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The use of Micro-Photogrammetry and Geometric Morphometrics for identifying carnivore agency in bone assemblages

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ABSTRACT

Before sedimentation, bones are exposed to an important amount of biostratinomic taphonomic processes. One of them is related to the action of carnivores, which is reflected in conspicuous tooth marks, such as pits, scores, punctures or furrowing. Different carnivores damage bone assemblages differently. Thus, several researches have tried to identify carnivore agency based on different parameters such as skeletal profiles, tooth mark frequencies and dimensions, breakage patterns, or more recently, taphotypes. Here we propose a new methodology based on the analysis of tooth scores to determine the carnivore type involved in bone modification. For this purpose, we have built 3D models of several tooth scores produced by wolves, lions, jaguars, foxes and hyenas using photogrammetric techniques. These models were later analyzed by means of Geometric Morphometrics and multivariate statistics. We show that although there is a high degree of overlap in tooth mark morphology, the combined action of tooth score dimensions and morphology enables the identification of some of the tooth scores made by lions from those of the other carnivores with a higher degree of confidence than any other inter-carnivore comparison.

1. Introduction

Archaeological and paleontological bone assemblages are the result of potential longitudinal exposure to a variety of destructive processes. Different physic, fossil-diagenetic and biologic phenomena can affect fossil integrity and ultimately bias produce the taphonomic process. Carnivores are one of the most destructive biological agents, so they have been subject of research by several authors (e.g. Hughes, 1954; Sutcliffe, 1970; Haynes, 1980, 1981; Binford, 1981; Brain, 1981; Solomon and David, 1990; Cruz Uribe, 1991; Domínguez Rodrigo, 1999; Selvaggio and Wilder, 2001; Brugal and Fosse, 2004; Coard, 2007; Egeland, 2008; Kuhn et al., 2010; Domíguez-Rodrigo and Pickering, 2010; Yravedra et al., 2011; Gidna et al., 2013; Arriaza et al., 2016).

Bone modifications and accumulations produced by carnivores are distinguishable from those produced by humans (e.g. Cruz Uribe, 1991; Kuhn et al., 2010). Conspicuous tooth marks produced by carnivores include pits, scores, punctures and furrowing (Sutcliffe, 1970; Haynes, 1980; Binford, 1981; Shipman, 1981) (Fig. 1). All carnivores are capable of producing such surface modifications, and consequently the identification of the carnivore responsible for the bone assemblage based on the appearance of tooth marks is rather difficult.

Some authors have tried to distinguish between carnivores based on the characteristics usually left by each type of carnivore on different element and bone portions (Brugal et al., 1997; Brugal and Fosse, 2004; Domíguez-Rodrigo and Pickering, 2010; Domínguez Rodrigo et al., 2012; Domínguez-Rodrigo et al., 2015; Gidna et al., 2013; Arilla et al., 2014). Felids, hyaenids and canids create different skeletal profiles (Brugal and Fosse, 2004; Domíguez-Rodrigo and Pickering, 2010; Domínguez Rodrigo et al., 2012), tend to accumulate different preys (Brugal and Fosse, 2004), and break bones differently. For instance, hyenas fracture bones more intensively than felids (Domínguez-Rodrigo et al., 2007, 2015; Domínguez Rodrigo et al., 2012). Domínguez-Rodrigo et al. (2015) developed a new technique based on the

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Fig. 1. Main surface modifications produced by carnivores.

Table 1
Main characteristics of the sample used in this study.

Carnivore	State	Section	No bones	No scores	Prey
Lion	Captivity	Shaft	12	30	Horse
Hyena	Captivity	Shaft	12	33	Horse
Jaguar	Captivity	Shaft	9	34	Horse
Wolves	Wild	Shaft	1	30	Horse
Fox	Wild	Shaft	6	21	Sheep

identification of "*taphotypes*", which allows the differentiation between hyenas, lions and jaguars based on anatomical patterning of bone damage. In addition, the action of certain carnivores can be indentified due to exclusive behavioural patterns exhibited by specific carnivores, as is the case among bears. The bears break axial elements producing peeling, a pattern that has not been documented among other non-human carnivores (Arilla et al., 2014). Thus a body of research has led to the effective distinction among carnivores based on the traces they leave on bones.

However, sometimes evidences are not conclusive enough. For instance, the dimensions of pits or scores have long been used distinguish between carnivores (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Coard, 2007; Delaney-Rivera et al., 2009; Andrés et al., 2012), but these studies have not managed to properly isolate the marks produced by each carnivore, and have rather established carnivore groups according to their size (e.g. large carnivores like hyenas or lions, and small carnivores like foxes or intermediate-small felids).

Here we present a new technique with the aim of differentiating carnivores at the taxon level. Our methodology implies the three-dimensional reconstruction of scores and the use of Geometric Morphometrics to statistically analyze marks.

2. Materials and methods

2.1. Materials

For the present study, we have analyzed scores produced by wild carnivores and carnivores in captivity. Recent works have demonstrated that studies based on carnivores in captivity have to be carefully interpreted since their behaviors differ from those in the wild (Gidna et al., 2013; Arilla et al., 2014; Sala et al., 2014a). However, such cautions do not affect our study because score morphology and size do not present morphological differences depending on the environment but are the physical results of the application of forces and bone surface modification.

