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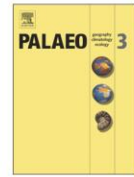
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## On applications of micro-photogrammetry and geometric morphometrics to studies of tooth mark morphology: The modern Olduvai Carnivore Site (Tanzania)

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## ABSTRACT

Recent application of photogrammetric and geometric morphometric approaches to the study of cut marks on bones has yielded positive results in discriminating different types of tools and even some raw materials. Here, we apply this analytical technique to the study of carnivore tooth scores. The goal is twofold: on the one hand, we intend to differentiate carnivore types and on the other one, we show the application of this approach to a sample of tooth scores from long bones documented at the modern assemblage of the Olduvai Carnivore Site (OCS). Previous taphonomic work at OCS suggested that this bone assemblage constituted a good evidence of a carcass accumulation behavior by lions, followed by hyena ravaging. The application of these 3D techniques to the selected sample of tooth marks shows that lions, as well as spotted hyenas, did indeed impart marks on the OCS assemblage. This reinforces the dual nature of the assemblage and the implication of lions in its formation.

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## 1. Introduction

During the last decades a significant part of the research carried out in taphonomy has been focused on carnivore neotaphonomy. Bone assemblages created by spotted hyenas (*Crocuta crocuta*) have been intensively studied (e.g., Egeland et al., 2008; Kerbis Peterhans, 1990; Lam, 1992; Pickering, 2002; Sutcliffe, 1970). Additionally, controlled experiments have also been carried out simulating intervention in anthropogenic bone assemblages, in order to quantify the degree of post-depositional hyena ravaging after hyena consumption of part of the bones (Blumenschine, 1988; Domínguez-Rodrigo, 1997). Some features were proposed as typical characteristics of hyena bone assemblages (e.g., low abundance of compact bones, different age class profiles of the preys or abundance of carnivore remains) (Cruz-Urbe, 1991;

Stiner, 1991). Subsequent studies have shown the great variability of this carnivore as taphonomic agent (Lam, 1992) and have revealed that only few criteria can be used to distinguish such bone assemblages (Pickering, 2002). Further research was carried out to understand the variability of the taphonomic signature among hyenid species (Egeland et al., 2008; Faith, 2007; Fourvel et al., 2015; Kuhn, 2011), taking into account that different ecological contexts can impact the outcome of the taphonomic property set of any given bone assemblage. These studies are crucial to create accurate analogues that serve to interpret archaeological assemblages.

Felids have also been targeted by neotaphonomic research. Leopards (*Panthera pardus*) have been proposed as potential bone accumulators in the savanna ecosystem (Brain, 1981; Kerbis Peterhans, 1990) and some interpretations consider felids as the primary accumulating agent of some of the early archaeological sites (Domínguez-Rodrigo et al., 2007). Research in modern savannas has analyzed the carcass consumption process at lion (*Panthera leo*) kills (Domínguez-Rodrigo, 1999; Gidna et al., 2014) and has provided descriptions of modern leopard dens (Brain, 1981; Ruitter and Berger, 2000).

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## ARTICLE IN PRESS

2

M.C. Arriaza et al. / Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2017) xxx–xxx

Despite the efforts made to determine the modifications that different carnivores leave on the bone assemblages, there is no consensus about an unequivocal feature that helps to discern the carnivore species involved and the access order. Sometimes, it is especially difficult because more than one species have been involved in the modification of the carcasses found at sites. Additionally, there is always some degree of equifinality, as documented through skeletal part representation or the tooth mark sizes generated by carnivore species with similar body mass (Andrés et al., 2012). Furthermore, neotaphonomic studies are subject to several shortcomings: the variables which quantify the skeletal part representation are diverse, results are not differentiated depending on body mass of the prey, sample size of the experiments is sometimes inadequate, the body mass of the prey in the experiments is not analogous to the ungulate size found at the sites, or experimental sets are based on the action of carnivores in captivity (Andrés et al., 2012; Gidna et al., 2013; Yravedra and Domínguez-Rodrigo, 2009).

Recently, new methods for analyzing classical taphonomic features have been proposed. Such methodology is primarily based on multivariate statistics. This is the case of the new term “taphotype” which integrates the differential quadrant bone destruction according to element type (Domínguez-Rodrigo et al., 2015). This method has proved that furrowing and tooth mark frequencies inflicted by several carnivores can be distinguished using multivariate statistics (Domínguez-Rodrigo et al., 2015). Moreover, the use of machine learning methods allows the distinction of skeletal part representations generated by felids from those seen in hyena dens (Arriaza and Domínguez-Rodrigo, 2016). That is also true when multivariate statistic is combined with the five-age class method for ungulate preys hunted by spotted hyenas and lions (Arriaza et al., 2015). Thus, multivariate approaches facilitate the identification of carnivores involved in the accumulation or modification of bone assemblages.

