



The Pleistocene archaeology and environments of the Wasiriya Beds, Rusinga Island, Kenya

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ABSTRACT

Western Kenya is well known for abundant early Miocene hominoid fossils. However, the Wasiriya Beds of Rusinga Island, Kenya, preserve a Pleistocene sedimentary archive with radiocarbon age estimates of >33–45 ka that contains Middle Stone Age artifacts and abundant, well-preserved fossil fauna: a co-occurrence rare in eastern Africa, particularly in the region bounding Lake Victoria. Artifacts and fossils are associated with distal volcanic ash deposits that occur at multiple localities in the Wasiriya Beds, correlated on the basis of geochemical composition as determined by electron probe microanalysis. Sediment lithology and the fossil ungulates suggest a local fluvial system and associated riparian wooded habitat within a predominantly arid grassland setting that differs substantially from the modern environment, where local climate is strongly affected by moisture availability from Lake Victoria. In particular, the presence of oryx (*Oryx gazella*) and Grevy's zebra (*Equus grevyi*) suggest a pre-Last Glacial Maximum expansion of arid grasslands, an environmental reconstruction further supported by the presence of several extinct specialized grazers (*Pelorovis antiquus*, *Megalotragus* sp., and a small alcelaphine) that are unknown from Holocene deposits in eastern Africa. The combination of artifacts, a rich fossil fauna, and volcanoclastic sediments makes the Wasiriya Beds a key site for examining the Lake Victoria basin, a biogeographically important area for understanding the diversification and dispersal of *Homo sapiens* from Africa, whose pre-Last Glacial Maximum history remains poorly understood.

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Introduction

The Middle and Late Pleistocene record of eastern Africa provides the most important dataset for understanding the origins of modern human diversity. Fossil and genetic data are consistent with an eastern Africa origin for *Homo sapiens* during the later Middle Pleistocene (~200 ka), with the Late Pleistocene history of

our species characterized by complex demographic shifts and population movements within Africa (Ambrose, 1998b; Lahr and Foley, 1998; Howell, 1999; Excoffier, 2002; McDougall et al., 2005; Behar et al., 2008; Tishkoff et al., 2009; Verdu et al., 2009). By 50 ka, portions of one or more African populations had dispersed to Eurasia and Australia (e.g., Prugnolle et al., 2005; Mellars, 2006; O'Connell and Allen, 2007). Because of this history, fully understanding the biological and behavioral diversity of present day modern humans requires a more complete understanding of the variation among early African populations of *H. sapiens*. This includes both the biological diversity suggested by the fossil and genetic data (Lahr and Foley, 1998; Howell, 1999; Pearson, 2008; Crevecoeur et al., 2009; Gunz et al., 2009), and the geographic and temporal variation evident in the Middle Stone Age (MSA)

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archaeological record (McBrearty and Brooks, 2000; Henshilwood and Marean, 2003; Marean and Assefa, 2005; Barham and Mitchell, 2008; Jacobs et al., 2008).

The relative roles of social or environmental factors in shaping the diversity of Pleistocene populations of *H. sapiens* in eastern Africa remain understudied. The appearance of symbolic artifacts (e.g., beads) at some Late Pleistocene sites (Ambrose, 1998a; Bouzouggar et al., 2007; d'Errico and Vanhaeren, 2007; Assefa et al., 2008) suggests the socially mediated use of material goods to maintain personal and probably group boundaries (Wobst, 1977; Kuhn and Stiner, 2007), boundaries that may also be suggested by the distribution of other artifact forms, including points (Clark, 1988; McBrearty and Brooks, 2000). However, environmental variation also strongly patterns some aspects of hominin forager behavior (Kelly, 1995; Binford, 2001; Kuhn and Stiner, 2001), and eastern Africa is topographically and environmentally complex, resulting in spatially diverse habitats and localized adaptations by recent foragers (e.g., Ambrose, 2001; Cornelissen, 2002; Kusimba, 2005; Barham and Mitchell, 2008). Past climate shifts that resulted in the fragmentation and reorganization of plant and animal communities (Kingston, 2007) may have played a key role in establishing some of the variability among populations of early *H. sapiens* by providing novel adaptive contexts (Ambrose and Lorenz, 1990; Marean et al., 2007; McCall, 2007) and the accumulation of genetic and behavioral differences by drift (e.g., Mayr, 2001; Eerkens and Lipo, 2005) among isolated populations.

A number of authors have recently argued for a strong role for climate change in shaping Late Pleistocene environments and the dispersal of *H. sapiens* within and out of Equatorial Africa (e.g., Cohen et al., 2007; Scholz et al., 2007; Vaks et al., 2007; Cowling et al., 2008; Carto et al., 2009; Castañeda et al., 2009). However, at this stage we have at best an incomplete understanding of the complex spatial and temporal patterns of climate change in Pleistocene Africa. For example, Scholz et al. (2007) and Cohen et al. (2007) demonstrate multiple episodes of Late Pleistocene hyperaridity or 'megadroughts,' far more extreme than observed during the Last Glacial Maximum (LGM) arid interval (19–26.5 ka; Clark et al., 2009). Their data suggest that Lakes Malawi and Tanganyika (Fig. 1) had 'megadroughts' between ~135 and 70 ka, out of phase with arid intervals predicted by orbital-scale precessional forcing. In contrast, high lake stands provide strong evidence for precessional insolation-forced periods of increased humidity at Lake Naivasha from ~150 to 60 ka and later intervals during the Pleistocene (Fig. 1; Trauth et al., 2001, 2003; Bergner et al., 2009), similar to patterns from localities elsewhere in Africa (see discussion in Scholz et al., 2007). These differences suggest that climate changes within different (sub) regions of the eastern portion of continent were out of phase, perhaps with a sharp climatic boundary near the Equator as predicted by some paleoclimate models (Clement et al., 2004). This marked contrast in aridity between the southern hemisphere Lakes Malawi and Tanganyika and the northern hemisphere Lakes Nakuru and Naivasha may be the result of the different latitude positions of the lake basins in the East Africa Rift system, due to different responses to orbitally-driven insolation variations or caused by variations in high latitude ice volumes in the northern and southern hemispheres, or to zonal gradients in atmospheric heating that affect the local hydrologic cycle (Burns et al., 2001; Clark et al., 1999; Clement et al., 2004; Scholz et al., 2007; Bergner et al., 2009). Whatever the cause, such a pattern could have resulted in different regions of eastern Africa experiencing very different climate regimes, with resulting sharp boundaries between plant and animal communities that shifted over time, a scenario more complex than most models of past environments in the region (cf. Marean and Assefa, 2005; Basell, 2008). If we are to understand the role of environmental

change in shaping modern human diversity and evolution, we require detailed environmental and archaeological data from Late Pleistocene eastern Africa, the time and region where *H. sapiens* originated and persisted.

In this context, we describe here our continuing investigation of pre-LGM artifact- and fossil-bearing tuffaceous sediments from Rusinga Island, Kenya (Figs. 1 and 2). Rusinga lies near the eastern shore of Lake Victoria, which has the largest surface area of any lake in Africa. It is a biogeographically important area (White, 1983; Kingdon, 1989) for understanding plant and animal dispersals whose pre-LGM history remains poorly understood. As the Pleistocene sediments on Rusinga have not previously been the focus of extensive research, we first describe our efforts to provide a detailed geological context for the recovered stone tools and fauna. These include the first measured stratigraphic sections and detailed lithological analyses, the only radiometric age estimates, and a tephrostratigraphic framework that facilitates correlations among localities on Rusinga and potentially with more distant areas. Our excavations have documented the first *in situ* archaeological sites on Rusinga, and the recovered MSA artifacts include points and Levallois flakes, associated with cut-marked fauna. Unlike most Pleistocene archaeological sites in the Lake Victoria region, the fauna is relatively abundant and well preserved. The fauna indicates that these hominins inhabited an open, arid grassland environment substantially different from the present, providing the foundation for our inquiry into pre-LGM environmental and archaeological variation in the region.

Biogeographical, evolutionary, and archaeological significance of the Lake Victoria region

Lake Victoria spans the Equator, is the largest lake in Africa as measured by surface area [66,400 km², Adams, 1996], and today supports diverse ecosystems and dense human populations. Although the formation of Lake Victoria began perhaps as early as 400 ka, little is known of the pre-LGM history of the lake or surrounding region (Johnson et al., 1996, 2000; Stager and Johnson, 2008). Seismic profiles of Lake Victoria suggest multiple periods of lake contraction and expansion, but sediment cores have only penetrated the uppermost of these, which shows complete desiccation during the LGM and a high stand from ~7 to 10 ka that may have doubled the surface area of the lake (Kendall, 1969; Johnson et al., 1996, 2000; Stager et al., 1997; Stager and Johnson, 2008), a pattern seen in other eastern African lakes (Goudie, 1996). Historic records document smaller scale variance in lake level (~4 m) over the last 200 years due to changes in mean annual rainfall (Nicholson, 1998). Because water level is controlled primarily by rainfall, Lake Victoria today serves as a particularly sensitive indicator of moisture availability and climate change. As the lake is shallow (mean and maximum depths are 40 and 68 m, respectively), even modest changes in lake volume due to precipitation change can cause substantial changes in lake surface area and surrounding habitats.

Seismic data demonstrate that the water level and size of Lake Victoria fluctuated considerably throughout the history of the lake, likely as a result of moisture availability (Johnson et al., 1996). Precise correlation with Pleistocene climatic oscillations is not currently possible due to a lack of chronological control, but it is clear that these changes that would have had substantial impacts on regional floral and faunal communities. Pollen data (Kendall, 1969) and geochemical proxies (Talbot and Laerdal, 2000; Talbot et al., 2006) from the terminal Pleistocene and Holocene suggest a shift from swamp margins and C₄ grasslands to more forested areas in the vicinity of Lake Victoria with progressive lake level increase. The Pleistocene expansion, contraction, and

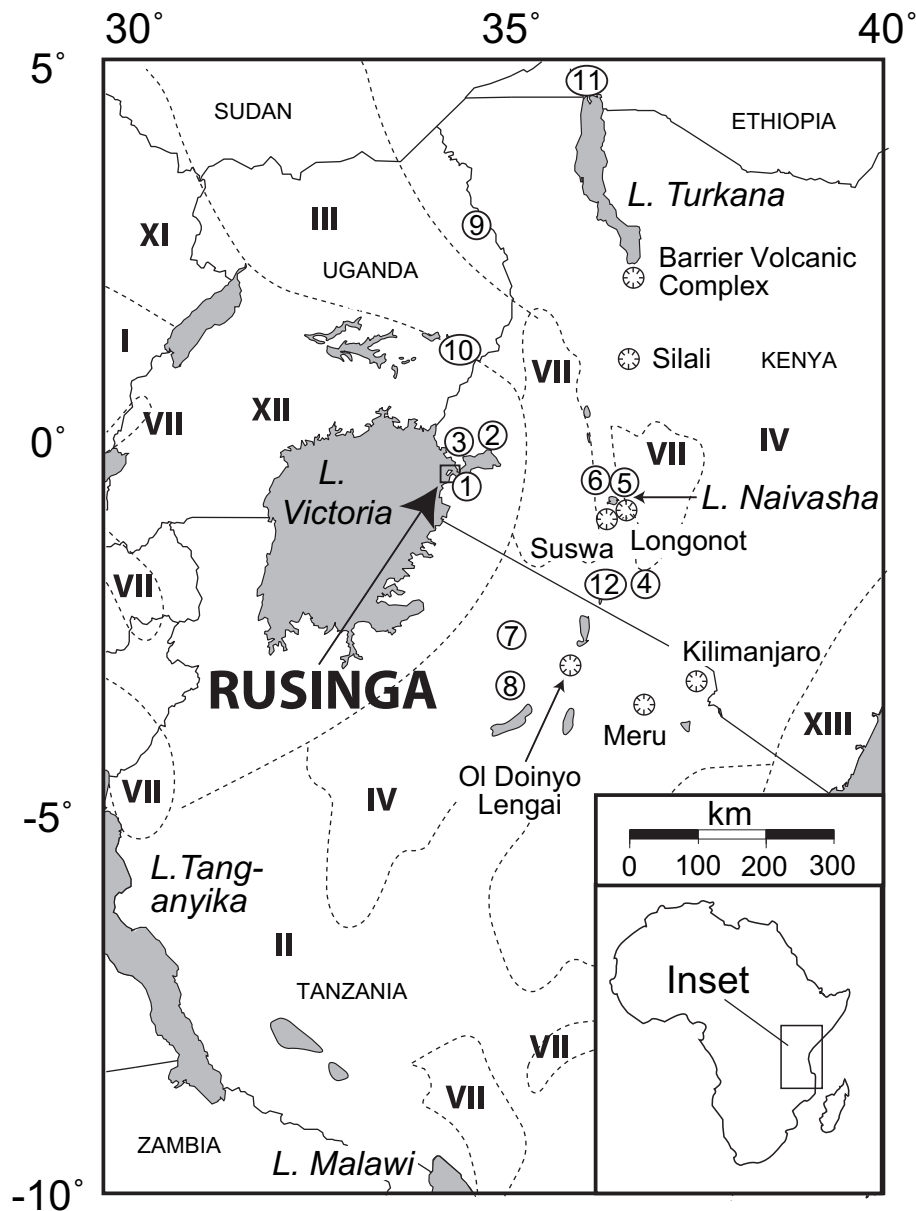


Figure 1. Schematic map of eastern Africa showing the major topographic features, biogeographic zones, and sites discussed in text. Major lakes are shaded grey. The location of the Quaternary volcanoes the Barrier Complex, Silali, Longonot, Suswa, Ol Doiyo Lengai, Meru, and Kilimanjaro are also shown (not to scale). Bold Roman numerals correspond to each of the major vegetation zones identified by White (1983) bounded by dashed lines. The Lake Victoria regional mosaic is zone XII. It is bounded by regional centers of endemism: Guineo-Congolian (I.), Zambezian (II.), Sudanian (III.), Somalia-Masai (IV.), and Afro-alpine (VIII.). Pleistocene archaeological and paleontological sites discussed in the text shown as circled Arabic numerals: (1) Kanjera, (2) Mugurk, (3) Randhore, (4) Lukenya Hill, (5) Cartwright's Site, (6) Prolonged Drift, (7) Nasera, (8) Mumba, (9) Magosi, (10) Walasi Hill, (11) Omo Kibish, (12) Lainyamok. Aduma and Porc-Épic, both in Ethiopia are not shown.

fragmentation of these woodland, grassland, and lakeside habitats may have provided dispersal avenues and/or refugia for flora and fauna, including hominins (White, 1983; Kingdon, 1989; Lahr and Foley, 1998; Marean and Assefa, 2005; Cowling et al., 2008). Biogeographic data support this hypothesis, as the region bounding Lake Victoria is a mosaic habitat between adjacent regional centers of floral and faunal endemism (Fig. 1). The distribution of extant taxa suggests that the Lake Victoria region was an important area of dispersal during periods of environmental change (Fig. 1; Kingdon, 1974, 1989; White, 1983; Grubb et al., 1999; Wronski and Hausdorf, 2008). As described below, the Pleistocene sediments from Rusinga document pre-LGM faunal communities without modern analogues in the Lake Victoria region, and include taxa beyond their historic ranges.