The samples consist of bone assemblages modified by captive lions, hyenas and jaguars from the Cabárceno Reserve "Parque de la Naturaleza de Cabárceno", in Cantabria (North of Spain). Carnivores in Cabárceno live in large open areas of several thousands of square meters (http://www.parquedecabarceno.com). For more details about the lion sample see Gidna et al. (2013), and for the hyena and jaguar samples see Domínguez-Rodrigo et al. (2015).

The sample of scores created by wolves was obtained in the Campelo Mount, near Sobrado Dos Montxes, Galicia (see Yravedra et al., 2011, 2012), and the one generated by foxes comes from Ayllón (Segovia), in the interior of the Iberian Peninsula.

Table 1 summarizes the sample composition used in this study (Table 1). A total of 148 scores produced by lions, hyenas, jaguars, wolves and foxes were analyzed. Most of the carcasses exploited belong to adult horses, except for one juvenile equid consumed by wolves, and 6 sheep consumed by foxes. Surface modifications produced by foxes on large carcasses are not significant (Yravedra et al., 2014), therefore small carcasses were selected for this study. We also selected scores identified on shafts for two main reasons: 1) diaphyses are denser than epiphyses, so teeth tend to penetrate less through the cortical layers of the first ones, and 2) diaphyses show a higher survival rate in the archaeo-paleontological record, so the use of a sample based on shafts would be a more useful framework for future analogies. Bone epiphyses usually are more exposed to different natural processes related to the action of carnivores (e.g. furrowing) or of water runoffs (Lyman, 1994), and tend to disappear faster.

2.2. Methods

The methodology applied in the analysis of scores is based on a previous study where we employed photogrammetry (Structure from Motion) and Geometric Morphometrics for the analysis of cut marks (Maté-González et al., 2015). Scores are similar to cut marks, as both marks share some characteristics. Scores, as well as cut marks, are longer than they are wide, though they differ in depth: scores present a shallower "U" shape, while cut marks are characterized by a "V" section that is deeper, narrower (although highly variable) and more rectilinear (Maté-González et al., 2016).

Scores were selected on the basis of their preservation and general conditions. We excluded those scores that present a bad cortical preservation or some type of post-depositional alteration. Neither superficial nor inconspicuous tooth marks that provided a bad resolution were selected for the study.

High-resolution images obtained through Micro-Photogrammetry and computer vision techniques were used for the three-dimensional modelling of scores sections. Following the methodology of Maté-González et al. (2015), Micro-Photogrammetry was used to generate precise metrical models of scores when using images taken with oblique

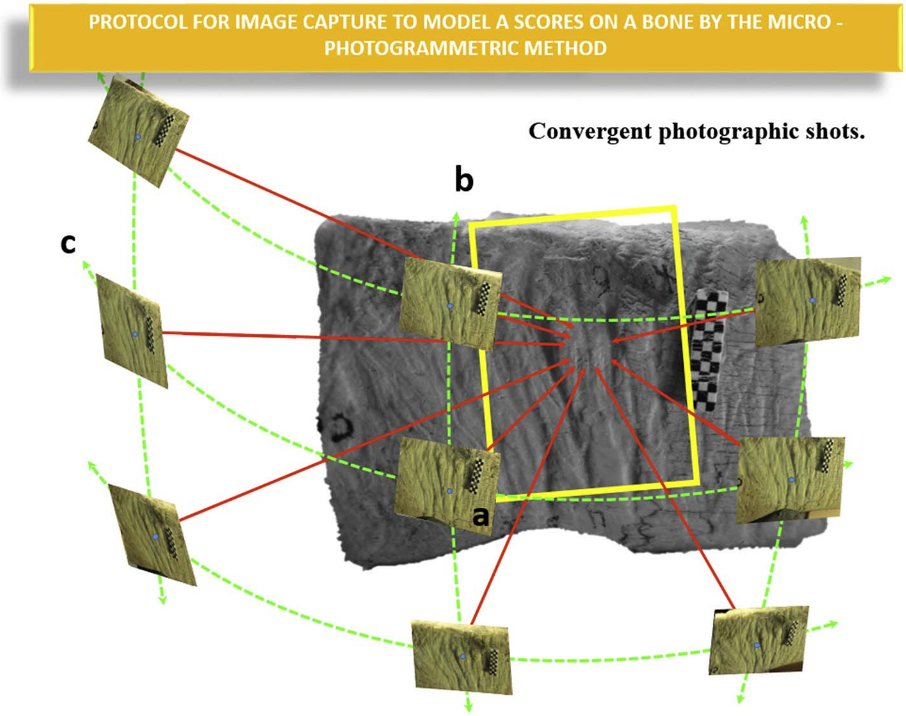

Fig. 2. Protocol for image capture to model scores on bone using the micro-photogrammetric method, with convergent photographic shots. (a) Master and dependent images in central position, (b) vertical subordinate images, and (c) horizontal subordinate images.

Table 2
Technical specifications of the photographic sensor with macro-lens.

Canon E OS 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

stereo-photography (Fig. 2). A Canon EOS 700D reflex camera (Table 2) 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. The methodology required placing a millimetric scale next to the cut mark to be photographed so as to provide a precise measurement reference.

Photographs were then taken following the specified protocol (Fig. 2). Once the photographs had been taken, they were processed to generate a 3D model for each mark. Subsequently, the photographs were treated with a photogrammetric reconstruction software GRAPHOS (inteGRAted PHOtogrammetric Suite) (Fig. 3) (González-Aguilera et al., 2016a, 2016b) or an alternative 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. 2 and 3).

