

New data about Neanderthal subsistence strategies in El Cierro cave (Ribadesella, Asturias) during the MIS 3

Rodrigo PORTERO, Mikelo ELORZA,
Jesús F. JORDÁ PARDO & Esteban ÁLVAREZ-FERNÁNDEZ



DIRECTEURS DE LA PUBLICATION / PUBLICATION DIRECTORS :

Gilles Bloch, Président du Muséum national d'Histoire naturelle
Étienne Ghys, Secrétaire perpétuel de l'Académie des sciences

RÉDACTEURS EN CHEF / EDITORS-IN-CHIEF: Michel Laurin (CNRS), Philippe Taquet (Académie des sciences)

ASSISTANTE DE RÉDACTION / ASSISTANT EDITOR: Adenise Lopes (Académie des sciences; cr-palevol@academie-sciences.fr)

MISE EN PAGE / PAGE LAYOUT: Audrina Neveu (Muséum national d'Histoire naturelle; audrina.neveu@mnhn.fr)

RÉVISIONS LINGUISTIQUES DES TEXTES ANGLAIS / ENGLISH LANGUAGE REVISIONS: Kevin Padian (University of California at Berkeley)

RÉDACTEURS ASSOCIÉS / ASSOCIATE EDITORS (*, took charge of the editorial process of the article/a pris en charge le suivi éditorial de l'article):

Micropaléontologie/Micropalaeontology

Lorenzo Consorti (Institute of Marine Sciences, Italian National Research Council, Trieste)

Paléobotanique/Palaeobotany

Cyrille Prestianni (Royal Belgian Institute of Natural Sciences, Brussels)

Anaïs Boura (Sorbonne Université, Paris)

Métazoaires/Metazoa

Annalisa Ferretti (Università di Modena e Reggio Emilia, Modena)

Paléoichthyologie/Palaeoichthyology

Philippe Janvier (Muséum national d'Histoire naturelle, Académie des sciences, Paris)

Amniotes du Mésozoïque/Mesozoic amniotes

Hans-Dieter Sues (Smithsonian National Museum of Natural History, Washington)

Tortues/Turtles

Walter Joyce (Universität Freiburg, Switzerland)

Lépidosauromorphes/Lepidosauromorphs

Hussam Zaher (Universidade de São Paulo)

Oiseaux/Birds

Jingmai O'Connor (Field Museum, Chicago)

Paléomammalogie (mammifères de moyenne et grande taille)/Palaeomammalogy (large and mid-sized mammals)

Grégoire Métais (CNRS, Muséum national d'Histoire naturelle, Sorbonne Université, Paris)

Paléomammalogie (petits mammifères sauf Euarchontoglires)/Palaeomammalogy (small mammals except for Euarchontoglires)

Robert Asher (Cambridge University, Cambridge)

Paléomammalogie (Euarchontoglires)/Palaeomammalogy (Euarchontoglires)

K. Christopher Beard (University of Kansas, Lawrence)

Paléoanthropologie/Palaeoanthropology

Aurélien Mounier (CNRS/Muséum national d'Histoire naturelle, Paris)

Archéologie préhistorique (Paléolithique et Mésolithique)/Prehistoric archaeology (Palaeolithic and Mesolithic)

Nicolas Teyssandier* (CNRS/Université de Toulouse, Toulouse)

Archéologie préhistorique (Néolithique et âge du bronze)/Prehistoric archaeology (Neolithic and Bronze Age)

Marc Vander Linden (Bournemouth University, Bournemouth)

RÉFÉRÉS / REVIEWERS: <https://sciencepress.mnhn.fr/fr/periodiques/comptes-rendus-palevol/referes-du-journal>

COUVERTURE / COVER:

Made from the Figures of the article.

Comptes Rendus Palevol est indexé dans / *Comptes Rendus Palevol* is indexed by:

- Cambridge Scientific Abstracts
- Current Contents® Physical
- Chemical, and Earth Sciences®
- ISI Alerting Services®
- Geoabstracts, Geobase, Georef, Inspec, Pascal
- Science Citation Index®, Science Citation Index Expanded®
- Scopus®.

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Comptes Rendus Palevol* sont référencés par /
Articles and nomenclatural novelties published in Comptes Rendus Palevol are registered on:

- ZooBank® (<http://zoobank.org>)

Comptes Rendus Palevol est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris et l'Académie des sciences, Paris
Comptes Rendus Palevol is a fast track journal published by the Museum Science Press, Paris and the Académie des sciences, Paris

Les Publications scientifiques du Muséum publient aussi / The Museum Science Press also publish:

Adansonía, Geodiversitas, Zoosystema, Anthropolozologica, European Journal of Taxonomy, Naturae, Cryptogamie sous-sections *Algologie, Bryologie, Mycologie*.

L'Académie des sciences publie aussi / The Académie des sciences also publishes:

Comptes Rendus Mathématique, Comptes Rendus Physique, Comptes Rendus Mécanique, Comptes Rendus Chimie, Comptes Rendus Géoscience, Comptes Rendus Biologies.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)

Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

© This article is licensed under the Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>)

ISSN (imprimé / print): 1631-0683/ ISSN (électronique / electronic): 1777-571X

New data about Neanderthal subsistence strategies in El Cierro cave (Ribadesella, Asturias) during the MIS 3

Rodrigo PORTERO

University of La Rioja, Department of Human Sciences,
C. Luis de Ulloa 2, 26004 Logroño, La Rioja (Spain)
and Estudios de prehistoria de la Península Ibérica (PREHUSAL) Research Group,
University of Salamanca, C. Cerrada de Serranos s/n, 37008 Salamanca, Castilla y León (Spain)
and Scope Research Group, International Institute of Prehistoric Research of Cantabria (IIIPC),
University of Cantabria, Santander, Avenida de los Castros s/n, 39005 Cantabria (Spain)
rodrigo.portero@unirioja.es (corresponding author)

Mikelo ELORZA

Aranzadi Science Society, Zorroagaina 11, 20014 Donostia, Gipuzkoa (Spain)

Jesús F. JORDÁ PARDO

Estudios de prehistoria de la Península Ibérica (PREHUSAL) Research Group,
University of Salamanca, C. Cerrada de Serranos s/n, 37008 Salamanca, Castilla y León (Spain)
and National University of Distance Education, Department of Prehistory and Archaeology,
Faculty of Geography and History, Paseo Senda del Rey 7, 28040 Madrid (Spain)

Esteban ÁLVAREZ-FERNÁNDEZ

Estudios de prehistoria de la Península Ibérica (PREHUSAL) Research Group,
University of Salamanca, C. Cerrada de Serranos s/n, 37008 Salamanca, Castilla y León (Spain)
and University of Salamanca, Department of Prehistory, Ancient History and Archaeology,
C. Cerrada de Serranos s/n. 37008 Salamanca, Castilla y León (Spain)

Submitted on 14 June 2024 | Accepted on 4 April 2025 | Published on 24 July 2025

[urn:lsid:zoobank.org:pub:FB21DF75-A120-4B3B-A21F-18D1ADDFD9DF](https://zoobank.org/pub:FB21DF75-A120-4B3B-A21F-18D1ADDFD9DF)

Portero R., Elorza M., Jordá Pardo J. F. & Álvarez-Fernández E. 2025. — New data about Neanderthal subsistence strategies in El Cierro cave (Ribadesella, Asturias) during the MIS 3. *Comptes Rendus Palevol* 24 (19): 363-379. <https://doi.org/10.5852/cr-palevol2025v24a19>

ABSTRACT

In recent decades, research on the subsistence strategies of Neanderthal groups in the Spanish Cantabrian region has advanced our knowledge of the ways in which these hunter-gatherer groups organised subsistence-related tasks during MIS 3. This paper offers new insights on this issue through El Cierro cave (Asturias), a site with one of the most complete archaeological sequences in Cantabrian Spain, with chronologies ranging from the late Pleistocene to the early Holocene. Here we present the results of the archaeozoological and taphonomic analysis of the Mousterian level (Cierro N), whose faunal remains come from the archaeological campaigns carried out in the cave in 2016. In this research we present a new radiocarbon dating for Cierro N, which places the archaeological deposit between *c.* 57 and 45 ky cal BP. The results obtained from the archaeozoological study indicate the presence of macromammals and birds at Cierro N, the first being the most abundant. Taphonomic analysis has revealed the anthropic manipulation of the remains of red deer, Iberian ibex and large bovids by Neanderthal groups. Carnivores are present at the site and have generated modifications on some elements of the archaeozoological record. In addition, a series of natural taphonomic alterations has been documented, which have allowed us to determine the processes of transformation of the stratigraphic level. These aspects have allowed us to compare the subsistence patterns of the Mousterian groups from El Cierro with other sites of similar chronology in Cantabrian Spain.

KEY WORDS

Zooarchaeology,
taphonomy,
Mousterian,
Neanderthals,
palaeoeconomy,
Cantabrian Spain.

RÉSUMÉ

Nouvelles données sur les stratégies de subsistance des Néandertaliens dans la grotte d'El Cierro (Ribadesella, Asturias) pendant le MIS 3.

Au cours des dernières décennies, les recherches sur les stratégies de subsistance des groupes Néandertaliens dans la région cantabrique ont fait progresser nos connaissances sur la façon dont ces groupes de chasseurs-cueilleurs organisaient les tâches liées à la subsistance au cours du MIS 3. Cet article offre de nouvelles perspectives sur cette question grâce à la grotte d'El Cierro (Asturies), un site avec l'une des séquences archéologiques les plus complètes de l'Espagne cantabrique, avec des chronologies allant de la fin du Pléistocène au début de l'Holocène. Nous présentons ici les résultats de l'analyse archéozoologique et taphonomique du niveau moustérien (Cierro N), dont les restes fauniques proviennent de la campagne archéologique menée dans la grotte en 2016. Dans cette recherche, nous présentons une nouvelle datation radiocarbone pour Cierro N, qui situe le dépôt archéologique entre environ 57 et 45 ky cal BP. Les résultats de l'étude archéozoologique indiquent la présence de macromammifères et d'oiseaux à Cierro N, les premiers étant les plus abondants. L'analyse taphonomique a révélé la manipulation anthropique des restes de cerfs, de bouquetins ibériques et de grands bovidés par des groupes néandertaliens. Les carnivores sont présents sur le site et ont provoqué des modifications sur certains éléments de l'enregistrement archéozoologique. En outre, une série d'altérations taphonomiques naturelles a été documentée, ce qui nous a permis de déterminer les processus de transformation du niveau stratigraphique. Ces aspects nous ont permis de comparer les modes de subsistance des groupes moustériens d'El Cierro avec d'autres sites de chronologie similaire en région cantabrique.

MOTS CLÉS

Zooarchéologie,
taphonomie,
Moustériens,
Néandertaliens,
paléoeconomie,
région cantabrique.

INTRODUCTION

The analysis of the subsistence strategies of the Neanderthals that inhabited the Iberian Peninsula has been a topic that has aroused great interest in the scientific community, giving rise to a large number of studies that address the socio-economic behaviour of these hominins from, among other topics and methods, archaeozoology and taphonomy (e.g. Hockett & Haws 2009; Cortés-Sánchez *et al.* 2011; Yravedra 2013; Nabais 2018; Blasco *et al.* 2022), human-carnivore interaction (e.g. Camarós *et al.* 2016; Luret *et al.* 2020; Linares-Matás & Yravedra 2024), lithic and bone industry (e.g. Thiébaud *et al.* 2012; Cuartero *et al.* 2015; Alonso-García *et al.* 2020; Romero *et al.* 2023), plant consumption (e.g. Hardy *et al.* 2001; Salazar-García *et al.* 2013;

Hardy 2022), experimental studies (e.g. Yravedra *et al.* 2005; Yravedra & Uzquiano 2013; Nabais *et al.* 2024), environment (Fernández-García *et al.* 2023; Pederzani *et al.* 2023; Vidal-Cordasco *et al.* 2023), and isotopic analysis (e.g. Jones *et al.* 2018; Fernández-García *et al.* 2022; Jaouen *et al.* 2022); as well as some synthesis (Yravedra *et al.* 2016; Marín-Arroyo & Sanz-Royo 2022; Romagnoli *et al.* 2022).

