Quaternary International 322-323 (2014) 7–31

Contents lists available at ScienceDirect

Quaternary International

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

Geo-archaeological and geometrically corrected reconstruction of the 1.84 Ma FLK Zinj paleolandscape at Olduvai Gorge, Tanzania

D. Uribelarrea [a,*], M. Domínguez-Rodrigo [b,c], A. Pérez-González [d], J. Vegas Salamanca [e], E. Baquedano [b], A. Mabulla [f], C. Musiba [g], D. Barboni [h], L. Cobo-Sánchez [b,c]

[a] Department of Geodynamics, Complutense University, c/José Antonio Novais 12, 28040 Madrid, Spain
[b] IDEA (Instituto de Evolución en África), Museo de los Orígenes, Plaza de San Andrés 2, 28005 Madrid, Spain
[c] Department of Prehistory, Complutense University, Prof. Aranguren s/n, 28040 Madrid, Spain
[d] CENIEH (Centro Nacional de Investigación sobre la Evolución Humana), Paseo Sierra de Atapuerca s/n, 9002 Burgos, Spain
[e] IGME (Instituto Geológico y Minero de España), Ríos Rosas 23, 28003 Madrid, Spain
[f] Department of History and Archaeology, University of Dar es Salaam, Dar es Salaam, P.O. Box 35050, Tanzania
[g] Department of Anthropology, University of Colorado Denver, 1201 5th Avenue, Suite 270, Denver, CO 80217, USA
[h] CEREGE, Aix-Marseille University, UM34, CNRS, IRD, Europole de l'Arbois, BP80, 13545 Aix-en-Provence cedex 4, France

ARTICLE INFO

Article history:
Available online 8 January 2014

ABSTRACT

A geomorphological, sedimentological, stratigraphic, and geometric study of 30 trenches excavated around FLK Zinj (Bed I, Olduvai Gorge) has enabled the partial reconstruction of the paleolandscape surrounding this site for a radius of ~1000 m. This is the largest sample of geological and archaeological information yet available to reconstruct the topography, ecology, and geomorphology of the Zinj paleosurface and the hominin activities preserved within it. Contrary to previous interpretations, which place FLK Zinj on an isolated and narrow peninsula, it appears that the site was located on the edge of an elevated platform traceable for hundreds of meters. Hominins created FLK Zinj (and other sites, such as the recently discovered PTK and AMK) within the wooded habitats of this platform rather than the more open and grassy environments situated on lower portions of the lacustrine floodplain. Input areas, probably in the form of alluvial fans, existed to the south, following a North-South direction. These input areas are partially responsible for changes in the type sequence. Restricted erosion documented on the wooded platform was mostly caused by runoff processes. An archaeological study of the excavated trenches reveals a sharp contrast in fossil and stone tool density between FLK Zinj and the surrounding landscape, further supporting the contention that the site may have acted as a "central place" where repeated carcass transport, butchery, and consumption took place. Taphonomic studies indicate that at this stage of human evolution, hominins had primary access to carcasses and were not dependent on other carnivores for obtaining meat.

1. Introduction

Leakey (1971) interpreted FLK Zinj (Bed I, Olduvai Gorge, Tanzania) as an example of a prehistoric living floor and home base. Sites similar to FLK Zinj discovered at Koobi Fora (Kenya) served as the basis for Isaac's (1978) "home base" or "food-sharing" model, in which he proposed that Plio-Pleistocene hominins selected specific locations for toolmaking, butchery, and collective food consumption activities. Bunn's (1982) subsequent taphonomic analysis of the site led him to conclude that hominins at the FLK Zinj site had primary access to meat through hunting or power scavenging (Bunn, 2001). This empirical evidence was used by Isaac (1983) to revise his "home-base" model and propose a new one borrowed from ethology: "central-place" foraging. In this model, he claimed that hominins selected specific spots on the landscape to which they repeatedly brought raw materials that were turned into tools, and carcasses that were shared. Potts (1988) argued that FLK Zinj was merely a stone cache used for quick carcass processing, but De la Torre and Mora (2005) convincingly showed the virtual lack of "manuports", and the palaeoecological context of the site, suggests low competition and, therefore, a prolonged stay at the site by hominins during the performance of their activities (see extensive discussion of this in Domínguez-Rodrigo et al., 2007).

* Corresponding author.
E-mail address: uriben@geo.ucm.es (D. Uribelarrea).

1040-6182/$ – see front matter © 2013 Elsevier Ltd and INQUA. All rights reserved.
http://dx.doi.org/10.1016/j.quaint.2013.12.023

It has now been well established that most of the carcass remains accumulated at the site were transported, processed, and exploited by hominins (Isaac, 1978, 1983; Bunn, 1982, 1983, 1991; Bunn and Kroll, 1986, 1988; Potts, 1988; Bunn and Ezzo, 1993; Oliver, 1994; Blumenschine, 1995; Capaldo, 1995, 1997;Rose and Marshall, 1996; Domínguez-Rodrigo, 1997; Domínguez-Rodrigo and Pickering, 2003). For several years, zooarchaeologists debated whether this site was the result of hominins (1) hunting and selectively transporting those carcass parts (Isaac, 1978, 1983; Bunn, 1982, 1983, 1991; Bunn and Kroll, 1986, 1988; Bunn and Ezzo, 1993; Oliver, 1994; Rose and Marshall, 1996; Domínguez-Rodrigo, 1997; Domínguez-Rodrigo and Pickering, 2003; Bunn and Pickering, 2010), (2) transporting complete skeletons from partially defleshed carcasses (Capaldo, 1995, 1997) or (3) scavenging the brain and marrow-bearing bones from defleshed felid kills (Blumenschine, 1986, 1991). This latter interpretation is increasingly questioned by traditional partisans of the passive scavenging model (see recent re-interpretations by Pante et al., 2012) and has been disproved by a wealth of taphonomic analyses (see review and recent reassessment by Domínguez-Rodrigo et al., 2007, 2014). These taphonomic studies have also shown that carcasses were neither partially defleshed when hominins acquired them nor acquired fully fleshed from mass deaths near the site (Domínguez-Rodrigo et al., 2010).

This evidence, coupled with a widespread distribution of cut marks on all anatomical parts, including most importantly the midshafts from upper limb bones, that reflect a diversity of butchery behaviours from dismembering and filleting to evisceration (Domínguez-Rodrigo et al., 2007), clearly indicates primary access to fully-fleshed carcasses that were undisturbed by previous carnivore consumption. Isaac's "central-place" foraging model is therefore reinforced, at least by currently available taphonomic data.

More than 50 years after its discovery, FLK Zinj still is the most important early Pleistocene site for understanding hominin carcass consumption behavior and its relationship to the evolution of the genus *Homo*. The site's paleoecological setting has long been described as a barren lacustrine plain (Cole, 1963; Blumenschine and Masao, 1991). More recent work at the site and its surrounding landscape have revealed that it lay on a topographic high point in proximity to a wetland created by the presence of an underground spring (Ashley et al., 2010). Several trenches excavated on the paleolandscape surrounding FLK Zinj also showed that bone deposition in the vicinity of the site was significantly less dense and, further, that no evidence for carcass butchering was preserved outside the space containing the FLK archaeofaunal assemblage, indicating that butchery was repeatedly carried out at the spot where the site was formed (Domínguez-Rodrigo et al., 2010). The recovery of abundant phytoliths within the FLK Zinj paleosol also showed that the site and its surroundings sampled a closed-vegetation habitat dominated by palm trees (Ashley et al., 2010), which would have provided shelter from predation and easy access to water, both of which would have encouraged prolonged stays by hominins at the site (contra Blumenschine and Masao, 1991).

Independent research carried out near the site has confirmed part of this paleoecological interpretation (Blumenschine et al., 2012). Domínguez-Rodrigo et al.'s (2010) and Ashley et al.'s (2010) work focused on the reconstruction of the paleolandscape to the north of FLK Zinj, but they did not provide enough information to reconstruct the paleolandscape to the south of the site. The present work expands Ashley et al.'s (2010) previous work and incorporates a more detailed reconstruction of the northern, eastern, and southern portions of the FLK Zinj paleolandscape.

The lower and middle sequence of Bed I around FLK is dominated by lake-margin facies, corresponding to a shallow lake with predominantly fine-grained sedimentation. Sedimentation is dominated by decantation of clay in mudflats with few or no evaporitic sedimentation (Hay, 1976). The environmental bends are wide and the lateral changes very progressive. Shallow lakes are typically considered to be flat and homogeneous landscapes, which matched well with earlier interpretations of FLK Zinj's paleoecological location (Leakey, 1971; Hay, 1976; Blumenschine and Masao, 1991). With the exception of saline lakes and lakes with carbonatic sedimentation, shallow lakes form mudflats and hardly show any differences between margin and central areas (Hutchinson, 1957). Only detailed survey within the frame of geo-archaeological research allows sub-zones with subtle differences in topography and sedimentary/erosive processes to be distinguished. In the FLK area, at least two of the geomorphological and environmental zones in lakes (Glen and Kelts, 1991) can be identified in lowermost Bed I: 1) A supra-littoral zone, dominated by subaerial exposure, rooted vegetation, and controlled by the water table; 2) A littoral (lake-margin) zone, which is a more complex area controlled by lake level variations and, therefore, comprises both aerial exposure and flooding features. Generally, this latter setting is an oxygenated and photic environment where sediment input occurs and would have been less suitable for hominin activities. This areal division was already established in the first reconstruction of the Zinj paleolandscape (Ashley et al., 2010; Domínguez-Rodrigo et al., 2010). These authors discriminated two main zones, the topographically higher supralittoral, where a palm and *Acacia* woodland developed (FLK-Zinj proper), and the topographically lower littoral with a freshwater spring surrounded by a wetland (FLK-NN) (see also Ashley et al., 2010).

Table 1
Description of the sample of trenches used for this study and their content of bones and stone tools. All specimens are longer than 2 cm. The geological columns indicate trenches that were sampled for stratigraphic and sedimentological analyses.

	Area (m^2)	Lithics		Bones		Used for geological study		Petrography
		Upper	Lower	Upper	Lower	Stratigraphy	Sedimentology	
FLK Zinj								
Site area								
FLKT1	12	5	2	14	7	x	x	x
FLKT2[a]						x		
FLKT4	4	2	0	13	2	x		
FLKT5	5	0	0	0	2	x		
FLKT6b	2	0	0	2	0	x	x	
FLKT7	4	1	0	0	0			
FLKT10	1	0	0	2	0	x	x	
Wetland (FLKN-FLKNN)								
Core								
FLKNWT1	16	1	3	20	31			

Table 1 (*continued*)

	Area (m^2)	Lithics		Bones		Used for geological study		Petrography
		Upper	Lower	Upper	Lower	Stratigraphy	Sedimentology	
FLKNWT2	9	0	0	7	0			
FLKNWT3	1	0	0	0	0			
FLKNWT4	1	0	0	0	0			
FLKNN2	2	0	0	0	0	x		
FLKNN1&2						x	x	x
Edge								
FLKN4	5	0	0	1	4	x		
FLKN5	4	11	0	6	3	x		
FLKN7	4	0	0	4	0	x		
FLKN8	2	0	0	1	0	x		
FLKN10	2	2	0	1	0	x		
South Zinj								
Proximal sector								
S1	1	0	0	0	0			
S2	2	0	0	0	0	x		
S3	2	0	0	0	0	x	x	
S4	1	0	0	0	0	x	x	
S6	1	0	0	0	0	x		
S7	1	0	0	0	0	x	x	x
S8	1	0	0	0	0	x		
S9	2	0	0	2	0	x		
S17	2	0	0	0	0	x		
Distal sector								
S15	8	0	0	41	0	x		
S16	2	1	2	2	0	x		
Eastern Sector								
E1	5	1	1	4	1	x		
E2	4	1	0	1	0	x		
E3	1	0	0	0	0	x		

[a] The Zinj clay had been removed by prior excavations. Used only for geological purposes.

Table 2
Nomenclature of geological units and archaeological levels. Information on sample number and analysis type is also shown.

Leakey, 1971; Hay 1976				Present work		Analysis		
FLK-NN		FLK Zinj		FLK-NN, FLK-N, FLK-Zinj, PTK		Sample	Texture	Petrography
Geology	Archaeology	Geology	Archaeology	Geology	Archaeology			
Hard buff-yellow tuff. Tuff 1C		Hard buff-yellow tuff. Tuff 1C		Tuff 1C		100	•	•
						101	•	
						111	•	
Clay with limestone nodules	(FLKNN-1) "Equiv. Zinj level"	Green silty clay	(Level 22)	Zinj clay	(Zinj upper)	103 (Zinj)	•	
						123 (FLK-NN)	•	
						PTK-02	•	
					(Zinj lower)	104 (Zinj)	•	
						124 (FLK-NN)	•	
						PTK-01	•	
Fine-grained buff-white tuff	(FLKNN-2) OH-7, OH-8 inside	Fine grained whitish-buff tuff		Reworked tuff CHT	Level 3 in PTK OH-7, OH-8 equiv.	105		•
						106	•	
Clay	(FLKNN-3) OH-7, OH-8 over	Silty clay		Tuffaceous clay	Other units in PTK	107	•	
Clay		Tuff		Local reworked tuff (only in Zinj)		108	•	
						114	•	
		Clay		Tuffaceous clay		122	•	
				Clay tuff		112, 113	•	
Tuff 1B		Tuff 1B		Tuff 1B				•
Bentonitic clay		Bentonitic clay		Green waxy clay		119	•	

The Olduvai Lake was a low energy environment, with very little capacity to move sediment. Sedimentation occurred mainly by decantation of clay, usually transformed from volcanic sediments (Hay, 1976). The geological record consists of clayey facies with a great lateral continuity and normally diffuse limits due to the homogeneity of the sediments and the intense bioturbation. The rarity of coarse-grained sediments is noticeable in lower and middle Bed I around the FLK sites. With the exception of some tuffs, most of the sedimentation consists of clay (70%) and only 1% is sand. These values suggest a very low energy environment. In lakes of this sort, because of very low slopes, even sediment input takes place through terminal fans (Turnbridge, 1984; Kelly and Olsen, 1993). Although coarse-grained sediments are available to the southeast (Hay, 1976), an extremely low gradient precluded their transport to FLK and its surroundings. As in other lakes associated with the African Rift, the Olduvai Basin experienced important inputs of pyroclastic sediments, transported generally by the wind or by drainage runoff systems. This volcanic material can become mixed with lacustrine sediments to form reworked tuffs. The shallow lacustrine condition favors intense bioturbation that makes the differentiation of internal structures difficult.

Lakes are dominated by three primary factors: climate, geologic context, and biota (Gierlowski-Kordesch and Kelts, 1994). Important changes in landscape (paleosurface) will be caused by fluctuation of the base level, which is controlled in turn by climate and tectonics. Therefore, a tectonic movement or an increase in aridity causes the descent of the lake level, stimulating the retreat of the lake margins towards the central area. Withdrawal and retrieval events will expose a wide surface in the lake-margin. The descent of the base level causes an increase of the potential energy, reactivating the whole drainage network and the surficial erosive processes. The geomorphological response will be more or less evident depending on the capacity of the drainage network. An increase of the base level or lake transgression, on the other hand, will produce the deposition of more lacustrine facies and the interruption of the processes linked to subaereal exposure (e.g., pedogenesis). New fine sediment layers will simultaneously adapt to and smoothen the previous surface and underlying topography.

In addition to these primary factors, lake morphometrics should also be highlighted, not only in sedimentation processes and stratigraphic architecture (Frenegal-Martínez and Meléndez, 2010), but also in landscape formation. Specifically, in a shallow lake-margin area, small differences in elevation and slope can determine the lake zonation, the time of subaerial exposure, the drainage pattern, and other associated processes. Frequently, the reconstruction of such subtle differences cannot be based on sedimentology alone.

The paleoenvironmental reconstruction presented here is based on detailed geological work and provides valuable information regarding the paleotopography of the landscape north, south and east of FLK Zinj. A large number of trenches sampling a paleolandscape spanning thousands of square meters uncovered an extensive paleosurface blanketed by Tuff IC. This paleotopography is devoid of any indication of fluvial activity or other high-energy processes in the vicinity of FLK Zinj. Most of the bed contacts are macroscopically laminar and non-discomformable on the FLK Zinj paleosurface, and they adapt to previous paleosurfaces. Discomformable contacts have been observed overlying the paleosurface covered by Tuff IC, as minor exceptions on the Zinj paleosurface, several dozens of meters away from FLK Zinj itself. The lack of typical fluvial structures and the identification of similar erosive topographies in modern lacustrine floodplains suggest that erosion south of FLK Zinj resulted as a combination of lacustrine transgressive cycles and rills formed by wet season run-off and sheetwash processes. Hominin activity on the landscape south of FLK Zinj is still less conspicuous than that documented at the site itself, again stressing the exceptional nature of the bone and stone tool accumulation unearthed there. The discovery of a dense concentration of fossils and stone tools at the southernmost end of the tuff IC outcrops in the Side Gorge (Philip Tobias Korongo, PTK), in which bones occur in densities of dozens per square meter, also contrasts with the surrounding paleolandscape where bones occur in the form of scatters, with densities on average smaller than five bones per square meter. PTK and FLK Zinj are, thus, dense patches created by hominins on a non-productive landscape where bone deposition by natural processes contrasts sharply in density with those unearthed at these sites.

The paleotopography presented here will correct previous descriptions of FLK Zinj as a narrow peninsula, (~ 50/100 m wide) formed by fluvial incision, (Blumenschine et al., 2012), which was due to the limited information available by an insufficient number of sampling trenches. The present work will show that the FLK Zinj-PTK strip was a topographically high platform with no evidence of large rivers crossing it or high-energy processes affecting it.

2. Method and sampling

2.1. Geological study: sedimentary, stratigraphic and geomorphological analyses

The paleotopographic and paleogeomorphological study presented here was based on three different techniques: a) stratigraphy and facies analysis, b) geomorphology, and c) structural tectonics. The stratigraphic analysis was carried out using information retrieved from 28 excavated trenches (Table 1) and 5 exposed sections between the FLK and KK faults (Fig. 1). Most of the trenches are concentrated near the classic Bed I sites of FLK-NN, FLK-N and FLK-Zinj, all of which are located on the southern margin of the main Gorge. The stratigraphic sections published by Leakey (1971), corresponding to FLK Zinj and FLK NN (her Figures 19 and 23 respectively), were also compared to the data in our study. Facies analysis was carried out by analyzing the type of sediment (texture and composition), their internal structures, and the boundaries and relationships with contiguous exposures. Special emphasis was laid on the description of the contact of tuff IC and the underlying Zinj paleosurface. Erosional shapes, small deposits, or evidence of subaerial exposure just under tuff IC denote the active processes occurring during the formation of the Zinj paleolandscape. Here, we will refer to the paleosurface underlying tuff IC as the Zinj paleosurface or Zinj paleolandscape. An ubiquitous horizon throughout the studied area is what we call “Zinj clay”, which is equivalent to layer 22 from the FLK Zinj sequence as described by Leakey (1971).

Facies description was carried out in the field and subsequently supported with laboratory analysis. Grain-size analysis allows quantifying the size distribution of particles, giving accurate information of the sedimentation processes (see Supplementary Information). Grain size and petrographic analyses were made with a Robinson’s pipette at the CENIEH (Centro Nacional de Investigación de la Evolución Humana) and in the Geodynamic laboratory of the Geology Faculty of the Complutense University of Madrid. Correlation was established combining all these criteria (see Table 2). Finally, petrographic analyses were carried out in several tuffs to quantify post-sedimentary compaction, although no conspicuous evidence of compaction was identified during fieldwork.

The analysis of compaction is of utmost relevance because inferences of different degrees of compaction can lead to over-estimations or under-estimations of landscape features (e.g., channels and slopes) depending on how compacted sediments are. For instance, Blumenschine et al. (2012) have reconstructed deeper fluvial channels on the FLK Zinj paleolandscape than stratigraphically documented, based on inferred high compaction values (145–205%, following Hay, 1976). Determining the accuracy of those compaction values is crucial to determine if the reconstruction of the shape of those channels and strata contacts is correct.

