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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).

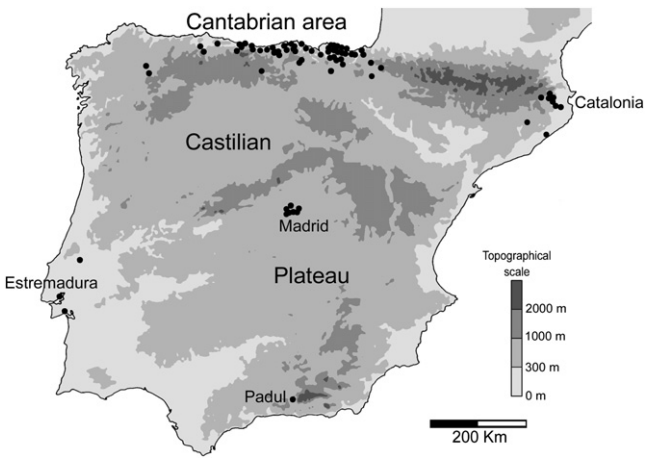

Fig. 1. Map of the Iberian Peninsula with the location of the sites with Pleistocene cold-adapted large mammal remains and the main geographic areas indicated in the text.

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

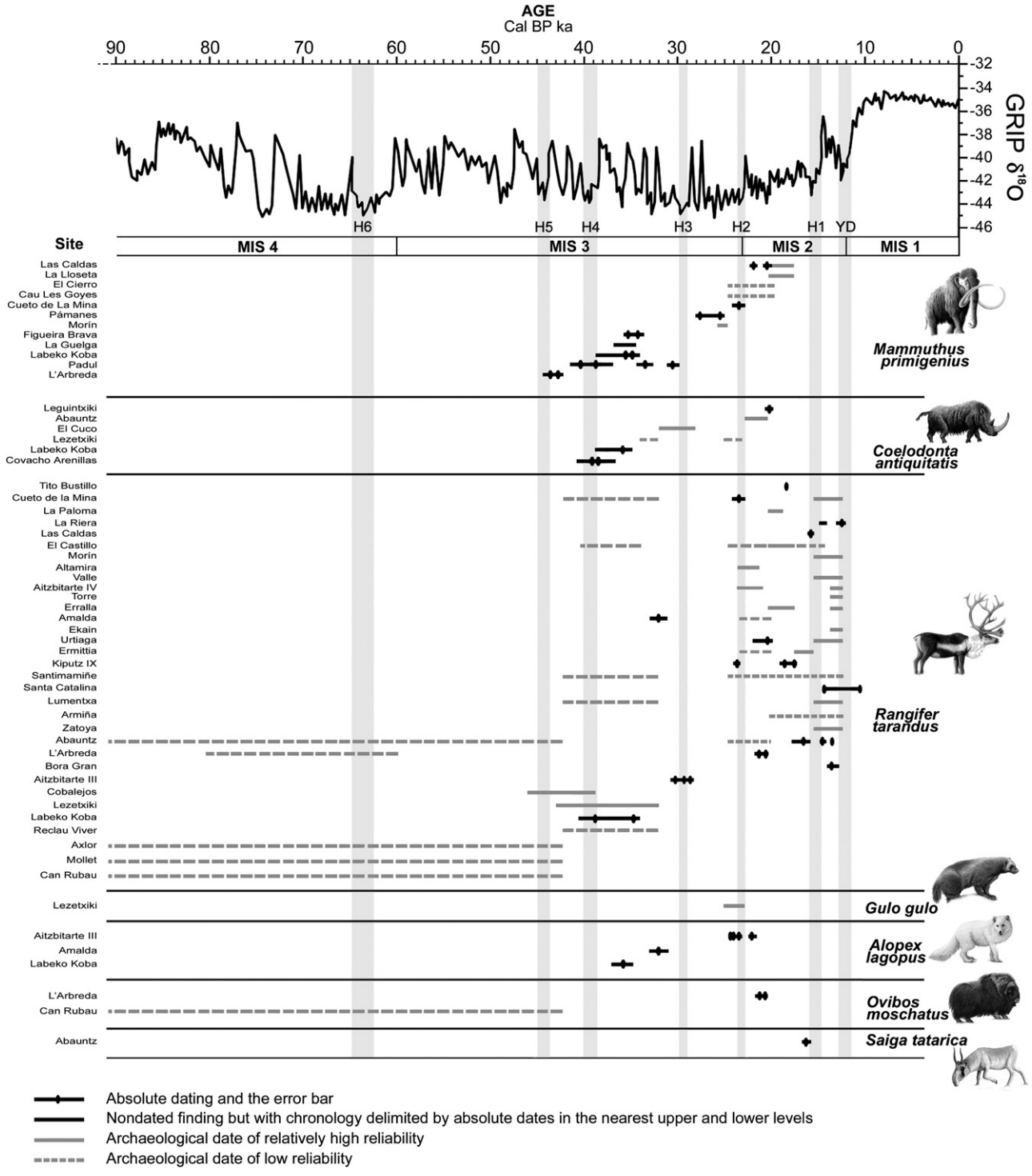

Fig. 2. Chronological distribution of the Late Pleistocene Iberian cold-adapted large mammal finds compared to the GRIP paleoclimatic oxygen curve and the Marine Isotope Stages (MIS). The vertical grey bands indicate the main cold episodes: Heinrich events and YD (from Álvarez-Lao and García, 2010).

has been estimated, generally by stratigraphic correlation, between the late Middle Pleistocene and the early Late Pleistocene. Remains have been found at: Casa Eulogio, Arriaga, Aldehuela (Sesé and Soto, 2002), Butarque and Edar Culebro (S. Bárez and J. Yravedra pers. com., 2006), indicating that the mammoths southernmost reach extended to at least 40° N during that time interval. Because of the limited number of sites, the true geographical distribution of this species during this particular time interval remains uncertain.

Second episode: The following episode is well documented, occurring between 43 and 31 cal ka BP based on the dating of five sites (Fig. 2; Álvarez-Lao and García, 2010). The absolute southernmost spread of this species in Iberia corresponds to this interval, reaching the Padul peat bog, at latitude 37°01′01′N (Álvarez-Lao et al., 2005, 2009), and also the Portuguese site of Figueira Brava (Antunes and Cardoso, 1992), at 38′48′N, at the westernmost limit of the Iberian territory. Woolly mammoth remains are recognized in northern Iberia during this interval at

Table 1
Iberian sites with fossil remains of *Mammuthus primigenius* and chronology of the finds.

