

**Paleobiological and taphonomic analysis of a site with cold-adapted fauna
in Iberia: Baio (Zestoa, Gipuzkoa, Northern Iberian Peninsula)**

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Abstract

The study of cold-adapted faunas in Iberia is of great interest for paleontologists because this peninsula represents the southernmost limit of distribution in western Europe of species such as mammoths, reindeer and woolly rhinoceros. Additionally, the direct dating of paleontological assemblages can provide important information regarding the paleoecology of Paleolithic humans. This study aims to study the fossil assemblage recovered on the surface of the Baio cave (Zestoa, Northern Iberia), which includes cold-adapted species remains. This site has yielded an assemblage that includes herbivores, carnivores and a small number of rodents. The radiocarbon dating of a reindeer and a red deer remains has yielded chronologies consistent with the Châtelperronian and Late Aurignacian occupations in the area, indicating a diachronic accumulation. Taphonomic observations suggest carnivores as the main accumulation agents, with a minimal human contribution, and the probable accumulation of some remains due to natural causes and/or the cave acting as a natural trap. This new evidence contributes to the existing record from other sites, such as Ekain and Mainea, suggesting severe climatic pulses during the transition from the Middle Paleolithic to the Upper Paleolithic, which coincides with a complex pattern of Neanderthal extinction and the replacement by modern humans.

Keywords: Pleistocene, *Rangifer tarandus*, Iberian Peninsula, taphonomy.

1. Introduction

In the coldest phases of the Pleistocene, in northern Eurasia and North America ice sheets advanced southward. These episodes led to shifts in the paleobiogeography of cold-adapted faunas, also known as the *Mammuthus-Coelodonta* faunal complex, entering the southernmost peninsulas of Eurasia (Kahlke, 2014 and references therein). The Iberian Peninsula became the southwestern boundary of tundra-steppe habitats during these periods, especially during the Last Glacial Maximum (LGM) (Álvarez-Lao and García, 2010, 2011a). However, the Pyrenees acted as a natural boundary for the expansion of cold-adapted faunas, except for its westernmost and easternmost borders that acted as natural passages (see e.g., Gómez-Olivencia et al., 2014 and references therein). Therefore, the Western Pyrenees area plays a crucial role in comprehending cultural and faunal exchanges between Iberia and the rest of South-Western Europe (Álvarez-Lao and García, 2011a; Arrizabalaga and Rios-Garaizar, 2012).

The most prevalent cold-adapted species in the Iberian Peninsula, particularly in the Cantabrian fringe and northeastern Catalonia, are the reindeer (*Rangifer tarandus* Linnaeus, 1759), the woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach, 1799) and the woolly mammoth (*Mammuthus primigenius* Blumenbach, 1799). To a lesser extent, the Iberian cold-adapted fauna also encompasses ungulates like the musk ox (*Ovibos moschatus* Zimmermann, 1780) and the saiga antelope (*Saiga tatarica* Linnaeus, 1766), along with carnivores like the arctic fox (*Vulpes lagopus* Linnaeus, 1758) and the wolverine (*Gulo gulo* Linnaeus, 1758) (Álvarez-Lao and García, 2011a, 2011b and Gómez-Olivencia et al., 2014 for reviews; Álvarez-Lao et al., 2020; Sala et al., 2020; Rodríguez-Almagro et al., 2021; Arceredillo et al., 2023).

The oldest records of woolly rhinoceros and the reindeer are found in the northern regions of the Iberian Peninsula during the Middle Pleistocene: between 188-141 ka BP for

the woolly rhinoceros (La Parte, Asturias) and c. 200 ka for the reindeer (Mollet, Girona) (Álvarez-Laó and García-García, 2006, 2011a). The woolly rhinoceros is distributed across northern and central Iberia, appearing in up to 36 sites and its chronological range spans the Middle and Late Pleistocene, being the most recent records those from Legintxiki (18,430-17,830 cal BP) and the Solutrean level f from Abauntz (Arceredillo et al., 2023 for a review).

The reindeer is the most abundant cold-adapted macromammal in the Iberian Peninsula, appearing in up to 56 sites in the northern region (Rios-Garaizar et al., 2019). The highest concentration of cold-adapted faunas in the Iberian Peninsula, particularly during the Late Pleistocene and covering the LGM, is observed in this region between 31 and 14 ka (Álvarez Lao and García, 2010, 2011a). Unlike *M. primigenius* and *C. antiquitatis*, *R. tarandus* is not present in central and southern regions of Iberia (Gómez-Olivencia et al., 2014) and the number of remains recovered per site is generally low, except in two sites in the Eastern Cantabrian region close to the natural pass of the Pyrenees: a natural trap (Kiputz IX; Castaños, 2014) and an anthropic site (Santa Catalina, Berganza et al., 2012).

The study of cold-adapted faunas in the southern European peninsulas, including precise taxonomic identifications, direct dating and taphonomic studies, provide essential paleobiogeographic and palaeoecological information for understanding how faunal communities respond to Quaternary climate pulses. Additionally, these studies contribute to the understanding of the paleoecology of the Palaeolithic human occupations in this area (e.g., Rodríguez-Almagro et al., 2021). The Baio site (Basque Country) is one of the locations where the presence of cold-adapted species has been recorded (Altuna and Mariezkurrena, 2010) but no precise chronological framework was available for this site. Hence, the general objectives of this study are to conduct a comprehensive quantitative paleobiological and taphonomic analysis of the paleontological remains found on the surface of the Baio cave and to provide a first chronological framework for this deposit. We aim to understand the origin of

this deposit, to improve the chronological framework of the presence of cold-adapted species in the region and to discuss its potential significance within the current comprehension of the transition from the Middle to the Upper Palaeolithic in this area.

