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Taphonomic study of the cave bears (*Ursus* cf. *deningeri* and *U. spelaeus*) from the Sima I of the El Polvorín cave (Northern Iberian Peninsula)

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ABSTRACT

Cave bears used caves for hibernation and giving birth. Caves maintain stable conditions of temperature and humidity, which facilitates the preservation of fossil accumulations. Causes of mortality in caves are related to starvation during hibernation, which affects mainly juveniles and old adults, predation and accidents, affecting bears of all ages. The Iberian Peninsula is located in one of the extremes of the geographical range of this species and has yielded an abundant cave bear fossil record, particularly in karstic systems in the northern fringe. The origin of the accumulation of bear fossil sites in Iberia has been investigated mostly based on selected paleobiological variables (sex-ratio and age-at-death profiles) and qualitative taphonomic assessment. The objective of this paper is to delve into the origin of a bear accumulation with a large proportion of hyaena remains, the Sima I of El Polvorín cave (Biscay, Northern Iberian fringe, Spain). For that end a combination of quantitative paleobiological (age-at-death and sex) and taphonomic (bone fracture patterns and surface modifications) data is used. This analysis has ruled out humans and hyenas as the origin of the accumulation but, due to the limited number of fossil remains available it is not possible to ascertain whether the bear accumulation was the result of a natural trap within the cave, natural mortality during hibernation, or a combination of both causes. This study underscores the necessity of integrated methodological approaches and the potential of old paleontological collections to provide new important paleobiological and taphonomic information under these approaches.

1. Introduction

The cave bear, an icon of the Pleistocene megafauna, is a medium to large sized ursid that traditionally comprises the species *U. deningeri* and *U. spelaeus sensu lato*, which are considered chronospecies. Cave bears inhabited in Europe from the late Early Pleistocene until they went extinct in the Late Pleistocene (Madurell-Malapeira et al., 2010; Baca et al., 2016).

Cave bears hibernated in caves that they frequented for repeated years in a solitary fashion or mothers with their offspring (Kurtén, 1958). Ancient DNA studies have also revealed that when hibernating, cave bears were faithful to their place of birth (Fortes et al., 2016). These habits may have helped to create the large accumulations of cave bear remains (Kurtén, 1958). Bear fossil accumulations may have different origins: dead during hibernation (Kurtén, 1958, 1976), predation by other carnivores, attack in dens by humans while hibernating or even predation on already weakened specimens by other bears in times of food shortage, though the latter are very isolated events (Pinto Llona

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et al., 2005). Hibernation-related deaths are the product of starvation, often caused by a low food supply during the rest of the year (Kurtén, 1976; Garshelis and Pelton, 1980; Stiner, 1998). It affects mostly cubs and subadult age groups, especially if the hibernation period is prolonged, which has been detected in both extant brown bears (Schoen et al., 1987) and cave bears (Debeljak, 2004), while adults tend to wake up and attempt to get supplies (Glenn et al., 1976). However, old adults tend to be more susceptible to die of inanition as their nutrition previous to hibernation tend to be less efficient due to their eroded teeth and possible health problems derived from such teeth wear (Debeljak, 2004). The major frequency of juvenile and old individuals compared to prime adults is characteristic of an attritional or "U" shaped mortality model. This model is related to natural death of the groups of age more susceptible and prone to die. In the Iberian Peninsula it has been documented in many caves such as Reguerillo (Torres, 1976) or Amutxate (Torres et al., 2014).

Other causes of mortality in caves are predation and accidents. Hunting of hibernating bears by other predators is not common nowadays, but may have happened more frequently during Pleistocene considering, for example, that recent hyenas are capable of killing solitary lions (Debeljak, 2004). Specifically, in the case of bears, the age profiles studied in accumulations of this kind reveal that the most affected individuals are juveniles, prime adults and old adults, resulting in a living structure (LS) model (Stiner, 1998).

Accidents such as falling in a natural trap within a cave system encompass several factors, including the presence of skeletal remains and the specific cave morphology (comprising areas where animals fall and perish due to either falling or starvation). In sites associated with these types of accumulations, it is common to find a lack of evidence of bone modifications of human origin (such as cut marks) as well as a low frequency of marks made by carnivores (e.g., Sima de los Osos, Pinto et al., 2005; Kiputz IX, Castaños et al., 2012; Sima de los Huesos, García García, 2003; Sala and Arsuaga, 2018; Mainea, Rodríguez-Almagro et al., 2021). Regarding bears, previous studies of sites where the origin of the accumulation has been interpreted as a natural trap (Sima de los Huesos, García García, 2003; and Sima de los Osos, Pinto et al., 2005), show a higher representation of infant individuals while the proportion between sub-adults and old individuals is similar, resulting in an "L" shaped mortality pattern. Therefore, it is of great importance to better understand the origin of the ursid accumulation.

In the Iberian Peninsula, the largest accumulations of cave bear remains are found in the karstic systems of the northern fringe, although there are also other accumulations in the northeast and central Iberia (Torres Pérez Hidalgo, 1988a; Grandal d'Anglade and Vidal Romaní, 1997; Torres et al., 1998; García García, 2003; Pinto Llona et al., 2005; Rabal-Garcés et al., 2012; Villaluenga Martínez, 2013).

The origin of the accumulation and partial taphonomic studies have been published for different cave bear collections from the northern fringe of the Iberian Peninsula (e.g., Torres Pérez Hidalgo, 1988a; Castaños Ugarte et al., 2012; Villaluenga et al., 2012, 2014; Torres et al., 2014). While many of these works deal with important aspects such as the age-at-death, sex determination and anatomical representation, other important taphonomic aspects are only approached in a qualitative way. Therefore, studies that combine quantitative taphonomic observations with paleobiological information of cave bear assemblages are needed in order to fully comprehend the origin of these important bone accumulations. Bear accumulations may also comprise, though to a lesser extent, other carnivore remains such as large felids or hyenas. In fact, the analysis of hyenas can provide additional insights, given that it is one of the main accumulator agents of bone remains in caves during the Pleistocene (Henschel et al., 1979; Skinner and Ilani, 1979; Skinner et al., 1980; Skinner and van Aarde, 1991; Lam, 1992; Leakey et al., 1999; Kuhn, 2005, Kuhn et al., 2010; Lacruz and Maude, 2005; Skinner, 2006). This is the case of the Sima I of the El Polvorín cave which has yielded a paleontological assemblage consisting mostly of cave bears but which also has yielded a relatively large hyaena collection (Castaños, 1986, 1987).

Previous studies of the Sima I of El Polvorín cave have only tackled paleobiological aspects of the faunal remains (Castaños, 1986, 1987). Here, we present for the first time a taphonomic analysis integrating paleobiological aspects with quantitative taphonomic observations about bone fracture analysis and bone surface modifications. The objective of this work is to understand the origin of the bear assemblage of this cave. We determine ages-at-death for the bear assemblage in order to infer whether this accumulation follows an attritional or a catastrophic demographic profile. Additionally, we determine the sex in order to assess potential sex bias in the association. We perform an analysis of fracture patterns in order to understand the timing and mechanisms of fracturing to understand if the bones were fractured when they still preserved collagen or in later post-depositional phases. This allows testing the potential of the possible biological (produced by carnivores or humans) or geological origin of the fossil accumulations. We also assess the surface modification to test for potential human or carnivore origins of this accumulation, as well as to assess whether the faunal remains have suffered transport or not or whether they were accumulated in the outside or inside of the cave. Finally, the results of the paleobiological information and the taphonomic quantitative analysis will be compared with other sites in order to discuss the origin of the bear accumulation of the Sima I of El Polvorín site.

El Polvorín cave, also known as Ventalaperra D (180 m a.s.l.; Karrantza, Biscay, Northern Iberian Peninsula) is located in the SE slope of the Carlista peak (part of the Ranero crag, in the mountainous foothills of access to the Karrantza river gorge, on its right margin (Fig. 1). This cave develops in Cretaceous (Aptian-Albian) reef limestones. The cave entrance has a rounded shape (6 × 6 m) and shows a complex development with three intercommunicated levels (Garate Maidagan, 2012). The current entrance is an archaeological site which has yielded evidence of different human occupations during the Paleolithic, among others (Barandiarán Ayerbe, 1958, 1978; Ruiz Idarraga, 1992/93; Ruiz Idarraga and Berganza, 2003; Garate Maidagan, 2012). From the cave entrance, after c. 50 m, a lateral conduit connects with the rest of the karst system. Taking this conduit and after descending more than 30 m through a vertical conduit and a ramp, cavers also found a paleontological site in a lower gallery, called the Sima I (Fig. 1). An "ossiferous breccia" was discovered in the explorations carried out between November and December 1982 by the speleological group *Iluntasunaren Lagunak*, and in 1983 a cave bear skull and numerous bones were extracted from the bottom of Sima I of El Polvorín (González and Reyes, 1985; Castaños, 1986; Reyes, personal communication) (Fig. 1). The speleological group was accompanied by the geologist V. Ibarra who suggested that the paleontological remains were in a secondary position. The fossil remains extracted in 1983 were studied by P. Castaños (1986) who described the presence of *Ursus spelaeus*, *Crocuta spelaea* (including a coprolite), *Sus* sp. and *Vulpes* sp. In a subsequent study, Castaños (1987) suggests that the dimensions of the hyena remains from Sima I of El Polvorín cave are closer to *Crocuta intermedia* from Lunel Viel. According to the records of the Arkeologi Museoa (Bilbao), the speleologists recovered new fossil remains from this site in 2000, and to our notice these remains have never been published.

2. Material and methods

2.1. Material

In the present study all the faunal remains recovered during the 1983 and 2000 interventions carried out by the *Iluntasunaren Lagunak* speleological group in Sima I of El Polvorín cave have been analyzed. All the collection from this site is currently stored in the Arkeologi Museoa in Bilbao.

