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

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ABSTRACT

During the coldest episodes of the Late Pleistocene, the cold-adapted large mammal faunas moved southward, reaching southern regions such as the Iberian Peninsula. Thus, during the Late Pleistocene, remains of *Mammuthus primigenius, Coelodonta antiquitatis* and *Rangifer tarandus* were found in Iberia. In addition, four other cold-adapted species (*Gulo gulo, Alopex lagopus, Ovibos moschatus* and *Saiga tatarica*) were present, although in very low proportions. All published chronologies from these Iberian findings, as well as new radiocarbon dates, were compiled and subsequently correlated with the published paleoclimatic information for the Iberian Late Pleistocene.

These cold-adapted faunas were present in the Iberian Peninsula from at least the late Middle Pleistocene (MIS 6), and several findings, although chronologically imprecise, were dated to the first half of the Late Pleistocene. After about 44 ka BP, these faunas became relatively abundant on the Iberian Peninsula. However, there is a chronological gap between 31 and 26 ka, in which these faunas were practically absent in Iberia. Subsequently, during MIS 2, the presence of these species was again well documented. The last Iberian occurrences of most of these species have been registered during the LGM, except the reindeer, that survived until the end of the Younger Dryas. The chronology of the Iberian findings of cold-adapted large mammal faunas is consistent with the paleoclimatical evidence provided by other sources.

1. Introduction

The Iberian Peninsula constituted one of the southernmost limits of the steppe-tundra expanse during the Pleistocene. The cold-adapted large mammals, also known as *Mammuthus–Coelodonta* faunal complex (Kahlke, 1999), that were common in a wide area of Eurasia during the Late Pleistocene, reached the Iberian Peninsula in the coldest time periods. In the peninsular fossil record, the presence of these cold-adapted mammal faunas is occasional and restricted to specific time spans and, in most cases, to specific geographical areas.

Since the mid-19th century a number of works regarding Iberian findings of cold-adapted large mammals have been published (Leith Adams, 1877; Harlé, 1912; Altuna, 1966, 1972; Altuna and Mariezkurrena, 2000, 2006). Nevertheless, radiocarbon dates have only been carried out on part of them. Furthermore, most of these works deal with only one site or one restricted geographical area. Compilation works were previously carried out by Altuna (1996) and García and Arsuaga (2003). These authors stated that the presence of cold-adapted large mammals in the Iberian Peninsula was very scant and, although the findings were widely distributed over the Peninsula, most of them were located in the north and were mainly restricted to the Upper Pleistocene. In the present paper additional radiocarbon dates which update and complete this information are provided. These chronologies have been correlated with the published paleoclimatic knowledge of the Iberian Late Pleistocene.

Over the last few decades several detailed paleoclimatic works were carried out from Iberian records on the basis of the study of diverse features. One of the main sources of information is the pollen record that provides outstanding knowledge about the vegetation cover and, therefore, the environmental conditions, in a certain geographical area and period. Pollen analysis were carried out in Iberian marine records (Roucoux et al., 2001, 2005; Turon et al., 2003; Sánchez Goñi and d'Errico, 2005) as well as in continental ones (Florschütz et al., 1971; Pons and Reille, 1988; García-Ruiz et al., 2002; Jiménez Sánchez et al., 2003; Moreno et al., 2005;

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González-Sampériz et al., 2006; Moreno et al., 2007). The climatic oscillations were also recorded in the Iberian marine margin by the variation of isotopes, marine organisms (Turon et al., 2003) and the presence of ice rafted detritus (IRD) (Roucoux et al., 2005).

From the above-mentioned works it can be stated that the coldest time spans are characterized in Iberian pollen records by the southern spread of steppe taxa (mainly *Artemisia, Ephedra* and Chenopodiacidae) and a strong decrease in tree pollen proportions. In marine records, high proportions of cold affinity organisms and IRD have also been detected. The warmer episodes were characterized by reduction in pollen of steppe taxa and increase of arboreal taxa. This is a general pattern for the areas where the fossil remains studied in this work were found. However, at lesser scale, there were detected several glacial refugia areas where temperate and Mediterranean vegetation remained, especially in South Iberia (Carrión, 2002; Carrión et al., 2003; Finlayson et al., 2008).

According to the cited papers, climatic oscillations during the Upper Pleistocene in Iberia are in agreement with the sequence of oscillations recorded in the Greenland ice cores GRIP and GISP 2 (Dansgaard et al., 1993; Grootes and Stuiver, 1997), considered of global validity. The coldest Late Pleistocene episodes in Iberia corresponds with the Heinrich events (H1–H6), the Last Glacial Maximum (LGM) and the Younger Dryas (YD), whereas the warmest moments correspond with the interstadials.

On the basis of the cited references, the following climatic evidence for the marine isotope stages MIS 2 and MIS 3 in the Iberian Peninsula can be established: (a) the MIS 3 (from 60 to 23 ka) is characterized in the Iberian records by strong oscillations of extreme cold episodes with brief warm episodes. Steppe environments extended widely in Iberia during the most of this stage; (b) during MIS 2 (between about 23 and 12 ka) the climate in Iberia was very cold and arid, with long periods of steppe landscape predominance. The great climatologic oscillations recorded during the MIS 3 are not present at this time; and (c) the last cold oscillation, known as Younger Dryas (between about 11.3 and 12.7 ka), is also well documented in Iberian paleoclimatic records.

2. Materials and methods

The selected taxa are mainly the following species: woolly mammoth (*Mammuthus primigenius*), woolly rhino (*Coleodonta antiquitatis*) and reindeer (*Rangifer tarandus*), and represent the most abundant cold-adapted large mammals during the Iberian Late Pleistocene. Four other species, scarcely represented in Iberia, were also considered in this work: wolverine (*Gulo gulo*), arctic fox (*Alopex lagopus*), musk ox (*Ovibos moschatus*) and saiga antelope (*Saiga tatarica*).

These taxa come from 76 Iberian sites, 65 of them from the North (Galicia, Asturias, Cantabria, Basque Country and Catalonia), and the rest from the center (Madrid, Estremadura) and South (Granada) (Álvarez Lao, 2007).

