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Geo-Pal Uganda

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5 Production

Uganda Museum, P.O. Box 5718, Kampala

Contents

Alan Cyril Walker (1938-2017)

As this monograph on the Bukwa Fossil Sites was nearing completion, the editors were saddened to learn that Dr Alan Walker, a pioneer researcher at Bukwa, passed away on 20th November, 2017.

Alan Walker was educated at St. John's College, Cambridge, where he earned an Honours Degree in Natural Sciences which was followed by higher degree studies at The University of London.

Arriving in Uganda soon after the country's independence, Dr Walker taught at Makerere University College, Kampala (1965-1969). During this time he was involved in the organisation of the survey and excavations at the Bukwa fossil locality which was discovered in 1965 by R. MacDonald and R. Old of the Geological Survey of Uganda, along with P. Brock. Indeed, it was at Bukwa that Alan Walker cut his field palaeontology teeth, an experience that determined his life-long commitment to the discipline, in particular to palaeoanthropology. The results of his researches at Bukwa were published in local and international journals. In collaboration with W.W. Bishop, at the time Director of the Uganda Museum, Dr Walker also collected and studied fossils from Napak and Moroto and curated fossils from the Western Rift Valley. He contributed to the construction of displays on fossils at the Uganda Museum in collaboration with C. Sekintu and J. Nzabonimpa. Details of his interpretations and discoveries are to be found in the present monograph, which attest to the breadth of his interests and the energy that he devoted to palaeontology. On leaving Uganda, he moved to Kenya, where he taught at the University of Nairobi, before moving to the United States of America where he completed his career.

In conversations with Alan Walker during the late 1990's concerning the surveys of Bukwa carried out by the Uganda Palaeontology Expedition, it became clear to me that he held a particular fondness for Uganda and its people, which is why the socio-political events that occurred in the country after he had left Makerere University saddened and appalled him deeply, not just for himself, but above all for the Ugandan people.

Throughout his academic career, Alan Walker was appreciated for his openness to, and encouragement of students and colleagues, as well as for the panorama of his interests and knowledge which he shared freely with anyone who was ready to listen. He was never dogmatic; on the contrary he enjoyed scientific debate and open-minded interaction with other scientists.

The Palaeontology Section of the Uganda Museum retains the original card catalogue of fossils compiled by Dr Walker, although it has suffered from termite activity, an interaction beween paper and insects that would undoubtedly have amused him, given his holistic approach to understanding biology and palaeobiology. This catalogue and the register numbers written on the fossils by Dr Walker, as well as the collection of hominoid casts that he amassed, attest to his activity and interest in this domain while he was in Uganda. He was of the opinion that science has no frontiers and can be practised by anyone, anywhere, which is one of the reasons why he contributed scientific articles to the local publication (*Uganda Journal*) as well as to international outlets. By this means he endeavoured to promote and encourage Science within the country. His publications on Bukwa Geology and Palaeontology are to be found in the reference lists in this monograph.

Martin Pickford, November, 2017

A brief history of the Early and Middle Miocene fossil sites at Bukwa, Uganda : discovery, research, protection

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ABSTRACT

The Bukwa fossil sites of Early and Middle Miocene age, were discovered in 1965, just three years after Uganda's Independence from Colonial Rule, and since then they have been studied sporadically by geologists and palaeontologists. From 1970 until 1985 security concerns in the country hampered progress. The Bukwa sites comprise an important part of Uganda's cultural and scientific heritage, and they warrant proper protection. Despite being protected by the 1967 Monuments Act of Uganda, the sites have suffered encroachment, notably from agricultural activity. In the late 1990's and the first decade of this century, liaison between the Uganda Museum, the Uganda Palaeontology Expedition (UPE) and Local Council officials of Bukwo District, resulted in a rise in awareness of the scientific importance of the sites, not only among government officials and civil servants, but also among local farmers. After 2002, when a team from America briefly visited the sites, there was a long period during which nothing happened, a state of affairs which was interpreted by local inhabitants to mean that the sites had been abandoned by the scientifiv community, which gave the false impression that the sites were of little scientific value. In 2012, in order to rectify this misinformation, after three years of central and local government interaction, a panel was erected at the site by the Uganda Museum, pointing out that the site is protected by law.

Local leaders and citizens of Bukwa are proud of the fact that an important scientific site exists in their area, one deposit of which represents a geological period not represented elsewhere in Uganda, and there are plans to gazette the sites and to create an Interpretation Centre for educational, scientific and tourism purposes. There remains, however, the possibility of further encroachment because, in the district, there is pressure on the land from the agricultural fraternity. The aim of this paper is to provide a succinct history of scientific activity and competing land use interests at the Bukwa fossil sites, and to discuss issues of protection and local development so that the fossil-bearing deposits can be preserved in order that future generations of Ugandan and international scientists can study the geology and palaeontology of the deposits, which are of world-class interest. Much remains to be investigated at the Bukwa fossil sites and several enigmas await elucidation, including the stratigraphy and ages of the localities.

Key Words : Bukwa Fossil Site, Miocene, History, Protection, Research, Local Development

INTRODUCTION

Fossils were discovered at Kwongori Hill in Bukwa District, Uganda (Fig. 1) by MacDonald & Old (1969) while mapping the geology of the Bukwa-Greek River map sheet (Fig. 2). Palaeontological activity was soon undertaken by scientists based at Makerere University, the Uganda Museum and the Geological Survey of Uganda, which also involved scientists from Britain and the United States of America (Walker, 1968, 1969; Hill & Walker, 1972). Many of the fossils collected during these expeditions are curated at the Uganda Museum, Kampala, but other specimens were sent to scientists in

Kenya and Britain for study, but the current whereabouts of these specimens are unknown. During these surveys, the first radio-isotopic dating was performed on samples of lava collected from the base and the summit of Kwongori Hill, which indicated an Early Miocene age for the lavas and the underlying flaggy tuffs (ca 19-20 Ma). The sedimentary deposits at Bukwa II are, however, considerably younger than this, the fossil fauna indicating an age of less than 17.5 Ma (probably ca 16 Ma).

The palaeontological importance of the Bukwa sites lies in four main areas : A) the presence of a high diversity of mammalian and other vertebrate fossils at Bukwa II (Walker, 1968), B) an abundance of land snails at Bukwa I (Pickford, 2002), C) a rich and diverse fossil flora at Bukwa I (Hamilton, 1968; Pickford, 2002 ; this monograph) and 4) it reveals unexpected biogeographic relationships with North African Middle Miocene localities such as Gebel Zelten, Libya, and Wadi Moghara, Egypt. There are few localities in Africa which combine the first three of these sources of information about the fossil record in such a small space. Thus, Bukwa is one of the few places where Early and Middle Miocene palaeoenvironments and palaeoecology can be studied in close combination with palaeobotany, invertebrate palaeontology and vertebrate palaeontology, all within a distance of less than 400 metres. The fact that Bukwa II has yielded two taxa of fossil ape-like primates, makes it an attractive research target for palaeoanthropologists.

Despite the high scientific potential of the Bukwa sites, there has been a curious poverty of scientific descriptions of the fossils, fewer than a dozen specimens having been figured and described in detail. This lack was partly related to particular historical events in the country which hampered the studies, but also because some of the fossil samples were scanty. The monographic coverage presented in this volume of Geo-Pal Uganda seeks to rectify the situation, in order to make the Bukwa fossil record more readily accessible to the scientific community.

Furthermore, because the fossiliferous deposits occur in volcanic strata, they can be dated by radio-isotopic methods (Brock & MacDonald, 1969; MacLatchy *et al*., 2006; Pickford, 2017) although, as usual, the geological and stratigraphic contexts of the dated samples needs to be securely established before wide-ranging correlations are made. Otherwise, there is a risk that the «absolute» dates so obtained may mislead (MacLatchy *et al*., 2006) rather than clarify the timing of geological and palaeontological events in the region (Pickford, 2017).

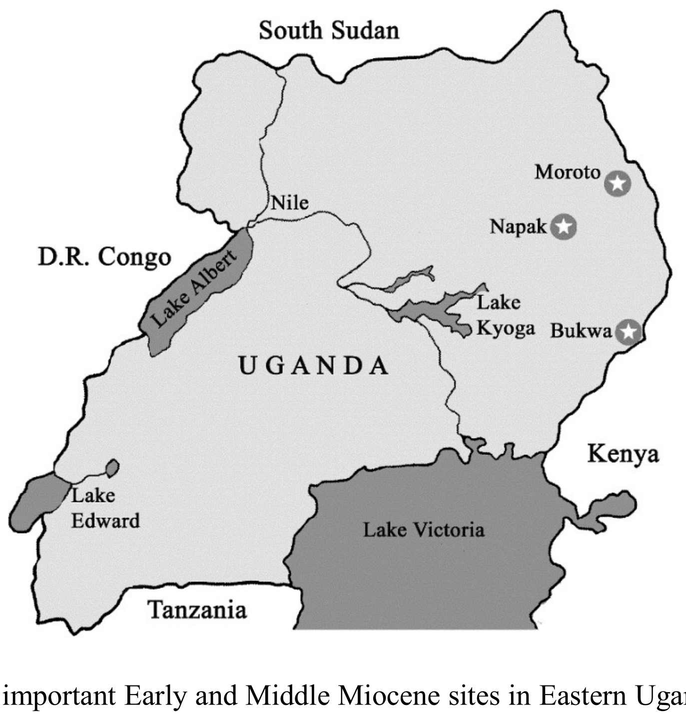

Figure 1. Location of important Early and Middle Miocene sites in Eastern Uganda. Bukwa is located in the eastern foothills of Mount Elgon, not far from the Kenya border.

Figure 2. Vertical satellite image of Kwongori Hill (image from Google Earth) showing the positions of the fossil-rich exposures at Bukwa I and Bukwa II.

Table 1 : Co-ordinates of fossil sites at Kwongori Hill, Bukwa, Uganda

SITE	GPS LOCATIONS (WGS 84)
Bukwa I Rhino phalanx site	01°17'14.4"N : 34°47'18.1"E
Bukwa I *Renefossor* jaw site	01°17'00.0"N : 34°47'07.8"E
Bukwa I Snail site	01°16'58.4"N : 34°47'12.2"E
Bukwa II Vertebrate site	01°17'04.8"N : 34°47'18.1"E

BRIEF HISTORY OF THE BUKWA FOSSIL SITES

The presence of Miocene fossils at Kwongori Hill, Bukwa (Table I) has been known for slightly more than half a century. Scientific study of the sites has been sporadic, not because of lack of scientific interest, but mainly because of security issues, allied to limitations of the fossil record of some of the taxa. Table 2 presents a summary of the main events which have occurred at the sites.

By the late 1980's security had been re-established in Uganda, and the Uganda Palaeontology Expedition (UPE) obtained permission to carry out research at Bukwa and other fossiliferous sites in Eastern Uganda, in collaboration with government funded organisations (Uganda Museum, Geological Survey of Uganda) and local District level organisations, not forgetting the inhabitants of the area around Kwongori Hill, where the fossils occur. Field surveys were carried out by the UPE in 1997 and 1998, but in 1999 the permit to study the site was transferred to a palaeontology team from the United States of America, and this upset and caused delays in the research programme of the UPE. Nevertheless, some results were published (Pickford, 2002). In 2002 an American team visited the Bukwa site (MacLatchy *et al*., 2006) but did not visit the area again for more than a decade, a fallow period that was taken by the local people to mean that the sites were of little scientific value and had, effectively, been abandoned. In 2009, 2011, 2012 and 2013, the Uganda Museum received information from district officials that the fossiliferous sites risked encroachment by local farmers, and this prompted visits to Bukwa by museum personnel in order to ensure the proper protection of the sites by reiterating the scientific and cultural heritage value of the deposits to local leaders, government officials and people living close to the sites. In effect, because of the long delay following the brief visit to the site in 2002 by the international team that had the permit from central government to study the site, the deposits were considered by local government officials and local inhabitants to have been abandoned by the scientific community, and thus to be open for exploitation by other interests, including agriculture. During the visits by the Uganda Museum in 2009, 2010 and 2013, aimed at rectifying the misunderstanding, a few fossils were rescued from recently cleared and ploughed parts of Bukwa II. The American team then visited the site in 2015.

Table 2. Main events at Bukwa fossil sites in chronological order.

1965	Discovery of fossiliferous sediments at Kwongori Hill near Lamitina, Bukwa, north-east Elgon, by MacDonald & Old
1965 December	Surface collection of fossils at Bukwa I (south flank of hill) by Henderson and Walker
1966	Bukwa II discovered on the north side of Kwongori Hill by Bishop & Walker, surface collections of fossils made. Isotopic date samples taken
1967	Lumitina, Bukwo Fossil Site, protected by the 1967 Monuments Act of Uganda
1967 December	Excavation at Bukwa II by Walker *et al*., Makerere University
1968 January	Excavation at Bukwa II by Walker *et al*., Makerere University
1970	Excavation and taphonomic study at Bukwa II by Hill & Walker
1997 October	Surface collections and screening at Bukwa I and Bukwa II by the Uganda Palaeontology Expedition (UPE)
1998 November	Surface collections and screening at Bukwa I and Bukwa II by the UPE
2002	Surface collections and screening at Bukwa II by MacLatchy *et al*. Date samples collected
2009 August	Elgon added to UPE excavation permit. Date samples collected by Franco-Japanese team
2010	Surface collections at Bukwa I and Bukwa II by Uganda Museum during administrative visit
2011 January	Administrative visit by Uganda Museum, fossils rescued from ploughed land at Bukwa II
2012	Erection of Information Panel at Bukwa Fossil Site by the Uganda Museum
2015	Collections at Bukwa II by MacLatchy *et al*.,

CONSERVATION ISSUES AT BUKWA FOSSIL SITES

In 1967, the Bukwa sites were protected by the Monuments Act of Uganda, but the boundary of the fossiliferous deposits was never defined and gazetted. From 1970 until 1997 there was no scientific activity in the region, due mainly to insecurity in the region. During this lengthy period, local farmers extended their fields, and thereby encroached onto the lower slopes of Kwongori Hill, principally on its northern flanks where there is thin soil overlying the fossiliferous strata. There was also partial deforestation of the hill, not so much for charcoal burning, but for obtaining poles for building and fencing. In addition, cattle graze the grass and goats browse the bushes that grow on the hill, and this activity leads to trampling of fossils (Fig. 3-10).

Due to the fact that the flaggy tuffs exposed over most of the hill are impossible to plough and the sloping ground is not suitable for building, the deposits at Bukwa I have remained largely intact. The same cannot be said of Bukwa II, which, in 2011 was cleared of trees and bushes, and ploughed in preparation for sowing maize by local farmers, despite an administrative visit by Uganda Museum staff in 2010, specifically to raise awareness among government officials, local leaders and farmers, concerning the scientific value of the site, and to prevent precisely this sort of activity (Fig. 3, 5-7). Because of this encroachment, the Uganda Museum decided to liaise more closely with local leaders and in 2012 it erected a panel at the site, which informs passers-by that the site is protected by the Monuments Act of 1967 (Fig. 4). This panel represents a preliminary phase of continued involvement between the Uganda Museum and the Bukwa community. Phase 2 will be the gazettement of the fossil sites such that all persons concerned will be clear about the boundaries of the monument while Phase 3 will entail the construction of an Interpretation Centre where children and adults can learn about the past, using the fossils and strata exposed at Kwongori Hill as the focus of the development.

Figure 3. Bukwa II in August 2009, showing dense vegetation between the fossiliferous outcrops and the neighbouring maize shambas. Note the two *Euphorbia* trees in the background (one half hidden by vegetation) which serve as landmarks (see Fig. 5-7).

Figure 4. Information panel erected in 2012 by the Uganda Museum at the foot of Kwongori Hill close to Bukwa II fossil site.

Figure 5. Bukwa II in January 2011, cleared of vegetation prior to ploughing.

Figure 6. Bukwa II site in January, 2011, trees and bushes cleared in preparation for ploughing

Figure 7. Exposures of sediment at Bukwa II in July, 2011. Note the maize shamba in the background, bordering the fossiliferous exposures and overlying fossiliferous strata. The two *Euphorbia* trees in the background serve as landmarks to highlight the changes that took place between August 2009 (see Fig. 3 and 6) and July, 2011.

Figure 8. Close-up photograph of fossiliferous deposits at Bukwa II in July, 2011, cleared of vegetation and roughly ploughed by a local farmer using oxen pulling a simple, hand-held plough. Numerous fossils were rescued from the surface of the ploughed land.

Figure 9. Bukwa I fossiliferous beds on the south flank of Kwongori Hill, Bukwa District. Image taken in July, 2010.

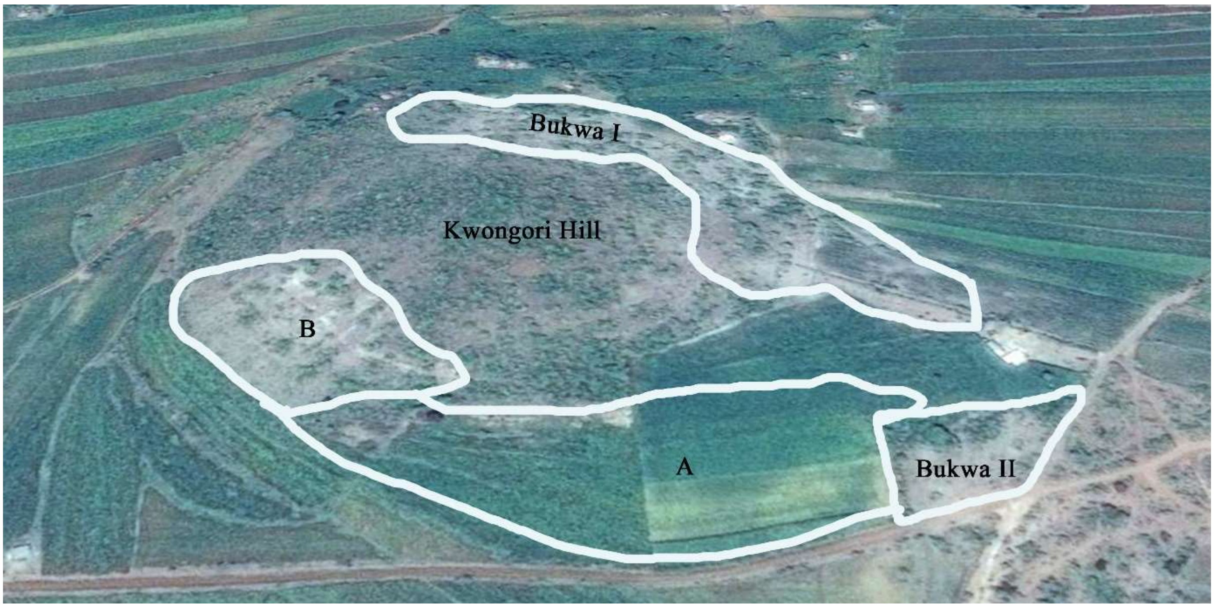

Figure 10. Oblique view of Kwongori Hill from the north, showing the fossiliferous areas Bukwa I and Bukwa II. Area 'A' comprises fossiliferous deposits incorporated into a maize field; Area B comprises tuffs containing fossil plants and scarce mammals. The summit of the hill is comprised of basanite lava.

DISCUSSION

The fossiliferous deposits at Kwongori Hill, commonly known in scientific circles as Bukwa I and Bukwa II, were discovered half a century ago, soon after Uganda's independence. After a few years of study and excavations by a palaeontological team based at Makerere University, there followed a long period during which no scientific research could be done at the sites, but activity picked up again at the end of the last century with surveys by the Uganda Palaeontology Expedition, a collaborative project between the Uganda Museum, Kampala, the Muséum National d'Histoire Naturelle, Paris, and local inhabitants of Bukwa District. In 1999, authorisation to study the Bukwa sites was transferred to a team based in the United States of America, which visited the region in 2002, after which the sites lay unstudied for more than a decade. Because of this long delay between field surveys, the site was considered by many people in Bukwa District to have been abandoned. In 2009, in order to underline the scientific potential of the sites to local government and inhabitants of Bukwa District, the Uganda Museum added Elgon to the Uganda Palaeontology Expedition's excavation permit as an integral part of the research activities jointly undertaken by the Uganda Museum and the UPE, not only for scientific reasons, but also to stress to government officials and local inhabitants at Bukwa that the sites are of real scientific value and had not, in effect, been abandoned by the scientific community.

Most authors have accepted that the Bukwa sites I and II correlate to the Early Miocene, older than 19 Ma, but this monograph indicates that, whereas Bukwa I is indeed of Early Miocene age, the deposits and fossils at Bukwa II are considerably younger, correlating to the Middle Miocene ca 16 Ma (Ogg *et al*. 2016). This is the only deposit of this geological period known in Uganda. Its protection and proper scientific study is evident.

The Bukwa fossiliferous deposits are protected by the 1967 Monuments Act of Uganda, but since the 1970's there has been encroachment onto the strata by local farmers and other people. The damage to the site has been limited mainly to the northern flanks of Kwongori Hill, the southern slopes being devoid of ploughable soil. Nevertheless, the deposits are damaged by cattle and goats which access the area in search of grazing and browse. Local inhabitants have exploited the vegetation in search of building poles and other plant products, and this has led to destruction of soil cover and erosion, especially along foot paths that traverse the hill.

Proper protection of the fossiliferous deposits is essential if the cultural integrity of the site is to be maintained and its scientific potential fully realised. The Uganda Museum plans to survey the locality in order to define its boundary, followed by gazettement, so that local inhabitants and government officials are clear about the limits of the monument. The main value of the locality lies in its scientific potential, but it has merits as a tourist destination, because the flaggy tuffs exposed on the southern slopes of the hill contain abundant plant fossils, including grass in its position of growth, which at ca 19.5 Ma, are the earliest documented occurrence of a grassland ecosystem in Africa (Fig. 11). With this in mind the Uganda Museum and Bukwa District officials intend to create an Interpretation Centre focused on the fossil sites.

CONCLUSIONS

Bukwa I (Early Miocene) and Bukwa II (Middle Miocene) are important fossiliferous localities cropping out on the southern slopes and northern flank of Kwongori Hill, Bukwa District, Uganda, respectively. Bukwa I site preserves grass fossils *in situ* in palaeosols that developed on volcanic tuffs some 19-20 million years ago. These are currently the oldest known grass fossils in Africa (Bamford & Pickford, 2017). A variety of mammalian fossils including two taxa of hominoid primates have been recovered from the younger deposits at Bukwa II, aged about ca 16 Ma. Being the only known site in Uganda aged ca 16 Ma, Bukwa II is an essential locality for protection, preservation and scientific study.

Figure 11. Fossils from Bukwa I, Elgon, Uganda. Top row: grass stems (left) and bulrush leaf (right) preserved in fine-grained volcanic ash, bottom row: diverse snails, a bone and an insect cocoon (left) and a snail in volcanic ash (right).

There continues to be concern about maintaining the scientific and cultural integrity of the Bukwa sites because there is pressure from local inhabitants who wish to exploit the plant resources on Kwongori Hill and from farmers who are anxious to enlarge their shambas by ploughing its lower slopes, especially on the northern side of the hill, where a large tract of potentially fossiliferous strata is already under cultivated maize. The 1967 Monuments Act of Uganda provided legal protection, but the boundaries of the sites need to be clearly defined in order to prevent any further misunderstandings about the area.

The Bukwa sites not only have scientific, educational and cultural heritage value, but also are potentially of interest to tourists. The present monograph provides detailed information about the fossil plants, mammals and gastropods from Bukwa which underline its scientific potential. Much remains to be done at the Bukwa palaeontological sites, not only for science but also for local development and education. The scientific community needs to interact with the local community on a regular (annual) basis, not just at national and district government levels, but also at the grass roots level, by involving local inhabitants in the scientific research at the sites.

ACKNOWLEDGEMENTS

In Bukwa District, councillors and leaders, government officials, farmers and local inhabitants are thanked for their interest in ensuring the scientific integrity of the Bukwa sites at national and international contexts, and for their collaboration at national government and local grass-roots socio-political levels.

REFERENCES

Bamford, M., & Pickford, M., 2017 - Bukwa Palaeovegetation. *Geo-Pal Uganda*, **11**: 23-28.

Brock, P.W.G. & MacDonald, R., 1969 - Geological environment of the Bukwa mammalian fossil locality, Eastern Uganda. *Nature*, **223**: 593-596.

Hamilton, A., 1968 - Some plant fossils from Bukwa. *Uganda Journal*, **32**: 157-164.

Hill, A. & Walker, A., 1972 - Procedures in vertebrate taphonomy; notes on a Uganda Miocene fossil locality. *Journal of the Geological Society of London*, **128**: 399-406.

MacDonald R. & Old, R., 1969 - Geology of the Bukwa - Greek River Area. *Report of the Geological Survey of Uganda*.

MacLatchy, L., Deino, A. & Kingston, J., 2006 - An updated chronology for the early Miocene of NE Uganda. *Journal of Vertebrate Paleontology*, **26** (**3**, Supplement): 93A.

MacLatchy, L. & Cote, S., 2017 - Mixing and matching "endemic" primate taxa: A distinct combination of Catarrhine Primates from an Early Miocene site at Bukwa, Uganda. *Society of Vertebrate Paleontology, 77th Annual Meeting, Calgary, Abstracts of Papers*, pp. 155-156.

Ogg, J.G., Ogg, G.M. & Gradstein, F.M., 2016 - *A Concise Geologic Time Scale 2016,* Elsevier, 240 pp.

Pickford, M., 2002 - Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda. *Comptes Rendus Palevol*, **1**: 213-219.

Pickford, M., 2017 - Bukwa Dating. *Geo-Pal Uganda*, **11**: 12-22

Walker, A., 1968 - The lower Miocene fossil site of Bukwa, Sebei. *Uganda Journal*, **32** (**2**): 149-156.

Walker, A., 1969 - Fossil mammal locality on Mount Elgon, eastern Uganda. *Nature*, **223**: 591-593.

Bukwa dating

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ABSTRACT

Estimates of the age of the fossiliferous localities at Bukwa I and Bukwa II, Uganda, have varied tremendously, the oldest published estimate being 23 Ma, and the youngest 16.5 Ma. Previous researchers have usually assumed that Bukwa I and Bukwa II are almost the same age, which is not the case. Two categories of chronological evidence have been cited : 1) radio-isotopic dates obtained from lavas subjacent to, and overlying, the sediment outcrops which overall indicate an Early Miocene eruption age, and 2) biostratigraphy, which for some authors indicated correlation to the Early Miocene in agreement with the radio-isotopic dates, while for others, the fauna suggested a Middle Miocene correlation in apparent contradiction of the radio-isotopic dates. This paper provides new radio-isotopic age determinations which are compatible with previous analyses, save for the K-Ar analyses which indicate a slightly younger age than previously obtained. The restricted mammalian fauna from Bukwa I indicates an Early Miocene age in agreement with the radio-isotopic age determinations. The fauna from Bukwa II, in contrast, suggests a Middle Miocene correlation, equivalent to European Land Mammal Zone MN 5 and East African Faunal Set IIIb. It post-dates the rich faunas of Rusinga Island and Karungu (Faunal Set II) being closer in age to Kipsaraman and Maboko (15-16 Ma) and is older than Fort Ternan (Faunal Set IV : 13.7 Ma). The sediments at Bukwa II are deduced to repose unconformably on the flaggy tuffs of Bukwa I. The nature of the unconformable relationship between the Bukwa II and Bukwa I deposits needs to be investigated (faulted relationship, channel infill, karst or pseudokarst, piping?).

Key words : Uganda, Middle Miocene, Radio-isotopic analyses, K-Ar, Ar-Ar, Faunal correlation.

INTRODUCTION

Estimates of the ages of the fossiliferous clays, tuffs and lavas at Kwongori Hill, near Lamitina (also spelled Lumitina), more commonly known in the palaeontological literature as Bukwa I and Bukwa II, (also spelled Bukwo) have varied tremendously, ranging from 23 Ma (Van Couvering, 1977; Van Couvering & Van Couvering, 1976; Sanders *et al*., 2010) to as young as 16.5 Ma (Pickford, 2009) with a variety of other estimates in between (Bishop *et al*., 1969; Brock & MacDonald, 1969; Cote *et al*., 2017; Geraads, 2010a, 2010b; Guérin, 2011; Harrison, 1982, 2010; Jacobs, 2004; Jacobs *et al*., 2010; MacLatchy & Cote, 2017; MacLatchy *et al*., 2006; Murray *et al*., 2017; Pickford, 1981, 1986, 1998, 2001, 2002, 2007; Sanders *et al*., 2010; Werdelin, 2010; Winkler & Avery, 2010; Winkler *et al*., 2005, 2010).

The first radio-isotopic analyses on samples of lavas collected at the base and summit of Kwongori Hill yielded ages of 20.1±1.3, 22.0±0.2, 21.9±0.2 and 17.4±0.3 Ma (Walker, 1968, 1969). However, the youngest age was associated with the lava at the base of the hill, against which the fossiliferous sediments were thought to be banked (MacDonald & Old, 1969) and the older ages were obtained from the lava at the top of the hill considered to cap the sequence. Baker *et al*. (1971) re-published the dates but appear to have made an error in one of them and added another (22.0±0.2, 21.9±0.2, 19.8±1.5, 17.2±0.4 and 17.4±0.3 Ma). Walker (1969) suggested that the 17.4 Ma date for the «lower» lava at Bukwa was discrepant, re-sampled it and obtained dates of 24.2±0.7 and 24.3±0.7 Ma (Bishop, 1972).

Table 1. Original provisional list of the Bukwa II fauna (Walker, 1969), the modifications by Van Couvering & Van Couvering (1976) and identifications in this paper.

Walker, 1969	**Van Couvering & Van Couvering, 1976**	**This paper**
Limnopithecus legetet	*Limnopithecus legetet*	«*Micropithecus*» *leakeyorum* («*Limnopithecus*» sp. Kipsaraman) Genus indet. medium-sized ape, in new collections
Myohyrax oswaldi	*Myohyrax oswaldi*	*Myohyrax oswaldi*
Other Insectivora as yet unidentified	Not listed	Not seen in old collections
Megalohyrax championi	*Pachyhyrax championi*	*Afrohyrax championi*
Meroehyrax bateae	*Meroehyrax bateae*	*Prohyrax bukwaensis*
Dinotherium hobleyi	*Prodeinotherium hobleyi*	*Deinotherium hobleyi* sensu lato
Indeterminate mastodonts	*Platybelodon kisumuensis* (?)*Gomphotherium* sp.	Indeterminate mastodont
Chilotherium sp.	*Chilotheridium pattersoni*	*Victoriaceros kenyensis*
Dicerorhinus sp.	*Brachypotherium heinzelini*	*Brachypotherium*
Brachyodus aequatorialis	*Masritherium aequatorialis*	cf *Brachyodus* sp.
(?)*Hyoboops africanus*	(?)*Brachyodus africanus*	Not seen in old collections
Diamantohyus africanus	*Xenochoerus africanus*	*Diamantohyus nadirus*
Lystriodon jeanneli	*Bunolistriodon jeanneli*	*Hyotherium namaquense*
Dorcatherium parvum	*Dorcatherium parvum*	cf *Afrotragulus parvus*
Dorcatherium pigotti	*Dorcatherium pigotti*	«*Dorcatherium*» *pigotti*
Large tragulid (not *Dorcatherium chappuisi*)	Not listed	Not seen in old collections.
Palaeomeryx sp. (the large species of Whitworth, 1958)	Not listed	*Prolibytherium magnieri* *Canthumeryx sirtensis*
Megapedetes pentadactylus	*Megapedetes pentadactylus*	Not seen in old collections
Other rodents as yet unidentified	*Paraphiomys stromeri*, *Paraphiomys pigotti*	See MacLatchy *et al*., 2006 ; *Diamantomys morotoensis* this paper
Small and medium sized indeterminate carnivores	Not listed	Small creodont (nov. gen. in prep.)
Ciconiiform birds	Not listed	Aves
Crocodylia sp.	Not listed	Crocodylia
Trionychid and Pelomedusid water tortoises	Not listed	Trionychid, Pelomedusid
Medium-sized and tiny freshwater fish	Not listed	See Murray *et al*., 2017
Heterocypris sp.	Not listed	Not seen in old collections
(?)*Archachatina*	Not listed	*Tholachatina*
Burtoa	Not listed	*Burtoa*
Gulella	Not listed	Not seen in old collections. *Haplonepion*, *Silvigulella* in new collections
Helicarion	Not listed	*Chlamydarion*, *Calidivitrina*
Homorus	Not listed	*Homorus* + other subulinids
Limicolaria	Not listed	Not present in old collections. *Pseudoglessula*, *Edouardia* in new collections
Maizania	Not listed	*Maizania*
Opeas	Not listed	*Opeas*, *Curvella*, *Pseudopeas*
Tayloria	Not listed	*Artemonopsis*, *Gonaxis*
Thapsia	Not listed	*Thapsia*
Melanoides tuberculata	Not listed	*Melanoides* sp.
Potamid crabs	Not listed	Crabs
Millipedes	Not listed	Not seen in old collections

The position of some of the lavas at Kwongori relative to the sediments is enigmatic. Bishop (unpublished field notes reproduced in Musalizi *et al.,* 2009) thought that the lava at the base of the hill had been down-faulted, in which case the sediments could be older than the lava rather than younger than it. Other authors (Walker, 1968, 1969; Hill & Walker, 1972) wrote that the sediments at Bukwa II are banked against the lava at the base of the hill, which would indicate that they are younger than it. This discrepancy has never been resolved.

The initial faunal list published by Walker (1968, 1969) gave the impression that the fauna was similar to the rich Rusinga and Karungu (Kenya) assemblages of Early Miocene age. It should be recalled that at the time of his studies, the subdivision of the so-called «Lower Miocene» faunas of East Africa had not been achieved, with the result that the term «Lower Miocene» as employed by palaeontologists working on East African fossils, encompassed faunas from a wide range of time, spanning the period 23 to 15 Ma (Pickford, 1981). It is also clear that Walker (1968, 1969) identified the Bukwa II fossils largely on the basis of the literature, which was focussed on fossil remains from rich Early Miocene localities rather than the poorer Middle Miocene ones, and this introduced a bias in the taxonomy and thence the biochronology.

Walker (1968, plate 1) illustrated a rhinocerotid upper cheek tooth row from Bukwa, but he did not describe or provide any measurements or figures of the other fossil specimens from the site, which rendered it difficult or impossible for other researchers to verify or revise the list on the basis of what was published. For many years insecurity in Uganda discouraged researchers from revising the material curated in the Uganda Museum, with the result that authors either accepted the faunal lists as published (Pickford, 1981) or modified them according to changes in taxonomy that were occurring at the time (Van Couvering & Van Couvering, 1976). Modification of the faunal list by Van Couvering & Van Couvering (1976) introduced several errors which enhanced the impression that the Bukwa fauna was close to that of Karungu, at the time thought to be securely dated ca 23 Ma (revision by Drake *et al*., 1988, indicates that Karungu is 17.8 Ma). With the re-establishment of security and peace in Uganda in 1985, some of the fossils were studied by the authors, and have been re-examined recently. Many of the published identifications have turned out to be erroneous or doubtful, or could not be verified, some of the specimens being absent from the collections studied in the Uganda Museum, Kampala.

Apart from a deinothere tooth, all previous faunal correlations of Bukwa were based on the fossils from Bukwa II. In 1998 and 1999, the Uganda Palaeontology Expedition collected some rodents at Bukwa I which indicate correlation to Faunal Set I (ca 19-20 Ma) which accords with the radio-isotopic age determination of the lava at the top of Kwongori Hill. The same expedition collected suids, ruminants and other mammals at Bukwa II which indicate a considerably younger age for the deposits at this site, inviting correlation to Faunal Set IIIb (ca 16 Ma) i.e. the base of the Middle Miocene (Ogg *et al*., 2016).

The aim of this paper, therefore, is to provide new age determinations for the lava flows at Kwongori Hill, and to discuss the biostratigraphic implications of the mammalian faunas from Bukwa I and Bukwa II.

MATERIALS AND METHODS

In 2009, samples of lava were collected at the top of Kwongori Hill, and angular cobbles of basalt were sampled from sediment within the Bukwa succession (Fig. 1-3). Whole rock and minerals within the lavas were analysed to determine the K content, radiogenic 40Ar and non-radiogenic 40Ar. We employ a recently published geological time scale for anchoring the Early Miocene / Middle Miocene boundary at 15.97 Ma (Ogg *et al*. 2016).

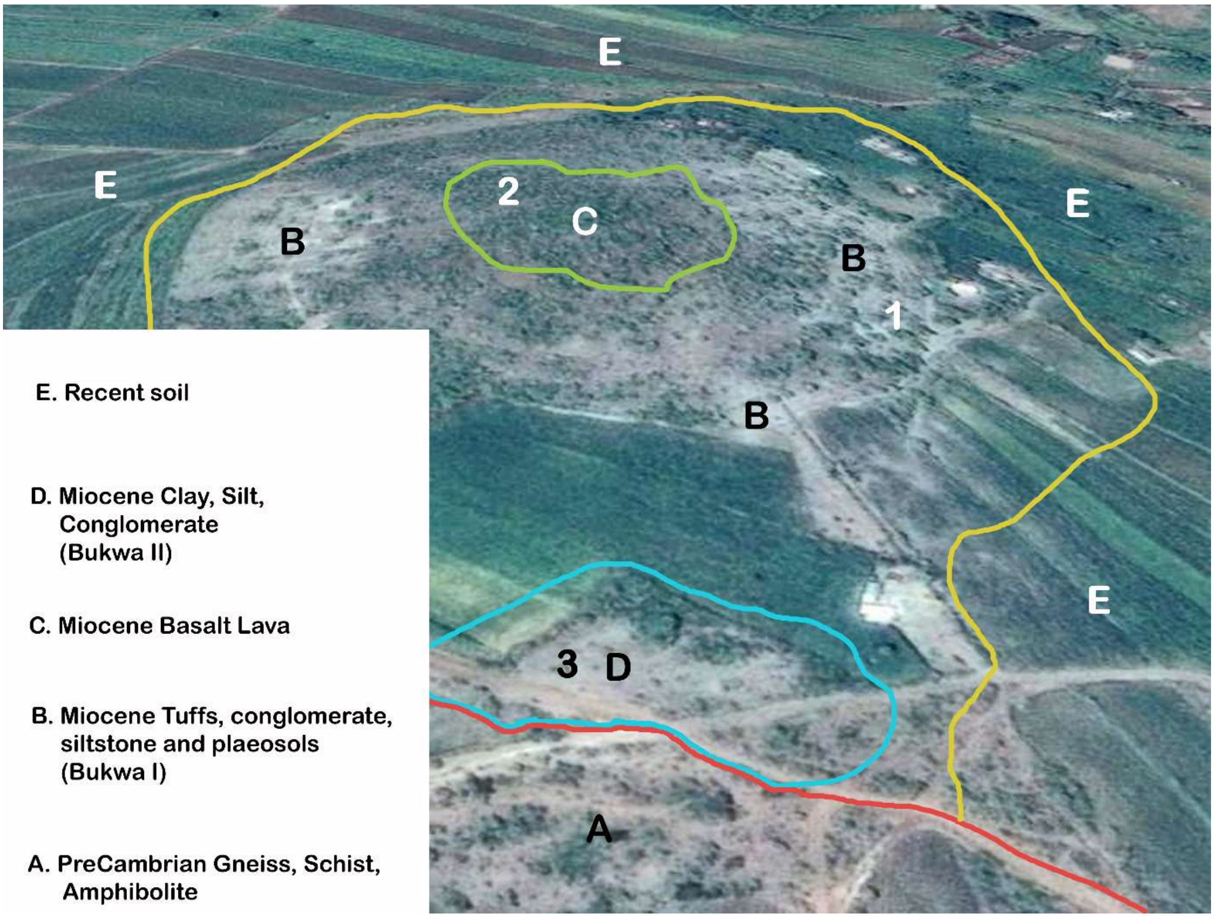

Figure 1. Geological interpretation of Kwongori Hill showing sampling locations for radio-isotopic analyses (1 – Conglomerate UG09082203; 2 – Lava UG09082201, UG09082202; 3 – Conglomerate UG09082204).

