The Jou Puerta cave (Asturias, NW Spain): A MIS 3 large mammal assemblage with mixture of cold and temperate elements

Diego J. Álvarez-Lao *

Departamento de Geología, University of Oviedo, C/Jesús Arias de Velasco s/n, 33005 Oviedo, Spain

ABSTRACT

The cave of Jou Puerta (Asturias, NW Spain), provided an interesting large mammal assemblage including cold-adapted elements like *Coelodonta antiquitatis* and *Mammuthus primigenius*, which are not frequent in Iberian sites. The chronology of the fossils ranges from 36.6 to 30.2 Cal ka BP, corresponding to MIS 3, an episode characterized by fast climate changes, from extreme cold to temperate conditions.

The origin of the bone accumulation is related to a natural trap, so most of the fossils were unusually well preserved. The woolly rhinoceros remains yielded one of the most numerous and well preserved populations of this species from the Iberian Peninsula, which allowed carrying out a detailed comparative anatomical study.

The faunal composition of Jou Puerta was statistically analyzed in comparison with other Iberian and Western European fossil assemblages where *C. antiquitatis* and/or *M. primigenius* occurred. The results showed that temperate ungulate species are predominant at most of the Iberian assemblages, including Jou Puerta, resulting in a particular mixture of temperate and cold elements which does not reflect the typical faunal composition of the Eurasian mammoth steppe. This particular situation supports the idea that these cold taxa only reached the Peninsula occasionally, during the coldest episodes of the Pleistocene, resulting in a mixing of cold and temperate faunas, instead of a faunal replacing.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Cold-adapted large mammals constituted a faunal community known as "mammoth fauna" (Vereschagin and Baryshnikov, 1982) or "*Mammuthus–Coelodonta* faunal complex" (Kahlke, 1999, in press), that was common in a wide area of Eurasia and North America during the Late Pleistocene. The Iberian Peninsula constituted the Southwestern limit of this faunal community. Occurrences of these species are normally very scarce in Iberian Pleistocene assemblages, but they are relatively more frequent during Marine Isotope Stage (MIS) 3 (Álvarez-Lao and García, 2010, 2011a), an episode marked by numerous and fast climate changes, from extreme cold to temperate conditions (Barron and Pollard, 2002; van Andel, 2002).

A new fossil assemblage with cold adapted taxa was discovered in April 2011 during the excavation works for a highway in Llanes (Asturias, NW Spain, Fig. 1), in a cave placed under a sinkhole. The cave, named Jou Puerta after a local name, was located at about 800 m of the current coastline and at 28 m above sea level. Numerous large mammal bones were scattered over the cave floor, most of them preserved in good condition, suggesting that a rich bone assemblage remained still into the sediments. Fossil remains were recovered during an intensive excavation campaign in the summer of 2011, few weeks before the cave was definitively destroyed by the highway works. An outstanding assemblage consisting of 1064 fossil remains was recovered. The assemblage includes an interesting faunal complex composed by a predominance of temperate species but with a remarkable presence of cold elements such as woolly rhinoceros (*Coelodonta antiquitatis*) and woolly mammoth (*Mammuthus primigenius*) (see Section 4).

Geologically, the cave formed in the carboniferous limestone of the Picos de Europa Formation (Martínez, 1980). There is a high density of karstic cavities in the area of Llanes (East Asturias), related to extensive carboniferous limestone masses, comprising more than 45 fossiliferous caves in a geographic area smaller than 30 km in length (Adán, 1997; Álvarez Laó, 2003). Some of these caves are known since the early 20th century (Harlé, 1912; Obermaier, 1916; Vega del Sella, 1916, 1930).

A paleontological comparative description of the ungulate fossil remains with special attention to the woolly rhinoceros (*Coelodonta antiquitatis*) population, the third largest assemblage of this species in the Iberian Peninsula, is provided in this work.

The ecological composition of the assemblage is statistically analyzed together with a number of faunal associations including *C. antiquitatis* and/or *M. primigenius* from the Iberian Peninsula and mainland Europe in order to verify if the Jou Puerta assemblage reflects the typical composition of the mammoth fauna.

2. Origin of the fossil accumulation

The origin of the Jou Puerta cave was related to a collapse sinkhole. The sinkhole, measuring 10 m in diameter and 8 m in depth, showed

* Tel.: +34 98 556 5435; fax: +34 98 510 3103.
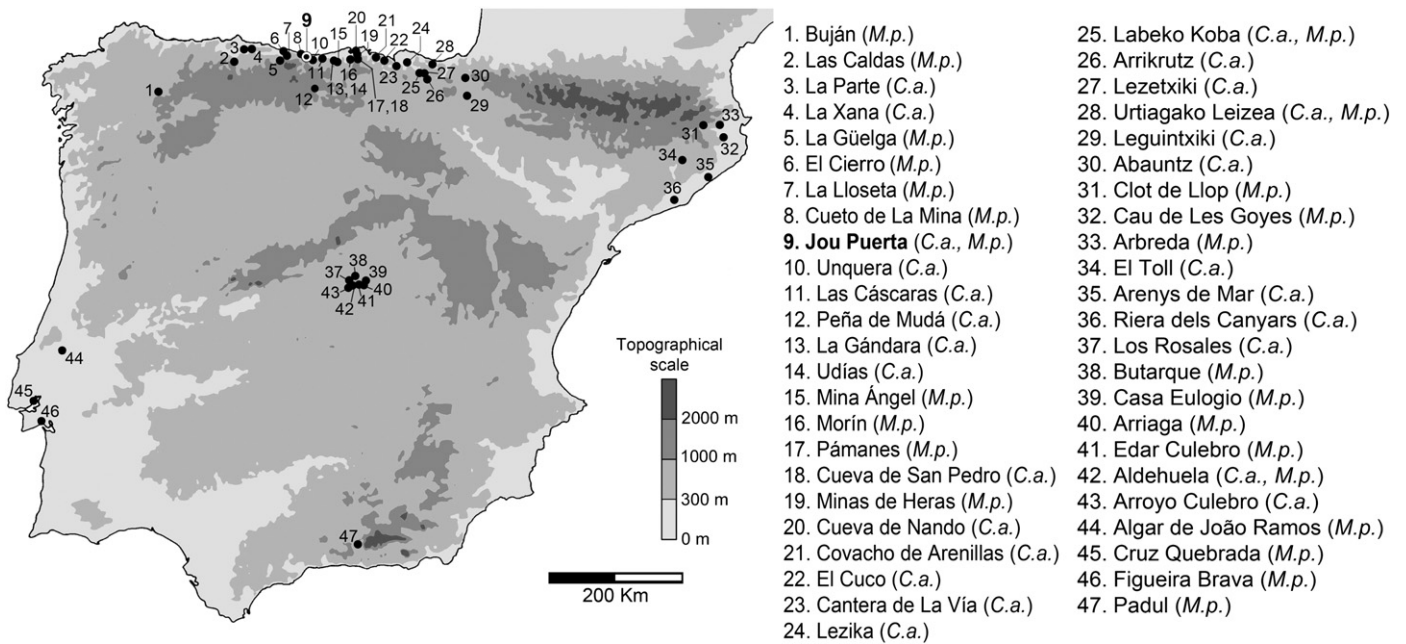 E-mail address: dalao@geol.uniovi.es.

1. Buján (*M.p.*)
2. Las Caldas (*M.p.*)
3. La Parte (*C.a.*)
4. La Xana (*C.a.*)
5. La Güelga (*M.p.*)
6. El Cierro (*M.p.*)
7. La Lloseta (*M.p.*)
8. Cueto de La Mina (*M.p.*)
9. Jou Puerta (*C.a., M.p.*)
10. Unquera (*C.a.*)
11. Las Cáscaras (*C.a.*)
12. Peña de Mudá (*C.a.*)
13. La Gándara (*C.a.*)
14. Udías (*C.a.*)
15. Mina Ángel (*M.p.*)
16. Morín (*M.p.*)
17. Pámanes (*M.p.*)
18. Cueva de San Pedro (*C.a.*)
19. Minas de Heras (*M.p.*)
20. Cueva de Nando (*C.a.*)
21. Covacho de Arenillas (*C.a.*)
22. El Cuco (*C.a.*)
23. Cantera de La Vía (*C.a.*)
24. Lezika (*C.a.*)
25. Labeko Koba (*C.a., M.p.*)
26. Arrikrutz (*C.a.*)
27. Lezetxiki (*C.a.*)
28. Urtiagako Leizea (*C.a., M.p.*)
29. Leguintxiki (*C.a.*)
30. Abauntz (*C.a.*)
31. Clot de Llop (*M.p.*)
32. Cau de Les Goyes (*M.p.*)
33. Arbreda (*M.p.*)
34. El Toll (*C.a.*)
35. Arenys de Mar (*C.a.*)
36. Riera dels Canyars (*C.a.*)
37. Los Rosales (*M.p.*)
38. Butarque (*M.p.*)
39. Casa Eulogio (*M.p.*)
40. Arriaga (*M.p.*)
41. Edar Culebro (*M.p.*)
42. Aldehuela (*C.a., M.p.*)
43. Arroyo Culebro (*C.a.*)
44. Algar de João Ramos (*M.p.*)
45. Cruz Quebrada (*M.p.*)
46. Figueira Brava (*M.p.*)
47. Padul (*M.p.*)

Fig. 1. Situation of the Jou Puerta site (no. 9) and other Iberian sites with *Coelodonta antiquitatis* (*C.a.*) and/or *Mammuthus primigenius* (*M.p.*). Modified from Álvarez-Lao and García (2011a,b, 2012).

a visible opening in the bottom which communicated with the cave below. The cave, measuring 48 m in length, 25 m in width and 12 m in depth (Fig. 2), was opened outwards after the collapse of the sinkhole above and, after a time lapse, it was closed again blocked by debris. The

fossils were associated to two main deposits: a pyramidal accumulation of debris located under the sinkhole, and a smaller debris fan placed in the lowest part of the cave (Fig. 2). A number of the fossils were found on the cave floor, occasionally covered by flowstone, and many others
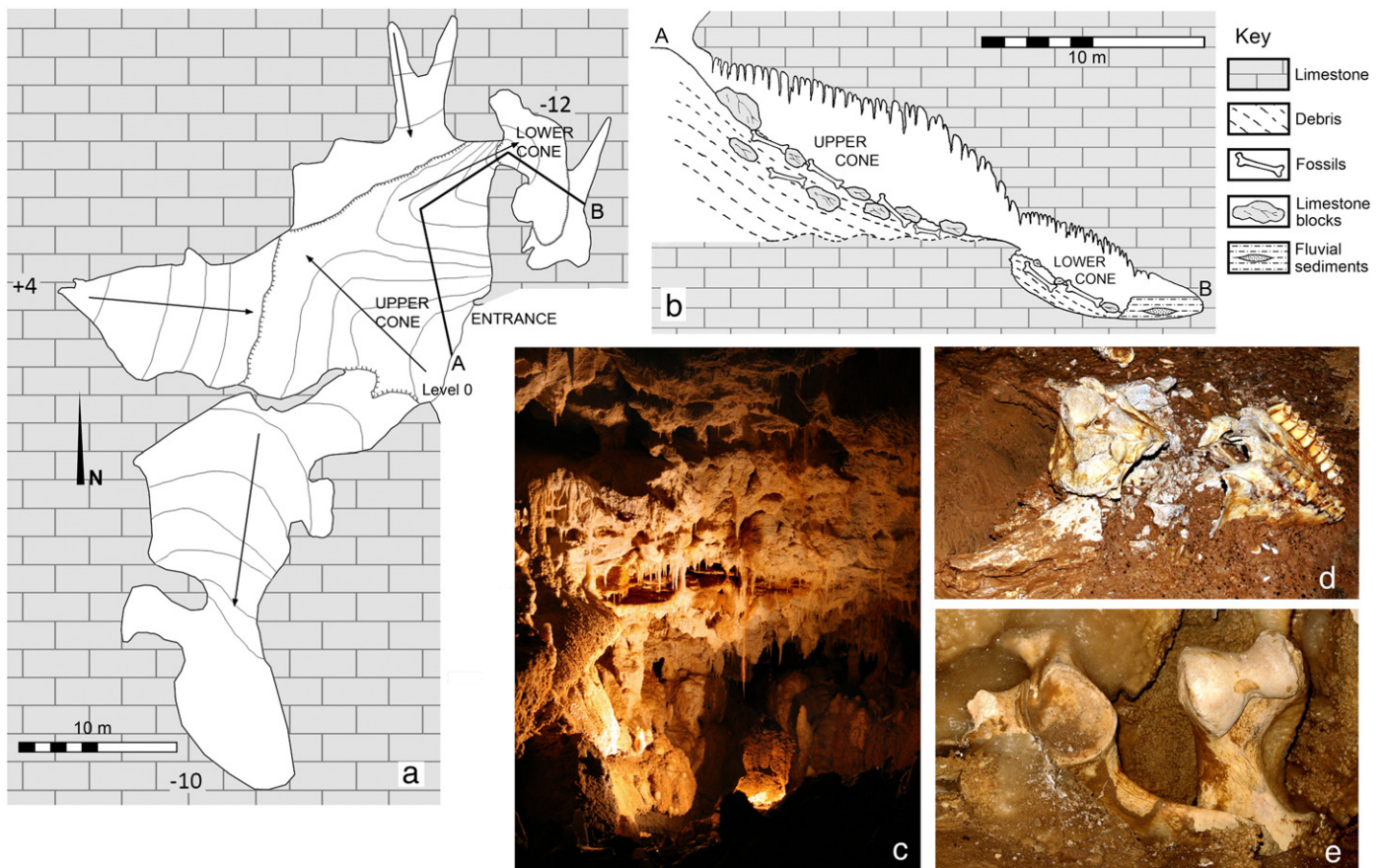

Fig. 2. The cave and the fossils before the excavation: site map showing the main debris deposits (upper and lower cones) where the fossils were recovered (a), sections A–B of the cave across the main fossiliferous deposits (b), view of the main gallery from the entrance (c), ibex skull on the floor of the cave (d), woolly rhinoceros innominate and humerus partially covered by flowstone (e).

were embedded in the debris. There was no clear stratigraphy in the fossiliferous deposits, which were associated to the input of debris into the cavity. Moreover, different anatomical elements corresponding to a single individual were found in different parts of the cave suggesting that episodic water flows scattered the sediments and fossils. The input of debris eroded a previous sedimentary sequence, probably of fluvial origin, that was examined but did not provide any fossils.

