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RESEARCH ARTICLE

Multidisciplinary approach to *Mammuthus meridionalis* from the late-Early Pleistocene archaeological site of Barranc de la Boella (Tarragona, North-East Iberia)

Darío Fidalgo[1], Antonio Rosas[1], Antonio Pineda[2,3], Iván Ramírez-Pedraza[2], Sergio Ros-Montoya[4], David Rodríguez de la Fuente[2,5], Lucía López-Polín[2], Laura Gómez-Morgado[2], Bienvenido Martínez-Navarro[2,5,6], Elena Moreno-Ribas[2,5], Antonio García-Tabernero[1,7], Rosa Huguet[2,5,8], Andreu Ollé[2,5], Josep Vallverdú[2,5,8] and Palmira Saladié[2,5,8]

[1]Department of Palaeobiology, Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain; [2]Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain; [3]Département Homme et Environnement, Muséum National d'Histoire Naturelle, Paris, France; [4]Departamento de Ecología y Geología, Universidad de Málaga, Málaga, Spain; [5]Departament d'Història i Història de l'Art, Universitat Rovira i Virgili, Tarragona, Spain; [6]ICREA, Barcelona, Spain; [7]Área de Antropología Física, Departamento de Biodiversidad y Gestión Ambiental, Universidad de León, León, Spain; [8]Unit Associated to CSIC, Department of Palaeobiology, Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain

ABSTRACT
Proboscideans have been used as a keystone in Quaternary palaeoecology and biostratigraphy studies throughout Europe, with genera such as *Mammuthus* and *Palaeoloxodon* widely represented in their fossil record. This study presents a multidisciplinary analysis of proboscidean remains from the late-Early Pleistocene site of Barranc de la Boella (Tarragona, Iberian Peninsula; 1.07–0.87 Ma), offering new insights into their biochronology, palaeoecology and human interactions. The fossil assemblages includes several fossils attributed to *Mammuthus meridionalis* advanced form, based on biometric, morphological and Schreger angle analyses. Stable carbon isotope ($\delta^{13}C$) data in the enamel indicate a diet related to C_3 grasslands under a Mediterranean climate, consistent with previous palaeoenvironmental reconstructions. Taphonomic evidence reinforces the published idea of an archaeological context with anthropogenic processing of a mammoth carcass, including cut marks and spatial association with Acheulean lithic tools. In addition, carnivore modifications suggest the hyenas activity. These findings underline the ecological importance of proboscideans in Early Pleistocene ecosystems and provide decisive evidence for human-megafaunal interactions during the early Acheulean dispersal in Europe. The study reinforces the importance of *Mammuthus meridionalis* as a palaeoenvironmental and biochronological proxy and contributes to broader debates on the role of large herbivores in Pleistocene ecosystems.

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Introduction

Proboscideans, particularly elephants and their relatives, played a crucial role in the ecosystems of Europe during the Quaternary (Lister & Bahn, 2007). Mammoths (*Mammuthus* spp.) are present in European faunal associations from the Late Pliocene to the Pleistocene/Holocene boundary, and the straight-tusked elephants (*Palaeoloxodon antiquus*) are common in the continent since the base of the Middle Plestocene until the latest Pleistocene (Lister, 2015; Lister & van Essen, 2003; Stuart et al., 2002). Indeed, proboscidean fossils have been classically used as biostratigraphic markers to help date and correlate Quaternary deposits from different regions (see Ros-Montoya et al., 2012, 2018; Iannucci & Sardella, 2023; and references therein). The presence, distribution and geographic movements of different proboscidean species have been used by different specialists as a proxy for the reconstruction of past climates and environments (Kahlke, 2013). For example, the woolly mammoth has been closely associated with cold and glacial conditions (Lister & Sher, 2015), while the straight-tusked elephant seems more closely related to interglacial times and forested environments (Pushkina & Raia, 2008). The distribution of

CONTACT Darío Fidalgo dario.fidalgo@mncn.csic.es Department of Palaeobiology, Museo Nacional de Ciencias Naturales (CSIC), st/ José Gutiérrez Abascal 2, Madrid 28006, Spain

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proboscideans in Europe during the Quaternary appears to reflect more complex biogeographic patterns, including migrations and extinctions in response to glacial-interglacial cycles (Palombo, 2014).

At an ecological level, these megaherbivores have acted as ecosystem engineers across the European continent (Bakker et al., 2015). Their dynamics, which can be observed in their present-day representatives, included uprooting trees and trampling vegetation and have been linked to the maintenance of open landscapes and the creation of mosaic habitats that supported a diverse range of local plant and animal species (Bakker et al., 2015). In turn, during this process, their role in seed dispersal has been described, particularly in the case of large-seeded plants. Their ability to consume and transport seeds over long distances would have contributed to the spread and genetic diversity of several plant species (Johnson, 2009). The extinction of proboscideans in Europe is linked to the loss of entire ecosystems such as the tundra-steppe (Kuzmin, 2010). This regional extinction occurred in the early Holocene (about 10,000 years ago; Stuart et al., 2002) and is part of a broader pattern of megafaunal extinctions on a global scale (Nogués-Bravo et al., 2008). The history of proboscideans in Europe offers lessons for modern conservation efforts, particularly in understanding the ecological roles of large herbivores and the potential consequences of their loss (Svenning et al., 2015). Efforts to restore wilderness areas with large herbivores, such as elephants, are partly inspired by the ecological roles that proboscideans once played and can today be considered lost (Lorimer et al., 2015).

In recent years, the great impact of the presence of proboscideans has been highlighted not only as modifiers of the environment, but also as one of the most important characters of fauna in interactions with humans (see Konidaris et al., 2021 for more details on the species of the genus *Homo* involved). On the one hand, the large size of proboscideans also conditions the high percentage of animal biomass they provide within the ecosystems in which they are found (Byers & Ugan, 2005). Proboscideans were an important resource for early humans in Europe. Evidence of trophic exploitation and/or hunting, such as cut marks on bones and the association of tools and proboscideans carcases, indicates that humans relied on these animals for food, tools, and other materials (de la Torre et al., 2025; Espigares et al., 2013; Konidaris et al., 2021; Pineda et al., 2024; Yravedra et al., 2024). The exploitation of proboscideans may have influenced human migration patterns and settlement strategies (Surovell et al., 2005). Proboscideans also held cultural significance for prehistoric humans, as evidenced by cave paintings and carvings depicting these animals. They likely played a role in the symbolic and spiritual lives of early human communities (Paillet & Wolf, 2017).

A remarkable example of this type of interaction has been documented at the Pit 1 site within the Barranc de la Boella ravine. Previous research on this archaeological context reveals evidence of direct exploitation of proboscidean carcasses by early human groups in the eastern Iberian Peninsula (Mosquera et al., 2016; Vallverdú et al., 2014). What makes this case particularly significant is its association with the earliest presence of the Acheulean (Mode 2) technocomplex in Europe (Lombao et al., 2024; Ollé et al., 2023). This finding underscores the critical relationship between early humans and megafauna (Belmaker, 2010, 2018; Palmqvist et al., 2022; Rodríguez-Gómez et al., 2024), as well as the need for a better understanding of the ecosystems in which these hominins lived in order to understand how the environment conditioned their evolutionary processes and cultural changes (Faith et al., 2019; Potts, 2013). This work takes a multidisciplinary approach to the study of these proboscideans recorded at the Barranc de la Boella site (Tarragona, North-East Iberia; 1.07–0.87 Ma; Vallverdú et al., 2014) with special interest in their scientific potential in areas such as the biochronology of the deposits, the palaeoecological reconstruction of the sites and the interaction of humans with the ecosystem.

