Beitr. Paläont., **30**:361–386, Wien 2006

# Early Middle Miocene Mammals from Moroto II, Uganda

by

**Martin Pickford[1] & Pierre Mein[2]**

Pickford, M. & Mein, P., 2006. Early Middle Miocene Mammals from Moroto II, Uganda. — Beitr. Paläont., **30**:361–386, Wien.

## Abstract

The Uganda Palaeontology Expedition collected fossils at Moroto II in 1985, and 1997 - 2004. Prior research at the site in the 1960's yielded only six species of mammals, several of which were represented by incomplete teeth and post-cranial bones, and as a result it was difficult to correlate the deposits to other localities and to estimate the age of the site. The new collections contain 34 species of mammals which collectively suggest that the deposits are latest Early Miocene or basal Middle Miocene in age (ca. 17.5 - 17 Ma) at variance with recent K-Ar age estimates of their age (> 20.6 Ma). This paper describes and interprets the non-catarrhine mammals from the site. The anthropoid primates have been described in a separate paper.

**Keywords**: Moroto, Uganda, Miocene, Mammalia, Fauna

## Zusammenfassung

Die Uganda Palaeontology Expedition hat 1985 und von 1997 bis 2004 in Moroto II Fossilien aufgesammelt. Frühere Forschungen in den 60er-Jahren haben nur sechs Säugetierarten erbracht von denen einige nur von Zahnfragmenten und ebensolchen postcranialen Skelettelementen repräsentiert waren. Dadurch war es schwierig, die Sedimente mit anderen Fundstellen zu korrelieren und das Alter der Fundstelle festzustellen. Die neuen Aufsammlungen umfassen 34 Säugetierarten, die alle darauf hindeuten, daß die Ablagerungen oberstes Untermiozän oder basales Mittelmiozän darstellen (ca. 17,5 - 17 Ma), anders als die neuen K-Ar-Daten ergeben haben (> 20,6 Ma). In diesem Artikel werden die Säugetiere aus Moroto II mit Ausnahme der Catarrhini beschrieben und interpretiert. Die Menschenaffen wurden in einem eigenen Artikel beschrieben.

## 1. Introduction

Moroto II is a complex of fossiliferous localities near Kogole Hill, 7 km north of Nakiloro, Moroto District, Uganda (Fig. 1, 2). There are two main deposits at Kogole, one in a steep valley east of the summit of the hill, the other in a shallower valley south of the hilltop (Fig. 1, 2). The eastern valley drains into the Gregory Rift in Kenya, whereas the southern valley drains westwards, eventually into the Nile. The southern exposures are visible from the Nakiloro-Kaabong track, and were the first ones prospected for fossils (Allbrook & Bishop, 1963; Bishop, 1963, 1964, 1968; Bishop & Whyte, 1962; Tricker et al., 1963). The eastern outcrops were found later, and whilst they are thicker and more extensive in outcrop area, they have yielded far fewer fossils than the southern outcrops. Initially, fossils from the site were simply catalogued as coming from Moroto II, but as research progressed in the 1960's the exposures were given different letters A, B, C, but the precise location of these sediment patches is not known and it is clear from conjoining pieces that have different letters, that there was a mixup in the various collections from the sub-sites, even during the 1960's. Bishop's field notes suggest that the Moroto hominoid snout came from the eastern gully (Pickford & Tassy, 1980).

Bishop (1967) provided a composite faunal list for Moroto I and II which contained *Proconsul major* based on the Moroto hominoid palate (now identified as *Afropithecus turkanensis*), *Brachyodus aequatorialis*, *Dissopsalis pyroclasticus* (now identified as *Hyainailourus sulzeri* and known only from Moroto I), *Trilophodon angustidens* (now identified as *Progomphotherium maraisi*), *Deinotherium* sp., mastodont gen. nov. (now known as *Eozygodon morotoensis*), Rodentia (now identified as *Diamantomys morotoensis* sp. nov.), and ruminant (now attributed to *Walangania africanus*). Subsequent research on the origi-

---

[1] Dr. Martin Pickford, Chaire de Paléoanthropologie et de Préhistoire du Collège de France, GDR 983 et UMR 5143 du CNRS, 8, rue Buffon, 75005 Paris, e-mail: pickford@mnhn.fr

[2] Dr. Pierre Mein, Département des Sciences de la Terre, Université Claude Bernard I, 27-43 Boulevard du 11 Novembre, 1918, 69621 Villeurbanne, Cedex. e-mail: pierre.mein@univ-lyon1.fr.

nal Moroto fossils was carried out by Pickford (1979), Pickford & Tassy (1982), and Tassy & Pickford, (1983). A review of the fauna taking into account fossils collected in 1985 was published by Pickford et al. (1986). Other papers on Moroto mammals were published by Pickford (1998), whilst the Moroto primates have been intensively studied (Allbrook & Bishop, 1963; Bishop, 1963, 1964a, b; Bishop & Whyte, 1964; Gebo et al., 1997; MacLatchy & Pilbeam, 1999; MacLatchy et al., 1995, 1998; Pickford, 2002; Pickford et al., 1999, 2003; Pilbeam, 1969; Sanders & Bodenbender, 1994; Senut et al., 2000; Walker & Rose, 1968; Young & MacLatchy, 2000, 2004).

In 1997, Gebo et al., erected the genus and species *Morotopithecus bishopi* which is in fact a synonym of *Afropithecus turkanensis* (Pickford, 2002), although MacLatchy and colleagues have maintained that it belongs to a separate genus, *Morotopithecus* (MacLatchy & Pilbeam, 1999; MacLatchy et al., 1995, 1998, 2000; Young & MacLatchy, 2004). A major problem with the Moroto fossil hominoids is that there are two large species represented by craniodental and postcranial remains (Pickford et al., 1999) (*Afropithecus turkanensis* and *Ugandapithecus* sp.). To which of these two taxa do the Moroto large primate vertebrae belong? Pickford et al., (1999) and Pickford (2002) consider that they belong to *Ugandapithecus* whereas Gebo et al., (1997), MacLatchy & Pilbeam (1999), MacLatchy et al., (1995) and Young & MacLatchy (2000, 2004) include them in *Morotopithecus*. The importance of these vertebrae is that they provide the earliest known evidence of a shortened lumbar region among catarrhines, and have been interpreted as heralding the evolution of the great ape clade. Thus it is of interest to determine to which genus these vertebrae belong.

The Uganda Palaeontology Expedition (UPE) has concentrated its reseach on the southern outcrops, as they are the richest, but fossils were collected in the eastern valley in 1985 and 1999. However, the latter valley yielded only fragmentary material intermixed with Pleistocene fossils (suids, bovids, rodents) which are not taken into account in this paper. Some of the historic collections came from the eastern outcrops, but we cannot be sure about which ones, except in cases where the preservation characters indicate the original site. For example, fossils from the eastern exposures are usually broken pieces, heavily rolled and polished, usually pale orange, yellow or white in colour, but some are purple. Fossils from the southern outcrops in contrast are better preserved, unrolled and often have a thin but discontinuous pellicle of deep red 'rusty' sand grains attached to the specimens, notably dentine, tooth roots and sometimes bone. Teeth are orange or grey in colour, and are sometimes chalky in appearance when they have lain on the surface for some time.

In 1998 the UPE cleared the surface boulders from two outcrops of sediment in the southern exposures and removed vegetation. Every year since 1998, it has carried out surface prospecting and screening of weathered and *in situ* sediments. By February 2004 over 100 tons of sediment had been screened with the result that the faunal list for the site is now 34 Miocene mammals, compared to only 6 after the 1960's surveys (Bishop, 1967; Pickford, 1981). In addition there are some Pleistocene fossils (rodents, bovids, suids, equids, *Struthio* eggshell fragments) which are not treated in this paper.

## 2. Geology

The geological succession in the vicinity of Kogole is relatively simple (Fig. 1). The area is underlain by Basement Complex gneisses (Mozambique Belt) (Fleuty, 1968) and has small outcrops of Neogene deposits comprising Miocene sediments infilling valleys cut into the gneisses (Bishop, 1967, 1968, 1971, 1972; Bishop et al., 1969; Pickford & Tassy, 1980) and capped by basalt lava, presumably from Moroto Mountain which is 8-12 km to the south (Fleuty, 1968; Horne, 1953; Varne, 1966, 1967). A thin veneer of fossiliferous Pleistocene sediments occurs in several of the valleys in the region.

The Miocene sediments are named the Kogole Beds, and comprise valley infillings east and south of Kogole Hill (Fig. 1). The eastern exposures have a weathered basalt flow intercalated in the sediments and topographically the lowest sediments are about 100 metres below the summit of Kogole Hill and about 80 metres below the general level of the Basement complex plains. This drainage flows to the Gregory Rift Valley, and indicates that the Rift was already at least 100 metres deep by the time of erosion of the valley.

Bishop (ms notes) considered that the uphill and downhill occurrences of basalt in the eastern valley were part of a single lava eruption that flowed down the drainage line (see Pickford & Tassy, 1980). However, it is now clear that the lower outcrop is a different unit from the capping basalt, as it is intercalated within the Miocene sediments some 25 metres below the capping basalt and is itself covered by sediments. It is possible that this basalt flowed into the drainage line from the nascent rift valley to the east, and that it is not necessarily from Moroto Volcano. Once in place, sediments accumulated on top of it almost to the general level of the countryside before the capping basalt was deposited. This flow is widespread in the region north of Nakiloro, with several outliers forming prominent flat-topped hills in the area, of which Kogole is one (Fig. 1) and Loitakero (Moroto I) another (Fig. 2) (Pickford & Tassy, 1980).

The southern valley is much shallower than the eastern one (Fig. 2), topographically the lowest sediments being only about 30 metres below the summit of Kogole Hill. The sediments in both valleys are overlain by basalt lava, and they each contain small patches of Pleistocene sediments and palaeosols (with carbonate nodules) (not shown on the map) which yield fossils (ostrich egg shell fragments, rodents, equids, suids and bovids).

### 2.1. Age of the deposits

There has been some debate about the age of the Moroto deposits, partly because the faunal list was scanty

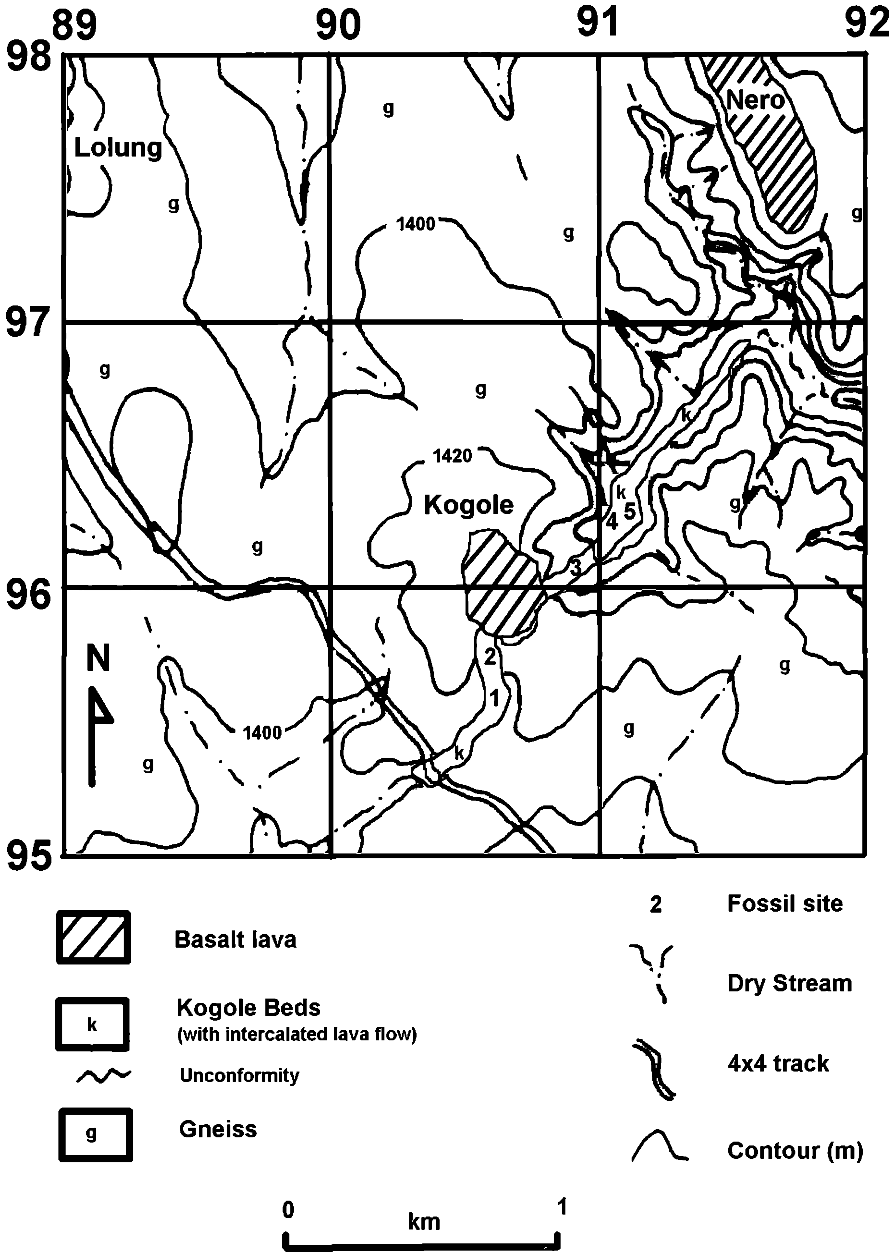


**Figure 1**: Geology of Kogole Hill and surroundings, Moroto II, Karamoja District, Uganda.

and partly because the basalt overlying the sediments is weathered. Bishop et al., (1969) initially reported an age older than 14.3 +/- 0.3 Ma. In various papers Pickford (1986a, b, c, 1981; Pickford & Tassy, 1980; Pickford et al., 1986, 1999) has suggested a late Early Miocene or basal Middle Miocene age for the sites (ca 17-17.5 Ma). This was challenged by Gebo et al., (1997) who published an age of greater than 20.6 Ma on the basis of K-Ar age determinations from the capping basalt at Moroto I.

As more and more species of mammals are found at Moroto II, the fauna appears increasingly similar to those of the sites of Locherangan, Kalodirr and Buluk in Kenya, all of which are aged ca 17.2 Ma (Anyonge, 1991; Boschetto et al., 1992; MacDougal & Watkins, 1985, 1988). The fauna has elements, including some of the rodents and the palaeochoerid *Morotochoerus*, that suggest an age younger than Rusinga, Kenya, which is aged 17.8 Ma (Drake et al., 1988). If Moroto II is really older than 20.6 Ma, then it would have the earliest records for almost the entire mammal fauna, which seems unlikely. Aged between 17.5 and 17 Ma, it would have some earliest records and some last records, the usual situation for a fossiliferous locality.

## 2.2. Palaeoenvironment of Moroto II

The Miocene sediments at Moroto II accumulated in valleys draining in two directions and over different topographic settings. The southern deposits are in a shallow valley which drained westwards across relatively planar topography similar to the modern Karamoja Plain, and the eastern deposits occur in a deeper valley that drained eastwards across more rugged terrain towards the nascent Rift Valley. Both valleys at Moroto II contain marly deposits and cross-bedded sands indicating overall similarity in depositional environments, dominated by sluggish, shallow rivers or streams. The presence of several aquatic and amphibious animals at Moroto II (crabs, frogs, fish, crocodiles, aquatic turtles, and anthracotheres) reveal that the rivers or streams may have been permanent, or that permanent pools of water occurred even during dry seasons.

One of the commonest fossils in the southern valley at Moroto II is the terrestrial snail *Nothapalinus*, which today occurs most typically in grassy areas (Pickford, 1995). It is likely that the vegetation in the palaeovalleys was dominated by grass, just as the extant shallow valleys of Karamoja are. Today, the interfluves between valleys are covered in open woodland and bushland, but during the Miocene the region was probably more thickly vegetated, as indicated by the presence in the deposits of a scaly-tailed flying squirrel (*Zenkerella*), galagos, monkeys and four species of hominoids. The presence of three taxa of proboscideans at Moroto II, two of which (*Deinotherium*, *Eozygodon*) were likely folivorous, indicate the same thing.

**Figure 2**: Moroto II, Uganda. (1) View of Moroto II site 1, looking south. Loitakero (Moroto I) is the flat topped hill in the middle distance. Moroto Mountain forms the backdrop. (2) Close-up of Moroto II site 1, looking west. A - *Progomophotherium* upper teeth; B - *Eozygodon* upper molar; C - *Ugandapithecus* M2; D - *Ugandapithecus* P3; E - *Kogolepithecus* lower teeth; F - *Ugandapithecus* upper canine; G - *Diamantomys* specimens and *Prohylobates* teeth; H - *Meroehyrax* tooth fragment and *Morotochoerus* teeth.

## 3. Systematic descriptions

### Order incertae sedis ?Marsupialia Illiger, 1811

**Material**: Mor II, 48'04, left m1 or m2.

**Measurements:** m1 or m2 (1.63 x 0.93 trigonid x 0.94 talonid)

**Description**: The lower molar (Fig. 5 (1)) is from a small insectivorous mammal with a relatively high trigonid, a paraconid that is clearly inclined anteriorly, and a metaconid in line with the protoconid. The talonid is slightly shorter than the trigonid and much lower, with three cuspids. The entoconid is broken in the specimen. The buccal surface shows a basal anterior cingulid which fades out before reaching the protoconid and there is a small cingulid between the protoconid and hypoconid. The hypoconid is low and forms a curved crest on the distal margin of the tooth.

**Discussion**: The presence of lower molars in which the talonid has three cuspids is unknown in Miocene Tenrecoids and Chrysochloridae (Butler & Hopwood, 1957). The specimen belongs to a hitherto undescribed insect-eating mammal but the material is too restricted for us to be able to determine its precise affinities. It could represent a marsupial, but the African fossil record of this group is currently restricted to the Palaeogene (Jaeger & Martin, 1984; Simons & Bown, 1984).

Order Chiroptera Blumenbach, 1779
Suborder Microchiroptera Dobson, 1875
Family Emballonuridae Gervais, 1855

### Genus *Taphozous* Geoffroy Saint-Hillaire, 1818

### *Taphozous incognita* (Butler & Hopwood, 1957)

**Material**: Mor II, 49'03, proximal humerus.

**Description**: The proximal humerus from Moroto II is from a large bat. The proximo-distal head diameter is 1.92 mm, and the maximal breadth of the proximal end is 2.70 mm. The lip next to the head measures 1.44 mm antero-posteriorly and 0.61 mm medio-laterally, measured from the point where it leaves the caput.