In the Spanish Cantabrian region, studies on the subsistence of Neanderthal populations have been approached mainly from a comparative perspective with the early Anatomically Modern Humans (AMH) (see, for example, Yravedra 2000, 2013; Yravedra *et al.* 2016; Marín-Arroyo *et al.* 2018, 2020; Marín-Arroyo & Sanz-Royo 2022; Linares-Matás & Yravedra 2024). This is due to the fact that in recent decades archaeological excavations have multiplied at sites with levels

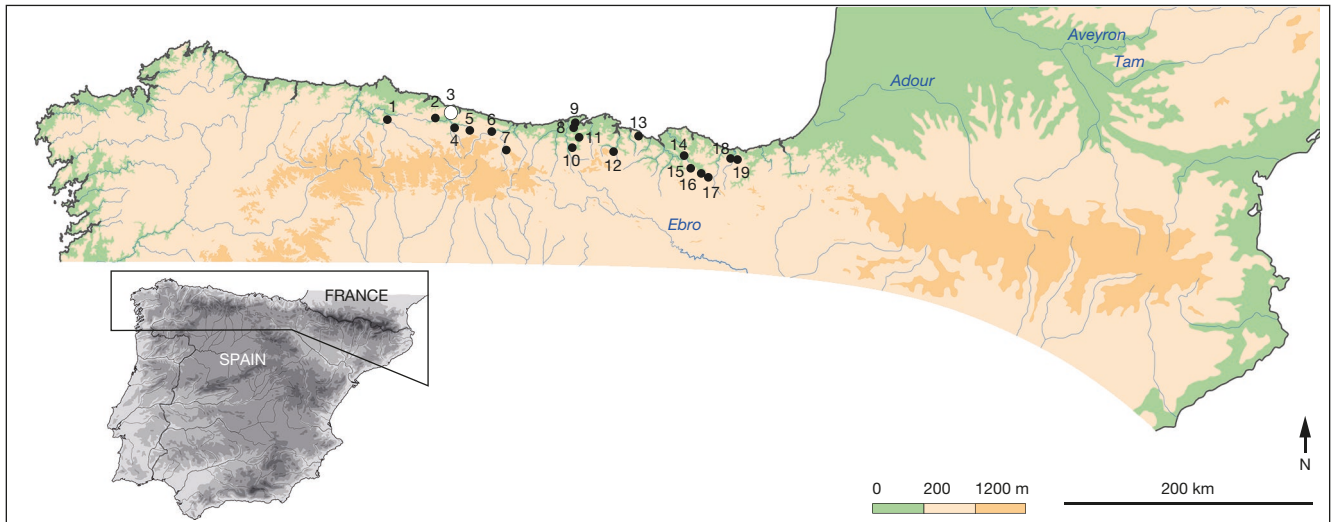


FIG. 1. — Map showing the location of the El Cierro Cave and other Mousterian sites in Cantabrian Spain mentioned in the text: 1, La Viña; 2, El Sidrón; 3, El Cierro; 4, La Güegla; 5, Sopeña; 6, Llonin; 7, El Esquilleu; 8, Covalejos; 9, El Ruso; 10, Hornos de la Peña; 11, Morín; 12, El Mirón; 13, El Cuco; 14, Arlanpe; 15, Axlór; 16, Lezetxiki; 17, Labeko koba; 18, Ekain; 19, Amalda. Credits: map by L.C. Teira.

ascribed to transitional periods between Middle and Upper Palaeolithic, such as Covalejos (Montes Barquín & Sanguino 2021), El Esquilleu (Baena & Carrión 2014), El Mirón (Straus & González Morales 2012), El Sidrón (de la Rasilla *et al.* 2020), Hornos de la Peña (Sanz-Royo *et al.* 2023), El Cuco (Muñoz *et al.* 2007) or Axlór (González-Urquijo *et al.* 2014). This quantitative increase of the archaeological record has generated an important scientific production, constituting one of the richest regional records of palaeo-ecological and palaeoeconomic behaviours during Marine Isotopic Stadial3 (*c.* 57–30 ky cal. BP).

In general, all these works have shown that the groups from the end of the Mousterian period (between *c.* 57 and 45 ky cal BP) in the north of the Iberian Peninsula exploited mainly red deer, especially in those places where the environment was favourable for their captures, such as at El Ruso (Yravedra *et al.* 2010) or Covalejos (Castaños 2021). Iberian ibex and chamois were the taxa most consumed in sites located in mountainous areas with strong slopes, such as El Esquilleu (Yravedra & Gómez Castanedo 2014), Arlanpe (Arceredillo-Alonso *et al.* 2013) or Axlór (Castaños 2005); whereas in sites located in open areas and close to different ecological niches, hunting patterns were more diversified (Yravedra & Cobo-Sánchez 2015; Yravedra *et al.* 2016), as is the case of El Mirón (Marín-Arroyo *et al.* 2020), Sopeña (Yravedra *et al.* 2023), Cueva Morín (Yravedra & Gómez-Castanedo 2011) or Lezetxiki (Villaluenga *et al.* 2012).

The characterisation of Mousterian human occupations and their interaction with carnivores at different sites has also been a recurrent topic of study (Altuna 1989; Castaños 2005; Yravedra 2010a; Sanz-Royo *et al.* 2023; Linares-Matás & Yravedra 2024). Thus, some sites are presented as places of prolonged occupation by Neanderthal groups, as Covalejos (Castaños 2021), Esquilleu (Yravedra 2006b) or La Güelga (Rojo 2020), while other sites alternate human and carnivore occupations in relatively short periods of time, as Amalda

(Yravedra 2010a; Sánchez-Romero *et al.* 2020), El Ruso (Yravedra *et al.* 2010), La Viña (de la Rasilla *et al.* 2020), Hornos de la Peña (Yravedra 2010b) or El Llonin (Sanchís *et al.* 2019). Interpreting this type of relationship between hominids and carnivores involves several problems, such as the fact that some faunal data come from early excavations, that some levels present stratigraphic ascription problems and that there is a great imbalance in the volume of faunal remains between different sites, making comparisons difficult (Yravedra *et al.* 2016, 2023; Marín-Arroyo & Sanz-Royo 2022).

All these aspects highlight the need, on the one hand, to address the regional contexts of areas that have been little studied through significant bone samples and, on the other hand, to review the archaeological contexts of the period in order to clarify the interactions between hominids and carnivores, as well as the ways in which Neanderthal groups exploited the territory (Marín-Arroyo & Sanz-Royo 2022; Yravedra *et al.* 2023; Linares-Matás & Yravedra 2024).

In this paper we analyse the faunal remains from the Mousterian level (Cierro N) of El Cierro cave (Ribadesella, Asturias) from an archaeozoological and taphonomic perspective. The main objective of this research is to determine who were the agents responsible for the accumulation of the faunal remains in the cave. In case it was the Neanderthals, to characterise the type of exploitation carried out on these resources and to analyse their diachronic evolution throughout El Cierro sequence, providing new data on the subsistence strategies of the Neanderthal groups that inhabited the Sella valley during MIS 3.

The results obtained at Cierro N are compared with the information available in other Mousterian contexts from the Spanish Cantabrian region dated between the beginning of MIS 3 (*c.* 57 ky cal BP) and the end of the Mousterian (*c.* 45 ky cal BP) (Marín-Arroyo *et al.* 2018, 2020), offering an updated view on the subsistence strategies of these groups in their regional context. To make these comparisons more

TABLE 1. — Radiocarbon dating of Cierro N with indication of material, specie, laboratory code, radiocarbon date in BP, calibrated date (2σ at 95.4%) with IntCal20 curve (Reimer *et al.* 2020) with Oxcal v.4.4.2 and 13C parameters.

Level	Material	Species	Ref. lab.	Dates BP	Cal. BP 2σ	¹³ C
Cierro N	Tooth	<i>Bos/Bison</i> sp. (without cutmarks)	OxA-X-2620-13	49 000 ± 3 800	>50 000-46 963	−19.6

accurate, we have selected only those sites with radiocarbon-dated levels, containing faunal remains studied by archaeozoologist and data from excavations carried out with modern recovery techniques.

EL CIERRO CAVE

El Cierro is a karstic cave located at the eastern end of the Asturian Massif in the Cantabrian Mountains (Fig. 1). The cave opens at 83 m above sea level in a pre-coastal depression 3.1 km from the mouth of the River Sella and 2.1 km from the current coastline (Álvarez-Fernández *et al.* 2016, 2022; Jordá Pardo *et al.* 2018a, b).

The faunal remains analysed in this paper come from the main room of the site, specifically from an old core from the excavations carried out by F. Jordá Cerdá in the 1950s. It was excavated for the first time between 1977 and 1979 by F. Jordá Cerdá and A. Gómez-Fuentes who, after cleaning it, carried out an excavation below the shell midden levels that were cemented at the top of the sequence. The objective was to characterise the archaeological sequence of the cavity; however, the excavation was interrupted before reaching the base, after the excavation of the Magdalenian levels (Cierro G1). Work was restarted in 2016 by E. Álvarez-Fernández, who excavated the lower levels (Cierro H1 to N), with the Mousterian level (Cierro N) resting on the bedrock. In Cierro N, the excavated area was 100 × 60 × 50 cm and the extracted sediments were sieved with meshes of 8 to 0.5 mm light (Álvarez-Fernández *et al.* 2014, 2018).

These campaigns revealed a broad stratigraphic sequence for the site, composed of 14 levels (Cierro N to Cierro A), with occupations ascribed to the Mousterian, Aurignacian, Gravettian, upper Solutrean, lower Magdalenian, Azilian and Mesolithic (Fig. 2).

Level Cierro N is 20 cm thick and is lithostratigraphically composed of clayey sands and yellowish-greyish silts. Very altered limestone pebbles are documented here, which are laid out flat. The sands are quartz, angular and rounded, with sizes varying from medium to fine. The origin of the sedimentary deposit has a tabular geometry with a horizontal arrangement whose formation is due to a dense mudflow type current (Jordá Pardo *et al.* 2018a). The archaeological materials documented in this stratum date it to the end of the Middle Palaeolithic (Álvarez-Fernández *et al.* 2018; 2022).

For this level we have a radiocarbon dating by AMS carried out at the Oxford Radiocarbon Accelerator Unit. This dating was done on a tooth of *Bos/Bison* sp. and gave a date of 49 000 ± 3 800 BP (Table 1). In its calibration this date exceeds the lower radiocarbon limit of 50 000 cal BP and

would range up to 46 963 cal BP. Therefore, we can date the deposit between the beginning of MIS 3 (c. 57 ky cal BP) and the disappearance of the Mousterian in the northern Iberian Peninsula (c. 45 ky cal BP).

METHODOLOGY

All the faunal remains recovered at Cierro N were analysed from an archaeozoological and taphonomic point of view. The sediment from the level was sieved with fine meshes, which allowed us to recover and analyse bone fragments >0.5 mm (Álvarez-Fernández *et al.* 2018). Faunal remains from both excavation and sieving have been accounted for in this work.

The faunal remains were identified anatomically and taxonomically using the reference collections of the Zooarchaeology Laboratory at the University of Salamanca, the Aranzadi Science Society and the International Institute of Prehistoric Research of Cantabria. In addition, various animal anatomy atlases were used for the different mammal species (Barone 1966; Schmid 1972; Pales & Garcia 1981a, b; Varela & Rodríguez 2004; Hillson 2005) and birds (Kraft 1972).

To evaluate the skeletal profiles, each anatomical element was classified by anatomical region, differentiating between cranial (antler, skull, maxilla and mandible), axial (vertebra, rib, sternum, scapula, pelvis, sacrum and flat bone), forelimb (humerus, radius, ulna, carpal, metacarpus) and hindlimb (femur, patella, tibia, fibula, tarsal and metatarsal) elements. Those that could not be classified in an appendicular region were included in the category limb (metapodial, phalanx, sesamoid and diaphysis and epiphysis of long bone) (Yravedra 2006a; Portero *et al.* 2024a). Mammals that could not be identified at the taxonomic level were classified into three size categories; large (>300 kg), medium (between 100-300 kg) and small (5-100 kg), according to the criteria of thickness and robustness of the cortical bone (Bunn & Kroll 1986; Portero 2022).

The number of remains (NR), the number of identified specimens (NISP), the minimum number of elements (MNE) and the minimum number of individuals (MNI) have been calculated for the quantification of the archaeofaunal record (Bunn 1983; Marean & Spencer 1991; Lyman 1994; Reitz & Wing 2003). Age of death has been calculated through the state of fusion of epiphyses and patterns of dental eruption and wear for different mammalian species (Grigson 1982; Mariezkurrena 1983; Mariezkurrena & Altuna 1983; Węgrzyn & Serwatka 1984; Pérez Ripoll 1988; Brown & Chapman 1991; Azorit *et al.* 2002; 2003). Based on the estimated age, we have classified the individuals according to three age categories, considering the biological cycles of the current species (Portero *et al.* 2024a).

