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Uganda Museum, P.O. Box 5718, Kampala

Revision of the Miocene Hominoidea from Moroto I and II, Uganda

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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 the boundary zone between East African Faunal Sets IIIa and IIIb (i.e. ca 15±0.5 Ma).

Key words: *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 underestimated 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) (Fig. 1-3). The fluvial deposits are dominated by clays and silts, with subordinate grits and conglomerates. The silts show evidence of sub-aerial exposure in the form of yellowish and reddish upper parts of the beds, representing incipient palaeosols. The clay fraction swells when wet and shrinks when dry, a process

that fractures many of the fossils into pieces which however, remain more or less in their correct position relative to one another (Fig. 4)

The hominoid fossils from Moroto (Allbrook & Bishop, 1963; Gebo *et al*., 1997; Gommery, 2006; 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; Senut, 2012; 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), Suoidea (Pickford, 1998; Bishop, 2010) Rodents and other micromammals (Pickford & Mein, 2006; Winkler *et al*., 2010), Ruminants (Cote, 2010), Bats (Gunnell, 2010), and Macroscelidea (Holroyd, 2010).

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).

Figure 2. MOR I 1’08, *Nacholapithecus kerioi* juvenile right maxilla with D3/ and D4/ at the time of discovery (see Fig. 1) lying exposed on the surface of deeply fissured red silty clay deposits at Moroto I. Matrix attached to the fossil indicate that it was derived from the red clay with calcareous nodules.

Figure 3. 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 4. 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 divergent 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, 1983, 1986; Pickford & Senut, 1999, Pickford *et al*., 1986, 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, 2006; Pickford & Senut, 1999) and Kipsaraman (ca 14.5 Ma, Pickford & Kunimatsu, 2005). From a faunal and evolutionary perspective an age between 16.5 and 15.5 Ma is most likely for the Moroto sedimentary deposits, close to the base of the Middle Miocene (Ogg *et al*., 2016).

Abbreviations

CA - Chamtwara (fossils housed in KNM)
BAR - Baringo (fossils curated at OCO)
BD - Bishop's Dump (at Moroto II)
BG - Baragoi (fossils housed in KNM)
FT - Fort Ternan (fossils housed in KNM)
KNM - Kenya National Museum, Nairobi, Kenya
MB – Maboko (fossils housed in KNM)
MOR – Moroto (fossils housed at the Uganda Museum)
NHMUK - Natural History Museum, London, England
OCO - Orrorin Community Organisation, Kipsaraman, Kenya
SO - Songhor
UM - Uganda Museum, Kampala, Uganda
UMP – Uganda Museum Palaeontology Collection
WK - Kalodirr (fossils housed in KNM)

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 (Fig. 5). 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 (Fig. 5) 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 between 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 measurements of m/3 in the Moroto II large ape mandible (UMP 62-10) are 15.1 x 13.0 mm (crown heavily abraded) which link the mandible with *Ugandapithecus* rather than with *Afropithecus*.

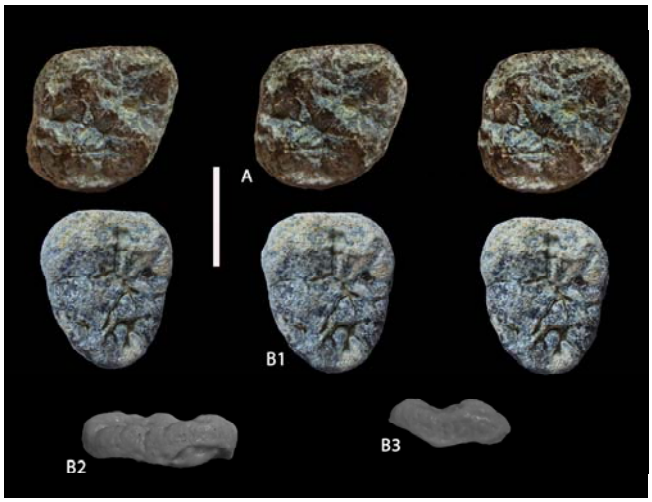

Figure 5. *Ugandapithecus gitongai* from Moroto II, Uganda. A) MOR II 2'98, left M2/ (stereo triplet occlusal view), B) MOR II 10'08, lightly worn left m/3 (B1 - stereo triplet occlusal view, B2 - lingual view of cast, B3 - mesial view of cast) (scale 10 mm).

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, Fig. 6) 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 6. *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, 1986a

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

Species *Afropithecus turkanensis* Leakey & Leakey, 1986a

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, 1986a; 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 paracone and protocone, 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, 1986a; 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/ (Fig. 7). 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.

The lower jaw (UMP 62-10) 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 (Fig. 8). 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, 1986a).

Figure 7. *Afropithecus turkanensis* from Moroto II, Uganda. MOR II UMP 62-11, the Moroto snout, A) left lateral and B) occlusal views (scale : 5 cm).

A lower molar, MOR II 1'08 (Fig. 8) 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).

