Evidence for rapid faunal change in the early Miocene of East Africa based on revised biostratigraphic and radiometric dating of Bukwa, Uganda

Cote, Susanne[a, *]; Kingston, John[b]; Deino, Alan[c]; Winkler, Alisa[d]; Kityo, Robert[e]; MacLatchy, Laura[f]

[a]Department of Anthropology and Archaeology, University of Calgary, 2500 University Drive NW, Calgary, Alberta, T2N 1N4, Canada

[b]Department of Anthropology, University of Michigan, Ann Arbor, Michigan, 48109, USA

[c]Berkeley Geochronology Center, Berkeley, California, 94709, USA

[d]Roy. M. Huffington Department of Earth Sciences, Southern Methodist University and Department of Cell Biology, University of Texas Southwestern Medical Center, Dallas, Texas 75390, USA

[e]Department of Zoology, Makerere University, Kampala, Uganda

[f]Department of Anthropology and Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, 48109, USA

[*]Corresponding author.
E-mail address: scote@ucalgary.ca (S. Cote)

Keywords: Africa, Neogene, *Limnopithecus*, 40-argon 39-argon dating, Biochronology, Faunal list

Abbreviations:
BAR – Baringo; BUK – Bukwa; FAD – first appearance date; KNM – Kenya National Museums; RU – Rusinga; UMP – Uganda Museum, Paleontology; SAM PQ RK – South African Museum, Ryskop Locality; SAES - Società Apparecchi Electrici e Scientifici (manufacturer of vacuum systems for scientific applications); MD – mesiodistal; BL – buccolingual; P4 – upper fourth premolar; M3 – upper third molar.

Abstract

Field expeditions to Bukwa in the late 1960s and early 1970s established that the site had a small but diverse early Miocene fauna, including the catarrhine primate *Limnopithecus legetet.* Initial potassium-argon radiometric dating indicated that Bukwa was 22 Ma, making it the oldest of the East African early Miocene fossil localities known at the time. In contrast, the fauna collected from Bukwa was similar to other fossil localities in the region that were several million years younger. This discrepancy was never resolved, and due to the paucity of primate remains at the site, little subsequent research took place.

We collected new fossils at Bukwa, reanalyzed the existing fossil collections, and provided new radiometric dating. $^{40}Ar/^{39}Ar$ incremental heating ages on lavas bracketing the site indicate that the Bukwa fossils were deposited ~19 Ma, roughly 3 Ma younger than the original radiometric age. Our radiometric dating results are corroborated by a thorough reanalysis of the faunal assemblage. Bukwa shares taxa with both stratigraphically older localities (Tinderet, Napak) and with stratigraphically younger localities (Kisingiri, Turkana Basin) perfectly corresponding to our revised radiometric age.

This revised age for Bukwa is important because it indicates that significant faunal turnover may have occurred in East Africa between 20 and 19 Ma. Bukwa samples immigrant taxa such as large suids, large ruminants, and ochotonids that are absent from stratigraphically older but well-sampled localities in the region, such as Tinderet (~20 Ma) and Napak (20 Ma). Further age refinements for Bukwa and the

entire East African early Miocene sequence will help to constrain the timing of this faunal turnover event, of particular importance in paleoanthropology since this temporal sequence also provides us with what is currently our best window into the early evolution of cercopithecoid and hominoid primates.

Introduction

Bukwa is an early Miocene fossil site in eastern Uganda with a small but diverse assemblage of early Miocene mammals. Unlike many contemporary early Miocene fossil localities in East Africa, early expeditions to Bukwa produced very few primates, with only two isolated catarrhine teeth attributed to *Limnopithecus legetet* (Walker, 1968, 1969; Harrison, 1988).

The precise age of the Bukwa locality has been the subject of considerable debate. Potassium-argon (K-Ar) radiometric ages on mafic lavas indicated that the site was at least 22 Ma, making it the oldest catarrhine fossil locality known in East Africa at the time by roughly 3 Ma (Bishop et al., 1969; Brock and Macdonald, 1969; Bishop, 1971). Pickford (1981, 2002) suggested that the original radiometric dating may be inaccurate and proposed a much younger age of about 17.5 Ma based on biostratigraphic comparisons of the limited faunal remains available at the time.

This discrepancy between the K-Ar age and faunal affinities clearly demonstrates both the need for more precise and accurate geochronology, and for a reanalysis of the faunal remains that incorporates both the original and newly recovered collections. Resolving the chronology and nature of faunal assemblages at Bukwa and other early Miocene localities in East Africa is particularly significant, as this sequence chronicles the mammalian faunal transition from archaic afrotherian-dominated communities to more modern assemblages, in which hominoids and cercopithecoids are important components. Only with a more comprehensive understanding of the chronology and biogeography of associated mammalian communities will we be able to refine hypotheses about how environmental change and community composition in the East African early Miocene may have influenced catarrhine evolution.

Here, we report the results of our fieldwork at Bukwa, including new $^{40}Ar/^{39}Ar$ age determinations and biostratigraphic comparisons of previous and new faunal collections from Bukwa to those from other early Miocene fossil localities in Kenya and Uganda.

Background

Bukwa fossil localities

Bukwa is located on the northeastern slopes of the Mount Elgon volcano at 34° 47.085' E, 1° 17.098' N, approximately 2.25 miles east of the town of Bukwa, Uganda (Fig. 1). The site has two main fossil localities—Bukwa I and Bukwa II. Although Bukwa I was discovered first (Macdonald and Old, 1966), almost all of the mammalian fossils were collected in subsequent years from the Bukwa II locality. Bukwa I is located on the southeastern slope of Kwongori Hill and consists primarily of paleosols that have produced few vertebrate fossils but numerous plant fossils. Bukwa II is comprised of a series of lacustrine horizons exposed in gullies at the base of the western side of Kwongori Hill. The Bukwa II locality is threatened by encroaching agricultural planting and is now fairly limited in surface exposure.

There have been multiple expeditions to Bukwa since Macdonald and Old discovered the site during a regional geologic mapping expedition in 1965 (Macdonald and Old, 1966; Brock and Macdonald, 1969). Macdonald and Old found only invertebrate and plant remains, but a Makerere University expedition led by Walker and Henderson in December 1965 uncovered proboscidean remains at Bukwa I (Walker, 1968). The following year, Walker and Bishop visited the site and found additional fossils from a second collecting area located approximately 100 m away, which they designated Bukwa II. Excavations of the Bukwa II locality took place in 1967, 1968, and 1970 (Walker, 1968, 1969; Hill and Walker, 1972). Pickford and colleagues from the Uganda Palaeontology Expedition visited Bukwa in 1997 and 1998 and collected plants, gastropods, and some mammals (Pickford, 2002). As part of a larger program of research into the Ugandan early Miocene, our team initiated new paleontological, stratigraphic, and geochronological research at Bukwa in 2002.

Stratigraphic and depositional context

Brock and Macdonald (1969), Walker (1968, 1969), and Hill and Walker (1972) provide an overview of the stratigraphy and depositional environments of the fossiliferous sequence at Bukwa. The deposits have been referred to as the Lamitina Beds and consist primarily of silts, tuffs, agglomerates, and lava flows with localized lacustrine sediments that were deposited in a basin (the Lamitina Basin) on topographically irregular, faulted basement gneiss. Sediments exposed at Kwongori Hill consist of a series of lacustrine claystones and siltstones, paleosols, and subaerial and epiclastic tuffs containing invertebrate, plant, and vertebrate fossils (Fig. 2). These deposits are bracketed below by under-saturated lavas that in turn are in depositional contact with the basement complex. Above, the fossiliferous sediments are capped by approximately 4.5 m of a resistant lava flow, which prevented complete erosion of the underlying sedimentary strata (Walker, 1968; Fig. 2). Lacustrine facies indicate at least two intervals of lake transgressions within the sequence, possibly as a result of damming of local drainages by volcanic flows/tuffs or faulting activity. Difficulty in tracing the lake facies laterally suggests that the lake was relatively limited in extent. Although plant and invertebrate fossils are scattered throughout the section, the vertebrate fossils are concentrated in lacustrine facies (corresponding generally to the green ostracod clay[1] described in Walker, 1969) near the base of the section (Walker, 1969; Hill and Walker, 1972; Winkler et al., 2005).

Age of the Bukwa deposits

In the 1960s, K-Ar dating of the lavas bracketing the Bukwa fossil horizons indicated that the site was approximately 22 Ma (Walker, 1968, 1969; Bishop et al., 1969). These first K-Ar samples from Bukwa came from the bracketing lavas above and below the fossil localities and were processed in two different laboratories. The nephelinitic lava that caps the sequence and sits at the top of Kwongori Hill (Lava 5 in Brock and Macdonald, 1969) produced ages of 20.1 ± 1.3 Ma by Armstrong at Yale (Walker, 1968; Brock and Macdonald, 1969; reported as 19.8 +/- 1.5 Ma in Bishop et al., 1969) and 22.0 ± 0.2 Ma and 21.9 ± 0.2 Ma by Miller at the Geochronology Laboratory at Cambridge (Walker, 1968; Bishop et al., 1969:Table 2; Brock and Macdonald, 1969). A

[1] In a previous publication (Winkler et al., 2005), we noted that William Downs, who collected sedimentary samples for screening, believed the fossils were coming from the junction between the green claystone and an overlying brown "marl." We hereafter consider the “marl” to be a tuff.

sample from the underlying lava flow at the base of Kwongori Hill (Lava 2 in Brock and Macdonald, 1969) yielded a K-Ar date of 17.4 ± 0.3 Ma (Walker, 1968; Brock and Macdonald, 1969; reported as 17.2 ± 0.4 Ma in Bishop et al., 1969) but was considered anomalous because it was stratigraphically inconsistent with the age of the overlying lava and the sample exhibited alteration features that may have resulted in argon leakage (Walker, 1968; Brock and Macdonald, 1969). The lower lava flow was later resampled and produced two age determinations of approximately 24 Ma (Bishop, 1971; Bishop and Miller, 1972:Appendix I, p. 469; actual dates reported in Pickford, 1981) that were chronostratigraphically consistent with the age of the capping lava. Attempts to constrain the age of the site by a preliminary paleomagnetic study of four lavas underlying the site proved inconclusive (Brock and Macdonald, 1969).

K-Ar dating for Bukwa therefore produced seemingly consistent results, indicating that the site was at least 22 Ma (bracketing dates at 22 and 24 Ma; Bishop, 1971). This made Bukwa the oldest of the early Miocene catarrhine fossil localities known at the time (Bishop et al., 1969; Bishop, 1971). Walker (1968, 1969) immediately recognized that the fossils found at Bukwa resembled those from younger sites in the region such as the Kisingiri sequence exposed on Rusinga Island, which at the time was dated to 17.0–18.5 Ma (Van Couvering and Miller, 1969). Thus, given the available geochronological evidence, it appeared to Walker that “East African faunas remained substantially unchanged for the period from 22.0 to 17.0 Ma” (Walker, 1969:593).

Further studies have since demonstrated that faunas across East Africa were not stable throughout the early Miocene. The discovery of early Miocene localities in the

Turkana Basin (Arambourg, 1933; Savage and Williamson, 1978; Boschetto et al., 1992; Leakey et al., 2011), as well as additional fossil collecting at Kisingiri and Tinderet in Western Kenya, and at Napak and Moroto in Uganda, have provided unequivocal evidence for faunal evolution throughout the early Miocene (Fig. 1; Pickford and Andrews, 1981; Pickford, 1986b; Pickford et al., 1986a, b; Drake et al., 1988; Cote, 2008; Peppe et al., 2009). Unfortunately, this perceived faunal change remains untethered to accurate absolute ages at several localities.

While Bukwa clearly has early Miocene affinities, no effort has yet been made to reassess the age using more advanced dating techniques, such as the incremental heating $^{40}Ar/^{39}Ar$ technique (Merrihue and Turner, 1966; McDougall and Harrison, 1999). Pickford (1981) questioned the K-Ar age for Bukwa, based on the faunal similarities he observed between Bukwa and other sites between 18–16.5 Ma, and suggested that the site was younger than 22 Ma. More recently, Pickford (2002:216) has suggested an age “younger than Rusinga” at 17.5 Ma, based on limited faunal comparisons of material he collected from Bukwa in 1997 and 1998. In subsequent publications, he has suggested an age as young as 17.2 Ma (Pickford, 2009) or even “basal middle Miocene” (Pickford, 2007:88). Other authors seem to have accepted a tentative date of ~17.5 Ma (e.g., Werdelin, 2010; Geraards, 2010a, b; Harrison, 2010), but this date is based on biostratigraphic comparisons of only a few taxa, rather than the complete fossil assemblage, and is at odds with the original published radiometric dates for the site.