The geomorphology of the landscape was obtained through the topographic documentation of the main geological units, such as the surface of the basalt, the marker tuffs, the Zinj clay, and several other marker units (see below). Measurements were done with sub-centimeter precision using a laser total station (TOPCON) within a triangulated network of 9 stations along the whole study area (Fig. 1). A total of 480 control points have been taken along the outcrops in the FLK-KK block. Spatial data were analyzed with GIS software (ArcGis 10.1). Uneven density and spatial distribution of data make it difficult to interpolate what is a wide and complex surface; however, the projection of X-Y-Z values enables the reconstruction of accurate geometric sections and calculations of real distances, depths, and slopes. A very accurate 2D section results from data aligned along FLK-NN, FLK-N, FLK-Zinj, Maiko Gully, the Road and the Junction areas (see Fig. 1). The correlation among

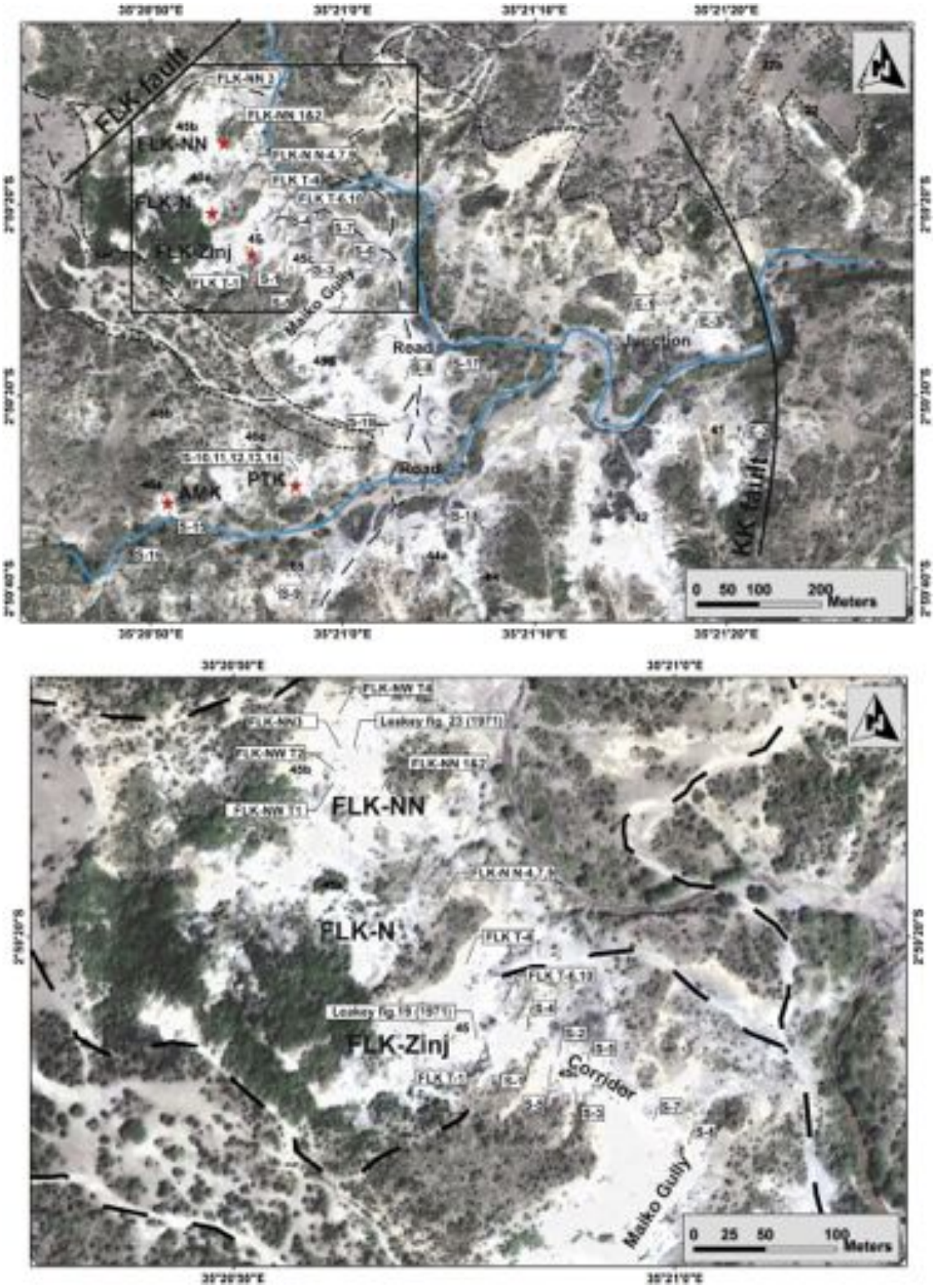

Fig. 1. Map of the study area, showing locations of TOPPP trenches exposing the Tuffs IB-IC interval. Below, close-up of the FLK-NN, FLK-N and FLK-Zinj area. Latitude and longitude are in degrees, minutes and seconds. Intervals of 10 s. Datum: WGS_1984. Background: Google Earth images.

units was also done using the resulting geometry, instead of the traditional stratigraphic sections, where correlation is "hung" on one arbitrary layer.

Olduvai Gorge has undergone synsedimentary and post-sedimentary tectonic movements, both of which can distort the palaeolandscape geometry. Tectonic deformation has two components: (1) folding and faulting of the sedimentary sequence and (2) rotation of the basement. To calculate them properly, the change of thickness of the Olduvai Beds as well as the displacement of fault escarpments have been taken into account. This goal was

complicated by the uneven distribution of outcrops along the FLK-KK block.

The study area corresponds to the block defined by the normal FLK and KK faults. These North-South faults affect the actual tilting of the entire block. Slopes and elevation differences must not be considered along an East-West direction before any correction. In contrast, North-South topographic values are only slightly affected by the main tectonic movement. The base of the FLK-KK sub-basin consists of pahoehoe lavas and olivine basalts. Numerous thin, tongue-like 30 cm to 1 m thick sheets may be stacked on top of one another, as observed near HWK (loc. 42), where there are many elongated lava mounds or tumuli, with a variable height of 1–4.5 m (Hay, 1976). In order to determine the exact paleotopography of the lava surface, it would be necessary to perform a geophysical survey, as the outcrops are randomly distributed. As a preliminary approach, the topography of the basalt surface was estimated with a total station between the FLK and KK faults. In such survey, the areas affected by the modern Olduvai river incision have been avoided.

Sedimentary records can be altered by post-sedimentary deformation. This deformation can be tectonic (faulting and/or folding) or mechanic compaction. The former distort the topography (e.g., slopes and heights), whereas the latter also modify internal sedimentary structures (stratification, layer contact or fabrics). The interpretation of a deformed record would lead to biased reconstructions of the paleolandscape. In this situation, a geometric correction of the deformation is required prior to the interpretation of the paleolandscape.

Prior to reconstructing the Zinj paleolandscape, tectonic movement has to be considered, specifically, the possible rotation of the FLK-KK block. The FLK and KK faults affect directly the FLK paleosurface tilting, although other larger faults and regional movements should also be considered. In these cases, the more wide the tectonic movement is, the more difficult it is to measure it. The precise analysis of tectonic movements in Olduvai is also difficult due to the absence of topographical maps. Even Hay's (1976) sections are not useful for this purpose, because total thickness data in sections are not accurate enough. That work should be carried out in the field, by measuring directly the exposed fault steps and the thickness variation of the Beds.

The most evident tectonic feature in the study area is the wall of the KK normal fault. It is 12 m high and the restitution of this vertical movement would suppose 0.52° of FLK-KK block rotation. But this movement was not considered, since the KK fault corresponds to a pop-up structure with the same step (12 m) as the 4th fault, (also measured with total station). Therefore, wider or regional movements should be invoked.

The main thickness variation corresponds to Bed III, but measuring it in the field is very difficult because of the irregularity of the basalt, the absence of Bed III sections in the northern side of the study area, and the unworkable cliffs to the south (i.e. locality 40b). Due to these difficulties, the geometric correction will be based on stratigraphic, sedimentological, and geometric criteria. To rotate the FLK-KK block, counterclockwise, the following criteria have been used to create a quantitative model:

a) The maximum energy area (S-8 and S-17) must be the lowest part of the section, as a local thalweg.
b) The maximum lacustrine facies (E-1 and E-3) must also be in the lower part of the basin. This facies can never be above less lacustrine areas, such as the FLK sites.
c) The actual geometry of the sequence must be conserved. Namely, the entire block FLK-KK should be rotated but not deformed.
d) Tuff IC should be left as horizontal as possible, as it preserves a palaeosurface developed along the margin of a shallow lake. The aim was to reduce the maximum height difference.

2.2. Archaeological study: fossil density and distribution analysis

The FLK Zinj site occupies the southernmost gully of the area comprised by the FLK sites (FLK, FLK N and FLK NN) (Leakey, 1971). The FLK NN 1 paleosurface was pene-contemporaneous with the FLK Zinj paleosol (Leakey, 1971). Since FLK NN occupies the northernmost part of the area covered by the three sites, previous work by TOPPP (The Olduvai Paleoanthropology and Paleoecology Project) sampled the area between FLK Zinj and FLK NN by excavating large test trenches between them in outcrops that contain the waxy clay (previously referred to as Zinj clay) sediments overlain by Tuff IC, which capped the FLK Zinj archaeological level time period (Domínguez-Rodrigo et al., 2010). Recent excavations in the area have exposed a larger portion of the paleolandscape, completing some gaps in between trenches. A summary of all the previous trenches was reported in Domínguez-Rodrigo et al. (2010). All previously and newly opened trenches opened in the northern sector are listed in Table 1, resulting in a total of 30 trenches excavated between 2008 and 2013. During this research, a new high-density site (PTK) was discovered ~500 m away from FLK Zinj on the same paleosurface. This site will not be used in the present study since it is currently being excavated.

Our work has sampled a diameter of ~1000 m of Zinj paleolandscape, significantly more than previously sampled (Domínguez-Rodrigo et al., 2010; Blumenschine et al., 2012). This paleolandscape has been divided into different areas. The Wetland Area is located between FLKN and FLKNN, where a spring system was identified (Ashley et al., 2010). This area was subdivided into the core wetland area (comprising FLKNN and FLKNW) and the wetland edge (FLKN). South of the FLK Zinj gully, the southern sector was divided into a proximal section (~500 m south of FLK Zinj) and a distal sector (the area covered by the Zinj paleosurface on the Side Gorge west of PTK). Then a stretch of paleosurface comprised between the junction area and the KK fault was denoted as the Eastern Sector.

Excavations of these trenches involved the use of large tools (picks and shovels) to remove the overburden of sterile sediment across thick stratigraphic sequences and small tools (trowels, brushes, screwdrivers, and small wooden and metal digging sticks) when reaching any fossiliferous level. Dry sieving with 5 mm mesh was systematically carried out. Only selected sediment for microfaunal research was wet-sieved with a finer mesh (1 mm). The lithological criterion (excavation followed natural layers) was superior to the artificial spit criterion in deciding the way the excavation preceded. Artefacts and fossils were carefully documented including their orientation and inclination. Bone counting included every meso- or macromammal specimen (microfauna are excluded here) longer than 2 cm.

3. Results

3.1. Geological study

3.1.1. Lower and Middle Bed I. The FLK-KK Block

In general, the surface of the basalt slopes 1.8% from south to north. It has a strong influence in the sedimentary record, not only in thickness but also in grain size and facies. There is a progressive increase of the thickness of the Bed I deposits to the North, and the sedimentary texture tends to be finer. The successive layers form "onlap" geometries over the basalt. Tuff IC overlies directly the basalt in several points along the south side of the Main Gorge.

Regarding the composition of the deposits, the proportion of volcanic components increases southward, in accordance with the expected input of volcanigenic sediment from the footslopes of Lemagrut to the south. Reworked volcanic sediments reached the FLK-KK sub-basin through alluvial fans, probably similar to those descending along the Lemagrut slopes nowadays (Hay, 1976).

When examined in detail, the basalt surface is very irregular. Local slopes vary from 1% to 10% along the entire study area. The steepest slope is 45%, corresponding to the margins of large lava thongs in S-18 (Fig. 1). There are also local depressions, such as the one located below the Zinj site, which is 3.5 m deep. This could be due to a concave base between two lava tongues, but it also matches the location of a minor fault located at FLK Zinj. It has a complex movement resulting in the deformation of tuff IB. The different sedimentary units tend to adapt to this purported concave shape.

3.1.2. Type section. Spatial distribution of sedimentation and associated processes

A Type Section was constructed that included the main sequence between Tuffs IB and IC, which could be traced along most of the transect line between FLK Zinj and PTK. The main units identified are, from bottom to top: tuff IB, clayey tuff and tuffaceous clay, intermediate reworked tuff (Chapati tuff, CHT), the Zinj clay, and Tuff IC (Fig. 2). Due to the irregularity of the basalt, the thickness of the sequence varies from 6 m to 30 cm and every identified unit overlies the basalt in someplace. A description of each unit (from older to younger) is as follows:

3.1.2.1. Tuff IB, in the vicinity of FLK, is an ash-fall tuff, both primary and reworked, that is 50 cm to 1 m thick (Hay, 1976), and has been dated to 1.845 ± 0.002 Ma and 1.839 ± 0.005Ma in the western part of the Gorge (McHenry, 2005). Here, it has been identified as a 15 cm to 1 m thick, primary, fining upwards, and laminated tuff. It is yellow and contacts are always sharp and horizontal. It was identified as a one-meter thick deposit by Leakey (1971) at the Zinj trench just above the "bentonitic clay with desert roses crystals". However, in the trenches opened by TOPPP in the same place, Tuff IB is only 50 cm thick. In contrast, in the FLK-NN trenches, this marker tuff is nearly 2 m thick, but decreases in thickness sharply towards the east. It is composed of a coarser term in the bottom and a very thin laminated one on top. That laminated term increases its thickness from 10 cm at FLK-Zinj to 80 cm at the KK fault.

Tuff IB overlies a waxy clay identified as bentonitic clay by Hay (Leakey, 1971). It is olive color and looks massive, probably due to abundant slickensides and bioturbation. At FLK-NN, FLK-N, and FLK-Zinj, this stratum has numerous desert roses of calcium carbonate close the top of the layer (10–15 cm in thickness).

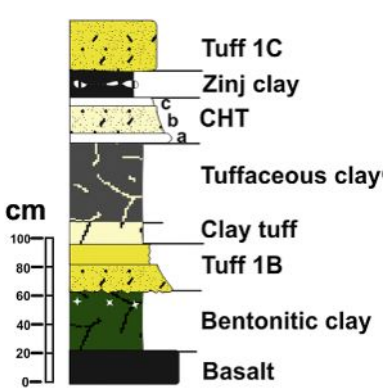

Fig. 2. Schematic type section corresponding with the main units described in the lower-middle Bed I in the area sampled, from the basalt to Tuff IC. For legend see Fig. 8.

3.1.2.2. Clay facies (clayey tuff and tuffaceous clay). Clay lake-margin facies are formed primarily of clay and a variable proportion of ashes, silt, and fine sand. Pure clay is therefore difficult to find. In all cases, bioturbation is very intense and it tends to distort the boundaries of different clay units. In the field, two main units can be distinguished based on the proportion of tuffaceous material: a) Clay Tuff and b) Tuffaceous Clay. They are considered as "Clay facies" because of their similar origin and nature.

The Clay Tuff is not very thick and usually appears above tuff IB. It has a light and compact aspect, with pale yellow (5Y 8/2) and light olive grey colors (5Y 6/2) with 5% dark components. It has some porosity (<1 mm) and appears intensively bioturbated with carbonated roots. The textural classification is clay, composed of 67% clay, 25% silt, and 6% sand. The lower contact is planar and the upper contact is occasionally irregular, perhaps as a result of erosive processes subsequent to its deposition.

Tuffaceous Clay is the most abundant sediment between tuffs IB and IC. It usually appears above the Clay Tuff. The color is green olive (5Y 4/2) and it has fragments of tuff and mudclasts. It is compact and massive, with numerous slickenside, as well as root, marks. The intensity of the dark color increases towards the upper contact, probably due to pedogenetic processes. No sedimentary interruptions or internal lamination can be observed due largely to the effect of bioturbation.

Both sediments correspond to low energy environments and decantation processes. Shallow water and subaerial exposure is documented by the abundant root marks. At FLK-NN, the top of this tuffaceous clay is the surface of OH-7 and OH-8, the archaeological level of FLK-NN3.

3.1.2.3. Chapati Tuff (CHT). Overlying the Tuffaceous Clay and below the Zinj clay, there is a laminated reworked tuff. Due to its multilayer composition, this intermediate tuff has been named the Chapati Tuff (CHT). It can be used as a marker layer because it is present along the whole study area. It is always composed by 3 main layers (Fig. 3), from bottom to top: a) a thin layer (1–5 cm), always laminated, white to light yellow color. It is composed of a tuffaceous sand and silty sand, interbedded with laminates (1 mm–20 mm thick) of green tuffaceous clay; b) a thicker layer (10–20 cm), gray colored and massive. It is composed of a tuffaceous clay with abundant fine to medium-sized tephra fragments, rounded and matrix-supported; c) a thin, massive, white tuff layer (1–3 cm) with very thin laminates of carbonate.

Layer B is a matrix-supported vitric tuff. The pyroclastic rock is formed by 20% sharp juvenile crystals (<2 mm), mainly anortoclase, hornblende, augite, and titanomagnetite. There is a 15% component of cognate fragments, such as rounded lava fragments and glass lapilli. Quartzite clasts of metamorphic rocks appear as accidental fragments (<1%). There is a 64% component of vitric matrix with abundant plagioclase microlites and titanomagnetite. Porosity is less than 1%. This tuff has a low selection, in which crystals and cognate fragments are floating in the vitric matrix. Thus, there is no evidence of compaction of this sediment.

Although grain size within this unit can change along the study area, the proportional thickness of the three layers, their lamination, and their relative position under the Zinj clay remain constant. The basal contact is always sharp, horizontal, and laminated. This reworked tuff was formed under low energy events as evidenced by the small grain size and the association with clay, even in the laminated layer. The origin of CHT is complex, as it comprises several types of sediments and structures. It could have a direct relationship with volcanism, as it increases in thickness towards the east as do the other marker tuffs in Bed I. At the 4th fault, it is 30 cm thick.

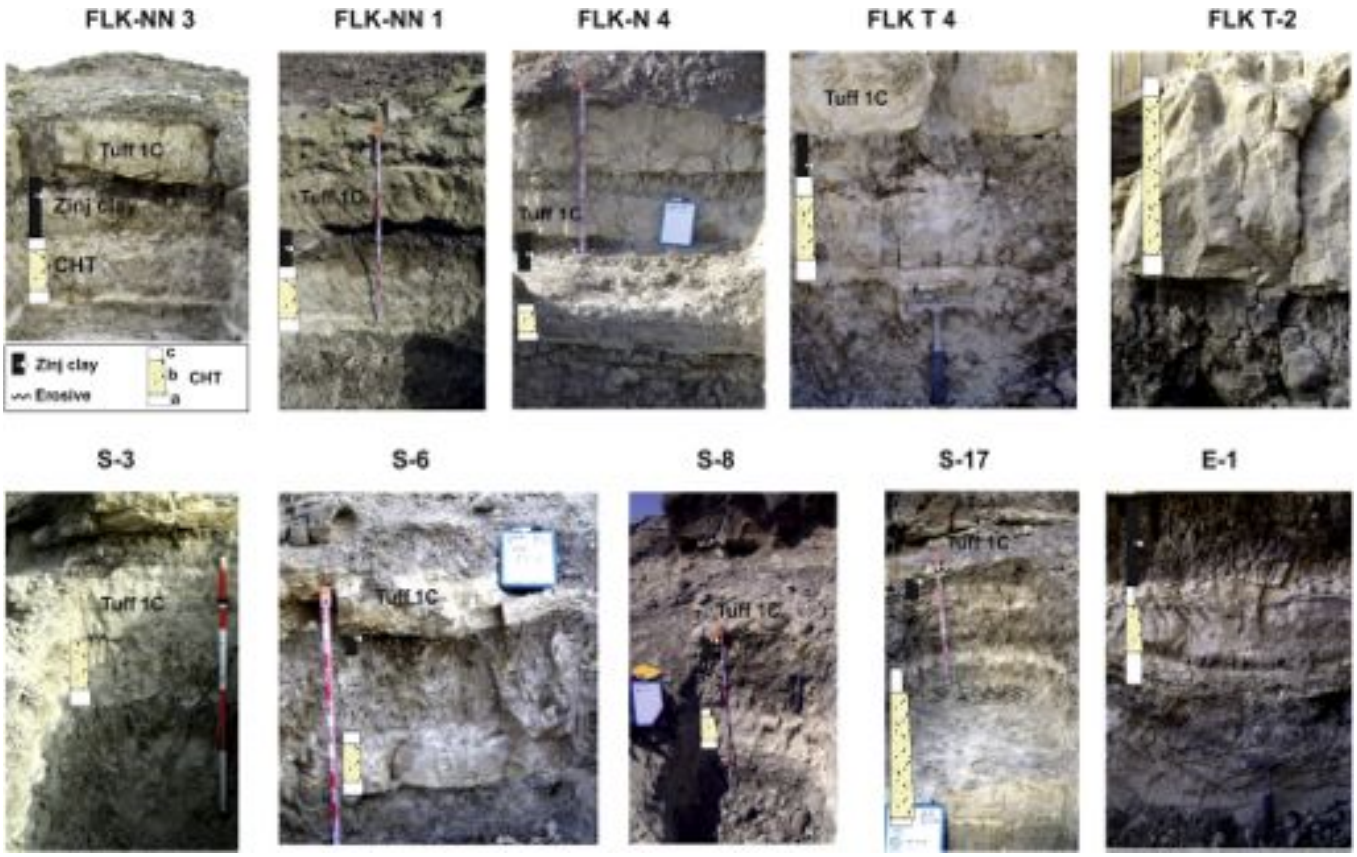

Fig. 3. Photograhps from different trenches showing the stratigraphic location of the Chapati Tuff (CHT).

