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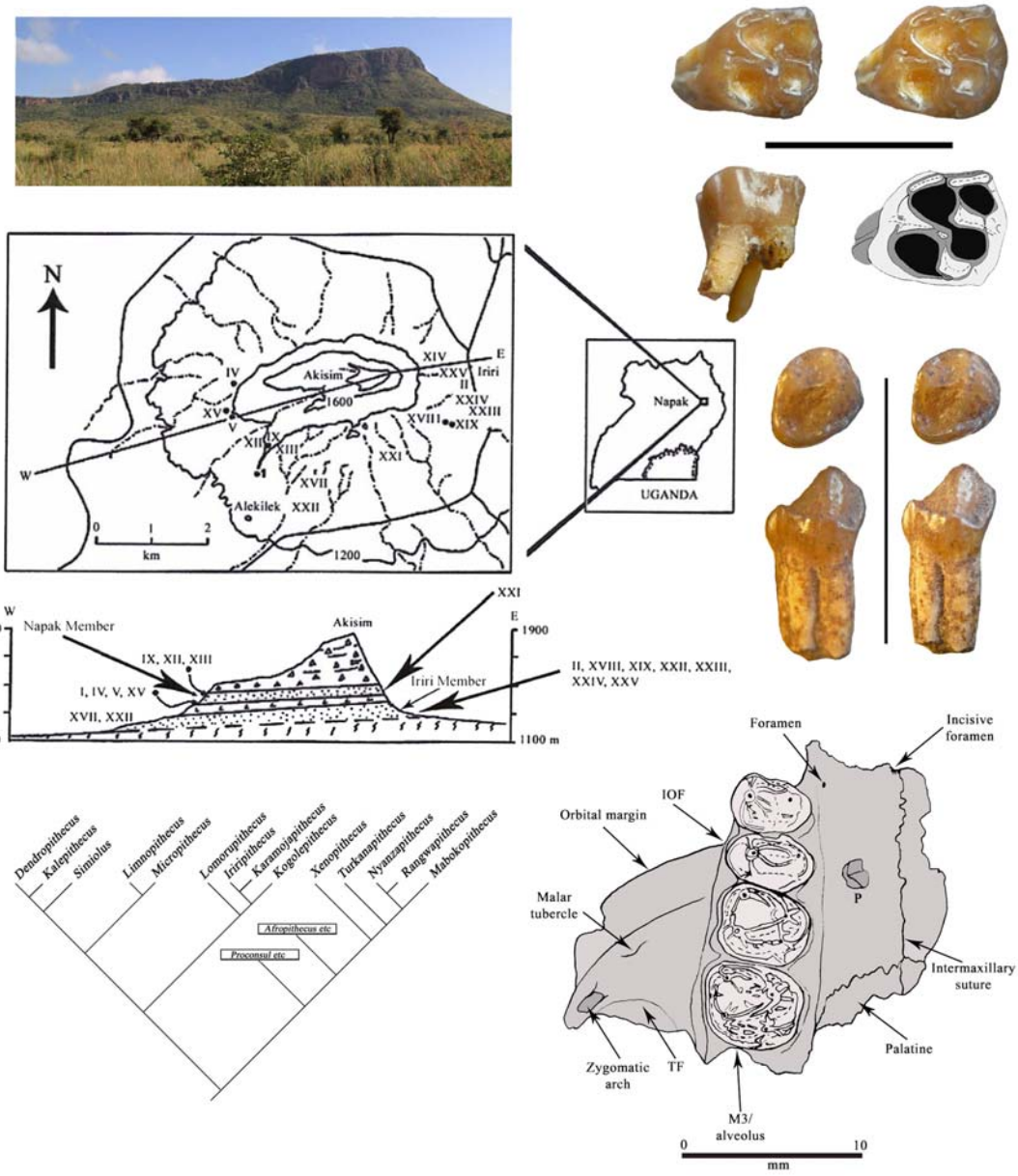

Uganda Museum, Kampala

Geo-Pal Uganda

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Uganda Museum, P.O. Box 5718, Kampala, Uganda

Small Apes from the Early Miocene of Napak, Uganda

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ABSTRACT

The sample of small hominoid dento-gnathic fossils from Napak, Uganda, has risen from 46 specimens in 1968 to 158 in 2010. Small ape post-cranial bones, of which many have been collected, will be treated in a separate paper. This improvement in the fossil record allows the resolution of some of the difficulties that scientists have experienced in their interpretations of the Napak hominoids. Four main points emerge from this study.

The first is that neglect of the holotype of *Limnopithecus legetet*, which got relegated to an insignificant role in all interpretations of East African small apes from 1951 onwards, has far-reaching effects on the interpretations of these apes. From 1952 until this study, another mandible, KNM KO 8, has replaced it as the reference specimen by which attributions of other fossils were decided, in contravention of the international code of zoological nomenclature. Eventually, even the diagnosis of the species was based on this specimen, with the result that the holotype of the species no longer fits the diagnosis. Restudy of the holotype of *Limnopithecus legetet* reveals that it is similar to mandibles subsequently attributed to *Micropithecus clarki* and the paratype of *Lomorupithecus harrisoni*. This means that *Micropithecus* may fall into synonymy with *Limnopithecus*, but because fossils from Napak are smaller than those from the Koru area, the Uganda fossils belong to a different species, *Micropithecus clarki*, the holotype of which is a palate, and therefore not directly comparable to the type specimen of *Limnopithecus legetet*. Until the fossil record of both these taxa improves, we retain the two genera. The Chamtwara and Legetet fossils previously attributed to *Micropithecus clarki* by Harrison (1982, 1988) are transferred to *Limnopithecus legetet*. This leaves the bulk of fossils similar to KNM KO 8, hitherto called *L. legetet*, without a name.

The second point to emerge from this study is that the Napak small ape assemblage contains some taxa that have not previously been recorded from the much richer Kenyan Early Miocene sites, which explains, to some extent, why previous authors have experienced difficulties interpreting them. These include two new genera, as well as new species of *Dendropithecus* and *Turkanapithecus*, although it needs to be pointed out that, although *Turkanapithecus* has not been reported from Western Kenya, it is indeed present there (Mfwangano, Rusinga and Songhor), its remains having been misattributed to *Dendropithecus*, *Rangwapithecus*, *Nyanzapithecus*, and even to *Proconsul*. Five genera are common to Napak and Western Kenya : *Limnopithecus* (as here reinterpreted), *Kalepithecus*, *Dendropithecus*, *Turkanapithecus* and *Lomorupithecus* (we consider that *Lomorupithecus harrisoni* is a junior synonym of *Limnopithecus evansi* : the combination we use is *Lomorupithecus evansi*) and there are some taxa that are present in Kenya but which are absent from Napak (*Rangwapithecus gordoni*, *Nyanzapithecus*

vancouveringorum, and other species of *Nyanzapithecus*). Likewise, *Simiolus* is not represented among the Napak fossils, but may be present at Moroto II, and it is present at Kipsaraman (*Simiolus cheptumoae* Pickford & Kunimatsu, 2005) and Fort Ternan, Kenya (*Simiolus andrewsi* Harrison, 2010).

Third, the distribution of small apes in East Africa speaks of local to regional environmental diversity during the Early Miocene, with Napak possibly lying in a more seasonal, more arid, palaeoclimatic belt (woodland-forest mosaic on the slopes of a volcano) than the sites at Koru (humid tropical forest) and Songhor (drier tropical forest).

Fourth, with the recognition of *Turkanapithecus* and *Simiolus* in Early Miocene sites in the Winam Rift and the Tugen Hills, Kenya, and *Kalepithecus* at Napak, previous assessments of the biogeography of the small hominoids in East Africa need to be re-examined. The perception of the existence of major differences between the small ape faunas of Western Kenya and the Turkana Basin, Northern Kenya, is rendered less divergent by the new identifications.

Key Words : Hominoidea, Small apes, Uganda, Early Miocene, Systematics, Taxonomy

INTRODUCTION

During the 1950's and 1960's, the fossiliferous volcano-sedimentary deposits at Napak, Uganda, yielded 46 dento-gnathic specimens of small apes (Andrews, 1978, 1980; Bishop, 1964; Fleagle, 1975; Fleagle & Simons, 1978; Harrison, 1981, 1982, 1988; Leakey, 1958, 1962; Pilbeam & Walker, 1968; Simons & Delson, 1979) comprising mainly isolated teeth, but there were four mandible fragments containing two or more teeth, and a snout containing almost complete cheek tooth rows.

The early studies of the Napak material, prior to the mid-1970's, were hampered by several factors. Firstly, there was, in general, a poor understanding of the diversity of small apes in the Kenyan fossil record, the only sample with which the Uganda assemblage could be compared – until that time, most authors severely underestimated the number of genera and species of such apes, and for many years all material was lumped into two species, *Limnopithecus legetet* for small material and *Limnopithecus macinnesi* for larger specimens (Le Gros Clark, 1952; Le Gros Clark & Leakey, 1951). The latter species was renamed *Dendropithecus macinnesi* by Andrews & Simons, 1977.

Secondly the stratigraphic succession of East African Early Miocene faunas was poorly understood, with the result that faunas which were in reality widely separated in time, were generally thought to be contemporaneous, an "a priori" that fed back to support the "lumping" of fossil taxa together.

Thirdly, even from Kenya, there was a paucity of fossil specimens in several of the taxa.

Fourthly, there was a lack of associated upper and lower dentitions (*Limnopithecus macinnesi* (now *Dendropithecus macinnesi*) was the only exception) and it was in cases difficult to determine the meristic position of isolated teeth, especially first and second molars. A few upper deciduous fourth molars (DM4/) were misidentified as permanent teeth and vice versa.

Fifthly, for many years taxonomic decisions had been heavily influenced by dimensions rather than by morphology (Andrews, 1978) and there was a great deal of misunderstanding concerning the degree of sexual dimorphism in hominoids (Simons & Pilbeam, 1965; Pickford & Chiarelli, 1986). There has also been a certain amount of shuffling of specimens between taxa, as explained by Pickford, 1986b, and quite a few non-primate specimens have been misidentified as hominoids.

Sixth, and most troubling for this and previous studies, is the moderate wear on the teeth of the holotype of *Limnopithecus legetet* Hopwood (1933a, 1933b) although it is by no means a hopeless fossil, the main morphological features of the m/1 and m/2 being clear. But because of the wear and slight damage that the crowns have suffered, reference has usually been made to other specimens

thought to belong to the species (KNM KO 8, from Koru; KNM SO 385, 386, 387, and 444 from Songhor, and other specimens (see Le Gros Clark, 1952; Harrison, 1982, 1986; Leakey & Leakey, 1987). However, close examination of the type material reveals that it differs radically in morphology from all material subsequently attributed to *Limnopithecus legetet*, which evidently represents a distinct species and even genus.

There has been a tendency to issue composite descriptions and interpretations of small hominoids from East Africa, and to attribute isolated teeth and dentognathic fragments to taxa despite differences in morphology from the holotype. Whilst this is completely understandable as the focus has been on taxonomy and phylogeny, it means that there is a lack of detailed description and iconography of all the available specimens. This makes it difficult for researchers to make comparisons unless original fossils or good casts can be accessed, and it makes it impossible to verify the sorting of the fossils into taxa. It is quite clear from the fossils and casts that we have been able to examine that there is a serious problem with attribution of fossils to taxa. For example, in the monograph on the large Kenyan hominoids by Andrews (1978) 10% of the fossils attributed to apes are not primate and a significant proportion of material identified as *Proconsul* has subsequently been rejected from it (Bosler, 1981). These non-primate specimens include suids, hyracoids, and even a fish tooth. It is also evident that almost every hominoid taxon has been assigned fossils that do not belong to it. *Dendropithecus macinnesi*, for example, contains fossils that are closer to *Turkanapithecus* than to *Dendropithecus*, and there is even a specimen of *Turkanapithecus* from Rusinga previously identified as *Proconsul africanus* (Andrews, 1978). For this reason, we adopt a different approach for the Napak small apes, describing and illustrating every available specimen. Thus, even if we make an incorrect attribution of a fossil to a taxon, the reader is enabled to judge for himself from the illustrations, measurements and descriptions that we provide, whether the attribution is valid or not. We arrange the Napak fossils by taxonomic group, but fully realise that there may well be some re-sorting of fossils by our colleagues, an inevitable outcome considering the fragmentary nature of many of the fossils.

We have been fortunate to find specimens in which several teeth are associated. For example we have found the first maxilla *Micropithecus clarki* in which the upper canine is *in situ* along with the P3/ and P4/. This specimen reveals that some of the previous attributions of canines from Napak are incorrect. We also found the first mandible fragments confidently attributed to *Micropithecus clarki* with both premolars and the canine alveolus, allowing the confident attribution of lower canines to this species. We also found mandible fragments with two molars, which clearly belong to taxa that are larger than *Micropithecus clarki*.

During the late 70's and early 80's some of the drawbacks to the study of the East African small hominoid fossil record were cast aside by a new generation of students, who not only collected a great deal of additional fossil material, but also re-examined the geological context of the fossils, determined their ages and based their taxonomic studies on a combination of morphological and metrical data, carried out within a more realistic biological framework which took into account the main factors responsible for variation within populations (individual variation, sexual dimorphism, ontogenetic changes, evolutionary changes over geological time spans, taphonomic factors affecting preservation). In addition, palaeoecological studies were undertaken, which permitted the visualisation of the palaeoenvironments in which the faunas lived. The outcome of all this activity over the past four decades, has been a revised understanding of the faunas, especially of their taxonomy, biochronology and palaeoenvironments. Nevertheless, several problems persist, especially with the genus *Limnopithecus*, of which the holotype of the type species is a fragmentary mandible containing two damaged molars (Hopwood, 1933b).

Phylogenetic studies were pursued during the past three decades, with cladistics playing a predominant role, but the proposals published by the various authors who focused on this approach have varied tremendously, resulting in extended debates from which little consensus has emerged. Atomisation of characters has led to atomisation of phylogenetic trees, with the proposal of numerous named branching points about which there is almost no consensus in the literature (Begun, 2007; Harrison, 2010) (see Table 16). The presence of chimaeras in the "species" being analysed also poses an

insurmountable problem for this and other kinds of analyses, as do uncertainties about the taxonomic identification of much of the material.

Detailed geological mapping and biostratigraphic studies (Pickford, 1981) carried out in Western Kenya, allied to the application of radio-isotopic dating to the deposits (Pickford, 1998, and references therein) led to the realisation that the so-called "Lower Miocene" faunas of Kenya, which for more than 40 years had been thought to comprise a unit fauna, in reality consisted of an inhomogeneous suite of faunas which changed strongly over time. The arrangement of the faunas from the sites in their chronological order led to the establishment of the East African land mammal zonation, known as Faunal Sets (Pickford, 1982, 1986a, 1986c, 1986d, 1998). The Napak sites belong to Faunal Set I (FS I : core fauna Songhor), NAP V, IX and XV being late in the set, close to the base of FS II, the core fauna of which is Rusinga.

MATERIALS AND METHODS

The bulk of the fossils described here are housed at the Uganda Museum, Kampala. Reference has been made to collections of casts and original fossils housed at the Natural History Museum, London, and the Institute of Primate Research, Kyoto University, Inuyama, Japan. Measurements were made with sliding calipers to the nearest tenth of a mm. Images of fossils were made with a Sony Cybershot Digital Camera, either attached to a binocular microscope or free, the resultant images enhanced, cropped and contrasted using Photoshop Elements 3. Scales were added to the images after processing, as it has been found that scales included in images at the time of taking them are often incorrect due to the frustrum effect and parallax. Where necessary, images of casts are included, as they sometimes show the morphology more clearly, especially if the original fossil is dark. Simplified interpretive drawings of key specimens have also been prepared.

The nomenclature of tooth cusps, basins, grooves and crests is provided in Figs 1 to 6.

Abbreviations are as follows:- BAR – Baringo, fossil housed at the Orrorin Community Organisation (OCO), BUMP – Boston University–University of Makerere Palaeontology, KNM – Kenya National Museum, KO – Koru, M followed by a number – Natural History Museum, London, Ma – millions of years (Mega-annum), MW - Mfwangano, NAP – Napak, RU – Rusinga, SO – Songhor, UMP – Uganda Museum Palaeontology.

Abbreviations applied to the teeth are as follows :- capital letters followed by the position and a forward slash denote upper teeth (12/, C1/, P3/, DM4/, M2/, for incisor, canine, premolar, deciduous molar, permanent molar respectively), and lower case letters followed by a forward slash and then the position denote lower teeth (i/1, c/1, p/3, dm/4, m/3, for incisor, canine, premolar, deciduous lower molar and permanent lower molar respectively). Measurements are MD – mesio-distal length, BL – bucco-lingual breadth, Ll – labio-lingual breadth.

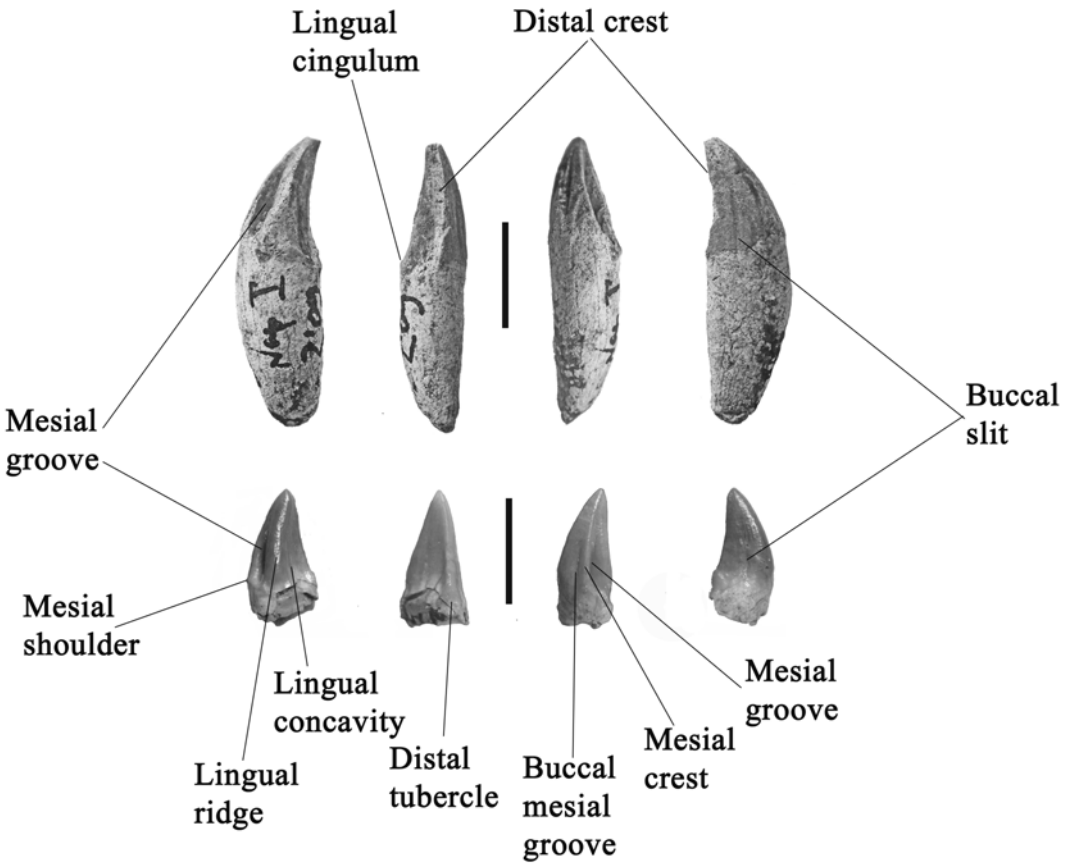

Figure 1. Nomenclature of hominoid upper canines, using NAP I 2'09 left C1/, upper frame from left to right, lingual, distal, mesial and buccal views) and NAP IV 14'07 left C1/, lower frame from left to right lingual, distal, mesial and buccal views. (Scales : 10 mm).

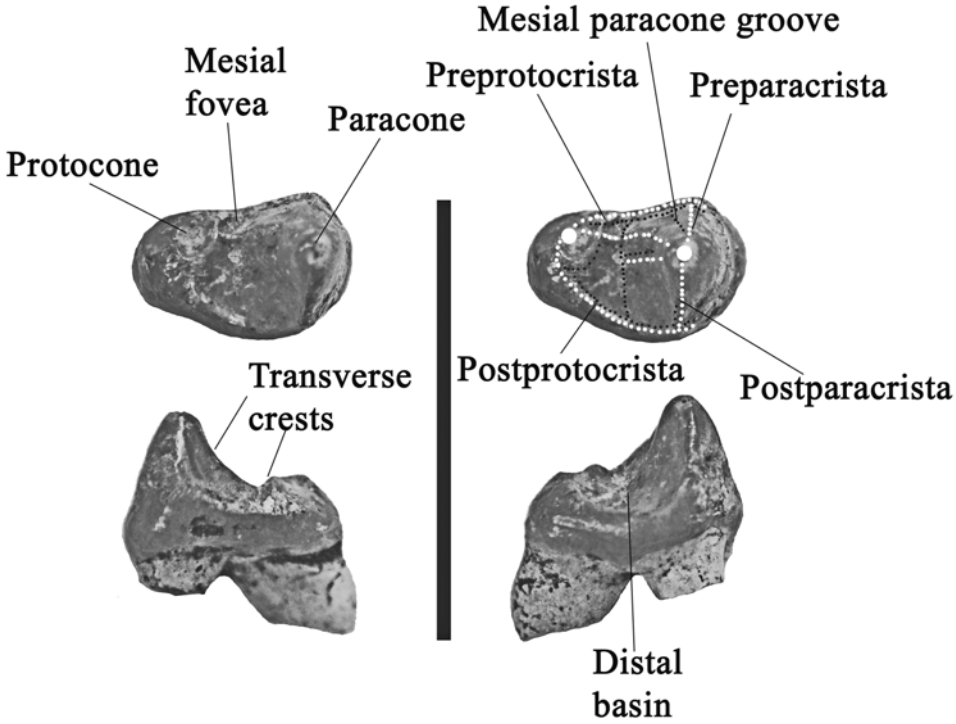

Figure 2. Nomenclature of hominoid upper P3/s, using stereo occlusal images of NAP XV 36'08 left P3/ (top row stereo occlusal view; second row from left to right, mesial and distal views). (Scale : 10 mm).

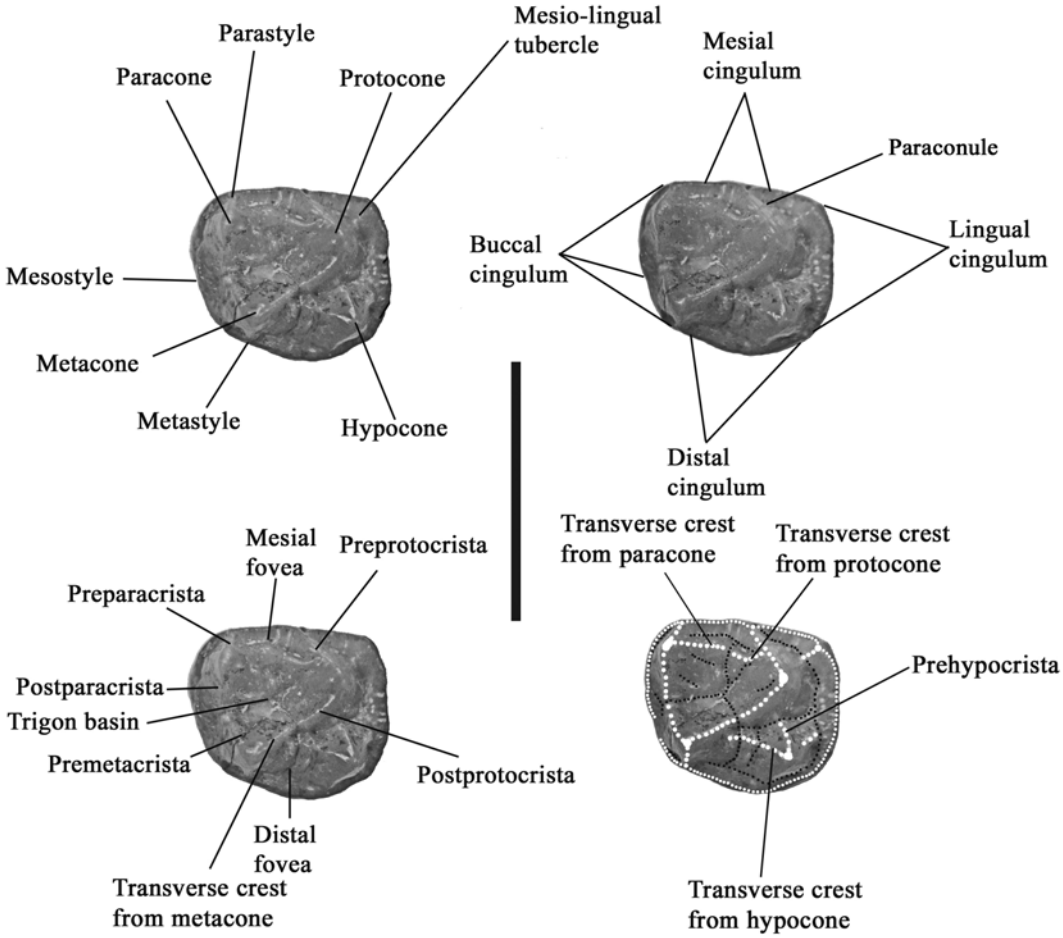

Figure 3. Nomenclature of cusps, basins, grooves and crests in hominoid upper molars (right) based on NAP XV 101’08, stereo occlusal images (crests – white dots; grooves - black dots). (Scale : 10 mm).

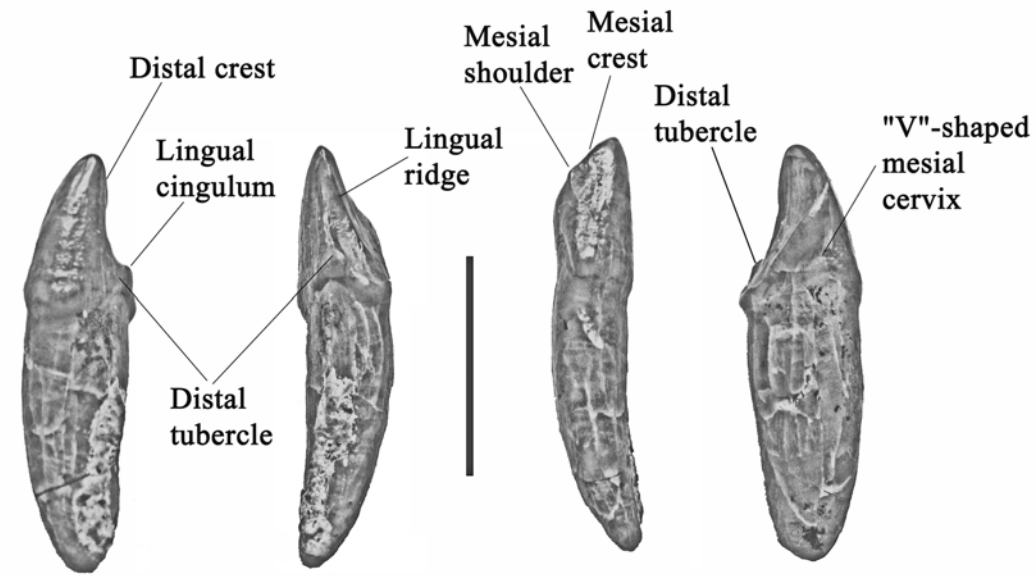

Figure 4. Nomenclature of hominoid lower canines based on NAP V 6’85, left c/1, from left to right, buccal, distal, mesial and lingual views. (Scale : 10 mm).

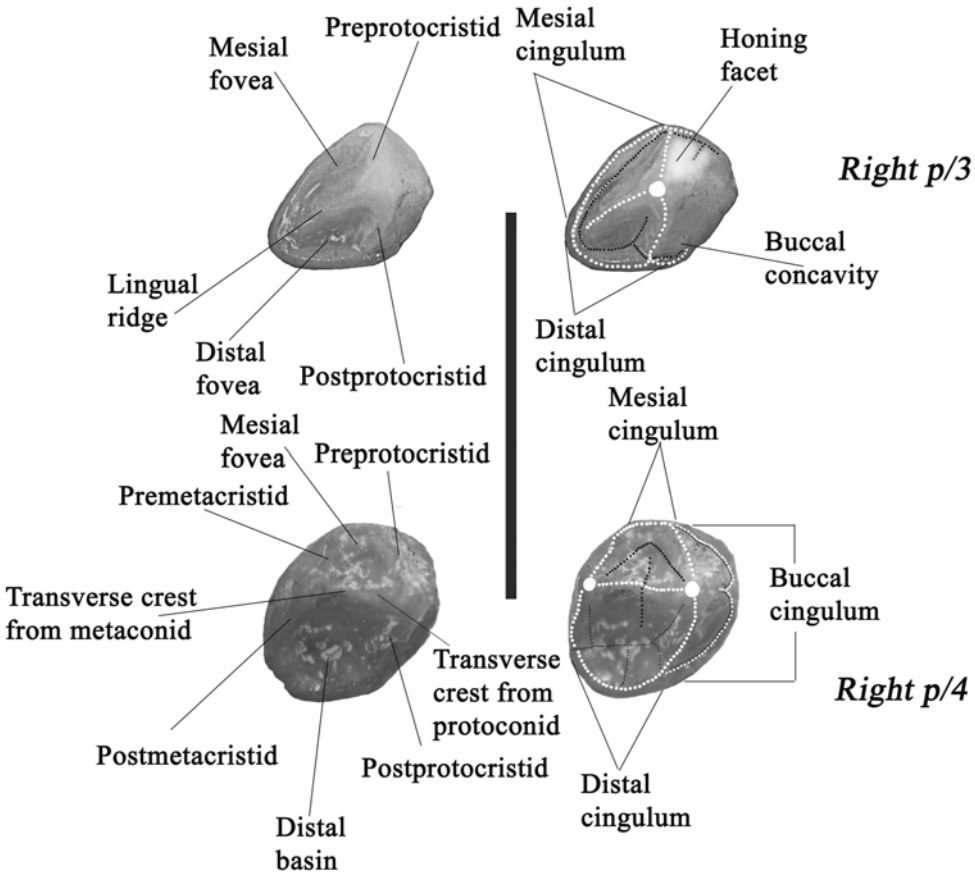

Figure 5. Nomenclature of hominoid lower premolars based on NAP IV UMP 66-05, right p/3 upper frame, and NAP IV 27'99, right p/4 lower frame, stereo occlusal images. (Scale : 10 mm).

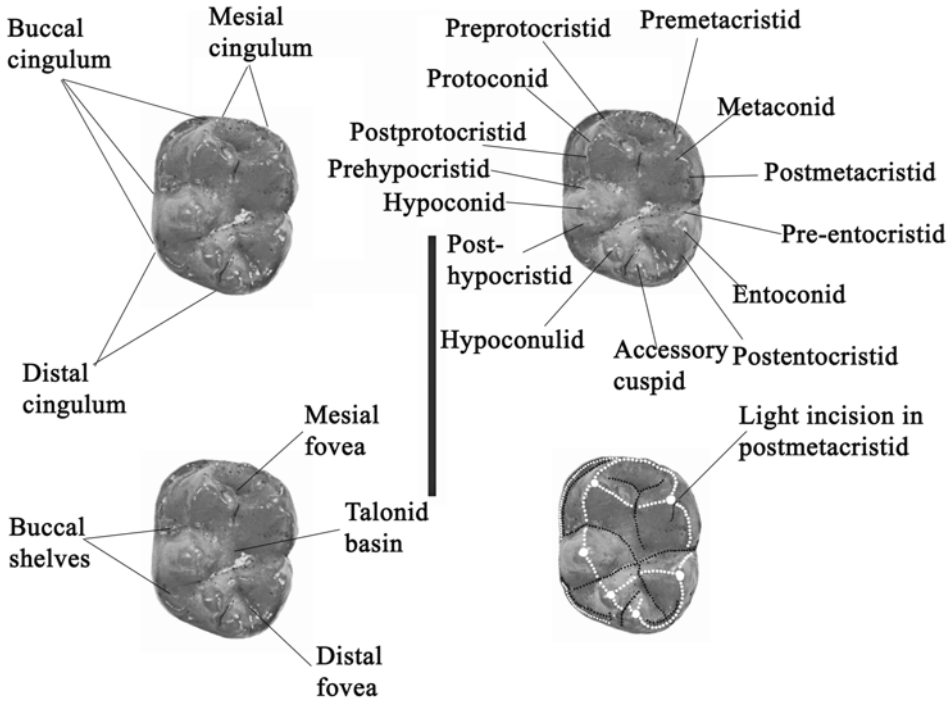

Figure 6. Nomenclature of cusps, basins, grooves and crests in hominoid lower molars based on NAP XV 183'08, stereo images of unworn left lower molar (crests – white dots; grooves - black dots). (Scale : 10 mm).

GEOLOGY AND STRATIGRAPHY

Small ape fossils have been collected from volcano-sedimentary deposits and palaeosols exposed at several sites on the slopes of the remnant of Napak Volcano known as Akisim (Bishop, 1962) (Fig. 7-8). The fossils come from the Napak Member (Pickford *et al*., 1986) which overlies a nephelinite lava flow that forms a prominent bench in the southern, western and northern flanks of the hill. NAP I, NAP IV and NAP CC are a few metres above the lava flow, whereas NAP IX, NAP V and NAP XV are higher in the sequence, ca 15–30 metres above the lava flow. NAP XII is at the same level as NAP IX, but NAP XXI may well be stratigraphically beneath the nephelinite lava, and thus the oldest hominoid-bearing deposits in the region (Figs 9-15).

Pickford (2002) demonstrated that the tragulid faunas from the various sites at Napak were not homogeneous, those near the base of the member containing only the species *Dorcatherium songhorensis*, whereas the upper levels yield *Dorcatherium parvum*, *Dorcatherium piggoti*, and *Dorcatherium iririensis*. On this basis, it was concluded that the lower levels of the Napak Member correlate to the sites of Songhor, Koru, and Legetet in Kenya (ca 19.5 Ma)(Pickford, 1981), whereas the upper levels are younger, being closer in age (ca 18.5 Ma) to Rusinga (17.8 Ma)(Drake *et al*., 1988).

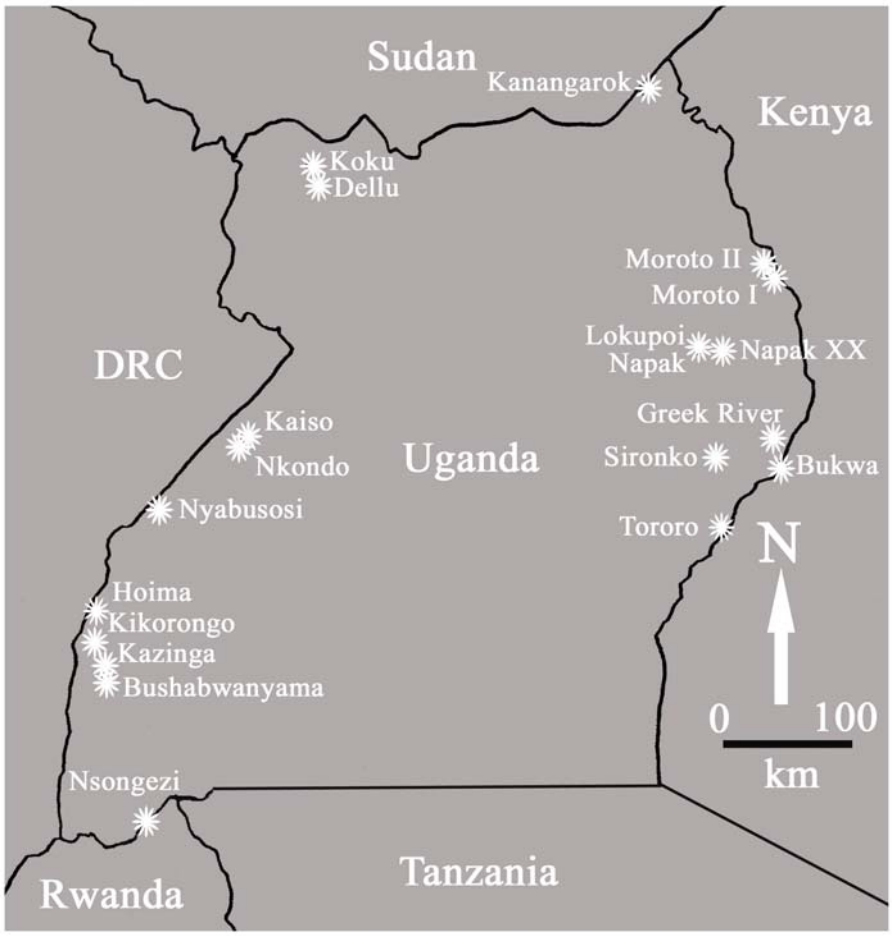

Figure 7. Neogene and Quaternary fossiliferous localities of Uganda (several areas contain sediments of diverse ages).
Pleistocene – Hoima, Lokupoi, Kanangarok, Kikorongo, Nsongezi, Nyabusosi, Tororo.
Pliocene – Bushabwanyama, Kaiso, Kazinga, Nyabusosi,
Late Miocene – Dellu, Koku, Nkondo, Nyabusosi
Middle Miocene – Moroto I, Moroto II
Early Miocene – Bukwa, Greek River, Napak, Napak XX, Sironko

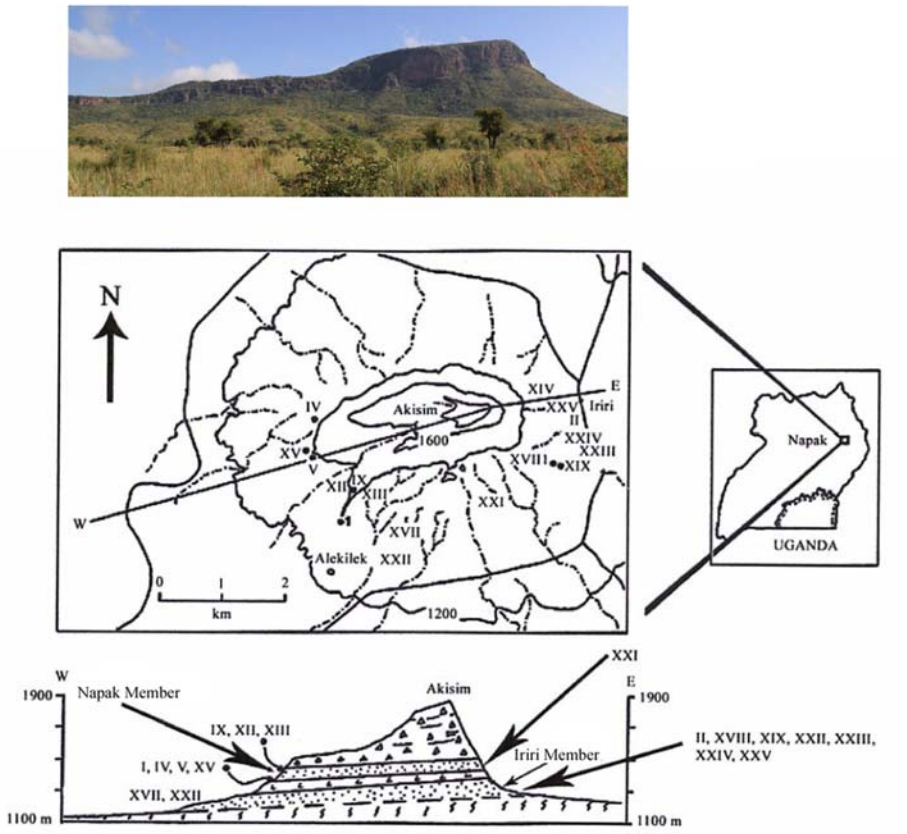

Figure 8. The remnant of Napak Volcano known as Akisim, where all the fossils described herein were found (NAP I, IV, V, IX, XIII, XV, XXI).

Figure 9. View from the southwest towards the Akisim remnant of Napak Volcano, with the cliffs of Alekilek in the foreground. Napak I is the pale grassy area on the ridge to the left of Alekilek.

Figure 10. Napak I, southern slopes, with Napak IX and Napak XIII in the background (2010).

Figure 11. Napak IV, Karamoja, Uganda, in 2007, the most prolific of the Early Miocene fossil localities.

Figure 12. Napak V, Karamoja, Uganda, in 2007. This site has yielded abundant remains of *Ugandapithecus* and small apes, including key specimens of *Micropithecus clarki*.

Figure 13. Napak IX and Napak XIII, Karamoja, 2010. Napak IX is the crest of the ridge beneath the steep cliffs, Napak XIII is the steep grassy slope to the right of the cliffs.

Figure 14. Napak XV, an important fossil site found in 2007, which has yielded abundant and varied hominoid fossils. This image was taken soon after the discovery, and shows the team clearing the grass in order to expose the sediments.

Figure 15. Napak XXI (2010) where a partial skeleton of a tragulid was recovered, along with a high diversity of seeds, snails and a tooth of *Micropithecus clarki*. Napak Mountain in the background.

NAPAK PALAEOPRIMATOLOGY

Fleagle (1975; Fleagle & Simons, 1978) published the first substantial studies of the Ugandan small apes, during which the new taxon *Micropithecus clarki* was erected. These authors recognised that, in the sample available from Napak at that time, there were a few specimens that probably belonged to other taxa (UMP 66-14 and UMP 66-16 which they attributed to *Limnopithecus legetet*, and UMP 62-19 which was listed as an unknown taxon). Pickford *et al*., 2009, dealt with the abundant remains of *Ugandapithecus* that have been found at the same sites.

Andrews (1978, 1980) focussed his research on the Miocene fossil apes from Kenya, and created the genus *Dendropithecus* (Andrews & Simons, 1977) for the species *L. macinnesi*, initially concluding that it was a Hylobatidae (Andrews, 1978) but subsequently classifying it within Pliopithecidae (Andrews, 1980).

The Western Kenya Project, led by one of the authors (MP) from 1976-1984, collected over 350 dento-gnathic specimens of small apes from Koru, Legetet, Chamtwara and Maboko, which comprised the basis for a PhD Thesis by Harrison (1982). This much expanded sample of small apes from Western Kenya provided a more secure foundation from which to make comparisons, but there remained several problematic areas, such as the lack of associated upper and lower dentitions, and a relatively weak appreciation of the degree of sexual dimorphism in these apes.

In Table 1 we summarise the history of identification of the Bishop collection of small hominoids from Napak.

Table 1. Successive identifications of the historical collection of small catarrhines from Napak, Uganda, and revised identifications in this paper. The improved fossil record has led to a better representation of several of the taxa, and has removed some of the doubt that was present in previously published interpretations. Nevertheless many of the identifications have proved to be resilient to change. (* - doubt expressed about the assignment).

