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NEW GEOLOGICAL CONTEXT AND SITE FORMATION PROCESSES OF THE SANTA ISABEL DE RANERO PALAEONTOLOGICAL SITE (MIDDLE PLEISTOCENE; KARRANTZA, BISCAY, NORTHERN IBERIAN PENINSULA)

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Abstract. The Santa Isabel de Ranero (SIR) assemblage is one of the most significant collections of *Ursus deningeri* in the Iberian Peninsula. This study aims to characterise the formation processes of the site using a combined palaeobiological, geological and taphonomic approach. Fossil remains were recovered from four different sectors of the cave: Entrance and Esparta, which produced small surface collections, Bear, and Lion. The Bear Sector has provided evidence of, at least, 16 *U. deningeri* individuals and one lion dated to c. 300 ka (MIS 8). Two thirds of the bears are either late juveniles or early prime adults, and the sex of nine of these individuals has been determined: seven females and two males. Based on the presence of all anatomical parts, the absence of anthropogenic marks, and the low percentage of carnivore modifications, humans and hyaenas can be ruled out as the primary accumulating agents. Based on the demographic profile and the absence of shed deciduous dentition, we can also rule out the possibility that this accumulation is related to mortality during birthing or hibernation. We propose that this bear accumulation is the result of a natural endokarstic trap, probably originating from the upper conduit where the Esparta Sector is located. The Lion Sector yielded a limited assemblage from the Late Pleistocene, associated with allochthonous anorthic ferruginous nodules, which would suggest a natural trap directly connected to the exterior. The SIR assemblage highlights the important role of natural traps in reconstructing Pleistocene ecosystems in the Cantabrian region.

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Introduction

Caves are an exceptional environment for preserving Quaternary fossil vertebrates. The use of caves by bears, in particular, has resulted in significant accumulations of fossils of this species, especially during the Late Pleistocene (Kurtén 1976; Torres 2014). Bears competed directly or indirectly with Palaeolithic humans inhabiting Eurasian ecosystems for much of the Pleistocene (Stiner 1999; Grayson & Delpech 2003; Stiller et al. 2010). Therefore, cave bear accumulations are crucial for understanding past ecosystems and interactions between carnivores and humans in the fossil record. To interpret site formation processes, palaeoecology, and chronology, a multiproxy investigation is essential. Combining geologic, palaeobiological, and taphonomic information is vital to understand the formation of archaeological and palaeontological cave sites. Stratigraphic, sedimentological, granulometric and micromorphological studies provide information on the geological processes involved in or affecting bone accumulation (Bosch & White 2004; White 2007; Goldberg & Berna 2010). The general geological setting and geometry of the basin/cave can also provide important additional information on these processes (Arriolabengoa et al. 2020). If feasible, geochronological studies can provide information on when these processes occurred. Taxonomic composition and diversity, anatomical representation, sex ratio, and age-at-death profiles provide information on which species accumulated and whether partial or complete carcasses are preserved at the site. They also indicate whether the fossil association follows or departs from an age-at-death distribution like that of a living population (e.g. Stiner 1994; Marín et al. 2017; Rodríguez-Hidalgo et al. 2017; Rodríguez-Almagro et al. 2024). Furthermore, biochronological studies can provide insights into the age of the fossil deposits. Taphonomy studies may reveal how different agents—anthropic, carnivore, or other biological and physico-chemical agents—have acted upon preserved bones (Lyman 1994). Within this framework, analysing bone fractures can be particularly informative, as it enables researchers to determine whether the bone broke while it still contained collagen (at or shortly after the time of death), or after collagen was lost, indicating *post-mortem* breakage (Sala et al. 2014a).

The cave bear lineage, traditionally comprising *Ursus deningeri* von Reichenau, 1904 and *Ursus spelaeus* Rosenmüller, 1794, was a paradigmatic element of the Pleistocene megafauna, spreading across Eurasia during the Middle and Late Pleistocene. The Iberian Peninsula provides an abundant fossil record of the Upper Pleistocene cave bear (*U. spelaeus*) but a more limited, though growing (see e.g. Villalba de Alvarado et al. 2025) record of its Middle Pleistocene ancestor (*U. deningeri*). In this region, cave bears have a more abundant fossil record than brown bears during the Pleistocene (e.g., Torres Pérez-Hidalgo 1984; Villaluenga 2009; Villalba de Alvarado et al. 2022). This could be due to a different use of the caves for hibernation (Torres 2014), as most of the fossil record has been found in caves (but see Madurell-Malapeira et al. 2010). Recently, several studies have attempted to investigate the origin of the cave bear accumulations in the northern part of the Iberian Peninsula. While many cave sites with abundant bear remains have long been known in this region, the action of treasure hunters (e.g. for bear canines) and/or illegal excavations have altered the deposits of many of these caves. In 1995, the Satorrak speleological group discovered a pristine cave bear site (Amutxate, Aralar, Navarre), leading to an excavation that focused on the taphonomic analysis of the bear bone accumulation, given its untouched status (Torres 2014).

The accumulation of bear bones in Amutxate (c. 48,000 and 39,000 years BP; Torres et al. 2007) appears to derive primarily from natural deaths during hibernation followed by various taphonomic processes such as scavenging (most likely by hyaenas), gravitational transport, and natural rockfalls, which resulted in the fragmentation and bias in the anatomical representation. Excavations at this site have yielded a minimum of 31 adult individuals, 54 juvenile individuals, and 148 skeletal elements belonging to newborns or late-term foetuses. Additionally, many of the deciduous teeth found in this assemblage are the result of natural tooth replacement. The proportion of males to females in this assemblage is similar (53% and 47% respectively), with most of the bears dying either before reaching the first year of life or at a very late age (Torres 2014). Many Upper Pleistocene cave bear sites in the Iberian Peninsula have been interpreted as being primarily the result of natural deaths during hibernation (e.g., Torres et al. 1991).

Conversely, information on the formation and age of Middle Pleistocene cave bear sites in the Iberian Peninsula is more limited, but growing (Villaluenga et al. 2012; Martínez-Pillado et al. 2024). The Sima de los Huesos (SH) site has yielded remains belonging to a minimum of 176 *U. deningeri*, as well as other carnivore and human remains (García & Arsuaga 2011; Arsuaga et al. 2014, 2015; García et al. 2024). Its mortality profile does not correspond to that of a hibernation den (similar to Troskaeta or El Reguerillo; Torres et al. 1991), neither to a birthing den. Rather, it is consistent with the site being a natural trap for the carnivores found there (García García 2003) coming from adjacent areas of the cave. Analysis of the carnivore remains from this site revealed scarce evidence of carnivore activity, limited mainly to furrowing of spongy tissue and a few tooth pits and scores. In contrast, the fracture patterns in the bear remains are consistent with *post-mortem* processes caused by sediment pressure and show no evidence of carnivore involvement (Sala et al. 2014a, 2015). The metric data on the toothmarks were consistent with them having been made by bears. In any case, the survival of trapped carnivores, which would have been responsible for the marks, was an unusual circumstance given the low percentage of bones with carnivore modification (Sala et al. 2014a). The near-total absence of bias in the anatomical representation of the bears also points to the accumulation of complete carcasses, with minimal post-depositional processes (García García 2003). The Middle Pleistocene (MIS 9) La Rampa site at La Lucia cave (Lamasón, Cantabria), which has yielded 2,417 *U. deningeri* remains belonging to at least 22 individuals, has been interpreted as an accumulation that occurred over a prolonged period due to the cave being occupied by adult male and female cave bears (Torres et al. 2005). Based on the number of *U. deningeri* individuals represented, Santa Isabel de Ranero (Karrantza, Biscay) is currently the third most important Middle Pleistocene site in the Iberian Peninsula, for the knowledge of this species. According to Torres et al. (2001), the Middle Pleistocene cave bears used this cave as a hibernation den. They entered through a different entrance, and the cave has a complex geological history involving siliciclastic and carbonate sedimentation phases, followed by erosion and collapse phases. Torres et al. (2001) mention the presence of corrosion and carnivore marks on the bones due to scavenging. However, to our knowledge, no detailed taphonomic study has yet been conducted on this collection. Furthermore, a recent assessment of the cave site indicates that its geological history is even more complex than previously thought. Moreover, additional fossil remains have been found in three additional zones of the cave.

The main objective of this study is to characterise the formation of the Santa Isabel de Ranero site using a combined geological, palaeobiological, and taphonomic approach. Specific aims include providing a geological description of the cave and identifying the allostratigraphic units (sedimentary sequences bounded by unconformities or other mappable discontinuities), which will be organised sequentially to establish the general stratigraphy of the cave. A more detailed account of the stratigraphy of the main site is provided, alongside an updated inventory of the fossil remains found there, including their anatomical representation. A complete taphonomic study of the remains is also conducted, including an analysis of the bone surfaces and breakage patterns.

The Santa Isabel de Ranero cave: the sites

The Santa Isabel cave (UTM 30T, 469680, 4789556, 301 m a.s.l., ETRS89) is located in the Ranero neighbourhood (Karrantza, Biscay) and currently has two entrances (Fig. 1; Torres et al. 2001), with an approximate length of 500 m. The first topography of the cave was performed by the Grupo Espeleológico Vizcaíno in 1956 (Torres et al. 2001). During the 1970s, a speleological group from Catalonia (G.E. Badalona) explored the cave system and discovered over a hundred fossils, which they gave to the palaeontologist F. Villalta. The bear mandible remains from the Villalta collection were described by Torres Pérez-Hidalgo et al. (1978).

During the spring of 1985, the Grupo Espeleológico Esparta conducted further exploration of the cave, uncovering new fossil remains, including a complete skull. Due to the risk posed by visitors to the cave, an excavation was carried out in 1991 to gather all the fossils present at the site. A second visit took place in 1994 to sample the site for ESR dating (Torres et al. 2001, 2014).

Torres et al. (2001) proposed a general model for the evolution of the cave, which included the following phases: a first phase of phreatic speleogenesis forming elliptical/subcircular conduits; a second