Table 2. Published age estimates of lavas and faunas associated with the Bukwa fossiliferous deposits.

Reference	**Age estimates of Bukwa deposits**	**Comments**
Baker, Williams, Miller & Fitch, 1971	22.0±0.2, 21.9±0.2, 19.8±1.5, 17.2±0.4, 17.4±0.3 Ma	Lavas at base and top of Kwongori Hill ; K-Ar
Bishop, Miller & Fitch, 1969	Older than 22.0±0.2 Ma (21.9±0.2; 22.0±0.2) Ma	Lava at top of hill ; K-Ar
Brock & MacDonald, 1969	Lava at top of hill : 22.0±0.2, 21.9±0.2 Ma, 20.1±1.3 Ma; Lava flow against which the mammalian beds are banked : 17.4±0.3 Ma	Lavas at base and top of Kwongori Hill ; K-Ar
Drake *et al*., 1988	Not mentioned	Re-dated Karungu to 17.8 Ma
Geraads, 2010a	17.5 Ma	Elasmotheriinae?
Geraads, 2010b	17.5 Ma	Tragulidae *D. parvum* & *D. pigotti*
Guérin, 2011	between 18.5 and 17.5 Ma	*Brachypotherium heinzelini*
Guérin, 2011	ca 18 Ma	*Chilotheridium pattersoni*
Harrison, 1988	22.3 Ma	*Limnopithecus legetet*
Harrison, 2010	?22 Ma or same age as Rusinga? 17.8 Ma	*Limnopithecus*
Jacobs *et al*., 2010	22 or 17.5 Ma	Plants
MacLatchy *et al*., 2006	19.5-19.1 Ma	Ar-Ar
MacLatchy & Cote, 2017	19.5-19.1 Ma	Primates; Ar-Ar
Murray *et al*., 2017	19.5-19.1 Ma (Burdigalian)	Fish, Ar-Ar,
Pickford, 2007	17.5 Ma	*Kenyasus namaquensis*
Pickford, 2009a	17.5 Ma	*Prohyrax bukwaensis*
Pickford, 2009b	17.5, 16.5 Ma	*Silvigulella*
Pickford, 1981	Faunal Set II, 18-16.5 Ma	(*Diamantohyus*, large pecora)

Pickford, 1998	ca 18.5 Ma	Biochronology
Pickford, 2002	ca 17.5 Ma	Grassland ecosystem Bukwa I
Pickford & Mein, 2011	17.5 Ma	*Megapedetes pentadactylus* (Walker, 1969)
Rasmussen & Gutierrez, 2010	Early Miocene	*Afrohyrax championi* and *Meroehyrax bateae*
Sanders *et al*., 2010	19.5-19.1 (alternative 23) Ma	Proboscidea
Van Couvering & Van Couvering, 1976	23 Ma	General review
Van Couvering, 1977	23 Ma	Fish
Walker, 1968	Upper lava : 20.1±1.3, 22.0±0.2, 21.9±0.2 Ma; Lower lava : 17.4±0.3 Ma (high possibility of Argon leakage). Upper age limit of the sediments is about 22 Ma.	Lavas at base and top of Kwongori Hill; K-Ar
Walker, 1969	ca 22 Ma	Lava at top of Kwongori Hill; K-Ar
Werdelin, 2010	18-19 Ma	General review
Winkler & Avery, 2010	19.5-19.1 Ma	Ochotonidae; K-Ar
Winkler, MacLatchy & Mafabi, 2005	22 Ma	Rodents, Ochotonidae; Ar-Ar
Winkler *et al*., 2010	19.5-19.1 Ma	Rodentia; K-Ar

K-Ar AND ^{40}Ar/^{39}Ar AGES

Samples and sample preparation for dating

Two gravel samples (UG09082203) were collected in order to provide a lower age limit for the fossiliferous deposits and were analysed by K-Ar and ^{40}Ar/^{39}Ar methods. However the gravel samples were not suitable for age determination, because they are extremely weathered. The basanite lava samples from the summit of Kwongori Hill (UG09082201, UG09082202) (Fig.1, 2) were collected in order to provide an upper age limit for the fossiliferous deposits and were analysed by K-Ar and ^{40}Ar/^{39}Ar methods.

The basanite samples were prepared by crushing and sieving of pumice samples. Grains in the size range 254–423 µm were used for K-Ar age determination. An anorthoclase phenocryst and groundmass of 0.3-1 mm size were prepared for ^{40}Ar/^{39}Ar age determinations. The separated fractions were washed with water, then dried in an oven at 110ºC. Magnetic minerals were then removed manually by magnet from the dried sieve fractions for K-Ar age determination.

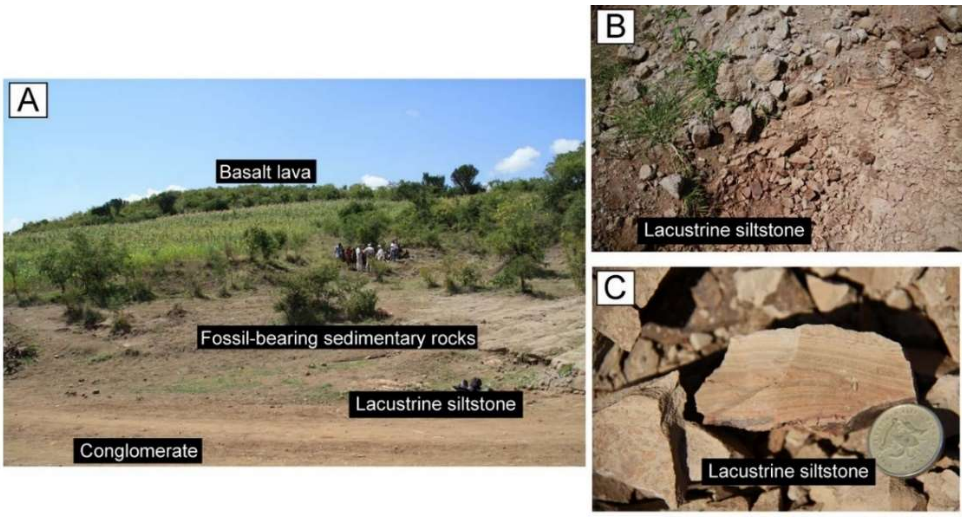

Figure 2. Outcrops of fossiliferous sedimentary rocks unconformably overlying Pre-Cambrian schist and overlain by basalt lavas. The sedimentary rocks are composed mainly of conglomerate, associated with sandstone and minor siltstone. In the lower part of the exposed section, parallel-laminated lacustrine siltstone occurs overlying basal conglomerate.

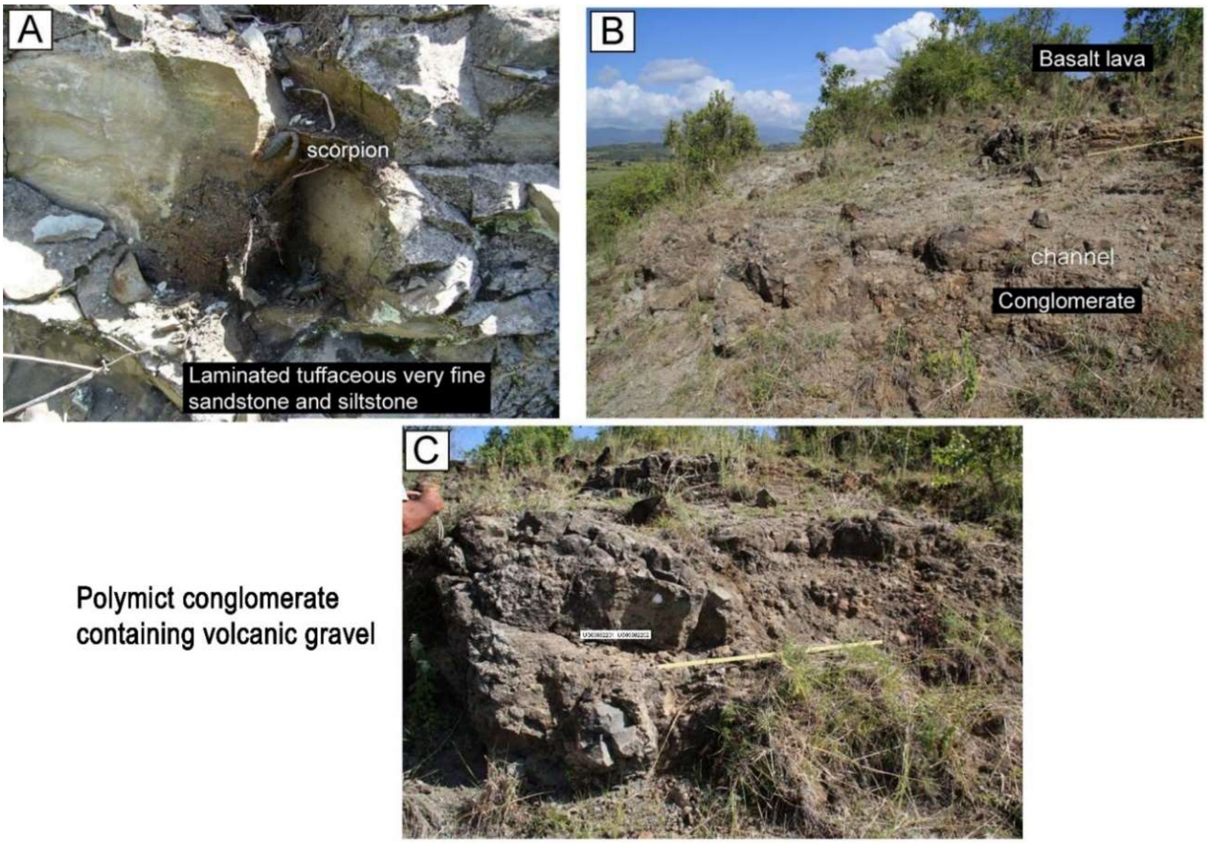

Figure 3. Sediment facies at Kwongori Hill dominated by volcanic clasts ranging from silt to coarse conglomerate.

Analytical procedures for K-Ar age determinations

The analytical procedures for potassium and argon and calculations of ages and errors were based on the methods described by Nagao *et al*. (1984) and Itaya *et al*. (1991). Potassium was analyzed by flame photometry using a 2000 ppm Cs buffer. The potassium data has an analytical error of less than 2% at the 2σ confidence level. Argon isotopes were analyzed with a 15 cm radius sector type mass spectrometer with a single collector system, using the isotopic dilution method and a ^{38}Ar spike. Multiple runs of the standard (JG-1 biotite, 91 Ma) gave an error of about 1% at a 2-sigma confidence level (Itaya *et al*., 1991). The decay constants for ^{40}K to ^{40}Ar and ^{40}Ca, and ^{40}K content used in the age calculations are 0.581×10^{-10}/ year, 4.962×10^{-10}/year and 0.0001167, respectively (Steiger & Jäger, 1977).

Analytical procedures for dating of $^{40}Ar/^{39}Ar$ age determinations

Individual mineral grains (0.3-1 mm in size) were placed in 2 mm holes on a pure aluminum tray. Neutron flux and interference factors were monitored by age standard grains (3gr hornblende; Roddick, 1983), and calcium ($CaSi_2$) and potassium (synthetic $KAlSi_3O_8$ glass) salts for Ca and K corrections. Subsequently the tray was vacuum-sealed in a quartz tube. The samples were irradiated neutron in the core of 5 MW Research Reactor at Kyoto University (KUR) for 5 hours. The fast neutron flux density is $3.9\ x10^{13}$ n/cm^2/sec, and is confirmed to be uniform in the dimension of the sample holder (ϕ16 x 18 mm^3) as little variation in J-values of the evenly spaced age standards was observed (Hyodo *et al*., 1999). Averaged J-values, potassium and calcium correction factors are J = 0.00550 + 0.00002, $(40/39)_K$ = 0.0041 + 0.0074, $(36/37)_{Ca}$ = 0.000158 + 0.000022 and $(39/37)_{Ca}$ = 0.000711 + 0.000039, respectively.

A mineral grain was analyzed by the step-heating technique using a 5W continuous argon ion laser. Temperatures of samples were monitored by an infrared thermometer with a precision of 3 degrees in an area of 0.3 mm diameter (Hyodo, 2008). A crystal grain was heated under a defocused laser beam at a given temperature for 30 seconds. The extracted gas was purified with a SAES Zr-Al getter (St 101) kept at 400 degrees for 5 minutes. Argon isotopes were measured using the custom-made mass spectrometer with a relatively high resolution ([M/ΔM]>400), which allows the separation of hydrocarbon peaks except for mass 36 (Hyodo *et al*., 1994). Typical blanks of extraction lines were 3.7×10^{-13}, 1.3×10^{-13}, 1.5×10^{-13}, 3.4×10^{-14} and 1.5×10^{-12} ccSTP for ^{36}Ar, ^{37}Ar, ^{38}Ar, ^{39}Ar and ^{40}Ar, respectively.

Results of K-Ar and ^{40}Ar/^{39}Ar age determinations

K-Ar ages of whole rock analyses of UG09082201 and UG09082202 are listed in Table 3. Whole rock ages of UG09082201 and UG09082202 are 17.44±0.42Ma and 17.96±0.42 Ma, respectively (Fig. 4, 5).

The ^{40}Ar/^{39}Ar analysis of the anorthoclase phenocryst from UG09082201 did not yield a plateau age. The ^{40}Ar/^{39}Ar plateau age of groundmass from UG09082202 was 19.71±0.46Ma.

Table 3. Analyses and age determinations of lava samples from Bukwa, Elgon, Uganda. (WR - whole rock) (data courtesy of H. Hyodo and Y. Sawada)

Sample N°	Age	Context	For K-Ar	For Ar-Ar	Material grain size
UG09082201	17.441	Covering fossil bed	WR	Feldspar	WR (#60-100)
UG09082202	17.964	Covering fossil bed	WR	Feldspar	WR (#60-100)
UG09082203-1	13.02	Gravel in fossil bed	Pyroxene	Feldspar	WR (#60-100)

Sample N°	Age	K content Weight %	Radiogenetic 40Ar (10-8cc STP/g)	Non-radiogenic 40Ar %
UG09082201	17.441	0.756±0.015	51.416±0.693	19.95
UG09082202	17.964	1.16±0.023	81.27±1.019	20.26
UG09082203-1	13.02	0.132±0.007	6.694±0.582	81.56

Sample N°	Rock type	Mineral	Ar-Ar age	Mineral	K-Ar age
UG09082201	basalt	WR-2	--	WR	17.44±0.42
UG09082202	basalt	WR-2	19.71±0.46	WR	17.96±0.42
UG09082202	basalt	WR-2	19.71±0.46	WR	17.70±0.42

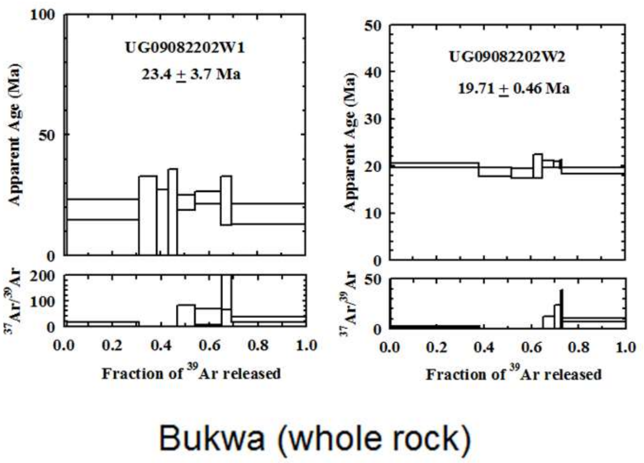

Figure 4. Age spectra and 37ArCa/39ArK ratios of sample UG 09082202W1 and UG 09082202W2 from Bukwa, Uganda.

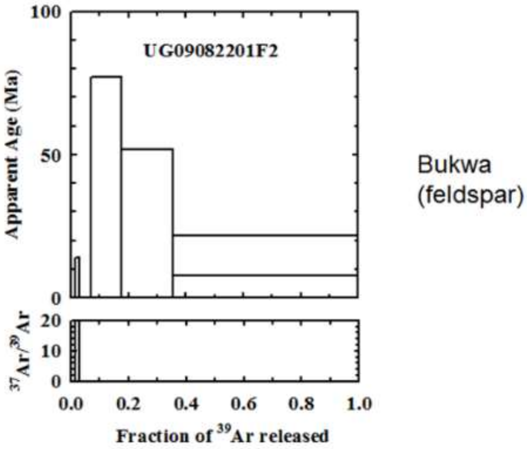

Figure 5. Age spectra and 37ArCa/39ArK ratios of sample UG 09082201F2 from Bukwa, Uganda

DISCUSSION

It is noted that Ar-Ar age determinations of the Bukwa lavas yielded results (19.7 Ma) that are greater than those calculated from the K-Ar analyses (17.4, 18.0, 17.7 Ma). Overall, though, the age determinations are compatible with those of previous researchers (Walker, 1968; MacLatchy *et al*. 2006) and they imply an Early Miocene eruption age.

If a normal superpositional relationship exists between the Bukwa sediments and the lava that caps Kwongori Hill, then the K-Ar analyses of the lavas would suggest that the age of the sediments at the Bukwa fossil sites is greater than 17.5-18 Ma, the upper limit of the estimate being somewhat younger than age estimates based on Ar-Ar analyses published by MacLatchy *et al*. (2006 : 19.1-19.5 Ma) and our own Ar-Ar analyses (this paper : 19.7 Ma). This estimate agrees with the restricted sample of mammals from Bukwa I, which yielded remains of the large bathyergoid rodent *Renefossor songhorensis* which is known only from Faunal Sets I and II (Mein & Pickford, 2008) implying that the flaggy tuffs exposed in the southern flank of Kwongori Hill are older than 17.8 Ma.

The fauna from Bukwa II, in contrast, indicates that the deposits at this site are much younger than the strata at Bukwa I, correlating closely to faunas from Kipsaraman (14.5 Ma : Pickford & Kunimatsu, 2005) and Ombo-Maboko (15.0 Ma : Faunal Set IIIb) and differing markedly from those of Rusinga and Karungu (17.8 Ma : Faunal Set II) (Drake *et al*., 1988). The Bukwa II fauna indicates that the sedimentary deposits at the site are older than Fort Ternan (Pickford *et al*., 2006 : 13.7±0.3 Ma, Faunal Set IV). This interpretation of the fauna from Bukwa II runs counter to the conclusion of MacLatchy & Cote (2017) that the medium-sized ape from Bukwa II is the oldest known example of the genus *Ekembo* : on the contrary, this ape could be descended from *Ekembo* rather than being its ancestor.

The long-lived assumption that the fossiliferous palustral deposits at Bukwa II underlie the flaggy tuffs of Bukwa I is called into question by the faunal correlations. It is inferred that the deposits at Bukwa II repose unconformably on an eroded surface of flaggy tuffs and are thus younger than the tuffs, not older than them. The precise nature of the unconformable relationship is currently unknown, but the palustral deposits could represent an infilling of a channel eroded into the flaggy tuffs. Alternatively, they could represent a superficial karst infilling. Several caves and many rock shelters are known in the flanks of Mount Elgon, incised into Miocene volcanic agglomerates and tuffs, including one example close to Bukwa, at Keben cho Kumus (Kumus Cave - 1°18'49"N : 34°45'28.9"E). The latter cave occurs in an analogous geomorphological situation to the palustral deposits at Bukwa II, being eroded into the tuffs and agglomerate at the foot of Tulwa Hill, 4.3 km northwest of Bukwa II. The floor of Kumus Cave has been infilled by sediments younger than the rocks comprising the hill. Finally, as W.W. Bishop (unpublished notes) wrote in his field notebook, there could have been tectonic activity resulting in faulted relationship between the lava at the base of the hill and the rest of the deposits. Detailed mapping may throw light in the matter.

CONCLUSIONS

Radio-isotopic analyses of lava from the top of Kwongori Hill, Bukwa District, Uganda, yielded a spectrum of ages. K-Ar analyses gave younger age estimates (17.5-18 Ma) than Ar-Ar analyses (19.7 Ma) compatible with the age of the lavas (19.1-19.5 Ma) obtained by MacLatchy *et al*. (2006) and previous authors (summarised in Baker *et al*., 1971). These and other authors suggested that as a consequence, all the sedimentary deposits at Kwongori Hill were of Early Miocene age, possibly as old as 23 Ma (Van Couvering & Van Couvering, 1976). The flaggy tuffs at Bukwa I that underlie the lava are of Early Miocene age, in agreement with the restricted mammalian fauna found there. In contrast, the mammalian fauna from Bukwa II has clear affinities with East African faunas correlated to Faunal Set IIIb, of Middle Miocene age (Ogg *et al*., 2016; Pickford, 1981, 1998) such as Kipsaraman, Maboko, Nyakach, Nachola, Losidok, Moruorot, and Kalodirr. The Bukwa II fauna is younger than that from Rusinga (Faunal Set II). It is older than the upper Middle Miocene fauna from Fort Ternan, Kenya (Faunal Set IV).

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REFERENCES

Baker, B.H., Williams, L.A.J., Miller, J.A. & Fitch, F.J., 1971 - Sequence and geochronology of the Kenya rift volcanics. *Tectonophysics*, **11**: 191-215.

Bishop, W.W., 1972 - Stratigraphic succession 'versus' calibration in East Africa. *In*: Bishop W.W. (Ed.) *Calibration of Hominoid Evolution*. London, Scottish Academic Press, pp. 219-246.

Bishop, W.W., Miller, J.A. & Fitch, F.J., 1969 - New potassium-argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *American Journal of Science*, **267**: 669-699.

Brock, P.W.G. & MacDonald, R., 1969 - Geological environment of the Bukwa mammalian fossil locality, Eastern Uganda. *Nature*, **223**: 593-596.

Cote, S., Mugume, A., Kityo, R., Kingston, J. & MacLatchy, L., 2017 - New fossil primate remains from Bukwa, Eastern Uganda. *5th EAQUA Workshop, Mukono, Uganda*, 4-7 July, 2017, Decades of Quaternary Research in East Africa : Implication for Sustainable Development, Conference Booklet, pp. 31-32.

Drake, R., Van Couvering, J.A., Pickford, M., Curtis, G.H. & Harris J.A., 1988 - New chronology for the early Miocene mammalian fauna of Kisingiri, western Kenya. *Journal of the Geological Society of London*, **145**: 479-491.

Geraads, D., 2010a - Rhinocerotidae. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, University of California Press, Berkeley, pp. 669-683.

Geraads, D., 2010b - Tragulidae. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, University of California Press, Berkeley, Los Angeles, London, pp. 723-729.

Guérin, C., 2011 - Les Rhinocerotidae (Mammalia, Perissodactyla) miocènes et pliocènes des Tugen Hills (Kenya). *Estudios Geologicos*, **67** (**2**): 333-362.

Harrison, T., 1982 - *Small-bodied Apes from the Miocene of East Africa*. Unpublished PhD Dissertation, University of London, 647 pp.

Harrison, T., 1988 - A taxonomic revision of the small catarrhine primates from the early Miocene of East Africa. *Folia Primatologica*, **50**: 59-108.
Harrison, T., 2010 - Dendropithecoidea, Proconsuloidea, and Hominoidea. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, University of California Press, Berkeley, Los Angeles, London, pp. 429-469.
Hill, A. & Walker, A., 1972 - Procedures in vertebrate taphonomy ; notes on a Uganda Miocene fossil locality. *Journal of the Geological Society of London*, **128**: 399-406.
Hyodo, H., 2008 - Laser Probe $^{40}Ar/^{39}Ar$ dating: History and development from a technical perspective *Gondwana Research*, **14**: 609-616.
Hyodo, H., Kim, S.-W., Itaya, T. & Matsuda, T., 1999 - Homogeneity of neutron flux during irradiation for $^{40}Ar/^{39}Ar$ age dating in the research reactor at Kyoto University. *Journal of Mineralogy, Petrology and Economic Geology*, **94**: 329-337.
Hyodo, H., Matsuda, T., Fukui, S. & Itaya, T., 1994 - $^{40}Ar/^{39}Ar$ age determination of a single mineral grain by laser step heating. *Bulletin of the Research Institute of Natural Science, Okayama University of Science*, **20**: 63-67 (in Japanese with English abstract).
Itaya, T., Nagao, K., Inoue, K., Honjou, Y., Okada, T. & Ogata, A., 1991 - Argon isotope analysis by a newly developed mass spectrometric system for K-Ar dating. *Mineralogical Journal*, **15**: 203-221.
Jacobs, B.F. 2004 - Palaeobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes. *Philosophical Transactions of the Royal Society of London*, B **359**: 1573-1583.
Jacobs, B.F., Pan, A.D. & Scotese, C.R., 2010 - Review of the Cenozoic Vegetation History of Africa. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, University of California Press, Berkeley, pp. 57-72.
MacDonald R. & Old, R., 1969 - Geology of the Bukwa – Greek River Area. *Report of the Geological Survey of Uganda*.
MacLatchy, L. & Cote, S., 2017 - Mixing and matching "endemic" primate taxa: A distinct combination of Catarrhine Primates from an Early Miocene site at Bukwa, Uganda. *Society of Vertebrate Paleontology, 77th Annual Meeting, Calgary, Abstracts of Papers*, pp. 155-156.
MacLatchy, L., Deino, A. & Kingston, J., 2006 - An updated chronology for the early Miocene of NE Uganda. *Journal of Vertebrate Paleontology*, **26**(**3**, Supplement): 93A.
Mein, P. & Pickford, M., 2008 - Early Miocene Rodentia from the Northern Sperrgebiet, Namibia. *Memoir of the Geological Survey of Namibia*, **20**: 235-290.
Murray, A.M., Argyriou, T., Cote, S. & MacLatchy L., 2017 - The fishes of Bukwa, Uganda, a lower Miocene (Burdigalian) locality of East Africa. *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2017.1324460. 10 pp.
Musalizi, S., Senut, B., Pickford, M. & Musiime, E., 2009 - Geological and palaeontological archives relating to Early Miocene localities of Uganda, 1957-1969. *Geo-Pal Uganda*, **1**: 2-96.
Nagao, K., Nishido, H., Itaya, T. & Ogata, K., 1984 - K-Ar age determination method, *Bulletin of Hiruzen Research Institute*, **9**: 19-38 (in Japanese).
Ogg, J.G., Ogg, G.M. & Gradstein, F.M., 2016 - *A Concise Geologic Time Scale 2016*, Elsevier, 240 pp.
Pickford, M., 1981 - Preliminary Miocene mammalian biostratigraphy for western Kenya. *Journal of Human Evolution*, **10**: 73–97.
Pickford, M., 1986 - The geochronology of Miocene higher primate faunas of East Africa. *In*: Else J. & Lee P. (Eds) *Primate Evolution*, Cambridge, Cambridge University Press, pp. 19-45.
Pickford, M., 1998 - Dating of the Neogene Old World anthropoid fossil record: essential base for phylogenetic analysis, biogeography and palaeoecology. *Primatologie*, **1**: 27-92.
Pickford, M., 2001 - The biochronological importance of Kubanochoerinae (Mammalia, Suidae) together with a description of new material of *Megalochoerus khinzikebirus* and *Libycochoerus massai* from Kenya. *Comptes Rendus de l'Académie des Sciences de Paris*, **332**: 193-200.
Pickford, M., 2002 - Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda. *Comptes Rendus Palevol*, **1**: 213-219.
Pickford, M., 2007 - Suidae and Hippopotamidae from the Middle Miocene of Kipsaraman, Kenya, and

other sites in East Africa. *Paleontological Research*, **11**: 85-105.
Pickford, M., 2009a - New Neogene hyracoid specimens from the Peri-Tethys region and East Africa. *Paleontological Research*, **13**: 265-278.
Pickford, M., 2009b - Land snails from the Early Miocene Legetet Formation, Koru, Kenya. *Geo-Pal Kenya*, **2**: 1-88.
Pickford, M. & Kunimatsu, Y., 2005 - Anthropoids from the Middle Miocene (ca 14.5 Ma) of Kipsaraman, Tugen Hills, Kenya. *Anthropological Science*, **113**: 189-224.
Pickford, M. & Mein, P., 2011 - New Pedetidae (Rodentia: Mammalia) from the Mio-Pliocene of Africa. *Estudios geologicos*, **67** (**2**): 455-469.
Pickford, M., Sawada, Y., Tayama, R., Matsuda, Y., Itaya, T., Hyodo, H. & Senut, B., 2006 - Refinement of the age of the Middle Miocene Fort Ternan Beds, Western Kenya, and its implications for Old World biochronology. *Comptes Rendus Geoscience*, **338**: 545-555.
Rasmussen, T. & Gutierrez, M., 2010 - Hyracoidea. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, University of California Press, Berkeley, pp. 121-145.
Roddick, J.C., 1983 - High precision intercalibration of ^{40}Ar-^{39}Ar standards. *Geochimica Cosmochimica Acta*, **47**: 887-898.
Sanders, W., Gheerbrant, E., Harris, J.M., Saegusa, H. & Delmer, C., 2010 - Proboscidea. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, University of California Press, Berkeley, pp. 161-251.
Steiger, R. & Jäger, E., 1977 - Subcommission on geochronology: convention on the use of decay constants in geo- and cosmo-chronology. *Earth and Planetary Science Letters*, **36**: 359-62.
Van Couvering, J.A.H., 1977 - Early records of freshwater fishes in Africa. *Copeia*, **1977**: 163-166.
Van Couvering, J.A. & Van Couvering, J.A.H., 1976 - Early Miocene mammal fossils from East Africa : Aspects of geology, faunistics and palaeoecology. *In*: Isaac, G. & McCown, E. (Eds) *Louis Leakey and the East African Evidence*, Berkeley, University of California Press, pp. 155-207.
Walker, A., 1968 - The lower Miocene fossil site of Bukwa, Sebei. *Uganda Journal,* **32** (**2**): 149-156.
Walker, A., 1969 - Fossil mammal locality on Mount Elgon, eastern Uganda. *Nature*, **223**: 591-593.
Werdelin, L., 2010 - Chronology of Neogene Mammal Localities. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, University of California Press, Berkeley, Los Angeles, London, pp. 27-42.
Winkler, A. & Avery, M., 2010 - Lagomorpha. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, University of California Press, Berkeley, Los Angeles, London, pp. 305-317.
Winkler, A., Denys, C. & Avery, M., 2010 - Rodentia. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, University of California Press, Berkeley, Los Angeles, London, pp. 263-304.
Winkler, A., MacLatchy, L. & Mafabi, M., 2005 - Small rodents and a lagomorph from the early Miocene Bukwa locality, Eastern Uganda. *Palaeontologia Electronica*, **8** (**1**): 24A; aeo-electronica.org/.

Bukwa Palaeovegetation

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ABSTRACT

Flaggy tuffs exposed at Bukwa I, Kwongori Hill, Uganda contain abundant examples of fossilised grass preserved in its position of growth, the root systems in palaeosols, and the above-ground parts in fine grained sub-aerial tuffs above the palaeosols. The same tuffs also yield occasional leaves and fruit of trees, but none of these were observed in their growth positions. The succession of sediments in the hillside also yield a low diversity of land snails, and a few mammals, notably a deinothere tooth, a rhinocerotid metapodial and a mandible of the large bathyergid rodent *Renefossor*, a fauna which indicates an Early Miocene correlation. The palaeobotanic ensemble indicates that the Early Miocene palaeovegetation around Kwongori was dominated by clump grasses, with stands of trees in the vicinity, possibly in riparian forests bordering streams and rivers.

Key Words: Fossil grasses, Dicot leaves, Early Miocene, Uganda, Palaeoenvironment.

INTRODUCTION

Among the first fossils found at Bukwa in 1965 were leaves, fruit and a flower derived from trees (Hamilton, 1968). He also mentioned a "Grass leaf Bed" with monocots (grasses and a rush or sedge) preserved in growth position and lying horizontally. Hamilton (1968) proposed that the rhizomes represented plants growing around an alkaline lake. The palaeovegetation was visualised as being tropical forest, but soon afterwards the presence of grass at the site was indicated by Bishop (unpublished field notes).

The palaeovegetation at Bukwa was later considered to have been dominated by grassland with stands of trees and forest in the vicinity (Pickford, 2002). However, the latter scenario has been criticised by Cote *et al*. (2017) who wrote that they considered that "the setting was a small lake surrounded by forest and/or woodland".

The presence of abundant and diverse *in situ* grass fossils at Bukwa I cannot be ignored or minimised. Part of the polemic derives from the definition of vegetation categories, 'woodland', by many peoples' definitions, usually being well-endowed with grass between the trees (Vesey-Fitzgerald, 1973). So the differences in opinions between Pickford's (2002) and Cote *et al*'s (2017) interpretations are more apparent than real. The aim of this paper is to illustrate the grass fossils from Bukwa I in order to re-establish their place within palaeovegetation interpretations of the area. Some fossil tree leaves are also illustrated.

Figure 1. Exposures of flaggy tuffs along a footpath on the north side of Kwongori Hill, Uganda, Locality Bukwa I, known for its exquisitely preserved plant fossils, many of which are in their positions of growth.

DESCRIPTIONS AND COMMENTS

Monocotyledon culms and leaves

A variety of monocot culms has been preserved in the fine sediments (Fig. 2a-g, 3a-b) as well as some leaves with parallel venation (Fig. 2d, 3c).

Grass culms are shown in Fig. 2. An *in situ* bunch or tussock grass (Fig. 2a) comprises numerous culm bases, close together and showing a bird's eye view of the hollow cylindrical culms as the length of the culm has been removed prior to preservation (a result of fire, grazing or seasonal die-back). These are grasses because other plants with a similar growth form, such as sedges, are round or triangular but have a solid pith. Only a few sedges have nodes along the culm but all grasses do. Rushes are similar to sedges but do not grow in bunches or tussocks.

Figure 2. A) View looking down onto a bunch or tussock grass with all the culms removed before preservation. Note the hollow basal culms. Culm diameter = 3 mm. B) Several grass culms, 2.5 mm diameter in a fragile block of grey-white mudstone. Culms are more or less parallel and diverge from the base. C) Clump of plant debris and broken culms. D) Monocot leaves – left side shows a grass leaf-sheath fragment just before it expands at the node and ligule into the leaf. Culm diameter = 4 mm. Right shows the parallel-veined lamina of bulrush or reed, *Typha australis*. E-G) Separate clumps of grass culms ranging in diameter from 4.5 mm (E) to 2 mm (G). Note longitudinal striations on the top of the left culm in F.

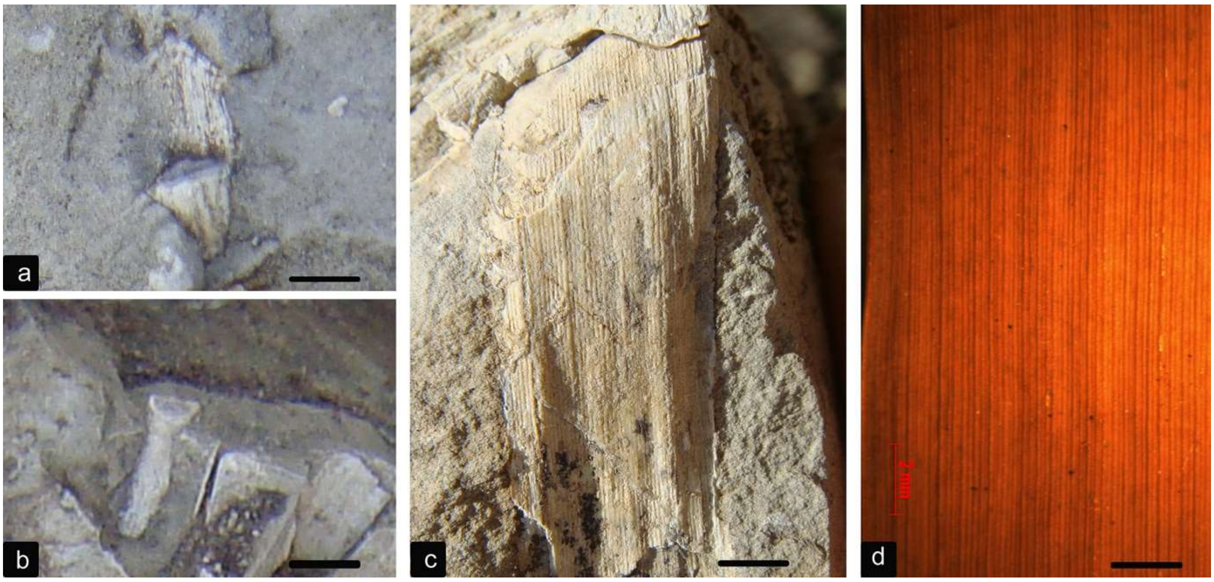

Figure 3. A) Enlarged culm-ligule section of a grass leaf (from 2e). B) Hollow culms (from 2g, top centre). C) Enlarged leaf lamina from (2d) to show the parallel veins and slightly wider every 8^{th}-9^{th} vein. D) Extant *Typha australis* leaf surface to show that every 8^{th} or 9^{th} vein is slightly wider. Material from the Palaeobotany Herbarium, Evolutionary Studies Institute, University of the Witwatersrand (scale bars : 2 mm)

The fossil grass culms are long and smooth or have fine longitudinal striations (Fig. 2f, left hand culm). Culms are preserved mostly parallel to one another and are probably in growth position as they diverge slightly from the base (Fig. 2b, e, f, g). A broken node is visible in Fig. 2c (top, centre). A clasping leaf blade with lamina expansion at the ligule is shown in Fig. 2d and 3a. Grass leaf venation preserved here is very fine and all the veins are the same thickness except for the midvein (partially preserved on the lower side), which is stronger than the laminar veins. Hollow culms are clear in Fig. 2a and 3b. Based on the diameters of the culms there are at least four species of grasses preserved here; the culms range in diameter from 5 to 8 mm and the longest preserved length is 25cm.

