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A comparative taphonomic study of tooth marks caused by Iberian wolves (*Canis lupus signatus*) and domestic hunting dogs (Rehala) (*Canis familiaris*) on bovine scapulae, for taxonomic differentiation

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A R T I C L E I N F O

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A B S T R A C T

For many years, the conflict between humans and wolves has persisted due to the death of livestock attributed to the attack of these animals and dogs, causing high economic costs to owners and governments. To remedy this problem, differential compensation programs have been established for the affected owners, depending on the attacker. Obtaining these benefits requires evidence to demonstrate the veracity of the complaint. Reliable approaches are needed nowadays to detect the predator, beyond any reasonable doubt. Although the analysis of teeth marks on bones has been used to differentiate carnivores, especially for archaeological purposes, its interpretation for forensic purposes is still ambiguous, due to the high range of factors that can influence tooth mark patterns, and it has scarcely been considered in previous work. This study analyzed and compared the tooth marks caused by captive Iberian wolves and by a group of domestic hunting dogs (rehala) on fresh, and disarticulated (isolated) bovine scapulae, for taxonomic differentiation purposes. Wolves showed a higher rate of modification throughout the study and, although tooth marks caused by wolves tend to be larger and wider than those caused by dogs, in most cases it was possible to find overlap between the two subspecies. Bone modifications are conditioned by a number of factors intrinsic to the scavenger or predator species, and intrinsic to the aggressor and the environment, that must be considered during the interpretation of tooth marks found on bones at a crime scene. Along with the comprehensive analysis of all evidence, the analysis of new variables of tooth marks on bones, using novel image processing methodologies and statistical analysis, has shown high potential to identify the morphological and/or morphometric variables that allow taxonomic differentiation

1. Introduction

The wolf (*Canis lupus*) preferably predates wild animals (Imbert et al., 2016; Miller et al., 2016), and domestic ungulates (Kaartinen et al., 2009), for this reason causing greater conflicts with humans and their economic interests regarding livestock (Murray, 2006). Furthermore, dogs (*Canis familiaris*) are widely distributed in southern European countries, coexisting with wolves, thus wolf predation can

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sometimes be confused with those caused by other carnivores (Cozza et al., 1996). It should also be noted that the attacks on humans by wolves or dogs are not isolated acts, and Spain is not immune to them (Rosado et al., 2009; González et al., 2017; Linnell et al., 2021). The unreliable methods used for identification (Cozza et al., 1996; Yravedra et al., 2019), and the absence of reliable data that can be used to identify the responsible predator (Caniglia et al., 2012; Yravedra et al., 2019) often make it difficult to achieve any successful and acute discrimination between whether the attackers are wolves or dogs. For this reason, wolves are blamed and systematically eliminated without solid scientific and technical reasons, according to the non-profit organization - Fondo para la Protección de los Animales Salvajes (FAPAS, 2016) cited by González et al. (2017). These strategies are inefficient due to rising compensation costs, which even encourage some farm breeders to make false accusations of predation (Caniglia et al., 2012). Some studies have tried to provide information to distinguish between different carnivores responsible for the slaughter of livestock (Project, 2011; Caniglia et al., 2012), however, the problem with these types of variables is that they are ostensibly affected by the decay process, leaving only skeletal remains for analysis. Like wolves, domestic and wild dogs can form packs and attack animals in order to feed, but they can also act as scavengers (Beaver, 2009) causing modifications on the bones during meat/bone exploitation. Although determining the predator responsible for an animal death is often difficult (Sundqvist et al., 2008; Caniglia et al., 2012), a few studies have focused on the identification and differentiation of wolves or dogs, through the analysis of tooth marks on bone remains, mainly in archaeological, zoo archeological, or taphonomic contexts, but rarely in forensics (Binford, 1981; Andres et al., 2012; Yravedra et al., 2014; Courtenay et al., 2019; 2020a; 2021 Yravedra et al., 2019). This is because wolves and dogs can also behave as scavengers, feeding on the carcasses of dead animals (Beaver, 2009; Young et al., 2015), creating tooth marks on the bone surfaces. Several simple and combined methodologies of analysis have been used to differentiate dog, wolf and other animal bite mark patterns (Delaney-Rivera et al., 2009; Dominguez-Rodrigo et al., 2012; Parkinson et al., 2014; Aramendi et al., 2017; Yravedra et al., 2017). However, from a strictly forensic point of view, we must consider that scavengers can alter the bone surfaces in many ways, depending on several variables. This differs according to the characteristics of the carcass (victim), scavengers (aggressor) and environmental factors (Haynes, 1980, 1982; Delaney-Rivera et al., 2009; Gidna et al., 2013; Sala et al., 2014), which were not included or only partially included in previous studies, as well as the context/scenes in which these marks occurred (e.g., hunting, scavenging, etc.). Consequently, efficient and accurate predator identification tools need to be developed (Caniglia et al., 2012). Forensic taphonomy, forensic odontology and, forensic veterinary combined, could allow the analysis and interpretation of tooth marks created in various contexts/scenes for forensic investigation. For these reasons, this is the first study focused on complementing and providing new information for the identification of attacks caused by domestic dogs and / or Iberian wolves through the analysis of the tooth patterns created on flat, fresh bovine bones and under controlled/standardized conditions.

2. Material and methods

The sample comprised tooth marks caused on fresh and carefully defleshed and disarticulated bovine (*Bos taurus*) scapular bones. The biting animals were seven captive Iberian wolves and a group of seven mixed hunter dogs with a known owner. In the Iberian Peninsula, this group of dogs is known as “rehala”. This type of dogs was chosen because they share certain physical (e.g., size, weight, and high biting force) and etiological (e.g., hunting in packs) characteristics with Iberian wolves. The wolves were individually housed in spaces constructed simply by fencing in natural areas to keep their environment as natural as possible. They had reduced contact with unknown humans and were fed a whole chicken carcass diet on some days every week. Eye contact between them was almost non-existent. The dogs were temporally separated during the study but they had direct eye contact with each other during the experiment. The wolves’ tooth mark patterns were obtained at the Centro de Fauna José Peña (Navas del Rey, Madrid, Spain) and the Centro de Educación Ambiental La Dehesa (Albacete, Riópar, Spain). The hunter dogs’ tooth mark patterns were registered in the city of Albacete (Riòpar, Spain). Only adult wolves and dogs, weighing over 25 kg, with no sex differentiation and healthy teething were included in the study. The experimental set included 84 scapular bones obtained from a local slaughter house (Carsana SL., Madrid, Spain). The selected scapulae were treated separately and the musculature was carefully detached from the bone to avoid causing tool marks on the bone surfaces. The procedure was carried out under the supervision of two veterinarians (co-authors). Forty-two scapulae from different bovines were offered to the groups of wolves and dogs during the study. Each day, two scapulae of one side (left or right) were given to the wolves. The dogs group received the two opposite scapulae from the same animals. This procedure was conducted to eliminate possible differences between the substrates used by the two groups, which may influence the results. Therefore, over the three days of the experiment, six bones were left exposed to each wolf and six to each dog. The carnivores worked on the bones for five hours, then the bones were removed for recording the tooth marks, while preventing the complete destruction of the bone. To stimulate bone consumption by the wolves, the bones were left inside the enclosure where the animals spent the day when not receiving scheduled feeding. They ate chicken carcasses several times a week, every other day. Likewise, the dogs received the bones 2 h before their normal feeding time and on the same day as the wolves. To avoid them focusing on just one of the bones and to verify consumption behavior, the two bones were left on the field in separate places and at an equal distance from each animal. Each bone was labeled with a different number in order to identify the specific animal that fed upon it and the date and location where they bit.