This tuff was described by Leakey as a fine-grained whitish-buff tuff at FLK Zinj and fine-grained buff-white tuff at FLKNN. It overlies the archaeological level FLKNN 3 (OH7 and OH8) and contains level FLKNN2. It is also the sedimentary context where another archaeological level is documented at PTK (see Table 2).

3.1.2.4. The Zinj clay. The Zinj clay overlies CHT, usually with a sharp contact. This clay corresponds to the archaeological level 22 at FLK Zinj or level 1 at FLKNN. It actually consists of two clay deposition events, each containing separate archaeological levels. The similarity of both types of sediments makes the identification of both archaeological levels difficult. Leakey (1971) grouped them into just one. The upper part of this unit is more earthy than the lower, which is more waxy and always contains more clay. At FLK Zinj, for example, the lower unit has 89% clay and the upper 71%. At FLKNN, the amount of clay increases in both the lower and upper units to 95% and 85%, respectively. This pattern is also seen in trench S-10 (PTK), where the upper Zinj clay level is composed of 59% clay and the lower 73%. Color varies in these levels, but tends to be darker in the lower (dark olive grey 5Y 3/2) relative to the upper (olive 5Y 4/2).

Carbonate nodules frequently accumulate between levels and are more common and continuous to the West at FLKN and especially at FLKNN. The Zinj clay is widely represented along the entire FLK-KK block and even eastward of the 4th fault, although it only contains archaeological remains in the more elevated northwestern area.

This clay represents a low energy environment corresponding to lake-margin sedimentation during a high stand of the lake. To the east, the proportion of clay increases as well as its thickness (E-1 and E-3). In that area (Junction), the Zinj clay is an olive waxy clay, massive and with plenty of slickensides. This is the area most influenced by lake sedimentation.

3.1.2.5. Tuff IC. Tuff IC is a crystal tuff that erupted as an airfall tephra. It has conformed nearly perfectly to the underlying topography and maintains a constant thickness throughout the study area. Eighty percent of this pyroclastic rock is sharp juvenile crystals (<2 mm), mainly of anorthoclase, hornblende, augite, and titanomagnetite. Cognate fragments, such as altered glass lapilli, make up 5% and quartzite clasts of metamorphic rocks occasionally appear as fragments (1%). There is only a 9% vitric matrix and less than 1% of closed porosity.

This tuff has low selection and contacts between crystals are well-defined. No deformation of cognate fragments and cementation is visible. Thus, there is no compaction evidence in this unit.

Tuff IC is in direct contact with the archaeological remains of the upper Zinj level. It preserves the paleosurface of the landscape intact and therefore allows a unique opportunity to reconstruct the surficial processes that were contemporaneous with the formation of the sites. Importantly, it also preserves the geometry of the contacts and the unaltered sedimentary deposits, as the lower contact of Tuff IC is nearly always planar and sharp. The infrequent undulations on the paleosurface, such as the shallow channel-shaped contacts in trenches FLK-N 4, S-7, S-8 and S-17, are due to post-depositional processes.

3.1.3. Local variations

3.1.3.1. Tufa at FLK-NN

A spatially restricted but environmentally important tufa developed within the Zinj clay at FLK-NN. The resulting

carbonate mound probably stood out in the homogeneously horizontal landscape. Its origin is explained by the presence of a meteoric water source associated with the FLK fault (see Ashley et al., 2010; Domínguez-Rodrigo et al., 2010). This freshwater spring is in direct relationship with the wetland identified around FLK-NN and is contemporaneous with the Zinj level. It is difficult to establish the lateral limits of the Zinj clays within the tufa mound, as they are mixed with calcium carbonate that form lenses and carbonate-rich clay layers. The mound margins themselves are discontinuous due to trampling and interbedded with the surrounding clay. The base of the mound lies on a clay layer, which may be the lower Zinj level. The bands of clay and carbonate inside the mound, and the presence of surficial water (the wetland), suggest decantation rather than a precipitation origin for the carbonates, although subaerial exposure of the spring would have favored the precipitation of calcium carbonate. Perhaps the spring terminated during one of these cycles when a thin clay layer (2–3 cm) formed on top of the mound. The geometry of these elements is complex and irregular, however, and it is certainly possible that other water sources of various sizes existed throughout the FLK fault area.

3.1.3.2. Sediment input area

In trench S-18, Tuff IC lies directly over volcanic sandstone, which is the only location in the entire study area where Tuff IC does not lie atop fine sediments. In S-18, it is massive, pale yellow, and rootmarked. No lamination, lag, channel features, or coarsening upwards have been identified. This section could represent an alluvial fan coming from the south towards the north or northeast, following the direction of a large lava tongue in S-18 (4.5 m high).

Fortunately, and despite the rarity of outcrops in this sector of the gorge, the zone of input sediment can be traced about 150 m north of S18. In S-8 and S-17, coarser sediments and thicker sections occur between tuff IB and IC. More specifically, the tuffaceous clay and the laminated layer of Tuff IB are replaced by massive silt. The intermediate unit of CHT is composed of a 15 cm thick conglomerate of tuff fragments. Clasts are rounded, matrix supported, and less than 2 cm in diameter. In S-17, between CHT and Tuff IC, 30–40 cm of tuffaceous clay and two reworked tuffs are documented (Fig. 3). Above it, the Zinj clay contains mud clasts and small tuff fragments. Finally, Tuff IC shows shallow channel features (15 cm in depth) eroding into the Zinj clay, which is not well preserved in the Maiko Gully and the Road area (S-6, S-8 and S-17).

This input alluvial system was active at least between the Tuff IB and Tuff IC interval, but shows gradually less influence in the sequence. Tuff IB is partially eroded and silt, rather than clay, is present. Later, CHT was not replaced, but it is coarser than at other places, and finally, the Zinj clay was deposited but partially eroded. Especially during FLK Zinj times, the capability of this area to move sediment downstream was very limited. At the same time, volcanic sand was deposited in S-18 and clay in S-17. As discussed below, this represents the lowest point in the paleolandscape, so a stream could possibly have flowed through S-17. However, the homogeneity of sediment in S-18 and S-17, the absence of current features, and the reduction of energy all point to an alluvial fan rather than a fluvial system.

Another input area can be placed around S-15, also coming from the south. It transported alternating layers of tuffaceous silt and volcanic reworked sands before the deposition of Tuff IC.

3.1.3.3. Water runoff area

East of FLK-Zinj, from S-4 to S-7 (Corridor), the thickness of the sequence between Tuffs IB and IC decreases because of erosional processes. In S-4, for example, Tuff IC directly overlies CHT rather than the Zinj clay. In S-3 and S-5, the upper part of CHT is also eroded and, finally, in S-7, Tuff IC overlies the Tuffaceous Clay. These erosional processes are probably due to water runoff and rills. With the exception of Trench S-7, where a small channel feature can be identified (Fig. 4), the contact of Tuff IC is sharp and flat. Even in S-7 no evidence for channel infilling prior to the Tuff IC deposit was found. Other erosional features, again probably due to the presence of rills, have been identified at FLK-N (FLKN-7), where Tuff IC overlies the lower Zinj clay (Fig. 5).

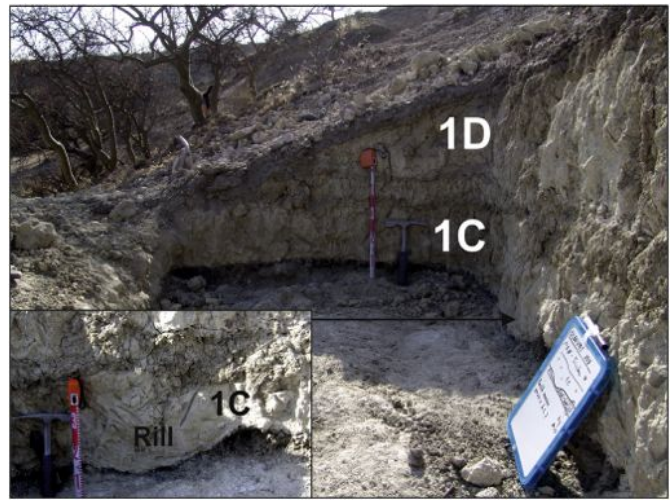

Fig. 4. Trench FLK-N7. Contact between the tuffaceous clay and Tuff IC.

3.1.3.4. Reworked tuffs

Locally, thin layers of reworked tuff occur within the Tuffaceous Clay unit. They are composed of fine to medium-sized sand tephra, silt, and clay. The tephra is always rounded and well sorted. Although the basal contact has been eroded slightly, these tuffs are always massive. They fill local shallow depressions and are invariably thinner and structurally different from CHT.

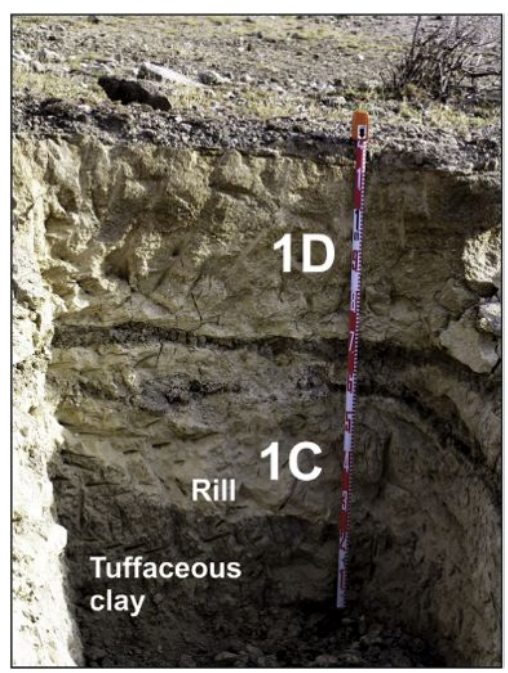

Fig. 5. Trench FLK S-7. Contact between the Zinj clay and Tuff IC. Note the horizontal and sharp contact and rill channel.

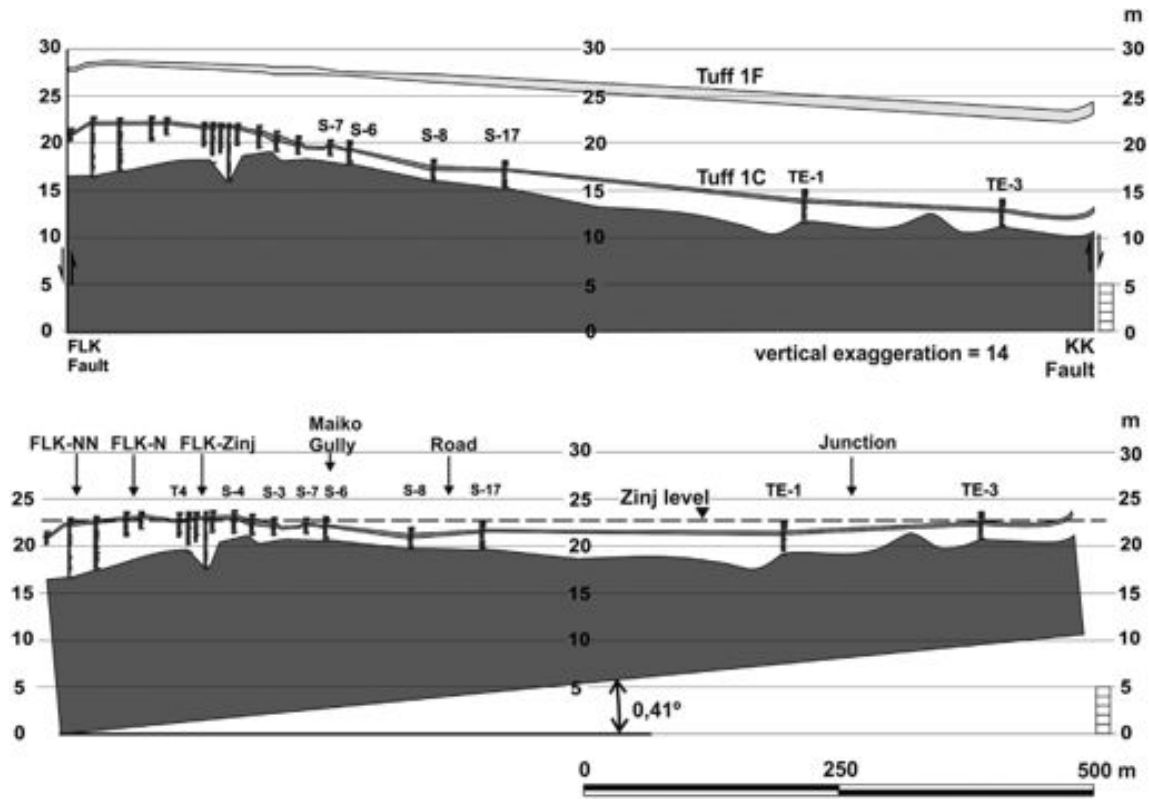

Fig. 6. Geometric correction of the FLK-KK block. Above, the actual position of the analyzed sections. Geometries of basalt and Tuffs Ic and IF are also based on control points along the study area. Below, the resulting geometry after applying an anticlockwise rotation of 0.41°. See text for description.

Unfortunately, they cannot be used as marker layers due to their spatially restricted distribution. They also bear no relationship to any archaeological level, although punctuated events of surface water movement, always occurring before the formation of the CHT (except at S-7 and FLKT 6, where a local minor tuffaceous layer overlies it), can be identified. The best examples can be seen in the FLK Zinj site area and in trenches S-17, E-1, and E-3.

3.1.4. Geometry correction

Following the guidelines laid out in the Methods section, the FLK-KK block has been rotated 0.42° counterclockwise (as seen from the south) using AutoCad software (Fig. 6). The two ends of the profile (FLK-NN 3 and E-3) are probably deformed because of the drag effect of the FLK and KK faults, respectively.

Sediment compaction was also considered to correct the geometry. The petrographic analysis made on Tuff IC and CHT indicates that there is no mechanical compaction (contra Blumenschine et al., 2012, Fig. 7). No evidence of deformation in the matrix was found, with even the thinnest pyroclasts unmodified. In coarse-grained tuffs such as Tuff ID, the coarse components, including pumices, are rounded and show no compaction fabrics. If other interbedded sediments, such as the clays, had undergone any mechanical compaction, important load cast figures should be observed.

Geometric correction of all the stratigraphic columns results in a 2D stratigraphic profile (Fig. 8). Deformation by drag effect at the FLK fault was also corrected for in the FLK–NN–3 section, using the minimal deformation values of tuff IF in the same point as all layers between Tuff IC and Tuff IF.

The reconstruction of the landscape combines the facies descriptions and this quantitative model, which make it possible to calculate real distances, heights, slopes, and paleosurfaces. Combining the topographic points collected along the whole study area and the sections in the south margin results in a 3D diagrammatic reconstruction (Fig. 9). It is also quantitative, though less accurate, at the south side. In both cases, 2D and 3D drawings were exaggerated 14 times so that features could be more easily identified. Two new sites equivalent to FLK Zinj and occurring on the same paleosurface were included in the 3D reconstruction: PTK and AMK (Amin Mturi Korongo), which were discovered during the 2012 and 2013 field seasons, respectively. Both PTK and AMK show the same horizontal height above the lake level as FLK-NN.

3.1.5. The Zinj paleolandscape

The resulting stratigraphic profile shows two clear areas. To the west, there was a raised platform and to the east a shallow depression (~2.2 m lower than FLK Zinj) that extended towards the KK fault. FLK-NN, FLK-N, and FLK-Zinj are all located on this raised platform, which extends 300 m from FLK-NN to S-2. FLK-N and FLK-Zinj lie at nearly the same horizontal level. At FLK-NN, which is ~40 cm below FLK N and FLK Zinj, a freshwater spring and wetland developed (see Domínguez-Rodrigo et al., 2010 and Ashley et al., 2010). This slight difference in elevation makes the growth of arboreal plants such as palms at FLK Zinj more feasible (see Barboni et al., 2010).

The runoff area extents 125 m from the platform (S-4) to the east, and has the highest East-West slope average (0.8%) in the study area. The steepest zone (3.5%) extends for 20 m between S-2 and S-5. The deepest erosion occurred in trench S-7, where a distinct rill feature was documented (Fig. 5).

The Zinj clay was deposited over CHT in the whole study area except within the highest energy area, where sediment input

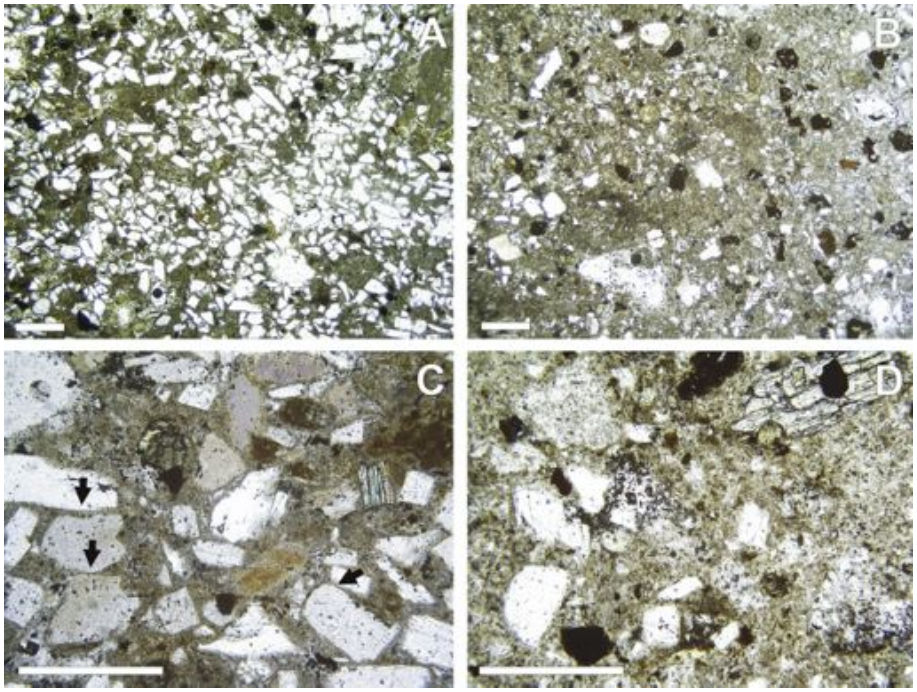

Fig. 7. Petrographic microscope images of thin-sections. A and C: Grain-supported crystal tuff (Tuff IC). White crystals are anortoclase. Brown crystals are hornblende and black grains are titanomagnetite. This tuff has low selection and contacts between crystals are punctual. Neither deformation of cognate fragments nor cementation are visible. B and D: Matrix-supported crystal-vitric tuff (CHT) formed by sharp juvenile crystals, mainly anortoclase, hornblende, augite and titanomagnetite. It contains rounded lava fragments and glass lapilli. There is a 64% of vitric matrix with abundant plagioclase microlites and titanomagnetite. This tuff has low selection, where crystals and cognate fragments are floating on the brown vitric matrix. White scale bar is 1 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

processes created a 40–50 cm thick deposit of tuffaceous clay and some reworked tuffs. The environment was quiet enough afterwards to allow the decantation of the Zinj clay. It was probably reactivated after the deposition of Tuff IC, a process that reworked the tuff and formed small channels. The Zinj clay appears between trench S-6 (runoff area) and the KK fault (including the highest energy area), but this portion of the paleolandscape is nearly devoid of archaeological remains. East of the high energy area, the slope drops close to 0% and lies 2 m below the FLK Zinj site.

