Journal of Human Evolution 179 (2023) 103368

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Short Communications

First presence of *Macaca sylvanus* at the late Early Pleistocene of Barranc de la Boella (La Mina locality, Francolí Basin, NE Iberia)

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ARTICLE INFO

Article history:
Received 29 December 2022
Accepted 23 March 2023
Available online 23 April 2023

Keywords:
Primates
Cercopithecidae
Macaque
Iberian Peninsula
Mediterranean
Early-Middle Pleistocene transition

1. Introduction

1.1. The discovery

On 13 June 2013, a right upper canine of a cercopithecine primate was found at the locality of La Mina, in the Barranc de la Boella complex (BB; Vallverdú et al., 2014). The presence of hominins at the archaeopaleontological levels of three localities in the BB is widely documented thanks to a stone tool assemblage with the oldest known Acheulean evidence in Europe (Vallverdú et al., 2014; Mosquera et al., 2016), but no other primate remains had been found previously.

The presence of primates in the Early Pleistocene of Europe, apart from the genus *Homo*, is attested by fossils of the catarrhine genera *Macaca*, *Paradolichopithecus*, and *Theropithecus* (Eronen and Rook, 2004; Marigó et al., 2014; Alba et al., 2018). Species of the genus *Macaca* are regularly found in Europe from the Late Miocene to the Late Pleistocene (Rook et al., 2001; Fooden, 2007), the latest occurrence being detected in sites dated to Marine Isotope Stages 5 and 4 (e.g., Cova Negra; Perez Ripoll, 1977; Arsuaga et al., 2007). On the other hand, *Theropithecus oswaldi* (Andrews, 1916) is a very rare species, only identified within Europe at the site of Cueva Victoria (Gibert et al., 1995). Previous determinations at the Pirro Nord site (Rook et al., 2004) have been dismissed (Alba et al., 2014). In parallel, in the first half of the Villafranchian, the last references of the species *Paradolichopithecus arvernensis* (Depéret, 1929) are found in French (Senèze, ca. 2.2–2.1 Ma; Nomade et al., 2014; Paquette et al., 2021), Greek (Dafnero-3, ca. 2.3 Ma; Bennami et al., 2020; Kostopoulos et al., 2018), or Romanian (Grăunceanu, ca. 2.2–1.9 Ma; Terhune et al., 2020) sites.

Here we describe, compare, and contextualize the specimen determined as an upper right canine of a male *Macaca sylvanus* cf. *florentina*, reporting the presence of this species in the late-Early Pleistocene (1.07–0.87 Ma) archaeopaleontological context of Barranc de la Boella. This occurrence corresponds to one of the 21 finds of this species in Iberian sites and the teen dated from the Early Pleistocene.

1.2. Barranc de la Boella

Barranc de la Boella is located in the northeast of the Iberian Peninsula, in the Francolí river basin (UTM coordinates of the

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https://doi.org/10.1016/j.jhevol.2023.103368

central point: 31T, X 4.346.559, Y 4.555.526; Fig. 1A). This site complex is composed of three localities where archaeopaleontological excavations have been carried out since 2007 (El Forn, La Mina, and Pit 1; Vallverdú et al., 2008; Fig. 1B). Geologically, the exposed sequence is made up of sand, gravel, and pebbles with little stratification and lateral variations that have been eroded by the torrential flows of the current ravine. Six lithostratigraphic units have been characterized and correlated in the three localities in the entire 9-meter sequence. Among the archeaopaleontological levels, a large number of fossil skeletal elements, coprolites, and lithic tools including picks and cleaver-like elements considered representative of an Early European Acheulean have been found, mainly located in unit II (Vallverdú et al., 2014; Mosquera et al., 2016).

Specifically, the fossil analyzed here comes from lithostratigraphic unit II, archaeological level II.2 (square Z13, at 1297 cm below the reference level) from the locality of La Mina. This unit has been dated using magnetostratigraphic, geochronological, and biostratigraphic techniques, approximating its absolute chronology between 1.07 and 0.87 Ma (Vallverdú et al., 2014; Lozano-Fernández et al., 2014; Fig. 1C). In this context, an environment with a strong aquatic influence is inferred. The palynological analyses point to a Mediterranean climate, and the paleoenvironmental reconstructions are consistent with a depositional context of a torrential regime that would alternate areas with abundant vegetation and grasslands (Vallverdú et al., 2008; Lozano-Fernández et al., 2015; Rosas et al., 2015; Pineda et al., 2017a). The faunal community represented includes a good sampling of macrofaunal taxa, with very few microvertebrate specimens (Supplementary Online Material [SOM] Table S1).