Materials and methods

$^{40}Ar/^{39}Ar$ dating

Two nephelenitic alkaline mafic lava flows were sampled for dating by the laser incremental heating $^{40}Ar/^{39}Ar$ method (Fig. 2): 'Lava 5' of Brock and Macdonald (1969) capping the Kwongori Hill above the Bukwa fossil site, and 'Lava 2' (Brock and Macdonald, 1969) immediately underlying the Bukwa fossiliferous sequence and overlying the gneissic metamorphic basement. 'Lava 2' was sampled once (sample designation BU-1016: Lab ID 22688), while 'Lava 5' was sampled twice (sample BU-1015: Lab ID 22686; sample BU-1014: Lab ID 22687). Groundmass in the size range 250–400 microns was prepared from these samples using conventional separation techniques and irradiated in a single package for three hours in the CLICIT facility of the Oregon State University TRIGA reactor, using sanidine from the Fish Canyon Tuff of Colorado as a monitor mineral (orbitally tuned age of 28.201 ± 0.023 1σ Ma; Kuiper et al., 2008). Reactor-induced isotopic production ratios for this irradiation were: $(^{36}Ar/^{37}Ar)_{Ca} = 2.65 \pm 0.02 \times 10^{-4}$, $(^{38}Ar/^{37}Ar)_{Ca} = 1.96 \pm 0.08 \times 10^{-5}$, $(^{39}Ar/^{37}Ar)_{Ca} = 6.95 \pm 0.09 \times 10^{-4}$, $(^{37}Ar/^{39}Ar)_{K} = 2.24 \pm 0.16 \times 10^{-4}$, $(^{38}Ar/^{39}Ar)_{K} = 1.220 \pm 0.003 \times 10^{-2}$, $(^{40}Ar/^{39}Ar)_{K} = 2.5 \pm 0.9 \times 10^{-4}$. Atmospheric $^{40}Ar/^{36}Ar = 298.56 \pm 0.31$ (Lee et al., 2006) and decay constants were according to Min et al. (2000).

Following irradiation, $^{40}Ar/^{39}Ar$ gas extractions were performed under ultra-high vacuum using a CO_2 laser fitted with an integrator lens to yield a quasi-uniform, 6 X 6 mm beam for progressive, step-wise heating of ~5–25 mg of groundmass. Two to four aliquots from each sample were analyzed in 13–16 steps of increasing laser power until all gasses were extracted. The sample gasses were exposed for several minutes to an approximately -130°C cryosurface to trap H_20 and to hot SAES getters to remove reactive compounds (CO, CO_2, N_2, O_2, and H_2). Cleanup was followed immediately by measurement of five argon isotopes on one of two MAP 215-50 mass spectrometers for approximately 30 minutes. Further details of irradiation procedure, argon analysis, and data reduction are provided in Deino et al. (2010).

Paleontology

We visited Bukwa in 2002, 2003, and 2015 to collect fossils and samples for radiometric dating. Our paleontological surface collections were augmented through wet-screening sediments from the green clay deposits in the upper portion of the lacustrine sequence at Bukwa II (Fig. 2; see also Winkler et al., 2005). Preliminary faunal interpretations (Winkler et al., 2005) and age determinations (MacLatchy et al., 2006) were based on results from the 2002 and 2003 field seasons[2].

In addition to faunal identification of specimens collected as part of this study, we reanalyzed all of the mammalian fossil specimens from earlier expeditions (Walker,

[2] All fossils collected by our team have been re-accessioned using a new numbering system mandated by the Uganda National Museum consisting of the abbreviation for the museum division name (Uganda Museum, Paleontology or UMP), followed by the three-letter site abbreviation and site number in roman numerals (Bukwa II is BUKII and Bukwa I is BUKI), the last two digits of the year of discovery, an apostrophe, and the accession number: [museum] [site] [year]’[number]. In this paper, we refer to the specimens previously published as BUMP (Boston University/Uganda Museum/Makerere University Paleontology Project) by their new designations. For example, BUMP 1022 is now UMP BUKII 02'1022. In this re-accessioning process, none of the numerical portions of previous specimen designations have changed.

1968, 1969; Hill and Walker, 1972; Pickford, 2002). Most of the previously collected fossils from Bukwa are housed at the Uganda Museum in Kampala, although some of the material that was originally found at Bukwa could not be relocated, including a lagomorph tooth found in the original collections (A. Walker, pers. comm.) and much of the material from the controlled excavation in 1970 (Hill and Walker, 1972). Some of the material from the 1970 excavation is now housed in the National Museums of Kenya in Nairobi, perhaps brought over during a period of political instability in Uganda (A. Hill, pers. comm.). This material includes some of the most complete material from Bukwa II, including many identifiable specimens. All new material from our team's field collections is housed in the Uganda Museum, Kampala.

We identified the fossils from Bukwa through detailed comparisons with original material from other early Miocene fossil sites in the region. These included: the Ugandan localities of Napak (20 Ma; MacLatchy et al., 2006) and Moroto (>20.6 Ma; Gebo et al., 1997); the Kisingiri sequence in Western Kenya that outcrops on Rusinga and Mfangano Islands (~ 18 Ma; Drake et al., 1988); the Tinderet sequence, also located in Western Kenya and including the localities of Songhor, Koru, Legetet, Chamtwara, Mteitei Valley, and Kapurtay (~ 20 Ma; Bishop et al., 1969); and the Turkana Basin localities of Kalodirr, Moruorot, Loperot, and Buluk (all likely <17.5 Ma; McDougall and Watkins, 1985; Boschetto et al., 1992). See Discussion for further information on recent updates to the age constraints for the comparative material.

Results

^{40}Ar/^{39}Ar dating

Incremental-heating spectra for the completed experiments are shown in Figure 3; full analytical data are supplied in Supplementary Online Material (SOM) Appendix A, while evaluation of the incremental heating data is summarized in Table 1. Yields of radiogenic versus atmospheric ^{40}Ar were fairly high (~25–100 % ^{40}Ar*) after initial low-temperature outgassing steps. Atomic ratio Ca/K values were ~0.1–1.0 in the central portions of the release spectrum, except in the latter stages of the release when more retentive Ca-bearing phases were contributors (e.g., augite and hornblende). Most aliquots yielded apparent-age plateaus. These plateaus are used to identify the most geologically representative eruption age from a particular experiment, and as is conventional, are defined as a minimum of three contiguous steps encompassing at least 50% of the total ^{39}Ar yield, wherein all steps meet an inclusion criterion. In this analysis, the criterion used to judge whether a step should be included is that all candidate steps together must yield a valid isochron derived through isotope correlation analysis (^{36}Ar/^{40}Ar vs. ^{39}Ar/^{40}Ar). A valid isochron is where analytical scatter alone can explain the observed dispersion about the isochron fit line (at the 95% probability level). Two aliquots failed to yield a plateau and showed pronounced step-wise increasing ages through the initial 25–80% of the experiments. These two were performed on a different extraction line/mass spectrometer setup than the others. The spectrometer data for these aliquots exhibit the effects of incomplete removal of non-noble gasses (non-linear isotope abundances vs. time of measurement in the mass spectrometer), hence are considered invalid.

The identified plateaus range from ~19.6–18.6 Ma and yield weighted-mean ages of 19.37 ± 0.22 Ma (2σ SE), 19.08 ± 0.18, and 19.0 ± 1.1 for samples BU-1014, BU-1015, and BU-1016, respectively (Table 1). The first two samples are from the lava capping the hill at Bukwa, and when combined give an overall minimum age for the fossiliferous strata of 19.16 ± 0.14 Ma. The maximum age is 19.0 ± 1.1 given by the lava underlying the site (BU-1016). The ages of the bounding lavas are in fact indistinguishable due to the order-of-magnitude higher uncertainty in the age of the lower lava. These ages differ slightly from those originally reported in an abstract (MacLatchy et al., 2006) due to revision of the age of the dating standard used, and use of the new plateau/isochron identification algorithm described above.

Paleontology

Our team recovered fossils from both the Bukwa I and II localities. At Bukwa I, we recovered gastropods, plant fossils, and some indeterminate bone fragments. The majority of fossils, and all mammals, came from Bukwa II. Therefore, this paper will focus on the material from Bukwa II.

The total sample of fossils that we collected from Bukwa II is small, but contains mammals, other vertebrates, gastropods, crabs, and plants. In total, we have collected approximately 200 vertebrate specimens identifiable to taxon and/or body part. Non-mammal vertebrates collected include fish vertebrae and teeth, crocodile teeth and osteoderms, and turtle scutes. This mixture of terrestrial and aquatic fauna is consistent with the depositional setting of Bukwa II, which is primarily lacustrine. Almost all specimens were recovered from the surface of the deposits, except for small samples of vertebrate teeth and bone collected via wet-screening of discrete samples of the green claystone unit (Winkler et al., 2005; Murray et al., 2017).

In general, the Bukwa mammalian fauna is biased towards larger taxa, and small species are relatively poorly sampled, particularly in comparison to other early Miocene sequences in the region such as Tinderet, Napak, and Kisingiri. In addition, remains from Bukwa II are generally quite fragmentary, making identification challenging. This is reflected in the faunal list, which includes several taxa that are identified only to the genus level or above. This pattern of bone preservation fits with Hill and Walker's (1972) hypothesis that fossil remains were likely accumulated through fluvial action associated with small lakes or ponds, and that the assemblage may have been subjected to post-depositional trampling.

Table 2 provides a composite mammalian faunal list for Bukwa II. In addition to new material reported for the first time, the identifications of some previously collected fossils have been revised, and others have been updated to reflect current taxonomy for African fossil mammals (e.g., Werdelin and Sanders [2010] and references therein). Through new collections and reanalysis of existing collections, we have added several taxa to the Bukwa II assemblage, including an ochotonid (Lagomorpha), an erinaceid (Erinaceomorpha), the rodents *Ugandamys downsi* (Winkler et al., 2005), *Afrocricetodon songhori*, *Lavocatomys* sp., *Diamantomys* sp., the chalicothere "*Butleria" rusingensis*, the rhinocerotid *Brachypotherium heizelini*, two additional species of pecoran ruminants, and two additional species of catarrhine primates (Cote and MacLatchy, 2017; MacLatchy and Cote, 2017).

Notable changes from previous identifications in the literature include the rhinocerotids. All of the original rhinocerotid dental material found in the early expeditions (Walker, 1968, 1969; Hooijer, 1971, 1978) can be attributed to *Chilotheridium* cf. *pattersoni.* Two astragali likely belong to a single individual and are attributed to *Brachypotherium heizelini*. Other previously reported rhinocerotid taxa do not appear to be present. We see no evidence for the rhinocerotid genera "*Dicerorhinus"* (Walker, 1968, 1969; now referred to as *Rusingaceros* [Geraards, 2010a]) or for an elasmotherine (Geraards, 2010a). These changes are of limited biostratigraphic significance because the general taxonomy of African Miocene rhinocerotids is in need of major revision.

The biostratigraphic hypothesis that Bukwa was only 17.5 Ma largely rests on Pickford's interpretations of the Bukwa suids and hyraxes (2001, 2007, 2009). Our own analysis of the taxonomic affinities of the Bukwa suids and hyracoids are markedly different and fully congruent with our radiometric dating results (see SOM Appendix B for a detailed discussion on the taxonomy of Bukwa hyracoids and suids).

Pickford (2009) named a new species of hyrax from Bukwa, *Prohyrax bukwaensis,* based on a single mandible collected in the 1960s and previously referred to *Meroehyrax bateae* (Walker, 1968, 1969; Meyer, 1978). *Prohyrax* is a middle Miocene taxon and central to Pickford's argument that the Bukwa fauna shows middle Miocene affinities. In contrast, we see strong similarities between the Bukwa specimen and the type material from Kisingiri and concur with others that the best attribution is *M. bateae* (Meyer, 1978; Rasmussen and Gutierrez, 2009, 2010).

Pickford (2001, 2009) identified fragmentary suid teeth from Bukwa as *Kenyasus namaquensis,* which is also found in early Miocene Namibian deposits (Pickford and Senut, 1997) and the middle Miocene locality of Kipsaramon in Kenya (Pickford, 2007). This is significant because it could suggest that Bukwa has faunal ties to southern African localities, and/or affinities with the middle Miocene of East Africa. In our opinion, because the Bukwa material is poorly preserved and lacks the diagnostic features of *K. namaquensis*, there is insufficient evidence to tie the Bukwa *Kenyasus* material to *K. namaquensis* rather than to the East African early Miocene species *Kenyasus rusingensis*.