An exhaustive compilation of all published radiocarbon dates from Iberian findings of these taxa was carried out in order to approach a chronologic view to delimit in which moments the Iberian Peninsula worked as a refuge area for these cold-adapted faunas (Tables 1 and 2). Some of the dates, still unpublished, were kindly provided by Drs. Mario Menéndez, Pedro Castaños and Julià Maroto. Five new radiocarbon dates are also provided from woolly mammoth remains coming from Padul (Granada) and Pámanes (Cantabria).

All the radiocarbon dates have been calibrated by means of the CalPal program to 1σ (68% range), in order to obtain calendar ages that could be correlated with the paleoclimatic scale GRIP. Therefore, all the radiocarbon dates are also expressed in calBP years (calendar years before present). All radiocarbon and calendar dates are detailed in Table 1 and represented in Fig. 1. The location of the sites mentioned in the text is represented in Fig. 2.

About half of the cold-adapted large mammal remains have not been radiocarbon dated, although the archaeological context can provide an estimate of the time range for most of them (Table 2 and Fig. 1). These dates should be used with caution since the degree of accuracy varies, but are more reliable for more recent times. Thus, the findings associated with a "Mousterian technocomplex" encompass a large time span (80 ka or considerably more, depending on the authors) (Rodríguez Asensio, 2001; Arrizabalaga, 2005), and are of low reliability. In contrast, younger findings, such as those during the Upper Magdalenian period, encompass more restricted time spans (3 kyr) (Adán, 1997), and provide a relative high reliability.

Although the accepted chronological limits of the "technocomplexes" may differ slightly among researchers and geographical areas, we have relied on the time spans inferred for each "technocomplex" in northern Iberia (Cantabrian Mountain Range and Catalonia) (De La Rasilla, 1994; Adán, 1997; Arrizabalaga, 2000, 2005; Rodríguez Asensio, 2001; Cabrera Valdés et al., 2002; Maroto et al., 2005), as most of the sites are concentrated in this region.

3. Results

3.1. Chronological distribution of Mammuthus primigenius

Woolly mammoth remains have been discovered in 24 sites on the Iberian Peninsula (Álvarez Lao, 2007; Álvarez-Laó and García, 2007). In most of the sites molar remains and tusk fragments were the predominant specimens recovered. However, at the Padul site (Granada) several cranial and postcranial elements were also recovered (Álvarez-Laó et al., 2005).

Among the Iberian sites with woolly mammoth remains, 12 of them yielded chronologies based on radiocarbon dates or in connection with archaeological context (Tables 1 and 2). The chronological distribution of these remains is detailed in Fig. 1.

The first presence of woolly mammoth in the Iberian Peninsula is uncertain, but seems to correspond with the end of the Middle Pleistocene or the first episodes of the Late Pleistocene (Sesé and Soto, 2002). The mammoth findings coming from Madrid province have an imprecise chronology. None of them have radiocarbon values, and in all cases, the age is estimated by stratigraphic correlations indicating ages, of likely late Middle Pleistocene (Casa Eulogio and Arriaga) or early Late Pleistocene (Aldehuela) (Sesé and Soto, 2002). The recent findings of Butarque and Edar Culebro have an approximate age of about 100 ka, based in stratigraphic correlations (S. Bárez and J. Yravedra pers. com., 2006). Some of these specimens (Aldehuela, Arriaga, Butarque) show primitive features, which is in agreement with the estimated age (Álvarez Lao, 2007). The lack of accuracy does not allow any palaeoenvironmental correlation. A woolly mammoth molar plate was found in a Mousterian level dated between 50 and 60 ka, in l'Arbreda cave (Gerona) (J. Maroto, pers. com., 2007).

The 12 previous cited woolly mammoth dates belong to the second half of the Late Pleistocene. On the basis of these chronologies, is possible to identify two moments at which the presence of the woolly mammoth in the Iberian Peninsula has been stated. The first occurrences are approximately recorded between 30 and 43 calBP ka, with higher density of findings between 33 and 40 calBP ka. Five *Mammuthus primigenius* Iberian findings belong to this time span, all of them radiometrically dated. Padul (Granada) is the southernmost European locality (37° 01′ N) with presence of woolly mammoth remains (Álvarez-Lao et al., 2005). Four dates obtained from different specimens from Padul yielded chronologies that cover a wide chronological span: 30.6, 33.5, 38.6 and 40.4 ka

Table 1
Numerical chronologies and calendar data of Iberian cold-adapted large mammal findings.