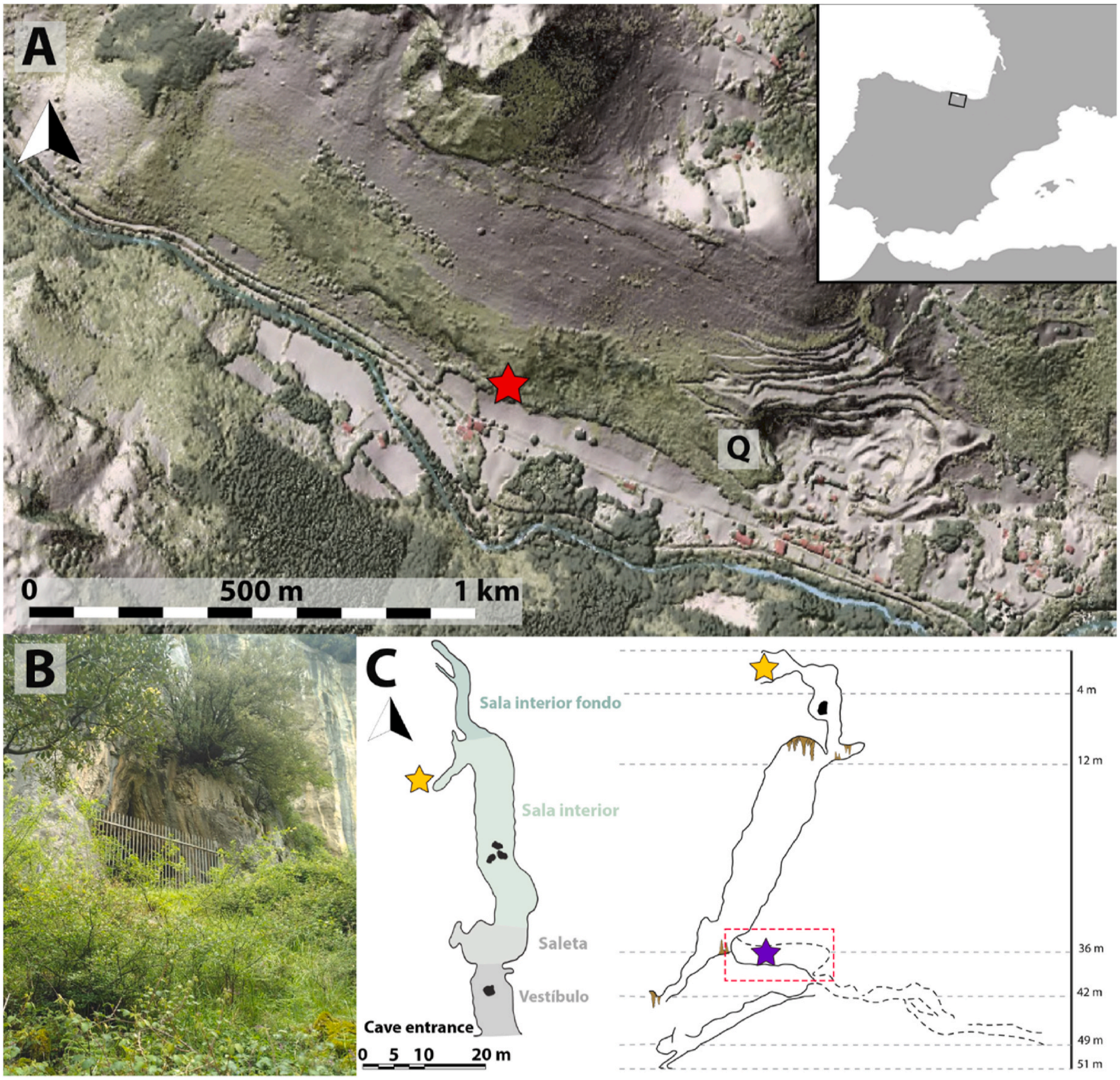

Fig. 1. A) Location of Sima I of El Polvorín (red star). B) Cave entrance. C) Left: Topographic scheme of the site map showing the different sectors, highlighting the access area to Sima I (yellow star) (modified from Garate Maidagan, 2012); Right: Topographic scheme in section of Sima I and location of the area where the fossil remains were recovered (violet star) (modified from Castaños, 1986). Base map in A made with QGIS 2.18.17 (QGIS Development Team, 2009). Q: Carranza Quarry, La Cadena neighborhood, Karrantza, Biscay. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.2. *Paleobiological analysis*

For the bear remains, the taxonomic assessment was performed on craniodental and metapodial remains, which are the most diagnostic anatomical regions (Torres Pérez Hidalgo, 1988c; 1988d; 1988e; 1988f). The age-at-death was estimated using the cranium, mandibles and teeth. Nine age cohorts were defined following Stiner (1998), which are based on the tooth eruption, root development and crown wear, and classify the population into juveniles, prime adults and old adults. We followed Fosse and Crégut-Bonnoure (2014) and Torres et al. (2007), to determine the age-at-death of the cranium and the mandibles, respectively. The postcranial remains were determined as juvenile, subadults and adults by their dimensions, and the state of fusion of their epiphysis (Torres et al., 2014). Age-categories followed Debeljak (2004): juveniles (0–2 years), subadults (3–4 years), prime adults (5–20 years), and old adults (+20 years). Sex was determined by the dimensions of the cranium and the upper and lower canines following Torres Pérez Hidalgo (1988b, 1988c). We followed Stiner (1990, 1998) mortality pattern classification of non-violent attrition (NNVA) or U shaped mortality profile represented by juvenile and old adults age cohorts, and living structure mortality profile (LS) represented by juvenile, prime adults and old adult age cohorts. We used the number of identified specimens (NISP) of the dentition to quantify each age cohort.

We have assessed the age-at-death of the spotted hyena remains following Brugal et al. (1997) and Jimenez et al. (2019). The minimum number of elements (MNE) and minimum number of individuals (MNI) was established based on anatomical replication, side, and age-at-death and morphological incompatibilities.

2.3. *Taphonomic analysis*

A sample of 245 macrovertebrate remains (after reffitings) from Sima I of El Polvorín were analyzed. The small sample of hominin remains were excluded from this study. The remains not included in this analysis correspond to undetermined fragments less than 2 cm in size. Dentition has been considered exclusively for the following attributes:

manganese oxides staining, calcium carbonate precipitates (crusts) and dissolution domes.

Experimental collections of modifications caused by living ursids of the Institut Català de Paleoecologia Humana i Evolució Social in Tarragona (Saladié et al., 2013) and the Centro Mixto UCM-ISCIII de Evolución y Comportamiento Humanos in Madrid (Sala and Arsuaga, 2018) have been used for the identification of the taphonomic attributes.

The observations of the remains at both macro and microscopic levels and the detailed photographs were taken with a binocular device SMZ-161-TP, a DINO-LITE AM-TFVW-A microscope using Dino-Capture 2.0 software and an Olympus OM-D camera with an OLYMPUS M. ZUIKO macro lens.

2.3.1. Biological modifications and physical-chemical alterations

Several agents, including carnivores, humans, rodents, plants, fungi, or bacteria can cause biologically induced modifications of bone surfaces (Lyman, 1994). For this reason, this assemblage has been analyzed at both macro and microscopic levels to clarify the presence or absence of such alterations.

In endokarst contexts, carnivores may play a leading role as carcass-accumulating agents. However, their modifying influence may be restricted to more or less sporadic scavenging of carcasses deposited inside the caves by other agents. In order to characterize the role of carnivores in this assemblage, an analysis of the bone surfaces has been developed focusing the observations on tooth marks and perimortem fracturing that could indicate the access of carnivores to the skeletal remains. In order to investigate the prevalence of carnivores in the Sima I of El Polvorín cave collection, we utilized a classification system for tooth marks including pits, punctures, furrowing, and scores (Haynes, 1980; Maguire et al., 1980; Binford, 1981; Sala and Arsuaga, 2018). Pits and punctures are marks of more or less circular morphology produced by the pressure of a tooth cusp on the surface of a bone, whose difference lies in whether this mark goes through the bone or not. Punctures are generated when this pressure passes through the cortical bone. The pits do not cross the cortical but are imprints that remain on the surface of the bone. They are usually, together with scores, the most common conspicuous marks after consumption by carnivores. Scores are elongated U-shaped section marks made by the continuous movement of the cusps of the teeth on the cortical surface of the bone. Furrowing is the result of gnawing action on the bone leading to loss of trabecular or cancellous tissue, and following the description of Haynes (1983), it can be light, moderate, or heavy depending on the portion of cancellous tissue removed.

The length and width of pits and punctures have been measured using the DINO-LITE digital microscope functions following the criteria of previous studies (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Sala et al., 2014a; Sala and Arsuaga, 2018).

Another modification that may be characteristic of the action of carnivores on bones is the partial dissolution of bones by gastric acids produced after the consumption of bone portions, and their subsequent expulsion in feces or regurgitation. Bones affected by gastric dissolution usually show characteristic features such as scalloping of the bone surface, presence of holes and/or thin, sharp edges (Sutcliffe, 1970; Sala and Arsuaga, 2018). The presence or absence of peeling has also been considered in this study. Peeling is defined as a roughened surface with parallel grooves or fibrous texture, produced when the bone is broken by bending (White, 1992; Pickering et al., 2013). Peeling is very common in primate and human feeding activities, as it involves two hands or the conjunction of teeth and hands to produce bone bending (Fernández-Jalvo and Andrews, 2011; Pickering et al., 2013; Saladié et al., 2013). However, carnivores, such as lions or hyenas, can also sporadically create this modification (Pickering et al., 2013; Haynes and Hutson, 2020). In fact, experimental work with bears has shown that this type of modification can be relatively common due to bear consumption (Arilla et al., 2014; Blasco et al., 2020).

Rodents may occasionally access skeletal remains to obtain minerals contained in the bone or to wear down their incisors, causing modifications that are preserved in the fossil record (Brain, 1981; Lyman, 1994; Klippel and Synstelien, 2007). These modifications can be made at any stage of carcass decomposition (Haglund, 1997). The remaining rodent marks are characterized by straight, parallel, flat-bottomed grooves (Shipman and Rose, 1983; Johnson, 1985).

