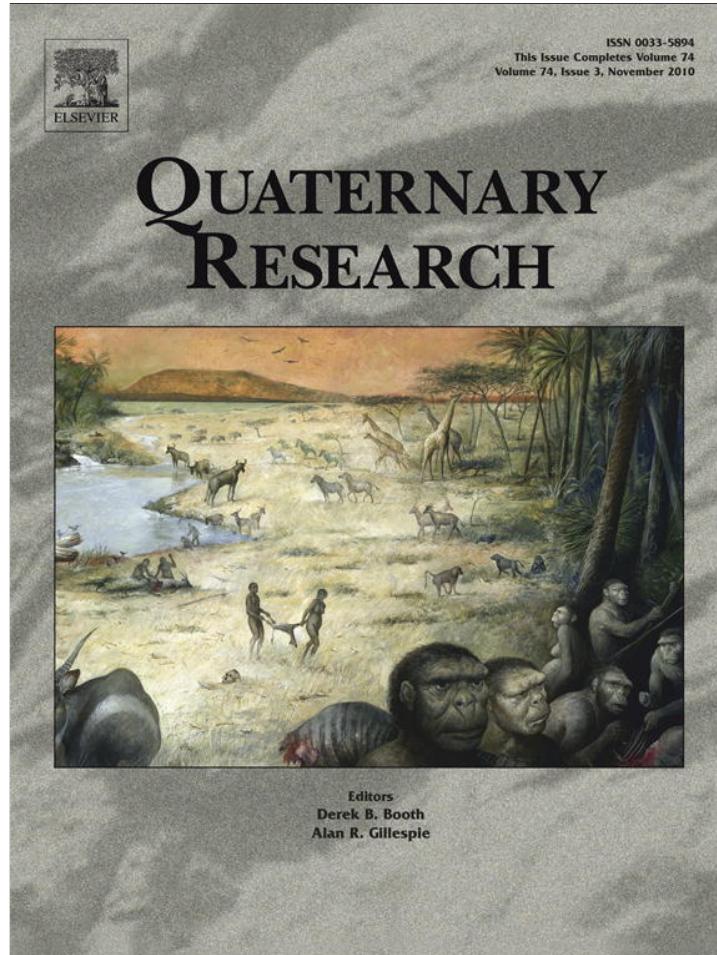


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Disentangling hominin and carnivore activities near a spring at FLK North (Olduvai Gorge, Tanzania)

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ABSTRACT

FLK North is one of the densest concentrations of fossils found in Olduvai Gorge. A recent taphonomic re-evaluation of the collection excavated by Leakey at the site suggests that it was a palimpsest in which most of the animals were accumulated and modified by carnivores. The lithic tools therefore seem to have an independent depositional history from most of the fauna. The present study, based on new excavations, expands the evidence supporting this interpretation and demonstrates a thicker deposit than was reported by Leakey, including new archaeological levels. It also shows that in the few instances where hominins butchered carcasses, meat, not marrow, was their main target. This argues against passive scavenging hypotheses, which emphasize the dietary role of marrow, and instead underscores the importance of meat in the diet of early Pleistocene hominins.

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Introduction

A taphonomic review of some of the most important early Pleistocene archaeological sites in Africa revealed that most sites that include indication of hominin behavior are also palimpsests (Domínguez-Rodrigo et al., 2007). Taphonomic and geological data for some of these palimpsests, which sometimes span impressive thicknesses of several meters of slowly deposited clays, indicate repeated occupation of the same place by hominins and other agents (e.g., carnivores) over hundreds and even thousands of years. The reasons why the same spots were visited recurrently by hominins remained unclear, however, as did the functionality of the sites and what they actually represent for the understanding of the origins of human behavior.

One of the most impressive palimpsests where hominins used the same place repeatedly, probably over several millennia, is FLK North (FLK N, Olduvai Gorge, Tanzania). There, an impressive accumulation of stone tools and bones was created over a long period of time

spanning >6 m of clays and tuffs. What drew hominins to the same spot for so long? What was special about that location, within a lacustrine floodplain, that caused hominins and other agents to overlap in the use of that space? Was the site a brief stop in the hominin foraging home range, and thus visited only for specific expedient activities, or was it used for something more complex that required a more prolonged stay? Our recent re-excavation of the site has aimed to address these questions.

FLK N is situated in uppermost Bed I. It is <100 m north of the famous FLK 22 *Zinjanthropus* (FLK Zinj) site. FLK N is the thickest early Pleistocene archaeological deposit currently known. Leakey (1971) uncovered three archaeological levels overlying Tuff IF, two in lowermost Bed II (FLK N clay with root casts and FLK N *Deinotherium* level) and one situated in the middle of Bed II (FLK N sandy conglomerate). Underlying Tuff IF, she excavated six archaeological levels (FLK N 1–6), which she interpreted as hominin “living floors” (levels 1–2 to 5) and the lowermost one (level 6) as an elephant butchery site (Leakey, 1971). Table 1 provides a geological description of these levels. The criteria that Leakey used for differentiating levels was mainly a change in the color or in the lithological properties of the sediments, although in some cases (e.g., levels 1–3) she separated the levels by their varying density of included materials and their differential vertical distribution within the same geological layer. A

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Table 1

Description of the lithology of the archaeological levels.

Archaeological level	M. Leakey	TOPPP
Levels 1–2 and 3	A single 2–3 ft. horizon of a gray-brown silty clay	A light waxy clay deposit spanning a maximum of 80 cm
Level 4	A dark chocolate brown silty clay varying in thickness from 1.5 ft. to 3–4 in.	A dark waxy clay spanning 60 cm maximum
Level 5	A greenish-yellow clay with ferruginous bands and a fine-grained white tuff towards the base	Same definition as in Leakey (1971)
Level 6	A dark grayish-brown silty clay with white streaks about 1.5 ft.	Dark waxy clay with carbonate nodules and white streaks spanning between 20 cm and 50 cm
Level 7		Light-gray clay with white streaks spanning between 15 cm to 20 cm and containing large concretions
Level 8		Light-gray to yellowish clay spanning 13 cm to 18 cm separated from level 7 by a thin layer of white carbonate/limestone and a ferruginous band
Level 9.		Dark waxy clay between 16 cm to 31 cm. The lowest part shows an abundance of oncolites, underlain by a tuffaceous clay

(Olduvai Landscape Palaeoanthropology Project) in Bed II sediments on both sides of our excavation, which we agreed not to reopen. Trench 1 measures 2×3 m and is situated approximately to the south of Leakey's Trench IV. Trench 2 measures 4×2 m (Fig. 1D) and is situated to the south of Leakey's Trenches III and part of II. One of our trenches exposed a deeper stratigraphic sequence than exposed by Leakey (1971) (Fig. 2) and yielded comparable and higher densities of archaeological materials as the densest areas excavated by Leakey (1971). This indicates to us that the bulk of the site was not completely excavated by Leakey and that an extensive area of it is still unexcavated. We also opened a 1-m-wide geological step-trench ~25 m to the east of the site to expose its boundary (Fig. 3A), which is described in more detail in Ashley et al. (2010a).

Initially, excavation in both trenches proceeded from the "clay with root casts" level in Bed II through Tuff IF. Given the high density of remains in level 1–2, the different excavation seasons (Trench 1 was initiated in 2007 and Trench 2 in 2008) and the size difference between the trenches, Trench 1 was further excavated through levels 1–2 to 6 and then, after removing the tuffaceous limestone, excavation proceeded deeper, uncovering three more archaeological levels (Fig. 2), described below and in Table 1. Trench 2 is still in the process of being excavated and will be presented separately. Analysis of the faunal and lithic remains from level 1–2 is found, respectively, in Bunn et al. (2010) and Diez-Martin et al. (2010). We ceased excavation in Trench 1 after reaching level 9, not because the deposit became sterile, but because the small size of the trench did not allow us to continue any further without compromising the quality and safety of the excavation.

Excavation was carried out systematically with the aid of small tools. We used large picks only when digging through Tuff IF, cemented sections, and the tuffaceous limestone separating the first five levels from the lower ones. The term "level" is applied here following the same definitions established by Leakey (1971) in her excavation of the site; that is, it mainly follows geological criteria and identifies each level according to its lithological properties. The exceptions are the upper three levels, which, following Leakey, are based on changes in the densities of artifacts and fossils and a partial sedimentary hiatus in between vertical concentrations of materials, which we have done for the sake of comparing the retrieved materials from Leakey's and our excavations. All sediment was sieved through 5-mm mesh. Each fossil and artifact ≥ 2 cm was plotted with a laser total station and each level was drawn, following Leakey's example. The total station was used to plot individual archaeological items.