2. Materials and methods

2.1. Preservation, preparation, and reproduction

The specimen (BB′13C2IIZ.1302) was found in situ, embedded in sandy sediments, and isolated from the maxillary bone or any other

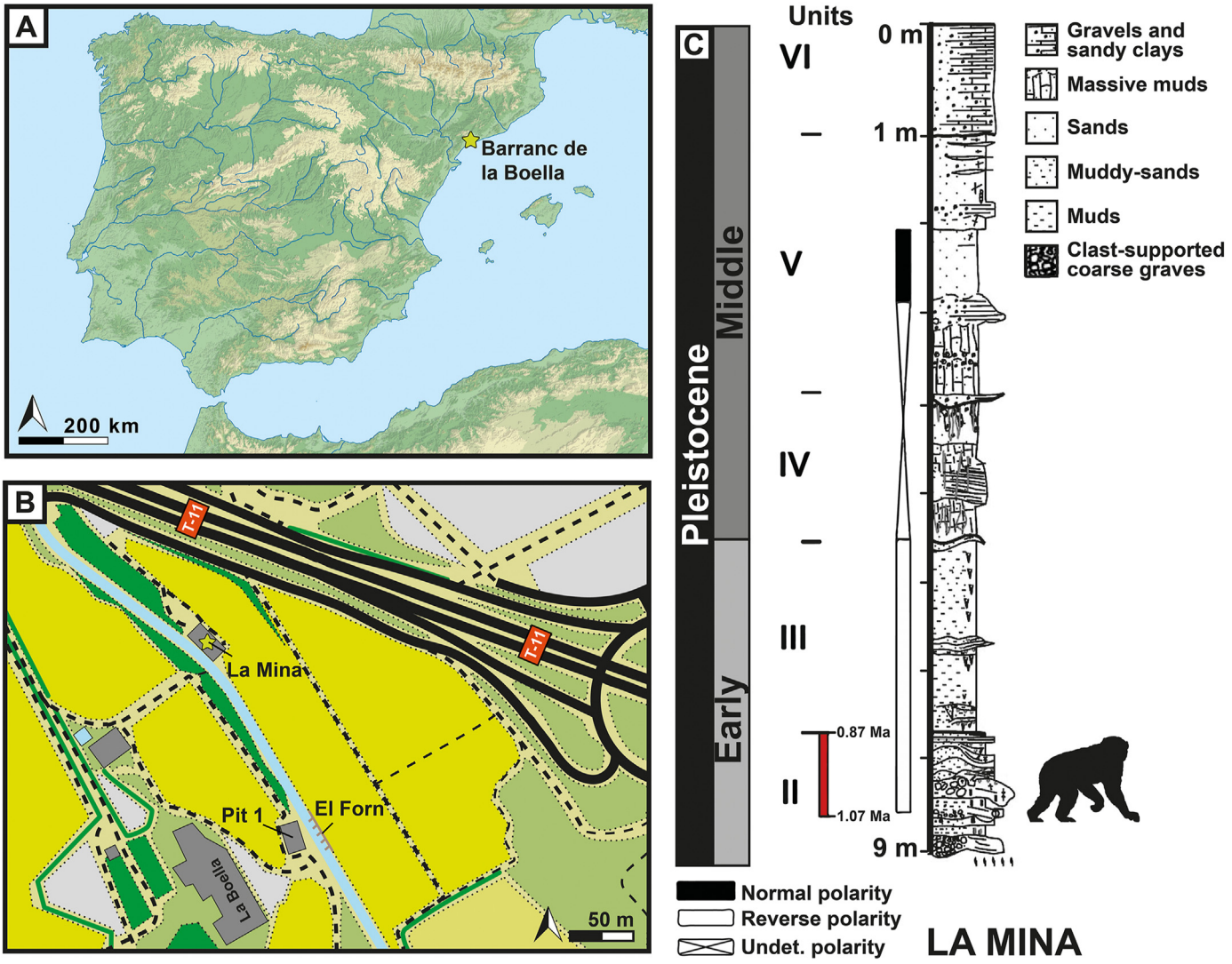

Figure 1. Location map and stratigraphic sequence of the Barranc de la Boella sites (Francolí Basin, NE Iberia). A) Location in the Iberian Peninsula; B) location of the La Mina, El Forn, and Pit 1 localities within the Barranc de la Boella complex; C) stratigraphy of the La Mina locality (Modified from Vallverdú et al., 2014). The macaque fossil was found in the lithostratigraphic unit II, within the 9-m stratigraphic sequence described for the Barranc de la Boella complex. Within this unit, three sedimentary packages are distinguished: 1) oxide-bearing sands, 2) discontinuous lenses of washed sands, and 3) gravels of different grain size with limestone pebbles (Rosas et al., 2015). Unit II has been dated with a chronological range between 0.86 and 1.07 Ma, thanks to the analysis of cosmogenic nuclides, magnetostratigraphy, and micromammal studies (Vallverdú et al., 2014). The macaque silhouette marks the level within the stratigraphic sequence where this specimen was found.

dental remains. It was complete but broken into several pieces as a result of diagenetic fractures. No preservation product was used on-site, and the fragments were wrapped in gauze and stored in a rigid plastic box.

Once in the laboratory, after gentle cleaning, photographs were taken of the disconnected fragments for subsequent inspection. The specimen is temporarily on loan to the Paleoanthropology Group of the Museo Nacional de Ciencias Naturales (CSIC, Madrid), although its final destination is the Institut Català de Paleoecologia Humana i Evolució Social (Tarragona).

