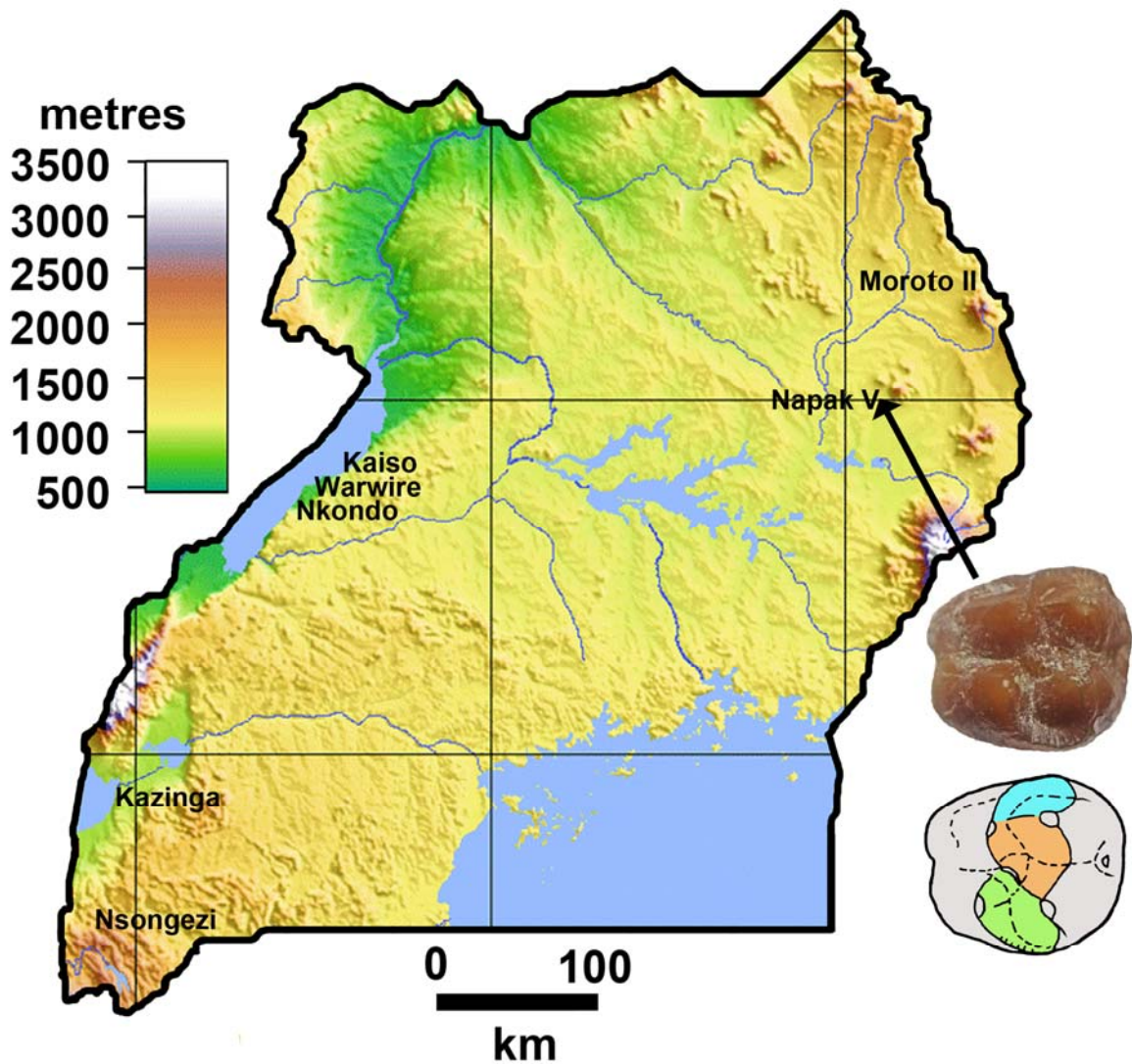


# GEO-PAL UGANDA



Uganda Museum, Kampala

# Geo-Pal Uganda

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# Early Miocene Victoriapithecoid Monkey from Napak, Uganda

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## ABSTRACT

The discovery in 2015 of a victoriapithecoid upper molar at Napak V, Uganda, is important because it confirms the presence of the superfamily Cercopithecoidea at the site. Doubts have been expressed about the identification of previously described cercopithecooid material from the deposits but we here confirm that the upper molar described in 1968 does indeed belong to this group of primates. The frontal bone, in contrast, is more likely to represent a small-bodied ape. The preservation of the new fossil tooth is excellent, and its unworn condition permits detailed observation of crests, grooves and other occlusal features, which indicate that its affinities lie with the family Victoriapithecidae rather than with Colobinae or Cercopithecinae, and that it is more likely to belong to the genus *Victoriapithecus* than to *Noropithecus*. Some of the morphological features indicate affinities, albeit quite remote, with some early Oligocene primates from Northern Africa, such as *Apidium*, and with the Oreopithecidae. Its relationships to other late Oligocene and early Miocene Old World Monkey genera such as *Nsungwepithecus*, *Alophia*, *Prohylobates* and *Zaltanpithecus* cannot be assessed because upper teeth of these genera are unknown.

**Key words:** Cercopithecoidea, Victoriapithecidae, East Africa, Early Miocene, Upper molar, Occlusal morphology

## INTRODUCTION

Monkey fossils of pre-Miocene and early Miocene age are exceedingly rare (Pilbeam & Walker, 1968; Stevens *et al.* 2013; Rasmussen *et al.* 2019). The first record of the presence of monkeys at Napak, Uganda, was by Pilbeam & Walker (1968) at the time of its description being the oldest known cercopithecooid in the fossil record, significantly older than the next oldest specimens, *Victoriapithecus* from Maboko, Kenya (MacInnes, 1943; Von Koenigswald, 1969).

Cercopithecooids have recently been reported from the late Oligocene of Tanzania (*Nsungwepithecus* Stevens *et al.* 2013) and from the early Miocene of Kenya (*Alophia* Rasmussen *et al.* 2019) but neither of these taxa are represented by upper teeth, a fact that poses problems for interpreting their phylogenetic and systematic positions. The Napak fossils, in contrast comprise upper molars but so far no lower teeth of monkeys have been found at the site.

In contrast, collections of *Victoriapithecus* from Maboko Island, Kenya (Benefit, 1993, 1994; Benefit & McCrossin, 1989, 1991, 1993, 1995, 1997; Blue *et al.* 2003) and of *Noropithecus* from Kipsaraman, Kenya (Pickford & Kunitatsu, 2005) and Buluk, Kenya (Leakey, 1985; Miller *et al.* 2009) include upper and lower teeth, so are more confidently interpreted, although there are differences of opinion about the quantity of species represented at these sites.

We describe the Napak specimens in order to fill out the fossil record of early cercopithecoids, especially that which provides evidence concerning upper molar morphology. One of the Napak specimens is particularly valuable in the sense that it is a fully formed but unworn crown showing the fine details of occlusal morphology, and it thereby reveals several peculiarities which have not been noticed on the moderately worn previously available sample (Pilbeam & Walker, 1968).