For data collection, a total of 6–9 photos are taken for each score. 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 took 30–45 min depending on the final number of photos taken.

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 favourable, 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:

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

where, scaling is the scaling precision established as 1/3 of the pixel (Luhmann et al., 2013), ePHO 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 geometric and statistical level.

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 cut marks, the values for the sections between 30% and 70% of the mark length would be the most representative ones (Fig. 4). A series of measurements including WIS, WIM, WIB, OA, D, LDC, RDC (sensu Bello et al., 2013) were taken on the mark section and used as quantitative variables (see Fig. 5).

The measurements for each mark section were later compared using statistical methods. Pandora is a specific program created in R for the analysis of taphonomic marks. Pandora automatically analyzes the marks from a statistical and morphometric perspective (Palomeque-González et al., 2017). This method facilitates a fast analysis of a large number of variables and samples. Pandora incorporates several statistical tests.

In order to test if there was any difference in the dimensions of tooth marks (Fig. 5) of the different carnivores, several statistical tests were

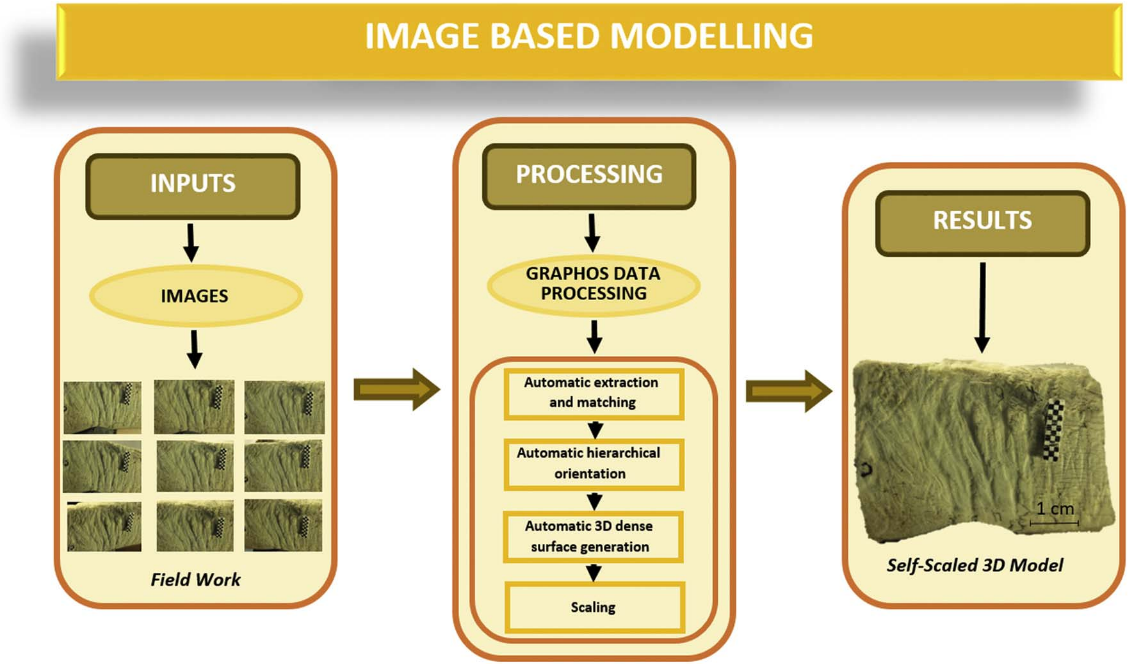

Fig. 3. Workflow of the image-based modelling technique.

applied. First, Analyses of Variance (ANOVA) and Multivariate Analyses of Variance (MANOVA) were applied to assess differences between group means. Second, a multivariate Principal Components Analysis (PCA) of the biometric data was performed with the library FactoMiner (Lê et al., 2008) using the R (www.rproject.org) software (Core R-Team, 2013). The PCA estimates similarities and differences of marks on a bidimensional Euclidean space and 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 was subsequently performed as a supplementary alternative to the Multivariate Metric Analysis (Fig. 5), focusing on shape rather than on dimensions. This technique uses information captured in the form of homologous points (landmarks, see Fig. 5) and normalizes the information by the application of superimposition procedures, known as Generalized Procrustes Analysis (GPA). This involves the translation, rotation and scaling of shapes defined by landmark configurations. After GPA, there are always some remaining differences 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). In this case, seven identical landmarks per section - as shown in Fig. 5 (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. 5. LandMark 1

