



## Study of the SHK Main Site faunal assemblage, Olduvai Gorge, Tanzania: Implications for Bed II taphonomy, paleoecology, and hominin utilization of megafauna



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### ABSTRACT

Recent excavations at the SHK Main Site, Olduvai Gorge, Tanzania, have unearthed a dense concentration of stone tools and faunal remains. Here, we describe how the site contributes to the understanding of hominin subsistence strategies and paleoecology during Bed II times (1.78–1.34 Ma). This palimpsestic site is located within, and on the over-bank of, a river channel. Taphonomic analyses suggest that a heterogeneous set of taphonomic agents played a role in the accumulation and modification of the faunal assemblage. Although hominins played a rather marginal part in this assemblage's faunal accumulation and modification, the recovered faunal assemblage includes evidence that is consistent with hominin exploitation of hippopotamus and equid. This evidence underscores the possibility that by 1.5 Ma hominins were diversifying their diet and enlarging their ecological niche by exploiting, probably opportunistically, megafaunal remains more commonly than previously documented. Taphonomic spatial analysis shows differences in bone preservation and modification according to whether faunal specimens were located inside the river channel or on its over-bank. We also show that spatial taphonomic analysis can contribute to the understanding of palimpsest-site formation, as well as to the reconstruction of diverse taphonomic agents responsible for that formation. A comparative analysis of taxonomic diversity between SHK *versus* other upper Bed II sites supports the notion that the environment was fairly open prior to the beginning of the Bed III deposits. The large number of lithic artifacts concentrated at the SHK Main Site, when considered in conjunction with the small amount of evidence for carcass-processing, suggests that hominins engaged in a diversity of activities beyond butchery.

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### 1. Introduction

There is only a small number of anthropogenic sites dated to the African Lower Pleistocene in which a functional association between stone tools and faunal remains can be clearly established (e.g., Pickering et al., 2004a, 2004b; Pobiner et al., 2008; Domínguez-Rodrigo, 2009). Included in this sample are a few of the

Bed I and Bed II sites at Olduvai Gorge, Tanzania (Domínguez-Rodrigo et al., 2007; Egeland and Domínguez-Rodrigo, 2008). Of the Bed II sites, only the archaeofaunal assemblage of BK (Bell Korongo) appears to have been predominately created by hominin exploitation of carcasses (Egeland and Domínguez-Rodrigo, 2008). Here, we present further evidence for hominin involvement in carcass exploitation during Bed II times with findings recovered from SHK (Sam Howard Korongo). We also describe findings from SHK relevant to the paleoecological reconstruction of the environment around the Olduvai paleo-lake basin in which middle to upper Bed II hominins lived.

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SHK was discovered in 1935 (Leakey, 1971), and the site was excavated in 1953, 1955 and 1957. It lies on the right bank of the side gorge approximately 1 km from BK (Bell Korongo). The site is comprised of two areas: (1) the Main Site and (2) the Annexe. The Main Site consists of a fluvial channel and its over-bank, while the Annexe is part of an alluvial plain situated nearby the channel. The stratigraphic sequence (from bottom to top) as defined by Leakey (1971: 165–166) is as follows: a thick (>9.0 m) chestnut brown clay; a conglomerate inside the fluvial channel (1.8 m wide by 0.75 m deep) almost entirely composed of artifacts and bone fragments at the Main Site, and a hominin occupation level at the Annexe; and a 2.4 m clayey tuff overlying both the conglomerate in the channel as well as the clay present in the over-bank. The hominin occupation level on the surface of the clay at the Annexe site was interpreted as penecontemporaneous with the conglomerate of the Main Site because the brown clay upon which the archaeological level occurs at the Annexe is the same as the one the fluvial channel eroded at the Main Site (Leakey, 1971).

Leakey (1971) described 915 stone artifacts from SHK, but the site's faunal specimens were not quantified or described beyond the brief mention of a complete *Hippopotamus gorgops* skull, and the remains of small antelopes (*Antidorcas recki*). The number of reported stone artifacts was an underestimation of what was actually present, given that a large proportion of the “débitage” and other artifacts were not collected and immediately discarded at the site (Leakey, 1971: 166–167). Furthermore, during the 1950s excavations Leakey (1971: 166) reports that due to financial limitations only a minimum number of staff could be maintained and sieving was not always carried out. As such, the curated faunal collection of SHK from these earlier excavations lacks small elements and comprises mainly of horn cores, dentition, and fairly complete or moderately fragmented long bones with a set of compact elements. Egeland and Domínguez-Rodrigo (2008) reported 282 specimens in total from this collection, representing 140 elements, during an analysis of the assemblage curated at the National Museums of Kenya. That 2008 specimen count does not include the aforementioned *Antidorcas* remains, which are stored at London's Natural History Museum. However, that omission is probably insignificant to the overall interpretation of hominin behavior at SHK because those remains were found in a different stratigraphic provenience from that of the hominin occupation at the site as documented by Leakey (1971) and our own excavations (described below). As already noted above, Leakey (1971) described the hominin occupation floor at SHK as occurring in the brown clay at the Annexe, and in the fluvial channel at the Main Site. The *Antidorcas* remains were found in the overlying clayey tuff (Gentry, 1966; Gentry and Gentry, 1978), and a study currently in progress suggests that these remains accumulated via a non-anthropogenic catastrophic event.

Here, we present the results of a taphonomic analysis carried out on the first faunal assemblage from SHK recovered systematically using modern excavation techniques. A site-oriented taphonomic study such as this one is essential for addressing other broader questions about hominin behavior and paleoecology during that crucial period of human evolution encompassed by Bed II at Olduvai Gorge. This new assemblage was retrieved from the Main Site, which we interpret to be a palimpsest, and includes both the fluvial channel containing the conglomerate as well as the adjacent over-bank (See Diez-Martín et al., 2014). Our results show that the formation history of the site is more complex than previously suggested (Egeland and Domínguez-Rodrigo, 2008), and involved hominin manipulation of bones. This manipulation included hominin processing of hippopotamus, an early possible instance of megafaunal exploitation, which is otherwise usually documented only after 1.5 Ma at sites such as BK, Olduvai Gorge, Tanzania (Domínguez-Rodrigo et al., 2009, 2014) and Koobi Fora (Kenya) (Bunn, 1994).

## 2. Method and sample

### 2.1. Faunal analysis

We chose methods designed to assess site integrity, site formation processes, and the relative contribution of different biogenic agents to the formation of the faunal assemblages. First, we looked at site integrity and formation processes. Size-sorted faunal assemblages created by water jumbles, such as those documented in rivers or streams, tend to be biased towards larger fragments; therefore we measured the maximum length of fragments and used the distribution of specimen sizes to detect any possible preservation bias. We also looked for signs of polishing or abrasion, which would be expected in transported assemblages, but also in non-transported assemblages exposed to circulating water and mobile sediments, such as those encased in sand strata (Thompson et al., 2011). Determining whether or not the assemblage is in primary versus secondary position was particularly important given the fluvial depositional context of the site.

Appendicular and axial elements, including all limb shaft fragments were identified to element whenever possible. In our consideration of skeletal part representation, carcasses were divided into anatomical regions: skull (horn, cranium, mandible and teeth), axial (vertebrae, ribs, pelvis, and scapula), and appendicular (limb bones). (We are aware that pelvis and scapulae have traditionally been classified separately. However, given their overall similarity in bone texture and taphonomic properties, we chose here to categorize pelvis and scapulae together with vertebrae and ribs, since these elements are mostly cancellous and fragile. In other instances, this approach has been useful for the classification of specimens from the most fragmented assemblages [see Domínguez-Rodrigo et al., 2007].) Long limb bones were further divided into upper (humerus and femur), intermediate (radius and tibia), and lower (metapodials) limb bones (Domínguez-Rodrigo, 1997). Skeletal part profiles were based on NISP (Number of Identified Specimens) and estimates of the MNE (Minimum Number of Elements). We also considered profiles by carcass size. “Small” refers to Bunn's (1982) sizes 1 and 2, “medium-sized” refers to size 3, and “large” refers to sizes 4 through 6.