The spatial plots shown in this work do not present horizontal long shapes (produced by plotting the ends of each item), which may be potentially useful to infer paleosol topography, because most levels have been identified in geological layers that lack paleosols, and also because bones with a clearly defined long axis (length >3 times width) showed a variety of degrees of vertical tilting. This phenomenon has been experimentally documented in clay contexts where the sediment is either periodically wet and dry and/or trampled (Domínguez-Solera, 2010). This ample range of vertical tilting would prevent the documentation of the shape of any paleosurface accurately. The use of the total station, though, allowed a three-dimensional reconstruction of the deposit, which is an improvement of the two-dimensional information provided by Leakey for each archaeological level that she excavated by showing the vertical location of each artifact and fossil. This has been shown to be important when considering the diachronic deposition of materials (especially when comparing lithics to fossils) prior to making any functional inference of their spatial association (Domínguez-Rodrigo et al., 2009) because it can contribute to detecting depositional histories of materials that appear more closely associated if displayed on a two-dimensional plot.

recent taphonomic re-evaluation of Leakey's collections concluded differently from Leakey that most of the FLK N archaeological levels are (1) palimpsests that were accumulated almost exclusively by carnivores killing and/or consuming animals on the spot or (2) mixed assemblages where carnivores and hominins contributed independently (the latter in a much more marginal way) to the accumulation and modification of animal bones (Domínguez-Rodrigo et al., 2007).

The present study aims to analyze new archaeological and paleontological data from FLK N to test this new palimpsest hypothesis, and to further refine the reconstruction of hominin roles in each of the archaeological levels. We aim to define the lowermost boundary of FLK N site, which could not be investigated earlier by Leakey (1971), who finished her excavation after the removal of the materials from level 6 because the underlying and overlying sediments (depending on the area) were highly compacted limestone (Leakey, 1971, 64). We also provide higher resolution spatial information on the position of archaeological materials in order to ascertain if Leakey's (1971) division of archaeological layers is supported. Finally, we investigate whether the vertical dispersion of archaeological materials in each level was due to the continuous occupation of the site, with multiple depositional events, or to more discrete depositional intervals but with trampling or vertical migration of materials.

Methodology and sample description

The characteristics of the new trenches and the excavation

When Leakey excavated FLK N in 1960, she opened five trenches of variable dimensions according to level (no level was exposed for more than 100 m²). We, as part of The Olduvai Palaeoanthropology and Palaeoecology Project (TOPPP), opened two archaeological trenches, separated by a 1 m wall, at the back of Leakey's trenches, continuing from near the back wall of Leakey's trenches IV (which showed the highest density of remains in level 1–2), III and a small part of II (Fig. 1). The location of the new trenches was also determined in part by multiple trenches opened by OLAPP

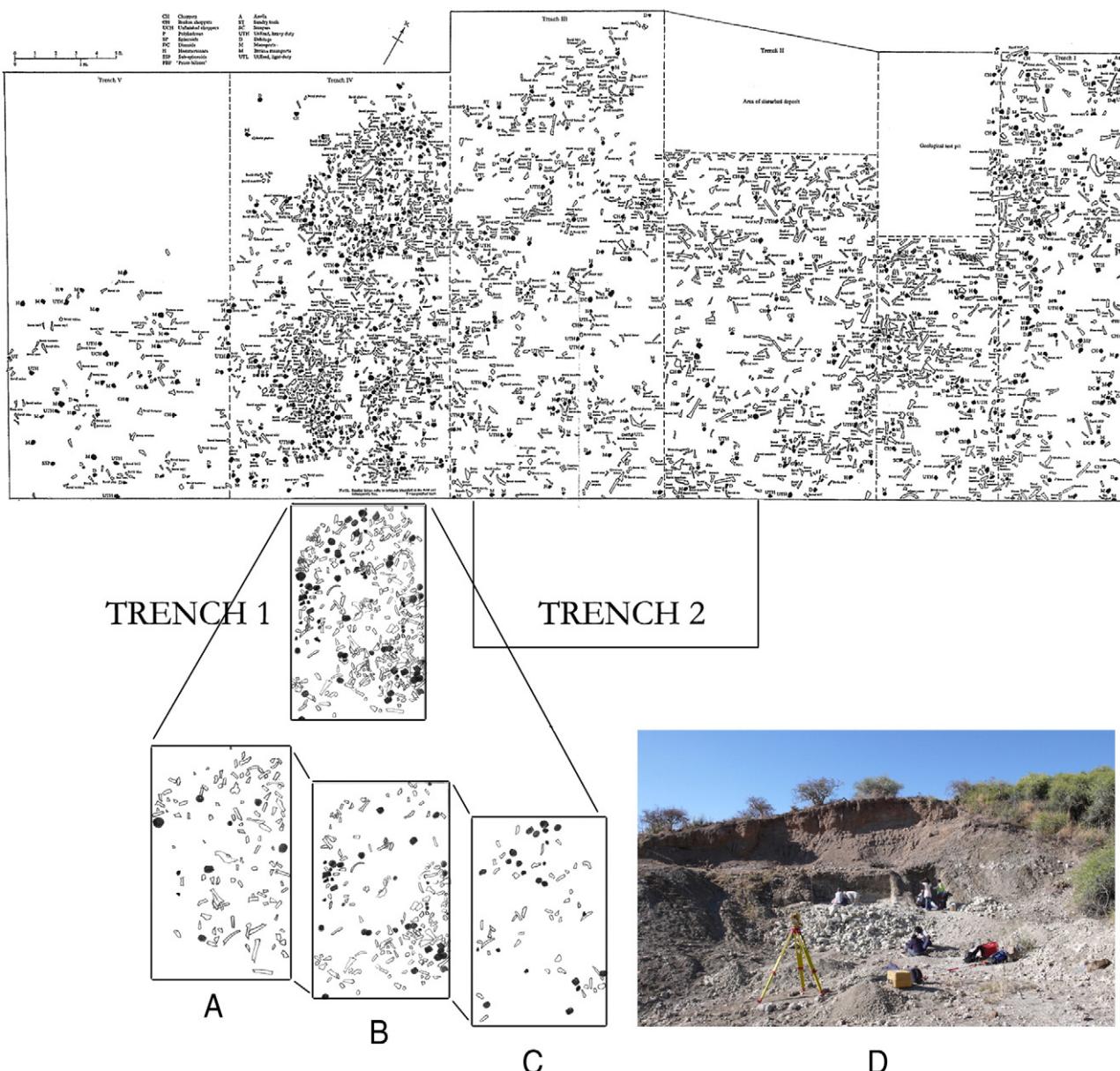


Figure 1. Map of the distribution of lithic artifacts and fossil bones at FLK North level 1–2 as drawn by Leakey (1971) and the approximate location of TOPPP's trenches. Distribution of artifacts and fossils is also shown in Trench 1, lumping all the materials retrieved together vertically (as M. Leakey did). The lower three trenches show the distribution of materials in Trench 1 according to depth: the upper 10 cm of FLK N1–2 (A), the middle 10 cm (B) and the lowermost 10 cm (C). The upper 10 cm in FLK North 1–2 (A) show a high density of fossils with very few stone tools, and the lowest 10 cm (C) show the opposite pattern; a substantial amount of stones (clustered in the northern area) with very few bones spatially associated with them. This casts more doubts on any inferred functional association of artifacts and bones. D, Location of Trench 1 (right) and Trench 2 (left) at FLK North.

Testing the vertical distribution of archaeological materials

FLK N is a deep vertical deposit (Figs. 2 and 4). Fossils and stone tools occur almost continuously in varying density across the deposit. Within each of the thick vertically distributed levels, depositional processes could have operated on a multi-occupational scale, with each occupation being discrete or, in contrast, with a continuous deposition of materials because of continuous occupation of the site. Alternatively, it could be argued that post-depositional processes could account for such an apparent clustering and the overall vertical dispersal of fossils. The problem is that taphonomists lack the proper analogs to choose between these interpretations. An experimental study analyzing how archaeological materials migrate vertically in clay by gravitational factors when the sediment is wet (expanding) or dry (contracting) or influenced by factors such as trampling—and how these are reflected in bone orientation in the vertical plane—has been

used as an analogy to interpret the vertical arrangement of fossils in FLK N (Domínguez-Solera, 2010).

