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# Taphonomic data from the transitional Aurignacian of El Castillo cave (Spain) reveals the role of carnivores at the Aurignacian Delta level



Alicia Sanz-Royo<sup>a,\*</sup>, Gabriele Terlato<sup>a</sup>, Ana B. Marín-Arroyo<sup>a,\*\*</sup>

<sup>a</sup> Grupo de I+D+i EVOADAPTA (Evolución Humana y Adaptaciones durante la Prehistoria), Dpto. Ciencias Históricas, Universidad de Cantabria, Av/Los Castros 44, 39005, Santander, Spain

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Keywords: Middle/upper palaeolithic Subsistence strategies Carnivores Taphonomy Iberia	Palaeolithic sites are complex palimpsests due to the recurrent presence of human groups and carnivores through time, as documented in several European caves and rock shelters. Within these contexts, it can be challenging to identify the main contributors to bone accumulations and interpret human subsistence strategies and the role of carnivores. Consequently, taphonomic analyses are crucial for distinguishing the origins of these occupation episodes. One example of alternating occupations is found at El Castillo cave (Cantabria, Spain), specifically in the so-called Transitional Aurignacian level (~46-42 ka uncal BP). According to a recent study conducted at this level (Luret et al., 2020), the human groups had a hunting specialisation focused on red deer, while carnivores had little influence on the assemblage. However, these interpretations were based only on the faunal assemblage from the recent excavations (1980–2011). A previous excavation phase was conducted on this site from 1910 to 1914, and after that, the faunal remains recovered were separated across several institutions, lacking a complete archaeozoological and taphonomic analysis of the whole level. In this work, a new taxonomic assessment and, for the first time, a taphonomic study of the macrofauna recovered in the Aurignacian Delta level during the initial

structing new hypotheses to interpret this relevant archaeological level.

# 1. Introduction

During the Late Pleistocene, caves and rock shelters were usually alternately inhabited by humans and carnivores, as attested in different European archaeological sites (i.e., Straus, 1982; Valente, 2004; Costamagno et al., 2005; Diedrich, 2015; Sanchis et al., 2019; Sánchez-Romero et al., 2020; Marín-Arroyo and Sanz-Royo, 2021; Zilio et al., 2021; Hussain et al., 2022; among others). In these contexts, it is challenging to interpret Neanderthal and Anatomically Modern Humans (AMH) subsistence strategies and evaluate the role played by carnivores in the accumulation of archaeological faunal assemblages. Palaeolithic sites are complex palimpsests, usually accumulated for thousands of years, where the presence of several human groups could be alternated by carnivore occupations. Identifying the main bone accumulator/accumulators at this stage is not easy. Thus, taphonomic analyses of the macrofaunal remains are essential to identify who occupied the site and to determine the origin of any archaeo-paleontological accumulation.

The Transitional Aurignacian level (~46-42 ka uncal BP) of El Castillo cave (Cantabria, Spain) is an example of alternating humancarnivore occupation. Since the discovery of the cave, two excavation phases were conducted (from 1910 to 1914 and from 1980 to 2011), discovering the exceptional archaeological richness of the site. Numerous multidisciplinary works have taken place, such as those carried out in the lithic industry (Cabrera Valdés, 1979; Cabrera Valdés et al., 2001; Bernaldo de Quirós et al., 2010) and chronology (Cabrera Valdés and Bischoff, 1989; Hedges et al., 1994; Cabrera Valdés et al., 1996; Rink et al., 1997; Wood et al., 2018). Also, the study of the paleoenvironmental context through pollen analysis (Dari and Renault-Miskovsky, 2001), sediments (Cabrera Valdés et al., 1993), as well as recent isotopic analysis in the Middle-to-Upper Palaeolithic transition levels (Jones et al., 2019). Of great relevance and interest are the human remains recovered at this level identified as Neanderthals (Garralda, 1992, 2005; Estalrrich and Marín-Arroyo, 2021; Garralda et al., 2022). Regarding the faunal materials, abundant remains were

excavations, stored at Museo Nacional y Centro de Investigación de Altamira (Cantabria, Spain), is carried out. This work provides new information about the human and carnivore groups that occupied El Castillo, con-

\* Corresponding author.

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<sup>\*\*</sup> Corresponding author.

E-mail addresses: aliciasanzr@gmail.com (A. Sanz-Royo), marinab@unican.es (A.B. Marín-Arroyo).

recovered along the different excavations. However, after the old excavations, faunal samples were sent to various specialists across American, French, and Spanish museums and institutions, producing a high dispersion of the collections. This has caused the lack of a complete archaeozoological and taphonomic analysis of the macrofauna and a synthesis of the work up until now. Different studies were conducted on the faunal remains recovered in the Transitional Aurignacian level from the old (Cabrera Valdés, 1979; Klein and Cruz-Uribe, 1994; Dari, 2003; Landry, 2005; Landry and Burke, 2006; Castaños, 2018) and from the most recent excavations (Luret, 2017; Luret et al., 2020) Nevertheless, Luret (2017) and Luret et al. (2020) are the only works in which a complete taphonomic analysis has been carried out, while from the ancient collections not detailed taphonomic data are available.