Paleoanthropological work in the Lake Victoria region, particularly in western Kenya, has focused primarily on Miocene (Oswald, 1911, 1914; Kent, 1942, 1944; Le Gros Clark and Leakey, 1951; McCall, 1958; Andrews, 1981; Pickford, 1986) or Plio-Pleistocene sites (Ditchfield et al., 1999; Plummer et al., 1999, 2009; Braun et al., 2008). In fact, the Lake Victoria area has not featured prominently in discussions of the origins of *H. sapiens* since L.S.B. Leakey's work at Kanjera and Kanam in the 1930s (see Ditchfield et al., 1999 for a historical review). Collections and detailed excavations from Pleistocene sites on islands within and around the perimeter of Lake Victoria have contributed large samples of stone artifacts and clarified the stratigraphic succession of various Stone Age industries (O'Brien, 1939; Leakey and Owen, 1945; Van Riet Lowe, 1952; Cole, 1967b; Nenquin, 1971; Van Noten, 1971; McBrearty, 1981,

1988; Pickford, 1982, 1991, 1992; Posnansky et al., 2005). However, few of these sites contain both stone artifacts and fauna as fossil preservation is typically poor and limited to isolated teeth, or when fauna is well preserved, fossils come from uncertain, complex, or largely unexplored stratigraphic contexts (e.g., the Apoko Formation at Kanjera, see Plummer et al., 1994; Behrensmeyer et al., 1995; Ditchfield et al., 1999). The paucity of fauna and the near total lack of chronological control hinder our understanding of Pleistocene biogeography and archaeology in the Lake Victoria region, limiting the contribution of this area to our understanding of modern human diversity. The presence of *in situ* MSA artifacts and associated fossil fauna in dated sediments at Rusinga therefore marks a major step towards resolving the Quaternary archaeology and biogeography of the Lake Victoria region.

Historical and geological context of the Wasiriya Beds

Fossil- and artifact-bearing deposits that overlie the Miocene strata on Rusinga have been noted since detailed paleoanthropological exploration of the island by L.S.B. Leakey began in the 1930s (Kent, 1942; MacInnes, 1956; Van Couvering, 1972; Leakey, 1974; Pickford and Thomas, 1984; Pickford, 1986). However, these younger beds have been examined primarily as an adjunct to work in the rich Miocene deposits (Le Gros Clark and Leakey, 1950, 1951; Napier and Davis, 1959; Andrews, 1981; Pickford, 1986; Walker and Teaford, 1988; Collinson et al., 2009). Renewed fieldwork on Rusinga initiated in 2006 (McNulty et al., 2007; Peppe et al., 2009) continued this trend, but in January 2009 was expanded to include the first formal archaeological surveys and excavations. While Pleistocene fossils have been reported across much of the island (Van Couvering, 1972; Pickford, 1986), our research thus far has focused on exposures on the southern portion of Rusinga, where both fossils and stone artifacts

have been recovered, particularly from the Wakondo, Nyamita, and western Nyamsingula (Kakrigu) localities (Fig. 2).

Pickford and Thomas (1984) introduced the term, 'Wasiriya Beds,' to describe sediments first mapped by Van Couvering (1972) as the Wasiriya Terrace, following terminology introduced by Kent (1942). The Wasiriya Beds crop out discontinuously over an area of <10 km² around the perimeter of Rusinga Island, at elevations ranging from ~15 to 36 m above the present level of Lake Victoria (Fig. 2). Wasiriya Beds sediment thickness varies, generally thinning towards the island margin from >10 m near the uplands at the island's center (Van Couvering, 1972) to <5 cm near the modern shore of Lake Victoria. The exposed sediments sample valley fill deposits that overlie a complex eroded topography of indurated Miocene sediments. Previous researchers (Van Couvering, 1972; Pickford and Thomas, 1984; Pickford, 1986) have described from the Wasiriya Beds sediments that range from poorly stratified clays to silts and coarse sands, as well as stony, clayey soils with lava clasts. Fig. 3 shows measured stratigraphic sections from Wakondo and Nyamita, the first described from the Wasiriya Beds. These record a complex cut-and-fill fluvial environment with substantial lateral facies variation among silts, sands, conglomerates. Preliminary work suggests that the channels in these sequences were <1 m to several meters wide. Further work describing the dimensions of the channels and the channel complexes is part of our ongoing research goals. Pedogenic silcrete and carbonate nodules, rootcasts, and reworked and airfall tephra deposits are also locally abundant.

Radiometric age estimates for the Wasiriya Beds

Previous researchers have suggested ages for the Wasiriya Beds ranging from the Middle Pleistocene (Kent, 1942; Van Couvering,

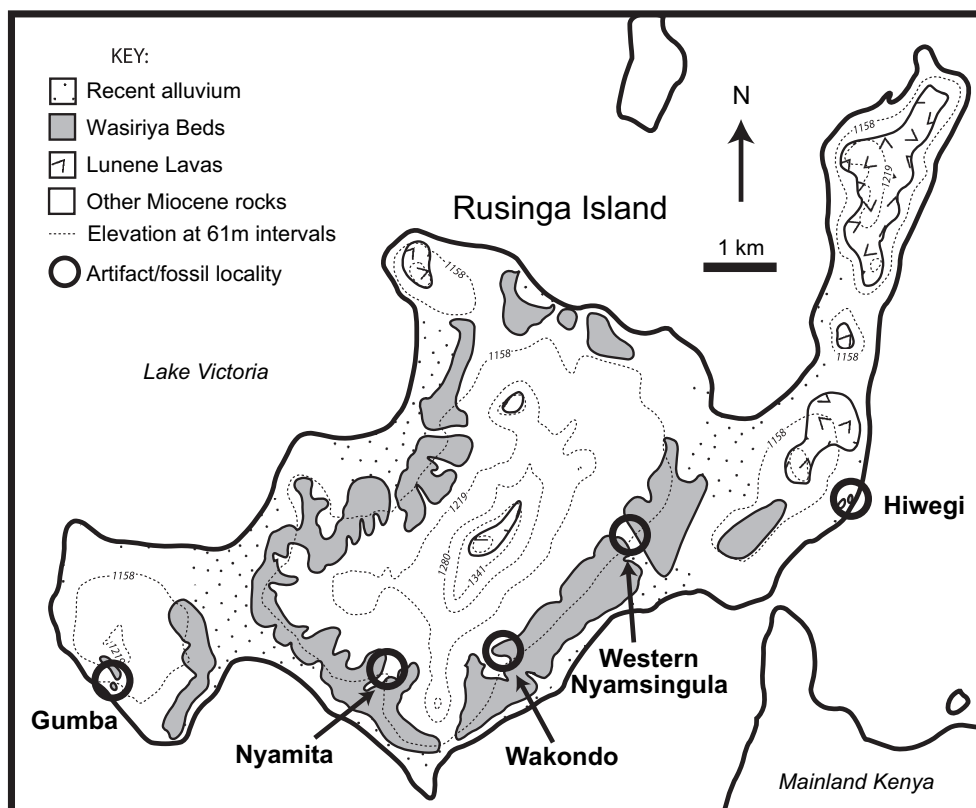


Figure 2. Schematic map of Rusinga Island, Kenya, showing topography, selected geological units and the position of artifact and fossil localities discussed in the text. After Van Couvering (1972) and Pickford (1986).

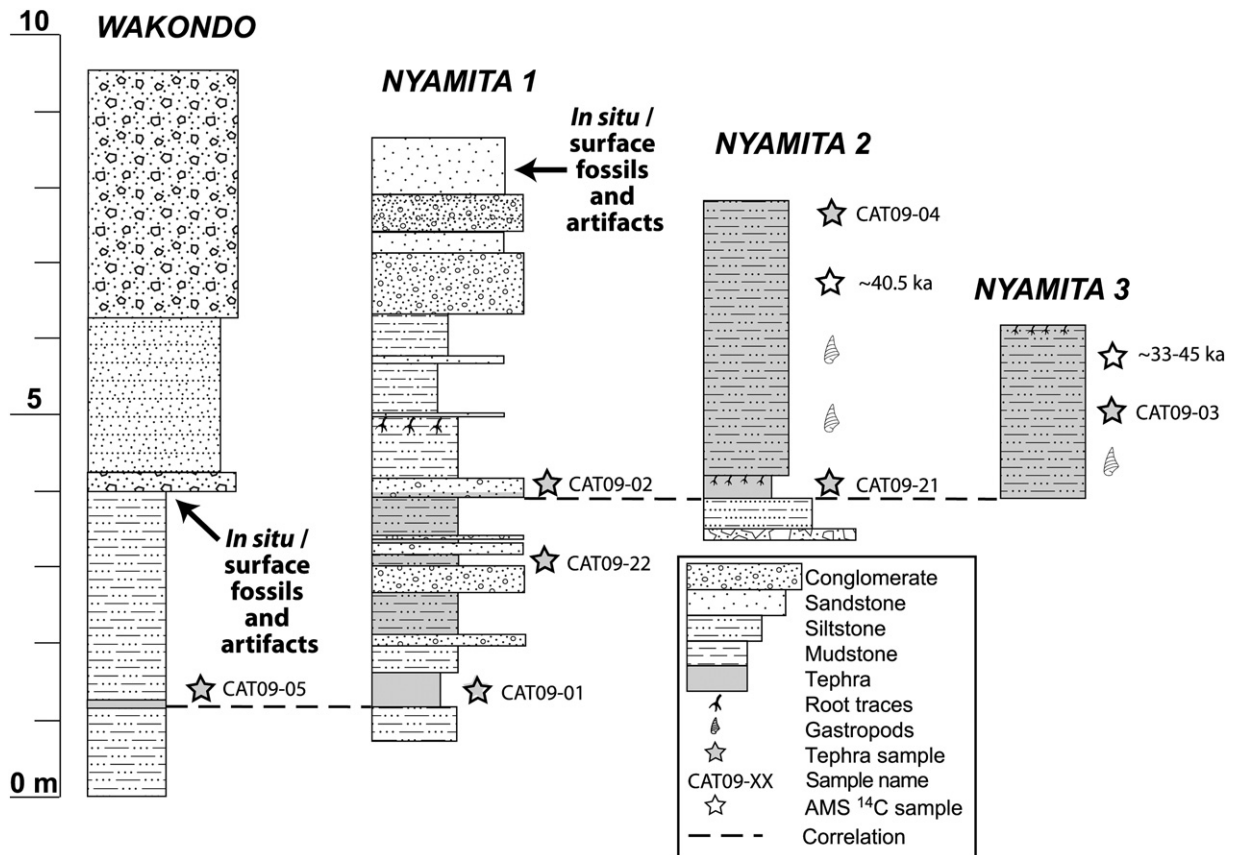


Figure 3. Stratigraphic sections measured at the Wakondo and Nyamita localities in 2009. Nyamita 1–3 are different exposures at the same locality. Dashed lines indicate correlations made on the basis of electron probe microanalyses of tephra. Gastropod shells at Nyamita have calibrated AMS radiocarbon age estimates between ~33 and 45 ka. See text for discussion.

1972) to the Holocene (Pickford and Thomas, 1984), based on artifact typology and a fossil fauna that consisted primarily of extant taxa. Our work in 2009 resulted in the first radiometric age estimates available, based on AMS radiocarbon dates on the carbonate fractions of three gastropod shells (*Limicolaria* cf. *L. martensiana*) from Nyamita (Fig. 3). The absence of calcite in the shells and thus their suitability for dating was determined using X-ray diffraction and thermogravimetric/differential thermal analysis. The samples yielded ages of $41\,700 \pm 1\,400$ (AA-85425), $35\,730 \pm 690$ (AA-86524), and $28\,670 \pm 600$ (AA-85426) radiocarbon years before present, or calibrated ages of $45\,355 \pm 1\,456$, $40\,494 \pm 1\,048$ and $33\,120 \pm 645$ calendar years BP (based on the CalPal-2007_{Hulu} ^{14}C calibration curve of Weninger and Jöris (2008)).

These dates provide approximate minimum ages for the Wasiriya Beds. Because gastropods incorporate ingested calcium carbonate into their shells, radiocarbon dates from them are often anomalously old, with a maximum offset of ~3 kyr (Goodfriend and Stipp, 1983; Goodfriend, 1987), and a 0.6 kyr offset recorded for specimens of sister taxa (*Limicolaria kambeul chudeaui*) from northwestern Sudan (Haynes and Mead, 1987). The gastropods at Nyamita are found within a ~3-m-thick indurated tuffaceous deposit, for which the precise stratigraphic relation to the artifact- and fossil-bearing strata is uncertain (Fig. 3). The snails presumably burrowed into this sediment after deposition (but prior to lithification) to aestivate. The ~12 kyr range among the ages, combined with preserved rootcasts, suggests incipient pedogenesis and a prolonged period of landscape stability. Given the complex paleotopography suggested by the present exposures of an ancient complex cut-and-fill fluvial sequence, the relation of the dated specimens to other fossils and artifacts remains imprecise.

Nevertheless, the radiocarbon ages are the first and only radiometric dates available, and although near the limit of the radiocarbon method, strongly suggest that the Wasiriya Beds pre-date the LGM.

Wasiriya Beds tephra composition and correlation

A more finely resolved understanding of local Wasiriya Beds stratigraphic sequences is provided by distal reworked and fallout tephra deposits at Wakondo and Nyamita (Figs. 2 and 3). Geochemical compositional analysis of tephra allows the determination of the stratigraphic equivalence of layers among disparate outcrops on Rusinga, and provides the potential for tephrostratigraphic correlation with pyroclastic deposits and volcanic sources elsewhere. Polished thin sections were prepared from each sample collected at the outcrop (shown in Fig. 3) to facilitate petrographic inspection and compositional analysis by electron microprobe. Samples CAT09-01 and CAT09-21 are primary tephra-fall (or minimally reworked) well-sorted ash-sized vitric tuffs, following the terminology of Schmid (1981), whereas the remaining samples are variably reworked but contain fresh volcanic glass shards and crystals set in a predominantly clay-to-silt-sized groundmass.

