



## Biotic and abiotic processes affecting the formation of BK Level 4c (Bed II, Olduvai Gorge) and their bearing on hominin behavior at the site



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### ABSTRACT

Excavations at BK have provided insights into the behavior of early hominins through the study of several archaeological levels. The present study shows the results for a new archaeological sub-level (BK4c). The main goal is to contribute to the knowledge of the different taphonomic processes that shaped BK4c and to better understand the role played by hominins in its formation. Due to the presence of a fluvial depositional context and a slight channel in BK4c, a spatial analysis has been applied in order to determine the impact caused by water flows. We conclude that water played a role in the rearrangement of the assemblage. However, the spatial properties of the assemblage indicate a limited impact of post-depositional disturbance processes, supporting the autochthonous nature of the site. The taphonomic study of this sub-level indicates that hominins had a primary role in the accumulation, bulk defleshing and demarrowing of carcasses. BK4 assemblages (BK4b and BK4c) indicate a repeated occupation of the site for short time periods. This is interpreted by the overall fast sedimentation recorded in the fluvial system and the paucity of highly-weathered bones showing extensive periods of sub-aerial exposure in between sedimentary episodes. The site functionality is potentially different from that inferred for earlier Oldowan periods, where sites were smaller and showed less marked spatial clustering of lithics and stone tools caused by hominin behavior.

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### 1. Introduction

A central issue in taphonomy is the problem of site integrity and resolution. Several faunal assemblages excavated in Bed I of Olduvai Gorge (Tanzania) were initially interpreted as the result of hominin butchering activities (Bunn, 1982, 1986; Bunn and Kroll, 1986; Leakey, 1971; Potts, 1982, 1988). A more recent reevaluation of those sites has shown that hominids contributed marginally or nothing to their formation (Domínguez-Rodrigo et al., 2007a,b; Egeland, 2007), except for FLK Zinj (Domínguez-Rodrigo and Barba, 2006; Domínguez-Rodrigo et al., 2007a, 2010, 2014a). In Bed II, several sites have also been interpreted as palimpsests produced by the action of different processes and agents, with hominins and carnivores acting independently over time

(Domínguez-Rodrigo et al., 2014b; Egeland and Domínguez-Rodrigo, 2008; Yravedra et al., 2015).

The first excavations in Bell's Korongo (BK) were conducted in the 1950s, with the intensive excavation at the BK site by the Leakey's, (1971). Research at the site was resumed in 2006. The Olduvai Paleoanthropology and Paleoecology Project (TOPPP) exposed a large area (>45 m<sup>2</sup>) containing a large amount of fossils and stone tools. This allowed the reconstruction of the behavior of early hominins for several archaeological levels (from 1 to 5) at the site (Domínguez-Rodrigo et al., 2009a, 2014c; Organista et al., 2015). The site also yielded a new date for the underlying Tuff IID of 1.35 Ma (Domínguez-Rodrigo et al., 2013). In this paper, we present the results obtained from the analysis of a new archaeological level at BK: the 4c level. This sub-level is differentiated solely on a lithological basis from the overlying levels 4a and 4b mostly encased within a clay matrix (Domínguez-Rodrigo et al., 2009a, 2014c). Level 4c is found in a more detritic sedimentary matrix than BK4b, including a well-defined channel. The main objective of this work is to

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contribute to the knowledge of the different formation processes of BK4c and understand its relationship to BK4b.

Throughout the sequence (Levels 1–5), the BK materials are preserved in low-energy fluvial deposits within a wide channel that has eroded the upper part of Bed II, including Tuff IID. The ancient river flowed from south to north and its former course is currently only visible on the paleochannel's right margin. The overbank shows a minimum depth of 4 m and a width of 50 m, although it appears to be both wider and deeper to the west. The fluvial infill is composed of four sedimentary units that thin upwards and overlap towards the right margin (Fig. 1). The two lowermost units (Units 1 and 2) are gently undulated, tilt to the west, and increase in thickness towards the left margin of the paleochannel. These units show a lateral accretion to the west. The overlying units (Units 3 and 4) completely fill the channel basin and spread over the bank.

Sub-level 4c is the lowest within the archaeological Level 4, composed also of sub-levels 4a and 4b (Fig. 1). All of them correspond to the facies association of the B sedimentary unit (see Domínguez-Rodrigo et al., 2014c). Each level is variable in thickness and consists of massive silts, very fine sands, and clay. Some of them are floored by channel-lags of coarse sands and low density aggregates, composed of clay, silt, and edaphic carbonate (pelletoids). BK4c occupies a smaller area than 4b, with a maximum extension in the excavated trench of 22 m<sup>2</sup> and an average depth of 5–10 cm outside the area occupied by a small channel. The bottom of the level is irregular, but in the central

part it contains an elongated depression, which slightly define a channel of 1 m of width and 20 cm of maximum depth.

In the months of June–July of 2012, three trenches (1.3 × 5.5 m each) were excavated. A large amount of fossils and associated stone tools were discovered (Fig. 2, Supplementary Fig. S1). At the northern end of the third trench we documented a higher density of fossil remains within the channel, so it was decided to identify the specimens as belonging to Cluster 1 (the “channel” cluster). Subsequently, other clusters were observed in the assemblage. As revealed in Fig. 3, the surface of BK4c shows three clusters with high density of materials. The application of a Chi-square test on the sample confirms that the distribution is inhomogeneous with  $p$  value < 0.05 ( $\chi^2 = 723.47$ ,  $df = 14$ ;  $p$ -value  $\leq 0.05$ ) (Baddeley and Turner, 2005). Furthermore, the use of allstats function representing the K, F, G, and J tests, indicates an agglomerative pattern at BK4c (Fig. 4) (Baddeley and Turner 2005). For this reason, and because of the fluvial depositional environment, we focused on the study of the role of hydraulic flows in the assemblage.

For years, several actualistic works have been made aimed at detecting possible alterations caused by water on any given assemblage (e.g., Badgley, 1986a,b; Badgley and Behrensmeier, 1980; Behrensmeier, 1975, 1982; Boaz, 1982; Boaz and Behrensmeier 1976; Coard, 1999; Coard and Dennell, 1995; Dodson, 1973; Frison and Todd 1986; Frostick and Reid 1983; Gifford, 1977; Gifford and Behrensmeier, 1977; Hanson, 1980; Isaac, 1967; Korth, 1979; Petraglia and Nash

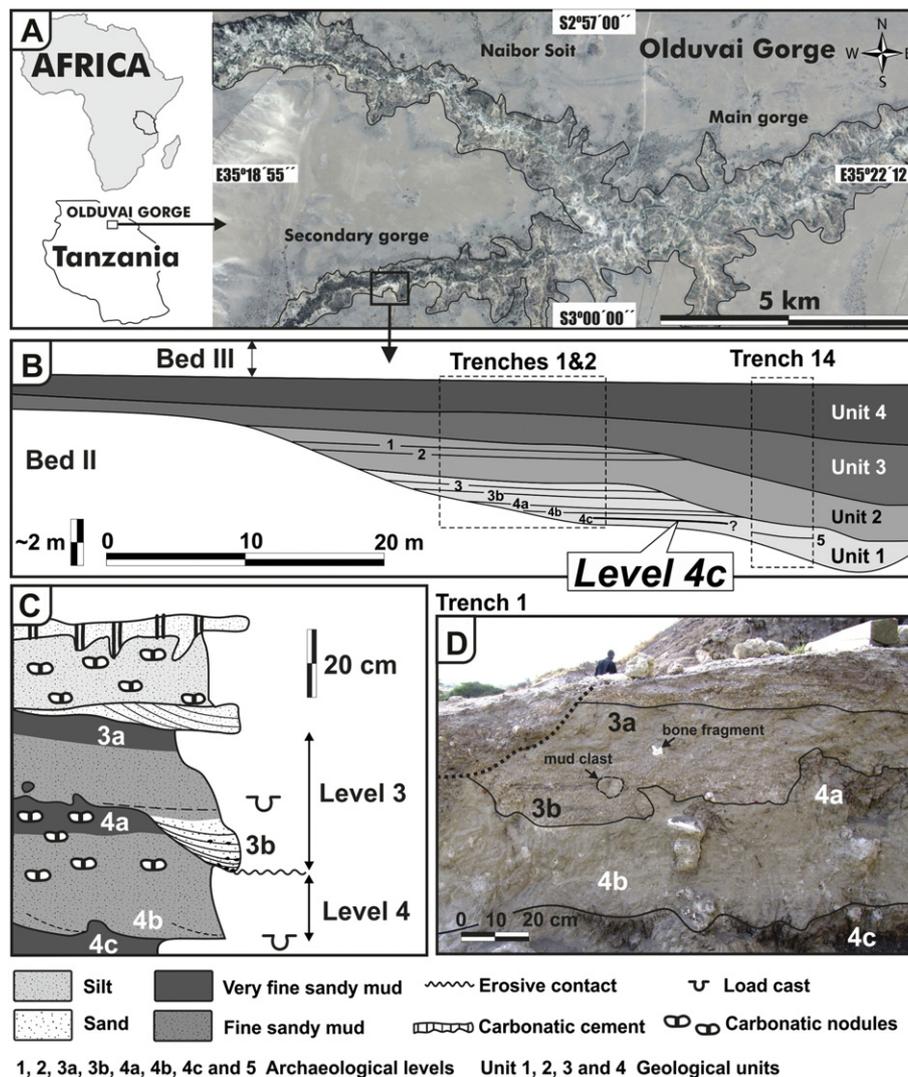
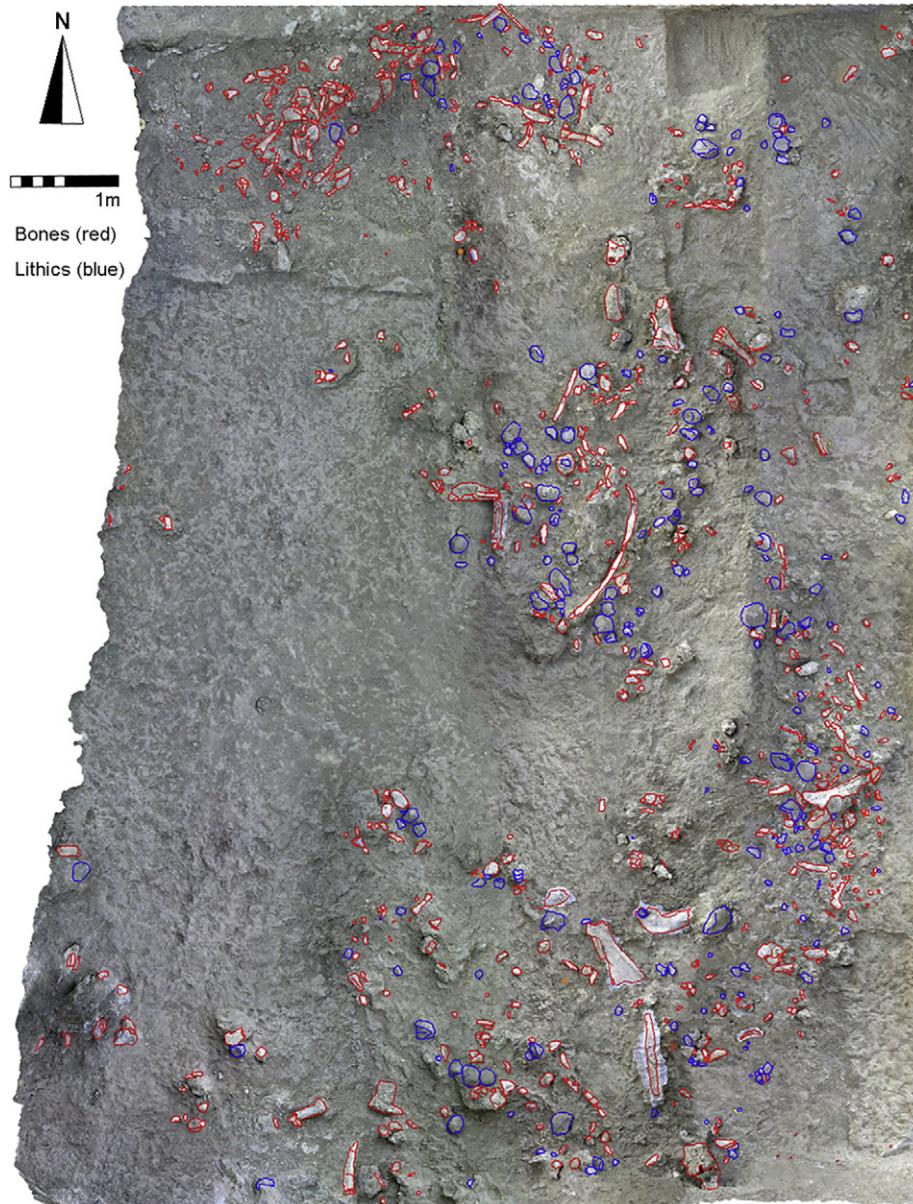


Fig. 1. A: Location of BK in the Olduvai Gorge. B: Detailed stratigraphic section of the four geological units with the different archaeological levels identified at BK. C: Detailed stratigraphic section of levels 3 and 4. D: contact shape between the strata 3 and 4.



**Fig. 2.** Photogrammetric surface of BK4c showing fossils (red) and stone tools (blue). It has been reconstructed in interactive 3D via photogrammetry and can be seen in Supplementary Online Information. Scale = 1 m.

1987; Petraglia and Potts, 1994; Schick, 1984, 1987; Voorhies, 1969; Wolff, 1973). While several of the experiments developed by these authors were performed with complete elements (that do not reflect the reality of the archaeological assemblages where most of the bones are hammerstone-broken), new experiments with fragmented bones have further refined these referential frameworks (Domínguez-Rodrigo et al., 2014d; Pante and Blumenschine, 2010).

