



Southern dispersal and Palaeoecological implications of woolly rhinoceros (*Coelodonta antiquitatis*): review of the Iberian occurrences

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ABSTRACT

Cold-adapted large mammal populations spread southward during the coldest and driest phases of the Late Pleistocene reaching the Iberian Peninsula. Presence of woolly rhinoceros (*Coelodonta antiquitatis*) can be identified from 23 Iberian sites, which is compiled and analyzed herein, and the fossil specimens from seven of these sites are described here for first time.

Morphological and biometrical analyses demonstrate that the Iberian woolly rhinoceros did not significantly differ from individuals of other European populations, but represent the westernmost part of a continuous Eurasian belt of distribution.

The first presence of woolly rhino in the Iberian Peninsula has been identified during the late Middle Pleistocene and early Late Pleistocene. However, the highest abundance of this species is recorded during MIS 3 and 2. The latest Iberian occurrences can be dated around 20 ka BP. The presence of woolly rhinoceros in the Iberian Peninsula correlates with periods of extreme dry and cold climatic conditions documented in Iberian terrestrial and marine sediment sequences.

From a palaeobiogeographic point of view, the maximum southern spread of *C. antiquitatis* on the Iberian Peninsula was registered during the late Middle Pleistocene or early Late Pleistocene, reaching the latitude of Madrid (about 40°N). Subsequently, during MIS 3 and 2, all Iberian finds were restricted to the Northern regions of Iberia (Cantabrian area and Catalonia). The southern expansion of *C. antiquitatis* during the Late Pleistocene in the Iberian Peninsula reached similar latitudes to other Eurasian regions.

The ecological composition of fossil assemblages with presence of woolly rhinoceros was statistically analyzed. Results show that temperate ungulate species are predominant at Iberian assemblages, resulting in a particular mixture of temperate and cold elements different of the typical Eurasian cold-adapted faunal associations. This particular situation suggests two possible explanations: a) Eventual migrations during the coldest time spans, resulting in a mixing of cold and temperate faunas, instead a faunal replacing; b) Persistence of woolly rhinoceros populations in the Iberian Peninsula during interglacial episodes confined at cryptic southern refugia.

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1. Introduction

The Iberian Peninsula constituted the south-western boundary in the distribution of the Late Pleistocene Eurasian tundra-steppe. The cold-adapted large mammal faunas, also called *Mammuthus-Coelodonta* faunal complex, reached its widest Palaearctic distribution during the Late Pleistocene, covering about 190° of longitude and 40° of latitude (Kahlke, 1999). During the coldest time spans of the Late Pleistocene, this faunal complex expanded through the southernmost regions of Europe reaching the Iberian

Peninsula (Altuna, 1996; García and Arsuaga, 2003; Álvarez-Lao and García, 2010).

The woolly rhinoceros (*Coelodonta antiquitatis*) is a large grazer closely dependent on the tundra-steppe ecosystem. This species morphologically changed throughout the Pleistocene with adaptations towards increasing tolerance to extreme cold and arid environments as well as to the abrasive food resources of open steppe (Guérin, 1980; Kahlke, 1999; Kahlke and Lacombat, 2008). This species became extinct at the end of the Late Pleistocene (Kahlke, 1999), when the tundra-steppe disappeared from most regions of Eurasia.

Iberian woolly rhino fossils were first identified by Naranjo y Garza (1875). Several other findings correspond to the late 19th and early 20th centuries (González Linares, 1876; Carballo, 1910;

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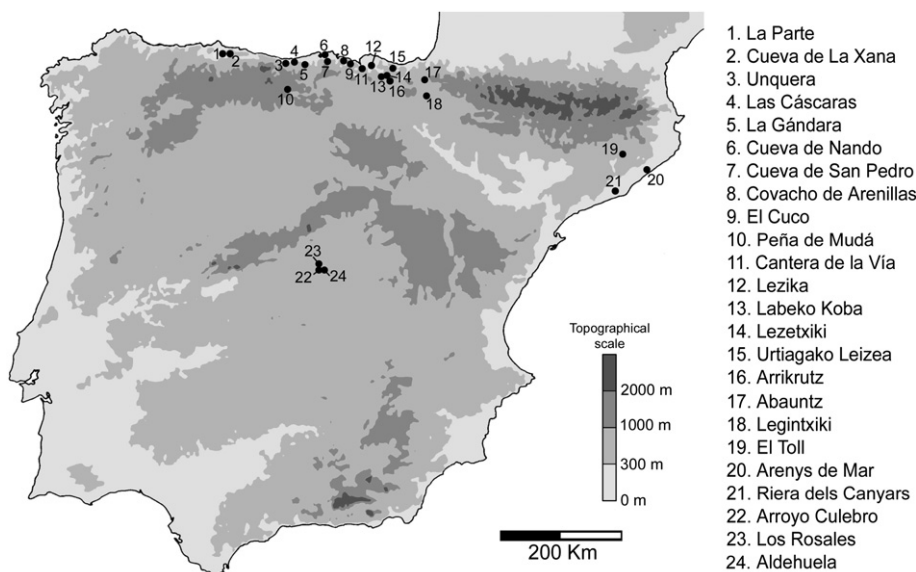


Fig. 1. Iberian sites with *Coelodonta antiquitatis* remains.

Harlé, 1912), come from mining and archaeological prospecting. Most of the fossils from the early discoveries could not be traced to their current location. Later discoveries include some outstanding assemblages, including the skulls from Arroyo Culebro (Arsuaga and Aguirre, 1979), the remains from Cueva de Nando (Fuentes and Meijilde, 1979), and Labeko Koba (Altuna and Mariezkurrena, 2000).

Remains of woolly rhinoceros have so far been recovered from 23 Iberian sites (Altuna, 1996; García and Arsuaga, 2003; Álvarez-Lao, 2007; Álvarez-Lao and García, 2010), particularly coming from the north, but also from some sites near the center of the peninsula.

In the present work a compilation of all the currently known Iberian finds, including new fossils and first descriptions of old findings, has been carried out. The morphology of the Iberian C.

Table 1
Iberian sites containing woolly rhinoceros remains.

Site	Nisp/MNI	Other cold taxa	Absolute Chronology ^a or Archaeologic context	Actual storage	First Citation of <i>Coelodonta</i>	Description of the fossils
La Parte	8/1	Rt.	188.5; 141.4 ka BP ^b	Ovd.	Álvarez-Lao and García-García, 2006	Álvarez-Lao and García-García, 2006
La Xana	1/1		Unknown	Ovd.	This paper	This paper
Unquera	1/1		Unknown	Unknown	Harlé, 1912	Harlé, 1912
Las Cáscaras	2/1		Unknown	Unknown	Carballo, 1910	None
La Gándara	2/1		Unknown	Unknown	Naranjo y Garza, 1875	Naranjo y Garza, 1875
Cueva de Nando	48/1		Unknown	Sant.	Fuentes and Meijilde, 1979	Fuentes and Meijilde, 1979
Cueva San Pedro	1/1		Unknown	MNCN	Domingo et al., 2005	This paper
Covacho Arenillas	1/1		38.4; 39.1 cal ka BP	Sant.	Castaños, 1996	Castaños, 1996
El Cuco	9/1		Gravettian	Sant.	Castaños and Castaños, 2007	Castaños and Castaños, 2007
Peña de Mudá	1/1		Unknown	Mgm.	This paper	This paper
Cantera de La Vía	1/1		Unknown	Bilb.	Altuna, 1974	Altuna, 1974
Lezika	144/5		Unknown	Bilb.	Castaños et al., 2009	Castaños et al., 2009
Labeko Koba	122/13	Mp. Rt.	35.8–38.9 cal ka BP	SSb.	Altuna and Mariezkurrena, 2000	Altuna and Mariezkurrena, 2000
Lezetxiki	3/1	Rt. Gg.	Aurignac.; Gravett.–Solutr.	SSb.	Altuna, 1972	Altuna, 1972
Urriagako Leizea	1/1	Mp. Rt.	33.9 cal ka BP	SSb.	Altuna, 1984; Altuna and Mariezkurrena, 2010	Altuna, 1984
Arrikruz	1/1		Unknown	SSb.	Altuna, 1979	Altuna, 1979
Abauntz	1/1	Rt.	Upper Solutrean	Nav.	Altuna et al., 2002	Altuna et al., 2002
Legintxiki	2/1		20.3 cal ka BP	Nav.	Castaños, 1996	Castaños, 1996
El Toll	4/1		Unknown	Barc.	Thomas and Villalta, 1957	This paper
Arenys de Mar	1/1		Unknown	Barc.	Harlé, 1920	Harlé, 1920; this paper
Riera dels Canyars	3/2		Under study	Under study	García et al., 2010	Under study
Arroyo Culebro	5/3		Unknown	Orig.	Arsuaga and Aguirre, 1979	Arsuaga and Aguirre, 1979; Soto and Sesé, 1991
Los Rosales	1/1		Unknown	MNCN	Cerdeño, 1990	This paper
Aldehuela	1/1	Mp.	Unknown	Orig.	Sesé and Soto, 2002	This paper

Abbreviations: Nisp. Number of identified specimens; MNI: Minimum Number of Individuals.

Taxa abbreviations: Rt. – *Rangifer tarandus*; Mp. – *Mammuthus primigenius*; Gg. – *Gulo gulo*.

Institutions: Ovd. – Geology Department, Oviedo University; Sant. – Museo de Prehistoria y Arqueología de Santander; MNCS – Nacional Museum of Natural Sciences, Madrid; Mgm. – Museo Geominero, Madrid; Bilb. – Museo Vasco, Bilbao; SSb. – Centro de Custodia de Materiales Arqueológicos y Paleontológicos de Guipúzcoa, San Sebastián; Nav. – Museo de Navarra; Barc. – Museo de Ciencias Naturales de Barcelona; Orig. – Museo de los Orígenes, Madrid.