Site – level	Province	Taxa	^{14}C years BP	Source	CalBP years and 68% range
Las Caldas – IV	Asturias	Rt.	13,400 ± 150	(2), (3)	15,918 (16,171–15,635)
Las Caldas – 4	Asturias	Mp.	17,050 ± 290	(2), (3)	20,405 (19,910–20,900)
Las Caldas – 3	Asturias	Mp.	18,200 ± 260	(2), (3)	21,878 (21,470–22,285)
Cueto de la Mina – E	Asturias	Mp. Rt.	19,700 ± 500	(4), (5)	23,577 (22,930–24,223)
La Güelga	Asturias	Mp.	>30,210 < 32,000	(28)	>34,407 < 36,809
La Parte – Inf.	Asturias	Ca. Rt.		(6), (7)	188,497 ± 11,000*
La Parte – Inf.	Asturias	Ca. Rt.		(6), (7)	141,479 ± 8500*
La Riera – 24	Asturias	Rt.	10,830 ± 430	(9), (10)	12,579 (12,022–13,136)
La Riera – 22	Asturias	Rt.	>12,360 < 12,620	(9), (10)	>14,100 < 14,800
Tito Bustillo – 1b	Asturias	Rt.	14,930 ± 70	(3), (11)	18,220 (17,977–18,463)
Covacho Arenillas – II	Cantabria	Ca.	33,780 ± 1700	(12)	38,437 (36,384–40,490)
Covacho Arenillas – II	Cantabria	Ca.	34,660 ± 1600	(12)	39,108 (37,223–40,903)
Pámanes	Cantabria	Mp.	21,255 ± 240	(1)	25,420 (25,013–25,826)
Pámanes	Cantabria	Mp.	23,050 ± 305	(1)	27,601 (27,103–28,098)
Santa Catalina – I	Vizcaya	Rt.	9100	(29), (13)	10,300
Santa Catalina – III	Vizcaya	Rt.	12,400	(29), (13)	14,400
Aitzbitarte III – V	Guipúzcoa	Al.	18,400 ± 215	(14)	22,025 (21,662–22,388)
Aitzbitarte III – V	Guipúzcoa	Al.	19,715 ± 234	(14)	23,557 (23,119–23,994)
Aitzbitarte III – V	Guipúzcoa	Al.	20,290 ± 260	(14)	24,111 (23,713–24,509)
Aitzbitarte III – V	Guipúzcoa	Al.	20,405 ± 130	(14)	24,346 (24,025–24,666)
Aitzbitarte III – VI	Guipúzcoa	Rt.	23,830 ± 345	(31)	28,751 (28,274–29,228)
Aitzbitarte III – VI	Guipúzcoa	Rt.	24,545 ± 415	(31)	29,353 (28,704–30,001)
Aitzbitarte III – VI	Guipúzcoa	Rt.	25,380 ± 330	(31)	30,326 (29,879–30,773)
Amalda – IV	Guipúzcoa	Rt. Al.	27,400 ± 1000	(15)	32,056 (31,102–33,009)
Kiputz IX – D	Guipúzcoa	Rt.	14,360 ± 130	(16)	17,524 (17,256–17,792)
Kiputz IX – D	Guipúzcoa	Rt.	15,590 ± 50	(16)	18,854 (18,653–19,055)
Kiputz IX – F	Guipúzcoa	Rt.	19,870 ± 150	(16)	23,806 (23,469–24,142)
Labeko Koba – V	Guipúzcoa	Mp. Rt.	30,615 ± 820	(17), (18)	34,913 (34,155–35,670)
Labeko Koba – VII	Guipúzcoa	Mp. Ca. Al.	31,455 ± 915	(17), (18)	35,790 (34,800–37,139)
Labeko Koba – IX sup.	Guipúzcoa	Mp. Ca. Rt.	>31,455 < 34,215	(17), (18)	>35,790 < 38,906
Labeko Koba – IX inf.	Guipúzcoa	Rt.	34,215 ± 1265	(17), (18)	38,906 (37,204–40,607)
Urtiaga – F	Guipúzcoa	Rt.	17,050 ± 140	(19)	20,387 (19,993–20,780)
Abauntz – 2r	Navarra	Rt.	11,760 ± 90	(20), (21)	13,643 (13,492–13,794)
Abauntz – 2r	Navarra	Rt.	12,340 ± 160	(20), (21)	14,534 (14,117–14,951)
Abauntz – E	Navarra	Rt. St.	13,500 ± 160	(20), (21)	16,413 (15,960–16,875)
Leguintxiki – IIb	Navarra	Ca.	17,000	(12)	20,279 (19,969–20,589)
L'Arbreda – C	Gerona	Rt. Om.	17,320 ± 290	(22)	20,764 (20,335–21,192)
L'Arbreda – D	Gerona	Rt.	17,720 ± 290	(22), (23)	21,225 (20,711–21,739)
L'Arbreda – H	Gerona	Mp.	38,500 ± 1000	(22), (23)	42,791 (42,140–43,801)
Bora Gran	Gerona	Rt.	11,470 ± 500	(22)	13,526 (12,914–14,138)
Mollet	Gerona	Rt.		(24), (30)	200,000*
Padul	Granada	Mp.	25,680 ± 610	(25)	30,606 (29,932–31,279)
Padul	Granada	Mp.	29,335 ± 990	(1)	33,564 (32,711–34,417)
Padul	Granada	Mp.	33,855 ± 1215	(1)	38,655 (36,895–40,414)
Padul	Granada	Mp.	35,790 ± 960	(1)	40,467 (38,281–41,653)
Figueira Brava – 3	Estremadura	Mp.	30,050 ± 500	(26), (27)	34,227 (33,796–34,657)
Figueira Brava – 2	Estremadura	Mp.	30,930 ± 700	(26), (27)	35,174 (34,512–35,835)

All the provinces are Spanish, except Estremadura, that belongs to Portugal. Taxa abbreviations: Mp.- *Mammuthus primigenius*; Ca.- *Coelodonta antiquitatis*; Rt.- *Rangifer tarandus*; Al.- *Alopex lagopus*; Om. *Ovibos moschatus*; St.- *Saiga tatarica*. The dates signed with * have been carried out by means of U-Th series. Sources: (1) Own data; Álvarez-Laó and García-García (2) Corchón, 1991–1992; (3) Adán, 1997; (4) Stuart et al., 2002; (5) Castaños, 1982; (6) Álvarez Laó et al., 2002; (7) Álvarez-Laó and García-García, 2006; (9) Strauss and Clark, 1986; (10) Altuna, 1986; (11) Moure Romanillo, 1990; (12) Castaños, 1996; (13) Elorza, 2005; (14) Altuna and Mariezkurrena, 2006; (15) Altuna, 2004; (16) Castaños et al., 2006; (17) Arrizabalaga, 2000; (18) Altuna and Mariezkurrena, 2000; (19) Altuna, 1972; (20) Altuna et al., 2001–2002; (21) Altuna and Mariezkurrena, 1996; (22) Galobart et al., 1996; (23) Maroto et al., 1996; (24) Solés and Maroto, 2002; (25) García and Arsuaga, 2003; (26) Sousa and Figueiredo, 2001; (27) Antunes and Cardoso, 1992; (28) Mario Menéndez, pers. com., 2006; (29); Pedro Castaños pers. com., 2006; (30) Julià Maroto pers. com., 2007; (31) Altuna, 1992.