**Discussion**: The humerus is close in size and morphology to that of other *Taphozous* species and accords with the Early Miocene species *T. incognita* (Butler & Hopwood, 1957).

Family Vespertilionidae Gray, 1821

### Genus ?*Chamtwaria* Butler, 1984

### Species indet.

**Material** : Mor II 50'03, left upper canine.

**Measurements**: (in mm) of the tooth

**C** (1.92 x 1.09) (crown height 1.89; total height 3.55)

**Description**: Mor II 50'03 is a canine-like tooth with a central cuspid. The base of the crown is surrounded by a cingulum which is higher anteriorly than elsewhere, and which is bent in the middle of the lingual side. It is an upper canine of a vespertilionid, and on the basis of its size could represent *Chamtwaria pickfordi* Butler, 1984.

Order Macroscelidoidea Gill, 1872
Family Macroscelididae Bonaparte, 1838

### Genus *Miorhynchocyon* Butler, 1984

### Species indet.

**Material**: Mor II, 49'04a, p2; Mor II 49'04b, p3 fragment.

**Measurements**: (in mm) of the teeth, **p2** (3.05 x 1.40), **p3** (– x 1.80).

**Description**: The p2 is a low, elongated, heavily worn, two rooted tooth with a rounded paraconid and a weakly projecting protoconid located in a very anterior position, a talonid which is almost flat with slightly raised buccal and lingual margins.

Order Insectivora Bowdich, 1821
Family ?Tenrecidae Gray, 1821

### Genus and species indet.

**Material**: Mor II 61’04, upper canine?
**Measurement**: (in mm) of the tooth, **C?** (1.00 x 0.47)
**Description**: Mor II 61’04 is a small uniradiculate tooth in which the crown is obliquely disposed on the root. The posterior margin is better developed than the anterior one. The distal part of the tooth rises upwards to form a pointed distal cusplet. This tooth could represent an upper canine of a small tenrecid.

Order Rodentia Bowdich, 1821
Family Pseudocricetodontidae Ünay-Bayraktar, 1989

### Genus ?*Pseudocricetodon* Thaler, 1969

### ?*Pseudocricetodon* sp. indet.

**Material**: Mor II, 43’03, right M1; Mor II, 44’03, damaged right M1; Mor II, 45’03, left m1; Mor II, 46’03, right m1; Mor II, 47’03, left m2; Mor II, 48’03, left m2; Mor II 53’04, right m3; Mor II, 58’04 (Fig. 6 (1)).
**Measurements**: (in mm) of the teeth.
**M1** (1.45 x 0.99) (-- x 0.98)
**m1** (1.36 x 0.85) (1.22 x 0.90)
**m2** (1.15 x 0.92) (1.26 x 0.99)
**m3** (1.08 x 0.97)
**Description**:

**The M1** (Fig. 3 (1)) has an undivided anterocone which is wider than in European forms of *Pseudocricetodon*, which is prolonged by a strong lingual anteroloph and a buccal cingulum which reaches the paracone. The paracone and protocone are at the same transverse level, but the protoloph reaches the front of the protocone, and not at its rear as in *Pseudocricetodon*. The protocone is devoid of an anterior spur which also occurs in *Pseudocricetodon*. The ectoloph has two short mesolophs, the distal one being a little longer than the mesial one. There is no trace of an entomesoloph. The metaloph is slightly oblique towards the front and ends before the hypocone. The posteroloph connects to the apex of the metacone. There are anterior and posterior crests on the metacone, the anterior one closing off the occlusal basin on its buccal side. The sinus is median in position in Mor II, 43’03 edged by the ectoloph which reaches the top of the protocone, but in specimen Mor II, 44’03, the ectoloph ends more centrally, so that the anterior end of the sinus extends further forwards.

**The m1** (Fig. 3 (2-4)) has a simple reduced lingual anteroconid connected to the protoconid by a buccal crest, but there is no buccal anteroconid. The anteroconid is connected to a high lingual anterolophid which reaches the apex of the metaconid. The metalophid is slightly oblique towards the rear, and arrives directly onto the protoconid. Centrally it has a small posterior spur. From the summit of the metaconid there is a distal crest which descends, but fails to close off the occlusal basin. The ectolophid has a mesolophid and an ectomesolophid which are equally short. There is no ectostylid. The sinusid is not oblique towards the rear. The posterior part of the tooth has a large hypoconid and a smaller entoconid. The hypoconid receives the hypolophid in its centre. Anteriorly there is the ectolophid and distally there is a posterolophid which swing across the back of the tooth to reach the base of the entoconid. There are no supplementary crests between the hypolophid and the posterolophid, and there is no crest behind the posterolophid. There are two round roots, the anterior one smaller than the distal one.

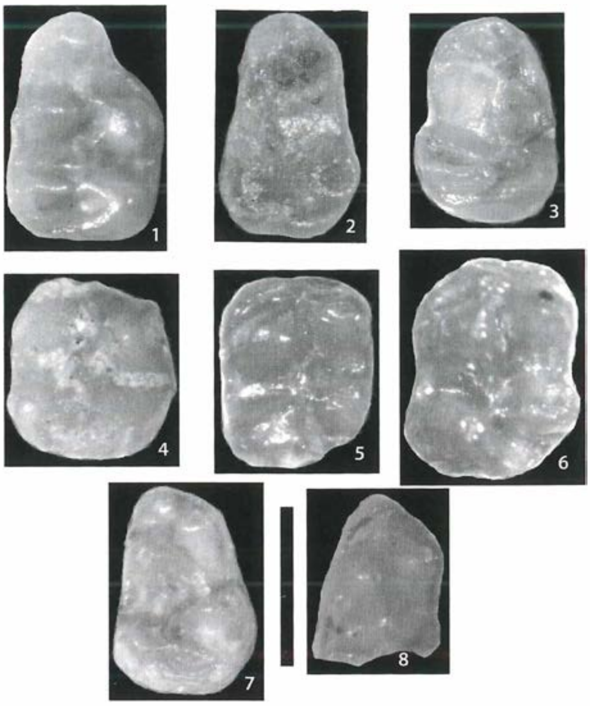


**Figure 3**: Rodentia from Moroto II, Uganda (Scale bar: 1 mm). (1) Mor II, 43’03, ?*Pseudocricetodon* sp. right M1, occlusal view, (2) Mor II, 45’03, ?*Pseudocricetodon* sp. left m1, occlusal view, (3) Mor II, 46’03, ?*Pseudocricetodon* sp. right m1, occlusal view, (4) Mor II, 44’03, ?*Pseudocricetodon* sp. right m1, occlusal view, (5) Mor II, 47’03, ?*Pseudocricetodon* sp. left m2, occlusal view, (6) Mor II, 48’03, ?*Pseudocricetodon* sp. left m2, occlusal view, (7) Mor II, 35’03, *Notocricetodon gommeryi* nov. sp. holotype, left m1, occlusal view, (8) Mor II, 50’04, *Notocricetodon gommeryi* nov. sp. fragment of left m1, occlusal view

**The m2** has four main cusps (Fig. 3 (5-6)). The anterior half has a triangular medially positioned anteroconid, from which a short and high lingual anterolophid and a large and descending buccal anterolophid which ends at the base of the protoconid. The metalophid is slightly arched towards the front, and reaches the anteroconid. The ectolophid has a small mesolophid, but no ectomesolophid. The entoconid has a hypolophid which arrives just in front of the hypoconid. The hypoconid is larger than the protoconid, and is followed distally by the posterolophid, which ends at the base of the entoconid. There is no structure behind the hypoconid. The valleys are not deeply excavated.

**The m3** is large relative to its length. The buccal anterolophid has a crest descending along the antero-buccal margin of the tooth. The lingual anterolophid reaches the base of the metaconid in the antero-lingual angle. The metalophulid is transverse and inserts directly onto the protoconid. Two fine longitudinal wrinkles depart towards the rear from the metalophid of which one rejoins the mesolophid. The mesolophid is short, and at its insertion on the ectolophid this crest broadens slightly. The sinusid is clearly oblique towards the rear. Two small entostylids are present at the labial end of the sinusid. The hypoconid is as voluminous as the protoconid. The posterolophid behind the hypoconid does not extend distally but courses directly transversely, which shortens the crown. The tooth, from which a small flake is missing, appears to have lacked an entoconid.

**Discussion**: These six teeth indicate the presence of a minuscule «cricetid» at Moroto which has never before been noted in Africa, which shows some analogies with Oligocene *Pseudocricetodon* of Europe and Asia Minor. It is not impossible that at the end of the Oligocene several rodent lineages migrated from Turkey to Africa, one of which culminated in the Moroto species, attributed here with reservation to the genus *Pseudocricetodon*. The major difference between the Moroto species and *Pseudocricetodon* species from Eurasia concerns the morphology of the protoloph and its connections to the protocone. The genus survives in Europe into the base of the Early Miocene (MN3), so the Ugandan material could represent the latest survivors of this group.

Family Afrocricetodontidae Lavocat, 1973

### Genus *Notocricetodon* Lavocat, 1973

#### *Notocricetodon gommeryi* sp. nov.

**Holotype**: Mor II 39'03, right m3 Mor II, 35'03, left m1 (holotype Fig. 3 (7)).

**Referred material**: Mor II, 34'03, right M2; Mor II, 36'03, left m2; Mor II, 37'03, left m3; Mor II, 38'03, right m3; Mor II, 39'03, right ?m2 or ?m3; Mor II, 40'03, distal half of right M2; Mor II, 41'03, damaged right M2.

**Measurements**:

**M1** (1.58 x 1.09)
**M2** (1.38 x 1.27) (– x 1.17) (1.20 x 1.17)
**m1** (1.57 x 1.12)
**m2** (1.43 x 1.22)
**m3** (1.33 x 1.08) (1.40 x 1.07) (1.42 x 1.07)

**Diagnosis**: Species of *Notocricetodon* smaller than the type species *N. petteri*. Posterior arm of the hypoconid is less extensive than in *N. petteri*; the sinus in M2 more sharply oblique towards the mesial end than in *N. petteri*.

**Derivatio nominis**: The species is named in recognition of Dominique Gommery for his contribution to the success of the Uganda Palaeontology Expedition.

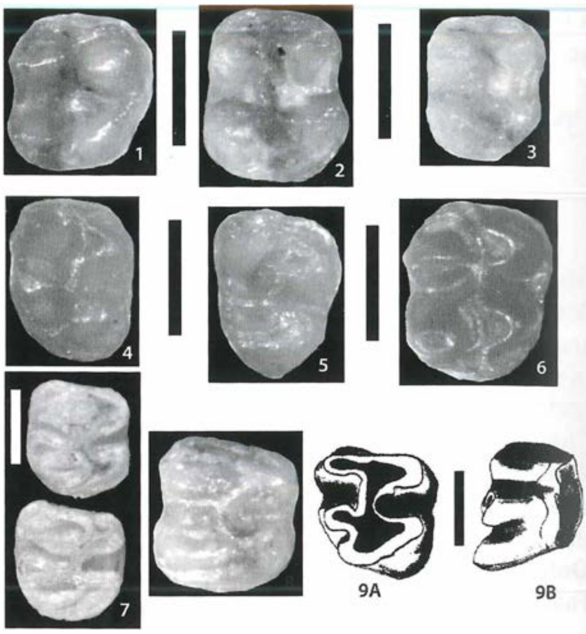


**Figure 4**: Rodentia from Moroto II, Uganda (Scale bar: 1 mm). (1) Mor II, 34'03, *Notocricetodon* sp. right M2, occlusal view, (2) Mor II, 36'03, *Notocricetodon* sp. left m2, occlusal view, (3) Mor II, 37'03, *Notocricetodon* sp. left m3, occlusal view, (4) Mor II, 50'04, *Notocricetodon* sp. left m2, occlusal view, (5) Mor II, 38'03, *Notocricetodon* sp. right m3, occlusal view, (6) Mor II, 42'03, *Protarsomys* cf. *lavocati*, left m2, occlusal view, (7) Mor II, 35'04, *Simonimys genovefae*, left mandible with m1 - m2, occlusal view, (8) Mor II, 28'01, *Simonimys genovefae*, right m2, occlusal view, (9) Mor II, 45'04, *Geofossor* sp. right m2, a) occlusal, b) lingual view

**Description**: These teeth are attributed to the genus *Notocricetodon* because they possess a posterior arm on the protoconid and hypoconid. They are small for cricetids.

**The m1** has a simple and short anteroconid (Fig. 3 (8)). Buccally it has a cingulum and lingually the cingulum joins the apex of the metaconid. In the holotype the longitudinal crest is interrupted so that the anteroconid is isolated from the protoconid, but in another specimen it is joined to it. The metaconid is triangular and more elevated lingually and lower centrally. It has two crests, one anterior which swings towards the anteroconid, the other distal which descends into the lingual sinus before climbing up towards the apex of the entoconid. The protoconid is triangular and lower than the metaconid and slightly distal to it. It has a posterior crest leading obliquely distally towards the centre of the tooth. The ectolophid connects the distal part of the protoconid to the mesial part of the hypoconid. In its middle it has a slight swelling forming a mesoconid with a small lingual spur. Lingually the entoconid possesses crests anteriorly and posteriorly. Lingually the entoconid has a transverse hypolophid which reaches the ectolophid well mesial to the hypoconid. The hypoconid is lower and larger than the entoconid. It has a well-developed posterior transverse arm which crosses the tooth, reaching the lingual end of the posterolophid. Behind the hypoconid, there is a transverse posterolophid which swings round the back of the tooth before extending upwards to the apex of the entoconid. On the buccal side, the tooth has three valleys, a narrow anterior one, a long sinusid with a narrow elongated ectostylid, and a small posterior valley behind the hypoconid which is bordered centrally by a cingulum emanating from the posterolophid. Lingually the occlusal basins are closed by lingual crests and are shallower than the buccal valleys. The m1 is widest at the entoconid-hypoconid pair. It has two roots, the anterior one elongated antero-posteriorly, the distal one elongated transversely.

**The m2** (Fig. 4 (2, 4)) is slightly wider distally than mesially. It has an anteroconid attached to buccal and lingual cingula, the lingual one reaching the apex of the metaconid, the other one ending at the base of the protoconid. There is a posterior arm of the protoconid which is oblique towards the rear and which swings round to join the mesolophid. The buccal base of the metaconid has a longitudinal swelling that lies parallel to the posterior arm of the protoconid. The longitudinal ectostylid is angular at its junction with the hypolophid which is transversely oriented. The hypoconid is similar to the protoconid and has a transverse posterior arm which stops short of the posterolophid. As in the m1 there is a small posterior buccal valley between the hypoconid and the posterolophid bordered distally by a cingular crest. There are two transversely elongated roots, the distal one being more voluminous than the mesial one.

**The m3** (Fig. 4 (3, 5)) is slightly wider mesially than distally, the opposite of the m2. Overall the tooth recalls an m2 save for the fact that the distal buccal valley is positioned further lingually, almost in the centre line of the crown, and in one specimen out of three, the posterior arm of the hypoconid points obliquely anteriorly towards the entoconid, rather than transversely. The other two specimens are devoid of this arm.

**The M2** (Fig. 4 (1)) has an anterocone with a buccal anteroloph which does not reach the border of the tooth, and a lingual anteroloph which reaches the foot of the protocone. In occlusal view the protocone and paracone are almost at the same level. The protoloph is slightly oblique towards the front, and ends at the junction between the ectoloph and the protocone. The protocone is voluminous lingually but pinches in towards the centre of the crown. The paracone has a disto-buccal crest which encloses the external valley and connects to the apex of the metacone. A continuation of this crest descends the distal part of the metacone. The metacone is slightly lower than the paracone and it has a transverse metaloph that connects to the hypocone. The ectoloph descends from the hypocone to the junction with the protoloph. It has a transverse mesoloph which stops well short of the buccal border of the tooth. In two other specimens which are damaged, the metaloph subdivides lingually into two portions, a distal one which connects to the posteroloph, and a mesial one that joins the mesoloph, thereby forming a fossette. The sinus is long and swings deeply anteriorly behind the protocone.

**Discussion**: Apart from some minor differences in morphology and its inferior size, the new species, *N. gommeryi*, is close to *N. petteri*, the type species (Lavocat, 1973), which is common in the Early Miocene deposits at Songhor and Koru, Kenya.

Family Cricetidae Fischer von Waldheim, 1817
Subfamily Democricetodontinae Lindsay, 1987

### Genus *Protarsomys* Lavocat, 1973

### *Protarsomys* cf. *macinnesi* Lavocat, 1973

**Material**: Mor II 51'04, left M1 (Fig. 6 (2)); Mor II 56'04 (Fig. 6 (3)); Mor II 59'04, anterior half of left M2; Mor II 61'04, posterior part of right M2; Mor II 60'04, left m1; Mor II 50'04, incomplete left m1; Mor II, 48'03, left m2.

**Measurements**: (in mm) of the specimens.

**M1** Mor II 51'04, (1.58 x 1.09)

**M2** Mor II 59'04, (-- x 1.19); Mor II 61'04, (-- x 1.14)

**m1** Mor II 60'04, (1.51 x 0.96)

**m2** Mor II, 48'03, (1.26 x 0.99)

**Description**: This small cricetid has a dental structure that is simpler and of more modern aspect than the *Pseudocricetodon* and the *Notocricetodon* from the locality. Contrary to the specimens figured by Lavocat (1973: pl. 32) the mesoloph and mesolophid are almost absent, as is the case in the mandible from Legetet figured by Flynn et al. (1985:599).

**The M1** has a paraconid which lacks the posterior protolophid which connects to the anterolophule. The M2 has a transversal protolophule reaching the protocone.

**The m1** has a simple anteroconid (Fig. 6 (3)) which is more projecting than the specimen figured by Lavocat, the buccal anterolophid is long and the lingual anterolophid absent. The metaconid inserts onto the anterolophulid linking the protoconid to the anteroconid. In contrast, the Rusinga specimen figured by Lavocat (1973) has a metaconid which has a poterior connection with the protoconid, a connection that is considered to be more archaic.

**The m2** is characterised by the very mesial position of the metaconid close to the short lingual anterolophid. This metaconid has a crest descending disto-lingually which reaches the base of the entoconid. The greatest breadth occurs in the posterior half of the tooth.

### *Protarsomys* cf. *lavocati* Mein & Pickford, 2003

**Material**: Mor II, 42'03, left m2.

**Measurements**: (in mm) of the tooth. **m2** (1.53 x 1.24).

**Description**: The m2 (Fig. 4 (6)) is wider distally than mesially. It has a small anteroconid with a lingual anterolophid which touches the metaconid (not the protoconid as was erroneously described in Mein & Pickford, 2003). The mesolophid is short. The tooth falls just above the range of metric variation of the species *P. lavocati* from Arrisdrift, Namibia.