Site	Province	Absolute chronology/Archaeological context[a]	Source
Buján	Lugo	Unknown	Torre Enciso, 1962
Las Caldas	Asturias	20.4; 21.8 cal ka BP; Lower Magdalenian	Corchón, 1991–1992; Adán, 1997
La Güelga	Asturias	>34.4<36.8 cal ka BP	M. Menéndez, pers. com., 2006
El Cierro	Asturias	Solutrean	Corchón, 1999
La Lloseta	Asturias	Lower Magdalenian	Álvarez-Lao, 2007
Cueto de la Mina	Asturias	23.5 cal ka BP	Castaños, 1982; Stuart et al., 2002
Mina Dolores	Cantabria	Unknown	Leith Adams, 1877; Harlé, 1912
Mina Angel	Cantabria	Unknown	Harlé, 1912
Morín	Cantabria	Gravettian	Altuna, 1971a,b
Minas de Heras	Cantabria	Unknown	Álvarez-Lao, 2007
Pámanes	Cantabria	25.4; 27.6 cal ka BP	Carballo, 1912; Álvarez-Lao and García, 2010
Labeko Koba	Guipúzcoa	34,9; 35,8; >35,8<38.9 cal ka BP	Altuna and Mariezkurrena, 2000
Urtiagako Leizea	Guipúzcoa	Unknown	Altuna, 1984
Clot de Llop	Gerona	Unknown	Harlé, 1912
Arbreda	Gerona	42.8 cal ka BP	Galobart et al., 1996; Maroto et al., 1996
Cau de les Goyes	Gerona	Solutrean	Obermaier, 1925
Butarque	Madrid	Unknown	S. Bárez, pers. com., 2006
Aldehuela	Madrid	Unknown	Sesé and Soto, 2002
Edar Culebro	Madrid	Unknown	J. Yravedra, pers. com., 2006
Arriaga	Madrid	Unknown	Sesé and Soto, 2002
Arenero Casa Eulogio	Madrid	Unknown	Sesé and Soto, 2002
Algar de João Ramos	Estremadura	Unknown	Cardoso, 1996; Sousa and Figueiredo, 2001
Cruz Quebrada	Estremadura	Unknown	Cardoso and Regala, 2002
Figueira Brava	Estremadura	35.1; 34.2 cal ka BP	Antunes and Cardoso, 1992
Padul	Granada	40.4; 38.6; 33.5; 30.6 cal ka BP	Álvarez-Lao and García, 2010

[a] Calibrated radiocarbon dates as well as more precise information about the chronology is provided in Álvarez-Lao and García, 2010.

three sites: La Güelga, in Asturias (M. Menéndez, pers. com., 2006), Labeko Koba, in Guipuzcoa (Altuna and Mariezkurrena, 2000), and Arbreda cave at Gerona (Galobart et al., 1996; Maroto et al., 1996).

Third episode: The most recent interval with the presence of *M. primigenius* on the peninsula ranges between 25 and 17.5 cal ka BP. Seven sites from this time interval have been identified, of which five have absolute dates and five are in an archaeological context.

During this interval all the records originate from the north (Table 1). Six sites are from the Cantabrian area and one from Gerona (Fig. 3). The last Iberian occurrences of woolly mammoth are all located within the Asturias region: La Paloma (Castaños, 1980), Las Caldas (Corchón, 1991–1992) and La Lloseta (Álvarez-Lao, 2007). These sites are found in Lower Magdalenian context (between approximately 20.2 and 17.6 cal ka BP). The northwest boundary of woolly mammoth on the Iberian Peninsula is marked by the site of Buján, (Lugo, Galicia) (Torre Enciso, 1962), whose chronology remains unknown.

The southern boundary of the Holarctic geographical spread of *M. primigenius* during the Late Pleistocene is mainly placed above the latitude of 40°N. A detailed map of the woolly mammoth

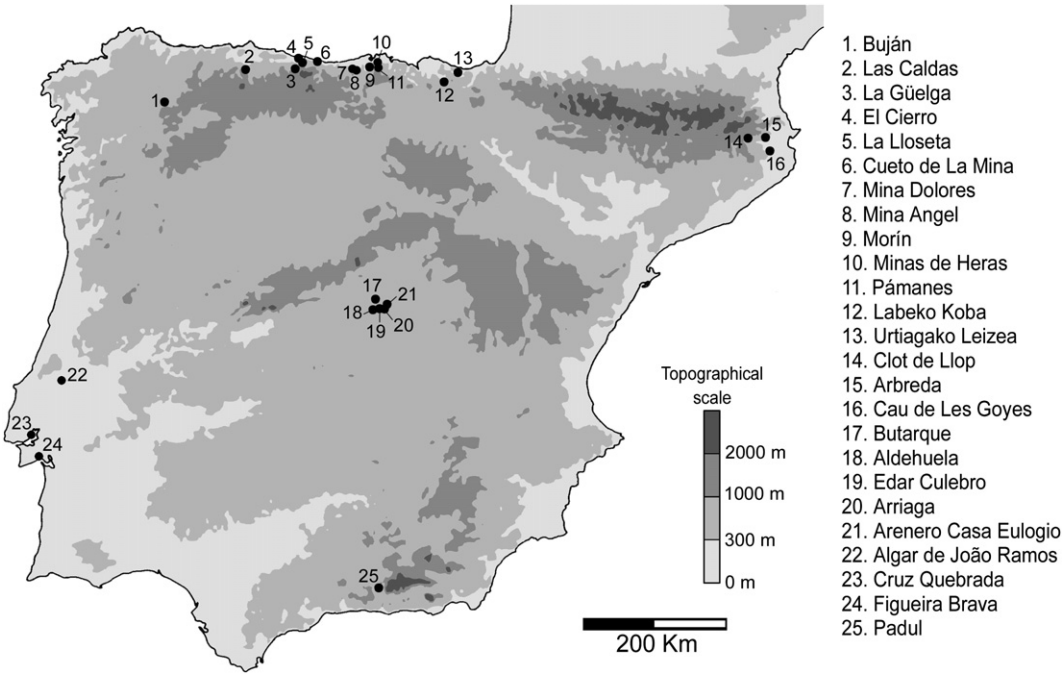

Fig. 3. Situation of the Iberian sites with *Mammuthus primigenius* remains.

Table 2
Iberian sites with fossil remains of *Coelodonta antiquitatis* and chronology of the finds.