2. The Baio cave: geographical and geological setting

The Baio cave is located on the western slope of the Mendigaña hill, called Baiomendi, in the municipality of Zestoa (Gipuzkoa). The cave is located 43 meters above the Urola River (Fig. 1), 100 meters above current sea level and the entrance measures 0.90 m in height and 2.70 m in width. The Baio cave does not exceed 30 meters in length (Fig. Sup. 1) and the passages are practically filled with sediment.

The site was discovered by the Antxieta Arkeologi Elkartea in 1990 (Altuna et al., 1995). This group intervened in two sectors: in the interior of the cave, they collected the paleontological material found on its surface. They also carried out a 1 m² test pit at the entrance of the cave that revealed the presence of at least 6 meters of sedimentary sequence (Altuna et al., 1995). Altuna and Mariezkurrena (2010) published a preliminary faunal list that encompassed both the material recovered from the surface of the interior of the cave and the material from the test pit at the cave entrance, and emphasized the prevalence of carnivores, particularly cave bears.

Geologically, the cave develops in the Aptian-Albian reef limestones with rudist bivalves and corals (Fig. 1), which are overthrust by Albian siliciclastic rocks (Garrote et al., 1986), that emerged during the Alpine orogeny between the Late Cretaceous and Miocene (García-Mondéjar et al., 1985). These rocks were subsequently excavated by river incision, which occurred in a changing manner, alternating between phreatic stability phases and incisive phases, creating cave levels and terraces along its course (Aranburu et al., 2015; del Val et al., 2019).

On the ceiling and the wall of the cave passages roof pendant morphologies, ceiling channels, and horizontal notches can be identified, indicating the cave's formation through paragenesis processes and revealing the presence of at least one cave level (Farrant and Smart, 2011). Inside, most of the surface consists of fine detrital sediment arranged relatively horizontally, with several areas showing collapse features in the form of several-meter-wide sinkholes (Fig. Sup. 2), functioning similarly to dropout dolines (Waltham et al., 2005). Some of the cave lateral conduits are sealed by debris cones, consisting of limestone blocks, decimeter- and centimeter-sized speleothem clast, and finer detrital sediments (Fig. Sup. 2). These debris cone deposits and the upward direction of the ceiling indicate the sealing of cave entrances from the upper surface, located 2-4 meters above the cave's median ceiling.

Lastly, in the electrical resistivity tomography profile conducted on the Baio cave (Fig. 1) (Supplementary text S1), besides detecting the cave itself, a zone with higher resistivity has been detected 7-10 meters below and around 35 meters to the southwest (Fig. Sup. 3), suggesting the existence of a lower cave conduit. Both the sedimentary potential of the cave and the sinkholes at the cave reinforce the presence of a lower cave level. All of this indicates that what is currently observed is likely a small part of a complex multi-level cave system. In this regard, it should be noted that approximately 50 meters north to Baio the Amabiturrieta cave is located (Fig. 1), which displays four cave levels. The Baio cave would correspond in elevation to the third level of the Amabiturrieta cave, and the lower cavity through electrical tomography would coincide with the second cave level. While both multi-level cave systems are likely genetically distinct, based on their levels, they would reflect a common evolution based on the lowering of the water table marked by the Urola River.

3. Material and methods

3.1. Material

In this study, all the faunal remains (NR = 277) retrieved from the surface of the Baio Cave have been examined. The collection consists of fossil remains that were retrieved by the Antxieta Arkeologi Taldea in the 1990s scattered throughout the cave (labelled as “Sup” and “Ext”) and an additional small collection recovered by us in 2021 (Table 1). Currently, the collection recovered in the 1990s is housed at the Gordailua Bildumen Zentroa (Irún, Gipuzkoa) and the remains recovered in 2021 are temporarily housed at the University of the Basque Country (UPV/EHU; Leioa, Biscay).

3.2. *Palaeobiological analysis*

The taxonomic assessment utilized both contemporary and fossil samples from various research centers, complemented by osteological atlases and specialized literature (e.g. Arceredillo, 2016; Castaños, 2014). The metric analysis of ungulates adhered to the standards established by Von den Driesch (1976) and Arceredillo (2016). For rhinoceros, the guidelines outlined by van der Made (2010) were followed. The taxonomic assessment of the bear remains was accomplished following Torres Pérez Hidalgo (1988) and using both modern and fossil samples from the Iberian Peninsula. The identification criteria and the metrics considered during small-mammal analysis were based on Chaline (1972) and Nadachowski (1982).

3.3. *Bone surface analysis*

A comprehensive taphonomic analysis was conducted on 228 of the total of 277 remains from Baio Cave, encompassing dentition as well. The focus of the dentition examination was limited to the following attributes: manganese oxides staining, calcium carbonate precipitates (crusts), and dissolution domes.

The remains were observed at both macro and microscopic levels, and detailed photographs were taken using a binocular loupe, a DINO-LITE AM-TFVW-A microscope with Dino-Capture 2.0 software, and an Olympus OM-D camera equipped with an OLYMPUS M.ZUIKO macro lens.

3.3.1 Biological modifications and physical-chemical alterations

Several agents, including plants, carnivores, humans, rodents, fungi, or bacteria can cause biologically induced modifications of bone surfaces (Lyman, 1994). For this reason, this assemblage has been analyzed to document the presence or absence of such alterations. Plant roots and acid-secreting fungi resulting from plant decomposition have the capability to dissolve bone surfaces as well. This process manifests as distinctive shallow dendritic groove patterns, grooves with smoothed bottoms, and sinuous trajectories (Andrews and Cook, 1985; Lyman, 1994 and references therein).

Carnivores and humans are the main accumulators of macromammal bone remains in caves. Stone tool marks have been classified as slicing marks, saw marks, scraping marks and chop-marks. To assess the involvement of carnivores in this assemblage, a detailed analysis of the bone surfaces has been undertaken, with particular emphasis on tooth marks and perimortem fracturing. To investigate the prevalence of carnivores within the Baio cave collection, a classification system for tooth marks, comprising pits, punctures, furrowing, and scores, was employed (Haynes, 1980; Binford, 1981). The measurements (length and width) of both pits and punctures were taken utilizing the functionalities of the DINO-LITE digital microscope, following the criteria established in previous studies (Domínguez-Rodrigo and Piqueras, 2003).