The most suitable explanation for the origin of the bone accumulation is that during the time between the opening and the closing of the cave, the sinkhole acted as a natural trap: a number of large mammals fell down into the cave and were either killed by the fall or unable to scramble out and thus starved to death, and their skeletons were preserved. Three radiometric dates of the bone assemblage comprise a time range of about 6 ka (see Section 5), which agrees with the idea that the cave was opened outwards during a relatively short geologic time lapse. In addition, half of the individuals in the assemblage (17 of 34) are young or immature (see Section 4), which also supports the hypothesis of a natural trap origin for the accumulation, since young individuals are relatively inexperienced and, as a consequence, are more likely to get into potentially fatal situations. The possibility that carnivores or humans were responsible for the bone accumulation should be discarded since most of the fossils are well preserved (Figs. 3, 4, 5). Normally, when bones are carried by humans or carnivores into a cave they are partially or totally destroyed (in order to extract the marrow) and show conspicuous biting and gnawing marks (in the case of carnivores) or cut marks by artifacts (in the case of humans). In the Jou Puerta assemblage there is no evidence of human activity, but a few elements (less than 5% of the remains), including some shed antlers, show biting and gnawing marks by carnivores (Fig. 5r). These marks can be interpreted as occasional carnivore activity, perhaps occurring at the end of the period at which the cave was opened, when it was almost obstructed by debris, thus allowing carnivores to exit the cave. Carnivores would be responsible of bringing the shed antlers (see Section 4.1.1.1.) and produce tooth marks in some bones which were previously in the cave but, in any case, they cannot be considered the authors of the bone accumulation.

3. Material and methods

A bone assemblage comprising 1064 fossil remains was recovered. The preservation degree was good in most cases; consequently, 91.3% of the remains (NISP = 971) were found to be taxonomically identifiable, and all belonged to large mammals, almost all of them ungulates (Table 1). The ungulate assemblage is composed by the species *Cervus elaphus* (red deer), *Megaloceros giganteus* (giant deer), *Capreolus capreolus* (roe deer), Bovini or *Bos/Bison* (aurochs/bison), *Capra pyrenaica* (ibex), *Rupicapra pyrenaica* (chamois), *Equus ferus* (horse), *Coelodonta antiquitatis* (woolly rhinoceros) and *Mammuthus primigenius* (woolly mammoth). Carnivores provided one single remain, a deciduous molar corresponding to a felid classified as cf. *Panthera pardus*.

Some of the bones were covered by flowstone, which hampered their recovery, requiring the use of an electric carbide saw to cut the speleothem. Some others were found in extreme fragility conditions due to moisture, so that an in situ consolidation of the bone with Paraloid B-72 was necessary, as well as its protection with a polyurethane foam crust. In most of the cases fossil preparation consisted only of removing the clay from the bones and consolidating them with Paraloid B-72. Exhaustive and careful laboratory work was necessary to remove the speleothem from some fossils, as well as to recompose and restore some others.

Three bone samples were AMS radiocarbon dated (see Section 5) by Beta Analytic (Florida). Two-sigma calibrated dates (95% probability) were used in order to correlate them with the paleoclimatic record represented in the Greenland Ice Core Project (GRIP). Therefore, calibrated dates are expressed in Cal ka BP (calibrated kiloannum before present).

Measurements taken on bones and teeth followed the standards of Driesch (1976) for artiodactyls and equids, Guérin (1980) for woolly rhinoceros, and Aguirre (1968) and Maschenko (2002) for woolly mammoth. All measurements are given in millimeters.

Morphometric data were compared with an extensive sample, mainly from Western Europe, published by a number of authors specified in Section 4 and in the captions of Tables 2 to 14.

Fig. 3. Cervid cranial and postcranial remains from Jou Puerta. *Cervus elaphus*: shed antler fragment in lateral view (a), right P^2–M^3 series in labial view (b), left P$_3$–M$_3$ series in lingual view (c), left humerus in posterior view (d), left femur in anterior view (e), right metatarsal in anterior view (f), left metacarpal in anterior view (g). *Capreolus capreolus*: female skull in right lateral view (h), right mandible fragment with the series P$_2$–M$_3$ in labial view (i); left humerus in posterior view (j); left metacarpal in anterior view (k). *Megaloceros giganteus*: shed antler basal fragment in posterior (l) and anterior (m) views, antler palm fragment and tine in anterior view (n).
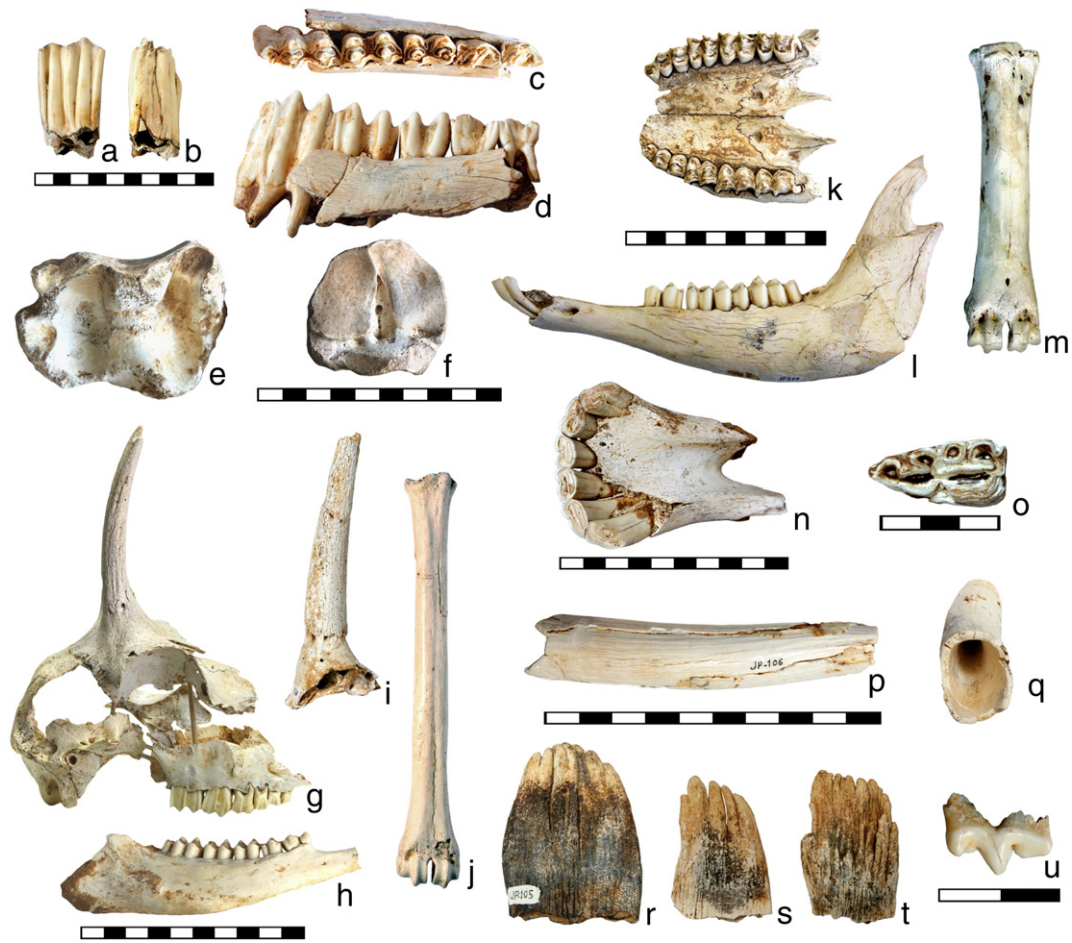
Fig. 4. Large mammal cranial and postcranial remains from Jou Puerta. *Bovini*: right M^2 in labial (a) and posterior (b) views, left P$_3$-M$_3$ series in occlusal (c) and lingual (d) views, right tibia in distal view (e), left metacarpal in proximal view (f). *Rupicapra pyrenaica*: female skull in right lateral view (g), right mandible fragment with the series P$_2$–M$_3$ in labial view (h), male right horn core in lateral view (i), left metatarsal in anterior view (j). *Capra pyrenaica*: palate with left and right P^2-M^3 series in occlusal view (k), left mandible with the series P$_3$–M$_3$ in labial view (l), left metacarpal in anterior view (m). *Equus ferus*: mandible fragment with the symphysis and the complete incisor series in occlusal view (n), left P$_2$ in occlusal view (o). *Mammuthus primigenius*: calf tusk in posterior (p) and apical (q) views, three deciduous molar plates in anterior view (r, s, t). cf. *Panthera pardus*: right D^3 in lingual view (u).

The age at death in some of the species has been estimated on the basis of molar wear and, in some cases, on the epiphyseal fusion degree of the limb bones. Age estimations followed the criteria published by diverse authors indicated in Section 4.

The fossils are stored at the Geology Department of the University of Oviedo (Spain).

4. Systematics: description of the remains and discussion

4.1. Order Artiodactyla (Owen, 1848)

4.1.1. Family Cervidae (Goldfuss, 1820)

4.1.1.1. Cervus elaphus (Linnaeus, 1758). Red deer was the dominant species in the Jou Puerta assemblage, comprising 40.67% of the remains (Table 1). The sample (Fig. 3a–g) included almost all anatomical elements, especially limb bones but also fragmentary cranial remains, axial elements, scapulae and a complete pelvis.

Age of death was estimated in cranial and postcranial elements following the criteria of Mariezkurrena (1983) and Brown and Chapman

(1991), and revealed the presence of a minimum number of eleven individuals in the assemblage. Concerning the age groups, two of the individuals were aged less than five months, five were aged between 15 and 36 months, three were aged between six and seven years and only one individual was older than ten years.

M$_3$ are the most numerous elements in the Jou Puerta assemblage and they were compared with a sample of Pleistocene red deer from Western Europe (Table 2). Although skeletal elements were well preserved, most of them belonged to young individuals (seven of the individuals were aged less than 36 months), and so their postcranial elements were still not fully developed at the time of death and were not useful for comparative studies. Only one of the four individuals older than six years provided a fairly complete skeleton, whereas the other three were basically represented by teeth. The most abundant postcranial elements were metapodials, but only three of them (two metacarpals and one metatarsal), all belonging to one single individual, were suitable for comparative purposes. Postcranial information was, therefore, very limited and I assume it is not representative enough for the whole sample. Size comparisons (Table 2) showed that specimens from Jou Puerta are more similar in size than those from Lezetxiki, Labeko Koba (both of MIS 3