Site	Province	Absolute chronology/Archaeological context[a]	Source
La Parte	Asturias	150 ka BP	Álvarez-Lao and García-García, 2006
Unquera	Cantabria	Unknown	Harlé, 1912
Las Cáscaras	Cantabria	Unknown	Carballo, 1909, 1910
La Gándara	Cantabria	Unknown	Naranjo y Garza, 1875; González Linares, 1876
Cueva de Nando	Cantabria	Unknown	Fuentes and Meijilde, 1979
San Pedro	Cantabria	Unknown	Domingo et al., 2005; Álvarez-Lao, 2007
Covacho de Arenillas	Cantabria	39.1; 38.4 cal ka BP	Castaños, 1996
El Cuco	Cantabria	Gravettian	Castaños and Castaños, 2007
Mudá	Palencia	Unknown	Prado, 1864; Álvarez-Lao, 2007
Cantera de la Vía	Vizcaya	Unknown	Altuna, 1974
Labeko Koba	Guipúzcoa	>35.8<38.9; 35.8 cal ka BP	Altuna and Mariezkurrena, 2000
Arrikrutz	Guipúzcoa	Unknown	Altuna, 1979
Lezetxiki	Guipúzcoa	Gravettian-Solutrean; Aurignacian	Altuna, 1972
Urtiagako Leizea	Guipúzcoa	Unknown	Altuna, 1984
Abauntz	Navarra	Solutrean	Altuna et al., 2001–2002
Leguintxiki	Navarra	20.2 cal ka BP	Castaños, 1996
El Toll	Barcelona	Unknown	Thomas and Villalta, 1957; Crusafont, 1961
Arenys de Mar	Barcelona	Unknown	Harlé, 1920; Gómez-Alba, 1997
Arroyo Culebro	Madrid	Acheulian	Arsuaga and Aguirre, 1979
Los Rosales	Madrid	Unknown	Royo y Gómez, 1935; Cerdeño, 1990
Aldehuela	Madrid	Unknown	Sesé and Soto, 2002

[a] Calibrated radiocarbon dates as well as more precise information about the chronology is provided in Álvarez-Lao and García, 2010.

distribution by R.-D. Kahlke (in Álvarez-Lao et al., 2009) shows that only two areas yielded woolly mammoth remains south of this latitude: the Iberian Peninsula and China. Padul is the southernmost European site where this species is recognized (Álvarez-Lao et al., 2005, 2009). The Chinese site of Ji'nan at Beidasha River (Shandong province) is placed at 36°35′N, representing the world's most southerly-recorded *M. primigenius* (Takahashi et al., 2007).

3.2. Geographical distribution of C. antiquitatis in the Iberian Peninsula

Twenty-one Iberian sites have yielded woolly rhinoceros remains (Table 2; Fig. 4), 18 of which are in northern regions: 16 in the Cantabrian area and Navarra (west from Pyrenees) and two in Catalonia (east from Pyrenees). Three more sites are situated in central Spain, at Madrid (Álvarez-Lao, 2007; Álvarez-Lao and García, 2010). No one site located between these two areas has provided remains of this species. Lack of woolly rhino at many sites between north and central Iberia may be due to taphonomic reasons, as above described for the mammoth. As with the mammoth, woolly rhino was present in the Iberian Peninsula during at least three episodes.

First episode: The oldest occurrence from La Parte Site, Asturias, was dated by $^{234}U/^{230}Th$ to 150 ka BP (Álvarez-Lao et al., 2002; Álvarez-Lao and García-García, 2006). In Madrid,

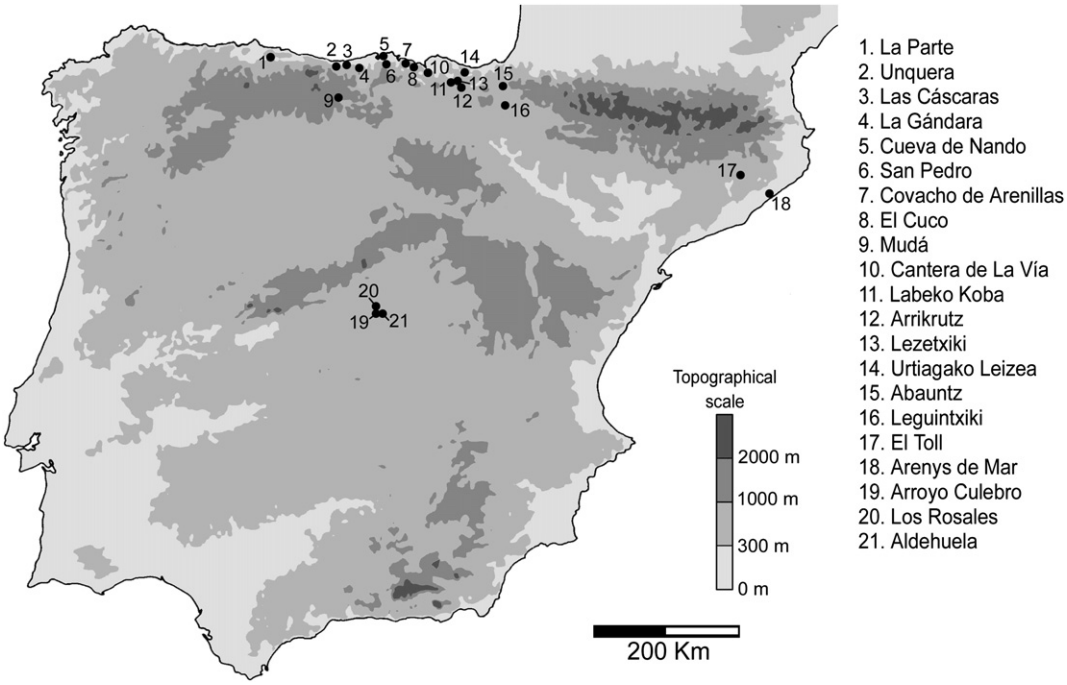

Fig. 4. Situation of the Iberian sites with *Coelodonta antiquitatis* remains.

remains from Arroyo Culebro were recovered but did not yield positive results through radiocarbon analysis. However, these fossils were recovered in association with Lower Palaeolithic tools, which suggest a late Middle Pleistocene or early Late Pleistocene chronology (Arsuaga and Aguirre, 1979). Fossils recovered at Los Rosales and Aldehuela, also from Madrid, have an imprecise chronology, estimated on the basis of stratigraphic correlation between the end of the Middle Pleistocene and the beginning of the Late Pleistocene (Sesé and Soto, 2002), and could have a similar age to Arroyo Culebro; however, a different episode cannot be discarded. During this period, therefore, woolly rhino reached its maximum southern spread in central Iberia, at the latitude of Madrid (about 40°N).

Second episode: The next episode of woolly rhinoceros presence in Iberia is identified between 41 and 29 cal ka BP (Fig. 2). Two finds from this time span have been radiocarbon dated while two others are associated with archaeological evidence. All four sites come from the Cantabrian Area west of the Pyrenees (Table 2, Fig. 4).

Third episode: The latest episode with woolly rhinoceros occurring in the Iberian Peninsula is placed between 24 and 20 cal - ka BP. One radiocarbon date and two archaeologically associated remains (Fig. 2) are identified from sites in the Cantabrian Area and western Pyrenees (Fig. 4).

