



A spring and wooded habitat at FLK Zinj and their relevance to origins of human behavior

Gail M. Ashley^{a,*}, Doris Barboni^b, Manuel Dominguez-Rodrigo^{c,d}, Henry T. Bunn^e, Audax Z.P. Mabulla^f, Fernando Diez-Martin^g, Rebeca Barba^c, Enrique Baquedano^{d,h}

^a Dept of Earth & Planetary Sciences, Rutgers University, Piscataway, NJ 08854-8066, USA

^b CEREGE (UMR6635 CNRS/Université Aix-Marseille), BP80, F-13545 Aix-en-Provence cedex 4, France

^c Dept. of Prehistory, Complutense University of Madrid Ciudad Universitaria s/n 28040 Madrid, Spain

^d IDEA (Instituto de Evolución en África), Museo de los Orígenes, Plaza de San Andrés 2, 28005, Madrid, Spain

^e Dept. of Anthropology, University of Wisconsin, Madison, WI 53706, USA

^f Archaeology Unit, P.O. Box 35050, University of Dar es Salaam, Dar es Salaam, Tanzania

^g Dept. of Prehistory and Archaeology, University of Valladolid, Plaza del Campus s/n 47011 Valladolid, Spain

^h Museo Arqueológico Regional de Madrid, Plaza delas Bernardas, Alcalá de Henares, Madrid, Spain

ARTICLE INFO

Article history:

Received 15 November 2009

Available online 19 September 2010

Keywords:

Spring

Phytoliths

Palm trees

Oldowan

Tufa

Hominin

ABSTRACT

The 1959 discovery of the hominin fossil *Zinjanthropus boisei* brought the world's attention to the rich records at Olduvai Gorge, Tanzania. Subsequent excavations of archaeological level 22 (FLK Zinj) Bed I uncovered remains of *Homo habilis* and a high-density collection of fossils and Oldowan stone tools. The occurrence of this unusual collection of bones and tools at this specific location has been controversial for decades. We present paleoecological data that provide new insights into the origin of FLK Zinj. Our recent excavations 200 m north of the site uncovered a 0.5-m-thick tufa mound draped by Tuff IC, in the same stratigraphic horizon as level 22. Stable isotope analyses indicate that the carbonates were deposited by a freshwater spring. Phytolith analysis of the waxy clay under Tuff IC revealed abundant woody dicotyledon and palm phytoliths, indicating that the site was wooded to densely wooded. The time equivalency and close physical proximity of the two environments indicate the two are related. This study has provided the first documented evidence of springs in Bed I and these data have important implications for the interpretation of hominin behavior in meat acquisition and the ongoing debate on scavenging versus hunting.

© 2010 University of Washington. Published by Elsevier Inc. All rights reserved.

Introduction

Mary and Louis Leakey discovered *Zinjanthropus boisei* (Zinj) at FLK, Olduvai Gorge, Tanzania in 1959, then the oldest hominin fossil (Fig. 1). From the 1960–61 excavation of a 315-m² area of level 22, i.e. the FLK Zinj layer, Leakey reported approximately 2500 Oldowan stone artifacts and 3500 fossil bone specimens including remains of *Homo habilis* and *Zinjanthropus* (later renamed *Paranthropus boisei*) (Leakey, 1971). Subsequent analyses have refined these numbers, but based on Leakey's first report, the site is recognized as one of the prime examples of a localized, high-density co-occurrence of Oldowan tools and fossilized bones. But, why this unique archaeological site occurred at this specific location in the Olduvai Basin has remained a mystery. The “junction area” (confluence of the main and side gorges) of Olduvai Gorge represents only a small portion of the fluvial-lacustrine sedimentary outcrop of the basin, but it contains a large proportion, perhaps as much as 75%, of the hominin paleontology and archaeological sites found in the Gorge (Hay, 1976).

The significance of the site for understanding the origins of sophisticated hominin behavior, such as foraging strategies, is documented by abundant butchered bones and evidence of repeated transport of portions of at least 48 large mammal carcasses (mostly Bovidae) to this location on the paleolandscape (Bunn, 2007; Dominguez-Rodrigo et al., 2007). Since its discovery, the unusually large collection of human-butchered bones at the FLK Zinj, has been debated and interpreted as a “living floor” (Leakey, 1971), a “home base” (Isaac, 1978, 1984; Bunn, 1982, 2007), a “refuge” or “stone-cache” for butchering and marrow-processing activities by hominins (Potts, 1988), and a “central-foraging place” where food-sharing of fleshed carcasses took place (Isaac, 1983; Bunn and Kroll, 1986; Rose and Marshall, 1996; Dominguez-Rodrigo et al., 2007; Dominguez-Rodrigo et al., 2007). These models of early Pleistocene hominin behavior, however, are completely dependent on the paleoenvironmental context. For example, Binford (1981) hypothesized that FLK Zinj was an open space site, and a palimpsest or a time-averaged assemblage where hominin participation was marginal. However, the paucity of arboreal refuge in mudflat would suggest that any visit by hominins must have been brief and limited to the fast processing of some carcass parts (Blumenshine and Masao, 1991). Another model proposed that

* Corresponding author. Fax: +1 732 445 3374.

E-mail address: gmaskley@rci.rutgers.edu (G.M. Ashley).

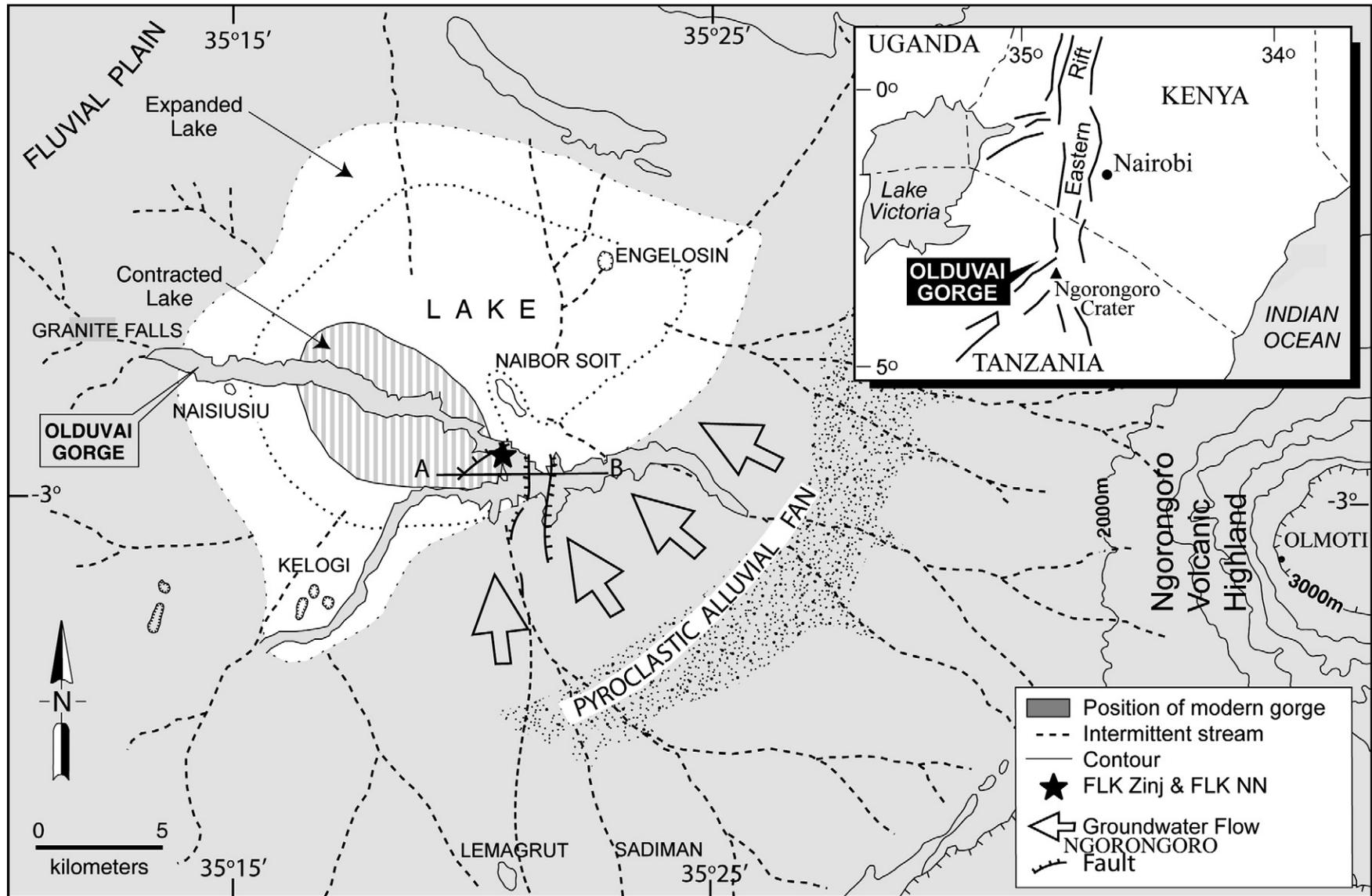


Figure 1. Paleogeographic reconstruction of Olduvai Gorge at Bed I time shows location of the Ngorongoro Volcanic Highland, the pyroclastic alluvial fan, proposed regional groundwater flow direction, outline of shorelines during expanded and contracted lake phases, and location of the FLK Zinj archaeological site (star). A-B cross section is shown in Figure 4. The outline of the modern gorge is indicated. Inset map depicts location of Olduvai Gorge in northern Tanzania.

hominins were creating “stone caches” on the lake margin floodplain to process carcasses. The model implies that hominins would be competing with carnivores for resources and thus the environment was not likely extensively wooded (Potts, 1988). In contrast, a closed-vegetation habitat supports models involving more advanced foresight and complex behaviors, such as “central-foraging place,” “homebase” or “resource-defense” models (Isaac, 1983; Dominguez-Rodrigo et al., 2007; Domínguez-Rodrigo et al., 2007). Carnivore competition in wooded habitats is low, thereby enhancing the likelihood of prolonged stay in those places (Dominguez-Rodrigo et al., 2007).