^a All radiocarbon dates have been calibrated at 68%.

^b Dates have been carried out by means of U–Th series.

antiquitatis remains was examined individually and as a whole in order to characterize the individuals and confirm whether their anatomy differs from that of contemporaneous populations from other regions of Eurasia.

2. Materials and methods

Woolly rhinoceros remains have been identified at 23 Iberian sites indicated in Fig. 1 and Table 1. Most of these sites correspond with caves and sediment fillings of karstic cavities, with the exception of Arenys de Mar (Barcelona) and those coming from Madrid, which are associated with fluvial deposits. Most of the Iberian woolly rhino fossils, kept at different Spanish museums and scientific institutions, were studied and measured to carry out this work. Some of the remains, especially those coming from old findings, cannot be currently traced. An exhaustive bibliographic review was also undertaken.

All published chronologies from Iberian woolly rhino findings were compiled in order to constrain the episodes when this species arrived in the Iberian Peninsula. This chronologic information was subsequently correlated with the published palaeoenvironmental information for the Late Pleistocene of Iberia. All radiocarbon dates have been calibrated by means of the CalPal program to 1σ (68% range), in order to obtain calibrated ages which could be correlated with the paleoclimatic record represented in the Greenland Ice Core Project (GRIP). Therefore, radiocarbon dates are expressed in cal ka BP (calibrated *kiloanne* before present) in Table 1 and also occasionally in the text. Uncalibrated radiocarbon dates are indicated as ^{14}C ka BP. Chronology of the findings associated with archaeological contexts has been estimated as indicated by Álvarez-Lao and García (2010).

Taxonomic classification of the rhino species follows the criteria of Guérin (1980). Nomenclature of *Stephanorhinus* species followed Fortelius et al. (1993). Measurements taken on skulls are detailed in Fig. 2. Measurements on teeth, mandibles and postcranial elements follow the standards of Guérin (1980) and Driesch (1976). Morphometric data from Iberian specimens (Tables 2–10) was compared with an extensive sample, mainly coming from Western Europe (Guérin, 1980) as well as data from other European and Siberian populations (Bonifay, 1961; Friant, 1961; Teobald and Szymanek, 1963; Badoux, 1964; Jörg, 1971; Borsuk Białynicka, 1973). The age at death based on complete dental series was estimated on the basis of molar wear by analogy with living African white rhinoceroses (*Ceratotherium simum*), following Hillman-Smith et al. (1986). The proposed ages are estimations assuming an equivalent ontogeny with the extant species.

3. Origin and description of the remains

The studied fossils come from 23 archaeo-paleontological Iberian sites indicated in Fig. 1 and Table 1. Although most of the findings had been previously described, five of these sites report the presence of woolly rhino remains without a description, which is here provided along with two other new finds. Revision of the Iberian fossils suggested us that some of the rhino citations which were previously identified as *C. antiquitatis* are actually ascribed to other species. A list of these sites is also added.

3.1. Cueva de la Xana (Nava, Asturias)

A right M^3 of a woolly rhino (Fig. 3h, Table 3) without stratigraphic context was found through prospecting a small cavity in 2007. The crown has highly hypsodont. Both anterior and posterior valleys are deep and V-shaped, but the anterior valley is much narrower than the posterior one. The enamel is very rough and

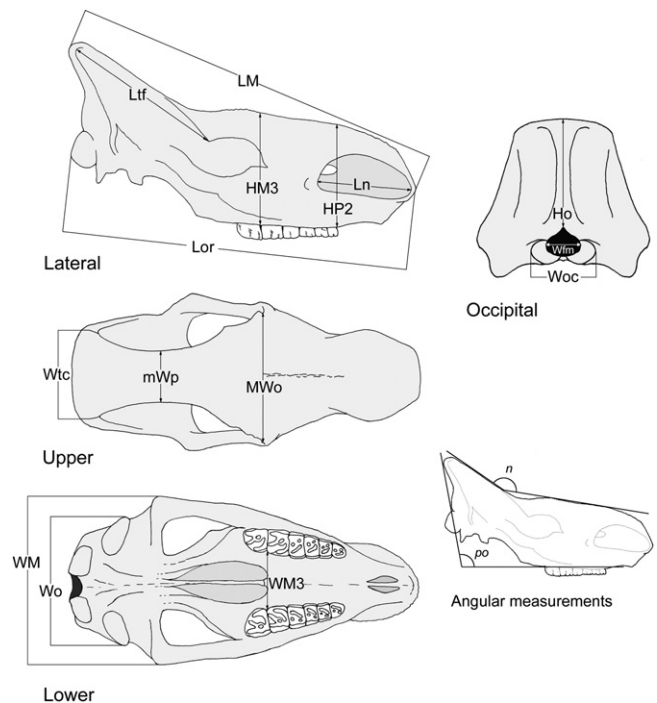


Fig. 2. Skull measurements. LM: maximum length; Lor: length occiput-rhinium; Ltf: length of the temporal fossa; Ln: length of nares; HP2 skull height at the level of the P²; HM3: skull height at the level of the M³; MWo: maximum width between orbits; Wtc: width between temporal crests measured at the posterior edge; mWp: minimal width between parietal crests; WM: maximum width; Wo: maximum occipital width; WM3: palatal width between M²/M³; Ho: occipital height from the upper edge of the foramen magnum to the upper edge of the occipital crest; Woc: width at the occipital condyles; Wfm: width of the foramen magnum; n: angle formed by the parietal surface and the tangent to the horn bosses; ρ : angle formed by the palatal surface and the opisthocranium-opisthion line.

thick, especially the lingual wall. Cement is lacking. The crown is worn approximately one-third of the height and the dentine is present on the paralophid, metalophid and hypolophid occlusal surfaces. Morphology and dimensions fall within normal values of *C. antiquitatis*.

3.2. Cueva de San Pedro (Navajeda, Cantabria)

A sole developing M^3 germ of a woolly rhino (Fig. 3d, Table 2) was recovered in 1906 (Domingo et al., 2005). The piece preserves only enamel and is totally unworn. It lacks the buccal wall of the protoloph. A pyramidal outline characterizes this molar, and is very hypsodont. A small metalophid is developing, which is an exclusive feature of *C. antiquitatis*. The presence of a well-developed medio-fossette and a rough enamel surface are other diagnostic traits. The wear stage suggests, this specimen belonged to a young individual, likely younger than 12 years.

3.3. Peña de Mudá (Mudá, Palencia)

One woolly rhino P³ is on display in the collections of the Museo Geominero of Madrid. This site was first mentioned in the 19th century (Prado, 1864; Calderón, 1876) where the presence of *Rhinoceros merkkii* (sic.) was reported but the woolly rhino fossil was not mentioned.

The P³ (Table 2) shows advanced wear. The medio-fossette, post-fossette and anterior valley are well defined as enamel islets. Cement is abundant, which is typical for this species.

Table 2Comparative dimensions of *Coelodonta antiquitatis* Iberian upper dentition and comparison with other European sites. Measurements are given in mm.

Site	p ²		p ³		p ⁴		M ¹		M ²		M ³		
	L	W	L	W	L	W	L	W	L	W	L	W	
Cueva de Nando ^a		32.4	42	38	49.3	47	59.5	57	56.6	51	52.3		
Cueva de San Pedro ^a										55			
Mudá ^a		36.3	44.2										
Labeko Koba ^b	Left serie								59	58.5	59	50.5	
	Isolated teeth							55	58		53.5	49	
								49	60		57	48	
								54	59				
Arrikrutz ^c						49							
Leguintxiki ^d				35.5	49						52.2	50.4	
Arenys de Mar ^a	Left	32	41.5	36.5	49	43.8	54.5	41.8	60.5	63.7	54		
	Right	32.5	41	34.5	51.2	43.5	49.5	48.5	59	64	58		
Arroyo Culebro ^e	Left							37		49	62	55	
	Right							35		46	60	56	
Aven de Coulon ^f				33	42	32		51	48	52	55	40	
Ordos ^f				38	43	42		50	56	50			
Abbeville ^f				38	47	40		49	56	48	55	46	
Rigney ^g	20	30	25	40	45	45			55				
European Sites ^h	n	26	29	56	57	47	52	43	47	59	62	69	67
	Mean	32.1	34.4	38.3	42.1	43.2	48.5	50.8	52.7	56.4	55.8	58	51.1
	Min.	25	27.5	33	35	37	44	43.5	43.5	47	45	44	40
	Max.	37	42	43	47.5	51.5	55.5	58.5	61	65.5	63	70	60

L: maximum crown length; W: maximum crown width.

^a Own data.^b Altuna and Mariezkurrena (2000).^c Altuna (1979).^d Castañós (1996).^e Arsuaga and Aguirre (1979).^f Bonifay (1961).^g Teobald and Szymanek (1963).^h Guérin (1980).**Table 3**Comparative dimensions of *Coelodonta antiquitatis* Iberian lower dentition and comparison with other European sites. Measurements are given in mm.