For comparative purposes, the smaller experimental sample was bootstrapped 200 times (with replacement) to make it more equivalent to the archaeological samples. ANOVA, Tukey HSD, Bonferroni (assuming equal variance) and Dennett T3 (assuming unequal variances) tests were applied.

The taphonomic analysis of the fauna

Vertebrate fossils, including all long limb bone shaft fragments were identified to element whenever possible. In our consideration of skeletal part representation, skeletons are divided into anatomical regions: skull (horn, cranium, mandible and teeth), axial (vertebrae, ribs), appendicular (limb bones), pelvis and scapula as specified in Yravedra and Domínguez-Rodrigo (2009). Long limb bones were

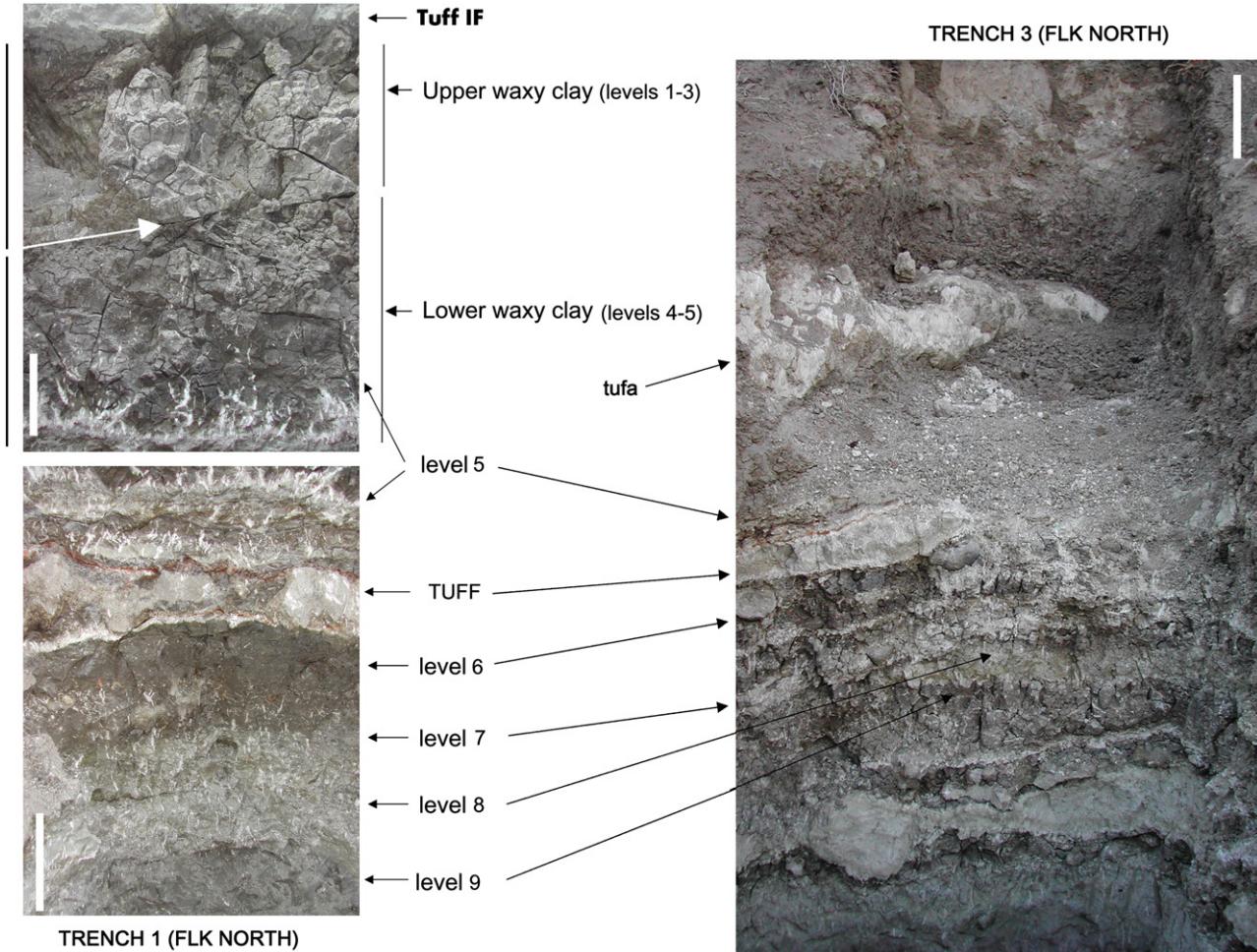


Figure 2. Stratigraphy of Trench 1 and Trench 3 at FLK North. Scale = 20 cm.

further divided into upper (humerus and femur), intermediate (radius and tibia) and lower (metapodials) types (Domínguez-Rodrigo, 1997). Skeletal part profiles were based on estimated NISP (number of identified specimens) and MNE (minimum number of elements) counts (Lyman, 1994). We considered profiles by the inferred size of the carcass from which specimens derived. "Small" refers to Bunn's (1982) sizes 1 and 2, "medium" refers to size 3 and "large" refers to size 4 and bigger.

Estimates of long limb bone MNEs at the Olduvai sites often differ substantially depending on whether epiphyses or shafts are employed analytically (Domínguez-Rodrigo et al., 2007). In the present analysis, MNE estimation for long limb bones has been based on the combined use of shafts and ends (Pickering et al., 2003). To calculate MNEs, some researches use a GIS-based method (Marean et al., 2001). We feel more confident calculating estimates by documenting specimen overlap by hand. As described in Yravedra and Domínguez-Rodrigo (2009), we further refined our analysis by integrating the systems of Patou-Mathis (1984, 1985), Münzel (1988) and Delpach and Villa (1993), for specifying bone section represented by each fossil specimen. Following Delpech and Villa (1993) and Münzel (1988), long limb bone shafts were divided by equally sized sections irrespective of the areas of muscular insertion and other anatomical landmarks. These sectors (upper shaft, mid-shaft, lower shaft) can be easily differentiated and oriented (cranial, caudal, lateral, medial). Yravedra and Domínguez-Rodrigo (2009) describe the criteria used in the division of each shaft sector, taking into account the orientation of each specimen. We also considered

the criteria used by Barba and Domínguez-Rodrigo (2005) for long limb element identification, based on shaft thickness, section shape and properties of the medullary surface of each shaft specimen. After identifying long limb bone specimens to element and shaft sector using these methods, we quantified the MNE by laying out all specimens from the same element and size group together.

When long limb bones are broken by humans or carnivores (namely, hyenas) they typically produce numerous shaft fragments, some intact articular ends, and the latter are then often consumed by carnivores. Bunn (1982) was the first to realize that humans and carnivores modify long limb bone shafts in a different way regarding the amount of section preserved in the fragments surviving marrow extraction. Generally, the articular ends of a broken limb bone have a section of shaft that retains its complete original circumference (Bunn's type 3), while the isolated shaft fragments are less than complete in circumference—Bunn's types 2 (more than half the circumference) and 1 (less than half the circumference). We quantified these circumference types for long limb bone specimens in our sample.

We also evaluated the cortical surfaces of fossils and recorded bone surface modifications: cut marks, tooth marks, percussion marks and natural marks (biochemical and abrasion marks) (Domínguez-Rodrigo and Barba, 2006). Surficial modifications were identified using 10–20x hand lenses under strong direct light, following the methodological and mark diagnostic criteria specified by Blumenschine (1988, 1995) and Blumenschine and Selvaggio (1988, 1991) for tooth and percussion marks, and by Bunn (1981) and Domínguez-Rodrigo (1997, 2002) for cut marks.