A high-resolution mold of the crown was made (with a vinyl polysiloxane resin Exaflex, GC America Inc.) before the parts were glued with a reversible adhesive (Paraloid® B 72). Photographs were then taken from all views (Fig. 2A–D), linear biometric data were taken, and a μCT scan (scanner Nikon XT H 160; voxel size 0.03559013 mm; projections 1800; kV/mA 160/55; exposure time 1000 ms; filter/thickness Copper/0.75 mm) of the specimen (Fig. 2E–G) was performed at the Servicio de Técnicas No Destructivas of the Museo Nacional de Ciencias Naturales (Madrid, Spain). The images obtained from the μCT have been used for the routine evaluation of the internal structure of the specimen and the Paleoanthropology Group of the Museo Nacional de Ciencias Naturales and the Institut Català de Paleoecologia Humana i Evolució Social in curating the data. The μCT data have been uploaded to the MorphoSource platform to facilitate access to other researchers (SOM File S1).

2.2. Measurements and comparative material

A phenotypic comparison of the specimen has been carried out by qualitative analysis of the anatomy (Fig. 2) and quantitative analysis by linear biometry (Fig. 3). The measurements used in the analysis of Figure 3 are the maximum mesiodistal diameter (MD) and the maximum buccolingual diameter (BL). A scatterplot has represented the results, generating a legend and colored areas for the specimens of each taxonomic and biological class considered. The sample considered in both analyses includes data from accessible specimens of European Pleistocene cercopithecines and specimens of extant *M. sylvanus*. For more information on each specimen, see SOM Table S2.

3. Results

3.1. Description

The specimen is a characteristically dagger-shaped tooth with an extensive wear facet on its lingual side, a long mesiolingual facet, and a mesial groove extending onto the root that is characteristic of the upper canines of papionin cercopithecid monkeys (Strasser and Delson, 1987). The size and shape of the tooth, the broadly flat buccal face, the location of the mesial groove on the crown and root, and the location of the wear facets (especially the sharpening facet) rule out its attribution to the genus *Theropithecus* and fit perfectly