The paleoecological setting of the Olduvai Bed 1 sites has also been used to discuss the importance of meat eating in the earliest representatives of our genus. Models relying on a paleoecological reconstruction of the site which describes FLK Zinj in an open mudflat support scavenging hypotheses in which meat and food sharing were

unimportant, given the overall high carnivore competition and the associated predation risks (Binford, 1981; Blumenschine and Masao, 1991). In contrast, models that recreate FLK Zinj in a habitat with dense arboreal component support the idea that meat was the main target in carcass exploitation and that food sharing was a natural result of the food surpluses repeatedly transported to the site (Isaac, 1978, 1983; Bunn, 1982; Bunn and Kroll, 1986; Rose and Marshall, 1996; Bunn, 2007; Dominguez-Rodrigo et al., 2007; Domínguez-Rodrigo et al., 2007). For these models, meat represents a high-quality movable resource that was transported to specific places that offered spatially fixed defensible resources such as fresh water, trees and plant foods and where predation risk was very low (Rose and Marshall, 1996).

In order to test these ecologically based models of early hominin behavior, we carried extensive field work at Olduvai in 2008 and 2009, and opened test trenches both at and in the surroundings of the

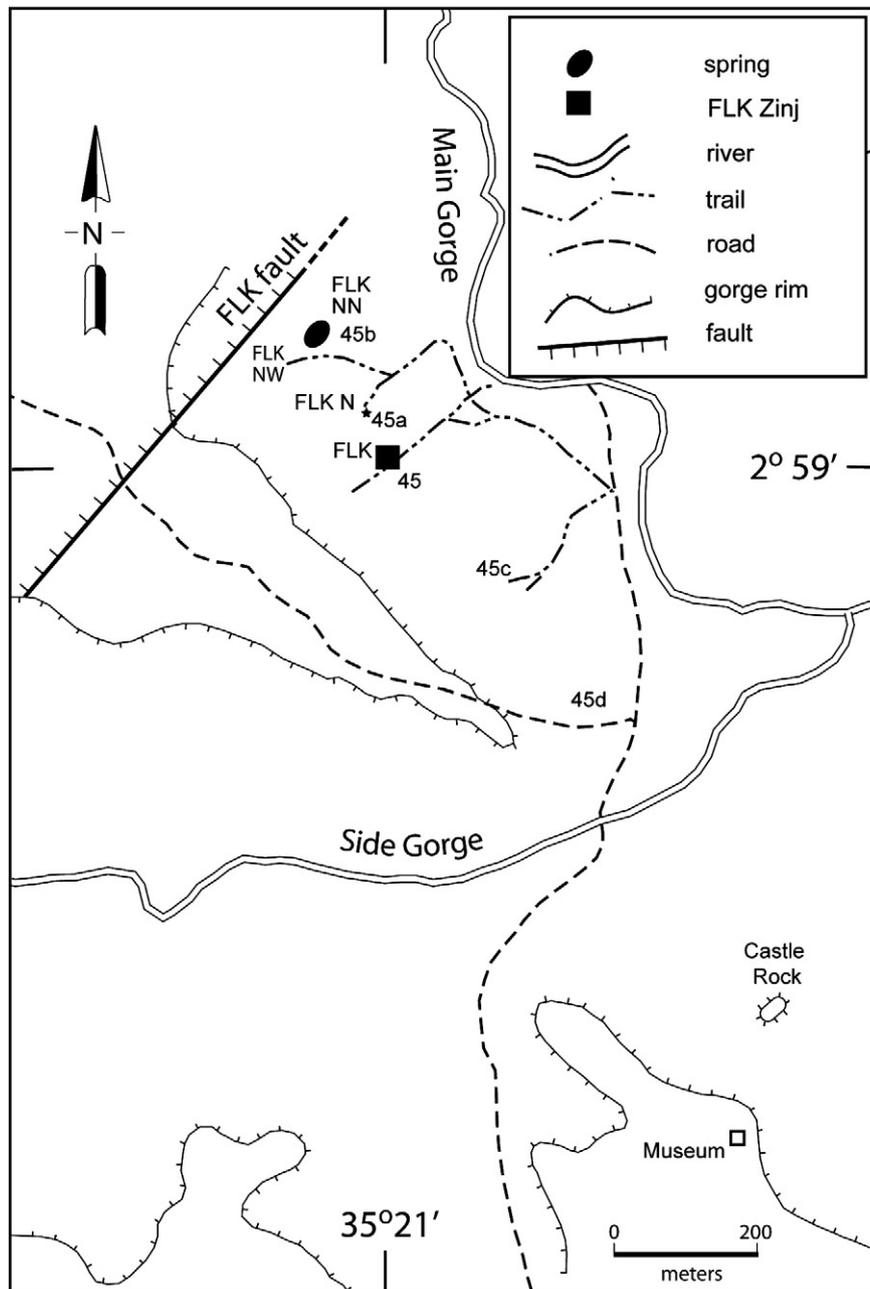


Figure 2. Location map within the “junction area” of Olduvai Gorge that depicts modern cultural features (road, trails, and museum), natural features (river and fault) and the interpreted paleoecological features. The interpreted groundwater-fed spring is circle at FLK NN. The interpreted wooded habitat is around the spring at FLK NN and archaeological site FLK Zinj (square), but its spatial extension over the area depicted in this map could not be ascertained by our phytolith data. Data are restricted to FLK Zinj, FLK NN, and FLK NW (Fig. 2).

site as far north as FLK NN (Fig. 2), where a tufa was found in the same stratigraphic position as FLK Zinj archaeological level 22 (Fig. 3). Detailed lithostratigraphic analyses were carried out and this stratigraphic layer systematically sampled for paleobotanical remains. Given the paucity of palynological content in Bed I sediments (Bonnieffle and Rioulet, 1980), phytolith analysis of the first few centimeters of the waxy clay below Tuff IC was used to investigate the distribution and density of vegetation in the ca. 2000-m² area encompassing the archaeological site and the newly discovered spring site at FLK NN and Location 45b (Hay, 1976). This paper presents new geological and biological evidence and examines the results of this high-resolution reconstruction of the landscape in terms of its bearing on our understanding of early hominin behaviors.

Geologic and hydrologic setting

The Olduvai Gorge cuts across a 50-km-wide rift-platform basin located between Precambrian basement to the west and the Pleistocene Ngorongoro Volcanic Highland to the east (Hay 1976) (Fig. 1). The basin fill is now disrupted by rift-parallel faults and separated into blocks. The sediments are quite thin (100 m) and composed largely of reworked volcanoclastic sediment and air-fall tuffs deposited in a shallow semiarid fluvial-lacustrine basin (Hay, 1976). The basin was hydrologically closed and astronomically forced

climate cycles raised and lowered lake levels on a time scale of 21 ka (Ashley, 2007). The Highland today acts as a rain shadow for the predominantly easterly winds from the Indian Ocean. The modern Ngorongoro Highland receives ~1150 mm/yr (Deocampo, 2004), whereas Olduvai receives only ~550 mm (Hay, 1976). Evaporation in East Africa is estimated to be 2500 mm/yr and very few perennial rivers can persist with this highly negative water budget.

A geological section across the basin reveals a prominent basalt high at the base of Bed I, related to extensional tectonics associated with the East Africa Rift and to a horst (1.5 km wide, up to 20 m local relief) created by rift parallel faults (Figs. 1 and 4). Hay's detailed stratigraphic reconstruction of Bed I sediments shows thinning of beds over the basalt high in the junction, documenting its presence at the time of deposition of Bed I (Fig. 4) (Hay, 1976). The complex geologic structure would have affected the flow of water moving in the basin.

Materials and methods

In order to identify the origin of carbonates deposited at FLK NN, we selected sixteen samples from ten locations within the tufa mound and analyzed them for C and O at the Stable Isotope Laboratory at Rutgers University on a Micromass Optima Mass Spectrometer. Samples were loaded into a Multi-Prep peripheral and reacted in phosphoric acid at 90 °C for 13 min. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are reported relative to V-PDB through the analysis of an internal laboratory standard which is routinely checked vs. NBS-19 (Coplen et al., 1983). The deviations of the internal lab standard from NBS-19 are 0.10 and 0.04‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively. The 1-sigma deviations of the lab standards analyzed during the sample analyses are 0.05 and 0.08‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively.