Other monkey fossils have been found in Uganda, in middle Miocene deposits at Moroto II (Pickford *et al.* 2003), in late Miocene to Pliocene and Pleistocene strata in the Western Rift (Cooke & Coryndon, 1970; Senut, 1994; Jablonski & Frost, 2010) and in archaeological contexts at Nsongezi (Pearce & Posnansky, 1963). Thus the fossil record of monkeys in Uganda is exceptionally long, but it has significant gaps.

The fossils described herein are relevant to understanding the taxonomic and phylogenetic positions of other early and middle Miocene cercopithecoids from Africa, found at Gebel Zelten, Libya (Delson, 1979), Wadi Moghara, Egypt (Fourtau, 1918; Simons, 1969; Miller *et al.* 2009), Buluk, Kenya (Leakey, 1985), Kipsaraman, Kenya (Pickford & Kunimatsu, 2005), Maboko, Majiwa and Ombo, Kenya (MacInnes, 1943; Von Koenigswald, 1969; Benefit & McCrossin, 2002; Senut, 1986a, 1986b), Nyakach, Kenya (Senut, 1987) and possibly Ongoliba, Democratic Republic of Congo (Hooijer, 1963). Also of interest are the primitive fossil monkeys from Nakwai, Kenya (Rasmussen *et al.* 2019) and the Rukwa Rift, Tanzania (Stevens *et al.* 2013).

As was pointed out when the presence of monkey fossils at Napak was first announced, the specimens are potentially important for throwing light on aspects of the evolutionary history and phylogeny of Old World Monkeys, e.g. for estimating the time that colobines split from the cercopithecines, thought to be prior to 19 Ma by Pilbeam & Walker (1968). Successively however, doubts have been expressed about the appurtenance of the Napak fossils to the superfamily Cercopithecoidea, the frontal bone being transferred to Hominoidea by Radinsky (1974) subsequently referred to a small-bodied ape close to *Limnopithecus* by Fleagle (1975), then to *Micropithecus clarki* by Fleagle & Simons (1978) and then re-attributed to Cercopithecoidea by Rossie & MacLachy (2006) only to be removed again by Harrison (2010). Doubts have been raised about the identification of the Napak upper molar by Grossman *et al.* (2014). If these doubts are valid, then these two fossils cannot be used to infer split times between subfamilies of Cercopithecoidea nor for determining the relationships of Cercopithecoidea to other primates.

At a higher taxonomic level, Benefit & McCrossin (2002) estimated that Cercopithecoidea split from Hominoidea about 25 Ma.

For this reason, it is important to examine carefully the fossils from Napak that have at one time or another been included in Cercopithecoidea and subsequently removed from this superfamily. Were the exclusions valid? One also needs to consider the possibility that Victoriapithecidae may belong to a superfamily distinct from the Cercopithecoidea, but we here accept that it is a 'monkey' in a broad sense of the term, and we accordingly classify it in Cercopithecoidea. The discovery of new material presented herein, supports the occurrence of the superfamily in early Miocene deposits at Napak.

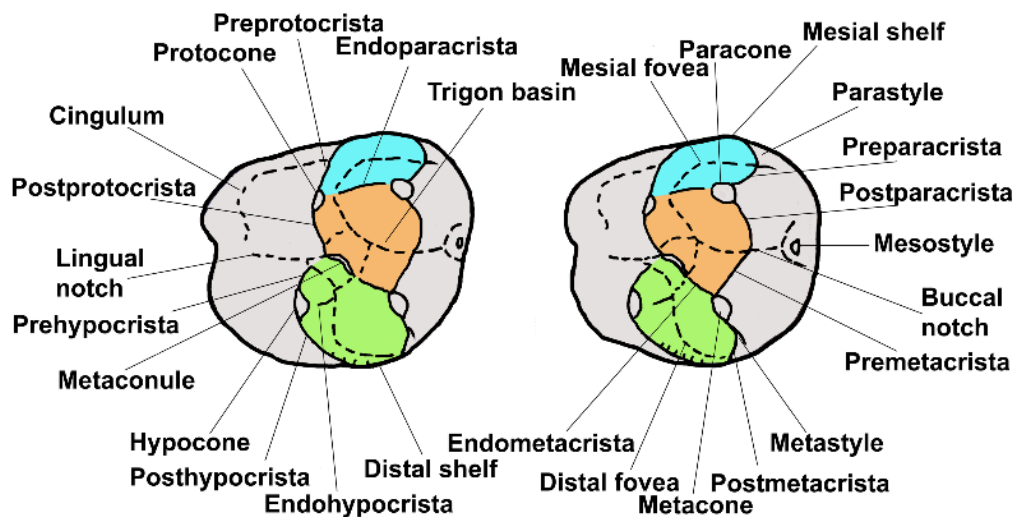
## MATERIALS AND METHODS

The fossil molar described herein is curated at the Palaeontology Section of the Uganda Museum (UM), Kampala and has been compared with fossils housed in the Orrorin Community Organisation (OCO), Kipsaraman, and the National Museum of Kenya (KNM), Nairobi. Measurements were taken with sliding calipers accurate to 0.1 mm (mdl – mesio-distal length, blb – bucco-lingual breadth). Images were obtained by placing the lens of a Sony Cybershot Camera over the eyepieces of a binocular microscope, treating the resulting images with Photoshop Elements 15 and then mounting them to prepare stereo-pairs. The scales were added manually.

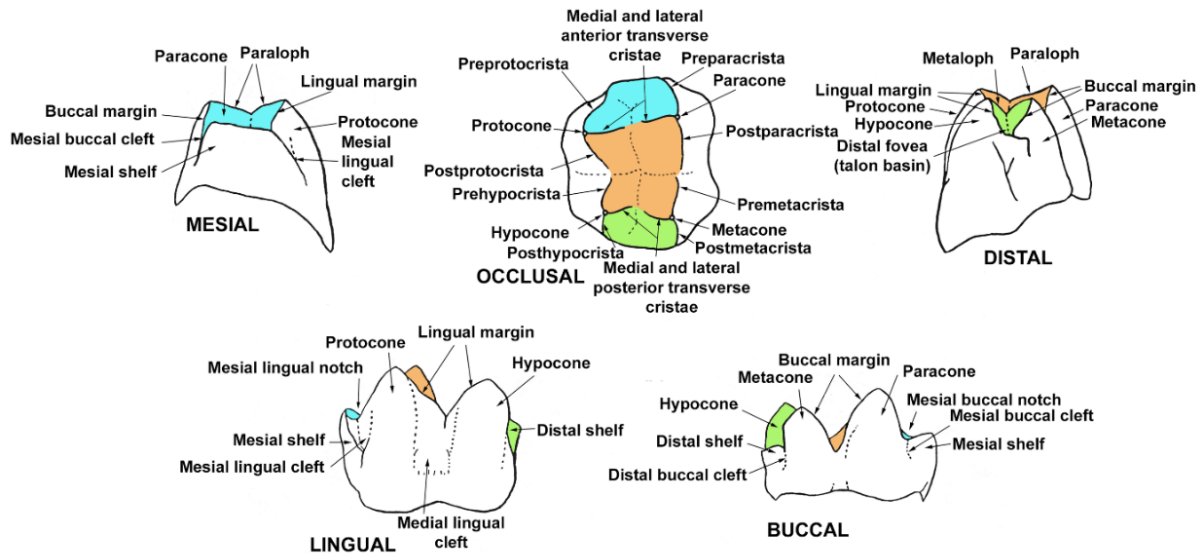
Nomenclature of the cusps, crests and other occlusal features of cercopithecoid upper molars is presented in Figures 1 and 2. Each of the cusps has crests running from its apex mesially (pre-) and distally (post-) and some of the cusps have a crest running towards the centre-line of the tooth (endo-). Thus preprotocrista means the crest on the protocone which runs mesially and the endoparacrista is the crest that extends from the apex of the paracone lingually towards the base of the protocone. Kay (1977) employed a similar nomenclature for the mesially and distally directed crests, but note that he used medial and lateral anterior transverse cristae for the endocrista of the paracone and that of the protocone, and medial and lateral posterior cristae for the inwardly directed crests on the metacone and hypocone.

