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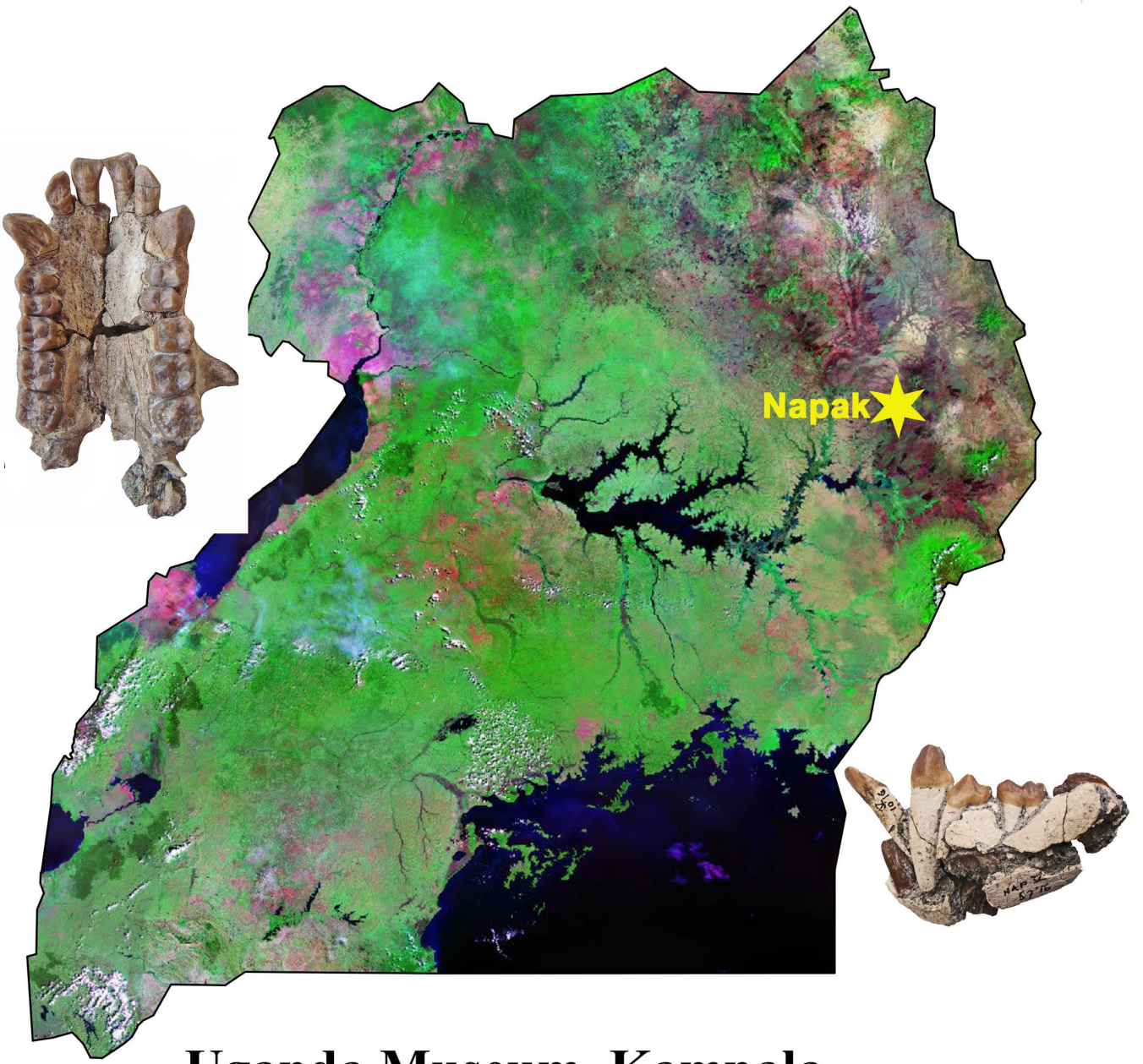
GEO-PAL UGANDA



Uganda Museum, Kampala

Geo-Pal Uganda

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Uganda Museum, P.O. Box 5718, Kampala

Descriptive catalogue of large ape dento-gnathic remains from the early and middle Miocene of Napak, Uganda : 2010-2020 collections

Martin Pickford

Centre de Recherche en Paléontologie - Paris (CR2P), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, CP 38, 8 rue Buffon, 75005 Paris, France (martin.pickford@mnhn.fr)

Brigitte Senut

Centre de Recherche en Paléontologie - Paris (CR2P), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, CP 38, 8 rue Buffon, 75005 Paris, France (brigitte.senut@mnhn.fr)

Dominique Gommery

Centre de Recherche en Paléontologie - Paris (CR2P), CNRS, Muséum national d'Histoire naturelle, Sorbonne Université, Campus Pierre et Marie Curie-SU, T.46-56, E.5, 4 Place Jussieu, 75005 Paris, France (dominique.gommery@sorbonne-universite.fr)

Sarah Musalizi

Uganda Museum, Kira Road, Kampala, Uganda
(saramussasarah@gmail.com)

Christopher Ssebuyungo

Uganda Museum, Kira Road, Kampala, Uganda
(jacksseb@yahoo.com)

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ABSTRACT

Between 2010 and 2020, abundant dentognathic remains of large apes were collected at Napak, Uganda. The Iriri Member (basal Miocene) yielded its first fossil ape specimens from the lowermost beds of the volcano-sedimentary succession in 2014 (assigned to *Ugandapithecus legetetensis* and *Ugandapithecus major*), the Napak Member (basal Miocene) yielded many specimens of the same two species while the younger strata attributed to the Akisim Member (middle Miocene) yielded two specimens of large ape which accord in dimensions and morphology with *Afropithecus turkanensis*.

Key Words :- Hominoidea, Early Miocene, dento-gnathic, palaeoecology, enamel hypoplasia, large apes

INTRODUCTION

Since 2010, the Uganda Palaeontology Expedition has collected a substantial quantity of fossilised large ape remains from Napak, Uganda, including an adult skull with its entire dentition and an infant mandible with mixed dentition. Several new localities have been discovered which yielded well-preserved but mostly isolated teeth. The historical collection (pre-1970) from Napak contained 16 large ape teeth which were attributed at the time to *Proconsul major* Le Gros Clark & Leakey (1951) (Leakey, 1962; Bishop & Whyte, 1962; Allbrook & Bishop, 1963; Pilbeam, 1969; Andrews, 1978). Between 1985 and 2000 ten teeth were found (some associated in mandibles), between 2000 and 2009, 31 teeth were found (Pickford *et al*, 2009) and from 2010-2020, 93 teeth have been collected, many of which are

associated in maxillae and mandibles. The total now stands at 150 teeth (Fig. 1) which is sufficient for most tooth positions to obtain a reasonable idea of morphological and metric variability (much of the deciduous dentition is still poorly known).

Previous work on *Ugandapithecus* from Napak was summarised by Pickford *et al*. (2009). Relevant publications are by Bishop (1958, 1962, 1964) Allbrook & Bishop (1963), Pilbeam (1969), Senut *et al*. (2000), Gommery *et al*. (2002), and MacLatchy *et al*. (2005). The latter authors concluded that *Ugandapithecus* was a junior synonym of *Proconsul*, but the new skull from Napak XV indicates otherwise – In *Ugandapithecus* the M3/ (MDL x BLB : 14.4 x 17.5 mm) is not reduced in dimensions but is larger than the M2/ (14.3 x 16.5 mm), unlike *Proconsul africanus* in which the M3/ (7.9 x 10.5 mm) is smaller than M2/ (9.2 x 11.3 mm) and has the same mesio-distal length as the M1/ (7.9 x 9.6 mm) (Andrews, 1978); In *P. africanus* the P4/ (5.7 x 9.0 mm) is slightly narrower than M1/, whereas the P4/ in *Ugandapithecus major* (7.5 x 14.8 mm) is broader than the M1/; the burin-like apical morphology of the upper canine is not as well-developed in *Proconsul* and the distal concavity in the upper canine is shallower; the buccal cingulum in the upper molars is stronger in *Proconsul* than in *Ugandapithecus*. Other distinguishing features will be presented in a forthcoming paper dealing with the skull of *U. major* from Napak XV.

The aim of this paper is to describe and illustrate the fossils collected during the past decade so that colleagues can access the data for their own researches.

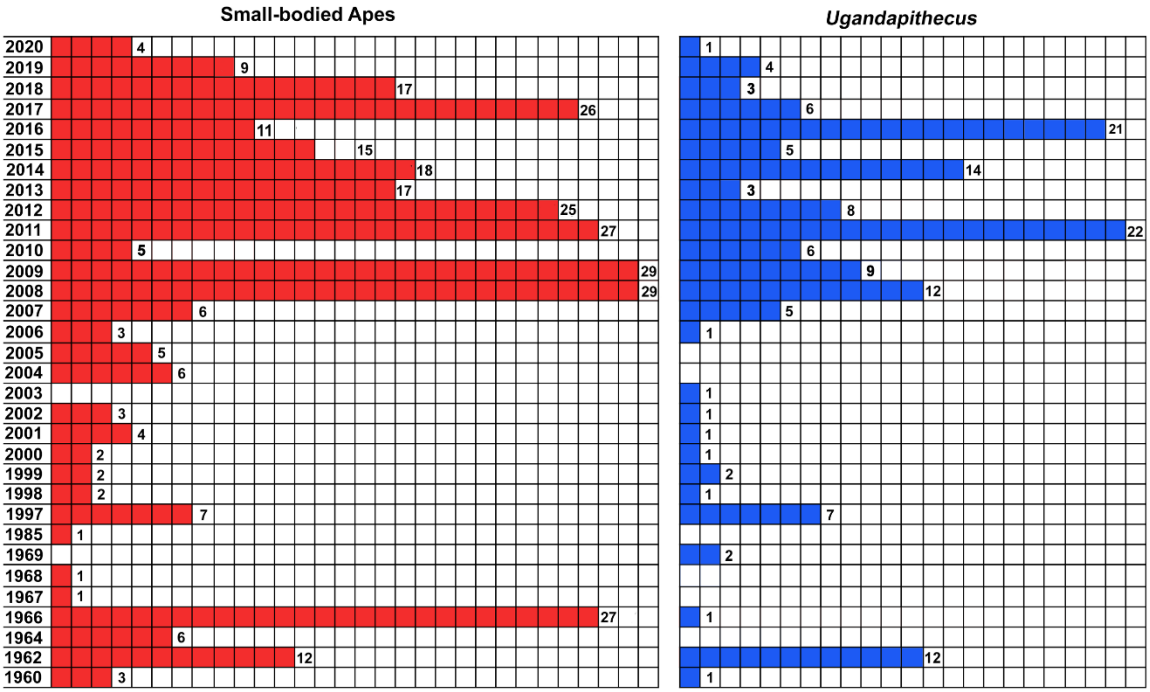

Figure 1. Yearly count of teeth of small-bodied apes and large apes collected at Napak, Uganda.

GEOLOGICAL CONTEXT AND AGE

All the fossil apes from Napak have been collected from the Akisim remnant of the volcano (Table 1). The fossils occur in early Miocene volcanic tuffs and palaeosols that developed on the tuffs during quiescent phases of volcanic activity. Several of the specimens show gnawing marks made by rodents prior to fossilisation (Figs 10, 72), and others show signs of predator activity, one small ape tooth being found in a coprolite at Napak IV (Fig. 2).

Figure 2. NAP IV 10'19, a lower third molar of *Micropithecus clarki* in a coprolite collected from Napak IV, Uganda.

The stratigraphic succession at the Akisim remnant has been subdivided into several members (Fig. 3). At the base of the succession, overlying Basement Complex gneiss of PreCambrian age and silicified sandstones (cf African Erosion Surface, locally of late Oligocene age) there is a series of palustral deposits of terrigenous and tuffaceous origin, containing oncoids, freshwater molluscs, crocodiles, fishes and turtles assigned to the Iriri Member. Palaeosols in this member are red. Above this is the Lomorutoit Nephelinite Lava flow, above which is the Napak Member, comprised mainly of subaerial tuffs, black palaeosols that developed thereon, and volcanic slope deposits, some of which are fluvial (small streams flowing down the flanks of the volcano yielding a few crocodiles (NAP V, NAP XV) and many plants and mammals. Above the Napak Member is the tuffaceous and agglomeratic Akisim Member which crops out in the steep parts of the mountain and, at the summit, comprises the thick agglomerate capping the sequence.

The Iriri Member is ca 20.5 Ma, the Napak Member ca 19-20.5 Ma, and the Akisim Member is ca 16 Ma. The Napak Member has been calibrated by radio-isotopic age determinations (Bishop *et al*. 1969).

More detailed stratigraphic work is in progress, but for the moment the currently established stratigraphic scheme is presented in Figure 3.

The Iriri Member has yielded a few primate fossils (one tooth from Napak XVIII and several from NAP XXX and XXXI which are considered to belong to this member because the palaeosols from which they came are red). The Napak Member (black palaeosols) has yielded the bulk of fossil primates, whereas the Akisim Member has yielded a few primates at NAP XXXII associated with proboscideans, chalicotheres, rhinocerotids, ruminants, hyracoids and rodents which indicate a Miocene correlation (Fig. 4).

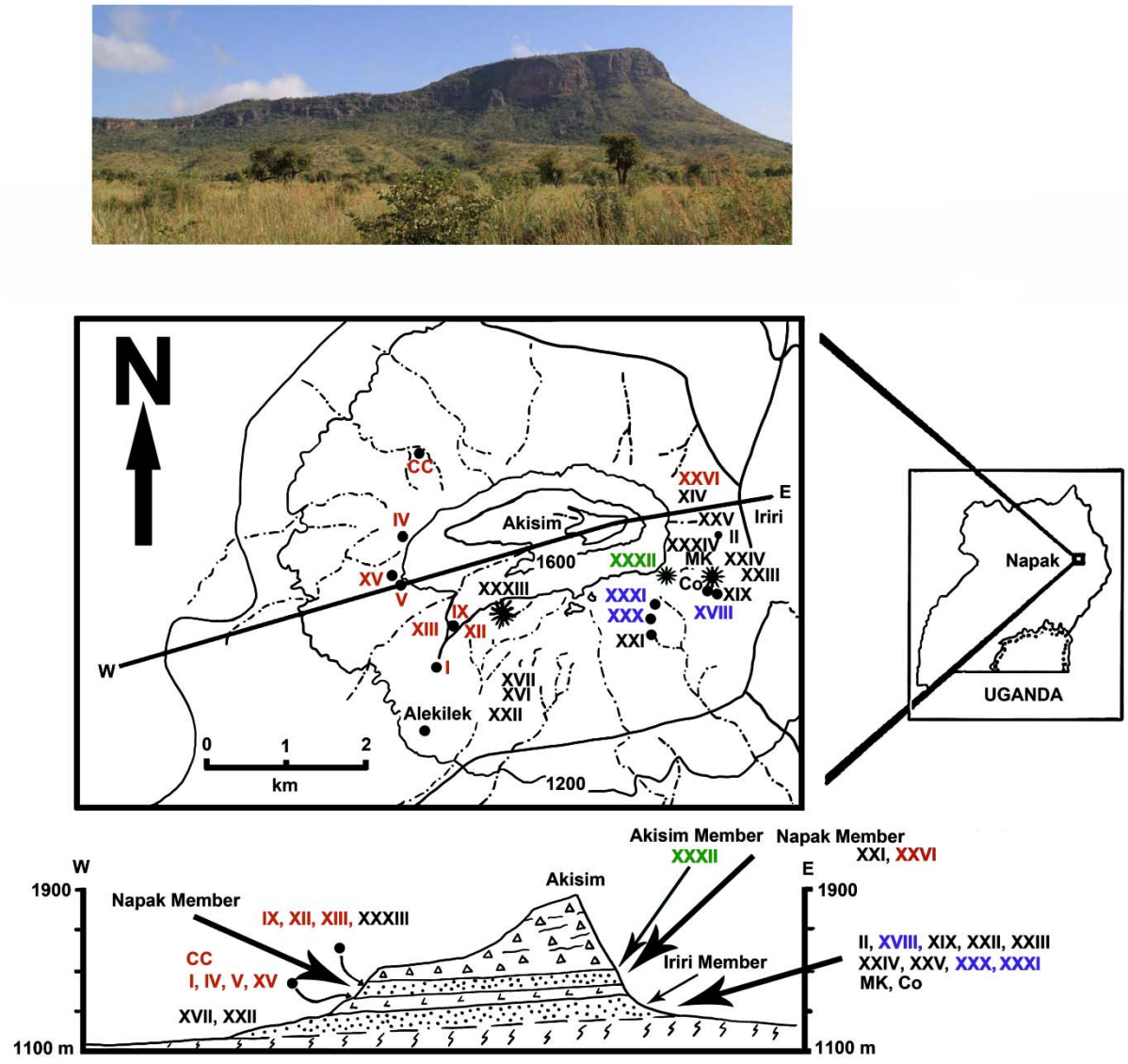

Figure 3. Geological sketch map and stratigraphy of the Akisim remnant of Napak Volcano. In blue are localities in the Iriri Member that have yielded specimens of *Ugandapithecus*, in red are localities in the Napak Member, while in green is the locality in the Akisim Member that yielded specimens attributed to cf *Afropithecus*.

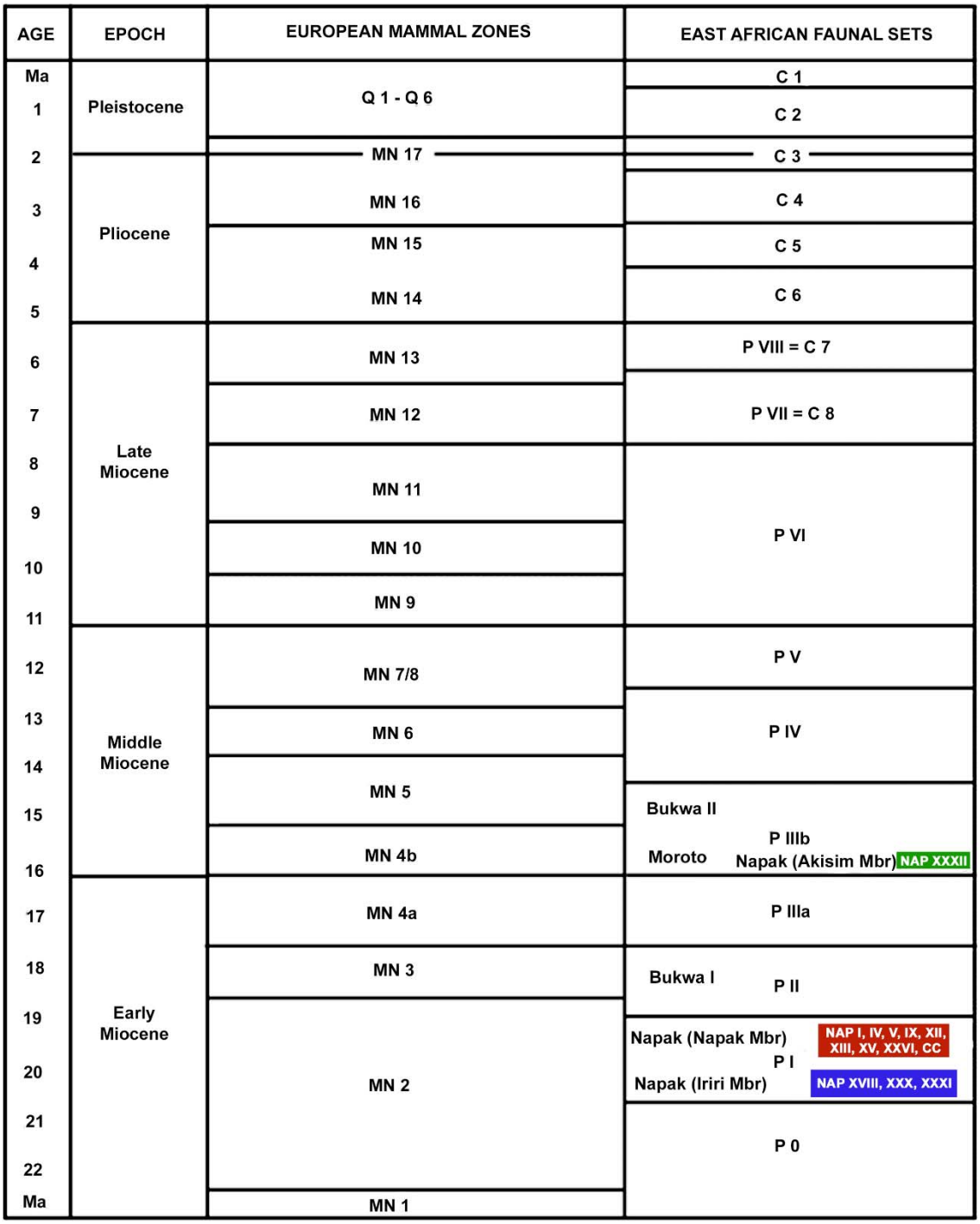

Figure 4. Biochronology of African fossiliferous localities, with the positions of the Napak succession highlighted (Discrete fossiliferous localities are underlined in blue, red and green).

Table 1. Localisation of Fossiliferous Sites at the Akisim Remnant of Napak Volcano

NAP I : 02°06'10.7''N : 34°11'30.8''E
NAP IV : 02°07'03.5''N : 34°11'17.1''E
NAP V : 02°06'43.4''N : 34°11'15.6''E
NAP IX : 02°06'24.0''N : 34°11'37.1''E
NAP XII : 02°06'17.2''N : 34°11'37.0''E
NAP XIII : 02°06'21.2''N : 34°11'32.2''E
NAP XV : 02°06'47.6''N : 34°11'12.6''E
NAP XVIII : 02°06'25.3''N : 34°13'14.3''E
NAP XXVI : 02°07'09.5''N : 34°13'03.8''E
NAP XXX : 02°06'24.1''N : 34°12'49.8''E
NAP XXXI : 02°06'28.5''N : 34°12'53.9''E
NAP XXXII : 02°06'48.6''N : 34°12'51.8''E
NAP CC : 02°07'32.1''N : 34°11'25.3''E

ABBREVIATIONS

BLB – Bucco-lingual breadth
KNM - Kenya National Museum, Nairobi
NHMUK - Natural History Museum of the United Kingdom, London
MDL - Mesio-distal length
NAP - Napak, Uganda
UM - Uganda Museum, Kampala
UPE - Uganda Palaeontology Expedition

MATERIALS AND METHODS

Fossils from Napak collected by the Uganda Palaeontology Expedition are catalogued on the day of collection with the locality abbreviation **NAP** followed by the site number, the catalogue entry and the year of collection. Thus **NAP V 4'12** signifies that the specimen was collected at Napak V in 2012 and is the fourth entry in the catalogue for that site and that year.

All specimens collected by the UPE are curated at the Uganda Museum, Kampala.

Most of the images were captured with a Sony Cybershot camera and treated with Photoshop Elements15 to enhance contrast and remove unwanted background. Scales were added manually. Measurements were made with sliding calipers to the nearest tenth of a mm (Tables 2-4).

Specimens that required extraction from the matrix were cleaned using a micrograveur followed by a brief bath in 7% formic acid buffered by calcium triphosphate (less than a minute to remove dust and thin layers of calcite adhering to the fossils). In the field, 6% vinegar served well for cleaning fossils with a thin layer of sediment or calcite adhering to them.

The meristic position of isolated molars can be tricky to determine. In order to avoid skewing the statistical analyses, isolated first and second molars were pooled rather than attributing them to position on the basis of their dimensions. The meristic positions of teeth in jaws are more readily determined and are kept as such. The lower m/3 is easier to distinguish from the m/1 and m/2 because it has an enlarged hypoconulid and a single distal root, and the M3/ is also more readily distinguished from the other upper molars on account of the smaller metacone that it usually possesses compared to that in the other upper molars, but the metacone on the M2/ can also be somewhat reduced.

The focus of this paper is on the specimens collected during the past decade, images of other specimens being available in Pickford *et al*. (2009).

DENTAL NOMENCLATURE

In this paper we employ the same nomenclature for cusps and crests of the teeth as that defined in Pickford *et al*. (2010) (Figs 5-7). For incisors and canines we use 'labial' for the outer surface of the teeth near the lips, 'lingual' for the inner surface close to the tongue, 'mesial' for the side of the tooth facing towards the anterior part of the sagittal plane, and 'distal' for the side facing towards the posterior part of the same plane. For the premolars and molars we employ 'buccal' for the sides of the teeth close

to the cheeks, 'lingual' for the sides close to the tongue, 'mesial' for the anterior end of the tooth, and 'distal' for the posterior end. One of the reasons for defining the orientations as such, is that for the incisors, the words 'anterior' and 'posterior' will signify the labial and lingual sides of the teeth, whereas for the premolars and molars, the same words will signify mesial and distal, thereby causing confusion - which exists in the literature. Measurements are mesio-distal length (**mdl**) and bucco-lingual breadth (**blb**) (also for the incisors in order to avoid too many abbreviations in Tables 2-4).

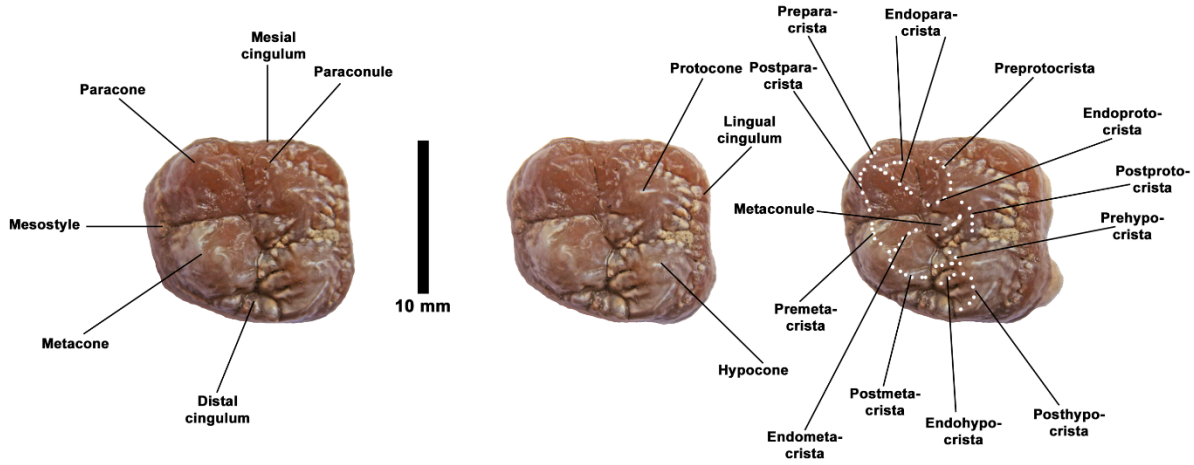

Figure 5. Nomenclature of the upper molars (NAP V 80'10, right M3/) (scale : 10 mm).