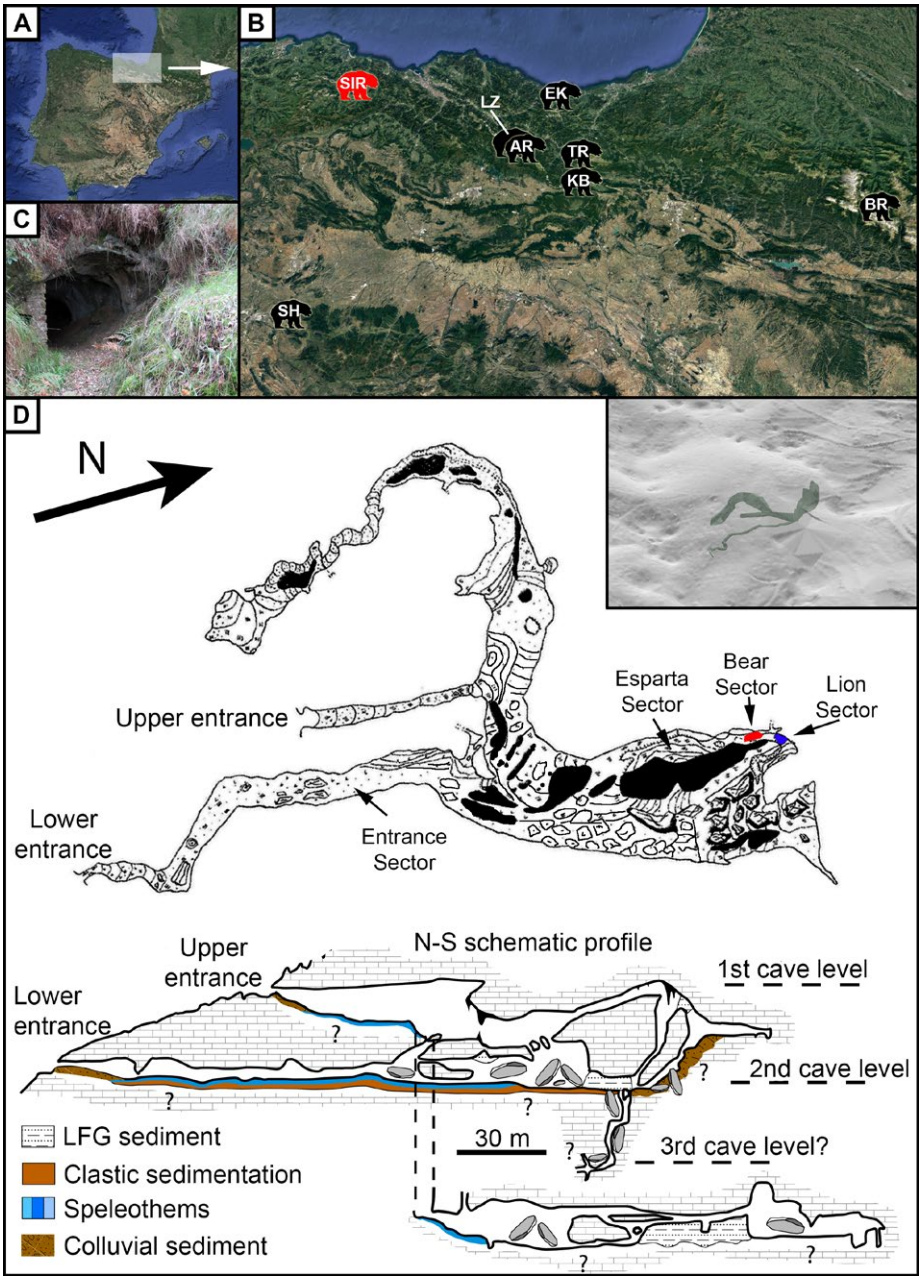


Fig. 1 - General location in the Iberian Peninsula (A) of Santa Isabel de Ranero (SIR; Karrantza, Biscay; Torres et al. 2001, 2014) and other Middle and Upper Pleistocene cave bear sites (B). Lower entrance (C) to the cave system, general topography (D; originally drawn by the Esparta Speleological Group; Torres et al. 2001) and N-S schematic profile showing the three cave levels. AR = Arrikrutz (Oñati, Gipuzkoa, Late Pleistocene; Torres et al. 2001); BR = Brecha del Rincón (Hecho, Huesca; Middle Pleistocene?; Rabal-Garcés and Sauqué 2015); EK = Ekain (Deba, Gipuzkoa; Late Pleistocene; Torres Pérez-Hidalgo 1984); KB = Koskobilo (Middle and Late Pleistocene; Arlegi et al. 2018; Gómez-Olivencia et al. 2020); LZ = Lezetxiki (level VII; late Middle Pleistocene; Altuna 1972; de-la-Rúa et al. 2016); SH = Sima de los Huesos (Torres 1978; García García 2003; García and Arsuaga 2011; Arsuaga et al. 2014); TR = Troskaeta (Ataun, Gipuzkoa; Late Pleistocene; Torres et al. 1991). LFG = Laminated fine-grained sediment.

phase of lowering of the phreatic level which led to the conduits widening in an epiphreatic regime; and finally, an alternation of clastic sedimentation, chemical sedimentation and erosion, within which the formation of the Bear Sector can be located. Additionally, Vidal et al. (2001) provided a broader geomorphological context for the cave within the valley. They emphasised the presence of periglacial sediments and evidence of a general lowering of the zone's phreatic level, such as the presence of three different fluvial terraces and exokarstic formations.

Our new explorations have confirmed the existence of four fossiliferous sectors in the cave (Fig. 1). The main site, which was excavated by Torres and G.E. Esparta in 1991, and which yielded the fossils in the Villalta collection, is now called Bear Sector (SIR-Bear, or just SIR). Around 6 m laterally and stratigraphically above SIR-Bear, J. Rios-Garaizar discovered the first fossils in another area, which yielded, among other remains, a very complete mandible of *Panthera spelaea* Goldfuss, 1810. We named this area "Lion Sector" (SIR-Lion). A few fossils were also found on the surface of the sediment in one of the corridors towards the "Bear Sector", and we called this the "Entrance Sector" (SIR-Entrance). Finally, additional fossils were found in the same conduit as the Bear and Lion

Sectors are, although topographically above them. This area is now called the "Esparta Sector" (SIR-Esparta).

Materials and methods

Materials

Bear Sector. The SIR collection from the Bear Sector is currently housed in three different institutions. The materials recovered by the G.E. Badalona in the 1970s are mainly housed at the Museu de Ciències Naturals de Barcelona (n = 159, plus one pottery fragment and two modern *Sus* sp. not included in this study), but a small sample (n = 5) is at the Institut Català de Paleontologia Miquel Crusafont. The materials found by the G.E. Esparta, those excavated by Torres in the 1990s (c. 2,200 remains; Torres 1992; but see below), and those recovered by our team are housed at the Arkeologia Museoa (Bilbao) and comprise the largest part of the collection. We have re-organised the Torres collection (labelled SI-1 to SI-2179) and found some discrepancies between the inventory that he provided and the current collection housed at the Arkeologia Museoa. Firstly, the dental remains attributed to *P. spelaea* are missing from the current collection. However, we have identified some postcranial remains of this species in the collection, though not the metapodials and phalanges enumerated by Torres (1992). Additionally, at least 319 labelled fragments are missing, including all types of skeletal elements, but particularly the vertebrae (n = 141). Secondly, additional fossil remains from SIR-Bear housed at the Arkeologia Museoa, which were encrusted inside blocks, have been cleaned and inventoried. These additional remains have been labelled SI-3000 to SI-3133 (Supplementary Fig. S1-S2). Thirdly, we have refitted around 50 bone fragments. Therefore, the Bear Sector collection from the Torres excavation currently comprises c. 1,900 remains after the refitting.

Additional fossil remains were recovered in the 2015 (SI-5000 to SI-5244) and 2016 (SI-5500 to SI-7169) field seasons. Most of these are small, indeterminate fragments. We mainly recovered fossils that were either: a) on the surface or at the top of the Bear Sector sequence, or from the sediment dumped by the Torres excavation ("escombrera"). This sediment was removed in order to search for micro-faunal remains. Within this sediment, we found one fossil remain which refitted with fossils found during the Torres excavation (SI-683+SI-1019+SI-5001, an immature right bear radius). Only one bone from the main fossil level and five indeterminate fragments from the top of the sequence were recovered *in situ*.

Lion Sector. Fossil remains from this sector were recovered during the 2015 (labels SI-10000 to SI-10147), the 2016 (labels: SI-10500 to SI-10599) and the 2017 (labels: SI-11000 to SI-11039) field seasons and are housed at the Arkeologia Museoa. This was not a systematic excavation, but rather the gathering of partially encrusted fossil remains from the surface, together with the surrounding sediment.

Entrance Sector. Fossil remains from this sector were recovered during the 2015 field season and labelled SI-15000 to SI-15005 and are housed at the Arkeologia Museoa. These fossil remains were found on the surface of the gallery.

Esparta Sector. Fossil remains from this sector were recovered during the 2016 (labels: SI-20000 to SI-20050), and 2017 (labels: SI-20500 to SI-20501) field seasons, and are housed at the Arkeologia Museoa. These fossil remains were found on the surface.

Stratigraphic analysis methods

We have identified and described the geomorphological elements within the SIR cave in order to determine the processes that have occurred there. Due to the intense erosion processes, our aim was to identify the different sedimentary sequences bounded by unconformities, i.e. the allostratigraphic units, and organise them sequentially to establish the various speleogenetic phases of the cave.

Granulometric and mineralogical studies of the sediments were performed to provide a detailed characterisation of the allostratigraphic units of the SIR-Bear Sector. Granulometric analyses were performed using a Coulter LS13350 granulometric analyser. Mineral phase identification using X-ray diffraction (XRD) was performed on bulk samples and on the clay fraction were performed at the SGIker laboratories (University of the Basque Country-EHU). For bulk mineralogy, each sample was manually ground in an agate mortar and studied using a Philips PW1710 diffractometer (PW1729 generator; 40 KV and 20 mA) equipped with a cop-

per tube (l CuKa mean = 1.541874 Å, lCuKa1 = 1.540598Å and lCuKa2 = 1.544426Å), a vertical PW1050/25 goniometer (Bragg-Brentano geometry), an automatic PW1386/55 divergence slit, an automated PW1170 sample changer, a secondary graphite monochromator, and an automatised control panel connected to an IBM PS/2 computer, which controls the diffractometer through specific software (Philips APD v.3.). The procedure for identifying the minerals present in the XRD can be found in Supplementary Text S1. The mineralogy of the clay fraction (<2 μm) was identified using a PANalytical X'Pert Pro diffractometer. The samples were first decarbonated by treatment with 0.1 M HCl and washed several times with deionised water to avoid calcium chloride precipitation. The clay fraction was then collected by centrifugation. The oriented aggregates were prepared by carefully pipetting the clay suspension onto glass slides, which were then placed in a glass desiccator for 24 hours for ethylene glycol solvation. Thermal treatments at 300ºC and 550ºC were also applied to identify the clay minerals, in accordance with the procedures detailed by Arostegui et al. (2006). Following each treatment step, the glass slides were measured by XRD with CuKa radiation (40 kV, 40 mA), a graphite monochromator, a programmable divergence slit, and a PIXcel detector.

U/Th dating was performed on two speleothems. SIR-a3 (layer a3) is a flowstone overlying some fossil remains in the Bear Sector (Fig. 3), which would provide a minimum age estimate for the main bone assemblage. Four subsamples were extracted from its lowermost part (Fig. S3). SI-5074 is a small calcitic crust covering a lion calcaneus from the Bear Sector (Fig. S4), which also provides a minimum age estimate as well for this bone. Due to the thickness of the crust, a single subsample was extracted. Sampling, chemical processing and analysis were performed at the U-series laboratory of the CENIEH (Burgos, Spain). The detailed protocol can be found in the Supplementary Text S2.

Anatomical and taxonomical determination

Macromammals. The anatomical and taxonomic assessment of the macro-fossils coming from our excavations and the various collections we studied was based on specialised literature (e.g., Pales & Lambert 1971; Pales & Garcia 1981; Torres 1988a, b, c, d, e, f; García García 2003; Varela & Rodríguez 2004; Prat-Vericat et al. 2020, 2022), as well as on modern and fossil collections housed at various institutions, including the Arkeologia Museoa (Bilbao) and the Centro Mixto UCM-ISCIII (Madrid). Age-at-death was estimated using the crania, mandibles, and teeth. Following Stiner (1998), nine age cohorts were defined based on the tooth eruption, root development, and crown wear. These cohorts classify the population as juveniles, prime adults and old adults. This methodology was initially applied to remains that were more complete and preserved multiple teeth (maxillae and mandibles), before being applied to isolated remains.

To determine the sex of the macromammal remains, the size of the canines was assessed. In the case of the bear remains, cluster and k-means analyses (where $k = 2$) were performed (Arceredillo et al. 2011). The scarce lion remains were compared to other samples in the literature (Manjón García 2024, and references therein).

Small vertebrates. Around 125 litres of sediment were removed from the Bear Sector (excavation spoil from the previous excavation), 5 litres from the Lion Sector, and 2.5 litres from the Esparta Sector. These were water-sieved in an attempt to find micro-vertebrates, using 0.5 mm and 2 mm sieves at the University of the Basque Country (EHU). The coarse fraction was selected directly and yielded a significant quantity of new macro-vertebrate remains (see above). Acetic acid was used to treat the fine fraction (i.e. < 2 mm) in all the sectors due to its high content of calcium carbonate, in order to reduce its volume and facilitate its sorting. The resulting fraction was then sieved into three further fractions: 0.5-1 mm, 1-1.6 mm, and 1.6-2 mm. Sorting was performed using a binocular loupe for the two smallest fractions.

The taxonomic assessment of the remains and the dental morphology (primarily occlusal) of the small mammal remains were performed using standard methods (García-Alix 2006; Minwer-Barakat 2006; Oliver & Peláez-Campomanes 2013). The length and width of all the dental remains were measured using a Nikon Kosata KK measuring microscope. Photographs of the molars were taken using an Environmental Scanning Electron Microscope (ESEM) FEI Quanta 200 at the Laboratory Non-Destructive Techniques at the Museo Nacional de Ciencias Naturales-CSIC.