Other distinct alterations produced by carnivores involve the partial dissolution of bones caused by gastric acids produced during the consumption of bone fragments, followed

by their subsequent expulsion through feces or regurgitation. Bones affected by this acid-etching process exhibit specific features, including scalloping of the bone surface, the presence of holes, and/or fine and sharp edges (Sutcliffe, 1970).

The analysis of various physicochemical modifications observed on bone surfaces has been categorized based on their presence or absence. In endokarst contexts, bone accumulations typically exhibit the precipitation of manganese oxides and calcium carbonate crusts on the bones (White and Culver, 2012). Trampling events lead to the formation of linear marks or sinuous scratches, due to the sediment abrasion on bone surfaces, that can resemble cut marks. The assessment of such alterations has been conducted following the criteria established by Domínguez Rodrigo et al. (2009). Another distinctive type of alteration found in endokarst environments is the dissolution of bone surfaces, characterized by dome-shaped morphologies resulting from soil acidity (Sala et al., 2023). Finally, the presence or absence of weathering has been documented in the bones according to the criteria of Behrensmeyer (1978).

3.3.2. Fracture patterns

This study has prioritized the analysis of fractures in long bones because they are the most informative remains for interpreting the timing of fracturing: fresh bone that still preserved soft tissues and/or collagen (perimortem) or on dry bone devoid of collagen preservation (postmortem). The following aspects were assessed: (a) Fracture outline, indicating the alignment of the fracture concerning the long axis of the bone, identified as longitudinal, transverse, or oblique/curved; (b) Fracture angle, representing the angle formed between the fracture surface and the cortical surface of the bone, categorized as either right or oblique; (c) Fracture edge, referring to the texture of the fracture surfaces, classified as either smooth or jagged; (d) Length of the diaphysis fragment, with four groups: (1) less than $\frac{1}{4}$ of

the total diaphysis, (2) between $\frac{1}{4}$ and $\frac{1}{2}$ of the total diaphysis, (3) between $\frac{1}{2}$ and $\frac{3}{4}$ of the diaphysis, (4) greater than $\frac{3}{4}$ of the diaphysis; (e) Circumference of the diaphysis, estimating the preservation of the long bone diaphysis circumference, with three categories: (1) less than half of the circumference, (2) more than half of the circumference, and (3) full circumference, found in at least a portion of the bone diaphysis. Fresh-bone fractures exhibit distinctive features, such as curved or spiral outlines, oblique angles of the fracture plane, and smooth edges (Villa and Mahieu, 1991).

The presence or absence of peeling has been considered in this study. Peeling is defined as a rough surface with parallel grooves or a fibrous texture, which is produced by breaking bones either by bending them with hands or chewing the bones and bending them with hands (White, 1992; Pickering et al., 2013). Carnivores such as lions, bears, and hyenas may occasionally engage in this type of modification, although it is prevalent during carcass consumption activities among primates and humans (Arilla et al., 2014 and references therein).

3.4. Direct dating

Collagen extraction for obtaining direct radiocarbon dating via AMS ultrafiltration was conducted on a *Rangifer tarandus* left metatarsal (#600+601) and on a *Cervus elaphus* right tibial fragment (Baio.2021.Sup.6) at Beta Analytic. We also sampled a rhinoceros femur fragment recovered in 2021 (label: Baio.2021.Sup.1) but the sample did not preserve collagen. The obtained dates were calibrated using the OxCal v.4.4 software (Bronk Ramsey, 2009) and the IntCal20 calibration curve (Reimer et al., 2020).

4. Results

4.1. Systematic paleontology

268 A total of 277 remains have been identified, belonging to a total of 5 orders and 11
 269 families (Table 1).
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 271 Order Perissodactyla Owen, 1848
 272 Family Equidae Gray, 1821
 273 Genus *Equus* Linnaeus, 1758
 274 *Equus ferus* Boddaert, 1785
 275 **Remarks:** Four remains have been identified, corresponding to a minimum of one individual.
 276 These include a lower molar, a fragment of a molariform (Table S1), an axis vertebra, and a
 277 proximal phalanx, which is entirely encased in a calcium carbonate crust. As a result, it has
 278 not been feasible to obtain measurements or conduct a more detailed identification (Fig. 2).
 279
 280 Family Rhinocerotidae Gray, 1821
 281 **Rmarks:** Three remains corresponding to this taxon have been identified: two cervical
 282 vertebrae (probably a C5 (#595) and a C6 (#596) and a femur diaphysis
 283 (#603+604+Baio.2021.Sup.1+2+3; Fig. 5). The measurements of the cervical vertebrae are
 284 shown in Table S2.
 285
 286 Order Artiodactyla Owen, 1848
 287 Family Cervidae Goldfuss, 1820
 288 Genus *Rangifer* Smith, 1827
 289 *Rangifer tarandus* (Linnaeus, 1758)
 290 **Remarks:** Four remains found in the Baio cave surface assemblage have been identified as
 291 belonging to a single adult reindeer individual. These remains include an almost complete

lumbar vertebra (#620), a distal fragment of a left metatarsal (#600+601), an intermediate phalanx (#606), and a distal lateral phalanx (#607) (Fig. 2).

The measured dimensions of the distal epiphysis of metatarsal #600+601 and the intermediate phalanx #606 are similar to those found in other Iberian sites such as Kiputz IX, and other fossil European assemblages (Table S3, S4).

