

The larger mammal palimpsest from TK (Thiongo Korongo), Bed II, Olduvai Gorge, Tanzania

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Abstract:

Ever since Mary Leakey's initial excavations in the 1960s, TK (Thiongo Korongo) has been recognized as one of Olduvai Gorge's most important Acheulean sites. The significant concentrations of lithics and fauna reported by Mary Leakey have been augmented in recent years by Santonja et al., who argue that human activities appear to be largely related to the manufacture of lithic implements. In contrast, the faunal remains have been interpreted to be of uncertain origin, and their anthropogenic nature remains in question. This paper presents new data on the formation of the TK bone accumulation. Our results reveal a diverse list of taxa, many of which reflect open habitats. Only limited evidence of anthropogenic activity is documented.

Keywords: Olduvai Gorge | *Homo erectus* | Paleoecology | Taphonomy | Acheulean | Palimpsest

Article:

1. Introduction

At Olduvai Gorge (Tanzania), multi-taxonomic faunal sites are particularly numerous, although their interpretation remains contentious. The large and well preserved lithic and faunal assemblages from FLK (Frida Leakey Korongo), for instance, have generated a more-or-less continuous debate, from Leakey's (1971) pioneering work to the recent studies of Domínguez-Rodrigo et al. (2014a). The collection from Level 22 (the *Zinjanthropus* Floor, or FLK-Zinj) has been presented as the earliest evidence for repeated hunting of small and medium-sized ungulates (Domínguez-Rodrigo and Barba, 2006, Domínguez-Rodrigo et al., 2007, Domínguez-Rodrigo et al., 2010, Domínguez-Rodrigo et al., 2014a), although models based on opportunistic scavenging have also been prevalent in the literature (Blumenschine and Selvaggio,

1988, Blumenschine, 1989, Blumenschine, 1991, Blumenschine, 1995, Capaldo and Blumenschine, 1994, Capaldo, 1997, Pante et al., 2012).

Other Bed I occurrences such as those at FLKN and FLKNN preserve deep, multi-leveled deposits of taxonomically diverse faunal assemblages in association with lithic artefacts (Leakey, 1971). Unlike FLK-Zinj, however, taphonomic analyses on these assemblages suggest only limited hominin, and significant carnivore, intervention with the bone accumulations (Domínguez-Rodrigo et al., 2007, Bunn et al., 2010). This mirrors the situation in Bed II, which preserves numerous sites with diverse taphonomic histories.

At BK (Bell's Korongo), for example, hominins enjoined recurrent primary access to numerous carcasses from a wide range of sizes, from about 50 kg to >5000 kg (Egeland and Domínguez-Rodrigo, 2008, Domínguez-Rodrigo et al., 2009, Domínguez-Rodrigo et al., 2014b). Other sites experienced more complex taphonomic histories. SHK (Sam Howard Korongo) yielded a large lithic accumulation associated with the remains of different animals (Díez-Martín et al., 2014). Taphonomic studies demonstrated that hominids had access to the flesh of hippopotamids and equids, although most of the bone accumulation is interpreted as a palimpsest of uncertain origin (Domínguez-Rodrigo et al., 2014c). The bone accumulations from other Bed II sites such as MNK or HWK East Levels 3–5 are reconstructed to be largely of carnivore origin with only very limited human intervention (Domínguez-Rodrigo et al., 2007, Egeland, 2007, Egeland, 2008, Egeland and Domínguez-Rodrigo, 2008). Sites such as TK (Thiongo Korongo) and FC West contain very poorly preserved faunal assemblages, which hinders definitive taphonomic interpretations (Egeland, 2007, Egeland, 2008, Egeland and Domínguez-Rodrigo, 2008). Some authors consider TK to be a Type A assemblage due to the contrast between the large number of lithics and the scarcity of bone remains (Isaac and Crader, 1981, de la Torre, 2004). This paper discusses the zooarcheology and taphonomy of the Lower Floor at TK (TKLF) based on recent re-excavation of the site.

Our work shows that the site comprises assemblages with different depositional histories and these reflect hominin stone tool manufacture activity with no securely identified indication of any significant bone modification. This casts doubts on functional interpretations of lithics and bones at sites where taphonomic studies have not been made. One of the most relevant examples in this regard can be found in the analysis of Olduvai Bed I sites. These sites were once interpreted as living floors (e.g., Leakey, 1971) given the discrete vertical clustering of spatially-associated stone tools and fossils bones, and subsequent taphonomic research showed a lack of functional association between most stone tools and bones at several of these sites (Domínguez-Rodrigo et al., 2007). Therefore, most of these sites were palimpsests with either a lack of hominin input or very marginal participation of hominins in the accumulation and modification of fauna. TK is another example of a similar type of palimpsest.

2. TK (Thiongo Korongo), Olduvai Gorge, Tanzania

2.1. The site

TK is located in a lateral north-south running korongo (gully) situated on the north slope of Olduvai's Main Gorge approximately 2 km east of the junction with the Side Gorge (Fig. 1). The

site was identified in 1931 by L. Leakey, who noted the presence of hand axe made on quartzite slabs and correctly identified the stratigraphic position of the site within Bed II (Leakey, 1951: 85). However, excavations were not conducted until 1963 when two areas, Trench I and Trench II, around 46.4 m² and 40.5 m² respectively, were excavated by M. Leakey (1971: 172–197). Although materials were found scattered throughout the deposits, M. Leakey identified two main archaeological levels, termed the Upper Floor (TKUF) and Lower Floor (TKLF), as living floors. Leakey (1971), as well as Isaac and Crader (1981), argued that both TKLF and TKUF were only minimally altered during burial. Petraglia and Potts (1994), in contrast, suggested that the site experienced prolonged exposure prior to burial, which resulted in the displacement of small items and reorganization of the site down slope.

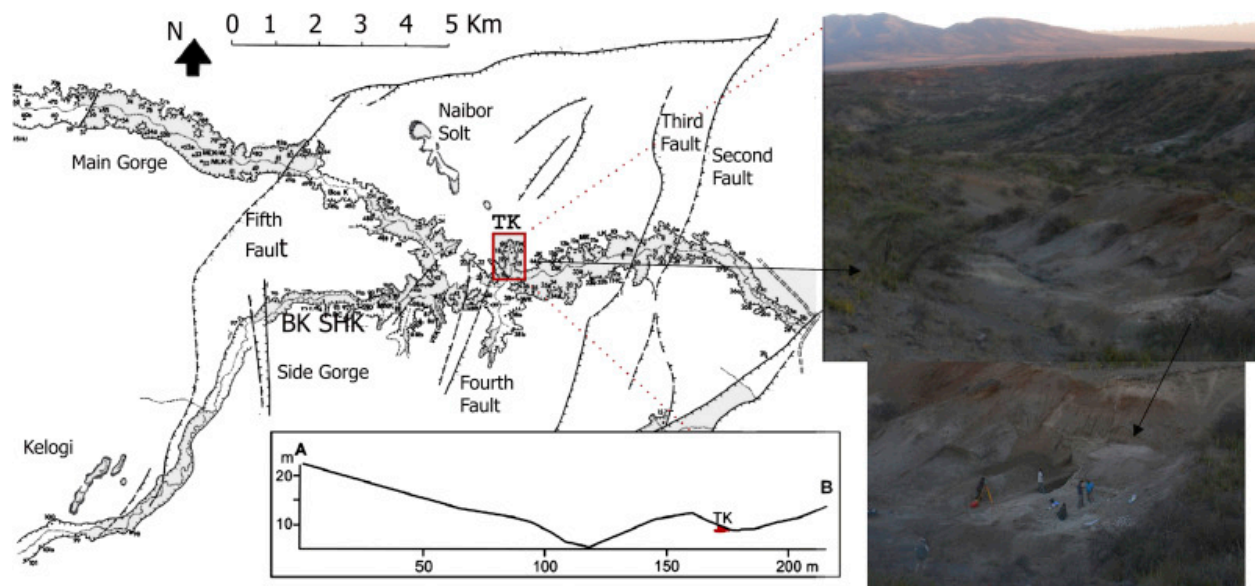


Fig. 1. Position of TK in a lateral korongo in Olduvai Gorge (modified from Hay, 1976) and two pictures of the 2011 excavation.