The analysis of physical-chemical modifications in the skeletal remains has been considered in terms of the presence or absence of the following alterations. Trampling, which is produced by sediment abrasion on bone surfaces, can leave more or less linear or sinuous scratches on the bone tissue. These marks, which can sometimes be similar to cut marks, have been analyzed comparatively using the criteria of Domínguez-Rodrigo et al. (2009). The precipitation of minerals on the bones is especially pronounced in calcium carbonate crusts or manganese oxides in cave interior facies (White and Culver, 2012). Also, in endokarst contexts, the soil acidity may affect the bones causing partial dissolution of bone surfaces with a dome morphology (Pinto Llona et al., 2005). Plant roots and acid-secreting fungi derived from plant decomposition can also dissolve bone surfaces, leaving a modification characterized by shallow dendritic groove patterns (Behrensmeyer, 1978), smoothed-bottom of the grooves (Morlan, 1980), and sinuous trajectory (Andrews and Cook, 1985; Lyman, 1994). Finally, the presence or absence of weathering has been documented in the bones according to the criteria of Behrensmeyer (1978).

2.3.2. Fracture patterns

Fracture patterns have primarily been analyzed in long bones to determine the timing and mechanisms of fractures and establish whether they occurred on fresh bone still preserving soft tissues and collagen (perimortem), or on dry bone that no longer retained collagen (postmortem). In this study, priority has been given to the analysis of fractures in long bones, as these, together with the cranial remains, are the most diagnostic remains when interpreting the time and causes of fracturing (Villa and Mahieu, 1991; Sala et al., 2015, 2016). Criteria established by Villa and Mahieu (1991) and Bunn (1983) were used to evaluate the following aspects: (a) fracture outline which refers to the orientation of the fracture with respect to the bone's long axis (longitudinal, transverse, or oblique/curved); (b) fracture angle, which is the angle formed by the fracture surface and the bone cortical surface. This angle can be right or oblique; (c) fracture edge, which is the texture of the fracture's surfaces, categorized as either smooth or jagged; (d) length of the diaphysis fragment, with four groups: (1) less than ¼ of the total diaphysis, (2) between ¼ and ½ of the total diaphysis, (3) between ½ and ¾ of the diaphysis, (4) greater than ¾ of the diaphysis; (e) circumference of the diaphysis, which estimates the preservation of the long bone diaphysis circumference, establishing three categories: (1) less than half of the circumference, (2) more than half of the circumference, (3) full circumference, in at least a portion of the bone diaphysis. Fresh-bone breakage is characterized by curved or spiral outlines, oblique angles of the fracture plane, and smooth edges (Sala et al., 2015).

3. Results

3.1. Paleobiological analysis

The preliminary taxonomic assessment of the Sima I of El Polvorín assemblage is roughly consistent with previous assessments (i.e., Castaños, 1986). This includes 323 labeled fossil fragments (representing 339 bone fragments; 308 after refittings), with a good degree of preservation (Tables 1 and 2). From these, it was possible to taxonomically assess 218 specimens (189 after refittings). The fossil assemblage is mainly constituted by carnivores: cave bears *s.l.*, followed by spotted hyenas and a few lion remains. The number of non-carnivore remains is very restricted, and comprises 9 hominin remains belonging to the Neandertal lineage (Gómez-Olivencia et al., 2022), a single suid and two

Table 1
Composition of El Polvorín-Sima I fossil assemblage.

Taxon	Year		Total
	1983	2000	
Artiodactyla indet.		2	**2**
Sus sp.	1		**1**
Homo sp.	9 (8[a])	1	**10 (9[a])**
Crocuta sp.	29	3	**32**
Ursus spelaeus	13	11 (10[a])	**24 (23[a])**
Ursus cf. *deningeri*	3	1	**4**
Ursus sp. (*Ursus* cf. *deningeri* or *U. spelaeus*)	91 (80[a])	50 (33[a])	**141 (113[a])**
Panthera sp. (lion-sized)	1	3	**4**
Indet.	109 (106[a])	12	**121 (120[a])**
Total Result[b]	**256 (241[a])**	**83 (65[a])**	**339 (308[a])**

[a] After refittings.

[b] In this recount it is not taken into account the four bone breccia blocks recovered in 2000 containing additional fossil remains that have not been isolated yet.

indeterminate Artiodactyla remains. Regarding the bear taxonomy, two cave bear chronospecies have been identified: *Ursus spelaeus* (NISP = 23, after refittings; see Table 1) and *Ursus* cf. *deningeri* (NISP = 4: a lower right m2, a left second metatarsal, and two fourth metatarsals, one left and one right). Following a conservative approach, the rest of the bear remains were classified as *Ursus* sp.

3.1.1. The cave bears

The Sima I of El Polvorín cave has yielded 140 bear remains (NISP after refittings), 96 from 1983 to 44 from 2000. The adult individuals are represented by a total of 75 anatomical elements (MNE), 14 from the cranium and 61 from the postcranium. Juvenile bears are represented by 30 remains, 12 from the cranium and 18 from the postcranium. Finally, for 17 additional anatomical elements (6 cranial and 11 from the postcranium) it has not been possible to determine the age-at-death (Tables 2 and 3). In general, all the anatomical regions are present, except those of small size (e.g., distal phalanges, hyoid bones) that could be due to a sampling bias due to the relatively small number of fossil remains of the collection, together with the lack of a systematic sediment retrieval. The collection from the Arkeologi Museoa currently contains less bear remains than those studied by Castaños (1986), as 9 isolated dental remains as well as several postcranial remains are missing. Nearly all the anatomical regions are represented, which would be consistent with complete bears being accumulated, given the small sample size and the fact that it was a surface recovery.

These remains belong to a minimum of eight individuals, representing three juveniles, three prime adults (two of them showing an advanced stage of wear within their age-class compared to the third one), and two old adult individuals (Fig. 2). Based on our preliminary taxonomical assessment, seven of the cave bear individuals are classified as *Ursus spelaeus* and one as *Ursus* cf. *deningeri*.

The first of the three *U. spelaeus* juvenile individuals is represented by a complete cranium and both hemimandibles (P.2000.70; stage II-III according to Stiner, 1998, Fig. 3), which preserve the decidual

Table 3
Minimum number of cranio-dental elements (MNE) of the juvenile and adult cave bear assemblage from Sima I of El Polvorín.[a]

Anatomical region		Juvenile	Adult		
			Prime	Old	Indet.
Cranium+maxilla		1	1	1	1
Hemimandible		4	2		
Isolated teeth	Upper incisor			1	
	Upper canine	3	1		
	M1			1	
	M2	1			
	Lower incisor	1			
	Lower canine	1			1
	m2	1	3	1	
	m3		1		
Total		12	8	4	2

[a] Those of indeterminate age-at-death from Table 2 are not included here.

Table 2
Minimum number of specimens (NISP before refittings) and elements (MNE) of the carnivore assemblage from Sima I of El Polvorín.

Anatomical region	Cave bears						Cave hyenas				Lion	
	Adults		Juvenile		Indet		Adults		Juvenile/Subadult		Adult	
	NISP	NME	NISP	NME	NISP	NME	NISP	NME	NISP	NME	NISP	NME
Complete Cranium	2	1	1	1								
Cranial fragments					2	1						
Maxilla	2	2										
Hemimandible	2	2	4	4								
Isolated teeth	9	9	7	7	5	5	13	13	5	5		
Cervical vertebrae	18	6	3	1	1							
Thoracic vertebrae	6	3	2	1	6	3	1	1				
Lumbar vertebrae	1	1					1	1				
Indeterminate vertebra	1		4									
Axis	1	1										
Sacrum			1	1								
Ribs	5	4	2	2	9	6						
Scapula			1	1								
Humerus	3	2	2	2			2	2			1	1
Radius	1	1	2	1			1	1	1	1	2	1
Ulna	2	2	2	1	5		1	1			1	1
Carpal bones	3	3							1	1		
Metacarpals	4	4			1	1						
Coxal bones			1	1								
Femur	5	3	3	3			1	1	2	2		
Tibia	2	2	2	2								
Fibula	2	1										
Tarsal bones	9	9										
Metatarsals	5	5			1	1	1	1				
Proximal phalanges	9	9	2	2			1	1	1	1		
Intermediate phalanges	5	5										
Indeterminate long bone			1		2							
Total	97	75	40	30	32	17	22	22	10	10	4	3