Nowadays, with the aid of a set of taphonomic variables stemming from these analogs, we can analyze the potential distortion of fluvial processes in any given assemblage. In this paper, we apply this information to infer what processes took place acting on Level 4c and to understand the role of hominins in its formation.

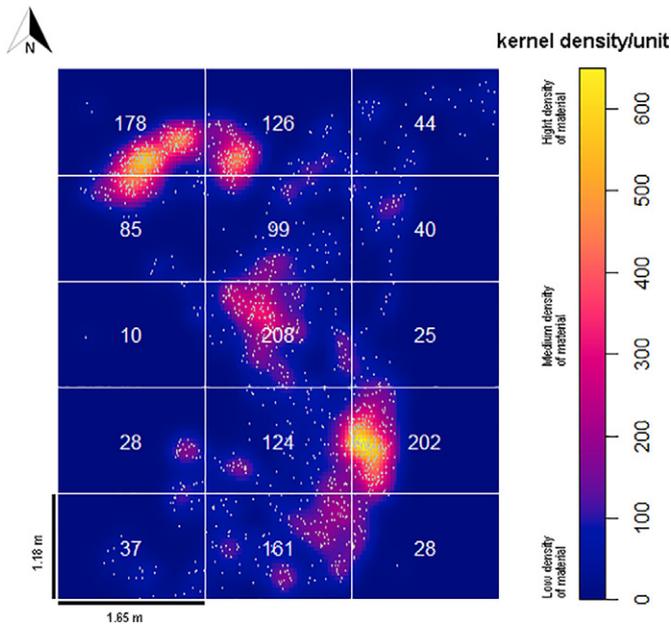
## 2. Methods

### 2.1. Site integrity: detecting the impact of fluvial processes

We made a sedimentary analysis of the matrix where the archaeological materials are embedded. Coarse-grain sediments indicate higher

energy contexts and silt and clay deposits imply low energy environments (e.g., Aslan and Behrensmeyer, 1996; Badgley 1986a,b; Behrensmeyer, 1975, 1982; Hanson, 1980; Korth, 1979; Schick, 1984).

Water flowing may modify the spatial position of archaeological materials, generating a preferential orientation of specimens (Badgley, 1986a,b; Behrensmeyer, 1990; Coard and Dennell, 1995; Domínguez-Rodrigo et al., 2014d; Isaac, 1967; Kreutzer, 1988; Schick, 1984; Toots, 1965; Voorhies, 1969;) although this also can be caused by other processes like gravity or even trampling (Peterhans, 1990; Domínguez-Rodrigo and Martínez-Navarro, 2012; Krajcarz and Krajcarz, 2014). The combination of artifact inclination and orientation is a sensitive indicator of water flow direction and intensity in experimental situations. We georeferenced archaeological specimens bigger than 2 cm. Compasses and clinometers were used to measure the horizontal and vertical orientations of each artifact or bone (Voorhies, 1969; Fiorillo, 1991; Alcalá, 1994, and Howard, 2007) with a longitudinal axis at least twice as long as its width. Measurements were taken along an A-axis that divided the specimen symmetrically along its longitudinal axis, since elongated objects tend to orient according to this axis (Toots,



**Fig. 3.** Spatial point pattern analysis, showing variations in intensity at BK4c. The scale bar represents the kernel density estimates of the intensity (expected number of observations per measuring unit) of the spatial point pattern (SPP). SPP is measured in meters. Statistical analysis was carried out using the “spatstat” R library.

1965, Voorhies, 1969; Domínguez-Rodrigo and García-Pérez, 2013). The data obtained from the orientations were graphically displayed using data crowns (software Oriana w4) and stereograms (software OpenStereo). The statistical analysis was performed using Oriana and the software package RStudio (<http://www.r-project.org>). The uniformity of the archaeological assemblage was statistically evaluated by combining tests that can detect isotropy/anisotropy. The Rayleigh test (R) was used to evaluate anisotropy (Fisher, 1995), and the omnibus Kuiper (V) and Watson (W) tests were further used to determine if the orientation of the archaeological assemblage was bimodal or polymodal (Fisher, 1995) in the likely event of an anisotropic distribution. The three tests were applied in this study using the functions “rayleigh”, “kuiper” and “watson” from the R “circular” library and subsequently confirmed with Oriana. The von Mises distribution was employed to evaluate the normal distribution of the circular data. For this distribution, the dispersion is quantified by the parameters of force ( $c$ ) and concentration ( $k$ ), where  $k$  and  $c$  values between 0 and <1 correspond to an isotropic distribution whereas values exceeding 1 indicate a trend towards anisotropy. These tests were complemented graphically with a Woodcock diagram (Woodcock, 1977). However, Domínguez-Rodrigo et al.’s (2014d) experiments showed that autochthonous assemblages can display anisotropy. To determine if the anisotropy is the result of a water flow transporting elements or the local rearrangement of an autochthonous assemblage, long bone shaft size distribution was also analyzed. Since long bones tend to stabilize in the direction of water flow and settle quickly, and they tend to be transported differently according to their size, we analyzed the shaft fragments independently (Domínguez-Rodrigo et al., 2014d).

Overall, smaller elements are underrepresented in assemblages which have undergone moderate to high-energy water flows (Badgley, 1986a,b; Domínguez-Rodrigo and García-Pérez, 2013; Pante and Blumenschine, 2010; Petraglia and Nash 1987; Schick, 1984, 1987). We examined specimen length distribution in several ways. First, fragment length distribution was tallied for all bone specimens. Then, only length distributions for long bone fragments were considered, since they are denser than cancellous axial bones and have different transportation properties (Domínguez-Rodrigo and Martínez-Navarro, 2012). Finally, length distributions for only green-broken

long bone fragments were analyzed, since diagenetic breakage is very common and tends to bias the original fragment size representation. Shaft specimens from different carcass sizes were analyzed, representing the small (<31 mm), intermediate (31–60 mm) and large (>60 mm) specimen size categories. The presence of unworn shaft specimens corresponding to all these categories are suggestive of autochthony (Domínguez-Rodrigo et al., 2014d).

The presence of polishing and abrasion in a substantial part of any given assemblage is indicative of water transport (Behrensmeier, 1975; Schick, 1984; Stein, 1987; Shipman and Rose, 1988; Fernández-Jalvo and Andrews, 2003). However, Thompson et al. (2011) showed that in non-transported assemblages in a sand context, the specimens exposed to circulating water and mobile sediments also created these modifications on locally-deposited bone specimens. Furthermore, chemical weathering and aeolian processes also may mimic water-flow rounding (Borden, 1971; Schiffer, 1987). For this reason, here we present a spatial taphonomic analysis which takes into account all these modifications according to specimen size. The spatial distribution of specimens was carried out using the “sp” R library.

Some researchers also report that the shape and composition (more and less dense) of a specimen exerts a strong influence on whether it is transported and how it is transported e.g., rolling, saltation, suspension (e.g., Schick, 1984; Visher, 1969; Reineck and Singh, 1980; Stein, 1987). Depending on the anatomical region and the animal age, bones react differently to water flows (Voorhies, 1969; Behrensmeier, 1975; Kaufmann et al., 2011). Bone fragments were measured to determine their shape (flat, tube and cube) and composition (dense, trabecular) following Domínguez-Rodrigo et al.’s (2014d) system. The BK4c data were compared to two experimental assemblages. One of them (referred to as “transported”) underwent transport and other was non-transported (referred to as “lag”). Finally, we compared the BK4c assemblage to an ethnoarchaeological assemblage (referred to as “Masai Camp”) that had not undergone any hydraulic disturbance (Table 1). Data were treated statistically using Bootstrapped Confidence Regions for Correspondence Analysis (Ringrose, 2012). This was done with the R “caboot” library, which performs correspondence analysis on a two-way contingency table and produces bootstrap-based elliptical confidence regions around the projected coordinates for the categories.

## 2.2. Faunal analysis

Skeletal profiles were analyzed by carcass size according to Bunn’s (1982) carcass size classification. Small refers to sizes 1 and 2, medium-sized refers to size 3, and large refers to sizes 4 through 6. Carcasses were divided into anatomical regions: skull (horn, cranium, mandible and teeth), axial (vertebrae, ribs, pelvis, and scapula), and appendicular (limb bones). Long limb bones were further divided into upper (humerus and femur), intermediate (radius and tibia), and lower (metapodials) limb bones (Domínguez-Rodrigo, 1997a). Zooarchaeological measures of skeletal part abundance employed in this study are: number of identified specimens (NISP), minimum number of elements (MNE), minimum number of animal units (MAU), and minimum number of individuals (MNI) (see Lyman, 1994) and survivor index (IS) (Faith and Gordon, 2007). MNE estimates were made taking into account the size, side, landmarks, and age of each identifiable specimen. MNEs were based on the systematic inclusion of shaft specimens, using a manual overlap approach (Yravedra and Domínguez-Rodrigo, 2009).

Skeletal element frequencies are more informative if analyses focus on high-survival elements (Marean and Frey, 1997; Marean and Cleghorn, 2003; Cleghorn and Marean, 2004, 2007) such as some skull sections, teeth, and limb shafts, which are more likely to survive due to their high density. Faith and Gordon (2007), argued that decisions to transport made by humans depend on the distance to carry a carcass; a high frequency of cranial and long limb bones would indicate an unselective transport of carcasses over short distances or no transport. The Shannon evenness index has been applied to measure the uniformity

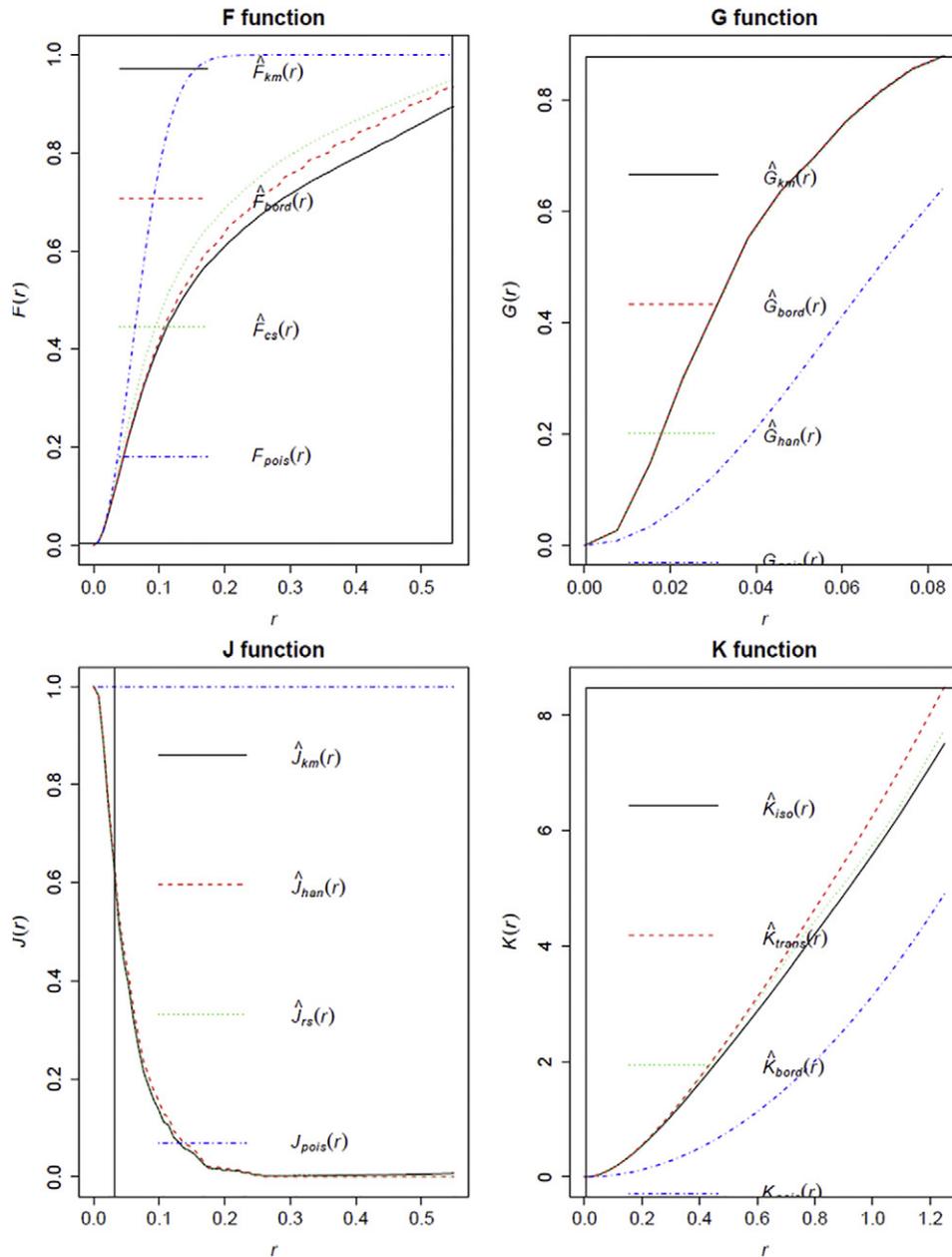


Fig. 4. Allstats functions representing the K, F, G, and J tests, indicating an agglomerative point pattern at BK4c. Statistical analysis was carried out using the “spatstat” R library.

of the distribution of skeletal elements in relation to a complete carcass-0.0 is the lowest evenness value and 1.0 is highest evenness value-(Faith and Gordon, 2007). This evenness index was obtained for BK4c for each carcass size group.

Since destructive processes like carnivore ravaging and water flows tend to eliminate or at least underrepresent less dense bones (Voorhies, 1969; Brain, 1967, 1969; Marean and Spencer, 1991; Marean et al., 1992; Capaldo, 1998; Pickering et al., 2003), element representation (measured by %MAU) was also examined in relation to the modified

general utility index (MGUI) and bone density. The MGUI was obtained from Binford (1978) for small carcasses, Outram and Rowley-Convy (1998) for medium size carcasses, and Emerson (1990) for large carcasses. Density values were acquired from Lam et al. (1999) for wildebeest and Kreutzer (1992) for bison. Regression and Spearman’s rank-order correlation were used to compare both variables.

