Did *Homo erectus* kill a *Pelorovis* herd at BK (Olduvai Gorge)? A taphonomic study of BK5

By: Elia Organista, Manuel Domínguez-Rodrigo, Charles P. Egeland, David Uribelarrea, Audax Mabulla and Enrique Baquedano

Abstract:

New research and excavations at Bell Korongo (BK, Olduvai Gorge, Upper Bed II) have uncovered a dense concentration of megafauna that contributes to our understanding of *Homo erectus* subsistence strategies around 1.34 Ma. Recent work has yielded clear taphonomic evidence for the exploitation of large-sized animals. The frequency and distribution of cut marks, for example, indicates that hominins enjoyed early access to substantial amounts of meat. This degree of carcass processing, particularly megafauna, suggests that the human group(s) exploiting them were large and had significant nutritional needs. Here, we build upon this work by presenting the first comprehensive taphonomic analysis of the faunal material excavated by the Leakeys at BK between 1952 and 1957 corresponding to 24 *Pelorovis oldowayensis*. Leakey's assemblage was biased due to selective collection of the most readily identifiable specimens, among which long bone shafts were not included. The recent assemblage reflects the relevance of using long bone shafts to overcome the equifinality of the alternative scenarios proposed to explain the accumulation of *Pelorovis*. The analysis of The Olduvai Paleoanthropology and Paleoecology Project's (TOPPP) recent assemblage sheds light on the reconstruction of hominin strategies of carcass acquisition at BK.

Keywords: Olduvai George | Lower Pleistocene archeology | Megafaunal | Taphonomy | Percussion marks | Cut marks | Hunted

Article:

Introduction

Due to the presence of numerous megafaunal remains and their association with stone tools, Bell Korongo (BK, Olduvai Gorge, Upper Bed II) was the first site in the gorge selected by the

Leakeys in the 1950s for large-scale excavation. Eventually, the remains of over 2 doz of *Pelorovis*, *Syncerus*, and *Sivatherium* individuals, in addition to thousands of stone tools, were uncovered within a small area near an ancient river channel. The assemblage was initially interpreted as the earliest evidence for the mass killing of animals exceeding 1000 kg (Leakey 1954; Cole 1963). The spatial association of lithics and bones from these and other animals also led the Leakeys to interpret the site as a swamp to which most of these animals were driven and then dispatched and later consumed by hominins (Leakey 1954; Leakey 1971; Cole 1963). Leakey (1954) argued that the smaller game, represented by a handful of individuals, was hunted elsewhere and transported to the site, which was thought to have functioned as a camp.

The fallout of the hunting-scavenging debate over the past 30 years left little room for interpretations of early Pleistocene hominins as successful hunters, or even exploiters, of megafauna (see review in Domínguez-Rodrigo et al. 2007a). However, the number of fossils representing a diversity of megafaunal taxa (*Pelorovis*, *Syncerus*, and *Sivatherium*) at BK is a taphonomic anomaly that has yet to be satisfactorily explained. Recent excavations within a level stratigraphically just above the Leakey's concentration (BK4b) on an ancient sand bar a few meters away from the "swamp" show that hominins, at least occasionally, were indeed thoroughly exploiting the carcasses of megafauna (Domínguez-Rodrigo et al. 2014a). The question remains as to whether the *Pelorovis* "herd," and the other large animals found in association with it, were accumulated and/or processed by hominins. Here, we present some of the results from recent excavations by TOPPP within the Leakey's main trench in an attempt to improve our knowledge of the formation of this exceptional site.

The BK site was first discovered in 1935, although excavations did not begin until 1952. During the 1950s, several trenches were opened to the west of BK and in 1963 additional trenches were opened in the east. The excavation of a total of 10 trenches revealed a large fossil assemblage rich in bovids, equids, and suids. Along with these herbivores were found a large number of lithic tools classified by Mary Leakey (1971, 1967) as Developed Oldowan type B. In trenches 5, 6, and 7, a particularly dense accumulation of fossils was found, including a minimum of 24 individuals attributed to *Pelorovis oldowayensis* (Fig. 1). One of the *Pelorovis* individuals, a nearly complete skeleton, was found in a vertical position, further suggesting that this particular animal had died in a standing position after sinking in the mud. Due to the occurrence of lithic tools in association with faunal remains, BK was initially described as a largely anthropogenic deposit 1.5 m thick (Leakey 1971). However, the thickness of the deposit in fact varies across the extent of the site. In those areas most distant from the main channel, the vertical thickness of the archeological deposit exceeds 3 m and is composed of several identifiable archeological levels (Domínguez-Rodrigo et al. 2009a).

Taphonomic studies of Leakey's 1963 assemblage by Monahan (1996) and Egeland (2007) determined that the faunal assemblage was largely anthropogenic but preserved evidence of post-depositional carnivore modification. Both authors nevertheless noted the low overall percentage of bones with hominin-imparted marks in comparison to the hominin-carnivore experimental models and other documented anthropogenic sites (e.g., Frida Leakey Korongo (FLK) Zinj). However, because Leakey (1971) did not record the stratigraphic position of the faunal remains, both Monahan (1996) and Egeland (2007) were forced to treat the entire 1.5-m-thick deposit as a

single assemblage. Both researchers therefore cautioned that the faunal assemblage could have resulted from several multi-agent depositional events spread out over many years.
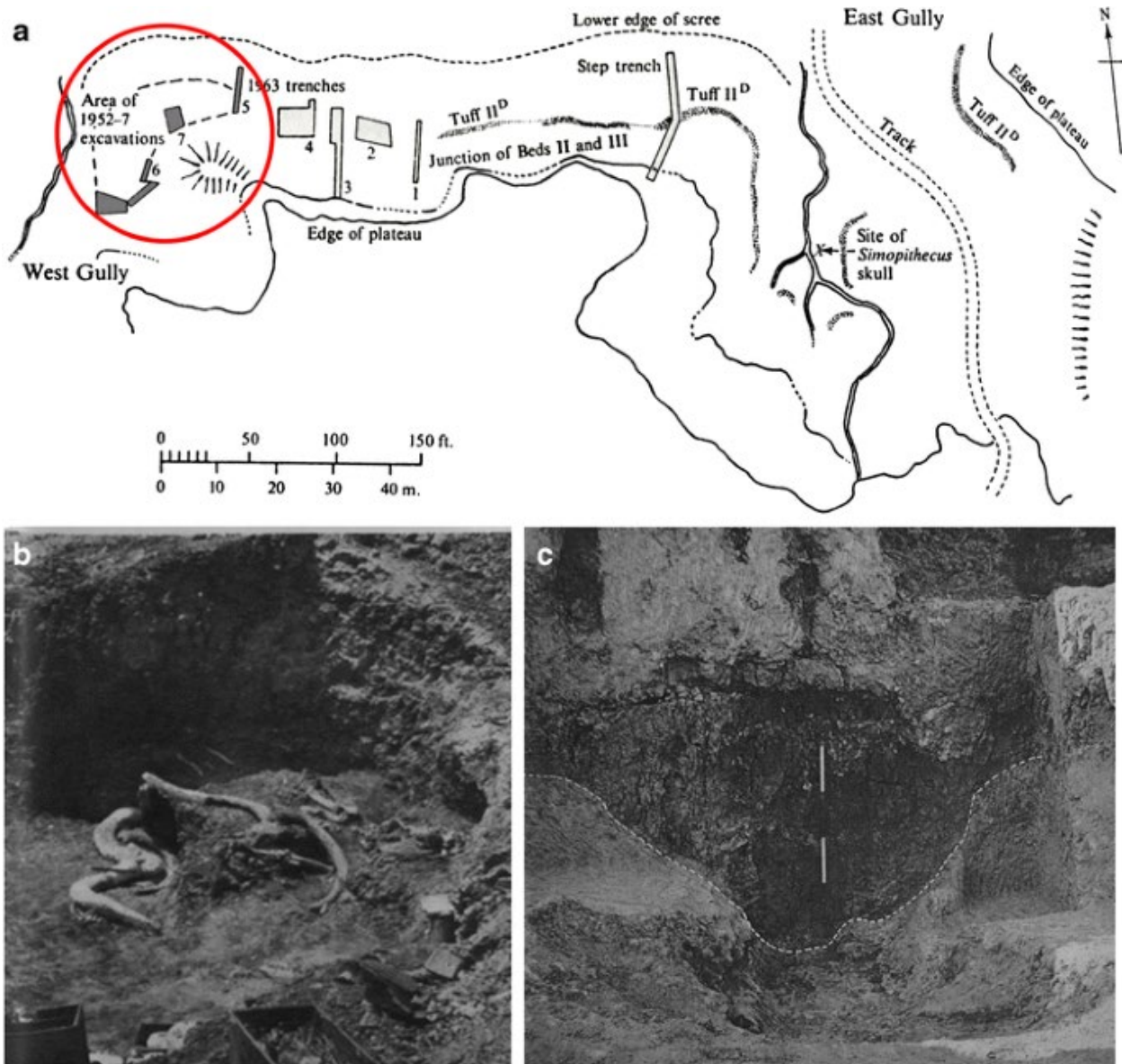

Fig. 1. a Sketch map of BK site (Leakey 1971). **b** *Pelorovis* crania in different vertical intervals (from Leakey 1954). **c** Part of the clay-filled channel that yielded many remains of large mammals (Leakey 1971). *Two vertical lines* indicates the scale = 1 meter

In 2006, TOPPP resumed excavations at BK in the area adjacent to Leakey's trenches 1–4 (Leakey 1971), all of which sample a river bar where the edge of the alluvial plain meets the river channel. Over the course of several years, a paleosurface of 46 m^2 with abundant stone tools and faunal remains was exposed. Several discrete archeological levels were identified. Levels 1 to 3 have a variable depth spanning 15 cm to 1 m, but the majority of the material appears concentrated in 20–15-cm horizons with a limited vertical distribution (Domínguez-Rodrigo et al. 2009a). Level 4 (BK4) preserves a high density of fossils and artifacts within a

vertically discrete horizon that varies between 20 to 40 cm in thickness (Domínguez-Rodrigo et al. 2014a). Taphonomic studies of the assemblages from these four levels suggest that hominins processed carcasses of various sizes, although the frequency of large-sized carcasses exceeds that seen at other Early Pleistocene archeological sites.

This work presents the first detailed taphonomic analysis of the BK material from the 1952–1957 excavations (trenches 6–9) together with materials recently discovered by TOPPP in the same re-excavated area. All these fossils belong to BK5, which is the only identified archeological level in this area of the site, and the one that contained the large concentration of megafauna excavated by the Leakeys in the 1950s. A cursory examination of the remains excavated in the 1950s reveals a good deal of selective retention, with an obvious bias towards large, complete, and taxonomically identifiable fossils. The TOPPP excavations in BK5, on the other hand, practiced complete recovery of remains regardless of preservation or size. As we will see, this excavation protocol has been crucial to understanding the formation dynamics of this level (Fig. 2). These excavations (TOPPP's trench 14) have exposed an area of 9 m^2, and stone tools and the fossil remains of a taxonomically diverse set of carcasses have been retrieved.
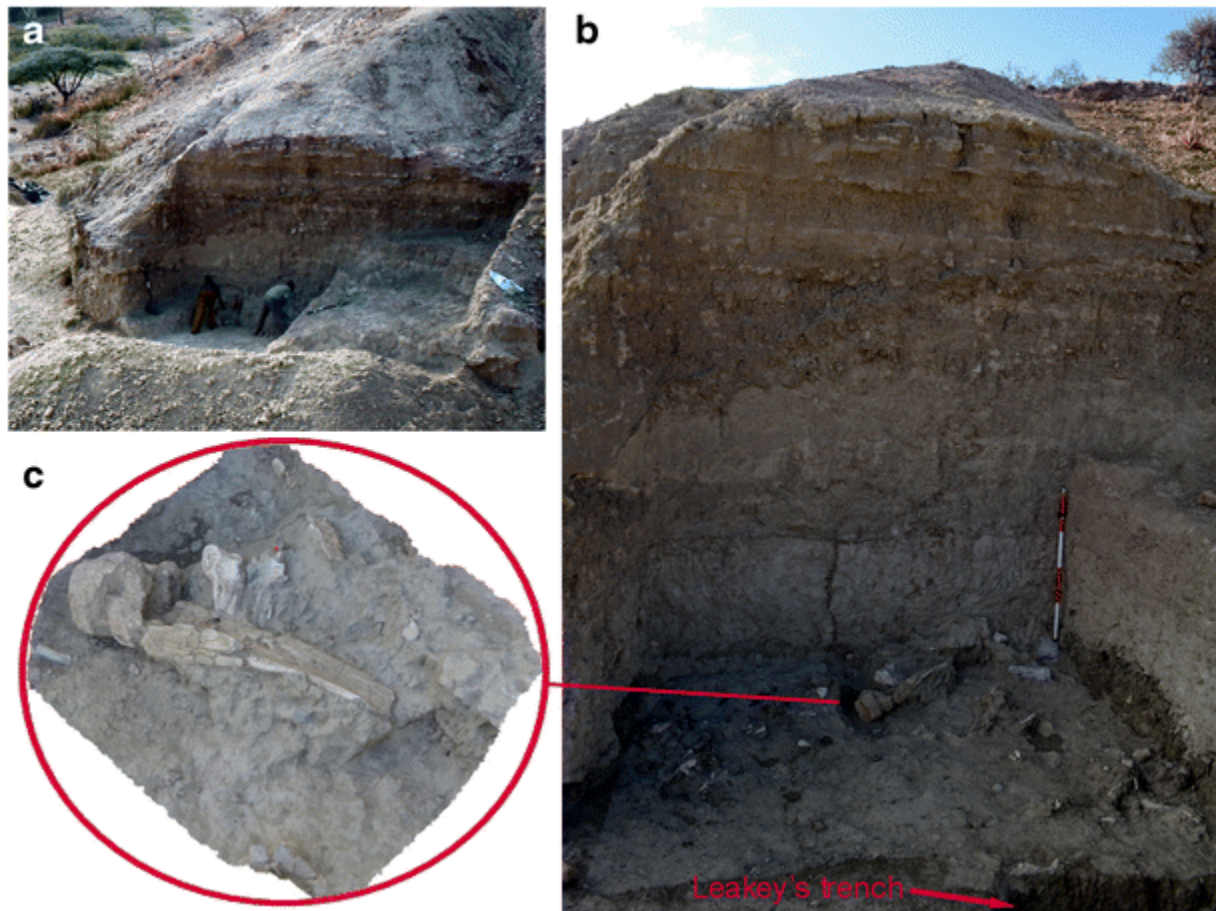