Locality	Catalogue	Specimen	Identifications A - Andrews; B - Bishop; D - Delson; F - Fleagle; H - Harrison; L - Leakey; P - Pilbeam; S - Simons; W - Walker	This paper
NAP IV	M 36371	Left P3/	*Dendropithecus macinnesi*, H. 1982, 1988 (as a p/3)	*Ugandapithecus meswae*
NAP I	UMP 62-17	Right mandible	*Limnopithecus* L.1958, 1962; *M. clarki*, F&S. 1978; anthropoid indet., H. 1982	*Limnopithecus legetet*
NAP IV	UMP 62-18	Left lower canine	*M. clarki*, F&S. 1978; anthropoid indet., H. 1982	*Micropithecus clarki*
NAP IV	UMP 62-19	Left lower molar	Hominoid indet., F&S. 1978; cf *Dendropithecus macinnesi*, H. 1982; *D. macinnesi*, H. 1988	*Iriripithecus alekileki*
NAP V	UMP 62-20	Left lower canine	*M. clarki*, F&S. 1978, H. 1982, 1988	*Limnopithecus legetet*
NAP V	UMP 62-21	Right upper molar	Cercopithecine, P&W. 1968; *Victoriapithecus* sp., S&D. 1979; H. 1982	*Victoriapithecus macinnesi*
NAP V	UMP 62-22	Mandibular symphysis	*M. clarki*? F&S. 1978; anthropoid indet., H. 1982	*Micropithecus clarki*
NAP IV	UMP 64-02	Snout	*Limnopithecus* sp., P&W. 1968; *M. clarki*, F&S. 1978, cf *L. legetet*, A. 1978; *D. clarki*, A. 1980; *M. clarki*, H. 1982, 1988	*Micropithecus clarki*
NAP IV	UMP 66-05	Right p/3	*M. clarki*, F&S. 1978; *L. legetet*, H. 1981; anthropoid indet., H. 1982	*Dendropithecus ugandensis*
NAP IV	UMP 66-06	Right p/3	*M. clarki*, F&S. 1978; anthropoid indet., H. 1982	*Kalepithecus songhorensis*
NAP IV	UMP 66-07	Right mandible c/1-p/3	*M. clarki*, F&S. 1978; anthropoid indet., H. 1982	*Limnopithecus legetet*
NAP IV	UMP 66-08	Left m/1	*M. clarki*, F&S. 1978; H. 1982, 1988	*Micropithecus clarki*
NAP IV	UMP 66-09	Left M1/	*M. clarki*, F&S. 1978; H. 1982, 1988	*Micropithecus clarki*
NAP IV	UMP 66-11	Left M2/	*M. clarki*, F&S. 1978; H. 1982, 1988	*Limnopithecus legetet*
NAP IV	UMP 66-12	Right p/3	*M. clarki?* F&S., 1978; *L. legetet*, H. 1981; anthropoid indet., H. 1982	*Limnopithecus legetet*
NAP IV	UMP 66-13	Right m/3	Not primate, L. 1962; *M. clarki*, F&S. 1978; H. 1982, 1988	*Micropithecus clarki*
NAP IV	UMP 66-14	Left M2/	*L. legetet*, F&S. 1978; H. 1981, 1982, 1988	*Karamojapithecus akisimia*
NAP IV	UMP 66-16	Right m/1	*L. legetet*, F&S. 1978; H. 1981, 1982, 1988	*Lomorupithecus evansi*
NAP V	UMP 66-17	Left p/3	*M. clarki*, F&S., 1978; H. 1981, 1982, 1988	*Micropithecus clarki*
NAP V	UMP 66-19	Left C1/	*M. clarki**, F&S. 1978; H. 1982	*Limnopithecus legetet*
NAP V	UMP 66-20	Right DC1/	*M. clarki**, F&S. 1978; *Proconsul major*, H. 1982	*Ugandapithecus major*
NAP IX	UMP 66-23	Right mandible m/2-m/3	*Limnopithecus* sp. B. 1964; *M. clarki*, F&S. 1978; *M. clarki*? H. 1982; *M. clarki*, 1988	*Dendropithecus ugandensis*
NAP IV	UMP 66-24	Right I1/	*M. clarki*, F&S. 1978; Anthropoid indet., H. 1982	*Limnopithecus legetet*
NAP IV	UMP 66-25	Right dc/1	Anthropoid indet., H. 1982	Anthropoid indet.
NAP IV	UMP 66-25b	Left i/1	*M. clarki*, F&S. 1978; *L. legetet*, H. 1982, 1988	*Micropithecus clarki*
NAP IV	UMP 66-26	Right dI2/	Anthropoid indet., H. 1982	Anthropoid indet.
NAP IV	UMP 66-27	Right DC1/ ?	Anthropoid indet., H. 1982	Anthropoid indet.
NAP V	UMP 66-28a	Left M2/ fragment	*M. clarki*, H. 1982, 1988	*Micropithecus clarki*
NAP IV	UMP 66-29	Right DC1/	cf *L. legetet*, H. 1982	Anthropoid indet.
NAP IV	UMP 66-30a	Left p/4	*M. clarki*, F&S. 1978; H. 1982, 1988	*Micropithecus clarki*
NAP IV	UMP 66-30c	Left c/1	Anthropoid indet., H. 1982	*Walangania africanus*
NAP IV	UMP 66-31	Molar crown fragment	Confusion with UMP 66-30c?	
NAP IV	UMP 66-32	Right c/1	Anthropoid indet., H. 1982	*Micropithecus clarki*
NAP IV	UMP 66-33a	Right I2/	*M. clarki*, F&S. 1978; H. 1982, 1988	*Lomorupithecus evansi*
NAP IV	UMP 66-33b	Left DM3/	*M. clarki*, H. 1982, 1988	*Micropithecus clarki*
NAP V	UMP 66-34	Left i/2	*M. clarki**, F&S. 1978; *L. legetet*, H. 1981, 1982, 1988	*Micropithecus clarki*
NAP IV	UMP 68-03	Left C1/	*M. clarki*? F&S. 1978; *Victoriapithecus* sp. H. 1982	*Lomorupithecus evans*
NAP IX	UMP 68-25	Frontal bone	Colobine, P&W. 1968; *M. clarki*, F&S. 1978; cf *M. clarki*, H. 1982	Anthropoid indet.

Despite the improvement in the Kenyan fossil sample, interpretation of the Napak fossils continued to be problematic because of the restricted nature of the available collection. Harrison (1982) for example, felt uncertain enough about the Napak specimens to list 13 of them as "anthropoid indet.", and four as "cf" or with a question mark after the species name. This suggested that Napak contains species not present in the Kenyan sites.

Harrison (1982, 1986, 1988, 1989, 2003) demonstrated the high diversity of small apes in the Early and Middle Miocene of East Africa. He resurrected the species *Limnopithecus evansi* (holotype from Songhor, Kenya (MacInnes, 1943)), erected the genus *Nyanzapithecus* (with two species, *N. pickfordi* (from Maboko, Kenya), *N. vancouveringorum* from Rusinga, Kenya) (Harrison, 1986), created the species *Micropithecus leakeyorum* for material from Maboko (Harrison, 1989), and the genus *Kalepithecus* (for *Dendropithecus macinnesi songhorensis*) as the combination *Kalepithecus songhorensis* (holotype from Songhor). However, he accepted the attribution of KNM KO 8 to *Limnopithecus legetet*, and indeed based his diagnosis for the mandible and lower dentition of the species on this mandible, rather than the holotype. By extension, this affected the diagnosis of the genus.

Among the Napak fossils, Harrison (1982) attributed the small to medium primate specimens to the following taxa:- *Micropithecus clarki* (14 specimens of which one was doubtfully assigned), *Dendropithecus macinnesi* (2 specimens, one of which was listed as cf), *Limnopithecus legetet* (5 specimens of which one was cf), and a monkey, *Victoriapithecus* (2 specimens). He also assigned to *Proconsul major* an isolated deciduous upper canine (UMP 66-20) formerly thought by Fleagle & Simons (1978) to be a lower canine which was attributed with doubt to *Micropithecus clarki* (Table 1).

In 1985, the authors launched the Uganda Palaeontology Expedition and since then have carried out research in the country on an annual basis. The first visit to Napak in 1985 yielded a few small hominoid specimens (Pickford *et al*., 1986). Insecurity in the region prevailed for a number of years after that, but since 1997 the team has collected at Napak every year, amassing a reasonable sample of ape fossils. As with the historical collections, the new specimens consist mainly of isolated teeth and postcranial elements, but there are 9 jaw fragments containing partial tooth rows, and 81 isolated teeth. Simultaneously, Rossie & MacLatchy (2006) worked at the sites and found some material including a snout and a juvenile mandible at Napak IX which formed the basis for the description of the genus and species *Lomorupithecus harrisoni*.

There are now 80 upper teeth and 75 lower teeth of small catarrhines from Napak, which we describe and interpret in this report. There are several deciduous canines and incisors in the sample, which we omit from this work. Despite the much improved fossil sample, there are still some residual difficulties with the study of the small hominoids from Uganda. Some of the teeth are heavily worn, much of the material is in the form of isolated teeth, and there is a high diversity of species present, partly due to the fact that the Napak sedimentary sequence spans an appreciable period of time from ca 19.5 to ca 18.5 Ma, during which palaeoenvironmental shifts took place and evolutionary changes occurred in some of the mammalian lineages (tragulids and pecorans for example (Pickford, 2002)) : the primates were probably not an exception. Furthermore, there is a degree of sexual dimorphism in *Micropithecus clarki*, and probably also in the other small ape lineages from the area, which has caused difficulties in the past. It is clear that the original hypodigm of *Micropithecus clarki* (Fleagle & Simons, 1978) contains specimens of at least four taxa (*Micropithecus*, *Limnopithecus*, *Ugandapithecus* and *Dendropithecus*) and the hypodigm of *Lomorupithecus harrisoni* (Rossie & MacLatchy, 2006) contains two (*Lomorupithecus* and *Limnopithecus*).

SYSTEMATIC DESCRIPTIONS

Genus *Dendropithecus* Andrews & Simons, 1977

Diagnosis: Small anthropoid primate approximating in dental size to *Symphalangus syndactylus*. Incisors high-crowned and mesio-distally relatively narrow. i/2 asymmetrical in shape with a convex

distal margin. Canines strongly sexually dimorphic in size and morphology. Canines high-crowned and bilaterally compressed in males; lower crowned and less compressed in females. Upper canines in males with double mesial groove. Upper premolars short and broad with strongly projecting buccal cusps. p/3 sectorial, with high and bilaterally compressed crown and extension of enamel onto buccal aspect of mesial root. Upper molars short and broad, and rectangular in occlusal outline, with high and voluminous cusps, sharp and well-developed occlusal crests, well-defined mesial and distal foveae and trigon basin, and broad, shelf-like lingual cingulum. M1/ smaller than M3/ smaller than M2/. Lower molars long and quite broad, with high conical cusps, sharp and well-developed occlusal crests, broad and transverse mesial fovea, large, well-defined and slightly oblique distal fovea, broad and deep talonid basin and moderately developed buccal cingulum. m/1 smaller than m/2 smaller than m/3. Marked increase in size from m/1 to m/3. Incisors relatively small in comparison with size of molars. Palate long and narrow, with large incisive foramina. Nasal aperture narrow and extends inferiorly quite close to the alveolar margin of the premaxilla. Maxillary sinus extensive. Body and symphysis of mandible low and robust, particularly below m/3. Moderately well-developed superior and inferior transverse tori. Limb bones long and relatively slender, lacking conspicuous muscle markings (from Harrison, 1988).

Type species : *Dendropithecus macinnesi* (Le Gros Clark & Leakey, 1951)

Species *Dendropithecus ugandensis* nov.

Diagnosis : Species of *Dendropithecus* 15-20% smaller than the type species, *D. macinnesi*.

Holotype : NAP I 1’00, right mandible fragment containing lightly worn m/2 and m/3 (Fig. 23-24).

Material from Napak
NAP IV 14’07, left upper canine; NAP XV 90’09, right M1/; NAP IV 25’02, left M2/; NAP IV 1’05, left lower canine; NAP I 1’01, edentulous right mandible fragment containing the roots of i/2-m/1; NAP V UMP 62-20, left c/1; NAP IV 66-05, right p/3; NAP IX UMP 66-23, right mandible fragment containing m/2 and m/3 (Figs 16-22, 25).

Descriptions

Figure 16. NAP IV 14’07, left upper canine, *Dendropithecus ugandensis* sp. nov., A) lingual, B) distal, C) mesial, and D) buccal views. (Scale : 10 mm).

NAP IV 14’07 (Fig. 16) is a germ of a left upper canine lacking the root which had evidently not formed by the time of death. The crown is compressed as in KNM RU 1860. It has an extensive and broad mesial groove, accompanied by a buccal mesial groove, which are separated from each other by a sharp mesial crest. On the buccal aspect of the crown there is a vertical slit as in KNM RU 1860. The distal crest is sharp, and terminates basally in a small tubercle. The lingual surface is concave distally, but mesially it is convex due to the presence of a lingual ridge which is mesio-distally broad near cervix, narrowing gently apically. In mesial view, the crown is seen to curve lingually, the buccal surface being strongly convex in profile.

Figure 17. NAP XV 90’09, right M1/, *Dendropithecus ugandensis* sp. nov., stereo occlusal view. (Scale : 10 mm).

NAP XV 90’09 (Fig. 17), a right upper molar is lightly worn, showing a tiny dentine depression on the apex of the protocone. The surface of the tooth is smooth, as though it has been polished. The protocone is the largest cusp, the paracone and metacone are sub-equal in dimensions and the hypocone is the smallest of the four main cusps. Because the protocone is in an interior position, the mesial fovea is cramped into the buccal half of the crown, and is narrow mesio-distally. The crests defining the distal margin of the mesial fovea are so low and subtle that the fovea is almost contiguous with the trigon basin. The two buccal cusps are compressed bucco-lingually. The transverse crest from the metacone which defines the distal margin of the trigon basin is almost transversely oriented and is accompanied by a low sub-parallel crest that subdivides the distal fovea into two sub-basins. The distal fovea itself is large. The protocone is bordered mesially and lingually by a large cingulum which gives rise to two swellings, one where it merges with the preprotocrista, the other near the disto-lingual corner of the protocone. The hypocone sends a tiny prehypocrista mesially, where it links with an extremely diminutive crista obliqua. There is thus a free connection between the trigon basin and the valley between the protocone and hypocone. There is a low buccal cingulum. A strange feature of this tooth is that the enamel extends between the roots distally. There are three roots, two buccal ones that have broken off, and a single lingual one.

Figure 18. NAP IV 25’02, left M2/, *Dendropithecus ugandensis* sp. nov., stereo occlusal view (scale : 10 mm).

NAP IV 25’02 (Fig. 18) is a left upper molar in light wear with dentine islands on the protocone and hypocone. The protocone is in an interior position, the mesial fovea is therefore cramped into the buccal half of the tooth. The trigon basin is large and has a very low wall separating it from the mesial fovea. The wall separating it from the distal fovea is somewhat taller, but it is in any case quite low. The hypocone is isolated from the protocone by a valley which is unobstructed, even by the low prehypocrista. The distal fovea is large and has a low ridge crossing it transversely. The buccal cingulum is continuous from rear of the metacone round to the front of the paracone. The lingual

cingulum is broad. The lingual surface of the protocone shows low enamel ridges descending towards the cingulum. There are three roots, two buccal ones, of which the mesial one is broken, and a single lingual root.

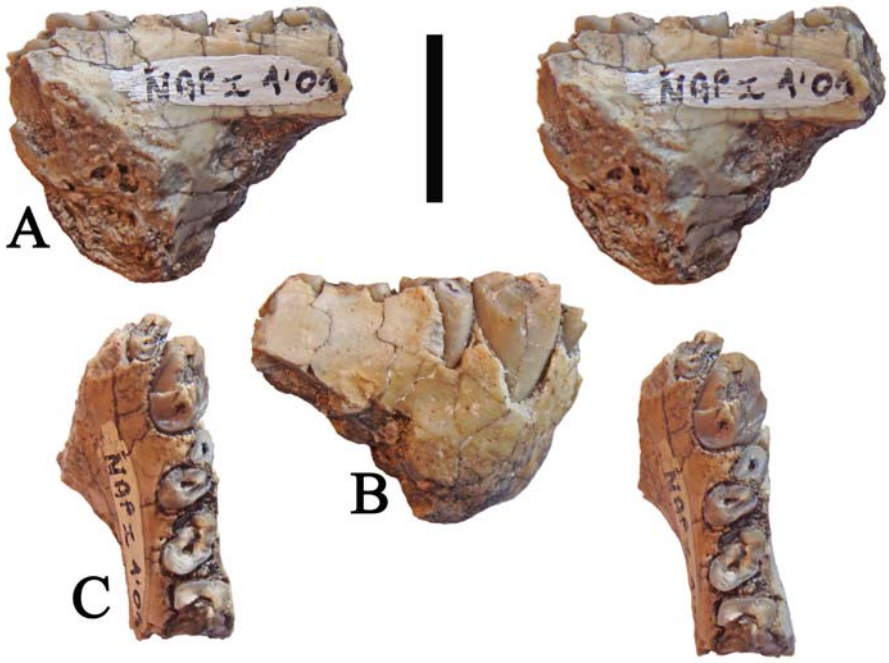

Figure 19. NAP I 1’01, right mandible with roots of i/2-m/1, oriented with the alveolar margin horizontal, *Dendropithecus ugandensis* sp. nov., A) stereo lingual, B) buccal, and C) stereo alveolar views. (Scale : 10 mm).

NAP I 1’01 (Fig. 19) is an edentulous right mandible fragment containing the roots of the right i/2, the canine, premolars and anterior root of the m/1. The canine root has similar dimensions to an isolated canine NAP IV 1’05. The symphyseal section shows a sloping planum alveolare, a superior transverse torus, beneath which is a shallow genial depression and a weak inferior transverse torus.

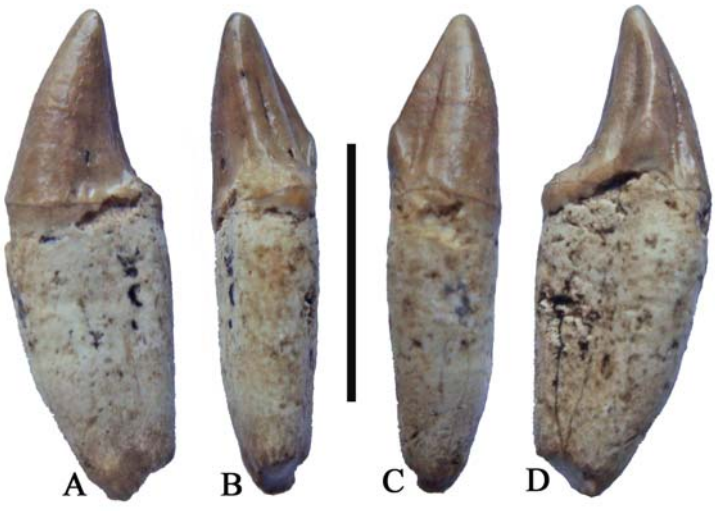

Figure 20. NAP IV 1’05, left lower canine, *Dendropithecus ugandensis* sp. nov., A) buccal, B) distal, C) mesial and D) lingual views. (Scale : 10 mm).

NAP IV 1’05 (Fig. 20), is a lower left canine. In mesial view it has a convex surface into which is scored a shallow groove which extends from near the cervix to about ¾ the height of the crown. The mesial crest is strongly developed and swells basally to produce a low tubercle at the junction between it and the lingual cingulum. The lingual pillar is almost in the centre of the lingual surface and extends

from near cervix almost to the apex, and has constant width throughout. It is bordered by two furrows, which separate it from the mesial crest anteriorly and the distal crest posteriorly. The distal crest is sharp, but swells basally to produce a basal tubercle, and on its mesio-lingual side there is a shallow vertical groove. Buccally, low down on the crown, there is a concave area, but the rest of the surface is convex. The root is stout and possesses a shallow lingual groove.

Figure 21. NAP V UMP 62-20, left lower canine, *Dendropithecus ugandensis* sp. nov., A) distal, B) buccal, C) mesial, and D) lingual views. (Scale : 10 mm).

NAP V UMP 62-20 (Fig. 21) is a slightly abraded, but unworn, left lower canine. The mesial shoulder of the tooth, where the lingual cingulum meets the mesial cristid, is low down. The lingual ridge is not well marked but rises from a small swelling in the lingual cingulum. There is no distal tubercle, and the distal marginal cristid is weak.

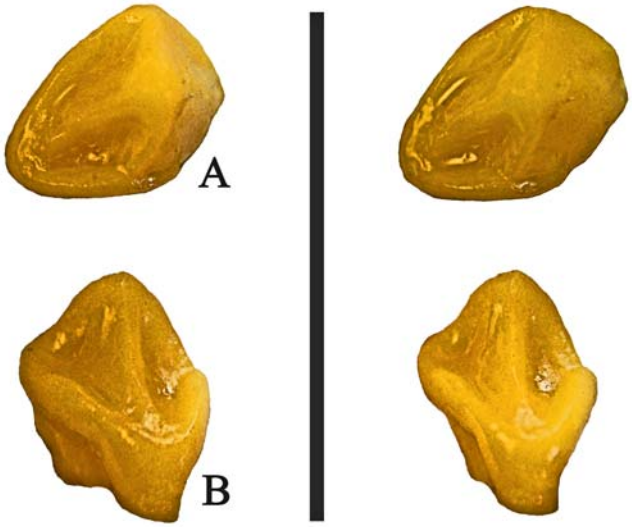

Figure 22. NAP IV UMP 66-05, right p/3 cast, *Dendropithecus ugandensis* sp. nov., A) stereo occlusal view, B) stereo lingual view. (Scale : 10 mm).

NAP IV UMP 66-05 (Fig. 22), an unworn right p/3 has strong pre- and post- cristids descending from the protoconid towards the cingulum mesially and distally, and a well developed lingual ridge, which rises from inside the junction of the lingual and distal cingula, upwards to the apex of the main cusp.

As a result of the central position of the lingual ridge, the mesial fovea is somewhat larger than the distal one. The lingual and distal cingula are strong and swollen. The honing surface is slightly flattened mesially, but the buccal surface of the crown is gently convex elsewhere.

Figure 23. NAP I 1’00, right mandible containing m/2 and m/3, holotype of *Dendropithecus ugandensis* sp. nov., A) stereo occlusal view, B) lingual, and C) buccal views. (Scale : 10 mm).

The holotype of the species is NAP I 1’00, a right mandible fragment containing lightly worn m/2 and m/3 (Fig. 23, 24). There are tiny dentine exposures at the tips of the protoconid, hypoconid and hypoconulid of the m/2, but none in the m/3. The mandibular body is robust at the level of the m/3 where the root of the ascending ramus sweeps upwards. The base of the jaw is broken so its depth cannot be assessed. The m/2 is rectangular in occlusal outline, with the protoconid only very slightly in advance of the metaconid, and the hypoconid slightly mesial to the entoconid, the hypoconulid just buccal to the centre line of the tooth. There is a buccal cingulum interrupted on the face of the hypoconid, which places the three buccal cusps some distance from the buccal margin of the tooth. The mesial fovea is mesio-distally narrow, but bucco-lingually extensive. The talonid basin dominates the crown, the crests entering it from the surrounding cusps being low and smooth, although there is a clear, but low, ridge entering it from the hypoconid directed towards the metaconid. The crests that define the front of the distal fovea are low. The m/3 is built on a similar plan to the m/2, but it tapers distally more, due to the greater dimensions of the hypoconulid, the distal buccal shelf and its larger distal fovea. A particularity of this tooth is that the crest running into the talonid basin from the hypoconid crosses the basin to reach the base of the entoconid rather than towards the metaconid.

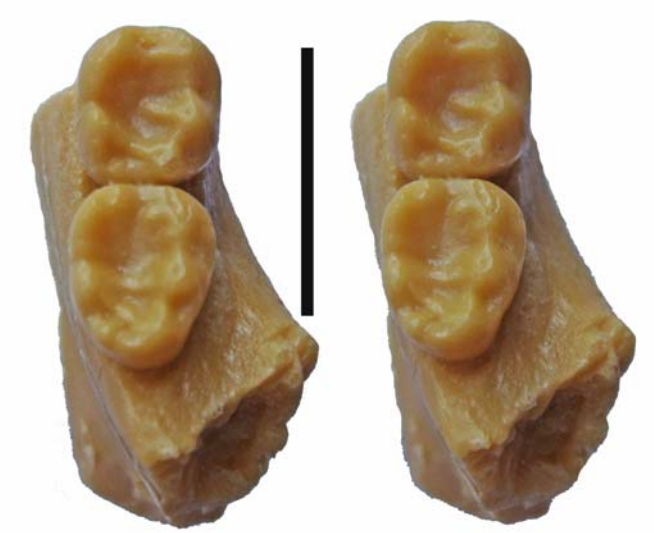

Figure 24. NAP I 1'00, right mandible containing m/2 and m/3, cast of holotype of *Dendropithecus ugandensis* sp. nov., stereo occlusal view to show better the cresting in the occlusal surface. (Scale : 10 mm).

Figure 25. NAP IX UMP 66-23, right mandible containing m/2 and m/3, *Dendropithecus ugandensis* sp. nov., stereo occlusal view. (Scale : 10 mm).

NAP IX UMP 66-23, is a right mandible fragment containing m/2 and m/3 in medium wear (Fig. 25). The mandible is robust opposite the m/3 where the ascending ramus sweeps upwards. There is dentine exposed at the apices of all five cusps in the m/2 and on all the cusps save for the entoconid in the m/3. The buccal cusps are located some distance from the buccal margin of the crown. The talonid basin occupies much of the crowns of the teeth, the mesial and distal fovea being quite small and the crests separating these structures, low. The protoconid is slightly in advance of the metaconid and the hypoconid is mesial to the entoconid, the hypoconulid slightly to the buccal side of the midline of the crown. The m/2 is rectangular in occlusal outline, the m/3 tapers distally.

Discussion

Harrison (1982) suggested that male and female canines of *Dendropithecus macinnesi* were strongly sexually dimorphic (males – large, females – small). Upper molars from the same sites fall into a single cloud of points, indicating the presence of a single species at Rusinga, the type locality. The main morphological difference between the large and the small canines of *Dendropithecus macinnesi* is the presence of a vertical slit on the buccal surface of the crown in large specimens, and the absence of such a slit in the small ones. The Napak fossil possesses a clear buccal slit. Bivariate plots (Fig. 26) of the Napak teeth and those attributed to the genus by Harrison (1982) and Andrews (1978) reveal

that the Ugandan specimens are consistently smaller than those from Rusinga, save for the canine from Napak (NAP IV 14'07), which plots close to, but just outside the range of variation of small canines from Rusinga.

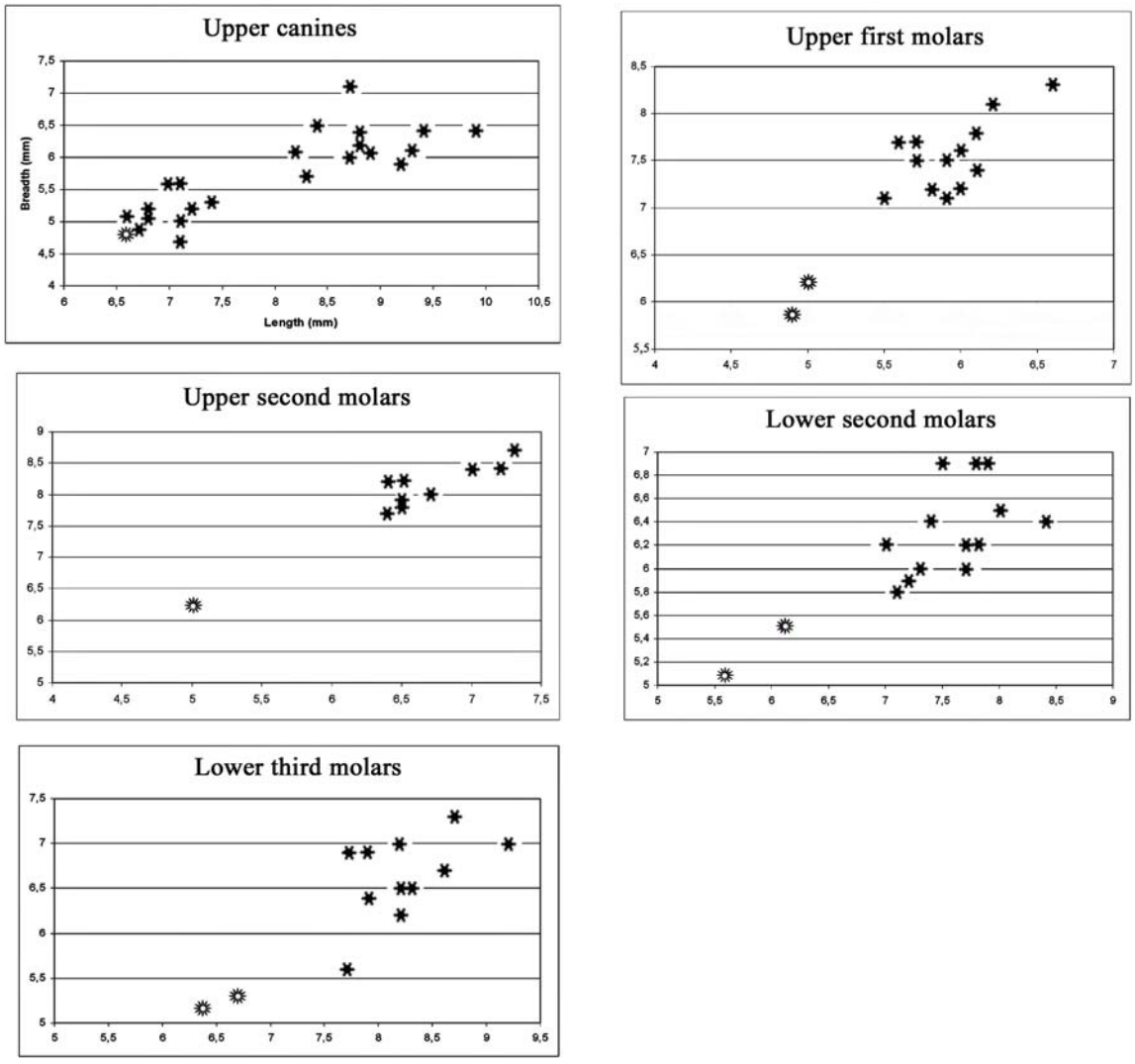

Figure 26. Bivariate (length – breadth at cervix) scatter plot of upper canines, and upper and lower molars attributed to *Dendropithecus macinnesi* (snow flake symbol – Rusinga) and *Dendropithecus ugandensis* nov. sp. (hollow starburst symbol – Napak). (Measurements of the Kenyan material are from Harrison, 1982). NAP IV 25'02 is considered to be an M2/ but, because it is an isolated tooth, it is also plotted in the M1/ graphic for the sake of comparison.

Genus *Kalepithecus* Harrison, 1988

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).

Species : *Kalepithecus songhorensis* (Andrews, 1978)

Diagnosis : As for the genus (from Harrison, 1988).

Referred material from Napak : NAP V UMP 67-06, left I1/; NAP IV 2'05, left I2/; NAP I 2'09, left upper canine (male morphology); NAP IV 2'09, heavily worn right M3/; NAP IV 33'08, right i/2; NAP V 6'09, right lower canine; NAP V 7'09, edentulous mandibular symphysis; NAP IV UMP 66-06, right p/3; NAP IV 12'08, right p/4 (Figs 27-35).

Description

Figure 27. NAP V UMP 67-06, *Kalepithecus songhorensis*, left I1/, A) labial, and B) lingual views. (Scale : 10 mm).

NAP V UMP 67-06 is an unworn upper central incisor crown with a low lingual swelling, weak mesial and distal marginal ridges, and a weakly spatulate distal part of the crown (Fig. 27). The base of the crown is missing, so information about the lingual cingulum is lacking.

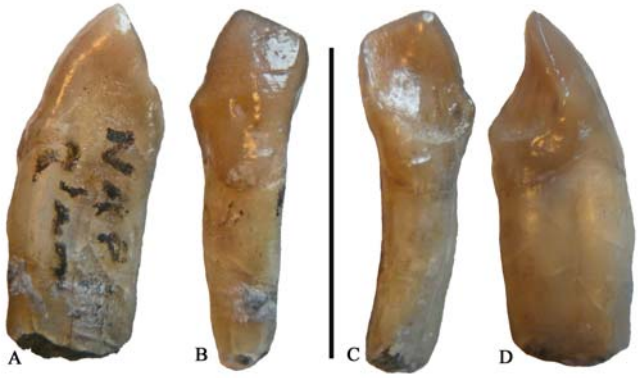

Figure 28. NAP IV 2'05, left I2/, *Kalepithecus songhorensis*, A) mesial, B) labial, C) lingual, and D) distal views. (Scale : 10 mm).

NAP IV 2'05 (Fig. 28) is similar in morphology and dimensions to the I2/ in KNM SO 417, attributed to *Kalepithecus songhorensis*. The crown is larger than the root. The lingual surface is concave, rectangular in outline, with a short apical cutting edge and a long distal one. These two edges meet at a

right angle. There is a weak lingual cingulum and equally weak mesial and distal marginal ridges. The distal ridge and the lingual cingulum join each other to form a small tubercle at the base of the crown distally. The buccal surface is convex throughout. The root is relatively short and is a compressed oval, with a slight curve in lingual view.

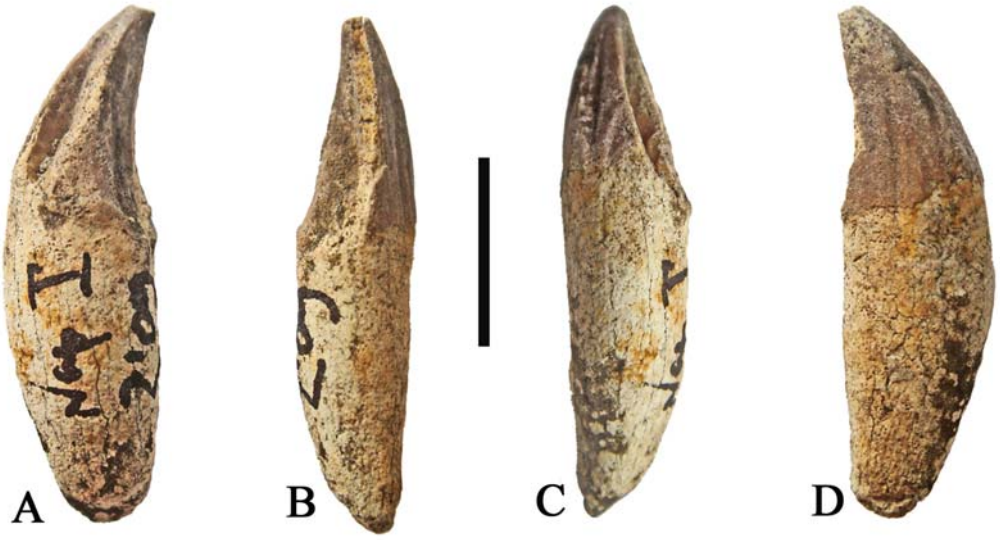

Figure 29. NAP I 2'09, left upper canine, *Kalepithecus songhorensis*, A) lingual, B) distal, C) mesial, and D) buccal views. (Scale : 10 mm).

NAP I 2'09 is a left upper canine with a robust root and crown (Fig. 29). The crown is moderately compressed, but not to the extent seen in *Dendropithecus macinnesi*. The mesial groove is broad and deep, and is accompanied by a smaller, shallower buccal mesial groove. On the buccal surface, there is a narrow buccal slit which extends from near cervix to about half the height of the crown. The distal crest is lightly worn, exposing dentine in a strip running from the apex to the cervix. The lingual concavity is patterned by fine vertical ridges of enamel either side of a vertical groove. The lingual ridge is broad at cervix and narrows gradually towards the apex. There is a weak lingual cingulum terminating mesially in a small tubercle. The root is more massive than the crown suggesing that this is a male individual.

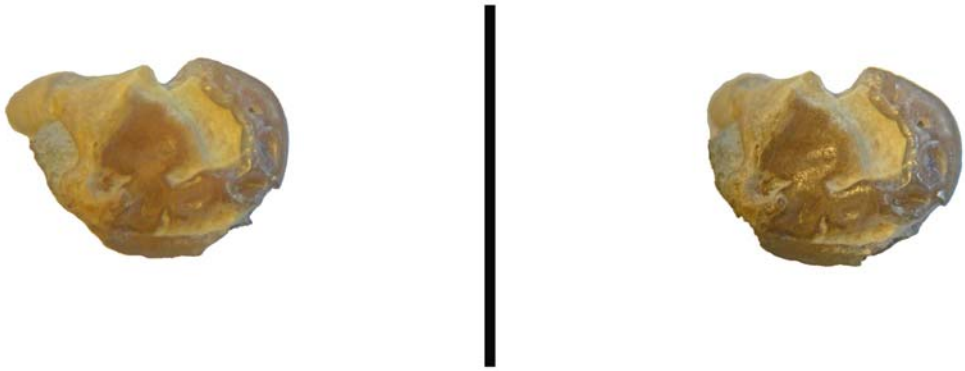

Figure 30. NAP IV 2'09, right M3/, *Kalepithecus songhorensis*, occlusal view. (Scale : 10 mm).

NAP IV 2'09, is a deeply worn right M3/ (Fig. 30), with extensive dentine exposures on the protocone and hypocone, and with a damaged buccal side. The main features visible on this rather poor specimen, are the presence of a broad lingual cingulum with a beaded margin with small connections to the protocone. The distal part of the tooth is reduced, the hypocone being a quarter of the dimensions of the protocone, and the metacone tiny (even if damaged). The trigon basin is large and the mesial and distal fovea, cramped. There are three roots, two small vertical ones buccally, and a larger lingual one which slants distally.

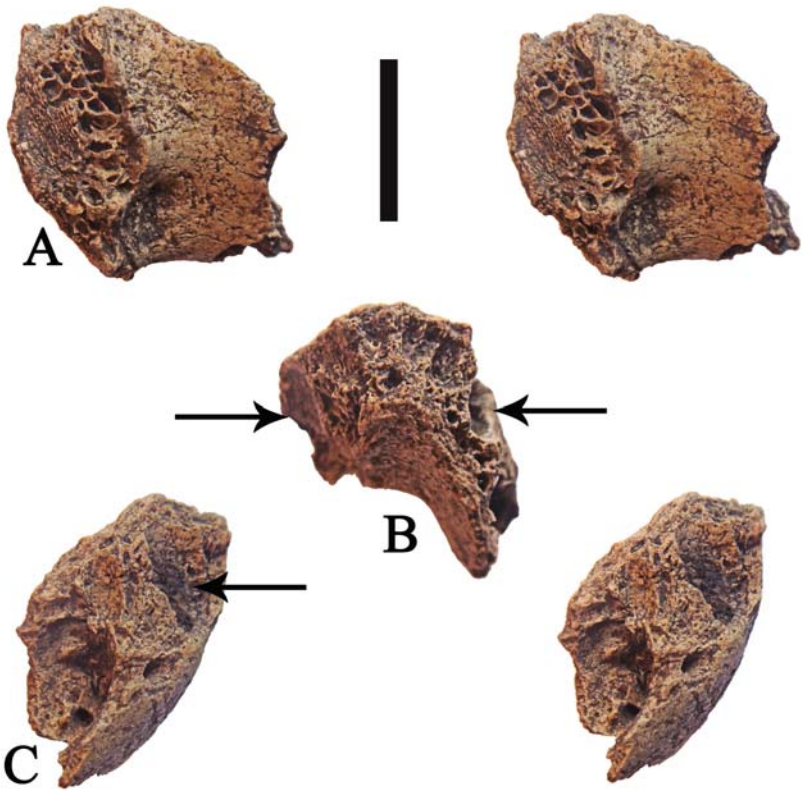

Figure 31. NAP V 7’09, mandibular symphysis oriented with the base of the mandible horizontal, *Kalepithecus songhorensis*, A) stereo lingual, B) alveolar, and C) stereo buccal views (arrows show the canine alveoli. (Scale : 10 mm).

The overall build and dimensions of NAP V 7’09 (Fig. 31), are similar to the symphysis of KNM RU 900. The planum alveolare slopes uniformly towards the base of the jaw, and is undercut beneath the superior transverse torus, which is in any case weakly expressed, to form a capacious genial fossa. The alveoli, or partial alveoli of the incisors and both canines are preserved, and the mental foramen pierces the jaw just behind the canine alveolus, at about 1/3 the height of the body of the mandible.

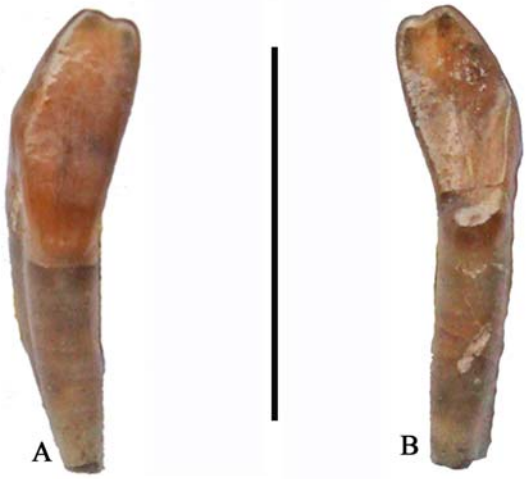

Figure 32. NAP IV 33’08, right i/2, *Kalepithecus songhorensis*, A) labial, and B) lingual views. (Scale : 10 mm).

NAP IV 33’08, a right i/2 (Fig. 32), is close in morphology and dimensions to that of KNM RU 900, a left mandible and symphysis containing all four incisors, the left canine, both premolars, and first molar. The crown is as tall as the root, and has a characteristic bend in its distal profile. The central lingual ridge is present but weak. The mesial and distal marginal ridges are also weakly developed, as

is the lingual cingulum. The lingual cingulum and distal marginal ridge meet at a junction located about half the height of the tooth, forming a bend in the profile of the crown. The labial surface is convex.

Figure 33. NAP V 6'09, right lower canine, *Kalepithecus songhorensis*, A) lingual, B) distal, C) buccal, and D) mesial views. (Scale : 10 mm).

NAP V 6'09, a right lower canine (Fig. 33), is extremely similar in morphology and overall dimensions to the canine in KNM RU 900. The mesial and buccal surface is convex. The lingual ridge is prominent, and merges with the lingual cingulum at about half the height of the tooth. This makes the upward "V"-ing of the cervix quite marked. The lingual surface is slightly concave but with a crest of enamel extending from the apex of the tooth to the cervix. The distal crest is bordered lingually and buccally by shallow grooves, and basally it appears not to form a tubercle, although slight damage in this area prevents certainty in the matter. The root is robust, almost as large as the crown, suggesting that this is a male individual.

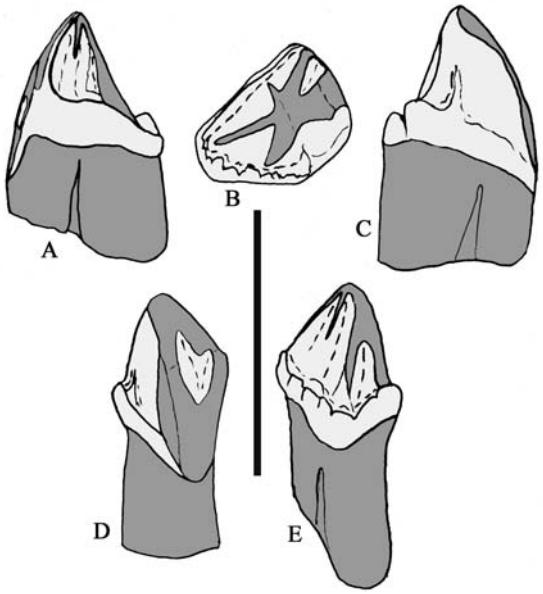

Figure 34. NAP IV UMP 66-06, right p/3, *Kalepithecus songhorensis*, probable male individual, A) distal, B) occlusal, C) mesial, D) buccal, and E) lingual views. Note the large honing facet in B, C and D, which extends slightly onto the root. (Scale : 10 mm).

NAP IV UMP 66-06, a right p/3 (Fig. 34), is extremely similar in morphology and dimensions to the p/3 in KNM RU 900. It is comprised of a single cusp with three strong crests directed cervically from the apex, the strong precristid, a weaker postcristid, and a well developed lingual cristid.

The lingual and distal cingula are well developed, whereas the buccal one is weaker and only covers the rear half of the buccal surface of the main cusp. The mesio-buccal surface of the tooth is worn by a large honing facet which shows a central depression where part of a groove is preserved. The honing facet passes onto the root, suggesting that this was probably a male individual. There are two roots, the anterior one broken, but the distal one complete and slender.

Figure 35. NAP IV 12'08, right p/4, *Kalepithecus songhorensis*, stereo occlusal view. (Scale : 10 mm).

NAP IV 12'08, an unworn right p/4 is short and broad (Fig. 35), just as its counterpart in KNM RU 900. The protoconid and metaconid are subequal in height, although the protoconid is appreciably more voluminous than the metaconid. The mesial fovea is moderately capacious, separated from the distal basin by a tall wall formed by crests running towards each other from the apices of the protoconid and metaconid. The distal cingulum provides a prominent wall for the distal fovea, and buccally it forms a small stylid where it merges with the postprotocristid. In this unworn tooth, it is possible to make out subtle wrinkles in the enamel, especially in the floor of the distal basin. NAP IV 12'08 looks similar to the p/4 in the type specimen of *Kalepithecus songhorensis*, KNM SO 378, and is close to the same tooth in KNM RU 900.

Discussion

The presence of *Kalepithecus songhorensis* at Napak is indicated by several teeth which closely resemble their counterparts in the holotype mandible KNM SO 378 (the p/3 and p/4) and KNM RU 900, a mandible from Rusinga that used to be classsified with *Dendropithecus macinnesi*, but which is more likely to belong to *Kalepithecus songhorensis*.