Figure 2. Upper canines of *Macaca sylvanus* males. A–D) Specimen BB′13C2IIZ.1302 from La Mina site. E) BB′13C2IIZ.1302 microtomographic buccal view. F) BB′13C2IIZ.1302 microtomographic axial plane (slice) at the root-enamel junction. G) BB′13C2IIZ.1302 microtomographic sagittal plane (slice) in the middle of the tooth. H–K) Right C^1 of extant *Macaca sylvanus sylvanus* cast (UVA3358, cast). L–O) Mirror image of the left C^1 of *M. sylvanus* from a possible Late Pleistocene site in the North Sea (HHO-0420; modified from Reumer et al., 2018). P, Q) Right C^1 (MCSNBS PA11138) of *M. s. pliocena* from the Middle Pleistocene site of Quecchia quarry (modified from Bona et al., 2016). R, S) Mirror image of the left C^1 (MUPE GCP-CV4052) of *Macaca sylvanus florentina* from the Early Pleistocene site of Quibas (modified from Alba et al., 2011). A, H, L, P, and R: buccal view; B, I, and M: mesial view; C, J, N, Q, and S: lingual view; D, K, and O: distal view. Scale: 2 cm.

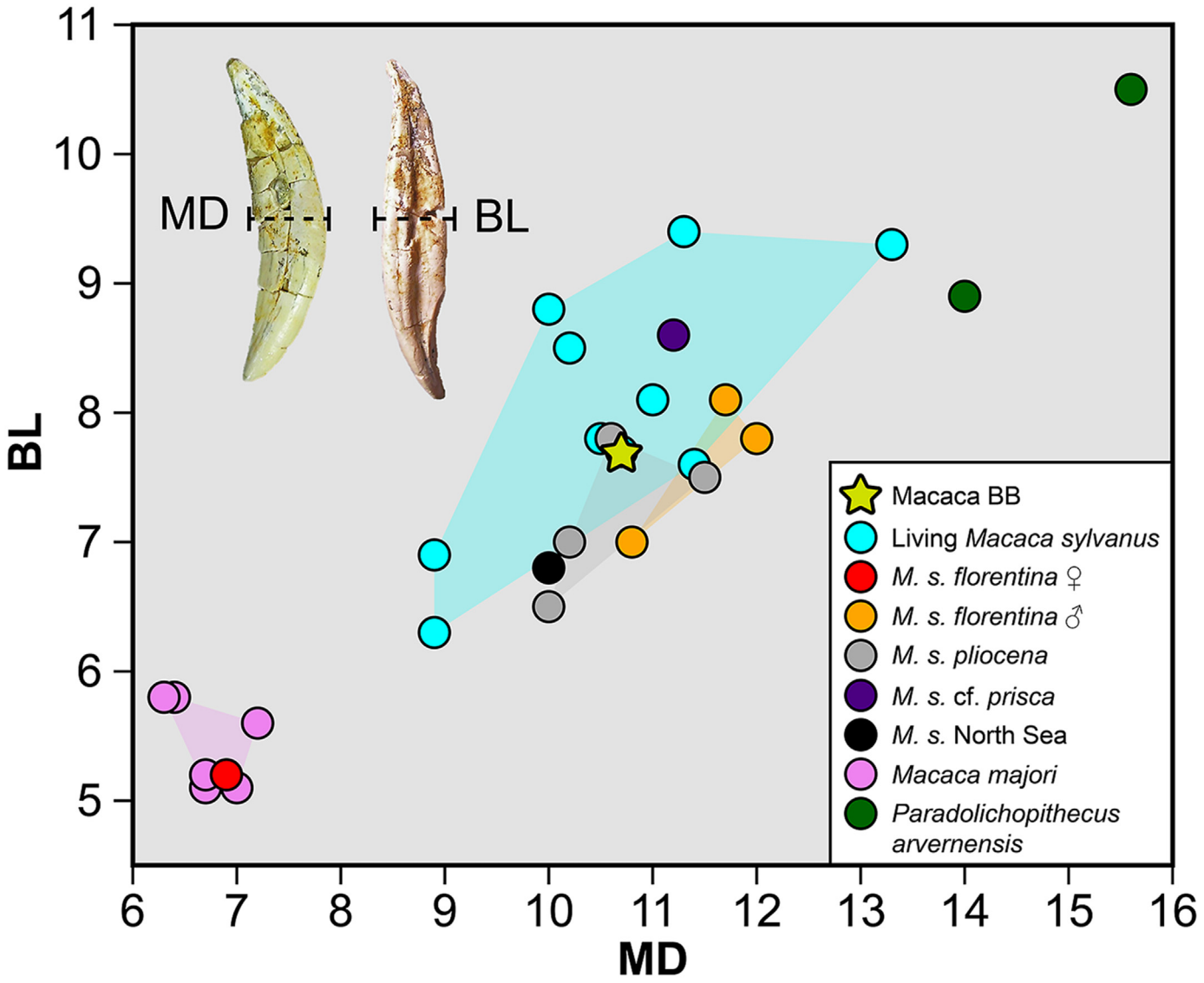

Figure 3. Scatterplot of maximum mesiodistal diameter (MD) and maximum buccolingual diameter (BL) of the upper canines of *Macaca* and *Paradolichopithecus* included in this study, highlighting the one found in the La Mina site. For the specimens lists and associated measurements, see SOM Table S2. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

with the shape of a male upper canine of a species of the genus *Macaca*. In particular, these features resemble those present in male individuals of the representative species of this genus in the Pleistocene European record, *M. sylvanus* (Linnaeus, 1758; Swindler, 2002; Fig. 2).

As in the canines of the extant representatives of *M. sylvanus*, in the BB specimen, the mesial pillar is located in lingual position, resulting in a relatively wide mesial groove. The mesial groove runs continuously along the root and crown, but without reaching the tip of the canine. The wear against the mandibular canine is well developed, being 20 mm long and 2 mm wide, reducing the relief of the internal abutment. The wear facet that occurs with the wear against the lower third premolar is also extensive (Fig. 2A–D).

