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## ABSTRACT

Moroto I and Moroto II, Uganda, are Middle Miocene sites that have yielded fossil mammalian remains, notably of primates, proboscideans, small and large anthracotheres, hyracoids and rodents. New discoveries of hominoid teeth at both localities indicate that the diversity of this superfamily was greater than previously understood. Taxa currently recognised from the sites are *Ugandapithecus gitongai*, *Afropithecus turkanensis*, *Nacholapithecus kerioi*, *Kalepithecus kogolensis* sp. nov., *Kogolepithecus morotoensis*, *Simiolus enjiessi*, and *Micropithecus leakeyorum*. The Moroto deposits have also yielded a cercopithecid and a galagid, and there can be litttle doubt that, during the Middle Miocene, the region was appreciably more humid and well-wooded to forested than it is today. The primate fauna indicates correlation to East African Faunal Set IIIa (ca 17.0-16.5 Ma).

**Key word**s: *Afropithecus*, *Ugandapithecus*, *Nacholapithecus*, *Kogolepithecus*, *Kalepithecus*, *Simiolus*, *Micropithecus*

## INTRODUCTION

Moroto I and Moroto II are Middle Miocene fossiliferous localities north of Moroto Mountain, northeastern Uganda. This contribution describes fossil hominoid remains collected at Moroto I and II since 2009 and reassesses the taxonomic position of material found between 1958 and 2008. The ensemble of hominoid remains from the two localities reveals that previous authors have tended to underestimate the taxonomic diversity. Two taxa of large apes were recognised by Pickford *et al*. (2009) but there are in fact three taxa in the collection, and only two small ape species were previously reported from the sites, whereas there are at least four taxa there. Admittedly, three of the small apes were poorly represented in the collections made prior to 2009, which made it difficult to infer a diversity greater than two, but informative samples collected in 2014, 2015 and 2017, have removed residual doubts concerning the diversity of small hominoids at Moroto.

## DISCOVERY CONTEXT AND ASSOCIATED FAUNA

The geological context of the Moroto I and Moroto II deposits has already been described in detail (Pickford *et al*., 2003). The sediments at the sites accumulated in valleys incised into PreCambrian gneiss and schist, and at both localities they were buried by basalt lavas that erupted from Moroto Volcano (Bishop, 1958, 1964; Fleuty, 1968; Tricker *et al*., 1963; Musalizi *et al*., 2009).

**Figure 1**. Moroto I exposures in July 2017, showing the discovery locus (white square) of a juvenile maxilla of *Nacholapithcus kerioi* (Mor I, 1'08).

The hominoid fossils from Moroto (Allbrook & Bishop, 1963; Gebo *et al*., 1997; Gommery *et al*., 1998, 2002; Harrison, 2010b; MacLatchy & Pilbeam, 1999; MacLatchy & Rossie, 2005; MacLatchy & Young, 2004; MacLatchy *et al*., 2000; Nakatsukasa, 2008; Patel & Grossman, 2006; Pickford, 2002; Pickford *et al*., 1999, 2003, 2009; Pilbeam, 1969; Sanders & Bodenbender,1994; Young & MacLatchy, 2000, 2004) are accompanied by a diverse mammalian fauna comprising other primates (Pickford *et al*., 2003; Harrison, 2010a), proboscideans (Pickford & Tassy, 1980; Sanders *et al*., 2010; Tassy & Pickford, 1983), Creodonta (Lewis & Morlo, 2010), Carnivora (Werdelin & Peigné, 2010), Anthracotheres (Holroyd *et al*., 2010; Pickford, 1998, 2011; Pickford & Mein, 2006), Hyracoidea (Pickford & Mein, 2006), Rhinocerotidae (Geraads, 2010), Rodents and other micromammals (Pickford & Mein, 2006; Winkler *et al*., 2010), Ruminants (Cote, 2010), Bats (Gunnell, 2010), and Macroscelidea (Holroyd, 2010).

**Figure 2**. Moroto II, Point 1, type locality of *Kalepithecus kogolensis* sp. nov. The teeth were found near the small clumps of grass in front of co-author Sarah Musalizi. Moroto Mountain in the background. Image taken in 2012.


**Figure 3**. The holotype of *Kalepithecus kogolensis* (Mor II, 1'17) weathering out of sandy silt at Moroto II, Point 1. Visible are the p/3, p/4, lower molars and mandible shattered into fragments by repeated swelling and contraction of the sediments following occasional rainfalls.

## THE AGE OF THE MOROTO FOSSILIFEROUS DEPOSITS

There has been a great deal of debate about the age of the Moroto deposits with two opinions commonly reported in the literature :- 1) that the deposits are of Early Miocene age, older than Napak, Uganda (Faunal Set I, ca 19.5-20.5 Ma) and thus correlating to Faunal Set 0 (Gebo *et al*., 1997). Werdelin (2010) positioned the sites at 20-21 Ma. :- 2) that the fauna indicates a Middle Miocene correlation (Pickford, 1981; Pickford & Senut, 1999, who positioned the sites at ca 16.5 Ma). The hominoid remains described herein indicate that the deposits accumulated penecontemporaneously with those at Kalodirr (17.6-16.8 Ma : Werdelin, 2010) the Aka Aiteputh Formation at Nachola (ca 16 Ma, Sawada *et al*., 1998; Pickford & Senut, 1999) and Kipsaraman (ca 14.5 Ma, Pickford & Kunimatsu, 2005). From a faunal and evolutionary perspective an age between 17.5 and 16 Ma is thus most likely for the Moroto sedimentary deposits.

## Abbreviations

KNM - Kenya National Museum, Nairobi, Kenya
NHMUK – Natural History Museum, London, England
OCO - Orrorin Community Organisation, Kipsaraman, Kenya
UM - Uganda Museum, Kampala, Uganda

## SYSTEMATIC DESCRIPTIONS

### Order Primates Linnaeus, 1758

### Suborder Anthropoidea Mivart, 1864

### Infraorder Catarrhini E. Geoffroy, 1812

### Superfamily Hominoidea Gray, 1825

### Genus *Ugandapithecus* Senut, Pickford, Gommery & Kunimatsu, 2000

**Type Species** : *Ugandapithecus major* (Le Gros Clark & Leakey, 1950)

### Species *Ugandapithecus gitongai* Pickford & Kunimatsu, 2005

**Diagnosis** : Species of *Ugandapithecus* plotting within the upper part and beyond the range of metric variation of *Ugandapithecus major* but with higher cusp relief than in this species, cusps more blocky in appearance, lingual cingulum in upper molars extremely broad, having the tendency to form an accessory cusplet at the mesio-lingual corner of the crown and to extend onto the mesial half of the hypocone; protocone more buccally positioned than in *Ugandapithecus major*; buccal cingulum present in upper molars, even if sometimes weak; trigon basin of upper molars deeper and more voluminous than in *Ugandapithecus major*; enamel more coarsely wrinkled and thus fewer wrinkles on occlusal surface than in *Ugandapithecus major* (visible mainly in unworn or slightly worn specimens); distal fovea of upper molars deeper than in *Ugandapithecus major*; M1/ slightly larger than in *Ugandapithecus major*; m/3 with metaconid subdivided into two cusplets, separated from entoconid by an additional small cusplet; accessory cusplet between entoconid and hypoconulid; hypoconulid has tendency to form accessory cusplets lingually and mesially; cingulum on buccal and distal aspects of hypoconulid, mesial fovea reduced in bucco-lingual breadth (modified from Pickford & Kunimatsu, 2005).

**Holotype** : OCO Bar 737’02, left M1/, OCO Bar 210’02, left M2/, representing the same individual on the basis of the form and size of the interstitial contact facets between the two teeth and their close proximity at the time of discovery.

**Type locality** : Kipsaraman Main (GPS WGS 84 datum, 00°44'53.7" N: 35°49'33.6" E).

**Stratigraphy and age** : Muruyur Formation, Middle Miocene, ca. 14.5 Ma, Faunal Set P IIIb.

**Description and comments**
Mor II 2’98, is an unworn left upper molar (probably M2/) of a large ape. As was pointed out by Pickford *et al*. (2009) this tooth resembles those of *Ugandapithecus* in a number of features, including the greater separation of the paracone and metacone than is the case in *Afropithecus*. The mesial fovea is mesio-distally broader than it is in *Afropithecus*, and the buccal edges of the paracone and metacone are more vertically oriented than they are in *Afropithecus*. The tooth recalls *Ugandapithecus gitongai* in its dimensions and the blocky nature of the main cusps (Table 1).

Mor II, 10’08 is a lightly worn left m/3 which is compatible in dimensions and morphology to teeth of *Ugandapithecus gitongai*, in particular by the presence of a secondary cusplet associated with the metaconid, and a small cusplet berween the metaconid and entoconid. The m/3 of *Ugandapithecus gitongai* from Kipsaraman, the type locality, measures 16.1 x 12.7 mm, which is close in length to the Moroto II tooth but is slightly narrower than it. Apart from its greater dimensions, the tooth is broader relative to its length (16.1 x 13.4 mm) than the equivalent teeth of *Afropithecus turkanensis* (KNM WK 16840 : 13.7 x 10.6 mm; KNM WK 24300 : left m/3, 15.7 x 11.3 mm, right m/3, 15.5 x 11.1 mm) (Rossie & MacLatchy, 2013). For comparison, the minimum mesurements of m/3 in the Moroto II mandible are 15.1 x 13.0 mm (crown heavily abraded) which link the mandible with *Ugandapithecus* rather than *Afropithecus*.


**Figure 4**. *Ugandapithecus gitongai* from Moroto II, Uganda. A) Mor II 2’98, left M2/ (stereo triplet occlusal view), B) Mor II 10’08, lightly worn left m/3, B1) stereo triplet occlusal view, B2) lingual view of cast, B3) mesial view of cast (scale 10 mm).

**Table 1**. Measurements (in mm) of teeth of *Ugandapithecus gitongai* from Moroto II, Uganda (e = estimated measurement.

| Catalogue | Tooth | Mesio-distal length | Bucco-lingual breadth |
|---|---|---|---|
| Mor II 2'98 | M2/ left | 14.2 | 14.5 |
| Mor II, UMP 62.10 | c/1 left | 18.7 | 13.0e |
| Mor II, UMP 62.10 | m/1 left roots | 10.1e | 9.8e |
| Mor II, UMP 62.10 | m/2 left | 12.7e | 12.9e |
| Mor II, UMP 62.10 | m/3 left | 15.1e | 13.0e |
| Mor II 10'08 | m/3 left | 16.1 | 13.4 |

The large ape mandible from Moroto II (UMP 62.10) has traditionally been linked with the Moroto snout (Pilbeam, 1969). However, as explained above, it is more likely to represent *Ugandapithecus gitongai* than *Afropithecus turkanensis*, which has relatively slender mandibles and smaller teeth. The dimensions of the canine in the mandible indicate that it was probably a male individual. The molars in this mandible are broader relative to length than in *Afropithecus* from Kalodirr (Rossie & MacLatchy, 2013).

**Figure 5**. *Ugandapithecus gitongai* from Moroto II, Uganda. Mor II, UMP 62.10, parts of left and right mandibles with damaged crowns of left m/2 and m/3 and roots of left canine, p/3-m/1 and right p/4-m/3 (stereo triplet occlusal view of cast of reconstructed mandible) (scale : 10 cm).

## Genus *Afropithecus* Leakey & Leakey, 1986

**Type species** : *Afropithecus turkanensis* Leakey & Leakey, 1986

## Species *Afropithecus turkanensis* Leakey & Leakey, 1986

**Diagnosis** : Skull with the following characteristics: long, broad and domed muzzle; palate shallow, long and narrow, with toothrows parallel sided or converging slightly posteriorly; incisive foramen comprising large paired openings; large diastema between C1/ and I2/; premaxilla narrow but anteriorly protruding, with contact superiorly with the nasals steeply inclined frontal; strong postorbital constriction; temporal lines strongly marked and converge in the midline far anteriorly to form a frontal trigon; frontal sinus present in the glabellar region; supraorbital costae slender; supraorbital notch at the medial angle of the orbital margin; broad interorbital region; nasals long and narrow, with midline keeling and concave contour in lateral view; pyriform aperture only slightly higher than broad, and oval in shape; subnasal clivus relatively short; canine jugum prominent, with shallow canine fossa; distinct maxillary fossa just below and anterior to the orbit; double infraorbital foramina; anterior root of the zygomatic arch deep, superiorly sloping, and attaches relatively low on the face; maxillary sinus extensive; orbit broader than high, and asymmetrical in shape; orbital process of frontal narrow; lacrimal fossa extends onto the face just anterior to the margin of the orbit; mandible with very deep corpus, distinct mandibular fossa, single mental foramen, ramus set at an oblique angle to the corpus, symphysis with strong inferior transverse torus and lacking superior transverse torus, and steeply sloping subincisive planum (Allbrook & Bishop, 1963; Pilbeam, 1969; Andrews, 1978; Leakey & Leakey, 1986; Leakey *et al*., 1988; Leakey & Walker, 1997; Pickford,

2002). Upper incisors strongly procumbent, and angled obliquely toward the midline; I1/ relatively broad, and much larger than I2/; lower incisors broad, especially i/2; upper canine in males broad and tusk-like, with an almost circular basal cross section, a deep mesial groove and a bladelike tip as in *Ugandapithecus major*, lower canine stout, bilaterally compressed and relatively low crowned; strong sexual dimorphism in canine size; P3/ larger than P4/; upper premolars broad, with only moderate difference in height between paraconid and protoconid, and lacking a lingual cingulum; upper premolars relatively large in relation to M1/; p/3 relatively large, narrow and sectorial; p/4 generally broader than long; upper premolars and molars have marked bucco-lingual flare; upper molars relatively narrow, with bunodont cusps, wrinkled enamel, small mesial fovea, moderate to weak development of lingual cingulum, and large hypocone (subequal in size to protocone); M1/ < M2/ ≤ M3/; lower molars relatively broad; m/1 < m/2 < m/3; enamel of cheek teeth thick with heavy wrinkling (Leakey & Leakey, 1986; Leakey *et al*., 1988; Leakey & Walker, 1997; Smith *et al*., 2003) (modified from Harrison, 2010b).

