GEO-PAL UGANDA

SUDAN

Moroto II ⭐

CONGO

Nile

Lake Albert

Lake Kyoga

U G A N D A

KENYA

Lake Edward

Lake Victoria

TANZANIA

Uganda Museum, Kampala

Geo-Pal Uganda

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Landslide geology and taphonomic context of Moroto II, Uganda

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ABSTRACT

Moroto I and Moroto II are fossiliferous sites in northeastern Uganda known principally for the large hominoid remains of basal middle Miocene age found there in association with a diversity of other vertebrates. What is less known is that Moroto II also yielded fossils of Plio-Pleistocene vertebrates and invertebrates, including warthog (*Phacochoerus* sp.) bovids, rodents, ostrich eggshells and landsnails. Furthermore, there are stone tools of diverse palaeocultures scattered on the surface

The aim of this paper is to reassess the Cainozoic deposits that occur in the vicinity of Kogole Hill and to establish the context and taphonomy of the fossils that were collected there.

Key Words :- Middle Miocene, Plio-Pleistocene, Stratigraphy, Preservation characters, In situ, Landslide, Geomorphology, Palaeovalley, Basalt.

INTRODUCTION

The discovery of fossils at Moroto I (Loitakero) was made by J.G. Wilson in 1959. During the subsequent decade many visits were made to the site by W.W. Bishop and colleagues, and a second site, Moroto II (Kogole, Bissett's Sands, Primate Site) was found during these surveys (Bishop & Whyte, 1962; Allbrook & Bishop, 1963) (Figs. 1-3). Although precise records of the discovery loci of the various fossils found at Moroto II were not made (MacLatchy et al. 2019) there are two screening dumps beneath trees at the so-called « Primate Site » where field workers screened the surface lag in search of additional fossils. It is thus possible to determine within ca 10 metres where the main fossils of exceptional interest were found (Bishop field notes – see Musalizi et al. 2009, p. 74). The Moroto anthropoid vertebrae were likely to have been found close to the main stream descending the valley at Moroto II, where there is a dump that contains numerous fragments of rounded, abraded and polished Miocene fossils. The most complete vertebra is labelled MOR II 61, indicating that it was probably collected in 1961. Bishop's field note book records the discovery of a vertebra on the

10th February, 1965 (Musalizi et al. 2009, p. 77 and p. 79). An interesting and possibly crucial piece of evidence is that the following line in the note book mentions « *two fragments of matrix containing pieces of bone* ». This is the only mention of fossils found at Moroto II which were included in matrix. The most discussed vertebra from Moroto (UMP 67-28) comprises the body plus two fragments glued onto it (Fig. 16).

The Moroto hominoid palate was most probably found ca 40 metres away from the vertebra, in a side gulley, close to the largest of the screening dumps left by Bishop's teams. The femora came from a third locale, 30 metres west of the « palate » site and 30 metres south of the « vertebra » site, part of the same fossil being found by E. Musiime of the Uganda Museum in 2007 during a routine inspection of the site (Fig. 8, 10). There is thus no close spatial association between the vertebra, the palate and the femora, in contradiction to the oft-repeated assumption that the remains could belong to a single individual (Walker & Rose, 1968; Sanders & Bodenbender, 1994; Gebo et al. 1997;

MacLatchy & Pilbeam, 1999; MacLatchy et al. 1995, 1998, 2000, 2019; Senut et al. 2000; Young & MacLatchy, 2004; MacLatchy, 2004, 2010; Gommery, 1998, 2006; Nakatsukasa et al. 2007; Nakatsukasa, 2008). Pilbeam (1969) was suitably cautious about the association of the Moroto II large anthropoid fossils to each other, but later researchers appear not to have been overly concerned about the lack of precise data concerning their discovery context.

MATERIALS AND METHODS

The Moroto II sediments infill shallow valleys dissected into Basement Complex gneisses and are overlain by horizontally disposed basalt flows (Bishop & Whyte, 1962) (Figs 1-3, 6, 7). The thickness of sediment varies from zero at the margins of the palaeovalleys, to maximal close to the axis of the palaeovalleys, in the case of Moroto II ca 37 metres. Under such circumstances, the most reliable datum is the horizontal sediment/lava contact, and not the base of the sediment pile which varies enormously in altitude according to where one observes the contact with the underlying gneiss. In this paper therefore, we use the horizontal sediment/lava plane as the datum for determining the positions of fossils.

GEOGRAPHIC LOCATIONS AND GEOMORPHOLOGICAL SETTING OF FOSSILIFEROUS EXPOSURES AT MOROTO II
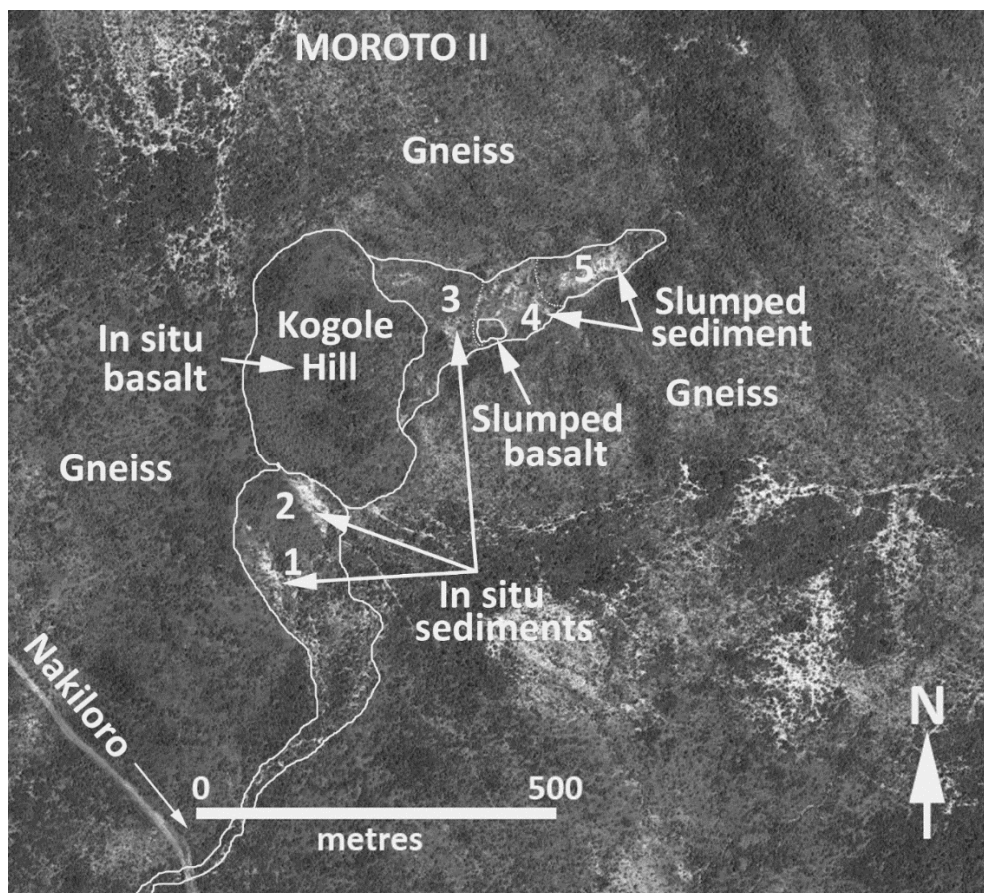
Figure 1. Moroto II, Uganda, geology and fossiliferous sites. N°s 1-5 correspond to fossiliferous exposures listed by Pickford & Mein (2006). N°4 is the « Primate Site ». Dotted lines show the limits of the slumped sediment masses. Not shown are the Plio-Pleistocene sediments (Base map from Google Earth).