Geographical, geological and archaeological context

Barranc de la Boella complex is situated in the north-eastern region of the Iberian Peninsula, within the Francolí River basin (UTM coordinates: 31T, X 4,346,559, Y 4,555,526). This complex comprises three archaeological localities – El Forn, La Mina, and Pit 1—where systematic archaeo-palaeontological excavations have been conducted since 2007 (Vallverdú et al., 2008, 2014). Geologically, the exposed stratigraphic sequence consists of poorly stratified sands, gravels, and pebbles, exhibiting lateral variations that have been subject to erosion by the torrential flows of the present-day ravine. A total of six lithostratigraphic units have been identified and correlated across the three localities, spanning a sedimentary sequence of approximately nine metres. Among the archaeo-palaeontological levels, numerous fossilised skeletal remains, coprolites, and lithic tools – particularly picks and cleaver-like implements characteristic of the Early European Acheulean – have been recovered, predominantly from unit II (Mosquera et al., 2016; Ollé et al., 2023; Vallverdú et al., 2014).

The majority of the fossils in Barranc de la Boella originate from lithostratigraphic unit II. This unit has been dated using magnetostratigraphic, geochronological, and biostratigraphic methodologies, yielding an estimated chronological range between 1.07 and 0.87 million years ago (Lozano-fernández et al., 2014; Vallverdú et al., 2014). The sedimentary and paleoenvironmental evidence suggests a depositional environment strongly influenced by aquatic dynamics. Palynological analyses indicate a Mediterranean climate, while paleoenvironmental reconstructions are consistent with a torrential regime alternating between densely vegetated areas and grassland-dominated landscapes (Lozano-Fernández et al., 2015; Pineda, Saladié, Expósito, et al., 2017; Rosas et al., 2015; Vallverdú et al., 2008). The associated faunal assemblage comprises a diverse representation of macrofaunal taxa, with only a limited presence of microvertebrate specimens.

For a geological and archaeo-stratigraphical context, see Vallverdú et al. (2008, 2014). For a more detailed archaeological context, see Vallverdú et al. (2014), Mosquera et al. (2015, 2016), Ollé et al. (2023), Lombao et al. (2024) and Pineda, Saladié, Expósito, et al., 2017. For a palaeontological, palaeo-ecological and taphonomic context see Lozano-fernández et al. (2014), Rosas et al. (2015), Pineda et al. (2015, 2017), Madurell-Malapeira et al. (2019), Fidalgo, Rosas, Madurell-Malapeira, et al. (2023, 2023).

Material and methods

Material

Most of the mammoth remains recovered from Barranc de la Boella up to 2024 come from level II.2 of Pit 1 (n = 486), the major part of which came from a single individual carcass composed mainly of cranial remains (including both tusks [Figure 5; A2B], teeth [Figure 2] and bone fragments), but also axial, mainly rib fragments, two scapulae and some long bone remains (Figure A3A), such a complete femur. At least a fragment of a mandibular corpus and two teeth fragments (Figure 2G,H) belong to a second, juvenile individual. Other mammoth remains were also recovered in the level II.3 of Pit 1, including both tusks (Figure 1, A2A), four molars (Figure 2) and bone fragments

Figure 1. Virtual preparation process of the *Mammuthus meridionalis* tusks of level II.3 of Pit 1 (Barranc de la Boella). (A) Photogrammetric model. (B) Tusks virtually separated. (C) Relative positioning of the tusks. (D) Virtual reconstruction of the unpreserved parts.

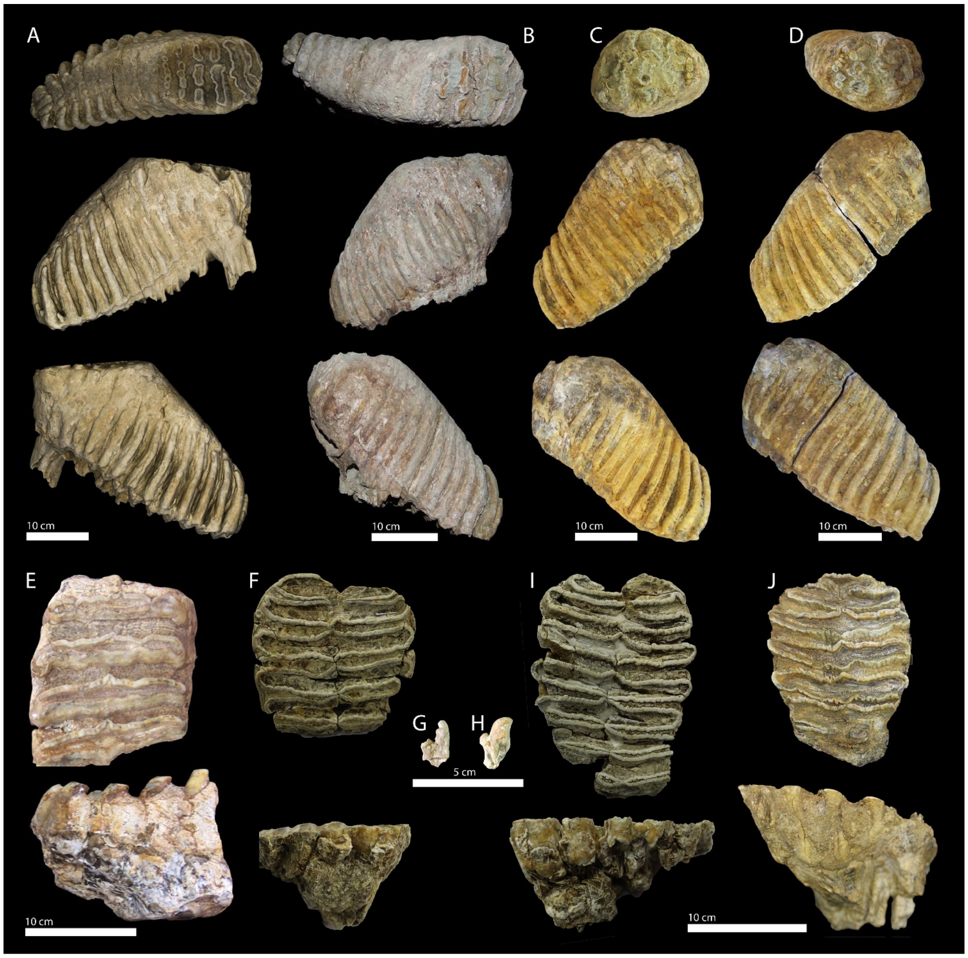

Figure 2. Molars of *Mammuthus meridionalis* from Barranc de la Boella. (A) BB07_C1_II_P13_11. (B) BB07_C1_II_O12_4. (C) BB07_C1_II_II_P13_57. (D) BB07_C1_II_II_P13_58. (E) bo1 (Villalta collection). (F) BB07_C1_II_II_O13_76. (G) BB07_C1_II_P14_5. (H) BB07_C1_II_II_O14_22. (I) BB07_C1_II_II_O13_78. (J) BB07_C1_II_O12_84. Anatomical data for each specimen can be found in the Description part of Systematic palaeontology in the text.

belonging to the cranium. Additionally, a petrosal bone was recovered from La Mina, level II.2, two dental fragments from levels II.2 and II.3 of El Forn, and six remains (a metatarsal, astragalus, tibia [Figure A3B], dental fragment, and two ribs) of the level II.4, a few specimens collected by Dr. Josep Fernández de Villalta in old surveys of the Barranc de la Boella complete the fossil record.