Fig. 2. **a** Insert of the excavation trench into the outcrop. **b** View from the west of trench 14 at BK. **c** Details of the bone accumulation where an elephant tibia can be seen, reconstructed with photogrammetry (see Supplementary Information)

Location and geology

The BK site is located on the south wall of the Side Gorge, 3 km upstream from its junction with the Main Gorge. The Side Gorge is only 20 m deep in the BK area, and therefore only the uppermost part of Bed II in addition to small sections of Bed III and Ndutu are exposed (Fig. 3c). Stratigraphically, the site's archeological deposits are located just above Tuff IID, which was previously dated to 1.2 Ma (Leakey 1971; Hay 1976) and, more recently, to 1.35 Ma (Domínguez-Rodrigo and García-Pérez 2013). In this area, Bed II is made up of the alluvial and fluvial deposits of a medial to distal fan zone and floodplain facies association. The sediment supply originated in the eroding slopes of Lemagrut, a volcano located at the south of the Olduvai Basin.
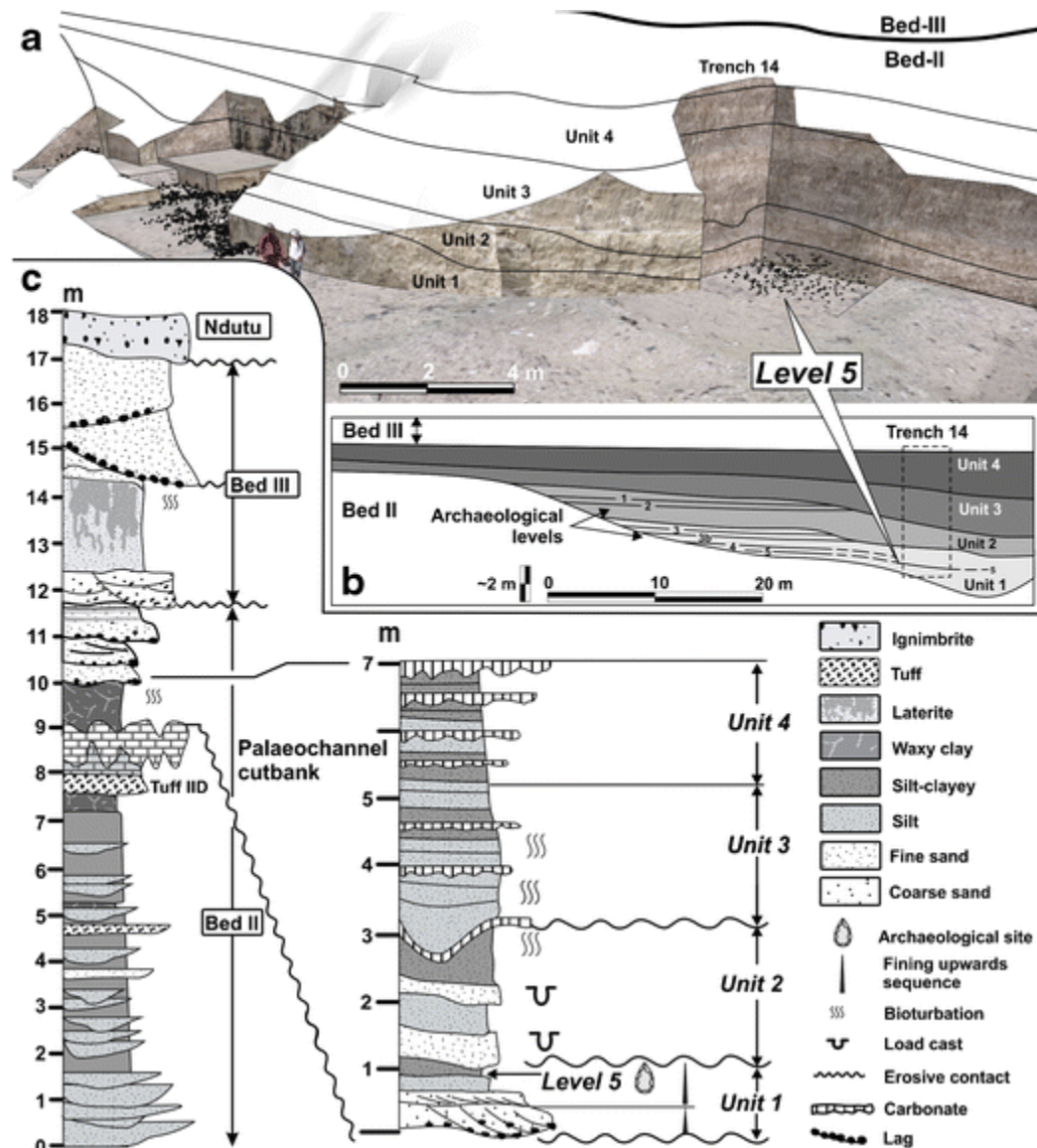
Fig. 3. **a** Location of level 5 at BK. **b** Detailed stratigraphic section of the four units with the different archeological levels identified. **c** Stratigraphic section across the Bed II-Bed III and Ndutu units (locality 94) in the Side Gorge

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 is currently only visible on the paleochannel's right margin. The cutbank 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. 3a, b). 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. Unit 1 contains the archeological levels 3, 3b, 4, and 5 and unit 2, levels 1 and 2. Units 1, 2, and 3 show a lateral accretion sequence to the west. Towards the west, unit 3 partially eroded the top of unit 2, including part of archeological levels 1 and 2. Similarly, unit 2 has partially eroded unit 1, and westward the archeological levels 3, 3b, and 4 disappear (Fig. 3b). The overlying unit 4 completely fills the channel basin and spread over the bank.

Fig. 4. Surface of BK 5 showing fossils and stone tools. This area has been reconstructed in 3D via photogrammetry and can be seen in the Supplementary Information

Level 5, identified in TOPPP's trench 14, lies atop a fining-upward sequence (60 cm thick) that corresponds to a flood event. It begins at the bottom with 30 cm of cross stratified bedload composed of 6 % gravels (<5 mm), 75 % sand, and 19 % silt. The velocity of the flood declined rapidly and the sedimentation process continued with tuffaceous silt, leaving a 20-cm-thick layer of massive, bioturbated, and pale (5Y 7/2) sediment. Finally, the decantation process became dominant as shown by a 10-cm-thick layer of silty-clay, 5 % of which is composed of small alluvial aggregates (clay pellets and pelletoids). These aggregates consist of clay (54 %), silt (35 %), and very fine sand (11 %) (silty-clay) with a brown color (7.5 years/4) massive structure due to bioturbation and trampling. Archeological remains (level 5) are interbedded on top of this silty-clay sediment (Fig. 4). The bones and stone tools accumulated after the flood event once the fine sediment was consolidated. Neither the bedload in the bottom nor the tuffaceous silt contains any bone fragment or artifact. The rise of the phreatic level or perhaps rain water later softened the fluvial deposit, which favored the interbedding of archeological remains into the top

layer and therefore furnished ideal conditions for preservation. The top of the sequence is partially eroded by unit 2, creating a gently tilted contact to the N-NW (<4°) and locally undulated shapes.

Methods

Orientation analysis

Experimental studies have shown that autochthonous groups affected by hydraulic processes can adopt anisotropic fabrics (Domínguez-Rodrigo et al. 2014b; Cobo-Sánchez et al. 2014). In addition to water flows, other processes such as gravity, wind, or trampling can produce orientation patterns (e.g., Frostick and Reid 1983; Petraglia 1987; Olsen and Shipman 1988; Bertran et al. 1997; Lenoble et al. 2008; Eren et al. 2010; Domínguez-Rodrigo et al. 2012; Krajcarz and Krajcarz 2013).

During the excavation of BK5, total stations were used to georeference every archeological item, and 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). 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 1965 and Voorhies 1969; Domínguez-Rodrigo and Garcia-Pérez 2013). Orientation measurements were taken on all specimens with a longitudinal axis at least twice as long as its width (Domínguez-Rodrigo and Garcia-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 archeological 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 used to determine if the orientation of the archeological assemblage was uniform, bimodal, or polymodal (Fisher 1995). The three tests were applied in this study using the functions "rayleigh.test," "kuiper.test," and "watson.test" 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 toward anisotropy. These tests were complemented graphically with a Woodcock diagram (Woodcock 1977).

Faunal analysis

The study of the frequency distribution of bone specimen length conveys information about the preservation biases that have affected a site. The absence or scarcity of small-sized fossil fragments may be the result of water transport as documented in lag assemblages (Schick 1984; Domínguez-Rodrigo and Garcia-Pérez 2013). Fluvial experiments show that transported sets

exhibit specific size distributions and skeletal element patterning, in addition to abrasion, polishing, and a total lack of refits (Toots 1965; Isaac and Behrensmeyer 1997; Voorhies 1969 and Schick 1984). To evaluate the role of hydraulic processes, we examined fragment length distribution in several ways. First, fragment length distribution was tallied for all bone specimens. Second, length distributions for long bone fragments only were considered, since they are denser than cancellous axial bones and have different fragmentation patterns (Domínguez-Rodrigo and Martínez-Navarro 2012). Finally, length distributions for green-broken long bone fragments were analyzed separately, as diagenetic breakage is very common and presents a different size distribution than the original green-broken assemblage. Modifications caused by abrasion and polishing were also documented, as they are evidence of fluvial activities within a site (Behrensmeyer 1975; Schick 1984; Stein 1987; Shipman and Rose 1988; Fernández-Jalvo and Andrews 2003; Thompson et al. 2011). These modifications are not conclusive because, although they may be found in transported assemblages, they may also appear in non-transported assemblages continuously exposed to moving water in detritic sediment (Thompson et al. 2011). In addition, we compared BK5's specimen size distribution to percussion experimental assemblages (Domínguez-Rodrigo 1999) and modern faunal collections obtained from hyena dens: Syokimau (Egeland et al. 2008) and Eyasi (Prendergast and Domínguez-Rodrigo 2008).

Specimens were identified as cranial, axial, or appendicular elements. Long bone shafts were included in all identifications when possible, as it is now well established that minimum number of elements (MNE) estimates differ substantially if shafts are included (e.g., Bunn and Kroll 1986 and Bunn et al. 1988; Marean and Frey 1997; Marean and Kim 1998; Marean 1998; Domínguez-Rodrigo et al. 2007a; Yravedra and Domínguez-Rodrigo 2009). Skeletal part profiles were analyzed by dividing the carcass into anatomical regions: head (horn, skull, and jaw), axial (vertebrae, ribs, pelvis, and scapula), and appendicular (limb bones). Long bones were also divided into three groups: upper limb bones (humerus and femur), intermediate limb bones (radio-ulna and tibia), and lower limb bones (metacarpal and metatarsal) (Domínguez-Rodrigo 1997a).

Skeletal part profiles were based on the number of identified specimens (NISP) and estimation of the MNE. Skeletal profiles were analyzed by carcass size according to Bunn's (1982) size groups: sizes 1 and 2 reach up to 120 kg (small carcasses), sizes 3a and 3b range from 120 to 450 kg (medium-sized carcasses), and sizes 4–6 with live weights exceeding 450 kg (large carcasses).

MNE estimates took into account the size, side, landmarks, and age of each identifiable specimen. The final result was obtained using a manual overlap approach. This integrative approach as outlined by Yravedra and Domínguez-Rodrigo (2009) was built on the bone section methods of Patou-Mathis (1984, 1985), Münzel (1988), and Delpeche and Villa (1993). Shafts were divided into equally sized sectors (proximal, mid, and distal) independent of muscle insertion sites. This method also takes into account the criteria used by Barba and Domínguez-Rodrigo (2005) for the identification of elements using features of long bone diaphyses such as cortical bone thickness, cross-sectional shape, and properties of the medullary surface.

Bones, after their initial deposition on the ground, are susceptible to a number of taphonomic processes that affect their survival, such as subaerial weathering (Behrensmeyer 1978), sediment compaction (Klein and Cruz-Uribe 1984: 69–75; Marean 1991), and especially carnivore modification (Brain 1967, 1969, 1981; Capaldo 1998a; Marean et al. 1992; Pickering et al. 2003; Richardson 1980). Skeletal part profiles are typically 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), based on optimal foraging theory, argued that decisions to transport certain parts of a carcass can be best interpreted using high-survival elements. This can be measured using Shannon's evenness index: $(\Sigma pi * \ln pi)/\ln S$, here pi is the proportional representation of a particular skeletal element measured using minimum animal units (MAU), and S is the number of elements per type. If transport decisions made by humans depend on the distance from acquisition locus to camp, a high frequency of cranial and long limb bones would indicate an unselective transport of carcasses over short distances or no transport (Bunn et al. 1988; Bartram 1993a, b; Faith and Gordon 2007; Faith et al. 2009). A lower value of Shannon's index implies selective transport, most likely due to long transport distance. This index was obtained for BK5 for each carcass size group.