In previous studies, all the outcrops of Miocene sediments and lavas in the vicinity of Kogole Hill were thought to be *in situ* (Gebo et al. 1997; Pickford & Mein, 2006; MacLatchy et al. 2006, 2019) but exposures N°4 and N°5 down the valley east of Kogole Hill represent slumped masses of sediment and lava (landslides) (Fig. 2, 4, 7). These masses were originally at the same altitude as the *in situ* lava and sediment at the head of the valley (exposure N°3), but were undercut by erosion concentrated downstream which deepened the valley eroded into the basement complex gneisses. The sediment and lava pile upstream eventually became unstable and sections of it then slumped into the depths of the deepened valley as relatively coherent landslides (i.e. not as debris flows). Exposure N°5 slumped before N°4, which is why it is more deeply eroded than the latter one. The lava at the top of exposure N°4 is still horizontal as are the sediments beneath it, indicating that the slumped mass did not rotate during its descent but retained its horizontality. The sediment/lava contact of the *in situ* outcrop at the head of the valley is at an altitude of ca 1435 metres above sea level (masl), whereas the same datum at exposure N°4 is at ca 1397 masl, indicating that the slumped mass moved ca 38 metres downwards. The lateral component of movement was less than 100 metres (Fig. 2).
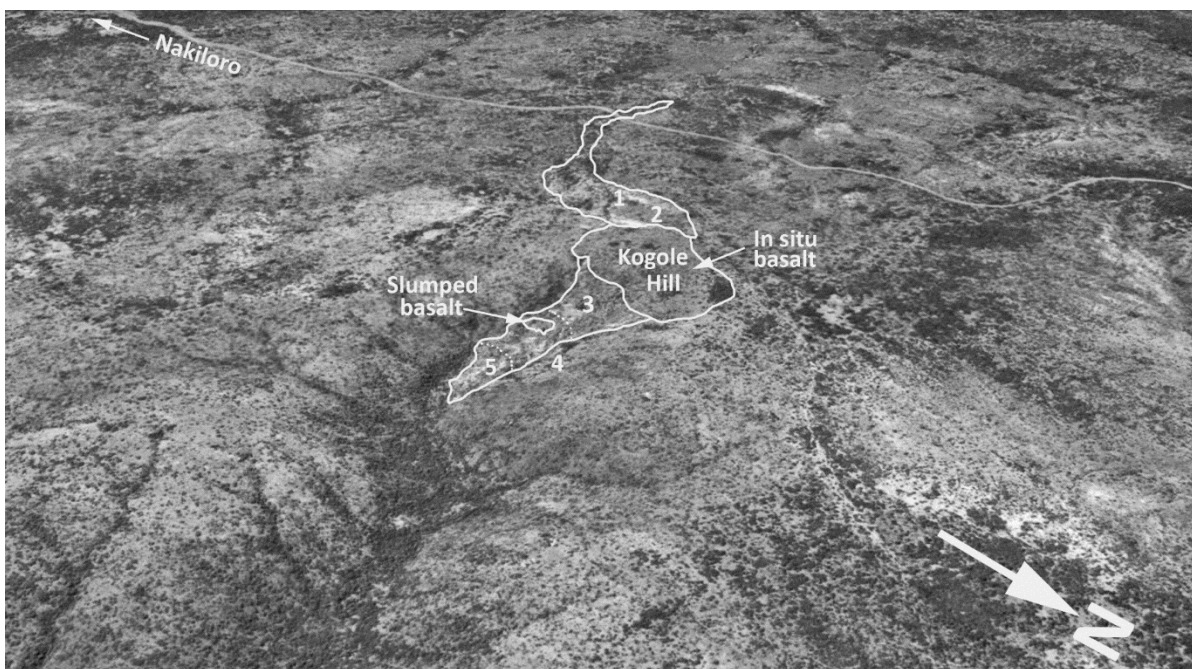
Figure 2. Oblique perspective view towards the southwest of the Moroto II site complex. N°s 1-5 correspond to sediment exposures listed by Pickford & Mein (2006). N°4 is the so-called « Primate Site » that yielded the Moroto snout, mandible, vertebrae and femora. Note the slumped lava and sediments in exposures N°4 and N°5. Sediments in exposures N°1-N°3 are *in situ* as is the basalt at Kogole Hill. Plio-Pleistocene sediments are not shown, but overlie the Miocene sediments in areas N°1, N°3 and N°4 (view is from Google Earth).

GEOLOGICAL CONTEXT OF THE MOROTO II « PRIMATE SITE »

The Moroto II « Primate Site » covers an area of ca 2500 square metres, in which there are three main exposures of Miocene sediments (pale areas labelled A, B and C in Fig. 3) overlain by a thin, discontinuous cover of Plio-Pleistocene and Recent sediment, much of which is covered in vegetation. The bottoms and sides of gullies draining the area are the sites of reworked, transient sediment that contains an admixture of Miocene and Plio-Pleistocene fossils. The Miocene fossils are often rolled and broken, the case with the Moroto snout, both of the mandibles and the two femora. The Pleistocene fossils, although rare, tend to be unrolled and are somewhat better preserved than the Miocene ones.

Descriptions of the work done at Moroto II « Primate Site », recorded in W.W. Bishop's field notes (Musalizi et al. 2009) together with

the positions of two screening dumps made by him and his teams, help to tie down the areas of focussed activity. The position of the Moroto II « Primate Site » is clearly established (Fig. 3). Area A (2°40'32.15''N : 34°43'04.53''E) is probably where the Moroto snout was collected and is where the mandible (UMP MOR II 03'551) was found (MacLatchy et al. 2019). Area B is likely the place where the vertebrae and the mandible (UMP 62-10 + 66-01) were found, whereas Area C is the place from which the femora came, as shown by a fragment of diaphysis found there in 2007 which fits onto one of the previously described specimens (Gebo et al. 1997) and two small fragments recovered by Bishop in the 1960's. These three areas are immediately downstream from the slumped lava/sediment mass.
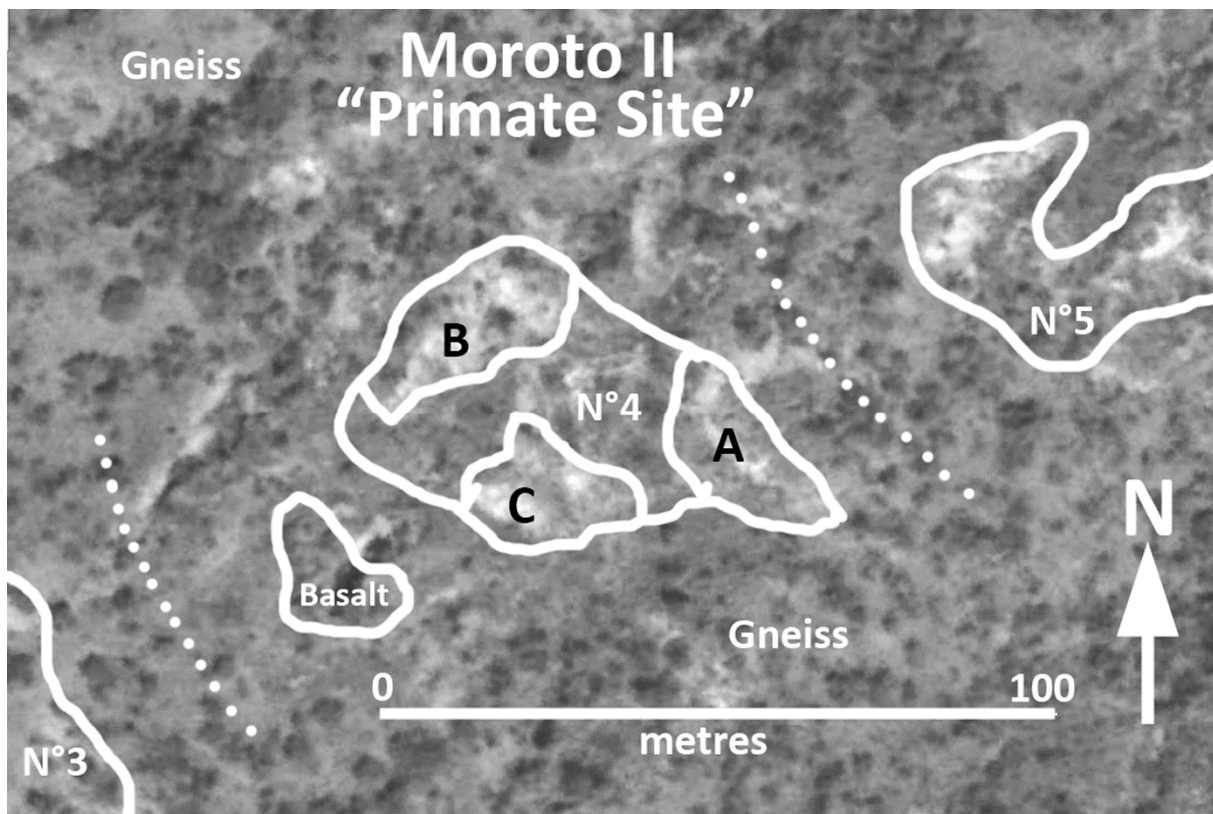
Figure 3. Fossiliferous spots within the Moroto II « Primate Site » (Exposure N°4). A) probable area of the Moroto snout, B) probable area of the Moroto vertebrae and mandible UMP 62-10 + 66-01, C) area of the Moroto femora. Area A is at 2°40'32.15''N : 34°43'04.53''E. The two screening dumps are in shady vegetated positions within areas A and B. Dotted lines indicate the approximate margins of the slumped masses (Base map from Google Earth).
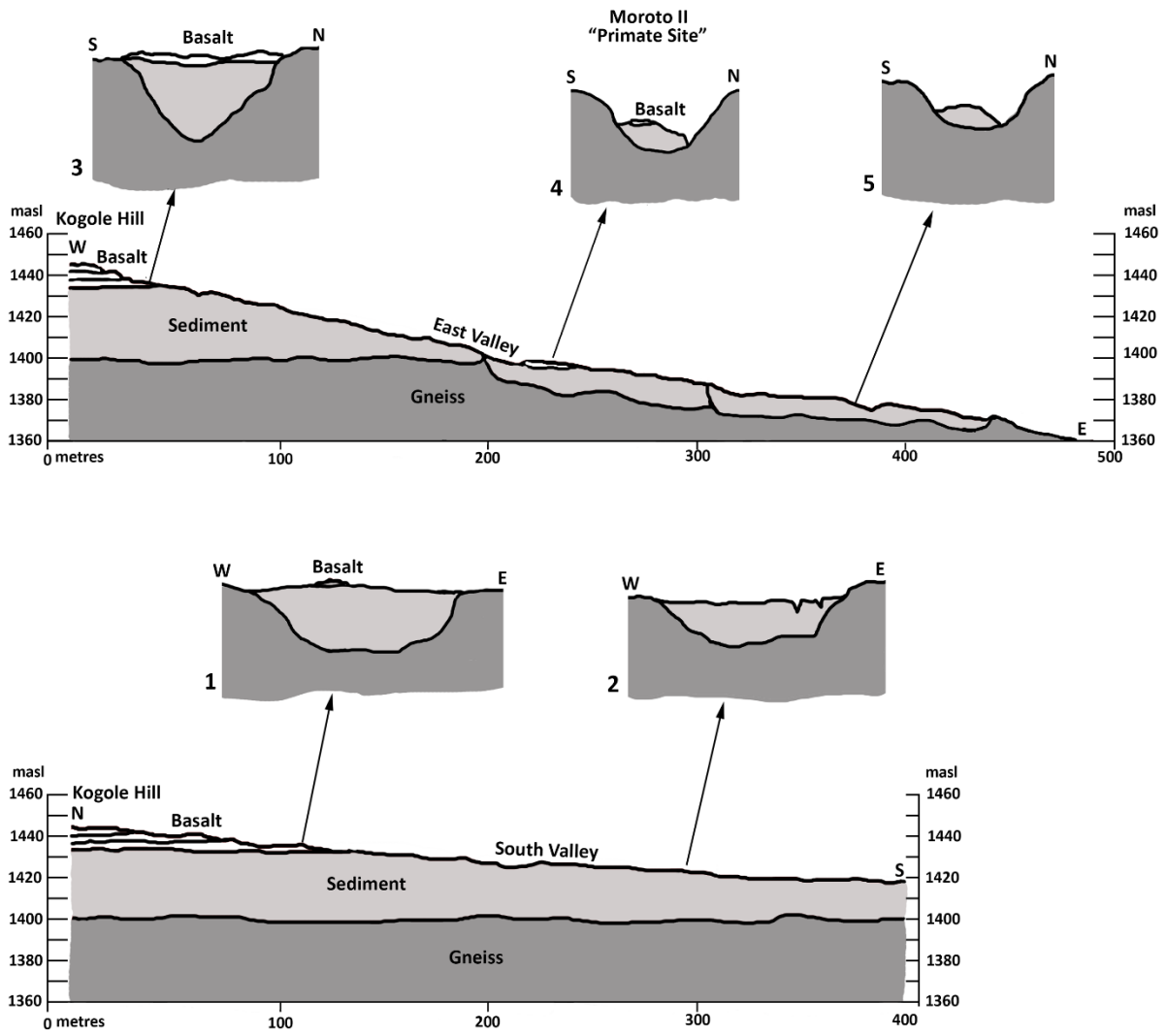
Figure 4. Profiles down the axial part of, and across the Miocene palaeovalleys east and south of Kogole Hill, Karamoja, Uganda. N°1-N°5 correspond to the sediment exposures in figures 1 and 2.