Genus *Limnopithecus* Hopwood, 1933a

Diagnosis: A gibbon-like primate with very low-crowned cheek-teeth in the lower jaw. Lower molars with distinct external cingulum between the cusps; length-breadth index exceeding 90 per cent (original diagnosis from Hopwood (1933a)).

Upper central incisors broad and relatively low-crowned. Lower incisors low-crowned and spatulate. Canines relatively small. Upper molars and premolars moderately long and broad, with well-defined occlusal crests. p/3 ovoid to almost circular in outline and non-sectorial. p/4 broad and ovoid to circular. Lower molars broad and rectangular with high sharp cusps and occlusal crests, and large, well-defined talonid basin. Mesial and distal foveae broad and slightly oblique in m/1 and m/2, and very oblique in m/3. m/3 relatively large, with entoconid situated transversely opposite hypoconid (emended diagnosis from Harrison, 1988).

Note that the diagnosis of the lower dentition by Harrison (1988) is based on KNM KO 8. The holotype of the species does not accord with this diagnosis : in M 14079, the lower molars are narrower anteriorly than posteriorly, not rectangular, the cusps are not as high and sharp as those of KNM KO 8, nor are the occlusal crests as sharp, and the mesial foveae are more pinched in. There are other differences evoked below.

Type species : *Limnopithecus legetet* Hopwood, 1933a

Species *Limnopithecus legetet* Hopwood, 1933a

Diagnosis : A gibbon-like primate with very low-crowned cheek-teeth in the lower jaw. Lower molars with distinct external cingulum between the cusps; length-breadth index exceeding 90 per cent (original diagnosis from Hopwood (1933a)).

Holotype : M 14079, right mandible fragment containing the roots of p/4 and the crowns of m/1 and m/2.

Type locality : Koru, Kenya.

Age : Early Miocene, Faunal Set I, ca 20-19 Ma.

Resolving the status of *Limnopithecus legetet*

Limnopithecus was the first genus of small fossil ape to be described from East Africa, and understanding its status is essential for interpreting other Miocene small apes from Africa. The type species is *Limnopithecus legetet* Hopwood, 1933a, and the type specimen is M 14079, from Maize Crib Site, Koru, Kenya, an Early Miocene deposit (Pickford, 1986a, 1986c, 1986d) in the Legetet Formation. It was associated with several other small hominoid specimens, including a juvenile mandible containing dm/3 and dm/4 attributed to *L. legetet*, and the type specimen of *Xenopithecus koruensis*, as well as various isolated teeth and jaw fragments.

In his type description of *Limnopithecus legetet*, Hopwood (1933a) wrote that "the second molar is now about 3 mm below the first. This gives the second molar the appearance of rising from the crypt to replace a lost deciduous tooth. But such is not the case". However, this description is incorrect – the second molar is in fact above the first, not below it, having risen slightly out of its alveolus prior to fossilisation. He also wrote that "the metaconid of the first molar and the protoconid and metaconid of the second molar have lost the peripheral enamel. Hence the teeth have a false appearance of an anterior narrowing". Although the appearance of anterior narrowing has been slightly enhanced by enamel spalling off the cusps, the tips of the cusps are preserved and are close together, indicating that anterior narrowing was a feature of these teeth, and not simply an artefact of preservation. This is confirmed by an examination of the cervical levels of the teeth which are well preserved. The illustration published by Hopwood (1933b) is inaccurate to the extent that he did not illustrate the dentine exposed at the tip of the entoconid. This has led to the erroneous interpretation that the entoconid is very internally positioned in this individual.

Because the holotype of *Limnopithecus legetet* is fragmentary and the crowns of the teeth are damaged and worn, there has been a consistent tendency since 1952, to base comparisons of other small ape specimens from East Africa to another specimen from Koru, KNM KO 8, a mandible of a young adult individual containing the lower incisors, canine, premolars and molars (p/4 lacking the mesial half), attributed to the species by Le Gros Clark (1952) (Harrison 1982, 1988). This specimen, although comparable in general dimensions to the type specimen of *Limnopithecus legetet*, possesses molars that are different in morphology from it, the cusps being peripheral, the occlusal outline more rectangular (not narrowing anteriorly), the buccal cusps are not bulbous, and there is no accessory cusplet in the talonid basin at the base of the entoconid. From this erroneous attribution, much confusion has flowed. It should also be noted that Le Gros Clark (1952) wrote that KNM KO 8 came from the same site as the holotype, but our photocopy of the reprint has a marginal note in the handwriting of L.S.B. Leakey, "NO, different site at Koru".

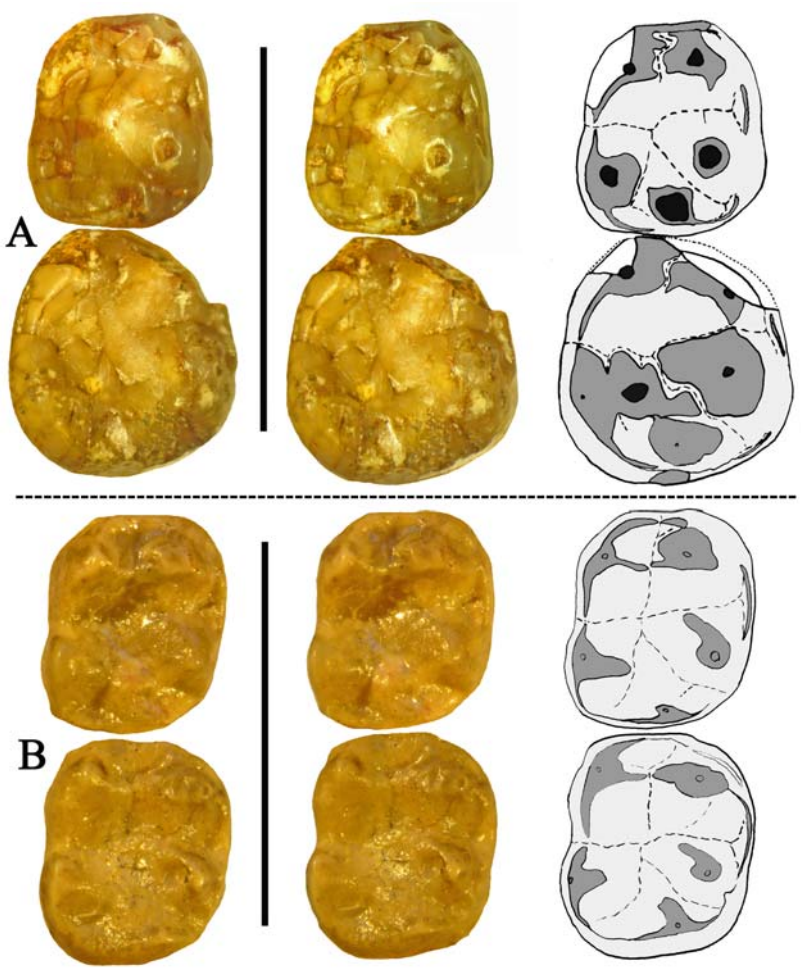

Figure 36. Comparison of first and second lower molars of M 14079, the holotype of *Limnopithecus legetet* (A) with a cast of KNM KO 8 (B) highlighting the major morphological differences between the two specimens. The latter specimen has been consistently used since 1952 as the basis for defining the species. (Scale : 10 mm).

M 14079 is a right mandible with the roots of p/4, and slightly damaged but lightly worn m/1 and m/2 (Fig. 36, 37). The m/2 is slightly out of its alveolus and has twisted anticlockwise with respect to the long axis of the tooth row. The most notable features of the molars in this specimen are as follows:- the m/1 (5.7 x 4.9 mm) is substantially smaller than the m/2 (6.3 x 6.0 mm), the mesial halves of the molar crowns are narrower bucco-lingually than the distal halves, especially evident in the m/1. The mesial fovea is cramped, the talonid basin is capacious, the apices of the buccal cusps are far from the buccal margin of the crown, the buccal cingulum and shelf are reduced to a small remnant between the two buccal cusps, the hypoconulid is centrally positioned in the distal margin of the crown only slightly distal to the line between the hypoconid and entoconid, the enamel is relatively thick and its surface smooth (possibly due in part to wear), and in light wear the dentine exposures at the cusp tips are triangular to rounded. In the m/2, the entoconid is close to the lingual edge of the tooth, but at its base in the talonid basin there is an additional cusp, as is evident from the illustration in Hopwood (1933b, Pl. 6, Fig. 1) which gives a good idea of its position relative to the lingual margin of the tooth but note that Hopwood (1933b) failed to observe the small exposure of dentine on the entoconid. This is an unusual morphology in hominoids, but it also present in specimens from Napak most notably in the paratype of *Lomorupithecus harrisoni* described by Rossie & MacLatchy (2006) (Fig. 37) and an isolated right m/2, NAP IV 82'08, in which the enamel in the talonid basin is lightly, but distinctly wrinkled, producing knots of enamel (Fig. 49). The crown of m/2 is not high, the cusps projecting little above the occlusal basin (taking into account the stage of wear) and the roots are separate from each other immediately beneath cervix (partly obscured by matrix).

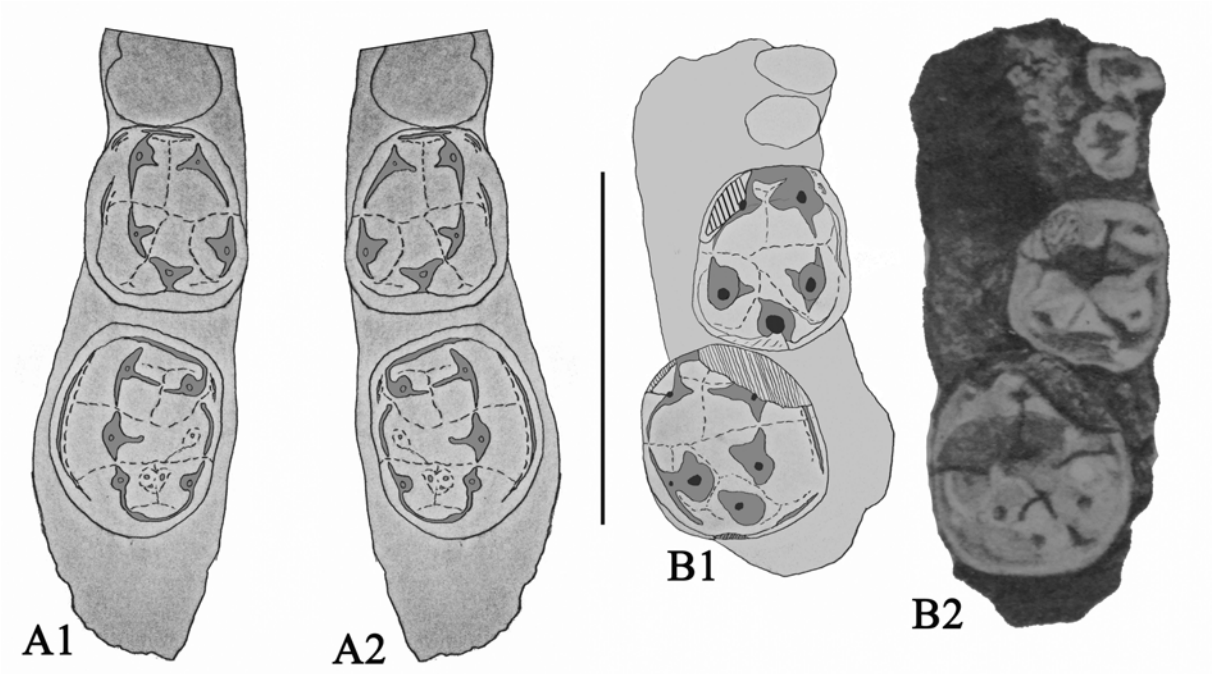

Figure 37. Comparison of the holotype of *Limnopithecus legetet* (B) with the paratype of *Lomorupithecus harrisoni* (A) here classified as *Lomorupithecus evansi*. A1) left mandible as preserved, A2) mirror image for ease of comparison. (Scale : 10 mm). Note in both specimens, the presence of a cusp in the talonid basin at the base of the entoconid, the hypoconid is the largest cusp, the anterior narrowing of the molars, the large difference in dimensions between m/1 and m/2, the buccal cingulum, the cingular remnant on the mesio-buccal surface of the protoconid, the buccal cusps flare greatly from their apices towards the buccal margin (B1 – present study, B2 – drawing from Hopwood, 1933b).

There are some superficial morphological resemblances between the teeth in mandible KNM KO 8 and the type specimen of *Kogolepithecus morotoensis* described by Pickford *et al*., (2003) from the basal Middle Miocene of Moroto II, Uganda. Among these are the similar extremely low-crowned incisors, stubby canine, and broad pyramidal lower third premolars, and lower molars with a tendency to possess a small cusplet on the post-cristid of the protoconid, but it clearly belongs to a smaller species and a different genus.

The attribution of KNM KO 8 to a genus different from *Limnopithecus* impacts on all studies of East African small apes subsequent to the publication of Le Gros Clark & Leakey (1951). Many fossils previously identified as *Limnopithecus legetet* belong in fact to this other genus and species.

Referred material from Napak : NAP IV UMP 66-24, right I1/; NAP V 25’08, left maxilla fragment containing roots I1/ and I2/, canine (lacking the apex) and P3/; NAP IV UMP 68-03, left C1/; NAP V UMP 66-19, left C1/; NAP IV 110’09, left M1/; NAP IV 176’09, left M1/; NAP IV UMP 66-11, left M1/; NAP IV 29’09, left M3/; NAP I UMP 62-17, distorted right mandible containing roots of c/1 and p/3, and heavily worn crowns of p/4, m/1 and m/2; NAP IV UMP 66-07, right mandible fragment containing c/1 (apex broken) and p/3; NAP IV UMP 66-12, right p/3; NAP IV 82’08, right m/2; NAP IX BUMP 268, left mandible containing roots dm/3, dm/4 and crowns of m/1 and m/2.

Descriptions

Figure 38. NAP IV UMP 66-24, right upper central incisor, *Limnopithecus legetet*, A) lingual, B) labial, C) mesial views. (Scale : 10 mm).

NAP IV UMP 66-24 is a right upper central incisor, low crowned, small and with a weakly spatulate distal half (Fig. 38). The lingual pillar is extensive, and forms a prominent boss within the generally gently concave lingual surface of the crown. The lingual cingulum merges with the mesial and distal marginal ridges, and the labial surface is convex save for a planar zone towards the mesial side.

Figure 39. NAP V 25’08, left maxilla containing roots of I1/ and I2/, canine lacking its apex, and complete P3/, *Limnopithecus legetet*, views of entire specimen, A) lateral view, B) stereo occlusal view. (Scale : 10 mm).

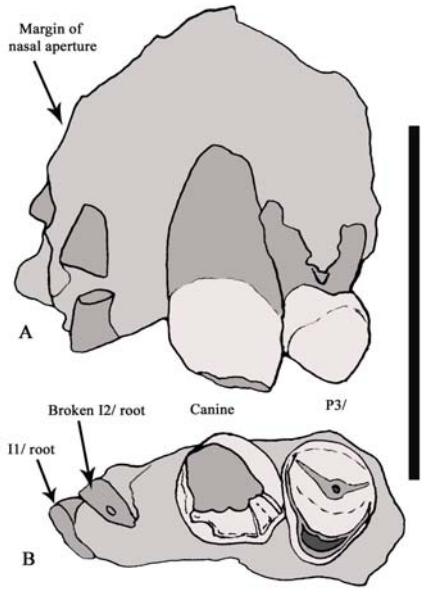

Figure 40. NAP V 25’08, left maxilla, *Limnopithecus legetet*, interpretive drawings, A) lateral and B) occlusal views (scale : 10 mm).

NAP V 25’08 is a fragment of left maxilla containing parts of the roots of both upper incisors, a canine lacking its apex, and a complete P3/ (Fig. 39-41). There is a small sector of the margin of the nasal aperture preserved, which shows a steep inclination sub-parallel to the root of the central incisor. There are two small nutritive foramina in the palate just lingual to the upper canine. The lingual part of the canine lies lateral to the lingual part of the P3/, as in NAP IX BUMP 266.

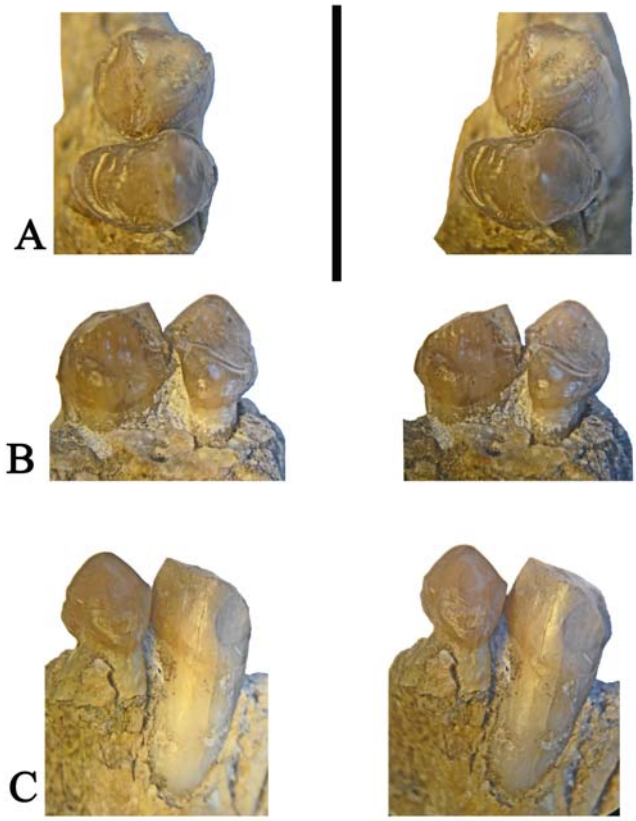

Figure 41. NAP V 25’08, left maxilla fragment containing C1/ and P3/, *Limnopithecus legetet*, detailed images of canine and premolar, A) stereo occlusal, B) stereo lingual, and C) stereo buccal views. (Scale : 10 mm)

The canine has a sharp lingual cingulum and there are two low relief enamel ridges rising towards the apex. About half the crown is missing. The P3/ is complete and shows a tall buccal cusp, accompanied lingually by a much lower protocone. The protocone is in a mesial position, and this effectively reduces the dimensions of the mesial fovea lingually. The preparacrista descends rootwards mesially, and a second crest descends towards the centre of the mesial cingulum, and between these two crests there is a mesial groove, but it is small. The distal fovea is large, and is bordered lingually by a strong crest that curves down from the protocone to merge with the distal cingulum. In buccal view there are tiny para- and mesostyles where the mesial and distal cingula meet the preparacrista and postparacrista respectively. There are three roots, two buccal and one lingual.

The crown of upper left canine NAP IV UMP 68-03 (Fig. 42) is blade like, moderately to strongly compressed bucco-lingually, and shows a prominent mesial groove on the lingual side and a shallow, weak one on the buccal side of the anterior crest. In mesial view, the crown is not canted on the root, instead the crown curves slightly lingually towards its tip. There is no waisting (beneath cervix the root is slightly bucco-lingually broader and mesio-distally longer than the crown) suggesting that this tooth represents a male individual. On the buccal surface of the crown there is a shallow, open, vertical groove extending about 2/3 up the crown, unlike the slit-like groove reported in male upper canines of the species *Dendropithecus macinnesi*. The lingual cingulum is weak but sharp and there is a distinct posterior cusplet at the base of the distal crest and a low tubercle where it rises towards the base of the mesial groove. The distal crest curves markedly lingually as it descends towards cervix, closing off the

posterior lingual concavity of the tooth. The buccal profile of the root is straight, whereas the lingual side curves buccally towards the apex, in opposition to the crown which curves lingually towards its apex.

Figure 42. NAP IV UMP 68-03, upper left male canine attributed to *Limnopithecus legetet*, A) distal, B) buccal, C) mesial, and D) lingual views. (Scale : 10 mm).

NAP IV UMP 68-03 (Fig. 42), which was attributed, with doubt, to *Micropithecus clarki* by Fleagle & Simons (1978) can be excluded from this taxon – it is here attributed to *Limnopithecus legetet*. The crown is not canted on the root (indeed the apex of the crown curves lingually to a slight extent), the mesial groove is prominent and is bordered distally by a well proportioned lingual pillar which reduces the dimensions of the distal concavity, the lingual cingulum is weak, but sharp edged, and produces a small swelling where it meets the mesial crest, and there is a weak groove on the mesio-buccal aspect of the tooth. Furthermore, the lingual side of the root is not flattened, the section being oval rather than D-shaped.

Harrison (1982) considered that upper canine NAP IV UMP 68-03 represented *Victoriapithecus*, but the mesial groove does not extend onto the root, meaning that it is unlikely to belong to a cercopithecoid. In his study, Harrison (1982, 1988) did not recognise any upper canines of *Micropithecus* from the Koru and Chamtwara in Kenya, sites at which other teeth of the genus are quite common. A re-examination of the Kenyan specimens needs to be carried out, keeping in mind the morphology of the canine associated with upper premolars in NAP V 221’09 (*Micropithecus clarki*).

Figure 43. NAP V UMP 66-19, left upper canine, *Limnopithecus legetet*, A) buccal, B) distal, C) lingual, and D) mesial views. (Scale : 10 mm).

NAP V UMP 66-19 (Fig. 43), is a left upper canine. The mesial groove is very lingually positioned, and the mesio-buccal groove is absent, making this specimen look similar to the upper canines of *Micropithecus clarki*. However, it is somewhat larger than other canines of the latter species, and the root is too long to fit into either of the maxillae of the species that are available. The distal concavity on the lingual side is broad and the lingual ridge narrow, partly due to wear. There is an indent beneath the cervix distally.

Figure 44. NAP IV 110’09, left M1/, *Limnopithecus legetet*, stereo occlusal view. (Scale : 10 mm).

NAP IV 110’09 is an unworn left upper molar with slight damage to the apex of the metacone and the distal cingulum, but otherwise in excellent condition (Fig. 44). The protocone is the largest cusp, almost conical, with prominent, sharp preprotocrista and postprotocrista. The paracone is smaller than the metacone and its preparacrista and postparacrista are small. The metacone sends a well developed crest towards the crista obliqua, which walls off what is a small trigon basin. The mesial fovea is tiny, but the distal one is as capacious as the trigon basin. This is due to the very lingual position of the hypocone and the weak stature of the crests entering the fovea. The hypocone sends a well developed crest mesio-lingually which fuses into the protocone quite high up. There is thus no direct connection between the trigon basin and the lingual shelf, the prehypocrista and the crista obliqua intervening between them. The metacone and hypocone send low ridges into the distal fovea. The buccal cingulum is weak, forming a tiny tubercle (mesostyle) beneath the junction of the paracone and metacone. The lingual cingulum is broad, and its edge is beaded. It extends onto the mesial part of the hypocone, but does not pass along its rear. The roots of the tooth are gracile, the lingual one flares strongly lingually, and the two buccal ones flare gently buccally.

Figure 45. NAP IV 176’09, left M1/ *Limnopithecus legetet*, stereo occlusal view. (Scale : 10 mm).

NAP IV 176’09 is a heavily worn upper molar, with large dentine exposures on the protocone and hypocone (which are contiguous) and smaller ones on the paracone and metacone (Fig. 45). The crown is worn almost flat. Nevertheless the mesial fovea can be discerned and it is cramped into the buccal half of the crown. The trigon basin is large and so is the distal fovea. Remnants of the buccal cingulum show that it was broad, and there are remains of low enamel ridges on the lingual face of the protocone. The buccal cingulum has been abraded but can be discerned running the entire length of the buccal side of the tooth. The two buccal roots have broken off, but the lingual one is complete.

Figure 46. NAP IV 29’09, left M3/, *Limnopithecus legetet*, stereo occlusal view. (Scale : 10 mm).

The left M3/, NAP IV 29’09, is reduced distally, the metacone being significantly smaller than the paracone, and the hypocone vestigial and separated from the protocone by a groove (Fig. 46). Nevertheless, the two anterior cusps are large and pyramidal, the protocone being almost conical. The lingual cingulum is crenulated and broad and wraps round the mesial side of the protocone, where it ends at the base of the preprotocrista. It extends distally where it surrounds the reduced hypocone. The mesial cingulum extends across the anterior base of the paracone closing off a mesial fovea that is about half the breadth of the tooth. The trigon basin is capacious and shaped like an inverted pyramid, with a narrow buccal slit at the base between the paracone and metacone. The distal fovea is small and complicated by enamel which is raised into small pustules or cusplets. The roots are quite small, and are inclined gently to the rear, the two buccal ones being closely applied to each other and quite a bit shorter than the lingual root.

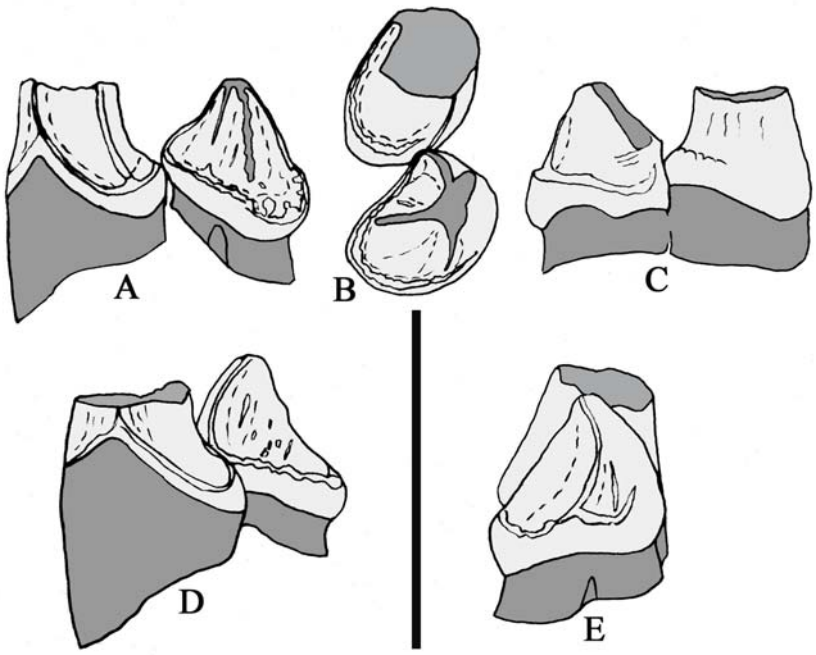

Figure 47. NAP IV UMP 66-07, right mandible fragment containing c/1 and p/3, *Limnopithecus legetet*, A) lingual, B) occlusal, C) buccal view showing small honing facet, D) slightly oblique mesial view, and E) distal view. (Scale : 10 mm).

Nap IV UMP 66-07, is a small fragment of right mandible containing part of the canine and the p/3 (Fig. 47). The canine has a strong lingual cingulum and a high mesial shoulder (broken in this specimen, but its position is not low). The lingual ridge is robust, the mesial and distal lingual concavities, small. The p/3 is a short, broad tooth with a prominent lingual ridge. The mesial and distal foveae are small, and there is a low depression on the buccal side of the crown, just anterior to the posterior stylid. A low crest rises up this depression. The honing facet is large.

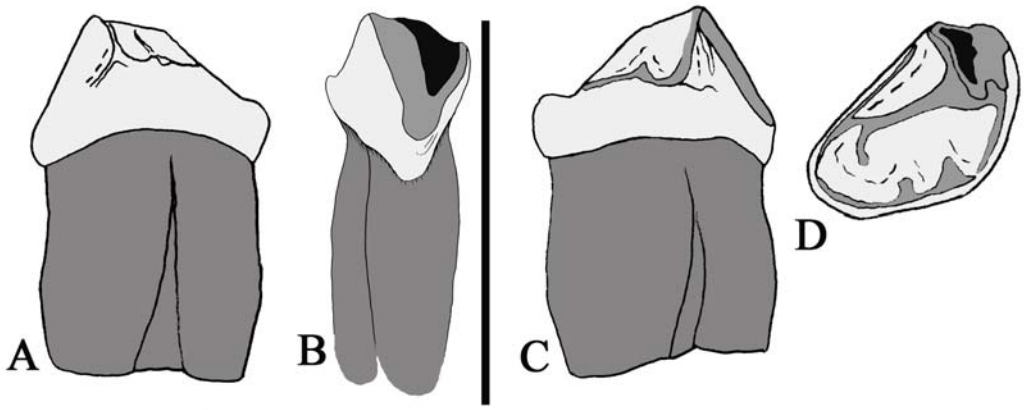

Figure 48. NAP IV UMP 66-12, right p/3, *Limnopithecus legetet*, A) mesial, B) buccal view showing extent of honing facet, C) distal, and D) occlusal views (light grey - unworn enamel, medium grey - worn enamel, dark grey – root, black – dentine). (Scale : 10 mm).

NAP IV UMP 66-12 is a moderately worn right p/3, with dentine exposed at the apex and down the mesial surface where it forms a distinct honing facet (Fig. 48). The lingual ridge extends from the middle of the distal cingulum, upwards to apex, and for this reason the mesial fovea is much larger than the distal one, which is almost vestigial in this specimen.

Figure 49. NAP IV 82’08, right m/2, *Limnopithecus legetet*, stereo occlusal view. (Scale : 10 mm).

NAP IV 82’08, a right m/2 which has just entered wear, shows a well proportioned mesial fovea bordered anteriorly by a thick mesial cingulum (Fig. 49). The mesial part of the crown is somewhat narrower than the distal part. The distal part of the fovea connects with the talonid basin, the crests forming the distal wall being rather low and separated by a slit. Likewise the connection to the buccal shelf between the protoconid and hypoconid is not encumbered by crests. The distal fovea is contiguous with the talonid basin, and the shelf between the hypoconid and hypoconulid is reduced due to the fact that these two cusps are close together, the so-called “twinning” of Rossie & MacLatchy, 2006. The enamel in the floor of the talonid basin is rugose, especially at the base of the entoconid. The lingual spout of the talonid basin is low and slit-like. There are two stout, transverse ovoid roots.

NAP I UMP 62-17 (Fig. 50) is a plastically deformed mandible containing deeply worn cheek teeth (p/4-m/2) and the roots of the canine and p/3. Little detail can be discerned from the remains of the teeth, save for the fact that the p/4 is short and broad, the m/1 distinctly narrower mesially than distally, and significantly smaller than the m/2, which is also narrower mesially than distally. The buccal shelves are capacious, the distal fovea small and the talonid basin expansive. In these features, and in terms of its dimensions, this specimen is close to the holotype of *Limnopithecus legetet* and to NAP IX BUMP 268. Like the latter specimen, there is a strong connection between the hypoconulid and the entoconid, which are now joined to each other by an exposure of dentine.

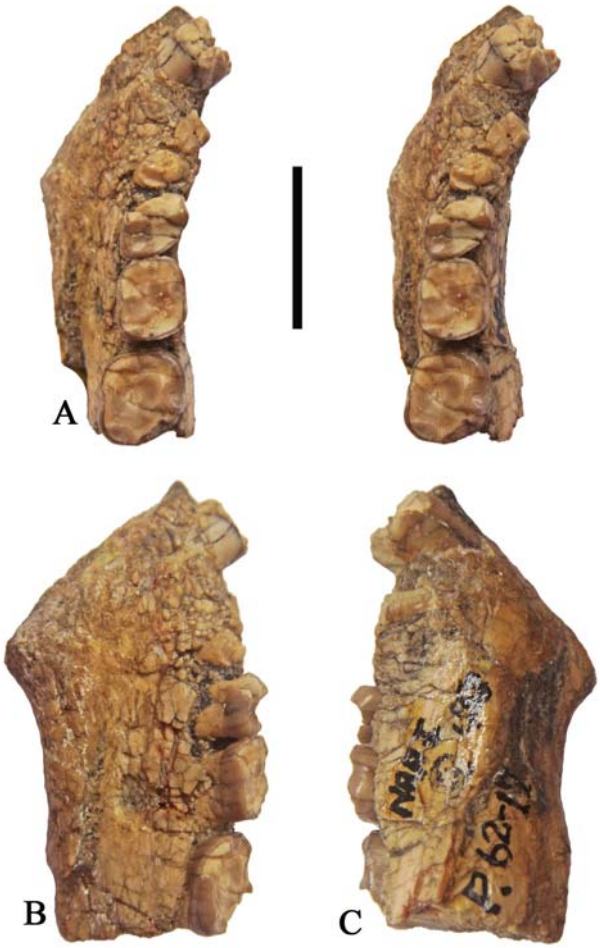

Figure 50. NAP I UMP 62-17, plastically deformed right mandible with damaged and deeply worn cheek teeth, *Limnopithecus legetet*, A) stereo occlusal view, B) lingual, and C) buccal views. (Scale : 10 mm).

Discussion

The presence of *Limnopithecus legetet* at Napak is based on comparisons with the holotype of the species from Koru (M 14079). The mandible NAP IX BUMP 268 (paratype of *Lomorupithecus harrisoni*) in particular, has molars which are close morphologically and metrically to those in the holotype of *Limnopithecus legetet* (Fig. 37).

There are resemblances between teeth attributed to *Limnopithecus legetet* and those of *Micropithecus clarki*, but the teeth of the former species are larger than those of the latter. Most of the specimens from Kenya identified as *Micropithecus clarki* belong to *Limnopithecus legetet*, which raises questions concerning the validity of the genus *Micropithecus*. We here retain the genus, because the fossil record of both species is not yet good enough to remove the doubt that persists.

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 clarki* Fleagle & Simons, 1978

Diagnosis: A species with dental and cranial dimensions similar in size to those of *Cebus albifrons* and significantly smaller in cheek teeth dimensions than any described species of *Limnopithecus*, *Dendropithecus*, *Dryopithecus* or *Pliopithecus* (Original diagnosis from Fleagle & Simons, 1978).

Holotype: NAP IV UMP 64-02, snout with left canine root, M1/-M3/ and right P3/-M3/ (P3/ lost but cast available).

Type locality : Napak IX, Uganda.

Referred material from Napak : NAP V 87'02, right I1/; NAP V 7'98, left I1/; NAP V 8'98, right C1/; NAP V 65'08, right C1/; NAP IV UMP 66-33b, left DM3/; NAP XV 36'08, left P3/; NAP V 221'09, right maxilla fragment containing C1/-P4/; NAP IV 221'08, right maxilla containing P3/-M2/; NAP IV 26'04, left P4/; NAP IV 70'05, left DM4/; NAP IV 85'08, right DM4/; NAP IV 51'04, left maxilla fragment containing M1/-M2/; NAP IV UMP 66-09, left M1/; NAP V 103'06 + UMP 66-28a, left M2/; NAP IV 16'07, right i/1; NAP IV UMP 66-28b right i/2; NAP V UMP 66-34, left i/2; NAP IV 81'08, right i/2; NAP IV UMP 62-18, left c/1; NAP IV UMP 66-32, right c/1; NAP IV 15'07, right c/1; NAP V 117'09, left mandible fragment containing alveolus of canine, and crowns of p/3 and p/4; NAP IV 6'85, left c/1; NAP I 6'10, right c/1; NAP V UMP 66-17, right p/3; NAP V UMP 66-22, right mandible fragment containing roots of i/1 and i/2, c/1 (lacking the apex) and p/3; NAP IV UMP 66-30a, left p/4; NAP XX1 15'10, right p/4; NAP IV 229'09, right p/4; NAP IV 175'09, left m/1; NAP V 89'09, right m/1; NAP IV UMP 66-08, left m/1; NAP IV UMP 66-13, right m/3; NAP I edentulous right mandible fragment containing roots of p/3-m/1; NAP IV 225'09, right m/2; NAP XV 325'08, edentulous mandibular symphysis.

Stratigraphic context: Napak Member above the nepehlinite lava flow, Akisim, Uganda.

Age: Early Miocene, Faunal Set P I, levels with *Dorcatherium songhorensis*, as well as younger levels with *Dorcatherium iririensis* and *Dorcatherium piggoti*. One specimen, a p/4 is from Napak XXI, which is probably below the nephelinite lava.

Description of new material

The most informative new specimen from Napak attributed to *Micropithecus clarki*, is a right maxilla (NAP IV 221'08) containing P3/-M2/, and parts of the alveoli of the canine and M3/ (Fig. 51, 52). In ventral view, part of the gutter that borders the palate opposite the M2/ and M3/ is preserved, the remaining parts resembling those of the holotype of the species (NAP IV UMP 64-02) in which this gutter is deep and wide, curving buccally behind the third molar. In its depths, there is a tiny foramen that communicates with the nasal cavity. The maxillo-palatine suture, which is missing in the holotype due to damage, is seen to climb out of this gutter opposite the second molar and then to zigzag slightly obliquely across the palate to the midline.

The incisive foramen has been almost obliterated by damage, but a tiny remnant is preserved near midline opposite the canine, as in the holotype. Also like the type specimen, there is a tiny nutritive foramen in the palate close to the canine. A significant difference between these two specimens is the position of the zygomatic process of the maxilla. It is positioned further anteriorly in NAP IV 221'08 than it is in NAP IV UMP 64-02. The malar tubercle is distinct in both specimens, but is opposite the rear of M2/ in the holotype specimen and opposite the rear of M1/ in NAP IV 221'08. The infraorbital foramen is a single large hole in NAP IV 221'08, positioned above the P3/. In NAP IV UMP 64-02 in

contrast, there are two small foramina, one above and behind the other, but both located above the P4/. The rear of the root of the zygomatic process, where it departs from the main body of the maxilla, is located above the middle of M2/ in NAP IV 221’08, and above the M3/ in NAP IV UMP 64-02.

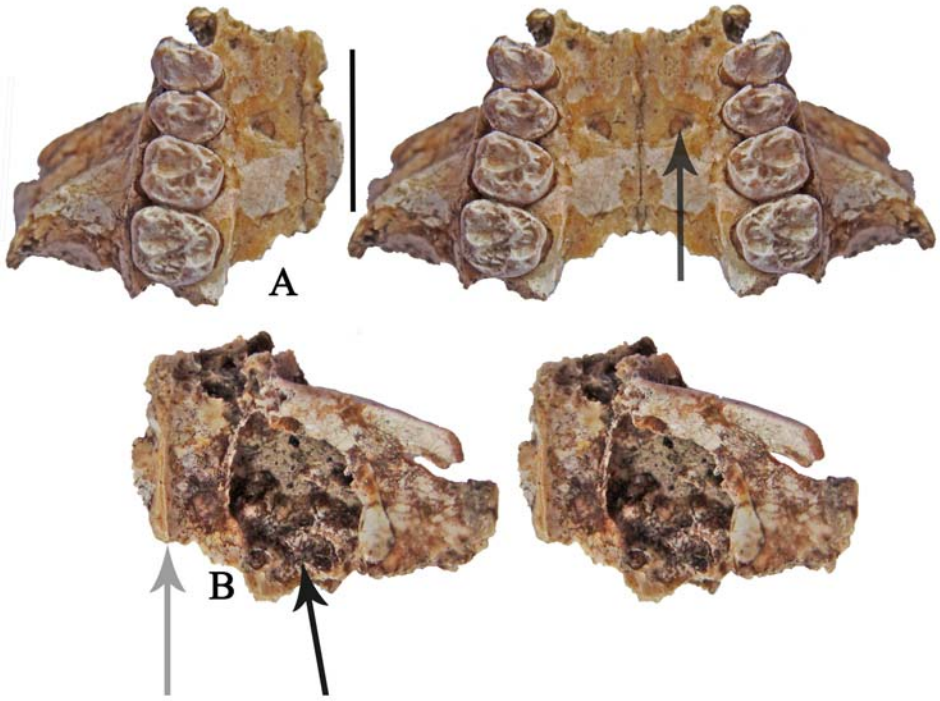

Figure 51. NAP IV 221’08, *Micropithecus clarki*, right maxilla containing P3/-M2/, A) stereo occlusal view with mirror image, B) stereo dorsal view (Grey arrow in B. - intermaxillary suture, black arrow in A. - perforation in palate, black arrow in B. - maxillary sinus). (Scale : 10 mm).

In lateral view, the maxillo-jugal suture ascends obliquely from above the malar tubercle anteriorly towards the orbital margin where it terminates above the infra-orbital foramen. A similar suture occurs in the holotype of *Micropithecus clarki*. Distally, behind the malar tubercle, this suture descends when it reaches the temporal fossa, such that the posterior wall of the fossa is comprised of the jugal bone rather than the maxilla. The anteriormost part of the orbital margin is positioned above the front of P3/, immediately above the infra-orbital foramen, the apex of the canine alveolus lying just in front of, and beneath this point. In the holotype, this part of the orbital margin is broken.

In dorsal view, NAP IV 221’08 is seen to possess a vast maxillary sinus that extends from immediately behind the canine to above the M3/, where its distal part is broken. The sinus invaginates between the tooth roots, which are protected by bony capsules which poke up out of the floor and walls of the sinus. Laterally, opposite the level of the front of M1/, there is a thin sliver of bone separating the sinus into two locules. The bone in the vicinity of the sinus appears to be extremely thin and fragile. In the holotype in contrast, the maxillary sinus is not as deeply invaginated between the tooth roots, but apart from that it seems similar in dimensions and general lay out.

In posterior view, the zygomatic arch of NAP IV 221’08 is seen to be gracile and dorso-ventrally shallow (thickness : 2.3 mm, height : 5 mm) which contrasts with the more robust arch in the holotype (thickness : 2.7 mm, height : 8 mm).

In anterior view, although the premaxillae are missing, what is preserved of the nasal cavity reveals that it is broad low down and narrows slightly dorsally. The orbits in NAP IV 221’08 are more complete medially and laterally than those of the holotype. They are wide and large, the distance between the lateral margins of the orbits as preserved (25 x 2 = 50 mm, implying a figure somewhat greater than this prior to breakage) is double the breadth of the palate measured between the lateral walls of the alveolar processes (palatal breadth opposite M1/ – 12.7 x 2 = 25.4 mm). These figures

indicate that *Micropithecus clarki* was endowed with large orbits, a point already mentioned by Fleagle & Simons (1978) and Harrison (1988).

The teeth of NAP IV 221'08 are less worn than those of the type specimen (Fig. 52), and because of this, they have suffered less interstitial wear than the latter individual. Partly for this reason, the mesial and distal foveae of the premolars in particular, are mesio-distally longer than they are in the type specimen. The subsidiary wrinkles in the enamel of the occlusal surface of the molars have been eradicated by wear in the type specimen, but are clearly preserved in NAP IV 221'08. The buccal cusps of the P3/ and P4/ are appreciably taller than the lingual cusps, a point that could not be ascertained in the holotype due to the advanced wear. The expanded lingual cingulum in the upper molars is clear in both specimens, imparting as it does a rounded profile to the tooth, rather than the more usual rectangular occlusal outline common to many hominoids.

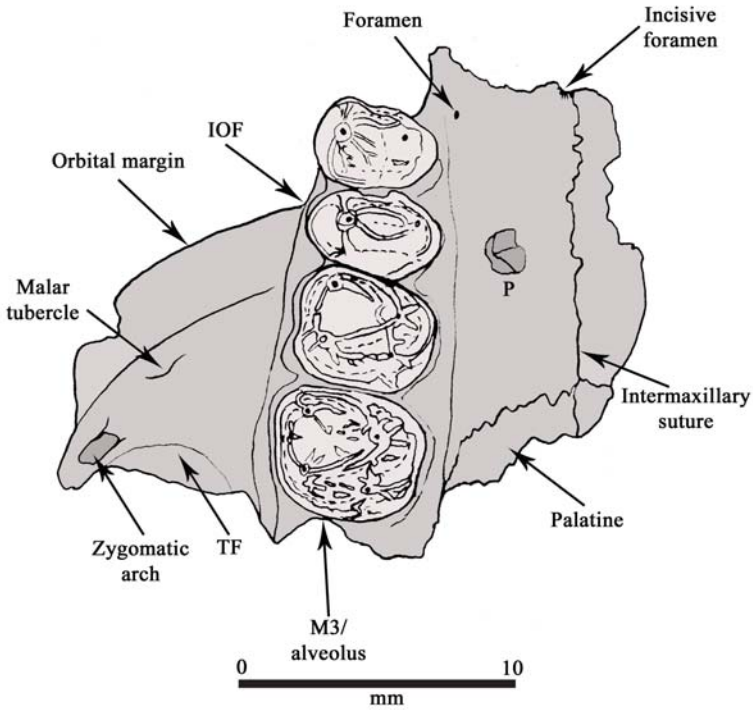

Figure 52. NAP IV 221'08, *Micropithecus clarki*, right palate containing unworn P3/-M2/, ventral view. (IOF – infra-orbital foramen, P – perforation in palate, TF – temporal fossa). (Scale : 10 mm).