In addition to the cited sites, two woolly rhinoceros findings from Catalonia as well as nine recoveries from the Cantabrian area have uncertain chronology (Álvarez-Lao, 2007).

The Holarctic spread of *C. antiquitatis* during the Late Pleistocene covers much of Eurasia. However, unlike the woolly mammoth, this species never reached North America. The maximum southern spread of the woolly rhinoceros is placed above 40°N latitude in the majority of its range. The southernmost European occurrence corresponds to the Megalopolis site, in Greece, at 37°2′N (Malez, 1972). The world's southernmost occurrence of this species is in China (Kahlke, 1999) reaching 33°N (Chow Ben Shun, 1978).

3.3. Geographical distribution of *R. tarandus* in the Iberian Peninsula

Reindeer remains have been found in 41 Iberian sites (Table 3), representing the cold-adapted species from the largest number of sites. Reindeer do not occur southwards of the Cantabrian Mountain Range and Gerona (Fig. 5). Most of the sites (36) are located in the Cantabrian Area and west of the Pyrenees (provinces of Lugo, Asturias, Cantabria, Vizcaya, Guipúzcoa and Navarra). The remaining sites (5) come from Gerona (Catalonia).

With respect to the density of sites with reindeer remains, an east-west gradient is observed in the Cantabrian area. The greatest

Table 3
Iberian sites with fossil remains of *Rangifer tarandus* and chronology of the finds.

Site	Province	Absolute chronology/Archaeological context[a]	Source
A Valiña	Lugo	Unknown	Fernandez Rodríguez and Ramil Rego, 1996
La Paloma	Asturias	Lower Magdalenian	Castaños, 1980
La Parte	Asturias	150 ka BP	Álvarez-Lao and García-García, 2006
Tito Bustillo	Asturias	18.2 cal ka BP	Moure Romanillo, 1990; Adán, 1997
El Bufón	Asturias	Unknown	Menéndez, 1923
Cueto de La Mina	Asturias	23.5 cal ka BP, Aurignacian & Upper Magdalenian	Castaños, 1982
La Riera	Asturias	12.5 cal ka BP; >14,100<14,800 cal ka BP	Strauss and Clarck, 1986; Altuna, 1986
Altamira	Cantabria	Upper Solutrean	Altuna and Strauss, 1976
El Castillo	Cantabria	Acheulian, Aurignacian, Solutrean & Magdalenian	Obermaier, 1925; Cabrera, 1984
Cobalejos	Cantabria	Late Mousterian to Lower Aurignacian	Castaños, 2005
Morín	Cantabria	Upper Magdalenian	Altuna, 1971a,b
Ojebar	Cantabria	Unknown	Harlé, 1912
Valle	Cantabria	Upper Magdalenian	Harlé, 1912
Palomas	Cantabria	Unknown	Harlé, 1912
Lumentxa	Vizcaya	Upper and Late Magdalenian	Castaños, 1984
Santa Catalina	Vizcaya	14.4; 10,3 cal ka BP; Upper Magdalenian & Azilian	Elorza, 2005; Castaños pers. com., 2006
Armotxe	Vizcaya	Unknown	Altuna, 1971b, 1972
Armiña	Vizcaya	Magdalenian	Obermaier, 1925; Altuna, 1972
Santimamiñe	Vizcaya	Aurignacian, Solutrean, Magdalenian	Castaños, 1984
Atxuri	Vizcaya	Unknown	Altuna, 1972, 1996
Axlor	Vizcaya	Mousterian	Altuna, 1971b, 1980
Kiputz IX	Guipúzcoa	23,8; 18,8; 17,5 cal ka BP	Castaños et al., 2006
Urtiaga	Guipúzcoa	Upper and Late Magdalenian	Altuna, 1971b
Astigarraga	Guipúzcoa	Unknown	Altuna, 1971b, 1972
Ermittia	Guipúzcoa	Solutrean and Middle Magdalenian	Altuna, 1971b
Ekain	Guipúzcoa	Late Magdalenian	Altuna and Mariezkurrena, 1984
Labeko Koba	Guipúzcoa	34.9; >35.8<38.9; 38.9 cal ka BP	Altuna and Mariezkurrena, 2000
Lezetxiki	Guipúzcoa	Proto Aurignacian, Aurignacian, Upper Aurignacian	Altuna, 1971b
Urtiagako Leizea	Guipúzcoa	Unknown	Altuna, 1984
Erralla	Guipúzcoa	Lower and Late Magdalenian	Altuna and Mariezkurrena, 1985
Amalda	Guipúzcoa	Solutrean, Middle-Upper Solutrean	Altuna, 1990, 2004
Aitzbitarte III	Guipúzcoa	30.3; 29.3; 28.7 cal ka BP	Altuna, 1992, 1996
Aitzbitarte IV	Guipúzcoa	Middle-Upper Solutrean, Late Magdalenian	Altuna, 1963a, 1971b
Torre	Guipúzcoa	Late Magdalenian	Altuna, 1971b, 1972
Abauntz	Navarra	16.4; 14.5; 13.6 cal ka BP; Mousterian, Solutrean	Altuna et al., 2001–2002
Zatoya	Navarra	Upper Magdalenian	Mariezkurrena and Altuna, 1989
Reclau Viver	Gerona	Aurignacian	Maroto et al., 1996
Bora Gran	Gerona	13,5 cal ka BP	Galobart et al., 1996
Arbreda	Gerona	21.2; 20.7 cal ka BP; Mousterian	Estévez, 1987; Maroto et al., 1996
Mollet	Gerona	Mousterian	Maroto pers. com., 2009
Can Rubau	Gerona	Mousterian	Maroto, pers. com., 2007

[a] Calibrated radiocarbon dates as well as more precise information about the chronology is provided in Álvarez-Lao and García, 2010.

