Iberian Neandertal fossils: Exploring funerary practices in a paleoclimatic context

Nohemi Sala[1], Edgar Téllez[1], Andion Arteaga-Brieba[1,2], Daniel Rodríguez-Iglesias[1], Manuel Rodríguez-Almagro[1], Ana Pantoja-Pérez[1], Jonas Grabbe[1], and Adrián Pablos[1,3]

[1]Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Burgos, Spain
[2]IPHES, Tarragona, Spain
[3]Universidad Complutense de Madrid, Spain

Abstract

The Iberian Peninsula is essential to our understanding of Neandertal populations due to its rich Middle Paleolithic archaeological record, boasting over 40 sites containing remains of Neandertals and their ancestors. This paper presents an updated review of the human remains from MIS-12 to MIS-3 found on the Iberian Peninsula from a taphonomic perspective. The goal is to explore whether there is a relationship between mortuary or funerary behaviors and the paleoclimatic context of each chronological period. The results show that most of the human remains found on the peninsula do not provide sufficient resolution to determine whether their deposition had a mortuary or funerary component. This is mainly due to the fact that the fossils are often found as isolated remains, which do not allow for comprehensive analysis. However, it has been possible to trace behaviors related to a culture of death with roots in the Middle Pleistocene. It is also noteworthy that in MIS-3, a time nearing the end of the Neandertals' existence, the most diverse taphonomic contexts are observed, including cannibalism, funerary practices, and carnivore-related contexts. To date, no proper burials have been documented in the Iberian Peninsula, in contrast with certain Euroasiatic regions. The absence of clear burial practices does not necessarily mean Neandertals did not engage in funerary behavior. Neandertal funerary traditions in the Iberian Peninsula may have differed from those elsewhere in Europe, thus calling for a re-evaluation of the funerary practices associated with Neandertals and a greater focus on alternative manifestations of the culture of death that could have been present in southern Europe..

1. Introduction

The Neandertal lineage, including both classic Neandertals and their Middle Pleistocene ancestors, managed to occupy different European territories. Europe's southern peninsulas are considered strategic regions for different species, especially during the Quaternary period, when climatic fluctuations could have been deciding factors for the habitability of different areas and the ways of life for the populations that occupied them (Carrión, et al., 2008, Cascalheira, et al., 2022, Ochando, et al., 2022, Taberlet, et al., 1998). The Iberian Peninsula in particular is located at the southwestern limit of Neandertal distribution. Neandertal populations were

shaped by recurrent local extirpations driven by climatic changes (Hublin and Roebroeks, 2009), followed by the recolonization of vast geographic areas by different genetic lineages (Dalén, et al., 2012). This can be traced to the genetic analyses conducted in recent decades, both from skeletal remains, such as the individuals of the Sima de los Huesos (Meyer, et al., 2014, Meyer, et al., 2016), and directly from sediments without requiring human fossils samples, as demonstrated by recent discoveries (Vernot, et al., 2021). The documented radiations, which have been discussed in a groundbreaking article by Rosas, et al. (2023), could be summarized as follows: a divergence 145–130 ka (MIS-6) involving Altai Neandertals (Siberia), early European groups (e.g., Hohlenstein-Stadel, Scladina), and Iberian sites, such as in the lower levels of Galería de las Estatuas (Vernot, et al., 2021) and Valdegoba (Andreeva, et al., 2022); a second radiation 105 ka, where western populations expanded into Siberia, replacing Altai Neandertals; and a third radiation 55 ka (MIS-4) producing "late Neandertals" across Europe and the Caucasus, with a second population replacement 47–39 ka. In Iberia, these dynamics are reflected in genetic shifts in Galería de las Estatuas, El Sidrón, and possibly Chatelperronian-bearing populations 43 ka, highlighting the peninsula's role as both a refuge and a region influenced by broader Neandertal evolutionary patterns (Rosas, et al., 2023). The Iberian Peninsula features a rich orography that provides a vast ecological and climatic diversity (Sala, et al., 2024a, Vidal-Cordasco, et al., 2022). However, we still do not know how paleoclimatic conditions, or these genetic exchanges and replacements, may have influenced the cultural traditions of Iberian Neandertal populations, specifically their mortuary and/or funerary behavior. One of the most distinctive behaviors of Neandertals and other Paleolithic hominins is their mortuary and/or funerary practices (Pettitt, 2011). According to Pettitt (2018), mortuary activities refer to practices that occur between the living and the dead at the time of death and do not involve symbolism or cultural practices. However, funerary behavior goes beyond simply doing something with the dead—i.e., a mortuary practice—and includes commemoration, designating spaces for the dead, and making time for commemoration. In other words, it involves symbolism and cultural practice (Pettitt, 2011, Pettitt, 2018, Pomeroy, et al., 2020). The Iberian Peninsula has a rich record of Neandertals, including pre-Neandertal populations (Cortés-Sánchez, et al., 2025, Garralda, 2005, Rosas, et al., 2023). In addition to the Middle Paleolithic sites that provide evidence of Neandertal activity, fossil remains have been directly recovered from a significant number of sites (Supplementary Information). The presence of human remains in Paleolithic sites can be attributed to different accumulation agents. Notably, a significant portion of the human fossils was recovered as isolated, fragmented, or decontextualized remains. This complicates their interpretation in terms of their accumulation origin and whether they can be linked to funerary behaviors. Nonetheless, their analysis remains invaluable because these remains may still provide important insights into when they were integrated into the broader Iberian fossil record, offering clues about the ecological and cultural contexts in which these populations lived. In some cases, paleontological contexts suggest that human remains were accumulated by carnivores (Arsuaga, et al., 2012a, Camarós, et al., 2016a, Camarós, et al., 2016b). Although it is not possible to infer funerary behaviors in these cases, the presence of Neandertal fossil remains in carnivore dens provides valuable information about the interactions between past human populations and other species with whom they likely competed for resources. This is inexorably linked to the paleoclimatic and paleoecological conditions in the different contexts where the fiercest competition for re-

sources played out. In other contexts, human remains show signs of having been processed by other humans. These butchery practices imply a complex range of behaviors, from cannibalism to funerary practices (Andrews and Fernández-Jalvo, 2003, Bello, et al., 2015, Boulestin, 1999, Carbonell, et al., 2010, Defleur, et al., 1999, Fernández-Jalvo, et al., 1999, Rougier, et al., 2016, Saladié and Rodríguez-Hidalgo, 2017, Trinkaus, 1985, Villa, 1992, White, 1992). Over the decades, much debate has arisen regarding the implications of cannibalistic practices and the objectives these practices may serve to achieve: survival (Rosas, et al., 2006, Saladié and Rodríguez-Hidalgo, 2017), violence-related (Boulestin and Coupey, 2015, Saladié, et al., 2012, Saladié and Rodríguez-Hidalgo, 2017), or funerary cannibalism (Marsh and Bello, 2023, Sala and Conard, 2019). In this case as well, it is important to understand the paleoclimatic conditions that were present in order to help contextualize cannibalistic practices with a paleoecological approach and to determine whether they were a result of cultural practices or a response to the search for food resources during times of scarcity. Finally, the Iberian Peninsula also provides evidence of funerary practices in the Neandertal lineage, some of which are incipient, in the form of the intentional accumulation of bodies. The goal of this study is to undertake a comprehensive review of the Neandertal fossil record in the Iberian Peninsula, analyzing mortuary and funerary behavior across its full spectrum—from its earliest possible manifestations to more developed expressions. By compiling and synthesizing the available archaeological evidence, we aim to explore potential patterns between ecological conditions and such behaviors, in cases where they can be reasonably identified. This is approached through a thorough bibliographic review of sites with Neandertals and their predecessors in the Iberian Peninsula, with the objective of integrating all published data to date. Lastly, the study seeks to assess whether observed mortuary practices may be linked to climatic factors or, alternatively, reflect shifts in population dynamics or cultural traditions.

