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Discerning carnivore agency through the three-dimensional study of tooth pits: Revisiting crocodile feeding behaviour at FLK- Zinj and FLK NN3 (Olduvai Gorge, Tanzania)

Julia Aramendi [a,b,*], Miguel Angel Maté-González [c,d], José Yravedra [a,b], María Cruz Ortega [e], Mari Carmen Arriaza [b,f], Diego González-Aguilera [c], Enrique Baquedano [b,g], Manuel Domínguez-Rodrigo [a,b]

[a] Department of Prehistory, Complutense University, Prof. Aranguren s/n, 28040 Madrid, Spain
[b] IDEA (Institute of Evolution in Africa), Covarrubias 36, 28010 Madrid, Spain
[c] Department of Cartography and Terrain Engineering, Polytechnic School of Avila, University of Salamanca, Hornos Caleros 50, 05003 Avila, Spain
[d] C.A.I. Arqueometry and Archaeological Analysis, Complutense University, Profesor Aranguren s/n, 28040 Madrid, Spain
[e] Universidad Complutense de Madrid-Instituto Carlos III (UCM- ISCIII), Centro de Investigacion de la Evolucion y Comportamiento Humanos, Madrid, Spain
[f] School of Geography, Archaeology and Environmental Studies, Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, 2050, South Africa
[g] Museo Arqueológico Regional, Plaza de las Bernardas s/n, 28801 Alcalá de Henares, Madrid, Spain

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ABSTRACT

Hominins and carnivores have shared similar habitats in Africa, evolving as direct competitors for the same prey and spaces. The overlap of their ecological niches has raised an important debate on the role that carnivores played in archaeological site formation. Different analytical techniques differentiate the action of carnivores and humans and identify the type of carnivore involved of which tooth mark analyses are prominent. However, available taphonomic studies present some limitations given the great overlap among tooth mark sizes from different carnivores, enabling only the distinction of size groups, not specific carnivores. In this work, we use a new technique combining three-dimensional (3D) reconstruction and geometric morphometrics (GMM) of tooth pits on equid and bovid bone created by different carnivores (including crocodiles, hyenas, jaguars, lions and wolves) in controlled settings. The 3D methodology we present isolates and differentiates tooth marks generated by different carnivores. We also test the applicability of the technique to ascribe tooth pits recorded on some hominin specimens from FLK Zinj and FLKNN 3 (Bed I, Olduvai Gorge). The tooth marks on the Olduvai OH8 and OH35 hominin fossils, previously assigned to crocodiles show that while OH8 tooth pit morphology falls in the range created by crocodiles, the pits on OH35 can not be interpreted as crocodile-inflicted marks.

1. Introduction

Bone accumulations including human bones with carnivore modifications are common in the paleoanthropological record. Modern (Horwitz and Smith, 1988; Milner and Smith, 1989) and fossil human bones seem to have been ravaged by carnivores in the past (e.g., Brain, 1981; Baquedano et al., 2012; Domínguez-Rodrigo et al., 2013; Camarós et al., 2015). The competition between humans and carnivores is not only reflected in the possible role of humans as prey, but also in the exploitation of carnivore carcasses by humans during the Lower (Yravedra, 2007; Blasco et al., 2010), Middle (Auguste, 1995; Arribas et al., 1997) and Upper Paleolithic (Yravedra, 2005; Münzel et al., 2011). Niche overlap also necessarily affects site formation processes fostering situations, where both agents might have had access to the same carcasses (Straus, 1982; Blasco, 1997; Turner, 2004; Valente, 2004; Yravedra et al., 2010; Patrocinio et al., 2012). Several studies show for example, that humans evolved under an important trophic pressure, with humans and carnivores sharing the same ecosystems and competing for similar resources, as is the case in Olduvai Gorge Beds I and II (Domínguez-Rodrigo et al., 2007, 2010; Aramendi et al., 2017).

Numerous Pleistocene sites evince interactions between humans and carnivores lending to focused taphonomic research over the past two decades identifying the characteristic traces generated by various carnivores. Different parameters such as skeletal and age profiles, fracturing patterns or the study of tooth marks according to their morphology, dimensions and anatomical distribution have been established in order to determine carnivore agency. Several studies demonstrate that different carnivores show characteristic behavioral patterns generating different skeletal profiles (e.g., Brugal and Fosse, 2004) and different patterns of modification, accumulation, and dispersion of carcasses at feeding

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[*] Corresponding author at: Department of Prehistory, Complutense University, Prof. Aranguren s/n, 28040 Madrid, Spain.
E-mail address: juliaram@ucm.es (J. Aramendi).

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sites (Domíguez-Rodrigo and Pickering, 2010; Domínguez-Rodrigo et al., 2015; Yravedra et al., 2011, 2012; Arilla et al., 2017).

Thus, the action of different carnivores can be inferred through the study of several factors. The direct study of tooth marks (Fig. 1) is one of the most common taphonomic techniques. An advantage of this type of analysis is that the study of tooth marks – including pits and scores does not depend on the habitat of the carnivores (wild or captive) since the morphology and dimensions of the marks do not vary (Sutcliffe, 1970; Haynes, 1980; Binford, 1981; Shipman, 1981). This is an important point because recent works demonstrate that captive and free carnivores behave differently (e.g., Gidna et al., 2013; Sala et al., 2014).

So far, studies based on pit dimensions have only managed to identify groups of carnivores by size, e.g. large carnivores like hyenas or lions, and small carnivores like foxes or intermediate-small felids (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Coard, 2007; Delaney-Rivera et al., 2009; Andrés et al., 2012; Saladié, 2009; Saladié et al., 2013; Bello et al., 2015). Recent studies such as those by Pante et al. (2017) or Arriaza et al. (2017) present new methods for the identification of carnivore tooth marks. Pante et al. (2017) offered a three-dimensional reconstruction of taphonomic modifications, but they did not compare marks made by different carnivores. Arriaza et al. (2017), on the other hand, do differentiate carnivores based on tooth scores, but do not provide a methodology focused on pits.

A current study comparing three-dimensional Digital Microscope (3D DM), Laser Scanning Confocal Microscopy (LSCM) and Micro-Photogrammetry (M-PG) techniques for the study of cut marks, demonstrated that these three techniques produced overall statistically similar results and imply that they are equally valid for the study of conspicuous bone surface modifications (Maté-González et al., 2017).