Physical restoration of the specimens

The mammoth remains were in poor overall condition, with bones and teeth that crumbled easily, requiring protective measures to prevent damage during excavation, lifting, transport, and handling (Figure A1A,B,C). Conservation efforts began in the field and continued at the IPHES conservation laboratory (López-Polín et al., In press). To ensure their preservation, all remains were treated with an acrylic consolidant, Paraloid B72 dissolved in acetone, before being meticulously cleaned and reassembled for study. This treatment applies to the entire faunal assemblage of the site. However, conserving the larger and heavier mammoth elements posed additional challenges. The internal stresses within these larger fossils were more difficult to control, and simple consolidation alone did not provide sufficient structural strength (Figure A1D,E). To address this, additional reinforcement techniques were employed, including facing with cotton gauze impregnated with consolidants and encasing in polyurethane foam to facilitate safe lifting and handling. Custom mounts were also created to ensure the secure transport and storage of the restored fossils. Beyond the conservation work, research has been conducted to better characterise and assess the state of preservation of the remains, evaluate the sensitivity of bone surfaces to various cleaning techniques, and analyse the penetration of consolidating products (Díaz-Cortés et al., 2022, 2024; Valtierra et al., 2023). So far, the findings support the continued use of Paraloid B72 consolidant and provide valuable insights for selecting the most suitable small tools for dry, wet, and solvent-based cleaning techniques.

Virtual reconstruction of the tusks

The tusks excavated in 2007 in level II.3 of Pit 1 belong to an adult individual, are approximately 1.8 metres long and were found intertwined, which is why they were extracted in a single block and are currently preserved in the same position (Figure A2A; Mosquera et al., 2015; Saladié et al., 2008; Vallverdú et al., 2014). For the moment, separating them has not been considered due to the level of complexity of the process and the risks it could pose to the remains, which could lead to cracks, detachments or fractures. The decision not to physically separate the tusks has led to the intervention being carried out using digital techniques such as 3D documentation, virtual reconstruction or 3D reproduction (Gómez-Morgado, 2018).

3D digitisation of the proboscidean tusks from the level II.3 of Pit 1 was carried out by digital photogrammetry, using a Nikon D5300 camera and various lighting and support equipment. The photographic sessions were carried out on three different days, with a total of 300 photographs taken to ensure complete coverage of the piece. For the capture, parameters such as aperture and shutter speed were adjusted according to the lighting conditions. Subsequently, the RAW images were background masking in Adobe Photoshop CC to facilitate processing. Agisoft Photoscan was used to generate the point cloud, the 3D mesh and the final texture, ensuring an accurate reconstruction of the model (Figure 1A; Gómez-Morgado, 2018).

The separation of the tusks was achieved by duplicating the model in Agisoft Photoscan and removing the mesh of one of them in each copy, generating two independent models (Figure 1B). Then, the gaps generated in the separation were cleaned. In Blender, the meshes were reconstructed using quad patches and tools such as Snap and Proportional Editing. To optimise the 3D models and facilitate their use in digital platforms and Virtual or Augmented Reality environments, the mesh resolution was reduced with Blender's Decimate modifier. In addition, alteration maps were created in Texture Paint to document pathologies and assess the state of conservation of the tusks in detail (Olazábal, 2016; Sánchez, 2016).

The virtual reconstruction of the tusks was based on similar fossil references and previous studies (Agostini et al., 2012; Brugal, 1995; Cioppi et al., 2020; W. E. Garutt, 1998; Maschenko et al., 2011; Rossi et al., 2017). Its original position was deduced by comparing its morphology with images of other tusks and reconstructions (Figure 1C). In Blender, the missing points were modelled using tools such as Shrinkwrap and Curve to obtain a shape consistent with the existing structures (Figure 1D).

Finally, the 3D models that have been uploaded to the Sketchfab platform are: the original photogrammetric model of the tusks that can be seen in the Figure 1A and in the link: https://skfb.ly/6BzAU; the 3D alteration map is in the Spanish version in the link: https://skfb.ly/6BzB8; the 3D reconstruction of the tusks that can be seen in the Figure 1D and in the link: https://skfb.ly/6ByxN.

For more detailed information on the virtual restoration protocol, see Gómez-Morgado (2018).

Schreger angles

During ontogenetic development, the proboscidean tusks progressively form a series of dentine cones, these cones intersect with the bundles of tubules which contain the processes of odontoblasts (Trapani & Fisher, 2003). This pattern is easily distinguishable from the others because, if a cross section is made, a pattern of intersecting lines can be seen. The two different sets of intersecting curved lines, one clockwise and one anticlockwise, constitute the so-called 'Schreger lines'. These lines form concave and convex angles. The set of lines and angles form the 'Schreger Model' (Espinoza & Mann, 1993). This tissue pattern of dentine has been proposed as a character with taxonomic value in the determination of different species of proboscideans through the tusks (M. R. Palombo & Villa, 2001; Trapani & Fisher, 2003). In our case, we have measured the angulation of the Schreger's lines observed in the tusks of level II.3 of the Pit 1 locality (Figure A2).

Anatomy and biometry of molars

In order to make assessments with detailed systematic implications, the anatomical and biometric study of the most complete upper third molars has been used. Anatomical terminology used follows Todd (2010). Dental measurements after Lister & Sher (2015). Previously published data from a large number of

Table 1. Systematically relevant metrics of the proboscidean upper third molars from Barranc de la Boella.

Nº	Element	Plate number (Nº)	Enamel thickness (mm)	Hypsodonty Index
BB07_C1_II_P13_57	Right M3	X13-	3.2	131.2
BB07_C1_II_P13_58	Left M3	X14-	3.5	138.6
BB07_C1_II_O12_4	Left M3	X14x	3.3	119.3
BB07_C1_II_P13_11	Right M3	X14x	–	–

'x' indicates the talons and "-" indicates the tooth may be incomplete.

localities (see Table 1 and Table A1) have been used to make comparative biometric assessments, including information from the species *Paleoloxodon antiquus*, *Mammuthus rumanus*, *Mammuthus meridionalis*, *Mammuthus trogontherii* and *Mammuthus primigenius* (Aguirre, 1969; Konidaris et al., 2020; Maglio, 1973; Ros-Montoya, 2010; Ros-Montoya et al., In press). Data for the chronosubspecies of *M. meridionalis* (*M. m. gromovi*, *M. m. meridionalis*, *M. m. vestinus*, *M. m. depereti* and *M. m. tamanensis*) are from those compiled by Konidaris et al. (2020). The molar biometric data were plotted in scatter plots along with the maximum and minimum values (and average values where available) for each species and chronosubspecies considered using Past 4.03 software (Hammer et al., 2001; Figure 3).

Stable isotope analysis

Stable carbon ($\delta^{13}C$) isotope analysis was performed on 13 specimens of proboscideans molars from Pit 1 (Figure 4). Buccal or lingual surfaces were systematically cleaned with a tungsten abrasive drill bit to remove any extraneous material. Enamel powder for bulk analysis was extracted using a diamond-tipped drill along the entire buccal or lingual surface, following a line from apical to cervical extremities, to ensure the most representative measurement for the whole period of enamel formation.

Powdered enamel samples, ranging between 3 and 5 mg, were sampled at the Biomarkers Laboratory of the Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA). The $\delta^{13}C$ values of carbonates were determined using an automated carbonate preparation device (KIEL-III) coupled to a gas-ratio mass spectrometer (Finnigan MAT 252) at the Environmental Isotope Laboratory, University of Arizona, U.S.A.. Powdered samples were reacted with dehydrated phosphoric acid under vacuum at 70°C. The isotope ratio measurement is normalised using a two-point method based on repeated measurements of the calcium carbonate international standards of NBS-19 ($\delta^{13}C = +1.95‰$ VPDB) and NBS-18 ($\delta^{13}C = -5.014 \pm 0.035‰$ VPDB) with a precision of ± 0.08‰ for $\delta^{13}C$ (1 sigma). Samples are typically run in sessions of 46 measurements with precision and normalisation determined for each session. Standards make up 13% of all measurements. Carbon and oxygen isotope composition was reported in δ notation, where $\delta^{13}C = [(Rsample/Rstandard) - 1]$, $R = {}^{13}C/{}^{12}C$, and δ is expressed in per mil, ‰. Carbon values were reported relative to the Vienna Pee Dee Belemnite (VPDB) standard.

