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Geographical distribution of Pleistocene cold-adapted large mammal faunas in the Iberian Peninsula

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ABSTRACT

Cold-adapted large mammal faunas reached the Iberian Peninsula during the coldest periods of the Late Pleistocene. A total of 75 Iberian sites yielded remains of the cold-adapted faunal complex which is composed of the species, *Mammuthus primigenius* (woolly mammoth), *Coelodonta antiquitatis* (woolly rhinoceros), *Rangifer tarandus* (reindeer) and, to a lesser extent, *Gulo gulo* (wolverine), *Alopex lagopus* (arctic fox), *Ovibos moschatus* (musk-ox) and *Saiga tatarica* (saiga antelope).

All published information about localities containing cold-adapted large mammal species has been compiled and interpreted according to its geographical location and chronology.

Discussion is focused on examining European faunal corridors into Iberia, particularly during cold phases and concentrating on routes to the central and southern part of the peninsula. Three main episodes with presence of cold-adapted faunas appear to occur within the Iberian Peninsula. The geographic distribution of sites containing the remains of cold-adapted species differs among the three episodes. The oldest occurrence of cold-adapted taxa has been dated around 200–100 ka BP. During this time, the southern limit appears to be about 40°N latitude (~Madrid). During the following episode, between 42 and 31 ka BP, the southernmost limit of cold-adapted fauna is identified by woolly mammoth (*M. primigenius*) remains at Padul, Granada, (37°01′01′N) near the southernmost part of the peninsula. Cold-adapted species appear to be limited to the northern part of the Iberian Peninsula during the last episode, which occurred during the Last Glacial Maximum (LGM) and Younger Dryas (YD).

1. Introduction

The cold-adapted large mammal faunas also known as "mammoth fauna" (Vereschagin and Baryshnikov, 1982) or "*Mammuthus-Coelodonta* faunal complex" (Kahlke, 1999), were common in a wide area of Eurasia over about 40°N, from the Iberian Peninsula to Beringia during the Late Pleistocene. This faunal community is closely related with the steppe-tundra or "Mammoth Steppe" (Guthire, 1982), an herbaceous ecosystem characteristic of the Pleistocene glacial periods, which disappeared at the end of the Pleistocene. Consequently, the mammoth fauna disappeared at the same time. After the end of the Pleistocene some of these species (reindeer, musk-ox and arctic fox) moved northward to arctic areas, a few others (as saiga antelope) migrated to the central Asian steppe and some other species (as woolly mammoth and woolly rhinoceros) became extinct.

The Iberian Peninsula constituted one of the southernmost limits of the steppe-tundra expanse and was occupied by these faunas during the coldest periods (Álvarez-Lao and García, 2010). In the Iberian fossil record, the presence of cold-adapted mammal species is occasional and restricted to specific time spans and, in most cases, to limited geographical areas.

Finds of Pleistocene cold-adapted large mammals from the Iberian Peninsula have been identified since the mid-19th century and published by several authors (Leith Adams, 1877; Harlé, 1912; Altuna, 1966, 1972; Altuna and Mariezkurrena, 2000, 2006). Compilation works about these finds have been carried out by Altuna (1996) and García and Arsuaga (2003). Subsequently, an exhaustive revision along with taxonomic, morphologic and biometric analyses of all the Iberian fossils of these species has been conducted (Álvarez-Lao, 2007). The chronological context of these remains based on a large number of absolute dates has been correlated with paleoclimatic data of the Iberian Late Pleistocene (Álvarez-Lao and García, 2010). According to these authors, cold-adapted faunas were present in the Iberian Peninsula from at least the late Middle Pleistocene (from about 200 to 150 ka BP,

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corresponding to MIS 6). Several findings are dated to the first half of the Late Pleistocene, and at about 44 ka BP these fauna became relatively abundant on the Iberian Peninsula. A chronological gap is detected between 31 and 26 ka BP, where this fauna appears almost absent from Iberia. However, during MIS 2, the fauna becomes relatively frequent again. The last Iberian occurrences for the majority of the cold-adapted species have been registered during the LGM and H1 (between about 23 and 15 ka BP), except in the case of reindeer, which survived beyond the Younger Dryas (12.7–11.3 ka BP), with a last date of 10.3 calibrated ka BP (Álvarez-Lao and García, 2010). The chronology of the Iberian findings of cold-adapted large mammal faunas is consistent with other paleoclimatic evidence suggesting cold climates such as pollen analysis, variation of oxygen isotopes, proportions of cold affinity marine organisms and the presence of Ice Rafted Detritus (IRD) (Roucoux et al., 2005; Álvarez-Lao and García, 2010).

The sites which have yielded cold-adapted species are distributed irregularly along the Iberian Peninsula (Fig. 1), most of them being concentrated in a few areas. Geographical, topographical, and latitudinal effects likely have created this geographic distribution. Most of these sites are located in the north, where the climatology and landscapes are more similar to central European localities. It is likely that the Pyrenees and Cantabrian Mountain Range functioned as geographic barriers for some of these species.

