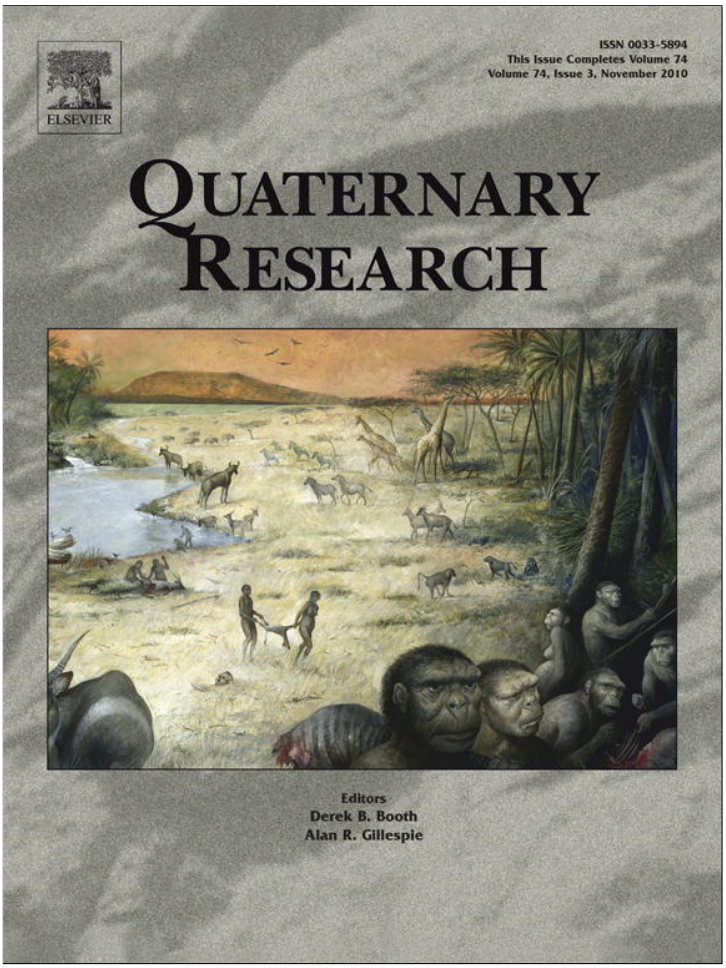

Quaternary Research 74 (2010) 315–332

Contents lists available at ScienceDirect

Quaternary Research

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

New excavations at the FLK *Zinjanthropus* site and its surrounding landscape and their behavioral implications

M. Domínguez-Rodrigo [a,b,*], H.T. Bunn [c], A.Z.P. Mabulla [d], G.M. Ashley [e], F. Diez-Martin [f], D. Barboni [g], M.E. Prendergast [h], J. Yravedra [b], R. Barba [b], A. Sánchez [i], E. Baquedano [a,j], T.R. Pickering [c,k]

[a] IDEA (Instituto de Evolución en África), Museo de los Orígenes, Plaza de San Andrés 2, 28005 Madrid, Spain
[b] Department of Prehistory, Complutense University, Prof. Aranguren s/n, 28040 Madrid, Spain
[c] Department of Anthropology, University of Wisconsin-Madison, 1180 Observatory Drive, Madison, Wisconsin, 53706, USA
[d] Archaeology Unit, University of Dar es Salaam, Dar es Salaam, P.O. Box 35050, Tanzania
[e] Department of Geological Sciences, Rutgers University, 610 Taylor Road, Piscataway, NJ 08854, USA
[f] Department of Prehistory and Archaeology, University of Valladolid, Plaza del Campus s/n, 47011 Valladolid, Spain
[g] CEREGE (UMR6635 CNRS/Université Aix-Marseille), BP80, F-13545 Aix-en-Provence cedex 4, France
[h] Department of Anthropology, Harvard University, Cambridge, MA 02138, USA
[i] Catalonian Institute of Paleontology, Autonomous University of Barcelona, 08193 Cerdanyola, Spain
[j] Museo Arqueológico Regional, Plaza de las Bernardas s/n, 28801 Alcalá de Henares, Madrid, Spain
[k] Institute for Human Evolution, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa

ARTICLE INFO

Article history:
Received 17 November 2009
Available online 21 August 2010

Keywords:
Olduvai Gorge
Landscape archaeology
Palaeoecology
Site formation
Taphonomy

ABSTRACT

Renewed excavations at FLK Zinj and its surrounding landscape have yielded valuable information regarding its paleoecological situation and the prehistoric behavioral function of the site. The density of materials at the main cluster of the site excavated by Leakey contrasts with the bone and lithic scatters surrounding the site. The location of FLK Zinj, situated a few hundred meters away from a freshwater spring, would have enabled hominins access to water, plants and game. The appeal of the spot for hominins (also explained by the presence of a wooded habitat) is confirmed by inferences of its redundant use prior and during the formation of the FLK Zinj paleosol, as witnessed by materials accumulated both under and on the waxy clay deposit that constitutes the FLK Zinj stratum. The single-cluster nature of the site indicates central-place behavior and evidence is provided that hominins occupied the site at a time of very low predation hazards in the area.

Introduction

The FLK 22 *Zinjanthropus* (FLK Zinj) site (1.84 Ma) in Bed I, Olduvai Gorge (Tanzania), has played a pivotal role in the reconstructions of early Pleistocene hominin behavior for the past three decades. Paleoanthropological data from the site have been used to infer "home base", "central place foraging" and "food sharing" behaviors by early hominins (Isaac, 1978, 1981, 1983; Bunn, 1982, 1983; Bunn and Kroll, 1986, 1988; Rose and Marshall, 1996; Domínguez-Rodrigo, 2002), where ungulate carcasses were transported to the site after having been obtained through hunting and/or confrontational scavenging (see review in Domínguez-Rodrigo et al., 2007). FLK Zinj has also been used to support passive scavenging models based on the interpretation of the site as a time-averaged carnivore kill site (Binford, 1981), a hominin refuge (Blumenschine, 1991; Blumenschine et al., 1994) and a carcass processing spot with stone caching (Potts, 1988) resulting as an epiphenomenon of hominin stone raw material transport and discard behavior (Potts, 1991). Under the latter group of models, FLK Zinj was considered as an unremarkable area in a barren lacustrine floodplain (Blumenschine and Masao, 1991), based on Hay's (1976) original interpretation of its geological context as a "near-lake" location. It was also claimed that the site, as well as others from Olduvai Beds I and II, are not necessarily paleoanthropologically high-density anomalies on the landscape—since, in the specific case of FLK Zinj, it was initially conceived as a patch (localized concentration of bones and lithics) in contrast to the surrounding, low-density scatters of materials—but similar to other unremarkable patches in the nearby paleoenvironments (Blumenschine and Masao, 1991). If this is true, it means that the biotic agents who accumulated the bones at FLK Zinj did not intentionally select the spot over others to carry out their taphonomically documented activities.

FLK Zinj and all other Bed I sites (except DK) are clustered in a very small area of Olduvai Gorge. There are at least two possible reasons that this is the case. First, it could be mere coincidence. Second, it could be a reflection of specific landscape and/or habitat feature(s) that attracted prehistoric hominins and carnivores to preferentially carry-out some of their subsistence activities in this discrete area. The ecotones in modern savannas where carnivore predation occurs most frequently and where

* Corresponding author. Department of Prehistory, Complutense University, Prof. Aranguren s/n, 28040 Madrid, Spain.
E-mail address: manueldr@ghis.ucm.es (M. Domínguez-Rodrigo).

0033-5894/$ – see front matter © 2010 University of Washington. Published by Elsevier Inc. All rights reserved.
doi:10.1016/j.yqres.2010.07.003

subsequent hominin scavenging is theoretically feasible are obviously not favorable for "central place foraging" behaviors by hominins. Instead, paleoanthropological indications of hominin central places are predicted in reconstructed paleohabitats that are inferred to have had low carnivore competition and risk (Domínguez-Rodrigo, 2001), or where such risk was reduced by the presence of natural features like climbable trees. Determining whether FLK Zinj was created in such a habitat or ecotone is of utmost relevance, given that the use of such ecotones by hominins does not seem to have been unusual (e.g., FxJj50 at Koobi Fora, Kenya (Bunn et al., 1980)). However, other than the rather ambiguous "near-lake" location of FLK Zinj provided by Hay (1976), no more detailed paleoecological reconstruction of the locale has been elaborated in the half-century since it was excavated.

That type of fine-scale paleoecological reconstruction is essential for a fuller picture of the site's prehistoric function for early hominins and other animals. The taphonomic indicators suggesting primary access to complete ungulate carcasses by hominins, presumably through hunting and/or confrontational scavenging (Bunn and Kroll, 1986; Domínguez-Rodrigo et al., 2007) has elicited alternative scenarios that hominins may have acquired large amounts of carcass flesh from herd ungulates who died in mass drownings (Capaldo and Peters, 1995) or in droughts (Lam, 2008). These alternatives to hominin hunting/confrontational scavenging obviously required opposing ecological conditions: mass drownings occur in wet conditions (wet season) and droughts occur in very arid and dry circumstances (prolonged dry season). Again, prior to the current work discussed here, there was little information to test these alternative hypotheses or any other proposed climatic scenarios involving ancient FLK Zinj.

Fifty years after Mary Leakey excavated FLK Zinj, the advance of the analytical techniques currently available (soil isotope signatures, bone and teeth isotopic components, study of phytoliths, soil mineral composition) allows us to now test these alternative hypotheses about the paleoecology and behavioral dynamics of FLK Zinj. In order that TOPPP (The Olduvai Paleoanthropology and Paleoecology Project) could apply some of these techniques to FLK Zinj, we necessarily had to expose and sample from a larger surface of the FLK Zinj paleoanthropological level both on- and offsite. The offsite work provides the clues about the vital, wider paleoecological context and the conditions that led to the formation of FLK Zinj in its precise locale and not somewhere else. This expansive field approach allowed us to thoroughly test the various hominin behavioral reconstructions for FLK Zinj discussed above.

Our results support the hypothesis that the FLK Zinj locality functioned as a spot consciously selected by hominins to carry out specific activities, as a result of which anthropogenic materials and hominin feeding refuse accumulated there in a much higher density than observed in the immediate area surrounding the site. The significance of these results are amplified because FLK Zinj is one of only two (the other being BK, upper Bed II, (Domínguez-Rodrigo et al., 2009)) primarily anthropogenically derived sites >1.0 Ma from Olduvai Gorge (Domínguez-Rodrigo et al., 2007). The site is truly a rare gem among paleoanthropological localities.

Sample and methods of data recovery and analysis

Excavating the FLK Zinj area

The FLK Zinj site occupies the southernmost gully of the area comprised by the FLK sites (FLK, FLK N and FLK NN) (Leakey, 1971). It was hypothesized that the FLK NN 1 site was contemporaneous with FLK Zinj (Leakey, 1971). Since FLK NN 1 occupies the northernmost part of the area covered by the three sites, we decided to sample all the area between FLK Zinj and FLK NN by excavating large test trenches between them in outcrops that contain the waxy clay sediments overlain by Tuff IC, which enclose the FLK Zinj archaeological level time period.

In addition, to test both the FLK Zinj level around Leakey's main excavation at FLK and the areas away from the site toward the north (Fig. 1), three trenches were opened to the east and south of the main excavation (FLK T1, FLK T5, and FLK T6), and two more were opened across from the gully into the sedimentary wall that transitions between FLK and FLK N (FLK T4 and FLK T7). Two other elongated trenches along a profile exposed by Leakey's excavation of the site were opened at FLK NN (FLK NNT1 and FLK NNT2). These two latter trenches were excavated strictly for geological purposes, and given that they were not archaeological trenches and that no archaeological materials were found in them, they will not be counted when adding the total area of the FLK Zinj level exposed in analyses discussed here. Between FLK N and FLK NN, two trenches were opened following an outcrop that is exposed to the west of both sites (FLK NWT1 and FLK NWT2). In all these trenches described, the FLK Zinj paleosurface was exposed and excavated. In total, seven trenches were excavated exposing 57 m^2 of FLK Zinj paleosurface. In other words, our excavations increased the area of FLK Zinj paleosol previously exposed (that corresponding to the main excavation by Leakey) by ~20%. The total area sampled by these trenches in the FLK Zinj gully alone extends over 3000 m^2 (Fig. 2).

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 2-mm mesh was systematically carried out. Only selected sediment for microfaunal research was wet-sieved with a finer mesh (1 mm). Trenches were not divided into smaller one-meter squares (except for FLKT1) since our use of total stations guaranteed extreme accuracy in plotting the spatial distribution of stone artifacts and fossil bones. Due to its larger size compared to other trenches, FLK T1 was excavated in a 1-m^2 grid upon reaching the FLK Zinj level. The lithological criterion (excavation followed natural layers) was hierarchically superior to the artificial spit criterion in deciding the way the excavation proceeded. Excavations through the sedimentary sequence at each trench was by 10-cm spits within each of the geological layers.

Trenches

A description of the trenches targeting the FLK Zinj stratum follows, but does not repeat previously published information on the geological sequence of Olduvai Bed I (for those details, see Hay (1976) and Ashley et al. (2010)) (Fig. 1).

FLK T1 is a 4×3 m trench, excavated from just above the Nge'ju Tuff, down to the tuffaceous clay underlying the waxy clay, which comprises the FLK Zinj level (Fig. 1). FLK T1 is situated on the east wall of Leakey's main excavation. The FLK Zinj geological layer in FLK T1 averages 20 cm in thickness and consists of green waxy clay, with a minor silt component.

FLK T5 is a 2×2 m trench placed ~20 m to the southeast of the main excavation. Vertically, it extends from the top of Tuff ID to the base of the FLK Zinj level waxy clay. Thickness of the clay is 18–21 cm.

FLK T6 is a 2×2 m trench located 18 m to the east of the main excavation, extending from the top of Tuff IC to the top of Tuff IB. The Tuff IC and the FLK Zinj clay levels are disturbed in the east side of the trench. The undisturbed waxy clay has an average thickness of 23 cm.

FLK T4 is a 2×2 m trench that occupies the bottom of a geological step-trench, which exposes the stratigraphy from the base of Tuff IF to the FLK Zinj level. The trench is located on the north side of the main Leakey excavation and about 30 m north from FLK T1. The mean thickness of the FLK Zinj waxy clay is 20–22 cm.