We divide the 3D model of the Zinj paleolandscape into four areas (1–4) based on depositional energy, topography, and facies (Fig. 10).

Area 1 corresponds to the supralittoral environmental belt, i.e. the border of the lake. In this area, features of subaerial exposure dominant and vegetation was largely controlled by water table oscillations. It represents the highest elevation and, in this case, connects with the lava slopes to the south. Sediment inputs, such as alluvial fans, can occur spreading along this rim. Coarser and more tuffaceous sediments are interbedded with earthy or even finer (e.g., waxy claystone) sediments. Relative to nearby areas, depositional energy in Area 1 was high, although still suitable for the formation preservation of archaeological sites (i.e. AMK).

During FLK Zinj times, the lake border curved as it conformed to the existing lava mounds. Tuff IC lies directly over the basalt, which means there were no soils in the surrounding areas to the south. In that case, the landscape close to lake Olduvai may have been a wasteland composed exclusively of lava layers and water.

Area 2 is very similar to Area 1, but the former was influenced substantially less by sediment input and experienced a lower energy depositional environment. Because it developed over a thicker substratum of sediment, the area's soils can be deeper and the water table was probably permanent during the dry seasons than it was over the nearby basalts. Area 2 would also have been well drained during the wet seasons due to its relatively high elevation. This sustained elevation differential may have favored the development of continuous surface runoff, especially on the steepest slopes during the rains. The drainage network probably was of a radial type, draining out from the center to lower areas. Because of Area 2's higher elevation and relatively flat geometry, it could be considered as a kind of lacustrine terrace.

Area 3 was assigned to the deepest and most lacustrine of the areas. Depositional energy is the lowest documented across the paleolandscape, although sedimentation events (inputs) did occur and are represented by thin layers of tuffaceous silt. In Area 3 both the Zinj clay and the tuffaceous clay are waxy claystones. This area is interpreted here as a mudflat. Very few archaeological remains have been found in the 8 square meters opened in area's trenches (E-1 and E-3).

Area 4 preserves local sediment input coming from the south and probably represents the medial to distal facies of an alluvial fan. Due to the scarcity of outcrops, it is not possible to establish their limits. It is likely, however, that a well-established drainage network existed upstream. Depending on hydroclimatic conditions, the discharge consisted of bedload (intermediate reworked tuffs), suspension (silt under CHT), or just water flow. Its effects on the Zinj clay were minor in S-8 and S-17, but upstream it either eroded the deposit (S-18) or prevented its formation.

3.1.6. Evolution of the Zinj paleolandscape

Considering the complete stratigraphic record from the basalt to Tuff IC, the Zinj palaeosurface seems to have adapted to the topographic shape of the underlying FLK-NN3 paleosurface. The Zinj paleosurface, as the sedimentological and geometric evidence suggests, was therefore not formed as a result of significant changes to the base level or to major erosional processes. The major landscape changes occurred well before Zinj times, before even CHT was deposited. The sequence follows a series of stages:

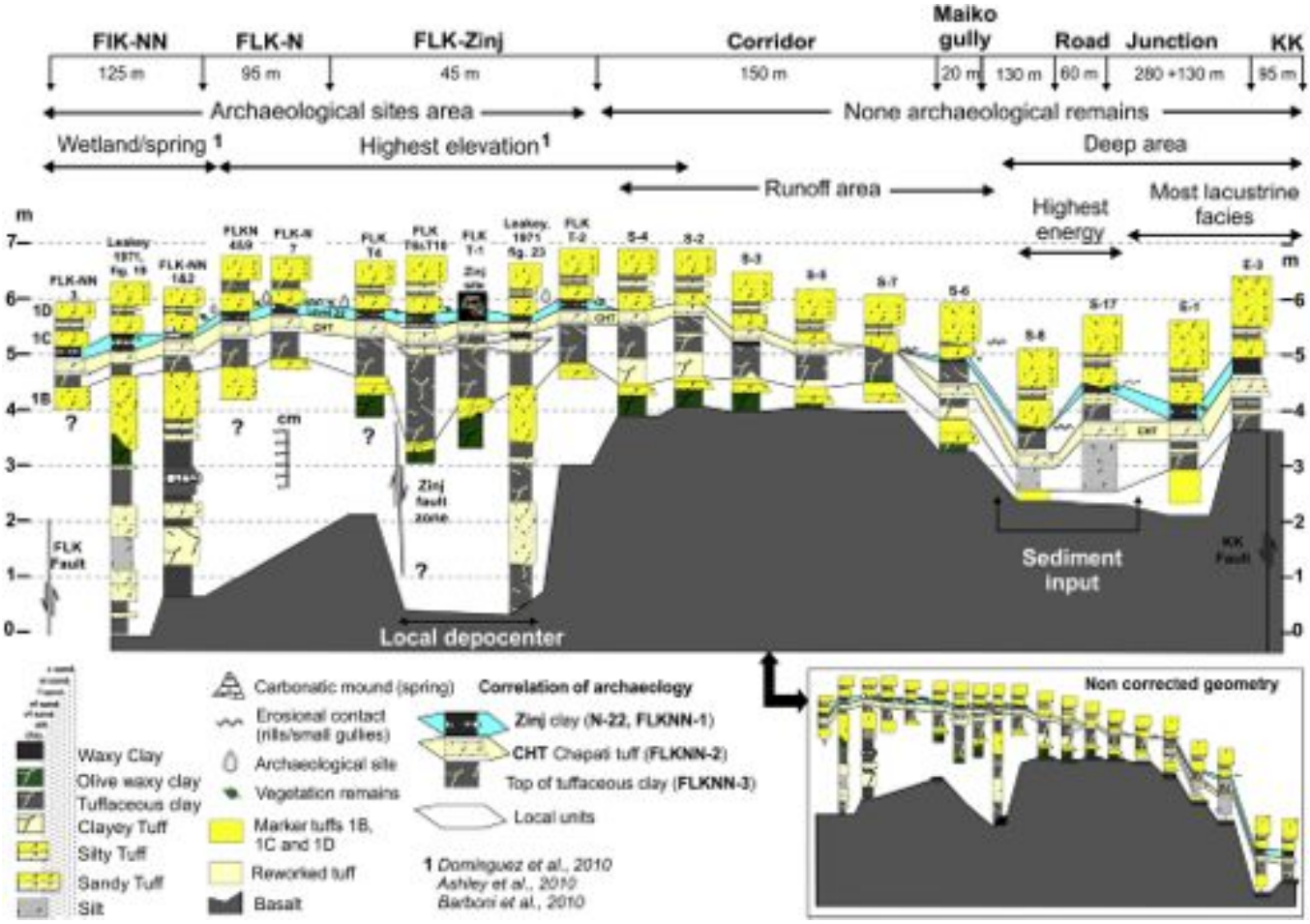

Fig. 8. Schematic stratigraphic profile for the lower-middle Bed I (basalt-Tuff ID interval), in the FLK-KK block. Bottom, the actual geometry, tilted by tectonic movements. Above, same geometry after applying the geometric correction (0.42°).

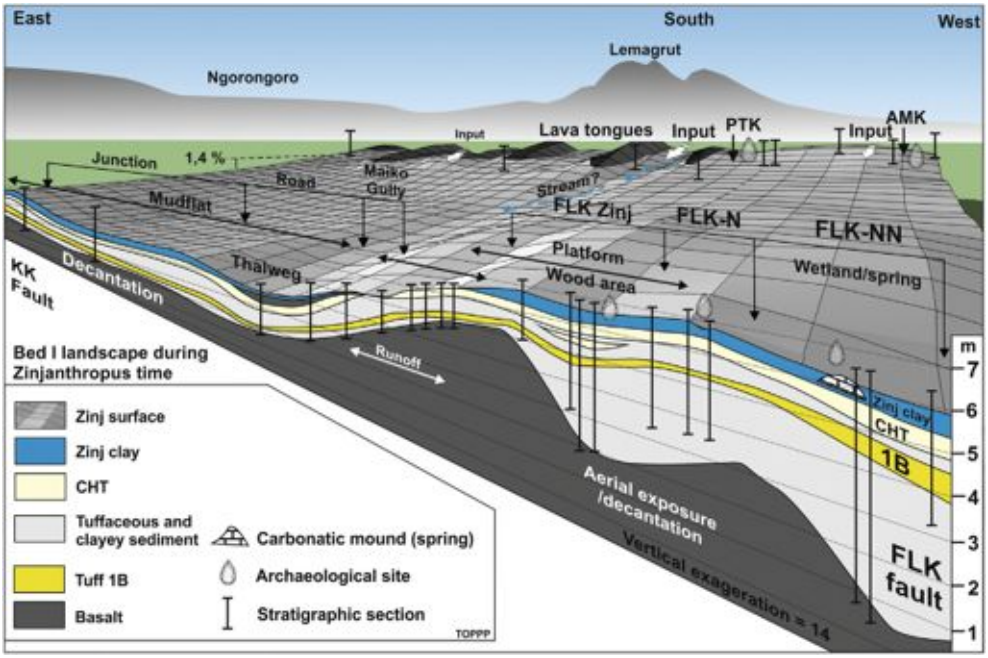

Fig. 9. 3D reconstruction of the *Zinj* paleosurface based on topographic control points (vertically corrected), stratigraphic sections and facies analysis. References to paleocology are based on previous work by Domínguez-Rodrigo et al. (2010), Ashley et al. (2010) and Barboni et al. (2010). The model decreases in precision towards the south.

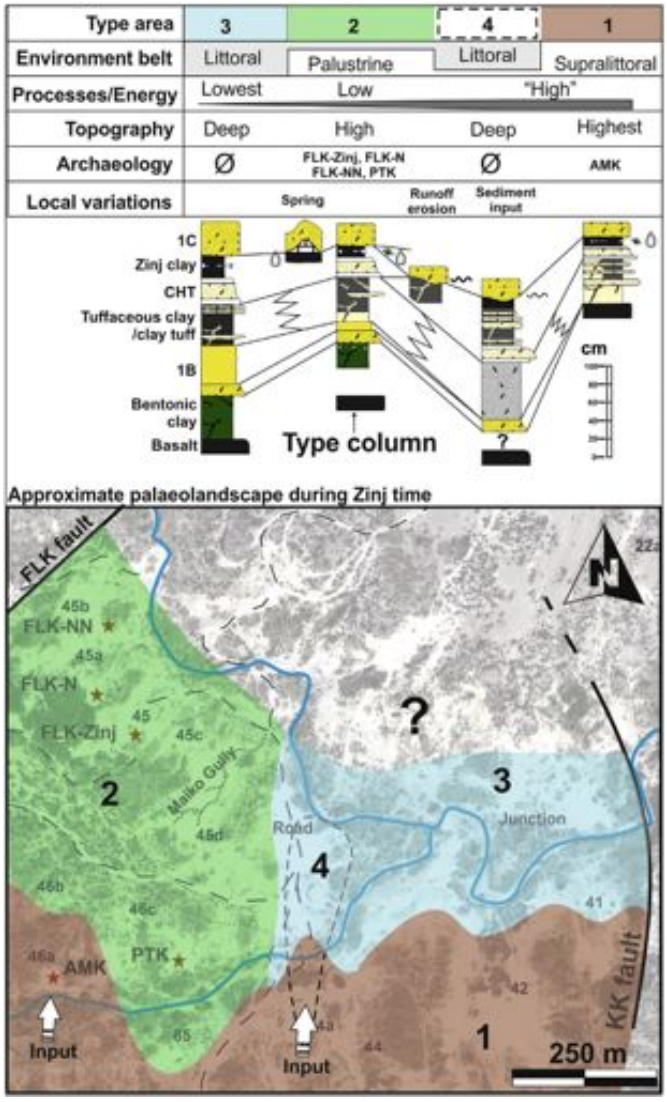

Fig. 10. Cartography of the main zones identified in the *Zinj* paleolandscape, within the lake-margin zone of lower-middle Bed I between the FLK and KK faults. Above, type column and lateral changes. The table comprises the main characteristics of each type zone.

Stage 1: The base level was 5–6 m below FLK Zinj during lowermost Bed I in the FLK-KK block (Fig. 11). At this time, the depocenter was situated in the west, towards the main lake. Sedimentation began there, whereas to the east the basalt outcropped 3–4 m above the lake. **Stage 2**: when the base level reached the basalt, two depocenters developed. The fine-grained lake-margin sediments and Tuff IB adapted to, and partially smoothed, this paleosurface, and in so doing created a new surface. The elevation differences between these concave topographies was less than 1.5 m. **Stage 3**: a lake transgression led to the deposition of the Tuffaceous Clay, which filled the local depressed areas and formed a nearly flat surface. The subsequent lake withdrawal reactivated the drainage network. These processes were concentrated in the modern Road area, where the main loss of stratigraphic sections is documented. In most of the area, erosion was probably not intense, given that the lower contact of CHT is consistently flat. The resultant surface was quite similar to the Zinj surface. **Stage 4**: the archaeological deposit of FLK-NN3 was formed on the Stage 3 landscape. CHT conformed to the FLK-NN3 surface, with some lateral variations, and created the FLK-NN2 and PTK-3 levels. Finally, the Zinj clay was deposited over the CHT surface in two continuous transgressive events, forming one archaeological level each time (Domínguez-Rodrigo et al., 2010).

3.2. Archaeological study of fossil density on the FLK Zinj paleolandscape

As observed in Fig. 12, there is a sharp contrast in artifact and fossil density when comparing the FLK Zinj main cluster to its surrounding paleolandscape (Table 3). Bone density at the FLKNN wetland is fairly low (1.7 bones/m^2). Fossil density in the central wetland (2 bones/m^2) is only slightly higher than at the edge of the wetland (1.2 bone/m^2). Blumenschine et al.'s (2012) higher fossil density values for the latter are just an artifact of sampling. FLKN5, situated close to Blumenschine et al.'s (2012) high-yielding trench also provided a higher density of fossils ($n = 9$; 2.25 per m^2) and stone tools ($n = 11$; 2.8 artefacts per m^2), which are not representative of fossil density at the edge of the wetland, as shown by data from the other FLKN trenches (Tables 1and 3). Bone density in this area is similar to that reported for the FLK Zinj periphery, where fossil density is also low (1.5 bones/m^2).

Table 3
Density values for stone tools and fossil bones on the excavated trenches on the FLK Zinj paleolandscape.

	Bones	Lithics	m^2	Bones/m^2	Lithics/m^2
FLK Zinj site[a]					
ZW	290	111	127	2.3	0.8
ZS	177	81	45	4	1.8
ZC	816	556	77	10.6	7.2
ZCC	553	463	21	26.3	22
Zinj periphery					
FLKT4	15	2	4	7.5	0.5
FLKT5	2	0	5	0.4	0
FLKT6b	2	0	2	1	0
FLKT7	0	1	4	0	0.25
FLKT10	2	0	1	2	0
Wetland core					
FLKNWT1	51	4	16	3.2	0.25
FLKNWT2	7	0	9	0.8	0
FLKNWT3	0	0	1	0	0
FLKNWT4	0	0	1	0	0
FLKNN2	0	0	2	0	0
Wetland edge					
FLKN4	5	0	5	1	0
FLKN5	9	11	4	2.25	2.75
FLKN7	4	0	4	1	0
FLKN8	1	0	2	0.5	0
FLKN9	1	2	2	0.5	1
Southern Sector (Corridor, Maiko Gully, Road, Side Gorge)					
S1	0	0	1	0	0
S2	0	0	2	0	0
S3	0	0	2	0	0
S4	0	0	1	0	0
S6	0	0	1	0	0
S7	0	0	1	0	0
S8	0	0	1	0	0
S9	2	0	2	1	0
S17	0	0	2	0	0
S15	41	0	8	5.1	0
S16	2	3	2	1	1.5
Eastern Sector (Junction)					
E1	5	2	5	1	0.2
E2	1	1	4	0.25	0.25
E3	0	0	1	0	0

[a] ZW (Zinj West), ZS (Zinj South), ZC (Zinj cluster), ZCC (Zinj cluster core). ZW, ZS and ZC as defined in Domínguez-Rodrigo et al. (2010). ZCC, the densest part of ZC. Estimates are an underestimation of the original frequencies, since Leakey (1971) only drew a portion of the assemblage.

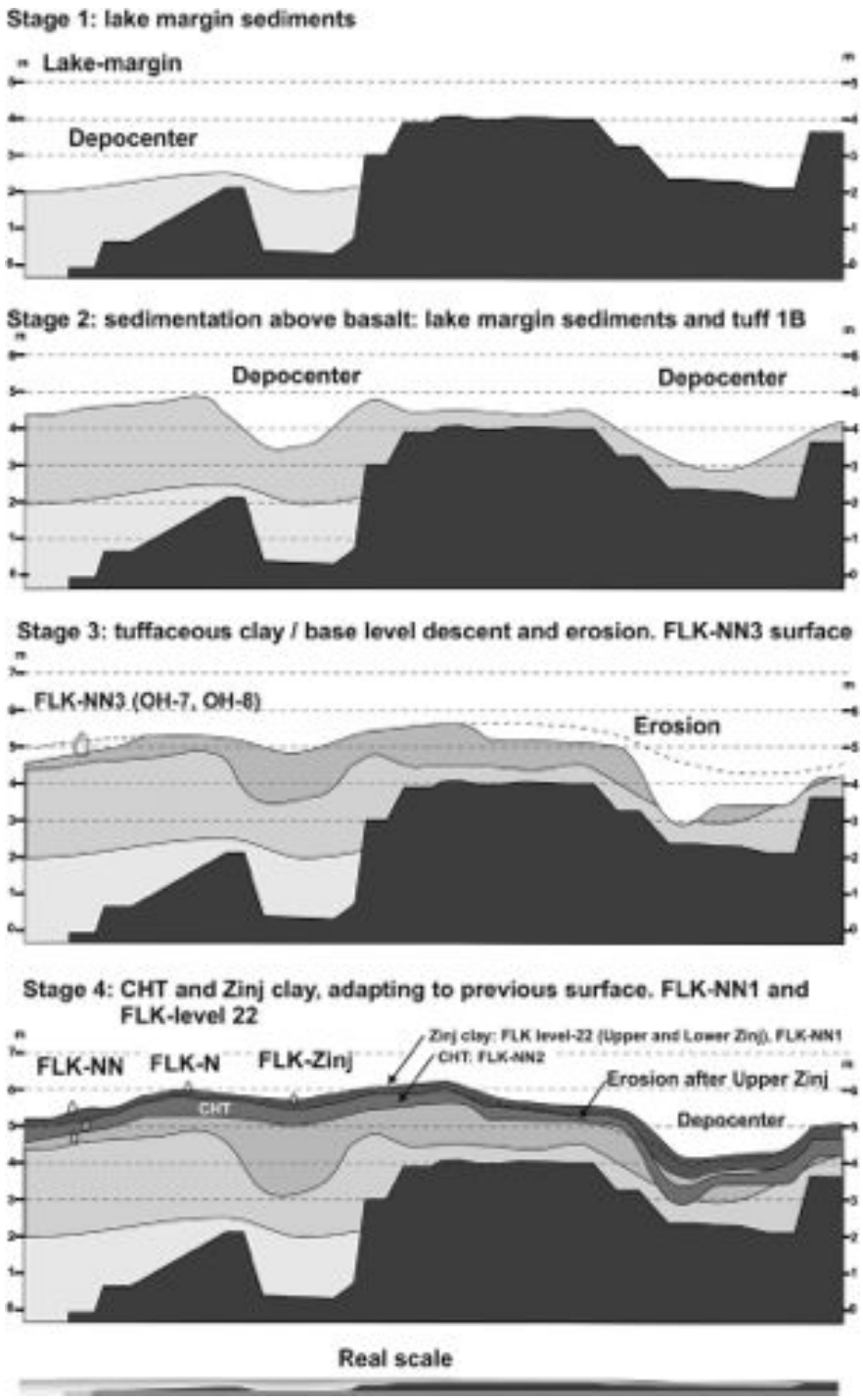

Fig. 11. Evolution of lower–middle Bed I sedimentation between the basalt and the Zinj clay. See text for description. Stage 4 represents the *Zinj* paleosurface just prior to the deposition of Tuff IC.