Other techniques that have recently been applied in neotaphonomy include geometric morphometric and micro-photogrammetric methods. Such techniques have been used for the analysis of cut (Maté-González et al., 2015, 2016) and tooth marks (scores), obtaining satisfactory results in order to differentiate scores produced by different carnivores (Muttart et al., 2016; Yravedra et al., submitted). Micro-photogrammetry affords three-dimensional high quality reconstructions, so that marks can be analyzed with high accuracy. Studies using three-dimensional reconstructions can be based on different techniques. Apart from the micro-photogrammetric approach (Maté-González et al., 2015, 2016), other researchers have worked with 3D digital microscopes (Boschin and Crezzini, 2012; Crezzini et al., 2014) or the Alicona

3D Infinite Focus Imaging microscope (Bello and Soligo, 2008; Bello et al., 2009; Bonney, 2014). In any case, these techniques have been employed in multiple contexts providing very useful results. For instance, such studies have succeeded in differentiating the raw materials used in the processing of carcasses (Boschin and Crezzini, 2012; Maté-González et al., 2016). They have also helped to interpret cannibalistic and funerary practices (Bello and Soligo, 2008; Bello et al., 2011a) as well as study teeth and the use of the mouth as a third hand (Bello et al., 2011b; Hillson et al., 2010). They contributed to the interpretation of engraved bones and antlers (Bello et al., 2013a) and the use of these materials as retouched tools and hammers (Abrams et al., 2014; Bello et al., 2013b) or for engraved pottery (Montani et al., 2012) and prehistoric art (Güth, 2012).

Recently a new modern bone assemblage – the Olduvai Carnivore Site (OCS) – has been presented as the first bone assemblage accumulated by lions (Arriaza et al., 2016). Several independent taphonomic analytic tools provided evidence that a large-size felid (namely, lions), rather than other types of carnivores, may have been responsible for the accumulation of more than 50 wildebeest carcasses at the OCS (Arriaza et al., 2016). In the present work, we show the results obtained by means of micro-photogrammetric and geometric morphometric techniques in the study of the scores identified at the OCS. It is the first time that such a technique is applied to this type of assemblages, given its potential utility to identify the carnivore(s) involved in the consumption of carcasses and to establish the access order. Our results show that both lions and spotted hyena have modified the OCS bones, corroborating the interpretations suggested in previous taphonomic and ecological analyses of the den (Arriaza et al., 2016). With this example we show that the use of this technology is an effective way of extracting further taphonomic information from any carnivore modified bone assemblage.

## 2. Material and methods

### 2.1. The Olduvai Carnivore Site (OCS)

During TOPPP's (The Olduvai Paleoanthropology and Paleocology Project) 2012 field season in Olduvai Gorge (Tanzania), a modern carnivore site was found close to the third fault of the gorge (Fig. 1). The carnivore assemblage was located in the short grassland ecological unit of the Serengeti National Park. The OCS includes 55 wildebeest carcasses accumulated at least during 2 or more seasons. The skeletal part representation comprised 4533 bone specimens that belong to the same



Fig. 1. Location of the Olduvai Carnivore Site (OCS) (yellow star) and a wildebeest carcass found at the site. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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M.C. Arriaza et al. / Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2017) xxx–xxx

3

SECTION TYPES SCORE PRODUCED VARYING CARNIVORES

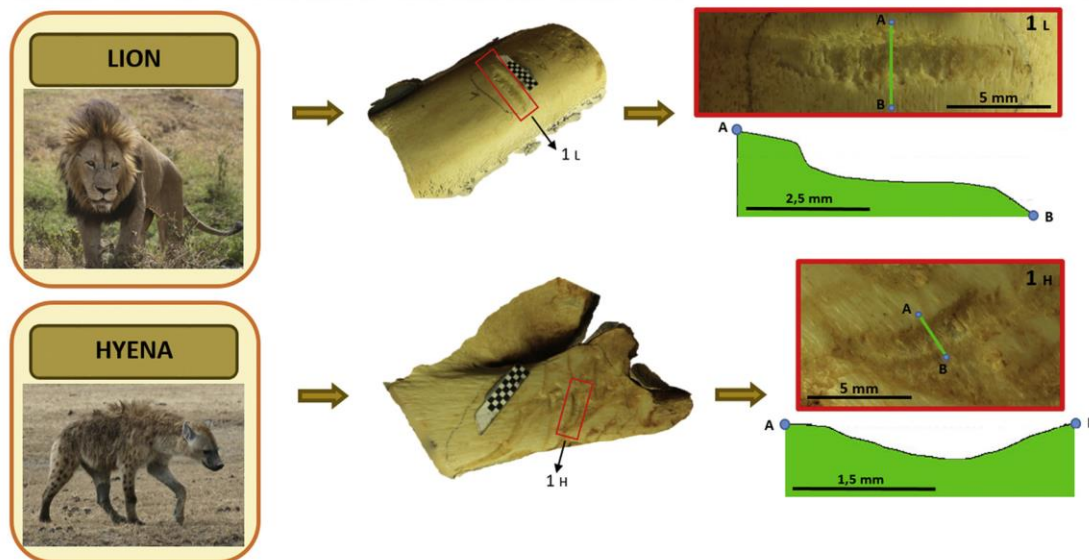


Fig. 2. Section types scores produced by the spotted hyena and lion.

species, the blue wildebeest (*Connochaetes taurinus*). Some of the carcasses were complete or almost complete. The taphonomic study carried out showed a low frequency of tooth marks, a low degree of bone breakage, and typical felid bone modifications on the axial skeleton and on the epiphyses. However, some long bones present bone destruction patterns carried out by a durophagus carnivore, such as those inflicted by spotted hyenas (Arriaza et al., 2016). The bone assemblage is dominated by young adults or mature adults, including only 5

yearlings (Arriaza et al., 2015). This data along with the high bone accumulation rate, the body mass of the prey, the prey specialization (only one ungulate species), and the behavioral ecology of the carnivores present in the short-grassland ecologic unit of the Serengeti, suggest that the primary accumulating agent was a felid, probably a nomad lion. However, spotted hyenas also modified the sample, scavenging part of the bones. The OCS may be the first documented bone assemblage accumulated by a lion. This constitutes a new framework for