Shaft circumference type distribution provides information about the agent of breakage (Bunn, 1982, 1983) and the integrity (Marean et al., 2004; Pickering and Egeland, 2006) of a site. Based on data from experimental hammerstone-broken assemblages and hyena dens, three types of shaft circumference were established following Bunn’s (1982) classification: Type 1 fragments retain <50% of the original circumference, Type 2 retain >50% and Type 3 preserve the complete shaft circumference (Bunn, 1982, 1983).

Cortical surface preservation was evaluated by taking into consideration the stages of sub-aerial exposure (Behrensmeier, 1978) and water-induced modification. Cortical surfaces were examined with 10 × 40 hand lenses under a strong oblique light source. Several types

Table 1  
Percentage of sample size and characteristics.

	Dense	Trabecular	Cube	Flat	Tube
BK level 4c	39%	60%	30%	60%	10%
lag	92%	7%	0%	96%	3%
Masai camp	40%	59%	39%	54%	6%
Transported	26%	73%	16%	40%	43%

of marks were identified: cut marks, percussion marks, tooth marks, trampling, abrasion/polish, microabrasion and biochemical marks (following criteria outlined by Bunn, 1981, Domínguez-Rodrigo et al., 2009a, De Juana et al., 2010 for cut marks; Blumenschine, 1988, 1995, Blumenschine and Selvaggio 1988, Pickering and Egeland, 2006 for tooth marks, cut and percussion marks; and Behrensmeier et al., 1986, Domínguez-Rodrigo et al., 2009b, for trampling). Our analysis applied a “configurational approach” where mark morphology, the anatomical placement of marks, and the sedimentary context of the specimen were taken into consideration (White, 1992; Fisher, 1995; Pickering and Wallis, 1997; Pickering et al., 2000, 2004; Domínguez-Rodrigo et al., 2005).

In all comparisons with modern control assemblages, only those fossil specimens with good cortical preservation and green breakage were considered. In assessments of cortical preservation, a score of “poor”, “moderate” or “good” was assigned to each specimen. Good preservation implied the presence of all the original cortical surface unaffected by weathering or other diagenetic processes. Moderate preservation implied at least half of the unaffected original cortical surface. Poor preservation implied that the original cortical surface was weathered or non present. Corrected estimates were obtained following the method of Pickering et al. (2008). This method excludes specimens with poor preservation, which bias the preserved frequencies of marks; and it compensates for the duplication of specimens resulting from the dry breaking. Mark frequencies were tallied by element and bone section for long limb bones (Bunn and Kroll, 1986; Domínguez-Rodrigo, 1997a,b). Bone sections were divided into proximal epiphyses, shaft, and distal epiphyses. This correction method is necessary to properly compare with modern experimental assemblages where dry bone breakage and cortical preservation are not an issue.

Finally, we analyzed simultaneously all marks in reference to different experimental models: Felid-Hominin (F-H) (Gidna et al., 2014); Felid-Hominin-Hyena (F-H-H) (Domínguez-Rodrigo, 1997a,b); and Hominin-Carnivore (H-C) (Domínguez-Rodrigo, 1997b; Pante et al., 2012 and Gidna et al., 2014). Were used a multiple discriminant analysis (MDA) that it maximizes intergroup variance and thus more readily enables factor discrimination. Prior to statistical analysis, samples were bootstrapped (1000 replications, with replacement), which not only expanded the smaller original samples but normalized distributions; this is a prerequisite to apply standard parametric tests such as MDA. The “lda” MASS library function from R ([www.r-project.org](http://www.r-project.org)) was used for this analysis. Graphic representation of the biplot was carried out with the R library “BiplotGUI”.

### 3. Results

#### 3.1. Site integrity: detecting fluvial impact

The depositional environment of Level 4c is composed of silt, fine sand and coarse sand, as well as a small proportion of alluvial aggregates (clay pellets and pelletoids cemented with carbonate) and mud-clasts (10–20 mm) which configure a low density bedload. Sediment selection is very low and neither imbricated clasts nor lamination structures have been found. Chiefly, the highest concentrations of faunal remains are in the depressions, forming a clast-supported conglomerate of bones, with a matrix of silts and sands. This set of features suggests a relative fast process of deposit. It also suggests rearrangement of items by sedimentary processes, moving and clustering items from higher topographic positions to lower ones. The BK4c bed load contexts composed of silt and sand are indicative of low and medium-energy sedimentary conditions, implying the potential of some degree of hydraulic modification of the archaeological assemblage.

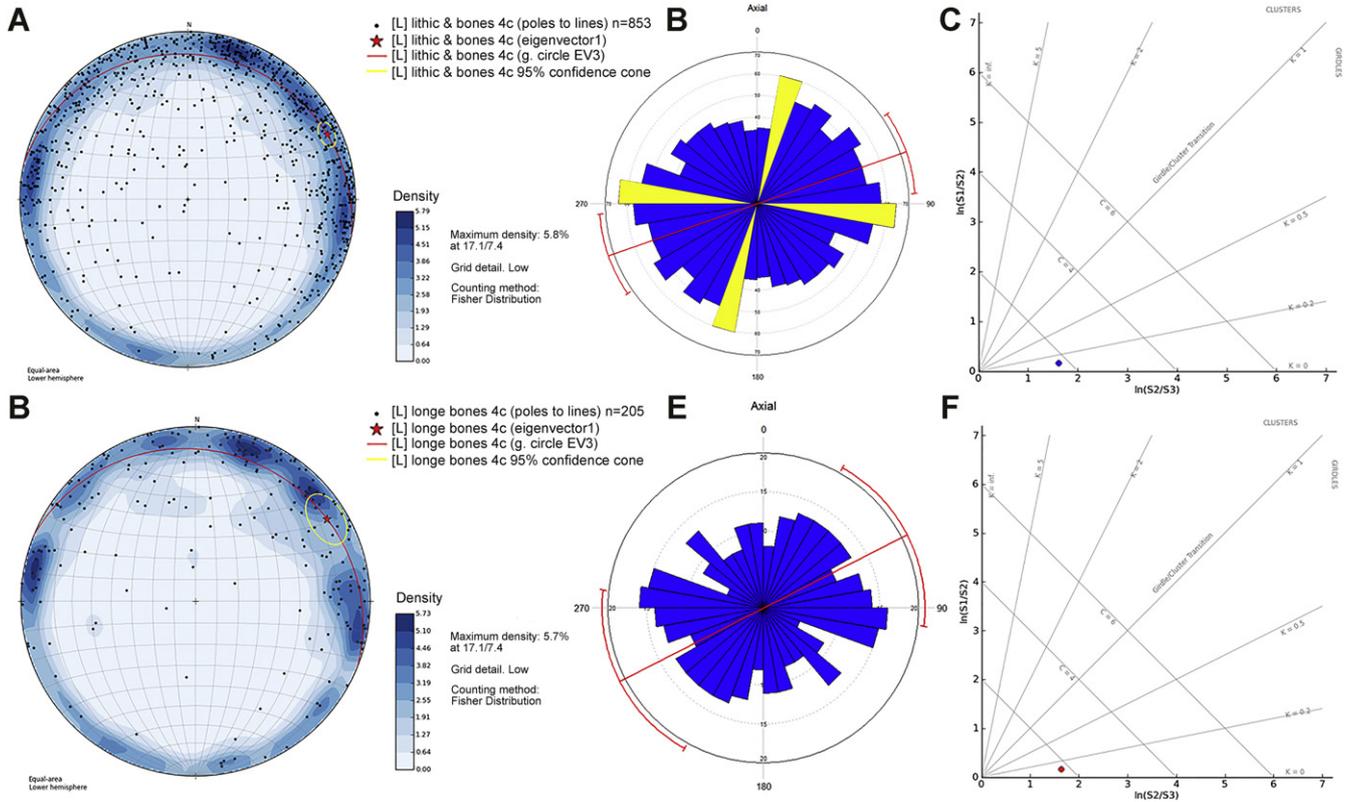
The orientation of archaeological items (bones and lithics) show only slight plunge and no horizontal trend (Fig. 5A). The mean direction is about 63° East–249° West as shown by the 95% confidence interval of the stereogram, but, as the rose diagram shows (Fig. 5B), most of the azimuth confidence interval shows clearly identifiable anisotropic

orientation. The Woodcock diagram shows an isotropic fabric for the assemblage, with a von Mises distribution  $k$  concentration value lower than 0.2 (Fig. 5C). Statistical tests show that the null hypothesis of uniform distribution have to be rejected. This is supported by a Rayleigh test of a general unimodal alternative ( $R = 0.44, p < 0.05$ ), a Kuiper test of uniformity ( $V = 9.028, p < 0.05$ ), and a Watson goodness-of-fit test of circular uniformity ( $U^2 = 8.349, p < 0.05$ ). These tests suggest that the assemblage has more than one preferential orientation. When the same analyses are applied to only long bone specimens, the result is different (Fig. 5D–F). Statistical tests suggest that long bones have a uniform distribution, with Rayleigh ( $R = 1.39, p = 0.24$ ), Kuiper ( $V = 1.47, p \geq 0.15$ ) and Watson ( $U^2 = 0.09, p = 0.5$ )  $p$ -values  $> 0.05$ . This implies that water circulation has different effects on bones types. Long bone shafts get more easily embedded in the sandy matrix and undergo less movements than bigger and more trabecular bones specimens (Domínguez-Rodrigo et al., 2014d).

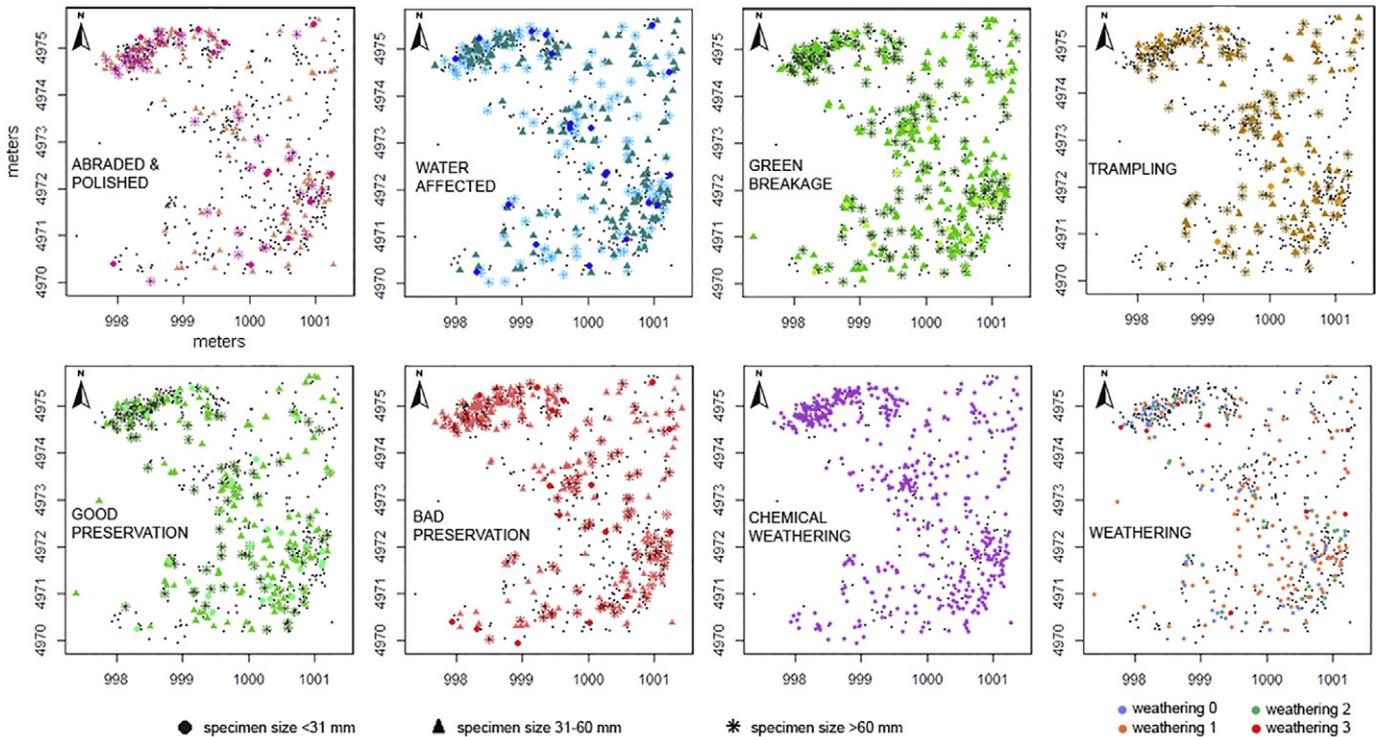
At BK 4c, we found 833 specimens, of these only 19.5% ( $n = 163$ ) showed a carbonate matrix and 40% ( $n = 330$ ) showed water-caused modification. The bulk of the bone collection (73%,  $n = 605$ ) shows exfoliation, and chemical weathering characteristic of bones exposed to water or humidity for extended periods of time. But only 200 (24%) specimens exhibited abrasion or polishing independently of their size, while the majority (76%) of specimens are unworn (Fig. 6). In addition, when documenting abrasion or polishing, these modifications often affect one or two of the surfaces but not the complete specimen. This suggests that rather than being transported into the site, polished bones more likely resulted from in situ physical modification, probably due to the slow abrasion of water circulation within the sedimentary matrix (Thompson et al., 2011).