Taphonomic analysis

A total of 776 non-dental macro-vertebrate remains from the SIR-Bear Sector were analysed at the Arkeologia Museoa. Of these, 764 belonged to *U. deningeri*, one to *P. spelaea*, and 11 were of an indeterminate taxonomic affinity. Observations and detailed photographs were taken using a stereoscopic zoom Olympus SZX10 microscope. The taphonomic observations were categorised as follows: a) physical alterations: weathering (following Behrensmeyer, 1978), dissolution (presence/absence), mineral precipitations (presence/absence of manganese oxides) and encrusting (presence/absence); and b) biological alterations: dissolution produced by plant roots (presence/absence), trampling, anthropogenic marks (butchery marks such as cut marks as well as evidence of combustion), rodent activity, and carnivore activity (tooth-marks and gastric acids). Finally, a breakage analysis was performed. The tooth-marks left by carnivores were classified as pits, punctures, furrowing and scores (Haynes 1980, 1983; Maguire et al. 1980; Binford 1981). Pits, punctures and scores were measured (length and width) following different authors (Selvaggio & Wilder 2001; Domínguez-Rodrigo & Piqueras 2003; Delaney-Rivera et al. 2009; Andrés et al. 2012). The metric data were then compared with experimental data obtained from living carnivores (Andrés et al. 2012; Sala 2012; Sala & Arsuaga 2013, 2018; Saladié et al. 2013; Sala et al. 2014a), as well as with data from palaeontological collections such as the Sima de los Huesos (Sala et al. 2014b) and sites that have been interpreted as hyaena dens (Arsuaga et al. 2012; Sala et al. 2012). The size of the tooth-marks in the SIR-Bear Sector was compared to that of other samples using a Kruskal-Wallis test. As the hypothesis of similar sizes was rejected for the measured variables, a Mann-Whitney test (Mann and Whitney 1947) was performed as a *post-hoc* procedure to establish the potential authorship of the carnivore responsible for the tooth-marks found at the SIR-Bear Sector.

Breakage analysis, which provides valuable data on the timing of the fracture, distinguishing between fresh-bone or *perimortem versus* dry-bone or *postmortem*. This analysis focused on the long bone elements. The following parameters were studied: fracture outline (longitudinal, transverse, or oblique/curved), fracture angle (right or oblique); fracture edge (smooth or jagged); shaft circumference (1: <50% of the circumference; 2: >50% of the circumference; 3: complete circumference); and shaft fragment (1: <25% of the total diaphysis; 2: 25-50% of the total diaphysis; 3: 50-75% of the diaphysis; 4: >75% of the diaphysis) (Bunn 1983; Villa & Mahieu 1991; Sala et al. 2015). Previous studies have demonstrated that transverse fractures to the long axis of long bones, with complete circumferences and fracture edges that are right-angled and jagged surfaces, are commonly associated with dry-bone fractures (i.e. those that occur *postmortem*), while oblique fractures with oblique angles of the fracture plane, incomplete circumferences and smooth surfaces are commonly associated with fresh or green-bone fractures (i.e. those that occur *perimortem*) (Villa & Mahieu 1991; Sala et al. 2015).

To compare the fracture patterns present in the SIR-Bear Sector sample with those in other fossil remains, we performed a multiple correspondence analysis (MCA) using STATISTICA 8.0 (StatSoft 2007). The samples used in the MCA analysis included two groups. The first group comprises fossil associations dominated by fresh fractures of the bones due to hyaena activity such the sites of Cueva del Búho and Zarzamora sites (Sala et al. 2012), and the Cueva del Camino site (Arsuaga et al. 2012). The second group comprises hominin and bear remains from the Middle Pleistocene site of Sima de los Huesos (Arsuaga et al. 2014, 2015), which are examples of dry-bone breakage due to the weight of the sediment (Sala et al. 2015).

Geological and stratigraphical context of the different fossiliferous sectors within Santa Isabel de Ranero

The topography of the cave reveals two distinct cave levels and suggests the potential for a third, as indicated by a narrow pit on the lower level (Fig. 1). There are currently two entrances: one on the upper cave level and one on the middle level. The cave exhibits a general anastomosing appearance, with evidence of various sedimentation and erosion events. From a geomorphological perspective, paragenetic morphologies are particularly prominent throughout the cave (e.g., Farrant & Smart 2011). In this regard, two distinct sets of ceiling channels have been observed at different elevations. One of these starts at the upper entrance and can be traced

Layer	Sample	Bulk sample					Clay minerals		
		Quartz	Calcite	Clay minerals	Potassium feldspar	Plagioclase	Illite	Vermiculite	Kaolinite
a4	Si_1	52	18	30	-	-	55	32	13
a4-a6	Si_10	55	13	32	-	-	70	17	13
a9	Si_9	3	97	-	-	-	51	28	21
a10	Si_2	49	16	35	-	-	45	44	11
a11	Si_3	17	55	28	-	-	46	43	11
a12	Si_4	63	3	34	-	-	61	31	8
a13	Si_5	89	1	8	1	1	84	8	8
a14	Si_6	48	30	22	-	-	68	13	19
a15	Si_7	52	-	48	-	-	87	6	7
LFG sediment	R_SI_2	57	-	43	-	-	66	19	15
	R_SI_3	62	-	38	-	-	65	22	13
	R_SI_4	41	-	59	-	-	67	14	19

Tab. 1 - Comparison of the results of the X-ray diffraction (XRD) of both bulk sample and clay minerals of the Bear Sector compared to three laminated fine-grained (LFG) samples from different parts of the cave.

throughout the entire cavity. The second starts at the lower entrance and can be traced to where the two levels converge. Several anastomosing half-tubes have been observed on the roof. The few scallops observed indicate a paleoflow direction from NE to SW. Associated with these paragenetic morphologies, massive and patchy deposits of laminated fine-grained (silt-clay) sediments (LFG) can be found in various locations within the cave (Supplementary Fig. S5). These sediments are well sorted (Supplementary Fig. S6) and display a similar mineralogical composition, particularly in terms of clay mineralogy and the absence of calcite (Tab. 1). Furthermore, they are consistently preserved as erosional remnants and do not overlap with deposits associated with other sedimentary phases. Taken together, these deposits are interpreted as representing the earliest sedimentary phase recorded in the cave, associated with paragenetic processes, and have therefore been identified as the first allostratigraphic unit.

The fossils from the Bear and Lion Sectors form part of the same sedimentary sequence (Fig. 2; Supplementary Fig. S7-S10), whereas the fossils from the Entrance and Esparta Sectors were found on the surface, without any clear stratigraphic context. From south to north, the Esparta, Bear, and Lion palaeontological sectors are located within the same conduit, at different points and heights (Fig. 1). This conduit contains relict patches of LFG sediment deposits (first allostratigraphic unit) at both its bottom and its highest point, with a distance of more than 10 m between them. The fossils from the Bear Sector are within an allostratigraphic unit deposited after the erosion of the previous underlying LFG deposits and are therefore assigned to the second allostratigraphic unit. This unit comprises a minimum of 15 preserved sedimentary layers, ranging from a1 (top) to a15 (bottom), with a minimum preserved thickness of c. 75-80 cm in the Bear Sector excavation area (Fig. 3; Supplementary Fig. S11). The lower layers (a15-a13) are sandier; the intermediate layers (a12-a4) are siltier with fine speleothem alternation; and the upper layers (a3-a1) are essentially flowstones (see below). This entire sequence collapsed in a roughly organised fashion from its original position between 40 and 120 cm, probably due to reactivation processes that eroded and transported part of the sediment from this cave level to the lower one (Supplementary Fig. S8). Most of the fossil remains from the site were recovered in previous excavation projects. Our field observations indicate that the Bear Sector fossils were deposited roughly contemporaneously with layers a7-a4 and were subsequently covered by the a3 flowstone. U/Th dating of this flowstone would provide a minimum age for this fossil association. The fossils were mainly located in the eastern half of the conduit. We have also recovered a few indeterminate long bone shaft remains in layer a2, which are not considered further here.

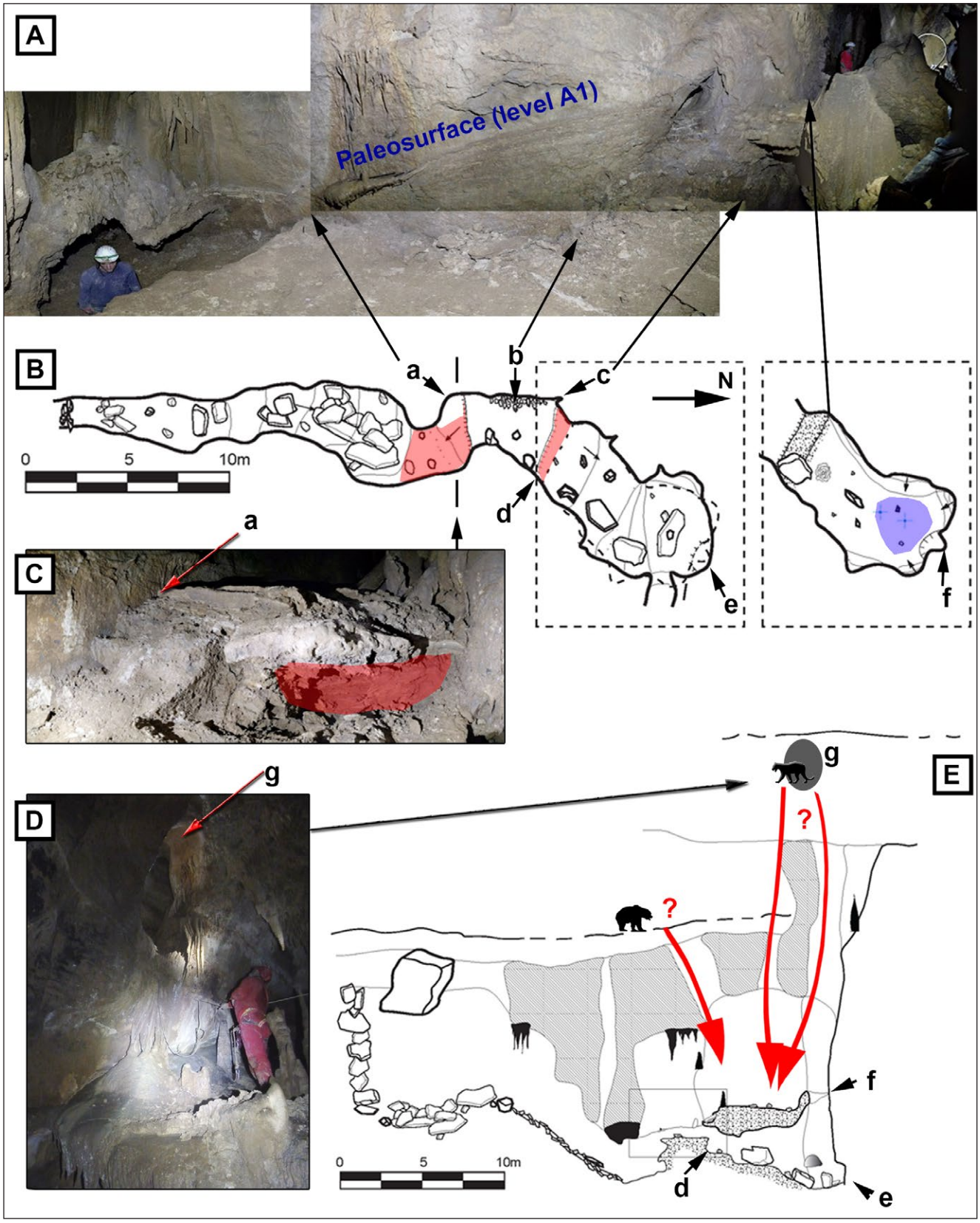


Fig. 2 - General view (A) and topographic plan (B) of the Bear and Lion Sectors of Santa Isabel de Ranero. The lower case letters indicate equivalent areas across the different images of this figure. Letter "b" represents the sediment dump where additional fossils from the Bear Sector were recovered (see main text). Red surfaces indicate where fossils of the Bear Sector were found and the blue surface indicates the location of the Lion Sector. C) Area within the Bear Sector where the stratigraphy can be observed. D) View from the upper part of the gallery of one of the old potential accesses to the karst system (g). E) Gallery profile (viewed from the south) showing both the Bear and Lion Sectors, the floor of the upper gallery (further to the west would be the Esparta Sector) and our hypotheses for the origin of the fossils: intra-karstic, from the upper floor of the gallery in the case of the Bear Sector and exo-karstic (from f) for the Lion Sector (see Discussion and Conclusions). See Supplementary Fig. S5-S9 for additional information.