The canine alveolus of NAP IV 221'08 is partly preserved. Its depth implies a small root ca 7 mm tall, or perhaps very slightly more. This contrasts with a root about 11 mm tall (measured along the anterior side) in the holotype. In both specimens, the canine alveolus is narrower bucco-lingually than the alveoli of the P3/, implying a relatively narrow tooth, confirmed by the dimensions of the root remaining in the holotype (maximum diameter : 4.3 mm, minimum diameter : 3.5 mm).

The P3/ of the holotype was broken during preparation, but its roots remain, showing two slender buccal roots that are fused together for much of their length, and a single lingual root. A flake of bone missing from the alveolus of the P3/ in NAP IV 221'08, reveals similar root morphology. The crown of P3/ is asymmetrical, longer buccally than lingually, with the distal fovea longer than the mesial one. The crests separating the fovea from the central basin are low and narrow, and would rapidly disappear with wear.

In the P4/, the buccal cusp is marginally taller than the lingual cusp. The crests bordering the foveae are stronger, a feature also occurring in the holotype. The distal basin of NAP IV 221'08 is mesio-distally longer than that in the holotype.

The M1/ of NAP IV 221’08 differs in slight ways from its counterpart in the type specimen. The broadest part of the crown is opposite the centre of the protocone, whereas in NAP IV UMP 64-02 it is slightly further back, opposite the rear of this cusp. Apart from that, the differences are slight and are mostly due to the different states of wear of the teeth. The same observations apply to the M2/s.

Interpretation of the differences between NAP IV UMP 64-02 and NAP IV 221’08

Some of the differences between the NAP IV UMP 64-02 and NAP IV 221’08 are flagrant, including the presence of a shorter face in the latter specimen (as discerned by the position of the facial structures relative to the tooth row). Other differences are more subtle and are due to individual variation or to differences in wear states of the teeth. However, the dimensions of the canine alveolus in NAP IV 221’08 indicate that the tooth would have been substantially smaller than that of NAP IV UMP 64-02 (root height 7 mm versus 10 mm). Canines of extant primates are, in general, sexually dimorphic, only a few taxa possessing monomorphic or unimodal canines (gibbons for example (Pickford, 1986)). Typically size differences between the sexes are marked (more than 10% ranging up to 30% in extreme cases). Molars of species with highly dimorphic canines, in contrast, show almost complete morphometric overlap between the sexes.

The obvious morphometric similarities between the posterior cheek teeth of NAP IV 221’08 with those of NAP IV UMP 64-02, combined with the difference in canine root height of the two specimens, suggest that the holotype was probably a male individual, and NAP IV 221’08, a female. Female catarrhines usually possess shorter faces than males (extremely marked in baboons, but also generally the case in colobines and macaques) and this may explain the differences in facial structure between NAP IV 221’08 and NAP IV UMP 64-02.

On this basis we conclude that NAP IV 221’08 is a member of *M. clarki*, despite the morphological differences in facial architecture and position of the face relative to the cheek teeth.

Taphonomy of NAP IV 221’08

NAP IV 221’08, comprises the right maxilla of a young adult small ape comparable in dimensions to the White fronted Capucin (*Cebus albifrons*) (Defler, 1979; Harrison, 1988), the body weight of which is ca 3 kg (males range in weight from 1.7 to 3.2 kg : females from 1.4 to 2.2 kg). The fossil is missing the parts anterior to the middle of the canine alveolus, and is broken obliquely distally at the level of the mesial part of the M3/ alveolus. A small sliver of palatine is preserved between the distal break and the maxilla. A small part of the left maxilla is preserved opposite the P4/-M1/. In lateral view the specimen shows the base of the orbit curving upwards and backwards where it ends at a jagged break just anterior to the level of the zygomatic root. The zygomatic arch is broken at the level of the junction between M2/ and M3/. In dorsal aspect, the roof of the maxillary sinus is missing, exposing a vast sinus beneath. Two prominent capsules that contain the lingual roots of M1/ and M2/ respectively, rise from the floor of the sinus at its medial border, and laterally, the capsules for the buccal roots of the M2/ can be seen rising as rounded ridges up the lateral wall of the sinus. The maxillary sinus thus extends deeply between the roots of the cheek teeth, almost to gingival level, and the roof of the sinus was apparently extremely thin, judging by the slimness of its broken edges. Ventrally, opposite the P4/, midway between the intermaxillary suture and the alveolar process, there is an ovoid depression ca 2 mm broad, in which three flakes of bone have been forced upwards, displacement being maximal near the alveolar process, decreasing towards the periphery of the depression medially. The apex of the depression forms a fine point (Fig. 52).

The depression in the palate of NAP IV 221’08, resembles those produced on young monkey skulls by the talons of Crowned Hawk-Eagles (Sanders *et al*., 2003). Typically, perforations due to Hawk-Eagle talons range in diameter from 2-10 mm. Typically also, the depression is not symmetrical. Even though the puncture mark in the fossil falls at the low end of the range of variation observed by Sanders *et al*., (2003), the perforation is asymmetrical, suggesting that it is more likely to have been made by a raptor than by the canine of a carnivore, which tends to produce almost symmetrical perforations in which the apex is blunter. The rest of the damage to the Napak specimen accords with such a scenario, but on its own would not be sufficient to postulate predation of the individual by such

a raptor. It is thus possible that during the early Miocene small hominoids sometimes fell victim to raptors, just as small monkeys continue to do so today.

Other raptors are known to prey on small monkeys, hyracoids and other prey in the size range of the Napak hominoid (see references in Sanders *et al*., 2003). One of these is Verreaux' Eagle, which is endemic to Africa. Given that NAP IV 221'08 has an exceptionally short face, judging from the position of the anterior margin of the orbit and the infra-orbital foramen relative to the position of the canine and P3/, it was likely a highly arboreal mammal. There may also be a contribution from sexual dimorphism – the fossil could represent a female individual. The slenderness of the maxillary bone surrounding the roots of the upper molars indicates that this species consumed foods that did not require heavy mastication or prolonged chewing, which indicates a diet likely comprised of soft, ripe fruit. Crowned Hawk-Eagles frequently prey on forest animals, whereas Verreaux' Eagles tend to hunt in more open country (rocky kopjes, grassy plains). Thus, it is perhaps more likely that NAP IV 221'08 fell prey to a Crowned Hawk-Eagle than to a Verreaux' Eagle, but clearly, the identification of the predator will remain uncertain.

Damage to NAP IV UMP 64-02

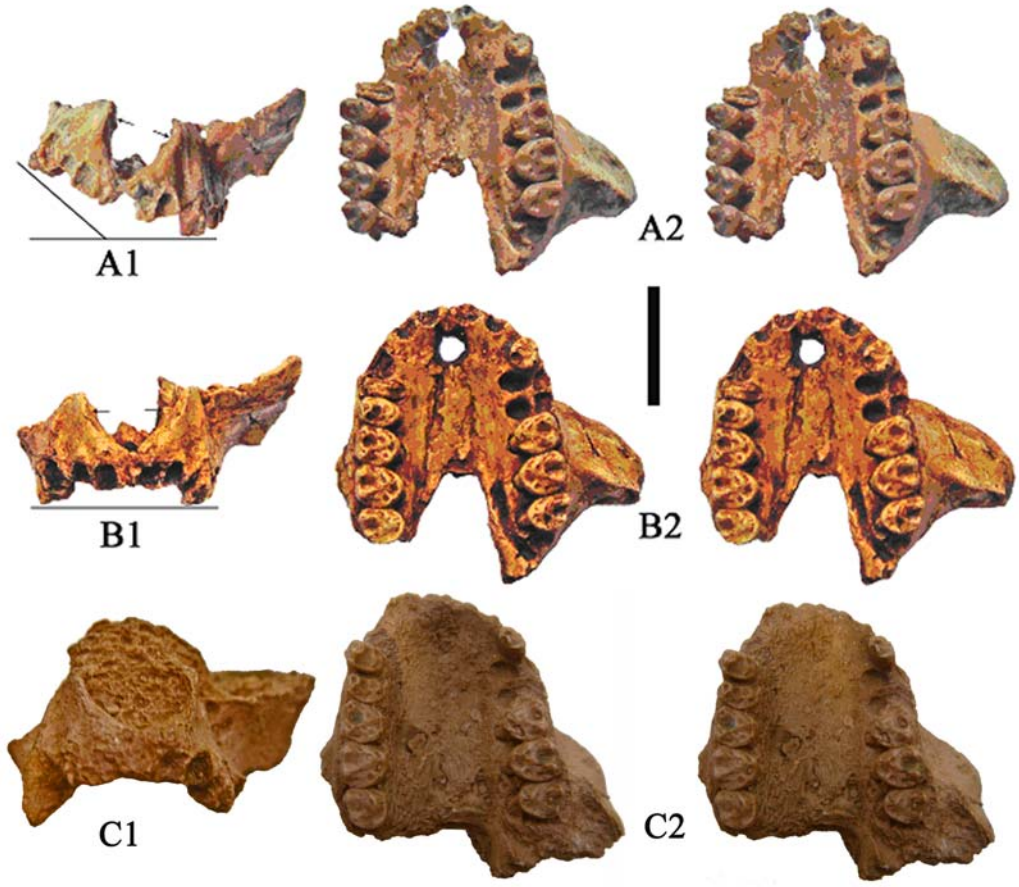

Figure 53. NAP IV UMP 64-02, *Micropithecus clarki*, successive stages of damage to the snout caused during preparation and casting, A) specimen as reconstructed after suffering damage between January 2003 and January 2004, B) cast of the specimen made in 2002, before the specimen was damaged for the second time, C) cast of the specimen made before the right P3/ was lost. Note in A) the high angle at which the two halves of the palate have been joined together, resulting in a narrowed nasal cavity, and a broadened palate (pieces aligned using the better preserved left maxilla as the baseline). Note also the loss of substantial bone mass in the vicinity of the palatines in C2 and B2, and the narrowing of the nasal aperture between C1 and B1. (A1, B1 and C1 - anterior views, A2, B2 and C2 - palatal views). (Scale : 10 mm).

NAP IV UMP 64-02 has suffered extensive damage since it was collected in the early 1960's (Fig. 53).

Even before it was described, the right P3/ was lost during preparation and casting (Fleagle & Simons, 1978). A cast made by the UPE in 2002 shows that at that time the two halves of the palate were in their original condition, with only a slight angle between the occlusal planes of the cheek teeth as is normal in primates. Between January 2003 and January 2004, when the fossil was on loan in America, the palate was severely damaged, and stuck together with a product that separates the two halves of the palate along a jagged fracture to the left of midline. A similar fracture has affected the right side which has been glued back with a slight gap between the pieces and some misalignment of the palatal surface. The outcome of this damage and faulty reconstruction, is that the tooth rows are no longer properly aligned, and the angle between the occlusal planes of the cheek teeth is severely distorted.

Measurement	**Original prior to damage**	**Current after damage**
Distance between lingual margins of M1/s	13 mm	16.5 mm
Distance between lingual margins of M3/s	14.1 mm	17.6 mm
Internal distance between margins of nasal cavity	11 mm	7.8 mm

NAP IX UMP 68-25

At the same time that the holotype snout of *Micropithecus clarki* was fractured and badly reconstructed, the frontal bone attributed to *Micropithecus clarki* was also severely damaged (Fig. 54). This specimen was returned to Uganda in January, 2004 by Dr L. MacLatchy, Boston University, who had had it on loan since January, 2003. The fossil was broken along the metopic suture and stuck together with a thick layer of transparent glue - the two halves of the frontal are no longer in their natural alignment and the endocranial mold no longer fits snugly into the endocranial space as it did in 2002.

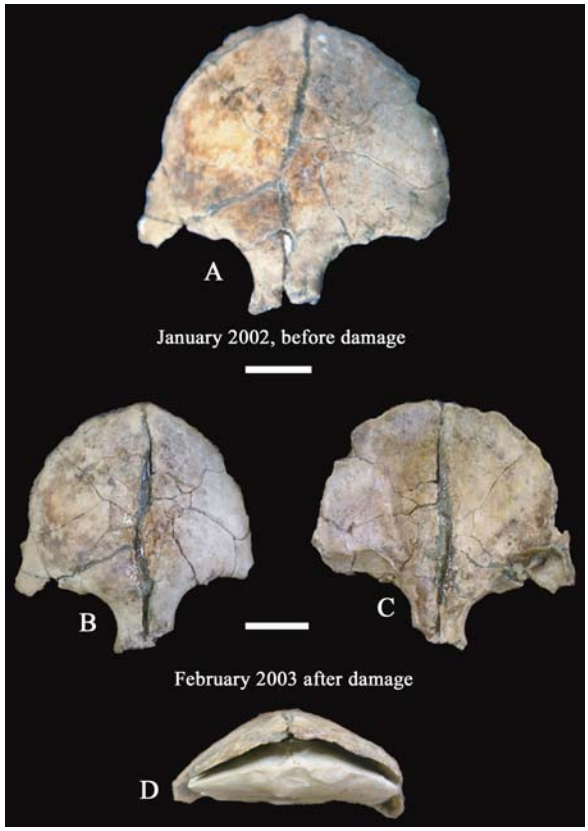

Figure 54. NAP IX UMP 68-25, small ape frontal bone. A) image taken in January 2002 before the specimen was damaged, and B-D) images taken in February 2004 after the fossil had been damaged. B) external view, C) internal view, D) posterior view showing the distortion of the frontal relative to the original endocranial mold beneath it. (Scale : 10 mm).

Upper incisors

Figure 55. NAP V 7’98, left upper central incisor, *Micropithecus clarki*. A) lingual, B) labial, C) mesial, and D) distal stereo views. (Scale : 10 mm).

The left upper central incisor, NAP V 7’98, is small, low crowned and with a spatulate distal margin (Fig. 55). It shows a prominent lingual ridge emanating from a swelling in the lingual cingulum, and narrowing apically, fading out beneath the cutting edge of the tooth. The lingual cingulum rises gently towards the mesial marginal ridge, with which it merges without any obvious change in direction. The distal part of the lingual cingulum, in contrast, descends gently before curving distally and apically to merge with the distal marginal ridge at the most distal point of the crown. The labial surface is gently convex throughout.

Figure 56. NAP V 87’02, *Micropithecus clarki*, right I1/, A) stereo lingual, B) distal, C) labial, and D) mesial views. (Scale: 10 mm).

NAP V 87’02, a right upper central incisor has a small crown with a spatulate distal half, and a small lingual ridge (Fig. 56). The latter structure is not linked to the lingual cingulum at its base, and it fades out apically. The lingual cingulum rises towards the mesial marginal ridge, and descends distally before curving apically to merge with the distal marginal ridge. The labial side is convex save for a small planar zone near the mesial edge of the crown.

Upper canines

Figure 57. NAP V 8’98, unworn upper right canine with incompletely formed root, *Micropithecus clarki*, probably a female individual, A) lingual, B) distal, C) mesial, and D) buccal views. (Scale : 10 mm).

From Napak V, there is an unworn right upper canine (NAP V 8’98) (Fig. 57) similar to the specimen *in situ* in maxilla fragment, NAP V 221’09. The mesial groove is deep and prominent, the lingual pillar robust, the crown is convex buccally from apex to base, the lingual side is strongly scooped out, the distal crest curves lingually as it descends towards cervix, there are well developed swellings where the sharp lingual cingulum meets the mesial and distal crests and there is a deep waisting beneath cervix : the root is appreciably narrower than the crown, usually a sign that the tooth belongs to a female individual.

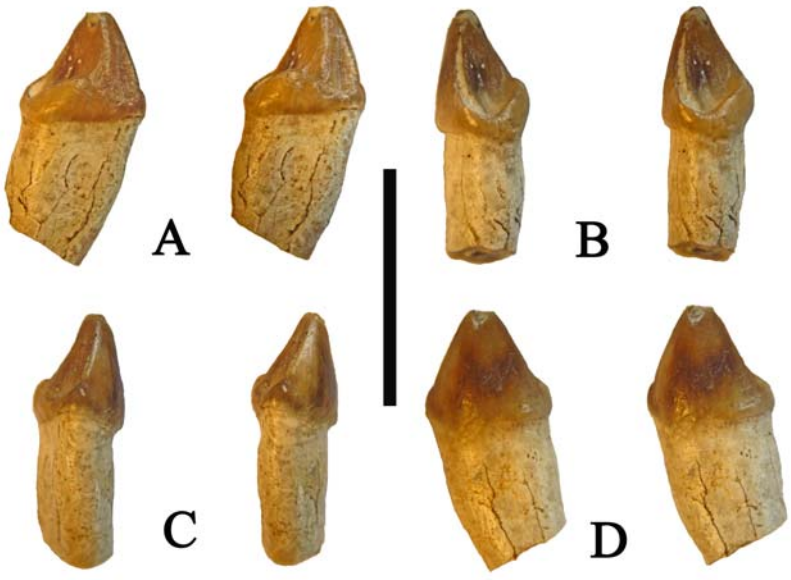

Figure 58. NAP V 65’08, right upper canine, *Micropithecus clarki*, A) lingual, B) distal, C) mesial, and D) buccal views. (Scale : 10 mm).

NAP V 65’08 is a lightly worn upper right canine of a small hominoid (Fig. 58). There is distinct waisting beneath cervix, and the crown is low, suggesting that we are dealing with a female individual. The apex of the root is missing, but we estimate from the half that remains, that the original height could not have exceeded 10 mm. The basic morphology of the tooth is compatible with that of NAP V

221’09, including a marked buccal cant of the crown on the root, a well developed lingual cingulum, a distal concavity on the lingual surface which is appreciably more extensive than the mesial one, absence of a mesial groove or depression on the buccal aspect of the tooth, the development of a low swelling basally where the anterior crest meets the lingual cingulum, the flattened lingual side of the root (in this specimen even sporting a shallow depression running from cervix apically) producing a D-shaped section. The crown is distinctly lower than that of NAP V 221’09 (5.1 mm, allowing for the presence of an apical wear facet which has removed a tiny amount of enamel, versus 7 mm in NAP V 221’09) (Fig. 59). On the basis of NAP V 65’08 and NAP V 221’09, which are from the same site, we conclude that *Micropithecus clarki* possessed sexually dimorphic and bimodal canines.

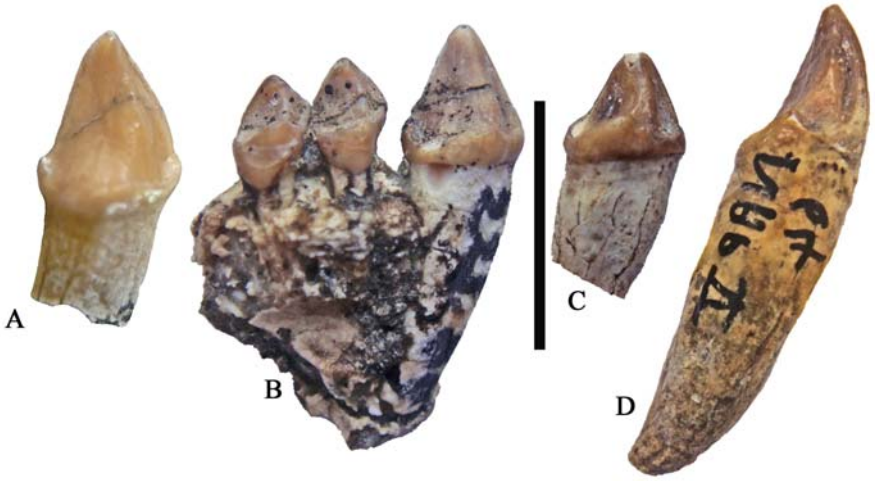

Figure 59. Four upper canines of small apes from Napak V, Uganda, in lingual view, cervix oriented horizontally. A-C) *Micropithecus clarki*, D) *Limnopithecus legetet*. A) NAP V 8’98 right upper canine, B) NAP V 221’09, right canine in maxilla associated with P3/ and P4/, C) NAP V 65’08, right canine, D) NAP V UMP 66-19, left canine (image reversed). (Scale : 5 mm).

Maxilla NAP V 221’09

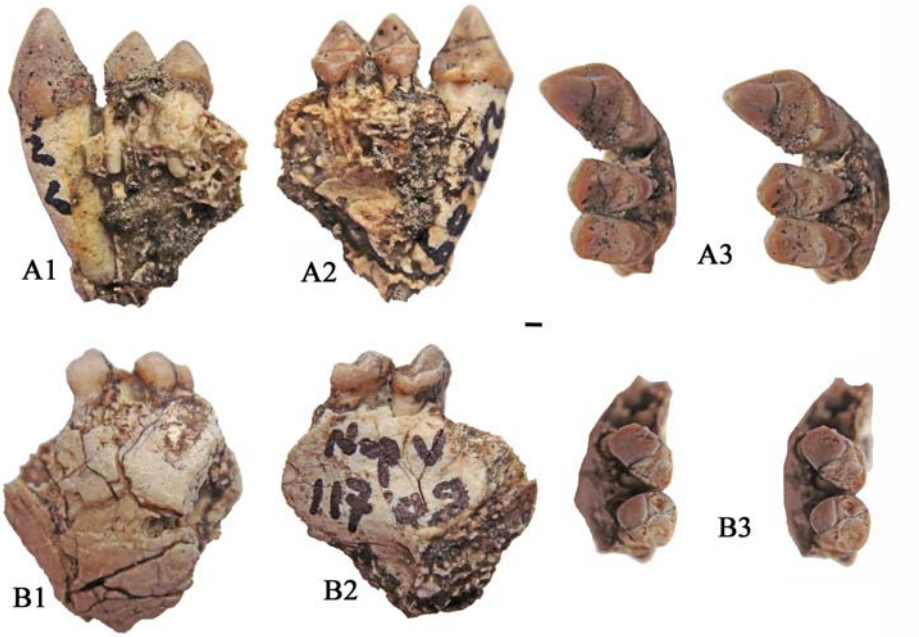

Figure 60. *Micropithecus clarki*, A) NAP V 221’09, right maxilla fragment containing C1/-P4, A1) buccal, A2) lingual and A3) stereo occlusal views, B) NAP V 117’09, left mandible fragment containing p/3 and p/4, B1) buccal, B2) lingual, and B3) stereo occlusal views. (Scale 10 mm).

By coincidence, a right maxilla with three teeth found at Napak V during the 2009 field season was given the same number as a specimen from the 2008 field season collected at Napak IV. Thus attention should be paid to the site and year of collection which serve to distinguish the specimens, both of which are attributed to *Micropithecus clarki*. The specimen from Napak V (Fig. 59, 60A) is a poorly preserved right maxilla fragment containing the well preserved canine and both premolars, all unworn. This is the first specimen of *Micropithecus clarki* to have these teeth associated with each other, which is important for attributing isolated canines to their relevant taxa. As we shall see, most previous attributions of canines to this genus are doubtful for one reason or another.

The canine in NAP V 221'09 is unusual in a hominoid context, as its mesial groove is extremely shallow and the lingual pillar has low relief. In many hominoids there is a shallow mesial groove on the buccal side of the tooth, close to the anterior crest. In NAP V 221'09, however, there is no sign of such a groove. The root of the tooth is compressed, producing a D-shaped section, and the crown is distinctly canted buccally on the root, such that in mesial view, the long axis of the root lies at a marked angle to the mesial crest of the crown.

The lingual side of the upper canine of NAP V 221'09 is concave save for the presence of a low relief lingual pillar, the disto-lingual concavity being appreciably more capacious than the mesio-lingual one. There is a prominent lingual cingulum extending from the base of the anterior crest to the base of the distal crest. Where the cingulum joins the anterior crest it forms a low swelling. The distal crest is in line with the anterior one, and both are in line with the buccal cusps of the upper premolars. The cervix is horizontal round the tooth save for the buccal side where it extends further up the root than elsewhere. The crown is slightly longer and broader than the root, but there is no obvious waisting beneath the crown. From this, and on the basis of the dimensions of the root (12 mm from cervix to apex measured along the anterior margin) we conclude that this specimen may represent a male individual.

The P3/ in NAP V 221'09 is useful in that its counterpart in the holotype was broken during preparation and casting, although Fleagle & Simons (1978) were able to describe it on the basis of a cast and photographs. The description of this tooth in NAP V 221'09 thus helps to complete that of the species. In occlusal view the crown is asymmetrical, the buccal side being longer mesio-distally than the lingual side. The buccal cusp is distinctly taller than the lingual one. The mesial fovea is narrow mesio-distally whereas the distal one is elongated. The anterior crest running from the buccal cusp lingually is small and low, ending on the mesial edge of the tooth about 1/3 in from the lingual side. The distal crest is barely visible. There is a low lingual cingulum, as in the P4/. The P3/ shows two buccal roots which diverge apically, as in the type specimen.

The P4/ in NAP V 221'09 is close in dimensions and basic morphology to its counterpart in NAP IV UMP 64-02. The main differences reside in the fact that this tooth is unworn in NAP V 221'09, and moderately worn in NAP IV UMP 64-02. The buccal cusp is distinctly taller than the lingual one, the mesial fovea is short mesio-distally and the distal fovea is not separated from the central basin by a ridge, unlike the condition in the type specimen. The lingual cingulum is comparable in the two specimens. The buccal root in NAP V 221'09 is a simple column with a hint of a buccal groove. This appears to be similar to the condition in the holotype. Despite the minor differences between these teeth, which we take to represent individual variation, we conclude that NAP V 221'09 fits comfortably within *M. clarki*.

***Discussion of the upper canines of* Micropithecus clarki**

Fleagle & Simons (1978) attributed two upper canines to *Micropithecus clarki*, one (NAP IV UMP 68-03) with some doubt, the other without hesitation. NAP V UMP 66-19 (Fig. 61) is somewhat bigger than NAP V 221'09, and in anterior view its crown is not as markedly canted on the root. The mesial groove on the lingual side is better developed, and unlike NAP V 221'09, the buccal side possesses a weak, shallow groove mesially. Like NAP V 221'09, the lingual side of the root is moderately compressed, but not to the extent of producing a D-shaped section. The leading edge of the canine is

more steeply oriented than in either NAP V 221'08 or NAP V 65'08 and its profile is convex rather than straight as in the other two specimens.

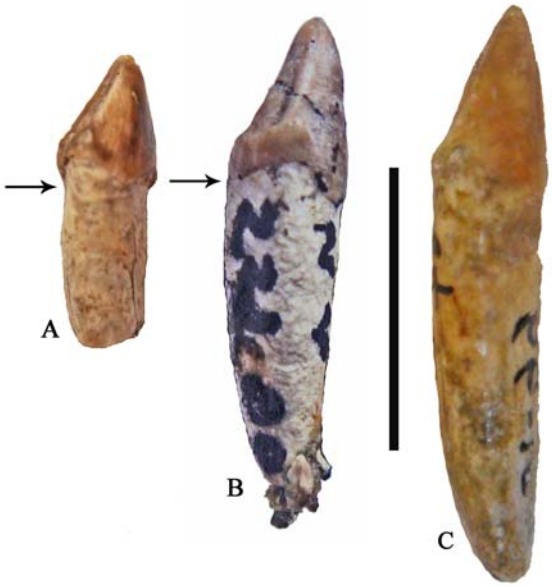

Figure 61. Mesial views of upper canines of small apes from Napak V. A-B) *Micropithecus clarki*, showing the marked buccal cant of the crown on the root. A) NAP V 65'08, right canine considered to represent a female, B) NAP V 221'09, right canine, C) NAP V UMP 66-19, left upper canine (image reversed) attributed to *Micropithecus clarki* by Fleagle & Simons (1978) but here considered to represent *Limnopithecus legetet*. Arrows point to the waisting beneath cervix. Note the difference in crown and root heights in specimens B and C. (Scale : 10 mm).

There are basically two possibilities regarding these three canines. Either, all of them could belong to *M. clarki*, in which case NAP V UMP 66-19 would represent a male and the other two specimens from Napak V would represent females, or, there are two taxa represented, one by NAP V UMP 66-19 which would not belong to *M. clarki*, but to another taxon. Its root is 16.2 mm long (Harrison, 1982), about 35% longer than that of NAP V 221'09. As such it would be far too long to fit with the holotype snout, NAP IV UMP 64-02, in which the canine root height was at most ca 10 mm, 11 mm if we are generous. UMP 66-19 has male morphology (lack of waisting beneath cervix, tall crown, long root) in contrast to NAP V 8'98, NAP V 221'09 and NAP V 65'08 which have the hallmarks of females (waisting beneath cervix, low crown, short root). On balance, therefore, we conclude that three upper canines (NAP V 8'98, NAP V 221'09 and NAP V 65'08) belong to *M. clarki*, whereas specimen NAP V UMP 66-19, is likely *Limnopithecus legetet*.

Deciduous upper molars

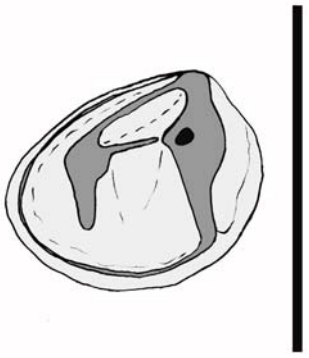

Figure 62. NAP IV UMP 66-33b, left DM3/, *Micropithecus clarki*, interpretive drawing, occlusal view. (Scale : 5 mm).

NAP IV UMP 66-33b, a left DM3/, is bicuspid, with a large paracone and smaller, lower protocone (Fig. 62). The mesial fovea, which is much smaller than the distal fovea, is separated from it by a well developed transverse crista extending between the paracone and protocone. The lingual cingulum is bucco-lingually broad but is low in relief.

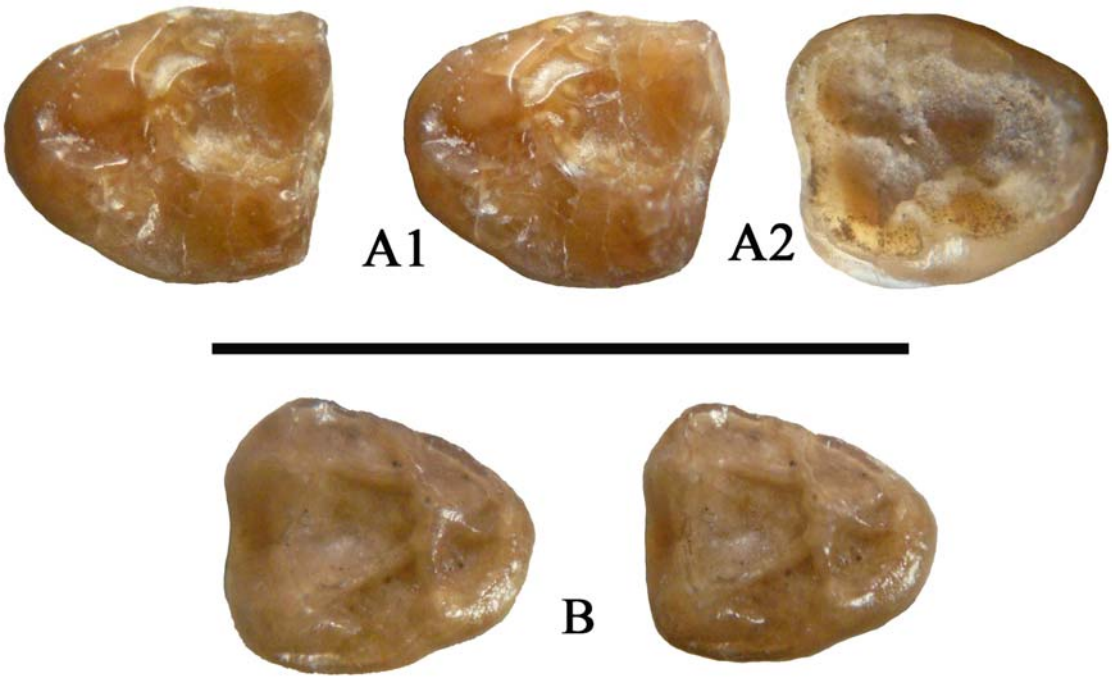

Figure 63. Upper deciduous molars from Napak attributed to *Micropithecus clarki*. A) NAP IV 70'05, left DM4/, A1) stereo occlusal view, A2) basal view showing resorption of roots, B) NAP IV 85'08, right DM4/, stereo occlusal view. (Scale : 10 mm).

NAP IV 70'05 is an upper left deciduous tooth (DM4/) in which the roots have been resorbed as is typical of teeth that are about to be shed (Fig. 63A). In occlusal view it is like a permanent molar save for the smaller hypocone and protocone which impart a more triangular outline to the tooth, the protocone cingulum is not as broad and is sharp edged rather than rounded, the buccal cusps are more trenchant (more bucco-lingually compressed) and it is smaller (MD x BL : 4.0 x 4.7 mm compared to 4.2 x 5.1 mm for the M1/ in the holotype specimen). In buccal view, the parastyle is more prominent than in the permanent molars.

NAP IV 85'08 is an informative specimen because it is unworn, and preserves all the cristae in excellent condition (Fig. 63B). There is a strong crest between the hypocone and protocone joining the protocone near the start of the crista obliqua, but not touching it. The crista obliqua extends across the tooth bucco-distally as far as the metacone. The preprotocone crista ends at the mesial cingulum in the midline of the tooth. It is joined on its way by a transverse crest emanating from the paracone. The latter crest and the crista obliqua separate the trigon basin from the mesial fovea in front and the distal fovea posteriorly. The metacone has a second crista descending disto-lingually but not as far as the hypocone, and thereby incompletely separates the distal fovea into two halves. The protocone has two short cristae descending towards the protocone cingulum. The parastyle is prominent. The lingual root is slanted strongly towards the palate, more so than in the permanent molars.

Upper premolars

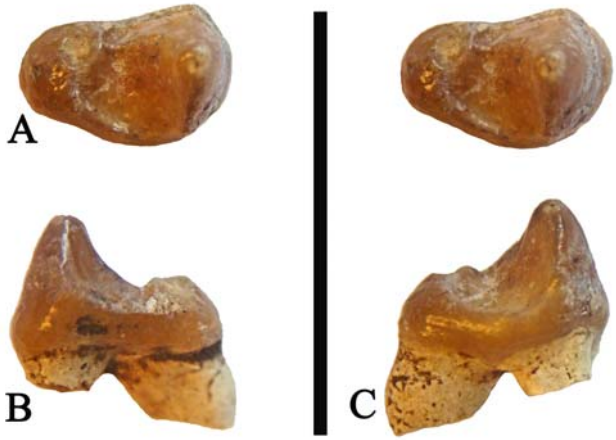

Figure 64. NAP XV 36’08, left P3/, *Micropithecus clarki*, A) stereo occlusal, B) mesial and C) distal view. (Scale : 10 mm).

NAP XV 36’08, is a very small upper left P3/, lacking much of the roots, but it is possible to see that there were two closely applied buccal ones, and a larger lingual one (Fig. 64). The paracone is appreciably taller and larger than the protocone. It has a shallow mesial groove between the preparacrista which leads directly mesially, and the crista that descends towards the centre of the tooth mesially. The mesial fovea is tiny. The distal basin is large with a relatively high wall between it and the mesial fovea. Its floor is smoothly concave and it is walled off distally by a well developed distal cingulum. The protocone, which is in an anterior position, and thus cramps the mesial fovea, has a dentine exposure at its apex. It sends a crista distally which merges into the distal cingulum. In buccal view, there are the merest hints of the parastyle and mesostyle.

Figure 65. NAP IV 26’04, left P4/, *Micropithecus clarki*, A) stereo occlusal, B) mesial, and C) distal views. (Scale : 10 mm).

NAP IV 26’04, a left P4/ in light wear, has dentine exposed on the apex of the paracone, and on the swelling located at the base of the preprotocone crista (Fig. 65). The mesial fovea is bucco-lingually broad, but because the protocone and paracone are in mesial positions, it is cramped mesio-distally. The distal basin, in contrast is capacious, bordered distally by a cingulum, which forms a small mesostyle where it meets the postparacrista. The two buccal roots are coalescent for most of their extent, but bifurcate near the apex. The apices of the two buccal roots and that of the lingual root curve sharply distally near their apices.

Upper molars

Figure 66. NAP V 103’06 + UMP 66-28a, left M2/, *Micropithecus clarki*, stereo occlusal view. (Scale : 10 mm).

Harrison (1982) identified the buccal half of a tooth (UMP 66-28a) as a left M2/ of *M. clarki*. The locality was unknown to Harrison (1982) but a label with the specimen erroneously recorded the locality as Napak IV. In 2006 the UPE collected the lingual half of the tooth at Napak V (NAP V 103’06) – the two pieces fit together perfectly (Fig. 66). The rounded lingual profile is characteristic of *M. clarki*, as is the large hypocone which is more lingually positioned than the protocone. The protocone cingulum is vast, forming a broad shelf accompanied by a mesial fovea and at the end of the median transverse valley. There is a crest leading from the hypocone to the protocone, but none between the hypocone and the crista obliqua.

Figure 67. NAP IV 51’04, left maxilla fragment containing M1/-M2/, *Micropithecus clarki*, stereo occlusal view of molars. (Scale : 10 mm).

NAP IV 51’04, is a left maxilla fragment containing the M1/ and M2/ (Fig. 67). The two molars are moderately worn, with dentine exposures on the apices of all four cusps. In addition, in the M1/, there is a small dentine exposure on the mesial end of the protocone cingulum, and in the M2/ there are dentine islands on the cingulum opposite the hypocone, and along its distal margin. The M2/ has a distal interstitial facet. The teeth in this maxilla are close in morphology to those of the holotype of *Micropithecus clarki*, which came from the same locality. In particular, the lingual position of the hypocone with respect to the protocone, and the protocone cingulum is broad. Both teeth have tiny buccal cingula, and the distal fovea is almost as large as the trigon basin. The mesial fovea is subdivided into two halves by the preprotocrista which terminates in the midline of the tooth.

Mandible

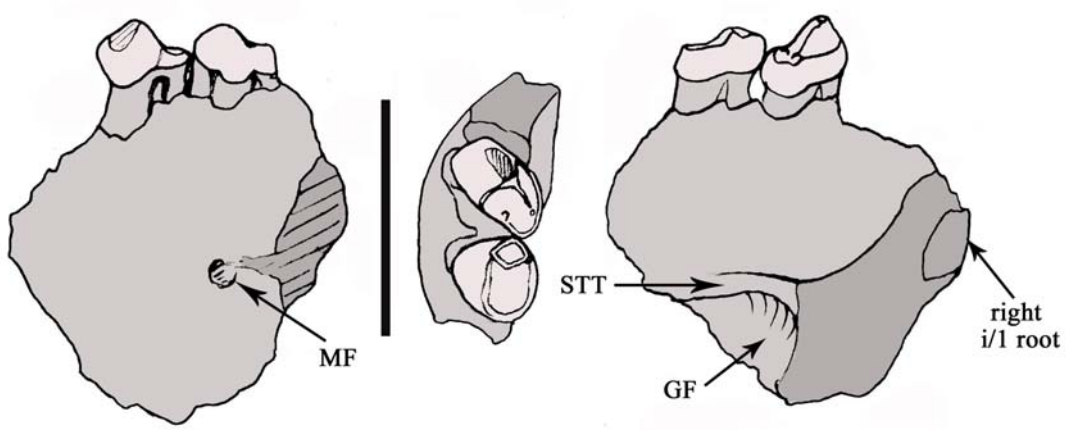

Figure 68. Interpretive drawing of NAP V 117'09, left mandible fragment containing p/3 and p/4, *Micropithecus clarki*. (GF – genial fossa, MF - mental foramen, STT – superior transverse torus)(from left to right, buccal, occlusal and lingual views). (Scale : 10 mm).

NAP V 117'09 is a left mandible fragment containing p/3 and p/4 and the alveoli of the incisors, the canine and the front root of m/1 (Fig. 60B, 68, 79). Medially it preserves part of the symphysis which shows a well developed genial fossa beneath a superior transverse torus. The ventral margin is damaged so it is not possible to determine whether it possessed an inferior transverse torus or not. In buccal view the mental foramen is observed beneath the gap between p/3 and p/4 lower than mid-height of the jaw. There are no gaps between the alveoli of the teeth. The canine alveolus is oval, oblique to the cheek tooth row.

Figure 69. NAP XV 325'08, fragment of left mandibular symphysis lacking teeth, *Micropithecus clarki*, stereo lingual view. (Scale : 10 mm).

NAP XV 325'08 is a small fragment of left mandibular symphysis containing the partial alveoli of the left second incisor, the canine and the p/3 (Fig. 69). The mental foramen is between the roots of the canine and p/3 in the lower part of the jaw. The incomplete symphyseal section shows part of the planum alveolare sloping distally to form a small superior transverse torus, beneath which is a capacious genial fossa.

Lower incisors

Figure 70. NAP IV 16'07, right i/1, *Micropithecus clarki*. A) mesial, B) labial, C) lingual, and D) distal views. (Scale : 10 mm).

NAP IV 16’07 is a lightly worn central lower incisor, probably from the right side (Fig. 70). In lingual view the apex of the root curves gently to the left and in labial view the root is bent towards the left with respect to the crown. The central lingual ridge is subtle, but clearly visible, and it extends from above cervix towards the cutting edge but fades out before reaching it. The mesial and distal marginal ridges are low and rounded. The labial side of the crown is evenly and gently convex.

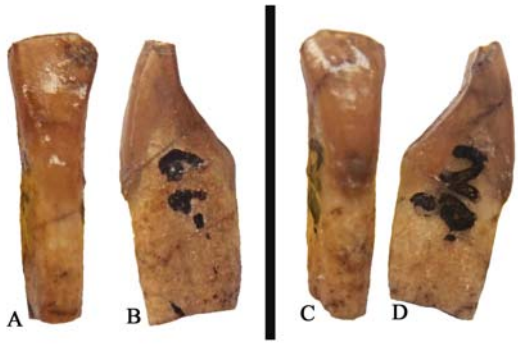

Figure 71. NAP IV UMP 66-28b, right i/1, *Micropithecus clarki*, A) lingual, B) mesial, C) labial, and D) distal views. (Scale : 10 mm).

NAP IV 66-28b is a heavily worn lower right i/1, which has lost a substantial part of the apex due to wear (Fig. 71). What is left of the crown is similar to NAP IV 16’07.

Figure 72. NAP IV 81’08, right i/2, *Micropithecus clarki*, stereo lingual view. (Scale : 10 mm).

NAP IV 81’08 is a right i/2 in light wear. In lingual view there are two sharp crests that rise towards the cutting edge, one in the centre of the tooth and one towards the distal side emanating from the lowest part of the lingual cingulum (Fig. 72). The mesial and distal marginal ridges are sharp and merge into the lingual cingulum. There is a distal groove between the distal marginal ridge and the central ridge. The distal margin of the tooth is curved, but not to the extent seen in *Dendropithecus*. The labial surface of the tooth is gently convex.

Figure 73. NAP V UMP 66-34, *Micropithecus clarki*, left i/2, A) lingual, B) distal, C) labial, and D) mesial views. (Scale : 10 mm).

NAP V UMP 66-34 is a small, almost unworn, left i/2 (Fig. 73). It has a sharp but low lingual crest in the centre of the lingual side, and the mesial and distal marginal ridges merge into the lingual cingulum. The distal basin on the lingual side is shallow, and the distal edge of the tooth is gently curved. The labial side is gently convex.

Lower canines

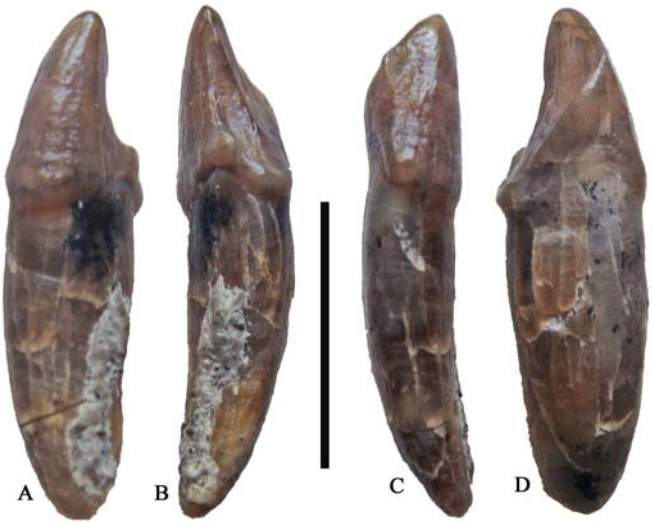

Figure 74. NAP IV 6'85, left lower canine, *Micropithecus clarki*, A) buccal, B) distal, C) mesial, and D) lingual views. (Scale : 10 mm).

