Journal of Human Evolution 116 (2018) 95–107

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

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

Susanne Cote [a, *], John Kingston [b], Alan Deino [c], Alisa Winkler [d], Robert Kityo [e], Laura MacLatchy [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, MI, 48109, USA
[c] Berkeley Geochronology Center, Berkeley, CA, 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, TX 75390, USA
[e] Department of Zoology, Makerere University, Kampala, Uganda
[f] Department of Anthropology and Museum of Paleontology, University of Michigan, Ann Arbor, MI, 48109, USA

ARTICLE INFO

*Article history:*
Received 17 May 2017
Accepted 10 December 2017

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

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 have 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.



## 1. 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

*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.

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

https://doi.org/10.1016/j.jhevol.2017.12.001
0047-2484/

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.

## 2. Background

### 2.1. 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.

### 2.2. 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

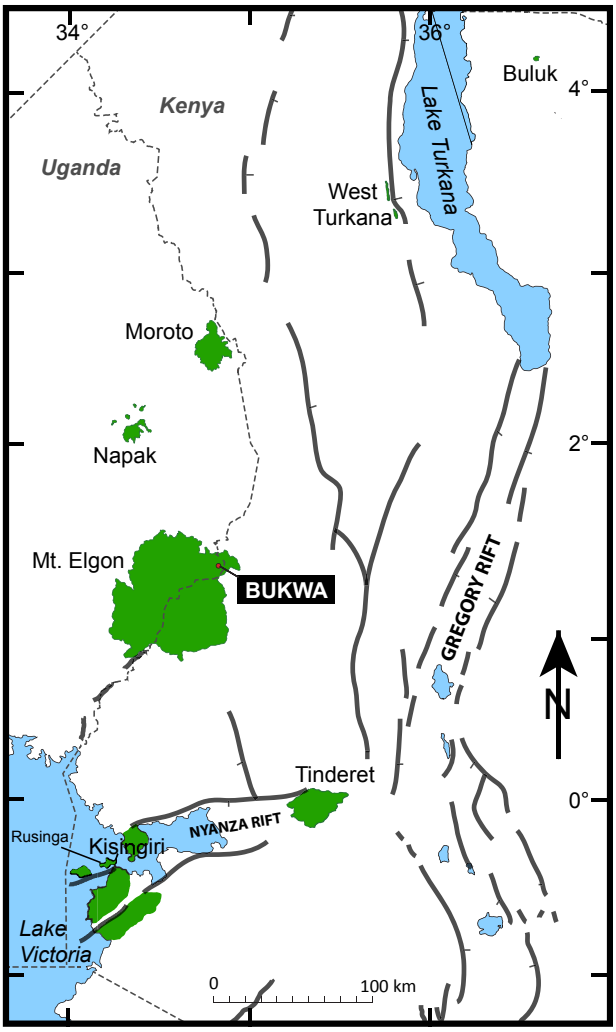


**Figure 1.** Regional map showing the location of the Bukwa fossil locality and other early Miocene fossil localities mentioned in the text. The green (shaded) areas denote the current exposures of the ancient volcanoes of Napak, Moroto, Elgon, Tinderet, and Kisingiri. In the Turkana Basin, the green areas indicate the location of sedimentary sequences that have yielded fossil material. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

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