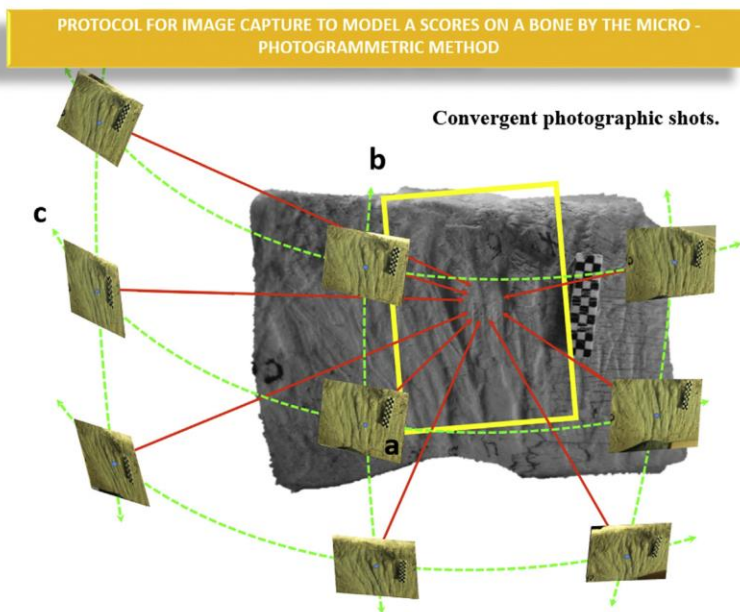


Fig. 3. Protocol for image capture to model a tooth mark on a bone by the micro-photogrammetric method, with convergent photographic shots. (a) Master and dependent images in central position, (b) vertical slave images, and (c) horizontal slave images.

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## ARTICLE IN PRESS

4

M.C. Arriaza et al. / Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2017) xxx–xxx

**Table 1**

Technical specifications of the photographic sensor with macro-lens.

Canon EOS 700D	
Type	CMOS
Sensor size	22.3 × 14.9 mm <sup>2</sup>
Pixel size	4.3 μm
Image size	
5184 × 3456 pixels	
Total pixels	18.0 MP
Focal length	60 mm
Focused distance to object	100–120 mm

future taphonomic studies that is relevant for the interpretation of classical paleoanthropological sites such as those of Olduvai Gorge (Arriaza et al., 2016).

## 2.2. Material

Traditionally, the access order of the different kind of carnivores (felid versus hyenid) has been tested based on the frequency and the distribution of tooth marks on long bones. The focus on long bones is due to the fact that carnivore taphonomy has been developed primarily on these elements to test hominin-carnivore potential interactions in the formation of prehistoric bone assemblages (e.g., Blumenschine, 1988; Gidna et al., 2014) and long bones are usually the most frequent elements in most of the archaeological sites. Thus, 23 OCS long bones bearing tooth marks were selected for the present study aiming at differentiating tooth marks inflicted by lions and hyenas. The sample of study includes 1 ulna, 1 metacarpal, 5 femora, 4 tibiae, 6 humerus and 6 radii. For this study we have only analyzed tooth scores, since previous experimental analyses have demonstrated that scores are the only type of tooth marks that yield reliable results when trying to differentiate carnivore types (Yravedra et al., submitted). A total of 25 scores were selected randomly but on the basis of their preservation and general groove integrity. We excluded those scores that present a bad cortical preservation or some type of alteration, such as the appearance of biochemical modifications or exfoliation. Neither superficial nor inconspicuous tooth marks that provided a bad resolution when photographed stereographically have been selected for the study.

The experimental samples that we used to compare carnivore types and the OCS tooth score sample are from Cabárceno Reserve “Parque de la Naturaleza de Cabárceno”, Cantabria (Northern Spain). For further detail on bone samples used in this work see Gidna et al. (2013) and Domínguez-Rodrigo et al. (2015). A total of 30 scores produced by

lions on 12 adult equid long bone shafts and 33 hyena scores on 12 adult equid long bone shafts were analyzed (Yravedra et al., submitted). This sample is small and is presented here as a preliminary study given its clearly diagnostic value.

## 2.3. Methods

According to previous taphonomic analyses, the OCS tooth marks should have been made either by spotted hyenas or lions, or both (Arriaza et al., 2016). In this work, we tested this hypothesis using micro-photogrammetric and morphometric techniques.

High-resolution images were obtained through micro-photogrammetry and computer vision techniques and these were then used for the three-dimensional modeling of score sections (Fig. 2). Following the methodology of Maté-González et al. (2015), precise metrical models of scores were generated using images taken with oblique photography (Fig. 3). It was demonstrated that more stable and precise sensors captured better quality images, producing more significant results. A Canon EOS 700D reflex camera (Table 1) with 60 mm macro lenses was used. Specimens were individually placed on a photographic table with lighting adjusted to keep the bone permanently well illuminated. The photographic sensor had to be configured at the beginning of the process to adjust focus and brightness. A tripod was used to stabilize the camera during the photographic process. Both the exposition moment of the camera and lighting remained constant during the image data capture. Noise removal was not required since the protocol for data acquisition and the controlled environmental conditions guaranteed high-quality point clouds. The methodology required placing a millimetric scale next to the score mark to be photographed so as to provide a precise measurement reference.