In order to evaluate the abundance of skeletal elements, MAU were calculated and standardized (%MAU) (Binford 1978; Binford and Bertram 1977). Element representation measured by %MAU was examined in relation to the modified general utility index (MGUI). Indices were obtained from Binford (1978) for small carcasses, Outram and Rowley-Conwy (1998) for medium-size carcasses, and Emerson (1990) for large carcasses.

Controlling for bone density is important because destructive processes like carnivore ravaging and water flows tend to eliminate or at least underrepresent less dense bones (axial and epiphyseal sections) (Voorhies 1969; Brain 1967, 1969; Marean and Spencer 1991; Marean et al. 1992; Capaldo 1998b; Pickering et al. 2003). Composition of the BK5 faunal assemblage was analyzed by Spearman correlations between %MAU and raw mineral density of wildebeest (Lam et al. 1999) and bison (Kreutzer 1992).

A detailed analysis of bone surface modifications is essential because it provides crucial information on the involvement of hominins and/or carnivores in the formation and modification faunal assemblages. Cortical surface preservation was evaluated by taking into consideration the stages of subaerial exposure (Behrensmeyer 1978) and water-induced modification. Cortical surfaces were examined with 10×40 hand lenses under a strong oblique light source. Several types of marks were identified: cut marks, percussion marks, tooth marks, trampling, abrasion/polish, and biochemical marks (Bunn 1981; Domínguez-Rodrigo et al. 2009b; Blumenschine 1988, 1995; Blumenschine and Selvaggio 1988; Pickering and Egeland 2006; Behrensmeyer et al. 1986). 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. 2008; 2003; Barba and Domínguez-Rodrigo 2005). The identification of tooth and percussion marks was made following the methods and diagnostic criteria outlined by Blumenschine (1988, 1995) and Blumenschine and Selvaggio (1988, 1991). Cut marks were identified and tallied following Bunn (1981), Domínguez-Rodrigo (2002) and Domínguez-Rodrigo et al. (1997a,

2009b, 2010). Since comparisons of archeological data with modern experimental assemblages involve processes that do not apply to the latter (diagenetic bone breakage or differential bone surface preservation), mark frequencies were calculated both in raw and corrected form following Pickering et al. (2008). This method attempts to correct for both the inflation of specimen frequency through dry breakage and artificial reduction of mark frequencies on poorly preserved cortical surfaces.

Tooth and percussion mark frequencies were tallied by element and bone section for long limb bones. The bone sections were divided into proximal epiphysis, diaphysis, and distal epiphysis according to Blumenshine (1988). Near-epiphyseal parts were not included in analyses because of problems with the way this part is defined and thus how marks are counted (Domínguez-Rodrigo and Barba 2006). Cut marks were tallied by element and section following Domínguez-Rodrigo (1997a). The precise location of the marks relative to areas identified by muscle and tendon insertions or areas representing flesh bulk extraction was also taken into account (Domínguez-Rodrigo et al. 2007a; Barba and Domínguez-Rodrigo 2008).

Primary and secondary access to carcasses by hominins produces different anatomical associations and frequencies of tooth, cut, and percussion marks. Such associations can only be detected when analyzing simultaneously all marks in reference to different experimental models: Felid-Hominin (F-H) (Gidna, et al. 2014), Felid-Hominin-Hyenid (F-H-H) (Domínguez-Rodrigo 1997a and b), and Hominin-Carnivore (H-C) (Domínguez-Rodrigo 1997b; Pante et al. 2012; Gidna et al. 2014).

Finally, we note that, due to sedimentary processes, several skeletal remains exhibit an adhering carbonate matrix that prevents their inclusion in the present taphonomic study.

Statistical analysis

We used a multiple discriminant analysis (MDA) to differentiate among distinct experimental groups and to classify the BK5 data accordingly. This type of statistical analysis was selected because whereas principal component analysis (PCA) maximizes sample variance, MDA 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.rg) was used for this analysis. Graphic representation of the biplot was carried out with the R library "BiplotGUI."

Results

Analysis of Leakey's *Pelorovis* herd

Faunal analysis

Leakey's excavations at BK5 recovered a total of 228 specimens belonging to 24 adult individuals of *P. oldowayensis* (Table 1). When the NISP was quantified by skeletal part and

bone section, we found a complete lack of isolated diaphyseal fragments (Table 2). The likely reason for this bias is that Leakey did not collect the more heavily fragmented material, which was more difficult to identify.

Table 1. Minimum number of individuals documented in BK5 by TOPPP and Leakey

	MNI BK5		MNI Leakey's material
	Juvenile	**Adult**	**Adult**
Hystrix sp.		1	
Theropithecus sp.		1	
Crocodylus sp.		1	
Antilopini	1	1	
Antidorcas recki		1	
Alcelaphini		1	
Pelorovis oldowayensis		1	24
Metridiochoerus compactus	1	1	
Equus oldowayensis	1	2	
Giraffa sp.		1	
Hippopotamus sp.	1	1	
Elephas sp.		1	
Total		17	24

Skeletal part profiles measured by MNE show that cranial and vertebral elements are the most abundant bones (Fig. 5). However, when comparing MNE to minimum number of individuals (MNI), following Brain (1981) percent survival method, skeletal representation varies substantially. In this case, and relative to what is expected based on the assemblage's MNI, cranial elements are well represented whereas the axial skeleton and compact bones are rare (Fig. 5).
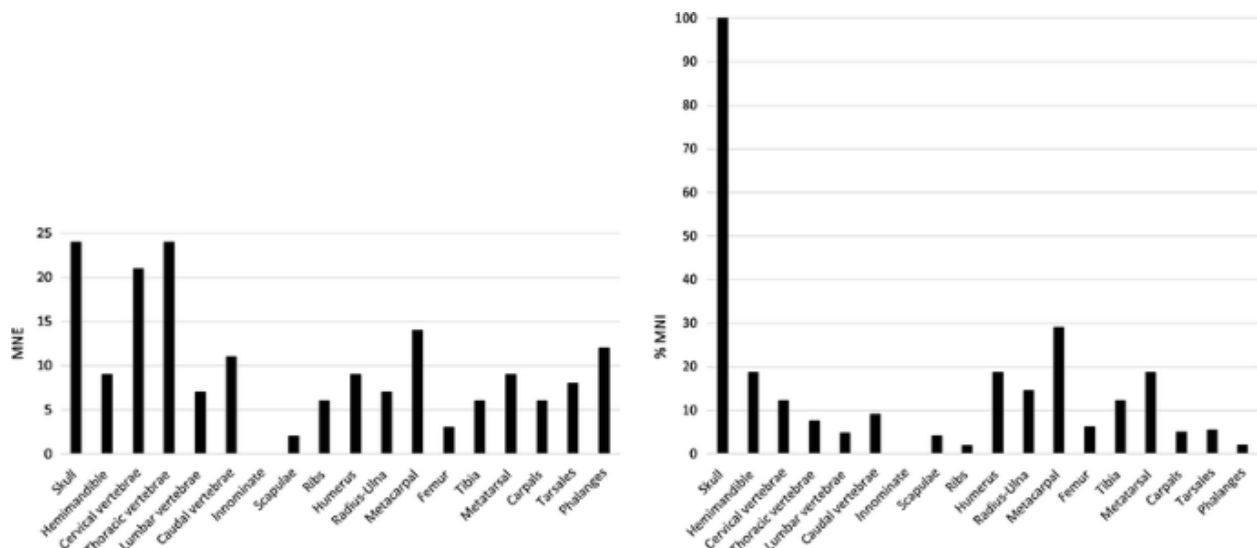
Fig. 5. *Left*: Frequency of skeletal parts measured by MNE for Leakey's *Pelorovis* herd. *Right*: MNE to MNI skeletal representation for Leakey's *Pelorovis* herd

Table 2. Number of specimens identified (NISP) and minimum number of elements according to the carcass size presents in BK5 (TOPPP) and in the *Pelorovis*/*Syncerus* Leakey collection from trenches 6–9

	BK level 5 (TOPPP)						BK level 5 (Leakey)	
	Small size		Medium size		Large size		Large size	
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
Horn	4	4	5	2	2	1		
Skull		1	1	9	2	23	23	
Hemimandible			2	1	5	3	10	9
Teeth	2	2	7	5	10	4		
Cervical vertebrae					1	1	21	21
Thoracic vertebrae			1	1	3	1	32	24
Lumbar vertebrae			1	1			7	7
Caudal vertebrae							11	11
Indet. vertebrae			1					
Scapulae			3	3	3	2	2	2
Ribs	2	2	4	2	8	2	31	6
Innominate	1	1	3	2	3	2		
Humerus		3		3		6		9
Complete							2	
Proximal end			1				3	
Shaft	3		8		11			
Distal end	1		1		1		6	
Radius-ulna		2		5		4		7
Complete							2	
Proximal end	1		2		1		2	
Shaft	1		2		5			
Distal end			3				4	
Metacarpal						3		14
Complete					1		2	
Proximal end							2	
Shaft					2			
Distal end					1		13	
Femur		1		3		2		3
Complete							2	
Proximal end					1		11	
Shaft	2		4		5			
Distal end								
Tibia		3		2		5		6
Complete							2	
Proximal end			1		1			
Shaft	5				16			
Distal end			1				5	
Metatarsal		1		2		2		9
Complete							1	
Proximal end	1		1				3	
Shaft	2		2		2			
Distal end			1				5	
Patella			3	3				

	Small size		Medium size		Large size		Large size	
			BK level 5 (TOPPP)				**BK level 5 (Leakey)**	
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
Carpals/tarsals			2	2	1	1	6/8	6/8
Phalanges			1	1	1	1	12	12
Other								
ULB	1				3			
ILB			1		1			
LLB	1		2					
Indet.	6		12		28			
Total	33	19	76	40	125	42	228	177

ULB upper limb bones, *ILB* intermediate limb bones, *LLB* lower limb bones

The paucity of low-density specimens like axial elements and compact bones (Voorhies's groups I and II) could be the result of their susceptibility to water transport. It is also possible that these remains were consumed post-depositionally by carnivores. However, a high percentage of the vertebral elements (63 out of 71) and the long bones recovered (11 out of 65) are complete bones. This, together with the presence of epiphyses ($n = 54$), the virtual lack of tooth marks (see below), and the underrepresentation of abraded and polished elements, argues against water flows or carnivores as culprits for the distortion of the original assemblage (Table 2). Although the rarity of low-density elements in the assemblage indicates that biotic or abiotic post-depositional processes did occur, the initial bias during the collection of the assemblage precludes further interpretations.

The analysis of bone surfaces reveals that 58 % of the sample is poorly preserved. Subaerial weathering on the long bones ($n = 62$) shows several stages: stage 0 has been documented on 55 % ($n = 34$) of the sample, stage 1 on 15 % ($n = 9$), stage 2 on 22 % ($n = 13$), stage 3 on 2 % ($n = 2$), and stage 4 on 2 % ($n = 2$) of the sample. This variability, together with the differential preservation patterns, imply several different moments of faunal deposition over time. The specimens belonging to stage 0 indicate that part of the assemblage was accumulated over a short period of time or, alternatively, at relatively constant pace over a longer period of time with high sedimentation rates. We discard the interpretation of a mass drowning or killing suggested by Leakey (1954) because the remains were found in different vertical intervals throughout the 1-m deposit excavated by Leakey (1954, 1971).

A total of 51 % of the assemblage shows green breakage; the remainder preserves evidence of dry breakage. Green breakage is present mostly on long bones, and tooth marks and percussion marks were only documented on 9 % ($n = 4$) and 4.5 % ($n = 1$) of bones, respectively. Cut marks were found on only 2.2 % ($n = 2$) of the specimens. The low percentage of tooth marks on long bone epiphyses and on the axial skeleton suggests limited carnivore involvement with the carcasses.