FLK T7 is a 2×2 m trench that is positioned 10 m east of FLK T4, following the front of the same outcrop across from the gully where the main excavation lies. The sedimentary sequence started on the clays overlying Tuff IC and continued down to the tuffaceous clays

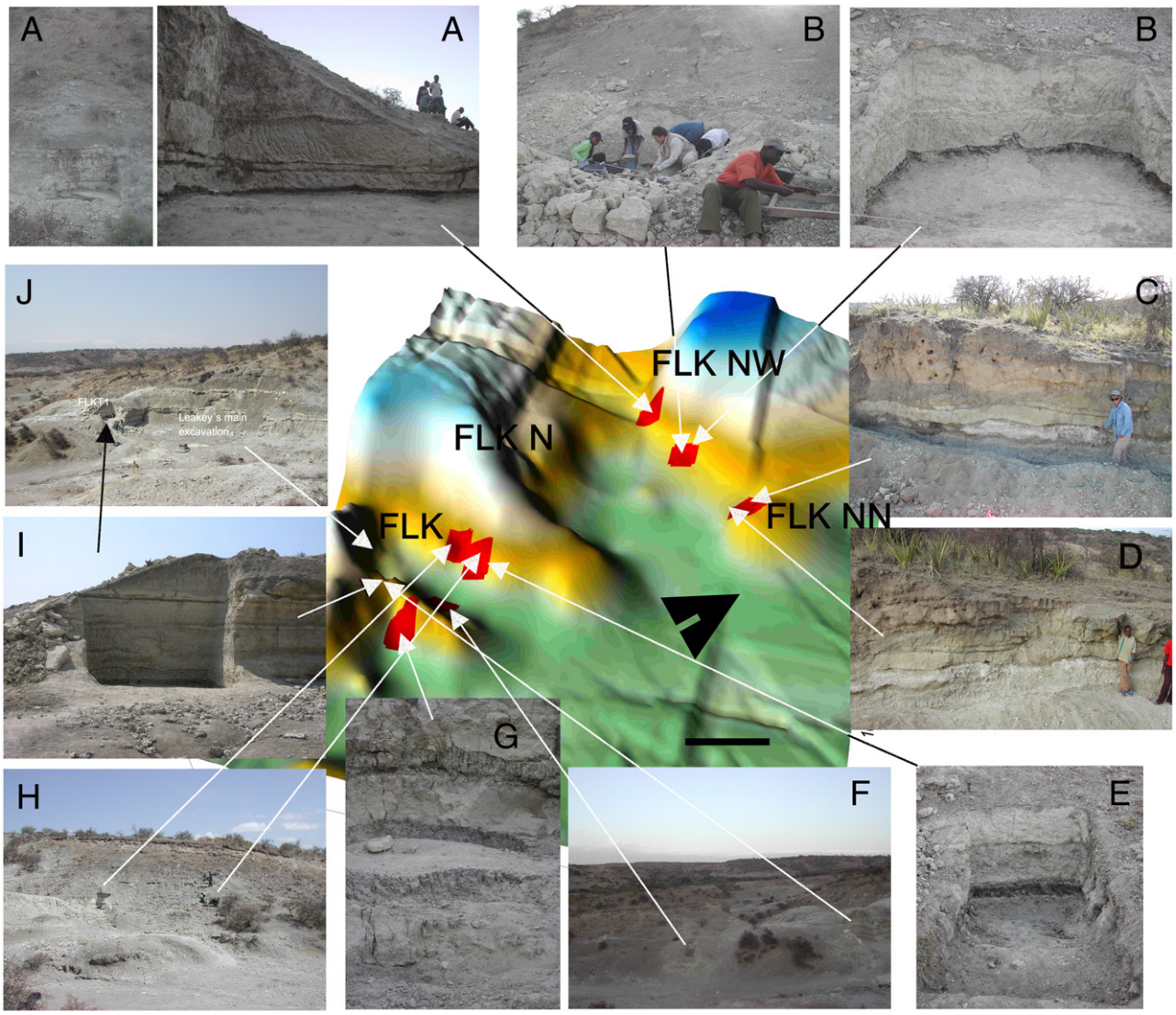

Figure 1. Distribution of all the test trenches carried out in the FLK, FLK NW and FLK NN gullies. Photos show images of trenches. A, FLK NWT1; B, FLK NWT2; C, FLK NN (east side); D, FLK NN (west side); E, FLK T7; F, location of FLK T1 (right) and FLK T6 (left); G, FLK T5; H, location of FLK T4 (left) and FLK T7 (right); I, FLK T1; J, location of FLK T1 by Mary Leakey's main excavation. See Fig. 2 for a scale of the area. Scale bar in the reconstructed topography = 50 m. Black arrow points north.

underlying the FLK Zinj waxy clay. The waxy clay is homogeneous in texture and its thickness varies from 18 to 22 cm.

FLK NWT1 is a 4 × 4 m trench situated between FLK N and FLK NN. When combined with FLK T1, these two trenches comprise the largest area we excavated. FLK NWT1, located on a corner of the outcrop where the western and northeastern walls meet, extends from just above the Nge'ju Tuff to the bottom of the FLK Zinj waxy clay. The average thickness of the FLK Zinj waxy clay on the two exposed walls is slightly thinner than at the FLK trenches: 12 cm in the north wall and 17 cm in the west wall.

FLK NWT2 is a 3 × 3 m trench that is set 25 m north of FLK NWT1, following the same outcrop. Excavation of FLK NWT2 started at the top of Tuff IC, which reaches a considerable thickness in this trench and is harder here than at any other trench, making excavation more difficult. The underlying FLK Zinj level was also slightly thinner in FLK NWT2 than in the FLK area, with an average thickness of 16 cm. The trench showed a small fault in the middle of the excavation, which occurred prior to depositions of Tuff IC.

The FLK Zinj waxy clay in the FLK NW trenches is different than in the FLK area. Whereas in the latter, the geological layer is almost pure waxy clay from top to bottom, in the FLK NW trenches the clay shows white laminated bands (Fig. 3) reminiscent of what in the geo-trenches, a few meters away at FLK NN, is a carbonate deposit of tufa, resulting from the diagenesis of soil due to the presence of fresh water (Fig. 4) (Ashley et al., 2010). When acid was applied to the clay in the FLK NW trenches, it was revealed as diatomite lenses, indicating the ancient presence of water. This interpretation is supported by the abundant aquatic fauna, including fish, turtle and waterfowl bones, recovered from FLKNWT1.

The analytical sample

The samples used for analysis consists of the stone artifacts and the fossils retrieved in each trench (Table 1). Analyses were carried out measuring the density of remains contained in the FLK Zinj waxy clay layer in each trench and comparing them to detect meaningful differences in material density across the landscape. The statistical tests applied in the analysis are described below. Fossil bones, identified to skeletal part, carcass size and taxon (when possible), were also carefully inspected for bone surface modifications. In addition to fossil and stone tool densities, a comparison of the FLK Zinj bovid diversity to bovid diversity in several modern African ecosystems was conducted to provide a more accurate reconstruction of the FLK Zinj paleoecology.

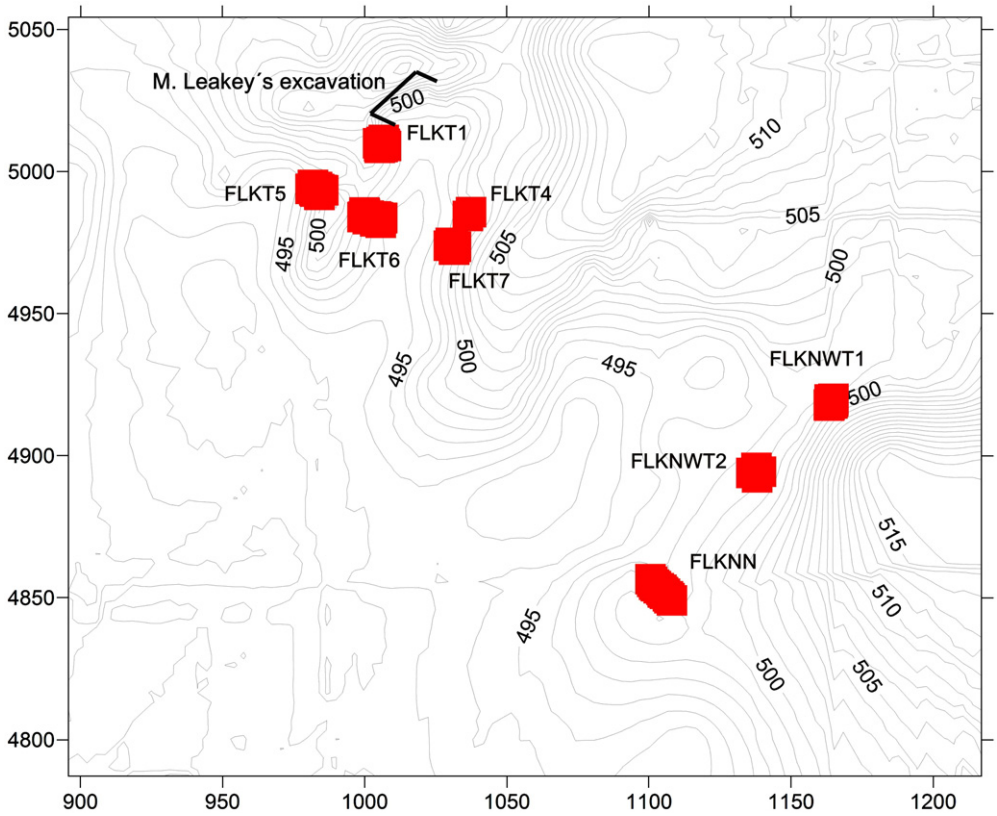

Figure 2. Topographic distribution of all the trenches excavated. Symbols do not show the actual trench sizes.

Statistical treatment of data

Samples from the densities of stone tools and fossils from each trench were inspected for normality using Shapiro–Wilks tests, which are more adequate for small samples than are Kormogorov–Smirnov tests. The non-normal distribution of the samples required the use of non-parametric tests. For the purpose of comparing densities of materials across the Zinj landscape, Kruskal–Wallis H test was used. This test is a nonparametric alternative to one-way analysis of variance. It tests the null hypothesis that samples do not differ in mean rank for the criterion variable. By taking rank, instead of median, it is very powerful in situations of skewed distribution of data and reveals differences among multiple groups. For pairwise comparisons between trenches, the Mann–Whitney U test was used. Although less powerful when the basic assumptions are not met, one-way ANOVA post-hoc statistical tests such as Bonferroni test (for unequal group sizes) were used for pairwise comparisons, so that Type I errors could be avoided. This will be shown as a contrast to the nonparametric tests.

Comparisons between the FLK Zinj bovid diversity and the bovid tribe representation of a large array of ecosystems were made in order to provide ecological proxies for the site. For this purpose, a hierarchical agglomerative cluster analysis of several African national parks representing wooded biomes and more open savanna landscapes was made. The proximity matrix was obtained using the square Euclidean distance and the dendrogram was constructed using the method of average linkage between groups. This was a preferred method over Ward's, because the latter's algorithm is biased towards producing clusters with the same number of members and requires a normal distribution of the sample. To strengthen the conclusions of the cluster analysis, a ternary graph was programmed in R, using all the data from each bovid group and bootstrapped 10,000 times with replacement.

Measuring the density of remains at FLK Zinj

All the trenches, except FLK T6, yielded lithic artifacts and/or fossils in the FLK Zinj paleosol, implying that hominins did not concentrate *all* their material-discard activities just in Leakey's main excavation area. Unexpectedly, the revealed archaeological materials occurred both at the top of the waxy clay, at the contact with the base of Tuff IC and in the top 10 cm of the clay (as documented by M. Leakey, 1971), *and* at the base of the waxy clay, in contact with the underlying tuffaceous clay; this was, again, the case for every trench but FLK T6, which was likely disturbed (Fig. 5). In Leakey's excavated collection, some archaeological specimens are so heavily encrusted in consolidated sediment, that they were preserved with the adhering sedimentary matrix. In our newly excavated sample from Leakey's main site, we have only observed this phenomenon on bones recovered from the lower level of the FLK Zinj clay. The only other newly excavated sample in which we have documented this consolidated sediment is in the upper level of the FLK Zinj waxy clay at FLK NWT1 (see Fig. 5A). This indicates that there were at least two distinct intervals during which hominins used the area and discarded materials on the ground during the formation of the FLK Zinj waxy clay. How these new details impact previous interpretations of FLK Zinj remains to be seen. Leakey (1971) clearly described that her assemblage from FLK Zinj was excavated from the upper 10 cm of clay, most specifically in contact with the overlying Tuff IC. In fact, Leakey comments that she had to wet the tuff the evening before each excavation in order to detach the underlying bones from the base of the tuff surface. Thus, we have no reason to believe that the contents of the FLK Zinj paleosol have a different provenience. However, it is necessary to emphasize that several of the specimens Leakey retrieved were very possibly located at or near the base of the waxy clay, as we have documented in FLK T1, FLK T4, FLK T5, FLK NWT1, and FLK NWT2.

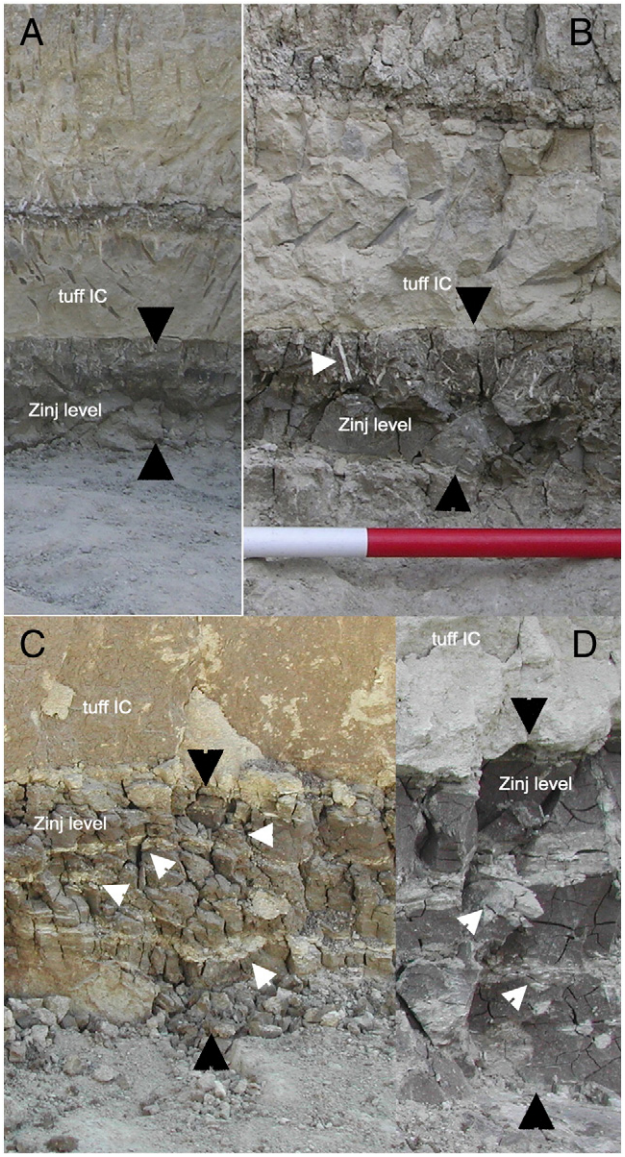

Figure 3. Aspect (at different scales) of the waxy clay level containing the FLK Zinj archaeological horizon: A, FLK T1; B, FLK T4; C, FLK NW1; D, FLK NW2. A and B show the typical clay texture found in trenches made in the FLK gully, with carbonated bioturbations (white arrows) on top of the sequence and waxy clay on the remaining part of the sequence. C and D show the structure of the same geological level at FLK NW, where the waxy clay is interbedded with carbonate levels and concretion nodules (white arrows), showing a greater presence of humidity in the paleoenvironment. Black arrows show the upper and lower boundaries of the FLK Zinj waxy clay level.