Figure 5. Sediment/lava contact at Moroto II exposure N° 2 (Bissett's Sands). Note the dark red « baked » sediments which underlie the basalt which crops out in the heavily vegetated slopes of Kogole Hill beyond the sediments (above the fallen tree at top centre of image). The red colour fades out downwards, and fossils from this part of the sequence are covered in dark red to purple stains (the excavated area shows a proboscidean limb bone *in situ*).

Figure 6. *In situ* outcrop of basalt at exposure N°3, overlying Miocene sediment which has been baked to a depth of 2-3 metres, below which the reddening fades out to a pale cream colour. The base of the lava is at ca 1435 metres asl. The gneiss in the foreground is the southern margin of the palaeovalley.
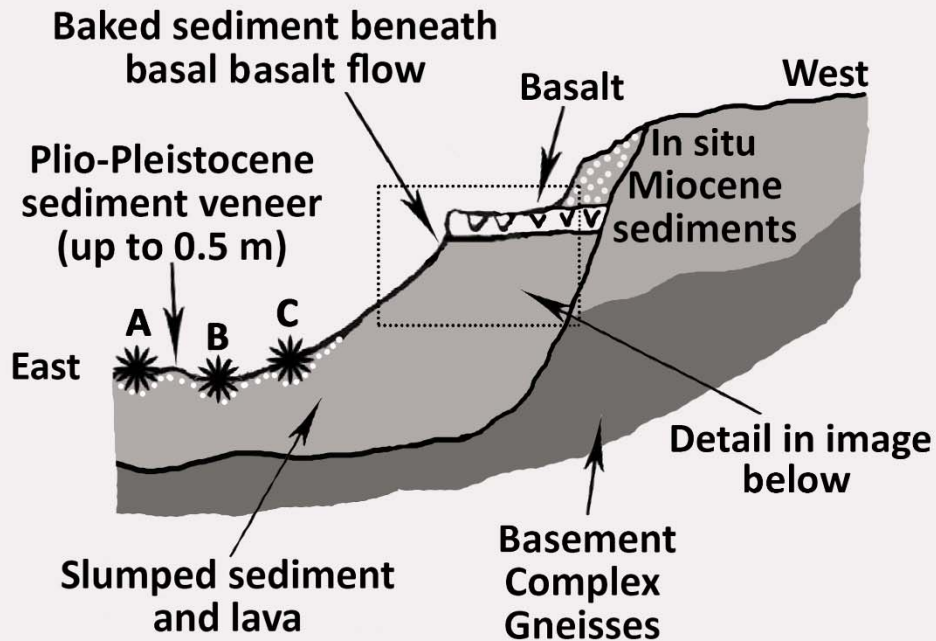
Figure 7. Sketch of the deposits at the Moroto II « Primate Site » (exposure N°4) in the valley east of Kogole Hill. **Upper frame** – East-West sketch section through the deposits showing the slumped mass of Miocene sediment and lava, the reconstructed positions of fossils (stars) and the thin layer of Plio-Pleistocene sediment (white dots). A – *Afropithecus* snout, B – vertebrae, C – femur. The dotted box shows the approximate extent of the view in the lower frame. **Lower frame** – Field view of the slumped lava and the underlying Miocene sediments immediately uphill from the « Primate Site » (view southwards). Note the reddened, baked sediment beneath the lava. The base of this lava is at ca 1397 metres asl, implying a slump downwards by ca 38 metres from its original *is situ* position.

None of the fossils from the Moroto II « Primate Site » were excavated from *in situ* Miocene deposits (Fig. 8-10). They were either collected from the surface or were recovered by screening the transient sediments in the gullies and lags in the flatter areas where there is a veneer of superficial Plio-Pleistocene to Recent deposits. This is why most of the Miocene fossils are broken or rolled and polished (Musalizi et al. 2009).

MacLatchy et al. (2019, fig. 15) proposed that the fossils from the « Primate Site » came from a layer of sediment 15.2 metres above the base of a **47.4** metre thick succession and 32.2 metres beneath the lava flows which cap the sediments at Kogole Hill. However, this proposal is not secure. They wrote « *Although the location within Moroto II where the hominoid vertebrae were found some fifty years ago is not known, we do know the* **exact** *stratigraphic location of UMP MORII 03'551, UMP MORII 03'559 and UMP MORII 94'80 (right and left femora). UMP MORII 03'551 and UMP MORII 94'80 were found at the same stratigraphic level 15.2 m from the base of over* **50 m** *of section* ».

Unfortunately, this « **exact** » level described by MacLatchy et al. (2019) corresponds to the topographic position of the fossils at the time of discovery (in the lag deposit covering the area) not to their stratigraphic position. None of these fossils was *in situ* when collected – all of them were reworked into the surface lag and soil. The part of the section in the same figure labelled « *covered* » corresponds to the slumped lava and sediment about 10 metres thick, and this is most likely the original context of the snout, the mandibles and the femora (see section on preservation characters below). If so then these specimens are coeval with the isolated fossil hominoid tooth from the upper part of the same valley (UMP MOR II 03'559) as well as with the bulk of fossils collected from the valley infilling south of Kogole Hill (exposures N°1 and N°2) (Pickford et al. 2017).

The discovery loci of the fossils at the « Primate Site » are thus not 32.2 metres below the lava as proposed by MacLatchy et al. (2019), but are only about 10 metres below it. This means that all the Miocene primate fossils from Moroto II, including most of the other fossils collected in exposures N°1, 2, 3 and 4, were derived from a short interval of the stratigraphic column, and can thus be treated as a coeval assemblage. Most of the fossils were in secondary context when found. Exceptions are some of the *in situ* fossils excavated from exposures N°1 and N°2 described by Pickford & Mein (2006) and Pickford et al. (2017).