There are several systems of nomenclature in the literature (Swindler, 2002). Szalay & Delson (1979) equate the crista obliqua with their « hypometacrista », but we call this crest the endometacrista because it does not make contact with the hypocone nor does it descend towards the hypocone but rather towards the protocone. Swindler (2002, fig. 4.6) in contrast used crista obliqua for the postprotocrista not the endometacrista. Von Koenigswald (1969) considered the entire crest system between the protocone and metacone to be the crista obliqua (i.e. postprotocrista + metaconule + endometacrista in the terminology used in this paper). At the base of the endometacrista there is a small tubercle called the metaconule by Swindler (2002) and Szalay & Delson (1979) which is in contact with the postprotocrista.

Stereoscopic drawings were prepared for defining the nomenclature of features of the occlusal surface (Fig. 1).



**Figure 1.** Nomenclature of occlusal features in the cercopithecoid left upper molar from Napak V (UM Nap V 100'15). Stereo occlusal drawings (blue is the mesial fovea, brown is the trigon basin, green is the distal basin and fovea). Note the weakly developed endohypocrista, the lack of endoprotocrista and the absence of crests between the metacone and hypocone, the endometacrista contacting the metaconule rather than the endohypocrista (dashed lines - grooves, solid lines - crests).



**Figure 2.** Nomenclature of morphological features of a cercopithecoid left upper molar (*Theropithecus*) modified from Kay (1977). Note the absence of crista obliqua, and the presence of well-developed endocristae (medial and lateral transverse cristae).

## COMPARATIVE SAMPLES

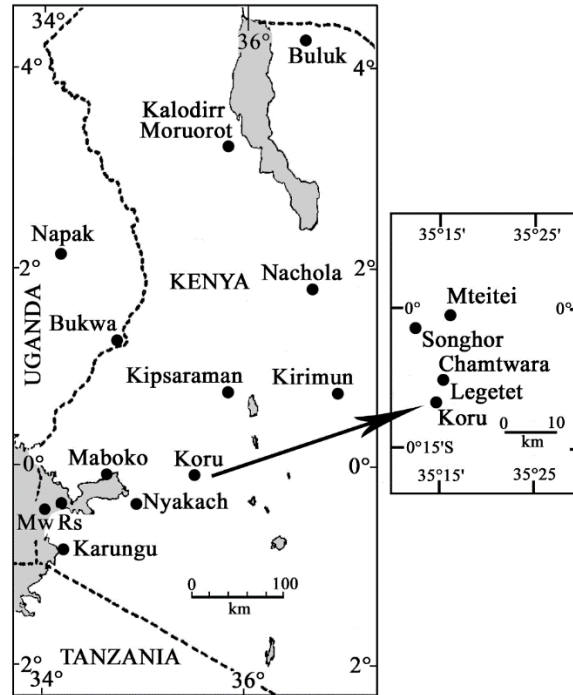
Where possible, comparisons of the Napak fossils have been made with other late Oligocene and early to middle Miocene cercopithecoids (Table I).

**Table I.** Oligocene and early to middle Miocene cercopithecoids of Africa, which can or can't be compared (where possible) with the Napak monkey.

Taxon	Locality	Upper molars	References
<i>Victoriapithecus</i> sp.	Ngorora	No	Hill <i>et al.</i> 2002; Rossie <i>et al.</i> 2013
<i>Victoriapithecus macinnesi</i>	Moroto II	No	Pickford <i>et al.</i> 2003
<i>Victoriapithecus macinnesi</i>	Ombo	No	Miller <i>et al.</i> 2009
<i>Victoriapithecus macinnesi</i>	Majiwa	No	Miller <i>et al.</i> 2009
<i>Victoriapithecus macinnesi</i>	Nyakach	No	Pickford, 1986; Senut, 1987
<i>Victoriapithecus macinnesi</i> (= <i>V. leakeyi</i> )	Maboko	Yes	MacInnes, 1943
<i>Victoriapithecus macinnesi</i>	Loperot	No	Miller <i>et al.</i> 2009 ; Grossman <i>et al.</i> 2014
<i>Victoriapithecus</i> sp.	Aka Aiteputh (Nachola)	No	Nakatsukasa & Kunimatsu, 2012
Genus indet. <i>mogharensis</i>	Wadi Moghara	No	Fourtau, 1918
<i>Prohylobates tandyi</i>	Wadi Moghara	No	Fourtau, 1918
<i>Zaltanpithecus simonsi</i>	Gebel Zelten	No	Delson, 1979; Benefit, 2008
Indeterminate cercopithecoid	Ongoliba (age uncertain)	No	Hooijer, 1963
<i>Noropithecus kipsaramanensis</i>	Kipsaraman	Yes	Pickford & Kunimatsu, 2005
<i>Noropithecus bulukensis</i>	Buluk	Yes	Miller <i>et al.</i> 2009
<i>Noropithecus fleaglei</i>	Nabwal	No	Miller <i>et al.</i> 2009
<i>Alophia metios</i>	Nakwai	No	Rasmussen <i>et al.</i> 2019
<i>Nsungwepithecus gunnelli</i>	Rukwa Rift	No	Stevens <i>et al.</i> 2013