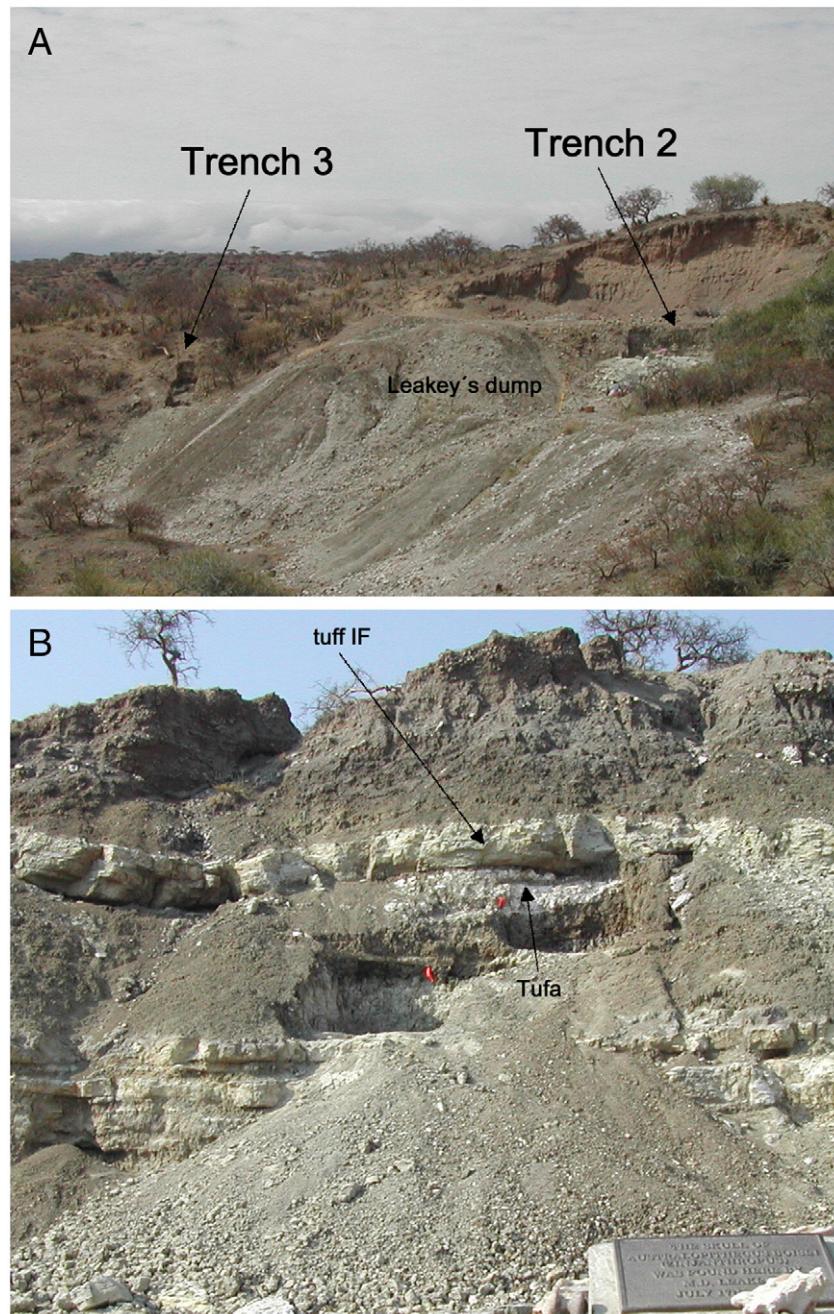


Figure 3. A, location of Trench 2 (within FLK North) and Trench 3. B, identification of a tufa signaling the presence of fresh water, under Tuff IF at FLK.

Results

The geological reconstruction of the site

The excavation of the upper levels in Bed I uncovered six lithostratigraphic levels as defined by Leakey (1971), but with some important differences. A tilted 40–65 cm layer of light-colored gray-brown waxy clay occupied the top of the sequence, underlain by a darker gray-brown silty clay of similar depth (see separation marked by white arrow in Fig. 2). We named these units Upper and Lower Waxy Clay. At the bottom of the latter, the occurrence of carbonate streaks and a more greenish-yellow clay with ferruginous bands overlay a 20-cm layer of fine-grained light gray tuff (which corresponds to Leakey's fine-grained white tuff overlying level 6). This tuffaceous layer showed an irregular distribution across the surface, being observed in half of the trench, whereas it was reduced to

a thin concreted iron band in the remainder of the trench, separating the two clay units. Under this tuff, a 30-cm unit of dark brown silty clay with white streaks and iron patches was found. Under this layer, there was a 20-cm unit of light gray clay with white streaks containing limestone and tuffaceous nodules, followed by a 40-cm layer of darker gray clay with fewer nodules.

Leakey's (1971) level 1–2 were differentiated from level 3 by a few centimeters of sterile sediment. Although clearly seen in the field, this is not easy to perceive in the vertical plotting of materials (Fig. 4), because the distribution of the levels is not quite horizontal. The tilting of the layers together with the fact that the "levels were contorted and faulted on a local scale" (Leakey, 1971, p. 62) explain why the plot does not show layering that was visible during excavation. Despite the irregular shape of each surface (Fig. 2) (see also Leakey, 1971, plate 12), the spatial plotting shows three high-density bands corresponding to level 1–2 (dense), 3 (more diffuse)

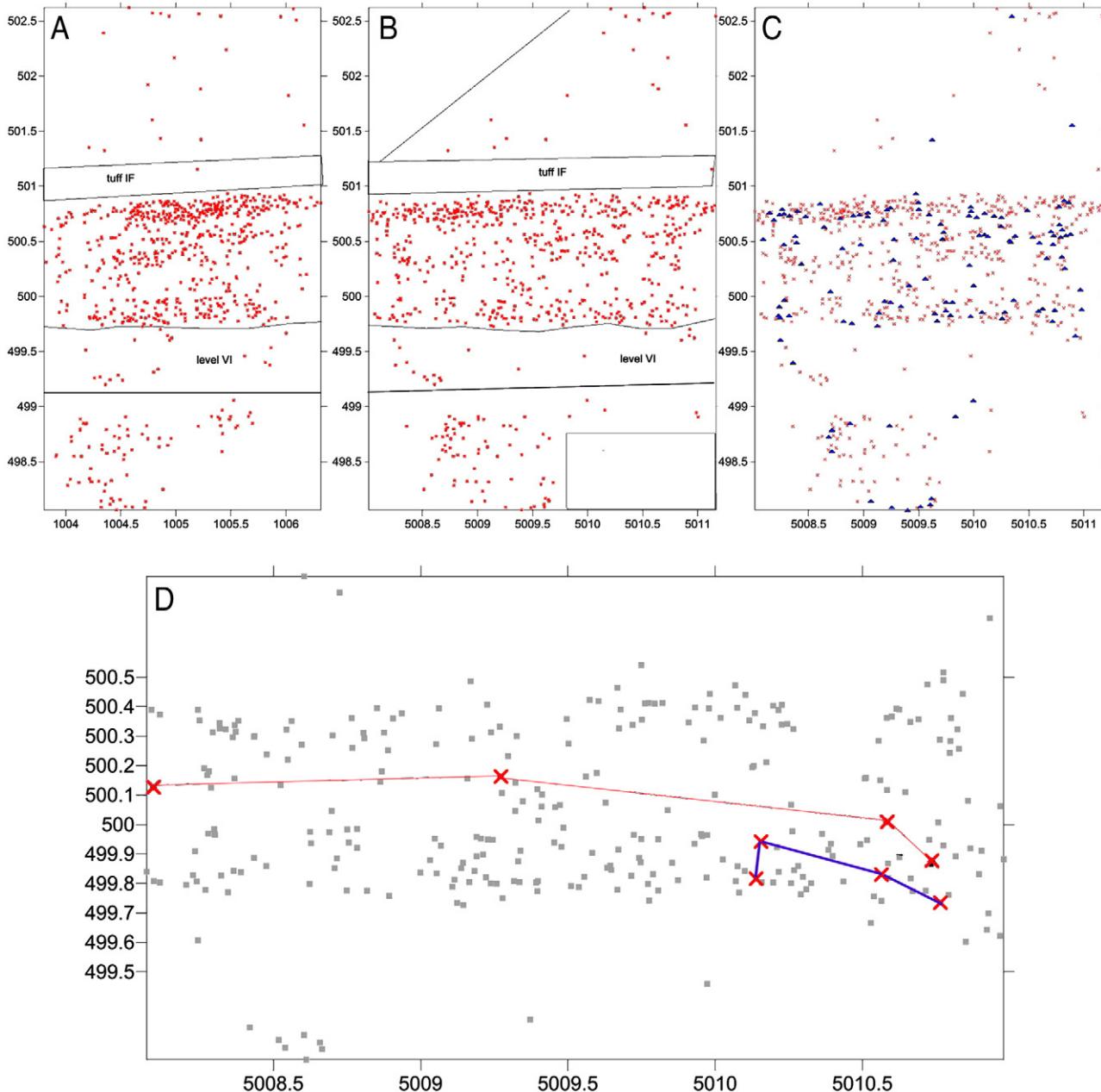


Figure 4. Vertical distribution of archaeological materials in Trench 1 as seen in north-south view (A) or east-west view (B and C). Dots in A and B represent the archaeological materials (stone tools and bones) plotted together. C, vertical distribution of stone tools (triangles) and fossil bones (crosses) plotted separately. D, vertical distribution of remains belonging tentatively to the same individuals: a giraffid (thin line) and an equid (thick line).

and 4–5 (dense). A small, highly localized hiatus also allowed us to separate level 3 from the underlying levels 4–5.