**Holotype** : KNM WK 16999, snout with complete dentition.

**Type locality** : Kalodirr, Kenya (3°20'N, 35°40'E)

**Age** : Middle Miocene, Faunal Set IIIa (<17.5 - >16.8 Ma).

**Description and comments**

UMP 62-11 is a fossilised snout of a large ape containing all the teeth save the right I1/ and parts of the upper canines and left P3/. The specimen was described in detail by Pickford (2002) so it is not necessary to redescribe it. However, an illustration is provided in order to complete the coverage of the hominoids from Moroto. In the old collections there is an upper left canine (UMP 62-12) which likely represents a male individual of the species.

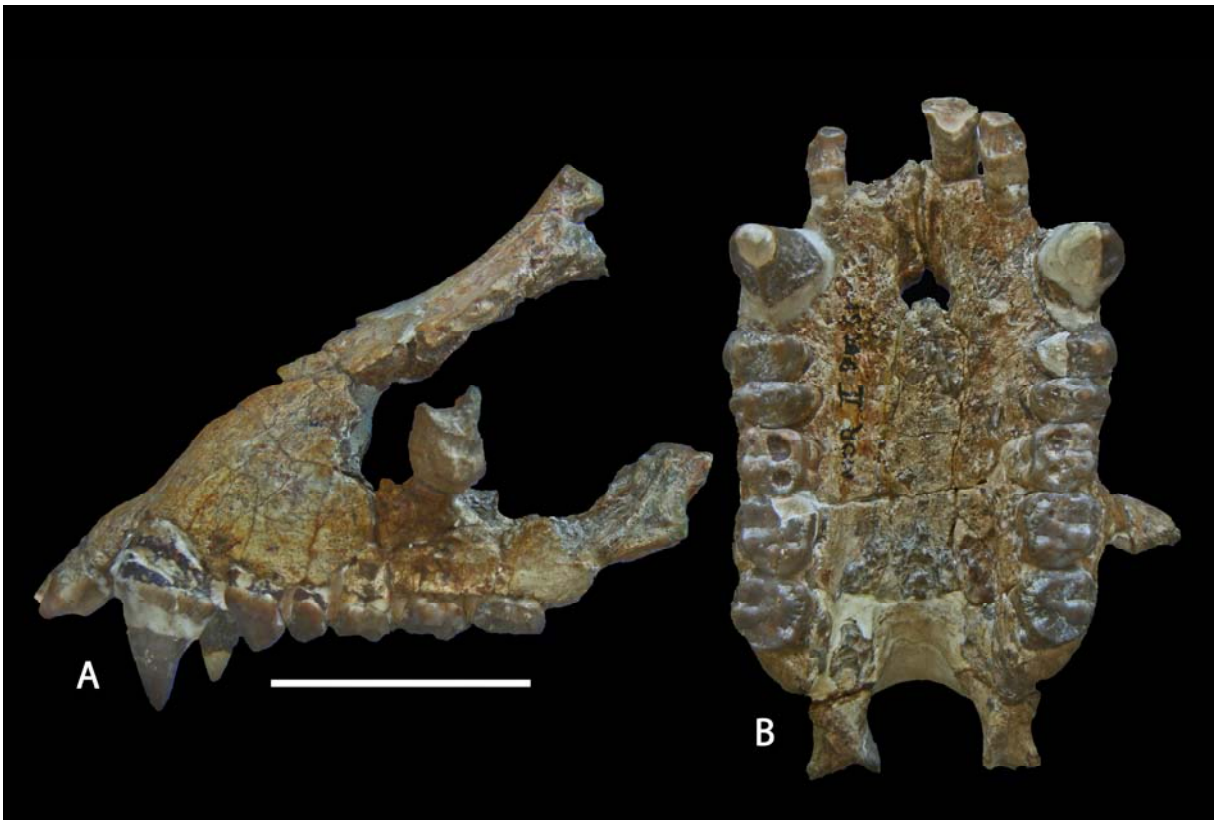


**Figure 6**. *Afropithecus turkanensis* from Moroto II, Uganda. Mor II UMP 62-11, the Moroto snout, A) left lateral and B) occlusal views (scale : 5cm).

The lower jaw long associated with the snout (Pilbeam, 1969) is in poor condition and yields little information save that concerning the general dimensions of the mandible which indicate not only that it does not represent the same individual as the snout (the teeth are deeply worn) but also that it does not belong to the same genus (anterior part of mandible is slender in *Afropithecus*, robust in *Ugandapithecus*).

There are several other specimens from Moroto which are attributed to *Afropithecus turkanensis*. They are Mor II 11'08, an upper right central incisor, Mor II 10'07, the distal half of an upper right central incisor. One of these teeth was tentatively attributed to *Ugandapithecus gitongai* by Pickford *et al*. (2009) but further comparisons indicate that the lightly worn upper central incisor, which has lost part of the lingual tubercle, accords well with the upper central incisor in the holotype of *Afropithecus turkanensis* from Kalodirr, Kenya (Leakey & Leakey, 1986).

A left lower canine lacking much of the crown (Mor II, 1'14) is attributed to *Afropithecus turkanensis* on the basis of its dimensions. The root is tall and curves distally at its apex. The base of the crown is quite compressed labio-lingually.

A lower molar, Mor II 1'08, is lightly worn and corresponds well with the m/2 of *Afropithecus turkanensis*, in particular the relative narrowness of the crown compared to its length (Rossie & MacLatchy, 2013) (Table 2).

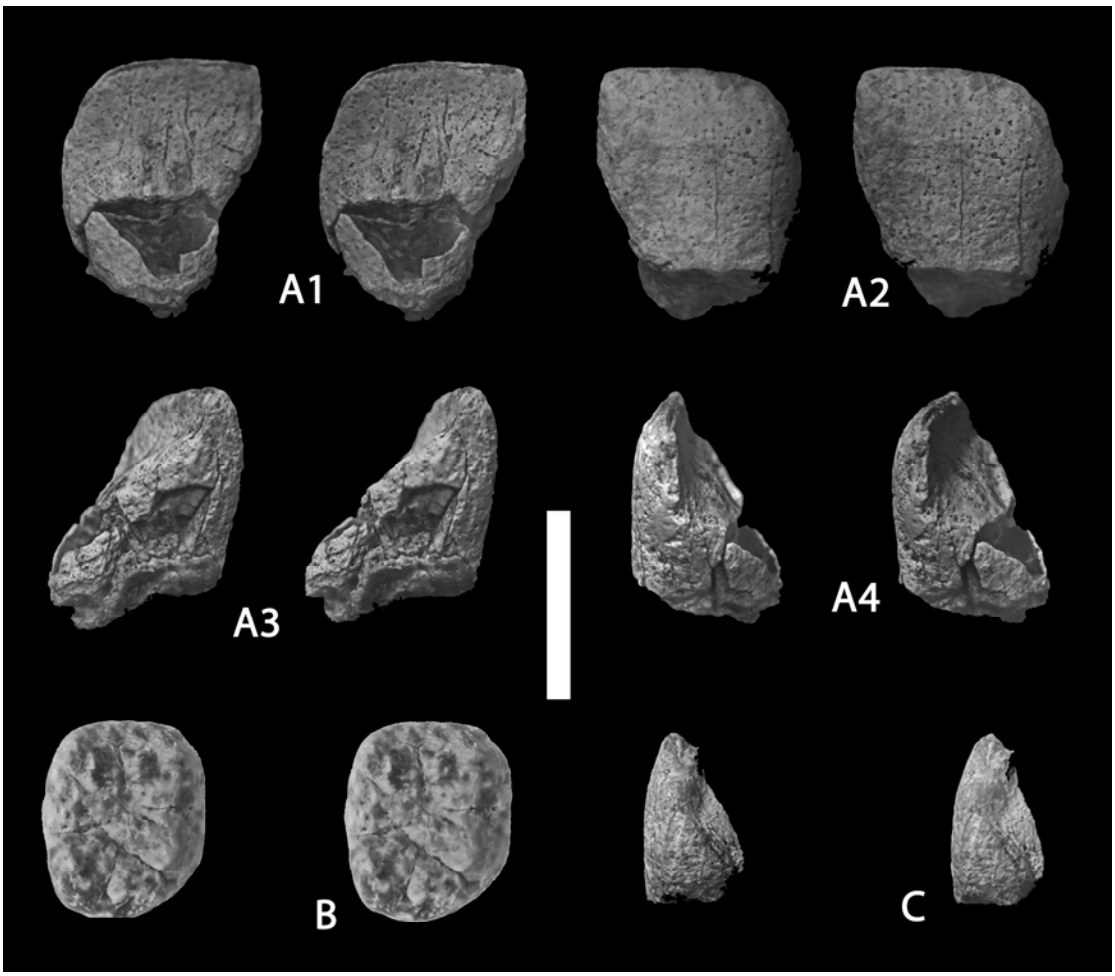


**Figure 7**. *Afropithecus turkanensis* from Moroto, Uganda. A) Mor II 11'08, right I1/, stereo views, A1) lingual, A2) labial, A3) distal and A4) mesial; B) Mor II 1'08, right m/2, stereo occlusal view, C) Mor II 10'07, right I1/ distal half, stereo distal view (scale : 10 mm).

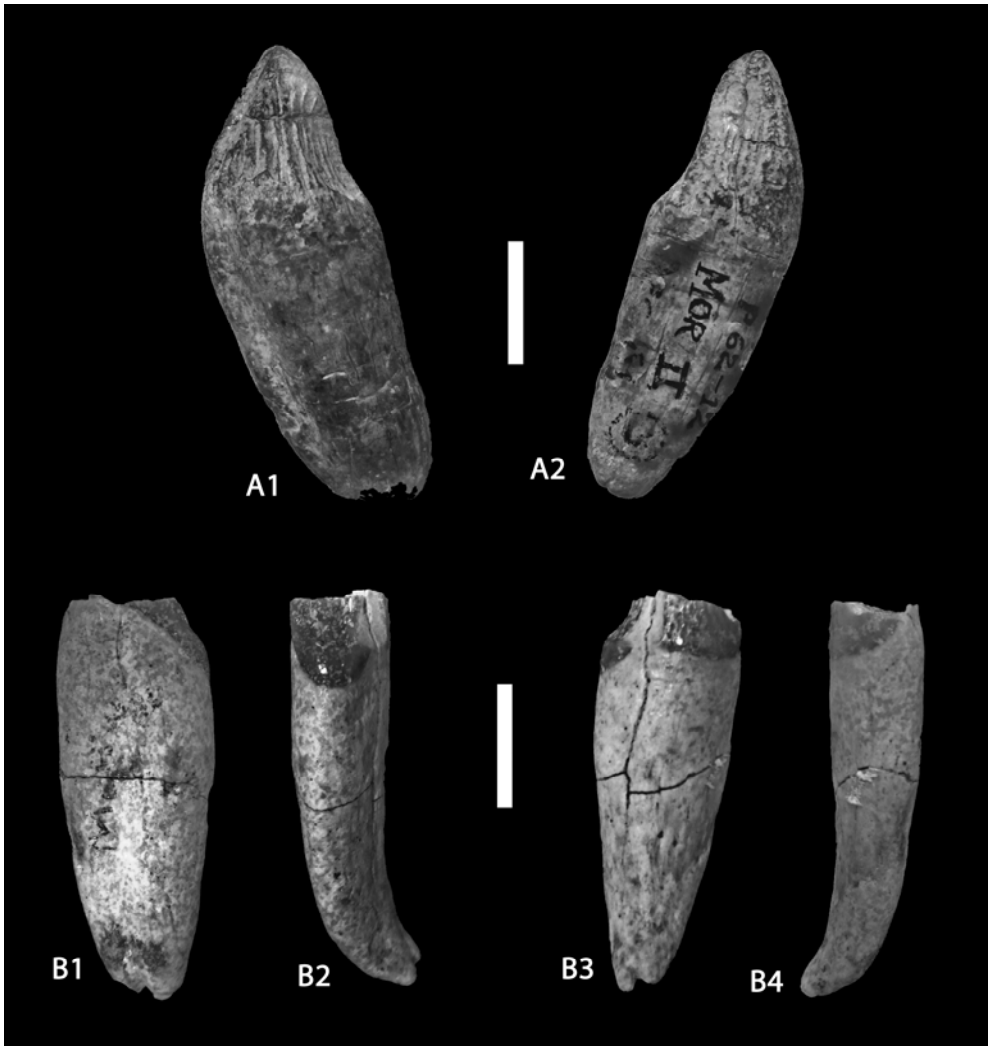


**Figure 8**. Canines from Moroto II attributed to *Afropithecus turkanensis*. A) UMP 62-12, left upper canine probably male, A1) mesial and A2) distal views, B) Mor II Mor II, 1'14, left lower canine, possibly female, lacking much of the crown, B1) mesial, B2) lingual, B3) distal and B4) labial views (scale : 10 mm).