The monocot leaf shown on the right side of Fig. 2d and magnified in Fig. 3c is 18 mm wide with strictly parallel margins and veins. The veins are very similar in width but it is just possible to see that every eighth or ninth vein is slightly wider. This pattern is typical of *Typha* species and illustrated in Fig. 3d which is a photograph of extant *Typha australis.* The leaves can reach more than 2m length and the plants grow in seasonally inundated wetlands or seeps that have fresh water.

Dicotyledon leaves
The impression in fine-grained matrix shows a broadly elliptic leaf with missing apex and base (Fig. 4a). Estimated length is 128 mm and width is 60 mm and the margin is entire. From the stout midvein arise secondary veins at about 70°. The secondary veins are irregularly spaced and between adjacent veins are, in some instances, a narrower inter-secondary vein. Between the secondary veins there can be two inter-secondary veins. Tertiary veins are only just visible in the centre left and they are perpendicular to the secondary veins. This type of primary venation is known as craspedodromous.

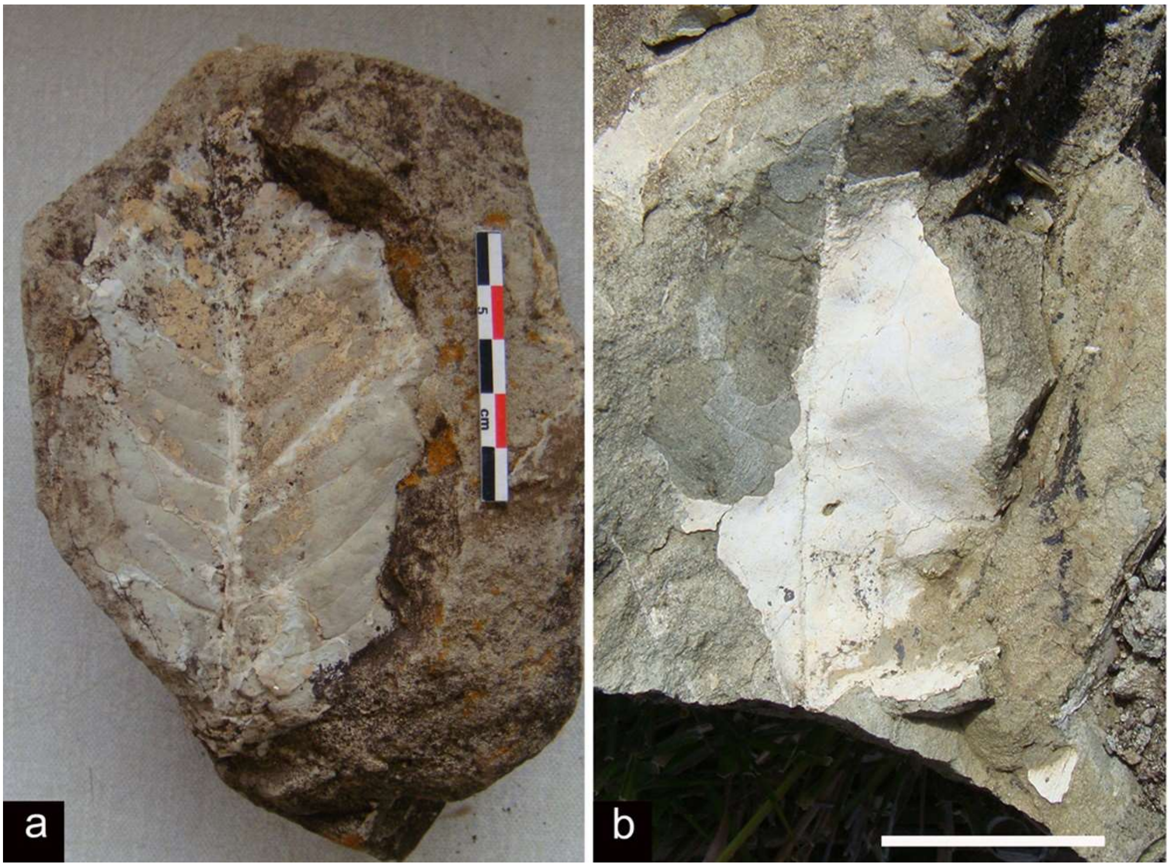

Figure 4. A) Dicot leaf with craspedodromous primary venation and entire margin. B) Dicot leaf with the same venation and size but with an opaque white infill (scale bar : 4 cm).

Another leaf is shown in Fig. 4b and is probably the same as the previous leaf but the details are indistinct. The right half of the leaf is obscured by an opaque white infill but veins are visible on the left side.

DISCUSSION AND CONCLUSIONS

The dicot leaf from Bukwa I is fairly large and is typical of more mesic environments. At least four types of grasses are preserved at Bukwa 1 and also some leaves of the cattail or bulrush, *Typha* sp. From a general survey of grasses (Vesey-Fitzgerald, 1963; Gibbs-Russell *et al*., 1990; van Oudtshoorn, 2012) broad-leaved grasses are generally taller than narrow-leaved grasses. While it is unlikely that the fossil grasses can be identified from the culms and leaves alone, a further study of the grasses, especially if any inflorescences can be found, would clarify the diversity of the grasses. The presence of *Typha* sp. confirms that a seasonally inundated wetland or a seep was in the vicinity. The wetland would have been a freshwater setting as *Typha* does not tolerate alkaline conditions. As the spatial and temporal relationships between the *Typha* and alkaline tolerant sedge or rush are not known it is not possible to determine whether they represent different settings or local conditions in the landscape or represent different times and conditions.

Dicot leaves, if venation and other leaf features such as apex and base, can be identified to generic level and would be useful for vegetation and climate reconstructions. Furthermore a physiognomic analysis (such as CLAMP; Wolfe, 1993; Spicer, 2007) of the dicot leaves, when more have been found, would provide an indication of the vegetation and type(s) of woodlands or woody grasslands that were present.

This preliminary study of the macrobotanical remains shows that there were a number of different grasses as well as wetland taxa such as *Typha*, and broad-leaved trees. Further research is warranted so that a more precise description can be given, for example wooded grassland, grassy woodland, mixed woodland and so on.

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REFERENCES

Cote, S., Mugume, A., Kityo, R., Kingston, J. & MacLatchy, L., 2017 - New fossil primate remains from Bukwa, Eastern Uganda. *5th EAQUA Workshop, Mukono, Uganda*, 4-7 July, 2017, Decades of Quaternary Research in East Africa : Implication for Sustainable Development, Conference Booklet, pp. 31-32.

Hamilton, A., 1968 - Some plant fossils from Bukwa. *Uganda Journal*, **32** (**2**): 157-164.

Gibbs-Russell, G.E., Watson, L., Koekemoer, M., Smook, L., Barker, N.P., Anderson, H.M. & Dallwitz, M.J., 1990 - Grasses of southern Africa. *Memoirs of the Botanical survey of South Africa*, N° **58**. 437pp.

Pickford, M., 2002 - Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda. *Comptes Rendus Palévol*, **1**: 213-219.

Spicer, R.A., 2007 - Recent and future developments of CLAMP: building on the legacy of Jack A. Wolfe. *Courier Forschungsinstitut Senckenberg*, **258**: 109-118.

Van Oudtshoorn, F., 2012 - *Guide to Grasses of Southern Africa*. 3rd Edition. Briza Publications, Pretoria. 287pp.

Vesey-Fitzgerald, D.F., 1963 - Central African Grasslands. *The Journal of Ecology*, **51** (**2**): 243-274.

Wolfe, J.A., 1993 - A method of obtaining climatic parameters from leaf assemblages. *United States Geological Survey Bulletin*, **2040**: 1-73.

Bukwa Gastropoda

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ABSTRACT

Gastropod fossils are common in flaggy tuffs at Bukwa I, Uganda, but are rare in the palustral sediment facies at Bukwa II, where only one shell of *Melanoides* sp. is known. The diversity of land snails at Bukwa I is low (17 genera) but it permits reasonable assessment of the palaeoecological and palaeoenvironmental conditions that existed at the site between 19 and 20 Ma (Early Miocene). It is concluded that there were patches of forest and/or woodland in the region, but near the site of deposition of the tuffs there was alot of grass. This paper complements previous analyses of fossil gastropods from Bukwa.

Key Words : Early Miocene, Gastropoda, Bukwa I, Uganda, Palaeoenvironment,

INTRODUCTION

Gastropods were among the first fossils found at Bukwa I (Walker, 1968). Walker (1969) listed ten land snail genera and one species of freshwater snail (Table I).

Table 1. Gastropods from Bukwa I and Bukwa II, Uganda.

Walker, 1969	Locality	Identification this paper
Gulella	Bukwa I	Not in the old collections
Limicolaria	Bukwa I	Not in the old collections
Maizania	Bukwa I	*Maizania lugubrioides*
Not listed	Bukwa I	*Edouardia*
Homorus	Bukwa I	*Oreohomorus*
Opeas	Bukwa I	*Pseudopeas*
Not listed	Bukwa I	*Curvella*
Not listed	Bukwa I	*Pseudoglessula*
(?)*Archachatina*	Bukwa I	*Tholachatina*
Burtoa	Bukwa I	*Burtoa nilotica*
Tayloria	Bukwa I	*Artemonopsis*
Not listed	Bukwa I	*Gonaxis*
Not listed	Bukwa I	*Silvigulella*
Not listed	Bukwa I	*Haplonepion*
Not listed	Bukwa I	*Crenatinanina*
Not listed	Bukwa I	*Trochonanina*
Thapsia	Bukwa I	*Thapsia*
Helicarion	Bukwa I	*Calidivitrina*
Not listed	Bukwa I	*Chlamydarion*
Melanoides tuberculata	Bukwa II	*Melanoides* sp.

Following the pioneer descriptions and interpretations of African land snails by Verdcourt (1963, 1983) Pickford (1995, 2009) revised the fossil land snails from the Neogene of East Africa, describing many more of the smaller taxa which were not represented in the collections available to Verdcourt (1963). The ecological and environmental meanings of the snails made by Verdcourt (1963, 1983) are valid, but some of the genus and species names have changed because better preserved specimens have been collected, or because changes have occurred to the taxonomy of snails.

Figure 1. *Maizania lugubrioides* in situ in flaggy tuff at Bukwa I, Uganda (shell ca 20 mm diameter). At present, this genus is commonly found in damp leaf litter on forest floors.

The Bukwa I snails were interpreted by Pickford (2002) who pointed out that there was probably grassland at the site at the time of deposition of the tuffs, but that some taxa indicated forested or wooded conditions nearby.

This paper illustrates the land snails from Bukwa I, and the single available specimen of freshwater snail from Bukwa II, and reiterates the interpretation of the palaeoecosystem made by Pickford (2002) that during the period of deposition, some 20-19 Ma, the Bukwa area was vegetated predominantly by grassland, but with forest patches and woodland close by. This contrasts with the slightly more forested conditions which prevailed at Napak, Uganda (22 genera of land snails, Pickford, 2004) and the humid tropical forest conditions that prevailed at Legetet (Koru), Kenya (Pickford, 2009) during the Early Miocene, where the snail fauna is somewhat different from that of Bukwa I, notably by its greater diversity (48 taxa at Legetet, Pickford, 2009) and by the presence of many different taxa, a few ubiquitous genera being common to all the faunas.

In order to avoid needless repetition of the descriptions of these taxa, which were already published by Pickford (2009) only a few remarks are made about the Bukwa I occurrences, most of which are not as well preserved as those from Koru which feature in that publication.

SYSTEMATIC DESCRIPTIONS

GASTROPODA FROM BUKWA I, UGANDA

Family Maizaniidae Tielecke, 1940

Genus *Maizania* Bourguignat, 1889

Species *Maizania lugubrioides* Verdcourt, 1963

Description and comments

A dozen shells from Bukwa I are confidently attributed to *Maizania* on the basis of the almost circular aperture, the relatively exserted spire, the indented sutures and the overall dimensions of the shells (Fig. 1, 2). The adult specimens closely resemble *Maizania lugubrioides* Verdcourt, 1963.

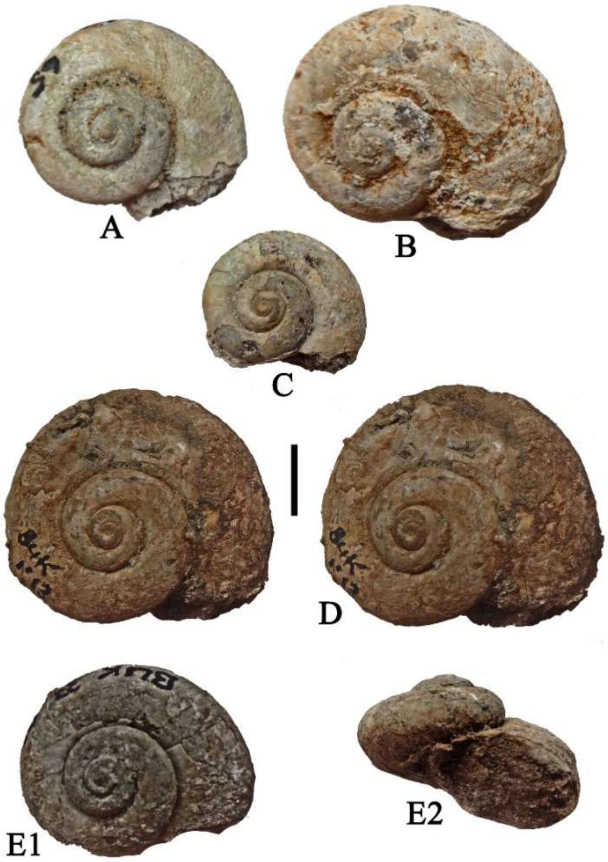

Figure 2. *Maizania lugubrioides* from Bukwa, Uganda. A-C) BUK I P 67-40, three shells in apical view; D) BUK I 1'13, stereo apical view; E) BUK I 37'97 (E1 - apical view, E2 - apertural view) (scale : 10 mm).

Extant *Maizania* prefer shady habitats with damp leaf litter. They are common in forests as well as in well-wooded areas close to rivers or streams where the vegetation is dense. At Napak, Uganda, they are found in leaf litter on the floor of riparian forest that grows along streams in regional wooded grassland. In this area, the strips of riparian forest are often only a few metres wide, giving way laterally to grassland with bushes and trees.

Family Cerastidae Wenz, 1923

Genus *Edouardia* Gude, 1914

Description and comments

The cerastid snail *Edouardia* is not common at Bukwa, but some well-preserved specimens show the angled whorl margin and pointed spire that typifies this genus (Fig. 3). The Bukwa specimens are taller relative to their breadth than *Edouardia mfwanganensis* Verdcourt, 1963. They are also somewhat larger in overall dimensions (ca 25 mm tall versus ca 15 mm for *Edouardia mfwanganensis*).

Cerastids are most commonly encountered in semi-arid and sub-humid environments which experience strong seasonality (arid-humid cycles) although they also occur in patches of forest (Pickford, 2009). The same applies to the genus *Edouardia*.

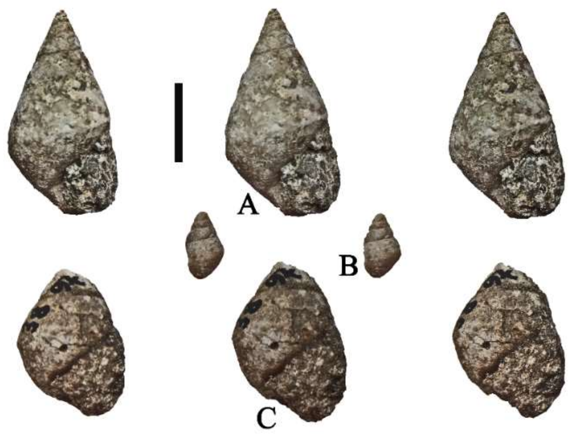

Figure 3. *Edouardia* sp. from Bukwa I, Uganda. A, C) BUK I 38'97, stereo apertural views, B) BUK I 33'97, juvenile apex, stereo side view to show angled whorl profile (scale : 10 mm).

Family Subulinidae Fischer & Crosse, 1877

Genus *Oreohomorus* Pilsbry, 1919

Description and comments

Subulinids are the commonest gastropod fossils found at Bukwa I, several dozen specimens having been collected (Fig. 4, 5). None of the specimens preserves the apex, so it is not possible to determine the generic affinities with any degree of confidence (apex pointed in *Oreohomorus*, more globose in *Subulona*). However, five large specimens are likely to represent the genus *Oreohomorus*.

In general, large subulinids occur in forested areas, whereas small ones are found in more open country (Pickford, 1995). The Bukwa sample suggests the presence of forest in the vicinity of the site.

Figure 4. BUK I 41'97, a typical collection of broken shells of *Oreohomorus* sp. from Bukwa I, Uganda (scale : 10 mm).

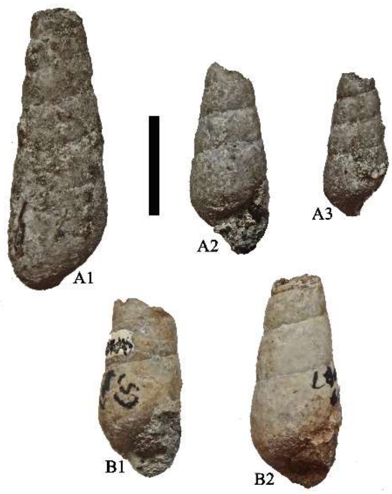

Figure 5. Large individuals of Subulinidae (probably *Oreohomorus* sp.) from Bukwa I, Uganda. A1-A3) BUK I 9'98; B1-B2) BUK I P67-41 (scale : 10 mm).

Genus *Pseudopeas* Putzeys, 1899

Description and comments

The presence of *Pseudopeas* at Bukwa is based on fossil shells which have the overall shape of this genus together with its diminutive dimensions (Fig. 6). None of the specimens is well enough preserved to show the radial ribbing that occurs on the shell.

At present, *Pseudopeas* is most commonly encountered in humid areas, but it can exist in regionally dry areas, such as the Larogi Hills, Kenya, where hilltop mists are common, which thereby increases the local humidity regime to the point where mist-forests can grow.

Genus *Curvella* Chaper, 1885

Description and comments

The small subulinid *Curvella* is identified at Bukwa on the basis of the overall shape of the shells and their diminutive dimensions (Fig. 6). The outer surface of the shells is not well-preserved, so it is not possible to discern the characteristic curved growth lines that adorn the shell of this genus of snail.

Curvella is usually found in forested areas, but is also known from humid, wooded grassland areas such as the zone between Mbarara and Entebbe in Uganda.

Figure 6. BUK I 33'97, small subulinids from Bukwa I, Uganda. A-B) *Curvella* sp. (stereo apertural views); C-D) *Pseudopeas* sp. (C - stereo apertural view, D - stereo side view) (scale : 10 mm).

Genus (?)*Pseudoglessula* Boettger, 1892

Description and comments

Two shells from Bukwa are provisionally identified as (?)*Pseudoglessula* on the basis of their dimensions and shell shape (Fig. 7).

The environmental significance of these specimens should not be overstressed on account of the fact that they are poorly preserved and incomplete. They are included in this paper in order to complete the list of snails from the deposits. Better material is required to settle their affinities.

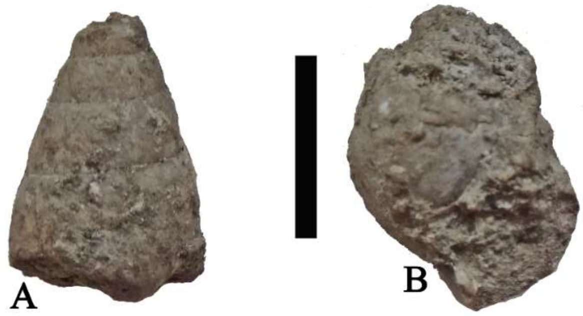

Figure 7. BUK I 16'98, (?)*Pseudoglessula* sp. from Bukwa I, Uganda (scale : 10 mm).

Family Achatinidae Swainson, 1840

Genus *Tholachatina* Bequaert, 1950

Description and comments

Bukwa I yielded several large achatinid shells up to 60 mm tall, close in overall morphology to the genera *Tholachatina* and *Archachatina*. The obtuse shape of the protoconch rules out the genera *Achatina* and *Limicolaria*. The lightly indented suture is characteristic, as is the granular aspect of the ornamentation of the outer surface of the shell (Fig. 8).

Tholachatina is common in montane forests of East Africa, but it also occurs in drier areas in the Natal and Zululand, South Africa. At Bukwa I it likely signifies the former presence of forest in the neighbourhood.

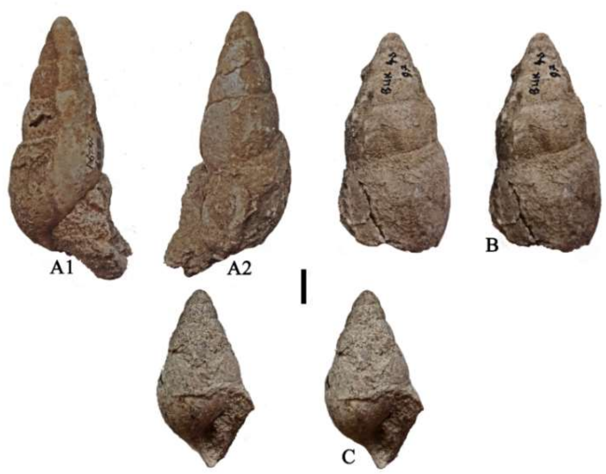

Figure 8. *Tholachatina* from Bukwa I, Uganda. A) BUK I UMP 67-42 (A1 - apertural view, A2 - posterior view); B) BUK I 40'97, stereo posterior view, C) BUK I 40'97, stereo apertural view (scale : 10 mm).

Genus *Burtoa* Bourguignat, 1889

Species *Burtoa nilotica* (Pfeiffer, 1870)

Description and comments

Several well-preserved bulimoid shells from Bukwa I are attributed to *Burtoa nilotica* on the basis of their dimensions (up to 45 mm tall) and their height-breadth ratio (breadth ca 30 mm) (Fig. 9). The protoconch is small and the spire short, both features characteristic of *Burtoa* (Crowley & Pain, 1959, 1963).

Pickford (2009) wrote that "*extant* Burtoa nilotica *is most common in mid-altitude woodland and forested areas where there are two rainy seasons per year, but it is also known from the eastern parts of the tropical forest in Congo (Crowley & Pain, 1959). It is possible that the high degree of variation in shell shape and size in* B. nilotica *relates to the changeable environment where it thrives. Individuals that grow in years with low rainfall are likely to be smaller than individuals that grow in years with high rainfall. Given that the rainfall throughout its range is quite variable on a year by year basis, then the genetic code of the genus may well allow a certain degree of variability in shell size and shape. This flexibility in conchological features was already present in the Early Miocene, and speaks for some degree of seasonality in East Africa as far back as 20 Ma*". The Bukwa fossils agree with this assessment of the genus, and indicate the presence of marked seasonality at the site during the Early Miocene.

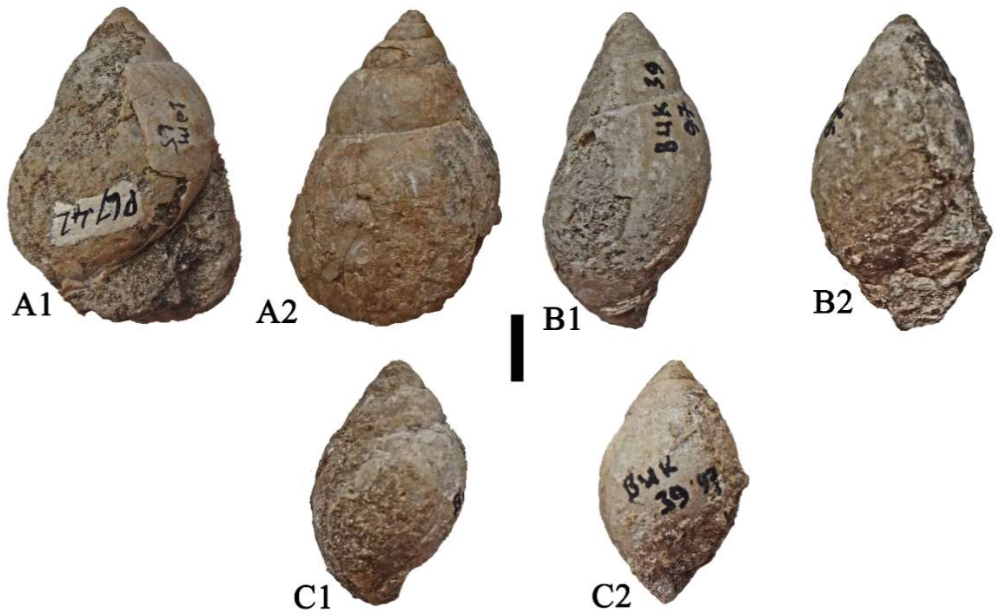

Figure 9. *Burtoa nilotica* from Bukwa I, Uganda. A) BUK I UMP 67-42 (A1 - apertural view, A2 - dorsal view); B-C) BUK I 39'17 two shells, (B1 - side view, B2 - apertural view; C1 - dorsal view, C2 - side view) (scale : 10 mm).

Family Streptaxidae Gray, 1860

Genus *Artemonopsis* Germain, 1908

Description and comments

Streptaxid shells with a depressed habitus and marked sinuous growth ribs are quite common at Bukwa I. These rather flat shells with slightly impressed sutures also have a large, open umbilicus, and fit well with the genus *Artemonopsis* (Fig. 10).

Artemonopsis is often found in forest, but also occurs in more open, arid country such as the Matthews Range in Kenya, where denser vegetation can grow due to the common presence of mist at the tops of the hills.

Genus *Gonaxis* Taylor, 1877

Description and comments

Slightly globose streptaxid shells with marked sinuous growth ribs are represented at Bukwa I by two almost adult shells and several fragments of juveniles (Fig. 10). The spire is taller than in *Artemonopsis*, but otherwise the two genera share certain resemblances in shell shape and fine structure. *Gonaxis* tends to be larger than *Artemonopsis*, and this is the case at Bukwa.

Gonaxis is often found in forest and dense woodland growing along river courses in sub-humid country.

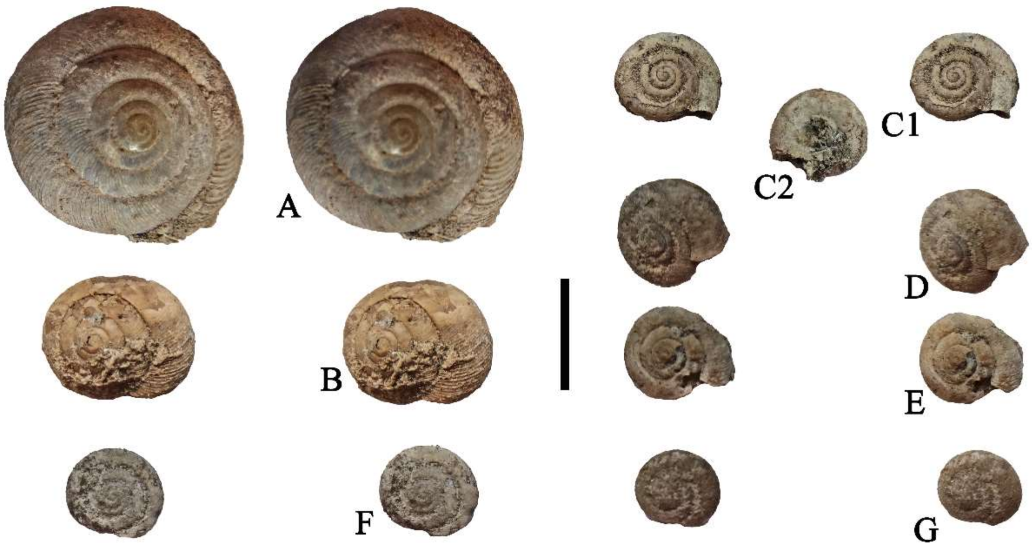

Figure 10. Streptaxidae from Bukwa I, Uganda. A-B) *Gonaxis* sp. stereo apical views; C-G) *Artemonopsis* sp. stereo apical views and ventral view (C2) (scale : 10 mm).

Genus *Silvigulella* Pilsbry, 1919

Description and comments

The very small streptaxid *Silvigulella* is represented at Bukwa I by a single shell ca 3 mm tall, preserved in a block of limey tuff (Fig. 11A). The round-shouldered whorls (about 10 of them) are tightly coiled round a tall axis and have deeply indented sutures. The spire is tall and pointed, and the body whorl is narrower than the rest of the shell, which imparts a spindle-shape to the whole shell.

At present *Silvigulella* occurs mainly in upland forest areas of Kenya and Uganda.

Genus *Haplonepion* Pilsbry, 1919

Description and comments

Haplonepion is represented at Bukwa I by a single fusiform shell some 10 mm tall, which is comprised of seven whorls (Fig. 11B). The spire is low, the body whorl narrower than the rest of the shell. The outer side of the body whorl has two deep grooves incised into its surface, a defining feature of this genus.

Haplonepion, like *Silvigulella* is most often encountered in forest.

Figure 11. Tall Streptaxidae from Bukwa I, Uganda. A) *Silvigulella* sp., stereo side view of specimen in a block of limey tuff; B) *Haplonepion* sp. (B1 - stereo dorsal view, B2 - apertural view) (scale : 10 mm).

Family Urocyclidae Simroth, 1889

Genus *Crenatinanina* Germain, 1920

Description and comments

Bukwa I yielded several specimens of shelled urocyclids (Fig. 12). A specimen with a slightly concave dorsal profile adorned with closely spaced oblique ribs can be confidently attributed to the genus *Crenatinanina*. There are 5 to 5.5 whorls, and the periphery of the shell is sharp.

These "Chinese-hat" snails are commonly collected in forest habitats of East Africa.

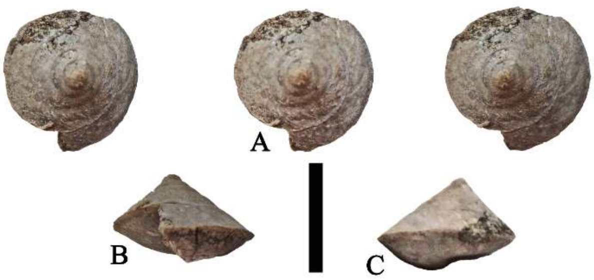

Figure 12. *Crenatinanina* from Bukwa I, Uganda. BUK I 13'98 (A - stereo apical views, B - side view, C - posterior view) (scale : 10 mm).

Genus *Trochonanina* Mousson, 1869

Description and comments

The shells of *Trochonanina* from Bukwa I show the characteristic slightly convex dorsal surface of the shell and a small, pointed apex (Fig. 13). Otherwise the shells of this genus resemble those of *Crenatinanina*. The ribs on the dorsal side of the shell of *Trochonanina* are less densely packed than they are in *Crenatinanina*. The periphery of the shell is angled, not rounded as in the genus *Bloyetia*.

Trochonanina is widespread in humid and sub-humid parts of equatorial Africa, and is often found in grassy areas, such as Napak, Uganda. Here it is sometimes found hiding in clumps of grass near the base of the grass stems, where humidity is higher than in the surroundings. One of the fossil specimens from Bukwa was found inside a clump of fossil grass, suggesting that this adaptation is an ancient one.

Figure 13. *Trochonanina* from Bukwa I, Uganda. BUK I 34'97, A - stereo apical view, B - dorsal view (scale : 10 mm).

Genus *Thapsia* Albers, 1860

Description and comments

There are two "thapsiform" shells from Bukwa I which have smooth, almost shiny shells, rounded peripheries and narrow but deep umbilicus (Fig. 14). They have about 4 whorls and low spires. These specimens are confidently attributed to the genus *Thapsia*.

Thapsia is usually found in forest floor leaf litter and other relatively humid habitats.

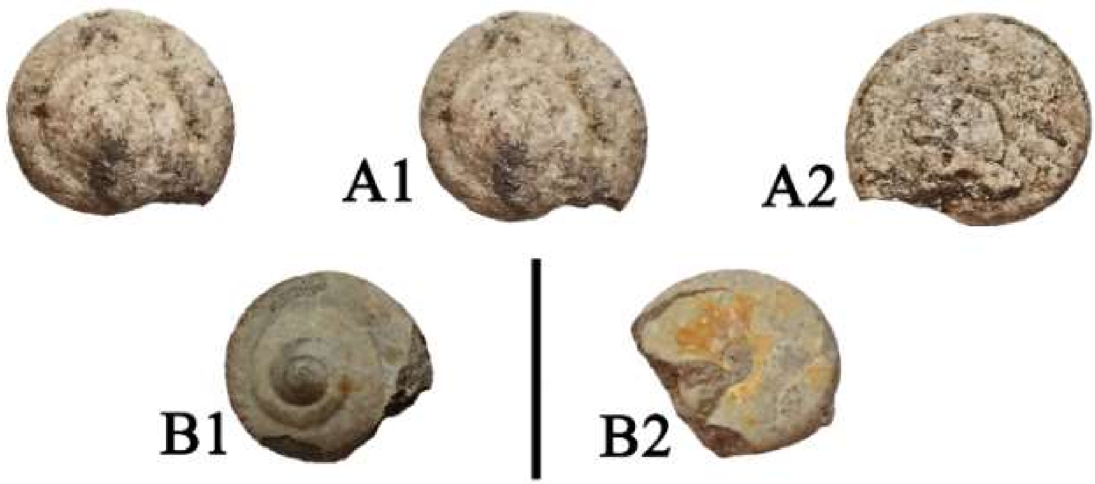

Figure 14. *Thapsia* from Bukwa I, Uganda. A) BUK I 17'98 (A1 - stereo apical view, A2 - basal view); B) BUK I P67-40, (B1 - apical view, B2 - basal view) (scale : 10 mm).

Family Vitrinidae Fitzinger, 1833

Genus *Calidivitrina* Pilsbry, 1919

Description and comments

The record of *Calidivitrina* from Bukwa I is based on a small (diameter ca 10 mm) thin-shelled specimen which is slightly crushed (Fig. 15b). The aperture is vast when compared to the size of the rest of the shell. Its dorsal surface is almost flat.

Calidivitrina is a slug-like snail and its body is larger than the shell, so it is unable to retract its body into the shell. It is confined to upland and mountainous areas of tropical Africa, where conditions are permanently humid and often very cold, with extreme daily variations in temperature. The shell is thin which is why it is easily crushed, the case with the specimen from Bukwa.

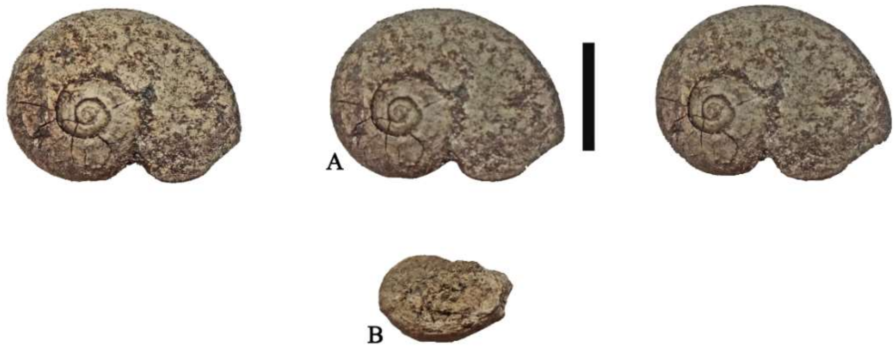

Figure 15. Urocyclidae and Vitrinidae from Bukwa I, Uganda. A) *Chlamydarion* sp. BUK I 15'98, stereo apical views; B) BUK I 32'97, *Calidivitrina* sp. ventral view (scale : 10 mm).

Urocyclidae Simroth, 1889

***Chlamydarion* Van Mol, 1968**

Description and comments

Superficially, the shell of the urocyclid snail, *Chlamydarion*, looks like that of *Calidivitrina*, with a vast body whorl much bigger than the rest of the shell, and an almost flat dorsal surface (Fig. 15). However it differs from the latter genus by its generally greater dimensions and its thicker, more robust shell. The Bukwa specimen is close in dimensions and morphology to specimens of extant *Chlamydarion hians*, a species which is common in sub-humid and semi-arid regions of Kenya.

GASTROPODA FROM BUKWA II (BASAL MIDDLE MIOCENE) UGANDA

Family Thiaridae Troschel, 1857

Genus *Melanoides* Olivier, 1804

Description and comments

A single shell from Bukwa II represents a small (ca 6 mm tall) turriform thiarid, a family of freshwater snails. The shell is poorly preserved but under the microscope it is possible to make out the presence of small bumps and spiral ridges characteristic of the genus (Fig. 16). The specimen is likely to represent the genus *Melanoides*, as was the opinion of Walker (1968) but the material is too poorly preserved to determine its specific affinities.

This genus of snail is typical of freshwater habitats in Africa and other parts of the tropical world.

Figure 16. *Melanoides* sp. from Bukwa II, Uganda (uncatalogued specimen, old collection) (scale : 10 mm).

Family Urocyclidae Simroth, 1889

Genus indet. (Slug)

Description and comments

At Bukwa II, an internal shell (slug plate) of an urocyclid snail was found (Fig. 17). It is not clear whether the specimen is fossilised, slug plates often being dense and thereby resembling fossils even in recently dead specimens.

Verdcourt (1963) illustrated several specimens of slug plates from Rusinga and other Early Miocene sites in Western Kenya. The Bukwa specimen could belong to one of several genera of slugs, the internal shells of the various genera resembling each other in many ways. *Polytoxon* is a possible identification.

Figure 17. BUK II 54'97, Urocylidae slug plate from Bukwa II (possibly sub-fossil) (scale : 10 mm).

DISCUSSION

The flaggy tuff deposits at Bukwa I have yielded a land snail fauna comprising 17 genera. The palaeoecological and palaeoenvironmental signals yielded by the fossils are mixed, with several taxa signifying the presence of forest or dense woodland, while others indicate the presence of grassland. Such was the view already articulated by Pickford (2002) but this reconstruction was recently challenged by Cote *et al*., (2017) who stressed the "forested" nature of the Bukwa palaeoenvironment. However, the discussion by the latter authors was based mainly on fossils from Bukwa II, which is a much younger deposit than Bukwa I (base of the Middle Miocene (Ogg *et al*. 2016)).