In this work, we have developed a complete taphonomic study of the macrofauna collection from the old excavations of El Castillo cave, stored at Museo Nacional y Centro de Investigación de Altamira (Cantabria, Spain), to evaluate the role played by humans and carnivores during the formation of the Transitional Aurignacian level. More detailed results, presenting a fresh interpretation of the findings obtained from the excavations between 1980 and 2011, are now being provided, following the preliminary results introduced in Sanz-Royo et al. (2022).

# 2. Regional settings

El Castillo is located in Puente Viesgo (Cantabria), Northern Iberia (Fig. 1). The cave dominates the Pas valley at an altitude of 195 m.a.s.l. from the North-Eastern side of El Castillo mount, a karstic massif of which this cave is part together with four others: Las Chimeneas, Las Monedas, La Cantera and La Pasiega. They all contain Palaeolithic rock art and were declared World Heritage Sites by UNESCO in 2008.

El Castillo cave was discovered in 1903 by Alcalde del Río, 1906 and contained a total of 26 archaeological levels and different human occupation phases, from the Acheulean to the Azilian (Breuil and Obermaier, 1912; Cabrera Valdés, 1984; Cabrera Valdés et al., 2001, 2005). After some preliminary research, early excavations were developed from 1910 to 1914 under the supervision of H. Obermaier, mainly in the vestibule zone (Cabrera Valdés, 1984). However, the arrival of World War I forced the campaigns to stop. In 1980, a second phase began, directed by V. Cabrera Valdés and F. Bernaldo de Quirós, whose main objective was to excavate Middle-to-Upper Palaeolithic transition levels in the vestibule area, as well as the correlation with the levels excavated by Obermaier (Cabrera Valdés et al., 2001). Currently, a third phase of excavation, directed by J.M. Maíllo Fernández and J. Marín from UNED, is mainly focused on the Mousterian levels.

The faunal remains from Cabrera Valdés and Bernaldo de Quirós excavations were deposited in 2008 at the Museo de Prehistoria y Arqueología de Cantabria (MUPAC) in Santander (Spain), while those from the old excavations were sent for study to different specialists based at national and international institutions. According to Castaños (2018), currently, there are five main collections located at i) Laboratory of Dr. Guérin in Lyon (France) (DPL); ii) Institut de Paléontologie Humaine (IPH) in Paris (France); iii) Museo Nacional y Centro de Investigación de Altamira (MCA) in Santillana del Mar (Spain); iv) Museo de Prehistoria y Arqueología de Cantabria (MUPAC) in Santander (Spain); and v) Museo Arqueológico Nacional (MAN) in Madrid (Spain). Other small collections were deposited in different Spanish institutions (i.e., Museo Nacional de Ciencias Naturales in Madrid, Universidad Nacional de Educación a Distancia (UNED), the Archaeological Museum of Navarra, and the Archaeological Museum of Oviedo), and the American Museum of Natural History in New York.

This work is focused on the Delta Aurignacian level, attributed to Transitional Aurignacian, identified during Obermaier's excavations. This is a rich archaeological level composed of yellowish-brown siltysandy clays, with a maximum depth of 65 cm. It was also excavated and named Level 18 during the modern excavations. Stratigraphically, this unit is located between two sterile levels and divided into three sublevels (from base to the top): 18C, 18B and 18A (Cabrera Valdés, 1984; Cabrera Valdés et al., 2001) (Fig. 2). Through the two lower sublevels, a dense concentration of faunal remains and lithic industry was discovered, in addition to hearths and human remains attributed to Neanderthals (Garralda, 1992, 2005; Garralda et al., 2022), although their taxonomic identification have been debated. In contrast, the uppermost sublevel 18A is practically sterile. Several radiocarbon and ESR dates



Fig. 1. Location of El Castillo cave (Cantabria, Spain) and other close archarological sites with similar chronology in Northern Iberia (image: M. Vidal-Cordasco and L. Agudo-Pérez).