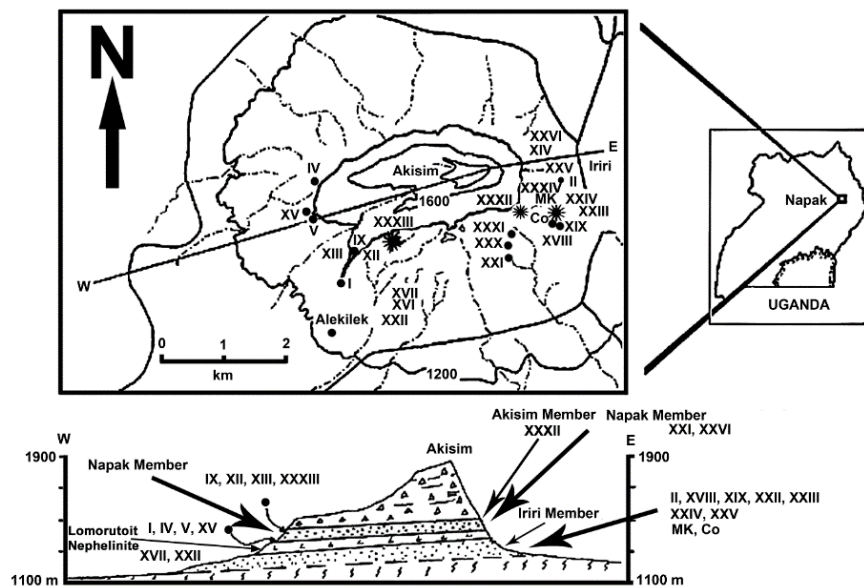
## GEOLOGICAL CONTEXT

The geology and stratigraphy of Napak, Uganda, have been described on several occasions (Bishop, 1958, 1962, 1963a, 1963b, 1964a, 1964b, 1967, 1968, 1971, 1972; Bishop, *et al.* 1969; Bishop & Trendall, 1967; Bishop & Whyte, 1962; Pickford *et al.* 1986; Gundling & Hill, 2000; Musalizi *et al.* 2009). The deposits are associated with Napak Volcano in the northeast of Uganda (Fig. 3, 4).



**Figure 3.** Location of early and middle Miocene fossiliferous localities in East Africa.

The stratigraphic succession in the Akisim remnant of the Napak volcano-sedimentary edifice has been subdivided into several members (Fig. 4). Overlying Precambrian Basement gneisses, there is a thin, 3-4 metre thick silicified palaeosol and regolith, best exposed at Opopwa, which is overlain by the Iriiri Member (predominantly waterlain volcanoclastic deposits interfingering with subaerial tuffs) which is succeeded by the Lomorutoit Nephelinite lava, which is in its turn overlain by the Napak Member (sub-aerial tuffs with incipient palaeosols and debris flows) which is succeeded by the Akisim Member (volcanic agglomerates with intercalations of coarse slope debris).



**Figure 4.** Stratigraphy of the Akisim remnant of Napak Volcano, Karamoja, Uganda, and the position of the main fossiliferous localities. Napak V is in the Napak Member, above the Lomorutoit Nephelinite Lava.

Radio-isotopic dates obtained from biotite crystals in the Napak Member indicate eruption ages ranging in age from 20.5 to 19 Ma (Bishop *et al.* 1969). This span of ages agrees with faunal correlations which indicate that the Iri and Napak faunas correlate closely with those from the Koru Formation and the Songhor Beds in Kenya (East African Faunal Set I, ca 20 Ma) and are appreciably older than those from Rusinga, Kenya (Faunal Set II, ca 17.8 Ma) (Pickford, 1981), and much earlier than the middle Miocene faunas of Maboko Island, Kenya (Faunal Set IIIa, ca 16-14.5Ma) which yield *Victoriapithecus* (Fig. 5).

Ma	North Africa	Arabian Peninsula	East Africa	Southern Africa	Ma
12	Bled Douarah inférieure, Tozeur Nementcha Oum Douil, Sehib Beni Mellal		Ngorora C-D Kisegi Ngorora A-B *	Hondeklip Bay	12
13	Pataniak 6, Testour	Al Jadidah	Napudet Tambach Kapsibor, Fort Ternan, Serek	Rooilepel (corbetti zone) Berg Aukas (MM 1) Rooilepel (oshanai zone)	13
14		Ajfar		Karingarab (oshanai zone)	14
15	Foum el Guelta		Kirimun Mbagathi Ombo *		15
16	Wadi Moghara * Gebel Zelten *	Ad Dabtiyah As Sarrar Tayma Rotem Yerovem	Majiwa * Maboko * Kaloma Nyakach * Nachola * Bukwa II Akisim Mbr Kipsaraman * Cheparawa, Muruyur Loperot *	Ryskop Bosluis Pan	16
17	Kabylie Kouif	Jabal Midra	Kalodirr Moruorot Moroto II *		17
18	Wadi Faregh Siwa	Wadi Sabya Ghaba	Rusinga, Karungu, Chianda Adi Ugri Bukwa I	Auchas	18
19			Loncherangan Meswa Bridge Napak Mbr * Koru, Songhor Iri Mbr Chamtwara	Zebra Hill Langental E-Bay, Fiskus, Bohrloch Grillental, Elisabethfeld	19
20					20
21			Nakwai *		21
22					22

**Figure 5.** Biostratigraphic correlations of early and middle Miocene localities of Africa, several of which have yielded cercopithecoids (stars). The position of Ongoliba is uncertain (possibly late Miocene) so it is omitted from the chart.

### BRIEF HISTORY OF STUDY OF NAPAK MONKEYS

Before entering into details of the history of study of Napak cercopithecoid fossils, it is worth pointing out that the Ugandan fossils have provided fuel for debates concerning monkey origins, niche partitioning between early monkeys and small apes, and aspects of locomotion and diet. Thus, even though in the beginning, the material basis of the debate was limited (one molar, one frontal bone) the specimens have played a significant role in subsequent scientific debates, even on occasion being eliminated from Cercopithecoidea on the grounds that the specimens may not, after all, be from monkeys. The partial elbow joint from Napak described by Senut (1986b) added fuel to the debate about locomotion in these early monkeys.

These identifications were played out against an intellectual background concerning niche competition between monkeys and small apes, starting with the proposals of Andrews (1981) up to the writings of Rossie & Hill (2018) as well as in studies concerning the timing of the split between apes and monkeys. Allied to these debates is the question of the affinities between Victoriapithecidae and Oreopithecidae, some authors seeing resemblances between them. For example, the presence of a crista obliqua in upper molars of *Victoriapithecus* and *Oreopithecus* (Von Koenigswald, 1969; Szalay & Delson, 1979; Harrison, 1982) has been interpreted to approach the taxa to each other and to distance both from Cercopithecidae (Colobinae, Cercopithecinae) which do not have a crista obliqua in the upper molars (Kay, 1977).



The first mention of the presence of fossil monkeys at Napak was by Pilbeam & Walker (1968) who described an upper molar (UMP 62-21 from Napak V) and a frontal bone (UMP 68-25 from Napak IX). On the basis of these two fossils the authors proposed that the subdivision of the Cercopithecidae (i.e. the dichotomy between Cercopithecinae and Colobinae) had already occurred by 19 Ma.

Pilbeam (in Pilbeam & Walker, 1968) thought that the length/breadth ratio of the upper molar from Napak meant that the species to which it belonged was orthognathic (short-faced). This was an interesting inference, to a great extent supported by the subsequent discovery of a skull of *Victoriapithecus* at Maboko, which has a relatively short splanchnocranium relative to the neurocranium (Benefit & McCrossin, 2002). The side from which the tooth came was not mentioned in the paper by Pilbeam & Walker (1968).

