Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Beavers and marmots in a Neanderthal cave palimpsest: small-prey consumption at Valdegoba Cave (Burgos, Spain)

Ona Redon

onaredon@gmail.com

Universidad de Burgos

J. Carlos Díez

Universidad de Burgos

César Laplana

Universidad de Alcalá (UAH)

Research Article

Keywords: Castor fiber, Marmota marmota, Valdegoba Cave, Neanderthals, small prey, rodent exploitation

Posted Date: October 15th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11319217/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

Abstract

Large rodents occupy a poorly explored gap in Neanderthal subsistence research, between the well-documented exploitation of small ungulates and small-bodied prey such as lagomorphs and tortoises. Here we present a zooarchaeological and taphonomic analysis of an unusually rich large-rodent assemblage from Valdegoba Cave (northern Iberia), a Middle Palaeolithic site associated with Neanderthal occupations during the late Marine Isotope Stage (MIS) 6 – early MIS 5 transition. Far from representing a single accumulation event, the *Castor fiber* (Eurasian beaver) and *Marmota marmota* (alpine marmot) assemblage at Valdegoba reveals a complex palimpsest shaped by carnivore activity, natural mortality, post-depositional processes and occasional Neanderthal exploitation, directly attested by cut marks on both taxa. Most notably, the cut-marked marmot provides rare evidence for Neanderthal exploitation of this taxon and extends the record of marmot processing beyond the better-documented Late Pleistocene examples. These findings broaden the known spectrum of animal resources occasionally exploited by Neanderthals and highlight the importance of disentangling multiple accumulation agents when assessing medium-sized prey.

Highlights

• Valdegoba represents the earliest known site with joint beaver and marmot Neanderthal exploitation.

• Valdegoba fills a poorly explored prey-size gap in Middle Palaeolithic Neanderthal subsistence

• Neanderthals exploited prey beyond their main ungulate resources

• Cut marks on beaver () and marmot () remains record direct evidence of hominin processing

• Large rodents formed a mixed assemblage shaped by several accumulation agents

1. Introduction

Neanderthal meat consumption has traditionally been reconstructed through the exploitation of large ungulates, overlooking the significant contribution of small-bodied prey from a wide range of taxa in Palaeolithic diets. At Bolomor Cave, for instance, rabbits, birds and tortoises were incorporated into the diet, showing that small-prey exploitation long predated the Upper Palaeolithic (Blasco & Fernández Peris 2012). The role of small prey across Neanderthal contexts was highly variable, ranging from occasional exploitation to recurrent procurement (Laroulandie et al. 2022), and archaeological and ethnographic studies show that small body size does not intrinsically imply negligible dietary or economic importance (Yellen 1991; Quintana et al. 2002).

Identifying the hominin exploitation of small prey remains is often archaeologically challenging. Since these carcasses can be processed and consumed with limited or no use of lithic technology, leaving few or no diagnostic bone modifications (Laroulandie et al. 2022; Nabais et al. 2024), their archaeological contribution tends to be underestimated. Nevertheless, small-mammal exploitation is documented

across several Palaeolithic sites. The earliest evidence of micromammal consumption is from hedgehogs at Olduvai Gorge (1.76 Ma, Tanzania) (Fernández-Jalvo et al. 1999), and the earliest micromammal processing comes from Early Pleistocene leporids at Sima del Elefante (Atapuerca, Spain) (Huguet 2007). Similar direct evidence includes exploitation of beavers at Bilzingsleben (Germany) and Caune de l'Arago (France), and marmot exploitation at Grotta del Clusantin and Grotte di Pradis (Italy) (Lebreton et al. 2017; Heinrich & Maul 2020; Nannini et al. 2022).

This study presents new data relevant to understanding Middle Palaeolithic hominin diet breadth during the Marine Isotope Stage (MIS) 6–MIS 5 transition at Valdegoba Cave (Burgos, Spain). Large rodents such as the Eurasian beaver (*Castor fiber*) and the alpine marmot (*Marmota marmota*) occupy an intermediate position between these small-bodied prey and ungulates. Both provide substantially more edible biomass than microfauna and could have been attractive occasional resources, and their pelts may also have been valued. Their remains can also enter caves through carnivore activity, natural mortality, burrowing, fluvial transport or sedimentary reworking, and human consumption may leave only a weak taphonomic signature when processing involves limited dismemberment or focuses on skin and soft-tissue removal. Consequently, the archaeological challenge is not simply to establish whether these animals were available, but to distinguish anthropogenic accumulation from natural processes. Neanderthal exploitation of beavers and marmots has been reported at a few European sites (e.g. Romandini et al. 2018, 2023; Verheijen et al. 2026), such evidence remains scarce, particularly in the Iberian Peninsula.

Valdegoba Cave (Burgos, Spain) provides an appropriate context to examine these processes, as the site has yielded Neanderthal remains (Quam et al. 2001), Mousterian lithic assemblages and a diverse fauna dating to the late MIS 6–early MIS 5 transition (Terradillos-Bernal et al. 2025). Previous zooarchaeological and taphonomic research has documented Neanderthal exploitation of a broad range of animal resources at Valdegoba, including ungulates, particularly chamois, as well as smaller prey such as rabbits and birds (Díez Fernández-Lomana et al. 2014; Rodríguez-Gómez et al. 2022; Alonso-Caño et al. 2025). Within this framework, the aim of this study is to assess through the large-rodent assemblage whether beavers and marmots were accumulated primarily by carnivores, by natural processes, by hominins, or by a combination of these agents.

2. The Valdegoba Cave site

Valdegoba Cave is a small karst cave with Middle Palaeolithic deposits located near Huérmeces, approximately 28 km northwest of Burgos city (42° 32' 36" N, 3° 46' 27" W). It lies at the transition between the southern margin of the Cantabrian Mountains and the northern plateau of the Iberian Peninsula, above a narrow canyon cut by the Úrbel River through Turonian limestones (Fig. 1). The archaeological deposit occupies the central cavity of a three-cavity system, at approximately 930 m a.s.l. and 35 m above the present course of the Úrbel River. Excavations were conducted between 1987 and 1991, and in 2006. The main archaeological deposits occur in Unit D (Levels 4–6), a clastic sequence containing Mousterian lithic artefacts, faunal remains and Neanderthal fossils. Sedimentary

displacement and reworking affected most of the sequence and Test Pit 4 is the only excavated sector preserving an intact deposit (Díez Fernández-Lomana et al., 2014; Terradillos-Bernal & Díez Fernández-Lomana 2018; Terradillos-Bernal et al. 2025). The beaver and marmot remains examined in this study, both come from Levels 4 (including Level 4 inferior), 5 and 6 of Test Pit 4, as well as additional specimens from unassigned or disturbed contexts. The chronology of the site places the Neanderthal-bearing Levels 4 and 5 at approximately 140–120 ka, around the late MIS 6–early MIS 5e transition (Terradillos-Bernal et al. 2025).

The faunal assemblage is dominated by herbivores but also includes a diverse carnivore guild, comprising *Crocuta crocuta*, *Canis lupus*, *Vulpes vulpes*, *Ursus arctos*, *Ursus spelaeus*, *Panthera pardus*, *Felis silvestris*, *Lynx pardinus*, *Meles meles*, *Lutra lutra* and *Martes* sp. (Díez Fernández-Lomana et al. 2014). Previous taphonomic studies of the faunal remains have documented both anthropogenic and carnivore modifications (Díez Fernández-Lomana et al. 2014; Alonso-Caño et al. 2025).

The associated fauna indicates a heterogeneous landscape combining rocky and mountainous areas, deciduous woodland and open habitats (Feranec et al., 2010; Díez Fernández-Lomana et al. 2014; Rodríguez-Gómez et al. 2022; Terradillos-Bernal et al. 2025).

3. Materials and methods

3.1. Sample and taxonomic identification

The analysed sample comprises all specimens attributed to *Castor fiber* and *Marmota marmota* recovered from Valdegoba Cave from all excavation campaigns (1987–2006). Four dental remains of *Hystrix* sp. (NISP = 4; MNI = 2) were also identified and given this limited porcupine sample, the detailed zooarchaeological and taphonomic analyses focus on *C. fiber* and *M. marmota*.

Anatomical identification and laterality were assessed using published reference material specific to each taxon.

For beavers, cranial and dental remains were identified using De Iuliis & Pulerà (2019); Heinrich (1991); Hugueney (1999), and postcranial remains were identified using Fischer (1991). For marmots, cranial and dental morphology and morphometrics were assessed following Estraviz-López et al. (2021); Kalthoff (1999); Radulesco & Kovács (1970); Salari et al. (2025). Postcranial elements were identified using Tomé (1998); Tukša (2019). Taxonomic identifications were further supported through comparison with skeletal and dental reference elements from the University of Alcalá and the CENIEH Comparative Anatomy Osteological Collection (COAC). Taxonomic composition was calculated as NISP (number of identified elements) and percentage of the total NISP. MNI was estimated conservatively from combinations of diagnostic and, where possible, laterality elements.

3.2. Age classification

All teeth with a visible occlusal surface were classified as showing slight, moderate or advanced wear. For *C. fiber*, wear stages were adapted from Heinrich and Maul (2020); for *M. marmota*, they followed the criteria described by Gay (2015).

Age estimates were based on taxon-specific criteria. In *C. fiber*, lower fourth premolars were assigned to the relative age groups of Heinrich and Maul (2020), based on dp4 replacement, p4 eruption and wear, dentine deposition and basal-cavity closure. Postcranial age estimates followed the epiphyseal-fusion calendar of Fandén (2005). Upper incisors preserving a measurable mesiodistal width were also compared with the age-related ranges of Borodina (1970), as reported by Volokh (2021).

For *M. marmota*, age attribution followed the four-stage system of Tomé (1998, 2005), based on eruption and wear of the lower tooth series. Specimens lacking the diagnostic structures required by these methods were left unassigned.

3.3. Mortality profiles

Mortality profiles were represented as age-frequency histograms and ternary diagrams based on the relative abundance of juveniles, prime adults and old adults (Stiner 1990; Discamps & Costamagno 2015).

For *C. fiber*, the age groups of Heinrich and Maul (2020) were combined as follows: groups 0–2, up to approximately 1.5 years, were classified as juveniles; groups 3–4, approximately 1.5–2.5 years, as prime adults; and groups 5–7, older than approximately 2.5 years, as old adults. For *M. marmota*, Tomé's stages 2, 3 and 4 were treated as juvenile, prime adult and old adult, respectively.

Age ranges spanning more than one category were divided equally among the compatible classes, so that each specimen contributed a total weight of one. The zones proposed by Discamps and Costamagno (2015) were used for visual comparison.

3.4. Taphonomic recording

All specimens were examined macroscopically under oblique light for surface modifications. Selected marks were inspected with a Dino-Lite digital microscope and photographed with an Olympus DSX1000 microscope. Structured recording included manganese and ochre staining, cracking, sediment cementation, root etching, exfoliation, rounding or abrasion, digestion, and corrosion/compression alterations. Cut marks were identified and described following standard zooarchaeological criteria (Olsen & Shipman, 1988; Noe-Nygaard, 1989). Selected cut marks were further examined using a JEOL JSM-6460LV scanning electron microscope (SEM) to assess diagnostic microfeatures, including internal microstriations, shoulder effects and Hertzian cones (Andrews & Fernández-Jalvo 2012). Carnivore damage was recorded as the number of pits, scores and punctures, while possible gnawing, trampling and burning were retained in the descriptive observations (Binford 1981; Dominguez-Rodrigo et al. 2019; Shipman et al. 1984).