Rare Plio-Pleistocene fossils occur in the soils, surface lag and sediments that accumulated on top of the Miocene deposits at exposures N°1 and N°4.
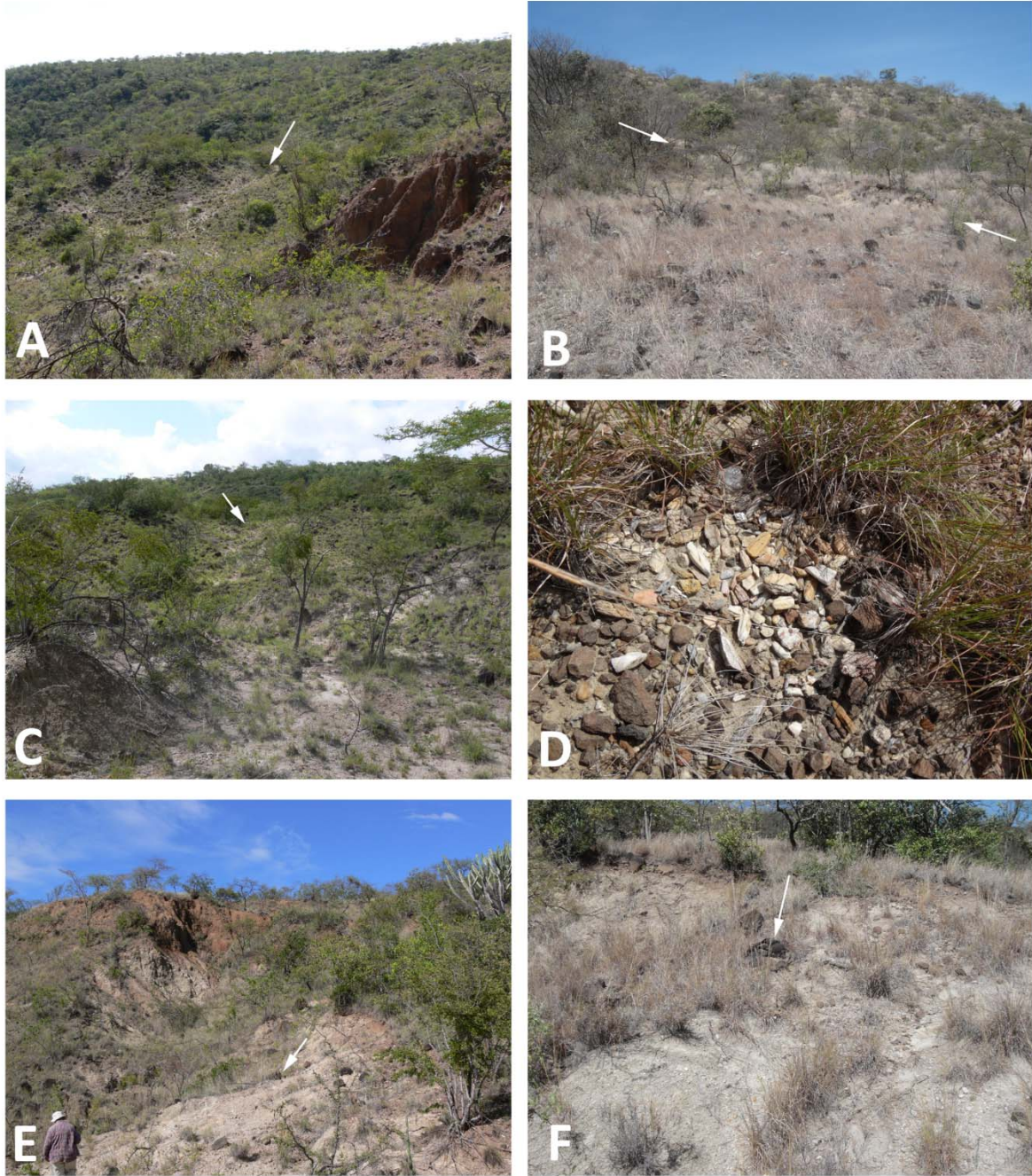
Figure 8. Views of the Moroto II « Primate Site ». A) View from the top of the slumped lava downstream towards Area A (Moroto snout site – white arrow), B) The gulley in Area A (white arrows) viewed southwards, C) Area B in the foreground with Area A in the background (white arrow), D) part of the screening dump at Area B with discarded, abraded and rounded fossilised bone fragments, E) Area C with the slumped lava (brown cliffs) in the background (white arrow shows cairn marking the spot where a femur fragment was found in 2007, F) close-up view of the cairn in Area C. Note the thin layer of Plio-Pleistocene sediment covering the well-vegetated area in the background.
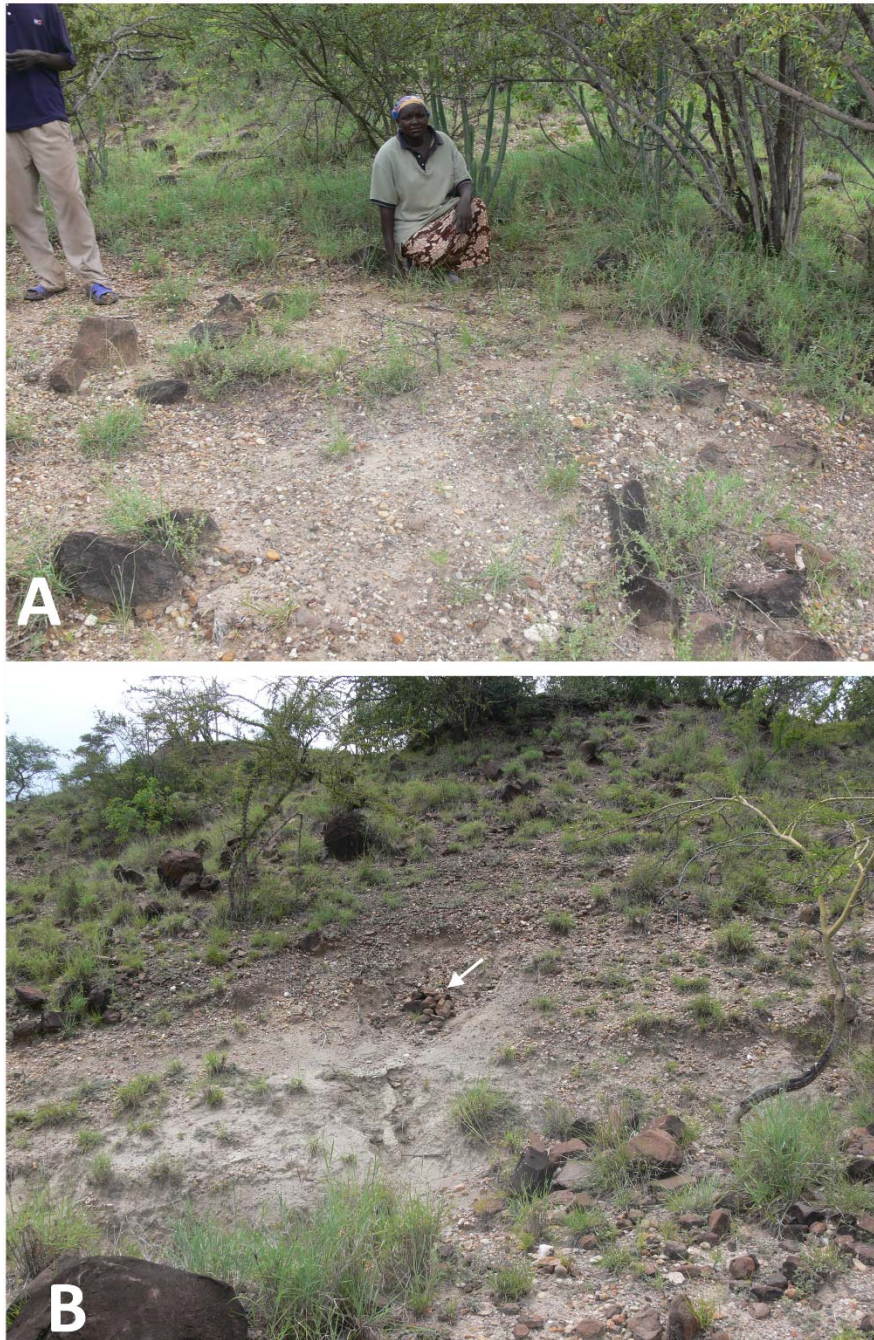
Figure 9. Area A at the Moroto II « Primate Site ». A) Bishop's screening dump beneath the bushes at the top of the exposures, B) cairn (arrow) close to the gully showing the discovery locus of the mandible UMP MOR II 03'551. Note the basalt boulders littering the surface and the fact that the mandible was above the interface between the pale grey sediment and the overlying Plio-Pleistocene to Recent surface deposits.