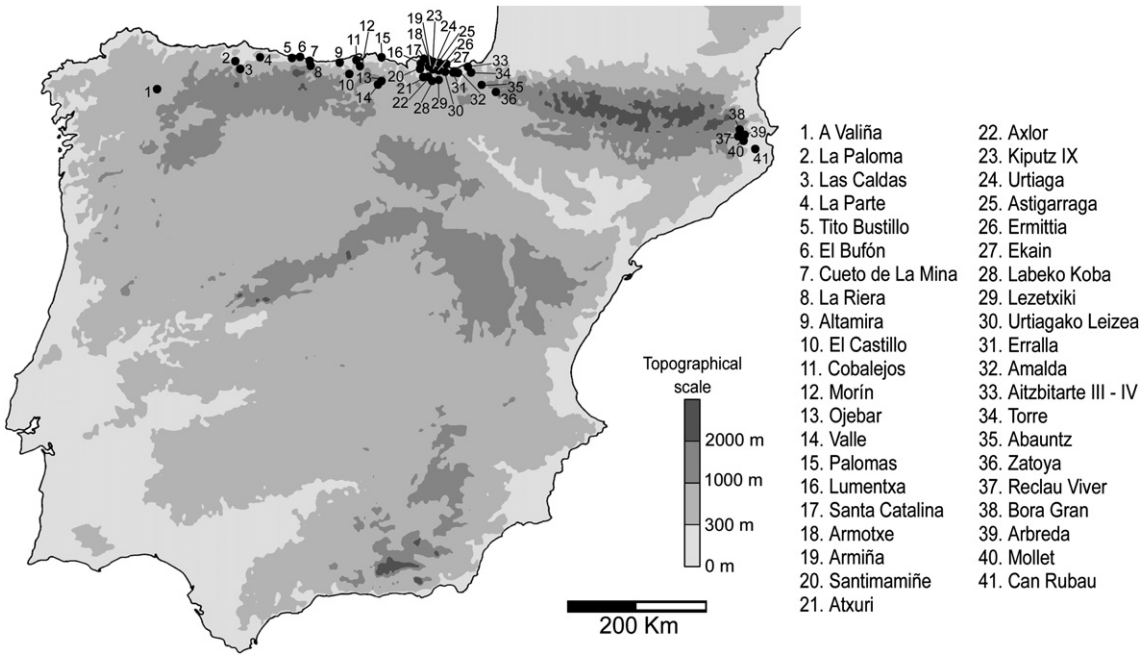

Fig. 5. Situation of the Iberian sites with *Rangifer tarandus* remains.

concentration is registered in the provinces of Vizcaya and Guipúzcoa, especially between the localities of Arteaga and Deva, where 11 sites have yielded reindeer remains in an area less than 20 km apart. This density decreases gradually westwards, with a fewer number of sites in Cantabria, even fewer in Asturias, and only one occurrence in Lugo (Fig. 5; Álvarez-Lao, 2007). This gradient suggests an entrance of this species from France through a corridor west of the Pyrenees and a later spread towards northwest Spain. A similar pattern can be noted east of the Pyrenees, with five sites at the eastern edge of the Pyrenees (Gerona), suggesting a reindeer dispersal through the narrow pass located between the end of this mountain range and the Mediterranean Sea. The occurrence of Iberian reindeer can be ascribed to the same three episodes as for the woolly mammoth and woolly rhino.

First episode: the oldest Iberian remains of this species corresponds to the late Middle Pleistocene and early Late Pleistocene and come from two sites: La Parte (Asturias) and El Castillo (Cantabria). These sites are dated by $^{234}U/^{230}Th$ series (La Parte) or by association with Lower Palaeolithic tools (El Castillo), between approximately 180 and 120 ka BP (Obermaier, 1925; Cabrera, 1984; Álvarez-Lao and García-García, 2006; Álvarez-Lao and García, 2010).
Second episode: Reindeer remains came from nine sites located in the Cantabrian area and Catalonia. Two localities yielded radiocarbon dates, while the other seven were associated with archaeological contexts (Fig. 2), and imply a range between 41 and 31 cal ka BP (Álvarez-Lao and García, 2010).
Third episode: The most recent episode with occurrence of this cervid is dated between approximately 24 and 12 cal ka BP. Twenty-five Iberian reindeer finds from the Cantabrian Area and Catalonia correspond with this time span. Nine sites have been radiocarbon dated whereas the ages of the other 16 sites have been interpreted based on their association with well defined archaeological levels (Fig. 2; Álvarez-Lao and García, 2010).

Of the remaining sites, five from the Cantabrian area and one from Catalonia, did not yield reliable dates (Álvarez-Lao, 2007; Maroto pers. com., 2009).

The Holarctic spread of *R. tarandus* during the Late Pleistocene covers much of Eurasia and North America. The southern boundary of reindeer reaches its extent at about 42°N in the Iberian Peninsula (Álvarez-Lao, 2007), at the east end of Siberia (Kahlke, 1999), and in the Balkan Peninsula and Crimea (although slightly northwards) (Malez, 1972). In most of central Siberia, the boundary appears to be more northerly at about 50°N.

3.4. Geographical distribution of *G. gulo*, *A. lagopus*, *O. moschatus* and *S. tatarica* in the Iberian Peninsula

The presence of these four species in the Iberian Peninsula is sporadic, with only one to three occurrences per species (Table 4). All sites occur in north Iberia very close to the Pyrenees at the western margins of the provinces of Álava, Guipúzcoa and Navarra, and eastern Gerona (Fig. 6).

Therefore, the dispersal of these species into the Iberian Peninsula is considered only occasional, probably coming from populations in France, and likely coinciding with extreme cold and dry episodes.

The Pleistocene range of the Eurasian wolverine (*G. gulo*) reaches its highest southern boundary in China, at slightly lower latitude than 40°N. The southernmost European occurrences of this mustelid are located in the Iberian and Italian peninsulas and the Caucasus (Kahlke, 1999) between 42° and 43°N. The Iberian finds come from level II of Lezetxiki Cave (Guipúzcoa), dated between about 25 and 23 cal ka BP, and Mairuelegorreta Cave (Álava) of unknown chronology (Altuna, 1972; Altuna and Baldeón, 1986).

The chronology of the finding from Lezetxiki fits into the third episode at which the three previously described species were present in Iberia.

The arctic fox (*A. lagopus*) is a species adapted to colder environments, living today in the tundra and the high arctic ice fields. Its Pleistocene southern spread reaches its maximum in the Iberian Peninsula (43°03′ N), where this species has been identified at three sites from the province of Guipúzcoa: Amalda, Labeko Koba and Aitzbitarte III caves (Altuna, 2004; Altuna and Mariezkurrena,

Table 4
Iberian sites with fossil remains of *Gulo gulo*, *Alopex Lagopus*, *Saiga tatarica* and *Ovibos Moschatus*; and chronology of the finds.

Species	Site	Province	Absolute chronology/ Archaeological context[a]	Source
Gulo gulo				
	Mairuelegorreta	Álava	Unknown	Altuna and Baldeón, 1986
	Lezetxiki	Guipúzcoa	Late Gravettian-Lower Solutrean	Altuna, 1963b, 1972
Alopex lagopus				
	Labeko Koba	Guipúzcoa	35.8 cal ka BP	Altuna and Mariezkurrena, 2000
	Amalda	Guipúzcoa	32.0 cal ka BP	Altuna, 2004
	Aitzbitarte III	Guipúzcoa	24.3; 24,1; 23,5; 22,0 cal ka BP	Altuna, 1992, 2004
Saiga tatarica				
	Abauntz	Navarra	16.4 cal ka BP	Altuna and Mariezkurrena, 1996
Ovibos moschatus				
	Arbreda	Gerona	20.7 cal ka BP	Estévez, 1978; Galobart et al., 1996
	Can Rubau	Gerona	Mousterian	J. Maroto, pers. com., 2007

[a] Calibrated radiocarbon dates as well as more precise information about the chronology is provided in Álvarez-Lao and García, 2010.