When compared with other fossil representatives, the morphology of the BB specimen fits perfectly with the description provided by Alba et al. (2011) for the upper canines of *M. s. florentina* (Cocchi, 1872) from the Early Pleistocene sites of Quibas (Murcia; Fig. 2R and S). No significant differences are observed in the anatomy of the canines of the different *M. sylvanus* subspecies proposed in Europe beyond the development of the wear facets. These similarities can be observed in the samples figured so far, from Puerto de la Cadena (Early Pliocene; Alba et al., 2018), Quibas (Early Pleistocene; Alba et al., 2011; Fig. 2R and S), Quecchia quarry (Middle Pleistocene; Bona et al., 2016; Fig. 2P and Q), and the North Sea (possible Late Pleistocene; Reumer et al., 2018; Fig. 2L–O).

3.2. Crown dimensions and comparisons

Although the dimensions of the canine are variable and not particularly diagnostic on small taxonomic scales, it is possible to make some assessments with the data evaluated. With dimensions of 10.7 mm maximum MD and 7.7 mm maximum BL, the BB specimen is notably smaller than those assigned to *P. arvernensis* and larger than those present in *Macaca majori* (Azzaroli, 1946) or the females of *M. sylvanus*. The canine studied here is very similar in size to some of the specimens of male extant *M. sylvanus*. As far as

Figure 4. Paleoartistic reconstruction of the environment of Barranc de la Boella (Francolí Basin, NE Iberia) in the Early Pleistocene, highlighting the presence of *Macaca sylvanus* in the ecosystem. Illustration by Domingo López González, under the supervision of A.R.

fossils are concerned, its measurements and proportions are close to those published for the PA11139 specimen from the Middle Pleistocene site of Quecchia quarry (Bona et al., 2016). The MD measurement of the BB specimen distances it from the proportions of the specimens from the Quibas site, the closest geographically and chronologically to BB (Alba et al., 2011; Fig. 3 and SOM Table S2). In terms of buccolingual compression (BL/MD index, 72%), the data from BB are consistent with some specimens of extant *M. sylvanus* and close to the proportions of the Quecchia quarry specimens, although the biometric range observed for *M. sylvanus pliocena* Owen, 1846 and *M. s. florentina* is practically the same (SOM Table S2).

