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Stable isotope paleoecology of Late Pleistocene Middle Stone Age humans from the Lake Victoria basin, Kenya

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A B S T R A C T

Paleoanthropologists have long argued that environmental pressures played a key role in human evolution. However, our understanding of how these pressures mediated the behavioral and biological diversity of early modern humans and their migration patterns within and out of Africa is limited by a lack of archaeological evidence associated with detailed paleoenvironmental data. Here, we present the first stable isotopic data from paleosols and fauna associated with Middle Stone Age (MSA) sites in East Africa. Late Pleistocene (~100–45 ka, thousands of years ago) sediments on Rusinga and Mfangano Islands in eastern Lake Victoria (Kenya) preserve a taxonomically diverse, non-analog faunal community associated with MSA artifacts. We analyzed the stable carbon and oxygen isotope composition of paleosol carbonate and organic matter and fossil mammalian tooth enamel, including the first analyses for several extinct bovids such as *Rusingoryx atopocranion*, *Damaliscus hypsodon*, and an unnamed impala species. Both paleosol carbonate and organic matter data suggest that local habitats associated with human activities were primarily riverine woodland ecosystems. However, mammalian tooth enamel data indicate that most large-bodied mammals consumed a predominantly C_4 diet, suggesting an extensive C_4 grassland surrounding these riverine woodlands in the region at the time. These data are consistent with other lines of paleoenvironmental evidence that imply a substantially reduced Lake Victoria at this time, and demonstrate that C_4 grasslands were significantly expanded into equatorial Africa compared with their present distribution, which could have facilitated dispersal of human populations and other biotic communities. Our results indicate that early populations of *Homo sapiens* from the Lake Victoria region exploited locally wooded and well-watered habitats within a larger grassland ecosystem.

Introduction

Environmental change has been associated with a number of key events in human evolutionary history, including the dispersal of modern humans within and out of Africa (e.g., Scholz et al., 2007; Cowling et al., 2008; Carto et al., 2009; Compton, 2011; deMenocal, 2011; Blome et al., 2012; Potts, 2012; Faith et al., in press). Fossil and genetic data point to an East African origin of *Homo sapiens* between 200,000 and 100,000 years ago (McDougall et al., 2005; Gonder et al., 2007), with Middle Stone Age (MSA) archaeological sites providing the behavioral context for these early populations (McBrearty and Brooks, 2000; Tryon and Faith, 2013). Recent genetic evidence indicates that an East African population, ancestral to many sub-Saharan African lineages and to all non-African lineages, began to disperse within and out of Africa between 70 and 60 ka (thousands of years ago) (Soares et al., 2012). Several recent studies have focused on the role of Late Pleistocene (126–12 ka) environmental change in driving these modern human dispersal events (Carto et al., 2009; Blome et al., 2012), including population retreat to well-watered refugia during periods of increased aridity (Basell, 2008; Brandt et al., 2012). However, the impact of these studies is limited because the relevant data archives—particularly proxies for temperature, moisture availability, and vegetation—are poorly resolved spatially and temporally (reviewed in Blome et al.,

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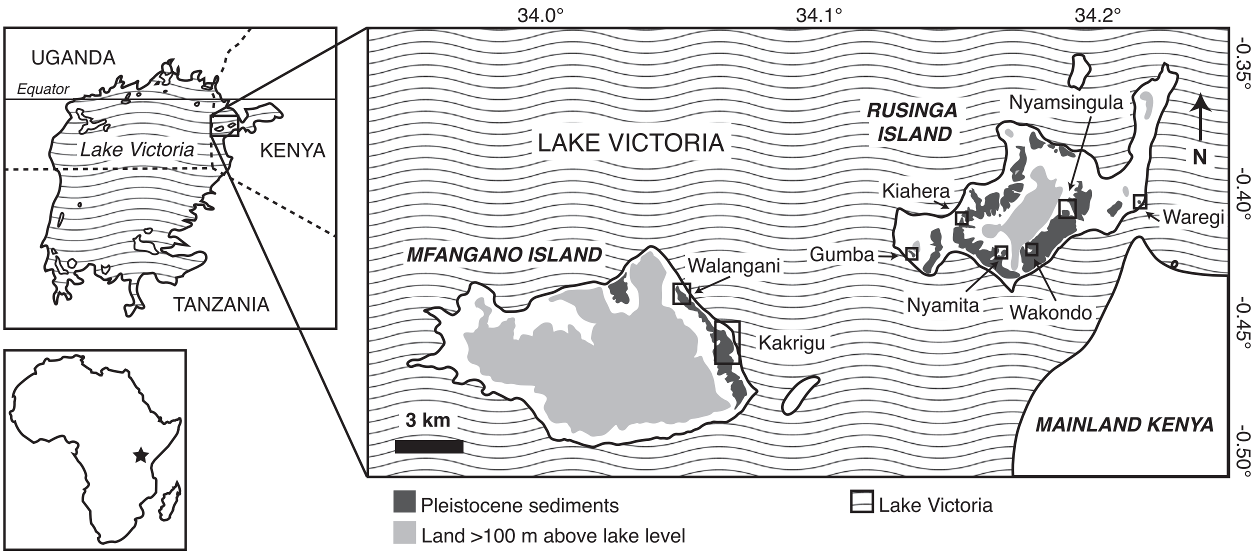

Figure 1. Map of Rusinga and Mfangano Islands, Kenya, showing the Pleistocene sediments and the positions of localities mentioned in the text.