Figure 10. Moroto II « Primate Site » area C. The backpack on the pale cream sediment exposure is at the spot where part of the left femur was found in 2007. The slumped lava cliff is partly obscured by the branches at the top left corner of the image.

STRATIGRAPHY AT MOROTO II

MacLatchy et al. (2019, fig. 15) presented a stratigraphic section of Moroto II in which the sediments were reported to be 47.4 metres thick (stated to be over 50 metres in the text), of which ca 10 metres in mid-section is described as being « *covered* ». Our own measurements at the various outcrops at Moroto II indicate a maximum sediment thickness of ca 34 metres. Because the sediments are infilling a palaeovalley, the thickness of deposits is generally less than 30 metres, wedging out to zero metres near the shoulders of the palaeovalley.

At exposures N°1 and N°2, the maximum thickness of sediment is ca 21 metres (Fig. 4). There are small exposures of disturbed sediment 500 metres downstream, close to the Nakiloro track, that are ca 33 metres lower than the lava-sediment contact at the head of the valley. However, the distorted nature of these

sediments indicate that they may have slumped downwards, and thus do not support a thickness of deposits greater than 21 metres.

At exposure N°3 east of Kogole Hill, the lava-sediment contact is at an altitude of ca 1435 metres above sea level. The lowermost sediments at this exposure lie at ca 1404 metres, indicating a minimum sediment thickness of 31 metres, but the base of the section is not exposed, being obscured by the slumped mass of lava and sediment of exposure N°4, as well as by an accumulation of a thickness of two to three metres of Plio-Pleistocene debris upstream from the slumped mass. The landslide formed a dam-like structure across the valley behind which sediments accumulated. The 'dam' has been breached by subsequent erosion which has produced a narrow but deep gulley along its northern edge, but this gulley does not expose the basement gneisses in its floor.

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The small exposure of basalt in the valley east of Kogole Hill (exposure N°4) was initially thought to be intercalated in the Miocene sediments (Pickford & Mein, 2006) but it is in fact part of the same flow as the one at the base of Kogole Hill. Part of this lava slumped down into the valley along with a ca 15-20 metre thickness of sediments underlying it. At this outcrop the sediments immediately beneath the lava were baked to a deep red colour which fades out with increasing depth, precisely as the *in situ* outcrops at the southern (exposure N°2) and eastern (exposure N°3) edges of Kogole Hill. The measured thickness of sediments at exposure N°4 is ca 10 metres but the sediment-gneiss contact is not observed.

At exposure N°5, downstream from N°4, a thickness of ca 5 metres of sediments is observed overlying Basement Complex gneisses. The form of the sediment outcrop and the presence of large boulders of basalt at the top of the exposure suggest that it is also a slumped mass which has been eroded deeply enough to have degraded its basalt cover and to have removed the uppermost part of the sediment column, leaving only the lowermost five metres in place.

In summary, the sediments beneath the slumped basalt in exposure N°4 (the « Primate Site ») are not near the base of a stratigraphic succession more than 50 metres thick as proposed by MacLatchy et al. (2019) but are only ca 5-10 metres beneath the base of the slumped basalt. The Miocene fossils therefrom are thus coeval with specimens from exposures N°1, N°2 and N°3, and are not significantly older than them (MacLatchy et al. 2019).

Secondly, the maximum thickness of sediment in the Kogole Palaeovalley was of the order of 34 metres of which the lowermost ten metres are poorly fossiliferous to unfossiliferous.

Finally, overlying the Miocene sediments and lava at Moroto II, there is a thin (up to 2 metres in places) discontinuous layer of fossiliferous Plio-Pleistocene and Recent sediment, soil and lag deposits, especially in exposures N°1 and N°4.

PRESERVATION CHARACTERS OF FOSSILS FROM MOROTO II « PRIMATE SITE »

Fossils from the Moroto II « Primate Site » show a diversity of preservation characeristics (Fig. 11-16). The Moroto snout (UMP 62-11) preserves thin patches of dense, brown to dark purple ferruginous staining which penetrates into cracks in the bone and tooth roots and which colours the dentine of the molars (Fig. 11). Some of this stain was lost when the fossils were eroded from their original context, and some was removed during preparation, but enough remains to indicate that much of the fossil was originally covered by such colouration. The two mandible fragments, UMP 62-11 and UMP 66-02, also show similarly stained patches and infillings of cracks. The mandible (UMP MOR II 03'551) described by MacLatchy et al. (2019) has quite extensive patches of similar staining and cracks in the bone and the tooth roots are infilled with similar mineral (Fig. 12).

Figure 11. Palatal view of UMP 62-11 to show the deep red-purple staining that affects the dentine exposures in the M1/ and M2/ and which infills cracks in the bone. The isolated tooth next to the right M1/ in the palate is MOR I 2'07, attributed to *Nacholapithecus kerioi* by Pickford et al. (2017).
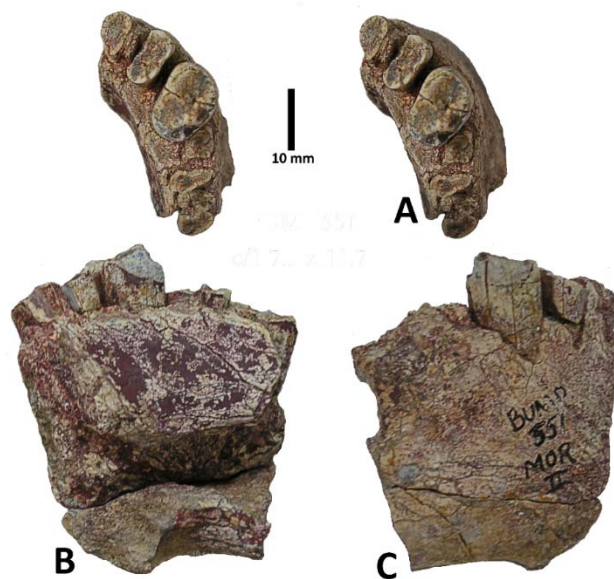
Figure 12. UMP MOR II 03'551, right mandible fragment containing roots of i/1-p/4. A) stereo dorsal view, B) lingual view, C), lateral view. Note the dark purple stain covering parts of the bone and infilling cracks in the bone and tooth roots.

Figure 13. Part of primate femoral diaphysis preserving the base of the lesser trochanter from Moroto II « Primate Site » Area C. The large piece found in 2007 has patches of red-purple stain and dark mineral infillings in cracks, as do the two small pieces collected by Bishop during the 1960's. Broad arrows, dark red-purple surface stain; narrow arrow, infillings of cracks in the bone.

In general, fossil bones from the Miocene sediments at Moroto II, not only those from the « Primate Site » in the valley east of Kogole Hill (exposure N° 4), but also from the exposures south of the hill (N°1 and N°2), show similar

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brown-purple staining (Fig. 14-15). Specimens of *Kogolepithecus*, *Kalepithecus*, *Prohyrax*, *Diamantomys*, other rodents, *Eozygodon*, *Progomphotherium*, *Deinotherium*, *Moroto-choerus* and ruminants all show similar stains
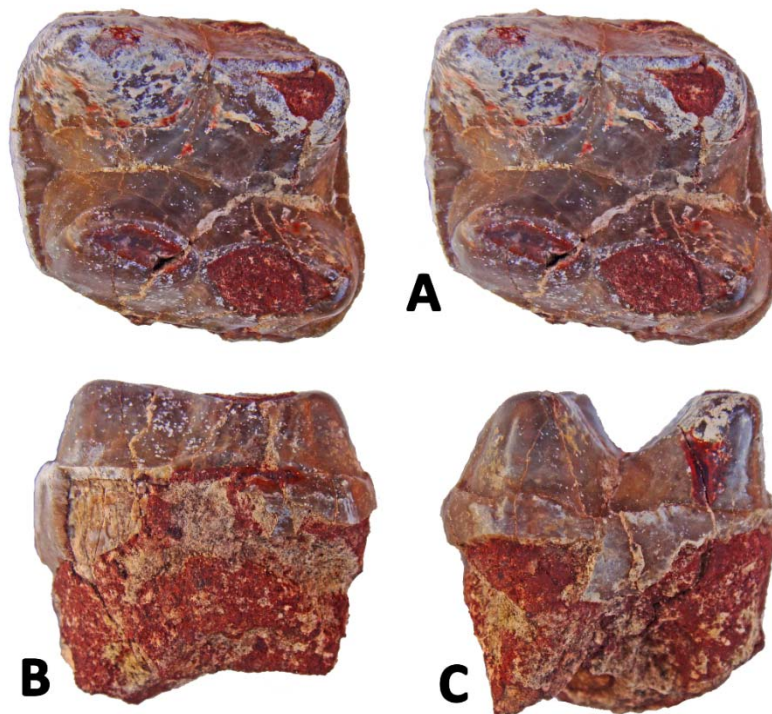
Figure 14. Mor II 1'10, right P4/, *Eozygodon morotoensis*, A) stereo occlusal view, B) mesial view, C) lingual view (mesio-distal length - 34.5 mm, mesial bucco-lingual breadth - 35.1 mm, distal bucco-lingual breadth - 38.0 mm). Note the red-purple staining on the dentine and roots.
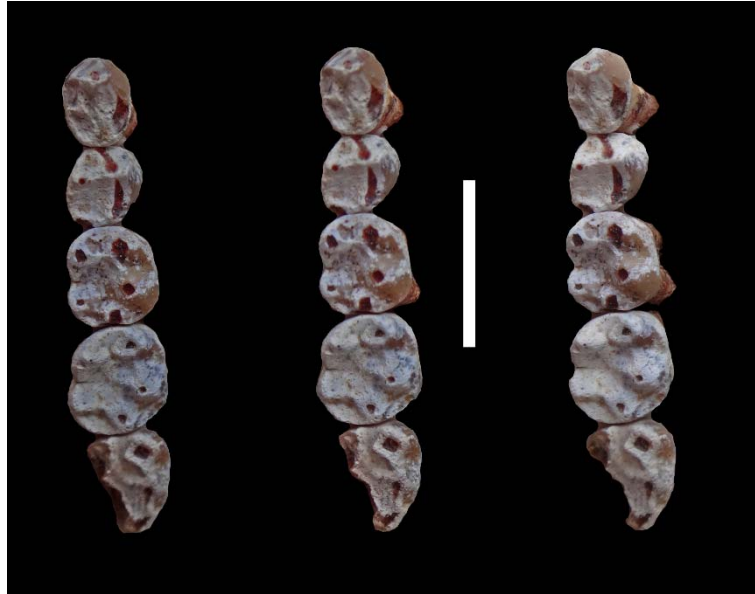
Figure 15. Stereo occlusal views of MOR II 1'17, right p/3-m/3 of *Kalepithecus kogolensis* (scale : 10 mm). Note the deep red to purple stain affecting the dentine and roots.