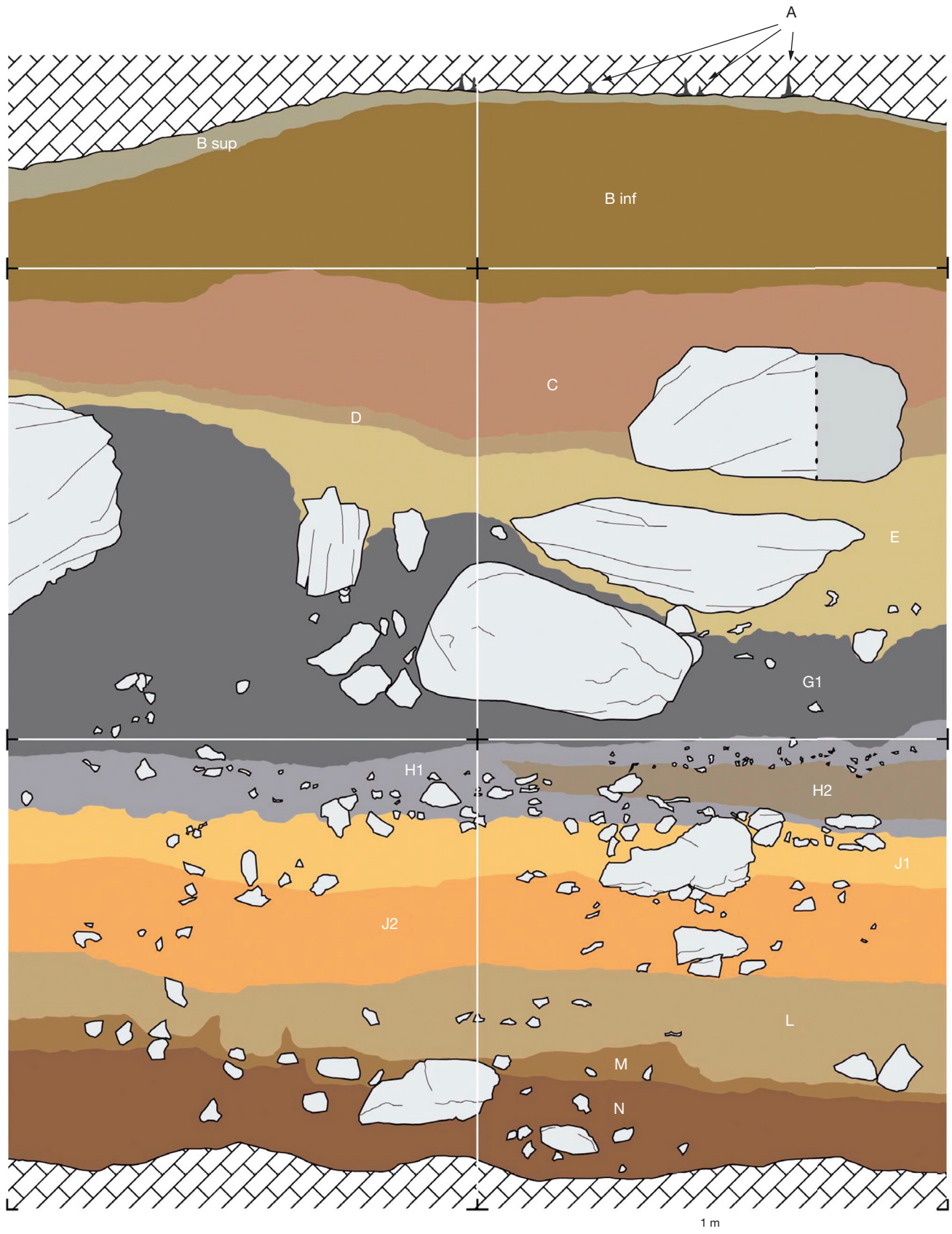


FIG. 2. — Stratigraphic sequence of the main room of El Cierro Cave (Álvarez-Fernández *et al.* 2016).

To evaluate the degree of fragmentation of the faunal remains, the fragmentation rate was calculated as the ratio between the NISP and the MNE (Marshall & Pilgram 1991; Lyman 1994). This rate gives a figure ≥ 1 and the further the value is from unity, the more fragmented the assemblage is.

Taphonomic analysis was carried out by observing bone surfaces through different hand magnifiers (5 $\times$, 10 $\times$, and 15 $\times$), combined with a Leica EZ4 HD (6.5–32 $\times$) and Teslong MS100 (10–200 $\times$) microscopes. We have taken into account the damage generated by natural and biological agents on the bone surfaces. This damage can lead to the destruction of the cortical surfaces of the bones, conditioning the interpretations of the agents causing the bone accumulations at the site. For this reason, in the first place we have considered the alterations related to the formation of the archaeological deposit and post-depositional processes (Behrensmeyer 1978; Behrensmeyer *et al.* 1986; Marín-Arroyo *et al.* 2008; Fernández-Jalvo & Andrews 2016).

The cutmarks were analysed in order to determine their function within the meat processing chain (Binford 1981). To this end, we have considered the morphology, location and orientation of the cutmarks on each bone, counting each of them individually (Bunn & Kroll 1986; Costamagno *et al.* 2019). Anthropogenic breakage of the bone with the aim of extracting the marrow has been analysed through angles, line, morphology, and type of fracture (Villa & Mahieu 1991; Pickering & Egeland 2006; Vettese *et al.* 2020). The percentage of preservation of the circumference of the diaphysis of the long bones was also taken into account, classifying them into four categories according to the preserved part (<25 % of the preserved diaphysis, between 25–50 %, between 50–75 %, and between 75–100 %). Similarly, the percentage of preserved length of the diaphysis has been counted in four categories (<25 % of the total length; between 25–50 %; between 50–75 %, and between 75–100 %) (Bunn 1983; Villa & Mahieu 1991; Villa *et al.* 2004). The degree of thermoalteration has been calculated from the colour of the bone surfaces (Stiner *et al.* 1995), which has allowed us to approximate the temperature to which they were exposed (Nicholson 1993). To determine the function of cremation for the roasting of meat or for the use of bone as fuel, differential burning processes were recorded by counting bone surfaces with double and triple colouration, as well as their location in the bone (Nicholson 1993; Cáceres *et al.* 2002; Costamagno *et al.* 2005; Yravedra *et al.* 2005; Yravedra & Uzquiano 2013). Moreover, carnivore marks have been classified according to their morphology (Haynes 1980; Selvaggio 1994).

Palaeoeconomic analysis has been carried out considering the nutritional contribution and the economic profitability of the prey hunted by the Mousterian groups of El Cierro. For this purpose, we have applied the following procedure (Portero *et al.* 2019, 2024b):

- establishing the mean weight of each taxon from the proportion of males and females of each species, based on current animal populations (Clutton-Brock & Iason 1986). For Cierro N, we used the mean weights for males and females of red deer (Carranza 2017), Iberian ibex (Alados & Escós 2017) and Bison (Kraśnińska & Kraśniński 1995, 2002);

- calculation of the weight of meat plus fat for each animal, based on the observations of L.W. Binford (1978) for caribou and sheep, applicable in the Cantabrian region to cervids and small bovines. In addition, as the contribution of mammals' meat and fat varies significantly depending on the age of the individual, we have established a reduction in the weight of the adult animal of 33 % for juveniles and 66 % for immature individuals, broadly coinciding with the weights established in their life cycles (Portero *et al.* 2022, 2024b). In this way, we have obtained the weight of the exploitable part of each of the animals;

- we estimated the calories per kilo of meat and fat for each of these animals, based on the data provided by the food tables of the US Department of Agriculture (USDA 2020). These figures have allowed us to document the total energy provided by each specimen when multiplied by the weight contributed by its meat and fat. To ensure that the contribution of the mammals documented in these sites is due to human activity, we only use those species that show signs of anthropic manipulation indicating that they were contributed to and consumed by human groups.

From this estimate, we have established which were the prey that contributed the greatest energy intake to the diet of the Mousterian groups of El Cierro. These data serve as an estimate of the economic profitability of these species, since they do not consider search time, handling time and return rates, which affect the costs of obtaining prey (MacArthur & Pianka 1966; Simms 1987; Marín-Arroyo 2010; Portero *et al.* 2019, 2024b).

RESULTS

Cierro N has 1399 faunal remains, of which 99 have been determined. Only 23 have been taxonomically classified. From the NISP, red deer is the most abundant species with 11 remains, followed by hyena with four and large bovid with two. The other specimens are represented with a single element, among them horse, Iberian ibex, and cave bear. In addition, we recovered an ivory fragment belonging to a tusk of *Elephas* sp., a proximal fragment of humerus of *Alectoris/Perdix* sp., a fragment of lumbar vertebra from a small indeterminate carnivore and the diaphysis of a tibiotarsus from an indeterminate bird. In the size categories, medium-size mammals are the most abundant (NR = 52) followed by the small (NR = 22) and large (NR = 2) (Table 2).

As for the MNE, its distribution is similar to the NISP, with the red deer having the greatest number of elements, followed by the hyena (MNE = 3), the large bovid (MNE = 2) and the rest of the taxa, documented with a single element. Red deer is represented by seven elements: a tibia, an ulna, a fragment of antler, and four teeth. All the elements of hyena, cave bear and *Elephas* sp. correspond to teeth. There is a metapodial fragment for large bovid, a third phalanx for Iberian ibex, and a first phalanx for horse. In the size categories, the medium mammal is the one with the greatest number of elements (MNE = 11), with all regions of the

TABLE 2. — Number of remains (NR), number of identified specimens (NISP), minimum number of elements (MNE) and minimum number of individuals (MNI) by age categories of animal remains documented in Cierro N. Abbreviations: AD, adult; IMM, immature; JU, juvenile.

	NR	NISP	MNE	MNI	IMM	JU	AD
<i>Cervus elaphus</i> (Linnaeus, 1758)	11	11	7	2	1	–	1
<i>Bos/Bison</i> sp.	2	2	2	1	–	–	1
<i>Capra pyrenaica</i> (Schinz, 1838)	1	1	1	1	–	–	1
<i>Equus ferus</i> (Boddaert, 1785)	1	1	1	1	–	–	1
<i>Ursus spelaeus</i> (Rosenmüller, 1794)	1	1	1	1	–	1	–
<i>Crocota crocuta</i> (Erxleben, 1777)	4	4	3	1	–	–	1
<i>Elephas</i> sp. (Linnaeus, 1758)	1	1	1	–	–	–	–
Carnivora	1	1	1	–	–	–	–
Large size mammal	2	–	1	–	–	–	–
Medium size mammal	52	–	11	–	–	–	–
Small size mammal	21	–	9	–	–	–	–
Subtotal large mammals	97	22	38	7	–	–	–
<i>Alectoris/Perdix</i> sp.	1	1	1	1	–	–	1
Indeterminable bird	1	–	1	–	–	–	–
Subtotal birds	2	1	2	1	–	–	–
Indeterminable	1300	–	–	–	–	–	–
Total	1399	23	40	8	1	1	6

TABLE 3. — Skeletal remains in Cierro N. Abbreviations: L.M., large-size mammal; M.M., medium-size mammal; S.M., small-size mammal.

	<i>Elephas</i> sp.	<i>Cervus elaphus</i>	<i>Bos/Bison</i> sp.	<i>Capra pyrenaica</i>	<i>Equus ferus</i>	<i>Ursus spelaeus</i>	<i>Crocota crocuta</i>	Carnivora	<i>Alectoris/Perdix</i> sp.	L. M.	M. M.	S. M.
Antler	–	2	–	–	–	–	–	–	–	–	–	–
Skull	–	–	–	–	–	–	–	–	–	–	–	2
Tooth	1	4	1	–	–	1	2	–	–	–	5	4
Mandible	–	–	–	–	–	–	–	–	–	–	1	2
Hyoid	–	–	–	–	–	–	–	–	–	–	1	–
Lumbar v.	–	–	–	–	–	–	–	1	–	–	–	–
Vertebrae ind.	–	–	–	–	–	–	–	–	–	–	6	3
Rib	–	–	–	–	–	–	–	–	–	1	1	1
Flat bone	–	–	–	–	–	–	–	–	–	–	10	2
Humerus	–	–	–	–	–	–	–	–	1	–	–	1
Radius	–	–	–	–	–	–	–	–	–	–	1	–
Ulnae	–	2	–	–	–	–	–	–	–	–	–	–
Femur	–	–	–	–	–	–	–	–	–	–	4	1
Tibiae	–	2	–	–	–	–	–	–	–	–	–	–
Metapodial	–	–	1	–	–	–	–	–	–	–	3	–
Long bone	–	–	–	–	–	–	–	–	–	1	19	4
Phalanx 1	–	–	–	–	1	–	2	–	–	–	–	–
Phalanx 3	–	–	–	1	–	–	–	–	–	–	–	1

skeleton represented. In the small mammal we do not have forelimbs, while the cranial elements are the most abundant, and in the case of the large mammal we only have a rib and a diaphysis of a long bone (Tables 2; 3).

Regarding the MNI, red deer is the only taxa with two individuals represented: an immature under four months, and an adult, whose age we have not been able to determine. There is one young adult hyena, given the lack of dental wear in the documented specimens. There is also one adult in the case of horse, Iberian ibex, large bovid, and *Alectoris/Perdix* sp. The cave bear is represented by a juvenile individual, given the scarce wear on the teeth.

The faunal assemblage from Cierro N is highly fragmented. We have only been able to identify 6.94 % of the remains and only four dental pieces are complete. In the case of determinable remains, 78.4 % are <3 cm, with the range between

2 and 3 cm being the best represented (49.5 %). The fragmentation rate (NISP/MNE) for the determinable remains shows a value of 1.61; therefore, there is a high degree of fragmentation in the archaeozoological sample. This is one of the factors that prevents us from having a greater number of identifiable remains in the Mousterian level of El Cierro.

Despite the high fragmentation of the bone record, the preservation state of the fossil remains is generally good, with 72 % of the surface's observable. Although 79 % of the faunal remains have been affected by natural agents, most of them have not caused alterations in the visualisation of the cortical surfaces. The concretions have made it impossible to see the surfaces properly, affecting 5.11 % of the remains, although only half of them have completely covered the surface of the bone. Water action has generated corrosion on 6.12 % of the NR, generating degradation of the bone surfaces.



FIG. 3. — Taphonomic alterations of the faunal remains from Cierro N: **A**, rolled and manganese-coated medium-size mammal long bone; **B**, diaphysis of medium-size mammal long bone partially stained with manganese; **C**, **D**, cutmarks on diaphysis of long bones of medium-size mammal; **E**, impact notches in a medium-size mammal femur diaphysis; **F**, flakes; **G**, burnt bones with different tones of colour; **H**, fragment of medium-size mammal flat bone with pits; **I**, digested indeterminate bone. Scale bar: A, B1, C1, D1, E-H1, I1, 2 cm; B2, 1.2 x 1.8 cm; C2, D2, 1 x 0.8 cm; H2, 0.8 x 1.7 cm; I2, 1.2 x 1.2 cm

TABLE 4. — Anthropogenic alterations documented in Cierro N by taxa and size categories.