2012). Available faunal evidence indicates that early modern human populations in East Africa were part of extinct non-analog animal communities that were distinct in terms of taxonomic composition compared with regional modern mammal communities (Marean and Gifford-Gonzalez, 1991; Marean, 1992, 1997; Tryon et al., 2010; Faith et al., 2011; Faith et al., 2012, 2013, 2014; Tryon et al., 2012), and, as such, the paleoecology of these ancient populations remains poorly understood. Previous paleoenvironmental reconstructions of East African MSA sites using isotopic data have been restricted to the analysis of paleosols from site A5 (dated to ~100–80 ka) at Aduma, Ethiopia (Yellen et al., 2005), and no published studies to date have examined the stable isotope composition of fossil mammals from this interval. Thus far, the rarity of detailed paleoenvironmental reconstructions from MSA archaeological and hominin fossil sites has obscured the ecological contexts that shaped the biology and behavior of East African modern humans.

Here we describe the first isotopic reconstruction of the paleoenvironmental context of early *H. sapiens* from the MSA of East Africa, using data from MSA archaeological sites on Rusinga and Mfangano Islands. These sites are dated to ca. 100–45 ka, overlapping with major dispersals of human populations out of East Africa. We combine the carbon ($\delta^{13}C$)[1] and oxygen ($\delta^{18}O$) isotopic compositions of sediments (pedogenic carbonates, bulk sedimentary organic matter) and fossil mammalian tooth enamel to reconstruct local vegetation composition, assess habitats in the broader landscape sampled by mobile large-bodied ungulates, and estimate regional moisture availability. Taken together, these analyses inform our knowledge of the paleoecological context of early modern humans during this critical time period.

Pleistocene records from Rusinga and Mfangano Islands

Rusinga (0°24′S, 34°0′E) and Mfangano (0°27′S, 34°0′E) are near-shore islands in Lake Victoria (Fig. 1) that today receive approximately 1400 mm rainfall per year (Crul, 1995; Fillinger et al., 2004). Prior to substantial human habitation, the islands were likely covered by variably dense woodlands (Andrews, 1973), with the surrounding area on mainland Kenya including woodlands, bushlands, thickets, and forested habitats (White, 1983). Rusinga and Mfangano are remnants of the eruption and deposition of lavas and sediments of the Kisingiri volcano, inactive since the middle Miocene. Both islands share a similar bedrock lithology of Miocene lavas and volcaniclastics, unconformably overlain by poorly consolidated Pleistocene sediments (e.g., Peppe et al., 2009; Tryon et al., 2010). The Pleistocene Wasiriya Beds of Rusinga and the Waware Beds of Mfangano are primarily made up of tuffaceous alluvial and fluvial sediments and weakly developed paleosols suggestive of a relatively unstable landscape dominated by episodic depositional events (Figs. 1–2; Tryon et al., 2012, 2013, 2014). Rare tufa deposits at the Nyamita locality (Rusinga) are indicative of small, local springs (Figs. 1–2; Tryon et al., 2014). The Wasiriya and Waware Beds comprise identical sedimentary facies and show remarkable similarities in the fauna, the chemical composition of tephra deposits, and age estimates from fossil gastropods, suggesting that the Wasiriya Beds on Rusinga and Waware Beds on Mfangano likely sample the same general interval of time during the Late Pleistocene (Tryon et al., 2012, 2014). This is confirmed by tephra correlations made between all fossil-bearing Pleistocene sites on Rusinga, Mfangano, and other nearby sites in the region (Blegen et al., 2014). We estimate that the artifact and fossil bearing strata on both islands range in age from ca. 100–45 ka. The minimum age for the deposits is constrained by calibrated radiocarbon dates on fossil gastropods (*Limicolaria* cf. *L. martensiana*) that have burrowed into the deposits, and the maximum age is defined by the eruption time of the inferred source volcanoes that produced distal tephra deposits found near the base of the sedimentary sequence (Tryon et al., 2010, 2012).

Both the Wasiriya and Waware Beds contain multiple archaeological sites with MSA artifacts, such as bifacial points and Levallois flakes and cores (Tryon et al., 2010, 2012, 2014). Controlled excavations in 2009–2011 from three locations on Rusinga Island (one at Nyamita and two at Wakondo, including the Bovid Hill sub-locality and a second unnamed sub-locality) totaling 28 m^2 produced artifact densities of 1.20–6.50 lithic artifacts/m^2 (Tryon et al., 2010; Jenkins et al., 2012). These in situ artifact densities are within the range expected from the ‘scatter between the patches’ (Isaac, 1981) or the ‘veil of stones’ (Roebroeks et al., 1995), typical of open-air Paleolithic artifact scatters across ancient landscapes

[1] $\delta^{13}C$ and $\delta^{18}O$ values are presented in parts per thousand (permil, ‰), where $\delta X = (R_{sample}/R_{standard} - 1)$ *1000, X is ^{13}C or ^{18}O, R is $^{13}C/^{12}C$ and $^{18}O/^{16}O$, respectively, and the standard for carbon is Vienna Pee Dee Belemnite (V-PDB) and for oxygen is Vienna Standard Mean Ocean Water (V-SMOW).