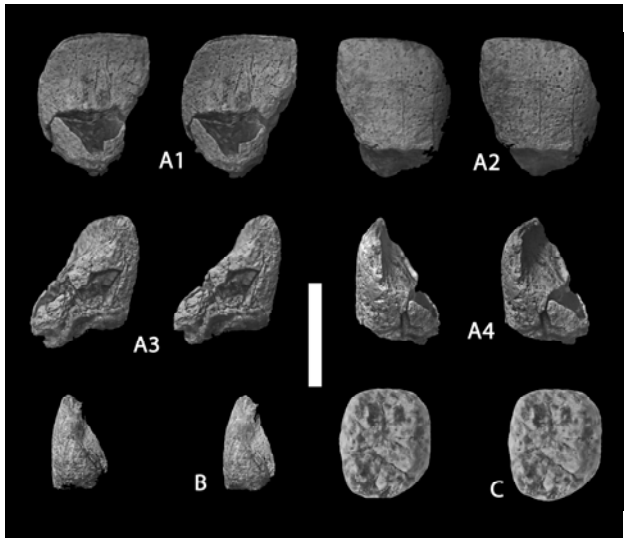

Figure 8. *Afropithecus turkanensis* from Moroto, Uganda. A) MOR II 11'08, right I1/, stereo views, (A1 - lingual, A2 - labial, A3 - distal and A4 – mesial); B) MOR II 10'07, right I1/ distal half, stereo distal view, C) MOR II 1'08, right m/2, stereo occlusal view (scale : 10 mm).

A left lower canine lacking much of the crown (MOR II 1'14, Fig. 9) 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.

Figure 9. 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 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, bucco-lingually stout, with a broad lingual pillar. I2/ narrower, with mesio-distal 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 mesio-distally 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 juvenile right maxilla fragment containing fully erupted D3/ and D4/, and the canine and M1/ in crypto (Fig. 10-11). 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.

Turkanapithecus Leakey & Leakey (1986b) has a shortened facial skeleton, but its post-canine dentition differs markedly from that of *Nacholapithecus*, notably by the deep crown bases upon which the main cusps are posed (Pickford *et al*., 2010). *Turkanapithecus* is also appreciably smaller than *Nacholapithecus*.