The geochemical processes that led to the development of the red to purple staining and infillings of cracks in the Miocene fossils from the various outcrops at Moroto II, both east and south of Kogole Hill, were related to the eruption of basalt lava which « baked » the uppermost layers of the sediments over which the lava flowed. The heat from the lava not only « baked » the sediments a deep red colour, but it also affected the colouration of fossils enclosed in the sediments which were probably damp at the time of the eruption. The fossils collected at the Moroto II « Primate Site » were evidently subjected to the same short-lived hydrothermal processes as those at exposures N°1, N°2 and N°3. The slumped lava close to the « Primate Site » is underlain by baked sediments, the reddening fading out with increasing depth, just as in the outcrops south of Kogole Hill and at the head of the valley east of the hill. This suggests that the sediments from which the affected fossils came were not deeper than 10 metres beneath the lava. Sediments deeper than this are poorly fossiliferous and show few if any signs of staining because they largely escaped the hydrothermal « baking » processes.

In contrast to the snout, the mandibles and the femora, all of which show the red-purple stains, the Moroto vertebrae do not show any obvious signs of red or purple staining, neither are cracks infilled with dark minerals (Fig. 16). Further analysis is required because it is possible that surface stains may have been removed during cleaning of the fossils. However, our impression is that the Moroto II vertebrae had a different taphonomic history from that of the snout and mandibles.
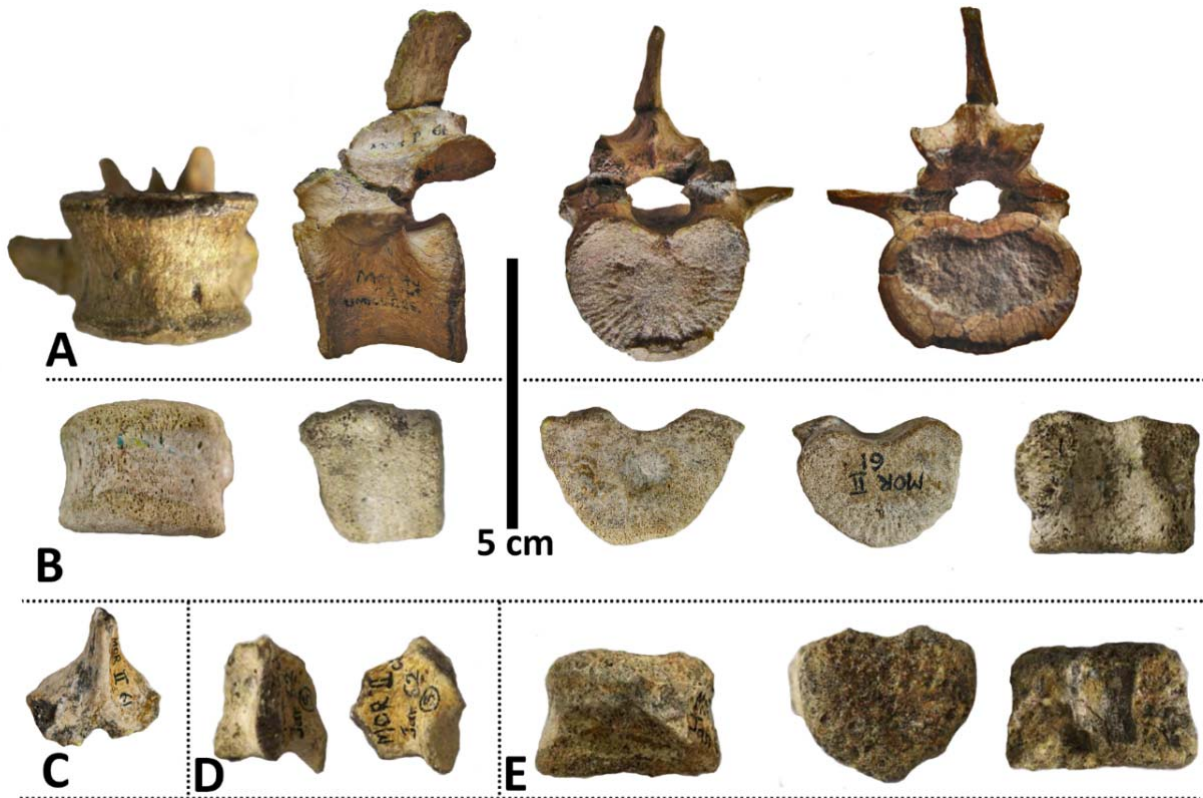
Figure 16. Surface details of vertebrae from Moroto II « Primate Site ». A) UMP 67-28, B) UMP 68-06, C) UMP 68-08, D) UMP 68-07, E) UMP 68-05. There are no obvious signs of a dark brown or purple staining or of dark minerals infilling cracks in the bone (images B. Senut, D. Gommery and M. Nakatsukasa).

FAUNA FROM MOROTO II, UGANDA

The fauna from Moroto II is listed in Tables 1 and 2. The composition of the mammalian assemblage indicates a basal middle Miocene correlation (Faunal Set P IIIa).

Table 1. Miocene mammalian fauna from Moroto II (emended from Pickford & Mein, 2006, with additions from Pickford et al. 2017). Pending confirmation, the report of the presence of Nyanzapithecinae at Moroto II by Jansma & MacLatchy, 2015, is not included.

Marsupialia ?	Indet.
Insectivora	Tenrecidae indet.
Macroscelididae	*Miorhynchocyon* sp.
Chiroptera	*Taphozous incognita*
	?Chamtwaria pickfordi
Rodentia	*?Pseudocricetodon* sp.
	Notocricetodon gommeryi
	Protarsomys cf *macinnesi*
	Protarsomys cf *lavocati*
	Megapedetes cf *pentadactylus*
	Zenkerella wintoni
	Diamantomys morotoensis
	Diamantomys ugandensis
	Paraphiomys piggoti
	Apodecter cf *stromeri*
	Apodecter orangeus

	Andrewsimys cf *parvus*
	Simonimys genovefae
	Geofossor cf *corvinusae*
Carnivora	?*Hecubides* sp.
Galagidae	*Komba* sp.
Catarrhini	*Victoriapithecus macinnesi*
	Kogolepithecus morotoensis
	« *Micropithecus* » *leakeyorum*
	Simiolus enjiessi
	Kalepithecus kogolensis
	Nacholapithecus kerioi
	Afropithecus turkanensis
	Ugandapithecus gitongai
Hyracoidea	*Meroehyrax bateae*
Proboscidea	*Deinotherium hobleyi*
	Progomphotherium maraisi
	Eozygodon morotoensis
Rhinocerotidae	Indet. sp.
Anthracotheriidae	*Brachyodus* cf *aequatorialis*
	Morotochoerus ugandensis
Ruminantia	cf *Prolibytherium* sp.

Table 2. Plio-Pleistocene Fauna from Moroto II (from Pickford & Senut, 2003, with additions)

Gastropoda	*Nothapalinus* sp.
Aves	*Struthio camelus* (eggshell fragments)
Mammalia	*Arvicanthis* cf *neumanni*
	Tatera sp.
	Hominidae
	Phacochoerus sp.
	Bovidae sp.