Fig. 2. Plan of El Castillo cave with the location of the excavation areas during the Obermaier's excavation (left), and the stratigraphy based on the studies of Cabrera Valdés (1984) (right) (image: A. Agudo-Pérez).

were carried out in Level 18 (Rink et al., 1997; Cabrera Valdés and Bischoff, 1989; Hedges et al., 1994; Cabrera Valdés et al., 1996) concluding no significant chronological differences among sublevels nor different cave areas were apparent. In addition, recent ultrafiltration AMS dates proposed a chronology for this level between 42,000  $\pm$  1500 BP (OxA-22203) and 46,000 ± 2400 BP (OxA-21973) (Wood et al., 2018), suggesting a correlation between Level 18 excavated in 1980-2011 and the Aurignacian Delta level excavated during 1910-14 (a compilation of dates is provided in SI1). The stratigraphy and lithic industries also show similarities, supporting the correlation between both. Culturally, due to its transitional industry with mosaic characters related to the Mousterian (with the presence of elements such as sidescrapers) and also with Upper Palaeolithic features, such as bladelets and typical Aurignacian bone industry (i.e., split base points), this level was attributed as Transitional Aurignacian during the 1980s excavations (Cabrera Valdés, 1984; Cabrera Valdés et al., 2001; Gimenez La Rosa, 2006; Morán and Tejero, 2006; Bernaldo de Quirós et al., 2010; Tejero et al., 2012; Pastoors and Tafelmaier, 2013). However, these characteristics resemble neither the Châtelperronian nor any other documented transitional industry in Europe. For this reason, its cultural attribution and the integrity of the level have been (and continue today) widely debated (Zilhão and d'Errico, 2000; Zilhão, 2006).

# 3. Materials and methods

The materials included in this work are the macrofaunal remains recovered in the level identified as Aurignacian Delta during the 1910-14 excavations, where no sublevels were identified as it happened in the 1980s excavations. The analysed faunal assemblage corresponds to the collection deposited in the Museo Nacional y Centro de Investigación de Altamira (MCA) in Santillana del Mar, Cantabria (Spain).

Different researchers previously carried out taxonomic identifications of the mentioned materials (see Castaños, 2018). However, taphonomic analyses were not performed in any of these studies. For this reason, we have reviewed the taxonomic identification, and for the first time, a taphonomic analysis is carried out. This study was conducted in the MCA.

For the anatomical and taxonomical identification, we used the comparative osteological collection of EvoAdapta Group (University of

Cantabria, Spain) and different osteological atlases (Barone, 1976; Pales and García, 1981; Varela and Rodríguez, 2004; among others). Measurements were taken following the standards of von den Driesch (1976) and compared with other Spanish and European Late Pleistocene sites. Specifically for equids, the taxonomic identification follows Eisenmann et al. (1988) and Sanz-Royo et al. (2020), and the collection of Los Rincones site (MPZ, 2015) from Museo de Ciencias Naturales of the Universidad de Zaragoza (Spain). The differentiation between Bos primigenius and Bison priscus has been conducted following Buitrago (1992), Gee (1993), and Sala et al. (2010). The taxonomic identification of ursids is based on morphological and metric criteria (Kurtén, 1955; Torres Pérez-Hidalgo, 1988; Argant, 1989; Grandal-d'Anglade, 1993; García, 2003; Torres et al., 2005; Crégut-Bonnoure et al., 2011; Rabal-Garcés, 2013; among others). The collection of Los Rincones site (Museo de Ciencias Naturales de la Universidad de Zaragoza - MPZ, 2015) and the criteria of Ghezzo and Rook (2015) have facilitated the identification of Panthera pardus. The differentiation between Canis lupus and Cuon alpinus has been carried out following Pérez-Ripoll et al. (2010), Pionnier-Capitan et al. (2011) and Sanchis et al. (2020). Non-identified remains were grouped into five mammal-sized classes (Bunn, 1986): Size 1- small-sized mammals such as mustelids; Size 2lagomorphs and small carnivores <20 kg; Size 3- medium-sized animals weighing between 20 and 30 kg (i.e., Capreolus capreolus or Canis lupus); Size 4- medium-large sized animals weighing between 30 and 160 Kg (i. e., Cervus elaphus and Capra pyrenaica); and Size 5- larger over 300 Kg (i. e., Bos primigenius or Equus ferus).

We have considered four age classes, following Couturier (1962), Silver (1969), Harris (1978), Mariezkurrena (1983), Habermehl (1992), Gipson et al. (2000), Azorit et al. (2002), Tomé and Vigne (2003), Weinstock (2009), and Geiger et al. (2016): fetus/newborn (deciduous teeth and epiphyses unfused), juvenile (worn deciduous teeth and permanent teeth emerging, and epiphyses unfused or fusing), subadult/adult (permanent teeth and fused epiphyses) and senile (very worn permanent teeth). Specifically for ursids and hyenas, we have followed Stiner (1994, 1998). The age of death has been plotted using ternary plots with R *Software* (4.2.3 version) to interpret the mortality profiles proposed by Stiner (1990).