To characterise the isotopic signature of different environments (closed-canopy forest, woodland to woodland-mesic C_3 grassland, and open woodland-xeric C_3 grassland), we applied the cut-off values defined by Domingo et al. (2013). The $\delta^{13}C$ of atmospheric CO_2 was corrected for Pleistocene conditions (Tipple & Pagani, 2010), and the diet-to-enamel fractionation was adjusted (+14.7%) according to body mass (~5000 kg) following Tejada et al. (2018).

To compare the proboscideans from Barranc de la Boella with other proboscideans in Europe from the Plio-Pleistocene to the Middle Pleistocene, a graphical representation of the $\delta^{13}C$ (‰, VPDB) against the chronology of the specimens has been made using the R (Figure 4). Information previously published in scientific literature has been included in the database together with that from our new analyses (Table A2).

Taphonomic analysis

Mammoth remains were identified by element, side, and portion, indicating the presence of anatomical landmarks. Other skeletal remains, not anatomically identified as belonging to a mammoth but described as belonging to a very large carcass (> 1,000 kg according to Saladié et al., 2011), and which, due to their size and characteristics, could only correspond to this taxon, have also been considered.

Bone surfaces were macroscopically and microscopically examined (using an OPTECH stereomicroscope, up to 45x). Striae of undetermined origin, but with characteristics that could link them to cut marks, were analysed, the location and features of which have been described following Domínguez-Rodrigo et al. (2009) and Pineda et al. (2014) for chemically altered cut marks and trampling striae. Carnivore-induced modifications identified were pits, scores, furrowing, scooping

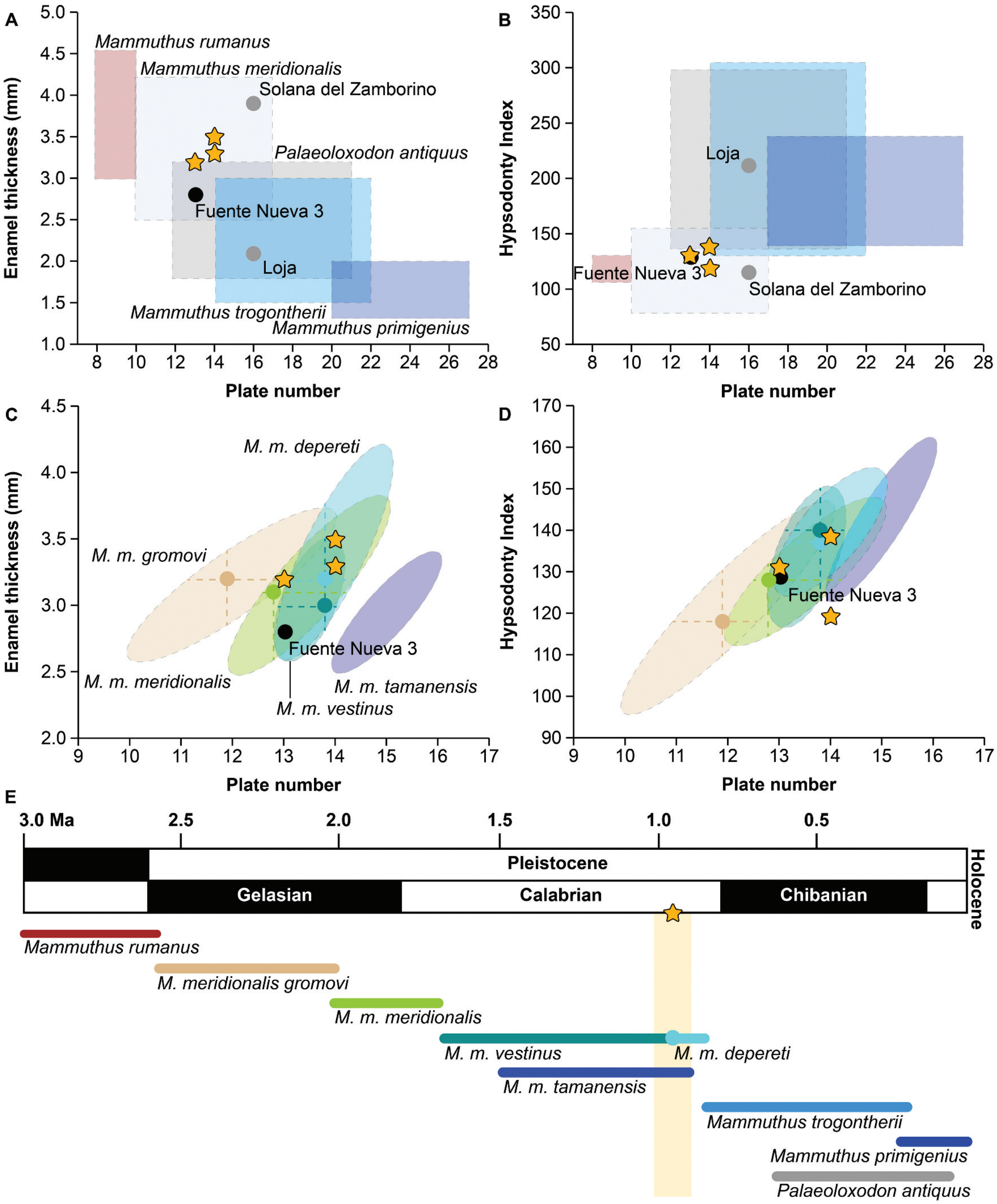

Figure 3. Scatter plots of the measurements taken on the upper third molars of European proboscideans and explanatory diagram of the systematic and biochronological hypothesis followed. Ranges of variability of measurements in continental European Quaternary proboscidean species together with specific data from Barranc de la Boella (yellow stars), Fuente Nueva 3, Solana de Zamborino and Loja: (A) plate number versus enamel thickness (mm), (B) plate number versus hypsodonty index. Ranges of variability of measurements in *Mammuthus meridionalis* chronosubspecies from Europe together with specific data from Barranc de la Boella and Fuente Nueva 3: (C) plate number versus enamel thickness (mm), (D) plate number versus hypsodonty index. (E) Systematic and biochronological hypothesis of proboscideans from continental Europe during the Quaternary modified from Konidaris et al. (2020).

out, and shaft cylinders (Binford, 1981; Brain, 1981; Haynes, 1980; Maguire et al., 1980). Post-depositional modifications (oxide coating, cracking, trampling, rounding, and polishing) have been recorded in terms of presence/absence. Finally, weathering and loss of cortical tissue were documented according to the stages proposed by Behrensmeyer (1978) (Table A3).