When considering the frequency of specimens according to their size and animal size class, the fragments between 31 and 60 mm, and  $> 100$  mm are the most abundant. It could be due to intense dry fragmentation of the assemblage because the distribution of green-broken specimens is different from the plotted distribution of all specimens irrespective of breakage type. If we consider green broken long bones (LB) only, the pattern is the same. Distribution of green-broken LB specimens is virtually similar to the plotted distribution of all LB specimens irrespective of breakage type. The presence of bones from large animals increases the portion of specimens longer than 40 mm. Plotted bone fragments  $< 20$  mm there are underrepresented because they were retrieved in the sieved sediment. Several bags containing sieved material were not included in this analysis. These bags contain thousands of small bone fragments and splinters  $< 2$  cm, which further show that the preservation of these small specimens indicate minor post-depositional effects by sedimentary processes. The majority of the fragments between 20 mm and 30 mm belong to small and medium-sized carcasses. Specimens longer than 40 mm are represented by long bone fragments from large carcasses (Fig. 7). When distributing long bone specimens according to size, animal size and if they are abraded or not, it can be seen that specimens  $< 31$  mm from large and medium-sized carcasses are underrepresented. Small carcasses show an even distribution of LB specimens (Fig. 8). Indeed, the high frequency of very small specimens indicate a limited impact of postdepositional disturbance processes, supporting the largely autochthonous nature of the site, although several of the spatial properties of the assemblage, as generated by hominins, may have been lost due to rearrangement by water.

Statistical analyses applied to BK, compared to the Masai camp and the referential transported and lag assemblages are also informative. The bootstrapped Correspondence Analyses shows a two-dimension solution, which accounts for 99.7% of the inertia. Dimension 1 (inertia = 75.1%) shows that shape and composition of bones discriminate efficiently among the three assemblages. This is also observable in Dimension 2 (inertia = 24.6%) (Supplementary Table S1; Fig. 9). The 95% confidence ellipses of the three models do not overlap, further reinforcing the difference, which in the case of the transported group is also the most prominent in Dimension 1 (Supplementary Table S1). The



**Fig. 5.** A: Stereogram showing the azimuth orientation of all the specimens with a longitudinal axis at BK4c. The first eigenvalue comprising most of the inertia, as well as the confidence interval of the mean trend/plunge orientation (in yellow) are shown. B: rose diagram showing non-uniform bone orientation. C: Woodcock diagram showing an isotropic fabric for the assemblage, with von Misses distribution  $k$  concentration values under 0.2. D: Stereogram showing the azimuth orientation of long bones with a longitudinal axis at BK4c. The first eigenvalue comprising most of the inertia is shown, as well as the confidence interval of the mean trend/plunge orientation (in yellow). E: rose diagram showing uniform bone orientation. F: Woodcock diagram showing an isotropic fabric for the assemblage, with von Misses distribution  $k$  concentration values under 0.2.



**Fig. 6.** Spatial distribution of all archaeological materials from BK4c (see Fig. 2). All the plotted images show the spatial distribution of each bone specimen according to selected taphonomic variables.

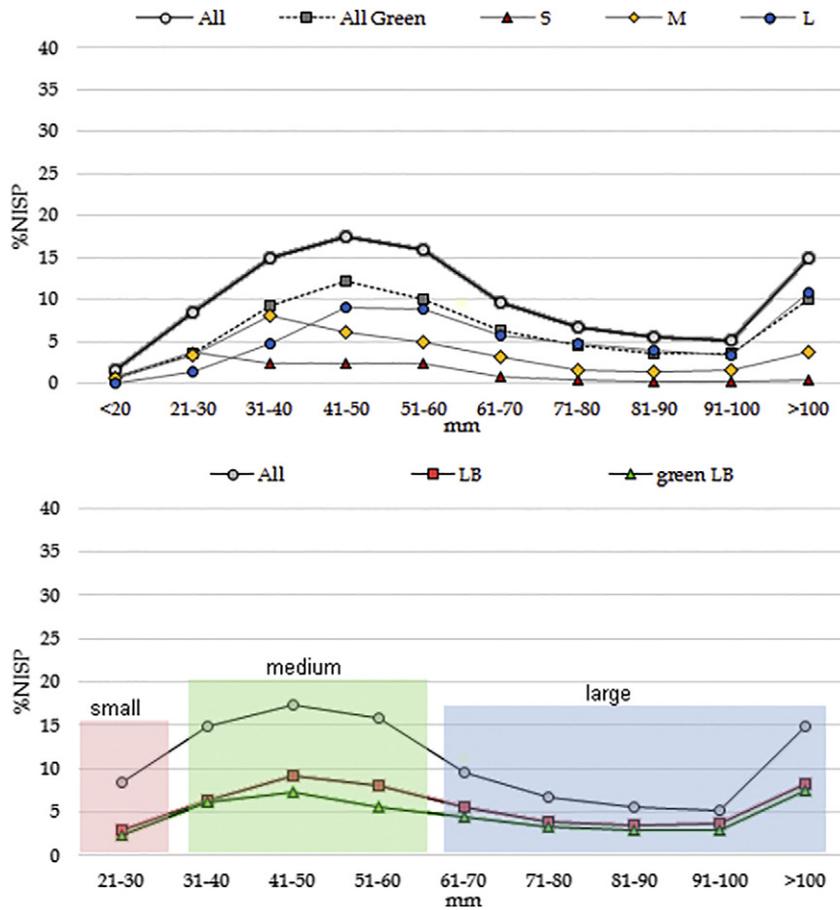


Fig. 7. Specimen size distribution at BK4c, quantified by %NISP and absolute NISP values. Each size category range appears highlighted in different color: specimen size < 31 mm (red), specimen size between 31 and 60 mm (green) and specimen size > 60 mm (blue).

transported assemblage shows more tube-shaped specimens, the Masai camp shows more cube-shaped and trabecular specimens, while the lag assemblage shows a higher presence of flat and dense bones. The spatial location of BK near the Masai camp assemblage indicates that Level 4c did not undergo any significant transportation by water.

3.2. Faunal analysis

During the 2012 excavation, a total of 22 m<sup>2</sup> from level BK4c were uncovered. Fig. 2 illustrates the close spatial association of stone tools

and fossils. A total of 833 specimens were recovered, but only 594 have been attributed to carcass size. A total of 29 individuals were identified (Table 2). Small animals were represented by 4 individuals, medium-sized animals by 16 individuals and large animals by 9 individuals.

Tables 4–6 present the skeletal profiles per carcass size. When we consider the relationship of MNE to MNI for each carcass size, small carcasses show that mandibles and appendicular limb bones are better represented than axial bones, such as ribs and vertebrae. These latter are considerably underrepresented. The appendicular skeleton retains several epiphyses ( $n = 13$ ) although they are fewer in number than shafts

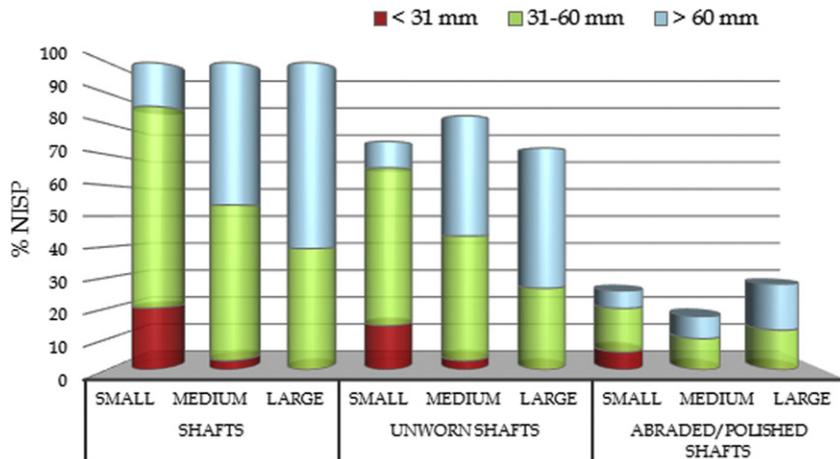
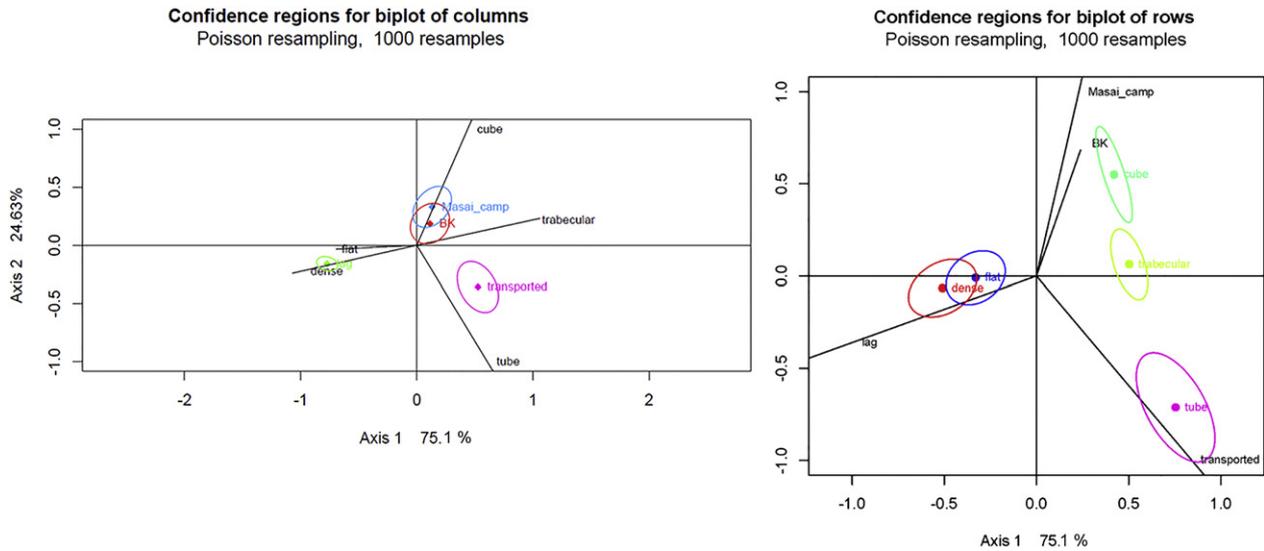


Fig. 8. Frequencies of shaft fragments, unworn shafts and abraded/polished shafts by specimen size and carcass size.



**Fig. 9.** Biplots of the bootstrapped CA of bones at BK4c showing the relationship between referential models (Masai camp, lag and transported modern assemblages) with respect to the shape and composition of bones at BK4c. Data from Domínguez-Rodrigo et al. (2014d). Ellipses with 95% confidence intervals for referential models (left) and shape and composition of bones (right) are also displayed. Loading scores for the variables are displayed in Table 1 and Supplementary Table S1. Length of the axes shows the importance of the contribution of each variable to the inertia.

( $n = 36$ ). Both epiphyses from humeri, and the proximal end of metatarsals are the most abundant long bone portions. Compact bones are underrepresented (Table 3). Medium-sized animals are mainly represented by dense elements, horns, mandibles and long bones. The axial skeleton and compact bones were marginally represented. Similarly to small-sized carcasses, some long limb bones are better represented by epiphyses than shafts portions (e.g., proximal end of radius) (Table 4). A similar pattern was documented for larger carcasses. The axial skeleton is slightly better represented than in smaller carcasses, probably because of a larger sample size. The appendicular skeleton is represented

mostly by shaft fragments and by some of the densest epiphyses such as distal humeri, proximal radius and distal metacarpals. Compact bones like phalanges, carpals and tarsals or patellae are almost completely absent (Table 5).

Overall, the skeletal part data exhibit assemblages dominated by skulls and limbs, with axial elements and compact bones highly under-represented, and scapulae and pelvis variably present. This general pattern is compared favorably to modern assemblages where carnivores have a significant input in damaging remains abandoned by hominins (Capaldo, 1998). However, the frequency of epiphyses may indicate a limited degree of postdepositional destruction. Epiphyses of long bones at BK 4c are well represented, even better than shafts in the case of the humerus, radius and metatarsal. The underrepresentation of shafts may be related to the impact of water flow during sedimentation.

Given the amount of individuals represented, the number of skeletal elements of each of them is small, which is probably the combined consequence of the following factors: the excavated surface (22 m<sup>2</sup>) is only a small portion of the total area covered by the site (see Domínguez-Rodrigo et al., 2014c; Organista et al., 2015), the minor but local rearrangement by water may have redeposited specimens outside the excavated area and even brought some in from its periphery, carnivore activity may have been responsible for the deletion of an uncertain amount of elements (especially from the axial skeleton) (see below), and the bulk of the individuals represented were identified by just isolated teeth, which frequently exaggerates the actual number of individuals represented by postcranial elements. Several of them may even belong to background scatters that frequently get deposited in the same hominin-activity areas without any functional relationship. In addition, the quasi-continuous nature of the Level 4 deposit, makes it likely that some of the elements identified in sub-level 4b may belong to individuals documented in sub-level 4c and viceversa.

Linear regression and Spearman's rank-order statistics show a non significant relationship between the minimum number of animal units and meat utility, for all carcass sizes (Table 6). The high survival elements are positively correlated with skeletal part representation for medium-sized carcasses (Table 6). The evenness values for small carcasses (0.94,  $n = 16$ ), medium-sized carcasses (0.96,  $n = 30$ ) and large carcasses (0.96,  $n = 29$ ) indicates that the high survival skeletal set is evenly represented in the assemblage. This supports the interpretation that the animals were not selectively transported to the site. This

**Table 2**

Minimum number of individuals documented in BK4c.