The elements were quantified using: NR (Number of Remains), NISP (Number of Identified Specimens), MNE (Minimum Number of

Elements) and MNI (Minimum Number of Individuals) (Grayson, 1984; Klein and Cruz-Uribe, 1984; Lyman, 1994).

For the taphonomic analyses, a specialised bibliography and taphonomic atlases were consulted (Behrensmeyer, 1978; Blumenschine et al., 1996; Fernández-Jalvo and Andrews, 2016; among others). Evidence of anthropogenic modifications on the faunal remains includes cut marks (Binford, 1981; Potts and Shipman, 1981; Shipman and Rose, 1983; Lyman, 2008), intentional bone breakage (differentiating among fresh, dry or indeterminate fractures) and percussion marks (Blumenschine and Selvaggio, 1988; Villa and Mahieu, 1991; Galán et al., 2009; Sala et al., 2015; Vettese et al., 2017, 2020). Carnivore modifications were documented when tooth marks and different marks related to chewing activity were present (Haynes, 1980, 1983; Binford, 1981; Domínguez-Rodrigo and Barba, 2006; Sala, 2012). Other post-depositional alterations comprise the presence/absence of root marks, fungi/bacteria, modifications made by rodents, weathering, trampling, water dissolution, concretion, abrasion and manganese (Behrensmeyer, 1978; Lyman, 1994; Shahack-Gross et al., 1997; Cukrowska et al., 2005; among others). When necessary, microscopic analyses, measurements, and image captures were carried out using Leica M125 microscope.

To identify the carnivore which might be responsible for the accumulation, we considered metric data of the tooth marks left on the bone surface, their morphology and location, and the anatomical element and animal species where they were observed. The measurements used in this work are the maximum diameter of the pits, complemented by the minimum diameter and the maximum width of the scores, and indicating their location in cortical, flat or cancellous bones. Nevertheless, this information must be taken cautiously as there is a critical overlap among the size ranges produced by different animals. The data obtained have been compared with metrical data provided in several experimental works with extant bears, lions, hyenas, leopards and wolves (with a priority of large samples with animals in freedom/semi-freedom conditions) (Domínguez-Rodrigo and Piqueras, 2003; Sala, 2012). Other specialised works have also been considered (Delaney-Rivera et al., 2009; Sala and Arsuaga, 2013, 2018; Sala et al., 2014; Rosell et al., 2019; Blasco et al., 2020; Toledo González et al., 2021; Domínguez-Rodrigo et al., 2022; among others). R Software has been used to represent these

mark measurements.

# 4. Results

# 4.1. Taxonomic review

A total of 327 faunal remains from the Aurignacian Delta level deposited at the Museo Nacional y Centro de Investigación de Altamira (MCA) have been analysed (Table 1).

91% of the assemblage has been identified taxonomically, where carnivores are predominant (72 % of NISP) with a wide variety of species, while the representation of herbivores is much lower (28 % of NISP). In general, except for slight variations, the taxonomic composition coincides with Castaños (2018). Both in terms of NISP and MNI, *Ursus spelaeus* is the most represented species, followed by *Bos/Bison* sp., *Crocuta spelaea*, and *Cervus elaphus*. Although scarce, ungulates such as *Bos primigenius, Equus ferus, Rupicapra rupicapra*, and *Sus scrofa* have also been identified, as well as *Panthera* cf. *spelaea*, *Panthera pardus, Canis lupus*, and *Vulpes vulpes* (Fig. 4) (additional information about the taxonomic identification is provided in **Supplementary Information**).

#### 4.2. Skeletal profiles and mortality profiles

In the Aurignacian Delta level, isolated teeth are the most common anatomical elements, comprising over half of the sample (58%), followed by the appendicular skeleton. When examining the skeletal profile of the most abundant taxa, a clear difference between herbivores and carnivores is observed. Whereas large bovines, horses and red deer are mainly represented by its appendicular skeleton and with scarce cranial and axial elements, carnivores are primarily characterised by cranial and isolated dental remains, with cave bears having the highest proportion at 83% of MNE (Fig. 3a).

Adult individuals dominate, although juvenile individuals are also present (Table 1). Cave bear is the only species represented by all age profiles, from newborn to senile. Three right lower deciduous teeth (Fig. 4h) indicate that a minimum of three bear cubs died shortly after birth inside the cave, suggesting winter seasonality at the death time.

Table 1

Number of Remains (NR), Number of Identified Specimens (NISP), Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) identified at the Aurignacian Delta level (F/NB = fetus/newborn, J = juvenile, SubA = subadult, A = adult, S = senile) (see **SI2** for more details about MNE).