Briefly: The scapula is a pair of bones and the first bone of the forelimb, which is positioned on the lateral surface of the trunk, at the junction of the ribs and neck. Externally, the scapula is formed by two blades of cortical bone, which create two faces (medial and lateral). The cortical bone covers areas with or without spongy bone (trabecular /cancellous bone/diploe). This bone articulates with the head of the humerus (long bone) forming the shoulder joint (Structures of bovine scapula in Supplementary Material, Fig. S1). Among the diploe fibers, the bone marrow is deposited in variable amounts. The scapula has several points of muscular insertion on both surfaces (König and Liebich, 2020). This bone is held and attached to the trunk only by muscular masses, which makes it a potential target for bites and, consequently, a potential source of tooth mark patterns caused during the disarticulation of the carcass and feeding (Haynes, 1982). In order to use more standardized samples, the bones were selected from 42 bovines (8–24 months old), farmed for human consumption. All of them were raised under similar management and feeding conditions. The bones were frozen, following the methodology performed by Sala et al. (2014) until 72 h before the experimentation. In order to relate the bone density with the degree/type of modification, the thawed bones were scanned using computed tomography equipment (Spiral CT Scanner System, Philips, MX 4000 Dual, Shenyang, China) facilitated by Servicio de Policlínica at the Centro Militar de Veterinaria de la Defensa (Madrid España). For bone density determination, the analysis considered the mean of the Hounsfield Units, averaging the density of three different points of different and well-known anatomical regions of the scapula (values closer to −1000 indicate lower density) (Schwarz and Saunders, 2011). Areas with different densities constitute the points of interest for the study of marks. To visualize the macroscopic changes caused to the bones by the two groups of animals before and after the experiment, and prior to the cleaning and analysis of the tooth marks, the thawed bones were photographed with a DSRL digital camera (Nikon D60®,Tokyo, Japan) mounted on a tripod (Hama®, Barcelona, Spain). The photos were taken at a natural 90-degree angle (Fig. 1). For the same purpose, the osteological gross integrity was also registered 48 h before the experiment through X-ray analysis (Trasportix LW AL, TXLW-4 kW model, Milan, Italy). The parameters used were: Voltage: 54 – 58 KVp; Current: 50 mA; and exposition time: 0.08 s. During the investigation, the bones remained in a sealed box, protected from the sun and insects, and covered with cold gel packs. As in similar previous studies (Delaney-Rivera et al., 2009), the animals were presented with defleshed bones to avoid significantly modifying their diet. Only small fibers of muscle tissue, tendons and ligaments were still present on the bones before the experiment (Fig. 1a). These fibers were not removed to avoid creating artifacts and tool marks on the bone surface before the experiments. For that reason, the bones were transported separately in plastic bags, to avoid creating scuffmarks. In addition, the bones were weighed (in grams) just a few minutes before and after the experiment with an electronic weighing scale (Gold Balance JL6001GE, Mettler-Toledo GmbH, Germany). The weight loss was used as an indirect way to determine the degree of modification or percentage of bone loss. The scapula weights, given to each group, were statistically analyzed before the experiment to verify homogeneity and to rule out the weight factor in the results. External factors, such as Temperature (°C) and relative humidity (%), were registered during the experiment with a data logger (Cryopak iMINI, Cryopak Europa, France). To confirm the possible interaction and participation of wolves and dogs in consumption, and to relate the tooth mark patterns with consumption behavior, the animals were monitored/recorded during consumption using a video camera (Legria HF G40, Canon Europa N.V, Bovenkerkerweg, Netherlands) following reported protocols (Sala et al., 2014). For the experimental part, the animals needed to adapt to the researchers' presence and filming equipment, in order to avoid the distress exhibited due to the proximity of human observers for a long time. Hence, the researchers attended the filming locations and facilities daily for two weeks prior to the experiment, accompanied by the animals' caregivers. Once the remains were recovered, the bones were photographed (Fig. 1b) and macerated in cold drinking water (Ajayi et al., 2016) for two weeks to remove the remaining soft tissues. Prior to the tooth mark analysis, the bones were cleaned, air-dried, and photographed (Fig. 1c). The bite mark pattern analysis was performed using a Stereoscopic microscope (MZ 16 A, Leica Microsystems, Spain) with a Digital camera (LEICA DFC550, Leica Microsystems, Spain) and LED light source (KL 1600 LED, SCHOTT, France SAS) belonging to the National Museum of Natural Sciences (Madrid, Spain). The comparative analysis of bite marks between the two groups included: the presence/absence, type, number, and dimensions of the tooth marks, the percentage of bones with tooth marks, and the survival rate of anatomical structures according to their density. The tooth marks were identified on the basis of the published Binford criteria (Binford, 1981). Tooth pits were defined as circular to oval/circular depressions resembling the shape of an individual tooth crown or cusp. Punctures were defined as circular/oval and irregular-shaped marks in which the entire thickness of the compact bone was breached. Tooth scores were defined as marks with a length measuring twice their breadth. Furrows were defined as broad and linear gouges where the thin cortical bone had been torn away, exposing the underlying cancellous bone. In some cases, crenulated edges were described as the result of punctures of the cortical bone, and chipping of the edges of fractured bones. The survival rate of each anatomical section analyzed was calculated as the number of structures found post-consumption divided by the total number of bones delivered to each group ($n = 42$) x 100. For the bite mark pattern analysis, two independent observers measured the length and breadth of the tooth marks (in mm), which included a perimeter marked by any modification of the original cortical surface. The analysis included only superficial and isolated tooth marks with good cortical preservation and general condition.

2.1. Statistical analysis

Data collection was recorded in a spreadsheet (Office Excel, Microsoft, Washington, USA). A descriptive analysis of the data was carried out, for which the mean ($\overline{X}$) and its respective standard deviation (SD) were determined. The following tests were also performed with 95% reliability: Shapiro-Wilk normality tests, independent samples t-test, Kruskal-Wallis non-parametric test, one-way ANOVA test, and Tukey's test for multiple comparisons. For construction of confidence intervals, a reliability of 95% was used. For data analysis, the statistical program IBM SPSS Statistics (version 23.0, IBM-Corp Armonk. USA) was used. A value of $p < 0.05$ was chosen as the threshold of significance. This study was approved by the University of Alcalá Ethics Committee (code: CEI: CEI/UAH/AN/2021–008).

3. Results

Both carnivore groups were able to create tooth marks on the osseous surface of the scapulae during the three days of the experiment and under similar environmental conditions. The average temperatures and relative humidity recorded during the first, second and third days, were:

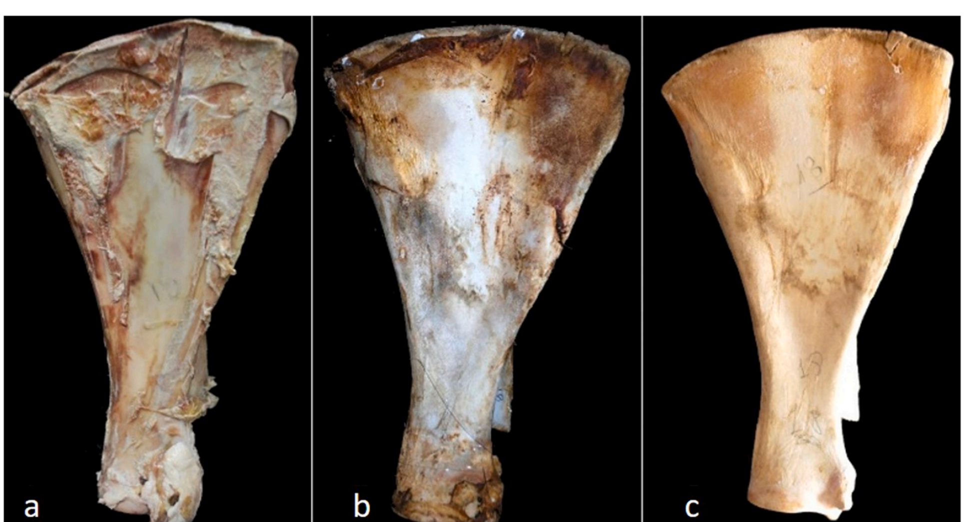

Fig. 1. Left bovine scapula (medial view). (a) Scapula previous the experimentation (some fresh soft tissue is still present); (b) Post experimentation (scarce dry soft tissue is still present); (c) Clean bone, prior to analysis.

27 °C and 26.6%, 24 °C and 44%, and 21.7 °C and 37.3%, respectively. In both groups, most of the bones suffered some degree of modification with the gross presence and overlapping of tooth mark patterns within each group. In percentage terms, the number of modified bones was higher in the wolf group than in the dog group after the three days of the experiment (95.2% vs. 83.3% of bones, respectively). Table 1 shows the percentage value of the daily weight loss of the bones, for the wolf and dog groups, which is an indirect way of determining the degree of bone modification/utilization of the bones.

There was a statistically significant difference ($p < 0.05$) in the degree of modification between the two groups. The wolves caused a higher level of modification than the dog group at the end of the study (33.6% ± 10.8 vs. 25.7% ± 7.6, respectively). This is considering that the bone sets used for each group before the study did not show significant differences ($p = 0572$, Independent samples t-test) in terms of average weight (711.4 g ± 75.3 vs. 723.7 g ± 72.8 for the wolf and dog groups, respectively). However, both wolf and dog groups presented significant differences ($p = 0.011$, U-Mann Whitney test) in the rate of modification on the first day of the experiment (Table 1). Although, for both groups, the modification rate was successively smaller with every new day of the experiment, the percentage of variation per day was less in the dog group throughout the study. In fact, the level of modification was only statistically significantly different in the wolf group ($p = 0.001$, U-Mann Whitney test) each day of the experiment while in the dog group, only the third day of the experiment showed a significant difference (day1 vs. day 3 ($p = 0004$) an, day 2 vs. day 3 ($p = 0.033$), Tukey's post hoc test) compared to the previous two days (Table 1). In addition, it became clear in the wolf group, that the degree of bone modification/utilization caused by the same individuals significantly decreased as the research progressed. In other words, the same individual modified the bones less and less with each new day of the experiment. This behavior was not observed in the dog group (Table 1). Conversely, not only was the quantity of tooth marks increasingly scarce, but also their intensity was reduced. This behavior was more pronounced in the wolf group.

3.1. Structure densities vs. modification

There were variations in the thickness of the blades depending on the part of the bone (Results of the comparative statistical analysis between the densities of the bone structures of the bovine scapula in Supplementary Material (Supplementary Tables S1, S2 and Supplementary Figs. S2, S3-left). According to these preliminary results the following anatomical regions (bone areas/zones) were selected for bite mark pattern analysis (Fig. S3-right). (a) the proximal area of the scapula; (b and c) the cranial and caudal borders, respectively; (d and e) the supraspinous and infraspinous fossae, respectively (central portion of the blades); (f) Acr; (g) the supraglenoid tubercle (including the coracoid process); (h) the glenoid cavity (articular cavity to the humeral head); (i) the margin of the glenoid cavity and SS. In order to position the tooth marks more precisely on the SS, this structure was divided into two parts: the base of spine of scapula, as the region close to the blade, and "border of the spine of the scapula (BSS)" as the most lateral area of the spine. The names "base" and "BSS" were arbitrarily assigned. Table S1 shows the number and percentage of bones with the presence/absence of tooth marks and their distribution according to the average cortical

Table 1
Percentage of bone weight loss per individual and comparative degree of modification in each group per day of the experiment.