**Discussion**: The Moroto specimen is closer morphologically to material from Arrisdrift, Namibia, than it is to the type species, notably in the shortness of the mesolophid,

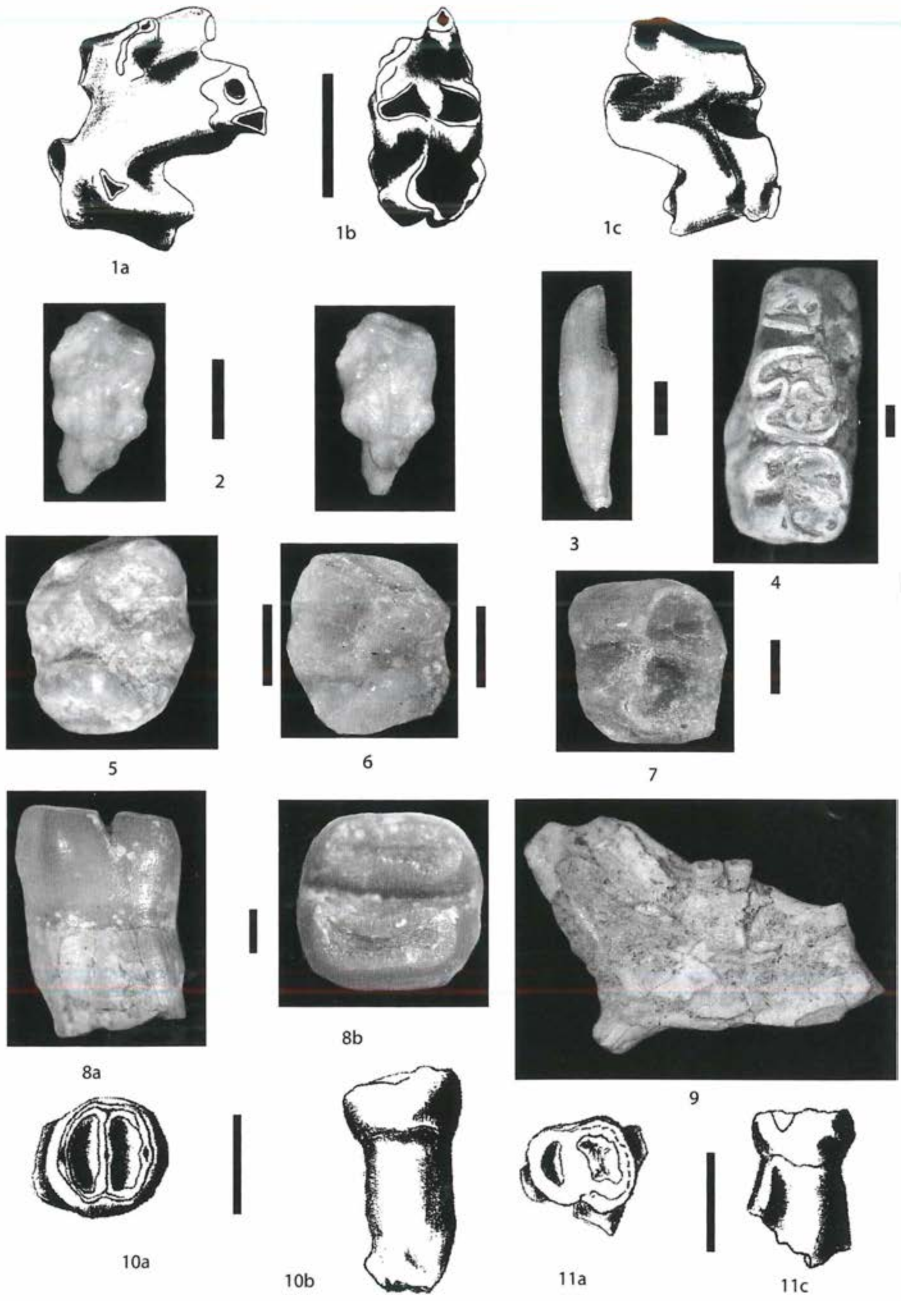


**Figure 5**: Small mammals from Moroto II, Uganda (Scale bar: 1 mm). (1) Mor II, 48'04, ?marsupial or insectivore, left m1 or m2, a) lingual, b) occlusal and c) buccal views, (2) Mor II, 23'02, *Komba* sp. left m3, stereo occlusal view, (3) Mor II, 24'02, *Komba* sp. p2, lingual view, (4) Mor II, 13'98, *Paraphiomys pigotti*, left maxilla with P4-M2, occlusal view, (5) Mor II, 40'04, *Apodecter orangeus*, left m2, occlusal view, (6) Mor II, 25'04, *Apodecter orangeus*, right m2, occlusal view, (7) Mor II, 36'01, *Paraphiomys pigotti*, right m1, occlusal view, (8) Mor II, 33'04, *Megapedetes pentadactylus*, p4, a) lingual and b) occlusal views, (9) Mor II, 14'98, *Zenkerella wintoni*, left mandible with m2-m3, oblique lingual view, (10) Mor II, 46'04, *Zenkerella wintoni*, left P4, a) occlusal, b) mesial view, (11) Mor II, 47'04, *Zenkerella wintoni*, left p4, a) occlusal, b) buccal view

which is much longer in material from Songhor and Koru, Kenya. It is slightly larger than the biggest of the Arrisdrift specimens.

In our opinion, *Protarsomys* is closer to the genus *Democricetodon* than to *Afrocricetodon*. If this is so, then it would belong to the family Cricetidae.

Family Pedetidae Gray, 1825

### Genus *Megapedetes* MacInnes, 1957

#### *Megapedetes* cf. *pentadactylus* MacInnes, 1957

**Material**: Mor II, 8'04, right lower incisor, Mor II 33'04, right P4

**Measurements**: (in mm) of the teeth.

**i1** (tr 3.2 mm)

**P4** (3.85 x 4.0)

**Description**:

**The P4** (Fig. 5 (8)) is low crowned, bilophodont with a substantial fused root base. The absence of an anterior interstitial facet indicates that it is an anterior cheek tooth. The buccal flexus is wider than the lingual one. The crown is slightly higher posteriorly than anteriorly, the usual condition for upper teeth. The root is slightly inclined anteriorly. The hypostria and mesostria have almost the same depth and terminate 2.7 mm above the cervix, and given that the crown is not deeply worn, then it means that the flexus is very shallow.

**The incisor** lacks much of the posterior dentinal part. The enamel has a squared section, with a low ridge laterally on the outer surface. The external part of the enamel is more developed than it is on the mesial side.

**Discussion**: Morphologically, these teeth are closest to *Megapedetes pentadactylus*, but they are somewhat smaller than the type series from Songhor, Kenya. Particular resemblances are the depth of the flexus, the remarkable brachyodonty of the molars and its thick enamel. The teeth are slightly smaller than specimens from Napak, but are larger than material from Kipsaraman and other sites in Kenya.

## Family Anomaluridae Gervais, 1849

### Genus *Zenkerella* Matschie, 1898

### ***Zenkerella wintoni* Lavocat, 1973**

**Material**: Mor II, 14'98, left mandible fragment with ml and m2; Mor II, 33'03, right molar fragment (left m3?); Mor II, 46'04, left P4; Mor II, 47'04, left p4.

**Measurements**: (in mm) of the teeth.

**P4** (1.09 x 1.19)

**il** (ap 3.0 x tr 1.30)

**p4** (1.04 x 0.95)

**ml** (1.33 x 1.30)

**m2** (1.43 x 1.37)

**molar fragment** (– x 1.25)

**Description**:

**The upper P4** (Fig. 5 (10)) is circular in occlusal outline, with a single root. The crown comprises two equal halves separated by a transverse valley. The mesial edge is circular and the distal margin is slightly flattened, allowing the orientation of the tooth to be determined. In *Zenkerella insignis* the posterior loph is slightly oblique and the occlusal outline of the tooth is in consequence elliptical.

**The mandible** (Fig. 5 (9)) deepens from mesial to distal, the depth at ml is 6.5 mm. The mental foramen is slightly anterior to the p4 and is in the upper third of the body of the mandible. The masseteric crests are weak, but the masseteric fossa is well defined.

**The incisor** is extremely flattened mesio-distally and the enamel extends further on the lateral side than on the mesial one.

**The lower p4** (Fig. 5 (11)) is subtriangular in occlusal outline with two lophids, wider at the rear than anteriorly. It has a marginal crest and a median lophid. It has three roots that are fused together for most of their depth.

**The lower molars** are rounded in occlusal outline. There is a ring of enamel surrounding the crown and a single transverse ridge of enamel that subdivides the occlusal surface into two parts, an antero-posteriorly narrower mesial portion, and a longer distal one. The fossettes are shallow and have flat bottoms.

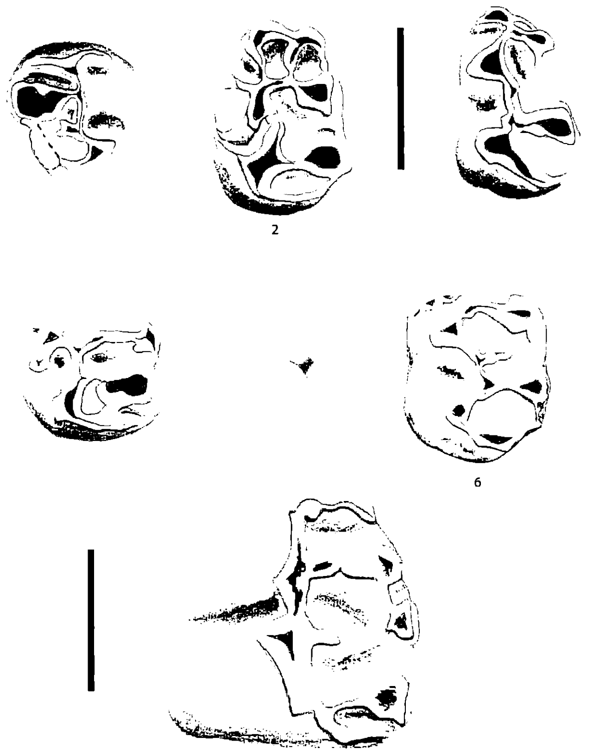


**Figure 6**: Small mammals from Moroto II, Uganda (Scale bar: 1 mm). (1) Mor II 58'04, *Pseudocricetodon* sp. right m3, occlusal view, (2) Mor II 51'04, *Protarsomys* cf. *macinnesi*, left M1, occlusal view, (3) Mor II 56'04, *Protarsomys* cf. *macinnesi*, left m1, occlusal view, (4) Mor II 52'04, *Andrewsimys* cf. *parvus*, left M3, occlusal view, (5) Mor II 54'04, *Andrewsimys* cf. *parvus*, P3 occlusal view, (6) Mor II 53'04, *Andrewsimys* sp. left m2, occlusal view, (7) Mor II, 44'04, *Apodecter stromeri*, left P4, occlusal view.

**Discussion**: The Moroto lower molars are similar to the type specimen of *Zenkerella wintoni* from Songhor (Lavocat, 1973) as well as to those of the extant species *Z. insignis*. Lavocat wondered whether the type specimen might not be much younger than the rest of the fauna from the site, which is Early Miocene, but he pointed out that the genus had never been reported from the region. At Moroto, there are thin deposits of Late Pleistocene age which have yielded remains of *Equus*, *Phacochoerus*, *Arvicanthis*, *Tatera*, *Struthio*, and hypsodont bovids, but it is unlikely that the *Zenkerella* is from this younger fauna as three of the specimens were screened from *in situ* Miocene deposits. In addition the upper and lower premolars from Moroto II differ from those of the extant species *Z. insignis*. Recent screening in Early Miocene deposits at Koru, Kenya, resulted in the discovery of *in situ* remains of *Zenkerella*, proving that the genus occurs in the Early Neogene deposits of East Africa.

## Family Diamantomyidae Schaub, 1958

### Genus *Diamantomys* Stromer, 1922

### ***Diamantomys morotoensis* sp. nov.**

**Holotype**: Mor II, 7'01, left mandible with p4 to m3 (Fig. 7 (1)).

**Paratype**: Mor II 7'03, palate with left and right P4-M1 + Mor II, 26'03b, right maxilla with M2 to M3 (same individual).

**Additional material**: Mor II 6'98, left mandible with p4-ml (Fig. 8 (1)); Mor II 7'98, premaxilla with incisor; Mor II 8'98 three lower cheekteeth associated (right ml, left m2, m3); Mor II 20'98, 8 isolated teeth and tooth fragments (a ninth specimen belongs to *D. ugandensis*); Mor II 23'98,

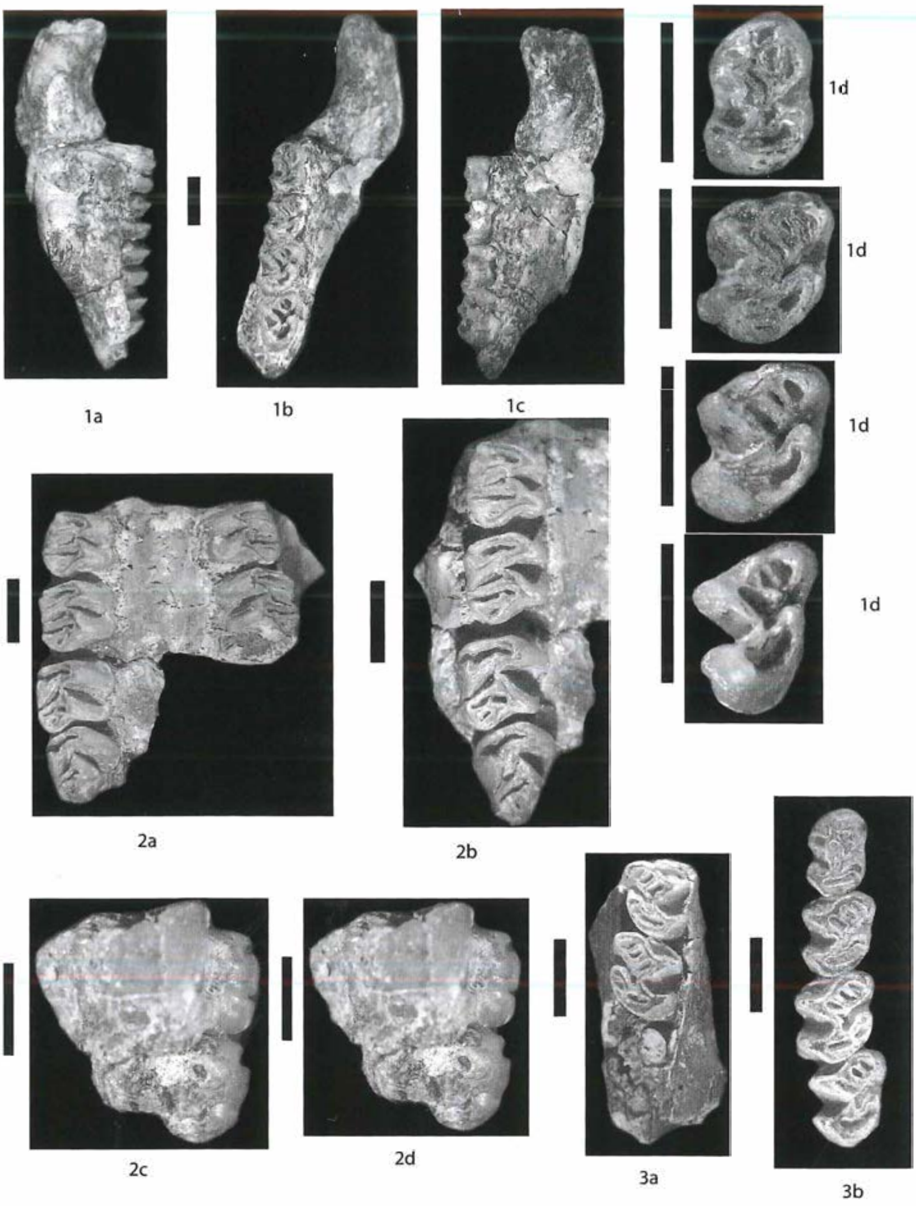


**Figure 7**: *Diamantomys morotoensis* sp. nov. from Moroto II, Uganda (Scale bar: 5 mm). (1) Mor II, 7'01, left mandible with p4-m3, a) buccal, b) occlusal c) lingual and d) enlarged occlusal view of tooth row, (2) Mor II, 7'03 + 26'03, palate with left P4-M1 and right P4-M3, a) occlusal view, b) enlargement of left tooth row, c) buccal and d) lingual views of Mor 11, 26'02, right maxilla with M2-M3, (3) Mor II, 9'04, a) right mandible with m1-m2, and b) left p4-m3 occlusal view

8 incisor fragments; Mor II 31'98, left maxilla fragment with M1-M2 (Fig. 8 (4)); Mor II 8'01, right mandible with p4 to m2; Mor II 9'01, right mandible with m1 to m3; Mor II 10'01, lower incisor; Mor II 31'01, right I1, right i1; Mor II 13'03, upper molar fragment; Mor II 18'03, right p4 (Fig. 8 (2)); Mor II 26'03a, left P4; Mor II, 26'03b, M2; Mor II, 26'03c, m3; Mor II, 9'04 parts of left and right mandibles with left i1, p4-m3 and right i1, m1-m2 (Fig. 7 (3a, 3b)); Mor II, 12'04a, left m3 (Fig. 8 (5)); Mor II, 12'04b, left M1, (Fig. 8 (6)); Mor II, 14'04, incisor; Mor II, 27'04, incisor; Mor II, 33'04a, P4; Mor II 33'04b, left M2; Mor II, 36'04, right m2 (Fig. 8 (3)); Mor II, 43'04, P3.