Fig. 5. *Coleodonta antiquitatis* cranial and postcranial remains from Jou Puerta: subadult mandible in occlusal (a) and right lateral (b) views, right D^4-M^1 series in labial (c) and occlusal (d) views, left D$_4$-M$_1$–M$_2$ series in occlusal (e) and labial (f) views, cervical vertebra in anterior view (g), right scapula fragment in anterior view (h), mature left humerus in posterior (i) and medial (j) views, subadult right humerus in posterior view (k), subadult left humerus distal fragment in posterior view (l), mature left radius in posterior view (m), subadult right radius in dorsal view (n), subadult right forelimb with articulated humerus, radius and ulna, in medial view (p), left innominate in ventral view (o), subadult right femur fragment in anterior view (q), the same specimen in proximal-posterior view showing tooth marks by carnivores (r), left scaphoid in posterior view (s), articulated left metacarpals II, III, IV and unciform, in anterior view (t).
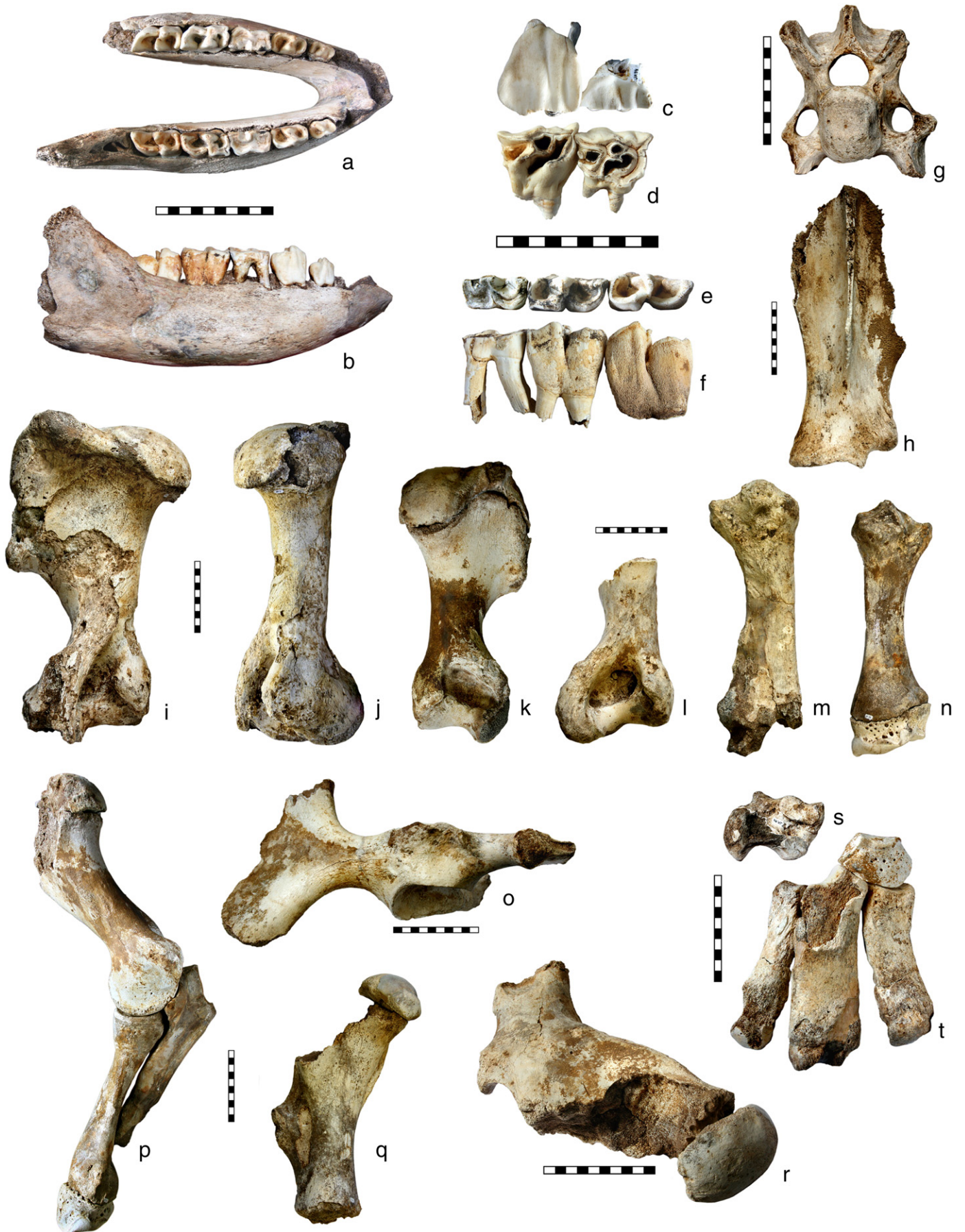
Table 1
Composition of the Jou Puerta faunal assemblage.

Taxa	NISP	% NISP	MNI	% MNI
Cervus elaphus	395	40.67	11	32.35
Megaloceros giganteus	8	0.82	1	2.94
Capreolus capreolus	101	10.4	4	11.76
Rupicapra pyrenaica	117	12.05	5	14.7
Capra pyrenaica	77	7.92	3	8.82
Bovini	159	16.37	4	11.76
Equus ferus	4	0.41	1	2.94
Coelodonta antiquitatis	105	10.81	3	8.82
Mammuthus primigenius	4	0.41	1	2.94
cf. *Panthera pardus*	1	0.1	1	2.94
Total	971	100	34	100

age; Altuna, 1972; Altuna and Mariezkurrena, 2000) and Zatoya (MIS 2; Mariezkurrena and Altuna, 1989), all them from cold stages and associated to cold-adapted taxa (reindeer, woolly rhinoceros). Furthermore,

specimens from these sites are larger than others corresponding to temperate stages, such as the ones from Swanscombe (MIS 7; Lister, 1986), Cova Negra and Camino Cave (both of MIS 5 age; Pérez Ripoll, 1977; Álvarez-Lao et al., 2013), suggesting that populations from cold stages are larger in body size than those from temperate phases. These size differences were previously observed by authors like Mariezkurrena and Altuna (1983) for Iberian red deer, and might reflect either Bergmann's rule (cold climate selects larger body sizes for survival) or perhaps differences in available resources under different environmental conditions: high quality vegetation from the cold stages favored ruminants like the red deer allowing them to reach a larger body size (Guthrie, 1990).

Fragments of eight shed antlers were also recovered. It is not easy to explain how such an amount of shed antler fragments could get into a natural trap. The only way by which these skeletal elements can get inside a cave is carried by humans or carnivores. As previously indicated, the possibility that carnivores or humans were responsible of the fossil accumulation should be discarded, since most of the bones are well

Table 2
Selected comparative measurements on *Cervus elaphus* cranial and postcranial elements.

Site		M$_3$ L	Mtc. PW	Mtc. DW	Mtt. PW	Mtt. DW
Jou Puerta[a]	Mean (n)	32.1 (4)	45.78 (2)	46.42 (2)	40.3 (1)	45.95 (1)
	Min–max	30.15–34.3	45.77–45.8	46.55–46.3		
Camino Cave[b]	Mean (n)	29.88 (11)	40.95 (5)	41.4 (5)	34.47 (4)	41.43 (3)
	Min–max	28.1–32.3	38.2–45.95	38.4–42.8	32.5–34.4	38.4–42.9
Cova Negra[c]	Mean (n)	30 (7)				
	Min–max	25.2–32.8				
Lezetxiki[d]	Mean (n)	32.26 (3)				
	Min–max	28.2–34.6				
Aitzbitatrte IV[d]	Mean (n)	34.6 (6)	47.65 (4)	47.73 (3)		
	Min–max	31.5–36.1	43.2–53.8	45.1–51.1		
Urtiaga D[d]	Mean (n)	34.8 (30)			38.98 (5)	46.65 (7)
	Min–max	30.1–38.1			35.6–44	42.7–53
Morín[e]	Mean (n)	35.27 (14)		43.13 (3)		
	Min–max	31–39.5		40–45,7		
Tito Bustillo[f]	Mean (n)	34.86 (13)		42.76 (15)		44.58 (12)
	Min–max	32–39		40–49		42–49.5
Zatoya[g]	Mean (n)	32.12 (4)				
	Min–max	28–34.5				
Labeko Koba[h]	Mean (n)	32.93 (12)	46.35 (7)	48.59 (11)	41.41 (11)	49.31 (8)
	Min–max	31–35	42.5–48	44–51	37–45	45–50.5
La Paloma[i]	Mean (n)	34.29 (89)	43.91 (6)	42.67 (70)	38.25 (4)	43.66 (43)
	Min–max	29.5–39	37.5–50.5	38.5–50.5	32–43.5	40.5–48.5
Las Caldas[j]	Mean (n)	34.96 (3)				
	Min–max	33.5–36.8				
Romain-la-Roche[k]	Mean (n)	31.8 (4)				
	Min–max	30–33.4				
Lazaret C II[l]	Mean (n)	34.5 (18)				
	Min–max	31.8–38.3				
Piégu[l]	Mean (n)	32.4 (10)				
	Min–max	29.3–37.4				
La Ferrassie[m]	Mean (n)	33.3 (7)				
	Min–max	31–37				
Vaufrey[n]	Mean (n)	32.2 (8)				
	Min–max	28.3–35.1				
Swanscombe[o]	Mean (n)	28 (3)				
	Min–max	27.8–28.3				

Mtc.: metacarpal; Mtt.: metatarsal; L: maximum length; PW: proximal width; DW: distal width.
[a] This study.
[b] Álvarez-Lao et al. (2013).
[c] Pérez Ripoll (1977).
[d] Altuna (1972).
[e] Altuna (1971).
[f] Altuna (1976).
[g] Mariezkurrena and Altuna (1989).
[h] Altuna and Mariezkurrena (2000).
[i] Castaños (1980).
[j] Soto and Meléndez (1981).
[k] Auguste (2010).
[l] Liouville (2007).
[m] Delpech (1984).
[n] Delpech (1988).
[o] Lister (1986).

Table 3
Selected comparative measurements on *Capreolus capreolus* cranial and postcranial elements.

Site		L P[2]–P[4]	LM[1]–M[3]	M[3] L	Hum. DW	Mtc. PW	Mtc. DW	Tib. DW
Jou Puerta[a]	Mean (n)	29.2 (1)	34.74 (1)	17.2 (2)	29.75 (5)	21.64 (3)	23.15 (4)	27.66 (4)
	Min–max			16.29–18.11	28.15–31.4	20.99–22.54	22.28–23.9	26.5–28.65
Urtiaga[b]	Mean (n)	29.8 (1)	38.9 (2)	16.53 (24)	31.15 (12)	19.2 (1)	24.4 (13)	30.7 (2)
	Min–max		38.7–39.1	14.5–17.6	28.2–33.4		21.3–27.9	29.9–31.5
Marizulo[b]	Mean (n)		34.7 (1)	15.2 (1)	28.45 (4)			
	Min–max				27–30			
Aitzbitarte IV[b]	Mean (n)	32.5 (1)			32.25 (2)			
	Min–max				31.5–33			
Santimamiñe[c]	Mean (n)	27.81 (8)	32.33 (12)	16.05 (27)	29.8 (13)			
	Min–max	26–29	30–35	14.2–17.6	28–32.5			
La Riera[d]	Mean (n)	29 (1)		16.88 (8)	29.4 (5)		24 (2)	
	Min–max			15.5–18	22.5–32		23.5–24.5	
Recent roe deer from Asturas[e]	Mean (n)	29.88 (7)	31.28 (7)	15.43 (3)				
	Min–max	25.01–41	24.4–34–98	15.1–15.77				

P[2]–P[4]: upper premolar series; M[1]–M[1]: upper molar series; Hum.: humerus; Mtc.: metacarpal; Tib.: tibia; L: maximum length; DW: distal width; PW: proximal width.

[a] This study.
[b] Altuna (1972).
[c] Castaños (1984).
[d] Altuna (1986).
[e] Álvarez-Lao (unpublished data).

Table 4
Selected comparative measurements on *Megaloceros giganteus* antlers.

	Jou Puerta[a]	Labeko Koba[b] (n = 4)		Ireland and Isle of Man[c] (n = 78)	
	JP-412	Mean	Min–Max	Mean	S.D.
MdR	92.1	88.25	83–93	107.07	12.06

MdR: maximum diameter of the rose.

[a] This study.
[b] Altuna and Mariezkurrena (2000).
[c] Gould (1974).

preserved. However, some carnivore activity (tooth marks) could be detected in the assemblage (see Section 2), so it is assumed that these shed antler fragments were carried into the cave by carnivores. The finding of shed antlers in assemblages produced by carnivores is not infrequent. At Guattari Cave (Mount Circeo), a typical hyena den, 56 shed antlers were recovered (Piperno and Giacobini, 1991; Stiner, 1991). In Northern Iberia, shed antlers carried by hyenas are noticed from sites like A Valiña, Lugo (Fernández Rodríguez, 2000), and Labeko Koba and Torre, Guipúzcoa (Altuna and Mariezkurrena, 2000, 2010).

One of the red deer shed antlers, which preserved the rose and part of the beam under the third tine (JP-296, Fig. 3a), is of extraordinary large size. Several carnivore gnawing marks were observed in the beam and in the bases of the tines. Some measurements are: maximum diameter of the rose—90.9 mm; circumference of the rose—273 mm; circumference of the beam between the first and second tines—265 mm; circumference of the beam between the second and third tines—207 mm. The unusually large size of this specimen is closer to the current wapitis (*Cervus elaphus canadensis*) than to the European

Table 5
Selected comparative measurements on *Bovini* cranial and postcranial elements.

Site		M[2] L	L M[1]–M[3]	M[3] L	Tib. DW
Jou Puerta[a]	Mean (n)	36.63 (1)	106.42 (1)	48.01 (1)	84.6 (2)
	Min–max				81.9–87.3
Lezetxiki[b]	Mean (n)		97 (1)	45.5 (1)	83.7 (4)
	Min–max				79.5–87.3
Leibar[b]	Mean (n)		92 (2)	38.75 (2)	
	Min–max		91–93	38.5–39	
Labeko Koba[c]	Mean (n)	32.57 (7)	104.25 (6)	46.47 (18)	82.87 (4)
	Min–max	28.5–37	103–105	38–53	79–85.5
Santimamiñe[d]	Mean (n)		104.75 (2)	41.94 (9)	95 (1)
	Min–max		93–116.5	37–52	
Lumentxa[e]	Mean (n)			46 (1)	89 (1)
	Min–max				
Bolinkoba[e]	Mean (n)			48 (2)	
	Min–max			47–49	
Aitzbitarte III[f]	Mean (n)	30.6 (1)		44.5 (1)	
	Min–max				
Kiputz IX (*Bison priscus*)[g]	Mean (n)				84.88 (25)
	Min–max				70–104
Habarra (*Bison priscus*)[h]	Mean (n)	33.14 (7)	102.83 (6)		84.07 (7)
	Min–max	26–35.5	93.5–112.5		77.5–93.5

M[1]–M[3]: lower molar series; Tib.: tibia; L: maximum length; DW: distal width.

[a] This study.
[b] Altuna (1972).
[c] Altuna and Mariezkurrena (2000).
[d] Castaños (1984).
[e] Castaños (1986).
[f] Altuna and Mariezkurrena (2011).
[g] Castaños et al. (2012).
[h] Prat et al. (2003).