Sample	^{238}U (ng g^{-1})	^{232}Th (ng g^{-1})	$^{230}Th/^{232}Th$ (atomic x10-6)	$\delta^{234}U$	$^{230}Th/^{238}U$ ratio activity	^{230}Th age (BP years)	^{230}Th corrected age (BP years)
SIR.a3 a	14.19 ± 0.14	34.2 ± 0.3	6.26 ± 0.6	639.7 ± 2.7	0.9224 ± 0.004	84,084 ± 18,770[a]	
SIR.a3 b	16.77 ± 0.16	35.2 ± 0.3	6.80 ± 0.7	404.9 ± 2.8	0.874 ± 0.003	160,560 ± 35,840[a]	
SIR.a3 c	12.32 ± 0.12	29.0 ± 0.3	6.44 ± 0.6	724.5 ± 2.8	0.927 ± 0.002	78,624 ± 17,550[a]	
SIR.a3 d	9.60 ± 0.10	23.6 ± 0.3	5.30 ± 0.5	443.4 ± 2.8	0.797 ± 0.002	117,515 ± 26,230[a]	
SI-5074	1347.7 ± 13.7	14.04 ± 0.15	162 ± 10	277.9 ± 4.6	0.972 ± 0.056	64,500 ± 2,300	62,100 ± 2,200

Tab. 2 - Contents of 238U, 232Th, 230Th/232Th ratio, δ234U and 230Th/238U ratio (activity) and obtained age for the ages sampled in the Bear Sector: four samples from the a3 layer block (SIR.a3) and a small calcitic crust covering a lion calcaneus (SI-5074) (Supplementary Fig. S3-S4). [a]The obtained ages were not corrected due to a high content of detritic thorium (^{232}Th). BP (*before present*) age: present is considered 1950. Decay constants following Cheng et al. (2013).

The SIR-a3 speleothem exhibits well-defined, albeit altered, dendritic calcite crystal growth characterised by creamy-brown hues, suggesting the presence of clays within the intercrystalline porosity. The lower part of the speleothem shows layers with a less porous appearance, and clear but darker laminae. The four subsamples for U/Th dating were taken from these laminae. SI-5074 shows a very much clear calcite crystals with a columnar fabric, and an absence of clays or impurities (Supplementary Fig. S3-S4). The U/Th results are shown in Tab. 2. The results from the SIR-a3 speleothem, ranging from ~80 to 160 ka BP (uncorrected ages for ^{232}Th), should be treated with caution due to the high detrital thorium content. The crust covering the lion calcaneus SI-5074 has yielded an age of ~62 ka BP, providing a minimum age for this bone.

The sedimentological study of the Bear Sector allostratigraphic unit (second allostratigraphic unit) excludes the flowstone levels a8, a7, a3 and a1, as well as the very thin layer a2. The granulometric study shows that there is generally poor sorting, especially compared to the LFG sediments. However, the basal layer a15 shows a relatively better

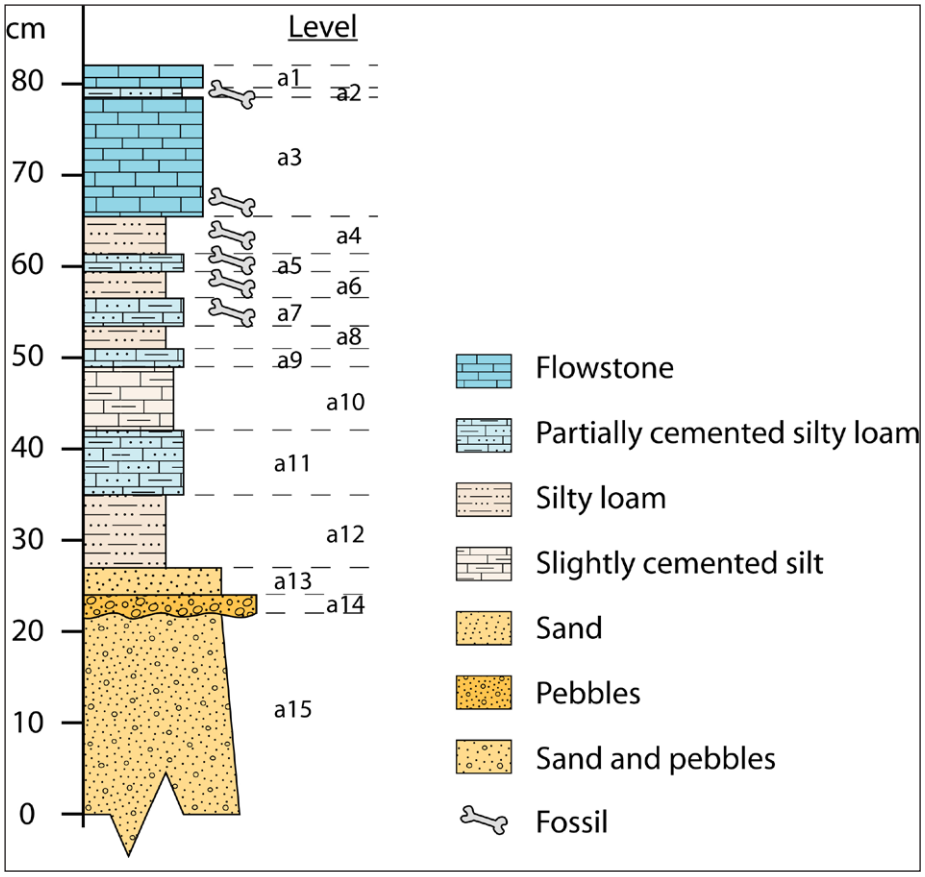


Fig. 3 - Stratigraphic column of the Santa Isabel de Ranero-Bear Sector. The main accumulation of fossil remains occurs in levels a7-a4 (Supplementary Fig. S11).

Taxon	Entrance Sector		Esparta Sector		Bear Sector				Lion Sector	
					NISP			MNI		
	NISP	MNI	NISP	MNI	Arkeologia Museoa (including new excavations)	Villalta collection (MCNB)	ICP		NISP	MNI
Ursus sp.			3	2		2			1	1
Ursus deningeri	2*	2			794	91	1	16		
Panthera spelaea					5	29	4	1	11	1
Canis cf. *lupus*									12	1
Carnivora indet.					5				7	
Indet	4		46		3001	41			240	
Apodemus cf. *sylvaticus*					15			3	1	1
Terricola cf. *duodecimcostatus*									19	2
Arvicolinae indet (*Iberomys* ?)									1	1
Arvicolinae indet					2			1		
Rodentia indet.			2		20				56	
Sorex sp.					3			1	1	1
Microvertebrate indet.			10	-	39			-		
Lacertidae indet.					1			1		
Total	6	2	61	2	3885	163	5	23	349	8

Tab. 3 - Composition of the Santa Isabel de Ranero fossil vertebrate assemblage. NISP = Number of identified specimens. MNI = Minimum number of individuals.* *Ursus* cf. *deningeri;* ICP = Institut Català de Paleontologia Miquel Crusafont; MCNB = Museu de Ciències Naturals de Barcelona.

sorting (Supplementary Fig. S6). The mineralogical results reveal a certain degree of variation, including the alternating presence of speleothem calcite and variation in the relative abundance of different clay minerals (illite, vermiculite and kaolinite). We can underline: a) the lower proportion of vermiculite relative to illite in the lower layers, which increases towards the top of the sequence, b) layer a13 being essentially composed of quartz grains, and c) layer a9 being essentially composed of calcite (Tab. 1).

The Lion Sector is located 4-5 m north of the Bear Sector and 2-3 m above it (Fig. 2). A correlation between the two sectors can be established based on the a3 and a1 flowstones from the top of the sequence (layers a3-a1). These flowstone levels are thicker towards the north (i.e. towards the Lion Sector), where the water sheet that originated the speleothem should have come from. The palaeontological remains from the Lion Sector are found on top of an erosion surface that cuts layer a1, and thus, they would be part of a third allostratigraphic unit. They are accompanied by sandy clay sediments containing millimetric to centimetric anorthic ferruginous nodules and are covered by flowstones from a later (possibly recent) phase.

Palaeontological associations

Entrance Sector

The Entrance Sector yielded six remains that were found on the surface of the cave (Tab. 3). Only two of these can be taxonomically assessed: a left upper M2 (SI-15001) and a left lower m1 (SI-15000), both of which have been assigned to *U.* cf. *deningeri* (Fig. 4). These two bear remains fall within the morphological and metrical variation of the Deninger's bear remains from the Bear Sector (Villalba de Alvarado et al. in preparation). The wear on the M2 is consistent with age stage III-IV, leaning towards stage IV. The lower m1 shows wear compatible with age stage IV. Due to the relatively small size of the M2 compared to the m1, we consider that these two teeth belonged to two different individuals (Villalba de Alvarado in preparation), which would be consistent with the slight degree of age incompatibility.

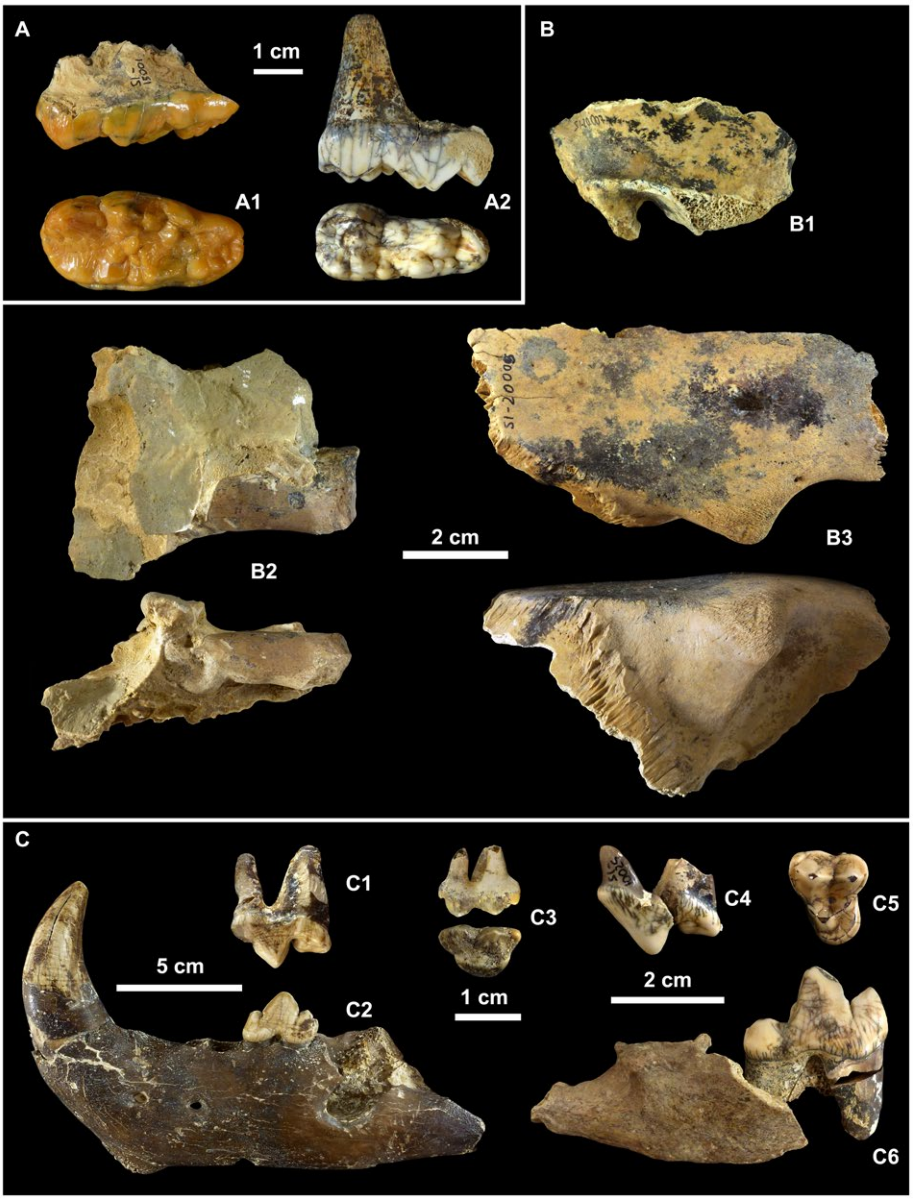


Fig. 4 - Selected remains from other palaeontological sectors of Santa Isabel de Ranero cave. A) Entrance Sector (*Ursus deningeri*): labial (top) and occlusal (bottom) views of the upper left M2 SI-15001 (A1) and lower left m1 SI-15000 (A2). B) Esparta Sector (*Ursus* sp.): lateral view of the immature temporal bone SI-20007 (B1), dorsal (top) and side (bottom) views of the adult proximal phalanx SI-20048 (B2), superior (top) and lateral (bottom) views of the right immature frontal bone SI-20005 (B3). C) Lion Sector: *Panthera spelaea*: lateral views of the left upper P4 SI-10005 (C1) and the left hemimandible preserving the canine and the p4 SI-10000 (C2; note the abnormal erosion present on the corpus of this specimen below the alveolus for the m1); *Ursus* sp.: labial (top) and occlusal (bottom) views of the left upper D4 SI-10003 (C3); *Canis lupus*: labial view of the left upper P4 SI-10025 (C4), occlusal view of the left upper M1 SI-10026 (C5), and lateral view of the corpus fragment of a right hemimandible preserving the m1 SI-10024 (C6).