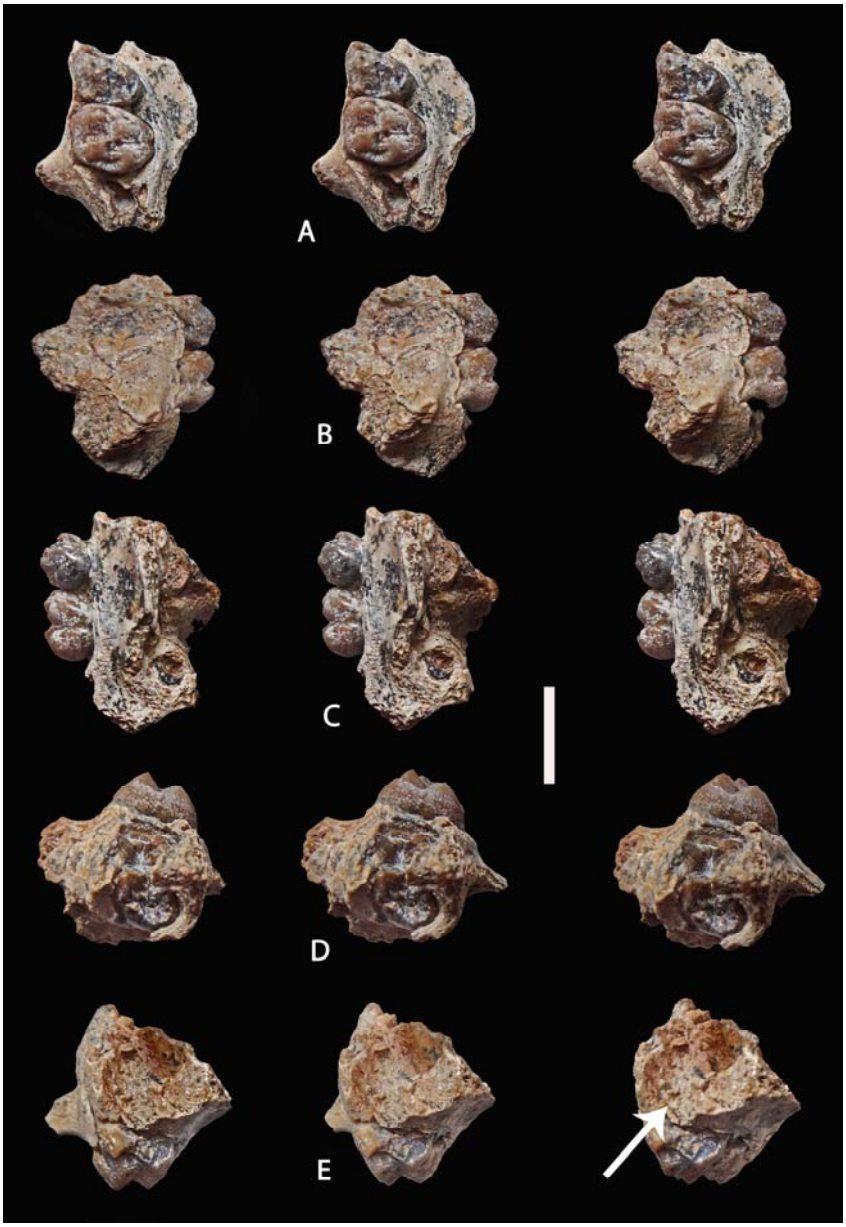

Figure 10. MOR I 1'08, right maxilla of *Nacholapithecus kerioi* containing D3/ and D4/ in occlusion and C1/ and M1/ in crypt, stereo triplet views. A) occlusal, B) lateral, C) lingual, D) posterior view to show unerupted M1/, and E) anterior view. The white arrow shows the alveolus of the deciduous canine (scale : 10 mm).

The only known 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).

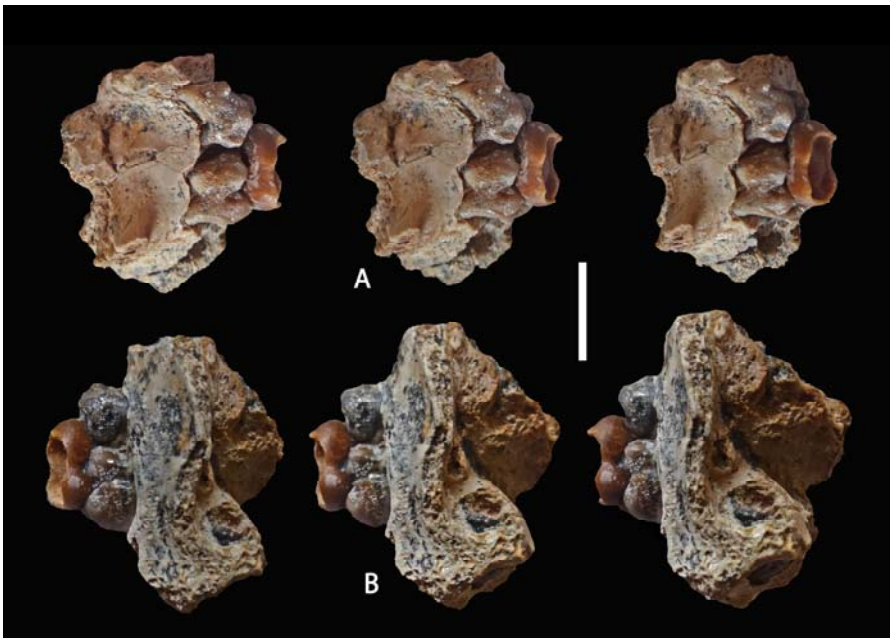

Figure 11. *Nacholapithecus kerioi*, right d/4 (MOR I 22'11) occluded with the D3/-D4/ in the juvenile maxilla (MOR II 1'08), stereo views A) buccal, B) lingual (scale : 10 mm).

Two lower incisors are attributed to *Nacholapithecus kerioi* on the basis of their dimensions (Fig. 12). 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.

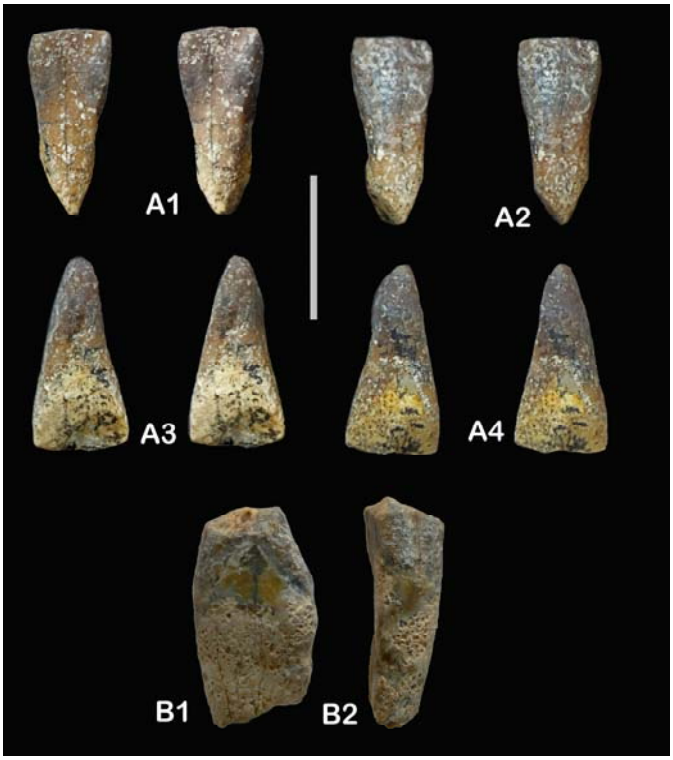

Figure 12. Lower incisors from Moroto I and Moroto II attributed to *Nacholapithecus kerioi*. A) MOR II 1'07, right i/1, stereo views (A1 - lingual, A2 - labial, A3 - mesial and A4 - distal views); B) MOR I 60'06, right i/2 (B1 - mesial and B2 - lingual views) (scale : 10 mm).