Table 6
Selected comparative measurements on *Rupicapra pyrenaica* cranial and postcranial elements.

Site		M^1 L	M^2 L	M_3 L	Hu. DW	Ti. DW	Mtt. PW
Jou Puerta[a]	Mean (n)	12.0 (4)	13.59 (4)	19.3 (1)	32.16 (2)	27.22 (3)	20.86 (5)
	Min–max	10.53–13.8	12.9–14.24		30.96–33.36	26.4–28.87	20–22.4
Conde Cave[b]	Mean (n)	11.5 (7)	13.08 (7)	18.14 (1)			
	Min–max	10.75–12.01	12.05–13.67				
Naranco[b]	Mean (n)	13.34 (5)	13.82 (2)	17.46 (4)	30.42 (7)	26.26 (10)	21.81 (10)
	Min–max	12.75–14.04	13.65–14	16.3–18.88	29.46–33.4	25.36–27.92	21.05–23.09
Malverde[b,c]	Mean (n)			17.4 (20)	31.35 (4)	26.32 (5)	21.45 (6)
	Min–max			15.2–19	31–32	25–27.6	20–23.3
Aitzbitatre IV[d]	Mean (n)				33.55 (23)	32 (2)	
	Min–max				30.3–28.4	30–34	
Lezetxiki[d]	Mean (n)			17.96 (19)	33.25 (2)	27.88 (6)	
	Min–max			16.4–19	32.1–34.4	26.3–29.5	
Urtiaga[d]	Mean (n)			18.95 (16)		29.91 (8)	
	Min–max			15.3–20.6		27.6–32.8	
Amalda[e]	Mean (n)			17.83 (3)		28.75 (2)	
	Min–max			17.3–18.5		28.5–29	
Ekain[f]	Mean (n)			17.4 (6)			
	Min–max			16.1–18.5	31 (1)		22.66 (3)
Erralla[g]	Mean (n)			18.62 (4)			
	Min–max			18.3–19			
Abauntz[h]	Mean (n)			18.16 (6)	32.65 (4)	28,5 (2)	
	Min–max			17.1–18.7	31.5–33.5	28–29	
La Paloma[i]	Mean (n)			16,73 (2)	31.5 (3)	28.5 (1)	
	Min–max			14.72–18.75	31–32		
Santimamiñe[j]	Mean (n)			18.5 (8)	32.21 (7)		22–23.4
	Min–max			17–19.7	30.5–35		
Lumentxa[k]	Mean (n)			17.9 (2)		26.75 (2)	20.36 (3)
	Min–max			17.4–18.4		25.5–28	18.9–23
Valdegoba[l]	Mean (n)				30,73 (8)	26,32 (27)	22.61 (16)
	Min–max				28.8–33	23.2–28.5	20.6–26
Recent Cantabrian chamois (Asturias)[b]	Mean (n)	11.43 (63)	12.58 (58)	15.56 (129)			
	Min–max	8.5–13.42	11.04–13.95	13.31–17.95			

Mtc.: metacarpal; Mtt.: metatarsal; L: maximum length; PW: proximal width; DW: distal width.

[a] This study.
[b] Álvarez-Lao (unpublished data).
[c] Lorenzana (1982).
[d] Altuna (1972).
[e] Altuna (1990).
[f] Altuna and Mariezkurrena (1984).
[g] Altuna and Mariezkurrena (1985).
[h] Altuna et al. (2002).
[i] Castaños (1980).
[j] Castaños (1984).
[k] Castaños (1986).
[l] Arceredillo et al. (2011).

red deer: considering that very few wapitis on the record exceed 279 mm of beam circumference between tines one and two (Geist, 1999), the antler from Jou Puerta could correspond to an individual as large as the largest current wapitis.

4.1.1.2. Capreolus capreolus (Linnaeus, 1758). Roe deer comprised 10.4% of the assemblage (Table 1), including one complete female skull, isolated teeth and almost all postcranial elements (Fig. 3h–k), well preserved, corresponding to at least four individuals (three adults and one immature). Selected measurements were compared with a sample of fossil and recent roe deer from Iberian sites (Table 3), showing that size of the Jou Puerta remains is not significantly different from the comparison sample.

Roe deer is in general very poorly represented in Western European Pleistocene sites, as was also noted by Lister (1986) for British localities. This author suggested that there might be a general taphonomic bias against this species. However, in Jou Puerta this cervid was relatively abundant, probably due to a lack of bias in connection with the natural trap-related origin (i.e. lack of human or carnivore activity) of the assemblage.

The presence of roe deer in Jou Puerta is interesting from a paleoecologic point of view, since this cervid is infrequent or lacking in assemblages associated to cold-adapted elements such as *Mammuthus*

primigenius and *Coelodonta antiquitatis*. This aspect is widely discussed in Section 6.

4.1.1.3. Megaloceros giganteus (Blumenbach, 1799). Giant deer was represented by eight antler fragments which, most probably, corresponded to the same left shed antler. The largest fragment (JP-412, Fig. 3l–m) preserved the basal portion with the rose or burr, the base of the brow tine, and part of the beam until the starting of the palm. Other remains include some broken tines and palm fragments (Fig. 3n). The size of the basal portion (Table 4) was compared with a sample from Ireland and the Isle of Man published by Gould (1974) and with several specimens from Labeko Koba, Guipúzcoa (Altuna and Mariezkurrena, 2000). The specimen from Jou Puerta is similar in size to the ones from Labeko Koba but is slightly smaller than the average values provided by Gould (1974), suggesting that it probably corresponded to an immature individual.

These fragments of a single antler constitute the sole evidence of *Megaloceros giganteus* presence in this assemblage. Considering that shed antlers are not infrequent in assemblages produced by carnivores, as was previously argued for the red deer (see Section 4.1.1.1), it is interpreted that this antler was carried into the cave by carnivores. A similar pattern is noticed in Labeko Koba, Guipúzcoa, where giant deer is represented mainly by shed antler fragments, which are interpreted to have been carried into the cave by hyenas (Altuna and

Table 7
Selected comparative measurements on *Capra pyrenaica* cranial and postcranial elements.

Site		L P²–P⁴	LM¹–M³	M₃ L	Mtc. PW	Mtc. DW	Tib. DW
Jou Puerta[a]	Mean (n)	24.58 (1)	53.6 (1)	25,52 (2)	34.17 (4)	37.63 (3)	38.26 (2)
	Min–max			24.54–26.5	29.65–36.29	36.72–38.11	37.69–38.83
Urtiaga[b]	Mean (n)			26.82 (31)	35.1 (1)	37.62 (12)	33.25 (3)
	Min–max			23.5–29.3		33.3–41.7	31–36.5
Lezetxiki[b]	Mean (n)			27.4 (2)			
	Min–max			26.5–28.3			
Morín[c]	Mean (n)						32.16 (3)
	Min–max						31–33.5
Tito Bustillo[d]	Mean (n)	22.85 (2)			35.5 (1)	35,75 (2)	33,5 (1)
	Min–max	21.7–24				34–37.5	
La Riera[e]	Mean (n)	24.5 (2)		23.78 (23)	29 (2)	35.66 (3)	31 (6)
	Min–max	23.5–25.5		19.5–28.5	28–30	30–39	29.5–34.5
Amalda[f]	Mean (n)			27,5 (2)	32 (1)		33 (1)
	Min–max			26–29			
Ekain[g]	Mean (n)			25.06 (3)		39.5 (1)	32.33 (3)
	Min–max			18.2–28.5			30.5–35.5
Erralla[h]	Mean (n)	25.62 (4)	48.62 (4)	25.92 (7)	34.66 (3)	37.5 (4)	34.5 (8)
	Min–max	23.5–29	44.5–54	23–29	33.5–35.5	33–41	29–39
Abauntz[i]	Mean (n)			24.83 (3)			
	Min–max			22.5–26.5			
Zatoya[j]	Mean (n)			25 (7)			
	Min–max			22–28			
Santimamiñe[k]	Mean (n)	25.5 (4)	48.62 (4)	26.81 (8)		35.3 (5)	35.33 (3)
	Min–max	22.5–31.5	44.5–54	21.5–32.5		30.5–41	33.5–38.5
Bolinkoba[l]	Mean (n)	27 (1)		26.03 (37)	29.73 (3)	39.5 (3)	
	Min–max			22–28.5	29.5–30	33–43.5	

P²–P⁴: upper premolar series; M¹–M¹: upper molar series; Mtc.: metacarpal; Tib.: tibia; L: maximum length; PW: proximal width; DW: distal width.

[a] This study.
[b] Altuna (1972).
[c] Altuna (1971).
[d] Altuna (1976).
[e] Altuna (1986).
[f] Altuna (1990).
[g] Altuna and Mariezkurrena (1984).
[h] Altuna and Mariezkurrena (1985).
[i] Altuna et al. (2002).
[j] Mariezkurrena and Altuna (1989).
[k] Castaños (1984).
[l] Castaños (1986).

Mariezkurrena, 2000). Occurrences of *M. giganteus* in Iberia are of special interest since, up to date, only nine other reliable citations of this species are known from NW Iberia (Altuna, 1972; Fuentes Vidarte, 1980; Altuna and Mariezkurrena, 1984; Altuna, 1990; Altuna and Mariezkurrena, 2000; Domingo et al., 2005; Álvarez-Lao and García-García, 2006; Mariezkurrena-Gastearena, 2011).

Table 8
Selected comparative measurements on *Equus ferus* cranial and postcranial elements.

Site		P₂ L
Jou Puerta[a]	Mean (n)	36.6 (1)
	Min–max	
Lezetxiki[b]	Mean (n)	39.6 (2)
	Min–max	39.1–40.1
La Riera[c]	Mean (n)	32.06 (11)
	Min–max	28–35
Labeko Koba[d]	Mean (n)	32.81 (8)
	Min–max	31–35.5
Cueto de La Mina[e]	Mean (n)	33 (10)
	Min–max	32–35.5
Santimamiñe[f]	Mean (n)	33.68 (10)
	Min–max	31.9–36.1

P₂L: maximum length of P₂.
[a] This study.
[b] Altuna (1972).
[c] Altuna (1986).
[d] Altuna and Mariezkurrena (2000).
[e] Castaños (1982).
[f] Castaños (1984).

4.1.2. Family Bovidae (Gray, 1821)

4.1.2.1. Tribe Bovini (Gray, 1821).
Bovines were the second taxon in abundance in the Jou Puerta assemblage, making up 16.4% of the remains (Table 1). Cranial and postcranial remains were present in the assemblage, most of them belonging to young individuals. Identification at species level was difficult in this assemblage, as is discussed below.

One adult M² (JP-1018, Fig. 4a–b) shows the entostyle very projected lingually (especially visible in mesial view), which is accepted by Slott-Moller (1988) as an indicative feature of *Bos primigenius*. Anterior and posterior lobes (corresponding to protocone and hypocone, respectively) are projected toward the lingual side in a similar degree, which is proposed by Byrne (1979) as a typical feature of *B. primigenius* and different from *Bison priscus* (in which the anterior lobe is visibly more lingually projected than the posterior one).

One adult left mandible fragment preserved the P₃–M₃ series (JP-760, Fig. 4c–d). The M₃ hypoconulid draws a wide angle, of about 180°, with the hypoconid (in occlusal view), which is admitted by Koken (1885) and Stampfli (1963) as a typical feature of *Bos primigenius*. However, the taxonomic validity of this character is discussed by other authors such as Delpech (1983).

A horn core fragment (JP-560), corresponding to a large specimen, shows an ellipsoidal shape in cross section, which is more comparable to *Bos primigenius* than to *Bison priscus* (whose horn core is round shaped in cross section).

One adult right tibia fragment (JP-984, Fig. 4e) preserved the distal epiphysis showing both the anterior and posterior malleolar facets

Table 9
Selected comparative measurements on *Coelodonta antiquitatis* teeth.