**Measurements**: of the teeth (in mm - cheek teeth mesiodistal length x bucco-lingual breadth, incisors anteroposterior diameter x transverse diameter)

**I1** (Mor II, 31'01b, ap 5.1 x tr 3.2) (Mor II, 7'98, ap 5.0 x tr 3.4)

**P3** (Mor II 43'04, 1.65 x 1.67)

**P4** (Mor II, 7'03 rt, 4.67 x 4.33) (Mor II, 7'03 lt, 4.47 x 4.20) (Mor II, 33'04a, 4.28 x 4.65)

**M1** (Mor II, 7'03 rt, 4.88 x 4.42) (Mor II, 7'03 lt, 4.57 x 4.16) (Mor II, 31'98, 4.52 x 4.50) (Mor II 12'04b, 4.49 x 4.06)

**M2** (Mor II, 26'03b, 5.28 x 4.62) (Mor II, 26'03a, 4.78 x 4.55) (Mor II, 31'98, 4.64 x 4.52) (Mor II, 33'04b, 4.40 x 5.30)

**M3** (Mor II, 26'03b, 5.25 x 4.43)

**i1** (Mor II, 9'04 rt, ap 5.0 x tr 3.4) (Mor II, 9'04 lt, ap 5.3 x tr 4.0) (Mor II, 6'98, ap 5.6 x tr 3.9)

**p4** (Mor II, 8'01, 5.10 x 3.73) (Mor II, 7'01, 5.50 x 3.95) (Mor II, 18'03, 5.60 x 3.65) (Mor II, 9'04, 5.8 x 3.9) (Mor II, 6'98, 6.0 x 3.8) (Mor II, 20'98 rt, 5.32 x 3.60)

**m1** (Mor II, 7'01, 5.19 x 4.58) (Mor II, 8'01, 5.50 x 3.89) (Mor II, 9'01, 5.44 x 4.07) (Mor II, 9'04 rt, 5.0 x 4.9) (Mor II, 9'04 lt, 5.3 x 4.9) (Mor II, 6'98, 5.3 x 4.3) (Mor II, 8'98, 5.20 x 3.77)

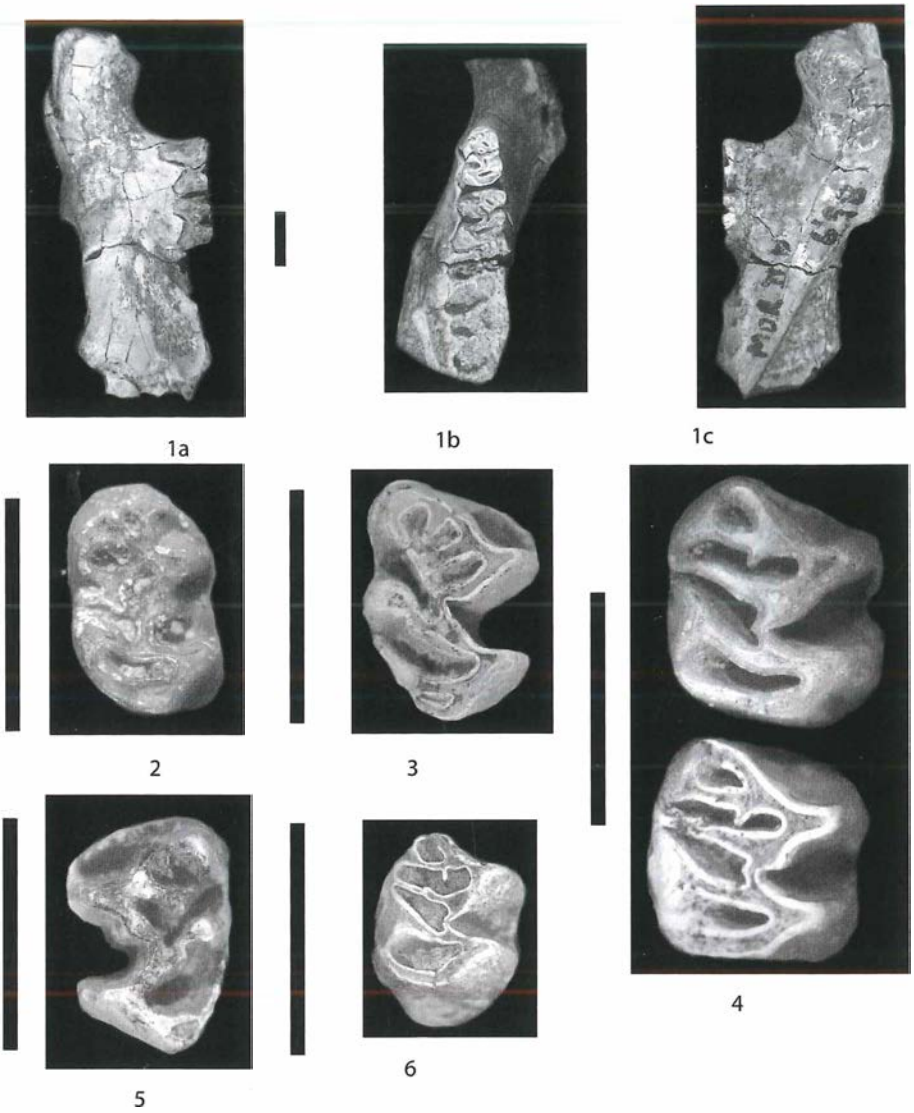
**m2** (Mor II, 7'01, 5.25 x 4.05) (Mor II, 8'01, 5.36 x 4.29) (Mor II, 9'01, 5.66 x 4.40) (Mor 9'04 rt, 5.9 x 5.1) (Mor II, 9'04 lt, 5.7 x 5.2) (Mor II, 8'98, 5.26 x 4.36) (Mor II, 36'04, 5.12 x 3.95)

**m3** (Mor II, 26'03c, 6.55 x 4.87) (Mor II, 7'01, 6.08 x 4.80) (Mor II, 9'01, 6.15 x 4.92) (Mor II, 9'04 lt, 6.4 x 4.8) (Mor II, 8'98, 5.45 x 4.30) (Mor II, 12'04a, 5.34 x 3.78)

**m1-m3** (Mor II, 7'01, 16.2) (Mor II, 9'04, 16.9) (Mor II, 6'98, 17.5)

**Diagnosis**: *Diamantomys* species larger than *Diamantomys luederitzi*, in which there is an addition of supplementary crests on the anterior part of all the lower cheek teeth (p4 to m3) and the posterior part of M1 and M2; p4, m1 and m2 possess a small fossettid on the posterolophid; lower cheek teeth increase in size from p4 to m3; M3 narrows sharply distally imparting a triangular, and not rectangular, outline to the occlusal surface. Mental foramen in upper

**Figure 8**: *Diamantomys morotoensis* sp. nov. from Moroto II, Uganda (Scale bar: 5 mm). (1) Mor II, 6'98, left mandible with p4-m1, a) buccal, b) occlusal and c) lingual views, (2) Mor II, 18'03a, right p4, occlusal view, (3) Mor II, 36'04, left m2, occlusal view, (4) Mor II, 31'98, left maxilla with M1-M2, occlusal view, (5) Mor II, 12'04a, right m3, occlusal view, (6) Mor II, 12'04b, left M1, oblique occlusal view



third of mandibular body beneath the rear of the diastema and above the incisor root.

**Derivatio nominis**: The species name refers to Moroto District, north-eastern Uganda.

**Description**: The holotype mandible (Fig. 7 (1)) shows a high mental foramen located below the p4. The masseteric crest is weak.

Some authors refer to the anterior cheek tooth of *Diamantomys* as a deciduous molar, while others consider it to be a permanent tooth. Without resolving the debate we refer to these teeth as premolars, and not deciduous molars. The labial surface of the upper and lower incisors is rounded. The enamel is thick with a chagriné surface.

**The p4** has a high anteroconid which is followed on the buccal side by a cingulum.The metaconid has a lingual crest departing distally which terminates close to or on the ectolophid. There is another spur which is longitudinal and terminates in the centre of the tooth or which joins the mesolophid. The protoconid is connected to the metaconid and anteroconid by an oblique crest, and is connected by a second crest to the metaconid, enclosing an anterior fossettid. Thus, between the metaconid and protoconid, there can be up to three fossettids. The ectolophid behind the protoconid is oblique, leading towards the centre of the tooth. The mesolophid is short, but it can receive the crest emanating from the metaconid. Opposite the mesolophid there is a short spur, the entomesolophid. This entomesolophid subdivides the sinus into two portions, the distal one of which is deeper than the mesial one. The hypoconid is connected to the entoconid by a curved hypolophid which departs from the hypoconid from its anterocentral corner and terminates lingually by turning distally. The posterolophid is quite thick and closes lingually onto the entoconid. On this posterolophid there is a small fossettid which is smaller than in *Diamantomys luederitzi* and *D. ugandensis*.

**The molars** are constructed almost on the same lines as the p4, but they are wider and the ectoloph is more w-shaped. The antero-buccal cingulum terminates occlusally in the m1, at mid-crown height in m2 and even lower in the m3. Between the protoconid and metaconid, the metalophulid has two spurs directed obliquely towards the rear sub-parallel to the longitudinal crest. These spurs are joined distally by a crest which is as high emanating from the metaconid which connects to the longitudinal crest at the level of the mesolophid. As a result, the anterior part of the tooth has three fossettids, the largest is buccal and the smallest is central. The entomesolophid subdivides the sinusid into two, the distal part being deeper than the mesial part. The anterior crest departing from the hypoconid swells before joining the entoconid. Towards the rear, the hypoconid communicates with a thick posterolophid, which sports a fossettid in its distal part, before swinging anteriorly to join the entoconid. In one specimen (Mor II, 9'04) the posterior fossettid is subdivided into two portions by an accessory longitudinal crest.

**The m3** is like an m2 but narrows distally and does not

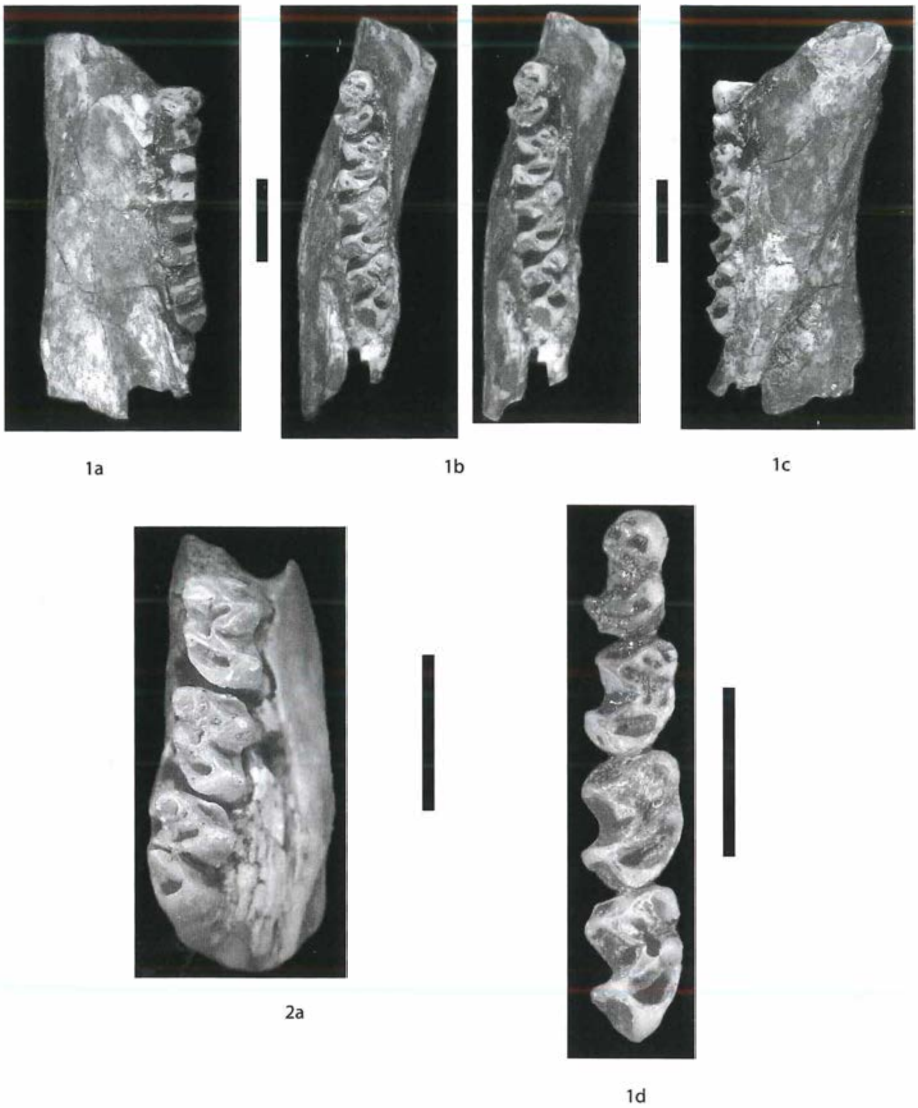


**Figure 9**: *Diamantomys ugandensis* sp. nov. (Scale bar: 5 mm). (1) Mor II, 30'04, left mandible with i1, p4-m3, a) buccal, b) stereo occlusal, c) lingual and d) enlargement of occlusal surface, (2) Mor II, 17'03, right mandible with m1-m3, occlusal view

have a fossettid on the posterolophid. The buccal part of the crown is more hypsodont than the lingual side, and in this respect is similar to *Diamantomys luederitzi*.

**The maxilla** (Mor II, 26'03b + Mor II, 7'03) (Fig. 7 (2)) reveals that the cheek teeth are more vertically oriented than they are in *Diamantomys luederitzi* in which the lingual surfaces of the cheek teeth are inclined steeply laterally. As a result the occlusal surface of the cheek teeth is less inclined linguo-buccally in the Moroto species than in *D. luederitzi*.

**The P4** is slightly smaller than the M1 and has a slightly oblique hypocone and a distal margin which is not very oblique. The metaloph is devoid of a metaconule.

**The M1** has a more oblique and curved distal margin and the metaloph sends a small crest (metaconule) anteriorly. This crest is stronger in the M2 in which the metaconule is more developed and closer to the buccal side.

**The M2** is slightly longer than wide, being almost square in occlusal outline with strongly w-shaped ectoloph. There are two halves separated by a transverse valley. The anterior half has two lophs which unite lingually at the protocone, the anteroloph which is straight, and the protoloph which connects the paracone to the protocone. Buccally the protoloph is oblique and becomes transverse at the swollen protoconule. The protoconule has a posterior spur which separates the transverse valley into two portions, and which, with wear becomes part of the ectoloph. The paracone has two crests, one anterior, the other posterior on the buccal side of the crown. The posterior half has three lophs, a long mesoloph which begins at the mesocone on the ectoloph, which is slightly oblique distally and which buccally joins the anterior crest of the metacone. The posteroloph is well developed and forms the distal border of the tooth ending at the hypocone. In its centre there is a swelling that is probably the metaconule. The metacone has a finer crest directed transversely towards the metaconule. The metaconule has a longitudinal spur pointing anteriorly. Finally, the metacone has anterior and posterior crests which enclose two fossettes.

**The front of the M3** is similar to the front half of the M2. The distal half, however, is pinched in, so that the occlusal outline narrows distally to a marked degree. The basic structure of the distal half is similar to that of the M2 save for the absence of the hypocone which makes the distal part of the ectoloph rounded rather than v-shaped. The orientation of the lophs in the distal half of the crown is more oblique.

**Discussion**: The upper and lower molars of *Diamantomys luederitzi* (Stromer, 1926) differ from those of *D. morotoensis* by the lack of accessory spurs, and thus the crown pattern is simpler. Within East Africa, there are clear differences between *Diamantomys* from Napak, Uganda, and younger material from Kipsaraman, Kenya, and Moroto, but a complete revision of the genus is beyond the scope of this article.

### *Diamantomys ugandensis* sp. nov.

**Holotype**: Mor II, 30'04, left mandible with incisor root and p4-m3 (Fig. 9 (1)).

**Paratypes**: Mor II, 17'03, right mandible with m1-m3; Mor II, 20'98, right upper molar.

**Measurements**: (in mm) of the teeth.
**Upper molar** (Mor II, 20'98, 3.7 x 4.0)
**i1** (Mor II, 30'04, ap 4.2 x tr 3.2)
**p4** (Mor II, 30'04, 4.29 x 2.54)
**m1** (Mor II, 17'03, 4.26 x 2.9) (Mor II, 30'04, 3.97 x 2.77)
**m2** (Mor II, 17'03, 3.60 x 2.84) (Mor II, 30'04, 4.3 x 3.23)
**m3** (Mor II, 17'03, 3.77 x 2.70) (Mor II, 30'04, 4.65 x 3.08)
**m1-m3** (Mor II, 17'03, 11.53) (Mor II, 30'04, 12.5)

**Diagnosis**: Small species of *Diamantomys*, (m1-m3 ca 12 mm long (known range 11.53 - 12.5 mm long, n = 2) (Fig. 10) cheek teeth morphologically simpler than in *D. morotoensis* but more complicated than in *D. luederitzi*. Smaller than *D. luederitzi* (length m1-m3 range 12.7-15.9 mm, mean 14.7, n = 32) and *D. morotoensis* (length m1-m3, 16.2-17.5 mm, n = 3). Mental foramen in lower third of mandibular body beneath the rear part of the diastema and next to the middle of the incisor root.

**Derivatio nominis**: The species name *ugandensis* refers to the country from which the type series came.

**Description**:

Mor II, 30'04, is a left mandible with all the cheek teeth and part of the diastema containing the rootward extremity of the incisor (Fig. 9 (1)). The mental foramen is low down beneath the rear of the diastema and on the same level as the midline of the incisor.

Mor 17'03 is a small right mandible with m1-m3 (Fig. 9 (2)). The root of the ascending ramus is at the anterior end of m3 where it forms a sharp, almost horizontal ridge with a more rounded anterior part that fades into the surface of the mandible below m2, just as in *D. luederitzi*.

The p4 is relatively elongated and narrow. The posterior valley between the hypolophid and posterolophid is mesio-distally longer than in *D. luederitzi* and much bigger than in *D. morotoensis*. The same applies to the anterior fossettid.

The lower molars are typical of the genus *Diamantomys* but are proportionally narrower than in *D. luederitzi* and *D. morotoensis*. The structure is simpler than in *D. morotoensis* the anterolophid possessing only two anterior fossettids rather than three. The anterior cingulum is well formed and decreases in size from m1 to m3.

In *D. luederitzi* and *D. morotoensis* the molars increase in size from m1 to m3. In Mor II, 17'03, however, the m2 is smaller than m1. The other specimen from Moroto II is normal in this respect.

The upper cheek tooth is from the right side and is of a size that accords with the lower molars of *D. ugandensis* and is appreciably smaller than cheek teeth of *D. morotoensis*. It is wider than long and only slightly oblique. The almost rectangular outline of the tooth suggests that it is a P4 rather than a molar. The metacone is separated from the metaloph which is fused to the posteroloph.