(all calBP ka). These dates show woolly mammoth presence during a long time span in that area. This could be interpreted as an isolated population living continuously during that long period or, more likely, as an intermittent presence according to the succession of cold and warm periods. The first and second of these dates occurred during an extreme cold period, the H4 event (Fig. 1). The third and fourth of them correspond with cold episodes within MIS 3. Another southern site, Figueira Brava (Estremadura, Portugal), provided two radiocarbon dates of 30.05 and 30.9 ka (34.2 and 35.1 calBP ka) (Antunes and Cardoso, 1992) on proboscidean samples, most probably woolly mammoth (although without absolute certainty). These dates are chronologically placed between H3 and H4 events, into a period in which extreme cold episodes alternate with brief warmer moments. Two archaeological levels with woolly mammoth remains from Labeko Koba cave (Guipúzcoa) yielded ages of 34.9 and 35.8 calBP ka (Altuna and Mariezkurrena, 2000), and another mammoth finding from this place has been dated between 35.8 and 38.9 calBP ka. These dates are also placed between H3 and H4, but closer to this last event. The mammoth molar fragment from La Güelga site also has a similar age (Mario Menéndez, pers. com., 2006).

A proboscidean ivory fragment from L'Arbreda cave (Gerona) comes from a level radiocarbon dated at 38.5 ka (42.7 calBP ka) (Maroto et al., 1996). This piece is not taxonomically diagnostic and given the age, it could correspond either to the species *Mammuthus primigenius* or to *Paleoloxodon antiquus*. Nevertheless, the radiocarbon age falls close to the H5 cold event, and it might be cautiously interpreted as belonging to the former species.

The second episode with presence of woolly mammoth in Iberia is clear, and it ranges approximately between 28 and 18 calBP ka. This time span includes the Heinrich event 2 and a great part of the Last Glacial Maximum, and therefore, it corresponds with a cold

Table 2
Chronologies of Iberian cold-adapted large mammal findings associate to archaeological contexts.

Site – level	Province	Taxa	Archaeological context	Source	Likely age (calBP ka)
Las Caldas – XI	Asturias	Mp.	Lower Magdalenian	(1)	20.2–17.6
El Cierro – 6	Asturias	Mp.	Solutrean	(2)	24.8–20.2
Cueto de la Mina – B	Asturias	Rt.	Upper Magdalenian	(3)	15.6–12.4
Cueto de la Mina – H	Asturias	Rt.	Aurignacian	(3)	42.5–32
La Lloseta	Asturias	Mp.	Lower Magdalenian	(4)	20.2–17.6
La Paloma – 8	Asturias	Rt.	Lower Magdalenian	(5)	20.2–17.6
Altamira	Cantabria	Rt.	Upper Solutrean	(6)	22.9–20.2
El Castillo – 26	Cantabria	Rt.	Acheulean	(7), (8)	>120?
El Castillo – 14	Cantabria	Rt.	Aurignacian	(7), (8)	42.5–32
El Castillo – 10	Cantabria	Rt.	Solutrean	(7), (8)	24.8–20.2
El Castillo – 8	Cantabria	Rt.	Lower Magdalenian	(7), (8)	20.2–17.6
El Castillo – 6 and 7	Cantabria	Rt.	Middle Magdalenian	(7), (8)	17.6–15.6
Cobalejos – J	Cantabria	Rt.	Late Moust. to Lower Aurign.	(9)	44–40
El Cuco	Cantabria	Ca.	Gravetian	(24)	32–28.1
Morín – 2	Cantabria	Rt.	Upper Magdalenian	(10), (11)	15.6–12.4
Morín – 4	Cantabria	Mp.	Gravettian	(10), (11)	32–24.8
Valle	Cantabria	Rt.	Upper Magdalenian	(12)	15.6–12.4
Armiña	Vizcaya	Rt.	Magdalenian	(7), (13)	20.2–12.4
Axlor – III, IV	Vizcaya	Rt.	Mousterian	(11), (14)	About 120–42.5
Lumentxa – IV	Vizcaya	Rt.	Late Magdalenian	(15)	13.5–12.4
Lumentxa – V	Vizcaya	Rt.	Upper Magdalenian	(15)	15.6–13.5
Santimamiñe – VI	Vizcaya	Rt.	Magdalenian	(15)	20.2–12.4
Santimamiñe – VII	Vizcaya	Rt.	Solutrean	(15)	24.8–20.2
Santimamiñe – VIII	Vizcaya	Rt.	Aurignacian	(15)	42.5–32
Aitzbitarte IV	Guipúzcoa	Rt.	Late Magdalenian.	(11), (16)	13.5–12.4
Aitzbitarte IV	Guipúzcoa	Rt.	Middle–Upper Solutrean	(11), (16)	23.9–20.2
Amalda – IV	Guipúzcoa	Rt.	Solutrean	(17), (18)	24.8–20.2
Ekain – VI	Guipúzcoa	Rt.	Late Magdalenian	(19)	13.5–12.4
Ermittia	Guipúzcoa	Rt.	Middle Magdalenian	(11), (13)	17.6–15.6
Ermittia	Guipúzcoa	Rt.	Solutrean	(11), (13)	24.8–20.2
Erralla – III	Guipúzcoa	Rt.	Late Magdalenian.	(20)	13.5–12.4
Erralla – V	Guipúzcoa	Rt.	Lower Magdalenian.	(20)	20.2–17.6
Lezetxiki – II	Guipúzcoa	Ca. Gg.	Late Gravett.–Lower Solutr.	(13)	25–23
Lezetxiki – IIIa	Guipúzcoa	Ca. Rt.	Upper Aurignacian	(11), (13)	32–34
Lezetxiki – IIIb	Guipúzcoa	Rt.	Aurignacian	(11), (13)	40–34
Lezetxiki – IVc	Guipúzcoa	Rt.	Proto Aurignacian	(11), (13)	42.5–40
Torre	Guipúzcoa	Rt.	Late Magdalenian	(11), (13)	13.5–12.4
Urtiaga – D	Guipúzcoa	Rt.	Late Magdalenian	(11), (13)	13.5–12.4
Urtiaga – E	Guipúzcoa	Rt.	Upper Magdalenian	(11), (13)	15.6–13.5
Abauntz – f	Navarra	Ca. Rt.	Solutrean	(21)	24.8–20.2
Abauntz – g	Navarra	Rt.	Mousterian	(21)	About 120–42.5
Zatoya – IIb	Navarra	Rt.	Upper Magdalenian	(22)	15.6–12.4
L'Arbreda – 36	Gerona	Rt.	Mousterian	(25)	About 80–60
Can Rubau	Gerona	Rt. Om.	Mousterian	(25)	About 120–42.5
Cau les Goyes	Gerona	Mp.	Solutrean	(7)	24.8–20.2
Reclau Viver	Gerona	Rt.	Aurignacian	(23)	32–24.8