Given the impossibility of separating the materials from the upper FLK Zinj level (first 10 cm of the waxy clay) from the few retrieved from the lower FLK Zinj level (the surface of the underlying tuffaceous clay and the overlying 5 cm of the waxy clay separated by an archaeologically sterile mid-section of the waxy clay) in Leakey's collection, we analyze their density by combining trench data for that from the top and bottom of the FLK Zinj waxy clay level in each trench. Unfortunately, the best way to compare the background density of fossils and artifacts to that excavated by Leakey from FLK Zinj began by counting the number of fossil specimens and lithics per square meter plotted on her original site map. We overlaid a grid composed of 1 m^2 units on Leakey's (1971) site distribution map to accomplish these counts per square meter: only remains from complete squares were counted and, because they do not include materials recovered during sieving, our counts underestimate the actual totals from Leakey's original excavations (Fig. 6). As a result of these counts, Leakey's map was divided into three areas: one containing a dense cluster of materials and surrounding areas to its south and west containing scatters of materials (Fig. 6).

The archaeological materials that we excavated from the new trenches were also tallied per square meter. Statistical analysis of the density of materials between the areas at the main excavation and each of the new trenches was carried out by using non-parametric tests since the samples are not normally distributed and heterocedastic despite logarithmic and square-rooted transformations (see above Sample and methods of data recovery and analysis).

There is a sharp contrast between the FLK Zinj cluster and all other areas in density of recovered materials (Table 1; Fig. 7). The scatter south of the main cluster at FLK Zinj is also materially denser than the rest of the sampled surrounding landscape. The trenches in the FLK gully show a higher density of lithics than those from FLK NW. Based on mean material density values, the cluster area and the south scatter at FLK Zinj seem to contrast with the density of materials across the sampled surrounding landscape. Interestingly, FLK T4 shows a higher fossil density value than does the west scatter at FLK Zinj, suggesting that early hominin activities (assuming the bones in FLK T4 are of anthropogenic derivation) were not restricted just to the vicinity of the main cluster area.

A Kruskall–Wallis test (Table 2) shows that there are significant differences ($H(\chi^2) = 55.3$; $p = .000$) in bone density values across the landscape sampled, with the highest concentrations in the FLK Zinj main cluster area, in the south scatter, in FLK T4 and in the west scatter. This is also the case for lithic densities ($H(\chi^2) = 48.6$; $p = .000$) (Table 3), but with a more defined contrast between the FLK Zinj main cluster and the south scatter compared to the other trenches, and a marked decrease in density according to distance from the main cluster. This suggests that most stone tool-discarding activities were spatially concentrated around the FLK Zinj main cluster and south scatter areas. It also shows that lithic and bone densities are independent phenomena, given the significantly higher presence of bones at FLK NWT1 due to natural non-anthropogenic processes (see below).

A pairwise comparison (Mann–Whitney tests) of fossil densities from all the excavated areas demonstrates important differences between the west and the south FLK Zinj bone scatter areas and the fossil densities in the newly excavated trenches, but these differences are not statistically significant. However, all the pairwise comparisons between the main FLK Zinj cluster and the other trenches (areas) reveal that there are important and significant differences in densities of bones distributed across the landscape (Table 4). Even the west and south scatter areas show significant contrasts in bone concentration values.

When the Mann–Whitney test is applied to the lithic density data, the FLK Zinj main cluster is also significantly denser in artifact concentration than is the rest of the sampled surrounding landscape, as are the south and the west FLK Zinj scatters in several comparisons (Table 5). The greater number of significant values in Table 4 for lithics when compared to bones (Table 4) indicates a greater contrast in lithic densities, which suggests that stone tools are more spatially concentrated at FLK Zinj than bones and that their occurrence along the paleolandscape is less diffuse. This indicates that hominin butchery activities were focused at the site; an inference corroborated by the lack of hominin modified bones in any of the newly excavated trenches and their concentration at the FLK Zinj main cluster and south and west scatter areas.

Because of the heterocedastic nature of our sample, one predicts that Bonferroni tests of our data should not yield powerful results, but these results, nonetheless, lead to similar interpretations as our Mann–Whitney results (Table 6). Applying Bonferroni tests only to the materials showing the smallest number of significant density values (in this case, bones) the results from the nonparametric tests are validated. In all cases, the FLK Zinj main cluster shows a significant

Figure 4. Tufa exposed at FLK NN, resulting from an underground spring system under tuff IC, contemporaneous with the FLK Zinj paleosurface.

contrast in material density with all the compared areas (trenches), with mean values up to ten times higher.

The higher density of fossils excavated from FLK T4 than recovered from the scatter west of the FLK main excavation area may be circumstantial, since FLK T4 has a much smaller sampled area (4 m^2) than does the FLK Zinj west scatter (124 m^2). The smaller size of FLK T4 would not allow any room for spatial variation in density. In fact, the FLK T4 values compare very well with any of the denser parts of the west scatter. This is suggestive of a similarly diffuse scatter around a large area of the periphery of the main cluster, much larger than previously assumed by the extent of Leakey's excavation.

Likewise, the high-density of fossils from FLKNWT1 is due to the presence of the partial carcass of a subadult suid, which was buried undisturbed by carnivores and hominins. This also indicates that natural processes, and not just hominin butchery behaviors, can also account for important accumulations of bone remains in these same places.

In sum, our new excavations and statistical analyses corroborate the earlier anecdotal suspicion that FLK Zinj is a materially dense anomaly on the Olduvai landscape. Bones are more densely concentrated at the site than in any other of the sampled areas. Stone tools are even more concentrated there than are bones when compared to the rest of the sampled landscape. These results prompt the following questions: (1) What did that ancient site have to offer to hominins so that it was selected during a minimum of two independent depositional events? (2) More specifically, what exactly did the site hold of attraction to hominins' second depositional interval, which is the only one when hominins apparently created a clearly defined cluster of materials significantly denser than in the remaining landscape? Geologically, this latter interval is represented by 10 cm of a clay deposit containing mostly unweathered bones and overlain by an airfall ash layer.

Table 1
Number of bone and lithic specimens found at the new trenches excavated in the Zinj waxy clay stratum.

	Lithic		Bone	
	Upper Zinj	Lower Zinj	Upper Zinj	Lower Zinj
FLK NWT1	1	3	20	31
FLK NWT2	0	0	7	0
FLK T5	2	0	1	2
FLK T4	2	0	13	2
FLK T7	1	0	0	0
FLK T6	0	0	0	0
FLK T1	5	2	14	7

Paleoenvironmental setting of FLK Zinj

One feature that is striking about the FLK, FLK N, FLK NW and FLK NN gullies beyond their clustering in a very small area is that each shows a recurrent presence of hominins and carnivores throughout most of their geological sequences. At FLK, Leakey (1971) uncovered various multiple artifact- and fossil-bearing levels; from top to bottom they are levels 7, 10, 11, 12, 13, 15, 16, 17, 21 and 22 (Zinj level). This is illustrated in Fig. 8, where most of the sequence exposed at FLK T1 is shown with the distribution of archaeological materials spanning an important part of the sequence and some preliminary correlations of the levels we uncovered with those reported by Leakey (1971). The same levels were detected in FLK NWT1, where even level 20 has a higher density of archaeological materials than does Level 22.

At FLK North, FLK N 1–2 occur directly under Tuff IF. Our on-going excavations at the site have expanded the number of archaeological levels discovered there by Leakey, meaning that if the records at FLK and FLK N are combined, there is a fairly continuous sequence of stone tools and fossils from the bottom of middle Bed I to the top of Bed I. Most of the low-density assemblages throughout the Bed I sequence are interpreted as the result of natural abiotic processes, but with an important input from carnivores (Domínguez-Rodrigo and Organista, 2007). In all events, the repeated use of the space around these three localities over such a vast time span suggests that there was something extraordinary about the paleoecological situation of the area.

In FLK NWT1, our excavation unearthed a wealth of microfaunal fossils (Fig. 9), a partial carcass of a juvenile suid (*Kolpochoerus limnetes*) and some ribs and vertebrae of a medium-sized bovid. The suid bones (including both scapulae, humeri, radii, femora, tibiae, one ulna, one innominate, both hemimandibles, some loose teeth, three rib fragments, and several isolated skull specimens) are very fragile and show multiple

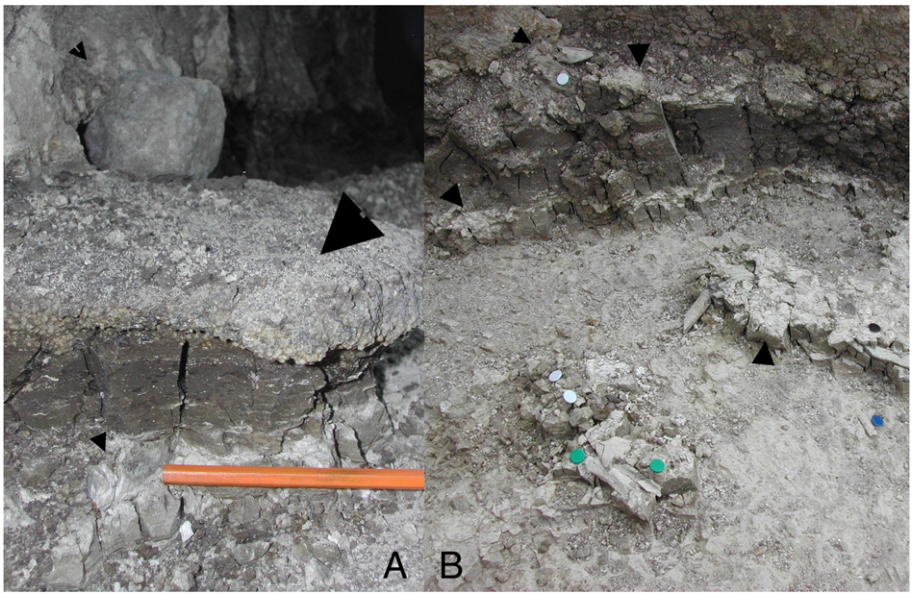

Figure 5. Vertical distribution of archaeological materials at FLKNWT1. A, small arrows show the location of a stone tool and a fossil bone at the top and the bottom of the Zinj waxy clay stratum respectively. Big arrow shows a clay patch with intense cemented sediment similar to some specimens documented in Leakey´s collection. B, small arrows show the carbonated layers interbedded with the Zinj waxy clay. Color pins show the presence of fossil bones on top and bottom of the sequence. Those at the bottom in the foreground belong to a partial carcass of a juvenile suid (see Fig. 10).

diagenetic cracks but have good cortical preservation and show no sign of subaerial weathering. The distribution of the macrofaunal remains and a couple of lithic artifacts might initially suggest some functional association between these classes of evidence at the site (Fig. 10). However, the lack of butchery marks on the bones, which show excellent cortical preservation, argues against that association. The skeleton also lacks carnivore-inflicted damage, so, our current best inference based on the skeleton's taphonomy is that a suid carcass was deposited at the site without hominin or carnivore intervention. Corroborating this inference, the distribution of fossils and lithics occupies a different vertical position than the suid in the FLK Zinj waxy clay stratum (Fig. 5). The lithics and bovid ribs were excavated from the upper FLK Zinj paleosol and the suid skeletal remains were found in the lower FLK Zinj paleosurface. Bones belonging to a snake, a turtle, and several fishes were also retrieved from the upper part of the FLK Zinj stratum. However, the most abundant microfaunal remains are those of birds, and they are important for the paleoecological information they provide.

FLK NWT1: paleoenvironmental interpretation of avian remains

There are very few studies of late Pliocene and early Pleistocene avian paleontology in East Africa (see though, Brodkorb and Mourer-Chauviré, 1982, 1984a,b). The FLK outcrops at Olduvai house the localities with the highest density of avian fossils and broadest taxonomic diversity of birds known from any African fossil site. And, FLK NWT1 is probably the densest spot among all the FLK outcrops surveyed and excavated so far: abundant bird fossils were recovered from both its upper and lower FLK Zinj levels. In fact, the bird remains are so abundant in FLK NWT1 that they covered significant areas of the FLK Zinj paleosurfaces as our excavations progressed (Fig. 9). Table 7 shows preliminary estimates, based on a sample of 479 individual fossils, of the occurrence of avian taxa from this trench. Twenty-two of the fossils (4.6% of the total bird fossil sample) could not be identified any more specifically than Aves. Among the remaining, identified remains, most are exclusively African taxa. There is a high representation of migratory species: charadriiforms (85.4%), followed by anseriforms (5.2%) constitute the bulk of the sample. In fact, taxa that are ecologically reliant on bodies of water like lakes, rivers, pools, swamps, etc.—i.e. anseriforms, charadriiforms, podicipediforms and rallids—amount to 445 fossil bones, representing 92.9% of the total sample.

More specifically, we identified abundant remains of birds that move on floating vegetation. Taxa linked to more open habitats (galliforms and columbiforms) make up only 1.0% of the sample. Passeriforms, which show preference for wooded and bushy environments constitute 1.2%. It is extremely unlikely that the remarkably large proportion of aquatic bird species is attributable to simply stochastic events or taphonomic bias. Instead, it is probably a fairly accurate reflection of the actual taxonomic structure of the local bird paleocommunities.