Photographs were then taken following the specified protocol (Fig. 3). Once the photographs had been taken, they were processed so as to generate a 3D model for each mark. Consequently, the photographs were treated with the photogrammetric reconstruction software GRAPHOS (inteGRATED PHOTogrammetric Suite) (Fig. 4) (González-Aguilera et al., 2016a, 2016b) or another reconstruction software such as Agisoft PhotoScan, PIX4D or PW (González-Aguilera et al., 2013). After producing scaled 3D models, Global Mapper software was used to define and measure mark profiles (Figs. 3 and 4).

For data collection, a total of 6–9 photos are taken for each mark. The number of photos varies depending on the geometry of the bone and the shape of the mark. The three-dimensional reconstruction of each mark takes 30–35 min depending on the final number of photos taken.

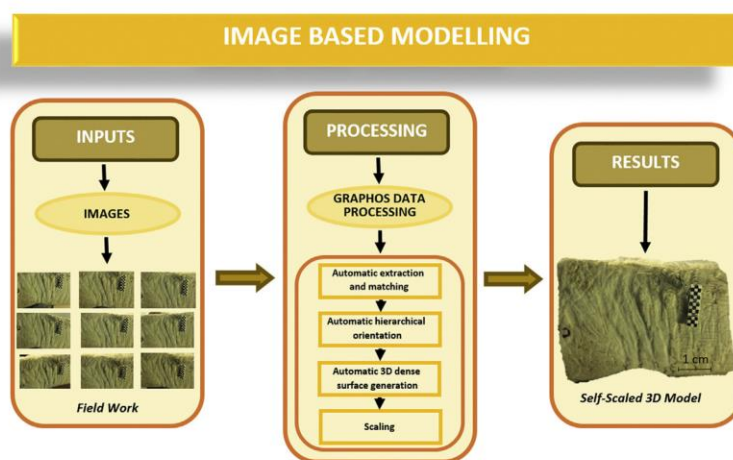


Fig. 4. Workflow of the image-based modeling technique.

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M.C. Arriaza et al. / Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2017) xxx–xxx

5

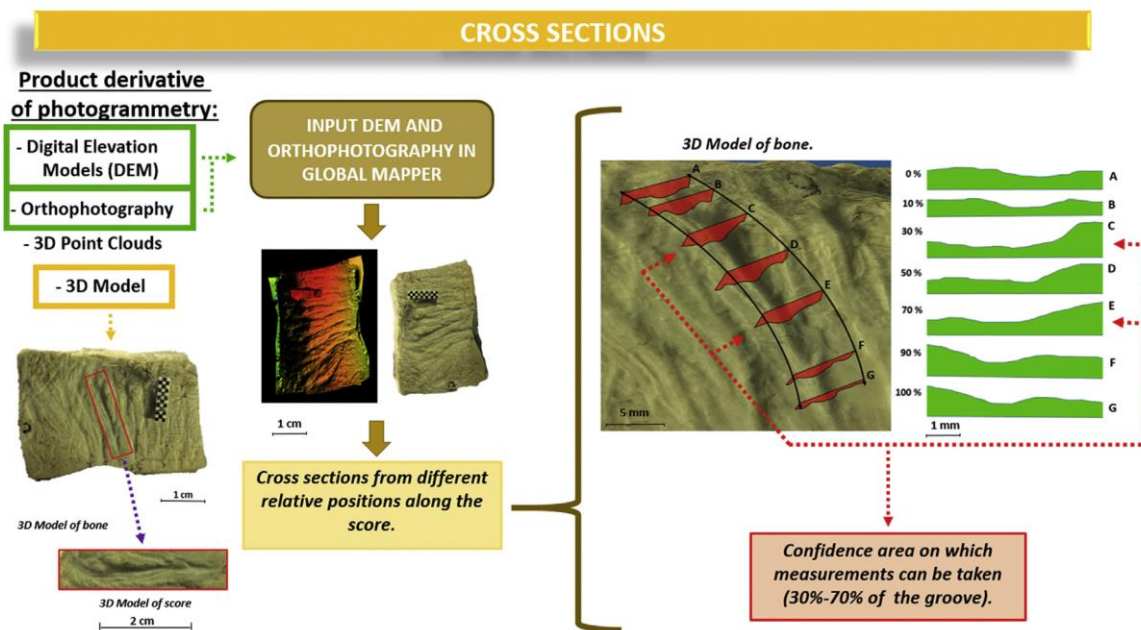


Fig. 5. Representation of the a–g sections of the tooth mark regarding its length.

Our goal with the reconstructions is to maximize both, accuracy and completeness. If the separation among images (baseline) increases, the accuracy will improve as the intersection of the perspective rays is more favorable, but the completeness of the object decreases due to the dense cloud algorithms. By contrast, if the separation among images (baseline) decreases, a better completeness of the object will be obtained, but the accuracy will be poorer because of a worse intersection of the perspective rays.