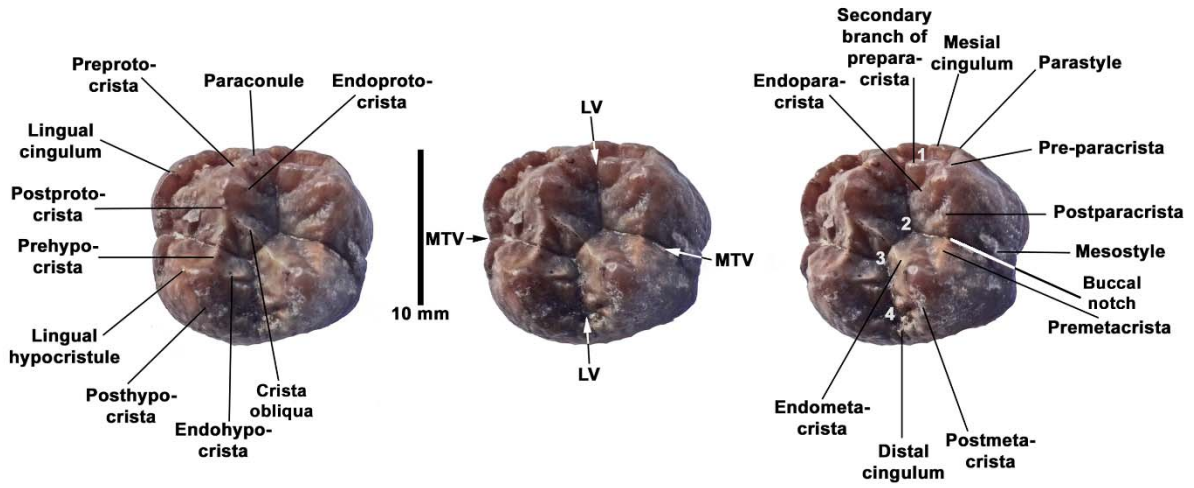

Figure 6. Nomenclature of crests, basins and valleys in an unworn upper molar (NAP XV 24'18, left M2/) of *Ugandapithecus major*. LV - longitudinal valley; MTV - median transverse valley; 1 - mesial fovea, 2 - trigon basin, 3 - talon basin, 4 - distal fovea (scale : 10 mm).

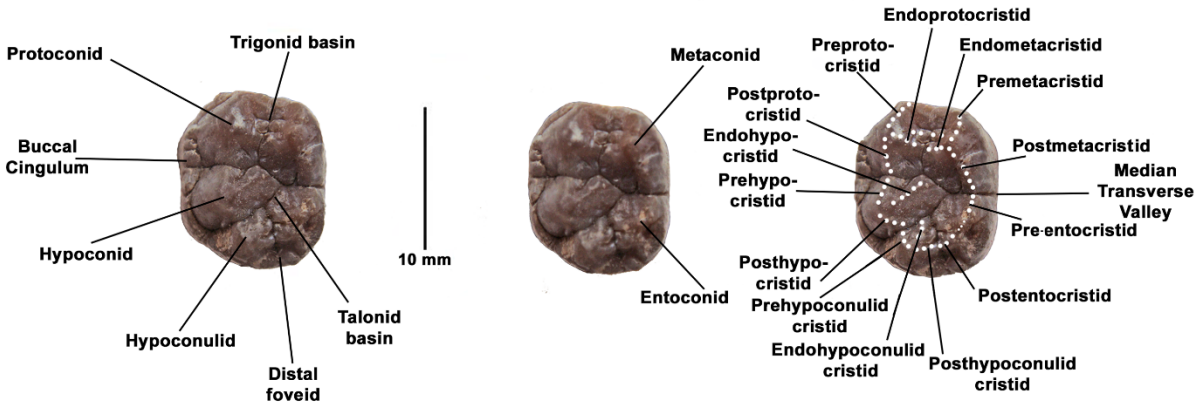

Figure 7. Nomenclature of the lower molars (NAP XIII 1'10, left m/1) (scale : 10 mm).

ORGANISATION OF DATA AND ASPECTS OF TAPHONOMY

In this paper, the fossils are described locality by locality. The main reason for this decision is that several isolated teeth and jaw fragments have been found to comprise single individuals. For example, NAP V yielded a set up right upper teeth which evidently belong to a single individual on the basis of the interstitial facets between the teeth (Fig. 8). The first tooth (a canine UMP 61.02) was found in 1961, the P3/ (NAP V 220'09) was collected in 2009, the P4/ (UMP 69.01) was found in 1969, the M1/ (NAP V 1'03) was collected in 2003, the M2/ (NAP V 5'09) was found in 2009 and the M3/ (NAP V 80'10) in 2010. The dispersal of the teeth seems to have been the result of recent bioturbation in the soils that have formed on the early Miocene tuffs. Plant roots and fungi loosen the matrix around fossils, and rodents and bush pigs burrow in the soils and disturb any fossils that occur therein. As the soils erode the diverse pieces of fossil can become dispersed downslope.

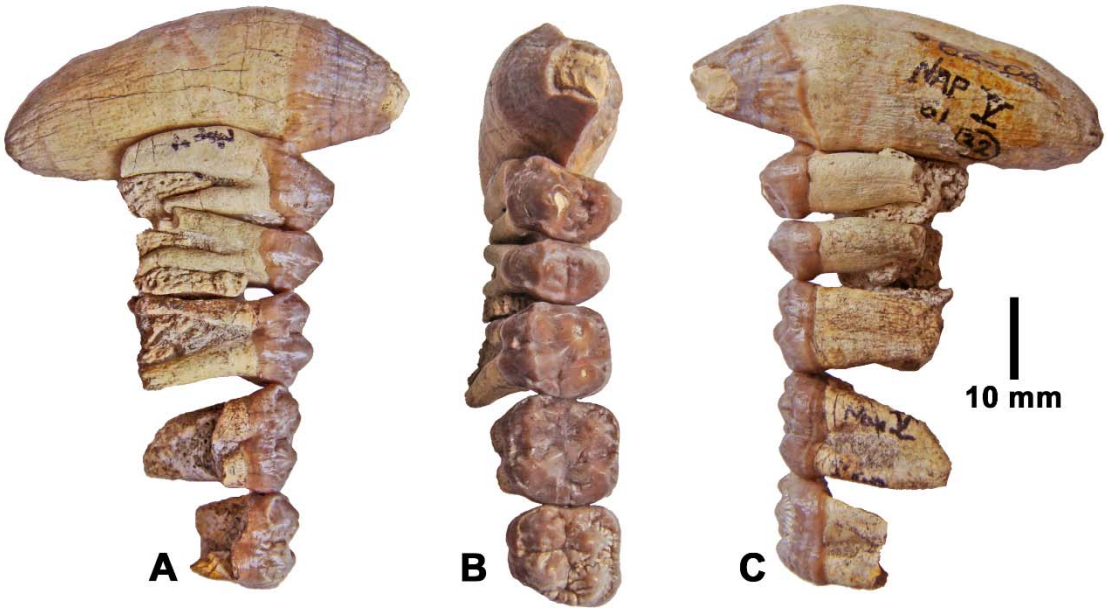

Figure 8. Reassembled right upper tooth row of *Ugandapithecus major* from NAP V, Uganda. A) buccal view, B) occlusal view, C) lingual view (scale : 10 mm).

Metrically, the reassembled tooth row from Napak V is larger than specimens of *Ugandapithecus legetetensis* in all dimensions except the breadth of M2/. It is likely to represent a female individual of *Ugandapithecus major* on the basis of its dimensions, which agrees with the morphology of the canine.

A second example is provided by an infant mandible with mixed dentition from Napak V. This specimen was found weathering out of the pedogenised tuffs at the site, the di/2 (NAP V 10'16) being found several months before the rest of the jaw (NAP V 57'16) (Fig. 9). Some isolated teeth probably from the same individual were found in the recent soils that had formed on the tuffs. The state of the specimen is extremely fragile, and it would certainly have broken into several pieces had it been allowed to weather out naturally. Interestingly, the same few square metres of deposit yielded several juvenile teeth from the upper jaw, and it is inferred that they could represent the same individual.

A series of teeth from NAP XXXI are also likely to belong to a single individual.

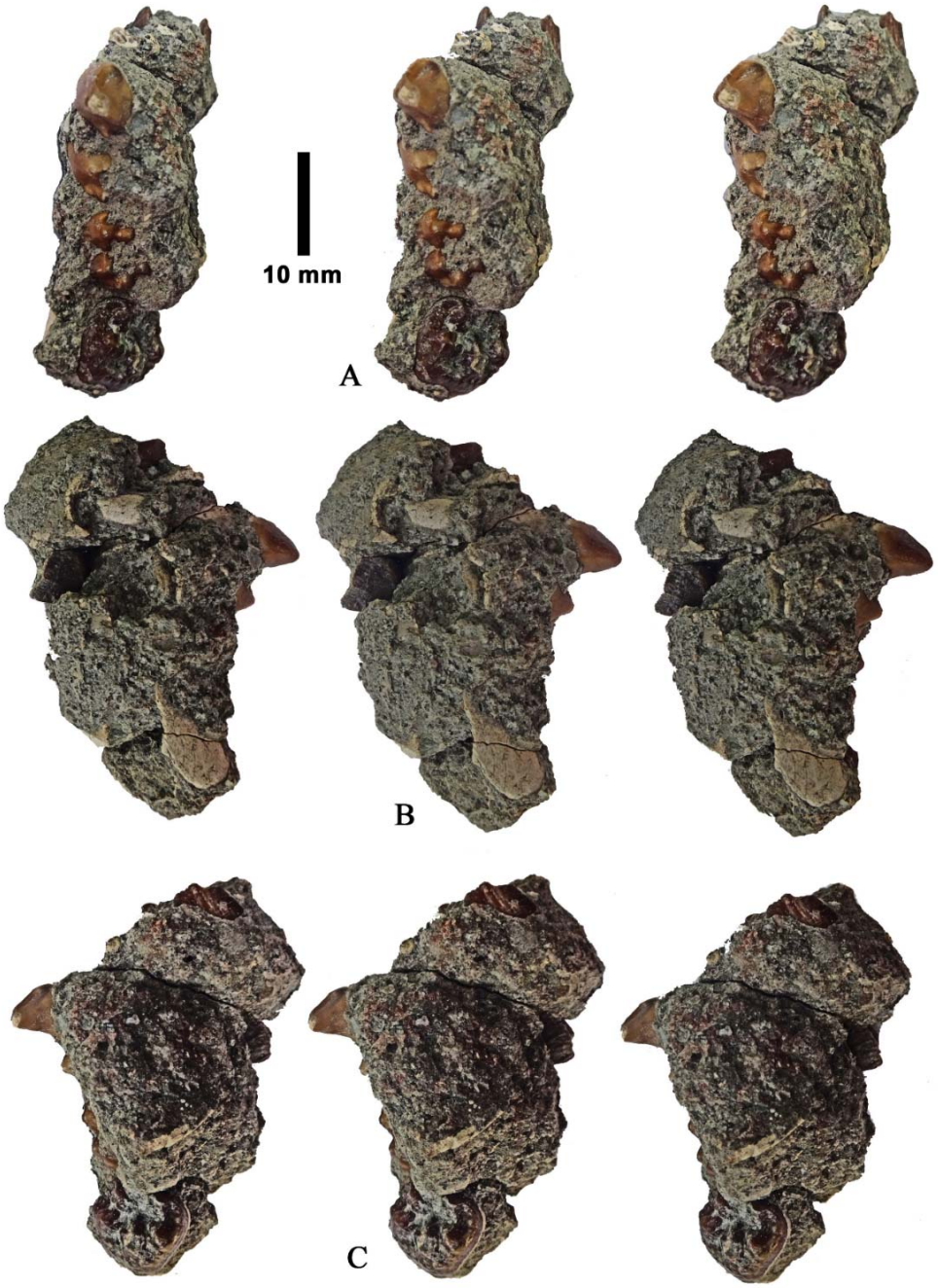

Figure 9. NAP V 57'16, infant left mandible of *Ugandapithecus major* as found in pedogenised tuffs already breaking up into several fragments A) stereo occlusal views, B) stereo buccal views, C) stereo lingual views showing the right i/2 and left m/1 in their crypts) (scale : 10 mm).

DESCRIPTIONS

Napak IV

During the past decade, four isolated teeth of *Ugandapithecus* have been found at Napak IV. This contrasts with the wealth of small-bodied ape specimens that occur there (77 teeth as of 2020).

<u>Upper dentition</u>

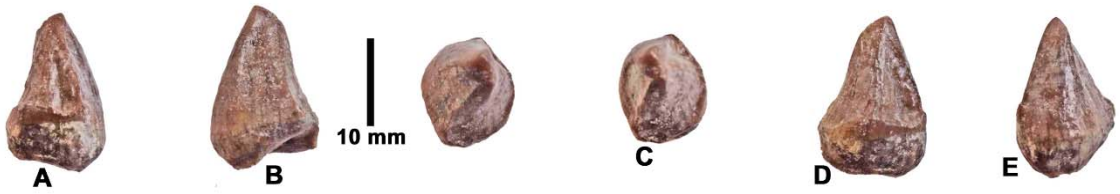

Figure 10. NAP IV 60'14, right upper canine of *Ugandapithecus* from Napak IV, Uganda. A) mesial view, B) disto-labial view to show the broad but shallow concavity that extends beneath the burin-like apex to the cervix, C) stereo occlusal view, D) mesio-lingual view, E) labial view (scale : 10 mm).

NAP IV 60'14 is an unworn canine lacking the root (gnawed off by rodents) (Fig. 10). The crown is conical with a distinct mesial groove which fades out apically, a shallow lingual concavity or depression and a low lingual cingulum. The apex is burin-like. There is a cingulum on the mesial and lingual sides. On the labial side, the height of the crown is 15.3 mm. On the basis of its shape and dimensions this tooth is interpreted to belong to a male individual of *Ugandapithecus legetetensis*.

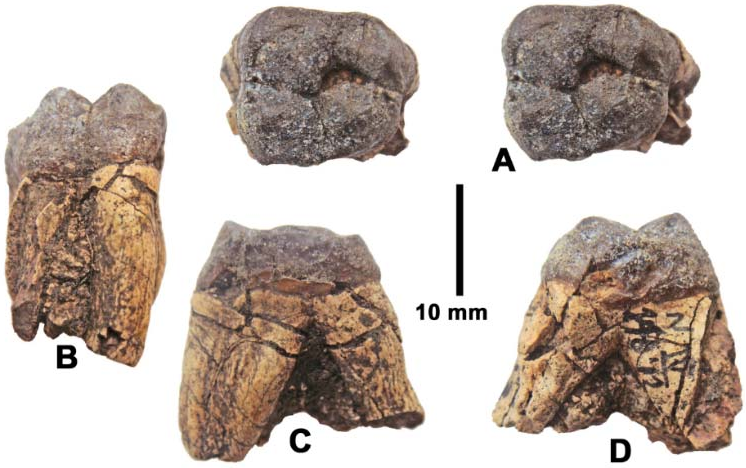

Figure 11. NAP IV 146'12, left upper molar of *Ugandapithecus* from Napak IV, Uganda. A) stereo occlusal view, B) buccal view, C) mesial view, D) distal view (scale : 10 mm).

NAP IV 146'12 is a moderately worn left upper molar complete with roots (Fig. 11). The occlusal surface is missing enamel between the paracone and metacone, the surface of which suggests that the damage represents a caries lesion, and there is similar damage distally where there was contact with the succeeding tooth, which also seems to have been affected by caries. The protocone is slightly smaller than the hypocone but is as big as the metacone, the paracone being the smallest of the main cusps. On the buccal aspect of the crown, there is a fold of enamel descending from the paracone towards a small tubercle of cingular origin. There is a low parastyle at the mesial end of the preparacrista which sends a narrow cingular fold onto the mesio-buccal edge of the tooth. The mesial cingulum is well-developed and extends lingually onto the base of the protocone but fades out along the mesial side of the hypocone. Occlusal wear has advanced to the stage where it is difficult to discern the detailed morphology of the crests and styles, but overall the tooth resembles those of other large ape specimens from Napak.

Lower dentition

Figure 12. Stereo occlusal views of NAP IV 70'16, germ of left lower molar of *Ugandapithecus* from Napak IV, Uganda (scale : 10 mm).

The lower molar germ from Napak IV (NAP IV 70'16) reveals many details of the occlusal surface (Fig. 12). There are five main cusps, protoconid and hypoconid buccally, metaconid and entoconid lingually and a small hypoconulid distally, close to the hypoconid. The metaconid has a distal cristid that is separated from it at the apex by a broad groove mainly on the buccal side of the cusp but extending onto the lingual part near the apex of the cusp. The premetacristid extends towards the mesial cingulid which is thick and forms a wall to the trigonid basin. The endometacristid reaches buccally towards the endoprotocristid to close off the rear of the trigonid basin. The hypoconid is the largest cusp, but its apex (and that of the hypoconulid) was not completely formed at the time of death. Nevertheless, it shows a prominent prehypocristid reaching towards the postprotocristid, thereby blocking off the buccal end of the median transverse valley. Outside this ridge, the buccal end of the median transverse valley is the site of a cingular remnant. The entoconid is well-separated from the hypoconid and hypoconulid by a deep slit. The enamel on the occlusal surface is coarsely wrinkled. The fact that the mesial lophid is somewhat narrower than the distal one suggests that this tooth is an m/1 rather than an m/2.

Figure 13. NAP IV 56'14, heavily worn left m/1 of *Ugandapithecus* from Napak IV, Uganda. A) buccal view, B) stereo occlusal view (scale : 10 mm).

Napak IV yielded a deeply worn left m/1 (NAP IV 56'14) of *Ugandapithecus* (Fig. 13). Not much can be said about the occlusal morphology except that it comprises two basins from which almost all the enamel has been worn away. The trigonid basin mesially is smaller than the talonid basin distally. The trigonid and talonid basins are completely worn away. The roots are tall and massive.

Napak V

Since 2010, a total of 32 of large ape teeth have been collected at Napak V, several of them in a mandible of an infant.

Upper dentition

Figure 14. NAP V 56'11 left dI1/ of *Ugandapithecus* from Napak V, Uganda. A) stereo lingual view, B) apical view, C) buccal view (scale : 10 mm).

NAP V 56'11 is a heavily worn deciduous upper central incisor (Fig. 14). The apex is worn flat, but lingually the basal cingulum is still evident as are short parts of the mesial and distal lingual ridges. The enamel is thin.

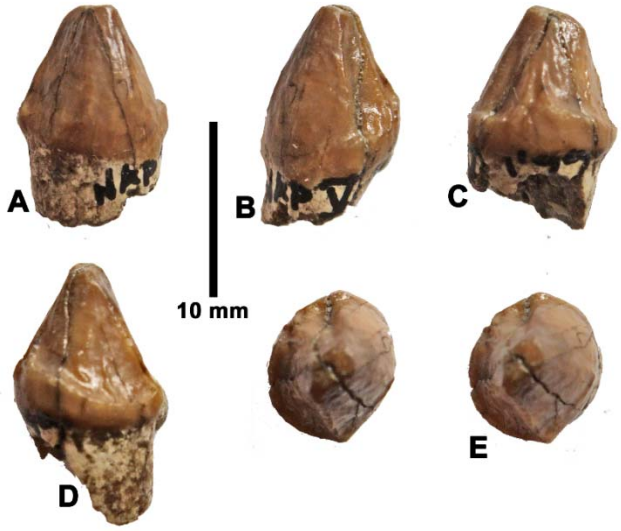

Figure 15. NAP V 1'99, left dC1/ of *Ugandapithecus* from Napak V, Uganda. A) labial view, B) mesial view, C) distal view, D) lingual view, E) stereo occlusal view (scale : 10 mm).

The deciduous upper canine (NAP V 1'99) is a conical tooth with a mesial groove, a low lingual cingulum and a distal crest (Fig. 15). The apex is lightly worn. The labial surface is convex, the lingual side concavo-convex, forming a shallow lingual depression. The mesial groove is weak apically, but broadens and deepens as it approaches the cervix. The distal crest ends cervically at a small style (distal tubercle) which overhangs the root, and it makes a clear demarcation between the labial and lingual surfaces of the crown.

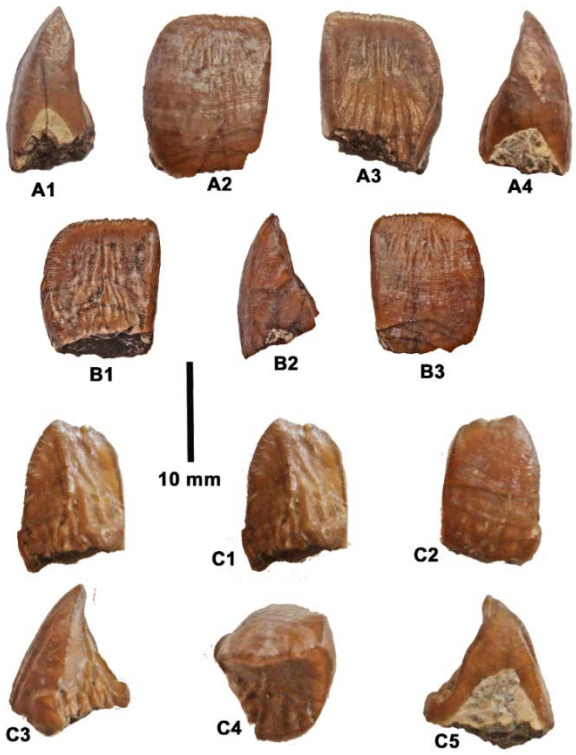

Figure 16. Germs of upper incisors of *Ugandapithecus* from Napak V, Uganda. A) NAP V 7'11, left I1/ (A1 - mesial view, A2 - labial view, A3 - lingual view, A4 - distal view) B) NAP V 131'12, right I1/ (B1 - lingual view, B2 - distal view, B3 - labial view) C) NAP V 140'08, right I2/ (C1 - stereo lingual view, C2 - labial view, C3 - distal view, C4 - occlusal view, C5 - mesial view) (scale : 10 mm).

Two upper central incisors and a lateral upper incisor likely belong to a single individual (Fig. 16A, 16B). The germ of the I1/ is spatulate in lingual view, with a relatively straight mesial edge, and a convex distal edge. The apical edge is straight and is oriented at right angles to the mesial edge but curves slightly as it approaches the distal edge of the crown. The lingual surface is concave with numerous wrinkles oriented more or less vertically diverging towards cervix as they approach the basal swelling. The mesial edge of the lingual side comprises a vertical blunt crest and the distal crest is also blunt but curved. In mesial and distal views the cervix rises a short distance towards the apex. The roots of these upper central incisors had not yet formed, indeed the basal part of the crown is incomplete on the lingual side, so it is not possible to determine whether there was a basal lingual cingulum. There are several hypoplastic lines in these teeth and perikymata are clearly visible (Kelley & Smith, 2003).

The I2/ is also a germ with no root (Fig. 16C). In lingual view it is trapezoidal in outline, narrower at the apex than at the cervix. The apex has a shallow notch to the mesial side of the central ridge which runs vertically from apex to cervix, thereby separating the lingual side into two unequal halves. The mesial depression is shallow, the distal one scoop-shaped. The enamel is coarsely wrinkled on the lingual surface but smooth labially. There is a small cingulum on the lingual side close to the mesial edge, fading out distally. On the labial side of the crown there is mesial crest (precrista) delimiting the otherwise gently convex surface and basally there is a low distal tubercle. The cervix rises about half the height of the tooth on the mesial side, but is not yet formed on the distal edge.

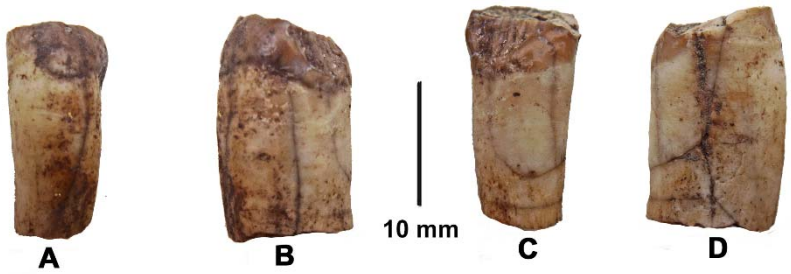

Figure 17. NAP V 3'10, right I2/ lacking the crown apex of *Ugandapithecus* from Napak V, Uganda A) labial view, B) distal view, C) lingual view, D) mesial view (scale : 10 mm).

An upper second incisor from Napak V (NAP V 3'10) is missing its apex, but basally it shows some morphology (Fig. 17). The enamel in the floor of the lingual basin is coarsely wrinkled and there is a low lingual cingulum which descends slightly distally. The preserved part of the root is stout and ovoid in section. This tooth has an interstitial contact facet where it rubbed against the upper canine, indicating that there was no diastema between the incisors and the canine in this individual (perhaps a female).

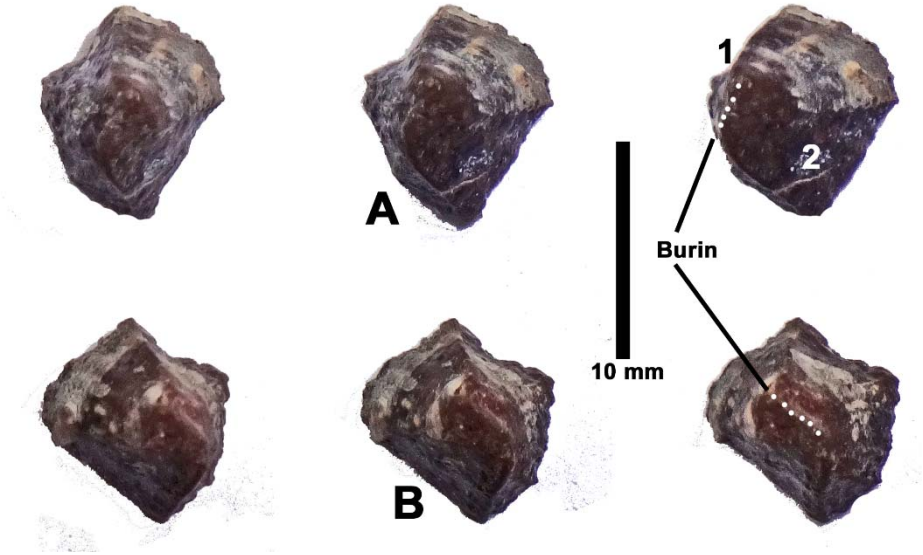

Figure 18. Stereo apical views of NAP V 57'16, upper canine germs of *Ugandapithecus majo*r from Napak V, Uganda. A) left C1/, B) right C1/. The burin-like apex is shown as a dotted line. 1 - mesial groove, 2 - disto-buccal concavity (scale : 10 mm).