2. Methods

To examine the geographical and chronological distribution of sites yielding Neandertal remains, we documented 55 archaeological units containing Neandertal or pre-Neandertal fossil remains, distributed across 46 distinct sites. This analysis is based on both bibliographic references and original sources. Far from being a minor undertaking, this review compiles essential data that are often scattered or only partially addressed in the literature, thereby providing a broader framework for interpreting the variability of mortuary or funerary practices. The Supplementary Material provides a comprehensive compilation of the information used to review the Iberian paleontological record. Some Neandertal fossils have not been discussed in the text because they are only known through press reports, such as the cranium fragment of Cueva Fantasma in Atapuerca, or because their exact chronological attribution is unknown, as in the case of the San Isidro site in Madrid or the Neandertal sites in Gibraltar. For each collection, the region was categorized into the Atlantic coast, Mediterranean coast, Cantabrian coast, northern central third of the peninsula, and central peninsula. The quantification of the samples was based on the Number of Identified Specimens (NISP) and the Minimum Number of Individuals (MNI). The chronology of the deposit was taken into consideration when available in bibliographic sources, along with the dating methods used in each case. The interpretation of the accumulation's origin,

as described in the bibliographic sources for each assemblage, was also taken into account. To estimate the corresponding Marine Isotope Stage (MIS) for each case, we used the chronological ranges defined by Lisiecki and Raymo (2005). The geographic coordinates of the archaeological sites were initially obtained from bibliographic references and subsequently cross-checked and standardized using Google Earth, ensuring that all sites are represented within a consistent spatial reference system (WGS 84 - EPSG:4326). The spatial data were visualized through a georeferenced map using the terra package (v.1.7-71) (Hijmans, 2025) in R (v. 4.4.2), providing an overview of the spatial distribution of Neandertal fossil sites. All the information gathered throughout this research—including the database, shapefiles, and R script used to produce Figure 1—has been made openly available in a public repository on Zenodo (Arteaga-Brieba, et al., 2025) under a CC BY 4.0 license (https://doi.org/10.5281/zenodo.15683451), ensuring transparency and reproducibility.

3. Results

3.1. MIS-12 to MIS-6. Middle Pleistocene Pre-Neandertals and Neandertals

During the Middle Pleistocene, different human populations occupied the Iberian Peninsula (Figure 1). Some of these populations share derived Neandertal traits, such as those found in the Sima de los Huesos site in Atapuerca (Arsuaga, et al., 2014, Arsuaga, et al., 2015). Others, however, display features characteristic of other early Middle Pleistocene European specimens, in which no derived Neandertal features have been identified, as seen in the Aroeira 3 cranium in Portugal (Conde-Valverde, et al., 2018, Daura, et al., 2017). In other cases, such as in Galería, also in Atapuerca, the fossil remains are isolated and fragmentary, providing limited information about their anatomy and, consequently, about their evolutionary lineage (Arsuaga, et al., 1999). At the Sima de los Huesos site, the remains of nearly thirty individuals were recovered from the base of a shaft, with the deposit dated to a maximum age of 450 ka (Aranburu, et al., 2017, Arnold, et al., 2014, Arsuaga, et al., 1997, Arsuaga, et al., 2014, Bermúdez de Castro, et al., 2021, Demuro, et al., 2019). The origin of the accumulation at this site has been widely debated for decades (Andrews and Fernández-Jalvo, 1997, Arsuaga, et al., 1990, Carbonell and Mosquera, 2006, Egeland, et al., 2018). The latest research has ruled out several accumulating agents, such as geological processes, carnivores, and accidental falls (Aranburu, et al., 2017, Sala, et al., 2014, Sala, et al., 2015a, Sala, et al., 2015b, Sala, et al., 2016, Sala, et al., 2024b, Sala, et al., 2024c). The only scenario that has not yet been dismissed is the intentional accumulation of corpses. Whether this accumulation reflects an incipient funerary behavior, or a mortuary practice devoid of any funerary component, is currently under investigation. In any case, this site is considered the most robust candidate for tracing the origins of funerary behavior in the fossil record. Considering the estimated chronology of the deposit, it can be said that the humans from the Sima de los Huesos were accumulated during Marine Isotope Stage 12 (MIS-12) (Demuro, et al., 2019), one of the most extreme glacial periods that occurred in the European continent over the past million year (Butiseacă, et al., 2024, Martínez-Dios, et al., 2021, Voelker, et al., 2010). The Middle Pleistocene record of the Iberian Peninsula includes another significant site with fossil remains that may be contemporaneous with Sima de los Huesos: the Gruta da Aroeira (Torres Novas, Portugal), which preserves evidence of human occupation dating back to