Analysis of TOPPP's trench 14

Orientation analysis

A stereographic projection of specimens shows a uniform distribution and a horizontal trend (Fig. 6a). The average mean direction is about 90° east–270° west as shown by the 95 % confidence interval of the stereogram, but, as the crow data show (Fig. 6b), no clearly identifiable anisotropic orientation exists. The Woodcock diagram also suggests an isotropic fabric for the assemblage with a von Mises distribution K concentration value of 0.08 (Fig. 6c). The values obtained from the Rayleigh test ($R = 1.78$, $p \geq 0.16$), Kuiper test ($V = 1.5$, $p \geq 0.10$), and Watson test ($U^2 = 0.12$, $p \geq 0.15$) show a uniform distribution where the null hypothesis of isotropy cannot be rejected. This all suggests an autochthonous assemblage in which post-depositional processes do not seem to have been prominent. Furthermore, the dearth of specimens with abrasion and/or polishing ($n = 7$; 2.2 %) led us to reject the hypothesis that water flows were a significant agent of post-depositional bias.
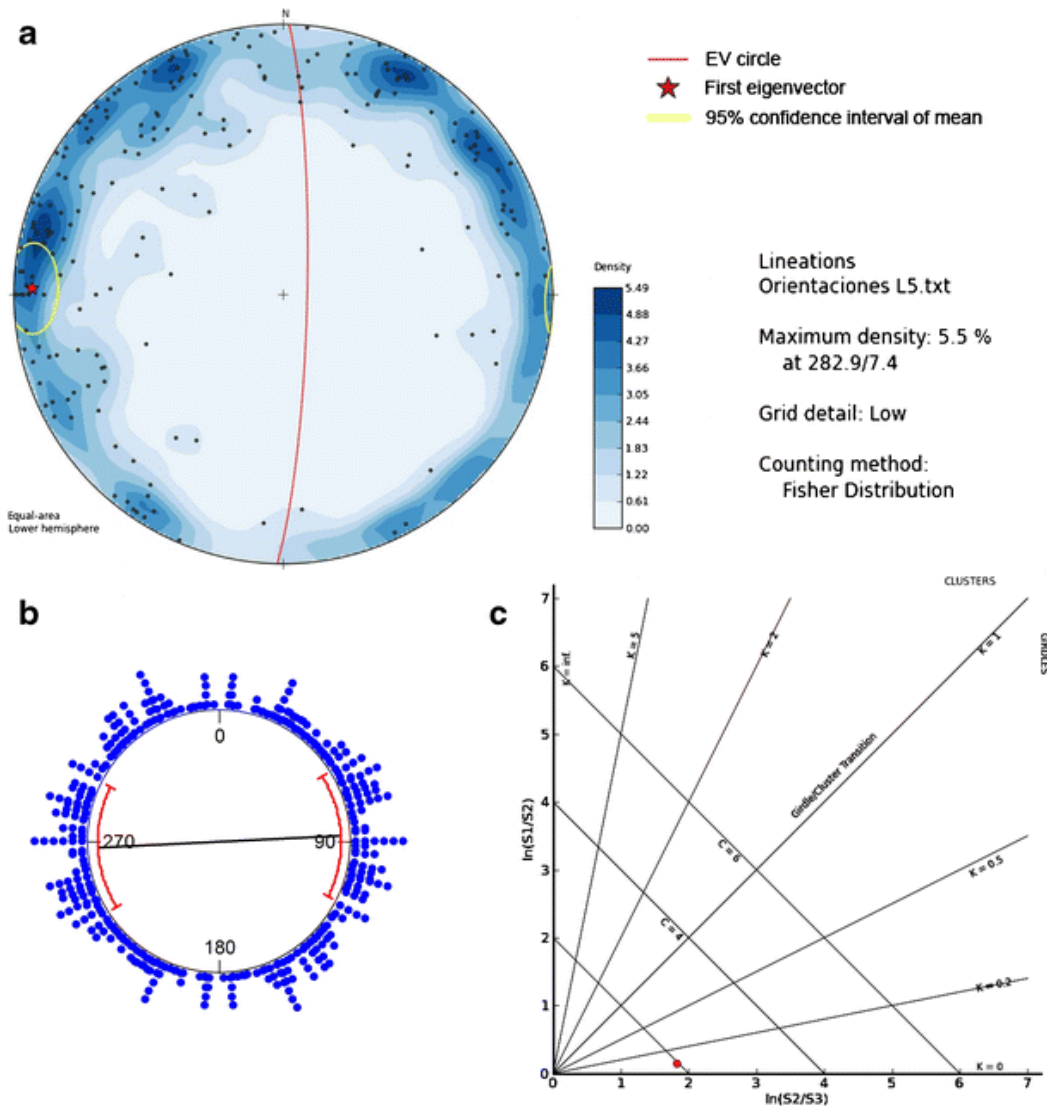
Fig. 6. a Stereogram showing the azimuth orientation of all specimens with a longitudinal axis from BK5. The first eigenvalue comprising most of the inertia is presented here, as well as the confidence interval of the mean trend/plunge orientation (in *yellow*). b Data crown showing uniform bone orientation. c Woodcock diagram shows an isotropic fabric for the assemblage, with von Mises distribution K concentration values under 0.2

Faunal analysis

The BK5 bone assemblage is composed of 306 specimens, of which only 245 could be attributed to carcass size, resulting in a minimum of 17 individuals (Table 1). Small carcasses are the least represented ($n = 33$) followed by medium- ($n = 76$) and large-sized ($n = 125$) carcasses (Table 2). A total of 59 lithic objects were also recovered from BK5 (Fig. 7). The diversity of taxa found in this level suggests a variety of habitats. Hippopotamus and crocodiles reveal the existence of permanent water while the presence of equids, alcelaphines, and *Theropithecus* suggest an open environment with riverine woodlands (Domínguez-Rodrigo et al. 2014c).
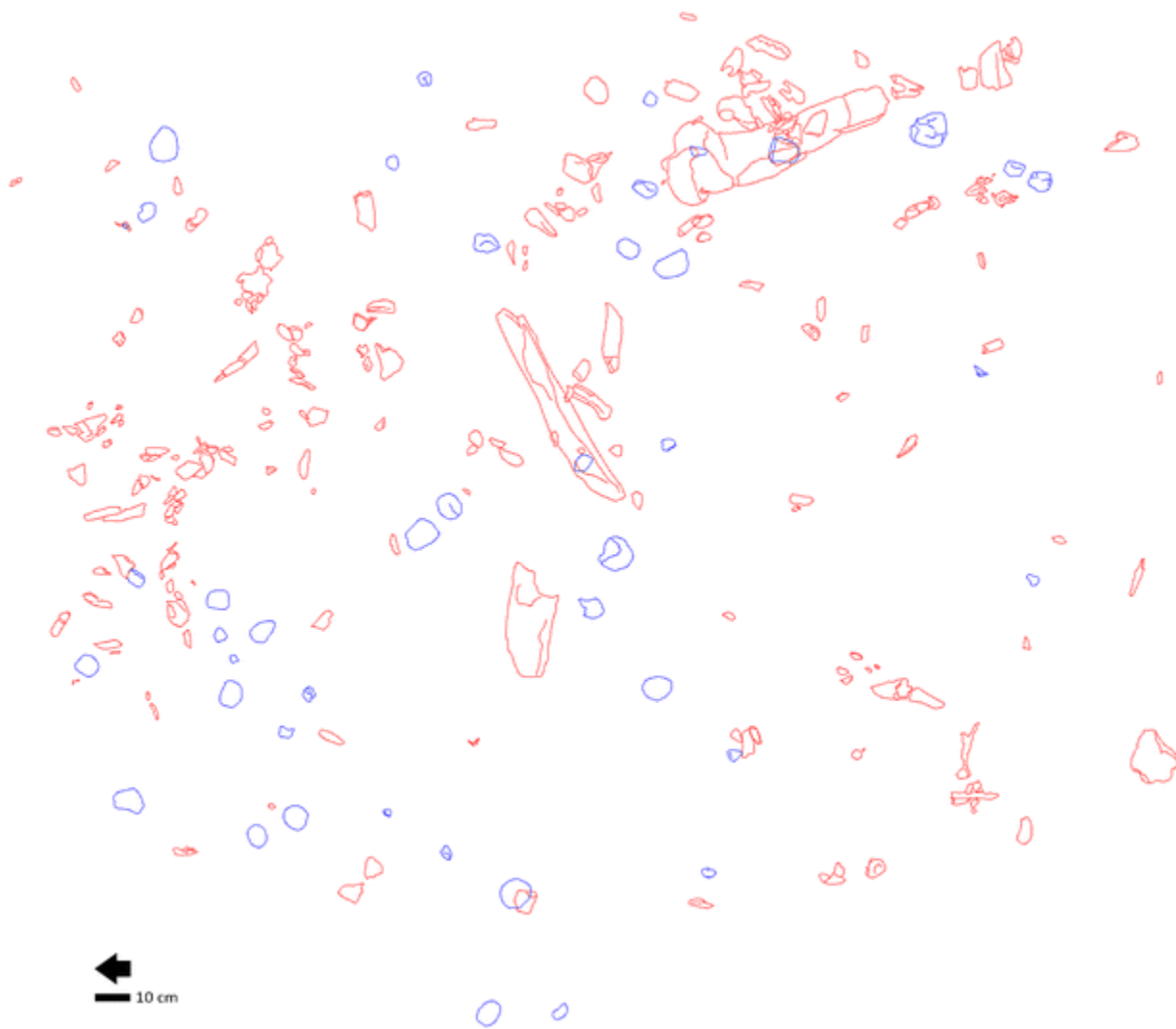
Fig. 7. Map of the archeological remains. *Blue color* represents the lithic artifacts and *red color* the fossil bones at BK5. This map shows the close spatial association between lithics and bones

The analysis of size distribution shows that specimens smaller than 20 mm are poorly represented, specimens longer than 100 mm are the most abundant, and fragments between 31 to 50 mm fall in between (Fig. 8). This suggests that biotic agents like carnivores or physical process like water flows may have modified the assemblage, despite the isotropy documented

above. However, the presence of impact flakes and refitting fragments ($n = 12$) suggest that such disturbance was only minor. When green-broken long bones only are considered, the pattern is slightly different. In this case, fragments smaller than 40 mm are underrepresented, which mirrors carnivore bone breaking (Fig. 8). However, it is important to emphasize that no adequate hammerstone-broken experimental sample exists to compare the specimen size distribution of long bones from large animals.
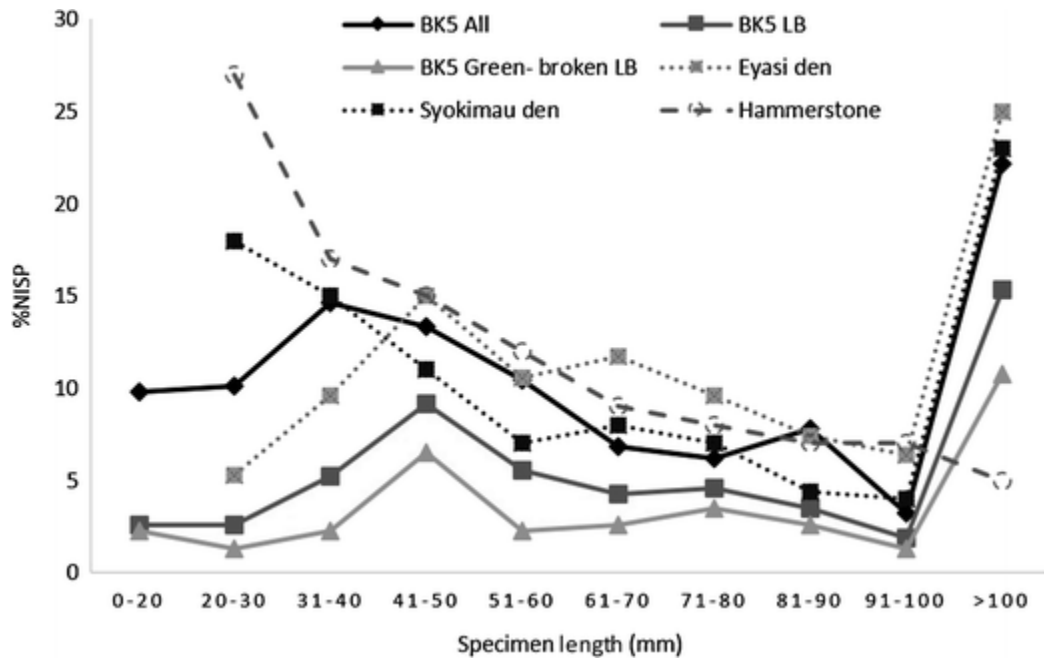
Fig. 8. Distribution of frequencies of bone specimen lengths from BK5, divided according to the complete sample, long bones only, and green-broken long bones only, compared to actualistic samples from Domínguez-Rodrigo (1999), Egeland et al. (2008), Prendergast and Domínguez-Rodrigo (2008)