The paleoecological implication of these results is that major bodies of non-moving or slowly moving water must have existed in the vicinity of the FLK NWT1 when its upper and lower FLK Zinj paleosurfaces were forming. The prominent presence of charadriiforms indicates that part of the body of water contained a somewhat shallow silty bottom, which was accessible to limnicole birds. In addition, the presence of podicipediforms, and rallids and the abundance of birds adapted to floating vegetation all suggest that there were deeper areas with ample floating vegetation covers, as can be found in modern ponds created by springs.

FLK NWT1: paleoecological information provided by fish remains

Very few fish remains were recovered from FLKNWT1 (total number of identified specimens [NISP] = 153, minimum number of individuals [MNI] = 10). A high recovery rate is indicated by the very small size of some specimens, such as vertebrae measuring just 2 mm in diameter. In addition, the presence of some very fragile cichlid cranial bones indicates excellent preservation. Therefore, the paucity of fish remains likely reflects their scarcity at the site, rather than inadequate recovery or poor preservation.

Only two taxa were identified: *Clarias* sp. (catfish) and Cichlidae (tilapia). *Clarias* dominates both levels, with 54 fragments belonging to a minimum of four individuals in the upper level, and 79 specimens attributable to another four individuals in the lower level. Cichlids are rare, with just six remains attributable to one individual in level 22 upper, and 14 remains attributable to another individual in level 22 lower (Table 8). Based on measurements of the first vertebra

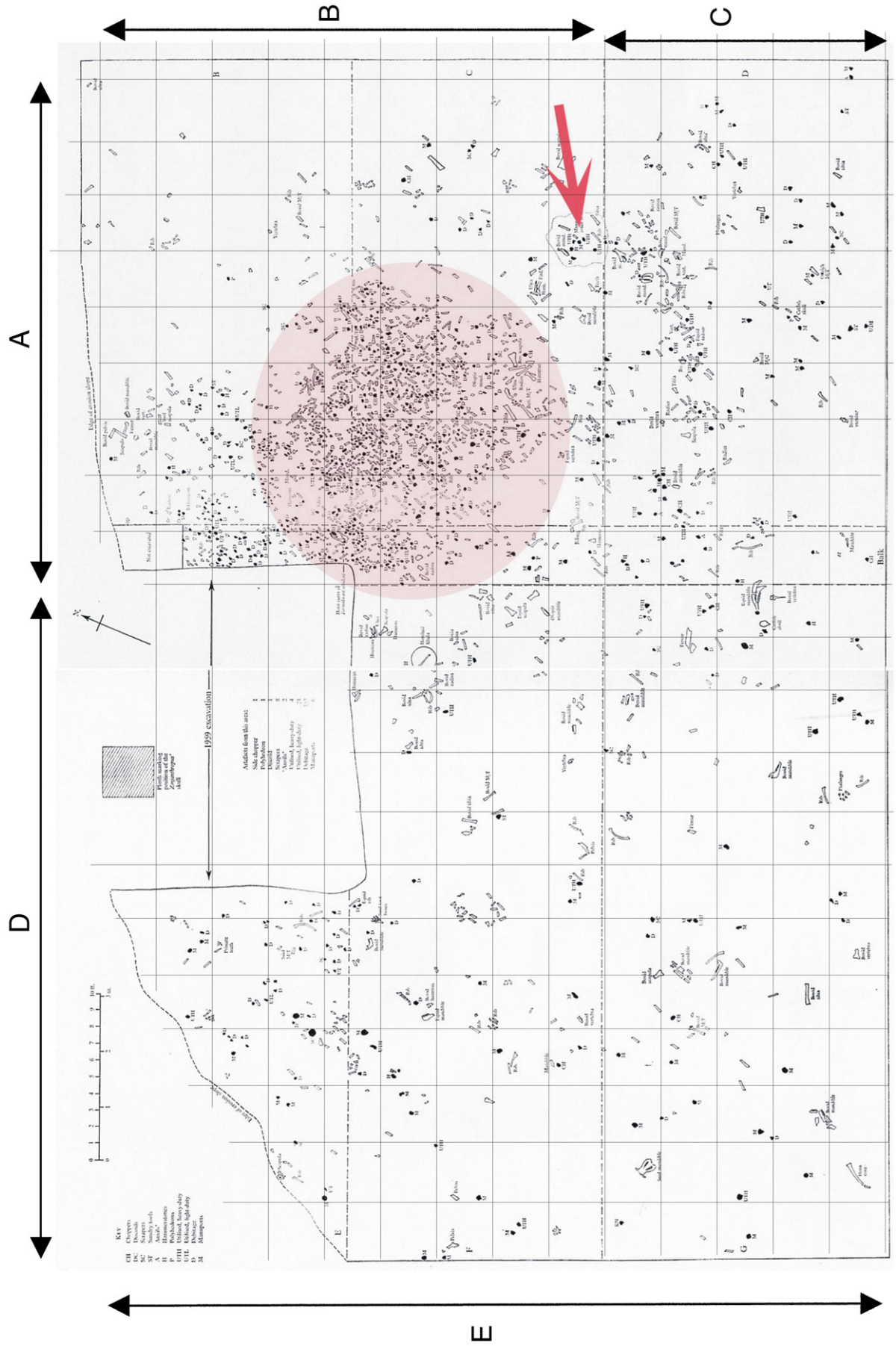

Figure 6. Map of the FLK Zinj main excavation by M. Leakey (1971) overlaid by a 1-m^2 grid. The areas defined are: FLK Zinj West (comprised by the grid DxE), FLK Zinj South (comprised by the grid AxC), and FLK Zinj Cluster (comprised by the grid AxB). The shaded circle shows the densest part of the cluster. Arrow points at microfaunal accumulation including bird bones, which could also indirectly indicate the presence of trees used by raptors as roosting places.

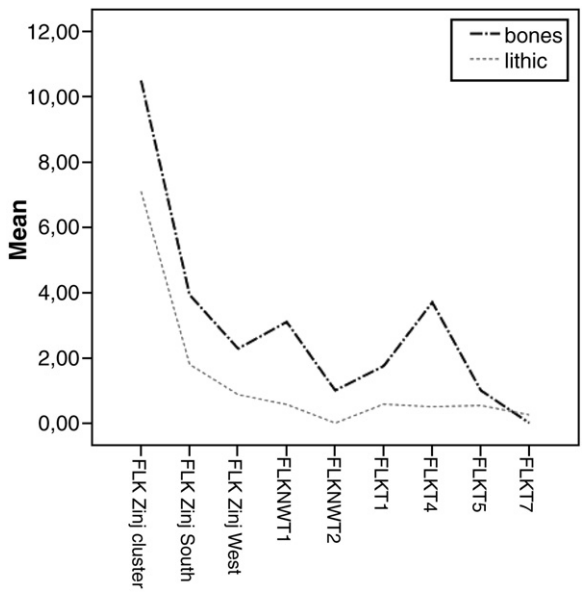

Figure 7. Mean values per square meter of fossil bones and lithic artifacts in each of the excavated trenches.

(following Van Neer and Lesur, 2004), a single tilapia was estimated to be 16 cm in total length, and it was certainly a juvenile since tilapia mature at ca. 25 cm. Based on measurements of the pectoral spine and articular, 14 specimens of *Clarias* have estimated total reconstructed live lengths averaging 25–35 cm; these are also quite small and young individuals, since *Clarias* mature at ca. 50 cm.

Clarias and Cichlidae were also identified as the only two taxa present at 11 Olduvai Gorge sites by Greenwood and Todd (1970) and Stewart (1994). At these sites, Stewart saw little to no evidence of hominin modification on the fish bones, with the possible exception of BK, and she interpreted most sites as the result of natural deposition. At FLKNWT1, we also interpret the fish remains to be the result of natural deposition in shallow, fresh water. *Clarias* can survive in very poor water conditions and are usually found in muddy-bottomed, shallow waters at the edges of lakes and swamps (Witte and de Winter, 1995). The dominance of *Clarias* at FLK NWT1 fits well with our interpretation of the trench's location as a spring (see Ashley et al., 2010). It is also consistent with Stewart's (1994) observation that *Clarias* dominated lake-margin sites in lower and middle Bed I, while cichlids were more abundant in upper Bed I and Bed II times. Cichlids thrive in a number of habitats but prefer shorelines or other shallow waters, and juveniles, in particular, are found in papyrus stands at the edges of lakes or ponds, where nesting takes place (Witte and de Winter, 1995). Although our sample size is far too small to make a strong argument, it is worth noting that the two individuals documented at FLK NW are certainly juveniles based on their small size. Considering these habitat data together, it seems likely that the fish recovered at FLK NW died *in situ* in a shallow-water setting, perhaps being stranded as the spring dried up. Similar stranding of fish in receding waters at several Olduvai sites was suggested by Leakey (1971) and again by Stewart (1994).

Table 2
Mean rank values (Kruskal–Wallis test) of bone densities at each excavated trench.

Ranks			
	Trenches	N	Mean rank
Bone	FLK NWT1	16	120.22
	FLK NWT2	7	90.71
	FLK T5	5	95.80
	FLK T7	4	40.00
	FLK T4	4	166.12
	FLK Zinj West	127	129.29
	FLK Zinj South	45	149.97
	FLK Zinj Cluster	78	205.05
	FLK T1	12	127.21
	Total	298	

Table 3
Mean rank values (Kruskal–Wallis test) of stone artefact densities at each excavated trench.

Ranks			
	trenches	N	Mean rank
Lithic	FLKNWT1	16	91.44
	FLKNWT2	7	69.00
	FLKT5	5	110.20
	FLKT7	4	94.75
	FLKT4	4	120.50
	FLK Zinj West	127	133.17
	FLK Zinj South	45	182.16
	FLK Zinj Cluster	78	187.02
	FLKT1	12	124.67
	Total	298	

The spring at FLK NN

Two north–south oriented exposures (~35 m long and at least 10 m wide) at FLK NN were scraped, dug, measured and sampled to determine the depositional environment during Middle Bed I time. The exposure located 200 m to the north of the main FLK Zinj excavation, is stratigraphically equivalent to Level 22 and reveals a large carbonate (tufa) mound draped with Tuff IC (Fig. 4). The stratigraphy and vertical and lateral changes in sediment composition suggest that the tufa was deposited at the same time as the FLK Zinj fossil and artifact horizon. The sequence of sediments starts with a tuff (0.35 m thick) overlain with a thin waxy clay which grades into the carbonate bed which, in turn, is overlain with a thin waxy clay (3 cm) and capped with Tuff IC. The tufa and waxy clay sandwich are equivalent to the ~20 cm thick waxy clay at FLK Zinj. At its thickest point (~0.5 m), the tufa bed is white to light beige in color and relatively pure (i.e., homogeneous). On the margins of the tufa mound the carbonate thins and pinches out and is noticeably mixed with waxy clay. The two lithologies are admixed creating sedimentary structures that are similar to the trampling and general bioturbation by ungulates observed at modern watering holes (LaPorte and Behrensmeyer, 1980; Ashley and Liutkus, 2002).

Stable isotope analyses of the tufa mound documents that the carbonate was deposited from a freshwater source, i.e., a spring fed by groundwater (Ashley et al., 2010). The reported $\delta^{18}O$ values of −4.0 to −1.0 are robust evidence for a meteoric-fed surface water source located in the midst of rich fossil sites in the environs of FLK.

The FLK Zinj site and its vegetational context

The prehistoric location of FLK Zinj, just a few meters from a permanent source of potable water means it probably was surrounded by abundant tree and bush cover. Indeed, this reconstruction agrees with Sikes's (1994) earlier soil isotope data, which indicate a, riverine or ground water forest in a 1-km^2 area covered by Blumenschine and Masao's (1991) initial landscape study area in lowermost Bed II in 1989. The isotopic signal detected in middle Bed I (FLK Zinj level) was similar to that documented in lower Bed II (Sikes, 1994). Although Sikes (1994, Fig. 1), demonstrated that carbon isotope values for wetland soils and sediments can be similar to those of non-wetland soils, she, for two reasons (personal communication), settled on a non-wetland soil interpretation for the FLK Zinj paleosol carbon isotope values. First,

Table 4
Mann–Whitney U values for pairwise comparisons of bone density values (number of specimens per square meter) between newly excavated trenches and areas at FLK Zinj. Numbers in bold and with * indicate a significant value ($p<.05$).

Bones	FLK NWT1	FLK NWT2	FLKT5	FLKT7	FLK T4	FLK ZINJ WEST	FLK ZINJ SOUTH	FLK ZINJ CLUSTER	FLK T1
FLK NWT1									
FLK NWT2	48.5								
FLK T5	36.5	15.5							
FLK T7	14	6	4						
FLK T4	24	6.5	5	**2***					
FLK ZINJ WEST	930	313	238	**78***	181				
FLK ZINJ SOUTH	282	89	67	**20***	79	2440			
FLK ZINJ CLUSTER	**309***	**85***	**62.5***	**20***	**19***	**2395.5***	**1065.5***		
FLK T1	85	26.5	19.5	**6***	16	753.5	226.5	**205.5***	

Cerling et al. (1989) showed that there is a systematic difference of 14–7‰ between the carbon values for coexisting soil carbonate and soil organic matter (SOM). The bottom of her Table 2 shows that there is a 14.1‰ difference between the FLK Zinj SOM and $CaCO_3$, so this fits with theoretical expectations. Second, as also argued in Sikes' (1994) paper on the basal Bed II paleosols, the existence of the pedogenic carbonate and its oxygen isotope values supports a non-wetland terrestrial interpretation. However, whether one argues on the basis of organic carbon, inorganic carbon or both, the isotopic data show that there is still a significant woody C_3 component present in Olduvai Bed I. Cerling and Hay (1986) presented carbonate istope data for Bed I, specifically. Carbon values for seven reported pedogenic carbonates (three just above the basal lava in the western lake margin; four in the eastern lake margin—the Zinj carbonate between Tuffs IB and IC, one from FLK N about a meter below Tuff IF, and two more just below IF) range from 5.8 to 3.7‰. This indicates the presence of 45 to 60% C_4 plants. Four data points represent grassy woodland; three fall into an interpretational overlap zone of grassy woodland or wooded grassland. Because of isotopic effects during carbonate precipitation, there is an overlap of up to 2‰ between physiognomic categories. The FLK Zinj carbonate—referenced in Sikes's (1994) Table 2 with a value of 5.7‰—falls into the grassy woodland category. Recent results on middle and upper Bed I soil sediments support this previous interpretation and show that the landscape at that time was a mosaic of grassy woodland and wooded grassland (Sikes and Ashley, 2007). In other words, the basin was significantly wetter and contained many more C_3 plants than it does today.