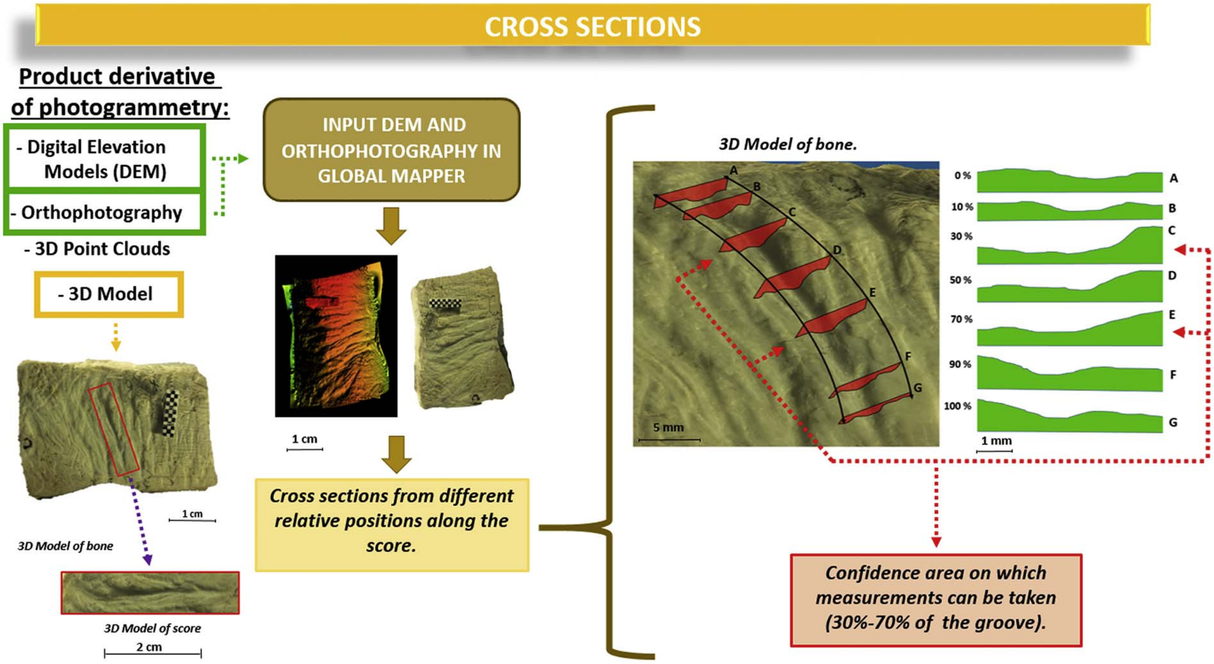

Fig. 4. Representation of the a-g sections of the score regarding its length.

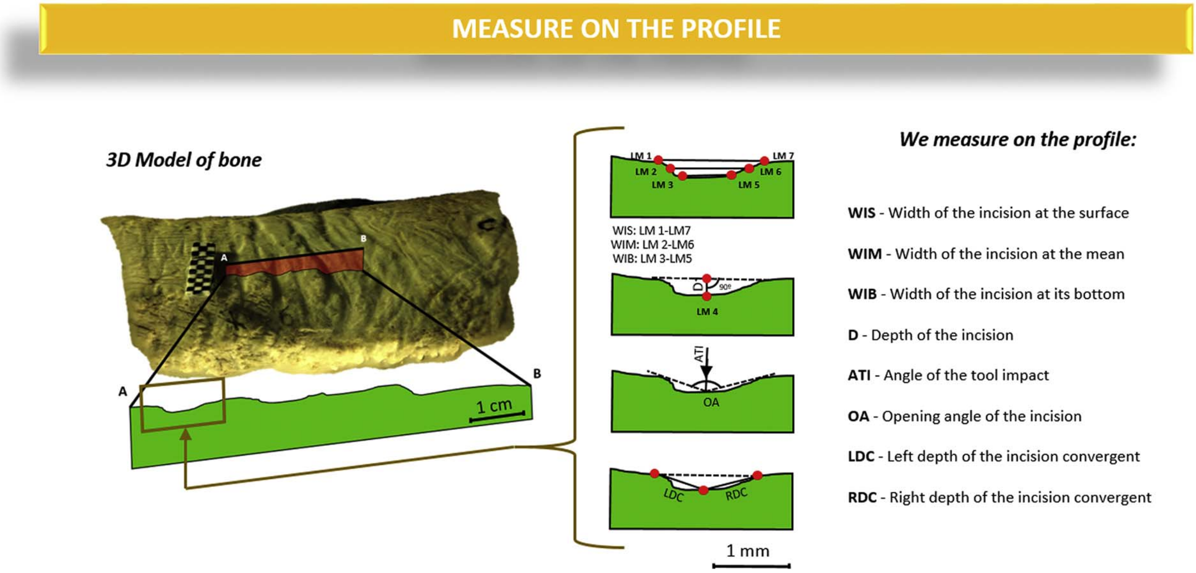

Fig. 5. Location of measurements sensu Bello et al. (2013). Landmarks (LM1–7) used for the morphometric model.

(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. 3). 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 and calculate a confusion matrix including all the scores analyzed. The LDA function included in the MASS R package was used.

3. Results

A total of 148 high quality 3D models were developed through the micro-photogrammetric method based on oblique photography. We used a reflex camera with a macro lens to generate the models of the scores on bone (average GSD (mm) = ± 0,0078; average scaling error (mm) = ± 0,0157; average precision (mm) = ± 0,0238). This method fulfils the requirements of quick capture, automatic processing of images and high precision.

The statistical tests applied on all these models show different results (Figs. 4–5).

The results obtained with the MANOVA (Table 3) and ANOVA tests (see supplementary file) tests, suggest that each carnivore group can be clearly distinguished based on the score dimensions except for wolves and jaguars (Fig. 6). Hyenas and wolves also show a certain degree of similarity; however, here it is possible to distinguish both carnivores according to the types of scores that they produce.

Table 3
MANOVA probability results obtained for the measurements (mm) taken on the scores according to the protocol explained in Figs. 4 and 5.