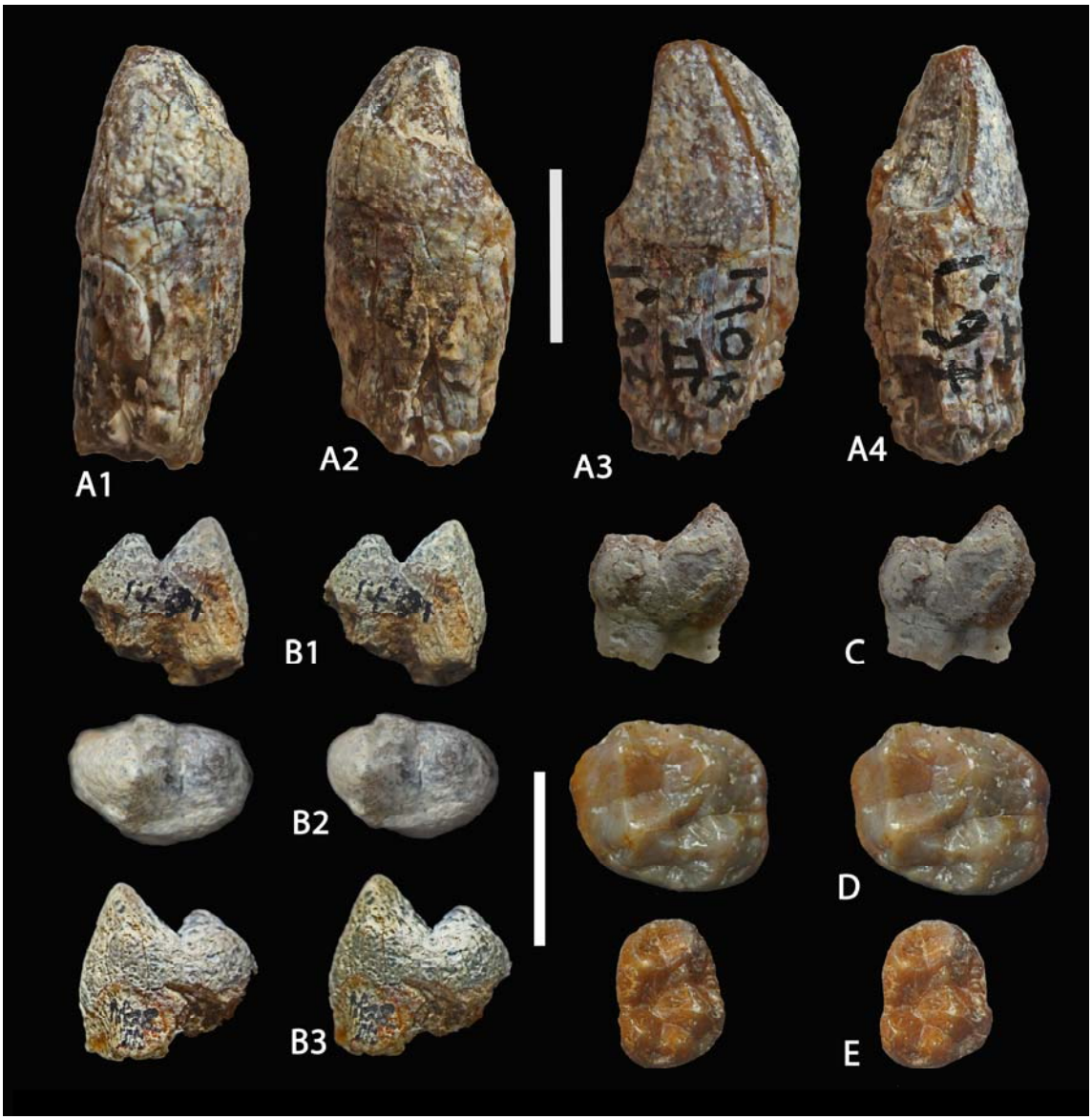

Figure 13. Isolated teeth from Moroto I and Moroto II attributed to *Nachalapithecus kerioi*. A) MOR II 1'97, left upper canine, probably female (A1 - labial, A2 - mesial, A3 - distal and A4 - labial views); B) MOR II 14'01, right P3/, stereo views (B1 - mesial, B2 - occlusal and B3 – distal); C) MOR 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).

The d/4, MOR I 22'11, is an unworn germ, lacking roots (Fig. 13E). It occludes well with the juvenile maxilla (MOR I 1'08, Fig. 11) 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, Fig. 13C) 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.

An upper canine, MOR II 1'97 (Fig. 13A) 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 (MOR 14'01, Fig. 13B) 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 mesial depression near cervix into which the root of the upper canine fits.