Associated in the matrix surrounding an infant mandible from Napak V, there were apices of two upper canines, probably from the same individual (Fig. 18). They show a well-developed burin-like apex, from which four cristae descend towards the cervix, two delimiting the mesial groove, the other two forming the margins of the disto-buccal concavity of the crown.

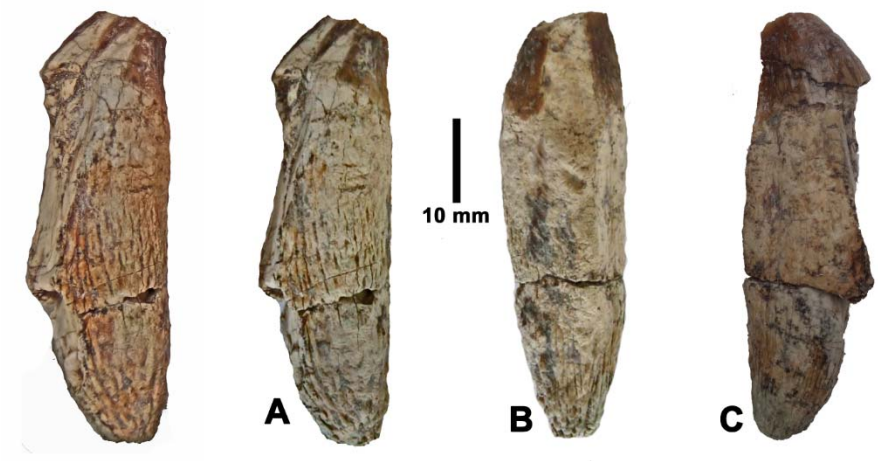

Figure 19. NAP V 10'19, left upper canine of *Ugandapithecus* from Napak V, Uganda. A) slightly oblique stereo mesial view, B) distal view, C) labial view (scale : 10 mm).

A large upper canine from Napak V (NAP V 10'19) has the apex broken off, but the base of the crown and the root are almost complete (Fig. 19). There are two prominent wear facets on this tooth, a large one mesially interrupted by the mesial groove (due to contact with the lower canine) and another distally due to abrasion against the p/3. The latter wear facet extends onto the root. Damage to the mesial side of the tooth prevents assessment of the extent of the mesial wear facet, but it seems likely that it extended onto the root. The root itself is massive and apically it is scored by numerous vertical folds and ridges.

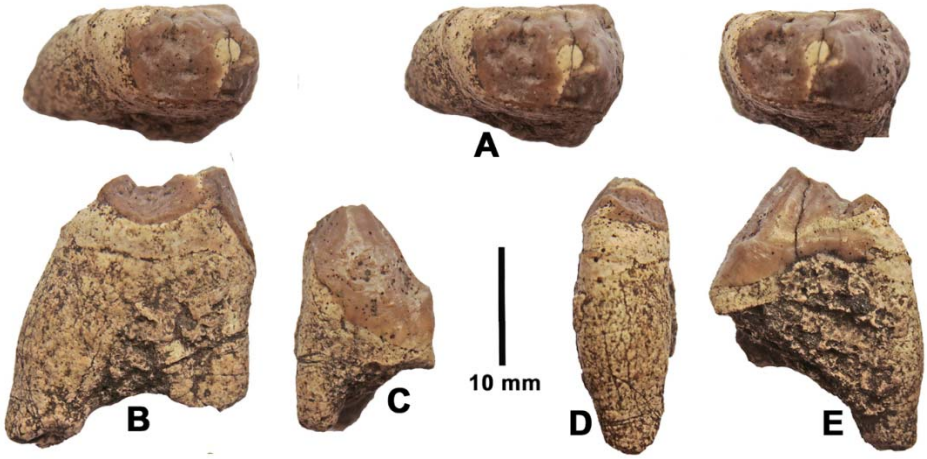

Figure 20. NAP V 54'11, left P3/ of *Ugandapithecus* from Napak V, Uganda. A) stereo occlusal views, B) distal view, C) buccal view, D) lingual view, E) mesial view (scale : 10 mm).

Some enamel has spalled away from the lingual and distal sides of the crown of the left P3/ (NAP V 54'11) but enough is left to reveal some of the occlusal morphology (Fig. 20). Wear at the apex of the paracone exposes a small dentine lake. The paracone is mesio-distally longer than the protocone, and it has a prominent parastyle at the cervical end of the steep preparacrista. The protocone is lower than the paracone, and has pre- and post-cristae that reach the mesial and distal cingula respectively (damaged distally) thereby closing off two foveae. In buccal view, the parastyle extends much further rootwards than the mesostyle, forming an extensive sloping mesio-buccal surface. There are three roots, the mesio-buccal one broken off near cervix, the other two are robust, the disto-buccal one vertical, the lingual one slanting slightly lingually.

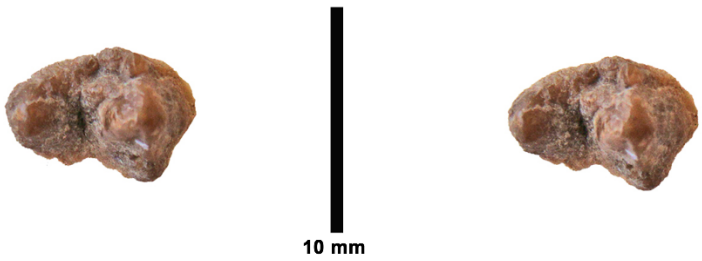

Figure 21. NAP V 30'12, incompletely formed germ of left P4/ of *Ugandapithecus* from Napak V, Uganda (stereo occlusal view) (scale : 10 mm).

As preserved the P4/ germ from Napak V (NAP V 30'12) measures 6.2 x 8.5 mm (mdl x blb) but the tooth would surely have been bigger when completely formed (Fig. 21). The paracone is larger than the protocone and there is a mesial cingular complex enclosing a mesial fovea. The preparacrista ends at a tall parastyle. The mesostyle is lower than the parastyle but is clearly visible in buccal view. The distal fovea is large, but its distal margin has not yet formed.

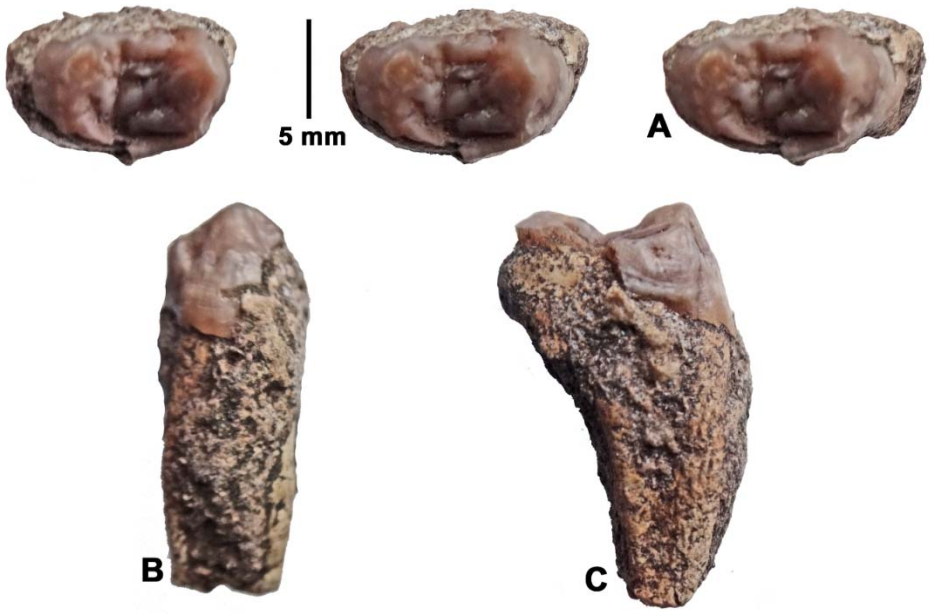

Figure 22. NAP V 134'12, left P4/ of *Ugandapithecus* from Napak V, Uganda. A) stereo occlusal views, B) buccal view, C) distal view (scale : 5 mm).

There is a reasonably well-preserved, lightly worn left P4/ (NAP V 134'12) of *Ugandapithecus* from Napak V (Fig. 22). Some enamel is missing mesially and from the lingual surface of the protocone. The crown is mesio-distally compressed, the occlusal outline being oval. The paracone has prominent parastyle (the base of which is missing) and mesostyle. On its lingual surface the paracone shows four low crests of enamel (more like wrinkles than crests) which descend lingually into the central basin, the mesial one coalescing with the mesial cingulum, the distal one distinct from the distal cingulum. The protocone is slightly angled such that its apex is mesially positioned almost above the mesial cingulum. The postprotocrista curves disto-buccally to blend into the distal cingulum. The two buccal roots are close to each other.

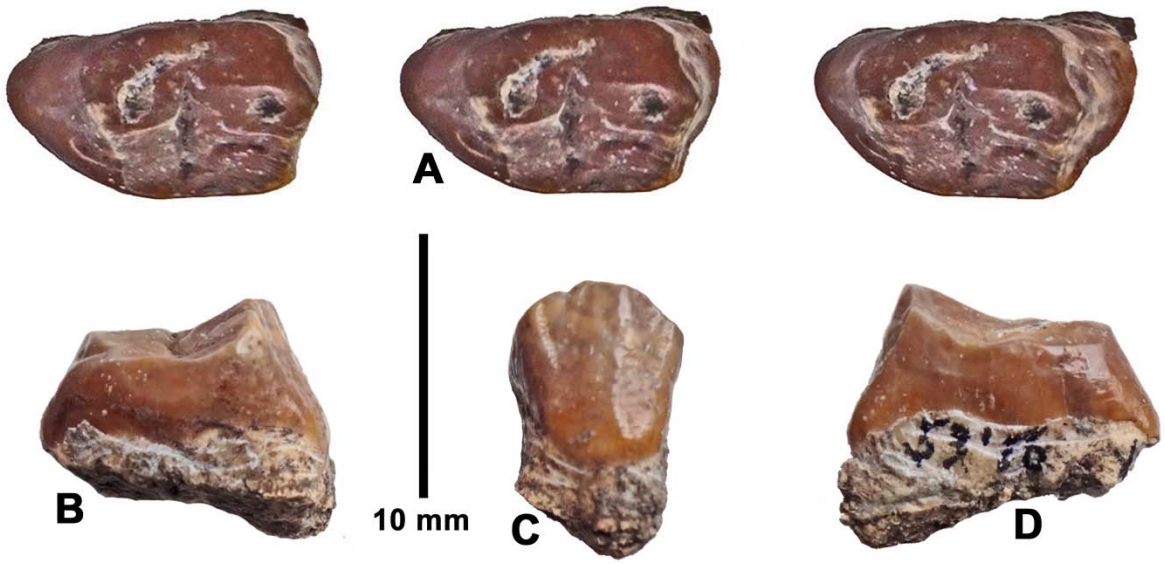

Figure 23. NAP V 53'16, left P4/ of *Ugandapithecus* from Napak V, Uganda. A) stereo occlusal views, B) distal view, C) buccal view, D) mesial view (scale : 10 mm).

A moderately worn left P4/ (NAP V 53'16) from Napak V is mesio-distally compressed (Fig. 23). It has two main cusps, a small mesial fovea and a larger distal basin. The paracone has a parastyle mesially and a mesostyle distally but they fade out towards the cervix. The protocone has a cingular structure on its disto-lingual corner. The mesial cingulum walls off the anterior part of the mesial fovea, and distally there is a low cingulum (deeply worn) closing off the distal basin. The longitudinal valley is interrupted by the endoparacrista reaching across towards the mesial base of the protocone. The preprotocrista extends mesio-buccally towards the centre-line of the crown where it blends into the mesial cingulum.

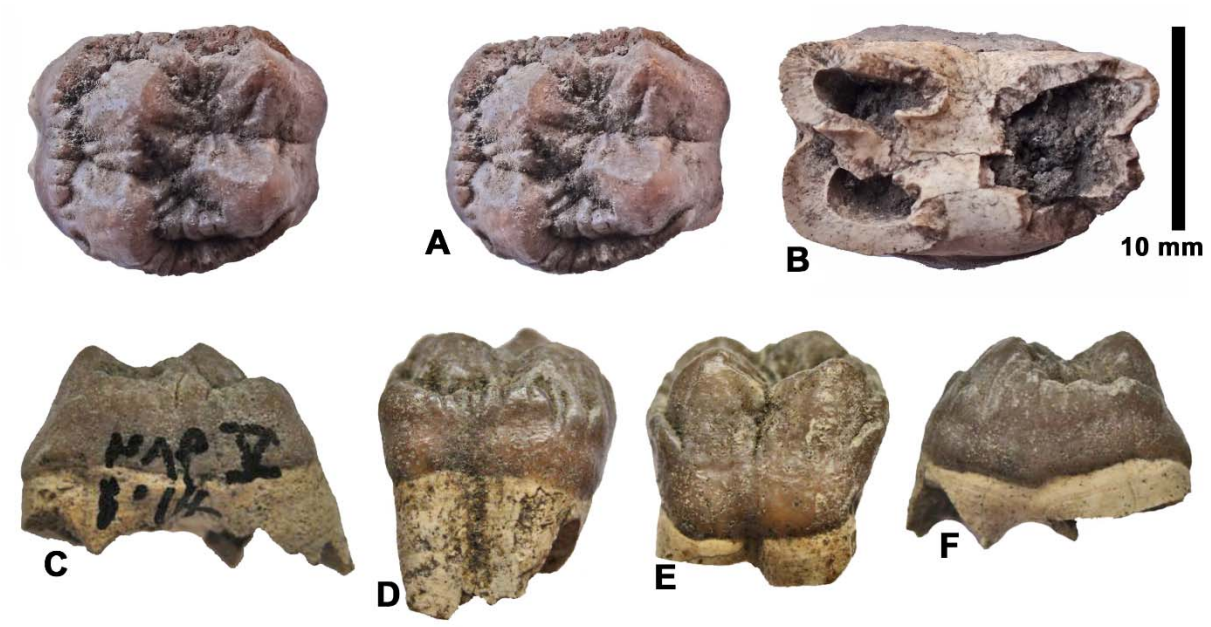

Figure 24. NAP V 1'14, unworn left upper molar of *Ugandapithecus* from Napak V, Uganda. A) stereo occlusal view, B) radicular view, C) mesial view, D) lingual view, E) buccal view, F) distal view (scale : 10 mm).

NAP V 1'14 is a fully formed but unworn left upper molar (Fig. 24). The protocone is the largest cusp, followed by the hypocone, the metacone and then the paracone. There is a prominent mesial cingulum which terminates buccally in a low but sharp parastyle. The mesial cingulum continues uninterrupted onto the lingual side of the protocone and it extends distally as far as the disto-lingual corner of the hypocone where it fades out. Lingually the cingulum is beaded. There is a small paraconule at the mesial end of the preprotocrista which is distinct from the mesial cingulum. There is a low crest linking it to the paracone. The preparacrista descends steeply mesially towards the parastyle. The postprotocrista leads distally towards the prehypocrista. On the way, a distinct crista obliqua branches off from the postprotocrista, reaching disto-bucally to meet the endometacrista, from which it is separated by a shallow slit. There is a low rounded, beaded crest on the middle of the protocone (endoprotocrista) that descends buccally into the trigon basin. The paracone has a low postparacrista descending steeply into the median transverse valley opposite the premetacrista, forming a low sill at the buccal end of the median transverse valley. At the buccal end of the median transverse valley, there is a low interruption in the profile of the buccal surface, but not to the extent of producing a style or a cingulum. The paracone has an endoparacrista that descends disto-lingually into the floor of the trigon basin. The metacone has a weak premetacrista, a stronger endometacrista leading towards the crista obliqua and a weak postmetacrista which forms a beaded ridge joining it to the middle of the hypocone. The hypocone has a subtle posthypocrista which descends distally a short way where it coalesces with the beaded distal cingulum which is broad lingually but narrows buccally, fading out at the disto-buccal corner of the metacone. The metacone also has a secondary endocrista which runs lingually to end opposite an endohypocrista, the two crests forming a low wall between the talon basin and the distal fovea.

The two buccal roots are missing but their bases are separated from each other, and lingually the roots beneath the protocone and hypocone have broken off, but what remains indicates that they were coalescent with a groove on the lingual aspect.

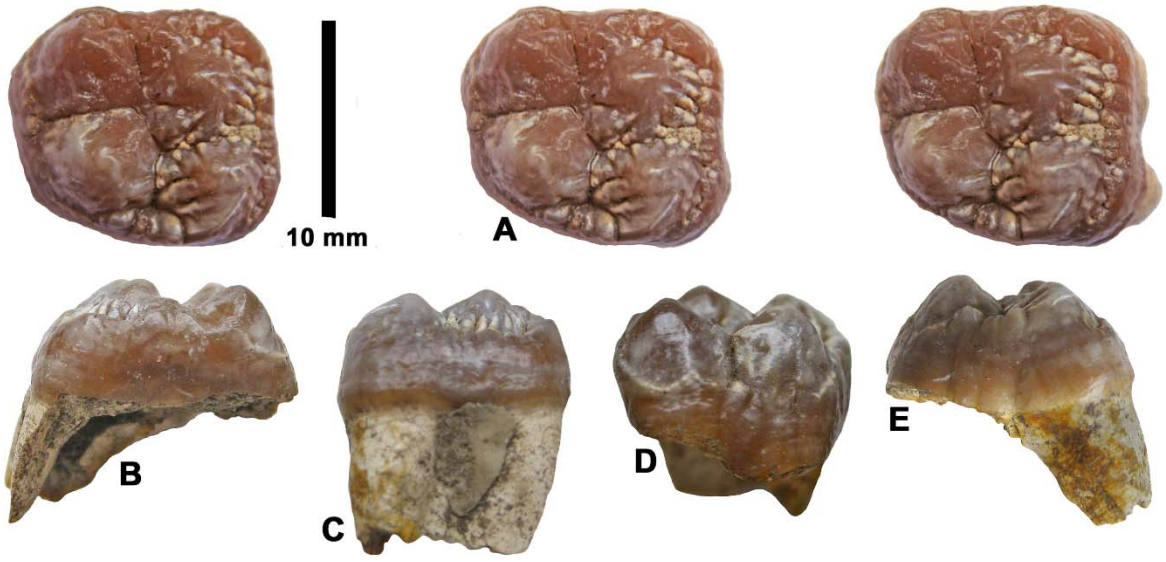

Figure 25. NAP V 80'10, right M3/ of *Ugandapithecus* from Napak V, Uganda. A) stereo occlusal views, B) mesial view, C) lingual view, D) buccal view, E) distal view (scale : 10 mm).

An unworn right M3/ (NAP V 80'10) shows the occlusal morphology clearly (Fig. 25). The interstitial wear facet caused by the tooth in front indicates that it probably belongs to the same individual as a tooth row already partly reassembled by Pickford *et al*. (2009, fig. 14 A, E, F). The buccal cusps have smooth enamel, whereas the two lingual cusps have coarsely wrinkled surfaces. The mesial and distal cingula are well-beaded.

The protocone is accompanied mesially by a distinct paraconule which is fused mesially with the cingulum and its crista obliqua swells to form a small cusplet (metaconule). The metacone is smaller than the paracone and hypocone which means that the occlusal outline is trapezoidal rather than rectangular or square. This indicates that the tooth is probably an M3/. Buccally there is a low cingular structure beneath the buccal end of the median transverse valley (mesostyle).

The postprotocrista swells at its disto-buccal end and has grooves mesially and distally that almost separate it from the protocone, forming a small cusplet like a metaconule that intervenes between the bases of the paracone and hypocone.

Lower dentition

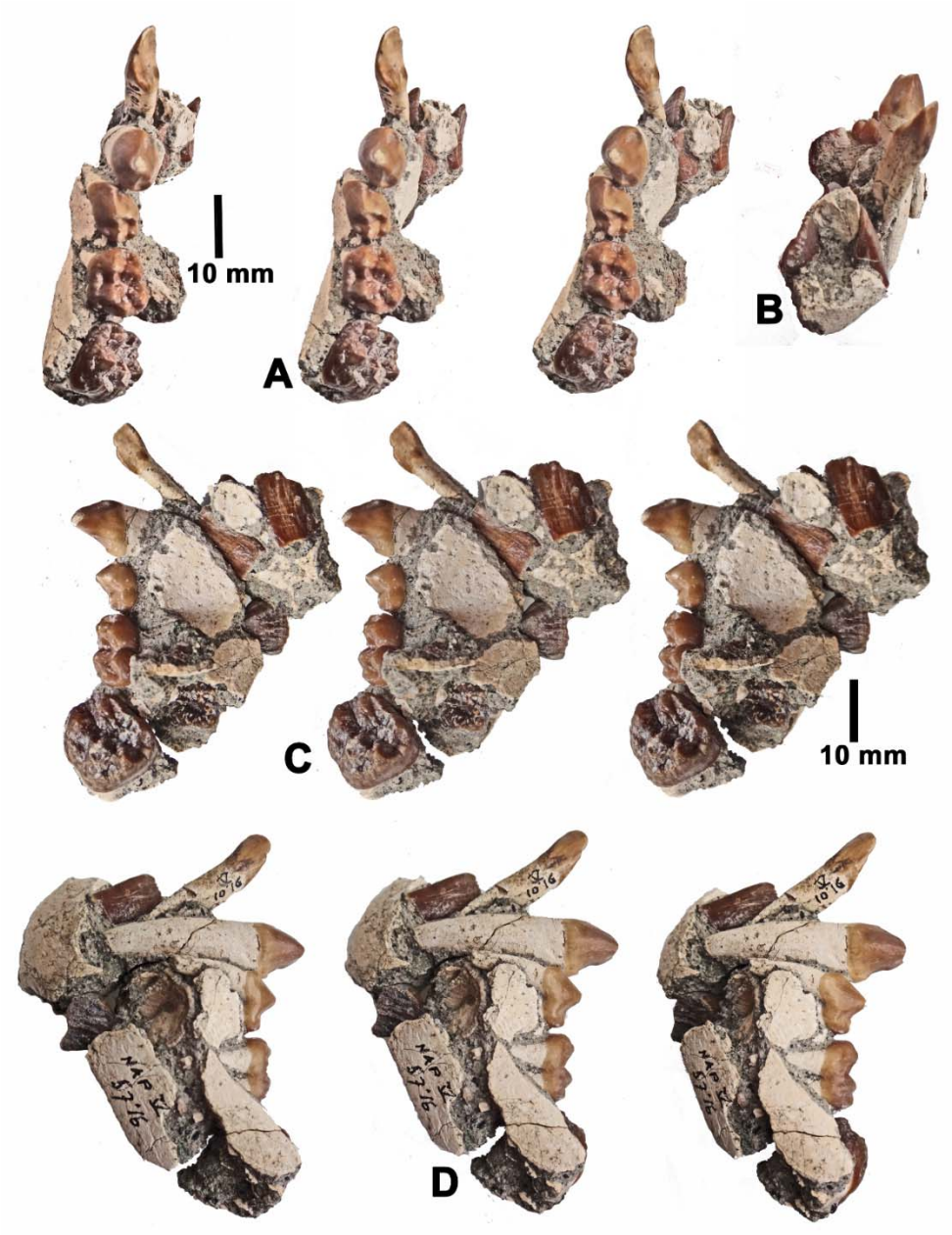

Figure 26. NAP V 57'16 + 10'16, infant left mandible of *Ugandapithecus* from Napak V, Uganda. A) stereo occlusal views, B) anterior view showing the left i/1 and right i/2, C) stereo lingual views, D) stereo buccal views, (scale : 10 mm).

The infant mandible from Napak V (NAP V 57'16 + 10'15) (Figs 26-28) contains the left di/2, the left deciduous canine and two deciduous molars (d/3 and d/4) fully erupted, the deciduous canine having a small wear facet apically. In crypto are some permanent teeth, the left central incisor, left and right i/2, the canine apex, the p/3, p/4 and m/1. In the matrix surrounding the mandible, there were two apices of upper canines at a similar stage of development as the lower canine in the mandible, indicating that parts of the upper jaws perhaps of the same individual, were preserved alongside the mandible. Two other teeth were found nearby with similar preservational features, a germ of a right i/1 (NAP V 9'16) and an incomplete lower molar (NAP V 134'17) which are described below.

The deciduous teeth are pale brown, the permanent teeth darker brown (incisors) or almost black (cheek teeth) a difference possibly related to the thickness of enamel. The jaw is somewhat crushed and the pieces are displaced from each other but the teeth are more or less in their natural positions, even if twisted out of alignment.

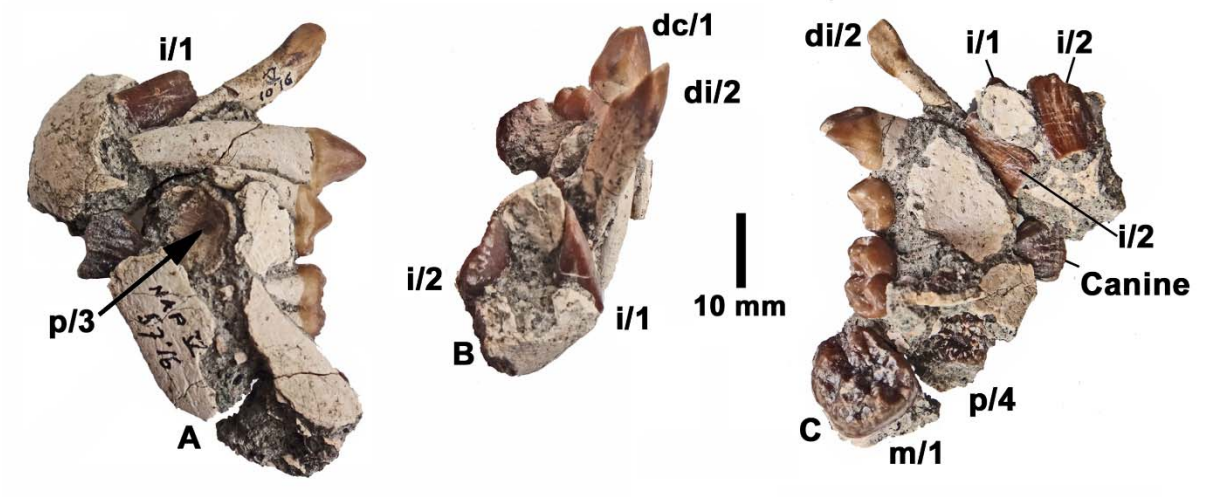

Figure 27. NAP V 57'16, infant left mandible of *Ugandapithecus*. Images with the teeth labelled. A) buccal view, B) anterior view, C) lingual view (scale : 10 mm).