Esparta Sector

The Esparta Sector yielded 49 macro-mammal remains, which were also found on the surface of the cave (Tab. 3). Most (n = 46) of these remains are indeterminate macro-mammal remains. One frontal bone and one temporal bone belonged to a bear cub of indeterminate taxonomic affinities (*Ursus* sp.) and three additional remains may be associated with this cranium (Fig. 4). A second bear individual is represented by the presence of a complete proximal phalanx that has completed its development. The size of this phalanx falls within the size range of the proximal phalanx sample from the Bear Sector (Supplementary Fig. S12 and Tab. S1). The small-vertebrate assemblage includes two indeterminate rodent remains and ten indeterminate small-mammal remains (Tab. 3).

Bear Sector

The Bear Sector is the most important palaeontological area of the cave, yielding a large assemblage of macro-vertebrates as well as a limited collection of small vertebrate remains (Fig. 5 and Supplementary Fig. S14). The macro-vertebrate assemblage of the Bear Sector is dominated primarily by *U. deningeri* (Torres et al. 2001), though remains of a pantherine felid the size of a lion have also been identified as *P. spelaea* (Tab. 3).

A total of 886 bear remains representing 618 anatomical units have been excavated from this sector (see Tab. 3 and Tab. 4). While all anatomical regions are represented, most of the vertebral remains present in a previous inventory have not been found in the Arkeologia Museoa collection. This assemblage represents a minimum of 16 Deninger's



Fig. 5 - Selected fossil remains from the Santa Isabel de Ranero-Bear Sector. *Ursus deningeri*: A) Lateral views of the virtually complete SI-1234 skull, the left hemimandible V7119 and the right hemimandible SI-295. B) Occlusal (top) and lateral view of the SI-3051 right hemimandible belonging to a cub. Observe the unerupted m1. C) Selected upper right (SI-244, SI-232) and lower left (SI-191, SI-193) canines in labial view. Note the sexual dimorphism in the size of the canines. *Panthera spelaea*: D) Selected remains: from left to right lateral view of the symphyseal part of both hemimandibles V7120, side views of the distal phalanx V7054; anterior and posterior views of the distal portion of a right humerus SI-1023.

bears. Fourteen of these are identified based on the repetition of the lower left m2 (earlier studies indicated the presence of 16 lower left m1s and m2s; Torres et al. 2001). Two additional individuals are identified due to age-at-death inconsistencies: the mandible SI-3051, which belongs to a juvenile (stage I, according to Stiner 1998), and the lower right m3 SI-228, which belongs to an old adult (stage VIII, according to Stiner 1998). We have observed that within the same age cohort teeth that erupt later (i.e. m2 and m3) tend to show relatively less dentine exposure than illustrated in Stiner (1998). Thus, the initial assessment of age-at-death relied on m1s, and the stage for m2s was modified accordingly (Supplementary Fig. S14). Approximately two thirds of the individuals correspond to late juveniles or early prime adults (wear stages III and IV of Stiner 1998) (Fig. 6; Supplementary Tab. S2). Based on the size of the lower canines, the presence of at least two males and seven females could be determined (Fig. 7; Supplementary Tab. S3 and Tab. S4).

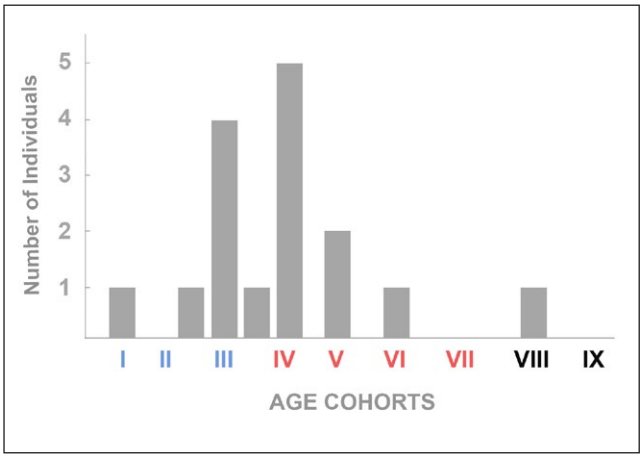


Fig. 6 - Graphical representation of the minimum number of individuals (MNI). Age cohorts are based on the tooth crown emergence and wear (Stiner 1998), adapted for the differences observed in this collection. Two of the individuals display intermediate age cohorts (II-III and III-IV).

The lion remains comprise cranial and postcranial elements, probably belonging to a single adult individual (Fig. 5; Tab. 3 and Tab. 4), which

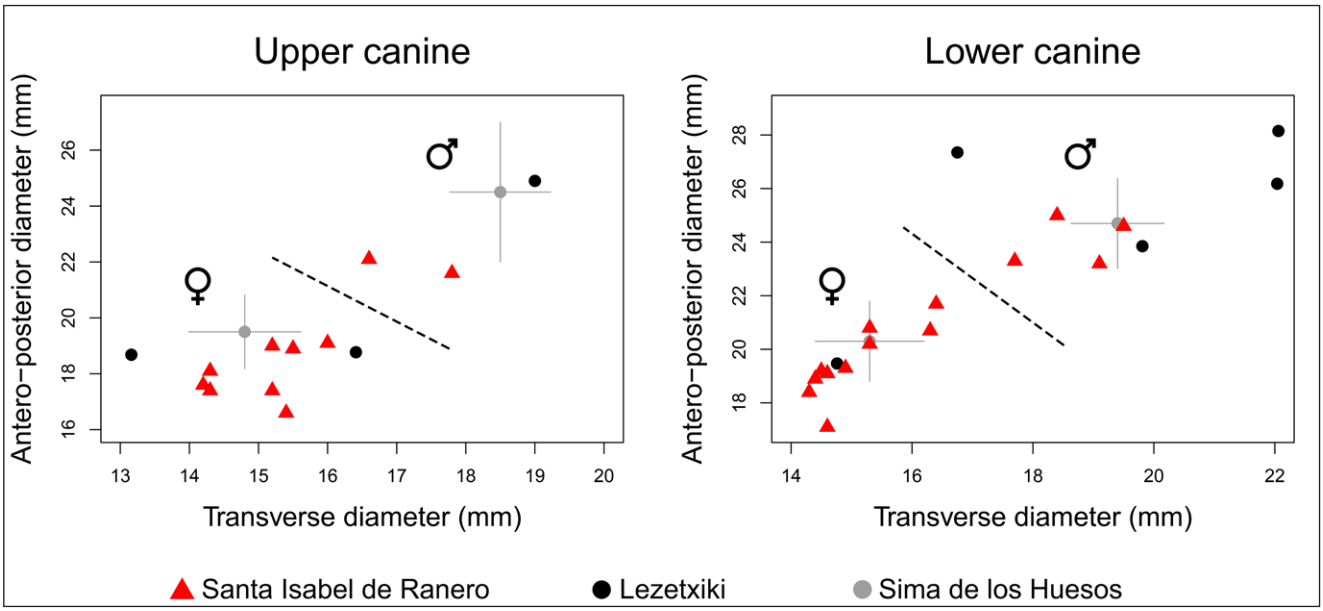


Fig. 7 - Bivariate scatterplots of the measurements of *Ursus deningeri* upper and lower canines from Santa Isabel de Ranero-Bear Sector (red triangles; Supplementary Tab. S3-S4), Lezetxiki-Levels VII and VIII (Arrasate; Gipuzkoa; black circles; Villaluenga Martínez 2013) and Sima de los Huesos (Sierra de Atapuerca, Burgos; grey circle and grey cross that represents the mean ± 1 standard deviation; Torres 1988e, 1988f).

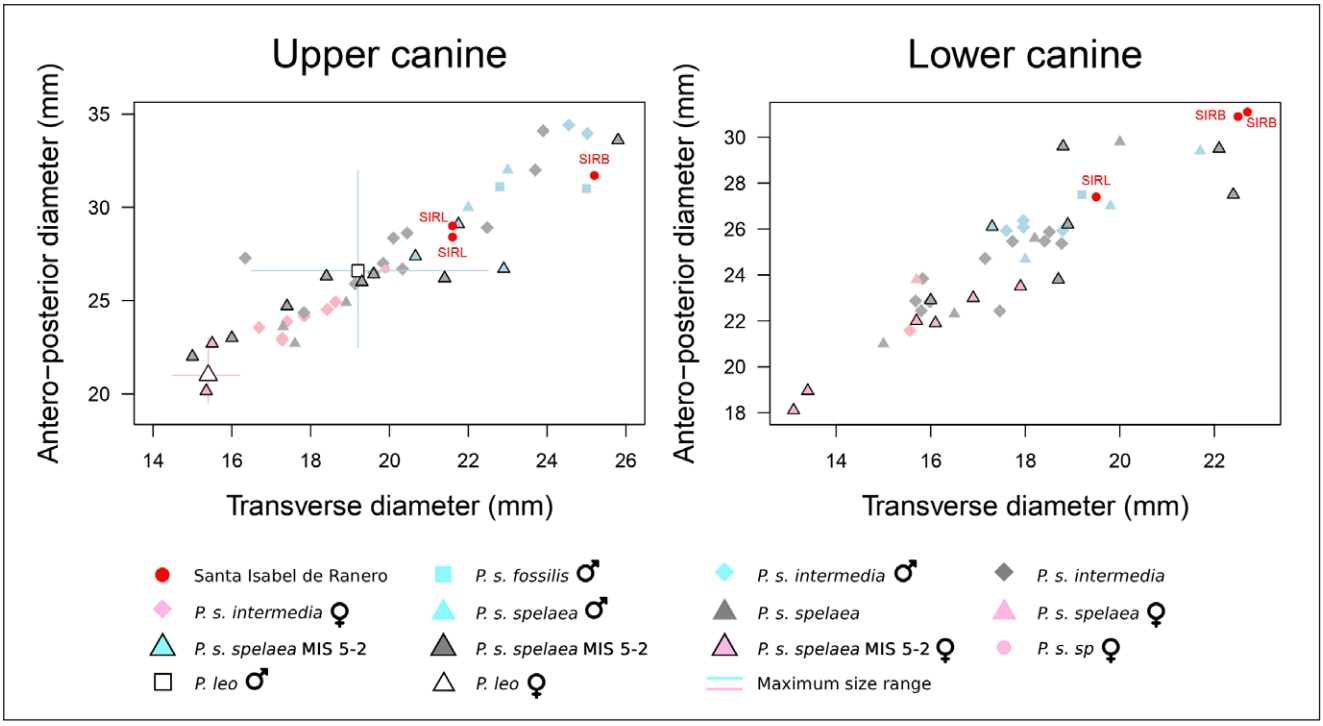


Fig. 8 - Bivariate scatterplots of the measurements of the Middle Pleistocene (Bear Sector; SIR-Bear) and Late Pleistocene (Lion Sector; SIR-Lion) *Panthera spelaea* canines. Original data can be found at Supplementary Tabs. S5-S6.

is consistent in size with other Middle Pleistocene lions attributed to *Panthera spelaea fossilis* (Manjón García 2024; Manjón-García et al. in preparation). The size of the canines suggests that these remains belonged to a male individual (Fig. 8; Supplementary Tab. S5 and Tab. S6), while the dental wear pattern, compared to that of modern lions, suggests that the individual was about 5-6 years old at death (Smuts et al. 1978).