Estimates of MNE at Olduvai sites often differ substantially depending on whether epiphyses or shafts are used for element identification (Pickering et al., 2003; Cleghorn and Marean, 2004; Marean et al., 2004; Domínguez-Rodrigo et al., 2007). As such, some researchers have used a GIS-based method to calculate MNEs (Marean et al., 2001). However, we feel more confident in element estimation if overlap among specimens is documented by hand. Thus, we employed an integrative approach using the bone section division proposed by Patou-Mathis (1984, 1985), Münzel (1988), and Delpeche and Villa (1993), as described in detail in Yravedra and Domínguez-Rodrigo (2009). Following Delpeche and Villa (1993) and Münzel (1988), shafts were divided by equally-sized sectors, irrespective of areas 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) described the criteria used in the division of each shaft sector, taking into account the orientation of each specimen. We also used the criteria of Barba and Domínguez-Rodrigo (2005) for long limb element identification, which is based on shaft thickness, section shape, and medullary surface properties. After identifying specimens to element and shaft sector according to these methods, MNE was quantified by laying out together all specimens from the same element and size group. This procedure allowed all the criteria used in our comprehensive analysis (Lyman, 1994), such as element size, side, age, and biometrics, to be observed by comparing specimens side by side.

Given the importance of determining the relative influence (and possible interaction) of hominins and carnivores on the faunal assemblage, the study bone surface modifications was an essential part of our analysis. We evaluated cortical surfaces and identified bone surface modifications, such as cut marks, tooth marks, percussion marks, and “natural” marks (biochemical and abrasion marks). Marks were identified using 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 et al. (2009) for cut marks. In order to robustly compare the archaeological data to referential frameworks created via modern experiments, where there is no diagenetic bone breakage or differential bone surface preservation, frequencies of marks are shown as both “raw estimates” and “corrected estimates”. Corrected estimates were obtained following the method of Pickering et al. (2008), which jointly considers the artificial inflation of specimens through dry breakage along with the artificial reduction of mark frequencies when specimens with poor cortical preservation are compared to those possessing good cortex. This method is cogent, since it (1) excludes specimens with poor preservation, which bias the preserved frequencies of marks; and it (2) compensates for the duplication of specimens resulting from the dry breaking of single specimens, which artificially inflates the bone sample.

Tooth marks and percussion marks were analyzed using epiphyseal and mid-shaft long limb bone portions, following Blumenschine (1988; see also Capaldo, 1995, 1998). However, we did not use the near-epiphyseal portion because of ambiguity in the way this portion is defined and how marks are tallied (Domínguez-Rodrigo and Barba, 2006). For example, consider a 10 cm shaft specimen that preserves 1 cm of spongy/trabecular tissue on its medullary surface. This specimen could be classified as a near-epiphyseal portion even if marks clearly occur on the mid-shaft part, which comprises 90% of the specimen. Given that the identification of epiphyseal specimens (following Blumenschine's nomenclature) is straightforward, we tallied marks on epiphyseal fragments because they could be reliably interpreted via the experimentally-derived referential frameworks currently available. However, given that the proportions of near-epiphyseal fragments identified in Blumenschine's (1988) analogical sample and our fossil sample would certainly differ, we decided to exclude this category from our analysis because it could not be unambiguously compared to the current published experimental database and, therefore, be adequately interpreted.

Following Bunn and Kroll (1986) and Domínguez-Rodrigo (1997), cut marks were tallied by element type and bone section. In an experimental sample of felid-consumed carcasses Domínguez-Rodrigo et al. (2007) and Barba and Domínguez-Rodrigo (2008) showed that a useful approach for differentiating primary *versus* secondary access to carcasses by hominins involves focusing on bone sections where flesh scraps would not have survived. In the present study, cut marks were not identified according to these general bone sections because the small number of marks allowed their location to be described detail.

During excavation, we had to overcome sediment compaction and its effects on bones. Several bone specimens showed cracks and diagenetic breakage planes that caused fragmentation as specimens were excavated. Several specimens fractured during excavation were glued before removal and/or in laboratory treatment. The identification of green and dry (including diagenetic) breakages was carried out following Villa and Mahieu's (1991) criteria. Dry breaks result in numerous breakage planes that are longitudinal and transverse to the axis of the bone; the angle measured between the cortical and medullary surfaces is close to 90°; and the breakage

plane surface is uneven, with micro-step fractures and a rough uneven texture. In contrast, green breaks result more frequently in smoother surfaces and more numerous oblique breakage planes.

Breakage patterns were analyzed using two complementary techniques outlined by Domínguez-Rodrigo et al. (2007). First we examined notches, which we define as semi-circular outlines along the otherwise rectilinear edge of a fracture surface, associated with a negative flake scar on the medullary surface. These were measured to differentiate between bone breakage processes. Capaldo and Blumenschine (1994) showed experimentally that the dynamic force of hammerstone percussion produces notches that are broader and shallower in cortical view than are the notches created by the static loading of carnivore teeth. They measured notch shape using two ratios: (1) notch breadth: notch depth (in cortical view), and (2) flake scar breadth: notch depth.

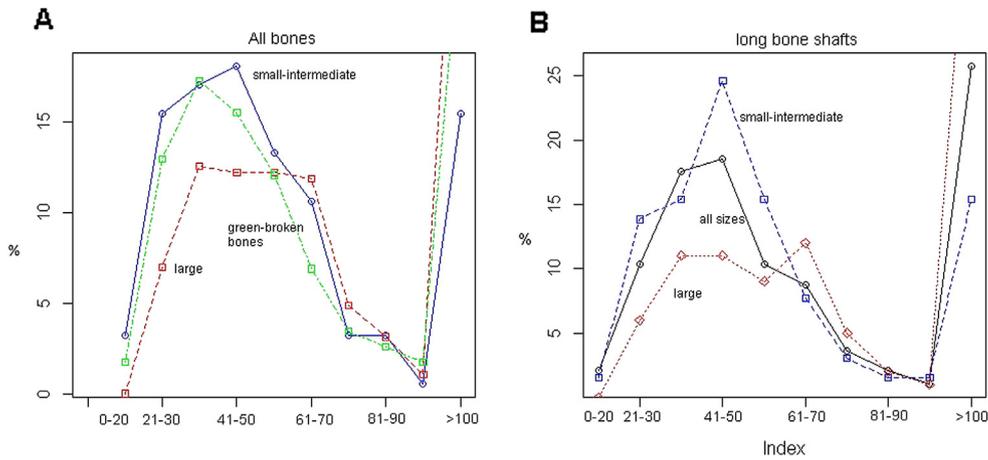
The platform angles of bone flakes removed as a result of percussion also tend to be more acute than those of flakes removed during carnivore bone breakage (Pickering et al., 2005). Using a goniometer, the platform angle was measured at the loading point on the negative scar of the detached flake. We note, however, that notch measurement still lacks an extensive interpretive referential framework. The sample sizes used by Capaldo and Blumenschine (1994), especially for middle-sized carcasses, are small, and yield ambiguous, overlapping ranges of variation when static and dynamic bone breakage processes are compared. Given this situation, the analysis of notch measurement was used only tentatively in our overall interpretations.

The second approach for analyzing breakage patterns involved the frequency of notch morphology categories. Capaldo and Blumenschine (1994) differentiated seven categories of “notch”, including “double-overlapping” and “double-opposing” notches, which are thought to be more abundant in carnivore bone breakage (Domínguez-Rodrigo et al., 2007). In our pilot experimental work, we observed that particular notch categories varied in frequency depending on whether static or dynamic loading was applied to a bone. “Double-overlapping” and “double-opposing” notches on bones from small- and middle-sized carcasses occurred in higher frequencies in assemblages of broken bovid fragments created through static loading (Domínguez-Rodrigo et al., 2007).

## 2.2. Spatial and geostatistical analysis

Spatial point pattern analysis was performed by applying Complete Spatial Randomness tests (Bivand et al., 2009). These tests analyze if points are independently and randomly distributed over any given area, or if they occur in clusters or any other pattern. The function used for this purpose was the G (Gest) function, which measures the distribution of distances from arbitrary points to the nearest point (nearest event). The compatibility of complete spatial randomness with the point pattern is evaluated by plotting the empirical function G against the theoretical expectation. The latter is simulated by multiple pair-wise estimations, which create envelopes or confidence intervals of expected complete spatial randomness, which can be used to assess if the observed (empirical) function is contained inside (Bivand et al., 2009). These envelopes are computed by randomly simulating a number of point patterns so that the summary function is computed for all of them jointly (using Monte Carlo computation methods).