Day	Id	Scapular weight (g) Pre and post experiment (wolves)	(DM) Percentage weight loss* (%)	Scapular weight (g) Pre and post experiment (dogs)	(DM) Percentage weight loss* (%)
1	1	1669 – 1023	32.7	1590 – 1081	32.0
	2	1514 – 940	37.9	1383 – 919	33.6
	3	1550 – 520	66.5	1545 – 1057	31.6
	4	1565 – 986	37.0	1474 – 1079	26.8
	5	1528 – 995	34.9	1416 – 1070	24.4
	6	1524 – 905	40.6	1517–918	39.5
	7	1400 – 804	42.6	1396–1017	27.2
2	1	1513 – 1038	31.4	1370 – 974	28.9
	2	1581 – 1088	31.2	1492 – 1164	22.0
	3	1446 – 714	50.6	1313 – 950	27.7
	4	1365 – 991	27.4	1679 – 1178	29.8
	5	1275 – 863	32.3	1497 – 1014	32.3
	6	1576 – 1067	32.3	1523 – 1279	16.0
	7	1320 – 888	32.7	1149 – 731	36.4
3	1	1226 – 998	18.6	1280 – 1164	9.1
	2	1219 – 846	30.6	1365 – 1109	18.8
	3	1560 – 1190	23.7	1390 – 1162	16.4
	4	1247 – 988	20.8	1451 – 1177	18.9
	5	1420 – 974	31.4	1512 – 1087	28.1
	6	1260 – 1040	17.5	1605 – 1262	21.4
	7	1269 – 860	32.2	1450 – 1163	19.8
		Total average percentage loss	33.6 ± 10.8 ($\overline{X}$ ± SD)		25.7 ± 7.6 ($\overline{X}$ ± SD)
Rate of bone modification/utilization within each group per day of the experiment					
Day		Wolves ($\overline{X}$ ± SD)	Dogs ($\overline{X}$ ± SD)		
1 *		41.7 ± 11.4^{a}	30.7 ± 5.1^{a}	p = 0011 * (U-Mann Whitney test)	
2		34.0 ± 7.6^{b}	27.6 ± 6.7^{a}	p = 0128 (U-Mann Whitney test)	
3		25.0 ± 6.4^{c}	18.9 ± 6.1^{b}	p = 0085 Independent samples t-test	

(Id) Individual; (DM) degree of modification; (*) for calculation of the DM, the difference between the total weight of both scapulae before and after each day of the experiment was considered and rounded up or down to one decimal place; (*) Statistical difference between groups ($p < 0.05$) (Different superscript letters indicate significant differences within each group ($p < 0.05$)); ($\overline{X}$): mean values; (SD) standard deviation.

density of each structure and their survival, for both groups. The differences between groups were found in the degree rather than the kind and distribution of tooth marks, while the type of tooth mark across the bone was non-random. The degree of modification and the type and quantity of tooth marks showed was related to the density of the cortical bone of each scapula portion. Four points were more intensively gnawed by the animals: (1) the proximal area of the scapula; (2) the transition zone; (3) the supraglenoid tubercle (and coracoids process); (4) the BSS, and (5) the margin of the glenoid cavity. Among the structures with the lowest cortical bone density, the proximal area of the scapula suffered the heaviest use, and was usually destroyed. In the wolf group the cranial and caudal portions of the proximal area (Fig. 2) were completely removed in more than 92–95% of the bones. In the dog groups, a smaller and more variable degree of destruction of the cranial and caudal portions (71% −91%) of the proximal area was found. However, the central portion of the same area presented less damage in both groups (Table S1, Fig. 2). Other structures with statistically similar cortical bone density (Table S2, Fig.S3-left) suffered variable modification, but never experienced complete destruction. Considering the wolf and dog groups, the acromion remained intact in 52% vs. 77% of the bones, and was gnawed in varying degrees in 39% vs. 19% of the bones, and completely destroyed in 9% vs. 4% of the bones, respectively. In the wolf group, the coracoid process (on the supraglenoid tubercle) remained unchanged in 21% of the bones and was completely destroyed in 79% of cases. In the dog group, the coracoid process registered a variable degree of modification. The coracoid process was never fully destroyed in 81% of the bones and remained intact in 19% of the bones. In all cases, in percentage values, the wolves registered a higher degree of bone modification than the dogs. Varying degrees of modification were observed on the margins of the glenoid cavity (with intermediate density of cortical bone), but there was never complete destruction. The regions with higher density preserved a large part of their structure. Wolves and dogs caused modification of 2% and 5% of the bones, respectively. In both groups, the caudal and cranial borders remained unchanged. However, the entire structure of the supraspinous and infraspinous fossae was preserved without tooth marks in 93% of the bones bitten by dogs and 64% of the bones bitten by wolves. The base of the spine of the scapula remained intact in a high percentage of the bones. Finally, the transition zone displayed a survival rate of 61% for wolves and 88% for dogs.

3.2. Tooth marks on the bones

In both groups, furrows were the most frequently occurring type of tooth mark, followed by pits. The maximum percentage of furrowed bones was 60% vs. 83% and the maximum of pitted bones was 43% vs. 74% for wolves and dogs, respectively. The supraglenoid tubercle, the BSS and the margin of the glenoid cavity presented variable degrees of modification, especially in bones gnawed by wolves (Tables S1, S2 and Fig. 3a-c). The number of furrowed bones on the proximal area caused by dogs was percentage-wise higher than that caused by wolves. However, the intensity of the damage caused by the wolves in this same area was much higher than that caused by dogs. In 36% and 7% of the bones bitten by wolves and dogs, respectively, a crenulated edge was created by removal of circular pieces of bones (Table S1) in the transition zone and central portion of the blades of the scapula (Fig. 3d). In some cases, the zones of BSS (with the exception of TSS and Acr) presented with chipped edges in 43% vs. 40% for wolves and dogs, respectively (Fig. 3e). The surviving structures displayed pits (Fig. 3f-i) and scores (Fig. 3j, k) tooth marks. Pits and scores were present in 43% vs. 74% and 14% vs. 36% of the bones, for wolves and dogs, respectively. In decreasing order, pits were more visible and concentrated in the transition zone (Fig. 3f-h), the proximal area, the margin of the glenoid cavity (Fig. 3i), the supraglenoid tubercle, the glenoid cavity and the base of the spine of the scapula. There was significant overlap of pitted tooth marks on these structures, making it almost impossible to make accurate measurements, especially in the group of dogs. The wolves caused pitted tooth marks on a smaller number of bones than the dogs on the majority of the analyzed structures, except for the glenoid cavity. Scoring tooth marks were observed in a smaller number of bones than pitted tooth marks for both species. However, the group of dogs caused a higher number of scored bones than wolves (52% vs. 21%), respectively). The marks were mainly placed in the transition zone, the proximal area (Fig. 3j, in the glenoid cavity and its margin, and exceptionally on the base of the scapula and the TSS. The degree of destruction caused by the wolves eliminated the possibility of finding a greater number of pits or scores, especially on the zones covered by low-density cortical

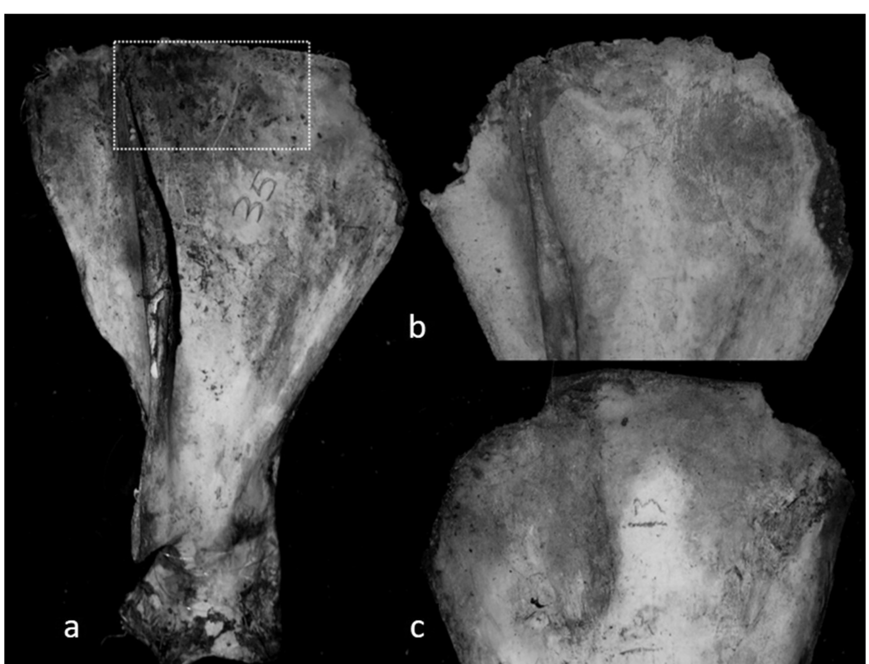

Fig. 2. (a, b) left and (c) right bovine scapula gnawed by wolves or dogs**.** The rectangle of dotted white lines corresponds to the central portion of the proximal area of the scapula. Note the major activity on the cranial and caudal portions of this area, and minor activity in the central one.