Species	NR	NISP	%NISP	MNE	MNI				
					F/NB	J	SubA	А	S
Bos primigenius	1	1	0.3	1				1	
Bos/Bison sp.	43	43	14.5	26		1	1	2	
Equus ferus	7	7	2.4	7		1		1	
Cervus elaphus	26	26	8.8	19		1	1	2	
Rupicapra rupicapra	3	3	1	3				1	
Sus scrofa	2	2	0.7	2		1			
Capra/Cervus	1	1	0.3						
Rupicapra/Capreolus	1	1	0.3						
Ungulata size 4-5	3								
Ungulata size 3-4	6								
Total Ungulates	93	84	28.3	58	2	8	0	7	0
Ursus spelaeus	155	155	52.2	75	3	3	5	16	7
Crocuta spelaea	37	37	12.5	22		3	1	4	
Panthera cf. spelaea	1	1	0.3	1			1		
Panthera pardus	5	5	1.7	5		1		2	
Canis lupus	9	9	3.0	7		1		2	
Vulpes vulpes	5	5	1.7	3		1	1	1	
Felidae	1	1	0.3						
Carnivora indeterminate	1								
Total Carnivores	214	213	71.7	113	3	9	8	25	7
Mammal size 5	12								
Mammal size 4	6								
Indeterminate	2								
Total	327	297	100	171	3	13	10	32	7



Fig. 3. 3.a) Skeletal profiles represented in the most abundant species of Aurignacian Delta level, indicated by the percentage of Number of Identified Specimens (% NISP) (the group "extremities" includes metapods, sesamoids, and phalanges); **3.b**) Ternary plot showing the mortality profiles proposed by Stiner (1990) of the most abundant species in terms of MNI.

The ternary plot made with the most abundant species of this level (MNI  $\geq$ 5) shows that the age of death of large bovines (including *Bos/Bison* sp. and *Bos primigenius*) is dominated by adults. In contrast, hyenas and cave bears show a catastrophic profile, representing all ages that could be found in life (Fig. 3b).

## 4.3. Taphonomic analysis

In general, the preservation state of the faunal remains is good. The most relevant postdepositional alteration throughout this level is the presence of manganese and weathering (both in a low grade).



**Fig. 4.** Faunal remains identified in Aurignacian Delta level (Museo Nacional y Centro de Investigación de Altamira, Ministerio de Cultura y Deporte de España). From a to h, dental remains of *Ursus spelaeus*: **4.a**) left upper  $M^1$  (buccal side); **4.b**) left upper  $M^2$  (lingual view); **4.c**) left upper  $M^1$  (occlusal view); **4.d**) left upper  $M^2$  (occlusal view); **4.e**) left lower  $M_1$  (occlusal view); **4.f**) right lower  $M_2$  (occlusal view); **4.g**) canines; **4.h**) right mandible of a newborn individual (lingual view). **4.i**) Left mandible of *Canis lupus* (buccal view). **4.j**) Left distal epiphysis tibia of *Bos primigenius* (dorsal and caudal view). **4.k**) Right lower  $M_1$  and upper  $P^4$  of *Crocuta spelaea* (buccal view).

Trampling, bacterial activity, roots or water dissolution are also present, although not significantly, facilitating the study of the bone surfaces.

# 4.3.1. Bone breakage pattern

Indeterminate fractures are the most frequent within the assemblage (68% of remains). The 6% of the total remains present fresh fractures, most with an oblique angle and a curved profile, being identified on

large bovines and red deer remains (Fig. 5b). Approximately 33% of fresh fractures are associated with cut marks. Dry fractures appear in 19%, of which 41% are associated with carnivore marks. This fracture type occurs in practically all species, both herbivores and carnivores, being most abundant in cave bear.



Fig. 5. Anthropogenic and carnivore modifications in Aurignacian Delta level (Museo Nacional y Centro de Investigación de Altamira, Ministerio de Cultura y Deporte de España): 5.a) mandible of *Equus ferus* (buccal left and right sides) with scores (red arrow) and cut marks (black arrow); 5.b) right tibia of *Cervus elaphus* with fresh fracture and cut marks. Carnivore chewing activity (red arrows) in carnivore mandibles (buccal view): 5.c) left mandible of *Panthera pardus*, 5.d) right mandible of *Crocuta spelaea*, 5.e) right mandible of *Ursus spelaeus*, 5.f) right mandible of *Crocuta spelaea*. 5.g) pits and scores in a rib of *Bos/Bison* sp. 5.h) atlas of *Ursus spelaeus* (cranial view) with scores and gnawing marks (red arrows).

#### Table 2

Number of Identified Specimens (NISP) in which different anthropogenic and carnivore marks have been observed in the Aurignacian Delta level of El Castillo.