The M1/ from Moroto II (MOR 2'07, Fig. 13D) 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*.

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.

Holotype : MOR II 28'03, left m/2.

Paratypes : MOR II 27'03, left p/4; MOR II 29'01 right m/2; MOR II 10'03, left m/3 (probably the same indivisual as the holotype)

Additional material : see Table 4.

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 *Kogolepithecus morotoensis*, further screening at the discovery site has yielded additional teeth of the same individual (Fig. 14). The teeth that have already been described (Pickford *et al*., 2003) are the left p/4 (MOR II 27'03), left m/2 (MOR II 28'03, holotype) and left m/3 (MOR II 10'03) and the right m/2 (MOR II 29'03). 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).

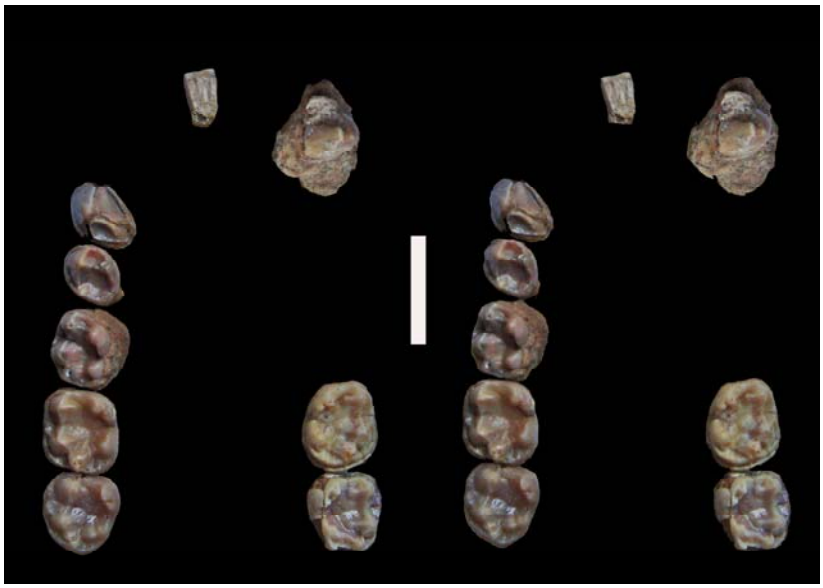

Figure 14. *Kogolepithecus morotoensis* holotype individual, stereo occlusal view of the ensemble of lower teeth (MOR II 63'04, left i/1; MOR II 21'04, right c/1; MOR II 3'04, left p/3; MOR II 27'03, left p/4; MOR II 1'04, left m/1; MOR II 28'03, left m/2; MOR II 29'03, right m/2; MOR II 10'03, left m/3; MOR II 2'04, right m/3 (scale : 10 mm).

The lower central incisor (MOR II 63'04) 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 central ridges.

The base of the lower canine (MOR II 21'04) 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 (MOR II 3'04) 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 (MOR II 1'04) is similar in morphology to the m/2 (MOR II 28'03) (Pickford *et al*., 2003) but is smaller.

The P4/ (MOR II 15'06) has two main cusps, a tall paracone and a lower protocone, accompanied by a tiny hypocone (Fig. 15). 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.

The M1/ (MOR II 2'05) has subequal protocone, paracone and metacone, and a slightly smaller hypocone (Fig. 15). 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.

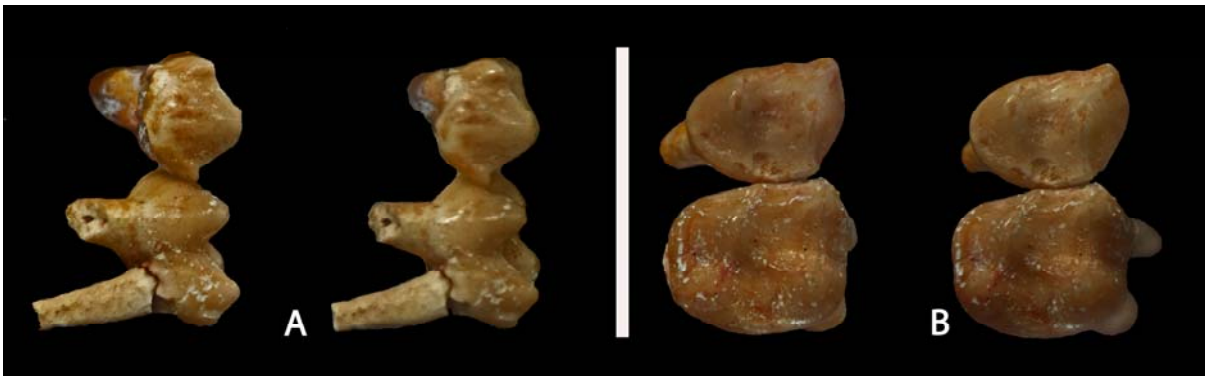

Figure 15. Left upper cheek teeth from the *Kogolepithecus* type locality, comprising the complete P4/ (MOR II 15'06) and M1/ (MOR II 2'05) shown here in A) stereo buccal and B) stereo occlusal views. The P4/ and M1/ occlude well with the holotype lower dental series (scale : 10 mm).