Site	p ²		p ³		p ⁴		M ¹		M ²		M ³		
	L	W	L	W	L	W	L	W	L	W	L	W	
La Parte ^a	29.6	19.7	32.5	25	43	31.4							
Cueva de La Xana ^a											55.5	33	
Cueva de Nando ^a	Left				38	26.2	41.9	27.8	47	28.6	49.5	27.3	
	Right				38.8	26.2	40.2	27.3	47.7	27.2	49	27.8	
Labeko Koba ^b	Left serie	27	18.6	32	24	41	27.5	42.5	32.5	51.5	32.5	52	31
	Left serie	29.5	18.5	37	24								
	Right serie			38	24	44	29	54	31	57	32.5		
	Isolated	34	27	45	28				31			57	30
	Teeth	35.5	26.5	45	28.5				31			52	25.5
Arroyo Culebro ^{c,d}	Left	29.5	20.5	37	24.5			52	31	54			
	Right	30	20	38.5	26			51.5	30.5	54			
	Left											55.2	34.2
Aldehuela ^a											53	27.6	
Aven de Coulon ^e				34	28	34	31	45	29	51	31		
Starunia ^e				35	15	48	21	40	18	27	15		
Kesslerloch ^e				46.2	29	50.7	33.6	58.7	32.3				
Ordos ^e				44	27	53	30	58	34				
Wieringermeer ^f	18.5	13.4	27.6	18.5	29	24.6	35.5	29.5	42	29.7	48	27.8	
European Sites ^g	n	13	14	27	30	29	32	31	43	45	52	49	51
	Mean	29	18.7	34.2	24	41.5	26.8	47.7	29.3	50.7	31.4	53.5	31.3
	Min.	23	16	29	18	35	22	38	23	42.5	24	47	28
	Max.	35.5	22	39.5	29	48.5	31.5	56	33	58.5	38.5	62	37

L: maximum crown length; W: maximum crown width.

^a Own data.^b Altuna and Mariezkurrena (2000).^c Arsuaga and Aguirre (1979).^d Soto and Sesé, 1991.^e Bonifay (1961).^f Badoux (1964).^g Guérin (1980).

Table 4Comparative dimensions of *Coelodonta antiquitatis* Iberian deciduous dentition and comparison with other European sites. Measurements are given in mm.

Site	D ¹		D ²		D ³		D ⁴		D ₁		D ₂		D ₃		D ₄		
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	
Covacho de Arenillas ^b													26	15.1			
Lezika ^c	23.3	19	29.4	31.6	40.5	35.6	44	39.3									
Labeko Koba ^d	Isolated teeth	22	19	32.5	31.5	42	35.5	44.5		20.5	11.4	35.5	19	35.5	19	40	20.5
		23.5	18.3	29	28	44	40	46	38.5	20.5	11.4					46.5	24
				32	32		40	46	38								
								52	45								
Arroyo Culebro ^a	Left															41.5	25.5
	Right															43	25
European sites ^e	n	3	3	27	31	27	28	20	23	1	1	11	12	21	24	12	13
	Mean	21.2	17.7	30.5	29.3	41.9	37.1	48.6	43.3	17.5	12	27.2	16.3	37.2	20.4	42.3	22.5
	Min.	21	17	28	26	31	31.5	44	39			26	15	34.5	17	37	19
	Max.	21.5	18	33	32.5	45.5	42	57	55			29.5	18.5	41.5	24	51	25.5

L: maximum crown length; W: maximum crown width.

^a Own data.^b Castaños (pers. com.).^c Castaños et al. (2009).^d Altuna and Mariezkurrena (2000).^e Guérin (1980).

3.4. El Toll (Moiá, Barcelona)

Thomas and Villalta (1957) and Crusafont (1961) reported the presence of woolly rhino remains from El Toll. One lower molar fragment, one right magnum, one carpal bone fragment and one right III metacarpal fragment were recovered. The lower molar fragment presents a high rugosity of the enamel surface. The magnum (Fig. 5m,n; Table 8) is almost complete, lacking part of the distal portion. The great width/length ratio of the distal articular surface is a diagnostic trait of *C. antiquitatis*. The morphology and dimensions fit well with this species (Guérin, 1980). The third metacarpal (Fig. 5i,j; Table 9) preserves the proximal end and part of the diaphysis. The equidimensional shape of the proximal articular surface, the large size of the specimen, and its general outline, correspond to woolly rhino (Guérin, 1980).

3.5. Arenys de Mar (Barcelona)

A *C. antiquitatis* skull was found in a sand layer (Harlé, 1920). The dentition of this specimen was first described by Harlé (1920) and figured by Gómez-Alba (1988).

The skull, (Fig. 4d–f; Table 5) lacks most of the neurocranium, (from the middle of the temporal fossa), while the rest of the fossil appears well preserved. The skull seems narrow although the maximum width measurement is not available. The preorbital tubercle is well developed, indicating the specimen might be a male. The rim of the nasal notch is located above P³–P⁴ and the anterior rim of the orbits is placed over the M³. The post-palatine notch rim is located at the level of the M². The nasal septum is ossified at the level of the anterior two-thirds. The nasal bone fuses anteriorly with the palatal bone constituting the typical “beak” that *C. antiquitatis* skulls present. The frontal horn boss is placed at a higher position than the nasal one, which is also a characteristic feature of this species. The angle of the nasal horn boss is very pronounced which, along with the relative narrowness of the skull, are considered typical features of Late Pleistocene *C. antiquitatis* forms (Kahlke and Lacomat, 2008).

The dentition (Fig. 3b, Table 2) is complete (both P²–M³ series) and well preserved. M³ are unworn and still emerging which, together with an incomplete nasal septum ossification, suggests that this fossil belonged to a young-adult individual. The age at death of this specimen ranges between 10 and 15 years. A thick

cement layer covers the buccal and lingual surfaces of the pieces, which is indicative of this species.

3.6. Los Rosales (Villaverde, Madrid)

Royo y Gómez (1935) reported *Rhinoceros merckii?* (sic.) remains from this sand quarry. A complete rhino right radius was attributed by Cerdeño (1990) to *C. antiquitatis* and by Sesé and Soto (2002) to *Stephanorhinus mercki* (synonym of *Stephanorhinus kirchbergensis*). Radiometric analyses are lacking, although Sesé and Soto (2002) suggest a Middle Pleistocene age. The radius (Fig. 5c,d; Table 7) is complete and well preserved. A comparative analysis of this specimen was undertaken including an extensive sample taken from Guérin (1980) of *C. antiquitatis*, *Stephanorhinus hemitoechus* and *S. kirchbergensis*. The values of Los Rosales radius fit well in the *C. antiquitatis* range, very close to the mean values, and differ considerably from the other species. The morphology of the proximal-medial articular surface is anterior-posteriorly elongated in *C. antiquitatis*, a trait also observed in the specimen from Los Rosales. In contrast *S. kirchbergensis* is equidimensional (Guérin, 1980). Based in the dimensions and morphology, this radius should be attributed to *C. antiquitatis*.

3.7. Aldehuela (Getafe, Madrid)

A left M₃ of a woolly rhino recovered from this sand quarry. Sesé and Soto (2002) studied the fauna from this site and attributed a Late Pleistocene age to this molar on the basis of the associated fauna, which includes *Mammuthus cf. intermedius* (sic.) and *Megaloceros cf. giganteus*.

The woolly rhino M₃ (Fig. 3e, Table 3) is an unworn developing germ; a high hypsodonty (55 mm height) of the crown is observed. The paralophid is lacking and the anterior valley is V-shaped. The enamel is very rough and no cement is preserved.

3.8. Revision of misidentified and doubtful citations of *Coelodonta*

Rhinoceros remains from the sites of Carihuela, Granada (Koby and Spahni, 1956) and Coscobillo, Navarra (Ruiz de Gaona, 1958) were incorrectly identified as *C. antiquitatis*. We propose this material belongs to *S. hemitoechus*. Other woolly rhino identifications from Cerecinos, (León) (Ezquerria, 1854), and from an

Table 5
Comparative dimensions and angles of *Coelodonta antiquitatis* Iberian skulls and comparison with other European sites. Metrical measurements are given in mm.

	Arroyo Culebro ^b		Arenys de Mar ^a	Coulon ^c	Ordos (Boule) ^c	Starunia ^c	Mannheim – Kafertal ^d	Western European sites ^e			Poland ^f			Hofstade ^g		Rigney ^h	Siberia and Europe. Late Pleistocene Sample ⁱ		
	A	B						n	Mean	Min–Max	n	Mean	min–Max	1	2		n	Mean	min–Max
LM	820			850	870–895–950	800	720	45	781	706–883	15	741.5	672–807	760	870	720	34	775.68	655–872
Lor	750			635			695	49	720.8	666–800				677	766	670			
Ltf	320	320		340	420–450–460			50	335.2	295–385						330			
Ln	230		205	190	220–230–240	140	215	52	205.2	183–237	13	218.8	209–238			180			
HP2	180		184					34	196.1	173–228						190			
HM3	210		203					32	206.8	166–242						292			
WM		370						35	334	296–383	13	334.1	306–366	323	357	260	32	340.2	303–360
Wo	300	280						52	273.1	245–313	15	247.9	230–268			260	34	277.33	247–316
Wtc	250	215		158		150		55	206.9	150–257						180			
mWp	90	70		82		80		53	90.5	53–136						80	6	74.17	60.7–92.2
MWo	300	350	273	270	264–270		303	39	248.6	213–320			301	323	250		23	96.65	80–116
WM3			110.5					29	98	79–112									
Ho	153	150		181				51	175.2	141–208						150			
Wfm	44	42		58		55	52	55	59.9	43–76						50			
Woc	160	153					160	53	157.4	142–177			146	174	130	34	157.52	141–171	
n	161°			157°			155°									149°			
ρo	105°			92°			98°									92°			

Abbreviations of the measurements are detailed in Fig. 2.

^a Own data.

^b Arsuaga and Aguirre, 1979.

^c Bonifay, 1961.

^d Jörg, 1971.

^e Guérin, 1980.

^f Borsuk Białynicka, 1973.

^g Friant, 1961.

^h Teobald and Szymanek, 1963.

ⁱ Kahlke and Lacomat, 2008.

Table 6

Comparative dimensions of *Coelodonta antiquitatis* Iberian mandibles and comparison with other European sites. Measurements are given in mm.