NAP IV 6'85 is an unworn left lower canine showing distinct hypoplasia on its buccal surface (Fig. 74). The crown is distinctly canted on the root, which curves distally towards its apex. The concave lingual surface is subdivided into two halves by a tall central ridge which extends from the lingual cingulum to the apex of the tooth. Mesially, the lingual cingulum rises high to merge with the mesial marginal crest where it forms a low stylid. The distal part of the cingulum rises a short distance to meet the distal cristid, where it forms a distinct distal tubercle. The buccal surface of the crown is convex. The morphology and dimensions of this tooth indicate that it is a male individual.

Figure 75. NAP IV UMP 62-18, left lower canine, *Micropithecus clarki*, A) distal, B) lingual, C) mesial, and D) buccal views. (Scale : 10 mm).

NAP IV UMP 62-18, is a slightly worn left lower canine, with a worn apex (Fig. 75). The lingual cingulum is well marked and curves upwards to the high mesial shoulder formed by its junction with the mesial crest. Distally the lingual cingulum continues a short distance onto the buccal side of the crown but does not form a distal tubercle. The crown is distinctly canted on the root. The dimensions and morphology of this tooth indicate that it is likely from a female individual, a possibility supported by the presence of waisting beneath the cervix.

Figure 76. NAP IV UMP 66-32, right lower canine, *Micropithecus clarki*, A) distal, B) buccal, C) mesial, and D) lingual views. (Scale : 10 mm).

Nap IV UMP 66-32 is a deeply worn right lower canine (Fig. 76). The lingual cingulum is sharp, and rises to a high shoulder mesially. A large wear facet cuts into the disto-lingual surface of the crown, making a notch above the distal basal tubercle.

Figure 77. NAP IV 15’07, right lower canine, *Micropithecus clarki*, A) lingual, B) distal, C) mesial, and D) buccal views. (Scale : 10 mm).

NAP IV 15’07 is a heavily worn right lower canine with an extensive wear facet descending from apex down the distal crest to the distal tubercle where it has incised a deep cleft into the crown, but not affecting the root at all (Fig. 77). The lingual cingulum is well developed and rises mesially to merge with the mesial crest at a high shoulder. The dimensions and morphology of the tooth indicate that it represents a female.

Figure 78. NAP I 6’10, right c/1, *Micropithecus clarki* (note the notch incised into the distal edge beneath cervix level, caused by contact against the upper canine), A) lingual, B) distal, C) buccal, and D) mesial views. (Scale : 10 mm).

NAP I 6’10 is a small right lower canine, probably female (Fig. 78). The lingual cingulum rises to a high shoulder where it meets the mesial crest. There is a prominent wear facet running down the distal crest which has cut into the lingual cingulum and even onto the root, obliterating the distal tubercle. The crown is canted on the root.

Lower premolars

The p/3 in NAP V 117’09 is strongly compressed and obliquely oriented in the mandible (Fig. 79). The main cusp sends a prominent crest disto-lingually which ends in a low tubercle situated in the lingual basin. Dentine is exposed down the entire length of this crest. Behind the main cusp, the post-cristid descends towards a low distal cusplet on which the dentine is exposed. A crest extends lingually from this cusplet, and it also exposes dentine. There is a clear, but small honing facet down the mesio-buccal surface of the tooth, but near the apex of the tooth and along the mesial surface the enamel has been damaged, so its apical extent is not discernible, nor is the extent of the mesial fovea, although it must have been mesio-distally short. Buccally the enamel extends rootwards a short distance onto the anterior root. This, and the presence of a small honing facet, possibly suggest that NAP V 117’09 is a female individual. The lingual ridge is centrally positioned, as a result of which the central basin and distal fovea are subequal in dimensions.

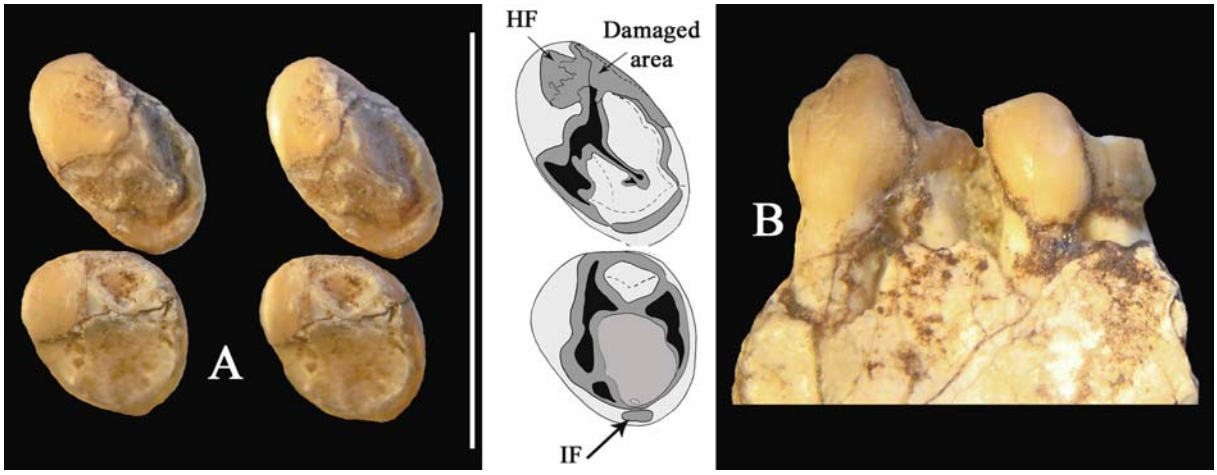

Figure 79. NAP V 117’09, left mandible containing p/3 and p/4, female individual, *Micropithecus clarki*. A) stereo occlusal view and interpretive drawing (light grey - unworn enamel, dark grey – wear surface, black – dentine, medium grey - distal basin of p/4) (HF – honing facet, IF – interstitial facet caused by abrasion against m/1) B) buccal view. (Scale : 10 mm).

The p/4 is longer than broad and only slightly obliquely inserted in the mandible (Fig. 79). The mesial fovea is mesio-distally long, and bucco-lingually short, the two main cusps are worn to the same height and they are almost linked together transversely by short cristids, which close the distal border of the mesial fovea. The distal basin comprises about half the occlusal surface of the tooth, and is rimmed by a low rounded crest which terminates buccally at a low cusp located behind and lower than the buccal main cusp which is itself linked to a low cusp distal to the buccal main cusp. The buccal main cusp has slight buccal flare, but there is no sign of a buccal cingulum, nor even of slight folds in the enamel. There is a distinct distal interstitial facet caused by abrasion against the first molar.

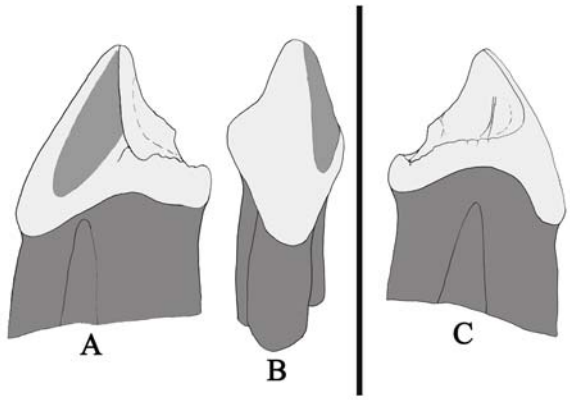

Figure 80. NAP I UMP 66-17, left p/3, male individual, *Micropithecus clarki*, A) mesial, B) buccal, and C) distal views. (Scale : 10 mm).

NAP I UMP 66-17 is a lightly worn left p/3 (Fig. 80). It has two stout compressed, obliquely oriented roots which are positioned en echelon. The crown is compressed bucco-lingually. Mesially there is a honing facet, and the enamel extends a slight distance down the mesial root. The distal cingulum is sharp and well developed, extending from the base of the distal crest to the rear of the tooth where it merges with the lingual cingulum, which itself reaches mesially to the base of the mesial crest. The lingual ridge extends from near the cingulum to the apex of the tooth, but does not touch the cingulum. Because of its central position, the mesial and distal fovea are sub-equal in size.

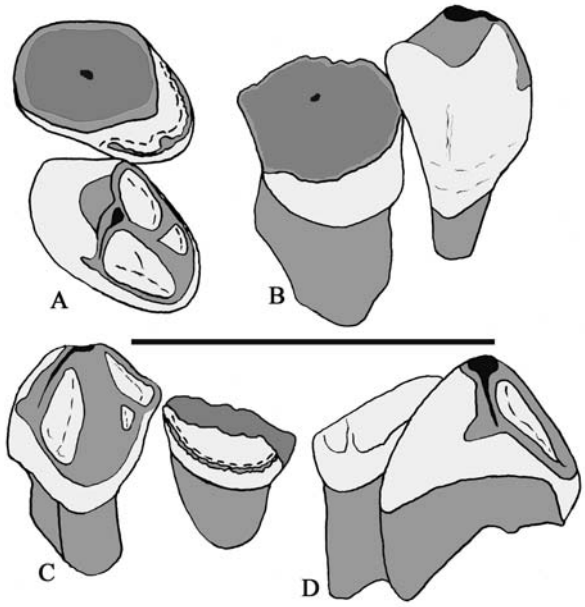

Figure 81. NAP V UMP 66-22, left mandible containing c/1-p/3 and roots i/1-i/2, *Micropithecus clarki*, probably a female individual, A) occlusal view of canine (lacking its apex) and p/3, B) buccal view showing small honing facet near apex, C) oblique lingual view, D) distal view (light grey – unworn enamel, dark grey – wear facets, black – dentine). (Scale : 10 mm).

The left mandible fragment labelled NAP V UMP 66-22 contains the root and small part of the canine, and the complete p/3, as well as the roots of both incisors and the p/4 (Fig. 81). All that is left of the canine crown shows a sharp lingual cingulum. The p/3 is lightly worn, producing a honing facet mesially which is confined to the apical part of the crown. The lingual ridge is centrally positioned, meaning that the mesial and distal fovea are sub-equal in dimensions. In this specimen the lingual ridge reaches the lingual cingulum but before merging with the cingulum it sends a short crest mesio-lingually which also touches the cingulum. This little crest subdivides the mesial fovea into two parts.

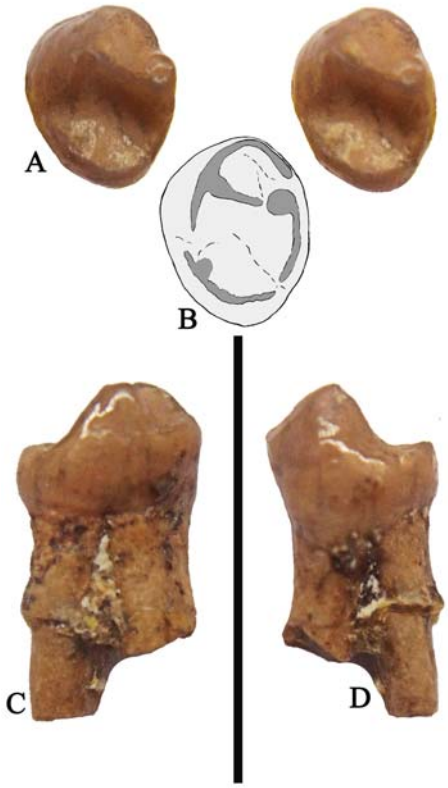

Figure 82. NAP IV UMP 66-30a, left p/4, *Micropithecus clarki*, A) stereo occlusal view, B) interpretive drawing, C) lingual, D) buccal views. (Scale : 10 mm).

NAP IV UMP 66-30a is a lightly worn left p/4 with a short, weak buccal cingulum (more a depression in the enamel than a proper cingulum) in the distal part of the buccal cusp (Fig. 82). The only significant morphological difference from its counterpart in NAP V 117'09 is the lower lingual opening of the mesial fovea. The unworn condition of this tooth enhances the appearance of the low spout-like opening, but even if this tooth were to be worn down to the same degree as NAP V 117'09, there would still remain an opening.

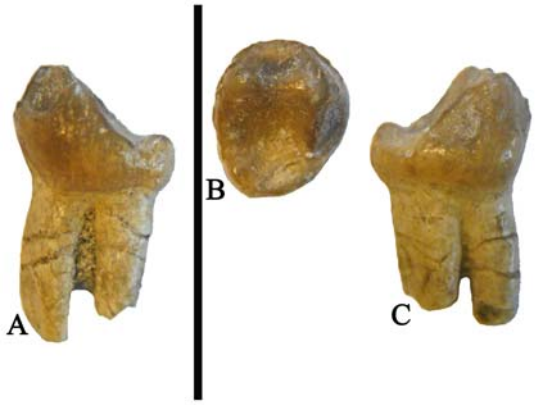

Figure 83. NAP IV 229'09, right p/4, *Micropithecus clarki*, A) lingual, B) occlusal, and C) buccal views. (Scale : 10 mm).

NAP IV 229'09, a lightly worn right p/4 (Fig. 83), is similar to NAP V 117'09 and NAP IV UMP 66-30a, but it possesses a partially developed buccal cingulum, interrupted beneath the main buccal cusp. NAP IV 229'09 and NAP IV UMP 66-30a are morphologically close to, but are slightly smaller than, a left lower p/4 from Mteitei Valley, Kenya (KNM MV 12) attributed by Harrison (1982) to *Limnopithecus evansi*. Like the Napak teeth, the one from Mteitei Valley shows only traces of a weak buccal cingulum.

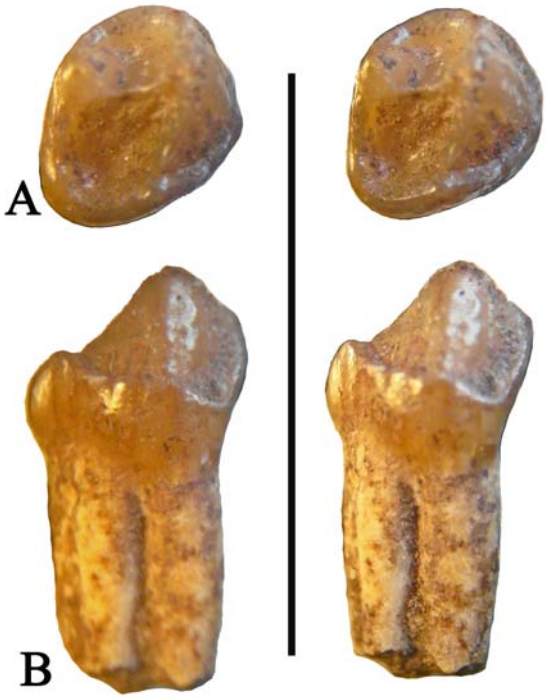

Figure 84. NAP XXI 15’10, right p/4, *Micropithecus clarki*, A) stereo occlusal, and B) buccal views. (Scale : 10 mm).

NAP XXI 15’10 is an unworn right p/4 (Fig. 84) with a prominent buccal cingulum extending along the entire side of the tooth, rising steeply mesially to form a low stylid. Distally it merges with the distal cingulum where it forms a small tubercle. The mesial fovea is about a third of the size of the distal basin. The lingual cusp is only slightly lower than the buccal one. The two roots are coalescent for much of their length.

Lower molars

Figure 85. NAP V 89’09, right m/1, *Micropithecus clarki*, stereo occlusal view. (Scale : 10 mm).

NAP V 89’09, a damaged right m/1 is deeply worn, with large dentine exposures on the five main cusps (Fig. 85). Some enamel is missing distally. The mesial fovea is quite large, the talonid basin occupies about half the surface of the tooth, and the distal fovea is reduced. The buccal shelves and cingulum are quite large. The mesial root is compressed and transversely oriented and is quite far back from the front of the tooth, the distal root is broken off.

Figure 86. NAP IV UMP 66-08, left m/1, *Micropithecus clarki*, stereo occlusal view. (Scale : 10 mm).

NAP IV UMP 66-08 is an unworn left m/1 (Fig. 86). The mesial fovea is oblique due to the fact that the metaconid is slightly more distally positioned than the protoconid. A low crest enters the mesial fovea from the apex of the protoconid, but it does not cross the entire extent of the fovea. The distal fovea is small, partly because the crests separating it from the talonid basin are thick. The buccal shelves are small and the buccal cingulum weak. The hypoconulid is centrally positioned. The two roots are bucco-lingually broad ovals and are transversely oriented.

Figure 87. NAP IV 175’09, *Micropithecus clarki*, left m/2, stereo occlusal view. (Scale : 10 mm).

NAP IV 175’09, is a slightly worn left m/2 (Fig. 87) which occludes well with the holotype of *Micropithecus clarki*. The mesial fovea is large and not oblique. The metaconid has a bifid apex, but the incision is small and with wear it would disappear. The distal fovea is small, and the talonid basin accordingly large. The buccal cingulum is sharp, and the buccal shelves narrow due to the rather peripheral positioning of the buccal cusps. The divides between the mesial fovea, the talonid basin and the distal fovea are tall, as are the divides between the talonid basin and the buccal shelves. There are two oval roots oriented transversely.

Figure 88. NAP IV 225’09, right m/2, *Micropithecus clarki*, stereo occlusal view. (Scale : 10 mm).

NAP IV 225’09, a right m/1 in light wear (Fig. 88). The specimen shows tiny dentine exposures at the tips of the main cusps, except for the entoconid. The mesial fovea is small and slightly oblique, due to the fact that the metaconid is slightly distal to the protoconid. The hypoconid is the largest cusp, the protoconid, metaconid and entoconid are subequal in stature, and the hypoconulid, small. The buccal cingulum is discontinuous, forming shelves between the protoconid and hypoconid, and the hypoconid and hypoconulid. The talonid basin is vast, occupying much of the surface area of the crown, and the

distal fovea is cramped. The lingual cusps are moderately compressed bucco-lingually, the buccal ones more voluminous. There are two stout oval roots oriented transversely.

Figure 89. NAP IV UMP 66-13, right m/3, *Micropithecus clarki*, stereo occlusal view. (Scale : 10 mm).

NAP IV UMP 66-13, a right m/3 in advanced wear (Fig. 89), shows extensive dentine lakes on the buccal cusps and smaller ones lingually. The crown is broad anteriorly narrowing distally. The mesial fovea was reasonably large, the talonid basin occupied about half the surface of the crown, and the distal fovea is small. There is a remnant of a buccal shelf between the protoconid and hypoconid. The two roots slant distally, indicating that this is a third lower molar.

Discussion

Harrison (1988) wrote that « none of the (9) upper molars from Koru attributed to *Micropithecus clarki* is as small as the those of the holotype, UMP 64-02. The possibility exists, therefore, that the Koru material may represent a somewhat larger species of *Micropithecus* ». The augmented sample of specimens now available from Napak, reveal that the fossils attributed to *Micropithecus clarki* from

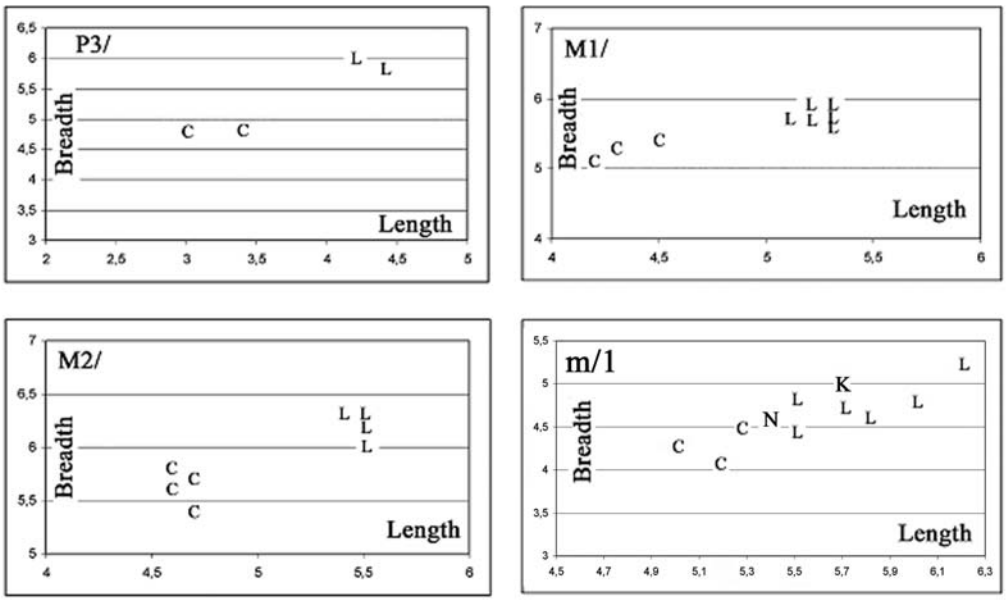

Figure 90. Bivariate plots (mm) of cheek teeth attributed to *Limnopithecus legetet* and *Micropithecus clarki*, showing no overlap in the clouds of points, indicating the likely presence of two species as surmised by Harrison (1988) on the basis of only 9 upper molars from Koru and one from Napak. The Napak sample is now seven upper molars. Lower first molars accord with this pattern, with the holotype of *Limnopithecus legetet* plotting into the middle of the range of variation of the Chamtwara specimens hitherto identified as *Micropithecus clarki*, but here attributed to *Limnopithecus legetet*. (C – *Micropithecus clarki* from Napak; K – Koru holotype of *Limnopithecus legetet*; L – *Limnopithecus legetet* from Chamtwara; N – NAP IX BUMP 268). (Measurements of the Chamtwara (L) fossils are from Harrison, 1982).

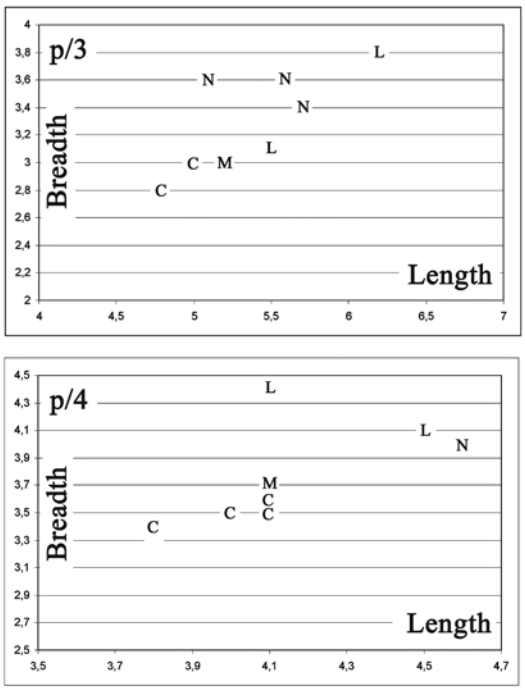

Figure 91. Bivariate plots (mm) of lower premolars attributed to *Limnopithecus* and *Micropithecus*. (C – *Micropithecus clarki*; L – *Limnopithecus legetet* from Chamtwara; M – *Micropithecus leakeyorum* from Maboko; N – *Limnopithecus legetet* from Napak). (Measurements of the Chamtwara (L) and Maboko (M) specimens are from Harrison, 1982).

Koru and Napak do not overlap in dimensions, and thus likely represent two species (Fig. 90, 91). The realisation that the holotype mandible of *Limnopithecus legetet* differs from the new material attributed to *Micropithecus clarki*, as well as from the rest of the mandibular hypodigm of *Limnopithecus legetet*, has the consequence that *Micropithecus* as previously understood is a chimera, containing specimens belonging to *Limnopithecus legetet* as well as to *Micropithecus clarki* (Fleagle & Simons, 1978). We conclude that the Chamtwara and Koru specimens attributed by Harrison (1982) to *Micropithecus clarki* belong instead to *Limnopithecus legetet* Hopwood, 1933a.

Genus *Lomorupithecus* Rossie & MacLatchy, 2006

Diagnosis: Differs from all other Miocene catarrhines (including pliopithecids) in the combination of extreme mesio-distal brevity of the upper premolar crowns, the ovoid and symmetrical shape of the P4/ crown, the twinning of the m/2 hypoconid and hypoconulid, the expansion of the m/2 distal fovea, and the prow-like paracristid. It differs from all other African Miocene catarrhines for which the region is preserved (*Proconsul*, *Turkanapithecus*, *Afropithecus*, Rae, 1999) in retaining a platyrrhine-like configuration of the contact between the premaxillae and nasal bones. *Lomorupithecus* differs from *Dendropithecus*, *Limnopithecus*, *Kalepithecus* and *Simiolus* in having the protoconid mesial to the metaconid on m/1 and m/2; from *Dendropithecus* and *Micropithecus* in having less heteromorphic P3/ cusps; from *Kalepithecus* and *Dendropithecus* in having a more sloping lingual face of P3/; from *Dendropithecus* and *Simiolus* in having a less pronounced P4/ lingual cingulum, and less bucco-lingually compressed upper canines; from *Simiolus* in having no P3/ lingual cingulum; from *Limnopithecus* and *Kalepithecus* in lacking an evenly convex distal margin of the P3/ crown; from *Kalepithecus*, *Micropithecus*, and *Simiolus* in having a mesio-distally shorter M1/; from *Kogolepithecus* (Pickford *et al*., 2003) in lacking a bifid metaconid and entoconid, and retaining a hypometacristid on m/2; from *Laccopithecus*, *Epipliopithecus*, and *Pliopithecus antiquus* in having a less obliquely oriented cristid obliqua; and from *Micropithecus* in having a pronounced mesio-lingual cingulum on M1/, a molar trigon considerably wider than long, rounded, barlike (as opposed to sharp) inferior orbital rim, and orbits positioned higher on face. *Lomorupithecus* differs from all

nyanzapithecines in having bucco-lingually broader upper premolars and M1/, and from all cercopithecoids in lacking bilophodont molars (from Rossie & MacLatchy, 2006).

Note that, as concerns the lower molars, this diagnosis accords with the type specimen of *Limnopithecus legetet* Hopwood (1933a).

Type species : *Lomorupithecus harrisoni* Rossie & MacLatchy, 2006 = *Limnopithecus evansi* MacInnes, 1943.

Species : *Lomorupithecus evansi* (MacInnes, 1943)

Diagnosis: as for the genus; a species with a body mass of approximately 4.3 kg based on m/1 size (Conroy, 1987) (from Rossie & MacLatchy, 2006). The second part of this diagnosis applies to *Limnopithecus legetet*, following transfer of the paratype mandible of *Lo. harrisoni* to *Li. legetet*. A species of *Limnopithecus* distinguished from the type species by the following features: upper central incisor slightly narrower and higher-crowned. Lower incisors much higher-crowned and relatively more slender. Canines slightly larger. Upper premolars and molars relatively broader, with less well-defined occlusal crests. Distal cusps of M3/ less well developed. p/3 narrower with moderately developed honing surface on mesio-buccal aspect of the crown. p/4 comparatively long and narrow with large mesial fovea. Lower molars narrower with low and rounded cusps and occlusal crests; posterior transverse crest poorly defined or entirely lacking; distal fovea small, poorly defined and communicating directly with the talonid basin. m/3 relatively smaller in size, with more distally positioned entoconid relative to the hypoconid. Mandibular corpus relatively higher (from Harrison, 1988).

Holotype : KNM SO 385, right mandibular fragment with the crowns of p/4-m/2 and the roots of p/3 and m/3.

Type locality : Songhor, Kenya.

Referred material from Napak: NAP IX BUMP 266 snout; NAP IV 11’08, left I1/; NAP V 22’08, left I1/; NAP IV UMP 66-33a, right I2/; NAP IV 25’04, left C1/; NAP V 31’06, left DM3/; NAP V 113’09, left P3/; NAP IV 10’08, right P4; NAP IV 71’05, right M1/ germ; NAP I 2’10, right M1/; NAP IV UMP 66-16, right m/1; NAP IV 13’08, right mandible fragment containing lightly worn m/2-m/3.

Age : Early Miocene, Faunal Set I, levels with *Dorcatherium songhorensis* as well as slightly younger levels with *Dorcatherium piggoti* and *Dorcatherium iririensis*.

Descriptions
Upper incisors

Figure 92. NAP IV 11’08, left upper central incisor, *Lomorupithecus evansi*, A) labial, and B) stereo lingual views. (Scale : 10 mm).

NAP IV 11’08, a left upper central incisor with minor wear along the apex, has a small central lingual pillar rising apically from the lingual cingulum to about half the height of the crown (Fig. 92). The cingulum descends rootwards sharply beneath the distal side of the central pillar, but rises gently mesially towards the mesial marginal ridge. Where the distal part of the lingual cingulum meets the distal marginal ridge, there is a v-shaped depression but no slit. The distal margin of the crown is spatulate, and the labial surface is gently convex. The root is compressed and somewhat taller than the crown, and has a slight distal curvature.

Figure 93. NAP V 22’08, left I1/, *Lomorupithecus evansi*, lingual view. (Scale : 10 mm).

NAP V 22’08, a left I1/ lacking its root, is in light wear, which has reduced the height of the crown (Fig. 93). The central lingual pillar has lost some mass due to wear, but it rises apically to just beneath the apical cutting edge. The lingual cingulum descends rootwards distal to the central pillar, and it forms a V-shaped junction with the distal marginal ridge. The mesial part of the lingual cingulum rises gently mesially and merges into the mesial marginal ridge. The distal part of the tooth is spatulate, and the labial side is convex save for a slightly planar area near the apex on the mesial half.

Figure 94. NAP IV UMP 66-33a, *Lomorupithecus evansi*, right I2/, A) lingual, B) distal, C) labial, and D) mesial views. (Scale : 10 mm).

NAP IV UMP 66-33a, a right I2/ is well preserved, with almost no wear (Fig. 94). The crown is ovoid in lingual view, the mesial and distal edges sub-parallel. The lingual cingulum is strongly developed centrally weakening as it approaches the mesial and distal marginal ridges, which it meets at obtuse angles. A subtle central ridge rises from the centre of the lingual cingulum but does not reach the apex of the tooth. The labial surface of the crown is gently convex. The root is almost twice the height of the crown.

The snout, NAP IX BUMP 266 (Fig. 95) has been described in detail and interpreted by Rossie & MacLatchy (2006). It is necessary to point out that the M1/s in this specimen are deeply worn, to such an extent that little can be deduced of the original morphology. The premolars are in better condition, although the P4/ has suffered moderate wear that has eliminated some features of the tooth. Very little remains of the crown of the canine, principally the part containing the lingual cingulum which is sharp, and shows a hint of low ridges of enamel rising towards the apex.

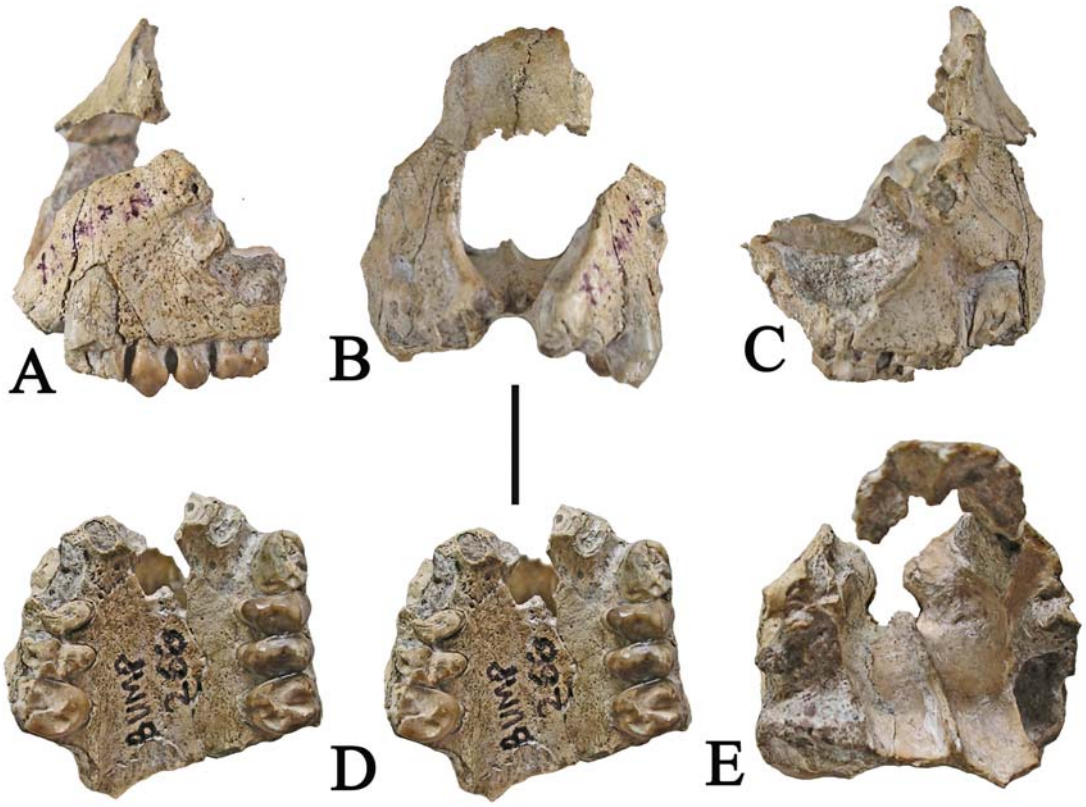

Figure 95. NAP IX BUMP 266, snout of *Lomorupithecus evansi*, A) left lateral, B) anterior, C) right lateral, D) stereo occlusal, and E) posterior views. (Scale : 10 mm).

Canine

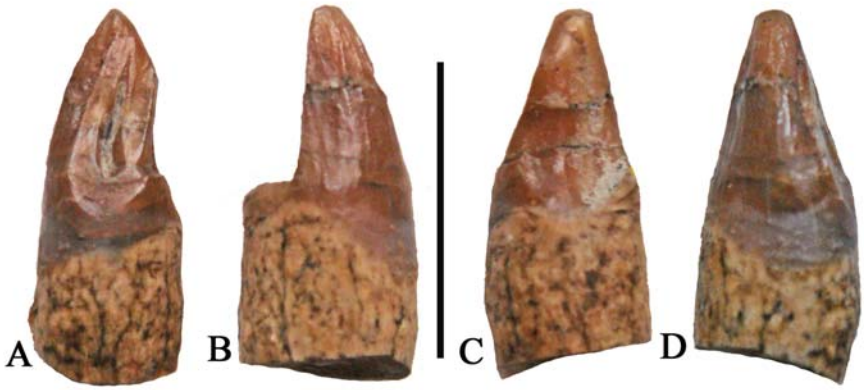

Figure 96. NAP IV 25'04, left upper canine, attributed to *Lomorupithecus evansi*, A) mesial, B) buccal, C) distal and D) mesio-buccal views. (Scale : 10 mm).

NAP IV 25'04 is a moderately worn crown and part of the root of an upper left canine (Fig. 96). The root is almost circular in section, as in the canine of the snout NAP IX BUMP 266. There is a prominent mesial groove, accompanied by a shallower mesio-buccal groove. The mesial wear facet has isolated the mesial groove from the lingual and buccal surface of the crown. There is a low tubercle where the lingual cingulum rises towards the base of the mesial groove. The distal wear facet is deeply indented basally where it has cut a notch into the cervix which even encroaches slightly onto the root, suggesting that this is possibly a male individual. This facet has cut away much of the distal part of the lingual ridge. There is no sign of a fissure on the buccal surface of the crown, which is uniformly convex.

Upper premolars

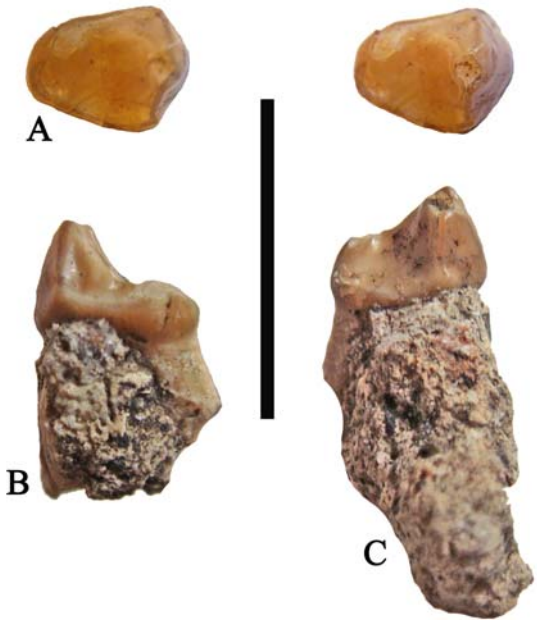

Figure 97. NAP V 113’09, left P3/, *Lomorupithecus evansi*, A) stereo occlusal view, B) mesial, and C) distal views. (Scale : 10 mm).

NAP V 113’09, is a lightly worn left P3/ (Fig. 97). The buccal cusp is taller and mesio-distally longer than the lingual cusp, and it shows a prominent mesial groove between its precrista and the lingually directed crest which descends towards the mesial cingulum but stopping short before the cingulum and not touching the lingual cusp. The lingual cusp is in a mesial position and merges with the mesial cingulum, making for a tiny mesial fovea. The distal basin in contrast is vast, with smooth enamel. The postcrista of the buccal cusp slopes towards the cervix, where it merges into a low, small, posterior tubercle or style. There is no distal cingulum, but posterior to the lingual cusp there is a low cusplet or tubercle in the disto-lingual corner of the crown, formed by a swelling in the postcrista of the lingual cusp.

Figure 98. NAP IV 10’08, right P4/, *Lomorupithecus evansi*, stereo occlusal view. (Scale : 10 mm).

NAP IV 10’08 is a moderately worn right P4/ (Fig. 98). The paracone is somewhat taller than the protocone, and both cusps are located in an anterior position, which makes the mesial fovea narrow mesio-distally, but broad bucco-lingually. The distal basin, in contrast, is vast. There is a low lingual cingulum on the protocone and two quite prominent styles on the buccal surface of the paracone. The buccal root bifurcates apically, and there is a single lingual root.

Upper deciduous teeth

Figure 99. NAP V 31’06, left DM3/, *Lomorupithecus evansi*, from left to right, stereo occlusal view and interpretive drawing. (Scale : 10 mm).

NAP V 31’06 is a left DM3/ in medium wear (Fig. 99). It is attributed to *Lomorupithecus evansi* on account of its dimensions, and the compatible morphology that it shows. The mesial fovea is moderately large, confined to the buccal half of the crown due to the inward position of the protocone, which sends a strong preprotocrista obliquely across the tooth towards the parastyle. The distal fovea is large and shows two low crests entering it, one each from the paracone and protocone, but they do not meet in the centre of the crown. Distally the distal fovea is enclosed by the distal cingulum which merges with the postparacrista to form a small mesostyle. Lingually, it merges with the lingual cingulum which encircles the protocone. There are three roots, two buccal and one lingual, which show the characteristic splayed out disposition of deciduous teeth.

Upper molars

Figure 100. NAP I 2’10, right M1/, *Lomorupithecus evansi*, stereo occlusal view. (Scale : 10 mm).

NAP I 2’10, an unworn M1/ germ (Fig. 100), is almost fully formed but evidently had not developed roots at the time of death, as shown by the jagged edge of the incompletely mineralised cervix. The protocone is positioned relatively far from the lingual margin, which restricts the mesial fovea to the buccal half of the crown. The distal wall of the mesial fovea is low, and with slight wear, there would be a low connection between it and the trigon basin. Likewise the crests from the metacone and protocone which define the mesial wall of the distal fovea, are low, making for an easy connection between it and the trigon basin. The distal fovea is large, only slightly less capacious than the trigon basin. The lingual cingulum is well defined, but not very broad. The hypocone is isolated from the protocone, its prehypocrista being low and making a weak link with the postprotocrista.

Figure 101. NAP IV 71’05, right M1/ incompletely formed germ, *Lomorupithecus evansi*, stereo occlusal view. (Scale : 10 mm).

NAP IV 71’05, is an incompletely formed upper molar germ (Fig. 101). The lingual cingulum is discernible near its incompletely formed cervix, indicating that the individual died very young. The occlusal enamel has not yet been completely laid down, but the main structures can be made out. The protocone is internally positioned, the hypocone apparently isolated from the protocone, the distal fovea almost as large as the trigon basin, and the mesial fovea extremely cramped into the buccal half of the tooth.

Lower molars

Figure 102. NAP IV UMP 66-16, right m/1, *Lomorupithecus evansi*, stereo occlusal view. (Scale : 10 mm).

NAP IV UMP 66-16, is an unworn right m/1 (Fig. 102) similar to the lightly worn m/2 in NAP IV 13’08. The mesial and distal fovea are narrow mesio-distally with high connections to the talonid basin. The mesial fovea is oblique, the metaconid being slightly behind the level of the protoconid. The cristids running towards each other from the apices of the protoconid and metaconid meet in the midline of the tooth and form a tallish wall separating the mesial fovea from the talonid basin. The same applies to the cristids running between the entoconid and hypoconid which wall off the distal fovea from the talonid basin. The enamel in the talonid basin is patterned with subtle wrinkles, but not as obviously as in the molars of *Rangwapithecus gordoni*. There is no buccal cingulum, but the buccal shelves between the protoconid and hypoconid and between the hypoconid and hypoconulid are prominent. The entoconid shows a slight hint of having a bifid apex, but it is extremely subtle and would disappear even with slight wear. The lingual cusps are not particularly compressed bucco-lingually and the buccal cusps have lingual surfaces that slope into the talonid basin, somewhat reducing its capacity.

NAP IV 13’08 is a well preserved right mandible fragment containing the m/2 and m/3 in light wear (Fig. 103). The mandible is extremely slender, even at the level of the m/3 where the ascending ramus sweeps upwards. The base of the jaw is preserved and it was shallow (12.2 mm from alveolar margin to base beneath the front of m/3, and its thickness in the same place is 6.6 mm). The fossa for the masseter is shallow and largely distal to the m/3. The sublingual fossa is shallow, and the jaw deepens

slightly posterior to the m/3. The root of the ascending ramus is far back, starting at the front of m/3. In mesial view, the broken section of the jaw shows a large mandibular canal extending over about half the height of the jaw, its superior part lying lingual to the distal alveolus of the root of m/1.

Figure 103. NAP IV 13’08, right mandible fragment containing m/2 and m/3, *Lomorupithecus evansi*, A) stereo occlusal, B) lingual, and C) buccal views. (Scale : 10 mm).

The m/2 shows small wear facets at the apices of the cusps, but no dentine is exposed. The metaconid is slightly distal to the protoconid, which makes the mesial fovea somewhat oblique. The mesial fovea is small, and the wall separating it from the talonid basin is low. The entoconid is well behind the line of the hypoconid, which makes for a vast talonid basin. The cristids which close the rear of the talonid basin are small and low and the postparacristid and preentocristid are weakly developed, meaning that the lingual outlet of the talonid basin is low, and slit-like. The apex of the metaconid is bifid, but with additional wear evidence of this would disappear. The distal fovea is moderate in dimensions and its distal outlet is very low. There is an incomplete buccal cingulum which forms shelves between the protoconid and hypoconid, and between the hypoconid and hypoconulid. The connections between these shelves and the talonid basin are high. The enamel is smooth or patterned by low enamel folds.

The m/3 is built on the same plan as the m/2, but it is narrower distally and the tooth itself is slightly smaller than the m/2. The entoconid has broken away.

The distal alveolus for the m/1 is partly preserved, and reveals that the roots in this species were exceptionally gracile, in accordance with the slenderness of the mandible, and they are short, not even penetrating to half the depth of the mandible.

The molars in NAP IV 13'08 are similar in dimensions and morphology to those in KNM SO 444, attributed to *Limnopithecus evansi*.

Discussion.
The genus *Lomorupithecus* was poorly known, and as originally defined was a chimera of two species, *Lomorupithecus evansi* (the holotype of *Lomorupithecus harrisoni*) and *Limnopithecus legetet* (the paratype of *Lomorupithecus harrisoni*). The dentition in the snout is deeply worn, so the discovery of unworn upper molars is important as it reveals that, in this genus, the molar crowns are low with isolated pyramidal cusps. The mandible is gracile, and the lower molars long and narrow with compressed lingual cusps, and large occlusal basins, quite different from the mandible (NAP IX BUMP 268) previously attributed to the genus.

Genus *Iriripithecus* nov.