The comparison between MNE and MNI shows that the survival frequencies for the three carcass sizes are dominated by dense bones (cranial and long bones). In contrast, elements and bone portions composed of cancellous tissue, such as vertebrae, ribs, scapulae, compact bones, and long bone epiphyses, are underrepresented (Fig. 9). Small carcasses show a higher percentage of cranial elements and long bone shafts relative to axial elements belonging to ribs and innominates. Compact bones are completely absent (Fig. 9a). Medium-sized carcasses show a similar pattern of skeletal representation. However, medium-sized carcasses show a higher percentage of cranial elements and long bone shafts with a moderate presence of compact bones (carpals, tarsal) and the axial skeleton, mostly scapulae and innominates, and a more reduced presence of ribs and vertebrae. The low frequency of bones with cancellous tissue is also documented for long bones, although the presence of epiphyseal ends from humeri, radii, tibiae, and metatarsals is documented (Fig. 9b). Large carcasses reflect the same general pattern, although long bone shafts, especially from humeri and tibiae, are better represented (Fig. 9c).
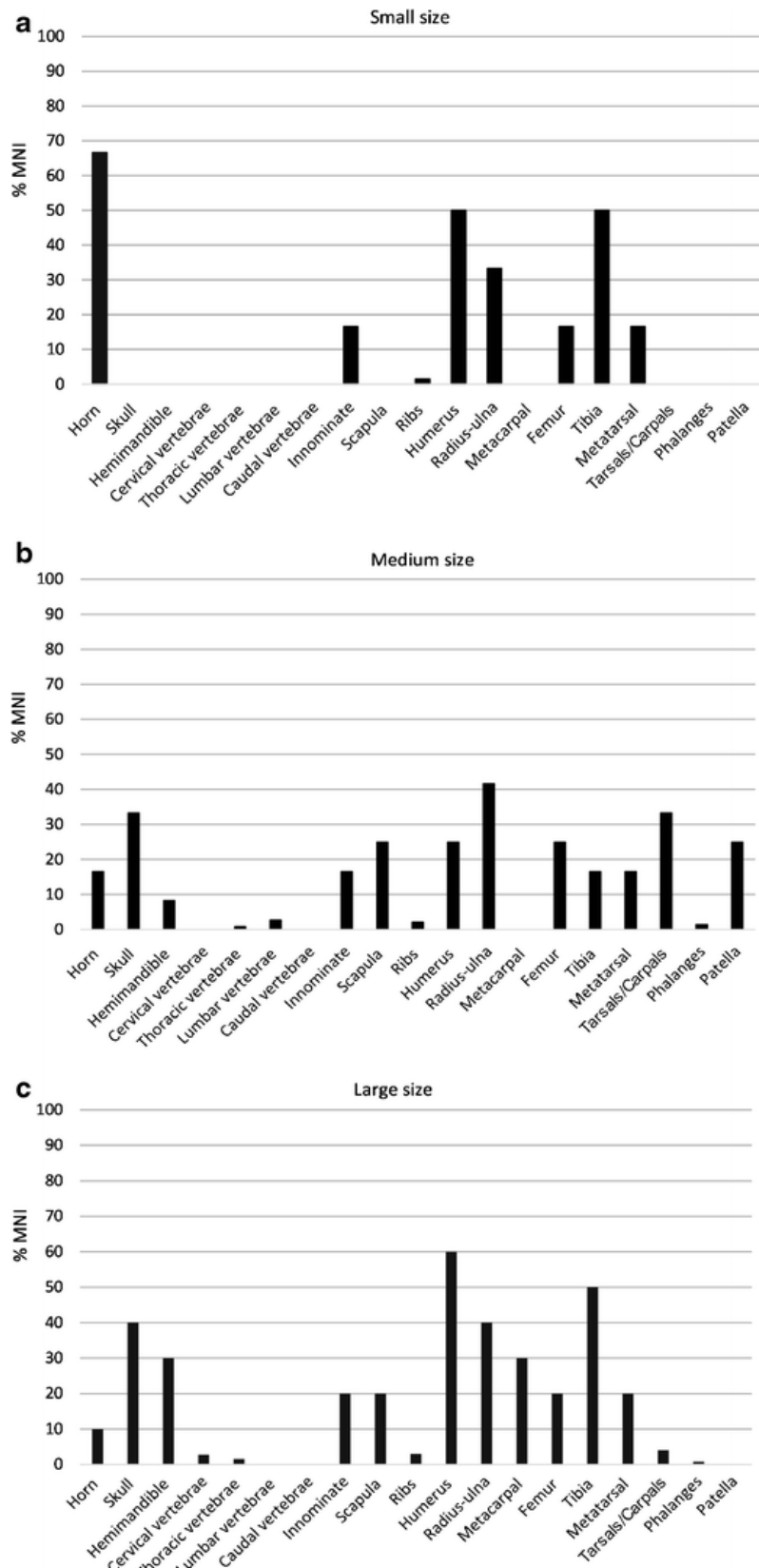
Fig. 9. MNE to MNI skeletal representation frequency at BK5 from **a** small carcasses, **b** medium-sized carcasses, and **c** large carcasses
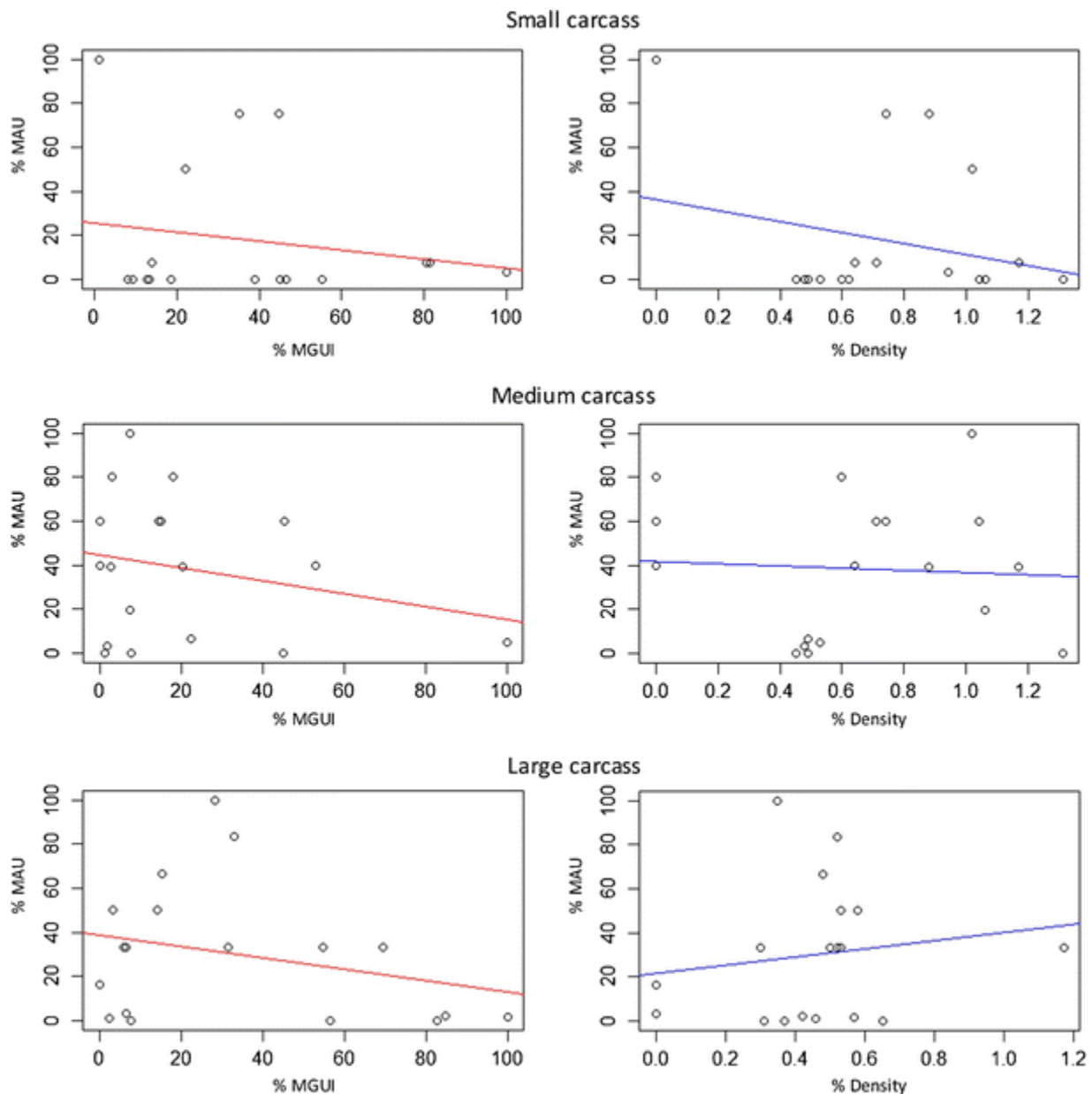
Fig. 10. *Left*: Scatterplots of %MAU values against %MGUI values for each carcass size at BK5. MGUI values are obtained from Binford (1978) for small carcasses, Outram and Rowley-Conwy (1998) for medium carcasses, and Emerson (1990) for large carcasses. *Right*: Scatterplots of %MAU values against %density values for each carcass size at BK5. Density values are obtained from Lam et al. (1999) for small and medium carcasses and Kreutzer (1992) for large carcasses

Skeletal profiles quantified through Shannon's evenness index (Faith and Gordon 2007) show values of 0.83 for small carcasses and 0.89 for medium-sized carcasses. These values suggest uneven carcass representation, possibly the result of selective transport. Large carcasses appear to be more evenly represented (index = 0.95), which suggests that these carcasses were initially acquired at or very near the site itself. The low representation of axial elements, epiphyseal ends, and compact bones at BK5 could be due to the destruction of certain skeletal parts by carnivore

ravaging and/or removal by weak hydraulic flows. The low values of Shannon's index for small and medium-sized carcasses are due to the underrepresentation of cranial and metapodial remains. This is most likely accounted for by selective transport than by post-depositional ravaging by carnivores (Faith et al. 2009). A high evenness index would be expected if complete carcasses had been transported and undergone subsequent post-depositional deletion.

When comparing %MAU to MGUI, it can be observed that small carcasses are represented largely by bones of low utility. Low-density bones are also well represented, which suggests that small carcasses did not suffer significant post-depositional modification (Fig. 10). MAU and MGUI percentages for medium-sized carcasses also show few bones of high utility (Fig. 10). However, the comparison of %MAU with density shows a clear presence of high-yielding and low-density elements (Fig. 10). Large carcasses also show a high percentage of low-yielding and high-density anatomical units, indicating also a post-depositional bias against less dense parts (Fig. 10, Table 3). The low-utility profiles of small and medium-sized carcasses can be explained by a combination of small sample size and the virtual non-existence of the axial skeleton. If these carcasses were selectively transported to the site, axial bones were either abandoned at the acquisition site or deleted if deposited at the consumption site. This is not contradictory with early access and carcass selection to carcasses by hominins. Bunn (2007) has shown that Hadza transport the flesh from the axial skeleton separately from the axial bones themselves, which are transported also (especially vertebrae) only because they have the boiling technology to extract grease from them. In the absence of such a technology, there would be no incentive for the transport of axial bones.

Table 3. Spearman's statistics for the relationship between %MAU and %MGUI, %MAU and density for carcass size and skeletal parts at BK5

Spearman's	BK level 5		
%MAU—%MGUI	Small	Mid-size	Large
cor	0.10	−0.08	−0.17
p	0.66	0.73	0.48
%MAU—density			
cor	0.12	−0.04	0.15
p	0.61	0.87	0.53
Spearman's	Appendicular BK level 5		
%MAU—%MGUI	Small	Mid-size	Large
cor	0.80	0.22	0.53
p	0.004	0.58	0.17
%MAU—density			
cor	0.22	0.58	−0.58
p	0.52	−0.22	0.12

For these reasons, when considering only long bone representation for each carcass size, the correlations between meat yield and part representation become positive. The higher meat-yielding elements are best represented for all three carcass sizes. Long bones of small carcasses show a positive correlation with meat yield (Fig. 11). Medium-sized carcasses also show a higher percentage of meat-yielding anatomical units, but in contrast with small carcasses, the least dense bones are also well represented, indicating that medium carcasses suffered only minimal

post-depositional carnivore ravaging (Fig. 11). Large carcasses have not undergone any bias. High yield and low-density long bones are both well represented (Fig. 11, Table 3).
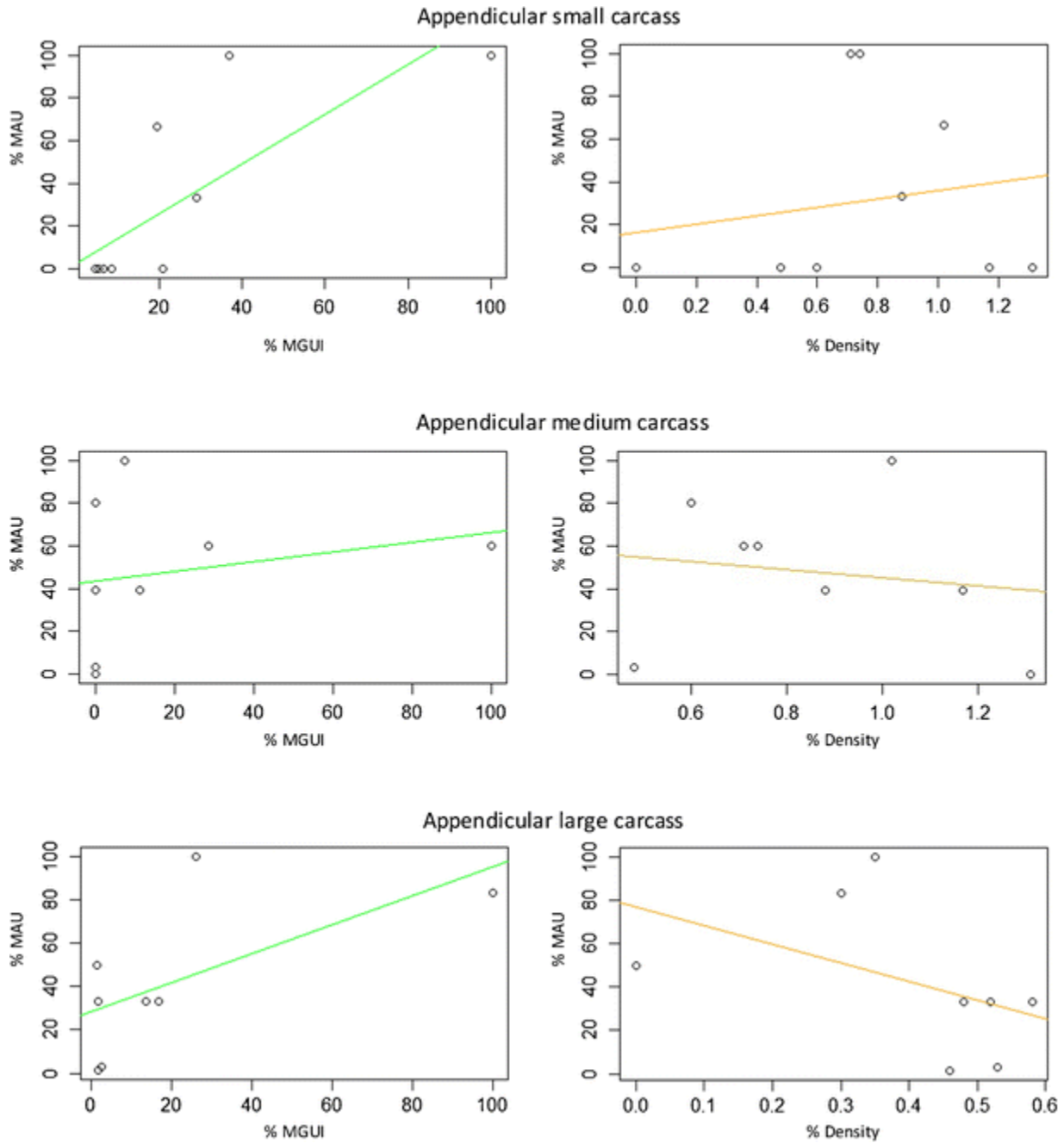
Fig. 11. *Left*: Scatterplots of %MAU values against %MGUI values for each appendicular carcass size at BK5. MGUI values are obtained from Binford (1978) for small size carcass, Outram and Rowley-Conwy (1998) for medium-sized carcass, and Emerson (1990) for large-sized carcass. *Right*: Scatterplots of %MAU values against %density values for each size carcasses at BK5. Density values are obtained from Lam et al. (1999) for small and medium-sized carcasses and Kreutzer (1992) for large carcass

These data suggest that BK5 hominins were transporting protein-rich anatomical portions of small and medium-sized animals into the site, whereas large carcasses were obtained and processed directly on the spot.