Genus *Cervus* Linnaeus, 1758

Cervus elaphus Linnaeus, 1758

Remarks: A total of 13 remains belonging to *Cervus elaphus* have been identified. Six of these have been attributed to an adult individual, including a remarkably complete deer antler (#1647), a distal fragment of a left humerus (#3067), two fragments of tibia diaphysis (#2977 -indeterminate side-, and Baio.2021.Sup.6, from the left side), a fragment of the posterior section of the diaphysis of a left metatarsal that still preserves a portion of the proximal epiphysis (#2983+2984+2985+2986), and a complete intermediate phalanx (#2974). Three of the remains associated with this species, comprising a fragment of the calcaneus tubercle (Baio.2021.Sup.5) and two phalanges with unfused epiphyses (#2973 and #2975), are indicative of an immature individual. Four other fragmented remains could not be definitively attributed to any of these individuals: an antler fragment (#2979), two fragments of metapod diaphysis (#2981 and #2982), and a fragment of calcaneus (#2976) (Fig. 2). Only a phalanx #2974 was complete enough to be compared metrically, and its maximum length and width closely align with those recorded at the nearby site of Kiputz IX (Table S5).

Family Bovidae Gray, 1821

Genus *Capra* Linnaeus, 1758

Capra pyrenaica Schinz, 1838

317 **Remarks:** Two remains have been assigned to *Capra pyrenaica* representing an adult
318 individual: a left innominate bone fragment preserving the acetabulum (#3016) and a right
319 metacarpal, which lacks the distal epiphysis(#3068) (Fig. 2). The measurements obtained
320 from the proximal epiphysis of metacarpal #3068 closely resembles those documented in
321 other Iberian sites (Table S6).

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323 Genus *Rupicapra* Blainville, 1816

324 *Rupicapra pyrenaica* (Bonaparte, 1845)

325 **Remarks:** Four chamois remains have been identified, indicating the presence of at least one
326 adult individual. These include a fragment of a right maxilla with the P4-M3 series (#630 +
327 #631), a fragment of a right mandibular condyle (#3064), a fragment of a right distal radius
328 (#3062), and a complete left talus (#3063) (Fig. 2; see Tables S7 to 12 for the metric data).

329

330 Genera *Bos* Linnaeus, 1758 or *Bison* Hamilton Smith, 1827

331 *Bos primigenius* Bojanus, 1825 or *Bison priscus* Bojanus, 1825

332 **Remarks:** Six fragmentary remains have been classified as large bovid (either *Bos*
333 *primigenius* or *Bison priscus*). Two individuals are represented: an adult by a left patella
334 (#3036) and two tibial distal fragments from the right (#3037) and the left (#3039) sides, and
335 a juvenile individual by a right incomplete scapula (#3040) and a nearly complete tibia with
336 unfused epiphyses (#3041). The sixth remain correspond to a distal diaphyseal fragment of a
337 humerus that was not ascribed to any of these individuals.

338

339 Order Carnivora Bowdich, 1821

340 Family Hyaenidae Gray, 1821

341 Genus *Crocota* Kaup, 1828

342 *Crocota spelaea* Goldfuss, 1823

343 **Remarks:** Two hyena remains, a left upper canine (#611) and a left fifth metatarsal (#609),
344 have been identified as belonging to *Crocota spelaea*, representing at least one adult
345 individual (Fig. 3). The maximum length and width measurements of the upper canine from
346 Baio fit within the variation found in the late Middle and Late Pleistocene sites from the
347 Iberian Peninsula (Tables S13-S14). The metric values of the metatarsal are at the upper end
348 or exceed those recorded for specimens from our Iberian sample but fall within the ranges
349 observed for a Marine Isotope Stage 3 sample from Austria (Tables S15 and S16).

350

351 Family Canidae Fischer von Waldheim, 1817

352 Genus *Canis* Linnaeus, 1758

353 *Canis lupus* Linnaeus, 1758

354 **Remarks:** A complete upper left canine corresponding to an adult individual (#594) has been
355 identified (Fig. 3). The measured dimensions of this tooth are slightly larger than those from a
356 present-day wolf sample (Table S17).

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358 Genus *Vulpes* Frisch, 1775

359 *Vulpes vulpes* (Linnaeus, 1758)

360 **Remarks:** 27 bone labeled remains have been identified belonging to this species
361 corresponding to a minimum of 3 adult individuals based on the presence of 3 right
362 hemimandibles (#746-749, #751-753, #754-757) (Fig. 3 and Tables S18 and S19).

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364 Family Ursidae Fischer von Waldheim, 1817

365 Genus *Ursus* Linnaeus, 1758

366 *Ursus* sp.

Remarks: The Baio surface ursid assemblage comprises nine remains, representing a minimum of two individuals. Five specimens have been identified as *Ursus* sp.: two dental remains belonging to a juvenile individual (a fragmentary M2, #285 and a canine #286) and three postcranial remains not associated to any of the two identified individuals: a partial cervical vertebra, and two partial to nearly complete thoracic vertebrae (#597+598+599 and #3023).

Ursus arctos Linnaeus, 1758

Remarks: Four bear remains are attributed to a single *Ursus arctos* adult individual: a right radius (#592), a right ulna (#593) (Fig. 4), a fragmentary right talus (#291) and a distal phalanx (#287) (Supplementary Text S2). Metrically, the radius, the ulna and the distal phalanx fit well within *U. arctos* variation. The radius and ulna are relatively narrow and gracile, while *U. spelaeus* bones are relatively wider and more robust. The distal phalanx is shorter in length and relatively low in height compared to the *U. spelaeus* comparative sample (Fig. S4; Tables S20-S22).

Family Felidae Fischer, 1817

Genus *Felis* Linnaeus, 1758

Felis silvestris Schreber, 1777

Remarks: Five wild cat remains, representing at least one adult individual, have been identified. These include a right maxilla, preserving C1, P2, P3, and P4 (Table S23); two hemimandibles: the right one (#3086), where only the corpus has been preserved without the dentition, and a left one (#3087), which lacks the incisors and the mandibular ramus (Fig. 3). Additionally, there is an axis fragment preserving the vertebral body and the odontoid process, and a femoral head.