Taxa	Cutmarks	Percussion marks	Thermoalterations
<i>Cervus elaphus</i> Linnaeus, 1758	2	1	—
<i>Bos/Bison</i> sp.	—	1	—
<i>Capra pyrenaica</i> Schinz, 1838	—	—	1
Large-size mammal	—	1	—
Medium-size mammal	9	6	5
Small-size mammal	—	1	2
Indeterminable	—	—	547

Manganese oxides have covered the surfaces of 66.3 % of the bones. Most of them have a shiny black colour, and in most cases, they are evenly distributed. Regarding the intensity of the shades, 50.75 % of the affected bones show a black shade, 40.30 % dark-brown and 8.95 % show light-brown shades. Regarding the area affected by the manganese oxides, most of them (53.73 %) have affected less than a quarter of the bone, 25.37 % have stained around 50 % of the bones, 14.93 % three quarters of the remains and 5.97 % have completely covered the bone (Fig. 3A, B). Weathering affected 20.41 % of the remains, generating small cracking in most of them, but no signs of deep degradation of the cortical surfaces, so their exposure to atmospheric conditions was not very prolonged. The rolling of bones due to water activity has also been documented in Cierro N, having affected 11.22 % of NR. In some cases, this rolling has been of great intensity, completely polishing the edges of the bone and affecting the visualisation of the cortices. One aspect to point out is that all of them were stained by manganese oxides (see Fig. 3A). The roots of the plants have generated vermiculations in 10.20 % of NR. Roots generally appear in isolation and in no case have they occupied more than a quarter part of the bone surfaces. The imprints generated by the roots present the same colour as the surface of the bones, which indicates that they were generated in the moments prior to the burial of the bones (Fernández-Jalvo & Andrews 2016). Additionally, we have documented another series of alterations that have affected <8 % of NR, including trampling, flattening, and microorganisms.

Taphonomic analysis of the faunal remains indicates the presence of anthropogenic manipulation. Evidence of this activity can be seen from cutmarks, bone breakage and thermoalteration processes (Table 4). Regarding the first, we have documented the processing of the bone carcasses of red deer and medium-size mammals. In the case of red deer, we have two tibiae with oblique and longitudinal incisions in the diaphysis, which would be related to the tasks of defleshing the animal. For the medium-size mammals, we have 10 remains with cutmarks consisting of incisions, scrapes and sawing marks located mainly on the diaphysis of long bones, also present on a femur and a metapodial (Fig. 3C, D). These marks are mainly related to the defleshing processes of these animals, but we have also documented traces related to the disarticulation of the appendicular skeleton on a metapodial, and the scraping of the periosteum on a femoral diaphysis and a long bone fragment.

We have found some evidence of intentional fracturing of green bones in the 34.09 % of NR. In the case of the medullary bones, the fracture occurs in 70.47 % of remains in order to gain access to the medullary fat. 14.77 % of NR had both green and dry fractures, combining acute and obtuse angles with right angles and mixed delineations. A large percentage of NR (51.14 %) had dry fractures, with straight angles and perpendicular and longitudinal delineations. Regarding the percentage of preservation of the circumference and length of the diaphysis, we observed that most of the remains present <25 % of the circumference and <25 % of the length of the shaft. Only 3 elements present 100 % of the circumference of the diaphysis (Fig. 4).

All the impact notches and counterblows documented to extract the marrow contents have been made on the diaphysis of the long bones (Fig. 3E). In the case of red deer, the impacts are on the lateral side of a tibia. In large bovids, they are located in the lateral side of a metapodial, where a point of impact is located together with a counterblow. In medium-size mammals, the impacts are located on the lateral faces of the femurs and the diaphysis of long bones, and evidence of counterblows and adhering flakes has been documented. The only percussion mark documented in small mammals is a diaphysis of a long bone with an impact point. In addition to these fracture marks, we have recovered 18 flakes from the fracturing process of the bones (Fig. 3F).

Thermoalteration has been the anthropic evidence that has affected the greatest number of remains ($n = 554$), affecting Iberian ibex, small and medium-size mammals and indeterminable remains. Although we have all the burnt colourations in the faunal record from Cierro N, most of the remains have grey and white tones, with black colourations also being abundant (Fig. 3G). Based on the classification of M. C. Stiner *et al.* (1995), 40.7 % of the cremated remains would correspond to grade 6. This suggests that they were exposed to temperatures above 800°C (Nicholson 1993), although these shades may also be due to prolonged exposure of the remains to low temperatures (Gallo *et al.* 2023). In addition, many of these remains show evidence of reduction in size and cracking of the surface of the bones, which could indicate that they did not contain meat when exposed to fire. This large number of bones exposed with these colourations could be related to their use as fuel by human groups, or to cleaning tasks. On the other hand, we have a smaller number of remains exposed to low temperatures (<400°C) that show brown and brown-black shades of their surfaces.

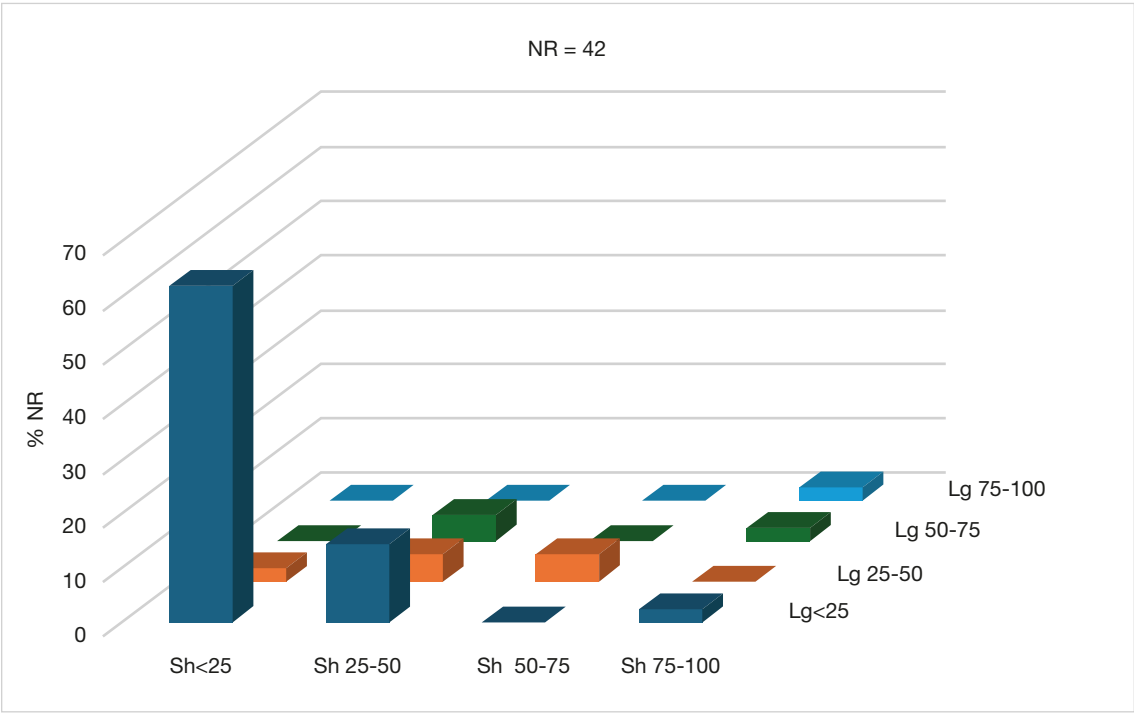


FIG. 4. — Three-dimensional bar diagrams showing the frequencies of shaft length categories (Lg <25%; Lg 25-50%; Lg 50-75%; Lg 75-100%) by shaft circumference (Sh <25%; Sh 25-50%; Sh 50-75%; Sh 75-100%) of long bones.

TABLE 5. — Caloric energy provided by taxon and age category of the macromammal species documented in Cierro N, based on the average weight of both sexes and the proportion of meat and fat provided by each individual per age category. Abbreviation: **AD**, adult; **IMM**, immature; **MNI**, minimum number of individuals.

Taxon	Age cat.	Middle weight (Kg)	Meat + fat (Kg)	Energy (Kcal/Kg)	MNI	Total meat + fat (Kg)	Total energy (Kcal)
<i>Cervus elaphus</i>	AD	93.5	36.7	1 110	1	36.7	40 737
Linnaeus, 1758	IMM	31.1	12.2	1 110	1	12.2	13 542
<i>Capra pyrenaica</i>	AD	51.2	19.4	1 140	1	19.4	22 116
Schinz, 1838							
<i>Bos</i> Linnaeus, 1758/ <i>Bison</i> Smith, 1827	AD	600	300	1 220	1	300	366 000

In these cases, they show a tonality compatible with the exposure of bones with soft tissue to heat sources for a relatively short period of time, which could be indicative of meat roasting by Neanderthal groups at El Cierro. Although remains with this type of double shades are scarce and most of them are documented in indeterminable remains, the location in a third phalanx of *Capra pyrenaica* (see Fig. 3G), in the metaphysis of a long bone of a small-size mammal and the proximal diaphysis of a medium-size mammal could be reflecting this practice.

Carnivores have partially modified the faunal record, generating pits, grooves, and digestion traces in three medium-size mammal remains and an undeterminable one (Fig. 3H, I). Two of the determinable remains affected by carnivores correspond to flat bones of the axial skeleton and one to the diaphysis of a metapodial. The poor preservation of their surfaces has not allowed us to measure the depressions to determine the carnivore responsible for the modifications.

Regarding the energy contribution of the faunal remains to the diet of the Neanderthal groups of El Cierro, we have calculated the amount of meat and fat that animals with some type of anthropogenic alteration at the level would have provided (Table 5). Although there are very few individuals with anthropogenic alterations, the full exploitation of hunted prey could have provided *c.* 368.3 kg of meat and fat with around 442,395 kcal.

DISCUSSION

The faunal remains studied at the Mousterian level, although scarce, provide an approach to the subsistence strategies of the Neanderthal groups of El Cierro.

Red deer is the best represented ungulate at the level with 50 % of the NISP, followed by the bovid with two remains, while the rest of them are represented by a single element.

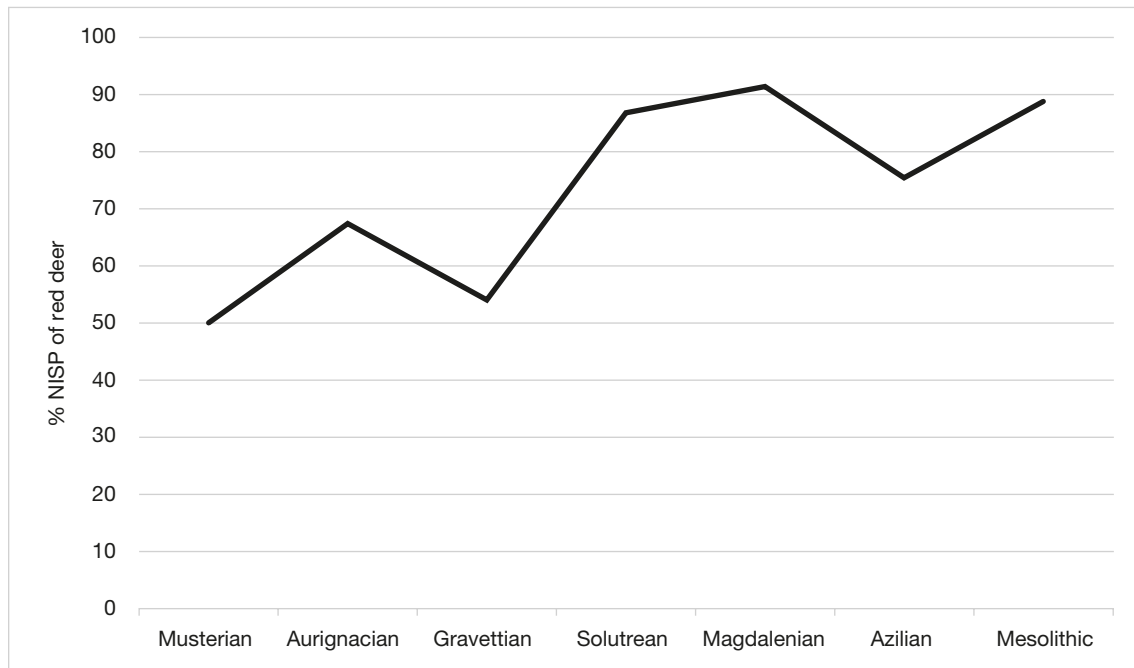


Fig. 5. — Percentage of NISP of red deer in the different periods of El Cierro sequence.