Samples for phytolith analyses were collected in archaeological trenches and localities in the FLK and FLK NN areas of Olduvai Gorge (Fig. 2, Table 1). All samples are from the same olive-brown waxy clay layer beneath Tuff IC, equivalent to archaeological level 22. At each sampling spot, three to four sub-samples were excavated less than 5 cm below Tuff IC and less than 1 m apart, and placed together into a clean polyethylene ziplock bag.

Samples were prepared for phytolith analyses by treatment of 8–10 g of sediments with pure HCl (33%) in Pyrex beakers for 4 h to remove carbonates, and then with pure H₂O₂ (30%) at 70 °C to remove organic matter. H₂O₂ was changed daily until reaction ceased. Clays were deflocculated using a solution of sodium polyphosphate (NaPO₃) at pH 7, and removed by decantation and centrifugation until supernatant was clear. Separation of organic silica from the mineral fraction and concentration of phytoliths was achieved using ZnBr₂ heavy liquid at a specific gravity of 2.30. Residue including phytoliths was rinsed and dried before storage in glass vials. Slides were prepared using a small amount of dry residue mixed with glycerin as mounting medium to allow rotation of the phytoliths during microscope observations. Slides were observed at 500× magnification. Phytolith micrographs were taken on extra slides prepared with Canada balsam. All particles that were black under crossed-polarizers were described, drawn, and counted separately. Phytoliths were classified according to their three-dimensional morphology and size, and only later were given (or not) some taxonomic attribution (Appendix 1). Counting was carried out until reaching 200 phytoliths, except for samples DB08-geo15 (material exhausted) and samples DB08-geo18a and DB08-19, which were found sterile (Table 1).

Results

Geological and geochemical evidence for a persistent freshwater spring

Geological excavation at FLK NN (200 m north of FLK Zinj) uncovered a thick persistent carbonate deposit (tufa) (Fig. 5A). The tufa is blanketed by Tuff IC air fall and thus is equivalent to the level 22 archaeological horizon at FLK (Fig. 5B). Tuff IC cannot be physically

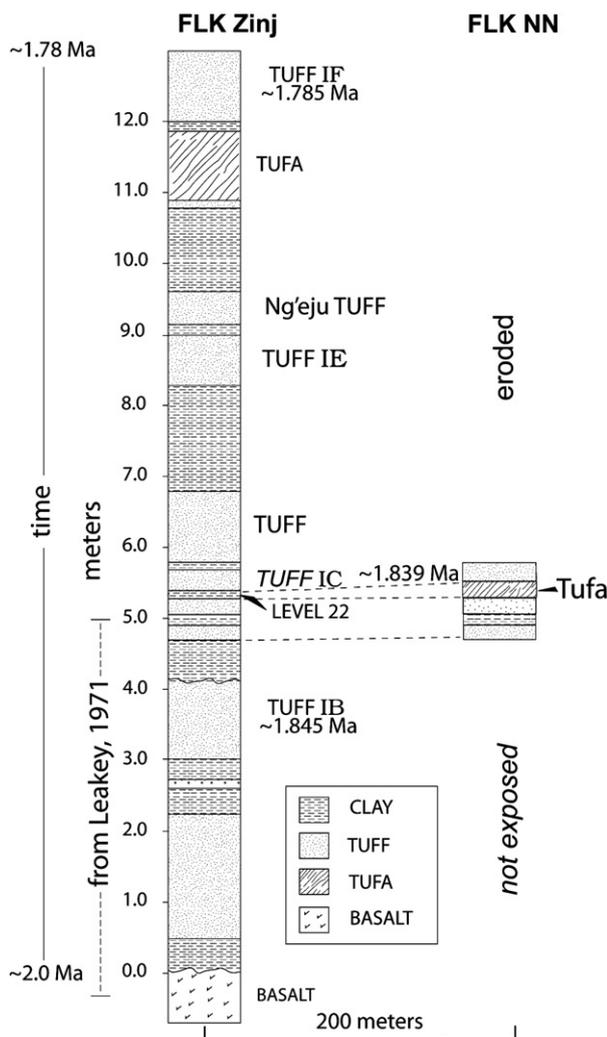


Figure 3. Stratigraphic columns of Bed I at FLK Zinj site and FLK NN, located 200 m to the north. Ages of Tuff IB and Tuff IC (Blumenschine et al., 2003). Age of Tuff IF (Hay and Kyser, 2001). Archaeological level 22 occurs immediately beneath Tuff IC and is stratigraphically equivalent with the tufa at FLK NN.

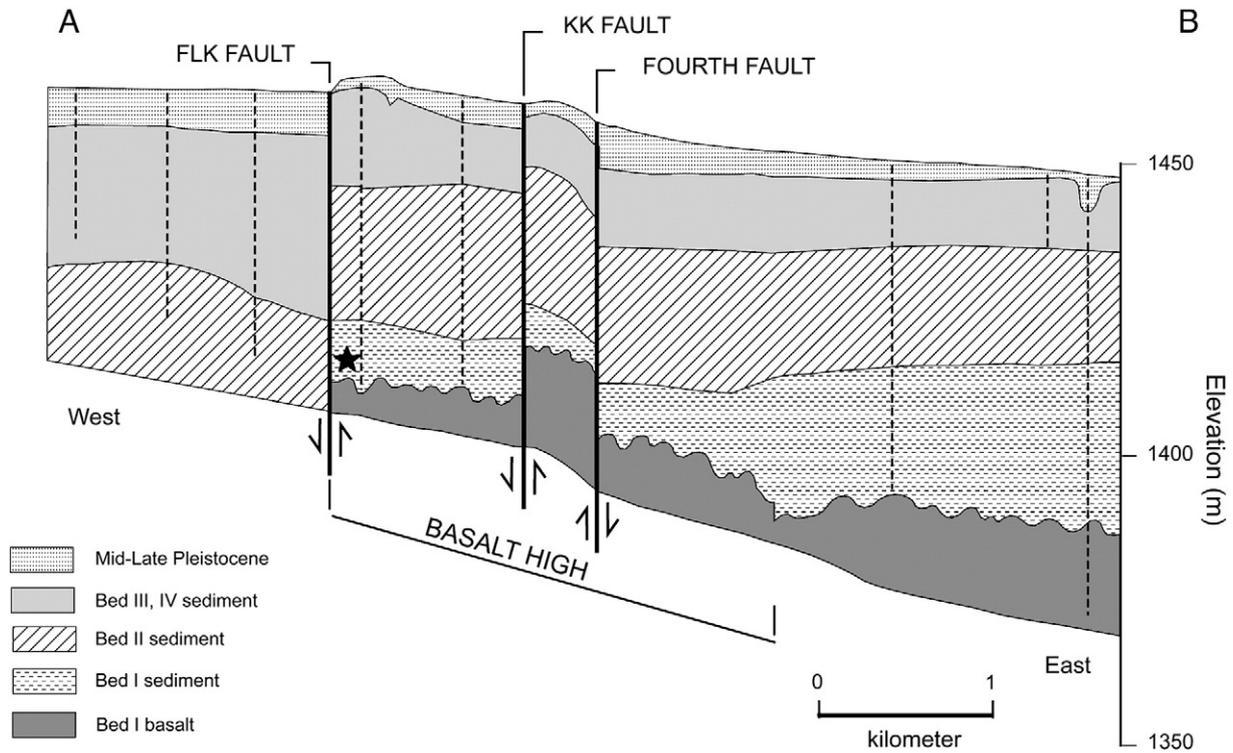


Figure 4. Geologic cross section (A–B) of the junction area depicting Olduvai Beds I–IV. Dashed lines represent geologic sections. FLK (Zinj and NN sites) (solid star) are located in Bed I and depicted here adjacent to the FLK fault and above the basalt. The Bed I basalt which is relatively impermeable forms a local high in the junction compared to adjacent areas. This basalt high may have focused groundwater flowing from the Ngorongoro Volcanic Highland to the surface creating freshwater seeps and springs in the junction area (Fig. 6B).

Table 1
Phytolith samples and phytolith counts summarized.

		Localities ^a sampled under Tuff IC / Sample #									
		FLK Zinj					FLK NN			FLK NW	
		GA-Old-17-07	DB08-geo15	GA-Old-113-07	GA-Old-114-07	DB08-geo16	DB08-geo4	DB08-geo17	DB08-geo18a	DB08-geo18b	DB08-geo19
Latitude	(°S)	2°59'22.48"	2°59'13.1"	2°59'21"	2°59'21"	2°59'21"	2°59'14.1"	2°59'22.16"	2°59'17.1"	2°59'17.1"	2°59'19.2"
Longitude	(°E)	35°20'55.7"	35°20'53"	35°20'54.9"	35°20'54.9"	35°20'54.9"	35°20'52.7"	35°20'56.48"	35°20'53.7"	35°20'53.7"	35°20'51.6"
Distance to trench FLK-03	(m)	0	0	0	0	~10	~25	~10	~200	~200	~200
Phytolith categories/ types ^b	Taxonomy										
Globular granulate	FI	28	57	82		78	115	101		7	
Globular echinate	Palm	20	14	3	70	4	2			16	
Globular echinate/micro- echinate/ridges	Ma/Cos?	13			21						
Globular tuberculate/ faceted/smooth	FI	35	18	27	37	26	30			50	
Striated/onion-like bodies	FI	7		8	37	13					
Plates (other)	Unknown	3	2	19	4	1		14		2	
Plates (Grass)	Grass/Sedge?			1	1						
Plates (FI)	FI						3				
Sclereids	FI	1					4	4		7	
Elongate (others)	Unknown		18		1	4	19	22		2	
Elongate (FI)	FI				4		1			1	
Blocky bodies (FI)	FI	30		29	17			10		7	
Blocky bodies (others)	Unknown	7	6	13	4	10	6	18		69	
Acicular hair cells	Grass/Sedge					2					
Fan-shaped bulliform cells	Grass/Sedge			2			19	2			
Grass silica short cells	Grass	38	3.5	12.5	26	14.5	4	16		6	
Dubious	–	34	19.5	9	11	61	1.5	16		37.5	
SUM Phytoliths		216	138	205.5	233	213.5	204.5	203	0	204.5	0
D°/P index		2.2	25.4	9.0	4.1	7.4	36.8	6.3	–	12.2	–

FI: forest indicators, Mar/Cos?: tentatively assigned to Maranthaceae/Costaceae.