The di/2 is like a small replica of a permanent second incisor. The root is slightly more than twice the height of the crown (crown height - 9 mm, root height - 18.7 mm). The root has a long groove on its mesial aspect. The apex of the crown is horizontal in the mesial half, but it slopes cervically distally slightly overhanging the root. There is a swelling near the lingual base of the crown which is separated from the distal marginal ridge by a shallow depression.

The deciduous canine has a slightly ovoid conical crown posed on a root that is 3.5 times taller than the crown. The precristid descends steeply from the apex towards the mesio-lingual end of the cervix, and has a shallow groove on its lingual side. Because of this the wear facet is not round, but has a re-entrant on its mesio-lingual side. The postcristid is rounded and descends steeply towards the disto-lingual part of the cervix. There is a lower postcristid to the buccal side of the main postcristid, and between these two cristids there is a shallow depression with a basal cingulum.

The d/3 is comprised of a large main cusp with three small cusplets distally, a large centrally positioned one, a small one lingually, and a very small one buccally. The precristid is prominent and is directed towards the mesio-lingual corner of the crown where it joins a small stylid-like cusplet (metaconid). There are three distal cristids, a large one directed disto-lingually where it forms a small stylid separated at its apex from the cristid, the central one oriented distally where it meets the largest of the three distal cusplets, and the third one which is the least developed of the three crests is directed disto-buccally. The three distal cusplets are well separated from each other, the central one being the larger of the three. As is usual in deciduous teeth, the mesial root is splayed anteriorly leaving room beneath the tooth for the developing permanent p/3 which can be seen in its crypt beneath the d/3.

The d/4 is constructed along the lines of a permanent lower molar, but the mesial lophid is appreciably narrower than the distal part of the crown. The five cuspids that comprise this tooth are the protoconid and metaconid mesially, the hypoconid and entoconid in the middle and the hypoconulid in a central position distally. The metaconid is located slighly distally with respect to the protoconid and the same applies to the entoconid with respect to the hypoconid. The mesial cingulum forms a sort of anterior shelf (mesial foveid or trigonid basin) between the mesial ends of the protoconid and metaconid. The distal cingulum is disposed lingually and buccally of the hypoconulid and there is a hint of the presence of a buccal cingulum at the end of the median transverse valley.

The left permanent central incisor is partly hidden under matrix, but what is visible shows that it is tall with an ovoid, almost rectangular section. The lingual surface has a low central ridge, the buccal surface is smooth. The apex is crenulated.

The left and right permanent second incisors are preserved, slightly distal to the first incisors. In lingual view, the crown is tall with a scoop-shaped distal margin. The central lingual ridge is tall and broad at the base narrowing apically.

Only the apex of the developing canine can be seen. It was incompletely formed at the time of death, corresponding to the upper third of the crown. As has been observed on several occasions, the apices of permanent canines of *Ugandapithecus* often break off due to the presence of a deep hypoplastic groove at this position. The timing of the formation of this groove is informative in that it correlates in time with the onset of weaning in the individual. In extant large primates this groove is informally termed the weaning line, and it signifies developmental disturbance of crown formation due to nutritional and emotional stresses that occur during this phase ontogeny. It is inferred that the Napak individual may have died as a result of such weaning stress.

The left p/3 is in its crypt directly beneath the d/3. The crown is hidden but the base can be measured.

Of the p/4 only the talonid basin and its surrounding cusps and cingulum can be observed. It looks like other p/4s from Napak.

Figure 28.Stereo occlusal views of left m/1, NAP V 57'16, *Ugandapithecus* (scale : 10 mm).

The crown of the m/1 is fully formed but there is no sign of root formation. It has shifted and twisted postmortem and now lies behind the d/4 at an unnatural angle The tooth is comprised of the usual five cusps, the narrow mesial lophid (large protoconid – smaller metaconid), the slightly broader middle lophid (hypoconid slightly larger than the entoconid) and a distally positioned hypoconulid slightly to the buccal side of the mid-line of the crown. Cristids from the entoconid and hypoconulid meet to form a mesial wall to the distal foveid, thereby separating it from the talonid basin. There is a suggestion of cingular structures at the buccal end of the median transverse valley and between the hypoconid and hypoconulid.

Finally, the two upper canine apices (NAP V 57'16) found in the same matrix as the mandible are described above with the other upper teeth from the locality (see above).

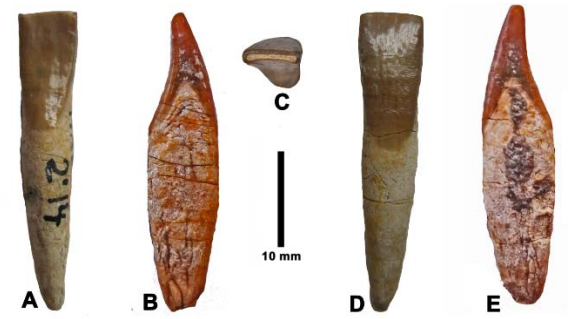

Figure 29. NAP V 2'14, left i/1 of *Ugandapithecus* from Napak V, Uganda. A) lingual view, B) mesial view, C) apical view, D) labial view, E) distal view (scale : 10 mm).

NAP V 2'14 is a complete but lightly worn left i/1 (Fig. 29). The lingual ridge is low and centrally positioned. The buccal surface is smooth. The mesial and distal lingual marginal ridges are low and the cervix rises towards the apex in both the mesial and distal views. The root is oval in section, the long axis of the root being at right angles to the mesio-distal long axis of the crown. Mesially and distally the cervix is v-shaped with the 'v' closer to the apex of the crown on the mesial side. Some hypoplastic lines are visible.

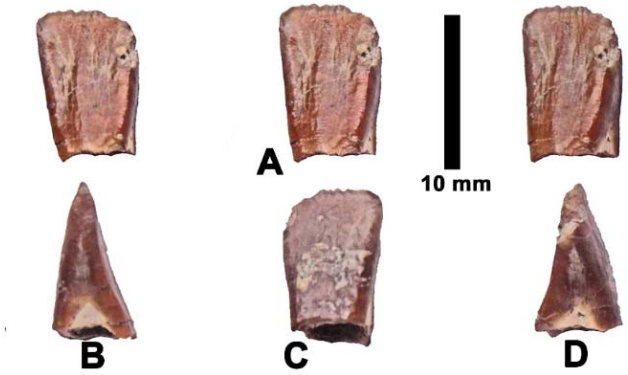

Figure 30. NAP V 9'16, germ of right i/1 of *Ugandapithecus* from Napak V, Uganda. A) stereo lingual views, B) mesial view, C) labial view, D) distal view (scale : 10 mm).

NAP V 9'16 is a germ of a right i/1 very likely representing the same individual as the infant jaw (NAP V 57'16) (Fig. 30). The apical margin is horizontal mesially but distally it curves towards the cervix. The distal marginal ridge is broad and the distal margin is not scoop-shaped. The lingual ridge is low and slants from the middle of the tooth apically towards the mesial edge cervically. The mesial and distal marginal ridges are low. The cervix rises apically on the mesial and distal sides. The base of the crown is incompletely formed. The apex of the crown is lightly crenulated.

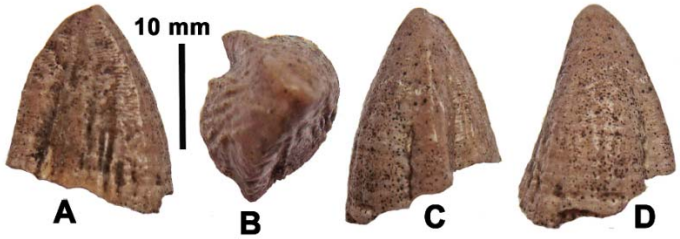

Figure 32. NAP V 25'11, unworn apex of right lower canine of *Ugandapithecus* from Napak V, Uganda. A) lingual view, B) apical view, C) distal view, D) labial view (scale : 10 mm)

The apex of a lower canine (NAP V 25'11) has a slightly burin-shaped apex, with prominent mesial and distal crests descending towards the cervix (Fig. 32). Several hypoplastic lines and perikymata are evident. The enamel is coarsely wrinkled producing low vertical ridges, especially on the lingual surface.

It is noted that most of the canines of *Ugandapithecus* from Napak are broken about one third of the crown height down from the apex. Some specimens that are complete show a hypoplastic groove all around the crown at the same general height, which is interpreted to be a possible sign of metabolic disturbance related to weaning stresses (dietary and emotional) (Pickford & Ishida (1998).

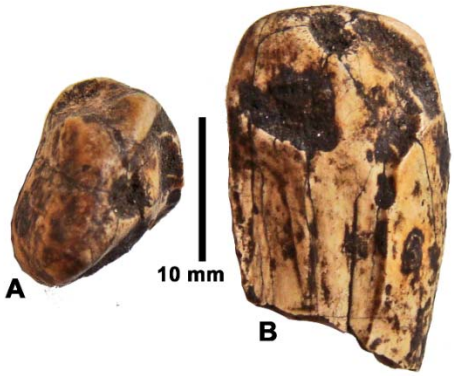

Figure 33. NAP V 179'09, damaged and polished apex of lower canine of *Ugandapithecus* from Napak V, Uganda, A) apical view, B) distal view (scale : 10 mm).

NAP V 179'09 is a damaged right lower canine (Fig. 33). The enamel is missing and the dentine surface is polished and rounded. It appears that the tooth was broken while the individual was alive, and that continued use ended up polishing and rounding the damaged surface. This tooth has the same preservation features as a diseased mandible from the same site (NAP V 2'12, the rear part of the left ramus containing the m/3 and the distal root of the m/2 and NAP V 4'01, other parts of the ramus and symphysis).

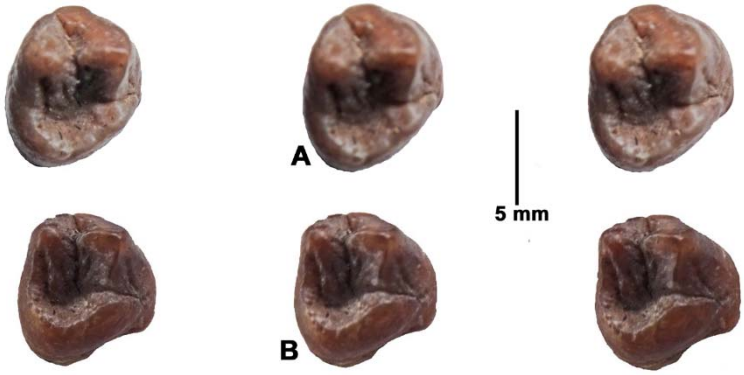

Figure 34. NAP V 54'16, lightly worn right p/4 of *Ugandapithecus* from Napak V, Uganda. A) stereo occlusal views, B) stereo oblique distal views to highlight the distal cingular complex (scale : 5 mm).

A right p/4 (NAP V 54'16) is in light wear (Fig. 34). There are two main cusps, protoconid and metaconid, with a mesial cingulum enclosing a small trigonid basin. The distal cingulum is larger and rims a capacious talonid basin. The buccal half of the distal cingulum rises, almost forming a hypoconid.

Figure 35. NAP V 46'14, left p/4 of *Ugandapithecus* from Napak V, Uganda. A) stereo occlusal view, B) buccal view (scale : 10 mm).

A moderately worn left p/4 (NAP V 46'14) (Fig. 35) is constructed along the same lines as the tooth described immediately above (NAP V 54'16) but the apices of the protoconid and metaconid are worn down almost to the level of the distal cingulum. The trigonid and talonid basins are still present. In buccal view one observes weak mesial and distal stylids. The lingual part of the distal cingulum is separated from the rest by a narrow slit, giving the impression of a small entoconid.

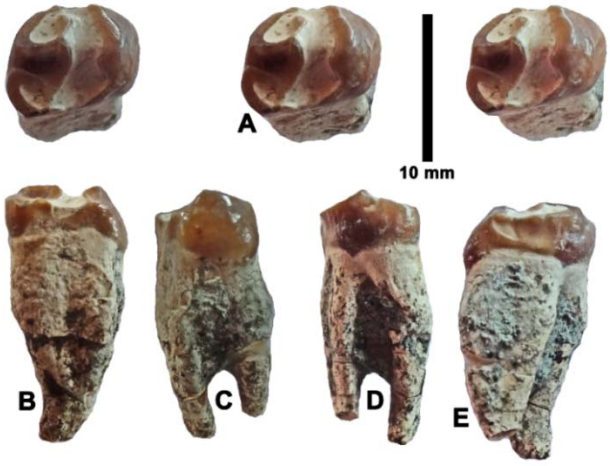

Figure 36. NAP V 1'15, right p/4 of *Ugandapithecus* from Napak V, Uganda. A) stereo occlusal views, B) mesial view, C) buccal view, D) lingual view, E) distal view (scale : 10 mm).

NAP V 1'15 is a deeply worn right p/4 with two large roots preserved (Fig. 36). Wear has advanced to the stage where there is a large dentine lake with a tiny remnant of the mesial fovea like an island between the protoconid and metaconid. The dentine lake extends distally then curves lingually to join a small wear facet on the entoconid.

Figure 37. Stereo occlusal views of NAP V 81'10, left m/1 of *Ugandapithecus* from Napak V, Uganda (scale : 5 mm).

NAP 81'10 is a lightly worn left m/1 lacking parts of the hypoconid and hypoconulid (Fig. 37). The mesial lophid of the tooth is appreciably narrower than the distal part. The protoconid is slightly more mesially positioned than the metaconid, and there is a mesial cingulum which extends onto the buccal side of the protoconid. The trigonid basin is minuscule. The median transverse valley is deep and opens lingually between the metaconid and entoconid. There is a distal foveid between the distal parts of the

entoconid and hypoconulid, separated from the talonid basin by endocristids from the entoconid and hypoconid.

Figure 38. Stereo occlusal views of NAP V 134'17, left lower molar germ of *Ugandapithecus* from Napak V, Uganda (scale : 10 mm).

NAP V 134'17 is an incomplete left lower molar in which the distalmost cusps had not yet mineralised (Fig. 38). It was found close to the infant mandible described above and could belong to the same individual. If so then this tooth is likely to be an m/2. The protoconid has a buccal cingulum which extends distally as far as the hypoconid. The mesial cingulum is strongly beaded. The metaconid and entoconid appear to be low, but this is because they are incompletely formed.

Figure 39. Stereo occlusal view of NAP V 69'14, left lower molar germ from Napak V, Uganda (scale : 10 mm).

An almost complete left lower molar germ (NAP V 69'14) shows the main morphological details of he mesial lophid clearly, but the fine details on the entoconid had not yet formed at the time of death (Fig. 39). There are five main cusps, the distalmost one (hypoconulid) being centrally positioned behind the rear of the hypoconid and entoconid. There is a weak buccal cingulum (perhaps not completely formed), and a strong mesial cingulum. At the distal end of the tooth, just to the lingual side of the hypoconulid, there is a low cusplet between the postendocristid and the posthypoconulid cristid.

Figure 40. Stereo occlusal views of NAP V 80'11, unworn left m/3 of *Ugandapithecus* from Napak V, Uganda (scale : 10 mm).

NAP V 80'11 is a well-preserved left lower third molar, fully formed and unworn (Fig. 40). As such it shows all the details of crown morphology in pristine condition. An immediately noticeable aspect of this tooth is that the mesial lophid is broader than the distal one, suggesting that it is not a first or second lower molar. There are five cusps, the hypoconulid being in the midline of the tooth between the rear parts of the hypoconid and entoconid. The protoconid has prominent pre- and postcristids that descend mesially and distally respectively and an endoprotocristid that reaches towards the metaconid, leaving a slit between it and the endometacristid. The trigonid basin is shallow and rimmed anteriorly by a cingulum. The metaconid has pre- and postcristids, the latter descending into the median transverse

valley towards the pre-entocristid, but separated from it by a low stylid which blocks the lingual end of the median transverse valley. The hypoconid has an endocristid descending mesio-lingually into the talonid basin. The entoconid has a buccally directed endocristid which bifurcates at its extremity, one branch curving mesially, the other distally to reach towards one of the cristids emanating from the hypoconulid, thereby defining the anterior wall of the distal foveid, and separating it from the talonid basin. The hypoconulid has two low cristids reaching mesio-lingually and mesio-buccally. The hypoconulid is coalescent with the distal cingulum. Finally, there is a clear buccal cingulum extending along the entire buccal side of the crown to join the mesial and distal cingulids, but it is thin on the buccal face of the protoconid.

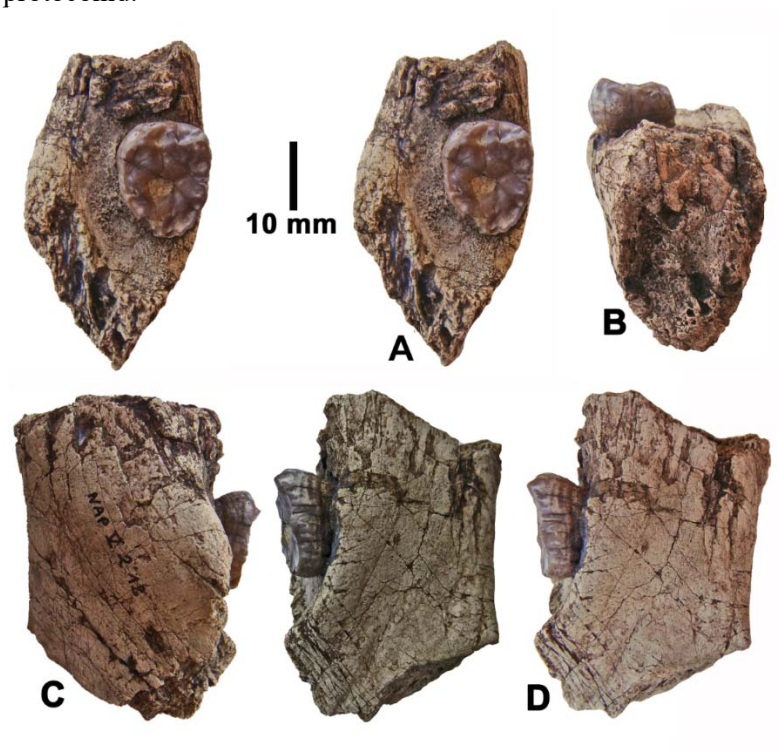

Figure 41. NAP V 2'12, left mandible fragment of *Ugandapithecus* containing the m/3 and roots of m/2. A) stereo occlusal view, B) mesial view, C) buccal view, D) stereo lingual view (scale : 10 mm).

NAP V 2'12 is the rear part of the left ramus containing the m/3 and the roots of the m/2 (Fig. 41). The mandible is thickened and represents the same individual as a diseased specimen (NAP V 4'01) described by Pickford *et al*. (2009) and a broken and polished lower canine (NAP V 179'09). The m/3 is deeply worn, leaving few occlusal details to be observed, but one can make out a mesial cingulum and a broad buccal cingulum. There is dentine exposure on the protoconid and hypoconid but not on the lingual cusps, suggesting that the dentinal horns are of low relief. The ascending ramus starts rising opposite the front of m/3 and the ventral profile of the horizontal ramus beneath the m/2 and m/3 is slightly concave. The depth of the ramus beneath the m/3 is 31.3 mm measured on the lingual side.

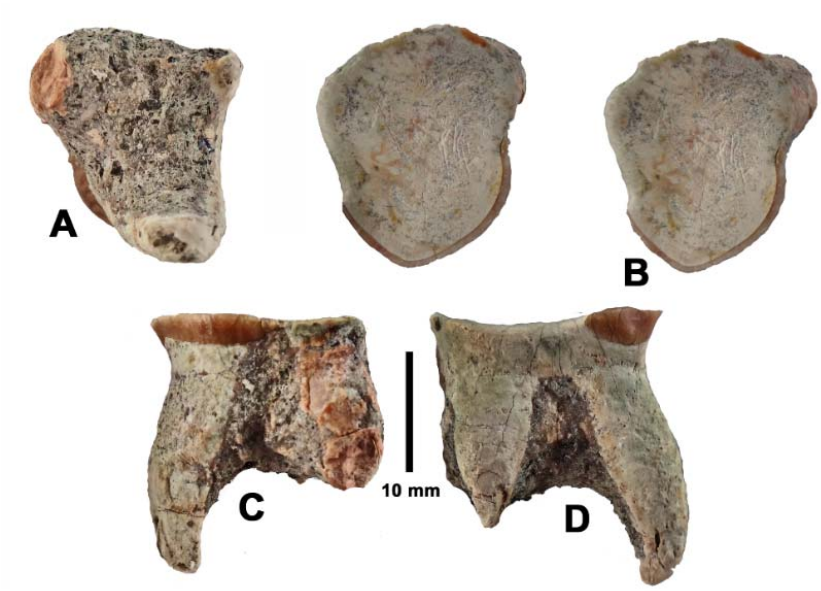

Figure 42. NAP V 133'17, heavily worn right m/3 of *Ugandapithecus* from Napak V, Uganda. A) radicular view, B) stereo occlusal view, C) buccal view, D) lingual view (scale : 10 mm).

NAP V 133'17 is an extremely deeply worn right m/3 in which all that remains of the crown is an incomplete ring of enamel mesially, on the hypoconid and entoconid (Fig. 42). There are three large roots, two mesially and one distally.

Napak XII

Napak XII yielded five large ape teeth in the past ten years, two of them in a mandible.

Upper dentition

Figure 43. Stereo occlusal views of NAP XII 2'13, right upper molar of *Ugandapithecus* from Napak XII, Uganda (scale : 10 mm).

A lightly worn, but well-preserved upper molar (NAP XII 2'13) (Fig. 43) has four main cusps and a prominent, broad lingual cingulum which is particularly strongly developed on the mesial and lingual sides of the protocone. The preprotocrista is sharply defined and where it meets the preparacrista it forms the distal wall of the mesial fovea. In the middle of the mesial cingulum there is a swollen part where the preparacrista coalesces with the cingulum, forming a tubercle that recalls a paraconule. There is also a cingular structure (mesostyle) on the buccal side of the crown beneath the end of the median transverse valley. It fades out distally but picks up again at the distal half of the metacone and then continues round the rear of the cusp to join the distal cingulum. The protocone, paracone and metacone form a triangular complex, with the hypocone separated from it by a deep slit. The lingual cingulum is coarsely wrinkled, but wear has removed the fine surface structures over most of the crown. There is a small interstitial facet on the distal edge of the tooth, indicating that it is not an M3/.

Lower dentition

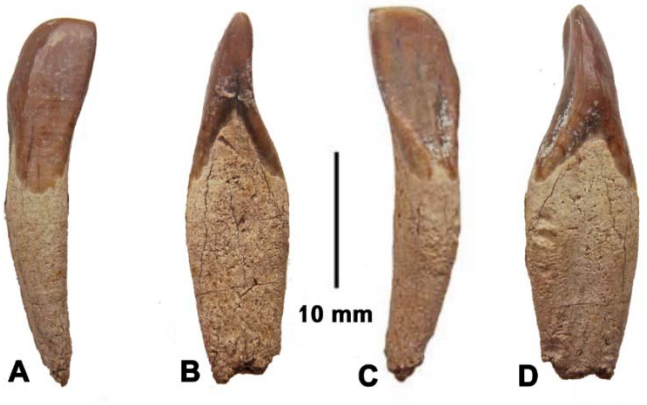

Figure 44. NAP XII 1'10, right i/2 of *Ugandapithecus* from Napak XII, Uganda. A) labial vew, B) mesial view, C) lingual view, D) distal view (scale : 10 mm).

The lateral incisor (NAP XII 1'10) is a tall slender tooth with a root that is slightly taller than the crown (Fig. 44). In lingual view the crown is curved, the apex is horizontal for two thirds of its mesio-distal extent, then curves cervically in the distal third. There is a low central ridge and the mesial and distal marginal ridges are low and rounded, converging towards each other cervically. In labial view the crown is smooth with the distal part curved a bit towards the lingual side. In mesial and distal views, the cervix is seen to rise apically about half the height of the crown mesially and about one third of the height of the crown distally.

Figure 45. NAP XII 10'19, right lower molar of *Ugandapithecus* from Napak XII, Uganda. A) buccal view, B) stereo occlusal view (scale : 10 mm).

A lower molar (NAP XII 10'19) is worn to the point of exposing dentine on the protoconid, metaconid, hypoconid and entoconid, with a tiny exposure on the hypoconulid (Fig. 45). There is a large cingular mass at the buccal end of the median transverse valley which is affected by wear. There are two stout roots, each comprised of two coalescent roots.

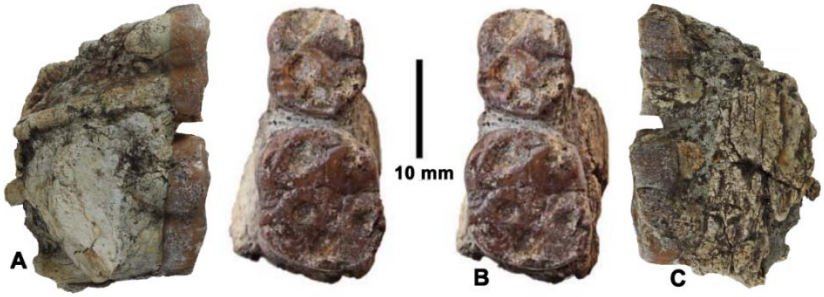

Figure 46. NAP XII 1'13, left mandible fragment of *Ugandapithecus* containing m/1 and m/2, from Napak XII, Uganda. A) buccal view, B) stereo occlusal view, C) lingual view (scale : 10 mm).

NAP XII 1’13 is a left mandible fragment containing the first and second molars (Fig. 46). It is an informative specimen in that it shows clearly the significant difference in size between the two molars, the m/1 being appreciably smaller than the m/2. Both teeth are deeply worn, the m/1 showing a large dentine lake on the protoconid and a small dentine lake on the metaconid. The distal dentine lakes on the entoconid, hypoconid and hypoconulid are linked by narrow straits. There is a prominent buccal cingulum. The m/2 is worn to the stage in which each of the five cusps has its own dentine exposure still separated from its neighbours. The buccal cingulum is broad. The m/2 shows a small interstitial facet caused by contact with the m/3.

The dimensions of the teeth in this mandible correspond to those of *Ugandapithecus legetetensis* and are smaller than those of *Ugandapithecus major*.

Napak XIII

During the past six years Napak XIII has yielded eight large ape teeth, three of them in a maxilla.