Diagnosis : A small hominoid primate approximating the size of *Hylobates pileatus* (Lucas *et al*., 1986) in which the molar cusps are tall and pyramidal, with minimal enamel wrinkling, cusp crests fine and sharp when unworn, not swollen. Upper molar crowns slightly broader than long. Protocone is the largest cusp followed by paracone, metacone and hypocone. Prominent unbeaded lingual cingulum linked to protocone by tiny low crests, mesial cingulum strong; low but sharp buccal cingulum extending from the mesial aspect of the paracone to the distal part of the metacone where it weakens before joining the distal cingulum. Hypocone separated from the trigon by a deep slit. Crista obliqua short, emanating from near the base of the postprotocrista. Mesial fovea tiny, posterior fovea capacious, rear profile of tooth convexly curved, and, in lateral view overhanging the distal root. Trigon basin deep, with low openings to the mesial fovea, distal fovea and the buccal side of the tooth. Marked molar wear gradient (M1/ in wear at the same time that only the mesial cusp tips of M3/ are forming). Lower molars mesio-distally elongated, with large talonid basin with a slit-like opening to the lingual side. Fine buccal cingulum between protoconid and hypoconid, and between hypoconid and hypoconulid, rises towards the apices of the protoconid and hypoconid. Lingual cusps compressed bucco-lingually, buccal cusps broader. Mesial fovea cramped at its base broadening bucco-lingually upwards, obliquely oriented, distal fovea larger, lingually positioned with low spout disto-lingually. Grooves between main cusps of lower molars narrow and deep. p/4 slightly longer than broad, without buccal cingulum, lingual cusp slightly lower and distinctly more distally positioned than the buccal cusp.

Differential diagnosis : Upper molars of *Iriripithecus* differ from those of *Karamojapithecus* by their simpler cusp form, lacking accessory folds and cusplets, unadorned floors in the mesial and distal foveae, smaller hypocone, deeper slits between main cusps and between hypocone and trigon, and less beaded cingulum. Lower molars of *Iriripithecus* differ from those of *Karamojapithecus* by the narrower, finer, buccal cingulum, the more compressed lingual cusps, the more open talonid basin, and the tendency for the postmetaconid cristid to be detached at its apex (disappears with light wear).

Iriripithecus differs from *Simiolus* by its greater dimensions, by its less elongated lower molars, and by the lack of transverse crests in the floor of the distal fovea in upper molars.

Iriripithecus differs from *Micropithecus* by its much greater dimensions, its more isolated molar cusps, the more compressed lingual cusps in lower molars, the more isolated cusps in the molars and the unadorned molar enamel. The upper canines are tall with a weak buccal mesial groove which contrasts with the upper canines of *Micropithecus* in which there is no buccal mesial groove, and the lingual one is very lingually positioned.

Iriripithecus differs from *Limnopithecus* by the more compressed lingual and buccal cusps in the lower molars, the more isolated molar cusps, the lack of enamel wrinkling in the floor of the talonid basin and the absence of cusplets or thick enamel wrinkles in the talonid basin at the base of the entoconid.

Iriripithecus differs from *Lomorupithecus* by its greater dimensions, but is otherwise quite close to it in its upper molar morphology.

Iriripithecus differs from *Dendropithecus* by the less well developed buccal cingulum in the upper molars, and its tall isolated molar cusps, lack of transverse crests in the occlusal basins and foveae of the molars.

Iriripithecus differs from *Turkanapithecus* by its low crown with tall isolated cusps which contrast with the tall crown and low cusps in *Turkanapithecus*.

Iriripithecus differs from *Kogolepithecus* by the lack of, or reduced, bifid incision in the metaconid and entoconid of the lower lower molars, and by the weaker buccal cingulum.

Iriripithecus differs from *Kalepithecus* by the morphology of the upper canines, which in *Kalepithecus* have two mesial grooves and a buccal slit, while in *Iriripithecus*, the buccal mesial groove is shallow and there is no buccal slit. The lower fourth premolars are radically different, short and broad in *Kalepithecus*, long and narrower in *Iriripithecus*, with the lingual cusp well back from the buccal one.

Iriripithecus differs from *Rangwapithecus* by the almost square outline of the upper molars, by the smooth enamel, and by its smaller dimensions.

Iriripithecus differs from *Xenopithecus* by its low crown with tall cusps, contrasting with the tall crown with low cusps of *Xenopithecus*.

Iriripithecus differs from *Mabokopithecus* by the external position of the hypoconid in lower molars, and by its larger dimensions.

Iriripithecus differs from *Nyanzapithecus* by its low crown with tall, isolated cusps which contrast with the high crown and low, bulbous cusps of *Nyanzapithecus*.

Etymology : Iriri is the name of the small village at the foot of Akisim, a remnant of Napak Volcano which yielded all the fossils described herein and “pithecus” is the latinised form of the Greek “pithekos”, trickster or ape.

Type species *Iriripithecus alekileki* nov.

Diagnosis : As for the genus.

Etymology: Alekilek cliffs form a prominent landmark close to the fossil sites that yielded the material described herein.

Holotype : NAP IV 20’07, left maxilla fragment containing the erupted, but lightly worn M1/, the M2/ in crypt and the anterior part of M3/ in an incomplete germinal state.

Referred material : NAP IV 80’08, right I1/; NAP IV 1’10, left upper canine; NAP XV 4’10, unworn left P3/; NAP XV 11’08, heavily worn right M2/; NAP IV 9’08, left M3/; NAP IV 8’08, left i/2; NAP XV 385’08, right lower canine lacking its apex; NAP XV 120’09 left dm/4; NAP XV 185’08, right p/4; NAP IV UMP 62-19, left m/2; NAP XV 183’08, left m/2.

Type Locality : Napak IV, Uganda.

Stratigraphic context: Napak Member, above the nephelinite lava flow.

Age : Early Miocene, Faunal Set 1, ca 19 – 20 Ma.

Description:

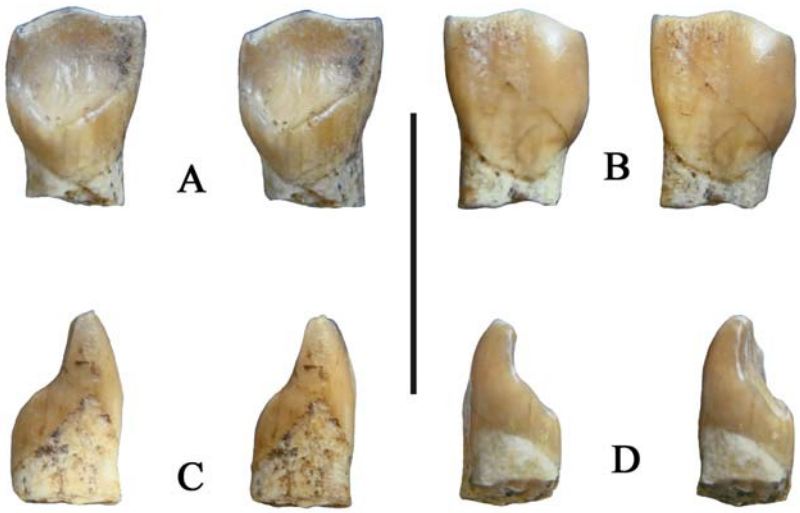

Figure 104. NAP IV 80’08, right upper central incisor, *Iriripithecus alekileki* nov. gen. nov. sp., A) lingual, B) labial, C) mesial, and D) distal stereo views. (Scale 10 mm).

NAP IV 80’08, a right I1/ in early wear is remarkable for the slightly concave aspect of the labial surface, especially the mesial moiety (Fig. 104). Whether this is due to malformation or is a constant feature of the species remains to be determined, but a result is that the labial profile of the root is flat in section. In lingual view the absence of a lingual pillar is evident, but the distal and mesial marginal ridges are well developed, and are connected via a slanting lingual cingulum, which descends distally to form a V-shaped junction with the distal marginal ridge. There are no fissures or slits interrupting the cingulum and marginal ridges. The cutting edge of the incisor is divided into two parts, a slightly broader mesial part which occludes with the lower central incisor, and a distal part which slopes distally, corresponding to the i/2. Apically, on the lingual side of the crown there is a very subtle groove separating the two halves of the tooth, but with increased wear this feature would be abraded away. The mesial and distal edges of the tooth are sub-parallel near their apices, but the distal margin curves towards the root at a sharp angle in the profile of the tooth, best observed in distal view. The tooth is low crowned.

Figure 105. NAP IV 1’10, left C1/, *Iriripithecus alekileki* nov. gen. nov. sp., A) lingual, B) distal, C) buccal, and D) mesial views. (Scale : 10 mm).

NAP IV 1’10, is a left upper canine (Fig. 105), probably male, judging from the high crown, and the fact that the root is slightly broader and longer than the base of the crown. The root section is ovoid, slightly compressed bucco-lingually. The crown is tall and strongly curved from cervix to apex, both the mesial and distal edges curving concave distally. The mesial groove is tall and broad and is separated from the lingual concavity of the tooth by a tall but narrow lingual pillar. Buccally, there is a shallow buccal mesial groove about half the height of the crown. Both crests either side of the mesial groove are lightly worn, exposing small patches of dentine, and the wear facet extends rootwards but not affecting the root itself. The groove itself is smooth, save for its cervical part which shows finely wrinkled enamel. The buccal surface of the tooth is marked by sub-parallel flute-like ridges which extend from the cervix to the apex. There is a large distal wear facet affecting the entire height of the distal crest, revealing a large area of dentine, and incidentally showing that the enamel in this tooth is remarkably thin. The lingual concavity is smooth enamelled but has a low ridge extending from cervix to apex, and in the linguo-mesial corner of the cervix there is a low swelling producing a tubercle.

Figure 106. NAP XV 4’10, left P3/, *Iriripithecus alekileki* gen. nov. sp. nov., A) distal, B) stereo occlusal, and C) mesial views. (Scale : 10 mm).

The left P3/ NAP XV 4’10 (Fig. 106) is metrically close to the P3/ in KNM SO 417, attributed to *Kalepithecus songhorensis* (Harrison, 1988) but the protocone is more conical and isolated, mirroring the morphology of the molar cusps in *Iriripithecus*. The paracone is taller and more voluminous than the protocone, which is about half the height of the buccal cusp. The buccal surface of the tooth is steep and convex, with a straight profile in mesial and distal views. The preparacrista and postparacrista are in line with each other and both terminate at small tubercles to form a parastyle anteriorly and a mesostyle posteriorly. The mesial face of the paracone is scored by a groove located between the preparacrista and a ridge directed from the apex of the cusp towards the midline of the tooth mesially. This groove extends basally just behind the mesial cingulum, and comprises the mesial fovea, which is cramped. The distal basin is vast, but has some low enamel folds crossing it from the paracone towards the protocone, but not subdividing it into separate basins, more providing it with a rugose or undulating surface. The protocone sends short crests mesially and distally, the latter one curving buccally to merge with the distal cingulum. There is a change in slope of the lingual surface of the protocone, hinting at a cingulum. There are three roots, two buccally and one lingually. Mesially, there is a deep depression in the root profile beneath cervix, and this is presumably where the root of the canine would fit in life. The distal part of the crown is swollen basally, producing an overhanging cingular-like distal margin.

The holotype maxilla of *Iriripithecus alekileki* (Fig. 107) contains M1/ in light wear, the M2/ emerging from its crypt and the M3/ incompletely formed, only the apices of the protocone and paracone being evident, joined together by crests that descend towards the midline of the tooth. The fact that M1/ already shows wear along the main crests at the same time that M3/ is in a very incomplete stage of formation suggests strongly that, in *Iriripithecus alekileki*, there was a significant time period between the eruption of successive molars.

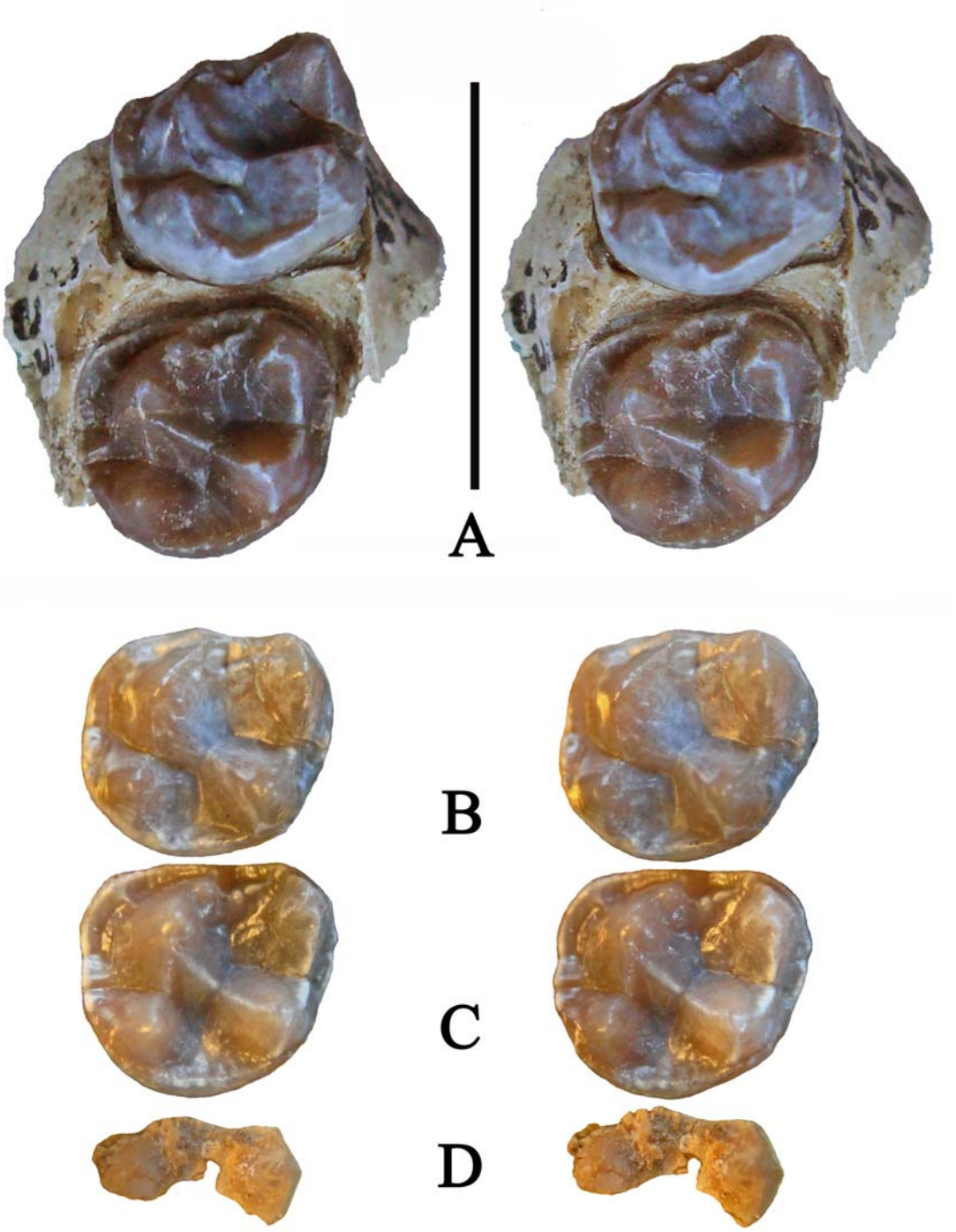

Figure 107. NAP IV 20’07, holotype upper left molar row, *Iriripithecus alekileki* nov. gen. nov. sp., A) stereo view of ensemble, B) M1/, C) M2/, D) M3/ germ (apices of protocone and paracone joined in the midline) stereo occlusal views. (Scale 10 mm).

The four main cusps of the M1/ and M2/ show an exceptionally simple morphology, with reduction of the crests, enamel wrinkling, cingular beading and other superficial structures. As a result the enamel is remarkably smooth or only very lightly wrinkled, such that even with light wear, surface ornamentation is abraded away. The trigon is an equilateral triangle, and the cusp surfaces that descend into it are relatively planar. The crista obliqua extends towards the lingual crest of the metacone which is in line with it, the two meeting at a slit which connects the trigon basin to the distal fovea. The mesial fovea is tiny, cramped between the mesial cingulum, the lingually directed crest of the paracone which is in a very mesial position, and the preprotocrista which bifurcates near its base, one branch forming the distal margin of the mesial fovea, the other closing it off lingually. The

connection between the trigon basin and the mesial fovea is about half the height of the tooth, the buccal outlet of the trigon basin and that to the distal fovea are somewhat lower. The hypocone is slightly smaller than the trigon cusps, but is in any case quite large and almost as tall as the protocone, and it is separated from the protocone by a deep, narrow slit. The distal fovea is capacious, floored by smooth enamel, and unencumbered by any crests or ridges from the metacone and hypocone. There is a wide lingual cingulum which passes round the lingual margin of the tooth from the mesial cingulum to the distal one, but on the hypocone, its stature is reduced (M2/) or even interrupted (M1/). There is a fine buccal cingulum extending along the entire buccal aspect of the tooth, rising mesially towards the mesial cingulum, and distally towards the distal cingulum.

The M3/ of the holotype is represented by a partial germ, in which only the apices of the protocone and paracone are well mineralised. The distance between the apices of these cusps is almost the same as that of the M2/, suggesting that M3/ was not reduced in this genus, at least in its mesial part.

Figure 108. NAP XV 11’08, deeply worn right M2/, *Iriripithecus alekileki* nov. gen. nov. sp., stereo occlusal view. (Scale : 10 mm).

NAP XV 11’08, a deeply worn right M2/ (Fig. 108), shows large areas of dentine at the protocone and hypocone, and smaller areas at the apices of the paracone and metacone. The mesial fovea is small, the trigon basin large and the distal fovea quite expansive and unencumbered by transverse crests. The buccal cingulum is well developed, although interrupted on the buccal surface of the metacone. The lingual cingulum is broad, and retains evidence of its wrinkled and beaded edge. The hypocone is slightly more lingually positioned than the protocone.

Figure 109. NAP IV 9’08, left M3/, *Iriripithecus alekileki* nov. gen. nov. sp., stereo occlusal view. (Scale : 10 mm).

NAP IV 9’08, a left M3/ in light wear (Fig. 109), is similar to its counterpart in the holotype, the only significant difference being the better developed buccal cingulum and slightly more marked distal narrowing of the crown. The distal fovea is large without transverse crests in its floor, and the hypocone is completely detached from the protocone.

NAP XV 385’08 is a right lower canine lacking the apices of the crown and root (Fig. 110). It possesses a wear facet disto-basally where the basal tubercle is positioned. The lingual ridge is large and makes the lingual surface convex. The lingual cingulum is sharp and rises apically where it merges into the mesial crest, thereby forming a marked inverted “V” in the cervix. The root is bucco-lingually compressed with a shallow sulcus on the lingual side.

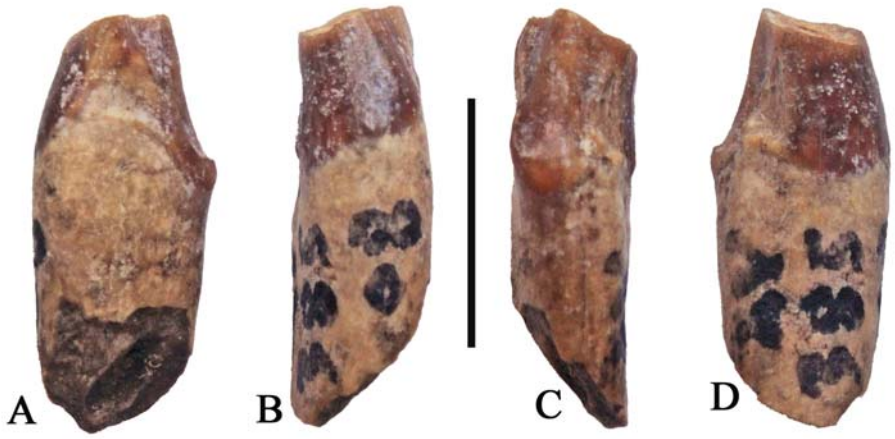

Figure 110. NAP XV 385’08, right lower canine missing its apex, *Iriripithecus alekileki* nov. gen. nov. sp., A) lingual, B) mesial, C) distal, and D) buccal views. (Scale : 10 mm).

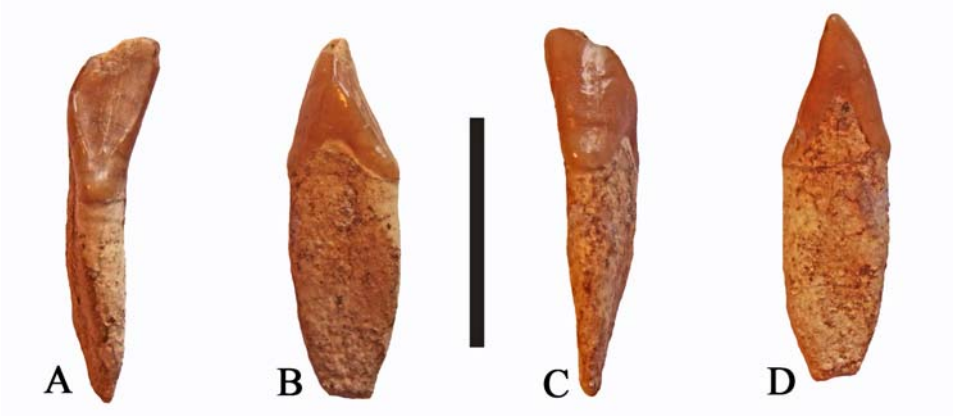

Figure 111. NAP IV 8’08, left i/2, *Iriripithecus alekileki* nov. gen. nov. sp., A) lingual, B) distal, C) labial, and D) mesial views. (Scale : 10 mm).

NAP IV 8’08, a left i/2, is slightly worn, and is missing a small chip of enamel on the distal part of the apex (Fig. 111). Nevertheless it is well preserved and informative. The crown is relatively low and broad, with the cutting edge sloping strongly. There is a low central ridge and more strongly expressed distal marginal ridge. The mesial marginal ridge is subtle, the entire lingual surface slightly convex mesio-distally, almost flat. The cervix rises apically quite strongly on both the mesial and distal aspects, revealing that this would have been an extremely low-crowned tooth when inserted in the mandible. The labial surface is convex.

Figure 112. NAP XV 120’09, left dm/4, *Iriripithecus alekileki* nov. gen. nov. sp., stereo occlusal view. (Scale : 10 mm).

NAP XV 120’09 is an unworn left dm/4 (Fig. 112), its deciduous status revealed by the presence of an oblique cristid invading the mesial fovea from the apex of the protoconid, and by the shape of the

broken root, which shows an oblique distal root and a transverse mesial one. The roots had not formed completely at the time of death. The accessory cristid which divides the mesial fovea into two halves, reduces its capacity and borders two pits. The protoconid is markedly in advance of the metaconid, making the anterior part of the tooth, including the mesial fovea, oblique. The talonid basin is vast, and has high margins separating it from the mesial fovea, the buccal shelf, the distal fovea and the lingual side of the tooth. The buccal cingulum is well formed and the buccal shelves are large. The distal fovea is reduced in dimensions, occupying a small area on the disto-lingual corner of the tooth between the entoconid and hypoconulid. The apices of the hypoconid and hypoconulid have broken off.

Figure 113. NAP XV 185’08, right p/4, *Iriripithecus alekileki* nov. gen. nov. sp., stereo occlusal view. (Scale : 10 mm).

NAP XV 185’08, a right p/4 in light wear is longer than broad, with the lingual cusp only slightly lower than the main buccal cusp (Fig. 113). Tiny enamel islands are exposed at the apices of the two main cusps and at the tubercle at the base of the postprotocristid. The mesial fovea is large with well formed buccal, mesial and lingual walls and with a high wall distally, separating it from the distal basin. The latter structure is enclosed lingually, distally and buccally by a low rounded cingulum. There is a well developed postprotocristid which descends distally to merge with the distal cingulum. There is no buccal cingulum, although on the buccal surface of the tooth there are small folds of enamel distally and mesially. The form of the roots reveal that the tooth was markedly obliquely oriented in the mandible.

Figure 114. NAP XV 183’08, left lower molar, *Iriripithecus alekileki* nov. gen. nov. sp., stereo occlusal view. (Scale 10 mm).

NAP XV 183’08 is an unworn left lower molar without root development (Fig. 114). We take it to be a fully formed but unerupted first lower molar, although, considering the subequal dimensions of the upper first and second molars, this tooth could be a second lower molar. It occludes well with the first molar in the holotype, NAP IV 20’07, but seems to be slightly too small for the second molar.

The crown consists of six cusps, the usual protoconid, metaconid, hypoconid, entoconid and hypoconulid, but with an additional low cusplet on the lingual side of the hypoconulid, slightly invading the distal fovea.

The unworn state of the tooth allows important observations to be made. All the cristids which emanate from near the apices of the main cusps are reduced in stature, meaning that each cusp stands almost isolated from its neighbours, with deep slits or low valleys between them. There is a weak buccal cingulum confined to the mesial and buccal wall of the protoconid, interrupted on the buccal face of the hypoconid, but present again on the hypoconulid. The buccal shelves between the protoconid and hypoconid, and hypoconid and hypoconulid are therefore quite capacious. The buccal cusps have steep buccal surfaces and in occlusal outline they are almost conical. The lingual cusps are slightly bucco-lingually compressed. The mesial fovea is oblique, due to the fact that the metaconid is slightly distal to the protoconid. The buccal side of the mesial fovea is closed off by a weak preprotocristid which runs mesially and only slightly lingually, where it joins the weakly beaded mesial wall of the fovea which itself merges into the premetacristid emanating from the apex of the metaconid. The distal margin of the mesial fovea is comprised of a low medially directed cristid emanating from the protoconid, which swells near its base to form a small accessory cusplet, which is separated by a slit from the buccally directed cristid coming from the metaconid. The postmetacristid is weakly developed, but on its lingual surface, near apex, it is possible to see that the metaconid is bifid, but not to the exaggerated extent observed in *Kogolepithecus* lower molars. Indeed, the separation of the apex of this cusplet would disappear even with slight wear. The base of this postmetacristid ends at a deep slit which separates it from the preentocristid. The cristid that runs buccally from the entoconid is directed towards the hypoconulid, and this leaves the talonid basin unobstructed, and therefore vast. The connection between the talonid basin and the mesial fovea is via a low wall with a slit in its midline between the protoconid and metaconid. The other four outlets of the talonid basin are low, 1) lingually via a slit between the postmetacristid and preentocristid, 2) distolingually between the entoconid and hypoconulid, 3) buccally into the buccal shelf via the low connection between the postprotocristid and prehypocristid, and 4) disto-buccally into the distal buccal shelf via a slit between the posthypocristid and the prehypoconulid cristid. The distal fovea is broad lingually but is encumbered buccally by a sharp, conical, tuberculum sextum which is applied to the base of the hypoconulid. The distal fovea connects to the talonid basin via a low wall, as described above, and it has a low outlet disto-lingually between the postentocristid and the tuberculum sextum.

It is necessary to point out that the enamel beading, and fine structures on the cristids in this unworn molar are extremely diminutive and even with slight wear would disappear leaving a crown with smooth enamel.

Figure 115. NAP IV UMP 62-19, left m/3, *Iriripithecus alekileki* nov. gen. nov. sp., stereo occlusal view. (Scale : 10 mm).

NAP IV UMP 62-19 is a peculiar tooth with a large carie-like depression occupying the entire talonid basin (Fig. 115). Its roots indicate that it is a left lower third molar, yet there appears to be a small abrasion facet on the lingual part of the distal wall of the hypoconulid. There is a small anterior

interstitial facet caused by abrasion against the m/2. There are small circular dentine islands exposed at the apices of all five cusps. The five main cusps are subequal in dimensions, the lingual cusps slightly smaller than the buccal ones, and the cristids between the cusps are reduced in stature, leaving each cusp standing on its own. The three buccal cusps (protoconid, hypoconid and hypoconulid) are conical with steep buccal walls, whereas the two lingual cusps (metaconid and entoconid) are bucco-lingually compressed. The metaconid is slightly distal to the protoconid and the entoconid is marginally distal to the hypoconid. The hypoconulid is slightly to the buccal side of the mesio-distal axis of the crown. There is a weak buccal cingulum, accompanied by buccal shelves between the protoconid and hypoconid, and the hypoconid and hypoconulid. The mesial fovea is oblique, mesio-distally wide and bucco-lingually broad, bordered buccally by the preprotocristid which runs anteriorly and only slightly medially. The premetacristid runs mesio-buccally and walls off the mesial fovea anteriorly. The talonid basin is vast, and connects to the mesial fovea via a low wall comprised of a cristid directed mesially from the apex of the protoconid where it joins a small cristid running buccally from the apex of the metaconid. The talonid basin has four other outlets, all low down, one lingually between the metaconid and entoconid, one to the distal fovea, one to the buccal shelf between the hypoconulid and hypoconid, and the fourth to the buccal shelf between the hypoconid and protoconid. The distal fovea is obliquely oriented, broad bucco-lingually and short mesio-distally. The anterior root is a mesio-distally compressed oval, whereas the distal root is more triangular in section, with a groove on the buccal aspect where the part supporting the hypoconid joins the part that supports the hypoconulid. This tooth occludes extremely closely with the holotype specimen, the enlarged protocone fitting snugly into the talonid basin of the lower molar, the hypocone fitting well into the distal fovea and the distal fovea of the upper molar accepting the large hypoconulid of the lower one. At the same time the metacone and hypocone fit neatly into the two buccal shelves of the lower molar and the entoconid fits into the lingual shelf of the upper molar between the protocone and hypocone. The reduction of the size of the cristids emanating from the main cusps in this tooth accords with the same kind of reduction seen in the upper molars.

Discussion

The only specimen of *Iriripithecus* in the Bishop collection from Napak is NAP IV UMP 62-19, an isolated lower molar with a deep carie-like depression in the talonid basin. Fleagle & Simons (1978) considered it to belong to an indeterminate anthropoid, but Harrison (1982, 1988) thought it belonged to *Dendropithecus macinnesi*.

The recovery of additional specimens, and of upper teeth which occlude well with this enigmatic specimen reveals that it represents a hitherto undescribed genus and species, which is here named *Iriripithecus alekileki*, with, as holotype, a maxilla fragment with fully formed M1/ and M2/, and the anterior part of M3/ in crypt in a very juvenile stage of formation.

This genus differs from all other genera of small apes from East Africa by its tall, isolated cusps with short low crests, and unadorned enamel, large foveae, and expansive trigon basin and talonid basin. It is perhaps related to *Kogolepithecus morotoensis* from younger deposits at Moroto II (Pickford *et al*., 2003), but it differs from this genus by a number of characters (lack of bifid entoconid, bifid tip of metaconid not well developed, buccal cingulum weaker, posterior wall of mesial fovea in lower molars complete, even if low). Its closest relative, however, is from Napak, *Karamojapithecus akisimia*, which differs from it by having better developed occlusal crests, more beaded cingula, and substantial crests entering the distal fovea of upper molars from the hypocone and metacone.

Karamojapithecus also has its hypocone in a markedly distal position relative to the metacone, which imparts a trapezoidal outline to the crown, unlike the more rectangular outline in *Iriripithecus*. *Iriripithecus* differs from *Simiolus* by its greater dimensions, and by the less elongated outline of the lower molars, and the less well developed transverse crest crossing the distal fovea in upper molars.

Genus *Karamojapithecus* nov.

Diagnosis: Hominoid approximating *Hylobates pileatus* in dental dimensions (M1/ 5.6 x 6.1 mm and 5.2 x 6.1 mm; M2/ 6.8 x 7.8 mm) (Lucas *et al*., 1986). Upper molars with pyramidal cusps, hypocone more lingually positioned than the protocone, and more distally positioned than the metacone, large lightly beaded lingual cingulum contiguous with mesial and distal cingulum, sometimes forming a low tubercle in the mesio-lingual corner of the crown, weaker buccal cingulum, low but thick crests separating the mesial and distal fovea from the trigon basin, preprotocone crista terminates in the midline of the crown where it merges into the mesial cingulum, a low but thick crest extends buccally from the protocone and touches a lingually directed crest emanating from the paracone, the two forming the distal wall of the mesial fovea, distal fovea invaded by two low but thick crests from the hypocone and metacone respectively. Lower molars with voluminous, uncompressed lingual cusps, thin but continuous buccal cingulum, and two prominent buccal shelves, a large one between the protoconid and hypoconid, a smaller one between the hypoconid and hypoconulid, ridges bordering the mesial and distal fovea thick, mesial fovea slightly oblique due to more distal position of metaconid with respect to the protoconid; distal fovea small; p/4 longer than broad, with buccal cingulum, lingual cusp only slightly lower than the buccal cusp, large mesial fovea, distal basin bordered by a raised cingulum.

Differential diagnosis : *Karamojapithecus* differs from *Iriripithecus* by the better developed occlusal crests in its cheek teeth, the presence of transverse ridges in the floor of the distal fovea in upper molars, and more beaded cingulum. The lower fourth premolar has a distinct buccal cingulum in *Karamojapithecus*, whereas there is none in *Iriripithecus*.

Karamojapithecus differs from *Simiolus* by its greater dimensions, and by its less elongated lower molars.

Karamojapithecus differs from *Micropithecus* by its much greater dimensions, its more isolated molar cusps, the more compressed lingual cusps in lower molars, and the more isolated cusps in the molars.

Karamojapithecus differs from *Limnopithecus* by the more compressed lingual and buccal cusps in the lower molars, the more isolated molar cusps.

Karamojapithecus differs from *Lomorupithecus* by its greater dimensions, and by the presence of enamel wrinkles in the occlusal basins and foveae of the molars.

Karamojapithecus differs from *Dendropithecus* by the less well developed buccal cingulum in the upper molars, and its tall isolated molar cusps.

Karamojapithecus differs from *Turkanapithecus* by its low crown with tall isolated cusps which contrast with the tall crown and low cusps in *Turkanapithecus*.

Karamojapithecus differs from *Kogolepithecus* by the lack of, or reduced, bifid incision in the metaconid and entoconid of the lower molars, and by the weaker buccal cingulum.

Karamojapithecus differs from *Kalepithecus* by the lower fourth premolars which are radically different, short and broad in *Kalepithecus*, long, narrow and endowed with a buccal cingulum in *Karamojapithecus*.

Karamojapithecus differs from *Rangwapithecus* by the almost square outline of the upper molars, by the less wrinkled enamel (intensely wrinkled in *Rangwapithecus*), and by its smaller dimensions.

Karamojapithecus differs from *Xenopithecus* by its low crown with tall cusps, contrasting with the tall crown with low cusps of *Xenopithecus*.

Karamojapithecus differs from *Mabokopithecus* by the external position of the hypoconid in lower molars, and by its larger dimensions.

Karamojapithecus differs from *Nyanzapithecus* by its low crown with tall, isolated cusps which contrast with the high crown and low, bulbous cusps of *Nyanzapithecus*.

Etymology: "Karamoja" is the district in Uganda in which the fossils were found; "pithecus" latinised form of the Greek "pithekos", trickster or ape.

Type species: *Karamojapithecus akisimia* nov.

Holotype: NAP XV 101'08, unworn right M2/.

Diagnosis : as for the genus.

Etymology: "Akisim" is the name of the remnant of Napak Volcano from which the fossils were found. The suffix "ia" is added so that the species name terminates in "simia" Latin for ape or monkey.

Referred material: NAP XV 102'08, right I1/; NAP XV 65'09, right I1/; NAP V 1'07, left I1/; NAP XV 64'09, right M1/ lightly worn (possibly same individual as NAP XV 46'09); NAP XV 46'09, left M1/ in medium wear; NAP IV UMP 66-14, left M1/; NAP XV 173'08, left c/1; NAP IV 3'09, left dm/4; NAP IV 27'99, right p/4; NAP V 30'06, left m/1; NAP XV 177'08, right m/2 lightly worn; NAP XV 91'09, heavily worn left m/3; NAP XV 63'09, edentulous mandibular symphysis.

Type locality: Napak XV (02°06'47.3"N : 34°11'11.0"E), Akisim, Karamoja District, Uganda.

Stratigraphic context: Napak Member, above the nephelinite lava.

Age: Early Miocene, late in Faunal Set 1, levels with *Dorcatherium iririensis* and *Dorcatherium piggoti*.

Description:

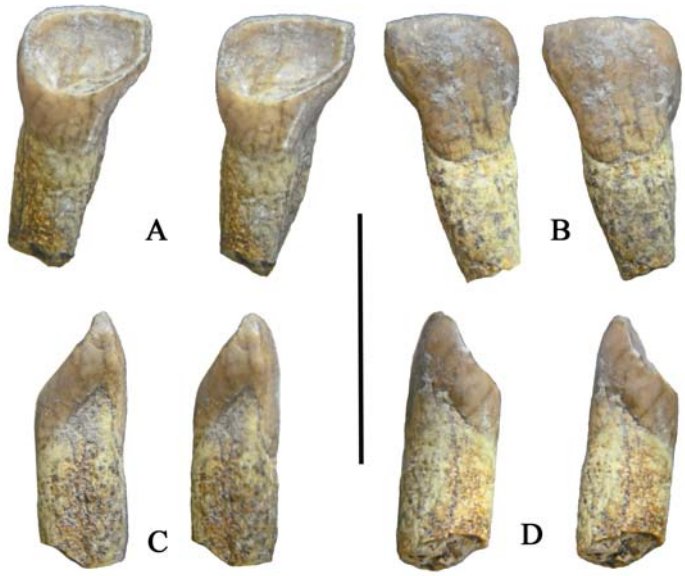

Figure 116. NAP XV 65'09, right upper central incisor *Karamojapithecus akisimia* nov. gen. nov. sp., A) lingual, B) labial, C) mesial, and D) distal stereo views. (Scale 10 mm).

NAP XV 65’09, a right upper central incisor (Fig. 116) is moderately worn apically, but the remaining part of the crown is well preserved with sharp lingual cingulum and marginal ridges, and a weak central lingual pillar. The crown is low and spatulate, and the labial surface gently convex.

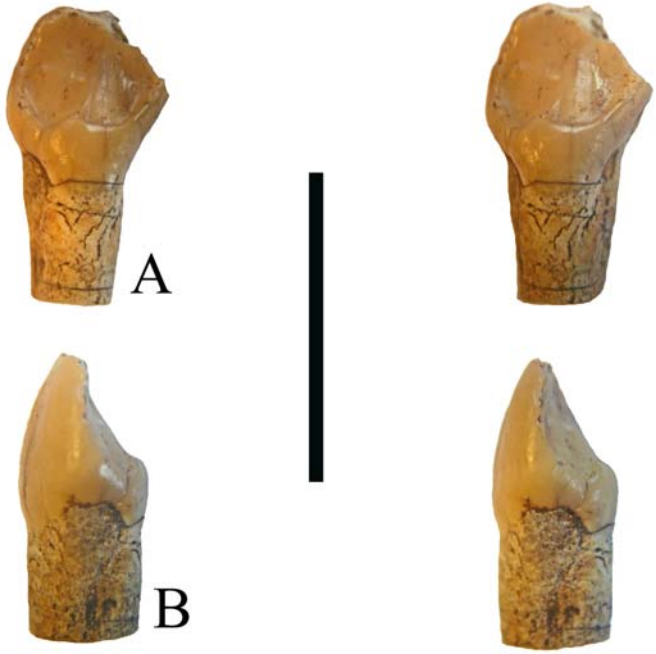

Figure 117. NAP XV 102’08, right I1/, *Karamojapithecus akisimia* nov. gen. nov. sp., A) stereo lingual and B) stereo distal views. (Scale : 10 mm).

NAP XV 102’08 is a barely worn right I1/ lacking a chip of enamel mesially and apically (Fig. 117). The central lingual pillar is weak, more a swelling in the enamel than a pillar. The mesial and distal marginal ridges are sharp and merge with the lingual cingulum. There is a poorly developed slit between the distal marginal ridge and the lingual cingulum where they meet in a V-shape. The labial surface is gently convex.

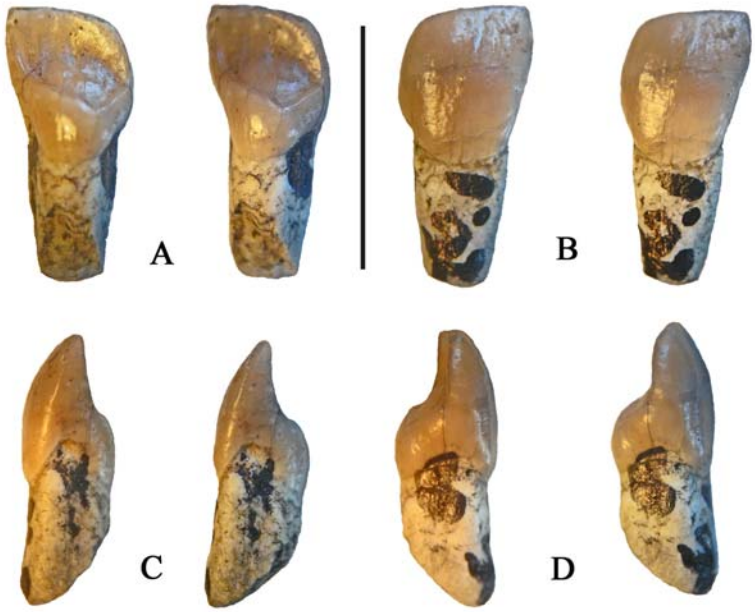

Figure 118. NAP V 1’07, left upper central incisor, *Karamojapithecus akisimia* nov. gen. nov. sp., A) stereo lingual view, B) stereo labial view, C) stereo mesial view, D) stereo distal view. (Scale : 10 mm).

NAP V 1’07, a lightly worn left I1/ is a low crowned tooth with no lingual pillar (Fig. 118). The mesial and distal marginal ridges merge with the lingual cingulum, the latter sloping distally, where it meets the distal marginal ridge at a V-shaped junction. The distal edge of the tooth is spatulate, with a sharp change in slope in the lower third of the crown. The labial surface is gently convex and the enamel lightly rugose.

Figure 119. NAP XV 64’09, left M1/, *Karamojapithecus akisimia* nov. gen. nov. sp., stereo occlusal view. (Scale : 10 mm).

NAP XV 64’09, a left M1/ is in medium wear (Fig. 119), with small dentine exposures on the protocone and hypocone, and tiny ones on the paracone and metacone, and also at the low tubercle (the paraconule) formed at the base of the preprotocrista. The hypocone is more lingually positioned than the protocone. The mesial fovea is extremely narrow mesio-distally, but broader bucco-lingually. The trigon basin is large and closed off distally by ridges running from the protocone (crista obliqua) and the metacone. The distal fovea is large, but it is invaded by broad ridges emanating from the metacone and hypocone which reduce its depth. The lingual cingulum is broad and wrinkled and passes round the protocone and hypocone. There is a clear buccal cingulum that rises mesially to join the mesial cingulum, and distally near the metacone.

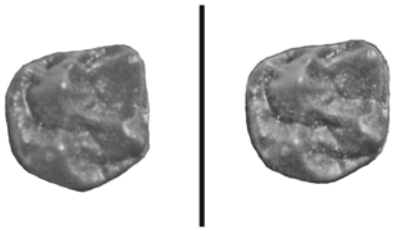

Figure 120. NAP IV UMP 66-14, left M1/, *Karamojapithecus akisimia* nov. gen. nov. sp., stereo occlusal view of cast. (Scale : 10 mm).

NAP IV UMP 66-14, is an unworn left M1/ (Fig. 120) displaying many of the features of the holotype, including a well formed accessory tubercle in the distal fovea, a tubercle in the mesio-lingual corner of the tooth, and rugose enamel in the trigon basin and distal fovea. The distal cingulum is thicker than in the holotype and the paraconule ridge is well developed.

Figure 121. NAP XV 46’09, left M2/, *Karamojapithecus akisimia* nov. gen. nov. sp., stereo occlusal view. (Scale : 10 mm).

NAP XV 46’09 is a lightly worn left M2/ (Fig. 121) exposing dentine at the very tips of the protocone, paracone and hypocone. The enamel is smooth, as though the tooth has been rolled or abraded, and this has removed some of the surface texture of the crown. Nevertheless it is possible to see that the trigon cusps had well developed crests which form the margins of a large trigon basin, separated by a substantial wall from the mesial fovea. The latter structure is mesio-distally cramped, but bucco-lingually extensive. The hypocone has well developed crests, one directed towards the protocone which it touches, and another directed into the distal fovea. The metacone also sends a ridge into the distal fovea, thereby thickening its base and reducing its capacity. The buccal cingulum is reduced in strength beneath the paracone and metacone, but this could be due to the abrasion that the tooth has suffered. The lingual cingulum is broad and encircles the protocone and hypocone. An unusual feature about this tooth is the distal position of the hypocone, which produces a marked asymmetry to the distal contour of the crown. This is due to the fact that the hypocone is larger than the metacone. The hypocone is also more lingually positioned than the protocone. The presence of wear on the distal wall of the crown suggests that this tooth is not a third molar.