D°/P index: ratio of globular granulate/echinate/tuberculate/smooth phytoliths over grass silica short cells.

^a After Hay (1976).

^b Detailed counts of phytolith types are in Appendix 1.

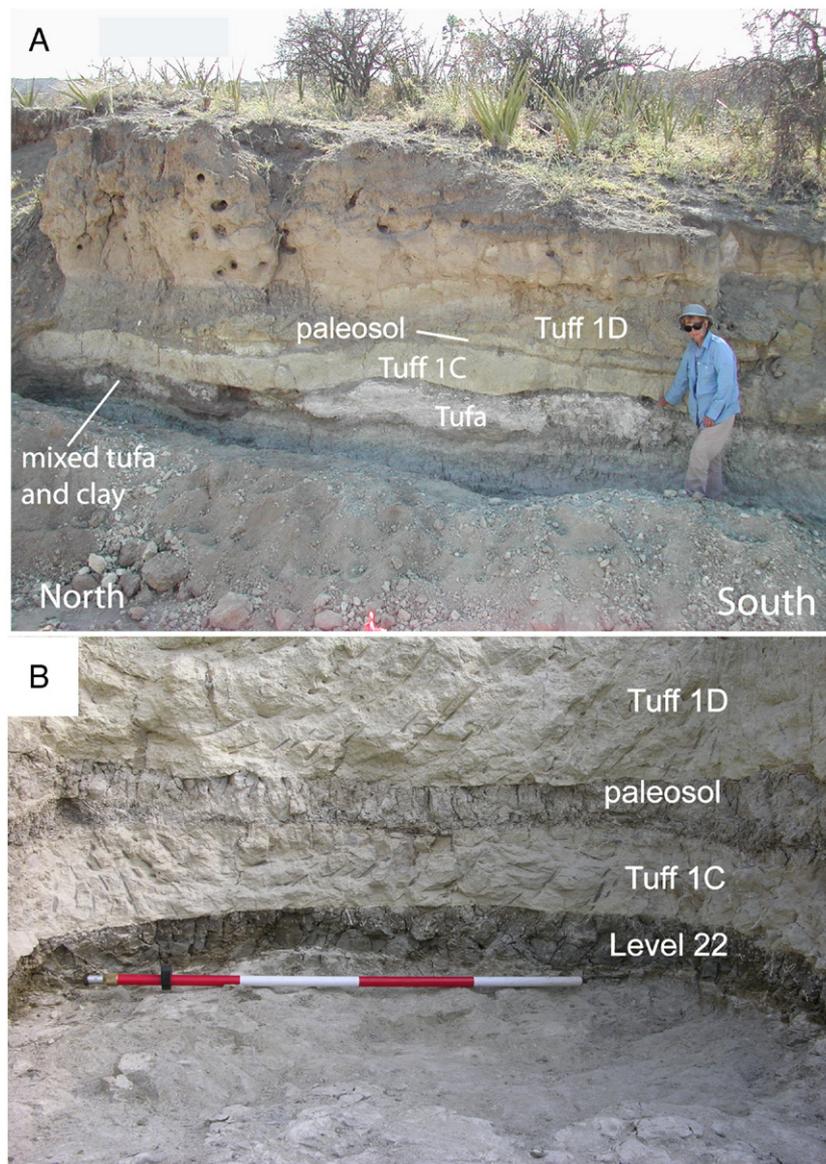


Figure 5. A. Photo of a north–south oriented exposure of stratigraphic section at FLK NN. White carbonate (tufa) occurs in an undulating mound draped with Tuff A. A thin paleosol and Tuff ID overlie Tuff IC. At the north end of our crop the tufa and underlying sediments (thin tuff and clay beds) are noticeably mixed with the tufa; likely bioturbation by vertebrates. B. Photo of Bed I outcrop at FLK Zinj showing level-22, Tuff IC, a thin paleosol and Tuff ID. Phytoliths (Fig. 8) are from level 22.

traced from FLK Zinj to FLK NN because of gully (korongo) erosion down to basalt between the outcrops. But, Tuff IC appears in both FLK Zinj and FLK NN detailed stratigraphic sections (Leakey, 1971). It is described as a medium- to coarse-grained vitric tuff of trachyte composition, and is depicted in stratigraphic sections of FLK Zinj and FLK NN; FLK Zinj being the type section (Hay, 1976). The tuff was characterized geochemically from samples collected throughout the Gorge (McHenry, 2004, 2005) and dated 1.839 ± 0.005 Ma from samples collected at the OH65 archeological site on the western side of the basin (Blumenschine et al., 2003). Level 22 is a 20-cm-thick green to olive-brown silty clay layer in and on which Oldowan stone tools and fossilized bones co-occur (Leakey, 1971) (Figs. 3 and 5B). Green smectitic clays with varying amounts of silt are intercalated with tuffs throughout Bed I. Interpreted to be lacustrine in origin (Hay, 1976), the green clays were deposited during high lake levels when water flooded onto the lake margin, and then modified by pedogenic processes and turning them brown during times of lower lake levels (Sikes and Ashley, 2007).

The tufa occurs in a mound-like form and is at least 35 m by 10 m and ~0.5 m thick (Fig. 5A). It is chalky and friable, white, when pure,

but mixed with underlying sediment in places. We interpret the admixing of the lithologies as bioturbation similar to that which occurs at modern watering holes (Behrensmeier and Laporte, 1981; Ashley and Liutkus, 2002).

The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signatures of tufa record the geochemistry of the water and carbonate-precipitating environment (Pentecost, 2005). $\delta^{18}\text{O}$ reflects the original signature inherited from precipitation plus any fractionation that occurred during the precipitation of carbonate and thus considered a faithful record of the paleoenvironment. The $\delta^{13}\text{C}$ signature is less straightforward as contributions of carbon are made from weathered rock and soil that the groundwater has moved through, as well as diffusion of carbon from the atmosphere.

The tufa has a robust “freshwater” isotopic signature. $\delta^{18}\text{O}$ values range from $\sim -5.0\%$ to -1.0% (Fig. 6A), which indicates a groundwater-fed water source (Cerling and Quade, 1993). Compared to the $\delta^{18}\text{O}$ average value of -4.0% for modern regional rainfall, $\delta^{18}\text{O}$ values of the newly discovered tufa indicate a meteoric source for the water as well as a fractionation toward more positive values, as found under evaporative conditions when groundwater discharges onto the surface (Cerling et al., 1993). Compared to the carbonate record of a

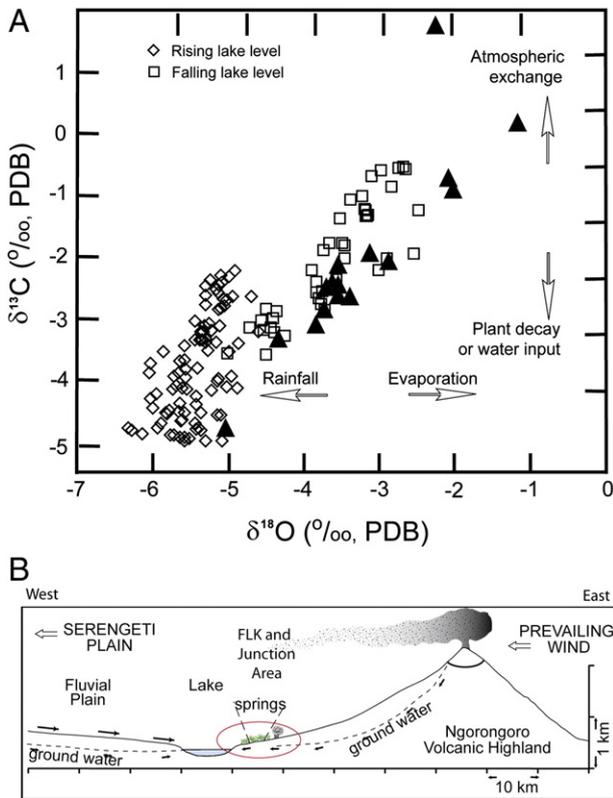


Figure 6. A. Oxygen and carbon stable isotopes of the Bed I tufa uncovered at FLK NN (solid triangles) compared with data of carbonate rhizoliths from lowermost Bed II that were interpreted as phreatic, formed in a freshwater wetland on the lake margin flats during an entire lake cycle. Squares: falling lake levels (lake regression); diamonds: rising lake level (lake transgression) (Liutkus et al., 2005). Falling lake levels are considered more evaporative conditions, whereas rising lake levels reflect wetter climate and a more direct input from rainfall (from surface runoff or groundwater). B. A paleoenvironmental reconstruction of the Olduvai basin during low lake levels and presumably drier periods. Groundwater-fed springs sourced from the Ngorongoro Volcanic Highland formed on the east side of the lake (adapted from Ashley et al., 2008). Prevailing winds from the east brought moisture from Indian Ocean.

freshwater wetland in lowermost Bed II, where phreatic rhizoliths formed during both rising and falling lake levels (Liutkus et al., 2005), the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ are slightly more positive for the Bed I tufa suggesting evaporative conditions and more atmospheric exchange, consistent with an interpretation of subaerial groundwater discharge. The oxygen signature of Bed I tufa is more positive than the Bed II example, which is also consistent with a spring discharging on the land surface and being subjected to continuous evaporation.