The higher frequency of fossils and stone tools at FLKN5 (and Blumenschine et al.'s adjacent trench) can be explained taphonomically. These trenches occupy the lowest portion of the FLK N gully front. The location of FLKN5 in a depressed area made it exposed to gravitational processes, such as slope gravity and water circulation. This latter process is documented indirectly through the presence of occasional small pebbles in FLKN5 and a clear NW-SE orientation of both fossils and stone tools in this trench (Fig. 13). A Rayleigh test ($Z = 8.013$, $p < 0.000$) and a Kuiper test ($V = 2.696$, $p < 0.01$) show clear anisotropy of fossils in this trench. A combined analysis for FLKN7 and FLKN8 also shows multimodal anisotropy ($V = 1.804$, $p < 0.05$), although a Rayleigh's test fails to show unimodal anisotropy ($Z = 2.646$, $p = 0.064$) probably because of the small sample size. The divergent orientation of fossils in these trenches is suggestive of rills instead of fluvial processes as the agent of anisotropy. The average thickness of the Zinj clay in the FLK North front (10.3 cm–15 cm) is also thinner than at FLK Zinj and its surrounding trenches. This is probably due to the fact that FLKN is

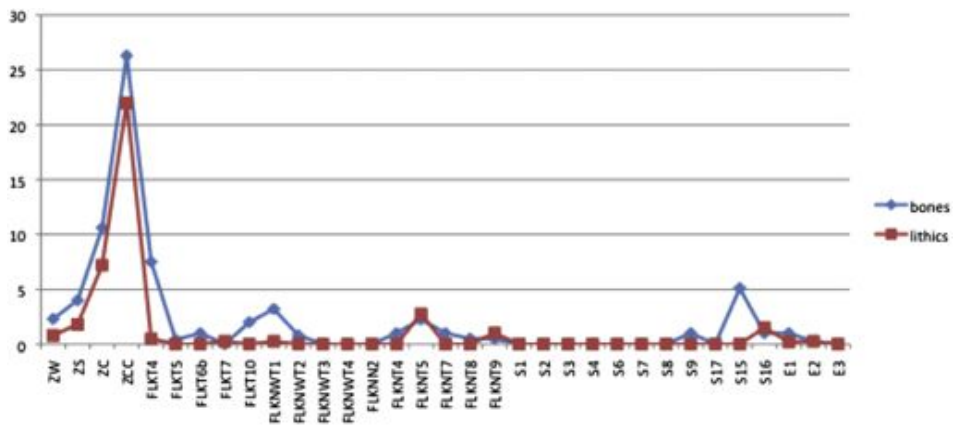

Fig. 12. Bone and lithic artefact density (number/m^2) at the main FLK Zinj areas (ZW, West Zinj; ZS, South Zinj; ZC, Zinj cluster; ZCC, Zinj cluster core), and the TOPPP trenches on the Zinj paleosurface.

slightly more elevated than FLK Zinj and therefore spatially-limited erosion of the top of the clay by, for example, small rill channels such as those documented at FLKN7 (Fig. 5), resulted in a very thin clay horizon. The thinnest clay at FLKN corresponds to those trenches that are situated within the depression of the local topography (Fig. 13), with the exception of FLKN6, which was eroded by the Ndutu unit. The location of this depression at the FLKN front (wetland edge) is roughly similar to that documented between the FLKT6 and FLKT10 interval, in which a thin tuffaceous layer is present within the clay overlying the CHT. This indicates that a drainage system was operating East of the FLK sites in a North-South direction. This may have been a rill network, since orientation of objects is different among trenches (Fig. 13). It should be stressed that the paleotopography of the wetland edge is lower to the East, towards the lake and input areas, and more elevated to the West, toward the inner part of the platform.

Bones are virtually absent in the southern sector (S1-9), either because of low landscape productivity or erosion caused by rills and sheetwash. In contrast, fossils become more abundantly represented in the distal section of the southern sector (4.6 bones/m^2), surrounding the high-density site of PTK. The eastern Sector also yielded a low-productivity landscape, with only 0.6 bones/m^2.

The area sampled within the Zinj paleolandscape (>106 m^2, comprising 30 trenches) is statistically comprehensive and shows a markedly lower fossil density when compared to the main cluster at FLK Zinj itself (>30 bones/m^2). Although we will not elaborate further here, it should be noted that the newly discovered PTK also shows much higher find densities than the surrounding landscape (>40 bones/m^2 at the main cluster)(work in progress). In our study, although some green fractures were identified on the landscape fossils (some of which bear tooth marks), not a single specimen bearing cut marks or percussion

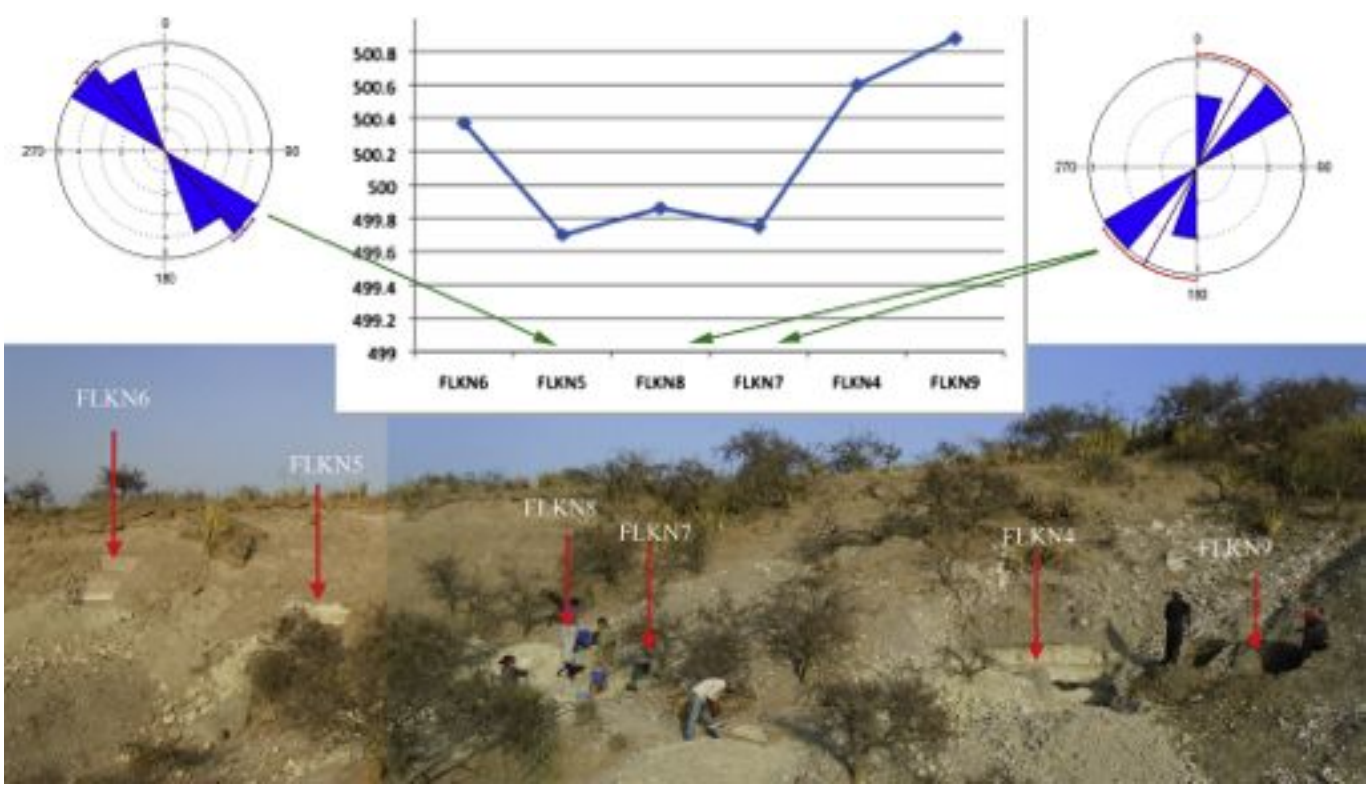

Fig. 13. Location of the FLKN trenches and depth of the Zinj clay in each of them. Orientation of FLKN5, FLKN7 and FLKN8 (combined) is shown.

marks has been observed outside the FLK Zinj or PTK areas. These results support the statistically-based fossil density contrast between FLK Zinj and its paleolandscape previously reported by Domínguez-Rodrigo et al. (2010). High-density bone patches existed on the Zinj paleolandscape, and these patches stand in stark contrast to the surrounding low-density scatters. Most of the evidence of hominin carcass butchery behavior and stone tool use is documented at these patches.

4. Discussion

4.1. Zinj paleolandscape

In denudational contexts, the geometric component is the most important analytical element for reconstructing ancient landscapes (see e.g., a fluvial valley evolution; Strahler, 1997; Summerfield, 1991). Successive surfaces or terraces are fragments of past landscapes that can be correlated with each other. Base level movements and associated processes can be established using quantifiable geomorphological maps (Chorley et al., 1984; Summerfield, 1991). Geometry is, therefore, the most important component, whereas sedimentology is ancillary. Furthermore, in sedimentary contexts, the reconstruction of landscapes can be much more complex and, at least geomorphologically, less accurate if based solely on stratigraphic profiles. Results can, and should, be compared with actual environments to elaborate a model. In those cases, geometry is in the background as it depends on the quantity of outcrops and the capability to measure them. The resulting models are, however, very useful to identify the distribution of habitats and reconstruct basin evolution. A good example is the abundant stratigraphic profiles made by R. Hay (1976) at Olduvai. In the specific case of Bed I, this produced evidence of, from East to West, alluvial fan, lake-margin, and lake systems. In all of them, sequences were "hung" on an arbitrary unit, which deformed the true geometry. While this approach is useful for those interested in interpreting the basin's history, it is not sufficient on its own for a detailed landscape reconstruction. When an originally tilted or undulated marker horizon is assigned as horizontal, the resulting topography is biased and a false relief is inferred. This must be taken into account, especially in flat landscapes such as the paleolake basin during lower and middle Bed I at Olduvai.

In the present work, attention to geometry in the stratigraphic analysis resulted in a more accurate landscape reconstruction. Such methodology is especially suited to the relatively flat Zinj paleolandscape, where subtle variations in elevation resulted in important variation in environmental conditions and sedimentological processes. Water distribution and subsequent erosive processes in particular can vary greatly on even slightly irregular surfaces.

The present case study shows that low energy sediments, even on flat landscapes, can and will follow previous surfaces, a process that results in topographically non-horizontal layers. In lower and middle Bed I, four different units (Tuff IB, clays, CHT, and the Zinj clay) show nearly the same geometry. They adapt to each other, or, more precisely, to the underlying topography, because low energy processes dominated regardless of the type of sediment (clayey or volcanic). Physical characteristics, drainage network, and slope changed very little throughout the Tuff IB-IC time interval even as climate and volcanic activity remained major regulatory factors in the basin's sediment input. The low energy environment promoted decanting processes as opposed to bed load transport. The landscape relief from Tuff IB to Tuff IC is progressively smoothed and was only disrupted by local processes in the water runoff area between FLK Zinj and Maiko Gully.

Despite the homogeneity of the depositional environment, the composition and thickness of the tuffaceous clay, CHT, and the Zinj clay change along the study area. Such variety could explain changes in the paleogeography. Finer proportions of sediments and thicker sections would be expected in deeper and lower-energy areas (Area 3). In contrast, coarser sediment and thinner layers correspond to more elevated zones, close to the border of the basin (Area 1 facies). Nevertheless, such variation in sedimentological characteristics cannot be used by itself particularly in a quantitative way, to accurately reconstruct a palaeosurface: the geometry of layers along outcrops must also be considered.

This method, and the resulting landscape reconstruction, contrasts with the interpretations recently offered by Blumenschine et al. (2012). These authors propose that the Zinj paleosurface was produced by fluvial erosion. This model is based on a stratigraphic section between FLK-NN and FLK-S (more specifically, Road in this work). In their section (Fig. 2, page 367), the authors assume: a) Tuff IB is horizontal; b) the presence of two volcaniclastic sandstones between tuffs IB and IC at FLK Zinj mean the site is on a topographic high point; c) the FLK Zinj level is not composed of two different layers of clay, but is only a single paleosurface; d) compaction values of 205% (clays), 145% (volcaniclastic sandstones) and 160% (tuffs).

The first assumption alone forces the creation of a false relief, because Tuff IB is not horizontal. Such a biased relief shows a more elevated area in the thickest section between Tuff IB and Tuff IC, which occurs below FLK Zinj. Thinner sections correspond to depressions (Maiko Gully, FLK-N and FLK-NN). The FLK-Zinj elevation is also justified by the presence of two layers ("volcaniclastic sandstones") between tuffs IB and IC. The lower one is present along FLK-NN to the Road, whereas the upper one is only in the Zinj area (approx. 150m between Tr 140 FLK and Tr 141 Maiko Gully North). To justify this scheme, the authors describe the sedimentation of the two layers as interbedded in the clay between Tuff IB and IC. The lower one represents the equivalent of level FLK-NN2 and overlies the OH-7 and OH-8 surface (FLK-NN3). After that, a lake withdrawal leads to a profound disconformity, forming the Zinjanthropus land surface (Blumenschine et al., 2012).

As can be seen at the FLK-Zinj site (Fig. 14), there are two tuffaceous layers below the Zinj clay. The upper one is the laminated CHT, which can be followed 1 km along the FLK-KK block. Below CHT there is another sandy reworked tuff, but it is less than 20 m wide, between trenches FLK T-2 and FLK T-4. It is clearly a very local layer, filling a shallow depression (<10 cm) and even forming an onlap shape (Fig. 14). It is not present outside the modern FLK Zinj gully and it has no relationship with any archaeological level. Both layers were plotted by Leakey (Fig. 23, Leakey, 1971) and can be seen in trenches FLK T-1, 6 and 10, aligned North-South. The upper tuffaceous layer of Leakey's corresponds to CHT and cannot be correlated with the local reworked tuff in the FLK North trenches. In trench FLKT6, a thin reworked tuff is observed between CHT and the Zinj clay, but it corresponds to a shallow depression, given that the Zinj clay top is exactly at the same horizontal elevation as the Zinj clay at FLK Zinj. By assuming that this local layer was originally regionally deposited, Blumenschine et al. (2012) justify that its absence north and south of FLK Zinj was the result of erosion. In contrast, we show that this layer was not deposited over the FLK Zinj paleolandscape beyond the modern FLK Zinj gully (Fig. 12). This has serious repercussions for the reconstruction of the topography of the Zinj paleosurface.

The Zinj clay was deposited over CHT (the upper tufaceous layer). At FLK-N and FLK-NN, CHT forms the archaeological level of FLK-NN2, which overlies the OH-7 and OH-8 paleosurface, which itself developed at the top of the tuffaceous clay (FLK-NN3) (Leakey, 1971). In the present reconstruction, the Zinj paleosurface developed over the same clay along the FLK-KK block. At the same time, hominins formed the FLK sites on the more elevated and exposed

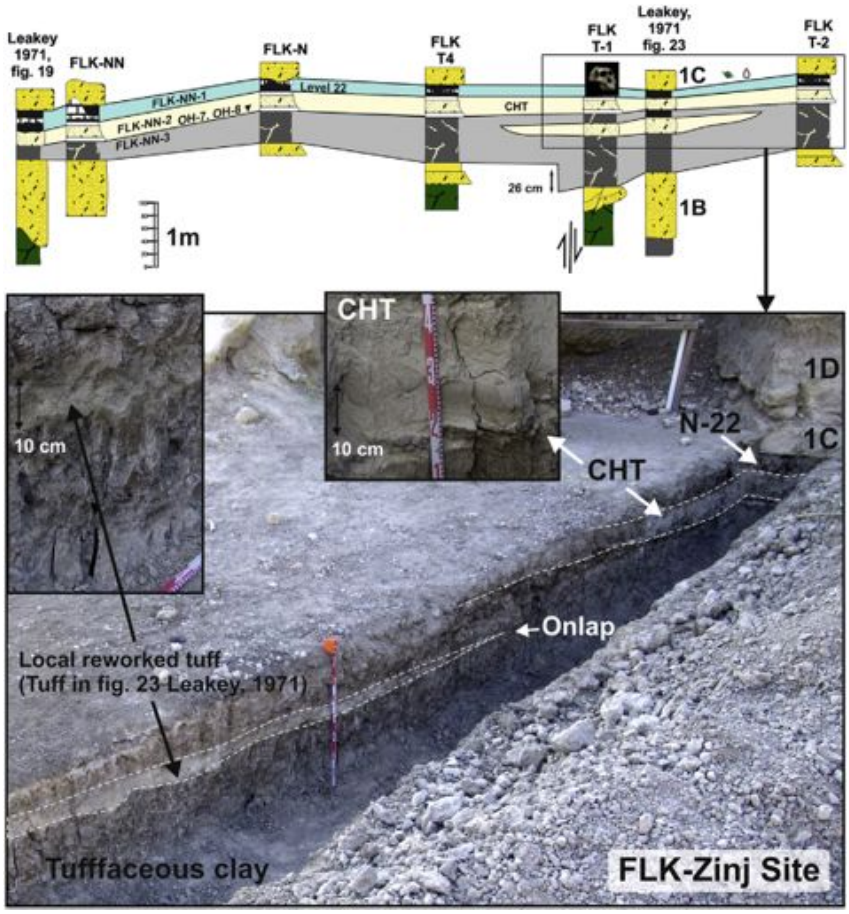

Fig. 14. Trench FLK T-1 at FLK Zinj, where the CHT and a local reworked tuff (Fine-grained whitish-buff tuff and Tuff respectively in Leakey, 1971; Fig. 23) can be observed. Note that the lower tuff has a shallow channel shape within the tuffaceous clay.

areas (FLK-N and FLK-Zinj) while decantation of clay occurred in the deeper areas to the east.

Given that the thickest sequence between tuffs IB and IC coincides with FLK Zinj, Blumenschine et al. (2012) argue that the resulting landscape fits with that initially proposed by Ashley et al. (2010), where FLK Zinj occurred on an elevated wooded area while a wetland was developed less than 0.5 m below it, at FLK-NN. The identification of such a depression to the northwest of Zinj at FLKN and FLKNN results from the misinterpretation of the intermediate tuffs (i.e., "siliciclastic sandstones"). Specifically, the correlation of FLK-NN2 with the lower intermediate tuff in FLK-Zinj is inaccurate, since it actually corresponds to the upper tuff (here CHT). Based on this correlation, a second landscape is constructed by Blumenschine et al. (2012, Fig. 4, page 370) where the correlation is hung on the contact between units equivalent to Leakey's FLK-NN Levels 1 and 2 (straight horizontal line). Not only the correlation, but also the assumption of horizontal levels, leads to a misinterpretation of the paleolandscape.

Regarding the energy of the Zinj paleolandscape, Blumenschine et al. (2012) suggest that it is periodically flooded by an anastomosing river system, whose thalwegs are in Maiko Gully and FLK-S (Road). The corresponding river channel style "was analogous to active and abandoned, low-gradient (<1:3400) river channels described from the modern Okavango Fan" Blumenschine et al., 2012: 371). However, the gradient of Tuff IC, measured from the road area to the south, is 1:140, more than twenty times greater that the Okavango Fan channels. Moreover, Tuff IC overlies steeper slopes of basalt in the south margin of the Gorge, whose gradient is 1:55. That means that the slopes projecting southward from the lake-margin are even greater. Sedimentologically, no fluvial deposit has been identified just below Tuff IC in the location pointed out by Blumenschine et al. (2012). Typical elements of anastomosing rivers, including cohesive and steep-sided channel banks, frequent crevasses and levees (see Miall, 2006) are not present in the outcrops and trenches.

What is more, their reconstruction (see Fig. 4 of Blumenschine et al., (2012)) requires the river to reach more than 1 m in depth before overflowing onto the Zinj site. This entails a minimum river cross-section of 200 m^2 (even more as the right margin is not represented). If one combines that cross-section with the calculated gradient, the result is a huge river system that should have left obvious evidence for its existence (e.g., bedload bars). In our corrected scheme (Fig. 6), the "flooded" cross-section should be much greater: at least 2.2 m in depth and more than 600 m wide.

As further conclusive proof of the lack of a river by the Zinj "peninsula", a new site (PTK) was found at the same horizontal height as FLK Zinj and FLK-N in the middle of the purported river channel (N30E, Fig. 6 of Blumenschine et al., (2012)). This site is also overlaid by Tuff IC and preserves two clay levels similar to those reported at FLK Zinj, both of which contain archaeological levels (Domínguez-Rodrigo et al., 2010). If a river existed in the area, a site would not have been formed in a clay deposit that preserved even the casts of plants on its surface. Therefore, the presence of a river or other high-energy geological processes in the vicinity of FLK Zinj should be discarded.