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Order Rodentia Bowdich, 1821

Family Sciuridae Fischer von Waldheim, 1817

Genus *Marmota* Blumenbach, 1779

Marmota marmota Linnaeus, 1758

Remarks: The marmot collection consists of five elements, namely an occipital fragment (#646), an intact petrous bone (#644), a complete right hemimandible (#642), a right humerus missing its distal epiphysis (#645), and a proximal fragment of a right ulna (#643) (Fig. S5 and Table S24).

Family Cricetidae Fischer, 1817

Genus *Arvicola* Lacépède, 1799

Arvicola amphibius Linnaeus, 1758

Remarks: Two hemimandibles (labels: Baio.2021.Sup.12 -left- and Baio.2021.Sup.13 -right-) were recovered from the surface of the cave in 2021 and could correspond to the same individual (Fig. S5 and Table S25).

Arvicola sapidus Miller, 1908

Remarks: A single left *Arvicola sapidus* hemimandible (#638) has been identified (Fig. S5 and Table S25).

Order Lagomorpha Brandt, 1855

Family Leporidae Fischer, 1817

Leporidae indet.

Remarks: Two remains corresponding to an indeterminate leporid are represented by a sacral bone (#3061; Fig. S5) and a left tibia (#3060) probably belonging to the same adult individual.

4.2. Taphonomic analysis

4.2.1. Bone surface modifications

The bones exhibit excellent preservation, with a small percentage of recent fractures (4.3%), easily distinguishable due to their distinct coloration and texture compared to intact bone surfaces. Particularly noteworthy are the typical alterations observed in endokarst environments, such as the precipitation of manganese oxides, corrosion of bone surfaces, and the formation of calcium carbonate concretions. No alterations suggestive of subaerial exposure processes (weathering) have been observed, but evidence of anthropic activity and signs of slight rounding of some bones has been documented. In a minimal proportion of the remains, there are marks of abrasion caused by dragging in the sediment (or trampling) and bone surface dissolution due to root activity (Table 2).

Regarding anthropic alterations, a group of four parallel linear marks has been identified on the cortical surface of an unidentified long bone shaft fragment from a medium-sized ungulate and present characteristics described by other authors for cut marks (Domínguez-Rodrigo et al., 2009). All marks follow a straight trajectory. V-shaped marks have been observed in, at least, two of them, while the rest display wider grooves (Fig. 5). Microstriations are evident along the path of these grooves and at least one of them shows shoulder effect and flaking of the shoulder, being consistent with possible slicing marks.

Notably, we did not identify any anthropic percussion marks, despite the presence of a fragment (the right tibia of a deer Baio.2021.Sup.6) exhibiting perimortem cone fractures. However, it remains challenging to discern whether these fractures were caused by human

activity or resulted from carnivore consumption. Additionally, no traces of bone combustion have been observed, suggesting no evidence of possible anthropic exploitation of the carcasses through the use of fire.

Carnivore activity marks were identified in 53 cases (23.2% of the studied sample). These tooth marks primarily consist of pits, scores, and furrowing (Fig. 5, Table S26). These pits and scores, along with evidence of furrowing, are usually found in the long bone diaphysis (Table S26). No punctures have been observed in the cancellous bone, but they are present in the cortical bone in both cranial and postcranial remains. Lastly, at least one specimen shows signs of corrosion resulting from the action of gastric acids (Fig. 5).

4.2.2. Fracture patterns

195 of the analyzed remains (85.5% of the analyzed sample) showed fractures. Remains with evidence of recent fracturing ($n = 11$; 4.3% of the sample) were excluded from the analysis.

In terms of fracture properties, oblique fractures were the most common, accounting for 44.5% of the cases, followed closely by transverse fractures at 31.8%. 51.8% of the fractures displayed oblique, while 36.3% had right angles (close to 90°), and 12.7% had both right and acute angles. When examining the texture of the fracture edges, rough edges were prevalent (70.9%).

Finally, both complete circumferences and those in which only $1/4$ of the diaphysis circumference are amongst the most common. Fracturing in long bones was found to be significant, with a predominance of fragments representing only $1/4$ of the diaphysis portion. Right angles are characteristic of fractures that occur during the fossilization phase in already mineralized bones, along with the rough texture of the fracture edges and the presence of complete circumferences in the diaphyses (Villa and Mahieu, 1991).

In summary, the Baio collection is characterized by bone surface modifications typical from karstic systems (i.e. manganese oxide staining and carbonate precipitation in the form of crusts) and the absence of weathering suggests that bones did not suffer subaerial exposure during the biostratigraphic phase. Modifications by carnivores include pits and scores on the cortical surfaces of the diaphysis of long bones, although they are not as numerous as in the dens of large carnivores such as hyenas. Fracturing in long bones is high and a large part of these fractures show typical characteristics of fracturing during the fossil diagenetic phase (i.e. right angles and irregular surfaces). The presence of anthropic modifications is anecdotal. In the case of the cold-adapted species, no signs of cut or percussion marks nor modifications by carnivores have been observed.

4.3. Radiocarbon dating

Two direct AMS ultrafiltration radiocarbon datings, from the left *Rangifer tarandus* metatarsal (#600+601) and the right *Cervus elaphus* tibia (Baio.2021.Sup.6) yielded ages of $38,370 \pm 430$ uncal. a BP ($42,765-42,067$ 2σ cal. a BP) for the reindeer and $30,020 \pm 180$ uncal. a BP ($34,786-34,136$ 2σ cal. a BP) for the red deer (Table 3). The isotopic values for both the reindeer and red deer samples are similar to those from other Basque sites as Kiputz IX (Castaños., 2014).