Site		D_4 L	D_4 W	P_2 L	P_2 W	P_3 L	P_3 W	M_1 L	M_1 W	M_2 L	M_2 W	D^4 L	D^4 W	M^1 L	M^1 W
Jou Puerta[a] (Series)	JP-5 left	39.4	23.25	24.3	15.17	32.81	18.35	44.01	26.07	47.3					
	JP-5 right	38.55	23.3	24.2	14.8	33.35	19.5	45.1	26.3	46.73					
	JP-96-97-98	41.85	21.84					51.41	28.85	54.74	29.92				
	JP-99-100-101	41.55	22.27					50.64	28.97	54.66	29.44				
	JP-94-95											46.24	40.55	50.04	50.17
La Parte[b]				29.6	19.7	32.5	25								
Cueva de Nando[c]	Upper r.													47	59.5
	Lower l.							41.9	27.8	47	28.6				
	Lower r.							40.2	27.3	47.7	27.2				
Arenys de Mar[c]	Upper l.							41.8	60.5						
	Upper r							48.5	59						
Arrikrutz[d]								49	54						
Labeko Koba[e]	Lower l.			27	18.6	32	24	42.5	32.5	51.5	32.5				
	Lower l.			29.5	18.5	37	24								
	Lower r.					38	24	54	31	57	32.5				
	Isolated Teeth	40	20.5	34	27	45	28				31	44	39.3	55	58
		46.5	24	35.5	26.5	45	28.5				31	46	38.5	49	60
												46	38	54	59
												52	45		
Arroyo Culebro[f,g]	Lower l.	41.5	25.5	29.5	20.5	37	24.5	52	31	54					
	Lower r.	43	25	30	20	38.5	26	51.5	30.5	54					
Lezika[h]				44	39.3										
European Sites[i]	n	12	13	13	14	27	30	31	43	45	52	20	23	43	47
	Mean	42.3	22.5	29	18.7	34.2	24	47.7	29.3	50.7	31.4	48.6	43.3	50.8	52.7
	Min.	37	19	23	16	29	18	38	23	42.5	24	44	39	43.5	43.5
	Max.	51	25.5	35.5	22	39.5	29	56	33	58.5	38.5	57	55	58.5	61
Aven de Coulon[j]								34	31	45	29			32	51
Starunia[j]								48	21	40	18				
Kesslerloch[j]								50.7	33.6	58.7	32.3				
Ordos[j]								53	30	58	34			42	50
Wieringermeer[k]				18.5	13.4	27.6	18.5	35.5	29.5	42	29.7				

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

[a] This study.
[b] Álvarez-Lao and García-García (2006).
[c] Álvarez-Lao and García (2011b).
[d] Altuna (1979).
[e] Altuna and Mariezkurrena (2000).
[f] Arsuaga and Aguirre (1979).
[g] Soto and Sesé, 1991.
[h] Castaños et al. (2009).
[i] Guérin (1980).
[j] Bonifay (1961).
[k] Badoux (1964).

clearly separated by a prominent notch, which is considered by Gee (1993) as a reliable character for the identification of *Bison*.

The left metatarsal JP-1000 (Fig. 4f) shows another interesting character of taxonomic significance: the two largest proximal facets (for the 2nd/3rd tarsal and the cubonavicular) are anteriorly clearly confluent and demarcated by a small ridge, which is also considered a reliable character for *Bison* by Gee (1993).

In sum, cranial remains are more comparable with *Bos* while post-cranial features resemble those of *Bison*. Considering this contradictory taxonomic information, a definitive assignation of the remains to a single species is very difficult, so I considered more favorable to maintain the classification as Bovini.

The remains belonged to a minimum of four individuals: three calves and one adult. The age at death was estimated on the basis of teeth wear by analogy with living American Bison (*Bison bison*), assuming an equivalent ontogeny with the extant species, following Frison et al. (1976), Frison (1978), Todd et al. (1990) and Niven and Hill (1998). The age of the three calves was estimated to be around one month (the youngest), 4–5 months and 6–7 months (the oldest one). The adult individual (corresponding to mandible JP-760, Fig. 4c–d) was around 5–6 years at the time of death.

Since most of the fossils belonged to young individuals, their post-cranial elements were still not fully developed at the time of death and they were not considered useful for comparative studies. Some

metric features from the adult individual are included in Table 5. Although sample size is small, it is interesting to observe that teeth from Jou Puerta are larger in size than the average values of the comparison sample. The postcranial values (taken in the tibia) are also larger than in most of the comparison populations.

4.1.2.2. Rupicapra pyrenaica (Bonaparte, 1845). Chamois comprised 12.05% of the fossil remains (Table 1). Cranial elements are relatively numerous, including a female skull partially preserved, and postcranial elements were also conserved (Fig. 4g–j).

Remains corresponded to a minimum of five individuals: three adults and two calves. Although elements were relatively well preserved, the sample was too small to allow reliable comparative analyses. However, some measurements (Table 6) indicate that their size is similar to other fossil populations.

An interesting feature seen in the female skull JP-395 is that horn cores are visibly curved forward (Fig. 4g). Moreover, the horn core is also slightly curved forward in the male skull fragment JP-336 (Fig. 4i), suggesting that this trait is not an individual malformation but perhaps a particular feature of the population. Compared with a sample of 62 recent chamois skulls coming from Asturias (where the cave is placed), this trait was not observed in any specimen (horn cores of recent chamois were vertical, straight or slightly bent backwards at its top, in all observed cases). Nevertheless, features similar to the Jou Puerta chamois horn core

Table 10
Selected comparative measurements on *Coelodonta antiquitatis* scapula and humeri.

Site		Scapula		Humerus							
		sDC	GDP	GL	WP	DP	Wtd	sWd	sDd	WD	DD
Jou Puerta[a]	JP-13	114.2	146.5								
	JP-1			445	242	216	188	90	90.5	176	134
	JP-2									160	119
	JP-3			384	201		139	74.2	74.8		119
Cueva de Nando[b]		133	170	225	180						
Labeko Koba[c]		124	162.5								
		128.5									
European Sites[d]	n	34	33	41	35	28	33	79	78	62	63
	Mean	128.1	153.2	429.4	195.3	187.8	160.7	83.5	87.1	165.5	127
	Min.	112	128	360	172	160	139	55.5	72	135	101
	Max.	147	178	475	218	220	181	99	107	194	141
Zapug[e]		113	142	433			161	70		143	
MG-1[e]				394			150	73		155	
PS-2[e]				415			167	74		159	
PS-3[e]				424				77		156	
Aven de Coulon[f]			154	435	205			84		172	
Starunia[f]			170								
Ordos[f]				455	206			80		158	

sDC: smallest depth of the *Collum*; GDP: greatest depth of the *Processus articularis*; GL: greatest length; WP: proximal width; DP: proximal depth; Wtd: Width of diaphysis at the level of the deltoid tuberosity; sWd: smallest diaphysis width; sDd: smallest diaphysis depth; WD: distal width; DD: distal depth.
[a] This study.
[b] Álvarez-Lao and García (2011b).
[c] Altuna and Mariezkurrena (2000).
[d] Guérin (1980).
[e] Borsuk Białynicka (1973).
[f] Bonifay (1961).

are also observed with relative frequency in recent *R. pyrenaica* from the Pyrenees, as indicated by Ricardo García-González (pers. com., 2013). Additionally, Sandro Lovari (pers. com., 2013) also detected this trait in the current Pyrenean chamois, but in no other recent population.

Different geographically isolated current chamois populations are ascribed to two species on the basis of morphological and behavioral characters: *R. rupicapra* and *R. pyrenaica* (Lovari and Scala, 1980; Nascetti et al., 1985; Pérez et al., 2002). Recent Iberian chamois are included in the species *R. pyrenaica* (Scala and Lovari, 1984).

Table 11
Selected comparative measurements on *Coelodonta antiquitatis* radius.

Site		Radius						
		GL	WP	DP	sWd	sDd	WD	DD
Jou Puerta[a]	JP-9		121.5	80	77.9	45		
	JP-10		109.8	73.6	57.1	33.8		
	JP-11	359	112.2	76.5	56.6	36.6	112.2	69.3
Los Rosales[b]		373	111.7	78.5	60	35	111.5	68
Labeko Koba[c]			113	79.5	65.5	46.5		
			111	82.5	57	40.5		
Lezika[d]		390	113	79.2	61.6	42.8	128	76
European Sites[e]	n	81	109	106	103	102	84	80
	Mean	380.3	112.8	77.5	63.4	45.6	117.7	76.6
	Min.	334	97	55	54	38	95	62
	Max.	413	126	93	75.5	57	142	92
Zapug[f]		348	102		54	39	110	
ZIN 17220[f]		385	117		70	47		
ZIN 5087[f]		343	105		53	35	110	
Aven de Coulon[g]		385	111				105	
Ordos[g]		450	114		66		112	

GL: greatest length; WP: proximal width; DP: proximal depth; sWd: smallest diaphysis width; sDd: smallest diaphysis depth; WD: distal width; DD: distal depth.
[a] This study.
[b] Álvarez-Lao and García (2011b).
[c] Altuna and Mariezkurrena (2000).
[d] Castaños et al. (2009).
[e] Guérin (1980).
[f] Borsuk Białynicka (1973).
[g] Bonifay (1961).

The divergence time between *R. rupicapra* and *R. pyrenaica* was estimated on the basis of genetic distance, but different methods provided different ages: an estimation based in molecular clock methods shows an initial split of both species on 1.7 ma (Rodríguez et al., 2010), whereas phylogenetic analyses of the Y-chromosome provided a younger age of 655 ka for this divergence (Pérez et al., 2011). Therefore, genetic results imply that Late Pleistocene fossil chamois from the Iberian Peninsula should be included in the species *R. pyrenaica*. In addition, the unusual morphology of the horn cores in the Jou Puerta individuals was also observed in specimens from the Pyrenees, as indicated above, which would also support its taxonomic classification as *R. pyrenaica*.

The size of the Jou Puerta chamois does not differ significantly from other Iberian Late Pleistocene populations (Table 6). Nevertheless, a comparison with an extensive sample of recent chamois from the geographically closest population (Western Cantabrian mountains, see Table 6), showed that fossil specimens, including the Jou Puerta sample, are visibly larger in size than recent ones, which is especially visible in the M₃ length. More in-depth morphologic and morphometric studies, which are currently being carried out, are necessary to accurate know the phylogeny of the genus *Rupicapra* in the Iberian Peninsula from a paleontological point of view.

The presence of this species in the assemblage is also of interest from a paleoenvironmental point of view (see Section 6), indicating rocky mountain areas in the vicinity of the site.

4.1.2.3. Capra pyrenaica (Schinz, 1838). Ibex provided 77 remains (7.92% of the assemblage), including one partially preserved skull (Fig. 2d) and other cranial and postcranial elements, most of them preserved in good conditions (Fig. 4k–m). These remains corresponded to a minimum of three adult individuals.

Selected measurements are included in Table 7, compared with a sample of fossil ibex from Iberian sites. Dentition size is very similar to the average values of the comparison sample. Postcranial values are also similar or slightly larger than the averages of the sample, which was especially visible in the two tibiae, which correspond to a same large individual.

As with the chamois, the presence of ibex in the assemblage indicates rocky mountain areas in the surroundings of the site (see Section 6).

Table 12

Selected comparative measurements on *Coelodonta antiquitatis* carpal and tarsal elements.

Site		Scaphoid				Unciform				Pisiform			Astragalus	
		GL	GH	LPs	LDs	GL	GH	GW	Lan	GL	GH	GW	GW	WDs
Jou Puerta[a]		92	66.4	63.5	71.6	90,1	52.9	70.4	73.5	75	53.8	33.8	91.2	82.86
La Parte[b]		67.6		44.3										
El Toll[c]														
Labeko Koba[d]													92	84
Lezika[e]													96	90
European Sites[f]	*n*	41	40	42	35	34	43	43	34	16	16	16	112	107
	Mean	88.4	64.1	60.5	72.6	92.6	53.8	73.7	73.1	67.7	46.2	33.9	95,7	80.9
	Min.	76.5	57	50	63.5	75	45	62	61	56.5	39	30	84	68
	Max.	97	70.5	68	83	105	59.5	84	82	75	54	41	112	91
Aven de Coulon[g]													85	
Ordos[g]													87	
Zapuj[h]		86	60			75	48	66		58	31	27	91	71

GL: greatest length; GH: greatest height; LPs: length of the proximal articular surface; LDs: length of the distal articular surface; GW: greatest width; Lan: anatomic length; WDs: width of the distal articular surface.

[a] This study.
[b] Álvarez-Lao and García-García (2006).
[c] Álvarez-Lao and García (2011b).
[d] Altuna and Mariezkurrena (2000).
[e] Castaños et al. (2009).
[f] Guérin (1980).
[g] Bonifay (1961).
[h] Borsuk Białynicka (1973).

Table 13

Selected comparative measurements on *Coelodonta antiquitatis* metacarpals.

		GL	WP	DP	sWd	sDd	WD	DD	WDs
Metacarpal II									
Jou Puerta[a]	JP-41	162			43.5			40.15	
European sites[b]	*n*	60	61	57	60	60	55	58	59
	Mean	164.2	52.9	46.9	42.4	27.3	48.8	43.1	43.5
	Min.	148	41	40	31.5	23	37.5	35	35
	Max.	180	66.5	58	50	34.5	57	52.5	55
Zapuj[c]		139	51				48		
Metacarpal III									
Jou Puerta[a]	JP-40	192	66	56.3	60.23	31.38	64.74		
El Toll[d]			67	55					
Labeko Koba[e]		186	66.5	50	51.5	26	64.5	49.5	55
			81	56.5	59.5	27			
European sites[b]	*n*	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
Zapuj[c]		161	60				57		
Ordos[f]		205	66				54		
Aven de Coulon[f]		181	64				61		
Metacarpal IV									
Jou Puerta[a]	JP-39	152.9	54.05	50.18	43.65	28.82	54.32	43.24	50.07
La Parte[g]		148			34	21		36.5	
Labeko Koba[e]		149	48	49	37.5	23.5		42.5	41.5
European sites[b]	*n*	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
Zapuj[c]		130	44				43		
Ordos[f]		183	63				48		
Aven de Coulon[f]		146	54				53		

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] This study.
[b] Guérin (1980).
[c] Borsuk Białynicka (1973).
[d] Álvarez-Lao and García (2011b).
[e] Altuna and Mariezkurrena (2000).
[f] Bonifay (1961).
[g] Álvarez-Lao and García-García (2006).

4.2. Order Perissodactyla (Owen, 1848)

4.2.1. Family Equidae (Gray, 1821)

4.2.1.1. Equus ferus (Boddaert, 1785). Four remains constituted the single evidence of horse, representing 0.41% of the ungulate assemblage (Table 1). The remains (Fig. 4n–o) included a mandible fragment (with the symphysis and the incisors), one isolated P_2 and one second phalanx, likely corresponding to the same adult individual. Although Jou Puerta material was very limited and not representative enough of the whole population, the P_2 did not show distinguishing features in comparison with a sample from northern Iberia sites (Table 8).