The application of geometric morphometrics (GMM) has also changed biological analyses over the past two decades, substituting traditional descriptive methods for statistical ones allowing the study of size and shape variation, and also allowing for the visualization of resultant covariation in terms of warpings and transformation grids (see review in Rohlf and Marcus, 1993; Slice, 2005). GMM procedures have been successfully applied to paleoanthropology (Bastir et al., 2007; Bruner, 2004; Cobb and O'Higgins, 2004; Freidline et al., 2012; Gunz and Bulygina, 2012) and archaeology, with studies focused on stone tools (Chacón et al., 2016; Buchanan and Collard, 2010; Lycett et al., 2010), paleolithic art (Nelson et al., 2017; Charlin and Hernández Llosas, 2016) and taphonomy (Maté-González et al., 2016; Yravedra et al., 2017; Arriaza et al., 2017) among others.

In this paper, we enhance these previous analyses by proposing a new methodology for the study of tooth pits. This new methodology combines a three-dimensional reconstruction of the pits through Micro-Photogrammetry and computer visualization techniques, as well as a three-dimensional geometric morphometric study and a multivariate statistical analysis. This study offers promising results that enable the differentiation of specific carnivores regardless of mark size. Finally, we applied these techniques to assess pits found on the Olduvai Gorge OH8 and OH35 hominin fossils, both previously interpreted as modified by crocodiles (Njau and Blumenschine, 2006; Baquedano et al., 2012), as an example of its applicability.

2. Methods and samples

2.1. Sample

For the purpose of this study, we first analyzed a total of 89 pits created by different carnivores in a controlled setting. In order to avoid possible discrepancies due to the different size modified by these carnivores, we have limited our sample to 20 pits on adult horse long bones generated by wolves, hyenas, jaguars and lions in captivity at the Cabárceno Nature Park, and 9 pits on adult cow long bones inflicted by captive crocodiles in Faunia. For more details about the lion sample see Gidna et al. (2013), for the hyena and jaguar samples see Domínguez-Rodrigo et al. (2015) and for the crocodile sample see Baquedano et al. (2012).

Along with this experimental sample, we analyzed 8 pits recorded on OH8 and 6 pits on OH35 from Olduvai Gorge. In this case, we used replicas of these fossils to virtually reconstruct and analyze the pits.

2.2. Micro-photogrammetry and virtual reconstruction

Micro-Photogrammetry and computer visualization techniques were used to create high-resolution three-dimensional models of the pits. Precise metrical models were generated using images taken with oblique photography using a CANON EOS 700D with a 60-mm macro lens (Table 1) and following the specified protocol explained in Maté-González et al. (2015). The camera was self-calibrated to simultaneously compute the interior and exterior camera parameters (Fraser, 1980). For data collection, a total of 6–9 photos were taken for each mark. The

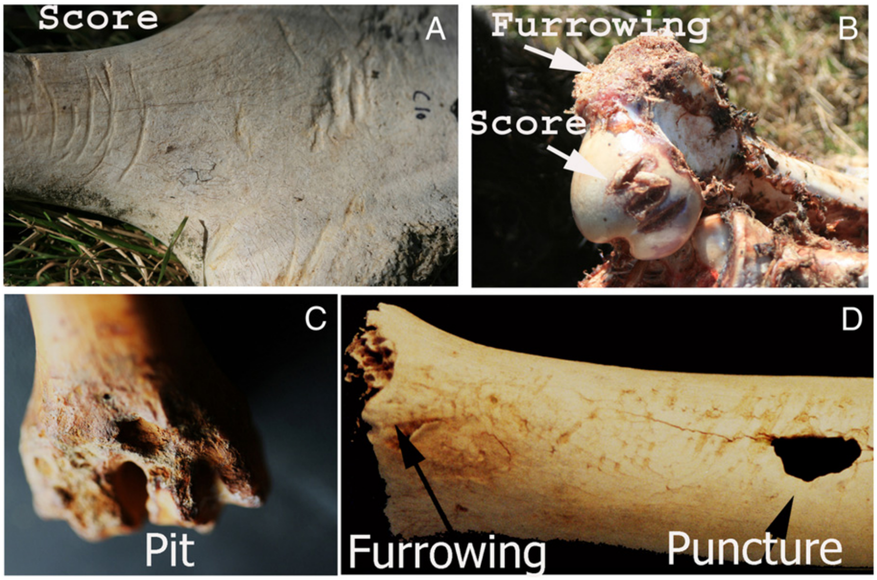

Fig. 1. Types of tooth marks generated by carnivores.

Table 1
Technical specifications of the photographic sensor with macro-lens.

Canon EOS 700D	
Type	CMOS
Sensor size	22.3 × 14.9 mm^2
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

number of photos varies depending on the geometry of the bone and the shape of the mark. Photographs were then taken following the protocol described in Maté-González et al. (2015). Once the photographs had been taken, they were processed so as to generate a 3D model for each mark with the open-source photogrammetric reconstruction software GRAPHOS (inteGRAted PHOtogrammetric Suite) (González-Aguilera et al., 2016a, 2016b).

Fossil virtual reconstructions were also performed by means of Photogrammetric and computer visualization techniques. OH8 and OH35 photographs were taken following the norms of convergent Photogrammetry from several horizontal and vertical angles (Fig. 2), using a CANON EOS 700D reflex camera with a 60 mm macro lenses (Table 1). An almost complete overlap between photographs was necessary. The separation between photographs increases 15° in the horizontal axis and 20° in the vertical axis. Lighting remained constant during the image data capture. A tripod was used to stabilize the process and photographs were taken rotating around the replica. The methodology requires placing a millimetric scale so as to provide a precise measurement reference necessary to scale the models. For data collection, a total of 100–120 photos were taken for each fossil. The number of photos varies depending on the geometry of the fossil. The three-dimensional reconstruction of each fossil takes 70–80 min depending on the final number of photos taken. Photographs of the cranial and caudal section were captured so as to generate two overlapping three-dimensional models that were later merged to create a complete 3D model of OH8 (Fig. 3) and OH35 (Fig. 4) with CloudCompare (Girardeau-Montaut, 2016). The 3D models were aligned using a least squares optimization to better arrange the final model. Three high-quality 3D models (average GSD (mm) = ±0.0078; average scaling error (mm) = ±0.0157; average photogrammetric error (mm) = ±0.0058; average precision (mm) = ±0.0168) were obtained for OH8 and OH35 (see Supplementary File 1).

2.3. Geometric morphometrics analysis

Shape and size information is contained in the form of landmarks, homologous points that can be identified among different specimens, and that keep the information for study and comparison in the form of Cartesian coordinates (O'Higgins and Johnson, 1988; Bookstein, 1991; Hall, 2003; Klingenberg, 2008).