In the field, we also measured the fine-scale, local relief on the basalt surface due to pahoehoe or ropey texture formed during cooling of the lava, and observed a difference of ~2.5 m in elevation in the study area. Hay (1976) reported has much as 5 m relief within the larger area of the junction (Fig. 4). Our measurements showed the basalt is 1.8 m higher at the FLK Zinj site than at the tufa locality (FLK NN) 200 m to the north (Fig. 2). The uneven basalt surface would have produced an undulating lake margin surface as sediment accreted, at least in the lower part of the section.

Botanical evidence for wooded to densely wooded environment

We identified 84 different phytolith types in the eight productive samples of clay that were collected immediately below Tuff IC (Appendix 1). Types were grouped into several main categories (Table 1). Phytoliths with unknown taxonomical origin represent 4% to 36% of the total assemblages, and phytoliths with dubious 3D-morphology that could not be classified in a definite category are

relatively abundant (>10% in several samples) and represent up to 30% in sample DB08-geo18b at FLK NN tufa locality (Fig. 7).

Grass silica short cells (GSSCs) are rare in all samples (2% to 18%), while forest indicator phytoliths are abundant (43% to 71%) (Fig. 7), which argues for abundant woody plants such as trees and/or shrubs or bushes in the paleo-vegetation. Among the grass phytoliths, the only categories we observed were Bilobate, Pyramidal, Rondel (diameter <15 μm), and Trapeziform short cells (Fig. 8, Appendix 1). Forest indicator phytoliths (FI) include the globular granulate type (Fig. 8), which occurs mainly in tropical woody dicotyledons (e.g., Geis, 1973) and which relative abundance in soils increases with increasing density of broadleaved trees and shrubs at low and middle elevations (Bremond et al., 2005, 2008; Barboni et al., 2007). FI phytoliths also include the globular echinate and micro-echinate types produced by palms (Arecaceae) (Tomlinson, 1961), and the globular echinate bodies with more or less marked ridges (Glo-18, -19, -23, and -24, Appendix 1) that strongly resemble phytoliths produced by some forest species of the Maranthaceae and Costaceae families (Strömberg, 2003). Some types among the categories Striated/onion-like bodies, Plate, Sclereid, Elongate, and Blocky bodies are also associated to woody plants and are, thus, considered forest indicators (Barboni et al., 2010).

$\text{D}^{\circ}/\text{P}$ phytolith index, which is the ratio of woody dicotyledon and palm phytoliths over grass phytoliths is another way to measure the relative importance of woody plants over grasses in a vegetation. Values $\gg 1$ are typical for sites in African wet evergreen forests, while $\text{D}^{\circ}/\text{P}$ values <1 are typical for savannas where trees and shrubs are scarce (Alexandre et al., 1997; Bremond et al., 2005). In the clay samples we studied here, $\text{D}^{\circ}/\text{P}$ values range from 2 to >36 (Table 1), which clearly suggest a wooded to densely wooded paleo-vegetation.

There are no major differences in the phytolith assemblages among the samples, except that the highest amount of palm phytoliths is found in sample GA-Old-114-07 from Trench FLK Zinj 04, a sample taken few centimeters below sample GA-Old-113-07.

Discussion

The isotopic signature of the tufa coeval to the FLK Zinj archaeological level 22 that we uncovered at FLK NN by our recent excavations at Olduvai Gorge indicates that less than 200 m away from the high-density patch of stone tools and butchered bones observed at FLK Zinj, a fresh water source was available to hominins. In the area surrounding FLK Zinj itself, including FLK NN where the spring was found, abundant plant silica bodies (phytoliths) from woody dicotyledons and palms were found, which attest to the presence of trees and/or shrubs or bushes. Hence, the paleoenvironmental context at FLK Zinj appears to offer a spring-fed watering hole and wooded to densely wooded habitat that would have provided a location relatively safe from carnivores for hominins to butcher animals.

Despite considerable recent advances in the field of phytolith research, which now allow for the identification of some important crops in fossil sediments (bananas, bottle-gourd, squash, maize, rice; e.g., Piperno, 2006), silica bodies, in general, can only relate to broad ecological groups or plant types (e.g., woody dicots, palms, and grasses). Even within the phytolith-rich Poaceae family, it is rarely possible to identify types that are diagnostic to the species-, genus-, or even sub-family level (e.g., Barboni and Bremond, 2009). Recent work on the modern miombo flora of Mozambique showed that few arboreal taxa, such as *Uapaca nitida* and *Podocarpus falcatus* produce unique diagnostic phytoliths, but in such low numbers compared to other phytoliths typical for woody dicotyledons that their detection is most unlikely unless extremely high total phytolith counts are carried out (Mercader et al., 2009). In the clay samples we studied here, despite the fact that forest indicator phytoliths are diverse and most abundant (>40%) compared to grass silica short cells ($\text{D}^{\circ}/\text{P}$ ratio $\gg 1$), we cannot identify if their abundance reflects the abundance of trees, shrubs, or bushes, or all three plant types in the paleovegetation.

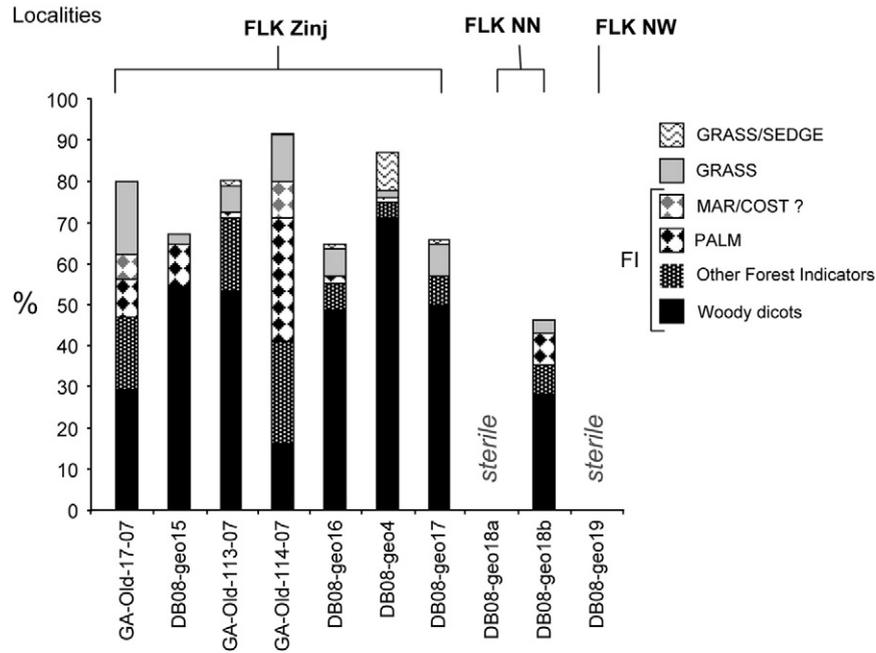


Figure 7. Relative abundance of phytolith indicators of grasses, grasses and/or sedges, and of forest taxa, including Maranthaceae/Costaceae?, Arecaceae (palms), and undifferentiated woody dicotyledons observed in the samples collected from 10 sites from the green silty clay layer under Tuff IC. Totals would reach 100% if the relative abundance of phytoliths with unknown taxonomical origin and dubious 3D-morphology would be null. See Appendix 1 for taxonomic attribution of phytolith types.