A total of 224 specimens from the BK5 assemblage bear green or/and dry breakage. Of these, 94 (30 %) specimens showed dry breakage and 129 (42 %) green breakage. Fifty-one percent ($n = 48$) of the dry breaks occur on long bones, followed by 39.9 % ($n = 30$) on axial bones and 17 % ($n = 16$) on cranial bones. Most of the green breakage (80.6 %; $n = 104$) was documented on long bones with the remainder documented on axial bones (14.7 %; $n = 19$) and a few cranial specimens (4.6 %; $n = 6$). The high percentage of green breakage suggests that some agent (hominin and/or carnivore) broke the bones at the site and in doing so generated specimens with diaphyseal circumference type 1 ($n = 170$) followed of specimens of type 3 ($n = 18$) and finally of type 2 ($n = 10$). Comparison with experimental assemblages shows that BK5 is more similar to the hammerstone-percussion model from Pickering and Egeland (2006) than to any other alternative scenario.

Only eight notches were documented: one "single" notch, three "incomplete," and four "double overlapping." Unfortunately, this sample was quantitatively insufficient to address the agent of bone breakage. However, the presence of percussion marks and a few impact flakes ($n = 6$) indicate that dynamic loading (i.e., .hammerstone) was probably responsible for the fragmentation of long bones.

Of the 306 specimens in the study sample, only 31 % ($n = 95$) have well-preserved cortical surfaces. The remainder ($n = 65$; 21.2 %) has been affected by chemical modifications caused by the presence of water or prolonged exposure to humidity. About 8.4 % ($n = 8$) of the assemblage was affected by water but still retained well-preserved cortical surfaces. A total of 11.4 % ($n = 35$) of the sample is affected by biochemical modifications caused by fungi and bacteria, and only 2.2 % ($n = 7$) is affected by abrasion or polishing of their surfaces due to water action.

Subaerial weathering was evaluated on a sample of 131 specimens. Fifty-five percent ($n = 72$) of these specimens displayed weathering stage 0, 16.7 % ($n = 22$) stage 1, 18.3 % ($n = 24$) stage 2, and 9.9 % ($n = 13$) stage 3. Stages 4 and 5 were not documented on the assemblage. In relative terms, these data indicate a very long exposure time for at least some of the remains accumulated at BK5, probably spanning several years, although over half of the sample was apparently accumulated relatively quickly.

Trampling was observed on 21.2 % ($n = 65$) of the total assemblage and on 30.5 % ($n = 29$) of the well-preserved subsample. Microabrasion was documented on 9.8 % ($n = 30$) of the total sample. Both modification types suggest that sediment abrasion (macro and micro) affected the assemblage even though a majority of the encasing sediments were clay.

The percentage of tooth-marked bones from total sample is 4.2 % ($n = 13$), which includes specimens that could not be classified to carcass size. Only one tooth-marked shaft specimen (0.3 %), from a small-sized carcass, was documented (Fig. A1 Supplementary information). Medium-sized carcasses preserve four tooth marks (1.3 %) one each on a scapula, vertebra, rib, and radius. Large carcasses show tooth marks on eight specimens (2.6 %): one hemimandible,

two scapulae, one cervical vertebra, one rib, and two radii-ulnae. However, to compare tooth mark percentages from BK5 to analogical experimental samples, which are made up only of green-broken bone fragments, it is necessary to correct for the bias introduced by dry breakage and poor cortical preservation in the BK5 assemblage (Pickering et al. 2008). The corrected estimate for tooth marks on shafts with good cortical preservation ($n = 85$) and dry breakage ($n = 23$) is 5.4 % ($n = 4$). If we consider only the long bone subsample, the percentage of tooth-marked specimens is slightly higher (Table 4). Three tooth-marked specimens have been documented (5.6 %): one epiphysis of a proximal ulna, one mid-shaft radius, and one mid-shaft of a metacarpal, all corresponding to large carcasses (Fig. 12) except one mid-shaft radius corresponding to a medium-sized carcass (3.2 %) (Fig. A2 Supplementary information) and one mid-shaft tibia belong to small carcasses (5.5 %) (Fig. A1 Supplementary information). Such low frequencies of tooth-marked long bone shafts are below the 95 % confidence interval of experiments modeling secondary access of carnivores to hammerstone-broken bones by hominins (Blumenschine 1988; Blumenschine 1995; Capaldo 1997).

Table 4. Frequencies of bone surface modifications according to carcass size for all bone specimens on each skeletal part from level 5

	Small size			Mid-size			Large size		
	TM	PM	CM	TM	PM	CM	TM	PM	CM
Horn	0/4	0/4	0/4	0/5	0/5	0/5	0/2	0/2	0/2
Skull				0/1	0/1	0/1	0/9	0/9	0/9
Teeth	0/2	0/2	0/2	0/7	0/7	0/7	0/10	0/10	0/10
Mandible				0/2	0/2	0/2	1/5 (20)	0/5	2/5 (40)
Cervical vertebrae							1/1 (100)	0/1	0/1
Thoracic vertebrae				0/1	0/1	0/1	0/3	0/3	0/3
Lumbar vertebrae				1/1 (100)	0/1	0/1			
Sacral vertebrae									
Vertebrae indet.				0/1	0/1	0/1			
Pelvis	0/1	0/1	0/1	0/3	0/3	0/3	0/3	0/3	0/3
Scapula				1/3 (33)	0/3	0/3	2/3 (66.6)	0/3	1/3 (33)
Ribs	0/2	0/2	0/2	1/4 (25)	0/4	0/4	1/8 (12.5)	1/8 (12.5)	0/8
Humerus									
Proximal end				0/1	0/1	0/1			
Shaft	0/3	1/3 (33)	0/3	0/8	1/8 (12.5)	0/8	0/11	0/11	1/11 (9)
Distal end	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1
Radius-Ulna									
Proximal end	0/1	0/1	0/1	0/2	0/2	0/2	1/1 (100)	0/1	0/1
Shaft	0/1	0/1	0/1	1/2 (50)	1/2 (50)	0/2	1/5 (20)	2/5 (40)	2/5 (40)
Distal end				0/3	0/3	0/3			
Metacarpal									
Complete							0/1	0/1	0/1
Proximal end									
Shaft							1/2 (50)	0/2	1/2 (50)
Distal end							0/1	0/1	0/1
Femur									
Proximal end							0/1	0/1	0/1
Shaft	0/2	0/2	0/2	0/4	0/4	1/4 (25)	0/5	2/5 (40)	0/5
Distal end									

	Small size			Mid-size			Large size		
	TM	PM	CM	TM	PM	CM	TM	PM	CM
Tibia									
Proximal end				0/1	0/1	0/1	0/1	0/1	0/1
Shaft	1/5 (20)	1/5 (20)	0/5				0/16	1/16 (6.2)	4/16 (25)
Distal end				0/1	0/1	0/1			
Metatarsal									
Proximal end	0/1	0/1	0/1	0/1	0/1	0/1			
Shaft	0/2	0/2	0/2	0/2	0/2	0/2	0/2	0/2	1/2 (50)
Distal end				0/1	0/1	0/1			
Patella				0/3	0/3	0/3			
Carpals/tarsals				0/2	0/2	0/2	0/1	0/1	0/1
Phalanges				0/1	0/1	0/1	0/1	0/1	0/1
Other									
ULB	0/1	0/1	0/1				0/3	0/3	0/3
ILB				0/1	0/1	0/1	0/1	0/1	0/1
LLB	0/1	0/1	0/1	0/2	0/2	0/2			
Indet.	0/6	0/8	0/8	0/12	0/12	0/12	0/28	3/28 (9.6)	028
Total	1/33 (3)	2/33 (6)	0/33 (0)	4/75 (5.3)	2/75 (2.6)	1/75 (1.3)	8/125 (6.4)	9/125 (7.2)	12/125 (9.6)
Epi. fragments	0/3 (0)	0/3 (0)	0/3 (0)	0/12 (0)	0/12 (0)	0/12 (0)	1/7 (14.2)	0/7 (0)	0/7 (0)
Shaft fragments	1/15 (6.6)	2/15 (13)	0/15 (0)	1/19 (5)	2/19 (10)	1/19 (5)	2/46 (4.3)	7/46 (11.9)	9/46 (21.4)

Numbers in numerators are for the number of specimens bearing marks; numbers in denominators are the total number of specimens; numbers in parentheses are the percentage

TM tooth marks, *CM* cut marks, *PM* percussion marks, *ULB* upper limb bones, *ILB* intermediate limb bones, *LLB* lower limb bones

Percussion marks appear on 4.2 % ($n = 13$) of the total sample. Using the well-preserved long bone subsample corrected for dry breakage, the percussion mark percentage rises to 14.9 %. Eleven percent of the small carcass fragments show percussion marks (two percussed shaft fragments, one each from a humerus and tibia) (Fig. A1, Supplementary information). Medium-sized carcasses are percussion marked at a rate of 6.4 %, corresponding to two shaft fragments (humerus and radius) (Fig. A2, Supplementary information), whereas large carcass shafts are marked at a rate of 13.2 % ($n = 7$) (Fig. 12, Table 4). These frequencies of percussion-marked long bone shafts on large carcasses fall within the 95 % confidence interval of hammerstone-to-carnivore experiments (Blumenschine 1988, 1995; Capaldo 1995). The sample of percussion-marked bones from small and medium carcass is too small for a meaningful behavioral analysis.

The cut mark percentage for the total sample is 4.2 % ($n = 13$). Most of these marks occur on long limb bones ($n = 9$), cranial bones ($n = 2$), and axial bones ($n = 1$) from large-sized carcasses. Only a single femur shaft from a medium-sized carcass bears cut marks (Fig. A2, Supplementary information). Using the well-preserved sample corrected for dry breakage, cut mark frequencies rise to 16.3 %. Overall, nearly all cut marks appear on larger carcasses. A total of nine long limb bone specimens show cut marks (21.4 %), documented on shaft fragments of a humerus, radius, ulna, metacarpal, tibia, and metatarsal (Fig. 12, Table 4). Cut marks are also found on two hemimandibles and one scapula. All cut marks documented are the result of defleshing except those on the metapodials, which are related to skinning and scraping of periosteum.
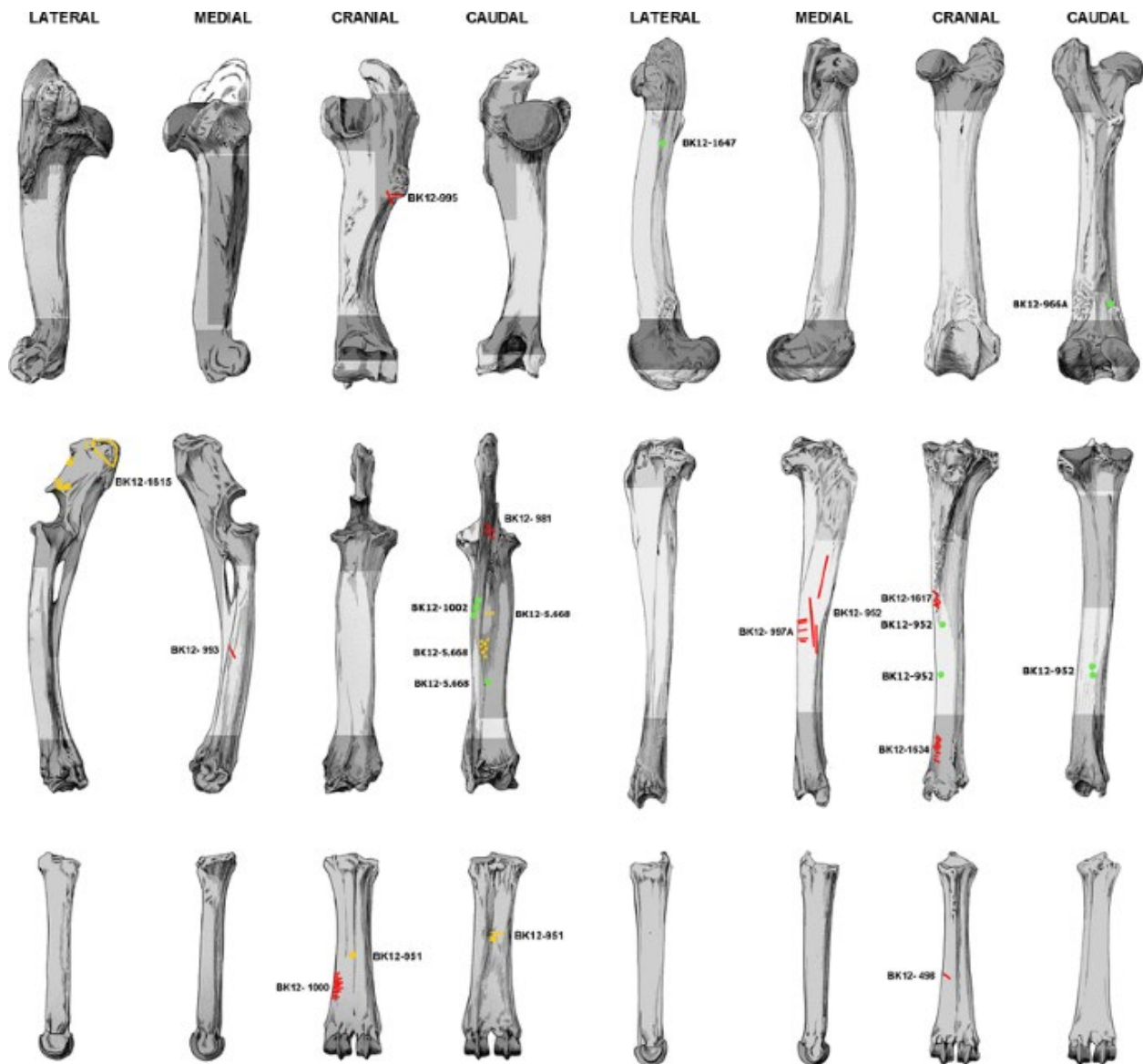
Fig. 12. Anatomical distribution of percussion, cut, and tooth marks on limb bones from large carcasses at BK5. Bones are redrawn from Pales and Lambert (1971)