This predominance of red deer is something observed throughout the entire sequence of El Cierro (Álvarez-Fernández *et al.* 2018, 2022; Portero *et al.* 2019, 2024a), although in this case, the representation percentages are lower than at other Upper Pleistocene periods in the sequence, especially in comparison with the lower Magdalenian levels (Fig. 5). Something similar happens at other levels of Asturian sites such as Viña XIII and XIV (de la Rasilla *et al.* 2020) and Güelga 4 (zone D Exterior) (Rojo 2020), and from Cantabrian and Basque Country sites, as Hornos de la Peña 13 and 14 (Sanz-Royo *et al.* 2023), Amalda VII (Yravedra 2010a) and Lezetxiki IV (Villaluenga *et al.* 2012), where red deer is the predominant taxon, but shares importance in subsistence strategies with other mammals such as chamois or horse. In contrast, we have a series of sites in which there is specialized hunting of this ungulate, such as Covalejos I (Yravedra *et al.* 2016), Ruso V (Yravedra *et al.* 2010) and Cuco VII to XIV (Rasines del Río *et al.* 2020), where this taxon exceeds 60 % representativeness. In sites close to mountain areas, where rock animals are very abundant, we observe that the trend is towards specialized hunting for Iberian ibex and chamois, as in Mirón 130 (Marín-Arroyo *et al.* 2020), Arlanpe D (Arcereditillo-Alonso *et al.* 2013), Esquilleu 3 to 6 (Yravedra & Gómez Castanedo 2014) or Axló 3 to 8 (Castaños 2005). This tendency to specialize in a taxon that we find in many sites in Cantabrian Spain contrasts with the sequences of those sites that clearly present a diversification in their subsistence strategy, such as Llonín VIII (Sanchís *et al.* 2019) and Sopena XV (Yravedra *et al.* 2023). Studies for the last Neanderthal groups in the north of the Iberian Peninsula seem to indicate that when the

hunting strategy was directed at a specific type of prey, they did so in a quite specialized way, focusing on a narrow range of other species (Linares-Matás & Yravedra 2024).

The presence in Cierro N of a tusk fragment of *Elephas* sp. indicates the existence of large herbivores at this time in the Sella valley. However, their presence does not imply the consumption of these animals, since they could have selected the use of ivory for the manufacture of bone industry. The presence of these proboscideans in Neanderthal sites in Cantabrian Spain is attested in sites such as Mirón 130 (Marín-Arroyo *et al.* 2020), Güelga 4 (Zona D exterior) (Rojo 2020), Cuco XII (Rasines del Río *et al.* 2020) and Ruso V (Yravedra *et al.* 2010).

Carnivores are present in Cierro N, represented by the hyena and the cave bear. Their presence is greater than in the rest of the levels of the sequence and these large carnivores have only been documented in Aurignacian levels. These large carnivores are very common in Mousterian sites in the Cantabrian Spain, such as in La Viña XII (de la Rasilla *et al.* 2020), Llonín VIII (Sanchís *et al.* 2019) or Amalda VII (Yravedra 2010a). In the case of El Cierro, its presence could indicate the use of the cave by these animals when it was not occupied by human groups. This is supported by evidence of carnivore marks on some remains and by the limited anthropic activity detected at the Mousterian level, which would indicate a short occupation of the cave by Neanderthal groups in El Cierro. This type of sporadic occupation and human-carnivore interactions are common in Mousterian sites in northern Spain. In particular, the caves would have been ideal places for bears to hibernate, as the remains documented in Lezetxiki 6, Arlanpe D, Amalda VII and Llonín VIII seem to indicate (Linares-Matás & Yravedra 2024).

On the other hand, the presence of hyenas in cavities is often associated with the use of these spaces as dens; however, in the case of Cierro N, the absence of deciduous teeth, the scarcity of digestion traces and the lack of coprolites of these animals would indicate that the cave was not used as a hyena den, something that also occurs, for example, in Covalejos (Yravedra *et al.* 2016).

Birds are very scarce in Cierro N, represented only by a remain of *Alectoris/Perdix* sp. and another of an undetermined bird. We do not know if the presence of a partridge in the site is due to anthropic action since it does not show signs of meat processing. In the other levels of El Cierro something similar occurs, birds are present in all periods, mainly corvids and passerines, but there are no traces of anthropic processing. The exploitation of birds in the Mousterian period of the Cantabrian Spain is attested in Axlør cave, where cutmarks are documented on remains of corvids and golden eagles, determining the use of these resources for food purposes by Neanderthal groups (Gómez-Olivencia *et al.* 2018). Although data on bird consumption are scarce in the north of Spain, the case of Axlør adds to other evidence in the Iberian Peninsula that allows us to determine the use of birds for consumption by Neanderthals, as evidenced, for example, in the caves of Bolomor (Blasco & Fernández Peris 2012), La Abreda (Lloveras *et al.* 2018), Cova Negra (Martínez Valle *et al.* 2016), Gruta da Oliveira (Nabais *et al.* 2023) or Figueira Brava (Mourer-Chauviré & Antunes 2000).

Regarding anthropogenic activity, the presence of cutmarks, fracture patterns and thermoalterations documented in Cierro N indicate that the origin of the faunal accumulations is due to human action. Although cutmarks and percussion marks have been scarce, the high rate of fragmentation of the remains, the absence of cylinders and the few traces of carnivores would exclude a cumulative pattern on the part of these predators. The meat and marrow processing of faunal remains is documented in red deer, Iberian ibex and large bovid, as well as in all size categories. The anthropic alteration that has left the greatest evidence is thermoalteration. Most of the burned remains correspond to high degrees of cremation and exposure temperatures above 800°C (Nicholson 1993; Stiner *et al.* 1995), almost entirely affecting remains included in the categories of indeterminable size and bones. This large number of bones exposed to high temperature could be related to their use as fuel (Théry-Parisot 2001; Costamagno *et al.* 2005, 2009; Yravedra *et al.* 2005). The great fragmentation of the bones burned at high temperature and the presence of axial elements and fragments of burnt epiphysis could indicate this use by the Mousterian groups of El Cierro. This type of practices seems to have also been documented in other Mousterian sites in the Cantabrian Spain such as El Esquilieu and Labeko Koba (Yravedra *et al.* 2005; Yravedra & Uzquiano 2013). However, a small percentage of the burned remains have brown and black tones, as well as double and triple colouring on the same surfaces of the remains, which could indicate meat roasting tasks by the Neanderthal groups of El Cierro (Buikstra & Swegle 1989; Stiner *et al.* 1995; Blasco *et al.* 2013; Goizane Alonso *et al.* 2024).

The scarce MNI and the potential calories provided by the hunted taxa seems to indicate a short occupation for the Mousterian of El Cierro. This contrasts with the occupation of the cave during the Lower Magdalenian, which, given the large volume of documented remains, could have been occupied throughout the year (Portero *et al.* 2024a). This phenomenon of short-intensity occupations in Mousterian sites is well attested in the north of the Iberian Peninsula, such as Viña XIV, Llonín VIII or Esquilieu 3 (Yravedra 2013; Yravedra & Gómez Castanedo 2014; Sanchís *et al.* 2019; de la Rasilla *et al.* 2020), especially considering the dynamics of interaction between humans and carnivores in these sites (Linares-Matás & Yravedra 2024). On the other hand, it must be taken into account that the excavated volume of Cierro N is *c.* of 1 m³, so we must be cautious regarding the duration of the occupations, since we only have a small part of the faunal record to understand the intensity of the inhabitation.

Finally, the natural agents that have affected the faunal remains of Cierro N indicate the presence of humidity during the formation process of the level, as we have been able to attest from the large number of bones stained with manganese oxides, the rolling of bones due to low-intensity water drag, and corrosion caused by water and plant roots on bone surfaces. Additionally, weathering has damaged bone surfaces causing cracking. These factors have influenced the conservation of the remains, making it difficult in some cases to identify anthropogenic processes.

CONCLUSION

The faunal sample analysed in this article has offered us an approach to the subsistence strategies of the Neanderthal groups that inhabited the El Cierro cave during MIS 3 in its regional context.

The archaeological analysis has revealed that red deer is the main prey hunted, a phenomenon that is highly consistent with what has been documented throughout the stratigraphic sequence of El Cierro during the Upper Pleistocene and early Holocene. Other ungulates consumed (Iberian ibex and large bovid) are scarcely represented, but they formed part of the diet of the Neanderthals in the cave, as we have been able to demonstrate from the anthropic evidence documented. Other herbivores, such as horse or proboscidean, are present in Cierro N, but we have not been able to determine their anthropic contribution. Within the traces of anthropic manipulation, thermoalterations have been very abundant and have allowed us to determine tasks related to the roasting of meat but, above all, the use of bone as fuel.

Birds are scarcely represented at Cierro N, with only one partridge, which shows no evidence of anthropic manipulation, nor traces of consumption by carnivores. The presence of hyena and cave bear, together with some marks produced by carnivores on the faunal remains, has allowed us to document the activity predators. Although the tooth marks have not enabled us to determine the carnivore that produced

them, the low volume of bones with anthropic alterations seems to indicate a short occupation of the cave by human groups, and cave bears and hyenas may have taken advantage of this circumstance to use the cave when it was not occupied by people. However, the low activity of carnivores, together with the scarcity of cylinders and evidence of coprolites, would rule out the use of the cave as a den.

The studied faunal assemblage has also allowed us to assess the processes of formation and transformation of the archaeozoological record of Cierro N due to natural agents. These phenomena have allowed us to conclude that the time of formation of the stratum, the humidity and the phenomena of rolling had a great impact on the archaeological material, having documented many remains with manganese staining and abrasions on the surfaces of the bones due to water activity.

The results provided in this study are inserted within the subsistence dynamics of the Neanderthal groups of the Sella valley and the Spanish Cantabrian region, contributing with a case study to the complex panorama that develops during MIS 3.

Acknowledgements

This research was made possible thanks to a Margarita Salas postdoctoral fellowship awarded to R. Portero by the University of Salamanca and the Spanish Ministry of Science (Plan de Recuperación, Transformación y Resiliencia) with EU-Next-Generation funds. This work was undertaken in the context of the PaleontheMove Project PID2020.114462 GB-I00 (PI: Esteban Álvarez Fernández) and CantabricOIS2 PID2020.115192 GB-I00 (PI: Jesús F. Jordá Pardo) funded by the Programa Estatal de Fomento de Generación de Conocimiento y Fortalecimiento Científico y Tecnológico of the Spanish Ministry of Science and Innovation. We thank the referees for their careful reading of the manuscript and for their comments.

REFERENCES

- ALADOS C. L. & ESCÓS J. 2017. — Cabra montés – Capra pirenaica, in SALVADOR A. & BARJA I. (eds), *Enciclopedia Virtual de los Vertebrados Españoles*. Museo Nacional de Ciencias Naturales, Madrid: 1-32.
- ALONSO-GARCÍA P., NAVAJO M. & BLASCO R. 2020. — Use and selection of bone fragments in the north of the Iberian Peninsula during the Middle Palaeolithic: bone retouchers from level 4 of Prado Vargas (Burgos, Spain). *Archaeological and Anthropological Sciences* 12: 218. <https://doi.org/10.1007/s12520-020-01097-z>
- ALTUNA J. 1989. — La subsistence d'origine animale pendant le Moustérien dans la région Cantabrique (Espagne), in PATHOU M. & FREEMAN L. G. (eds), *L'Homme de Néandertal. La Subsistance, Actes du colloque international de Liège*. ERAUL, Liège: 41-43.
- ÁLVAREZ-FERNÁNDEZ E., BÉCARES J. & PORTERO R. 2014. — Excavaciones arqueológicas en Cova Rosa y en El Cierro (Ribadesella, Asturias): pasado, presente y futuro, in ÁLVAREZ-ALONSO D. & FERNÁNDEZ DE CÓRDOBA J. (coords), *F. Jordá Cerdá (1914-2014), maestro de prehistoriadores*. APPIA (Anejos de NAILOS 2), Oviedo: 73-97.
- ÁLVAREZ-FERNÁNDEZ E., ÁLVAREZ-ALONSO D., BÉCARES J., CARRAL P., CARRIOL R.-P., CHAUVIN A., CUBAS M., CUETO M., DOMINGO R., DOUKA K., JORDÁ PARDO J. F., MURELAGA X., PORTERO R., RIVERO O., TAPIA J., TARRIÑO A. & TEIRA L. C. 2016. — Nouvelles données sur le Magdalénien inférieur de la Région Cantabrique : le Niveau F de la grotte de El Cierro (Ribadesella, Asturias, Espagne). *L'Anthropologie* 120 (5): 537-567.
- ÁLVAREZ-FERNÁNDEZ E., BÉCARES J., JORDÁ PARDO J. F., AGUIRRE A., ÁLVAREZ-ALONSO D., ANDRÉS-HERRERO M. DE., APARICIO M. T., BARRERA I., CARRAL P., CARRIOL R.-P., CHAUVIN A., CUBAS M., CUETO M., DOMINGO R., DOUKA K., DUARTE C., ELORZA M., FERNÁNDEZ-GÓMEZ M. J., GABRIEL S., HABER M., IRIARTE M. J., JULIÁN M.-A., LEPAGE J., LLAVE C., MARTÍN-JARQUE S., MURELAGA X., OSETE M. L., PALENCIA A., PORTERO R., RIVERO M., RIVERO O., TAPIA J., TARRIÑO A., TEIRA L. C., UZQUIANO P. & ARIAS P. 2018. — Excavaciones arqueológicas en El Cierro (Fresnu, Ribadesella). Campañas de Excavación e Investigación 1977-1979, 2014 y 2016, in *Excavaciones Arqueológicas en Asturias 2013-2016*. Consejería de Educación y Cultura del Gobierno del Principado de Asturias, Oviedo: 93-106.
- ÁLVAREZ-FERNÁNDEZ E., ARIAS P., BÉCARES J., CUBAS M., ELORZA M., GABRIEL S., MARTÍN-JARQUE S., PORTERO R. & JORDÁ PARDO J. F. 2022. — Intervenciones arqueológicas en la cueva de El Cierro (Fresnu, Ribadesella, Asturias): síntesis de los datos disponibles procedentes de los recientes trabajos realizados en tres zonas del yacimiento, in JORDÁ PARDO J. F., MARTÍN-JARQUE S., PORTERO R. & ÁLVAREZ-FERNÁNDEZ E. (eds), *Descendiendo el río Sella. Una (re) visión de la Arqueología Prehistórica del valle del Sella (Asturias, España)*. UNED, Gijón: 133-162, (Entemu XIX).
- ARCEREDILLO-ALONSO D., GÓMEZ-OLIVENCIA A., SAN PEDRO-CALLEJA Z. 2013. — La fauna de macromamíferos de los niveles pleistocenos de la Cueva de Arlanpe, in *La cueva de Arlanpe (Lemoa): Ocupaciones humanas desde el Paleolítico Medio Antiguo hasta la Prehistoria Reciente*. Diputación Foral de Bizkaia, Bilbao: 123-160.
- AZORIT C., ANALLA M., CARRASCO R., CALVO J. A. & MUÑOZ-COBO J. 2002. — Teeth eruption pattern in red deer (*Cervus elaphus hispanicus*) in southern Spain. *Anales de Biología* 24: 107-114.
- AZORIT C., ANALLA M., CARRASCO R. & MUÑOZ-COBO J. 2003. — Determinación de la edad por desgaste dental en el ciervo ibérico (*Cervus elaphus hispanicus* Erxleben, 1777) (Mammalia, Cervidae). *Boletín de la Real Sociedad Española de Historia Natural (Sección biológica)* 98 (1-4): 123-134.
- BAENA J. & CARRIÓN E. 2014. — Esquilleu, in SALA RAMOS R., CARBONELL E., BERMÚDEZ DE CASTRO J. M. & ARSUAGA J. L. (coords), *Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait. The Current Archaeological Record*. Universidad de Burgos, Servicio de Publicaciones, Burgos: 82-87.
- BARONE R. 1966. — *Atlas de mammifères domestiques*. Vol. 1. *Ostéologie*. Masson, Paris, 811 p.
- BEHRENSMEYER A. K. 1978. — Taphonomic and ecological information from bone weathering. *Paleobiology* 4 (2): 150-162. <https://doi.org/10.1017/S0094837300005820>
- BEHRENSMEYER A. K., GORDON K. D. & YANAGI G. T. 1986. — Trampling as a cause of bone surface damage and pseudocut-marks. *Nature* 319: 768-771. <https://doi.org/10.1038/319768a0>
- BINFORD L. R. 1978. — *Nunamiut Ethnoarchaeology*. Academy Press, New York, 509 p.
- BINFORD L. R. 1981. — *Bones: Ancient man and modern myths*. Academy Press, New York, 320 p.
- BLASCO R. & FERNÁNDEZ PERIS J. 2012. — Small and large game: Human use of diverse faunal resources at Level IV of Bolomor Cave (Valencia, Spain). *Comptes Rendus Palevol* 11 (4): 265-282. <https://doi.org/10.1016/j.crpv.2012.01.003>