To complement the “nearest event” approach, a “second-order property” approach was also used. This measures interaction types among points and detects clustering. This uses the K (Kest) function, which measures the number of cases found at a given distance of any particular point. By comparing the estimated K value to the theoretical value, the type of interaction among points can be



**Fig. 1.** A. Distribution of specimen size categories for small-intermediate (Bunn's [1982] sizes 1–3) (circle, blue) and large (Bunn's [1982] sizes 4–6) (square, red) carcasses, including dry and green breakage, and for specimens with green breakage only (circle, green). B. distribution of specimen size ranges on long bone shafts, including all carcass sizes (circle, black), small-intermediate carcasses (square, blue), and large carcasses (diamond, red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

determined. Envelopes using Monte Carlo methods are also generated (Bivand et al., 2009).

Spatial distributions of specimens, which were designated according to specific taphonomic variables (bone preservation, chemical modification of cortical surfaces, polishing and abrasion, trampling and tooth marking), was carried out using the “sp” R library. Statistical tests comparing the spatial expression of taphonomic variables according to location (within-channel or channel over-bank) were carried out by using  $\chi^2$  tests for categorical variables and regression linear models for numerical variables (e.g., specimen size distribution).

For the latter type of variable, a variogram was used. Variograms model spatial correlations between distance and any specific variable and offer a good indication of anisotropy. In the present study, a variogram was used to assess whether specimen size distribution was spatially determined. Anisotropy was measured using a range ellipse using four main directions (0, 45, 90 and 135°). The analysis was carried out using the “geoR” and “gstat” R libraries (Bivand et al., 2009).

For specimen size distribution, class boundaries were assigned Fisher–Jenks natural break method (Bivand et al., 2009) by using the “classInt” R library.

### 2.3. Paleocological analysis

Here, we make provisional paleocological interpretations from the fossil assemblages. It is well-known that fossil assemblages are partial and selective collections of biocoenoses conditioned by a wide array of taphonomic processes (Domínguez-Rodrigo and Musiba, 2010). Therefore, we acknowledge that paleocological interpretations are always incomplete in the sense that they are based on only portions of paleo-biocoenoses. However, partial representation of biocoenoses does not prevent small samples from being efficiently used to characterize past environments (e.g., Lacruz and Maude, 2005).

To better understand Bed II paleoecology here, SHK bovid diversity was compared to the bovid tribe representation found in a large array of modern ecosystems in order to provide ecological proxies for the site (see list in Shipman and Harris, 1988). Although the SHK bovid sample size is small, this analysis was conducted to suggest preliminary conclusions regarding the paleocological context of the site. However, since a small sample size limits the

paleocological conclusions drawn for the temporal period represented by middle to upper Bed II, larger bovid samples from sites overlying SHK, namely BK4b and TK, were also included in our analysis (see Supplementary Information). A hierarchical agglomerative cluster analysis of several African national parks representing wooded biomes and open savanna landscapes was conducted, the results of which served as an analogical framework against which the SHK data were compared. The cluster analysis combined clustering and principal component analysis (PCA) methods. A proximity matrix was obtained using the square Euclidean distance and a dendrogram was constructed using the Ward method. PCA eliminates the least contributing dimensions, retaining the components that are responsible for a high percentage of inertia. Then a hierarchy analysis is conducted to interpret the results from the PCA. Both statistical methods were carried out using the R “FactoMineR” library.

To strengthen the conclusions of this combined PCA/cluster analysis, a ternary graph was programmed in R, using all the data from each bovid group and bootstrapped 10,000 times with replacement. In Shipman & Harris' (1988) list of parks with their respective census, some parks had extremely large faunal counts (e.g., Serengeti  $\geq$  700,000 individuals) whereas other parks possessed extremely small counts (e.g., Bicular = 2500 individuals). This wide variation could influence the perceived proportion of certain bovid tribes, because some are more likely to be better (or differently) represented in larger than in smaller samples. In order to avoid this possible bias from inter-park sample size variation, we performed a statistical analysis aimed at homogenizing sample sizes and correcting for small samples sizes. Namely, we bootstrapped all the data 10,000 times in each national park and plotted them in two separate groups: one corresponding to wooded ecosystems and the other one corresponding to open savanna biomes.

## 3. Results

### 3.1. Anatomical profiles and specimen size representation

A total of 20 individuals have been identified out of a sample of 875 bone specimens (Table 1). The near-lack of complete dental specimens made species attribution difficult for some individuals; often only genus or tribe could be reliably identified. Only some

partial dentition from alcelaphini size 3a could tentatively be attributed to *Parmularius*. The diversity of animals represented includes open-habitat bovidae, equidae, and water-dependent species, like crocodile and hippopotamus.

**Table 1**  
Minimum number of individuals (MNI) identified at the SHK Main Site.

	Subadult	Adult
<i>Elephas</i> sp.	1	
<i>Hippopotamus</i> sp.	2	1
<i>Sivatherium maurusium</i>		1
<i>Pelorovis</i> sp.		1
<i>Megalotragus</i> sp.		2
<i>Connochaetes</i> sp.		1
Alcelaphini size 3a		1
<i>Redunca</i> sp.		1
<i>Equus</i> sp.	1	1
<i>Hipparion</i> sp.		1
<i>Kolpochoerus</i> sp.	1	1
<i>Crocodylus</i> sp.	1	1
Chelonia		1
<i>Canis</i> sp.		1

Skeletal representation per carcass size shows that for small animals there was only a scarce representation of cranial and postcranial material (Table 2). Only the densest parts of the appendicular skeleton survived (distal humerus, proximal radius, long bone shafts, and metapodial condyles), with a near-total absence of cancellous parts. Ribs, compact bones, and vertebrae were only marginally present, suggesting a strong taphonomic bias in their preservation.

**Table 2**  
Number of identifiable specimens to carcass size and skeletal part at SHK. Besides the data displayed in this table, there are 253 unidentifiable specimens which could not confidently be assigned to any carcass group.

	Size 1-2	Size 3	Size 4-6
Skull	3	3	23
Mandible		5	2
Teeth	6	58	28
Vertebrae	1	7	26
Ribs	5	21	73
Scapula		3	4
Pelvis	3	4	14
Humerus	Proximal end	1	1
	Shaft	6	8
	Distal end	1	3
Radius-ulna	Proximal end	1	4
	Shaft	3	2
	Distal end	1	
Metacarpal	Complete		1
	Proximal end	3	
	Shaft	4	1
Femur	Distal end	3	3
	Proximal end	1	3
	Shaft	7	4
Tibia	Distal end		1
	Complete	1	
	Proximal end		
Metatarsal	Proximal end	3	5
	Shaft	8	5
	Distal end	2	
Carpal/tarsal	1	7	13
Phalanges	1	1	7
Other		1	1
Indeterminate	17	49	134
Total	45	217	363

Similarly to small-sized carcasses, only limited number of bones preserved for medium-sized carcasses, especially when one considers the relatively larger number of individuals represented (Table 2). The axial skeleton and compact bones were marginally represented, which suggests either carnivore attrition or hydraulic disturbance. Long bones were represented by their densest parts (e.g., distal humerus, proximal radius, shafts). It should be noted that there was a scarcity of shaft fragments relative to the number of long bones present.

A similar pattern was documented for larger carcasses. Although vertebrae and ribs were better represented, the larger carcasses overall were a very fragmented collection from which most of the axial and appendicular skeletons were missing. The high fragmentation of elements also affected teeth, which occurred mostly as small fragments. This intense fragmentation of dentition suggests a prolonged exposure to weathering, which may also have been a major cause for the underrepresentation of cancellous bones.

When considering long bone elements, the relationship of MNE to MNI indicates that a large part of the original sample is underrepresented (Table 3). In this instance, skeletal part profiles suggest that carnivore post-depositional ravaging, hydraulic disturbance, and long exposure to subaerial weathering might have shaped the characteristics of the assemblage.