	MNI	
	Juvenile	Adult
Antilophini		
<i>Gazella</i> sp.		2
Alcelaphini		
Size 3 Alcelaphini	1	
<i>Parmularius</i> sp.		1
<i>Parmularius angusticornis</i>		1
<i>Megalotragus</i> sp.		1
Tragelaphini		
Size 3 Tragelaphini		1
<i>Taurotragus oryx</i>	1	
Bovini		
Size 4 Bovini		1
<i>Pelorovis oldowayensis</i>		1
Suidae		
<i>Metrochoerus compactus</i>	2	2
<i>Kolpochoerus olduvaiensis</i>		1
Suidae	2	
Equidae		
<i>Hipparion cornelianum</i>	1	1
<i>Equus olduvaiensis</i>	2	2
Rhinocerotidae		
<i>Ceratotherium simum</i>		1
Hippopotamidae		
<i>Hippopotamus</i> sp.	1	1
Elephantidae		
<i>Elephas</i> sp.		1
Giraffidae		
<i>Sivatherium</i> sp.		1
Giraffidae indet.		1
Total	29	

**Table 3**  
Skeletal part profiles of small (sizes 1, 2) carcasses.

BK 4c small	NISP	NISP good preservation	TM	PM	CM	MNE
Horn						
Skull						
Teeth	5	2				
Mandible	2	1				2
Cervical vertebrae						
Thoracic vertebrae	4	4				3
Lumbar vertebrae						
Vertebrae indet.						
Scapulae	1	1				1
Ribs	9	8				3
Pelvis	1	1				1
Humerus						4
Proximal end	2	1			1	
Shaft	2					
Distal end	4					
Radius-ulna						4
Proximal end	2	3	1	1		
Shaft	3	1				
Distal end						
Metacarpal						1
Complete						
Proximal end	1					
Shaft						
Distal end	1					
Femur						2
Proximal end	1					
Shaft	1	1				
Distal end						
Tibia						1
Proximal end						
Shaft	3	3		1		
Distal end						
Metatarsal						2
Proximal end	2					
Shaft	1	1				
Distal end						
ULB <sup>a</sup>	6	2			1	
ILB <sup>a</sup>	1					
LLB <sup>a</sup>	5					
Indet. shaft	14	6	1	1	1	
Patella						
Carpals/tarsals	1	1				1
Phalanges	3	1				2
Indet no shaft						
Total	75	37	2	3	3	27

NISP, number of identified specimens; TM, tooth marked specimens; PM, hammerstone-percussed specimens; CM, cut marked specimens; MNE, Minimum number of elements.

<sup>a</sup> ULB upper limb bones, ILB intermediate limb bones, LLB lower limb bones. In addition to the data displayed in this table, there are 233 unidentifiable specimens which could not confidently be assigned to any carcass group.

may be due to carcasses being acquired at or very close to the site, although small sample sizes preclude definitive interpretations. High evenness indices of high-survival skeletal elements in modern referent assemblages usually show that no discard decision was made prior to transport, which is frequently documented in modern foragers when transport distances from kill site to consumption site are short (Faith and Gordon, 2007; Faith et al., 2009). Longer distances involve weight reduction strategies implying the discard of the least nutritious parts.

A total of 483 bone specimens could be identified as bearing green or/and dry breakage, the rest ( $n = 341$ ) are isolated teeth and indeterminate specimens. Of these, 272 specimens showed green breakage only, and 101 had dry breakage only, and 110 specimens showed a combination of green and dry breakage. Most of the green breakage was produced on long bones ( $n = 165$ ), with the rest documented on crania ( $n = 33$ ), axial bones ( $n = 31$ ), compact ( $n = 4$ ), and indeterminate elements ( $n = 22$ ). Dry breakage was documented in higher numbers on axial bones ( $n = 33$ ), long bones ( $n = 26$ ), and more marginally on cranial ( $n = 19$ ) and compact bones ( $n = 3$ ). When analyzing long bones only, we found 315 long bone shaft fragments, of them 165 (52%) specimens bear green fractures only, 66 (21%) specimens bear both green

**Table 4**  
Skeletal part profiles of medium-sized (size 3a, 3b) carcasses.

BK 4c medium	NISP	NISP good preservation	TM	PM	CM	MNE	
Horn	3	2				2	
Skull	1	1				1	
Teeth	66	26					
Mandible	6	5				5	
Cervical vertebrae							
Thoracic vertebrae	1	1		1		1	
Lumbar vertebrae	2	1				2	
Vertebrae indet.	1	1					
Scapulae	2	1				2	
Ribs	28	22			1	5	
Pelvis	1					1	
Humerus						5	
Proximal end	1	1					
Shaft	11	3			1	1	
Distal end							
Radius-Ulna						5	
Proximal end	3	3					
Shaft	5	3		2	2		
Distal end	2	2					
Metacarpal						5	
Complete	2	1			1		
Proximal end							
Shaft	6	4					
Distal end	2						
Femur						3	
Proximal end							
Shaft	4	2					
Distal end	2	2					
Tibia						4	
Proximal end							
Shaft	8	4		1	2		
Distal end	1						
Metatarsal						3	
Proximal end	2						
Shaft	3	1					
Distal end							
ULB <sup>a</sup>	7	3					
ILB <sup>a</sup>	1						
LLB <sup>a</sup>	6	2			1		
Indet. shaft	18	6		2	3		
Patella	1					1	
Carpals/tarsals	2					2	
Phalanges	4	3			1	4	
Indet no shaft	3	2			1		
Total	205	102		4	9	7	51

NISP, number of identified specimens; TM, tooth marked specimens; PM, hammerstone-percussed specimens; CM, cut marked specimens; MNE, Minimum number of elements.

<sup>a</sup> ULB upper limb bones, ILB intermediate limb bones, LLB lower limb bones. In addition to the data displayed in this table, there are 233 unidentifiable specimens which could not confidently be assigned to any carcass group.

and dry fractures, 26 (8%) specimens showed dry breaks only, and 68 (19%) specimens showed ambiguous breakage planes. Specimens bearing green breakage planes make up 73% of the identifiable breakage planes when the entire long bone shaft sample is considered, or 89.7% if the ambiguous specimens are discarded. Shaft circumference types show that Type 1 is predominant with 92.3% ( $n = 291$ ), Type 2 and Type 3 show a lower frequency with a 3.1% ( $n = 10$ ) and 4.7% ( $n = 15$ ) respectively. This suggests a biotic agent of bone breaking. Only twelve specimens bearing notches were documented; seven single notches and three incomplete notches and two “double-opposing” notches. The fact that notches appear on larger carcasses ( $n = 10$ ) prevents a sure attribution of the breakage agent based on notch morphology (De Juana and Domínguez-Rodrigo, 2011).

Bone surfaces at BK4c are poorly preserved, independently of location within the excavated area. Good preservation of cortical surfaces is documented in 271 (32.5%) specimens of the total bone sample (Fig. 6). One hundred seventy-six specimens (21% of total sample; 69% of the well-preserved sample) showed traces of trampling (Fig. 6) and 124 specimens (14.8% of total sample; 48.8% of the well-preserved sample) showed microabrasion. The sediment-induced modification seems

**Table 5**  
Skeletal part profiles of large (sizes 4–6) carcasses.

BK 4c large	NISP	NISP good preservation	TM	PM	CM	MNE
Horn	5					2
Skull	7					3
Teeth	43	11				
Mandible	3	2	1	1		2
Cervical vertebrae	5	2	1			3
Thoracic vertebrae	3	2	1	1		2
Lumbar vertebrae	3	3				3
Vertebrae indet.	5	2	1			
Scapulae	6	4	1		1	3
Ribs	36	9			1	9
Pelvis	4	2				2
Humerus						8
Proximal end						
Shaft	16	3		1		
Distal end	8	1				
Radius-ulna						4
Proximal end	6	4	1		3	
Shaft	5	4	1	2	1	
Distal end						
Metacarpal						3
Complete						
Proximal end						
Shaft						
Distal end	3	1				
Femur						3
Proximal end						
Shaft	5	4		3		
Distal end	1	1				
Tibia						10
Proximal end						
Shaft	25	11	1	3	1	
Distal end	1	1				
Metatarsal						2
Proximal end						
Shaft	3	1				
Distal end						
ULB <sup>a</sup>	4	2				
ILB <sup>a</sup>	4	1				
LLB <sup>a</sup>	11					
Indet. shaft	73	13	2	1	1	
Patella						
Carpals/tarsals	10	4				10
Phalanges	1					1
Indet no shaft	17	3				
Total	313	91	10	12	8	70

NISP, number of identified specimens; TM, tooth marked specimens; PM, hammerstone-percussed specimens; CM, cut marked specimens; MNE, Minimum number of elements. NISP, number of identified specimens; TM, tooth marked specimens; PM, hammerstone-percussed specimens; CM, cut marked specimens; MNE, Minimum number of elements.

<sup>a</sup> ULB upper limb bones, ILB intermediate limb bones, LLB lower limb bones. In addition to the data displayed in this table, there are 233 unidentifiable specimens which could not confidently be assigned to any carcass group. In addition to the data displayed in this table, there are 233 unidentifiable specimens which could not confidently be assigned to any carcass group.

to have had an important role in the modification of bone surfaces at the BK 4c faunal assemblage. Biochemical modification by fungi or plants was documented on 121 specimens (14.5% of total sample; 48% of the

well preserved sample). The BK4c bone collection includes 315 long bone shaft specimens; 99 (31.4%) showed good cortical preservation. Sub-aerial weathering could confidently be documented on 87 long bone shaft specimens, out of which 41 showed weathering stage 0 (47%); 27 specimens showed weathering stage 1 (31%); 16 specimens showed weathering stage 2 (18%); and 3 specimens showed weathering stage 3 (3%). These specimens (with weathering 3) are located within Cluster 1 (Fig. 6). The majority of long bones ( $n = 228$ ) showed exfoliation and chemical weathering, typical of bones exposed to water or humidity for extended periods of time (Fig. 6).

Tooth marks occur in low frequencies (Supplementary Fig. S2). Only one tooth-marked shaft specimen was documented in small carcasses. Taking into account only shaft bones with good surface preservation ( $n = 14$ ) and correcting for dry breakage ( $n = 6$ ) (Pickering et al., 2008) the percentage of tooth-marked specimens for this carcass size is 9% (Supplementary Table S2). Medium-sized carcasses show three tooth-marked shafts out of a total of 29 good surface preservation sample and correcting for dry breakage ( $n = 2$ ) the percentage is 11% (Supplementary Table S2). Finally, large carcasses show 4 tooth-marked shaft bones out of a total of 39 well-preserved specimens and correcting for dry breakage ( $n = 6$ ) the percentage is 11% (Supplementary Table S2). A total of six tooth-marked bones occurred on mandible, vertebrae and scapula for medium and large carcasses. Only three epiphyses (olecranon and radius) show tooth marks for small and large carcasses. These results suggest a low activity by carnivores on the assemblage. Indeed, tooth mark frequencies for shafts are within the hammerstone to carnivore range (Blumenschine, 1988, 1995; Capaldo, 1997), but also are within or exceed the values reported for felid to hammerstone model (Domínguez-Rodrigo et al., 2007b; Organista et al., 2016).

A total of 24 specimens bearing percussion marks were identified (Supplementary Fig. S2). Only three percussion marks occurred on a mandible, a thoracic vertebrae and an indeterminate specimen. The percussion mark percentage for small carcasses show 18% (2 percussed shaft fragments out of a sample of 11 well-preserved and corrected for dry breakage) (Supplementary Table S2). Medium-sized carcasses show 32% of shaft specimens with percussion marks (9 out of a sample of 28), while large carcasses show 18% of their shaft sample bearing percussion marks (10 out of a sample of 36) (Supplementary Table S2). These percussion-marked specimens extended across the entire range of carcass sizes: one radius, one tibia and one indeterminate shaft of a small animal; one humerus, two radii, two tibiae, one metapodial, and three indeterminate shafts of medium-sized carcasses; one humerus, two radii, three tibiae, three femurs, and one indeterminate large-sized shaft. This result fits with the range documented in experimental models where bones are broken with hammerstones (Blumenschine, 1988, 1995; Capaldo, 1997) before carnivores intervene. Most of the re-fits documented are on specimens showing green fractures, indicating local bone breakage by hominins.

A total of eighteen cut-marked specimens have been documented (Supplementary Fig. S2), three of them occurred on a scapula, a rib and a first phalanx specimen. The cut mark percentage on mid-shaft specimens that are well preserved and corrected for dry-breakage for small carcasses is 18%. Medium-sized carcasses show 14% of specimens

**Table 6**  
Regression and Spearman's statistics for each carcass size at BK4c.

% MAU-%MGUI	Regression			%MAU-density			
	Small	Medium	Large	Regression	Small	Medium	Large
$r^2$	-0.104	-0.141	-0.079	$r^2$	-0.041	0.526	-0.158
$F$	0.337	0.009	0.485	$F$	0.719	9.9	0.044
$p$	0.58	0.92	0.51	$p$	0.42	<b>0.01</b>	0.84
Spearman's	Small	Medium	Large	Spearman's	Small	Medium	Large
$r_s$	0.527	0.079	0.626	$r_s$	0.049	0.670	0
$p$	0.17	0.83	0.09	$p$	0.90	<b>0.04</b>	1

Regression and Spearman's statistics for the relationship between %MAU and %MGUI, %MAU and density for high survival elements. Significant values are in bold.

with cut marks, while large carcasses show 8% of their sample bearing cut marks (Supplementary Table S2). When comparing the distribution of cut-marked specimens for each appendicular section with Gidna's experimental model (2014) it can be seen that the percentages belonging to large carcasses fall within the range of an early access (Table 7). Small and medium-sized carcasses show lower percentages than documented by Domínguez-Rodrigo (1997a,b) for primary access experiments in which carcasses were thoroughly defleshed, even removing all flesh scraps (Table 7). However, 14% is higher than documented in experiments replicating secondary access to felid-consumed carcasses (Gidna et al., 2014) (Table 7). The cut mark frequencies are also similar to several recent sites where primary access is not disputed (Domínguez-Rodrigo and Yravedra, 2009c). The presence of cut marks on a rib, a radius and an ulna belonging to *Sivatherium* and one indeterminate shaft corresponding to elephant also suggest defleshing by hominins of large carcasses. In addition, several cut marks on the medial and lateral side of a first phalanx (Fig. 10) show that hominins were in some cases skinning carcasses at BK4c intentionally.