5. Discussion

5.1 Taphonomic inferences

The paleontological assemblage recovered on the surface of the Baio cave is taxonomically diverse, despite its restricted size, exhibiting faunas typical of the MIS 3 in the area and consistent with the ecotone diversity surrounding the cave. This assemblage includes herbivores from open environments, such as horses, rhinoceros and reindeer, from mountain

habitats like capra and chamois, as well as others that can inhabit diverse habitats, such as red deer and large bovids. Carnivores account for the 23.8% with the presence of hyaenids, felids and canids. Finally, it was recovered a small sample of rodents, including marmot and two species of genus *Arvicola*.

The analysis of bone surfaces and fracture patterns has made it possible to elucidate different modifying agents of the bone remains that can provide information on the formation processes of the analyzed assemblage. However, we must take into account the limitations derived from the fact that the association of analyzed elements does not correspond to an *in situ* stratigraphic level, but rather to materials recovered from the surface of the cave. In addition, we do not know the precise location of the recovered elements and the possible active entrances to the karst system at the time of the accumulation of bone remains.

However, we can observe that the association as a whole shares the traces of bone modification produced in the fossilization phase, that is, those modifications typical of endokarst environments such as: absence of signs of weathering implying subaerial exposure and the presence of manganese oxide patinas, carbonate crusts, and some bone dissolution. This indicates that the skeletal remains have been accumulated inside the karst system in a biostratigraphic phase and that they have shared postdepositional conditions.

Regarding biostratigraphic processes, we can observe a variety of modifications that can provide us with information about the origin or origins of accumulation of the different elements. The surface taphonomic analysis suggests the intervention of both carnivores, and, to a minimum extent, of humans. Tooth marks have been documented in 23.2% of the sample, especially in the remains of ungulates. This suggests an intervention of carnivores, perhaps related to the accumulation of some bone elements. However, the percentage of carnivore-induced marks is relatively low compared to sites in which carnivores are the main accumulation agent, such as Iberian hyena den sites, such as Portalón del Tejadilla (37.4%).

Additionally, the absence of hyena juveniles and coprolites suggests that this taxon was not the main accumulation agent (Sala et al., 2020 for a review). In any case, the percentage of carnivore intervention is notably higher than in other contexts interpreted as natural traps, such as Mainea (11.6%; Rodríguez-Almagro et al., 2021). 29.1% of the analyzed fractures occurred in fresh bone but no evidence suggesting fractures of anthropogenic origin has been observed, with only one specimen in the entire collection exhibiting cut marks. This scarcity of anthropogenic evidence, coupled with the absence of lithic industry and burned bones, leads us to rule out humans as the primary contributors to the fossil accumulation at Baio. Finally, it cannot be ruled out that the cave may have acted as a natural trap, or some animals, such as bears, could have died naturally when using the cave as a shelter.

Taphonomic inferences could indicate that we are dealing with a heterogeneous assemblage, probably the product of different taphonomic processes and agents over time. This observation is compatible with the results of the direct dating which indicates that the surface collection of this cave corresponds to a diachronic accumulation over several millennia (see below). In this sense, additional geochronological data and the ongoing systematic excavation at the entrance of the cave could provide additional insights on the accumulation dynamics of the fossil assemblage recovered on the surface of the cave.

5.2 Chronological framework and cold-adapted taxa of the Baio cave surface assemblage in the regional context

The number of direct dating of reindeer remains in the Iberian peninsula is still very restricted. To our knowledge, C14 direct dating of reindeer remains is restricted to Kiputz IX, Arlanpe, Atxuri and Santa Catalina (Gómez-Olivencia et al., 2014 and references therein). However, the date of Santa Catalina, which suggests a late survival of this species in the eastern Cantabrian region is not consistent with the extinction of this species in south-western

France (Costamagno et al., 2016). In the rest of the cases, the obtained dates are within the regional chronological range of the Upper Paleolithic in the region. In most cases, the chronological framework of the reindeer remains comes from the combination of direct dating obtained from other faunal elements of their level and/or the techno-typological analysis of archaeological material (see Gómez-Olivencia et al., 2014 and references therein). However, there are some other paleontological sites, in the Gipuzkoa province (e.g., Aitz-gaizto II, Urtiagako leizea) that despite having interesting faunal assemblages, including cold adapted faunas, do not have a established chronological framework. The case of Urtiagako leizea is especially interesting as it has yielded the third largest reindeer assemblage (NISP = 96; 28.5% of the assemblage) from the Iberian peninsula, and a mammoth remain (Altuna and Mariezkurrena, 2010).

The age obtained from the Baio reindeer remain (42,765-42,067 a cal BP) fits perfectly in the time range of the Châtelperronian (43.7-39.2 ka cal BP) (Rios-Garaizar et al., 2022). It is slightly younger than other Châtelperronian contexts such as the open air site of Aranbaltza II (Barrika) (ca. 43.5 ka BP), slightly older than Labeko Koba (Arrasate) (43.8-40.9 ka BP) (Wood et al., 2014) which also has yielded reindeer remains (Altuna and Mariezkurrena, 2000), and older than Ekain Xa (Deba) (40.7-37.7 ka BP). The Châtelperronian technological complex in the Northern Iberian Peninsula has been interpreted as a population replacement of previous Neandertal populations, with Middle Paleolithic technology, by other Neandertal groups, coming from Southwestern France (Rios-Garaizar et al., 2022). In the region there is a time gap of at least 1 kyr between these two populations, meaning that the region was probably unoccupied during this time (Marín-Arroyo et al., 2018). Diverse causes for the Neandertal depopulation previous to the Châtelperronian in this region have been explored but certainly climate deterioration played an important role as has been evidenced by various climatic proxies (Rodríguez-Almagro et al., 2021; Sánchez-Goñi et

al., 2008; Jones et al., 2018). Even more, during the Châtelperronian, the current evidence suggests a very low density population with sites acting as ephemeral hunting camps and others functioning as workshops for the manufacture of flint tools (Rios-Garaizar et al., 2022).