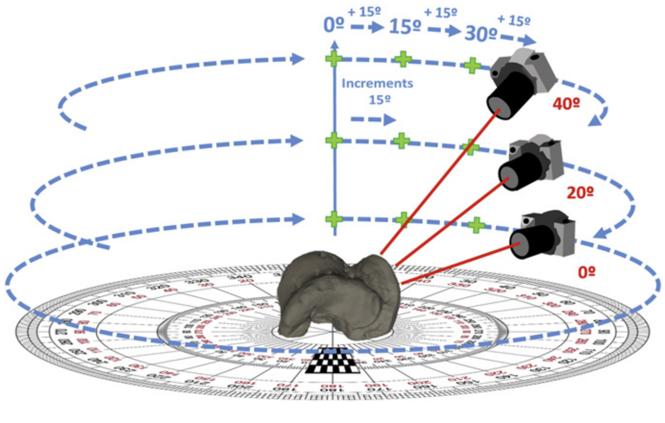

Fig. 2. Protocol for image capture to model the hominin fossils by the Photogrammetric Method.

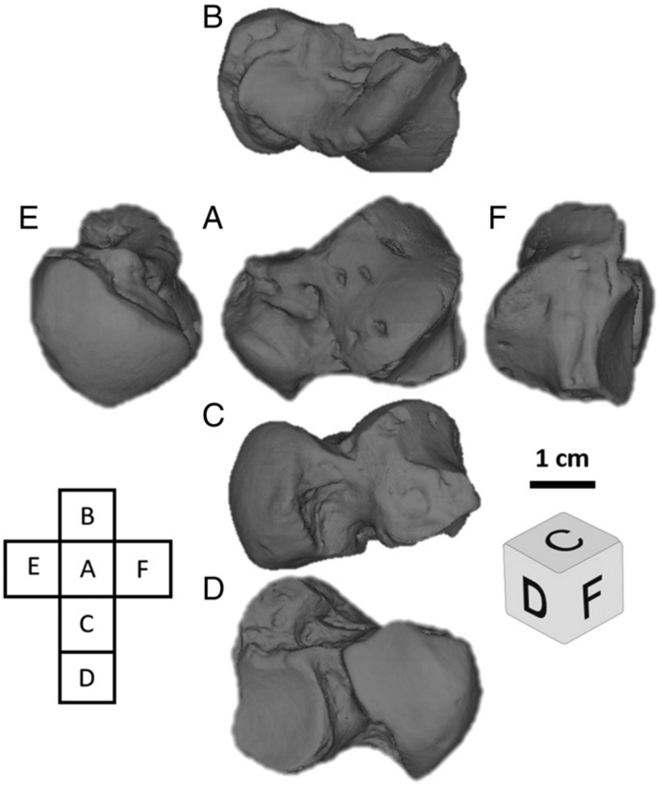

Fig. 3. OH8 three-dimensional reconstruction.

For this analysis, pits were landmarked using 17 three-dimensional points (Table 2), on the exterior and interior surfaces (Fig. 5). This fairly descriptive set of fixed landmarks allows assessing the morphological differences that might characterize each carnivore pit (see Supplementary File 2). The landmarking step was performed in Avizo (Visualization Sciences Group, USA). A preliminar reliability test was performed to evaluate data colection. First, two pits corresponding to different carnivores were landmarked several times by different individuals to prove that landmarks can be easily reproduced. Second, pits generated by the same carnivore (crocodile) on different sized-carcasses (*Ovis aries* vs.

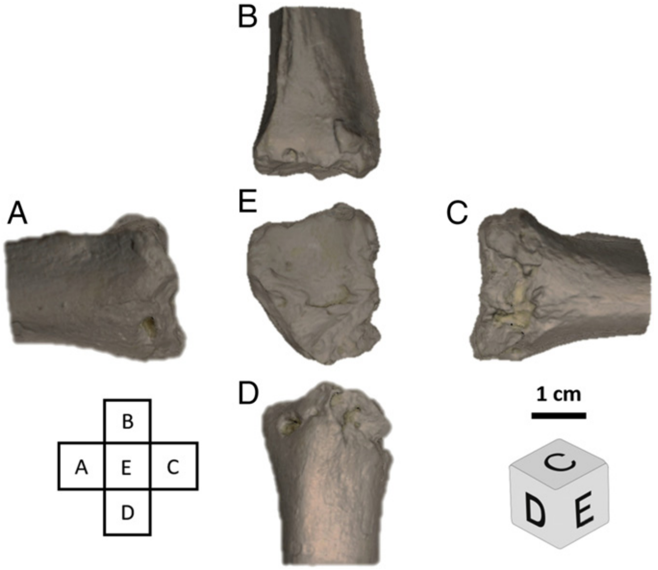

Fig. 4. OH35 three-dimensional reconstruction.

Table 2
List of landmarks used in the study and their description.

N	Landmark	Description
1	Length A	Upper limit of the longitudinal axis
2	Length B	Lower limit of the longitudinal *axis*
3	Width A	Left limit of the breadth axis
4	Width B	Right limit of the breadth axis
5	Depth	Most centered lowest point of the pit
6	Left upper half A	Point at the first third between the upper limit of the long axis and the left limit of the breadth axis
7	Left upper half B	Point at the second third between the upper limit of the long axis and the left limit of the breadth axis
8	Left lower half A	Point at the first third between the left limit of the breadth axis and the lower limit of the long axis
9	Left lower half B	Point at the second third between the left limit of the breadth axis and the lower limit of the long axis
10	Right upper half A	Point at the first third between the upper limit of the long axis and the right limit of the breadth axis
11	Right upper half B	Point at the second third between the upper limit of the long axis and the right limit of the breadth axis
12	Right lower half A	Point at the first third between the right limit of the breadth axis and the lower limit of the long axis
13	Right lower half B	Point at the second third between the right limit of the breadth axis and the lower limit of the long axis
14	Interior length A	Upper inflection point on the longitudinal axis
15	Interior length B	Lower inflection point on the longitudinal axis
16	Interior width A	Left inflection point on the breadth axis
17	Interior width B	Right inflection point on the breadth axis

Bos taurus) were compared to identify morphological differences and delimit the sample according to the results obtained.