**Discussion**: Up til now, only one species of *Diamantomys* has been recognised (*D. luederitzi*), first described from Namibia, but later found in great abundance in Early Miocene localities in Kenya and Uganda (Lavocat, 1973) and a few Middle Miocene localities (Moruorot, Kipsaraman, Kenya). The molars of *D. luederitzi* are unadorned by accessory crests and fossettes, whereas both of the new species from Moroto II possess these additional structures. The small species *D. ugandensis* has fewer accessory crests than the larger one *D. morotoensis*. It would appear that throughout the Early Miocene the genus was remarkably uniform in its dental morphology and body size but then at the onset of the Middle Miocene it evolved new dental structures, followed by a divergence in size (Fig. 10), the end result of which was two species, one smaller than the precursor and one larger than it, while the precursor itself continued to survive for a while (at Moruorot and Kipsaraman in Kenya, for example) before going extinct.

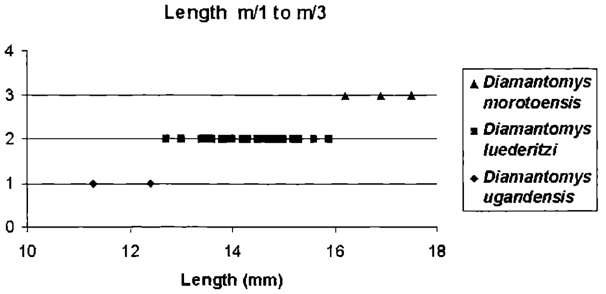


**Figure 10**: Univariate plot of length of m1-m3 of *Diamantomys* species.

Family Phiomyidae Wood, 1955

### Genus *Paraphiomys* Andrews, 1914

#### ***Paraphiomys pigotti*** **Andrews, 1914**

**Material**: Mor II, 13'98 left maxilla with P4-M2; Mor II 36'01, right m1.

**Measurements**: (in mm) of the teeth.
**M1** (3.05 x 3.00)
**M2** (3.14 x 3.67)
**m1** (3.32 x 2.97)

**Description**: The maxilla with three teeth (Mor II 13'98) (Fig. 5 (4)) is slightly smaller than usual for *Paraphiomys pigotti*. The P4 and M1 are deeply worn so that most details of crown morphology have been destroyed. The M2 shows four main cusps joined by transverse lophs. The paracone has two transverse crests - an anterior one that joins the anterior cingulum which reaches across the front of the tooth to join the protocone, and a median one that reaches directly towards the protocone but does not touch it. The metacone and hypocone are joined anteriorly by a transverse crest and centrally they are separated by a deep fovea. The metacone sends a short crest into the rear of this fovea. The hypocone has a distal crest that reaches across the rear of the tooth as a distal cingulum which extends as far as the buccal margin of the tooth. The lingual notch between the protocone and hypocone is deep and curves anteriorly as it extends into the tooth. The median valley between the paracone and metacone is shallow buccally but becomes deeper in the centre of the tooth where it ends in a deep fovea. The rear of the crown of m1 (Mor II, 36'01) (Fig. 5 (7)) is more developed than the front and it has a low but clear buccal anteroconid. The posterior arm of the protoconid is well developed, more so than in Rusinga specimens, and it is curved into a hook directed distally. The specimen corresponds to a small population or variant of the species. The metalophid and hypolophid are transversely oriented, whereas at Rusinga the metalophid is slightly oblique. The posterolingual border of the hypolophid forms a crest leading obliquely distally.

**Discussion**: The Moroto teeth fall within the range of metric variation of *Paraphiomys pigotti* from Kenya (LAVOCAT, 1973). *Paraphiomys pigotti* was first described from Karungu (ANDREWS, 1914) and has since been described from many other East African localities (LAVOCAT, 1973) including Songhor, Koru, Rusinga, Napak 1, Napak IV and Moruorot.

### Genus *Apodecter* HOPWOOD, 1929

#### *Apodecter* cf. *stromeri* HOPWOOD, 1929

**Material**: Mor II 44'04, left P4 (Fig. 6 (7)).
**Measurement**: of specimen (in mm).
**P4** (1.72 x 1.69)

**Description**: This tooth, which is unfortunately corroded, has the typical structure of the P4 of *Apodecter* (Fig. 6 (7)). The middle mesoloph extends transversely as a fine crest which reaches the mesostyle on the buccal margin. The paracone has a disto-buccal crest which joins the mesostyle. The metaloph curves distally and is almost interrupted before it joins the posteroloph in its middle. This tooth is too small to belong to *Apodecter orangeus* and is close in size to specimens of *Apodecter stromeri* from Elisabethfeld, Namibia.

#### *Apodecter orangeus* MEIN & PICKFORD, 2003

**Material**: Mor II, 39'01, left m3 fragment; Mor II, 25'03, right m2; Mor II, 40'04, left m2.
**Measurements**: of the teeth (in mm).
**m2** (2.36 x 2.01) (2.33 x 2.0)
**m3** (– x 2.03)

**Description**: Specimens Mor II, 25'02 (Fig. 5 (6)) and Mor II, 40'04 (Fig. 5 (5)) are the same size as the m2 of *Apodecter orangeus* from Arrisdrift, Namibia (MEIN & PICKFORD, 2003). It has a large and low buccal anteroconid. There is no sign of a posterior arm on the protoconid. The anteroconid is strong. There is a buccal valley between the protoconid and anteroconid. This feature is more accentuated than in Arrisdrift specimens.

**Discussion**: The second species of *Apodecter* from Moroto II is larger than the type species *A. stromeri* HOPWOOD, 1929, from Langental, Namibia. It is larger than specimens from Rusinga, Kenya, attributed to this species by LAVOCAT, 1973, but which are themselves appreciably larger than *A. stromeri* from Namibia. The Moroto specimen is closest in size and morphology to the sample of *A. orangeus* from Arrisdrift. Namibia. It is smaller than *A. australis* from Harasib 3a, Otavi Mountains, Namibia, but is slightly larger than *A. roessneri* from the same site.

A right m1 from Maboko, Kenya, (2.90 x 2.60) attributed to *Paraphiomys* sp. by FLYNN et al. (1983) lacks the posterior arm of the protoconid, and for this reason we prefer to class the specimen in the genus *Apodecter*.

### Genus *Andrewsimys* LAVOCAT, 1973

#### *Andrewsimys* cf. *parvus* LAVOCAT, 1973

**Material**: Mor II, 30'03, right M2; Mor II, 31'02, M2 fragment; Mor II 52'04, left M3 (Fig. 6 (4)); Mor II 53'04, left m2 (Fig. 6 (6)); Mor II 54'04, P3 (Fig. 6 (5)).
**Measurements**: (in mm) of the teeth.
**P3** (0.62 x 0.68)
**M2** (1.17 x 1.20) (– x 1.14)
**M3** (1.01 x 1.26)
**m2** (1.27 x 1.09)
**Description**:
Mor II 54'04 is a small button-like tooth with a single root (Fig. 6 (5)). It is almost circular in occlusal outline with slight apical wear, and has a well-developed interstitial facet on its distal surface. It closely recalls the P3 of the thryonomyid illustrated by LAVOCAT (1973) save for its greater dimensions.

**The M2s** from Moroto are tiny teeth. There are four transverse lophs with a connection between the mesoloph and the metaloph and between the mesoloph and posteroloph, enclosing a fossette, with a centrocone on its anterolingual corner. The lingual sinus is very oblique anteriorly. The paracone has a spur directed posteriorly which ends at the base of the transverse valley.

**The M3** has a rounded contour of which the posterior margin is the narrowest (Fig. 6 (4)).

**An m2** is attributed to this species (Fig. 6 (6)), the lower dentition of which was hitherto unknown. It consists of a minuscule, low lingual anterolophid, a high metaconid, and a protolophulid forming the mesial wall of the tooth. Its ectolophid is straight but runs diagonally and in its anterior part has a short mesolophid oriented towards the metaconid, after which the ectolophid bends sharply buccally before rejoining the hypoconid. A small hypolophid spur (the anterior horn of the hypoconid) extends lingually in the same diagonal direction of the ectolophid. The posterolophid is well developed and closes onto the summit of the entoconid, thereby closing off a metafossetid. The sinusid is deep and opens obliquely towards the rear. The tooth possesses three roots, two small circular ones anteriorly, and a single transversely oriented distal one which is subdivided at its apex.

**Discussion**: In the type specimen of *A. parvus*, the mesoloph is transversely oriented (LAVOCAT, 1973) but in the Moroto specimen it is directed distally and closes off a fossette. This morphology is derived compared to that from Songhor. The Moroto and Songhor specimens are similar in size.

Family Kenyamyidae LAVOCAT, 1973

### Genus *Simonimys* LAVOCAT, 1973

### ***Simonimys genovefae* LAVOCAT, 1973**

**Material**: Mor II 28'01, right m2 in mandible fragment (Fig. 4 (8)); Mor II, 32'02, right m3; Mor II 22'04, left mandible with p4-m2; Mor II, 35'04, left mandible with m1-m2 (Fig. 4 (7)); Mor II, 42'04, right m2.
**Measurements**: (mesio-distal length x bucco-lingual breadth in mm) of the teeth
**p4** (2.0 x 1.51)
**m1** (1.88 x 1.74) (1.54 x 1.39)
**m2** (2.05 x 1.96) (1.96 x 1.93) (1.59 x 1.46) (2.17 x 1.98)
**m3** (1.55 x –)
**Description**: The p4 has a small enamel crest in the middle of the anterior of the tooth which is absent in material from Napak.
The lower molars have four transverse lophids connected by a longitudinal crest. The buccal cusps have sharply angled corners, the one on the hypolophid pointing obliquely forwards, that on the mesolophid being transverse. The mesolophid and hypolophid enclose fossettids, but the valley between the two lophids opens lingually. The m1 has a small longitudinal crest in the bottom of the anterior fossettid. The m2 does not have a corresponding crest in its anterior fossettid (Fig. 4 (7, 8)). The m3 is smaller than the m2, but is damaged, so that it is not possible to provide a detailed description.
**Discussion**: In comparison with specimens from Songhor (LAVOCAT, 1973) the lingual cusps of the lower molars are joined together at a higher level, enclosing fossettids at an earlier stage of wear, probably a derived condition, and thus suggesting a younger age for Moroto II than for Songhor.

Family Bathyergidae WATERHOUSE, 1841

### Genus *Geofossor* MEIN & PICKFORD, 2003

### ***Geofossor* cf. *corvinusae* MEIN & PICKFORD, 2003**

**Material**: Mor II, 45'04, right m2.
**Measurements**: of the tooth (in mm).
**m2** (1.68 x 1.69)
**Description**: The bathyergid tooth from Moroto II (Fig. 4 (9)) is appreciably larger than those of *Proheliophobius* and is wider than those of *Richardus* but its crown is similar in height and crown morphology to the Arrisdrift species *Geofossor corvinusae*. The main difference concerns the wider mesoflexid and the more vertical metaconid which is higher than the other cusps in lingual view.
**Discussion**: In view of the similarities in size and overall morphology we attribute the specimen to *Geofossor* but because there are slight differences in the mesoflexid and metaconid, there is some doubt about its specific identity to *G. corvinusae*. We prefer to assign the tooth to *Geofossor* cf. *corvinusae*. The latter species was defined on the basis of material from Arrisdrift, Namibia, aged ca 17.5 Ma, and as such, the discovery of a similar species at Moroto II provides further evidence that the Ugandan locality is about 17-17.5 Ma.

Order Carnivora BOWDICH, 1821
Suborder Fissipeda BLUMENBACH, 1791
Family ?Amphicyonidae TROUESSART, 1885

### Genus ?*Hecubides* JOURDAN, 1862

### **Species indet.**

**Material**: Mor II Jan 67, right lower canine.
**Measurements**: (in mm) of the tooth.
**c1** (11.3 x 7)
**Description**: The only carnivore found at Moroto II is an isolated canine lacking most of the crown. It is mediolaterally slender, slightly curved from crown to root and has a shallow open groove on the lingual aspect of the root. At cervix the tooth measures 11.3 ap x 7 bl and the root is 27.5 mm high.
**Discussion**: Such a specimen is unidentifiable, but it is noted that it is compatible in size with lower canines of *Hecubides euryodon*.

Order Primates LINNAEUS, 1758
Suborder Strepsirrhini GEOFFROY SAINT-HILAIRE, 1812
Family Galagidae GRAY, 1825

### Genus *Komba* SIMPSON, 1967

### ***Komba* sp. indet.**

**Material**: Mor II 23'02, left m3; Mor II 24'02, right lower canine.
**Measurements**: (in mm) of the teeth.
**p2** (1.15 x 0.7 mm; crown + root height = 4.32; crown height = 1.81).
**m3** (2.00 x 1.24).
**Description**: The lower left m3 (Fig. 5 (2)) is almost unworn. It has five main cusps peripherally located round a long wide occlusal basin. The protoconid is more anteriorly located than the metaconid and is joined to it by a strong crest. The hypoconid has a long, slightly oblique anterior arm that descends gradually towards the base of the protoconid almost in the centreline of the tooth. Its posterior arm leads obliquely backwards to join the anterobuccal crest of the hypoconulid. The entoconid is bucco-lingually compressed and has sharp anterior and posterior crests, the anterior one being oriented antero-posteriorly, the posterior one being slightly oblique and reaching the antero-lingual crest of the hypoconulid. The talonid basin is voluminous. Anterior to the protoconid and metaconid there is a wide cingular shelf. There are two roots, the anterior one being comprised of fused buccal and lingual parts, the distal one being comprised of three fused parts, buccal, lingual and distal, suggesting a five rooted ancestral condition.
The p2 Mor II, 24'02 (Fig. 5 (3)) is unworn. It is a single

rooted tooth in which there is a buccal and lingual groove, suggesting a two rooted ancestral condition. The crown has a main cusp with a mesial crest that descends from apex to cervix, and a distal crest that ends in a small tubercle near cervix. The mesial and distal crests are separated from the main cusp by grooves on the lingual side of the crown.

**Discussion**: The m3 is small, falling well below the m3 bivariate scatters of *Komba* and *Progalago* species (Fig. 11). The tooth is significantly smaller than those of *Komba robustus* and *Komba minor.* Unfortunately, no m3 of *Komba winamensis* has been described in the literature (McCrossin, 1992), but the latter is the largest of the three species. The tooth probably does not belong to the Lorisidae *Mioeuoticus bishopi* since this species is about the same size as *Progalago dorae* (Simpson, 1967). Nor does it belong to *Mioeuoticus shipmani* which is larger than *M. bishopi* (Phillips & Walker, 2000). It would appear from the evidence that the Moroto galagid represents a hitherto undescribed species much smaller than any of the other known Early Miocene East African forms, and smaller even than the Pliocene *Galago sadimanensis* from Laetoli (Tanzania) and the Mabaget Formation, Kenya (Walker, 1987). We tentatively attribute the specimen to *Komba.*

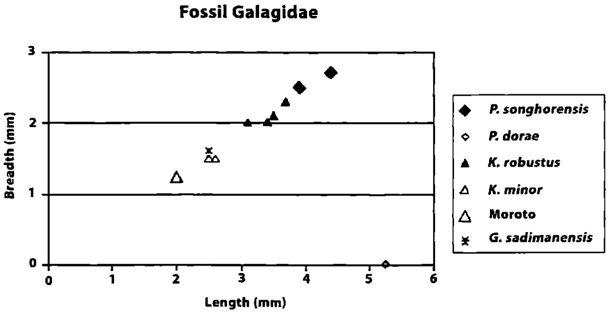


**Figure 11**: Bivariate plot of lower m3s of fossil galagids from East Africa.

Order Hyracoidea Huxley, 1869

Family Saghatheriidae Andrews, 1906

### Genus *Meroehyrax* Whitworth, 1954

### *Meroehyrax bateae* Whitworth, 1954

**Material**: Mor IIb 11'98, upper cheek tooth fragment (Site 1) (Fig. 12 (1)); Mor II, 14'03, magnum (Site 1); Mor II 4'04, lightly worn right upper 3rd molar; Mor II 5'04 left mandible fragments with moderately worn p4, ml, broken m3 and broken right m3 (all Site 1).

**Measurements**: of the teeth (in mm)

**M3** (12.2 x 11.6)

**p4** (7.5 x 5.2)

**ml** (9.0+ x 5.9)

**m3** (14.6 x 7.0 (length estimated by combining left and right m3s) anterior two lophs are 10.6 mm long)

**Description**:

**The M3** (Mor II 4'04) (Fig. 12 (2)) has four main cusps and a distal transverse crest and cingulum forming a low distal loph. The protocone is obliquely oriented, the anterior crest terminating in the centre line of the tooth just behind the anterior cingulum. The distal crest of the protocone is high and drops abruptly into the median transverse valley but does not block it, even at its base. The anterior surface of the protocone is concave. The base of the cusp is voluminous but it narrows sharply apically. The apex is blade-like in this unworn specimen. There is no lingual cingulum on the protocone but there is one in the lingual end of the median transverse valley. The paracone is selenodont with prominent parastyle and mesostyle. Both these styles are swollen at the base of the crown but pinch in apically. The buccal rib of the paracone is weakly expressed. The hypocone is conical with a sharp steep antero-buccal crest descending into the central valley terminating before reaching the median transverse valley. There is no trace of a cingulum on its lingual aspect. The ectoloph is almost straight with kinks where the styles are located. The metacone is selenodont with a prominent but low metastyle which is swollen basally and which birfurcates apically, one low crest blending into the distal crest of the metacone, the other reaching disto-lingually to form a small 'fifth' cusplet. The distal crest of this cusplet reaches lingually and blends into a distal cingulum that emanates from the disto-buccal corner of the hypocone. There is a low distal crest just anterior of the distal cingulum forming a small distal fossette. The enamel is finely wrinkled. There are three roots buccally and two lingually. Wear is minimal, being confined to outer cusps where it affects the apices of the paracone and metacone and their mesial and distal crests.

Mor II 11'98 is the distal part of an upper cheek tooth of a hyracoid (Fig. 12 (1)). It preserves part of the ectoloph and the hypocone together with the posterior fossette and is similar to the complete molar described immediatey above.