4. Discussion

4.1. Taxonomic determination of the Barranc de la Boella macaque

Based on current data, the most widely held hypothesis considers that during the Plio-Pleistocene, the macaques present in Europe belong to the extant species *M. sylvanus* (Shearer and Delson, 2012). A subspecific classification of the European populations of this species is more problematic. Current proposals include the consideration of three chronologically delimited subspecies, albeit with few diagnostic anatomical features (Szalay and Delson, 1979): *Macaca sylvanus prisca* Gervais, 1859 for earlier Pliocene specimens, *M. s. florentina* from the Late Pliocene to the Early Pleistocene and *M. s. pliocena* for the Middle and Late Pleistocene.

Following the criteria outlined in the previous section, the BB specimen would tentatively be assigned to the subspecies *M. s.* cf. *florentina*, increasing the overall Iberian record of macaques to 21 localities and the Early Pleistocene record to teen finds (see SOM Table S3).

4.2. Paleobiogeographical, paleoecological, and taphonomic implications

Macaques (genus *Macaca*) have been widely distributed throughout Europe from the Late Miocene to the Late Pleistocene (Mecozzi et al., 2021). Specifically, the first European record of this taxon is found in the Iberian Peninsula at the Almenara-Casablanca M site (MN13, 5.9–5.3 Ma), probably associated with the inflows of African faunas with the drying of the Mediterranean during the Messinian Salinity Crisis (Köhler et al., 2000; Alba et al., 2018). From this time onwards, there are various fossils in the Iberian Peninsula included in the taxon *M. sylvanus* in the Pliocene sites of Canal Negre I (putatively Miocene–Pliocene; Marigó et al., 2014), Puerto de la Cadena (Early Pliocene; Alba et al., 2018), Orrios 7 (Late Pliocene, MN15; Eronen and Rook, 2004), and Cova Bonica (Late Pliocene, MN 16; Delson, 1971; Crusafont-Pairó and Golpe-Posse, 1984; SOM Table S3).

During the Early Pleistocene, specimens from sites located near the Mediterranean coast are well known (Incarcal: Alba et al., 2016; Vallparadís: Alba et al., 2008; Cal Guardiola: Alba et al., 2008; Puebla de Valverde: Heintz et al., 1971; Quibas: Alba et al., 2011; Cueva Negra del Estrecho del Quípar: Walker et al., 2016; SOM Table S3). Despite the scarce anatomical evidence available, the specimen analyzed here from Barranc de la Boella is included in this chronological and geographical range. This record, together with

the findings from southern France, Italy, and Greece (Mecozzi et al., 2021), could contribute to the consideration of *M. sylvanus* populations as representatives of the Mediterranean fauna during the Early Pleistocene (Elton and O'Regan, 2014). Nevertheless, the synchronous records from the TE9 level of the Sima del Elefante (Atapuerca; Rosas et al., 2006) demonstrate a wider Iberian distribution during the Early Pleistocene that would reach latitudes farther away from the meso-Mediterranean influence. More decisive is the broadly contemporaneous presence in Dutch (Tegelen; van Kolfschoten, 2020) and German (Untermassfeld; Reumer and Kahlke, 2022) sites at latitudes much further north, probably suggesting that Early Pleistocene macaques (as extant macaques) had a wider ecological tolerance than we have assumed. Considering that extant Barbary macaques live in harsh, mountainous environments and have to face snow while foraging (Elton and O'Regan, 2014), it would not be surprising to find them in northern latitudes during warm climatic phases (as in the case of Untermassfeld or Tegelen; van Asperen and Kahlke, 2017; Villa et al., 2018).

The sedimentary environment of the materials excavated in the Barranc de la Boella indicates a fluviodeltaic environment with high-density flows and a torrential hydrographic regime (Vallverdú et al., 2014; Rosas et al., 2015). Pollen analyses of hyena coprolite samples highlight the presence of Mediterranean vegetation composed of pines, cypresses, evergreen *Quercus*, Oleaceae, Poaceae, Asteraceae, Liliaceae, or Cyperaceae (Pineda et al., 2017a). Approaches to the reconstruction of this Mediterranean environment from the faunal association (SOM Table S1) allow us to infer the alternation of permanently wet areas with areas of open grasslands and environments with greater vegetation cover (Vallverdú et al., 2008; Lozano-Fernández et al., 2015; Pineda et al., 2017a; Madurell-Malapeira et al., 2019; Fidalgo et al., in press; Fig. 4). This environmental context fits perfectly with the range described for *M. sylvanus* populations, with the presence of permanent watercourses and areas with some tree cover, as discussed in more detail by Alba et al. (2011, 2016). In particular, European populations of this taxon are considered to be part of the so-called Pleistocene warm-adapted faunas, with range expansions northward during interglacial periods and contraction toward southern refugia during glacial periods (Fooden, 2007; Alba et al., 2011; Elton and O'Regan, 2014). The apparently continuous record of macaques on the Iberian Peninsula during the Pleistocene (Mecozzi et al., 2021), as well as that of other components of faunas associated with warm climates (e.g., hippopotamuses; Fidalgo et al., 2023), point to the potential of this area as a climatic refuge in the cold and arid phases that worsen from the Early-Middle Pleistocene transition onwards (Head and Gibbard, 2015; Maslin and Brierley, 2015; Strani et al., 2019; Berends et al., 2021).