**Table 3**  
Number of minimum number of elements (MNE) from long bones according to carcass size identified at SHK.

Carcass size	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal
Very large (5-6)		1	1	2		1
Large (4)	2			1	2	2
Medium	3	3	4	4	6	3
Small	2	3	3	1	2	3

The frequency distribution of specimens according to their size (Fig. 1) shows that specimens under 20 mm are underrepresented, while the remaining size categories are distributed as would be expected in slightly disturbed assemblages (Domínguez-Rodrigo et al., 2007). The small (<50 mm) fraction is well-represented, both when considering all elements (Fig. 1A) or just long bone shafts (Fig. 1B). It could be reasonably argued that this situation would have been due to intense dry fragmentation of the assemblage; however, the distribution of green-broken specimens is virtually identical to the plotted distribution of all specimens irrespective of breakage type (Fig. 1A). Furthermore, the presence of bones from large animals would initially increase the portion of specimens larger than 50 mm. In contrast, the distribution of specimens from large fauna is similar to the plotted distribution of smaller carcasses as well as green-broken specimens irrespective of carcass size (Fig. 1A). Only when splitting the sample according to carcass size and using only long bone shafts (Fig. 1B) do some differences emerge between small-intermediate and large carcasses (with a greater frequency of larger specimens represented in the latter); but these differences are minor, and the overall pattern is the same. This suggests that water disturbance played a minor role in the configuration of the faunal assemblage at SHK, although it could have been a cause for the underrepresentation of the smallest (<20 mm) fraction of the sample, while simultaneously removing small cancellous elements (such as carpals, tarsals, rib and vertebral fragments) from the site.

### 3.2. Bone breakage

An analysis of 219 long bone shaft fragments showed that 62 (28.3%) specimens bear green fractures only, 12 (5.4%) specimens

bear both green and dry fractures, 87 (39.7%) specimens showed dry breaks only, and 58 (26.4%) specimens showed ambiguous breakage planes. Specimens bearing green breakage planes make up 33.7% of the identifiable breakage planes when the entire long bone shaft sample is considered, or 46.0% if the ambiguous specimens are discarded. This suggests a biotic agent of bone breaking. Only four specimens bearing notches were documented; three single notches and one “double-opposing” and “double overlapping” notch set. Unfortunately, this notch sample size was quantitatively insufficient to address the agent of bone breakage.

### 3.3. Bone surface modifications

Bone preservation varied according to each specimen's location within the excavated area (see below). Good preservation of cortical surfaces is documented in 377 (43.0%) of the total bone sample. A total of 168 (19.2% of total sample; 44.5% of the sample with good preservation) of the specimens exhibited abrasion or polishing, suggesting that water was an important taphonomic agent. Indeed, 215 specimens (24.5% of the total sample) showed a carbonate matrix, exfoliation, and chemical weathering typical of bones exposed to water or humidity for prolonged periods of time. One hundred and fifty specimens (17.0% of total sample; 39.7% of the well-preserved sample) showed traces of trampling and/or microabrasion, which indicates that biotic agents modified cortical surfaces. Bioturbation of cortical surfaces in the form of biochemical modification by fungi or plants was documented only on 17 specimens (1.9% of total sample; 4.5% of the well-preserved sample). Weathering (excluding chemical weathering) could be confidently be documented on 116 long bone shaft specimens, out of which 98 showed weathering stage 0 (84.4%); 10 specimens showed weathering stage 1 (8.6%); 3

specimens showed weathering stage 2 (2.5%); 3 specimens showed weathering stage 3 (2.5%); and 2 specimens showed weathering stage 4 (1.7%).

The SHK bone collection includes 208 long bone shaft specimens. Only 91 (43.7%) showed good cortical preservation. The majority of these well-preserved shaft fragments exhibited no traces of subaerial weathering. The distribution, following Behrensmeier's (1978) weathering stages, is: stage 0 = 66 specimens (72.5%); stage 1 = 22 specimens (24%); stage 2 = 2 specimen (2.2%); stage 3 = 1 (1.1%). This suggests that the bulk of the assemblage was not exposed to subaerial weathering for a long period of time.

When considering all carcass sizes in the assemblage, a total of 33 tooth marks were documented (Fig. 2, Table 4). Only 24 of these tooth marks occurred on long bones. Although Table 4 shows that the frequencies of tooth-marked epiphyseal and diaphyseal specimens remain low for all carcass sizes, the addition of six tooth-marked specimens, which could not be reliably attributed to carcass size, in addition to a correction for bone preservation, showed that this percentage is slightly higher. Eighteen tooth-marked shafts make up 19.7% of the well-preserved shaft specimen sample ( $n = 91$ ). Furthermore, when further correction was applied to compensate for the intensity of bone diagenetic breakage, this percentage increased again. When considering the well-preserved shaft specimen sample, a high frequency of dry breaks ( $n = 40$ ; 44.0%) was documented. When correcting for dry breakage, following Pickering et al.'s (2008) method, it can be conservatively argued that there was originally 71 green-broken fragments. When tallying tooth-marked specimens against this corrected estimation of green-broken specimens, we can calculate a final percentage of 33.8% tooth-marked shaft specimens. This result points to moderate activity by carnivores on the assemblage.



Fig. 2. A, furrowing on both caudal epicondyles and part of the trochlea of a distal equid humerus. B, Furrowing and tooth pits on a proximal humeral epiphysis. C, Gnawing on the proximal end of an equid tibia. D, Furrowing on the iliac crest of a hippopotamus innominate.

Tooth mark frequencies for shafts are higher than those reported for felids (Domínguez-Rodrigo et al., 2007), but substantially lower than those reported for experiments conducted with hyenids as primary bone modifiers (Blumenschine, 1988, 1995).

**Table 4**

Number of tooth-marked specimens per skeletal part and carcass size at SHK. Numerator is for number of tooth-marked specimens. Denominator is for total number of specimens of each part. Parentheses are for percentages.

		Size 1–2	Size 3	Size 4–6
Skull		0/3 (0)	0/3 (0)	0/23 (0)
Mandible			0/5 (0)	0/2 (0)
Vertebrae		0/1 (0)	1/7 (14.2)	2/26 (7.6)
Ribs		0/5 (0)	0/21 (0)	3/73 (4.1)
Scapula			0/3 (0)	0/4 (0)
Pelvis		1/3 (33.3)	0/4 (0)	3/14 (21.4)
Humerus	Proximal end		1/1 (100)	0/1 (0)
	Shaft		2/6 (33.2)	0/8 (0)
	Distal end	0/1 (0)	1/2 (50)	1/3 (33.3)
Radius-ulna	Proximal end	0/1 (0)	1/4 (25)	
	Shaft		1/3 (33.3)	0/2 (0)
	Distal end		0/1 (0)	
Metacarpal	Complete			1/1 (100)
	Proximal end		0/3 (0)	
	Shaft		1/4 (25)	0/1 (0)
Femur	Distal end		1/3 (33.3)	0/3 (0)
	Complete		0/1 (0)	
	Proximal end		0/1 (0)	0/3 (0)
Tibia	Shaft		2/7 (28.5)	0/4 (0)
	Distal end		0/1 (0)	0/1 (0)
	Complete	1/1 (100)		
Metatarsal	Proximal end		0/2 (0)	0/1 (0)
	Shaft		0/8 (0)	1/5 (20)
	Distal end	0/2 (0)	0/2 (0)	
Carpal/tarsal		0/7 (0)	0/13 (0)	
Phalanges	0/1 (0)	0/1 (0)	0/7 (0)	
Other		0/1 (0)	0/1 (0)	
Indeterminate	1/17 (5.8)	5/49 (10.2)	2/134 (1.4)	
Total	3/39 (7.6)	17/159 (10.6)	13/335 (3.8)	
Epiphyseal fragments	1/6 (16.6)	3/22 (13.6)	2/15 (13.3)	
Shaft fragments	0/12 (0)	9/57 (15.7)	3/65 (4.6)	

When tallying tooth marks per bone portion (epiphysis, diaphysis) and carcass size, using only the well-preserved shaft sample, the frequencies are similar to those described above (Table 5). This result further supports the notion that carnivores moderately modified the bone assemblage. This result also fits within the lower range of tooth-marked specimen frequencies documented in spotted hyena dens (especially, given the higher representation of specimens whose size ranges from 20 to 50 mm, as opposed to those whose size is between 50 and 100 mm, see Domínguez-Rodrigo and Martínez-Navarro, 2012).

**Table 5**

Number of tooth-marked specimens from long bones per portion type and carcass size.

	Small	Medium	Large
Epiphyseal fragments <sup>a</sup>	1/6 (16.6)	3/22 (13.6)	2/15 (13.3)
Shaft fragments <sup>a</sup>	0/5 (0)	9/40 (22.5)	3/38 (7.8)
Epiphyseal fragments <sup>b</sup>	1/6 (16.6)	3/22 (13.6)	2/15 (13.3)
Shaft fragments <sup>b</sup>	0/4 (0)	9/33 (27.2)	3/28 (10.7)

<sup>a</sup> Well-preserved fragments identifiable to carcass size.