It is possible to interpret the palaeoenvironmental and palaeoclimatic meaning of the Bukwa I land snail fauna in greater depth. For example, the presence of *Burtoa nilotica* suggests that the region was under a seasonal climatic regime (dry season-wet season) with possibly two rainy seasons per year. At present the distribution of the genus *Burtoa* is centred on regions enjoying this kind of climate (Crowley & Pain, 1959; Pilsbry, 1919). The genus does not often occur below an altitude of 1,200 metres.

Some of the Bukwa I taxa are common in grassy areas of tropical Africa, which are often wooded, or have strips of riparian forest along streams and rivers. Among these are *Maizania*, *Edouardia*, *Pseudoglessula*, *Trochonanina* and *Chlamydarion*, although it is pointed out that these genera tolerate a wide variety of habitats and climate categories, including forests. Among taxa which are more restricted in their habitat requirements, there are several forest-adapted genera at Bukwa I - *Oreohomorus*, *Pseudopeas*, *Curvella*, *Tholachatina*, *Artemonopsis*, *Silvigulella*, *Haplonepion*, *Crenatinanina*, *Thapsia* and *Calidivitina*. But as with the other land snails from Bukwa I, several of these genera can occur in more open vegetation categories in sub-humid climates (riparian forest, woodland groves).

At first glance, this faunal composition gives the misleading impression that Bukwa I was covered in forest because its snail fauna appears to be dominated by forest-adapted snail taxa. However, such is unlikely to be the case because localities such as Legetet (Koru), Kenya (Early Miocene) which preserve truly forested palaeofaunas have a far higher diversity of land snails (48 genera at Legetet) with a high diversity of *Gulella* (none at Bukwa I, despite the mention of one species by Walker, 1968) and

Pseudogonaxis as well as other streptaxids, pupillids, chondrinids, ferussaciids, charopids and halolimnohelicids, none of which have been observed at Bukwa I (see Pickford, 2009, for details).

The relatively low diversity of land snails at Bukwa I (17 genera) suggests strongly that the site does not preserve elements of a widespread humid forested environment, even though some taxa do indicate that there were well-wooded tracts nearby, possibly riparian forest close to streams and rivers and ponds.

This reconstruction of the palaeoenvironment of Bukwa I on the basis of the land snails accords with the presence of abundant grass fossils in the flaggy tuffs at Bukwa I, comprising clump grasses in their position of growth, roots in palaeosols, above-ground stems and leaves preserved in fine ash which buried them during volcanic eruptions. Bukwa I also yields leaves and fruit from trees (Hamilton, 1968) some of which may have formed groves or clumps of denser vegetation, but which do not necessarily denote the former presence of humid tropical forest at the site.

CONCLUSIONS

Seventeen genera of land snails occur at Bukwa I (Early Miocene), and one genus of freshwater snail and a slug have been found at Bukwa II (Middle Miocene). The diversity of land snails at Bukwa I is low, which indicates that it was probably not covered in humid tropical forest at the time of deposition. Localities such as Legetet, near Koru, Kenya (48 genera) accumulated under tropical forest conditions, whereas others such as Napak, Uganda (22 taxa of land snails) formed under slightly drier climatic conditions (upland woodland to forest on the slopes of a volcano). By comparison, the diversity of land snails at Bukwa I is much lower, and signifies a more seasonal palaeoclimate with extended dry seasons interspersed with rainy seasons. This does not mean that there were no trees at Bukwa. On the contrary, there were likely to have been strips of riparian forest fringing stream banks and surrounding ponds, and there would have been clumps and groves of trees within the neighbourhood. Such a palaeoenvironmental reconstruction is borne out by the fossil flora from Bukwa I, which is dominated by clumps of grass, of which the root systems are preserved in palaeosols and the above-ground parts preserved in volcanic ash. Leaves and fruit of trees are also preserved in the tuffs, and these attest to the presence of groves of trees in the vicinity at the time of deposition of the tuffs.

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REFERENCES

Albers, J.C., 1860 - *Die Heliceen nach natürlicher Verwandtschaft systematisch geordnet. 2. Ausgabe, herausgegeben von E. von Martens*. Leipzig. 359 pp.

Bequaert, J.C., 1950 - Studies in the Achatininae, a group of African land snails. *Bulletin of the Museum of Comparative Zoology, Harvard*, **105**: 1-216.

Boettger, O., 1892 - Neue Stenogyren aus Westafrika und ein neues *Aperostoma* aus Honduras. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, **24** (**3/4**): 202-204.

Bourguignat, J., 1889 - *Mollusques de l'Afrique equatoriale de Moguedouchou à Bagamoyo au Tanganika* (sic). Paris, Dumoulin, pp. 1-210.

Chaper, M., 1885 - Description de quelques espèces et genres nouveaux de coquilles vivantes de diverses provenances. *Bulletin de la Société zoologique de France*, **10**: 42-54.

Cote, S., Mugume, A., Kityo, R., Kingston, J. & MacLatchy, L., 2017 - New fossil primate remains from Bukwa, Eastern Uganda. *5th EAQUA Workshop, Mukono, Uganda*, 4-7 July, 2017, Decades of Quaternary Research in East Africa : Implication for Sustainable Development,

Conference Booklet, pp. 31-32.
Crowley, T.E. & Pain, T., 1959 - A monographic revision of the African land snail genus *Burtoa* (Mollusca, Achatinidae). *Annales du Musée Royale Belge*, *Série. Zoologie*, Tervuren, **79**: 7-35.
Crowley, T.E. & Pain, T., 1963 - Achatininae. *In*: Verdcourt, B., 1963 - The Miocene non-marine Mollusca of Rusinga Island, Lake Victoria, and other localities in Kenya. *Palaeontographica*, (A) **121**: 1-37.
Fischer, P. & Crosse, H., 1877 - *Mission scientifique au Mexique et dans l'Amérique centrale. Recherches zoologiques*, Trouble Nationale, Paris, (7) **1** (6): 1-731.
Fitzinger, L.J., 1833 - Systematisches Verzeichniss der im Erzherzogthume Oesterreich verkommenden, Weichthiere, als Prodrom einer Fauna derselben. *Beiträge zur Landeskunde von Oestereich's unter der Enns*, **3**: 88-122.
Germain, L., 1908 - Mollusques terrestres et fluviatiles receuillis par M. A. Chevalier à la Côte d'Ivoire (1907). *Journal de Conchyliologie*, **56**: 95-115.
Germain, L., 1920 - Mollusques Terrestres et Fluviatiles. *Voyage de M. Guy Babault dans l'Afrique orientale anglaise. Résultats scientifiques*. Paris, Gaultier & Thébert, pp. 1-258.
Gray, J.E., 1860 - On the arrangement of the land pulmoniferous Mollusca into families. *Annals and Magazine of Natural History*, (Series 3), **6**: 267-269.
Gude, G., 1914 - *The Fauna of British India, including Ceylon and Burma. Mollusca. II. (Trochomorphidae - Janellidae)*. London, pp. 1-520.
Hamilton, A. 1968 - Some plant fossils from Bukwa. *Uganda Journal*, **32**: 157-164.
Mousson, A., 1869 - Faune malacologique terrestre et fluviatile des îles Samoa, publiée d'après les envois de M. le Dr E. Graeffe. *Journal of Conchology*, **17**: 323-390.
Ogg, J.G., Ogg, G.M. & Gradstein, F.M., 2016 - *A Concise Geologic Time Scale 2016***,** Elsevier, 240 pp.
Olivier, G.A., 1804 - *Voyage dans l'Empire Othoman, l'Egypte et la Perse, fait par ordre du gouvernement, pendant les six premières années de la République*. Tome second. Paris, Agasse.
Pfeiffer, L., 1870-1876 (cited in paper as 1870) - *Novitates Conchologicae*, *Series prima, Mollusca extra-marina*, **4**: 1-171. Kassel.
Pickford, M., 1995 - Fossil land snails of East Africa and their palaeoecological significance. *Journal of African Earth Sciences*, **20 (3-4)**: 167-226.
Pickford, M., 2002 - Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda. *Comptes Rendus Palevol*, **1**: 213-219.
Pickford, M., 2004 - Palaeoenvironmental reconstruction of Early Miocene hominoid-bearing deposits at Napak, Uganda, based on terrestrial molluscs. *Annales de Paléontologie*, **90**: 1-12.
Pickford, M., 2009 - Land snails from the Early Miocene Legetet Formation, Koru, Kenya. *Geo-Pal Kenya*, **2**: 1-88.
Pilsbry, H. 1919 - A review of the land mollusks of the Belgian Congo, chiefly based on the collections of the American Museum Congo Expedition, 1909-1915. *Bulletin of the American Museum of Natural History*, **40**: 1-370.
Putzeys, S., 1899 - Diagnoses de quelques coquilles et d'un sous-genre nouveau provenant de l'État indépendant du Congo. *Annales de la Société malacologique Belgique Bulletin des séances*, **34**: LV-LX.
Simroth, H., 1889 - Beiträge zur Kenntniss der Nacktschnecken. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curisorum*, **54** (**1**): 1-91.
Swainson, W., 1840 - *A Treatise on Malacology; or the Natural Clasification of Shells and Shell Fish*. Longman, Orme, Brown, Green & Longmans and John Taylor, London, viii & 419 pp.
Taylor, J.W., 1877 - Descriptions of new species of land shells from the East Coast of Africa. *Quarterly Journal of Conchology*, **1**: 251-255.
Tielecke, H., 1940 - Anatomie, Phylogenie un Tiergeographie der Cyclophoriden. *Archiv für Naturgeschichte*. New series, **9** (**3**): 317-371.
Troschel, F.H., 1857 (1856-1863) - *Das Gebiss der Schnecken zur Begründung einerntürlichen Classification*. Nicolaische Verlagsbuchhandlung, Berlin.

Van Mol, J.-J., 1968 - Désignation du néotype de *Granularion duporti* Germain, 1912, définition du genre *Granularion*, et description de *Chlamydarion* gen. nov. (Mollusca, Pulmonata, Urocyclidae. Note 2). *Revue de Zoologie et de Botanique africains*, Bruxelles, **77**: 253-266.
Verdcourt, B., 1963 - The Miocene non-marine Mollusca of Rusinga Island, Lake Victoria, and other localities in Kenya. *Palaeontographica*, (A) **121**: 1-37.
Verdcourt, B., 1983 - A list of the non-marine Mollusca of East Africa. *Achatina*, **11**: 200-239.
Walker, A., 1968 - The lower Miocene fossil site of Bukwa, Sebei. *Uganda Journal*, **32** (**2**): 149-156.
Walker, A., 1969 - Fossil mammal locality on Mount Elgon, eastern Uganda. *Nature*, **223**: 591-593.
Wenz, W., 1923 - *Gastropoda extramarina tertiaria Fossilium catalogus, I: Animalia.* 3387 pp. published in parts: Part **IV**, Pars **21**: 1069–1420.

Bukwa Rodentia and Creodonta

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ABSTRACT

Bukwa I and Bukwa II have yielded few small mammalian fossils among which there are rare rodents and carnivorans. Wet-screening and sharp-eyed surface searches have resulted in the collection of a few rodent jaws and teeth and an isolated small creodont premolar. These specimens are described but, because of their rarity, they do not, for the moment, yield much information of a chronological nature, but they indicate a broadly Early to Middle Miocene age.

Key Words : Rodentia, Creodonta, Early Miocene, Middle Miocene, Bukwa, Uganda

INTRODUCTION

The presence of small mammals at Bukwa II was first reported by Walker (1968, 1969) but none of the specimens was described or illustrated, and *Megapedetes pentadactylus* was the only species named, the remainder being listed as "others as yet unidentified". Searches for these fossils in the old collections were fruitless.

Rodents were collected at Bukwa I by the Uganda Palaeontology Expedition in 1997. In 2002, additional rodent specimens were collected at Bukwa II, including a new genus and species, *Ugandamys downsi* and a tooth listed as cf *Paraphiomys* (Winkler *et al*., 2005). Some isolated teeth of a large species of *Diamantomys* were collected at Bukwa II in 2010 during an administrative survey of the site by staff from the Uganda Museum.

Walker (1968, 1969) listed small and medium-sized carnivores at Bukwa II, but did not describe or illustrate the specimens. In the Uganda Museum there is an isolated upper premolar of a small creodont, which is described herein, but there is no evidence of a medium-sized carnivoran in the collection of the Uganda Museum, Kampala.

SYSTEMATIC DESCRIPTIONS

Order Rodentia Bowdich, 1821

Family Renefossoridae Mein & Pickford, 2008

Genus *Renefossor* Mein & Pickford, 2008

Species *Renefossor songhorensis* Mein & Pickford, 2008

Description and comments

BUK I 25'97, is an almost complete mandible of a large renefossorid rodent (Fig. 1). Both the m/3s are missing, as are the apices of the incisors, and the p/4s are damaged. The m/1 shows two transverse lophids joined in the centre, but separated from each other buccally and lingually by deep sinusids. The distal lophid of the m/2 has a deep additional sinusid on the lingual side, which results in three cusps on the lingual side of the crown, and two on the buccal side. The dimensions of the specimen are :- length of tooth row p/4-m/3 left – 14.8 mm; length of tooth row p/4-m/3 right – 16.0 mm; mesio-distal diameter i/1 left – 4.2 mm; mesio-distal diameter i/1 right – 4.0 mm.

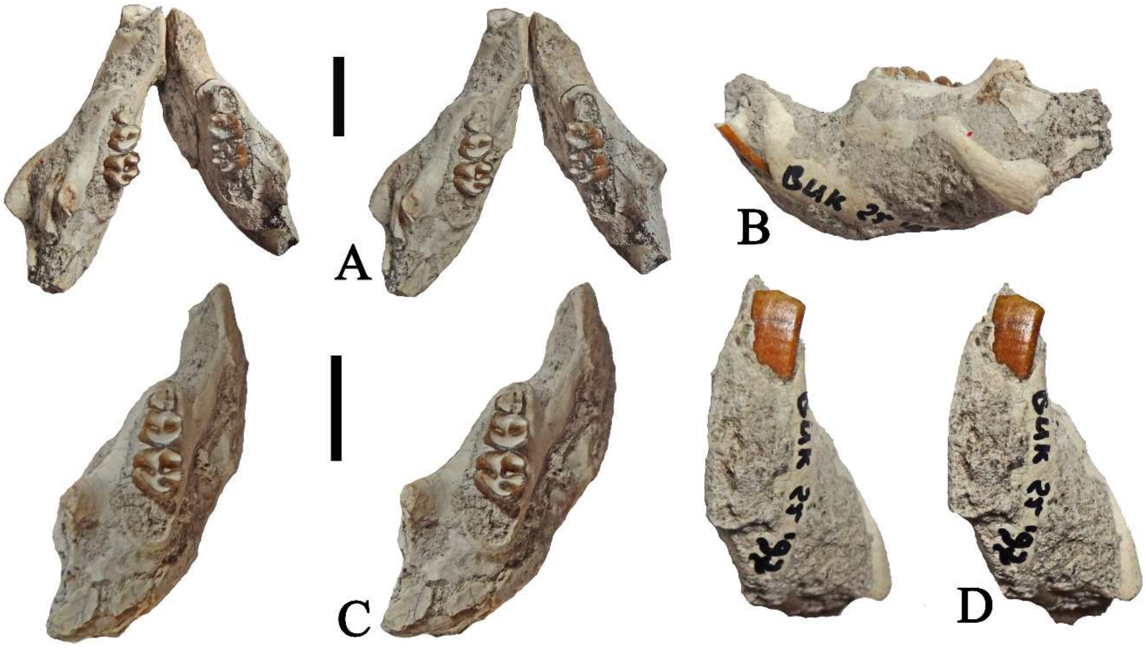

Figure 1. BUK I 25'97, left and right mandibles of *Renefossor songhorensis* from Bukwa I, Uganda. A) Stereo occlusal view, B) lateral view of left mandible, C) stereo occlusal view of left mandible to show details of molar morphology, D) stereo anterior view to show the lower incisor (scales : 10 mm).

The m/1 in the holotype specimen of *Renefossor songhorensis* Mein & Pickford (2008) (KNM SO 710) has three sinusids on the lingual side of the crown, but the distal one is shallow. The Bukwa I specimen is heavily worn, such that all trace of this distal sinusid has been eradicated. Apart from this difference, the Bukwa I specimen is close to that from Songhor, and we have little hesitation in referring it to the same species.

Renefossor songhorensis is restricted in its distribution to East African Faunal Sets I and II (Mein & Pickford, 2008) which means that the flaggy tuffs on the southern flank of Kwongori Hill are of Early Miocene age, compatible with the radio-isotopic age estimates (19-20 Ma).

Family Diamantomyidae Schaub, 1958

***Diamantomys morotoensis* Pickford & Mein, 2006**

Description and comments

A lower p/4 from Bukwa II measures 5.6 x 3.7 mm (length x breadth) which is appreciably larger than the corresponding tooth in *Diamantomys luederitzi* (4.15 x 2.65; 4.47 x 3.17; 4.43 x 3.05 mm) from Namibia but agrees with *Diamantomys morotoensis* from Moroto (range of length - 5.1-6.0 x range of breadth – 3.60-3.95mm). On the basis of the morphology and dimensions, we attribute this tooth to *Diamantomys morotoensis*.

The species *Diamantomys morotoensis* has not been recorded in any of the fossil sites arranged in Faunal Sets I and II. It was defined on the basis of specimens from Moroto, a site which was correlated to Faunal Set III by Pickford & Mein (2006) and an age of ca 17.5-17 Ma estimated for it. However, Moroto is more likely to be about 15±0.5 Ma (Pickford *et al*., 2017).

Rodentia Family indeterminate

Description and comments

From Bukwa I, there is a tiny rodent mandible in which the p/4-m/3 is 5.4 mm long, and the i/1 is 1.0 mm in mesio-distal diameter. The crowns of the cheek teeth are broken off, so it is not possible to identify the genus or species, but it is noted that this rodent is compatible in size with *Kenyamys* and *Epiphiomys*.

DISCUSSION

Bukwa I (Early Miocene) and Bukwa II (Middle Miocene) have yielded rodent fossils, but they are rare and generally comprise isolated teeth. However, the Uganda Palaeontology Expedition found two mandibles at Bukwa I : a large fossorial rodent, *Renefossor songhorensis*, the other a tiny species, possibly *Kenyamys* or *Epiphiomys*.

Bukwa II yielded isolated teeth attributed to *Ugandamys downsi* and cf *Paraphiomys* (Winkler *et al*., 2005; listed as *Paraphiomys pigotti* in Lòpez Antoñanzas *et al*., 2004), as well as *Diamantomys morotoensis* (this paper).

The biochronological significance of some of the Bukwa II rodents is not clear. *Paraphiomys* is a long-lived lineage (Early Miocene to Latest Miocene, Mein & Pickford, 2006) and *Ugandamys* is unique to Bukwa. Other taxa are more informative : *Renefossor songhorensis* from Bukwa I is common at Koru, Legetet and Napak (Faunal Set I) and Rusinga (Faunal Set II) and *Diamantomys morotoensis* from Bukwa II occurs at Moroto, a middle Miocene site (Faunal Set III).

Order Creodonta Cope, 1875

Genus nov. gen

Species nov. sp.

Description and comments

In the old collections from Bukwa housed in the Uganda Museum, there is an isolated upper premolar of a small creodont (Fig. 2). This is presumed to be the specimen upon which Walker (1968) based his listing of a small carnivore at the site.

The crown is dominated by a single, tall cusp with steep mesial and distal surfaces, accompanied basally by a low bulge mesially and a small cusplet distally bordered buccally and lingually by a cingular swelling. The lingual face of the main cusp is scored by a narrow vertical groove which descends towards the disto-lingual hollow formed between the cingulum and the main cusp. The anterior root is small, but the posterior one large and broad, suggesting that this is an anterior or second upper premolar. The tooth is probably from the left maxilla. The dimensions of the tooth are 5.7 x 3.2 mm (length x breadth).

Such a tooth is difficult to identify with confidence, but it most likely represents a creodont. It resembles an undescribed new genus and species of small creodont from Napak (Morales, pers. comm.).

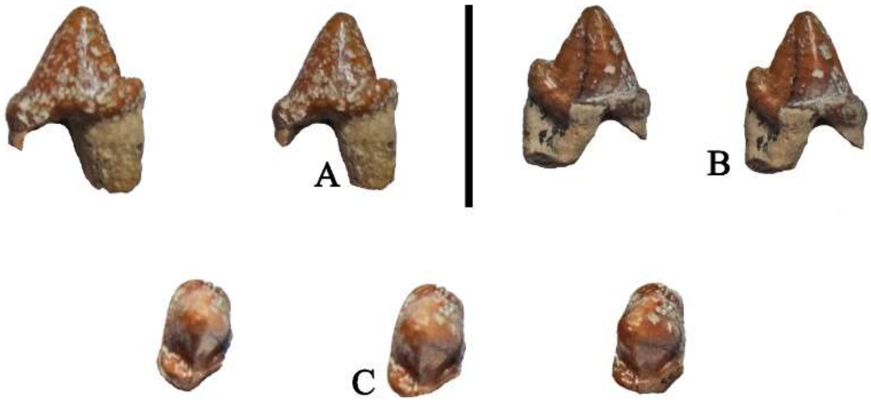

Figure 2. Creodonta from Bukwa II, left upper premolar, A) stereo buccal view, B) stereo lingual view, C) stereo occlusal views (scale : 10 mm).

DISCUSSION

Rodents and carnivorans are poorly represented at the Bukwa sites, and consequently they do not throw much light on the age of the deposits, although a broad correlation to the Early Miocene is indicated for Bukwa I and a Middle Miocene correlation for Bukwa II (Ogg *et al*. 2016).

CONCLUSIONS

Bukwa I has yielded two taxa of rodents, *Renefossor songhorensis*, which is a large fossorial species, and a tiny rodent of indeterminate affinities. The fauna from Bukwa I is correlated to Faunal Set I or II. Bukwa II has yielded isolated teeth attributed to *Ugandamys downsi*, cf *Paraphiomys* sp. and *Diamantomys morotoensis*, the latter species indicating correlation to Faunal Set III. The only carnivoran from the Bukwa complex of sites belongs to a new genus and species of small creodont, so in the present state of knowledge about these carnivorans, does not yield much information of geochronological interest.

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REFERENCES

Bowdich, T.E., 1821 - *An Analysis of the Natural Classifications of Mammalia for the use of Students and Travellers*. Paris, J. Smith. pp. 1-115 (+31).

Cope, E. D. 1875 - On the supposed Carnivora of the Eocene of the Rocky Mountains. *Proceedings of the Academy of Natural Sciences, Philadelphia*, **27**: 444-448.

Lòpez Antoñanzas, R., Sen, S. & Mein, P., 2004 - Systematics and phylogeny of the cane rats (Rodentia: Thryonomyidae). *Zoological Journal of the Linnaean Society*, **142**: 423-444

Mein, P. & Pickford, M., 2006 - Late Miocene micromammals from the Lukeino Formation (6.1 to 5.8 Ma), Kenya. *Bulletin mensuel de la Société linnéenne de Lyon*, **75**: 183-223.

Mein, P. & Pickford, M., 2008 - Early Miocene Rodentia from the Northern Sperrgebiet, Namibia. *Memoir of the Geological Survey of Namibia*, **20**: 235-290.

Ogg, J.G., Ogg, G.M. & Gradstein, F.M., 2016 - *A Concise Geologic Time Scale 2016,* Elsevier, 240 pp.

Pickford, M. & Mein, P., 2006 - Early Middle Miocene Mammals from Moroto II, Uganda. *Beiträge zur Paläontologie*, **30**: 361-386, Wien.

Pickford, M., Senut, B., Gommery, D., Musalizi, S. & Musiime, E., 2017 - Revision of the Miocene Hominoidea from Moroto I and II, Uganda. *Geo-Pal Uganda*, **10**: 1-32.

Schaub, S., 1958 – Simplicidentata. *In*: Piveteau, J. (Ed.) *Traité de Palaéontologie*, **6** (**2**): 659-818, Paris, Masson et Cie.

Walker, A., 1968 - The lower Miocene fossil site of Bukwa, Sebei. *Uganda Journal*, **32** (**2**): 149-156.

Walker, A., 1969 - Fossil mammal locality on Mount Elgon, eastern Uganda. *Nature*, **223**: 591-593.

Winkler A.J. & Downs W.R., 2002 - Rodents from the Early Miocene of Uganda: preliminary results of renewed investigations. *Journal of Vertebrate Paleontology*, **22** (**3**, supplement): 120A.

Winkler, A., MacLatchy, L. & Mafabi M., 2005 - Small rodents and a lagomorph from the early Miocene Bukwa locality, Eastern Uganda. *Palaeontologia Electronica*, **8** (**1**): 24A; aeo-electronica.org/2005_1/winkler24/issue1_05.htm.

Bukwa Afrotheria

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ABSTRACT

The Bukwa fossiliferous deposits have yielded a low diversity of Afrotheria, comprising five taxa : one macroscelidid, two hyracoids and two proboscideans, of which one is indeterminate at the family level. Of these the only fossils that have been described are the hyracoids. This paper describes the other taxa and discusses the biochronological implications of the fauna.

Key Words : Uganda, Basal Middle Miocene, Macroscelididae, Hyracoidea, Proboscidea

INTRODUCTION

Walker (1968, 1969) listed five Afrotheria at Bukwa : *Myohyrax oswaldi* Andrews, 1914, *Megalohyrax championi* (Arambourg, 1933), *Meroehyrax bataeae* (sic) Whitworth, 1954, *Dinotherium* (sic) *hobleyi* Andrews, 1911, and indeterminate mastodonts. Van Couvering & Van Couvering (1976) emended the list and added a genus of proboscidean : *Myohyrax oswaldi*, *Pachyhyrax championi*, *Meroehyrax bateae*, *Prodeinotherium hobleyi*, *Platybelodon kisumuensis*, (?)*Gomphotherium* sp. The hyracoids *Afrohyrax championi* and *Prohyrax bukwaensis* were published by Pickford (2009) but none of the other material has reached the scientific literature, a lack that is rectified herein.

SYSTEMATIC DESCRIPTIONS

Order Macroscelidea Butler, 1956

Family Myohyracidae Andrews, 1914

Genus *Myohyrax* Andrews, 1914

Species *Myohyrax oswaldi* Andrews, 1914

Description and comments

The material of *Myohyrax oswaldi* from Bukwa II mentioned by Walker (1968) seems to be missing from the collections in the Uganda Museum. During an administrative visit to the site, personnel of the Uganda Museum found a specimen (BUK II 9'10) in recently ploughed land at Bukwa II (Fig. 1).

The specimen comprises a lower cheek tooth, probably a premolar, 3.2 mm long x 1.7 mm broad. The crown is hypsodont, supported on two well-developed roots. The occlusal surface is worn to the stage where little detail of cusp morphology remains. There is a deep, slightly curved buccal sinus and a broad lingual one, but there is no sign of cementum. The specimen is similar to material from the Sperrgebiet, Namibia, especially the sample from Arrisdrift (Senut, 2003, 2008).

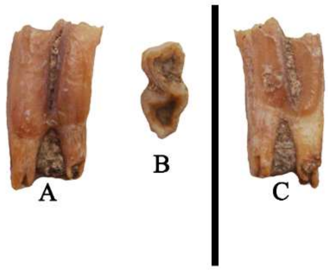

Figure 1. BUK II 9'10, *Myohyrax oswaldi*, left lower premolar: A) buccal, B) occlusal and C) lingual views (scale : 10 mm).

Order Hyracoidea Huxley, 1869

Family Titanohyracidae Matsumoto, 1926

Genus *Afrohyrax* Pickford, 2004

Species *Afrohyrax championi* (Arambourg, 1933)

Description and comments

The only specimen of *Afrohyax championi*, from Bukwa II, an upper cheek tooth, possibly the M1/, was described by Pickford (2009) (Fig. 2). The specimen is 15.0 mm long x 16.8 mm broad. The occlusal surface is worn flat, typical of this genus of hyracoid. Little morphological detail of the occlusal surface remains, but the characteristic shape of the hypocone can be observed, as can the inflated mesostyle and the position of the metastyle almost in the midline of the tooth.

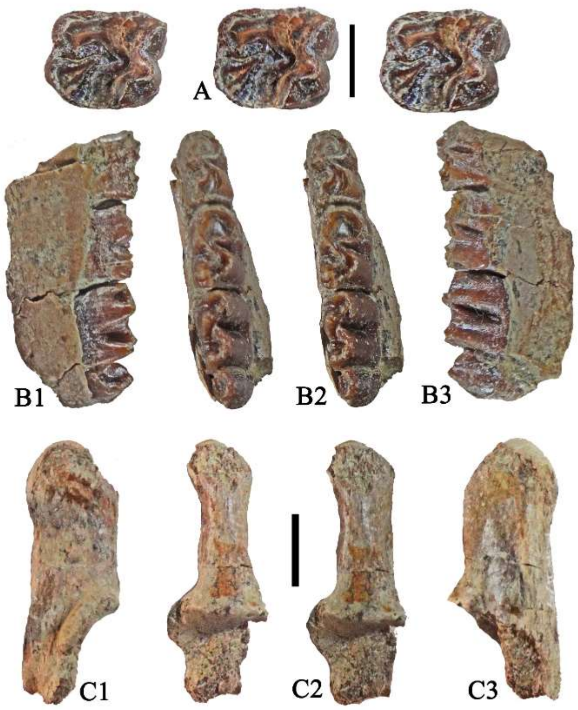

Figure 2. Hyracoidea from Bukwa II, Uganda. A) BUK II, left upper premolar, *Afrohyrax championi*, stereo occlusal views; B) BUK II, right mandible containing m/1-m/3, *Prohyrax bukwaensis*, holotype specimen (B1 - lingual view, B2 - stereo occlusal view, B3 - buccal view); C) BUK II'67, left calcaneum of *Prohyrax bukwaensis* (C1 - lateral view, C2 - stereo anterior view, C3 - medial view) (scales : 10 mm).

Family Pliohyracidae Osborn, 1899

Genus *Prohyrax* Stromer, 1923

Species *Prohyrax bukwaensis* Pickford, 2009

Description and comments

There are two hyracoid fossils from Bukwa II which are attributed to *Prohyrax bukwaensis* Pickford, 2009. The holotype mandible was described by Pickford (2009) and it is not necessary to repeat the description, but the fossil is illustrated again for ease of reference (Fig. 2). The teeth have the following measurements: m/1 - 9.8 x 6.7; m/2 - 11.1 x 7.3; m/3 - 16.8 x 7.8 mm.

Bukwa II also yielded a slightly damaged hyracoid calcaneum which is in the old collections from the site (Fig. 2). The tuber is long and robust, and the sustentaculum is weakly salient on the lateral side. Pickford (1994, 2009) illustrated calcanea of *Prohyrax hendeyi* and *Afrohyrax championi*. The dimensions of the Bukwa specimen link it to *Prohyrax* rather than to *Afrohyrax* which is an appreciably larger species.

Order Proboscidea Illiger, 1811

Family Deinotheriidae Bonaparte, 1845

Genus *Deinotherium* Kaup, 1829

Species *Deinotherium hobleyi* Andrews, 1911

Description and comments

An almost complete, lightly worn left M3/ of *Deinotherium hobleyi* was one of the first mammalian fossils found at Bukwa (Fig. 3). It was collected from Bukwa I, on the south flank of Kwongori Hill during the first palaeontological survey of the site (Walker, 1968). The tooth (UMP 67-35, Fig. 3) measures 60 x 62 mm (length x breadth) and thus falls into the range of metric variation of *Deinotherium hobleyi*. The crown is comprised of two lophs with no sign of an antero-posterior sulcus. The pre- and post-crista are subtle, as is usual in this species and deinotheres in general. There is no hint of the convolute, a small knot of enamel on the distal wall of the metaloph (distal loph) which is common in large species of the genus.

Figure 3. UMP 67-35, BUK I, *Deinotherium hobleyi*, left M3/, A) stereo occlusal view, B) lingual view (scale : 10 mm).

DISCUSSION

Among the Afrotheria from Bukwa, Walker (1968, 1969) listed *Myohyrax oswaldi*, *Megalohyrax championi*, *Meroehyrax bataeae* (sic), *Dinotherium* (sic) *hobleyi* and indeterminate mastodonts, which is a fair assessment of the fossils, taking into account the taxonomy during the period that he worked.

Van Couvering & Van Couvering (1976) in contrast, recorded *Platybelodon kisumuensis* and (?)*Gomphotherium* sp. in addition to the macroscelidids and hyracoids. However, the enamel fragments upon which these identifications of proboscideans were based are unidentifiable, even at the family level.

The fossil attributed to *Meroehyrax* by Walker (1968) was transferred to *Prohyrax* by Pickford (2009) who erected a new species for it, *Prohyrax bukwaensis*.

The biochronological meaning of the Bukwa afrotheres is delicate to assess, but the hyracoids from Bukwa II plead for an age younger than Rusinga, *Prohyrax bukwaensis* being closest in morphology and dimensions to *Prohyrax hendeyi* from Arrisdrift, Namibia (Pickford, 1994, 2009) which is considered to be about 17.2 Ma (Pickford & Senut, 2003). The deinothere from Bukwa I falls into the range of variation of *Deinotherium hobleyi*, which has a long chronological range (20.5-14.5 Ma, if not even longer). The species *Myohyrax oswaldi* is common at Rusinga and Karungu, Kenya, but it has been found in younger deposits at Bosluis Pan, South Africa (ca 16 Ma, Senut *et al.*, 1996) and Arrisdrift, Namibia, where it is particularly well represented (Senut, 2003). It also occurs at Maboko, Nyakach and Kipsaraman, Kenya, all sites correlated to Faunal Set IIIb, but is also common in localities correlated to Faunal Set II, such as Karungu, Rusinga and Nyakongo, and its earliest records in East Africa are from Faunal Set I, at sites such as Napak, Uganda, and Koru, Kenya.

CONCLUSIONS

The Bukwa fauna contains five taxa of Afrotheria. An isolated tooth is attributed to the hypsodont macroscelidid *Myohyrax oswaldi*, a species that probably grazed on grass. Hyracoidea are represented at Bukwa by two species, *Afrohyrax championi* and *Prohyrax bukwaensis*, both of which are brachyodont, and thus probably browsers. Finally there are two proboscideans, the folivorous *Deinotherium hobleyi* and a bunodont omnivore of gomphothere grade, but currently unidentifiable at the family level.

As an assemblage the afrothere fauna from Bukwa suggests an Early or Middle Miocene correlation, with the species *Prohyrax bukwaensis* from Bukwa II indicating preference for the latter possibility, because it is intermediate in dimensions between the Early Miocene species *Prohyrax tertiarius* on the one hand, and the Middle Miocene species *Prohyrax hendeyi*, on the other (Pickford, 2009).

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REFERENCES

Andrews, C.W., 1911 - On a new species of *Dinotherium* from British East Africa. *Proceedings of the Zoological Society of London*, **1911**: 943-945.

Andrews, C.W., 1914 - On the lower Miocene vertebrates from British East Africa, collected by Dr Felix Oswald. *Quarterly Journal of the Geological Society of London*, **70**: 163-186.

Arambourg, C., 1933 - Mammifères miocènes du Turkana, Afrique orientale. *Annales de Paléontologie*, **22**: 121-148.

Bonaparte, C.L., 1845 - *Catalogo Metodico dei Mammiferi Europei*. Valenciennes, Milan, 36 pp.

Butler, P.M., 1956 - Erinaceidae from the Miocene of East Africa. *Fossil Mammals of Africa*, **11**: 1-75.

Huxley, T.H., 1869 - *An Introduction to the Classification of Animals*. London, John Churchill and Sons, 147 pp.

Illiger, C.D., 1811 - *Prodromus systematis mammalium et avium additis terminis zoographicis uttriusque classis*. Berlin, Salfeld.
Kaup, J., 1829 - *Deinotherium giganteum*, eine Gattung der Vorwelt aus der Ordnung der Pachydermen, aufgestellt und beschreiben. *Isis*, **22**: 401-404.
Matsumoto, H., 1926 - Contribution to the knowledge of the fossil Hyracoidea of the Fayum, Egypt, with a description of several new species. *Bulletin of the American Museum of Natural History*, **56**: 253-350.
Osborn, H.F., 1899 - On *Pliohyrax kruppi* Osborn, a fossil hyracoid from Samos, Lower Pliocene in the Stuttgart collection. A new type and first known Tertiary hyracoid. *Proceedings of the 4th International Congress of Zoology, Cambridge*, pp. 172-173.
Pickford, M., 1994 - A new species of *Prohyrax* (Mammalia, Hyracoidea) from the middle Miocene of Arrisdrift, Namibia. *Communications of the Geological Survey of Namibia*, **9**: 43-62.
Pickford, M., 2004 - Revision of the Early Miocene Hyracoidea (Mammalia) of East Africa. *Comptes Rendus Palevol*, **3**: 675-690.
Pickford, M., 2009 - New Neogene hyracoid specimens from the Peri-Tethys region and East Africa. *Paleontological Research*, **13**: 265-278.
Pickford, M. & Senut, B., 2003 - Miocene palaeobiology of the Orange River valley, Namibia. *Memoir of the Geological Survey of Namibia*, **19**: 1-22.
Senut, B., 2003 - The Macroscelididae from the Miocene of the Orange River, Namibia. *Memoir of the Geological Survey of Namibia*, **19**: 119-141.
Senut, B., 2008 - Macroscelididae from the Lower Miocene of the Northern Sperrgebiet, Namibia. *Memoir of the Geological Survey of Namibia*, **20**: 185-255.
Senut, B., Pickford, M., de Wit, M., Ward, J., Spaggiari, R. & Morales, J., 1996 - Biochronology of sediments at Bosluis Pan, Northern Cape Province, South Africa. *South African Journal of Science*, **92**: 249-251.
Stromer, E. 1923 - Ergebnisse der Bearbeitung mitteltertiär Wirbeltierreste aus Deutsch-Südwestafrika. *Sitzungsberichte der Bayerische Akademie der Wissenschaften*, **1923**: 253-270. München.
Van Couvering, J.A. & Van Couvering, J.A.H., 1976 - Early Miocene mammal fossils from East Africa : Aspects of geology, faunistics and palaeoecology. *In*: Isaac G. & McCown E., (Eds) *Louis Leakey and the East African Evidence*. Berkeley, University of California Press, pp. 155-207.
Walker, A., 1968 - The lower Miocene fossil site of Bukwa, Sebei. *Uganda Journal*, **32** (**2**): 149-156.
Walker, A., 1969 - Fossil mammal locality on Mount Elgon, eastern Uganda. *Nature*, **223**: 591-593.
Whitworth, T., 1954 - The Miocene hyracoids of East Africa. *Fossil Mammals of Africa*, **7**: 1-58.