Regarding the small vertebrate assemblage, it derives from the wet sieving of sediments that were left by the previous intervention. Thus, we assume

Anatomical region	*Ursus deningeri*	*Panthera spelaea*
	MNE	MNE
Cranium	3	
Maxilla	3	
Hemimandible	5	2
Isolated teeth	70	6
Atlas	2	
Axis	2	1
Cervical vertebrae	3	3
Thoracic vertebrae	7	5
Lumbar vertebrae	6	1
Caudal vertebra	10	2
Sacrum		
First ribs*	1	
Scapula	3	
Humerus	15	1
Radius	8	2
Ulna	18	1
Carpal bones	64	
Metacarpals	57	1
Coxal bones	3	1
Femur	14	2
Patella	10	2
Tibia	11	2
Fibula	6	1
Talus	15	
Calcaneus	16	1
Other tarsal bones	17	1
Metatarsals	55	
Proximal phalanges	102	
Intermediate phalanges	48	
Distal phalanges	44	1
Total	618	36

Tab. 4 - Anatomical representation of the *Ursus deningeri* and *Panthera spelaea* remains from the Bear Sector of Santa Isabel de Ranero. *Due to the fragmentation no further attempt has been made to identify the MNE on the rib sample.

that it comes from the layers in which the bear remains were found, since this sediment also yielded fossil remains that refitted with the previous collection. Taxonomic analysis of this assemblage revealed the presence of 15 *Apodemus* cf. *sylvaticus* (Linnaeus, 1758) remains, three *Sorex* sp. remains, and one Lacertidae indet. remain, as well as 61 additional remains for which precise taxonomic identification was not possible (Tab. 3; Supplementary Fig. S13; Supplementary Tab. S7; Supplementary Text S3).

Lion Sector

The Lion Sector has also yielded remains of both large and small vertebrates. The macro-vertebrate remains include 11 remains from a pantherine felid the size of a lion, 19 canid remains (12 attributed to *Canis* sp.), and a single upper D4 of a bear (*Ursus* sp.) (Fig. 4C). The lion remains are smaller compared to those from the Bear Sector and are consistent with the size of Upper Pleistocene cave lions (*Panthera spelaea spelaea;* Manjón García 2024; Manjón-García et al. in preparation). The size of the canines indicates that these remains belonged to a male individual (Fig. 8) and the degree of dental wear suggests that the animal was 5-6 years old at the time of death (Smuts et al. 1978). Radiocarbon dating was attempted on one of the lion remains, but it was unsuccessful due to the absence of collagen.

The small vertebrate assemblage includes one *Apodemus* cf. *sylvaticus* remain (an M3), 19 *Terricola* cf. *duodecimcostatus* (de Sélys-Longchamps, 1839) remains, one indeterminate arvicoline remain (an upper M1-M2), whose morphology suggests that it probably belongs to the genus *Iberomys*, 56 additional rodent remains, and one remain belonging to the genus *Sorex* (Tab. 3; Supplementary Fig. S15; Supplementary Tab. S8 and Tab. S9; Supplementary Text S4).

Taphonomic analysis of the Bear Sector

Bone surface modifications

The SIR-Bear Sector collection is characterised by the exceptional preservation of the bone surfaces. Of the analysed bones, 414 (53.4% of the total studied) are intact in terms of surface marks or breakage. There is no evidence of subaerial weathering or long-distance transport, such as bone polishing. Trampling marks were found in very low proportions (Tab. 5). The most frequent

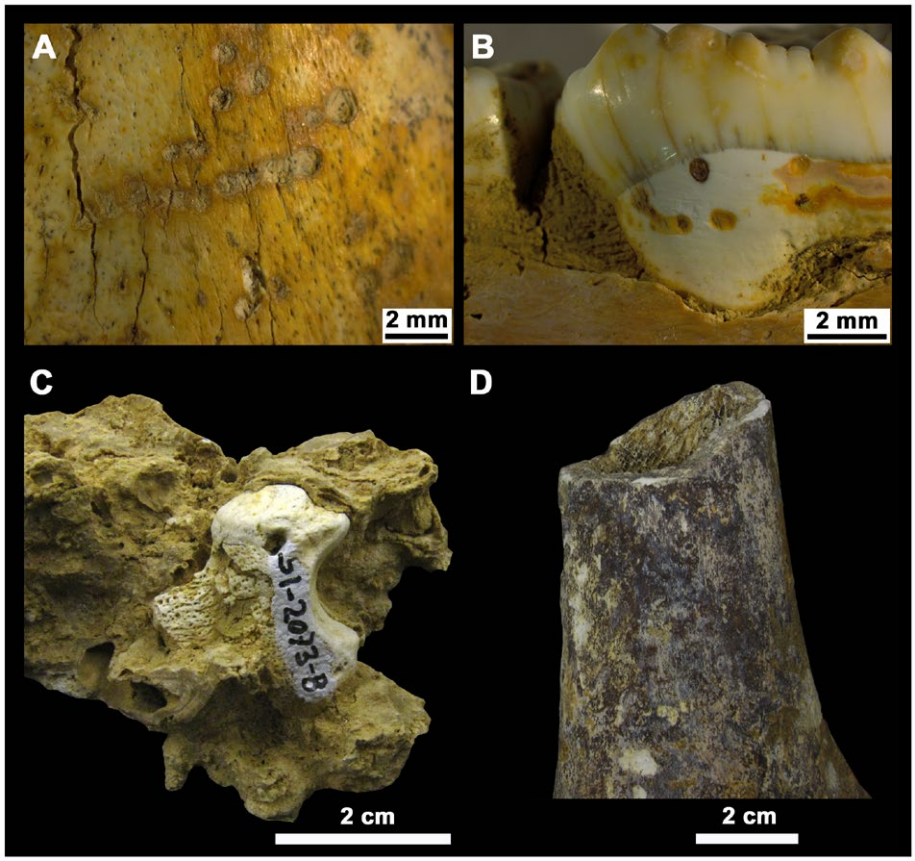


Fig. 9 - The most frequent taphonomic alterations in Santa Isabel de Ranero-Bear Sector: A and B) dissolution affecting a bone (A) and a tooth root (B); C) distal phalanx embedded in a calcitic crust; D) long bone showing the precipitation of manganese oxides on its surface.

alterations are those typical of endokarstic environments, such as calcite precipitation on bone surfaces (crusts), manganese oxide precipitation and dissolution holes in bone surfaces (Fig. 9). Regarding anthropogenic marks, no evidence of cut-marks or anthropogenic breakage (percussion marks) has been found. There is no evidence of rodent activity on the bone surfaces either.

Taphonomic alterations	**NISP (%)**
Anthropogenic marks (e.g., cut-marks, percussion marks)	0 (0.0%)
Carnivore activity	23 (2.9%)
Manganese oxides	382 (49.3%)
Trampling	8 (1.0%)
Weathering	0 (0.0%)
Dissolution/corrosion	69 (8.9%)
Calcite precipitations	73 (9.4%)[a]
Rodent activity	0 (0.0%)
Dissolution produced by roots	0 (0.0%)

Tab. 5 - Number and frequency of the taphonomic observations in the Bear Sector of Santa Isabel de Ranero. [a] This should be considered as a minimum value due to the fact that some bones were cleaned and liberated from crusts.

Carnivore activity was observed in 23 cases, accounting for less than 3% of the analysed remains. This frequency is low compared to contexts in which carnivores are the primary accumulator agents, such as hyaena dens (Arsuaga et al. 2012; Sala et al. 2012). Nevertheless, it is consistent with the frequency observed at the Middle Pleistocene Sima de los Huesos (SH) site, which is the largest accumulation of *U. deningeri* in the Iberian Peninsula (García & Arsuaga 2011; Sala et al. 2014b). The marks observed were essentially pits and scores on the proximal epiphyses and diaphyses of long bones, as well as on the cortical parts of flat bones, with furrowing occurring to a lesser extent (Fig. 10 and Tab. 6). No punctures were observed on either cortical or spongy bone. Peeling was observed in a bear rib (SI-450), which also showed tooth-marks (Fig. 10B). Tab. 7 shows the dimensions of the tooth-marks (pits and scores) in both cortical and trabecular bone. Their large size suggests that these tooth-marks were made by a large carnivore.

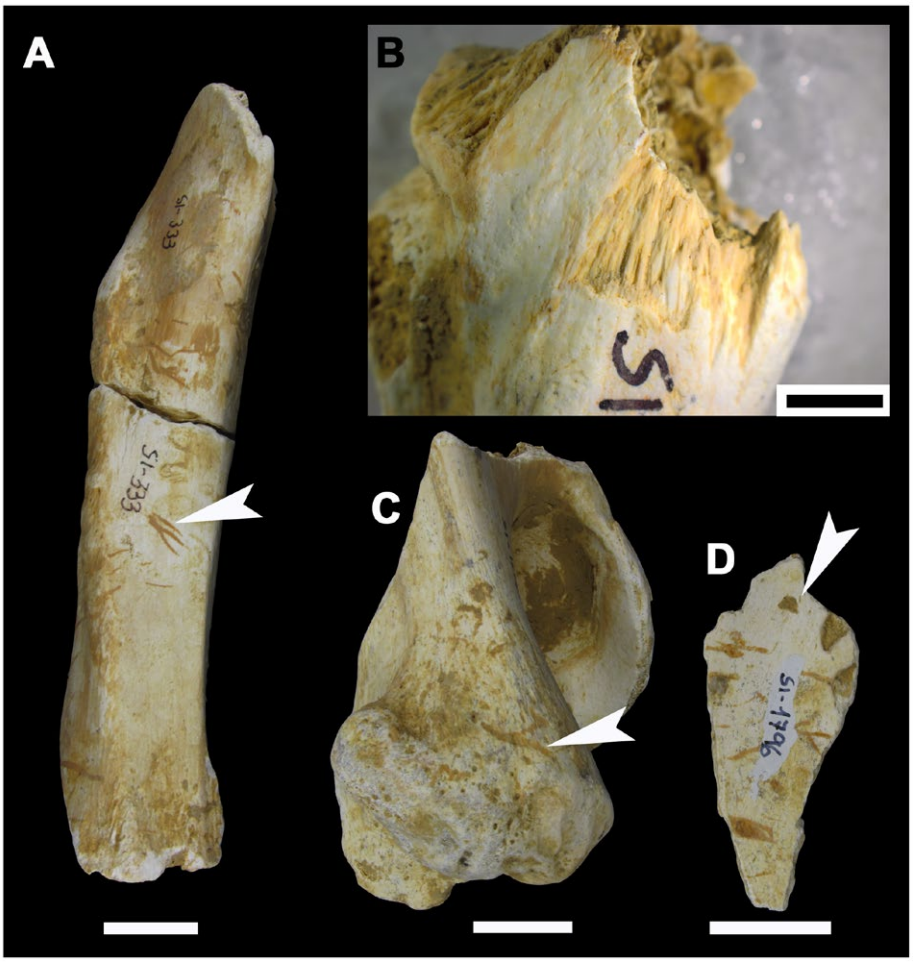


Fig. 10 - Selected remains from the Santa Isabel de Ranero-Bear Sector collection affected by carnivore activity: A) scores in the humeral diaphysis SI-333; B) peeling in the rib SI-450; C) scores in the distal epiphysis of the humerus SI-1041; D) scores and pits on a flat bone (SI-1796). Scale-bar: 2 cm except in (B) in which the scale = 2 mm.

Tab. 6 - Frequency and location of the tooth marks on the Santa Isabel de Ranero remains[a,b].
[a]All the studied bones belonged to *U. deningeri*.
[b]Vertebrae were not included in this study (see main text).

Type of tooth-mark	Long bones (NISP = 257)			Flat bones (NISP = 236)		Phalanges, carpal, and tarsal bones (NISP = 276)
	Proximal epiphysis	Diaphysis	Distal epiphysis	Cortical	Spongy	
Pits	6 (2.3%)	6 (2.3%)	0	3 (1.3%)	0	1 (0.3%)
Scores	2 (0.8%)	7 (2.7%)	1 (0.4%)	8 (3.4%)	0	1 (0.3%)
Furrowing	2 (0.8%)	0	0	0	1 (0.4%)	0

Tab. 7 - Dimensions (in mm) of the tooth-marks measured in the Santa Isabel de Ranero fossil assemblage depending on the bone type. CI = Confidence interval.