MOROTOPITHECUS BISHOPI – A THREE-WAY CHIMAERA

The fossils attributed to *Morotopithecus bishopi* came from two localities, Moroto II « Primate Site » (the holotype snout, mandible fragments, femora and vertebrae) and Moroto I (the scapula glenoid). The original hypodigm comprised 10 fossils (Gebo et al. 1997) many of which had been described previously (Allbrook & Bishop, 1963; Rose & Walker, 1968; Pilbeam, 1969). One fossil, a mandible, was added to the hypodigm by MacLatchy et al. (2019) (Table 3).

Table 3. The original hypodigm of *Morotopithecus bishopi* Gebo et al. 1997, with an addition of a mandible collected in 2003. (*) In MacLatchy et al. (2019) the glenoid was erroneously listed as MORII 94'60 and the catalogue numbers UMP 62-10 and UMP 62-01 were transposed.

Locality and field data	Specimen (Gebo et al. 1997, MacLatchy et al. 2019)	Identification this paper
Moroto II, Aug'61, Dec'61, Jan'64, Feb'65	UMP 62-11, snout	*Afropithecus turkanensis*
Moroto II, Jan'64	UMP 62-10*, mandible fragments	*Ugandapithecus gitongai*
Moroto II, Jan'64	UMP 66-01*, mandible fragment	*Ugandapithecus gitongai*
Moroto II, Jan'64	UMP 62-12, left upper canine	*Afropithecus turkanensis*
Moroto II 61	UMP 67-28, middle lumbar vertebra	Hominoid,
Moroto II, Jan'64	UMP 68-05, middle lumbar vertebra fragment	Hominoid
Moroto II, Jan'64	UMP 68-06, last thoracic vertebra	Hominoid, probably lumbar

| Moroto II, Jan'64	UMP 68-07, lamina and base of spine of lumbar vertebra	Hominoid
Moroto II, 1994	MUZM 80, UMP MOR II 94'80, right and left partial femora	Right femur - Hominoidea indet. a Left femur - Hominoidea indet. b
Moroto I, 1994	MUZM 60, UMP MOR I 94'60*, left scapula glenoid	Probably artiodactyl *Morotochoerus ugandensis*
Moroto II, 2003	UMP MOR II 03'551, partial mandible	*Afropithecus turkanensis*

The holotype snout of *Morotopithecus bishopi* is similar in its comparable parts and dimensions to the holotype of *Afropithecus turkanensis* (Pickford, 2002; Pickford et al. 2003; Patel & Grossman, 2006; Harrison, 2010). Deane (2017) considered that the Moroto snout differed from *Afropithecus* at the generic level, an interpretation that was answered by Pickford et al. (2017) (Fig. 17-18).

Figure 17. Glass teaching slide prepared by W.W. Bishop showing fossil catarrhines from Moroto II and various sites at Napak, Uganda. A) part of left maxilla and premaxilla lacking the crowns of I1/-P4/ (UMP 62-11), B) edentulous fragment of right mandible with roots of m/2 and anterior root of m/3 (UMP 62-10). The other fossils in the slide are from Napak.

10 cm
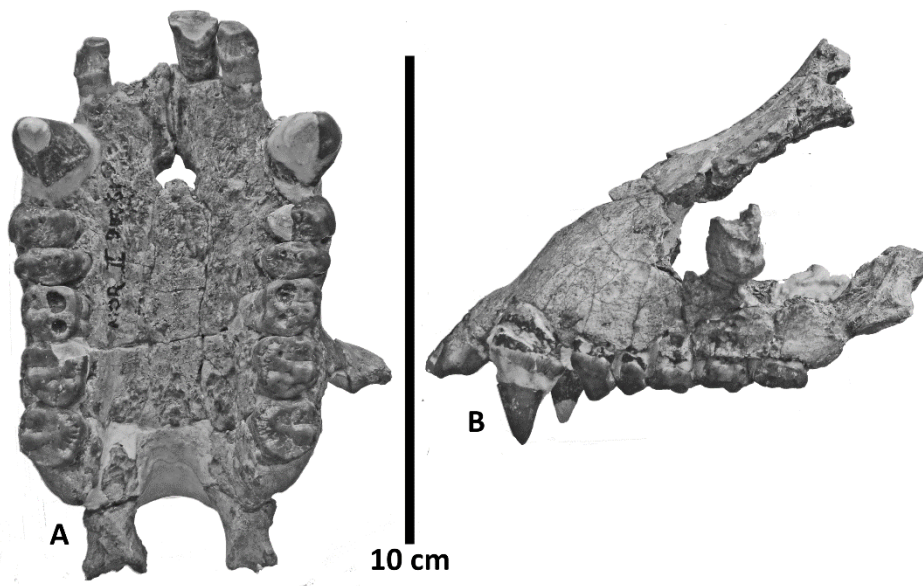
Figure 18. UMP 62-11, snout of *Afropithecus turkanensis* from Moroto II « Primate Site ». A) palatal view, B) left lateral view.

The mandible fragments, UMP 62-10 and UMP 66-01 (Fig. 19) are compatible in dimensions with *Ugandapithecus gitongai* (Pickford et al. 2017). MacLatchy et al. (2019) transposed the catalogue numbers (see Pilbeam, 1969, fig. 20 for the correct numbers) and they considered that it could represent the same individual as the holotype of *Morotopithecus bishopi*.
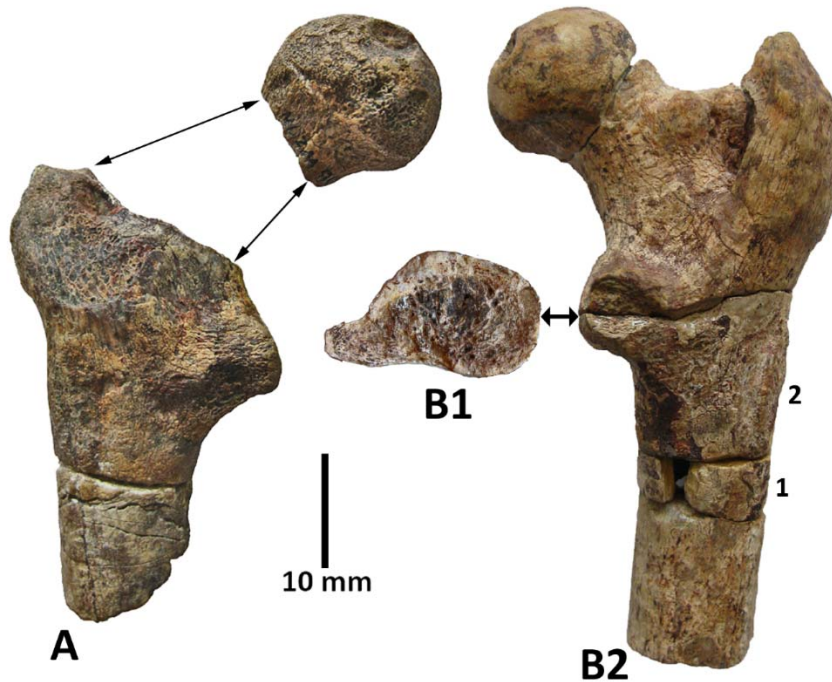

10 cm
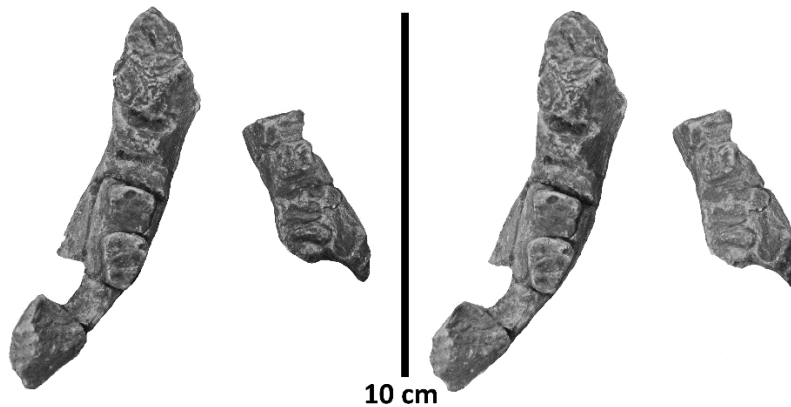
Figure 19. Stereo occlusal view of right (UMP 62-10) and left (UMP 66-01) mandible fragments from Moroto II « Primate Site » attributed to *Ugandapithecus gitongai* (cast in NHMUK).

Pickford et al. (1999) Senut et al. (2000) and Senut (2012) argued that the scapula glenoid from Moroto I is not from a primate, the fossil resembling specimens of medium-sized suoids. In terms of dimensions it would fit with the anthracotherioid artiodactyl *Morotochoerus ugandensis* Pickford, 1998 (Pickford, 2011).