Tooth marks were identified following Blumenschine et al. (1996) and Fernández-Jalvo and Andrews (2016). Their anatomical position was recorded, and maximum length and width were measured for 22 pits for exploratory comparison with published carnivore datasets (Domínguez-Rodrigo & Piqueras, 2003; Young et al., 2015).

Long-bone fractures were analysed following Villa and Mahieu (1991). Fracture angle, outline and edge were recorded for each fracture surface, whereas preserved shaft circumference and shaft length were recorded once per element.

3.5. Body-mass estimation

Body mass was estimated with the family-specific regression equations for Castoridae and Sciuridae of Freudenthal and Martín-Suárez (2013), applied to the summed mean occlusal lengths of the lower and upper cheek-tooth rows, with m1/m2 and M1/M2 counted twice and P3 excluded, as in the original method. Estimates were back-transformed with the correction factor CF = exp(SEE²/2) (Smith 1993), and the final value is the mean of the lower- and upper-row estimates.

4. Results

4.1. Odontometric variation

The dental measurements obtained are summarised in Table 1. They fall within the metric variability documented for fossil European populations of *C. fiber* and *M. marmota* (Heinrich 1991; Cuenca-Bescós et al. 2017, 2021; Estraviz-López et al. 2021) and are therefore consistent with the morphological identification of the Valdegoba remains. The observed dispersion is compatible with intraspecific variation related to age, dental wear, sex and geographical origin, unequal comparative sample sizes or the uncertain attribution of isolated first and second molars. The odontometric results provide a taxonomic basis for the subsequent taphonomic and zooarchaeological analyses.

Table 1
Dental measurements (mm) of Castor fiber and Marmota marmota from Valdegoba Cave, by dental position.

Taxon	Dental position	n length	Length, mean ± SD (mm)	n width	Width, mean ± SD (mm)
C. fiber	I	11	7.81 ± 0.52	9	8.24 ± 0.56
	i	7	8.14 ± 0.45	4	8.64 ± 0.69
	dp4	1	5.54	1	5.59
	p4	12	10.01 ± 1.49	12	7.94 ± 0.57
	P4	9	8.49 ± 0.83	9	7.92 ± 0.86
	m1/m2	23	8.18 ± 0.87	24	7.66 ± 0.73
	M1/M2	47	7.42 ± 0.88	48	7.39 ± 0.87
	m3	5	7.63 ± 0.75	5	7.17 ± 0.81
	M3	6	6.57 ± 0.36	6	6.59 ± 0.63
M. marmota	I	15	4.70 ± 0.35	14	6.05 ± 0.27
	i	14	4.12 ± 0.30	13	5.87 ± 0.43
	P3	1	3.00	1	2.50
	p4	6	4.97 ± 0.92	7	5.03 ± 0.55
	P4	1	5.31	1	5.32
	m1/m2	14	4.64 ± 0.54	14	4.80 ± 0.74
	M1/M2	13	4.98 ± 0.33	13	5.26 ± 0.45
	m3	3	5.27 ± 0.84	3	5.38 ± 1.11
	M3	10	5.59 ± 0.58	10	5.67 ± 0.18

Counts include isolated teeth and teeth preserved in situ. Upper teeth are indicated by uppercase letters and lower teeth by lowercase letters; “d” denotes deciduous teeth. The M1/M2 and m1/m2 categories combine both molar positions. Length and width refer to occlusal measurements in premolars and molars, and to mesiodistal (MD) and labiolingual (LL) dimensions, respectively, in incisors. SD is the sample standard deviation and is omitted when n = 1.

The *M. marmota* sample shows partial overlap with the comparative dataset compiled by Estraviz-López et al. (2021). Valdegoba marmot measurements fall closer to the variability of Late Pleistocene and recent samples than to the Early Pleistocene specimens. Overlap with recent *M. marmota* is especially evident for M3 and the lower molars, while the single P4 also falls within the observed ranges of both recent *M. marmota* and Parmorari. In contrast, M1, M2 and p4 present greater dispersion. Some of these

specimens overlap with or approach the Late Pleistocene Parmorari sample from the Estraviz-López dataset.

The *C. fiber* measurements show broad overlap with European fossil populations, without a consistent geographical pattern. Among the individual comparative datasets, overlap is most evident with Gruta da Aroeira (Cuenca-Bescós et al. 2021), particularly for p4 and the first and second molars, although Valdegoba shows a wider dispersion and some large comparative M1/M2.

The published values for Bilzingsleben, Süßenborn and Weimar-Ehringsdorf (Heinrich 1991) were compared directly with the mean occlusal length and width of the corresponding dental positions from Valdegoba and showed a particularly close correspondence with Bilzingsleben for P4, M3 and m1/m2. The Valdegoba p4 values on the other hand, were especially close to those reported for Taubach. Other dental positions fall within or close to the ranges reported for several of these comparative populations, including Süßenborn and Weimar-Ehringsdorf. These comparisons show the metric overlap among European beaver populations and do not indicate a consistent chronological or geographical relation.

4.2. Body-mass estimation

Body-mass estimates obtained with the equations of Freudenthal and Martín-Suárez (2013) are approximately 19.7 kg for *C. fiber* and 3.5 kg for *M. marmota*. Each value is the mean of the lower and upper row estimates after the correction factor was applied. For *C. fiber* these are 21.2 kg (lower row) and 18.2 kg (upper row); for *M. marmota* they are 3.2 kg (lower row) and 3.8 kg (upper row). The family-specific equations have standard errors of estimate (SEE, natural-log units) of 0.274 (lower row) and 0.390 (upper row) for Castoridae, and 0.382 and 0.340 for Sciuridae (Freudenthal and Martín-Suárez 2013, Table 3). These correspond to ranges of 15.5–26.8 kg (lower row) and 11.5–25.0 kg (upper row) for *C. fiber*, and 2.0–4.3 kg and 2.6–5.1 kg for *M. marmota*. Approximate 95% prediction intervals are 8.5–48.8 kg and 3.2–90.6 kg for *C. fiber*, and 1.4–6.3 kg and 1.9–7.1 kg for *M. marmota*. The wide Castoridae intervals reflect that these equations are based on only five and four extant species, respectively.

4.3. Taxonomic abundance

C. fiber is the dominant large rodent at Valdegoba, with 171 identified specimens and an MNI of 12. *M. marmota* is less abundant but still well represented, with 60 specimens and an MNI of 9 (Table 2). The relatively high MNI compared with NISP reflects the importance of diagnostic dental and mandibular material.

Table 2
Taxonomic composition of beavers and marmots from Valdegoba Cave.

Taxon	NISP	% NISP [a]	MNI
C. fiber	171	74.0	12
M. marmota	60	26.0	9
Total	231	100.0	21

[a] Percentages are calculated relative to the combined marmot and beaver NISP.

4.4. Skeletal representation

Skeletal representation is summarised in Table 3. Both taxa are dominated by cranial and dental remains, but appendicular elements are much better represented in *C. fiber* (28.1%) than in *M. marmota* (3.3%) which is almost exclusively represented by cranial and dental remains. In *M. marmota*, the postcranial sample is restricted to a left calcaneus and a phalanx of indeterminate laterality. This pronounced skeletal imbalance substantially reduces the number of surfaces available for identifying carnivore and anthropogenic modifications in *M. marmota*.

Table 3
Broad skeletal representation by taxon. Values are NISP (% within taxon).

Taxon	Cranial [a]	Isolated teeth [b]	Appendicular	Axial	Total
C. fiber	121 (70.8)	110 (64.3)	48 (28.1)	2 (1.2)	171
M. marmota	58 (96.7)	43 (71.7)	2 (3.3)	0	60

[a] Cranial includes cranial elements, isolated teeth, indeterminate teeth and tooth germs.

[b] Isolated teeth category includes tooth germs and is integrated in the count of elements of the cranial category and are not added separately to the total.

4.5. Age profiles

Age-at-death estimates for the ternary diagram were available for 75 *C. fiber* elements. Juveniles accounted for 42.4% of the weighted sample, prime adults for 41.8% and old adults for 15.8% (Fig. 2a). Juveniles and prime adults are represented in almost equal proportions, whereas old adults are less frequent. In the ternary diagram, the sample falls within the Juvenile–Prime–Old dominated (JPO) zone. The more detailed age distribution (n = 65, Fig. 2b) shows that individuals younger than one year are uncommon and frequencies increase through the second and third years of life, reaching their highest values in the 2–4 year (35.2%) intervals; older age classes are less represented with specimens older than four years distributed across the 4–6-year (10.3%), 6–8-year (13.4%) and ≥ 8-year (12.4%) categories.

The *M. marmota* ternary diagram is based on 22 age-informative specimens. Old adults are the most frequent category, accounting for 40.9% of the weighted sample, followed by juveniles at 31.8% and prime adults at 27.3% (Fig. 3a). In the ternary diagram, the sample is plotted in the Juvenile–Old–Prime (JOP) zone zone, although no single age category strongly dominates. The more detailed age-of-death distribution (n = 15, Fig. 3b) points to a broadly U-shaped distribution, with higher proportions of juveniles and old adults than prime adults, and is compatible with an attritional mortality profile. 33.3% fall within the 1.5–29-month interval and specimens older than five years form the largest category (60.0%). Individuals aged approximately 3–5 years are rare (6.7%).

The mortality profiles reveal differences between the two taxa. The *C. fiber* sample falls within the JPO zone, with juveniles and prime adults in similar proportions, whereas the *M. marmota* sample is within JOP zone, dominated by juveniles and old adults.

4.6. Fractures and surface modifications

The fracture analysis included 22 *C. fiber* long bones, of which two were complete and 20 preserved 54 fracture surfaces. Oblique angles predominated (63.0%), with curved outlines (46.3%) and smooth edges (63.0%), and 19 out of the 20 fractured bones retained the complete shaft circumference (Fig. 4). This combination is consistent with breakage while the bone was fresh or semi-fresh, although jagged edges were also frequent (37.0%). Jagged edges have traditionally been associated with dry-bone fracture, but fracture-edge morphology alone does not reliably discriminate between fresh- and dry-bone breakage, and the type of force applied (dynamic versus static) may also influence edge morphology (Villa & Mahieu 1991). Jagged fracture margins have also been documented in carnivore-generated assemblages and, when associated with other taphonomic evidence, support an interpretation of carnivore activity (Arilla et al. 2020).

Mandibles and maxillae are the most frequently represented cranial bone elements and show recurrent fracture patterns. *M. marmota* maxillae generally preserve only the tooth row and part of the palatal process. In both taxa, mandibles tend to fracture at the base of the incisor and immediately posterior to the tooth row, whereas the horizontal ramus is usually preserved intact.

Bone surface modifications are summarised in Fig. 5. Manganese staining is the most common modification, affecting 54.4% of the *C. fiber* remains and 71.7% of the *M. marmota* sample. Cracking and corrosion or compression damage are more frequent in *C. fiber* (24.0% and 15.2%, respectively) than in *M. marmota* (8.3% and 3.3%). Ochre staining, sediment cementation and root etching occur at lower frequencies, while exfoliation and rounding or abrasion are rare and were recorded only on *C. fiber*. These differences probably reflect variation in skeletal composition and preservation, particularly the much greater representation of postcranial remains in *C. fiber*, which increases the representation of surfaces susceptible to alterations such as cracking and compression damage, with the complex depositional and reworking history of the cave.