In order to contextualize the accuracy analysis of photogrammetry and geoinformatics (PG) methods vs. microscopy, given that geometric data are dependent from two different sources (scaling and photogrammetric reconstruction-PHO), the variance of the PG could be estimated

as follows:

$$\sigma_{PG} = \pm \sqrt{(\sigma_{\text{scaling}} \cdot \text{GSD})^2 + (e_{\text{PHO}} \cdot \text{GSD})^2} \tag{1}$$

where,  $\sigma_{\text{scaling}}$  is the scaling precision established as 1/3 of the pixel (Luhmann et al., 2013),  $e_{\text{PHO}}$  is the reprojection error of the photogrammetric bundle block adjustment expressed in pixels and GSD is the ground sample distance expressed in m/pixel. In this way, it is possible to obtain a comprehensive and complete comparison, at a geometric and statistical level.

MEASURE ON THE PROFILE

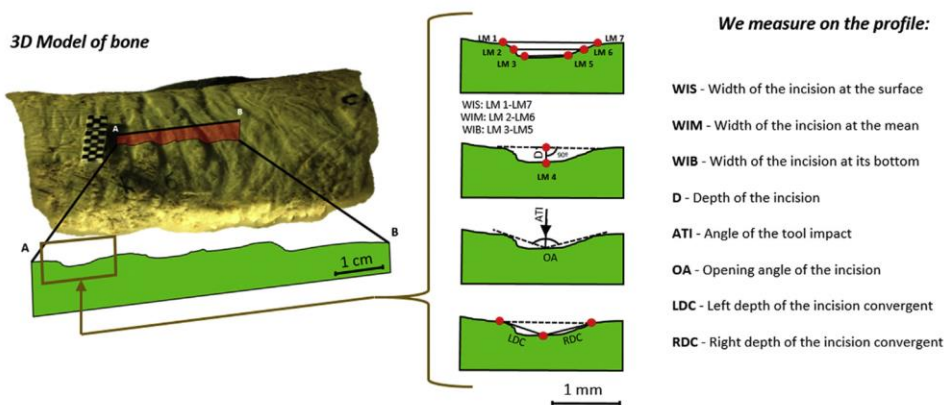


Fig. 6. Location of measurements sensu Bello et al. (2013a). Landmarks (LM1–7) used for the morphometric model are also represented.

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## ARTICLE IN PRESS

6

M.C. Arriaza et al. / Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2017) xxx–xxx

**Table 2**  
Measurements taken on the profile.

Width of the incision at the surface	WIS
Width of the incision at the mean	WIM
Width of the incision at its bottom	WIB
Opening angle of the incision	OA
Depth of the incision	D
Left depth of the incision convergent	LDC
Right depth of the incision convergent	RDC

Scores were measured at mid-length (about 50% of the mark length) as suggested in Maté-González et al. (2015). According to such description, for a confident comparison of scores, the values for the sections between 30% and 70% of the mark length would be the most representative ones (Fig. 5). A series of measurements including WIS, WIM, WIB, OA, D, LDC, RDC (sensu Bello et al., 2013a) were taken on the mark section and used as quantitative variables (see Fig. 6 for measurements and Table 2).

The measurements for each score section were later compared using several statistical tests. In order to test if there was any difference in the several measurement of carnivores, a multivariate Principal Component Analysis (PCA) of the biometric data was performed with the library FactoMiner (Lê et al., 2008) in R ([www.rproject.org](http://www.rproject.org)) software (Core-Team, R, 2015). The PCA estimates mark similarities and differences on a bidimensional Euclidean space. In the present study we used the mark measurements transformed through scaling. Plotting of the PCA results with confidence ellipses was made with the ggplot2 R library.

A geometric morphometric analysis based on a Generalized Procrustes Analysis (GPA) was conducted as a supplementary alternative to the Multivariate Metric Analysis (Fig. 6). Such analyses use information captured in the form of homologous landmarks that describe each specimen independently. This technique takes the landmark data (coordinates) and normalizes the form information by the application of superimposition procedures. This involves the translation, rotation and scaling of shapes defined by landmark configurations. In this case, seven identical landmarks per section – as shown in Fig. 6 (LM1–7) – were considered from each mark. Landmarks were digitalized using tpsUtil (v. 1.60.) and tpsDig2 (v. 2.1.7), as explained in Maté-González et al. (2015). The location of the landmarks responded to the measures considered for the statistical analysis, as seen in Fig. 6. LandMark 1 (LM) was found at the beginning of the left line in the mark section; LM2 appeared in the middle of this line; LM3 was placed approximately at 10% of the right end of the mark; LM4 was at the very end; LM5, LM6 and

LM7, in a opposed position to LM3, LM2 and LM1, respectively (Fig. 6). The resulting tps file was imported into R and analyzed using the “geomorph” library (Sherratt, 2014). Lastly, a Linear Discriminant Analysis (LDA) was performed to estimate the differences among the several groups of tooth marks. The LDA function included in the MASS R package was used.

A total of 88 high quality 3D models were generated with a reflex camera with a macro lens (average GSD (mm) =  $\pm 0.0078$ ; average scaling error (mm) =  $\pm 0.0157$ ; average photogrammetric error (mm) =  $\pm 0.0058$ ; average precision (mm) =  $\pm 0.0168$ ). This method fulfills the requirements of quick capture, automatic processing of images and high precision, so as to enable a precise and reliable statistical analysis.