All the provinces are Spanish. Taxa abbreviations: Mp.- *Mammuthus primigenius*; Ca.- *Coelodonta antiquitatis*; Rt.- *Rangifer tarandus*; Gg.- *Gulo gulo*; Om. *Ovibos moschatus*. Sources: (1) Corchón, 1991–1992; (2) Corchón, 1999; (3) Castaños, 1982; (4) Álvarez Lao, 2007; (5) Castaños, 1980; (6) Altuna and Strauss, 1976; (7) Obermaier, 1925; (8) Cabrera, 1984; (9) Castaños, 2005; (10) Altuna, 1971a; (11) Altuna, 1971b; (12) Harlé, 1912; (13) Altuna, 1972; (14) Altuna, 1980; (15) Castaños, 1984; (16) Altuna, 1963; (17) Altuna, 1990; (18) Altuna, 2004; (19) Altuna and Mariezkurrena, 1984; (20) Altuna and Mariezkurrena, 1985; (21) Altuna et al., 2001–2002; (22) Mariezkurrena and Altuna, 1989; (23) Maroto et al., 1996; (24) Castaños and Castaños, 2007; (25) Julià Maroto, pers. com., 2007.

and dry period with steppe landscapes extending widely in the Iberian Peninsula. Eight of the Iberian findings of woolly mammoth remains belong to this time span, of which three are radiocarbon dated. The other five are in connection with archaeological contexts belonging to the Late Gravettian, Solutrean and Lower Magdalenian technocomplexes. One mammoth molar fragment coming from Cueto de La Mina (Asturias) has yielded a radiocarbon age of 19.7 ka (Stuart et al., 2002) which corresponds with 23.5 calBP ka and falling exactly into the H2 event. Two radiocarbon analysis made on the same mammoth specimen from Pámanes (Cantabria) (and in the same laboratory), yielded different dates: 25.4 and 27.6 calBP ka. This difference shows that radiocarbon dates can show a moderate degree of variability. Such dates correspond with the predominant cold period between H2 and H3. The youngest Iberian remains of *Mammuthus primigenius* were found in the caves of Las Caldas, Asturias (Corchón, 1991–1992) and La Lloseta, Asturias (Álvarez Laó, 2007), both in connection with Lower Magdalenian archaeological context, chronologically, into the LGM.

3.2. *Chronological distribution of* Coelodonta antiquitatis

Although there are 21 Iberian sites with presence of the woolly rhino (Álvarez Lao, 2007), absolute dates or archaeological context are known for only seven of these. The earliest evidence for the presence of this species in the Iberian Peninsula is found at the site of La Parte (Asturias) where *Coelodonta antiquitatis* remains are associated with a level radiometrically dated (by $^{234}U/^{230}Th$ method) to 188.5–141.4 ka, with a likely age of around 150 ka BP (MIS 6) (Álvarez Laó et al., 2002; Álvarez-Laó and García-García, 2006). Although the finds at Arroyo Culebro (Madrid) (Arsuaga and Aguirre, 1979) lack absolute dates, the association with Lower Palaeolithic tools could indicate a late Middle Pleistocene or early Late Pleistocene chronology. The rest of the dated findings correspond to the second half of the Late Pleistocene (Fig. 1).

Based on the radiocarbon dating of three of these finds (Table 1), at least two episodes with presence of woolly rhino in Iberia are detected during MIS 2 and 3. The first episode covers about