Few remains have been found in the Castilian Plateau, most of them in Madrid, originating from building and road construction, quarries, as well as in sands and gravel from aggregates in fluvial sediments. In the northernmost regions of western (Galicia, Asturias), central (Cantabria, Basque Country), and eastern (Catalonia) Iberia, caves preserve the Pleistocene cold-adapted faunas. Additionally, the presence of woolly mammoth remains in southern sites, like Padul (Aguirre et al., 1973; Álvarez-Lao et al., 2009), indicates that the distribution of the woolly mammoth reached the southernmost regions of the peninsula. Further, the substantial distance between Padul and the next closest mammoth site (Arriaga, Madrid; ~300 km N), implies a much wider geographic distribution for this species which has not yet been reflected in the fossil record.

2. Material and methods

The cold-adapted mammal species selected for this work are generally the three most abundant in the Iberian Late Pleistocene fossil record: the woolly mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*) and reindeer (*Rangifer tarandus*). Four other species also have been considered in these cold-adapted faunas although their Iberian record is scarcer: wolverine (*Gulo gulo*), arctic fox (*Alopex lagopus*), musk ox (*Ovibos moschatus*) and saiga antelope (*Saiga tatarica*).

Remains of woolly mammoth, woolly rhino, and reindeer are recognized from 75 Iberian sites (Fig. 1), 64 from the north (Cantabrian area and Catalonia), and the rest from the central (Madrid, Estremadura) and south (Granada) areas (García and Arsuaga, 2003; Álvarez-Lao, 2007; Álvarez-Lao and García, 2010).

In general, most of the fossil remains have been verified taxonomically by the authors, especially in those cases corresponding to undescribed older findings or those only briefly described in the literature. In a few rare cases, some older findings have been untraceable.

The chronology of most of the analyzed sites (Fig. 2) is known either by radiometric analysis (e.g., ^{14}C) or by correlation with archaeological materials (Álvarez-Lao and García, 2010). In this examination, all radiocarbon dates have been calibrated and are expressed in cal ka BP (calibrated kiloannae before present).

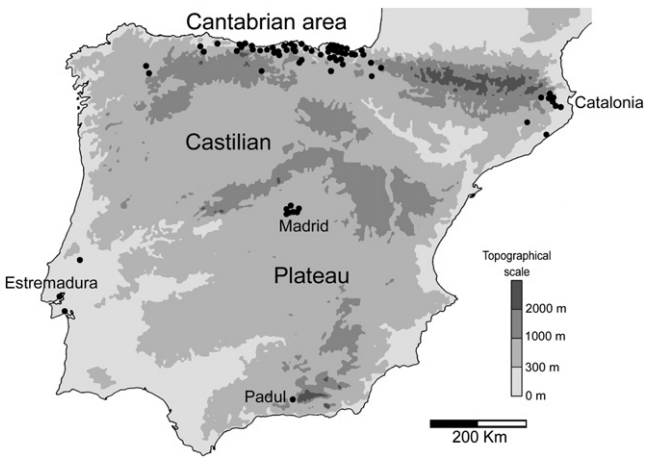

Fig. 1. Map of the Iberian Peninsula with the location of the sites with Pleistocene cold-adapted large mammal remains and the main geographic areas indicated in the text.

3. Paleogeography of the species in the Iberian Peninsula

3.1. Geographical distribution of *M. primigenius* in the Iberian Peninsula

Woolly mammoth remains are found in 25 archaeo-palaeontological Iberian sites (Table 1). Sixteen of these sites are in the north (Fig. 3), 13 of which are in the Cantabrian area, west of the Pyrenees (provinces of Lugo, Asturias, Cantabria and Guipúzcoa). The other three northern sites containing woolly mammoth are in the Gerona province (Catalonia), east of the Pyrenees. The remaining nine sites are distributed about the Peninsula, but appear concentrated in three main areas: Madrid (central Spain) and Estremadura province (central Portugal) both in central Iberia, and Padul in south Iberia (Granada province, southern Spain). The total distribution of this species appears quite extensive, although its density is very low in the central-southern regions. Given that mammoths reached the south, their presence in central Iberia may indicate a corridor from the north to the southern regions. The lack of this species at many sites between north and south Iberia may be due to taphonomic reasons. Perhaps, the central region of the Iberian Peninsula only represented a migration corridor to other favourable places (like Padul), so that the presence of woolly mammoths in these areas would only have been occasional. That type of situation may explain the current and very scanty fossil record of this species in this region.

In the south, Padul peat bog has exceptional conditions for fossil preservation. Padul likely represented an excellent living area for these proboscideans. The area has high altitude environmental characteristics (given the closeness of the Sierra Nevada), a predominant steppe vegetation (recorded by pollen data), and favourable geographic conditions (a basin surrounded of mountains with moderate topography). The abundant fossil record, with at least four specimens found at this site, supports this idea (Álvarez-Lao et al., 2005, 2009).

There is evidence of at least three clear episodes in which woolly mammoth was present in the Iberian Peninsula, two of them are chronologically well defined and one is older and more imprecise (Álvarez-Lao and García, 2007, 2010). The geographical distribution of Iberian woolly mammoth sites varied depending on these periods.

First episode: All the oldest Iberian woolly mammoth sites come from fluvial sediments in the province of Madrid. Its chronology