The only fluvial or alluvial processes recorded in lower and middle Bed I corresponds to those already described in the input area (S-18) and probably in S-17 (150 m north). Even smaller channels of no more than 2–3 m of width and 1 m of depth transported large-sized grain loads, including gravel and sand, on the 1:100 gradient of the reconstructed mudflats (Diez-Martin et al., 2014).

Blumenschine et al., (2012) also justify their river interpretation through the presence of small overflow channels at FLK-Zinj that follow an East-West direction. More specifically, they categorize one channel feature described by Leakey (1971) at FLK-Zinj and another in identified in Trench 138 as a distributary channel similar to those documented in the modern Okavango delta. Leakey (1965) mentions the presence of "a small channel exposed in the Trial Trench, 1 ft. 9 in. (53 cm) of width and 1 ft. 2 in. (35 cm) deep (W/D = 1.5), infilled with a broken-down earthy clay similar to the paleosol level" of the Zinjanthropus floor (pg. 49). In her Fig. 23, Leakey (1971) depicts a channel 64 cm wide and 24 cm deep (W/D = 2.6). An infill of silty clay different from the Zinj clay is also identified. Blumenschine et al., (2012) argue that high levels of compaction (145%–205%) must have operated in order to obtain smaller W/D ratios (~0.9) and the possible presence of peat in the channel. However, these authors did not find any evidence of peat in their excavations and neither did Ashley et al. (2010). In addition, petrographic analyses carried out by TOPPP on these sediments indicate that mechanic compaction is 0%.

The Tuff IC deposit is a unique opportunity to identify the geological processes affecting the Zinj paleolandscape, since it contributed to the preservation of the microtopography, the surface geometry, and the associated deposits. Given the ashfall nature of Tuff IC, it has not modified the original position of any underlying deposit and any materials contained therein.

In addition, practically all contact planes of Tuff IC with the underlying sediments are virtually flat and straight. Only two clear channel-shape contacts were identified, in Trench S-7 (150 m. East of Zinj) and at Trench FLK-N 7 (FLK-N). The former was 40 cm wide and 15 cm deep and was infilled with tuffaceous clay (Fig. 4). This exceptional contact resembles channels created by rills. In FLK-N, another rill, (15 cm deep and 60 cm wide) is eroding the upper layer of the Zinj clay (Fig. 5).

Channel features make up less than 1% of the total documented Tuff IC-Zinj clay contact. Flat erosive contacts are more frequent (<5%) and are concentrated in the runoff area (127 m) east of the Zinj site (S-2 to S-6). Sheetflow runoff eroded the Zinj clay and the top of CHT without leaving any lag or deposits of greater grain size. In both cases, runoff erosion starts near the border of the platform containing the archaeological sites. This process was more pronounced on the east side, probably because water could more easily drain out to the deepest point in S-8 (Road). Potential energy is higher at this location, coinciding with the steepest slopes in the study area: 0,8% between S-2 and S-8 (127 m) and 3.5% along the 20 m between S-2 and S-5. Note that slopes are previous to runoff because of layer adaptation processes (see Fig. 11). Headwater erosion could also have occurred towards the west. All these suggest water runoff as the most likely erosional factor on the Zinj paleolandscape, as it occurred on the topographically high platform upon which the archaeological sites rest (Area 3). As the clay is cohesive and erosion is due to precipitation runoff, without external inputs, this process has not left any deposit. After the deposition of a non-cohesive and very low-density sediment (Tuff IC), the same process could generate structures including laminations and cut-fill channels in Tuff 1C.

Runoff rills are extremely common in the lacustrine floodplains of modern African lake systems Africa (Fig. 15). They are very active during the rainy season and produce uneven "discomforming"

Fig. 15. A, Irregular topography of Lake Masek margin, including a rill channel. B, same channel showing typical fluvial structures including lamination and fining upwards sedimentation.

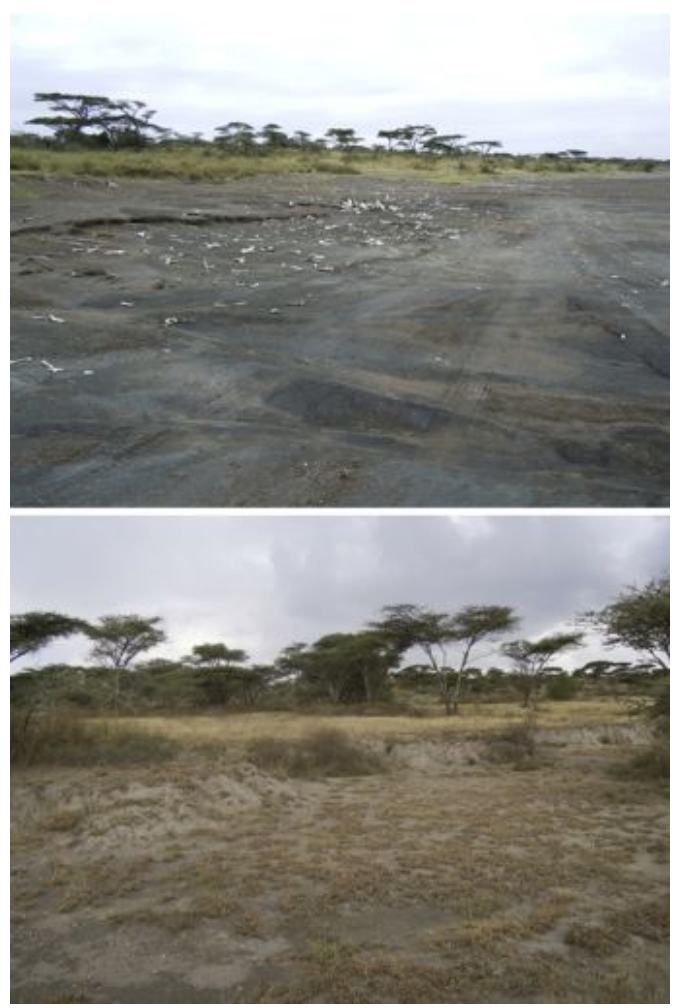

Fig. 16. Two examples from Lake Masek (upper) and Lake Ndutu (lower) showing classical lacustrine terraces creating elevated platforms with wooded vegetation. The erosive steps are created by lake transgression–regression cycles and headwater erosion. Small rills are visible on the Lake Masek margin. These modern examples could be good proxies for the erosion documented south of FLK Zinj.

surfaces because of their great erosive capacity (Fig. 16). Although very shallow rills do not show fining upwards structures in a clayey environment, those wider than one meter usually do when clastic sediment is available upstream (Fig. 15). If such observations pertain to such small channels, fluvial channels >100 m should certainly also show these structures. None of this has been documented for the purported mega-channel south of FLK Zinj reconstructed by Blumenschine et al. (2012). Observations of modern lake floodplains also show that bank erosion occurs in those areas that mark the transition between the outermost reach of lake transgression and the non-flooded alluvial plains (Fig. 16). This creates a topographic high surrounded by small escarpments formed by headwater erosion that enhances inland rill formation during the wet season.

Blumenschine et al. (2012) argue that the hydroplasticity of the clay accounts for the distribution of fossils and artefacts from the FLK Zinj surface into the underlying units of Leakey's trench. This statement is also unsupported, given that experimentation on clay plasticity shows that when this happens, items occur vertically without hiatus (Domínguez-Solera and Domínguez-Rodrigo et al., 2010). In the FLK Zinj clay stratum, what is observed is that most fossils occur on the top few cm and the bottom of the stratum with almost no fossils found in between (see Figs. 5 and 8 in Domínguez-Rodrigo et al., [2010]). This indicates that these fossils belong at least to a minimum of two independent depositional events. Furthermore, hydroplasticity is easily identified by non-linear contacts and waxy or globular contacts in between strata. None of this is documented at FLK Zinj, where the Zinj paleosurface and the overlying Tuff IC contact is mostly planar and horizontal.

4.2. Hominin behavior and productivity of the FLK Zinj paleolandscape

Despite a wealth of taphonomic evidence, some authors still argue (without clear taphonomic support [see Domínguez-Rodrigo et al., 2014]) that hominins visited FLK Zinj to passively scavenge from other carnivores (Pante et al., 2012) and that the site "was not an isolated occupation floor but a part of the land surface used intensively by hominins" (Blumenschine et al., 2012: 364), implying that bone deposition surrounding FLK Zinj was as intense as at the site. Furthermore, these authors also argue that "the high predation risk, evidenced by large carnivore feeding traces" shows that strong carnivore-hominin competition prevented the site from being a home base (Blumenschine et al., 2012: 364). We argue that both statements are taphonomically unsupported. Domínguez-Rodrigo et al. (2010) performed a sampling of >10000 m^2 of the paleolandscape surrounding FLK Zinj and encountered a statistically-supported significant contrast in bone density between the strict boundaries of the site and the remainder of the landscape. Most of the trenches are either devoid of macromammal fossils or preserve them in very low numbers. This supports the central-place character of FLK Zinj and refutes the claim that it represents part of a continuum of densely bone-covered areas.

Blumenschine et al.'s (2012) sample ($n = 13$ trenches covering >500 m) is substantially more reduced than TOPPP's sample ($n = 30$ trenches covering a larger distance). In none of their trenches have Blumenschine et al. (2012) reported any accumulation that could be statistically comparable to the core area of FLK Zinj. For example, in their trenches adjacent to the site they document ~4 bones/m^2, in contrast to the dozens of fossils per square meter documented at the site's main cluster (see highlighted area in Domínguez-Rodrigo et al.'s (2010) Figure 6). A similar density (~5 bones/m^2) is documented on their reconstructed wetland edge in the vicinity of FLK N. Blumenschine et al. (2012) argue that bone densities on parts of the landscape surrounding FLK Zinj, especially on the "edge of the peninsula" are greater than those reported by Leakey (1971) at the site. However, Domínguez-Rodrigo et al. (2010) point out that bone density at FLK Zinj itself varies according to area. Leakey (1971) excavated a high-density cluster of fossils and a peripheral area virtually devoid of bones. Average estimates of the whole excavated area are bound to underestimate the true bone density at the site's main locus. Leakey unearthed 300 m^2 to make sure she delimited the boundaries of the site. She could have excavated a bigger area and, had she done so, the lower density areas away from the core would have depressed the overall site bone density. For this reason, only the core area of the site (i.e., the main cluster) will reflect the true bone density at FLK Zinj. In the main cluster (Domínguez-Rodrigo et al., 2010, Fig. 6 for a gridded division of the site), for instance, 17 m^2 of the site show >20 macrovertebrate bones/m^2, several orders higher than the values reported by OLAPP in their highest bone-yielding area, the wetland edge, with 5.2 bones/m^2 (Blumenchine et al., 2012, Table 1). Some squares show a density higher than 40 specimens. Surrounding the densest area, 10 squares show densities >15 specimens/m^2. It should be emphasized that these figures are underestimates, since Leakey (1971) drew only a portion of the assemblage. Despite this, none of the trenches excavated by OLAPP or TOPPP show comparable densities. In the FLK Zinj core area, 27 m^2 (that is, less than one tenth of the excavated area) contain 667 bones out of the 1283 bones (>50%) drawn by Leakey for the whole site. About 90% of Leakey's excavated area, peripheral to the main cluster, shows <13 specimens/m^2. This contrast provides solid confirmation that nowhere on the paleolandscape (not even in the periphery of the site) was bone accumulated at a rate comparable to the FLK Zinj main area.

Given that Leakey drew only a portion of the excavated assemblage (excluding the smallest specimens), the density figures reported above surely underestimate the true density of the main cluster (Domínguez-Rodrigo et al., 2012). OLAPP does not specify if their bone counts include fragments <2–3 cm, which were not usually drawn by Leakey (1971). If these fragments are included in their counts, the comparisons are potentially misleading, since Leakey drew only 1283 fossils out of >40.000 faunal remains. Excluding micromammals and avian remains, Leakey's Zinj vertebrate sample (including indeterminate fragments) is composed of ~15.000 fossils, which provides a conservative estimate of 50 bones/m^2 within the entire excavated area and a substantially higher number if only the main cluster is considered.

The high degree of carnivore feeding traces in the FLK Zinj archaeofaunal assemblage and the associated inference of intense carnivore-hominin competition at the site are also incorrect, based as they are on the misinterpretation of biochemical marks by Blumenschine (1995), Selvaggio (1994), and Capaldo (1995) as carnivore-made marks (Domínguez-Rodrigo and Barba, 2006, 2007). The actual number of tooth marks on midshafts from all carcasses at FLK Zinj is <20%, which is lower than any Carnivore-first experimental model. These low carnivore estimates at FLK Zinj have recently been replicated by Parkinson (2013). According to Blumenschine's own experiments (1995), this would be indicative of primary access to fleshed carcasses by hominins. The FLK Zinj assemblage represents one of the least carnivore-modified assemblages in all of Bed I (Domínguez-Rodrigo et al., 2007). The intermittent activities of carnivores at FLK Zinj seem to coincide with their general scarcity in the surrounding landscape as taphonomically documented in the pene-contemporaneous assemblage of FLK NN and the fossils found in the areas around the junction, very few of which bear tooth marks (Domínguez-Rodrigo et al., 2010, and present work).

The lingering idea that hominins used FLK Zinj as a scavenging provisioning arena is at odds with current taphonomic evidence (Bunn and Pickering, 2010; Domínguez-Rodrigo et al., 2014). This view of hominin survival has never satisfactorily explained exactly which carnivore(s) hominins were actually scavenging from. What carnivore, for example, could have provided hominins with *Antidorcas* and *Kobus*, which are the most frequently butchered animals at FLK Zinj? Such different carcass sizes would imply more than one carnivore type. Furthermore, what carnivore would allow other carnivores (including hominins) to repeatedly steal its prey (~50 carcasses were exploited by hominins at FLK Zinj) and then permit the thief to remain on-site to consume its spoils? Why would hominins be exploiting carnivore kills at FLK Zinj while overlooking posteriorly the dozens of carcasses that were accumulated by felids only tens of meters away FLK N? (The fauna at FLK N was accumulated mainly by carnivores over an extended period of time, and hominin presence throughout the nine archaeological levels is evidenced by stone tools that apparently were not used for systematic carcass butchery (Domínguez-Rodrigo et al., 2007; Bunn et al., 2010).

4.3. Hominins and crocodiles at FLK Zinj

Blumenschine et al.'s (2012) interpretation that hominins may have been accumulating carcass parts obtained from crocodile kills in the wetland is based on six specimens with purported crocodile tooth marks among a sample of thousands of bones found at FLK Zinj and FLKNN.

If the setting where FLK Zinj and FLKNN were formed were hazardous because of crocodile presence, a strong taphonomic signature of crocodile activities would be expected on the bones accumulated at the sites and their surrounding landscape. Baquedano et al. (2012) showed that bisected marks could represent >40% of marks inflicted by crocodiles. In a crocodile-infested environment, one would expect high number of carcass remains both accumulated and consumed by crocodiles, with correspondingly high frequencies of bones (80%) bearing at least one bisected mark (Njau, 2006; Baquedano et al., 2012). This is supported by actualistic studies, where the 75% of the bones from presumed prey of crocodiles in pond and riverine settings show carinated marks (Njau, 2006). In contrast, Njau (2006) and Blumenschine et al. (2012; Table 3) claim that only 2 bones from FLK Zinj (1.1%), 2 bones from FLKNN3 (4.6%) and 2 bones from their trenches bore bisected marks. This suggests a rather marginal presence of crocodiles in the paleolandscape and, thus, a low risk of predation. The specimen numbers of the bones with bisected marks as identified by Njau (2006) and Njau and Blumenschine (2006, 2012) were not reported, and thus cannot be corroborated by other researchers, but in another independent taphonomic study of the FLK Zinj and FLK NN assemblages, no clear bisected mark caused by crocodiles was identified (Domínguez-Rodrigo et al., 2007). In addition, in a recent landscape study of 10,000 m^2 of the FLK 22 paleolandscape did not identify a single bone showing any trace of crocodile-inflicted modifications (Domínguez-Rodrigo et al., 2010). This argues against the location being hazardous because of crocodile presence or that crocodiles could have been a potential source of carcasses for scavenging hominins. This underscores that no secure crocodile damage is identifiable on fossils from the Zinj paleosurface other than the specimens reported by OLAPP. It is suggestive that while FLKNN (another small portion of exposed land in Blumenschine et al.'s [2012] interpretation) is situated at the heart of a wetland, no crocodile-damaged bones or crocodile fossils are reported from this site.

Baquedano et al. (2012) provided compelling arguments against the felid-crocodile interpretation in the modification of the hominin fossil OH35 found at FLK Zinj (Njau and Blumenschine, 2012; Blumenschine et al., 2012). They argued that the marks on the distal tibia are effectively indistinguishable from those inflicted by a small mammalian carnivore. It is known that OH35 and OH8 derive from different strata (with the latter bearing more compelling crocodile-imparted marks). The available evidence cannot be used to determine whether a leopard-like mammalian carnivore or a crocodile modified the OH35 tibia as opposed to a jackal or other small-sized carnivore. Blumenschine et al.'s (2012) assertions about the hazards of carnivore predation at the site, the socio-economic function of FLK Zinj, and hominin interactions with other biotic elements are, thus, logically unlikely and empirically unsupported.

4.4. Paleobotanical evidence of paleolandscape vegetation

Several questions regarding the "central-place" nature of FLK Zinj are crucial. Why did hominins select that specific spot to carry out activities? It has been traditionally argued that the Olduvai Bed I sites, particularly those in the junction area, were located on a lacustrine floodplain not far from the lake shoreline (Leakey, 1971; Hay, 1976; Blumenschine and Masao, 1991). However, most of the space in a floodplain is open and, thus, subject to rather intense competition on a seasonal basis. If the Olduvai sites are the result of repeated transport of carcasses by carnivores and hominins, it is unlikely that these spots were located in open spaces.

Recent geochemical work has shown that FLK Zinj was situated a few meters away (200 m) from a permanent source of potable water, which probably enabled the existence of tree cover and bush vegetation at and around the site (Ashley et al., 2010). This interpretation received support from soil isotope data published by Sikes (1994) in which she identified a riverine or ground water forest within a 1 km^2 area covered by Blumenschine and Masao's (1991) initial landscape study area in lowermost Bed II in 1989.

The presence of woody plants, trees, and shrubs is also attested by the discovery of abundant micro-botanical remains in the form of globular silica bodies (phytoliths) in the archaeological level 22 (Ashley et al., 2010). In modern soils, the abundance of globular granulate phytoliths typical of woody dicots (mainly trees and shrubs) and globular echinate phytoliths typical of palms (Piperno, 1988) reflects the density of the tree cover (Barboni et al., 2007) and therefore may be used to reconstruct past vegetation types at paleoanthropological sites (i.e., WoldeGabriel et al., 2009). At Zinj, globular (arboreal) phytoliths make up nearly 95% of some samples. Percentages do not necessarily reflect the density of tree cover, however, since phytoliths are prone to poor preservation and preferential dissolution may have biased the fossil assemblage.

Blumenschine et al. (2012: 364) state that the "FLK Peninsula supported groves of trees" and that their "…landscape reconstruction delimits the vegetation mosaic indicated by previous work" but they fail to provide any botanical evidence for 1) trees contemporaneous with the FLK Zinj site, and 2) a vegetation mosaic. First, a "vegetation mosaic" can only be identified at the landscape scale (i.e. tens of km) and therefore cannot be sampled within a 530 m long transect between FLK S (their trench 148) and FLK NN (their trench 135). *A* <1 km long transect only provides a vegetation reconstruction at the local, site scale. Their paleoecological reconstruction is thus incorrectly referred to as a "refined landscape context" (Blumenschine et al., 2012: 379). The macrobotanical remains they recovered from Trenches 147 and 134 only partly support the presence of trees: "Silicified woody plant stems and/or branches of 2–3 cm in diameter and up to 1 m long" and"…woody plants the size of herbs and shrubs…" are not proof for single stem woody perennial plants >2 m high; that is, trees as defined by botanists and ecologists. The presence of trees or any other woody plant is also not attested by the phytolith data because

they write that "Most phytoliths derive from grasses and possibly other monocots such as sedges". Therefore, the only evidence for woody plants and palms comes from a reference the authors failed to cite (Ashley et al., 2010). This earlier work shows high relative abundance of forest indicator phytoliths (43%–71%, mainly globular granulate and globular echinate types) at FLK Zinj, which can be interpreted as clear evidence for the presence of woody plants and palms.