Pairwise MANOVA		
1	Wolf fox	0.00000000000226779434326676
2	Lion fox	0.00438941350166583
3	Lion wolf	0.000000000000457362637500933
4	Jaguar fox	0.00000000000681482540766344
5	Jaguar wolf	0.407575579390673
6	Jaguar lion	0.00000000000195081432373783
7	Hyena fox	0.000000519800895882058
8	Hyena wolf	0.0274397931792291
9	Hyena lion	0.0000000377271793144022
10	Hyena jaguar	0.00878817347543753

The PCA based on the measurements from Figs. 4 and 5 shows similar results to the ones obtained with the ANOVA and MANOVA tests, despite the intensive overlap among some carnivores. The jaguar group shows intensive overlap with other groups. Jaguars and wolves sometimes overlap hyenas, but hyena score variability is more significant, so that a certain portion of marks occurring outside the overlapping area could be more indicative of hyena's action. On the other hand, lion scores can be more clearly distinguished from the rest of the carnivores, being the most identifiable group.

We included the fox data in a second PCA analysis, which brings the small carcass size into the comparative sample. Here we obtained a similar figure (see Figs. 7 and 8) that only differs in the appearance of the overlapping area between the lion and the fox (Fig. 8). As explained in the previous section, fox action was studied on small carcasses; that is why such overlap could just be incidental.

Even if some ellipses clearly overlap (Figs. 7 and 8), there are also some exclusive areas for each carnivore.

A LDA analysis (Table 4) highlights that jaguars and lions can be relatively easily identifiable, with more than 70% of their marks classified correctly. In contrast, other carnivores present an important degree of misclassification (almost 60% or higher).

Morphometric tests (based on semi-landmark data) excluding the fox show similar results to the ones exposed above. We observe that wolves, hyenas and jaguars are grouped separated from lions, which are partly differentiated from the rest of carnivores (Fig. 9).

The morphometric test including the fox data is too confusing to provide any conclusion, as all carnivore tooth marks are plotted together in the same cloud (Fig. 10).

The LDA verifies that differences between carnivores are larger according to morphometry (Table 5) than to biometric data. Scores produced by wolves and foxes are better classified with this method (Table 5), being almost 50% of their marks correctly classified. The results obtained for the hyenas also improve, but the classification of the hyena scores still does not exceed 50% of the total. However, we do not get conclusive results for lions, as 62% of the scores produced by this felid are not well classified (Table 5).

The results obtained using the morphometric data can only classify marks correctly between 37%–55%, depending on the carnivore type, whereas data from LDA based on biometric measurements range from 24% to 76%. In both cases, the percentage of misclassification is so high that neither morphometrics nor dimensional values can effectively differentiate among most carnivore types.

Since previous tests did not provide conclusive results for all

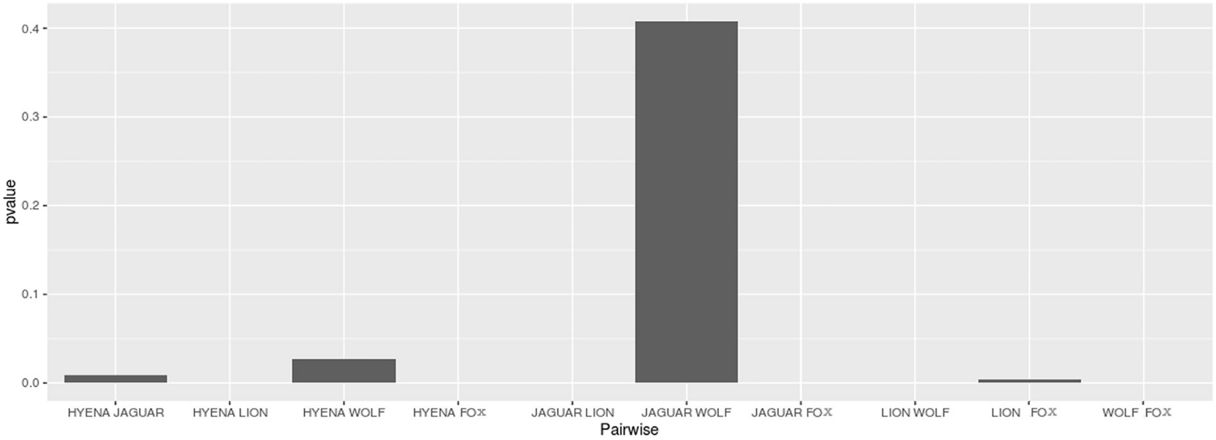

Fig. 6. Plot of the MANOVA probability results where the similarity between the scores produced by jaguars and wolves stands out above the other comparisons.

carnivores, we present a GPA plot including all landmarked specimens as a graphical aid. Fig. 11 summarizes the GPA results of wolf, hyena, lion and jaguar. Fig. 11 displays in grey the LMs of each specimen, and in black the common centroid. Several morphological differences among carnivores can be observed. The scores produced by lions are slightly different from those of the rest of the carnivores. This supports the results obtained with the previous tests. Lion scores morphology is more superficial, showing an open "U" section. Hyenas generate deeper "U"-shaped scores. Scores produced by jaguars are similar to those of hyenas, but the first one presents a higher variability, being most of the landmarks more dispersed and distant from the centroid. Wolf scores present the deepest and narrowest "U" section of all the carnivores studied.