approximately 400,000 years ago. Although initial publications placed it within MIS 11 (Daura, et al., 2017)—a significantly warmer and wetter period compared to the harsh conditions of MIS-12 (Crow, et al., 2022, Dabkowski and Limondin-Lozouet, 2022)—recent research supports its attribution to MIS-12, based on stratigraphic, palaeoclimatic, and faunal evidence (Sanz, et al., 2024, Zilhão, 2023). Unfortunately, Aroeira fossils are much scarcer compared to Sima de los Huesos; only three human remains have been recovered: two teeth, Aroeira 1 (an inferior canine) and Aroeira 2 (an upper third molar), and the partial cranium of Aroeira 3. These fossil remains were found in a context of human occupation, specifically interpreted as a residential base camp (Daura, et al., 2017, Sanz, et al., 2018, Sanz, et al., 2024). Despite the scarcity of fossil remains, the detailed taphonomic analysis of the Aroeira 3 cranium, in addition to its archaeological context, made it possible to rule out certain scenarios as explanations for its accumulation, such as postmortem manipulation by humans (e.g., cannibalism or butchering) or carnivore activity (Sanz, et al., 2018). Whether the remains were gathered by other humans as part of a funerary ritual remains a hypothesis that, at present, cannot be confirmed or refuted. Despite the fragmentary nature of the paleoanthropological collection, which does not lend itself to further interpretation of the funerary capacities of this Middle Pleistocene population, the human presence in the Almonda karst system near the Portuguese Atlantic coast during MIS 11 is confirmed by the human, lithic, and faunal remains recovered from the site (Daura, et al., 2017, Daura, et al., 2018, Sanz, et al., 2018). With the exception of the pre-Neandertal sites of Sima de los Huesos and Aroeira, no additional human remains have been identified from MIS-12 to MIS-9. The subsequent fossils in the Iberian record belong to Neandertals from isotopic stage MIS-8. The absence of human fossils from these periods appears to be related to the following possibilities: mortuary practices with a low probability of preservation, or simply the fact that human remains from these periods have yet to be discovered. This absence of human fossils from the MIS-10 interval aligns with the broader pattern observed across the European continent, where no human remains have been identified for this period. Furthermore, MIS-9 is characterized by a scarcity of human fossils, with notable exceptions, including the German sites of Steinheim and possibly Reilingen (Berckhemer, 1936, Czarnetzki, 1989, Dean, et al., 1998, Hublin, 2009), as well as the Italian sites of Polledrara di Cecanibbio and Castel di Guido (Anzidei, et al., 2012, Mariani-Costantini, et al., 2001, Pereira, et al., 2017). Other human remains from the Middle Pleistocene found in the Iberian Peninsula were recently presented to the scientific community, corresponding to the onset of MIS-8 (García-Martínez, et al., 2024, Palancar, et al., 2024, Torres-Medina, et al., 2024). These remains, recovered in Los Villares de Ruidera, in Ciudad Real and interpreted as originating from a shelter that was dismantled during road construction, were chronologically assigned to 290 ± 24 ka, based on OSL dating. These human remains were associated with a faunal assemblage showing evidence of anthropogenic manipulation (García-Martínez, et al., 2022). However, since these human remains have not yet been described, their taphonomic interpretation is still outstanding. Other Middle Pleistocene sites in the Iberian Peninsula containing human remains are characterized by the scarcity of such findings, which complicates their taphonomic characterization. This is the case for the Galería site in the Sierra de Atapuerca, which is located very close to the Sima de los Huesos. In 1976, a human mandible fragment was recovered from sediment debris from previous excavations and was analyzed by Bermúdez de Castro and Rosas (1992), Rosas and Bermúdez de Castro (1999).

Since it was not found in situ, its original stratigraphic position has yet to be determined and, consequently, its chronology is not easily determined. Fortunately, in 1995, a cranial fragment was discovered, this time in unaltered sediments at the base of the G-III lithostratigraphic unit (Arsuaga, 1999), with an estimated chronology around 220-260 ka, corresponding to MIS-8 and early MIS-7 (Demuro, et al., 2014). The scarcity of these remains poses a challenge when it comes to ascertaining the origin of their deposition. Nevertheless, the presence of funerary behavior in this case seems unlikely, as several taphonomic and depositional factors—such as the existence of a natural trap, carcass exploitation by human groups, and scavenging by carnivores (García-Medrano, et al., 2017, Ollé, et al., 2005), provide alternative explanations for the accumulation of remains and make it improbable that this space was used for mortuary and/or funerary activities. Nonetheless, given the geological complexity and the time potentially represented in the stratigraphic units, it cannot be ruled out that multiple scenarios—including sequential and independent uses—may have occurred when interpreting the presence of isolated human remains. The Cova Negra site has so far yielded 37 human remains corresponding to at least eight individuals, recovered from different units of the stratigraphic sequence (Arsuaga, et al., 1989, Villaverde-Bonilla and Eixea, 2024). New dates of the deposits indicate ages ranging from MIS-8 to MIS-6, with human remains from the base of the sequence (level XII) dating to 273 ± 26 ka and those from level XI to 261 ± 42 ka (Richard, et al., 2019). Taphonomic analyses of the human remains examined in the present study suggest that most modifications occurred postmortem, except for two instances of trauma with signs of healing observed in cranial remains. No evidence of butchery activities has been identified, ruling out accumulation in a cannibalistic context. Regarding carnivore modifications, a study conducted on perforations found in the parietal bone CN42174b suggests modification by a leopard (Camarós, et al., 2016a). However, even if these marks are confirmed as carnivore damage, they appear to result from secondary scavenging rather than active predation or primary accumulation. The absence of typical features associated with systematic carnivore accumulation—such as green bone fractures, high frequencies of tooth marks, or the selective transport and consumption of specific skeletal elements—strongly supports this interpretation. In this sense, the few modifications present are better understood as isolated instances of scavenging that occurred after deposition. Considering the abundance of individuals at the site, the predominantly postmortem nature of the bone modifications, and the absence of taphonomic patterns consistent with carnivore accumulation, the most plausible hypothesis is that the remains were accumulated by other hominins, possibly as a manifestation of some form of funerary behavior. This interpretation, however, does not imply deliberate preparation or modification of the space (i.e., formal burial), for which no clear evidence has been identified. For these reasons, this site is undoubtedly a promising candidate for more detailed investigation in future research. Within the Valencian Community, the Bolomor site also stands out for containing human fossils in different stratigraphic units (Arsuaga, et al., 2001, Arsuaga, et al., 2012b, Blasco and Fernández-Peris, 2024). Although the exact position - and therefore the chronology - of some fossils is unknown, human remains have been identified in Unit XIII, corresponding to MIS-7 (Arsuaga, et al., 2012b). Unfortunately, these consist of a single isolated dental remain, a canine, making it impossible to infer the origin of the accumulation. The remaining fossils were found in Unit IV, corresponding to MIS-5, which will be addressed in this study. With respect to the context of MIS-7 and the Mediterranean

region, the Mollet I site (Serinyà, Girona) yielded an upper right molar from an immature individual (Maroto, et al., 2012). Although no hypothesis has been proposed regarding the accumulation processes responsible for this specimen, faunal analyses from the site indicate that the cave likely served as a den for carnivores, particularly the spotted hyena (Maroto, et al., 2012). There are two Iberian sites that have yielded Neandertal remains dating to the MIS-6 glacial period: the Arbreda and Lezetxiki sites. At the Arbreda site, two human teeth were recovered from Level N, one belonging to an adult and the other to an infant, dated to over 120 kyr (Lozano, et al., 2024). Despite their poor preservation and significant dental wear, which prevent definitive taxonomic classification, their crown dimensions and certain tissue proportions are consistent with an attribution to Homo neanderthalensis. These teeth were found in a context reflecting prolonged and recurrent occupations of the cave (Lozano, et al., 2024). At Lezetxiki, a complete humerus was recovered from Level VIII. Initially classified as pre-Neandertal, it was later reassigned as Neandertal (Arrizabalaga, et al., 2005, Basabe, 1966, de la Rúa, et al., 2016). This specimen is thought to belong to an individual who was approximately 35 years of age, possibly a female (Basabe, 1966). Since these remains are isolated in both cases, it is not possible to draw inferences about the mortuary or funerary behaviors of these populations, which limits the interpretation of their practices in this regard. Finally, a promising paleontological site has been identified in northern Iberia, where fossil remains of the Neandertal lineage have recently been documented. This site, known as Sima I of the Polvorín cave (Karrantza), has yielded 16 human fossils to date (Gómez-Olivencia, et al., 2022, Gómez-Olivencia, et al., 2023, Gómez-Olivencia, et al., 2024), all compatible with a single adult individual. This accumulation of human remains is located at the bottom of a vertical shaft, where mainly carnivore remains have been found alongside the human fossils, including Ursus deningeri, U. spelaeus, and Crocuta crocuta. Taphonomic analyses conducted on the carnivore remains thus far rule out both humans and carnivores as accumulation agents (Rodríguez-Almagro, et al., 2024). The chronological context of the human fossils remains uncertain; however, some anatomical features are consistent with Middle Pleistocene human populations, specifically with those from the Sima de los Huesos site (Gómez-Olivencia, et al., 2022, Gómez-Olivencia, et al., 2023, Gómez-Olivencia, et al., 2024). Future research will be crucial for establishing the chronological and taphonomic context for this site, given its significant potential.