It should be noted that camera was self-calibrated to simultaneously compute the interior and exterior camera parameters. In particular, a complete calibration, which includes 12 interior parameters (focal length (1), principal point (2) and distortion center (2), radial (3) and tangential (2) distortion, scaling and affinity factors (2)) (Fraser, 1980), was applied. This self-calibration is suitable and valid when we work with reflex cameras and some theoretical parameters are known.

### 3. Results

Statistical tests comparing the OCS score sections and those of the experimental sample from Cabárceno (Figs. 5 and 6) prove that there are certain features that allow the differentiation and identification of both, lions and hyenas, according to the way they score bone surfaces.

The PCA analysis shows that lion scores are clearly differentiated from those produced by hyenas (Fig. 7). Hyenas present a greater variability in the morphology of their scores, generating a certain overlap with lions. OCS scores are grouped into the ellipse corresponding to the lions (Fig. 7), being 68% of the marks directly associated with the lion ellipse (Table 3). The 32% remaining scores are grouped differently: 24% appear associated with hyena scores and 8% lie outside the range of variability described by both carnivores (marked with arrows in Fig. 7). This result is not surprising considering previous taphonomic analysis (Arriaza et al., 2016), where hyenas were described as secondary agents scavenging the carcasses after the primary consumption by lions. The PCA plot (Fig. 7) shows that most of the den scores match the lion sample.

On the other hand, the morphometric test described in Fig. 8 is more confusing: the scores produced by lions (in red) are grouped on the right of the plot, hyena scores (in black) lie on the left, while the OCS

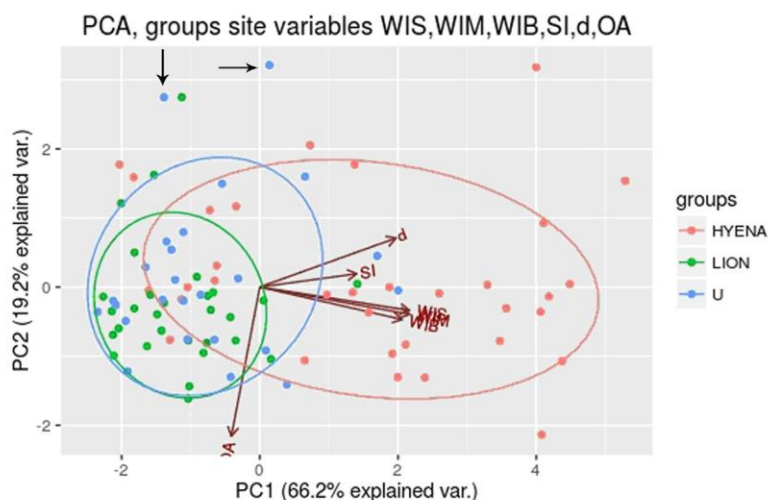


Fig. 7. PCA plot of the measurements indicated in Figs. 6 and 7. U refers to the OCS. Arrows indicate the scores that are outside the variability range of hyenas and lions.

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## ARTICLE IN PRESS

M.C. Arriaza et al. / Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2017) xxx–xxx

7

**Table 3**  
LDA confusion matrices based on biometric data.

	Hyena	Lion
Hyena	28 (0.85)	5 (0.15)
Lion	2 (0.07)	27 (0.93)
OCS	8 (0.32)	17 (0.68)

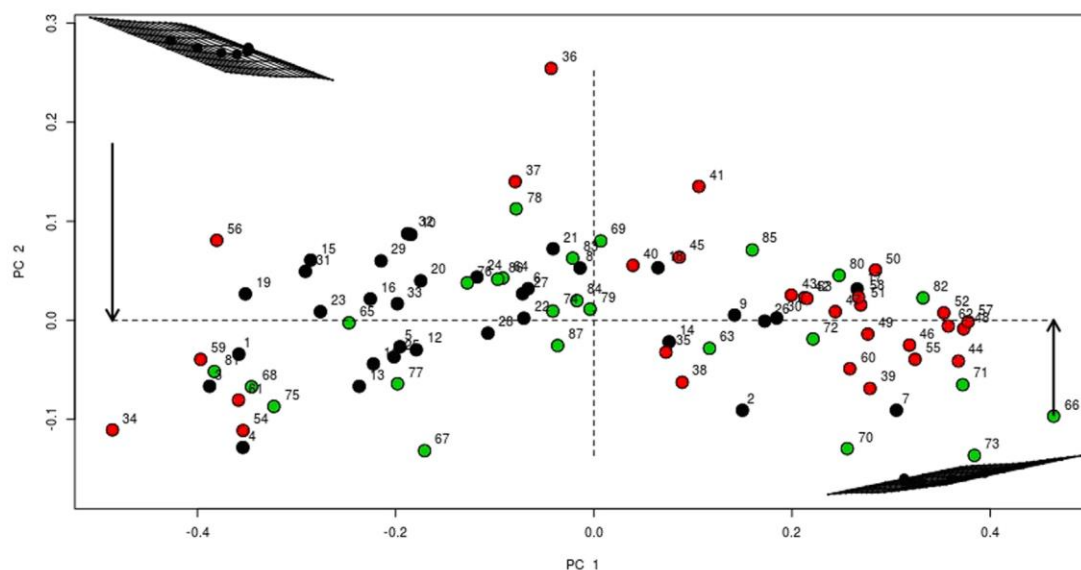
marks (in green) occupy the whole graph. Comparative matrices do not provide conclusive results, since the OCS scores are placed between the lion and the hyena data (Table 4). This morphometric test is not conclusive and the degree of variation explained is lower than the one obtained with the biometric PCA (Fig. 8 vs Fig. 7).