Between 2010 and 2012, The Olduvai Paleoanthropological and Paleoecological Project (TOPPP) has excavated an additional 113 m² in two zones (Fig. 2), Sector A (SA) and Sector B (SB) (Santonja et al., 2014), immediately adjacent to M. Leakey's 1963 trenches. This new work reveals that the materials in M. Leakey's (1971: 186) Trench II correspond stratigraphically and topographically to TKLF and, hence, do not correspond with TKUF (see discussion in Santonja et al., 2014: 184). This has significant consequences, as some authors have assumed that the lithic material from Leakey's Trench II, as those from Trench I, can be ascribed to TKUF (de la Torre, 2004: 258 ff), when they belong to TKLF.

Recent technological and paleoeconomic study of 5805 artifacts (including 3812 pieces of shatter) from TKLF and the channel in SA show that a majority of the raw material is quartzite that likely derives from Naibor Soit, an inselberg located a few hundred meters from the site. Two different *chaînes opératoires* were identified in TKLF: one based on obtaining flakes from volcanic rocks and quartzite, and the second on the manufacture of standardized hand axe that were produced, used, and abandoned at the site (Santonja et al., 2014). In addition to the artifacts, numerous small cobbles between 6 and 29 g and sizes from 2 × 2 to 3 × 4 cm have been

observed. Santonja et al. (2014) argue that these materials may have been incorporated via natural mechanisms such as fluvial transport or overland flow conditioned by a small channel.

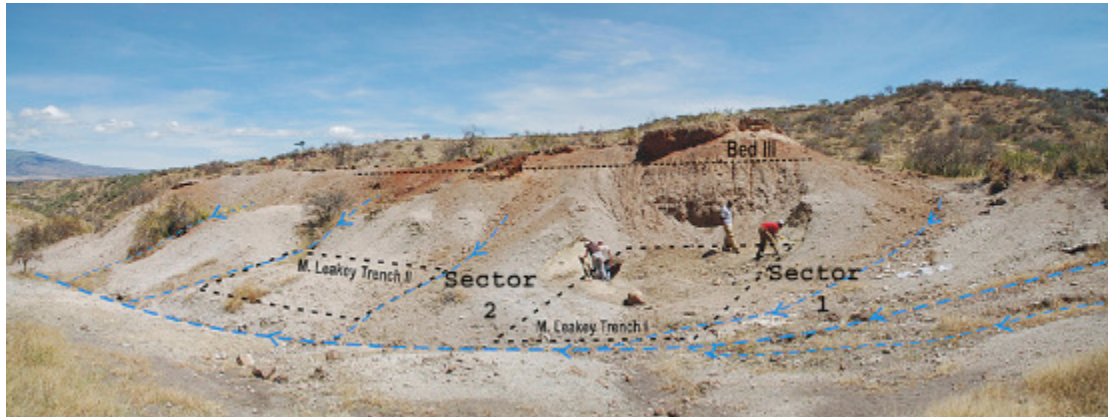


Fig. 2. General view of the TK site in June 2010, showing the location of Trenches I and II (excavated by M. Leakey in 1963) and the seasonal streams that drain this sector of the korongo.

2.2. Geology

From bottom to top, the volcanic and sedimentary outcrops of TK display parts of Hay's (1976) Beds II, III, and IV. The stratigraphic section (Fig. 3) is about 8.90 m thick, of which 7.25 m corresponds to Bed II, 1.25 m to Bed III, and 0.40 m to Bed IV (Santonja et al., 2014).

In the TK area, Bed II begins with dark gray clays (10 YR 4/1, Munsell Soil Color Charts, 1994) and a channel facies of yellowish (10 YR 5/6) sandy clay loam. Over this level appears alternating light brownish (10 YR 6/2) and sandy clay eroded by sandy clays with cross-stratification that form a channel 1.5 m wide and 0.5 m deep, following a north-south direction.

The upper sequence is more complex. Light gray (2.5 Y 7/2) or pale yellow (2.5 Y 8/2) tuffs of several textures are observed, ranging from clay loam to sandy clay, particularly towards the top. A loamy sand channel facies is also interblended, displaying planar cross-stratification with a NW–SE depositional direction. In the NNE–SSW transversal cut, the size of the outcrop section is approximately 12 m in SA, with a maximum thickness of 0.40 m. This thin channel facies rests upon and partially covers TKLF, which in turn overlies a very pale brown (10 YR 8/2) calcrete layer some 7–8 cm thick.

TKUF is found in a stratigraphic discontinuity about 1 m above TKLF and between two tuff levels. It is limited by a discontinuous calcrete some 10–15 cm thick, thicker towards the east and west.

The upper sequence of Bed II is characterized by several brown (10 YR 5/3) or pale brown (10 YR 6/3) clay sublevels with carbonate nodules and root casts. A very pale brown chalky horizon (10 YR 8/2), containing up to 60% calcium carbonate, intercalates in the clay sequence. On top of this level there is light gray tuff (10 YR 7/2) that was eroded and subsequently filled by a pale brown (10 YR 6/3) sandy clay loam that is cross-stratified north-south. The upper part of Bed II is a clay deposit with calcium carbonate nodules and root casts.

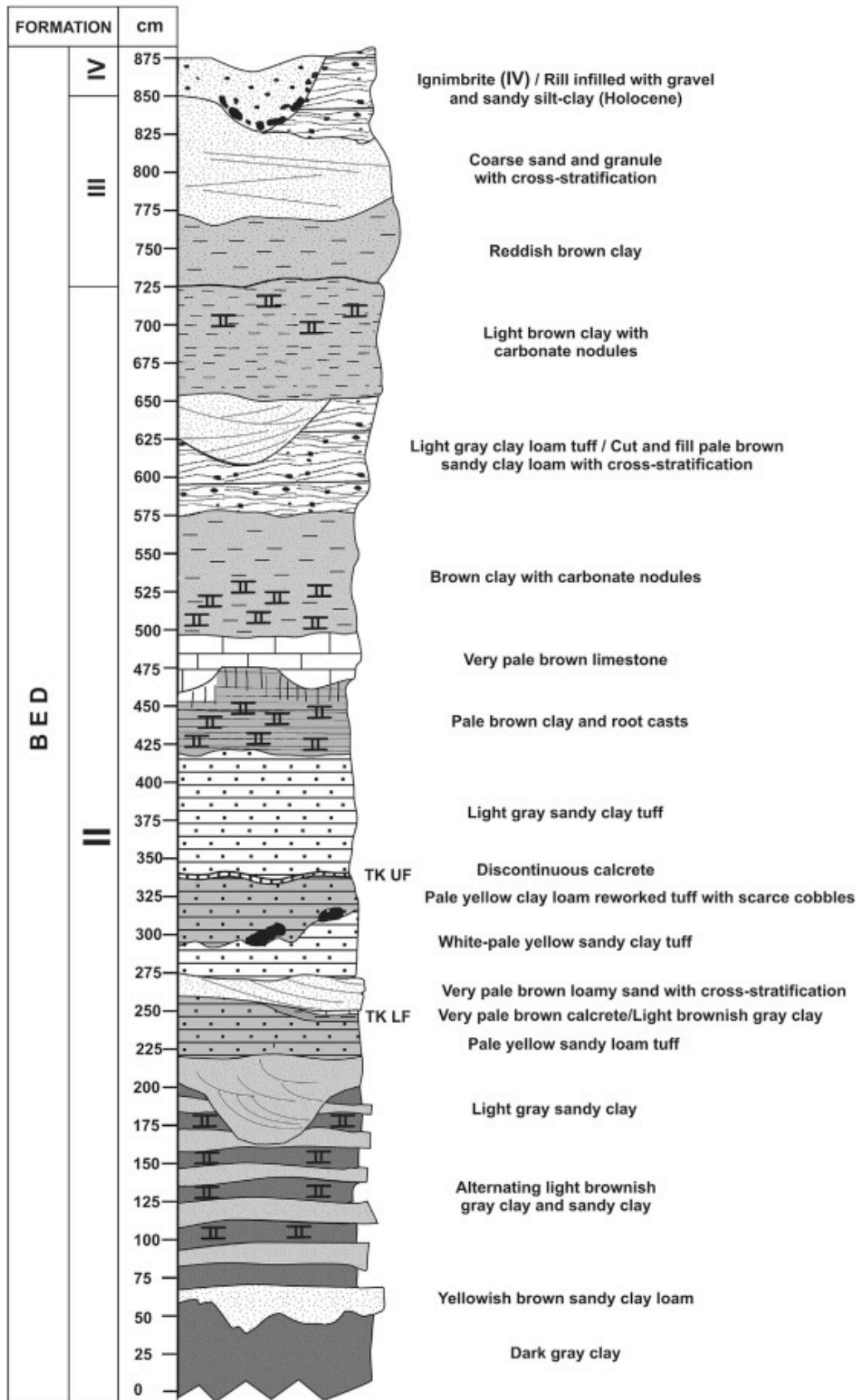


Fig. 3. Stratigraphic section of TK.