Statistical analysis

The multivariate analysis of the three types of marks (cut, tooth, and percussion) together provides a more clear-cut conclusion regarding order of hominin access. The MDA results show a single solution that explains 99.6 % of the sample variance, where the first dimension represents 90 % of variance and the second dimension represents 9.6 %. The most determinant variables in the first dimension are total cut marks on all bone parts and percentage of cut marks on shafts. The second dimension is largely determined by the percentage of tooth marks (Table 5). The MDA correctly classified 86.4 % of sample. The MDA shows that the confidence intervals of alternative hypotheses overlap slightly (Fig. 13). The BK5 megafaunal assemblage occurs within the overlapping area of primary access and secondary access to partially defleshed

carcasses (Fig. 13). This is probably due to the lack of experimental modeling with large carcasses.

Table 5. Discriminant coefficient scores for the first two functions of the MDA tests. CM, cut marks; PM, percussion marks; TM, tooth marks. Notice how cut marks appear as the most discriminant variables

	Dimension 1	**Dimension 2**
Total_CM	−0.073617522	0.007138463
CM_shafts	−0.041906461	−0.012620043
PM	0.000446310	−0.019706902
Total_TM	−0.028076257	0.117655095
TM_shafts	−0.002684796	0.203996347
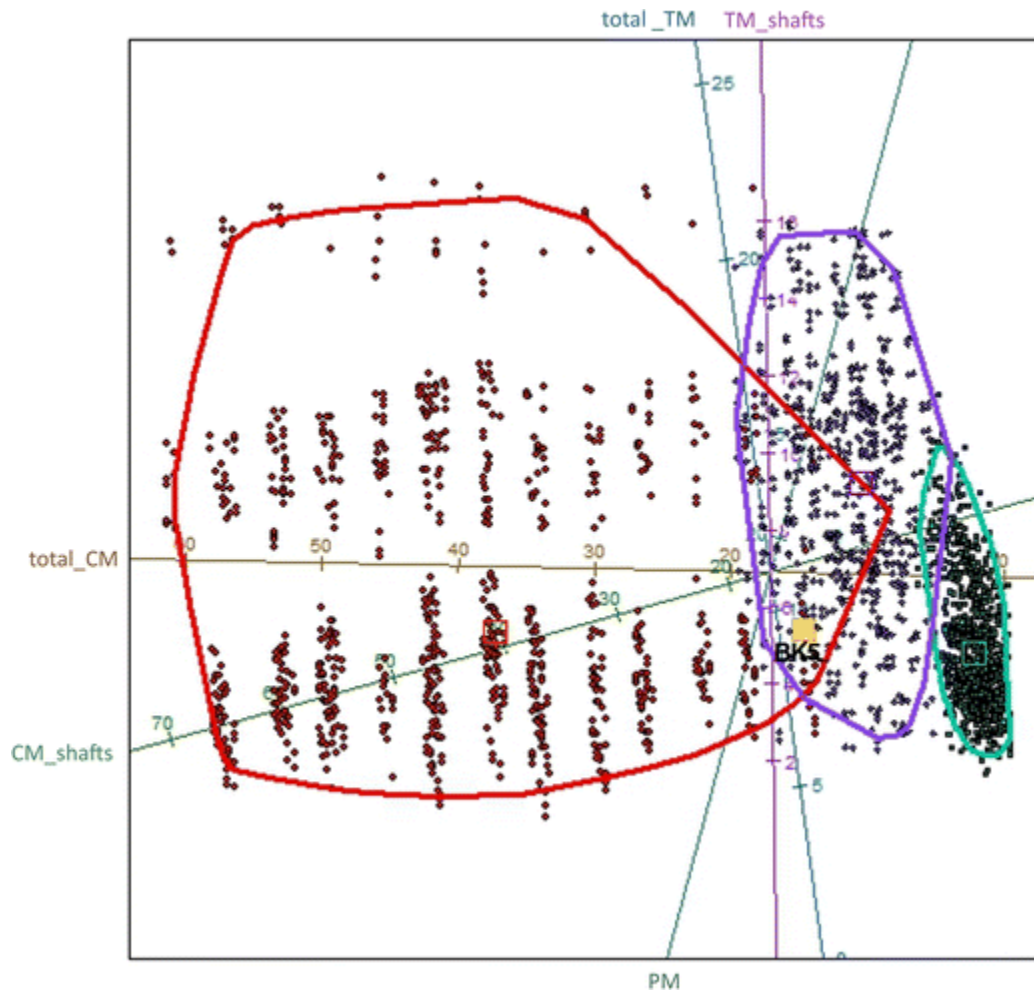
Fig. 13. Multiple discriminant analysis (using a canonical variate approach) on a bootstrapped sample of experimental sets: primary access to completely fleshed carcasses butchered with stone tools reproducing the H-C model (*large red alpha bag to the left*), secondary access to variously defleshed carcasses in the F-H-H model (*medium-sized blue alpha bag*), and secondary access to defleshed carcasses from the F-H model (*small green alpha bag to the right*). Centroid location within each alpha bag is also shown (*squares*)

Looking at long bones from large carcasses by NISP and bone section reveals that 19 % of the BK5 sample is cut marked. This percentage is higher than the 10 % established as the minimum to differentiate between primary and secondary access according to butchery experiments conducted by Gidna et al. (2014) on fleshed and scavenged buffalo carcasses. Cut marks on the BK5 samples are distributed as follows: 5.5 % for upper long bones (humerus and femur), which is within the 95 % confidence interval (0–22.15) for those experiments reproducing primary access to completely fleshed large carcasses by hominins. Intermediate long bones (radio-ulna and tibia) show a high percentage of cut marks (26 %) that exceeds the 95 % confidence interval (2.56–21.13) of the experimental sample of primary access to buffalo carcasses (Fig. 14). Therefore, when we compare cut mark frequencies by element and bone portion with experimental models, BK5 shows values similar to those resulting from experiments that reproduce early access to carcasses of this size (Gidna et al. 2014). This information should be taken as preliminary and should be contrasted with an increased sample from an expanded excavation.
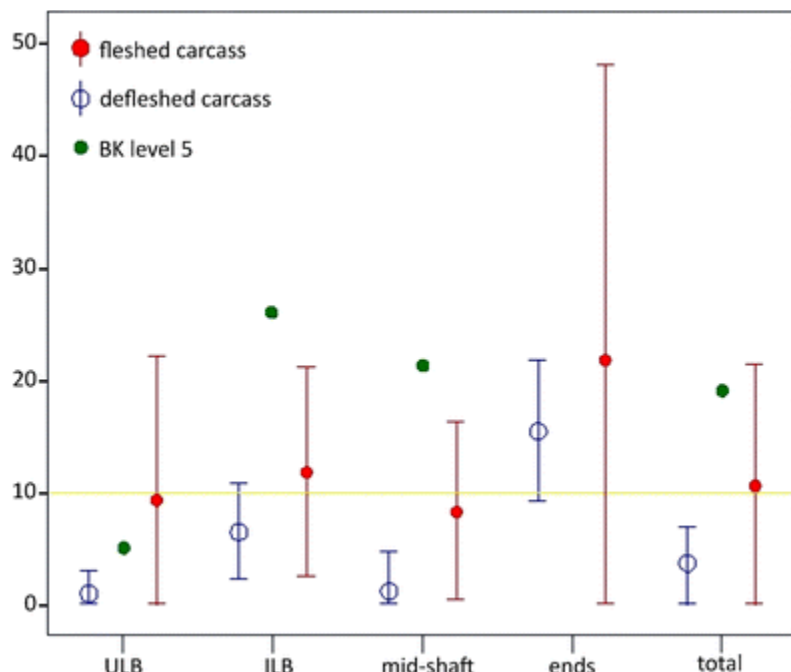
Fig. 14. Percentage of cut marked specimens (*Y*-axis) and range of variation (95 % confidence intervals) for experiments simulating primary and secondary access to fleshed (*red*; mean = *filled circle*) and defleshed (*blue*; mean = *open circle*) large size carcasses. *ULB* upper limb bones, *ILB* intermediate limb bones

Discussion

A stark contrast in skeletal part profiles was documented between the Leakeys' 1950s excavation of the BK megafaunal assemblage and that excavated by TOPPP. Such a contrast is expressed mainly in the virtual absence of long bone shaft fragments from the Leakey assemblage (probably because of selective collection) and their predominance in the TOPPP assemblage. This bias is important for several reasons. Most significantly, it underscores the relevance of using long bone shafts (Bunn and Kroll 1986; Bunn et al. 1988; Marean and Frey 1997; Marean

and Kim 1998; Marean 1998; Pickering et al. 2003; Yravedra and Domínguez-Rodrigo 2009) because (a) different skeletal profiles and their relationship to meat utility are produced and (b) all bone surface modifications at BK5 were documented on these sections. This unbiased assemblage provided an avenue through which to overcome the equifinality presented by the alternative scenarios proposed to explain the accumulation of *Pelorovis* in the Leakey collection (i.e., hominin-made accumulation versus natural death assemblage with or without intervention by hominins). The analysis of the TOPPP assemblage sheds light on these issues. The evidence at hand, particularly the weathering stages and the different vertical depths of individual skulls, shows that the assemblage is the result of several depositional events widely separated in time. It also shows that the assemblage is composed of at least a single natural death, as represented by a single unmodified *Pelorovis* individual, and by either naturally dead and/or hunted animals that were subsequently processed by hominins. Bone surface modifications on the megafauna indicate a primary role by hominins in the exploitation of these carcasses. Cut marks further show that carcasses were substantially fleshed at the moment of hominin intervention. Tooth marks also show that carnivores played a secondary role. Carnivores alone or in conjunction with water flows could be responsible for the poor representation of axial and compact bones. However, the lack of preferred orientation and the presence of different specimen sizes indicate that the collection does not represent a lag assemblage.

TOPPP's excavation unearthed not only *Pelorovis* but also *Syncerus*, *Sivatherium*, *Hippopotamus*, and *Elephas*, that is, a very diverse collection of megafaunal remains. All of them show traces of exploitation by hominins. What is particularly striking is the way hominins repeatedly broke open proboscidean bones. This was also documented in the Leakey collection from a different archeological level. BK's proboscidean remains are the earliest that show this sort of intensive breakage by hominins. Despite the scarcity of axial remains, the presence of several vertebrae and ribs as well as the high frequency of skulls indicates that megafaunal individuals died on the spot. Transport can be inferred for small and medium-sized individuals through the evenness index. Uneven representation of the high-survival skeletal elements (characterized by high bone density) supports inferences of selective transport by the accumulating agent. Modern foragers select carcass parts differently according to transport distances (Faith and Gordon 2007; Faith et al. 2009), and these strategies generate different bone accumulation patterns at consumption sites, namely camps (Yellen 1977; Bartram 1993a, b; Bunn et al. 1988; Faith and Gordon 2007; O'Connell et al. 1988a; O'Connell et al. 1988b; O'Connell et al. 1990).

There must have been a substantial amount of resedimentation at the site given the high degree of dispersal of bones and lack of articulated elements.