	HP ₂	HP ₃	HP ₄	HM ₁	HM ₂	HM ₃
Labeko Koba ^b		90	103	109	106	
Arroyo Culebro ^a	74	85	92	92	91	
Aven de Coulon ^c				104		110
Fulaerhtzi ^c				110		110
Heldn ^a				123	113	109
Wieringermeer ^d	89					107
European sites ^e	<i>n</i>	42	49	59	52	47
	Mean	81.6	88.5	96.8	101	100.9
	Min.	61	68	75	74	79
	Max.	106	110	126	124	126

The measurements correspond to the height of the horizontal branch just behind each indicated dental element.

^a Own data.

^b Altuna and Mariezkurrena (2000).

^c Bonifay (1961).

^d Badoux (1964).

^e Guérin (1980).

unknown site in Cantabria (Carballo, 1909) are not considered reliable.

The comprehensive study of the Iberian *C. antiquitatis* findings provided interesting results from anatomical, chronological, biogeographical and palaeoecological points of view, which are indicated in next sections.

4. Morphology and biometry

Body size might respond in an adaptive way to variation in a general factor that varies with latitude, possibly temperature. *C. antiquitatis* seemed to be an adequate candidate to test the idea that within a species, animals are larger in colder environments (Mayr, 1956, 1963). However the Iberian woolly rhino fossil sample is scarce as well as geographically and chronologically dispersed. For these reasons, statistical analyses on the Iberian woolly rhino fossils were not applied, although size comparisons between remains

coming from lower (Iberia) and higher (North and Central Europe) latitudes are here taken into consideration.

Teeth are the most abundant fossils in the Iberian sample. Comparing the Iberian values provided by Guérin (1980) for western European populations, upper premolars and molars of three Iberian specimens (from Cueva de Nando, Arenys de Mar and Arroyo Culebro; Fig. 3a–c) show relatively high width respect to the length. This ratio is not constant throughout the individual life, but increases with the ontogenetic age of the specimens, caused by the interdental attrition. The most likely explanation for this relatively high width respect to the length is that these three Iberian specimens are mature or old aged and show an advanced interdental attrition. Almost all the measurements of the upper teeth fall in to the ranges of the western European population provided by Guérin (1980). The lower dentition is more variable in size (Table 3), but in almost all cases the values also fall within the range observed by Guérin (1980). Interdental attrition is observed in the lower teeth from Cueva de Nando (Fig. 3f,g) and from La Parte (Álvarez-Lao and García-García, 2006), corresponding in both cases to old specimens. The Iberian tooth sample does not show morphological features distinct from the other Eurasian woolly rhinoceros populations, with the exception of the specimen from Arenys de Mar, whose M¹ shows a medio-fossette divided by a wall and also shows an additional *crista* in M³.

The Iberian woolly rhino sample includes three skulls, two of them from Arroyo Culebro and other, partially preserved, from Arenys de Mar. Specimen “A” from Arroyo Culebro (ref. ACU-62-19303, Fig. 4a, Table 5) is quite complete, but eroded on the surface, and is very large, close to the maximum values of length provided by Guérin (1980) for western European specimens. It lacks both zygomatic arches, so the maximum width cannot be measured. The nasal septum is almost completely ossified except in a small portion in the posterior area where is likely broken by erosion. The nasal horn boss shows a high ruggedness. Following Arsuaga and Aguirre (1979) this skull could have belonged to a female individual given the low development of the occipital and temporal crests and the orbital rims. Nevertheless the large size of the specimen suggests a male attribute. The dentition is extremely

Table 7

Comparative dimensions of *Coelodonta antiquitatis* Iberian fore limb elements and comparison with other European sites. Measurements are given in mm.

	Scapula		Humerus				Radius						Ulna		
	sDC	GDP	WP	DP	WPs	DPs	GL	WP	DP	sWd	sDd	WD	DD	WPs	
Cueva de Nando ^a	133	170	225	180	120	120									
Los Rosales ^a							373	111.7	78.5	60	35	111.5	68		
Labeko Koba ^b	124	162.5						113	79.5	65.5	46.5				90
		128.5						111	82.5	57	40.5				
Lezika ^c							390	113	79.2	61.6	42.8	128	76	81	
European Sites ^d	<i>n</i>	34	33	35	28		81	109	106	103	102	84	80	30	
	Mean	128.1	153.2	195.3	187.8		380.3	112.8	77.5	63.4	45.6	117.7	76.6	92.4	
	Min.	112	128	172	160		334	97	55	54	38	95	62	75	
	Max.	147	178	218	220		413	126	93	75.5	57	142	92	109	
Zapug ^e	113	142			107	103	348	102		54	39	110		95	
MG-1 ^e					103	106									
PS-3 ^e					108	99									
ZIN 17220 ^e							385	117		70	47				
ZIN 5087 ^e							343	105		53	35	110		91	
Aven de Coulon ^f		154	205				385	111				105		88	
Starunia ^f		170													
Ordos ^f			206				450	114		66		112			

sDC: smallest depth of the *Collum*; GDP: greatest depth of the *Processus articularis*; WP: proximal width; DP: proximal depth; WPs: width of the proximal articular surface; DPs: depth of the proximal articular surface; GL: greatest length; sWd: smallest diaphysis width; sDd: smallest diaphysis depth; WD: distal width; DD: distal depth.

^a Own data.

^b Altuna and Mariezkurrena (2000).

^c Castaños et al. (2009).

^d Guérin (1980).

^e Borsuk Białynika (1973).

^f Bonifay (1961).

Table 8Comparative dimensions of *Coelodonta antiquitatis* Iberian carpal and tarsal elements and comparison with other European sites. Measurements are given in mm.

	Scaphid				Magnum			Calcaneum					Astragalum					
	GL	GW	LPs	WPs	GW	GH	HA	GL	GW	GD	WT	DT	sWN	GL	GW	LDs	WDS	
La Parte ^a	67.6	51.13	44.3	49.1														
El Toll ^a					56	74	67											
Lezika ^b								129.5	85.5		56	70	470	83.3	96	65	90	
								129.5	85	72.5	58	74	460					
European Sites ^c	<i>n</i>	41	40	42	39	42	34	29	64	64	63	66	61	49	112	112	91	107
	Mean	88.4	60.1	60.5	58.1	50.9	66.7	63.6	129.3	80.2	71.72	55.18	75.24	44.12	86.9	95.7	51.3	80.9
	Min.	76.5	51	50	50	39	49.5	55.5	117.5	65	59.5	45	60	35	77	84	42	68
	Max.	97	71.5	68	70	58	75	70	141	93	86.5	66	90	59	102	112	79	91
Aven de Coulon ^d									136	91			70		78	85		
Ordos ^d									137	85			67		86	87		
Zapuj ^e		86	69			49				87	66	53	71		77	91	44	71

GL: greatest length; GW: greatest width; LPs: length of the proximal articular surface; LDs: length of the distal articular surface; WPs: width of the proximal articular surface; WDS: width of the distal articular surface; WPs: width of the proximal articular surface; GH: greatest height; HA: anterior height; GD: greatest depth; WT: width of the Tuberosity; DT: depth of the Tuberosity; sWN: smallest width of the calcaneal Neck.

^a Own data.^b Castaños et al. (2009).^c Guérin (1980).^d Bonifay (1961).^e Borsuk Białynika (1973).

worn preserving only the left M¹–M³ and right M²–M³ series (Fig. 3c, Table 2). The premolars have disappeared likely due to extreme wear; the left M¹ shows only 10 mm of crown whereas the crown of right M¹ is completely worn; both M³ present an advanced wear stage. Interdental attrition of the rows is pronounced. Based on these dental features this fossil likely belonged to an extremely old individual whose age at death has been estimated between 35 and 40 years, corresponding with age group XVI (Hillman-Smith et al., 1986). The skull “B” from Arroyo Culebro (ref. ACU-62-19304, Fig. 4b,c; Table 5) exhibits better condition although it lacks the nasal area, palate and dentition. It preserves the neurocranium, occipital, parietal and frontal areas,

orbits and zygomatic arches. Bone sutures are totally fused suggesting that it belonged to an adult individual. Temporal and occipital crests as well as orbit rims are much more pronounced than in skull “A”, suggesting that this individual was male. The occipital angle (ρ) is high and the zygomatic arches are straight which following Kahlke and Lacomat (2008) are typical features of Late Pleistocene *C. antiquitatis* forms. The skull from Arenys de Mar, as described in Section 3.5, lacks most of the neurocranium. The well developing of the preorbital tubercle suggests that the specimen might be a male. The angle of the nasal horn boss is very pronounced and the general shape of the skull is relatively narrow. All the measurements fall among typical values observed for this species in Eurasia (Table 5), most of them very close to the average values provided by Guérin (1980).

A number of morphological features, as a very pronounced angle of the nasal horn boss, a high occipital angle (ρ) and straight zygomatic arches, which are considered by Kahlke and Lacomat (2008) as typical for Late Pleistocene forms, are observed in these three Iberian skulls.

Mandibles are scarce in the Iberian woolly rhino record with only two specimens partially preserved. The juvenile mandible from Arroyo Culebro (ref. ACU-63-26281, Fig. 4g,h; Tables 3, 4 and 6; Soto and Sesé, 1991) preserves all the horizontal branches, the symphysis, and all the dentition. This specimen remains the last deciduous piece (D₄) extremely worn (Fig. 3i) and close to be replaced. M₁ shows incipient wear and a totally unworn M₂ is still emerging. Following Hillman-Smith et al. (1986) the ontogenetic age estimated for this specimen ranges between 4 and 7 years (age group VIII). Its size is smaller than the average European values published by Guérin (1980), which would be expected due to it corresponds to a young individual. The mandible from Labeko Koba is nearly complete (Table 6; Altuna and Mariezkurrena, 2000), which preserves almost the entire dental series (left P₂–M₃ and right P₃–M₃ rows). M₁ shows advanced wear but is only incipient in M₃. The age at death is estimated to between 20 and 28 years (age group XIII) following Hillman-Smith et al. (1986). The measurements of this robust specimen are slightly larger than the average values provided by Guérin (1980).