Bukwa II Hominoidea

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ABSTRACT

Bukwa II, Uganda has yielded several isolated teeth of two taxa of Miocene Hominoidea, a small ape close to «*Micropithecus*» *leakeyorum* from Maboko which is similar to the material from Kipsaraman, Kenya, previously attributed to «*Limnopithecus*» sp., and a medium-sized ape close in dimensions to small specimens of *Ekembo heseloni* from Rusinga, Kenya, but differing from it in morphology. The diversity of hominoids at Bukwa II is low, but this could be related to the relatively small sample of mammals from the site. Two hominoid specimens from Bukwa II have already been mentioned in the literature but have not been described. These and other fossils from the site are described and illustrated herein. As an assemblage, the primate fauna from Bukwa II suggests correlation to East African Faunal Set III.

Key Words : Hominoidea, Middle Miocene, Bukwa, Uganda, dentition

INTRODUCTION

The Middle Miocene (Faunal Set III) deposits at Bukwa II have yielded about 200 mammalian fossils (Walker, 1968; Cote *et al*., 2017 ; personal observations MP) among which there are several complete to subcomplete primate teeth. Eleven of the primate teeth are described and illustrated herein, but several fragmentary specimens are not included in this paper on account of uncertainties about their taxonomic identification.

In comparison with primate-rich sites such as Napak, Uganda, where there is a high diversity of primates (11 taxa of catarrhines), Bukwa II appears to have a low diversity of primates (2 taxa) but this could be related to the fact that the overall fossil record of mammals from the deposits is quite low. It could also be related to the fact that the vegetation near the site was dominated by grassland with woodland and forest patches in the vicinity (Pickford, 2002), a reconstruction of the vegetation based on fossils from Bukwa I, which are appreciably older than the deposits at Bukwa II. If the vegetation reconstruction applies to Bukwa II, which is open to discussion, it would be expected that primates would be less diverse than in localities that preserved remnants of humid forest palaeoenvironments such as Chamtwara and Legetet, Kenya (Harrison, 1982) or even slightly more open, but still predominantly forested, palaeoenvironments such as Napak, Uganda (Pickford *et al*., 2010). The presence of a grazing rhinoceros (Geraads *et al*., 2012) hypsodont afrotheres and rodents at Bukwa II indicate that, when the Bukwa II deposits accumulated, there was probably an important biomass of grass in the local environment.

Walker (1968, 1969) listed *Limnopithecus legetet* at Bukwa II, an identification that has been repeated many times. However, following the general review by Le Gros Clark & Leakey (1951), all the small hominoids from East Africa were attributed to *Limnopithecus* (*Limnopithecus legetet* for very small specimens and *Limnopithecus macinnesi* for slightly larger ones). As envisaged by Le Gros Clark &

Leakey (1951) the hypodigm of *Limnopithecus legetet* was a mixture of at least two genera, including what became known as *Kalepithecus*, while the fossils attributed to *Limnopithecus macinnesi* consisted of remains later classified in *Dendropithecus*, *Rangwapithecus* and *Nyanzapithecus* (Harrison, 2010). With this extreme version of taxonomic lumping which was commonly accepted during the 1960's, Walker's (1968) identification of the Bukwa II teeth was logical.

Since 1968, many genera of small-bodied apes have been erected for material from Kenya and Uganda (Harrison, 1982, 2010 ; Pickford *et al*., 2009, 2010) (Table 1), but no-one has re-appraised the taxonomy of the Bukwa material in light of these advances. This is undoubtedly due to the fact that the two specimens in the original Bukwa II collection are damaged : one (UMP 68-27) is an incomplete incisor crown, and the other (UMP 68-22) is a lower molar missing most of the metaconid, and the enamel has spalled off the rear of the crown, leaving a small remnant of the hypoconulid. Thus, the fossils are difficult to interpret.

Harrison (1982, 1988) mentioned the presence of the above-mentioned two hominoid teeth from Bukwa II, which he attributed to *Limnopithecus legetet*, a lower molar and an incomplete upper central incisor but he didn't enter into detail about the specimens (Pickford, 2002).

Table 1. Comparison of hominoid diversity at Bukwa II, Napak and two Kenyan sites (Chamtwara, Legetet)

Locality	List of Catarrhines	Reference
Chamtwara and Legetet, Kenya	*Micropithecus clarki* *Kalepithecus songhorensis* *Limnopithecus legetet* *Dendropithecus macinnesi* *Xenopithecus koruensis* *Proconsul africanus* *Ugandapithecus legetetensis* *Ugandapithecus major*	Harrison, 1982 Pickford *et al*., 2009
Napak, Uganda	*Micropithecus clarki* *Dendropithecus ugandensis* *Limnopithecus legetet* *Turkanapithecus rusingensis* *Lomorupithecus evansi* *Kalepithecus songhorensis* *Iriripithecus alekileki* *Karamojapithecus akisimia* cf *Ekembo nyanzae* *Ugandapithecus major*	Pickford *et al*., 2010
Bukwa II, Uganda	«*Micropithecus*» *leakeyorum* (= «*Limnopithecus*» sp. similar to the species from Kipsaraman) Genus indet. medium-sized ape	This paper This paper

Pickford *et al*. (2010) recorded *Afropithecus* sp., *Simiolus* sp. and an indeterminate hominoid species at Bukwa II, but the fossils were not described. The evidence is re-examined in this paper. The record for *Afropithecus*, for example, was based on half a deeply worn lower molar, which resembles worn molars of *Afropithecus*.

MacLatchy & Cote (2017) reported the presence of three hominoid taxa at Bukwa II : 1) a medium-sized ape tentatively attributed to *Ekembo* (M2/, worn upper molar fragment, worn lower molar), 2) the tentative presence of *Micropithecus* (upper canine), and 3) *Lomorupithecus* (upper premolar) but the fossils were not illustrated, nor measurements provided. These authors considered that the Bukwa deposits are aged between 19.5-19.1 million years old and on this basis assumed that the fossils attributed by them to *Ekembo* were the oldest known of the genus.

Materials - Abbreviations

The fossils described herein comprise specimens housed in the Uganda Museum, collected by two teams :- A) historical collections made by Walker (1968) (UMP catalogue), B) collections made by

Uganda Museum staff during administrative visits to the site (BUK 2009, 2010, 2011) (Mwanja *et al*., 2017).

Abbreviations are as follows :- BAR - Baringo (Kenya), BUK - Bukwa (Uganda), FT - Fort Ternan (Kenya), KO - Koru, (Kenya), MB - Maboko (Kenya), NAP - Napak (Uganda), UMP - Uganda Museum Palaeontology collection.

SYSTEMATIC DESCRIPTIONS

Superfamily Hominoidea Gray, 1825

Genus «*Micropithecus*» Fleagle & Simons, 1978

Species «*Micropithecus*» *leakeyorum* Harrison, 1989 (= «*Limnopithecus*» sp. from Kipsaraman, Pickford & Kunimatsu, 2005)

Description and comments

There are several lower molars from Bukwa II which are close in crown morphology, enamel thickness and dimensions to fossils of «*Micropithecus» leakeyorum* from Maboko, Kenya (Harrison, 1989) and to specimens from Kipsaraman, Kenya, attributed to *Limnopithecus* sp. by Pickford & Kunimatsu (2005) (Fig. 1, 2). The Bukwa fossils differ in morphology and interdental proportions from the type specimen of *Limnopithecus legetet*, and also from the type species of *Micropithecus* (*Micropithecus clarki*) suggesting that they represent a distinct genus, so in this paper we put the genus names in parentheses («*Limnopithecus*» sp. from Kipsaraman, «*Micropithecus*» *leakeyorum*) to distinguish it from both these genera. Harrison (1989) already evoked the possibility that the species *leakeyorum* might eventually be classified in a genus different from *Micropithecus*, and the Kipsaraman and Bukwa II fossils trend in this same direction, but we do not name a new genus here, pending recovery of more diagnostic fossils.

The upper central incisor (UMP 68-27) from Bukwa II (Harrison, 1982, 1988) (cast in NHMUK) lacks the root and part of the cervix (Fig. 1E). However, it is unworn and shows a deeply scooped lingual surface with a low central lingual ridge that does not extend upwards as far as the scoop. This tooth is remarkably similar to specimens from Maboko attributed to «*Micropithecus*» *leakeyorum*.

UMP 68-22 is a left lower molar from Bukwa II (Fig. 1) which was previously attributed to *Limnopithecus legetet* (Walker, 1968, 1969; Harrison, 1982, 1988; MacLatchy & Cote, 2017). Part of the metaconid and the distal end is slightly damaged. The tooth is unworn and shows a constricted talonid basin closed distally by the hypoconulid which is positioned between the distal parts of the hypoconid and entoconid, different from lower molars of *Micropithecus clarki* from Napak (Pickford *et al*., 2010). In particular, the hypoconid sends a large, swollen cristid obliquely forwards towards the centre of the tooth, and this structure effectively reduces the capacity of the floor of the talonid basin. The post-metacristid and pre-entocristid are steep and sharp-edged, and form a constricted sill between the talonid basin and the lingual side of the crown.

This m/1 differs from the type specimen of *Limnopithecus legetet* which has a vast talonid basin (Pickford *et al*., 2010) its crown being noticeably broader posteriorly than anteriorly. It also differs from its counterparts in *Micropithecus clarki* from Napak, and from KNM KO 8 from Koru, Kenya, which has a more capacious talonid basin. The latter specimen was for a long time included in *Limnopithecus legetet* (in fact it was used to refine the diagnosis of the species) but its molar morphology differs fundamentally from the type specimen in the cusp layout, the length/breadth ratio and the distal position of the hypoconulid (see discussion in Pickford *et al*., 2010). The anterior portion of the lower molars of KNM KO 8 is almost the same breadth as the posterior part, unlike the type specimen of *Limnopithecus legetet*.

In two other m/1s from Bukwa II (BUK II 35’10 and BUK II 36’10) the talonid basin is capacious, the protoconid and metaconid are closer to each other than are the metaconid and hypoconid, and the hypoconulid is large and in a distal position behind the rear parts of the metaconid and hypoconid. The hypoconid sends a large, swollen cristid obliquely forwards into the talonid basin. There is a buccal cingulum on the side of the protoconid which fades out on the hypoconid. The distal fovea is well defined, and is separated from the talonid basin by cristids running between the entoconid and hypoconulid.

The m/3 from Bukwa II (BUK II 25'09) is slightly larger than the m/2s from the same site, and its hypoconulid is retired distally in such a way as to leave openings, or low sills, on the disto-lingual and disto-buccal sides of the talonid basin separated by the hypoconulid. In addition, the cingulum extends along the entire buccal side of the tooth. The cristids between the entoconid and hypoconulid which separate the distal fovea from the talonid basin are absent, a feature which is common to m/3s of several small apes from the Miocene (*Lomorupithecus evansi*, *Kalepithecus songhorensis*, *Micropithecus clarki*) (Harrison, 2010).

The right M3/ from Bukwa (BUK II 1'10) attributed to «*Micropithecus*» *leakeyorum* is smaller than the homologous tooth in the species *Simiolus enjiessi* Leakey & Leakey, 1987, from which it differs by the reduced dimensions of the hypocone and metacone (large in *Simiolus*) but it is close in dimensions to the Kipsaraman fossil attributed to *Limnopithecus* sp. (BAR 772'02 ; 4.9 x 6.2 mm : length x breadth) by Pickford & Kunimatsu (2005). The protocone is by far the largest cusp, followed by the paracone, then a reduced metacone, and a low hypocone in a very distal position. There is a well-developed lingual cingulum, the trigon basin is walled off distally by the endo-protocrista, but the wall is low, the mesial fovea is reduced in mesio-distal diameter, and the posterior fovea is large. The enamel surface is heavily wrinkled where it is unaffected by wear.

In these morphological features, as well as in their dimensions, the small ape teeth from Bukwa II are compatible with the material from Maboko and Kipsaraman, but are slightly larger than specimens of *Limnopithecus legetet* from Napak (Pickford *et al*., 2010). The m/1s differ from those of *Lomorupithecus evansi* by the presence of clear cristids between the entoconid and hypoconulid which separate the distal fovea from the talonid basin, cristids which are lacking in *Lomorupithecus evansi* (Harrison, 2010).

The Bukwa II teeth differ from those of *Dendropithecus* Andrews & Simons, 1977, by the occlusal outlines, by the breadth-length proportions of the molars and by the less developed cingulids and cingulum. They differ from teeth of the genera *Nyanzapithecus* Harrison, 1986, and *Turkanapithecus* Leakey & Leakey, 1986b, by the shallower base of the molars beneath the cusps. The molars of *Simiolus* Leakey & Leakey, 1987, differ from those from Bukwa II by the less elongated occlusal outline of the crowns. There is some similarity in cusp layout between the teeth of *Kalepithecus* Harrison, 1988, and the Bukwa II sample, but in *Kalepithecus songhorensis*, the molars are relatively broader compared with the length than are the Bukwa teeth. This is probably due to the stronger development of the buccal cingulids in *Kalepithecus*. The lower molars of *Kogolepithecus* Pickford *et al*., 2003, differ considerably from the Bukwa II sample : they are larger, more elongated and the protoconid has a distinct post-protoconid cristid separated apically from the protoconid.

The Bukwa II small ape teeth differ from those of *Lomorupithecus* Rossie & MacLatchy, 2006, which has extremely smooth enamel almost devoid of wrinkles (Pickford *et al*., 2010). Harrison (2010) considered *Lomorupithecus harrisoni* to be a junior synonym of *Limnopithecus evansi*, whereas Pickford *et al*. (2010) recognised the validity of the genus *Lomorupithecus* but considered that the type specimen of the type species was the same species as *evansi*, making for the combination *Lomorupithecus evansi*. The mandible from Napak attributed to *Lomorupithecus harrisoni* by Rossie & MacLatchy, 2006, was classified as *Micropithecus clarki* by Harrison (2010).

The Bukwa II small ape molars differ from those of *Iriripithecus* Pickford *et al*., 2010 and *Karamojapithecus* Pickford *et al*., 2010 by their lesser dimensions, and by details of cusp layout. In addition *Iriripithecus* has more sectorial crista and cristids in the molars, and there is a large tuberculum sextum in the lower molars.

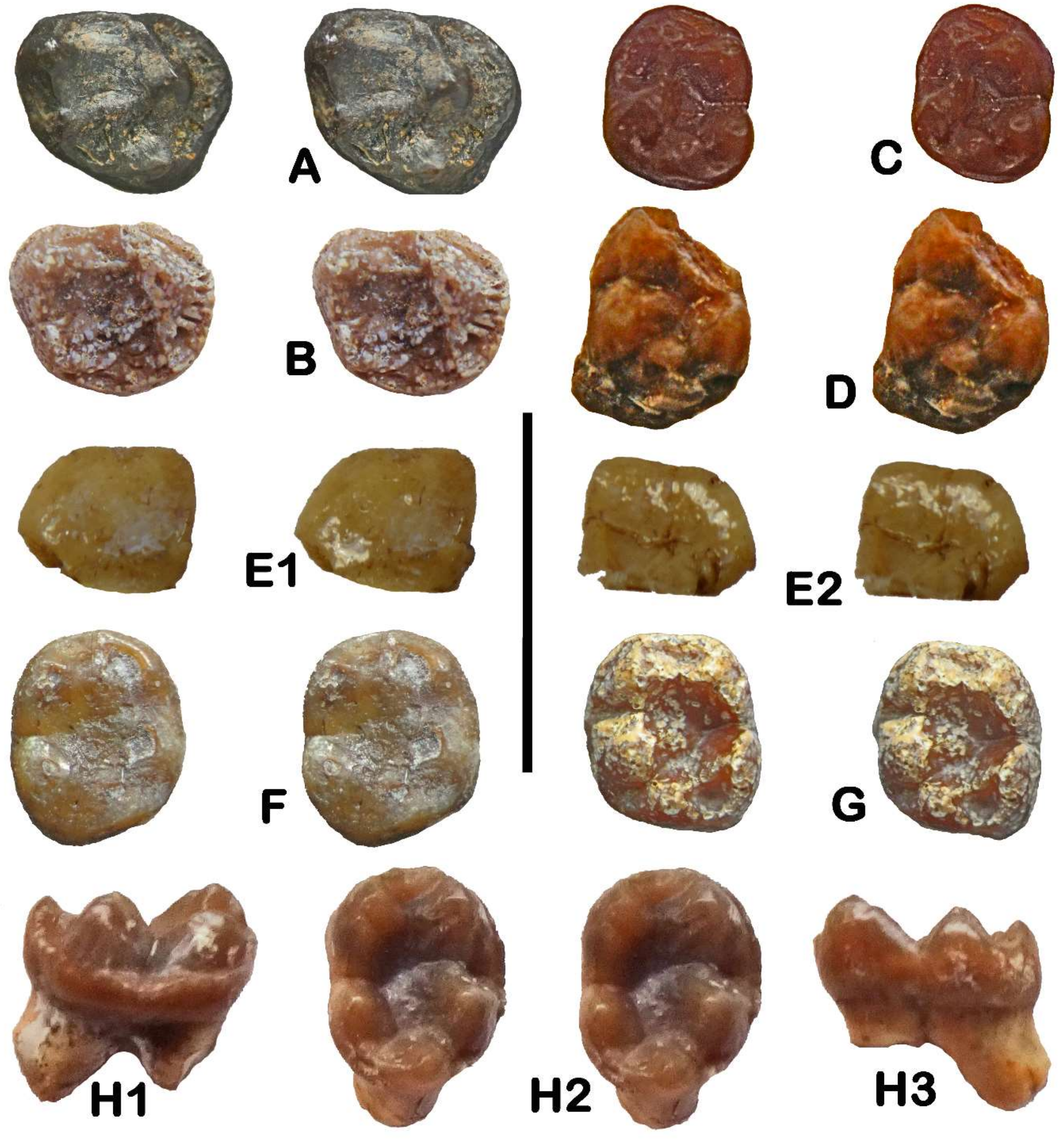

Figure 1. «*Limnopithecus*» cf sp. from Kipsaraman Kenya, «*Micropithecus*» *leakeyorum* from Bukwa II, Uganda, and *Micropithecus clarki* from Napak, Uganda. A) BAR 772'02, left M3/ (reversed stereo occlusal view) from Kipsaraman; B) BUK II 1'10, right M3/, sp. (stereo occlusal view); C) NAP, UMP 66-08, left m/1, *Micropithecus clarki* from Napak (stereo occlusal view); D) UMP 68-22, (BUK) left m/1 (stereo occlusal view); E) UMP 68-27, left I1/ (E1 - stereo labial view, E2 - stereo lingual view); F) BUK II 35'10, right m/1 (stereo occlusal view); G) BUK II 36'10, left m/1 (stereo occlusal view); H) BUK II 25'09, right m/3, (H1 - buccal view, H2 - stereo occlusal view, H3 - lingual view) (scale : 10 mm).

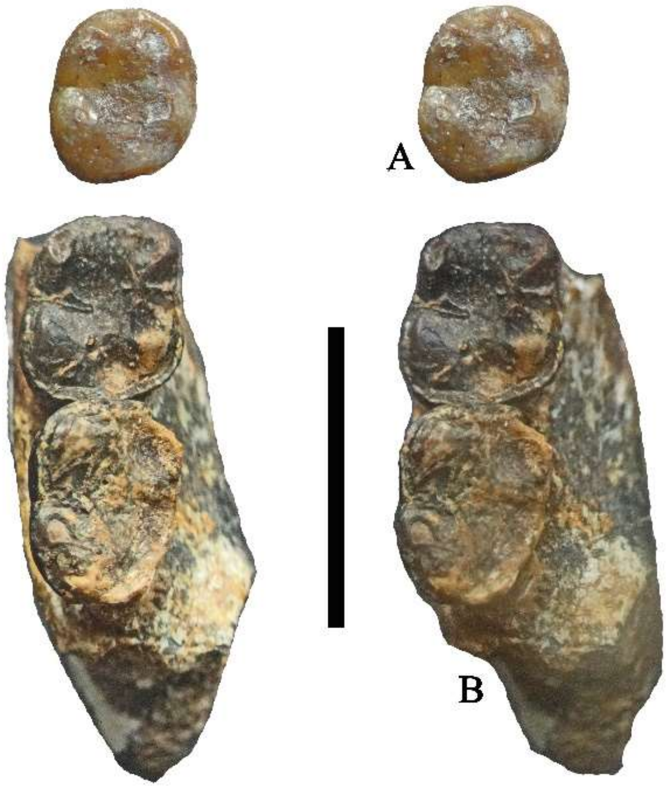

Figure 2. Comparison of lower molars of cf «*Limnopithecus*» sp. from Kipsaraman and «*Micropithecus*» *leakeyorum* from Bukwa II. A) BUK II 35’10, right m/1, B) BAR 216’02, right mandible fragment containing m/2 and m/3 (scale : 10 mm).

The Kipsaraman species has not yet been named on account of the fact that it’s fossil record is still poor, yet it seems clear that it represents a species distinct from *Limnopithecus legetet*. Furthermore, given the morphological differences from the type specimen of *Limnopithecus legetet*, it is likely that these teeth from Kipsaraman and Bukwa II do not in fact belong to *Limnopithecus* at all, but to an undescribed genus akin to «*Micropithecus*» *leakeyorum* from Maboko and Majiwa, Kenya (Harrison, 1989). We refrain from erecting a new genus, pending the recovery of more informative specimens, and merely note that the Bukwa II, Maboko and Kipsaraman small ape fossils are similar to each other, and differ from the type species *Micropithecus clarki* and *Limnopithecus legetet*.

Table 2. Measurements (in mm) of hominoid teeth from Bukwa II, Uganda (see Harrison, 1982, for alternative measurements of UMP specimens).

Catalogue N°	Tooth	Mesio-distal length	Bucco-lingual breadth	Identification
BUK II UMP 68-22	m/1 incomplete left	5.7	4.5	«*Micropithecus*» *leakeyorum*
BUK II 36’10	m/2 left	5.7	4.8	«*Micropithecus*» *leakeyorum*
BUK II 35’10	m/2 right	5.7	5.0	«*Micropithecus*» *leakeyorum*
BUK II 25’09	m/3 right	6.4	5.2	«*Micropithecus*» *leakeyorum*
BUK II 1’10	M3/ right	4.9	5.7	«*Micropithecus*» *leakeyorum*
BUK II UMP 68-26	I1/ left	4.9e	--	Indeterminate small ape?
BUK II 37’10	upper canine left	9.7	7.2	Genus nov.
BUK II 18’11	M3/ left	8.3	10.1	Genus nov.
BUK II 43’11	m/3 left	11.1	8.3	Genus nov.
BUK II 17’11	m/3 right	11.1	8.7	Genus nov.
BUK II 2’10	m/3 fragment right	--	8.6	Genus nov.
BUK II 1’11	m/3 left	12.9	9.0e	Genus nov.

The presence of this small ape species at Bukwa II invites correlation of the deposits to Maboko, Majiwa and Kipsaraman, Kenya, all localities correlated to Faunal Set IIIb (Pickford, 1981, 1998; Pickford & Kunimatsu, 2005).

Genus and species nov. medium-sized ape

Description and comments

Six isolated teeth from Bukwa II are attributed to an undetermined genus and species of medium-sized ape (Fig. 3), probably a new genus and species.

BUK II 37'10, an upper canine shows apical wear. The mesial groove is somewhat lingually positioned and there is a capacious concave distal surface which is moderately worn. The relatively low crown suggests that the specimen possibly represents a female individual.

BUK II 18'11 is a lightly worn left M3/. The protocone and paracone are large, but the hypocone and metacone are reduced, imparting a rounded margin to the distal half of the crown. The slight lingual cingulum on the protocone fades out before reaching the hypocone.

Two moderately worn m/3s (BUK II 17'11, BUK II 43'11) show dentine exposures on the protoconid and hypoconulid, but not on the other cusps. The protoconid, hypoconid and hypoconulid are sub-equal in size and are disposed in line with each other, whereas the endoconid is reduced in stature. Cingulum development is weak on the protoconid. A broken lower molar (BUK II 2'10) lacks the distal cusps, but the anterior half resembles the two m/3s, with the sole exception that the metaconid is low and rounded, not pointed, despite the fact that there is no dentine exposure on the protoconid suggesting a lesser degree of wear than in the other two specimens. There is a weak, discontinuous buccal cingulum. For these reasons, the tooth was previously interpreted to belong to *Afropithecus* (Pickford *et al*., 2010) but it now seems more likely that it represents the same unknown genus and species as the other medium-sized ape teeth from Bukwa.

Four of the five molars from Bukwa II plot out at the small end of the range of variation of *Ekembo heseloni* (Fig. 4) the smaller of the two species of the genus which is common at Rusinga Island (McNulty *et al*., 2015 ; Pickford, 1986, Pickford *et al*., 2009). However, the morphology of the teeth indicate that they do not belong to this taxon. The lingual cingulum in the upper molar is light and fades out before the hypocone, the buccal cingulum in the lower molars is weak and incomplete, the upper canine is stubby and shows apical wear, unlike equivalent teeth of *Ekembo*.

In addition to these four cheek teeth, there is a larger tooth, BUK II 1'11, a slightly damaged left m/3 (Fig. 3, 4) which is similar in morphology to other lower third molars from the site, but which is of significantly greater dimensions (length 12.9 mm versus 11.1 mm for the two other teeth). It plots near the middle of the gap that separates the scatter plots of *Ekembo heseloni* (Walker *et al*., 1993) and *Ekembo nyanzae* (Le Gros Clark & Leakey, 1950) from Rusinga (Fig. 4, Table 2). Despite the size difference we provisionally attribute it to the same taxon as the other medium-sized ape teeth from Bukwa.

The upper canine from Bukwa II looks similar to a specimen from Fort Ternan (KNM FT 39) which was attributed to *Dryopithecus nyanzae* by Andrews & Walker 1976, to *Proconsul nyanzae* by Andrews (1978) but to *Kenyapithecus wickeri* by Pickford (1985) and Harrison (1992). However, the Fort Ternan specimen is considerably larger (length x breadth - 15.5 x 11.7 mm) than the one from Bukwa II (9.7 x 7.2 mm). The difference in dimensions could be due to sexual dimorphism (Pickford, 1986).

The medium-sized ape cheek teeth from Bukwa II differ from their counterparts in *Proconsul* Hopwood, 1933, *Xenopithecus* Hopwood, 1933, *Rangwapithecus* Andrews, 1974, *Ugandapithecus* Senut *et al*., 2000 and *Ekembo* McNulty *et al*., 2015, by the feebleness of the buccal cingulid in the lower molars and of the lingual cingulum in the upper third molar. They resemble *Ekembo* in the kind of dentine penetrance in the buccal cusps of the lower molars, in the occlusal outline of the M3/ (reduced hypocone and metacone as noted by MacLatchy & Cote, 2017) and the protoconid, hypoconid and hypoconulid of the m/3s are in line with each other, but the difference in cingular development rules out appurtenance to this genus. In addition, the upper canine differs from that of *Ekembo* by the lingual position and strength of the mesial groove, the expansive scoop-shaped distal surface of the crown and the apical wear.

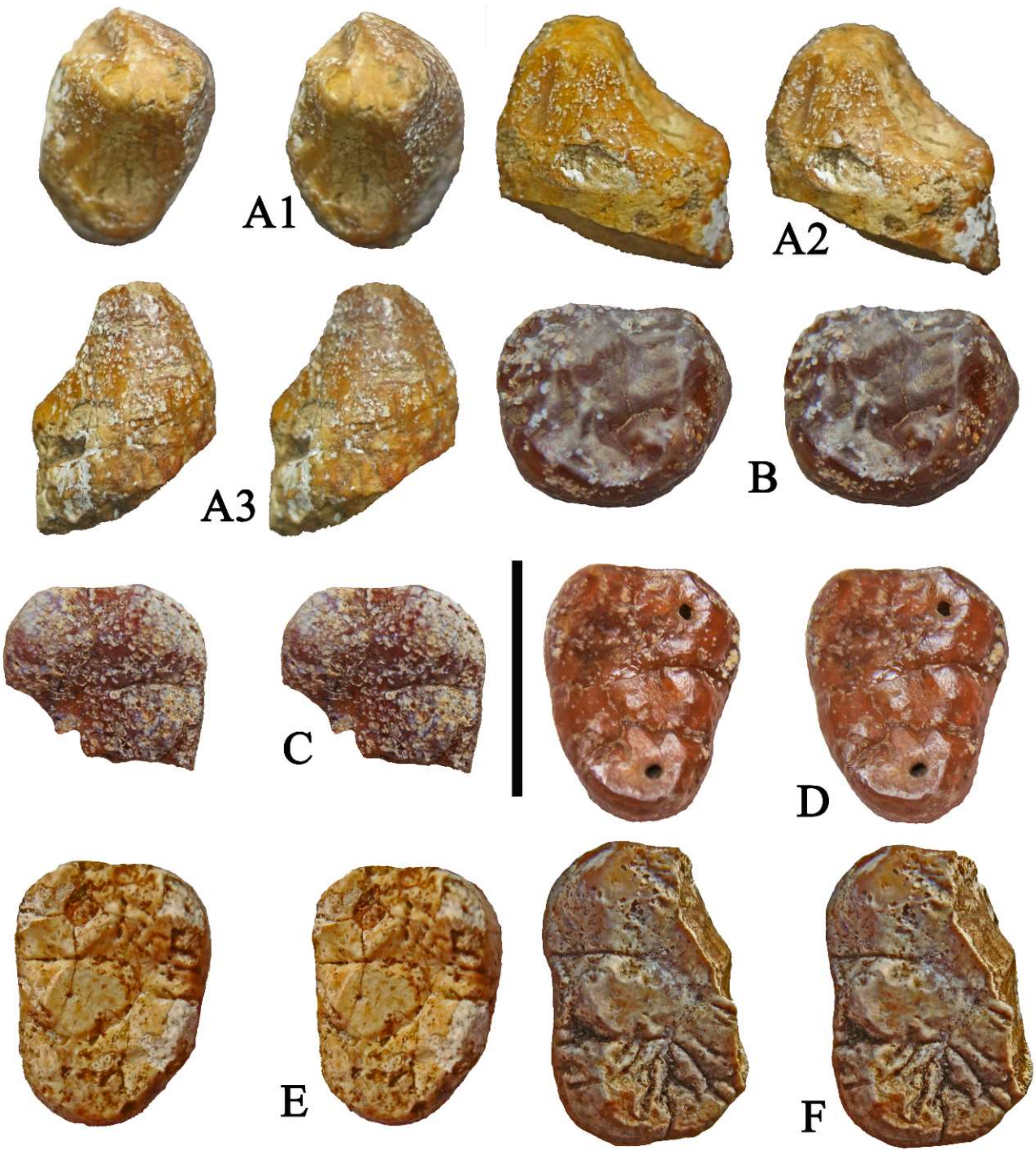

Figure 3. Genus and species indet. (medium-sized ape) from Bukwa II, Uganda. A) BUK II 37'10, left upper canine, (A1 - stereo occlusal view, A2 - stereo lingual view, A3 - stereo labial view); B) BUK II 18'11, left M3/, (stereo occlusal view); C) BUK II 2'10, right lower molar fragment (probably m/3) (stereo occlusal view); D) BUK II 17'11, right m/3, (stereo occlusal view); E) BUK II 43'11, left m/3, (stereo occlusal view); F) BUK II 1'11, left m/3 of a particularly large individual (stereo occlusal view) (scale : 10 mm).

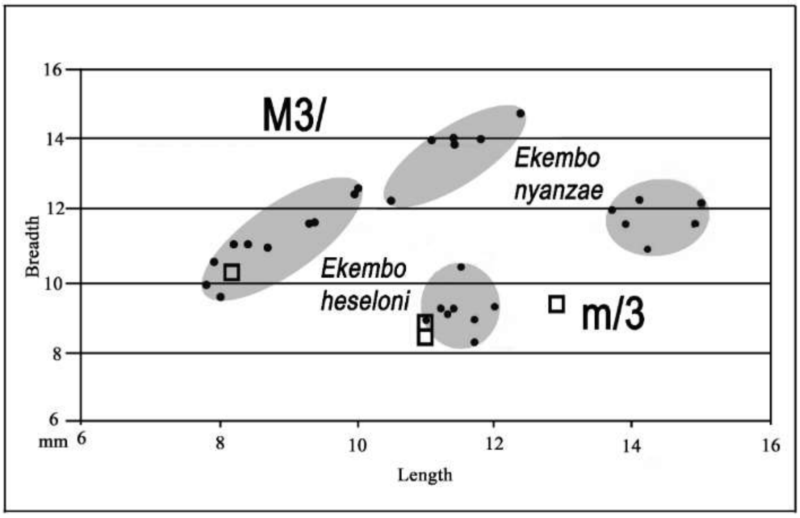

Figure 4. Bivariate plots of upper and lower third molars of *Ekembo* species from Rusinga Island (dots within grey ovals) and Genus and species indet. from Bukwa II (open squares). Apart from one specimen, the Bukwa material plots close to the lower end of the range of variation of *Ekembo heseloni* (Rusinga data from Pickford *et al*., 2009).

The Bukwa II teeth differ from those of *Kenyapithecus* Leakey, 1962, *Afropithecus* Leakey & Leakey, 1986a (we treat *Morotopithecus* Gebo *et al*., 1997 as a synonym of *Afropithecus*), *Mabokopithecus* Von Koenigswald, 1969, *Heliopithecus* Andrews & Martin, 1987, *Kamoyapithecus* Leakey, Ungar & Walker, 1995, *Nacholapithecus* Ishida *et al*., 1999 and *Equatorius* Ward *et al*., 1999, by the kind of dentine penetrance, suggestive of the presence of thinner enamel and taller dentinal horns in the Bukwa II teeth than in the above genera, but they approach them in the feebleness of the cingular structures. Two isolated teeth (P3/, M1/) from Fort Ternan, Kenya, were attributed to *Proconsul* sp. by Harrison (1992), but direct comparisons cannot be made with the Bukwa specimens because there are no tooth positions in common. However, some aspects of the morphology of the M1/ from Fort Ternan, approaches that of the M3/ from Bukwa – the relatively low cusps and thin enamel, and the presence of weak buccal cingular structure (not a full cingulum).

The m/3s from Bukwa II differ from the homologous tooth of *Otavipithecus* Conroy, Pickford, Senut & Mein, 1992, in which the hypoconulid in the m/3 is lingually positioned, not in line with the protoconid and hypoconid.

Comparisons of the teeth from Bukwa II with those of the European genus *Dryopithecus*, revealed some similarity in enamel thickness and dentine penetrance, but overall the differences in occlusal outline of the molars preclude appurtenance to this genus. Other Eurasian genera of medium-sized apes such as *Griphopithecus*, have thicker enamel and different molar occlusal outlines.

It is concluded that the Bukwa II medium-sized ape teeth belong to an undescribed genus and species, but we refrain from naming it, pending the recovery of a more informative sample.

DISCUSSION

Bukwa II, Uganda, has yielded 12 complete to sub-complete primate teeth and several fragments of teeth which are described herein. Two taxa are represented in the sample : A) «*Micropithecus*» *leakeyorum* slightly larger than *Limnopithecus legetet*, from which it differs in morphological details, but which is similar to specimens from Maboko (KNM MB 11660) and Majiwa attributed to *Micropithecus leakeyorum* by Harrison (1989) and to specimens from Kipsaraman, Kenya, attributed to *Limnopithecus* sp. by Pickford & Kunimatsu (2005), B) a medium-sized ape, three teeth of which plot at the lower end of the range of variation of *Ekembo heseloni* from Rusinga, and one of which (a large m/3) is intermediate in dimensions between *Ekembo heseloni* and *Ekembo nyanzae* (Fig. 4). The latter teeth could belong to the same genus and species as a poorly known taxon from Fort Ternan, previously identified as *Proconsul* sp. by Harrison (1992).

Harrison (2010) reviewed the history of interpretation of small ape fossils from Kenya and Uganda, which has become incredibly complicated. There has been repeated shuffling of specimens between species, and there has been the age-old matter of lumping versus splitting, which is further complicated by the lack of association between upper and lower dentitions. The latter problem, for example, affected the species *Lomorupithecus harrisoni* Rossie & MacLatchy, 2006 : the mandible included in the species was re-interpreted by Harrison (2010) to belong to *Micropithecus clarki*. In fact, this mandible is close to the type specimen of *Limnopithecus legetet* (see Pickford *et al*., 2010) but differs significantly from KNM KO 8, a mandible which for many years has been erroneously attributed to *Limnopithecus legetet*. The taxonomic identification of the Bukwa II and Kipsaraman small ape requires a more complete fossil record before it can be resolved. Pending this, we refer it to «*Micropithecus*» *leakeyorum*, noting similarities to material from Kipsaraman identified as *Limnopithecus* sp. by Pickford & Kunimatsu (2005) which could well represent the same species.

Whatever its taxonomic attribution turns out to be, the small ape species from Bukwa II indicates affinities with the sites of Maboko, Majiwa and Kipsaraman, Kenya, which are all Middle Miocene (Faunal Set III, Kipsaraman is ca 14.5 Ma according to Pickford & Kunimatsu, 2005). None of the primate specimens from Bukwa II shows affinities with the diverse fauna from Napak, Uganda (Pickford *et al*., 2010) nor with those from Koru, Chamtwara and Legetet in Kenya (Harrison, 1982) all of which are arranged in Faunal Set I (Pickford, 1981) and resemblances to apes from Faunal Set II, such as *Ekembo*, are weak, although the Bukwa II taxon might have descended from an *Ekembo*- or *Proconsul*-like precursor.

CONCLUSIONS

Bukwa II has yielded two taxa of Hominoidea : one small ape («*Micropithecus*» *leakeyorum*) and one medium-sized ape of undetermined taxonomic status representing an undescribed genus and species. The small ape from Bukwa has affinities with a species from Maboko and Kipsaraman, Kenya, suggesting that Bukwa correlates to Faunal Set IIIb (i.e. Middle Miocene : Ogg *et al*. 2016). The data suggests that Bukwa II is likely to be younger than Rusinga Island (17.8 Ma) but older than, or similar in age to, Kipsaraman (14.5 Ma). Overall, the fauna from Bukwa II indicates that the age of the deposits is most likely ca 16 Ma.

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REFERENCES

Andrews, P.J., 1974 - New species of *Dryopithecus* from Kenya. *Nature*, **249**: 188-196, 680.

Andrews, P.J., 1978 - A revision of the Miocene Hominoidea of East Africa. *Bulletin of the British Museum of Natural History (Geology)*, **30**: 85-224.

Andrews, P.J. & Martin L.B., 1987 - The phyletic position of the Ad Dabtiyah hominoid. *Bulletin of the British Museum (Natural History), Geology*, **41**: 383-393.

Andrews, P. & Simons, E., 1977 - A new Miocene gibbon-like genus, *Dendropithecus* (Hominoidea, Primates) with distinctive postcranial adaptations: Its significance to origin of Hylobatidae. *Folia Primatologica*, **28**: 161-169.