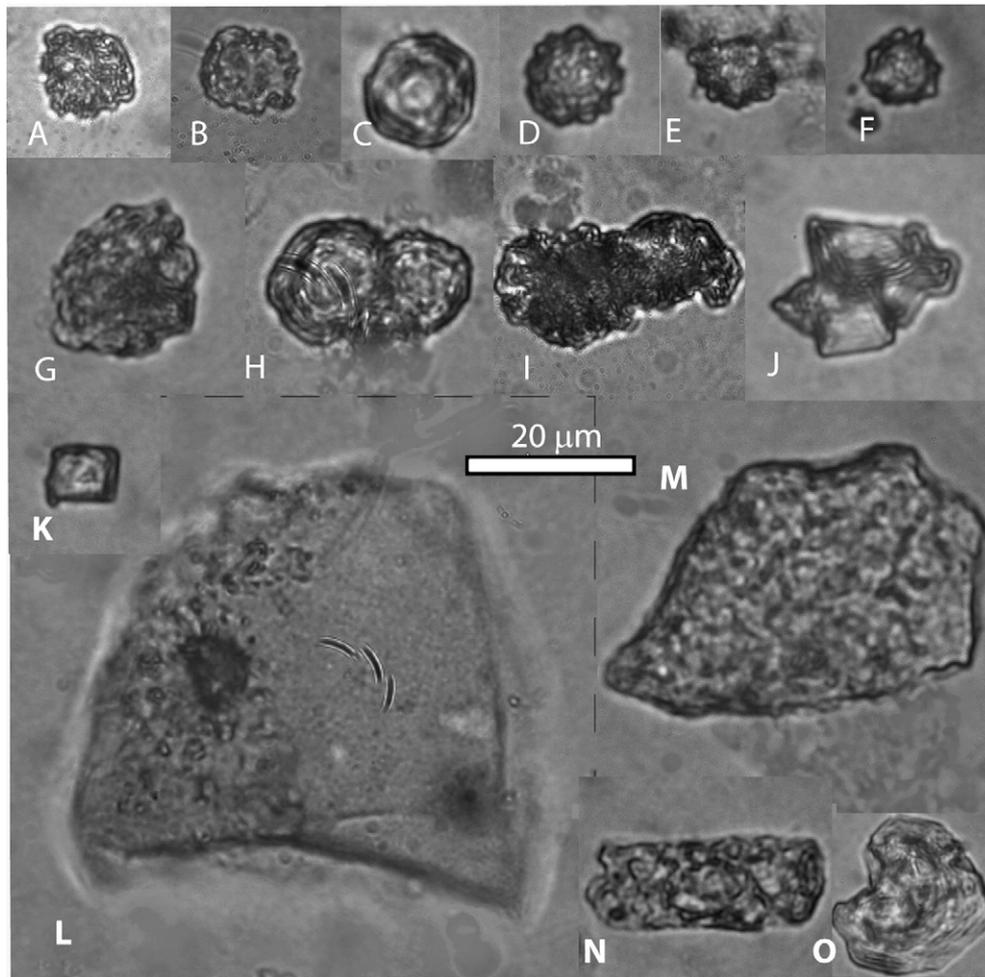


Figure 8. Optical micrographs of woody dicots, palm, and grass phytoliths from archaeological level 22 (FLK Zinj) (see Appendix 1 for detailed taxonomic attributions). A–D, phytoliths of the type Globular granulate (Glo-3, 4); E–G, phytoliths of the type Globular echinate (Glo-10); H, spherical phytolith with concentric striations (Str-3); I, globular phytolith micro-echinate oblong (Glo-32); J, dubious body made of imbricated cubes (Unid-9); K, trapeziform short cell phytolith (GSSC-42); L, Discoidal/spheroidal psilate phytolith, vaguely fan-shaped (Blo-7); M, Thin silicified plate, edge or surface lacunate (Pla-3); N, Elongate cylindrical phytolith, surface lacunate (El-10); O, vaguely key-stone phytolith with concentric striations (Str-2).

Palms (Arecaceae), which are big producers of phytoliths (Hodson et al., 2005) were most likely scattered because the relative abundance of globular echinate phytoliths is <10% in average in our fossil samples. For comparison, the percent of globular echinate phytoliths in a swamp dominated by *Raphia* palms is ~68% (Bremond et al., 2005). It is most likely that there were few open spaces between the woody plants because grasses which are ubiquitous and big phytolith producers contributed few silica bodies and types in all samples (Fig. 7, Table 1).

The paleoenvironment would have been a wooded lake margin setting with low-relief hummocks (undulating surface) created by sediment blanketing the irregular surface of the underlying basalt. The spring was in a depression 1–2 m lower than the FLK Zinj. Although the water table was likely high on the lake margin, the slight difference in local relief (i.e., hummocks) may have produced a better drained area at FLK Zinj, and thus a site near to the spring sought for meat consumption. The spring deposit is located a scant 50 m from the FLK Fault (Figs. 2 and 4) and groundwater likely flowed from the fault or related fractures associated with the extensional faulting prevalent in the Olduvai basin. However, the underlying geology needed to verify this pathway is not exposed.

The likely source for the fresh water at FLK NN was groundwater recharged by precipitation on the 3000-m-high Ngorongoro Volcanic Highland that lay to south and east (Ashley et al., 2008). Groundwater flow (and surface runoff) would have been northward from the Highland toward the Olduvai basin (Figs. 1 and 6B). The basalt high in the junction area was relatively impermeable compared to the overlying tuffs and sediments, and likely focused groundwater to the surface by restricting flow (Fig. 4).

The taphonomic analysis of level 22 revealed that the site was predominantly anthropogenic in origin with carnivores playing a minor role (Domínguez-Rodrigo et al., 2007). The spring would have provided an attraction and the woodland a temporary respite of safety for multipurpose activities of hominins producing tools and consuming animals (Dunnell and Dancey, 1983).

Even though the reconstruction of the site includes abundant evidence of hominin activity the context of the site has been problematic because prior reconstructions emphasize the location of the site on an exposed lake-margin flat. Lake Olduvai was a saline-alkaline playa, not a freshwater lake (Hay and Kyser, 2001; Hover and Ashley, 2003; Deocampo et al., 2009). During wetter periods the water flooded across the lake margin (Hay and Kyser, 2001) and during drier periods the lake withdrew to the west exposing a wide lake margin and the potential freshwater sources supplied from the highlands to the east (Ashley and Hay, 2002) (Fig. 3). FLK Zinj is found within this general paleoenvironmental scenario.

Tuff IC blanketed Olduvai basin at 1.839 ± 0.005 Ma, covering the tufa mound, botanical remains and the dense accumulation of stone tool tools and bones at FLK Zinj with a 30-cm-thick layer of volcanic ash. At the time of Tuff IC deposition, the climate was intermediate between the wettest and driest part of a precession cycle (Sikes and Ashley, 2007). The lake shore was estimated to be approximately a kilometer to the west of FLK Zinj, implying that archeological site was situated on an extensive mudflat or marshland (Hay, 1990). Mudflats are usually open-vegetation habitats with little likelihood of refuge. In contrast, the paleoecological reconstruction of FLK Zinj area from a variety of bio-indicators points to the presence of a grassy woodland (Sikes, 1994).

Riparian woodlands are often assumed to be sites frequented by hominins (Bunn and Kroll, 1986; Rose and Marshall, 1996; Domínguez-Rodrigo et al., 2007). However, there is little coarse sediment and no geological evidence for rivers *per se*, although Leakey (1971) noted a shallow drainage channel (<100 cm wide and 40 cm deep) incised into the FLK Zinj clay layer on the edge of excavation. This narrow steep-sided incision is more in keeping with the scale of a hippopotamus trail than a river channel (Ashley and Liutkus, 2002; Deocampo, 2002).

Our descriptive model of the paleoenvironment of the FLK Zinj site including the newly discovered evidence for a freshwater source (Figs. 2, 5A, 6) is consistent with the phytoliths reported in this study and a range of independently collected data from the site in the past 40 years. No pollen data from FLK Zinj level 22 or a stratigraphically equivalent layer are available (Bonniefile and Riollot, 1980); however, stable isotopes (Sikes, 1994), faunal data (bovids) (Kappelman, 1984; Potts, 1988), abundant remains of the *Acacia* rat *Thallomys* (Jaeger, 1976; Gentry and Gentry, 1978), freshwater snails and urocyclid slugs (Hay, 1973) have provided abundant evidence for woody C₃ floral habitats, like *Acacia* woodland or gallery forests.

Paleoenvironmental analyses of faunas, in particular rodents, from mid-Bed I indicate a very rich closed woodland environment (Fernandez-Jalvo et al., 1998). A recent analysis of bovid taxa excavated from the FLK Zinj horizon indicates animals with a mixed grazing and browsing diet and also suggests a significant presence of C₃ plants in the area (Plummer et al., 2009). Paleoenvironmental proxies, including our phytolith results from the archaeological site itself, point to a closed habitat made of undefined woody trees and/or shrubs or bushes and palms at the FLK Zinj site.

Our recent excavations have exposed a sharp difference in density of archaeological materials in most of the ca. 2000-m² area between FLK Zinj locality and the surroundings, including the FLK NN spring locality (Fig. 2). The high density patch at FLK Zinj contains the highest diversity of stone tool types and more completely butchered animal bones than the surrounding lower density samples (Domínguez-Rodrigo et al., 2010). Very few quartz and quartzite artefacts and flakes were found outside FLK Zinj, and cutmarked bones occur only at the FLK Zinj itself. None have been documented in our excavations of the surrounding landscape (Domínguez-Rodrigo et al., 2010). Carcass butchering activities were thus restricted to FLK Zinj site.

It appears that hominins were not simply using this as arboreal habitat as a refuge, otherwise, following the behaviours of modern non-human primates (Domínguez-Rodrigo et al., 2007), FLK Zinj would exhibit a much lower density of materials. The palaeoenvironmental evidence presented in this work refute all previous interpretations on the behavioral nature of the Olduvai sites based on an open mudflat environment, such as the refuge model and the related passive scavenging hypothesis (Blumenschine and Masao, 1991). These results single out FLK Zinj as a high-density spot within the woodland and supports inferences of the site as a focal site of subsistence (and maybe social) activity for a group of hominins during an uncertain period of time. The evidence from the site fits well the prediction of the “resource-defence” model, which infers that these focal sites offered spatial fixed and defensible resources such as fresh water, trees and plant foods (Rose and Marshall, 1996).