**Table 2**. Measurements (in mm) of teeth of *Afropithecus turkanensis* from Moroto II, Uganda.

| Catalogue | Tooth | Mesio-distal length | Bucco-lingual breadth |
|---|---|---|---|
| Mor II 1'14 | c/1 right | 7.4 | 11.7 |
| Mor II 1'08 | m/2 right | 10.8 | 9.2 |
| Mor II 10'07 | I1/ distal half | -- | 6.1 |
| Mor II 11'08 | I1/ right | 10.0 | 8.3 |
| Mor II UMP 62'11 | I1/ left | 10.4 | 8.8 |
| Mor II UMP 62'11 | I2/ left | 7.8 | 10.0 |
| Mor II UMP 62'11 | I2/ right | 8.0 | 10,5 |
| Mor II UMP 62'12 | C1/ left male | 16.1 | 11.6 |
| Mor II UMP 62'11 | C1/ left | 19.4 | 15.3 |
| Mor II UMP 62'11 | P3/ left | 10.0 | 14.8 |
| Mor II UMP 62'11 | P3/ right | 9.3 | 14.3 |
| Mor II UMP 62'11 | P4/ left | 7.6 | 14.6 |
| Mor II UMP 62'11 | P4/ right | 7.2 | 14.2 |
| Mor II UMP 62'11 | M1/ left | 11.9 | 12.4 |
| Mor II UMP 62'11 | M1/ right | 11.4 | 12.5 |
| Mor II UMP 62'11 | M2/ left | 12.5 | 13.5 |
| Mor II UMP 62'11 | M2/ right | 13.1 | 13.6 |
| Mor II UMP 62'11 | M3/ left | 12.3 | 14.4 |
| Mor II UMP 62'11 | M3/ right | 12.7 | 14.1 |

## Genus *Nacholapithecus* Ishida, Kunimatsu, Nakatsukasa & Nakano, 1999

**Type species** : *Nacholapithecus kerioi* Ishida, Kunimatsu, Nakatsukasa & Nakano, 1999

**Diagnosis** : Key features of the skull are as follows: Face relatively short. Nasal aperture tall and narrow, widest above mid-height, and tapering inferiorly. Subnasal clivus moderately low. Premaxilla overlaps slightly with the palatine process of maxilla to produce a "stepped" nasal floor and restricted incisive fossa (Ishida *et al*., 2004; Kunimatsu *et al*., 2004). Premaxilla slightly protruding, with procumbent upper incisors. Prominent canine jugum bordered posteriorly by a deep canine fossa in males; less well developed in females. Relatively large diastema between I2/ and C1/ in male individuals; small in females. Anterior root of zygomatic arch situated low on the face above M1/-M2/ and laterally projecting. Maxillary sinus not as extensive as in *Proconsul*, terminating anteriorly at M1/, and its floor is level with or slightly lower than the apices of the molar roots. Palate relatively shallow. Mandibular corpus moderately deep, with shallow postcanine fossa on the lateral side. Symphysis steeply inclined, with moderately well-developed inferior transverse torus (Ishida *et al*., 2004; Kunimatsu *et al*., 2004). I1/ is narrow, buccolingually stout, with a broad lingual pillar. I2/ narrower, with mesiodistal diameter about 75% that of I1/. Upper canines in males robust but relatively low crowned. Upper premolars moderately large, and quite broad. P3/ with paracone much more elevated than protocone and connected by a pair of transverse crests. P4/ ovoid, with paracone and protocone subequal in height. Upper molars rectangular, broader than long, with slightly longer lingual moiety than buccal moiety. Cusps low and voluminous. Large hypocone. Lingual cingulum weakly developed or absent. Upper molars increase in size from M1/ to M3/. M3/ tapers distally, with reduced distal cusps. Lower incisors tall and mesiodistally narrow. Lower canines in males robust, relatively low crowned, with strong bilateral compression. Lower molars rectangular, with moderately low and rounded cusps. Entoconid relatively small. Well-developed transverse crests demarcate the mesial and distal foveae. Buccal cingulum poorly developed. m/3 triangular in outline, with reduced entoconid, and large hypoconulid aligned with protoconid and hypoconid. m/3 is much larger than m/2 (Ishida *et al*., 1999, 2004; Kunimatsu *et al*., 2004) (modified from Harrison, 2010b).

## Species *Nacholapithecus kerioi* Ishida, Kunimatsu, Nakatsukasa & Nakano, 1999

**Diagnosis** : as for the genus.

**Holotype** : KNM BG 35250, much of a skeleton comprising parts of the face and mandibles and many post-cranial elements.

**Type locality** : Locality BG-K, Aka Aiteputh Formation, Nachola, Kenya

**Stratigraphy and age** : Middle Miocene, ca 16-15 Ma (Ishida *et al*., 2004)

**Description and comments**

There are several large ape specimens from Moroto I and Moroto II which are slightly smaller than *Afropithecus turkanensis*, and which differ significantly from this genus in osteological and dental features (Table 3). Three of the specimens were previously included in *Afropithecus* (Pickford *et al*., 2009) but are now recognised as belonging to *Nacholapithecus kerioi*.

Mor I, 1'08 is a right maxilla containing fully erupted D3/and D4/, and the canine and M1/ in crypto. The base of the zygomatic arch is in an anterior position above the D4/-M1/, and its base is close to the alveolar margin. The small portion of the palate preserved reveals that it was shallow. In *Afropithecus* the zygomatic arch is in a posterior position above the M2/, and its base is high above the alveolar margin. In the juvenile maxilla from Moroto, there is a deep canine fossa above the D3/ and the space between the canine jugum and the anterior root of the D4/ is short, unlike the shallow, but mesio-distally extensive canine fossa that occurs in *Afropithecus* and *Ugandapithecus*. In *Afropithecus*, the palate is somewhat deeper than in the juvenile maxilla, but with growth, the depth of the palate might change so we do not put alot of weight on this character.

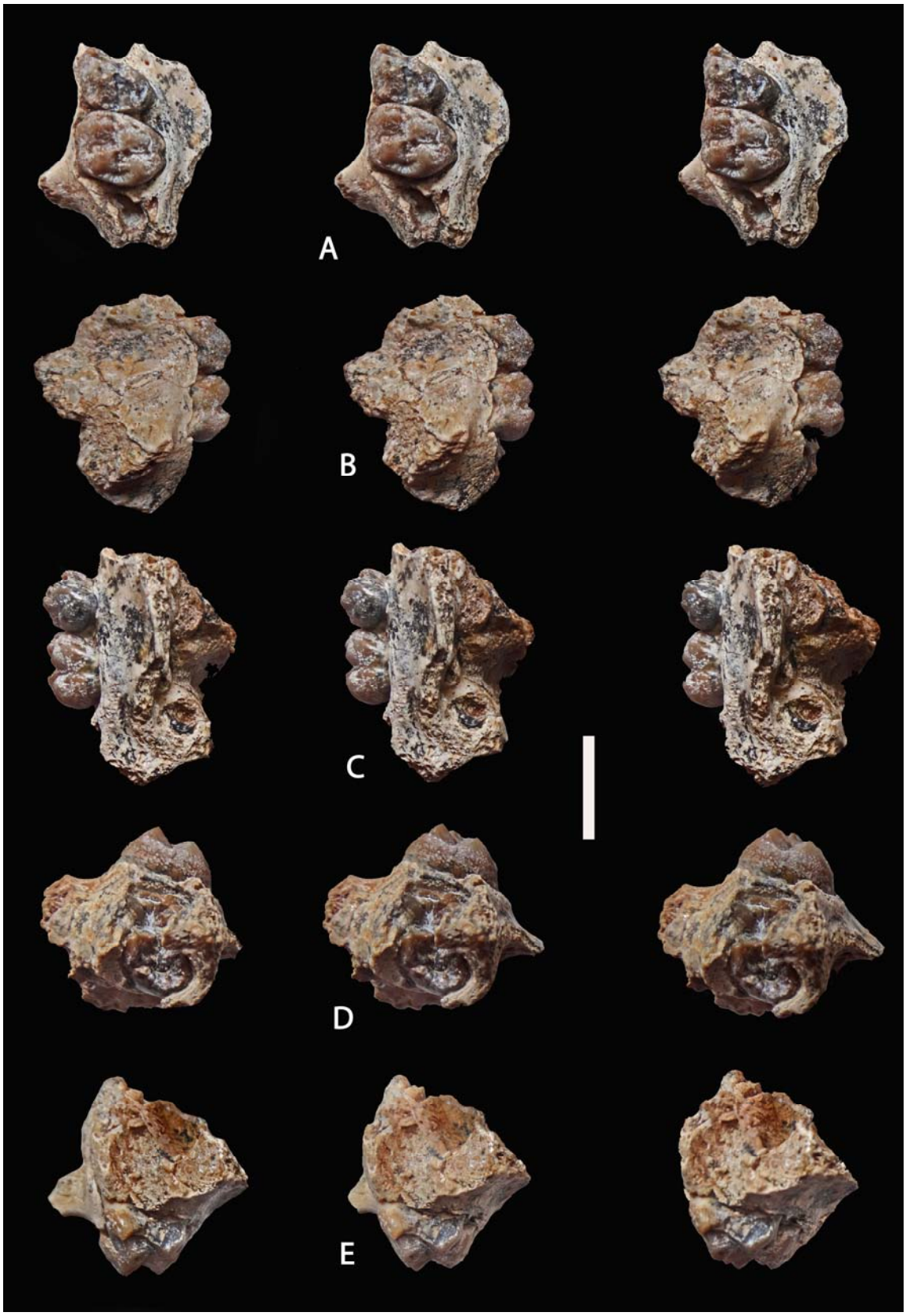


**Figure 9**. Mor I, 1’08, right maxilla of *Nacholapithecus kerioi* containing D3/ and D4/ in occlusion and C1/ and M1/ in crypt, stereo triplet views, A) occlusal, B) lateral, C) lingual, D) posterior and E) anterior (scale : 10 mm).

The only genus of Miocene African ape that has such a low zygomatic arch in such an anterior position, preceded by a deep but mesio-distally restricted canine fossa, is *Nacholapithecus kerioi*. In *Equatorius africanus* the base of the zygomatic arch is further from the alveolar margin than it is in *Nacholapithecus*, even though it is in an anterior position, and it also shows a canine fossa (Le Gros Clark & Leakey, 1951) as does the genus *Kenyapithecus* from Fort Ternan (Leakey, 1962).