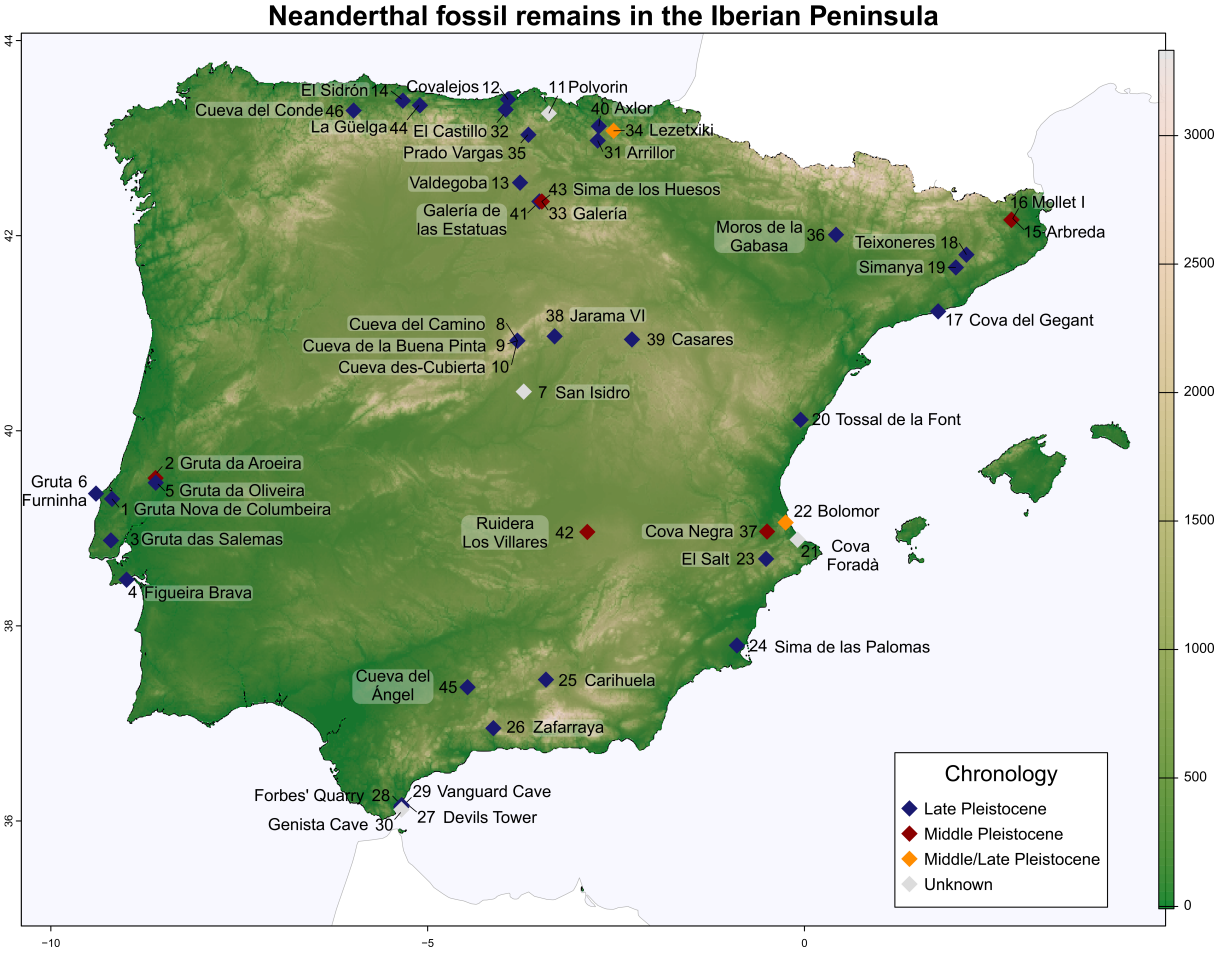

Figure 1: Map of the Iberian Peninsula showing all the sites that have yielded Neandertal fossil remains. Specific information about each site can be found in the Supplementary Information. The map was generated using R, and the complete dataset, R code, and shapefiles used are available on Zenodo (Arteaga-Brieba, et al., 2025). Site labels were manually adjusted for optimal readability 1: Gruta Nova da Columbeira; 2: Gruta da Aroeira: 3: Gruta das Salemas; 4: Figueira Brava; 5: Gruta da Oliveira; 6: Gruta Furninha; 7: San Isidro; 8: Cueva del Camino (Pinilla del Valle); 9: Cueva de la Buena Pinta (Pinilla del Valle); 10: Cueva Des-Cubierta (Pinilla del Valle); 11: Sima I Polvorín; 12: Covalejos; 13: Valdegoba; 14: El Sidrón; 15: Arbreda; 16: Mollet I; 17: Cova del Gegant; 18: Cova de les Teixoneres; 19: Cova Simanya; 20: Tossal de la Font; 21: Cova Foradà; 22: Bolomor; 23: El Salt; 24: Sima de las Palomas; 25: Carihuela; 26: Zafarraya; 27: Devils Tower; 28: Forbe's Quarry; 29: Vanguard Cave; 30: Genista cave; 31: Arrillor; 32: El Castillo; 33: Galería (Atapuerca); 34: Lezetxiki; 35: Prado Vargas; 36: Moros de la Gabasa; 37: Cova Negra; 38: Jarama VI; 39: Casares; 40: Axlor; 41: Galería de las Estatuas (Atapuerca); 42: Ruidera - Los Villares; 43: Sima de los Huesos (Atapuerca); 44: La Güelga; 45: Cueva del Ángel; 46: Cueva del Conde.