The multivariate discriminant analysis of cut, percussion and tooth marks provides information about order of hominin access. The MDA test produced a two dimension solution which accounted for 99.9% of the sample variance. The first dimension explained 90% of the total variance alone. This dimension was determined by two variables: total cut marks on all bone portions and the frequencies of cut marks on shafts with respect to the total cut marked sample (scores: 0.073 and 0.041 respectively). The second dimension is largely determined by tooth mark frequencies (scores: 0.203 and 0.117). Percussion marks are the least discriminatory of all the classes of bone surface modifications. The confusion matrix shows that MDA correctly classified 86.4% of sample. When the BK data were interpolated in the MDA test, the BK4c assemblage plots within the 95% confidence alpha bag of primary access (Fig. 11, Supplementary Table S3).

## 4. Discussion

### 4.1. The input of hydraulic processes at BK4c

According to the geometry of BK4c and its location within the stratigraphic record of BK, the archaeological level is on top of the point-bar, far away from the main channel and the bedload transport area. Frequently, small secondary channels rework the surface along the top of point-bars during bankfill stages, creating elongated depressions, scours and rills which will be infilled during and after flood events, as has happened in the main site. Secondary flows during a relative high flow stage tends to cluster bones and lithic remains dispersed over the bar surface, into nearby depressions, where they acquire greater stability, as seems

to be the case for Cluster 1. This would explain the presence of anisotropy and refits in the faunal assemblage and the absence of flow sedimentary structures. We examined all specimens and found a total of 16 refits, including three phalanges (BK12-381, BK12-382, BK12-383) belonging to a size 3a animal. Also a distal end of a humerus (BK12-1304) and a proximal end of radius-ulna (BK12-1334a and BK12-1334b) belonging to a *Sivatherium*, would indicate that the post-depositional disturbance of potential hydraulic flows was not strong (Fig. 12). However, it has been documented that specimens deposited within a loamy substrate can be stabilized since the sediment prevents their movement and allow *in locus* preservation despite strong water currents (Schick, 1984).

The spatial randomness tests including all specimens shows an anisotropic distribution; however, a taphonomic spatial analysis does not show any differences in bone preservation and modification according to their length or animal size (Fig. 6). Polished and abraded bone is equally documented in all size categories (Fig. 6). The overlap in the spatial distribution of bones with good and poor preservation also suggests differential modification due to the interaction of bone and soil properties (Fig. 6). This result suggests that BK4c was not significantly modified by water in terms of resedimentation, but that the chemical and physical modification of bones was probably due to circulation of water in a sandy matrix which slowly abraded autochthonous bone (Thompson et al., 2011). Recent studies have shown that assemblages affected even by low energy water flows show anisotropy although being autochthonous (Domínguez-Rodrigo et al., 2014d). Indeed, we find specimens of all shapes and compositions which according to the bootstrapped multiple correspondence analysis indicate that BK4c did not undergo any important hydraulic transport. Water may have rearranged the original assemblage, but the energy of the process was not strong.

### 4.2. Relationship between BK4c and BK4b

The discrete vertical distribution of the BK4b and BK4c assemblages indicates a repeated occupation of the site spread out in short intervals, because of the quasi-continuous nature of the fluvial sedimentation and the paucity of highly-sub-aerially weathered bones (Fig. 13). While both sub-levels show lithological differences and dissimilarities in the degree of bone alteration; BK4b shows an isotropic fabric, which was less affected by water, whereas the BK4c sub-level shows anisotropy and a poor preservation of bone cortical surfaces.

The evenness index for both sub-levels suggests that dense elements are evenly represented regardless of carcass size. This could represent short-distance transport of carcasses by hominins to the site (Faith et al., 2009). This index should be interpreted carefully, since the evenness index from modern Hadza assemblages shows 0.95 (small carcasses)

**Table 7**  
Mean percentages of cut-marked specimens in experimental assemblages and in the BK4c assemblage.

Primary access (Domínguez-Rodrigo, 1997b)				BK level 4c	Secondary access (Gidna et al., 2014)			
Small/mid-size carcasses	Mean	s.d.	95% i.c.	%	Small/mid-size carcasses	Mean	s.d.	95% i.c.
ULB	56.2	19.4	25.4–87	20	ULB	0.92	1.42	0.08–1.76
ILB	40.7	16.1	15.2–66.2	10.5	ILB	2.72	2.24	1.40–4.05
Mid-shafts	8.5	16.5	24.8–74.4	14	Mid-shafts	1.11	1.03	0.50–1.73
End	49.6	19	34.9–56.5	8.3	End	6.18	5.84	2.55–9.80
Total	45.7	6.8	26–64	13	Total	1.81	1.40	0.99–2.64
Primary access (Gidna et al., 2014)				BK level 4c	Secondary access (Gidna et al., 2014)			
Large size carcasses	Mean	s.d.	95% i.c.	%	Large size carcasses	Mean	s.d.	95% i.c.
ULB	9.4	6.50	0–22.15	0	ULB	1	1.41	0–3
ILB	11.85	4.73	2.56–21.13	24	ILB	6.5	3.11	2.18–10.81
Mid-shafts	8.35	4.03	0.45–16.24	8	Mid-shafts	1.25	1.76	0–4.71
End	21.75	13.76	0–47.94	37	End	15.5	4.52	9.22–21.77
Total	10.65	5.44	0–21.32	13	Total	3.7	2.26	0–6.9

Percentages of cut marked specimens in the reported samples of small, medium and large sized carcasses experimentally butchered with stone tools. ULB upper limb bones, ILB intermediate limb bones. Range of variation (95% confidence intervals) for experiments simulating primary and secondary access to fleshed carcasses. Data for experiments replicating primary and secondary access are from Domínguez-Rodrigo, 1997a,b and Gidna et al., 2014.



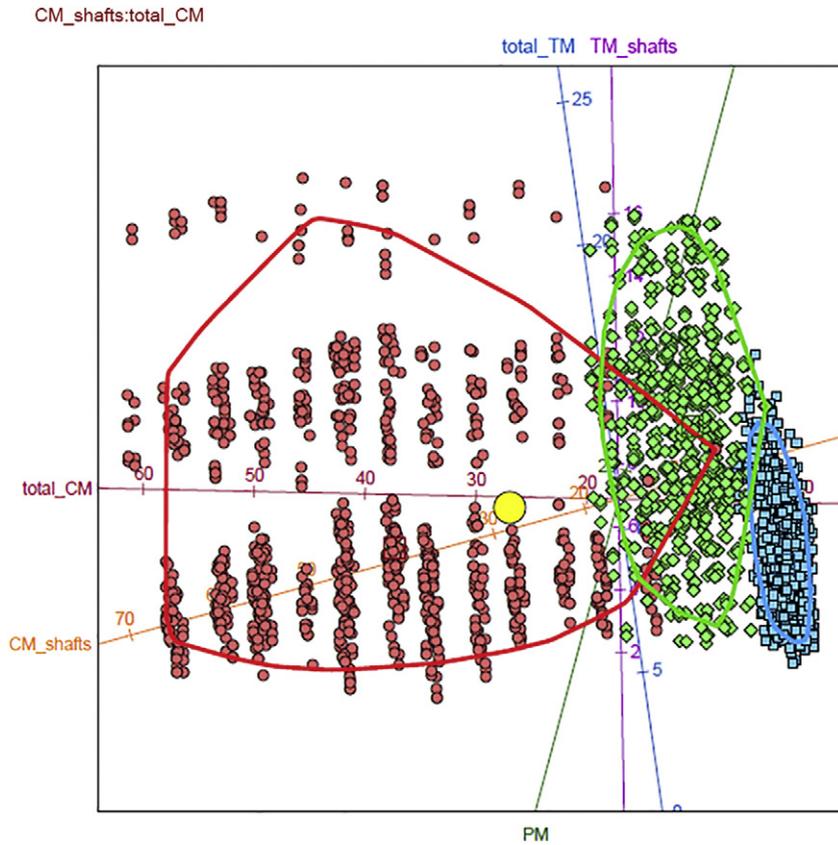
**Fig. 10.** Anatomical connection of three phalanges belonging to a size 3a carcass with several cut marks on the medial and lateral side of the first phalanx. Photo: Mario Torquemada.

and 0.99 (large carcasses) values, when often carcasses were transported several kilometers prior to being accumulated in camps (Egeland, 2007). Skeletal profiles show a similar pattern to some modern human-made assemblages where bones are post-depositionally ravaged by carnivores (Capaldo, 1998).

The analysis of BK4c improves our understanding of the BK4b assemblage and allows a more detailed interpretation of archaeological unit 4 at BK. The percentages of bone surface modifications on long bones reported at BK4b (Domínguez-Rodrigo et al., 2014a) were obtained using the total number of shaft specimens correcting for the number of specimens with dry breakage and poor preservation. In the present analysis, estimates of mark frequencies were obtained also using a correction method based on the well-preserved sample, from which the number of specimens with dry breakage were subtracted, and then added after having been divided by two according to Pickering et al. (2008). This method excludes the specimens with poor preservation, which would bias the preserved frequencies of marks, and compensates for the duplication of specimens resulting from the dry breaking of single specimens, which would artificially inflate the original bone sample.

The low frequency of tooth marks and the high percentage of specimens bearing percussion marks fit well with experiments modeling

primary access to carcasses by hominins. Cut mark distribution at BK4b shows that 62% of marks occur on long limb bones, mainly on mid-shafts from ULB (35%) and ILB (30%), which represent meat-bearing bones. These are the sections that would have already been defleshed by carnivores if they had had primary access to the carcass. On the other hand, the percentage of cut marks at BK4c is similar or slightly lower, but multivariate statistics show that they indicate primary access to carcasses. About 57% of cut marks occur on mid-shafts. Both sets (4b and 4c) present cut marks on ventral and dorsal sides of ribs, suggesting that hominins were not acquiring resources through passive scavenging of carnivore kills. Indeed, many of the cut marks and the percussion marks occur on large faunal specimens indicating that hominins were able to butcher megafauna as suggested by Monahan (1996a,b), Egeland (2007), Domínguez-Rodrigo et al. (2014a), and Organista et al. (2015). The overall taphonomic study of both sub-levels indicates that hominins had a primary role in the accumulation, bulk defleshing and demarrowing of carcasses at BK4. We cannot interpret if the head-limb skeletal representation in all carcass sizes represent a bias introduced by the selective transport of these elements to the site or a bias introduced by the combined action of carnivore postdepositional ravaging and fluvial winnowing of the trabecular axial bones.



**Fig. 11.** Multiple discriminant analysis (using a canonical variate approach) on a bootstrapped sample of experimental sets: primary access to completely fleshed carcasses butchered with stone tools reproducing the H-C model (red alpha bag), secondary access to variously defleshed carcasses in the F-H-H model (green alpha bag), and secondary access to defleshed carcasses from the F-H model (blue alpha bag). The *cm\_shaft* variable displays the frequency of cutmarked shaft specimens compared to the total sample of cutmarked fragments. Data from Domínguez-Rodrigo et al. (2014a).

## 5. Conclusions

The spatial analysis of taphonomic variables shows that fluvial impact on the assemblage was low with only local rearrangement of the preserved specimens, but no significant bone import into the site. The underrepresentation of axials could indicate that an important part of the lighter and more cancellous elements may have been transported away, creating a lag assemblage formed by the densest and most resilient elements. The percentage of cut marks and percussion marks

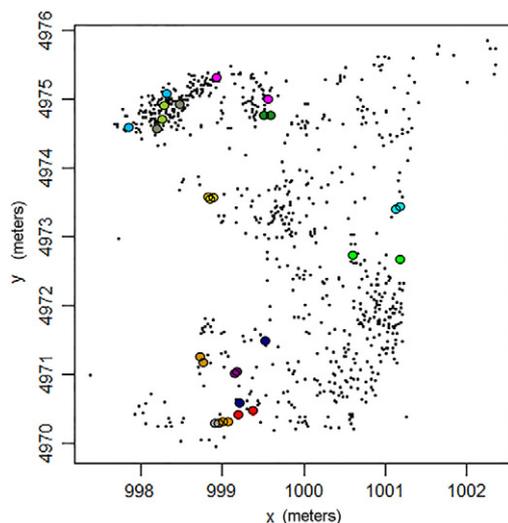
indicates that hominins played a primary role in the accumulation and processing of carcasses, while carnivores played a secondary role. The presence of cut marks and percussion marks on mid-shafts belonging to large carcasses suggest that hominins exploited large amounts of meat and marrow from megafaunal sources. This could be an indication of hominin groups being bigger than traditionally assumed.

The high frequencies of cut marks and percussion marks from such a small excavation suggest that BK4 could potentially contain a much larger number of hominin-modified bones. Indeed, a larger area should be exposed in order to better understand the behavior of early hominins, especially through the spatial analysis of the distribution of materials and make this site comparable to other sites such as FLK Zinj.