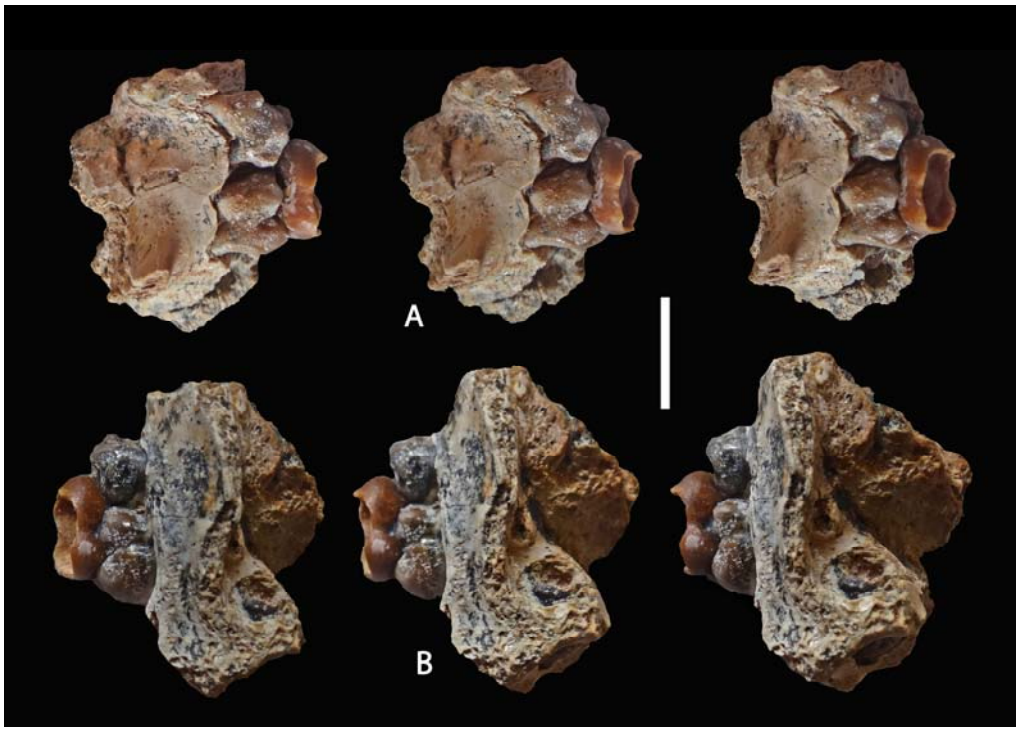


**Figure 10**. *Nacholapithecus kerioi*, right d/4 (Mor I, 22'11) occluded with the D3/-D4/ in the juvenile maxilla (Mor II, 1'08), stereo views A) buccal view, B) lingual (scale : 10 mm).


**Figure 11**. Lower incisors from Moroto I and Moroto II attributed to *Nacholapithecus kerioi*. A) Mor II, 1'07, right i/1, stereo views, A1) lingual, A2) labial, A3) mesial and A4) distal views; B) Mor I, 60'06, right i/2, B1) mesial and B2) lingual views (scale : 10 mm).

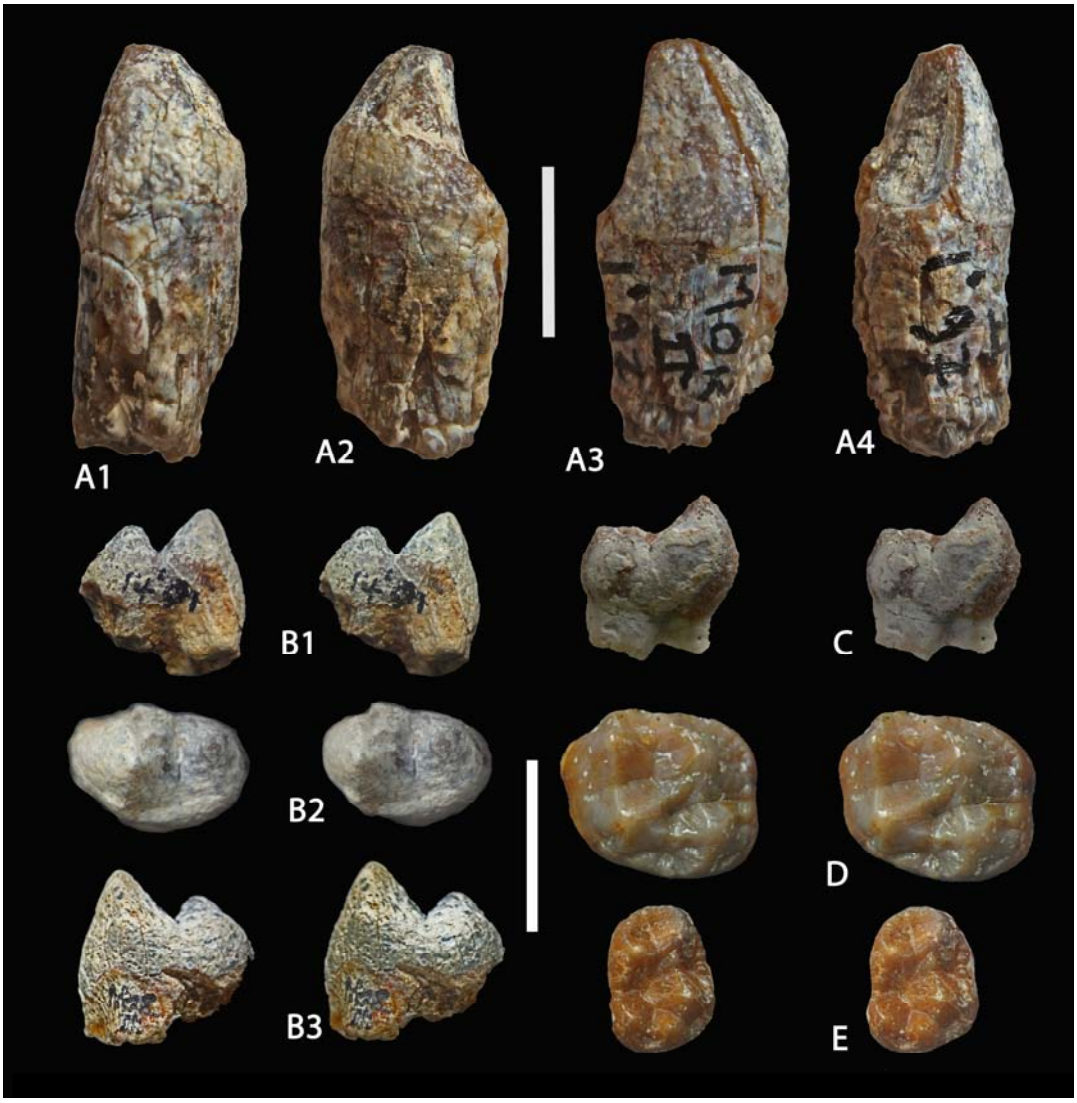


**Figure 12**. Isolated teeth from Moroto I and Moroto II attributed to *Nachalapithecus kerioi*. A) Mor II, 1'97 left upper canine, probably female, A1) labial, A2) mesial, A3) distal and A4) labial views; B) Mor II, 14'01, right P3/, stereo views B1) mesial, B2) occlusal and B3) distal; C) Mor I, 40'06, right p/4 buccal half, stereo view; D) Mor II, 2'07, right M1/ stereo occlusal view; E) Mor I, 22'11 right d/4, stereo occlusal view (scales : 10 mm).

An upper canine, Mor II, 1'97, was previously interpreted to represent a female of *Ugandapithecus gitongai* (Pickford *et al*., 2009) because it resembles a specimen from Kipsaraman attributed to this species (Pickford & Kunimatsu, 2005). However, comparison with specimens of upper canines of *Nacholapithecus kerioi* from the Aka Aiteputh Formation reveals close similarities between the specimens, not only in morphology, but also in dimensions. The crown is relatively low and of stubby appearance, the mesial groove is narrow, slit-like and not deep, the lingual cingulum is well developed, the distal scoop is broad and shallow and wear is mainly apical. We therefore include this canine in *Nacholapithecus*

The P3/ from Moroto II (14'01) was previously attributed to *Ugandapithecus gitongai* (Pickford *et al*., 2009) despite some morphological differences and its smaller dimensions. However, The specimen closely resembles material of *Nacholapithecus kerioi*, including the low protocone and taller paracone, and the shallowly scoop-shaped depression anteriorly into which the root of the upper canine fits.

The M1/ from Moroto II (2'07) is an unerupted crown lacking the roots. It is slightly polished, but is otherwise in good condition. The paracone and metacone are far apart, not close together as in *Afropithecus*. The lingual cingulum is strong on the protocone but fades out on the edge of the hypocone and the buccal cingular structure is weaker than it is in *Afropithecus*.

Two lower incisors are attributed to *Nacholapithecus kerioi* on the basis of their dimensions. Mor II, 1'07, a right i/1, has a shallowly concave lingual margin and a flat labial surface. The other specimen, Mor I, 60'06, a right i/2, is missing the apex of the crown, but has the right dimensions to belong to this taxon.

The d/4 from Moroto I (22'11) is an unworn germ, lacking roots. It occludes well with the juvenile maxilla (Mor I, 1'08) and on this basis we attribute it to *Nacholapithecus kerioi*. The buccal cingulum is strong and beaded.

The buccal half of a p/4 (Mor I, 40'06) is included in *Nacholapithecus kerioi* on the basis of its morphology and dimensions. The protoconid is appreciably taller than the talonid and the roots are stout.

**Table 3**. Measurements (in mm) of the teeth of *Nacholapithecus kerioi* from Moroto I and Moroto II, Uganda (+ : the tooth would probably have been 1-1.5 mm longer).

| Catalogue N° | Specimen | Mesio-distal length | Bucco-lingual breadth |
|---|---|---|---|
| Mor I 31'04 | i/1 right | -- | 6.9 |
| Mor II 1'07 | i/1 right | 6.5 | 7.0 |
| Mor I 60'06 | i/2 right | 5.2 | 8.4 |
| Mor I 22'11 | d/4 right | 8.5 | 6.6 |
| Mor I 40'06 | p/4 right | 9.1 | -- |
| Mor II 1'97 | C1/ left female | 11.3 | 9.4 |
| Mor II 14'01 | P3/ right | 7.0 | 10.8 |
| Mor I 1'08 | D3/ right | 6.5 | 7.7 |
| Mor I 1'08 | D4/ right | 8.0 | 9.5 |
| Mor I 1'08 | M1/ right | 9.7 | -- |
| Mor II 2'07 | M1/ right | 9.5 | 11.5 |
| Mor IIb 3'98 | M*/ fragment | 11+ | -- |

## Genus *Kogolepithecus* Pickford, Senut, Gommery & Musiime, 2003

**Type species** : *Kogolepithecus morotoensis* Pickford, Senut, Gommery & Musiime, 2003

**Diagnosis** : Small anthropoid with ape-like rather than monkey-like teeth, in which the lower molars tend to possess bifid metaconids and entoconids; with broad shelf-like cingulum enclosing protoconid and hypoconid; transverse crest from metaconid suppressed; voluminous occlusal basin bordered by trenchant cusps; anterior lophid of anterior lower molars narrower than the talonid; lower fourth premolar with well developed buccal cingulum; cheek tooth enamel thin; dentine penetrance high (Pickford *et al*., 2003).

### Species *Kogolepithecus morotoensis* Pickford, Senut, Gommery & Musiime, 2003

**Diagnosis** : as for the genus.

**Type Locality** : Moroto II, Point 1 in Pickford *et al*., 2003 (02°40'20.2''N : 34°42'52.4''E (WGS 84))

**Age** : Middle Miocene, Faunal Set IIIa.

**Description and comments**
Since the initial description of *Kogolepithcus morotoensis*, further screening at the discovery site has yielded additional teeth of the same individual. The teeth that have already been described (Pickford *et al*., 2003) are the left p/4, left m/2 (holotype) and left m/3 and the right m/2. The left p/3, left m/1,

right m/3 and right lower canine, as well as left P4/ and M1/ are described for the first time. Even though these teeth were isolated from each other, they likely represent a single individual as shown by their discovery in close proximity to one another, and the fact that they share the same stage of wear of the teeth (lightly worn to unworn crowns).