- BLASCO R., ROSELL J., DOMÍNGUEZ-RODRIGO M., LOZANO S., PASTÓ I., RIBA D., VAQUERO M., FERNÁNDEZ PERIS J., ARSUAGA J. L., BERMÚDEZ DE CASTRO J. M. & CARBONELL E. 2013. — Learning by heart: cultural Patterns in the faunal processing sequence during the Middle Pleistocene. *PLOS One* 8 (2): 1-20. <https://doi.org/10.1371/journal.pone.0055863>
- BLASCO R., COCHARD D., COLONESE A. C., LAROUANDIE V., MEIER J., MORIN E., RUFÀ A., TASSONI L. & THOMPSON J. C. 2022. — Small animal use by Neanderthals, in ROMAGNOLI F., RIVALS F. & BENAZZI S. (eds), *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*. Academic Press, Cambridge: 123-206. <https://doi.org/10.1016/B978-0-12-821428-2.00010-X>
- BROWN W. A. B. & CHAPMAN G. N. 1991. — The dentition of red deer (*Cervus elaphus*): a scoring scheme to assess age from wear of the permanent molariform teeth. *Journal of Zoology* 224 (4): 519-536. <https://doi.org/10.1111/j.1469-7998.1991.tb03783.x>
- BUKSTRA J. E. & SWEGLE M. 1989. — Bone modification due to burning: experimental evidence, in BONNICHSEN R. & SORG M. H. (eds), *Bone Modification*. University of Maine Centre for the Study of the First Americans, Orono: 247-258.
- BUNN H. T. 1983. — Comparative analysis of modern bone assemblages from a San hunter gatherer camp in the Kalahari Desert, Botswana, and from spotted hyena den near Nairobi, Kenya, in CLUTTON-BROCK J. & GRIGSON C. (eds), *Animals and Archaeology. Vol. 1. Hunters and their prey*. BAR Publishing (International Series; 163), Oxford: 143-148.
- BUNN H. T. & KROLL E. M. 1986. — Systematic butchery by Plio-Pleistocene hominids at Olduvai Gorge, Tanzania. *Current Anthropology* 27 (5): 123-149. <https://doi.org/10.1086/203467>
- CÁCERES I., BRAVO P., ESTEBAN M., EXPÓSITO I. & SALADIÉ P. 2002. — Fresh and heated bones breakage. An experimental approach, in DE RIENZI M., PARDO ALONSO M. V., BELINCHÓN M., PEÑALVER E., MONTOYA P. & MÁRQUEZ-ALIAGA A. (eds), *Current topics on taphonomy and fossilization*. Ayuntamiento de Valencia, Valencia: 471-481.
- CAMARÓS E., CUETO M., LORENZ C., VILLAVARDE V. & RIVALS F. 2016. — Large carnivore attacks on hominins during the Pleistocene: a forensic approach with a Neanderthal example. *Archaeological and Anthropological Sciences* 8: 635-646. <https://doi.org/10.1007/s12520-015-0248-1>
- CARRANZA J. 2017. — Ciervo – *Cervus elaphus*, in SALVADOR A. & BARJA I. (eds), *Enciclopedia Virtual de los Vertebrados Españoles*. Museo Nacional de Ciencias Naturales, Madrid: 1-28.
- CASTAÑOS P. 2005. — Revisión actualizada de las faunas de macromamíferos del Würn antiguo en la región cantábrica, in MONTES R. & LASHERAS J. A. (eds), *Actas de la reunión científica: neandertales cantábricos, estado de la cuestión*. Ministerio de Cultura, Madrid: 201-207.
- CASTAÑOS P. 2021. — Estudio de la fauna de macromamíferos de la cueva de Covalejos, in MONTES R. & SANGUINO J. (eds), *La cueva de Covalejos (Velo de Piélagos, Cantabria): ocupaciones neandertales y sapiens en la cueva baja del río Pas. Actuaciones arqueológicas 1997-1999 y 2002*. Museo de Prehistoria y Arqueología de Cantabria, Santander: 106-125.
- CLUTTON-BROCK T. H. & IASON G. R. 1986. — Sex-ratio variation in mammals. *Quarterly Review of Biology* 61 (3): 339-374. <https://doi.org/10.1086/415033>
- CORTÉS-SÁNCHEZ M., MORALES-MUÑOZ A., SIMÓN-VALLEJO M. D., LOZANO-FRANCISCO M. C., VERA-PELÁEZ J. L., FINLAYSON C., RODRÍGUEZ-VIDAL J., DELGADO-HUERTAS A., JIMÉNEZ-ESPEJO F. J., MARTÍNEZ-RUIZ F., MARTÍNEZ-AGUIRRE M. A., PASCUAL-GRANGED A. J., BERGADÀ-ZAPATA M. M., GIBAJA-BAO J. F., RIQUERME-CANTAL J. A., LÓPEZ-SÁEZ J. A., RODRÍGUEZ-GAMIZ M., SAKAI S., SUGISAKI S., FINLAYSON G., FA D. A. & BICHO N. F. 2011. — Earliest Known Use of Marine Resources by Neanderthals. *PLOS One* 6 (9): e24026. <https://doi.org/10.1371/journal.pone.0024026>
- COSTAMAGNO S., THÉRY-PARISOT I., BRUGAL J.-P. & GUILBERT R. 2005. — Taphonomic consequences of the use of bone as fuel. Experimental data and archaeological applications, in O'CONNOR T. (ed.), *Biosphere to Lithosphere: New studies in vertebrate taphonomy. Proceedings of the 9th ICAZ Conferences (Durham, August 2002)*. Oxbow Books, Oxford: 51-62.
- COSTAMAGNO S., THÉRY-PARISOT I., CASTEL J. C. & BRUGAL J.-P. 2009. — Combustible ou non? Analyse multifactorielle et modèles explicatifs sur des ossements brûlés paléolithiques, in THÉRY-PARISOT I., COSTAMAGNO S. & HENRY A. (eds), *Gestion des combustibles au paléolithique et au mésolithique. Nouveaux outils, nouvelles interprétations. Proceedings of the XV World Congress (Lisbon, 4-9 September 2006)*. BAR Publishing (International Series; 13), Oxford: 65-84.
- COSTAMAGNO S., SOULIER M.-C., VAL A. & CHONG S. 2019. — The reference collection of cutmarks. *Palethnologie* 10: 186-280.
- CUARTERO F., ALCARAZ-CASTAÑO M., LÓPEZ-RECIO M., CARRIÓN-SANTAFÉ E. & BAENA-PREYSLER J. 2015. — Recycling economy in the Mousterian of the Iberian Peninsula: the case study of El Esquilieu. *Quaternary International* 361: 113-130. <https://doi.org/10.1016/j.quaint.2014.11.059>
- DE LA RASILLA M., DUARTE E., SANCHÍS A., CARRIÓN L., CAÑAVARE J. C., MARÍN-ARROYO A. B., REAL C., NUÑEZ C., SÁNCHEZ S., GUTIÉRREZ-ZUGASTI I., JONES J., RIGAUD S., MARTÍNEZ R., CUESTA L., AGUDO L. & SANTOS G. 2020. — Environment and subsistence strategies at La Viña rock shelter and Llonín cave (Asturias, Spain) during MIS3. *Journal of Archaeological Science: Reports* 30: 102198. <https://doi.org/10.1016/j.jasrep.2020.102198>
- FERNÁNDEZ-GARCÍA M., LÓPEZ-GARCÍA J. M., ROYER A., LÉCUYER C., RIVALS F., RUFÀ A., BLASCO R. & ROSELL J. 2022. — New insights in Neanderthal palaeoecology using stable oxygen isotopes preserved in small mammals as palaeoclimatic tracers in Teixoneres Cave (Moià, northeastern Iberia). *Archaeological and Anthropological Sciences* 14: 106. <https://doi.org/10.1007/s12520-022-01564-9>
- FERNÁNDEZ-GARCÍA M., VIDAL-CORDASCO M., JONES J. R. & MARÍN-ARROYO M. 2023. — Reassessing palaeoenvironmental conditions during the Middle to Upper Palaeolithic transition in the Cantabrian region (Southwestern Europe). *Quaternary Science Reviews* 301: 107928. <https://doi.org/10.1016/j.quas-ciev.2022.107928>
- FERNÁNDEZ-JALVO Y. & ANDREWS P. 2016. — *Atlas of Taphonomic Identifications. 1001+ Images of Fossil and Recent Mammal Bone Modification*. Springer (Vertebrate Paleobiology and Paleoanthropology Series), New York, 339 p. <https://doi.org/10.1007/978-94-017-7432-1>
- GALLO G., USHAKOV S. V., NAVROTSKY A., STAHLSCHEIDT M. C. 2023. — Impact of prolonged heating on the color and crystallinity of bone. *Archaeological and Anthropological Sciences* 15:143. <https://doi.org/10.1007/s12520-023-01842-0>
- GOIZANE ALONSO A., RUFÀ A. & BLASCO R. 2024. — Cooked or discarded? Experimental distinction of rabbit burnt bones and its application to the archaeological record. *Journal of Archaeological Science: Reports* 56: 104541. <https://doi.org/10.1016/j.jasrep.2024.104541>
- GONZÁLEZ-URQUIJO J. E., IBÁÑEZ ESTÉVEZ J. J., LAZUÉN FERNÁNDEZ T. & MOZOTA HOLGUERAS M. 2014. — Axlór, in SALA RAMOS R., CARBONELL E., BERMÚDEZ DE CASTRO J. M. & ARSUAGA J. L. (eds), *Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait. The Current Archaeological Record*. Universidad de Burgos, Fundación Atapuerca, Burgos: 45-48.
- GÓMEZ-OLIVENCIA A., SALA N., NUÑEZ-LAHUERTA C., SANCHÍS A., ARLEGI M. & RÍOS GARAIZAR J. 2018. — First data of Neanderthal bird and carnivore exploitation in the Cantabrian Region (Axlór; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Scientific Reports* 8: 10551. <https://doi.org/10.1038/s41598-018-28377-y>