The geometric morphometric analysis is based on a Procrustes superimposition, commonly known as generalized procrustes analysis (GPA). This technique takes the landmark data and normalizes the form information by the application of superimposition procedures. This involves the translation, rotation and scaling of shapes defined by landmark configurations. After GPA, there are always some remaining differences (Procrustes residuals separated by Procrustes distances) that expose patterns of variation and covariation between structures that after being projected into a flat Euclidian space can be analyzed by means of common multivariate statistics (Richtsmeier et al., 2002; Slice, 2001; Rohlf, 1999).

GMM studies require techniques for dimension reduction are requiered in GMM studies since the number of variables tends to be much higher than the number of cases. Principal component analysis (PCA), a tool that reduces a large set of variables to few dimensions, and assess patterns of variation among the data is a common methos for simplification. Several PCAs were performed to identify differences between carnivore pits and to evaluate the classification of the pits observed on OH8 and OH35. Tests were performed in shape and form space to assess not only differences in shape but also in size. Form spaces containing size and shape information were obtained by re-scaling data using the natural logarithm of Centroid Size. Changes in shape and form space were visualized with the aid of transformation grids and warpings computed using thin-plate splines (TPS). TPS derived grids minimize the bending between forms and express changes in the relative location of the landmarks as a deformation of the grid (Bookstein, 1989). PCAs were performed in Morphologika 2.5 (O'Higgins and Jones, 1998).

The presence of defined groups was statistically tested using a multiple variace analysis (MANOVA) on the PC scores. The test was performed in the free software R (www.rproject.org, Core-Team, 2015) to assess differences among the pits generated by different carnivores and to identify similarities between OH8 and OH35 pits and the rest of the sample.

More detailed shape and size analyses were performed in MorphoJ (Klingenberg, 2011) to describe morphological changes among carnivore pits. Partial least square (PLS) analyses were conducted to assess the association among the interior and exterior morphology of the pits. PLS permits the evaluation of two different sets (blocks) of landmarks, without assuming that one block is dependent on the other (Rohlf and Corti, 2000). PLS extracts pairs of vectors (one set for each block) successively explaining diminishing proportions of covariance between blocks.

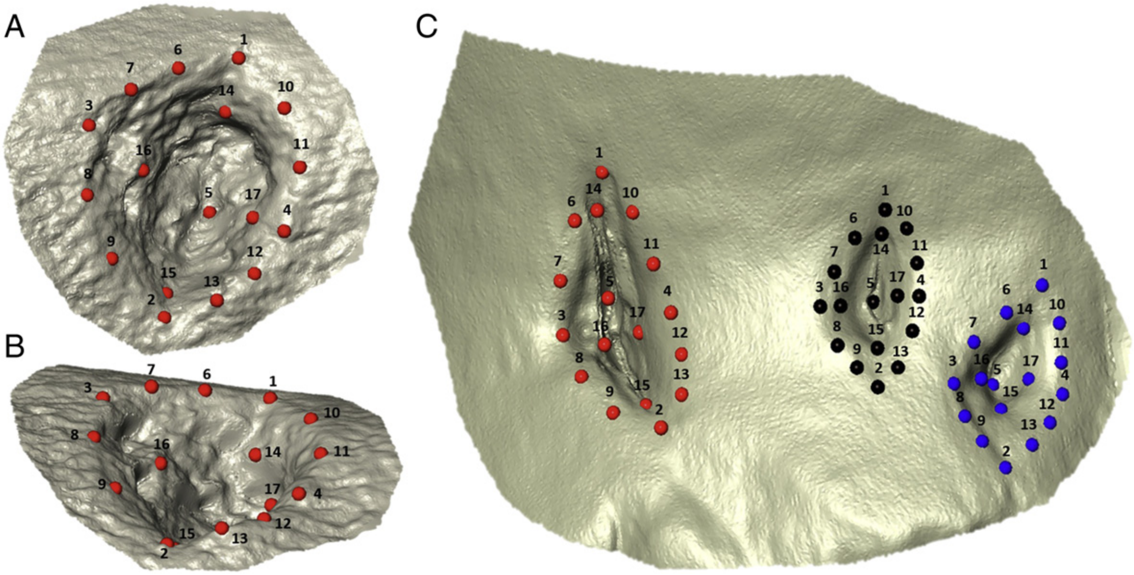

Fig. 5. Landmarks used in this study to describe carnivore pits. A) Frontal view of landmarks location on a crocodile pit; B) side view of landmarks location on a crocodile pit; C) frontal view of landmarks location on three pits observed on OH8. The numbers correspond to the description provided in Table 2.

Within configuration PLS analyses were conducted to fully address the covariation between the interior and exterior morphology of the pits in the context of the structure. This PLS technique includes changes related to the relative sizes, positions and orientations of data. Two-block PLS analyses were also performed. This allows the separate evaluation of shape and size.

Lastly, canonical variate analyses (CVA) and linear discriminant analyses (LDA) were performed to determine the shape features that best distinguish among carnivore pits (Timm, 2002). CVA and LDA provides differences among groups in Procrustes – the square root of summed squared landmark distances from their centroid – and Mahalanobis distances – distance between points scaled by the within-group variance and correlation (Klingenberg and Monteiro, 2005). A priori defined groups for crocodiles, lions, hyenas, jaguars and wolves were tested. OH8 and OH35 pits were included in a second CVA and LDA to assess their group assignation. LDA comparisons were performed in pairs and permutation tests were computed to assess differences between group means.

3. Results

3.1. Reliability test and descriptive method

The landmarks can be identified and placed reliably enough to distinguish different specimens. The PCA results are clearly polarized with the pits repeatedly landmarked plotted close to each other in shape space (Fig. 6). However, the individual pits belonging the same species do not appear as constrained in the graph. This result could be due to different variables affecting the sample. A total of 14 principal components (PCs) were obtained, with the two first PCs accounting for 57.2% of the total variance. The distance between pits generated by the same carnivore species could be conditioned by specific variables related to the single specimens.

Significant differences among carnivores on the basis of their pits could be ascertained with a MANOVA (Wilks' Lambda $= 0.03$, F $= 9.11$, $p < 0.001$). Though preliminary results suggest a clear differentiation of carnivore groups and, thereby highlight the robust reliability of the methodology, a pairwise MANOVA (Table 3) indicates that differences among mean samples are not always significant. However, possible overlapping between the pit means (see Wolf-Lion and Wolf-Jaguar) do not respond to the low reliability of the landmarking process or the repeatability of the landmarks, since repeated landmarked individuals form clear identifiable groups.