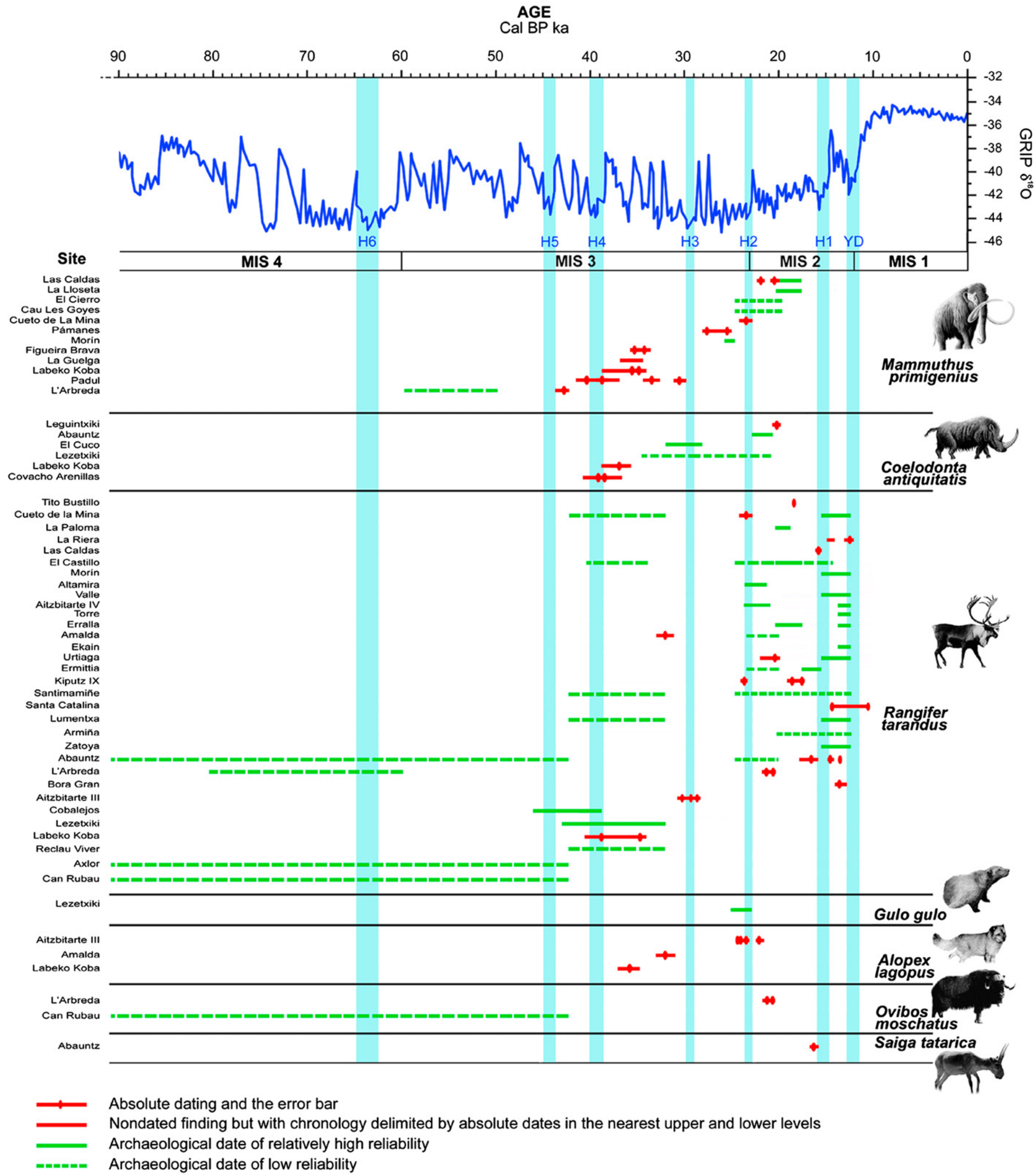

Fig. 1. Chronological distribution of the Late Pleistocene Iberian cold-adapted large mammal finds compared to the GRIP paleoclimatic oxygen curve and the marine isotope stages (MIS). The vertical blue bands indicate the main cold episodes: Heinrich events and YD.

36–41 calBP ka, coinciding with or very close to the H4 cold event, and includes two sites: (a) Labeko Koba (Guipúzcoa), where woolly rhino remains have been found in two levels (Altuna and Mariezkurrena, 2000), one of them dated at 31.4 ka (35.7 calBP ka) and other between 31.4 and 34.2 ka (35.7–38.9 cal BP ka); and (b) Covacho de Arenillas (Cantabria) with two radiocarbon dates of 33.7 and 34.6 ka (38.4 and 39.1 calBP ka) obtained on the level with woolly rhino remains (Castaños, 1996).

The second episode with occurrence of woolly rhino in the Iberian Peninsula is detected between 32 and 20 ka, a period that

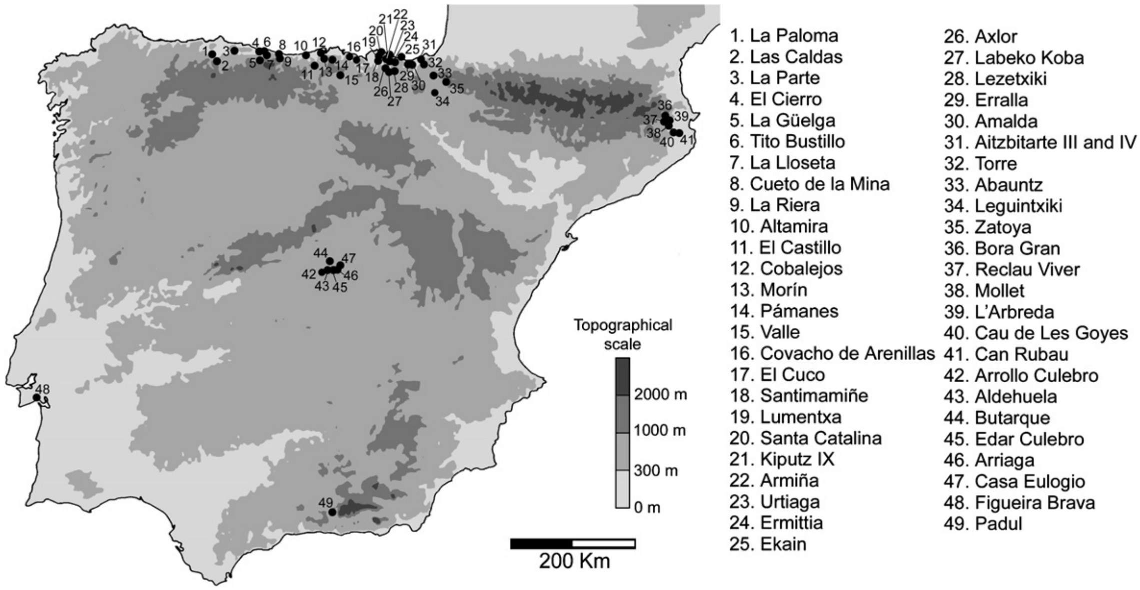

Fig. 2. Geographical situation of the paleontological and archaeological sites cited in the text and tables.

covers the H3, H2 and LGM cold events, during the great expansion of steppe environments. The Gravettian–Solutrean archaeological levels assigned by Altuna (1972) at the site of Lezetxiki (Basque Country) contain woolly rhino remains, and would also coincide with this time span, although no absolute dates were obtained. The specimen from Cueva del Cuco (Cantabria), was found in a Gravettian context just below a level dated to 28.1 calBP ka (Castaños and Castaños, 2007), corresponding to the H3 event.

The remains from Leguintxiki (Navarra), dated to 20.2 calBP ka (Castaños, 1996) and the fossils from Abauntz (Navarra), associated with Upper Solutrean industries (Altuna et al., 2001–2002) are the most recent dates of woolly rhino on the Iberian Peninsula.

3.3. *Chronological distribution of* Rangifer tarandus

The reindeer is the most common cold-adapted large mammal species found in Iberian Pleistocene sites, occurring at 41 sites, and most of the remains are in archaeological context. Forty one fossil remains, coming from 33 localities (Fig. 1), have yielded numerical dates or are in archaeological context (Álvarez Lao, 2007).