<sup>b</sup> Sample from above corrected for dry breakage: 2 NISP with dry breaks for small carcasses; 14 NISP with dry breaks for medium-sized carcasses and 21 NISP with dry breaks for large carcasses.

Only seven specimens bearing percussion marks were identified (7.6% of the well-preserved sample; 9.8% of the well-preserved shaft sample with correction for dry breakage). This result fits well within the range documented in experimental models in which bones are broken by hammerstones (Blumenschine, 1988). These percussion-marked specimens spanned across the entire range of carcass sizes: one tibia of a small animal; one humerus, one radius, and one metatarsal of medium-sized carcasses; two indeterminate medium-sized shafts; and one indeterminate size 5 (probably hippopotamus) shaft. Furthermore, three impact flakes were also documented (Fig. 3). However, similar flakes have been documented on bones broken by hyenas in modern and fossil assemblages (Domínguez-Rodrigo and Martínez-Navarro, 2012). Three cut-marked specimens have been documented (3.2% of the well-preserved sample). The first specimen was an equid pelvis; the remaining two were hippopotamus ribs (Fig. 4). One of the ribs shows clear green fractures in the form of “snap”. The cut marks on the pelvis occur on the ischium, at the area of insertion for the external obturator muscle, which inserts into the trochanteric fossa of the femur (Fig. 5). Thus, we can infer that these marks were probably created while detaching the limb from the pelvis. Given the hundreds of kilograms of lithic raw material present at the site, these three cut marked specimens suggest that butchery comprised only a minor component of overall hominin behavior displayed there — however, it is noteworthy that the butchery that was conducted appears to have involved the exploitation of a medium-sized and a large-sized carcass.

Overall, the bone modification surface data is consistent with the hypothesis that both hominins and carnivores contributed to SHK bone assemblage breakage. However, no taphonomic evidence of direct carnivore-hominin or hominin-carnivore interaction has been so far documented in the assemblage, since no single specimen exhibits both carnivore tooth marks and hominin-applied cut and/or percussion marks.

### 3.4. Spatial analysis of taphonomic variables

The use of *G* and *K* functions in the study of complete spatial randomness processes in the SHK sample showed that the distribution is generally isotropic and uneven, with some degree of local clustering, as indicated by the estimated functions occurring above the envelopes. The width of the envelopes shows limited variability of the null hypothesis of complete spatial randomness and the scale of interaction (Fig. 6).

When assessing specimen distribution and taphonomic properties according to location (inside the channel or on the over-bank), an interesting pattern was revealed (Fig. 7). Channel and over-bank assemblages differ statistically with regard to the distribution of bone preservation ( $\chi^2 = 84.93$ ,  $p = 0.000$ ). For instance, although well-preserved specimens are documented in both contexts, there is a higher clustering of well-preserved specimens on the over-bank than there is in the channel. As we then might predict, the distribution of bones with poor cortical preservation shows greater clustering inside the channel relative to that on the over-bank. The occurrence of bones with chemical modification and carbonate, induced by humidity or the presence of water, also cluster overwhelmingly more inside the channel, than on the over-bank ( $\chi^2 = 86.82$ ,  $p = 0.000$ ). The differences in degree of bone polishing and abrasion between both contexts are also significant ( $\chi^2 = 116.56$ ,  $p = 0.000$ ), and there is a significantly higher presence of tooth-marked bones on the over-bank than in the channel ( $\chi^2 = 5.89$ ,  $p = 0.015$ ). Trampled specimens significantly occur more often on the bank relative to the channel ( $\chi^2 = 29.37$ ,  $p = 0.000$ ). However, green and dry breakage does not differ significantly between the two contexts ( $\chi^2 = 0.00$ ,  $p = 0.953$ ).



Fig. 3. Impact flakes from long bone shafts of large (left and center) and small animals (right). Scale = 1 cm.

These results suggest that biotic agents were more active in modifying cortical surfaces (tooth-marking and trampling) on the over-bank than in the channel. They also support that chemical processes degraded bone more intensively in the channel. The higher degree of bone abrasion and polishing in the channel could also support the hypothesis that part of the channel archaeofaunal assemblage was allochthonous in origin. To test this hypothesis, we conducted a study of specimen size frequency and spatial distribution. Transported and lag deposits show dimensional patterns which should be detected if the SHK channel sub-assemblage was transported by water. A Fisher–Jenks selection of size class intervals and their spatial plotting (Fig. 8A and B) showed that all size classes are similarly represented in the channel as on the over-bank. A variogram targeting an ellipsoid range of orientations from the external axis of the channel also shows that there is a no relationship between specimen size and spatial distribution. This result is inconsistent with the idea that the channel assemblage

was significantly modified by water, and instead suggests that its chemical and physical modification was due to circulation of water in a sandy matrix which slowly abraded *autochthonous* bone, as experimentally modeled under controlled conditions (Thompson et al., 2011).

### 3.5. Paleocological analysis

A PCA showed a two-dimension solution, which accounted for 58.61% of the sample variance (Fig. 9). A hierarchical classification analysis produced four clusters. Cluster 1 is composed of a small group of diverse parks in which wooded vegetation is prominent and large bodies of water or humidity exist, which in turn determines the high presence of bovini. Cluster 2 is composed of parks with a dominant woodland or bushland component, and a dry open landscape. Cluster 3 is composed of parks that are mostly bushland (e.g., Omo) or grassland with small portions of forest.



Fig. 4. Hippopotamus rib showing green snapped fractures (upper right and left) produced by intentionally breaking it and cut mark on the edge (lower right), which shows V-section and microstriations inside the groove (lower left, magnification = 40; scale = 0.2 mm). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 5. Cut marked equid innominate from SHK.

Cluster 4 is composed of grassland-dominated or dry bushland parks, which possess the highest degree of vegetation openness and dryness. The most influential bovid groups in classifying parks in the PCA (correlation scores in parentheses) were alcelaphini (0.81), antilopini (0.77) and bovini (−0.56) in the first dimension of the components (explaining 32.99% of inertia), and reduncini (−0.91), aepycerotini (−0.64) and antilopini (0.38) in the second dimension (explaining 25.62% of the inertia). In other words, the first component shows the degree of openness of the landscape (positive values more open; negative values more wooded) and the second component indicates the degree of water influence (reduncini) or presence of bush (aepycerotini/antilopini interplay). If we compare with this model three Olduvai archaeological sites situated in mid-upper and upper Bed II (SHK, BK4b and TK), it is clear that the three sites show a higher degree of landscape openness than most of the parks used for comparison, except those belonging to Cluster 4 (Kalahari, Nairobi, Turkana, Serengeti, Ngorongoro, Etosha). SHK clusters near Tarangire and other parks showing a dry wooded landscape. BK 4b clusters near Omo, showing the combined effect of an open overall landscape in conjunction with the wooded component of a river. TK clusters near Serengeti and Ngorongoro, showing a very open landscape with the minor presence of wooded elements or bush. When the three sites

are plotted against bootstrapped estimates of bovid tribe distribution in the parks, SHK and BK 4b appear to be situated in the open and wooded ecosystem samples respectively, very close to the boundary that separates both ecosystem types (Fig. 10). TK is clearly situated within the range of variation characteristic of an open landscape.

These interpretations are further supported when other mammal taxa are considered. Giraffids are an important component of the BK 4b assemblage (see Domínguez-Rodrigo et al., 2014), which, together with the presence of tragelaphini, suggests the presence of at least some woodland or bush near the site. One of the tragelaphini types is the eland, which is the most grazing tragelaphini. Therefore, given the dominance of alcelaphini and equids in the BK 4b faunal assemblage, it could be reasonably argued that most of the landscape surrounding BK must have been fairly open, but some dense wooded/bush vegetation probably also existed at or near the site (Domínguez-Rodrigo et al., 2014). In SHK, despite its smaller sample size, alcelaphini also dominate the bovid assemblage, but the presence of bovini and hippopotamus indicates a water-dependent habitat. Therefore, the landscape was probably transitional between open and more wooded or bushy. Overall, the three sites suggest that dry open ecosystems were present and that local wooded vegetation may have influenced hominin foraging patterns.