2006). Occurrences of the arctic fox at similar latitudes are also identified in Romania (Malez, 1972) and Crimea (Kahlke, 1999).

The three Iberian sites have been radiocarbon dated (Table 4) resulting in a presence of this canid during two periods of the Late Pleistocene. The first one ranges between 32.05 and 35.8 cal ka BP (remains from Amalda and Labeko Koba), and is coincident with the second episode describer for the mammoth, woolly rhinoceros and reindeer. The second episode occurred between 22.2 and 24.3 cal ka BP (remains from Aitzbitarte III), corresponding with the third described episode.

The modern Eurasian geographic distribution of the musk ox (*O. moschatus*) is also essentially arctic, restricted to the tundra. Its southernmost Pleistocene Holarctic spread corresponds to the Iberian Peninsula (42°09′N), where it has been identified in two Catalonian sites at Gerona: the Arbreda cave and Can Rubau site (Estévez, 1978, 1987; Galobart et al., 1996; J. Maroto, pers. com., 2007). At Arbreda cave, Solutrean level radiocarbon dates are between 21.2 and 20.7 cal ka BP (Galobart et al., 1996). At Can Rubau, musk ox remains have been found associated with stone tools tentatively attributed to the Mousterian culture (Maroto, pers. com, 2007; Álvarez-Lao and García, 2010). Romanian musk ox remains reach similar latitude as the Iberian finds (44°32′N) (Malez, 1972; Raufuss and von Koenigswald, 1999). Asiatic finds (Siberia and Kazakhstan) are over 50°N (Kahlke, 1999).

The chronology of the remains from Arbreda fits into the third described episode. The imprecise chronology of Can Rubau findings could broadly corresponds with the second or even with the first episode.

The saiga antelope (*S. tatarica*) is a species adapted to arid environments (steppe). Its geographical distribution during the Pleistocene covered a great extension of Eurasia and also reached North America. In the Iberian Peninsula, only the Abauntz cave (Navarra) has yielded saiga remains which were found into Middle Magdalenian cultural context and radiocarbon dated to 16.4 cal - ka BP (Altuna and Mariezkurrena, 1996). The apparent incompatibility between the environmental conditions of this cave (mountainous) and the typical habitat of this small bovid (flat plains) suggests people likely hunted this animal in the vicinity and subsequently carried it to the Abauntz cave (Altuna and Mariezkurrena, 1996). The most probable area is in southwestern France where abundant appropriate habitat was present during this time (Delpech, 1983).

The southernmost boundary of saiga antelope during the Pleistocene reached latitudes lower than 30°N in the Balkan Peninsula and also in Turkmenistan, where it currently exist today

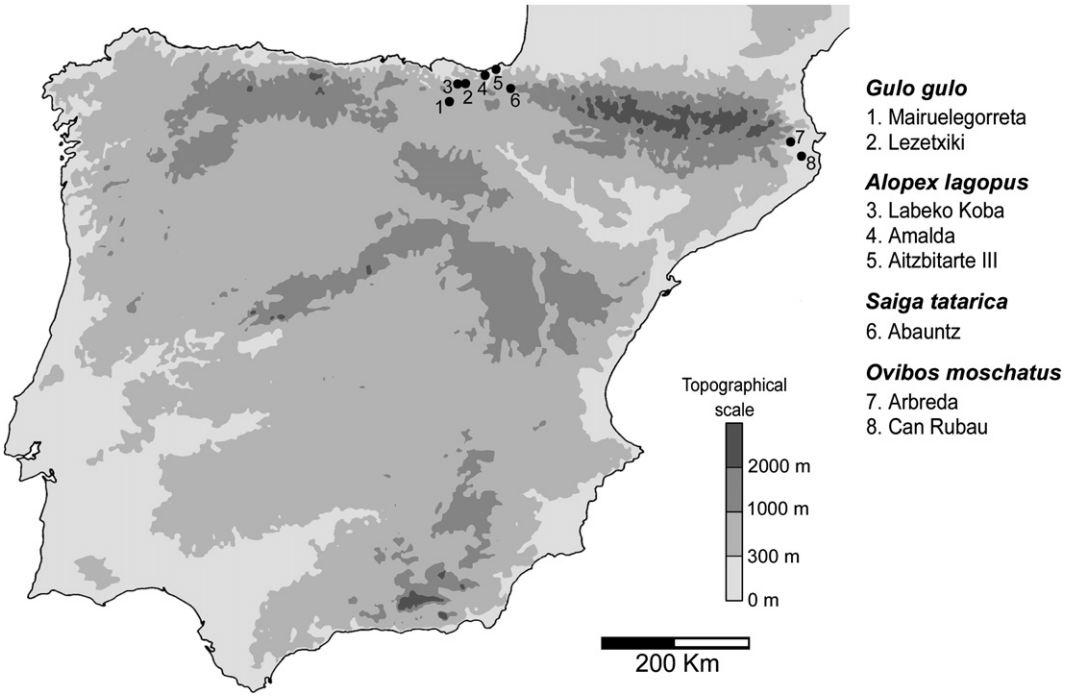

Fig. 6. Situation of the Iberian sites with *Gulo gulo*, *Alopex lagopus*, *Saiga tatarica* and *Ovibos moschatus* remains.

(Kahlke, 1992, 1999; Baryshnikov and Krakhmalnaya, 1994). The chronology of the Abauntz findings corresponds with the third episode describer for the mammoth, woolly rhinoceros and reindeer.

4. Discussion

4.1. Distribution of the Iberian sites with cold-adapted large faunas remains

Remains of cold-adapted large mammals were found in 75 Iberian sites (Fig. 1), 64 of which (85.3%) are placed in the north (Álvarez-Lao, 2007; Álvarez-Lao and García, 2010). Such distribution is in agreement with the geomorphologic context as the Iberian Peninsula is relatively isolated from continental Europe by the Pyrenees which acted as a barrier limiting dispersals. These cold-adapted species, which were abundant in southern France during the Upper Pleistocene (Delpech, 1983), could only enter into the Iberian Peninsula through narrow passes placed east and west of the Pyrenees (Guipúzcoa and Gerona provinces respectively).

Remains of cold-adapted species are rare in central and south Iberia, only 11 sites provided it. These sites are located in only three areas, and are geographically isolated from the northern sites (Álvarez-Lao, 2007; Álvarez-Lao and García, 2010): the provinces of Madrid (Spain), Andalucía (Spain), and at Estremadura (Portugal) (Fig. 1). This fact makes it difficult to ascertain the routes which these mammals used to come from north Iberia.