Geochemical composition of the vitric (glass) phase was determined by electron probe microanalysis (EPMA), using back-scattered and secondary electron images to identify areas of fresh glass for analysis. Samples were run using the JEOL JXA-8200 electron microprobe, housed in the Department of Earth and Planetary Sciences at Rutgers University, using a 40° takeoff angle. Analyses employed a 15 kV accelerating voltage, a 10 nA current, and used a rasterized beam over an area of ~25 μm^2 , with beam

size constrained by the fine grain size of some of the Wasiriya Beds samples, particularly CAT09-01. A time dependent intensity element correction with a 2 s (second) interval was applied using Probe for EPMA software (Donovan et al., 2009) to minimize volatile element loss, a persistent problem in the analysis of volcanic glass (Hunt and Hill, 1993, 1996, 2001). Counting times were from 10 to 20 s on-peak and 5–10 s off-peak. Reference materials used for calibration of the analyses include plagioclase (USNM 115900), microcline (USNM 143966), anorthite (USNM 137041), hornblende (USNM 143065), and fayalite (USNM 85276), characterized by Jarosewich et al. (1980; see also Jarosewich, 2002), as well as synthetic tephroite and orthopyroxene from the type specimen of the Tatahouine meteorite (Barrat et al., 1999 and references therein). Raw data were converted to concentrations using standard calculations with an Armstrong-Love/Scott ZAF matrix correction (Armstrong, 1988).

The elemental oxide abundances of nine major and minor elements were determined for each sample. Approximately 15 grains were analyzed per sample, with one analysis per grain for a total of 116 analyses. Results are summarized in Table 1. Samples with totals <92% were excluded from further analyses; this value is arbitrary, but is above acceptable levels noted by Froggatt (1992) and follows a natural break in the distribution of totals for all analyses (see Pollard et al., 2006). Sample CAT09-02 from Nyamita is subdivided into CAT09-02a and CAT09-02b on the basis of two populations of morphologically indistinguishable shards with distinct relative weight. % abundances of Al_2O_3 , FeO, MgO, and CaO (Table 1). Sample CAT09-02 was analyzed twice in order to obtain a representative sample of both shard (sub) populations. Data are not normalized except where required for comparison with whole rock analyses. Although there remains debate as to the advantages and disadvantages of sample normalization in tephrochronological research (cf. Hunt and Hill, 1993; Pollard et al., 2006; Pearce et al., 2008), the tephra correlations proposed here work with either raw or normalized data, providing further support for stratigraphic equivalence among the deposits. We report results from our analyses of raw data here.

There are diverse methods for correlating tephra deposits on the basis of geochemical composition (e.g., Denton and Pearce, 2008; Lowe et al., 2008; Quade and Wynn, 2008). For the Wasiriya Beds tephra, we infer sample equivalence (correlation) among those samples whose means overlap at one standard deviation in the wt. % abundance of all analyzed element oxides. As any correlation is best treated as a hypothesis (e.g., Feibel, 1999; Brown et al., 2006), we explore sample equivalence by principal components analysis (PCA) and test it using multivariate analysis of variance (MANOVA). PCA is used to visualize the distribution of samples in a low-dimensional space, with MANOVA and *post hoc* Hotelling's T^2 used to test whether geochemical centroids of different tephra samples are significantly different. This approach provides a conservative

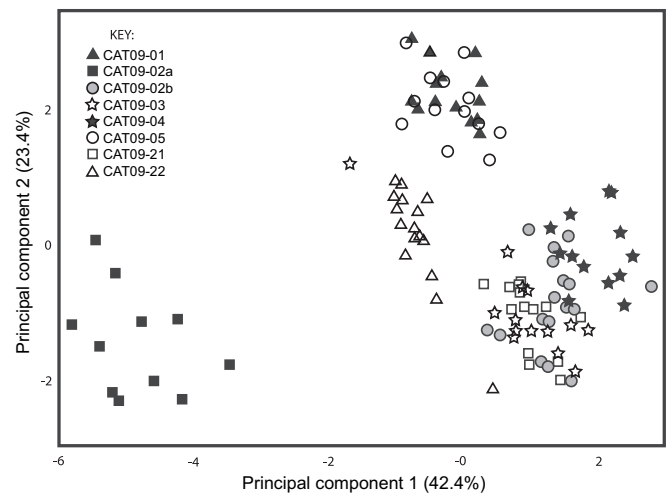


Figure 4. Bivariate plot of the first and second axes of a principal components analysis of element oxide weight percent abundances of Wasiriya Beds tephra determined by electron microprobe. Results suggest that samples CAT09-01 and CAT09-05 are correlative, as are samples CAT09-02b, CAT09-03, and CAT09-21. Sample location is shown in Fig. 3, with summary values listed in Table 1.

estimate of correlations. Canonical ordination is mathematically designed to maximize differences among groups (Neff and Marcus, 1980), and is computationally similar to discriminant analysis, a method widely used in tephrostratigraphy (e.g., Stokes and Lowe, 1988; Stokes et al., 1992; Charman and Grattan, 1999; Pollard et al., 2006; Tryon et al., 2009). Because of our very conservative approach, samples that are found not to differ statistically represent robust hypotheses of equivalence.

Results of a one-way MANOVA indicate that there are significant differences in the geochemical composition of different samples in the total sample pool, suggesting that it is highly unlikely that all sampled tephra deposits derive from a single eruption ($p < 0.0001$ for Wilk's lambda, Pillai's trace, Hotelling–Lawley trace and Roy's greatest root), confirming stratigraphic observations of multiple depositional events. Among our data set, the mean wt. % values of all element oxides overlap at one standard deviation for phonolitic samples CAT09-01 and CAT09-05, suggesting correlation. Trachytic samples CAT09-02b, CAT09-03, and CAT09-21 show the same overlap, suggesting that these three deposits are correlative but distinct from samples CAT09-01 and CAT09-05 (Table 1). As shown in Fig. 4, these correlations are well supported in a PCA multivariate ordination. Results of the pairwise Hotelling's T^2 tests statistically confirm the correlations suggested by single element examinations (Table 2). Samples CAT09-01 and CAT09-05 are significantly different from all other samples, but cannot be shown to differ from each other. Similarly, no differences were found between CAT09-03 and either CAT09-02b or CAT09-21.

Table 1

Major and minor element oxide abundances of Wasiriya Beds tephra determined by electron probe microanalysis, listed as mean and one standard deviation.

Sample	n	SiO ₂	TiO ₂	Al ₂ O ₃	FeO	MnO	MgO	CaO	Na ₂ O	K ₂ O	Total
CAT09-01 ^a	14	58.07 ± 0.99	0.53 ± 0.02	15.54 ± 0.13	7.34 ± 0.41	0.31 ± 0.05	0.29 ± 0.02	0.96 ± 0.08	8.53 ± 0.28	4.61 ± 0.12	96.18
CAT09-02a ^b	12	62.92 ± 0.98	0.58 ± 0.03	10.90 ± 0.35	8.63 ± 0.56	0.33 ± 0.08	0.11 ± 0.02	0.45 ± 0.14	7.31 ± 0.24	4.32 ± 0.12	95.56
CAT09-02b ^b	18	60.46 ± 1.42	0.61 ± 0.02	15.93 ± 0.20	6.31 ± 0.36	0.28 ± 0.07	0.33 ± 0.02	0.90 ± 0.16	7.42 ± 0.29	4.98 ± 0.18	97.21
CAT09-03 ^b	14	60.67 ± 0.85	0.61 ± 0.02	15.70 ± 0.28	6.45 ± 0.51	0.28 ± 0.09	0.33 ± 0.02	0.80 ± 0.12	7.42 ± 0.65	4.91 ± 0.20	97.18
CAT09-04 ^b	14	59.12 ± 0.81	0.58 ± 0.02	15.70 ± 0.21	6.16 ± 0.60	0.24 ± 0.04	0.34 ± 0.05	1.21 ± 0.08	7.11 ± 0.18	4.81 ± 0.29	95.28
CAT09-05 ^a	14	58.03 ± 1.46	0.54 ± 0.02	15.57 ± 0.19	7.59 ± 0.58	0.30 ± 0.03	0.28 ± 0.02	0.94 ± 0.07	8.41 ± 0.48	4.62 ± 0.15	96.27
CAT09-21 ^b	14	60.66 ± 0.81	0.60 ± 0.02	15.83 ± 0.22	6.38 ± 0.20	0.23 ± 0.07	0.32 ± 0.02	0.81 ± 0.10	7.26 ± 0.31	4.84 ± 0.28	96.94
CAT09-22 ^b	16	59.97 ± 1.01	0.55 ± 0.04	14.77 ± 0.28	7.33 ± 0.29	0.28 ± 0.07	0.30 ± 0.03	0.61 ± 0.05	7.56 ± 0.88	4.71 ± 0.16	96.06

n = number of analyses per sample

^a Phonolite composition according to the method of Le Bas et al. (1986).

^b Trachyte composition according to the method of Le Bas et al. (1986).

Table 2Pairwise Hotelling's T^2 results that test for sample differences on the basis of geochemical composition.

Sample	CAT09-01	CAT09-02a	CAT09-02b	CAT09-03	CAT09-04	CAT09-05	CAT09-21	CAT09-22
CAT09-01								
CAT09-02a	*							
CAT09-02b	*	*						
CAT09-03	*	*	0.0923					
CAT09-04	*	*	*	*				
CAT09-05	0.7181	*	*	*	*			
CAT09-21	*	*	0.0206 ^a	0.3119	*	*		
CAT09-22	*	*	*	*	*	*	*	

^{*} $p < 0.0001$.^a Not significant according to a Bonferroni correction for multiple comparisons.

Our tephrostratigraphic results permit us to correlate outcrops that could not be related in the field because of discontinuous exposure at Nyamita (samples CAT09-03, CAT09-2b, and CAT09-21; Fig. 3). The compositional similarity of subsample CAT09-02b with CAT09-03 and CAT09-21 suggests that the bimodal composition of CAT09-02 is due to mechanical admixture through post-depositional reworking of formerly distinct tephra, rather than a result of magma heterogeneity at eruption (cf. Shane et al., 2008). The same tephra deposit is found at both Nyamita and Wakondo (samples CAT09-01 and CAT09-05), indicating that both localities sample sediments, artifacts, and fossils of a similar temporal range (Fig. 3). Samples CAT09-02a, CAT09-04, and CAT09-22 have no correlates. Combined with the evidence for correlation presented above, the Wasiriya Beds preserve at least four geochemically distinct distal deposits of trachytic tephra and one widespread deposit of phonolitic tephra (Table 1).

Possible source and age of the Wasiriya Beds tephra

The volcanic sources closest to the Wasiriya Beds lie within the Nyanza Rift, but are Mio-Pliocene in age (Pickford, 1982; Woolley, 2001) and thus inconsistent with available age estimates for the Wasiriya Beds. Although it is possible that smaller unnamed vents or fissures close to Rusinga are the sources of the Wasiriya Beds tephra, their fine grain size, composition, and position relative to dominant wind patterns suggest sources to the west in the East African rift system, where large volumes of primarily trachytic (and rarely phonolitic) tephra were erupted from multiple Quaternary volcanoes (Dunkley et al., 1993; Pyle, 1999; Woolley, 2001; Macdonald and Scaillet, 2006), particularly in the Kenyan portion of the Gregory Rift. Most Quaternary eruptions in Ethiopia, Uganda, and Tanzania produced rhyolites, basalts, carbonatites (see Woolley, 2001 and references therein) or other volcanoclastic rocks compositionally distinct from the Wasiriya Beds trachytic and phonolitic tephra.

There are insufficient comparative data on the geochemical composition of tephra from the East African rift system volcanoes to make any confident source attributions, particularly for the trachytic deposits. However, fewer Quaternary volcanoes erupted phonolitic lava or tephra (Macdonald, 1987; Clarke et al., 1990; Dunkley et al., 1993; Skilling, 1993; Woolley, 2001; Dawson, 2008). Their locations are shown in Fig. 1. At >400 km away, the Barrier Volcanic Complex of northern Kenya (Dunkley et al., 1993) and Oldoinyo Lengai, Meru, and Kilimanjaro in northern Tanzania (Dawson, 2008) are the least likely sources. At Silali, the phonolites are limited to Holocene lava flows (Dunkley et al., 1993); Pleistocene explosive tephra-producing eruptions on Silali were trachytic (Tryon et al., 2008).

We consider Longonot and Suswa the most likely sources for the Wasiriya Beds tephra, although this hypothesis requires a considerable number of geochemical analyses to test it. At ~250 km,

Longonot and Suswa are the closest sources of phonolitic ash. Longonot and Suswa apparently share an eruptive history, with shield formation on each volcano beginning <400 ka (Scott and Skilling, 1999). On Suswa, pre-caldera deposits are trachytic overlain by exclusively phonolitic post-caldera deposits (Skilling, 1993). The lowermost post-caldera phonolites at Suswa have two K–Ar age estimates of 100 ± 10 ka (Baker et al., 1988), overlain by 1–25 m of phonolitic tephra fallout deposits (Skilling, 1993). Tephra from Longonot and Suswa, termed the Mau Ashes, have a maximum observed thickness of >220 m and have been mapped across an area up to 150 km west of their source (Randel and Johnson, 1991; Williams, 1991). This indicates past wind patterns that dispersed tephra primarily to the south as well to the west towards Lake Victoria, making it likely that discontinuous deposits of these tephra are preserved in more distal areas, such as in the Wasiriya Beds of Rusinga Island (cf. Pickford, 1982). Should a Longonot or Suswa source for the basal phonolitic tephra deposit at Wakondo and Nyamita be confirmed, it would suggest a maximum age of 100 ± 10 ka for these Wasiriya Beds exposures.