The oldest reindeer occurrence in the Iberian Peninsula corresponds to three localities placed in the Middle Pleistocene. In Mollet cave (Gerona), a reindeer molar has been dated to 200 ka (J. Maroto pers. com., 2007), constituting the oldest Iberian reindeer finding. La Parte site (Asturias) has been radiometrically dated to about 150 ka (Álvarez Laó et al., 2002; Álvarez-Laó and García-García, 2006), within the MIS 6 cold stage. Some remains of this cervid were found in the lowest levels of El Castillo cave (Cantabria), along with Acheulean tools (Obermaier, 1925; Cabrera, 1984). If the cultural context is assumed as an estimated age for the fossils, then these should be older than 120 ka, perhaps contemporary with the La Parte site.

There are four reindeer finds coming from Mousterian archaeological contexts, most of them without additional chronological details. Given that the Mousterian culture covers a wide chronological range (between about 120 and 42 calBP ka, depending on the author), and includes at least two cold events (H5 and H6), is not possible to reliably estimate their chronology.

Additional reindeer remains from nine sites were dated to between 41 and 31 calBP ka (MIS 3). Two of them are radiocarbon dated, while the rest come from layers attributed to Chatelperronian, Aurignacian and older Gravettian contexts (Fig. 1). This period is characterized by great climatic fluctuations and cold temperatures, with even lower minimum temperatures than those from MIS 2. One of the coldest time spans of this period corresponds to the H4 event. One reindeer find from Labeko Koba (Guipúzcoa) has been found in a layer dated of 34.2 ka (38.9 calBP ka) (Altuna and Mariezkurrena, 2000).

Only one reindeer find, coming from Aitzbitarte III, Guipúzcoa (Altuna, 1996), has been dated and corresponds to the H3 cold event. The archaeological level where this specimen was recovered, was radiocarbon dated to between 23.8 and 25.4 ka (between 28.7 and 30.3 calBP ka) (Altuna, 1990).

Twenty five Iberian sites contain remains of reindeer attributed to MIS 2. This stage includes the cold and dry events H2, H1, YD and also the LGM, characterized by a great expansion of steppe environments. Nine of these sites are radiocarbon dated whereas the rest were interpreted based on their association with well defined archaeological levels (Tables 1 and 2; Fig. 1). The quantity of specimens recovered increases at the end of this episode, and within the brief H2 event (correlated with the Solutrean culture) they are particularly abundant, with nine occurrences having been described (Fig. 1). During the H1 event (correlated to the Middle and Upper Magdalenian cultures) 13 finds are detected and the YD (time of the Late Magdalenian and Azilian cultures) has yielded 14 dates. The dates related to any archaeological context should be used with care, taking into account the wide time span which they cover, for which an exact age cannot be determined.

At La Riera cave (Asturias) remains of reindeers have been dated to 10.8 ka (12.5 calBP ka) (Altuna, 1986). Santa Catalina cave (Vizcaya), has yielded the youngest dates of reindeer in Iberia with radiocarbon dates from 12.4 to 9.1 ka (14.4–10.3 calBP ka) and associated Azilian artifacts support the chronologies obtained in this site (Castaños, pers. com., 2007). This continuous occurrence suggests that reindeer populations continued to inhabit this area close to France shortly after the end of the YD, the last cold and dry time span. Furthermore, not far from Santa Catalina, two sites, Duruthy and Dufaure (Southern Landas, France), have yielded reindeer remains in an Azilian context (Delpech, 1983; Altuna, 1996).

To date, only one reindeer find has yielded an age corresponding to the H3 event. A chronological gap of reindeer records ranging between 31 and 25 calBP ka (period in which Gravettian culture developed) is detected. The reason for this near absence of *Rangifer tarandus* during a time span that is expected to be favorable remains unclear and is discussed in more detail below.

3.4. Chronological distribution of Gulo gulo, Alopex lagopus, Ovibos moschatus and Saiga tatarica

Although rarer, four additional cold-adapted large mammal species occurred in the Iberian Peninsula: wolverine (*Gulo gulo*), arctic fox (*Alopex lagopus*), musk ox (*Ovibos moschatus*) and saiga antilope (*Saiga tatarica*). Fortunately, most are accurately associated with radiocarbon dates (Fig. 1).

Only a single wolverine remain has been recovered in archaeological context from the Iberian Peninsula at Lezetxiki cave (Guipúzcoa). The layer this specimen was found in is attributable to the Upper Gravettian–Solutrean culture (Altuna, 1972). This is a cold period ranging between about 25 and 23 calBP ka that covers the H2 event.

Three remains of arctic fox (*Alopex lagopus*) are associated with radiocarbon dates on the Iberian Peninsula. The most recent was found at Aitzbitarte III cave (Guipúzcoa). The level where it was recovered has yielded four dates from 24.3 to 22.02 calBP ka, respectively (Table 1) (Altuna and Mariezkurrena, 2006), all of them chronologically placed around the H2 event. Another specimen from Amalda cave (Guipúzcoa) comes from a level dated to 32.05 calBP ka (Altuna, 2004), placing it in MIS 3. The oldest finding of this species comes from Labeko Koba cave (Guipúzcoa) and is dated to 31.4 ka (35.8 calBP ka) (Altuna, 2004), also during MIS 3. This indicates that the presence of arctic fox in Iberia, although sporadic, can be stated between 36 and 22 calBP ka.

Two Iberian localities yielded *Ovibos moschatus* remains: one is L'Arbreda cave (Gerona) and was recovered from a level radiocarbon dated to 21.2 and 20.7 calBP ka (Galobart et al., 1996), contemporary with the LGM. Some other remains coming from Can Rubau (Gerona), were found associated with stone tools that have been cautiously attributed to the Mousterian culture. The chronological information from Cau Rubau is limited, but at least it suggests this species was present even earlier in Iberia.