Andrews, P. & Walker, A., 1976 - The Primate and other fauna from Fort Ternan, Kenya. *In*: G.L. Isaac & E.R. McCown (Eds) *Human Origins : Louis Leakey and the East African Evidence.* Menlo, W.A.Benjamin, pp. 279-304.

Conroy, G.C., Pickford, M., Senut, B., Van Couvering, J. & Mein, P., 1992 - *Otavipithecus namibiensis*, first Miocene hominoid from southern Africa. *Nature*, **356**: 144-148

Cote, S., Mugume, A., Kityo, R., Kingston, J. & MacLatchy, L., 2017 - New fossil primate remains from Bukwa, Eastern Uganda. *5th EAQUA Workshop, Mukono, Uganda*, 4-7 July, 2017, Decades of Quaternary Research in East Africa : Implication for Sustainable Development, Conference Booklet, pp. 31-32.

Fleagle, J. & Simons, E., 1978 - *Micropithecus clarki*, a small ape from the Miocene of Uganda. *American Journal of Physical Anthropology*, **49**: 427-440.

Gebo, D.L., MacLatchy, L., Kityo, R., Deino, A., Kingston, J. & Pilbeam, D., 1997 - A hominoid genus from the early Miocene of Uganda. *Science*, **276**: 401-404.

Geraads, D., McCrossin, M. & Benefit, B., 2012 - A new Rhinoceros, *Victoriaceros kenyensis* gen. et sp. nov., and other Perissodactyla from the Middle Miocene of Maboko, Kenya. *Journal of Mammalian Evolution*, **19**: 57-75.

Gray, J.E., 1825 - Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. *Annals of Philosophy*, **10**: 337-344.

Harrison, T., 1982 - *Small-bodied Apes from the Miocene of East Africa*. Unpublished PhD Dissertation, University of London, 647 pp.

Harrison, T., 1986 - New fossil anthropoids from the middle Miocene of East Africa and their bearing on the origin of the Oreopithecidae. *American Journal of Physical Anthropology*, **71**: 265-284.

Harrison, T., 1988 - A taxonomic revision of the small catarrhine primates from the early Miocene of East Africa. *Folia Primatologica*, **50**: 59-108.

Harrison, T., 1989 - A new species of *Micropithecus* from the middle Miocene of Kenya. *Journal of Human Evolution*, **18**: 537-557.

Harrison, T., 1992 - A reassessment of the taxonomic and phylogenetic affinities of the fossil catarrhines from Fort Ternan, Kenya. *Primates*, **33**: 501-522.

Harrison, T., 2010 - Dendropithecoidea, Proconsuloidea, and Hominoidea. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, Los Angeles, London. University of California Press, pp. 429-469.

Hopwood, A.T., 1933 - Miocene primates from Kenya. *Journal of the Linnaean Society, Zoology*, **38**: 437-464.

Ishida, H., Kunimatsu, Y., Nakatsukasa, M. & Nakano Y., 1999 - New hominoid genus from the middle Miocene of Nachola, Kenya. *Anthropological Science*, **107**: 189-191.

Le Gros Clark, W.E. & Leakey, L.S.B., 1950 - Diagnoses of East African Miocene Hominoidea. *Quarterly Journal of the Geological Society of London*, **105**: 260-263.

Le Gros Clark, W.E. & Leakey, L.S.B., 1951 - The Miocene Hominoidea of East Africa. *Fossil Mammals of Africa*, **1**: 1-117.

Leakey, L.S.B., 1962 - A new lower Pliocene fossil primate from Kenya. *Annals and Magazine of Natural History*, series 13, **4**: 689-696.

Leakey, R.E & Leakey, M.G., 1986a - A new Miocene hominoid from Kenya. *Nature* **324**: 143-146.

Leakey, R.E. & Leakey, M.G., 1986b - A second new Miocene hominoid from Kenya. *Nature*, **324**: 146-148.

Leakey, R.E. & Leakey, M.G., 1987 - A new Miocene small-bodied ape from Kenya. *Journal of Human Evolution*, **16**: 369-387.

Leakey, M.G., Ungar, P.S. & Walker, A., 1995 - A new genus of large primate from the late Oligocene of Lothidok, Turkana District, Kenya. *Journal of Human Evolution*, **28**: 519-531.

MacLatchy, L. & Cote, S., 2017 - Mixing and matching "endemic" primate taxa: A distinct combination of Catarrhine Primates from an Early Miocene site at Bukwa, Uganda. *Society of Vertebrate Paleontology, 77th Annual Meeting, Calgary, Abstracts of Papers*, pp. 155-156.

McNulty, K.P., Begun, D.R., Kelley, J., Manthi, F.K. & Mbua, E.N., 2015 - A systematic revision of *Proconsul* with the description of a new genus of early Miocene hominoid. *Journal of Human Evolution*, **84**: 42-61.

Mwanja, R., Musiime, E., Musalizi, S., Senut, B., Gommery, D., Ségalen, L. Pickford, M., 2017 - A brief history of the Early and Middle Miocene fossil sites at Bukwa, Uganda : discovery, research, protection. *Geo-Pal Uganda*, **11**: 1-11.

Ogg, J.G., Ogg, G.M. & Gradstein, F.M., 2016 - *A Concise Geologic Time Scale 2016*, Elsevier, 240 pp.

Pickford, M., 1981 - Preliminary Miocene mammalian biostratigraphy for western Kenya. *Journal of Human Evolution*, **10**: 73-97.

Pickford, M., 1985 - A new look at *Kenyapithecus* based on recent collections from Western Kenya. *Journal of Human Evolution*, **14**: 113-143.

Pickford, M., 1986 - Sexual dimorphism in *Proconsul*. *Human Evolution*, **1**: 111-148.

Pickford, M., 1998 - Dating of the Neogene Old World anthropoid fossil record: essential base for phylogenetic analysis, biogeography and palaeoecology. *Primatologie*, **1**: 27-92.

Pickford, M., 2002 - Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda. *Comptes Rendus Palevol*, **1**: 213-219.

Pickford, M. & Kunimatsu, Y., 2005 - Catarrhines from the Middle Miocene (ca. 14.5 Ma) of Kipsaraman, Tugen Hills, Kenya. *Anthropological Science*, **113**: 189-224.

Pickford, M., Musalizi, S., Senut, B., Gommery, D. & Musiime, E., 2010 - Small apes from the Early Miocene of Napak, Uganda. *Geo-Pal Uganda*, **3**: 1-111.

Pickford, M., Senut, B., Gommery, D. & Musiime, E., 2003 - New catarrhine fossils from Moroto II, early middle Miocene (ca 17.5 Ma) Uganda. *Comptes Rendus Palevol*, **2**: 649-662.

Pickford, M., Senut, B., Gommery, D. & Musiime, E., 2009 - Distinctiveness of *Ugandapithecus* from *Proconsul*. *Estudios geologicos*, **65** (**2**): 183-241.

Rossie, J.B. & MacLatchy L., 2006 - A new pliopithecoid genus from the early Miocene of Uganda. *Journal of Human Evolution*, **50**: 568-586.

Senut, B., Pickford, M., Gommery, D. & Kunimatsu, Y., 2000 - A new genus of Early Miocene hominoid from East Africa: *Ugandapithecus major* (Le Gros Clark & Leakey, 1950). *Comptes Rendus de l'Académie des Sciences, Paris*, **331**: 227-233.

Von Koenigswald, G.H.R., 1969 - Miocene Cercopithecoidea and Oreopithecoidea from the Miocene of East Africa. *In*: Leakey L.S.B. (Ed.) *Fossil Vertebrates of Africa*, vol. 1. Academic Press, London, pp. 39-52.

Walker, A., 1968 - The lower Miocene fossil site of Bukwa, Sebei. *Uganda Journal*, **32** (**2**): 149-156.

Walker, A., 1969 - Fossil mammal locality on Mount Elgon, eastern Uganda. *Nature*, **223**: 591-593.

Walker, A., Teaford, M.F., Martin, L. & Andrews, P., 1993 - A new species of *Proconsul* from the early Miocene of Rusinga/Mfangano Islands, Kenya. *Journal of Human Evolution*, **25**: 43-56.

Ward, S., Brown, B., Hill, A., Kelley, J. & Downs, W., 1999 - *Equatorius*: A new hominoid genus from the middle Miocene of Kenya. *Science*, **285**: 1382-1386.

Bukwa II Rhinocerotidae

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ABSTRACT

Rhinocerotid teeth and a talus from Bukwa II, Uganda, were described in the late 1960's and early 1970's and eventually attributed to two species, *Chilotheridium pattersoni* and *Brachypotherium heinzelini*. The fossils housed in the Uganda Museum, Kampala suggest that there are indeed two species at the site, but one is attributed to Elasmotheriinae by Geraads (2010) and Geraads *et al*., (2012), the other representing the genus *Brachypotherium*. The material is re-illustrated and its biochronological and palaeoenvironmental implications examined.

Key Words : Uganda, Middle Miocene, Rhinocerotidae, Elasmotheriinae, *Victoriaceros*, *Brachypotherium*

INTRODUCTION

Rhinocerotid teeth were the first fossil specimens from Bukwa II to be illustrated (Walker, 1968). They were initially attributed to *Chilotherium* by Walker (1969) (Fig. 1) but were soon transferred to *Chilotheridium pattersoni* by Hooijer (1971) when he described that species. Hooijer (1973) identified an incomplete talus from Bukwa as *Brachypotherium heinzelini*, and attributed an m/2 from the site to the same species (length – 59 mm, anterior breadth – 36 mm, posterior breadth – 38 mm). The latter tooth is not in the collection of the Uganda Museum.

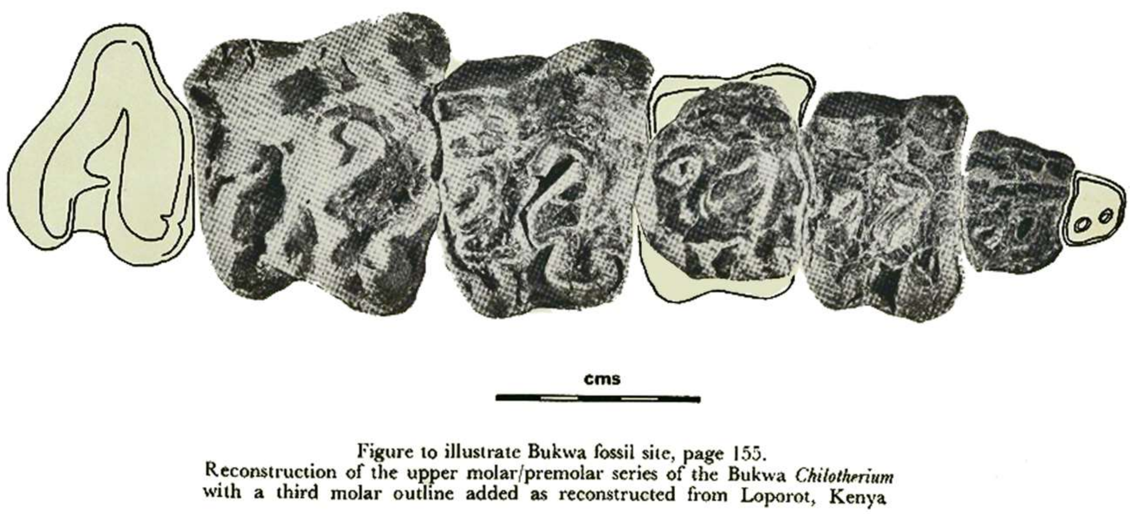

Figure 1. Reconstructed right upper cheek tooth row of the Bukwa II Rhinocerotidae published by Walker (1968) (image modified from the Uganda Journal). The whereabouts of the M2/ are unknown, although a cast is curated in the National Museum of Kenya, Nairobi. The other teeth are in Kampala (Table 1, Fig. 2).

Geraads (2010) summarised the fossil record of rhinocerotids in Africa, and considered that the Bukwa II fossils were more likely to belong to an Elasmotheriinae than to *Brachypotherium* or *Chilotheridium*.

Later, he and others (Geraads *et al*., 2012) erected the new genus and species *Victoriaceros kenyensis* on the basis of material from Maboko, Kenya, and mentioned that the species was similar to the upper teeth from Bukwa II described by Walker (1968) and Hooijer (1966, lapsus for 1973).

SYSTEMATIC DESCRIPTIONS

Family Rhinocerotidae Gray, 1821

Genus *Victoriaceros* Geraads *et al*., 2012

Species *Victoriaceros kenyensis* Geraads *et al*., 2012

Description and comments

The rhinocerotid upper teeth from Bukwa II are deeply worn, but the M1/ and M2/ retain details of the morphology of the protocone and hypocone, a tall ectoloph and the deeper parts of the medisinus and fossettes. The protocone has a somewhat flattened lingual part, marked in the M2/ by a vertical groove (Geraads *et al*., 2012) (Fig. 2E). The upper molars are hypsodont, which is one of the reasons why Hooijer (1971) included them in his taxon *Chilotheridium pattersoni*, but in this feaure the teeth are also close to *Victoriaceros*.

The lower cheek teeth from Bukwa II consist of two crescentic cusp complexes joined together close to the buccal side of the crown, making for a shallow buccal groove. There are traces of cementum in the buccal grooves, more marked in the posterior cheek tooth (G1 in Fig. 2). There is no sign of a buccal cingulid. These features, especially the presence of cementum, support the attribution of these lower teeth to *Victoriaceros kenyensis*.

Geraads *et al*., (2016) created a second species, *Victoriaceros hooijeri*, for material from Karungu, Kenya, which differs from the type species by the shallower dorsal concavity of the skull, laterally expanded nuchal crest, slightly inclined occiput and narrower nasals among other characters. None of these features can be evaluated in the Bukwa II specimens, but a dental character serves to demonstrate that the Bukwa II specimens do not belong to *Victoriaceros hooijeri*. It is the presence of a basal expansion of the hypocone towards the protocone on the molars, a feature which is absent in the Karungu species.

Table 1. Measurements (in mm) of the teeth of Rhinocerotidae from Bukwa II, Uganda

Tooth	Mesio-distal length	Bucco-lingual breadth
A (P4/)	25.6++	34.4++
B (P2/)	25.4	33.0
C (P3/)	40.1	57.2
D (M1/)	51.9	64.7
F (lower cheek tooth)	33.5	22.6
G (lower cheek tooth)	36.1	27.5
m/2 (Hooijer, 1973)	59	38

The upper and lower rhinocerotid teeth from Bukwa II illustrated in Figure 2 are confidently attributed to *Victoriaceros kenyensis* Geraads *et al*., 2012.

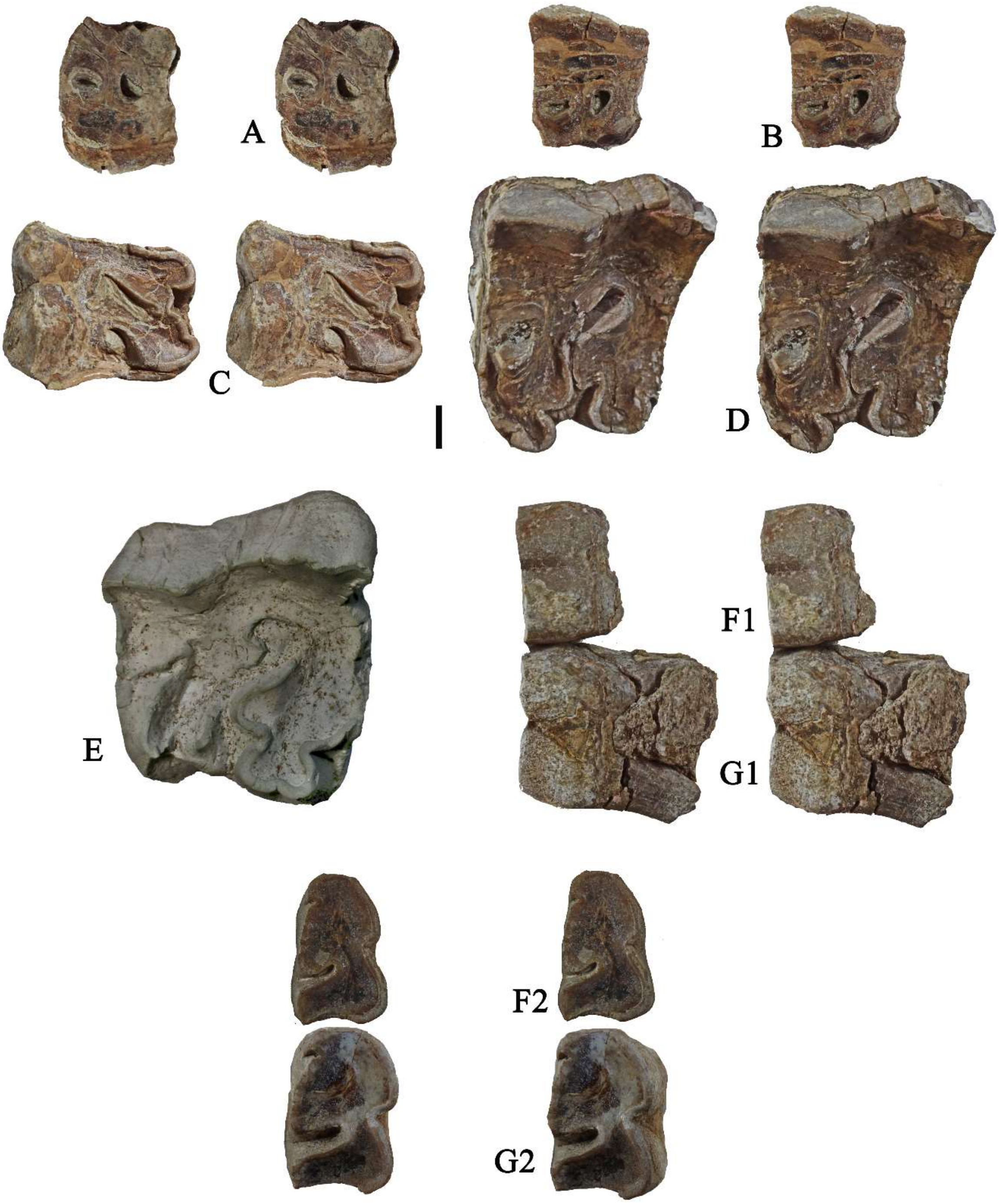

Figure 2. Rhinocerotidae teeth from Bukwa II, Uganda (stereo occlusal views except F1 and G1, which are stereo buccal views) A) right P4/, B) right P2/, C) right P3/, D) right M1/, E) cast of right M2/, F) right lower cheek tooth, G) right lower cheek tooth (Image 'E' courtesy of D. Geraads) (scale : 10 mm).

Genus *Brachypotherium* Roger, 1904

Description and comments

Hooijer (1973) attributed a talus and a lower molar from Bukwa II to *Brachypotherium heinzelini*. The collections in the Uganda Museum preserve a broken talus, but there is no sign of the lower molar mentioned by Hooijer (1973). The molar is reported to possess a buccal cingulid, which Hooijer (1973) considered to be a defining character of the genus *Brachypotherium*.

The talus from Bukwa II (Fig. 3) shows the extremely abbreviated navicular and cuboid portion typical of *Brachypotherium*. Thus although the evidence from Bukwa II is relatively poor, there does seem to be a rhinocerotid allied to *Brachypotherium* at the site.

Figure 3. BUK II/67, fragment of brachypothere talus from Bukwa II, Uganda (stereo tibial view) (scale : 5 cm).

DISCUSSION AND CONCLUSIONS

Geraads *et al*., (2012) erected the new genus and species *Victoriaceros kenyensis* for a comprehensive collection of rhinocerotid remains from the Middle Miocene deposits at Maboko Island, Kenya. These authors briefly discussed the Bukwa II upper molars and concluded that they were close to *Victoriaceros kenyensis*. From the same localities there is a restricted sample of fossils which agree with the short-footed rhinocerotid *Brachypotherium*.

The co-occurrence of *Victoriaceros kenyensis* and *Brachypotherium* at Bukwa II, supported herein, is repeated at Maboko, Kenya, inviting correlation. There has been discussion about the age of Maboko. Until 1981, Maboko was lumped into the so-called «Lower Miocene» of Western Kenya, but Pickford (1981) showed that the fauna from the site differed fundamentally from those of Karungu and Rusinga (which he arranged in Faunal Set II) and older sites such as Songhor and Napak (Faunal Set I). Thus Maboko was selected to be the core fauna for Faunal Set III, and the even younger fauna from Fort Ternan was selected to represent the core fauna for Faunal Set IV.

Geraads *et al*., (2012) discussed the dating of Maboko in detail, and concluded that it is most likely to be about 15 Ma, although an age of 16 Ma cannot be ruled out (Pickford, 1981) (i.e Middle Miocene : Ogg *et al*., 2016). The similarities between the rhino faunas from Maboko and Bukwa II, thus accord with a correlation of the latter site to Faunal Set III, although a precise age within the period of time spanned by this faunal set is difficult to tie down. The deposits at Bukwa are therefore concluded to be younger than those from Rusinga (17.8 Ma) but older than those of Fort Ternan (13.7 Ma).

The occurrence of a rhinocerotid at Bukwa II which possessed hypsodont cheek teeth endowed with cementum, which signifies that it was probably a grazing rhinoceros, accords with the presence of fossil grass at or near the site (Pickford, 2002).

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REFERENCES

Geraads, D., 2010 - Rhinocerotidae. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, University of California Press, Berkeley, pp. 669-683.

Geraads, D., Lehmann, T., Peppe, D.J. & McNulty, K.P., 2016 - New Rhinocerotidae from the Kisingiri localities (lower Miocene of Western Kenya). *Journal of Vertebrate Paleontology*, **36** (**3**): e1103247. doi:10.1080/02724634.2016.1103247.

Geraads, D., McCrossin, M. & Benefit, B., 2012 - A new Rhinoceros, *Victoriaceros kenyensis* gen. et sp. nov., and other Perissodactyla from the Middle Miocene of Maboko, Kenya. *Journal of Mammalian Evolution*, **19**: 57-75.

Gray, J.E., 1821 - On the natural arrangement of vertebrose animals. *London Medical Repository*, **15** (**1**): 296-310.

Hooijer, D.A., 1966 - Miocene rhinoceroses of East Africa. *Bulletin of the British Museum (Natural History) Geology*, **13**: 119-190.

Hooijer, D.A., 1971 - A new rhinoceros from the late Miocene of Loperot, Turkana District, Kenya. *Bulletin of the Museum of Comparative Zoology*, **142**: 339-392.

Hooijer, D.A., 1973 - Additional Miocene to Pleistocene rhinoceroses of Africa. *Zoologische Mededelingen*, **46**: 149-178.

Ogg, J.G., Ogg, G.M. & Gradstein, F.M., 2016 - *A Concise Geologic Time Scale 2016*, Elsevier, 240 pp.

Pickford, M., 1981 - Preliminary Miocene mammalian biostratigraphy for western Kenya. *Journal of Human Evolution*, **10**: 73-97.

Pickford, M., 2002 - Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda. *Comptes Rendus Palevol*, **1**: 213-219.

Roger, O., 1904 - Wirbelthierreste aus dem Obermiocän der bayerisch-schwabischen Hochebene. *Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg*, **36**: 1-22.

Walker, A., 1968 - The lower Miocene fossil site of Bukwa, Sebei. *Uganda Journal*, **32** (**2**): 149-156.

Walker, A., 1969 - Fossil mammal locality on Mount Elgon, eastern Uganda. *Nature*, **223**: 591-593.

Bukwa II Suiformes

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ABSTRACT

Bukwa II has yielded fossils belonging to three families of suiformes (Anthracotheriidae, Sanitheriidae and Suidae) but only one fossil has been described in detail in the scientific literature. The present article describes the remains of all three taxa from the site, revises the taxonomy and arrives at the conclusion that the deposits are considerably younger than previously thought, being ca 16 Ma (Middle Miocene).

Key Words : Uganda, Middle Miocene, Anthracotheriidae, Sanitheriidae, Suidae

INTRODUCTION

Fossil suiformes have been listed at Bukwa II on several occasions (Walker, 1968, 1969) but only one specimen, a sanithere tooth, has been illustrated, described and measured (Pickford, 1984).

Walker (1968, 1969) listed *Brachyodus aequatorialis* MacInnes, 1951, (?)*Hyoboops africanus* Andrews, 1914, *Diamantohyus africanus* Stromer, 1922, and (?)*Lystriodon* (sic) *jeanneli* Arambourg, 1933, at Bukwa II, but he provided no descriptions, measurements or figures. Van Couvering & Van Couvering (1976) modified the names in the list in order to comply with taxonomic revisions of African mammals current at the time: *Masritherium aequatorialis*, (?)*Brachyodus africanus*, *Bunolistriodon jeanneli*, *Xenochoerus africanus*, but they did not describe any of the material. From this these authors drew the conclusion that the Bukwa II fauna was as old as 23 Ma, the supposed age of the Karungu, Kenya, deposits, with which they compared the Ugandan fauna. However, none of the above identifications is correct.

Pickford (1984) described and illustrated a sanithere P4/ from Bukwa II, attributing the specimen to *Diamantohyus africanus* Stromer, 1922, and he later referred to the same tooth (Pickford, 2007). Subsequently, additional sanithere teeth were recognised in the Bukwa II collections, which reveal that, as an assemblage, the teeth are closer in morphology to specimens of *Diamantohyus nadirus* (Wilkinson, 1976) from Ombo and Kipsaraman, Kenya, than they are to teeth of *Diamantohyus africanus* from older strata.

Pickford (2007) attributed several suid teeth from Bukwa II to *Kenyasus namaquensis*, and estimated a basal Middle Miocene age (17.5 Ma) for the deposits.

The aim of this article is to describe the suiform fossils from Bukwa II. The revised suiform fauna from Bukwa II comprises three taxa, 1) cf *Brachyodus* sp. indet., 2) *Diamantohyus nadirus* and 3) *Hyotherium namaquense*, which means that it differs fundamentally from the older faunas from Rusinga, Karungu, Songhor and Napak, arranged in Faunal Sets I and II. There can be little doubt that Bukwa II correlates better with Kipsaraman, Maboko, Ombo, Nachola and other basal Middle Miocene localities arranged in Faunal Set III by Pickford (1981, 1998). As such the Bukwa II sediments are likely to be less than 17.5 Ma, probably ca 16 Ma (Middle Miocene : Ogg *et al*., 2016).

SYSTEMATIC DESCRIPTIONS

Order Artiodactyla Owen, 1848

Family Anthracotheriidae Gill, 1872

Genus cf *Brachyodus* Depéret, 1895

Species cf *Brachyodus* sp.

Description and comments

There are two fragments of upper teeth and a navicular from Bukwa II, which are attributed to a selenodont Anthracotheriidae (Fig. 1). The evidence is meagre, and does not permit confident identification at the generic level, although it is clear that the fossils do not belong to *Sivameryx*, *Afromeryx* or *Libycosaurus* (Pickford, 1991). By a process of elimination, this leaves *Brachyodus* as the most likely identification of the Bukwa fossils. However, the navicular is appreciably smaller than material attributed to *Brachyodus aequatorialis* MacInnes (1951). For this reason, the fossils from Bukwa II are provisionally identified as cf *Brachyodus* sp.

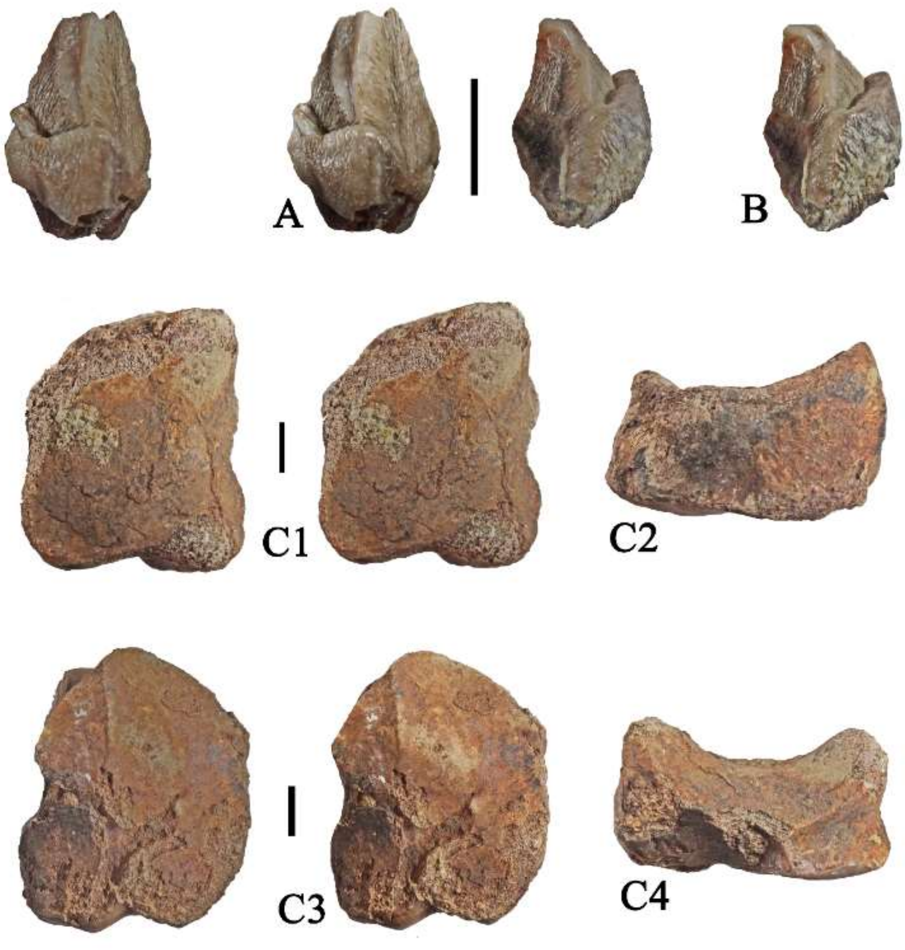

Figure 1. Anthracothere fossils from Bukwa II, Uganda, provisionally attributed to cf *Brachyodus* sp. indet. A) BUK II, fragment of upper premolar (stereo mesial view); B) fragment of upper tooth (stereo distal view); C) right navicular (C1 - stereo proximal view, C2 - medial view, C3 - stereo distal view, C4 - lateral view) (scales : 10 mm).

Family Sanitheriidae Simpson, 1945

Genus *Diamantohyus* Stromer, 1922

Species *Diamantohyus nadirus* (Wilkinson, 1976)

Description and comments

The p/4 of *Diamantohyus nadirus* has a metaconid which is as tall as, or taller than, the protoconid (Fig. 2), whereas in *Diamantohyus africanus* the metaconid is generally lower and less voluminous than the protoconid. The anterior cristid in the older species is sectorial whereas in the younger one it is swollen and puffy in appearance, as in the Bukwa specimen. Thus the Bukwa II fossil accords with the younger species, *Diamantohyus nadirus*.

A d/4 from Bukwa II (BUK II 67, Fig. 2) has somewhat more puffy cusps than those of *Diamantohyus africanus* from Namibia and Kenya (Pickford, 2004). It shows a clear root beneath the protoconid (Pickford, 2017).

The P4/ from Bukwa II, previously attributed to *Diamantohyus africanus* (Pickford, 1984) is similar to specimens of *Diamantohyus nadirus* from Nachola (Pickford & Tsujikawa, 2005) and Kipsaraman (Pickford, 2004) in particular by the more swollen crista which traverses the distal fovea of the crown (Fig. 2), a crest which is weaker and discontinuous in *Diamantohyus africanus* (Pickford, 2008).

Four teeth from Bukwa II belong to the family Sanitheriidae. One of them, UMP 68-01 was described by Pickford (1984). Two other teeth were collected by Walker (1968) while personnel from the Uganda Museum collected a specimen in 2011 during an administrative visit to the site. Pickford (2007) described good sanithere material from Kipsaraman, Kenya, which was attributed to *Diamantohyus nadirus* (Wilkinson, 1976). Examination of the additional specimens from Bukwa II indicates that they are closer morphologically to fossils from Kipsaraman, Nachola and Ombo, than to the Early Miocene species *Diamantohyus africanus* (Pickford & Tsujikawa, 2005).

The two species *Diamantohyus africanus* and *Diamantohyus nadirus* are similar in dimensions, the differences between the species residing in the more complicated dental morphology in the younger species. Continuation of this trend towards increasing molar complexity resulted in the evolution of the genus *Sanitherium*, best known from Middle Miocene deposits in Europe and the Indian Sub-Continent (Pickford, 1984).

For these reasons, the Bukwa II sanithere fossils are attributed to the species *Diamantohyus nadirus*, which is typically found in Faunal Set IIIb (Ombo, Kipsaraman, Nachola).

Table 1. Measurements (in mm) of the teeth of *Diamantohyus nadirus* from Bukwa II, Uganda.

Catalogue N°	Tooth	Mesio-distal length	Bucco-lingual breadth
UMP 68-01	P4/ left	7.7	8.1
BUK II 67	d/4 left	13.0	5.6
BUK II/6	p/4 right	10.2	5.9
BUK II 2'11	Lower molar, right	10.3	5.8

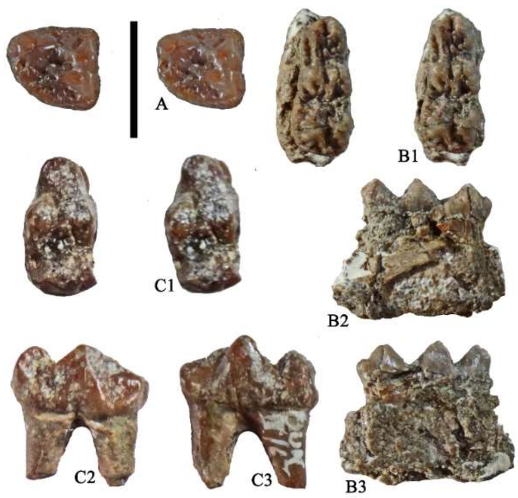

Figure 2. *Diamantohyus nadirus* from Bukwa II, Uganda. A) BUK II 68-01, left P4/, stereo occlusal view; B) BUK II 67, left d/4 (B1 - stereo occlusal view, B2 - buccal view, B3 - lingual view); C) BUK II/6, right p/4 (C1 - stereo occlusal view, C2 - buccal view, C3 - lingual view) (scale : 10 mm).

Family Suidae Gray, 1821

Genus *Hyotherium* Von Meyer, 1834

Species *Hyotherium namaquense* (Pickford & Senut, 1997)

Description and comments

Eleven suid teeth and three post-cranial bones from Bukwa II (Fig. 3) represent a medium-sized species of suid, larger than *Nguruwe kijivium* (Wilkinson, 1976) and *Kenyasus rusingensis* Pickford, 1986, but smaller than *Libycochoerus jeanneli* (Arambourg, 1933). The material closely matches the species *Hyotherium namaquense* from Namaqualand, South Africa (Pickford & Senut, 1997) which is best known from Kipsaraman, Kenya (Pickford, 2007). There is no sign of the presence of *Listriodon jeanneli* at Bukwa II, contra the provisional identification by Walker (1968).

The suid M3/ from Bukwa II (BUK II 20’97) is unworn. The main cusps are voluminous, with weakly expressed Furchen and the accessory cusplets are tall and swollen. The mesial cingulum is broad and beaded, and the hypoconule is centrally positioned. This combination of characters accords with the holotype of the species from Namaqualand (Pickford & Senut, 1997) and informative specimens from Kipsaraman, Kenya (Pickford, 2007).

BUK II 2’98 is a suid P3/ which closely resembles specimens from Kipsaraman (Pickford, 2007). The disto-lingual cusp is relatively smaller than in specimens of *Hyotherium medium* from Europe, but the overall impression is that this tooth is close to that species. The distal half of a P2/ (BUK II 9’11) is morphologically close to specimens of *Hyotherium medium* from Sandelzhausen, Germany (Pickford, 2016).

Two unworn lower molars from Bukwa II (BUK II 21'97 and BUK II 27’10) are highly informative, and reveal close similarities to European *Hyotherium medium*. The most telling feature of these teeth is the presence of strong, vertical postcristids on the posterior surface of the protoconid and metaconid, separated from the respective endocristids by open grooves, the four cristids forming a clear M-structure on the posterior face of the anterior lophid. These cristids are beaded as in fossils from Europe (Pickford, 2016) (Fig. 3, 4).

For the sake of completeness, a lower incisor (BUK II 3'10), a broken P4/ (UMP 68-02) and a damaged lower molar (BUK II 19'11) of the same species of suid are illustrated and measurements provided (Fig. 3).

Table 2. Measurements (in mm) of the teeth of *Hyotherium namaquense* from Bukwa II, Uganda.

Catalogue N°	Tooth	Mesio-distal length	Bucco-lingual breadth
BUK II 9'11	P2/ left broken	--	7.4
BUK II 2'98	P3/ right	14.8	10.1
UMP 68-02, BUK II	P4/ right broken	--	12.0e
BUK II 3'11	M1/ right	11.8	9.5e
BUK II 20'97	M3/ right	20.0	15.7
BUK II 3'10	i/2 right	--	5.1
BUK II 19'11	molar fragment	--	8.6
BUK II 4'10	m/1 fragment	--	10.6
BUK II 5'10	m/2 fragment	--	12.0
BUK II 21'97	m/2 left	16.0	13.2
BUK II 27'10	m/2 left	16.6	13.2

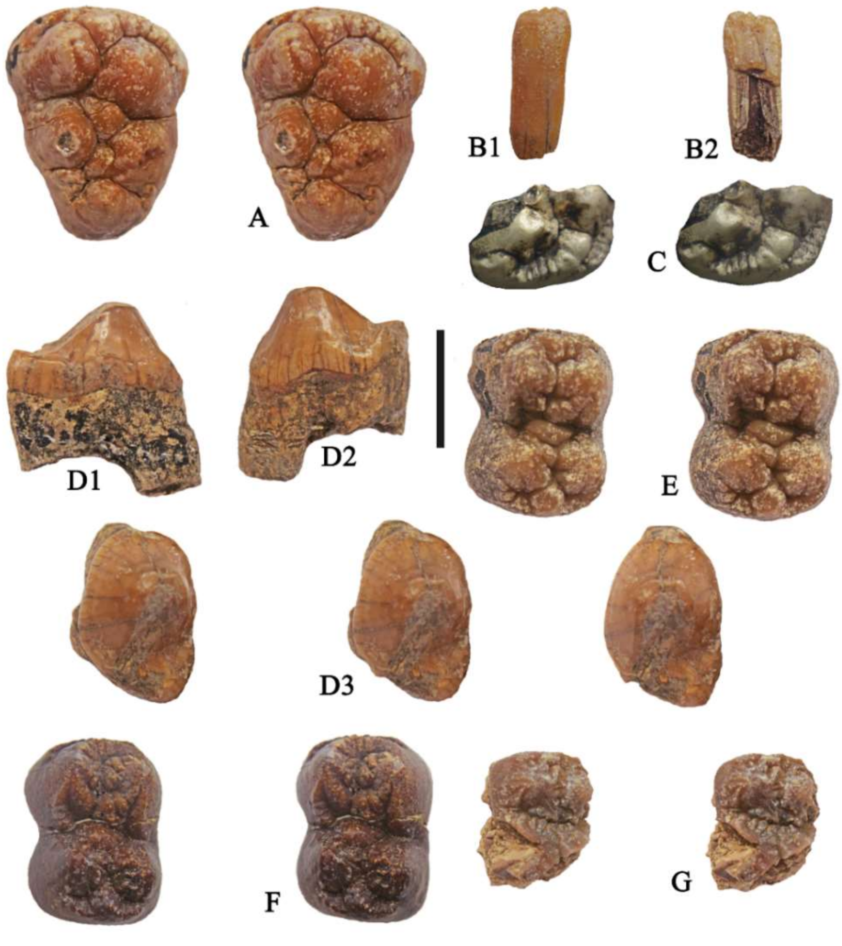

Figure 3. *Hyotherium namaquense* from Bukwa II, Uganda. A) BUK II 20'97, right M3/ (stereo occlusal view); B) BUK II 3'10, right i/2 (B1 - labial, B2 - lingual views); C) UMP 68.02, fragment of right P4/ (stereo occlusal view); D) BUK II 2'98, right P3/ (D1 - lingual, D2 - buccal, D3 - stereo occlusal views); E) BUK II 21'97, left m/2 (stereo occlusal view) F) BUK II 27'10, left m/2 (stereo occlusal view) G) BUK II 19'11, damaged molar tentatively attributed to this species (stereo occlusal view) (scale : 10 mm).