The archaeology of the Wasiriya Beds

Earlier researchers reported Acheulian and Sangoan implements from the Wasiriya Beds (identified by L.S.B. Leakey, reported in Kent, 1942; Van Couvering, 1972). These artifacts, primarily picks and handaxes, are stored in the National Museums of Kenya. Our re-inspection confirmed the initial typological diagnosis. These artifacts are rolled, substantially weathered, and have preservation states quite unlike the fresh, minimally altered typologically MSA material we have observed on Rusinga. Although we have yet to find such material *in situ*, the handaxes and picks hint at a long archaeological sequence on Rusinga, as such artifacts typically date to the Early or Middle Pleistocene elsewhere in eastern Africa (McBrearty and Tryon, 2005; Barham and Mitchell, 2008).

Although we collected sparse fossils and artifacts from the Gumba and Hiwegi localities (Fig. 2), our 2009 surveys and test excavations focused on the western Nyamsingula, Nyamita and Wakondo localities. We conducted excavations at Nyamita and Wakondo where artifacts and fossils were most densely distributed. Our tephrostratigraphic correlations show Nyamita and Wakondo to be approximately age-equivalent (Fig. 3), and our initial test excavations at both localities document the first *in situ* artifacts recovered from the Wasiriya Beds. We excavated 4 m² trenches to a depth of up to 0.7 m at both localities, followed arbitrary (10-cm thick) levels, sieved with 6.4 mm wire mesh, and plotted all surface and excavated finds relative to a site datum. Both Nyamita and Wakondo have spatially discrete (~50 m²) surface and *in situ* fossil and artifact concentrations that at each locality apparently derive from a single, although broad, stratigraphic interval.

Artifacts at Nyamita and Wakondo were recovered from a complex cut-and-fill fluvial sequence, and at Nyamita elongated artifacts were aligned parallel or perpendicular to local channel margins, suggesting reorientation by stream flow (Schick, 1986). *In situ* faunas were sparse at Wakondo, making comparable orientation data unavailable for the fauna. Because our focus in the analysis of fauna thus far has been on taxonomic identification of primarily cranio-dental elements, detailed taphonomic analyses of these and other specimens have only just begun. However, our initial study of the recovered fossils indicates well-preserved bone cortical surfaces and, like the artifacts, the fauna also suggests complex taphonomic histories at these localities. Based on field and preliminary laboratory observations, the type and range of bone weathering (Behrensmeyer, 1978) suggests rapid burial at Nyamita and western Nyamsingula (primarily weathering stages 0–1) and more prolonged exposure at Wakondo (primarily weathering stages 2–3). Carnivore damage, specifically tooth punctures and gnaw marks, is present at all localities, with gastric etching observed among the Wakondo material. The presence of multiple, deep, v-shaped butchery marks on a large bovid vertebral fragment from Wakondo demonstrates the active role of hominins in the accumulation of at least some of the fauna (Fig. 5). A more detailed study is in progress to assess the relative contribution of the different accumulation agents to the faunal assemblages at Wakondo and Nyamita, and until complete, the site formation processes at these localities remain unresolved. Despite this qualification, Wakondo joins the very small sample of open-air eastern African MSA sites with stone artifacts and associated fauna (reviewed by Domínguez-Rodrigo et al., 2007).

The artifacts ($n = 176$) consist of flaking debris (cores, flakes, and flake fragments) and rare ($n = 8$) retouched pieces, summarized in Table 3, with a sample illustrated in Fig. 6. Cores and core fragments include one multiplatform core with at least 10 removals (Fig. 6h) and three casual cores with <2 flake removals each. One small specimen (maximum dimension = 5.1 cm) may be

Table 3
Counts of surface and excavated (in parentheses) lithic artifacts collected from the Wasiriyia Beds in 2009.

	Nyamita	Wakondo	Nyamsingula	Artifact Type Total
Complete Flakes	15 (3)	13 (0)	0	31
Proximal Flake Fragments	19 (8)	7 (3)	2	39
Other flake fragments	50 (13)	23 (6)	0	92
Retouched Pieces	7 (0)	1 (1 ^a)	0	9
Cores	2 (2)	1 (0)	0	5
Locality Total	119	55	2	176

^a Found *in situ* but not from excavation.

either a discoidal core made on a flake or a Levallois core, from which the last Levallois flake overshot the core margins and removed most of the upper flaking surface prior to subsequent smaller flake removals (Fig. 6c). The small sample of complete flakes ($n = 31$) is dominated by pieces with plain striking platforms and few dorsal scars, most originating from the same direction as the striking platform. The combined Wasiriyia Beds sample includes 14 Levallois flakes or proximal flake fragments (Fig. 6a, b, f) as well as five blades and blade proximal fragments with relatively wide striking platforms (Fig. 6g, i, j). Formal tools include bifacially and unifacially flaked points or pointed pieces (Fig. 6d–e), a retouched elongated Levallois flake (Fig. 6a), and miscellaneous other retouched pieces. No hammerstones or other percussors were recovered.

The artifacts are made of chert ($n = 53$), quartzite ($n = 4$), quartz ($n = 2$), and at least 18 types of lava distinguished on the basis of color, texture, and phenocryst type and abundance seen macroscopically and under 10X magnification. The most abundant lava type ('type A', $n = 55$) is lithologically similar to the Lunene Lavas described by Shackleton (1950), outcrops of which cap the central highlands on Rusinga <2 km north of Nyamita and Wakondo

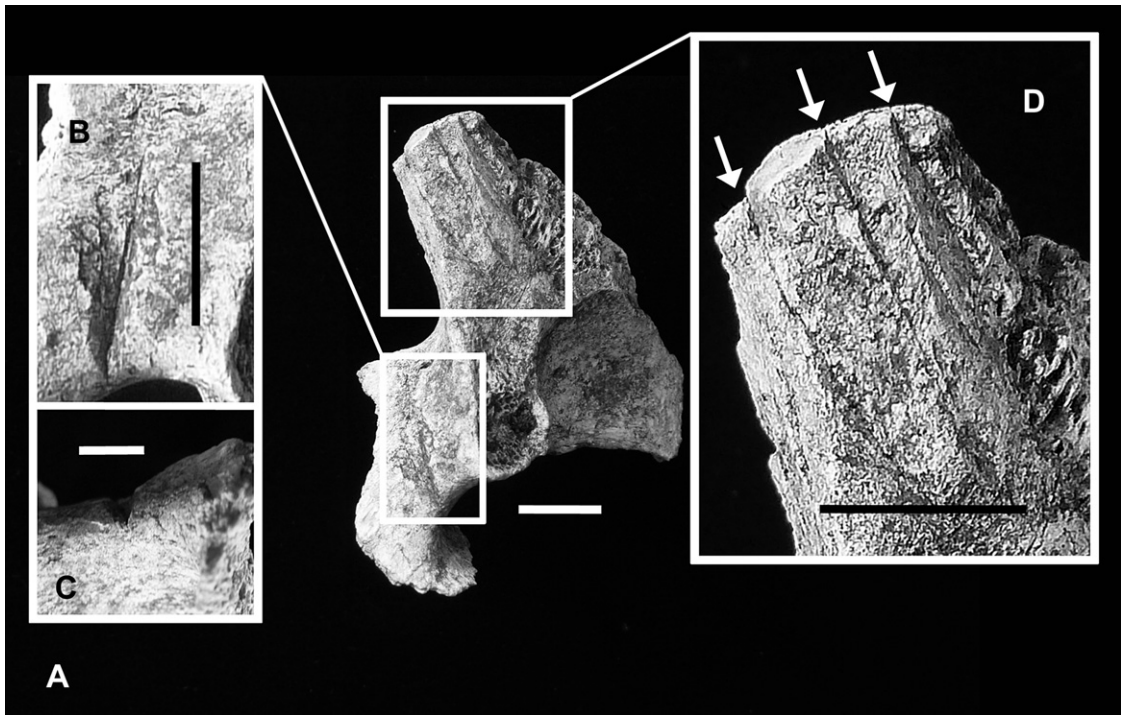


Figure 5. (A) Lateral view of a weathered bovid cervical vertebra fragment retaining large v-shaped butchery marks suggesting disarticulation at the base of the neck. (B) Close-up and (C) profile view of a large, v-shaped cutmark on the body of the vertebra. (D) Multiple parallel cutmarks on the transverse process. Scale bar in each image is equal to one cm.

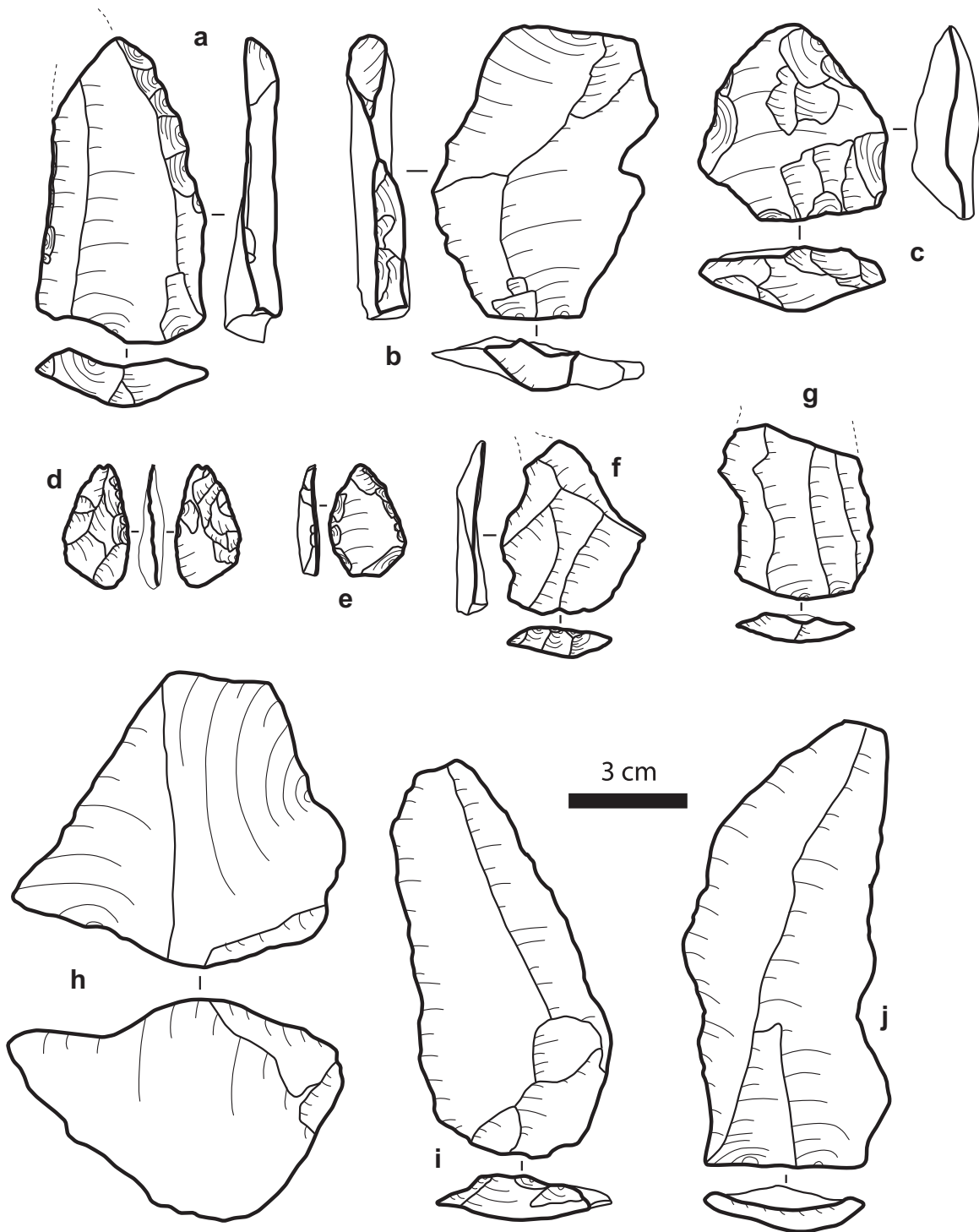
Wasiriya Beds Artifacts 2009 collections

Figure 6. Artifacts from the Wakondo and Nyamita localities in the Wasiriya Beds collected in 2009: (a) retouched elongated Levallois flake fragment, lava, *in situ*, Wakondo, (b) Levallois *eclat débordant* (edge of core or core trimming flake), lava, surface, Nyamita, (c) Levallois/discoidal core, lava, *in situ*, Nyamita, (d) bifacially retouched point, chert, surface, Nyamita, (e) unifacially retouched pointed flake, lava, surface, Nyamita, (f) Levallois flake fragment, lava, surface, Nyamita, (g) blade? fragment, lava, surface, Wakondo, (h) multiple platform core, lava, surface, Nyamita, (i) elongated flake or blade, lava, surface, Wakondo, (j) blade, lava, surface, Nyamita.

(Fig. 2). Cortex is present on only 8% ($n = 14$) of the complete artifact sample. Conglomerates exposed at both sites could have and likely did serve as raw material sources, but clasts in these juvenile sediments are angular and lack well-developed fluvial

cortex. The precise sources of the stone raw materials used remain unknown.

Levallois flakes and other retouched pieces are heavily represented among the raw material types identified by a single

Table 4

Taxonomic list and number of identified specimens (NISP) of mammalian fossils from the Wasiriya Beds.

Taxon	Common name	Nyamita	Wakondo	Nyamsingula	Other Localities	Wasiriya Beds Total
<i>Crocota crocuta</i>	Spotted hyena	3	0	0	0	3
<i>Orycteropus crassidens</i> ^a	Aardvark	1	0	0	0	1 ^c
Elephantidae cf. <i>Loxodonta africana</i>	Elephant	0	0	1	0	1
<i>Equus burchelli</i>	Burchell's zebra	0	0	1	3	4
<i>Equus grevyi</i> ^b	Grevy's zebra	2	2	1	0	5
<i>Equus</i> sp. indet.	Zebra	2	0	5	4	11
<i>Hippopotamus</i> cf. <i>H. amphibius</i>	Hippopotamus	3	0	0	1	4
<i>Phacochoerus</i> sp.	Warthog	1	3	3	2	9
<i>Taurotragus oryx</i> ^b	Eland	2	0	0	0	2
<i>Tragelaphus strepsiceros</i> ^b	Greater kudu	0	0	0	1	1
<i>Oryx gazella</i> ^b	Oryx	1	0	2	0	3
<i>Redunca</i> sp.	small Reedbuck	5	1	2	3	11
Reduncine sp.	larger Reedbuck/Waterbuck	1	1	3	0	5
<i>Connochaetes taurinus</i> ^b	Wildebeest	8	3	17	7	35
<i>Megalotragus</i> sp. indet. ^a	Giant wildebeest	1	1	1	0	3
<i>Alcelaphus buselaphus</i>	Hartebeest	0	2	1	8	11
Small Alcelaphine (cf. <i>Damaliscus</i>) ^a		5	4	10	7	26
Alcelaphini cf. <i>Alcelaphus/Damaliscus</i>	Alcelaphini	17	60	23	40	140
Alcelaphini indet.	Alcelaphini	5	14	9	6	34
<i>Gazella</i> cf. <i>G. thomsoni</i>	Thomson's Gazelle	2	0	1	4	7
<i>Gazella</i> cf. <i>G. granti</i>	Grant's Gazelle	4	0	1	2	7
Antilopini indet.	Antilopini	1	0	0	1	2
<i>Ourebia ourebi</i>	Oribi	3	0	2	3	8
<i>Synceus caffer</i>	Cape Buffalo	0	2	0	4	6
<i>Pelorovis antiquus</i> ^a	Giant Buffalo	0	1	1	0	2
Bovini indet.	Buffalo	0	1	0	1	2
ΣNISP		67	95	84	97	343

Note that specimens from localities other than Nyamita, Wakondo, and Nyamsingula include limited specimens from Hiwegi that we collected in 2009 as well as those collected from across the island by previous researchers, for which precise provenance cannot always be determined.