The age obtained for the red deer remain (34,786-34,136 ka cal BP) corresponds with a time period when anatomically modern humans were well established in the region. Similar ages have been obtained for the Late Aurignacian occupations from Ekain-level IXb (36.2-33.7 ka cal BP) and Aitzbitarte III-Vb (36.1-34.9 ka cal BP) (Marín-Arroyo et al., 2018), among others.

The hyaena remain would also be consistent with the direct C14 dates obtained in Baio, as this taxon disappeared in Western Europe c. 31 ka cal BP (Stuart and Lister, 2014). Unfortunately, the rhinoceros femur has not yielded collagen to be dated. Little is known regarding the potential differences between the femur and cervical vertebrae of *Stephanorhinus hemitoechus* and *Coelodonta antiquitatis* and therefore these remains in Baio have been classified as Rhinocerotidae indet. The extinction chronology for these species has been suggested to be 45 ka cal BP and 14 ka cal BP, respectively (Stuart and Lister, 2012). In the Eastern Cantabrian region, the *Coelodonta antiquitatis* fossil record is more abundant than the *Stephanorhinus hemitoechus* record and is present in different Upper Paleolithic contexts (e.g., Legintxiki, Abauntz, Labeko Koba, Lezetxiki), while the *Stephanorhinus hemitoechus* fossil record is more scarce and is present in early Upper Paleolithic and older (i.e., Middle Palaeolithic) contexts (Rodríguez-Almagro et al., 2021 and references therein). New findings of rhinoceroses preserving the anatomical regions missing in Baio could aid in the taxonomic determination of these remains.

The rest of the faunal remains can be usually found in Late Pleistocene assemblages of the region. However, we should mention that the brown bear remains are usually more scarce in Pleistocene contexts, when compared to cave bear remains (Villaluenga, 2009). Finally,

while the number of equid remains (and of the whole collection) is restricted in Baio, it is worth mentioning that, in this area, the presence of *Equus ferus* is, in proportion, more abundant in Châtelperronian and older chronologies of the Upper Paleolithic (e.g., Labeko Koba) than in more recent MIS3-2 chronologies (e.g., Kiputz IX; Castaños, 2014).

In summary, the paleontological assemblage recovered at the surface of the Baio cave helps us to understand the paleoecology of the last Neandertals and the first anatomically modern humans that inhabited the region.

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Table and Figure captions

Table 1. Composition of the Baio faunal assemblage by number of specimens (NISP), minimal number of elements (MNE) and minimal number of individuals (MNI).

Table 2. Frequency of alterations of bone surfaces.

Table 3. Dates and isotopic values from two ungulate remains from Baio.

Figure 1. A) Location of Baio (red star) and selected Paleolithic sites with human remains in the eastern Cantabrian Region and southwestern France. B) Geological setting of the Baio cave and the nearby Amabiturrieta multi-level cave system. C) Baio cave entrance. 1: Rascaño; 2: La Chora; 3: Mirón; 4: Arrillor; 5: Axlór; 6: Lezetxiki; 7: Santa Catalina; 8: Labeko koba; 9: Ekain; 10: Baio; 11: Erralla; 12: Aitzbitarte III. Base map in A made with QGIS 2.18.17 (QGIS Development Team 2009) with data by Jarvis et al. (2008).

Figure 2. Selected herbivore remains from Baio cave surface assemblage. From left to right and from up to bottom: *Cervus elaphus*: an almost complete antler (#1647); intermediate phalanx (#2974); fragment of metapodial preserving proximal epiphysis and diaphysis (#2981). *Rangifer tarandus*: left metatarsal preserving part of the diaphysis and distal articulation (#600+#601); intermediate phalanx (#606). *Capra pyrenaica*: left innominate bone (#3016); right metacarpal lacking distal articulation (#3068). Rhinocerotidae indet.: femoral diaphysis (#603+604+Baio.2021.Sup.1+2+3); almost complete cervical vertebrae (#595 and #596). *Rupicapra rupicapra*: distal half of a right radius (#3062); right

820 maxilla preserving P4-M3 (#630+#631); eroded but complete left talus (#3063). *Equus ferus*:
821 right lower molariform (#628). *Bos primigenius/Bison priscus*.: right tibia distal fragment
822 (#3037).

823

824 **Figure 3.** Selected carnivore remains from Baio cave surface assemblage. From left to right:
825 *Crocota spelaea*: left upper canine (#611); complete 5th left metatarsal (#609). *Canis lupus*:
826 complete left upper canine (#594). *Felis silvestris*: right maxilla fragment preserving C1, P2-
827 P4 (#3088); left hemimandible (#3087). Fox remains: from up to bottom: almost complete
828 right hemimandible preserving p1 and p3-m3 (#746+747+748+749); right hemimandible with
829 c1 and p1-m3 (#754+755+756); right hemimandible with m1 and corpus fragment with p2,
830 probably from the same individual (#751+752 and #753); almost complete cranium in left
831 lateral and inferior views with P1, P2 and P4-M2 on the left side and P3-M2 on the right side
832 (#763).

833

834 **Figure 4:** Selected ursid remains from Baio cave surface assemblage. *Ursus arctos*: right
835 radius (#592) and right ulna (#593) in anterior and posterior views. *Ursus sp.*: partial right M2
836 from a juvenile individual in occlusal view (#285); partial canine from a juvenile individual in
837 labial and lingual views (#286).

838

839 **Figure 5.** Fossil remains from Baio cave surface with taphonomic modifications. #3035:
840 detailed depression in the femur diaphysis of a large size ungulate; #3069: evidence of
841 corrosion caused by gastric acids in a small size ungulate ulna; #3016: pits and furrowing on a
842 *Capra pyrenaica* innominate bone; #2987: group of slicing marks observed on a diaphysis
843 fragment of an unidentified long bone from a medium-sized ungulate.

844

Supplementary information

Supplementary Text S1. Electric Resistivity Tomography

Supplementary Text S2. Morphological features of the *Ursus arctos* remains.