Bed III is composed of reddish brown (5 YR 5/4) clays and a coarse sand channel facies with granules (2–4 mm) and cross-stratification. At the top of the section a 60-cm-thick ignimbrite (Bed IV) was eroded on top by a rill saturated with gravel in a sandy clay loam matrix.

TKLF presents a stratigraphic discontinuity (Fig. 3) and a flat topography of light brownish gray (10 YR 6/2) clay in the westernmost area, covered by a calcrete level that increases in thickness towards the east. TKLF lies from west to east over both levels and is partially covered in the SA central section (Fig. 3) by a loamy sand channel facies in which a lamination structure typical of low-energy water flows can be observed. A pale yellow (2.5 Y 8/2) sandy clay tuff sits over both the loamy sand channel facies and the artifact level found in the eastern zone of SA.

The chronology for TK is tied largely to Tuff II^D, which outcrops about 0.8 km south-east of TK at the site of JK (Leakey, 1971:16–17, Fig. 1; Hay, 1976: plate 2). Recently, a ⁴⁰Ar/³⁹Ar date of 1.353 ± 0.035 Ma was acquired for Tuff II^D several kilometers from BK (Domínguez-Rodrigo et al., 2014d).

3. Study of the fauna

3.1. Previous faunal evidence

Leakey (1971) provided the first report on the fauna of TK, which consisted of 230 fragments from TKLF and 147 from TKUF. Their scarcity of bones, which contrasted starkly with the abundant lithic industry, persuaded Isaac and Crader (1981) to conclude that both levels were Type A sites. In taxonomic and ecological terms, open landscape animals dominated, with *Equidae* being the most numerous group (Leakey, 1971) followed by bovids, particularly Alcelaphinae (Gentry and Gentry, 1978). *Hippotragus gigas*, *Pelorovis oldowayensis*, *Rhinocerotidae*, *Suidae*, *Hippopotamidae* and *Giraffidae* were identified as well.

Hill (1983) observed a hole on a fragment of a hippopotamus jaw (TK OLD 63 I/L.F. 1972 2043), which he attributed to the behaviour of *Homo erectus*. Similar pits are created by people around Lake Turkana when they extract the nutritious pulp inside the large canine root. He also identified cuts that were in positions comparable to those seen on hippopotamus jaws consumed by the Dassanetch tribe. The absence of carnivore tooth marks or any other evidence for natural boring led Hill (1983) to propose that the jaw fragment may have been manipulated by *Homo erectus*. Although he did not specify if the bone was recovered from TKLF or TKUF, it likely derived from the former, as he noted its association with 2000 lithic artefacts, 15 hand axes, and an Oldowan living floor. This could fit the description for the Developed Oldowan proposed by Leakey (1971), which incorporated the 15 bifaces identified in Trench II ascribable to the Lower Floor, as suggested by Santonja et al. (2014).

A more recent faunal analysis (Egeland, 2007) studied 46 remains from TKLF and 78 from TKUF. *Bovidae* was the most numerous taxonomic group in the TKLF assemblage, comprising 47.8% of the remains, followed by *Equidae* (45.7%), *Hippopotamidae* (4.3%), and *Suidae* (2.2%). In the case of TKUF, *Bovidae* comprised 48.7% of the remains, followed by *Equidae* (37.2%), *Hippopotamidae* (10.3%), *Rhinocerotidae* (2.6%), and *Giraffidae* (1.3%). The

skeletal profiles for most taxa were characterized by the abundance of cranial elements. Only bovids and hippopotamus yielded appendicular elements at the site.

The surfaces of bones from the 1963 excavations were found to be poorly preserved, with only 8.8% and 5.5% of the bones from TKLF and TKUF, respectively, scored as “well preserved” (Egeland, 2007, Egeland, 2008; see also; Leakey, 1971, Monahan, 1996). This poor preservation may reflect an extended period of sub-aerial exposure and likely hindered the identification of surface modifications (only three tooth marks were observed). Although numerous bones preserved green fractures, it was unclear whether they resulted from the activities of hominins or carnivores. Given the incomplete representation of skeletons, it was suggested that some parts of the carcasses were transported off-site or otherwise scattered after their active accumulation (Egeland, 2007). Nevertheless, the origin of the bulk of the TK bone assemblage remained unknown, as no definite taphonomic evidence indicated that hominins played a substantial role in its formation (Egeland and Domínguez-Rodrigo, 2008).

4. Materials and methods

The materials discussed here were retrieved through the 2010–2012 excavations described by Santonja et al. (2014). A total of 1065 bone remains were recovered from TKLF.

Taxonomic identifications were based on reference material. However, in those cases when such determination was not possible, fragments were attributed to animal weight/size classes following Bunn (1982), where “small” refers to Bunn's (1982) sizes 1 (animals <50 kg, such as Thompson's gazelles) and 2 (50–125 kg, like impalas); “medium” to size 3a (125–250 kg, such as topis) and 3b (250–500 kg, like zebras); and “large” to sizes 4 (>500–1000 kg, such as elands or buffaloes), 5 (1000–4000 kg, rhinoceros) and 6 (>4000 kg, elephants).

Faunal remains were quantified by NISP, MNI, and MNE. NISP determination follows the protocol described in Yravedra and Domínguez-Rodrigo (2009). MNI estimates considered element side and ontogenetic age (Brain, 1969). For skeletal profiles were organized into four anatomical regions: cranial (i.e., horn, cranium, mandible, and teeth), axial (vertebrae, ribs, pelvis, and scapula, *sensu* Yravedra and Domínguez-Rodrigo, 2009); upper appendicular limbs (humerus, radius, ulna, femur, patella, and tibia), and lower appendicular limbs (metapodial, carpals, tarsals, phalanges and sesamoids). Long limb bones were further divided into upper (humerus and femur), intermediate (radius and tibia), and lower (metapodial) bones (Domínguez-Rodrigo, 1997). We are aware that pelvis and scapulae have traditionally been classified separately from axials, but given their overall similarity in bone texture and taphonomic properties to traditional axial bones, we decided to group them with vertebrae and ribs, as all respond exactly the same to post-depositional weathering and carnivore ravaging processes (see Yravedra and Domínguez-Rodrigo, 2009 for explanation).

It is now well-known that MNE estimates of long limb bone MNE at Olduvai and elsewhere often differ substantially depending on whether epiphyses or shafts were used for element identification (Pickering et al., 2003, Cleghorn and Marean, 2004, Marean et al., 2004, Domínguez-Rodrigo et al., 2007). The major issue with MNE estimates is to determine how best to determine overlap between specimens. have developed Although GIS-based approaches

(Marean et al., 2001) can be very useful with extremely large assemblages where physical overlap is difficult, for smaller assemblages such as that from TK we preferred to determine document overlap by hand. Thus, an integrative approach was applied using the bone section divisions proposed by Patou-Mathis, 1984, Patou-Mathis, 1985, Münzel, 1988, and Delpech and Villa (1993) and as described in detail by Yravedra and Domínguez-Rodrigo (2009). In this system, shafts were divided into equal-size sectors, regardless of the area of muscular insertion. 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. Long limb element identification considers Barba and Domínguez-Rodrigo's (2005) division by shaft thickness, section shape, and medullary surface properties. Following element and shaft sector identification, MNE is quantified by comparing all the specimens of the same element and size group by element size, side, ontogenetic age, and biometrics (Lyman, 1994).