The frontal bone from Napak IX was attributed to a colobine by Walker (in Pilbeam & Walker, 1968) but was interpreted to belong to a hominoid by Radinsky (1974) was subsequently interpreted by Fleagle (1975) as "most closely related to the small Kenyan hominoids formerly placed in the genus *Limnopithecus*" and was referred to *Micropithecus clarki* by Fleagle & Simons (1978) and to cf *Micropithecus clarki* by Harrison (1982). Rossie & MacLachy (2006) considered that the frontal bone belonged to a monkey. However, with the recognition of the existence of a highly diverse catarrhine fauna at Napak (Pickford *et al.* 2010) the Napak frontal bone could belong to one of the other small apes from the site : *Lomorupithecus evansi* (= *Lomorupithecus harrisoni*), *Iriripithecus alekileki*, *Turkanapithecus rusingensis*, *Dendropithecus ugandensis*, *Limnopithecus legetet* or *Karamojapithecus akisimia* but it is less likely to belong to a monkey as originally thought by its describer and by Rossie & MacLachy (2006). Napak IX, from which the frontal was collected, yielded a snout of *Lomorupithecus evansi*, a mandible of *Dendropithecus ugandensis* and a mandible of *Limnopithecus legetet*.

Szalay & Delson (1979, figure 214L) published the first illustrations of the Napak cercopithecoid upper molar which they considered to be a left upper M<sup>1or2</sup>, attributing the tooth to *Victoriapithecus* sp. However, the molar is from the right side. This mis-orientation may explain why some subsequent authors have been reticent to accept the cercopithecoid status of the tooth (Grossman *et al.* 2014).

Pickford *et al.* (1986) mentioned the discovery of post-cranial elements of a cercopithecoid at Napak V, the proximal radio-ulna featuring in a paper by Senut (1986b) in which the author inferred that it showed adaptations to terrestrial locomotion.

Pickford *et al.* (1999) listed *Victoriapithecus/Prohylobates* at Nachola (Aka Aiteputh Formation) Kenya, but the fossils were not described.

Benefit (1993, 1999) and Benefit & McCrossin (2002) classified the Napak tooth in *Victoriapithecus macinnesi*, an identification accepted by Miller *et al.* (2009) and Jablonski & Frost (2010).

Nakatsukasa & Kunimatsu (2012) in contrast, considered that the Napak fossil was indeterminate at the genus level, listing it as Cercopithecoidea indet. This uncertainty about the appurtenance of the fossil was followed up by Grossman *et al.* (2014) who went further when writing that the Napak upper molar described by Pilbeam (in Pilbeam & Walker, 1968) might, with further analysis, be removed from Cercopithecoidea. The authors appear to have been unaware of the fact that the tooth was illustrated by Szalay & Delson (1979).

This study responds to some of the scientific issues, but we recognise that the material basis is still rather restricted for reaching wide-ranging conclusions. Nevertheless, the excellent preservation and unworn condition of the new upper molar from Napak V reveals that it possesses some unexpected morphological features that potentially throw light on the group from which the Old World Monkeys may have emerged and to which other Catarrhini it might be closely related, in particular the Oreopithecidae. It does not throw light on the origins of the colobines or cercopithecines.

## SYSTEMATIC DESCRIPTION

Superfamily Cercopithecoidea Gray, 1821

Family Victoriapithecidae Von Koenigswald, 1969

Genus *Victoriapithecus* Von Koenigswald, 1969

**Type species:-** *Victoriapithecus macinnesi* Von Koenigswald, 1969

**Type locality and Age :-** Maboko, Kenya, Faunal Set PIIIa, (ca 15.5 Ma)

**Species *Victoriapithecus* sp.**

### **Material from Napak:-**

UM Nap V 100'15, left upper molar (mdl x blb - 6.5 x 7.4 mm) from Napak V.

UMP 62-21, right upper molar (mdl x blb - 7.2 x 8.1 mm) from Napak V.

UM Nap V 8'85, proximal ends of left ulna and radius from Napak V.

### **Description**

UM Nap V 100'15 is an unworn but completely formed crown of a left upper molar (M1/ or M2/) (Fig. 6). It has four main cusps (protocone and paracone forming the mesial loph, metacone and hypocone forming the distal loph) and a small but distinct cusplet (the metaconule) between the metacone and protocone. There are also mesial and distal cingular structures and a cingulum on the mesial surface of the protocone which extends onto the lingual surface of the cusp but weakening as it does so, producing a shallow groove and low ridge which terminates at the lingual notch. In addition, there is a low, small tubercle at the base of the buccal notch which is interpreted to be a mesostyle, much as in some New World Monkeys (Swindler, 2002). The parastyle and metastyle are clearly evident at the mesial and distal ends of the buccal margin of the crown.

The protocone possesses two cristae - preprotocrista and postprotocrista - the former of which descends mesio-centrally to blend into the mesial cingulum which forms a mesial shelf, the latter descending distally to touch the end of the metaconule.

The paracone has three cristae - preparacrista, postparacrista and endoparacrista. The preparacrista descends mesially and blends into the mesial cingulum, and it also contributes to the formation of the low parastyle. The postparacrista descends distally into the median transverse valley where it meets the premetacrista. The endoparacrista extends lingually towards the base of the protocone, thereby making a low wall between the mesial fovea and the trigon basin. In addition, the distal surface of the paracone has a low swelling descending from apex towards the lingual end of the median transverse valley.

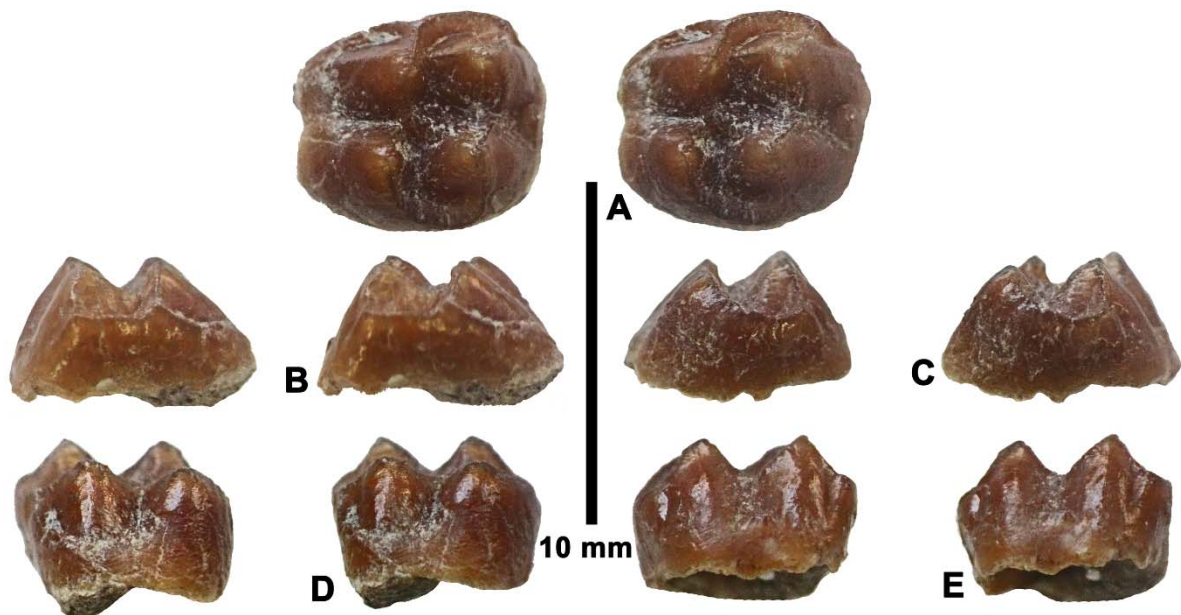
The premetacrista descends mesially from the apex of the metacone and terminates in the median transverse valley opposite the end of the postparacrista. The postmetacrista descends distally and blends into the distal cingulum which forms a distinct distal shelf. The endometacrista descends mesio-lingually towards the metaconule which separates the trigon basin from the distal fovea (talon basin).