Figure S1. Baio cave's topographic survey.

Figure S2. a) The current entrance appears to have clear signs of recession due to erosion caused by the slope; b) One of the debris cone mainly composed of limestone blocks and speleothems; c) Another debris cone made up of finer sediments, with one of the collapses of the soil on the side; d) A small passage with a collapsed floor.

Figure S3. a) The equipment used during the geophysical survey; b) electrode configuration; c) BAIO-2 profile.

Figure S4. Bivariate scatter plot of selected measurements of *Ursus arctos* radius #592, ulna #593 and distal phalanx #287 from Baio Superficie (red triangle) compared to recent *U. arctos* (grey circle) and *U. spelaeus* (black square). Variables measured taken from Tsoukala and Grandal d'Anglade (2002). Bone illustration taken from García-Vázquez (2015). X and Y from the bone illustration makes reference to X axis and Y axis respectively. All statistical analyses and graphical representations were executed using R (R Core Team 2020).

Figure S5. Selected cranio-dental material of the order Rodentia from Baio A: right mandible (#642) of *Marmota marmota* in lingual (top) and occlusal (bottom) views; B: *Arvicola sapidus* left m1(#638) in occlusal view; C: *Arvicola amphibius* left m1 in occlusal view (Baio.2021.Sup.12); D: sacrum of Leporidae indet (#3061) in cranial (top) and ventral (bottom) views.

Supplementary Table S1. Measurements (in mm) of the *Equus ferus* right lower molariform from Baio site.

Supplementary Table S2. Measurements (in mm) of the rhinoceros cervical vertebrae from Baio.

Supplementary Table S3. Measurements (in mm) of the left metatarsal of *Rangifer tarandus* (RT) from Baio (#600+601) compared to other European actual and fossil samples/individuals.

Supplementary Table S4. Measurements (in mm) of the intermediate phalanx of *Rangifer tarandus* from Baio (#606) compared to other European actual and fossil samples/individuals.

Supplementary Table S5. Measurements (in mm) of the intermediate phalanx of *Cervus elaphus* from Baio (#2974) compared to other Iberian samples.

Values between () indicate estimated values.

893 **Supplementary Table S6.** Measurements (in mm) of the metacarpal of *Capra pyrenaica*
894 from Baio (#3068) compared to other Iberian samples/individuals.
895
896 **Supplementary Table S7.** Measurements (in mm) of the upper P4 of *Rupicapra pyrenaica*
897 from Baio.
898
899 **Supplementary Table S8.** Measurements (in mm) of the upper M1 of *Rupicapra pyrenaica*
900 from Baio compared to other Iberian samples/individuals.
901
902 **Supplementary Table S9.** Measurements (in mm) of the upper M2 of *Rupicapra pyrenaica*
903 from Baio compared to other Iberian samples/individuals.
904
905 **Supplementary Table S10.** Measurements (in mm) of the upper M3 of *Rupicapra pyrenaica*
906 from Baio compared to other Iberian samples/individuals.
907
908 **Supplementary Table S11**
909 Measurements (in mm) of the radius of *Rupicapra pyrenaica* from Baio (#3062) compared to
910 other Iberian samples/individuals.
911
912 **Supplementary Table S12.** Measurements (in mm) of the talus of *Rupicapra pyrenaica* from
913 Baio (#3063) compared to other Iberian samples/individuals.
914
915 **Supplementary Table S13.** Measurements (in mm) of the upper canine of *Crocota spelaea*
916 from Baio (#611) compared to an Iberian sample.
917

Supplementary Table S14. Measurements (in mm) of the upper canine of *Crocota spelaea* of the comparative sample used in Supplementary Table S13.

Supplementary Table S15. Measurements (in mm) of the fifth metatarsal of *Crocota spelaea* from Baio (#609) compared to an Iberian and an austrian sample.

Supplementary Table S16

Measurements (in mm) of the fifth metatarsal of *Crocota spelaea* for the comparative sample used in Supplementary Table S15.

Supplementary Table S17. Measurements (in mm) of the upper C1 of *Canis lupus* from Baio compared to a present-day wolf sample.

Supplementary Table S18. Measurements (in mm) for the *Vulpes vulpes* upper dentition of the cranium #763 from Baio in comparison to other Iberian recent and Middle Pleistocene samples and a recent *Vulpes lagopus* sample.

Supplementary Table S19. Measurements (in mm) for the *Vulpes vulpes* lower dentition from Baio in comparison to other Iberian recent and Middle Pleistocene samples and a recent *Vulpes lagopus* sample.

Supplementary Table S20. Selected measurements (in mm) for the *Ursus arctos* radius from Baio Superficie, compared to *Ursus arctos* and *Ursus spelaeus* from the Iberian Peninsula. Variables measured taken from Tsoukala and Grandal d'Anglade (2002)

Supplementary Table S21. Selected measurements (in mm) for the *Ursus arctos* ulna from Baio Superficie, compared to *Ursus arctos* and *Ursus spelaeus* from the Iberian Peninsula. Variables measured taken from Tsoukala and Grandal d'Anglade (2002)

Supplementary Table S22. Selected measurements (in mm) for the *Ursus arctos* distal phalanx from Baio Superficie, compared to *Ursus arctos* and *Ursus spelaeus* from the Iberian Peninsula. Variables measured taken from Tsoukala and Grandal d'Anglade (2002)

Supplementary Table S23. Measurements (in mm) of the right maxilla of *Felis silvestris* from Baio.

Supplementary Table S24. Comparison of *Marmota marmota* measurements (in mm) from the mandible recovered in Baio (this work) with mandibular and dental remains from Koskobilo (Gómez-Olivencia et al., 2021).

Supplementary Table S25. Measurements (in mm) of the lower m1 of *Arvicola sapidus* and lower m1s of *Arvicola amphibius* from Baio.

Supplementary Table S26. Frequency of tooth mark type and location.

Supplementary references.