Carnivore damage (Fig. 6) was concentrated on the beaver remains. Tooth marks were recorded on 21 *C. fiber* specimens (12.3%), mainly postcranial elements (as shown in Fig. 6d-e), but on only one *M. marmota* specimen (1.7%). Some of the smaller pits and scores are compatible with modification by small carnivores. The exploratory 22 tooth pits measured on three *C. fiber* long bones had a mean maximum length of (1.26 ± 0.49) mm and a mean maximum width of (0.89 ± 0.41) mm. These mean values fall within the broad intervals reported for *Crocuta crocuta* pits on dense cortical bone but are substantially smaller than the published means (3.27 mm in length and 2.24 mm in width) (Domínguez-Rodrigo & Piqueras, 2003). The Valdegoba values are more similar to the values reported for wild red foxes by Young et al. (2015); 21/22 measurements fall within the published range, and several overlap with values reported for badgers and domestic dogs. The heavily gnawed *C. fiber* hemimandible (Fig. 6a) bearing nine pits and one score, shows extensive carnivore modification, as well as the maxilla (Fig. 6c). By contrast, the gnawing on the *M. marmota* hemimandible shows a different morphology from the carnivore modifications described above and is attributed to a rodent.

Digestive corrosion was identified on two specimens: a complete *C. fiber* talus (Fig. 6b) from the disturbed upper deposit and a *M. marmota* maxilla from Level 4. The *C. fiber* talus shows heavy digestive attrition, whereas the *M. marmota* maxilla displays moderate digestive attrition (Lloveras et al. 2014). Comparable digestive alteration has been documented in carnivore accumulations, including hyaenid dens (Fernández-Jalvo & Andrews 2016; Gatta et al. 2022; Linares-Matás et al. 2021). The alterations indicate ingestion by a mammalian carnivore.

4.6.1. Anthropogenic modifications

Cut marks confidently attributed to anthropogenic modification were identified on four remains (three *C. fiber* and one *M. marmota*), and an additional immature *C. fiber* mandible shows linear marks of uncertain origin (Fig. 7). Two of the four cut-marked specimens, the *M. marmota* hemimandible and the *C. fiber* tibia, come from disturbed contexts (Fig. 7b, d).

The *C. fiber* left hemimandible (Fig. 7a) bears two parallel cut marks on the labial surface. The *M. marmota* hemimandible (Fig. 7b) bears cut marks on the lateral surface close to the alveolar margin. SEM examination revealed microstriations within the base of one of the grooves. The *C. fiber* coxal (Fig. 7c) bears two short, subparallel incisions on the pubic portion, close to the fracture margin. The *C. fiber* tibia (Fig. 7d) bears a transverse linear mark on the diaphysis. SEM examination showed a V-shaped cross-section, internal microstriations and Hertzian cones; a shoulder effect and an associated external parallel incision were also observed. Numerous fine, oblique marks consistent with trampling were present on adjacent areas of the bone surface. Finally, an immature *C. fiber* right hemimandible (Fig. 7e) bears two parallel marks visible macroscopically anterior to the teeth in the symphyseal region. SEM examination did not reveal internal microstriations or Hertzian cones, and the groove bases appear relatively flat. Given the immature cortical surface and the absence of diagnostic microscopic features, it is not included among the confidently identified cut-marked remains.

5. Discussion

5.1. Formation and accumulation of the assemblage

The odontometric data support the taxonomic attribution of the Valdegoba large-rodent remains to *Castor fiber* and *Marmota marmota*, with measurements broadly comparable to those reported for other Pleistocene populations of these taxa. The available measurements do not support the recognition of a distinct local population in either taxon, and the observed variation is more readily explained by intraspecific, ontogenetic and geographical factors.

A primary accumulation of beaver remains in the cave through the animal's own activity is highly unlikely. The Eurasian beaver is currently the largest rodent in Europe, with strict ecological preferences, strongly associated with aquatic environments and riparian vegetation, and most of their activity takes place close to the water's edge, not in caves (Nolet & Rosell 1998; Donkor & Fryxell 1999). Beavers do not hibernate, although they reduce their activity during autumn and winter and establish underwater caches of woody vegetation (Campbell-Palmer et al. 2016). In cave contexts, the presence of *C. fiber* is more plausibly explained by secondary incorporation into the karst system. Natural mortality followed by sediment reworking may introduce isolated remains from nearby river valleys, as proposed for the Middle Pleistocene *C. fiber* accumulation of Gruta da Aroeira (Portugal) (Cuenca-Bescós et al. 2021), whereas predators, scavengers or humans may transport whole carcasses or selected body parts into the cave. Carnivore transport may instead be indicated by tooth marks, gnawing, disarticulation and selective skeletal representation, whereas anthropogenic involvement is supported by modifications related to carcass processing, such as cut marks associated with skinning, disarticulation or meat removal.

The accumulation history of marmots differs since marmots are burrowing, social rodents that spend much of their lives in underground burrows and hibernate for approximately six months. Although extant marmots normally use purpose-built burrows for hibernation, the use of caves has also been documented (Vincenzi & Bona 2024). Their remains may accumulate primarily in caves or karst cavities following natural mortality, particularly while hibernating. Archaeological examples such as East Brina Cave and Caverna Generosa have been interpreted as including natural accumulations of marmots, supported by evidence such as demographic composition, local burrow structures and weak or absent signs of human or carnivore modification (Oros Sršen et al. 2025; Vincenzi & Bona 2024). Natural mortality is not the only possible accumulation process. Carnivores may prey upon marmots and transport their remains, producing tooth marks, gnawing, disarticulation and selective skeletal-part representation (Oros Sršen et al. 2025). Furthermore, large raptors also present in Valdegoba could be considered potential accumulators, however, no bone modifications from these taxa were observed. Humans may also contribute to these accumulations. Anthropogenic exploitation of marmots has been documented at several Palaeolithic sites, including Grotta del Clusantin and Grotte di Pradis, where cut marks, burning, demographic profiles and skeletal representation have been used to identify hunting and carcass processing (Romandini et al. 2012; Nannini et al. 2022).

Large-rodent cave assemblages may result from several overlapping pathways. Natural mortality, fluvial transport, carnivore predation or scavenging, human activity and subsequent post-depositional processes may all contribute to the same assemblage. For this reason, the presence of *C. fiber* or *M. marmota* in an archaeological deposit cannot by itself be considered evidence of human exploitation, and their accumulation history must be evaluated through the combined analysis of skeletal representation, demographic profiles, surface modifications and archaeological and depositional context.

The Valdegoba large-rodent assemblage does not conform to a single accumulation model. The beaver remains (NISP 171, MNI 12) at Valdegoba are represented by 121 cranial and dental remains and 50 postcranial elements. The marmot remains (NISP 60, MNI 9) are dominated by cranial and dental remains, while postcranial elements are almost absent (NISP 2). These differences point to distinct histories of accumulation, transport, modification and preservation. The scarcity of marmot postcranial remains is difficult to explain with the *in situ* death during hibernation, which would be expected to leave more complete carcasses, and it substantially reduces the number of surfaces on which tooth marks and other modifications could be recognised. This difference in skeletal representation must be considered when comparing the taphonomic signals of the two taxa.

The structure of the *C. fiber* mortality profile reveals that age at death is concentrated among juvenile and prime-aged animals, possibly corresponding to individuals captured on natal dispersal at around 2 years of age. A pattern also observed in Bilzingsleben, where it is attributed to Palaeolithic hunters preying on beavers of the same age (Heinrich & Maul 2020). At Valdegoba, at least one beaver is compatible with death in late summer or early autumn, and several beavers fall within the approximately two-year age range associated with natal dispersal, which in modern populations occurs predominantly in spring after the thaw, when dispersing individuals may be more vulnerable. This would suggest more than one mortality event for the beaver accumulation, with individuals entering the assemblage at different times of the year.

On the other hand, the *M. marmota* profile is broadly attritional or U-shaped, dominated by individuals older than five years, with a secondary peak at 1.5–29 months and lacks predominance of prime-aged individuals expected under selective hunting and seen in other sites with documented marmot exploitation such as Grotte di Pradis (Nannini et al. 2022). Natural mortality, including deaths associated with burrow use or hibernation remains a plausible contributor to the marmot assemblage. In living alpine marmot populations, survival is low in the first year of life (Farand et al. 2002) and declines markedly after about five years of age (Berger et al. 2016), so natural mortality, including deaths associated with burrow use or hibernation, remains a plausible contributor to the marmot assemblage. This is supported by comparison to other modern marmot populations, Vancouver Island marmots (*Marmota vancouverensis*) mortality also increased during hibernation and the period immediately after emergence, although predation was the main cause of mortality in the modern population (McAdie et al. 2026). The youngest marmots are around 10–13 months old, their mortality would be compatible with spring to early summer, around the time of emergence from hibernation.

The fracture profile indicates that at least part of the *C. fiber* long bones were broken while the bones were fresh or semi-fresh, with oblique fracture angles, curved outlines, smooth edges and complete shaft circumference predominating. The signal is not unequivocal, as jagged fracture edges are also frequent (37.0%). Fresh-bone breakage cannot be attributed to a particular agent, since both carnivores and hominins are capable of producing such fractures. Post-depositional compression and sediment movement may also have modified fracture morphology, particularly given the frequency of cracking and compression-related damage in the beaver sample. Differences in manganese staining between beaver and marmot remains further suggest differential preservation within the assemblage (Laplana et al. 2015).

Carnivore activity is indicated by tooth marks on 21 beaver remains and one marmot, and by digestive alteration on a *C. fiber* talus and an *M. marmota* maxilla. Some of the smaller pits and scores fall within the range reported for small carnivores and are most compatible with *Vulpes vulpes* (Young et al. 2015). The presence of *V. vulpes* is documented in the Valdegoba faunal assemblage (Feranec et al. 2010). Modern observations confirm that red foxes can prey on young Eurasian beavers, and transport prey to dens or in cave-like settings (Kile et al. 1996; Krajcarz & Krajcarz 2014). They may have contributed to the accumulation or secondary modification of some beaver remains. Evidence for the involvement of larger carnivores complements this signal. The heavily gnawed *C. fiber* hemimandible and maxilla are consistent with modification by a large carnivore, possibly a hyaenid. The degree of digestive corrosion on the digested remains is likewise compatible with ingestion by a hyaenid or wolf than by a fox, both represented in the Valdegoba fauna. Stable-isotope data further indicate that *C. crocuta* exploited prey associated with relatively wooded environments, while *C. fiber* shows the most negative δ13C values among the herbivores analysed at the site (Feranec et al. 2010), making hyaena predation on beaver ecologically plausible. The gnawing on one *M. marmota* hemimandible, is attributed to a small rodent and represents a separate source of modification.

A comparable interpretation has been proposed for Gruta da Aroeira, where *C. fiber* remains occur in deposits contemporaneously used by hyaenas and other carnivores that potentially contributed to the accumulation of beaver remains (Cuenca-Bescós et al. 2021). At Valdegoba natural mortality may also have contributed to the assemblage, particularly in the case of marmots, while some beaver remains could have been introduced or reworked from the nearby river valley. Subsequent sediment displacement, compression and stratigraphic reworking would have further mixed remains with different depositional histories.

The Valdegoba large-rodent assemblage is best interpreted as the result of multiple inputs. Some individuals probably died naturally, others were preyed upon, scavenged or transported by carnivores, and a few were processed by hominins. These pathways were subsequently overprinted by post-depositional processes, producing a palimpsest rather than an assemblage attributable to a single accumulation agent.