The prehypocrista descends mesio-buccally to terminate at the lingual end of the metaconule but it is separated by grooves from the metaconule and postprotocrista. The posthypocrista curves disto-buccally as it descends towards the distal cingulum into which it blends without any obvious interruption. The occlusal surface of the distal shelf thus formed, has a corrugated aspect caused by a series of sub-parallel grooves oriented more-or-less mesio-distally. The buccal surface of the hypocone is slightly inflated, but does not produce a crista.

The lingual notch which separates the protocone from the hypocone is deep but not very broad, having a V-shaped profile. The notch shallows towards cervix. The buccal notch, in contrast, is broader, more vertically oriented and somewhat shallower than the lingual one, its profile being U-shaped. At the base of the buccal notch, immediately above cervix there is a low tubercle, the mesostyle.

The apices of the four main cusps are in very internal positions compared to the cervix of the tooth. The lingual flare is markedly greater than that on the buccal side. The mesial and distal shelves are mesio-distally broad, contributing about 12% to the length of the tooth, and they overstep the cervical margins beneath them by a small margin (i.e. the teeth are shorter at cervix than at the shelves).

The trigon basin is the largest of the three occlusal basins, followed in size by the distal fovea (talon basin) and the mesial fovea.



**Figure 6.** Stereo images of Nap V 100'15, left upper molar from Napak V, Uganda (A) occlusal, (B) mesial, (C) distal, (D) lingual, (E) buccal views. Note the relatively large mesostyle (visible in A and E) and the isolated nature of the metaconule between the protocone and metacone (scale : 10 mm).

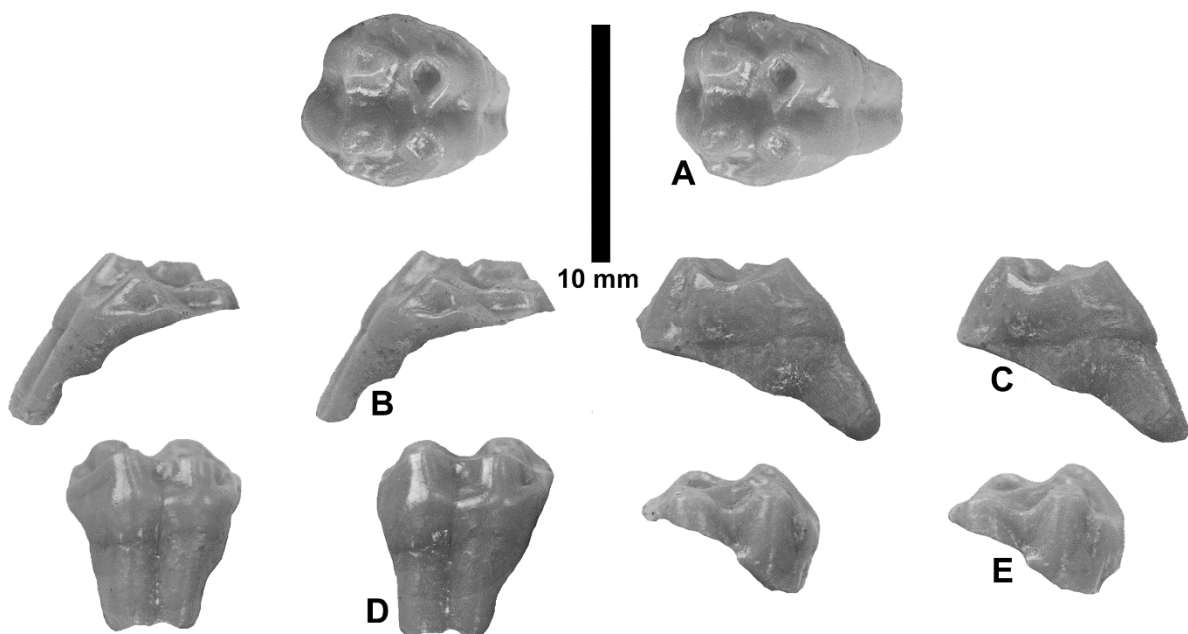
**Table II.** Measurements (in mm) of the upper molars of Cercopithecoidea from Napak V, Uganda. Measurements for UMP 62-21 are from Pilbeam (in Pilbeam & Walker, 1968) (\* estimated as the tooth is worn).

Measurement	UM Nap 100'15	UMP 62-21
Mesio-distal length in line with paracone-metacone	6.5	7.2
Mesio-distal length in line with protocone-hypocone	6.0	--
Bucco-lingual breadth anterior loph	7.5	--
Bucco-lingual breadth posterior loph	7.0	8.1
Distance between apices of protocone and paracone	2.6	--
Distance between apices of metacone and hypocone	2.8	4.0*
Distance between apices of protocone and hypocone	2.9	--
Distance between apices of paracone and metacone	3.1	--
Protocone height	4.2	--
Paracone height	4.4	--
Metacone height	4.1	4.0*
Hypocone height	4.0	--

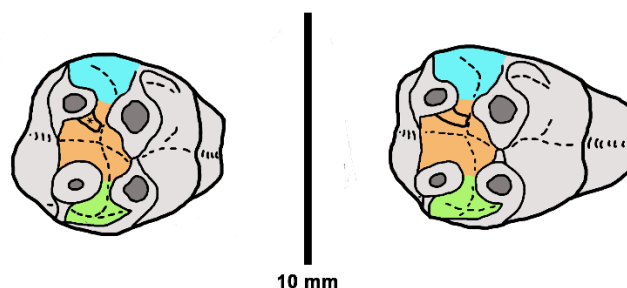
UMP 62-21, a right upper M1/ or M2/ was previously described by Pilbeam (in Pilbeam & Walker, 1968). The specimen retains the lingual root which has a prominent longitudinal groove on its lingual aspect. The buccal roots and part of the crown are missing mesially and buccally, but leaving most of the occlusal surface intact (Fig. 7-8).