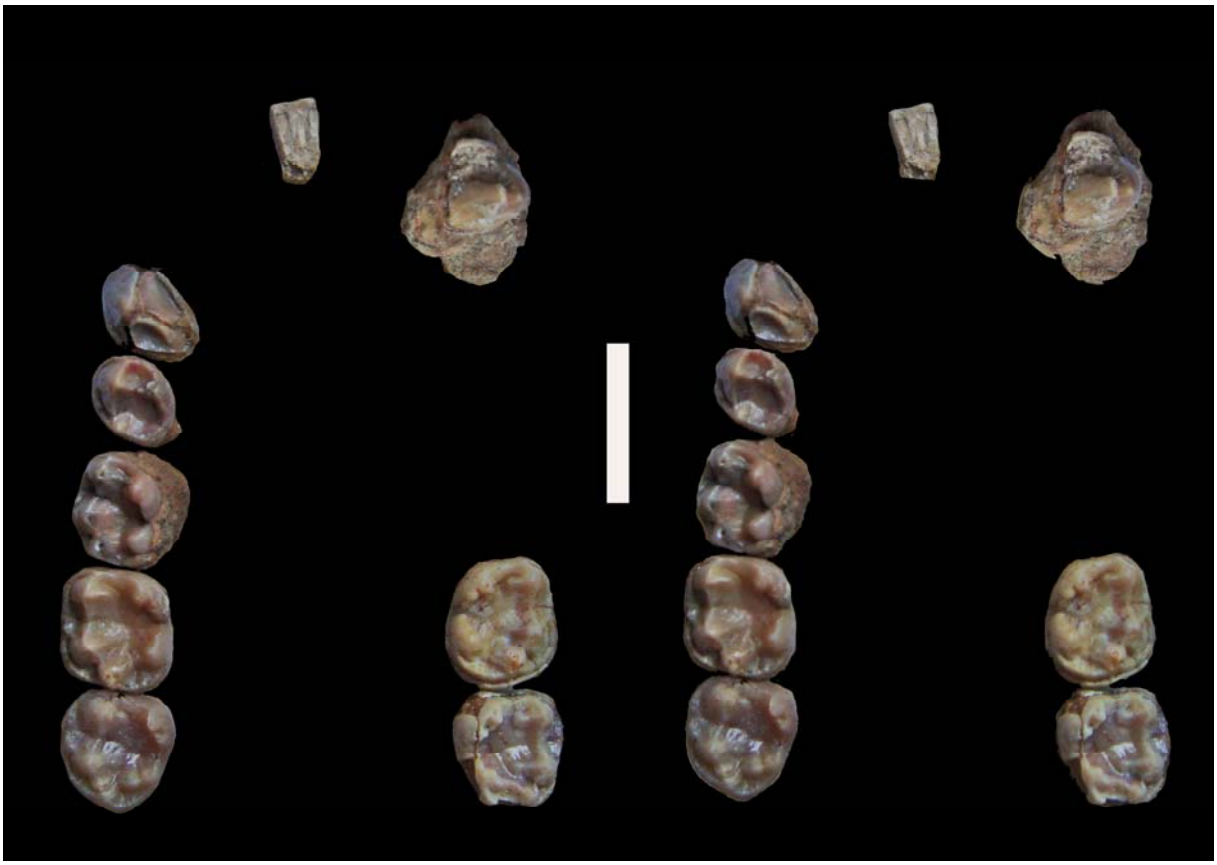

**Figure 13**. *Kogolepithecus morotoensis* holotype individual, stereo occlusal view of the ensemble of lower teeth (scale : 10 mm).

The lower central incisor lacks the root, but enough of the crown is preserved to show that it has a rectangular section, with parallel mesial and distal margins and weak lingual marginal and cenral ridges.

The base of the lower canine is partly obscured in bone, so its dimensions are difficult to access. The crown is bucco-lingually compressed and there are sharp pre- and post-cristids descending from the apex towards the cervix. There is also a cristid on the lingual side of the tooth, but it does not reach the apex of the crown.

The lower third premolar is broader bucco-lingually than its mesio-distal length. The protoconid has a convex buccal surface and sharp pre- and post-cristids, and there is a strong sloping lingual ridge (endoprotocristid) which extends towards the disto-lingual corner of the crown where it fuses with the lingual and distal cingulids. There are shallow mesial and distal fovea.

The m/1 is similar in morphology to the m/2 (Pickford *et al*., 2003) but is smaller.

The P4/ has two main cusps, a tall paracone and a lower protocone, accompanied by a tiny hypocone. The postparacrista ends in a pointed mesostyle and the preparacrista ends at a low parastyle. There are low but sharp mesial and distal cingula walling off the mesial and distal foveae respectively, and there is a weak lingual cingulum at the base of the protocone. The mesial fovea is mesio-distally short and

shallow, whereas the distal one is larger. There are two buccal roots close to each other and a single lingual one.

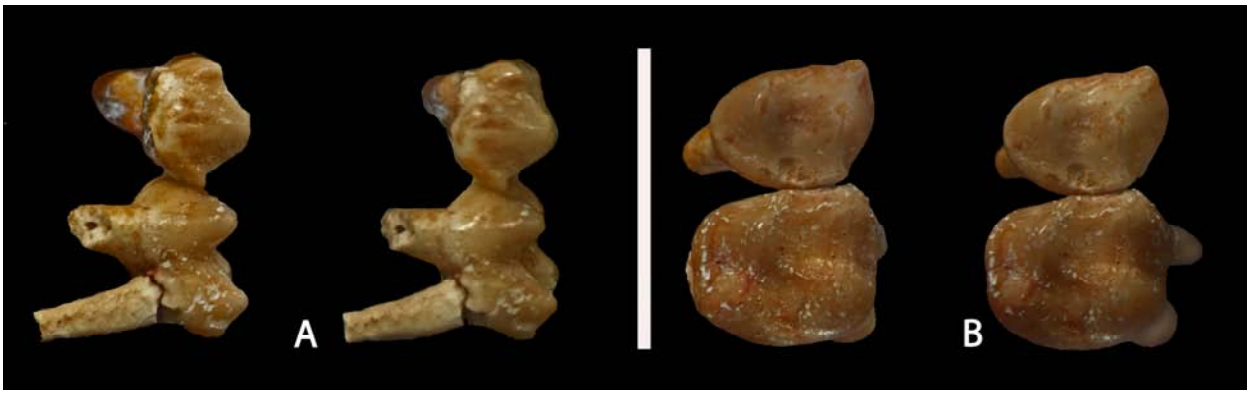


**Figure 14**. Left upper cheek teeth from the *Kogolepithecus* type locality, comprising the complete P4/ and M1/, shown here in A) stereo buccal and B) stereo occlusal views. The P4/ and M1/ occlude well with the holotype lower dental series (scale : 10 mm).

The M1/ has subequal protocone, paracone and metacone, and a slightly smaller hypocone. The two buccal cusps have sharp pre- and post-crista. The parastyle is low but distinct, whereas the mesostyle and metastyle are weak. There is a shallow buccal depression in the enamel between the paracone and metacone, but not really forming a cingulum. The mesial part of the paracone sends a well-formed crista lingually towards the preprotocrista. This structure is in a rather mesial position and thereby reduces the mesio-distal dimension of the mesial fovea. The mesial cingulum is interrupted in its centre by a small style-like cusplet at the end of the preprotocrista, whereupon it continues lingually to blend into a well-developed lingual cingulum which borders the mesial and lingual surfaces of the protocone. The metacone has three crista, the premetacrista running towards the paracone, the postmetacrista descending towards the tiny metastyle and a clear, oblique endometacrista which runs towards the protocone where it blends into the endoprotocrista, thereby forming the low distal wall of the trigon basin. The hypocone is more lingually positioned than the protocone, and it has no cingulum on its lingual side. It has a subtle posthypocrista which runs buccally to join the distal cingulum, walling off the distal fovea. There are three roots, two well-separated buccal ones, and a single lingual one.

The P4/ and M1/, which occlude well with the holotype mandibular dentition, were found in close proximity to it, and are of the same stage of wear. It is probable that these two upper cheek teeth comprise parts of the same individual as the holotype. Measurements are provided in Table 4.

**Table 4**. Measurements (in mm) of teeth of *Kogolepithecus morotoensis* from Moroto II, Uganda (e – estimated measurement).

| Catalogue | Tooth | Mesio-distal length | Bucco-lingual breadth |
|---|---|---|---|
| Mor II 63’04 | i/1 left | 3.2 | 2.6 |
| Mor II 21’04 | c/1 right | 6.4e | 5.3e |
| Mor II 3’04 | p/3 left | 4.9 | 6.7 |
| Mor II 1’05 | p/3 right fragment | 5.1 | -- |
| Mor II 27’03 | p/4 left | 5.5 | 5.4 |
| Mor II 1’04 | m/1 left | 7.0 | 6.4 |
| Mor II 28’03 | m/2 left | 7.7 | 7.1 |
| Mor II 29’03 | m/2 right | 8.1 | 7.1 |
| Mor II 10’03 | m/3 left | 7.5 | 6.9 |
| Mor II 2’04 | m/3 right | 7.0e | 7.2 |
| Mor II 33’06 | P4/ right buccal cusp | 4.2 | -- |
| Mor II 15’06 | P4/ left | 3.9 | 5.1 |
| Mor II 2’05 | M1/ left | 5.0 | 6.1 |

## Genus *Simiolus* Leakey & Leakey, 1987

**Type species** : *Simiolus enjiessi* Leakey & Leakey, 1987

**Diagnosis** : A small-bodied ape that differs from *Micropithecus*, *Limnopithecus* and *Dendropithecus* in the following features : the P3/ is almost triangular in occlusal outline, the P4/ has little lingual or buccal basal flare of the cusps, the upper molars, including M3/, have a large talon basin clearly defined distally by a distinct crest linking the hypocone and metacone, the M3/ is unreduced and the M2/ and M3/ are relatively elongated mesio-distally. It further differs from *Limnopithecus* and *Micropithecus* in the bucco-lingually compressed canines and the larger degree of extension of enamel onto the buccal root of P3/ and the more mesio-distally elongated m/2. It differs from *Micropithecus* in having lower molars with relatively high sharp cusps, and the mandibular superior and inferior transverse tori approximately equally developed. It differs from *Limnopithecus* in the female upper canines which lack a lingual pillar, the P3/ with only slight development of a buccal cingulum, the p/3 being high crowned and sectorial, the lower molars which have poorly developed buccal cingulum, and the mandible having an inferior transverse torus. It differs from *Dendropithecus* in having a relatively gracile mandibular body and symphysis.

Among the larger hominoids it differs from *Proconsul* and *Turkanapithecus* in having bucco-lingually compressed canines, a relatively shorter snout and both superior and inferior mandibular tori. It further differs from *Turkanapithecus* in having a P3/ that is less expanded bucco-lingually and upper molars that lack an additional cuspule between the mesial and lingual cingula. It differs from *Rangwapithecus* in having upper premolars that are relatively narrow mesio-distally and that lack a wide shelf-like distal cingulum, an M1/ that is relatively wider bucco-lingually than either M2/ or M3/ and lower molars that both lack a well developed buccal cingulum and a large buccal fovea indented between the mesial (protoconid) and distal (hypoconid) buccal cusps (from Leakey & Leakey, 1987).

**Other species in the genus** :
*Simiolus cheptumoae* Pickford & Kunimatsu, 2005
*Simiolus andrewsi* Harrison, 2010b

### Species *Simiolus enjiessi* Leakey & Leakey, 1987

**Diagnosis** : A species of *Simiolus* similar in dimensions to *Simiolus andrewsi* from which it differs in the following features: i/2 relatively lower crowned and slightly narrower, with a less distinctly angular distal margin, and a less well-developed lingual pillar; lower canine (comparing those of presumed females) is slightly less tall and less slender; p/3 more elongated and more bilaterally compressed, with a longer honing face; p/4 slightly narrower, with less widely spaced cusps, less oblique transverse crest linking the main cusps, and better developed buccal cingulum; m/2 relatively broader (average breadth-length index is 79.4 in *Simiolus enjiessi* and 75.7 in *Simiolus andrewsi*) with a lesser size differential between m/1 and m/2; m/2 with slightly shorter mesial fovea, less transversely aligned protocristid, narrower distal fovea, somewhat less well-developed buccal cingulum, and hypoconulid less buccally displaced; m/3 larger than m2, with a less transversely oriented protocristid, a less well-developed buccal cingulum, a relatively smaller entoconid, and a larger distal fovea; M3/ mesio-distally longer, relatively greater in size, with less markedly reduced distal cusps (average breadth-length indices for m/1 and m/3 are 73.1 and 74.6 in *Simiolus cheptumoae* and 81.4 and 77.8 in *Simiolus andrewsi*) (modified from Harrison, 1992, 2002).

*Simiolus enjiessi* is larger than *Simiolus cheptumoae* from which it also differs in the following morphological features :- buccal cingulum in p/4 strong; mesial fovea of p/4 not triangular; in lower molars, protoconid less mesially located than the metaconid with obliquely oriented protocristid and main cusps with well-developed crests; metaconid apex in molars not bifid; spout (lingual opening) of talonid basin higher than the rest of the basin; m/3 not reduced (modified from Pickford & Kunimatsu, 2005).

**Holotype** : KMN WK 16960, left mandible with i/1-m/3, left premaxilla and maxilla fragment with C1/-P3/, isolated upper right canine, left P3/ and left and right M1/-M3/.

**Type locality** : Kalodirr, Kenya (3°20'N, 35°40'E).

**Age** : Middle Miocene, Faunal Set IIIa (<17.5 - >16.8 Ma).

**Description and comments**
Two teeth from Moroto II are attributed to *Simiolus enjiessi*. The best preserved of the specimens is an unworn right m/3 (Mor II, 2'15). The main cusps are peripherally positioned and are sectorial rather than bunodont, the buccal cingulum is weak at the protoconid and hypoconid and fades out entirely at the hypoconulid but in the zone between the cusps it is well-developed. The trigonid basin is vast, and connects to the talonid basin, the cristids from the hypoconid and entoconid being low and not meeting each other, while the talonid basin connects to the distal fovea via a v-shaped valley. The entoconid has a small accessory cusplet between it and the metaconid. The occlusal outline of the crown is elongated.