5.2. Neanderthal exploitation of large rodents

Cut marks *C. fiber* and *M. marmota* remains provide direct evidence that both taxa were processed by hominins, presumably Neanderthals given the archaeological context. Their anatomical distribution indicates that anthropogenic modification was not restricted to a single skeletal region, but involved cranial, pelvic and hind-limb elements. The marks on the *C. fiber* tibia and coxal are compatible with defleshing and, in the os coxae, possibly also disarticulation, as suggested for comparable beaver remains from Krapina, Caune de l'Arago and Lehringen (Lebreton et al. 2017; Romandini et al. 2018; Verheijen et al., 2026). A similar occurrence of cut marks on a marmot pelvic element has also been reported at Vrbička Cave (poster from Borić et al. 2014). By contrast, the marks on *C. fiber* and *M. marmota* mandibles are more consistent with skinning, as documented in archaeological beaver and marmot assemblages (Tomé 2005; Romandini et al. 2012, 2018; Verheijen et al. 2026).

Within the European Middle Palaeolithic record, Krapina provides the closest comparative case for Valdegoba, since both *C. fiber* and *M. marmota* are represented there by cut-marked remains (Romandini et al. 2018). The Late Mousterian evidence from northern Italy is also relevant, beaver exploitation is documented at Grotta Maggiore di San Bernardino and Riparo del Broion and marmot processing is recorded at Riparo Tagliente (Romandini et al. 2018, 2023; Terlato et al. 2021). At Grotta Maggiore di San Bernardino *C. fiber* and *M. marmota* also occur within a faunal assemblage strongly dominated by ungulates (Romandini et al. 2018). Combined with Valdegoba cave, these sites indicate that large rodents could contribute to Palaeolithic hunters' subsistence as opportunistically exploited resources within a broad and variable prey spectrum.

There is no indication that either beavers or marmots were a specialised prey resource at Valdegoba. Anthropogenic modifications are uncommon, no recurrent butchery pattern or any burning remain has been identified, and the available age data do not indicate repeated selection of a particular demographic group. Among the three beaver specimens with confirmed cut marks there are three adult remains and at least one corresponds to an individual within the typical age range for natal dispersal. A further beaver hemimandible bearing uncertain anthropogenic marks corresponds to a juvenile. Lastly, the cut-marked *M. marmota* hemimandible belongs to an older adult. This differs from the more structured exploitation documented for chamois at Valdegoba (Rodríguez-Gómez et al. 2022) and cases of much more intensive rodent exploitation such as Bilzingsleben, where the larger beaver assemblage, recurrent cut marks and prime-dominated mortality profile support systematic hominin exploitation (Heinrich & Maul, 2020; Gaudzinski-Windheuser et al. 2023).

The taphonomic analysis of the total faunal assemblage reveals Neanderthal flexibility in exploiting a whole range of mammalian species, including beavers and marmots. Smaller-bodied prey, despite their lower meat yields, may have offered lower but less variable energetic returns and lower acquisition costs (Lupo & Schmitt 2016). Mineral pigments have been associated with symbolic practices in some Iberian Neanderthal contexts although the presence of ochre in the Valdegoba assemblage (n = 18 in *C. fiber* bones and n = 2 in *M. marmota*) does not necessarily imply symbolic behaviour (Zilhão et al. 2010). There is no contextual evidence for deliberate pigment use in Valdegoba, since ochre also occurs in the

surrounding burial matrix and the stains on the bones are randomly distributed across their surfaces which is consistent with natural iron-oxide staining.

With estimated mean body masses of approximately 20 kg for *C. fiber* and 3.5 kg for *M. marmota*, these taxa fall between the small-bodied prey and the ungulates exploited at Valdegoba, although the marmot estimate overlaps with the body mass of hares. The estimated mass of the Valdegoba marmots lies at the lower end of the body-mass range of extant *M. marmota* but given the uncertainty of the regression and the strong seasonal variation in marmot body mass, it should not be taken as evidence of particularly small individuals. This paper provides evidence of flexible use of available animal resources, where large rodents supplemented more regularly exploited prey without becoming specialised targets. This pattern also included the exploitation of smaller prey, as shown by the importance of chamois, one of the smallest ungulates of the Late Pleistocene, with several bird and lagomorph species.

5.3. Palaeoecological and palaeobiogeographical implications

The repeated occurrence of *C. fiber* and *M. marmota* in Level 4s, 4 inferior, 5 and 6, of Test Pit 4 supports their broad temporal association within the Valdegoba sequence. Levels 4 and 5 are dated to the late MIS 6–early MIS 5 transition, between ca. 140 and 120 ka (Terradillos-Bernal et al. 2025).

The two taxa provide complementary ecological information. *C. fiber* indicates the availability of permanent freshwater and riparian vegetation, most plausibly associated with the nearby Úrbel River. Its presence also adds to the Iberian Pleistocene record of the species and documents the persistence of suitable freshwater habitats during this period (Cuenca-Bescós et al. 2021). *M. marmota*, in contrast, is associated with open grasslands, rocky slopes and steppe-like environments. Although marmots are commonly linked to cold or continental conditions, their presence at Valdegoba should not be taken as evidence for a uniformly cold landscape. The wider faunal record instead points to a heterogeneous environment combining open, wooded and mountainous habitats (Feranec et al. 2010; Rodríguez-Gómez et al. 2022).

From a regional perspective, the occurrence of *M. marmota* is particularly relevant because the species is uncommon in the Iberian Pleistocene record. Its association with *C. fiber* documents the presence of both open-habitat and riparian taxa in the interior of northern Iberia around the Middle–Late Pleistocene transition. These records add to the still limited evidence for the palaeobiogeographical distribution of both taxa in Iberia during this period.

6. Conclusions

Valdegoba is the earliest known site with joint beaver and marmot Neanderthal exploitation. Their exploitation appears to have been occasional, not systematic as anthropogenic modifications are scarce, no recurrent processing pattern has been identified and mortality profiles show no strong age selection. The exploitation of several rodent species, as well as birds at Valdegoba indicates that

Neanderthals did not rely exclusively on large-bodied prey for their subsistence. Large rodents thus broaden the range of prey exploited at Valdegoba by hominins and help fill a poorly documented prey-size gap in Neanderthal subsistence between small-bodied prey, such as lagomorphs and tortoises, and small ungulates such as chamois and roe deer.

The large-rodent assemblage reflects a complex history of accumulation and modification. *C. fiber* and *M. marmota* were incorporated into the cave through several pathways, including natural mortality, carnivore activity and hominin exploitation, and were later affected by post-depositional reworking. Tooth marks on about one-eighth of the beaver specimens, fresh-bone fractures and digestive alteration suggest an important carnivore contribution, involving both small and larger carnivores.

From a palaeoecological perspective, *C. fiber* and *M. marmota* indicate the local availability of riparian and open habitats during the late MIS 6–early MIS 5 transition. The association of marmot with chamois, a dominant component of the Valdegoba ungulate assemblage, is also consistent with the cold and open conditions expected during a stadial phase such as MIS 6. The zooarchaeological and taphonomic evidence shows that the Valdegoba large-rodent assemblage resulted from the interaction of natural, carnivore and hominin processes within a heterogeneous landscape.

Declarations

Acknowledgements

We thank Nohemi Sala for her help and the Laboratory of Prehistory (I+D+i Building) at the University of Burgos for access to Valdegoba's archaeological collection, the comparative collections of the University of Alcalá, and the CENIEH Comparative Anatomy Osteological Collection (COAC) for the comparative skeletal and dental material. We also thank the Scientific and Technological Park of the University of Burgos for making available the scanning electron microscopy facilities.

This research was supported by the Junta de Castilla y León (Consejería de Educación y Consejería de Educación) through several funding projects, and by the University of Burgos through its support to the "Prehistoric Archaeology" research group.

References

1. Alonso-Caño G, Díez Fernández-Lomana JC, Sánchez-Marco A (2025) Insights into Neanderthal bird hunting practices during MIS 5–3: taphonomical analysis of avian remains from Valdegoba Cave (Burgos, Spain). J Archaeol Science: Rep 66:105266. https://doi.org/10.1016/j.jasrep.2025.105266
2. Andrews P, Fernández-Jalvo Y (2012) How to approach perimortem injury and other modifications. In: Bell L (ed) Forensic microscopy for skeletal tissues. Methods in Molecular Biology, vol 915. Humana Press, Totowa, pp 191–225. https://doi.org/10.1007/978-1-61779-977-8_12

3. Arilla M, Rosell J, Blasco R (2020) A neo-taphonomic approach to human campsites modified by carnivores. Sci Rep 10:6659. https://doi.org/10.1038/s41598-020-63431-8
4. Berger V, Lemaître J-F, Dupont P, Allainé D, Gaillard J-M, Cohas A (2016) Age-specific survival in the socially monogamous alpine marmot (*Marmota marmota*): evidence of senescence. J Mammal 97:992–1000. https://doi.org/10.1093/jmammal/gyw028
5. Binford LR (1981) Bones: ancient men and modern myths. Academic, New York
6. Blasco R, Fernández Peris J (2012) A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). Quatern Int 252:16–31. https://doi.org/10.1016/j.quaint.2011.03.019
7. Blumenschine RJ, Marean CW, Capaldo SD (1996) Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. J Archaeol Sci 23:493–507. https://doi.org/10.1006/jasc.1996.0047
8. Borodina MN (1970) Age-related variability of some morphological characters of the Moksha beaver population. Proceedings of the Mordovian State Reserve 5:91–130
9. Campbell-Palmer R, Gow D, Campbell R, Dickinson H, Girling S, Gurnell J, Halley D, Jones S, Lisle S, Parker H, Schwab G, Rosell F (2016) The Eurasian beaver handbook: ecology and management of *Castor fiber*. Pelagic Publishing, Exeter
10. Cuenca-Bescós G, Rosell Ardévol J, Morcillo-Amo Á, Galindo-Pellicena MÁ, Santos E, Moyà-Costa R (2017) Beavers (Castoridae, Rodentia, Mammalia) from the Quaternary sites of the Sierra de Atapuerca, in Burgos, Spain. Quaternary International 433 (Part A), 263–277. https://doi.org/10.1016/j.quaint.2015.10.072
11. Cuenca-Bescós G, Sanz M, Daura J, Zilhão J (2021) The fossils of *Castor fiber* from the Middle Pleistocene site of Gruta da Aroeira (Portugal) and human–beaver interaction. Quaternaire 32:1–10. https://doi.org/10.4000/quaternaire.14975
12. De Iuliis G, Pulerà D (2019) Cranial skeleton: supplement—comparative mammalian skulls. The dissection of vertebrates: a laboratory manual, 3rd edn. Academic, London, pp 189–195
13. Díez Fernández-Lomana JC, Jordá Pardo JF, Arceredillo Alonso D (2014) Valdegoba Palaeolithic site (Huérmeces, Burgos). In: Sala R (ed) Pleistocene and Holocene hunter-gatherers in Iberia and the Gibraltar Strait: the current archaeological record. Fundación Atapuerca and Universidad de Burgos, Burgos, pp 608–610
14. Discamps E, Costamagno S (2015) Improving mortality profile analysis in zooarchaeology: a revised zoning for ternary diagrams. J Archaeol Sci 58:62–76. https://doi.org/10.1016/j.jas.2015.03.021
15. Domínguez-Rodrigo M, Piqueras A (2003) The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. J Archaeol Sci 30:1385–1391. https://doi.org/10.1016/S0305-4403(03)00027-X
16. Domínguez-Rodrigo M, de Juana S, Galán AB, Rodríguez M (2009) A new protocol to differentiate trampling marks from butchery cut marks. J Archaeol Sci 36:2643–2654. https://doi.org/10.1016/j.jas.2009.07.017