^a Extinct

^b Outside historic range

^c Estimated from MacInnes (1956).

specimen. Eight types of lava are defined by one artifact each, but half of these artifacts ($n = 4$) are Levallois flakes or Levallois flake fragments, of which only 14 were recovered. Levallois flakes are thus significantly more abundant among the rare lava types than expected by chance (Fisher's exact test because of sparse cells, $p = 0.002$). The absence of associated manufacturing debris with these Levallois flakes suggests their preferential transport from manufacturing sites elsewhere, a feature of Levallois flakes also noted for some Eurasian Mousterian sites (e.g., Geneste, 1989). Similarly, the bifacially retouched point (Fig. 6d) is made of green chert, different from 51 of the 52 remaining pieces of cryptocrystalline silica recovered that are a white-and-red mottled material. Combined with the relatively few cores ($n = 5$), these data suggest that the sites studied thus far were largely areas of stone artifact use and discard rather than production.

Points, Levallois flakes, and perhaps blades at Nyamita, Wakondo, and western Nyamsingula indicate a Middle Stone Age (MSA) attribution for these assemblages (e.g., Clark and Kleindienst, 2001), consistent with the absence of handaxes, cleavers, microliths or other stone implements from these localities diagnostic of the Early or Later Stone Age. Although our small sample size precludes detailed comparison, the Wasiriya Beds assemblages are broadly similar to the few excavated and published (but as yet undated) MSA assemblages from the Lake Victoria region, including the Pundo Makwar Industry at Muguruk (McBrearty, 1988), and artifacts from Songhor (McBrearty, 1981) and the basal levels at Randhore rockshelter (Gabel, 1969). Our Wasiriya Beds sample lacks the distinctive Lupemban lanceolates, likely Middle Pleistocene in age (Barham, 2000), that are found at many sites in central and eastern Africa (see Banks et al., 2006). Instead, the diminutive, carefully worked points and pointed pieces such as those found at Nyamita (Fig. 6d–e) are more characteristic of assemblages found at a number of sites in eastern Africa dated to or presumed to date to

the Late Pleistocene, an age consistent with our estimates from radiocarbon and tephrostratigraphic data. These include site Gvjm16 at Lukenya Hill (Merrick, 1975; Marean, 1990), Songhor (McBrearty, 1981), Prolonged Drift (Merrick, 1975; Waweru, 2007), and Cartwright's Site (Waweru, 2007) in Kenya, Nasera and Mumba rockshelters in Tanzania (Mehlman, 1989, 1991), Walasi Hill (O'Brien, 1939) and Magosi in Uganda (Wayland and Burkitt, 1932; Clark, 1957; Cole, 1967a), and Aduma (Yellen et al., 2005) and Porc-Épic Cave (Perlès, 1974; Clark et al., 1984; Pleurdeau, 2005; Assefa et al., 2008) in Ethiopia. The combination of small points and large blades is unusual, but from our small sample size it is impossible to determine if this represents behavioral variation, time averaging, or even differences due to raw material as shown for MSA sites in the Kenya Rift Valley and areas to the north (Tryon et al., 2008).

Wasiriya Beds fauna and paleoenvironmental context

Available sedimentary evidence suggests that the Wasiriya Beds sample a range of subaerial fluvial depositional environments. Fossil fauna are relatively abundant in the Wasiriya Beds, and include numerous micromammals currently under study. The recovered macromammals suggest ancient habitats substantially different from the present.

Table 4 lists the mammalian fauna for the Wasiriya Beds, based on our surface collections and excavations through 2009, as well as the reanalysis of specimens collected by previous research teams. As a result, we have substantially increased the taxonomic range of recovered fauna (cf. Pickford, 1986). Surface collection focused primarily on specimens that could be identified to taxon. For bovids, this included primarily horn cores, crania, mandibles, and isolated teeth. Post-cranial elements were also collected, although our analysis presented here focuses only on taxonomically

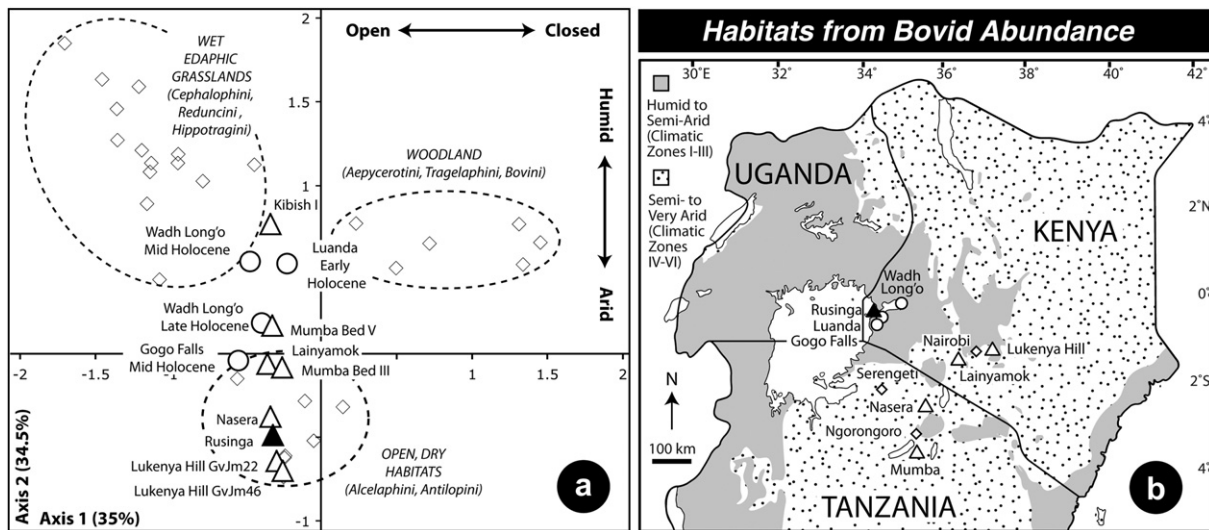


Figure 7. (a) Habitat distinctions from correspondence analyses of bovid abundances in African game parks (diamonds) and Pleistocene (triangles) and Holocene (circles) archaeological sites. Habitat boundaries encircled by dashed lines are arbitrary. (b) Schematic map of East Africa showing position of archaeological sites and selected game parks shown in (a), plotted against climatic zones of Pratt and Gwynne (1977).

identifiable specimens. Taxonomic identifications were made with the assistance of modern comparative material and fossil collections stored at the National Museums of Kenya (NMK), Nairobi, with taxonomic abundances quantified according to the number of identified specimens (NISP) (Grayson, 1984).

Water-dependent taxa, such as *Hippopotamus* and reedbucks, are consistent with the fluvial setting inferred from the sediments. However, the remaining fauna suggest that this fluvial setting represented a local habitat within a relatively dry, open, grassland environment. The faunal assemblage is dominated by alcelaphine bovids (73% of NISP), suggesting the predominance of open grassland vegetation (Vrba, 1980). The Wasiriya Beds fauna also includes arid-adapted ungulates, such as oryx (*Oryx gazella*) and Grevy's zebra (*Equus grevyi*), both of which are absent historically from this region and today are restricted to regions east and south of Lake Victoria (Kingdon, 1979, 1982; see also Table 4). Our sample also includes several extinct ungulates: the giant buffalo (*Pelorovis antiquus*), the giant wildebeest (*Megalotragus* sp.), and a small unnamed alcelaphine (cf. *Damaliscus*) also known from Late Pleistocene contexts at Lukenya Hill in south-central Kenya (Marean and Gifford-Gonzalez, 1991; Marean, 1992). The unnamed alcelaphine (cf. *Damaliscus*) material from the Wasiriya Beds was identified by direct comparison with the Lukenya Hill material housed at the NMK. The extinct bovids are associated elsewhere with faunas indicative of dry and open habitats (Klein, 1980; Vrba, 1987; Marean and Gifford-Gonzalez, 1991; Marean, 1992). The Wasiriya Beds fauna is similar to that from Lukenya Hill, although the Wasiriya Beds sample is distinguished from it by fewer numbers of the small extinct alcelaphine bovid. Much of the Lukenya Hill material has been interpreted as representing an expansion of arid grasslands during the LGM (Marean, 1992), although some strata pre-date this arid interval (Marean, 1992; Ambrose, 1998a).

An analysis of bovid community structure also suggests an open, dry, grassland setting for the Wasiriya Beds. Alemseged (2003) conducted correspondence analysis of abundance data from 29 African game parks and demonstrated that, at the tribal level, bovid taxonomic abundance distinguishes among open-dry, woodland, and edaphic grassland habitats, providing a model to infer paleoenvironment from fossil assemblages. In our correspondence analysis

(Fig. 7), the Wasiriya Beds bovids cluster with alcelaphine and antilopine bovids from African parks characterized by open and dry conditions: Nairobi (Kenya), Ngorongoro and Serengeti (Tanzania), Omo (Ethiopia), Etosha (Namibia), and Kalahari (Botswana). The Wasiriya Beds bovid abundances are also similar to other sites from the Middle and Late Pleistocene: GvJm22 and GvJm46 from Lukenya Hill, Kenya (Marean, 1992), levels 4–7 at Naseria rockshelter, Tanzania (Mehlman, 1989, 1991), and to a lesser extent, Lainyamok, Kenya (Potts and Deino, 1995), and Bed III at Mumba rockshelter, Tanzania (Mehlman, 1989, 1991). These game parks and fossil localities occur in areas that today are substantially drier than Rusinga (Fig. 7). Importantly, the correspondence analysis (Fig. 7) also suggests that the Wasiriya Beds assemblage differs substantially from Holocene (~2–8 ka) faunas of the Lake Victoria region in western Kenya, notably Gogo Falls (Robertshaw, 1991; Karega-Munene, 2002), Luanda (Robertshaw et al., 1983), and Wadh Long'o (Lane et al., 2007; Prendergast, 2008). Although now an island in a relatively semi-arid to semi-humid region (500–1000 mm per annum; Pratt and Gwynne, 1977), during the deposition of the Wasiriya Beds, Rusinga may have been a local topographic high point in a more arid grassland environment connected to the mainland. The extent to which this arid grassland setting is related to the possible contraction of Lake Victoria with reduced rainfall is currently uncertain.

Several other lines of evidence suggest that the Wasiriya Beds sample environments and animal communities substantially different from the present. The correspondence analyses show a strong similarity between the Wasiriya Beds assemblages and LGM strata from Lukenya Hill sites GvJm22 and GvJm46 (Marean, 1990; Miller, 1979) and Naseria rockshelter (Mehlman, 1989, 1991). Available radiocarbon age estimates and the presence of MSA artifacts suggest that the Wasiriya Beds are older than the LGM, but serve to stress the presence of taxa indicative of an arid grassland environment among each of these assemblages. *Pelorovis* and a small extinct alcelaphine bovid (cf. *Damaliscus*) occur at Lukenya Hill and the Wasiriya Beds, and both became extinct throughout sub-Saharan Africa with the return of relatively humid conditions during the Holocene (Klein, 1980, 1984; Marean and Gifford-Gonzalez, 1991; Marean, 1992). Like the Wasiriya Beds, the fauna reported from the LGM strata at Naseria (Mehlman, 1989) as well as Middle Pleistocene levels at Lainyamok (Potts and Deino,

1995) include oryx and Grevy's zebra, both beyond their historic range, suggesting considerable range shifts in these arid-adapted taxa. One consequence of range shifts is the formation of local refugia, and the *Megalotragus* from the Wasiriya Beds probably represents the last known occurrence of the genus in eastern Africa. Middle-to-Late Pleistocene fossil occurrences of *Megalotragus* are comparatively rare (cf. Harris, 1991), although in southern Africa its last securely dated record is in Late Pleistocene deposits at Nelson Bay Cave dated to ~16 ka (Klein, 1972, 1980), with an isolated tooth reported from 7 ka deposits at Wonderwerk Cave (Thackeray, 1982; Beaumont and Morris, 1990).

The gastropod evidence

Pickford (1986) reports the land snails *Limicolaria* sp., *Burtoa* sp., and *Trochonanina* sp. from the Wasiriya Beds encountered during his wide-ranging survey across Rusinga Island. Our own more limited survey identified only *L. cf. L. martensiana* which is locally abundant at Nyamita and Wakondo. Shell pigmentation and patterning are preserved on *in situ* specimens from tuffaceous sediments (Fig. 3), aiding in identification to the species level (see also Abbott, 1989). Today, *Limicolaria* species are widely dispersed across Equatorial Africa including the Lake Victoria region, and most of the known species (particularly in eastern Africa) live in upland woodland or woodland-savanna habitats and feed on leaf litter and new growth. Although the Lake Victoria region today receives from 500–1500+ mm of rainfall each year (Pratt and Gwynne, 1977), *Limicolaria* can occur in much more arid regions with a minimum of ~300 mm of rainfall per annum, but with prolonged periods of aestivation (Crowley and Pain, 1970; Haynes and Mead, 1987; Pickford, 1995). *Burtoa* and *Trochonanina* also both occur in woodland and savanna habitats in the Lake Victoria region today (Pickford, 1995). Although none of the land snails allow a precise paleoenvironmental reconstruction because of wide habitat tolerances, the taxa recovered from the Wasiriya Beds are consistent with a local fluvial setting within a savanna or grassland environment. As we noted above in our discussion of tephra, the gastropods may also significantly post-date the artifact- and fossil-bearing strata.