4.2.2. Family Rhinocerotidae (Owen, 1845)

4.2.2.1. Coelodonta antiquitatis (Blumenbach, 1799). The woolly rhinoceros provided 105 remains, comprising 10.8% of the assemblage (Table 1), and constituting the third most numerous collection of this species known to date in the Iberian Peninsula, after Lezika (NISP = 144; Castaños et al., 2009) and Labeko Koba (NISP = 122; Altuna and Mariezkurrena, 2000). Cranial and postcranial elements were present in the assemblage, including an almost complete mandible, isolated teeth, scapulae, pelvis, vertebrae, limb bones, carpus, metacarpus, tarsus and phalanges; corresponding to a minimum of three individuals. Most of the bones were preserved in excellent conditions. Since this woolly

Table 14

Selected comparative measurements on *Mammuthus primigenius* calf tusks.

Specimen	MTD	PCD	Age (yr)
JP-106[a]	27.3 × 21.2	73.1	
PIN 4353-1008[b]	24 × 18	20 (?)	1.5–2
PIN 4353-1000[b]	23 × 17	–	1.5–2
PIN 4531-25[b]	28 × 25	73	1.5–2
PIN 4353-933[b]	17 × 11	ca. 43	1
PIN 4531-24[b]	31 × 24	–	1.2

MTD: maximal transverse diameters; PCD: pulp cavity depth.

[a] This study.
[b] Specimens from Sevsk (Maschenko, 2002).

rhinoceros assemblage is one of the most relevant from the Iberian Peninsula, it is here described and discussed in detail. Morphometric data (Tables 9–13) were compared with an extensive sample mainly from the Iberian Peninsula (Álvarez-Lao and García, 2011b) and 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; Borsuk Białynicka, 1973). Anatomical descriptions of these elements are included below.

The mandible (JP-5, Fig. 5a–b) preserved its right horizontal branch in relatively good condition, but the left one, as well as the symphysis, were damaged and had to be partially restored. The size of this mandible was not considered useful for comparative studies since it was still not fully developed at the time of death. Teeth show the thick and rough enamel typical of *Coelodonta antiquitatis*. Cement is present, especially in the labial side. Both dental series show premolars P_2 and P_3 almost completely emerged but still unworn, the last deciduous piece (D_4) extremely worn and close to be replaced, M_1 already in wear and M_2 almost completely emerged and with slight wear. The right M_3 germ, still unmerged, is visible in the alveolus. Following Hillman-Smith et al. (1986), the ontogenetic age estimated for this specimen ranges between 7 and 8 years (age groups VIII–IX), which fits into the subadult period proposed by Shrader and Owen-Smith (2002) for modern African white rhinoceroses. The teeth in this mandible are smaller (Table 9) than the average values provided by Guérin (1980), suggesting that they probably belonged to a female.

Two upper teeth from the same series (right D^2 and M^1, JP-94 and JP-95, respectively, Fig. 5c–d) show exactly the same development degree as the mandible described here. Morphological features such as the presence of a well-developed mediofossette and the thick and rough enamel are diagnostic traits of *Coelodonta antiquitatis*. The size of these teeth (Table 9) is slightly smaller than the average values provided by Guérin (1980) for Western European populations.

Two lower series composed by left and right D_4–M_1–M_2 elements (JP-96, JP-97, JP-98 and JP-99, JP-100, JP-101 respectively; Fig. 5e–f), belonging to the same individual, were recovered in the assemblage. Enamel is thick and rough, and cement is relatively abundant in the labial side. The developing stage is similar to mandible JP-5: D_4 is extremely worn, M_1 presents incipient wear and M_2 is still unworn. The individual age of this specimen, following Hillman-Smith et al. (1986), can be estimated at between 6 and 7 years (age group VIII), corresponding to the subadult period. M_1 and M_2 (Table 9) are larger in length but slightly smaller in width than the average values published by Guérin (1980). This can be explained as the teeth belonging to an immature individual that was still not affected by dental attrition at the time of death. The size of both D_4 (Table 9) is similar to the average values provided by the mentioned author.

Five vertebrae remains were preserved: three cervical ones (the most complete of which is JP-22, Fig. 5g) corresponding to an adult individual (since epiphyses are completely fused); and two thoracic ones that lack their epiphyses (which remained unfused), and so must correspond to a young or subadult individual.

Two scapula fragments were present in the assemblage. One of them (JP-13, Fig. 5h), which preserved the glenoid process, neck and part of the spine, is of a size (Table 10) close to the average values provided by Guérin (1980). The other scapula is fragmented and eroded on the surface, not allowing reliable measurements.

Remains of four humeri were recovered, two of them preserved in excellent conditions, constituting the first almost complete humeri of *Coelodonta antiquitatis* reported from an Iberian site. One of them (JP-1, left side of the body, Fig. 5i–j) shows extraordinary large size and robustness. The preservation of this specimen is very good, although it is somewhat eroded in its distal end. Most of its measurements exceed the maximum values of the comparison sample (Table 10). Epiphyses fusion is complete. These characteristics indicate that it corresponded to an unusually large and robust mature individual, surely a male, different than the two subadult ones previously described by dentition. The other

almost complete humerus (JP-3, right side, Fig. 5k, p) corresponded to a young or immature individual, since the proximal epiphysis was not fused at the time of death (it was affixed to the diaphysis by flowstone/calcitic covering). The proximal and distal ends of the bone were eroded, preventing the taking of some of the measurements. Its size is small (Table 10), below the average values provided by Guérin (1980), which could be expected since its development is not complete. One humerus distal end, well preserved (JP-2, left side, Fig. 5l), is of a size very similar to specimen JP-3 (Table 10), suggesting that they probably corresponded to the same individual.

Three radii were present in the assemblage. Two of them, left and right (JP-10 and JP-11, respectively), are almost identical and most likely corresponded to the same immature individual, keeping their distal epiphyses unfused in both cases (Fig. 5n, p). Their size (Table 11) is slightly smaller than the average values provided by Guérin (1980). Both are perfectly articulated with humeri JP-2 and JP-3 (Fig. 5p), respectively. Another radius (JP-9, left side, Fig. 5m) is greatly eroded and had to be partially restored. It is large (Table 11), with values higher than the average ones published by Guérin (1980). This specimen is perfectly articulated with humerus JP-1, so most likely both specimens corresponded to the same individual.

One ulna fragment (JP-12, right side), which partially retained the proximal epiphysis and the diaphysis, did not provide any reliable measurement. It articulates very well with humerus JP-3 and with radius JP-11 (Fig. 5p), so these three elements were probably part of a same forelimb.

Three carpal bones were recovered: one scaphoid, one unciform and one pisiform. The scaphoid (JP-44, left side, Fig. 5s) was partially eroded. Measurements (Table 12) are similar to the average values published by Guérin (1980). The unciform (JP-42, left side, Fig. 5-t), well preserved, is slightly smaller than the average values provided by the mentioned author (Table 12). The pisiform is large compared with the sample indicated in Table 12.

Three metacarpals (II, III and IV, JP-41, JP-40 and JP-39, respectively, all from the left side, Fig. 5t), were found almost together. Preservation is good in Mc. IV, whereas the proximal and distal epiphyses in Mc. III were damaged and Mc. II was superficially eroded. The size of these elements (Table 13) is close to the average values provided by Guérin (1980). These three metacarpals articulate perfectly among themselves and with unciform JP-42 (Fig. 5t), so these four elements are supposed to correspond to a one single individual.

One well preserved left innominate bone (JP-16, Fig. 5o) was present in the assemblage. Some measurements are: length of the foramen obturatum—103.8 mm; length of the acetabulum—100.2 mm; smallest width of the ilium shaft—44.5 mm. This specimen was partially covered by flowstone and very close to humerus JP-3 (Fig. 2e), so they probably belonged to the same individual.

Two femur remains were recovered. One right diaphysys fragment (JP.15, Fig. 5q–r), which did not allow reliable measurements, shows both proximal and distal epiphyses unfused at the time of death, so it must have belonged to an immature individual. This was one of the few specimens in the assemblage that showed clear tooth marks produced by carnivores (Fig. 5r). The other femur fragment is a left distal epiphysis (JP-20) that remained unfused at the time of death, so it must have belonged to an immature individual, probably the same as specimen JP-15.

Tibiae were represented by two distal epiphyses (left and right, JP-18 and JP-19, respectively) which remained unfused at the time of death and most likely corresponded to the same immature individual.

Tarsal bones are scarce and fragmentary. Only one astragalus fragment and one calcaneus fragment were recovered. Some measurements taken in the astragalus (JP-56) indicated a slightly smaller size (Table 12) than the averages of the Western European sample (Guérin, 1980).

Only two phalanges, a first one and a second one, were recovered, both damaged and with eroded surfaces.

All these fossils corresponded to a minimum of three individuals: a) a subadult of small size (under the average values published by

Guérin, 1980), probably a female, is the best represented individual of the assemblage, to whom would correspond mandible JP-5, humeri JP-2 and JP-3, radii JP-10 and JP-11, ulna JP-12, innominate JP-16 and femur JP-15; b) a subadult individual of larger size, probably a male, represented by the two lower dental series JP-96 to JP 101; c) a mature individual of extremely large size and robustness whose fossil remains comprise humerus JP-1, radius JP-9 and the cervical vertebrae JP-22 to JP-24. The ontogenetic age of the subadult individuals is similar and was estimated at around 6 to 8 years following the criteria proposed by Hillman-Smith et al. (1986). It is not possible to accurately estimate the ontogenetic age of the third individual, since no teeth were preserved. Nevertheless, the complete fusion of all the epiphyses indicates that it corresponded to an adult.

As a whole, the woolly rhinoceros population from Jou Puerta did not show any singular anatomic features other than the extremely large size of the elements corresponding to the forelimb of the mature individual, which, for some of the measurements, exceed all in the comparison sample. Another remarkable singularity of this woolly rhinoceros assemblage, compared with the Iberian sample, is the very good preservation of the fossils, which that allowed in several cases to find different elements which articulate among them, corresponding to a same individual.

4.3. Order Proboscidea (Illiger, 1811)

4.3.1. Family Elephantidae (Gray, 1821)

4.3.1.1. Mammuthus primigenius (Blumenbach, 1799). The woolly mammoth provided only four remains (0.41% of the assemblage), consisting of one tusk and three molar plates corresponding to a calf.

The tusk (JP-106, Fig. 4p,q) was well preserved in approximately three fourths of its length, but the tusk end is lacking. The length of the preserved portion is 111.4 mm. The cross section is oval with the greater diameter in vertical position; the maximum transverse

diameters, located at the tusk base, are 27.3 × 21.2 mm. The depth of the pulp cavity is 73.1 mm. Measurements were compared with a sample of woolly mammoth calf tusks from Sevsk, Russia, published by Maschenko (2002) (Table 14). The tusk from Jou Puerta is very similar in size to specimen PIN 4531-25 from Sevsk, whose individual age was estimated at 1.5 to 2 years (Maschenko, 2002). Therefore, a similar age can be estimated for specimen JP-166. Despite this very young age, the tusk already shows a visible curvature (Fig. 4p) which is also shown in some tusks of similar individual age figured by Maschenko (2002) and can be considered an indicative character for Mammuthus primigenius.

The three isolated molar plates (Fig. 4r–t) were not completely formed at the time of death, since they are unworn and no cement is covering their surfaces. They were found almost together, so they were assumed to belong to one same tooth. An interesting morphological character of these plates is the deep space between the digits (especially visible in specimen JP-104, Fig. 4s) which, following Dick Mol (pers. com., 2011), is an indicative feature for Mammuthus primigenius. The width of the largest one (JP-105) is 44.3 mm, which fits into the range of a dp4 (upper and lower) woolly mammoth sample from several localities in Siberia and Europe, provided by Aguirre (1968) and Maschenko (2002). The other two plates are smaller in width, so they probably corresponded to the posterior edge of the same tooth. Enamel thickness is very thin, which can be also considered an indicative character for Mammuthus primigenius, providing values between 0.8 and 1 mm. These measurements fit in the range published by Maschenko (2002) for woolly mammoth dp4. Therefore, the three molar plates are assumed to belong to a not fully developed dp4.