Several procedures were followed to reconstruct site formation processes, assess site integrity, and evaluate the contribution of various biogenic agents to the faunal assemblage. The impact of water activity was estimated with fragment size distributions and the presence of abrasion, polishing, and carbonates.

The analysis of size distribution was carried out at three levels. First, size-sorting was examined for all fragments. Regarding bone fragmentation indices, bones were divided into several categories according to their length: <20 mm, 21–40 mm, 41–60 mm, 61–80 mm, 81–100 mm and >101 mm. At a second level, only long bone fragments were considered, as cancellous axial bones undergo different fragmentation patterns than do denser limb bones (Domínguez-Rodrigo and Martínez-Navarro, 2012). Based on the idea that anthropogenic bone concentrations yield greater fragmentation than those of carnivore, the amount of preserved shaft circumference is also considered. Bunn (1982) proposes three categories for shaft circumference where (1) stands for shaft circumference <50%; (2) covers the >50% range; and (3) the shaft circumference is 100 > 75%. At a third level, only those long bone fragments showing green breakage were considered. This distinction is important as diagenetic (dry) breakage is relatively common in the assemblage and thus the specimen size distribution at recovery may be quite different from the original deposit. Here, the term “breakage” is preferred to “fragmentation” (Brugal and Fosse, 2004), following the English-speaking tradition. Although the term “fragmentation” has been used to imply non-anthropogenic breakage, traditional studies on bone breaking processes refer to “bone breakage by carnivores” (Bunn, 1981: 575) and “bone breakage by humans and carnivores” (e.g., Capaldo and Blumenschine, 1994: 727). This terminology is preferred in the present work and both breakage and fragmentation will be used as synonymous. The segregation in the use of these terms, we believe, artificially emphasizes the distinctiveness of humans. Taphonomy usually embodies all organisms within the same natural scale and separates processes (i.e., breakage) from agency (dynamic or static loading by humans and other carnivores).

Signs of polishing or abrasion were recorded as a final estimation of fluvial activities at the site. Polishing or abrasion may be found in both transported and non-transported assemblages exposed to moving water and sediments, such as those found in sand strata (Thompson et al., 2011). Several bones show cracks and diagenetic breakage planes that caused further

fragmentation during excavation. Identification of breakage planes as green or dry (including diagenetic) followed Villa and Mahieu's (1991) classification: dry breakage planes tend to be longitudinal and/or transversal to the bone long axis, have a nearly 90° angle between the cortical and medullary surfaces, and show an uneven breakage plane surface with micro-step fractures and a rough texture. Green breakage planes show smoother surfaces and are more likely to be obliquely oriented to the bone long axis. Breakage pattern analysis followed methods outlined by Domínguez-Rodrigo et al. (2007). Weathering stages were also observed following Behrensmeier (1978) to estimate exposure time. A spatial analysis of bones with evidence of abrasion-polish, carbonate encrustation, trampling-microabrasion, and biochemical marks was carried out to evaluate if taphonomic phenomena are focused in specific areas.

Bone surface modifications such as cut, percussion, and tooth marks were systematically examined with 10X-20X hand lenses and strong light (Blumenschine, 1988, Blumenschine, 1995). The diagnostic criteria defined by Bunn, 1982, Potts and Shipman, 1981, and Domínguez-Rodrigo et al. (2009c) guided the identification of cut marks, whereas tooth marks were recorded following Binford (1981) and Blumenschine, 1988, Blumenschine, 1995. Finally, the identification of percussion marks was based on Blumenschine and Selvaggio (1988) and Blumenschine (1995). For comparative purposes, surface modification frequencies (based on NISP) were calculated separately for epiphyses and shafts (Blumenschine, 1988, Blumenschine, 1995) and quantified by element type and bone section (Domínguez-Rodrigo, 1997, Domínguez-Rodrigo and Barba, 2005) as well. The presence of tooth, percussion, and cut marks was considered for the whole assemblage, whereas estimated percentages included only well-preserved bone surfaces.

Taxonomic determinations were based mainly on teeth. However, in the case of *Sivatherium* and *Pelorovis*, species determination considered the biometrics of metapodials, and for *Gazella* sp. size 1 and 2, phalanx size was used due to the absence of teeth in the assemblage.

5. Results

5.1. Taxonomic profiles and skeletal patterns

A minimum of 47 individuals are represented by the skeletal remains from TKLF (Table 1). The estimation of MNI, is based on teeth. Several of these teeth appear highly fragmented, which implies long-term weathering and long exposure of carcasses prior to burial.

Unfortunately, carbonate concretions made species-level diagnosis difficult for most specimens. In most cases, only genus or tribe could be reliably identified. *Connochaetes* sp., *Megalotragus* sp., *Redunca* sp., *Kobus* sp., *Syncerus* sp., and *Metridiochoerus* sp. A partial dentition of a size 3a alcelaphine was tentatively identified as *Parmularius* sp.

Adult animals dominate the TKLF samples. The animals represent a diversity of habitats, with open-habitat species such as antilopines, alcelaphines, suids, and equids occurring with water-dependent fauna, crocodile and hippopotamus (Table 1). From a taxonomic point of view, equids and alcelaphines are the most abundant animals. Overall, and despite the fact that we did not

identify elephant or *Hippotragus* remains, this taxonomic list is more diverse than that reported by Leakey (1971).

Table 1. Minimum number of individuals (MNI) identified in TKLF where ad1: senile, ad2: adult, ad3: prime adult, J: juvenile, I: infant.

	TK lower				
	Ad1	Ad2	Ad3	J	I
<i>Equus oldowayensis</i>	3	2	1	2	
<i>Hipparion</i> sp.		1			
<i>Ceratotherium</i> sp.		1			
<i>Hippopotamus</i> sp.		1	1		
<i>Giraffidae</i> sp.		1			
<i>Sivatherium</i> sp.		1			
<i>Syncerus</i> sp.			1		
<i>Pelorovis</i> sp.		1			
<i>Alcelaphini</i> size 2		1	1		
<i>Parmularius</i> sp.		1	1		
<i>Alcelaphini</i> size 3a	1	3	2		
<i>Alcelaphini</i> size 3b		1	1		
<i>Connochatetes</i> sp.		1	1		
<i>Megalotragus</i> sp.		1			
<i>Antilopini</i> size 2		1			
<i>Antidorcas</i> sp.		1			
<i>Gacella</i> sp. Size 1		1			
<i>Gacella</i> sp. Size 2		1			
<i>Gacella</i> Thompson			1		
<i>Tragelaphini</i> size 4		1			
<i>Redunca</i> sp.		1			
<i>Kobus</i> sp.		1			
<i>Metridiochoerus</i> sp.		2			
<i>Suidae</i> size 3		1			
<i>Suidae</i> size 2		2		1	
<i>Bird</i>		1			
<i>Crocodile</i>		1			
Total	4	30	10	3	0

Of the total of 1065 specimens, only 526 (49.4%) could be attributed to carcass size (Table 2). Medium-sized carcasses (NISP = 262) are more common than either large (NISP = 156) or small carcasses (NISP = 108) (Table 2).

Table 2. Skeletal profiles in small (size 1–2), medium (size 3a, 3b) and large mammals (size 4–6) in NISP and MNE at TKLF.