Evidence of different interspecific interactions ranging from predation by carnivores (Pineda et al., 2015, 2017b) to human exploitation of faunal components (Vallverdú et al., 2014; Mosquera et al., 2015) has been found at the Barranc de la Boella sites. Although it is not possible to determine the origin of accumulation of this single *M. sylvanus* canine, different plausible scenarios can be analyzed. In depositional contexts similar to BB, it has been shown that Barbary macaques were frequently hunted by felids (Meloro and Elton, 2012). Scarce dental and postcranial specimens attributable to a lynx (*Lynx pardinus*) and a large pantherine felid (*Panthera* sp.) have been found at BB (Madurell-Malapeira et al., 2019), and this predation interaction may be a potential prediction to be tested with future discoveries at the site. Even so, in the BB, we also found specimens belonging to canids (*Canis mosbachensis*, *Vulpes* sp.), ursids (*Ursus deningeri*), and hyenas (indeterminate Hyaenidae; Pineda et al., 2017a; SOM Table S1), which makes it difficult to determine the simple trophic relationships in which these macaques would be included. Given the abundant record of lithic tools at the La Mina site (Vallverdú et al., 2014), direct predation by humans on the individual studied here cannot be ruled out (Meloro and Elton, 2012; Konidaris et al., 2022).

5. Summary and conclusions

The BB specimen is an upper right canine belonging to a male of the primate *M. sylvanus*. The agreement among the qualitative characteristics of the tooth and the chronology of the site suggest its identification as *M. sylvanus* cf. *florentina*, although the lack of consensus on the validity of the proposed subspecies and the large biometric overlap do not allow certainty of this subspecific assignment. *Macaca* cf. *sylvanus* fossils are known across Iberia and throughout Europe in the Pliocene and Pleistocene, mainly in warmer intervals. Data suggest that the species is limited to areas that are more southern in colder phases, whereas in warm phases, this taxon could extend its distribution further north. Predation by carnivore species is likely, while interaction with early humans is less definite.

Declaration of competing interest

The authors of this manuscript certify that they have no conflict of interest. They have no affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

Acknowledgments

We would especially like to thank the co-Editor-in-Chief (Clément Zanolli), the Associate Editor (Eric Delson), and the two anonymous reviewers for their helpful comments, which have significantly improved this paper. This research has been funded by Ministerio de Ciencia e Innovación, PID2021-122356NB-I00. D.F. is supported by the Ayuda del Programa de Formación de Profesorado Universitario (FPU20/03389) and is a Ph.D. student at the Programa de Doctorado en Biología at the Universidad Complutense de Madrid. A.E. is supported by H2020-MSCA-IF project No. 891529 (3DFOSSILDIET). A.P. is supported by the LATEUROPE project (Grant agreement ID 101052653) that has received funding from the European Research Council (ERC) under the European Union's HORIZON1.1 research program. The Barranc de la Boella fieldwork is supported by the Ajuntament de la Canonja and Departament de Cultura of Generalitat de Catalunya (ARQ001SOL-186-2022). The Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA) has received financial support from the Spanish Ministry of Science and Innovation through the 'María de Maeztu' program for Units of Excellence (CEX2019-000945-M).

Supplementary Online Material

Supplementary Online Material to this article can be found online at https://doi.org/10.1016/j.jhevol.2023.103368.

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