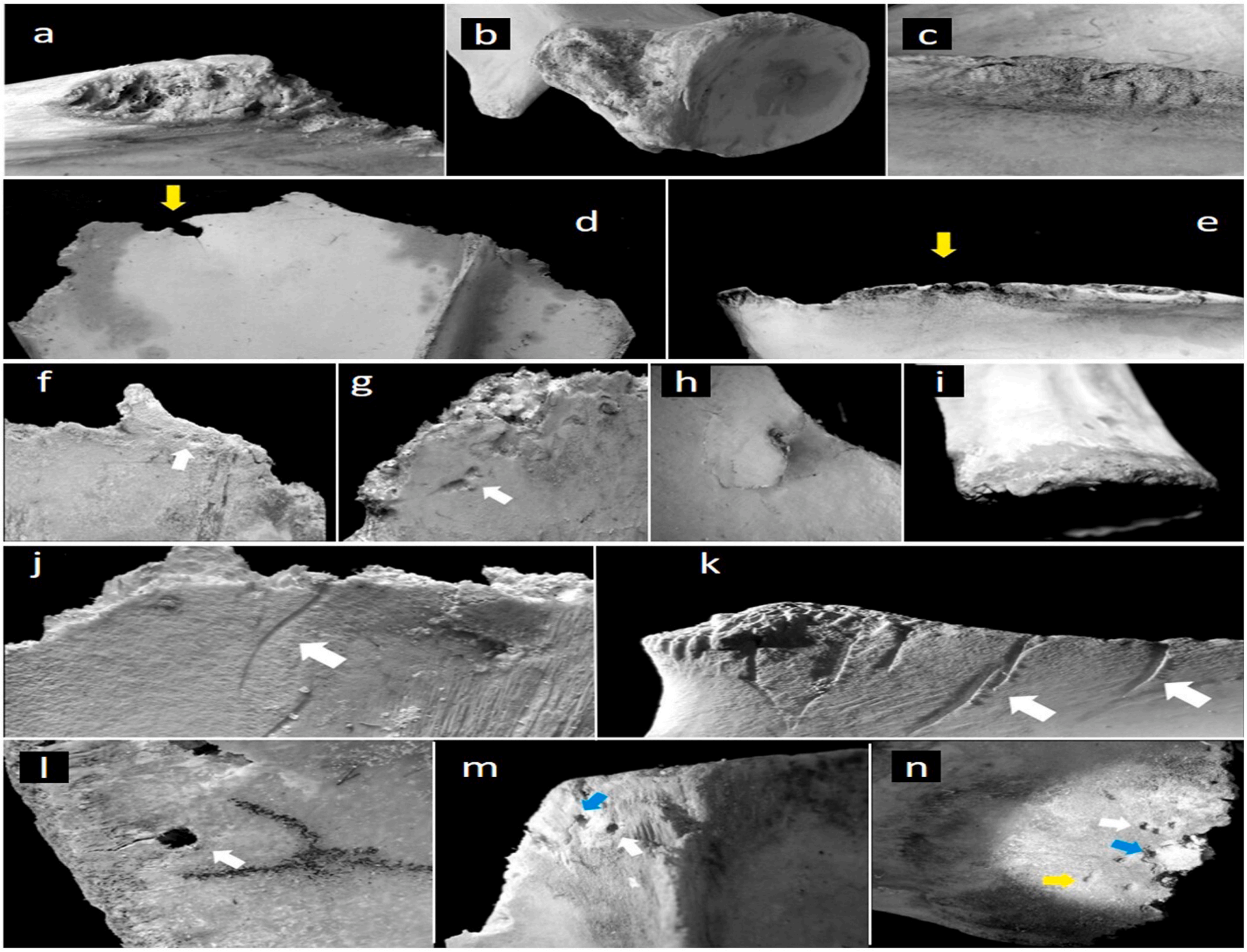

Fig. 3. Clean scapulae. Minor destruction (furrowing) caused by both groups of animals: (a) Dorsal border; (b) Supraglenoid tubercle and coracoid process; (c) TSS. (d) Crenulated edge of the clean scapula blade (yellow arrow). (e) Chipped back (features of a microdenticulate on the BSS, yellow arrow). (f, g) Pitting in the transition zone of the scapula. (h) Pitting in the central portion of the scapula (fossae). (i) Pitting around the margin of the glenoid cavity. Lateral view of the scapula: (j) Scores on the zone of transition and proximal area (white arrow). (k) Scores on the base of the SS, below the chipped edges present on the BSS (white arrows). Puncture tooth marks in the proximal area of the scapula: (l) Isolated circular puncture (white arrow); (m) Circular punctures (white arrow) and a puncture with associated fracture (blue arrow); (n) a group of circular punctures (white row), a puncture forming part of the fracture line (blue arrow) and pitted tooth marks (yellow arrow).

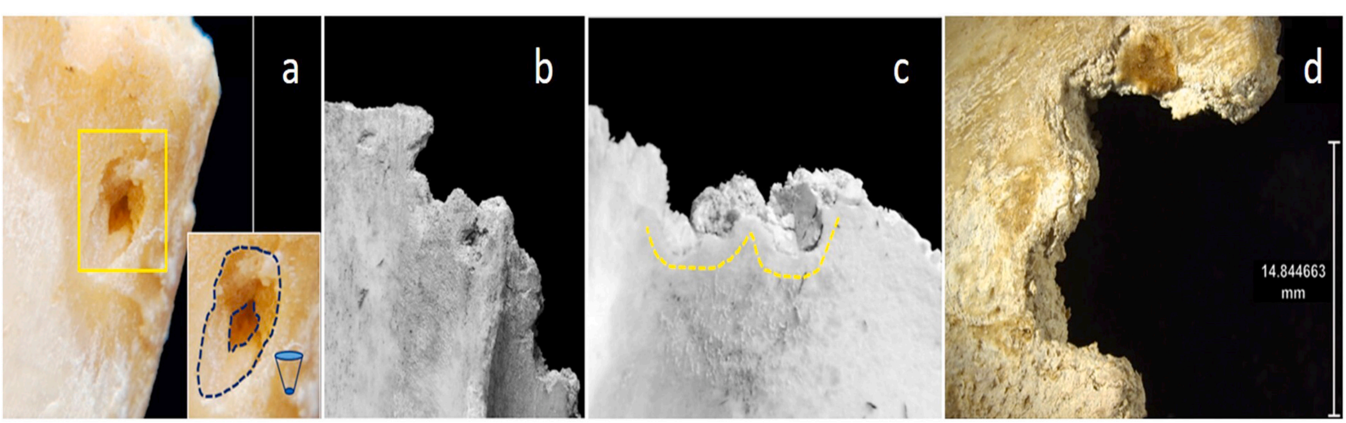

Fig. 4. (a) Puncture (yellow rectangle). Small and larger surfaces delimited by blue dotted lines corresponding to areas caused by canine tooth tip cusps and the surface of the canine tooth (central portion of the crown of the tooth), respectively; (b) Two C-shaped patterns on the zone of the cortical bone with low density; (c) Close up with yellow dotted lines indicating tooth mark patterns with irregular edges on the dorsal border of the scapula; (d) Microphotography with the dimensions of patterns found on the dorsal border of the scapula.

bone. Some scores observed on the base of the scapula were associated with chipped edges found on the BSS (Fig. 3k). Finally, a few but clear puncture marks (Fig. 3l-n) were found in 24% and 26% of bones on the proximal area of the scapula, for the groups of wolves and dogs, respectively. Dogs gnawed the glenoid cavity in 2% of the bones (not shown). On the thinner central blade of the scapula, puncture tooth marks were not generally preserved for measurements, creating just a crenulated edge. Contrary to expectations, the articular cartilage of the glenoid cavity remained intact in more than 50% of the scapulae in both groups.

3.3. Tooth mark morphology and dimensions

The tooth mark morphology mostly did not differ between the groups (Fig. 4). The punctures recorded in the thickness of the diploe had the shape of an inverted cone, while the edge of the tooth pattern was irregularly elliptical (Fig. 4a). Occasionally, in the softer areas punctures with more stable and clearer characteristics were found than in the denser or thicker cortical bone.

The pits also presented irregular borders. They had an oval shape in areas of low cortical bone density (Fig. 3 f, g). In higher density areas, the pitted tooth marks showed a more circular pattern and were bounded by an irregularly circular fracture line (Fig. 3 h). During the bite, minor displacement of the teeth on the surface of the bone generated the distortion of the pitting pattern, making it slightly rectangular (Fig. 3 g). Thus, marks on high-density sections showed a higher degree of ambiguity. Scoring tooth marks were sharp at one end, and rounded or square at the other. They had well-defined borders when located in isolated areas of increased cortical bone density (Fig. 3j, k), in contrast to those found in areas of low cortical bone density and a large amount of diploe. In addition, we found a few thin linear score-like marks, transversely oriented and oblique to the longest axis of the bone, possibly caused by claws when using the paws as a means of gripping. Since we cannot affirm that teeth caused these lines, any mark of dubious provenance was discarded from the analysis. Along the proximal area and over the transition zone, in both groups of animals, we repeatedly found two C-shaped bite patterns, slightly separated by an incomplete bony septum (Fig. 4b-d). This pattern was present in isolation from other similar patterns. Its morphology was much more irregular in areas of low cortical density and, although not measured, visually those caused by wolves were larger than those caused by dogs. Table 2 shows the locations, types and average values of the dimensions of tooth marks relative to the average bone density and underlying diploe, for both groups. Two individual and clear furrowed tooth marks were visible just once in the TSS. They had lengths of six and eight millimeters, respectively, as appreciated in Fig. 3c.

In general, within each group of animals, all the types of tooth marks measured showed larger dimensions over lower density zones than higher density. Comparatively, the length and breadth of all tooth marks caused by wolves tended to be greater and broader than those of dogs, regardless of the density of the osseous region. However, the statistical analysis indicated that only two dimensions (length and breadth) of the punctures, pits and scores caused by wolves on low-density structures with large amount of diploe were statistically larger (Table 2) than those caused by dogs. In addition, scores caused by wolves on areas of high density displayed statistical differences between groups (Table 2) for both dimensions, while the transition zone showed pits and scores with significant differences (Table 2) in only one of the dimensions. In some cases, the length of the score marks were four or more times greater than their breadth. On the transition zone and areas with denser cortical bone, it was not possible to find puncture tooth marks. Although it is not possible to be certain that the size of the crenulated edges corresponds to a particular tooth mark, it is visually evident that the crenulations created by the dogs were of smaller dimensions. In areas of high cortical bone density, the pits presented fewer differences in their dimensions, becoming more circular. In areas of less cortical density and a large amount of diploe, the pits were of an oval shape with dimensions that differed even to the naked eye. On the other hand, when comparing tooth marks within the groups of wolves, only the length of the scores showed significant differences (Table 2) between areas of low cortical

Table 2
Descriptive analysis of average of pitting, scoring and puncturing measurements in both canine groups, wolves and dogs. The data displayed in the table show the length and breadth of tooth marks according to the density of the cortical bone of the different analyzed structures (n: number of tooth marks analyzed; mm: millimeters).