17. Estraviz-López D, Rosell J, Blasco R, Rodríguez-Hidalgo A, Carbonell E (2021) The earliest record of marmots in Europe from the Early Pleistocene levels of Gran Dolina (Atapuerca, Spain). Quatern Int 602:53–94. https://doi.org/10.34637/crz1-da69
18. Fandén A (2005) Ageing the beaver (*Castor fiber* L.): a skeletal development and life history calendar based on epiphyseal fusion. Archaeofauna 14:199–213
19. Farand É, Allainé D, Coulon J (2002) Variation in survival rates for the alpine marmot (*Marmota marmota*): effects of sex, age, year, and climatic factors. Can J Zool 80:342–349. https://doi.org/10.1139/z02-004
20. Feranec RS, García N, Díez JC, Arsuaga JL (2010) Understanding the ecology of mammalian carnivorans and herbivores from Valdegoba cave (Burgos, northern Spain) through stable isotope analysis. Palaeogeogr Palaeoclimatol Palaeoecol 297:263–272. https://doi.org/10.1016/j.palaeo.2010.08.006
21. Fernández-Jalvo Y, Andrews P (2016) Atlas of taphonomic identifications: 1001 + images of fossil and recent mammal bone modification. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-7432-1
22. Fernández-Jalvo Y, Andrews P, Denys C (1999) Cut marks on small mammals at Olduvai Gorge Bed-I. J Hum Evol 36:587–589. https://doi.org/10.1006/jhev.1999.0292
23. Fischer K (1991) Postkraniale Skelettreste von Bibern (*Castor* L., *Trogontherium* Fischer, Castoridae, Rodentia, Mamm.) aus dem Mittelpleistozän von Bilzingsleben. In: Bilzingsleben IV: *Homo erectus* – seine Kultur und seine Umwelt. Deutscher Verlag der Wissenschaften, Berlin, pp 63–74
24. Freudenthal M, Martín-Suárez E (2013) Estimating body mass of fossil rodents. Scripta Geol 145:1–513
25. Gatta M, Fiorillo A, Salari L, Achino KF, Rolfo MF, Alessandri L (2022) The faunal assemblage from La Sassa cave (Latium, Italy): environmental perspective of a Late Pleistocene cave hyena–brown bear den. J Archaeol Science: Rep 46:103691. https://doi.org/10.1016/j.jasrep.2022.103691
26. Gaudzinski-Windheuser S, Kindler L, Roebroeks W (2023) Beaver exploitation, 400,000 years ago, testifies to prey choice diversity of Middle Pleistocene hominins. Sci Rep 13:19766. https://doi.org/10.1038/s41598-023-46956-6
27. Gay I (2015) La saisonnalité des occupations humaines au Tardiglaciaire dans les Alpes occidentales. Dissertation, Aix-Marseille Université. http://www.theses.fr/2015AIXM3058
28. Heinrich W-D (1991) Biometrische Untersuchungen an Fossilresten des Bibers (*Castor fiber* L.) aus der Fundstätte Bilzingsleben. In: Kaufmann D, Bilzingsleben IV (eds) *Homo erectus* – seine Kultur und seine Umwelt, vol 44. Deutscher Verlag der Wissenschaften, Berlin, pp 35–62
29. Heinrich W-D (1991) Biometrische Untersuchungen an Fossilresten des Bibers (*Castor fiber* L.) aus der Fundstätte Bilzingsleben. In: Bilzingsleben IV. Veröffentlichungen des Landesmuseums für Vorgeschichte in Halle 44, pp. 35–61
30. Heinrich W-D, Maul LC (2020) Mortality profiles of *Castor* and *Trogontherium* (Mammalia: Rodentia, Castoridae), with notes on the site formation of the Mid-Pleistocene hominin locality Bilzingsleben II

(Thuringia, Central Germany). Fossil Impr 76:40–58. https://doi.org/10.37520/fi.2020.004

31. Hugueney M (1999) Family Castoridae. In: Rössner GE, Heissig K (eds) The Miocene land mammals of Europe. Verlag Dr. Friedrich Pfeil, München, pp 281–300
32. Huguet R (2007) Primeras ocupaciones humanas en la península ibérica: paleoeconomía en la sierra de Atapuerca (Burgos) y la cuenca de Guadix-Baza (Granada) durante el Pleistoceno inferior. Dissertation, Universitat Rovira i Virgili
33. Kalthoff DC (1999) Ist *Marmota primigenia* (Kaup) eine eigenständige Art? Osteologische Variabilität pleistozäner *Marmota*-Populationen (Rodentia: Sciuridae) im Neuwieder Becken (Rheinland-Pfalz, Deutschland) und benachbarter Gebiete. Kaupia: Darmstädter Beiträge zur Naturgeschichte 9:127–186
34. Kile NB, Nakken PJ, Rosell F, Espeland S (1996) Red fox, *Vulpes vulpes*, kills a European beaver, *Castor fiber*, kit. Can Field-Naturalist 110:338–339. https://doi.org/10.5962/p.357466
35. Krajcarz M, Krajcarz MT (2014) The red fox (*Vulpes vulpes*) as an accumulator of bones in cave-like environments. Int J Osteoarchaeology 24:459–475. https://doi.org/10.1002/oa.2233
36. Laplana C, Sevilla P, Arriaza MC, Pérez-González A, Baquedano E, Arsuaga JL (2015) Un caso de asociaciones de microvertebrados pleistocenas mezcladas por reelaboración en ambientes cársticos: la Cueva de la Buena Pinta (Pinilla del Valle, Comunidad de Madrid). In: Reolid M (ed) XXXI Jornadas de Paleontología: libro de resúmenes. Universidad de Jaén, Jaén, pp 152–153
37. Laroulandie V, Blasco R, Thompson JC, Meier J, Rufà A, Tassoni L, Cochard D, Morin E, Colonese AC (2022) Small animal use by Neanderthals. In: Romagnoli F, Rivals F, Benazzi S (eds) Updating Neanderthals: understanding behavioural complexity in the late Middle Palaeolithic. Elsevier, pp 123–143. https://doi.org/10.1016/B978-0-12-821428-2.00010-X
38. Lebreton L, Moigne A-M, Filoux A, Perrenoud C (2017) A specific small game exploitation for Lower Palaeolithic: the beaver (*Castor fiber*) exploitation at the Caune de l'Arago (Pyrénées-Orientales, France). J Archaeol Science: Rep 11:53–58. https://doi.org/10.1016/j.jasrep.2016.11.023
39. Linares-Matás GJ, Fernández Ruiz N, Haber Uriarte M, López Martínez M, Walker MJ (2021) Hyaenas and early humans in the latest Early Pleistocene of South-Western Europe. Sci Rep 11:24036. https://doi.org/10.1038/s41598-021-03547-7
40. Lloveras L, Moreno-García M, Nadal J, Thomas R (2014) Blind test evaluation of accuracy in the identification and quantification of digestion corrosion damage on leporid bones. Quatern Int 330:150–155. https://doi.org/10.1016/j.quaint.2013.07.033
41. Lupo KD, Schmitt DN (2016) When bigger is not better: the economics of hunting megafauna and its implications for Plio-Pleistocene hunter-gatherers. J Anthropol Archaeol 44:185–197. https://doi.org/10.1016/j.jaa.2016.07.012
42. McAdie M, Larsen K, Raverty S, Whiteside D, Stephen C (2026) Causes of mortality in captive, captive-release, and wild Vancouver Island marmots (*Marmota vancouverensis*). J Wildl Dis. https://doi.org/10.7589/JWD-D-26-00045

43. Nabais M, Rufà A, Igreja M (2024) Experimental replication of early human behaviour in bird preparation: a pilot-study focusing on bone surface modification and breakage patterns. Front Environ Archaeol 3:1411853. https://doi.org/10.3389/fearc.2024.1411853
44. Nannini N, Duches R, Fontana A, Romandini M, Boschin F, Crezzini J, Peresani M (2022) Marmot hunting during the Upper Palaeolithic: the specialized exploitation at Grotte di Pradis (Italian pre-Alps). Q Sci Rev 277:107364. https://doi.org/10.1016/j.quascirev.2021.107364
45. Noe-Nygaard N (1989) Man-made trace fossils on bones. Hum Evol 4:461–491. https://doi.org/10.1007/BF02436295
46. Nolet BA, Rosell F (1998) Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems. Biol Conserv 83:165–173. https://doi.org/10.1016/S0006-3207(97)00066-9
47. Olsen SL, Shipman P (1988) Surface modification on bone: trampling versus butchery. J Archaeol Sci 15:535–553. https://doi.org/10.1016/0305-4403(88)90081-7
48. Oros Sršen A, Novak V, Šanjek R (2025) Taphonomy of the alpine marmot (*Marmota marmota*) remains from the Late Pleistocene deposits of the East Brina Cave, Croatia. Geologia Croatica 78:115–127. https://doi.org/10.4154/gc.2025.11
49. Quam RM, Arsuaga JL, Bermúdez de Castro JM, Díez CJ, Lorenzo C, Carretero M, García N, Ortega AI (2001) Human remains from Valdegoba Cave (Huérmeces, Burgos, Spain). J Hum Evol 41:385–435. https://doi.org/10.1006/jhev.2001.0486
50. Quintana CA, Valverde F, Mazzanti DL (2002) Roedores y lagartos como emergentes de la diversificación de la subsistencia durante el Holoceno tardío en sierras de la región Pampeana Argentina. Latin Am Antiq 13:455–473. https://doi.org/10.2307/972226
51. Radulesco C, Kovács A (1970) Contribution à la connaissance de la marmotte fossile (Marmota cf. bobac Müller) du bassin de Sf. Gheorghe (Dépression de Braşov). Travaux de l'Institut de Spéologie Émile Racovitza 9:231–243
52. Rodríguez-Gómez G, Pérez-Fernández E, Fernandez P, Arsuaga JL, Díez C, Arceredillo D (2022) Palaeoecology of the Southern chamois from Valdegoba Cave (Burgos, Spain) and its exploitation by the Neanderthals. Lethaia 55:1–25. https://doi.org/10.18261/let.55.4.3
53. Romandini M, Peresani M, Gurioli F, Sala B (2012) *Marmota marmota*, the most common prey species at Grotta del Clusantin: insights from an unusual case-study in the Italian Alps. Quatern Int 252:184–194. https://doi.org/10.1016/j.quaint.2011.03.016
54. Romandini M, Thun Hohenstein U, Fiore I, Tagliacozzo A, Perez A, Lubrano V, Terlato G, Peresani M (2018) Late Neandertals and the exploitation of small mammals in Northern Italy: fortuity, necessity or hunting variability? Quaternaire 29:61–67. https://doi.org/10.4000/quaternaire.8626
55. Romandini M, Silvestrini S, Real C, Lugli F, Tassoni L, Carrera L, Badino F, Bortolini E, Marciani G, Delpiano D, Piperno M, Collina C, Peresani M, Benazzi S (2023) Late Neanderthal menu from northern to southern Italy: freshwater and terrestrial animal resources. Q Sci Rev 315:108233. https://doi.org/10.1016/j.quascirev.2023.108233