Spatial relationship between faunal remains and lithic tools in the level II.2 of Pit 1 has been analysed through Spatstat package (v. 3.2–1) in R. A window

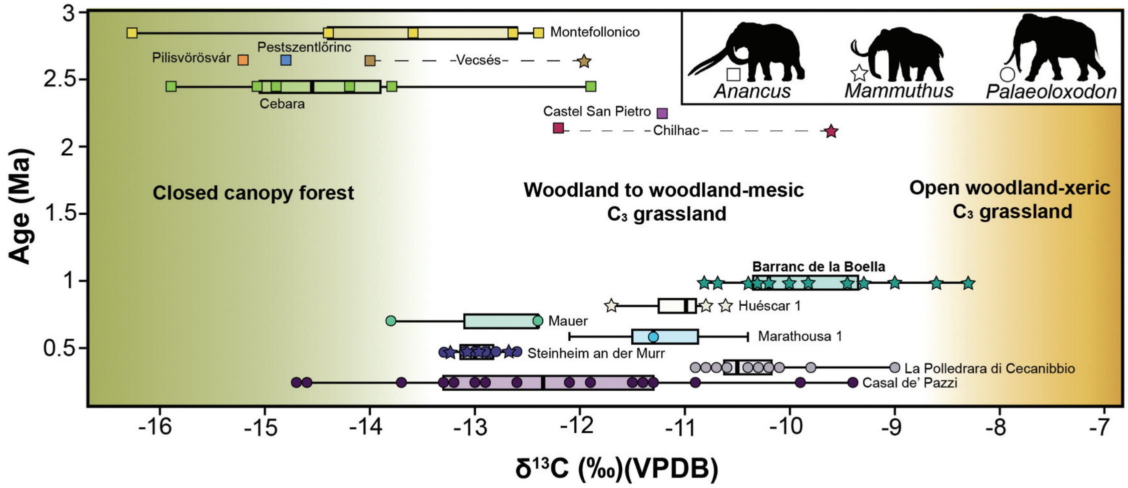

Figure 4. Boxplot of δ^{13}C values in tooth enamel in proboscideans in Europe on the chronological approach of each site. The specific methodology of the analyses can be found in the Stable isotope analysis of Material and methods section in the text and the data are accessible in Table A2.

of the archaeological site was built and window-effect was corrected for every method. Nonparametric Kernel maps were used to observe density, and both Clark-Evans and Hopins-Skellam tests were applied to assess clustering (Baddeley et al., 2015). The distribution of the remains has been analysed through the application of inhomogeneous L function (Ripley, 1976, 1977, 1979; Robert & Casella, 2004). Finally, a multitype approach was applied to assess spatial codependence using inhomogeneous cross-type L function (Ripley, 1979) (Figure 5). For more information on the analysis see Text Appendix 1.

Systematic palaeontology

Order PROBOSCIDEA Illiger, 1811
Family Elephantidae Gray, 1821
Subfamily Elephantinae Gray, 1821
Genus *Mammuthus* Brookes, 1828

Type species. *Mammuthus primigenius* (Blumenbach, 1799), fixed as type species by V. E. Garutt et al. (1990) (see also Lister, 2017; Reich et al., 2007).

Mammuthus meridionalis (Nesti, 1825)

Lectotype. cranium with M3, IGF-1054 (Natural History Museum, Geology and Paleontology Section, University of Florence, Italy), designated by Depéret & Mayet (1923), p. 126).

Type locality: Upper Valdarno (Italy).

Material examined. For the analysis of the systematic palaeontology and taxonomic determination of the proboscideans from Barranc de la Boella, we have focused on the teeth as the most informative element. Specifically, the best preserved tusks (Figure 1, A2) and molars (Figure 2; Table 1) of the fossil complex.

Description

Tusks

During the 18 years of excavation at Barranc de la Boella, four almost complete proboscidean tusks have been extracted at the Pit I locality (Figure 1, A2). All the tusks show a strong torsion (Figure A2), which is especially visible in the virtual reconstruction of the tusks of level II.3 (Figure 1). In the restored section of these same tusks, it has been possible to measure the angulations between several Schreger lines, obtaining an average value of approximately 74° (Figure A2A).

Molars

Among the specimens from the old surveys carried out by Dr. Josep Fernández de Villalta and those found in the excavations carried out since 2007, it has been possible to recover a minimum (due to fragmentary specimens) of 11 molars. Four of these specimens are complete upper molars belonging to two adult individuals over 30 years old (Figure 2A-D; Laws, 1966). These complete and well-preserved molars (Figure 2A-D) consist of between 13 and 14 enamel plates, plus anterior and posterior talon. The roots are the least

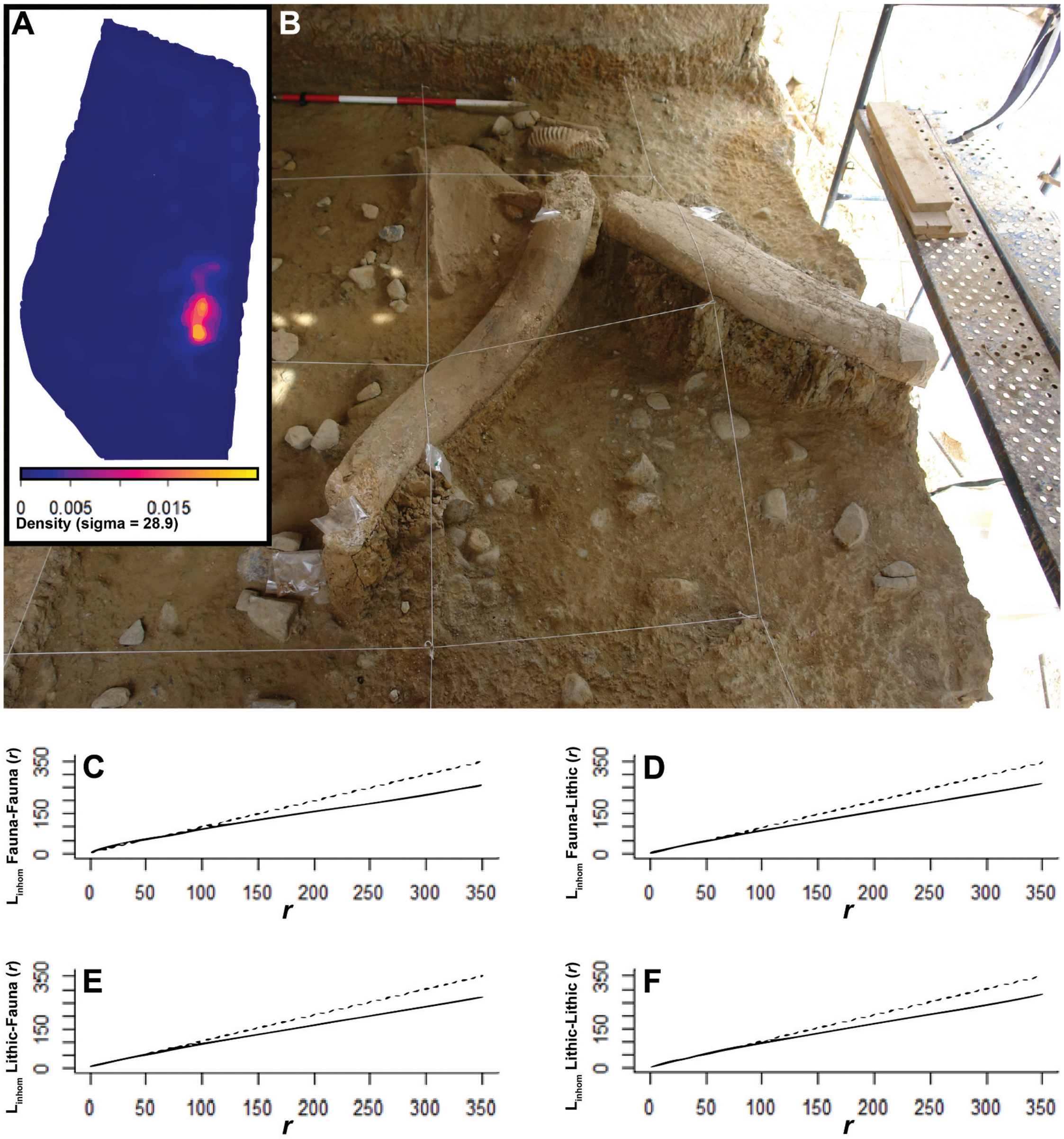

Figure 5. Evaluation of the proposed butchering site of *Mammuthus meridionalis* from level II.2 of Pit 1 (Barranc de la Boella). (A) Field image showing the arrangement of the archaeo-palaeontological materials. (B) Smoothing Kernel density map of faunal and lithic remains. (C-F) Inhomogeneous cross-type L function for faunal and lithic remains.