Species	Cut marks	Percussion marks	Carnivore marks		
Bos/Bison sp.	4	1	11		
Cervus elaphus	3		7		
Equus ferus	2		4		
Crocuta spelaea			4		
Panthera pardus			2		
Ursus spelaeus			8		
Mammal size 4-5	2		3		
Total NISP	11	1	39		

#### 4.3.2. Anthropogenic modifications

Anthropogenic modifications are scarce, appearing in 4% of the total remains (Table 2). However, it must be considered that more than half of the assemblage corresponds to isolated teeth. Excluding these elements, the percentage of anthropogenic modifications amounts to 8%. These modifications are mainly cut marks, mostly incisions (Fig. 5a and 5b). The morphology and location of the incisions observed in a large bovine metacarpal and a proximal phalanx may be related to skinning and disarticulation activity. In contrast, long cut marks in red deer are associated with defleshing of long bones. Large bovines, followed by red deer and horses, were highly butchered by human groups. No remains with signs of thermoalteration have been identified.

#### 4.3.3. Carnivore modifications

Carnivore modifications are present in 12% of the total remains (Fig. 5 and Table 2), including ungulates and carnivores, and mainly in adult individuals. Excluding the isolated teeth, carnivore activity is present in 20.3% of the remains. The species most affected by these activities are large bovines, followed by cave bears and red deer. The most common marks are pits, usually accompanied by scores and gnawing, mainly on long bones and mandibles (see **SI8** for more details). Occasionally, carnivore marks have been observed associated with fresh or indeterminate fractures, generating doubts about their anthropogenic origin. Furthermore, in three remains belonging to *Bos/Bison* sp. and *Equus ferus*, both cut marks and carnivore marks have been identified, although without the possibility of establishing a chronological order between them (Fig. 5a).

The variety in the morphology and size of the marks observed leads us to suspect that multiple carnivores may have been involved. Throughout this work, different carnivore species have been identified, all able of producing various bone modifications in skeletal assemblages. To determine the responsible carnivore/carnivores, the measurements taken on the marks observed during this analysis have been compared with those produced by extant bears, hyenas, lions, leopards and wolves (Domínguez-Rodrigo and Piqueras, 2003; Sala, 2012). Despite an overlap among measures, the similarity between the morphology and size range and those commonly produced by hyenas suggests that this carnivore species may have been the primary agent of the observed modifications at this level. On the other hand, in some cave bear and red deer remains, the size of the marks coincides with those typically produced by cave bears (Fig. 6).

# 5. Discussion

The chronological dates provided by ESR and AMS dates without and with ultrafiltration pretreatment (Cabrera Valdés and Bischoff, 1989; Hedges et al., 1994; Cabrera Valdés et al., 1996; Rink et al., 1997; Wood et al., 2018) confirmed that deposition of Level 18 excavated during the 1980–2011 campaigns ended between 44.9 and 42.1 ka cal BP, without relevant differences among sublevels and excavated areas of the cave. These dates are consistent with those obtained for the excavations of the Aurignacian Delta level during 1910-14 (see **SI1**). Level 18 and Aurignacian Delta level overlap with the end of the Mousterian and



**Fig. 6.** Comparison among measurements taken in this work on different specimens of El Castillo with those produced by extant bears, hyenas, lions, leopards and wolves (Domínguez-Rodrigo and Piqueras, 2003; Sala, 2012): **6.a**) Maximum diameter of pits in cortical long bones; **6.b**) Maximum diameter of pits in flat bones; **6.c**) Maximum diameter of pits in cancellous bones.

Châtelperronian, both at regional and European levels (Higham et al., 2014; Hublin, 2015; Marín-Arroyo et al., 2018; Rios-Garaizar et al., 2022; Vidal-Cordasco et al., 2022), and are older than the Proto-Aurignacian at the region, documented in Level 16 of El Castillo, Covalejos, and El Cuco (Wood et al., 2018; Marín-Arroyo et al., 2018; Marín-Arroyo and Sanz-Royo, 2021). According to these data, in this work, the integrity and stratigraphic delimitation of Aurignacian Delta level (Level 18 in recent excavations) is assumed to be consistent. However, the presence of split base points, which provided Aurignacian dates (Wood et al., 2018), does not rule out the possibility of some intrusions from the upper Aurignacian levels.

Differences have been observed when comparing the archaeozoological and taphonomic data obtained in this work with the data available for other collections of El Castillo. Regarding the taxonomic composition of the MCA collection (Museo Nacional y Centro de Investigación de Altamira), there is a predominance of carnivores, especially cave bears, which differs notably from the data presented previously by other authors (Dari, 2003; Castaños, 2018; Luret et al., 2020). As shown in Table 3, the MUPAC collection (Museo de Prehistoria y Arqueología de Cantabria) preserves the most significant number of faunal remains, where red deer is the most represented species. However, the diverse collections from the old excavations have a considerably smaller number of remains, with a large sample of equids in MAN (Museo Arqueológico Nacional of Madrid), a collection of rhinos in DPL (Laboratory of Dr. Guérin in Lyon), a high amount of red deer specimens in the IPH (Institut de Paléontologie Humaine), and a varied selection of ungulates in the UNED (Universidad Nacional de Educación a Distancia) with a minimal presence of carnivores.