Conclusions

Although long known for its rich deposits of Miocene fossils, our recent investigations have demonstrated the paleoanthropological potential of the Pleistocene Wasiriya Beds on Rusinga Island, Kenya. Sediments of the Wasiriya Beds, particularly at the Nyamita and Wakondo localities, sample a cut-and-fill sequence of fluvial sediments. Exposures at Nyamita and Wakondo include fallout and reworked distal tephra deposits that can be correlated on the basis of their geochemical composition as determined by electron probe microanalysis. Multiple AMS radiocarbon age estimates on gastropod shells indicate that these sediments pre-date the Last Glacial Maximum (LGM), consistent with recovered artifacts and fossils. Surface and *in situ* stone artifacts from Nyamita and Wakondo include a small, bifacially flaked point and unmodified as well as retouched Levallois flakes, consistent with a Middle Stone Age (MSA) attribution. A taxonomically diverse fossil fauna that includes at least one cut-marked specimen is associated with these artifacts, which is unusual among eastern African MSA sites. The fauna indicates environments substantially more arid than the present, and includes a number of extant forms beyond their current range (oryx and Grevy's zebra), as well as taxa largely extinct in sub-Saharan Africa by the Holocene, such as *Pelorovis antiquus*, *Megalotragus* sp., and a small, unnamed extinct alcelaphine bovid.

Rusinga's position within a biogeographically important region characterized by shifting floral and faunal communities make it a key location for understanding the complex dynamics of environmental variability, dispersal, and biological and behavioral diversity among Equatorial African hominins that included *H. sapiens*. Our continued research on Rusinga focuses on employing a multi-proxy approach to test the hypothesis of past aridity inferred from collected fossils, constructing a detailed chronological framework, broadening the sample of archaeological traces, and better understanding the depositional and taphonomic histories of artifact and faunal accumulations. These data should allow us to begin to document the timing of pre-LGM periods of aridity in the Lake Victoria region relative to the contrasting patterns of climate variation recorded in sedimentary archives in adjacent lake basins to the east and south (cf. Trauth et al., 2001, 2003; Cohen et al., 2007; Scholz et al., 2007), and to understand the role of climate change in shaping local environments and hominin populations.

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References

- Abbott, R.T., 1989. Compendium of Landshells: a Color Guide to More than 2,000 of the World's Terrestrial Shells. American Malacologists, Inc., Melbourne, Florida.
- Adams, W.M., 1996. Lakes. In: Adams, W.M., Goudie, A.S., Orme, A.R. (Eds.), The Physical Geography of Africa. Oxford University Press, Oxford, pp. 122–133.
- Alemseged, Z., 2003. An integrated approach to taphonomy and faunal change in the Shungura Formation (Ethiopia) and its implications for hominid evolution. *J. Hum. Evol.* 44, 451–478.
- Ambrose, S.H., 1998a. Chronology of the Later Stone Age and food production in East Africa. *J. Archaeol. Sci.* 25, 377–392.
- Ambrose, S.H., 1998b. Late Pleistocene human population bottlenecks, volcanic winter and differentiation of modern humans. *J. Hum. Evol.* 34, 623–651.
- Ambrose, S.H., 2001. Middle and Later Stone Age settlement patterns in the Central Rift Valley, Kenya: comparisons and contrasts. In: Conard, N.J. (Ed.), Settlement Dynamics in the Middle Paleolithic and Middle Stone Age. Kerns-Verlag, Tübingen, pp. 21–44.

- Ambrose, S.H., Lorenz, K.G., 1990. Social and ecological models for the Middle Stone Age in southern Africa. In: Mellars, P. (Ed.), *The Emergence of Modern Humans: An Archaeological Perspective*. Edinburgh University Press, Edinburgh, pp. 3–33.
- Andrews, P., 1981. A short history of Miocene field paleontology in western Kenya. *J. Hum. Evol.* 10, 3–10.
- Armstrong, J.T., 1988. Quantitative analysis of silicate and oxide materials: comparison of Monte Carlo, ZAF, and $\phi(\rho z)$. In: Newbury, D.E. (Ed.), *Microbeam Analysis-1988*. San Francisco Press, Inc., San Francisco, pp. 239–246.
- Assefa, Z., Lam, Y.M., Mienis, H.K., 2008. Symbolic use of terrestrial gastropod opercula during the Middle Stone Age at Porc-Epic Cave, Ethiopia. *Curr. Anthropol.* 49, 746–756.
- Baker, B.H., Mitchell, J.G., Williams, L.A.J., 1988. Stratigraphy, geochronology and volcano-tectonic evolution of the Kedong-Naivasha-Kinangop region, Gregory Rift Valley, Kenya. *J. Geol. Soc. London* 145, 107–116.
- Banks, W.E., d'Errico, F., Dibble, H.L., Kriskalka, L., West, D., Olszewski, D.I., Peterson, A.T., Anderson, D.G., Gillam, J.C., Montet-White, A., Crucifix, M., Marean, C.W., Sánchez-Göni, M.-F., Wohlfarth, B., Vanhaeren, M., 2006. Ecological niche modeling: new tools for reconstructing the geography and ecology of past human populations. *PaleoAnthropology*, 68–83.
- Barham, L., Mitchell, P., 2008. *The First Africans: African Archaeology from the Earliest Toolmakers to most Recent Foragers*. Cambridge University Press, Cambridge.
- Barham, L.S. (Ed.), 2000. *The Middle Stone Age of Zambia*. Western Academic & Specialist Press, Bristol.
- Barrat, J.A., Gillet, P., Lesourd, M., Blichert-Toft, J., Poupeau, G.R., 1999. The Tatahouine diogenite: mineralogical and chemical effects of sixty-three years of terrestrial residence. *Meteorit. Planet. Sci.* 34, 91–97.
- Basell, L.S., 2008. Middle Stone Age (MSA) site distributions in eastern Africa and their relationship to Quaternary environmental change, refugia and the evolution of *Homo sapiens*. *Quatern. Sci. Rev.* 27, 2484–2498.
- Beaumont, P.B., Morris, D., 1990. *Guide to Archaeological Sites in the Northern Cape*. McGregor Museum, Kimberley.
- Behar, D.M., Villemis, R., Soodyall, H., Blue-Smith, J., Pereira, L., Metspalu, E., Scozzari, R., Makkani, H., Tzur, S., Comas, D., Bertranpetit, J., Quintana-Murci, L., Tyler-Smith, C., Wells, R.S., Rosset, S., 2008. The dawn of human matrilineal diversity. *Am. J. Hum. Genet.* 82, 1130–1140.
- Behrensmeier, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150–162.
- Behrensmeier, A.K., Potts, R., Plummer, T., Tauxe, L., Opdyke, N., Norstad, T., 1995. The Pleistocene locality of Kanjera, western Kenya: stratigraphy, chronology, and paleoenvironments. *J. Hum. Evol.* 29, 247–274.
- Bergner, A.G.N., Strecker, M.R., Trauth, M.H., Deino, A., Gasse, F., Blisniuk, P., Dühnforth, M., 2009. Tectonic and climatic control on evolution of rift lakes in the Central Kenya Rift, East Africa. *Quatern. Sci. Rev.* 28, 2804–2816.
- Binford, L., 2001. *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building using Hunter-Gatherer and Environmental Data Sets*. University of California Press, Berkeley.
- Bouzouggar, A., Barton, N., Vanhaeren, M., d'Errico, F., Collcutt, S., Higham, T., Hodge, E., Parfitt, S., Rhodes, E., Schwenninger, J.-L., Stringer, C., Turner, E., Ward, S., Moutmir, A., Stambouli, A., 2007. 82,000-year-old shell beads from North Africa and implications for the origins of modern human behavior. *Proc. Natl. Acad. Sci.* 104, 9964–9969.
- Braun, D.R., Plummer, T., Ditchfield, P., Ferraro, J.V., Maina, D., Bishop, L.C., Potts, R., 2008. Oldowan behavior and raw material transport: perspectives from the Kanjera Formation. *J. Archaeol. Sci.* 35, 2329–2345.
- Brown, F.H., Haileab, B., McDougall, I., 2006. Sequence of tuffs between the KBS Tuff and the Chari Tuff in the Turkana Basin, Kenya and Ethiopia. *J. Geol. Soc. London* 163, 185–204.
- Burns, S.J., Fleitmann, D., Matter, A., Neff, U., Mangini, A., 2001. Speleothem evidence from Oman for continental pluvial events during interglacial periods. *Geology* 29, 623–626.
- Carto, S.L., Weaver, A.J., Hertherington, R., Lam, Y., Wiebe, E.C., 2009. Out of Africa and into an ice age: on the role of global climate change in the late Pleistocene migration of early modern humans out of Africa. *J. Hum. Evol.* 56, 139–151.
- Castañeda, I.S., Mulitz, S., Schefuß, E., Lopes dos Santos, R.A., Sinninghe Damsté, J.S., Schouten, S., 2009. Wet phases in the Sahara/Sahel region and human migration patterns in North Africa. *Proc. Koninklijke Akademie des Wetenschappen B* 106, 20159–20163.
- Charman, D.J., Grattan, J., 1999. An assessment of discriminant function analysis in the identification and correlation of distal Icelandic tephra in the British Isles. In: Firth, C.R., McGuire, W.J. (Eds.), *Volcanoes in the Quaternary*. Geological Society London, London, pp. 147–160.
- Clark, J.D., 1957. A re-examination of the industry from the type site of Magosi, Uganda. In: Clark, J.D. (Ed.), *Third Pan-African Congress on Prehistory, Livingstone, 1955*. Chatto & Windus, London, pp. 228–241.
- Clark, J.D., 1988. The Middle Stone Age of East Africa and the beginnings of regional identity. *J. World Prehist.* 2, 235–305.
- Clark, J.D., Kleindienst, M.R., 2001. The Stone Age cultural sequence: terminology, typology, and raw material. In: Clark, J.D. (Ed.), *Kalambo Falls Prehistoric Site. The Earlier Cultures: Middle and Earlier Stone Age*, vol. 3. Cambridge University Press, Cambridge, pp. 34–65.
- Clark, J.D., Williams, K.D., Michels, J.W., Marean, C.A., 1984. A Middle Stone occupation site at Porc Epic Cave, Dire Dawa. *Afr. Archaeol. Rev.* 2, 37–72.
- Clark, P.U., Alley, R.B., Pollard, D., 1999. Northern Hemisphere ice-sheet influences on global climate change. *Science* 286, 1104–1111.
- Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W., McCabe, A.M., 2009. The last glacial maximum. *Science* 325, 710–714.
- Clarke, M.C.G., Woodhall, D.G., Allen, D.J., Darling, G., 1990. Geological, Volcanological and Hydrogeological Controls on the Occurrence of Geothermal Activity in the Area Surrounding Lake Naivasha, Kenya. Ministry of Energy, Republic of Kenya. Nairobi.
- Clement, A.C., Hall, A., Broccoli, A.J., 2004. The importance of precessional signals in tropical climate. *Clim. Dynam.* 22, 327–341.
- Cohen, A.S., Stone, J.R., Beuning, K.R.M., Park, L.E., Reinthal, P.N., Dettman, D., Scholz, C.A., Johnson, T.C., King, J.W., Talbot, M.R., Brown, E.T., Ivory, S.J., 2007. Ecological consequences of early Late Pleistocene megadroughts in tropical Africa. *Proc. Natl. Acad. Sci.* 104, 16422–16427.
- Cole, G., 1967a. A re-investigation of Magosi and the Magosian. *Quaternaria* 9, 153–168.
- Cole, G.H., 1967b. The Later Acheulian and Sangoan of southern Uganda. In: Bishop, W.W., Clark, J.D. (Eds.), *Background to Evolution in Africa*. Chicago University Press, Chicago, pp. 481–528.
- Collinson, M.E., Andrews, P., Bamford, M.K., 2009. Taphonomy of the early Miocene flora, Hiwegi Formation, Rusinga Island, Kenya. *J. Hum. Evol.* 57, 149–162.
- Cornelissen, E., 2002. Human responses to changing environments in central Africa between 40,000 and 12,000 B.P. *J. World Prehist.* 16, 197–235.
- Cowling, S.A., Cox, P.M., Jones, C.D., Maslin, M.A., Peros, M., Spall, S.A., 2008. Simulated glacial and interglacial vegetation across Africa: implications for species phylogenies and trans-African migration of plants and animals. *Glob. Change Biol.* 14, 827–840.
- Crevecoeur, I., Rougier, H., Grine, F., Froment, A., 2009. Modern human cranial diversity in the Late Pleistocene of Africa and Eurasia: evidence from Nazlet Khater, Peștera cu Oase, and Hofmeyr. *Am. J. Phys. Anthropol.* 140, 347–358.
- Crowley, T.E., Pain, T., 1970. A Monographic Revision of the African Land Snails of the Genus *Limicolaria* Schumacher (Mollusca – Achatinidae). In: *Annales Serie In-8°, Sciences Zoologiques*, vol. 177. Musée Royal de l'Afrique Centrale. Tervuren.
- d'Errico, F., Vanhaeren, M., 2007. Body ornamentation as information technology: towards an understanding of the significance of early beads. In: Mellars, P., Boyle, K., Bar-Yosef, O., Stringer, C. (Eds.), *Rethinking the Human Revolution*. McDonald Institute Monographs, Cambridge, pp. 275–286.
- Dawson, J.B., 2008. The Gregory Rift Valley and Neogene-Recent Volcanoes of Northern Tanzania. In: *Geological Society Memoir*, No. 33 London.
- Denton, J.S., Pearce, N.J.G., 2008. Comment on “A synchronized dating of three Greenland ice cores throughout the Holocene” by B.M. Vinther, et al.: no Minoan Tephra in the 1642 B.C. layer of the GRIP Ice Core. *J. Geophys. Res.* 113 D04303.
- Ditchfield, P., Hicks, J., Plummer, T., Bishop, L.C., Potts, R., 1999. Current research on the Late Pliocene and Pleistocene deposits north of Homa Mountain, south-western Kenya. *J. Hum. Evol.* 36, 123–150.
- Domínguez-Rodrigo, M., Díez-Martín, F., Mabulla, A., Luque, L., Alcalá, L., Tarriño, A., López-Sáez, J.A., Barba, R., Bushozi, P., 2007. The archaeology of the Middle Pleistocene deposits of Lake Eyasi, Tanzania. *J. Afr. Archaeol.* 5, 47–78.
- Donovan, J.J., Kremser, D., Fournelle, J., 2009. Probe for EPMA: Acquisition, Automation and Analysis. Enterprise Edition. Probe Software, Inc., Eugene.
- Dunkley, P.N., Smith, M., Allen, D.J., Darling, W.G., 1993. The Geothermal Activity and Geology of the Northern Sector of the Kenya Rift Valley. In: *British Geological Survey Research Report SC/93/1*, Keyworth, Nottingham.
- Eerkens, J.W., Lipo, C.P., 2005. Cultural transmission, copying errors, and the generation of variation in material culture and the archaeological record. *J. Anthropol. Archaeol.* 24, 316–334.
- Excoffier, L., 2002. Human demographic history: refining the recent African origin model. *Curr. Opin. Genet. Dev.* 12, 675–682.
- Feibel, C.S., 1999. Tephrostratigraphy and geological context in paleoanthropology. *Evol. Anthropol.* 8, 87–100.
- Froggatt, P.C., 1992. Standardization of the chemical analysis of tephra deposits. Report of the ICCT Working Group. *Quatern. Int.* 13/14, 93–96.
- Gabel, C., 1969. Six rockshelters in the northern Kavirondo shore of Lake Victoria. *Afr. Hist. Stud.* 2, 205–254.
- Geneste, J.-M., 1989. Economie des ressources lithiques dans le Moustérien du sud-ouest de la France. In: Otte, M. (Ed.), *L'Homme de Néandertal. La Subsistance*, vol. 6. Etudes et Recherches Archéologiques de l'Université de Liège, Liège, pp. 75–97.
- Goodfriend, G.A., 1987. Radiocarbon age anomalies in shell carbonate of land snails from semi-arid areas. *Radiocarbon* 29, 159–167.
- Goodfriend, G.A., Stipp, J.J., 1983. Limestone and the problem of radiocarbon dating of land-snail shell carbonate. *Geology* 11, 575–577.
- Goudie, A.S., 1996. Climate: past and present. In: W.M.A., Goudie, A.S., Orme, A.R. (Eds.), *The Physical Geography of Africa*. Oxford University Press, Oxford, pp. 34–59.
- Grayson, D.K., 1984. *Quantitative Zooarchaeology*. Academic Press, Orlando.
- Grubb, P., Sandrock, O., Kullmer, O., Kaiser, T.M., Schrenk, F., 1999. Relationships between eastern and southern African mammal faunas. In: Bromage, T., Schrenk, F. (Eds.), *African Biogeography, Climate Change, and Early Hominid Evolution*. Oxford University Press, Oxford, pp. 253–267.
- Gunz, P., Bookstein, F.L., Mitteroecker, P., Stadlmayr, A., Seidler, H., Weber, G.W., 2009. Early modern human diversity suggests subdivided population structure and a complex out-of-Africa scenario. *Proc. Natl. Acad. Sci.* 106, 6094–6098.