Plummer and Bishop's (1994) ecomorphological analysis of the Olduvai bovids, contrary to a taxon-based approach of paleohabitat reconstruction, reconstructed middle Bed I as more closed and intermediate than inferred from species count, even when the representation of alcelaphines and antilopines is taken into account. FLK NN 1 shows a "high representation of bovids with the closed habitata morphology" and "FLK I is dominated by intermediate and closed-habitat morphologies" (Plummer and Bishop, 1994: 66). A recent study of bovid representation in some Oldowan sites (Plummer et al., 2008), using the frequencies of the triple bovid group suggested by Shipman and Harris (1988)—Alcelaphini and Antilopini, Reduncini and Bovini, Tragelaphini and Aepycerotini—shows that FLK Zinj, when compared with modern African biomes is similar to Fina National Park (Mali) and close to Kainji (Nigeria), which was the closest affinity to the site in Shipman and Harris's (1988) analysis. Both modern parks, each defined as 100% Sudanian woodland, are well-wooded. FLK NN 1 plots with even more modern wooded ecosystems than does FLK Zinj. Fig. 11b shows that where FLK Zinj shares the same cluster as Fina and Kainji, FLKNN 1 shares an independent cluster with Hluhluwe (94% woodland and 6% forest) and Bicuar (89% woodland and 11% forest). Therefore, the bovid groups from both Olduvai sites are represented in the same proportions as those observed densely wooded modern African biomes. This relationship is even more realized with the analytical inclusion of *all* large-sized bovids, instead of excluding hippotragines, as in the original analyses (Fig. 11a). Including this bovid tribe, whose representation in several national parks is highly variable, places FLK Zinj in a cluster with a group of parks that are 100% wooded or wooded and forested and FLK NN1 now shares a cluster with Cuelei (*Brachystegia* woodland with riverine ecosystems) and Bicuar, even more forested.

One could argue that the relationship revealed by these cluster analyses is also influenced by analytical artifacts (clustering method, proximity matrix method) as much as by the high variation of the analogical samples used. Review of Shipman and Harris's (1988) and Vrba's (1980) lists of parks with their respective census shows that some parks had extremely large faunal counts (e.g., Serengeti = >700,000 individuals) whereas others were extremely small (e.g., Bicuar = 2500 individuals). In order to avoid this bias that could result from this variation inter-park sample sizes, we performed a statistical analysis aimed at homogenizing sample sizes and correcting for small samples sizes. We did so by bootstrapping 10,000 times all the data from each national park and plotting them in two separate groups: one corresponding to wooded ecosystems and the other one corresponding to open savanna biomes (Fig. 12). When plotting the areas corresponding to the 95% confidence intervals of each group and that of the FLK Zinj and FLK NN 1 sites, a greater variability in bovid

Table 5
Mann–Whitney U values for pairwise comparisons of lithic artefact density values (number of specimens per square meter) between newly excavated trenches and areas at FLK Zinj. Numbers in bold and with * indicate a significant value ($p<.05$).

				LITHICS					
	FLK NWT1	FLK NWT2	FLK T5	FLK T7	FLK T4	FLK ZINJ WEST	FLK ZINJ SOUTH	FLK ZINJ CLUSTER	FLK T1
FLK NWT1									
FLK NWT2	45.5								
FLK T5	32.5	10.5							
FLK T7	30.5	10.5	8.5						
FLK T4	23	**7***	9	6					
FLK ZINJ WEST	**694***	**227.5***	261.5	179.5	229				
FLK ZINJ SOUTH	**127.6***	**35***	**50***	**32.5***	45	**1801***			
FLK ZINJ CLUSTER	**285.5***	**98***	**18***	**27***	**12***	**3191***	1523		
FLK T1	67.5	**21***	26	17.5	23	712.5	**145***	**283.5***	

Table 6
Bonferroni test values for pairwise comparisons of bone density values (number of specimens per square meter) between newly excavated trenches and areas at FLK Zinj.

Multiple comparisons						
Bone						
(I) trenches	(J) trenches	Mean difference (I–J)	Std. error	Sig.	95% Confidence interval	
					Lower bound	Upper bound
FLK NWT1	FLK NWT2	2.18750	2.85729	1.000	−7.0366	11.4116
	FLK T5	2.18750	3.23046	1.000	−8.2413	12.6163
	FLK T7	3.18750	3.52472	1.000	−8.1912	14.5662
	FLK T4	−.56250	3.52472	1.000	−11.9412	10.8162
	FLK Zinj West	.90404	1.67265	1.000	−4.4957	6.3038
	FLK Zinj South	−.74583	1.83526	1.000	−6.6705	5.1789
	FLK Zinj Cluster	**−7.27404***	1.73044	.001	−12.8603	−1.6877
	FLK T1	1.43750	2.40784	1.000	−6.3356	9.2106
FLK NWT2	FLK NWT1	−2.18750	2.85729	1.000	−11.4116	7.0366
	FLK T5	.00000	3.69196	1.000	−11.9186	11.9186
	FLK T7	1.00000	3.95200	1.000	−11.7581	13.7581
	FLK T4	−2.75000	3.95200	1.000	−15.5081	10.0081
	FLK Zinj West	−1.28346	2.44794	1.000	−9.1861	6.6191
	FLK Zinj South	−2.93333	2.56181	1.000	−11.2035	5.3368
	FLK Zinj Cluster	**−9.46154***	2.48779	.006	−17.4928	−1.4303
	FLK T1	−.75000	2.99873	1.000	−10.4307	8.9307
FLK T5	FLK NWT1	−2.18750	3.23046	1.000	−12.6163	8.2413
	FLK NWT2	.00000	3.69196	1.000	−11.9186	11.9186
	FLK T7	1.00000	4.22967	1.000	−12.6545	14.6545
	FLK T4	−2.75000	4.22967	1.000	−16.4045	10.9045
	FLK Zinj West	−1.28346	2.87475	1.000	−10.5639	7.9970
	FLK Zinj South	−2.93333	2.97231	1.000	−12.5287	6.6620
	FLK Zinj Cluster	**−9.46154***	2.90875	.046	−18.8517	−.0713
	FLK T1	−.75000	3.35621	1.000	−11.5847	10.0847
FLK T7	FLK NWT1	−3.18750	3.52472	1.000	−14.5662	8.1912
	FLK NWT2	−1.00000	3.95200	1.000	−13.7581	11.7581
	FLK T5	−1.00000	4.22967	1.000	−14.6545	12.6545
	FLK T4	−3.75000	4.45846	1.000	−18.1431	10.6431
	FLK Zinj West	−2.28346	3.20187	1.000	−12.6199	8.0530
	FLK Zinj South	−3.93333	3.28974	1.000	−14.5535	6.6868
	FLK Zinj Cluster	**−10.46154***	3.23243	.049	−20.8967	−.0264
	FLK T1	−1.75000	3.64032	1.000	−13.5019	10.0019
FLK T4	FLK NWT1	.56250	3.52472	1.000	−10.8162	11.9412
	FLK NWT2	2.75000	3.95200	1.000	−10.0081	15.5081
	FLK T5	2.75000	4.22967	1.000	−10.9045	16.4045
	FLK T7	3.75000	4.45846	1.000	−10.6431	18.1431
	FLK Zinj West	1.46654	3.20187	1.000	−8.8699	11.8030
	FLK Zinj South	−.18333	3.28974	1.000	−10.8035	10.4368
	FLK Zinj Cluster	**−6.71154***	3.23243	.049	−17.1467	3.7236
	FLK T1	2.00000	3.64032	1.000	−9.7519	13.7519
FLK Zinj West	FLK NWT1	−.90404	1.67265	1.000	−6.3038	4.4957
	FLK NWT2	1.28346	2.44794	1.000	−6.6191	9.1861
	FLK T5	1.28346	2.87475	1.000	−7.9970	10.5639
	FLK T7	2.28346	3.20187	1.000	−8.0530	12.6199
	FLK T4	−1.46654	3.20187	1.000	−11.8030	8.8699
	FLK Zinj South	−1.64987	1.09385	1.000	−5.1811	1.8813
	FLK Zinj Cluster	**−8.17807***	.90704	.000	−11.1062	−5.2499
	FLK T1	.53346	1.90421	1.000	−5.6138	6.6807
FLK Zinj South	FLK NWT1	.74583	1.83526	1.000	−5.1789	6.6705
	FLK NWT2	2.93333	2.56181	1.000	−5.3368	11.2035
	FLK T5	2.93333	2.97231	1.000	−6.6620	12.5287
	FLK T7	3.93333	3.28974	1.000	−6.6868	14.5535
	FLK T4	.18333	3.28974	1.000	−10.4368	10.8035
	FLK Zinj West	1.64987	1.09385	1.000	−1.8813	5.1811
	FLK Zinj Cluster	**−6.52821***	1.18032	.000	−10.3386	−2.7178
	FLK T1	2.18333	2.04852	1.000	−4.4298	8.7965
FLK Zinj Cluster	FLK NWT1	**7.27404***	1.73044	.001	1.6877	12.8603
	FLK NWT2	**9.46154***	2.48779	.006	1.4303	17.4928
	FLK T5	**9.46154***	2.90875	.046	.0713	18.8517
	FLK T7	**10.46154***	3.23243	.049	.0264	20.8967
	FLK T4	**6.71154***	3.23243	.049	−3.7236	17.1467
	FLK Zinj West	**8.17807***	.90704	.000	5.2499	11.1062
	FLK Zinj South	**6.52821***	1.18032	.000	2.7178	10.3386
	FLK T1	**8.71154***	1.95516	.000	2.3998	15.0233
FLK T1	FLK NWT1	−1.43750	2.40784	1.000	−9.2106	6.3356
	FLK NWT2	.75000	2.99873	1.000	−8.9307	10.4307
	FLK T5	.75000	3.35621	1.000	−10.0847	11.5847
	FLK T7	1.75000	3.64032	1.000	−10.0019	13.5019
	FLK T4	−2.00000	3.64032	1.000	−13.7519	9.7519
	FLK Zinj West	−.53346	1.90421	1.000	−6.6807	5.6138

(continued on next page)

Table 6 (*continued*)

Multiple comparisons						
Bone						
(I) trenches	(J) trenches	Mean difference (I–J)	Std. error	Sig.	95% Confidence interval	
					Lower bound	Upper bound
FLK T1	FLK Zinj South	−2.18333	2.04852	1.000	−8.7965	4.4298
	FLK Zinj Cluster	**−8.71154***	1.95516	.000	−15.0233	−2.3998

Data in bold are significant at a sigma level of .05.
*The mean difference is significant at the 0.05 level.

group representation can be documented among wooded biomes, which accounts for their widespread distribution in the whole area covered by the triangle. Open ecosystems are restricted to a large variability of Alcelaphini and Antilopini and Tragelaphini and Aepycerotini but a fairly small proportion of Reduncini and Bovini. The area occupied by FLK Zinj and FLK NN1 is outside the range documented for open ecosystems and well within the core of wooded biomes. The location of FLK Zinj close to the outermost boundary of the open ecosystems suggests a slightly more open woodland situation than the mere taxonomic comparisons with unbootstrapped samples.

Thus, the presence of woodland in the vicinity of the lacustrine plain, in relation to archaeological sites, seems to be indicated by the independent but converging studies of microfauna (Jaeger, 1976; Fernández-Jalvo et al., 1998), macrofauna (Shipman and Harris, 1988; Plummer and Bishop, 1994; Plummer et al., 2008), fossil pollen (Bonnefille, 1984) and carbonate isotopic analyses (Sikes, 1994). Ecomorphological analyses also suggest the same. The analyses of metapodials from bovids indicates that the most widely represented antilopini taxon (*Antidorcas recki*) during middle Bed I shows morphologies indicative of mixed habitats instead of open habitats as they do nowadays (Plummer and Bishop, 1994). This is supported by the ecomorphological analysis of cranial remains, where the morphology of the jaws is indicative of a mixed diet of grazing and browsing (Spencer, 1997). Therefore, the presence of antilopini is not indicative of open habitats as they are in modern savannas. When considering all the available evidence, it is thus fair to assume that the actual location of FLK Zinj was in a wooded setting.

One interesting feature that we documented while excavating the FLK Zinj paleosol was the profuse distribution of thick carbonated root casts, which could belong to various bush/tree plants (Fig. 13). This certainly supports the interpretation that the setting where the site occurred was not just grassy.

The presence of trees at FLK Zinj is also suggested by the recovery of abundant remains belonging to the Acacia rat, *Thallomys* (Jaeger, 1976). In addition, several fossils of bush baby (*Galago* cf. *senegalensis*), quite similar to the modern species found at the site (Leakey, 1965) suggest the presence of thicker tree cover, given that bush-baby primates are confined to woodland and forest (Kingdon, 1997).