Only one site, Abauntz (Navarra), has yielded *Saiga tatarica* remains, and the layer was radiocarbon dated to 13.5 ka (16.4 calBP ka) (Altuna and Mariezkurrena, 1996), corresponding to the end of the LGM, and close to the H1 event. During this time span, the highest densities of this bovid were recorded in the nearby French localities of Isturitz, Bisqueytan, Moulin–Neuf or Roc de Marcamps, among others (Delpech, 1983). The mountainous environment surrounding Abauntz site is not compatible with the habitat expected for the saiga antilope, which normally inhabits very flat plains, similar to those from Landas (South-western France). This suggests the Abauntz remains might have been hunted in South-western France and then transported to Navarra, perhaps within a skin. If this explanation is accepted, then the presence of this species in the Iberian Peninsula as a common inhabitant could not be supported.

4. Discussion and conclusions

There is some doubt surrounding the timing of the earliest appearance of cold-adapted large mammals in Iberia. The earliest presence of *Rangifer tarandus* can be verified at around 200 ka at the site of Mollet, and subsequently at 150 ka (MIS 6) at the La Parte site. *Mammuthus primigenius* probably first appeared at the end of the Middle Pleistocene or at the beginning of the Upper Pleistocene, based on finds coming from the province of Madrid. In Similarly, *Coelodonta antiquitatis* was first registered during MIS 6 at La Parte with a chronology of 150 ka. Thus, by MIS 6 times, or perhaps even earlier, climatic conditions on the Iberian Peninsula were favorable for the presence of these cold-adapted species.

There is scarce and imprecise evidence for the presence of these taxa during MIS 5 and 4. Four reindeer finds, together with one of woolly mammoth and one of musk ox, are ascribed to this period. Two main episodes of cold and dry environmental conditions are identified from the pollen record, and other features are registered in the Iberian marine margin during these times, particularly between 65 and 59 ka (Roucoux et al., 2005). The most likely explanation is that these finds probably fall within MIS 5–4, but there is presently not enough data to confirm this.

During MIS 3, drastic cold and dry conditions alternated with brief mild or warm periods. The presence of cold-adapted large mammals in the Iberian Peninsula is for the first time widely documented during the cold episodes, especially between 42 and 31 calBP ka. At this time, the widest geographic distribution of woolly mammoth was registered and woolly rhino and reindeer were frequently present, particularly in Northern Iberia. Arctic fox is also present during MIS 3, a time when many environmental fluctuations on a millennial scale are recorded in ocean cores SU-8118 and MD95-2039 (Turon et al., 2003; Roucoux et al., 2005), carried out in the Atlantic Iberian margin. Two main episodes of steppe vegetation expansion along with a high proportion of polar affinity organisms and IRD are identified corresponding with the H4 and H5 events (Roucoux et al., 2005). Very similar results were obtained in the core record MD95-2043, from the Alboran Sea (Western Mediterranean) (Moreno et al., 2005). In the continental pollen record of Padul peat bog, high proportions of the steppe taxa *Artemisia* and Poaceae are present within the same levels from where the mammoth remains were found (Florschütz et al., 1971; Pons and Reille, 1988).

The available chronological data evidence a gap between 31 and 26 ka, which coincides with the nearly complete disappearance of these species in Iberia. Only two woolly mammoth finds, other two of woolly rhino (one of them very imprecise) and one of reindeer, were dated pointing to this time span. The absence of these species during a period that includes the cold and dry H3 event, very favorable for their presence, is difficult to understand. However, it is important to point out that Gravettian technocomplex sites are less frequently recorded and often not as well defined chronologically as later periods (especially the Magdalenian). Northern Iberian archaeological sites such as La Riera, El Castillo, Ekain, Bolinkoba, Santimamiñe or L'Arbreda (some of them radiometrically dated) did not yield cold-adapted mammal faunas within Gravettian levels (Altuna and Mariezkurrena, 1984; Cabrera, 1984; Castaños, 1984; Altuna, 1986; Altuna, 1990; Galobart et al., 1996). We must also consider that not all the Iberian finds of these species are dated, so we cannot discard that some of these undated finds could belong to this moment.

Subsequently, during the cold and dry MIS 2, the occurrence of cold-adapted mammals in Iberia was common, especially between 25 and 18 ka (including the H2 event), when most of these species reached their highest abundance.

During the LGM (16–22.8 ka) all these species were present in Iberia and reached a relatively high abundance, but a reduction is noticed towards the end of this period. The latest occurrence of woolly rhino is dated to 20 calBP ka, and the youngest woolly mammoth Iberian records were dated to about 17.5 calBP ka. The last occurrence of the wolverine, arctic fox, musk ox and saiga antelope were noticed in Iberia during the LGM, and reindeer findings became even scanter at the end of this episode. Steppe environments were predominant through this episode in the Iberian Peninsula as the pollen records show from continental (Florschütz et al., 1971; Pons and Reille, 1988; Iriarte et al., 2005) and marine sequences (Turon et al., 2003; Roucoux et al., 2005). The different pollen taxa indicate that environmental conditions were cold during all this period, but much drier during the H2, with predominance of *Artemisia*, and more humid during the LGM, when taxa as Cyperaceae and Ericaceae were also present (Roucoux et al., 2005).

Subsequently, during the H1 event (14.6–16 ka), reindeer was the only cold-adapted species that survived in Iberia, becoming relatively frequent. The abundance of this taxa increases toward the YD (12.7–11.3 ka), and the youngest Iberian reindeer record has been dated to 10.3 calBP ka, shortly after the end of the YD. H1 and YD events are also well documented in Iberian pollen records, again with a great expansion of steppe taxa together with a decrease of tree pollen (Roucoux et al., 2005). Furthermore, IRD and organisms of polar affinity are significantly abundant in marine records during H1 (Turon et al., 2003; Sanchez Goñi and d'Errico, 2005).

This work represents an initial approach in our understanding of the chronological dynamics of cold-adapted large mammal fauna in Iberia. The results are consistent with the palaeoclimatic works carried out by different authors during recent years. Nevertheless, a more in depth study is necessary to clarify the occurrence of cold-adapted taxa in the Iberian Peninsula. Archaeological prospections for new sites covering the chronological periods when these species are likely to be present as well as additional radiometric data on older finds are necessary. These would widen our knowledge of the exact dates of arrival and disappearance of these fauna in Iberia and provide valuable information about the geographical and paleoecological constraints of these species.

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