In summary, we see no evidence that the Bukwa hyracoids or suids show any middle Miocene affinities. A comprehensive reanalysis of the entire Bukwa fauna instead shows that the fauna has clear early Miocene affinities, with strong similarities to the 20 Ma Tinderet and Napak sequences and the slightly younger Kisingiri and Turkana Basin sites.

Discussion

The $^{40}Ar/^{39}Ar$ results presented here indicate that the Bukwa I and II fossil localities formed approximately 19 million years ago, almost three million years younger than previously reported (Bishop et al., 1969; Brock and Macdonald, 1969). This result should not be surprising, as several of the original radiometric age determinations for

East African early Miocene localities have likewise been substantially revised using more modern dating techniques.

First, new radiometric dating using single crystal $^{40}Ar/^{39}Ar$ incremental heating analyses for new samples from Moroto have revised its age assignment from the middle Miocene (Bishop et al., 1969) to >20.6 Ma (Gebo et al., 1997). Similarly, preliminary $^{40}Ar/^{39}Ar$ results from the Napak localities suggest an age closer to 20 Ma (MacLatchy et al., 2006), not 19 Ma as originally suggested (Bishop et al., 1969). Finally, there have been substantial revisions to the age of the Kisingiri sequence on Rusinga and Mfangano Islands. Early K-Ar dates for the Kisingiri sequence were not internally consistent, but suggested that most of the fossiliferous deposits were between 18.5 and 17.0 Ma (Van Couvering and Miller, 1969). Drake et al (1988) re-dated the Kisingiri sequences using K-Ar dating. Their work substantially revised the age by condensing the age of the main fossil-bearing sequence to a short interval of approximately 0.5 million years at 17.8 Ma.

More recently, Peppe and colleagues (2011, 2016, 2017) have begun to reassess the age of the Kisingiri sequence using updated dating techniques. Their preliminary dating results using $^{40}Ar/^{39}Ar$ and paleomagnetism indicate that the oldest levels (Wayondo Formation) may be as old as 20 Ma, and that the top of the Hiwegi Formation is approximately 18 Ma (Peppe et al., 2009, 2011, 2016, 2017; McCollum et al., 2012). This indicates that deposition of the Kisingiri sequence may have occurred over a substantially longer period of time than suggested by Drake et al. (1988) and that previous analyses of the Hiwegi fossil faunas that have assumed near-contemporaneity of Hiwegi Formation localities may be inaccurate.

Other early Miocene East African localities have yet to be re-dated. Most critically, the original K-Ar dates from the 1960s for the Tinderet sequence have not been revised. The Biotite Tuff (part of the Calcified Tuff Member), located just below the main deposits at Songhor, produced ages of 19.9 +/-0.6 and 19.7 +/- 0.5 Ma (Bishop et al., 1969). Published radiometric dates from the nearby Koru localities are similar (19.5 +/- 0.3 Ma; 19.6 +/- 0.3 Ma; Bishop et al., 1969). If these K-Ar dates are corrected for revised decay constants (Min et al., 2000), then the Tinderet localities are estimated to be between 20.5 and 20 Ma, but this should be confirmed with $^{40}Ar/^{39}Ar$ dating and paleomagnetism.

Incorporating these revised radiometric dates into a provisional regional chronology places Bukwa in the middle of a sequence of East African fossil localities that documents both the in situ evolution of African mammals, including catarrhine primates, and the migration of Eurasian mammals into Africa throughout the Miocene (Fig. 4). If the preliminary revised dates for Kisingiri are correct (Peppe et al., 2011, 2016, 2017), then Bukwa would occupy a stratigraphic position roughly contemporaneous with the Wayondo Formation. It would be younger than the Tinderet and Napak sequences (~ 20 Ma), but older than most of the fossil localities in the Kisingiri sequence (Hiwegi Formation; 18.3–18.0 Ma) and the early Miocene sequence in the Turkana Basin with Kalodirr and Moruorot radiometrically dated to 16.8–17.5 Ma (Boschetto et al., 1992), Buluk to < 17 Ma (McDougall and Watkins, 1985), and Loperot presumed to be similar in age to these localities and Kisingiri (Leakey et al., 2011; Grossman et al., 2014).

The hypothesis that Bukwa is ~17.5 Ma (Pickford, 2002) or even younger (Pickford, 2007, 2009) based on perceived faunal similarities to Kisingiri and middle Miocene hyraxes and suids (see Results) is neither supported by new radiometric dating results, nor by a reanalysis of the mammalian fauna from Bukwa. If Bukwa were deposited at the end of the early Miocene or earliest middle Miocene, then its fauna should resemble that of the youngest Kisingiri localities (Kulu Formation) and even incorporate middle Miocene taxa known from localities such as Fort Ternan and Maboko. Instead, our biostratigraphic comparisons demonstrate that the Bukwa fauna shows strong similarities to both the Tinderet and Napak localities, which are slightly older, and the Kisingiri localities, which are slightly younger, in full agreement with its radiometric age (Table 2).

Most striking are the obvious similarities between Bukwa and the Kisingiri faunas, first noted by Walker (1968, 1969) and Pickford (1981). Bukwa samples ochotonids, large pecorans (cf. *Canthumeryx* and *Propalaeoryx*), the suid *Kenyasus*, and the hyracoids *Meroehyrax bateae* and *Afrohyrax championi*. These taxa are notably absent from the well-sampled fossil sequences at Napak and Tinderet (20 Ma); Bukwa is their first appearance (FAD) in East Africa at 19 Ma. All of these taxa are subsequently found at the Kisingiri localities and most are also known from the later Turkana early Miocene localities at Kalodirr, Moruorot, Loperot, and Buluk, though from relatively fragmentary material (Leakey et al., 2011).

The ochotonid *Kenyalagomys* occurs at all early Miocene localities 19 Ma and younger, namely throughout the Hiwegi sequence (Wayondo, Kiahera, Hiwegi, and Kulu

Formations) and also at Kalodirr (Table 2; Drake et al., 1988; Winkler and Avery, 2010; Leakey et al., 2011). *Australagomys*, another early ochotonid, is known from Elisabethfeld, Namibia (Winkler and Avery, 2010), which is poorly dated but generally considered 20–19 Ma (Werdelin, 2010). Therefore, the unnamed Bukwa ochotonid may not be the oldest in Africa, although it is the first known record of the group in East Africa.

The Bukwa hyracoid species *Meroehyrax bateae* and *Afrohyrax championi* are not known from any earlier fossil localities, though both genera have Oligocene representatives from the Turkana Basin (Rasmussen and Gutierrez, 2010). The only other described specimens of *M. bateae* are from Kisingiri, while *A. championi* is also found at Kalodirr and Moruorot in West Turkana (Table 2; Meyer, 1978; Rasmussen and Gutierrez, 2010).

Three of the artiodactyl taxa found at Bukwa are known only at sites 19 Ma and younger (Table 2). *Kenyasus* has been reported from Kalodirr and Moruorot, and Rusinga is the type locality for *K. rusingensis* (Pickford, 1986a; Leakey et al., 2011). The pecoran *Propalaeoryx* is known from Rusinga and Elisabethfeld (Whitworth, 1958; Drake et al., 1988; Cote, 2010), while *Canthumeryx* has been reported from Kalodirr, Moruorot, and Rusinga, as well as at Jebel Zelten in North Africa (Hamilton, 1978; Drake et al., 1988; Harris et al., 2010).

While the faunal similarities between Bukwa and Kisingiri are striking, it is important to note that all other large mammal taxa found at Bukwa are found at Tinderet and Napak as well (Table 2), with the exception of the rhinocerotid genus

Chilotheridium. Bukwa also shares some small mammalian taxa with Tinderet and Napak to the exclusion of the well-sampled Kisingiri localities. In East Africa, the rodents *Bathyergoides neotertiarius* and *Afrocricetodon songhori* are known exclusively from the set of early Miocene localities at ~ 20 Ma and now from Bukwa. Neither has been found at Kisingiri, despite an abundant record of small mammals, or at the early Miocene localities in the Turkana Basin. The observation that taxa are shared amongst both the older (Tinderet and Napak) and younger localities (Kisingiri and Turkana) is compatible with the radiometric data indicating that Bukwa is 19 Ma, intermediate in age between these well-sampled sequences.

It has long been recognized that faunal composition of the Kisingiri localities differs from earlier Miocene faunas found at Napak and Tinderet (corresponding to Faunal Sets I and II in Pickford, 1981). As reviewed above, the main faunal differences are in the ochotonids, ruminants, suids, and hyracoids. Several representatives of these groups are absent at Tinderet and Napak, but have their FAD at Bukwa. Our revised age for Bukwa allows us to constrain this faunal turnover event to between 20 and 19 Ma. Given the fact that most of these taxa are likely immigrants from Eurasia, we can characterize this faunal turnover event as one likely driven by immigration into the region.

While we believe that our faunal and radiometric dating strongly suggests a major faunal turnover event between Napak/Tinderet (20 Ma) and Bukwa (19 Ma), an alternative explanation is that the regional mammalian faunas are stable and that local variations are the result of habitat differences between these areas during the early

Miocene (e.g., Pickford, 1981). Pickford (2002) has suggested that the Bukwa fauna may be sampling a more open environment, including grasslands. The main evidence for this hypothesis is the paucity of primates at Bukwa, which Pickford (2002) interprets as signaling a lack of suitable catarrhine habitat (i.e., forest), the presence of fossilized grasses at Bukwa I, and paleoecological inferences from gastropod fossils.

While only two primate fossils have been published, new catarrhine specimens were recovered during our 2015 field season, adding at least two additional taxa (MacLatchy and Cote, 2017; Cote and MacLatchy, 2017, in prep). Catarrhines may actually not be less abundant than at other early Miocene fossil localities when overall fossil sample sizes are considered, since fossil collections from Bukwa are small (Cote and MacLatchy, 2017). Furthermore, Pickford's (2002) interpretations of the floral assemblage and gastropod fauna are at odds with the originally published interpretations. Hamilton (1968) states that the majority of fossil plants recovered at Bukwa indicate forested conditions, and that the grasses may represent a localized vegetation successional phase resulting from intermittent ecological disturbance by volcanic activity. In a review of African fossil floras throughout the Cenozoic, Jacobs et al. (2010) concur with Hamilton's interpretations and state that all Bukwa plant assemblages, including the grasses, are consistent with either forested or aquatic habitats. It is worth noting that aquatic habitats are not preserved at Napak or Tinderet, but are present in Kisingiri. This may account for some similarities in the corresponding mammalian faunas, although kubanochoeres, ochotonids, and large pecorans are not known to be hydrophilic taxa. In addition, Pickford's (2002) interpretation of gastropod paleoecology is at odds with that of Verdcourt, who suggests that the Bukwa gastropods indicate an evergreen forest receiving no less than forty inches of rain per year (Verdcourt reported in Walker, 1969). In summary, it seems that there is little compelling data to suggest that the habitats at Bukwa were substantially different from those sampled at other early Miocene localities, particularly those in the Kisingiri sequence that include lacustrine deposits (e.g., Drake et al., 1988).

Even if the habitats at Bukwa and other early Miocene localities are not substantially different, it may be that during this period, East Africa is characterized by strong faunal endemism likely rooted in regional habitat variation. Endemism could be driven partly by the nature of the volcanic edifices themselves, in that each volcano created its own local habitat that may have served as a 'refugium' of forest habitat separated from other volcanoes by considerable distances up to several hundred kilometers (e.g., Bishop, 1963) and by potentially different plant and animal communities. However, endemism seems an unlikely explanation for similarities between Bukwa and Kisingiri from a biogeographic perspective since Bukwa is located geographically between Tinderet and Napak and is more distant from Kisingiri (Fig. 1).

In summary, we propose that the early Miocene was a period of rapid faunal turnover across East Africa with the slightly older sequences at Tinderet and Napak (~20 Ma) possessing a more archaic fauna than the ~ 19–18 Ma localities at Kisingiri and Bukwa. Specifically, a relatively quick faunal turnover event, in which large ruminants and suids, ochotonids, and new hyraxes enter East Africa, took place between 20–19 million years ago, prior to the deposition of the Bukwa fossils. Testing this hypothesis requires additional information on the immigration of non-African taxa into East Africa, as well as the in situ evolution of African mammals on other parts of the continent during the early Miocene. Most critically, additional dating of the East African early Miocene sequence is needed, particularly for Tinderet and to corroborate preliminary revised age determinations for Napak and Kisingiri, in order to more fully resolve the biochronology of East Africa throughout the Miocene.