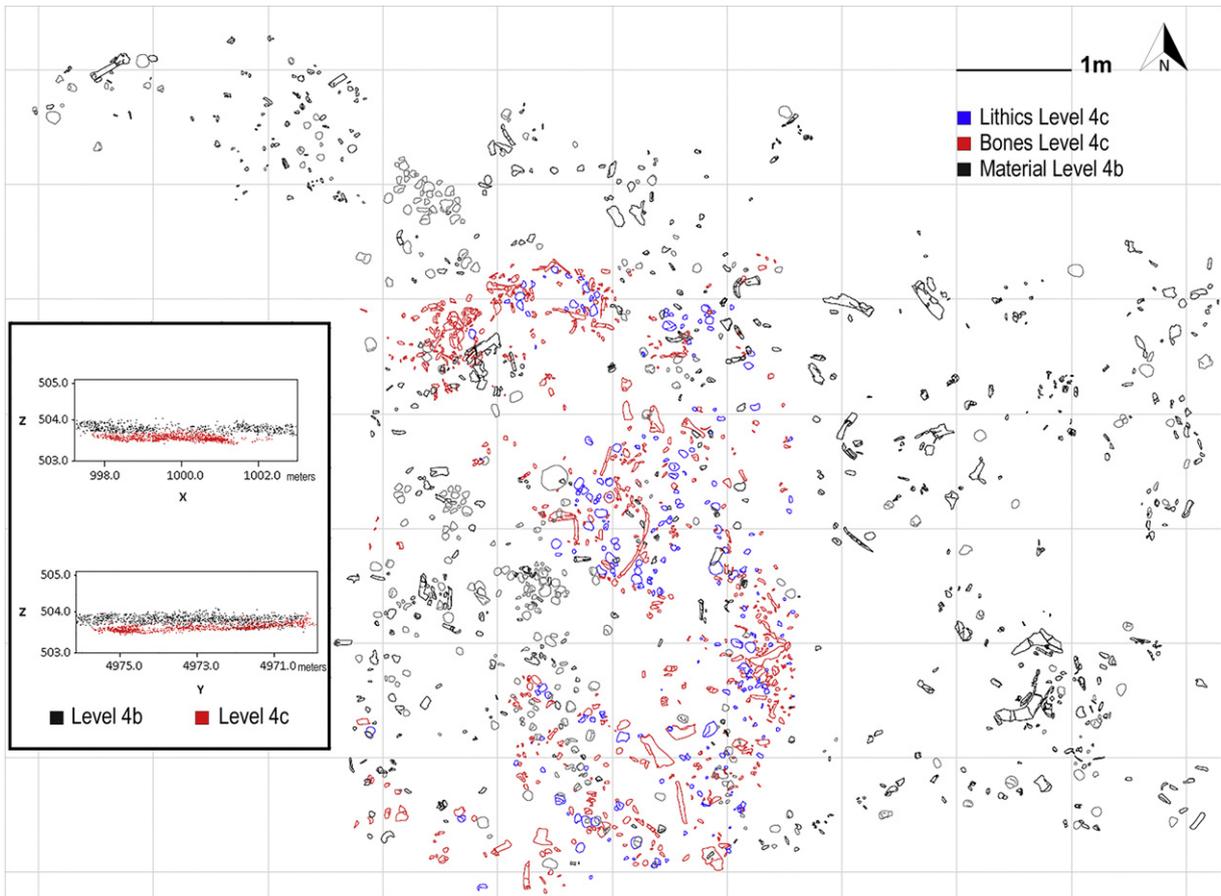
BK occupied an overall open landscape in conjunction with wooded and wet areas as suggested by avian anseriforme remains. The site was situated by the edge of a small river and was repeatedly occupied by hominins producing stone tools on several blank types. These were used to process different animal sizes, from gazelle to *Sivatherium* or elephant. The prolonged period of time represented in the unit 1, indicating sequential reoccupation of the site and the exploitation of such a large array of faunal resources is indicative of non-expedient behaviors of hominins at the site and a site functionality that is potentially different from that inferred for earlier periods, where sites were smaller and showed less marked spatial clustering of lithics and stone tools caused by hominin behavior. The extension of the small area excavated should yield more valuable information to the question of site functionality during the Acheulian times.

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**Fig. 12.** Bone refits (same color icons) at BK4c.



**Fig. 13.** Spatial distribution of the archaeological materials in BK4b (black) and BK4c (red = bones; blue = lithics). Vertical distribution of artifacts and fossils in BK4b (black) and BK4c (red) is shown in the left rectangle.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2017.03.001>.

#### References

- Alcalá, L., 1994. *Macromamíferos neógenos de la fosa Alfambra-Teruel*. Instituto de Estudios Turolenses, Zaragoza.
- Aslan, A., Behrensmeier, A.K., 1996. Taphonomy and time resolution of bone assemblages in a contemporary fluvial system: the East Fork River, Wyoming. *Palaios* 411–421.
- Baddeley, A., Turner, R., 2005. Spatstat: an R package for analyzing spatial point patterns. *J. Stat. Softw.* 12 (6):1–42 URL: [www.jstatsoft.org](http://www.jstatsoft.org) ISSN: 1548-7660.
- Badgley, C., 1986a. Counting individuals in mammalian fossil assemblages from fluvial environments. *PALAIOS* 1 (3), 328–338.
- Badgley, C., 1986b. Taphonomy of mammalian fossils remains from siwalik rocks of Pakistan. *Paleobiology* 12, 119–142.
- Badgley, C., Behrensmeier, A.K., 1980. Paleocology of middle siwalik sediments and faunas, North Pakistan. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 30, 133–155.
- Behrensmeier, A.K., 1975. The taphonomy and paleocology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. *Bulletin of the Museum of Comparative Zoology* 146 (10), 473–578.
- Behrensmeier, A.K., 1982. Time resolution in fluvial vertebrate assemblages. *Paleobiology* 8 (03), 211–227.
- Behrensmeier, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4 (2), 150–162.
- Behrensmeier, A.K., 1990. Transport-hydrodynamics: bones. *Paleobiology: a synthesis*. (D.E.G. Briggs y P.R. Crowther, eds.). Blackwell Scientific Publications, Oxford, pp. 232–235.
- Binford, L.R., 1978. *Nunamiut Ethnoarchaeology*. Academic, New York.
- Blumenschine, R.J., 1988. An experimental model of the timing of hominin and carnivore influence on archaeological bone assemblages. *J. Archaeol. Sci.* 15, 483–502.
- Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominin behavior. *Nature* 333, 763–765.
- Blumenschine, R.J., 1995. Percussion marks, tooth marks and the experimental determinations of the timing of hominin and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 29, 21–51.
- Boaz, D.D., 1982. *Modern Riverine Taphonomy: Its Relevance to the Interpretation of Plio-Pleistocene Hominid Paleocology in the Omo Basin, Ethiopia*. (Ph.D. Dissertation). University of California, Berkeley.
- Boaz, N.T., Behrensmeier, A.K., 1976. Hominid taphonomy: transport of human skeletal parts in an artificial fluvial environment. *Am. J. Phys. Anthropol.* 45, 53–60.
- Borden, F.W., 1971. The use of surface erosion observations to determine chronological sequence in artifacts from a Mojave Desert site. *Archaeological Survey*. Association of Southern California Paper 7.
- Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominins from Koobi Fora, Kenya. *Nature* 291, 574–577.
- Bunn, H.T., 1982. *Meat-Eating and Human Evolution: Studies on the Diet and Subsistence Patterns of Plio-Pleistocene Hominids in East Africa*. (Ph.D. Dissertation). University of California, Berkeley.
- Bunn, H.T., 1983. Evidence on the diet and subsistence patterns of Plio-Pleistocene hominids at Koobi Fora, Kenya, and at Olduvai Gorge, Tanzania. In: Clutton-Brock, J. (Ed.), *Animals and Archaeology. Hunters and their Prey*. B.A.R. International Series Vol. 163, pp. 21–30.
- Bunn, H.T., 1986. Patterns of skeletal part representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. *J. Hum. Evol.* 15, 673–690.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio Pleistocene hominids at Olduvai-gorge, Tanzania. *Curr. Anthropol.* 27, 431–452.
- Brain, C.K., 1967. Hottentot food remains and their bearing on the interpretation of fossil bone assemblages. *Sci. Pap. Namib. Desert Res. Station* 32, 1–7.
- Brain, C.K., 1969. The contribution of Namib Desert Hottentots to an understanding of australopithecine bone accumulations. *Sci. Pap. Namib. Desert Res. Station* 39, 13–22.