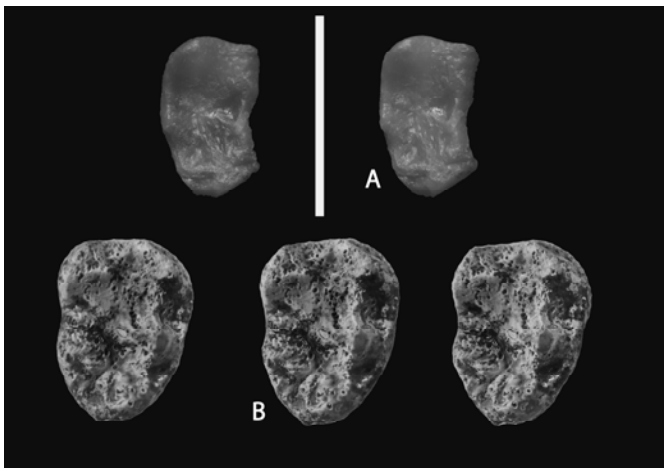


**Figure 15**. Lower teeth of *Simiolus enjiessi* from Moroto II. A) Mor II, 35'05, damaged right m/2, stereo occlusal view of a cast; B) Mor II, 2'15, right m/3, stereo triplet occlusal view (scale : 10 mm).

These two teeth differ markedly from those of *Kogolepithecus* by the weaker buccal cingulum, the more elongated m/3 and the weak cristids separating the talonid basin from the distal fovea. They match the corresponding teeth in the holotype of *Simiolus enjiessi* from Kalodirr (Leakey & Leakey, 1987).

**Table 5**. Measurements (in mm) of teeth of *Simiolus enjiessi* from Moroto II, Uganda.

| Catalogue | Tooth | Mesio-distal length | Bucco-lingual breadth |
|---|---|---|---|
| Mor II 35'05 | m/2 right fragment | 6.6 | -- |
| Mor II 2'15 | m/3 right | 8.0 | 5.7 |

The dimensions of the m/3 from Moroto II are close to those of the holotype of *Simiolus enjiessi* (KNM WK 16960, l x b – 7.8 x 5.9) (Leakey & Leakey, 1987) and are larger than specimens of *Simiolus andrewsi* (KNM FT 20-25, l x b – 6.3 x 4.9) (Harrison, 1992, 2010b) and *Simiolus cheptumoae* (OCO Bar 824'01, l x b – 5.9 x 4.4) (Pickford & Kunimatsu, 2005). It is concluded that the Moroto specimens represent *Simiolus enjiessi* (Table 5).

## Genus *Kalepithecus* Harrison, 1988

**Genus diagnosis :** A small anthropoid primate approximating *Hylobates lar* in dental size. Upper central incisor broad and spatulate. I2/ markedly bilaterally asymmetrical in shape and relatively much

smaller than I1/. Lower incisors very high-crowned, slender and relatively symmetrical in shape. Canines moderately high-crowned and robust, with only slight bilateral compression. Upper premolars long and narrow with well-developed transverse crests. p/3 moderately sectorial. p/4 relatively large and ovoid, and frequently broader than long. Upper molars relatively broad due to strong development of a lingual cingulum. Protocone voluminous and markedly buccally displaced away from the margin of the crown. Breadth of trigon only slightly greater than its length. Lower molars are short and broad, and rectangular to ovoid in shape, with a slightly oblique mesial fovea and a broad, but rounded and poorly defined buccal cingulum. m/1 smaller than m/2 smaller than or equal to m/3. Upper and lower molars have low, rounded and poorly developed occlusal crests. Anterior dentition large relative to the size of the cheek teeth. Nasal aperture very broad, particularly inferiorly. Subnasal portion of premaxilla relatively high. Mandible high with relatively deep and robust symphysis. Superior transverse torus well-developed. Inferior transverse torus poorly developed to absent (from Harrison, 1988).

**Type species** : *Kalepithecus songhorensis* (Andrews, 1978)

**Species diagnosis** : A small catarrhine primate similar in dental size to *Limnopithecus legetet* (Table 6) with an estimated body weight of ~5 kg. I1/ relatively broader and more spatulate compared with those in *Limnopithecus* or *Dendropithecus*; I2/ markedly bilaterally asymmetrical in shape, and relatively much smaller than I1/; lower incisors high crowned, slender and relatively bilaterally symmetrical; canines moderately high-crowned, with only slight bucco-lingual compression; upper premolars relatively narrow, with a well-developed transverse crest linking the main cusps; p/3 exhibits a moderate degree of sectoriality; p/4 relatively large and ovoid, frequently being broader than long; upper molars relatively broad due to the strong development of a lingual cingulum; protocone voluminous and markedly buccally displaced away from the margin of the crown; breadth of the trigon only slightly greater than its length; lower molars short and broad, and rectangular to ovoid in shape; mesial fovea slightly oblique; buccal cingulum broad, but rounded and poorly defined; $m/1 < m/2 \leq m/3$; molars have low rounded and voluminous cusps that restrict the extent of the foveae and occlusal basins; occlusal crests low, rounded, and poorly developed; anterior teeth large in relation to the size of the cheek teeth; unlike other early Miocene catarrhines, nasal aperture broad, particularly inferiorly, and nasoalveolar clivus relatively deep (from Harrison, 2010b).

**Table 6**. Measurements (in mm) of the type specimen of *Kalepithecus songhorensis* from Songhor, Kenya (data from Harrison, 1982).

| Catalogue | Tooth | Mesio-distal length | Bucco-lingual breadth |
|---|---|---|---|
| KNM SO 378 | p/4 right | 5.5 | 4.9 |
| KNM SO 378 | m/1 right | 5.7 | 5.0 |
| KNM SO 378 | m/2 right | 5.9 | 5.7 |
| KNM SO 378 | m/3 right | 6.5 | 5.4 |

**Species *Kalepithecus kogolensis* sp. nov.**

**Diagnosis** : Species of *Kalepithecus* in which the posterior molars are ca 20% larger than in the type species *Kalepithecus songhorensis* (Andrews, 1978) but in which m/1 is about the same diensions and the p/4 smaller. Lower second incisors with a distinct bend in the crown.

**Holotype** : UM Mor II, 1’17, right p/3-m/3.

**Paratypes** : UM Mor II, 2’14 (left and right i/1, right i/2, left and right canines, left p/3-m/2), UM MorII 3’15, left I1/, Mor II 4’15, right I1/, Mor II 5’15, left i/2 (probably the same individual as the holotype). The morphology of the canines indicate that the specimen is female.

**Type Locality** : Moroto II, Point 1 in Pickford *et al*., 2003 (02°40’20.2’’N : 34°42’52.4’’E (WGS 84))

**Age** : Middle Miocene, Faunal Set IIIa.

**Etymology** : Kogole is the name of the basalt hill immediately north of Moroto II, Point 1. It means Eagle's Nest or Eerie in Karimojong, often with the connotation of « Lookout Point ».

**Description and comments**

The holotype teeth (right p/3-m/3) collected in 2017, were found close together with fragments of the mandible (Fig. 3) and undoubtedly belong to a single individual. The paratypes were found in 2014 and 2015, all close to the same spot that yielded the holotype. The degree of wear of the cheek teeth indicates that they belong to a single individual. However, the premolars on the left side are somewhat different from those on the right side. Despite the differences, we consider that all these teeth represent a single individual, and that the differences in morphology constitute a case of unilateral teratogenic development, with the right p/3 and p/4 being aberrant, the left p/3 and p/4 representing the usual morphology of these teeth in the species.

A pair of upper central incisors from Moroto II (3'15, 4'15) evidently belong to a single individual and likely represent the same animal as a set of lower teeth found in the same square metre of sediment. There is slight apical wear which accords with the degree of wear in the lower incisor battery. The lingual surface of the crown is concave with a prominent central basal tubercle and crest rising to wards the middle of the apical edge. There is a low but sharp cingulum mesially, lingually and distally. The distal quarter of the apical edge curves disto-lingually. When occluded with the lower incisor battery, it is clear that the mesial half of the biting edge of the upper central incisors, mesial to the central lingual rib, corresponds to the lower central incisor, while the part distal to the central lingual rib corresponds to the second lower incisor. The labial surface of the upper incisors is shallowly concave, almost flat. The roots are robust and bend laterally about one-third of the way towards their apices. This leaves a broad gap between the mesial parts of the cervix of the two teeth, even though the apices of the crowns are in contact with each other

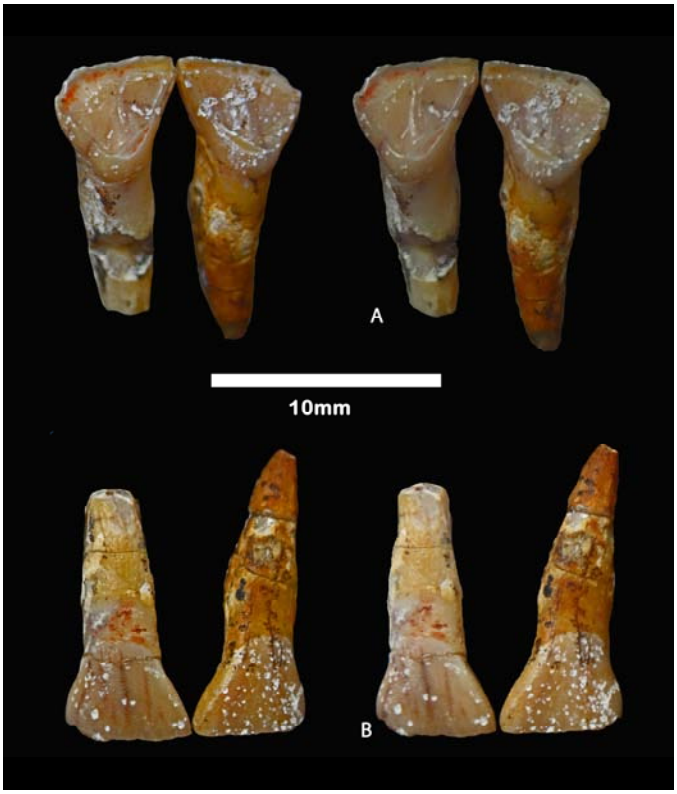


**Figure 16**. Upper central incisors of *Kalepithecus kogolensis* sp. nov. from Moroto II, A) stereo lingual and B) stereo labial views (scale : 10 mm).

The lower incisor battery from Moroto II is large relative to the dimensions of the cheek tooth rows. The central lower incisors have parallel mesial and lingual sides. The lingual surface is very lightly concave apically but becomes convex towards the cervix terminting at a low bulge. The lateral lower incisors are taller than the central incisors, and are remarkable for the bend in the crown, making for a longitudinally concave mesial surface and a convex distal one. The apical edge curves rootwards from mesial to distal, with an interruption between an apical part that occludes with I1/ and a distal part that is inclined cervically.There is a low lingual bulge near cervix, as in the i/1.


**Figure 17**. *Kalepithecus kogolensis* sp. nov. from Moroto II, upper and lower incisors in approximate occlusal relationship in A) labial view, and B) stereo occlusal view of lower incisors and canines. Note the curvature of the crowns of the i/2s (scale : 10 mm).

The lower canines are low crowned and stubby, suggesting that the specimen is female. The main wear facet is apical. There is a weak lingual cingulum that extends along the mesial side of the tooth. The distal scoop is shallow.

The left p/3 is mesio-distally elongated, more so than the right p/3 (Table 7). It has a lingual cristid which descends from the main cusp disto-lingually. The right p/3 also has a lingual cristid but it bifurcates basally. There is a honing facet on the mesio-buccal surface. We interpret these differences in morphology to be a case of teratogenic development of the right p/3 crown.

The p/4s have tall protoconid and metaconid joined togehter by a strong cristid. There are narrow wear facets down the preproto- and postprotocristid. The mesial fovea is small, the distal basin larger.

The m/1and m/2 are similar in occlusal morphology, but the m/2 is significantly bigger than the m/1. The mesial half of the crown is significantly narrower than the distal half. The main cusps are low and conical, with relatively subdued cristids. Wear on the cusps produces almost circular dentine lakes, with the buccal cusps slightly more deeply worn than the lingual ones. The protocoid and metaconid are obliquely positioned, such that the protoconid is more anteriorly positioned than the metaconid. As a result, the mesial fovea is slightly obiquely oriented, bordered anteriorly by a low cingulum, and distally by cristids that run between the protoconid and metaconid. The hypoconid is the largest cusp and is slightly anteriorly positioned relative to the entoconid. The hypoconulid is positioned in the centre-line of the tooth. The talonid basin is large and the buccal and lingual « spouts » are low and unencumbered by cristids or cingulids, and even the outlet between its hypoconulid and hypoconid is open. The distal fovea is separated from the talonid basin by cristids that run between the entoconid and the hypoconulid.