- GRIGSON C. 1982. — Sex and age determination of some bones and teeth of domestic cattle: a review of the literature, in WILSON B., GRIGSON C. & PAYNE S. (eds), *Ageing and Sexing Animal Bones from Archaeological Sites*. British Archaeological Reports (British Series; 109), Oxford: 7-24.
- HARDY K. 2022. — The use of plant by Neanderthals as food, medicine, and raw materials, in ROMAGNOLI F., RIVALS F. & BENAZZI S. (eds), *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*. Academic Press, Cambridge: 145-161. <https://doi.org/10.1016/B978-0-12-821428-2.00004-4>
- HARDY B. L., KAY M., MARKS A. E. & MONIGAL K. 2001. — Stone tool function at the paleolithic sites of Starosele and Buran Kanya III, Crimea: behavioral implications. *Proceedings of the National Academy of Sciences USA* 98: 10972-10977. <https://doi.org/10.1073/pnas.191384498>
- HAYNES G. 1980. — Evidence of carnivore gnawing on Pleistocene and recent mammalian bones. *Paleobiology* 6 (3): 341-351. <https://doi.org/10.1017/S0094837300006849>
- HILLSON S. 2005. — *Teeth*. Cambridge Manuals in Archaeology, Cambridge, 373 p. <https://doi.org/10.1017/CBO9780511614477>
- HOCKETT B. & HAWS J. 2009. — Continuity in animal resource diversity in the late Pleistocene human diet of Central Portugal. *Before Farming* 2009 (2): 1-14. <https://doi.org/10.3828/bfarm.2009.2.2>
- JAOUEN K., VILLABA-MOUÇO V., SMITH G. M., TROST M., LEICHLITER J., LÜDECKE T., MÉJEAN P., MANDROU S., CHMELEFF J., GUISEIX D., BOURGON N., BLASCO F., MENDES CARDOSO J., DUQUENOY C., MOUBTAHIJ Z., SALAZAR GARCIA D. C., RICHARDS M., TÜTKEN T., HUBLIN J.-J., UTRILLA P. & MONTES L. 2022. — A Neandertal dietary conundrum: insights provided by tooth enamel Zn isotopes from Gabasa, Spain. *PNAS* 113 (43): e2109315119. <https://doi.org/10.1073/pnas.2109315119>
- JONES J. R., RICHARDS M. P., STRAUS L. G., READE H., ALTUNA J., MARIEZKURRENA K. & MARÍN-ARROYO A. B. 2018. — Changing environments during the Middle-Upper Palaeolithic transition in the eastern Cantabrian Region (Spain): direct evidence from stable isotope studies on ungulate bones. *Scientific Reports* 8 (14842): 84-88. <https://doi.org/10.1038/s41598-018-32493-0>
- JORDÁ PARDO J. F., CARRAL P., ÁLVAREZ-ALONSO D., ARIAS P., BÉCARES J., CUBAS M., MARTÍN-JARQUE S., PORTERO R., TEIRA L. C. & ÁLVAREZ-FERNÁNDEZ E. 2018a. — Al oeste del Sella. Geoarqueología y cronoestratigrafía del registro del Pleistoceno Superior de la cueva de El Cierro (Fresno, Ribadesella, Asturias, España). *Boletín Geológico y Minero* 129 (1-2): 207-250.
- JORDÁ PARDO J. F., CARRAL P., MAESTRO A., ÁLVAREZ-ALONSO D., ARIAS P., BÉCARES J., CUBAS M., MARTÍN-JARQUE S., PORTERO R., TEIRA L. C. & ÁLVAREZ-FERNÁNDEZ E. 2018b. — La gran transgresión. La secuencia pleistoceno-holocena de la cueva de El Cierro (Fresno, Ribadesella, Asturias): geoarqueología, cronoestratigrafía y paleogeografía, in GARCÍA-IBAIBARRIAGA N., MURELAGA X., SUÁREZ A. & SUÁREZ O. (eds), *Paleoambiente y recursos bióticos del Pleistoceno superior cantábrico. Estado de la cuestión a la luz de las nuevas investigaciones*, Bizkaiko Foru Aldundia (Kobie, Serie Anejo, 18), Bilbao: 57-68.
- KRAFT E. 1972. — *Vergleichend morphologische Untersuchungen an Einzelknochen Nordund Mitteleuropäischer Kleinerer Hühnervogel*. Universität München, Munich, 194 p.
- KRASIŃSKA M. & KRASIŃSKI Z. A. 1995. — Composition, group size, and spatial distribution of European bison bulls in Białowieża Forest. *Acta Theriologica* 40 (1): 1-21. <https://doi.org/10.4098/AT.ARCH.95-1>
- KRASIŃSKA M. & KRASIŃSKI Z. A. 2002. — Body mass and measurements of the European bison during postnatal development. *Acta Theriologica* 47 (1): 85-106. <https://doi.org/10.1007/BF03193569>
- LINARES-MATÁS G. J. & YRAVEDRA J. 2024. — Competing forces: Subsistence strategies and human-carnivore interactions during the middle to Upper Palaeolithic transition in Northern Iberia. *Quaternary Science Reviews* 334: 108703. <https://doi.org/10.1016/j.quascirev.2024.108703>
- LLOVERAS L., GARCIA L., MAROTO J., SOLER J., & SOLER N. 2018. — The bird assemblage from the Middle Palaeolithic level I of Arbreda Cave: a taphonomic story. *Journal of Archaeological Science: Reports* 21: 758-770. <https://doi.org/10.1016/j.jasrep.2018.08.040>
- LURET M., BURKE A., BERNALDO DE QUIROS F. & BESSE M. 2020. — El Castillo cave (Cantabria, Spain): Archeozoological comparison between the Mousterian occupation level (unit 20) and the “Aurignacien de transition de type El Castillo” (unit 18). *Journal of Archaeological Science: Reports* 31: 102339. <https://doi.org/10.1016/j.jasrep.2020.102339>
- LYMAN R. L. 1994. — *Vertebrate Taphonomy*. Cambridge Manuals in Archaeology, Cambridge, 524 p. <https://doi.org/10.1017/CBO9781139878302>
- MACARTHUR R. H. & PIANKA E. R. 1966. — On optimal use of a patchy environment. *The American Naturalist* 100 (916): 603-609. <https://www.jstor.org/stable/2459298>
- MAREAN C. W. & SPENCER L. M. 1991. — Impact of Carnivore ravaging on zooarchaeology measures of element abundance. *American Antiquity* 56 (4): 645-658. <https://doi.org/10.2307/281542>
- MARIEZKURRENA K. 1983. — Contribución al conocimiento del desarrollo de la dentición y el desarrollo del esqueleto postcranial de *Cervus elaphus*. *Munibe* 35: 149-202.
- MARIEZKURRENA K. & ALTUNA J. 1983. — Biometría y dimorfismo sexual en el esqueleto de *Cervus elaphus* würrmiense, postwürrmiense y actual del Cantábrico. *Munibe* 35: 203-246.
- MARÍN-ARROYO A. B. 2010. — *Arqueozoología en el cantábrico oriental durante la transición Pleistoceno/Holoceno*. La Cueva del Mirón. PubliCan, Ediciones Universidad de Cantabria, Santander, 686 p.
- MARÍN-ARROYO A. B. & SANZ-ROYO A. 2022. — What Neanderthals and AMH ate: reassessment of the subsistence across the middle-upper palaeolithic transition in the Vasco-Cantabrian region of SW Europe. *Journal of Quaternary Science* 37 (2): 320-334. <https://doi.org/10.1002/jqs.3291> <https://doi.org/10.1002/jqs.3291>
- MARÍN-ARROYO A. B., LANDETE-RUIZ M. D., VIDAL G., SEVA-ROMÁN R., GONZÁLEZ MORALES M. R. & STRAUS L. G. 2008. — Archaeological implications of human-derived manganese coatings: a study of blackened bones in El Mirón Cave, Cantabrian Spain. *Journal of Archaeological Science* 35 (3): 801-813.
- MARÍN-ARROYO A. B., RIOS-GARAIZAR J., STRAUS L. G., JONES J. R., DE LA RASILLA M., GONZÁLEZ MORALES M. R., RICHARDS M., ALTUNA J., MARIEZKURRENA K. & OCIO D. 2018. — Chronological reassessment of the Middle to Upper Paleolithic transition and early Upper Paleolithic cultures in Cantabrian Spain. *PLOS One* 13: e0194708. <https://doi.org/10.1371/journal.pone.0194708>
- MARÍN-ARROYO A. B., GEILING J. M., JONES J. R., GONZÁLEZ MORALES M. R., STRAUS L. G. & RICHARDS M. P. 2020. — The middle to upper Palaeolithic transition at El Mirón cave (Cantabria, Spain). *Quaternary International* 544: 23-31. <https://doi.org/10.1016/j.quaint.2018.06.036>
- MARSHALL F. & PILGRAM T. 1991. — Meat versus within-bone nutrients: another look at the meaning of body part representation in archaeological sites. *Journal of Archaeological Science* 18 (2): 149-163. [https://doi.org/10.1016/0305-4403\(91\)90044-P](https://doi.org/10.1016/0305-4403(91)90044-P)
- MARTÍNEZ VALLE R., CALATAYUD P. M. G. & BONILLA V. V. 2016. — Bird consumption in the final stage of Cova Negra (Xàtiva, Valencia). *Quaternary International* 421: 85-102. <https://doi.org/10.1016/j.quaint.2016.01.068>