No difference could be established between levels 4 and 5 in our trench. They form a vertical continuum of materials, despite the difference in lithology. This reflects a general characteristic of the FLK N archaeological sequence: the vertical distribution of fossils is almost continuous. However, there are clearly areas with denser (more discrete) concentrations and others with fewer materials. This likely indicates that the processes of bone accumulation were more active during certain parts of the sedimentation process.

The continuity of fossil distribution also casts doubt on the reliability of differentiation of archaeological levels. Leakey (1971) used lithological criteria to separate levels, while admitting that the separation of some levels was arbitrary and based on density criteria (e.g., level 1–2 from level 3). Likewise, even when some lithostratigraphic details can be differentiated (e.g., the bottom of the lower

waxy clay [level 4] and the more yellow underlying clay [level 5]), no clear separation in the materials forming the archaeological deposit could be made. We would have liked to use a new nomenclature when differentiating archaeological levels that could reflect this situation, but decided to retain Leakey's (1971) level division for the sake of comparison with the materials already excavated. Whereas we feel more confident of the separation of level 1–2 from the underlying levels in our trench, we have to admit that the distinction among levels 3 and 4–5 is completely arbitrary and is based on linking lithostratigraphic and material density criteria. The presence of the tuffaceous layer and thick ferruginous bands, creating a true sedimentary hiatus, reflected in the absence of archaeological materials, helped to differentiate level 6 from the overlying levels.

The same problem applies to levels 7–9, which were differentiated solely on lithostratigraphic grounds, due to the clearly defined horizontal layering, whereas materials appear vertically dispersed

without showing any sedimentary hiatus. The lithology, coloring and texture of levels 7–9 are markedly different from those of the upper levels (Fig. 2). They are fairly thin layers with different lithological properties, which are easily differentiated from one another (Table 1). This enabled us to connect the layers between separate and distant trenches. This was done in a third trench (Trench 3), to delimit the site boundaries (Fig. 3A). There, levels 1–9 were identified and some more vertical layering under level 9 was also documented (Fig. 2).

Trench 3 revealed an interesting feature of paleoecological significance. Remnants of Tuff IF were identified. The underlying six clay levels were present on the right (west) side of the trench but more than one-half of the left (east) side was occupied by the edge of a tufa layer. The clay to the right (west) of the tufa contained fossil bones but none was retrieved from the left (east) side, where the tufa lay. The presence of this tufa indicates that a body of water was present extending up to the location where Trench 3 was dug. This body of water has been interpreted as a spring (see an extensive description in Ashley et al., 2010a). The tufa identified at Trench 3 can be traced along the FLK N outcrop and joins the tufa layer identified under Tuff IF all around the FLK gully (Fig. 3B). This tufa layer, right under Tuff IF, has also been identified at the exposures between FLK N and FLK N West (see Domínguez-Rodrigo et al., 2010). Therefore, in >500 m of exposure of Tuff IF around the FLK, FLK N and FLK N West gullies, the tufa sediment appears in the clay deposit under Tuff IF everywhere but at the FLK N site.

The paleo-spring in this area would have created a wetland with swampy areas where water was on the surface. The upper section of FLK N (levels 1–6, and more specifically, levels 3–5) thus was formed near the edge of one of these bodies of water. Figure 4A shows that there is a slight tilt of sediments eastwards, towards Trench 3. This tilting is better seen in Figure 2, where the stratigraphy of Trench 3 shows a tilting of strata under the tufa. This becomes more pronounced as one moves lower in the sequence, to the point of showing some cross-bedding. For instance, layer 7 cuts across layer 8. This could indicate the presence of a slope that could account for higher ground in the FLK N area, which might have been frequently protected from the spring water when the surrounding area was covered with it.

This all suggests the presence of a large wetland area with a sort of small peninsula, on which FLK N was situated in the past. FLK N was thus the only continuous dry land in the area (or at least, the only one identifiable in the available exposures), projecting into a wetland where water was covering most of the surrounding surface. This would have created a portion of dry land conducive to the accumulation of bones and tools in an otherwise wet area. Continuous reuse of this spot by carnivores and hominins over a long span thus seems to have created one of the largest accumulations of bones in Olduvai Gorge. The location of the site is also suggestive of some degree of closed-vegetation as documented in most spring wetland systems (Copeland, 2007) and supported by the abundant presence of wooded plant phytoliths (see data in Barboni et al., 2010).

Thus, the existence of a more open-vegetation landscape farther away from FLK N does not contradict the exceptional paleoecological situation of the site and its wooded nature (Ashley et al., 2010a; Barboni et al., 2010). If it was a small dry area surrounded by water and/or open habitats, it is easy to think of the site as a sort of natural trap for herbivores repeatedly approaching the water to drink and carnivores then preying on them.

This reconstruction is applicable to the upper five levels in Bed I, given the extensive presence of tufa under Tuff IF. However, the archaeology of levels 7–9 in Trench 1 is providing interesting hints that even if the wetland situation might have been present earlier—a spring wetland has also been discovered during the underlying FLK Zinj times (Ashley et al., 2010b)—the amount of dry land might have been greater. Although the area exposed through excavation in Trench 1 was small, it is evident that the highest density of remains is

located in the upper five levels. The underlying levels show a much lower density of remains (Fig. 4), slightly higher than the lowermost Bed II level (clay with rootcasts). That the levels with the lowest density of remains, both in Bed I and Bed II, occur in the absence of nearby evidence of water (tufa), seems to be more than a coincidence. This could imply a larger expanse of dry land and, therefore, no reason for bone-accumulating agents to cluster in the same space.

Experimental testing of vertical migration of materials

An experiment carried out to test vertical migration of materials in a clay deposit under cyclic wet/dry processes was used as an analogical framework (Domínguez-Solera, 2010). In this experiment, the vertical displacement of bones was not accompanied by a marked change in the degree of tilting. Bones moved vertically keeping broadly their original horizontal position. A high degree of tilting, therefore, is probably more indicative of biotic trampling of bones than the abiotic dynamics of bone movement throughout a deposit.

The vertical displacement of bones in this modern experiment counsels caution when dealing with archaeological deposits formed in clays for long periods of time. In Trench 1, some vertical movement of materials can be observed, which stresses the artificial differentiation of archaeological levels, either by using lithological criteria (Leakey, 1971) or material density criteria (present work). We can also consider the possibility of refitting or matching individuals across a level. Isolating bones from the same individual is not easy. However, in Trench 1 this was possible twice (Fig. 4D). In one instance, the only equid bones found in the level 3–6 sequence were stratigraphically identified and in the case of the forelimb, both the left humerus and radius were present and biometric criteria indicated their perfect fit. The occurrence of the equid bones in the same part of the trench but with a maximum vertical difference of 21 cm (using the locations of the humerus and radius) suggested that post-depositional vertical movement had taken place. In both cases no tilting was documented and therefore, the vertical difference cannot be attributed to trampling on wet clay.