The 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* Fleagle & Simons (1978), *Limnopithecus* Hopwood (1933a, 1933b) and *Dendropithecus* Andrews & Simons (1977) 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 m/2, 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 : KNM 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* (Fig. 16). 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 valley with a v-shaped profile. The entoconid has a small accessory cusplet between it and the metaconid. The occlusal outline of the crown is elongated.

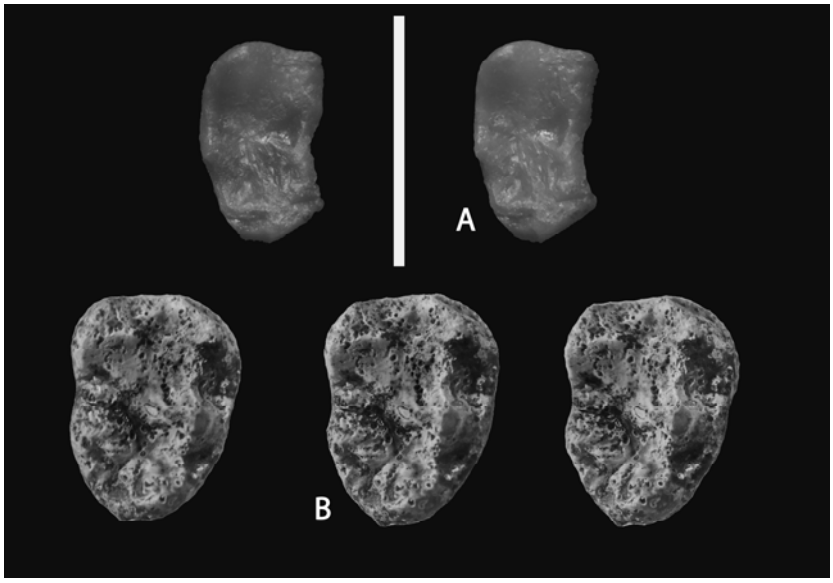

Figure 16. Lower teeth of *Simiolus enjiessi* from Moroto II. A) MOR II 35'05, damaged right m/2, stereo occlusal view of a cast; B) MOR II 2'15, right m/3, stereo triplet occlusal view (scale : 10 mm).

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 dimensions and the p/4 smaller. Lower second incisors have a distinct bend in the crown.

Holotype : MOR II 1'17, right p/3-m/3.

Paratypes : MOR II 2'14 (left and right i/1, right i/2, left and right canines, left p/3-m/2), MOR II 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 probably 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 Eyrie in Karamojong, 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. 4) 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 (MOR II 3'15, MOR II 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 (Fig. 17). 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 towards 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

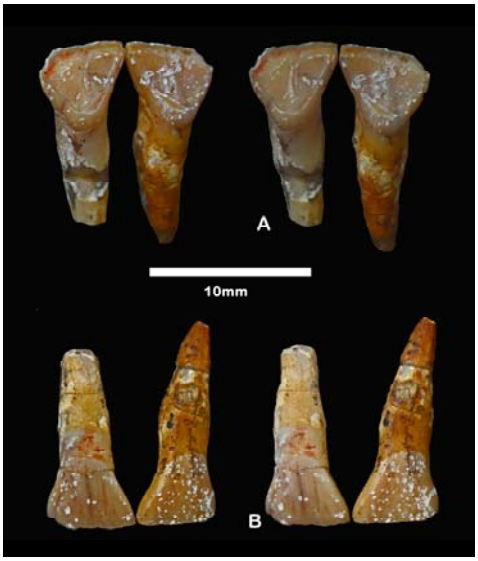

Figure 17. MOR II 3'15, left I1/ and MOR II 4'15, right I1/ of *Kalepithecus kogolensis* sp. nov. from Moroto II, A) stereo lingual and B) stereo labial views (scale : 10 mm).

The lower incisor battery from Moroto II is large relative to the dimensions of the cheek tooth rows (Fig. 18, 20). The central lower incisors have parallel mesial and lingual sides. The lingual surface is very lightly concave apically but becomes convex towards the cervix terminating 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 18. Upper and lower incisors of *Kalepithecus kogolensis* sp. nov. from Moroto II in approximate occlusal relationship. MOR II 3'15, left I1/, MOR II 4'15, right I1/, MOR II 2'14, left and right i/1s and lower canines, MOR II 5'15, left i/2 (A - labial view, 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 (Fig. 18, 20). 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 (Fig. 19, Table 7). It has a lingual cristid which descends from the main cusp disto-lingually. The right p/3 (Fig. 19) 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 (Fig. 19, 20) have tall protoconid and metaconid joined together 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/1 and m/2 are similar in occlusal morphology, but the m/2 is significantly bigger than the m/1 (Fig. 19). 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 protoconid and metaconid are obliquely positioned, such that the protoconid is more anteriorly positioned than the metaconid. As a result, the mesial fovea is slightly obliquely 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.