The m/3 lacks the lingual cusps, but what is preserved resembles the m/2 with the exception that the hypoconulid appears to be slightly more bucally positioned.

Measurements are provided in Table 7. The m/1 is the smallest molar, the m/2 is significantly bigger than it, and the m/3 is marginally longer than the m/2.

**Table 7**. Measurements (in mm) of teeth of *Kalepithecus kogolensis* sp. nov. from Moroto II, Uganda.

| Catalogue | Tooth | Mesio-distal length | Bucco-lingual breadth |
|---|---|---|---|
| Mor II 3'15 | I1/ left | 5.4 | 3.5 |
| Mor II 4'15 | I1/ right | 5.2 | 3.8 |
| Mor II 33'05 | M3/ right fragment | -- | -- |
| Mor II 2'14 | i/1 right | 2.5 | 3.0 |
| Mor II 2'14 | i/1 left | 2.6 | 3.0 |
| Mor II 5'15 | i/2 left | 2.8 | 3.7 |
| Mor II 2'14 | i/2 right | 3.0 | 3.6 |
| Mor II 2'14 | c/1 left | 3.9 | 5.4 |
| Mor II 2'14 | c/1 right | 3.7 | 5.2 |
| Mor II 2'14 | p/3 left | 6.2 | 3.5 |
| Mor II 1'17 | p/3 right | 4.8 | 3.6 |
| Mor II 2'14 | p/4 left | 4.8 | 4.0 |
| Mor II 1'17 | p/4 right | 4.7 | 4.2 |
| Mor II 2'14 | m/1 left | 6.1 | 5.2 |
| Mor II 1'17 | m/1 right | 5.8 | 5.1 |
| Mor II 2'14 | m/2 left | 6.7 | 5.9 |
| Mor II 1'17 | m/2 right | 6.7 | 6.1 |
| Mor II 1'17 | m/3 right | 7.0 | -- |


**Figure 18**. Lower dentition of *Kalepithecus kogolensis* sp. nov. from Moroto II, stereo occlusal view (scale : 10 mm).

### Genus *Micropithecus* Fleagle & Simons, 1978

**Diagnosis** : Dental formula 2.1.2.3. Upper molars differ from those of all other early Miocene apes in the more lingual position of the hypocone with respect to the protocone, the reduction of the cingulum in the mesio-lingual and disto-lingual aspect of the tooth, and the expansion of the posterior basin between hypocone and metacone. These features give the upper molars the appearance of an inflated triangle in contrast to the rhomboidal or rectangular shape seen in upper molars of *Aegyptopithecus*, *Pliopithecus*, *Dryopithecus* (sensu Simons & Pilbeam, 1965), *Dendropithecus*, and *Limnopithecus*. M2/ > M1/ > M3/. P4/ shows two subequal cusps; P3/ shows slightly enlarged buccal cusp. Lower molars show 5-cusped typical hominoid cusp pattern with centrally placed hypoconulid and little or no cingulum. m/1 smaller than or equal to m/3. Anterior dentition large relative to size of cheek teeth, with dagger-like canines and laterally compressed p/3. Nasal opening relatively broader than in *Dryopithecus*, *Pliopithecus*, and *Dendropithecus*. Orbits relatively much larger than in *Aegyptopithecus*, and *Dryopithecus*, but comparable to those of *Pliopithecus* (Original diagnosis from Fleagle & Simons, 1978).

### Species *Micropithecus leakeyorum* Harrison, 1989

**Diagnosis** : A species distinguished from *Micropithecus clarki* by the following features: p/3 more bilaterally compressed, with only moderate development of a honing face mesially; p/4 relatively longer and narrower; lower molars relatively narrower, with a more pronounced buccal cingulum and better defined mesial and distal fovea; m/3 subequal to or slightly larger in occlusal area than m/2, and no indication on m/3 of marked reduction of the cusps and occlusal crests distally; upper molars slightly broader, with a shorter and more restricted trigon and a larger hypocone; M3/ relatively larger with better-developed cusps distally; M1/ < M3/ < M2/ (from Harrison, 2010b).

**Description and comments**

Mor II BD, 1’07 is a right mandible fragment containing a lightly worn m/3 and the roots of the m/2 found in Bishop’s Dump at Moroto II. At the level of the m/3 the mandible is twice a thick as the breadth of the m/3, indicating a robust jaw. The root of the ascending ramus starts rising at the level of the middle of m/3, but in lateral view it does not hide the m/3. Judging from the roots of the m/2, the tooth would have been slightly shorter than, and about the same breadth as, the m/3 (Table 8).


**Figure 19**. Moroto II specimen attributed to *Micropithecus leakeyorum*. Mor II BD, 1’07, right mandible fragment containing m/3, A) stereo occlusal view, B) buccal view, C) lingual view (scale 10 mm).

The crown of m/3 has five main cusps, three buccal ones which are somewhat internally positioned and conical in form, with the hypoconulid closer to the midline of the tooth than the protoconid and hypoconid. The mesial lophid is almost as broad as the distal one, which makes the lingual and buccal sides of the crown almost parallel with each other. The metaconid and entoconid are positioned peripherally and are slightly sectorial in appearance. There is a weak buccal cingulum extending along the entire side of the tooth. The cristids from the main cusps are subtle, possibly reduced due to wear, but in any case not strongly formed. The mesial fovea is separated from the trigonid basin by the two cristids that emanate from the apices of the protoconid and metaconid to join in the midline of the tooth. There is no separation between the trigonid basin and the distal fovea, which itself is open distally.

The molar in this jaw fragment is similar in morphology to that in the most complete mandible referred to *Micropithecus clarki*, KNM CA 380 from locality 34, Chamtwara Formation (Harrison, 2010b, fig. 24.2b) but it is appreciably larger (7.1 x 5.6 mm for the Moroto specimen, versus 5.5 x 4.5 mm for the Chamtwara specimen). It is closer in dimensions to *Micropithecus leakeyorum* from Maboko Island (Harrison, 1989) the m/2 of which measures 6.2 x 4.9 mm which compares favourably with the root dimensions in the Moroto specimen (estimated length x breath 6.6 x 5.5 mm) (m/2 is 5.8 x 5.3 in the Chamtwara specimen).

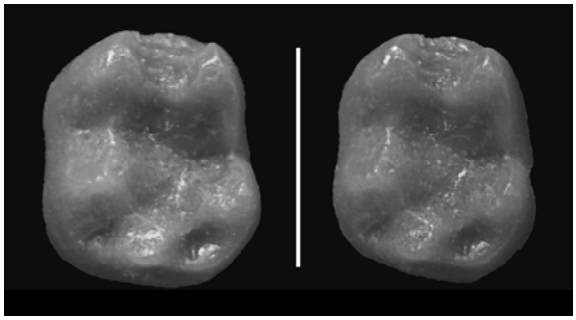

**Figure 20**. Mor II 20’04, left m/2 from Moroto attributed to *Micropithecus leakeyorum*, stereo occlusal view of a cast (scale : 5 mm).

Mor II 20’04 is an isolated, unworn left lower molar previously attributed to *Micropithecus* sp. by Pickford & Mein (2006). The mesial part of the crown is only marginally narrower than the distal part. The protoconid and hypoconid are conical with subdued, rounded crests. The hypoconulid is centrally placed at the rear of the tooth with weak, low crests leading towards the hypoconid and entoconid respectively. The metaconid and entoconid have slightly sectorial crests at the lingual end of the talonid basin, forming a low sill to the basin. The mesial fovea is shallow, walled off mesially by a cingular structure and posteriorly by crests from the protoconid and metaconid. The distal fovea is a deep dimple behind the crests which join the hypoconulid to the entoconid. The buccal sinusids are shallow and there is no sign of a cingulum on the bccal side of the crown.

**Table 8**. Measurements (in mm) of teeth attributed to *Micropithecus leakeyorum* from Moroto II and Maboko (e – estimated measurement). Maboko (MB) mesurements are from Harrison (1989).

| Catalogue | Tooth | Mesio-distal length | Bucco-lingual breadth |
|---|---|---|---|
| UM Mor II 20’04 | left lower molar | 5.4 | 4.9 |
| UM Mor II BD 1’07 | m/2 right roots | 6.6e | 5.5e |
| UM Mor II BD 1’07 | m/3 right | 7.1 | 5.6 |
| KNM MB 11660 | m/1 | 5.2 | 4.0 |
| KNM MB 11660 | m/2 | 5.8 | 4.5 |
| KNM MB 11797 | m/1 | 5.5e | 4.1e |
| KNM MB 14250 | m/1 | 5.3 | 4.1 |
| KNM MB 14250 | m/2 | 6.2 | 4.9 |
| KNM MB 14251 | m/3 | 6.3 | 5.1 |
| KNM MB 14258 | m/3 | 5.9 | 4.8 |

The morphology of Mor II, 20’04 is similar to that of the m/2 in the mandible attributed to *Micropithecus clarki* (KNM CA 380) by Harrison (2010b) but it also plots close to the size of the m/2 in *Micropithecus leakeyorum* (Table 8). In view of the uncertainty about the meristic position of this tooth (m/1or m/2) it is tentatively attributed to *Micropithecus leakeyorum* rather than to *Micropithecus clarki* on the grounds that it would be unlikely for the site to yield two species of *Micropithecus*.

## Unidentified small ape from Moroto II

### Description and comments

Mor II, 1’15 is a right lower canine with a heavy honing facet on the disto-labial side cutting slightly into the root beneath the cervix, indicating that it is probably from a male individual. The crown is canted buccally with respect to the root, the crown is tall and pointed, with a prominent disto-lingual cingulum that rises apically on the mesial side to join the mesial cristid which fades out at about half the height of the crown. The labial surface of the tooth is convex with a shallow depresssion near the mesial crest and the enamel extends slightly further rootwards here than elsewhere round the cervix. The mesial surface of the root has a shallow longitudinal groove.


**Figure 21**. Mor II, 1'15, stereo views of right lower canine, probably male, A) mesial, B) distal, C) lingual and D) labial (scale : 10 mm).

**Table 9**. Measurements (in mm) of a lower canine attributed to an unidentified small ape species from Moroto II.

| Catalogue | Tooth | Mesio-distal length | Bucco-lingual breadth |
|---|---|---|---|
| Mor II 1'15 | c/1 right male | 7.2 | 4.9 |

There are several taxa to which this lower canine could belong. It is evidently a male on the basis of the large honing facet which extends slightly onto the root. It is compatible in dimensions with *Kogolepithecus morotoensis*, *Micropithecus leakeyorum*, and *Kalepithecus kogolensis* (Table 9). The lower canine of *Kogolepithecus morotoensis* described above is more labio-lingually compressed than Mor II, 1'15. The lower female canines of *Kalepithecus kogolensis* could correspond to the male individual Mor II 1'15, but if this were the case, it would represent an extreme, but not unknown, degree of sexual dimorphism. No lower canines of *Micropithecus leakeyorum* have been described, so it is not possible to make comparisons with specimens from the type locality, although it is noted that the morphology of the tooth resembles the one in KNM CA 380, a mandible from Chamtwara attributed to *Micropithecus clarki* by Harrison (2010b), although it is considerably larger.

## GENERAL DISCUSSION

As was already mentioned by Pickford *et al*. (2009) the presence of two species of large ape at Moroto complicated the attribution of the post-cranial bones from the deposits. Initially assumed to belong to the same species as the Moroto snout (*Afropithecus turkanensis*), it was pointed out that some of the bones could represent a second taxon. Now, with the description of *Nacholapithecus kerioi* from the deposits, the situation is once again open to reinterpretation. The more complete of the two femora, in particular, which always seemed to be rather small for *Afropithecus* or *Ugandapithecus*, might represent *Nacholapithecus*, a possibility that can now be addressed because the post-cranial skeleton of the latter taxon is well-represented at the type locality, Nachola (Ishida *et al*., 2004).

A hominoid phalanx from Moroto I described by Pickford *et al*. (1999) was provisionally attributed to *Morotopithecus bishopi* (i.e. *Afropithecus turkanensis* in this paper). Additional finds of phalanges at Moroto I indicate that all of the specimens could belong to *Nacholapithecus kerioi*. They will be

described in a separate paper. An upper canine from Moroto II was initially considered to represent a female of *Morotopithecus* (Pickford *et al*., 1999) but the specimen is here considered to belong to *Nacholapithecus*. Last but not least, the juvenile maxilla from Moroto I was attributed to *Afropithecus turkanensis* by Pickford *et al*. (2009) but is here identified as *Nacholapithecus kerioi* on the basis of the osteological and dental characters that it shares with the fossils from Nachola, and by which it differs fundamenally from both *Afropithecus* and *Ugandapithecus*.