3.2. Late Pleistocene Neandertals

In the Late Pleistocene, the onset of MIS-5 marks one of the warmest interglacial periods, even surpassing present-day conditions (Rohling, et al., 2008). MIS-5, spanning approximately 130,000 to 71,000 years before present (BP) (Lisiecki, 2005), is divided into five substages: MIS-5e, 5d,

5c, 5b, and 5a. The MIS-5e substage (Eemian) represents the climatic optimum, characterized by global temperatures slightly higher than today's temperatures and sea levels 6–9 meters above current levels, driven by extensive melting of polar ice sheets (Rohling, et al., 2008). During MIS-5, the Iberian Peninsula experienced significantly warmer and more humid conditions, which facilitated the expansion of deciduous forests in northern regions and increased resource availability in both coastal and inland areas (Arsuaga, et al., 2012a, Ochando, et al., 2022). These favorable environmental conditions likely supported the expansion of Neandertal populations, potentially resulting in increased population densities. Such demographic growth could be associated with greater variability and complexity in their cultural and funerary behaviors. Outside the Iberian Peninsula, evidence of burials attributed to MIS-5 populations, including Neandertals and early Homo sapiens, has been documented. Noteworthy examples include sites in the Eastern Mediterranean, such as Tabun, Qafzeh, and Skhul (Been and Barzilai, 2024, Garrod and Bate, 1937, McCown and Keith, 1939, Tillier, 2022, Vandermeersch and Bar-Yosef, 2019), where evidence of intentional burial practices reflects increasing symbolic behaviors and the modification of spaces for funerary purposes. To date, 11 sites yielding Neandertal fossil remains and which were attributed to MIS-5 have been identified within the Iberian Peninsula. Unfortunately, all of these sites contained scarce human remains which have not been sufficiently analyzed from a taphonomic perspective (Supplementary Information). As a result, the depositional origin of most of these specimens remains unknown. This is the case for the fossils recovered from Phase IV of the Cova de Bolomor, where additional human remains were found. A recent taphonomic analysis conducted by the authors of the present study failed to identify any marks indicative of human or carnivore activity on these bones. While the exact process by which these remains were deposited at this location remains unclear, an asynchronous deposition could imply a form of intentional accumulation. However, this hypothesis requires further corroboration through additional lines of evidence. In the Galería de las Estatuas, one human remain has been described in the literature: a toe phalanx (Pablos, et al., 2019). Despite the scarcity of human remains, DNA has been successfully detected from at least two genetically distinct populations at this site (Vernot, et al., 2021). The presence of distal phalanges of the fourth and fifth toes in Neandertal fossil assemblages represents an exceptional rarity in the paleoanthropological record. Such elements have only been documented in contexts involving nearly complete skeletons, as in the intentional burials of Kiik-Koba 1, Regourdou 1, and Shanidar 4 (Bonch-Osmolovski, 1954, Maureille, et al., 2015a, Trinkaus, 1983, Trinkaus, et al., 2016), or within extensive paleoanthropological collections, such as those from Sima de los Huesos or Krapina (Pablos, 2015, Pablos, et al., 2017, Pablos and Arsuaga, 2024, Trinkaus, 1975, Trinkaus, 2016). The discovery of the distal phalanx of the fifth toe at this site makes this cave particularly significant in terms of its funerary potential (Pablos, et al., 2019). Portugal has also yielded interesting MIS-5 paleoanthropological findings, particularly at sites such as Gruta da Oliveira (Torres Novas), Gruta Furninha, Peniche, and Gruta Nova da Columbeira (Bombarral), where isolated remains of unknown depositional origin have been recovered (Figure 1; Supplementary Material). Finally, during MIS-5, human remains attributed to Neandertals were also recovered from the Figueira Brava site (Antunes and Cunha, 1992, Antunes and Cardoso, 2000, Zilhão, et al., 2020). At this site, three human remains were identified: an upper fourth premolar, a first metacarpal, and a proximal phalanx (Antunes and Cunha, 1992). These human remains are interpreted as belonging to a single male individual

who was approximately 16 to 20 years old at the time of death. A taphonomic study suggests a potential case of cannibalism, although no direct evidence of anthropogenic manipulation, such as cut marks, intentional breakage, or human bite marks, has been identified (Antunes and Cunha, 1992). It is worth noting that, if the cannibalism hypothesis at Figueira Brava is confirmed, it would represent the earliest evidence of cannibalism in the Iberian Peninsula occurring during the Late Pleistocene. Nevertheless, given the limited size of the collection and the lack of unequivocal evidence of cannibalism, this hypothesis should remain highly tentative. Lastly, there are two Iberian MIS-5 sites containing human remains that have been interpreted as assemblages corresponding to cave occupations by carnivores (Figure 2). One of these sites is the Cueva del Camino in Pinilla del Valle (Madrid), where two molars belonging to the same adult individual were recovered from level 5. These remains likely reached this deposit due to scavenging by spotted hyenas (Arsuaga, et al., 2012a). The other site is the Cova del Gegant in Barcelona, where a total of five remains, corresponding to four individuals, have been documented. These remains derive from different areas of the cavity, and recent studies indicate that they come from at least two distinct stratigraphic horizons, associated with different chronologies within the MIS-5 to MIS-4 range (Daura, et al., 2021, Daura, et al., 2022). Specifically, the mandible (Gegant-1) and the incisor (Gegant-2) from layer XVb in the Lateral Gallery date to around 52–60 ka (Daura, et al., 2021), while the humerus (Gegant-4) and the mandible (Gegant-5) from layer V in the Main Gallery are slightly older (93.7 ± 15.0 to 59.3 ± 1.4 ka cal. BP) (Daura, et al., 2021, Daura, et al., 2022). In this case, although carnivore activity is well documented at the site—particularly in layer V, as evidenced by bone damage patterns, coprolites, and partially digested remains—it cannot be confirmed whether the Neandertal fossils were accumulated by carnivores or resulted from the disturbance of intentionally deposited corpses. Given the presence of lithic artifacts and some anthropogenic modifications on faunal remains in the same layer, human presence in the cave is also documented. However, due to the complex taphonomic history of the site, including possible post-depositional disturbances and the impact of marine erosion near the entrance, the exact accumulation processes of the Neandertal bones remain uncertain (Daura, et al., 2005, Daura, et al., 2021). In the Axlor site, located in the Cantabrian region (Figure 1), several human remains have been recovered (Bailey, et al., 2024, Gómez-Olivencia, et al., 2019) throughout a sequence extending from MIS-5 to MIS-3 (Demuro, et al., 2023). Although a thorough taphonomic study was conducted, the absence of diagnostic marks on the bone surfaces made it difficult to determine the origin of the accumulation of Neandertal remains in the different units (Gómez-Olivencia, et al., 2019). The southern part of the Iberian Peninsula has also yielded some isolated records of Neandertal remains from MIS 5, such as a single fragmentary remain from Cueva del Ángel in Córdoba (Bermúdez, et al., 2023). Following the MIS-5 interglacial period, a gradual cooling phase began, encompassing MIS-4 and the dynamic climatic oscillations characteristic of MIS-3. This period was marked by rapid alternations between warmer interstadials and colder stadials, known as Dansgaard-Oeschger events, alongside episodes of significant ice discharge into the North Atlantic, referred to as Heinrich events. These fluctuations had profound effects on ecosystems and resource availability across Europe, shaping the environmental conditions in which Neandertals and other populations lived. Currently, there are few sites with Iberian Neandertal remains whose dating can be reliably corroborated as strictly corresponding to the cold MIS-4 period. One of these sites is Cueva de la Buena Pinta,