Our paleoecological interpretation is supported by the previous work of Gentry and Gentry (1978), who documented greater kudu and another smaller tragelaphini at SHK, as well as *Pelorovis* and *Syncerus*, *Kobus*, *Hippotragus*, a diversity of alcelaphini (*Parmularius*, *Damaliscus*, *Connochaetes*, and *Megalotragus*) and *Antidorcas*. The bovini and reduncini indicate the presence of water. The diversity and amount of alcelaphini and antilopini indicate a rather open environment, although bushy and closed vegetation must have also existed, as suggested by the presence of tragelaphini.

#### 4. Discussion

##### 4.1. Hominin behavior at SHK

Olduvai Bed II preserves evidence of hominid activity in more varied ecological settings than Bed I, since Bed II sites are not restricted to Hay's (1976) "lake-margin" zone but appear also along fluvial contexts away from the lake habitats. Bed II contains the presence of both Oldowan- and Acheulian-type stone tool industries. Furthermore, in terms of fauna, archaeological sites in

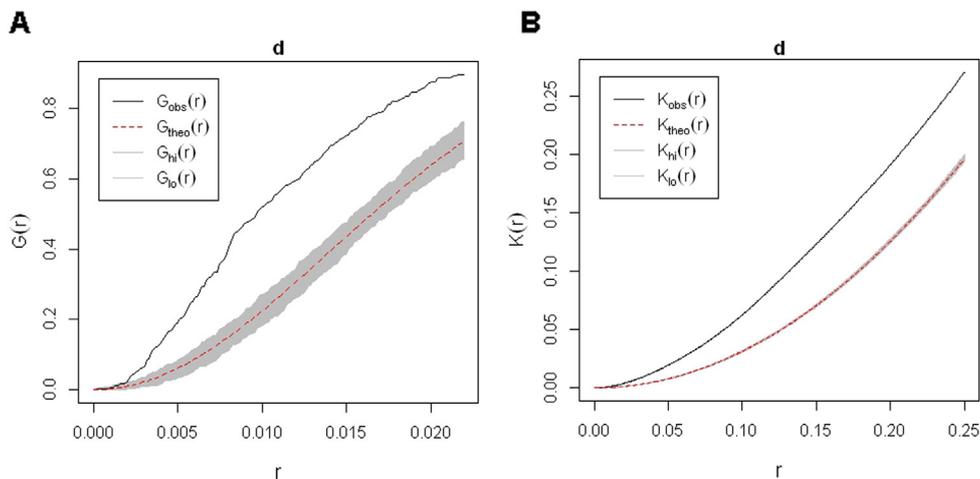
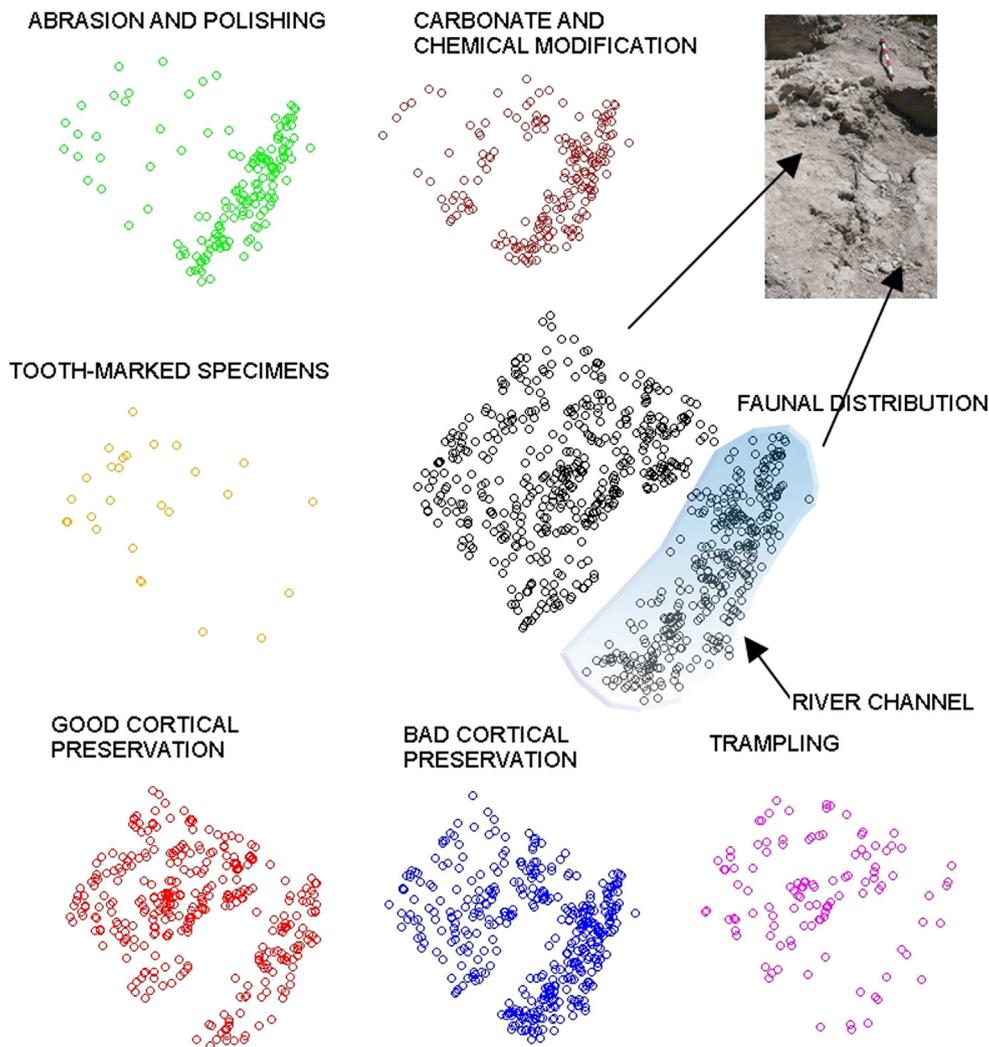


Fig. 6. Envelopes (grey) and observed values of the G function (A) and the K (B) function for the point pattern at SHK.