Pits generated by crocodiles on sheep and cow bones were compared. The results show that while the outer morphology of the mark does not vary based on the prey size (Wilks' Lambda $= 0.88$, F $= 0.36$, $p = 0.87$), when the interior morphology of the pit is considered in the analysis, differences in the morphology of the pits generated by the same carnivore on different carcass sizes are significantly different. Crocodile pits on bones from small and medium-sized animals can be distinguished when the depth of the incision and the inflection points are included in the analysis (Wilks' Lambda $= 0.26$, F $= 7.52$, $p = 0.002$), and when depth is excluded (Wilks' Lambda $= 0.26$, F $= 7.5$, $p = 0.002$). These results constrained our reference sample to medium-sized carcasses so as to avoid larger discrepancies and provide a homogeneous comparative sample.

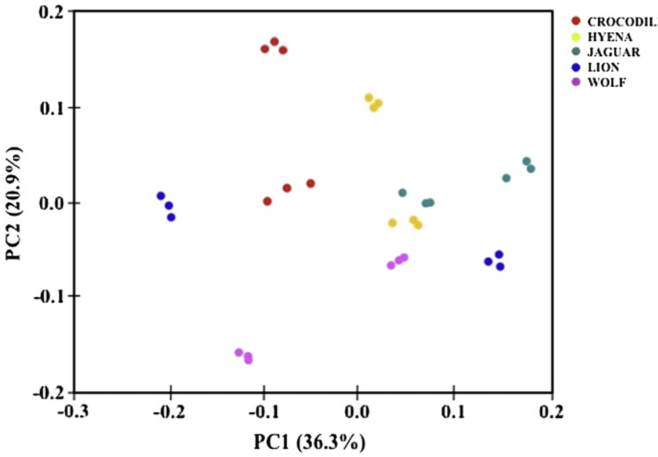

Fig. 6. Reliability test PCA with the distribution of the repeated measurements for the ten pits randomly selected in shape space. Two pits per carnivore species were selected.

Table 3
MANOVA Pairwise p values for reliability test of repeated landmarking process.

	Crocodile	Hyena	Jaguar	Lion	Wolf
Crocodile		<0.001	0.001	0.04	0.02
Hyena	<0.001		<0.001	<0.001	<0.001
Jaguar	0.001	<0.001		0.04	0.06
Lion	0.04	<0.001	0.04		0.96
Wolf	0.02	<0.001	0.06	0.96	

Since the inclusion of the interior area of the pit caused different results than when only comparing the external morphology of the mark, differences in the interior area in relation to the exterior area of the pits were assessed taking into account shape variance as well as changes related to the relative sizes, positions and orientations of the data (Table 4). The PLS shows the existence of a significant correlation ($p < 0.001$) between the structure of the inner and outer surface of the pits, though it is not very strong ($r = 0.43$). The covariation between the inner and the outer areas seem to be more strongly determined by the size ($r = 0.92$, $p < 0.001$) than by the shape ($r = 0.32$, $p < 0.001$).

The correlation of the interior and exterior areas of the pits was also examined for each carnivore independently. In all the cases, the covariation of both areas seem to be higher than when studying the whole sample. In some cases (e.g. jaguars and crocodiles) changes in the inner and outer part of the pits are strongly and significantly ($r > 0.7$, $p < 0.05$) correlated. The PLS performed for lions and wolves also show a strong overall association between the inner and outer structure ($r = 0.69$ and $r = 0.64$, respectively) that is statistically significant ($p < 0.05$). Only hyenas show a not significant and weak covariance of both areas ($r = 0.56$, $p = 0.15$).

3.2. Testing differences between carnivore groups

The PCAs of the carnivore pits in shape (Fig. 7) and form space (Fig. 8) show a non-polarized morphospace, defined by a high number of PCs. In shape space, the first two PCs explain only 34.1% of the total variance (PC1 = 18.3%, PC2 = 15.8%), while the variance expressed in the scatter-plot in form space is mainly explained by PC1 (86.8%) and PC2 (2.6%). These results might indicate that centroid size is an important factor affecting the variance of the sample, which is not surprising since carnivore groups have already been established based on pits

Table 4
PLS results obtained for the comparisons of the internal and external features of the pits.

Comparison	Sample	RV coefficient	p-value
Interior vs. exterior structure of the pit[a]	Total sample	0.435	<0.001
Interior vs. exterior shape of the pit	Total sample	0.324	<0.0001
Interior vs. exterior size of the pit	Total sample	0.921	<0.0001
Interior vs. exterior structure of the pit[a]	Lion	0.685	0.004
Interior vs. exterior structure of the pit[a]	Crocodile	0.772	0.028
Interior vs. exterior structure of the pit[a]	Hyena	0.557	0.152
Interior vs. exterior structure of the pit[a]	Jaguar	0.701	0.024
Interior vs. exterior structure of the pit[a]	Wolf	0.642	0.024

[a] Tests assesssing the structure of the pits include differences in shape, size and relative positions of the interior and exterior areas.