Figure 122. NAP XV 101’08, right M2/ (6.8 x 7.8 mm), holotype of *Karamojapithecus akisimia* nov. gen. nov. sp., stereo occlusal view. (Scale : 10 mm).

NAP XV 101’08 is an unworn, right M2/ (Fig. 122). The crown is completely formed, but the roots had not formed at the time of death, indicating that the tooth was unerupted, or in the process of erupting. Because of its exceptionally well preserved condition, this tooth has been selected as the holotype. The crown is trapezoidal in occlusal outline, due to the large dimensions of the hypocone, and its slightly distal position with respect to the metacone and its lingual position relative to the protocone. The protocone is the largest cusp and it has two main ridges descending mesio-centrally and disto-centrally to wall off the trigon basin. The preprotocrista sends a small crest buccally which forms the distal wall of the mesial fovea. Mesial to this crest lies the paraconule which merges into the mesial cingulum. The mesial crest joins a transverse crest that runs lingually from the apex of the paracone. Because the distal wall of the mesial fovea formed by these transverse crests is in a relatively anterior position, the mesial fovea is reduced in mesio-distal dimensions, and is broader bucco-lingually. Nevertheless it is a small and cramped mesial fovea, with its deepest pit in the centre-line of the crown. The paracone sends a preparacrista anteriorly where it forms the buccal wall of the mesial fovea before merging with the mesial cingulum. The postparacrista runs distally where it joins the premetacrista thereby forming a high buccal wall for the trigon basin. The metacone sends an oblique crest towards the postprotocrista, the two meeting to wall off the trigon basin from the distal fovea. The hypocone has five crests emanating from it, one mesially to reach the base of the protocone, one buccally into the distal fovea where it gives rise to a tubercle which helps to reduce the depth of the fovea, a third crest runs disto-buccally to join the distal cingulum, thereby defining the lingual wall of the distal fovea, a fourth one directed mesio-lingually which meets the lingual cingulum, and the fifth crest is small and runs disto-lingually to reach the lingual cingulum where it forms a small, low, tubercle. The lingual cingulum is broad and somewhat beaded or wrinkled, and in the mesio-lingual corner of the crown it forms a low tubercle, almost an accessory cusplet. The buccal cingulum is sharp edged, and is interrupted beneath the metacone. The distal cingulum is sharp. The enamel surfaces in the trigon basin and distal fovea are rugose.

Figure 123. NAP XV 63’09, mandibular symphysis, *Karamojapithecus akisimia* nov. gen. nov. sp., lingual and occlusal views. (Scale : 10 mm).

NAP XV 63’09 is a damaged mandibular symphysis (Fig. 123) with the roots of the left i/1, i/2, c/1, p/3 and the anterior root of p/4, and the alveoli of the right i/1, i/2 and c/1. The mental foramen is at mid height of the jaw beneath the p/3. There is a weak superior transverse torus, beneath which there is a genial fossa and a very slight inferior transverse torus. The planum alveolare is steeply inclined.

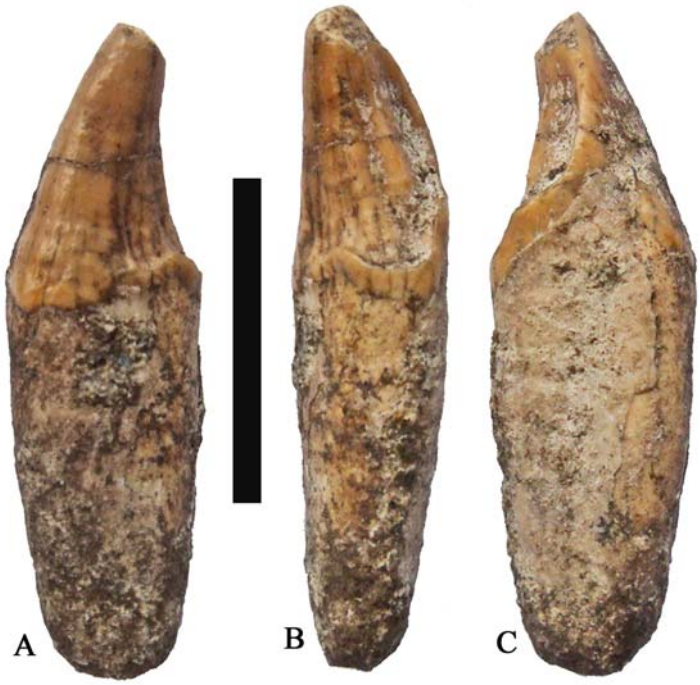

Figure 124. NAP XV 173’08, left lower canine, *Karamojapithecus akisimia* nov. gen. nov. sp., A) buccal, B) distal, and C) lingual views. (Scale : 10 mm).

The lower left canine, NAP XV 173’08, is a stout tooth with the crown canted onto the root in distal view (Fig. 124). The upward “V” of the cervix in mesial view is slight, not nearly as marked as it is in *Dendropithecus* or *Kalepithecus*. In mesial view, the surface is uniformly convex and the enamel lightly rugose, and there is a slight swelling, almost forming a weak tubercle at the base of the crown in its mesio-lingual corner. In lingual view, the lingual crest is seen to descend from the apex to the cervix, where it curves distally, forms a low tubercle, before merging with the distal cingulum. The lingual concavity next to the lingual crest is shallow. In distal view, the tooth has a distinct angulation between the crown and the root. There is a low but sharp distal ridge which fades out apically and basally. The basal cingulum is sharp and laterally it forms a low tubercle before fading out on the buccal side of the crown. The apex is slightly worn, producing a sloping apical wear facet, which extends a short way down the lingual crest.

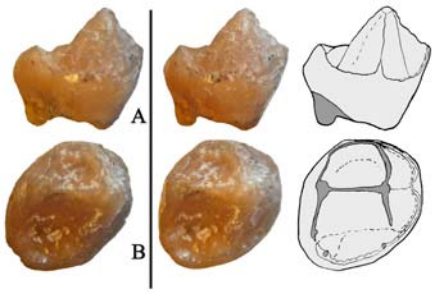

Figure 125. NAP IV 27’99, right p/4, *Karamojapithecus akisimia* nov. gen. nov. sp., A) buccal stereo view and interpretive drawing, B) stereo occlusal view and interpretive drawing. (Scale : 10 mm).

NAP IV 27’99, is an unworn right p/4 with a capacious talonid basin (Fig. 125). Its protoconid is only slightly taller than the metaconid, the two cusps being linked together via cristids that run towards each other from the apices of the cusps, forming a wall that separates the talonid basin from the mesial fovea. The mesial fovea is walled by the preprotocristid and premetacristid which merge with the mesial cingulum. The distal cingulum swells into tiny tubercles, one at the base of the postmetacristid, the other at the base of the postprotocristid, and the enamel between these tubercles is lightly beaded. A fine buccal cingulum is present, and runs all along the buccal side of the tooth, rising slightly beneath the tip of the protoconid, before descending anteriorly where it merges with the mesial cingulum.

Figure 126. NAP IV 3’09, left dm/4, *Karamojapithecus akisimia* nov. gen. nov. sp., stereo occlusal view. (Scale : 10 mm).

NAP IV, 3’09, is a left dm/4 in the beginning stages of wear (Fig. 126). Its deciduous status is indicated by two features, a) the presence of an oblique cristid entering the mesial fovea from the protoconid anterior to the usual mesially directed cristid, and thereby subdividing the mesial fovea into two halves, and b) its distal root is oriented at a sharp angle to the long axis of the tooth, and not bucco-lingually as in permanent molars.

The crown is comprised of five main cusps as in permanent lower molars. The buccal cingulum is discontinuous, forming a buccal shelf between the protoconid and hypoconid, and it forms a low cusplet or tubercle between the hypoconid and hypoconulid. The cristids emanating from the main cusps are sharp and well developed, and separate the talonid basin, which is vast, from the mesial and distal foveae and from its lingual and buccal outlets. The distal fovea is small and cramped, the mesial one bucco-lingually broader, but mesio-distally cramped due to the accessory cristid emanating from the protoconid.

Figure 127. NAP V 30’06, left m/1, *Karamojapithecus akisimia* nov. gen. nov. sp., stereo occlusal view (Scale : 10 mm).

NAP V 30’06 is a moderately worn lower molar with a chip of enamel missing from the mesio-lingual corner of the crown (Fig. 127). The three buccal cusps are placed some distance from the buccal margin of the tooth, so there are small buccal shelves between the protoconid and hypoconid, and between the hypoconid and hypoconulid. The mesial fovea is small, the talonid basin is vast, and the distal fovea is small. The protoconid and metaconid are at almost the same level.

Figure 128. NAP XV 177’08, right m/2, *Karamojapithecus akisimia* nov. gen. nov. sp., stereo occlusal view. (Scale : 10 mm).

NAP XV 177’08, is a lightly worn right lower molar showing tiny enamel exposures at the apices of the protoconid, metaconid and hypoconid (Fig. 128). The hypoconulid is lacking it tip due to damage. The crown is supported by two stout ovoid roots oriented transversely. The talonid basin is vast and connects to a cramped, transversely oriented mesial fovea, via a high wall formed of medially directed crests from the protoconid and metaconid. The distal fovea is moderately sized, walled off from the talonid basin by crests from the entoconid and hypoconulid. The buccal shelves are large, but the accompanying cingulum is not well developed on the buccal surface of the hypoconid. The cingulum rises mesially on the outer surface of the protoconid but doesn’t reach the mesial cingulum.

Figure 129. NAP XV 91’09, left m/3, *Karamojapithecus akisimia* nov. gen. nov. sp., stereo occlusal view. (Scale : 10 mm).

NAP XV 91’09 is a heavily worn left m/3 (Fig. 129) with deep dentine lakes in the position of the metaconid and hypoconid and shallower, smaller exposures of dentine at the protoconid and hypoconulid. The buccal shelf between the protoconid and hypoconid is large and the buccal cingulum extends mesially to merge with the mesial cingulum. The remnants of the mesial fovea show that it was relatively small and cramped. There are two roots, the anterior one vertical, ovoid in section, and transversely aligned, the distal one rounded triangular in section and slanting distally.

Discussion

An upper molar (NAP IV UMP 66-14) from Napak attributed to *Karamojapithecus akisimia*, was previously identified as *Limnopithecus legetet* (Fleagle & Simons, 1978; Harrison, 1982, 1986 (as an upper second molar)). It is here interpreted as a first upper molar of a somewhat larger taxon than *Limnopithecus legetet*. The crown morphology is close to that of the holotype of *Karamojapithecus akisimia*, even down to details of the secondary occlusal ridges in the distal fovea of the upper molars, the position of the hypocone relative to the metacone and the strength of the lingual cingulum.

Karamojapithecus is closest in overall morphology to *Iriripithecus*, yet there are significant differences between the two genera. Where *Karamojapithecus* has thicker enamel, better developed occlusal crests and more bulbous cusps, *Iriripithecus* is thinner enamelled, with finer occlusal crests,

more bucco-lingually compressed cusps and smooth enamel. Furthermore, the hypocone of the upper molars is more distally positioned in *Karamojapithecus* than in *Ririipithecus*.

Genus *Turkanapithecus* Leakey & Leakey, 1986

Diagnosis: A short-faced small hominoid approximately the size of *Colobus polykomos*. It is distinguished from all known hominoids by the upper M2/s, which have an additional cuspule between the pronounced and beaded mesial and lingual cingula, and the upper molars and P4/ which have small additional cuspules associated with a small buccal cingulum bordering the paracone. It is distinguished from Oreopithecidae by the relatively low relief of the dental occlusal surface, upper molars not mesio-distally elongated and lower molars not long and narrow, without bucco-lingual waisting and lacking a centroconid. It is distinguished from the larger *Rangwapithecus* by the upper M3/ approximately the same size or smaller than M2/ and the upper P4/ smaller than P3/. It is distinguished from the slightly larger *Proconsul africanus* by the distinct snout, the wide interorbital distance, the relatively thick supraorbital tori, the broad nasals, the relatively broad and low mandibular ramus and the upper premolars and molars not bucco-lingually expanded. It is distinguished from the similar sized *Pliopithecus vindobonensis* by the distinct snout, the long nasals and the zygomatic process of the maxilla approximately vertical and no protruding inferior orbital margin (from Leakey & Leakey, 1986).

Emendation : The crowns of the molars are tall, with diminutive cusps on the occlusal surface.

Type species : *Turkanapithecus kalakolensis* Leakey & Leakey, 1986.

Diagnosis: as for the genus (from Leakey & Leakey, 1986).

Holotype : KNM WK 16950 A and B, partial cranium and mandible.

Type locality: Kalodirr, Kenya.

Age : Basal Middle Miocene (ca 17.2 Ma).

Species *Turkanapithecus rusingensis* nov.

Diagnosis: Species of *Turkanapithecus* ca 15% smaller than the type species *T. kalakolensis*. The enamel has a tendency to spall off the sides of the molars.

Holotype: KNM RU 1680 (CMH 8) right mandible fragment containing m/2 and m/3.

Type locality: R3, Rusinga Island, Winam Gulf, Western Kenya.

Age: Early Miocene, Faunal Set 2, ca 17.8 Ma.

Other sites: Napak V (Uganda) Kipsaraman, Rusinga, Mfwangano, Songhor (Kenya).

History

Le Gros Clark & Leakey (1951) provided a description of the holotype, CMH 8 (= KNM RU 1680) from R3 on Rusinga Island, which they attributed to *Proconsul africanus*. The enamel has flaked off the sides of the teeth, but it is possible to make out that the crowns are tall with low cusps arranged on the occlusal surface, as in the type specimen of *Turkanapithecus kalakolensis*. Among the Hominoidea, such morphology of the cheek teeth is unusual, but it occurs in *Turkanapithecus* and to some extent in *Nyanzapithecus* (lower cheek teeth unknown for *Xenopithecus* and *Kamoyapithecus*). The mandible is relatively slender : Le Gros Clark & Leakey (1951) give measurements of 22 mm depth and 9 mm breadth at the first molar.

Table 2. Measurements (in mm) of the teeth of *Turkanapithecus* species (Measurements of *T. kalakolensis* are from Leakey & Leakey, 1986) the others are by MP.

Catalogue Number	Tooth	Length	Breadth	Locality	Identification
KNM RU 1680	m/1	7.8	6.0	Rusinga R3	*Turkanapithecus rusingensis*
BAR 17'03	m/1 or m/2	7.5	6.2	Kipsaraman	*Turkanapithecus rusingensis*
KNM WK 16950	m/2	9.2	7.0	Kalodirr	*Turkanapithecus kalakolensis*
KNM RU 1680	m/2	8.0	6.4	Rusinga R3	*Turkanapithecus rusingensis*
KNM WK 16950	m/3	9.2	7.4	Kalodirr	*Turkanapithecus kalakolensis*
KNM WK 16950	C1/	10.0	7.6	Kalodirr	*Turkanapithecus kalakolensis*
KNM WK 16950	P3/	6.4	8.0	Kalodirr	*Turkanapithecus kalakolensis*
KNM WK 16957	P3/	5.7	7.7	Kalodirr	*Turkanapithecus kalakolensis*
KNM WK 16950	P4/	5.5	--	Kalodirr	*Turkanapithecus kalakolensis*
KNM WK 16950	M1/	7.0	7.5	Kalodirr	*Turkanapithecus kalakolensis*
KNM SO 1134	M1/	6.0	6.1	Songhor	*Turkanapithecus rusingensis*
NAP V 10'04	M1/	6.0	6.8	Napak V	*Turkanapithecus rusingensis*
KNM WK 16950	M2/	8.6	9.0	Kalodirr	*Turkanapithecus kalakolensis*
KNM WK 16950	M3/	8.0	8.9	Kalodirr	*Turkanapithecus kalakolensis*
KNM MW 48	M3/	7.2	7.3	Mfwanganu	*Turkanapithecus rusingensis*

Andrews (1978, fig. 3) illustrated the type specimen as *Proconsul africanus*, but Bosler (1981) excluded it from the hypodigm of the species. We agree with this exclusion, and go further in attributing it to *Turkanapithecus*. Other material from Western Kenya belongs to the same kind of small ape, including KNM MW 48 an upper third molar with a tall crown, but low cusps. This specimen was previously identified as an M2/ of *Rangwapithecus vancouveringorum* (Andrews, 1978) and later as *Nyanzapithecus vancouveringorum* by Harrison (1986), but the differences from the holotype of the species are manifest. A similar morphology occurs in KNM SO 1134 from Songhor, also previously included in *R. vancouveringorum* (Andrews, 1978). An undescribed lower molar from Kipsaraman (BAR 17'03) also shows the characteristic tall crown base, with low cusps occlusally. It is concluded from this evidence that a small species of *Turkanapithecus* occurs in Western Kenya, but that fossils belonging to it have previously been incorrectly attributed to other genera. The Napak upper molar confirms the presence of a small species of *Turkanapithecus* in the Early Miocene of East Africa.

Material from Napak

NAP V 10'04, a left M1/ (Fig. 130), is a high-crowned molar posed on a substantial root base (moderate taurodonty). The cusps of the crown are worn flat, the outline of the wear facets reveals that they crowded the occlusal surface of the tooth, restricting the trigon basin and narrowing the mesial and distal foveae. The paracone is small and possesses clear parastyle and mesostyle. The wear facet on the parastyle is confluent with the one that surrounds the anterior margin of the mesial fovea. The parastyle is bordered bucco-distally by a shallow groove. The mesostyle is also bordered buccally by a groove which leads basally towards a low cingular swelling that almost forms a tiny cusplet. The protocone is the largest cusp, and is bordered anteriorly by a bucco-lingually broad but mesio-distally narrow fovea which is in effect the groove between the protocone and the cingulum. The preprotocone crista has been eradicated by wear, but its course is revealed by an extension of the dentine exposure towards the front of the tooth in its midline. Wear has progressed to the stage that the dentine exposure in the protocone has joined that of the metacone. Buccally the metacone has a short premetacone crista that descends towards the mesostyle, but does not join it, although with slightly greater wear there would be a link between them. The metastyle curves lingually where it joins the posterior margin of the distal fovea, their wear facets being contiguous. There is a small area of damage distally which obscures the dimensions and extent of the distal fovea. The trigon basin is extremely restricted between the paracone, protocone and metacone. The hypocone is almost the same dimensions as the protocone, but it is more lingually positioned, and is almost completely separated from the trigon. There is a low link between the hypocone and the crista obliqua, and a low ridge between the hypocone and the metacone. The prehypocone crista extends basally towards a low cingular cusplet, which is separated by a groove from another such cusplet at the disto-lingual base of the protocone.

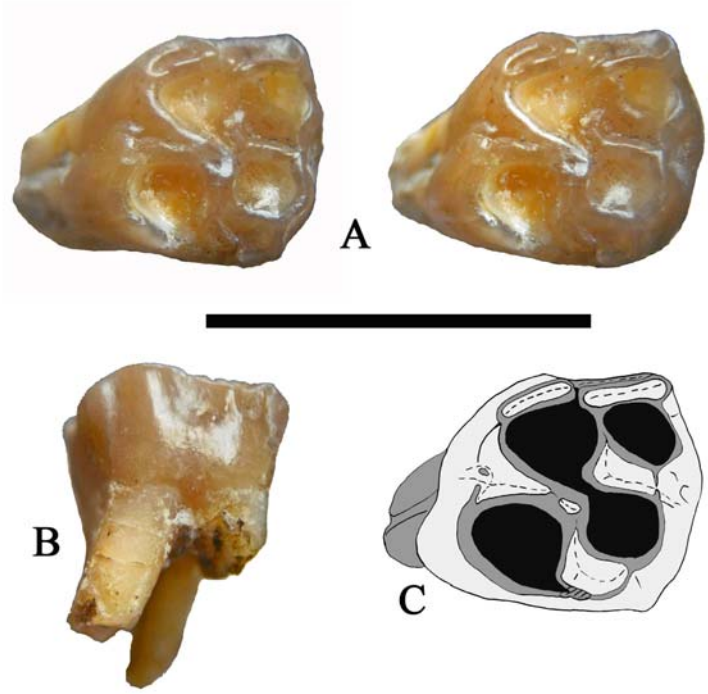

Figure 130. NAP V 10’04, left M1/, *Turkanapithecus rusingensis* sp. nov., A) stereo occlusal, B) buccal, and C) interpretive drawing of the occlusal surface. Note the short crest linking the hypocone to the crista obliqua and the posteriorly slanting disto-buccal root. (Scale : 10 mm).

There is a single mesio-distally elongated lingual root inclined palatewards and slightly distally and showing a groove lingually, and there are two buccal roots, both of which are mesio-distally compressed, with a prominent internal groove. The posterior buccal root is inclined gently distally. The occlusal surface is not at right angles to the height axis of the tooth, suggesting that the tooth was slightly inclined in the maxilla.

Discussion

There has been some confusion about small hominoids from East Africa which have tall molar bases with small cusps occlusally which wear flat. Leakey & Leakey (1986) erected the taxon *Turkanapithecus kalakolensis* for specimens from Kalodirr, Kenya (basal Middle Miocene, 17.2 Ma) and Rossie & MacLatchy (2006) erected the taxon *Lomorupithecus harrisoni* for a snout from Napak IX in which the first molar has worn flat, but its molars are not high-crowned and its roots are not taurodont. This specimen was found near a juvenile mandible which they included in the species. However, the mandible evidently does not represent the same species as the snout, but belongs instead to *Limnopithecus legetet*.

Turkanapithecus from Kalodirr, Kenya, has molars which possess taurodont roots as well as tall crowns with crowded occlusal surfaces which wear flat, like the Napak molar (and incidentally somewhat like the type specimen of *Xenopithecus koruensis*). The basic morphology of the upper molars of *Turkanapithecus kalakolensis* is compatible with the Napak molar, but in *Turkanapithecus kalakolensis*, the cingula are more strongly developed, and there is incipient cusplet formation at the mesio-lingual corner of the cingulum, as is also the case in *Xenopithecus koruensis* Hopwood, 1933a. *Turkanapithecus* is unusual among Hominoidea in that the teeth lean forwards in the maxilla. The Napak molar, being isolated, is difficult to orient, but the occlusal surface is not at right angles to the height axis of the tooth, suggesting that it too was slanting in the maxilla. On this basis, and its morphology, we consider that NAP V 10’04 belongs to *Turkanapithecus*, but it differs from the type species by its smaller dimensions and by some relatively minor details of molar morphology such as less exaggerated cingular structures and the posteriorly inclined disto-buccal root.

The upper first molar of *Lomorupithecus harrisoni* was described by Rossie & MacLatchy (2006) who showed that, despite the heavy wear, it has a small hypocone, is not particularly high crowned, and it is not taurodont. The morphology and dimensions of NAP V 10'04 differentiate it from *Lomorupithecus harrisoni*, especially its large hypocone, tall crown and taurodont roots.

Examination of casts in the Natural History Museum, London, reveals that *Turkanapithecus* is more widespread than has generally been acknowledged. KNM SO 1134 is a left M1/ (6.0 x 6.1 mm) of *Turkanapithecus*, and not of *Rangwapithecus vancouveringorum*. KNM MW 48, a left M3/ (6.8 x 6.1 mm) is morphologically close to, but smaller than, the M3/ in the holotype of *Turkanapithecus kalakolensis*, and KNM RU 1680, a right mandible containing m/1 and m/2 previously attributed to *Proconsul africanus*, is slender, as in *Turkanapithecus*, and the two lower molars (m/1 - 7.8 x 6.0, m/2 - 8.0 x 6.4 mm) possess tall crowns with small, low cusps on the occlusal surface, just as in the holotype of *T. kalakolensis*, but the teeth are slightly smaller (m/2 in *T. kalakolensis* 8.6 x 6.7 mm). From Kipsaraman, Kenya, there is an isolated lower molar (BAR 17'03) with the same distinctive tall crown base, with small cusps occlusally. We take all these occurrences as evidence that *Turkanapithecus* was widespread, even though rare, in Early Miocene deposits of East Africa, as it is now known from Napak, Songhor, Rusinga, Mfwangano and Kipsaraman. It could well be present at other sites, but we have not been able to examine all the relevant material (Table 2, Fig. 131).

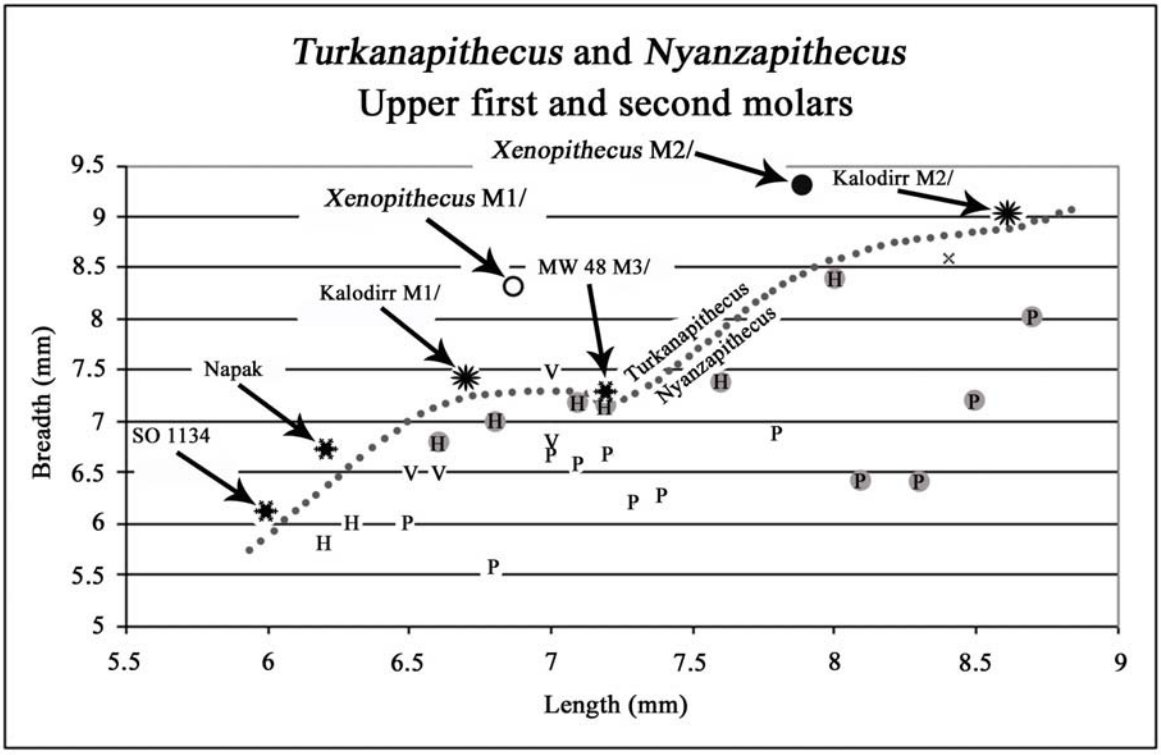

Figure 131. Length/breadth scatter diagram of upper 1st and 2nd molars of *Turkanapithecus kalakolensis*, *Nyanzapithecus* species and *Xenopithecus koruensis*. (Open symbols - M1/, shaded symbols – M2/)(P – *N. pickfordi*, V – *N. vancouveringorum*, H – *N. harrisoni*, X – Kipsaraman specimen attributed to *N. pickfordi*). Note the positions of KNM MW 48 and KNM SO 1134, two upper molars from Western Kenya attributed to *Turkanapithecus rusingensis* sp. nov. (Measurements of the Kenyan fossils are from Harrison, 1986; Kunimatsu, 1997; and Pickford & Kunimatsu, 2005).

NAP V 10'04 shows some resemblances to upper molars of *Nyanzapithecus*, but the cusps are not as bulky as those in *Nyanzapithecus*. Most of the morphological features of this tooth agree with the criteria highlighted by Harrison (1986) for *Nyanzapithecus*, but the crown is not as elongated and it does not narrow distally as much. But the high crown, voluminous cusps producing a crowded occlusal morphology, very restricted foveae and trigon basin, the strong development of the mesial

part of the cingulum on the protocone, the isolated nature of the hypocone, save for the presence of a short, low crest linking it to the crista obliqua, plus the extremely flat wear surface of the tooth, are all compatible with *Nyanzapithecus*. There is slight waisting of the base of the crown on the lingual side, but not on the buccal side, although at the level of the cusps, the waisting is well developed.

Harrison 1986) did not mention the presence of a substantial root base (taurodonty) in *Nyanzapithecus*. In the Napak tooth, this base consists of about 1 mm of fused root, beyond which the roots become separate entities. Radicular taurodonty generally increases with ontogenetic age, so young individuals may not have it as well developed as in this heavily worn tooth. Thus, despite the resemblances between NAP V 10'04 and *Nyanzapithecus*, we conclude that the Napak tooth does not belong to this genus, but is closer to *Turkanapithecus*.

NAP V 10'04 is shorter and broader than most reported material of *Nyanzapithecus* (Figure 131), but is closest in dimensions to *N. harrisoni* from the younger, Middle Miocene deposits at Nachola, Kenya (Kunimatsu, 1992). However, it is broader relative to length than *Nyanzapithecus*. In molar proportions it is close to *Turkanapithecus kalakolensis*, but it is substantially smaller (Fig. 131). We consider that this specimen represents a small new species of the genus *Turkanapithecus* which we name *Turkanapithecus rusingensis* with, as holotype, a mandible with two molars from R3 on Rusinga Island.

The combination of tall crowns, taurodont roots and heavy wear suggest that the species was probably consuming food that required strong chewing forces. The food may not have been excessively abrasive, but was probably hard, such as nuts.

MORPHOMETRIC ANALYSIS OF NAPAK SMALL APE DENTITIONS

Napak small ape upper central incisors

There are 10 upper central incisors of small apes from Napak, which comprise six morphotypes (Table 3). None have been found in direct association with cheek teeth, so some doubt remains about the identification of the specimens.

Table 3. Upper central incisors of small apes from Napak. Measurements are in mm.

Catalogue N°	Tooth	MD length	Ll breadth	Species
NAP V 7'98	I1/ left	4.5	3.4	*Micropithecus clarki*
NAP V 87'02	I1/ right	4.4	3.5	*Micropithecus clarki*
NAP IV UMP 66-24	I1/ right	4.4	3.7	*Limnopithecus legetet*
NAP IV 11'08	I1/ left	4.7	4.0	*Lomorupithecus evansi*
NAP V 22'08	I1/ left	4.7	4.4	*Lomorupithecus evansi*
NAP V 1'07	I1/ left	5.3	4.0	*Karamojapithecus akisimia*
NAP XV 102'08	I1/ right	5.2	4.2	*Karamojapithecus akisimia*
NAP XV 65'09	I1/ right	5.3	3.7	*Karamojapithecus akisimia*
NAP V UMP 67-06	I1/ left	4.7	3.6	*Kalepithecus songhorensis*
NAP IV 80'08	I1/ right	5.0	3.6	*Iriripithecus alekileki*

Upper central incisors attributed to *Micropithecus clarki* have low crowns, weak lingual pillars and quite spatulate distal halves, with a low junction between the distal marginal ridge and the lingual cingulum.

Two incisors attributed to *Lomorupithecus evansi* have low lingual pillars, and the junction between the lingual cingulum and distal marginal ridge forms a deep "V". Three upper central incisors are attributed to *Karamojapithecus*. They are low crowned and mesio-distally broad. The incisor identified as *Kalepithecus* is not very well preserved, but agrees in overall features with its counterpart in KNM SO 417. The upper central incisor of *Iriripithecus* has no lingual pillar, and its labial surface is flattened to concave in the mesial half.

Napak small ape upper lateral incisors
Only two upper lateral incisors of small apes have been found at Napak (Table 4). One is attributed to *Kalepithecus songhorensis* because it is extremely similar in morphology and dimensions to its counterpart in KNM SO 417. The other is attributed to *Lomorupithecus evansi*.

Table 4. Upper lateral incisors of small apes from Napak. Measurements are in mm.

Catalogue N°	Tooth	MD length	Ll breadth	Species
NAP IV 2'05	I2/ left	3.3	4.0	*Kalepithecus songhorensis*
NAP IV UMP 66-33a	I2/ right	3.7	3.8	*Lomorupithecus evansi*

Napak small ape upper canines
12 upper canines representing six morphotypes of small apes have been collected at Napak (Table 5). In addition there is a maxilla with a partial canine alveolus preserved and one specimen is associated with the upper premolars.

Table 5. Upper canines of small apes from Napak (bold represents specimens associated with other teeth in maxillae). Measurements are in mm.

Catalogue N°	Tooth	MD length	BL breadth	Root height	Crown height	Species
NAP V 221'09	C1/ left	5.3	4.2	10.0	7.0	*Micropithecus clarki*
NAP IV UMP 64-02	C1/ right	4.3	3.5	10.5		*Micropithecus clarki*
NAP V 65'08	C1/ right	5.2	3.8	10.0	4.7	*Micropithecus clarki*
NAP V 8'98	C1/ right	5.8	4.2		8.1	*Micropithecus clarki*
NAP IV 221'08	C1/ right alveolus	4.5	3.8	8.0		*Micropithecus clarki*
NAP V UMP 66-19	C1/ left	5.3	4.1	14.0	7.4	*Limnopithecus legetet*
NAP V 25'08	C1/ left	4.9	4.7			*Limnopithecus legetet*
NAP IV UMP 68-03	C1/ left	6.7	5.4	18.0	9.0	*Limnopithecus legetet*
NAP IV 25'04	C1/ left	5.9	5.0		10.0	*Lomorupithecus evansi*
NAP IX BUMP 266	C1/ left	6.0	5.0			*Lomorupithecus evansi*
NAP IV 14'07	C1/ left	6.6	4.8			*Dendropithecus ugandensis*
NAP I 2'09	C1/ left	8.1	6.7		12.4	*Kalepithecus songhorensis*
NAP IV 1'10	C1/ left	6.4	5.4	12.8		*Iriripithecus alekileki*

Four upper canines are attributed to *Micropithecus clarki*. The discovery of a specimen in a maxilla associated with the premolars is important, as this discovery establishes the association between the canines and the cheek teeth. Harrison (1982) for example did not recognise any upper canines of this genus. The teeth are unusual in a hominoid context on account of the fact that the mesial groove is extremely weakly developed, very lingually positioned and is overshadowed by the mesial crest. The crowns are low, mesial and distal shoulders are low (where the lingual cingulum meets the mesial and distal crests respectively).

Two complete upper canines and one broken specimen are identified as *Limnopithecus legetet*. The broken specimen is in a maxilla which also contains the P3/. The mesial groove is well developed, and bordered by a well developed mesial crest anteriorly, and a well formed lingual pillar behind. The crown is relatively tall and pointed.

The canine in the snout of *Lomorupithecus evansi* is broken, but it is possible to determine that its root was almost circular in section. There is an isolated canine from Napak IV which also has a stout circular root. The mesial groove is deep and bordered by two prominent crests, and there is a second groove immediately to the buccal side of the mesial crest. This morphology recalls that of *Dendropithecus*, but the crowns of the latter genus are much more compressed bucco-lingually, than is

the case in this tooth and there is no buccal slit. There is a deep wear facet distally, which has worn an angular notch into the base of the crown close to the distal tubercle.

The single upper canine attributed to *Dendropithecus ugandensis* is similar to its counterpart in *Dendropithecus macinnesi* but is small. There are two grooves mesially, the crown is compressed bucco-lingually and there is a distinct buccal slit.

A well preserved upper canine from Napak I is identified as *Kalepithecus songhorensis* on account of its dimensions and morphology, which are close to those in KNM SO 417. The canine in the Songhor specimen is broken apically, but enough is preserved to reveal the similarities between these two teeth. The description of the upper canine of this species can thus be completed. The bucco-lingual compression is moderate, less than that in *Dendropithecus* but more than in *Lomorupithecus*. There are two grooves mesially, a deep lingual one, and a shallower buccal one, separated by a sharp crest. On the buccal surface of the crown there is a vertical slit, as in *Dendropithecus*. The distal tubercle is weak. A long wear facet extends from the apex of the crown down its distal crest onto the root. The upper canine attributed to *Iriripithecus* was found close to the holotype maxilla. It has a prominent mesial groove, but the one on the buccal side of the mesial crest is weakly incised, and there is no buccal slit. The enamel on the buccal surface is fluted by low fine crests. Enamel is thin, and the distal wear facet extends from the tip of the crown to the root, and the basal tubercle is weak or absent.

Napak small ape upper P3/s

There are eight upper third premolars of small hominoids from Napak, which can be arranged into five morphotypes (Table 6). Four specimens belong to *Micropithecus clarki*, one to *Limnopithecus legetet*, two to *Lomorupithecus evansi* and one to *Iriripithecus alekileki*.

Table 6. Upper third premolars of small apes from Napak (bold represents specimens associated with other teeth in maxillae). Measurements are in mm.

Catalogue N°	Tooth	MD length	BL breadth	Species
NAP V 221'09	P3/ right	3.4	4.8	*Micropithecus clarki*
NAP IV 221'08	P3/ right	3.2	4.7	*Micropithecus clarki*
NAP IV UMP 64-02	P3/ right	3.1	4.7	*Micropithecus clarki*
NAP XV 36'08	P3/ left	3.0	5.0	*Micropithecus clarki*
NAP V 25'08	P3/ left	3.6	5.3	*Limnopithecus legetet*
NAP IX BUMP 266	P3/ left	3.9	6.1	*Lomorupithecus evansi*
NAP V 113'09	P3/ left	3.9	5.1	*Lomorupithecus evansi*
NAP XV 4’10	P3/ left	4.4	5.9	*Iriripithecus alekileki*

The three additional teeth attributed to *Micropithecus clarki* are similar to the holotype P3/, which has unfortunately been lost since it was first described. A cast in the NHM London, retains the P3/, and it is on this basis that the additional specimens are attributed to the species. The buccal cusp is taller and much larger than the lingual cusp. The lingual cusp is in a mesial position. There is an exceptionally weak lingual cingulum, more a small line in the enamel than a proper cingulum. The mesial fovea is cramped anteriorly, the distal basin is large. There is a single or double crest crossing the tooth from the buccal cusp, but these crests are low and narrow.

The P3/ identified as *Limnopithecus legetet* is similar to but larger than that of *Micropithecus clarki*, although there is no hint of a lingual cingulum. The mesial fovea is exceedingly cramped, the distal basin large.

The P3/ attributed to *Lomorupithecus evansi* has already been described by Rossie & MacLatchy (2006). It is broader than long, with an anteriorly positioned protocone and there is no lingual cingulum. The second specimen of P3/ (NAP V 113’09) attributed to *Lomorupithecus* is less worn than that in NAP IX BUMP 266. It differs from that of *Limnopithecus legetet* by its more upright buccal cusp and from that of *Kalepithecus* by its lack of lingual cingulum, and by the lower crests running from the protocone, which is in a more mesial position.

The P3/ attributed to *Iriripithecus alekileki* is similar in size to its counterpart in the maxilla and premaxilla KNM SO 417 but differs in the morphology of the protocone. The buccal cusp is tall, large and angular and the lingual cusp low, conical, pointed and with a lingual cingulum. There is a mesial groove lying between the preparacrista and a crest leading towards the centre of the mesial cingulum from the apex of the paracone. The mesial fovea is mesio-distally narrow, but bucco-lingually broad. The distal basin is large and the enamel in its floor is lightly but coarsely wrinkled. The postprotocrista is sharp.

Napak small ape upper P4/s

Only six upper fourth premolars have been collected at Napak, four attributed to *Micropithecus clarki*, and two to *Lomorupithecus evansi* (Table 7).

Table 7. Upper fourth premolars of small apes from Napak (bold represents specimens associated with other teeth in maxillae). Measurements are in mm.

Catalogue N°	Tooth	MD length	BL breadth	Species
NAP IV 221'08	P4/ right	3.3	5.0	*Micropithecus clarki*
NAP V 221'09	P4/ right	3.1	5.0	*Micropithecus clarki*
NAP IV UMP 64-02	P4/ right	3.2	5.0	*Micropithecus clarki*
NAP IV 26'04	P4/ left	3.3	5.3	*Micropithecus clarki*
NAP IX BUMP 266	P4/ left	3.6	6.2	*Lomorupithecus evansi*
NAP IV 10'08	P4/ right	3.9	5.8	*Lomorupithecus evansi*

The three additional specimens identified as *M. clarki*, have a weak lingual cingulum, more like a shallow groove in the enamel than a proper cingulum. In the holotype the lingual cingulum is clearly developed. There are usually two transverse crests crossing the tooth from the apex of the buccal cusp, across towards the lingual one, although these crests are fine, and disappear with light wear. NAP IV 10’08 is similar to its counterpart in the snout from Napak IX described by Rossie & MacLatchy, 2006. The lingual cusp is almost as big as the buccal one, and is in an anterior position. The outline of the tooth is almost symmetrical. There are two transverse crests crossing the distal basin, the mesial one defining the margin of the mesial fovea, the distal one subdividing the distal basin into two. There is a low but clear lingual cingulum.

Napak small ape deciduous upper molars

Two specimens of DM3/ and two of DM4/ of small apes have been found at Napak (Table 8). Three of the specimens are attributed to *Micropithecus clarki*, and one to *Lomorupithecus evansi*.

Table 8. Upper deciduous molars of small apes from Napak. Measurements are in mm.

Catalogue	Tooth	MD length	BL breadth	Species
NAP V 31'06	DM3/ left	3.7	5.0	*Lomorupithecus evansi*
NAP IV UMP 66-33b	DM3/ left	3.0	3.8	*Micropithecus clarki*
NAP IV 70'05	DM4/ left	4.0	4.7	*Micropithecus clarki*
NAP IV 85'08	DM4/ right	4.0	4.5	*Micropithecus clarki*

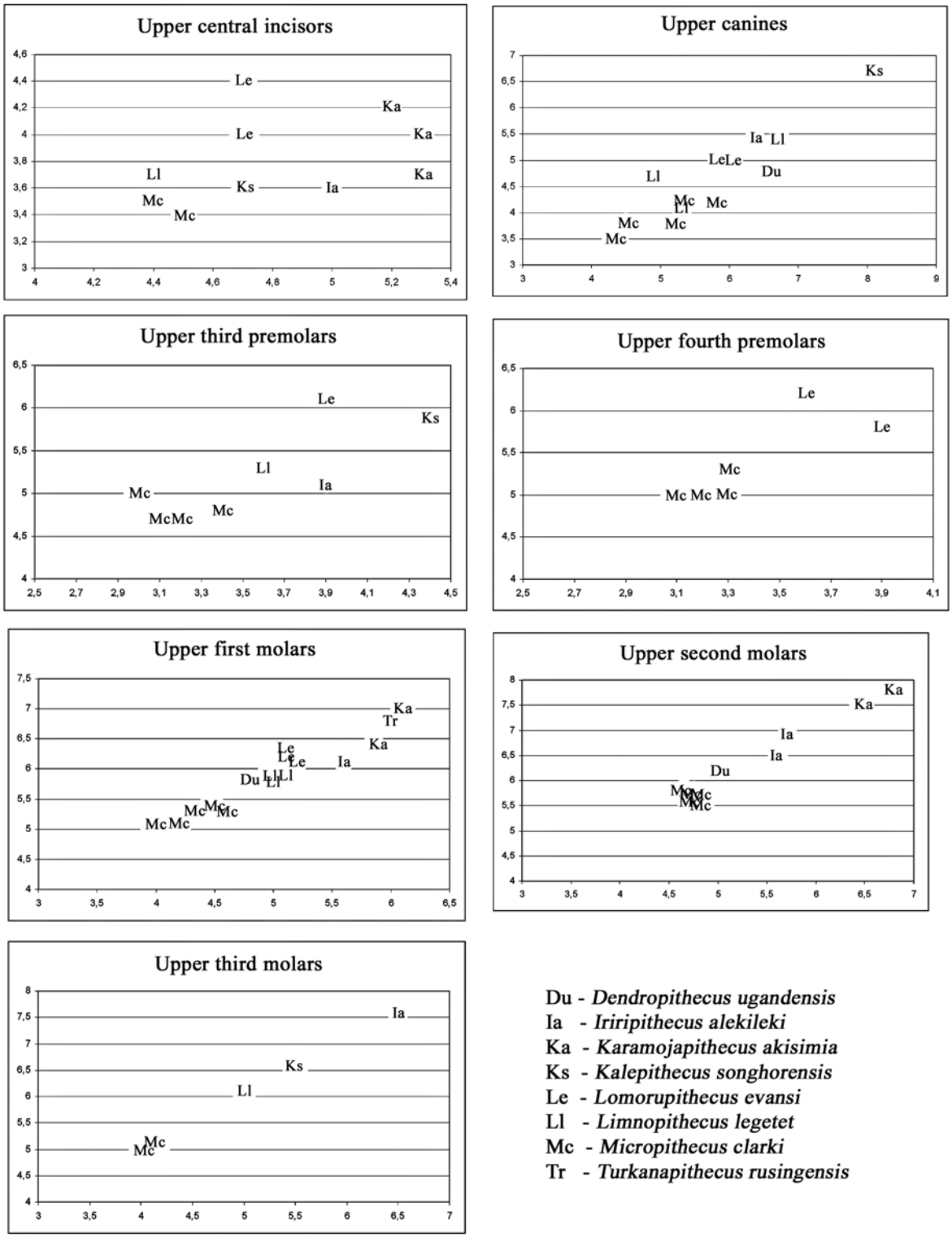

Figure 132. Bivariate plots of upper teeth of small apes from Napak, Uganda. (Length axis horizontal, breadth axis vertical).