Blumenschine et al. (2012: 365) believe that "wooded settings afford hominins more varied resources than open-vegetation settings, plus arboreal refuge from predation" but, again, no evidence is provided to validate this conceptual model. The only botanical evidence for a wooded to densely wooded environment at FLK Zinj was provided by the phytolith content of eight (over 10) samples collected directly below Tuff IC and published by Ashley et al. (2010).

We disagree with Blumenschine et al.'s (2012) belief that wood pieces (trees, shrubs) cannot co-occur with sedges (*Cyperaceae*), grasses (*Poaceae*), or other dicots (Blumenschine et al., 2012: 373). Sedges co-occur with large trees and lianas in the groundwater- or spring-forest at Manyara National Park, a forest which occurs as an azonal local vegetation patch within the zonal savanna shrubland that dominates the landscape (Greenway and Vesey-Fitzgeral, 1969). The cattail *Typha* and trees such as *Sesbania sesban, Acacia xanthophloea,* and the palm tree *Hyphaene petersiana* also co-occur in groundwater discharge areas, such as one can observe at several places on the northeast side of Lake Eyasi's floodplain (D.B. personal observation) (Fig. 17).

There are important methodological issues that determine Blumenschine et al.'s (2012) results and interpretations. One is time resolution. Sampling below the Zinj surface is not time-constrained. Because we cannot know how much of the sedimentary unit underwent erosion, time-constrained samples can only be found at the direct contact with a volcanic tuff. Hence, the phytolith samples that were collected from immediately below the clay unit named the "Zinjanthropus land surface" in OLAPP trenches (Blumenschine et al., 2012: 368) are unlikely to be of the same age. If they were, which is currently impossible to verify, it would be totally fortuitous. Only the samples collected directly below Tuff IC are contemporaneous and therefore can be compared and interpreted as local variation in the paleovegetation cover.

4.5. Why the acid insoluble fraction (AIF) is not an appropriate residue for a proper microscopic observation of fossil phytoliths

Phytoliths, which are biogenic silica bodies made of hydrated opal A (SiO_2, nH_2O), cannot be observed under the microscope without an adequate chemical preparation of the sediments. Such preparation consists of removing 1) the carbonates, 2) the organic matter, and 3) the minerals (e.g. Lentfer and Boyd, 1998). Carbonates and organic matter are removed by acid digestion, while minerals such as quartz and clays are removed mechanically. Acids such as HF cannot be used to destroy silicate minerals because they will destroy the phytoliths as well. Clays are therefore removed by decantation or centrifugation, and heavy minerals by densimetric separation using a heavy liquid (e.g. $ZnBr_2$ or Sodium polytungstate at $d = 2.3$). This protocol was successfully applied to Miocene paleosols from Central Africa (Novello, 2012), Pliocene paleosols

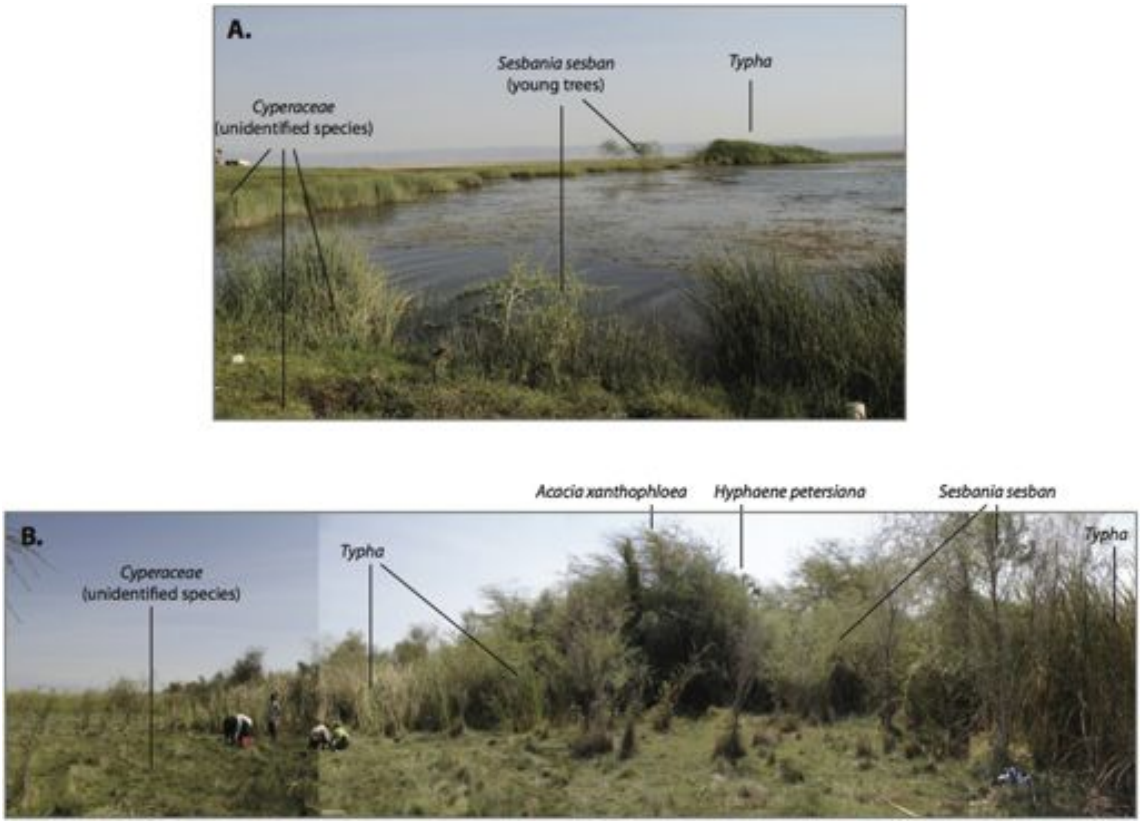

Fig. 17. Photographs of two groundwater discharge areas near the locality of Kisima Ngeda situated on the northeastern floodplain of Lake Eyasi. **A**. Freshwater pond with *Typha*, Cyperaceae, and young specimens of the water-loving tree *Sesbania sesban* (Fabaceae). Saline Lake Eyasi is located in the far background. **B**. Composite photograph of an ecotone between the *Typha* swamp and the *Acacia xanthophloea-Hyphaene petersiana* woodland at Kisima Ngeda. *Sesbania sesban* trees are pioneers that colonize the freshwater ponds. Photos by D. Barboni (June 2011).

from Ethiopia (Barboni et al., 1999; WoldeGabriel et al., 2009), and Pleistocene paleosols and sediments from Olduvai in Tanzania (Ashley et al., 2010; Barboni et al., 2010). The protocol used by R.M. Albert and M. Bamford to prepare their samples from Olduvai was obviously less successful, as it resulted in many sterile and sub-sterile samples, too poor to provide reliable phytolith counts despite repeated attempts (Albert et al., 2006; Bamford et al., 2006, 2008; Blumenschine et al., 2012). To carry out their microscopic observation of phytoliths, Albert et al. (2006) use the acid insoluble fraction of the sediment, i.e. the residue obtained after carbonates and organic matter were destroyed by HCl and H_2O_2. Their protocol lacks two important steps: 1) the removal of clays, and 2) the removal of heavy minerals. These time-consuming but unavoidable steps in the procedure are required in order to obtain residues that are highly concentrated in phytoliths and that are clean enough to allow the observation of phytoliths under the microscope.

At Olduvai, the sediment samples are rich in clays and in volcanic ashes. We accelerate the removal of clays by using a deflocculant (sodium hexametaphosphate at pH 7) and centrifugation. Centrifugation time and speed are calculated based on Jackson (1956)'s formula and take into account the characteristics of the centrifuge that is being used. Ashes are problematic, but we managed to partially remove them from the final residue by using a magnet of 500 micro-tesla. The residue was placed in a small beaker and soaked in distilled water. We moved the magnet on the glass walls of the beaker, which attracted the magnetic particles, notably the ashes.

4.6. The influence of count size on the sampling error for the percentages: a total sum of 200 phytoliths is usually not enough

Since the 1960s, ecologists and also palynologists have increasingly appreciated the importance of the sampling effort required to obtain, on the one hand, an accurate evaluation of species (or pollen taxa) diversity and, on the other hand, statistically sound percentages. In ecology, the sampling effort is represented by the size of the quadrant surveyed in the field. In palynology, it is represented by the number of pollen grains (or phytoliths) counted under the microscope. As a general rule, the greater the sampling effort, the greater the taxa diversity. However, after a certain threshold, the taxa diversity of a site levels off, such that it is not worth increasing the sampling effort to increase the number of taxa found. This threshold is, unsurprisingly, low for sites with low taxa diversity and correspondingly high for sites with high taxa diversity (e.g. Preston, 1962; D.; Barboni, 2000). Recently, Strömberg (2009) showed that the sampling error associated with percentages (e.g. of grass phytoliths) is influenced by the count size of the taxa in question (i.e. the grass phytoliths in our example), and by the value of the percentage, not by the total number of phytoliths counted. Explicitly, if grass phytoliths account for 10% in a sample, the sampling error is ±7% at a count of 50 grass phytoliths; it is ±4% at a count of 200 grass phytoliths. If grass phytoliths account for 30%, the sampling error is ±12% at a count of 50 grass phytoliths; it is reduced to ±6% at a count of 200 grass phytoliths. Blumenschine et al. (2012: 368) advocate "a minimum of 200 morphologically diagnostic phytoliths … to obtain a ca. 20% error margin in interpretation (Albert and Weiner, 2001)". These authors appear unaware that the sampling effort must vary according to the phytolith type diversity of each sample. They are also unaware that the quality of their data is impossible to evaluate because they do not provide the detailed description of the phytolith types they observed, the total phytolith sum obtained for each sample, and the taxonomical attribution they decided to apply to each phytolith type they observed.

4.7. Taxonomical attribution of phytolith types

Because one phytolith type is generally produced by many plant species, and because one plant species produces many different phytolith types, the interpretation of phytolith assemblages preserved in soils and sediments is not straightforward. The taxonomical attribution of phytoliths to plant taxa relies on 1) the observation of phytoliths extracted from botanical specimens, and 2) the statistical analysis of the modern reference material to evaluate the strength of the phytoliths-to-plant–taxon relationships. Thorough descriptions of the observed phytolith types eases comparisons with other published work, which are another way to evaluate the strength of the phytolith-plant taxon relationship. Few published studies include those two steps (Strömberg, 2003; Novello, 2012). The phytolith data interpretation by Blumenschine et al. (2012) rely heavily on a modern phytolith reference collection (Bamford et al., 2006), which lacks 1) rigorous phytolith type descriptions (as noted elsewhere Shillito, 2013), and 2) a statistical analysis of the phytolith types to plant taxa relationships. To date, we argue that their phytolith identification and assignment to botanical taxa such as "grass inflorescence," "grass stem," "monocots," and "dicots" is flawed, if not fallacious. For instance, although phytoliths produced in grass inflorescences are mainly of the rondel type (e.g. Mulholland, 1989; Novello, 2012), rondel phytolith types cannot be assigned only to "grass inflorescences" because many grass species (e.g., among the Chloridoideae subfamily) produce rondel phytolith types in the leaf epidermis (e.g. Barboni and Bremond, 2009). As noted by Shillito (2013), further work on inflorescences is still needed to fully evaluate the morphological overlap between grasses and other (non-grass) species. Silicified bulliform cells not only occur in grass epidermis as stated by Blumenschine et al. (2012; 373) but also in sedges (Novello et al., 2012).

The ever-increasing number of publications allows the taxonomical identification of phytoliths to continue improving, and therefore should help improve earlier paleoenvironmental reconstructions. In a publication, it is critical scientific practice to provide the phytolith-to-plant taxa assignment table used for the paleovegetation inference. Such a correspondence table, which allows for adjustments and corrections in light of increasing knowledge, has only been provided rarely for studies at Olduvai (Ashley et al., 2010; Barboni et al., 2010).

4.8. A tale of two paleoecological reconstructions

Blumenschine et al. (2012) argue that floodplains 1 km away from the perennial lake in modern settings analogeous to paleolake Olduvai indicate that FLK Zinj was situated within a mudflat on a treeless marshland. They further argue that only a river large enough to have created a topographic high point would have enabled an area where a lowered water table would have allowed the growth of trees. This high area would have been a narrow strip of trees, standing in contrast with the surrounding open landscape, thus acting as a magnet for carnivores and the hominins that scavenging their kills. This intense use of the high point is attested by the presence of hyena and jackal remains at the site.

This scenario has several shortcomings. One is the use of modern proxies. Tree-covered and bushy habitats are found well within 1 km of the lake shoreline at several African lakes similar to paleolake Olduvai, so there is no need to invoke the presence of a river or even a marshland. If one overlooks the overwhelming taphonomic evidence in favor of a Human–Carnivore scenario at FLK Zinj (see above and Domínguez-Rodrigo et al., 2014), and growing evidence for primary access by hominins to carcasses at even older sites (Sahnouni et al., 2012; Ferraro et al., 2013), the main logic of

Blumenschine et al.'s (2012) argument is that trees only existed at FLK Zinj and not FLK NN, which limited carnivore activity to FLK Zinj and therefore produced a common-amenity spot. According to these authors, the paucity of carcasses at FLKNN 1 means that this site was rarely visited by carnivores.

Blumenschine (1986) produced a wealth of data indicating that open vegetation landscapes were the most hazardous and carnivore-laden in African savannas. He also showed that wooded, closed-vegetation habitats were only sporadically visited by carnivores and, therefore, the least hazardous for hominins. He suggested that if hominins were using wooded habitats, it must have been as refuges and safe spots (Blumenschine, 1991; Blumenschine et al., 1994; Capaldo, 1995). This was corroborated by actualistic research in wooded alluvial habitats (Domínguez-Rodrigo, 2001). For this reason, he interpreted FLK Zinj as a very dangerous spot when reconstructed to have been situated in the middle of a barren floodplain (Blumenschine and Masao, 1991). Now, given the increasing evidence that FLK Zinj was in the middle of a densely wooded habitat, Blumenschine et al. (2012) argue that this paleo-setting was dangerous because carnivores may also have been attracted to it. As far as modern proxies go, wooded alluvial habitats are the least dangerous in savanna ecosystems because they are the least frequented habitats by large mammalian predators (Domínguez-Rodrigo, 2001). Blumenschine et al. (2012) conceive of the Zinj "peninsula" as a very narrow strip of vegetation surrounded by largely open landscapes. Blumenschine et al. (2012) depicted FLKNN 1 as another topographic high in the wetland, which lacked trees and did not invite carnivore presence. This is disproved by Barboni et al.'s (2010) work, which found compelling evidence of tree vegetation in the form of phytoliths (including woody dicots and palm trees) at this site as well as at FLK Zinj. In addition, it was at FLK NN1 and not FLK Zinj that a carnivore taphonomic signal was detected (Barba and Domínguez-Rodrigo, 2007). Phytoliths show that the area between FLK Zinj and FLKNN was densely covered in wooded vegetation. If this small paleo-landscape sample surrounding both sites is indicative of closed-vegetation, no intensive use of this space by carnivores can be a heuristic argument, if using similar modern savanna environments.

Considering the FLKNN sequence, a minimum of 65 macromammal carcasses is represented (~50 at FLK Zinj, combining its upper and lower levels). A minimum of 14 large mammals is represented at FLK NN1. Therefore, FLKNN does not seem to have been a less attractive site than FLK Zinj for animals in general and carnivores in particular. Isaac's (1983) conception of sites as common-amenity places did not necessarily involve hominin–carnivore interactions of the type described by Blumenschine et al. (2012), but simply the sequential and independent use of the space. A factor not properly considered by Blumenschine et al. (2012) is that sites are essentially diachronic palimpsests of varied length. The presence of hyenas and jackals at FLK ZInj do not necessarily indicate that they interacted directly with hominins, only that they visited, and died at, the site, perhaps well before or after its use by hominins. It is highly unlikely that hominins scavenged any remains from hyenas or jackals (Blumenschine, 1986), as shown taphonomically (Bunn and Kroll, 1986; Domínguez-Rodrigo et al., 2007) Given the lack of taphonomic indicators that felids were involved with the bone accumulation at FLK Zinj and that no remains of felids were found at the site, there is no empirical support for a felid presence at FLK Zinj as potential providers of carcasses for scavenging hominins. In contrast, strong felid taphonomic signals have been identified at the three levels of FLK NN. Furthermore, there is physical evidence of their presence at the site in the form of remains belonging to *Megantereon* at FLKNN 1 (Barba and Domínguez-Rodrigo, 2007). In sharp contrast, hominin presence at FLKNN 1 is documented by heavy-duty pounding stone tools, which they did not use to process any scavengeable remains, as reflected in the absence of hominin-imparted marks on the accompanying bone assemblages. If hominins were scavenging from felids on the Zinj paleosurface, it is at FLK NN that such evidence should be found. None exists in any of the FLKNN assemblages (Domínguez-Rodrigo et al., 2007).

The discovery of chemical and especially paleobotanical (phytoliths) evidence for tress at FLK NN also shows that far from being an isolated wooded spot, FLK Zinj was part of a larger tree-covered alluvial platform, although FLK Zinj does appear to have been situated within the most densely wooded part (Ashley et al., 2010), all of which attests to its non-hazardous nature: the more closed a habitat is, the lesser the impact of carnivores (Blumenschine, 1986; Domínguez-Rodrigo, 2001). Therefore, carnivores did not need to clutter FLK Zinj with carcasses. Evidence thus shows that a) the only documented carnivores to have been at FLK Zinj are hyenas and jackals, and their roles were limited to scavenging; b) other areas with trees (FLKNN) were used primarily by felids, as both bone modification patterns and felid fossils show (this is documented similarly in FLKN higher in the stratigraphic sequence) (Domínguez-Rodrigo et al., 2007) and, further, that hominins did not process the carcasses that felids were consuming at these sites; c) crocodiles must have been a marginal element in the FLKNN wetland, certainly not common enough to have been a regular source of scavengeable carcasses given the virtual absence of crocodile-modified bones on the Zinj paleosurface, in contrast with what is documented in alluvial spots where crocodiles are active bone-modifying agents (Njau, 2006).

5. Conclusions

FLK Zinj occupied a location on the southern edge of an elevated platform by the lake floodplain. Although previous work depicted this high point as a peninsula (Ashley et al., 2010), given the similar altitude of the paleosurface at both FLK Zinj to FLKNN, the evidence recently obtained and presented in this work is more suggestive of an extensive platform extending towards the north. Judging from the preserved sedimentary sequences, the northernmost point was occupied by a localized wetland, likely caused by a spring (FLKNN 1). Although Blumenschine et al. (2012) depict FLKNN1 as an island surrounded by water in the middle of the wetland, as in the Okavango delta, the FKNN sedimentary record argues otherwise. Taphonomic work carried out on FLKNN1, FLKNN2, and FLKNN3 shows that carcasses were being transported and modified almost exclusively by carnivores (probably felids) throughout the entire sequence (Domínguez-Rodrigo et al., 2007), clearly indicating that FLKNN was not completely surrounded by water. Due to the lack of sedimentary exposure, it cannot be determined whether the wetland continued northwards past FLKNN, but its use by mammals and the abundance of tree phytoliths found within the FLKNN1 level suggest that the site, rather than being completely covered by water, was probably accessible from the westward prolongation of the platform.

Although Blumenschine et al. (2012) emphasized the open nature of the landscape surrounding FLK Zinj, the available evidence shows its mixed character (Ashley et al., 2010; Domínguez-Rodrigo et al., 2010), as supported by abundant paleoecological data (Leakey, 1965; Jaeger, 1976; Bonnefille, 1984; Shipman and Harris, 1988; Plummer and Bishop, 1994; Sikes, 1994; Spencer, 1997; Fernández-Jalvo et al., 1998; Plummer et al., 2008; Domínguez-Rodrigo et al., 2010). Blumenschine et al. (2012) fail to provide convincing evidence that waterbucks grazing on the Zinj paleosurface are indicators of open landscapes, since a) their modern counterparts are not useful indicators of open versus closed-

vegetation habitats, and b) the Olduvai Bed I waterbucks showed a different limb morphology than their modern counterparts. Specifically, they have more elongated metapodials and shorter zygopodials (Gentry and Gentry, 1978), both of which are similar to modern kob and suggest an adaptation to marshy floodplains and the margins of adjacent woodlands.