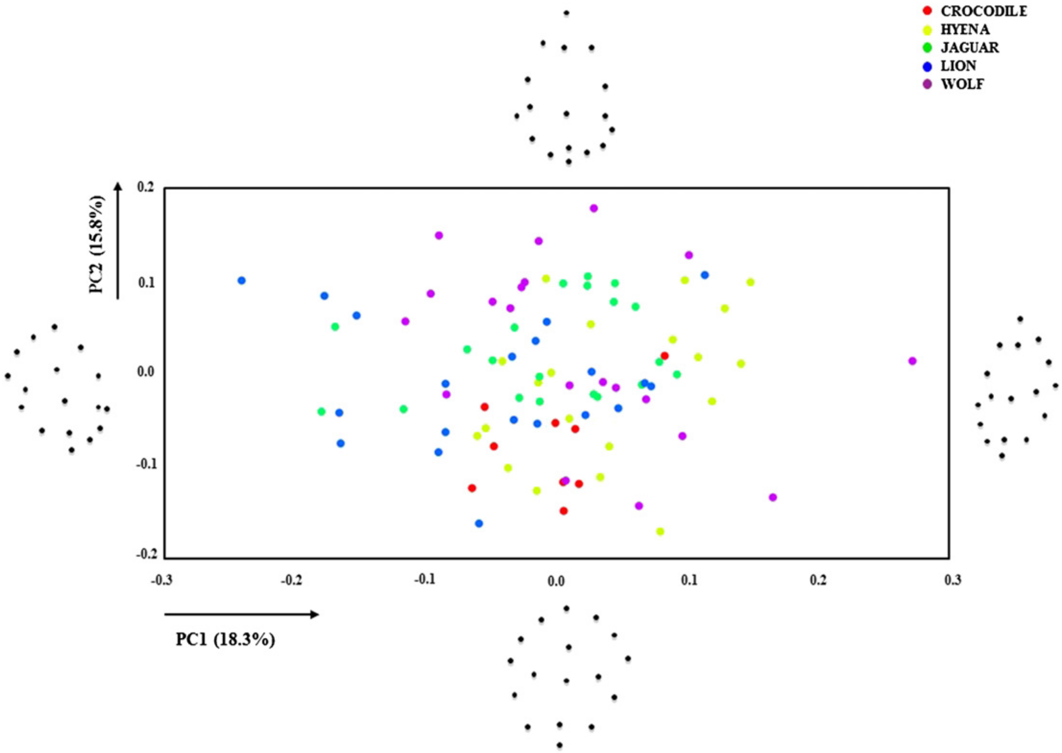

Fig. 7. Scatter-plot of the PCA in shape space. Extreme shape changes described by PC1 and PC2 are represented on the corresponding axis limit.

measurements (e.g. Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Andrés et al., 2012).

In the shape space scatter-plot (Fig. 7), the first PC appears to be approximately related to the distance between the upper inflection point and the exterior of the pit and the overall inclination of the pit. The second PC in shape space is related to the expansion of the interior area and to shape changes in the morphology of the outer area that are also characterized by the location of the widest axis of the pit. In PC1 as well as in PC2 changes in the depth of the pits are also relevant. PC3 (13.9%) was also observed as the first two PCs do not explain half of the variance of the sample. The third PC is characterized by changes in the interior surface of the pit (very constrained inflection points located in the lower part of the pit versus separated inflection points) and shape differences in the exterior area of the mark (elongated versus circular shape).

Shape changes among pits are explained differently by carnivore (Fig. 7). Wolves show the largest variability in changes expressed by PC2, while lion and jaguar variance is better explained by changes in PC1. Hyena pits vary in both axes, though its pits are usually close to the average shape and vary mostly towards the positive range, reaching the closest values between the interior and exterior points describing the pits.

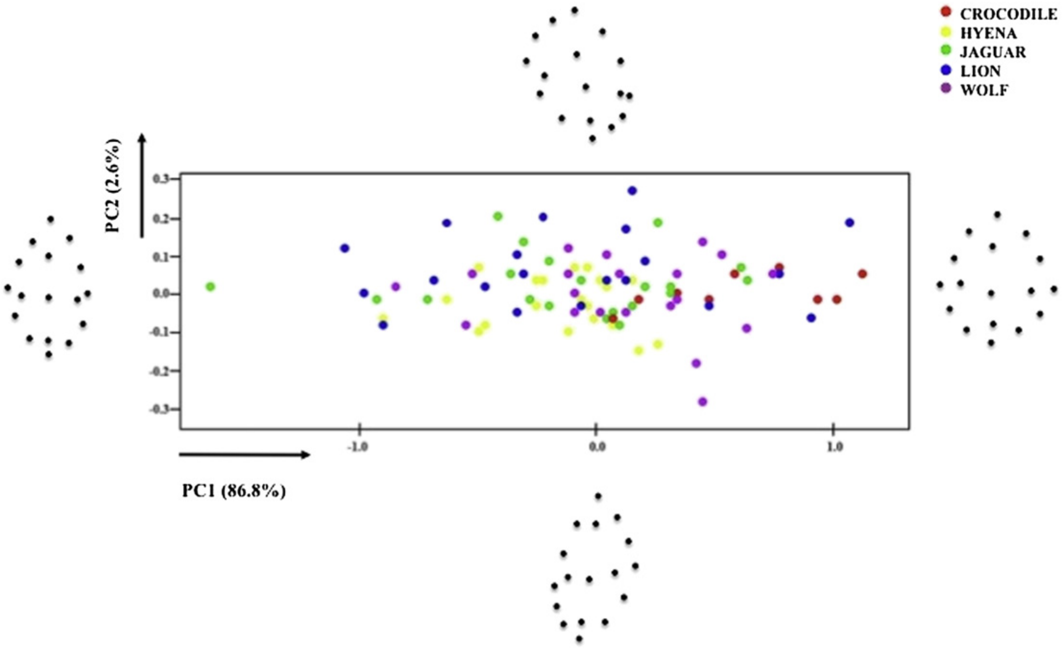

Fig. 8. Scatter-plot of the PCA in form space. Extreme form changes described by PC1 and PC2 are represented on the corresponding axis limit.

Crocodiles fall in the average range for PC1 and the negative PC2 axis, creating rounded pits and with a well-defined interior morphology that matches the pit morphologies observed among crocodiles that are not always defined by a bisected section (Baquedano et al., 2012).

In form space (Fig. 8), when the centroid size of the pits is considered, the variables that appear to mostly explain the variance in shape space, are comprised in the second PC. PC1 in form space is related to changes in the overall form of the pits with wider pits at the positive limit of the x-axis and longer and narrower pits at the negative limit of the x-axis. In form space, changes in depth are more prominent along PC1. PC2 and PC3 in form space are determined by the same variables that characterize PC1 and PC2 in shape space, respectively.

All pits in form space are mostly explained by PC1 (Fig. 8). Lions, jaguars and wolves show larger form changes, while crocodiles and hyenas are better grouped on opposite sides of the x-axis. While crocodiles generate larger, more rounded bisected pits, hyena pits are defined by an elongated smaller form whose interior is not as well defined.

Despite the visual overlapping of carnivores in shape (Fig. 7) and form space (Fig. 8), it must be acknowledged that those graphs are only a two-dimensional representation of the first two PCs. This, first, fails to explain the entirety of the variance expressed by the sample, and, second, cannot display the distance among groups in the z-axis. Therefore, further statistical tests are necessary to address differences and similarities among carnivore pits.

The MANOVAs performed on the PC scores to assess the differences among group means show significant results in shape (Wilks' Lambda $= 0.667$, $F = 1.729$, $p = 0.02905$) and form space (Wilks' Lambda $= 0.511$, $F = 3.811$, $p < 0.001$) with clear differences between the tested groups.

The CVA conducted for the entire carnivore sample support these results. The CVA is explained by only four canonical variates (CVs) that account for the variation among groups scaled by the inverse of the within-group variation. The scatter-plot of the CVA (Fig. 9) shows the dispersion of the pits generated by each carnivore according to the first two CVs that explain >76% of the differences (CV1 = 52.9%, CV2 = 23.1%). Carnivore groups are classified forming three separated areas. In the graph, crocodiles are clearly separated from the rest of the carnivores while lions and jaguars overlap, and wolves fall in the range described by hyenas. Despite graphical overlapping, most of the Procrustes distances calculated among all possible pairs of groups are significant (Table 5), except for the comparison wolf-jaguar ($p = 0.12$).