The presence of woody plants, trees or shrubs is also attested by the recent discovery of abundant micro-botanical remains in the form of globular silica bodies (phytoliths) in the archaeological level 22 (Ashley et al., 2010). In current soils, the abundance of globular granulate phytoliths typical for woody dicots (mainly trees and

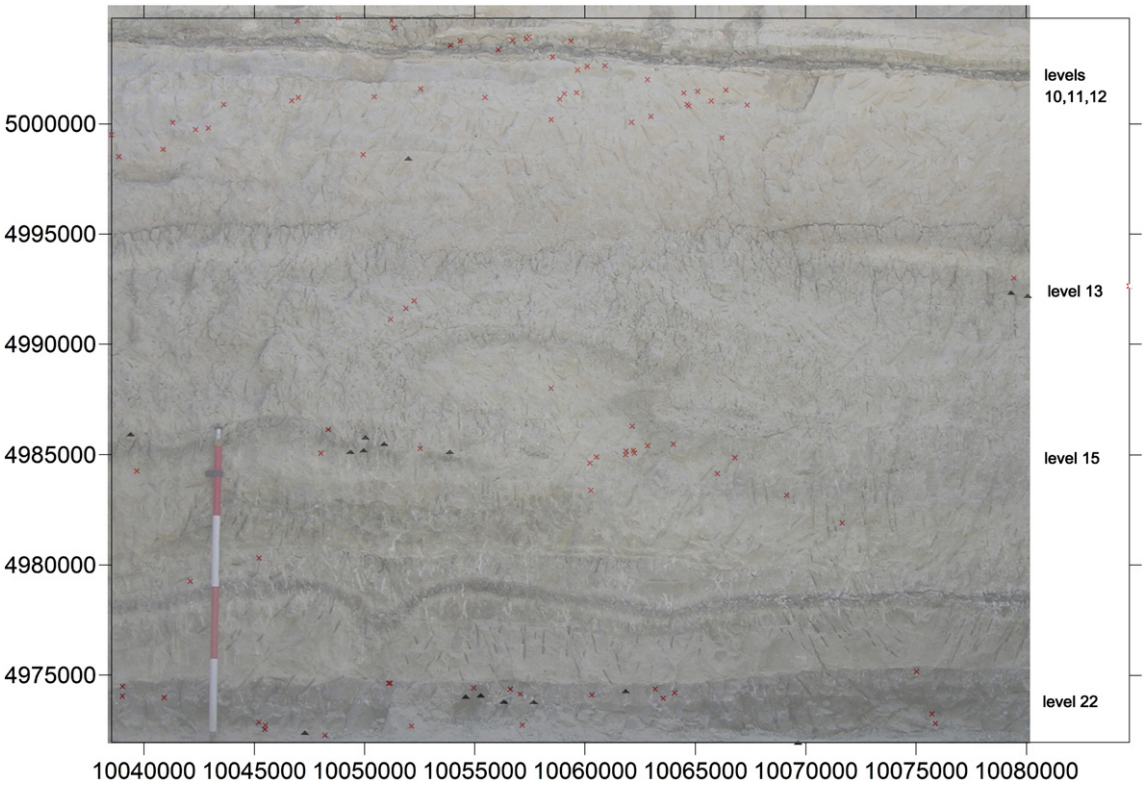

Figure 8. Main wall of FLK T1 exposed by excavation showing the geological strata (from under the Ngeju tuff to the bottom of the Zinj waxy clay underlying Tuff IC) and showing the vertical distribution of fossils and artifacts in various archaeological levels which tentatively correspond to those described by M. Leakey in the main excavation. Notice the distribution of archaeological materials on top and bottom of the Zinj waxy clay (lower part of the sequence) without materials distributed in the middle part of the sequence of the clay stratum. Light crosses are fossil bones; black triangles are stone tools.

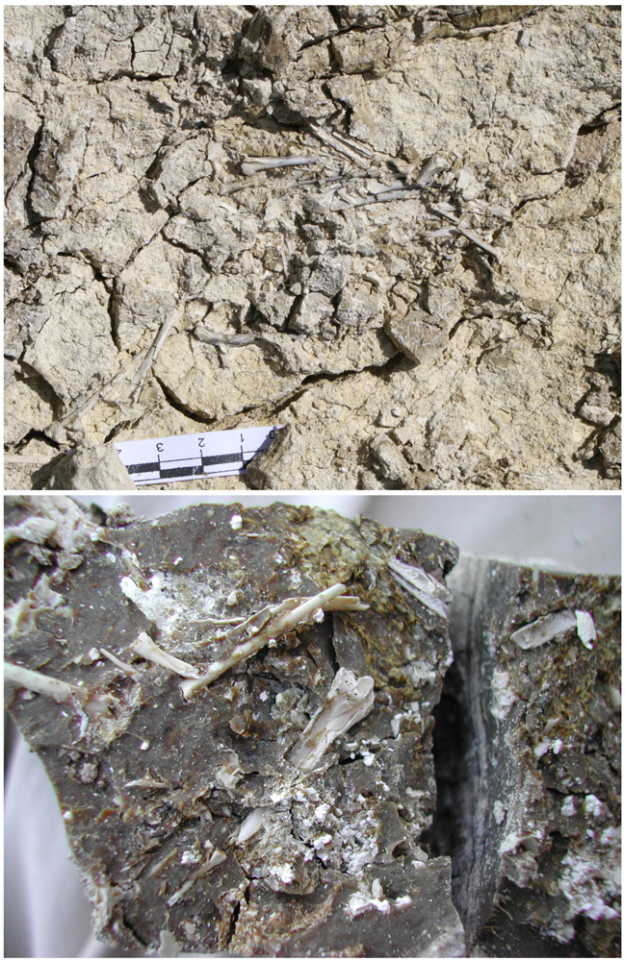

Figure 9. Example of concentration of microfaunal remains (dominated by bird bones) at FLK NWT1 (upper) and a close-up example thereof (bottom).

shrubs) and globular echinate phytoliths typical for palms (Piperno, 1988) reflects the density of the tree cover (Barboni et al., 2007) and may be used to reconstruct past vegetation types at paleoanthropological sites (WoldeGabriel et al., 2009). In the Zinj context, globular (arboreal) phytolith may account for up to 95% in some samples. Such high percentages, however, are difficult to interpret in terms of density of the tree cover because of the overall poor preservation of the phytoliths, which suggests that preferential dissolution may have occurred and biased the fossil assemblage.

A recent analysis of limb strength and locomotion in *Homo habilis*, through cross-sectional bone strength measurements of OH62 shows many affinities with chimpanzees, which indicates that even if fully bipedal when moving terrestrially, it engaged in frequent arboreal behavior (Ruff, 2008). This suggests that the presence of *Homo habilis* remains should be linked to the presence of arboreal cover. In Bed I, *H. habilis* fossils are conspicuously more abundant on the intersection of FLK NN–FLK than anywhere else in the gorge, maybe because trees were more abundant there than in other parts of the gorge.

Carnivores and hominins at the spring

Domínguez-Rodrigo et al.'s (2007) taphonomic re-evaluation of the Olduvai Bed I sites suggested that all the sites but FLK Zinj (the only anthropogenic site identified) were palimpsests in which carnivores had been responsible for the accumulation of most faunal remains. Their taphonomic results also suggested that the area where most of the Bed I sites cluster must have possessed some specific ecological conditions that prompted carnivores and hominins to overlap in the use of the same places. The presence of carnivores, such as lions, leopards, jackals, hyenas, and saber-toothed felids (*Megantereon*, *Dinofelis*), whose remains were found in the same area (Lewis, 1997), suggests that part of the area's prehistoric herbivore biomass must have used the floodplain edaphic grasslands on at least a seasonal basis, encouraging a high degree of carnivore activity in the area. Competition among carnivores could have prompted carcass transportation by solitary hunters (*i.e.*, medium-sized felids) and in some cases by larger felids to safe spots where bone remains were repeatedly accumulated.

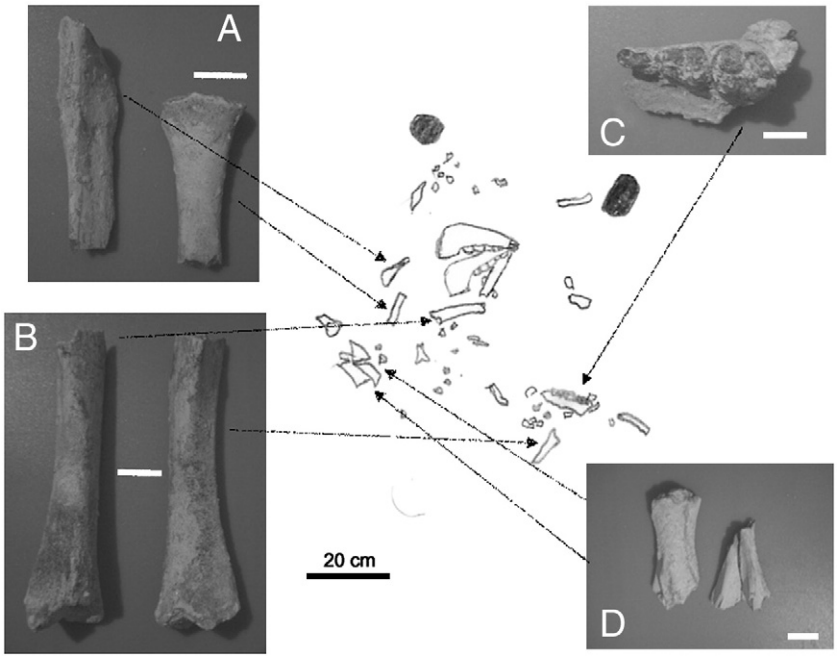

Figure 10. Map showing the suid remains clustered in the central part of the FLK NWT1 trench at the bottom of the Zinj clay stratum, with two stone tools (on the upper Zinj paleosol). A, ulna and radius; B, both tibiae; C, part of a fragmented maxillar bone with upper dentition; D, part of the scapular blades with the beginning of the spine. Scale in photos = 2 cm.

Table 7
Distribution of avian remains into major taxonomical groups in FLK NWT1. Numbers are for NISP and MNI (in parentheses).

	Podicipediforms	Anseriforms	Charadriiforms	Rallids	Galliforms	Columbiforms	Passeriforms	Accipitriforms	Others
Habitat preferences	Inland bodies of water	Inland bodies of water	Shorelines marsh, springs	Shorelines	Open country/woodland	Open country/parkland	Scrubland/parkland	Wide range	
NW 20			7 (2)	1 (1)				1 (1)	1 (1)
NW 22 A	1 (1)	19 (7)	274 (38)	8 (4)	1 (MNI: 1)	3 (1)	5 (2)		21 (3)
NW 22 B		4 (2)	126 (15)		1 (1)		1 (1)		
NW 22		2	2	1					
Total: 479	1	25	409	10	2	3	6	1	22
Percentages	0.2	5.2	85.4	2.1	0.4	0.6	1.2	0.2	4.6

It was suggested that lions, leopards and *Dinofelis* were likely candidates for the carnivore-generated accumulations discovered in sites that were previously believed to have been made by hominins (Domínguez-Rodrigo et al., 2007). According to Leakey (1971), FLK NN, which lies about 200 m away from FLK Zinj (Fig. 2), occupied a contemporaneous stratigraphic position as FLK Zinj during its upper level (FLK NN 1). This site, excavated by Leakey (1971), revealed three levels with fossil and/or stone artifacts. FLK NN 1 (the upper level) and FLK NN 3 (the lower level), previously considered anthropogenic, are clearly carnivore-made accumulations. Tooth mark frequencies, a very low degree of bone fragmentation and an abundance of complete elements seem to support a non-bone crunching carnivore as the main agent responsible for the accumulation of bones in both assemblages (Barba and Domínguez-Rodrigo, 2007; Domínguez-Rodrigo and Barba, 2007a).

FLK NN 2 was previously interpreted as a carnivore-created bone accumulation (Bunn, 1986; Potts, 1988). Egeland's (2007) taphonomic re-evaluation of the assemblage indicated that a medium- to large-sized felid could have been responsible for the accumulation, with hyenas acting as intermittent scavengers. Given that analyses of the materials from the under- and overlying levels provide sustained support for this hypothesis, the FLK NN site could, in fact, have resulted from repeated use of the same space primarily by felids as a hunting and feeding site, with the resulting bone residues subsequently scavenged by hyenas. The only indication of hominin involvement with the FLK NN faunas is in the form of just two cut-marked bone specimens from FLK NN 2, and the level lacks stone tools (Bunn, 1986). The few stone flakes recovered from FLK NN 1 and FLK NN 3 can be explained by hominins visiting the sites briefly, at times during which no activity related to carcass-processing took place, or at least left durable bone residues *in situ*. Most of the purported artifacts in both levels (Leakey, 1971; Potts, 1988) are instead likely natural ecofacts rather than "manuports," (personal observations) as was previously argued by Torre and Mora (2005).

Thus, for a long span, which is represented by the three excavated levels at FLK NN, carnivores used the same spot for predation and carcass consumption. The appeal of the locus is now apparent in its prehistoric proximity to a permanent water source. Based on observations in modern savannas, permanent water sources often become the focus of serial predation by carnivores during the dry season (Domínguez-Rodrigo, 1993, 1996). During the formation of the FLK NN tufa, by the action of a freshwater spring, the Olduvai paleolakeshore was quite a distance from the area where the sites are clustered. It is likely that the spot where the site was formed was the one of the few freshwater sources nearby during the dry season causing herd animals to congregate in the area during that season. That, in turn, would have drawn carnivores to the area, ultimately generating the bone accumulations around the spring as they hunted and fed.

By the time the FLK Zinj floor was forming, it seems that carnivore activity around the spring was quite reduced. For example, the FLK NN 1 fauna is composed of just a few bones fragments (NISP = 257), compared to the underlying levels, where carnivore activity at the site was at its apogee. Remains from a total of 14 carcasses have been identified in the FLK NN 1 assemblage, including a partial skeleton (mostly teeth and some axial elements) of a *Tragelaphus strepsiceros*. Very few elements per skeleton survived in the assemblage, which indicates a high degree of carcass destruction and/or time-averaging. The lack of hominin butchery marks and the presence of tooth marks on bone specimens suggest a carnivore origin for the assemblage. The identification of specimens showing Behrensmeyer's (1978) weathering stages from 0 to 4, especially on the larger component of the assemblage indicates the assemblage accumulated over a longer time than did the FLK Zinj fauna (Barba and Domínguez-Rodrigo, 2007; Domínguez-Rodrigo and Barba, 2007b). By extension, one can argue that when hominins created the cluster at FLK Zinj, carnivores were not as active around the spring as in earlier times. Further, these data suggest that when hominins created FLK Zinj, they did so by choosing a spot where carnivore activity was minimal, away from the spring area where carnivore risk may have been higher, at a time when carnivores were relatively inactive around the spring. This inference of minimal carnivore presence when hominins were using FLK Zinj is reinforced by the paucity of carnivore-modified bone in the sampled landscape surrounding the site. Only two recovered specimens (3.9% of the total NISP) bear tooth marks. Encephalized hominins were evidently up to the task of a level of complex decision-making, of developing a foraging strategy that capitalized on an evident availability of prey nearby in a setting that did not expose them to too much risk of becoming prey themselves.

The hominin-created ungulate skeletal part patterning at FLK Zinj, dominated by long limb bone and mandible specimens, has been explained in two different ways. Either hominins transported fleshed long limb bones from acquisition sites to FLK Zinj for butchery (Bunn and Kroll, 1986, 1988; Bunn, 1991) or axial elements were eventually deleted by feeding carnivores from whole or near-whole ungulate carcasses deposited at the site (Marean et al., 1992; Capaldo, 1995, 1997; Domínguez-Rodrigo et al., 2007). The latter idea is sustained by the fact that ungulate axial remains comprise nearly one third of all the bone MNE counts at the FLK Zinj site (Bunn, 1982; Domínguez-Rodrigo et al., 2007), although their percentage minimum animal unit (%MAU) values are substantially lower than those for long limb bones. Hominin transport of complete carcasses to FLK Zinj would mean a wider range of edible carcass parts and higher overall nutritional yield available to those hominins. Recently, Bunn (2007) argued that complete carcass transport by modern foragers is best explained by the fact that boiling technology allows them to extract grease from cancellous bone tissue, so the relatively nutritionally low-yielding axial elements are worth carrying

Table 8
Summary of fish remains from FLKNWT1.