Element	NISP lower			MNE lower		
	Small	Medium	Large	Small	Medium	Large
Horn	3			2		
Skull						
Mandible	1	1	1	1	1	1
Teeth	16	110	39	16	110	39

Element	NISP lower			MNE lower		
	Small	Medium	Large	Small	Medium	Large
Vertebrae	5	8	1	2	2	1
Ribs	7	11	2	2	5	1
Scapulae		1	2		1	2
Pelvis						
Humerus						
	Prox. ep.					
	Shaft		1			1
	Dist. ep.	1			1	
Femur						
	Prox. ep.					
	Shaft	1	4	1	2	
	Dist. ep.	1		1		
Hum.-fem. indet.						
	Epiph.		1			
	Shaft	4	14	8		
Radius-ulna						
	Prox. ep.					
	Shaft		2			1
	Dist. ep.	1	1	1	1	
Tibiae						
	Prox. ep.		1			1
	Shaft	5	11	6	2	7
	Dist. ep.		1		1	
Rad.-tib. Indet.						
	Epiph.					
	Shaft	1	2			
Metacarpal						
	Prox. ep.		2	2	2	2
	Shaft	2	2		2	1
	Dist. ep.		2	1	2	1
Metatarsal						
	Prox. ep.		1			1
	Shaft	3	3	2	4	3
	Dist. ep.	1	2	1	2	1
	Complete	1		1		
Metapodial						
	Epiph		3	1		
	Shaft	1		6		
Carpal						
		2	3	4	2	3
Tarsal						
			1	2	1	2
Phalanges						
		3	2	1	3	2
Sesamoid						
		1	1		1	
Indeterminate						
		49	76	71		
Total		108	262	156	43	147
		%NISP			%MNE	
Cranial		3.7	0.4	0.6	7.0	0.7
Tooth		14.8	42.0	25.0	37.2	74.8
Axial bones		11.1	7.6	3.2	9.3	5.4
Upper limbs		5.6	7.3	6.4	4.7	2.0
Medial limbs		6.5	5.7	5.8	7.0	6.1
Lower limbs		7.4	5.3	9.0	20.9	6.1
Compact bones		5.6	2.7	4.5	14.0	4.8
Indeterminate		45.4	29.0	45.5	0.0	0.0

The TKLF skeletal profiles are composed mainly of dense bone parts (Table 2). Cancellous bones such as axial elements (scapulae, pelvis, ribs and vertebrae), compact bones (carpals,

tarsals and phalanges), and long bone epiphyses are underrepresented in MNE counts. Although most taxonomic identifications were based on dental material, they are still underrepresented relative to MNI.

All animal sizes follow a similar pattern of skeletal part representation; namely, underrepresentation of axial bones. The MNE for this skeletal section is less than 10% of all elements. Ribs and vertebrae are only marginally represented and no pelvis has been identified in the assemblage. Compact bones are also scarce and appendicular specimens show a dominance of denser elements such as metapodials or tibial shafts, whereas humeri and femora are virtually nonexistent (Table 2).

Based on the MNE:MNI ratio, it is clear that most of the skeletons are incompletely represented. Many elements are only marginally present, which suggests a strong taphonomic bias in their preservation and/or deposition due to post-depositional carnivore ravaging, hydraulic disturbance, and/or prolonged exposure to subaerial weathering or a combination of all these processes.

5.2. Bone fragmentation and breakage

The TKLF faunal assemblage is highly fragmented, as 35% of specimens are smaller than 40 mm from large size carcasses (Fig. 4) and 60% from small and intermediate size carcasses (Fig. 5, Fig. 6). Bone fragments between 21 and 40 mm are the most abundant when considering all bone types (Fig. 4, Fig. 5, Fig. 6). The pattern is slightly different for long bone fragments and green broken limb fragments. In this case, a majority of the pieces are between 40 and 60 mm and there is a clear under-representation of specimens smaller than 20 mm (Fig. 4, Fig. 5, Fig. 6).

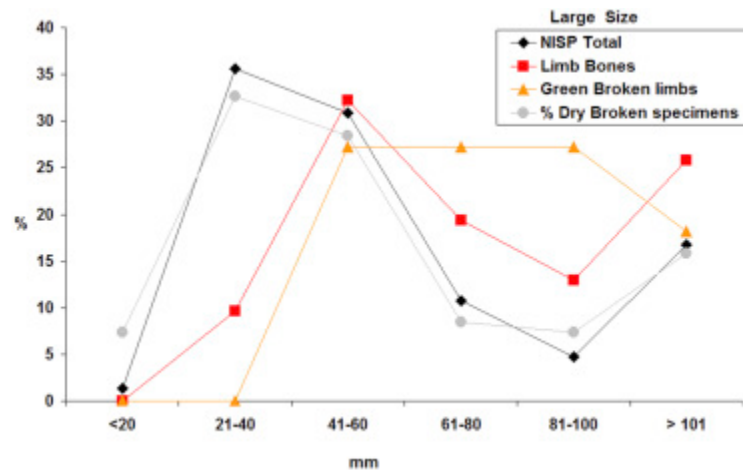


Fig. 4. Distribution of frequencies of bone specimens of Large size carcasses (size 4–6 after Bunn, 1982) from TKLF for the complete sample as well as for limb bones, green broken limbs and dry broken specimens. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

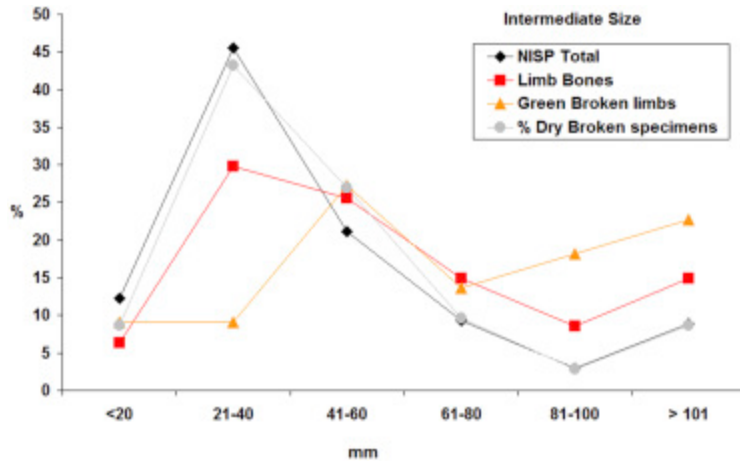


Fig. 5. Distribution of frequencies of bone specimens of Intermediate size carcasses (size 3a-3b after Bunn, 1982) from TKLF for the complete sample as well as for limb bones, green broken limbs and dry broken specimens. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

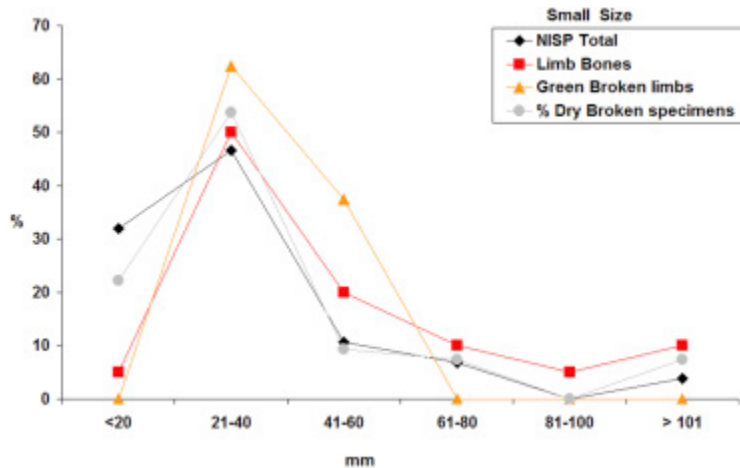


Fig. 6. Distribution of frequencies of bone specimens of Small size carcasses (size 1-2 after Bunn, 1982) from TKLF for the complete sample as well as for limb bones, green broken limbs and dry broken specimens. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

A significant degree of fragmentation is also reflected in the circumference index of long bones. There is a dominance of shafts with less than 50% of the original circumference. Only the more dense elements, such as metapodials, preserve larger circumferences. The analysis of 335 long bone shafts, including both identifiable and non-identifiable fragments, resulted in 87% of indeterminate shafts with circumferences smaller than 50% (Fig. 7). The high fragmentation of elements affect teeth as well, many of which are crushed into small fragments, making the estimation of species in 133 tooth specimens (57%) and of animal size in 165 teeth (70.8%) impossible.