Nevertheless, morphometric data suggest some morphological differences. Scores produced by lions are shallow and very wide with an open U-section, whereas hyena scores are deeper and their section is less open (Fig. 9).

In sum, the biometric test is more conclusive than the morphometric analysis. The biometric test and the corresponding confusion matrices (Fig. 7 and Table 3) show that a high percentage of the OCS scores were produced by lions, while hyenas exerted a minor and secondary impact on the assemblage. Bone accumulations produced by hyenas present a higher number of scores than pits, contrary to what happens in the samples primarily modified by lions (Domínguez-Rodrigo et al., 2012; Gidna et al., 2013, 2014). Most of the scores identified at the OCS describe the action of lions. If hyenas had been responsible for the OCS bone accumulation, the number of typical hyena scores would have been much higher than the amount of lion scores, which is not the case at the OCS. The morphometric test and its accuracy enhance the role hyenas might have played on the OCS accumulation (Fig. 8 and Table 4). Thus, our results agree that both lions and hyenas were involved in the consumption of the OCS assemblage. This confirms previously proposed hypothesis that suggested a primary access of lions to the wildebeest carcasses accumulated at OCS, and a subsequent intervention of the hyenas that would have scavenged some of the bones (Arriaza et al., 2016).

**4. Discussion**

The interaction of carnivores and hominins is a widely studied topic due to its great relevance in the understanding of the human evolutionary record. A very promising taphonomic variable concerns the tooth mark sizes generated by different carnivore species. This variable has been used to discuss bone assemblages as relevant as those from Sima de los Huesos or Olduvai Gorge (Andrews and Fernández-Jalvo, 1997; Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003). According to Selvaggio and Wilder (2001), the mean tooth pit size on cancellous bone from the FLK Zinj was similar to the ones observed in the sample consumed by hyenas and lions. However, the results on the cortical bone suggested that the sample from the FLK Zinj was similar to samples generated by cheetah, leopard or hyenas (Selvaggio and Wilder, 2001). Based on these data, they argued that the last carnivore modifying the FLK Zinj bone assemblage was the hyena. Either hyenas were ravaging carcasses left by hominins, or felids firstly defleshed the carcasses, followed by hominins demarrowing them and hyenas ravaging the abandoned bones (Selvaggio and Wilder, 2001). Further research analyzed the same carnivore taxa studied by Selvaggio and Wilder (2001). The results revealed that tooth mark size also reached equifinality (Domínguez-Rodrigo and Piqueras, 2003). Several species showed overlapping pit sizes, although it was possible to differentiate between small-medium carnivores and larger species in accordance with tooth mark sizes on both cancellous and cortical bone sections (Domínguez-Rodrigo and Piqueras, 2003). The great variability suggested by tooth mark size analysis could not support the three-stage model hypothesis (carnivore-hominin-carnivore) for the FLK Zinj. Subsequently, other carnivorous and omnivorous species were studied such as the tiger, bobcat or caracal (Delaney-Rivera et al., 2009). The body mass of the taxa and the bone portion where the tooth mark was inflicted may determine the tooth mark dimensions (Delaney-Rivera et al., 2009). Again, an overlap between different species was identified but small and large carnivores inflicted differentiable tooth pits on cortical bone (shafts). It was argued that this variable alone was not a good indicator of the carnivore species involved in the exploitation of fossil



**Fig. 8.** PCA plot where the morphometric data of the OCS scores are compared with the experimental sample. Black: hyena, Red: lion, Green: OCS. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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## ARTICLE IN PRESS

8

M.C. Arriaza et al. / *Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2017) xxx–xxx***Table 4**  
LDA confusion matrices based on morphometric data.

	Hyena	Lion
Hyena	25 (0.76)	8 (0.24)
Lion	7 (0.24)	22 (0.76)
OCS	14 (0.56)	11 (0.24)

assemblages (Delaney-Rivera et al., 2009). Recently, new studies have shown that the inadequate sample size of the experiments may create the overlap between taxa, in addition to the differential carnivore body mass and age (Andrés et al., 2012). Furthermore, some experiments have been made using the same prey for all the carnivore species involved, regardless of the body mass of the carnivore. Nevertheless, carnivore body mass normally constrains the selection of preys in wild environments (Andrés et al., 2012). Combining a larger sample and taking into account the prey size usually consumed by the different carnivore taxa, it is possible to differentiate the species according to the tooth marks inflicted on long bone shafts (Andrés et al., 2012). However, more taphonomic variables should be analyzed in order to develop solid hypotheses concerning the implication of carnivores in fossil assemblages (Delaney-Rivera et al., 2009; Andrés et al., 2012).