- Harris, J.M., 1991. Family Bovidae. In: Harris, J.M. (Ed.), *Koobi Fora Research Project. The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments*, vol. 3. Clarendon Press, Oxford, pp. 139–320.
- Haynes, C.V., Mead, A.R., 1987. Radiocarbon dating and paleoclimatic significance of subfossil *Limicolaria* in northwestern Sudan. *Quatern. Res.* 28, 86–99.
- Henshilwood, C.S., Marean, C.W., 2003. The origin of modern human behavior: critique of the models and their test implications. *Curr. Anthropol.* 44, 627–651.
- Howell, F.C., 1999. Paleo-demes, species clades, and extinctions in the Pleistocene hominin record. *J. Anthropol. Res.* 55, 191–243.
- Hunt, J.B., Hill, P.G., 1993. Tephra geochemistry: a discussion of some persistent analytical problems. *The Holocene* 3, 271–278.
- Hunt, J.B., Hill, P.G., 1996. An inter-laboratory comparison of the electron probe microanalysis of glass geochemistry. *Quatern. Int.* 34–36, 229–241.
- Hunt, J.B., Hill, P.G., 2001. Tephrological implications of beam size-sample size effects in electron microprobe analysis of glass shards. *J. Quatern. Sci.* 16, 105–117.
- Jacobs, Z., Roberts, R.G., Galbraith, R.F., Deacon, H.J., Grun, R., Mackay, A., Mitchell, P., Vogelsang, R., Wadley, L., 2008. Ages for the Middle Stone Age of Southern Africa: implications for human behavior and dispersal. *Science* 322, 733–735.
- Jarosewich, E., 2002. Smithsonian microbeam standards. *J. Res. Natl. Inst. Stan.* 107, 681–685.
- Jarosewich, E., Nelen, J.A., Norberg, J.A., 1980. Reference samples for electron microprobe analysis. *Geostandard. Newslett.* 4, 43–47.
- Johnson, T.C., Kelts, K., Odada, E., 2000. The Holocene history of Lake Victoria. *Ambio* 29, 2–11.
- Johnson, T.C., Scholz, C.A., Talbot, M.R., Kelts, K., Ricketts, R.D., Ngobi, G., Beuning, K., Ssemmanda, I., McGill, J.W., 1996. Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* 273, 1091–1093.
- Karega-Munene, 2002. *Holocene Foragers, Fishers and Herders of Western Kenya*. In: BAR International Series, vol. 1037 Oxford.
- Kelly, R.L., 1995. *The Foraging Spectrum*. Smithsonian Institution Press, Washington, D.C.
- Kendall, R.L., 1969. An ecological history of the Lake Victoria basin. *Ecol. Monogr.* 39, 121–176.
- Kent, P.E., 1942. The country round the Kavirondo Gulf of Victoria Nyanza. *Geogr. J.* 100, 22–31.
- Kent, P.E., 1944. The Miocene beds of Kavirondo, Kenya. *Q. J. Geol. Soc. London* 100, 85–118.
- Kingdon, J., 1974. *East African Mammals: An Atlas of Evolution in Africa*, vol. 1. University of Chicago Press, Chicago.
- Kingdon, J., 1979. *East African Mammals: An Atlas of Evolution in Africa*. In: *Large Mammals*, vol. IIIB. University of Chicago Press, Chicago.
- Kingdon, J., 1982. *East African Mammals: An Atlas of Evolution in Africa*. In: *Bovids*, vol. IIID. University of Chicago Press, Chicago.
- Kingdon, J., 1989. *Island Africa: The Evolution of Africa's Rare Animals and Plants*. Princeton University Press, Princeton.
- Kingston, J.D., 2007. Shifting adaptive landscapes: progress and challenges in reconstructing early hominid environments. *Yearb. Phys. Anthropol.* 50, 20–58.
- Klein, R.G., 1972. The late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province, South Africa): its implications for megafaunal extinctions and environmental and cultural change. *Quatern. Res.* 2, 135–142.
- Klein, R.G., 1980. Environmental and ecological implications of large mammals from Upper Pleistocene and Holocene sites in southern Africa. *Ann. S. Afr. Mus.* 81, 223–283.
- Klein, R.G., 1984. Mammalian extinctions and Stone Age people in Africa. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, pp. 553–573.
- Kuhn, S.L., Stiner, M.C., 2001. The antiquity of hunter–gatherers. In: Panter-Brick, C., Layton, R.H., Rowley-Conwy, P. (Eds.), *Hunter–Gatherers: An Interdisciplinary Perspective*. Cambridge University Press, Cambridge, pp. 99–142.
- Kuhn, S.L., Stiner, M.C., 2007. Body ornamentation as information technology: towards an understanding of the significance of early beads. In: Mellars, P., Boyle, K., Bar-Yosef, O., Stringer, C. (Eds.), *Rethinking the Human Revolution*. McDonald Institute Monographs, Cambridge, pp. 45–54.
- Kusimba, S.B., 2005. What was a hunter–gatherer? Variation in the archaeological record of eastern and southern Africa. *J. Archaeol. Res.* 13, 337–366.
- Lahr, M.M., Foley, R., 1998. Towards a theory of modern human origins: geography, demography, and diversity in recent human evolution. *Yearb. Phys. Anthropol.* 41, 137–176.
- Lane, P., Ashley, C., Seitsonen, O., Harvey, P., Mire, S., Odede, F., 2007. The transition to farming in eastern Africa: new faunal and dating evidence from Wadh Long'o and Usenge, Kenya. *Antiquity* 81, 62–81.
- Le Bas, M.J., Le Maitre, R.W., Streckeisen, A., Zanettin, B., 1986. A chemical classification of volcanic rocks based on the total alkali-silica diagram. *J. Petrol.* 27, 745–750.
- Le Gros Clark, W.E., Leakey, L.S.B., 1950. Diagnoses of East African Miocene Hominoidea. *Q. J. Geol. Soc. London* 105, 260–262.
- Le Gros Clark, W.E., Leakey, L.S.B., 1951. *Fossil Mammals of Africa 1: The Miocene Hominoidea of East Africa*. British Museum (Natural History), London.
- Leakey, L.S.B., 1974. *By the Evidence: Memoirs 1932–1951*. Harcourt Brace Jovanovich, New York.
- Leakey, L.S.B., Owen, W.E., 1945. A Contribution to the Study of the Tumbian Culture in East Africa. In: Coryndon Memorial Museum Occasional Papers, No. 1 (Nairobi).
- Lowe, D.J., Shane, P.A.R., Alloway, B., Newnham, R.M., 2008. Fingerprints and age models for widespread New Zealand tephra marker beds erupted since 30,000 years ago: a framework for NZ-INTIMATE. *Quaternary Sci. Rev.* 27, 95–126.
- Macdonald, R., 1987. Quaternary peralkaline silicic rocks and caldera volcanoes of Kenya. In: Fitton, J.G., Upton, B.G.J. (Eds.), *Alkaline Igneous Rocks*. Geological Society Special Publication, No. 30, pp. 313–333. London.
- Macdonald, R., Scailliet, B., 2006. The central Kenya peralkaline province: insights into the evolution of peralkaline silicic magmas. *Lithos* 91, 59–73.
- MacInnes, D., 1956. Fossil Tubulidentata from East Africa. *Fossil Mammals of Africa* 10, 1–38.
- Marean, C.W., 1990. *Late Quaternary Palaeoenvironments and Faunal Exploitation in East Africa*. Ph.D. Thesis, University of California.
- Marean, C.W., 1992. Implications of late Quaternary mammalian fauna from Luke-nya Hill (south-central Kenya) for paleoenvironmental change and faunal extinctions. *Quatern. Res.* 37, 239–255.
- Marean, C.W., Assefa, Z., 2005. The Middle and Upper Pleistocene African record for the biological and behavioral origins of modern humans. In: Stahl, A.B. (Ed.), *African Archaeology*. Blackwell Publishing, Malden, MA, pp. 93–129.
- Marean, C.W., Bar-Matthews, M., Bernatchez, J., Fisher, E., Goldberg, P., Herries, A.I.R., Jacobs, Z., Jerardino, A., Karkanas, P., Minichillo, T., Nilssen, P.J., Thompson, E., Watts, I., Williams, H.M., 2007. Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature* 449, 905–908.
- Marean, C.W., Gifford-Gonzalez, D., 1991. Late Quaternary extinct ungulates of East Africa and palaeoenvironmental implications. *Nature* 350, 418–420.
- Mayr, E., 2001. *What Evolution Is*. Basic Books, New York.
- McBrearty, S., 1981. Songhor: a Middle Stone Age site in western Kenya. *Quaternaria* 23, 171–190.
- McBrearty, S., 1988. The Sangoan–Lupemban and Middle Stone Age sequence at the Muguruk site, western Kenya. *World Archaeol.* 19, 379–420.
- McBrearty, S., 1991. Recent research in western Kenya and its implications for the status of the Sangoan Industry. In: Clark, J.D. (Ed.), *Cultural Beginnings: Approaches to Understanding Early Hominid Lifeways in the African Savanna*. Monographien, vol. 19. Romisch-Germanisches Zentralmuseum, Forschungsinstitut für Vor- und Frühgeschichte, Bonn, pp. 159–176.
- McBrearty, S., 1992. Sangoan technology and habitat at Simbi. *Nyame Akuma* 38, 34–39.
- McBrearty, S., Brooks, A., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* 39, 453–563.
- McBrearty, S., Tryon, C.A., 2005. From Acheulian to Middle Stone Age in the Kapthurin Formation, Kenya. In: Hovers, E., Kuhn, S.L. (Eds.), *Transitions before the Transition: Evolution and Stability in the Middle Paleolithic and Middle Stone Age*. Kluwer Press, New York, pp. 257–278.
- McCall, G.H.G., 1958. *Geology of the Gwasi Area*. Geological Survey of Kenya, Nairobi. Report 45.
- McCall, G.S., 2007. Behavioral ecological models of lithic technological change during the later Middle Stone Age of South Africa. *J. Archaeol. Sci.* 34, 1738–1751.
- McDougall, I., Brown, F.H., Fleagle, J.G., 2005. Stratigraphic placement and age of modern humans from Kibish, Ethiopia. *Nature* 433, 733–736.
- McNulty, K.P., Harcourt-Smith, W.E.H., Dunsworth, H.M., 2007. New primate fossils from Rusinga Island, Kenya. *Am. J. Phys. Anthropol.* 132 (S44), 170.
- Mehlman, M.J., 1989. *Late Quaternary Archaeological Sequences in Northern Tanzania*. Ph.D. Dissertation, University of Illinois.
- Mehlman, M.J., 1991. Context for the emergence of modern man in Eastern Africa: some new Tanzanian evidence. In: Clark, J.D. (Ed.), *Cultural Beginnings: Approaches to Understanding Early Hominid Life-Ways in the African Savanna*. Dr. Rudolph Habelt GMBH, Bonn, Germany, pp. 177–196.
- Mellars, P., 2006. Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. *Proc. Natl. Acad. Sci.* 103, 9381–9386.
- Merrick, H.V., 1975. *Change in Later Pleistocene Lithic Industries in Eastern Africa*. Ph.D. Dissertation, University of California.
- Miller, S.F., 1979. Lukenya Hill, Gvjm 46, excavation report. *Nyame Akuma* 14, 31–34.
- Napier, J.R., Davis, P.R., 1959. *Fossil Mammals of Africa*, No. 16: The Fore-limb Skeleton and Associated Remains of *Proconsul africanus*. British Museum (Natural History), London.
- Neff, N.A., Marcus, L.F., 1980. *A Survey of Multivariate Methods for Systematics*. Privately published, New York.
- Nenquin, J., 1971. Archaeological prospections on the islands of Buvuma and Bugaia, Lake Victoria Nyaza (Uganda). *P. Prehist. Soc.* 37, 381–418.
- Nicholson, S.E., 1998. Historical fluctuations of Lake Victoria and other lakes in the northern rift valley of East Africa. In: Lehman, J.T. (Ed.), *Environmental Change and Response in East African Lakes*. Kluwer Academic Publishers, Dordrecht, pp. 7–35.
- O'Brien, T.P., 1939. *The Prehistory of Uganda Protectorate*. Cambridge University Press, Cambridge.
- O'Connell, J.F., Allen, J., 2007. Pre-LGM Sahul (Pleistocene Australia-New Guinea) and the archaeology of early modern humans. In: Mellars, P., Boyle, K., Bar-Yosef, O., Stringer, C. (Eds.), *Rethinking the Human Revolution: New Behavioural and Biological Perspectives on the Origin and Dispersal of Modern Humans*. McDonald Institute Monographs, Cambridge, pp. 395–410.
- Oswald, F., 1911. Correspondence and Notes Concerning the Oswald Expedition to Victoria Nyanza. In: *Archives of the British Museum (Natural History)*. Department of Palaeontology, London.
- Oswald, F., 1914. The Miocene beds of the Victoria Nyanza, and the geology of the country between the Lake and the Kisii Highlands. *Q. J. Geol. Soc. London* 70, 128–162.