Postcranial elements (Fig. 5) are usually scattered fragments and not preserved in good conditions. However, a radius from Los Rosales (Fig. 5c,d) is complete and well preserved; it has been ascribed to *C. antiquitatis* based on morphology and size (close to

Table 9Comparative dimensions of *Coelodonta antiquitatis* Iberian metacarpals III and IV, and comparison with other European sites. Measurements are given in mm.

Metacarpal III	GL	WP	DP	sWd	sDd	WD	DD	WDS	
Labeko Koba ^b	186	66.5	50	51.5	26	64.5	49.5	55	
		81	56.5	59.5	27				
El Toll ^a		67	55						
European sites ^c	<i>n</i>	79	90	80	86	84	77	68	77
	Mean	189	68.2	52.2	56.44	28.71	65.7	50.8	56.1
	Min.	162	59.5	42.5	46	23	57.5	44	49
	Max.	213	79	61.5	66	36.5	74	57.5	65
Ordos ^d		205	66					54	
Aven de Coulon ^d		181	64					61	
Zapuj ^e		161	60					57	
Metacarpal IV									
La Parte ^a	148		34	21				36.5	
Labeko Koba ^b	149	48	49	37.5	23.5			42.5	41.5
European sites ^c	<i>n</i>	59	57	54	59	57	58	50	54
	Mean	151	53.3	44.9	37.5	24.4	47.9	42.2	45.2
	Min.	126	41	39	32	20	42	34	34.5
	Max.	176	62.5	52	46	30	62.5	48	50.5
Ordos ^d		183	63					48	
Aven de Coulon ^d		146	54					53	
Zapuj ^e		130	44					43	

GL: greatest length; WP: proximal width; DP: proximal depth; sWd: smallest diaphysis width; sDd: smallest diaphysis depth; WD: distal width; DD: distal depth; WDS: width of the distal articular surface.

^a Own data.^b Altuna and Mariezkurrena (2000).^c Guérin (1980).^d Bonifay (1961).^e Borsuk Białynika (1973).

Table 10Comparative dimensions of *Coelodonta antiquitatis* Iberian hind limb elements and comparison with other European sites. Measurements are given in mm.

	Fémur				Tibia					
	WP	WC	DC	sWd	GL	WP	sWd	sDd	WD	DD
La Parte ^a										63
Labeko Koba ^b	224	105	95	85.5 83 99 108			64	54.5	105.5	78
Lezika ^c					381	125	65	60.5	104.5	80
European sites ^d	<i>n</i>	17	27	25	45	67	50	85	82	88
	Mean	223	104.9	99.2	93	381.1	133.4	70.1	63.2	106.7
	Min.	195	94	87	65	323.5	111	59	51	92
	Max.	249	116	113	112	433	163	82.5	77	127
Aven de Coulon ^e		210	94			385	132	73		114
Ordos ^e						392		59		99
Fulaerhtzi ^e		175	110			374	135	67		115
Zapuj ^f		207	97	92	87	326	127	63	61	96
GI No. 9/1 ^f		225	100	100	91					79
ZIN No. 4071 ^f						368	144	75	67	107
										89

WP: proximal width; WC: width of the Caput femoris; DC: depth of the Caput femoris; sWd: smallest diaphysis width; sDd: smallest diaphysis depth; WD: distal width; DD: distal depth.

^a Own data.

^b Altuna and Mariezkurrena (2000).

^c Castaños et al. (2009).

^d Guérin (1980).

^e Bonifay (1961).

^f Borsuk Białynika (1973).

the average European values) (Table 7). Analyzed fragmented postcranial elements fall within the European range standard of Bonifay (1961), Borsuk Białynika (1973) and Guérin (1980) (Tables 7–10).

5. Chronological context

Only 7 out of 23 Iberian sites with woolly rhinoceros fossils have absolute dates or an archaeological context associated with them (Álvarez-Lao and García, 2010; Table 1, Fig. 6).

La Parte (Asturias) represents the earliest evidence for this species on the Iberian Peninsula. The fossil remains are associated with a stratigraphic level radiometrically dated ($^{234}\text{U}/^{230}\text{Th}$) to 188.5–141.4 ka, with a likely age of around 150 ka BP, which corresponds to MIS 6 (Álvarez-Lao et al., 2002; Álvarez-Lao and García-García, 2006). Tentatively, we attribute Arroyo Culebro to the early Late Pleistocene due to the morphological features discussed above and the associated Lower Palaeolithic tools present at the site.

At least two episodes during MIS 3 and 2 are identified in Iberia with presence of woolly rhino (Álvarez-Lao and García, 2010).

The first of these episodes ranges from about 41 to 36 ka BP, coinciding with or very close to Heinrich event 4 (H4), a suspected cold interval dated to about 36–41 ka. Two sites included in this range are: a) Labeko Koba, where woolly rhino remains are found in two layers (Altuna and Mariezkurrena, 2000), one of them dated at 31.4 ^{14}C ka BP (35.7 cal ka BP) and another between 31.4 and 34.2 ^{14}C ka BP (35.7–38.9 cal ka BP); and b) Covacho de Arenillas (Castaños, 1996) with two radiocarbon dates of 33.7 and 34.6 ^{14}C ka BP (38.4 and 39.1 cal ka BP). Several sites reveal cold-adapted faunas in Iberia during this period and include the southernmost geographic distribution of woolly mammoth (*Mammuthus primigenius*), which reached Padul (Granada) during this time (Álvarez-Lao et al., 2009). Relatively frequent reindeer remains (*Rangifer tarandus*) in Northern Iberia and the presence of arctic fox (*Alopex lagopus*) are also representative of this type of fauna (Altuna, 2004; Álvarez-Lao and García, 2010). Environmental

fluctuations on a millennial scale which occurred during MIS 3 are recorded in the Atlantic Iberian margin ocean cores SU-8118 and MD95-2039 (Turon et al., 2003; Roucoux et al., 2005). An episode of steppe vegetation expansion along with high proportions of polar-affinity organisms and ice rafted debris (IRD) was identified in the cores corresponding in time with the H4 event (Roucoux et al., 2005). Coincident results were obtained for the same time period in the Mediterranean from the marine record MD95-2043, from the Alboran Sea (Moreno et al., 2005), and from the continental pollen record of Padul peat bog, where high proportions of the steppe taxa *Artemisia* and Poaceae were recorded (Florschütz et al., 1971; Pons and Reille, 1988).

The last episode that identifies woolly rhino presence on the Iberian Peninsula is detected between 32 and 20 ka covering H3, H2 and the LGM cold events (also Gravettian and Solutrean archaeological cultures). Woolly rhino remains from Lezetxiki come from Gravettian-Solutrean archaeological contexts (Altuna, 1972). The specimen from Cueva del Cuco were also found in a Gravettian context just below a level dated to 28.1 cal ka BP (Castaños and Castaños, 2007), which corresponds to the H3 event. The most recent dates for woolly rhino on the Iberian Peninsula are at 20.2 cal ka BP, from Leguintxiki (Castaños, 1996), and from Abauntz, associated with Upper Solutrean artefacts (Altuna et al., 2002). Cold and dry environmental conditions are also identified throughout this episode. During MIS 2, the occurrence of cold-adapted mammals in Iberia was again relatively common, especially during the H2 event, when most of these species reached maximum abundance (Álvarez-Lao and García, 2010). During the Last Glacial Maximum (LGM), which occurred between the H2 and H1 events, cold-adapted species were present and abundant in Northern Iberia, although a reduction in their abundance is identified towards the end of this period. Steppe environments were predominant through this episode on the Iberian Peninsula as indicated by pollen records from continental and marine sequences (Florschütz et al., 1971; Pons and Reille, 1988; Turon et al., 2003; Iriarte et al., 2005; Roucoux et al., 2005).