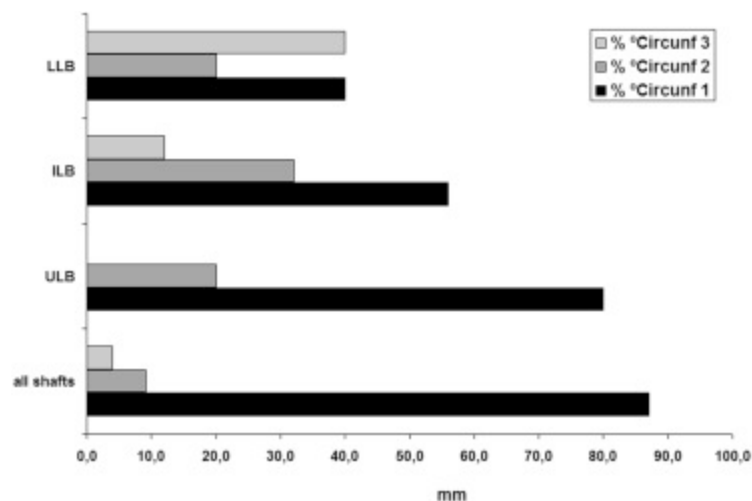


Fig. 7. Distribution (%NISP) of Bunn's (1982) long bone shaft circumference types in TKLF for ULB (Upper Limbs Bones, Humerus and Femur), ILB (Intermedial Limbs Bones, Tibia and Radius), LLB (Lower Limbs Bones, Metapodials) and all long bone shafts.

Table 3. Alterations on bones with poor cortical preservation at TKLF.

	NISP TKLF	%
NISP Total included determinable and non determinable	1065	100.0
Bones with poor cortical preservation	722	67.8
Bones with carbonate concretion	539	50.6
Bones with abrasion and polishing	407	38.2
	Bones with poor cortical preservation	
NISP	722	100.0
Bones with carbonate concretion	461	63.9
Bones with abrasion and polishing	288	39.9

Table 4. Bones with well-preserved surfaces and different alterations at TKLF.

	NISP	%
Bones good cortical preservation, excluding teeth	248	100
Microabrasion or trampling	58	23.4
Total bones with weathering	26	10.5
Total bones with weathering stage 1	11	4.4
Total bones with weathering stage 2	8	3.2
Total bones with weathering stage 3	7	2.8
Bones with biochemical alteration	35	14.1
Bones with teeth marks	4	1.6
Bones with percussion marks	1	0.4
Bones with cut marks	0	0.0
Bones with green fracture	99	39.9
Bones with dry fracture	149	60.1

The intense fragmentation documented here contrasts with the data provided by Leakey (1971), who did not mention bone specimens smaller than 40 mm. This suggests that the 1963 collection probably reflects selective retention of materials.

This intense fragmentation likely resulted from diagenetic processes, as the distribution of green-broken limb specimens is unlike the distribution found for the sum total of specimens, whereas the representation of dry-broken bones is identical (Fig. 4). Furthermore, nearly 87% of the 335 long bone shaft fragments experienced dry fragmentation. Conversely, only 67 (20%) of the fragmented shafts show green fractures. No notches were observed and the evidence of percussion marks or tooth marks is limited (Table 4). Thirty-one percent and 61%, respectively, of axial and long bone epiphysis fragments show dry fractures. This all suggests that biotic agents were not responsible for most of the bone breaking.

5.3. Bone surface modification

Leakey, 1971, Hill, 1983, Monahan, 1996, and Egeland, 2007, Egeland, 2008 all noted the poor preservation of the bones found at TK. Our sample shows a similar pattern, with poor preservation of cortical surfaces documented on 67.8% (NISP = 722) of the total number of specimens. This poor preservation may be conditioned by a series of phenomena. The most frequent process is post-depositional (and frequently diagenetic) alterations, such as concretions and carbonates, which affect 539 fragments (50.6% of the total sample) (Table 3). The severity of encrustation prevents the identification of many remains: 403 fragments (68.4% of the total sample with carbonates) are indeterminate specimens. Abrasion and polishing also affect bone surface preservation. In this case, 40% (NISP = 288) of the bones with poor cortical preservation show this kind of modification (Table 3).

Several specimens show modifications that indicate exposure to water, humidity, or other physical processes. Of those specimens with well-preserved surfaces, 149 (60.1% of well-preserved sample) exhibit diagenetic fractures. A total of 407 (38.2% of the total sample) specimens show abrasion or polishing (Table 3), and 262 of these (64.4% of the bones with abrasion or polishing) are smaller than 40 mm, which suggests that water could have been an important taphonomic agent. Biochemical modifications produced by fungi or plants were documented on 35 specimens (14.1% of the bones with good preservation surfaces), which suggests prolonged exposure to humidity. Furthermore, microabrasion and trampling was observed on 58 specimens (23.4% of the bones with well-preserved surfaces, excluding teeth) indicates that abiotic agents had modified cortical surfaces.

The distribution of weathering stages suggests that bones experienced some exposure, although the rarity of specimens in stages 2–3 of Behrensmeyer's (1978) classification indicates that subaerial weathering was not intense in the preserved sample (15 specimens, or 6% of bones with well-preserved surfaces; Table 4). On the other hand, the intense fragmentation of teeth and the skeletal bias of many remains relative to the MNI are typical of an extended period of pre-depositional exposure.

Similarly, the large percentage of bones with dry breakage and the incidence of polishing and abrasion, as well as biochemical modification, trampling, and microabrasion suggest some degree of exposure, and water activity is a likely source of disturbance. The small channel that contacts TKLF could have been responsible for the limited movement of small bones. Hydraulic flows have been shown to result in an under representation of several elements such as axial and compact bones (i.e. ribs, vertebrae, scapulae, phalanges, pelvis, carpals, or tarsals). These all fall

within Voorhies's (1969) easily transported Group 1 elements. Water action is thus a plausible explanation for the severe bias in the skeletal profiles. While carnivore ravaging could also explain such a pattern, only four specimens show tooth marks, representing only 1.6% of the bones with well-preserved surfaces (Table 4). These tooth marks are located on an indeterminate intermediate shaft of a medium-size animal (size 3 sensu Bunn, 1982), on the metatarsal of a small animal (size 1–2), and on two indeterminate specimens (one axial and shaft fragment).