Following Maschenko (2002), at the age of 1.5–2 years (the age estimated for the tusk, as indicated above), the woolly mammoth dp3 crown is heavily worn and the first plates of the pd4 begin to wear. A number of the dp4 plates are still in formation at this stage. For these reasons, I assume that both the tusk and the molar plates correspond to a same mammoth calf of 1.5–2 years of individual age.
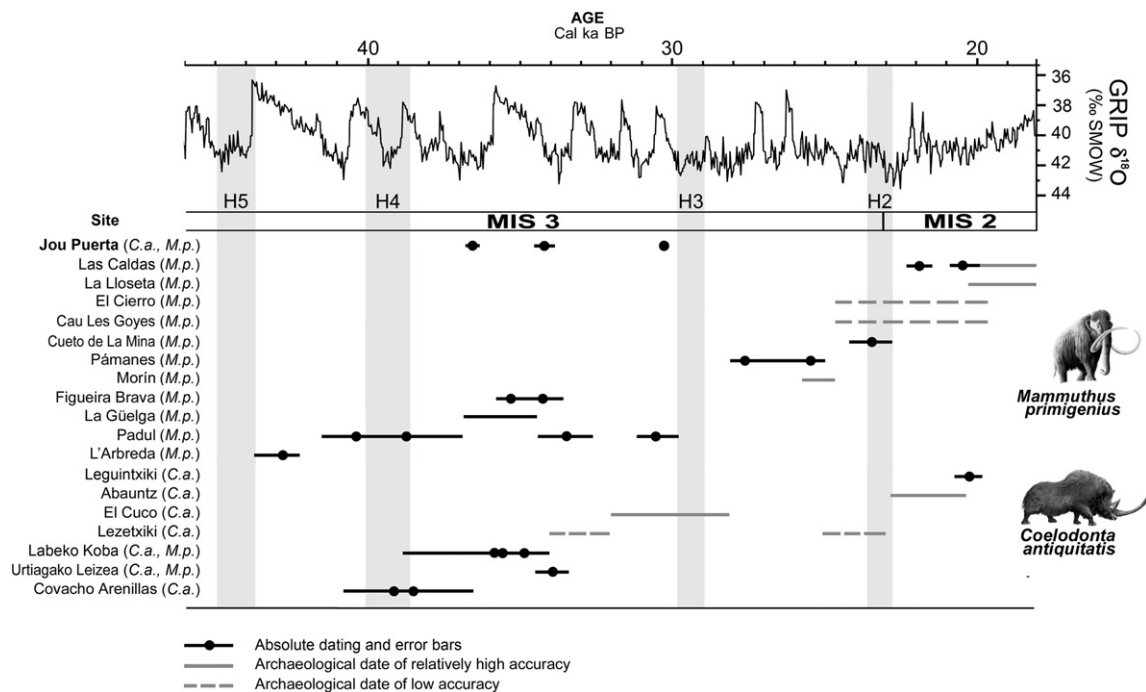

Fig. 6. Calibrated radiocarbon dates from Jou Puerta and other Iberian assemblages with *Coelodonta antiquitatis* (*C.m.*) and/or *Mammuthus primigenius* (*M.p.*), compared with the GRIP paleoclimatic oxygen curve.
Modified from Álvarez-Lao and García (2010, 2011b, 2012).

4.4. Order Carnivora (Bowdich, 1821)

4.4.1. Family Felidae (Fischer, 1817)

4.4.1.1. cf. *Panthera pardus* (Linnaeus, 1758). Carnivores only provided a single remain (0.1% of the assemblage), corresponding to an upper deciduous felid carnassial (D^3) of *Panthera pardus* size (Fig. 4u). The length of the crown is 18.8 mm, which is similar to the *Panthera pardus* D^3 described by Clot (1980) from Grotte de La Carrière (18.5 mm), and slightly larger than the one from Bolinkoba (17.9 mm) published by Castaños (1986). Other felid which could show a similar D^3 size is *Panthera gombaszoegensis*, but this species became extinct in Europe before the MIS 3 (O'regan et al., 2002), so the possibility that the Jou Puerta felid D^3 could belong to this species must be discarded.

Despite the scarcity of the material, based in the similarity in size with the mentioned sample, the most likely taxonomical attribution to this specimen is *Panthera pardus*.

5. Chronologic and biogeographical framework

The chronology of the fossil assemblage was determined by three AMS radiocarbon dates of 30,275 ± 105 Cal ka BP (Beta−313518), 34,235 ± 374 Cal ka BP (Beta−313520) and 36,655 ± 205 Cal ka BP (Beta−313519), all falling within the MIS 3. This time lapse corresponds to the episode when the greatest concentration of *Mammuthus primigenius* and *Coelodonta antiquitatis* Iberian occurrences is recorded (Fig. 6), coinciding with assemblages such as Labeko Koba, Lezetxiki, El Cuco, Covacho de Arenillas, Urtiagako Leizea, La Güelga, Figueira Brava and Padul (Álvarez-Lao and García, 2010, 2011b, 2012). Moreover, this episode is of special interest because the maximum registered southern spread of woolly mammoth occurred then both in Europe (in Padul, Spain, Álvarez-Lao et al., 2009) as in Asia (Beidasha River, China, Takahashi et al., 2007). MIS 3 was a period characterized by strong and brief climatic oscillations (Barron and Pollard, 2002; van Andel, 2002) recorded in the GRIP and GISP2 ice cores, which appear to be of global significance (Dansgaard et al., 1993; Grootes and Stuiver, 1997).

Biogeographically, the Jou Puerta site is located in the Cantabrian region (NW Iberia), which is the Iberian area where the greatest concentration of woolly rhinoceros and woolly mammoth occurrences was recorded (Álvarez-Lao and García, 2011a). A minor part of the finds of these species is located in Catalonia (NE Iberia), and a few more in Central and Southern Iberia, where cold adapted species are rare (Fig. 1). Such distribution is consistent with the geomorphologic context, as the Iberian Peninsula is relatively isolated from continental Europe by the Pyrenees, which acted as a barrier limiting dispersals. Cold-adapted species, which were abundant in southern France during the Upper Pleistocene (Delpech, 1983), could only enter the Iberian Peninsula through narrow passes placed east and west of the Pyrenees (Álvarez-Lao and García, 2011a).

6. The faunal composition

6.1. Paleoecological context

Woolly rhinoceros and woolly mammoth are two typical elements of the "mammoth fauna" (Vereschagin and Baryshnikov, 1982), also known as "*Mammuthus–Coelodonta* faunal complex" (Kahlke, 1999, in press), but they are two infrequent species in Iberian Pleistocene sites. Up to date, only 23 Iberian sites have yielded woolly rhinoceros fossils and other 25 Iberian sites have provided woolly mammoth remains (Álvarez-Lao and García, 2011b, 2012) (see Section 5 and Fig. 7). Nevertheless, the Iberian fossil assemblages containing woolly rhinoceros and woolly mammoth remains do not show the typical faunal composition of the Eurasian mammoth fauna, as was indicated by Álvarez-Lao and García (2011b, 2012). A revision of the faunal composition of Iberian sites with presence of these two cold-adapted taxa shows that high proportions of species associated to temperate environments, particularly red deer (*Cervus elaphus*), are generally included. This pattern, which can also be observed in the Jou Puerta site (Table 1), is very different to the contemporary faunal associations from Central and Western Europe, where the mammoth fauna was fully established (i.e. reindeer, woolly mammoth, woolly rhinoceros and other cold-adapted species were dominant while temperate taxa were scant or even lacking). These different associations that characterize the Iberian woolly rhinoceros and woolly mammoth records are here statistically analyzed to understand the ecological constraints and trophic limits of these species.
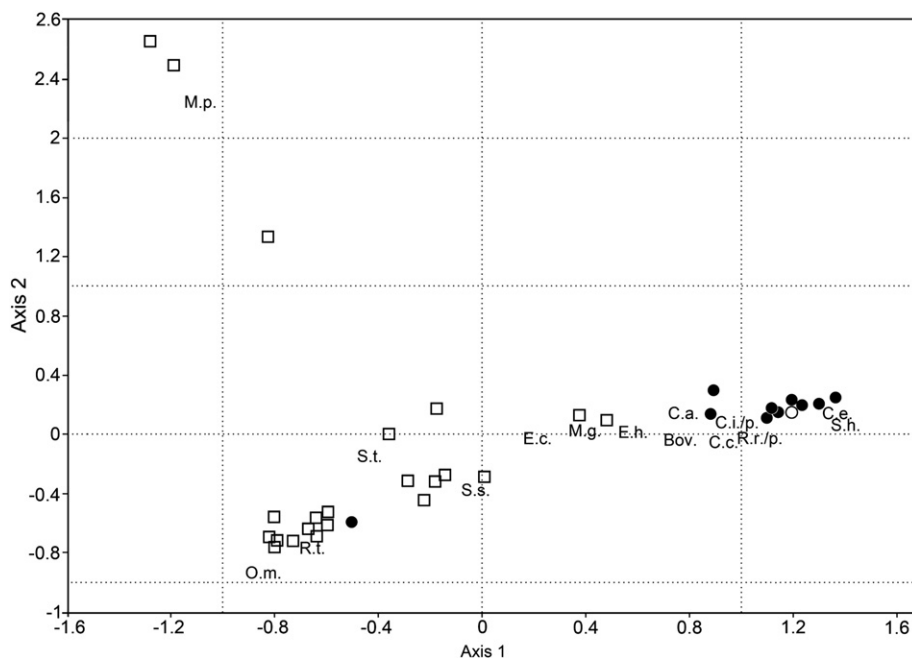

Fig. 7. Biplot of the two first axes extracted by the Correspondence Analysis (CA). Four main factors were extracted by the CA, with eigenvalues of 0.69, 0.62, 0.38 and 0.27, which explained 27.6%, 24.9%, 15.3% and 10.8% of the inertia in the data, respectively. Jou Puerta is indicated by an unfilled circle, other Iberian sites are indicated by black dots, Central-Western European sites are represented by unfilled squares. Taxa abbreviations as in the caption for Table 15.

Table 15
Percentages of ungulate taxa at Jou Puerta and other 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./p.	S.t.	Bov.	O.m.	S.s.	E.c.	E.h.	C.a.	S.h.	M.p.		
Jou Puerta	Spain	0	40.8	0.72	10.4	7.92	12.05	0	16.4	0	0	0.41	0	10.8	0	0,41	970	(1)
Cueto de La Mina (E)	Spain	0.4	67.3	0	0.8	6.7	0.8	0	5.6	0	0.4	15.5	0	0	0	0.4	251	(2)
Covacho de Arenillas (II)	Spain	0	16.5	0	3.5	76.4	0.4	0	0.8	0	0	1.2	0	0.4	0	0	254	(3)
Lezika	Spain	0.32	44.6	0	0	0	6.9	0	0.3	0	0	0	0	47.8	0	0	305	(4)
Lezetxiki (IIIa)	Spain	0.7	25.2	0	1	8.7	31.4	0	28.2	0	0.7	3.2	0	0.2	0.5	0	401	(5)
Las Caldas VII	Spain	0	79.5	0	0	12.3	0	0	0	0	0	7.4	0	0	0	0.8	122	(6)
Morín (4)	Spain	0	68.9	0	12.4	3.3	0.2	0	4.8	0	0	9.9	0	0	0	0.2	390	(7)
Urtiagako Leizea	Spain	83.4	5.3	0	5.2	0.8	2.6	0	0.8	0	0	0	0	0.8	0	0.8	115	(8)
Labeko Koba (IX sup.)	Spain	1.3	36.4	0.5	0.4	0	0.7	0	20.4	0	0,1	30.2	0	9.1	0	0.8	1008	(9)
Arbreda (H)	Spain	0	47.2	0	0.8	0	3.1	0	14.2	0	0	26.8	2.3	0	0	5.5	127	(10)
Figueira Brava (2–3)	Portugal	0	52.5	0	0	0	0	0	33.9	0	0	12.7	0	0	0.4	0.4	221	(11)
Jamblancs (3)	France	81.5	1.8	0	0	0	0	0.2	2.8	0	0	13.3	0	0	0	0.2	434	(12)
Abri Pataud (5 ext 2)	France	98.7	0.6	0	0.04	0.1	0.1	0	0.2	0.03	0	0.2	0	0	0	0.02	20992	(13)
Abri Pataud (5/6 a 10)	France	64.9	14.4	0	1.1	0.4	0.8	0	3.8	0	0.9	12.4	0.9	0	0	0.3	646	(13)
Laugerie Haute Ouest. (2–7)	France	97.4	0.2	0	0	0	0	0	0.1	0	0	0.8	0	0	0	1.5	1426	(13)
Laugerie Haute Ouest. (12 a + b)	France	96.8	0.1	0	0	0.2	0	0	0	0	0	2.4	0	0	0	0.5	1121	(13)
Roc de Combe (1)	France	87.5	3	0	0.1	0.7	2.9	0	0	0	0	3.4	0	0	0	0.05	1933	(13)
Roc de Combe (5)	France	92.5	0.3	0	0	0.7	0.2	0	0.9	0	0	0.3	0	0	0	5	1199	(13)
Roc de Combe (6)	France	83.6	1.1	0	0.5	0.5	0	0	5.4	0	2.7	2.7	0	0.5	0	2.7	183	(13)
Abri du Facteur (Perig. V)	France	95	0.7	0	0	1.5	0.7	0	0.7	0	0.7	0	0	0.7	0	0	133	(14)
Theillat	France	0.7	0.4	11.7	0	0	0	0	15.2	0	2.5	42.7	0	25.6	0	1	284	(15)
Morancourt	France	3.2	1.1	1.3	0.5	0	0	0	21.7	0	0.3	54.1	0.8	13.3	0	3.5	368	(16)
Roche à Pierrot (Saint-Césaire)	France	50.5	1.7	1.5	3.4	0	0	0	19.1	0	0.6	14.4	0.6	5.1	0	3	471	(17)
Arcy Sur Cure Gr. Renne (8)	France	78.6	0.8	0	0	0	2.1	0	1.8	0	0	14.1	0	0.3	0	2.3	1154	(18)
Kesslerloch (III)	Switzerl.	85	0	0	0	0.1	0	0	0.2	0.02	0	14.6	0	0.02	0	0.02	4149	(19)
Hohle Fels (IIb)	Germany	49.7	0	0	0	3.7	0.5	0	0	0	0	43.9	0	0.5	0	1.6	189	(20)
Geissenklösterle (AH III)	Germany	6.3	0.1	0	0.1	1.5	0.5	0	0.03	0	0	2.8	0	1.2	0	87.4	3634	(21)
Geissenklösterle (AH IV–VIII)	Germany	38.4	1.4	5.1	1.4	14.5	3.6	0	0	0	0	15.2	0	5.8	0	14.5	138	(21)
Brillenhöhle (VII)	Germany	44.4	0	0	0	7.4	0.7	1.5	0.7	0	0	34.1	0	0	0	11.1	227	(22)
Vogelherd (IV–V)	Germany	23.9	0.3	0	0	0	0.03	0	0.9	0	0.1	20.9	0	1.8	0	52	6810	(23)
Trou Magritte (2)	Belgium	50.5	0	0	0	17.2	0	0	0.5	0	4.4	21.6	0	3.9	0	1.6	180	(24)
Paviland, Goat's Hole Cave	G. Britain	42.2	5.3	1.6	0	0	0	0	28.3	0	1.6	8.6	0	11.5	0	0.8	224	(25)
Lynford	G. Britain	5.4	0	0	0	0	0	0	0.3	0	0	0.4	0	1.01	0	92.8	1347	(26)

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./p.*—*Rupicapra rupicapra/pyrenaica*; *S.t.*—*Saiga tatarica*; *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*.