Equally illustrative of this process is the vertical distribution of the few bones attributable to a giraffid individual. Two teeth (upper and lower molars), a skull fragment and half of a distal epiphysis of a metatarsal occur across the trench and span a vertical difference of 26 cm. In this case, the remains occur both in the artificially differentiated level 3 and in levels 4–5, which further proves the inaccuracy of the level differentiation when using lithological or material density criteria. It is tempting to think that this individual could be the same as the one represented by a metatarsal from level 6. A patella from a juvenile giraffid was also identified in level 7, suggesting a possible link with the level 6 individual. No direct link can be made between these remains in levels 6–7 and those from levels 3–5. But given that these are the only giraffid remains in this part of the sequence, if they belonged to the same individual, vertical dispersion could span >1 m, but, of course, this is untestable speculation.

However, the hippopotamus remains located in levels 6 and 7 could belong to the same individual, given the size of the carcass and the limited depth of level 7. Furthermore, an Antilopini humerus from level 7 and a radius from level 8 match perfectly, further suggesting that they could belong to the same individual, although in this case, the fit could be coincidental given the abundance of Antilopini remains throughout the sequence.

In contrast with the experimental situation, the FLK N deposit includes a higher number of bones with an acute degree of vertical tilting. A one-way ANOVA analysis shows a significant difference among assemblages ($F = 7.5$; $p = .000$).

Post hoc tests show that no significant differences exist when comparing all the archaeological levels from 1 to 5, but that each level is significantly different from the experimental set (Table 2). Levels 6

Table 2

Bonferroni, Dunnert and Tukey tests of intercomparability of mean values of the degree of vertical tilting among experiments and archaeological levels. Asterisks denote significant difference.

Multiple comparisons						
Dependent variable: degree of vertical tilting						
	(I) assemblage	(J) assemblage	Mean difference (I-J)	Std. Error	Sig.	95% Confidence Interval
						Lower bound
Tukey HSD	Level 1–2	Level 3	.59612	2.38102	.994	−5.5458 6.7381
		Levels 4–5	1.68151	2.44657	.902	−4.6295 7.9925
		Experiments	17.81774*	3.77193	.000	8.0879 27.5476
		Level 3	−.59612	2.38102	.994	−6.7381 5.5458
		Levels 4–5	1.08539	3.00819	.984	−6.6744 8.8452
		Experiments	17.22162*	4.15824	.000	6.4953 27.9480
		Level 1–2	−1.68151	2.44657	.902	−7.9925 4.6295
		Level 3	−1.08539	3.00819	.984	−8.8452 6.6744
		Experiments	16.13623*	4.19611	.001	5.3122 26.9603
		Level 1–2	−17.81774*	3.77193	.000	−27.5476 −8.0879
Bonferroni	Level 1–2	Level 3	−17.22162*	4.15824	.000	−27.9480 −6.4953
		Levels 4–5	−16.13623*	4.19611	.001	−26.9603 −5.3122
		Level 3	.59612	2.38102	1.000	−5.7161 6.9084
		Levels 4–5	1.68151	2.44657	1.000	−4.8045 8.1675
		Experiments	17.81774*	3.77193	.000	7.8181 27.8173
		Level 3	−.59612	2.38102	1.000	−6.9084 5.7161
		Levels 4–5	1.08539	3.00819	1.000	−6.8895 9.0603
		Experiments	17.22162*	4.15824	.000	6.1979 28.2454
		Level 1–2	−1.68151	2.44657	1.000	−8.1675 4.8045
		Level 3	−1.08539	3.00819	1.000	−9.0603 6.8895
Dunnett T3	Level 1–2	Experiments	16.13623*	4.19611	.001	5.0121 27.2604
		Level 1–2	−17.81774*	3.77193	.000	−27.8173 −7.8181
		Level 3	−17.22162*	4.15824	.000	−28.2454 −6.1979
		Levels 4–5	−16.13623*	4.19611	.001	−27.2604 −5.0121
		Level 3	.59612	2.05890	1.000	−4.8791 6.0714
		Levels 4–5	1.68151	2.24296	.973	−4.2986 7.6616
		Experiments	17.81774*	1.62028	.000	13.4972 22.1382
		Level 3	−.59612	2.05890	1.000	−6.0714 4.8791
		Levels 4–5	1.08539	2.43023	.998	−5.3980 7.5688
		Experiments	17.22162*	1.87094	.000	12.2012 22.2420
Dunnett T3	Level 4–5	Level 1–2	−1.68151	2.24296	.973	−7.6616 4.2986
		Level 3	−1.08539	2.43023	.998	−7.5688 5.3980
		Experiments	16.13623*	2.07178	.000	10.5702 21.7022
		Level 1–2	−17.81774*	1.62028	.000	−22.1382 −13.4972
		Level 3	−17.22162*	1.87094	.000	−22.2420 −12.2012
		Levels 4–5	−16.13623*	2.07178	.000	−21.7022 −10.5702

* The mean difference is significant at the .05 level.

and lower were excluded because of the much smaller sample size. Although most specimens in the archaeological sets from levels 1–2, 3 and 4–5 show tilting of less than 30°, 23% of bones from level 3 and 21% of bones from levels 4–5 show tilting higher than this value. The percentage of tilted bones documented in this level is similar to that documented in level 1–2 (23.5%). This suggests that some trampling occurred, which is also documented in the presence of trampling marks on some of the recovered fossils. For the levels analyzed (levels 3 and 4–5), trampling marks occur in lower frequencies than that reported for level 1–2 (Domínguez-Rodrigo et al., 2007). For level 3, trampling marks are documented in eight specimens (10%) and in levels 4–5, only five specimens (4.5%) bearing trampling marks were documented.

The taphonomic analysis of the faunal remains

There is a fairly high density of remains in Trench 1, which compares well to the highest density area excavated by Leakey (1971). We exclude our conclusions about the densest part of the deposit here (level 1–2) since those conclusions are presented in detail in Bunn et al. (2010). Table 3 summarizes the taxonomic representation and MNIs we documented per level. As from Leakey's more extensive excavations, the bovids *Antidorcas* and *Parmularius* predominate in our sample. However, we also document the important presence of very large, size-5 faunal remains.

Bovid skeletal part profiles are biased towards skull and long limb bone specimens (Table 4). Some long limb bones are better represented by epiphyseal than by shaft portions (Table 5); shafts are surprisingly scarce compared to the number of elements present.

Table 3

Minimum number of individuals (MNI) for each of the excavated levels (except level 1–2).

	Level 3	Levels 4–5	Level 6	Level 7	Level 8
Primate indet	1				
<i>Panthera cf. pardus</i>	1				
<i>Antidorcas recki</i>	1	2		1	
<i>Antilopini</i> size 1	1		1	1	1
<i>Parmularius altidens</i>	2	2			
<i>Kobus cf. sigmoidalis</i>	1				
<i>Alcelaphini</i> size 3a			1	1	1
Bovid size 3b	1	1			
<i>Tragelaphus cf. strepsiceros</i>				1	1
<i>Equus</i> sp.		1			
<i>Kolpochoerus limnetes</i>			1	1	
<i>Giraffa jumae</i>		1			
<i>Giraffa</i> sp.	1	1	1	1	
<i>Hippopotamus gorgops</i>			1	1	

Table 4

Skeletal representation by level and carcass size (small to large) for levels 3 to 7. Numerator indicates NISP and denominator shows MNE.

	Level 3			Levels 4–5			Level 6			Level 7		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	large
Horn	1/1			1/1	2/2							1/1
Skull	1/1	3/2		1/1	5/3	2/1		1/1				
Teeth	1/1	4/4	2/2	2/2	5/5	2/2		2/2				1/1
Mandible				2/2	1/1			1/1				
Cervical vertebrae				1/1	1/1			1/1				
Thoracic vertebrae		1/1		1/1	2/2			2/2				
Lumbar vertebrae					1/1							
Indet. vertebrae					1/1							
Pelves	2/2			1/1	3/2							
Scapulae		1/1			1/1							1/1
Ribs		2/2		2/1	12/10		1/1	2/2		1/1	1/1	1/1
Humerus	3/2	6/5		1/1	6/4		1/1			2/2	1/1	1/1
Radius	2/2	3/3		1/1	1/1			1/1		2/2		
Ulna	1/1			1/1								
Metacarpal		3/3		2/2	2/2							1/1
Femur	1/1	3/2		1/1	3/2			1/1				
Tibia	3/2	2/2		3/2	8/5			1/1				1/1
Metatarsal	3/3	2/2	1/1	1/1	2/2				1/1	1/1		
Carpal/tarsal	1/1	1/1		1/1	5/5		1/1			1/1		

This unexpected result may be related to a limited degree of post-depositional destruction. The distribution of shaft circumference types (Bunn, 1982, 1983) shows that the representation of shafts of type 1 (retaining <50% of their original diaphyseal circumferences) is almost half of what is expected in assemblages broken by either humans or hyenas. In contrast, complete circumference shafts and those with >50% of the original circumference are four to five times higher than in those experimental assemblages (Fig. 5). Collectively, these data indicate much more limited bone fragmentation than is documented among humans and hyenas. Therefore, we infer that neither of those agents played a major role in bone breakage at the site. This is further confirmed by the complete absence of percussion marks in the excavated assemblage.