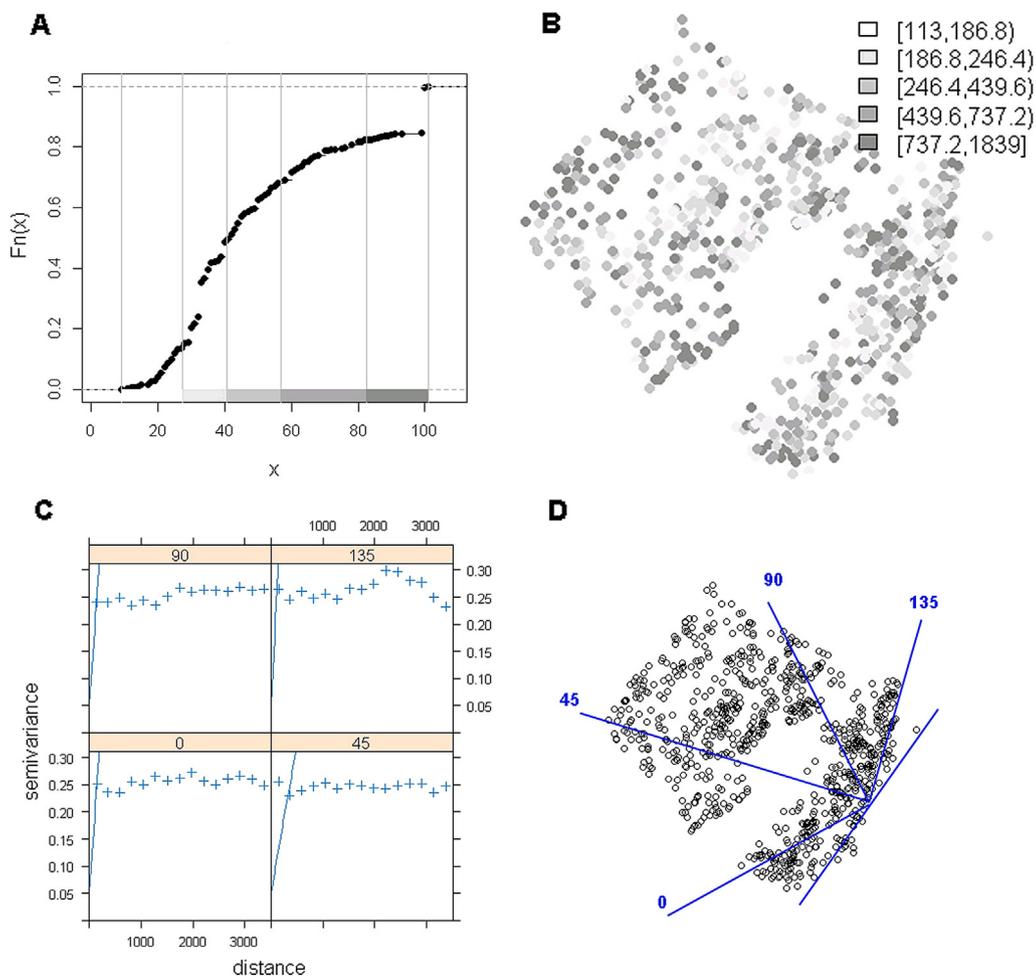


**Fig. 7.** Spatial distribution of all the faunal specimens from SHK (2008–2011) (center of image), showing their location in the channel and on the over-bank. All the plotted images show the spatial distribution of each bone specimen according to taphonomic variables. The upper right image shows the topography of the channel and the bank.

Bed II vary from very large macro-mammalian accumulations (HWK East 1–2, MNK Main Site, BK) to small bone concentrations (EF-HR, FC West, TK, MNK Skull, HKW East 3–5). Bone cortical preservation varies according to site, with sites such as HWK East 1–5, MNK Main and BK generally exhibiting very good cortical surfaces, while other sites yield bones that are highly modified and show poorer cortical preservation (as might be expected from varied depositional *loci*). The variability in ecological setting, as well as bone stone tool density and kind could, in theory, allow the identification of hominin behavioral variability along the landscape.

Monahan (1996) identified two-hominid created bone assemblages in Bed II: MNK Main and BK. He interpreted HWK East 1–2 as an accumulation created by hyenas, thereby suggesting that these bone-crunching animals were more active around riparian environments than in the present time, and thus criticizing the basis for the passive scavenging model created from modern savanna ecology (Blumenschine, 1986). His interpretation of MNK was revised by Domínguez-Rodrigo et al. (2007), who identified a more substantial carnivore component in the assemblage. Following this revisionist interpretation and based on renewed taphonomic work, Egeland and Domínguez-Rodrigo (2008) argued that SHK could have represented some sort of carnivore accumulation.

In the present study we document a minimum of three independent processes contributing to the formation of the SHK faunal assemblage: (1) natural death of megafauna (elephant and hippopotamus); (2) hominin processing of mega- and macrofauna (in the form of cut marks, percussion marks and impact flakes); and (3) activity by carnivores. This palimpsestic nature in the faunal assemblage has been extensively documented in other Oldowan and Acheulian sites (Gaudzinski-Windheuser, 2005; Domínguez-Rodrigo, 2009). While it is challenging to exactly determine the relative contribution of each of these agents in the formation of the site, the relatively marginal presence of taphonomic indicators supporting hominin manipulation of the bones *versus* the substantial amount of carnivore-modified bone suggests that hominins were not predominantly responsible for the majority of faunal accumulation at the site. Most of the fauna appears to have accumulated naturally, which makes sense given the presence of the channel. Channels acquire denser bone accumulations than at other *loci*, since animals need regular access to water and they may either die naturally, or fall to predation, more frequently in and around these environments. We feel it important to emphasize that evidence does exist at SHK consistent with hominin exploitation at least one equid and one hippopotamus. While this evidence is strong, it is not ubiquitous; and thus we infer carcass processing



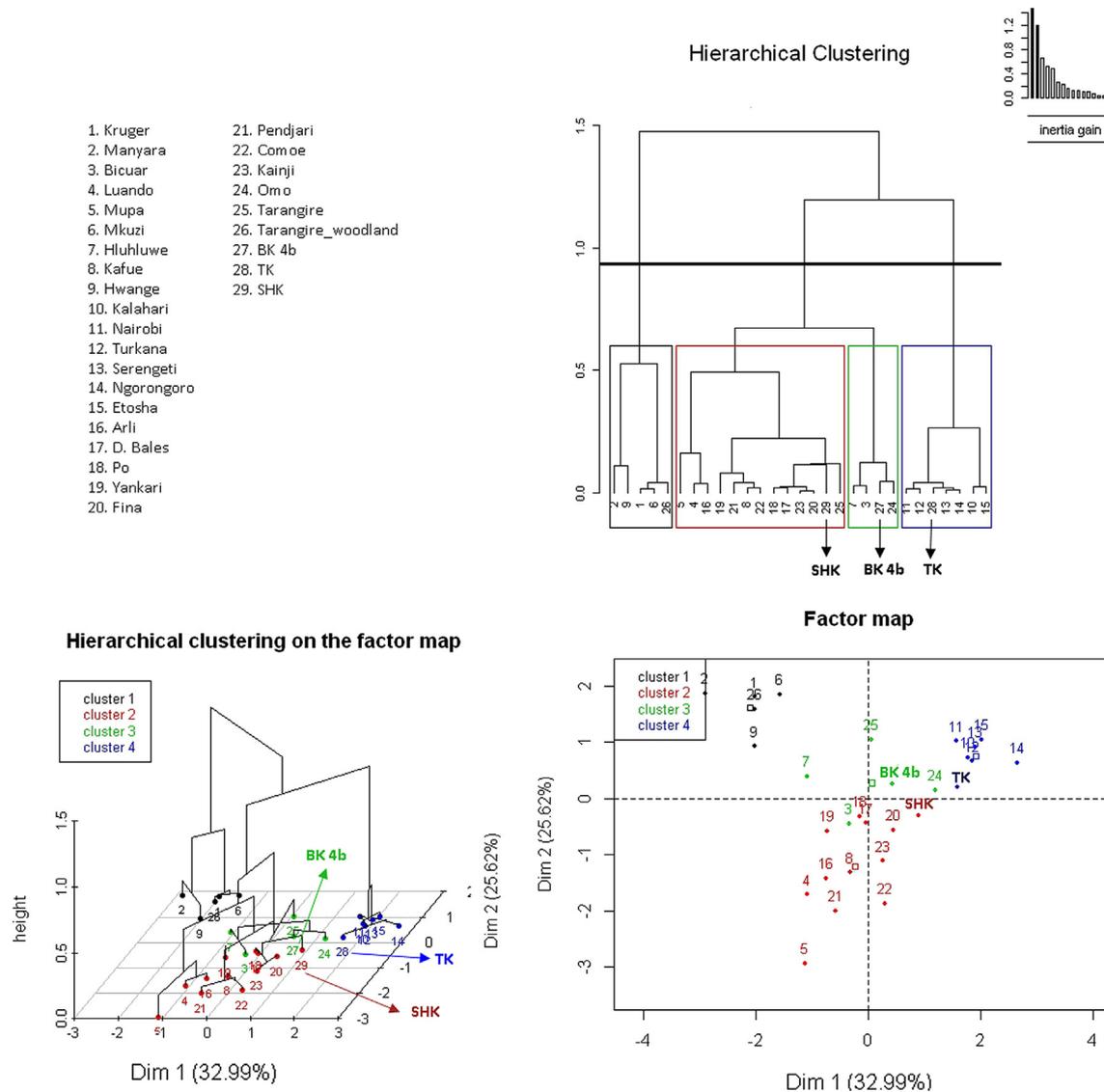
**Fig. 8.** A, Fisher–Jenks class distribution test according to specimen size. B, plotting of each of the five classes of sizes determined by the Fisher–Jenks test, showing homogeneous distribution of all size classes. C, Variogram showing lack of relationship in specimen size distribution and distance from the channel (in four different orientations). D, Sections of each of the orientations upon which the variogram is based.

cannot be the predominant explanation for the abundance of lithic artifacts present at the site. It follows that activities other than butchery probably better account for the high lithic production at SHK.