- Pearce, N.J.G., Bendall, C.A., Westgate, J.A., 2008. Comment on “Some numerical considerations in the geochemical analysis of distal microtephra” by A.M. Pollard, S.P.E. Blockley and C.S. Lane. *Appl. Geochem.* 23, 1353–1364.
- Pearson, O.M., 2008. Statistical and biological definitions of “anatomically modern” humans: suggestions for a unified approach to modern morphology. *Evol. Anthropol.* 17, 38–48.
- Peppe, D.J., McNulty, K.P., Cote, S.M., Harcourt-Smith, W.E.H., Dunsworth, H.M., Van Couvering, J., 2009. Stratigraphic interpretation of the Kulu Formation (Early Miocene, Rusinga Island, Kenya) and its implications for primate evolution. *J. Hum. Evol.* 56, 447–461.
- Perlès, C., 1974. Réexamen typologique de l'industrie du Porc-Épic (Éthiopie): Les pointes et pièces pointues. *L'Anthropologie* 78, 529–552.
- Pickford, M., 1982. The tectonics, volcanics and sediments of the Nyanza Rift Valley, Kenya. *Z. Geomorphol.* 42, 1–33.
- Pickford, M., 1986. Cainozoic paleontological sites of Western Kenya. *Münchner Geowissenschaftliche Abhandlungen* 8, 1–151.
- Pickford, M., 1995. Fossil land snails of East Africa and their paleoecological significance. *J. Afr. Earth Sci.* 20, 167–226.
- Pickford, M., Thomas, H., 1984. An aberrant new bovid (Mammalia) in subrecent deposits from Rusinga island, Kenya. *Proc. Koninklijke Akademie des Wetenschappen B* 87, 441–452.
- Pleurdeau, D., 2005. Human technical behavior in the African Middle Stone Age: the lithic assemblage of Porc-Epic Cave (Dire Dawa, Ethiopia). *Afr. Archaeol. Rev.* 22, 177–197.
- Plummer, T., Bishop, L.C., Ditchfield, P., Hicks, J., 1999. Research on Late Pliocene Oldowan sites at Kanjera South, Kenya. *J. Hum. Evol.* 36, 151–170.
- Plummer, T.W., Ditchfield, P.W., Bishop, L.C., Kingston, J.D., Ferraro, J.V., Braun, D.R., Hertel, F., Potts, R., 2009. Oldest evidence of toolmaking hominins in a grassland-dominated ecosystem. *PLoS ONE* 4, e7199.
- Plummer, T.W., Kinyua, A.M., Potts, R., 1994. Provenancing of hominid and mammalian fossils from Kanjera, Kenya, using EDXRF. *J. Archaeol. Sci.* 21, 553–563.
- Pollard, A.M., Blockley, S.P.E., Lane, C.S., 2006. Some numerical considerations in the geochemical analysis of distal microtephra. *Appl. Geochem.* 21, 1692–1714.
- Posnansky, M., Reid, A., Ashley, C., 2005. Archaeology on Lolui Island, Uganda 1964–5. *Azania* 40, 73–100.
- Potts, R., Deino, A., 1995. Mid-Pleistocene change in large mammal faunas of East Africa. *Quatern. Res.* 43, 106–113.
- Pratt, D.J., Gwynne, M.D., 1977. Rangeland Management and Ecology in East Africa. Hodder and Stoughton, London.
- Prendergast, M.E., 2008. Forager Variability and Transitions to Food Production in Secondary Settings: Kanyore and Pastoral Neolithic Economies in East Africa. Ph.D. Dissertation, Harvard University.
- Prugnolle, F., Manica, A., Balloux, F., 2005. Geography predicts neutral genetic diversity of human populations. *Curr. Biol.* 15, 159–160.
- Pyle, D.M., 1999. Widely dispersed Quaternary tephra in Africa. *Glob. Planet. Change* 21, 95–112.
- Quade, J., Wynn, J.G. (Eds.), 2008. The Geology of Early Humans in the Horn of Africa. Geological Society of American Special Paper, vol. 446 Boulder.
- Randel, R.P., Johnson, R.W., 1991. Geology of the Suswa Area. Republic of Kenya Ministry of Environment and Natural Resources, Mines and Geological Department, Nairobi. Report No. 97.
- Robertshaw, P., 1991. Gogo Falls: a complex site east of Lake Victoria. *Azania* 26, 63–196.
- Robertshaw, P., Collett, D., Gifford, D., Mbae, N.B., 1983. Shell middens on the shores of Lake Victoria. *Azania* 18, 1–44.
- Schick, K., 1986. Stone Age Sites in the Making: Experiments in the Formation and Transformation of Archaeological Occurrences. In: BAR International Series, No. 314 Oxford.
- Schmid, R., 1981. Descriptive nomenclature of classification of pyroclastic deposits and fragments: recommendations of the IUGS subcommission on the systematics of igneous rocks. *Geology* 9, 41–43.
- Scholz, C.A., Johnson, T.C., Cohen, A.S., King, J.W., Peck, J.A., Overpeck, J.T., Talbot, M.R., Brown, E.T., Kalindekale, L., Amoako, P.Y.O., Lyons, R.P., Shanahan, T.M., Castañeda, I.S., Heil, C.W., Forman, S.L., McHargue, L.R., Beuning, K.R., Gomez, J., Pierson, J., 2007. East African megadroughts between 135 and 75 thousand years ago and bearing on early modern human origins. *Proc. Natl. Acad. Sci.* 104, 16416–16421.
- Scott, S.C., Skilling, I.P., 1999. The role of tephrochronology in recognizing synchronous caldera-forming events at the Quaternary volcanoes Longont and Suswa, south Kenya Rift. In: Firth, C.R., McGuire, W.J. (Eds.), *Volcanoes in the Quaternary*. The Geological Society of London Special Publications, No. 161, pp. 47–67. London.
- Shackleton, R.M., 1950. A contribution to the geology of the Kavirondo Rift Valley. *Q. J. Geol. Soc. London* 106, 345–392.
- Shane, P., Nairn, I.A., Martin, S.B., Smith, V.C., 2008. Compositional heterogeneity in tephra deposits resulting from the eruption of multiple magma bodies: implications for tephrochronology. *Quatern. Int.* 178, 44–53.
- Skilling, I.P., 1993. Incremental caldera collapse of the Suswa volcano, Gregory Rift Valley, Kenya. *J. Geol. Soc. London* 150, 885–896.
- Stager, J.C., Cumming, B., Meeker, L., 1997. A high-resolution 11,400-yr diatom record from Lake Victoria, East Africa. *Quatern. Res.* 47, 81–89.
- Stager, J.C., Johnson, T.C., 2008. The Late Pleistocene desiccation of Lake Victoria and the origin of its endemic fauna. *Hydrobiologia* 596, 5–16.
- Stokes, S., Lowe, D.J., 1988. Discriminant function analysis of late Quaternary tephra from five volcanoes in New Zealand using glass shard major element chemistry. *Quatern. Res.* 30, 270–283.
- Stokes, S., Lowe, D.J., Froggatt, P.C., 1992. Discriminant function analysis and correlation of late Quaternary rhyolitic tephra deposits from Taupo and Okatana volcanoes, New Zealand, using glass shard major element composition. *Quatern. Int.* 13/14, 103–117.
- Talbot, M.R., Jensen, N.B., Laerdal, T., Filippi, M.L., 2006. Geochemical responses to a major transgression in giant African lakes. *J. Paleolimnol.* 35, 467–489.
- Talbot, M.R., Laerdal, T., 2000. The Late Pleistocene–Holocene paleolimnology of Lake Victoria, East Africa, based upon elemental and isotopic analyses of sedimentary organic matter. *J. Paleolimnol.* 23, 141–164.
- Thackeray, J.F., 1982. On Darwin, extinctions and South African fauna. *Discovery* 16, 2–11.
- Tishkoff, S.A., Reed, F.A., Friedlaender, F.R., Christopher, E., Ranciaro, A., Froment, A., Hirbo, J.B., Awomoyi, A.A., Bodo, J.-M., Doumbo, O., Ibrahim, M., Juma, A.T., Kotze, M.J., Lema, G., Moore, J.H., Mortensen, H., Nyambo, T.B., Omar, S.A., Powell, K., Pretorius, G.S., Smith, M.W., Thera, M.A., Wambebe, C., Weber, J.L., Williams, S.M., 2009. The genetic structure and history of Africans and African Americans. *Science* 324, 1035–1044.
- Trauth, M.H., Deino, A., Strecker, M.R., 2001. Response of the East African climate to orbital forcing during the last interglacial (130–117 ka) and the early last glacial (117–60 ka). *Geology* 29, 499–502.
- Trauth, M.H., Deino, A.L., Bergner, A.G.N., Strecker, M.R., 2003. East African climate change and orbital forcing during the last 175 kyr BP. *Earth Planet. Sci. Lett.* 206, 297–313.
- Tryon, C.A., Logan, M.A.V., Mouralis, D., Kuhn, S.L., Slimak, L., Balkan-Atli, N., 2009. Building a tephrostratigraphic framework for the Paleolithic of Central Anatolia, Turkey. *J. Archaeol. Sci.* 36, 637–652.
- Tryon, C.A., Roach, N.T., Logan, M.A.V., 2008. The Middle Stone Age of the northern Kenyan Rift: age and context of new archaeological sites from the Kapado Tuffs. *J. Hum. Evol.* 55, 652–664.
- Vaks, A., Bar-Matthews, M., Ayalon, A., Matthews, A., Halicz, L., Frumkin, A., 2007. Desert speleothems reveal climatic window for African exodus of early modern humans. *Geology* 35, 831–834.
- Van Couvering, J., 1972. Geology of Rusinga Island and Correlation of the Kenya Mid-Tertiary Fauna. Ph.D. Dissertation, Cambridge University.
- Van Noten, F., 1971. Excavations at Munyama Cave. *Antiquity* 45, 56–58.
- Van Riet Lowe, C., 1952. The Pleistocene Geology and Prehistory of Uganda. Part II: Prehistory. In: *Geological Survey of Uganda Memoir*, No. 6 Entebbe.
- Verdu, P., Austerlitz, F., Estoup, A., Vitalis, R., Georges, M., Thêry, S., Froment, A., Le Bomin, S., Gessain, A., Hombert, J.-M., Van der Veen, L., Quintana-Murci, L., Bahuchet, S., Heyer, E., 2009. Origins and genetic diversity of pygmy hunter-gatherers from Western Central Africa. *Curr. Biol.* 19, 312–318.
- Vrba, E.S., 1980. The significance of bovid remains as an indicator of environment and predation patterns. In: Behrensmeyer, A.K., Hill, A.P. (Eds.), *Fossils in the Making*. University of Chicago Press, Chicago, pp. 247–272.
- Vrba, E.S., 1987. A revision of the Bovini (Bovidae) and a preliminary revised checklist of Bovidae from Makapansgat. *Paleontologia Africana* 26, 33–46.
- Walker, A., Teaford, M.F., 1988. The Kaswanga Primate Site: an Early Miocene hominoid site on Rusinga Island, Kenya. *J. Hum. Evol.* 17, 539–544.
- Waweru, V.N., 2007. Middle Stone Age Technology at Cartwright's Site, Kenya. Ph.D. Dissertation, University of Connecticut.
- Wayland, E.J., Burkitt, M.C., 1932. The Magosian culture of Uganda. *J. R. Anthropol. Inst.* 62, 369–390.
- Weninger, B., Jöris, O., 2008. A ^{14}C age calibration curve for the last 60 ka: the Greenland-Hulu U/Th timescale and its impact on understanding the Middle to Upper Paleolithic transition in western Eurasia. *J. Hum. Evol.* 55, 772–781.
- White, F., 1983. The Vegetation of Africa, a Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa. UNESCO, Paris.
- Williams, L.A.J., 1991. Geology of the Mau Area. Republic of Kenya Ministry of Environment and Natural Resources, Mines and Geological Department, Nairobi. Report No. 96.
- Wobst, H.M., 1977. Stylistic behavior and information exchange. In: Cleland, C.E. (Ed.), *For the Director: Research Essays in Honor of James B. Griffin*. University of Michigan Anthropological Papers, vol. 61, pp. 317–342. Ann Arbor.
- Woolley, A.R., 2001. Alkaline Rocks and Carbonates of the World. Part 3: Africa. Geological Society, London.
- Wronski, T., Hausdorf, B., 2008. Distribution patterns of land snails in Ugandan rain forests support the existence of Pleistocene forest refugia. *J. Biogeogr.* 35, 1759–1768.
- Yellen, J.E., Brooks, A.S., Helgren, D.M., Tappen, M., Ambrose, S.H., Bonnefille, R., Feathers, J.K., Goodfriend, G., Ludwig, K., Renne, P., Stewart, K., 2005. The archaeology of Aduma Middle Stone Age Sites in the Awash Valley, Ethiopia. *PaleoAnthropology* 10, 25–100.