Tooth marks also occur in low frequencies, as expected given the limited bone breakage. A total of 13 tooth-marked bones were identified in level 3 (16.4%). Considering only long limb bone mid-shafts with good surface preservation, only one tooth-marked specimen in the small animal remains subsample (out of six; 16.6%) was identified and three tooth-marked specimens in the larger animal remains subsample (out of 10; 30%). In levels 4–5, one tooth-marked specimen in the small animal remains subsample (out of 10; 10%) and six tooth-marked mid-shafts in the larger animal remains subsample (out of 22; 27%) were identified. These low to intermediate frequency of tooth marks on mid-shaft portions of long limb bone specimens is higher than that produced by modern felids but significantly lower than that produced by modern hyenas (Domínguez-Rodrigo et al., 2007).

These frequencies of tooth-marked specimens are similar to those previously reported for the same levels from the collections excavated by Leakey and can be explained by felids being the initial agents in carcass consumption, occasionally followed by hyenas (Domínguez-

Rodrigo et al., 2007). This inference is supported by (1) the pattern of furrowing on the caudal side of the medial epicondyle of humeri and the olecranon process of the ulnae, typical of modern felid bone modification (Fig. 6), and (2) by the breakage of size-3 long limb bones, which preserve tooth marks and associated multiple opposing and overlapping tooth notches, typical of hyena modification of large bovid limb bones (Fig. 6).

The absence of percussion marks, despite the abundance of green fractures (65 long limb bone mid-shaft specimens out of 70 are green broken; 93%) indicates hominins did not break bones at the site. Following the previous interpretation of these levels as a palimpsest with marginal hominin participation (Domínguez-Rodrigo et al., 2007), only three bones with cut marks have been identified. One of them is a large giraffid metatarsal with its proximal epiphysis and almost half of the proximal shaft, found in level 6, with seven roughly obliquely aligned cut marks on the lateral metadiaphysis close to the epiphysis, where the tibio-metatarsal ligaments are attached (Figs. 7A, 7C, 7E). These cut marks are the result of dismembering this element from the limb. The surprising observation about this specimen is that the mid-shaft section clearly shows a green fracture, along which several conspicuous large tooth scores, which together with other tooth pits on the shaft indicates that a large carnivore (very likely a hyena) broke the bone. Post-breakage gnawing by hyenas is

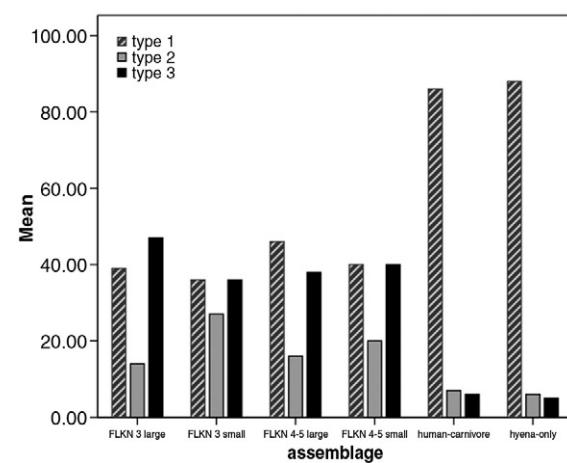


Figure 5. Bunn's (1982, 1983) shaft circumference type distribution in experimental assemblages and in the collection retrieved in Trench 1 levels 3–5.

Table 5

Number of identifiable specimens (NISP) according to bone portion (epiphysis and shaft) from long limb bones, lumping all levels together.

	Small carcasses		Medium-sized and large carcasses	
	Epiphysis	Shaft	Epiphysis	Shaft
Humerus	1	6	5	9
Radius	2	3	2	3
Metacarpal	1	2	4	1
Femur	0	2	3	4
Tibia	0	6	1	11
Metatarsal	2	3	5	1



Figure 6. A, location of carnivore furrowing on the caudal side of the medial epicondyle of humeri of various carcass sizes indicating typical modification caused by felids (Domínguez-Rodrigo et al., 2007). B, identification of chewing on the ulna olecranon of a size 3A carcass and the resulting tooth scoring, also typical of felid damage to bones. C, double-opposing and multiple overlapping notches typical of carnivore bone breakage. D, tooth pit on the shaft of an *Antidorcas* metapodial. C and D are typical modifications caused by hyenas.

discarded as an explanation because the breakage plane shows not only adjacent tooth scores but also a winding micro-notch outline in connection with the scoring showing that breakage resulted from gnawing. Hominins therefore did not exploit the substantial amount of marrow that such a large bone contained.

Another cut-marked specimen is a size 3a Alcelaphini proximal metatarsal from level 3, with one cut mark occurring in exactly the same location as on the giraffid specimen described above. The Alcelaphini specimen shows a green fracture, but the absence of percussion or tooth marks make it impossible to discern the agent of breakage. A third and final cut-marked specimen is a proximal femoral epiphysis of a size 3a Alcelaphini, also from level 3, which shows a cut mark at the base of the cranial side of the greater trochanter, in a position that has been identified as resulting from disarticulation (Nilssen, 2000), although defleshing could also produce sometimes cut marks on the same area. The specimen shows a green fracture on the metadiaphysis but the presence of three clear tooth pits near the breakage plane and the absence of percussion marks indicates that carnivores and not hominins broke the bone (Fig. 7F). Therefore, the evidence shows that hominins exploited at least one *Parmularius* across the vast time represented by levels 3–6.

Despite the ambiguity of marks previously interpreted as cut marks on the elephant bones from level 6, reinterpreted as trampling marks (Domínguez-Rodrigo et al., 2007), the indisputable evidence of cut marks on the giraffid metatarsal in the same level is suggestive of some access to and exploitation of resources from very large animal carcasses. This is further supported by the presence of cut marks on a hippopotamus metacarpal in the Leakey collection (Bunn, 1982). Although the empirical evidence is insufficient to reconstruct the strategy of acquisition and order of access by hominins to resources from these large-sized carcasses, the most parsimonious explanation is that they may have scavenged them, if they died near the edge of the spring, as the occurrence of two elephants, one hippopotamus and one giraffe in a small area in level 6 from FLK N seem to indicate. However, it should be emphasized that opportunistic exploitation of small- and medium-sized carcasses by hominins is not supported, confirming the previous analysis of the Leakey collection (Domínguez-Rodrigo et al., 2007). The absence of percussion marks

excludes any possibility of systematic marrow exploitation by hominins. Furthermore, the presence of disarticulation cut marks negates the possibility of secondary access, since from an optimal foraging point of view disarticulation is unnecessary if hominins had access to defleshed carcasses, and such behavior would have also unnecessarily blunted their tools (Braun et al., 2008).

Discussion and conclusions

The long sequence spanned at FLK N indicates that the place must have been a focus of attraction for both carnivores and hominins for a very long time, more than has been documented for any other early Pleistocene site. This is probably due to the specific paleoecological characteristics of the location of the site. Most paleoecological inferences of FLK N place it within a fairly open ecosystem, spanning a subdesertic steppe (Bonnefille, 1984) to an arid bushland and woodland (Fernández-Jalvo et al., 1998). The overwhelming presence of Alcelaphini and Antilopini also supports such ecological interpretations both taxonomically (Potts, 1988; Shipman and Harris, 1988; Plummer et al., 2008) and, to a lesser extent, ecomorphologically (Plummer and Bishop, 1994). Not much was known about bone scatters and densities underlying Tuff IF since no landscape archaeological approach had been applied to this time interval until now. However, we have opened four trenches exposing the clays underlying Tuff IF (three in the FLK gully and one lateral to the FLK North site), and very few fossils occurred in the latter whereas the three former trenches were completely bone-free. In contrast, FLK N contains the densest concentration of faunal remains for all the Bed I sites and is only second to BK for all the Olduvai sites. This dense concentration of bone remains over such a vast period has no modern analog and challenges the idea that it was formed in an open-vegetation habitat, given the limited amount of bones accumulated in such settings in modern savannas (Hill, 1979; Behrensmeyer and Boaz, 1980; Behrensmeyer, 1983; Hill and Behrensmeyer, 1984).