Modern foragers transport carcasses across long distances. In marked contrast, the high concentration of select parts at FLK Zinj suggests a different behaviour pattern (Faith et al., 2009). The presence of a nearby spring (the only documented source of fresh water in that part of the basin) would have been a magnet for herbivores during the dry season. Hence, hominins could have obtained carcasses at the nearby spring (FLK NN) and transported them a short distance (200 m) to FLK Zinj. Carcass availability and their exploitation in a low competition environment probably was one of the major appeals of the spring and woodland to hominins.

The dynamics of carcass acquisition and carcass transport are complex, and short-distance transport by hominins from the spring to FLK Zinj is one working hypothesis among several alternatives. For example, modern felids, such as lions and leopards, are known ambush hunters and kill their prey essentially on the spot. If similar felids were killing their prey near the spring at FLK NN, then it follows that hominins scavenging from such felid kills would face only a short transport distance. However, the bovid mortality profiles from FLK Zinj do not indicate that ambush hunting by felids was the predominant source of the bovid carcasses, and the bovid mortality

profiles call into question any form of scavenging or persistence hunting by hominins (Bunn and Pickering, this issue).

An alternative working hypothesis is that hominins themselves were ambush hunters. Ambush hunting by modern Hadza foragers (a local tribe near Lake Eyasi) using long bows and poison-tipped arrows usually does not yield on-the-spot kills, except for the rare, paralyzing shot to the spine. Large Hadza prey animals commonly run long distances before death and must be tracked by the hunters for distances ranging up to 5 km prior to field butchery and transport (Bunn et al., 1988). If hominins were hunting large animals near the spring and lacked such sophisticated weaponry, acquiring them and transporting portions to FLK may have involved considerable distances, rather than a short 200 m. This might be the case unless it can be demonstrated that hominins used wooden spears and that such weapons can produce severe wounds and on-the-spot kills. There is some ethnographic support for the latter, at least using metal-tipped spears (Hitchcock and Bleed, 1997), but it seems possible that wooden-tipped spears would be less effective in producing on-the-spot kills. This latter interpretation will have to be experimentally supported. As analyses proceed, we will continue to consider all of these alternatives and the evidence and analytical techniques underlying them.

In summary, the spectacularly high concentration of life in “the junction” appears to be caused by the interplay of rift valley-related tectonics and astronomically-controlled climate fluctuations that created localized freshwater environments in the Olduvai basin between ca 1.85–1.75 Ma (Ashley and Hay, 2002; Ashley, 2007). The consistent attraction of this site for hominins and animals from both the Ngorongoro Volcanic Highland and Serengeti grasslands was most likely the availability of fresh water at a time of increasing dryness and climate instability in Africa that coincided with early migrations out of the continent (deMenocal, 1995; Gabunia et al., 2000; Ashley et al., 2008; Ashley, 2009).

Conclusions

Field observations, isotopic analyses of the tufa found at FLK NN, in the same stratigraphic position as archaeological level 22 at FLK Zinj, and micro-botanical analyses of biogenic silica particles (phytoliths) attest to the presence of a freshwater source and a closed wooded vegetation (forest, shrub- or bushland). We conclude that the localized, high-density co-occurrence of stone tools and fossilized bones at FLK Zinj, was located approximately 200 m from a freshwater source in a wooded to densely wooded habitat. This new reconstruction suggests a site highly attractive to hominins, in stark contrast to the current consensus model of a lake margin flat with non-potable saline-alkaline water. Our study suggests that hominins selected this site for carcass transport, accumulation and processing. Future reconstructions of early Pleistocene hominin behavior will need to be tested against the taphonomic information retrieved from FLK Zinj (Fernandez-Jalvo et al., 1998), together with the new palaeoenvironmental evidence provided by this present study.

Supplementary materials related to this article can be found online at doi:10.1016/j.yqres.2010.07.015.

Acknowledgments

The raw data presented here were collected under permits from the Tanzania Commission for Science and Technology and the Tanzanian Antiquities Department to TOPPP (The Olduvai Paleoanthropological and Paleoecology Project), PIs M. Domínguez-Rodrigo, A.Z.P. Mabulla, H.T. Bunn and E. Baquedano. We appreciate funding provided by the Spanish Ministry of Education and Science through the European project I+D HUM2007-63815. We are grateful to J.S. Delaney for assistance with manuscript preparation, and C. Dominici for SEM-Energy Dispersive Analyses X. We appreciate the discussions

with D.M. Deocampo, T.E. Cerling, S.G. Driese, C.S. Feibel, C.M. Liutkus, J. Quade and J.C. Tactikos in helping to formulate our ideas and are indebted to the late R.L. Hay for his immense knowledge of the geology of Olduvai Gorge and his generosity in sharing his wisdom.

References

- Alexandre, A., Meunier, J.-D., Lézine, A.-M., Vincens, A., Schwartz, D., 1997. Phytoliths indicators of grasslands dynamics during the late Holocene in intertropical Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 213–219.
- Ashley, G.M., 2007. Orbital rhythms, monsoons, and playa lake response, Olduvai Basin, equatorial East Africa (1.85–1.75). *Geology* 35, 1091–1094.
- Ashley, G.M. (2009). The Olduvai Spring System: Freshwater resources at Olduvai Gorge (1.85–1.75 Ma) provided an important ecological niche. In “50th Golden Anniversaries of *Zinjanthropus* discovery and the current establishments of Serengeti National Park and Ngorongoro Conservation Area Authority, Tanzania.” Ministry of Natural Resources and Tourism, Dar es Salaam, Tanzania, Arusha International Conference Center, Arusha, Tanzania.
- Ashley, G.M., Hay, R.L., 2002. Sedimentation patterns in a Plio-Pleistocene volcanoclastic rift-margin basin, Olduvai Gorge, Tanzania. *Sedimentation in Continental Rifts*. SEPM Special Publication. SEPM, pp. 107–122.
- Ashley, G.M., Liutkus, C.M., 2002. Tracks, trails and trampling by large vertebrates in a rift valley paleo-wetland, lowermost Bed II, Olduvai Gorge, Tanzania. *Ichnos* 9, 23–32.
- Ashley, G.M., Tactikos, J.C., Owen, R.B., 2008. Hominin use of springs and wetlands: paleoclimate and archaeological records from Olduvai Gorge (1.79–1.74 Ma). *Palaeogeography, Palaeoclimatology, Palaeoecology* 272, 1–16.
- Barboni, D., Bremond, L., 2009. Phytoliths of East African grasses: an assessment of their environmental and taxonomic significance based on floristic data. *Review of Palaeobotany and Palynology* 158, 29–41.
- Barboni, D., Bremond, L., Bonnefille, R., 2007. Comparative study of modern phytolith assemblages from inter-tropical Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 246, 454–470.
- Barboni, D., Ashley, G.M., Dominguez-Rodrigo, M., Mabulla, A.Z., Bunn, H.T., Baquedano, E., 2010. Phytoliths infer locally dense and heterogeneous paleovegetation at FLK North and surrounding localities during upper Bed I time, Olduvai Gorge, Tanzania. *Quaternary Research* 74, 344–354.
- Behrensmeier, A.K., Laporte, L.F., 1981. Footprints of a Pleistocene hominin in Northern Kenya. *Nature* 289, 364–366.
- Binford, L.R., 1981. *Bones: Ancient Men, Modern Myths*. Academic Press, New York.
- Blumenschine, R.J., Masao, F.T., 1991. Living sites at Olduvai Gorge, Tanzania? Preliminary landscape archaeology results in the basal Bed II lake-margin zone. *Journal of Human Evolution* 21, 451–462.
- Blumenschine, R.J., Peters, C.R., Masao, F.T., Clarke, R.J., Deino, A.L., Hay, R.L., Swisher, C.C., Stanistreet, I.G., Ashley, G.M., McHenry, L.J., Sikes, N.E., van der Merwe, N.J., Tactikos, J.C., Cushing, A.E., Deocampo, D.M., Njau, J.K., Ebert, J.I., 2003. Lake Pliocene Homo and hominid land use from western Olduvai Gorge, Tanzania. *Science* 299, 1217–1221.
- Bonnefille, R., Rioulet, G., 1980. Palynologie, végétation et climats de Bed I et Bed II à Olduvai, Tanzanie. In: Leakey, R.E., Ogot, B.A. (Eds.), *Proc. 8th Pan-African Congress of Prehistory and Quaternary Studies*. The International Louis Leakey Memorial Institute for African Prehistory, Nairobi, pp. 123–127.
- Bremond, L., Alexandre, A., Hely, C., Guiot, J., 2005. A phytolith index as a proxy of tree cover density in tropical areas: Calibration with Leaf Area Index along a forest-savanna transect in southeastern Cameroon. *Global and Planetary Change* 45, 277–293.
- Bremond, L., Alexandre, A., Wooller, M.J., Hely, C., Williamson, D., Schafer, P.A., Majule, A., Guiot, J., 2008. Phytolith indices as proxies of grass subfamilies on East African tropical mountains. *Global and Planetary Change* 61, 209–224.
- Bunn, H.T. (1982). “Meat-eating and human evolution: studies on the diet and subsistence for meat-eating by Plio-Pleistocene hominids in East Africa,” Unpublished PhD thesis, University of California, Berkeley.
- Bunn, H.T., 2007. Meat Made us Human. In: Ungar, P. (Ed.), *Evolution of the Human Diet*. Oxford University Press, Oxford, pp. 191–211.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio-Pleistocene hominids at Olduvai Gorge, Tanzania. *Current Anthropology* 27, 431–452.
- Bunn, H.T., Kroll, E.M., Bartram, L.E., 1988. Variability in bone assemblage formation from Hadza hunting, scavenging and carcass processing. *Journal of Anthropological Archaeology* 7, 412–457.
- Cerling, T.E., Quade, J., 1993. Stable Carbon and Oxygen Isotopes in Soil Carbonates. In: Swart, P.K., Lohmann, K.C., McKenzie, J., Savin, S. (Eds.), *Climate Change in Continental Isotopic Records: Geophysical Monograph*, pp. 217–231.
- Cerling, T.E., Wang, Y., Quade, J., 1993. Global ecological change in the late Miocene: expansion of C4 ecosystems. *Nature* 361, 344–345.
- Coplen, T.B., Kendall, C., Hopple, J., 1983. Comparison of stable isotope reference samples. *Nature* 302.
- deMenocal, P.B., 1995. Plio-Pleistocene African climate. *Science* 270, 53–59.
- Deocampo, D.M., 2002. Sedimentary structures generated by *Hippopotamus amphibius* in a lake-margin wetland, Ngorongoro Crater, Tanzania. *Palaios* 17, 212–217.
- Deocampo, D.M., 2004. Hydrogeochemistry in the Ngorongoro Crater, Tanzania, and implications for land use in a World Heritage Site. *Applied Geochemistry* 19, 755–767.
- Deocampo, D.M., Cuadros, J., Wing-Dudek, T., Olives, J., Amouric, M., 2009. Saline lake diagenesis as revealed by coupled mineralogy and geochemistry of multiple