The faunas coming through the western route found an important topographic barrier, the Cantabrian Mountain Range, which prevented their southward spread. The pathways taken then were the coast and low valleys of the Cantabrian area. The concentration of fossil sites increases near the western margin of the Pyrenees (province of Guipúzcoa) and gradually decreases towards the west (Fig. 1). Nevertheless, the lack of paleontological sites over this time span on the southern slope of the Cantabrian Mountain Range and north of the Castilian plateau must be considered. The geological conditions, with mainly Neogene lacustrine and fluvial sediments, would imply a relevant lack of information that suggests that these faunas never crossed the Cantabrian Mountain Range southward.

The faunas entering into the peninsula through the eastern margin of the Pyrenees dispersed over the flat topography of Catalonian terrains (Gerona and Barcelona provinces). The highest concentration of sites with remains of cold-adapted large mammals was also observed in the area close to the Pyrenees, then decreasing southward (Fig. 1).

The access routes which explain central and south Iberian finds are a complex question and remain uncertain. The Madrid (seven sites) and Padul specimens might have dispersed from east of the Pyrenees southward near the Mediterranean coast, which is topographically even. The specimens recovered in the Portuguese margin (three sites) might have entered from the west, through the Cantabrian area and later southward by the Atlantic coast.

4.2. Description of the access areas to the Iberian Peninsula for the cold-adapted large mammal faunas

The entrance of these faunas into the Iberian Peninsula from southern France is only likely if made through the narrow passes located east and west of the Pyrenees. At the west end of the Pyrenees, the pass (placed around Irún, in Guipúzcoa) is very narrow today, the distance between the coast and the hills higher than 500 m over the sea level, is shorter than 10 km in some places. Nevertheless, during the Late Pleistocene's coldest stages, the ice sheet advances caused a great decrease in eustatic sea level of about 135 m (Clark and Mix, 2002; Jiménez-Sánchez et al., 2006). Consequently, the retreat of the coastline exposed a wide surface of the continental shelf, expanding the width of the pass area to around 20 km (Fig. 7), making the dispersal of the fauna easier.

At the east end of the Pyrenees, the pass area today is even narrower. Elevations of 500 m above sea level are just 5 km from the coast in the area of Creus Cape. The lowering of sea level during the Pleistocene also increased the area of this pass to about 20 km (Fig. 7).

4.3. Distribution of the Iberian sites according to its chronology

The presence of cold-adapted large mammal faunas in the Iberian Peninsula occurred principally during three wide-range episodes (Álvarez-Lao and García, 2010).

a) The oldest and more imprecisely defined of these episodes ranges from approximately 200 to 100 ka BP. The La Parte site (Asturias) was dated to 150 ka BP (Álvarez-Lao and García-García, 2006). The ages for most of the sites from Madrid were estimated around 100 ka (Arsuaga and Aguirre, 1979; Sesé and Soto, 2002). This oldest episode could correspond with more than one event, but the lack of more precise dating does not allow more accuracy. The presence of *M. primigenius* and *C. antiquitatis* was identified at the latitude of the province of Madrid (around 40°N), showing a wide southern spread during this early stage (Fig. 8).

An important gap is detected during MIS 5 and 4, when evidences of these taxa are scarce and imprecise in the Iberian Peninsula (only six finds: one woolly mammoth, one musk ox and four reindeers). Two main episodes of cold and dry environmental conditions are identified from the pollen record and other features registered in the Iberian marine margin during these times, particularly between 65 and 59 ka BP (Roucoux et al., 2005). The most likely explanation is that these finds probably fall within the cold Heinrich events 6 and 5, but there is presently not enough data to confirm this (Álvarez-Lao and García, 2010).

b) In the next episode, between 42 and 31 cal ka BP, the presence of these species in numerous Iberian sites has been registered. The chronology of this episode is well characterized by numerous radiocarbon dates in association with archaeological contexts (Fig. 2). This period corresponds with MIS 3, during which extreme cold and dry conditions alternated with brief mild or warm periods. The brevity of these alternating warm periods supports the latitudinal distribution of the cold faunas as known from the Iberian Peninsula and other Eurasian localities. At this time, the widest geographic distribution of woolly mammoth was registered (Fig. 8), reaching the extreme Iberian south (37°01′01′N) in the site of Padul (Álvarez-Lao et al., 2005, 2009), and the Portuguese Atlantic margin in Figueira Brava site (Antunes and Cardoso, 1992). Woolly rhino and reindeer were frequent during this time span, and arctic fox was detected. Woolly mammoth was the only cold taxon found in southern Iberian sites.

The available chronological data indicate a gap, shorter than the previous one, between 31 and 26 ka BP, which coincides with the nearly complete disappearance of these species in Iberia. The absence of these species during a period that includes the cold and dry H3 event, very favourable for their presence, is difficult to understand. However, it is important to point out that Gravettian technocomplex sites (corresponding to this episode) are less frequently recorded and often not as well defined chronologically as later periods (Álvarez-Lao and García,