4. Discussion and conclusions

The identification of specific carnivores based on the traces they leave in the fossil record is especially important because the presence of different carnivores may have different interpretative implications. For example, the Middle and Upper Paleolithic site of Amalda has been interpreted differently. On one hand, Yravedra (2007, 2011) claims that the bone assemblage shows no cut marks while tooth marks are significant, and that the accumulation at the site could be explained as a chamois accumulation primarily generated by leopards or lynx that was later scavenged by foxes. On the other hand, Altuna (1990) and Altuna et al. (2010) argue that the accumulation was anthropogenic, but later scavenged by foxes despite the lack of cut marks in the bone assemblage. Finally, Mallye et al. (2012) say that the chamois accumulation found at Noisetier reminiscent of the one in Amalda was produced by dholes. A micro-photogrammetric analysis followed by multivariate statistics and Geometric Morphometrics, like the one used in this study, could help dispel the doubts about the carnivore agency at these sites. The fossil accumulation at Sima de los Huesos (Atapuerca, Spain) is another worldwide example of uncertain interpretation of carnivore agency. While Andrews and Fernández-Jalvo (1997) argues that the humans found at Sima de los Huesos were eaten by lions, Arsuaga et al. (1997) and Sala et al. (2014b) claim that these fossils were modified by bears. Our methodology would be of great importance to differentiate whether the tooth marks found on these human bones were produced by lions or bears, and consequently reinterpret the deposit, since according to Andrews and Fernández-Jalvo (1997) lions were the main accumulators at this site, whereas Arsuaga et al. (1997) interpret the assemblage as an anthropogenic accumulation.

In this work we used a new technique to analyze scores based on the use of Micro-Photogrammetry to generate three-dimensional reconstructions that later enable the use of Geometric Morphometrics and

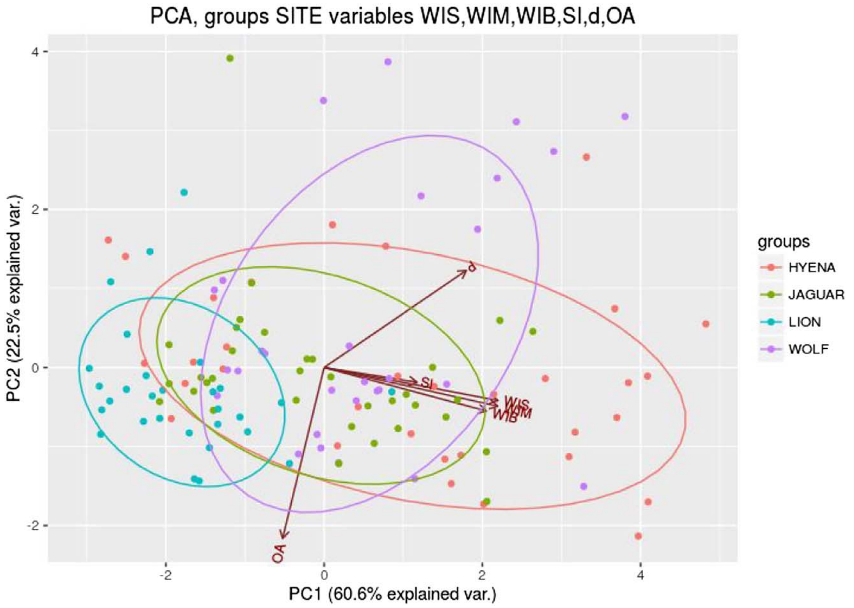

Fig. 7. PCA plot of the scores' measurements obtained following the protocol highlighted in Figs. 4 and 5.

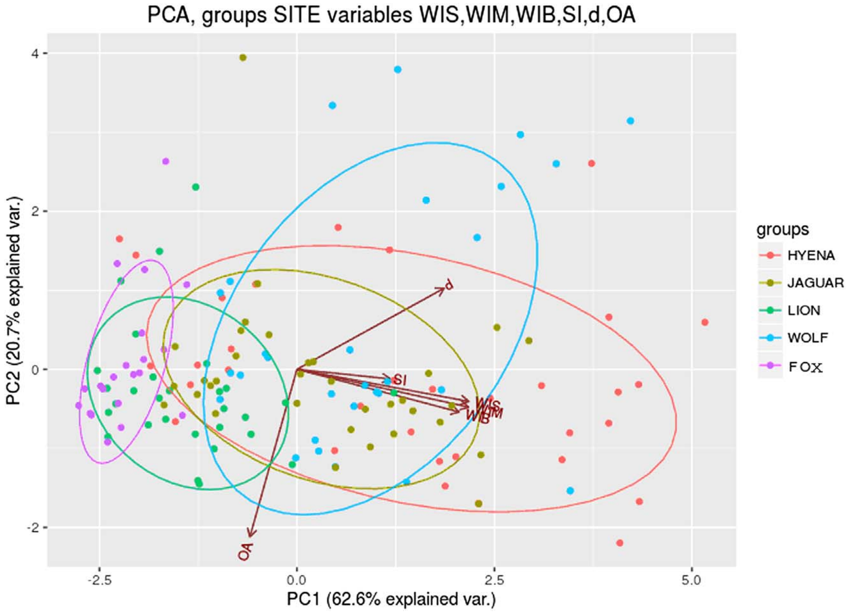

Fig. 8. PCA plot of the scores' measurements obtained following the protocol highlighted in Figs. 4 and 5. Here fox is also included.

Table 4
Confusion matrix resulting from the application of the Discriminate Lineal Analysis (DLA).