56. Salari L, Fiorillo A, Rolfo MF, Gatta M (2025) Late Pleistocene *Marmota marmota* from Grotta Mora Cavorso (central Italy): a morphological and osteometric contribution to the Western European fossil record. Quatern Int 749:110031. https://doi.org/10.1016/j.quaint.2025.110031
57. Shipman P, Foster G, Schoeninger M (1984) Burnt bones and teeth: an experimental study of color, morphology, crystal structure and shrinkage. J Archaeol Sci 11:307–325. https://doi.org/10.1016/0305-4403(84)90013-X
58. Stiner MC (1990) The use of mortality patterns in archaeological studies of hominid predatory adaptations. J Anthropol Archaeol 9:305–351. https://doi.org/10.1016/0278-4165(90)90010-B
59. Terlato G, Lubrano V, Romandini M, Marín-Arroyo AB, Benazzi S, Peresani M (2021) Late Neanderthal subsistence at San Bernardino Cave (Berici Hills—northeastern Italy) inferred from zooarchaeological data. Alp Mediterranean Quaternary 34:213–235. https://doi.org/10.26382/AMQ.2021.10
60. Terradillos-Bernal M, Díez Fernández-Lomana JC (2018) La tecnología lítica neandertal de Valdegoba en el contexto del Paleolítico medio de la Meseta norte. Trabajos de Prehistoria 75:320–332. https://doi.org/10.3989/tp.2018.12218
61. Terradillos-Bernal M, Demuro M, García-Martínez D, Arceredillo D, Arnold LJ, Jordá-Pardo JF, Torres T, Ortiz JE, Díez Fernández-Lomana JC (2025) Neanderthal morphology, behaviour and adaptation at Valdegoba Cave (Northern Spain) during late MIS 6–early MIS 5. Q Sci Rev 369:109649. https://doi.org/10.1016/j.quascirev.2025.109649
62. Tomé C (1998) Étude de la marmotte des Alpes (Marmota marmota L.) et de son exploitation par les chasseurs du Paléolithique final de la grotte Colomb (Méaudre–Vercors, France). Mémoire de maîtrise. Université Pierre Mendès France, Grenoble II
63. Tomé C (2005) Les marmottes de la grotte Colomb (Vercors, France). Revue de Paléobiologie. Volume spécial 10:11–21
64. Tukša I (2019) Metrijske analize skeletnih ostataka planinskih svizaca (*Marmota marmota* (Linnaeus, 1758)) iz gornjopleistocenskih naslaga Pećina u Brini kod Drniša. Master's thesis, University of Zagreb. https://urn.nsk.hr/urn:nbn:hr:217:504508
65. Verheijen I, Di Maida G, Russo G, Terberger T (2026) Faunal exploitation at the elephant hunting site of Lehringen, Germany, 125,000 years ago. Sci Rep 16:9836. https://doi.org/10.1038/s41598-026-42538-4
66. Villa P, Mahieu E (1991) Breakage patterns of human long bones. J Hum Evol 21:27–48. https://doi.org/10.1016/0047-2484(91)90034-S
67. Vincenzi M, Bona F (2024) Some thoughts regarding MIS3 marmots (*Marmota marmota*) of north-western Italy with particular reference to those from Caverna Generosa (Centro Valle Intelvi, Como). Hystrix, the Italian. J Mammal 35:123–132. https://doi.org/10.4404/hystrix-00685-2023
68. Volokh A (2021) Determination of age of the Eurasian beaver (*Castor fiber*). Theriologia Ukrainica 22:49–62. https://doi.org/10.15407/TU2206

69. Yellen JE (1991) Small mammals: Kung San utilization and the production of faunal assemblages. J Anthropol Archaeol 10:1–26. https://doi.org/10.1016/0278-4165(91)90019-T
70. Young A, Stillman RA, Smith MJ, Korstjens AH (2015) Scavenger species-typical alteration to bone: using bite mark dimensions to identify scavengers. J Forensic Sci 60:1426–1435. https://doi.org/10.1111/1556-4029.12839
71. Zilhão J, Angelucci DE, Badal-García E, d'Errico F, Daniel F, Dayet L, Douka K, Higham TFG, Martínez-Sánchez MJ, Montes-Bernárdez R, Murcia-Mascarós S, Pérez-Sirvent C, Roldán-García C, Vanhaeren M, Villaverde V, Wood R, Zapata J (2010) Symbolic use of marine shells and mineral pigments by Iberian Neandertals. Proceedings of the National Academy of Sciences of the USA 107:1023–1028. https://doi.org/10.1073/pnas.0914088107

Figures

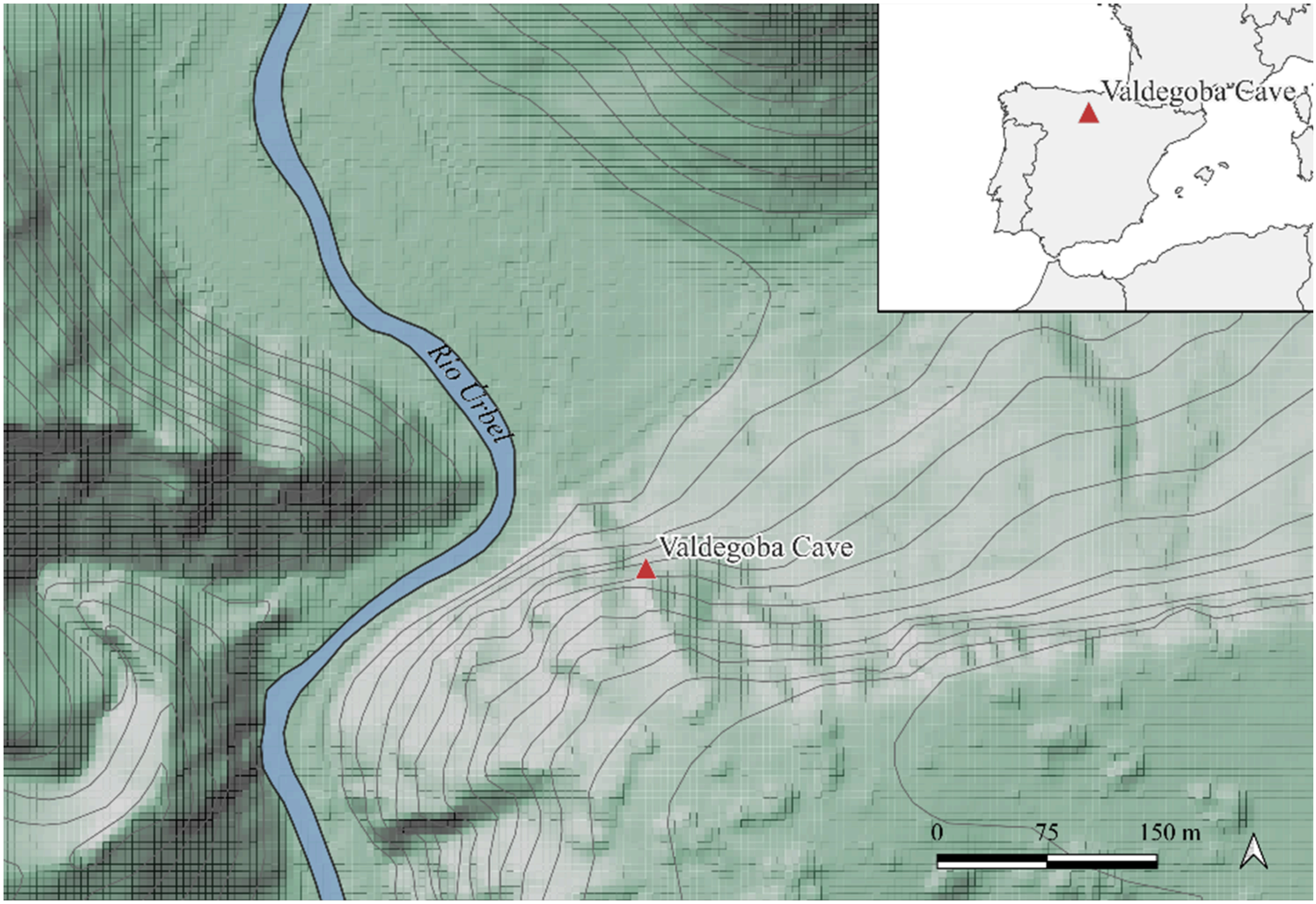


Figure 1

Location of Valdegoba Cave (Huérmeces, Burgos) in the Úrbel River gorge. Digital elevation model and hillshade based on the PNOA-LiDAR MDT05 (tile 0167); contour lines and hydrographic network from

BTN25 (© Instituto Geográfico Nacional, CC BY 4.0, scne.es). Location map: Natural Earth. Coordinate reference system: ETRS89 / UTM Zone 30N (EPSG:25830). Prepared using QGIS 3.44.

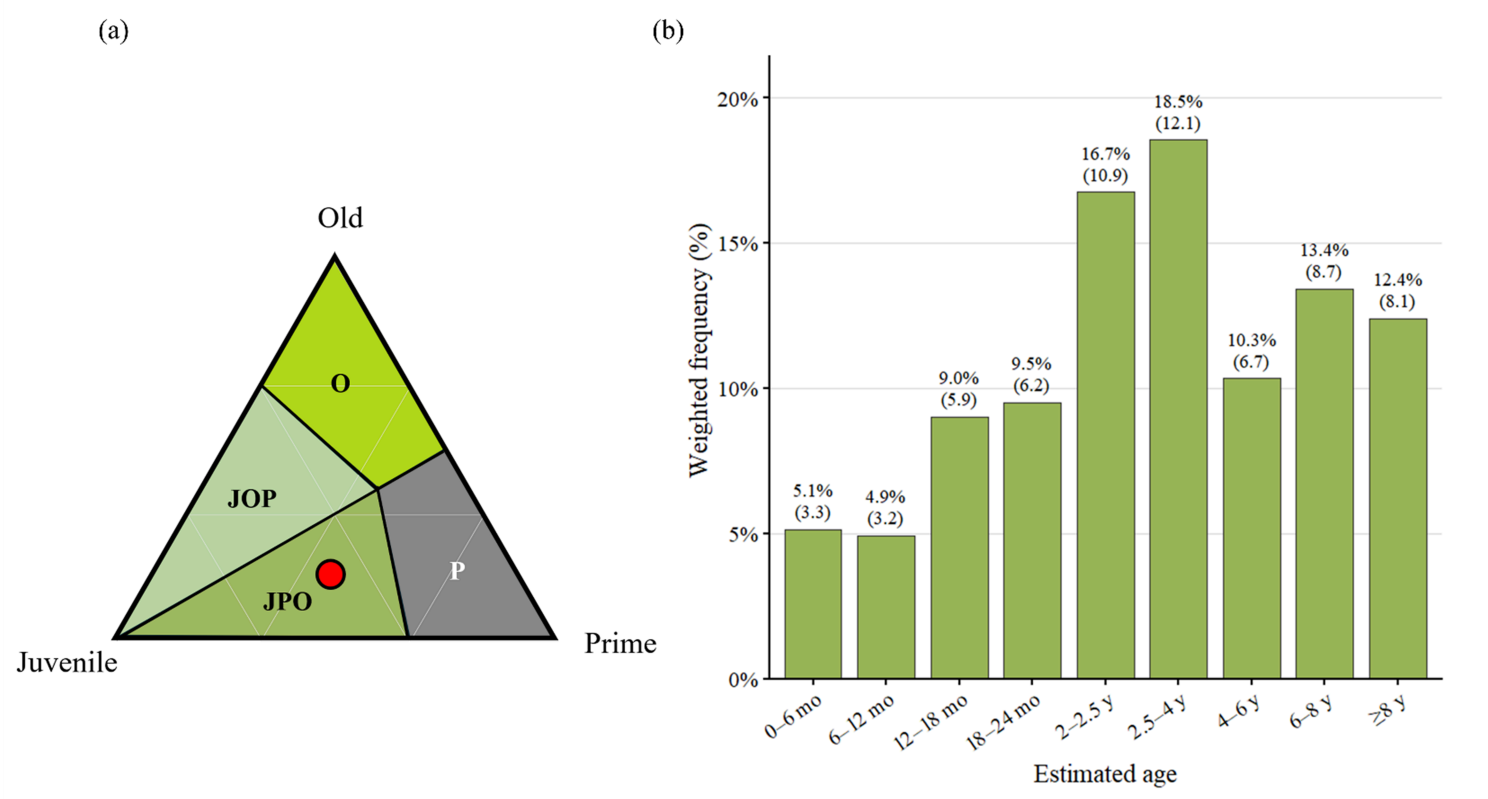


Figure 2

Age-at-death data for *Castor fiber* from Valdegoba Cave. (a) Ternary diagram showing the relative proportions of juvenile, prime-adult and old-adult *C. fiber* specimens from Valdegoba (n = 75 age-informative specimens). The sample falls within the Juvenile–Prime–Old dominated zone (JPO) (juvenile 42.4%; prime adult 41.8%; old adult 15.8%). Age estimates spanning more than one category were fractionally allocated so that each specimen contributed a total weight of one. Zone boundaries follow Discamps and Costamagno (2015). (b) Detailed age-of-death profile of *C. fiber* specimens from Valdegoba (n = 65 specimens). Specimens spanning more than one age interval were fractionally allocated among the compatible classes so that each specimen contributed a total weight of one. Bars represent weighted frequencies as percentages