preserved areas. The wear is not very pronounced, only seen in the first 4–6 lamellae. The enamel is thick and folded. Cementum is abundant in the front area, although this is not the case in the back, as the molars have not finished forming completely and are erupting. The interlamellar distance is approximately equal to or slightly larger than the lamella itself. The lamellar frequency is high. The shape of the posterior talon is straight, i.e. there is no thrust from any other molars, indicating that they correspond to third molars. The mesial talon is curved inwards due to the thrust on the anterior molar. The shape of the abrasion figure in occlusal view seen in the second plate is composed of a wide sub-rounded figure in the centre, flanked labially and lingually by an elongated and narrower oval.

In turn, four fragments of second or third upper molars have been found in a not very good state of preservation, made up of between four and seven complete plates, neither the talons nor the roots are preserved (Figure 2E,F,I,J). The enamel plates are in use, the wear is very marked and the enamel is thick and folded. Cement is abundant. The interlaminar separation is somewhat larger than the lamina itself. The molars have a relatively low laminar frequency. The abrasion pattern in occlusal view is not very visible due to wear, but it can be seen that in each lamella the pattern is composed of a central, subrounded and wide shape, flanked labially and lingually by two elongated and narrower ovals.

The collection of dental specimens is completed by a total of 45 tooth plates, which are not in a very good state of preservation; no complete plate has been recorded and no wear has been observed on any of them. The vast majority of the isolated plates studied could belong to the first germinal molars, which are in the process of formation, so there is no cement in any of the plates. Among the total number of plates analysed, two can be highlighted, which, according to their dimensions and morphology, possibly belong to one or two infant or neonate individuals (Figure 2G,H).

Taxonomic remarks

European population of the iconic Quaternary proboscidean genus *Mammuthus* have classically been divided into three chronospecies in this region (Maglio, 1973) from the Late Pliocene to the Late Pleistocene-Holocene: *Mammuthus meridionalis* (2.6–0.7 Ma); *Mammuthus trogontherii* (0.7–0.35 Ma) and *Mammuthus primigenius* (~0.35/0.20–0.01/0.004 Ma; Figure 3E). More recently, it has been proposed to have first appeared on the continent from Africa 3.2/3.0 Ma ago, more than 500,000 years before the so-called *Elephant-Equus* event (Iannucci & Sardella, 2023; Lindsay et al., 1980; Lister et al., 2004; Palombo & Ferretti, 2004). The oldest known remains have been found in the Middle Pliocene of Romania (Tulucesti) and ascribed to the species *Mammuthus rumanus* (Lister & van Essen, 2003; Radulescu & Samson, 2001; Spassov, 2003), considered to be a distinct and more primitive species than *M. meridionalis*. The straight-tusked elephant *Palaeoloxodon*, represented from the early Middle Pleistocene (ca. 0.6 Ma; Lister, 2015) to the Late Pleistocene by the single species *P. antiquus* (Falconer & Cautley, 1847), complete this diversity of proboscideans in continental Europe during the Quaternary.

Linear biometric analyses of the upper molars show that the selected measures (number of plates, enamel thickness, lamellar frequency and hypsodonty index) present a good resolution to rule out the assignment of individuals to the species *Mammuthus rumanus*, *Mammuthus trogontherii* and *Mammuthus primigenius* (Figure 3A,B; Table 1). It is widely known that the number of plates in these molars follows a clear upward trend along the lineage of the genus *Mammuthus*, with minimums in the species *M. rumanus* and maximum values in *M. primigenius* (Ferretti, 2003), clearly moving our data away from these two extremes. In the Barranc de la Boella molars measured, the higher values in tooth enamel thickness allow us to refine the ruling out of the species *M. trogontherii*. Taking into account the Quaternary fossil record of Europe, only the possibility remains that these individuals belong to *Mammuthus meridionalis* or *Palaeoloxodon antiquus* (Figure 2E). The number of plates in the M3 and the hypsodonty index would point to the discarding of *P. antiquus*.

The large torsion found in the Barranc de la Boella tusks is a feature generally indicative of the genus *Mammuthus* (Figure 1; Dimitrijević et al., 2015; Lister & Stuart, 2010). In the genus *Palaeoloxodon*, the straight-tusked elephants, torsion is almost non-existent, it can only be observed in some adult male specimens, although this torsion is minimal and not as strong as in these four cases (Larramendi et al., 2017). Likewise, the mean value of 74° for the Schreger's lines of the Pit 1 fenders (Figure A1A) indicates that they can only belong to the genus *Mammuthus*, since the values presented by this genus range between 52.5° and 92.5° while in the species *P. antiquus* the values vary between 92.5° and 132.5° (Palombo & Villa, 2001). The occlusal abrasion figure present in the complete upper molars is also typical of the genus *Mammuthus* (Figure 2). Taking into account the laminar frequency, enamel thickness, crown height and abrasion pattern, the molars agree with the characteristics described for the species *Mammuthus meridionalis* (Nesti, 1825).

There are several proposed chronosubspecific taxa within *M. meridionalis* that reflect its evolutionary progression across Europe and western Asia, most notably the following taxa within the Lower Pleistocene in Europe: *M. m. gromovi*, described within localities of the Khapry fauna near the northeastern Sea of Azov (Russia), dating to the middle Villafranchian (MNQ 17; Baygusheva & Titov, 2011; Garutt & Alexeeva, 1964; Garutt & Baygusheva, 1981). *M. m. meridionalis*, described from Upper Valdarno (Italy), shows more derived dental characteristics and correlates with the late Villafranchian, around 1.78 Ma (Ferretti et al., 2025; Nesti, 1825; Rook et al., 2013). *M. m. vestinus*, described from Madonna della Strada (Italy), is associated with the Farneta Faunal Unit, slightly older than 1.3 Ma (Ambrosetti et al., 1972; Palombo et al., 2005; Rossi et al., 2017). *M. m. depereti*, described from Saint-Prest (France), with advanced dental features and linked to the Epivillafranchian, around 1–0.9 Ma (Coppens & Beden, 1982; Kahlke et al., 2011). Finally, *M. m. tamanensis*, described from Sinyaya Balka (Russia), shows bimodal dental characteristics (see Lister & Sher, 2015 for an in-depth discussion of this phenomenon) and is dated to a late Villafranchian-Epivillafranchian age (1.5–1.1 Ma; Baygusheva & Titov, 2011; Dubrovo, 1964). For more detailed information on the proposed subspecies of *M. meridionalis* see Konidaris et al. (2020; Figure 2E).

The biometric analyses of the upper third molars with data assigned to the different described chronosubspecies of *M. meridionalis* show particularly extreme values for the specimens from Barranc de la Boella, which are far from the form of the first half of the Early Pleistocene (Figure 2C,D). Specifically, the parameters of the Barranca de la Boella upper third molars fall within the overlapping ranges of *M. m. meridionalis*, *M. m. vestinus* or *M. m. depereti*, suggesting a moderately derived condition. This pattern is also observed in the specimen from Fuente Nueva 3, with an even higher number of plates our specimens (Figure 2C,D). Considering the difference in the number of plates between the specimen BB07_C1_2_P13_57 and BB07_C1_II_O12_4 from Barranc de la Boella, it looks most appropriate to assign these individuals to an advanced form of the species, without a chronosubspecific attribution. These data reinforce the phenotypic variability described for the advanced forms of *M. meridionalis* from Western Europe and are consistent with a chronology previously proposed for the Barranc de la Boella deposits (Coppens & Beden, 1982; Ferretti, 1999; Konidaris et al., 2020; Vallverdú et al., 2014).