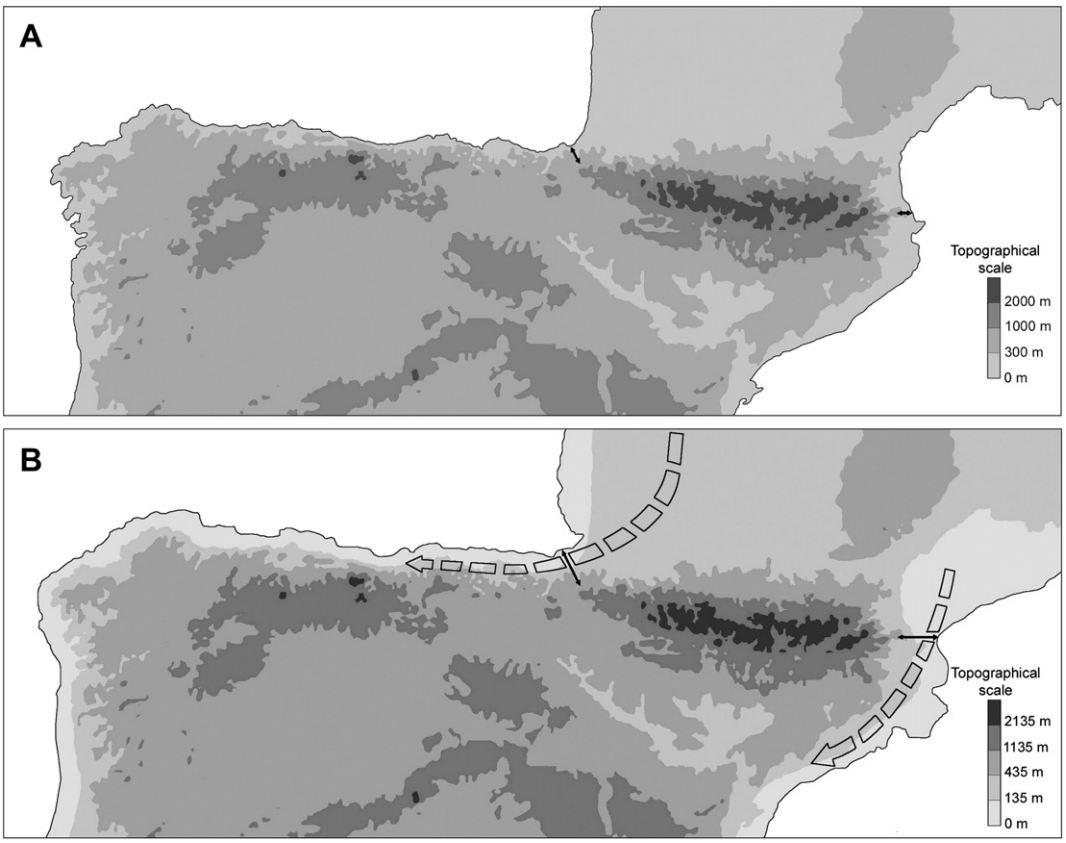

Fig. 7. A. Map of the northern Iberian Peninsula with the current coast configuration showing the narrow passes placed at the west and east of the Pyrenees (indicated by black arrows), with elevations from 0 m (sea shore) to 500 m over the sea level. B. The same map with the supposed coast configuration during the Late Pleistocene coldest episodes (corresponding to the actual isobath of 135 m) showing the extended passes at the west and east of the Pyrenees (little black arrows), with elevations from 0 to around 500 m. The discontinuous empty arrows indicate the access ways for the large mammal faunas from mainland Europe.

2010). As well, not all the Iberian finds of these species are dated, so some of these undated finds could belong to this time.

c) The last episode, which has an abundant and chronologically well defined fossil record, is framed during MIS 2. The highest number of finds of all these taxa is restricted to north Iberian localities, dated between 25 and 18 cal ka BP, and corresponding with the LGM (Fig. 8). All of the cold adapted taxa identified are present in Iberia at this time. Reindeer survives until the Younger Dryas (YD) cold event (between 12.7 and 11.3 ka BP) in several north Iberian sites and survival extends after this event (Álvarez-Lao and García, 2010), with a last occurrence in Santa Catalina cave (Guipúzcoa), dated to 10.3 cal ka BP (Elorza, 2005; P. Castaños, pers. com., 2006).

5. Conclusions

Presence of the cold-adapted mammal species *M. primigenius*, *C. antiquitatis*, *R. tarandus*, *G. gulo*, *A. lagopus*, *O. moschatus* and *S. tatarica*, has been reported at 75 Iberian sites, most of them located in the north and only a few in the Iberian center and south. This distribution was determined by geographical features of the Iberian Peninsula, most of the cases due to presence of mountain ranges

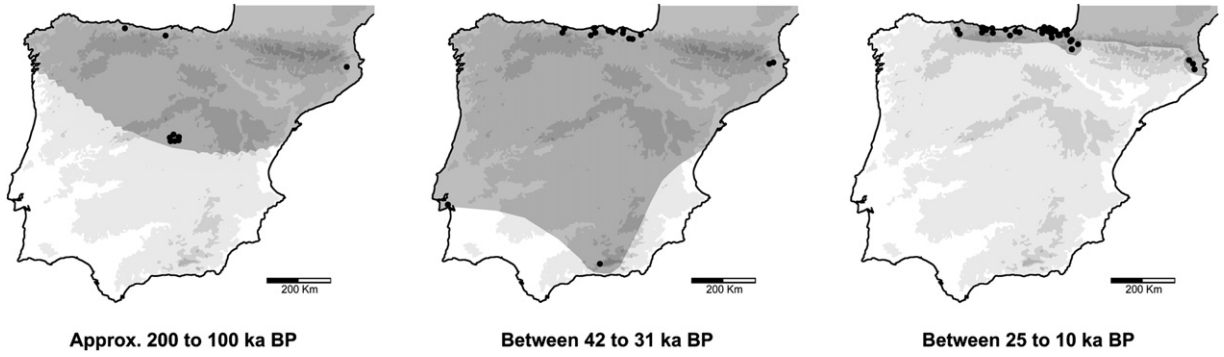

Fig. 8. Geographical distribution of the Iberian sites with cold-adapted large mammal remains and estimated distribution of these faunal complex (in grey background), during each of the three described main moments. This distribution can be indicative of the spread of the steppe-tundra biotope throughout the Iberian Peninsula during the coldest stages of the Pleistocene.

which acted as barriers. Entrance of cold-adapted faunas from continental Europe occurred by narrow passes placed east and west of the Pyrenees. Although these areas currently are narrow they were much wider during the coldest stages of the Pleistocene. Moreover, these corridors were topographically low, being near sea level, and would thus be ideal areas for these mammals to pass. Spread of these faunas into central and southern Iberia is not clear, but it was likely related with low relief areas.

The coldest and most arid episodes of the Pleistocene, therefore, favoured the entrance of cold-adapted large mammal faunas into the Iberian Peninsula in two ways: 1) the southward spread of the studied populations helped fauna to avoid the extremely cold and inhospitable conditions of northern Europe; and 2) the expansion of the access areas needed for dispersal allowed the large mammals to overcome a major geographic barrier (i.e., Pyrenees mountain range).

Occurrences of this faunal complex into the Iberian Peninsula were stated in, at least, three episodes from approximately 200 to 10 ka BP corresponding mostly to the coldest periods of the Late Pleistocene (Álvarez-Lao and García, 2010). The geographic distribution of these species changed among each episode. During the oldest episode, between about 200 and 100 ka BP, woolly mammoth and woolly rhinoceros populations expanded southward until 40°N. The maximum southern spread occurred between 42 and 31 cal ka BP, when the woolly mammoth reached the latitude 37°01′N (Álvarez-Lao et al., 2009). During the latest episode (25–10 cal ka BP), cold-adapted large mammals were only detected in the Iberian north (Cantabrian area and Catalonia, over 42–43°N).

The available data are insufficient for some areas, especially in the center of the peninsula (the Castilian Plateau), where the lack of Late Pleistocene fossil assemblages hinders obtaining a precise knowledge of the distribution and dispersal corridors of cold-adapted fauna. A gap in late Middle and early Late Pleistocene findings from the northern sites also is observed, where the majority of the deposits correspond to the second half of the Late Pleistocene (mainly to MIS 3 and MIS 2).

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