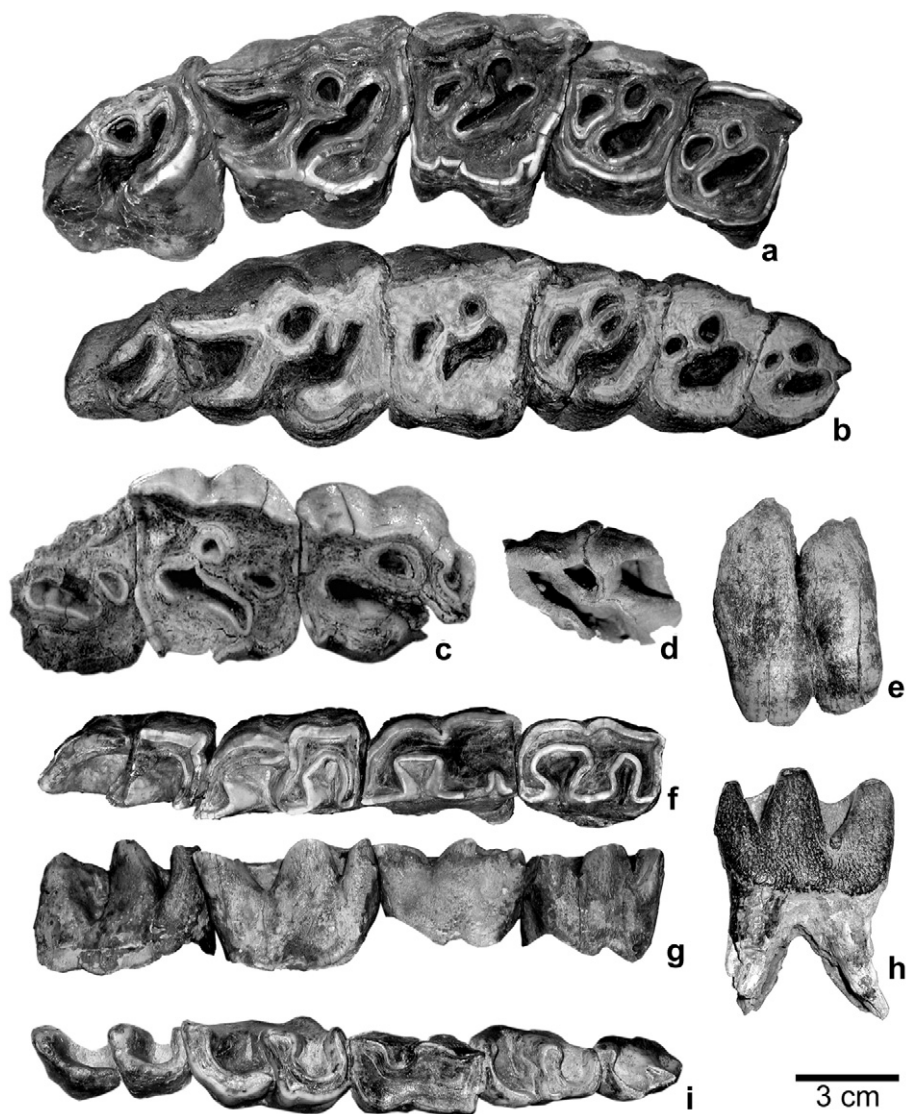


Fig. 3. *Coelodonta antiquitatis* dental elements from Iberian sites: Right P^2 – M^3 from Cueva de Nando in occlusal view (a). Right P^2 – M^3 from Arenys de Mar in occlusal view (b). Left M^1 – M^3 of skull "A" from Arroyo Culebro in occlusal view (c). Left M^3 germ from Cueva de San Pedro in occlusal view (d). Left M^3 germ from Aldehuela in labial view (e). Left P_4 – M_3 from Cueva de Nando in occlusal (f) and lingual (g) views. Right M_3 from Cueva de La Xana in lingual view (h). Right P_2 – P_3 – D_4 – M_1 – M_2 of the young mandible from Arroyo Culebro in occlusal view (i). All at the same scale.

6. Geographical distribution

Twenty of the 23 Iberian sites which yielded woolly rhinoceros remains are located in the north (18 in the Cantabrian area and 2 in Catalonia, Fig. 1) above $41^{\circ}35'N$ latitude, while the other 3 are in the central region (Madrid province) at about $40^{\circ}20'N$ latitude.

For the Madrid sites, the absolute chronology remains uncertain, although the data described above suggests the presence of woolly rhino during the early Late Pleistocene (from Arroyo Culebro) or during the Middle Pleistocene (from Los Rosales, following Sesé and Soto, 2002) at about $40^{\circ}N$ latitude.

The sites from Catalonia (north east Iberia), did not yield precise dates. The woolly rhino sites west of the Pyrenees (Asturias, Cantabria, Basque Country and Navarra) correspond to MIS 2 and MIS 3, with the exception of La Parte. Such a predominant northern distribution, westward and eastward of the Pyrenees, is in agreement with the suggestion that the Iberian Peninsula was relatively

isolated from continental Europe because the Pyrenees acted as a dispersal barrier (Álvarez-Lao and García, 2011).

Populations of woolly rhino coming from Southern France, where cold-adapted mammal faunas were abundant during the Late Pleistocene (Delpech, 1983), would likely come to the peninsula via the low topographic margins of the Pyrenees to the west (Basque Country) or the east (Catalonia). The fossil record agrees with this hypothesis. Given the lack of fossils between North and Central Iberia, is not easy to ascertain the tracks woolly rhinoceros made for Central Iberian.

The Iberian Peninsula constitutes the south-western boundary of the Eurasian distribution of *C. antiquitatis*. Its Holarctic geographical spread during the Late Pleistocene covers much of Eurasia, from the Iberian Peninsula to eastern Siberia and China, but this species never reached North America (Kahlke, 1999, 2006). The southernmost spread of woolly rhinoceros is mainly above latitude $40^{\circ}N$. In Europe, the southernmost site corresponds to Megalopolis, (Greece), at $37^{\circ}2'N$ latitude (Malez, 1972), while the world's



Fig. 4. *Coelodonta antiquitatis* cranial elements from Iberian sites: Skull "A" from Arroyo Culebro in lateral view (a). Skull "B" from Arroyo Culebro in lateral (b) and upper (c) views. Skull from Arenys de Mar in lateral (d), upper (e) and lower (f) views. Young mandible from Arroyo Culebro in occlusal (g) and lateral (h) views. All at the same scale.

southernmost recovery of this species is in China (Kahlke, 1999), reaching 33°N latitude (Chow, 1978).

7. Palaeoecological context

C. antiquitatis became widespread throughout Eurasia during the Late Pleistocene. However, it is never an abundant element of the typical cold-adapted faunas, which restricts palaeoecological analysis. In Sommer and Nadachowski (2006), European southern refugia were studied, although woolly rhinoceros was not included in the whole analysis. Moreover the northern half of the Iberian Peninsula represents the southern range limit of this species, which makes the Spanish finds of special interest from an ecological perspective.

7.1. Analysis of the faunal composition

Seven of the 23 studied Iberian sites provided precise data about the ungulate association, including percentages of each species (Table 11).

The ungulate composition of these Iberian samples and another 13 from Western and Central Europe which also included woolly rhinoceros, were compared (Table 11). The age of all the analyzed sites corresponds to either MIS 3 or MIS 2.

Percentages of each ungulate species into each assemblage have been calculated on the basis of the NISP (Number of Identified Specimens). We consider this estimator of good reliability (Lyman, 1994) since no taphonomic bias is indicated to any of the species of each assemblage.

In order to identify similarities and differences among the ungulate compositions of the Iberian assemblages with those from Western and Central Europe, they were statistically analyzed by means of a multivariate analysis, since the sample consists in a number of species by each assemblage. Because species proportions vary notably among the assemblages including the fact that some taxa are even absent at a number of the sites, a Correspondence Analysis (CA) was considered the most suitable statistical test, and was performed using the program PAST version 1.93 (Hammer et al., 2001).

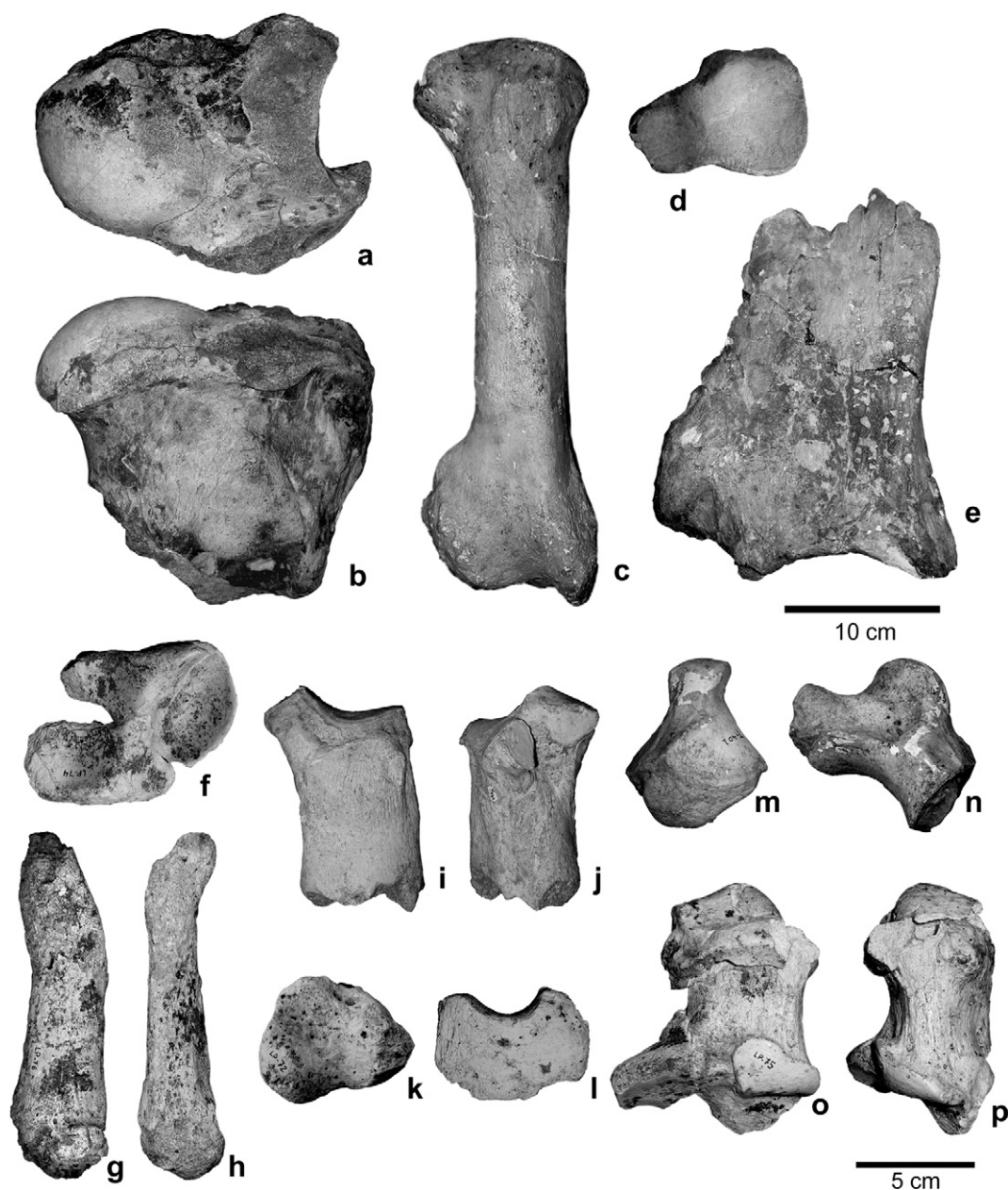


Fig. 5. *Coelodonta antiquitatis* postcranial elements from Iberian sites: Right humerus fragment from Cueva de Nando in proximal (a) and medial (b) views. Right radius from Los Rosales in anterior (c) and proximal (d) views. Right scapula fragment from Cueva de Nando in lateral view (e). Right tibia fragment from La Parte in distal view (f). Right metacarpal IV from La Parte in anterior (g) and lateral views (h). Right metacarpal III fragment from El Toll in anterior (i) and medial-posterior (j) views. Right scaphoid from La Parte in proximal (k) and anterior (l) views. Right magnum fragment from El Toll in anterior (m) and lateral (n) views. Left calcaneus from La Parte in medial (o) and caudal (p) views.