Conclusions

Revised $^{40}Ar/^{39}Ar$ dating for Bukwa I and II indicates that both localities are approximately 19 Ma. This is three million years younger than previously reported K-Ar dates, but is supported by mammalian biostratigraphic correlations with other fossil localities in the region. Faunal similarities between Bukwa and Kisingiri corroborate preliminary findings that the fossil localities at Rusinga and Mfangano range in age from ~20–18 Ma and are not all ~17.8 Ma, as was previously thought (Peppe et al., 2009, 2011, 2016, 2017; McCollum et al., 2012). Based on our faunal comparisons, we anticipate that re-dating of the Tinderet deposits using $^{40}Ar/^{39}Ar$, and additional $^{40}Ar/^{39}Ar$ dating to confirm our initial age for Napak (MacLatchy et al., 2006), will confirm that these two sequences are ~20 Ma.

Despite its relatively small fossil sample and limited catarrhine remains, Bukwa is important for our understanding of Miocene community evolution in East Africa because it occupies an intermediate stratigraphic position relative to other, better sampled fossil sequences. Bukwa represents the East African FAD for several immigrating Eurasian lineages (suids, pecoran ruminants, and ochotonids) and allows us to constrain the dates for a strong regional faunal turnover event taking place between the deposition of the Tinderet and Napak sequences at ~ 20 Ma and Bukwa at ~ 19 Ma—a critical period for catarrhine evolution in East Africa.

Acknowledgments

We thank the staff of the Uganda Museum, particularly Rose Mwanja and Amon Mugume, for research support and access to specimens under their care. Mrs. Mary Muungu, Dr. Fredrick Manthi, and Dr. Emma Mbua graciously provided access to comparative collections at the National Museums of Kenya. Alan Walker and Andrew Hill provided useful information on the history of Bukwa. Mercedes Gutierrez, Tab Rasmussen, William Sanders, and Pierre-Olivier Antoine provided expert advice on faunal identifications. Will Downs, Janet Nabaale, Moses Mafabi, Ezra Musiime, David Fox, Kirsten Jenkins, Betty Nalikka, Irisa Arney, Maire Malone, and Herbert Kasozi provided help in the field. Funding was provided by grants from the Wenner-Gren Foundation, the Leakey Foundation, the National Science Foundation (BCS 0215877, BCS 0456589, BCS 1208369, BCS 1241811 to LM; BCS 0524944 to SC; BCS 1241918 to AD), and by the Departments of Anthropology at Boston University and the University of Michigan and the Department of Anthropology and Archaeology at the University of Calgary. We thank all members of the NSF-funded REACHE Project (Research on East African Catarrhine and Hominoid Evolution). This is REACHE publication #7.

References

Arambourg, C., 1933. Découverte d'un gisement de Mammifères burdigaliens dans le Bassin du Lac Rodolphe (Afrique Orientale). C.R. Soc. Geol. Fr. 14, 221–222.

Bishop, W.W., 1963. The later Tertiary and Pleistocene in eastern equatorial Africa. In: Clark Howell, F., Bourliere, F. (Eds.), African Ecology and Human Evolution. Aldine Publishing Company, Chicago, pp. 248–275.

Bishop, W.W., 1971. The late Cenozoic history of east Africa in relation to hominoid evolution. In: Turekian, K.K. (Ed.), The Late Cenozoic Glacial Ages. Yale University Press, New Haven, pp. 493–527.

Bishop, W.W., Miller, J.A. (Eds.), 1972. Calibration of hominoid evolution. Scottish Academic Press, Edinburgh.

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. Am. J. Sci. 267, 669–699.

Boschetto, H.B., Brown, F.H., McDougall, I., 1992. Stratigraphy of the Lothidok Range, Northern Kenya, and K/Ar ages of its Miocene primates. J. Hum. Evol. 22, 47–71.

Brock, P.W.G., Macdonald, R., 1969. Geological environment of the Bukwa mammalian fossil locality, eastern Uganda. Nature 223, 593–596.

Butler, P.M., 1984. Macroscelidea, Insectivora and Chiroptera from the Miocene of east Africa. Palaeovertebrata (Montpellier) 14, 118–198.

Cote, S., 2008. Sampling and ecology in three Early Miocene catarrhine assemblages from East Africa. Ph.D. Dissertation, Harvard University.

Cote, S., 2010. Pecora *incertae sedis.* In: Werdelin, L., Sanders, B. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 731–739.

Cote, S., MacLatchy, L. 2017. Now they're everywhere: new fossil primate remains from Bukwa, Uganda demonstrate that catarrhine primates are ubiquitous at East African early Miocene fossil sites. Am. J. Phys Anthropol. 162 (S64),152.

Deino, A., Scott, G.R., Saylor, B., Alene, M., Angelini, J.D., Haile-Selassie, Y., 2010. $^{40}Ar/^{39}Ar$ dating, paleomagnetism, and tephrochemistry of Pliocene strata of the hominid-bearing Woranso-Mille area, west-central Afar Rift, Ethiopia. J. Hum. Evol. 58, 111–126.

Drake, R.E., Van Couvering, J.A., Pickford, M., Curtis, G.H., Harris, J.A., 1988. New chronology for the early Miocene mammalian faunas of Kisingiri, western Kenya. J. Geol. Soc. 145, 479–491.

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.

Geraards, D., 2010a. Rhinocerotidae. In: Werdelin, L., Sanders, B. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 669–683.

Geraards, D., 2010b. Tragulidae. In: Werdelin, L., Sanders, B. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 729–735.

Grossman, A., Liutkus-Pierce, C., Kyongo, B., M'Kirera, F., 2014. New fauna from Loperot contributes to the understanding of early Miocene catarrhine communities. Intl. J. Primatol. 35, 1253–1274.

Hamilton, A., 1968. Some plant fossils from Bukwa. Uganda J. 32, 157–164.

Hamilton, W.R., 1978. Fossil giraffes from the Miocene of Africa and a revision of the phylogeny of the Giraffoidea. Phil. Trans. R. Soc. Lond. B 283, 165–229.

Harris, J.M., Solounias, N., Geraards, D., 2010. Giraffoidea. In: Werdelin, L., Sanders, B. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 797–811.

Harrison, T., 1988. A taxonomic revision of the small catarrhine primates from the Early Miocene of East Africa. Folia Primatol. 50, 59–108.

Harrison, T., 2010. Dendropithecoidea, Proconsuloidea, and Hominoidea. In: Werdelin, L., Sanders, B. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 429–469.

Hill, A., Walker, A., 1972. Procedures in vertebrate taphonomy; notes on a Uganda Miocene fossil locality. J. Geol. Soc. 128, 399–406.

Holroyd, P.A., Stevens, N.J., 2009. Differentiation of *Phiomys andrewsi* from *Lavocatomys aequatorialis* (n. gen. n. sp.) (Rodentia: Thryonomyoidea) in the Oligo-Miocene interval on continental Africa. J. Vert. Paleontol. 29(4), 1331–1334.

Hooijer, D.A., 1971. A new rhinoceros from the late Miocene of Loperot, Turkana District, Kenya. Bull. Mus. Comp. Zool. 142, 339–392.

Hooijer, D.A., 1978. Rhinocerotidae. In: Maglio, V.J., Cooke, H.B.S. (Eds.), Evolution of African Mammals. Harvard University Press, Cambridge, pp. 371–378.

Jacobs, B., Pan, A., Scotese, C., 2010. A review of the Cenozoic vegetation history of Africa. In: Werdelin, L., Sanders, B. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 57–72.

Kuiper, K.F., Deino, A., Hilgen, F.J., Krijgsman, W., Renne, P.R., Wijbrans, J.R., 2008. Synchronizing rock clocks of earth history. Science 320, 500–504.

Lavocat, R., 1973. Les rongeurs du Miocène d'afrique orientale, Mémoires et travaux de l'institut de Montpellier de l'ecole pratique des hautes etudes, Volume 1. Ecole Pratique des Hautes Etudes, L'Institut de Montpellier, Montpellier.

Leakey, M.G, Grossman, A., Gutierrez, M., Fleagle, J., 2011. Faunal change in the Turkana basin during the late Oligocene and Miocene. Evol. Anthropol. 20, 238–253.

Lee, J.-Y., Marti, K., Severinghaus, J.P., Kawamura, K., Yoo, H.-S., Lee, J.B., Kim, J.S., 2006. A redetermination of the isotopic abundances of atmospheric Ar. Geochimica et Cosmochimica Acta 70, 4507–4512.

López-Antoñanzas, R., Sen, S., Mein, P., 2004. Systematics and phylogeny of the cane rats (Rodentia: Thryonomyidae). Zool. J. Linnean Soc. 142, 423–444.

Macdonald, R., Old, R.A., 1966. The geology of the Bukwa-Greek River Area. Geol. Surv. Uganda, Unpublished Report RM/30.

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. J. Vert. Paleontol. 37(S), 155–156.

MacLatchy, L., Deino, A., Kingston, J., 2006. An updated chronology for the early Miocene of NE Uganda. J. Vert. Paleontol. 26(S3), 93A.

McCollum, M., Peppe, D.J., McNulty, K.P., Dunsworth, H.M., Harcourt-Smith, W., Andrews, A.L., 2012. Magnetostratigraphy of the early Miocene Hiwegi Formation (Rusinga Island, Lake Victoria, Kenya). Geol. Soc. Am. Abstracts with Programs 44(7), 241.

McDougall, I., Harrison, T.M., 1999. Geochronology and Thermochronology by the ^{40}Ar-^{39}Ar Method. Oxford University Press, New York.

McDougall, I., Watkins, R.T., 1985. Age of hominid-bearing sequence at Buluk, northern Kenya. Nature 318, 175–178.

Merrihue, C., Turner, G., 1966. Potassium-argon dating by activation with fast neutrons. J. Geophys. Res. 71, 2852–2857.

Meyer, G.E., 1978. Hyracoidea. In: Maglio, V.J., Cooke, H.B.S. (Eds.), Evolution of African Mammals. Harvard University Press, Cambridge, pp. 284–314.

Min, K.W., Mundil, R., Renne, P.R., Ludwig, K.R., 2000. A test for systematic errors in ^{40}Ar/^{39}Ar geochronology through comparison with U/Pb analysis of a 1.1-Ga rhyolite. Geochim. Cosmochim. Acta 64, 73–98.

Murray, A., Argyrious, T., Cote, S., MacLatchy, L., 2017. The Burdigalian (early Miocene) fish fauna of Bukwa, Uganda. J. Vert. Paleontol. 37(3), e1324460.

Peppe, D.J., McNulty, K.P., Cote, S.M., Harcourt-Smith, W.E.H., Dunsworth, H.M., Van Couvering, J.A.H., 2009. Stratigraphic interpretation of the Kulu Formation (Early

Miocene, Rusinga Island, Kenya) and its implications for primate evolution. J. Hum. Evol. 56, 447–61.

Peppe, D., Deino, A., McNulty, K., Lehmann, T. Harcourt-Smith, W. Dunsworth, H., Fox, D., 2011. New age constraints on the early Miocene faunas from Rusinga and Mfangano Islands (Lake Victoria, Kenya). Am. J. Phys. Anthropol. 144 (Suppl.), 237.

Peppe, D.J., McNulty, K.P., Deino, A.L., Michel, L.A., McCollum, M.S., Driese, S.G., Dunsworth, H.M., Harcourt-Smith, W.E, Jenkins, K.E., Lehmann, T., 2016. Early Miocene paleoenvironments of the Hiwegi Formation on Rusinga Island (equatorial

Africa, Lake Victoria, Kenya) and their implications for hominoid evolution. Geol. Soc. Am. Abstracts with Programs 48(7), doi: 10.1130/abs/2016AM-280981.

Peppe, D.J., Deino, A., McNulty, K.P., McCollum, M., Mitchell, A., Driese, S.G., Dunsworth, H.M., Fox, D., Harcourt-Smith, W.E.H., Jenkins, K., Lehmann, T., Michel, L., 2017. Revised geochronology of the early Miocene faunas from Rusinga Island and Mfangano Island (Lake Victoria, Kenya): Implications for Miocene hominoid evolution and faunal succession. Am. J. Phys. Anthropol. 162(S64), 313.