The open landscape interpretation of FLK N has to be modified: in the lower levels, the presence of browsers like *Giraffa* and *Tragelaphus* indicates a mosaic environment, with presence of trees. This is further supported by the analysis of the microfaunal remains, which are

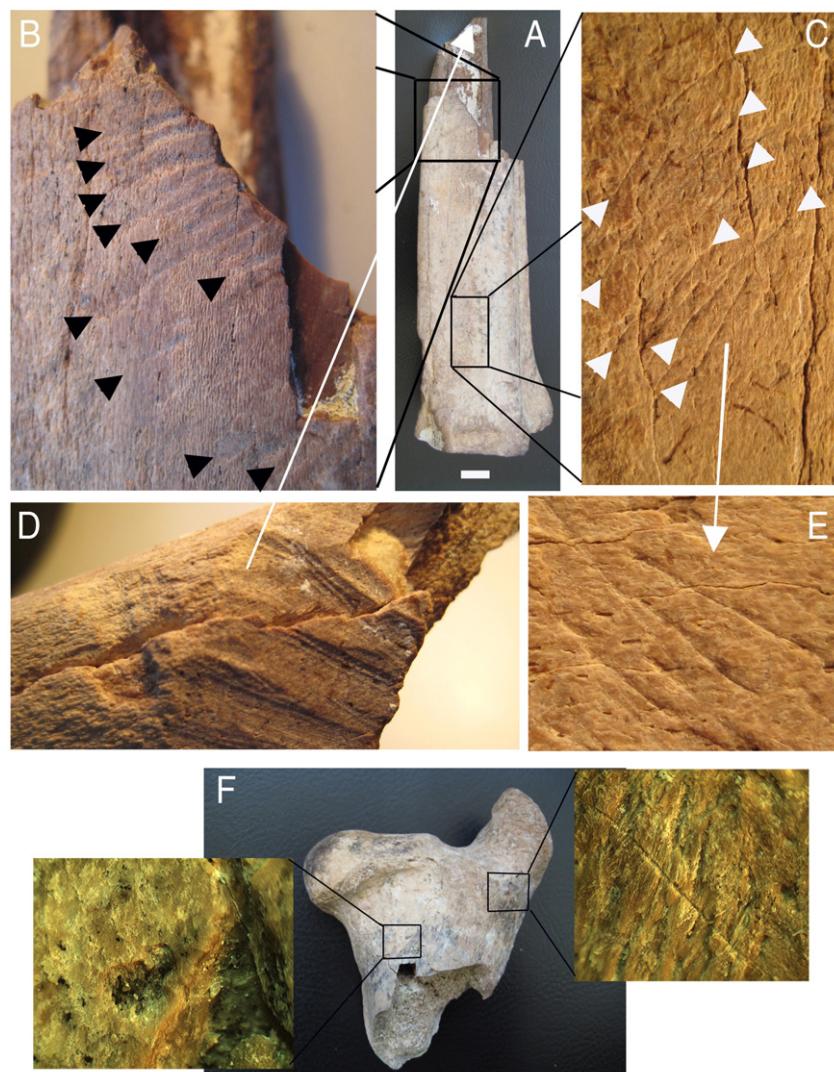


Figure 7. Biostratinomic modifications on a giraffe metatarsal by biotic agents. A, location of cut and tooth marks. B, multiple tooth scores near the edge of a green breakage plane, probably caused by hyenas. C and E, cut marks. D, gnawing marks created by porcupine. F, *Parmularius* proximal femur bearing cut marks (right) indicating disarticulation and a tooth mark by the breakage plane suggesting that carnivores (namely, hyenas) broke the bone.

abundant at the site (Fernández-Jalvo et al., 1998). Recent paleobotanical discoveries at the site shows that even at the upper levels, both at the site and its immediate surrounding area, the vegetation was very closed with a predominance of bushes and trees (Barboni et al., 2010). Given the overall openness of the remaining landscape, such a wooded habitat would have provided a respite for hominins and carnivores, especially given the presence of permanent potable water provided by the spring.

The present study has increased the number of archaeological levels found at FLK N in Bed I and has provided further evidence of the predominant carnivore authorship of the accumulation of all the faunal assemblages across the sequence. Hominin participation in faunal accumulation and modification was very marginal. However, the new discovery from the present analysis, which was not documented in Domínguez-Rodrigo et al.'s (2007) taphonomic re-evaluation of Leakey's collections, was that of large faunal remains modified by hominins. A giraffid metatarsal has been shown to bear cut marks. This supports Bunn's (1982) identification of a hippopotamus metapodial also modified by hominins (with cut marks) in level 6. The other two cut-marked specimens from smaller fauna show similar features to those reported from the Leakey collection: hominins butchered those carcasses but did not seem interested in exploiting their marrow-bearing bones. This has also been reported for the early Pleistocene in Koobi Fora (Kenya), where complete cut-

marked long bones, even from large fauna (hippopotamus), were left unbroken by hominins (Bunn, 1994). This disregard for marrow is especially evident throughout the sequence at FLK N, where complete long bones in spatial connection with stone tools comprise an important part of the assemblage (Domínguez-Rodrigo et al., 2007). Hominins during hundreds (maybe thousands) of years visited FLK N and did not exploit the marrow of the complete bones abandoned by felids at the site during all this time.

This type of evidence is repeated at other sites. For instance, at MK (lower Bed I, Olduvai Gorge), upper limb bones of middle-sized animals bear cut marks but were not broken by hominins (Fig. 8). The evidence for meat as the main target of butchering behaviors by early Pleistocene hominins in Africa is strong enough, at least in Olduvai Gorge, to claim that such a resource must have been obtained by means other than passive scavenging strategies.

The question remains as to why hominins visited the site if they were not scavenging the felid-accumulated remains. The technological analysis of the stone tools indicates that battering was the main function of the artifacts (Diez-Martin et al., 2010). The lack of evidence of hammerstone-broken bones in the faunal remains recovered in Trench 1 suggests that resources other than animal carcasses must have been the target of hominin stone tool use at the site.

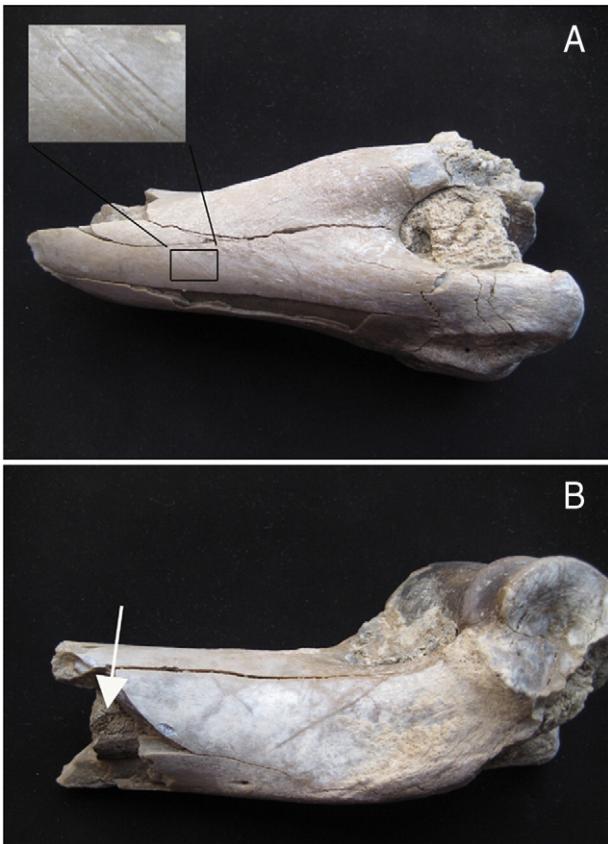


Figure 8. Bovid humerus found at MK, lower Bed I, with recent breaks. It bears cut marks on the caudal-medial side (A). The bone was not broken for marrow (arrow in B).

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