- Capaldo, S.D., 1997. Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (Zinjanthropus), Olduvai Gorge, Tanzania. *J. Hum. Evol.* 33 (5), 555–597.
- Capaldo, S.D., 1998. Methods, marks and models for inferring hominin and carnivore behaviour. *J. Hum. Evol.* 35, 323–326.
- Cleghorn, N., Marean, C.W., 2004. Distinguishing selective transport and in situ attrition: a critical review of analytical approaches. *Journal of Taphonomy* 2, 43–67.
- Cleghorn, N., Marean, C.W., 2007. The destruction of skeletal elements by carnivores: the growth of a general model for skeletal element destruction and survival in zooarchaeological assemblages. In: Pickering, T.R., Schick, K., Toth, N. (Eds.), *Breathing life into fossils: Taphonomic studies in Honor of C.K. (Bob) Brain*. Stone Age Institute Press, Bloomington, pp. 38–66.
- Coard, R., Dennell, R.W., 1995. Taphonomy of some articulated skeletal remains: transport potential in an artificial environment. *J. Archaeol. Sci.* 22, 441–448.
- Coard, R., 1999. One bone, two bones, wet bones, dry bones: transport potentials under experimental conditions. *J. Archaeol. Sci.* 26, 1369–1375.
- De Juana, S., Domínguez-Rodrigo, M., 2011. Testing analogical taphonomic signatures in bone breaking: a comparison between hammerstone-broken equid and bovid bones. *Archaeometry* 53, 996–1011.
- De Juana, S., Galán, A., Domínguez-Rodrigo, M., 2010. Taphonomic identification of cut marks made with lithic handaxes: an experimental study. *J. Archaeol. Sci.* 37, 1841–1850.
- Dodson, P., 1973. The significance of small bones in paleoecological interpretation. *University of Wyoming Contributions to Geology*, 12, pp. 15–19 Laramie.
- Domínguez-Rodrigo, M., 1997a. Meat eating by early hominids at FLK Zinj 22 site, Olduvai Gorge, Tanzania: an experimental approach using cut-mark data. *J. Hum. Evol.* 33, 669–690.
- Domínguez-Rodrigo, M., 1997b. A reassessment of the study of cut mark patterns to infer hominid manipulation of fleshed carcasses at the FLK Zinj 22 site, Olduvai Gorge, Tanzania. *Trab. Prehist.* 54, 29–42.
- Domínguez-Rodrigo, M., Pickering, T.R., Semaw, S., Rogers, M.J., 2005. Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. *J. Hum. Evol.* 48 (2), 109–121.
- Domínguez-Rodrigo, M., Barba, R., 2006. New estimates of tooth marks and percussion marks from FLK Zinj, Olduvai Gorge (Tanzania): the carnivore hominin-carnivore hypothesis falsified. *J. Hum. Evol.* 50, 170–194.
- Domínguez-Rodrigo, M., Barba, R., Egeland, C.P. (Eds.), 2007a. *Deconstructing Olduvai: A Taphonomic Study of the Bed I Sites*. Springer Verlag, New York.
- Domínguez-Rodrigo, M., Egeland, C.P., Pickering, T.R., 2007b. Equifinality in carnivore tooth marks and the extended concept of archaeological palimpsests: implications for models of passive scavenging in early hominids. In: Pickering, T.R., Schick, K., Toth, N. (Eds.), *Breathing Life into Fossils: Taphonomic Studies in Honor of C.K. (Bob) Brain*. Stone Age Institute Press, Bloomington, pp. 255–268.
- Domínguez-Rodrigo, M., Mabulla, A., Bunn, H.T., Barba, R., Diez-Martin, F., Egeland, C.P., Espílez, E., Egeland, A., Yravedra, J., Sánchez, P., 2009a. Unraveling hominin behavior at another anthropogenic site from Olduvai Gorge (Tanzania): new archaeological and taphonomic research at BK, Upper Bed II. *J. Hum. Evol.* 57, 260–283.
- Domínguez-Rodrigo, M., de Juana, S., Galán, A.B., Rodríguez, M., 2009b. A new protocol to differentiate trampling marks from butchery cut marks. *J. Archaeol. Sci.* 36, 2643–2654.
- Domínguez-Rodrigo, M., Yravedra, J., 2009c. Why are cut mark frequencies in archaeofaunal assemblages so variable? A multivariate analysis. *J. Archaeol. Sci.* 36 (3), 884–894.
- Domínguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Ashley, G.M., Diez-Martin, F., Barboni, D., Prendergast, M.E., Yravedra, J., Barba, R., Sánchez, A., Baquedano, E., Pickering, T.R., 2010. New excavations at the FLK Zinjanthropus site and its surrounding landscape and its behavioral implications. *Quat. Res.* 74, 315–332.
- Domínguez-Rodrigo, M., Martínez-Navarro, B., 2012. Taphonomic analysis of the early Pleistocene (2.4 Ma) faunal assemblage from AL894 (Hadar, Ethiopia). *J. Hum. Evol.* 62, 315–327.
- Domínguez-Rodrigo, M., Pickering, T.R., Baquedano, E., Mabulla, A., Mark, D.F., et al., 2013. First partial skeleton of a 1.34-million-year-old paranthropus boisei from Bed II, Olduvai Gorge, Tanzania. *PLoS One* 8 (12), e80347. <http://dx.doi.org/10.1371/journal.pone.0080347>.
- Domínguez-Rodrigo, M., García-Pérez, A., 2013. Testing the accuracy of different A-axis types for measuring the orientation of bones in the archaeological and paleontological record. *PLoS One* 8 (7), e68955.
- Domínguez-Rodrigo, M., Bunn, H.T., Yravedra, J., 2014a. A critical re-evaluation of bone surface modification models for inferring fossil hominin and carnivore interactions through a multivariate approach: application to the FLK Zinj archaeofaunal assemblage (Olduvai Gorge; Tanzania). *Quat. Int.* 322–323, 32–43.
- Domínguez-Rodrigo, M., Diez-Martin, F., Yravedra, J., Barba, R., Bunn, H.T., Mabulla, A., Baquedano, E., Uribealrrea, D., 2014b. A taphonomic study of the faunal assemblage of the main site at SHK (Bed II, Olduvai Gorge, Tanzania). *Quat. Int.* 322–323, 153–166.
- Domínguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Baquedano, E., Uribealrrea, D., Pérez-González, A., Gidna, A., Yravedra, J., Diez-Martin, F., Egeland, C.P., Barba, R., Arriaza, M.C., Organista, E., 2014c. On meat eating and human evolution: a taphonomic analysis of BK4b, (Upper Bed II, Olduvai Gorge, Tanzania) and its bearing on hominin megafaunal consumption. *Quat. Int.* 322–323, 129–152.
- Domínguez-Rodrigo, M., Uribealrrea, D., Santonja, M., Bunn, H.T., García-Pérez, A., Pérez-González, A., Panera, J., Rubio-Jara, S., Mabulla, A., Baquedano, E., Yravedra, J., Diez-Martin, F., 2014d. Autochthonous anisotropy of archaeological materials by the action of water: experimental and archaeological reassessment of the orientation patterns at the Olduvai sites. *J. Archaeol. Sci.* 41, 44–68.
- Egeland, C.P., 2007. *Zooarchaeological and Taphonomic Perspectives on Hominid and Carnivore Interactions at Olduvai Gorge, Tanzania*. (Ph.D. Dissertation). Indiana University, Bloomington.
- Egeland, C.P., Domínguez-Rodrigo, M., 2008. Taphonomic perspectives on hominin site use and foraging strategies during the Bed II times at Olduvai Gorge, Tanzania. *J. Hum. Evol.* 55, 1031–1052.
- Emerson, A.E., 1990. *Archaeological Implications of Variability in the Economic Anatomy of Bison Bison*. (Ph.D. Thesis). Washington State University, Washington, DC, U.S.A.
- Faith, J.T., Gordon, A.D., 2007. Skeletal element abundances in archaeofaunal assemblages: economic utility, sample size, and assessment of carcass transport strategies. *J. Archaeol. Sci.* 34, 872–882.
- Faith, J.T., Domínguez-Rodrigo, M., Gordon, A.D., 2009. Long-distance carcass transport at Olduvai Gorge? A quantitative examination of bed I skeletal element abundances. *J. Hum. Evol.* 56 (3), 247–256.
- Fernández-Jalvo, Y., Andrews, P., 2003. Experimental effects of water abrasion on bone fragments. *Journal of Taphonomy* 1, 147–163.
- Fiorillo, A.R., 1991. Taphonomy and depositional setting of Careless Creek Quarry (Judith River formation), Wheatland County, Montana, U.S.A. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 81, 281–311.
- Fisher, N.I., 1995. *Statistical Analysis of Circular Data*. Cambridge University Press, Cambridge.
- Frison, G.C., Todd, L.G., 1986. The Colby Mammoth Site. Taphonomy and Archaeology of a Clovis Kill in Northern Wyoming. University of New Mexico Press, Albuquerque.
- Frostick, I., Reid, I., 1983. Taphonomic significance of sub-aerial transport of vertebrate fossils on steep semi-arid slopes. *Lethaia* 16, 157–164.
- Gidna, A., Kisui, A.B., Domínguez-Rodrigo, M., 2014. An ecological neo-taphonomic study of carcass consumption in Tarangire National Park (Tanzania) and its relevance for human evolutionary biology. *Quat. Int.* 322–323, 167–180.
- Gifford, D.P., 1977. *Observations of Modern Human Settlements as an Aid to Archaeological Interpretation*. (Thesis doctoral). University of California, Berkeley, Ann Harbor, University Microfilms International.
- Gifford, D.P., Behrensmeier, A.K., 1977. Observed formation and burial of a recent human occupation site in Kenya. *Quat. Res.* 8, 245–266.
- Hanson, C.B., 1980. Fluvial taphonomic processes: Models and experiments. In: Behrensmeier, A.K., Hill, A.P. (Eds.), *Fossils in the Making: Vertebrate Taphonomy and Paleocology*. University of Chicago Press, Chicago, pp. 156–181.
- Howard, P., 2007. *Archaeological Survey and Mapping*. Taylor and Francis, London.
- Isaac, G.L., 1967. *Towards the Interpretation of Occupation Debris: Some Experiments and Observations*. 37. *Kroeber Anthropological Society Papers*, pp. 31–57.
- Kaufmann, C., Gutiérrez, M.A., Álvarez, M.C., González, M.E., Massigoe, A., 2011. Fluvial dispersal potential of guanaco bones (*Lama guanicoe*) under controlled experimental conditions: the influence of age classes to the hydrodynamic behavior. *J. Archaeol. Sci.* 38, 334–344.
- Krajcarz, M., Krajcarz, M.T., 2014. The red fox (*Vulpes vulpes*) as an accumulator of bones in cave-like environments. *Int. J. Osteoarchaeol.* 24 (4), 459–475.
- Kreutzer, L.A., 1992. Bison and deer bone mineral densities: comparisons and implications for the interpretation of archaeological faunas. *J. Archaeol. Sci.* 19, 271–294.
- Kreutzer, L.A., 1988. Megafaunal butchering at Lubbock Lake, Texas: a taphonomic reanalysis. *Quat. Res.* 30 (2), 221–231.
- Korth, W.W., 1979. Taphonomy of microvertebrate fossil assemblages. *Ann. Carnegie Museum* 4 (8), 235–285.
- Lam, Y.M., Chen, X., Pearson, O.M., 1999. Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record. *Am. Antiq.* 343–362.
- Leakey, M.D., 1971. *Olduvai gorge. Excavations in Beds I and II, 1960–1963*. 3. Cambridge University Press, Cambridge.
- Lyman, R., 1994. *Vertebrate Taphonomy*. Cambridge University Press, Cambridge.
- Marean, C.W., Spencer, L.M., 1991. Impact of carnivore ravaging of bone in archaeological assemblages. *J. Archaeol. Sci.* 18, 677–694.
- Marean, C.W., Spencer, L.M., Blumenschine, R.J., Capaldo, S.D., 1992. Captive hyaena bone choice and destruction, the Schlep effect and Olduvai archaeofaunas. *J. Archaeol. Sci.* 19, 101–121.
- Marean, C.W., Frey, C.J., 1997. The animal bones from caves to cities: reverse utility curves as methodological artifacts. *Am. Antiq.* 62, 698–711.
- Marean, C.W., Cleghorn, N., 2003. Large mammal skeletal element transport. Applying foraging theory in a complex taphonomic system. *Journal of Taphonomy* 1, 15–42.
- Marean, C.W., Domínguez-Rodrigo, M., Pickering, T.R., 2004. Skeletal element equifinality in zooarchaeology begins with method: the evolution and status of the "shaft critique". *Journal of Taphonomy* 2, 69–98.
- Monahan, C.M., 1996a. *New zooarchaeological data from Bed II, Olduvai Gorge, Tanzania: implications for hominin behavior in the early Pleistocene*. *J. Hum. Evol.* 31, 93–128.
- Monahan, C.M., 1996b. *Variability in the Foraging Behavior of Early Homo: A Taphonomic Perspective from Bed II, Olduvai Gorge, Tanzania*. (Ph.D. Dissertation). University of Wisconsin, Madison.
- Organista, E., Domínguez-Rodrigo, M., Egeland, C.P., Uribealrrea, D., Mabulla, A., Baquedano, E., 2015. *Did Homo erectus kill a Pelorovis herd at BK (Olduvai Gorge)? A taphonomic study of BK5*. *Archaeol. Anthropol. Sci.* 1–24.
- Organista, E., Pernas-Hernández, M., Gidna, A., Yravedra, J., Domínguez-Rodrigo, M., 2016. *An experimental lion-to-hammerstone model and its relevance to understand hominin-carnivore interactions in the archeological record*. *J. Archaeol. Sci.* 66, 69–77.
- Outram, A., Rowley-Conwy, P., 1998. Meat and marrow utility indices for horse (*Equus*). *J. Archaeol. Sci.* 25, 839–849.
- Pante, M., Blumenschine, R.J., 2010. Fluvial transport of bovid bones fragmented by the feeding activities of hominins and carnivores. *J. Archaeol. Sci.* 37, 846–854.
- Pante, M.C., Blumenschine, R.J., Capaldo, S.D., Scott, R.S., 2012. Validation of bone surface modification models for inferring hominin and carnivore feeding interactions, with reapplication to FLK 22, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 63, 395–407.

- Peterhans, J.K., 1990. The Roles of Porcupines, Leopards and Hyenas in Ungulate Carcass Dispersal: Implications for Paleoanthropology. (Doctoral dissertation), University of Chicago, Department of Anthropology.
- Petraglia, M.D., Nash, D.T., 1987. The impact of fluvial processes on experimental sites. *Natural Formation Processes and the Archaeological Record*. (D.T. Nash y M.D. Petraglia, eds.). BAR International Series 352, 108–130.
- Petraglia, M.D., Potts, R., 1994. Water flow and the formation of early Pleistocene artifact sites in Olduvai Gorge, Tanzania. *J. Anthropol. Archaeol.* 13, 228–254.
- Pickering, T.R., Wallis, J., 1997. Bone modifications resulting from captive chimpanzee mastication: implications for the interpretation of Pliocene archaeological faunas. *J. Archaeol. Sci.* 24 (12), 1115–1127.
- Pickering, T.R., White, T.D., Toth, N., 2000. Brief communication: cutmarks on a Plio-Pleistocene hominid from Sterkfontein, South Africa. *Am. J. Phys. Anthropol.* 111, 579–584.
- Pickering, T.R., Marean, C., Domínguez-Rodrigo, M., 2003. Importance of limb bone shaft fragments in zooarchaeology: a response to “on in situ attrition and vertebrate body part profiles” (2002), by M.C. Stiner. *J. Archaeol. Sci.* 30, 1469–1482.
- Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C., Brain, C.K., 2004. New data and ideas on the foraging behaviour of Early Stone Age hominins at Swartkrans cave, South Africa. *S. Afr. J. Sci.* 100, 215–219.
- Pickering, T.R., Egeland, C.P., 2006. Experimental patterns of hammerstone percussion damage on bones: implications for inferences of carcass processing by humans. *J. Archaeol. Sci.* 33, 459–469.
- Pickering, T.R., Egeland, C., Domínguez-Rodrigo, M., Brain, C.K., Schnell, A., 2008. Testing the “shift in the balance of power” hypothesis at Swartkrans, South Africa: hominin cave use and subsistence behavior in the Early Pleistocene. *J. Anthropol. Archaeol.* 27, 30–45.
- Potts, R., 1982. Lower Pleistocene Site Formation and Hominid Activities at Olduvai Gorge, Tanzania. (Ph.D. Dissertation). Harvard University, Cambridge.
- Potts, R., 1988. Early Hominid Activities at Olduvai. *Aldine de Gruyter*, New York.
- Reineck, H.E., Singh, I.B., 1980. Tidal flats. In *Depositional Sedimentary Environments*. Springer Berlin Heidelberg, pp. 430–456.
- Ringrose, T.J., 2012. Bootstrap confidence regions for correspondence analysis. *J. Stat. Comput. Simul.* 83 (10), 1397–1413.
- Schick, K.D., 1984. Processes of Palaeolithic Site Formation: An Experimental Study. (Thesis doctoral). University of California, Berkeley, Ann Harbor, University Microfilms International.
- Schick, K.D., 1987. Experimentally-derived criteria for assessing hydrologic disturbance of archaeological sites. In: Nash, D.T., Petraglia, M.D. (Eds.), *Natural Formation Processes and the Archaeological Record*. BAR International Series 352, pp. 86–107.
- Schiffers, M.B., 1987. *Formation Processes of the Archaeological Record*. University of Utah Press.
- Shipman, P., Rose, J.J., 1988. Bone tools: an experimental approach. In *Scanning electron microscopy in archaeology*. British Archaeological Reports, pp. 303–335.
- Stein, J.K., 1987. Deposits for archaeologists. *Adv. Archeol. Method Theory* 11, 337–395.
- Thompson, C.E., Ball, S., Thompson, T.J.U., Gowland, R., 2011. The abrasion of modern and archaeological bones by mobile sediments: the importance of transport modes. *J. Archaeol. Sci.* 38, 784–793.
- Toots, H., 1965. Sequence of disarticulation in mammalian skeletons. *Rocky Mountain Geology* 4 (1), 37–39.
- Visher, G.S., 1969. Grain size distributions and depositional processes. *J. Sediment. Res.* 39 (3).
- Voorhies, M.R., 1969. Taphonomy and population dynamics of an Early Pliocene Vertebrate Fauna, Knox County, Nebraska. *Contributions to Geology, Special Paper 1*. University of Wyoming.
- White, T.D., 1992. *Prehistoric cannibalism at Mancos 5MTUMR-2346*. Princeton, Princeton University Press.
- Wolff, R.G., 1973. Hydrodynamic sorting and ecology of a Pleistocene mammalian assemblage from California (U.S.A.). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 13, 91–101.
- Woodcock, N.H., 1977. Specification of fabric shapes using an eigenvalue method. *Geological Society of America Bulletin* 88, 1231–1236.
- Yravedra, J., Domínguez-Rodrigo, M., 2009. The shaft-based methodological approach to the quantification of long limb bones and its relevance to understanding hominin subsistence in the Pleistocene: application to four Paleolithic sites. *J. Quat. Sci.* 24, 85–96.
- Yravedra, J., Domínguez-Rodrigo, M., Santonja, M., Rubio-Jara, S., Panera, J., Pérez-González, A., Uribelarrea, D., Egeland, C.P., Mabulla, A., Baquedano, E., 2015. The Larger mammal palimpsest from TK (Thiongo Korongo), Bed II, Olduvai Gorge, Tanzania. *Quat. Int.* 113. <http://dx.doi.org/10.1016/j.quaint.2015.04.013>.