The Mahalanobis distances calculated for the same pairs of groups stress such differences, indicating a clear separation between all carnivore groups based on the pits they generate (Table 5). Mahalanobis distances are computed using a joint within-group covariance matrix that assumes that the within-group covariance matrices are identical. Differences in Mahalanobis and Procrustes distances among groups can indicate anisotropy of the variation within groups (Klingenberg and Monteiro, 2005).

In order to test Mahalanobis distances without assuming the equal values of within-covariance matrices, a jackknife cross-validated LDA was performed to assess minimal variance within carnivore groups and maximal variance between groups. Confusion matrices were extracted in pairs, that means that only two carnivores were compared at the same time. LDA results (Table 6) do stress more similarities between carnivore groups than the CVA. The confusion matrices calculated for each pair of groups indicate high confusion rates between jaguars and lions, wolves and lions, and hyenas and lions, with at least half percent of the pits incorrectly classified. The rest of group pairs could be correctly classified in most cases, with crocodiles showing the highest success rates.

3.3. Application of the 3D methodology to OH8 and OH35

The application of these techniques to tooth marks on OH8 and OH35 indicate that the pits observed on these two fossils might have been generated by different agents. PCA results in shape and form space show a non-polarized space determined by many variables, such that neither OH8 or OH35 pits can be related to any sampled carnivore. Here, we assume that wolves and jaguars are reasonable proxies for other carnivores with which hominins might have shared niches in Plio-Pleistocene Africa (e.g. wild dogs and leopards). CVA (Table 5) and LDA (Table 6) results indicate that OH8 pits cannot be differentiated from crocodile pits and are mistaken with those in >62% of the cases analyzed. On the contrary, OH35 pits differ significantly from crocodile pits (Table 5) and are more often classified as any of the other carnivores analyzed in this study (Table 6). Considering that crocodiles are the best defined and most identifiable group among the carnivores analyzed, the clear morphological separation of the OH35 pits suggests that these marks cannot

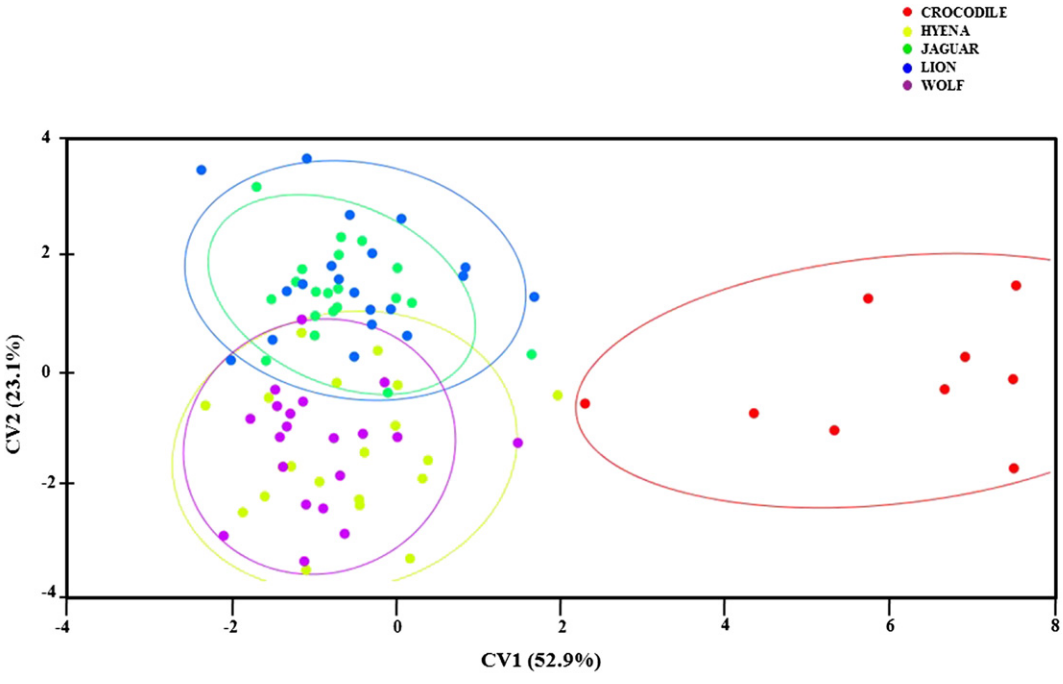

Fig. 9. Scatter-plot of the CVA.

Table 5
CVA results including Mahalanobis and Procrustes distances.

		Crocodile		Hyena		Jaguar		Lion		Wolf		OH8	
Mahalanobis D	Hyena	6.76	<0.0001										
Procrustes D		0.17	<0.0001										
Mahalanobis D	Jaguar	6.67	<0.0001	3.04	<0.0001								
Procrustes D		0.17	<0.0001	0.08	0.041								
Mahalanobis D	Lion	6.6	0.0001	2.96	<0.0001	2.54	0.001						
Procrustes D		0.17	<0.0001	0.1	0.003	0.08	0.045						
Mahalanobis D	Wolf	6.68	<0.0001	2.71	<0.0001	3.12	<0.0001	3.04	<0.0001				
Procrustes D		0.18	<0.0001	0.09	0.025	0.08	0.112	0.11	0.005				
Mahalanobis D	OH8	6.26	<0.0001	5.82	<0.0001	5.9	<0.0001	5.7	<0.0001	5.87	<0.0001		
Procrustes D		0.11	0.308	0.16	<0.001	0.18	<0.0001	0.18	<0.0001	0.17	0.001		
Mahalanobis D	OH35	6.96	<0.0001	5.91	<0.0001	6.34	<0.0001	6.55	<0.0001	6.57	<0.0001	7.4	<0.0001
Procrustes D		0.16	0.024	0.16	0.003	0.18	<0.001	0.21	<0.001	0.19	0.003	0.17	0.156

P values for Mahalanobis and Procrustes distances were obtained by means of permutation tests.

be associated with the action of crocodiles, and other carnivores are more likely to have been the modifying agent of the OH35 fossil.