Tooth-mark	Measurement	Type of bone	*n*	Mean	Standard deviation	Minimum	Maximum	CI -95%	CI + 95%
Pits	Maximum diameter	Spongy	11	4.44	1.17	2.85	6.25	3.65	5.23
		Cortical	14	3.29	0.98	1.83	5.23	2.72	3.86
	Minimum diameter	Spongy	11	3.15	0.77	1.82	4.60	2.63	3.67
		Cortical	13	2.28	0.65	1.50	3.42	1.89	2.67
Scores	Maximum width	Spongy	7	2.53	1.00	1.61	4.19	1.60	3.45
	Maximum width	Cortical	29	2.31	0.99	0.88	4.80	1.94	2.69

Fracture patterns

Of the total of analysed remains, 317 (40.9% of the studied sample) exhibited fractures. Those with clear evidence of recent breakage (i.e. differential colour on the fracture surface) were excluded from the analysis. Among the complete remains, those with high osseous density (i.e., carpal and tarsal bones, phalanges, metapodials and sesamoid bones) are prevalent. Regarding breakage properties (Supplementary Fig. S16), transverse fractures dominate the sample, being present in 69.23% of the long bones studied. Regarding the angle of the fracture plane, 80% of the sample showed right angles, 17.33% showed both right and acute angles, and only 2.67% of the sample showed angles different from 90º. Most fractures have jagged surfac-

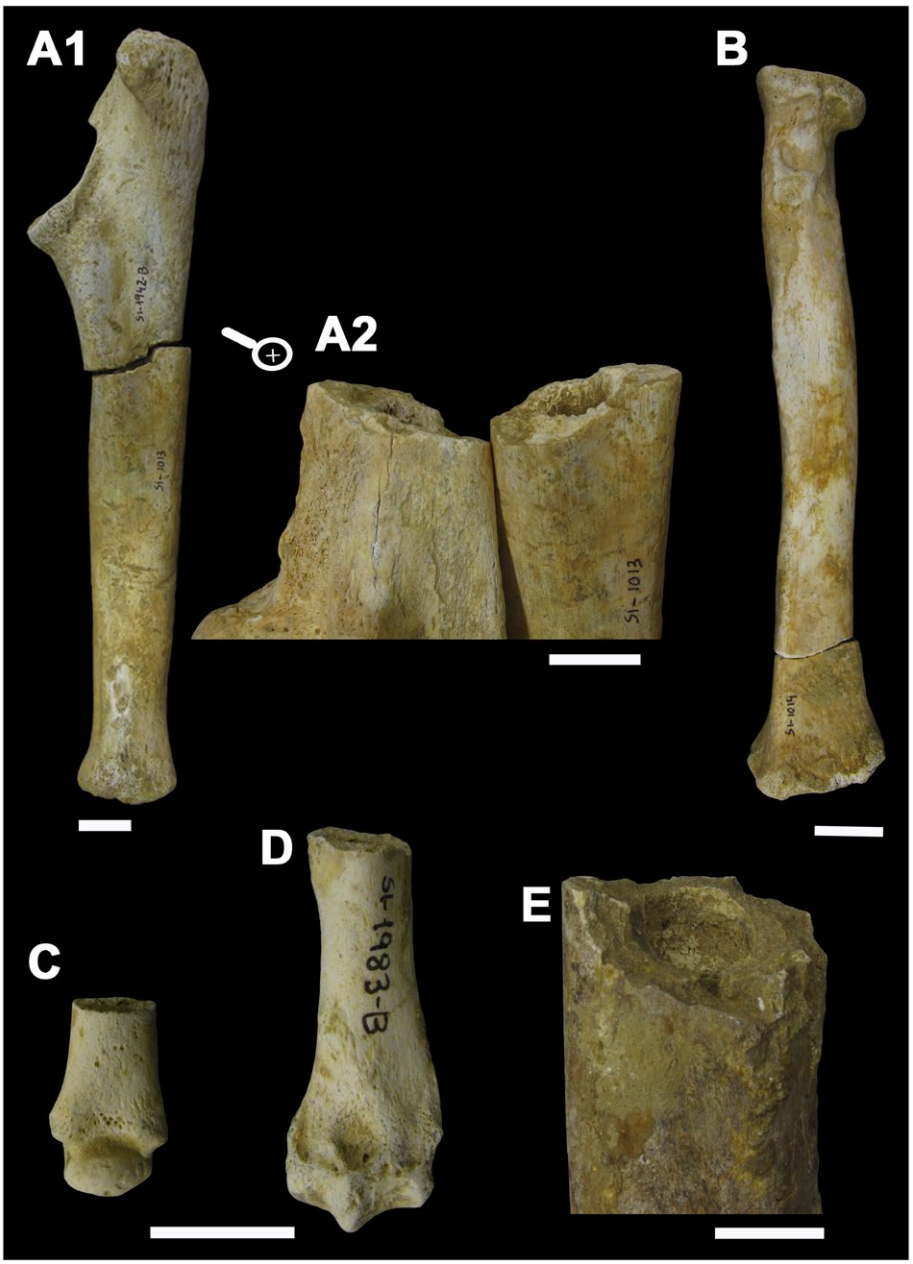


Fig. 11 - Most common fractures in the Santa Isabel de Ranero-Bear Sector fossil association. Transverse fracture of the ulna SI-1013+SI-1942 (A1: general view; A2: detail of the fracture surfaces); B) Fracture on the diaphysis of the radius SI-338+SI-1014; C) Transverse fractures in the SI-1964B metapodial (in dorsal view); D) Transverse fracture of the SI- 1983B metapodial (in plantar view); E) Detail of the fracture surface of the bear ulna SI-1288. Scale bars = 2 cm.

es and, despite differences in preserved diaphysis length, 88.46% of the studied bones have complete circumferences (Supplementary Fig. S17).

The SIR-Bear long bone sample shows a fracture pattern characterised by the dominance of transverse fractures along the long axis, complete circumferences, and fracture edges with right angles and jagged surfaces (Fig. 11). These features are all consistent with dry-bone fractures occurring during the fossil diagenetic phase. In archaeo-palaeontological sites, this type of fracture could result from sediment pressure (Villa & Mahieu 1991; Sala et al. 2015).

In addition, a comparison was made between the fracture patterns of SIR and the green bone breakage assemblages corresponding to Pleistocene hyaena dens (Zarzamora and Camino) and dry-bone breakage assemblages caused by sediment pressure (*U. deningeri* and hominins from the Sima de los Huesos site). The MCA showed a distinct grouping of the different comparative assemblages (Supplementary Fig. S18). Axis 1 (eigenvalue 0.75841; 33.71% of the inertia) and Axis 2 (eigenvalue 0.33524; 14.90% of the inertia) clearly distinguish two sets according to the fracture traits, depending on the state of the bone when it was fractured: transverse fractures, right angles, jagged surfaces and complete circumferences in the post-depositional state versus oblique outline fractures, oblique angles, smooth surfaces and incomplete circumferences in

the green bone breakage. Furthermore, the MCA also suggests a direct statistical relationship between the bear long bones from the SIR sample and the *U. deningeri* assemblage from the Sima de los Huesos Middle Pleistocene site, with post-depositional breakage by sediment pressure.

Discussion and conclusions

With regard to the number of identified fossil remains, the Santa Isabel de Ranero assemblage represents one of the most important Middle Pleistocene *U. deningeri* collections on the Iberian Peninsula, second only to those at Sima de los Huesos and La Lucia (Torres et al. 2005; García et al. 2024). Furthermore, the site has yielded highly complete *P. spelaea* remains, thus facilitating the assessment of the evolution of this taxon in the Iberian Peninsula (Castaños Ugarte 2025; Madurell-Malapeira et al. 2025) throughout the second half of the Pleistocene. The primary objective of this work is to characterise the site formation processes of Santa Isabel de Ranero using a combined geological, palaeobiological, and taphonomic approach. Recent explorations have indicated the presence of at least four distinct areas within the cave where fossil remains have been retrieved. Two of these areas (the Entrance and Esparta sectors) consist of small assemblages collected on the surface. The remaining two sectors, the Bear and Lion sectors, are found within the same sedimentary sequence but within two different allostratigraphic units, as there is at least one erosive phase in between. However, the fossil assemblage found at the Lion Sector is limited. Therefore, the focus will be on the origin of the bone accumulation of the Bear Sector, with a secondary focus on the Lion Sector.

Across the Cantabrian region, multi-level cave systems associated with base-level lowering are well documented (Aranburu et al. 2015). Following uplift related to the Alpine orogeny, the regional base level has progressively lowered, at least since the Miocene (Rosenbaum et al. 2002). However, this lowering was not continuous. Periods during which sediment supply to river valleys exceeded fluvial transport capacity promoted aggradation and temporary stabilisation of the local base level, favouring the formation of river terraces (del Val et al. 2019) and the development of cave levels through paragenesis (Arriolabengoa et al. 2019, 2020). Under these conditions, sediment accumulation within phreatic cave passages promoted paragenetic enlargement, as sediment infilling restricts dissolution along the lower part of the conduit and focuses water flow and dissolution towards the ceiling and upper walls (e.g., Pasini 2009; Farrant & Smart 2011; Audra & Palmer 2015). The geomorphological and sedimentological evidence from Santa Isabel de Ranero is consistent with this regional framework. The cave displays two clearly differentiated levels, together with a possible third, lower and currently inaccessible level. The two accessible levels preserve characteristic paragenetic morphologies, including ceiling channels and anastomosing half-tubes, spatially associated with remnants of laminated fine-grained sediments (LFG), which constitute the first allostratigraphic unit. Taken together, these features indicate that the early development of the cave was linked to phases of base-level stability, fine-grained sediment accumulation, and paragenetic enlargement of the passages.

Based on this framework and the available geomorphological and stratigraphic evidence, we propose a schematic evolution of the Santa Isabel de Ranero cave, particularly the Bear and Lion sectors, in several stages (Fig. 12). Initially, LFG sediments accumulated under phreatic conditions, promoting paragenetic enlargement, as evidenced by the ceiling channels and anastomosing half-tubes preserved in the cave (Fig. 12a). Following the cessation of sediment supply, a subsequent fall in the base level lowered the water table and promoted erosion of the previously deposited LFG sediments. The resulting erosional discontinuity defines the upper boundary of the first allostratigraphic unit. Continued base-level lowering eventually placed the Bear and Lion sectors above the active water table, allowing runoff-related erosion and sedimentation to occur within these passages (Fig. 12b). These processes mark the beginning of deposition of the second allostratigraphic unit. Within the Bear and Lion sectors, the dominant depositional processes subsequently changed through time. Runoff-related sedimentation prevailed during deposition of the lower layers (a15–a13), whereas infiltration through the overlying soil and epikarst became progressively more important during deposition of the intermediate layers (a12–a4). Speleothem formation finally dominated the uppermost part of the sequence