Pickford, M., 1981. Preliminary Miocene mammalian biostratigraphy for western Kenya. J. Hum. Evol. 10, 73–97.

Pickford, M., 1986a. A revision of the Miocene Suidae and Tayassuidae, (Artiodactyla, Mammalia) of Africa. Tertiary Res. Spec. Pap. 7, 1–83.

Pickford, M., 1986b. Cainozoic palentological sites of western Kenya. Münchner Geowissenschaftliche Abhandlungen 8, 1–151.

Pickford, M., 2002. Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda. C.R. Palévol 1, 213–219.

Pickford, M., 2007. Suidae and Hippopotamidae from the Middle Miocene of Kipsaraman, Kenya and other sites in East Africa. Paleontol. Res. 11, 85–105.

Pickford, M., 2009. New Neogene hyracoid specimens from the Peri-Tethys region and East Africa. Paleontol. Res. 13, 265–278.

Pickford, M., Andrews, P., 1981. The Tinderet Miocene sequence in Kenya. J. Hum. Evol. 10, 11–33.

Pickford, M., Mein, P. 2006. Early Middle Miocene Mammals from Moroto II, Uganda. Beitr. Paläont. 30, 361–386.

Pickford, M. Senut, B., 1997. Cainozoic mammals from coastal Namaqualand, South Africa. Paleontol. Afr. 34, 199–217.

Pickford, M., Senut, B., Hadoto, D., Musisi, J., Kariira, C., 1986a. Découvertes récentes dans les sites miocènes de Moroto (Ouganda Oriental): aspects biostratigraphiques et paleoécologiques. C.R. Acad. Sci. Paris Série II 302, 681–686.

Pickford, M., Senut, B., Hadoto, D., Musisi, J., Kariira, C., 1986b. Nouvelles découvertes dans le Miocène inférieur de Napak, Ouganda Oriental. C.R. Acad. Sci. Paris Série II 302, 47–52.

Rasmussen, D.T., Gutierrez, M., 2009. A mammalian fauna from the late Oligocene of northwestern Kenya. Palaeontographica Abteilung A 288, 1–52.

Rasmussen, D.T., Gutierrez, M., 2010. Hyracoidea. In: Werdelin, L., Sanders, B. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 123–145.

Savage, R.J.G., Williamson, P.G., 1978. The early history of the Turkana depression. Geological Society, London, Special Publications 6(1), 375–394.

Van Couvering, J.A., Miller, J.A., 1969. Miocene stratigraphy and age determinations, Rusinga Island, Kenya. Nature 332, 628–632.

Walker, A., 1968. The lower Miocene fossil site of Bukwa, Sebei. Uganda J. 32, 149–155.

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, B. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 27–43.

Werdelin, L., Sanders, W. (Eds.), 2010. Cenozoic Mammals of Africa. University of California Press, Berkeley.

Whitworth, T., 1958. Miocene ruminants of East Africa. Fossil Mammal. Afr. 15, 1–50.

Winkler, A.J., Avery, D.M., 2010. Lagomorpha. In: Werdelin, L., Sanders, B. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 305–317.

Winkler, A.J., MacLatchy, L., Mafabi, M., 2005. Small rodents and a lagomorph from the early Miocene Bukwa locality, eastern Uganda. Palaeontologia Electronica 8, 24A.

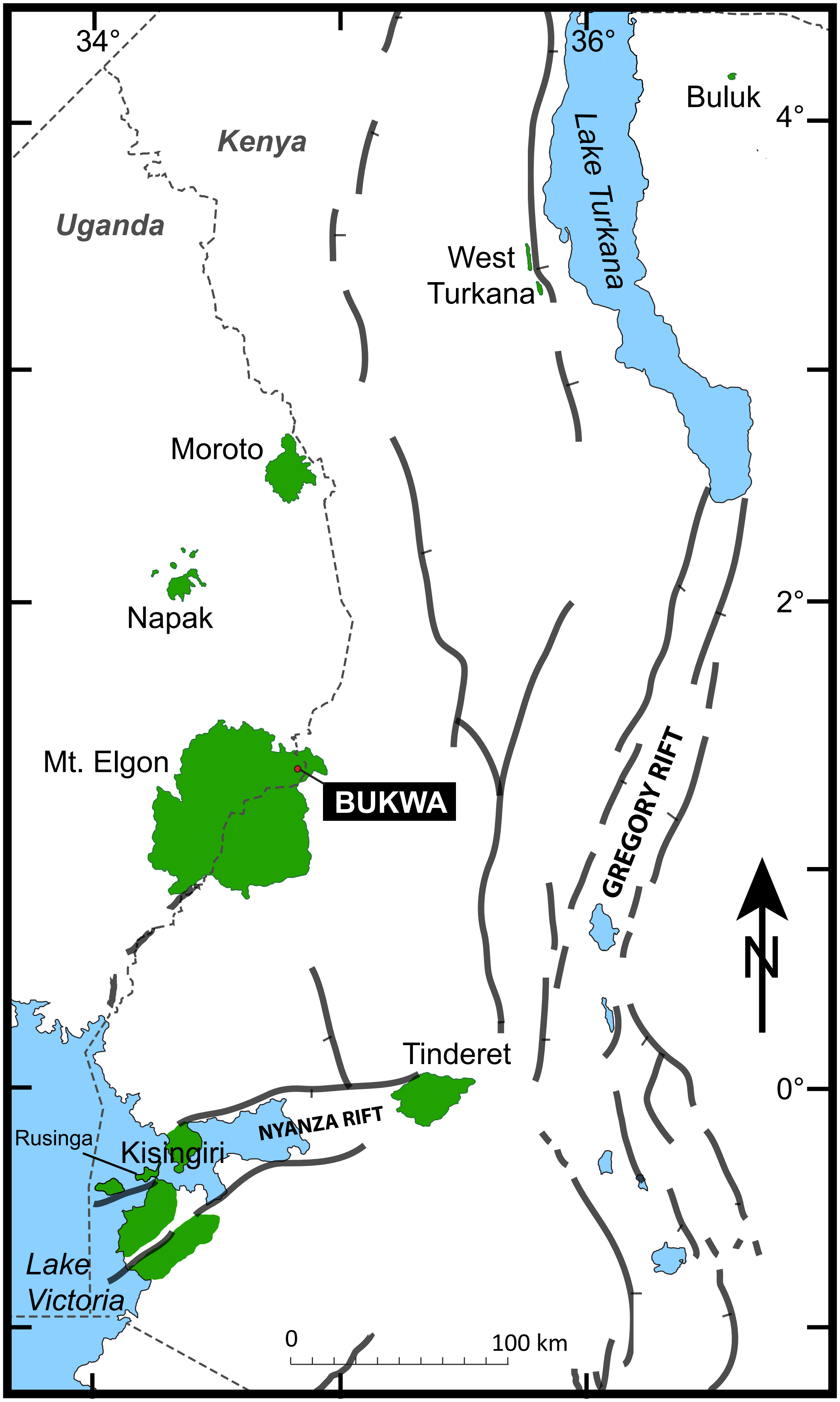
Figure legends

Figure 1. Regional map showing the location of the Bukwa fossil locality and other early Miocene fossil localities mentioned in the text. The green areas denote the current exposures of the ancient volcanoes of Napak, Moroto, Elgon, Tinderet, and Kisingiri. In the Turkana Basin, the green areas indicate the location of sedimentary sequences that have yielded fossil material.

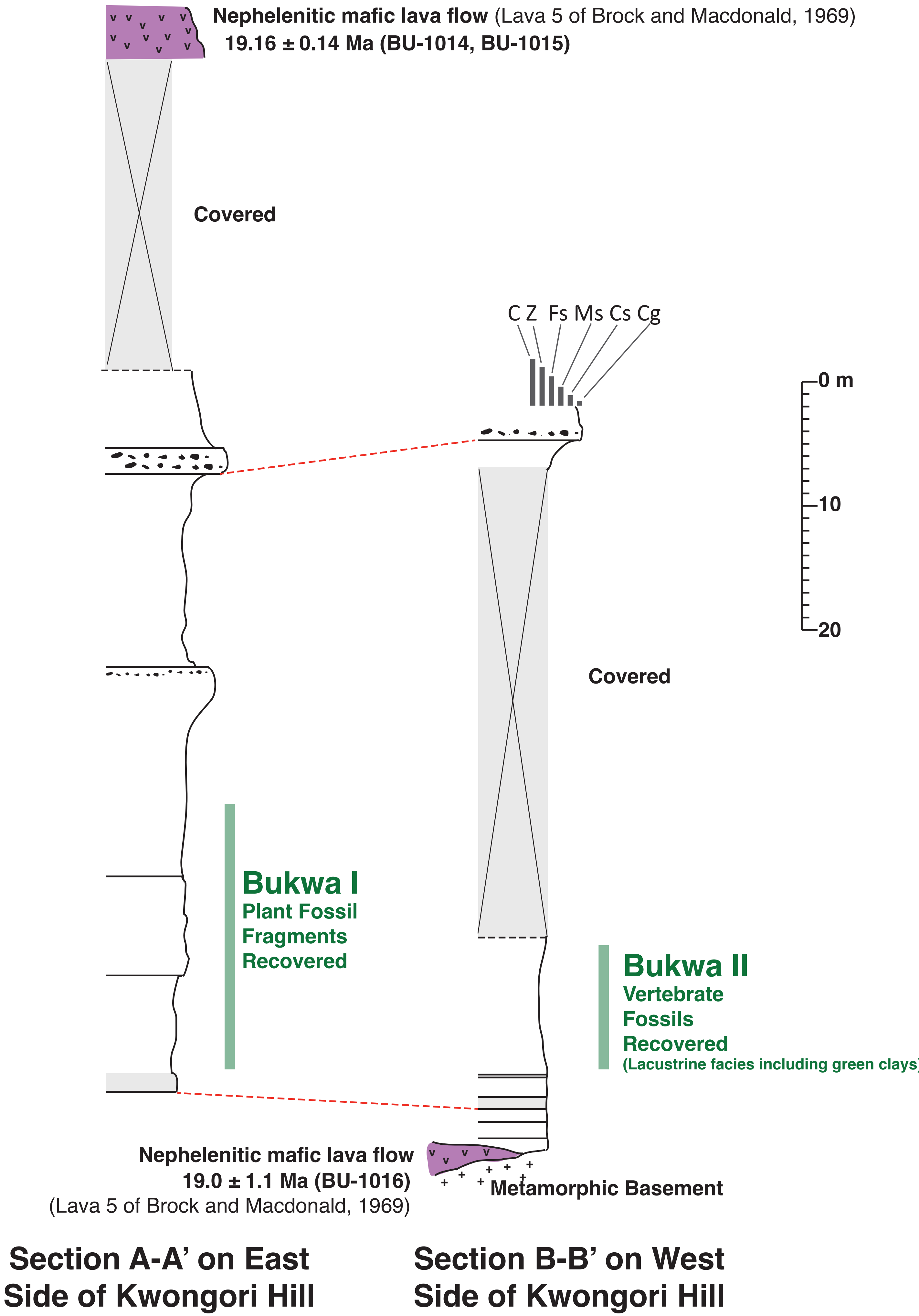
Figure 2. Stratigraphic section for the deposits at Kwongori Hill. Section A-A' was taken at the Bukwa I locality; section B-B' passes through the Bukwa II locality. Underlying and capping lavas with corresponding dates are shown. Grain size indicated.