DLA	Hyena	Jaguar	Lion	Wolf	Fox
Hyena	14	5	5	6	3
Jaguar	2	26	1	4	1
Lion	1	3	21	0	4
Wolf	6	16	0	7	0
Fox	1	0	12	0	8
% confianza	0.4242424	0.7647059	0.7241379	0.2413793	0.3809524

multivariate statistical analyses. The results presented here are preliminary since only small samples (less than 32 marks for each carnivore) have been analyzed, and results do not appear to be as conclusive as expected.

The diverse statistical tests carried out in this study show that carnivores can be distinguished only to a certain extent based on the morphology and dimensions of some of their scores. Lions, for instance, produce very inconspicuous scores that can be distinguished from those generated by other carnivores using the methodology presented here. Only foxes are capable of producing tooth marks that are morphologically and dimensionally similar to marks produced by lions. Nevertheless, the ethological behaviour of these two carnivores is very different and the carcass sizes on which these two carnivores operate are also very different. Thus, taking these two factors into consideration the identification of lions should not cause problems in archaeological and paleontological contexts. This is of utmost importance, since for example, in some Pleistocene sites (e.g., Olduvai Gorge Beds I and II) where hyenas and lions may have had an important impact on the bone assemblages, this technique can help to provide further arguments for differentiate between these two agents (Domínguez-Rodrigo et al., 2007; Arriaza et al., 2016).

While the action of lions could be potentially identifiable on the basis of this three-dimensional methodology, this was not the case for the rest of the carnivores analyzed. The diverse statistical tests do not show differences between the tooth scores produced by hyenas, wolves and jaguars. The MANOVA and ANOVA test (Table 3 and Fig. 6), and the PCAs based on biometric and morphometry data were not conclusive in some in these cases (Figs. 8–10),since jaguars overlapped with hyenas and wolves. A LDA based on biometric data provided better results, around 76% of the scores produced jaguars could be correctly classified. On the contrary, the analysis of scores produced by hyenas, wolves and foxes was not conclusive (Table 4). The LDA based on Geometric Morphometrics provides less conclusive results (Table 5). Only the GPA test provides graphical aid for the distinction of the

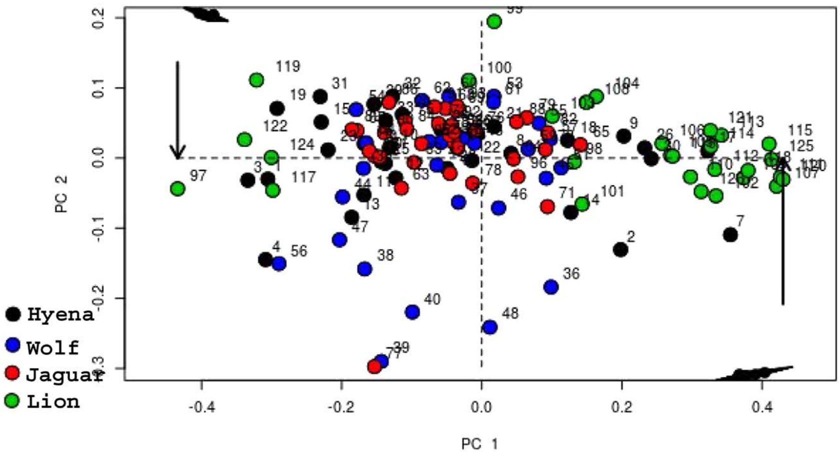

Fig. 9. Morphometric PCA plot excluding the fox.

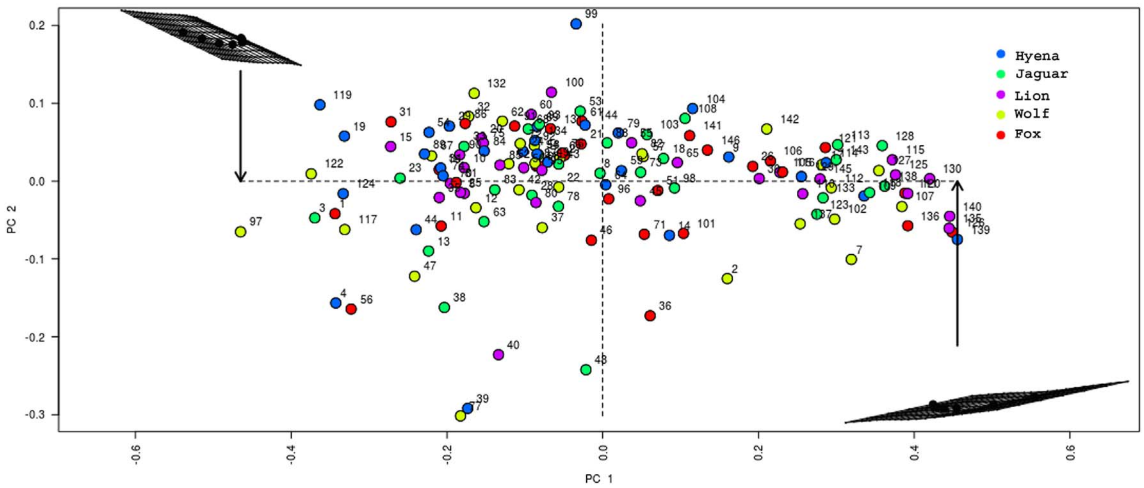

Fig. 10. Morphometric PCA plot including all carnivores.