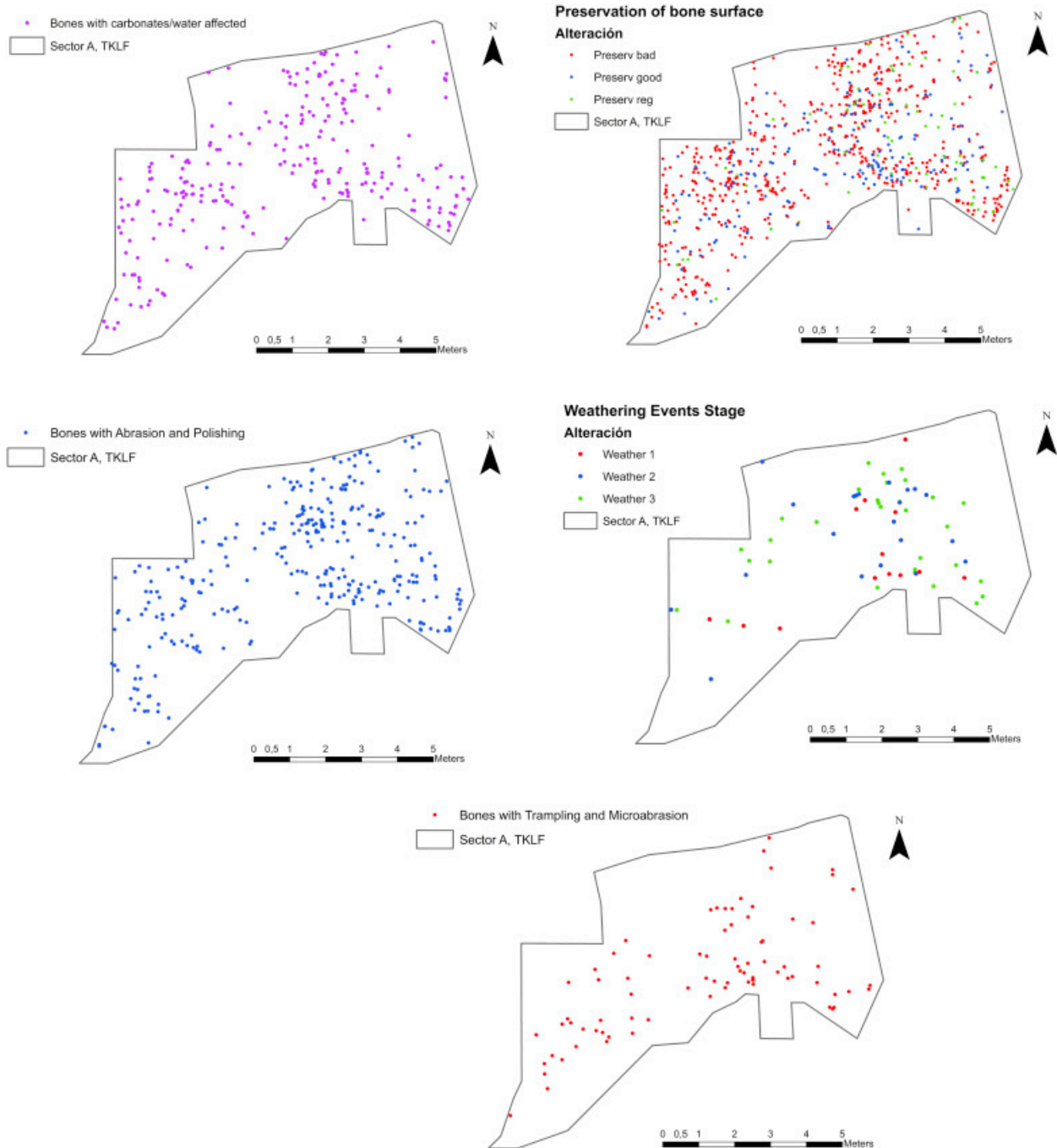


Fig. 8. Spatial distribution of the different alteration processes such as carbonate and water, preservation of bone surface, bones with abrasion and polishing, weathering stages (according to Behrensmeyer, 1978) and trampling-microabrasion.

Despite evidence for hydraulic flows, many of the bones present in TKLF certainly have an autochthonous origin. The presence of some bones with well-preserved surfaces, the absence of rounded bones larger than 40 mm, and the presence of green fractures on 39.9% of the sample suggests they were originally deposited and broken on-site (Table 4). Water alterations observed on the longer bones could have been produced by normal water flow, which can slowly abrade autochthonous bones without displacing them, and can also produce polished surfaces (as discussed in Thompson et al., 2011).

The spatial distribution of the different bone modifications shows no patterning, as all types of bone, regardless of modification, are in close association (Fig. 8). Hominin intervention on the assemblage is difficult to determine. No cut marks were identified and only one percussion mark was observed, on a tibial shaft from a medium-sized animal. Green fractures across long bones are recorded on 37 shafts. Fracture angles were measured on 31 shaft fracture planes with oblique and longitudinal breakage. The variation reflected in fracture angles overlaps with both anthropogenic and carnivore breakage.

6. Discussion: interpretation of the fauna in TKLF

Among Olduvai Gorge's Bed II sites, TKLF preserves the highest concentration of lithic artifacts (Leakey, 1971, Santonja et al., 2014). The contrast between the large amount of lithics and the few faunal remains led some scholars to consider TKLF to be a Type A site; that is, a site with lithic artefacts exclusively as the result of hominin activities (Isaac and Crader, 1981, de la Torre, 2004). This kind of site is frequent in the African Lower Paleolithic, exemplified by the Acheulean sites at Olorgesailie or Peninj (Isaac, 1977, Domínguez Rodrigo et al., 2009b). However, we have shown unequivocally that TKLF also preserves a large bone assemblage represented by several individuals from various species.

Leakey, 1971, Monahan, 1996 and Egeland, 2007, Egeland, 2008 were unable to assign authorship to the bone accumulation at TK due largely to poorly preserved bone surfaces. Despite the larger sample size considered here, we have also found that poor preservation is a notable characteristic of the faunal assemblage. Calcareous concretions and postsedimentary carbonation are largely responsible for the poor preservation, and it is likely that water flows and protracted sub-aerial exposure resulted in the deletion or removal of axial elements and compact bones.

Many of the fragments smaller than 40 mm are rounded, 67% of the remains excluding teeth have water-produced alterations, and 64% show dry fractures. It is possible that many of the smaller pieces were introduced by weak water currents from a channel, as suggested by Petraglia and Potts (1994) without the benefit of detailed stratigraphic studies. Larger elements, it seems, were deposited and buried at the site. After deposition, several lines of evidence suggest that the bones were exposed for long time periods, as indicated by the presence of microabrasion, trampling, weathering, biochemical alterations, and dry fractures.

The impact of carnivores appears to have been rather marginal. While some specimens were certainly broken by carnivores, only four fragments yielded tooth marks. No individual bone

preserved more than five tooth marks, all of which were pits and scores smaller than 3 mm and thus unsuitable for the identification of the specific type of carnivore. Such limited evidence for carnivore involvement argues against this agent being the cause of the anatomical bias in axial and compact bones or epiphyses.

There is virtually no direct evidence for hominin manipulation of carcasses, as only a single percussion mark was identified. The bone specimens at TKLF thus show that both hominins and carnivores intervened in the modification of the fauna at the site, albeit in very limited roles. Hence, TKLF, as with so many other Lower Pleistocene sites, represents a palimpsest (Gaudzinski-Windheuser, 2005, Domínguez-Rodrigo et al., 2007, Domínguez-Rodrigo et al., 2014c). The lithic and bone assemblages at TK may thus have resulted as the circumstantial succession of several independent events, some of which involved the manufacture of lithic implements in areas where faunal remains were naturally accumulated and deposited.

Table 5. MNE/MNI ratio in TKLF compared to the actualistic samples for the Serengeti and Ngorongoro, in Tanzania (Blumenschine, 1989), and the Galana and Kulalu reserves, in Kenia (Domínguez-Rodrigo, 1996). MNE values in TKLF only include the anatomical elements described in the actualistic samples, excluding teeth and sesamoidals, as well as the MNI for birds and reptiles.

Site	Characteristics	MNE	MNI	Ratio MNE/MNI
Galana and Kulalu	Bushy Plains	233	16	14.6
Galana and Kulalu	Lali Hills	119	3	39.7
Galana and Kulalu	Open Grassland	246	16	15.4
Galana and Kulalu	Riparian Woodland	388	26	14.9
Galana and Kulalu	Total	1461	95	15.4
Gnorongoro	Grass Plains	250	57	4.4
Serengeti	Grass Plains	377	62	6.1
Serengeti	Acacia Woodland	201	23	8.7
Serengeti	Riparian woodland	408	23	17.7
Serengeti	Total	986	108	9.1
TKLF	Total	74	47	1.6
Galana and Kulalu	Small	215	18	11.9
Galana and Kulalu	Medium	343	26	13.2
Galana and Kulalu	Lartge	428	15	28.5
Galana and Kulalu	Total	598	35	17.1
Serenget & Gnorongoro	Small	92	19	4.8
Serenget & Gnorongoro	Medium	747	122	6.1
Serenget & Gnorongoro	Lartge	297	24	12.4
Serenget & Gnorongoro	Total	2088	214	9.8
TKLF	Small	22	11	2.0
TKLF	Medium	31	26	1.2
TKLF	Large	21	8	2.6
TKLF	Total	74	45	1.6

There are, however, a number of peculiar aspects to the TK faunal assemblage. The most conspicuous is its high taxonomic diversity (>20 species). Comparisons of the TKLF assemblage with landscape taphonomic studies by Blumenschine (1989) and Domínguez-Rodrigo (1996), who present data on natural accumulations in various habitats in the modern Serengeti and

Ngorongoro ecosystems and Galana and Kulalu in Kenya, indicate that TK shows] extremely low MNE/MNI values (1.6 elements/individual). This is significantly lower than the ratio for the Serengeti, Ngorongoro, Galana and Kulalu (Table 5). Only the Grass Plains in Ngorongoro and the Serengeti display a lower MNE/MNI ratio, largely a consequence of the higher bone destruction produced by the carnivores living in those areas.