Previous knowledge about the small catarrhines from Moroto was extremely limited, three teeth of a primitive cercopithecid being described by Pickford *et al*. (2003) and a possible *Micropithecus* tooth being listed by Pickford & Mein (2006). The latter tooth is here attributed to *Micropithecus leakeyorum*. In the past few years several interesting discoveries have been made, including that of associated tooth rows which reveal that there are at least four taxa of small apes at Moroto II, *Kogolepithecus morotoensis*, *Kalepithecus kogolenis* sp. nov., *Simiolus enjiessi* and *Micropithecus leakeyorum* while an isolated canine of a small ape is left in open nomenclature.

The discovery of a diverse higher primate fauna at Moroto I and Moroto II throws light on the age of the deposits. When combined with the other faunal elements, the conclusion is that the Moroto sediments correlate best with East African Faunal Set III. The records of *Afropithecus turkanensis* and *Simiolus enjiessi* suggest correlation to FS IIIa, whereas the presence of *Nacholapithecus kerioi* and *Micropithecus leakeyorum* indicate correlation to FS IIIb. This means that the age of the Moroto sediments probably lies between ca 17.5 Ma and 16 Ma, and most likely is ca 16.5-17.0 Ma.

## CONCLUSIONS

Moroto I and Moroto II comprise a complex of Middle Miocene sites on the flanks of the Gregory Rift Valley, North-eastern Uganda, which have yielded a vertebrate fauna which compares reasobaly well with samples from Kalodirr, Moruorot, Nachola, Maboko and Kipsaraman. On the basis of faual similarities, we correlate Moroto I and II to Faunal Set III, with a preferred age range for the deposits between 17.0 and 16.5 Ma.

Among the vertebrates from Moroto I and II, the primates are more diverse than previously documented. There are now known to be three large apes at the sites (*Ugandapithecus gitongai*, *Afropithecus turkanensis* and *Nacholapithecus kerioi*) and at least four species of small apes (*Kogolepithecus morotoensis*, *Kalepithecus kogolensis* sp. nov., *Simiolus enjiessi* and *Micropithecus leakeyorum*). The deposits have also yielded a primitive cercopithecid (*Noropithecus* sp.) (Pickford *et al*., 2003) and a galagid (Pickford & Mein, 2006; Harrison, 2010a).

The presence of such a diverse primate fauna at the Moroto complex of sites indicates that during the Middle Miocene, the region north of Moroto Mountain was appreciably more humid (sub-humid to humid) than it is today (semi-arid steppe).

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## REFERENCES

Allbrook, D. & Bishop, W.W., 1963 - New fossil hominoid material from Uganda. *Nature*, **197**: 1187-1190.
Andrews, P., 1978 - A revision of the Miocene Hominoidea of East Africa. *Bulletin of the British Museum (Natural History), Geology*, **30**: 85–225.
Andrews, P. & Simons, E.L., 1977 - A new African Miocene gibbon-like genus, *Dendropithecus* (Hominoidea : Primates) with distinctive postcranial adaptations : Its significance to origin of Hylobatidae. *Folia Primatologica*, **28**: 161-168.
Bishop, L., 2010 - Suoidea. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 821-842.
Bishop, W.W., 1958 - Fossil apes and ivory. *Bulletin of the Uganda Society*, **1958**: 127-129.
Bishop, W.W., 1964 - More fossil Primates and other Miocene mammals from North-east Uganda. *Nature*, **203**: 1327-1331.
Cote, S., 2010 - Pecora *Incertae sedis*. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 731-739.
Fleagle, J. & Simons, E., 1978 - *Micropithecus clarki*, a small ape from the Miocene of Uganda. *American Journal of Physical Anthropology*, **49**: 427-440.
Fleuty, M.J., 1968 - Explanation of the Geology of Sheet 27 (Moroto). *Reports of the Geological Survey of Uganda*, **13**.
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.
Geoffroy Saint-Hillaire, E., 1812 - Tableau des Quadrumanes, ou des animaux composant le premier Ordre de la Classe des Mammifères. *Annales du Muséum d'Histoire Naturelle*, **19**: 85-122, 156-170.
Geraads, D., 2010 - Rhinocerotidae. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 669-683.
Gommery, D., Senut, B. & Pickford, M., 1998 - Nouveaux restes postcrâniens d'Hominoidea du Miocène inférieur de Napak, Ouganda. *Annales de Paléontologie*, **84**: 287-306.
Gommery, D., Senut, B., Pickford, M. & Musiime, E., 2002 - Les nouveaux restes du squelette d'*Ugandapithecus major* (Miocène inférieur de Napak, Ouganda). *Annales de Paléontologie*, **88**: 167-186.
Gray, J.E., 1825 - Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. *Annals of Philosophy*, **10**: 337-344.
Gunnell, G., 2010 - Chiroptera. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 581-597.
Harrison, T., 1982 - *Small-bodied Apes from the Miocene of East Africa*. Unpublished PhD Dissertation, University of London, 647 pp.
Harrison, T., 1988 - A taxonomic revision of the small catarrhine primates from the early Miocene of East Africa. *Folia Primatologica*, **50**: 59–108.
Harrison, T., 1989 - A new species of *Micropithecus* from the middle Miocene of Kenya. *Journal of Human Evolution*, **18**: 537–557.
Harrison, T., 1992 - A reassessment of the taxonomic and phylogenetic affinities of the fossil Catarrhines from Fort Ternan, Kenya. *Primates*, **33** (4): 501-522.
Harrison, T., 2010a - Later Tertiary Lorisiformes. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 333-349.
Harrison, T., 2010b - Dendropithecoidea, Proconsuloidea and Hominoidea. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 429-469.
Holroyd, P., 2010 - Macroscelidea. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 89-98.
Holroyd, P., Lihoreau, F., Gunnell, G. & Miller, E., 2010 - Anthracotheriidae. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 843-851.
Hopwood, A., 1933a - Miocene Primates from British East Africa. *Annals and Magazine of Natural History*, Series 10, **11**: 96-98.
Hopwood, A., 1933b - Miocene primates from Kenya. *Journal of the Linnaean Society of London (Zoology)*, **38**: 437-464.
Ishida, H., Kunimatsu, Y. Nakatsukasa, M. & Nakano Y., 1999 - New hominoid genus from the middle

Miocene of Nachola, Kenya. *Anthropological Science*, **107**: 189-191.
Ishida, H., Kunimatsu, Y. Takano, T. Nakano, Y. & Nakatsukasa, M., 2004 - *Nacholapithecus* skeleton from the middle Miocene of Kenya. *Journal of Human Evolution*, **46**: 69–103.
Le Gros Clark, W.E. & Leakey, L.S.B., 1950 - Diagnoses of East African Miocene Hominoidea. *Proceedings of the Zoological Society of London*, **105**: 260-262.
Le Gros Clark, W.E. & Leakey, L.S.B., 1951 - The Miocene Hominoidea of East Africa. *Fossil Mammals of Africa*, No. **1**. British Museum (Natural History), London, 117 pp.
Leakey, L.S.B., 1962 - A new lower Pliocene fossil primate from Kenya. *Annals and Magazine of Natural History*, series 13, **4**: 689-696.
Leakey, M.G. & Walker, A., 1997 - *Afropithecus* Function and Phylogeny. *In*: Begun, D.R., Ward, C.V. & Rose, M.D. (Eds) *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. New York and London, Plenum, pp. 225-239.
Leakey, R.E. & Leakey, M.G., 1986 - A new Miocene hominoid from Kenya. *Nature*, **324**: 143-146.
Leakey, R.E. & Leakey, M.G., 1987 - A new Miocene small-bodied ape from Kenya. *Journal of Human Evolution*, **16**: 369-387.
Leakey, R.E., Leakey M.G. & Walker A.C., 1988 - Morphology of *Afropithecus turkanensis* from Kenya. *American Journal of Physical Anthropology*, **76**: 289–307.
Lewis, M.E. & Morlo, M., 2010 - Creodonta *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 543-560.
Linnaeus, C., 1758 - *Systema Naturae, Ed. X. (Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis). Editio decima, reformata*. Tomus 1. Holmiae: Laurentius Salvius, Stockholm, 824 pp.
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. & 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.* London, Geological Society, pp. 15-26.
MacLatchy, L. & Rossie, J., 2005 - New hominoid dental specimens from Moroto II, Early Miocene, Uganda. *Journal of Vertebrate Paleontology, Abstracts*, **25**: 86A.
MacLatchy, L. & Young, N., 2004 - The phylogenetic position of *Morotopithecus*. *Journal of Human Evolution*, **46**: 163-184.
Mivart, S.-G.J., 1864 - Note on the crania and dentition of the Lemuridae. *Proceedings of the Zoological Society of London*, **1864**: 611-648.
Musalizi, S., Senut, B., Pickford, M. & Musiime, E., 2009 - Geological and palaeontological archives relating to Early Miocene localities of Uganda, 1957-1969. *Geo-Pal Uganda*, **1**: 2-96.
Nakatsukasa, M., 2008 - Comparative study of Moroto vertebral specimens. *Journal of Human Evolution*, **55**: 581–588.
Patel, B.A. & Grossman, A., 2006 - Dental metric comparisons of *Morotopithecus* and *Afropithecus*: implications for the validity of the genus *Morotopithecus*. *Journal of Human Evolution*, **51**: 506-512.
Pickford, M., 1981 - Preliminary Miocene Mammalian biostratigraphy for Western Kenya. *Journal of Human Evolution*, **10**: 73-97.
Pickford, M., 1983 - Sequence and environments of the lower and middle Miocene hominoids of Western Kenya. *In*: Ciochon, R. & Corruccini, R. (Eds) *New Interpretations of Ape and Human Ancestry*. New York, Plenum, pp. 421-439.
Pickford, M., 1986 - The geochronology of Miocene higher primate faunas of East Africa. *In*: Else, J. & Lee, P. (Eds) *Primate Evolution*. Cambridge, Cambridge University Press, pp. 19-45.
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 - New reconstruction of the Moroto hominoid palate and a reassessment of its affinities to *Afropithecus turkanensis*. *Human Evolution*, **17**: 1-19.
Pickford, M., 2011 - *Morotochoerus* from Uganda (17.5 Ma) and *Kenyapotamus* from Kenya (13-11 Ma): implications for hippopotamid origins. *Estudios geologicos*, **67** (2): 523-540.
Pickford, M. & Kunimatsu, Y., 2005 - Anthropoids from the Middle Miocene (ca 14.5 Ma) of Kipsaraman, Tugen Hills, Kenya. *Anthropological Science*, **113**: 189-224.

Pickford, M. & Mein, P., 2006 - Early Middle Miocene Mammals from Moroto II, Uganda. *Beiträge zur Paläontologie*, **30**: 361–386, Wien.

Pickford, M. & Senut, B., 1999 - Geology and Palaeobiology of the Namib Desert, Southwestern Africa. *Memoir of the Geological Survey of Namibia*, **18**: 1-155.

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*. London, Geological Society, pp. 27-38.

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 Palevol*, **2**: 649-662.

Pickford, M., Senut, B., Gommery, D. & Musiime, E., 2009 - Distinctiveness of *Ugandapithecus* from *Proconsul*. *Estudios geologicos*, **65** (2): 183-241.

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, Paris*, **302**: 681-686.

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, Monatshefte*, **4**: 235-251.

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.

Sanders, W., Gheerbrant, E., Harris, J., Saegusa, H. & Delmer, C., 2010 - Proboscidea. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 161-251.

Sawada, Y., Pickford, M., Itaya, T., Makinouchi, T, Tateishi, M., Kabeto, K., Ishida, S. & Ishida, H., 1998 - K-Ar ages of Miocene Hominoidea (*Kenyapithecus* and *Samburupithecus*) from Samburu Hills, Northern Kenya. *Comptes Rendus de l'Académie des Sciences, Paris*, **326**: 445-451.

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, Paris*, **331**: 227-233.

Smith, T.M., Martin, L.B. & Leakey M.G., 2003 - Enamel thickness, microstructure and development in *Afropithecus turkanensis*. *Journal of Human Evolution*, **44**: 283–306.

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.

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

Ward, C.V., 1998 - *Afropithecus*, *Proconsul*, and the primitive hominoid skeleton. *In*: Strasser, E., Fleagle, J., Rosenberger, A. & McHenry, H. (Eds), *Primate Locomotion: Recent Advances*. New York, Plenum, pp. 337-352.

Werdelin, L., 2010 - Chronology of Neogene Mammal Localities. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 27-43.

Werdelin, L. & Peigné, S., 2010 - Carnivora. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 603-657.

Winkler, A., Denys, C. & Avery, M., 2010 - Rodentia. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London, University of California Press, pp. 263-304.

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.