#### 4.2. Paleocology of middle-upper Bed II

Taphocoenoses are never complete or unbiased representations of paleobiocoenoses. The fossil record is biased because paleontological localities are always habitat-dependent (most sites occur in locations where sedimentary traps occur) and time-averaged (faunas fluctuate within the same habitats) (Domínguez-Rodrigo and Musiba, 2010). The idealistic notion of a paleoecological study sampling equally all the parts of a paleobiocoenosis is not currently possible. Sample sizes of fossil assemblages are relevant, but do not correlate directly with the quality of information about a paleobiocoenosis that may have existed in a given ecosystem. For instance, the Masek-Ndutu bone bed in the Serengeti, which has yielded thousands of wildebeests (Capaldo and Peters, 1995), would be a poor indicator of current biocoenosis in the area, especially when compared to much smaller samples from other bone-accumulating agents, such as hyena dens. A collection of fossils retrieved from any given geological stratum of an open air site should always be considered *a priori* to be biased via a combination of random erosional processes, the chosen retrieval

methods, the prehistoric depositional environment, and the limited range of ecological niches any single locality (often alluvial or lacustrine) might embody (Domínguez-Rodrigo and Musiba, 2010). When considering paleontological samples for paleoecological reconstruction purposes, one should always keep in mind that those samples may not be proportionally representative of a given ecosystem's paleocommunities, but instead be used as provisional paleoenvironmental indicators, potentially representative of specific portions of a paleoenvironment or paleoenvironments. In this sense, although the SHK bovid sample size is small and, therefore, almost certainly incomplete for sampling the paleobiocoenosis of the time, the site's palimpsestic nature may actually be a boon to paleoenvironmental reconstruction because it might possess a more indiscriminate portrayal of some of the most representative (abundant) taxa frequenting the site and its surroundings. This assertion is supported by studies comparing taxonomic diversity in modern hyena dens to the biocoenosis of the ecosystems where these dens occur, which show a strong correlation between taxa representation and the paleoecology of the surrounding environment, despite the fact that sample sizes for most of these dens are <10 MNI (Lacruz and Maude, 2005; see also Kuhn et al., 2008) — the same as SHK. The predominance of open-habitat bovids at SHK is thus consistent with an open ecosystem. This preliminary interpretation is further supported by the substantially larger sample size from TK and BK4b, both overlying SHK.



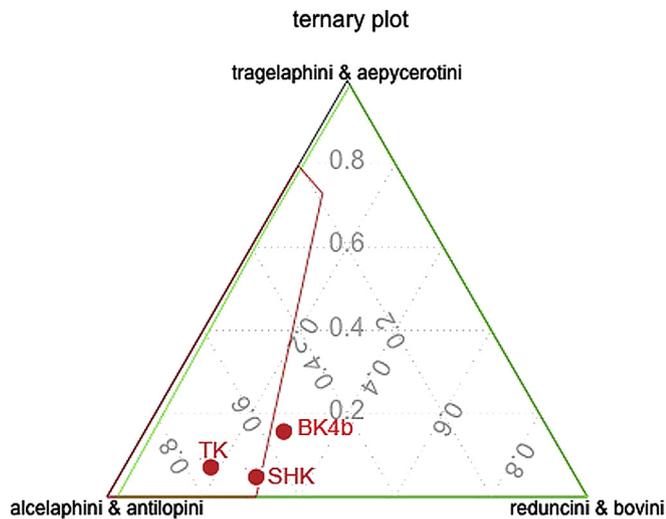
**Fig. 9.** Hierarchical agglomerative cluster analyses of several African national parks representing wooded biomes and open savanna landscapes (see description of each cluster in the text). Data on bovid tribe census for each park are from [Shipman and Harris \(1988\)](#) and [Vrba \(1980\)](#). The cluster dendrogram was obtained using all major bovid tribes, including alcelaphini, antilopini, reduncini, bovini, tragelaphini, aepycerotini and hippotragini. Upper left: List of parks used for the comparative statistical analysis. Upper right: Cluster analysis, showing the distribution of SHK and the other Olduvai upper Bed II sites. Lower left: Cluster analysis on the factor map produced by the PCA. Lower right: PC factor map showing the coordinates according to their correlation of all the parks and archaeological sites.

Although faunas in middle-upper Bed II suggest fairly open ecosystems with a strong riparian component, [Kovarovic et al. \(2013\)](#) recently proposed that faunas at the lower (LBII) and upper Bed II (UBII) indicate woodland habitats throughout the whole bed, *contra* previous works ([Gentry and Gentry, 1978](#)) and our results presented here. [Gentry and Gentry's \(1978\)](#) study of the Olduvai bovid fauna showed that there was an aridification trend occurring at uppermost Bed II with the disappearance of the lake, the lake's replacement by a series of shallow ponds ([Hay, 1976](#)), and the spread of grasslands ([Cerling and Hay, 1986](#)). We also note that fauna >100 kg, which comprise the majority of the Olduvai Bed II assemblages, can be extremely sensitive to ecology. This portion of fauna is not properly considered in [Kovarovic et al.'s \(2013\)](#) recent work. The taxa diversity of the bulk of the fauna in Upper Bed II (dominated by alcelaphini and to a lesser but important extent by the smaller antilopini) is strongly suggestive of a fairly open ecosystem, not a wooded one. An extensive dry or semi-dry woodland as suggested by [Kovarovic et al. \(2013\)](#) would be

reflected by the dominance of tragelaphini in the bovid profiles. However, alcelaphini and antilopini are overwhelming predominant and tragelaphini is, together with the smaller neotragini and cephalophini, the least represented bovid tribe.

## 5. Conclusions

Archaeologists have usually avoided archaeological sites in sandy sedimentary matrices or interpreted them as highly altered by sedimentary processes given their connection to fluvial systems, which usually carry high-energy hydraulic flows. The main site at SHK was previously interpreted as autochthonously affected by water since "most artefacts and bone fragments are in fresh condition, or show only very slight abrasion, but a few specimens, generally of the larger tools, are considerably rolled. Among the choppers the rolled specimens amount to 10 per cent of the total" ([Leakey, 1971: 166](#)). However, the presence of a massive conglomerate within the channel was suggestive of a strong energy depositional



**Fig. 10.** Ternary graph programmed in R, using all the data from each bovid group (alcelaphini & antilopini, reducini & bovini, and tragelaphini & aepycerotini) from Fig. 10 and bootstrapped 10,000 times. Large variability of data from wooded biomes accounts for the widespread overlap of this sample. Location of the Olduvai localities of SHK, BK4b and TK is also shown.

environment, which could have ostensibly impacted the preservation of the site. Egeland and Domínguez-Rodrigo (2008) inferred the assemblage to be substantially biased when they analyzed it, but rigorous interpretations were difficult to make due to selective collection of bones at the site. No modifications due to hominins were discovered on the curated assemblage from Leakey's (1971) excavations.

However, the newly excavated material shows that fluvial impact on the assemblage is smaller than originally suspected: the preservation of small fragments is suggestive of only minor displacement or transport, and there is only a small proportion of abraded bone. The bone abrasion can be explained by either (1) transport into the site or (2) *in situ* modification by circulating water within the sandy matrix embedding the faunal remains, as experimentally shown by Thompson et al. (2011). A spatial analysis of taphonomic attributes shows that no distribution of specimens according to size exists, that there are two distinctive zones (the channel and the over-bank) where taphonomic agents have operated differently, and that bone preservation is substantially worse inside the channel than on the over-bank. The small number of taphonomic indicators resulting from anthropogenic action (the presence of ten specimens bearing either percussion or cut marks), and the more abundant presence of carnivore-modified bone, indicates that SHK is a palimpsest in which several (probably independent) processes intervened. The presence of mega-faunal remains hints at the site having acted as a natural death spot for some of them. This may have attracted hominins, who processed them. Carnivores independently modified other taxa as would be expected in a time-averaged faunal assemblage in a savanna ecosystem with high trophic dynamics. The presence of a large canid tooth specimen (*Canis* sp.) further emphasizes the presence of carnivores at the site.

In sum, our analyses suggest that the assemblage is autochthonous, with only moderate postdepositional disturbance. However, the marginal hominin presence detected through the careful inspection of the faunal assemblage contrasts greatly with the massive accumulation of stone tools at the site. The site was originally described as a conglomerate "almost entirely composed of artefacts and bone fragments, the proportion of unmodified of cobblestones being no higher than that found on many living floors

where there had been no water action" (Leakey, 1971: 166). While we can reasonably infer that these hundreds of artifacts were not related to the exploitation of game, we are currently left to guess what other types of hominin activities they represent. Future analyses of the SHK lithic assemblage may shed light on this question.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2013.09.025>.

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