***Hyotherium medium* from Europe (MN 5, basal Middle Miocene)**

Of all the Eurasian suids, *Hyotherium medium* Von Meyer, 1841, is morphometrically closest to *Hyotherium namaquense*, so much so, that the two species are likely to be close in age and phylogenetically, the African form having diverged slightly from the European species from which it likely descended. A distinguishing feature of *Hyotherium medium* is the presence of postcristids on the rear surface of the protoconid and metaconid of the lower molars, located at the buccal and lingual margins of the cusps respectively (Fig. 4). These cristids are swollen and almost vertical, separated from the corresponding endocristids of the same cusps by prominent grooves. The complex of cristids thus formed, makes an M-shaped structure, similar in some respects to the M-structure in the lower molars of tragulids. The lower parts of the post-cristids are beaded in both the African and European species.

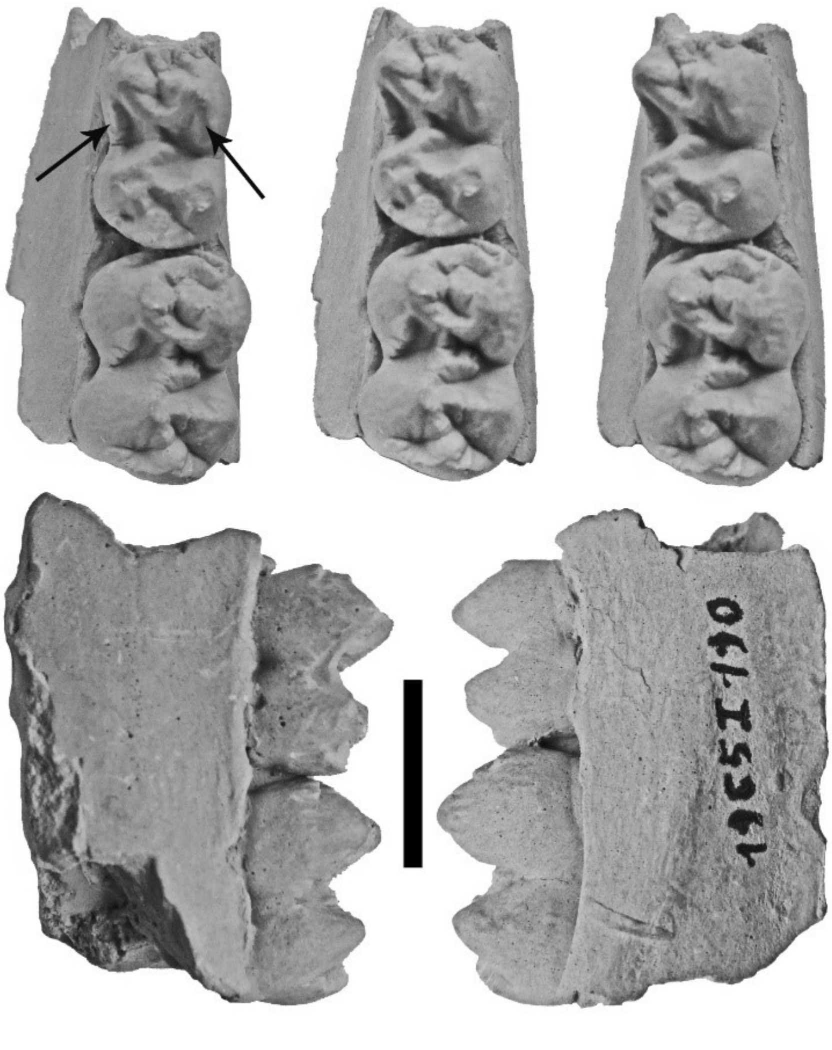

Figure 4. *Hyotherium medium*, cast of a left mandible with m/1-m/2 from Marbas (Maritsa Basin) Plovdiv, Bulgaria. A) Stereo occlusal views, B) buccal view, C) lingual view. The arrows show the post-cristids and the M-structure on the rear surface of the mesial lophid (scale : 10 mm).

Suid post-cranial bones from Bukwa II

Three post-cranial elements from Bukwa II, are attributed to *Hyotherium namaquense* on the basis of their morphology and dimensions, which are compatible with the dental remains from the same site (Fig. 5). A talus is similar to specimens of *Hyotherium medium* from Sandelzhausen, Germany (Van der Made, 2010) as are a distal metapodial pulley and a distal tibia (Table 3).

Table 3. Measurements (in mm) of postcranial bones of *Hyotherium namaquense* from Bukwa II, Uganda.

Catalogue N° / Bone	Anatomy	Measurement
BUK II, talus left	Length external	31.8
BUK II, talus left	Length internal	30.0
BUK II, talus left	Breadth proximal	14.2
BUK II, talus left	Breadth distal	15.5
BUK II 13'97, distal tibia	Breadth talar facet	ca 15
BUK II 13'97, distal tibia	Total breadth	20.5
BUK II 13'97, distal tibia	Height	16.0

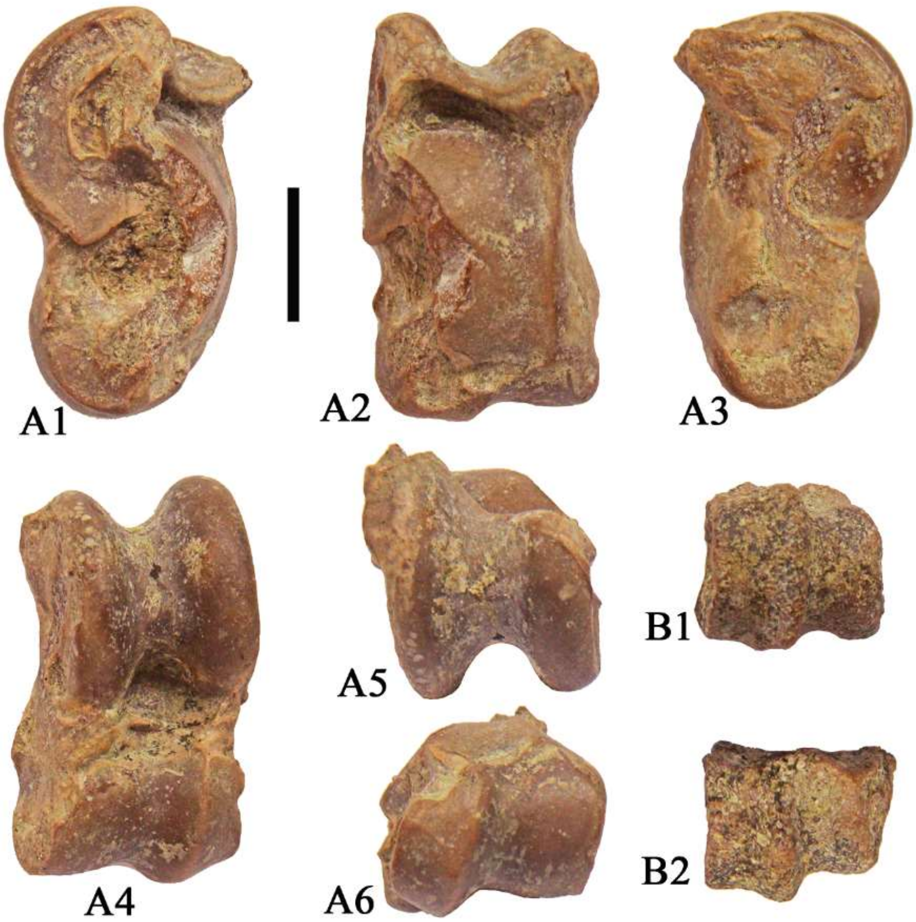

Figure 5. *Hyotherium namaquense* from Bukwa II, Uganda, A) left talus (A1 - lateral (external) view, A2 - caudal view, A3 - medial (internal) view, A4 - cranial view, A5 - proximal view, A6 - distal view); B), BUK II, distal epiphysis of metapodial (B1 - distal view, B2 - dorsal view) (scale : 10 mm).

DISCUSSION

Hyotherium namaquense was previously attributed to the genus *Kenyasus* by Pickford (2007) but new comparisons were made possible by the discovery of the type series of *Hyotherium medium* from Mösskirch housed in the Fürstlich Fürstenbergische Sammlung, Donaueschingen, Germany (Pickford, 2016). Subsequently, a cast of a mandible fragment of this species from Marbas (Maritsa Basin), Plovdiv, Bulgaria, containing unworn m/1 and m/2, was studied at the BSPG Munich, which revealed that the European and African species are close in morphology and dimensions, and that continued attribution of the African species to *Kenyasus* is no longer tenable. This taxonomic revision leaves

Kenyasus rusingensis (Pickford, 1986) as the sole species in the genus. In Europe, *Hyotherium medium* is a characteristic suid found only in deposits correlating to Land Mammal Zone MN 5 (basal Middle Miocene).

GENERAL DISCUSSION

The palustral deposits at Bukwa II, Uganda, have yielded three suiforms : an anthracothere, a sanithere and a suid. The anthracothere is allied to *Brachyodus*, but a confident identification of the species is not possible with the available fossils. The sanithere and the suid, in contrast, are well-enough represented to provide confident species determination, *Diamantohyus nadirus* and *Hyotherium namaquense* respectively. The latter two taxa are characteristic of Faunal Set III in East Africa, indicating that the deposits are younger than those of Rusinga (Faunal Set II) : an age of 16 Ma or younger is probable for Bukwa II, but the deposits are not as young as Fort Ternan (13.7 Ma, Faunal Set IV, Pickford *et al*., 2006). Furthermore, the resemblances between *Hyotherium namaquense* and *Hyotherium medium* from Europe are striking, and the two species are likely closely similar in age. *Hyotherium medium* is characteristic of European Land Mammal Zone MN 5, which is at the base of the Middle Miocene. From this we conclude that the Bukwa II deposits correlate to the base of the Middle Miocene rather than to the Early Miocene, as was thought by many reseachers for the past half century.

CONCLUSIONS

The suiform fauna from Bukwa II, Uganda, is restricted but is nevertheless highly informative about the age of the deposits. The combination of *Diamantohyus nadirus* and *Hyotherium namaquense* indicates correlation to East African Faunal Set III (more specifically to FS IIIb) and to European Land Mammal Zone MN 5, which correlates to the Middle Miocene (Ogg *et al*. 2016). An age of ca 16 Ma is indicated for Bukwa II.

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I thank the Uganda National Council for Science and Technology for authorisation to carry out research in the country and the Uganda Museum for an excavation permit. Particular thanks to Mrs Rose Mwanja (Commissioner, Uganda Museum) and Ms Sarah Musalizi (Curator of Palaeontology, Uganda Museum) and her predecessor Mr Ezra Musiime, for access to fossils in their care. The Uganda Palaeontology Expedition was supported by the Commission des Fouilles, the Collège de France, and the Muséum National d'Histoire Naturelle.

REFERENCES

Andrews, C.W., 1914 - On the lower Miocene vertebrates from British East Africa, collected by Dr Felix Oswald. *Quarterly Journal of the Geological Society of London*, **70**: 163-186.

Arambourg, C., 1933 - Mammifères miocènes du Turkana, Afrique orientale. *Annales de Paléontologie*, **22**: 121-148.

Depéret, C., 1895 - Über die Fauna von miocänen Wirbelthieren aus der ersten Mediterranstufe von Eggenburg. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch - Naturwissenchaftliche Klasse. Abteilung 1, Mineralogie, Biologie, Erdkunde*, **104 (4)**: 395-416.

Gill, T., 1872 - Arrangement of the families of mammals with analytical tables. *Smithsonian Miscellaneous Collection*, Volume **11,** article **1**, pp. i-vi, 1-98**.**

Gray, J.E., 1821 - On the natural arrangement of vertebrose animals. *London Medical Repository*, **15** (**1**): 296-310.

MacInnes, D.G., 1951 - Miocene Anthracotheriidae from East Africa. *Fossil Mammals of Africa*, **4**: 1-24.

Ogg, J.G., Ogg, G.M. & Gradstein, F.M., 2016 - *A Concise Geologic Time Scale 2016*, Elsevier, 240 pp.

Owen, R., 1848 - Description of teeth and portions of jaws of two extinct anthracotheroid quadrupeds

(*Hyopotamus vectianus* and *H. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight. *Quarterly Journal of the Geological Society of London*, **4**: 104-141.

Pickford, M., 1981 - Preliminary Miocene mammalian biostratigraphy for western Kenya. *Journal of Human Evolution*, **10**: 73-97.

Pickford, M., 1984 - A revision of the Sanitheriidae (Suiformes, Mammalia). *Geobios*, **17**: 133-154.

Pickford, M., 1986 - A revision of the Miocene Suidae and Tayassuidae of Africa. *Tertiary Research Special Paper*, **7**: 1-83.

Pickford, M., 1991 - Revision of the Neogene Anthracotheriidae of Africa. *In*: Salem, M.J. (Ed.) *The Geology of Libya*, Volume **4**: 1491-1525. Amsterdam, Elsevier.

Pickford, M., 1998 - Dating of the Neogene Old World anthropoid fossil record: essential base for phylogenetic analysis, biogeography and palaeoecology. *Primatologie*, **1**: 27-92.

Pickford, M., 2004 - Miocene Sanitheriidae (Suiformes, Mammalia) from Namibia and Kenya: systematic and phylogenetic implications. *Annales de Paléontologie*, **90**: 223-278.

Pickford, M., 2007 - Suidae and Hippopotamidae from the Middle Miocene of Kipsaraman, Kenya, and other sites in East Africa. *Paleontological Research*, **11**: 85-105.

Pickford, M., 2008 - Early Miocene Sanitheriidae from the northern Sperrgebiet, Namibia. *Memoir of the Geological Survey of Namibia*, **20**: 365-386.

Pickford, M., 2016 - Revision of European Hyotheriinae (Suidae) and Doliochoeridae. *Münchener Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie*, **44**: 1-270.

Pickford, M., 2017 - New evidence concerning relationships within Artiodactyla, Mammalia: radicular morphology of the dp/4. *Historical Biology*, DOI: 10.1080/08912963.2017.1320398. 18 pp.

Pickford, M. & Senut, B., 1997 - Cainozoic mammals from coastal Namaqualand, South Africa. *Palaeontologia Africana*, **34**: 199-217.

Pickford, M. & Tsujikawa, H., 2005 - A partial cranium of *Diamantohyus nadirus* (Sanitheriidae, Mammalia) from the Aka Aiteputh Formation (16-15 Ma), Kenya. *Palaeontological Research*, **9** (**4**): 319-328.

Simpson, G.G., 1945 - The principals of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, **85**: 1-350.

Stromer, E., 1922 - Erste Mitteilung über Tertiäre Wirbeltierreste aus Deutsch-Sudwestafrika. *Sitzungsberichte der Bayerische Akademie der Wissenschaften*, **1921** (**2**): 331-340.

Van Couvering, J.A. & Van Couvering, J.A.H., 1976 - Early Miocene mammal fossils from East Africa : Aspects of geology, faunistics and palaeoecology. *In*: Isaac G. & McCown E., (Eds) *Louis Leakey and the East African* Evidence. Berkeley, University of California Press, pp. 155-207.

Van der Made, J., 2010 - The Pigs and "Old World Peccaries" (Suidae and Palaeochoeridae, Suoidea, Artiodactyla) from the Miocene of Sandelzhausen (southern Germany): phylogeny and an updated classification of the Hyotheriinae and Palaeochoeridae. *Paläontologisches Zeitschriften*, **84**: 43-121.

Von Meyer, H., 1834 - Die fossilen Zähne und Knochen und ihre Ablagerung in der Gegend von Georgensgmünd in Bayern. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **8**: 1-126, Frankfurt am Main.

Von Meyer, H., 1841 - Letter in *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, **II** *Briefwechsel*, **9**: 101-104.

Walker, A., 1968 - The lower Miocene fossil site of Bukwa, Sebei. *Uganda Journal*, **32** (**2**): 149-156.

Walker, A., 1969 - Fossil mammal locality on Mount Elgon, eastern Uganda. *Nature*, **223**: 591-593.

Wilkinson, A., 1976 - The lower Miocene Suidae of Africa. *Fossil Vertebrates of Africa*, **4**: 173-282.

Bukwa II Ruminants

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ABSTRACT

Ruminant fossils are scarce at Bukwa II, but four taxa have been recognised : two tragulids, and two primitive pecorans. As an assemblage, the fauna indicates affinities with localities such as Maboko, Nyakach, Kipsaraman, Kalodirr and Moruorot in East Africa, Arrisdrift in Namibia and Gebel Zelten and Wadi Moghara in North Africa. All these localities are arranged in East African Faunal Set III, younger than Rusinga (Faunal Set II) and older than Fort Ternan (Faunal Set IV). The deposits at Bukwa II are likely to be younger than 17.5 Ma, probably ca 16 Ma. The ruminant fossils from Bukwa II are described for the first time.

Key Words : Uganda, Middle Miocene, Tragulidae, Climacoceratidae

INTRODUCTION

Ruminant fossils are scarce at Bukwa II, but four species have been identified on the basis of isolated teeth and post-cranial bones. There are two tragulids, one very small species of which there is a broken d/4 which is compatible in dimensions and morphology to specimens of *Afrotragulus parvus* (Whitworth, 1958). A slightly larger species is represented by a broken lower molar which is likely to belong to «*Dorcatherium*» *pigotti* Whitworth, 1958, a species also represented by a navicular-cuboid. There are two pecoran taxa at Bukwa II represented by isolated teeth and a few post-cranial bones : 1) a medium-sized species which semi-hypsodont molars showing close affinities to *Prolibytherium magnieri* Arambourg, 1961, and more remote resemblances to *Climacoceras africanus* MacInnes, 1936, *Climacoceras gentryi* Hamilton, 1978b, and *Orangemeryx hendeyi* Morales *et al*., 1999, and 2) a larger species which is similar to *Canthumeryx sirtensis* Hamilton, 1973. There are close affinities between the Bukwa ruminant fauna and that from Gebel Zelten, Libya, with three out four taxa common to the two localities.

Abbreviations

BU - Bristol University, England (specimens now in NHMUK)
BUK - Bukwa (specimens housed in Uganda Museum)
GSN - Geological Survey of Namibia, Windhoek, Namibia
KNM - Kenya National Museum, Nairobi, Kenya
MNHN – Muséum National d'Histoire Naturelle, Paris
NHMUK - Natural History Museum, London, UK
UM - Uganda Museum, Kampala, Uganda
Z - Gebel Zelten, Libya

SYSTEMATIC DESCRIPTIONS

Order Artiodactyla Owen, 1848

Suborder Ruminantia Scopoli, 1777

Tragulidae Milne-Edwards, 1864

Genus *Afrotragulus* Sanchez, Quiralte, Morales & Pickford, 2010a

Species *Afrotragulus parvus* (Whitworth, 1958)

Description and Comments

An isolated d/4 of a small tragulid from Bukwa II, lacking the posterior lophid, is preserved in the Uganda Museum. The second lophid shows the typical M-structure formed by the postcristids and endocristids of the protoconid and metaconid. The dimensions of the tooth (Table 1) are compatible with the small species *Afrotragulus parvus* (Whitworth, 1958) and are slightly too large for it to belong to the type species of the genus, *Afrotragulus moruorotensis* (Pickford, 2001).

Genus «*Dorcatherium*» Kaup & Scholl, 1834

Species «*Dorcatherium*» *pigotti* Whitworth, 1958

Description and comments

The front half of a lower molar from Bukwa II is curated in the Uganda Museum (Table 1). The rear surface of the lophid shows the typical M-structure that occurs in tragulid lower molars. The fragment is of the right dimensions and morphology to be classified as «*Dorcatherium*» *pigotti* Whitworth, 1958, rather than *Siamotragulus songhorensis* (Whitworth, 1958) but some doubt must reside in the identification because it is not clear whether the specimen is a first, second or third molar. A navicular-cuboid in the Uganda Museum collected in 1967, agrees in morphology and dimensions with «*Dorcatherum*» *pigotti* (Table 3) (Pickford, 1981).

The genus name is enclosed in parentheses because it is clear that this African species does not belong to the same genus as *Dorcatherium naui* Kaup & Scholl, 1834, the type species from Germany.

Family Climacoceratidae Hamilton, 1978b

Subfamily Prolibytheriinae nov.

Type genus : *Prolibytherium* Arambourg, 1961.

Other genera in subfamily : *Propalaeoryx* Stromer, 1926; *Sperrgebietomeryx* Morales, Soria & Pickford, 1999; *Orangemeryx* Morales, Soria & Pickford, 1999.

Genus *Prolibytherium* Arambourg, 1961

Species *Prolibytherium magnieri* Arambourg, 1961

Description and comments

Several isolated teeth and postcranial bones from Bukwa II belong to a small giraffoid pecoran artiodactyl. A left p/4 (Fig. 1C, 2A) has short anterior paired cristids (paraconid and parastylid) and well-formed posterior paired cristids (entoconid and entostylid) as well as a robust central lingual cusplet (metaconid) which has anterior and posterior apophyses marked lingually by a vertical groove (see Hamilton, 1978a, 1978b, and Gentry, 2010, for the nomenclature of giraffoid and bovid lower premolars). A P2/ from the same site shows strong buccal ribs, the mesial one in particular standing out from the ectoloph. The protocone is centrally positioned and is separated from the paracone by a deep longitudinal valley.

There is an ectoloph of a D3/ which shows strong buccal styles which are accompanied near their bases by lower accessory styles, one in front, one behind. These styles and the main cusp ribs make for a complex buccal surface of the tooth (Fig. 5C). The lingual side of the tooth is missing. All these teeth have the right dimensions (Table 1) to belong to *Prolibytherium*, *Climacoceras* or *Orangemeryx*.

Finally a medium-worn left upper molar from Bukwa II (BUK II 1'97) is hypsodont, with deep crescentic fossae, which have steep walls and smooth, thin enamel (Fig. 5A). The distal crescentic fossa has a spur entering it from the postmetaconulecrista, and opposite it, there is a shallow vertical groove in the postero-lingual surface of the metacone. Apically the parastyle and mesostyle form strong vertical ribs on the ectoloph, but the relief of both these structures fades out towards cervix. The metastyle is weakly expressed, even in this medium-worn tooth. The specimen (length x breadth 18.8 x 19.0 mm) shows no sign of a lingual cingulum nor of a basal lingual pillar. It resembles two molars of *Climacoceras africanus* from Maboko (Whitworth, 1958; Hamilton, 1978b) not only in dimensions (NHMUK M 15314a (18.2 x 17.9 mm) and M 15314b (17.8 x 17.7 mm) but also in morphology. It is also comparable to fossils of *Orangemeryx hendeyi*, but it is closest in dimensions and morphology to upper molars of *Prolibytherium magnieri* Arambourg, 1963 (NHMUK M 21901, left M2/ length x breadth : 18.5 x 20.0 mm). A specimen curated in the MNHN, Paris (Z 1961, Fig. 5B) has a spur entering the distal fovea from the postmetaconulecrista, much as in the Bukwa II specimen.

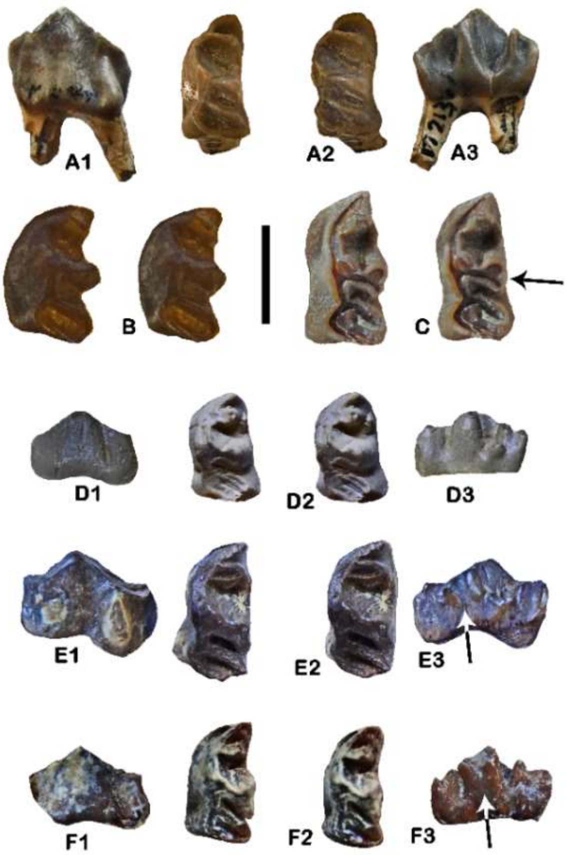

Figure 1. Comparison of p/4s of Climacoceratidae and Prolibytheriinae. A) *Climacoceras africanus* from Maboko, NHMUK M 21367, left p/4, A1 - buccal, A2 - stereo occlusal and A3- lingual views; B) *Climacoceras gentryi* from Fort Ternan, KNM FT 2950, right p/4 in a cast of a mandible (stereo image of p/4 reversed), C) *Orangemeryx* sp. from Bukwa II, UM BUK II, left p/4 stereo occlusal view, D) *Climacoceras* sp. from Nyakach, KNM NC 7816, left p/4, D1 - buccal, D2 - stereo occlusal, D3 - lingual views, E) *Orangemeryx hendeyi* from Arrisdrift, Namibia, GSN AD 710'97, left p/4 in mandible, E1 - buccal view, E2 - stereo occlusal view, E3 - lingual view, F) *Propalaeoryx stromeri* from Langental, Namibia, GSN LT 37'08, right p/4 (images reversed) F1 - buccal view, F2 - stereo occlusal view, F3 - lingual view (arrows show the groove in the lingual surface of the metaconid) (scale : 10 mm).

The morphology of the p/4 from Bukwa II resembles that of specimens in mandibles from Nyakach, Kenya, identified as *Nyanzameryx pickfordi* by Thomas (1984) a locality on the southern flank of the Nyanza Rift Valley, opposite Maboko, and of the same age (Faunal Set III) but the Bukwa specimen is larger (11.4 x 7.2 mm for the Nyakach specimen, KNM NC 7816, versus 15.3 x 8.3 mm for the Bukwa specimen). The Bukwa tooth resembles specimens of *Orangemeryx hendeyi* from Arrisdrift, Namibia, and falls within the range of metric variation of this species (Fig. 1E). Morphologically it is close to specimens of *Propalaeoryx austroafricanus* Stromer, 1926 and *Propalaeoryx stromeri* Morales *et al*., 2008 (Fig. 1F) but the p/4s of these species are appreciably smaller (length x breadth : 12.1 x 6.0 mm for *P*. *stromeri*). The Bukwa II specimen is considerably larger than the corresponding tooth in *Walangania africanus*. It is close in dimensions to the p/4 of *Prolibytherium magnieri* from Gebel Zelten, Libya, housed in the NHMUK (Table 1), but it is difficult to make detailed comparisons of the morphology because the Libyan fossils are heavily worn (Hamilton, 1973). Less worn specimens curated in Paris are close to the Bukwa II specimen, but there are minor differences in the form of the base of the metaconid and the area between the metaconid and the paraconid. What can be compared, however, indicates similar underlying morphology in the Bukwa II specimen and the p/4 of *Prolibytherium* and we interpret the minor differences between the samples as examples of individual variation.

Figure 2. Comparison of p/4s of A) *Prolibytherium magnieri* from Bukwa II (left p/4 image reversed) and B) Gebel Zelten (NHMUK M 21899, left mandible with p/2-m/3) stereo occlusal views (scale : 5 cm).

The P2/ from Bukwa (length x breadth : 12.3 x 9.3 mm) is comparable in dimensions to a specimen of *Prolibytherium magnieri* from Gebel Zelten, Libya (NHMUK M 21901 left P2/ : 12.8 x 9.5 mm). Both teeth are quite deeply worn, but the remaining parts are similar in morphology (Fig. 3, 4). It is not possible to make comparisons with *Climacoceras africanus* because the P2/ of this species has not been described. The tooth shows some resemblances to specimens of *Orangemeryx hendeyi* from Arrisdrift (Morales *et al*., 1999) but the Namibian fossils are slightly larger (AD 300’99 is 14.2 x 9.8 mm; AD 301’99 is 14.4 x 9.1 mm).

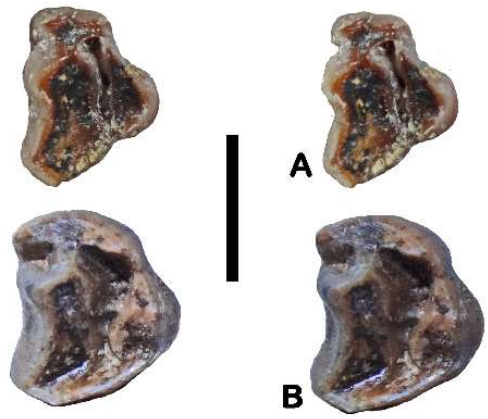

Figure 3. Comparison of right upper premolars of climacoceratids and prolibytheriines. A) Bukwa II specimen interpreted as a right P2/ to *Prolibytherium magnieri*, B) *Orangemeryx hendeyi*, GSN AD 26’97, right P3/ in maxilla fragment (scale : 10 mm).

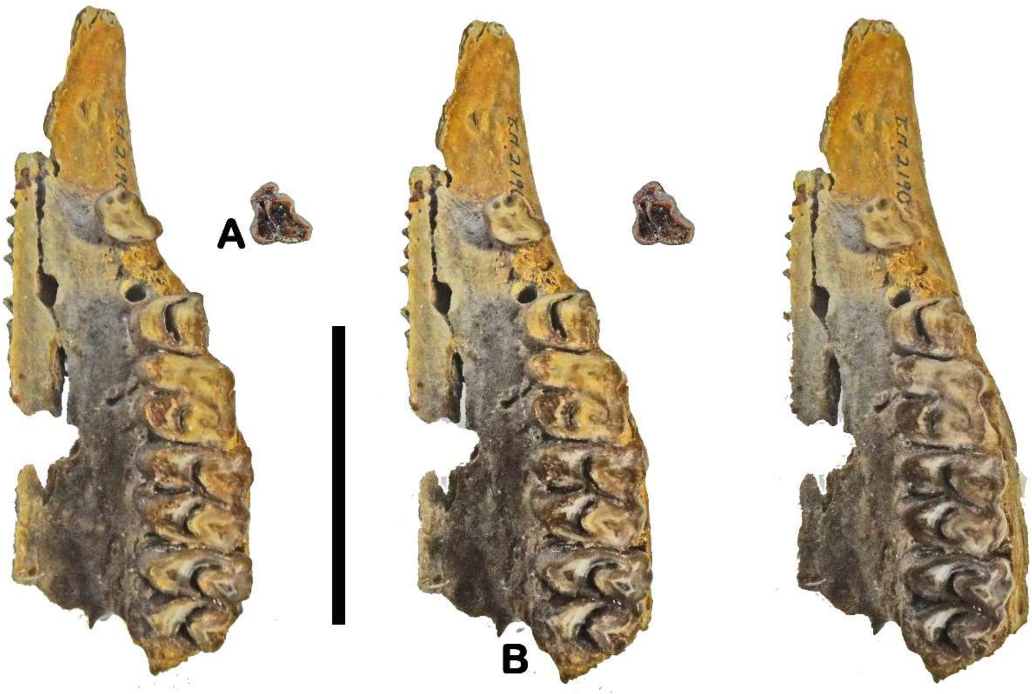

Figure 4. *Prolibytherium magnieri* from A) Bukwa II right P2/ (image reversed) and B) Gebel Zelten (M 21901, left maxilla with P2/, P4-M3) stereo occlusal views (scale : 5 cm).

Whitworth (1958) described some ‘prismatic’ ruminant teeth from Maboko Island, Kenya, which he attributed to Bovidae, some of which have since been identified as *Hypsodontus* by Morales *et al*., (2003b) and others as *Climacoceras* (Hamilton, 1978, figs 16, 17). Once the different wear stages have been taken into account, the Bukwa upper molar (Fig. 5A) compares well in morphology and dimensions with the Maboko climacoceratid specimens but it also agrees with the upper molars of *Orangemeryx* Morales *et al*., 1999 (Morales *et al*., 2003a) and *Prolibytherium magnieri* from Gebel Zelten (Hamilton, 1973) (Fig. 5B). It is similar to a specimen from the Nyakach Formation, Kenya (KNM NC 7803, left maxilla containing M2/ and M3/) described by Thomas (1984, text-fig. 6) and attributed to *Nyanzameryx pickfordi*. The type specimen of this species (from Maboko) is a bovid, but most of the dental remains from Nyakach attributed to this genus belong to a climacoceratid (Geraads, 1986) (probably *Orangemeryx* or *Propalaeoryx*).

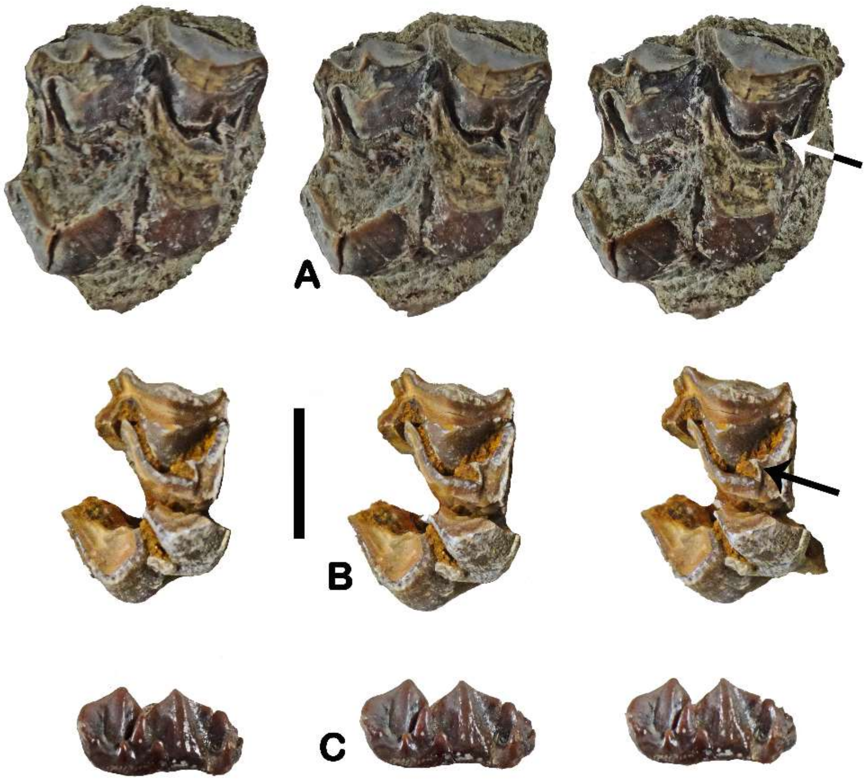

Figure 5. *Prolibytherium magnieri* from Bukwa II, Uganda and Gebel Zelten, Libya. A) BUK II 1'97, left M2/, stereo occlusal views; B) MNHN Z 1961, damaged right M1/ from Gebel Zelten (stereo occlusal images reversed); C) BUK II, ectoloph of left D3/, stereo buccal views. Arrows in A and B show the broad spur entering the distal fovea from the postmetaconulecrista (scale : 10 mm).

Family Giraffidae Gray 1821

Genus *Canthumeryx* Hamilton, 1973

Species *Canthumeryx sirtensis* Hamilton, 1973

Description and comments

A left upper molar from Bukwa II (BUK II 17'10) (Fig. 6A) shows a suite of features that links it to the giraffoid genus *Canthumeryx*. The enamel is wrinkled in the same style as the type species from Gebel Zelten, Libya (Hamilton, 1973) (Fig. 6C) and to material from Moruorot, Kenya (Fig. 6B). The layout of the protocone, paracone, metacone and hypocone is the same, and there is a spur entering the distal crescentic fossa from the postmetaconulecrista, precisely as in the Libyan and Kenyan fossils. The dimensions of this tooth (Table 1) accord with *Canthumeryx sirtensis* (the three upper molars in this genus are all close in dimensions : Hamilton, 1978b, table 16).