Type of tooth mark	Structures according to density	Wolves Length-breadth ($\bar{X}$ in mm)	Dogs Length-breadth ($\bar{X}$ in mm)	Comparison between bite measures (length and breadth) between groups of wolves and dogs (P-value)
Punctures	Structures with low density cortical bone and a large amount of diploe * * Zone of transition Structures with high density cortical bone	4.55–3.65 (n: 3) (SD: 0.41–0.18) Not found Not found	3.67–2.80 (n: 8) (SD: 0.27–0.27) Not found Not found	Length, p = 0.002 * * Breadth, p = 0.002 * *
Pits	Structures with low density cortical bone and a large amount of diploe * * Transition zone * Structures with high density cortical bone	3.86–3.16 (n: 4)[a] (SD: 0.20–0.17) 2.84–2.28 (n: 4)[b] (SD: 0.17–0.19) high overlapping high overlapping	3.06–2.63 (n: 4)[a] (SD:0.17–0.17) 2.06–1.93 (n: 5)[b] (SD: 0.36–0.37) high overlapping high overlapping	Length, p = 0.029 * * Breadth, p = 0.029 * * Length, p = 0.032 * Breadth, p = 0.111
Scores	Structures with low density cortical bone and a large amount of diploe * * Transition zone * Structures with high density cortical bone * *	10.87[a] - 3.20[a'] (n:3), (SD: 0.81–0.27) 9.13[ab] - 2.90[a'] (n: 3), (SD: 0.32–0.26) 7.19[b] - 2.62[a'] (n: 4), (SD: 0.59–0.43)	7.28[a] - 1.99[a'] (n: 5), (SD: 1.80–0.30) 6.53[a] - 2.02[a'] (n:6), (SD: 1.40–0.17) 4.50[a] - 0.88[b'] (n: 6), (SD: 0.84–0.3)	Length (wolves vs. dogs), p = 0.029 * * Breadth (wolves vs. dogs), p = 0.036 * * Length (wolves vs. dogs), p = 0.095 Breadth (wolves vs. dogs), p = 0.024 * Length (wolves vs. dogs), p = 0.01 * * Breadth (wolves vs. dogs), p = 0.01 * *

(**) Both dimensions (length and breadth) showed statistically significant differences ($p < 0.05$) between groups; (*) Only one dimension (length or breadth) displayed significant differences ($p < 0.05$) between groups; Different superscript letters for pitted tooth marks indicate significant differences for both dimensions within each group: (Wolves, length and breadth ($p = 0.029$); Dogs, length ($p = 0.016$) and breadth ($p = 0.032$). Different superscript letters and letters with apostrophes, for score tooth marks, indicate significant differences for both length and breadth, respectively within each group ($p = 0.001$); ($\bar{X}$) mean value; (SD) standard deviation. (Comparative statistical analysis of the density between structures of the bovine scapula (p-value) in Supplementary Material, table S2) density and a high amount of diploe, versus areas of high cortical density. The transition zone had intermediate values, with no significant difference (Table 2) from the others. In dogs, only the breath of the scores located in areas with high density differed from their counterparts. Despite some significant differences ($p < 0.05$) found among the dimensions of tooth marks, in absolutes terms, the length and breadth of the tooth marks showed variable degrees of overlapping between both studied groups.

3.4. Consumption behavior

The wolves sniffed and picked up bones before transporting them to another location which they used as a "feeding ground". Simultaneously and before consumption, they rubbed their body against the bones for a period not exceeding 20 s. This behavior did not recur either during or after consumption. Meanwhile, the dogs sniffed but did not accumulate the bones or move them to a specific area before consuming them. Immediately when they saw the bones they picked one and started biting into it. In addition, unlike the wolves, the dogs did not rub their body over the bones (Fig. 5a-c). Consequently, only the bones in contact with

Fig. 5. (a) Accumulation of bones before consumption. (b, c) Rubbing of the body with the bones**;** (d, e) Wolves using incisor and canine teeth to remove soft tissue on flat and wide surfaces; (f, g) Wolf and dog, respectively, using incisor and canine teeth to remove the remains of tendons on the supraglenoid tubercle; (h, i) Wolf and dog, respectively, licking surfaces before biting on chipped edges; (j, k) Dog and wolf, respectively, by positioning the dorsal border of the scapula in the mouth parallel to the orientation of the row of teeth with forelimbs helping; (l, m) Wolf and dog, respectively chip remolding after the shredding action of carnassial teeth; (n, o) Wolf causing chipping of edges on the BSS with incisor teeth.

Fig. S1. Macroscopic external anatomy of the left bovine scapula. A Lateral view. a Cranial angle; b caudal angle; c ventral (articular) angle; 1 dorsal scapular cartilage; 2 dorsal border; 3 cranial border; 4 caudal border; 5 supraspinous fossa; 6 infraspinous fossa; 7 neck of scapula; 8 glenoid cavity; 9 acromion; tubercle of the spine of the scapula (black circle of dotted lines); Supraglenoid tubercle (green). B Medial view, new structures. 1 dorsal scapular cartilage; 2 dorsal border; 3 cranial border; 4 caudal border;10 Subscapular fossa; 11 border of the glenoid cavity; 12 coracoid process. C Ventral view. 8 glenoid cavity; 12 coracoid process. D Cranial view. 3 cranial border; 5 supraspinous fossa; 9 acromion; spine of scapula (yellow); border of the spine of the scapula (BSS); supraglenoid tubercle (green).

Fig. S2. (A) Sagittal plane of the CT scans from the left bovine scapula showing the different analyzed points (yellow lines). (a – h). Cross-sectional CT images through the scapula illustrating variations in density according to the bone zones and structures. The green and yellows arrows show cortical bones (white zones – structures with a higher degree of attenuation), while the orange arrows show diploe (gray zones with bone trabeculae – structures with a lower degree of attenuation). The black zones (structures with the lowest degree of attenuation) surrounded by cortical bone, indicate the absence or a minimal quantity of diploe. Structures with a higher degree of attenuation are denser than structures with a lower degree of attenuation. (a) View of the articular surface of the glenoid cavity surrounded by its margin; (b) the cranial zone corresponds to the supraglenoid tubercle and coracoid process; (c) the neck of the scapula with a thick cortical bone and a large amount of diploe; (d) comparison of the cortical bone and diploe present in the neck and a portion of the acromion (Acr); (e) the cortical bone of the cranial and caudal border and the SS; (f) comparison between the caudal border and the SS. The tubercle of the spine of the scapula (TSS) presents a proportionally high amount of diploe; (g) the blades of the cortical bone (on the supraspinous and infraspinous fossae); and (h) the proximal area close to the dorsal border with a low density of cortical bone and the presence of a large amount of diploe.

Fig. S3.

(Left) Density in the different zones of the left bovine scapula. (a) Lateral view; (b) Ventral view; (c) Cranial view. Lower density zones (orange); Intermediate density zones (blue); High-density zones (red). The structures of the same color have densities without significant differences between them ($p > 0.05$). (Right) X-ray of the left bovine scapula and the anatomical zones studied in this work: a) the proximal area (white dotted lines); b) the cranial border; c) the caudal border; d) the supraspinous fossa; e) the infraspinous fossa; f) Acr; g) the supraglenoid tubercle; h) the glenoid cavity; i) the margin of the glenoid cavity; (SS).

the wolves had a large amount of hair adhering to them after the experiment and even after cleaning, although to a lesser degree. Although the "wolf feeding area" was usually hidden from the view of intruders, it was possible to observe and record some feeding habits. On the first day of the experiment, both groups caused the highest degree of bone modification. The wolves initially focused their attention on one of the bones causing the greatest degree of modification in a leisurely manner, with intervals between bites. After discarding it, they accessed the second bone, repeating the process, but with less attention. The second bone was occasionally consumed/gnawed. This behavior was repeated each day of the experiment. However, their interest in modifying the bones on two successive days of experimentation was increasingly diminished. In contrast, the dogs alternated their attention between the bones, spending more time gnawing on one bone and then occasionally taking a few seconds to chew on the other. Contrary to the wolves, the dogs chewed bones in a hyperactive, agile, continuous and non-stop manner. They also showed a higher degree of salivation than wolves during bone gnawing, and remained attentive to their surroundings. In fact, the wolves were observed to gnaw or remove soft tissue while lying down, unlike the dogs that alternated biting while standing and lying down. During the first access, both groups spend approximately 1 h biting the bones, without interruptions. They had second access to the bones but only the dogs modified them once again. In both groups, the tooth marks observed through the observation of feeding behavior were mainly attributed to carnassial teeth and secondarily to canines. Gnawing generally proceeded from soft to hard bone. Both groups of animals gnawed the soft cancellous parts of the bone first until they encountered progressively harder bone (with or without adjacent diploe in the transition zone). This was strong enough to not collapse under the gnawing causing by the same process, that is major and overlapping pitting and scoring patterns within each group. Both wolves and dogs began shearing and pulling at any soft tissue still present in the bone. The remains of fasciae, aponeurosis or muscle tissue present on the scapula were removed by them dragging their incisor and canine teeth repeatedly over its surface, causing overlapping of score marks with different dimensions and directionality. Scorings occurs when a tooth is dragged over the surface of the bone. The removal of denser soft tissue, such as the tendon of the biceps brachii muscle, whose origin is the supraglenoid tubercle, was caused by intense and repeated biting of this bony structure with the carnassial teeth. Literally, the supraglenoid tubercle was mashed aways. This caused a high degree of destruction of the tubercle, facilitating the removal of the tendon, using incisors and canines. Both groups spent the majority of their time using their cheek teeth to gnaw on grease-rich zones with low density and with a variable presence of tendons (e.g., the proximal area, supraglenoid tubercle). During modification, the dorsal border of the scapula was placed in the mouth, parallel to the orientation of the row of teeth. This action was performed with the molars on the left and right sides of the jaw; however, each individual tended to use one side more than other. The action of the carnassial teeth crushed the proximal area, causing furrowing marks. The canine teeth seemed to assist in this work. The action of the teeth in this area generated irregular detachment of the diploe and the splintering of the cortical bone, which was subsequently removed by the incisor and canine teeth. Both animals commonly swallow small splinters of bone. Only in the group of dogs was it possible to see small bone fragments remaining in the "feeding area", but it was not possible to verify their presence in the "wolf feeding zone". The wolves gnawed on the hard areas of the SS with their incisor teeth, breaking off small slivers of bone, resulting in a microdenticulate appearance (Figs. 3e and 5 n, o). To break harder areas of bone, the animals clenched their teeth whilst at the same time tilting their heads with the opposite end of the bone resting on the ground surface. This leverage allowed the bone edge to rut. On the other hand, the use of their forelimbs played a vital role in the correct positioning of the bone between the teeth, and enabled them to exert pressure while pulling a piece of bone, splintering or softening the tissue. Crushed areas and structures to be chewed were previously and repeatedly licked, especially by the dogs. During the study, the use of carnassial teeth on the SS, rather the use of incisors causing chipping back, and the use of canines and incisors to fracture bones in areas of high density was not observed. In addition, the use of canines in areas of high cortical density in order to drill the bone was also not observed. Fig. 5d-o shows some behavior during the consumption process by both species. After first access to the bones, they were almost totally abandoned by the wolves. After their daily ration of food, some dogs accessed them again spending some minutes biting at them, without much interest or enthusiasm.