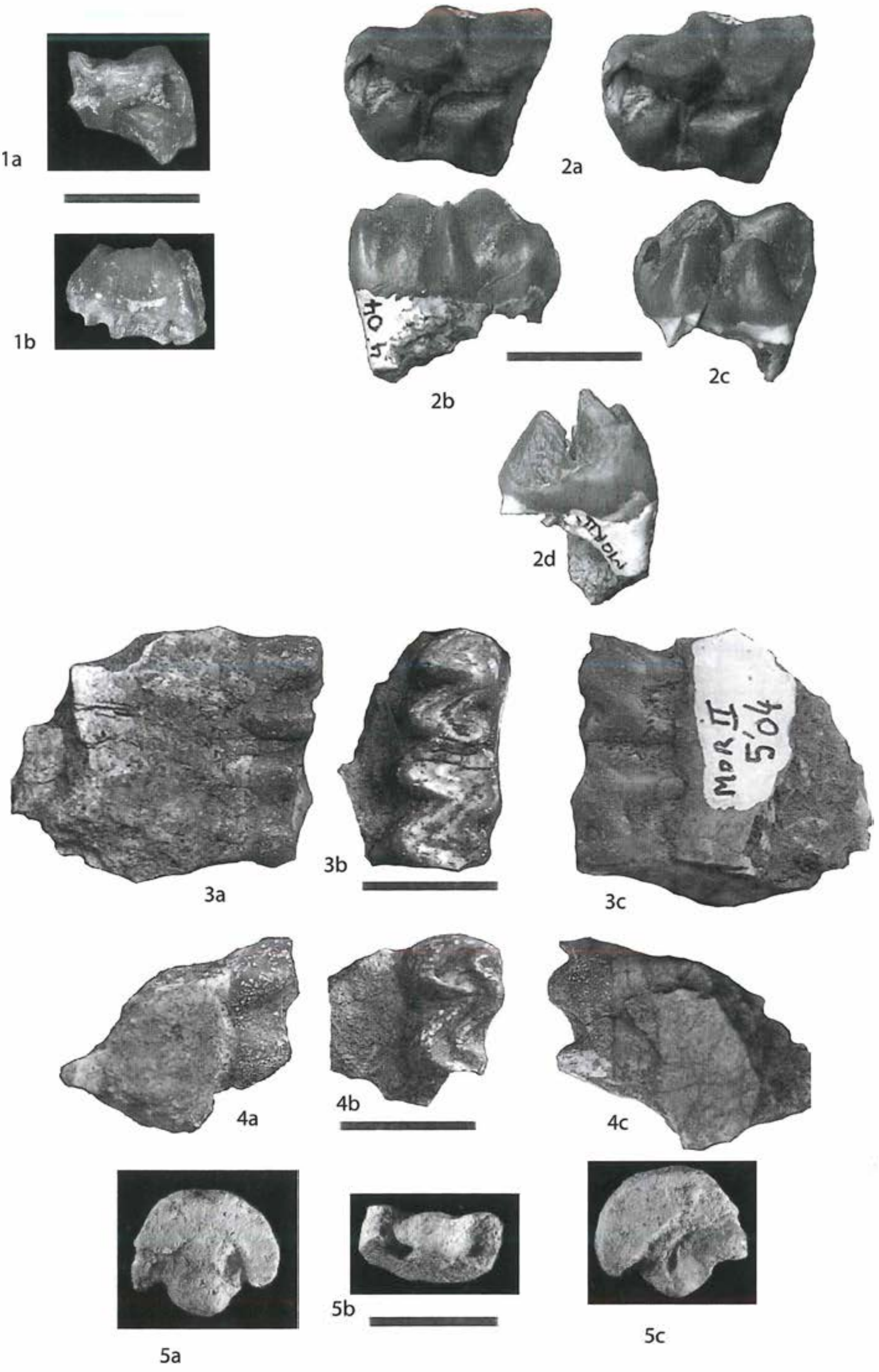
Mor II 5'04 (Fig. 12 (3, 4)) is a fragmentary mandible with four teeth, broken into three main pieces. The lingual surface of the jaw below p4-ml retains the upper edge of the lingual fossa which forms a low antero-posterior ridge along the specimen.

**The p4** in Mor II 5'04 is in medium wear with about half the height of the crown worn off. It consists of two crescents, the anterior one shorter than the posterior one. The anterior crests of the crescents are oriented at about 45° to the long axis of the tooth, while the distal part of the crescent is almost at right angles to the long axis of the tooth row. There is a hint of a buccal cingulum in the end of the buccal notch, but it is very low and insignificant. There is a light cingular fold on the antero-lingual corner of the tooth.

**The ml** is more deeply worn than the p4, which is typical of hyracoids, and because of this most of the crown morphology has been obliterated. However, it is possible to see that the anterior crescent is longer mesio-distally than the posterior crescent, the opposite of the situation in the p4.

**The left m3** is at a lesser stage of wear than the p4, again typical of hyracoids. It has lost about one third of the crown height due to wear and the hypoconulid is missing.

**Figure 12**: *Meroehyrax bateae* from Moroto II, Uganda (Scale bar: 10 mm). (1) Mor II, 11'98, distal portion of upper molar, a) occlusal, b) distal view, (2) Mor II, 4'04, right M3, a) stereo occlusal view, b) buccal, c) lingual and d) mesial views, (3) Mor II, 5'04, left mandible with p4-m1, a) buccal, b) occlusal and c) lingual views, (4) Mor II, 5'04, left mandible with m3 (lacking talonid), a) buccal, b) occlusal and c) lingual views, (5) Mor II, 14'03, magnum, a) proximal, b) posterior and c) distal views.



The right m3 retains the distal loph and the hypoconulid, so the total length of the m3 can be estimated to be 14.6 mm. The anterior loph is broader than the second one, and the hypoconulid is short, low and narrow, being 3.9 mm wide compared to the anterior crescent which is 7 mm wide. As in the p4, the anterior crests of the crescents are oriented at about 45° to the long axis of the tooth row, whereas the distal crests are almost at right angles to the same axis. There is no buccal cingulum, and only a small anterior lingual one. The hypoconulid is almost bilaterally symmetrical in occlusal view, and is not markedly selenodont.

Mor II 14'03 is a very characteristic hyracoid magnum (Fig. 12 (5)), being C shaped in proximal and distal view with a prominent volar process and highly compressed proximo-distally. It measures 11.4 mm medio-lateral breadth, 10 mm dorso-volar height and 4.4 mm proximo-distal length.

**Discussion**: The few hyracoid specimens from Moroto are interesting as they provide the first evidence of the upper dentition of the species *Meroehyrax bateae* associated with lower teeth. This species is extremely rare, WHITWORTH (1954) describing a single mandible and an isolated m3. The hypoconulid of m3 is almost identical to that in the holotype specimen from Rusinga Island (324'47) described by WHITWORTH (1954) and is divergent from the more selenodont hypoconulid that typifies most hyracoids, including *Megalohyrax* and *Prohyrax*. We can thus definitively reject the hypothesis that *Prohyrax* and *Meroehyrax* are synonyms (MEYER, 1978). The cheek tooth and carpal from Moroto are smaller than those of *Megalohyrax championi*, the common hyracoid of East African Early and Middle Miocene localities and we consider that they are also likely to represent *Meroehyrax bateae*.

From the point of view of their dimensions (Table 1) the Moroto II hyracoid teeth are close to those of *Meroehyrax bateae*.

The upper cheek teeth from Rusinga mentioned by WHITWORTH (1954) as possibly representing *Meroehyrax* were described as being «completely molarised teeth, only differing from upper molars of *Megalohyrax championi* in the low mesostyle, the shelf-like anterior cingulum, and the well developed transverse crests, similar to those found in *Prohyrax tertiarius* STROMER.» This description

| Tooth | Length | Breadth |
|---|---|---|
| p4 Moroto II, 5'04 | 7.5 | 5.2 |
| p4 Rusinga 324'47 | 8.0 (8.5) | 5.8 (5.8) |
| ml Moroto II, 5'04 | 9.0+ | 5.9 |
| ml Rusinga 324'47 | 10.0 (9.8) | 7.1 (6.8) |
| m3 Moroto II, 5'04 | 14.6 | 7.0 |
| m3 Rusinga 324'47 | 15.0 (15.1) | 7.2 (6.9) |
| m3 Rusinga 499'49 | 15.3 | 7.6 |

**Table 1**: Measurements of the teeth of *Meroehyrax bateae*. Values in brackets for Rusinga fossils are the author's measurements, those without brackets are from WHITWORTH, 1954. + The specimen is deeply worn and has lost a substantial amount of its original length due to interstitial wear mesially and distally. Its original length was probably about 9.5 mm. * WHITWORTH (1954) gives the breadth of the tooth as 7.1 mm. Inspection of the plate reveals that the tooth is narrower than this, probably 6.1 mm.

suggests that the specimens differ from the Moroto II upper molar, which has a high mesostyle, a narrow anterior cingulum and poorly developed transverse crests. The determination of the Rusinga fossils remains enigmatic but at least one of the specimens (548'47, now KNM RU 39) mentioned by WHITWORTH, is a chalicothere dM4. One of them (381'48, now KNM RU 55) is likely to belong to *Megalohyrax championi*. The third specimen (CMHy 98) may be lost, as no trace of it can be found in either the Natural History Museum, London, or the Kenya National Museum.

The discovery of the upper molar of *Meroehyrax* is important because it provides evidence concerning the origins of the extant hyracoid family Procaviidae. On the basis of the talar morphology we can rule out any close relationship between this family on the one hand and Titanohyracidae and Geniohyidae on the other (PICKFORD et al., 1997). This leaves Saghatheriidae and Pliohyracidae as the closest relatives of the Procaviidae. PICKFORD et al., (1997) placed Procaviidae as the sister group of Pliohyracidae, but the discovery that *Meroehyrax* has upper molars that are appreciably more similar to those of procaviids than are those of pliohyracids, shifts the relationship away from the pliohyracids, and back towards the Saghatheriidae, unless *Meroehyrax* is not a member of the latter family. However, examination of the upper molars of *Saghatherium* and *Meroehyrax* reveals that they are extremely similar, to the extent that if the genera were known only from the upper molars, they would be considered synonymous. Short of revising the saghatheriids keeping in mind the question of their detailed relationships to *Meroehyrax*, it is perhaps prudent to retain the genus in the family Saghatheriidae, rather than to place it either in its own family or in Procaviidae. Nevertheless, on the basis of upper molar morphology, we can rule out any particularly close relationship between pliohyracids and procaviids, the latter family having more in common with *Meroehyrax* than with any other genus of Hyracoidea. This means that Procaviidae are more closely related to Saghatheriidae than to any other family of hyracoids.

Order Proboscidea ILLIGER, 1811

Family Deinotheriidae BONAPARTE, 1845

### Genus *Deinotherium* KAUP, 1829

#### *Deinotherium hobleyi* ANDREWS, 1911

**Material**: Mor IIC Jan 62 (S), anterior loph of 2nd or 3rd lower molar; Mor II 3'85 enamel fragment (Site 1); Mor II 6'04, left dm3 germ.

**Measurements**: (in mm) of the teeth.

**dm3** (length ca 29.5, wl 19.2, w2 20.6)

**lower molar** (length – x wl 54.1, w2 –)

**Description**: The anterior lower molar loph (Mor IIC Jan 62 (S)) (Fig. 13 (2)) is typical of the genus *Deinotherium* being a simple transverse loph with anteriorly bent buccal and lingual ends, with a sharp-edged, distally sloping, flat, shearing wear facet running the entire width of the apex of the loph. The preserved part of the tooth is 54.1 mm bucco-lingual breadth. Its dimensions are compatible with the species *Deinotherium hobleyi.*

Mor II 6'04 is a broken left dm3 germ (Fig. 13 (3)). It has two transverse lophs and an anterior crest which is better developed than in the Napak deinothere (Nap I 125'99), which is a marginally larger individual. The anterior loph is 19.2 mm wide and the posterior one 20.6 mm. The length of the tooth is about 29.5 mm (there is no contact between the preserved parts of the anterior and posterior lophs, so the measurement is only approximate). The distal cingulum is well formed.

**Discussion**: The deciduous tooth is similar in size to specimens from Rusinga Island, Kenya, but has a better developed anterior ridge. However, there can be little doubt that it represents the species *Deinotherium hobleyi* which is known at almost all the Early and Middle Miocene localities in Eastern Africa. The molar loph is also compatible in size and morphology with this species.

Family Mammutidae CABRERA, 1929

### Genus *Eozygodon* TASSY & PICKFORD, 1983

#### *Eozygodon morotoensis* (PICKFORD & TASSY, 1980)

**Material**: Mor II 4'85, molar fragment (Site 1); Mor II 18'01, left M2 (Site 1); Mor IIC Jan 62, talus; ?Mor II 5'98, right lower i1 tip (Site 1).

**Measurements**: in mm of the tooth.

**M2** (89 x 60)

**lower incisor?** (15 x 8.2)

**Description**: The left upper second molar Mor II 18'01 is an almost complete though damaged specimen in medium wear (Fig. 13 (1)). The tooth has broken into sections which have drifted apart in the sediment, but have retained their positions relative to one another. There are three lophs and a beaded distal shelf-like cingulum. The thin enamel (3mm on the pretrite of the second loph), perfectly formed lophs with a central sulcus and a continuous beaded lingual cingulum are all features that are typical of *Eozygodon*

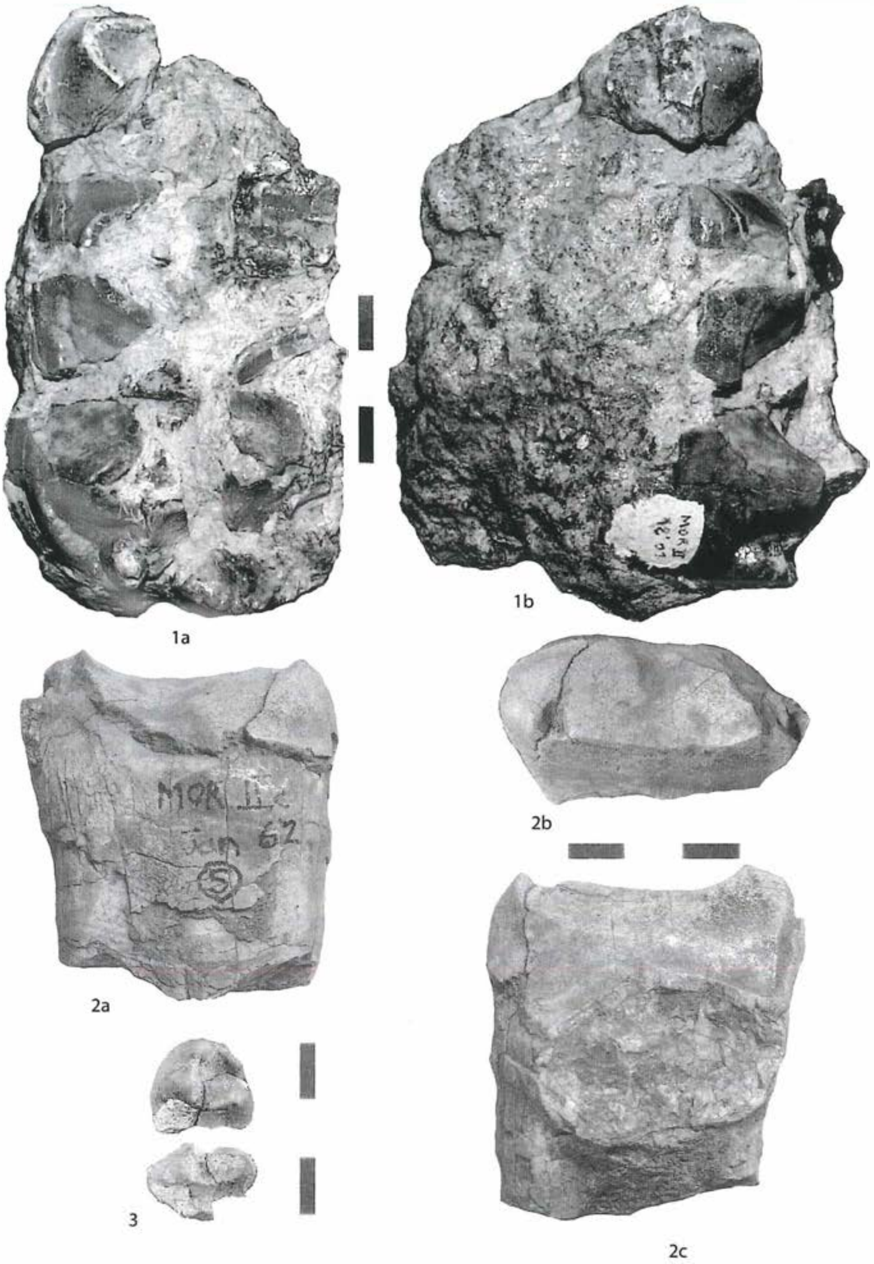


**Figure 13**: Proboscideans from Moroto II, Uganda. (Scale interval: 1 cm). (1) Mor II, 18'01, *Eozygodon morotoensis*, left M2, a) occlusal and b) lingual views, (2) Mor IIc, S, Jan 62, *Deinotherium hobleyi*, half molar, a) mesial b) occlusal and c) distal views, (3) Mor II, 6'04, *Deinotherium hobleyi*, left dm3 germ, occlusal view

*morotoensis*, the type locality of which is Moroto I (Pickford & Tassy, 1980; Tassy & Pickford, 1983). Taking into account the displacement of the various pieces, the crown measures ca 89 mm long by ca 60 wide at the second loph.

Mor II 5'98 is the tip of a lower central incisor. It is slightly scoop shaped and elongated from tip towards the root which is broken off. It is flattened supero-inferiorly, being 15 mm mesio-distal and 8.2 mm labio-lingually. It has a single wear facet running across the tip and along the distal edge. This tooth is similar in overall morphology to lower tusks of *Eozygodon* from Meswa Bridge (Pickford & Tassy, 1980) but it is much smaller. It could be a deciduous lower tusk, as the enamel is thin, but until better information is available about deciduous tusks in proboscideans, this tooth will remain enigmatic.

The talus Mor IIC Jan 62 (Fig. 14) is attributed to *Eozygodon morotoensis* on the basis of size; the tali of *Progomphotherium* and the deinothere are expected to have been smaller. The proximal surface is evenly curved from anterior to posterior and is almost hemicylindrical from medial to lateral with a slight depression centrally. The head is broken off leaving a small projection of the neck flaring from the body of the talus. The tibial facet is 92.4 mm medio-laterally.

**Discussion**: *Eozygodon morotoensis* is a distinctive proboscidean on account of its extremely lophodont cheek teeth and the almost square outline of the skull in lateral view (Pickford, 2003). It is known from Auchas and Elisabethfeld, Namibia, several sites in East Africa (Meswa Bridge, Rusinga, Moruorot, Moroto) and north Africa (Wadi Moghara, Egypt). In East Africa its known geochronological range is from ca 22.5 to 17.2 Ma.

Family Gomphotheriidae Hay, 1922

### Genus *Progomphotherium* Pickford, 2003

### *Progomphotherium maraisi* Pickford, 2003

**Material**: Mor IIb 1'85 + 1'98 + 22'03, upper right tooth row and half lower molar (Site 1) (Fig. 15 (1, 3)); Mor IIa 2'98, p3 (Site 2) (Fig. 15 (2)); Mor II 7'04, left M2 (Site 1) (Fig. 15 (4)).