which, together with Cueva del Camino, Navalmaíllo, and Cueva Des-Cubierta, forms part of the Pinilla del Valle archaeological complex located in the Lozoya Valley in Madrid. In this case, the remains consist of two teeth—a left upper second molar and third molar—both belonging to the same adult individual (Rodríguez, et al., 2016). The stratigraphic level where these dental remains were recovered, Level 3, has been interpreted as a hyena den (Huguet, et al., 2010). As in the neighboring Cueva del Camino, we cannot rule out the possibility that these remains were accumulated by carnivores. This unit has been dated by thermoluminescence to approximately 63.4 ± 5.5 ka BP (Pérez-González, et al., 2010), corresponding to a cold period, as indicated by various proxies, including the presence of the steppe pika (Ochotona cf. pusilla) (Laplana, et al., 2016). Additionally, a human remain was found in Level J of the previously mentioned Arbreda site, also corresponding to MIS-4, which is indicative of short and seasonal occupations of the cave (Lozano, et al., 2024); however, given that it is just one isolated tooth, it does not provide insights into the funerary practices of these Neandertals. Two other cases potentially correspond to either MIS-4 or MIS-3, as their chronological range overlaps with both isotopic stages. However, there is insufficient data to be able to assign them a more precise isotopic stage. Firstly, at the Des-Cubierta site, several deciduous teeth and a fragmentary mandible were recovered, representing a single immature individual. The age at death has been estimated to be between two and five years (Rodríguez, et al., 2016). The origin of the accumulation of these human remains, is difficult to establish due to their isolated nature. However, the underlying layer (Level 3) at this site has been interpreted as an accumulation of cranial remains of large herbivores, possibly with a symbolic component for that group of Neandertals (Baquedano, et al., 2023). In addition, Neandertal remains were documented in Mousterian Unit XX in the Cueva del Castillo in Cantabria, attributed to MIS-4 and early MIS-3. These remains include a left upper second premolar, a proximal hand phalanx fragment, and a femoral head fragment (Garralda, et al., 2023). Unfortunately, it appears that these remains did not provide sufficient taphonomic information that would allow us to determine whether their presence in Unit XX of this site can be explained by an accumulation with either a funerary or mortuary origin. At this same site, human remains were also recovered from Unit 18, with a firmly established chronology of 44,940–42,110 cal. ka BP, corresponding to a late population of Iberian Neandertals within MIS-3 (Garralda, et al., 2022, Wood, et al., 2018). In this case, the remains consist of deciduous teeth likely belonging to two individuals. For one of these individuals, the loss of teeth is attributed to the natural process of replacing deciduous teeth with permanent dentition, but in the case of the deciduous third molar, the tooth was likely lost during life due to a traumatic event, as it shows incomplete root resorption (Garralda, et al., 2022). The deposition of these teeth at this site can therefore be attributed to natural processes occurring during this site's occupation by this Neandertal group, ruling out any interpretations involving funerary behavior. The Marine Isotopic Stage 3 (MIS-3) was crucial for Neandertal populations, which is when their definitive extinction occurred (Finlayson and Carrión, 2007, Raia, et al., 2020, Staubwasser, et al., 2018, Wolf, et al., 2018). Regardless of the ultimate cause or causes behind their disappearance, it is possible that the rapid climatic oscillations present at the time posed a significant challenge for the Neandertal groups that remained on the Iberian Peninsula (Vidal-Cordasco, et al., 2022). However, if we focus on the Iberian paleoanthropological record, the units corresponding to MIS-3 have provided a rich record of human fossils compared to others. In fact, approximately 18 deposits containing

human fossils have been recorded for this marine isotopic stage (Supplementary Information). Moreover, during this period, mortuary practices were more diverse, with one of the most robust pieces of evidence of funerary practices found alongside more widespread instances of cannibalism than in previous stages, while still in other cases, carnivore-related contexts persisted. In other cases, such as Teixoneres Cave Neandertal fossil remains from the MIS-3 (Rufà, et al., 2014, Talamo, et al., 2016) have been recovered (Janković, et al., 2024) although the origin of the accumulation of these remains is currently unknown Some isolated remains were found in contexts interpreted as carnivore occupations (Figure 2) at the sites of Jarama VI (Lorenzo, et al., 2012) and, Casares (Basabe, 1973), both located in the province of Guadalajara, in central Spain, as well as in Moros de la Gabasa, located in Huesca (Lorenzo and Montes, 2001). On the other hand, there are several sites with isolated human remains of uncertain origin, such as Arrillor (Bermúdez de Castro and Saenz de Buruaga, 1999), El Salt (Garralda, et al., 2014), Gruta das Salemas (Ferembach, 1962), Lezetxiki (Basabe, 1970), Prado Vargas (Navazo Ruiz, et al., 2021), Covalejos (Montes Barquín and Sanguino González, 2021), La Güelga (Kehl, et al., 2018, Menéndez, et al., 2014) and Cueva del Conde (Adán, et al., 2011, Arbizu, et al., 2008) (see details in the Supplementary Information). There are two sites that have been interpreted as the result of cannibalistic practices. The first is the Sidrón site, located in the northern Iberian Peninsula, specifically in Asturias. This site is well known from a paleoanthropological perspective, as more than 2,500 human remains have been recovered from it, corresponding to a minimum of 13 individuals (Rosas, et al., 2012, Rosas, et al., 2017). Some elements in anatomical position (Rosas, et al., 2012) and elements associated with the same juvenile individual (Rosas, et al., 2017) were found there. Furthermore, this site is renowned for providing a rich record of ancient DNA, which has been crucial in molecular research conducted on Neandertals (Lalueza-Fox, et al., 2012). Cut marks have been found on the human fossils at this site, which have been interpreted as evidence of cannibalism (Rosas, et al., 2006). This site has been proposed in the literature as a possible case of survival cannibalism, as almost no animal remains were found associated with the deposit of human fossils (Rosas, et al., 2006). However, new taphonomic data from the deposit could provide new interpretations regarding this matter (Saladié and Rodríguez-Hidalgo, 2017). In addition to the Sidrón site, another MIS-3 Neandertal site has been interpreted as a case of cannibalism. This is the Zafarraya Cave site, located at the other end of the Iberian Peninsula, in the province of Málaga (Higham, et al., 2014, Michel, et al., 2013, Wood, et al., 2013). This site has yielded 16 Neandertal fossils, which are estimated to correspond to a minimum of 9 individuals (Barroso Ruiz and de Lumley, 2006, Hublin, et al., 1995). A recently revealed paleoanthropological collection from Cova Simanya (Barcelona) was discovered while reviewing old excavation collections in a museum (Morales, et al., 2023). It includes 54 human remains corresponding to at least three Neandertal individuals. One faunal bone has been dated to between 42,440–42,110 cal BP, while dates from charcoal samples fall outside the radiocarbon range (Morales, et al., 2023). Although the taphonomic characteristics remain unclear because a specific study has not yet been conducted, many fossils are complete, and almost all of the anatomical parts of the entire skeleton are represented (see inventory of human remains available in the supplementary information from Morales, et al. (2023)), including bones typically found in intentional burials, such as finger and toe phalanges. Therefore, this accumulation is possibly related to funerary behavior, though this hypothesis cannot be confirmed until the assemblage's