4. Discussion

This study demonstrated that Iberian wolves and domestic hunting dogs have the ability to cause bone modifications through their bite, and generate comparable tooth marking patterns in standardized, fresh, fleshed and slightly dried bovine scapulae. Given its position, the muscle masses that surround it and its relationship with other bones of the forelimb, the scapula becomes a potential source of tooth marks caused by wolves and dogs during disarticulation of a carcass and transport of bone pieces (see complementary material). The outcomes presented in this work can only be partially compared and in a referential way with previous studies, for reasons that will be discussed below. However, several methodological and analytical aspects are a great contribution to the forensic interpretation of tooth mark patterns caused by wolves and domestic dogs on bones, that can be further discussed.

4.1. Tooth marks vs. scapulae density

The results obtained show that the modification of the scapula was created from areas of lower cortical density to areas of higher density in both groups of animals. Thus, the proximal area of the scapula was the first area of attack and where the animals spent most time, causing the greatest degree of modification and, consequently, the lowest bone survival. Here the amount of diploe is high and the overlying cortical bone has low bone density. Other areas of the scapula with the same structural characteristics, but a smaller surface (e.g., supraglenoid tubercle, TSS) also underwent a proportionally high degree of modification in both groups. An intermediate degree of modification was suffered by the margin of the glenoid cavity and the transition zone, despite the latter being classified in the group of structures with high cortical density, but with a low amount of diploe between its bony tables. This area showed a higher survival rate in the bones bitten by dogs and a high rate of destruction in the group of wolves. In addition, a high rate and overlapping of tooth marks was shown. Finally, structures covered by high-density cortical bone, with or without adjacent diploe, showed only crenulated edges or the total absence of tooth marks. According our results, the scapulae present a structural analogy with the long bones described in Complementary material. Considering this analogy and previous studies on long bones (Haynes, 1980; Binford, 1981; Haynes, 1982; Parkinson et al., 2014; Sala et al., 2014), the strategy for consumption of the scapula follows a similar pattern to long bones, when considering only their density as a factor conditioning the characteristics of the tooth marks. Additionally, the size of the tooth marks increased inversely to the density of the cortical bone, as shown in this work. Delaney et al. (2009) also reported this. This is due to the greater depth that the teeth could reach during the bite in less dense areas, and the particular characteristics of Iberian wolf (Toledo González et al., 2020) and dog teeth (König and Liebich, 2020). In this study, it was possible to group three statistically distinct zones according to the density of the cortical bone. However, the high number of tooth patterns found in the transition zone, especially in the group of dogs, suggests that the amount of adjacent diploe seems to play a role in the degree of modification. This is in line with the type, distribution and degree of overlapping of tooth marks found on the different bone surfaces of the studied scapulae, mainly pits followed by scores.

4.2. The degree and patterns of bone modification according to the consumption behavior of wolves vs. dogs

Although the basic patterns of modification/tooth marks (furrowing, pitting, scores and puncture tooth marks) do not present great variation, the intensity and morphometric characteristics of the modification patterns showed some differences between and within both groups. In percentage terms, the results presented show a higher degree of modification by the wolves on each day of the experiment and, consequently, at the end of the study. However, the statistically significant difference between groups is determined exclusively by the degree of modification caused during the first day of the experiment. Although, in the following days, there was no significant average difference between the two groups, there was a significant difference in absolute terms. There were visual differences in consumption behavior that could be useful to consider for correct interpretation of tooth mark patterns, and to allow for differentiation and taxonomic forensic identification. Thus, as a group and individually, the wolves decreased their degree of modification significantly and progressively, while the group of dogs did so only at the end of the study and neither of them had a determined pattern. This indicates that both groups of animals lost their interest in modifying bones differentially (see below). Another difference was the time of interaction between the two groups with the bones set. The dogs bit the bone immediately, while the wolves started biting after their usual ritual of picking, rubbing against them and moving them to the "feeding area". Also the time spent biting the bones was different between groups. During the first access to the bones, dogs and wolves spent approximately the same amount of time biting them ($\approx$ 1 h). That is, they started biting without stopping until they lost their interest in the bone. However, the dogs, after receiving their daily food, again accessed the bones, spending slightly more time modifying them, but with less interest. The wolves, during a second or third access, did not cause any modifications or even ignored them. In the studies carried out by (Binford, 1981), on long bones and articulated scapulae in bison carcasses bitten by dogs and wolves accumulated for years, he obtained similar modification patterns to this work, although they were more intense on the acromion and the margin of the glenoid cavity. It is likely that the long exposure time to the animals and the environmental conditions (not described in his study) explain, at least in part, their results. The use of a completely articulated carcass may expose the bony structures forming the glenohumeral joint to a higher level of modification during the early stages of disarticulation, according to previous studies (Binford, 1981; Haynes, 1982; Haglund et al., 1989). This agrees with the lower degree of damage found in our study on the glenoid cavity and its margin, and the high survival rate of the articular cartilage when using isolated, fleshless bones for a short time in both groups of animals. Like Binford (1981), it was possible to find morphological similarities in tooth marks, such as crenulated edges and damage to the dorsal edge of the scapula. However, Binford (1981) did not provide differential results between the two subspecies comparable to the results reported here. At the same time, Haynes (1980), working with American wolves, analyzed tooth mark patterns on scapulae from bison collections, offering similarly scarce information. Only the extensive damage caused by wolves, the presence of splinters, fractures, and holes of 1–2 cm in diameter, without indicating the number and distribution of these, were reported. However, in his study, some factors were mentioned that could influence the degree and form of the modification of scapulae in our study.

4.3. The size of the corpse and the degree of bone modification

The size of the corpse could not be a preponderant factor, something that years later Haynes reevaluated together with other authors (Sala et al., 2014). They took up carcass size as an important factor in the number and frequency of tooth marks created on bones by wolves. However, they pointed out that it was only possible to differentiate patterns of tooth marks caused by large versus small animals. This has been also reported by other authors (Andres et al., 2012), remarking that large animals can generate both large and small marks, especially on small carcasses. This may be particularly true if some factors that allow smaller species to generate larger marks on the carcasses of large animals are not considered, for example, more individuals biting, more time to bite, lower bone strength, or more bites on top of pre-existing bites (overlapping marks). Moreover, recent studies with Iberian wolves and using advanced analytical techniques indicate that the effect of prey size on the morphology of tooth marks is still inconclusive (Courtenay et al., 2020b).

4.4. Captivity and free life as bone modification variables

Since the modification of teeth and dental markings may be conditioned by ecological factors (Haynes, 1982; Gidna et al., 2013), Sala et al. (2014) worked with captive and wild wolves on different types of carcasses articulated according to taxa. In their study, they tried to establish the impact of the age, body size and bone density of the carcass on bone modification. Following the methodology of Haynes (1982), they classified the damage caused to the bones, including the scapula. Their results range from extensive modification of the scapula caused by furrowing, to the presence of isolated bone fragments. Although they acknowledge the use of heterogeneous groups of wolves and non-homogeneous carcasses as a limitation of their work, they concluded that captive wolves caused greater bone modification in ungulate carcasses than their wild counterparts, something that has also been noted in other works (Gidna et al., 2013). This captivity may possibly correlate with the increased sedentary lifestyle reported where by Haynes (1982). Here, the animals that do not require hunting tend to gnaw bones more (Haynes, 1982). In our view, space limitation and guaranteed food in wolves and carnivores in general may not only encourage sedentarism, but also the previously reported "boredom" (Binford, 1981; Sala et al., 2014) causing animals to spend more time modifying bones by creating various types of tooth marks.