4. Discussion

The present study compares pits produced by five different carnivores (crocodiles, lions, hyenas, wolves and jaguars) using a new 3D technique based on the Micro-Photogrammetric reconstruction of the tooth marks and a geometric morphometric analysis. Our results show that the replicable and reliable techniques employed allow for specific differentiation of carnivores based on the tooth pits they create. Similar techniques based on the virtual reconstruction of marks have been already applied in taphonomic studies, demonstrating their utility (Pante et al., 2017; Bello, 2011; Bello and Soligo, 2008; Arriaza et al., 2017, among others). However, while some only address questions that do not imply significant problems to taphonomists (e.g. differentiating between tooth and cut marks: Pante et al., 2017), we elucidate a finer-grained method capable of distinguishing specific agents of carnivore modification. Our methodology could also be useful to analyze the way carnivores modify carcasses from an experimental perspective. For instance, it would be interesting to determine the teeth used in the exploitation of carcasses and relate each tooth with a certain mark morphology, as it has already been done by Diedrich (2012, 2015).

Previous analyses focused on the external morphology of tooth pits, particularly the length and breadth of marks, measurements that enable the classification of carnivores according to their body size (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Coard, 2007; Delaney-Rivera et al., 2009; Andrés et al., 2012). Our analysis not only addresses these axes, but it also accounts for variation in internal pit morphology, which helps differentiate carnivores, and also includes a more detailed morphological description of their external areas. Our analysis suggests that accounting for the internal structure of pits might be of greater relevance than hitherto envisaged. Several tests assessing the relation between their internal and external structures suggest that both factors are significantly correlated, especially due to changes in size, and that such correlation varies among carnivore species. These differences might respond to the degree of variance in shape and size in each species. Hyenas are known to produce a large and variable set of tooth marks (Domínguez-Rodrigo and Piqueras, 2003), which might also be reflected in the external and internal areas of their pits they create. Therefore, it is not surprising that hyenas are the only carnivores that show a low and insignificant correlation among pit areas.

The descriptive methods applied here lay the foundations for a deeper and more detailed investigation of pits that has produced promising results in the identification of carnivore action on bones. Nevertheless, our sample is small and other species could be added (e.g. leopard, cheetah, bear, African wild dog, jackal etc.). Our preliminary results also suggest that it would be beneficial to compare pits on different carcass sizes. Our data also demonstrate that the internal features of pits vary in shape depending on prey size, engendering a need for further research in this area. It would be also interesting to analyze the way tooth pits change according to carnivore age, since younger individuals may generate a wider range of variability. Further research should be done in this area in order to compare tooth pits made by adults and sub-adults and extrapolate the results to the paleontological and archaeological record.

Further refinement of this new methodology would provide an essential tool for the study of certain modifying agents that can only be identified by the tooth marks (scores and pits) they produce during the consumption process. This is particularly the case for crocodiles for which agency cannot be assigned by furrowing patterns or skeletal part representation alone (Baquedano et al., 2012). Increasing our reference sample would also help better distinguish different carnivores acting on the same bone assemblages.

Despite these current limitations, our methodology represents a critical baseline for future taphonomic studies, and can help test previous existing taphonomic interpretations (e.g. Njau and Blumenschine, 2012).

Njau and Blumenschine (2012) argued that two separate hominins at FLK NN3 and FLK Zinj (Bed I, Olduvai Gorge) were prey for crocodiles, contending based on their taphonomic analysis that these places were high-risk and not suited for prolonged occupations and associated subsistence tasks. The only empirical evidence for this interpretation is the

Table 6
LDA confusion matrices based on morphometric data.

	Lion	Hyena	Jaguar	Wolf	Crocodile	OH8	OH35
Lion		8 (40%)	9 (45%)	13(65%)	4 (20%)	3 (15%)	3 (15%)
Hyena	10 (50%)		7 (35%)	4 (20%)	5 (25%)	6 (30%)	5 (25%)
Jaguar	11 (55%)	8 (40%)		7 (35%)	4 (20%)	3 (15%)	4 (20%)
Wolf	10 (50%)	8 (40%)	7 (35%)		0 (0%)	4 (20%)	1 (5%)
Crocodile	2 (22.2%)	2 (22.2%)	3 (33.3%)	1 (11.1%)		3 (33.3%)	1 (11.1%)
OH8	2 (25%)	4 (50%)	3 (37.5%)	3 (37.5%)	5 (62.5%)		2 (25%)
OH35	4 (66.67%)	4 (66.67%)	4 (66.67%)	4 (66.67%)	2 (33.3%)	3 (50%)	

Only the misclassified pits per each pair comparison are expressed in the table.

purported presence of crocodile marks on the OH8 foot bones and on the OH35 tibia. Njau and Blumenschine (2012) also attributed the modification of OH35 to crocodiles based on corresponding tooth marks on the distal articular surface of the tibia and the trochlea of the talus. In contrast, Baquedano et al. (2012) argued that attributing OH35 modifications to crocodiles was not well supported. The main argument used by Njau and Blumenschine (2012) to interpret modifications on the distal end of OH35 as crocodile-made is the presence of one half bisected pit. In their analysis, Baquedano et al. (2012) did not identify any bisected mark on said specimen. In addition, the presence of a single bisected mark cannot be considered a definitive proof of crocodile intervention. The corresponding mark on the talus shows a deep elongated pit, which can only have been produced by the apex of the effector perpendicular to the articular surface; that is, in the same direction as the axis of the tibia in the reconstructed image. In contrast, the "corresponding" mark on the articular edge of the tibia can only have been produced by an effector acting parallel or obliquely to the horizontal plane of the articular surface of the talus. These opposing interpretations receive new light from our morphometric analysis.

Our analysis supports Baquedano et al.'s (2012) interpretation. According to the internal and external features registered, the OH8 pits can be only associated with crocodile pits, whereas OH35 cannot be clearly related to the action of any of the agents we studied. However, our results also suggest that the OH35 modifications might be preferentially assigned to other carnivores (e.g. hyena, lion, jaguar, wolf) but not to crocodiles.

5. Conclusions

This study presents a new methodology for identifying the action of different carnivores through the 3D reconstruction and geometric morphometric analysis of tooth pits. This work thus enhances recently published studies that successfully determine carnivore types according to modifying patterns and destruction processes. The development of this research and its application to archaeological and paleontological records, where the action of carnivores is evident is critical for segregating specific carnivore agents. We demonstrated the applicability of the technique through the analysis of the pits observed on two *Homo habilis* specimens (OH8 and OH35) found at Olduvai Gorge. The results obtained with this method might improve and be more diagnostic as the reference sample increases and using larger archaeological or paleontological samples.

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