Upper dentition

The upper canine (NAP XIII 3’14) (Fig. 47) is complete but was found in two pieces, the apex having separated from the rest of the tooth at a hypoplastic groove probably corresponding to the weaning line, as in many of the canines from Napak. There are also clearly visible perikymata on the crown. The apex is burin-like. The root is massive, being about twice as tall as the crown and mesio-distally somewhat larger than at cervix. The crown has a clear mesial groove which fades out cervically while disto-labially it has a concave surface. The disto-labial concavity of the crown is unusual in having a low but sharp accessory ridge in its middle extending from the cervix towards the apex, fading out about two-thirds of the way towards the apex. The root beneath the concavity is also concave for about half the height of the root.

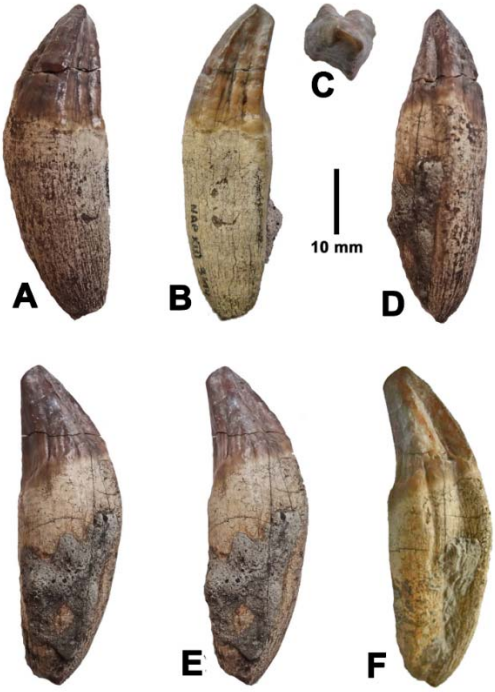

Figure 47. NAP XIII 3’14, right upper canine of *Ugandapithecus* from Napak XIII, Uganda. A) labial view, B) disto-labial view to show concavity, C) apical view slightly enlarged to show the burin-like apex, D) mesial view, E) stereo lingual view, F) mesio-lingual view to highlight the mesial groove (scale : 10 mm).

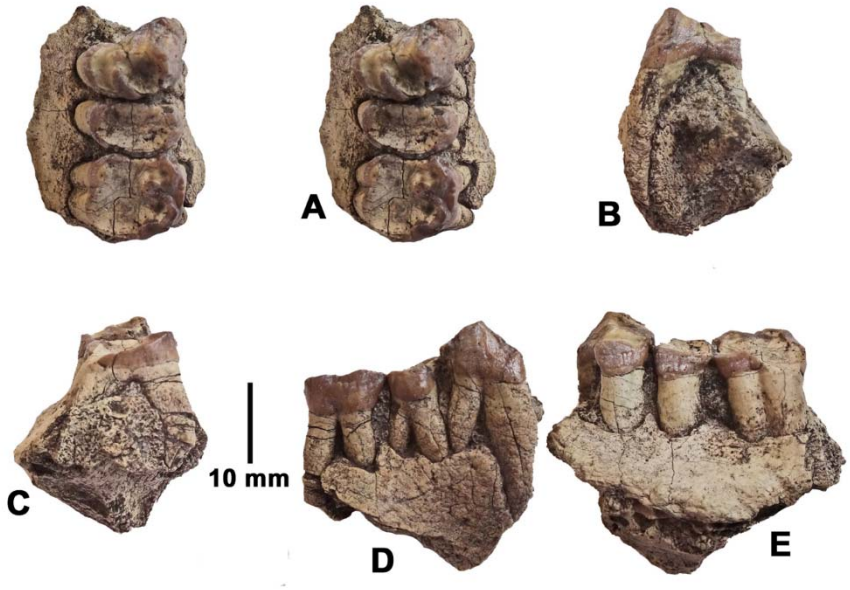

Figure 48. NAP XIII 1'14, left maxilla of *Ugandapithecus* containing P3/-M1/ from Napak XIII, Uganda. A) stereo occlusal view, B) mesial view (note the enlarged and elongated mesial root on the buccal side), C) distal view, D) buccal view, E) lingual view (scale : 10 mm).

A maxilla fragment with three teeth (NAP XIII 1'14) is useful in showing the two premolars and first molar in association (Fig. 48). Unfortunately, all three teeth are deeply worn with the occlusal enamel of the P4/ and M1/ almost completely eradicated. The P3/ shows a mesial extension of the paracone ending in a style supported by a stout anterior root. Buccally, the enamel extends a bit further rootwards mesially than distally. In occlusal view, the protocone is distinctly shorter in the mesio-distal direction than the paracone. Between the protocone, paracone and distal cingulum, there is a prominent distal fovea. There are three roots, one lingually, and two large ones buccally of which the mesial one is stouter and taller than the distal one. The mesial root on the buccal side is twice as tall as the lingual root. The overall morphology of the crown and roots of this tooth gives the impression that it is well-adapted for a honing function.

The p/4 has a mesio-distally compressed oval outline, very slightly convex mesially but more convex distally. It has three roots, two buccally, of which the mesial is the larger, and one root on the lingual side.

The M1/ is so deeply worn that no details of crown morphology remain. There are two buccal roots, and a single lingual root comprised of coalescent roots supporting the protocone and hypocone.

The dimensions of the teeth in this maxilla are close to those of *Ugandapithecus legetetensis*, and are appreciably smaller than those of *Ugandapithecus major*.

In dorsal view, the anterior part of the maxillary sinus is evident and shows a deep invagination between the roots of the M1/ in front of which the wall of the sinus rises sharply, such that the roots of the P4/ and P3/ are solidly anchored in a thick mass of bone.

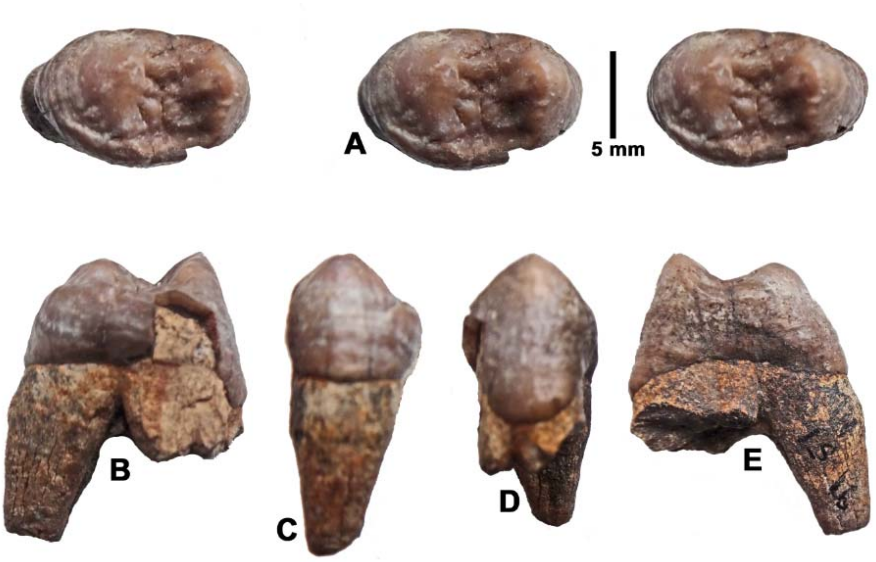

Figure 49. NAP XIII 13'16, left P4/ of *Ugandapithecus* from Napak XIII, Uganda. A) stereo occlusal views, B) distal view, C) lingual view, D) buccal view, E) mesial view (scale : 5 mm).

NAP XIII 13'16 is a lightly worn P4/ missing a chip of enamel from the distal side of the paracone (Fig. 49). It has two main cusps which have coarsely wrinkled occlusal enamel surfaces, the paracone being slightly taller than the protocone. Short swollen crests reach from the protocone and paracone meeting centrally, thereby walling off the mesial fovea from the central basin which opens into the distal fovea. The disto-buccal surface of the protocone has two short swollen crests leading towards the longitudinal valley. In occlusal view, the mesial margin of the tooth is rectilinear, but the distal margin is convex. There is cingular development on the disto-lingual aspect of the protocone. The enamel extends appreciably further rootwards on the buccal side than on the lingual one.

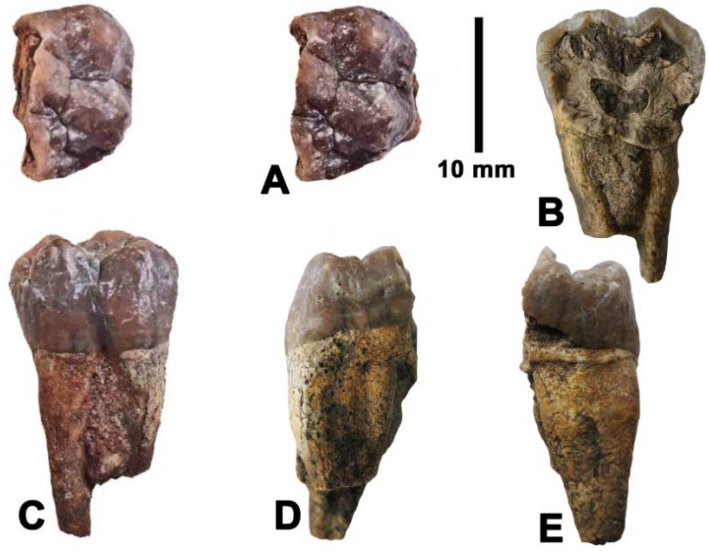

Figure 50. NAP XIII 2'14, broken left upper molar of *Ugandapithecus* from Napak XIII, Uganda. A) stereo occlusal view, B) lingual view of broken surface to show enamel thickness and pulp cavity, C) buccal view, D) mesial view, E) distal view (scale : 10 mm).

NAP XIII 2'14 is an upper molar lacking the lingual part of the protocone and hypocone (Fig. 50). It is lightly worn and shows coarsely wrinkled occlusal enamel. The metacone is larger than the paracone and the endometacrista is broad and swollen, extending towards the enlarged crista obliqua from which it is separated by a groove. There are two roots supporting the paracone and metacone respectively.

Lower dentition

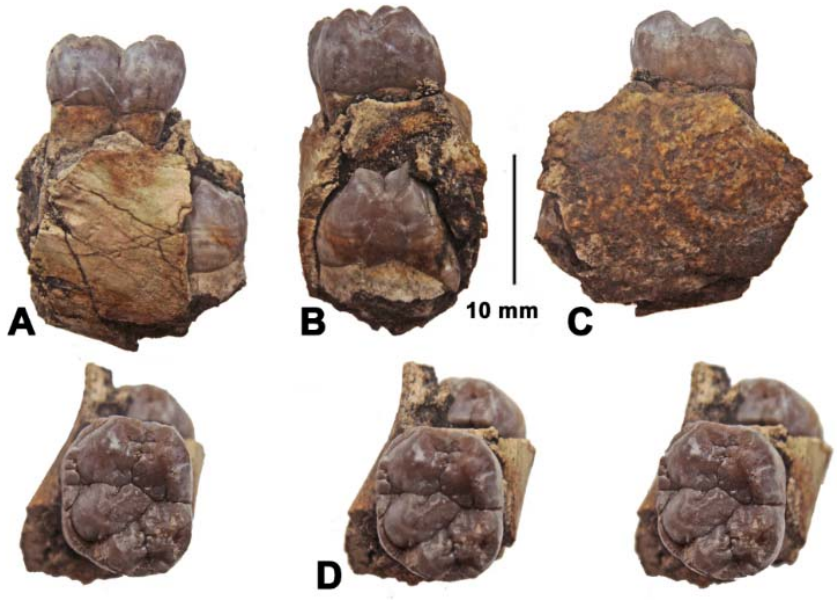

Figure 51. NAP XIII 1'10, left mandible fragment of a juvenile *Ugandapithecus* from Napak XIII, Uganda. A) lingual view, B) mesial view, C) buccal view, D) stereo occlusal view (scale : 10 mm).

A mandible fragment of a juvenile large ape (NAP XIII 1'10) contains the p/4 in its crypt and a fully erupted but almost unworn m/1 (Fig. 51). At the time of death, the p/4 had started root formation but had not yet begun erupting. The apices of the protoconid and metaconid are close together and there is a talonid basin between them and the mesial cingulum. The rest of the tooth is obscured but it is noted that the enamel extends further rootwards on the buccal side of the crown than it does on the lingual side.

The m/1 is comprised of the usual five main cusps and an extensive buccal cingulum. The hypoconid is the largest cusp, followed by the protoconid and then subequally sized metaconid and entoconid and a small hypoconulid. Beneath the buccal end of the median transverse valley, the cingulum is broad and beaded but elsewhere it is narrow and sharp. Anteriorly, there is a clear trigonid basin between the mesial cingulum and the endocristids of the protoconid and metaconid.

The teeth in this mandible agree in dimensions with those of *Ugandapithecus legetetensis* as does the juvenile jaw from Napak I (UMP 62.13) (Pickford *et al*. 2009).

Napak XV

During the past decade, Napak XV continued to yield important specimens of *Ugandapithecus* including an adult skull with all the teeth, the first time that both upper tooth rows of a single individual of this genus have been found (Figs 52-60). The same area yielded several fragments of mandible that could represent the same individual (NAP XV 62'08, Pickford *et al*. 2009). The collection from Napak XV since 2010 comprises 22 teeth of large apes and several of small-bodied apes.

Upper dentition

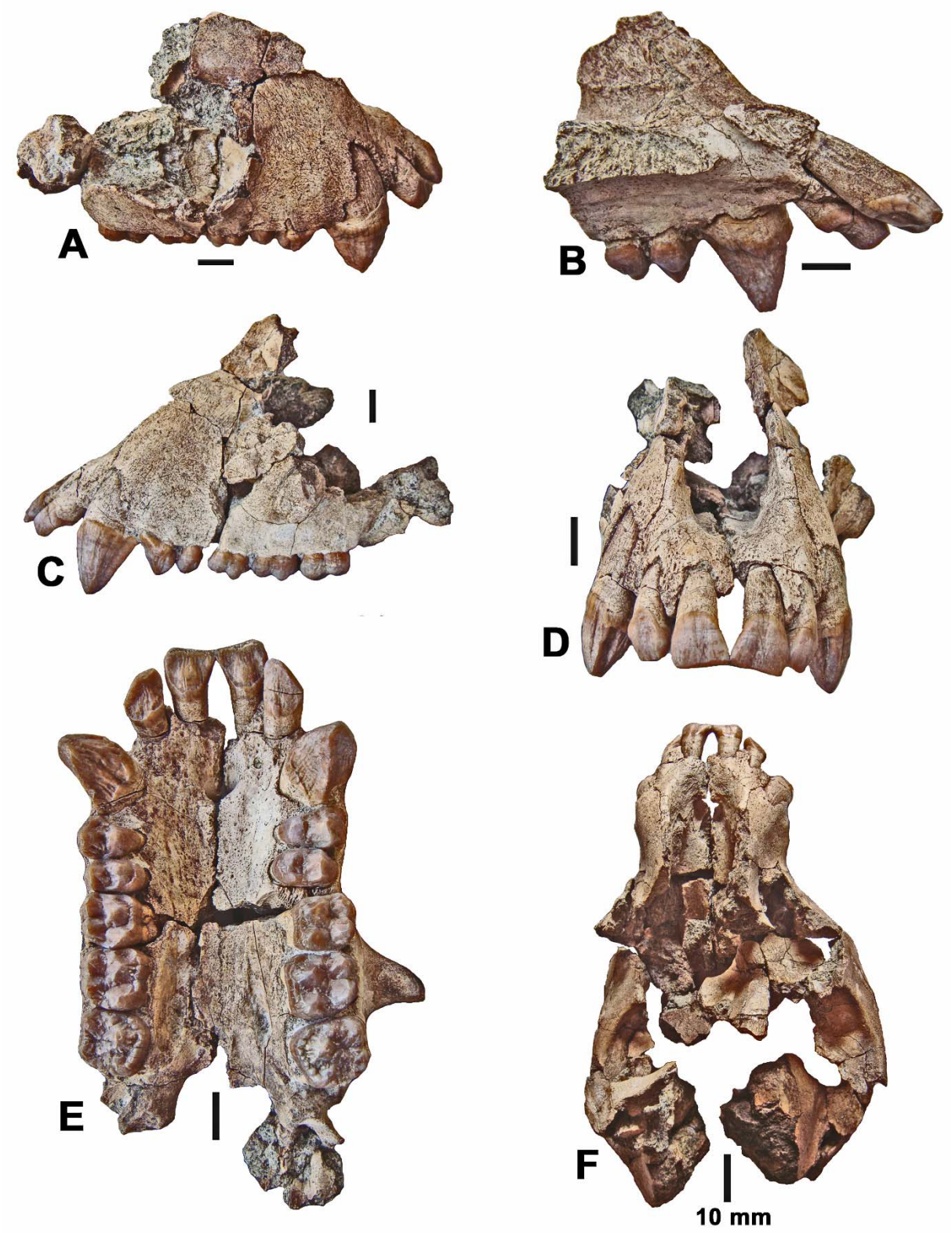

Figure 52. NAP XV 60'11, partial skull of *Ugandapithecus* from Napak XV, Uganda. A) right lateral view, B) lingual view of left anterior teeth, C) left lateral view, D) anterior view, E) palatal view, F) dorsal view (scales : 10 mm).

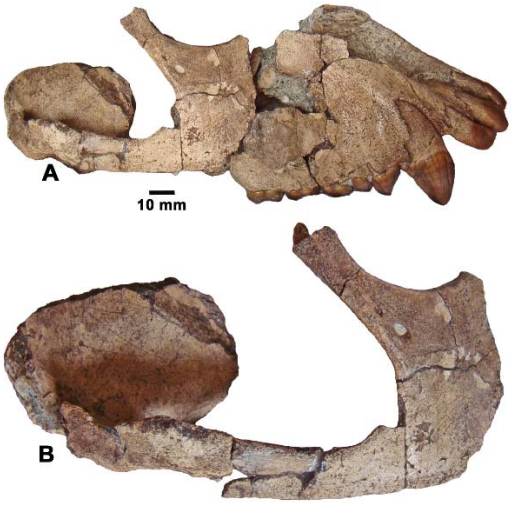

Figure 53. NAP XV 60'11, partial skull of *Ugandapithecus* from Napak XV, Uganda. A) right lateral view, B) oblique dorsal view of right orbit and zygomatic arch (scale : 10 mm).

A detailed description of the skull, NAP XV 60'11, is in preparation. Scans of the specimen reveal internal details which will be crucial for taxonomy, but they will not be discussed herein. Suffice to report that the muzzle is complete with all the mature dentition in a lightly worn condition, the right zygomatic arch is complete and is joined to the parietal behind and the maxilla in front which preserves the basal half of the right orbit. Various parts of the neurocranium are also preserved but are somewhat damaged.

There are large maxillary sinuses above the molar rows extending slightly mesially of the M1/, the mesial root of the zygomatic arch leaves the facial part of the maxilla above the mesial root of the M1/. There is a prominent sub-orbital foramen beneath the midline of the orbit, close to the edge of the temporal fossa. The incisive foramen is large and is not subdivided sagittally. The dimensions of the teeth in this skull agree with those of the large species *Ugandapithecus major*.

Figure 54. Stereo occlusal views of cast of right maxilla (NAP XV 60'11) of *Ugandapithecus major* from Napak XV, Uganda (scale : 5 cm).

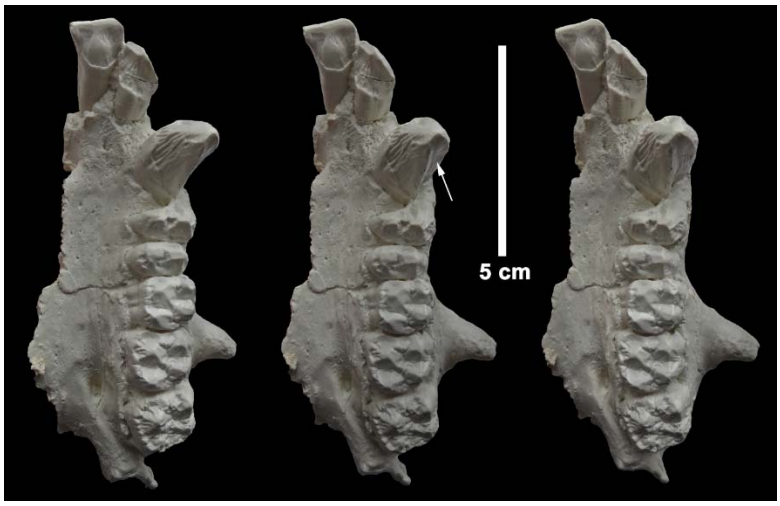

Figure 55. Stereo occlusal views of cast of left maxilla (NAP XV 60'11) of *Ugandapithecus major* from Napak XV, Uganda. Arrow points to the disto-labial concavity of the canine (scale : 5 cm).

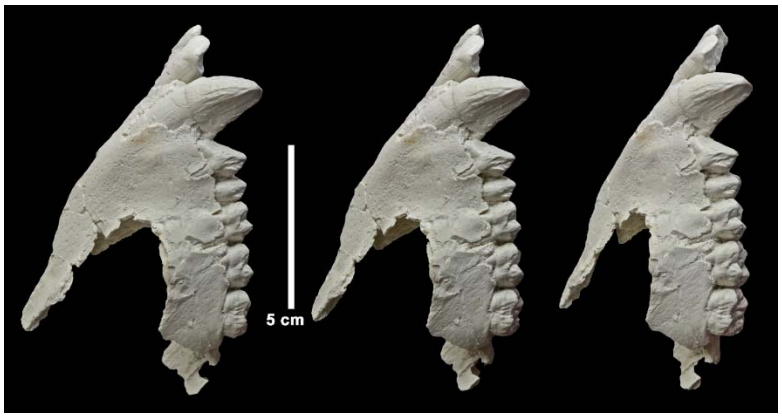

Figure 56. Stereo right lateral views of cast of right maxilla (NAP XV 60'11) of *Ugandapithecus major* from Napak XV, Uganda (scale : 5 cm).

Figure 57. Stereo left lateral views of cast of left maxilla (NAP XV 60'11) of *Ugandapithecus major* from Napak XV, Uganda (scale : 5 cm).

Figure 58. Stereo lingual views of cast of right maxilla (NAP XV 60'11) of *Ugandapithecus major* from Napak XV, Uganda (scale : 5 cm).

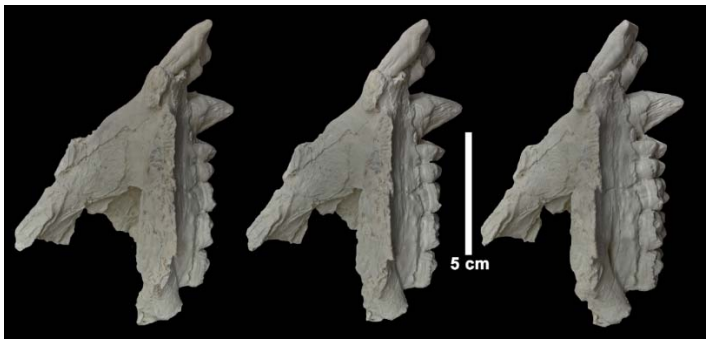

Figure 59. Stereo lingual views of cast of left maxilla (NAP XV 60'11) of *Ugandapithecus major* from Napak XV, Uganda (scale : 5 cm).

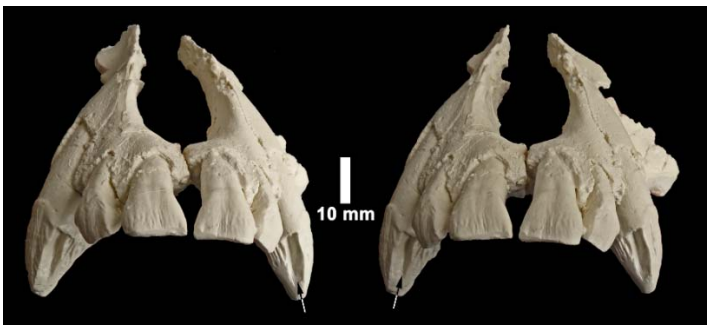

Figure 60. Stereo anterior view of cast of NAP XV 60'11, *Ugandapithecus major* from Napak XV, Uganda. Arrows point to the mesial groove in the upper canines (scale : 10 mm at I1/).

The teeth in the palate of NAP XV 60'11 will be described in detail in a forthcoming publication. Suffice to note that in this individual, as in other specimens of the upper dentition of *Ugandapithecus* (Pickford *et al*. 2009) the M3/ is the largest of the molars, the buccal surfaces of the molars have small mesostyle-like cingular complexes beneath the median transverse valley, the upper canines have a well-developed burin-like morphology at their apices, with a prominent disto-labial depression spanning the height of the crown.

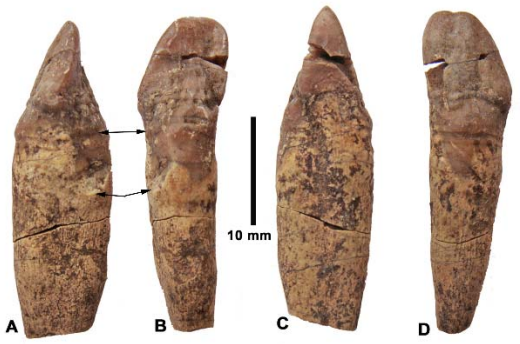

Figure 61. NAP XV 31'11, right I2/ of *Ugandapithecus* from Napak XV, Uganda. A) distal view, B) lingual view, C) mesial view, D) labial view. Arrows show the extent of the wear facet due to contact with the lower canine (scale : 10 mm).

NAP XV 31'11 is an adult I2/ of which only the apex of the root is missing (Fig. 61). In its preserved parts it is similar to the other lateral upper incisors described from Napak except that the crown is marginally taller than that in the skull NAP XV 60'11, and the lingual cingulum is weaker. The postcrista curves labially as it approaches the cervix and the enamel on the lingual surface is coarsely wrinkled basally. There is a clear wear facet caused by the lower canine, which extends from the base of the distal part of the crown a short way onto the root.

Figure 62. NAP XV 134'12, buccal half of right P4/ of *Ugandapithecus* from Napak XV, Uganda. A) occlusal view, B) buccal view (scale : 10 mm).

NAP XV 134'12 is the buccal half of a P4/ preserving the paracone, parastyle and mesostyle (Fig. 62). In occlusal view one observes a mesio-distally compressed mesial fovea and distally a more expansive distal fovea. Two prominent hypoplastic grooves are present on the buccal surface.

Figure 63. Stereo occlusal view of NAP XV 24'18, left upper molar of *Ugandapithecus* from Napak XV, Uganda (scale : 10 mm).