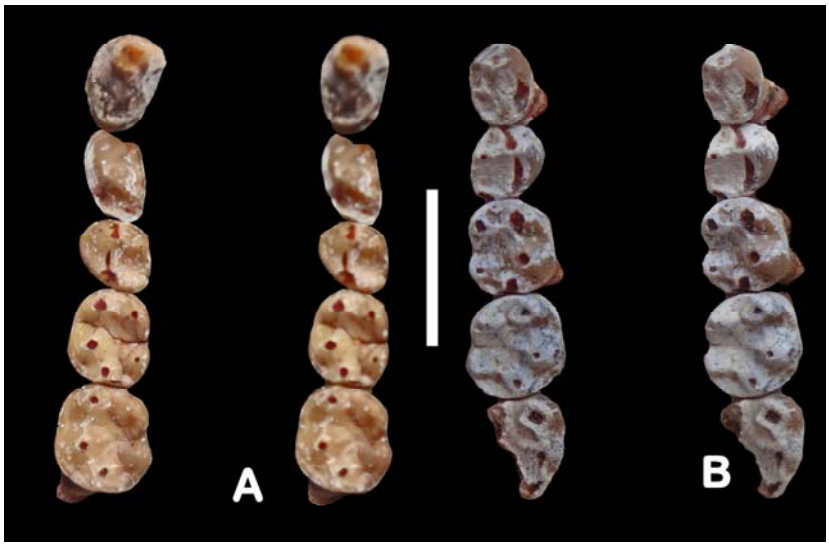

Figure 19. Stereo occlusal views of the post-canine mandibular dentition of *Kalepithecus kogolensis* sp. nov. from Moroto II. MOR II 2'14, left canine and p/3-m/2, MOR II 1'17 right p/3-m/3 (scale : 10 mm).

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 buccally positioned (Fig. 19, 20).

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 20. Stereo occlusal view of the reassembled lower dentition of *Kalepithecus kogolensis* sp. nov. from Moroto II. MOR II 2'14, left and right i/1s, lower canines, and left p/3-m/2, MOR II 5'15, left i/2, MOR II 1'17, right p/3-m/3 (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).

Note on the generic status of «*Micropithecus*» *leakeyorum*

At the time of the creation of the species *Micropithecus leakeyorum* for the Maboko small hominoid, Harrison (1989) noted that it differed in some features from the type species *Micropithecus clarki*, but that the hypodigms available were insufficient for the erection of a new genus for the material from Maboko. The same author (Harrison, 2010b) discussed the issue, mainly because Gitau & Benefit (1995) wrote that the Maboko fossils belonged to *Simiolus*. He concluded that «*Once the undescribed material from Maboko is fully analyzed, and the relationships between the taxa included in* Micropithecus *and* Simiolus *have been carefully and critically reassessed, it may prove necessary to*

designate a distinct genus for the species from Maboko». For this reason we employ the combination «*Micropithecus*» *leakeyorum* with quotation marks round the genus name.

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 (Fig. 21). At the level of the m/3 the mandible is twice as 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).

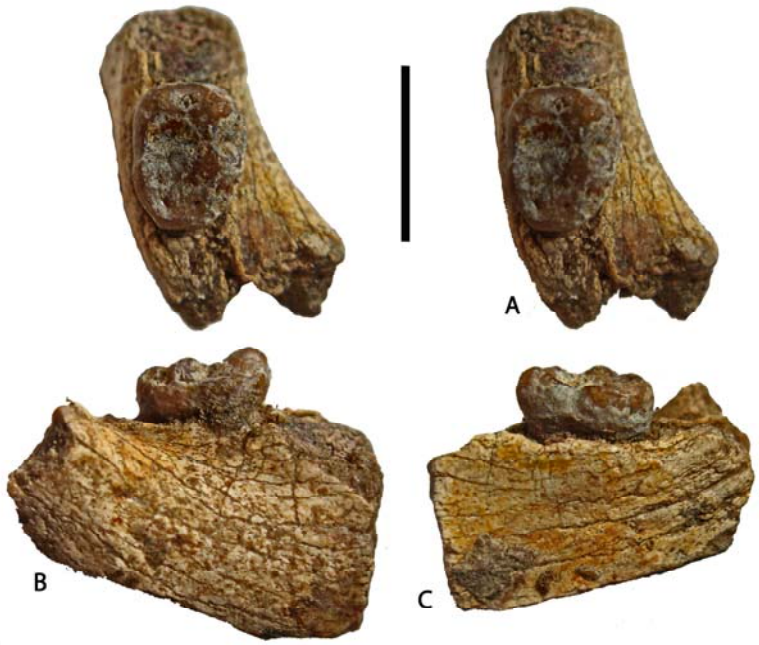

Figure 21. Moroto II specimen attributed to «*Micropithecus*» *leakeyorum*. MOR II BD 1'07, right mandible fragment containing m/3, A) stereo occlusal view, B) buccal view, C) lingual view (scale 10 mm).