- MONTES BARQUÍN R. & SANGUINO J. 2021. — *La cueva de Covalejos (Velo de Piélagos, Cantabria) ocupaciones neandertales y sapiens en la cueva baja del río Pas. Actuaciones arqueológicas, 1997-1999 y 2002*. Museo de Prehistoria y Arqueología de Cantabria, Santander, 466 p.
- MOURER-CHAUVIRÉ C. & ANTUNES M. T. 2000. — L'avifaune pléistocène et holocène de Gruta da Figueira Brava (Arrábida, Portugal), in *Últimos neandertais em Portugal: evidência, odontológica e outra*. Tomo XXXVIII. Memórias da Academia das Ciências de Lisboa, Lisboa, 129-161.
- MUÑOZ E., RASINES DEL RÍO P., SANTAMARÍA S. & MORLOTE J. M. 2007. — Estudio arqueológico del abrigo del Cuco, in MUÑOZ-FERNÁNDEZ E. & MONTES BARQUÍN R. (eds), *Intervenciones arqueológicas en Castro Urdiales, tomo III. Arqueología y arte rupestre paleolítico en las cavidades de El Cuco o Sobera y La Lastrilla*. Excmo. Ayuntamiento de Castro Urdiales. Concejalía de Medio Ambiente y Patrimonio Arqueológico, Castro Urdiales: 15-160.
- NABAIS M. 2018. — Neanderthal subsistence in Portugal: what evidence? *Archaeology International* 21 (1): 95-100. <https://doi.org/10.5334/ai-376>
- NABAIS M., PIMENTA C. & ZILHÃO J. 2023. — Human-bird interaction in last Interglacial Iberia: a combined approach using skeletal part analysis, bone surface modification, bird ethology and ethnography. *Journal of Archaeological Science: Reports* 49: 104023. <https://doi.org/10.1016/j.jasrep.2023.104023>
- NABAIS M., PORTERO R. & ZILHÃO J. 2024. — Neanderthal brown crab recipes: a combined approach using experimental, archaeological and ethnographic evidence. *Historical biology* 36 (8): 1487-1495. <https://doi.org/10.1080/08912963.2023.2220005>
- NICHOLSON R. 1993. — A morphological investigation of burnt animal bone and an evaluation of its utility in archaeology. *Journal of Archaeological Science* 20 (4): 411-428. <https://doi.org/10.1006/jasc.1993.1025>
- PALES L. & GARCIA M. A. 1981a. — *Atlas ostéologique pour servir à l'identification des mammifères du Quaternaire. I-Tête, rachis, ceintures scapulaire et pelvienne, membres: Herbivores*. CNRS, Paris, 177 p.
- PALES L. & GARCIA M. A. 1981b. — *Atlas ostéologique pour servir à l'identification des mammifères du Quaternaire. II-Tête, rachis, ceintures scapulaire et pelvienne, membres: Carnivores. Homme*. CNRS, Paris, 77 p.
- PEDERZANI S., BRITTON K., JONES J. R., AGUDO PÉREZ L., GEILING J. M. & MARÍN-ARROYO A. B. 2023. — Late Pleistocene Neanderthal exploitation of stable and mosaic ecosystems in northern Iberia shown by multi-isotope evidence. *Quaternary Research* 116: 1-25. <https://doi.org/10.1017/qua.2023.32>
- PÉREZ RIPOLL M. 1988. — Estudio de la secuencia del desgaste de los molares de *Capra pyrenaica* de los yacimientos prehistóricos. *Archivo de Prehistoria Levantina* 18: 83-128.
- PICKERING T. R. & EGELAND C. P. 2006. — Experimental patterns of hammerstone percussion damage on bones: Implications for inferences of carcass processing by humans. *Journal of Archaeological Science* 33 (4): 459-469. <https://doi.org/10.1016/j.jas.2005.09.001>
- PORTERO R. 2022. — *Estrategias de subsistencia a finales del Pleistoceno superior y comienzos del Holoceno en el Valle del Sella: La Cueva de El Cierro (Ribadesella, Asturias, España)*. Unpublished PhD thesis, Universidad de Salamanca, Salamanca, 595 p.
- PORTERO R., CUETO M., JORDÁ PARDO J. F., BÉCARES J. & ÁLVAREZ-FERNÁNDEZ E. 2019. — The persistence of red deer (*Cervus elaphus*) in the human diet during the Lower Magdalenian in northern Spain: insights from El Cierro cave (Asturias, Spain). *Quaternary International* 506: 35-45. <https://doi.org/10.1016/j.quaint.2019.01.016>
- PORTERO R., CUETO M., FERNÁNDEZ-GÓMEZ M. J. & ÁLVAREZ-FERNÁNDEZ E. 2022. — Surf and turf. — Animal resources in the human diet in Cantabrian Spain during the Mesolithic (11.5 – 7.5 Ky cal. BP). *Journal of Archaeological Science: Reports* 45: 103635. <https://doi.org/10.1016/j.jasrep.2022.103635>
- PORTERO R., CUETO M., ELORZA M., MARCHÁN-FERNÁNDEZ A., JORDÁ PARDO J. F. & ÁLVAREZ-FERNÁNDEZ E. 2024a. — Subsistence Strategies in the Lower Magdalenian at El Cierro Cave (Ribadesella, Asturias, Spain). *Journal of Paleolithic Archaeology* 7: 14. <https://doi.org/10.1007/s41982-024-00179-x>
- PORTERO R., FERNÁNDEZ-GÓMEZ M. J. & ÁLVAREZ-FERNÁNDEZ E. 2024b. — Revisiting macromammal exploitation in the Spanish Cantabrian region during the lower Magdalenian (ca. 20-17 ky cal BP). *Quaternary Science Reviews* 332: 108651. <https://doi.org/10.1016/j.quascirev.2024.108651>
- RASINES DEL RÍO P., MUÑOZ E., MAROTO J., MORLOTE J. M. & SANTAMARÍA S. 2020. — Los recursos bióticos de los niveles Musterienses del Abrigo de El Cuco (Castro Urdiales. Cantabria). *Kobie* 19: 201-212.
- REIMER P., AUSTIN W., BARD E., BAYLISS A., BLACKWELL P., BRONK RAMSEY C. J., BUTZIN M., CHENG H., EDWARDS R. L., FRIEDRICH M., GROOTES P. M., GUILDERTON T. P., HAJDAS I., HEATON T. J., HOGG A. G., HUGHEN K. A., KROMER B., MANNING S. W., MUSCHELER R., PALMER J. G., PEARSON C., VAN DER PLICHT J., REIMER R. W., RICHARDS D. A., SCOTT E. M., SOUTHON J. R., TURNER C. S. M., WACKER L., ADOLPHI F., BÜNTGEN U., CAPANO M., FAHRNI S. M., FOGTMANN-SCHULZ A., FRIEDRICH R., KÖHLER P., KUDSK S., MIYAKE F., OLSEN J., REINIG F., SAKAMOTO M., SOOKDEO A. & TALAMO S. 2020. — The IntCal20 northern Hemisphere radiocarbon age calibration curve (0-55 cal kBP). *Radiocarbon* 62 (4): 725-757. <https://doi.org/10.1017/RDC.2020.41>
- REITZ E. J. & WING E. S. 2003. — *Zooarchaeology*. Cambridge Manuals in Archaeology, Cambridge, 533 p.
- ROMAGNOLI F., RIVALS F. & BENAZZI S. 2022. — *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*. Academic Press, Cambridge, 361 p. <https://doi.org/10.1016/C2019-0-03240-2>
- ROMERO A. J., YRAVEDRA J., GRANDAL-D'ANGLADE A. & PINTO A. C. 2023. — Neanderthal use of animal bones as retouchers at the Level XV of the Sopena rock shelter (Asturias, northern Spain). *International Journal of Osteoarchaeology* 33 (6): 1064-1079.
- ROJO J. 2020. — *Neandertales y Humanos Modernos en el valle del Güeña. Estudio arqueozoológico, tafonómico y evolución de las pautas de aprovechamiento de la macrofauna del valle*. Unpublished PhD Dissertation, UNED, Madrid.
- SALAZAR-GARCÍA D. C., POWER R. C., SANCHIS A., VILLASVERDE V., WALKER J. & HENRY A. G. 2013. — Neanderthal diets in central and southeastern Mediterranean Iberia. *Quaternary International* 318: 3-18. <https://doi.org/10.1016/j.quaint.2013.06.007>
- SÁNCHEZ-ROMERO L., BENITO-CALVO A., MARÍN-ARROYO A. B., AGUDO-PÉREZ L., KARAMPAGLIDIS T. & RIOS-GARAIAR J. 2020. — New insights for understanding spatial patterning and formation processes of the Neanderthal occupation in the Amalda I cave (Gipuzkoa, Spain). *Scientific Reports* 10: 8733. <https://doi.org/10.1038/s41598-020-65364-8>
- SANCHIS A., REAL C., SAUQUÉ V., NÚÑEZ-LAHUERTA C., ÉGÜEZ N., TORMO C., PÉREZ RIPOLL M., CARRIÑO MARCO Y., DUARTE E. & DE LA RASILLA M. 2019. — Neanderthal and carnivore activities at Llonin Cave, Asturias, northern Iberian Peninsula: Faunal study of Mousterian levels (MIS 3). *Comptes Rendus Palevol* 18 (1): 113-141. <https://doi.org/10.1016/j.crpv.2018.06.001>
- SANZ-ROYO A., MARÍN-ARROYO A. B., RIVERO O. & RIOS-GARAIAR J. 2023. — Hornos de la Peña (Northern Iberia): new excavations, chronological and subsistence data of the Middle-to-Upper Palaeolithic transition. *Archaeofauna* 32 (1): 129-143. <https://doi.org/10.15366/archaeofauna2023.32.1.008>
- SCHMID E. 1972. — *Atlas of Animal Bones for Prehistorians, Archaeologist and Quaternary Geologist*. Elsevier, Amsterdam, London, New York, 159 p.

- SERVAGGIO M. M. 1994. — Carnivore tooth marks and stone tool butchery marks on scavenged bones: archaeological implications. *Journal of Human Evolution* 27 (1-3): 215-228. <https://doi.org/10.1006/jhev.1994.1043>
- SIMMS S. R. 1987. — *Behavioral ecology and hunter-gatherer foraging: an example from the Great Basin*. British Archaeological Reports (International Series; 381), Oxford, 157 p.
- STINER M. C., KUHN S. L., WEINER S., & BAR-YOSEF O. 1995. — Differential burning, recrystallization, and fragmentation of archaeological bone. *Journal of Archaeological Science* 22 (2): 223-237. <https://doi.org/10.1006/jasc.1995.0024>
- STRAUS L. G. & GONZÁLEZ MORALES M. R. 2012. — *El Mirón Cave, Cantabrian Spain*. University of New Mexico Press, Albuquerque, 444 p.
- THÉRY-PARISOT I. 2001. — *Economie des combustibles au Paléolithique*. CNRS (Dossiers de documentation archéologique; 20), Paris, 200 p.
- THIÉBAUT C., MOURRE V., CHALARD P., COLONGE D., COUDENEAU A., DESCHAMPS M. & SACCO-SONADOR A. 2012. — Lithic technology of the final Mousterian on both sides of the Pyrenees. *Quaternary International* 247: 182-198. <https://doi.org/10.1016/j.quaint.2011.05.028>
- USDA 2020. — *U.S. Department of Agriculture. National Nutrient Database for Standard Reference, Release 19. Nutrient data laboratory*. <https://fdc.nal.usda.gov> (Last visit: 19/05/2024).
- VARELA S. & RODRÍGUEZ J. 2004. — *Atlas osteológico. Carnívoros ibéricos*. CSIC, Madrid, 70 p.
- VETTESE D., BLASCO R., CACERES I., GAUDZINSKI-WINDHEUSER S., MONCEL M.-H., THUN HOHENSTEIN U. & DAUJEARD C. 2020. — Towards an understanding of hominin marrow extraction strategies: a proposal for a percussion mark terminology. *Archaeological and Anthropological Science* 12 (48): 1-19. <https://doi.org/10.1007/s12520-019-00972-8>
- VIDAL-CORDASCO M., TERLATO G., OCIO D. & MARÍN-ARROYO A. B. 2023. — Neanderthal coexistence with *Homo sapiens* in Europe was affected by herbivore carrying capacity. *Science Advances* 9 (38): eadi4099. <https://doi.org/10.1126/sciadv.adi4099>
- VILLA P. & MAHIEU E. 1991. — Breakage patterns of human long bones. *Journal of human Evolution* 20 (1): 1-22. [https://doi.org/10.1016/0047-2484\(91\)90041-S](https://doi.org/10.1016/0047-2484(91)90041-S)
- VILLA P., CASTEL J. C., BEAUVAL C., BOURDILLAT V. & GOLDBERG P. 2004. — Human and carnivore sites in the European Middle and Upper Paleolithic: Similarities and differences in bone modification and fragmentation. *Revue de Paléobiologie, Genève* 23 (2): 705-730.
- VILLALUENGA A., CASTAÑOS P., ARRIZABALAGA A. & MUJICA J. A. 2012. — Cave bear (*Ursus spelaeus* rosenmüller heinroth, 1794) and humans during the early upper Pleistocene (lower and middle palaeolithic) in Lezetxiki, Lezetxiki II and Astigarragako Koba (Basque country, Spain). Preliminary approach. *Journal of Taphonomy* 10 (3/4): 521-543.
- WĘGRZYN M. & SERWATKA S. 1984. — Teeth Eruption in the European Bison. *Acta Theriologica* 29 (9): 111-121.
- YRAVEDRA J. 2000. — Subsistencia en el Musteriense Cantábrico. *Cuadernos de Arqueología de la Universidad de Navarra* 8: 7-26. <https://doi.org/10.15581/012.8.27776>
- YRAVEDRA J. 2006a. — *Tafonomía aplicada a la zooarqueología*. UNED, Madrid, 412 p.
- YRAVEDRA J. 2006b. — Acumulaciones biológicas en yacimientos arqueológicos: Amalda VII y Esquilleu III-IV. *Trabajos De Prehistoria* 63 (2): 55-78. <https://doi.org/10.3989/tp.2006.v63.i2.17>
- YRAVEDRA J. 2010a. — A taphonomic perspective on the origins of the faunal remains from Amalda Cave (Spain). *Journal of taphonomy* 8 (4): 301-334.
- YRAVEDRA J. 2010b. — Zooarqueología y tafonomía del yacimiento de Hornos de la Peña, San Felices de Buelna, Cantabria. *Complutum* 21 (1): 69-86.
- YRAVEDRA J. 2013. — New contributions on subsistence practices during the Middle-Upper Palaeolithic in northern Spain, in CLARK J. & SPETH J. D. (eds), *Zooarchaeology and Modern Human Origins: Human Hunting Behavior during the Later Pleistocene*. Springer (Vertebrate Paleobiology and Paleoanthropology), New York: 77-95. https://doi.org/10.1007/978-94-007-6766-9_6
- YRAVEDRA J. & COBO-SÁNCHEZ L. 2015. — Neanderthal exploitation of ibex and chamois in southwestern Europe. *Journal of Human Evolution* 78: 12-32. <https://doi.org/10.1016/j.jhevol.2014.10.002>
- YRAVEDRA J. & GÓMEZ CASTANEDO A. 2011. — Análisis de los procesos tafonómicos de Cueva Morín. Primeros resultados de un estudio necesario. *Zephyrus* 67: 69-90. <https://revistas.usal.es/uno/index.php/0514-7336/article/view/8370>
- YRAVEDRA J. & GÓMEZ-CASTANEDO A. 2014. — Taphonomic implications for the late mousterian of south-west Europe at Esquilleu cave (Spain). *Quaternary International* 337: 225-236. <https://doi.org/10.1016/j.quaint.2013.09.030>
- YRAVEDRA J. & UZQUIANO P. 2013. — Burnt bone assemblages from El Esquilleu cave (Cantabria, Northern Spain): deliberate use for fuel or systematic disposal of organic waste? *Quaternary Science Reviews* 68: 175-190. <https://doi.org/10.1016/j.quascirev.2013.01.019>
- YRAVEDRA J., BAENA J., ARRIZABALAGA A. & IRIARTE M. J. 2005. — El empleo de material óseo como combustible durante el Paleolítico Medio y Superior en el Cantábrico. Observaciones experimentales, in LASHERAS CORRUCHAGA J. A. & MONTES BARQUÍN R. (eds), *Neandertales cantábricos estado de la cuestión: actas de la reunión científica: celebrada en el Museo de Altamira los días 20-22 de octubre de 2004*. Ministerio de Cultura, Santander, Subdirección General de Publicaciones, Información y Documentación, Museo de Altamira 20: 369-383.
- YRAVEDRA J., MUÑOZ E. & GÓMEZ-CASTANEDO A. 2010. — Estrategias de Subsistencia en el yacimiento del Ruso (Igollo, Camargo, Cantabria España). *Espacio, Tiempo y Forma* 3: 39-58. <https://doi.org/10.5944/etfi.3.2010.1963>
- YRAVEDRA J., GÓMEZ-CASTANEDO A., ARAMENDI-PICADO J., MONTES-BARQUÍN R. & SANGUINO-GONZÁLEZ J. 2016. — Neanderthal and *Homo sapiens* subsistence strategies in the Cantabrian region of northern Spain. *Archaeological and Anthropological Sciences* 8: 779-803. <https://doi.org/10.1007/s12520-015-0253-4>
- YRAVEDRA J., ESTACA-GÓMEZ V., GRANDAL-D'ANGLADE A. & PINTO-LLONA A. C. 2023. — Neanderthal subsistence strategies: new evidence from the Mousterian Level XV of the Sopena rock shelter (Asturias, northern Spain). *Archaeological and Anthropological Sciences* 16: 6. <https://doi.org/10.1007/s12520-023-01914-1>

Submitted on 14 June 2024;
accepted on 4 April 2025;
published on 24 July 2025.