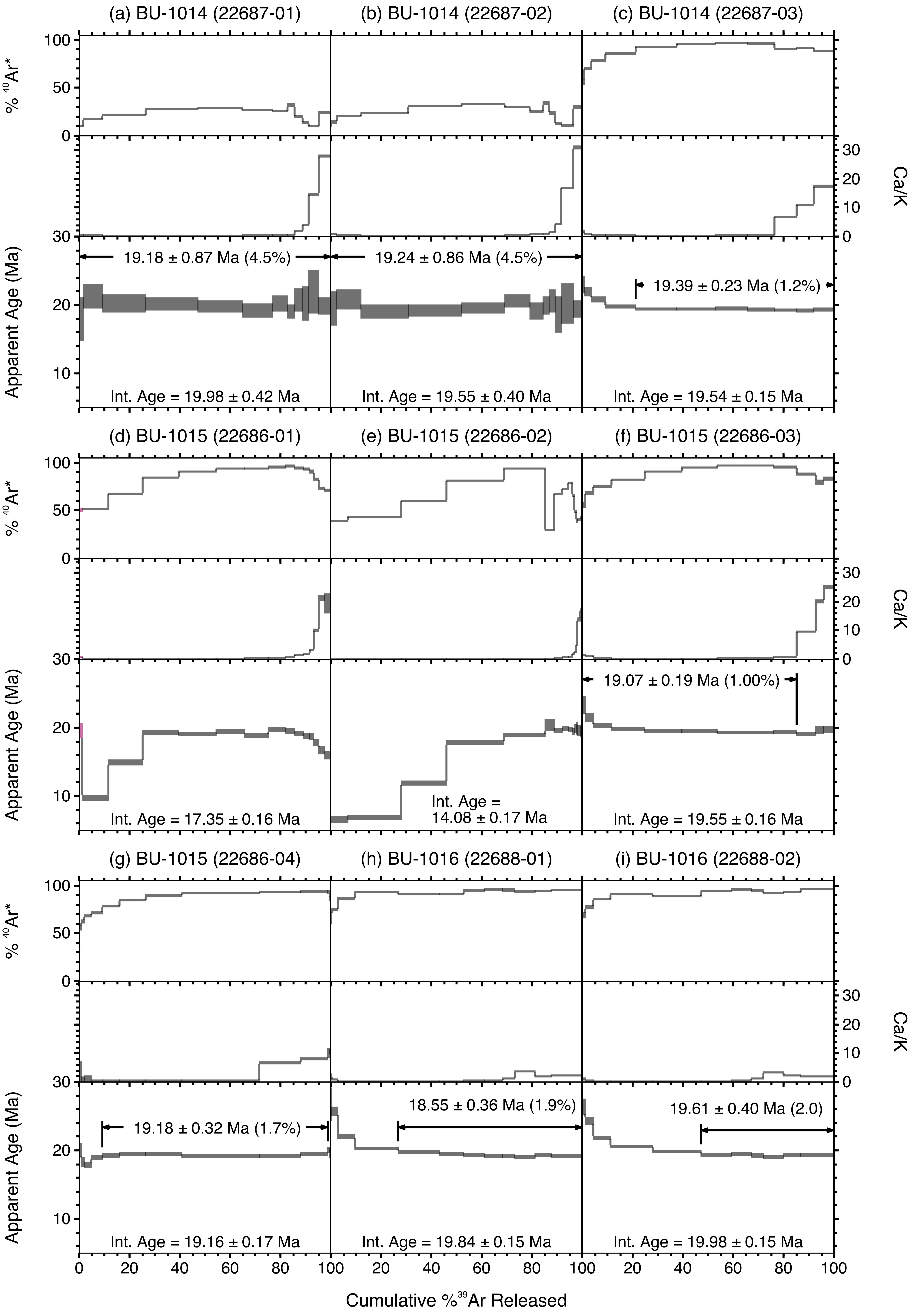
Figure 3. $^{40}Ar/^{39}Ar$ incremental heating release spectra obtained from the groundmass of mafic lavas at the Bukwa site. Age plateaus are identified and quantified by isotope correlation analysis (see text and Table 1). Plateau uncertainties are expressed as 2σ standard errors, expanded by root MSWD (mean square weighted deviation) if MSWD >1.

Figure 4. Chronological sequence of early Miocene fossil localities in East Africa (red) and important taxa that appear first (FAD) in East Africa at Bukwa, or have their last appearance (LAD) in East Africa at Bukwa (blue). See text for further description.

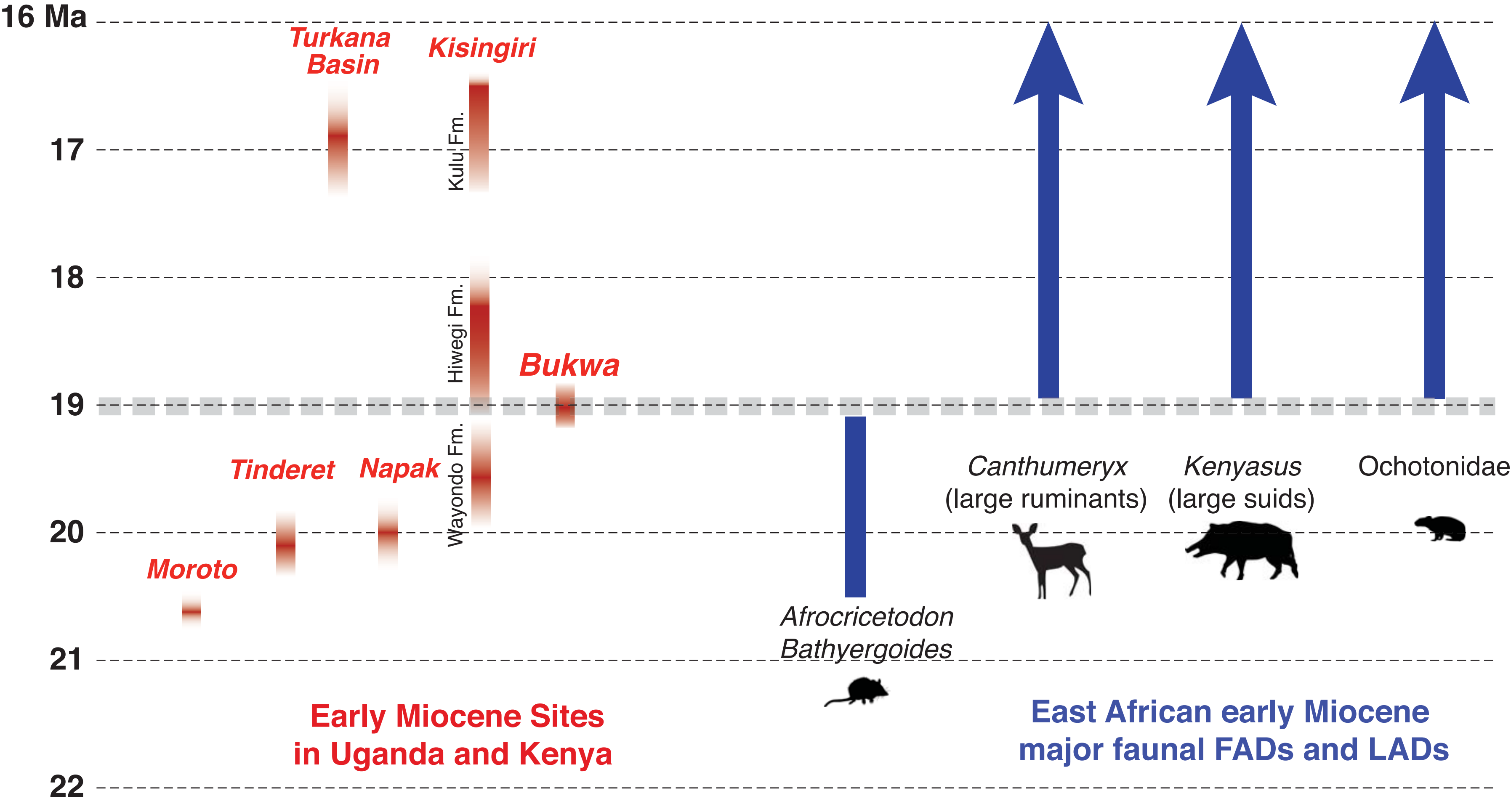


34°
36°
4°
2°
0°
Kenya
Uganda
Buluk
Lake Turkana
West Turkana
Moroto
Napak
Mt. Elgon
BUKWA
GREGORY RIFT
N
Tinderet
NYANZA RIFT
Rusinga
Kisingiri
Lake Victoria
0
100 km


Nephelenitic mafic lava flow (Lava 5 of Brock and Macdonald, 1969)
19.16 ± 0.14 Ma (BU-1014, BU-1015)
Covered
C Z Fs Ms Cs Cg
0 m
10
20
Covered
Bukwa I
Plant Fossil
Fragments
Recovered
Bukwa II
Vertebrate
Fossils
Recovered
(Lacustrine facies including green clays)
Nephelenitic mafic lava flow
19.0 ± 1.1 Ma (BU-1016)
(Lava 5 of Brock and Macdonald, 1969)
Metamorphic Basement
Section A-A' on East Side of Kwongori Hill
Section B-B' on West Side of Kwongori Hill



(a) BU-1014 (22687-01)
(b) BU-1014 (22687-02)
(c) BU-1014 (22687-03)
(d) BU-1015 (22686-01)
(e) BU-1015 (22686-02)
(f) BU-1015 (22686-03)
(g) BU-1015 (22686-04)
(h) BU-1016 (22688-01)
(i) BU-1016 (22688-02)
% 40Ar*
Ca/K
Apparent Age (Ma)
19.18 ± 0.87 Ma (4.5%)
19.24 ± 0.86 Ma (4.5%)
19.39 ± 0.23 Ma (1.2%)
Int. Age = 19.98 ± 0.42 Ma
Int. Age = 19.55 ± 0.40 Ma
Int. Age = 19.54 ± 0.15 Ma
19.07 ± 0.19 Ma (1.00%)
Int. Age = 17.35 ± 0.16 Ma
Int. Age = 14.08 ± 0.17 Ma
Int. Age = 19.55 ± 0.16 Ma
19.18 ± 0.32 Ma (1.7%)
18.55 ± 0.36 Ma (1.9%)
19.61 ± 0.40 Ma (2.0)
Int. Age = 19.16 ± 0.17 Ma
Int. Age = 19.84 ± 0.15 Ma
Int. Age = 19.98 ± 0.15 Ma
Cumulative %39Ar Released



16 Ma
17
18
19
20
21
22
Turkana Basin
Kisingiri
Kulu Fm.
Hiwegi Fm.
Wayondo Fm.
Bukwa
Tinderet
Napak
Moroto
Early Miocene Sites in Uganda and Kenya
Afrocricetodon Bathyergoides
Canthumeryx (large ruminants)
Kenyasus (large suids)
Ochotonidae
East African early Miocene major faunal FADs and LADs

Table 1. $^{40}Ar/^{39}Ar$ analytical data.[a]

	Integrated gas result				Isochron result									
Lab ID	*n*	Mol ^{39}Ar X 10^{-14}	Age (Ma) ± SD (2σ)		*n*	% Gas	MSWD	Prob.	$(^{40}Ar/^{36}Ar)_{tr}$ ± 2σ		Ca/K ± 2σ		Age (Ma) ± MSE (2σ)	
BU-1014; 'Lava 5' capping Kwongori Hill														
22687-01	14	3.6	19.98	± 0.40	14	100.0	0.8	0.61	301	± 4	21.76	± 0.22	19.18	0.86
22687-02	14	2.5	19.55	± 0.38	14	100.0	1.1	0.37	300	± 4	23.66	± 0.27	19.24	0.85
22687-03	13	4.5	19.54	± 0.07	7	78.7	0.9	0.46	279	± 35	14.07	± 0.17	19.39	0.18
											Weighted mean =		***19.37***	***0.22***
BU-1015; 'Lava 5' capping Kwongori Hill														
22686-01	16	11.4	17.35	± 0.11	No valid isochron									
22686-02	15	13.4	14.08	± 0.13	No valid isochron									
22686-03	13	3.6	19.55	± 0.08	10	85.4	1.1	0.38	356	± 12	20.31	± 5.39	19.07	0.13
22686-04	14	3.0	19.16	± 0.09	6	89.5	1.8	0.12	308	± 30	7.32	± 0.24	19.18	0.29
											Weighted mean =		***19.08***	***0.18***
BU-1016; 'Lava 2' underlying section														
22688-01	13	4.4	19.84	± 0.07	8	73.0	1.2	0.29	447	± 66	2.83	± 0.06	18.55	0.34
22688-02	13	4.3	19.98	± 0.07	6	52.8	1.0	0.42	211	± 81	2.68	± 0.05	19.61	0.37
											Weighted mean =		***19.0***	***± 1.1***

[a] n (integrated gas results) = total number of steps in the experiment; n (isochron result) = number of steps included in the isochron; % Gas = percentage of ^{39}Ar included in the isochron steps relative to the total ^{39}Ar yield; MSWD = 'Mean square weighted deviation' is the reduced chi-squared statistic; Prob. = probability that the data define an isochron based on MSWD and degrees of freedom. The assumption of an isochron is rejected if $p < 0.05$ ('No valid isochron'); $(^{40}Ar/^{36}Ar)_{tr}$ = 'Trapped' $^{40}Ar/^{36}Ar$ ratio determined from the isochron linear regression; MSE = modified standard error, equal to the standard error times root MSWD, if MSWD > 1.