Stable isotope analysis

δ^{13}C values indicate a dominance of C_3 plant consumption (trees, woody shrubs, bushes, herbs, and temperate grasses) by proboscideans (δ^{13}C range = −10.8‰ to −8.3‰; median = −10.2‰; $n = 13$), occupying an ecological niche that ranged from woodland to woodland-mesic C_3 grassland to open woodland-xeric C_3 grassland (Figure 4).

Carbon stable isotope analyses of *M. meridionalis* specimens from BB compared to proboscidean data from other chronologies across Europe show differences at various ecological levels between the localities included. At the level of trophic niche differences by taxa, only the much more positive δ^{13}C values in members of the genus *Mammuthus* than in those of the genus *Anancus* at the Vecsés (Hungary; Kovács et al., 2012) and Chilhac (France; Szabó et al., 2022) sites at the beginning of the Quaternary (Figure 4) stand out. Possibly, these differences are due to a more grazing behaviour in the genus *Mammuthus* than in *Anancus* (Rivals et al., 2015). In contrast, in the second half of the Quaternary there seems to be no clear dietary niche differences between members of the genus *Mammuthus* and those of the genus *Palaeoloxodon*, easily observable in the values from Steinheim (Pushkina et al., 2014; Figure 4). This observation is striking, since at the level of molar structure an increase in wear resistance has been recorded during the Plio-Pleistocene in different lineages of proboscideans (including *Mammuthus* and *Palaeoloxodon*) due to the increase in crown height (hypsodonty), the number of lamellae, the development of wider lamellae with a thinner cementum (increase in lamellar frequency, based on tooth dimensions), while the enamel is more recessed and thinner (Ferretti, 2003; Lister & Joysey, 1992). In the *Mammuthus* lineage, these changes have been related to a shift from a diet consisting mainly of leaves, shoots and bark to a diet consisting of a high percentage of grasses and herbs, with a high degree of silica and thus increased abrasion (Capozza, 2001; Palombo & Curiel, 2003; Rivals et al., 2012). However, in the Eurasian *Palaeoloxodon* lineage a contrary dietary shift has been proposed during the Middle Pleistocene (Rivals et al., 2012).

Considering our results, it seems that the differences observed in the δ^{13}C values between the specimens from the different sites from 1 Ma ago in Europe would be attributed to changes in the plant structure and climatic conditions in the environment in which the sites were located. It is evident that the data recorded at BB correspond to the highest values and mean of δ^{13}C in the European record and are more assimilated to relatively arid and grassland environments (Figure 4). In contrast, data from Plio-Pleistocene sites suggest more forested and humid environments. Something similar is observed in Middle Pleistocene sites such as Casal de' Pazzi (Italy), which has been associated with a wetland/near-wetland environment (Briatico & Bocherens, 2023; Palombo, 2023; Palombo et al., 2005). The closest data to those of BB are those of *Palaeoloxodon* at La Polledrara di Cecanibbio (Palombo et al., 2005), from 0.41–0.32 Ma ago and associated with a more arid environment than in the case of Casal de' Pazzi (Grube et al., 2010; Palombo, 2023).

Data from sites at higher latitudes than BB, such as the German sites Mauer or Steinheim (Pushkina et al., 2014) show δ^{13}C values associated with denser vegetation cover and wetter environments (Figure 4). In contrast, the Marathousa 1 (Greece) site also has values associated with wetter environments than BB and is located at a more southern latitude (Roditi et al., 2024), although it is true that chronologically it is associated with a cooler and more arid Marine Isotopic Stage (MIS 12; Konidaris et al., 2018; Panagopoulou et al., 2015, 2018). The closest site geographically and chronologically to BB for which data could be included in the analysis is Huéscar 1 (Domingo et al., 2013; Ros-

Montoya et al., 2018). This site is associated with a deltaic environment (Demuro et al., 2014) and is located at a lower latitude than BB. However, the $\delta^{13}C$ values indicate the presence of an ecosystem with greater vegetation cover. It is interesting to note that the advanced forms of *M. meridionalis* from Greece (Apollonia-1 and Kalamoto-1) show a more grazing component than the more browsing one of other *M. meridionalis* (see Tsakalidis et al., 2025).

The environmental inferences obtained for the BB sites from the $\delta^{13}C$ data of the molars of *Mammuthus meridionalis* align with the estimates made previously. Palaeoecological reconstructions inferred from the sedimentary environment (Vallverdú et al., 2014), micromammals (Lozano-Fernández et al., 2015), malacofauna (Vallverdú et al., 2008), palynological analyses (Pineda, Saladié, Expósito, et al., 2017) and macrofauna (Rosas et al., 2015; Pineda, Saladié, Huguet, et al., 2017; Fidalgo, Rosas, Madurell-Malapeira, et al., 2023,b) suggest a fluvio-deltaic environment under a Mediterranean climate with scattered vegetation habitats and seasonal rainfall in which there was a constant presence of water bodies. Our results indicate that these *Mammuthus* were feeding in open environments dominated by C_3 grasslands, likely in a relatively seasonally arid environment.

Taphonomic analysis

In Pit 1, the four upper third molars correspond to two adult individuals, although of a not very advanced age (ca. 30 years; Laws, 1966), as the distal part of the teeth has not been completely formed and the molars, which would have been erupting, show wear only on the mesial plates. It is also worth noting the presence of an infant or unborn individual, with two small, almost complete dental plates (Figure 2G,H) and a fragment of a mandible. At El Forn, all the specimens found may belong to adult individuals (judging by the size and anatomy of the talus); even so, the specimens are found in different archaeological levels, so the Minimum Number of Individuals (MNI) would be three adults. At La Mina there is certainly an MNI of one at Level II.2 (characterised by at least one petrous and a fragment of coxal) and scattered remains in the adjacent sectors probably belonging to at least one other individual.

Taphonomic data for the mammoth remains from La Mina and El Forn were previously published by Pineda, Saladié, Huguet, et al. (2017), as part of the faunal assemblages. In the case of Pit 1 level II.2, these remains were part of a multidisciplinary study on the anthropogenic exploitation of the proboscidean (Mosquera et al., 2015). Broadly speaking, the remains recovered from the different assemblages share common features: (a) poor preservation of bone surfaces due mainly to the dissolution of soluble elements from sediments (leaching; Pineda et al., 2014; Table A3) and, to a lesser degree, to weathering (stage 1 according to Behrensmeyer, 1978; Figure A3A); (b) signs of green and dry bone breakage, and trampling notches, some of them probably attributed to trampling by other mammoths, as in the case of the partial scapula found in level II.2 of Pit 1 (Haynes, 1988; Table A3; Figure A3C).

Mosquera et al. (2015) described three putative cut marks on two ribs from level II.2 of Pit 1, which may represent direct evidence of the anthropic processing of the carcass (0.4% of the remains; Table A3). A subsequent study suggested that at least two of these three cut marks could indeed be cut marks in an advanced stage of alteration (Pineda et al., 2018), reinforcing their identification. Beyond the cut marks, hominin access to this carcass is also attested by the clear spatial relationship between the stone tools and the remains of *M. meridionalis*, further supported by use-wear analysis of some flakes, which suggest the flakes were used for meat processing (Mosquera et al., 2015).