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 the one 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 breadth 6.6 x 5.5 mm) (m/2 is 5.8 x 5.3 in the Chamtwara specimen).

MOR II 20’04 is an isolated, unworn left lower molar (Fig. 22) 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 buccal side of the crown.

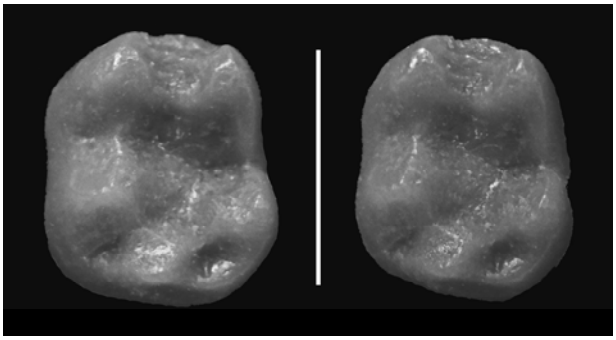

Figure 22. MOR II 20’04, left m/2 from Moroto attributed to «*Micropithecus*» *leakeyorum*, stereo occlusal view of a cast (scale : 5 mm).

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

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
MOR II 20’04	left lower molar	5.4	4.9
MOR II BD 1’07	m/2 right roots	6.6e	5.5e
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 in bivariate measurement plots it falls close to the m/2 of the larger species defined at Maboko, «*Micropithecus*» *leakeyorum* (Harrison, 1989) (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 deeply incised honing facet on the disto-labial side, cutting slightly into the root beneath the cervix, indicating that it is probably from a male individual (Fig. 23). 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 23. 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 (Ward, 1998). 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 fundamentally from both *Afropithecus* and *Ugandapithecus*.

Deane (2017) discussed the anterior dental arcade of simians and concluded that the Moroto snout does not represent the same species as *Afropithecus turkanensis*, and probably not the same genus, because the premaxillary dental arcades of these two apes appear to be different. However, the supposed differences between the morphology of the anterior dental arcade geometry of *Afropithecus turkanensis* and «*Morotopithecus bishopi*» are minimal, and have been exaggerated by two non taxonomic factors :- 1) the premaxillary arcade in «*Morotopithecus*» was altered during the life of the individual as a result of bone remodelling due to the presence of an abcess at the root of the right I2/ (which was lost during life) as described by Pickford (2002). One effect of this bone remodelling was to broaden out the anterior part of the snout. 2) The snout of *Afropithecus turkanensis* in contrast, is bilaterally compressed, severely at the level of the M3/ and less at the canines, but the fact that the left upper central incisor has been imbricated slightly dorsally and labially over the right upper central incisor, means that the anterior dental arcade appears to be narrower than it would have been in life. The combination of a teratogenically broadened arcade in «*Morotopithecus*» and a taphonomically narrowed arcade in *Afropithecus* is thus contributing to a misleading assessment of the taxonomy of these two specimens. In addition, the fact that the Moroto snout is of a fully mature individual (M1/s with large dentine exposures) and the Kalodirr individual is a young adult (no dentine exposure in the M1/s) could also be contributing to the supposed differences in premaxillary dental arcade curvature. In other respects, the minor differences in the osteology and odontology of the Kalodirr and Moroto snouts fall within the types of variation observed in extant ape species, which indicates that the two fossil snouts likely represent a single species, as was already concluded by Pickford (2002), Patel & Grossman (2006) and Harrison (2010b).

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 association of *Afropithecus turkanensis* and *Simiolus enjiessi* suggest correlation to FS IIIa (core fauna Buluk), whereas the association of *Nacholapithecus kerioi*, «*Micropithecus*» *leakeyorum* and *Simiolus enjiessi* invite correlation to FS IIIb (of which the core fauna is Maboko). The Middle Miocene locality of Maboko, Kenya, has yielded «*Micropithecus*» *leakeyorum* (Maboko is the type locality) as well as *Simiolus enjiessi* (Benefit, pers. comm, Gitau & Benefit, 1995) a combination which indicates that the site is similar in age to Moroto, from which we conclude that the age of the Moroto deposits is close to the transition between FS IIIa and FS IIIb, i.e. ca 16±0.5 Ma, considerably younger than the age (20-19.6 Ma) estimated by Gebo *et al*. (1997) and Werdelin (2010).

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 reasonably well with samples from Kalodirr, Moruorot, Nachola, Maboko and Kipsaraman. On the basis of faunal similarities, we correlate Moroto I and Moroto II to East African Faunal Set III (Pickford, 1983). The composition of the fauna suggests that Moroto lies close to the boundary between FS IIIa (core fauna Buluk 18-16 Ma, Werdelin, 2010) and FS IIIb (core fauna Maboko, 15-14 Ma, Werdelin, 2010) from which we deduce an age range for the Moroto deposits of ca 16±0.5 Ma, which is basal Middle Miocene in the scheme of Ogg *et al*. (2016).

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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