**Measurements**: (in mm) of the teeth

**M1** (51.8 x 44.1)
**M2** (82.6 x 49.8) (76 x 52)
**M3** (90.2 x 49)
**p3** (32.4 x 29.5)
**m2** (- x 47.9)

**Description**: The lower premolar Mor IIa, 2'98 is from the left side and was found at the uphill exposures of the southern valley (Fig. 15 (2)). It is comprised of four bu-

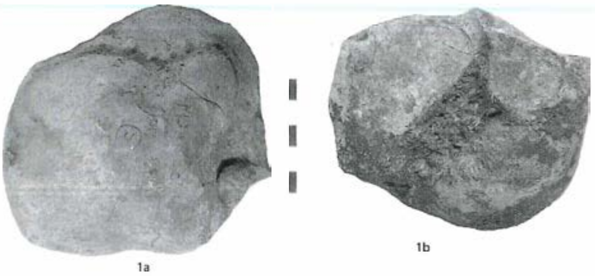


**Figure 14**: Proboscidea from Moroto II, Uganda (Scale interval: 1 cm). (1) Mor IIc, S, Jan 62, cf. *Eozygodon morotoensis*, left talus, a) proximal and b) distal views.

nodont cusps arranged in two pairs, with a small anterior accessory cusplet in the midline of the tooth, and another small cusplet in the transverse valley just to the buccal side of midline. The anterior loph is narrower than the posterior one. It has a prominent distal interstitial wear facet.

Mor II 1'85 + 1'98 + 22'03 is an upper tooth row (Fig. 15 (1)) from the downhill exposures of the southern valley (Site 1, Fig. 1). The interstitial contact facets reveal that the three teeth represent a single individual. The right M1 is deeply worn and lacks the two distal cusps on the buccal side and would be unidentifiable save for its association with the M2 and M3. It is a trilophodont tooth. Its dimensions are 51.8 mm anteroposterior length x 44.1 mm breadth of the anterior loph.

The right M2 is deeply worn on the two anterior lophs. It is trilophodont with a prominent but low distal cingulum, bundont with thick enamel. The pretrite cusps have a simple curved outline without any indentations, suggesting the presence of simple mesocones and conelets. The posttrite cusps are more oval in outline. The crown is 82.6 mm long. The first loph is 44 mm wide, the second is 47.0 mm and the third is 49.8 mm wide.

The right M3 is lightly worn and the first pretrite cusp is missing. It shows bunodont cusps, small mesocones in line with and almost fused to the pretrite and posttrite cusps, simple cusp layout with minimal multiplication of the conelets and cuspules. The lophs are almost straight across, except for the third one which is very slightly v-shaped, the apex of the v pointing anteriorly. The tooth narrows to the rear and the occlusal surface is helicoidally twisted from almost horizontal anteriorly to inclining buccally distally. When the interstitial facets are aligned, the M3 is seen to curve palatally with respect to the long axis of the M2, from which it is inferred that the palate narrowed distally. The M3 is composed of 3.5 lophs the distal loph being little more than a slightly expanded cingulum. Crown length is 90.2 mm, the first loph is estimated to have been ca 52 mm wide, the second is 49 mm and the third 40.7 mm. Half a lower molar (Mor II 1'98) is deeply worn. It is 47.9 mm broad.

**Discussion**: *Progomphotherium maraisi* is widespread in eastern and southern African deposits, but it is generally poorly represented which is why it has only recently been recognised as a new genus and species (PICKFORD, 2003). The type locality is Auchas, Namibia, the holotype being an almost complete skull with partly damaged dentition.

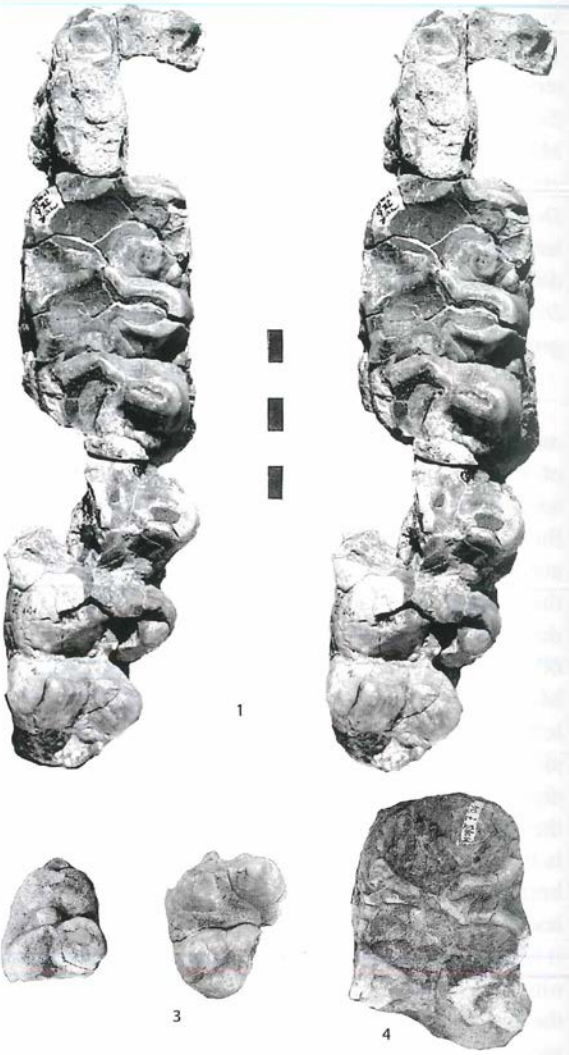


**Figure 15**: *Progomphotherium maraisi* from Moroto II, Uganda (Scale interval: 1 cm). (1) Mor IIb, 1'85, 1'98, right upper molar row, stereo occlusal view, (2) Mor II, 2'98, left p3, occlusal view, (3) Mor II, 1'98 + 4'01, rear loph of right M3, occlusal view (note cementum layer), (4) Mor II, 7'04, left m1, occlusal view

The genus is characterised by the presence of functional P3 and p3 in the permanent cheek tooth series still in position when M3 is erupted, the molars are simple, trilophodont, bunodont with mesocones in line with and almost completely fused to the pretrite and posttrite cusps. There is no multiplication of conelets and cuspules that characterise later gomphothere dentitions. The M3 has 3.5 lophs and the mesocones are in line with the main cusps. The lower tusks are peg-like but are higher than wide, the opposite of most other gomphotheres in which the lower tusks tend to be dorso-ventrally flattened. There are minor amounts of cementum in the bases of the valleys (Fig. 15 (3)), but in many specimens it is not preserved.

The species has been recorded from Mfwangano and Karungu, Kenya, where it is represented by lower tusks and well-preserved molars respectively, but it could also be present at several other sites in Africa such as Napak, where simple, small, bunodont gomphothere cheek teeth are known.

Order Perissodactyla Owen, 1848

Family Rhinocerotidae Owen, 1845

### Genus and species indeterminate

**Material**: Mor IIa, 1'98, phalanx (Site 1); Mor IIa 7'98, enamel fragments (Site 1); Mor IIb, 16'98, enamel fragments (Site 1); Mor II, 13'01, molar fragments (Site 1);

**Description**: All that can be said of these fragmentary rhinocerotid remains from Moroto II, is that the family is represented at the site. Even the phalanx cannot be unequivocally identified, although it is short and robust as in the genus *Brachypotherium*.

**Discussion**: The Moroto rhinos are too poorly preserved to be confidently identified, although there is the possibility that the phalanx represents a brachypothere.

Order Artiodactyla Owen, 1848

Family Anthracotheriidae Gill, 1872

### Genus *Brachyodus* Depéret, 1895

### *Brachyodus aequatorialis* MacInnes, 1953

**Material**: Mor IIb (S) Dec 61, complete femur; Mor II Jan 62 (S), proximal metatarsal; Mor II Jan 67, 2nd phalanx; Mor II 61, Ist phalanx; Mor II 19'01, left upper molar fragment (Site 1); Mor IIb 33'98, tooth fragment (Site 1); Mor II 19'01, upper molar fragment (Site 1).

**Description**:

Mor II 19'01 is the anterior portion of an upper molar (Fig. 16 (1)). It preserves the parastyle, part of the paracone and a bit of the protoconule. The enamel is finely wrinkled, the parastyle is hook-shaped anteriorly and the main cusps are selenodont. The dimensions and morphology of the specimen indicate that it belongs to *Brachyodus aequatorialis*.

Mor IIb Dec 61 (S) is a complete femur in three pieces (Fig. 16 (2)). It has a prominent spherical head on a short neck. The femur is ca 580 mm long and the midshaft is 67.5 x 48.2 mm in diameter. The distal end is damaged and slightly crushed, so meaningful measurements cannot be taken. The greater trochanter is robust and overhangs a deep and voluminous trochanteric fossa. There is no third trochanter.

Mor II Jan 62 (S) is a proximal end of a metatarsal with a trapezoidal articular facet which is wider on the dorsal side than on the plantar side (Fig. 16 (3)) The articulatioin is almost flat. It is 41 mm wide.

Mor II 61 is a 1st phalanx of a large anthracothere (Fig. 16 (4)). It is 58 mm long and has the characteristic divergently curved distal articulation for the 2nd phalanx and the more evenly curved proximal facet. Its proximal end is 32.3 mm wide and 31.0 mm high, while the distal end is 26.5 mm wide and 22.3 mm high.

Mor II Jan 67 is a 2nd phalanx 46.5 mm long (Fig. 16 (5)). In dorsal view it is wedge shaped with the distal end being sensibly narrower than the proximal one. The distal end is 32.3 mm wide by 20.4 mm high, whereas the proximal end is 39.7 mm wide by 25.5 mm high.

**Discussion**: The femur and both phalanges are typical of large anthracotheres, and the molar fragments reveal that the species present at Moroto II is *Brachyodus aequatorialis*, the common large anthracothere in East African Early and basal Middle Miocene localities. In East Africa, this species ranges in age from 22.5 Ma (Meswa Bridge, Kenya) to 17.2 Ma (Moruorot, Kenya) and the genus has been found as far south as the Orange River, (Auchas) and Grillental, Namibia (Pickford, 2003) as well as in North Africa (Wadi Moghara, Egypt; Gebel Zelten, Libya).

Family Palaeochoeridae Matthew, 1924

### Genus *Morotochoerus* Pickford, 1998

### *Morotochoerus ugandensis* Pickford, 1998

**Material**: Mor II 2'85, right M3 (Site 1); Mor II 12'98, right lower canine fragment; Mor II 20'01, right M2 (Site 1); Mor IIb 4'98, left M3 (Site 1).

**Measurements**: of the teeth (in mm):

**M2** (13.3 x 13.7)

**M3** (14.0 x 15.3) (13.0 x 14.5)

**c1** male (5.9 x 5.3 x 4.9)

**Description**

Mor 20'01 is a right M2 measuring 13.3 mm ap x 13.7 mm tr. It has four main cusps arranged in two lophs, and a prominent protoconule between the protocone and paracone and slightly in front of them. The cusps are slightly selenodont. The rear cusp pair is separated from the anterior one by a wide transverse valley unencumbered by any structures, which makes the tooth quite lophodont in appearance, despite the selenodont aspect of each of the main cusps.

Mor II 4'98 has four main cusps and a prominent protoconule between the protocone and paracone (Fig. 16 (6)). There is a clear anterior cingulum and on the lingual side there is a weak cingulum at the end of the median transverse valley. The rear pair of cusps is narrower than the anterior pair. The M3 Mor II 2'95 was described by Pickford (1998).

The fragment of lower canine (Mor II 12'98) is scrofic in section with a mesio-distally longer lingual surface (5.9 mm), a shorter buccal surface (5.3 mm) and a distal face that has no enamel, 4.9 mm in breadth.

**Discussion**: *Morotochoerus ugandensis* is a medium-sized palaeochoerid first described from Moroto I and Moroto II. Palaeochoerids are unknown from other prolific Early Miocene localities of East Africa such as Napak, Songhor, Rusinga, Karungu etc., and it seems likely that the family immigrated to Africa from Eurasia at the beginning of the Middle Miocene. The presence of this family at Moroto suggest that it is unlikely that the deposits are as old as 20.6 Ma, otherwise fossils of this lineage would likely have been found in at least one of the many Early Miocene sites, which, it should be remembered, are much more richly fossiliferous than Moroto.

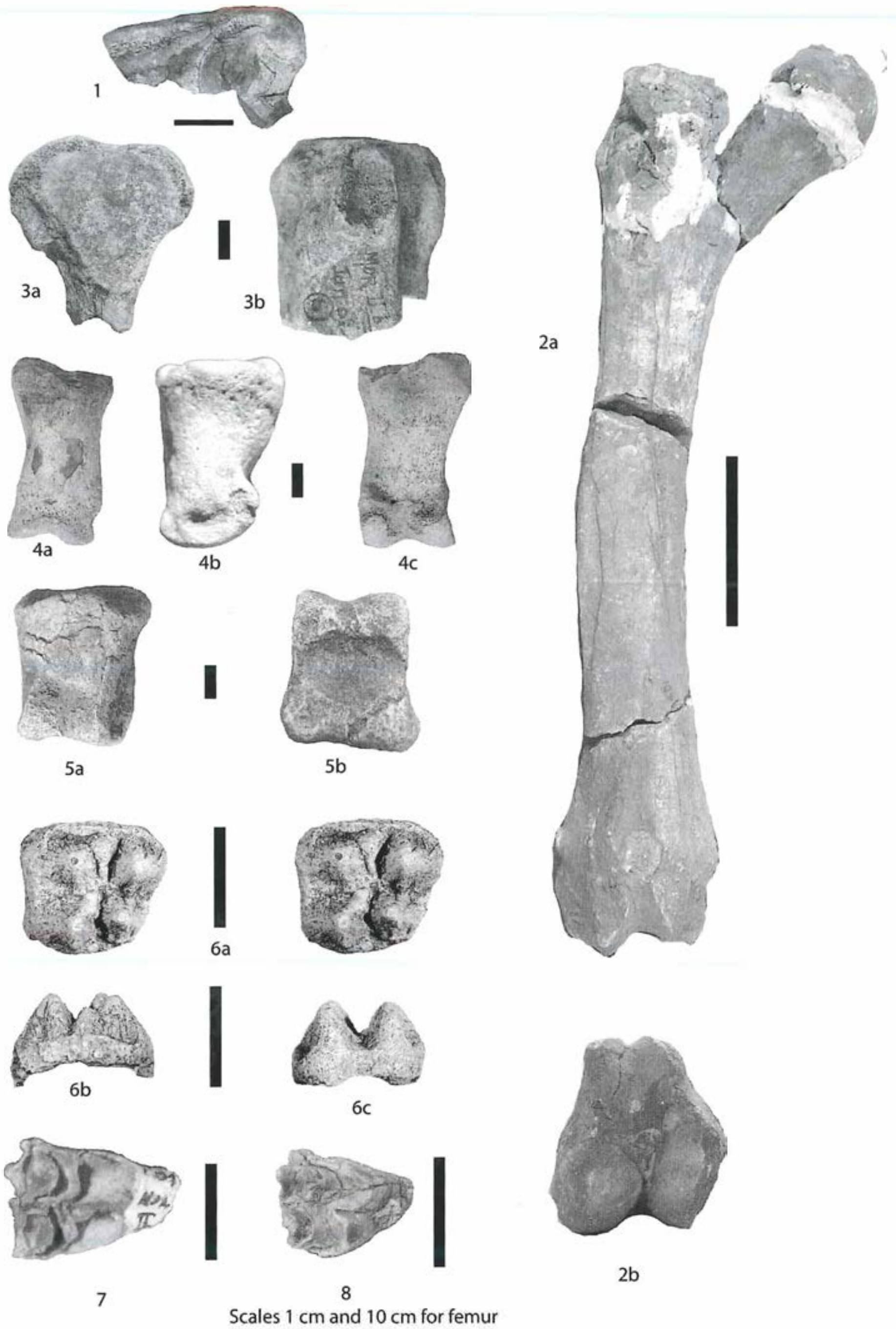


**Figure 16**: Artiodactyls from Moroto II (Scale bar: 1 cm except for femur which is 10 cm).

(1) Mor II, 19'01 *Brachyodus aequatorialis*, mesial part of left upper molar fragment, occlusal view, (2) Mor IIb, S, Dec. 61, *Brachyodus aequatorialis*, left femur, a) cranial view, b) distal view, (3), Mor II, S, Jan 62, *Brachyodus aequatorialis*, metatarsal, a) proximal view, b) plantar view, (4) Mor II, 61, *Brachyodus aequatorialis*, 1st phalanx, a)dorsal, b) lateral and c) volar views, (5) Mor II, Jan 67, *Brachyodus aequatorialis*, 2nd phalanx, a) dorsal and b) volar views, (6) Mor II, 4'98, *Morotochoerus ugandensis*, left M3, a) stereo occlusal, b) anterior and c) lingual views, (7) Mor II, 1'01, *Walangania africanus*, right upper molar, occlusal view, (8) Mor II, 19'03, *Walangania africanus*, right upper molar, occlusal view.

Suborder Ruminantia Scopoli, 1777

Genus *Walangania* Whitworth, 1958

***Walangania africanus* (Whitworth, 1958)**

**Material**: Mor II 1'01, right upper molar (Site 1); Mor II 19'03, right upper molar (Site 1).
**Measurements**: of the teeth (in mm).
**M*** (11.6 x 12.9) (10.4 x 11.5)
**Description**: Mor II 1'01 is a typical selenodont upper molar of *Walangania africanus* (Fig. 16 (7)). Mor II 19'03 (Fig. 16 (8)) is a right upper molar with similar morphology but slightly smaller dimensions.
**Discussion**: *Walangania africanus* is the most common pecoran in Early and basal Middle Miocene deposits of East Africa. It occurs at virtually all the known sites ranging in age between 20 Ma and 17.2 Ma and it may extend upwards towards the end of the Middle Miocene at sites such as Fort Ternan. It is well represented at Napak, Uganda (Pickford, 2002). The few teeth from Moroto II are typical of the species.