Table 5
Linear Discriminate Analysis (LDA) of scores to estimate differences among carnivores (based on morphometric data).

LDA morphometric	Hyena	Jaguar	Lion	Wolf	Fox
Hyena	16	7	3	4	3
Jaguar	10	17	0	7	0
Lion	5	5	11	0	8
Wolf	4	9	0	16	0
Fox	3	2	6	0	10
% confianza	0.4848485	0.5000000	0.3793103	0.5517241	0.4761905

scores, being the scores produced by hyenas and jaguars quite different from those produced by wolves and lions (Fig. 11).

Future analyses will include more samples, increasing the number of scores per carnivore and probably providing more conclusive results. This study opens up the possibility of conducting future studies that might enable a reliable identification based on the analysis of scores, going one step further than previous works (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009; Andrés et al., 2012). Our study has already proved that lions can be potentially distinguished based on the morphology and dimensions of the scores. Additionally, we also have also established that some tests might be more favourable for the identification of other carnivores such as jaguars, wolves and hyenas, according to the scores left on bones.

Hence, all general the methodology used in this study could be useful in order to finally find a way to determine carnivore activity through the analysis of scores. Nevertheless, more analyses are necessary. First, the sample must be increased to have a more solid statistical framework. Secondly, tooth marks on bones showing post-depositional modifications (e.g. abrasion, biochemical marks) should also be analyzed. Thirdly the technique has to be conducted with other carnivore's types. Fourth, the technique has to be conducted with carnivores sharing ecologic niches should be analyzed in order to test the reliability of the methodology in archaeological and paleontological contexts. In our case, we analyzed two carnivores sharing the same

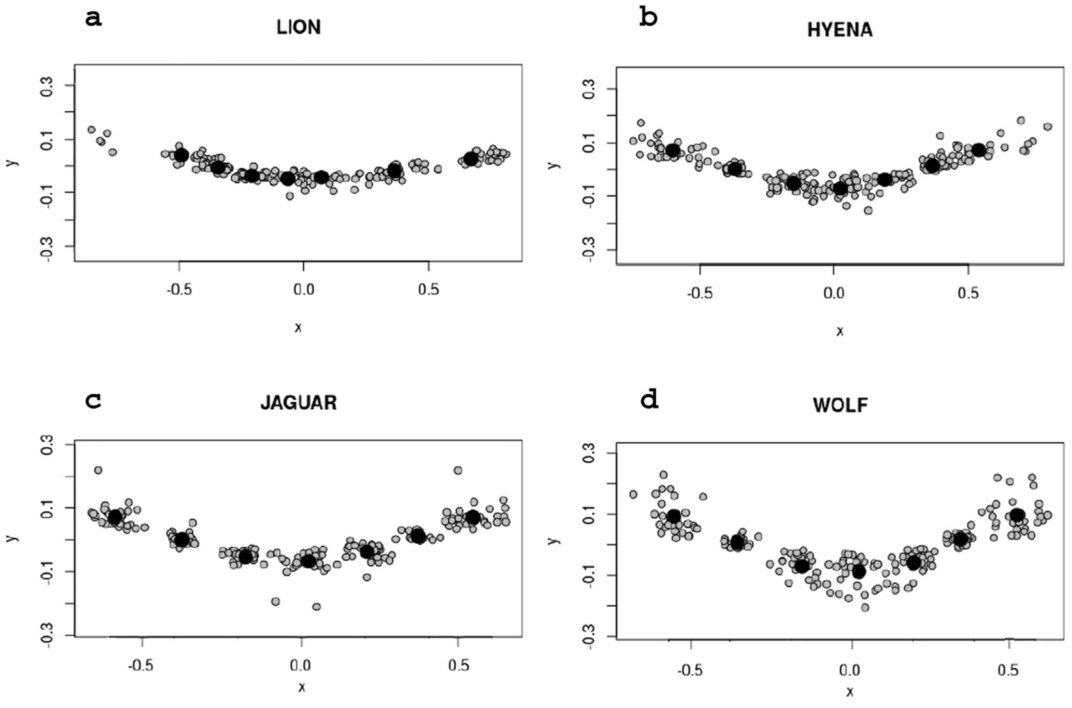

Fig. 11. GPA test including the profiles of the carnivore scores analyzed, where a: lion, b: hyena, c: jaguar and d: wolf.

habitat, lions and hyenas, that could be distinguished based on their scores. Hyenas, jaguars and wolves, do not appear in similar habitats; therefore it would be interesting to compare other pairs, e.g. bear-wolf-hyena, or jaguar-puma, etc. Finally, this technique could be also applied for the study of other tooth marks such as pits. Pits have been described as more conclusive tooth marks for the identification of carnivore types (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009; Andrés et al., 2012), thus, the use of the photogrammetric-morphometric methodology for the study of pits should definitely provide more additional results.

This technique, in addition to previous works, provides the necessary tools for the identification of the action of different carnivores such as hyenas, lions, jaguars, and wolves (Domínguez-Rodrigo et al., 2015; Domíguez-Rodrigo and Pickering, 2010; Domínguez Rodrigo et al., 2012; Brugal and Fosse, 2004; Yravedra, 2011; Arilla et al., 2014). The development of 3D and multivariate statistical techniques are largely contributing to the taphonomic knowledge of these carnivores, providing new and more precise tools for the identification of the agencies involved in the generation and modification of bone assemblages.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jasrep.2017.05.043.

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