Table 2. List of mammalian taxa from Bukwa.[a]

Order	Family	Previous faunal lists[b]	Revised identifications	New collection (Our expeditions and NMK material)	Other Miocene localities with this taxon[c]	Biostratigraphic range within early Miocene
Primates	**Catarrhini (Family *incertae sedis*)**	*Limnopithecus legetet* (UMP 68-22; UMP 68-26/27)[d]			Tinderet (Koru, Chamtwara, Legetet), Napak, Kisingiri (Rusinga)	<= 20 Ma
Macroscelidea	**Macroscelididae**	*Myohyrax oswaldi*	*Myohyrax* sp.[e] (unnumbered vial of teeth, UM)	*Myohyrax* sp. UMP BUKII 02'1746, UMP BUKII 15'2289—molars)	Genus is present but rare at Tinderet (Songhor, Chamtwara) and Napak; more common at Kisingiri (Rusinga, Mfangano, Karungu)	20 Ma–~ 18 Ma
Proboscidea	**Deinotheriidae**	*Deinotherium hobleyi*	*Prodeinotherium hobleyi* (BUK II 1967—deciduous premolar)		Moroto, Tinderet (Koru), Napak, Kisingiri (Rusinga, Mfangano), Turkana (Kalodirr, Moruorot, Buluk, Loperot)	Ubiquitous throughout early Miocene
	Gomphotheriidae	"Indeterminate Mastodonts"	Gomphotheriidae gen. and sp. indet. (BUK II P 67 33—tooth frag)	Gomphotheriidae gen. and sp. indet. (UMP BUKII 02'197—cheek tooth fragment)	Gomphotheres known from Tinderet (Songhor, Legetet), Napak, Kisingiri (Rusinga, Mfangano) and Turkana (Kalodirr, Moruorot, Buluk, Loperot)	<= 20 Ma
Hyracoidea	**Titanohyracidae**	*Megalohyrax championi*	*Afrohyrax championi* (BUK II unnumbered upper molar; Pickford, 2009)	*Afrohyrax championi* (NMK #1 maxilla)	Kisingiri (Rusinga, Mfangano), Turkana (Kalodirr, Moruorot, Buluk, Loperot)	<= 19 Ma
	Pliohyracidae	*Meroehyrax bateae*	*Meroehyrax bateae* (unnumbered mandible[f]; Pickford, 2009)		Kisingiri (Rusinga, Mfangano)	19–~ 18 Ma
Erinaceomorpha	**Erinaceidae**			Erinaceidae gen. and sp. indet. (NMK unnumbered specimen 'B'—lower molar)	Similar erinaceids from Tinderet, Napak, Kisingiri, and Turkana (Moruorot, Kalodirr)	<= 20 Ma
Carnivora/ Creodonta		Unidentified species	Not found[g]			
Lagomorpha	**Ochotonidae**			Ochotonidae gen. and sp. indet (UMP BUKII 02'1021; Winkler et al., 2005)	Ochontids known from Kisingiri (Rusinga, Mfangano), Turkana (Kalodirr)	<= 19 Ma
Rodentia	**Nesomyidae**			*Afrocricetodon songhori* (NMK unnumbered specimen 'A'—molar)	Tinderet (Songhor, Legetet, Chamtwara, Mteitei Valley), Napak	>= 19 Ma
	Pedetidae	*Megapedetes pentadactylus*	*cf. Megapedetes pentadactylus* (unnumbered distal phalanx, incisor fragment)	*cf. Megapedetes pentadactylus* (UMP BUKII 15'2236)	Tinderet (Songhor, Legetet, Chamtwara, Koru, Mteitei Valley), Napak, Kisingiri (Rusinga, Mfangano). A smaller species may be present at Kalodirr.	20 Ma–~ 18 Ma
	Bathyergidae	*Bathyergoides neotertiarius*	*Bathyergoides neotertiarius (* BUK 25'97—left and right mandibles)		Moroto, Tinderet (Songhor, Legetet, Chamtwara, Kapurtay, Mteitei Valley), Napak	>= 19 Ma
	Phiomyidae	*Paraphiomys* cf. *stromeri* "of small size" (specimen B11 and Thryonomyoidea B12 listed in Lavocat, 1973:158)	*Ugandamys downsi* (B12; B11 tentatively referred as cf. *U. downsi*— see also Winkler et al., 2005)	*Ugandamys downsi* (UMP BUKII 02'1022, UMP BUKII 02'1023, UMP BUKII 02'1024, UMP BUKII 02'1025; Winkler et al., 2005)	None	Exclusive to Bukwa
	Thryonomyidae	*Paraphiomys pigotti* (specimens B1-B5 listed in Lavocat, 1973:158)	*Paraphiomys pigotti* (B1, B3, B4, B5)	*Paraphiomys pigotti* (UMP BUKII 15'2237; NMK unnumbered specimens 'C' and 'D'—molars)	Large *Paraphiomys* known from all E.Af. early Miocene localities (Moroto, Tinderet, Napak, Kisingiri, Turkana)	Ubiquitous throughout early Miocene
		Paraphiomys stromeri (specimens B6-B8 in Lavocat, 1973:158)	*Paraphiomys* small sp. (B6-B8)	cf. *Paraphiomys* small sp. (UMP BUKII 02'1026; Winkler et al., 2005)	Similar small *Paraphiomys* known from Tinderet, Napak, Turkana (Kalodirr, Moruorot, Loperot), and Kisingiri (Rusinga, Mfangano)	<= 20 Ma
		Paraphiomys cf. *stromeri* "of small size" (specimen B10 of Lavocat, 1973:158)	*Paraphiomys* cf. *hopwoodi* (B10*)*		According to López-Antoñanzas et al. (2004), *P. hopwoodi* is restricted to Tinderet and Napak.	>= 19 Ma
	Thryonomyoidea (Family *incertae sedis*)	*Paraphiomys stromeri* "of small size" (specimen B9 in Lavocat, 1973:158)	*Lavocatomys* sp. (B9 right dp4)		Genus recognized at Songhor and Rusinga (Holroyd and Stevens, 2009)	20 Ma–~ 18 Ma
	Diamantomyidae		*Diamantomys sp.* (B2 half molar)		Genus known from all African early Miocene localities (Moroto, Tinderet, Napak, Kisingiri, Turkana)	Ubiquitous throughout early Miocene
Perissodactyla	**Rhinocerotidae**	*Chilotherium* sp. nov.	*Chilotheridium* cf. *pattersoni* (right upper premolar and molar series illustrated in Walker [1968], lower molars).	*Chilotheridium* cf. *pattersoni* (NMK unnumbered m3)	Similar to taxon from Loperot (Hooijer, 1971)	<= 19 Ma

		Dicerorhinus sp.	*Brachypotherium heinzelini*	*Brachypotherium heinzelini* (NMK #176—astragalus; unnumbered astragalus in UM)	Genus known from Napak, Kisingiri (Rusinga, Mfangano), and Turkana (Buluk)	20 Ma– ~ 18 Ma
	Chalicotheriidae			*"Butleria" rusingensis* (UMP BUKII 15'2279)	Tinderet (Songhor, Legetet, Chamtwara), Napak, Kisingiri (Rusinga and Mfangano), Turkana (Moruorot)	<= 20 Ma
Cetartiodactyla	**Anthracotheriidae**	*Brachyodus aequatorialis* (BUK II 1967)		*Brachyodus aequatorialis* (UMP BUKII 03'367—phalanx; UMP BUKII 15'2280—lower molar)	Moroto, Tinderet, Napak, Kisingiri, Turkana	Ubiquitous throughout early Miocene
		?Hyoboops africanus	Not found[g]			
	Sanitheriidae	*Diamantohyus africanus* (BUK II/67 - p4; UMP 68-01 - P4)		*Diamantomys africanus* (UMP BUKII 15'2207 - left maxilla; NMK #106—astragalus)	Napak, Kisingiri (Rusinga), Turkana (Kalodirr, Moruorot, Buluk)	<= 20 Ma
	Suidae	*?Listriodon (Libychochoerus) jeanneli*	Not found[g]			
		Kenyasus namaquensis	*Kenyasus* sp. (UMP 68-02—P4 fragment[h]; BUK II 67—metapodial; unnumbered astragalus)	*Kenyasus* sp. (UMP BUKII 15'2302—molar; UMP BUKII 03'381—molar fragment)	*K. rusingensis* known from Kisingiri (Rusinga) and Turkana (Kalodirr, Moruorot, ?Loperot)	<= 19 Ma
		Nguruwe kijivium	Not found[g]			
	Tragulidae	*Dorcatherium parvum*	*Dorcatherium* cf. *parvum* (unnumbered broken m3, UM)	*Dorcatherium* cf. *parvum* (UMP BUKII 15'2276, UMP BUKII 15'2277—upper molar fragments)	Tinderet (Songhor), Napak, Kisingiri (Rusinga, Mfangano)	<= 20 Ma
		Dorcatherium pigotti	*Dorcatherium pigotti* (BUK II/67—naviculo-cuboid; unnumbered lower molar)		Kisingiri (Rusinga and Mfangano) and Turkana (Kalodirr, Moruorot, Loperot, Buluk)	<= 19 Ma
		Large tragulid (not *D. chappuisi*)	Not found[g]			
	Pecora (Family *incertae sedis*)	*Paleomeryx* sp.	*Walangania africanus*	*Walangania africanus* (UMP BUKII 03'371)	Moroto, Tinderet (Songhor, Legetet, Chamtwara, Kapurtay, Mteitei Valley), Napak, Kisingiri (Rusinga, Mfangano), Turkana (Kalodirr, Moruorot)	Ubiquitous throughout early Miocene
		Paleomeryx sp.	*Propalaeoryx nyanzae* (BUK II/67—P3; BUK P 67.31—astragalus; BUK P67.29—naviculo-cuboid)	*Propalaeoryx nyanzae* (UMP BUKII 02'194—astragalus; UMP BUKII 02'195—mandible fragment; UMP BUKII 02'196–astragalus; UMP BUKII 03'375A–molar fragment; UMP BUKII 03'388–unciform; UMP BUKII 11'13—P3; NMK #100—tuber calcis; NMK #148—astragalus; NMK #164—lunate)	Kisingiri (Rusinga, Mfangano) and Turkana (Kalodirr, Moruorot)	<= 19 Ma
		Paleomeryx large sp.	cf. *Canthumeryx sirtensis* (unnumbered material in UM—p4, cuneiform, scaphoid, astragalus, phalanges, metapodial keels)	cf. *Canthumeryx sirtensis* (UMP BUKII 15'2244—phalanx; NMK #39—distal phalanx; NMK #72—radius; NMK #152 and NMK #181—metapodial fragments; NMK unnumbered complete tibia)	Kisingiri (Rusinga, Mfangano), Turkana (Kalodirr, Moruorot, Buluk, Loperot)	<= 19 Ma

[a]Columns represent the published faunal lists from previous publications (Walker and Pickford Collections) as well as new material from our own fieldwork and from the National Museums of Kenya (New Collections). Revisions to

[b]Faunal lists from the earlier collections published in Walker (1968, 1969), Lavocat (1973:158), and Pickford (2002:216).

[c]Lists other Miocene sites where the taxon is found. Data from published faunal lists (Pickford, 1986a; Drake et al., 1988; Pickford and Mein, 2006; Cote, 2008, 2010; Leakey et al., 2011; Grossman et al., 2014) with updates from Werdelin and Sanders (2010). Unpublished data are included for Moroto (S. Cote and L. MacLatchy, pers. obs.), Kalodirr and Moruorot (S. Cote, pers. obs.).

[d]Harrison (1988) stated that these two specimens represented *L. legetet* ; Harrison (2010) reports only one specimen of *L. legetet* from Bukwa, but does not specify which specimen is retained.

[e]Based on a jaw from Napak, Butler (1984) suggested that a second species of *Myohyrax* may be present in the East African early Miocene. It is not possible to definitively assign the Bukwa material to either species.

[f]Pickford (2009) published this specimen as *Prohyrax bukwaensis.* See text and SOM for details.

[g]We did not find specimens that represented all species described in Walker (1968, 1969). This is likely due to specimens being misplaced or lost from the Uganda Museum many years ago. Only species that we personally observed are listed in the 'Summary List' column.

[h]Pickford (2007) published UMP 68-02 as *Kenyasus namaquensis.* We conservatively identify the suid at Bukwa as *Kenyasus* sp. See text and SOM for details.