taphonomy is studied. At the Cova Foradà site (Oliva, Valencia), located on the Mediterranean coast, numerous Neandertal remains have been found. The cave preserves a long stratigraphic sequence ranging from the Middle Paleolithic – with lithic industry attributed to the Mousterian – (Eixea and Sanchis, 2022) to the Bronze Age (Aparicio, et al., 2014, Lozano, et al., 2013). Between 2000 and 2003, fossils, including a maxilla, four cranial fragments, a fibula fragment, and a deciduous molar, were recovered from Unit 29 in the Mousterian levels, for which it should be noted that absolute geochronological data is not yet available. These remains correspond to at least two individuals and were published by Lozano, et al. (2013), documenting toothpicking and periodontal disease in the maxilla. In addition to these isolated remains, a partial skeleton of an adult individual in anatomical position was recovered in 2010. The individual was found lying on its side within a calcareous concretion in a small natural cavity in the eastern wall at the end of the cave (Aparicio, et al., 2014). This skeleton, which preserves the skull, thoracic region, left arm and hand, and sacrum, is currently on display at the Museo de Prehistoria de Valencia. Unfortunately, detailed information about its stratigraphic position within the cave's sequence, its geochronology, and its taphonomic aspects is still lacking. Future studies may shed light on these questions to determine, among other things, whether the Cova Foradà skeleton could be added to the scarce catalog of Iberian Neandertals found in a clearly funerary context. Finally, the Sima de las Palomas site, located in the southeasternmost region of the Iberian Peninsula, has yielded one of the most extensive Iberian paleoanthropological collections of late Neandertals to date. Remains of at least 14 individuals have been recovered so far, including three associated partial skeletons (Trinkaus and Walker, 2017, Walker, et al., 2008, Walker, et al., 2012). This site is a cave system with vertical shafts. The three partial skeletons were discovered in a unit known as "Conglomerate A" composed of highly cemented sediments and blocks and dated to around 50,000 years ago. The skeletons were found in anatomical position. The most complete of these skeletons (SP-96), corresponding to an adult female individual, was found lying on her right side, with flexed arms and her hands near her facial region. This posture suggests to the authors that it may have resulted from intentional deposition. To date, no evidence has been found suggesting a burial pit excavation, nor have any items been found that could be considered grave goods or intentional arrangement of covering slabs. However, no signs of carnivore modification were found on the skeletons, despite the presence of remains indicating their presence at the site, thus suggesting a rapid burial preventing perimortem disturbances of the bodies. While the authors entertain the possibility of an accidental accumulation of the skeletons, they find the idea of intentional accumulation more plausible, suggesting a funerary purpose for the deposition within the cave (Trinkaus and Walker, 2017, Walker, et al., 2008, Walker, et al., 2012). Additionally, the three skeletons were found at different depths (Walker, et al., 2012), which may indicate recurrent use of the space for the accumulation of different individuals, further supporting the hypothesis of intentional accumulation for funerary purposes. Lastly, it is worth mentioning that in deeper units of the site, human remains attributed to MIS-4 and MIS-5 have also been recovered (Walker, et al., 2017). However, so far, only the presence of these remains has been reported, and therefore, details about them remain unknown.

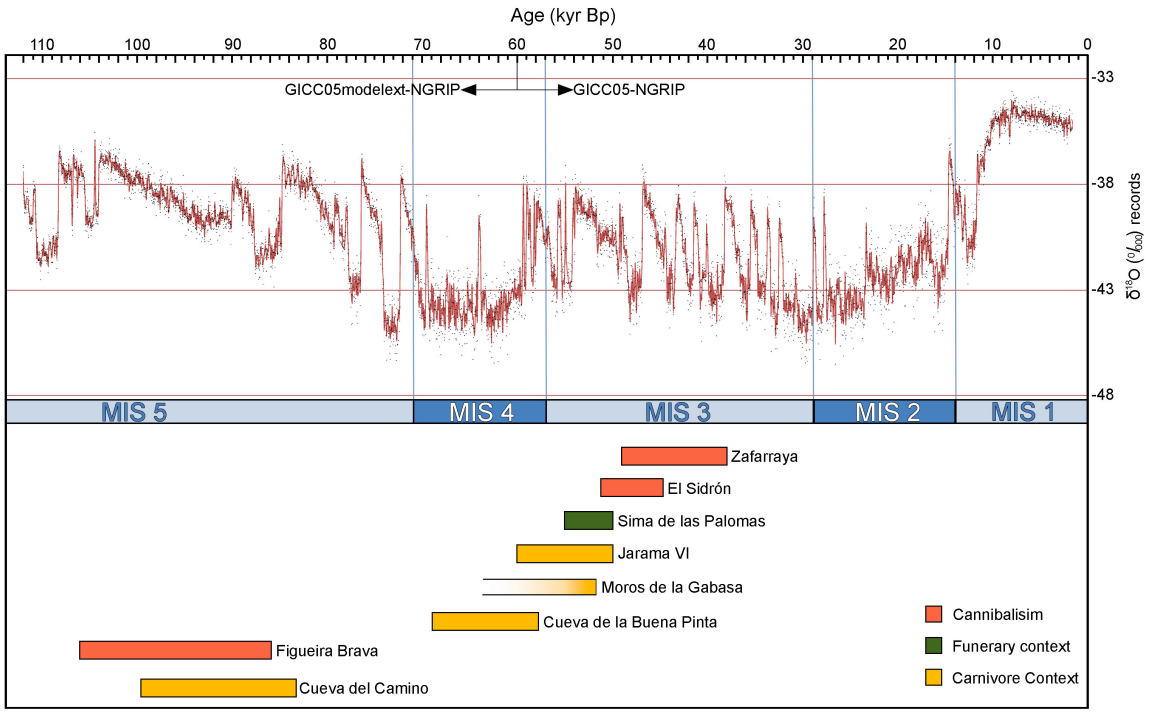

Figure 2: Paleoclimatic and chronological context of Iberian Neandertal sites for which there is a consensus as to the origin of the accumulation. The oxygen-isotope data (North Greenland Ice Core Project Members, 2004) adjusted to 60 year averages (data points are black circles and the red line is the 6-points running mean) are presented here on the GICC05 age scale dating back to 60 ka (Andersen, et al., 2006, Rasmussen, et al., 2006, Svensson, et al., 2008, Vinther, et al., 2006), and before that on the ss09sea modelled age scale (Johnsen, et al., 2001) shifted (by –705 years) to match GICC05 at 60 ka (Wolff, et al., 2010). Detailed chronological aspects of the sites are described in the Supplementary Information.