4.5. Competition as a variable in the bite patterns of wolves and hunting dogs

In this study, and from a forensic perspective, there is another behavioral aspect to consider for the analysis and interpretation of tooth marks on soft or hard tissues, such as bones. In the wild, wolves and wild dogs generally hunt in packs (Mech et al., 2015), as do hunting dogs. Dogs in general (e.g., stray, feral dogs) as well as wolves, exhibit predatory behavior, and domestic dogs can form packs that mount attacks against various types of animals and even humans (Beaver, 2009). They may also attack solitarily, due to many causes, or act as scavengers (Beaver, 2009; Young et al., 2015). Cooperation can lead to competition between animals for prey during an attack and/or consumption and/or immobilization, depending on the objective of each animal (e.g., predation, scavenging or simply immobilization during hunting) (Binford, 1981). Tension and competition may increase when there are a greater number of individuals trying to access food and/or food is scarce (Ioannidou, 2003; Santoro et al., 2011; Parkinson et al., 2014), which may cause differential patterns of destruction (Pokines and Symes, 2013; Fosse et al., 2014) and a high degree of mark overlap. It should be noted that a pack attack can also occur with non-hunting domestic dogs, against people and when dogs are part of a group, where this "pack instinct" is a motivation to escalate the attack (Pomara et al., 2011). It appears that the visual contact between the dogs in this work may have created this "false competition" and influenced the degree of bone modification, but not the pattern of scapula molting, as previously noted. During the three days of the experiment, a degree of anxiety shown by the dogs during consumption was noticeable, in contrast to the wolves. This is similar to what Burke (2013) reported working with other carnivores. Logistically, in this work it was not possible to isolate the dogs to verify the degree of impact of this factor on the degree of bone modification. However, the wolves spent less time biting the bones, and did so in a leisurely manner. They showed greater effectiveness of their bite on each day of the experiment.

4.6. Dimensional overlap of bite patterns between Iberian wolves and dogs

The presence of a high number of pits found in our study on fleshless scapulae leads us to infer that pitting tooth marks generally result only from the act of biting bones and not from the intention of eating or pulling meat from the skeleton of an animal, as occurs during hunting patterns. Binford (1981) also previously observed this, especially in bones found near dog and wolf dens. Although the tooth dimensions reported by Sala et al. (2014) relate to long bones, the length and width of punctures and pits were quite similar to those caused by the wolves in this study, and greater than those of the dog group, according to cortical density. In contrast, the width of the furrows in their study is more similar to that of the scores caused by the group of dogs, and not to that of the wolves in this study. Additionally, the scores created by wolves and dogs in our work did not always show significant differences for both dimensions (length and width), indicating that the morphometric analysis of pits and punctures could be more reliable for a taxonomic differentiation between the two subspecies. This is nothing new and has been pointed out by other authors in (Aramendi et al., 2017; Courtenay et al., 2021). In fact, Domínguez-Rodrigo, Piqueras (2003) already reported that they were not convinced that scores could be useful for taxonomic differentiation when the length varies in the same individual. Then Delaney-Rivera et al. (2009) determined the lengths of scores as three times their breadth. In our study, lengths up to 4 times the breadth were determined. This shows how variable and unreliable score tooth marks could be for identification. From an animal forensic perspective, it should be noted that the average values of bite marks created by carnivores that have been published previously are useful, but in many cases only referential. This is due to the overlap of marks between different canid species. In this study, although significant differences were found in the average values of tooth marks between groups, in absolute terms there was an overlap between their dimensions. This also occurred in the work of Andres et al. (2012) and Delaney et al. (2009) who compared the dimensions of the tooth markings of domestic dogs of the German Shepherd breed with the Iberian wolf and coyotes, respectively, although on very heterogeneous samples. Therefore, caution is recommended when interpreting dental marking patterns by considering only some characteristics of them.

4.7. Wolf and dog bite patterns on scapula: One more piece of evidence in the identification of an aggressor

Bite patterns on rigid elements (as scapulae) are more stable and reliable than those found on soft tissues, and their use in court has led to effective convictions (Rivera-Mendoza et al., 2018). Therefore, the analysis of tooth patterns on bones could also be used as part of an official investigation protocol in cases of wolf and/or dog attacks on livestock and humans. This evidence, together with other evidence (e.g., presence or absence of hairs as in our study), would allow from a forensic perspective to identify and/or exclude possible suspects with the certainty required in judicial cases, avoiding reasonable doubts. In fact, Domínguez-Rodrigo, Piqueras (2003) and Young et al. (2015) pointed out that tooth marks alone cannot be used reliably to identify a given carnivore taxon. Therefore, in cases of wolf and/or dog attacks on humans and other animals, a multidisciplinary team, as was also pointed out by Young et al. (2015) should carry out the investigation.

4.8. The bite force of dogs and wolves in the degree of modification

Regarding on the degree of modification or damage caused on bone structures, the bite force must also be incorporated. Past studies have determined, by morphometric analysis on skull images, that wolves exert a greater bite force than domestic dogs (Damasceno et al., 2013). Similar results have been obtained by incorporating weight as a factor in the bite force of canine and carnassial teeth (Christiansen and Wroe, 2007). However, following previous methodologies, Brassard et al. (2020) showed that breeds such as the German Shepherd and Husky could approach the force exerted by wolves, especially of the carnassial and canine teeth in the second instance, according to the angle of mouth opening. Other breeds, such as Rottweilers and Pitbulls would greatly exceed the bite force of a wolf, and even some breeds smaller than wolves would also be able to exert forces similar to them (Brassard et al., 2020). However, and according to previous studies in dogs, it would seem that the size and/or weight of the animal would not be 100% correlated with bite force and consequently with pattern sizes. This could explain, at least in part, the similarity between the tooth mark dimensions caused by the wolves in this study to those using American wolves (Haynes, 1980, 1982; Sala et al., 2014), considering that the mean size of the Iberian wolf is smaller than American wolves (Iglesias et al., 2017). The choice of hunting dogs for large animals in this study leads to a comparison of tooth patterns caused by the two canids with more homogeneous phenotypic characteristics, at least in weight, size and similarity in hunting behavior and bite force, eliminating the factor of the number of individuals, to obtain an individual and comparable standard pattern. Considering the above, in this study, the wolves showed a higher bite force than the dogs, since they created more damage in less time and in a slower manner in comparison to the lesser modification shown by the dogs who spent more time biting bones. Even the diet that the wolves received over a long period did not seem to affect their bite force and capacity. This lower bite force in dogs may explain the greater number and overlapping of tooth marks found on the bones (especially pitting and scoring in areas of higher cortical density) unlike in wolves, a fact also pointed out in Binford (1981). Thus, the dog bites were less effective than wolf bites, even if the competitive factor was potentially present as there was visual contact with other dogs.

4.9. The scapula as an energy source and its relationship with the degree of modification

Another factor that can influence the degree of modification of the scapulae is their energy content. Any carnivore must determine the energetic cost of a catch versus the return it will get (Mech et al., 2015; Iglesias et al., 2017). Marrow fat reserves and other nutrients presents in the bones can be energy source (Mech and Boitani, 2003). Thus, the low amount of bone marrow found in the scapulae and the assured food provided in the captive condition of wolves, could explains, the abruptly diminishes the interest every day, in unnecessarily expending energy biting denser areas of bone in the wolf group with the consequent absence of marks (e.g., the borders and neck of the scapulae). In dogs, on the other hand, the act of biting declined gradually. The biting action of the hunting dogs was almost a "conditioned reflex", since after receiving their daily food ration (higher than we considered required), they went back to biting the bones. Thus, the purpose of bone biting for wolves and dogs can be assumed to be different (see Supplementary material, Supplementary text).

4.10. The morphology of the scapula as a conditioning variable of its modification

The anatomical shape of the bone also seemed to be an important factor influencing the degree of modification caused by both groups of animals. High-density areas, such as the supraspinous, infraspinous and subscapular fossae, in their central region, were unreachable by the carnassial teeth due, apparently, to the width of the bone, preventing its modification and the presence of marks. They tried to access these areas by repeatedly changing the position of the scapula inside the mouth, with the help of their front paws, and by tilting and rotating the head. In less dense areas, this rotation could have probably increased the size of the marks. After a few attempts, they aborted the mission by exclusively licking the area and detaching soft tissue if it still existed.

4.11. The hypercarnivorous condition of wolves and the degree of modification

Considering that bite force and biting action depend on the animal's lifestyle and feeding habits, it seems logical to infer that hunting and scavenging patterns differ (Courtenay et al., 2020b) causing variations during meat/bone exploitation. Studies on wolves indicate that the trunk and proximal limb bones, such as the humerus and femur, are affected the most by fractures, while the radius-ulna (elbow) and tibia are the least affected (Yravedra et al., 2011; Fosse et al., 2014). When the amount of meat is abundant, the degree of marking may be less (Pokines and Symes, 2013) depending on other factors, such as the number of animals feeding on the carcass. In the case of scavenging patterns when the wolf/dog encounters an animal that has died by natural or accidental causes a short time before and its carcass is complete, the same pattern is expected. However, if animals encounter a carcass with little meat on it, they will bite into any area in search of nutrients, causing fractures and teeth marks in a scattered manner. It should be noted that carnivores prefer fresh bones, such as those used in our study, with soft tissue and fat/marrow attached as a source of nutrients, but they will bite dry bones if they have nutritional requirements (Pokines and Symes, 2013). In addition, Delaney et al. (2009), who used fleshed long bones, assumed that the marks found on them from different taxa were due to the absence of meat. This reflection may seem opposite to that expressed by Yravedra et al. (2014). They concluded that African wild dogs generated fewer marks than wolves because they were more oriented to meat consumption than bone gnawing, also indicating that a higher frequency of teeth marks was found in both on the upper bones. That is, the scapula would be among the most affected bones. Although they incorporated the scapula in their study, they do not provide specific results on the type and degree of modification it suffered. In fact, Fosse et al. (2014) reported that the greatest degree of destruction (isolated punctures) occurred in the thin areas of postcranial elements such as the scapula. Consequently, the scapulae used in the study by Yravedra et al. (2014), due to the large muscle masses surrounding them and their smaller thickness than long bones, were collaterally destroyed, so it was considered that a hypercarnivorous condition may not be exempt from causing tooth marks. In fact, in our study, both groups created large amounts of tooth marks on the fleshless scapulae. Focus on the scapula in future studies, as a source of tooth marks for forensic analysis, controlling its complete destruction, should to be considered. Although the absence of soft tissues and/or muscles in our samples hinders evaluation of their participation in the modifications, some aspects may be highlighted from a forensic perspective, according to our results. (1) Look for bite patterns on all bony structures, protected by muscle masses, such as the scapula, or unprotected, such as the distal bones of the limb, as found by other authors (Binford, 1981; Parkinson et al., 2014). (2) It is a real possibility to find tooth marks on relatively fresh, dry and isolated bones. The morphological and morphometric similarities of tooth mark patterns found in this work on scapulae compare with other studies (Haynes, 1980; Binford, 1981; Haynes, 1982) where bones were exposed to multiple factors for months and years, and prove the high degree of conservation and integrity that tooth marks can preserve over time on bones, especially in the densest areas. This characteristic may increase their value as evidence, not only in recently skeletonized victims, as long as they are interpreted together with other findings, especially in outdoor cases where the perpetrators are generally unknown. (3) The presence of marks may not be ruled out simply because of bone density. Thus, Faith (2007) and Kuhn et al. (2009) found that portions of elements with low bone density in most cases showed an inverse correlation with the frequency of dental pits. This is possible if there is no major bone destruction, as occurred in this work, and in another reported by Yravedra et al. (2014) on African wild dogs, where a high concentration of pitting marks was found in the epiphysis of long bones. This shows that bite patterns are multifactorial in origin, and are affected by and/or depend on the characteristics of the aggressor (the one causing the bites), the substrate or the victim (the one receiving the bites) and the context/scene in which the bites occur. Past studies indicated that the study of teeth marks was a good tool for taxonomic identification, as the morphology and dimensions of teeth marks do not vary according to habitat (Haynes, 1980; Binford, 1981). This remains the rationale for recognizing bite mark analysis as one of the most widely used taphonomic techniques to identify the action of different carnivores.