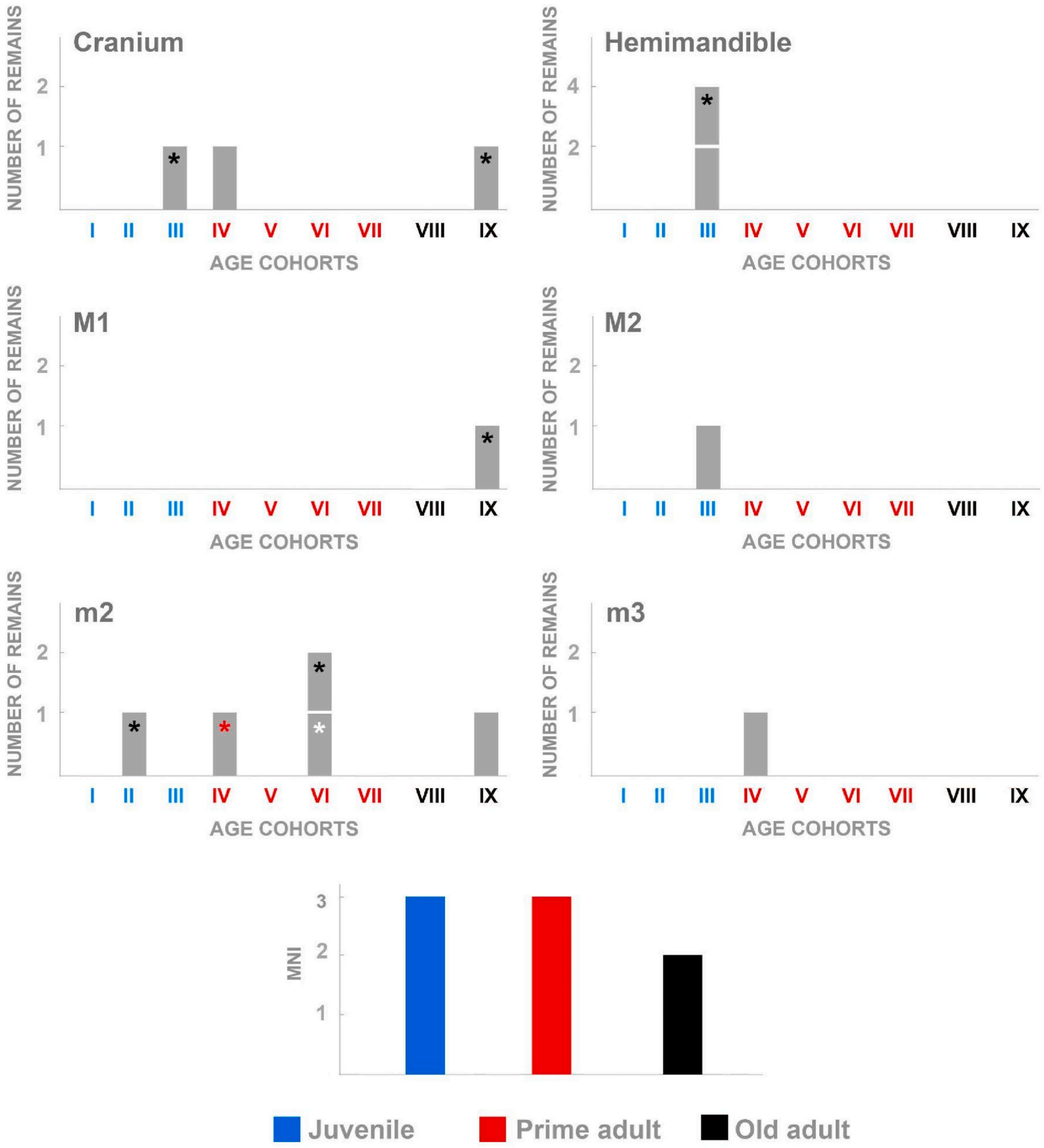

Fig. 2. Graphical representation of the ages-at-death of selected cranial, mandibula and dental remains (NISP), and the minimum number of individuals (MNI). Age cohorts are based on the tooth crown emergence and wear (Stiner, 1998). Asterisks (regardless of the color) indicate the elements used to calculate the MNI; the red asterisk indicates the *Ursus* cf. *deningeri* individual; the white asterisk indicates the *Ursus* sp. individual. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

canines, the permanent P4-M1 are erupted and the M2 is emerging. Its age-at-death is estimated between 5 and 11 months following Rausch (1969) and Fosse and Crégut-Bonnoure (2014). The second juvenile individual is represented by two hemimandibles (P-22 and P-32; stage III according to Stiner, 1998, Fig. 3) that preserve the mandibular corpus, the p4 and m2 with no signs of wear and the emerging m3. This individual has an estimated age-at-death of, at least, a year (*sensu* Torres et al., 2007). The third juvenile is represented by a lower right m2 with the root not formed and no signs of wear on the crown (P-28; stage II following Stiner, 1998; Fig. 3). The *U. spelaeus* prime adult individual is represented by a left lower m2 (P.2000.5; stage VI *sensu* Stiner, 1998, Fig. 4) which is morphologically different from the other adult m2s. The two *U. spelaeus* old adult individuals are represented by a right upper M1 (P-29; stage IX following Stiner, 1998, Fig. 4), and a cranium of a female bear (P-198; stage IX *sensu* Stiner, 1998, Fig. 4) from the same age stage. Additionally, an *Ursus* cf. *deningeri* prime adult individual is represented by a right lower m2 (P.2000.10; stage IV *sensu* Stiner, 1998) and an indeterminate ursid (*Ursus* sp., either *Ursus spelaeus* or *Ursus* cf. *deningeri*) is represented by a right lower m2 (P-30; stage VI according to Stiner, 1998, Fig. 4).

The postcranial remains with fused epiphysis were classified as adults (NISP = 83). Only a left radius (P-329; Figs. 5 and 6) and a left ulna (P.2000.64+P.2000.65; Figs. 5 and 6) could be classified as subadults based on their dimensions and unfused epiphyses. The remaining 23 postcranial remains that show unfused epiphyses, can be classified as belonging to juvenile individuals.

The dimensions of the upper and lower canines (NISP = 6) showed that the majority of them belonged to female individuals of different

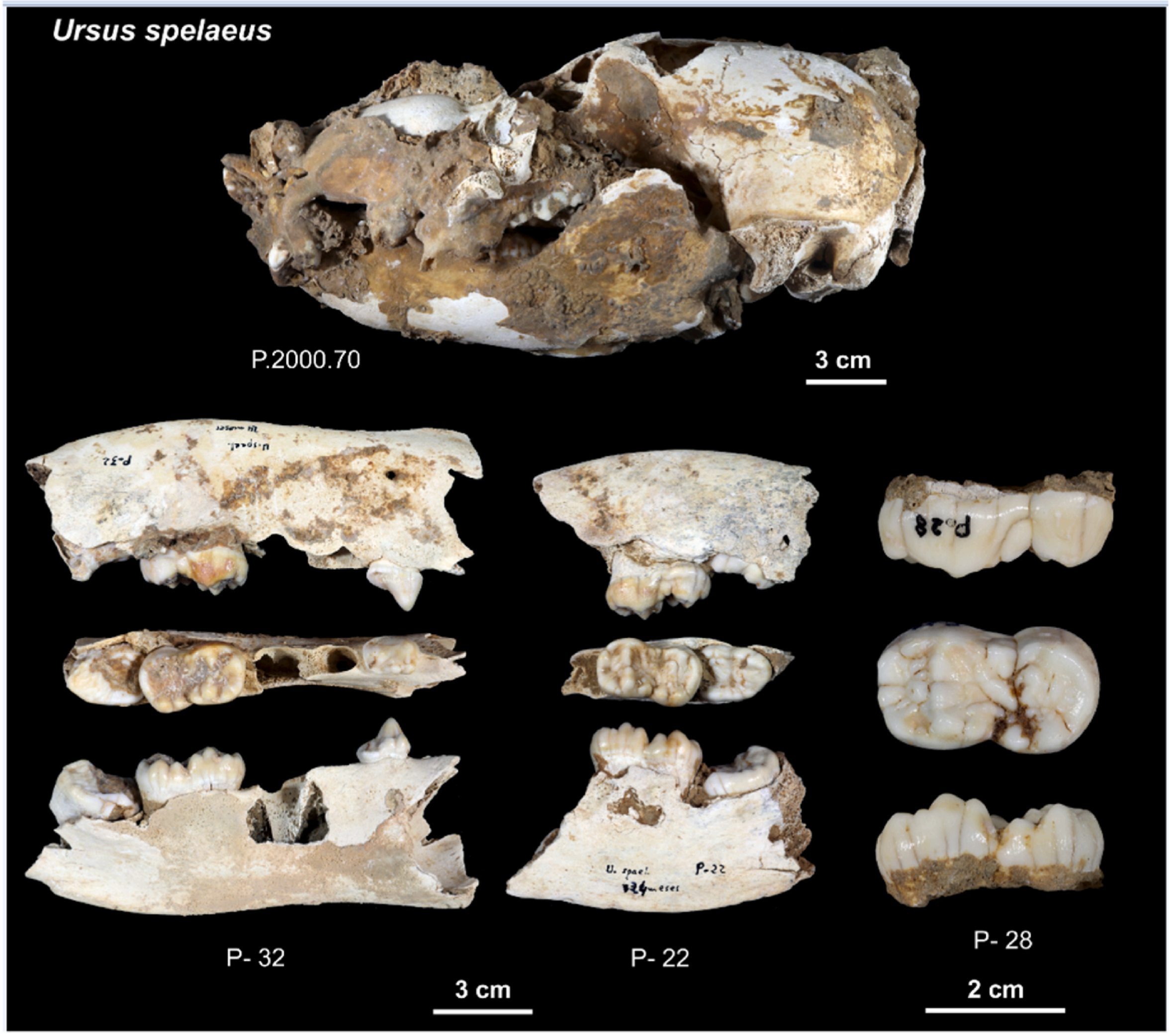

Fig. 3. Selected cranial remains of juvenile individuals of *Ursus spelaeus* from Sima I of El Polvorín. P.2000.70: complete cranium, preserving both hemimandibles (stage II-III *sensu* Stiner, 1998). P-32 and P-22: left and right hemimandibles (stage III according to Stiner, 1998). P-28: right m2 (stage II *sensu* Stiner, 1998).

ages-at-death (Fig. 7). This sample includes the upper canines P-13 (juvenile), P-17 (prime adult) and P-198 (old adult) and the lower canine P-2000.53 (prime adult) and P-16 (adult). Only the size of a lower canine was consistent with this fossil belonging to a male individual (P-18; juvenile). Finally, it was not possible to determine the sex for the canine P-12 (juvenile).

3.1.2. *The hyena remains*

We have identified 32 (NISP) spotted hyena (*Crocuta* sp.) remains: 29 recovered in 1983 and 3 recovered in 2000 (Table 1, Fig. 8). This is in contrast with the 37 hyena remains identified by Castaños (1987) in the 1983 collection. Additionally, one bone breccia block, retrieved in 2000 (P.2000.69), preserves a minimum of three well-preserved coprolites that we attribute to hyenas, alongside other bone remains (Fig. 9). Based on the dental dimensions, Castaños (1987) suggested that these hyenas were closer to *Crocuta intermedia* from Lunel Viel than to *Crocuta spelaea*. Given the potential diachronic nature of the hyaena accumulation, until a new reassessment is performed, we prefer to remain cautious and classify the hyaena remains as *Crocuta* sp.

There are four hyena individuals represented in the Sima I of El Polvorín collection: an old adult (stage VI according to Brugal et al., 1997; to which probably belonged the pathological right metapodial P-35), one prime adult (stage IV *sensu* Brugal et al., 1997) and two juvenile/subadult individuals between 8 and 24 months (stages 4–5 following Jimenez et al., 2019).

3.1.3. *Other carnivores*

Four remains have been attributed to a lion-sized felid. The fragmentary nature of these remains and the uncertainty regarding the chronology made us classify them as *Panthera* sp. as there is no criteria to classify them either as *P. spelaea* or *P. fossilis* (see Prat-Vericat et al., 2022). Castaños (1986) mentioned the presence of two fox remains (a cranial and a mandibular fragment) that we have not found in the Arkeologi Museoa collection.