4. Concluding discussion

In addition to its rich archaeological record, with numerous sites showing evidence of human occupation (see, for example Cortés-Sánchez, et al. (2025)), the Iberian Peninsula has a significant paleoanthropological record, including both classic Neandertals and their Middle Pleistocene ancestors (Figure 1 and Supplementary Material). This evidence indicates that these populations were capable of occupying a vast territory across the peninsula, ranging from the Atlantic, Mediterranean, and Cantabrian coastal areas to inland Iberia, intermittently throughout the Middle and Late Pleistocene (Figure 1 and Supplementary Information). Although the Iberian Neandertal paleoanthropological record offers a variety of information, most of the findings consist of isolated remains with unclear depositional contexts. In addition to these contexts of unknown origin, the diversity of contexts in which Neandertal remains have been found includes the following: cannibalism, accumulations that were likely carried out by carnivores, and intentional accumulations of corpses. The scarcity of human remains prior to the emergence of structured funerary practices—those involving deliberate modification of space, such as formal burials—appears to be conditioned by a combination of factors. Other mortuary practices that

do not involve rapid burial or other mechanisms conducive to the preservation of human remains are particularly vulnerable to post-depositional processes. In such cases, skeletal elements are more likely to be affected by natural agents of disturbance—such as bioturbation, erosion, or sediment reworking—which may lead to the displacement and mixing of remains from different temporal or contextual origins. As a result, human fossils can become incorporated into palimpsestic deposits, complicating their stratigraphic attribution and archaeological interpretation. No evident relationship appears to exist between MIS stages and the observed mortuary or funerary behavior in the analyzed contexts. The only possible exception is cases of cannibalism, which have been documented exclusively during MIS-3. Among the behaviors associated with specific MIS stages, cannibalism stands out as one of the most widely debated in terms of its purpose, with a range of hypotheses encompassing survival-related causes—such as famine-induced anthropophagy—as well as ritualistic, gastronomic, violent, or funerary contexts (Saladié and Rodríguez-Hidalgo, 2017). Instances of cannibalism have been documented in Europe since the Lower Pleistocene at Gran Dolina (Fernández-Jalvo, et al., 1996, Saladié, et al., 2012), as well as during the Middle Pleistocene (Arago) (de Lumley, 2015). For Neandertals, cannibalism was not an isolated phenomenon, as paleoanthropological assemblages with clear evidence of cannibalism have been documented at various sites across Europe, including Belgium (Troisieme caverne of Goyet, Rougier, et al. (2016)), the Czech Republic (Vindija, Smith, et al. (2024)) and France (Moula Guercy, Defleur, et al. (1999)), among others. In the Iberian Peninsula, two cases of Neandertal cannibalism have been identified, specifically at El Sidrón (Rosas, et al., 2006) and Zafarraya (Barroso Ruiz and de Lumley, 2006). Both sites date to MIS-3, a period in which genetic diversity has been observed in late Neandertals from Vindija, Spy, and Goyet (Vernot, et al., 2021), similar to the genetic patterns found in El Sidrón (Vernot, et al., 2021). These could correspond to the radiation event around 50 ka in the Iberian Peninsula. This data could indicate that cannibalism in the El Sidrón populations may be a manifestation of funerary behavior associated with genetically related groups, such as Goyet or Vindija, which are known for their cannibalistic practices. This could suggest that cannibalism might have been a cultural characteristic, possibly linked to funerary practices, which these populations brought along on their migrations and persisted in the populations that spread across the territory. This phenomenon is similar to what has been proposed for Magdalenian populations, as suggested by Marsh and Bello (2023), who argue that differences in funerary behaviors during the Magdalenian reflect distinct genetic ancestries indicative of population movements during the late Upper Paleolithic. Alternative explanations, such as cannibalism resulting from violent interactions, should also be considered, as they might carry significant cultural and behavioral implications. The documentation of funerary behaviors on the Iberian Peninsula spans from the Middle Pleistocene (as evidenced by sites such as Sima de los Huesos) to the final stages of the Neandertal presence during MIS-3 (such as Sima de las Palomas). In the absence of data for Foradà (Oliva) and Simanya, with the information currently at hand, we can surmise that there is no documented case of a proper burial in the Iberian Peninsula. Instead, the available evidence of funerary practices primarily consists of the intentional accumulation of human remains in karstic environments, where there is little to no indication of spatial modifications commonly associated with formal burials— such as pit excavation, corpse deposition, and subsequent covering with sediment or rocks. Of course, the geological conditions of the various contexts considered in this

study may play a critical role in the preservation of original depositional settings, potentially masking funerary behaviors involving spatial modification (i.e. proper burials) that we are currently unable to detect. Differential preservation—such as the presence of articulated remains in sites like Sima de las Palomas or Foradà, versus isolated elements in other locations—may reflect not only cultural variability but also taphonomic and geological factors such as breccia formation, concretion processes, or rapid sedimentation events like block collapses. Furthermore, it is important to acknowledge the inherently biased and fragmentary nature of the archaeological record. In comparison to other regions of Europe, where there is a clear record of intentional Neandertal burials, such as the rich Middle Paleolithic assemblages from MIS-5 to MIS-3 sites in the Middle East, where some of the most iconic sites include: Tabun (Garrod and Bate, 1937, Grün and Stringer, 2000, McCown and Keith, 1939), Amud (Kimbel, et al., 1995, Rak, et al., 1994), Kebara (Bar-Yosef, et al., 1988, Tillier, et al., 1991), Shanidar (Pomeroy, et al., 2020, Solecki, 1975, Trinkaus, 1983), and several French locations in MIS-4 and MIS-3, such as: La Ferrassie (Balzeau, et al., 2020, Gómez-Olivencia, et al., 2018, Heim, 1976, Heim, 1982, Maureille and Peer, 1998), La Chapelle-aux-Saints (Bouysonie, et al., 1908, Rendu, et al., 2014, Rendu, et al., 2016), or Regordou (Maureille, et al., 2015b), the Iberian Peninsula lacks any documented cases of formal burials in the traditional sense. In other words, these formal burials seem not to have extended south of the Pyrenees. The absence of formal burial practices in the Iberian Peninsula does not, however, exclude the presence of funerary practices. We must reconsider and expand our understanding of Neandertal funerary practices in this region. The repeated and systematic accumulation of bodies in designated locations over time, while not part of the "classic burial" practices conventionally required in the archaeological tradition, offers a behavioral pattern that undeniably indicates funerary behavior (Pettitt, 2011, Pettitt, 2018). This pattern may reflect a distinct mortuary manifestation, but it still represents a manifestation of the culture of death, highlighting alternative treatments of the dead that, while they do not involve full burial practices, they are meaningful within the broader context of funerary traditions. Therefore, we can surmise that Neandertals in the Iberian Peninsula engaged in complex social or ritual behaviors related to death and the afterlife, apparently regardless of prevailing paleoclimatic conditions. Thus, this study of Iberian Neandertal remains, in addition to evidence from other European contexts, sparks a broader exploration beyond traditional funerary practices and calls for the consideration of a wider array of mortuary repertoire that may have been part of the Neandertal funerary behavior in southern Europe.

Acknowledgements

This research is funded by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program: DEATHREVOL (no. 949330); Ministerio de Ciencia e Innovación PID2021-122355NB-C31 and PID2021-122355NB-C33 financed by MCIN/AEI/ 10.13039/ 501100011033/ FEDER, UE. NS and AP are supported by a Ramón y Cajal fellowship RYC2020-029656-I and RYC2023-045715-I respectively funded by the MCIN/AEI /10.13039/ 501100011033 and FSE invierte en tu future and FSE+. We deeply appreciate our colleague C. Calvo for her commitment and support. We thank the editors of this volume for allowing us to contribute to this special issue. Lauren Ames reviewed the English of the original manuscript.

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