During the last few years, new methodologies have been proposed to analyze the action of carnivores: taphotypes, skeletal part representation combined with machine learning methods or age profiles (five-age class method) classified through multivariate statistic may differentiate the taxa involved in the bone modification (Domínguez-Rodrigo et al., 2015; Arriaza et al., 2015; Arriaza and Domínguez-Rodrigo, 2016). Moreover, micro-photogrammetry and geometric morphometry have been applied in taphonomic studies (Maté-González et al., 2015, 2016). These techniques can reproduce three-dimensional models of the marks identified on bones facilitating its morphologic study. This has already been done to analyze the raw material used in the processing of carcasses (Maté-González et al., 2016). Although tooth mark dimensions alone cannot distinguish between carnivore taxa, the morphology of the tooth marks seems to be different depending on the carnivore species (Yravedra et al., submitted). A recent study carried out with bones consumed by spotted hyenas, lions, wolves, foxes and jaguars showed that the scores inflicted on the shafts by these carnivores can be differentiated when the tooth mark is reconstructed through micro-photogrammetry and analyzed using geometric morphometrics (Yravedra et al., submitted).

Here, the samples created by spotted hyenas and lions were compared with the tooth marks from the OCS, in order to test previous taphonomic hypotheses that argued that the bone assemblage was primary consumed by the lion followed by the hyena ravaging. The statistical analyses showed that the OCS score morphology is similar to the one created by lions and spotted hyenas in controlled experiments. The scores are located on the shafts, which means that both carnivores generated tooth marks on this bone portion. Lions usually deflesh carcasses in the consumption process of the prey and may inflict tooth marks on

the shafts of long bones during the consumption of flesh (Domínguez-Rodrigo, 1999; Gidna et al., 2014). Hyenas usually break long bones to access the bone marrow and grease (Sutcliffe, 1970). The scores which are morphologically similar to those inflicted by the spotted hyena may correspond to the secondary access to the carcasses by this durophagous carnivore. In sum, our morphometric analyses support the hypothesis raised previously through the taphonomic and the ecologic analyses. In spite of the low number of tooth marks analyzed from the OCS the hypothesis raised through the morphometric analysis meets the one proposed from a taphonomic and ecological point of view. The neotaphonomic collection contains spotted hyena, lion, fox, jaguar and wolf samples (Yravedra et al., submitted). Another relevant species that has been proposed as an accumulating agent in the African savanna is the leopard (Brain, 1981; Kerbis Peterhans, 1990; Ruitter and Berger, 2000). The morphometric analysis of the leopard tooth marks should be compared with the tooth marks inflicted by hyenids and other large felids such as the lion. Equally, jackals, which are usually the first bone modification agent in simulated archaeological sites in the African savanna (work in progress), should be compared to wild dogs (although this species does not modify bones greatly (Yravedra et al., 2014)).

The morphometric analyses of tooth marks may constitute a new research line in carnivore taphonomy and may be of great value in the study of paleoanthropological sites. High-resolution morphologic studies such as the one presented here may help determine the species involved in the bone modification of bone assemblages.

## 5. Conclusions and future perspectives

Recent morphometric studies of tooth marks successfully distinguished different carnivore species. This work presents a new methodology that opens up new and interesting perspectives for the identification of taphonomic processes. The application of photogrammetry for the modeling of two- or three-dimensional reconstructions in combination with the application of geometric morphometrics and multivariate statistics allows the examination of new horizons in taphonomy. In some recent works, these techniques have been applied to the study of cut marks, but this new methodology has the potential to also analyze other taphonomic marks such as trampling or biochemical alterations.

These new techniques have been used in the bone assemblage from the OCS to test the hypothesis that emerged from previous taphonomic analyses that the site resulted from a lion-hyena model. The results show that both hyenas and lions inflicted tooth marks on the long bones from the OCS. Thus, this variable supports that the bone assemblage was firstly consumed by lions and hyenas subsequently scavenged part of the remains. This constitutes a new framework where lions should be considered potential bone accumulators in the past. It is for this reason that the morphometric analysis of tooth marks may help in the taphonomic study of paleoanthropological sites.

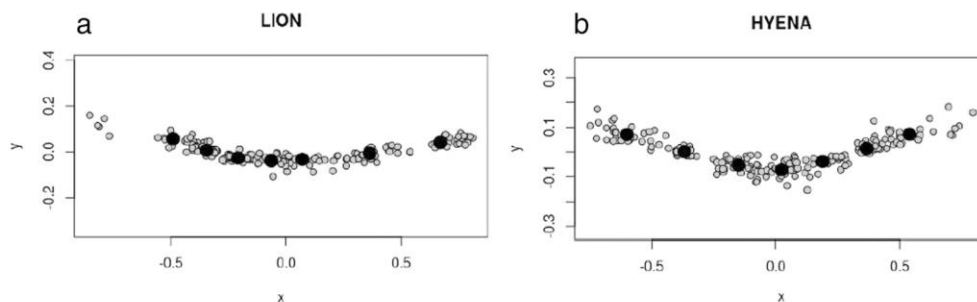


Fig. 9. GPA test including the profiles of the carnivore scores analyzed, where a: lion, b: hyena.

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## ARTICLE IN PRESS

M.C. Arriaza et al. / Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2017) xxx–xxx

9

Regarding future perspectives, graphical tests based on QQ-plots and robust estimators such as the median and the median absolute deviation would be desirable to check the reliability of data, especially if they do not follow a Gaussian distribution. Another important aspect for future works involves the automatic recognition of coded targets, so that 3D models can be automatically scaled, guaranteeing subpixel precision.

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## ARTICLE IN PRESS

10

M.C. Arriaza et al. / *Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2017) xxx–xxx*

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