3.2. *Taphonomic analysis*

3.2.1. *Bone surface modifications*

The bone surfaces from the Sima I of El Polvorín cave assemblage are well preserved. The presence of alterations typical of cave interior environments such as a high incidence of manganese oxides staining, precipitation of calcium carbonates and dissolution domes on bone surfaces is noteworthy (Fig. 9, Table 4). 58.3% of the bone sample contains some type of calcium carbonate precipitation. Different types of precipitates have been observed, the genesis of which can provide information on the formation of the deposit. Firstly, there are fossils that have adhered cemented clayey sediment partially covering their surface. This is the most common type of precipitate in the analyzed sample (1.6

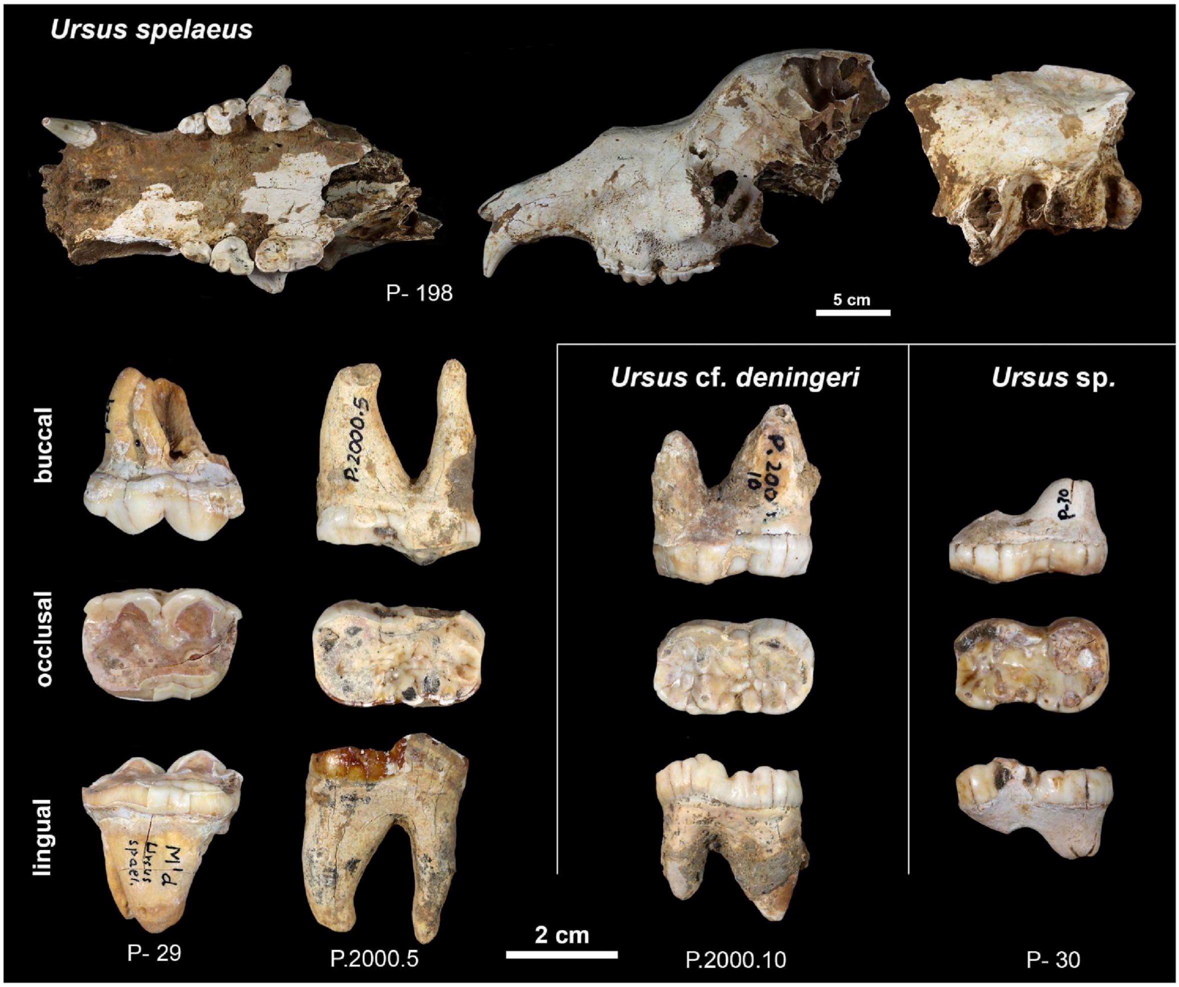

Fig. 4. Selected *Ursus spelaeus*, *Ursus* cf. *deningeri* and *Ursus* sp. cranial remains of adult individuals from Sima I of Polvorín. P-198: nearly complete cranium (stage IX); P-29: right M1 (stage IX); P.2000.5: left lower m2 (stage VI); P.2000.10: right lower m2 (stage IV); P-30: right lower m2 (stage VI). The stages correspond to those described by Stiner (1998).

%) which is not rare in endokarst contexts (White and Culver, 2012). On the other hand, four fragments of concreted ossiferous breccia have been recovered (Fig. 9), related by an intense carbonate precipitation, probably associated with supersaturated zones of $CaCO_3$. These breccia fragments were possibly found decontextualized from their original position, since the fossil collection was superficial as far as we know. Therefore, these clasts in secondary position could be indicating sectors or levels related to stalagmitic floors or areas of intense water dripping. Finally, two bear remains, a skull (P.2000.70; Fig. 5) and an ulna (P.2000.64; Fig. 6), and a decimetric bone breccia fragment (P.2000.72; Fig. 9) show a crust characterized by the presence of small stalagmites called "soda straws". These speleothems are formed by vertical dripping, and, therefore, would unequivocally indicate that these remains were once hanging or cemented to the walls or the ceiling of the cave. Their recovery on the cave surface indicates erosion processes of cemented units.

No alteration that implies subaerial exposure processes (weathering) or evidence of long-distance transport processes have been recorded, though a slight rounding of some bones has been observed. In a very low proportion, there are trampling marks (4.4%), indicating some movement and abrasion of the bones against the sedimentary matrix. Rodent activity has only been recorded in one case (P-141, Fig. 10). On the contrary, no case of dissolution of bone surfaces due to plant root activity have been documented (Table 4). No sign of fungal or bacterial modifications have been documented in the Sima I of El Polvorín cave assemblage.

No evidence of butchery activity on the skeletal remains, such as cut or percussion marks were recorded. Similarly burned bones were not identified in the collection (Table 4).

Carnivore activity has been observed in a very low proportion (4.8% of the studied sample. Table 4). The most characteristic marks are pits and scores in the diaphysis of the long bones together with furrowing (Table 5; Fig. 10) while crenulated edges have been observed in a single specimen (P-146). No punctures were found in either cortical or cancellous bone. There is also no evidence of bones partially dissolved by gastric acids that could indicate an intervention of durophagous carnivores. No tooth marks have been observed on both hyena and *Panthera* sp. remains and preferentially affect the diaphyses of long bones although they have also been detected on the cortical surfaces of the flat bones. In the case of cave bear remains, tooth marks are mainly represented by scores (30%, NISP = 10) in the diaphysis of long bones, followed by furrowing and pits (20%, NISP = 10) in the cortical surfaces of flat bones in adult bear remains. In juvenile individuals, furrowing is more prevalent in the diaphysis and distal epiphyses of long bones (40%, NISP = 5). Table 6 details the metric data obtained in the few marks that have been documented taking into account the affected bone region. These measurements are consistent with the activity of carnivores of large size such as bears, large-sized felids and hyenas. The ungulate sample (only three remains) are partially encrusted and no signs of carnivore activity have been observed.

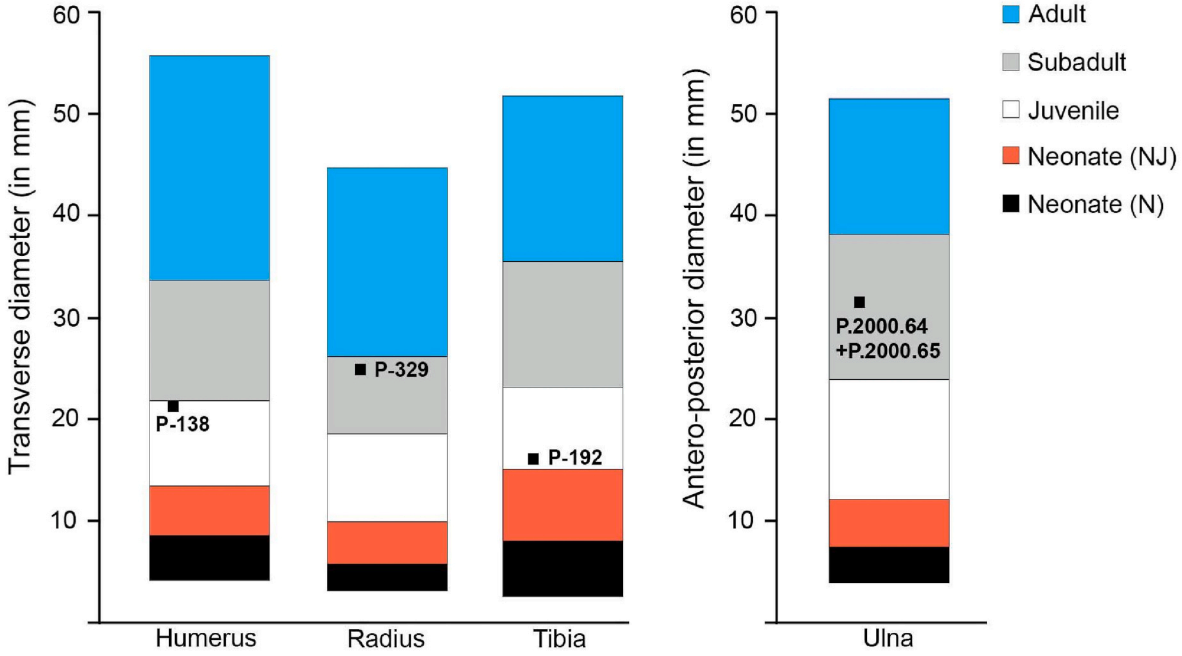

Fig. 5. Age-at-death of selected postcranial remains from Sima I of El Polvorín based on their dimensions. The age-at-death groups were established by Torres et al. (2014) and their limits are based on the measurements of cave bear postcranial remains from Amutxate cave. NJ: neonate-juvenile refers to individuals of 1-year age-at-death. Measurements are represented in millimeters.

Fig. 6. Selected juvenile cave bear postcranial remains (P-138: right humerus; P-192: left tibia) and subadult individuals (P-329: left radius; P.2000.64+P.2000.65: left ulna) from Sima I of El Polvorín cave.