This extensive woodland on the FLK Zinj-FLKNN1 platform would probably not have constrained carnivores within a small strip of trees as suggested by Blumenschine et al. (2012) but, rather, would have enabled trophic dynamics to operate similarly to modern lacustrine and riverine alluvial forests (Domínguez-Rodrigo, 2001). It is not yet known if the area surrounding PTK was also densely wooded as at FLK Zinj and FLK NN1 (work in progress). Available evidence indicate that the dense archeological assemblage of stone artifacts, cut-marked bones, and hominin fossils at FLK *Zinj* accumulated within the confines of an isolated forest patch just 200 m from a spring-fed wetland (Ashley et al., 2010).

The fossiliferous productivity of the FLK Zinj paleolandscape, apart from the site itself, was very low. Statistically significant differences exist between bones accumulated at the core area of the site and its surrounding landscape (Domínguez-Rodrigo et al., 2010). This can be measured by simple bone counts and by the number of carcasses represented per area. This shows that bone was being concentrated in very high densities at that particular spot, and nowhere else (until one hits the PTK concentration some 400 m to the south). The presence of 50 macromammal carcasses at FLK Zinj also contrasts with the substantially lower number of individuals (average <4 MNI) documented in the random sampling of 1500 m^2 (>4 times bigger than FLK Zinj) units at Amboseli (Hill, 1975; Behenrensmeyer, 1983), further attesting to the dynamic nature of the formation of the FLK Zinj bone assemblage. The taphonomic confirmation of the human–carnivore model at the site, and the lack of empirical evidence that carnivores preceded hominins in carcass exploitation reinforces the hypothesis that the site was formed by hominins who intentionally selecting that spot for systematic transport, butchery, and consumption of carcasses, probably in a communal setting. This makes FLK Zinj one of the oldest empirically-supported "central-place" sites known in human evolution to date.

Acknowledgements

We thank the Tanzanian Commission for Science and Technology (COSTECH), the Department of Antiquities and the Ministry of Natural Resources and Tourism for permission to conduct research at Olduvai Gorge. We thank the Spanish Ministry of Science and Technology and the Ministry of Culture for funding this research through the HAR2010-18952-C02-01 Project, the Comunidad de Madrid through the S2010/BMD-2330 I+D project, and the program of Archaeological Research Abroad of the Spanish Ministry of Culture. We also thank C.P. Egeland for his comments and editorial assistance on an earlier draft of this paper.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2013.12.023

References

Albert, R.M., Bamford, M.K., Cabanes, D., 2006. Taphonomy of phytoliths and Macroplants in different soils from Olduvai gorge (Tanzania) and the Application to Plio-Pleistocene Palaeoanthropological Samples. Quaternary International 148, 78–94. http://dx.doi.org/10.1016/j.quaint.2005.11.026.

Albert, R.M., Weiner, S., 2001. Study of phytoliths in prehistoric ash layers from Kebara and Tabun Caves using a quantitative approach. In: Meunier, J.D., Colin, F. (Eds.), Phytoliths, Applications in Earth Sciences and Human History. A.A. Balkema Publishers, pp. 251–266.

Ashley, G.M., Barboni, D., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Diez-Martin, F., Barba, R., Baquedano, E., 2010. A spring and woodland: new paleoenvironmental reconstruction of FLK-Zinj, Olduvai Gorge, Tanzania. Quaternary International 74, 304–314.

Bamford, M.K., Albert, R.M., Cabanes, D., 2006. Plio-pleistocene Macroplant fossil remains and phytoliths from lowermost bed II in the eastern Palaeolake margin of Olduvai gorge, Tanzania. Quaternary International 148, 95–112.

Bamford, M.K., Stanistreet, I.G., Stollhofen, H., Albert, R.M., 2008. Late Pliocene Grassland from Olduvai gorge, Tanzania. Palaeogeography Palaeoclimatology Palaeoecology 257 (3), 280–293.

Baquedano, E., Domínguez-Rodrigo, M., Musiba, C., 2012. An experimental study of large mammal bone modification by crocodiles and its bearing on the interpretation of crocodile predation at FLK Zinj and FLK NN3. Journal of Archaeological Science 39, 1728–1737.

Barba, R., Domínguez-Rodrigo, M., 2007. FLKNN1: "living floor" or natural accumulation? In: Domínguez-Rodrigo, M., Barba, R., Egeland, C.P. (Eds.), Deconstructing Olduvai. Springer, New York, pp. 217–228.

Barboni, D., Bonnefille, R., Alexandre, A., Meunier, J.D., 1999. Phytoliths as paleoenvironmental indicators, west side middle Awash valley, Ethiopia. Palaeogeography Palaeoclimatology Palaeoecology 152 (1–2), 87–100.

Barboni, D., 2000. Signal pollinique et climat de mousson en Inde du Sud. Doctorat (Ph.D. Thesis). Université de Droit, d'Economie et des Sciences d'Aix-Marseille III, Aix-Marseille, France.

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., 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 (1–2), 29–41.

Barboni, D., Ashley, G.M., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., 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 (3), 344–354.

Behrensmeyer, A.K., 1983. Patterns of natural bone distribution on recent land surfaces: implications for archaeological site formation. In: Clutton- Brock, J., Grigson, C. (Eds.), Animals and Archaeology: Hunters and their Prey. B.A.R. International Series, 163, pp. 93–106.

Blumenschine, R.J., 1986. Early Hominid Scavenging Opportunities. Implications of Carcass Availability in the Serengeti and Ngorongoro Ecosystems. B.A.R. International Series 283, Oxford.

Blumenschine, R.J., 1991. Hominid carnivory and foraging strategies, and the socioeconomic function of early archaeological sites. Philosophical Transactions of the Royal Society London 334, 211–221.

Blumenschine, R.J., 1995. Percussion marks, tooth marks and the experimental determinations of the timing of hominin and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. Journal of Human Evolution 29, 21–51.

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., Cavallo, J.A., Capaldo, S.D., 1994. Competition for carcasses and early hominid behavioral ecology: a case study and a conceptual framework. Journal of Human Evolution 27, 197–213.

Blumenschine, R.J., Stanistreet, I.G., Njau, J.K., Bamford, M.K., Masao, F.T., Albert, R.M., Stollhofen, H., Andrews, P., Prassack, K.A., McHenry, L.J., Fernández-Jalvo, Y., Camilli, E.L., Ebert, J.I., 2012. Environments and hominin activities across the FLK Peninsula during Zinjanthropus times (1.84 Ma), Olduvai Gorge, Tanzania. Journal of Human Evolution 63, 364–383.

Bonnefille, R., 1984. Palynological Research at Olduvai Gorge. Research Reports n. 17. National Geographic Society, pp. 227–243.

Bunn, H.T., 1982. Meat-eating and Human Evolution: Studies on the Diet and Subsistence Patterns of Plio-pleistocene Hominids in East Africa. Ph. Dissertation. University of California, Berkeley.

Bunn, H.T., 1983. Evidence on the diet and subsistence patterns of Plio-Pleistocene hominids at Koobi Fora, Kenya, and at Olduvai Gorge, Tanzania. In: Clutton-Brock, J., Grigson, C. (Eds.), Animals and Archaeology: Hunters and their Prey-B.A.R. International Series 163, pp. 21–30.

Bunn, H.T., 1991. A taphonomic perspective on the archaeology of human origins. Annual Review of Anthopology 20, 433–467.

Bunn, H.T., 2001. Hunting, power scavenging, and butchering by Hadza foragers and by Plio- Pleistocene Homo. In: Stanford, C.B., Bunn, H.T. (Eds.), Meat-eating and Human Evolution. Oxford University Press, Oxford, pp. 199–218.

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., 1988. Fact and fiction about the Zinjanthropus floor: data, arguments, and interpretations (a reply to Binford). Current Anthropology 29, 135–149.

Bunn, H.T., Ezzo, J.A., 1993. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. Journal of Archaeological Science 20, 365–398.

Bunn, H.T., Pickering, T.R., 2010. Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running–hunting and passive scavenging by early Pleistocene hominins. Quaternary Research 74, 395–404.

Bunn, H.T., Mabulla, A.Z.P., Domínguez-Rodrigo, M., Ashley, G.M., Barba, R., Diez-Martin, F., Remer, K., Yravedra, J., Baquedano, E., 2010. Was FLK North levels 1–2 a classic "living floor" of Oldowan hominins or a taphonomically complex palimpsest dominated by large carnivore feeding behavior? Quaternary Research 74, 355–362.
Capaldo, S.D., 1995. Inferring Hominid and Carnivore Behavior from Dual-patterned Archaeological Assemblages. Doctoral Dissertation. Department of Anthropology, Rutgers University, New Brunswick, New Jersey.
Capaldo, S.D., 1997. Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (Zinjanthropus), Olduvai Gorge, Tanzania. Journal of Human Evolution 33, 555–597.
Chorley, R.J., Schumm, S.A., Sugden, D.E., 1984. Geomorphology. Methuen, New York.
Cole, S., 1963. The Prehistory of East Africa. Mentor Books, New York.
Diez-Martin, F., Sánchez-Yustos, P., Uribelarrea, D., Domínguez-Rodrigo, M., Fraile-Márquez, C., ;Díaz-Muñoz, I., Obregón, R.A., Mabulla, A., Baquedano, E., Pérez-González., A., 2014. New archaeological and geological research at SHK main site (Bed II, Olduvai Gorge, Tanzania). Quaternary International (submitted for publication).
Domínguez-Rodrigo, M., 1997. Meat-eating by early hominids at the FLK 22 Zinjanthropus site, Olduvai Gorge, Tanzania: an experimental approach using cut mark data. Journal of Human Evolution 33, 669–690.
Domínguez-Rodrigo, M., 2001. A study of carnivore competition in riparian and open habitats of modern savannas and its implications for hominid behavioral modelling. Journal of Human Evolution 40, 77–98.
Domínguez-Rodrigo, M., Pickering, T.R., 2003. Early hominids, hunting and scavenging: a summary of the discussion. Evolutionary Anthropology 12, 275–282.
Domínguez-Rodrigo, M., Barba, R., 2006. New estimates of tooth marks and percussion marks from FLK Zinj, Olduvai Gorge (Tanzania): the carnivore-hominid-carnivore hypothesis falsified. Journal of Human Evolution 50, 170–194.
Domínguez-Rodrigo, M., Barba, R., 2007. Five more arguments to invalidate the passive scavenging version of the carnivore–hominid–carnivore model: a reply to Blumenschine et al., (2007). Journal of Human Evolution 53, 427–433.
Domínguez-Rodrigo, M., Barba, R., Egeland, C.P., 2007. Deconstructing Olduvai. Springer, New York.
Domínguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Ashley, G.M., Diez-Martin, F., Barboni, D., Prendergast, M.E., Yravedra, J., Barba, R., Sánchez, A., Baquedano, E., Pickering, T.R., 2010. New excavations at the FLK Zinjanthropus site and its surrounding landscape and its behavioral implications. Quaternary Research 74, 315–332.
Domínguez-Rodrigo, M., Bunn, H.T., Yravedra, J., 2014. A critical re-evaluation of bone surface modification models for inferring fossil hominin and carnivore interactions through a multivariate approach: application to the FLK Zinj archaeofaunal assemblage (Olduvai Gorge, Tanzania). Quaternary International 322-323, 32–43.
Fernández-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y., Humphrey, L., 1998. Taphonomy and palaeocology of Olduvai bed I (Pleistocene, Tanzania). Journal of Human Evolution 34, 137–172.
Ferraro, J.V., Plummer, T.W., Pobiner, B.L., Oliver, J.S., Bishop, L.C., Braun, D.R., Ditchfield, P., Seaman III, J.W., Binetti, K., Seaman, J.W., Hertel, F., Potts, R., 2013. Earliest archaeological evidence of persistent hominin carnivory. PLoS ONE 8 (4), e62174. http://dx.doi.org/10.1371/journal.pone.0062174.
Fregenal-Martínez, M.A., Meléndez, N., 2010. Lagos y sistemas lacustres. In: Arche, A. (Ed.), Sedimentología, del proceso físico a la cuenca sedimentaria. Consejo Superior de Investigaciones Científicas, Madrid.
Gentry, A.W., Gentry, A., 1978. Fossil bovidae (Mammalia) from Olduvai gorge, Tanzania. London, Bulletin of the British Museum 29 (29), 289–446.
Gierlowski-Kordesch, E., Kelts, K. (Eds.), 1994. Global Geological Record of Lake Basins. World and Regional Geology Series, vol. I. Volume 4. Cambridge.
Glen, C., Kelts, K., 1991. Sedimentary rythms inlake deposits. In: Einsele, G., Ricken, W., Seilacher, A. (Eds.), Cycles and Events in Stratigraphy. Springer–Verlag, Berlin, pp. 188–221.
Greenway, P.J., Vesey-Fitzgeral, D.F., 1969. Vegetation of lake Manyara National Park. Journal of Ecology 57 (1), 127–149.
Hay, R., 1976. Geology of the Olduvai Gorge. University of California Press, Berkeley.
Hill, A., 1975. Taphonomy of Contemporary and Late Cenozoic East African Vertebrates. Ph. D. dissertation. University of London.
Hutchinson, G.E., 1957. A Treatise on Limnology I, Geography, Physiscs and Chemistry. John Wiley and Sons, New York.
Isaac, G.L., 1978. The food-sharing behavior of protohuman hominids. Scientific American 238, 90–108.
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 1. Hunters and Their Prey, B.A.R. International Series, vol. 163. Archaeopress, Oxford, pp. 3–19.
Jaeger, J.J., 1976. Les rongeurs (Mammalia, Rodentia) du Pleistocene Inferieur d'Olduvai Bed I (Tanzanie), 1 partie: les muridés. In: Savage, R.J.G., Coryndon, S.C. (Eds.), Fossil Vertebrates of Africa, vol. 4Academic Press, London, pp. 57–120.
Jackson, M.L., 1956. Soil Chemical Analysis: Advanced Course. Wisconsin, Madison.
Kelly, S.B., Olsen, H., 1993. Terminal fans: a review with reference to Devonian examples. Sedimentary Geology 85, 339–374.
Leakey, L., 1965. Olduvai Gorge 1951–1961. A Preliminary Report on the Geology and Fauna. Cambridge University Press, Cambridge.
Leakey, M., 1971. Olduvai Gorge. In: Excavations in Bed I and II, vol. 3. Cambridge University Press, Cambridge, pp. 1960–1963.
Lentfer, C.J., Boyd, W.E., 1998. A comparison of three methods for the extraction of phytoliths from sediments. Journal of Archaeological Science 25, 1159–1183.
McHenry, L.J., 2005. Phenocryst composition as a tool for correlating fresh and altered tephra, Bed I, Olduvai Gorge, Tanzania. Stratigraphy 2, 101–115.
Miall, A.D., 2006. The Geology of Fluvial Deposits. Sedimentary Facies, Basin Analysis, and Petroleum Geology. Springer–Verlag, Berlin Heidelberg.
Mulholland, S.C., 1989. Phytolith shape frequencies in north Dakota grasses: a comparison to general patterns. Journal of Archaeological Science 16, 489–511.
Njau, J.K., 2006. The Relevance of Crocodilians to Oldowan Hominin Paleoecology at Olduvai Gorge. Ph.D. Dissertation. The State University of New Jersey, Rutgers.
Njau, J.K., Blumenschine, R.J., 2006. A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai basin, Tanzania. Journal of Human Evolution 50, 142–162.
Njau, J.K., Blumenschine, R.J., 2012. Crocodylian and mammalian carnivore feeding traces on hominin fossils from FLK 22 and FLK NN 3, Plio-Pleistocene, Olduvai Gorge, Tanzania. Journal of Human Evolution 42 (2), 408–417.
Novello, A., 2012. Les phytolithes, marqueurs des environnements mio-pliocènes du Tchad. Reconstitution à partir du signal environnemental des phytolithes dans l'Afrique subsaharienne actuelle. Doctorat (Ph. D. thesis). Université de Poitiers, Poitiers, France.
Novello, A., Barboni, D., Berti-Equille, L., Mazur, J.C., Poilecot, P., Vignaud, P., 2012. Phytolith signal of aquatic plants and soils in Chad, Central Africa. Review of Palaeobotany and Palynology 178, 43–58.
Oliver, J.S., 1994. Estimates of hominid and carnivore involvement in the FLK Zinjanthropus fossil assemblage: some socioecological implications. Journal of Human Evolution 27, 267–294.
Pante, M.C., Blumenschine, R.J., Capaldo, S.D., Scott, R.S., 2012. Validation of bone surface modification models for inferring hominin and carnivore feeding interactions, with reapplication to FLK 22, Olduvai Gorge, Tanzania. Journal of Human Evolution 63, 395–407.
Parkinson, D., 2013. A GIS Image Analysis Approach to Documenting Oldowan Hominin Carcass Acquisition: Evidence from Kanjera South, FLK Zinj and Neotaphonomic Models of Carnivore Bone Destruction. Ph. D. dissertation. Dept. Anthropology, University of New York.
Piperno, D.P., 1988. Phytolith Analysis — an Archaeological and Geological Perspective. Academic Press/Harcourt Brace Jovanovich, New York, USA.
Plummer, T.W., Bishop, L.C., 1994. Hominid paleocology at Olduvai gorge, Tanzania, as indicated by antelope remains. Journal of Human Evolution 27, 47–76.
Plummer, T.W., Bishop, L.C., Ditchfield, P.W., Ferraro, J.V., Kingston, J.D., Braun, D., 2008. Hominin activities at Kanjera south, Kenya. In: Hovers, E., Braun, D. (Eds.), Interdisciplinary Approaches to the Oldowan. Springer, New York, pp. 149–160.
Potts, R., 1988. Early Hominid Activities at Olduvai. Aldine, New York.
Preston, F.W., 1962. The canonical distribution of commonness and rarity: Part I. Ecology 43 (2), 185–215.
Rose, L., Marshall, F., 1996. Meat eating, hominid sociality, and home bases revisited. Current Anthropology 37, 307–338.
Selvaggio, M.M., 1994. Identifying the Timing and Sequence of Hominid and Carnivore Involvement with Plio-pleistocene Bone Assemblages from Carnivore Tooth Marks and Stone-tool Butchery Marks on Bone Surfaces. Unpublished Ph. D. Dissertation. Rutgers University.
Sahnouni, M., Rosell, J., van der Made, J., Vergés, J.M., Ollé, A., Kandi, N., Harichane, Z., Derradji, A., Medig, M., 2012. The first evidence of cut marks and usewear traces from the Plio-Pleistocene locality of El-Kherba (Ain Hanech), Algeria: implications for early hominin subsistence activities circa 1.8 Ma. Journal of Human Evolution 64, 137–150.
Shillito, L.M., 2013. Grains of truth or transparent blindfolds? A review of current debates in archaeological phytolith analysis. Vegetation History and Archaeobotany 22, 71–82.
Shipman, P., Harris, J.M., 1988. Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa. In: Grine, F.E. (Ed.), Evolutionary History of the "Robust" Australopithecines. Aldine de Gruyter, New York, pp. 343–382.
Sikes, N., 1994. Early hominid habitat preferences in East Africa: paleosol carbonate isotopic evidence. Journal of Human Evolution 27, 25–45.
Spencer, L.M., 1997. Dietary adaptations of Plio-Pleistocene Bovidae: implications for hominin habitat use. Journal of Human Evolution 32, 201–228.
Strahler, A.N., 1997. Physical Geography: Science and Systems of the Human Environment. John Wiley and Sons, United States of America.
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 Hypsodonty in Equids. PhD. University of California, Berkeley.
Strömberg, C.A.E., 2009. Methodological concerns for analysis of phytolith assemblages: does count size matter? Quaternary International 193, 124–140.
Summerfield, M.A., 1991. Global Geomorphology. Longman Scientific and Technical, Essex, UK.
De la Torre, I., Mora, R., 2005. Unmodified lithic material at Olduvai Bed I: manuports or ecofacts? Journal of Archaeological Science 32, 273–285.
Turnbridge, I.P., 1984. Facies model for a sandy ephemeral stream and clay playa complex; the Middle Devonian Trentishoe Formation of North Devon. U.K. Sedimentology 31, 697–715.
WoldeGabriel, G., Ambrose, S.H., Barboni, D., Bonnefille, R., Bremond, L., Currie, B., DeGusta, D., Hart, W.K., Murray, A.M., Renne, P.R., Jolly-Saad, M.C., Stewart, K.M., White, T.D., 2009. The geological, isotopic, botanical, invertebrate, and lower vertebrate surroundings of *Ardipithecus ramidus*. Science 326, 65e1–65e5.