4.12. Variables required for a forensic comparison between bite patterns caused by Iberian wolves and dogs

In order to be able to compare bite marks to differentiate between different species, Dominguez Rodrigo et al. (2012) indicate that comparisons must be made between homologous experimental sets, that is, that the elements participating in the study share the same components (substantially analogous), are structurally similar (structurally analogous) and share the same context (environmentally analogous). This was the basis for establishing the methodology in this work, where consideration was given to the use of highly homogeneous bones, dogs and wolves, as standardized as possible (physically and behaviorally), carrying out the study with as little intervention as possible and minimizing any possible differences. In our work, although the bone dimensions do not differ ostensibly from other publications on long bones (Toledo González et al., 2021) results cannot be extrapolated to the marks found in this study. Again, from a forensic perspective, knowing the context/scene in which the marks were created (e.g., predation, scavenging, hunting, defense, etc.) and recognizing the characteristics of the victim and its aggressor will lead us to understand the origin of these small morphological and morphometric differences in bite patterns, thus increasing their identification value. Create a database of tooth marks, using homologous experimental sets, and knowing the characteristics of those who participate, may allow us to find patterns to be compared with tooth marks found at a crime scene. It is not sufficiently reliable, for forensic purposes, to create tooth pattern standards using bone material from paleontological and zooarchaeological assemblages, because not all the taphonomic processes are known and many processes may have created these marks. This is also particularly important when the possibility exists to compare tooth marks found at a crime scene, on soft and rigid tissues, with the dentition characteristics of identified suspect canids, as has happened in the past (Santoro et al., 2011). The collection of data at the scene is of vital importance for this purpose, given the ethical and often logistical limitations for experimentation with live animals, and where the culprit that created the tooth marks is known with certainty. The analysis of bite patterns caused by animals on soft tissue is mainly performed by determining the distance between injuries, presumably caused by canines using on both sides of the jaw. This distance is compared to the intercanine distance recorded directly from the suspect's mouth (when known), or from casts or images (Dorion, 2011). Similarly, recording a dental arch on the victim would allow morphological analysis and recognition of specific dental peculiarities (e.g., fractures, twists, etc.) that may allow individualization of a suspect, for example, the higher dental wear of a particular tooth because of the tendency of a known dog or wolf to bite more on one side of the jaw, as seen in this research.

Measurement systems in the study of wolf and dog bite marks for forensic purposes The investigation of tooth mark patterns as a tool for differential identification of wolves and/or dogs has gone through many different phases. Studies have ranged from simple qualitative characterization, using direct analysis of markings on bones (Haynes, 1980; Binford, 1981; Fosse et al., 2014) to quantitative analyses using digital photographs, magnifying lenses, and stereoscopic zoom microscopes (Delaney-Rivera et al., 2009; Yravedra et al., 2011; 2014; Andres et al., 2012; Sala et al., 2014) As in this work, many of them used hand-held digital measurement systems (e.g., digital calipers). However, there are two major limitations of these tools: (i) their level of accuracy and sensitivity is not 100% and (ii) variability in the results can occur depending on inter- and intra-observer error when measuring and/or determining the measurement points. In the work of Aramendi et al. (2017), Yravedra et al. (2017), Yravedra et al. (2019) and Courtenay et al., (2019, 2020a, 2020b, 2021) the use of three-dimensional tooth mark analysis and geometric morphometrics created important advances in mark processing. This has contributed, in part, to correcting past deficiencies by reporting differentiation levels of over 90%. Image processing has gone hand in hand with the use of more complex data analysis, where qualitative and quantitative variables can be processed together. These multivariate analyses and the use of artificial intelligence show great promise. However, complete differentiation is not yet possible. Courtenay et al. (2020a), point out the difficulties of morphological and morphometric processing of wolf teeth marks, apparently because of their great variability. In our study, it was possible to demonstrate that both canids are capable of modifying fresh or relatively dry and fleshless scapula, creating differential tooth marks, through different consumption habits. However, a less subjective method of measurement, a three-dimensional analysis of the tags and a multivariate analysis, will need to be considered in future studies. There have been remarkable advances in trying to identify a possible biological agent by analyzing tooth marks on bones. However, this evidence may only indicate the presence of an animal in a certain place, but not whether it was responsible for the death of the animal or human being. Forensic investigation requires determination of whether the animal was alive or dead when the teeth marks were created, and to find evidence that a certain suspect caused the death. In this scenario, where many variables are involved and where subjectivity must be eliminated, the methods of analysis must be stricter and the results more accurate. At this point, the expert investigation becomes interdisciplinary work. Thus, forensic taphonomy and forensic odontology combined could strengthen the analysis of tooth marks as evidence in a judicial process, determining to whom a certain bite pattern belongs and whether it resulted in death. The first will allow us to identify the remains, investigate the circumstances surrounding the death, including the cause and manner of death and, where appropriate, the identification of clues (e.g., teeth marks on tissue and bones) that may lead to the perpetrator. This will incorporate the analysis of intrinsic (victim-specific) and extrinsic (perpetrator-specific and environmental) factors (Schotsmans et al., 2017). Forensic odontology, on the other hand, currently applied to veterinary medicine, will allow us to determine the forensic value of each of the bite marks, in order to exclude or include a possible suspect, according to the criteria established by the ABFO (American Board of Forensic Odontology, 2016) (Kling and Stern, 2018) by direct analysis of an animal's dentition, casts or three-dimensional images (Dorion, 2011). The wide range of factors that can affect the type and degree of bone modification indicates that the scavenge taxa's feeding behaviors could be more important than the size of the bite marks found at a crime scene in identifying the agent that caused them. There are many studies that can be carried out given the great potential that the scapula provides as a source of bite marks, to try to differentiate wolves from dogs with similar characteristics, despite the high degree of modification it can undergo. Using a highly standardized/homologous material, advanced methodologies, such as geometric morphometrics and artificial intelligence for image processing and analysis, and the availability of tools for multivariate analysis of samples, encourages us to work in an interdisciplinary way, creating blind studies to validate the results. The presence of hairs (present in all hair-modified bones), may be only one of many pieces of evidence found at a crime scene (Iglesias et al., 2017). Thus, the integration of complementary evidence will increase the value of bite patterns on bones as forensic evidence, as it will help us understand the context in which each type and degree of modification may have originated. Tooth marks or fractures on the bone that may have caused the death, histological studies to determine whether the injury was predation or scavenging (Cappella and Cattaneo, 2019) and DNA analysis, together, can significantly contribute to determining the aggressor agent. To integrate this information requires knowledge of the context in which the events occurred, so the presence of a professional with animal forensic expertise is necessary at the crime scene.

5. Conclusions

Captive Iberian wolves and semi-captive large-animal hunting dogs are capable of modifying relatively fresh, fleshless and isolated bovine scapulas in a differential manner by creating tooth marks on their bony surface during scavenging. This is despite the fact that their motivation may be different and the scapula may undergo a high degree of modification. However, taxonomic differentiation by two-dimensional morphometric analysis of these marks, using subjective methodologies and univariate statistical analysis still generates a degree of overlap between the two species. This makes it necessary to incorporate new morphological and morphometric variables in the analysis of tooth marks, using advanced technologies still under development, in three-dimensional form, with homologous experimental elements and multivariate analysis. For now, the overlap of tooth marks between the two species suggests their cautious use, as they only provide a frame of reference. Relating other evidence found at the crime scene to the pattern of teeth marks on bones will facilitate understanding of their variations according to the context in which they were created, increasing their value as forensic evidence. Given the wide range of extrinsic and extrinsic factors that may affect the degree and type of modification caused by these animals, on bones in general and scapulae in particular, the interdisciplinary evaluation of their characteristics is required. To this end, the combination of integrative disciplines, such as criminalistics, taphonomy, forensic odontology and forensic veterinary will improve the procedures for assessing the potential of tooth marks on bones as evidence, and allow the reconstruction of events, predation or scavenging.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2023.105988.

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