In a critical approach to the analogical frameworks and neo-taphonomic research that has allowed the determination of primary and secondary access to carcasses by hominins at sites like FLK Zinj or BK, Pante et al. (2015) argue that their single-variable bootstrapped approach indicates an opportunistic strategy by early Pleistocene hominins at Olduvai. We have criticized this conclusion, arguing that when a comparative sample size is small, a forced bootstrap on it will not provide a more adequate analogical framework (Domínguez-Rodrigo et al. 2014d; Domínguez-Rodrigo 2015). The assumption that for any sample size *n* the distribution for samples chosen at random is the sampling distribution inferred for the population can only be

justified if *n* is really representative of the original population. Chernick (1999) has specified that for *n* < 10, the set of possible bootstrap samples is not rich enough. Chernick and LaBudde (2011) devote extensive treatment to this question and stress that "for very small sample sizes like n <10, the bootstrap may not be reliable… because the sample may not be representative of the population and the bootstrap samples tend to repeat observations and they tend to differ even more from the population sampling distribution than the original samples do" (Chernick and LaBudde 2011: 191). This warning regarding the original *n* size prior to bootstrapping is also emphasized by Hall (1997). In sum, when *n* is small, no matter how sophisticated the algorithms implemented, they may not only misrepresent the original sample, but they may also be further biasing it. We stress that Pante et al. (2012) systematically used original samples (experimental models) in which *n* by category (model and carcass size types) is smaller than 10. For example, their carnivore-only model for small carcasses consists of two experiments. It does not matter if one bootstraps these two experiments separately prior to analyzing them combined, as Pante et al. did; if this set (*n* = 2) is too small to represent the range of carnivore-only behaviors, as confirmed when compared with other alternative experimental scenarios considering specific types of carnivores (e.g., Domínguez-Rodrigo et al. 2007b; Gidna et al. 2014), then the bootstrapped sample is not reproducing the range of behaviors originally present in a carnivore-only model. In this case, the statistical approach may be biasing it artificially because the "number of permutations grows faster than the number of bootstrap atoms" (Chernick and LaBudde 2011: 191). We showed this clearly in Domínguez-Rodrigo et al. (2014c).

Pante et al. (2015) rejected the information derived from cut mark data, but their conceptual frameworks are flawed for the following reasons: First, they claim cut mark frequency is not related to the amount of flesh, while it has been experimentally shown that cut mark frequency and anatomical distribution is statistically different in primary access to carcasses involving bulk defleshing from secondary access to defleshed or partially defleshed carcasses (Domínguez-Rodrigo 1997, 2012; Domínguez-Rodrigo et al. 2007a; Egeland 2012). Secondly, Pante et al. (2015) are also skeptical when confronted with the observational and experimental evidence that felids tooth mark bones in very low frequencies (Domínguez-Rodrigo et al. 2007b; Gidna et al. 2014). In addition, a study of felid modification of over 400 bones from small carcasses by Parkinson (2013) yielded a frequency of 12.1 % tooth-marked midshafts. Pobiner (2007) also showed that 33 % of the midshafts of her medium-sized collection modified by lions were tooth marked. These estimates are made on mostly complete bones and are bound to decrease significantly when these bones are hammerstone broken if replicating the scavenging model posited by Pante et al. for FLK Zinj. This decrease in tooth mark frequencies on shafts modified by felids can be observed in Gidna et al. (2014; Tables 3 and 4). Gidna et al. (2014) showed that on virtually "hammerstone broken" assemblages, tooth mark frequencies on shaft specimens ranged from 4.4 to 12-2 % for small and medium-sized carcasses (with an average of 8 % of tooth-marked shafts when lumping all element types).

Our taphonomic work has shown that Olduvai hominins had primary access to fleshed carcasses during the early Pleistocene (Domínguez-Rodrigo et al. 2014d). Hominin bulk defleshing and demarrowing at FLK Zinj has also been supported recently by Parkinson et al. (2015), who also reject that passive scavenging could have produced the taphonomic modifications documented in the Zinj faunal assemblage. The same taphonomic analogs and techniques show that hominins at BK had early access to a wider range of carcass sizes during Bed II.

The interpretation of early hominin access to carcasses of all sizes, including megafauna, at BK5 is similar to that documented in the overlying levels, especially BK4b (Domínguez-Rodrigo et al. 2014a). This indicates either that natural deaths occurred sequentially on the same spot for a long time period or that hominins were actively involved in acquiring faunal resources at the site. One way or another (these alternatives are currently difficult to test), what this sequence of archeological levels does show is that local trophic dynamics were unique. Although at present there are no natural faunal accumulations from Africa that show the same taxonomic diversity or skeletal elements per taxon as those documented at BK5, it could be argued that the site contained exceptional resources that drew numerous animals, including hominins. Given the site's location near a river, water could have been one of these resources. However, several other penecontemporaneous river channels (including larger ones) have been reported for the same period at sites like PLK, WK, and HK, and no bone accumulations like those of BK have been documented.

The exploitation of megafauna is rather exceptional compared to small and medium-sized fauna across time in both Africa and Europe (e.g., Smith 2015). The repeated exploitation of megafaunal individuals diachronically at BK is thus unique. It will therefore probably require unique explanations that can only be better understood with a larger excavation and increased sample sizes.

Conclusions

Taphonomic studies of both the excavated assemblage from BK5 and the collection excavated by Leakey in 1950s support the importance of diaphyseal fragments to interpretations of early Pleistocene hominin behavior.

The paleosurface data analysis obtained at BK5 has demonstrated a functional association of stone tools and fossil bones. However, it seems likely that BK5 represents a palimpsest formed over many years through various processes such as natural deaths, the processing of naturally dead or (possibly) hunted megafauna by hominins, and post-depositional ravaging by carnivores. The data show an abundance of green fractures, some of which occur with percussion marks; low frequencies of tooth-marked bones; and a high frequency of cut marks on elements and sections that would have already been defleshed by carnivores if they had had primary access. These results are consistent with Dominguez-Rodrigo's (2009a; 2014a) interpretations of the site where early carcass acquisition by hominins was surmised.

The distribution and frequency of cut marks on specimens belonging to large animals indicates that hominins enjoyed early access to substantial amounts of meat, and the extent to which these carcasses were defleshed and broken suggests that the human group was large and exhibited a degree of cooperative behavior that required a capacity for strategy, organization, communication, and physical effort. This, combined with a larger, more robust, and more muscular body (Sorensen and Leonard 2001), implies high energy demands that could only be obtained by consuming large quantities of animal resources.

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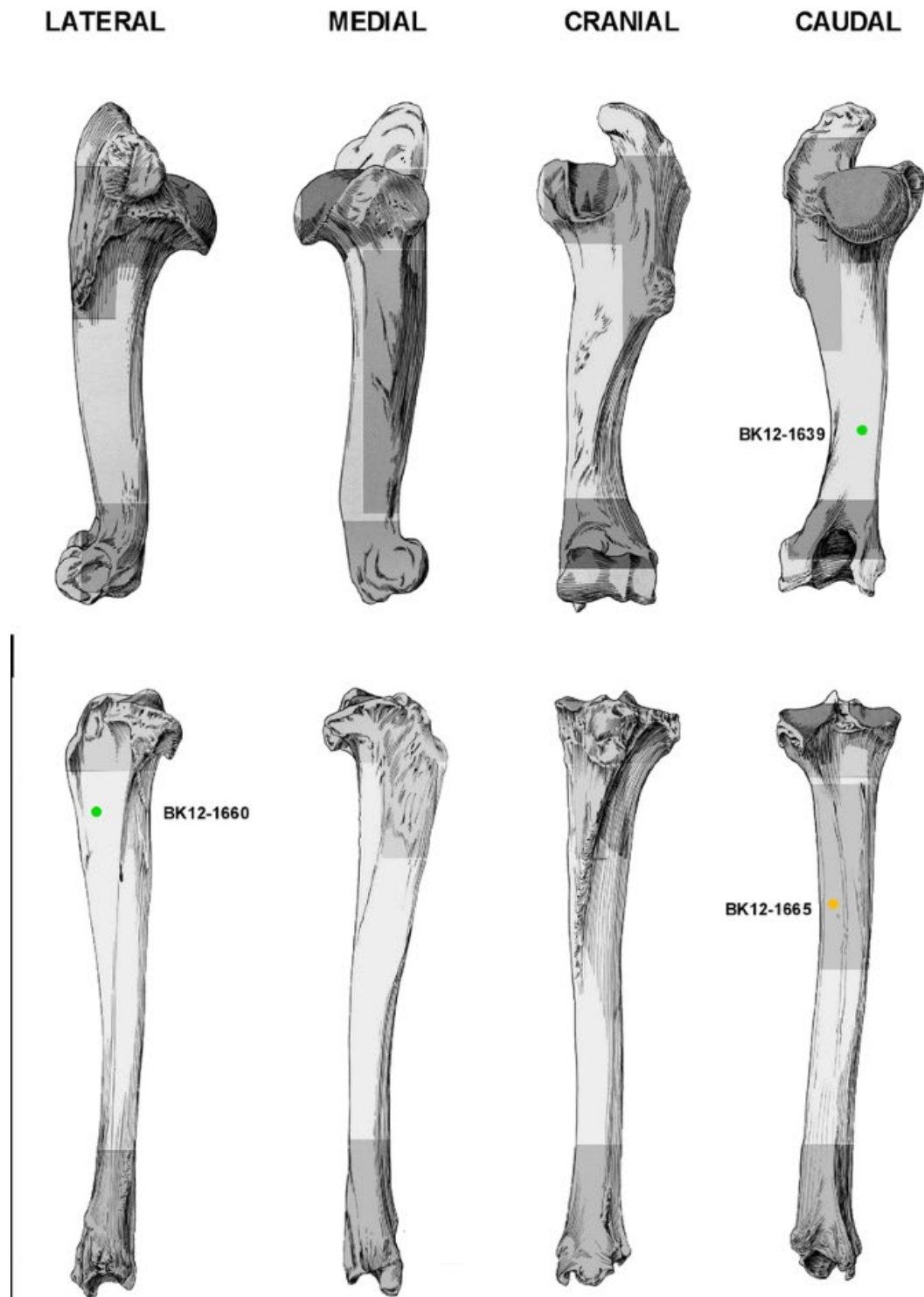
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Acknowledgments

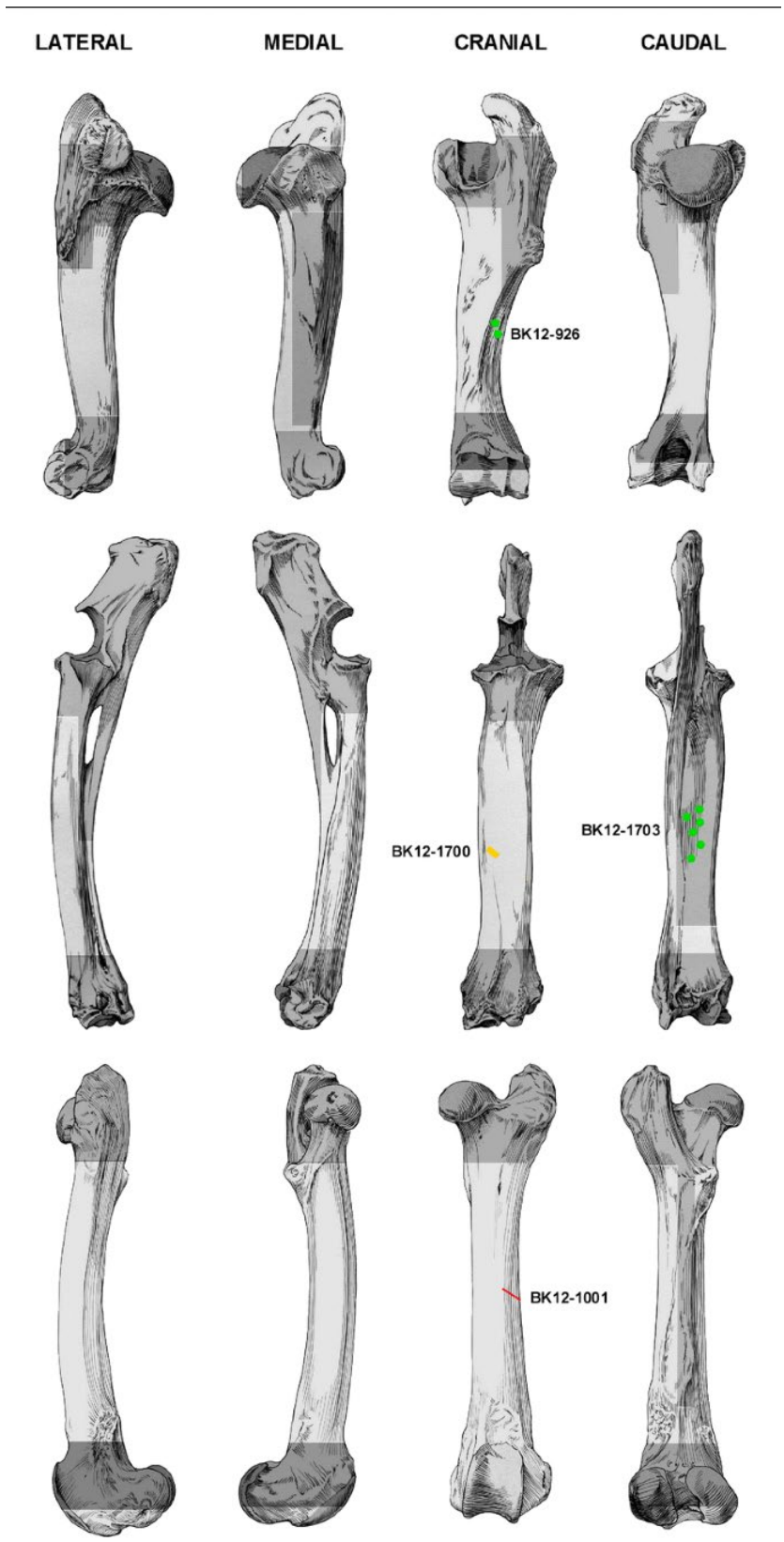**Fig. A1**. Anatomical distribution of percussion and tooth marks on limb bones from small carcasses at BK5. Bones are redrawn from Pales and Lambert (1971)

Fig. A2. Anatomical distribution of percussion, cut and tooth marks on limb bones from medium carcasses at BK5. Bones are redrawn from Pales and Lambert (1971)

ESM 1
Details of the bone accumulation where an elephant tibia can be seen

ESM 2
Surface of BK5 showing fossils and stone tools