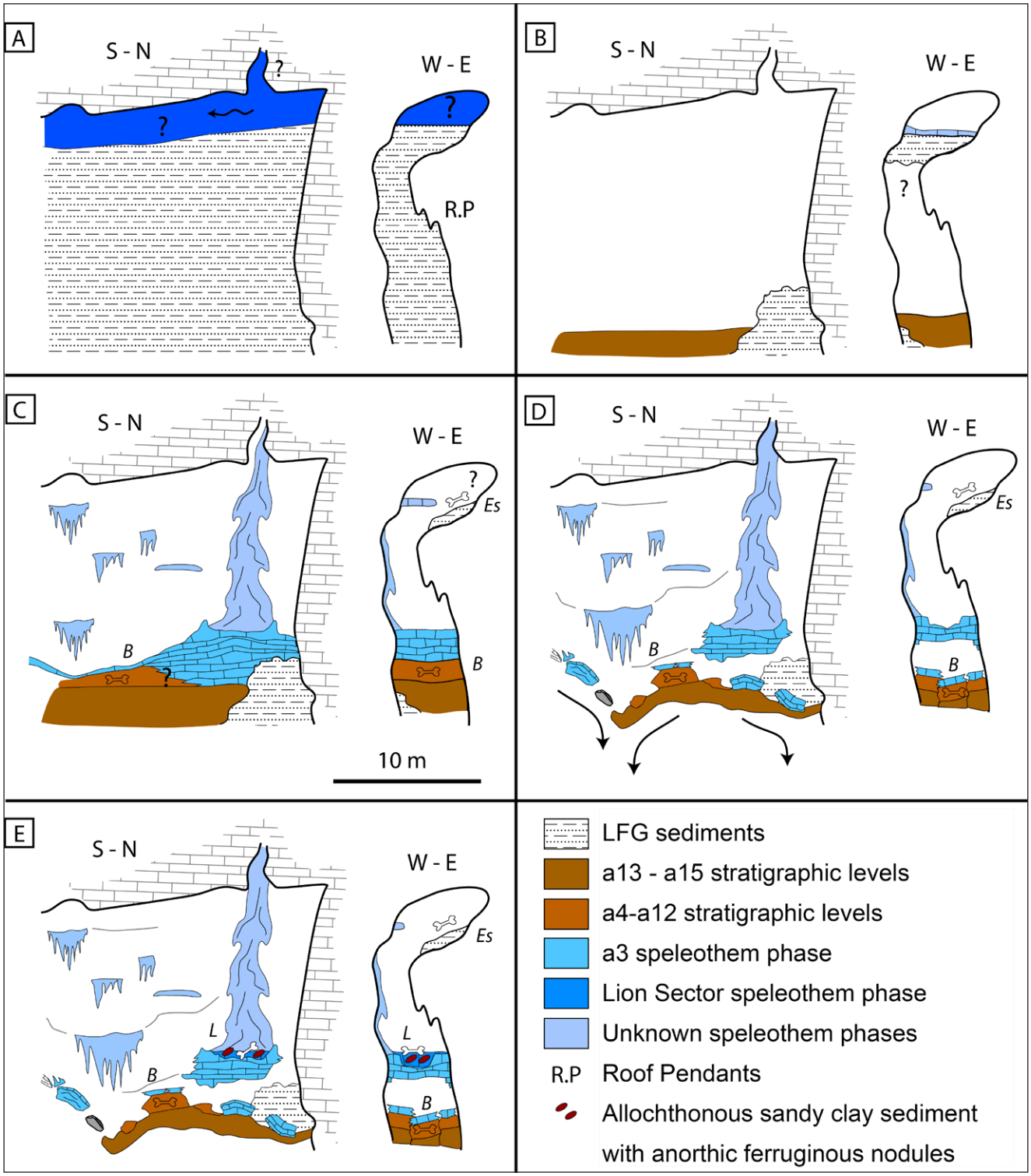


Fig. 12 - Schematic evolution of the Santa Isabel de Ranero cave and the Bear (B) and Lion (L) Sectors. a) Laminated fine-grained (LFG) sedimentation under phreatic conditions, and speleogenesis by paragenesis. b) Erosion and sedimentation by runoff. c) As time passes, sediments are deposited by infiltration processes rather than runoff, and speleothem formation dominates towards the top of the sequence. The fossils found at the Bear Sector and maybe those from the Esparta Sector (Es) were deposited during this phase. d) Partial erosion of the site, probably by an active water flow circulation in a cave level below the Bear Sector. e) Deposition of the fossils of the Lion Sector together with sediments and anorthic ferruginous nodules from outside the cave. Modified from Arriolabengoa et al. (2018). The detailed stratigraphic column of the Bear Sector can be found in Fig. 3. B = Bear Sector; L = Lion Sector. Es = Esparta Sector.

(layers a3–a1). The fossils recovered from the Bear Sector (layers a4–a8), and possibly those from the Esparta Sector, were likely deposited during this phase (Fig. 12c). Previous studies in Cantabrian cave sequences have shown that higher proportions of illite relative to vermiculite can reflect a greater contribution from fluviokarstic processes relative to soil-derived infiltration and have been associated with comparatively colder environmental conditions (Arriolabengoa et al. 2015). Conversely, speleothem formation in the Cantabrian region is generally favoured during warmer periods (Stoll et al. 2013; Aranburu et al. 2015). Accordingly, the sedimentological and mineralogical evidence from the Bear and Lion sectors suggests an upward transition within the second allostratigraphic unit from a comparatively colder phase, characterised by dominant runoff processes, to a relatively warmer phase characterised by increased soil-derived infiltration and, ultimately, speleothem formation.

The U/Th dating of SIR-a3 must be approached with a degree of caution due to detrital contamination. However, the results provide a minimum Middle Pleistocene age for the Bear Sector fossils, which is in agreement with the previously reported c. 300 ka ESR dating (Torres et al. 2014). Two samples from the SIR-a3 speleothems (samples a and c) would provide maximum ages for the fossils found within layer a2 and those from Lion Sector, and would locate these within the Late Pleistocene, which would be consistent with the overall size of the lion remains found in the Lion Sector. A partial erosion of the site, likely caused by active water flow circulation at a lower cave level (Fig. 12d) exposed part of the remains from layers a4-a8. It can be hypothesised that the result obtained for SI-5074 (~62 ka BP) could indicate the minimum age of the subaerial exposure of these fossil remains, with a subsequent carbonate precipitation. Finally, the deposition of the fossils from the Lion Sector occurred, accompanied by the anorthic ferruginous nodules that were formed within soils outside the cave (Fig. 12e).

The taphonomic analysis indicates that the carnivore remains from the SIR-Bear Sector do not show signs of sub-aerial exposure and, thus, were probably deposited in the cave during the biostratinomic phase. The absence of anthropogenic marks indicates that humans were not responsible for the accumulation (or the modification) of the bone remains. However, the SIR *U. deningeri* remains show carnivore modifications. Tooth-marks appear in a very low proportion (2.9%) and do not implicate long bone breakage. The most prevalent tooth-mark typologies were pits, scores, and, to a lesser extent, furrowing of the trabecular bone. In the context of hyaena dens, tooth-marks are more prevalent (with an average of 39.2%, ranging from 38.8% to 55.9% in hyaena dens from the Iberian Peninsula; Kuhn et al. 2010; Arsuaga et al. 2012; Sala et al. 2012). This low frequency, in conjunction with the absence of breakage related to the carnivore-marks and the absence of digested bones and coprolites, serves to eliminate hyaenas as the accumulation agent of the Bear Sector assemblage. As demonstrated by experimental works, the tooth pit length on cortical surfaces has been identified as the most useful variable in identifying the carnivore that produced the tooth-marks (Sala & Arsuaga 2018). The comparative metric analysis of the tooth-marks (Supplementary Tab. S10) demonstrates that the size of the pit length is significantly different from those produced by wolves and hyaenas, but not from those marks produced by bears and lions. Bears produce a low frequency of tooth-marks, but may produce the presence of peeling (Arilla et al. 2014). In the SIR assemblage we have found one rib showing peeling. Conversely, the SIR sample does not show significant differences when the size of the tooth pits is compared to those found in the Sima de los Huesos (SH) assemblage, which was sporadically scavenged by other bears (Sala et al. 2014b). The frequency of tooth-marks in the SH assemblage is low and similar to that present in the SIR sample (2.9%). The MCA analysis groups SIR with dry-bone breakage assemblages caused by sediment pressure (*U. deningeri* and hominins from the Sima de los Huesos site) and it is not grouped with the Pleistocene hyaena dens included in this analysis (Zarzamora and Camino). To summarise, it can be concluded that both humans and hyaenas can be disregarded as accumulation agents, and it is hypothesised that bears were the most probable carnivore responsible for the surface modifications observed on other bear remains. This scavenging behaviour of bears by other bears is known both in recent and Pleistocene contexts (Stiner 1994; Pinto et al. 2005; Rabal-Garcés et al. 2012). Finally, the fracture pattern of SIR is consistent with a dry-bone breakage caused by sediment pressure.

An in-depth taphonomic assessment of the fossil remains derived from the Lion Sector has not been performed, due to the limited number of remains available for analysis, and the fact that many of them are dental remains, which are less informative. However, a comparison of the fossil remains from this sector with those derived from the Bear Sector reveals notable differences in appearance, including a darker coloration and the presence of erosion on the surface of the bone in some specimens (Fig. 4C).

The presence of all anatomical regions in the SIR-Bear Sector collection indicates that entire bear carcasses were accumulated in this sector. The SIR-Bear Sector assemblage has not yielded any deciduous bear teeth that have fallen naturally, which contrasts with the presence of these elements in sites interpreted as hibernation and birthing dens (e.g., Amutxate; Torres et al. 2014). Also, the demographic profile of SIR-Bear Sector displays a large proportion of both older juveniles and young prime adults, which contrasts with hibernation/birthing dens, which include large proportions of very old and very young individuals, neonate remains, among others (e.g., Troskaeta, El Reguerillo, Amutxate; Torres et al. 1991, 2014). Something similar happens with mortality profile of Sima de los Huesos (Burgos), which does not correspond to a hibernation/birthing den, and is more similar to a catastrophic mortality profile. This would be consistent with this site being a natural trap for the carnivores found in this site (García et al. 1997). The age-at-death categories and methodology employed for the age profiles in both Sima de los Huesos and La Lucia-Ramp are different, and the number of individuals represented in the SIR-Bear Sector also precludes a more direct comparison between these Middle Pleistocene sites, which should be undertaken in the future, using the same methodology.

A minimum of 16 bear individuals is represented in the collection, and it has been possible to determine the presence of a minimum of seven female and two male individuals. It is not possible to exclude the possibility of representation bias, given that sex determination has been successfully achieved in only nine out of the 16 individuals from the SIR-Bear Sector. However, other Middle Pleistocene sites, such as Sima de los Huesos (SH; Spain) and Westbury-sub-Mendip (UK), demonstrate sex ratios in which female individuals are more represented than male individuals (Bishop 1982; García et al. 1997). In the case of SH, García et al. (1997) have interpreted this proportion as females using the part of the Cueva Mayor cave system adjacent to Sima de los Huesos for hibernation purposes, and falling into the Sima de los Huesos more frequently than males. A higher percentage of females (>70%) have also been identified in other Upper Pleistocene sites, including Ekain and El Reguerillo (Torres et al. 1991).

We propose that the fossil accumulations found at both the Bear and the Lion sectors are the consequence of that part of the cave acting as a natural trap, as indicated by the results obtained previously. Presently, this segment of the cave constitutes basically an isolated short passage, and cavers had to dig to gain entry. It is connected vertically to another conduit, which contains the Esparta Sector. It is hypothesised that, during the Middle Pleistocene, cave bears (*U. deningeri*) utilised other areas of the SIR cave as hibernation/birthing dens. Different bear individuals, mainly late juveniles and young prime adults (stages III and IV *sensu* Stiner 1998), and likely with a large ratio of female individuals fell into the Bear Sector, probably from the conduit in which we found the Esparta Sector. An adult Middle Pleistocene lion *P. spelaea fossilis* (von Reichenau, 1906) also fell into the Bear Sector, either by accident or attracted by the carrion stench. It is conceivable that some of the fallen bears may have arrived in this sector alive and may have produced some of the carnivore marks (i.e. bite marks, peeling) detected in the SIR-Bear Sector. These remains were subsequently covered by a speleothem and underwent the various geological and taphonomic (post-depositional) processes listed above. For the remains found in the Lion Sector, we propose a slightly different scenario, as these remains were found in sediment containing anorthic ferruginous nodules of exokarstic origin (Stoops et al. 2018). Vertically to the Lion Sector and above to the conduit from which we propose that the carnivores from the Bear Sector may have fallen, there is a sub-vertical conduit that eventually became blocked (Fig. 2). We hypothesise that this passage was accessible from the outside during the Late Pleistocene and could have acted as a natural trap for various animals, such as the lion, the canid, and the small vertebrates, and could be the origin of the accumulation in the Lion Sector. However,

the interpretation of the accumulation of the Lion Sector should be regarded as more tentative, as it is based on very limited fossil evidence, together with observations of cave morphology. In summary, based on geological, palaeobiological, and taphonomic evidence, we propose that the accumulations found in the Bear and Lion Sectors derive from animals that fell naturally from another conduit in the case of the Bear Sector, and likely from outside in the case of the Lion Sector. This study highlights the importance of natural traps for gaining insight into past ecosystems in the Cantabrian region (e.g. Gómez-Olivencia et al. 2015; Castaños et al. 2012).

Data Availability Statement. The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding author to obtain access.

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