The two fragmentary femora from Moroto II « Primate Site » show somewhat divergent morphology (Fig. 20). The right one has the lesser trochanter oriented laterally, the left one has this structure oriented somewhat more posteriorly (Pickford et al. 1999; Senut, 2012). There are also slight differences in dimensions. The observed morphometric differences could represent individual variation or might be due to sexual dimophism within a single taxon, or could imply the presence of two taxa.

Figure 20. UMP MOR II 94'80, proximal ends of femora from Area C at the Moroto II « Primate Site ». A) posterior view of right femur reconstituted from three eroded and polished fragments, B) left femur reconstituted from six fragments, B1) cross section at lesser trochanter, B2) posterior view (1 - two fragments from the old collections made by Bishop in the 1960's, 2 -fragment found by UM staff in 2007). Note the rounded and abraded surfaces of the fragments.

In conclusion, the presence of three large-bodied ape taxa (*Afropithecus*, *Ugandapithecus*, *Nacholapithecus*) in the Miocene deposits at Moroto II « Primate Site » and nearby localities (Pickford et al. 2003, 2017) together with remains of a hominid of Plio-Pleistocene age from the « Primate Site » renders attribution of the Moroto post-cranial elements delicate. It is evident that the original and extended hypodigms of *Morotopithecus bishopi* comprise elements of at least three taxa, one of which is likely an artiodactyl (Pickford, 1998). This finding renders previous phylogenetic analyses and some aspects of morphofunctional analyses of *M. bishopi* dubious to invalid. The phylogenetic analyses based on these hypodigms are chimaerograms, and are thus of no biological relevance (Pickford & Tsujikawa, 2019). The interpretations of *Morotopithecus* as a stiff-backed, orthograde biped (Filler, 2007a; Nakatsukasa et al. 2007) is compromised, because the lumbar vertebra linked to this hypothesis likely does not belong to *Morotopithecus* nor to any other Miocene ape-like creature, but could represent a Plio-Pleistocene hominid.

THE SIGNIFICANCE OF THE MOROTO II VERTEBRAE

The Moroto vertebrae, especially UMP 67-28, have played an important role in all discussions of the Moroto large hominoids. From the very beginning, lumbar vertebra UMP 67-28 was observed to share some morphological characters with extant African great apes and humans, and to differ markedly from the lumbar vertebrae of cercopithecoids (Rose & Walker, 1968). In particular the transverse processes of the vertebra are in a dorsal position on the pedicle some distance above the body of the vertebra. Later studies revealed marked differences from the corresponding vertebrae of proconsulids (*Ekembo*) and *Nacholapithecus* (Nakatsukasa, 2008).

20

The literature on the Moroto lumbar vertebrae is extensive (Andrews, 2015; Andrews et al. 1997; Begun, 2015; Finarelli & Clyde, 2004; Filler, 1981, 2007a, 2007b, 2007c, 2007d; Gallien, 2002; Gilbert et al. 2020; Gommery, 1998, 2006; Harrison, 2002, 2005, 2010; MacLatchy, 2004, 2010; MacLatchy et al. 1995, 2019; Moyà-Solà et al. 2004: Sanders, 1998; Shapiro & Russo, 2019; Ward, 1993, 1997, 1998, 2015). All of these authors stressed the morphological similarities of the vertebra to those of extant great apes and, on this basis, most of them inferred functional, locomotor, systematic and phylogenetic scenarios for *Morotopithecus*.

The assumed appurtenance of the vertebra to the same species as the Moroto II snout and mandibles played a role in the decision to create the new genus and species *Morotopithecus bishopi* by Gebo et al. (1997) and in the phylogenetic analysis that followed (Young & MacLatchy, 2004). It also impacted on interpretations of the supposed locomotor repertoire and posture of the genus. However, as discussed above, the original hypodigm of *Morotopithecus bishopi* is a three-way chimaera, comprising fossils of an artiodactyl and at least two species of catarrhine.

GEOLOGICAL CONTEXT AND INTERPRETATIONS THAT FLOW FROM IT

Determining the correct geological and stratigraphic context of fossils is of fundamental importance for interpreting the fossil record (Pickford, 1987, 2018). The same applies to the context of artefacts in the archaeological record (Dominguez-Rodrigo & Alcala, 2016, 2019; Pickford, 2018; Archer et al. 2020; Stollhofen et al. 2020).

In East Africa, the case of the Kanam human mandible is well-known (Leakey, 1935, 1936, 1970). Initially interpreted to be contemporaneous with the fauna from the Kanam Formation (early Pliocene, but at the time reported to be early Pleistocene on the basis of the presence of *Deinotherium* in the deposits) the mandible was in fact fossilised in the overlying Apoko Formation of late Pleistocene age. Recent erosive activity had released the Kanam mandible from its original context and it had come to rest in transient sediment which infills the Kanam gullies, which becomes hard when it dries out. The same recent sediment contains early Pliocene fossils that have eroded from the Kanam Formation and which have been temporarily recemented into the transient surface deposits (Pickford, 1987). Thus, when found, the Kanam human mandible was in secondary context along with some early Pliocene fossils. But for over 50 years Leakey (1970) maintained that it was 'in situ' when found, and was therefore contemporary with the early Pliocene fauna.

At Olduvai (Leakey, 1932) and Kanjera (Leakey, 1936), the situation was somewhat different, in that the human remains collected there reached their respective contexts via burial into pre-existing strata. This did not prevent their discoverers from initially interpreting them to be of greater age than they were.

At Rusinga Island, an admixture of early Miocene and Pleistocene fossils occurs at some of the sites, such that the record of Soricidae from site R3a on the island (Butler & Hopwood, 1957) was initially interpreted to mean that this family of insectivorous small mammal had existed in Africa since the early Miocene. However, the fossil is of Pleistocene age (Butler, 1984). The oldest known soricid in the continent is from Beni Mellal (late middle Miocene, Morocco) (Lavocat, 1961).

At Karungu, Kenya, the early Miocene strata are overlain by fossiliferous Pleistocene beds, and it is not unusual to find early Miocene and Pleistocene fossils side by side (Owen, 1936; Pickford, 1981, 1982, 1986).

Moroto II, Uganda, joins the list of African Neogene palaeontological localities that yield admixtures of fossils of diverse ages which may have influenced interpretations of the fossils collected there.

In particular, the Moroto lumbar vertebrae have been repeatedly interpreted as yielding evidence for the early acquisition (ca 21 Ma) of

orthograde posture in hominoids (Walker & Rose, 1968; Filler, 1981, 2007a, 2007b, 2007c, 2007d; MacLatchy et al. 2000) and of bipedal locomotion (Filler, 2007b; Alba, 2008). Not only is the age estimate of 21 Ma unlikely to be correct on the grounds that the bulk of the mammalian fauna from Moroto indicates a basal middle Miocene correlation (Pickford et al. 2003, 2017), but also, the presence of Plio-Pleistocene fossils in the same exposures opens up alternative avenues of interpretation. The rather great ape-like morphology and dimensions of the Moroto vertebrae are not called into question – however, the vertebrae could be 15 million years younger than the snout, mandibles and femora, or 18-19 million years younger if the less likely age estimate proposed by MacLatchy et al. (2019) is adopted. If so, then the evolutionary scenarios habitually attached to the vertebrae and snout would require somewhat radical rethinking.

CONCLUSIONS

The sediments at Moroto II infill a shallow valley incised into Basement Complex gneisses, and are capped by basalt flows that erupted from Moroto Volcano. There are two main areas of sediment outcrops separated by the basalt hill known as Kogole, both of which are fossiliferous. The commonest fossils are of basal middle Miocene age, but there are Plio-Pleistocene fossils in superficial deposits overlying the Miocene strata at exposures N°1 and N°4.

In the palaeovalley east of Kogole Hill there are three exposures of sediment, two of which (N°4 and N°5) are remnants of landslides. Exposure N° 3 is *in situ* and shows creamy white sediment at the base grading upwards into red sediment that was baked by the overlying basalt lava. Exposure N°5 is heavily degraded and all that remains there is a thickness of ca 5 metres of sediment, but N°4 retains ca 15 metres of sediment and its overlying basalt lava cap which baked the underlying sediment. The slumped mass in exposure N°4 retained its horizontality.

Fossils from the sediment beneath the basalt are stained red, whereas fossils from the Plio-Pleistocene deposits are not. The Moroto II snout, two mandibles and two femora from the Moroto II « Primate Site » (i.e. exposure N°4) all exhibit red staining, but the vertebrae from the same area do not show any obvious sign of such stains, suggesting that they went through a different taphonomic history from the snout, mandibles and femora. Further tests are recommended in order to establish the detailed geochemical history of the various fossils from the « Primate Site ».

Should it be confirmed that the taphonomic history of the vertebrae differs from that of the snout, lower jaws and femora from Moroto II, then some fundamental reinterpretation of the evolutionary scenarios, locomotion and posture of the Moroto large fossil catarrhines will be required.

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