The CA analysis extracted four main factors whose eigenvalues and inertia values (see caption of Fig. 7) indicate a close association between sites with similar relative abundances of ungulate taxa. Most of the sites are arranged in a continuous gradient running diagonally to the first and second ordination axes (Fig. 7).

All Iberian sites (black dots), are placed at one end of the gradient, with the exception of U. Leizea. This association is characterized by abundance of red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*), the ibex (*Capra ibex/C. pyrenaica*) and presence of steppe rhino (*S. hemitoechus*, only at Lezetxiki). At the opposite end of the same gradient, the sites (almost all from Western-Central Europe) are characterized by high abundances of reindeer (*R. tarandus*), with presence of musk-ox (*Ovibos moschatus*, only at Kesslerloch). U. Leizea is the only Iberian site falling at this

side, clearly separated from the rest of the Iberian localities. Sites in the middle part of the gradient are characterized by abundance of horse (*Equus caballus/E. ferus/E. germanicus*), bovines (*Bison priscus/Bos primigenius*), cervids (*Capreolus capreolus/Megaloceros giganteus*) and wild boar (*Sus scrofa*). These species do not show significant difference between Iberian and Central-Western European sites. Finally, Lynford and Vogelherd, associated to abundance of woolly mammoth (*M. primigenius*), fall apart from the remaining sites.

7.2. Palaeoecologic interpretation

The Iberian sites are dominated by temperate fauna, with high percentages of *C. elaphus*, presence of *S. hemitoechus* and low

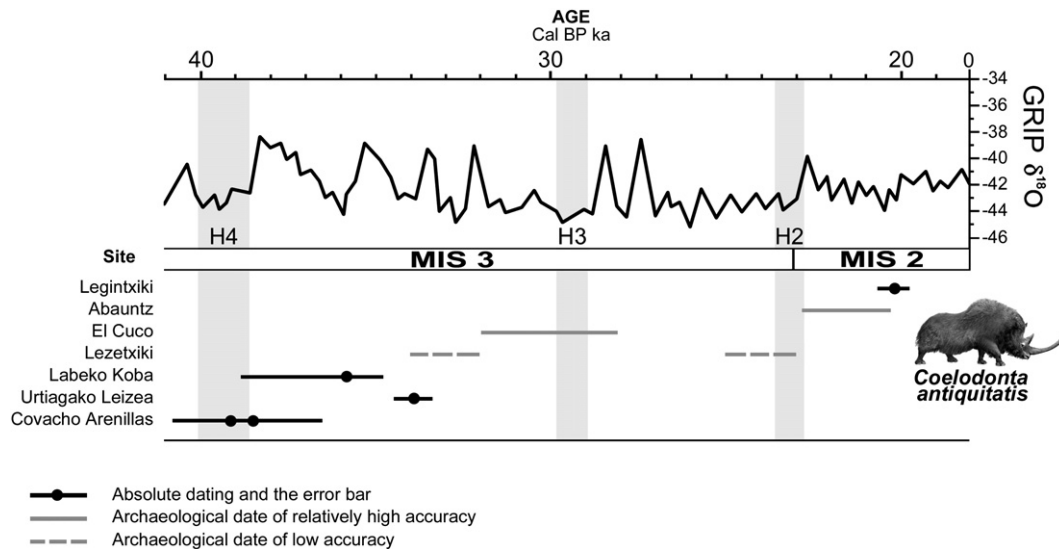


Fig. 6. Chronological distribution of the Late Pleistocene Iberian *Coelodonta antiquitatis* finds compared to the GRIP paleoclimatic oxygen curve and the marine isotope stages (MIS). The vertical grey bands indicate the main cold episodes (Heinrich events).

percentages of cold-adapted taxa such as *R. tarandus* and *M. primigenius*. The alpine taxa *R. rupicapra* and *Capra ibex/C. pyrenaica* are also abundant at the Iberian sites (Fig. 7), which may be explained by the topography. Iberian localities are clearly separated and placed at one extreme of the gradient. At the opposite extreme, the assemblages, almost all from Western-Central Europe, are dominated by cold-adapted species. In most of the cases, *R. tarandus* is the dominant species whereas *M. primigenius* is less frequent. Red deer (*C. elaphus*) are rare at these localities, with percentages below 2% at all the sites except in Wannan, where it reaches 15.4% (Turner, 1990). U. Leizea is the only Iberian site with a very similar faunal composition to the Western-Central European localities. This suggests it corresponds to an extreme cold episode of the MIS 3 stage (Fig. 6).

The faunal composition of the majority of the southern European peninsular sites (with the exception of Greece), as well as south-western France and the Carpathian region, indicates the co-occurrence of typical cold-adapted species alongside temperate species during the LGM (Sommer and Nadachowski, 2006). Studies focused on faunal communities that include *C. antiquitatis* are limited, reason why the Iberian data here analyzed are, in our opinion, of palaeoecological interest.

Iberian woolly rhinoceros assemblages show then a mixture of temperate and cold species which do not reflect the typical faunal composition of the Eurasian mammoth steppe (Guthrie, 1982) or *Mammuthus*–*Coelodonta* faunal complex (Kahlke, 1999), suggesting an interesting view on the palaeoecology of this ungulate in Iberia. These results do not contradict previous studies (Kahlke, 1999), and

Table 11
Percentages of ungulate taxa at different fossil assemblages from the Iberian Peninsula and Central-Western Europe.

Site (layer)	Country	Taxa													NISP	Source	
		R.t.	C.e.	M.g.	C.c.	C.i./p.	R.r.	Bov.	O.m.	S.s.	E.c.	E.h.	C.a.	S.h.			M.p.
Covacho de Arenillas (II)	Spain	0	16.5	0	3.5	76.4	0.4	0.8	0	0	1.2	0	0.4	0	0	254	Castaños, pers. com.
El Cuco (XIII)	Spain	0	68.2	0	0	0	2.3	9.1	0	0	6.8	0	13.6	0	0	44	Castaños and Castaños, 2007
Lezika	Spain	0.32	44.6	0	0	0	6.9	0.3	0	0	0	0	47.8	0	0	305	Castaños et al., 2009
Urtiagako Leizea	Spain	83.5	5.2	0	5.2	0.8	2.6	0.8	0	0	0	0	0.8	0	0.8	115	Altuna and Mariezkurrena, 2010
Lezetxiki (IIIa)	Spain	0.7	25.2	0	1	8.7	31.4	28.2	0	0.7	3.2	0	0.2	0.5	0	401	Altuna, 1972
Labeko Koba (IX sup.)	Spain	1.3	36.4	0.5	0.4	0	0.7	20.4	0	0.1	30.2	0	9.1	0	0.8	1008	Altuna and Mariezkurrena, 2000
Abautz (f)	Spain	1.3	23.4	0	0	16.9	33.7	5.2	0	2.6	15.6	0	1.3	0	0	77	Altuna et al., 2002
Lynford	G. Britain	5.4	0	0	0	0	0	0.3	0	0	0.4	0	1	0	92.8	1347	Schreve, 2006
Paviland, Goat's Hole Cave	G. Britain	44.6	0	1.7	0	0	0	29.9	0	1.7	9.1	0	12.1	0	0.8	212	Turner, 2000
Wannan (4-5)	Germany	6.1	15.4	0	0	0	0	0	0	0	35.4	0	41.5	0	1.5	65	Turner, 1990
Vogelherd (IV-V)	Germany	24	0.3	0	0	0	0.03	0.9	0	0.1	20.9	0	1.8	0	52	6810	Niven, 2007
Hohle Fels (IIb)	Germany	49.7	0	0	0	3.7	0.5	0	0	0	43.9	0	0.5	0	1.6	189	Münzel and Conard, 2004a
Geissenklösterle (AH IV-VIII)	Germany	38.4	1.4	5.1	1.4	14.5	3.6	0	0	0	15.2	0	5.8	0	14.5	138	Münzel and Conard, 2004b
Trou Magritte (2)	Belgium	50.5	0	0	0	17.2	0	0.5	0	4.4	21.6	0	3.9	0	1.6	180	Gautier, 1995
Kesslerloch (III)	Switzerl.	85	0	0	0	0.1	0	0.2	0.02	0	14.6	0	0.02	0	0.02	4149	Le Tensorer, 1998
Morancourt	France	3.2	1.1	1.3	0.5	0	0	21.7	0	0.3	54.1	0.8	13.3	0	3.5	368	Fosse, 1997
Theillat	France	0.7	0.4	11.7	0	0	0	15.2	0	2.5	42.7	0	25.6	0	1	284	Raynal et al., 1989
Roche à Pierrot (Saint-Césaire)	France	50.5	1.7	1.5	3.4	0	0	19.1	0	0.6	14.4	0.6	5.1	0	3	471	Pathou-Mathis, 2005
Abri du Facteur (Perig. V)	France	95	0.7	0	0	1.5	0.7	0.7	0	0.7	0	0	0.7	0	0	133	Bouchud, 1968
Roc de Combe (6)	France	83.6	1.1	0	0.5	0.5	0	5.4	0	2.7	2.7	0	0.5	0	2.7	183	Delpéch, 1984

Taxa abbreviations: R.t. – *Rangifer tarandus*; C.e. – *Cervus elaphus*; M.g. – *Megaloceros giganteus*; C.c. – *Capreolus capreolus*; C.i./p. – *Capra ibex/pyrenaica*; R.r. – *Rupicapra rupicapra*; Bov. – *Bovinae indet.*; O.m. – *Ovibos moschatus*; S.s. – *Sus scrofa*; E.c. – *Equus caballus*; E.h. – *Equus hydruntinus*; C.a. – *Coelodonta antiquitatis*; S.h. – *Stephanorhinus hemitoechus*; M.p. – *Mammuthus primigenius*.

