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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.

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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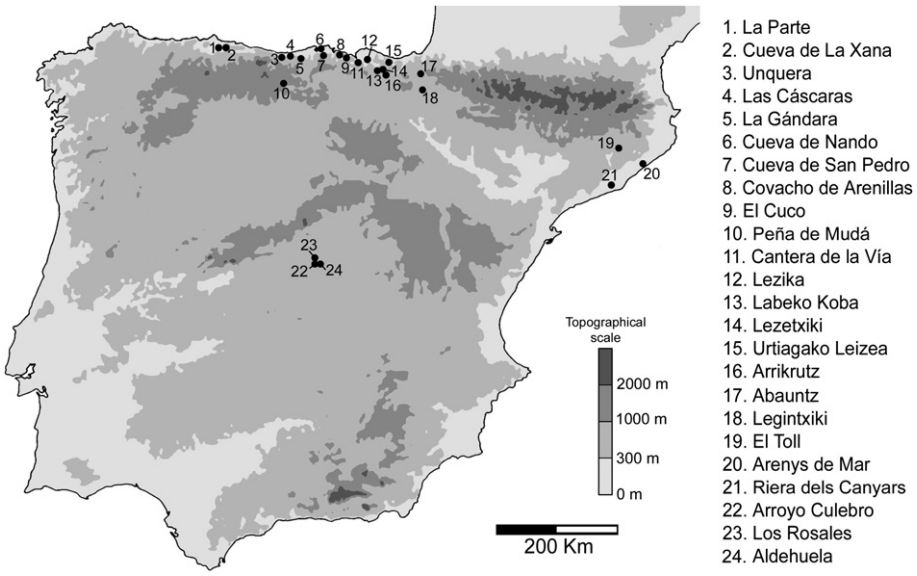

Fig. 1. Iberian sites with *Coelodonta antiquitatis* remains.

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 *Coelodonta*	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
Urtiagako Leizea	1/1	Mp. Rt.	33.9 cal ka BP	SSb.	Altuna, 1984; Altuna and Mariezkurrena, 2010	Altuna, 1984
Arrikrutz	1/1		Unknown	SSb.	Altuna, 1979	Altuna, 1979
Abauntz	1/1	Rt.	Upper Solutrean	Nav.	Altuna et al., 2002	Altuna et al., 2002
Leguintxiki	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; MNCN – 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.