Regarding the skeletal profiles in Table 6, the situation at TK also differs from natural accumulations in Tanzania and Kenya. Excluding teeth from the skeletal profiles, the cranial section is much less well represented relative to modern habitats. If, however, teeth are included, then the cranial section predominates. As shown in Table 2, this section for medium and large sized animals exceeds 60% of total MNE.

Table 6. Skeletal Profiles observed in natural assemblages from Serengeti, Ngorongoro (Blumenschine, 1989), Galana and Kulalu (Domínguez-Rodrigo, 1996), where GP: Grass Plains, AW: Accacia Woodland, RW: Riparian Woodland, BP: Bushy Plains, LH: Lali Hills, OG: Open Grassland. Cr: Cranial (cranium, mandible), Ax: Axial (Vertebrae, rib, scapula, pelvis), Up. Ap.: Upper appendicular limbs (humerus, femur, radius, tibia), Lw. Ap.: Lower appendicular limbs (metapodial, tarsal, carpal). Teeth have been excluded in TK.

	Anatomical elements profiles							TKLF
	Gnorongoro		Serengeti		Galna and Kulalu			
	GP	AW & GP	RW	RW	BP	LH	OG	
Cranial	40	44	11	10	7	3	5	2
Mandible	32	27	9	8	8	3	10	3
Vertebrae	64	84	43	145	92	43	67	5
Rib	5	14	13	62	63	47	81	8
Pelvis	4	32	9	12	6	3	3	0
Scapule	12	25	9	21	7	5	3	3
Humerus	11	12	2	21	8	5	12	2
Rad-Ulna	7	11	1	13	10	3	11	3
Carpal	0	0	1	4	0	0	1	9
Femur	6	13	2	24	10	2	12	3
Tibia	7	17	6	17	8	2	10	12
Tarsar	2	4	2	12	4	2	0	3
Metapodial	7	21	4	13	8	1	13	15
Phalange	0	1	0	26	2	0	18	6
Total	197	305	112	388	233	119	246	74
% Element Distribution according section								
Cr	36.5	23.3	17.9	4.6	6.4	5.0	6.1	6.8
Ax	43.1	50.8	66.1	61.9	72.1	82.4	62.6	21.6
Up Ap	15.7	17.4	9.8	19.3	15.5	10.1	18.3	27.0
Lw Ap	4.6	8.5	6.3	14.2	6.0	2.5	13.0	44.6

In the case of the other anatomical parts, axial bones in TKLF are less frequent than in modern savannas. Carcasses with ribs and vertebrae were recorded in the Galana, Kulalu, Ngorongoro, and Serengeti faunas. In the case of TKLF, however, several circumstances such as hydrological flows or the intervention of carnivores may have prevented their preservation. In contrast, lower appendicular elements, which are more resistant to these processes, yield a higher representation.

A number of circumstances such as the high overall MNI, the low MNE/MNI ratio, and the biased skeletal profiles in TKLF indicate that the faunal accumulation at TK is rather poorly preserved, and in all likelihood an important part of the original assemblage has been destroyed or otherwise removed from the site. Other phenomena such as the abundance of bones with dry fracture (40%) among the well-preserved bone sample, as well as the poor state of bone surfaces (which limited observations in 68% of the total sample), suggest that the site is a palimpsest where hominins may have played an incidental role reflected by a single percussion mark.

7. Conclusions

TK remains one of the most well-known sites in Bed II. Previous studies, based on the premise that faunal remains were scarce, classified it as a Type A site (*sensu* Isaac and Crader (1981) and de la Torre (2004)). Our results show that TKLF contains both lithic artifacts and the remains of several species of animals. According to Leakey (1971), *Equidae* is the best-represented animal at the site, and *Alcelaphinae* dominates the bovid assemblage (Gentry and Gentry, 1978). Our results confirm this, as *Equidae* is the most common taxon in our sample, and *Alcelaphinae* is the most common bovid. Age patterns show that adults dominate the demographic profiles (Table 1). Regarding skeletal representation, teeth are the most important anatomical element.

In both paleoecological and paleoenvironmental terms, our analysis confirms Gentry and Gentry's (1978) conclusions. The TKLF fauna is characteristic of open areas. The dominance of *Equidae* and *Alcelaphini*, as well as *Suidae* and *Antilopini*, are typical of the open savannas and arid environments of Bed II. The presence of other animals such as tragelaphines, bovines, reduncines, hippopotamus, and crocodile can be explained by the fluvial contexts near the site. Hippopotamus, bovines, and crocodile indicate water-dependent habitats that would have favored small woodland habitats for tragelaphines and reduncines.

Previous works on the fauna failed to find cut marks on the TK fauna, and the poor preservation of bone surfaces did not allow the identification of the agent involved in the bone accumulation with any certainty (Egeland, 2007). Only one altered hippopotamus jaw has been interpreted by Hill (1983) as an example of human intervention. Our analysis identified green fractures and a single percussion mark on the long bone sub-assemblage. This, in addition to a few tooth marks, indicate the presence of both hominin and carnivore activity, although the agent most responsible remains unclear. We therefore suggest that TKLF should be viewed as a palimpsest similar to other Lower Pleistocene sites such as SHK at Olduvai or Ubeidiya in the Levant (Gaudzinski-Windheuser, 2005, Domínguez-Rodrigo et al., 2014c).

In addition to the documented anthropogenic and carnivore action, a number of additional depositional and post-depositional processes altered the original skeletal representation. The large number of bones smaller than 40 mm demonstrates that Leakey's (1971) excavations only retained a selection of bones. This analysis has also shown that many of these bones show rounding, which indicates that they may have come from elsewhere, perhaps via water flow. This process may have caused an osteological bias against axial and compact bones, as they float rather easily according to Voorhies (1969). Some bones were also directly deposited at TK, as evidenced by green fractures and the absence of rounding. Polishing and abrasion are also a

consequence of water flow and the bones with these modifications may have been altered without significant spatial displacement (Thompson et al., 2011). The considerable carbonation and concretion on many bones is a consequence of post-depositional processes.

The bulk of the faunal remains accumulated at the site seem to correspond to background scatters, typical of assemblages formed in riverine settings, with and without intervention by carnivores. This cumulative palimpsest probably represents a vast time span. Most of the taxonomic diversity is represented at the site by teeth, suggesting the disappearance of the postcranial remains probably due to the combined action of weathering and carnivore ravaging. Teeth are also highly fragmented, probably due to prolonged exposure and to diagenetic processes. This work on the newly excavated material further elaborates on Egeland, 2007, Egeland, 2008 study of the Leakey's collection. This taphonomic study also shows that a large taxonomic diversity can be represented (albeit marginally, by teeth) due to natural processes in assemblages where the main anthropogenic input is tool manufacture.

Sites in Bed II show the complexity and variability of *Homo erectus* behavior. This involves a high and intense manipulation of a significant number of animals in BK, including very large specimens such as elephants, hippopotamus, *Sivatherium* and *Pelorovis*. Also, a more limited exploitation of large and medium-sized animals in SHK (Domínguez-Rodrigo et al., 2014c) and TK, where lithic activities are more important. This may imply a high competition with carnivores, as suggested by their activities in these three sites and in other locations such as HWK East and MNK, where they were the main agent for bone accumulations. However, taphonomic evidence from BK shows that by this time hominins may have outcompeted other carnivores and that functional differences in *H. erectus* behavior are the most likely explanation for the diversity of sites and palimpsests represented during this consolidation of the Acheulian.

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