Napak small ape upper molars

33 upper molars of small hominoids from Napak are attributed to eight different taxa, and in addition there is a single cercopithecid upper molar which does not concern us here (Table 9, Fig. 132).

Table 9. Upper molars of small apes from Napak (bold represents specimens associated with other teeth in maxillae). Measurements are in mm.

Catalogue N°	Tooth	MD length	BL breadth	Species
NAP IV 51'04	M1/ left	4.5	5.4	*Micropithecus clarki*
NAP IV UMP 64-02	M1/ left	4.0	5.1	*Micropithecus clarki*
NAP IV UMP 66-09	M1/ left	4.6	5.3	*Micropithecus clarki*
NAP IV 221'08	M1/ right	4.3	5.3	*Micropithecus clarki*
NAP IV UMP 64-02	M1/ right	4.2	5.1	*Micropithecus clarki*
NAP IV 176'09	M1/ left	5.1	5.9	*Limnopithecus legetet*
NAP IV 110'09	M1/ left	5.0	5.9	*Limnopithecus legetet*
NAP IV UMP 66-11	M1/ left	5.0	5.8	*Limnopithecus legetet*
NAP XV 90'09	M1/ right	4.8	5.8	*Dendropithecus ugandensis*
NAP IX BUMP 266	M1/ left	5.1	6.2	*Lomorupithecus evansi*
NAP I 2'10	M1/ right	5.2	6.1	*Lomorupithecus evansi*
NAP IX BUMP 266	M1/ right	5.1	6.3	*Lomorupithecus evansi*
NAP IV 71'05 (germ)	M1/ right	4.4+	5.2+	*Lomorupithecus evansi*
NAP IV 20'07	M1/ left	5.6	6.1	*Iriripithecus alekileki*
NAP IV UMP 66-14	M1/ left	5.9	6.4	*Karamojapithecus akisimia*
NAP XV 64'09	M1/ left	6.1	7.0	*Karamojapithecus akisimia*
NAP V 10'04	M1/ left	6.0	6.8	*Turkanapithecus rusingensis*
NAP IV UMP 64-02	M2/ right	4.7	5.6	*Micropithecus clarki*
NAP IV UMP 64-02	M2/ left	4.8	5.5	*Micropithecus clarki*
NAP IV 51'04	M2/ left	4.6	5.8	*Micropithecus clarki*
NAP V 103'06 + UMP 66-28a	M2/ left	4.8	5.7	*Micropithecus clarki*
NAP IV 221'08	M2/ right	4.7	5.7	*Micropithecus clarki*
NAP IV 25'02	M2/ left	5.0	6.2	*Dendropithecus ugandensis*
NAP IV 20'07	M2/ left	5.6	6.5	*Iriripithecus alekileki*
NAP XV 11'08	M2/ right	5.7	6.9	*Iriripithecus alekileki*
NAP XV 46'09	M2/ left	6.5	7.5	*Karamojapithecus akisimia*
NAP XV 101'08	M2/ right	6.8	7.8	*Karamojapithecus akisimia*
NAP UMP 62-21	M2/ left	7.1	7.5	*Victoriapithecus macinnesi*
NAP IV UMP 64-02	M3/ left	4.1	5.1	*Micropithecus clarki*
NAP IV UMP 64-02	M3/ right	4.0	5.0	*Micropithecus clarki*
NAP IV 29'09	M3/ left	5.0	6.1	*Limnopithecus legetet*
NAP IV 2'09	M3/ right	5.5	6.6	*Kalepithecus songhorensis*
NAP IV 9'08	M3/ left	6.5	7.6	*Iriripithecus alekileki*

Two new specimens of M1/, both in maxilla fragments, are attributed to *Micropithecus clarki*. NAP IV 221’08 reveals that the enamel is wrinkled when unworn, especially on the lingual aspect of the protocone. The distal fovea has a lightly wrinkled floor. The lingual cingulum is well developed and has a tendency to form a small tubercle in the mesio-lingual corner of the crown, but the buccal cingulum is weak, little more than a fold in the enamel. The hypocone is more lingually positioned than the protocone and is slightly distal with respect to the metacone. Three new specimens of M2/ are represented in the sample. They are like the M1/ but are slightly larger. No new M3/s of *Micropithecus clarki* have been found.

Three M1/s, and an M3/ are identified as *Limnopithecus legetet*, on account of their similarity to M 14082 (which was originally described as the paratype of *Xenopithecus koruensis* : DM4/ Hopwood, 1933a) and to the fact that they occlude well with the mandible NAP IX BUMP 268 and the holotype mandible of *Limnopithecus legetet* (M 14079, the holotype of the species). These teeth are basically upscaled versions of the teeth in *Micropithecus clarki*, but with a more rectangular outline due to the fact that the hypocone is not distal to the line of the metacone, although it is more lingually positioned than the protocone. The lingual cingulum is large, beaded, the buccal cingulum weaker but sharp edged. Crests are high and sharp, the mesial fovea is cramped and the distal one large. The distal half of the M3/ is reduced, with small, low metacone and hypocone.

Two new upper molars are identified as *Lomorupithecus evansi*. One of them is an incompletely formed germ, but the other, NAP I 2'10, is an unworn right M1/. Since the M1/s in the Napak IX snout are deeply worn, the latter tooth is important. It has tall conical cusps, weak crests which meet low down so that the cusps are almost isolated from each other. The lingual cingulum is relatively weak, the mesial fovea cramped, the distal one large, almost as big as the trigon basin. The buccal cingulum is weak. The hypocone is slightly more lingually positioned than the protocone, and very slightly more distally located than the metacone. The enamel is smooth.

There are two upper molars attributed to *Dendropithecus ugandensis* which differ from other molars from Napak by the presence of low rounded cusps, rounded lingual cingula and smooth enamel. One of the specimens has a prominent buccal cingulum, the other does not. Both specimens are broader than long.

Four upper molars are identified as *Iriripithecus*, two of them in the holotype maxilla (accompanied by the incompletely formed tips of the protocone and paracone of the M3/). The cusps are extremely simple, with low crests which meet low down, thereby making the cusps isolated from each other. Enamel is smooth, or very lightly wrinkled. The lingual and buccal cingula are strong. The mesial fovea is tiny, the distal one large.

Four upper molars are identified as *Karamojapithecus*. The teeth are constructed on similar lines to those of *Iriripithecus*, but the crests are stronger, and the enamel is more heavily wrinkled, to the extent of making the floors of the trigon basin and distal fovea coarsely rugose. The lingual cingulum is strong and has a tendency to form a small tubercle at the mesio-lingual corner of the crown and even at the mesial base of the hypocone. The buccal cingulum is present but weak. The hypocone is more distally positioned than the metacone, and more lingually positioned than the protocone, to such an extent that the occlusal outline is trapezoidal.

Because it is heavily worn, an M3/ (NAP IV 2'09) is provisionally attributed to *Kalepithecus* on the basis of its dimensions. The distal part of the crown is reduced, the hypocone and metacone small. Finally, a single upper molar from Napak is attributed to *Turkanapithecus* on the basis of its tall crown, with small cusps on the occlusal surface.

Napak small ape lower incisors

Only six lower incisors of small apes have been found at Napak (Table 10), and there are three mandibular symphyses two of which contain incisor roots. Incisors have been attributed to taxa mainly on the basis of their dimensions, although an i/2 is identified as *Kalepithecus* on account of its similarity to its counterpart in KNM RU 900.

Table 10. Lower incisors of small apes from Napak (bold represents specimens associated with other teeth in mandibles). Measurements are in mm.

Catalogue N°	Tooth	MD length	LL breadth	Species
NAP V UMP 62-22	i/1 left root	1.8	3.2	*Limnopithecus legetet*
NAP IV 16'07	i/1 right	3.0	3.7	*Micropithecus clarki*
NAP IV UMP 66-28b	i/1 right	2.7	3.5	*Micropithecus clarki*
NAP IV 8'08	i/2 left	3.3	5.0	*Iriripithecus alekileki*
NAP V UMP 66-34	i/2 left	2.7	4.0	*Micropithecus clarki*
NAP V UMP 62-22	i/2 left root	1.8	3.6	*Limnopithecus legetet*
NAP IV 33'08	i/2 right	2.9	4.0	*Kalepithecus songhorensis*
NAP IV 81'08	i/2 right	3.0	4.2	*Micropithecus clarki*
NAP I 1'01	i/2 right root	2.0	4.0	*Dendropithecus ugandensis*

Napak small ape lower canines

There are 17 lower canines (including canine roots lacking the crowns) from Napak comprising six morphotypes (Table 11).

Table 11. Lower canines of small apes from Napak, Uganda (specimens in bold are associated with other teeth in mandibles). Measurements are in mm.

Catalogue N°	Tooth	MD length	BL breadth	Root height	Crown height	Species
NAP IV 6'85	c/1 left	5.2	3.5	11.3	7.2	*Micropithecus clarki*
NAP IV UMP 62-18	c/1 left	5.1	3.7		7.5	*Micropithecus clarki*
NAP V 117'09	c/1 left alveolus	4.7	3.0	9.0		*Micropithecus clarki*
NAP I 6'10	c/1 right	5.8	3.8			*Micropithecus clarki*
NAP IV 15'07	c/1 right	5.2	3.3			*Micropithecus clarki*
NAP IV UMP 66-32	c/1 right	5.4	3.4	12.0	6.4	*Micropithecus clarki*
NAP V UMP 62-22	c/1 left	5.6	3.4			*Limnopithecus legetet*
NAP IV UMP 66-07	c/1 right	5.1	3.6			*Limnopithecus legetet*
NAP I UMP 62-17	c/1 right root	5.9	4.6			*Limnopithecus legetet*
NAP IV 1'05	c/1 left	6.3	4.3	10.5	8.5	*Dendropithecus ugandensis*
NAP V UMP 62-20	c/1 left	6.1	4.7	12.0	10.5	*Dendropithecus ugandensis*
NAP I 1'01	c/1 right root	6,4	4,7			*Dendropithecus ugandensis*
NAP XV 385'08	c/1 right	7.3	5.0	15.5	10.5	*Iriripithecus alekileki*
NAP V 6'09	c/1 right	6.3	4.2		11.4	*Kalepithecus songhorensis*
NAP V 7'09	c/1 right alveolus	6.0	3.8			*Kalepithecus songhorensis*
NAP XV 173'08	c/1 left	7.5	5.2			*Karamojapithecus akisimia*
NAP XV 63'09	c/1 left root	6.0	4.1	11.5		*Karamojapithecus akisimia*

Lower canines attributed to *Micropithecus clarki* are small with a high mesial shoulder (junction between the lingual cingulum and the mesial crest) and a low distal tubercle where the lingual cingulum and distal crest meet. Wear is dominantly down the distal crest and can cut a sharp, angular notch into the crown near the distal tubercle.

The three lower canines of *Limnopithecus legetet* from Napak are poorly preserved, lacking their crown apices, but all are associated with other teeth in mandible fragments, which is the basis for their identification.

Lower canines from Napak assigned to *Dendropithecus ugandensis* have a low mesial shoulder and a weak distal tubercle. They are relatively low crowned, robust teeth with stout roots. The lower canine attributed to *Iriripithecus* lacks its crown and root apices, but enough is preserved to show that the mesial shoulder is high, the lingual cingulum sharp and the distal tubercle modest.

One lower canine is attributed to *Kalepithecus songhorensis*, and there is a mandibular symphysis which preserves a partial canine alveolus. The mesial shoulder is high, the crown is tall, the distal tubercle low down and small. This tooth is close to that in KNM RU 900.

Two specimens are identified as *Karamojapithecus*, one of which is represented only by a root in a mandibular symphysis. The mesial shoulder is low, the distal tubercle weak, represented by a low rise in the lingual cingulum. The crown is not very tall, the root long and robust.

Napak small ape p/3s

The Napak deposits have yielded seven lower third premolars of small apes (Table 12). In the sample there are four morphotypes. Two premolars are associated with canines in mandibles, and one is in a mandible associated with a p/4 and a canine alveolus, providing a degree of control on dental associations. There are also four mandible fragments with the roots of p/3.

Table 12. Lower third premolars of small apes from Napak, Uganda (specimens in bold are associated with other teeth in mandibles). Measurements are in mm.

Catalogue N°	Tooth	MD length	BL breadth	Species
NAP V 117'09	p/3 left	4.8	2.8	*Micropithecus clarki*
NAP V UMP 66-17	p/3 left	5.0	3.0	*Micropithecus clarki*
NAP V UMP 62-22	p/3 left	5.6	3.6	*Limnopithecus legetet*
NAP IV UMP 66-07	p/3 right	5.1	3.6	*Limnopithecus legetet*
NAP IV UMP 66-12	p/3 right	5.7	3.4	*Limnopithecus legetet*
NAP IV UMP 66-05	p/3 right	5.9	3.8	*Dendropithecus ugandensis*
NAP IV UMP 66-06	p/3 right	6.0	4.1	*Kalepithecus songhorensis*

The two smallest specimens are attributed to *Micropithecus clarki* on the basis of occlusion tests against the holotype snout (NAP IV UMP 62-04). Three specimens, one of which is in a mandible associated with a canine, are attributed to *Limnopithecus legetet*. One specimen is identified as *Dendropithecus ugandensis* sp. nov. and one as *Kalepithecus songhorensis*. A specimen (M 36371) listed as a p/3 of *Dendropithecus macinnesi* by Harrison (1982) is the buccal half of an upper P3/ similar in morphology to those of *Ugandapithecus major*, but evidently of a smaller species, probably *Ugandapithecus meswae*.

The p/3s of *Micropithecus clarki* are strongly compressed and have a prominent but narrow lingual crest emanating from the main cusp and terminating in the distal basin but not touching the lingual cingulum. Buccally, there is no sign of a cingulum, and there is no depression buccal to the postcristid of the main cusp. NAP V UMP 66-17, a left p/3 is probably from a male individual on the basis of the strong honing facet and the relatively great extension of the enamel down the buccal root. NAP V 117'09, in contrast has a less well developed honing facet, and the enamel extension down the buccal root is less than in NAP V UMP 66-17, suggesting that it represents a female individual.

The lower third premolars attributed to *Limnopithecus legetet* are mesio-distally longer, relative to their breath, than in *Micropithecus*, and the lingual cristid descending from the buccal main cusp, joins the mesial cingulum about a third to a half of the distance from the lingual side of the tooth. As a consequence the distal basin is bucco-lingually small. The buccal surface of the tooth shows no sign of a cingulum, and in NAP IV UMP 66-12 and NAP IV UMP 66-07, there is only a very slight depression buccal to the postcristid descending from the apex of the main cusp. In NAP V UMP 66-22, in contrast there is no sign of a homologous depression. NAP IV UMP 66-12 possesses a strong honing facet, whereas NAP V UMP 66-22 and NAP IV UMP 66-07 do not, and this is possibly an expression of sexual dimorphism with the latter two specimens probably representing female individuals.

The two lower third premolars attributed to *Kalepithecus songhorensis* and *Dendropithecus ugandensis* sp. nov., differ from those of *Micropithecus* and *Limnopithecus* by having a bulky lingual cristid descending towards the angle between the lingual and distal edges of the tooth, but not joining the cingulum which extends along the lingual and distal margins of the tooth. This leaves the distal basin quite broad bucco-lingually. Furthermore, there is a distinct depression on the buccal surface of the tooth close to the postcristid of the main cusp, forming a triangular space bordered basally by a low cingular crest which fades out mesially. This morphology recalls that of the holotype of *Kogolepithecus morotoensis*. There is also a low depression on the buccal surface where the honing facet forms, so that in early wear stages, the honing facet has a low depression in its centre. NAP IV UMP 66-06 has a taller main cusp, a greater rootward extension of enamel on the buccal root, and a more prominent honing facet than the other tooth, NAP IV UMP 66-05. NAP IV UMP 66-05 resembles the p/3 of *Dendropithecus macinnesi* but is smaller, whereas NAP IV UMP 66-06 is close to that of *Kalepithecus songhorensis*.

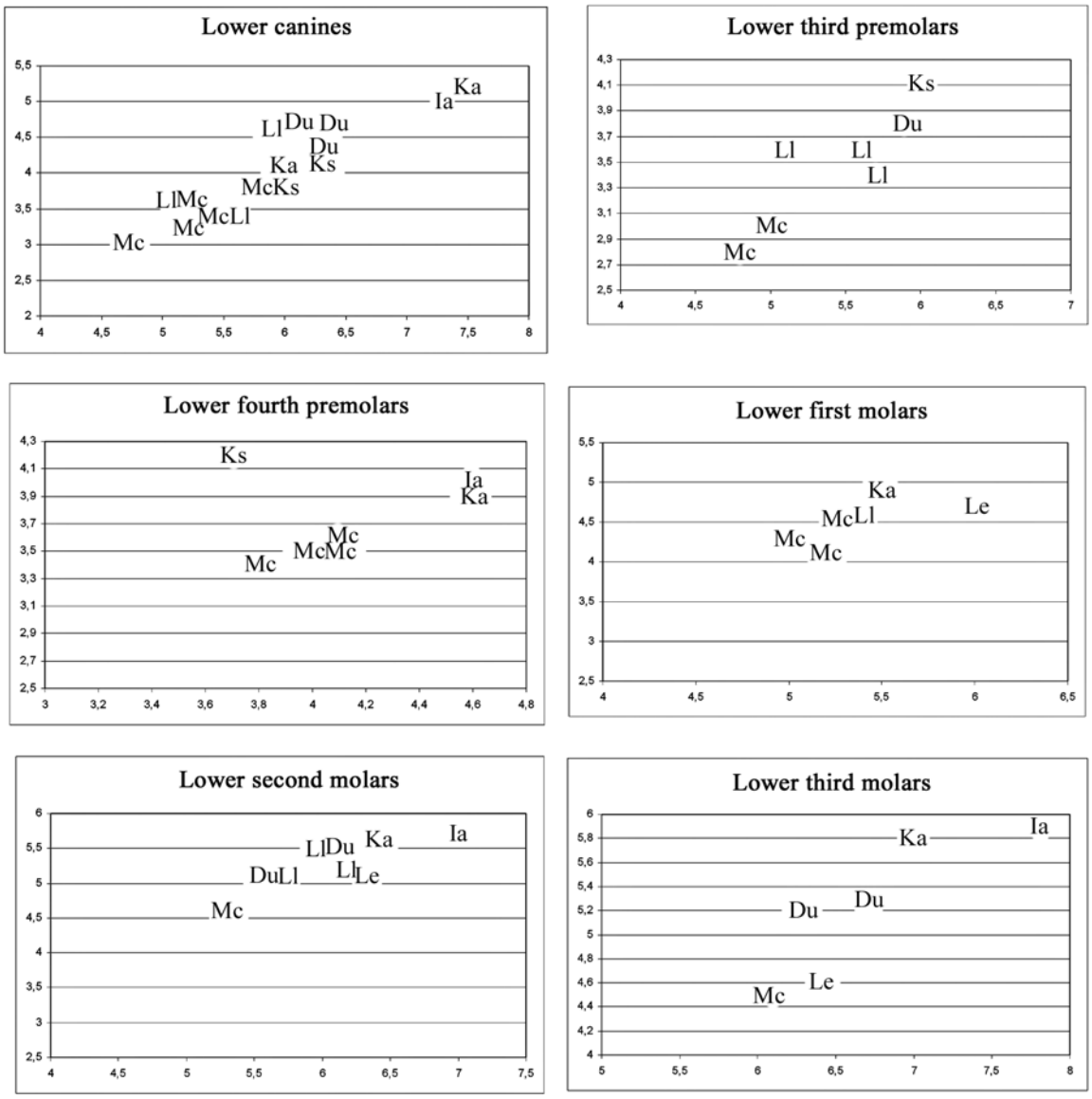

Figure 133. Bivariate plots of small ape lower teeth from Napak, Uganda. (Abbreviations as in figure 132, length – horizontal axis, breadth – vertical axis).

Napak small ape p/4s

There are eight lower p/4s of small apes from Napak which comprise five morphotypes (Table 13).

Table 13. Lower fourth premolars of small apes from Napak (bold represents specimens associated with other teeth in mandibles). Measurements are in mm.

Catalogue	Tooth	MD length	BL breadth	Species
NAP IV UMP 66-30a	p/4 left	4.1	3.6	*Micropithecus clarki*
NAP V 117'09	p/4 left	4.0	3.5	*Micropithecus clarki*
NAP IV 229'09	p/4 right	4.1	3.5	*Micropithecus clarki*
NAP XXI 15'10	p/4 right	3.8	3.4	*Micropithecus clarki*
NAP I UMP 62-17	p/4 right	4.6	4.0	*Limnopithecus legetet*
NAP IV 12'08	p/4 right	3.7	4.2	*Kalepithecus songhorensis*
NAP XV 185'08	p/4 right	4.6	4.0	*Iriripithecus alekileki*
NAP IV 27'99	p/4 right	4.6	3.9	*Karamojapithecus akisimia*

Four p/4s are attributed to *Micropithecus clarki*. The teeth are small, with the postprotoconid cristid positioned far from the buccal side of the tooth , which makes the buccal side concave behind the main cusp. Two specimens have no buccal cingulum, one has an incomplete one, and one sports a continuous buccal cingulum, but in other respects the fossils are similar to each other.

One extremely worn specimen in a mandible NAP I UMP 62-17, is attributed to *Limnopithecus legetet* but little can be said about its morphology. The species determination is based on the occlusal outline and dimensions of the associated molars. There is an unerupted p/4 in the juvenile mandible NAP IX BUMP 268.

One specimen, NAP IV 12'08, is so close in morphology and dimensions to the holotype of *Kalepithecus songhorensis* that we have little hesitation in attributing it to this species. It is broader than long with the two cusps almost the same height, the lingual one only slightly lower than the buccal one, but quite a bit smaller than it.

There are two slightly larger p/4s. NAP XV 185'08, identified as *Iriripithecus alekileki*, has no buccal cingulum, and the lingual cusp is more distally positioned than the buccal cusp and is somewhat lower than it. NAP IV 27'99, attributed to *Karamojapithecus akisimia*, has a buccal cingulum, the lingual cusp is only slightly behind the level of the main cusp, and the apices of the cusps are further apart than they are in NAP XV 185'08.

Napak small ape lower deciduous molars

Only two deciduous lower molars of small apes have been found at Napak (Table 14). One the basis of their dimensions and crown morphology they are attributed to *Iriripithecus* and *Karamojapithecus*.

Table 14. Lower deciduous molars of small apes from Napak. Measurements are in mm.

Catalogue N°	Tooth	MD Length	BL breadth	Species
NAP XV 120'09	dm/4 left	6.4	4.8	*Iriripithecus alekileki*
NAP IV 3'09	dm/4 left	6.1	4.7	*Karamojapithecus akisimia*

Napak small ape lower molars

There are seven lower m/1s, ten m/2s and five m/3s of small hominoids from Napak (Table 15). We recognise six morphotypes (Fig. 133).

Lower molars of *Micropithecus clarki* have weak, discontinuous buccal cingula with small to tiny buccal ledges between the protoconid and hypoconid, and the hypoconid and hypoconulid. The mesial fovea is small, and transversely to only slightly obliquely oriented. The talonid basin is large and capacious, and the distal fovea extremely small. The apex of the metaconid is incipiently to lightly bifid, but even slight wear removes the evidence of this. The enamel is smooth.

The lower molars of *Limnopithecus legetet* are narrower mesially than distally, and there is a tendency for the enamel in the floor of the talonid basin to be rugose, often to the extent of forming low cusps or tubercles at the base of the entoconid. The buccal cingulids (forming ledges) are quite marked despite the fact that the buccal cingulum is discontinuous. The buccal cusps are much more voluminous than the lingual ones. The mesial fovea is quite large and obliquely oriented, due to the more distal position of the metaconid with respect to the protoconid. The distal fovea is small.

The lower molars attributed to *Lomorupithecus evansi* are long and narrow, with well developed buccal cingulum which is interrupted at the base of the hypoconid, and forms large shelves between the protoconid and hypoconid, and a smaller one between the hypoconid and hypoconulid. The lingual cusps are bucco-lingually compressed, and the divides between the mesial fovea, the talonid basin and distal fovea are low and weak. The mesial fovea is oblique, and the hypoconulid is large. The apex of the metaconid is incipiently bifid, but wear soon eradicates evidence of this, leaving a shallow groove or indent to show its presence.

The lower molars assigned to *Karamojapithecus* have a well developed buccal cingulum, and buccal shelves. The mesial fovea is small, the distal fovea is a bit larger and the talonid basin large but its capacity is reduced by the internal positioning of the buccal cusps. The divides between the mesial fovea, the talonid basin and the distal fovea are quite high. The hypoconulid is tall, sub-equal in stature to the hypoconid and entoconid.

Table 15. Lower molars of small apes from Napak (bold represents specimens associated with other teeth in mandibles). Measurements are in mm.

Catalogue N°	Tooth	MD length	BL breadth	Species
NAP V 89'09	m/1 right	5.3	4.5	*Micropithecus clarki*
NAP IV UMP 66-08	m/1 left	5.2	4.1	*Micropithecus clarki*
NAP IV 175'09	m/1 left	5.0	4.3	*Micropithecus clarki*
NAP I UMP 62-17	m/1 right	5.4	4.6	*Limnopithecus legetet*
NAP IX BUMP 268	m/1 left	5.4	4.6	*Limnopithecus legetet*
NAP IV UMP 66-16	m/1 right	6.0	4.7	*Lomorupithecus evansi*
NAP V 30'06	m/1 left	5.5	4.9	*Karamojapithecus akisimia*
NAP IV 225'09	m/2 right	5.3	4.6	*Micropithecus clarki*
NAP IX BUMP 268	m/2 left	6.2	5.2	*Limnopithecus legetet*
NAP I UMP 62-17	m/2 right	6.0	5.5	*Limnopithecus legetet*
NAP IV 82'08	m/2 right	5.7	5.1	*Limnopithecus legetet*
NAP IV 13'08	m/2 right	6.3	5.1	*Lomorupithecus evansi*
NAP XV 177'08	m/2 right	6.4	5.6	*Karamojapithecus akisimia*
NAP I 1'00	m/2 right	6.1	5.5	*Dendropithecus ugandensis*
NAP IX UMP 66-23	m/2 right	5.6	5.1	*Dendropithecus ugandensis*
NAP XV 183'08	m/2 left	7.0	5.7	*Iriripithecus alekileki*
NAP IV UMP 62-19	m/2 left	7.8	5.9	*Iriripithecus alekileki*
NAP IV UMP 66-13	m/3 right	6.1	4.5	*Micropithecus clarki*
NAP IV 13'08	m/3 right	6.4	4.6	*Lomorupithecus evansi*
NAP I 1'00	m/3 right	6.7	5.3	*Dendropithecus ugandensis*
NAP IX UMP 66-23	m/3 right	6.3	5.2	*Dendropithecus ugandensis*
NAP XV 91'09	m/3 left	7.0	5.8	*Karamojapithecus akisimia*

The lower molars of *Dendropithecus ugandensis* have a well formed buccal cingulum and the buccal cusps are internally positioned. The crests separating the mesial fovea, talonid basin and distal fovea are low, allowing almost free communication between them. The hypoconulid is reduced in stature and the lingual cusps are low and bucco-lingually compressed. The third lower molar narrows distally.

Lower molars of *Iriripithecus* are peculiar, with tall conical cusps in which the cristids are reduced in size, leaving the main cusps isolated from each other even near their bases. The buccal cingulum is weak as are the buccal shelves. The enamel is smooth, even in unworn teeth. The mesial fovea is quite large, the talonid basin vast, due to the very buccal implantation of the buccal cusps, and the distal fovea is large, even when there is an accessory cusplet at the base of the hypoconulid.

DENTAL ADAPTATIONS AND NICHE PARTITIONING AMONG EARLY MIOCENE SMALL APES OF AFRICA

The small apes from the Early Miocene of East Africa can be sorted into several groups on the basis of dental morphology. On the basis of the available fossils we consider that the taxa cluster into the following trophic groups. The fact that these groups correspond to divergent dentitions, suggests a high degree of niche partitioning, with different groups consuming a variety of resources; leaves, soft fruit, harder fruit, and even possibly nuts for those taxa with tall molar crowns and low occlusal cusps.

Group 1.
Iriripithecus
Kogolepithecus

Lomorupithecus
Share low molar crowns with tall, almost isolated molar cusps, large hypocones detached from the protocone, large lingual cingula, smooth enamel. These taxa would likely have been mixed feeders, including leaves and soft fruit in their diets.

Group 2.
Micropithecus
Limnopithecus
Simiolus
Karamojapithecus
Share lingual cingula on the upper premolars, wrinkled enamel in the floors of the occlusal basins and foveae of the molars, thicker enamel than group 1. These taxa were probably soft fruit specialists.

Group 3.
Dendropithecus
Kalepithecus
Share upper canines with two mesial grooves and a buccal slit. Molars tend to have transverse occlusal crests. These taxa may have included a lot of leaves in their diet, but probably also fruit.

Group 4.
Xenopithecus
Mabokopithecus
Nyanzapithecus
Turkanapithecus
Share tall molar crowns with small cusps occlusally, tendency to develop accessory cusplets or tubercles in the mesio-lingual corner of the upper molars. These taxa were probably consuming harder fruit, and possibly even nuts.

Group 5.
Rangwapithecus
Cheek tooth enamel in *Rangwapithecus* is highly wrinkled. This genus was probably a mixed folivore/frugivore.

The presence of at least 14 genera of small apes in the Early Miocene of East Africa which can be sorted into five groups suggests a long period of prior evolution and occupation of a large range of niches. Add to this the presence of cercopithecid teeth and post-cranial bones at Napak (Senut, 1988) (and other cercopithecid genera at other sites in Kenya), and it is clear that small catarrhines were extremely diverse in tropical Africa during the period 20 Ma to 14 Ma. Small ape diversity diminished gradually in Africa through the Middle and Late Miocene. Cercopithecid diversity remained relatively low until the latest Miocene, by which time small hominoids had all but disappeared from Africa. The high diversity of small apes in the Early Miocene of Africa is mirrored by the high diversity of pliopithecids in the Middle Miocene and basal Late Miocene of Europe, and by that of extant hylobatids in south-east Asia.

PHYLOGENETIC RELATIONSHIPS AND CLASSIFICATION OF NAPAK SMALL APES

The relatively poor fossil record of small apes in general, poses enormous difficulties for phylogeny reconstruction. Many analyses have been done and a somewhat bewildering quantity of phylogenetic hypotheses has been proposed in the literature, out of which has developed an unwieldy nomenclature of all ranks higher than the genus. Almost no consensus has emerged during the past 30-40 years, not even about family level systematics (Table 16). Harrison (2010) for example, classified the East African Early and Middle Miocene apes into three Superfamilies (Dendropithecoidea, Proconsuloidea, Hominoidea) leaving several genera as *incertae sedis*, whereas Begun (2007) arranged the genera in markedly different groups, and at highly divergent ranks compared with those of Harrison (2010).

Table 16. Comparison of two recently published classifications of Miocene to Extant non-cercopithecoid Catarrhines (extracted from Harrison (2010) and Begun (2007)).

Harrison, 2010	**Begun, 2007**
Dendropithecoidea	Hominidea (Magnafamily, new rank)
Dendropithecus	Proconsuloidae (sic)
Micropithecus	*Proconsul*
Simiolus	cf. *Proconsul*
Proconsuloidea	*Samburupithecus*
Proconsul	*Micropithecus*
Afropithecus	Hominoidea
Heliopithecus	Hylobatidae
Nacholapithecus	*Hylobates*
Equatorius	Hominidae
Nyanzapithecus	*Pierolapithecus*
Mabokopithecus	*Dryopithecus*
Rangwapithecus	*Ouranopithecus*
Turkanapithecus	*Graecopithecus*
Xenopithecus	*Sivapithecus*
Otavipithecus	*Lufengpithecus*
Incertae sedis	*Khoratpithecus*
Limnopithecus	*Ankarapithecus*
Lomorupithecus	*Gigantopithecus*
Kalepithecus	*Sahelanthropus*
Kamoyapithecus	*Orrorin*
Kogolepithecus	*Homo*
Hominoidea	*Ardipithecus*
Kenyapithecus	*Praeanthropus*
Pongo	*Australopithecus*
Gorilla	*Paraustralopithecus*
Pan	*Paranthropus*
Australopithecus	*Pongo*
Homo	*Pan*
Ardipithecus	*Gorilla*
Orrorin	Crown hominoids of uncertain status
Sahelanthropus	*Kenyapithecus*
Samburupithecus	*Oreopithecus*
Chororapithecus,	Family *incertae sedis*
Nakalipithecus	*Afropithecus*
	Morotopithecus
	Heliopithecus
	Griphopithecus
	Equatorius
	Nacholapithecus
	Otavipithecus
	Superfamily *incertae sedis*
	Rangwapithecus
	Nyanzapithecus
	Mabokopithecus
	Turkanapithecus
	Magnafamily *incertae sedis*
	Kamoyapithecus
	Dendropithecus
	Simiolus
	Limnopithecus
	Kalepithecus

The position of *Limnopithecus* needs to be changed, as its classification in both schema is based on material that differs from the holotype, which is closer to *Micropithecus* than to anything else. The

new material of *Micropithecus* from Napak distances it from *Dendropithecus* (upper canines without double mesial groove, lack of buccal slit).

Kalepithecus is likely to be close to *Dendropithecus*, on account of its upper canine morphology (double mesial groove, buccal slit present).

We consider that the taxa with tall molar crowns, upon which are posed low cusps (*Turkanapithecus*, *Xenopithecus*, *Nyanzapithecus*) are highly divergent from *Proconsul*, and do not sit comfortably in the superfamily Proconsuloidea.

It is possible, on the basis of molar morphology, that *Lomorupithecus*, *Iriripithecus* and *Karamojapithecus* form a natural group.

We feel that, with the presently available small ape samples from Africa, it is difficult to make a convincing case in support of the classifications proposed by Harrison (2010) and Begun (2007). The species and genera are well enough represented to reveal the presence of a high diversity of forms which, at the species level, can be distinguished from each other on a reasonable basis, yet most taxa are too poorly known for inferring relationships at levels higher than the genus, a finding which naturally precludes the proposal of reliable phylogenies. Nevertheless, we propose a phylogeny (Fig. 134) which agrees in several details with that proposed by Harrison (2010).

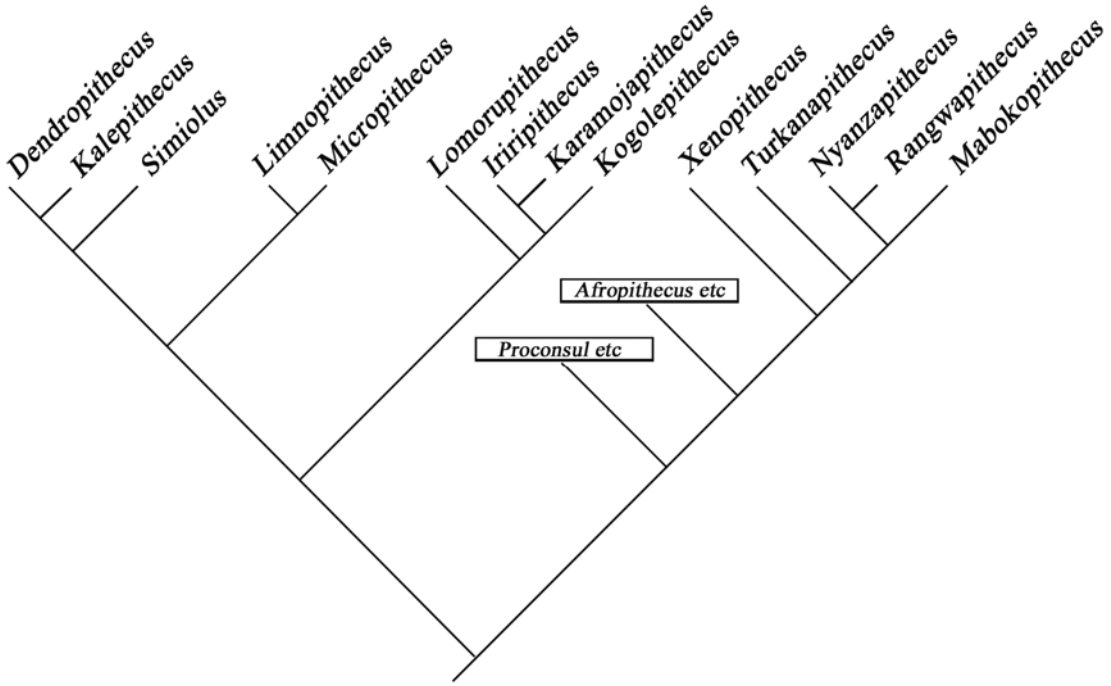

Figure 134. Hypothesis of relationships between genera of Early and Middle Miocene apes of East Africa.

CONCLUSIONS

Interpretation of the Napak small ape fossils was carried out by comparing them to type specimens of other small apes from Kenya and Uganda, and with material subsequently attributed to the various species. It became clear during the study that, all comparisons and interpretations of *Limnopithecus legetet* published since 1952, were based on KNM KO 8 and various fossils from Songhor, which differ radically in molar morphology from the holotype of the species (M 14079). A major revision of this genus and species needs to be carried out, using the holotype as the reference, rather than KNM KO 8.

The teeth in the paratype mandible of *Lomorupithecus harrisoni*, NAP IX BUMP 268, are close in morphology and dimensions to their counterparts in the holotype of *Limnopithecus legetet*. The holotype of *Lomorupithecus harrisoni*, NAP IX BUMP 266, is similar in cranio-dental features to *Limnopithecus evansi*, which we here transfer to the genus *Lomorupithecus* as the combination *Lomorupithecus evansi*, the species being highly divergent from the type species of *Limnopithecus*.

A new species of *Dendropithecus* (*D. ugandensis*) is created. It is comparable to the type species, *D. macinnesi*, but is substantially smaller.

Micropithecus clarki is the most common fossil ape at Napak. New fossils include dental associations that were previously not available. The canines of this taxon are described on the basis of specimens associated with cheek teeth and the lower premolars are described in detail for the first time. The relationship of this genus to *Limnopithecus* requires further study as it shows several similarities to it; *Micropithecus* could be a junior synonym of *Limnopithecus*, but for the time being we retain the two genera, pending a more comprehensive fossil record of *Limnopithecus*, in particular its upper teeth and facial structure, and a better representation of the mandibles of *Micropithecus*.

Several specimens from Napak are attributed to *Kalepithecus songhorensis*, but it is poorly represented at the various sites.

Two new genera of small apes, *Iriripithecus* and *Karamojapithecus*, are created on the basis of fossils from Napak. The taxa *Iriripithecus alekileki* and *Karamojapithecus akisimia* do not seem to occur in the Kenyan Early Miocene deposits, although a revision of the available material might reveal the presence of one or other, or perhaps both taxa there.

Some hitherto problematic fossils from Rusinga, Mfwangano, and Songhor (all in Western Kenya) are identified as a new species of *Turkanapithecus*, *T. rusingensis*, which is smaller than the type species *T. kalakolensis*. *Turkanapithecus rusingensis* also occurs at Napak (Uganda) and Kipsaraman (Kenya). It is a widespread but rare element of the early and basal Middle Miocene faunas of East Africa. In sum, therefore, the Early Miocene volcano-sedimentary deposits at Napak, Karamoja District, Uganda, have yielded a high diversity of small apes, attributed to eight species in eight genera (Table 17). One species (*Turkanapithecus rusingensis*) is represented at Napak by a single upper molar. The other taxa are more common, the richest sample being that of *Micropithecus clarki*. Recall that the same deposits have also yielded two species of *Ugandapithecus* (Pickford *et al*., 2009; Senut *et al*., 2000) and a species of cercopithecoid, *Victoriapithecus macinnesi* (Miller *et al*., 2009; Senut, 1988).

Table 17. Summary distribution of small apes at Napak, Karamoja District, Uganda.

Taxon	NAP I	NAP IV	NAP V	NAP IX	NAP XV	NAP XXI
Dendropithecus ugandensis	X	X	X	X	X	
Micropithecus clarki	X	X	X		X	X
Turkanapithecus rusingensis			X			
Limnopithecus legetet	X	X	X	X		
Lomorupithecus evansi	X	X	X	X		
Kalepithecus songhorensis	X	X	X		X	
Iriripithecus alekileki		X	X		X	
Karamojapithecus akisimia		X	X		X	

Because the Napak deposits span an appreciable time period (ca 1 million years) the faunas from the various levels show signs of evolution. The tragulids, for example, are represented by *Dorcatherium songhorensis* in the earlier deposits, and by *Dorcatherium parvum*, *D. piggoti* and *D. iririensis* at the higher levels. To some extent this explains why the Napak ape fauna is so diverse (9 genera) compared with prolific sites such as Songhor (6 genera) and Legetet and Chamtwara (5 genera each), but this does not account for all the diversity, because one site at Napak (NAP V) has yielded specimens of all nine apes, and another (NAP IV) has yielded eight of them.

Two new genera, *Iriripithecus* and *Karamojapithecus* and the four new species, *Dendropithecus ugandensis*, *Iriripithecus alekileki*, *Karamojapithecus akisimia*, and *Turkanapithecus rusingensis* indicate a relatively high degree of endemicity in the small ape fauna from this site. The first three new species appear to be confined to Napak. Another taxon confined to Napak is *Micropithecus clarki*, although a sister taxon (*Micropithecus leakeyorum*) is reported from the younger site of Maboko, Kenya (Harrison, 1988). *Turkanapithecus rusingensis*, in contrast, appears to be a widespread, but rare element of ape faunas at Napak, Rusinga, Mfwangano and Songhor, but the genus was hitherto only recorded from its type locality, Kalodirr, Kenya (Leakey & Leakey, 1986) (Fig. 135).

Genus \ Locality	Lothidok	Meswa	Napak	Songhor	Mteitei	Koru	Chamtwara	Legetet	Mfwanganu	Karungu	Rusinga	Moroto	Bukwa	Kalodirr	Maboko	Nachola	Kipsaraman	Fort Ternan	Ngorora	Otavi
Afropithecus												x	x	x						
Dendropithecus			x	x			x		x	x	x									
Equatorius															x		x			
Iriripithecus			x																	
Kalepithecus			x	x	x		x	x												
Kamoyapithecus	x																			
Karamojapithecus			x																	
Kenyapithecus																		x	x	
Kogolepithecus												x								
Limnopithecus			x			x	x	x			x						x			
Lomorupithecus			x	x	x															
Mabokopithecus															x					
Micropithecus			x												x					
Nacholapithecus																x				
Nyanzapithecus											x				x	x				
Otavipithecus																				x
Proconsul						x	x	x	x		x									
Rangwapithecus				x																
Simiolus												x	x	x			x	x		
Turkanapithecus			x	x					x		x			x			x			
Ugandapithecus		x	x	x		x	x	x				x					x			
Xenopithecus								x												
Indeterminate									x				x					x	x	

Figure 135. Distribution of Early and Middle Miocene hominoids in Africa. A few minor localities, such as William's Flat and Moruorot, have been omitted.

We provide a hypothesis of phylogeny of the East African small apes (Fig. 134), but note that phylogenetic analyses of the material published over the past 30 years have produced almost no signs of consensus among the researchers. Our hypothesis is closest in overall terms to one published by Harrison (2010), although there are some differences.

Finally, because the Napak small hominoids are so diverse, they reveal a high degree of dietary niche partitioning, some specialising in fruits, others more on leaves, some possibly on hard foods such as nuts, and yet others being mixed feeders. This in turn suggests that the Napak palaeoenvironment was variable, probably a mosaic of woodland and dry forest on the slopes of a large volcano. This interpretation is supported by the fossil land snails which indicate the presence of forest, woodland and grassland.

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