3.2.2. *Fracture patterns*

A high incidence of recent fractures (104 remains, 32.2% of the total sample) has been documented. These fractures are easily recognizable by their different coloring and texture when compared to intact bone surfaces and have been excluded from the analysis. Of the total number of remains analyzed, 40 out of 245 present postmortem fractures (15.4% of the total sample). With respect to fracture properties on long bones, transverse fractures predominate (29 remains; 56.9% of the analyzed sample) (Fig. 11). In terms of fracture patterns, 47.1% of the remains show fractures with both right and acute angles, while 33.3% show fractures at right angles (Fig. 11). Regarding the texture of the fracture pattern, all of them show jagged edges. Finally, complete circumferences dominate with 41.2% (21 remains of the analyzed sample), together with portions of diaphysis of bone between 25 and 50% of its length (Fig. 11).

Therefore, the fractures in long bones from the Sima I of El Polvorín cave are characterized by transverse outlines, fracture patterns at both right and acute angles, rough textures and a high representation of complete circumferences of the diaphysis.

4. Concluding discussion

4.1. *Origin of the cave bear accumulation in Sima I of El Polvorín cave*

Numerous studies have been conducted on cave bear collections in the northern part of the Iberian Peninsula, focusing on paleobiological

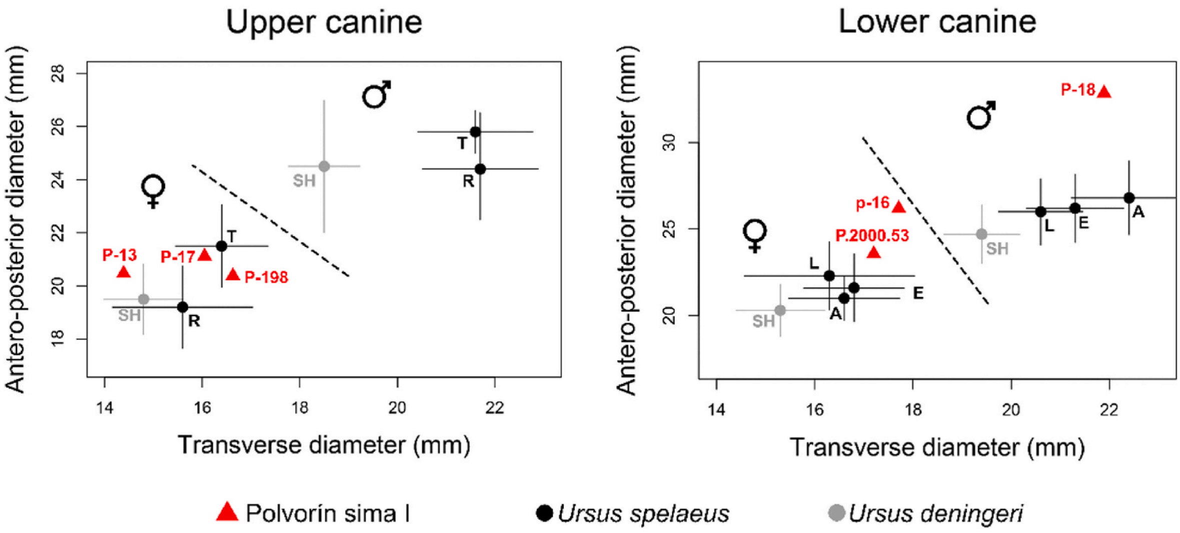

Fig. 7. Bivariate scatterplots of the upper and lower canines from Sima I of El Polvorín, compared to male and female individuals of *U. spelaeus* taken from Torres Pérez, 1988c). The dot represents the mean, and the cross represents the ± 1 standard deviations. SH: Sima de los Huesos. R: Reguerillo. T: EL Toll, L: Lezetxiki. A: Arrikrutz. E: Ekain.

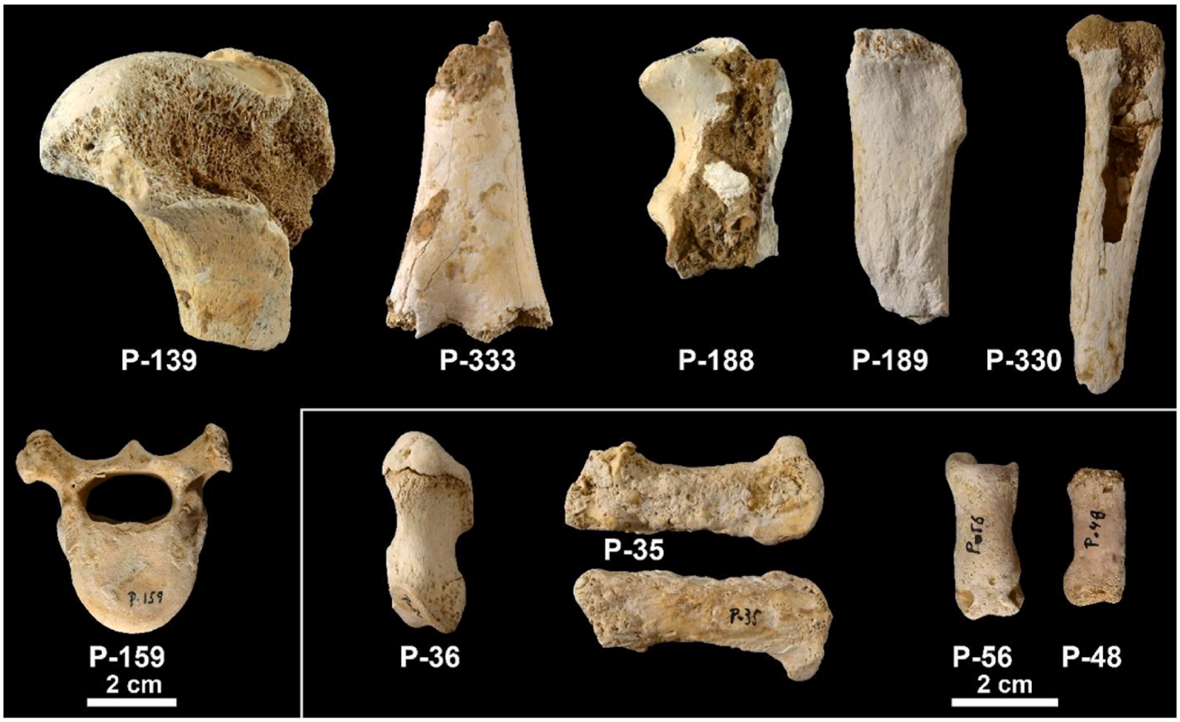

Fig. 8. Selected hyena postcranial remains from Sima I of El Polvorín. P-139: right humerus; P-333: left humerus; P-188: left ulna; P-189 and P-330: left juvenile radii; P-159: thoracic vertebra; P-36: right subadult pisiform; P-35: pathological right metapodial; P-56 and P-48: adult and juvenile (respectively) proximal phalanxes.

aspects such as age-at-death, sex, and anatomical representation. However, these studies often provide only qualitative information regarding important taphonomic aspects (e.g., Torres Pérez-Hidalgo, 1984; Castaños Ugarte et al., 2012; Villaluenga et al., 2012, 2014; Torres et al., 2014). To gain a comprehensive understanding of the origin of these bone accumulations, it is necessary to combine quantitative taphonomic observations with paleobiological information. While bear remains are the primary component of these accumulations, other carnivore remains such as large felids or hyenas may also be present, although in smaller quantities (Altuna et al., 1982; Altuna and Mariezkurrena, 1984; Torres Pérez Hidalgo et al., 1991; Torres et al., 2014; Pinto Llona and Andrews, 2002; Grandal d'Anglade and López-González, 2004; Villaluenga et al., 2012, 2014). The analysis of these carnivores can offer additional insights since they were the primary bone accumulators in Pleistocene caves. Previous research has delved into this topic (Kuhn et al., 2010), highlighting the need for further investigations in this area. Here we present the first study that encompasses paleobiological aspects of the recovered remains, as well as an exhaustive taphonomic study, including the analysis of both fracture patterns and modifications of bone surfaces.

Attempting to distinguish the agent responsible for the bone accumulations is crucial for an approximation of the formation of the deposit

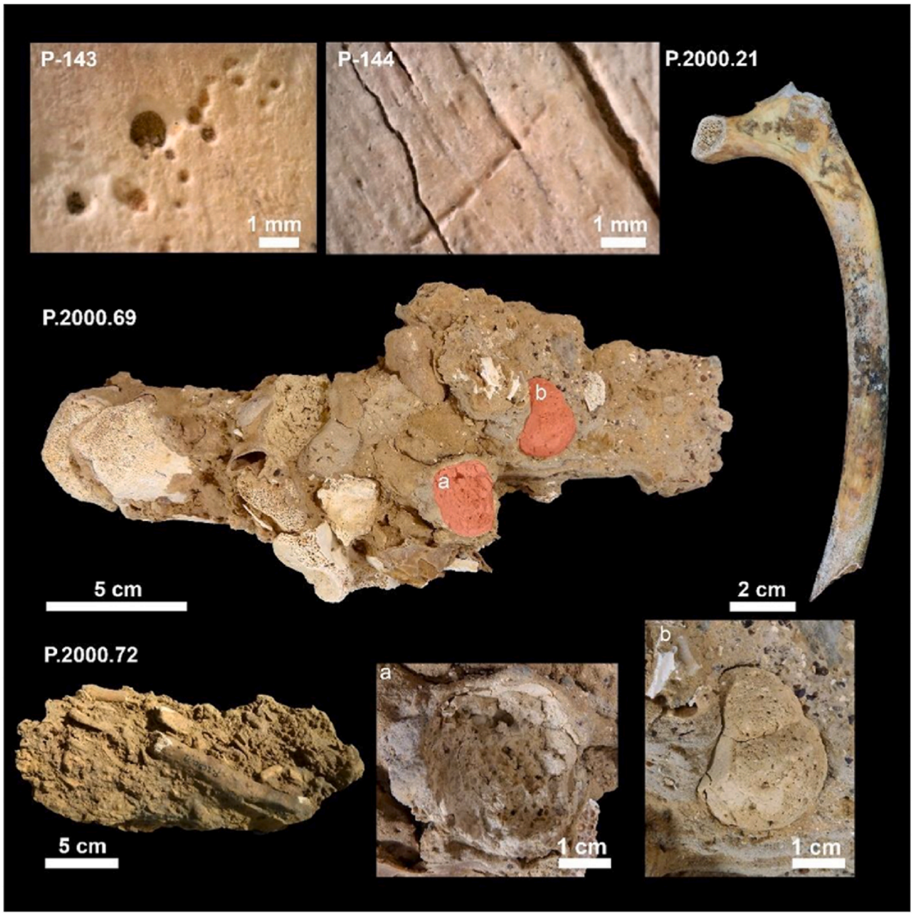

Fig. 9. Most frequent alterations documented in the Sima I of El Polvorín collection: P-143 and P-144: dissolution of the bone surface; P.2000.69: carbonate concretion affecting several bone remains and hyena coprolites; P.2000.21: precipitation of manganese oxides on an ursid rib. P.2000.72: ossiferous breccia.