## 4. Discussion and conclusions

The Moroto II mammals are much better known now than they were even five years ago thanks to surface prospecting and screening of sediments by the Uganda Palaeontology Expedition. Micromammals in particular are relatively diverse and abundant, although only a single rodent incisor figured in previous faunal lists from the site. Also

**Table 2**: Faunal List Miocene of Moroto II. * not counting many rodent incisors and unidentifiable tooth fragments.

| Group | Genus and species | Quantity of specimens* |
|---|---|---|
| **?Marsupialia** | indet. | 1 (1 tooth) |
| **Insectivora** | Tenrecidae indet. | 1 (1 tooth) |
| **Macroscelididae** | *Miorhynchocyon* sp. | 1 (1 tooth) |
| **Chiroptera** | *Taphozous incognita* | 1 |
|  | *?Chamtwaria pickfordi* | 1 (1 tooth) |
| **Rodentia** | *?Pseudocricetodon* sp. | 6 (6 teeth) |
|  | *Notocricetodon gommeryi* sp. nov. | 6 (6 teeth) |
|  | *Protarsomys* cf. *macinnesi* | 6 (6 teeth) |
|  | *Protarsomys* cf. *lavocati* | 1 (1 tooth) |
|  | *Megapedetes* cf. *pentadactylus* | 2 (2 teeth) |
|  | *Zenkerella wintoni* | 4 (6 teeth) |
|  | *Diamantomys morotoensis* sp. nov. | 20 (49 teeth) |
|  | *Diamantomys ugandensis* sp. nov. | 3 (9 teeth) |
|  | *Paraphiomys pigotti* | 2 (3 teeth) |
|  | *Apodecter* cf. *stromeri* | 1 (1 tooth) |
|  | *Apodecter orangeus* | 3 (3 teeth) |
|  | *Andrewsimys* cf. *parvus* | 5 (5 teeth) |
|  | *Simonimys genovefae* | 5 (8 teeth) |
|  | *Geofossor* cf. *corvinusae* | 1 (1 tooth) |
| **Carnivora** | *?Hecubides* sp. | 1 (1 tooth) |
| **Galagidae** | *Komba* sp. | 2 (2 teeth) |
| **Catarrhini** | *Prohylobates macinnesi* | 4 (4 teeth) |
|  | *Kogolepithecus morotoensis* | 9 (9 teeth) |
|  | *Micropithecus* sp. | 1 (1 tooth) |
|  | *Afropithecus turkanensis* | 7 (19 teeth) |
|  | *Ugandapithecus* sp. | 3 (3 teeth) |
| **Hyracoidea** | *Meroehyrax bateae* | 4 (5 teeth) |
| **Proboscidea** | *Deinotherium hobleyi* | 3 (3 teeth) |
|  | *Progomphotherium maraisi* | 3 (6 teeth) |
|  | *Eozygodon morotoensis* | 4 (1 tooth) |
| **Rhinocerotidae** | indet. | 4 (3 tooth fragments) |
| **Anthracotheriidae** | *Brachyodus aequatorialis* | 7 (1 tooth) |
| **Palaeochoeridae** | *Morotochoerus ugandensis* | 4 (4 teeth) |
| **Ruminantia** | *Walangania africanus* | 2 (2 teeth) |
| **$\Sigma$ Mammals** |  | **127 (182 teeth)** |

present are at least six species of primates, four of which have been discussed in detail in separate papers (PICKFORD et al., 2003).

The sediments in the eastern and southern valleys at Kogole are penecontemporaneous and both outcrops accumulated about 17.5 to 17 Ma. This is substantially younger than a radio-isotopic age of 20.6 Ma for the capping basalt flow published by GEBO et al. (1997), and it is likely either that there is something wrong with the samples of lava analysed (it is heavily altered) or that they carried excess argon at the time of eruption, a common problem with basalts. For example, mineral concentrates from dacite lava from the 1986 eruption of Mt St Helens, North America, have yielded K-Ar ages of 2.8 +/- 0.6 Ma. (AUSTIN, 1996). Perhaps the Moroto basalt also retained excess argon. In any case the fauna suggests that the K-Ar age estimate is more than three million years too old.

The depth of the sediment filled valley east of Kogole Hill, which drains into the Gregory Rift, indicates that relief in the region must have been at least 100 metres at the time of sediment accumulation. If the Kogole deposits really are more than 20.6 Ma, as suggested by the K-Ar dates, then that would mean that rifting activity started some 21 Ma or earlier, whereas the faunal and radio-isotopic evidence from within the Rift indicates an appreciably later onset for rifting, perhaps as recently as 17.5 Ma.

The valley south of Kogole Hill, which eventually drains into the Nile, is a shallow one, and would have resembled one of the present day silted up valleys of the Karamoja Plain. These are linear swamps which can dry up completely during severe and prolonged droughts, but which usually have pools of water or underfit streams in them. During rainy seasons these shallow valleys rapidly fill with water which can cause extensive flooding. They are attractive places for animals on account of the grass and water. At present the slightly higher ground between the valleys is covered with wooded savanna, but the valleys themselves are devoid of trees. It is probable that during the time of deposition of the Kogole Beds, the valleys did not dry out completely during dry seasons, because the common occurrence of anthracotheres, turtles and crocodiles indicates more permanent stands of water.

The Moroto II fauna now stands at 34 mammalian taxa based on over 127 identifiable specimens. Some taxa are still poorly known (carnivores, Rhinocerotidae, ?marsupial). The deposits are not richly fossiliferous, but continue to yield new taxa each year. Further surface prospecting and sediment screening will undoubtedly yield additional taxa.

## 5. Acknowledgements

The Uganda Palaeontology Expedition is a collaborative project between the Muséum national d'Histoire naturelle de Paris and the Uganda Museum, Kampala. We thank the

Uganda National Council for Science and Technology (Drs Nyiira, Kakule, Mugoya), the Uganda Museum (Dr E. Kamuhangire, Mr E. Musiime), Makerere University Geology Department (Mrs I. Ssemmanda), and the Ministry of Culture, Antiquities and Tourism (Dr S. Kagoda) for authorisation to carry out research and for co-operation within Uganda. The French Embassy in Kampala was of considerable aid to the Uganda Palaeontology Expedition. We particularly thank the District Administrator and Municipal Council of Moroto for help and encouragement to continue surveying in the region.

We are anxious to thank Professors Y. Coppens (Collège de France) and P. Taquet (Département Histoire de la Terre) for funds and other assistance. Funding was also supplied by the French Ministry of Foreign Affairs (Commission des Fouilles) and the CNRS (UMR 8569, UMR 5143, and Projet PICS). Drs. Brigitte Senut, Dominique Gommery and Mr. Ezra Musiime assisted in the field work at Moroto as did the villagers of Rupa, near Moroto, Uganda.

## 6. References

ALLBROOK, D. & BISHOP, W.W., 1963. New fossil hominoid material from Uganda. — Nature, **197**:1187–1190, London.

ANDREWS, C.W., 1914. On the lower Miocene vertebrates from British East Africa, collected by Dr. Felix Oswald. — Quarterly Proceedings of the Geological Society of London, **70**:163–186, London.

ANYONGE, W., 1991. Fauna from a new lower Miocene locality west of Lake Turkana, Kenya. — Journal of Vertebrate Paleontology, **11**:378–390, Norman.

AUSTIN, S., 1996. Excess Argon within mineral concentrates from the New Dacite lava dome at Mount St Helens. — CEN Technical Journal, **3**:335–343.

BISHOP, W.W., 1963. Uganda's animal ancestors. — Wildlife and Sport, **3** (**3**):1–8.

BISHOP, W.W., 1963. The later Tertiary and Pleistocene in eastern equatorial Africa. — [in:] HOWELL, F.C. & BOURLIÈRE, F. (eds.). African Ecology and Human Evolution, **36**:246-275, (Viking Fund Publ. Anthrop.) New York.

BISHOP, W.W., 1964. More fossil Primates and other Miocene mammals from North-east Uganda. — Nature, **203**:1327–1331, London.

BISHOP, W.W., 1964. Mammalia from the Miocene volcanic rocks of Karamoja, East Africa. — Proceedings of the Geological Society of London, **1617**:91–94, London.

BISHOP, W.W., 1967. The later Tertiary in East Africa - volcanics, sediments and faunal inventory. — [in:] BISHOP, W.W. & CLARK, J.D. (eds.). Background to Evolution in Africa, pp. 31-56, (Univ. Chicago Press) Chicago.

BISHOP, W.W., 1968. The evolution of fossil environments in East Africa. — Transactions of the Leicester Literary and Philosophical Society, **62**: 22–44.

BISHOP, W.W., 1971. The late Cenozoic history of East Africa in relation to hominoid evolution. — [in:] TUREKIAN, K. (ed.). Late Cenozoic Glacial Ages, pp. 493-527, (Yale Univ. Press), Cambridge.

BISHOP, W.W., 1972. Stratigraphic succession 'versus' calibration in East Africa. — [in:] BISHOP, W.W. & MILLER, J.A. (eds.). Calibration of Hominoid Evolution, pp. 219-246, (Scottish Academic Press) Edinburgh.

BISHOP, W.W., MILLER, J.A. & FITCH, F.W., 1967. New potassium-argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. — American Journal of Science, **267**:669–699, New Haven.

BISHOP, W.W. & WHYTE, F., 1962. Tertiary mammalian faunas and sediments in Karamoja and Kavirondo, East Africa. — Nature, **196**:1283–1287, London.

BOSCHETTO, H.B., BROWN, F.H. & MCDOUGALL, I., 1992. Stratigraphy of the Lothidok Range, northern Kenya, and K-Ar ages of its Miocene Primates. — Journal of Human Evolution, **22**:47–71, London.

BUTLER, P.M. & HOPWOOD, A., 1957. Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. — Fossil Mammals of Africa, **13**:1–35.

DRAKE, R., VAN COUVERING, J.A., PICKFORD, M., CURTIS, G. & HARRIS, J.A., 1988. New chronology for the early Miocene mammalian faunas of Kisingiri, Western Kenya. — Proceedings of the Geological Society of London, **145**:479–491, London.

FLEUTY, M.J., 1968. Explanation of the Geology of Sheet 27 (Moroto). — Reports of the Geological Survey of Uganda, **13**.

FLYNN, L., JACOBS, L. & SEN. S., 1983. Miocene diversity of *Paraulacodus* (Rodentia, Thryonomyidae) and its relatives. — Annales de Paléontologie, **69** (**4**):355–366.

FLYNN, L., JACOBS, L. & LINDSAY, E., 1985. Problems in muroid phylogeny: relationships to other rodents and origin of major groups. — [in:] LUCKETT, W.P. & HARTENBERGER, J.-L. (eds.). Evolutionary Relationships among Rodents: A Multidisciplinary Analysis. — NATO ASI Series, **92**:589–618.

GEBO, D.L., MACLATCHY, L., KITYO, R., DEINO, A., KINGSTON, J. & PILBEAM, D., 1997. A hominoid genus from the Early Miocene of Uganda. — Science, **276**:401–404, Washington.

HOPWOOD, A.T., 1929. New and little known mammals from the Miocene of Africa. — American Museum Novitates, **334**:1–9.

HORNE, R.G., 1953. The geology of the lower mountain slopes adjacent to Moroto Township. — Unpublished Report of the Geological Survey of Uganda, **1953**:1-47.

JAEGER, J.-J. & MARTIN, M., 1984. African marsupials - vicariance or dispersion? — Nature, **312**:379, London.

LAVOCAT, R., 1973. Les rongeurs du Miocène d'Afrique orientale. — Mémoirs et Travaux de l'Institut, Ecole Pratique des Hautes Etudes, Montpellier, **1**:1–284.

MCDOUGALL, I. & WATKINS, R.F, 1985. Age of hominoid-bearing sequence at Buluk, northern Kenya. — Nature, **318**:175–178, London.

MCDOUGALL, I. & WATKINS, R., 1988. Potassium-argon ages of volcanic rocks from northeast of Lake Turkana, northern Kenya. — Geological Magazine, **125**:15–23.

MacLatchy, L., Gebo, D., Kityo, R. & Pilbeam, D., 2000. Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. — Journal of Human Evolution, **39**:159–183.

MacLatchy, L., Gebo, D. & Pilbeam, D., 1995. New primate fossils from the Lower Miocene of Northeast Uganda. — American Journal of Physical Anthropology, Supplement **20**:139.

MacLatchy, L. & Pilbeam, D., 1999. Renewed research in the Ugandan Early Miocene. — [in:] Andrews, P. & Banham, P. (eds.). Late Cenozoic Environments and Hominid Evolution: a tribute to Bill Bishop, pp. 15-26, (Geological Society), London.

MacLatchy, L., Wunderlich, R. & Stern, J., 1998. Distal femora of *Morotopithecus* and *Sivapithecus*. — Journal of Vertebrate Paleontology, **18 (3)**:60A, Norman.

McCrossin, M., 1992. New species of bushbaby from the middle Miocene of Maboko Island, Kenya. — American Journal of Physical Anthropology, **89**:215–233.

Mein, P. & Pickford, M., 2003. Rodentia (other than Pedetidae) from the Orange River deposits, Namibia. — Memoirs of the Geological Survey of Namibia, **19**:147–160.

Meyer, G., 1978. Hyracoidea. — [in:] Maglio, V.J. & Cooke, H.B.S. (eds.). Evolution of African Mammals, pp. 284-314, (Harvard Univ. Press) Cambridge.

Phillips, E.M. & Walker, A., 2000. A new species of fossil lorisid from the Miocene of East Africa. — Primates, **41 (4)**:367–372.

Pickford, M., 1981. Preliminary Miocene mammalian biostratigraphy for Western Kenya. — Journal of Human Evolution, **10**:73–97, London.

Pickford, M., 1986. Dating the primate fossil record. — [in:] Else, J. & Lee, P. (eds.). Primate Evolution, pp. 1-2, (Cambridge Univ. Press) Cambridge.

Pickford, M., 1986. Geochronology of the Miocene higher primate faunas of East Africa. — [in:] Else, J. & Lee, P. (eds.). Primate Evolution, pp. 19-45, (Cambridge Univ. Press) Cambridge.

Pickford, M., 1986. Geochronology of the Hominoidea: A summary. — [in:] Else, J. & Lee, P. (eds.). Primate Evolution, pp. 123-128, (Cambridge Univ. Press) Cambridge.

Pickford, M., 1995. Fossil land snails of East Africa and their palaeoecological significance. — Journal of African Earth Sciences, **20 (3-4)**:167–226.

Pickford, M., 1998. A new genus of Tayassuidae (Mammalia) from the middle Miocene of Uganda and Kenya. — Annales de Paléontologie, **84**:275–285.

Pickford, M., 2002. Ruminants from the Early Miocene of Napak, Uganda. — Annales de Paléontologie, **88**:85–113.

Pickford, M., 2002. New reconstruction of the Moroto hominoid palate and a reassessment of its affinities to *Afropithecus turkanensis*. — Human Evolution, **17**:1–19.

Pickford, M., 2003. New Proboscidea from the Miocene strata in the lower Orange River Valley, Namibia. — Memoirs of the Geological Survey of Namibia, **19**:207–256.

Pickford, M., 2003. Early and Middle Miocene Anthracotheriidae (Mammalia, Artiodactyla) from the Sperrgebiet, Namibia. — Memoirs of the Geological Survey of Namibia, **19**:283–290.

Pickford, M., Senut, B. & Gommery, D., 1999. Sexual dimorphism in *Morotopithecus bishopi*, an early Middle Miocene hominoid from Uganda and a reassessment of its geological and biological contexts. — [in:] Andrews, P. & Banham, P. (eds.). Late Cenozoic Environments and Hominid Evolution: a Tribute to Bill Bishop. pp. 27-38, (Geological Society) London.

Pickford, M., Senut, B., Gommery, D. & Musiime, E., 2003. New Catarrhine fossils from Moroto II, Early Middle Miocene (ca 17.5 Ma) Uganda. — Comptes Rendus Palévol, **2**:649–662.

Pickford, M., Senut, B., Hadoto, D., Musisi, J. & Kariira, C., 1986. Découvertes récentes dans les sites miocènes de Moroto (Ouganda Oriental) aspects biostratigraphiques et paléoécologiques. — Comptes Rendus de l'Académie des Sciences de Paris, **302**:681–686, Paris.

Pickford, M. & Tassy, P., 1980. A new species of *Zygolophodon* (Mammalia, Proboscidea) from the Miocene hominoid localities of Meswa Bridge and Moroto (East Africa). — Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **4**:235–251, Stuttgart.

Pilbeam, D.R., 1969. Tertiary Pongidae of East Africa: Evolutionary relationships and taxonomy. — Bulletin of the Peabody Museum of Natural History, **31**:1–185.

Sanders, W.J. & Bodenbender, B.E., 1994. Morphometric analysis of lumbar vertebra UMP 67-28: Implications for spinal function and phylogeny of the Miocene Moroto hominoid. — Journal of Human Evolution, **26**:203–237, London.

Senut, B., Pickford, M., Gommery, D. & Kunimatsu, Y., 2000. A new genus of Early Miocene hominoid from East Africa: *Ugandapithecus major* (Le Gros, Clark & Leakey, 1950). — Comptes Rendus de l'Académie des Sciences de Paris, **331**:227–233, Paris.

Simons, E.L. & Bown, T., 1984. A new species of *Peratherium* (Didelphidae, Polyprotodonta): The first African marsupial. — Journal of Mammalogy, **65**:539–548.

Simpson, G.G., 1967. The Tertiary lorisiform primates of Africa. — Bulletin of the Museum of Comparative Zoology, **136**:39–61.

Stromer, E., 1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. — [in:] Kaiser, E. (ed.). Die Diamantenwuste Südwest-Afrikas, **2**:107-153, (Reimer) Berlin.

Tassy, P. & Pickford, M., 1983. Un nouveau mastodonte zygolophodonte (Proboscidea, Mammalia) dans le

Miocène inférieur d'Afrique orientale: systématique et paléoenvironnement. — Geobios, **16**:53–77, Villeurbanne.

Tricker, B., Taylor, W. & Bishop, W.W., 1963. Fossils from Karamoja. Brathay Exploration Group II. — Uganda Journal, **27**:109–114.

Varne, R., 1966. The petrology of Moroto Mountain, Eastern Uganda. — Proceedings of the Geological Society, **1629**:23.

Varne, R., 1967. The growth of the Moroto volcano, Eastern Uganda. — Bulletin of Volcanology, **31**:163–174.

Walker, A., 1987. Fossil Galaginae from Laetoli. — [in:] Leakey, M.D. & Harris, J. (eds.). Laetoli: A Pliocene Site in Northern Tanzania, pp. 85-90, (Oxford University Press) Oxford.

Walker, A. & Rose, M., 1968. Fossil hominoid vertebra from the Miocene of Uganda. — Nature, **217**:980–981, London.

Whitworth, T., 1954. The Miocene hyracoids of East Africa. — Fossil Mammals of Africa, **7**:1–58.

Young N. & MacLatchy, L., 2000. Is *Morotopithecus* a Great Ape?. — American Journal of Physical Anthropology, **30**:329–330.

Young, N. & MacLatchy, L., 2004. The phylogenetic position of *Morotopithecus*. — Journal of Human Evolution, **46**: 163–184, London.