Some remains from El Forn show carnivore-induced modifications (33.3% at level II.4; Table A3). The ends of a mammoth tibia show signs of scooping out and heavy furrowing, along with a shaft cylinder on a mammoth metapodial (Pineda, Saladié, Huguet, et al., 2017; Figure A3B). The intensity of these modifications suggests that hyenas acted as modifying agents of these remains (Faith & Behrensmeyer, 2006; Haynes & Klimowicz, 2014). It is also noteworthy that at level II.3, pits were documented on one rib of a very large animal, probably a mammoth. Finally, the remains recovered from La Mina level II.2 show no evidence of exploitation by any actor.

A total of 1448 remains from the level II.2 from Pit 1 have been spatially analysed, composed by 807 faunal remains and 641 lithic objects. Smoothing Kernel density maps showed a clear overlapping between both materials (Figure 5A,B). Clark-Evans test supported this trend to clustering when applied on lithic remains ($R = 0.6759$; P-value $< 2.2e-16$), showing a greater dispersion among faunal remains ($R = 0.47349$; P-value $< 2.2e-16$). On the other hand, Hopkins-Skellam test of complete spatial randomness showed a clear clustering of both lithics (A = 0.12857; P-value $< 2.2e-16$) and bones (A = 0.055331; P-value $< 2.2e-16$). According to the inhomogeneous L test (Linhom (r) function) (Figure A4) both lithic and faunal remains show a trend towards intraspecific spatial aggregation patterns. When the test is applied with a multitype approach (Lcross.inhom(r) function) (Figure 5C-F), there is a positive spatial correlation of regular dispersion between fauna and lithic industry, suggesting an important spatial relationship and denying the hypothesis of spatial randomness.

Barranc de la Boella has been described as an open-air site formed in a deltaic environment, where species from various nearby habitats (riparian, aquatic, and open and semi-open spaces) could find some of the daily resources (e.g. water, vegetal, animal resources or raw materials) for their survival (Fidalgo, Rosas, Bartolini-Lucenti, et al., 2023; Fidalgo, Rosas, Madurell-Malapeira, et al., 2023; Lozano-Fernández et al., 2015; Pineda, Saladié, Expósito, et al., 2017; Rosas et al., 2015; Vallverdú et al., 2008, 2014). As described by Haynes (1988, 1991) in ethological studies of modern elephants, these environments are commonly occupied by proboscideans in search of water and other resources and frequently serve as places of death for these animals, both old individuals that go to drink water before dying and animals that could become trapped in muddy areas. This behavioural pattern could explain the presence of isolated remains at different excavated levels in La Mina and El Forn and in the level II.3 of Pit 1, reflecting the more or less recurrent visits of mammoths to this area. Evidence from El Forn suggests the presence of a bone-cracking carnivore, likely a hyena, whose activity has been broadly documented at Barranc de la Boella (Pineda, Saladié, Expósito, et al., 2017). However, there are no signs of active predation by these animals. Research has shown that elephant remains can be exposed on the surface for several decades before complete burial, during which time spotted hyenas may access soft tissues or engage in bone gnawing (Haynes & Klimowicz, 2014).

A distinct scenario is observed in level II.2 of Pit 1, where access to the mammoth carcass is directly evidenced by possible cut marks and indirectly supported by the spatial association of fauna and lithic, as well as by the stone tools microwear analyses (Mosquera et al., 2015). The spatial analyses conducted in this study further reinforce the evidence of spatial association, not only through the interspecific aggregation of faunal and lithic remains but also through the positive correlation between these elements. This strengthens the argument that the assemblage resulted from the butchering activities of the mammoth carcass, although the available evidence is insufficient to determine the mode of access to the carcass (hominins could have found the individual already dead, killed it after encountering it trapped in the mud, or led it to a muddy area where it could not escape). Nevertheless, considering both the size and age of the individual (an adult that, in the present-day natural environment, lacks natural predators) the most parsimonious hypothesis is that no predator contributed to its death.

Data on modern African elephants (*Loxodonta africana*) indicate that, with an average weight of six tons, these individuals would provide between 2 and 2.5 tons of edible tissue (including brain, heart, liver, meat, tongue, and trunk) for consumption (Byers & Ugan, 2005). Recent biometric studies suggest that the average weight of *Mammuthus meridionalis* exceeded 11 tons (Romano et al., 2022), making it nearly twice the size of the African elephant. Therefore, despite the absence of specific studies on the amount of soft tissue available for consumption in this taxon, we could suppose that this quantity could exceed four tons. This scenario outlines a context in which these hominin groups would have had access to vast amounts of edible tissue, which could have sustained a large group (Figure 6). It also leaves open the possibility that other predators may have accessed the edible tissues not exploited by hominins, even though no direct evidence of such activity is recorded.

Conclusions

Thanks to the comprehensive collection of proboscidean specimens from Barranc de la Boella (Tarragona, North-East Iberia), recovered over 18 years of fieldwork and subjected to meticulous restoration and both physical and virtual reconstruction, multidisciplinary analyses have been conducted to thoroughly characterise the presence of this megahervibores at the site. TThe biometric analysis of the most complete third molars would support a referral to an advanced form of *Mammuthus meridionalis*, possibly similar to *M. m. depereti*, reinforcing the existence of deposits dating to late-Early Pleistocene at Pit 1, La Mina and El Forn, which align with the biogeographical and biochronological patterns of the last *Mammuthus meridionalis* in Europe. New palaeoecological inferences from this ca. 0.9 Ma environment from the dietary niche of *M. meridionalis* have helped us to refine the landscape reconstructions, reinforcing the presence of areas of extensive grassland with seasonal aridity (Figure 6).

The recurrent presence of proboscideans in European Pleistocene open-air archaeological sites, such as Barranc de la Boella, along with clear evidence of their exploitation by hominins, reinforces the hypothesis that these environments played a crucial role in human settlement and resource acquisition strategies since the Early Pleistocene. The archaeo-palaeontological record at Barranc de la Boella further

Figure 6. Palaeoenvironmental reconstruction of Barranc de la Boella (Francolí Basin, East Iberia) in the early Pleistocene, highlighting the presence of *Mammuthus meridionalis* in the ecosystem. Illustration by Domingo López, according to A.R. version.

suggests the potential for a commensal relationship between hominins and other predatory palaeoguilds, underscoring the complexity of ecological interactions in prehistoric landscapes.

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ORCID

Darío Fidalgo http://orcid.org/0000-0003-3646-4272
Antonio Rosas http://orcid.org/0000-0002-5829-9952
Antonio Pineda http://orcid.org/0000-0002-3767-8590
Iván Ramírez-Pedraza http://orcid.org/0000-0001-8673-212X
Sergio Ros-Montoya http://orcid.org/0000-0001-6895-807X
David Rodríguez de la Fuente http://orcid.org/0000-0003-4257-411X
Lucía López-Polín http://orcid.org/0000-0002-5810-4115
Bienvenido Martínez-Navarro http://orcid.org/0000-0002-8374-5109
Elena Moreno-Ribas http://orcid.org/0000-0002-0947-6457
Antonio García-Tabernero http://orcid.org/0000-0001-5400-5630
Rosa Huguet http://orcid.org/0000-0002-1750-6249
Andreu Ollé http://orcid.org/0000-0002-8643-5536
Josep Vallverdú http://orcid.org/0000-0002-3177-3263
Palmira Saladié http://orcid.org/0000-0002-1730-8461

Data availability statement

All data used in the preparation of this work are available in the manuscript or in the supplementary materials. Access to 3D models of some of the materials studied is available at the following links: https://skfb.ly/6BzAU; https://skfb.ly/6BzB8; https://skfb.ly/6ByxN; https://skfb.ly/onvFL

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