An unworn germ of an upper molar (NAP XV 24'18) shows the occlusal morphology clearly (Fig. 63). There are four main cusps and a well-developed lingual cingulum on the protocone, fading out distally on the hypocone but extending mesially to join the mesial cingulum which extends right across to the preparacrista. The protocone has a bulbous preprotocrista that is directed mesially towards the centre-line of the crown where it joins the mesial cingulum. On its way it has shallow grooves on either side forming an indistinct paraconule. The crista obliqua separates from the postprotocrista about half way down from the apex and is directed towards the endometacrista but is separated from it by a slit. In addition, the protocone has a third crest descending from its apex directly distally where it meets a crest emanating mesially from the hypocone, but separated from it by a slit. The protocone also has a swollen ridge (endoprotocrista) descending from its apex into the trigon basin. The paracone has four crests, the pre-paracrista descending mesially to join the buccal end of the mesial cingulum and forming a subtle parastyle. A second crest on the paracone (secondary branch of preparacrista) descends mesio-lingually to touch the paraconule, thereby walling off a mesial fovea. A third broad crest or ridge (endoparacrista) descends from the apex of the paracone lingually into the floor of the trigon basin where it ends opposite the protocone ridge (endoprotocrisrta). The postparacrista descends from the apex of the cusp distally towards the premetacrista but is separated from it by a slit. The metacone sends a broad crest mesio-lingually (endometacrista) to meet the postprotocrista (+ crista obliqua) from which it is separated by a slit. It also has a postmetacrista that descends distally and curves lingually to join the distal cingulum. The hypocone has four crests or ridges. Mesio-lingually there is bulky ridge that descends towards the lingual cingulum, but without joining it. Mesially there is a sharper crest (prehypocrista) that meets the distally directed crest (postprotocrista) from the protocone. Internally there is a broad ridge (endohypocrista) that splits into two as it approaches the longitudinal valley, and finally there is a distal crest that curves buccally as it descends from the apex until it joins the distal cingulum. On the buccal surface of the tooth, beneath the median transverse valley, there is a small cingular structure (mesostyle). Mesially and distally there are no interstitial contact facets.

Figure 64. Stereo occlusal view of NAP XV 9'18, eroded crown of right upper molar of *Ugandapithecus* from Napak XV, Uganda (scale : 10 mm).

NAP XV 9'18 is a poorly preserved upper right molar crown which has suffered some kind of etching (Fig. 64). Similar damage has been observed in teeth that have been partly digested by carnivores. All that can be said of this specimen is that it is comprised of four main cusps arranged as is usual in large ape teeth and that the hypocone shows signs of a subdivision disto-buccally.

Lower dentition

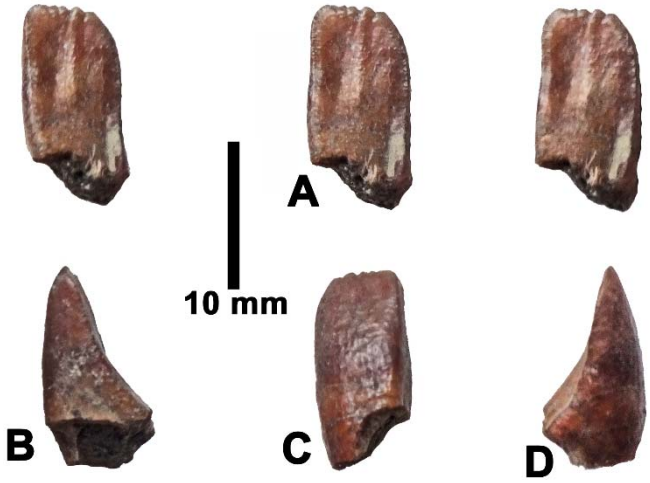

Figure 65. NAP XV 8'17, right i/2 germ of *Ugandapithecus* from Napak XV, Uganda. 1A) stereo lingual views, B) mesial view, B) labial view, C) distal view (scale : 10 mm).

NAP XV 8'17 is a germ of a right i/2 (Fig. 65). The apex shows three shallow subdivisions (crenulations) on the mesial side of the central lingual ridge which forms its own apical point, followed by another one distal to it (making five points in all). The apex is rectilinear in its mesial two-thirds, but curves cervically in the distal third. The central lingual ridge fades out cervically as it approaches the basal lingual swelling, which is incomplete cervically, not having mineralised at the time of death. In lingual view, the mesial marginal ridge is clear, as is the distal marginal ridge in its cervical half.

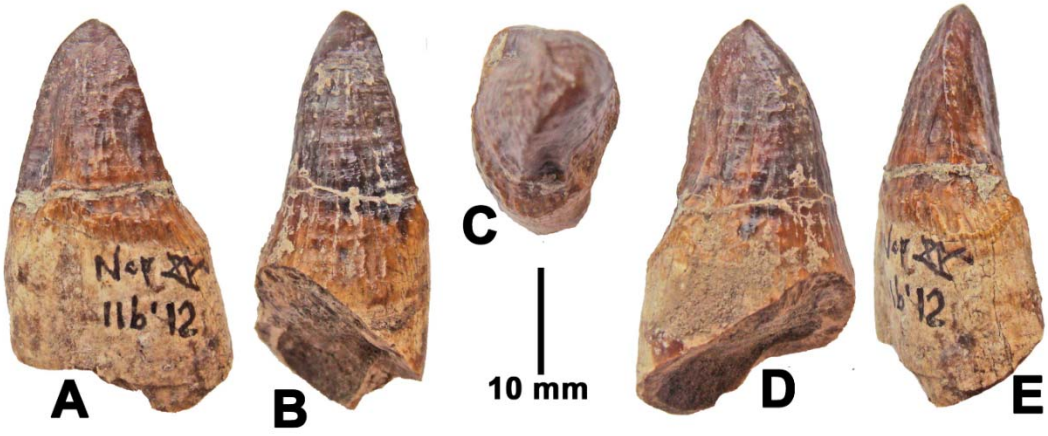

Figure 66. NAP XV 116'12, right lower canine of *Ugandapithecus* from Napak XV, Uganda. A) lingual view, B) mesial view, C) apical view, D) labial view, E) distal view, (scale : 10 mm).

Na XV 116'12 is a lower canine crown (Fig. 66), which judging from its dimensions probably represents a male individual. The tooth is unworn and shows clear hypoplastic grooves in the cervical third of the crown. Much of the root is missing, but what remains is longer and broader than the crown. The pulp cavity is large indicating young adult status.

In apical view, the crown has a triangular appearance, with prominent crests descending from the apex mesially and distally. There is a tall groove on the mesio-lingual side of the crown, and a short one

basally on the disto-labial side of the tooth. The enamel is somewhat rugose with hypoplastic growth lines and perikymata in evidence.

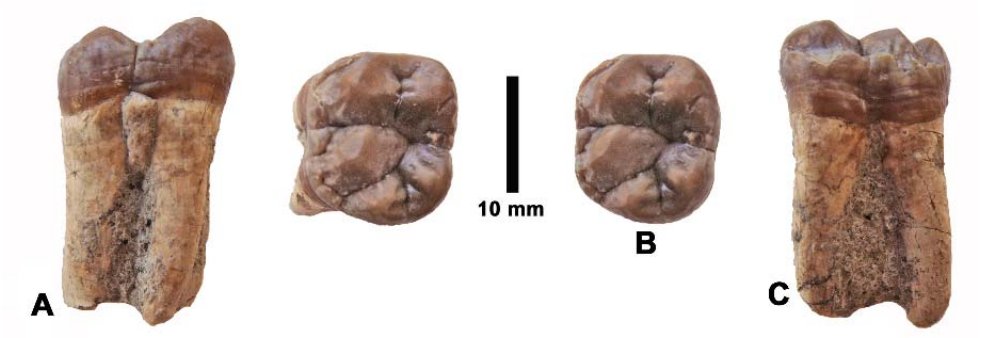

Figure 67. NAP XV 2'12, left lower molar of *Ugandapithecus* from Napak XV, Uganda. A) lingual view, B) stereo occlusal, C) buccal view (scale : 10 mm).

NAP XV 2'12 is a lightly worn lower molar supported by two stout roots (Fig. 67). Its crown morphology accords with that of other lower molars from Napak. The buccal cingulum is low on the protoconid but is strong and beaded on the hypoconid. Hypoplastic lines are visible on the buccal and lingual surfaces of the crown.

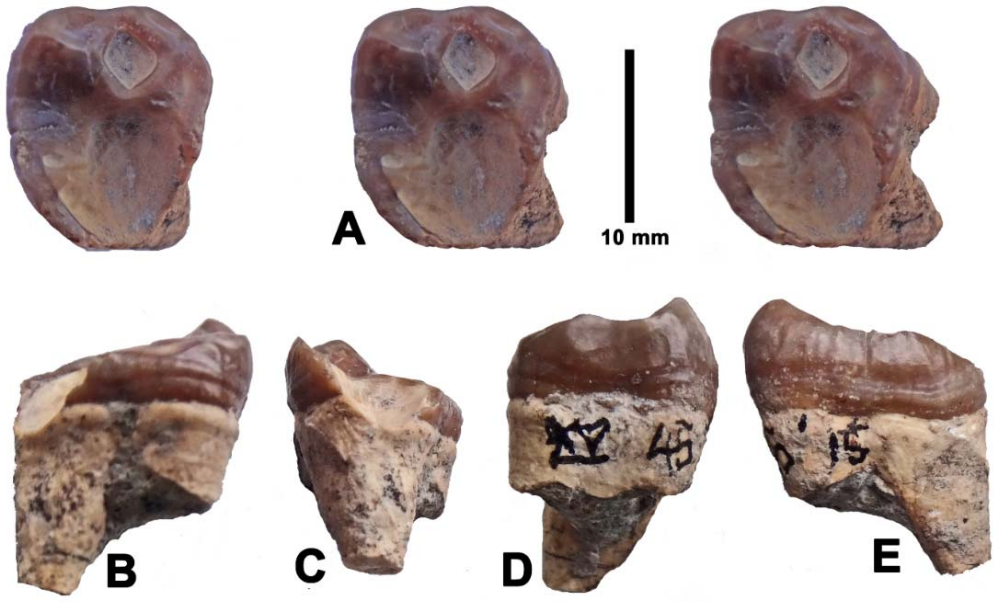

Figure 68. NAP XV 45'15, deeply worn left m/3 of *Ugandapithecus* from Napak XV, Uganda. A) stereo occlusal views, B) lingual view, C) distal view, D) mesial view, E) buccal view (scale : 10 mm).

NAP XV 45'15 is a heavily worn lower third molar (Fig. 68). Little can be said about crown morphology because wear on the distal part of the tooth has advanced so deeply that it affects the posterior root. The mesial root is compressed oval in outline, the distal one sub-rounded and tilted distally, indicating that this tooth is a lower third molar. There is a prominent hypoplastic groove just above cervix.

Napak XVIII

Napak XVIII is in the Iriri Member, and is thus older than the Napak Member which yielded most of the fossil apes from Napak. In 2019, the site yielded an upper molar of a large ape.

Upper dentition

Figure 69. NAP XVIII 1'19, right M3/ of *Ugandapithecus* from Napak XVIII, Uganda. A) stereo occlusal view, B) buccal view (scale : 10 mm).

The Iriri Member yielded a moderately worn upper molar (NAP XXVII 1'19) (Fig. 69). The morphology is characteristic of other upper molars from Napak. The protocone shows several crenulations in the enamel on its lingual and mesial surfaces where it approaches the lingual and mesial cingulum. The buccal surface of the crown shows a weakly developed cingular complex beneath the buccal end of the median transverse valley. Wear has produced a crystodont pattern on the four main cusps. There is an interstitial contact facet mesially, but none distally, suggesting that this could be an upper third molar, an inference supported by the relatively small dimensions of the hypocone.

Napak XXVI

In 2012, the bedded tuffs exposed in the steep slopes on the nose of Akisim Mountain above the village of Iriri yielded an isolated canine of a large ape.

Upper dentition

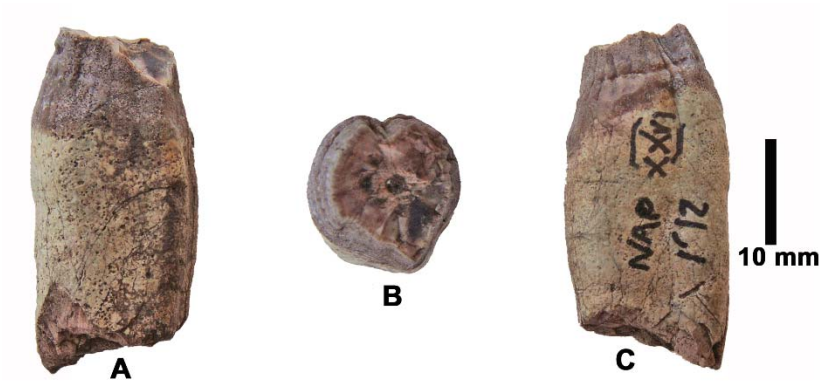

Figure 70. NAP XXVI 1'12, right upper canine of *Ugandapithecus* from Napak XXVI, Uganda. A) mesial view, B) apical view, C) distal view (scale : 10 mm).

The bedded tuffs at Napak XXVI yielded a single upper canine of a large ape (Fig. 70). The apex is missing as is often the case with canines from Napak, but this tooth also shows evidence of a second deep hypoplastic groove encircling the crown just above cervix.

In apical view the mesial groove is seen to be as deep as it is broad and it fades out before reaching the cervix. The distal crest is quite sharp. The root is somewhat longer and broader than the crown at cervix.

Napak XXX

The site of Napak XXX, discovered in 2014, yielded a rich assemblage of rodent and ruminant skeletons in a pipe-like deposit (Pickford, 2018). The bedded tuffs in which the pipe formed are poorly fossiliferous, but they have yielded some interesting mammal specimens including three teeth of *Ugandapithecus* and alot of fossil wood.

Lower dentition

Figure 71. NAP XXX 41'16, right lower deciduous canine of *Ugandapithecus* from Napak XXX, Uganda. A) mesial view, B) stereo apical view, C) distal view (scale : 10 mm).

The lower deciduous canine (NAP XXX 41'16) is similar to the tooth in situ in the infant mandible from Napak V (Fig. 71). The distal crest is prominent and curves as it descends from the apex, bordering a shallow lingual basin. There is a shallow but tall mesio-lingual groove which stops short 2 mm above the cervix.

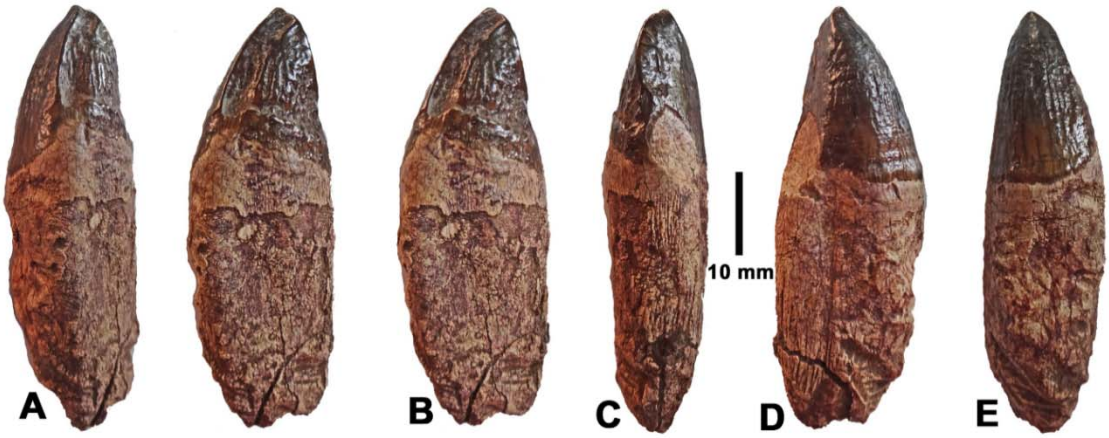

Figure 72. NAP XXX 185'14, right lower canine of *Ugandapithecus* from Napak XXX, Uganda. A) mesial view, B) stereo lingual view, C) distal view, D) lateral view, E) labial view (scale : 10 mm).

Napak XXX yielded a well-preserved lower canine (NAP XXX 185'14) which has a wear facet caused by abrasion against the upper canine extending from the distal part of the crown onto the disto-lateral side of the root (Fig. 72). Elsewhere the crown is not worn. Apically there is a burin-like form where the lingual crest is offset from the main cusp by a short distance, and then runs down towards cervix parallel to the mesial cristid. The post-cristid descends from the inner side of the burin-like apex about halfway towards cervix after which it curves labially to terminate at the top of the wear facet. The enamel is rugose, the mesial cristid clear and sharp. Just beneath cervix the root is slightly longer and broader than the crown. The root is twice as tall as the crown and apically it shows several corrugations on the distal and labial sides and on its lingual side it has a broad but shallow gutter. Near the apex of the root there are some rodent gnaw marks.

Figure 73. Stereo occlusal views of NAP XXX 31'16, worn right p/4 of *Ugandapithecus* from Napak XXX, Uganda (scale : 10 mm).

NAP XXX 31'16 is a heavily worn p/4 missing a chip of enamel from the mesio-lingual corner of the metaconid (Fig. 73). What remains conforms with other p/4s from Napak, but the specimen is rather small, probably representing the species *Ugandapithecus legetetensis* Pickford *et al*. (2009).

Napak XXXI

A new locality discovered in 2014 (Napak XXXI) has yielded 10 teeth of *Ugandapithecus* some of which which could represent a single individual.

Upper dentition

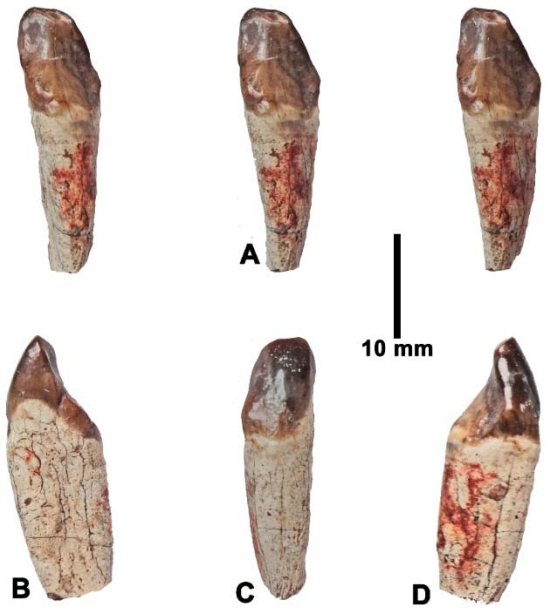

Figure 74. NAP XXXI 11'17, left I2/ of *Ugandapithecus* from Napak XXXI, Uganda. A) stereo lingual views, B) mesial view, C) labial view, D) distal view (scale : 10 mm).

NAP XXXI 11'17 is an upper lateral incisor with minor apical wear (Fig. 74). The distal scoop-like depression is clearly expressed, bordered mesially by a low, rounded central lingual ridge. The mesio-lingual depression is small and located near the apex. The cervix rises apically on the mesial side, but distally it barely rises at all.

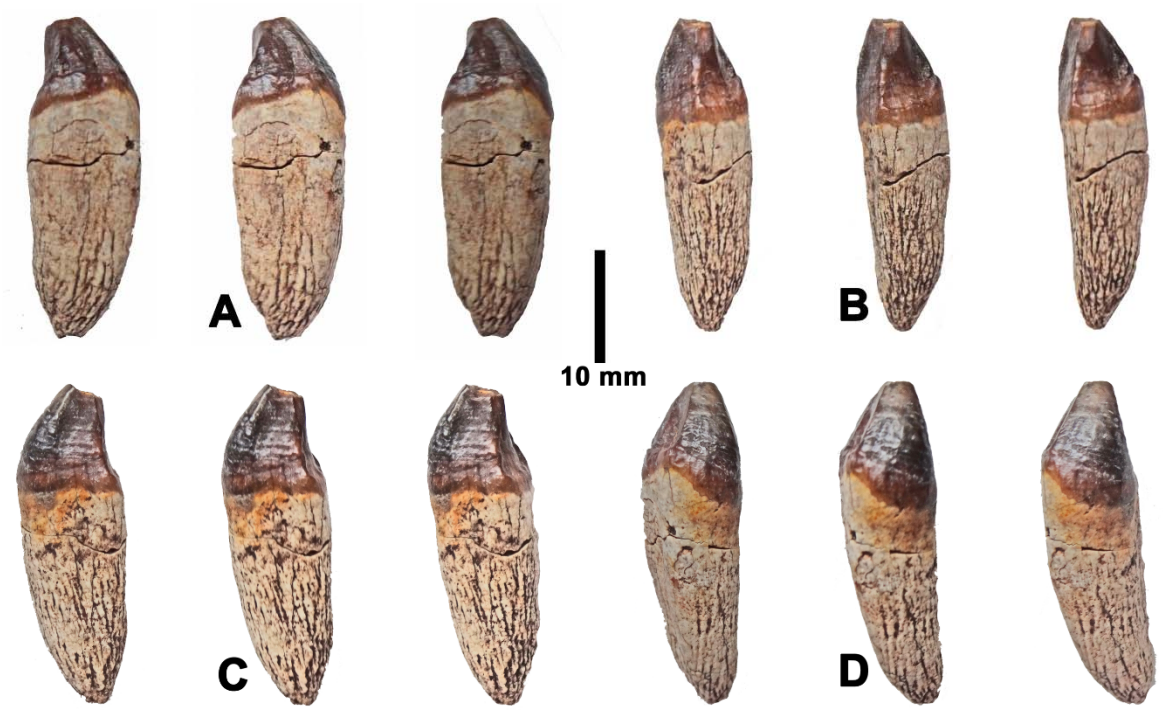

Figure 75. NAP XXXI 10'17, right upper canine of a female *Ugandapithecus* from Napak XXXI, Uganda. A) stereo lingual views, B) stereo distal views, C) stereo distal views, D) stereo labial views (scale : 10 mm).

NAP XXXI 10'17 is an upper canine of female morphology (Fig. 75). The apex is missing, likely broken off due to the presence of a hypoplastic groove and there is a second hypoplastic groove surrounding the crown just above the cervix. The root is three times as tall as the crown. The mesial groove is deep and is stopped cervically by a cingular fold. The distal crista is prominent but blunt and shows a wear facet near the apex. The mesial cingulum is low and narrow and rises apically a short distance at its mesial extremity. The surface of the root is scored by longitudinal grooves, especially extensive on the distal side.

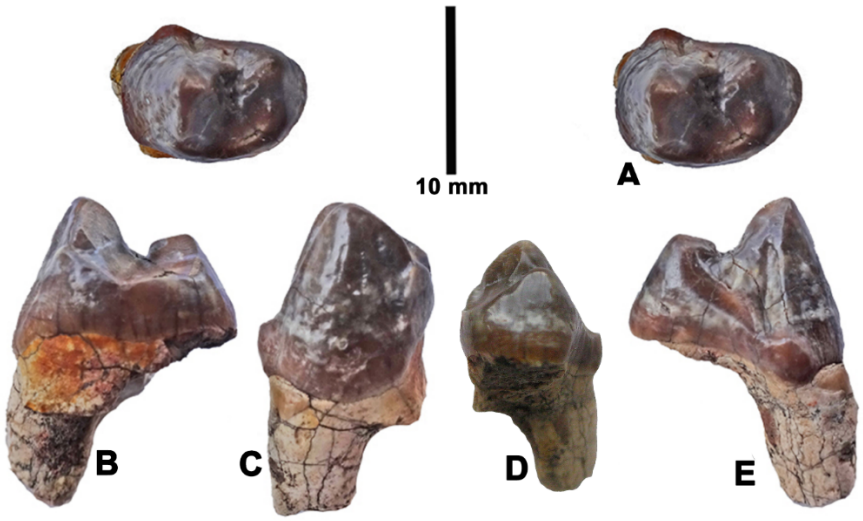

Figure 76. NAP XXXI 10'14, right P3/ of *Ugandapithecus* from Napak XXXI, Uganda. A) stereo occlusal view, B) distal view, C) buccal view, D) lingual view, E) mesial view (scale : 10 mm).

The P3/ (NAP XXXI 10'14) is lightly worn and shows the occlusal morphology reasonably clearly (Fig. 76). The paracone is appreciably larger and taller than the protocone. Mesially its precrista terminates at a parastyle and distally the mesostyle is small and low. The protocone is in a mesial position and its precrista runs buccally, the postcrista distally, and the endocrista leads down into the central basin. The mesial and distal cingula form walls for the mesial and distal foveae respectively. In buccal view the enamel extends appreciably further rootwards than elsewhere on the crown. Mesially the cingulum overhangs a hollow space where the upper canine would fit. The distal interstitial facet is compatible with the mesial facet in P4/ NAP XXXI 6'18, suggesting that the two teeth represent a single individual.

There are two buccal roots (one broken off) and a single lingual root (missing).

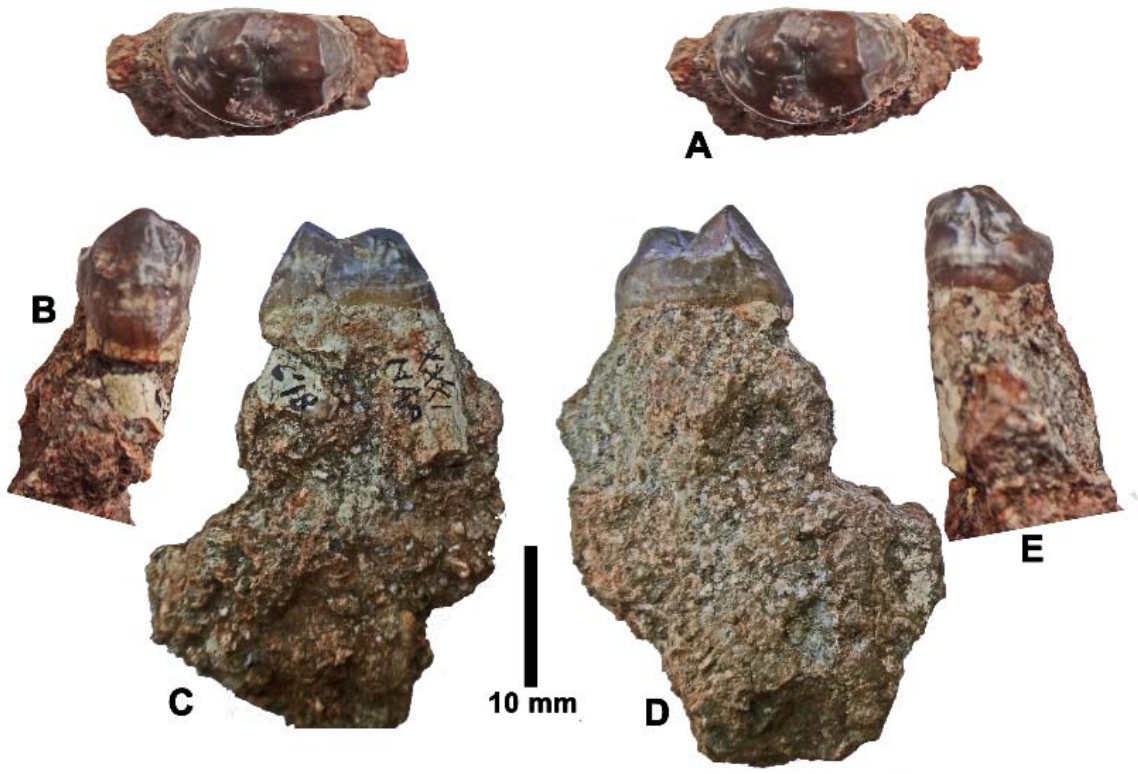

Figure 77. NAP XXXI 6'18, left P4/ of *Ugandapithecus* from Napak XXXI, Uganda. A) stereo occlusal view, B) buccal view, C) mesial view, D) distal view, E) lingual view (scale : 10 mm).