By looking at these data, a straightforward question arises: is there a differential distribution of macrofauna depending on the institutions where they are stored and therefore, this situation influence the archaeozoological interpretation of the assemblage?

This study concludes that there is a significant bias in the old collections, probably motivated by Obermaier's decision to distribute different bone animal species to specialists worldwide. Since then, the management of those collections has been maintained by those institutions, leading to independent studies. The skeletal profiles documented in this work are double influenced: first by this bias and second by the old excavation methods used during Obermaier's works, which prioritised the recovery of the most diagnostic and complete elements. Conversely, such biases may not have affected the faunal specimens from modern excavations. When examining the available taxonomic data of the collections as a whole assemblage (including our results) (Table 3), red deer is the predominant species and the most consumed by human groups. However, the data presented in this work demonstrate a higher presence of carnivores than previously documented.

Regarding the activity carried out by human groups and carnivores during the Transitional Aurignacian of El Castillo cave, Luret et al. (2020) proposed a hunting specialisation on red deer, while the carnivores had little influence on bone accumulation. These conclusions were based on the study of the 1980–2011 excavations deposited at MUPAC. They observed abundant fresh fractures (98% of the remains) with spiral morphology, and some cut and percussion marks, thermoalterations, and bone retouchers. On the contrary, the carnivore modifications were scarce despite the 987 fragments of hyena coprolites documented at this level. However, the results presented in this work, based on the study of the MCA collection from ancient excavations, show notable taphonomic differences indicating a higher carnivore activity and less anthropogenic activity than previously documented for this cultural level.

The comparison among measurements taken by us on the carnivore marks and those produced by extant carnivore species suggests that hyenas would have been the main modifying carnivore in the MCA faunal assemblage, acting primarily on large bovines, red deer and cave bears. In addition, the consumption pattern, and the morphology and location of the marks coincide with the consumption activity documented in hyenas (Domínguez-Rodrigo and Piqueras, 2003; Kuhn et al., 2010; Diedrich, 2011; Sala, 2012; Sala et al., 2012; Samper Carro and Martínez-Moreno, 2014: among others). Hyenas often produce pits, scores in long bones diaphysis of diverse ungulate sizes, and gnawing marks. Hyenids are the only ones capable of carrying out an intense consumption of large mammal bones, like cave bears. Hence, the observed marks on the mandibles of cave bears and hyenas in an advanced state of consumption could probably be the result of their activity.

On the one hand, hyenas are expert bone breakers and do not necessarily leave associated tooth marks, making them potentially responsible for some of the documented spiral or indeterminate fractures. Lions also have strong biting capabilities but do not leave such marks and fractures (Sala, 2012). Additionally, certain marks showed a metric range similar to those produced by leopards. However, these animals do not usually consume large prey, focusing their feeding behaviour on medium/small-sized ungulates, such as caprids (Sauqué and Sanchis, 2017; Domínguez-Rodrigo et al., 2022). On the other hand, in some cave bears and red deer remains, the size of the marks matches with those produced by bears (Sala, 2012; Sala and Arsuaga, 2013). Although the diet of cave bears is mainly herbivorous, they may include meat by scavenging after hibernation (Clevenger and Purroy, 1991; Rabal-Garcés et al., 2012; Krajcarz et al., 2016; Bocherens, 2019; Ramírez-Pedraza et al., 2022). This scavenging activity, even among the cave bears, has been documented in several works (i.e., Pinto-Llona and Andrews, 2003; Pinto-Llona et al., 2005; Rabal Garcés et al., 2012). Experimental data indicate that bears leave fewer bone marks of their activity than other carnivores. When they leave marks, they tend to be

#### Table 3

Number of identified specimens (NISP) in the Delta Aurignacian level and Level 18 of El Castillo collections (Dari, 2003; Castaños, 2018; Luret et al., 2020). Samples with complete taphonomic analysis are marked with an asterisk.