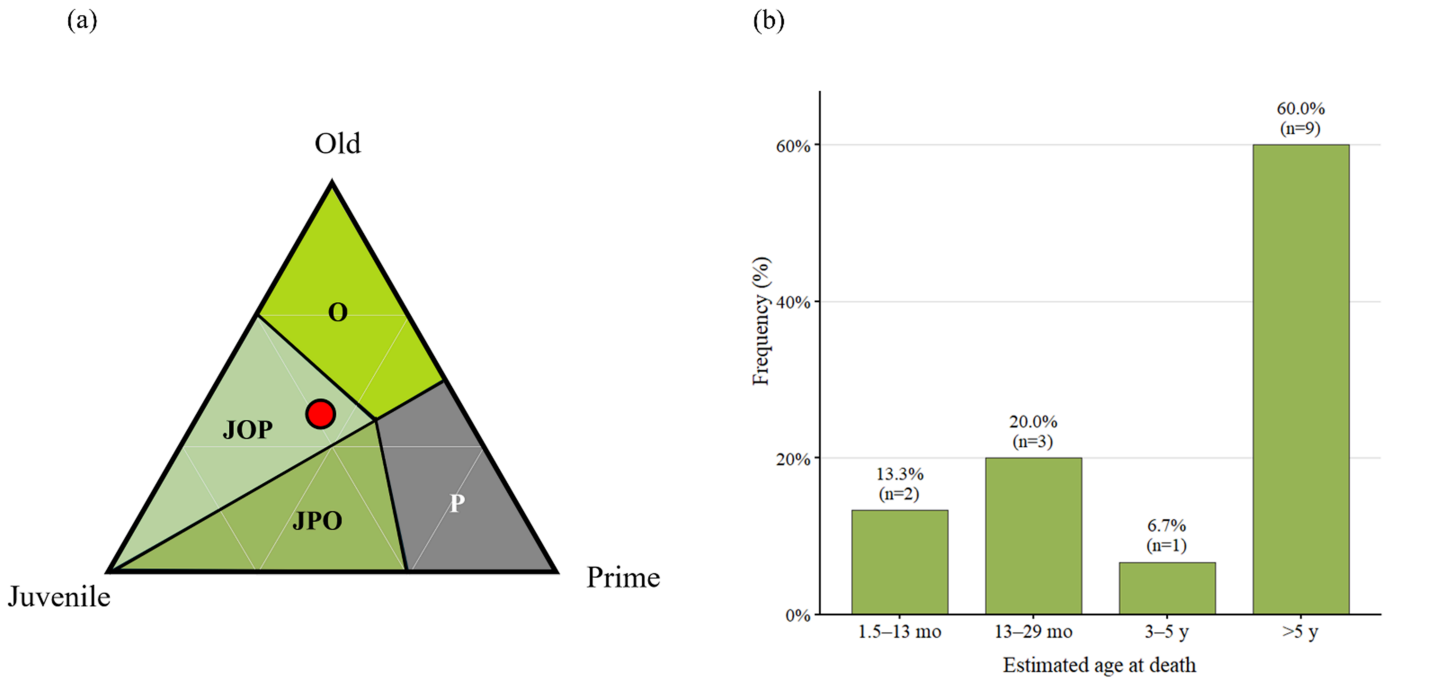


Figure 3

Age-at-death data for *Marmota marmota* from Valdegoba Cave. (a) Ternary diagram showing the relative proportions of juvenile, prime-adult and old-adult *M. marmota* specimens from Valdegoba (n = 22 age-informative specimens). The sample falls within the Juvenile–Old–Prime (JOP) zone (juvenile 31.8%; prime adult 27.3%; old adult 40.9%). Age estimates spanning more than one category were fractionally allocated so that each specimen contributed a total weight of one. Zone boundaries follow Discamps and Costamagno (2015). (b) Age-at-death distribution by age interval, following Tomé (1998, 2005) (n = 15 specimens). Specimens spanning more than one age interval were fractionally allocated among the compatible classes so that each specimen contributed a total weight of one. Bars represent weighted frequencies as percentages.

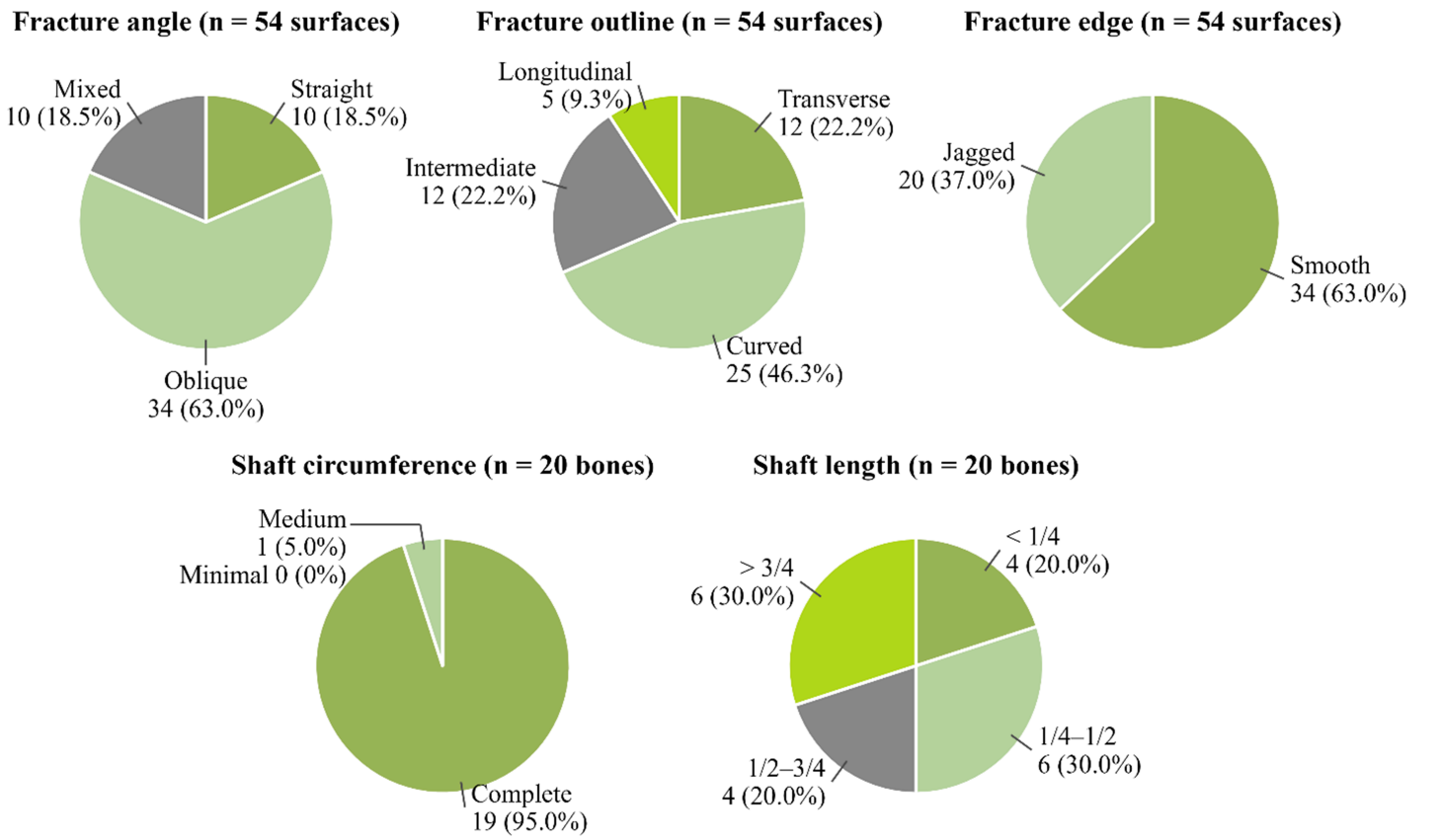


Figure 4

Fracture attributes of *C. fiber* long bones from Valdegoba Cave, recorded following Villa and Mahieu (1991). Fracture angle, outline and edge were recorded per fracture surface (n = 54 surfaces on 20 fractured bones); shaft circumference and shaft length were recorded per element (n = 20 fractured bones).