The upper molar is in medium wear, with dentine exposures on all four main cusps. The lingual cusps are more deeply worn than the buccal ones. The cristae of the four main cusps are disposed in the same way as those in Nap V 100'15 described above but, being more worn are no longer crest-like, but more like low round-shouldered ridges. The paracone shows a large, distinct wear facet on its disto-lingual side descending into the trigon basin. The mesostyle is represented by a subtle swelling in the base of the buccal notch. There is a remnant of a cingulum on the mesial aspect of the protocone, but it fades out on the lingual surface of the cusp only to pick up again on the surface close to the lingual notch. A slight change in slope of the lingual wall of the cusp hints that there may have been a complete cingulum in ancestral populations of the lineage as was remarked upon by Pilbeam (in Pilbeam & Walker, 1968).

As in the unworn tooth described above, the crown of UMP 62-21 is marked by great lingual and buccal flare, as was already noted by Pilbeam (in Pilbeam & Walker, 1968).

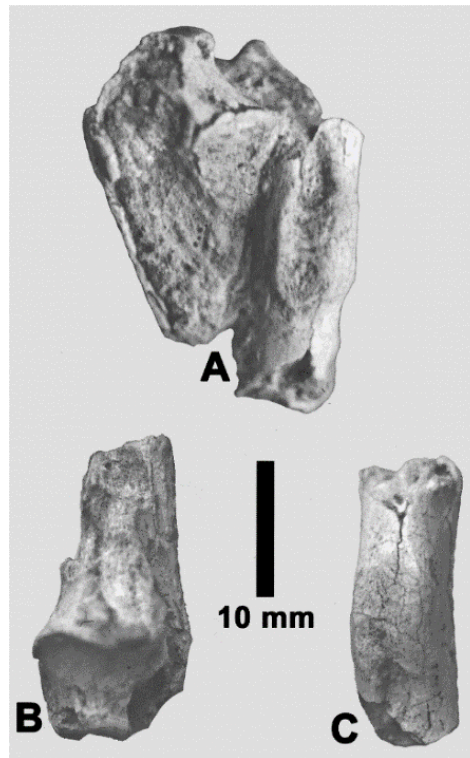


**Figure 7.** Stereo views of a cast of UMP 62-21, cercopithecoid right upper molar in medium wear (A) occlusal, (B) mesial, (C) distal, (D) lingual, (E) buccal views (scale : 10 mm).



**Figure 8.** Stereoscopic drawing of UMP 62-21, cercopithecoid right upper molar from Napak V (blue - mesial fovea, brown - trigon basin, green - talon basin (distal fovea) dashed lines - grooves, solid lines - positive relief features. Note the large wear facet on the disto-lingual surface of the paracone (star in left image), the remnants of a cingulum on the mesial face of the protocone and a minuscule, low mesostylar swelling (scale : 10 mm).

Napak V 8'85 comprises the proximal ends of a left radius and ulna which were in articulation when found (Senut, 1986a, 1986b, 1987, fig. 4). There is no need to redescribe the fossils, but illustrations are presented of the specimens after being extracted from the matrix (Fig. 9). Senut (1987) compared the fossils with specimens from Maboko Island, Kenya, where she documented two patterns of post-cranial bones, indicating the presence of two species at the site. However, the teeth of the two species are difficult to distinguish from each other. For this reason, the specific identification of the Napak monkeys is left open.



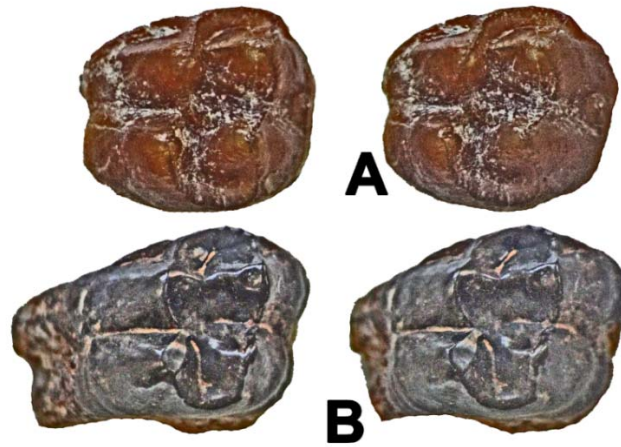
**Figure 9.** UM Nap V 8'85, proximal left radius and ulna attributed to *Victoriapithecus* sp. (A) lateral view of specimen as found, (B) anterior view of proximal radius, (C) posterior view of radius (scale : 10 mm).

## DISCUSSION

The new cercopithecoid upper molar from Napak V is valuable in the sense that it resolves doubts expressed in the literature concerning the presence or otherwise of monkeys at the locality. The fact that the specimen is unworn is a bonus because it shows clearly all the cristae and grooves, as well as the presence of minor structures such as a protoconal cingulum and a mesostyle in the buccal notch, as well as a clear, distinct metaconule, about 0.55 mm long, occupying the space between the ends of the postprotocrista and the endometacrista. All these features indicate appurtenance to the Victoriapithecidae rather than to any non-cercopithecoid mammalian group, but determining the generic and specific attribution of the tooth is more delicate. Some of these morphological features such as a mesostyle and/or metaconule are also present in Oreopithecidae and some Oligocene primates such as *Apidium*, and even occur in some lemuroids and platyrrhines, but the overall resemblances of the Napak fossil to these primates are not close.

Comparisons with other non-cercopithecoid cercopithecoids such as *Prohylobates*, *Zaltanpithecus*, *Nsungwepithecus* and *Alophia* are not possible, because the upper teeth of these four genera have not yet been described. The only victoriapithecids for which upper molars are known are *Victoriapithecus* and *Noropithecus*. Of these two genera, the former recalls the Napak teeth more closely than does the latter but in any case the differences between upper molars of these genera are subtle. Furthermore, the teeth of both *Victoriapithecus* and *Noropithecus* are quite variable in terms of the development of the lesser structures such as cingulum, cristae, metaconule (or crista obliqua), and styles (Von Koenigswald,

1969; Benefit, 1987; Pickford & Kunimatsu, 2005; Miller *et al.* 2009). However, *Noropithecus* generally shows a well-developed endoprotocrista extending buccally across the tooth towards the endoparacrista, thereby forming a continuous crest across the tooth separating the mesial fovea from the trigon basin (Fig. 10) unlike the absence of a corresponding endoprotocrista in the Napak specimens.



**Figure 10.** Comparison between (A) the Napak cercopithecoid upper molar (UM Nap V 100'15 : 6.5 x 7.5 mm) and (B) a lightly worn left upper molar (OCO BAR 34'03 : 6.8 x 8.9 mm) of *Noropithecus kipsaramanensis* from Kipsaraman, Kenya. The stereo occlusal images of the teeth have been brought to the same size for ease of comparison. Note the differences in the expression of the metaconule (or crista obliqua), the lingual cingulum and the mesostyle, which are well differentiated in the Napak specimen, but are subtle or absent in the Kipsaraman fossil. Note also the presence of an endoprotocrista in the Kipsaraman individual reaching towards the endoparacrista; the endoprotocrista is absent in the Napak fossil. Overall, however, the teeth are quite similar in proportions and gross morphology.