- ultrafine clay phases: Pliocene Olduvai Gorge, Tanzania. *American Journal of Science* 309, 834–868.
- Dominguez-Rodrigo, M., Barba, R., Egelund, C.P., 2007. Deconstructing Olduvai : A taphonomic study of the Bed I sites. *Vertebrate Paleobiology and Paleoanthropology Series*. Springer, AA Dordrecht, The Netherlands, p. 337+ xvi.
- Dominguez-Rodrigo, M., Barba, R., Egelund, C.P., 2007. Deconstructing Olduvai: A taphonomic study of the Bed I sites. Springer, AA Dordrecht, The Netherlands.
- Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Ashley, G.M., Diez-Martin, F., Barboni, D., Prendergast, M.E., Yravedra, J., Barba, R., Sanchez, A., Baquedano, E., Pickering, T.R., 2010. New excavations at the FLK *Zinjanthropus* site and its surrounding landscape and their behavioral implications. *Quaternary Research* 74, 315–332.
- Dunnell, R.C., Dancy, W.S., 1983. The siteless survey: a regional scale data collection strategy. *Advances in Archaeological Method and Theory* 6, 267–287.
- Faith, J.T., Dominguez-Rodrigo, M., Gordon, A.D., 2009. Long distance carcass transport at Olduvai Gorge? A quantitative examination of Bed I skeletal element abundances. *Journal of Human Evolution* 56, 247–256.
- Fernandez-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y., Humphreys, L., 1998. Taphonomy and palaeoecology of Olduvai Bed-I (Pleistocene, Tanzania). *Journal of Human Evolution* 34, 137–172.
- Gabunia, L., Vekua, A., Lordkipanidze, D., Swisher, C.C., Ferringer, R., Justus, A., Nioradze, M., Tsvachretidze, M., Anton, S.C., Bosinski, G., Joris, O., Lumtsey, M., Majsuradze, G., Mouskhelishvili, A., 2000. Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: taxonomy, geological setting, and age. *Science* 288, 1019–1025.
- Geis, J.W., 1973. Biogenic silica in selected species of deciduous angiosperms. *Soil Sciences* 116, 113–119.
- Gentry, A.W., Gentry, A., 1978. Fossil bovidae (mammalian) from Olduvai Gorge, Tanzania. *Bulletin of the British Museum London* 29, 289–446.
- Hay, R.L., 1973. Lithofacies and environments of Bed I, Olduvai Gorge, Tanzania. *Quaternary Research* 3, 541–560.
- Hay, R.L., 1976. *Geology of the Olduvai Gorge*. University of California Press, Berkeley.
- Hay, R.L., 1990. Olduvai Gorge: A Case History in the Interpretation of Hominid Paleoenvironments in East Africa. In: Laporte, L.F. (Ed.), *Establishment of a geologic framework for paleoanthropology*. Geological Society of America Special Paper. Geological Society of America, Boulder, Colorado, pp. 23–37.
- Hay, R.L., Kyser, T.K., 2001. Chemical sedimentology and paleoenvironmental history of Lake Olduvai, a Pleistocene lake in northern Tanzania. *Geological Society of America Bulletin* 113, 1505–1521.
- Hitchcock, R., Bleed, P., 1997. Each According to Need and Fashion: Spear and Arrow Use among San Hunters Of The Kalahari. In: Knecht, H. (Ed.), *Projectile Technology*. Plenum Press, New York, pp. 345–368.
- Hodson, M.J., White, P.J., Mead, A., Broadley, M.R., 2005. Phylogenetic variations in the silicon composition of plants. *Annals of Botany* 96, 1027–1046.
- Hover, V.C., Ashley, G.M., 2003. Geochemical signatures of paleodepositional and diagenetic environments: a STEM/AEM study of authigenic clay minerals from an arid rift basin, Olduvai Gorge, Tanzania. *Clays and Clay Minerals* 51, 231–251.
- Isaac, G.L., 1978. The food-sharing behavior of protohuman hominids. *Scientific American* 238.
- Isaac, G.L., 1983. Bones in Contention: Competing Explanations for the Juxtaposition of Early Pleistocene Artifacts and Faunal Remains. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology I: Hunters and their Prey*. Oxford, pp. 3–19.
- Isaac, G.L., 1984. The archaeology of human origins : studies of Lower Pleistocene in East Africa, 1971–1981. *Advances in World Archaeology* 3, 1–87.
- Jaeger, J.J., 1976. Les rongeurs (mammalia, Rodentia) du Pleistocene inferieur d'Olduvai Bed I (Tanzanie), 1ere partie : Les Murides. In: Savage, R.J.G., Coryndon, S.C. (Eds.), *Fossil Vertebrates of Africa*. Academic Press, London, pp. 57–120.
- Kappelman, J., 1984. Plio-Pleistocene environments of Bed land lower Bed II, Olduvai Gorge, Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoecology* 48, 171–196.
- Leakey, M.D., 1971. *Olduvai Gorge: Excavations in Beds I and II; 1960–1963*. Cambridge University Press, Cambridge, UK.
- Liutkus, C.M., Wright, J.D., Ashley, G.M., Sikes, N.E., 2005. Paleoenvironmental interpretation of lake-margin deposits using $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ results from Early Pleistocene carbonate rhizoliths, Olduvai Gorge, Tanzania. *Geology* 33, 377–380.
- McHenry, L.J., 2004. Characterization and correlation of altered Plio-Pleistocene tephra using a “multiple technique” approach: case study at Olduvai Gorge, Tanzania. Rutgers University.
- McHenry, L.J., 2005. Phenocryst composition as a tool for correlating fresh and altered tephra, Bed I, Olduvai Gorge, Tanzania. *Stratigraphy* 2, 101–115.
- Mercader, J., Bennett, T., Esselmont, C., Simpson, S., Walde, D., 2009. Phytoliths in woody plants from the Miombo woodlands of Mozambique. *Annals of Botany* 104, 91–113.
- Pentecost, A., 2005. *Travertine*. Springer-Verlag, Berlin.
- Piperno, D.R., 2006. *Phytoliths: A Comprehensive Guide for Archaeologists and Paleoeologists*. AltaMira Press, Lanham.
- Plummer, T.W., Bishop, L.C., Ditchfield, P.W., Ferraro, J.V., Kingston, J.D., Hertel, F., 2009. The environmental context of Oldowan hominid activities at Kanjera South, Kenya. In: Hovers, E., Braun, D. (Eds.), *Interdisciplinary approaches to the Oldowan*. New York, NY, Springer, pp. 149–160.
- Potts, R., 1988. Early hominid activities at Olduvai. *Aldine de Gruyter*, New York.
- Rose, L., Marshall, F., 1996. Meat eating, hominid sociality, and home base revisited. *Current Anthropology* 37, 307–338.
- Sikes, N.E., 1994. Early hominid habitat preferences in East Africa: Paleosol carbon isotopic evidence. *Journal of Human Evolution* 27, 23–45.
- Sikes, N.E., Ashley, G.M., 2007. Stable isotopic signatures of pedogenic carbonates as indicators of paleoecology in the Plio-Pleistocene (upper Bed I) western margin of Olduvai Basin, Tanzania. *Journal of Human Evolution* 53/5, 574–594.
- Strömberg, C.A.E., 2003. *The Origin and Spread of Grass-Dominated Ecosystems during the Tertiary of North America and How It Relates to the Evolution of Hipsodonty in Equids*. University of California.
- Tomlinson, P.B., 1961. *Anatomy of the Monocotyledons*. Oxford University Press, London.