The P4/ (NAP XXXI 6'18) is in a fragment of poorly preserved maxilla (Fig. 77). The crown is like other specimens from Napak, with the paracone and protocone in mesial positions, making for a small mesial fovea and a large distal fovea, both of which are bordered by cingula. The paracone is slightly taller than the protocone. The pre- and postcrista of the paracone are sharp and lie in line with each other and are oriented mesio-distally. The pre- and postcrista of the protocone in contrast are swollen and curve buccally. There is a cingular swelling on the lingual surface of the protocone. The roots, visible in mesial view, are stout. There is only one buccal root which is unusual for *Ugandapithecus*, and one lingual root.

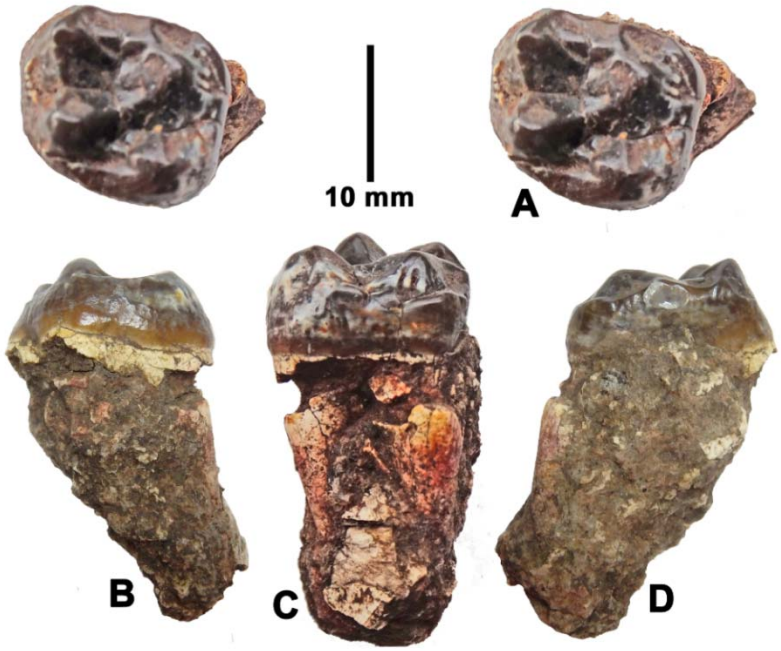

Figure 78. NAP XXXI 35'19, right M2/ of *Ugandapithecus* from Napak XXXI, Uganda. A) stereo occlusal view, B) distal view, C) lingual view, D) mesial view (scale : 10 mm).

An upper molar (NAP XXXI 35'19) is lightly worn (Fig. 78). The morphology of the crown is typical of other upper molars from Napak, but the buccal cingular structure is somewhat more in evidence than it is in other specimens. The lingual cingulum is also well developed on the protocone but is more subtle on the hypocone. Mesially and distally there are interstitial facets where the tooth contacted the neighbouring teeth.

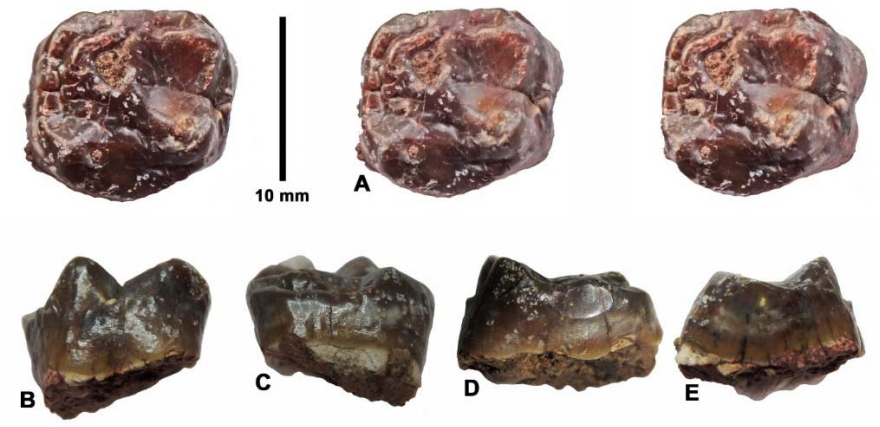

Figure 79. NAP XXXI 20'20, left M1/ of *Ugandapithecus* from Napak XXXI, Uganda. A) stereo occlusal views, B) buccal view, C) lingual view, D) mesial view, E) distal view (scale : 10 mm).

NAP XXXI 20'20 is an upper left molar (Fig. 79). Wear has advanced to the stage where there is dentine visible on the protocone but not yet at the apices of the paracone, metacone and hypocone. The buccal cingular complex beneath the end of the median transverse valley is prominent and beaded. The lingual cingulum is broad on the protocone and at the lingual end of the median transverse valley, but fades out on the hypocone. In other respects the morphology of the tooth is similar to that of other upper molars from Napak, the paracone being the smallest cusp, the protocone the largest. There is a slit between the paracone and metacone (buccal notch).

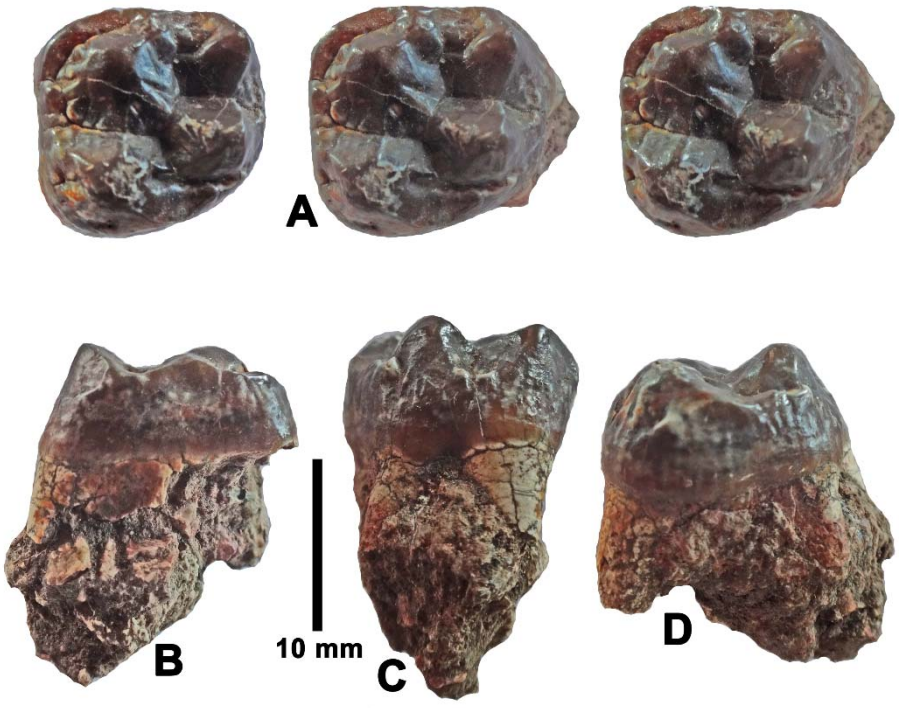

Figure 80. XXXI 3'15, left M2/ of *Ugandapithecus* from Napak XXXI, Uganda. A) stereo occlusal views, B) mesial view, C) buccal view, D) distal view (scale : 10 mm).

NAP XXXI 3'15 is an upper molar with damaged roots (Fig. 80). A noticeable feature of this tooth is the small stature of the paracone and the large dimensions of the protocone and hypocone. The lingual cingulum is broad and rises close to the lingual end of the median transverse valley, where it becomes beaded. The lingual and distal base of the protocone is scored by shallow but broad furrows. The buccal cingular complex beneath the buccal end of the median transverse valley is subtle. There are interstitial contact facets on the mesial and distal sides of the tooth.

Figure 81. Stereo occlusal views of NAP XXXI 3'16, right M3/ of *Ugandapithecus* from Napak XXXI, Uganda (scale : 10 mm).

A striking aspect of the upper third molar (NAP XXXI 3'16) is the presence of deep furrowing on the lingual surface of the protocone (Fig. 81). The lingual cingulum is tall and is also furrowed by grooves. These grooves could be related to a hypoplastic condition (Pickford & Ishida, 1998) rather than reflecting the the morphology had hypoplasia not occurred, and thus may not be relevant for phylogenetic analyses. This tooth is evidently an upper third molar because the metacone is reduced in dimensions, as is the hypocone. The protocone in contrast is large and occupies almost half the occlusal surface of the crown. The mesial edge of the crown has a depression that looks like a caries lesion. There is no distal interstitial contact facet.

Lower dentition

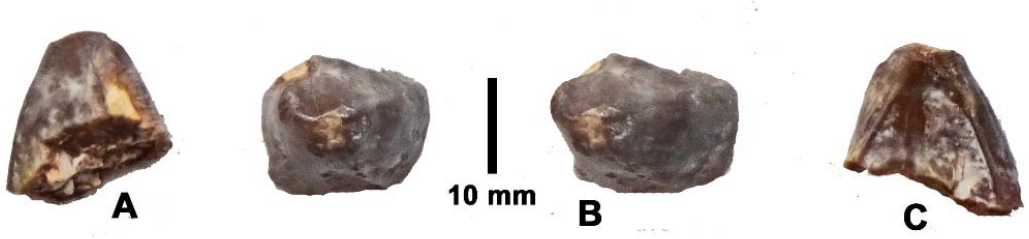

Figure 82. NAP XXXI 99'15, apex of lower canine of *Ugandapithecus* from Napak XXXI, Uganda. A) labial view, B) stereo occlusal view, C) lingual view (scale : 10 mm).

A lower canine apex (NAP XXXI 99'15) (Fig. 82) shows the apical burin-like morphology in which the precristid is offset from the apex somewhat before descending towards the cervix.

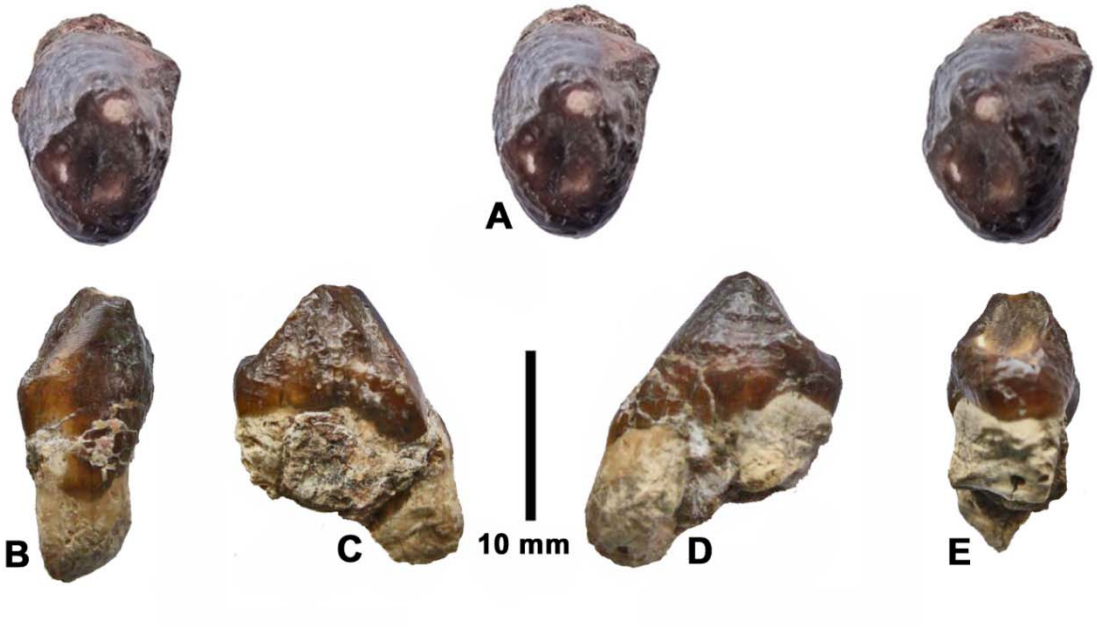

Figure 83. NAP XXXI 11'14, left p/3 of *Ugandapithecus* from Napak XXXI, Uganda. A) stereo occlusal views, B) mesial view, C) lingual view, D) buccal view, E) distal view (scale : 10 mm).

A p/3 (NAP XXXI 11'14) has a conspicuous main cusp (protoconid) on the distal edge of which is a low cuspid, probably the hypoconid (Fig. 83). The apices of both these cusps expose dentine despite the slight amount of wear. The mesial foveid is small and shallow, bordered buccally by the preprotocristid. The distal basin in contrast is large, but shallow, bordered buccally by the hypoconid and lingually by the endoprotocristid. There is an expansive wear facet on the mesio-buccal side of the crown, due to honing actions of the upper canine. In buccal and lingual views, the enamel is seen to extend further rootwards on the mesial root than on the distal one, evidently part of the honing complex. Perikymata are visible on the mesial and buccal surfaces of the crown.

Napak XXXII

The discovery of Napak XXXII in 2015 high on the hillside of Akisim was a surprise because it yielded an unusual fauna for Napak, comprising proboscideans, hyracoids, chalicotheres, rhinocerotids, huge suoids, ruminants and rodents, as well as two teeth of large apes and one of a small ape. The fauna indicates a middle Miocene age, and it is thus of interest to observe that the two great ape fossils do not belong to *Ugandapithecus*, but are more similar to specimens of *Afropithecus*. The associated fauna suggests an age of ca 16 Ma for this tooth, which is 3 to 3.5 million years younger than the bulk of large ape fossils from Napak (Pickford & Tsujikawa, 2019).

Upper dentition

From the Akisim Member there is an upper fourth premolar (NAP XXXII 2'17) which differs markedly from other examples of the corresponding tooth of large apes from Napak (Fig. 84).

Figure 84. NAP XXXII, 2'17, left P4/ of cf *Afropithecus* from Napak XXXII, Uganda. A) stereo occlusal view, B) mesial view, C) lingual view, D) buccal view (note the reduced distal root), E) distal view (scale : 5 mm).

The crown has two main cusps which are accompanied by a broad smooth lingual cingulum which continues uninterrupted onto the distal side of the tooth. The paracone is moderately worn, and is unusual in having a buccal surface that flares buccally to a significant extent, and then basally produces a secondary swelling just above the cervix. The parastyle and mesostyle are quite large, even if low. The protocone exposes a small patch of dentine apically and the cusp itself appears to have very thick enamel, the preprotocrista being broad and short, the postprotocrista also being swollen. There is a central basin, but the mesial and distal foveae are small. The distal root on the buccal side is reduced in mesio-distal direction (more so than in *Ugandapithecus*) but is broad bucco-lingually. The mesio-buccal root is large.

Comparisons with other Miocene hominoids reveals close correspondence to specimens of *Afropithecus turkanensis* from Kalodirr, Kenya, and Moroto II, Uganda (Leakey & Leakey, 1986; Pickford, 2002; Pickford *et al*. 1999; Harrison, 2010). The protocone and paracone are relatively close together, as in the Moroto specimen and the holotype of *Afropithecus turkanensis*.

Lower dentition

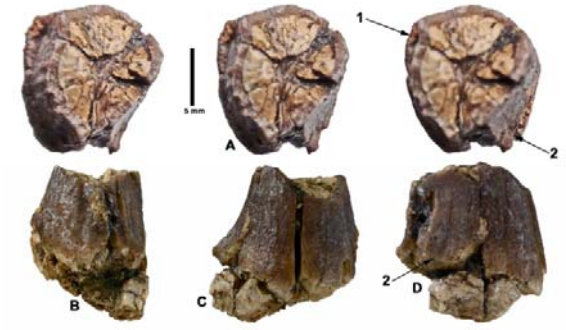

Figure 85. NAP XXXII 2'15, right lower canine fragment of a large ape from Napak XXXII, Uganda. A) stereo apical views, B) distal view, C) labial view, D) disto-labial view (1 - mesio-lingual groove, 2 - disto-labial wear facet) (scale : 5 mm).

For the sake of completeness, a badly damaged lower canine from the Akisim Member is illustrated (Fig. 85). Its apex is missing, as are those of many large ape canines from Napak, and basally the root is absent, the cervix being badly damaged. There is a low, narrow lingual cingulum, a mesial groove to the lingual side of the precristid, and a wear facet on the disto-labial side of the crown. The postcristid is sharp and is bordered lingually by a shallow vertical groove.

Measurements

Table 2. Measurements (in mm) of the currently available deciduous teeth of large apes from Napak. In **bold** are teeth associated in a mandible (lt - left, rt - right).

Catalogue	Tooth	MDL	BLB	Taxon
Nap V 10'16+57'16	di/2 lt	4.9	4.5	*U. major*
NAP V 57'16	dc/1 lt	8.6	6.8	*U. major*
NAP XXX 41'16	dc/1 rt	8.4	6.5	*U. major*
NAP V 57'16	d/3 lt	9.8	6.3	*U. major*
NAP XV 394'08	d/3 rt	8.3	6.0	*Ugandapithecus* sp.
NAP V 57'16	d/4 lt	10.7	8.9	*U. major*
NAP V 56'11	dI1/ lt	7.3	4.9	*Ugandapithecus* sp.
NAP V 1'99	dC1/ lt	8.6	7.5	*Ugandapithecus* sp.
NAP IV UMP 62.20	dC1/ rt	7.2	6.8	*Ugandapithecus* sp.
NAP I 28'01	D4/ lt	8.9	10.0	*Ugandapithecus* sp.

Table 3. Measurements (in mm) of the currently available permanent upper teeth of large apes from Napak. In **bold** are teeth associated in maxillae (lt - left, rt - right, * - meristic position unsure) (Some fragmentary teeth are not listed).

Catalogue	Tooth	MDL	BLB	Taxon
NAP V 7'11	I1/ lt	12.2	9.0	*Ugandapithecus* sp.
NAP XV 60'11	I1/ lt	12.4	8.5	*Ugandapithecus* sp.
NAP I 181'02	I1/ rt	11.3	8.6	*Ugandapithecus* sp.
NAP V 131'12	I1/ rt	12.4	9.0	*Ugandapithecus* sp.
NAP V 169'08	I1/ rt	--	7.6	*Ugandapithecus* sp.
NAP XV 60'11	I1/ rt	12.3	8.7	*Ugandapithecus* sp.
NAP XV 60'11	I2/ lt	9.9	10.2	*Ugandapithecus* sp.
NAP XXXI 11'17	I2/ lt	7.1	9.2	*U. legetetensis*
NAP I 1'09	I2/ rt	8.6	10.7	*Ugandapithecus* sp.
NAP V 140'08	I2/ rt	8.5	10.4	*Ugandapithecus* sp.
NAP V 3'10	I2/ rt	8.0	9.4	*Ugandapithecus* sp.
NAP XV 116'07	I2/ rt	--	--	*Ugandapithecus* sp.
NAP XV 60'11	I2/ rt	9.7	9.9	*Ugandapithecus* sp.
NAP XV 31'11	I2/ rt	8.3	9.2	*Ugandapithecus* sp.
NAP IV 60'14	C1/ rt m	12.6	10.4	*U. legetetensis*
NAP XXXI 10'17	C1/ rt f	10.0	10.0	*U. legetetensis*
NAP V 10'19	C1/ lt f	15.4	15.7	*U. major*
NAP XV 60'11	C1/ lt m	18.5	16.6	*U. major*
NAP XIII 3'14	C1/ rt f	16.0	14.6	*U. major*
NAP XV 60'11	C1/ rt m	18.8	16.2	*U. major*
NAP XXVI 1'12	C1/ rt f	15.6	15.2	*U. major*
NAP IX BUMP 763	C1/ m	17.5	15.3	*U. major*
NAP I UMP 62.05	C1/ lt m	18.9	16.3	*U. major*
NAP I UMP 62.03	C1/ rt f	16.4	13.6	*U. major*
NAP V 62.01	C1/ rt f	16.3	15.4	*U. major*
NAP V UMP 62.04	C1/ rt m	19.4	16.4	*U. major*
NAP V 54'11	P3/ lt	9.7	14.6	*U. major*
NAP XIII 1'14	P3/ lt	9.0	11.6	*U. legetetensis*
NAP XV 60'11	P3/ lt	12.2	15.0	*U. major*
NAP V 220'09	P3/ rt	10.0	14.5	*U. major*
NAP XV 60'11	P3/ rt	12.0	15.1	*U. major*
NAP XXXI 10'14	P3/ rt	10.3	13.7	*U. major*
NAP V 134'12	P4/ lt	8.0	11.5	*U. major*

NAP V 53'16	P4/ lt	6.7	12.2	*U. legetetensis*
NAP XIII 1'14	P4/ lt	7.0	11.6	*U. legetetensis*
NAP XIII 13'16	P4/ lt	9.1	15.2	*U. major*
NAP XV 60'11	P4/ lt	7.5	14.8	*U. major*
NAP XXXI 6'18	P4/ lt	8.1	13.7	*U. major*
NAP XXXII 2'17	P4/ lt	6.6	11.8	cf *Afropithecus*
NAP V MUZM 146	P4/ rt	7.0	12.1	*U. legetetensis*
NAP V UMP 69.01	P4/ rt	7.7	13.7	*U. major*
NAP XV 134'12	P4/ rt	8.3	--	*U. major*
NAP XV 60'11	P4/ rt	8.0	14.6	*U. major*
NAP XV 9'18	M1/ rt	10.0	10.9	*U. legetetensis*
NAP XXXI 20'20	M1/ lt	11.2	12.6	*U. legetetensis*
NAP XII 2'13	M1/ rt	11.2	12.4	*U. legetetensis*
NAP XIII 1'14	M1/ lt	10.3	11.4	*U. legetetensis*
NAP XV 60'11	M1/ lt	12.3	14.6	*U. major*
NAP XV 60'11	M1/ rt	12.7	14.5	*U. major*
NAP V 1'03	M1/ rt	11.5	14.0	*U. legetetensis*
NAP XXXI 35'19	M2/ rt	13.5	15.3	*Ugandapithecus* sp.
NAP XV 24'18	M2/ lt	13.0	15.3	*U. major*
NAP XXXI 3'15	M2/ lt	13.5	15.3	*Ugandapithecus* sp.
NAP XV 60'11	M2/ lt	14.3	16.5	*U. major*
NAP XV 60'11	M2/ rt	14.2	16.3	*U. major*
NAP XIII 2'14	M*/ frag	12.4	--	*Ugandapithecus* sp.
NAP IV 146'12	M*/ lt	14.3	16.1	*Ugandapithecus* sp.
NAP V 1'14	M*/ lt	12.8	16.1	*Ugandapithecus* sp.
NAP V UMP 62.07	M*/ lt	11.2	13.9	*Ugandapithecus* sp.
NAP I UMP 62.09	M*/ rt	11.1	13.0	*Ugandapithecus* sp.
NAP IV UMP 66.41	M*/ rt	11.7	13.5	*Ugandapithecus* sp.
NAP V UMP 69.02	M*/ rt	11.0	13.3	*Ugandapithecus* sp.
NAP V 5'09	M*/ rt	13.0	14.7	*Ugandapithecus* sp.
NAP XV 60'11	M3/ lt	14.4	17.9	*U. major*
NAP XV 60'11	M3/ rt	15.0	16.6	*U. major*
NAP V UMP 62.08	M3/ lt	15.0	16.8	*U. major*
NAP V 80'10	M3/ rt	12.2	13.8	*U. legetetensis*
NAP XVIII 1'19	M3/ rt	12.6	14.8	*U. legetetensis*
NAP XXXI 3'16	M3/ rt	12.2	15.8	*U. legetetensis*

Table 4. Measurements (in mm) of the currently available permanent lower teeth of large apes from Napak. In **bold** are teeth associated in mandibles (e - estimated measurement; lt - left, rt - right, * - meristic position uncertain) (Some fragmentary teeth are not listed).