Doubts which were raised recently by Grossman *et al.* (2014) about the superfamilial appurtenance of the fossil described by Pilbeam (in Pilbeam & Walker, 1968) can be laid to rest. The fossil does indeed belong to a monkey, in all likelihood *Victoriapithecus* or a closely related genus. The new material thus clears up the issue about the presence of victoriapithecids at Napak, but the fossils are still insufficient to verify the generic and specific status of the material, a point already articulated by Nakatsukasa & Kunimatsu (2012). On balance, we consider that appurtenance of the Napak cercopithecoid specimens to *Victoriapithecus* is more likely than to *Noropithecus* for the reasons outlined above. However, the presence of a clear metaconule and a mesostyle indicate that it is a remarkably primitive member of the Cercopithecoidea and it is not beyond the realms of possibility that these specimens from Napak represent an unknown genus of monkey. However, given that there are four genera of primitive monkeys from the Oligocene and early Miocene which are known only by their lower teeth, we cannot exclude the possibility that the Napak teeth could belong to one of them (*Nsungwepithecus*, *Alophia*, *Prohylobates*, *Zaltanpithecus*). We refrain from formally naming a new taxon in the hope that more instructive specimens will be found.

The victoriapithecoid from Napak represents one of the earliest known members of this family of Old World monkeys. *Nsungwepithecus* from the Rukwa Rift, Tanzania (Stevens *et al.* 2013) and *Alophia* from Nakwai, Kenya (Rasmussen *et al.* 2019) are probably older, but their appurtenance to Victoriapithecidae sensu stricto, requires a more comprehensive fossil record for both taxa, including upper teeth which are currently unknown.

In their monograph on the small apes from Napak, Pickford *et al.* (2010) described 80 upper and 75 lower teeth of small apes. Since then 112 additional small ape specimens have been found, including several mandibles and maxillae with two or more teeth, bringing the total tooth count to over 300. The abundance and high diversity of small apes at Napak contrasts strongly with the paucity of cercopithecoid specimens (two isolated teeth and one partial elbow joint) from the deposits. If we add

to this the abundant large ape fossils attributed to *Ugandapithecus major* and a few to *Ekembo nyanzae*, then the ratio of apes to monkeys at Napak becomes starker, with monkeys comprising less than 1% of the catarrhine primate fossils from the site. This contrasts with the situation at localities such as Maboko and Kipsaraman, Kenya, where monkey fossils are abundant and ape fossils less so, but still present in significant quantities.

The reasons for these differences in relative abundance are almost certainly ecological. The middle Miocene sites that have yielded abundant cercopithecoid fossils have also yielded the remains of large kubanochoerine suids, suggesting that the monkeys and large suids may have occupied comparable habitats. Some of the sites (Maboko, Aka Aiteputh) also yield fossil terrestrial gastropod assemblages typical of the more arid spectrum of habitats that occur in tropical Africa, such as Nyika woodland (Pickford 2004; Pickford & Senut, 1988). The rivers traversing such habitats generally have a dense gallery forest fringing them. We infer from this that the early and middle Miocene monkeys were probably adapted to slightly more open habitats than the majority of the small-bodied apes, as was discussed by Pickford & Senut (1988). The early Miocene localities where more humid palaeoenvironments are attested by the gastropod assemblages, such as Rusinga, Koru, Songhor and Mfwangano, yield small species of suids and abundant small ape fossils but no cercopithecoid specimens.

Napak V and the nearby site Napak XV are the only localities in the Napak Member which show evidence of fluvial deposition (conglomerates in channels) and faunal elements such as crocodiles and the large anthracothere *Brachyodus*. It also yielded remains of the large tragulid *Dorcatherium iririensis* (Pickford, 2002).

The palaeoenvironments at Napak were discussed by Pickford & Senut (1988) and Pickford (2004) who, on the basis of the terrestrial molluscs, documented the former presence of dense vegetation on the upper slopes of the volcano with some open probably grass-covered patches here and there forming a mosaic of vegetation categories covering the lower slopes of the volcano. The crocodiles, *Brachyodus* and possibly the monkey may have been excluded from much of the thickly vegetated parts of the mountain but could survive near well-wooded streams which drained the more sparsely vegetated lower slopes of the edifice.

It is pertinent to point out that recent discoveries at Napak include remains of a gigantic suid at Napak XXXII near the base of the Akisim Member which overlies the Napak Member (Pickford & Tsujikawa in press). This suid is a typical middle Miocene form, having been found at Nyakach, Kenya, and it is therefore not beyond the realms of possibility that some of the fossils from Napak V could be younger than the early Miocene. For the moment, however, we consider that the fossil monkeys are part of the Napak V assemblage which is typical of East African Faunal Set I (Pickford, 1981) aged between ca 19 and 20.5 Ma.

Whatever the case, the Napak monkey fossils are likely to be older than *Zaltanpithecus* and *Prohylobates* from northern Africa, but anatomical comparisons are not possible, these taxa being represented only by lower teeth and mandible fragments (Fourtau, 1918; Benefit, 2008).

Given the meagre nature of the Napak monkey sample, we do not think it necessary to perform a rigorous computer-assisted phylogenetic analysis, but merely note that it shares some presumably plesiomorphic features with early Oligocene *Apidium* and Miocene oreopithecids as well as some features (metaconule, mesostyle) that occur in some lemurs and even some New World Monkeys (Swindler, 2002) as well as Pliopithecidae (Hürzeler, 1954 : Göriach specimen originally attributed to *Pliopithecus antiquus* but now included in *Pliopithecus platyodon* Biedermann 1863).

The available evidence from Napak does not throw light on the timing of the split between colobines and cercopithecines as thought by Pilbeam & Walker (1968), nor does it clarify the question about which of the extant subfamilies of Cercopithecidae is the closest relative of the victoriapithecids.

## CONCLUSIONS

The discovery of an unworn upper molar of a victoriapithecoid at Napak V confirms the presence of the superfamily Cercopithecoidea at the site, previously hypothesised on the basis of a moderately worn upper molar and a frontal bone (Pilbeam & Walker, 1968) and a partial elbow joint (Senut, 1987). Doubts have been raised about the appurtenance of the upper molar, and the frontal bone was subsequently removed from the superfamily. The interest in these Napak monkey fossils lies in the fact that they are among the oldest known in the world, being rivalled only by incompletely known *Nsungwepithecus* from Tanzania (Stevens *et al.* 2013), and *Alophia* from Kenya (Rasmussen *et al.* 2019). They are appreciably older than the richer occurrences of victoriapithecoids at Maboko, Kenya (Benefit, 1993) and Kipsaraman, Kenya (Pickford & Kunimatsu, 2005). The details of crests, cingula, styles and other structures in the Napak molars indicate that they are exceedingly primitive within the context of Cercopithecoidea, sharing some dental features with early Oligocene fossils from Egypt, such as *Apidium*, as well as with the enigmatic primate *Oreopithecus* and other oreopithecoids and even with some lemurs and platyrrhines. However, the Napak monkey species requires a better fossil record before much more can be learned about its affinities and origins.

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