Species	NISP							
	MUPAC 18B*	MUPAC 18C*	MAN Delta Aur.	IPH < Delta Aur.	DPL Delta Aur.	UNED Delta Aur.	MCA Delta Aur. (This work)*	TOTAL NISP
Stephanorhinus hemitoechus	10	4			14			28
Bos primigenius							1	1
Bos/Bison sp.	135	143		1		6	43	328
Equus ferus	22	23	176			1	7	229
Cervus elaphus	3981	4541		256		251	26	9055
Capreolus capreolus	86	123				21		230
Capra pyrenaica	3	4				58		65
Rupicapra rupicapra	151	77				109	3	340
Sus scrofa	2						2	4
Total Ungulates	4390	4915	176	257	14	446	82	10280
Ursus spelaeus	15	4					155	174
Ursus arctos								0
Crocuta spelaea	2	1					37	40
Panthera cf. spelaea	1	4					1	6
Panthera pardus							5	5
Canis lupus	5	1					9	15
Vulpes vulpes							5	5
Total Carnivores	23	10					212	245
Total NISP	4413	4925	176	257	14	446	294	10525

located in long bone epiphyses, ribs, and vertebrae, with peeling, pits, scores or gnawing marks in the cancellous bones (Clevenger and Purroy, 1991; Domínguez-Rodrigo and Piqueras, 2003; Sala, 2012; Rabal-Garcés et al., 2012; Rabal-Garcés, 2013; Sala and Arsuaga, 2013; Blasco et al., 2020). Some of these marks have also been observed in the analysed sample. Furthermore, the presence of three newborn individuals indicates winter seasonality at the moment of the occupation and death of these animals, suggesting cave bears used the cave's interior to hibernate and probably died naturally. This pattern is typical in bear dens, where adult or senile individuals without enough reserves for the winter season fail to overcome hibernation, or cubs who die after birth (Kurtén, 1976; Romandini et al., 2018). Besides, the skeletal remains found in the bear den areas usually show dry fractures caused by the trampling produced during the transit of cave bears and other carnivores through the site. This type of fracture has been observed in this work, mainly in cave bear remains, in some cases with carnivore modifications.

According to the results presented, we propose cave bears and hyenas as the main biological agents involved in the taphonomic modifications of the faunal assemblage from the Aurignacian Delta level stored at the MCA. We suggest that the presence of hibernating cave bears and the decomposing bears that died during that phase would have attracted carnivores such as hyenas, which would probably visit the cavity with relative regularity in search of carrion (as indicated by the presence of coprolites and tooth marks). This situation has been documented in several Late Pleistocene caves (i.e., Diedrich, 2011, 2012). However, a possible minor participation of other carnivores can not be ruled out.

According to Luret et al. (2020), the presence of young and newborn red deer individuals indicates a seasonality between spring and autumn during the Transitional Aurignacian, while several ungulate foetal remains suggest that females were introduced pregnant into the cavity between the end of winter and spring. Equally, this study documents the presence of carnivores during the winter. This could suggest a higher human occupation of the cave during more temperate periods, while carnivore activity would have been more intense during the winter. Therefore, the analysis of both assemblages deposited at MUPAC and MCA lend support to the human-carnivore alternating cave use during Transitional Aurignacian. However, the lack of information about the spatial location of the old materials prevents a clear interpretation about this alternation in the Aurignacian Delta level.

Regarding the paleoenvironment data provided by the assemblage, the high representation of red deer and the presence of wild boar at this level might suggest a temperate climate with some wooden areas close to the cave during this period. However, this inference based on the faunal representation must be taken with caution since red deer is an eurytherm species and can adapt to diverse environments and temperatures. This suggestion is supported by pollen and charcoal analysis, which reflect a temperate climate and forested areas constant throughout the sequence. However, the tree mass was reduced compared to previous levels (Dari and Renault-Miskovsky, 2001; Uzquiano, 2005, 2008). The isotopic analysis carried out by Jones et al. (2019) and the recent regional palaeoenvironmental synthesis (Fernández-García et al., 2023) indicates little change in the δ13C values through this period, suggesting that ungulates were consistent over time in their feeding behaviour by consuming C3 plants in a relatively open environment.

#### 6. Conclusions

Although the sample studied in this work is small, our study allows confirming: 1) the subsistence strategies of human groups inside the cave were mainly focused on red deer consumption; 2) a higher carnivore presence and activity inside the cave previously undocumented, especially of cave bears and hyenas; and 3) a differential distribution of the archaeofaunal materials recovered during the ancient excavations into the Spanish, French and American institutions that prevents a complete taphonomic interpretation of the roles played by humans and carnivores during the level formation. The different occupations of the cavity by humans and carnivores created a palimpsest complicated to decipher. However, our results suggest alternated use of the cave according to different seasons, with a more relevant presence of carnivores during winter.

Our study indicates the necessity of carrying out a complete archaeozoological and taphonomic analysis on the whole faunal assemblage of the Transitional Aurignacian level to avoid more bias in the data obtained and its global interpretation. A synthesis of the results is necessary to correctly identify the human/carnivore occupation episodes, the role of carnivores inside the cave and the subsistence strategies that human groups carried out at El Castillo during this period.

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#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

# Data availability

https://github.com/ERC-Subsilience/El\_Castillo\_Aurignacian\_Delta

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# Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.qsa.2023.100147.

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