Caralogue	**Tooth**	**MDL**	**BLB**	**Taxon**
NAP V 2'14	i/1 lt	6.3	7.3	*Ugandapithecus* sp.
NAP V 57'16	i/1 lt	7.3	--	*U. major*
NAP V 50'06	i/1 rt	--	7.0	*Ugandapithecus* sp.
NAP XV 184'08	i/1 rt	7.4	7.0	*U. major*
NAP XV 270'08	i/1 rt	7.0	9.6	*U. major*
NAP V 4'09	i/1 rt root	4.9	5.7	*Ugandapithecus* sp.
NAP V 57'16	i/2 rt	7.4	--	*U. major*
NAP V 9'16	i/2 rt	6.8	6.2	*Ugandapithecus* sp.
NAP XII 1'10	i/2 rt	6.0	8.0	*Ugandapithecus* sp.
NAP XV 35'08 + 33'09	i/2 rt	8.0	12.6	*U. major*
NAP XV 8'17	i/2 rt	7.0	8.0	*Ugandapithecus* sp.
NAP V 4'09	i/2 rt root	5.3	9.8	*Ugandapithecus* sp.
NAP XIII 5'10	c/1 m	16.0	9.3	*U. legetetensis*
NAP IX 7'98	c/1 lt f	12.4	9.7	*U. legetetensis*
NAP V 57'16	c/1 lt apex	--	--	*U. major*
NAP XV 62'07	c/1 lt m	19.2	13	*U. major*
NAP V 179'09	c/1 rt f	15.3	--	*U. major*
NAP XXX 185'14	c/1 rt f	17.0	12.2	*U. major*
NAP XV 116'12	c/1 rt m	19.6	14.4	*U. major*
NAP XXXII 2'15	c/1 rt m	16.0	12.3	cf *Afropithecus*

NAP V 25'11	c/1 rt apex	--	--	*U. major*
NAP V 95'09	p/3 lt	12.5	7.4	*U. legetetensis*
NAP XV 61'07	p/3 lt	14.0	9.7	*U. major*
NAP XXXI 11'14	p/3 lt	16.0	9.6	*U. major*
NAP V 57'16	p/3 lt	11.2	9.2	*U. major*
NAP XV 62'08	p/3 rt	16.3	10.6	*U. major*
NAP V UMP 62.06	p/4	8.5	9.7	*U. legetetensis*
NAP I 2'99	p/4 lt	8.6	9.7	*U. legetetensis*
NAP V 46'14	p/4 lt	7.6	8.0	*U. legetetensis*
NAP XV 63'08	p/4 lt	9.3	11.6	*U. major*
NAP V 1'15	p/4 rt	6.7	9.0	*U. major*
NAP V 54'16	p/4 rt	9.0	9.7	*U. major*
NAP XV 62'08	p/4 rt	9.0	10.0	*U. major*
NAP XXX 31'16	p/4 rt	7.5	7.7	*U. legetetensis*
NAP V 57'16	p/4 lt	--	8.0e	*U. major*
NAP XII 1'13	m/1 lt	11.0	9.9	*U. legetetensis*
NAP XIII RS 1'10	m/1 lt	12.0	10.3	*U. legetetensis*
NAP I UMP 62.16	m/1 lt	10.5	9.3	*U. legetetensis*
NAP IV 56'14	m/1 lt	12.6	11.6	*U. major*
NAP IV 70'16	m/1 lt	10.6	9.5	*U. legetetensis*
NAP V 57'16	m/1 lt	12.4	11.3	*U. major*
NAP XV 100'08	m/1 lt	12.4	11.5	*U. major*
NAP V 69'14	m/1 lt	11.6	10.0	*U. legetetensis*
NAP V 81'10	m/1 lt	10.9	9.2e	*U. legetetensis*
NAP I BUMP 601	m/1 rt	12.6	11.4	*U. major*
NAP I UMP 62.13	m/1 rt	10.0	9.5	*U. legetetensis*
NAP XV 62'08	m/1 rt	12.3	11.4	*U. major*
NAP XV 8'08	m/1 lt	12.9	11.5	*U. major*
NAP XII 10'19	m/1 rt	11.1	10.3	*U. legetetensis*
NAP V 88'09	m/1 rt	12.6	11.2	*U. major*
NAP CC BUMP 269	m/1 rt	11.9	11.1	*U. legetetensis*
NAP I UMP 62.14	m/1 rt	11.8	10.4	*U. legetetensis*
NAP XII 1'13	m/2 lt	13.2	12.0	*U. legetetensis*
NAP XV 2'12	m/2 lt	14.9	13.2	*U. major*
NAP I BUMP 601	m/2 rt	14.3	12.7	*U. major*
NAP UMP 62.15	m/2 lt	12.4	11.0	*U. legetetensis*
NAP XV 174'08	m/2 lt	12.4	11.3	*U. legetetensis*
NAP V 134'17	m/2 lt germ	--	12.7	*U. major*
NAP I 49'00	m/3 lt	--	13.4	*U. major*
NAP XV 45'15	m/3 lt	14.0	11.1	*U. legetetensis*
NAP V 2'12	m/3 lt	17.0	13.2	*U. major*
NAP I BUMP 600	m/3 lt	18.2	13.8	*U. major*
NAP XV 117'07	m/3 lt	18.7	13.6	*U. major*
NAP XV 60'07	m/3 lt	18.9	14.0	*U. major*
NAP I BUMP 601	m/3 rt	17.8	14.1	*U. major*
NAP V 133'17	m/3 rt	19.0	17.0	*U. major*
NAP V 80'11	m/3 lt	12.1	11.7	*U. legetetensis*

DISCUSSION

The prevalence of hypoplastic grooves on the permanent canines of Napak apes

There are 24 large ape permanent canines from Napak, 10 lowers and 14 uppers (Table 5). Many of them lack the apices which have broken off at about the same place, suggesting a weakness in the teeth at this point.

Table 5. Permanent canines of large apes from Napak Uganda.

Tooth	Comments
Lower canines	
NAP XIII 5'10	Apex damaged
NAP IX 7'98	Complete
NAP V 57'16	Apex only
NAP XV 62'07	Apex missing
NAP V 179'09	Apex damaged and polished
NAP XXX 185'14	Complete
NAP XV 116'12	Complete but cracked across
NAP XXXII 2'15	Apex broken
NAP V 25'11	Apex only
NAP XXXI 99'15	Apex only
Upper canines	
NAP IX BUMP 763	Apex missing
NAP I UMP 62.05	Apex missing
NAP V 10'19	Apex missing
NAP XV 60'11 left	Complete
NAP XV 60'11 right	Complete
NAP I UMP 62.03	Apex missing
NAP V UMP 62.04	Apex missing
NAP IV 60'14	Complete
NAP XXXI 10'17	Apex missing + hypoplastic groove
NAP XIII 3'14	Apex cracked all round but not broken off
NAP XXV1 1'12	Apex missing
NAP V 61'02	Apex missing
NAP V 57'16 left	Apex only
NAP V 57'16 right	Apex only

Out of ten lower canine crowns, seven are missing the apex (or comprise only the apex) three are complete, of which one has the apex cracked all around but it has not broken off.

Out of 14 upper canine crowns ten are lacking the apex (or comprise only the apex) and four are complete, of which one has a crack all round the crown, but it has not broken off.

Thus fully two thirds of upper and lower canine crowns are broken, the damage occurring at more or less the same place on the teeth. Some of the specimens are well enough preserved to reveal the presence of a hypoplastic groove or grooves in the cervical third of the tooth, so it is inferred that the apices broke off post-mortem where they did, due to a zone of weakness related to the hypoplasia.

In extant large apes, there is often a hypoplastic groove on the canines which is considered to be related to stresses that occurred during the weaning phase of the individual, at ca 3 - 5 years of age (Dean & Wood, 1981; Ubelaker, 1978; Pickford & Ishida, 1998). In such cases the hypoplastic groove is referred to as the « weaning line ». At weaning, individuals suffer emotional stress, and sometimes ingest foods and other things that can cause digestive problems, thereby upsetting the normal functioning of the organism. Fevers in particular can interrupt proper formation of hard tissues such as teeth.

It is inferred that the damage to the permanent canine crowns in the Napak large apes during their formation, is most likely to be related to stresses during weaning, but other factors that can result in enamel hypoplasia, such as fevers caused by malaria and other diseases, cannot be eliminated from consideration.

The significant quantity of juvenile large ape individuals at Napak

Juvenile great ape teeth and jaws have been found at six of the fossiliferous localities at Napak (Table 6).

Table 6. List of infant and juvenile large ape specimens from Napak.

Catalogue	Specimen
NAP I 28'01	D4/
NAP I UMP 62.13	juvenile mandible
NAP IV 70'16	lower molar germ
NAP IV 62.20	deciduous upper canine/
NAP V 57'16	infant mandible and upper canines
NAP V 1'99	deciduous upper canine
NAP V 56'11	deciduous upper central incisor
NAP V 30'12	P4/ germ
NAP V 9'16	i/2 germ
NAP V 54'16	p/4 germ
NAP V 134'17	lower molar germ
NAP V 7'11	I1/ germ
NAP V 131'12	I1/ germ
NAP V 140'08	I2/ germ
NAP XIII 1'10	juvenile mandible
NAP XV 8'17	i/2 germ
NAP XV 116'07	I2/ germ
NAP XV 148'08	i/1 germ
NAP XV 394'08	d/3
NAP XXX 41'16	deciduous lower canine

The presence of juvenile individuals at six of the eleven Napak localities that have yielded large apes indicates that there was a significant rate of mortality among young individuals. There is perhaps nothing unusual about this, as it is known that a proportion of extant ape populations suffer early deaths. Kennedy (2005) reported that, among Gombe chimpanzees (Tanzania) more than 50% of deaths occurred before adulthood. What is unusual about Napak is that the remains were commonly preserved as fossils, possibly due the alkaline geochemical composition of the tuffs and palaeosols in which they were eventually buried.

We do not perform detailed age profiling using all the specimens, but it seems clear that weaning was a particularly problematic time for infants (see below), and that several sub-adults died in the year or two following weaning. It is also clear from the adult specimens, that some individuals lived to a great age, several m/3s being worn flat.

Age profile of NAP V 57'16

The infant mandible of *Ugandapithecus major* from Napak V has the deciduous teeth in occlusion with light wear on the canine. Preserved in the jaw are the left di/2, dc/1, d/3 and d/4. Still in their crypts are three of the permanent incisors, the apical third of the canine, the p/3, p/4 and m/1. There is no sign of root formation in any of the permanent teeth, although in some isolated teeth found nearby which could represent the same individual, there is minor root formation in the mesial and distal parts of the upper central incisors and the I2/. The m/2 from the same area has the four main cusps bound together but there is no sign of the hypoconulid.

In terms of the human developmental clock (Ubelaker, 1989; Blenkin & Taylor, 2012) the Napak infant *Ugandapithecus* jaw corresponds to individuals aged ca 3.75 +/- 1 year (female developmental clock Modern Australian population) or 3.8 +/- 1 year (male developmental clock). Of course, account needs to be made for differences in ontogenetic development between great apes and humans, which are even among themselves quite variable. Chimpanzees at Kanyawara, Uganda, have the m/1 emergent at 3.5-4 years of age (Smith *et al*. 2013), whereas in the Napak infant, the crown of the m/1 is still not fully formed and it had not yet started to emerge when the individual died. It is thus inferred that the Napak

individual died at an earlier neontological phase than the infant specimen of *Afropithecus turkanensis* from Moruorot, Kenya, in which the m/1 was in the process of erupting towards gingival level (Kelley & Smith, 2003).

Although the age of onset of the weaning process varies in chimpanzees (4 - 4.5 years : Kennedy, 2005) and gorillas (3.5 - 4 years : Fossey, 1979, 1983), there is a broad correlation between the eruption of the first permanent molar and the onset of consumption of solid foods as the main source of nutriment. From this it is inferred that the Napak infant died a short time prior to weaning, or perhaps during the onset of the weaning phase of the individual (possible some time between 3.5 and 4.5 years of age).

Metric analysis

Bivariate plots of the large ape teeth from Napak (Figs 86-89) indicate the presence of at least two taxa, each of which has sexually bimodal and dimorphic canines and P3/s. The P4/s and p/4s form two clusters of points, as do the M3/s and m/3s, but due to difficulties in identifying the meristic positions of the first and second molars it is not possible to allocate all the teeth satisfactorily except for the few teeth preserved in maxillae and mandibles. If these are taken into account, then two clusters of points can be distinguished for the first molars but the quantity of specimens is rather low, and even lower for the second molars.

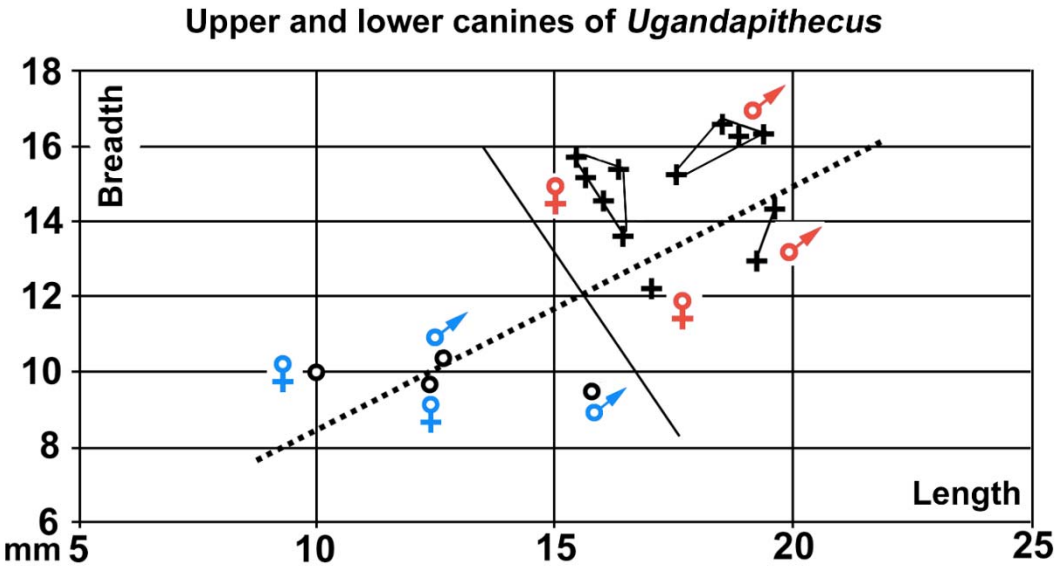

Figure 86. Bivariate plots of male and female upper and lower canines of *Ugandapithecus* from Napak. Blue gender symbols are *Ugandapithecus legetetensis*, red gender symbols are *Ugandapithecus major*. Both species shows a bimodal distribution.

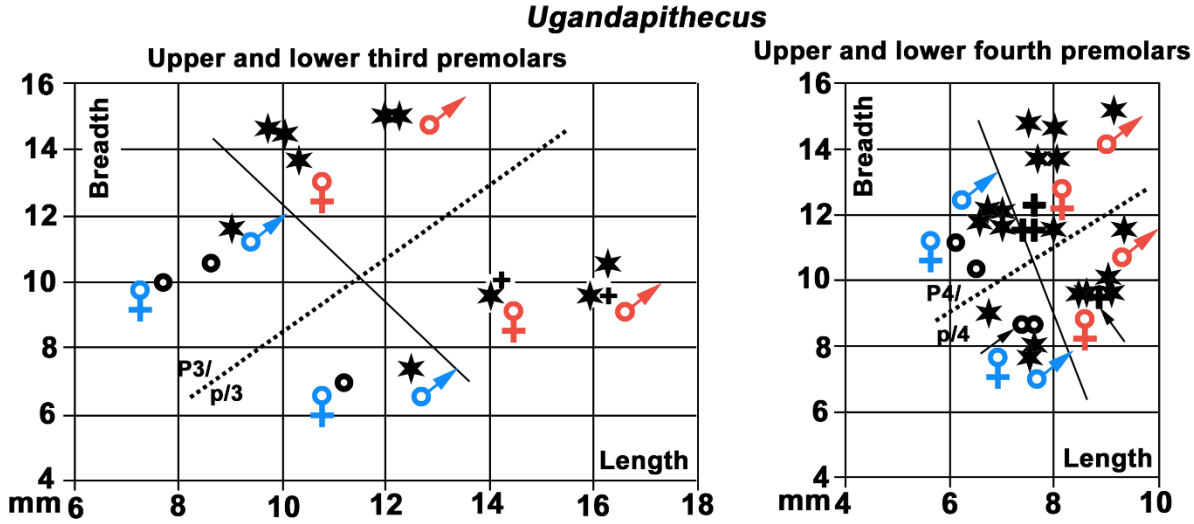

Figure 87. Bivariate plots of premolars of *Ugandapithecus major* and *U. legetetensis* from East Africa. The dotted lines separate the upper and lower teeth, the slanting black line separates specimens of *U. major* (red gender symbols) from those of *U. legetetensis* (blue gender symbols). Star - Napak fossils, **o** - *U. legetetensis*, + - *U. major*. The arrows show the type specimens of *U. major* and *U. legetetensis*. Even though the samples are small there appears to be a bimodal distribution in the p/3 and P3/ of *U. major*.

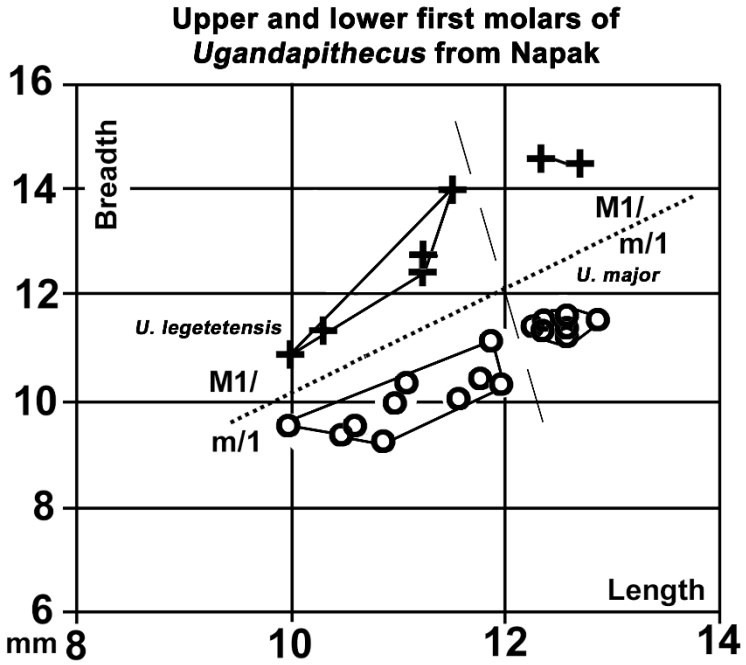

Figure 88. Bivariate plots of upper and lower first molars of *Ugandapithecus major* and *U. legetetensis* from Napak. (**o** – lower molars, + - upper molars).

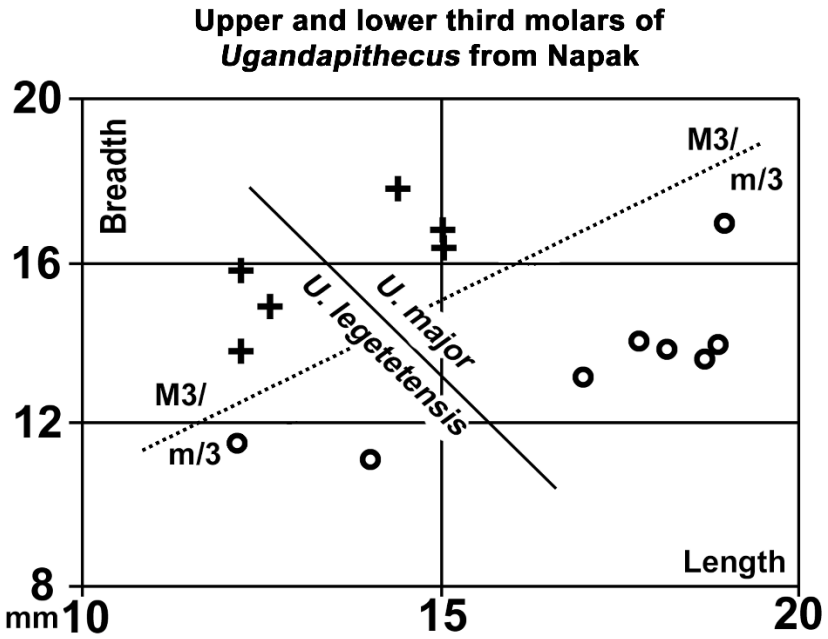

Figure 89. Bivariate plots of upper and lower third molars of *Ugandapithecus* from Napak. There are two clouds of points for each tooth, the large specimens corresponding to *U. major*, the small ones to *U. legetetensis*. (+ : M3/s, **o** : m/3s). The dotted line separates the upper teeth from the lowers. The slanting line separates the two taxa.

There is a third large ape taxon at Napak based on the morphology of the P4/ from Napak XXXII, which has similar dimensions to its counterparts in *Ugandapithecus legetetensis*, but morphology that departs greatly from that of P4/s of this species, resembling more closely the morphology of upper fourth premolars of *Afropithecus* : protocone and paracone relatively close together, large degree of buccal flare, thicker enamel, small disto-buccal root.

Taxonomy

MacLatchy & Rossie (2005) considered that *Ugandapithecus* was a junior synonym of *Proconsul*. As pointed out in the introduction, there are significant differences between the dentitions of *Proconsul africanus* on the one hand, and those of *Ugandapithecus major* and *Ugandapitheus legetetensis*, on the other. There are also osteological differences in the maxilla which will be described in detail in a forthcoming paper.

We here provide an illustration of the maxillary dentitions of the type specimen of *Proconsul africanus* Hopwood (1933) and those of two species of *Ugandapithecus* to emphasize the differences between the taxa (Fig. 90). For these reasons the authors consider that synonymy between these genera is unlikely, a viewpoint that has already been published (Pickford *et al*. 2009).

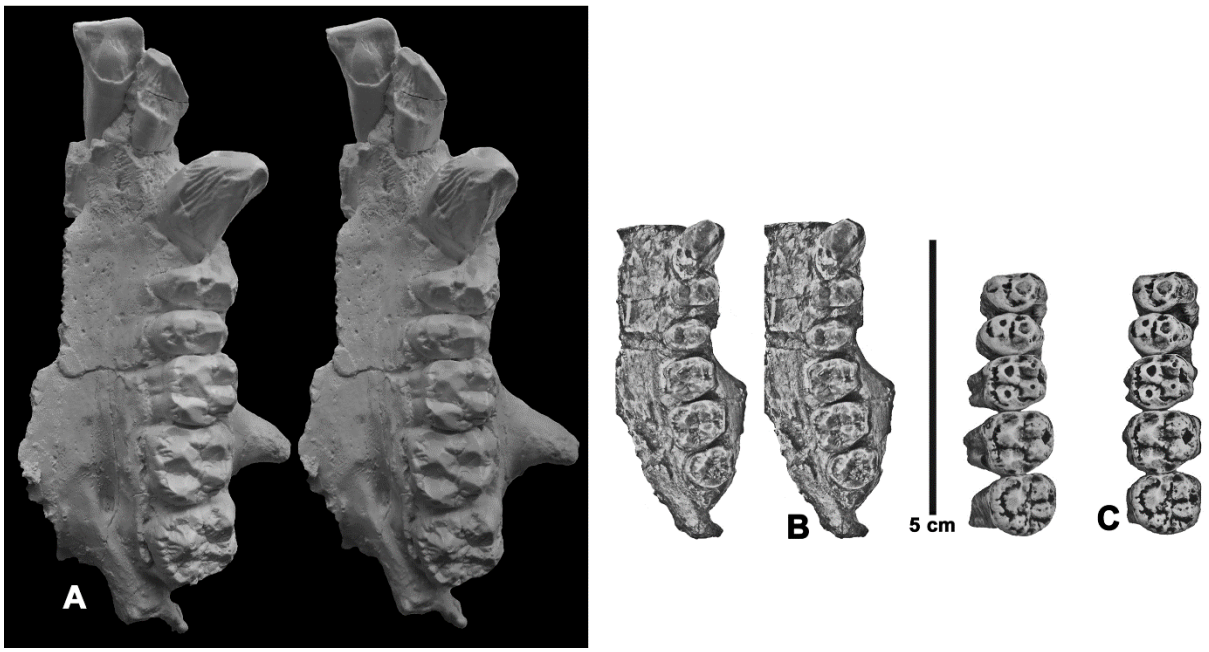

Figure 90. Comparison of left upper tooth rows of (A) *Ugandapithecus major* (NAP XV 60'11), (B) *Proconsul africanus* (NHMUK M 14084) and *Ugandapithecus legetetensis* (KNM CA 387-391, cast) (C). Stereo occlusal views, specimens aligned at the front of M1/ (scale : 5 cm).

Stratigraphic distribution

The basal Iriri Member of the volcano-sedimentary succession at Akisim Mountain has yielded 13 large ape teeth (Table 7). Comparisons with the *Ugandapithecus meswae* (Harrison & Andrews, 2009), *U. legetetensis* Pickford *et al*. (2009), and *U. major* (Le Gros Clark & Leakey, 1951) from the type localities in Kenya, indicate that there are two taxa in the Iriri Member, *U. legetetensis* and *U. major*, but some of the upper molars fall in between the range of variation of the two species, so for the time being they are left in open nomenclature.

Table 7. Species attribution of large ape teeth from the Iriri Member at Napak. Specimens identified as *Ugandapithecus* sp. are intermediate in dimensions between *U. major* and *U. legetetensis* (f - female).

Catalogue	Tooth	Taxon
NAP XXVI 1'19	M1/	*U. legetetensis*
NAP XXX 185'14	c/1 f	*U. major*
NAP XXX 31'16	p/4	*U. legetetensis*
NAP XXX 41'16	dc/1	*U. major*
NAP XXXI 10'14	P3/	*U. major*
NAP XXXI 10'17	C1/ f	*U. legetetensis*
NAP XXXI 11'14	p/3	*U. major*
NAP XXXI 11'17	I2/	*U. legetetensis*
NAP XXXI 20'20	M1/	*Ugandapithecus* sp.
NAP XXXI 3'15	M2/	*Ugandapithecus* sp.
NAP XXXI 3'16	M3/	*Ugandapithecus* sp.
NAP XXXI 6'18	P4/	*U. major*
NAP XXXI 99'15	c/1 apex	*Ugandapithecus* sp.

Large ape teeth from the Napak Member that can be attributed to species with confidence because their meristic position is clear, reveal that there are two taxa present, *Ugandapithecus legetetensis* and *U. major* (Tables 3-4). It is stressed that several isolated teeth from this member are left in open nomenclature because their meristic position is uncertain.

Finally, the youngest fossiliferous levels in the Akisim Member at Napak, have yielded two large ape teeth, one of which is of uncertain taxonomic affinities because it comprises a broken canine, the other of which is close in morphology and dimensions to corresponding teeth in *Afropithecus turkanensis* Leakey & Leakey (1986) from Kalodirr on the one hand, and Moroto II on the other (Pickford, 2002).

It is concluded that there are three taxa of large apes present at Napak - *Ugandapithecus major*, *Ugandapithecus legetetensis* and cf *Afropithecus turkanensis*. Whilst it is not possible at present to attribute every tooth to a specific taxon, due to overlapping dimensions and similar morphology among the molars in particular, it is clear from the teeth, the meristic position of which can be confidently identified because they are in mandibles or maxilla, that there are two size groups of *Ugandapithecus*, and two specimens of a different large ape, the P4/ of which is close in morphology and dimensions to corresponding teeth in *Afropithecus turkanensis*. Given the paucity of the Napak record of the last species, it is cited as cf *Afropithecus turkanensis*.

CONCLUSIONS

There are three species of large apes at Napak. The basal Iriri Member (NAP XVIII, XXX, XXXI) has yielded specimens of *Ugandapithecus legetetensis* and *U. major*. The same two species are abundant in the Napak Member (NAP I, IV, V, IX, XII, XIII, XV, XXVI, CC) whereas in the middle Miocene deposits at Napak XXXII two large ape fossil teeth have been found, which are attributed to cf *Afropithecus turkanensis*. Some of the isolated molars from the Napak Member are left in open nomenclature because it is difficult to be sure of their meristic position. Further discoveries may resolve some of the uncertainties. Finally it is concluded that *Proconsul* is a distinct genus of great ape, and that *Ugandapithecus* is not a junior synonym of it.

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