Table 4
Frequency of alterations of bone surfaces.

Alteration type	NISP (%)
Anthropic marks	0 (0%)
Carnivore marks	11 (4.8%)
Manganese staining	81 (33%)[a]
Trampling	10 (4.4%)
Weathering	0 (0%)
Dissolution domes	115 (46.9%)[a]
Crusts	143 (58.3%)[a]
Rodent activity	1 (0.4%)
Plant roots	0 (0%)
Fungal/bacterial activity	0 (0%)
Cemented clayey	4 (1.6%)

[a] Dentition has been considered only for the analysis of these attributes.

(Cruz-Uribe, 1991; Kuhn et al., 2010; Pickering, 2002; Stiner, 1991). Four potential, non-exclusive agents can be the responsible of the cave bear accumulations of the Sima I of El Polvorín cave: anthropic activity, carnivore activity, natural mortality and a catastrophic event.

First, there is no evidence of exploitation of the carcasses that would indicate anthropogenic activity (cut or percussion marks). The preservation of long bone epiphyses is low (21.2% among long bones, NISP = 67). This could be related to carnivore activity (Cruz-Uribe, 1991) but also to human action (Marín et al., 2017; Crezzini et al., 2023). Another important data to distinguish between accumulations made by carnivores and humans is the ratio between the presence of carnivores and ungulates. In anthropic accumulations, the MNI of carnivores in the assemblages is less than 13% (Cruz-Uribe, 1991). In the case of the assemblage of the Sima I of the El Polvorín cave, the presence of ungulates is minimal (only three remains have been identified, 1.7% of the total NISP and 11.8% of the total MNI) compared to that of carnivores (hyenas, a lion-sized felid and bears; NISP = 172, 98.3% of the total and 88.2% of the total MNI), as observed in other sites with no (or very little) human occupations were cave bear presence dominates, such as level IV of Astigarragako Kobea (carnivore %MNI: 75; ungulate %MNI: 16.7) and level N from Lezetxiki (carnivore %MNI: 82.3; ungulate %MNI: 11.7; Villaluenga et al., 2012). This allows us to rule out humans as accumulating agents, as opposed to carnivores (Cruz-Uribe, 1991), although it must be evaluated together with other factors to identify the possible carnivore responsible for the accumulation (Kuhn et al., 2010).

Second, carnivore activity has been observed on the fossil remains: tooth marks are present, though in a minimal proportion, and without any evidence of long bone fracturing related to carnivore activity. These marks commonly manifest as scores and pits on cortical tissue. The metric analysis of the marks (Table 6) is consistent with the activity of a large carnivore such as bears, hyenas, and large felids (e.g. lions) (Sala and Arsuaga, 2018 and references therein), but the low number of preserved marks prevents an exhaustive statistical analysis that would allow us to infer the carnivore responsible for these marks. Hyenas are recognized as highly significant taphonomic factors in the fossil record due to their ability to accumulate bones, making them one of the most productive bone collectors (Henschel et al., 1979; Skinner and Ilani, 1979; Skinner et al., 1980; Skinner and van Aarde, 1991; Lam, 1992; Leakey et al., 1999; Kuhn, 2005; Lacruz and Maude, 2005; Skinner, 2006). According to Kuhn et al. (2010), the most effective distinguishing features to differentiate hyena-generated accumulations are the

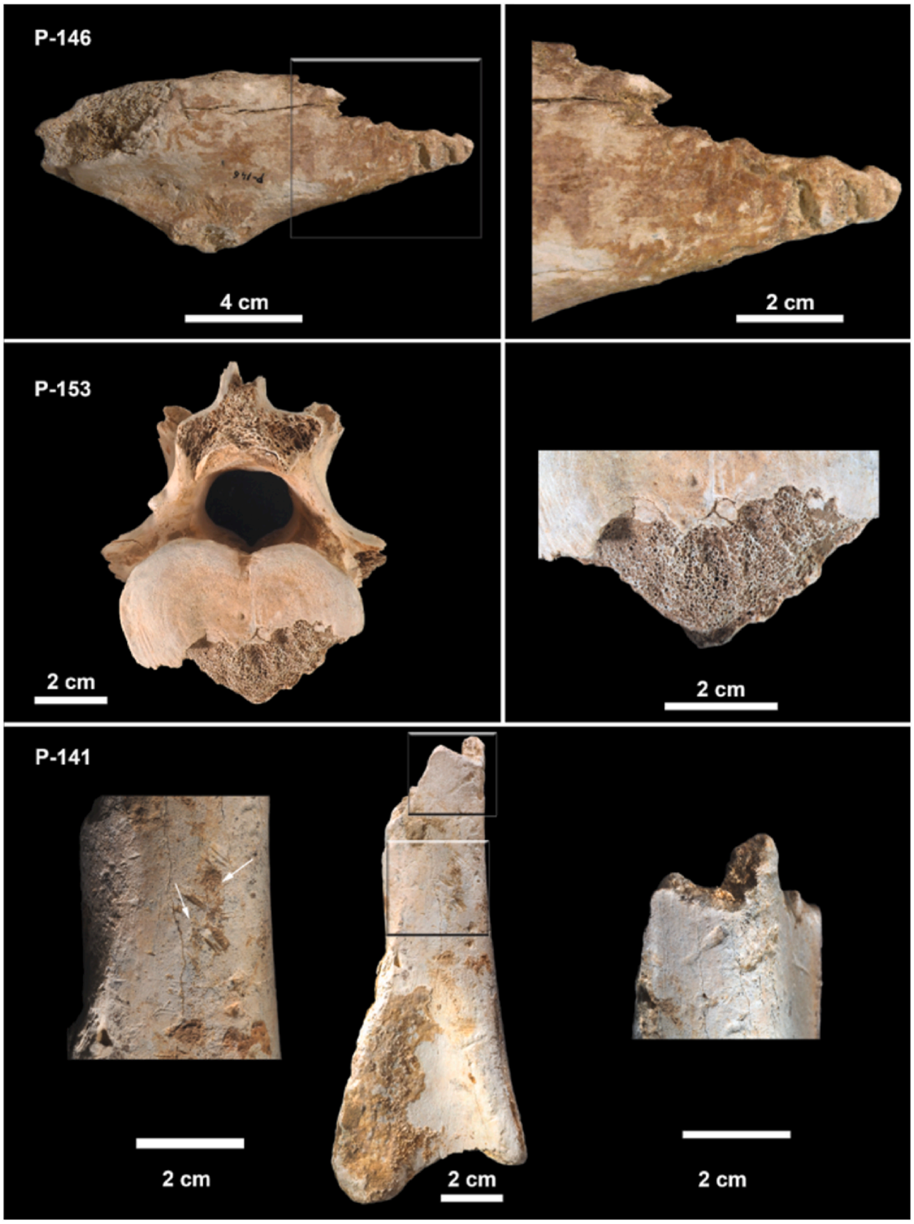

Fig. 10. Bear remains from the Sima I of El Polvorín assemblage with marks of carnivore activity: P-146: furrowing on the diaphysis of an ulna; P-153: scores on a lumbar vertebra; P-141: rodent activity on a humerus diaphysis and furrowing.

Table 5
Frequency of tooth mark type and location on different types of bone and bone portions.

Tooth mark	Type of bone					
	Long bones (NISP = 57)			Flat bones (NISP = 46)		Carpal/tarsal/phalanges (NISP = 32)
	Proximal epiphysis	Diaphysis	Distal epiphysis	Cortical	Spongy	Compact bone
Pits	1 (1.75%)	3 (5.2%)	2 (3.5%)	3 (6.5%)	0	0
Scores	0	6 (10.5%)	0	2 (4.3%)	0	0
Furrowing	0	2 (3.5%)	1 (1.75%)	4 (8.7%)	0	0

existence of their coprolites and the existence of juvenile remains of the species. In the case of the fossil collection from Sima I of El Polvorín, despite the relatively high representation of this taxa in the assemblage when in terms of minimum number of individuals represented, the presence of juvenile hyena individuals and the evidence of coprolites is very low compared to other bone accumulations produced by hyenas (Kuhn et al., 2010). Here, however, caution is necessary because the retrieval performed by the speleologists was not systematic, and there might be a potential bias in which smaller elements such as deciduous teeth are underrepresented in the collection. In any case, it is worth noting that the frequency of tooth marks is comparatively higher in contexts identified as hyena dens, such as the Búho and Zarzamora caves (38.8%; Sala et al., 2012), Portalón del Tejadilla (37.4%; Sala et al., 2020), the Camino cave (55.9%; Arsuaga et al., 2012), and an average of

Table 6
Descriptive statistics for measurements (in mm) of pits and scores studied at Sima I of El Polvorín. The data displayed in the table show length and breadth (n: number of cases; Min: minimum value; Max: maximum value and SD: standard deviation).

			n	Mean	SD	Min	Max
Pits	Maximum diameter	Spongy	0				
		Cortical	18	2.78	1.42	1.27	7.30
	Minimum diameter	Spongy	0				
		Cortical	18	2.16	1.31	0.97	6.10
Scores	Maximum width	Spongy	0				
	Maximum width	Cortical	34	2.89	2.26	0.67	8.31