Table 2. List of mammalian taxa from Bukwa.[a]

Order	Family	Previous faunal lists[b]	Revised identifications	New collection (Our expeditions and NMK material)	Other Miocene localities with this taxon[c]	Biostratigraphic range within early Miocene
Primates	**Catarrhini (Family *incertae sedis*)**	*Limnopithecus legetet* (UMP 68-22; UMP 68-26/27)[d]			Tinderet (Koru, Chamtwara, Legetet), Napak, Kisingiri (Rusinga)	<= 20 Ma
Macroscelidea	**Macroscelididae**	*Myohyrax oswaldi*	*Myohyrax* sp.[e] (unnumbered vial of teeth, UM)	*Myohyrax* sp. UMP BUKII 02'1746, UMP BUKII 15'2289—molars)	Genus is present but rare at Tinderet (Songhor, Chamtwara) and Napak; more common at Kisingiri (Rusinga, Mfangano, Karungu)	20 Ma–~ 18 Ma
Proboscidea	**Deinotheriidae**	*Deinotherium hobleyi*	*Prodeinotherium hobleyi* (BUK II 1967—deciduous premolar)		Moroto, Tinderet (Koru), Napak, Kisingiri (Rusinga, Mfangano), Turkana (Kalodirr, Moruorot, Buluk, Loperot)	Ubiquitous throughout early Miocene
	Gomphotheriidae	"Indeterminate Mastodonts"	Gomphotheriidae gen. and sp. indet. (BUK II P 67 33—tooth frag)	Gomphotheriidae gen. and sp. indet. (UMP BUKII 02'197—cheek tooth fragment)	Gomphotheres known from Tinderet (Songhor, Legetet), Napak, Kisingiri (Rusinga, Mfangano) and Turkana (Kalodirr, Moruorot, Buluk, Loperot)	<= 20 Ma
Hyracoidea	**Titanohyracidae**	*Megalohyrax championi*	*Afrohyrax championi* (BUK II unnumbered upper molar; Pickford, 2009)	*Afrohyrax championi* (NMK #1 maxilla)	Kisingiri (Rusinga, Mfangano), Turkana (Kalodirr, Moruorot, Buluk, Loperot)	<= 19 Ma
	Pliohyracidae	*Meroehyrax bateae*	*Meroehyrax bateae* (unnumbered mandible[f]; Pickford, 2009)		Kisingiri (Rusinga, Mfangano)	19–~ 18 Ma
Erinaceomorpha	**Erinaceidae**			Erinaceidae gen. and sp. indet. (NMK unnumbered specimen 'B'—lower molar)	Similar erinaceids from Tinderet, Napak, Kisingiri, and Turkana (Moruorot, Kalodirr)	<= 20 Ma
Carnivora/ Creodonta		Unidentified species	Not found[g]			
Lagomorpha	**Ochotonidae**			Ochotonidae gen. and sp. indet (UMP BUKII 02'1021; Winkler et al., 2005)	Ochontids known from Kisingiri (Rusinga, Mfangano), Turkana (Kalodirr)	<= 19 Ma
Rodentia	**Nesomyidae**			*Afrocricetodon songhori* (NMK unnumbered specimen 'A'—molar)	Tinderet (Songhor, Legetet, Chamtwara, Mteitei Valley), Napak	>= 19 Ma
	Pedetidae	*Megapedetes pentadactylus*	*cf. Megapedetes pentadactylus* (unnumbered distal phalanx, incisor fragment)	*cf. Megapedetes pentadactylus* (UMP BUKII 15'2236)	Tinderet (Songhor, Legetet, Chamtwara, Koru, Mteitei Valley), Napak, Kisingiri (Rusinga, Mfangano). A smaller species may be present at Kalodirr.	20 Ma–~ 18 Ma
	Bathyergidae	*Bathyergoides neotertiarius*	*Bathyergoides neotertiarius (* BUK 25'97—left and right mandibles)		Moroto, Tinderet (Songhor, Legetet, Chamtwara, Kapurtay, Mteitei Valley), Napak	>= 19 Ma
	Phiomyidae	*Paraphiomys* cf. *stromeri* "of small size" (specimen B11 and Thryonomyoidea B12 listed in Lavocat, 1973:158)	*Ugandamys downsi* (B12; B11 tentatively referred as cf. *U. downsi*— see also Winkler et al., 2005)	*Ugandamys downsi* (UMP BUKII 02'1022, UMP BUKII 02'1023, UMP BUKII 02'1024, UMP BUKII 02'1025; Winkler et al., 2005)	None	Exclusive to Bukwa
	Thryonomyidae	*Paraphiomys pigotti* (specimens B1-B5 listed in Lavocat, 1973:158)	*Paraphiomys pigotti* (B1, B3, B4, B5)	*Paraphiomys pigotti* (UMP BUKII 15'2237; NMK unnumbered specimens 'C' and 'D'—molars)	Large *Paraphiomys* known from all E.Af. early Miocene localities (Moroto, Tinderet, Napak, Kisingiri, Turkana)	Ubiquitous throughout early Miocene
		Paraphiomys stromeri (specimens B6-B8 in Lavocat, 1973:158)	*Paraphiomys* small sp. (B6-B8)	cf. *Paraphiomys* small sp. (UMP BUKII 02'1026; Winkler et al., 2005)	Similar small *Paraphiomys* known from Tinderet, Napak, Turkana (Kalodirr, Moruorot, Loperot), and Kisingiri (Rusinga, Mfangano)	<= 20 Ma
		Paraphiomys cf. *stromeri* "of small size" (specimen B10 of Lavocat, 1973:158)	*Paraphiomys* cf. *hopwoodi* (B10*)*		According to López-Antoñanzas et al. (2004), *P. hopwoodi* is restricted to Tinderet and Napak.	>= 19 Ma
	Thryonomyoidea (Family *incertae sedis*)	*Paraphiomys stromeri* "of small size" (specimen B9 in Lavocat, 1973:158)	*Lavocatomys* sp. (B9 right dp4)		Genus recognized at Songhor and Rusinga (Holroyd and Stevens, 2009)	20 Ma–~ 18 Ma
	Diamantomyidae		*Diamantomys sp.* (B2 half molar)		Genus known from all African early Miocene localities (Moroto, Tinderet, Napak, Kisingiri, Turkana)	Ubiquitous throughout early Miocene
Perissodactyla	**Rhinocerotidae**	*Chilotherium* sp. nov.	*Chilotheridium* cf. *pattersoni* (right upper premolar and molar series illustrated in Walker [1968], lower molars).	*Chilotheridium* cf. *pattersoni* (NMK unnumbered m3)	Similar to taxon from Loperot (Hooijer, 1971)	<= 19 Ma

		Dicerorhinus sp.	*Brachypotherium heinzelini*	*Brachypotherium heinzelini* (NMK #176—astragalus; unnumbered astragalus in UM)	Genus known from Napak, Kisingiri (Rusinga, Mfangano), and Turkana (Buluk)	20 Ma– ~ 18 Ma
	Chalicotheriidae			*"Butleria" rusingensis* (UMP BUKII 15'2279)	Tinderet (Songhor, Legetet, Chamtwara), Napak, Kisingiri (Rusinga and Mfangano), Turkana (Moruorot)	<= 20 Ma
Cetartiodactyla	**Anthracotheriidae**	*Brachyodus aequatorialis* (BUK II 1967)		*Brachyodus aequatorialis* (UMP BUKII 03'367—phalanx; UMP BUKII 15'2280—lower molar)	Moroto, Tinderet, Napak, Kisingiri, Turkana	Ubiquitous throughout early Miocene
		?Hyoboops africanus	Not found[g]			
	Sanitheriidae	*Diamantohyus africanus* (BUK II/67 - p4; UMP 68-01 - P4)		*Diamantomys africanus* (UMP BUKII 15'2207 - left maxilla; NMK #106—astragalus)	Napak, Kisingiri (Rusinga), Turkana (Kalodirr, Moruorot, Buluk)	<= 20 Ma
	Suidae	*?Listriodon (Libychochoerus) jeanneli*	Not found[g]			
		Kenyasus namaquensis	*Kenyasus* sp. (UMP 68-02—P4 fragment[h]; BUK II 67—metapodial; unnumbered astragalus)	*Kenyasus* sp. (UMP BUKII 15'2302—molar; UMP BUKII 03'381—molar fragment)	*K. rusingensis* known from Kisingiri (Rusinga) and Turkana (Kalodirr, Moruorot, ?Loperot)	<= 19 Ma
		Nguruwe kijivium	Not found[g]			
	Tragulidae	*Dorcatherium parvum*	*Dorcatherium* cf. *parvum* (unnumbered broken m3, UM)	*Dorcatherium* cf. *parvum* (UMP BUKII 15'2276, UMP BUKII 15'2277—upper molar fragments)	Tinderet (Songhor), Napak, Kisingiri (Rusinga, Mfangano)	<= 20 Ma
		Dorcatherium pigotti	*Dorcatherium pigotti* (BUK II/67—naviculo-cuboid; unnumbered lower molar)		Kisingiri (Rusinga and Mfangano) and Turkana (Kalodirr, Moruorot, Loperot, Buluk)	<= 19 Ma
		Large tragulid (not *D. chappuisi*)	Not found[g]			
	Pecora (Family *incertae sedis*)	*Paleomeryx* sp.	*Walangania africanus*	*Walangania africanus* (UMP BUKII 03'371)	Moroto, Tinderet (Songhor, Legetet, Chamtwara, Kapurtay, Mteitei Valley), Napak, Kisingiri (Rusinga, Mfangano), Turkana (Kalodirr, Moruorot)	Ubiquitous throughout early Miocene
		Paleomeryx sp.	*Propalaeoryx nyanzae* (BUK II/67—P3; BUK P 67.31—astragalus; BUK P67.29—naviculo-cuboid)	*Propalaeoryx nyanzae* (UMP BUKII 02'194—astragalus; UMP BUKII 02'195—mandible fragment; UMP BUKII 02'196–astragalus; UMP BUKII 03'375A–molar fragment; UMP BUKII 03'388–unciform; UMP BUKII 11'13—P3; NMK #100—tuber calcis; NMK #148—astragalus; NMK #164—lunate)	Kisingiri (Rusinga, Mfangano) and Turkana (Kalodirr, Moruorot)	<= 19 Ma
		Paleomeryx large sp.	cf. *Canthumeryx sirtensis* (unnumbered material in UM—p4, cuneiform, scaphoid, astragalus, phalanges, metapodial keels)	cf. *Canthumeryx sirtensis* (UMP BUKII 15'2244—phalanx; NMK #39—distal phalanx; NMK #72—radius; NMK #152 and NMK #181—metapodial fragments; NMK unnumbered complete tibia)	Kisingiri (Rusinga, Mfangano), Turkana (Kalodirr, Moruorot, Buluk, Loperot)	<= 19 Ma

[a]Columns represent the published faunal lists from previous publications (Walker and Pickford Collections) as well as new material from our own fieldwork and from the National Museums of Kenya (New Collections). Revisions to

[b]Faunal lists from the earlier collections published in Walker (1968, 1969), Lavocat (1973:158), and Pickford (2002:216).

[c]Lists other Miocene sites where the taxon is found. Data from published faunal lists (Pickford, 1986a; Drake et al., 1988; Pickford and Mein, 2006; Cote, 2008, 2010; Leakey et al., 2011; Grossman et al., 2014) with updates from Werdelin and Sanders (2010). Unpublished data are included for Moroto (S. Cote and L. MacLatchy, pers. obs.), Kalodirr and Moruorot (S. Cote, pers. obs.).

[d]Harrison (1988) stated that these two specimens represented *L. legetet* ; Harrison (2010) reports only one specimen of *L. legetet* from Bukwa, but does not specify which specimen is retained.

[e]Based on a jaw from Napak, Butler (1984) suggested that a second species of *Myohyrax* may be present in the East African early Miocene. It is not possible to definitively assign the Bukwa material to either species.

[f]Pickford (2009) published this specimen as *Prohyrax bukwaensis.* See text and SOM for details.

[g]We did not find specimens that represented all species described in Walker (1968, 1969). This is likely due to specimens being misplaced or lost from the Uganda Museum many years ago. Only species that we personally observed are listed in the 'Summary List' column.

[h]Pickford (2007) published UMP 68-02 as *Kenyasus namaquensis.* We conservatively identify the suid at Bukwa as *Kenyasus* sp. See text and SOM for details.