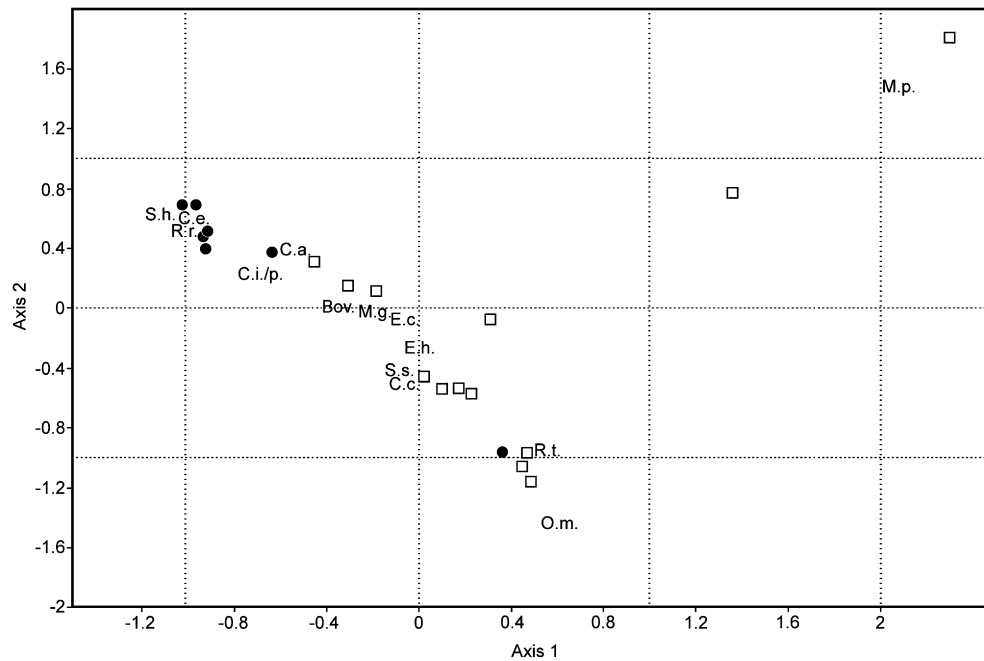


Fig. 7. Biplot of the two first axes extracted by the CA analysis. Four main factors were extracted by the CA, with eigenvalues of 0.6, 0.5, 0.4 and 0.3, which explained 27.2, 23, 19 and 11% of the inertia in the data, respectively. Iberian sites are indicated by black dots, Central-Western European sites are represented by unfilled squares. Abbreviations of the taxa are indicated in the caption of Table 11.

add new data on the southernmost European sites that represent a geographic limit of this species.

There are at least two reasonable explanations that could justify this particular situation of temperate faunas and woolly rhinoceros co-occurring at Iberian sites. These two hypotheses are not mutually exclusive and could be valid for different sites.

The first explanation could be that this faunal mixture supports the idea that woolly rhinoceros and the other cold-adapted taxa reached the Iberian Peninsula during the coldest and most arid episodes of the Late Pleistocene. When the conditions in the northernmost edge of the woolly rhino distribution range were inhospitable, they would have been pushed southwards and coexisted with, but not replaced, the local faunas. Other possible explanation could be the idea of a territorial expansion of woolly rhino populations during colder and dryer episodes caused by a southern expansion of areas with suitable environmental conditions. This hypothesis is especially suitable for sites like Abauntz, El Cuco and Covacho de Arenillas, whose absolute dates correspond to extreme cold episodes (LGM, H3 and H4 respectively, see Fig. 6). The faunal assemblage of U. Leizea, is the only one in the Iberian Peninsula which reflects a typical cold faunal composition that most likely corresponds to an extreme cold episode. The possibility of seasonal immigration of the woolly rhino towards southern areas during the winter is also considered. Sommer and Nadachowski (2006) compared the faunal composition of 47 LGM sites from traditional refuge areas in Europe, containing temperate mammal species. Three of them are clearly dominated by, *C. elaphus*, *C. capreolus* and *Vulpes vulpes*. Interestingly, nearly 40% of analyzed sites contained all three species together and red deer was the dominant species in 80% of all evaluated sites.

Second, the co-occurrence of cold-adapted and temperate faunas also suggests the possibility that the woolly rhinoceros reached the Iberian Peninsula during interglacial conditions, and confined within areas known as cryptic southern refugia, at which cold and arid steppe environments persisted.

The topic of Quaternary refugia, where the Iberian Peninsula plays an important role, is of great interest to a variety of

researchers. Among a number of definitions, we consider the one proposed by Stewart et al. (2010, p. 661) is especially flexible and capable of accommodating species that are adapted to different climatic conditions: “the geographical region or regions that a species inhabits during the period of a glacial/interglacial cycle that represents the species’ maximum contraction in geographical range”. There are several different categories of Quaternary refugia depending on the environmental conditions, the latitudinal location and the environmental preferences of each species. The cryptic refugia defined by Stewart and Lister (2001) are areas situated at different latitudes or longitudes than would normally be expected, and often resemble climatic islands in which conditions differ favourably from the surrounding areas. Cryptic southern refugia are interglacial refugia for cold-adapted species situated at lower latitudes (Stewart et al., 2010) and development of mountainous topography such as the Pyrenees (Angus, 1983). Furthermore, all these Iberian sites come from the vicinity of mountainous areas (Cantabrian Mountains and Pyrenees) which also agrees with the concept of cryptic southern refugia. Two of the analyzed Iberian woolly rhinoceros assemblages fit into the definition of cryptic southern refugia proposed by Stewart and Lister (2001) and Stewart et al. (2010) in which populations of cold-adapted species in cryptic southern refugia are often surrounded during interglacials by populations of temperate species that have expanded from their glacial refugia. Lezetxiki and Lezika are sites, that although have not yielded absolute dates (Altuna, 1972; Castaños et al., 2009), might likely correspond to a temperate phase during MIS 3. The woolly rhino fossils found in these sites might represent the traces of cryptic southern refugia, at which cold and arid steppe environments persisted, in the mountains of Guipúzcoa that might have existed at that temperate period, playing an important role for these taxa.

No evidence of a latitudinal gradient in the assemblage composition of ungulates, between the Iberian and the other European sites, was found. Abrí du Facteur and Roc de Combe (Southern France), which are relatively close to the Iberian Peninsula, show high percentages of reindeer (95% and 83.6% respectively), and low

percentages of red deer (0.75% and 1.09% respectively) (Bouchud, 1968; Delpech, 1984), differing largely from the Iberian values.

8. Discussion and conclusions

Twenty three Iberian sites yielded *C. antiquitatis* fossils. Morphological and biometrical analyses reveal that the upper dentition has high width to length values, which may be explained by advanced interdental attrition normally associated with mature or old specimens. The Iberian postcranial elements do not show remarkable differences from the rest of the European woolly rhino populations. The Iberian sample is not as abundant as in other Eurasian regions although it is abundant enough to show similar dimensions and morphology to those populations. Consequently, the Iberian *C. antiquitatis* population likely represents the westernmost distribution of the species, creating a continuous Eurasian belt of distribution.

The first episode of woolly rhino presence in the Iberian Peninsula can be placed during the late Middle Pleistocene and early Late Pleistocene, reaching a maximum southern spread in Madrid (about 40°N latitude). Later, during MIS 3 and 2, it was restricted to the Northern regions of Iberia occupying low regions west and east of the Pyrenees, likely adapted to the topography and natural barriers of the geography.

The southern expansion of *C. antiquitatis* during the Late Pleistocene in the Iberian Peninsula reached similar latitudes to other Eurasian areas, although the southernmost boundary is in China at latitude 33°N.

The presence of woolly rhinos on the Iberian Peninsula correlates to periods of extreme dry and cold climatic conditions documented in both Iberian terrestrial and marine sediment sequences as well as with cold climatic phases recorded in Greenland ice cores indicating transregional palaeoecological processes.

As Iberian *C. antiquitatis* finds are constrained to few concrete episodes and to specific geographic areas, it is most suitable to interpret these findings as sporadic entrances of individuals from European populations rather than assume established Iberian populations.

Association of woolly rhinoceros fossils with other taxa typically considered of temperate and forested environments, especially the red deer (*C. elaphus*), is frequent at Iberian sites, showing a mixture of temperate and cold elements which does not reflect the typical faunal composition of the Eurasian tundra-steppe. This particular situation suggests two possible explanations. First, migrations during the coldest time spans, resulting in a mixing of cold and temperate faunas, as opposed to faunal replacement. Second, persistence of woolly rhinoceros populations on the Iberian Peninsula during interglacial episodes, confined to cryptic southern refugia. These two hypotheses could be valid for different sites.

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