39.2% in other hyena dens, according to Kuhn et al. (2010). In sum, despite the presence of carnivore activity in the Sima I of El Polvorín collection, it is possible to discard hyenas as the agent responsible for this accumulation, though it is not possible to rule out that they were one of the agents responsibles for the observed tooth marks. The presence of a large-sized felid in the assemblage, the low representation of tooth marks, its location and the absence of punctures, could indicate some carnivore activity over the bear carcasses by this taxon (Fourvel et al., 2014). However, the low number of *Panthera* sp. remains (NISP = 4 and MNI = 1) requires us to be cautious about this taxon to be the main accumulation agent. Scavenging of bear carcasses that died during hibernation by other bears is not only common in present-day contexts, but is also a behavior that has been recorded in numerous Pleistocene sites with cave bears (Stiner, 1994, 1998, 1999; Pinto Llona and Andrews, 2002; Pinto Llona et al., 2005; Rabal-Garcés et al., 2012; Sala et al., 2014b). This non-strict vegetarian diet is consistent with isotopic results (Richards et al., 2008; Robu et al., 2013) and dental microwear (Ramírez Pedraza et al., 2020). One of the marks that could suggest bear activity would be the presence of peeling in the sample, especially on the ribs (Arilla et al., 2014). In the Sima I of El Polvorín sample, peeling has not been documented. However, this modification, when it appears, usually affects the ribs. In the Sima I of El Polvorín the number of ribs is low (NME = 12; Table 2) and therefore the absence of this modification could be simply a representation bias. The low percentage of tooth marks and fresh-bone breakage is consistent with those observed in carcass consumption by present-day ursids (Sala and Arsuaga, 2013). However, in monospecific bear sites, where bears have sporadic access to the carcasses of other bears such as Coro Tracito (Rabal-Garcés et al., 2012) or Tito Bustillo (Pinto Llona et al., 2005), the percentage of marks is much higher (c. 35% of the long bone sample at Coro Tracito).

Based on the study of cranial and postcranial remains, all age-at-death stages are represented in Sima I of El Polvorín, with the exception of neonates. The representation of juveniles, prime adults and old adults is consistent with a living structure (LS) model of mortality. However, several aspects must be considered. First, the number of bear individuals in the sample is relatively small, probably derives from two cave bear chrono-species and could be biased. This would result in a different population structure if the fossil collection is increased. Second, the way the bones were extracted from the cave surface may have resulted in a bias for the smallest remains such as decidual teeth or neonate long bones, that could have not been recovered, especially since no systematic sediment retrieval was performed. Also, when the number of juvenile remains is compared to adults, they show similar proportion in the cranial remains but a low proportion of the postcranial bones, which may be the result of a differential conservation due to their fragility or the action of scavengers (Torres et al., 2014). The low proportion of old individuals could be consistent with an attritional model that does not show a "U" shape (Debeljak, 2004; Grandal d'Anglade and Vidal Romaní, 1997; Weinstock, 2000, 2001), as sometimes there could be higher proportions of prime adults compared to old adults (Debeljak, 2004). This is explained because many adults die outside the cave, when they are starving during hibernation, they abandon the den and die looking for food (Debeljak, 2004).

The relation between the sex ratio and the mortality pattern is difficult to establish. In recent brown bear populations, females with cubs tend to hibernate for longer periods than males and single females, so they have more possibilities to starve, which makes the sex ratio to be a difficult determinant of the use of the cave (Schoen et al., 1987; Debeljak, 2004). Also, in several sites with cave bears, the sex ratio has resulted to be highly variable (Weinstock, 2000). According to this, the predominance of females with different ages-at-death in the Sima I of El

Fig. 11. Representative examples of the most common types of fractures in bear remains from Sima I of El Polvorín. P.2000.17: right fibula displaying fractures with transverse outlines, right angles and rough textures; P.2000.41: left femur showing acute angle fractures and rough textures as P-143: right humerus.

Polvorín, does not elucidate the origin of the accumulation.

The origin of cave bear accumulation is complex to approach, and in the majority of the occasions is based in the behavior of extant species (e.g., Craighead et al., 1976; Garshelis and Pelton, 1980; Schoen et al., 1987). Given the low number of remains recovered from the Sima I of El Polvorín cave, a paleontological assessment must be taken carefully. The morphology of the cave and of the gallery in which the fossils are found (at the bottom of a chasm more than 30 m deep from the current entrance) could suggest that Sima I from El Polvorín could have acted too as a natural trap, which would not contradict the current demographic profile.

Alternatively, the Sima I site would be located far from the original entrance of this area of the cave and the entrance is currently sealed by sediments/speleothems. In fact, these two hypotheses are not mutually exclusive. Additional speleological exploration will help to understand the cave geometry and locate ancient entrances.

In addition, the frequency of tooth marks in the Sima I assemblage from El Polvorín is very low (4.8%), as is the case in other Pleistocene contexts such as the Sima de los Huesos (4.4% in carnivores and 3.6% in humans), which acted as a natural trap for ursids, which have been considered as the main agents responsible for the scavenging marks (Sala et al., 2014b). Therefore, we do not rule out the intervention of other carnivores such as hyenas and/or large-sized felids that could have arrived to that part of the gallery, scavenged bear corpses and left their feces. However, as mentioned above, the taphonomic study clearly shows that hyenas were not the main fossil accumulating agent in Sima I of El Polvorín.

The results of the taphonomic analysis indicate that the remains from Sima I of El Polvorín cave show no signs of subaerial exposure and, therefore, were probably deposited in the cave in the biostratinomic phase. There is one aspect to be taken into consideration and that is the presence of large ossiferous breccia, as well as “soda straws” mentioned before. Given the conditions in which the fossils were collected, the presence of these large clasts in secondary position indicates that there were areas of the cave with intense water dripping, while the “soda straws” indicate that some fossils were left hanging from the walls or ceiling of the cave, which allowed these speleothem formations to originate. These cases are not very numerous with respect to the total sample but indicate that there is at least a part of the collection that, at the time of surface collection, was not in its original position. This raises another possible scenario in which the fauna represented in the site gained access through other areas of the cave, the fossil remains were deposited in the biostratinomic phase and, subsequently, different erosive processes transported these remains to the area of the cave where they were recovered. However, the good preservation of the bone surfaces indicates that the potential transport was minimal in terms of both intensity and distance.

The fracture patterns provide further insight into fracture times, i.e., whether the fractures were made in dry bone during the fossil-diagenetic phase or in fresh bone during the biostratinomic phase, when the bone still retains collagen. Right angles are typical of fractures during the fossil-diagenetic phase in already mineralized bones, as well as the rough texture of the fracture edges and the representation of complete circumferences in the diaphyses (Johnson, 1985; Villa and Mahieu, 1991). For the Sima I of El Polvorín, the fracture patterns suggest that the bone assemblage was fractured mainly during its postmortem phase due to diagenetic factors, despite the large number of recent fractures identified in the collection. The properties of the fracture surfaces in most cases are characterized by being jagged, while the presence of crenulated edges has only been noted in one remain (P-146, Fig. 10).

4.2. Biochronological implications

Given the current taxonomic assessment of bears and the previous assessment of the hyena remains (Castaños, 1987) a diachrony of the deposits could be hypothesized. First, we have identified the presence of a lower second molar (Fig. 4) and three postcranial remains (a second and two fourth metatarsals) that show *Ursus deningeri* affinities. Second, as suggested by Castaños (1987), the measurements of some of the hyena remains from Sima I of El Polvorín show measurements compatible with *Crocuta intermedia* (Lewis and Werdelin, 2022), described in Lunel-Viel (MIS 9-8; Bonifay, 1971; Brugal et al., 2020). On the one hand, the presence of *Ursus deningeri* remains would suggest a minimum chronology of MIS 7 for part of the deposit, which would be consistent with the presence of *Crocuta intermedia*. On the other hand, the abundant presence of *Ursus spelaeus* indicates that most of the deposit has either a late Middle Pleistocene (MIS 6) or a Late Pleistocene (MIS 5-3) chronology. Future studies should address a more indepth taxonomic assessment of the faunal remains and the chronology of the fossil accumulations in this site.

Based on paleobiological and taphonomic criteria, it is not possible to completely ascertain whether the bears accumulated in the Sima I of El Polvorín cave (Biscay, Northern Iberian Peninsula) either due to deaths during hibernation and/or, sporadic consumption by carnivores, fall from a natural trap (maybe from an upper gallery) or a combination of these. It is possible to discard humans as the main accumulation agent. Despite the relatively high presence of hyena individuals (MNI = 4 out of total carnivore MNI = 13) in comparison with other contexts interpreted as bear hibernation dens, there is insufficient taphonomic data to ensure the presence of a hyena den, also ruling them out as the main accumulating agent. In any case, slight carnivore activity has been recorded on the surface of the bear remains, indicating that the carcass consumption activities could have been carried out either by bears, a lion-sized felid and/or hyenas. Despite the difficulties due to the possible diachronic accumulation and the fact that the analyzed material corresponds to surface collections, here we demonstrate that integrative paleobiological and taphonomic analyses applied to paleontological collections excavated and deposited in museums decades ago, can still provide very relevant information regarding the origin of cave bear accumulations in endokarst contexts, and that studies comprising both paleobiological and taphonomic aspects are fundamental to discern processes on paleobiology (Stiner, 1991; Kuhn et al., 2010) and dynamics of occupation by carnivores and humans in the Pleistocene (e.g., Altuna, 1972; Castaños, 1986, 1987; Diedrich, 2008; Marín-Arroyo, 2013; Marín-Arroyo et al., 2014; Arlegi et al., 2018; Sala et al., 2021; Gómez-Olivencia et al., 2015, 2018, 2020; Rodríguez-Almagro et al., 2021). The study of this kind of collection has been able to advance in the origin of the accumulation of the bear remains of the Sima I of El Polvorín cave. Future studies of the cavity and more bone collection will help to further disentangle the origin of the bear accumulation of this site.

CRediT authorship contribution statement

Manuel Rodríguez-Almagro: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Asier Gómez-Olivencia:** Conceptualization, Investigation, Project administration, Supervision, Writing – original draft, Writing – review & editing, Funding acquisition. **Mónica Villalba de Alvarado:** Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Juan Luis Arsuaga:** Supervision, Validation, Writing – review & editing. **Nohemi Sala:** Conceptualization, Funding acquisition, Project administration, Supervision, Validation, Writing – original draft, Writing – review & editing.

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

Data will be made available on request.

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