Level	Taxon	NISP	MNI
22 upper	*Clarias* sp. (catfish)	54	4
	Cichlidae (tilapia)	6	1
	Total	60	5
22 lower	*Clarias* sp. (catfish)	79	4
	Cichlidae (tilapia)	14	1
	Total	93	5

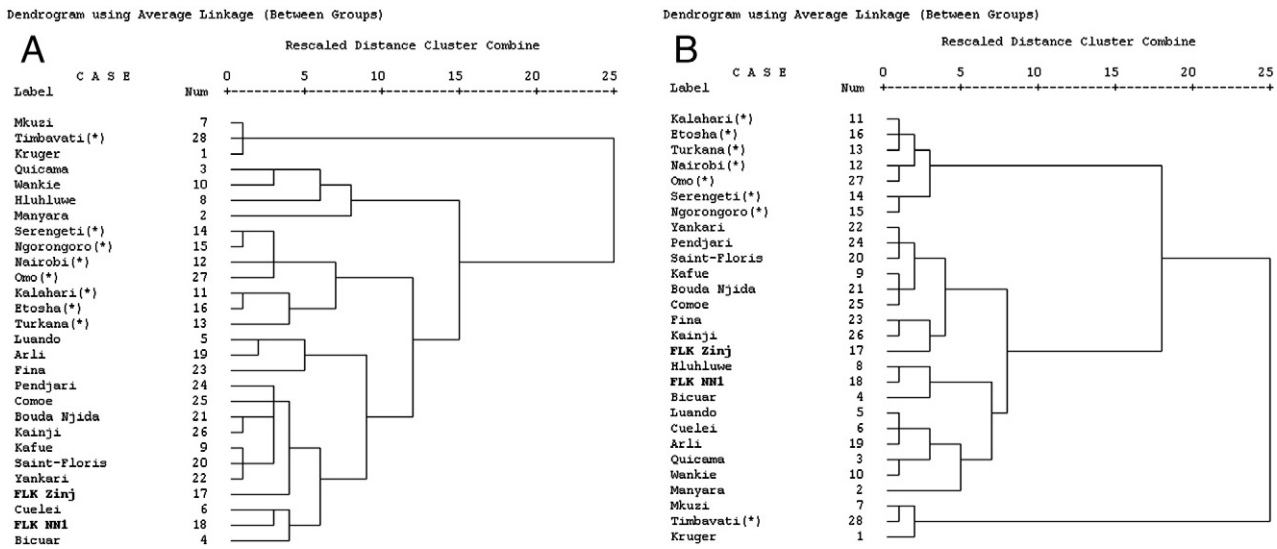

Figure 11. Hierarchical agglomerative cluster analyses of several African national parks representing wooded biomes and open savanna landscapes (with asterisks). Data on bovid tribe census for each park are from Shipman and Harris (1988) and Vrba (1980). The proximity matrix was obtained using the square Euclidean distance and the dendrogram was made using the method of average linkage between groups (UPGMA). A, cluster dendogram obtained using all major bovid tribes, including alcelaphini, antilopini, reduncini, bovini, tragelaphini, aepycerotini and hippotragini. B, cluster dendogram derived using Shipman and Harris (1988) three bovid groups: alcelaphini and antilopini, reduncini and bovini, and tragelaphini and aepycerotini.

over distance to camp. For example, modern Hadza foragers from Lake Eyasi (Tanzania) deflesh ungulate skeletons and transport the flesh separately from the vertebrae, which are carried to the camp only because they are boiled for grease extraction. Bunn (2007) argues that in the absence of a boiling technology in the early Pleistocene, the incentive for the transport of axial bones by modern humans was not present.

We harness current experimental taphonomic models and our new paleoecological data to assess if one of these two explanations better models the prehistoric reality of the formation of the FLK Zinj fauna. If, as we contend, carnivore activity on the landscape surrounding the FLK Zinj site was limited during the depositional phases of that archaeological level, how was it that they (carnivores) seemingly deleted the hundreds of missing axial bones that are necessary to account for the estimated number of carcasses that contributed to the FLK Zinj fauna? To answer this question, it is necessary to understand the impact of carnivore ravaging on human-accumulated bone assemblages and how that relates to the frequencies of the resulting bone deletion, comparing different anatomical parts of the same skeleton. Modern actualistic studies on carnivore ravaging can provide a useful insight into this process. Capaldo's (1995) large experimental sample provides a test of the interpretation that the missing skeletal portions in the FLK Zinj fauna were deleted by carnivores. His "hammerstone-to-carnivore" experiments modeled, in different African savanna settings, the destructive taphonomic behavior of hyenas on bone assemblages first modified by

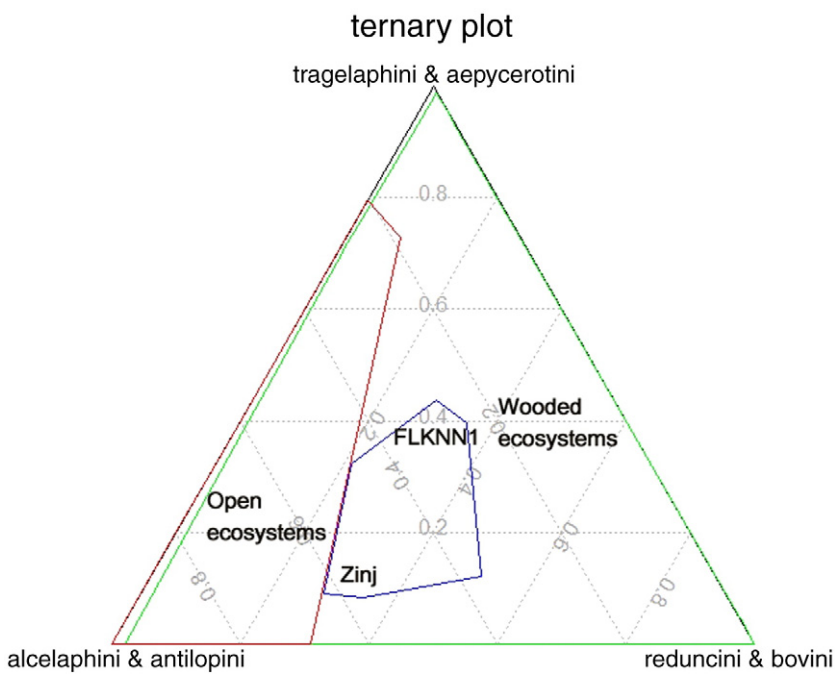

Figure 12. Ternary graph programmed in R, using all the data from each bovid group (alcelaphini and antilopini, reduncini and bovini, and tragelaphini and aepycerotini) from Fig. 13 and bootstrapped 10,000 times. Large variability of data from wooded biomes accounts for the widespread overlap of this sample.

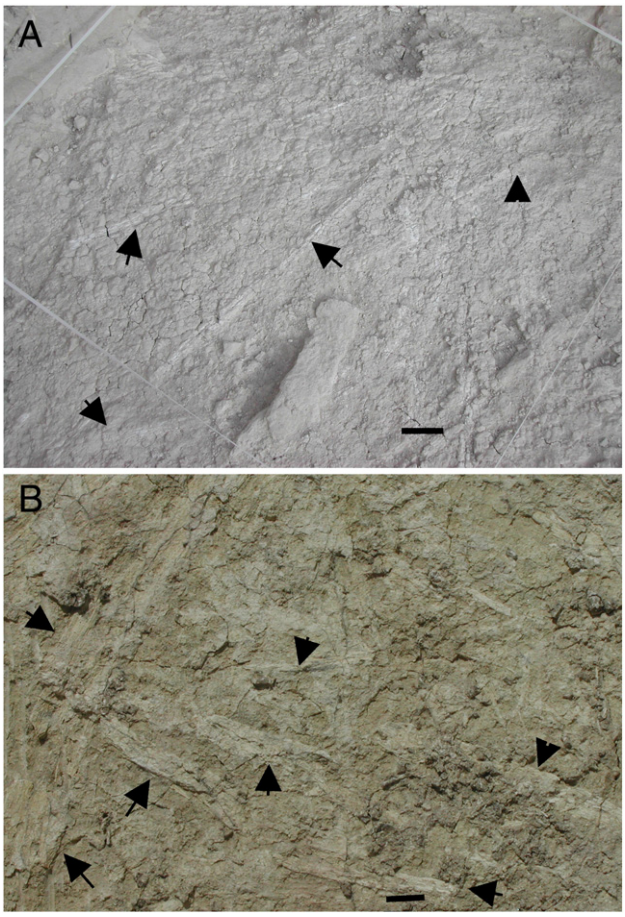

Figure 13. Arrows show some of the fossil root casts on the FLK Zinj paleosol (A) and FLK NWT1 (B). Scale = 5 cm.

humans defleshing and demarrowing ungulate carcasses. Capaldo (1995) reports that 93% of axial bones (vertebrae and ribs) were deleted by carnivore ravaging in this experimental sample, as well as 81% of long limb bone ends, when comparing element count before and after carnivore intervention. In addition, 53% of the surviving limb bone epiphyseal specimens were tooth-marked. It could be argued that the tooth-mark percentage of the surviving epiphyses is related to the survival of these portions and these, in turn, can be related to the survival of axial elements, since carnivores target axial elements before consuming long bone ends (Capaldo, 1995). Thus, with this assumption, a relationship is established among three variables: the more intense carnivore impact on a deposited fauna, the greater the deletion of axial elements from carcasses, the greater the deletion and frequency of tooth marks on long limb bone ends.

There are only 65 axial bone specimens from small animals (Bunn's (1982) size 1 and 2) and 90 from medium-sized animals (Bunn's (1982) size 3) in the FLK Zinj fauna (Domínguez-Rodrigo et al., 2007). Long limb bone end specimens (50 for small animals and 60 for medium-sized ones) represent, respectively, 45% and 42%, of the total minimal number inferred by the long bone MNE reconstruction (110 for small animals and 142 for medium-sized animals). That means that there is a loss of epiphyseal bone portions of 55% in small animals and 58% in medium-sized carcasses, according to the minimal number of complete bones inferred. A total of 24% of epiphyseal fragments from small carcasses and 28.3% of epiphyseal specimens from medium-sized carcasses are tooth-marked (Domínguez-Rodrigo et al., 2007). Using Capaldo's (1995) experimental dataset for comparison the tooth-marked frequencies of epiphyseal portions at FLK Zinj would indicate an epiphyseal loss of 36.7% for small animals and 43% for medium-sized animals. The mismatch between the actual documented loss in the FLK Zinj fauna and the expected loss according to tooth-marked epiphyseal frequencies is simply a product of employing a theoretical model. We utilize the documented loss and the expected loss of epiphyseal portions as the maximum and minimal estimates to interpret the loss of axial bones from the FLK Zinj assemblage in a broad perspective. For small animals a range of 41% to 62% of axial bones is estimated to have been deleted by carnivore ravaging, and between 49% and 66% of medium-sized animal axial bones.

Using teeth, Bunn (1982) and Bunn and Kroll (1986) estimated that 48 ungulate carcasses are represented at FLK Zinj. Using ungulate long limb bones, a more conservative estimate of a minimum of 21 carcasses potentially having been represented by some portions of the postcranial skeleton is inferred (Domínguez-Rodrigo et al., 2007). Reasoning from the most conservative estimate to minimize errors, a minimum of 1113 axial bones from 21 carcasses should have been once been present in at FLK Zinj if whole carcasses were originally transported to the site. Thus, the identification of just 155 ungulate axial bones in the FLK Zinj fauna implies that 86% of the axial skeletons of those carcasses were lost. This

Table 9
Theoretical estimates of axial and long bone end deletion using Capaldo's (1995) experimental data on bone placement and recovery after carnivore ravaging in savanna environments. Ratios of axial, and long bone end loss, and of long bone end loss:percentage of tooth-marked long bone specimens. Theoretical bone loss estimate for the Zinj faunal assemblage is shown. See the text for comparison with estimates based on MNI and MNE.

Capaldo (1995), Appendix 4. Part 1 and Part 3.				
Hammerstone-carnivore				
		Placement	Recovery	Percentage loss
Axial bones (ribs and vertebrae		1054	77	92.7
Long bone ends		460	88	81
				Percentage
TOOTH-marked long bone ends			47/88	53.4
Ratio %loss long bone end: %TM long bone end	1.53			
Ratio %loss axial bone: %loss long bone end	1.14			
				Estimated
FLK Zinj		Small carcasses	Large carcasses	Percentage loss according to Capaldo's data
Axial bones		65	90	
Long bone ends		50	60	
TM% long bone ends		24	28.3	
Ratio %loss long bone end: %TM long bone end		24 × 1.53	28.3 × 1.53	36.7 for small 42.8 for large
Ratio %loss axial bone: %loss long bone end		36.7 × 1.14	42.8 × 1.14	41.8 for small 49 for large

is a loss 30%–45% higher than the range estimated from the application of Capaldo's (1995) experimental data (Table 9). Together, these observations indicate to us that the early Pleistocene hominids who created the FLK Zinj fauna practiced a mixed carcass transport strategy: (1) The extreme paucity of ungulate axial elements at the site is probably not related to post-hominid, carnivore destruction of select parts of whole skeletons, but rather to selective transport of long limb bones from carcasses by hominids. (2) The presence, though, of *some* axial elements in the assemblage indicates that hominids did transport some carcasses to the site in a complete or nearly complete state, which carnivores may have subsequently ravaged. The predominant role of hominids and minimal role of carnivores in forming the FLK Zinj fauna is also supported by the paucity long limb bone epiphyseal specimens that are tooth-marked, especially those that are preserved as complete ends.

It has been argued (Domínguez-Rodrigo and Barba, 2006) that studies which suggested a high degree of tooth-marking on the FLK Zinj bones (Blumenschine, 1995; Capaldo, 1997) are flawed because those original estimates are inflated by the mistaken inclusion of natural biochemical marks in counts of carnivore tooth marks (and subsequent defenses of those original claims of high tooth mark frequencies (Blumenschine et al., 2007) have also been proved fatally flawed (Domínguez-Rodrigo and Barba, 2007c)).