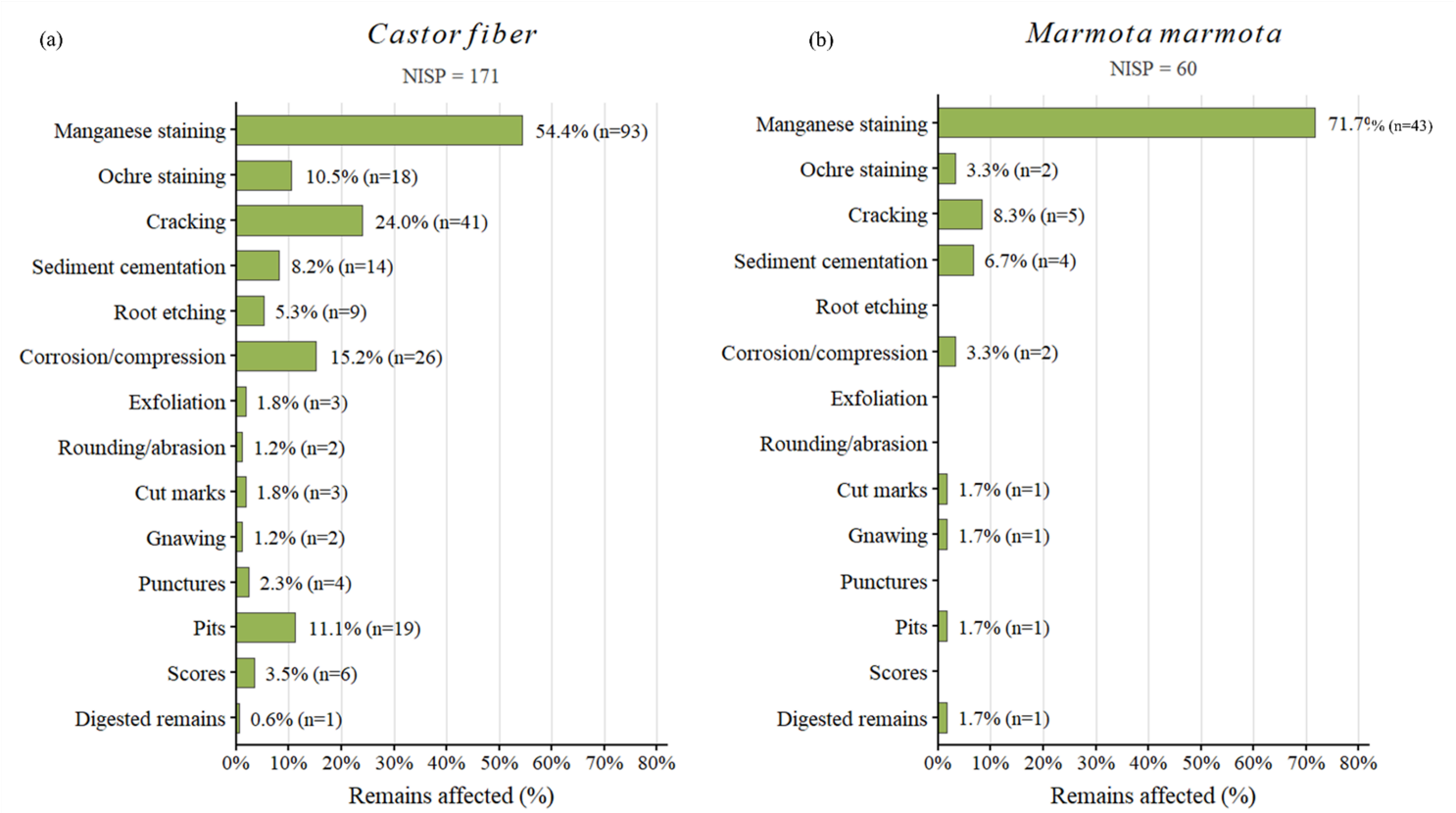


Figure 5

Frequency of bone surface modifications on (a) *C. fiber* (NISP = 171) and (b) *M. marmota* (NISP = 60) remains from Valdegoba Cave. Percentages are calculated relative to the NISP of each taxon; numbers in parentheses are the number of affected specimens. A specimen may display more than one type of modification

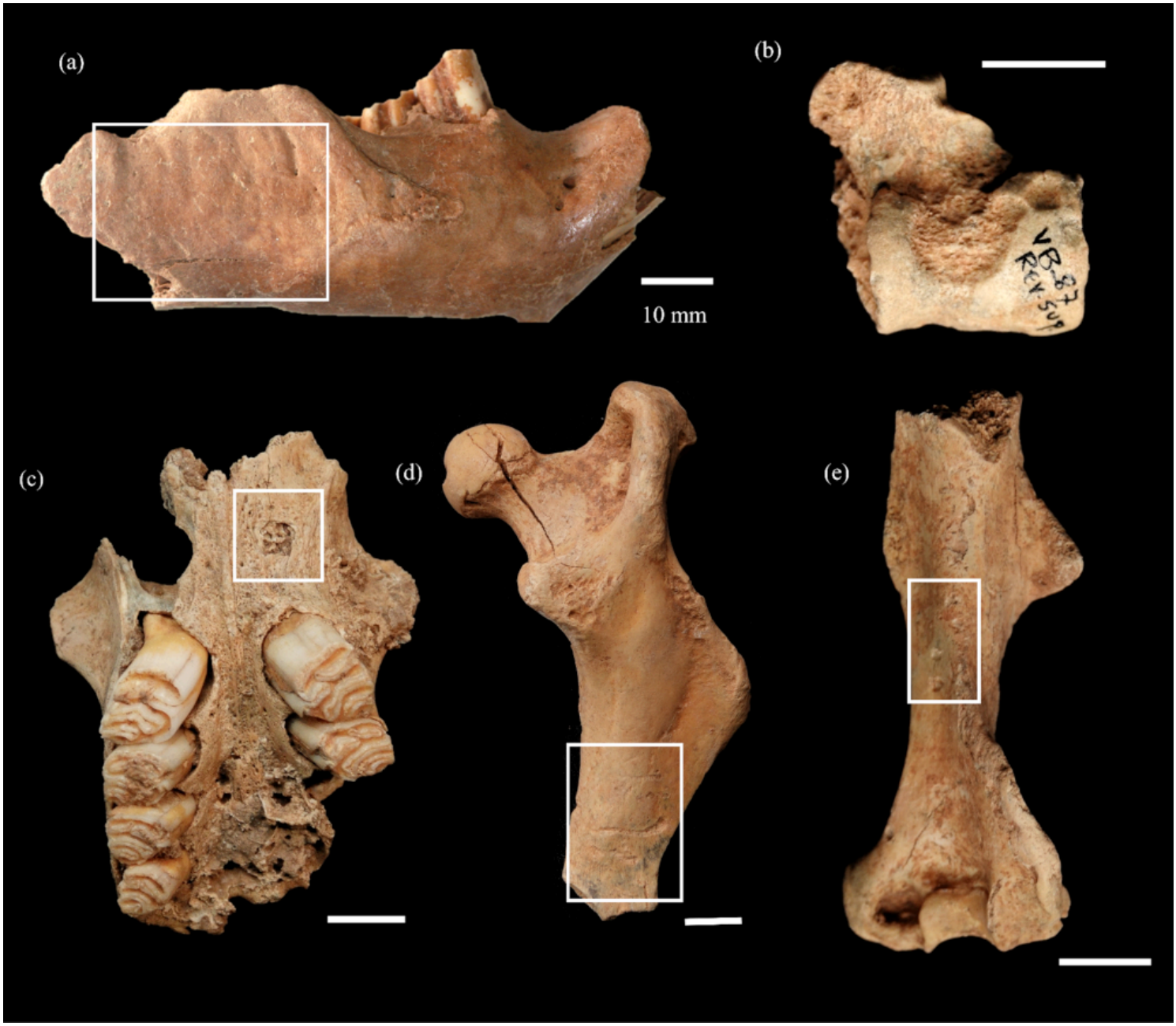


Figure 6

Carnivore-related modifications on large-rodent remains from Valdegoba Cave. (a) Heavily gnawed *C. fiber*right hemimandible (Vb06, L13 Ab, 45–60); (b) *C. fiber* right talus (Vb87, revuelto superior, 25) showing digestive corrosion; (c) *M. marmota*maxilla (Vb89, K13 Da, T8, 2) showing gnawing alterations; (d) *C. fiber*right femur (Vb87, revuelto superior, 8) showing punctures, pits and scores; (e) *C. fiber* right humerus (Vb06, L13 Ad, Da, 65–70) showing tooth pits.

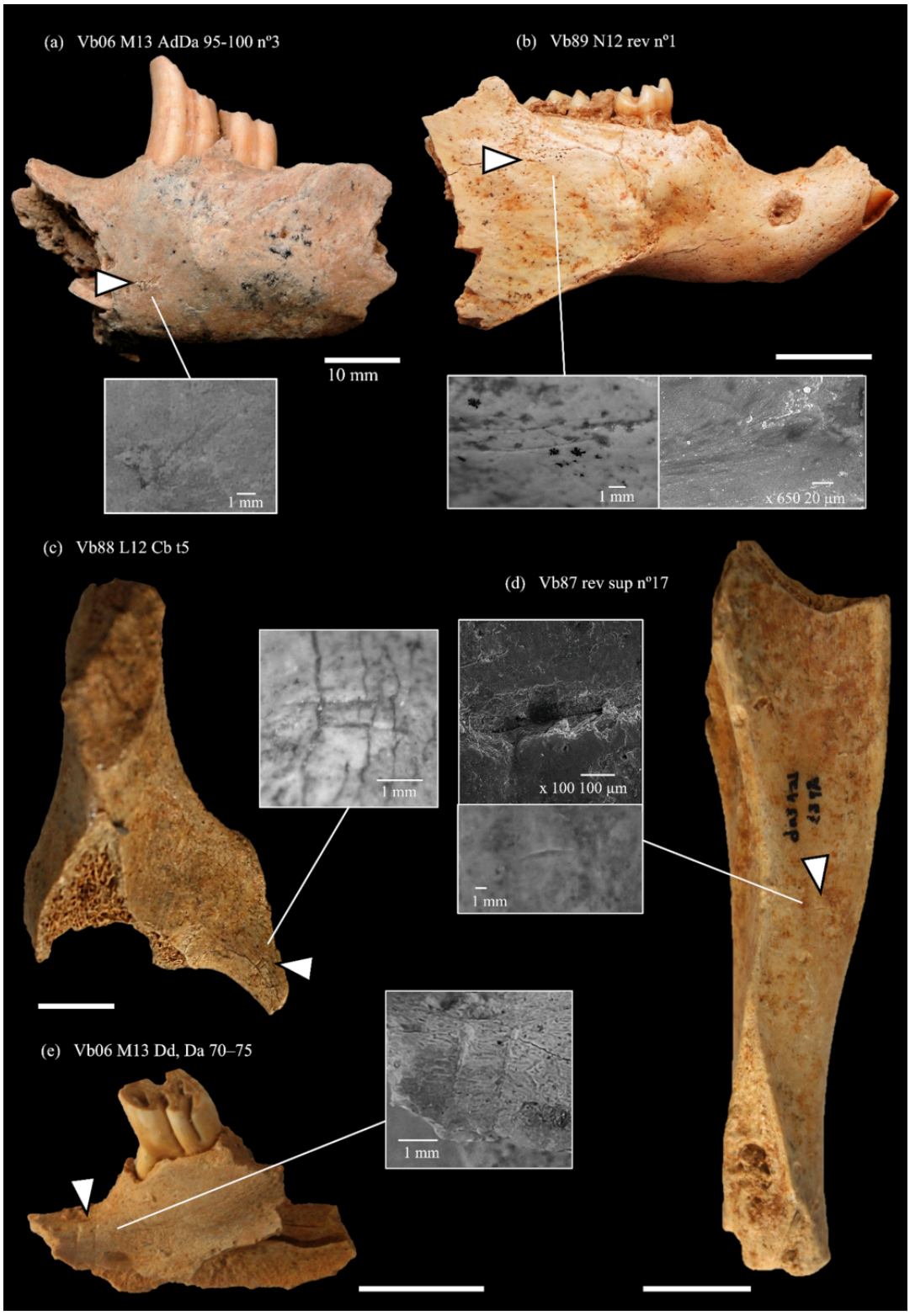


Figure 7

Cut marks on large-rodent remains from Valdegoba Cave. (a) *C. fiber* left hemimandible Vb06 M13 Ad,Da 95–100 3 showing two parallel cut marks on the labial surface. (b) *M. marmota* right hemimandible Vb89 N12 revuelto 1, with cut marks on the lateral surface close to the alveolar margin. SEM micrographs show the marked area at ×150 the internal microstriations; (c) *C. fiber* right coxal Vb88 L12 Cb, 40–50 cm, T5, showing two short, parallel cut marks on the proximal portion of the pubis, close to the fracture

margin. Image from Olympus DSX1000 at ×10; (d) *C. fiber* right tibia Vb87 revuelto superior 17, showing a transverse cut mark on the diaphysis. SEM micrographs at ×100 show the V-shaped groove and associated internal microstriations and Hertzian cones. White arrows indicate the location of the cut mark; (e) Immature *C. fiber* right hemimandible Vb06 M13 Dd,Da 70–75, showing linear marks anterior to the teeth in the symphyseal region, also visible on the amplified image.