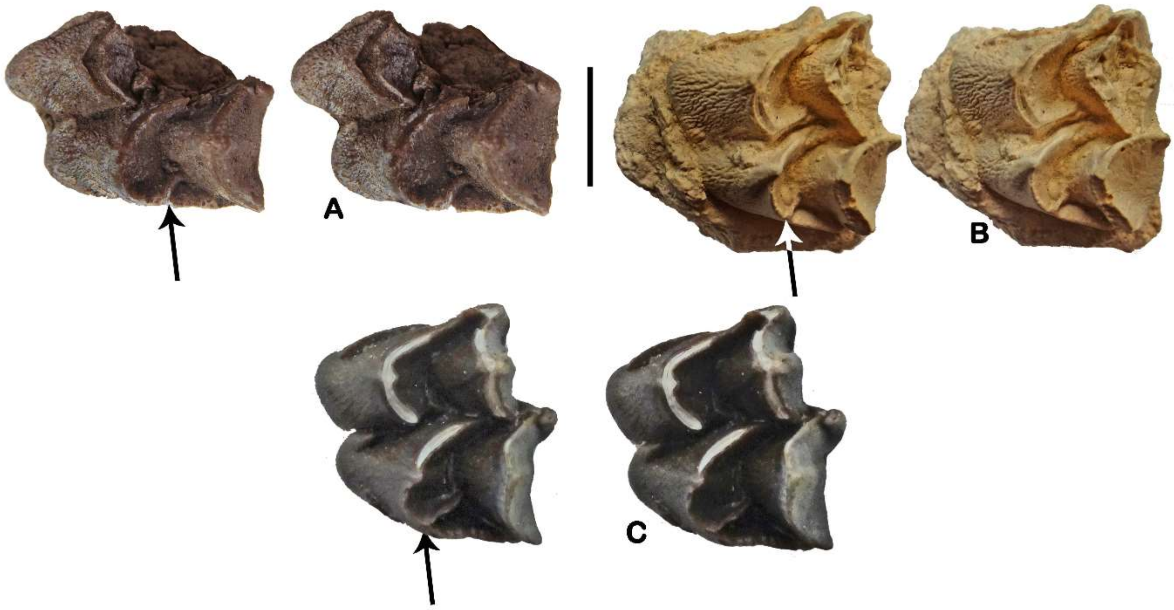

Figure 6. Upper molars of *Canthumeryx sirtensis*, A) BUK II 17’10, left M1/, B) NHMUK M 30179, cast of right M1/ (images reversed) from Moruorot, Kenya, C) NHMUK M 26672, left M1/ from a cheek tooth series D2/-D4/, M1/-M2/ (stereo occlusal views). Arrows show narrow spur on postmetaconulecrista entering the distal fovea (scale : 10 mm).

Table 1. Measurements (in mm) of ruminant teeth from Bukwa II, Uganda (BUK), Gebel Zelten, Libya (M 21***, M 26*** and Z) and Moruorot, Kenya (M 3****).

Taxon / Catalogue N°	Tooth	Mesio-distal length	Bucco-lingual breadth
Afrotragulus parvus BUK II	d/4 (incomplete)	--	2.6
“Dorcatherium” pigotti BUK II	lower molar, mesial half	--	5.3
Prolibytherium magnieri BUK II	p/4 right	15.3	8.3
Prolibytherium magnieri NHMUK M 21899	p/4 right	13.3	8.8
Prolibytherium magnieri MNHN Z 1961	p/4 left	13.3	9.0
Prolibytherium magnieri MNHN Z 1961	p/4 right	13.7	7.7
Prolibytherium magnieri BUK II	P2/ right	12.3	9.3
Prolibytherium magnieri BUK II	D3/ ectoloph left	13.0	--
Prolibytherium magnieri BUK II 1’97	M2/ left	18.8	19.0
Prolibytherium magnieri NHMUK M 21901	M1/ left	--	17.0
Prolibytherium magnieri NHMUK M 21901	M2/ left	18.5	20.0
Prolibytherium magnieri NHMUK M 21901	M3/ left	19.3	20.7
Prolibytherium magnieri MNHN Z 1961	M1/ right	--	17.8
Canthumeryx sirtensis BUK II 17’10	M1/ left	--	19.7
Canthumeryx sirtensis NHMUK M 26672	M1/ left	21.8	18.9
Canthumeryx sirtensis NHMUK M 26671	M1/ right	19.3	--
Canthumeryx sirtensis NHMUK M 30179	M1/ right	20.0	19.3
Canthumeryx sirtensis NHMUK M 33001	M1/ left	19.0	19.0
Canthumeryx sirtensis NHMUK M 26672	M2/ left	25.0	22.3
Canthumeryx sirtensis NHMUK M 26671	M2/ right	22.8	24.0
Canthumeryx sirtensis NHMUK M 26672	M3/ right	22.0	24.0
Canthumeryx sirtensis NHMUK M 33016	M3/ left	24.0	24.0

Some poorly preserved post-cranial elements from Bukwa II (Fig. 7) notably a talus and a distal metapodial pulley, are of the right dimensions to belong to this species (Tables 2 and 3).

Ruminant postcranial bones

Two tali, a navicular-cuboid and three distal metapodial pulleys from Bukwa II belong to a non-traguloid ruminant (Fig. 7) and are attributed herein to *Prolibytherium magnieri*. They are compatible in dimensions to specimens of *Climacoceras africanus*, and are somewhat smaller than those of *Climacoceras gentryi* (Pickford, 1981) (Table 2, 3).

Other rather fragmentary specimens from Bukwa II (a talus and distal metapodials) are from a considerably larger pecoran than *Prolibytherium magnieri* (Fig. 7) and are compatible in dimensions with *Canthumeryx sirtensis* from Moruorot, Kenya, and other sites (Antilopidé indéterminé in Arambourg, 1933). The internal lengths of the three Moruorot tali (MNHN 1933.9) are 36.0, 43.0 and 43.3 mm, and the Bukwa specimen measures 41.6 mm (Table 2). The Bukwa II distal metapodial pulley measures ca 19 mm in diameter which compares with 19.7 mm in a specimen of *Canthumeryx sirtensis* from Moruorot, Kenya. The metapodial pulleys of *Prolibytherium magnieri* (15.5 mm diameter in a metatarsal (LBE 616) from Gebel Zelten and 14.7 mm in a metacarpal (LBE 617) from Gebel Zelten) are smaller than those of *Canthumeryx sirtensis* (19 mm).

Table 2. Measurements (in mm) of ruminant tali from Bukwa II, Uganda (BUK) and Gebel Zelten, Libya (Data concerning Gebel Zelten (BU) is from Hamilton, 1973).

Catalogue N° (Taxon)	External length	Internal length	Minimum length	Proximal breadth	Distal breadth
BUK 67-34 (*Prolibytherium*)	34.9	31.3	--	19.4	20.7
BUK 67-31 (*Prolibytherium*)	--	33.5	--	18.9	22.7
BU 20165 (*Prolibytherium*)	32	--	26	20	18
BU 20166 (*Prolibytherium*)	36	--	30	20	20
BU 20167 (*Prolibytherium*)	33	--	26	20	19
BU 20168 (*Prolibytherium*)	33	--	25	18	18
BUK II (*Canthumeryx*)	--	41.6	--	--	--
BU 20120 (*Canthumeryx*)	49	--	40	29	29
BU 20121 (*Canthumeryx*)	41	--	40	30	29
BU 20122 (*Canthumeryx*)	53	--	41	32	30
MNHN Z 1961 (*Canthumeryx*)	53	48.6	--	30	34

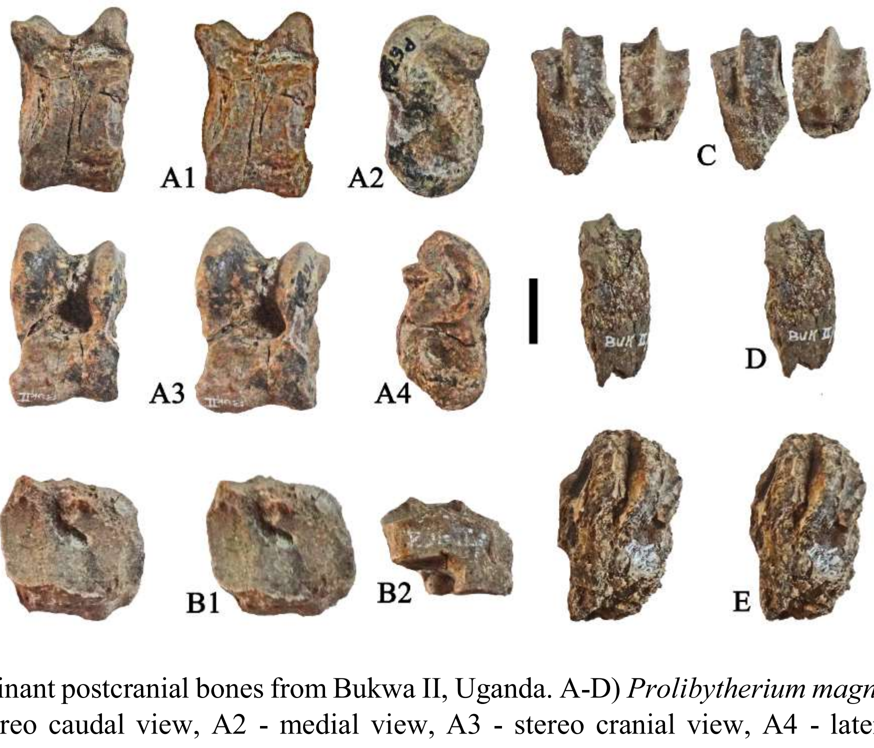

Figure 7. Ruminant postcranial bones from Bukwa II, Uganda. A-D) *Prolibytherium magnieri*; A - right talus (A1 - stereo caudal view, A2 - medial view, A3 - stereo cranial view, A4 - lateral view); B) navicular-cuboid (B1 - stereo proximal view, B2 - posterior view); C-D) distal metapodial pulleys (stereo cranial views); E) *Canthumeryx sirtensis*, damaged distal metapodial pulley (stereo cranial view) (scale : 10 mm).

Table 3. Measurements (in mm) of diverse ruminant post-cranial bones from Bukwa II, Uganda (BUK) and Gebel Zelten, Libya (LBE) (e : estimated measurement).

Catalogue N°	Taxon	Bone	Anatomy	Measurement
BUK II/67	«*Dorcatherium*» *pigotti*	navicular-cuboid	breadth talar facet	9.4
BUK II P67-29	*Prolibytherium magnieri*	navicular-cuboid	breadth talar facet	17.5
BUK II/67	*Prolibytherium magnieri*	metapodial distal pulley	internal diameter	12.3
BUK II/67	*Prolibytherium magnieri*	metapodial distal pulley	internal diameter	13.3
BUK II/67	*Prolibytherium magnieri*	metapodial distal pulley	internal diameter	13.5
MNHN LBE 618	*Prolibytherium magnieri*	metapodial distal pulley	internal diameter	15.5
MNHN LBE 617	*Prolibytherium magnieri*	metapodial distal pulley	internal diameter	14.7
BUK II/67	*Canthumeryx sirtensis*	metapodial distal pulley	internal diameter	19.0e

DISCUSSION AND CONCLUSIONS

There are two species of tragulid at Bukwa II, but their fossil representation is meagre, comprising two-thirds of a d/4 of a very small species, compatible in dimensions with *Afrotragulus parvus*, and the front half of a lower molar of a slightly larger species, comparable in morphology and dimensions to «*Dorcatherium*» *pigotti* (Whitworth, 1958). There is also a navicular-cuboid that has the right dimensions to belong to the latter species. Walker (1968) listed a «large tragulid (not *Dorcatherium chappuisi*)» at Bukwa II, but the fossils were never described. There are no large tragulids in the material that we have observed, and it is plausible that the specimens to which the author referred belong instead to *Prolibytherium magnieri*, which does occur at the site.

The Bukwa II lower premolar here attributed to *Prolibytherium magnieri* is somewhat more derived in morphology than the specimens of *Climacoceras* from Maboko, Kenya (the type locality of *Climacoceras africanus* MacInnes, 1936) and is similar in some respects to some mandibular specimens from Nyakach included in *Nyanzameryx pickfordi* by Thomas (1984). The holotype of the latter species, a cranial fragment with horn cores from Maboko, Kenya, belongs to a bovid (*Hypsodontus*) (McCrossin *et al*., 1998 ; Morales *et al*., 2003b) but the mandibles from Nyakach included in the hypodigm represent an undescribed species of *Climacoceras* according to Geraads (1986). In particular, the lingual central cusplet of the p/4 from Bukwa II has mesial and distal swellings at the lingual end, separated by a shallow lingual groove, like the material from Nyakach and Fort Ternan, as well as like the fossils of *Orangemeryx* from Arrisdrift, Namibia, and the specimens in mandibles of *Prolibytherium* from Gebel Zelten, Libya. The Maboko material figured by Hamilton (1978a) shows an undivided central lingual cusplet which broadens mesio-distally towards the cervix, but without developing a groove, whereas the fossils of *Climacoceras gentryi* from Fort Ternan (the type locality) (Hamilton, 1978a) show a subdivided lingual central cusplet, not very different from the Bukwa II fossil. The Bukwa II fossil is also closer in dimensions to the Fort Ternan material, but the difference is not very great. It is concluded that the morphology of the Bukwa II material is most similar to specimens of *Prolibytherium magnieri*. The tali from Bukwa II are slightly smaller than those of *Climacoceras gentryi*, but they fall into the range of variation of the material of *Climacoceras africanus* from Maboko Island and *Prolibytherium magnieri* from Gebel Zelten.

To conclude, the p/4s of *Prolibytherium magnieri*, *Orangemeryx hendeyi*, *Propalaeoryx austroafricanus*, *Propalaeoryx stromeri* and the material from Nyakach (Kenya) and Bukwa II resemble each other closely and form an internally coherent group. In contrast, the specimens from Maboko and Fort Ternan included in *Climacoceras* differ from the first group but resemble each other. From this we conclude that the Bukwa and Nyakach fossils do not belong to *Climacoceras*, but rather to the *Prolibytherium*-*Propalaeoryx*-*Orangemeryx* clade, here included in a new subfamily Prolibytheriinae, distinct from Climacoceratinae. Both these groups were considered to be climacoceratids by Pickford *et al*., (2001) differing from true giraffids and bovids in a suite of features. Cote (2010) suggested that the second group defined immediately above belonged to Pecora *Incertae sedis* and that *Climacoceras* is a giraffoid. The suggestion of separate systematic status for the two groups warrants further examination, as it finds support from the observations presented herein as well as from studies of the cranial appendages and some post-cranial elements mentioned by Sanchez *et al*. (2010b). Similarities are noted between the Bukwa II fossils attributed to *Prolibytherium* and Palaeomerycidae from Europe, such as *Xenokeryx* Sanchez *et al*., (2015, fig. 9) from Retama, Spain, in particular the morphology of the D3/ and the presence of a broad spur leading into the distal fovea of the upper molars from the postmetaconulecrista.

Harris *et al*., (2010) listed *Canthumeryx sirtensis* from Napak, Uganda, citing Bishop (1962, 1967) but the genus was not erected until later (Hamilton, 1973). The record is thus a lapsus. None of the ruminants from Napak are as large as this giraffoid, the largest pecoran from the deposits being *Walangania africanus* (Pickford, 2002). Thus the earliest record of the genus *Canthumeryx* is the scant material from Rusinga Island, dated ca 17.8 Ma (Faunal Set II) (Hamilton, 1978a). In contrast, the genus is common in Faunal Set III (Pickford, 1981) in deposits younger than 17.5 Ma, not just in Africa, but also the Middle East (Grossman & Solounias, 2016).

The ruminants from Bukwa II thus comprise two tragulids (*Afrotragulus parvus* and *«Dorcatherium» pigotti*) and two pecorans (*Prolibytherium magnieri* and *Canthumeryx sirtensis*). This combination indicates that the Bukwa II deposits are likely to be younger than Rusinga Island (Faunal Set II) and are most similar to a suite of localities that are correlated to Faunal Set III (Nyakach, Lothidok, Maboko, Ombo, Kipsaraman, Loperot, Buluk, Kalodirr and Moruorot in East Africa, Arrisdrift in Namibia, Gebel Zelten and Wadi Moghara in North Africa, and Yeroham and Al-Sarrar in the Arabian Peninsula) (Grossman & Solounias, 2016).

For this reason, from the point of view of the ruminant fauna, it is considered that the recently published age estimate for the deposits at Bukwa II (19.1-19.5 Ma) by MacLatchy *et al*., (2006) is far too old. An age some time between Kalodirr (17.5 Ma) and Fort Ternan (12.7 Ma, Pickford *et al*., 2006) seems most likely on the basis of the ruminants from Bukwa II. As an ensemble, the mammals from Bukwa II indicate an age of ca 16 Ma (Middle Miocene : Ogg *et al*., 2016).

Finally, it is noted that the Bukwa II ruminant fauna shares three out of four species with Gebel Zelten, Libya, indicating the likelihood of intriguing biogeographic relationships between these two localities.

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REFERENCES

Arambourg, C., 1933 - Mammifères Miocène du Turkana (Afrique orientale). *Annales de Paléontologie*, **22**: 123-146, 2 pls.

Arambourg, C., 1961- *Prolibytherium magnieri*, un Velléricorne nouveau du Burdigalien de Libye (Note préliminaire). *Comptes Rendus des Séances de la Société Géologique de France, Paris*, **3**: 61-63.

Bishop, W.W., 1962 - The mammalian fauna and geomorphological relations of the Napak volcanics, Karamoja. *Records of the Geological Survey of Uganda*, **1957-58**: 1-18.

Bishop, W.W., 1967 - The later Tertiary in East Africa - volcanics, sediments and faunal inventory. *In*: Bishop, W.W. & Clark, J.D. (Eds) *Background to Evolution in Africa*. University of Chicago Press, pp. 31-56.

Cote, S., 2010 - Pecora *Incertae sedis*. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, University of California Press, pp. 731-739.

Gentry, A.W., 2010 - Bovidae. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, University of California Press, pp. 741-796.

Geraads, D., 1986 - Remarques sur la systématique et la phylogénie des Giraffidae (Artiodactyla, Mammalia). *Geobios*, **19**: 465-477.

Gray, J.E., 1821 - On the natural arrangement of vertebrose animals. *London Medical Repository*, **15** (**1**): 296-310.

Grossman, A. & Solounias, N., 2016 - New fossil Giraffoidea (Mammalia : Artiodactyla) from the Lothidok Formation (Kalodirr Member, Early Miocene, West Turkana, Kenya) contribute to our understanding of early giraffoid diversity. *Zitteliana*, **B32**: 63-70.

Hamilton, W.R., 1973 - The lower Miocene ruminants of Gebel Zelten, Libya. *Bulletin of the British Museum (Natural History) Geology*, **21**: 75-150.

Hamilton, W.R. 1978a - Cervidae and Palaeomerycidae. *In*: Maglio, V.J. & Cooke, H.B.S., (Eds) *Evolution of African Mammals*, Cambridge, Harvard University Press, pp. 496-508.

Hamilton, W.R., 1978b - Fossil giraffes from the Miocene of Africa and a revision of the phylogeny of the Giraffoidea. *Philosophical Transactions of the Royal Society of London*, **B283**: 165-229.

Harris, J.M., Solounias, N. & Geraads, D., 2010 - Giraffoidea. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*, Berkeley, University of California Press, pp. 797-811.

Kaup, J.-J. & Scholl, J.-B., 1834 - *Verzeichniss der Gypsabgüsse von den ausgezeichnetsten urweltlichen Thierresten des Grossherzoglichen Museum zu Darmstadt*. Zweite Ausgabe. Darmstadt, J.P. Diehl. 28 pp.

MacInnes, D.G., 1936 - A new genus of fossil deer from the Miocene of Africa. *Journal of the Linnaean Society of Zoology*, **39**: 521-530.

MacLatchy, L., Deino, A. & Kingston, J., 2006 - An updated chronology for the early Miocene of NE Uganda. *Journal of Vertebrate Paleontology*, **26** (**3**, Supplement): 93A.

McCrossin, M.L., Benefit, B.R., Gitau, S.N., Palmer, A.K. & Blue, K.T., 1998 - Fossil evidence for the origins of terrestriality among old world higher primates. *In*: Strasser, E., Fleagle, J., Rosenberger, A. & McHenry H. (Eds) *Primate Locomotion: Recent Advances*, New York, Plenum Press, pp. 353-396.

Milne-Edwards, A., 1864 - Recherches anatomiques, zoologiques et paléontologiques sur la famille des chevrotains. *Annales de Science Naturelle*, *Paris*, **5**: 1-167.

Morales, J., Soria, D. & Pickford, M., 1999 - New stem giraffoid ruminants from the Lower and Middle Miocene of Namibia. *Geodiversitas*, **21**: 229-254.

Morales, J., Soria, D. & Pickford, M., 2008 - Pecoran ruminants from the Early Miocene of the Sperrgebiet, Namibia. *Memoir of the Geological Survey of Namibia*, **20**: 391-464.

Morales, J., Soria, D., Nieto, M., Pelaez-Campomanes, P. & Pickford, M., 2003a - New data regarding *Orangemeryx hendeyi* Morales *et al*., 2000, from the type locality, Arrisdrift, Namibia. *Memoir of the Geological Survey of Namibia*, **19**: 305-344.

Morales, J., Soria, D., Pickford M. & Nieto M., 2003b - A new genus and species of Bovidae (Artiodactyla, Mammalia) from the early Middle Miocene of Arrisdrift, Namibia, and the origins of the family Bovidae. *Memoir of the Geological Survey of Namibia*, **19**: 371-384.

Ogg, J.G., Ogg, G.M. & Gradstein, F.M., 2016 - *A Concise Geologic Time Scale 2016*, Elsevier, 240 pp.

Owen, R., 1848 - Description of teeth and portions of jaws of two extinct anthracotheroid quadrupeds (*Hyopotamus vectianus* and *H. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight. *Quarterly Journal of the Geological Society of London*, **4**: 104-141.

Pickford, M., 1981 - Preliminary Miocene Mammalian biostratigraphy for Western Kenya. *Journal of Human Evolution*, **10**: 73-97.

Pickford, M., 2001 - Africa's smallest ruminant: a new tragulid from the Miocene of Kenya and the biostratigraphy of East African Tragulidae. *Geobios*, **34**: 437-447.

Pickford, M., 2002 - Ruminants from the Early Miocene of Napak, Uganda. *Annales de Paléontologie*, **88**: 85-113.

Pickford, M., Attia, Y. & Abd El Ghany M., 2001 - Discovery of *Prolibytherium magnieri* Arambourg, 1961 (Artiodactyla, Climacoceratidae) in Egypt. *Geodiversitas*, **23**: 647–652.

Pickford, M., Sawada, Y., Tayama, R., Matsuda, Y., Itaya, T., Hyodo, H., Senut, B., 2006 - Refinement of the age of the Middle Miocene Fort Ternan Beds, Western Kenya, and its implications for Old World biochronology. *Comptes Rendus Geoscience*, **338**: 545-555.

Sanchez, I.M., Cantalapiedra, J.L., Rios, M., Quiralte, V., & Morales, J., 2015 - Systematics and Evolution of the Miocene Three-horned Palaeomerycid Ruminants (Mammalia, Cetartiodactyla). PLoS ONE, **10** (**12**) : e0143034.doi.org/10.1371/journal.pone.0143034.

Sanchez, I., Quiralte, V., Morales, J. & Pickford, M., 2010a - A new genus of tragulid ruminant from the early Miocene of Kenya. *Acta Palaeontologica Polonica*, **55**: 177-187.

Sanchez, I., Quiralte, V., Morales, J., Azanza, B., & Pickford, M., 2010b - Sexual dimorphism of the frontal appendages of the Early Miocene African Pecoran *Prolibytherium* Arambourg, 1961 (Mammalia, Ruminantia). *Journal of Vertebrate Paleontology*, **30** (**4**): 1306-1310.

Scopoli, J-A., 1777 - *Introdvctio ad historiam natvralem sistens genera lapidvm, plantarvm, et animalivm hactenvs detecta, caracteribvs essentialibvs donata, in tribvs divisa, svbinde ad leges natvrae*. Pragae, Gerle. 506 pp.

Stromer, E., 1926 - Reste Land- und Süsswasser-Bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: Kaiser E. (Ed.) *Die Diamantenwüste Südwest-africas*, vol. 2. Reimer, Berlin, pp. 107-153.

Thomas, H., 1984 - Les Giraffoidea et les Bovidae Miocènes de la formation Nyakach (Rift Nyanza, Kenya). *Palaeontographica*, **A183**: 64-89.

Walker, A., 1968 - The lower Miocene fossil site of Bukwa, Sebei. *Uganda Journal*, **32** (**2**): 149-156.

Whitworth, T., 1958 - Miocene ruminants of East Africa. *Fossil Mammals of Africa*, **15**: 1-50.

Updated Middle Miocene Mammalian Fauna and Biochronology of Bukwa II, Uganda

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ABSTRACT

Several of the mammals from Bukwa II, Uganda, show affinities with taxa from East African Faunal Set III, equivalent to European Mammal Zone MN 5. Most previous interpretations of the fossils indicated correlation to the Lower Miocene, in line with radio-isotopic age determinations which suggested an age greater than 19 Ma. However, many of the previous identifications of fossil specimens seem to have been made to accord with the expected age of the deposits rather than on the basis of the correct taxonomy of the fossils themselves. The strata at Bukwa I, in contrast (and their contained fauna and flora) are of Early Miocene age, probably Faunal Set I, ca 19-20 Ma. The deposits at Bukwa II (and the fauna) correlate with Faunal Set IIIb (ca 16 Ma) and indicate the presence of a discordance between the palustral deposits of Bukwa II, and the underlying flaggy tuffs of Bukwa I.

Key Words : Mammalian fauna, Bukwa II, Biostratigraphy, Middle Miocene, Unconformity

INTRODUCTION

This paper summarises the biostratigraphic meaning of the mammals from the fossiliferous deposits at Bukwa I and Bukwa II, Elgon, Uganda. The concept of Faunal Sets was articulated by Pickford (1981) who arranged the East African Miocene fossiliferous localities into various Faunal Sets on the basis of their contained faunas. As originally envisaged, the Miocene faunas were arranged into eight Faunal Sets spanning the period 20.5 Ma to 5 Ma. Subsequent modifications to the scheme (Pickford, 1998; Pickford & Senut, 1999) comprised the addition of Faunal Set 0 (23-20.5 Ma) at the base of the column, corresponding to the discovery of Meswa Bridge, in Kenya, and the subdivision of Faunal Set III into two, FS IIIa (17.5-16 Ma, Core fauna - Buluk) and FS IIIb (16-14 Ma, Core fauna - Maboko) (Pickford, 2017b).

Pickford & Senut (1999) published a correlation chart between the East African Faunal Sets and the European Land Mammal Zonation (MN Zones). Whilst there has been debate about the ages of the boundary zones between the faunal sets and those of the MN zones (see discussion in Pickford & Senut, 1999, fig. 1) there has been general acceptance of the succession of events. There are some residual disagreements about certain localities which don't fall clearly into one or another MN Zone or FS, but on the whole, the schemes appear to reflect the sequence and, to a significant extent, the timing of faunal events in Europe on the one hand (MN Zones) and East Africa (FS) on the other. However, extrapolation of these correlation schemes to other palaeobiogeographic realms of the world is not advisable, because biogeographic signals, especially latitudinal ones, can over-ride the faunal chronological signal, and thus lead to false positive correlation or to mismatches, as was pointed out by Pickford (1997).

The aim of this paper is to analyse the mammal fauna from Bukwa II in light of the East African biostratigraphic succession, and to make comparisons with European zones where applicable, the case with the suids.

THE MAMMAL FAUNA FROM BUKWA II

In East Africa, the sanithere *Diamantohyus nadirus* is known from Ombo, Maboko, Kipsaraman and Nachola, all arranged in FS IIIb, The Bukwa II sanithere is close to *Sanitherium* from Chios (Greece) and several Middle Miocene sites in Asia (Pickford, 2017a). The suid *Hyotherium namaquense* is known from Ryskop in South Africa, and Kipsaraman, Nyakach and Nachola in Kenya, the latter two localities in FS IIIb. The suid from Bukwa II is closest in morphology and metrics to specimens of *Hyotherium medium* from Europe arranged in MN 5 (Sandelzhausen, Mösskirch, Thannhausen) (Pickford, 2016, 2017f).

The pecoran ruminant genera from Bukwa II have not been reported from Europe, but *Prolibytherium* is known from FS IIIa (Gebel Zelten, Libya) while *Canthumeryx* is known from FS II, IIIa and IIIb in East Africa and from Gebel Zelten, Wadi Moghara, Yeroham and Al-Sarrar in North Africa and the Arabian Peninsula (Grossman & Solounias, 2016), which, with the exception of Wadi Moghara, were all correlated to FS III by Pickford & Senut (1999). Later, after a study of the Wadi Moghara fauna housed in the Geological Survey of Egypt, Cairo, during which a cranial fragment with ossicones of *Prolibytherium* was identified, Wadi Moghara was correlated to FS III by Pickford *et al*., (2001) and its age was estimated to be 17 Ma. Thus, as an assemblage, the ruminants from Bukwa II tell the same story as the suoids : the deposits correlate to FS III (Pickford, 2017g).

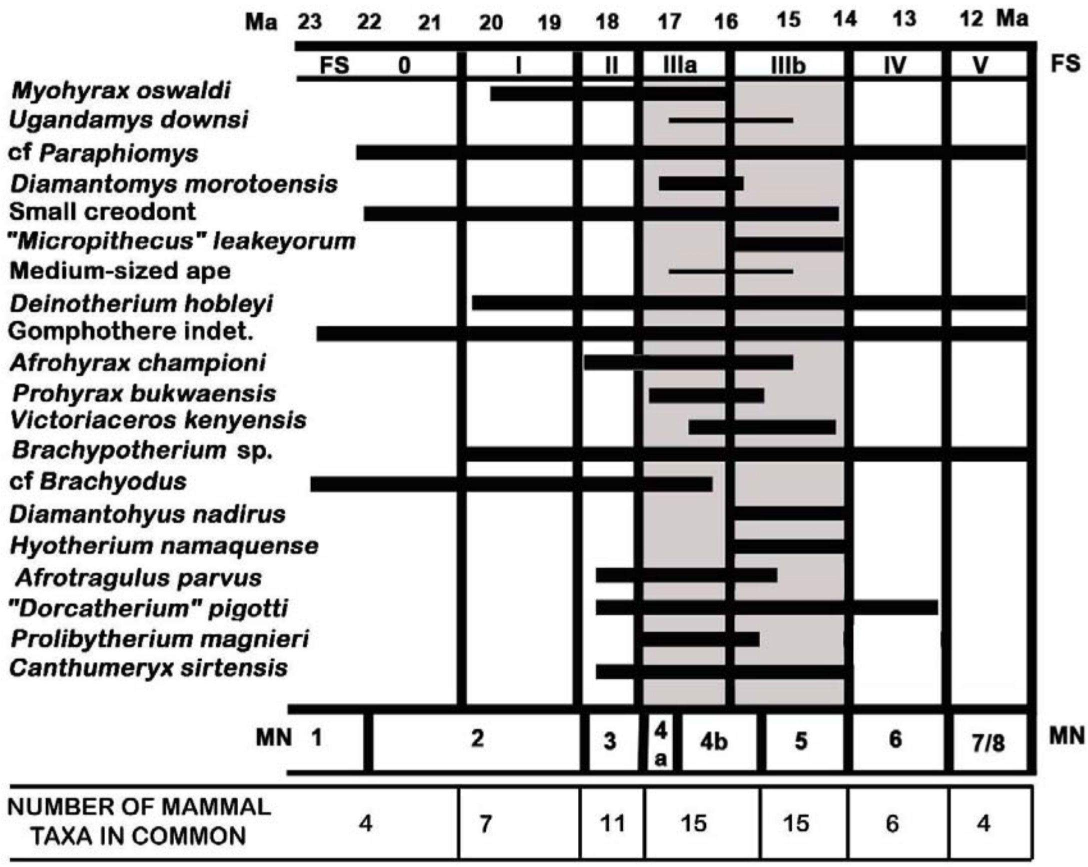

Figure 1. Chronological ranges of 20 mammalian taxa from Bukwa II, Uganda. The overall picture that emerges is that Bukwa II correlates to Faunal Set III (marked in grey) in particular the younger half of this set, FS IIIb. In terms of the European Land Mammal Zonation, the best correlation, on the basis of the suoids, is with MN 5, corresponding to FS IIIb. The most likely age of Bukwa is thus 16-15 Ma (Mammals unique to Bukwa II are marked in thin black lines and are not included in the calculations of the number of taxa from Bukwa II that are common to the different Faunal Sets).

A few poorly known taxa are omitted from this biostratigraphic analysis, including some rodents and a broken tooth interpreted to be that of a lagomorph (Winkler *et al*., 2005) (Pickford, 2017c).

Bukwa II has yielded several long-ranging mammalian taxa, but none of them contradict the correlations based on ruminants and suoids (Fig. 1) (Pickford, 2017d, 2017e). It has also yielded several shorter-lived lineages, including two genera of hominoid primates and two taxa of hyracoids (Pickford *et al*., 2017). One of the primates, a medium-sized ape could be the same species as a poorly represented taxon from Fort Ternan (reported as *Proconsul* sp. by Harrison, 1992). One of the hyracoids, *Afrohyrax championi*, occurs in FS II, but it also occur in FS III at Moruorot (its type locality) Maboko, Kipsaraman and Nachola in East Africa (Pickford, 2017d). The stratigraphic range of the rhinocerotid, *Victoriaceros kenyensis*, has not yet been fully determined, other than from its type locality, Maboko (FS IIIb) (Geraads *et al*., 2012), but the same genus has been recorded in FS II where it is represented by a distinct species, *Victoriaceros hooijeri* (Geraads *et al*., 2016). Thus the elasmotheriine rhinocerotid from Bukwa II does not disagree with correlation of the site to FS IIIb (Pickford, 2017e). The other mammalian lineages represented at Bukwa II, are either unique to the site (*Ugandamys*) or are poorly represented (cf *Paraphiomys*, small creodont) so are of little weight in deciding correlations (Pickford, 2017c).

Of the 18 mammal taxa from Bukwa II which carry biostratigraphic information (i.e. omitting the two species which are unique to Bukwa II) only four are found in Faunal Set 0 (22%), seven are recorded in Faunal Set II (38.9%), eleven occur in Faunal Set II (61.1%), fifteen are recorded from Faunal Sets IIIa and IIIb (83.3%), seven occur in Faunal Set IV (36.8%) and five in Faunal Set V (27.7%). There can be little doubt therefore, that the mammal fauna from Bukwa II invites correlation to Faunal Set III, with slightly more support for a correlation to FS IIIb than to FS IIIa.

DISCUSSION AND CONCLUSIONS

The mammalian fossils from Bukwa II, Uganda, were long thought to represent an early Miocene fauna comparable in detail to those from sites such as Rusinga and Karungu, Kenya (Walker, 1968, 1969). Detailed study of the fossils, however, reveals that there are several taxa present that indicate correlation to the Middle Miocene, there being two suoid taxa and two ruminants that occur frequently in the Middle Miocene of Eastern and Southern Africa, but which have never been found in Early Miocene deposits of Africa. One of the suids even indicates correlation to MN 5 in the European Land Mammal Zonation (Pickford & Senut, 1999) in agreement with this assessment, corresponding to the Middle Miocene (Ogg *et al*., 2016).

There can be little doubt therefore that the Bukwa II mammals signify correlation to Faunal Set III of East Africa, and more specifically to the base of FS IIIb, more or less equivalent to European zone MN 5, aged about 16 Ma. The restricted fauna from Bukwa I, in contrast, is of Early Miocene age, Faunal Set I - II, in accordance with the age determination of the lava that caps the succession at Kwongori Hill. It is inferred that the deposits at Bukwa II are in a disconformable relationship with the underlying flaggy tuffs of Bukwa I.

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REFERENCES

Geraads, D., Lehmann, T., Peppe, D.J. & McNulty, K.P., 2016 - New Rhinocerotidae from the Kisingiri localities (lower Miocene of Western Kenya). *Journal of Vertebrate Paleontology*, **36** (**3**): e1103247. doi:10.1080/02724634.2016.1103247.

Geraads, D., McCrossin, M. & Benefit, B., 2012 - A new Rhinoceros, *Victoriaceros kenyensis* gen. et sp. nov., and other Perissodactyla from the Middle Miocene of Maboko, Kenya. *Journal of Mammalian Evolution*, **19**: 57-75.

Grossman, A. & Solounias, N., 2016 - New fossils of Giraffoidea (Mammalia: Artiodactyla) from the Lothidok Formation (Kalodirr Member, Early Miocene, West Turkana, Kenya) contribute to our understanding of early giraffoid diversity. *Zitteliana*, **B32**: 63-70.

Harrison, T., 1992 - A reassessment of the taxonomic and phylogenetic affinities of the fossil catarrhines from Fort Ternan, Kenya. *Primates*, **33**: 501-522.

Ogg, J.G., Ogg, G.M. & Gradstein, F.M., 2016 - *A Concise Geologic Time Scale 2016,* Elsevier, 240 pp.

Pickford, M., 1981 - Preliminary Miocene mammalian biostratigraphy for western Kenya. *Journal of Human Evolution*, **10**: 73-97.

Pickford, M., 1997 - Reply to Van der Made, 1995. *Paleontologia I Evolucio*, **30-31**: 269-274.

Pickford, M., 1998 - Dating of the Neogene Old World anthropoid fossil record: essential base for phylogenetic analysis, biogeography and palaeoecology. *Primatologie*, **1**: 27-92.

Pickford, M., 2016 - Revision of European Hyotheriinae (Suidae) and Doliochoeridae. *Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie*, **44**: 1-270.

Pickford, 2017a - Revision of «peccary-like» Suoidea (Artiodactyla : Mammalia) from the Neogene of the Old World. *Münchener Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie*, **46**: 1-144.

Pickford, M., 2017b - Bukwa dating. *Geo-Pal Uganda*, **11**: 12-22.

Pickford, M., 2017c - Bukwa Rodentia and Creodonta, *Geo-Pal Uganda*, **11**: 44-48.

Pickford, M., 2017d - Bukwa Afrotheria, *Geo-Pal Uganda*, **11**: 49-53.

Pickford, M., 2017e - Bukwa II Rhinocerotidae, *Geo-Pal Uganda*, **11**: 66-70.

Pickford, M., 2017f - Bukwa II Suiformes, *Geo-Pal Uganda*, **11**: 71-79.

Pickford, M., 2017g - Bukwa II Ruminants, *Geo-Pal Uganda*, **11**: 80-91.

Pickford, M., Attia, Y.S. & Abd el Ghany, M.S., 2001 - Discovery of *Prolibytherium magnieri* (Climacoceratidae, Artiodactyla) in Egypt. *Geodiversitas*, **23** (**4**): 647-652.

Pickford, M., Musiime, E., Musalizi, S., Gommery, D. & Senut, B., 2017 - Bukwa II Hominoidea. *Geo-Pal Uganda*, **11**: 54-65.

Pickford, M. & Senut, B., 1997 - Cainozoic mammals from coastal Namaqualand, South Africa. *Palaeontologia Africana*, **34**: 199-217.

Walker, A., 1968 - The lower Miocene fossil site of Bukwa, Sebei. *Uganda Journal*, **32** (**2**): 149-156.

Walker, A., 1969 - Fossil mammal locality on Mount Elgon, eastern Uganda. *Nature*, **223**: 591-593.

Winkler, A., MacLatchy, L. & Mafabi M., 2005 - Small rodents and a lagomorph from the early Miocene Bukwa locality, Eastern Uganda. *Palaeontologia Electronica*, **8** (**1**): 24A; aeo-electronica.org/2005_1/winkler24/issue1_05.htm.

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