In sum, then, the limited evidence of significant carnivore ravaging (and biasing) of the FLK Zinj bone assemblage means that the fauna is much more indicative of hominin subsistence behavior than of non-anthropogenic taphonomic processes. Taking this into account, hominin behavior at FLK Zinj can now be better understood from the taphonomic study of the archaeofaunal assemblage and the analysis of carcass obtainment strategies that it reflects; hominins at FLK Zinj may have used the wooded/bushy character of the FLK Zinj paleolandscape to actively engage in ambushing ungulates (see Bunn and Pickering, 2010). As a result, hominins might have been able to choose which resources to transport to FLK Zinj to be processed and consumed.

Conclusions

The FLK, FLK N and FLK NN sites span most of the Bed I stratigraphic sequence, from lower Bed I (FLK NN 4) to uppermost Bed I (FLK N 1–2). Each of these sites shows evidence of hominin and carnivore use of the same spaces over a vast amount of time (thousands of years) when considering all sites collectively. The reason for site clustering could be ecological: a freshwater spring system would have fed the lake floodplain at that specific point, drawing herbivores to the plant resources, which are extremely diverse and abundant near springs (Copeland, 2004). Carnivores and hominins would have followed herbivores. Hominins would also have felt drawn to the area by the available plant resources (Copeland, 2004, 2007). The carbonate record of freshwater sources on the landscape migrated across the landscape through time likely due to rift-related tectonics. Carbonate spring deposits occur at FLK NN in middle Bed I time, at FLK in upper Bed I time and in VEK, HWK-E and MCK during the lowermost Bed II time (Ashley et al., 2009).

The recent paleoecological information discovered by TOPPP's on-going research also falsifies Capaldo and Peters (1995) and Lam's (2008) suggestions that the carcasses accumulated by hominins at FLK Zinj could have been passively obtained from either mass drowning or from carcass gluts caused by intensive droughts. Had any of these events occurred at the time the site was formed, this should be reflected by a high number of carcasses occurring at or near the spring. Given the paucity of carcass remains found at the spring (FLK NN 1 and on-going work around it) it is evident that animals were not drawn *en masse* to the spring due to a drought. No mass deaths are documented there either. Therefore, carcasses, obtained through more aggressive strategies, must have been those transported to the FLK Zinj locality.

Our work reinforces the hypothesis that FLK Zinj is a "central-place" (hominins selected the spot and repeatedly transported carcasses and raw materials to it), in a low-competition setting (wooded place), in an ecological context ~200 m away from a permanent source of potable water (spring). Hominin butchery activities are documented only at the site; no cut-marked or percussion-marked bone specimens were found anywhere else on the sampled landscape. This area seems to have been appealing for hominins and carnivores for thousands of years since there is almost continuous occupation from the FLK Zinj times until Bed II times. The FLK Zinj bone assemblage was formed at the time when the taphonomy of the landscape and the underlying and overlying sites indicates that carnivore presence was most marginal. This is probably not a coincidence. The single-cluster nature of the FLK Zinj site does not seem to be a consequence of site exposure and also suggests that the socio-economic organization of the hominin group(s) responsible for its formation was different from modern humans (characterized by multi-cluster home bases (Yellen, 1977)) and/or that site functionality was different from modern foragers' "central places".

Acknowledgments

We wish to thank COSTECH and the Antiquities unit for permits to conduct research at Olduvai. We appreciate the major funding provided by the Spanish Ministry of Science and Innovation through the European project I + D HUM2007-63815 and from the Ministry of Culture through the archaeological projects abroad program. Support was also provided by the Fundación Conjunto Paleontológico de Teruel. We also gratefully acknowledge supplemental funding from a University of Wisconsin Graduate School Faculty Research Grant that partially supported participation by H. Bunn and K. Remer. We are also thankful to P. Sánchez, K. Remer, L. Alcalá, A. Gidna, P. Bushozi, J. Ulumara, B. Mbasa, T. Ombari and the Dar es Salaam University field school for their contribution in the 2007 and 2008 field seasons. We also thank John Kumaro for his support. We appreciate the comments made by two anonymous reviewers.

References

Ashley, G.M., Liutkus, C.M., 2002. Tracks, trails and trampling by large vertebrates in a rift valley paleo-wetland, lowermost Bed II, Olduvai Gorge, Tanzania. Ichnos 9, 23–32.

Ashley, G.M., Tactikos, J.C., Owen, R.B., 2009. Hominid use of springs and wetlands: paleoclimate and archaeological records from Olduvai Gorge (1.79–174 Ma). Palaeogeography, Palaeoclimatology, Palaeoecology 272, 1–16.

Ashley, G.M., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Diez-Martin, F., 2010. A spring and wooded habitat at FLK Zinj and their relevance to origins of human behavior. Quaternary Research 74, 304–314.

Barba, R., Domínguez-Rodrigo, M., 2007. FLK North North I: "living floor" or natural accumulation? In: Dominguez-Rodrigo, M., Barba, R., Egeland, C.P. (Eds.), Deconstructing Olduvai. Springer, New York, pp. 216–228.

Barboni, D., Bremond, L., Bonnefille, R., 2007. Comparative study of modern phytoliths assemblages from inter-tropical Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 246, 454–470.

Behrensmeyer, K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4, 150–162.

Binford, L.R., 1981. Bones: Ancient Men, Modern Myths. Academic Press, New York.

Blumenschine, R.J., 1991. Hominid carnivory and foraging strategies, and the socio-economic 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 hominid 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? Preliminare lanscape 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., Prassack, K., Kreger, C.D., Pante, M., 2007. Carnivore tooth marks, microbial bioerosion and the invalidation of Domínguez-Rodrigo & Barba's (2006) test of Oldowan hominin scavenging behavior. Journal of Human Evolution 53, 420–426.

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

Brodkorb, P., Mourer-Chauviré, C., 1982. Fossil anhingas (Aves: Anhingidae) from early man sites of Hadar and Omo (Ethiopia) and Olduvai Gorge (Tanzania). Geobios 15 (4), 505–515.

Brodkorb, P., Mourer-Chauviré, C., 1984a. Fossil owls from early man sites of Olduvai Gorge, Tanzania. Ostrich 55, 17–27.

Brodkorb, P., Mourer-Chauviré, C., 1984b. A new species of cormorant (Aves: Phalacrocoracidae) from the Pleistocene of Olduvai Gorge, Tanzania. Geobios 17 (3), 331–337.

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, vol. 163, pp. 21–30.

Bunn, H.T., 1986. Patterns on skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. Journal of Human Evolution 15, 673–690.

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

Bunn, H.T., 2007. Butchering backstraps and bearing backbones: insights from Hadza foragers and implications for Paleolithic archaeology. In: Pickering, T., Schick, K., Toth, N. (Eds.), Breathing Life into Fossils: Taphonomic Studies in honor of C.K. (Bob) Brain. Stone Age Institute Press, Indiana, pp. 269–280.

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., 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., Harris, J.W.K., Isaac, G., Kaufulu, Z., Kroll, E., Schick, K., Toth, N., Behrensmeyer, A.K., 1980. FxJj 50: an early Pleistocene site in northern Kenya. World Archaeology 12, 109–136.

Capaldo, S. D. 1995. Inferring hominid and carnivore behavior from dual-patterned archaeological assemblages. Ph. D. Thesis. Rutgers University, New Brunswick.

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.

Capaldo, S.D., Peters, C.R., 1995. Skeletal inventories from wildebeest drownings at Lakes Masek and Ndutu in the Serengeti ecosystem of Tanzania. Journal of Archaeological Science 22, 385–408.

Cerling, T.E., Hay, R., 1986. An isotopic study of paleosol carbonates from Olduvai Gorge. Quaternary Research 25, 63–78.

Cerling, T.E., Quade, J., Wang, Y., Bowman, J.R., 1989. Carbon isotopes in soils and paleosols as ecology and palaeoecology indicators. Nature 341, 138–139.

Copeland, S.R., 2004. Paleoanthropological Implications of Vegetation and Wild Plant Resources in Modern Savanna Landscapes, with Implications to Plio-Pleistocene Olduvai Gorge, Tanzania. The State University of New Jersey, Rutgers.

Copeland, S.R., 2007. Vegetation and plant food reconstruction of lowermost Bed II, Olduvai Gorge, using modern analogs. Journal of Human Evolution 53, 146–175.

Domínguez-Rodrigo, M., 1993. La analítica espacial como herramienta tafonómica: aplicación al entorno de una charca africana. Procesos postdeposicionales, Arqueología espacial, pp. 16–17.

Domínguez-Rodrigo, M., 1996. A landscape study of bone preservation in the Galana & Kulalu (Kenya) ecosystems. Origini 20, 17–38.

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., 2002. Hunting and scavenging by early humans: the state of the debate. Journal of World Prehistory 16, 1–54.

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., 2007a. Five more arguments to invalidate the passive scavenging version of the carnivore-hominid-carnivore model: a reply to Blumenschine et al., (2007a). Journal of Human Evolution 53, 427–433.

Domínguez-Rodrigo, M., Barba, R., 2007b. Reanalysis of FLK North 3: yet another case of a palimpsest? In: Dominguez-Rodrigo, M., Barba, R., Egeland, C.P. (Eds.), Deconstructing Olduvai. Springer, New York, pp. 239–252.

Domínguez-Rodrigo, M., Barba, R., 2007c. The behavioral meaning of cut marks at the FLK Zinj level: the carnivore–hominid–carnivore hypothesis falsified (II). In: Dominguez-Rodrigo, M., Barba, R., Egeland, C.P. (Eds.), Deconstructing Olduvai. Springer, New York, pp. 75–100.

Domínguez-Rodrigo, M., Organista, E., 2007. Natural background bone assemblages and their ravaging stages in Olduvai Bed I. In: Dominguez-Rodrigo, M., Barba, R., Egeland, C.P. (Eds.), Deconstructing Olduvai. Springer, New York, pp. 201–216.

Domínguez-Rodrigo, M., Barba, R., Egeland, C.P., 2007. Deconstructing Olduvai. Springer, New York.

Domínguez-Rodrigo, M., Mabulla, Bunn, H.T., A., Diez-Martín, F., Barba, R., Egeland, C.P., Espílez, E., Egeland, A., Yravedra, J., Sánchez, P., 2009. Unravelling hominid behavior at another anthropogenic site from Olduvai Gorge (Tanzania): new archaeological and taphonomic research at BK, Upper Bed II. Journal of Human Evolution 57, 260–283.

Egeland, C.P., 2007. Zooarchaeology and taphonomy of FLK North North 2. In: Dominguez-Rodrigo, M., Barba, R., Egeland, C.P. (Eds.), Deconstructing Olduvai. Springer, New York, pp. 229–238.

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.

Greenwood, P.H., Todd, E.J., 1970. Fish remains from Olduvai. In: Leakey, L.S.B., Savage, R. J.G. (Eds.), Fossil Vertebrates of Africa, Vol. 2. Academic Press, London, pp. 225–241.

Hay, R., 1976. Geology of the Olduvai Gorge. University of California Press, Berkeley.

Isaac, G.L., 1978. The food-sharing behavior of protohuman hominids. Scientific American 238, 90–108.

Isaac, G.Ll., 1981. Archaeological tests of alternative models of early hominid behaviour: excavation and experiments. Philosophical Transactions of the Royal Society of London, Series B 292, 177–188.

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. 4. Academic Press, London, pp. 57–120.

Kingdon, J., 1997. Field guide to African mammals. Princeton University Press, Princeton.

Lam, Y.M., 2008. What have taphonomic studies taught us about early hominin behavior? Evolutionary Anthropology 17, 158–161.

LaPorte, L.F., Behrensmeyer, A.K., 1980. Tracks and substrate reworking by terrestrial vertebrates in Quaternary sediments of Kenya. Journal of Sedimentary Petrology 50, 1337–1346.

Leakey, L., 1965. Olduvai Gorge 1951–1961. A Preliminary Report on the Geology and Fauna. Cambridge University Press, Cambridge.

Leakey, M., 1971. Olduvai Gorge, vol. 3. Excavations in Bed I and II, 1960–63. Cambridge University Press, Cambridge.

Lewis, M.E., 1997. Carnivoran paleoguilds of Africa: implications for hominid food procurement strategies. Journal of Human Evolution 32, 257–288.

Marean, C.W., Spencer, L.M., Blumenschine, R.J., Capaldo, S., 1992. Captive hyaena bone choice and destruction, the Schlepp effect and Olduvai archaeofaunas. Journal of Archaeological Science 19, 101–121.

Piperno, D.R., 1988. Phytolith Analyses: an archeological and Geological Perspective. Academic Press, San Diego.

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.

Potts, R., 1991. Why the Oldowan? Plio-Pleistocene tool making and the transport of resources. Journal of Anthropological Research 47, 53–176.

Rose, L., Marshall, F., 1996. Meat eating, hominid sociality, and home bases revisited. Current Anthropology 37, 307–338.

Ruff, C., 2008. Relative strength and locomotion in *Homo habilis*. American Journal of Physical Anthropology 138, 90–100.

Shipman, P., Harris, J.M., 1988. Habitat prefeence 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: paeosol carbonate isotopic evidence. Journal of Human Evolution 27, 25–45.

Sikes, N., Ashley, G.M., 2007. Stable isotopes of pedogenic carbonates as indicators of paleoecology in the Plio-Pleistocene (upper Bed I), western margin of the Olduvai basin. Journal of Human Evolution 53, 574–594.

Spencer, L.M., 1997. Dietary adaptations of Plio-Pleistocene bovidae: implications for hominid habitat use. Journal of Human Evolution 32, 201–228.

Stewart, K.M., 1994. Early hominin utilisation of fish resources and implications for seasonality and behaviour. Journal of Human Evolution 27, 229–245.

Torre, de la, I., Mora, R., 2005. Unmodified lithic material at Olduvai Bed I: Manuports or Ecofacts? Journal of Archaeological Science 32, 273–285.

Van Neer, W., Lesur, J., 2004. The ancient fish fauna from Asa Koma (Djibouti) and modern osteometric data on 2 tilapiini and 2 Clarias catfish species. Documenta Archaeobiologiae 2, 143–160.

Vrba, E., 1980. The significance of bovid remains as indicators of environment and predation patterns. In: Behrensmeyer, A.K., Hill, A. (Eds.), Fossils in the Making. The University of Chicago Press, Chicago, pp. 247–271.

Witte, F., de Winter, W., 1995. Appendix II: Biology of the major fish species of Lake Victoria. In: Witte, F., Van Densen, W.L.T. (Eds.), Fish Stocks and Fisheries of Lake Victoria. A Handbook for Field Observations. Samara Publishing Ltd, Cardigan, UK, pp. 301–320.

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.

Yellen, J., 1977. Archaeological Approaches to the Present. Models for reconstructing the past. Academic Press, New York.