Sources: (1): This paper; (2): Castaños, 1982; (3): Castaños, pers. com., 2006; (4): Castaños et al., 2009; (5): Altuna, 1972; (6): Soto and Meléndez, 1981; (7): Altuna, 1971; (8): Altuna and Mariezkurrena, 2010; (9): Altuna and Mariezkurrena, 2000; (10): Maroto et al., 1996; (11): Cardoso, 1996; (12): Drucker et al., 2000; (13): Delpech, 1984; (14): Bouchud, 1968; (15): Raynal et al., 1989; (16): Fosse, 1997; (17): Pathou-Mathis, 2005; (18): Yravedra Sáinz de Los Terreros, 2006; (19): Le Tensorer, 1998; (20): Münzel and Conard, 2004a; (21): Münzel and Conard, 2004b; (22): Scheer, 2001; (23): Niven, 2007; (24): Gautier, 1995; (25): Turner, 2000; (26): Schreve, 2006;

6.1.1. Analysis of the faunal composition

Percentages of each herbivore (ungulate and subungulate) species from the Jou Puerta site were analyzed in comparison with 32 other assemblages that include woolly mammoth and/or woolly rhinoceros coming from Iberian sites and from Western-Central European sites (Table 15). All the associations involved in the comparative analysis correspond chronologically to Marine Isotope Stages 3 and 2. The percentages of the different herbivore species in each assemblage have been calculated on the basis of NISP (Number of Identified Specimens). This estimator is considered of good reliability (Lyman, 1994) since no taphonomic bias is detected toward any of the species of each assemblage. Only assemblages with NISP greater than 100 have been considered for the analysis.

With the purpose of identifying similarities and differences among the ungulate compositions of the different assemblages they were statistically analyzed by means of a multivariate analysis, since the sample consists of a number of species from each assemblage. Due to the high variation detected on the proportions of some of the species and the lack of some taxa in a number of assemblages, a Correspondence Analysis (CA) was considered the most suitable statistical test, and was performed using the program PAST version 2.15 (Hammer et al., 2001).

A close association between sites with similar relative abundances of herbivore taxa was evidenced by the eigenvalues and inertia values provided by the Correspondence Analysis (see Fig. 7 caption).

The CA evidenced a clear separation between Iberian and Western-Central European faunal associations (Fig. 7): almost all Iberian sites (black dots), excluding Urtiagako Leizea, are placed on the right part of the graph, associated with a high abundance of red deer and presence of steppe rhino (*Stephanorhinus hemitoechus*, only at Figueira Brava). The Jou Puerta assemblage, indicated by the unfilled circle, is included in the middle part of the Iberian sample, showing the same pattern of faunal composition. Sites in the central part of the graph, clearly separated from the Iberian sample, are characterized by a high abundance of horse species (*Equus caballus/E. ferus/E. germanicus/Equus hydruntinus*), woolly rhinoceros (*Coelodonta antiquitatis*), wild boar (*Sus scrofa*), giant deer (*Megaloceros giganteus*), roe deer (*Capreolus capreolus*), bovines (*Bison priscus/Bos primigenius*), chamois (*Rupicapra rupicapra*) and ibex (*Capra ibex/C. pyrenaica*). At the middle-left section of the graph the sites are associated with a high abundance of strictly cold-adapted taxa such as reindeer (*Rangifer tarandus*), and the presence of saiga antelope (*Saiga tatarica*) and musk-ox (*Ovibos moschatus*). Urtiagako Leizea is the only Iberian site placed on this area and separated from the rest of the Iberian localities. Three sites placed on the upper left quadrant of the graph, clearly apart from the remaining sites, are related to high abundances of woolly mammoth.

6.1.2. Paleoecologic interpretation

Herbivore compositions from Jou Puerta and the other Iberian assemblages with woolly mammoth and/or woolly rhinoceros are significantly different from those of Western-Central Europe of contemporary age. As a whole, Iberian assemblages are dominated by species indicative of temperate environments, with high percentages of

Cervus elaphus and low percentages (or a complete lack) of cold taxa such as *Rangifer tarandus*.

In the Western-Central European analyzed assemblages, faunal compositions are characterized by high percentages of cold taxa: *Rangifer tarandus* is the dominant species in most cases, while at a few sites *Mammuthus primigenius* is the most frequent taxon. Temperate species are scarce or lacking at these assemblages: red deer (*Cervus elaphus*) is infrequent in all these localities, with percentages below 2% with the single exception of Abri Pataud, where it reaches 14.39% (Delpech, 1983). There is a sole Iberian site with a very similar faunal composition to the Western-Central European localities (Fig. 7), Urtiagako Leizea (Altuna, 1984; Altuna and Mariezkurrena, 2010), which probably corresponded to an extreme cold episode within MIS 3.

The Jou Puerta site, as well as almost all other analyzed Iberian sites, shows a mixture of temperate and cold elements which does not reflect the typical faunal composition of the "Eurasian mammoth fauna" or "*Mammuthus–Coelodonta* faunal complex", as was described by Guthrie (1982), Vereschagin and Baryshnikov (1982) and Kahlke (1999, in press). Instead, it supports the idea proposed by Álvarez-Lao and García (2011b, 2012) that woolly rhinoceros and woolly mammoth only reached the Iberian Peninsula occasionally, probably during the coldest episodes of the Late Pleistocene, and coexisted with, but did not replace, the local faunas.

6.2. Paleoenvironmental context

The herbivore assemblage from Jou Puerta suggests an environmental complex composed of, at least, three different ecosystems.

a) *Coelodonta antiquitatis* and *Mammuthus primigenius* are two typical elements of the steppe-tundra or "Mammoth Steppe" (Guthrie, 1982; Guthrie, 1990; West, 2000), an herbaceous ecosystem characteristic of the Pleistocene glacial periods and indicative of cold and arid environmental conditions. *Equus ferus* and *Megaloceros giganteus* are also associated to herbaceous open grasslands (Kurtén, 1968; Geist, 1999).

b) The high abundance of *Cervus elaphus* and the occurrence of *Capreolus capreolus* suggest the presence of at least some forested areas in the vicinity of the site, which is not incompatible with the "Mammoth Steppe" (Ukraintseva, 1993).

c) The presence of *Rupicapra pyrenaica* and *Capra pyrenaica* indicates rocky mountain areas in the surroundings of the site. Although the cave was located at a low altitude (28 m above current sea level), the close presence of altitudes higher than 1000 m above sea level (Cuera Mountain Range), 5 km south of the cave, is consistent with the occurrence of these alpine species.

7. Conclusions

The origin of the Jou Puerta bone accumulation was related to a natural trap, as indicated by the morphology of the cavity (a collapse sinkhole) and by the unusually good preservation of the fossils.

The Jou Puerta site provided an outstanding fossil assemblage containing cold-adapted species such as *Coelodonta antiquitatis* and *Mammuthus primigenius*, which are infrequent in Iberian sites, yielding relevant information on the paleoenvironmental conditions in Northern Iberia during MIS 3. Since the bone accumulation was originated in a natural trap, fossils were unusually well preserved.

One of the Iberian largest and best preserved amounts of woolly rhinoceros fossils was here recovered. From an anatomical point of view it is interesting to note that the forelimb elements of a mature individual show extremely large size and robustness that, for some measurements, exceed all those in the comparison sample. The very good preservation degree of the fossils allowed, in several cases, to find different elements corresponding to the same individual which articulate among them.

Chronologically and biogeographically the assemblage coincides with the episode and region where the greatest concentration of *Mammuthus*

primigenius and *Coelodonta antiquitatis* Iberian occurrences are recorded. The presence of these cold taxa 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 (Álvarez-Lao and García, 2011b, 2012), indicating transregional paleoecological processes.

The faunal complex of the Jou Puerta site, as well as the majority of the Iberian assemblages with presence of *C. antiquitatis* and *M. primigenius*, was predominantly composed of temperate ungulate species, where red deer (*Cervus elaphus*) was the most abundant species. By contrast, contemporary Western-Central European ungulate associations were dominated by cold-adapted taxa, especially reindeer (*Rangifer tarandus*). These results provide an interesting view on the paleoecology of the woolly rhinoceros and the woolly mammoth in the south-western boundary of its Palearctic distribution. This mixture of temperate and cold elements at Iberian sites supports the idea proposed by Álvarez-Lao and García (2011b, 2012) that these species only reached the Iberian Peninsula occasionally, during the coldest episodes of the Pleistocene, cohabiting with the local faunas instead of replacing them totally. Consequently, these results suggest that the typical mammoth fauna was never completely established in Iberia as it was in mainland Europe.

The ungulate and subungulate assemblage in Jou Puerta evidences cold and arid environmental conditions and a diverse landscape complex with the presence of steppe-like environments, forested areas and rocky mountains.

References

Adán, G., 1997. De la caza al útil. La Industria ósea del Tardiglaciar en Asturias. Consejería de Cultura del Principado de Asturias, Oviedo 1–383.

Aguirre, E., 1968. Revisión sistemática de los Elephantidae por su morfología y su morfometría dentaria (I). Estud. Geol. 24, 109–167.

Altuna, J., 1971. Los mamíferos del yacimiento prehistórico de Morín (Santander). In: González Echegaray, J., Freeman, L.G. (Eds.), Cueva Morín. Excavaciones 1966–68, vol. 6. Publicaciones del Patronato de Cuevas Prehistóricas de Santander, Santander, pp. 367–398.

Altuna, J., 1972. Fauna de Mamíferos de los Yacimientos Prehistóricos de Guipúzcoa. Munibe (Antropol.-Arkeol.) 24, 1–464.

Altuna, J., 1976. Los mamíferos del yacimiento prehistórico de Tito Bustillo (Asturias). In: Moure, J.A., Cano, M. (Eds.), Excavaciones en la cueva de Tito Bustillo (Asturias). Bol. Inst. Estud. Asturianos, pp. 149–194.

Altuna, J., 1979. Nuevo hallazgo de rinoceronte lanudo (*Coelodonta antiquitatis* Blum.) en Guipúzcoa. Munibe (Antropol.-Arkeol.) 31, 281–282.

Altuna, J., 1984. Primer hallazgo de mamut (*Mammuthus primigenius* Blumenbach) en el País Vasco Meridional. Munibe (Antropol.-Arkeol.) 36, 27–32.

Altuna, J., 1986. The mammalian faunas from the prehistoric site of La Riera. In: Straus, L.G., Clarck, G. (Eds.), La Riera Cave, Stone Age Hunter Gatherer adaptations in Northern Spain. Anthropological Papers, 36. University of Arizona, pp. 237–274.

Altuna, J., 1990. Caza y alimentación procedente de Macromamíferos durante el Paleolítico de Amalda. In: Altuna, J., Baldeón, A., Mariezcurrena, K. (Eds.), La Cueva de Amalda (Zestoa, País Vasco). Ocupaciones paleolíticas y postpaleolíticas. Sociedad de Estudios Vascos, Serie B 4. Sociedad de Estudios Vascos, San Sebastián, pp. 149–192.

Altuna, J., Mariezkurrena, K., 1984. Bases de subsistencia, de origen animal, de los pobladores de Ekain. In: Altuna, J., Merino, J.M. (Eds.), El yacimiento prehistórico de la cueva de Ekain (Deba, Guipúzcoa). Sociedad de Estudios Vasco, Serie B 1. Sociedad de Estudios Vascos, San Sebastián, pp. 211–280.

Altuna, J., Mariezkurrena, K., 1985. Bases de subsistencia de los pobladores de Erralla: Macromamíferos. In: Altuna, J., Baldeón, A., Mariezcurrena, K. (Eds.), Cazadores

magdalenienses en Erralla (Cestona, País Vasco). Munibe (Antropologia-Arkeologia), 37, pp. 87–117.

Altuna, J., Mariezkurrena, K., 2000. Macromamíferos del yacimiento de Labeko Koba (Arrasate, País Vasco). In: Arrizabalaga, A., Altuna, J. (Eds.), Labeko Koba (País Vasco): Hienas y humanos en los albores del Paleolítico Superior. Munibe (Antropologia-Arkeologia), 52, pp. 107–181.

Altuna, J., Mariezkurrena, K., 2010. Tafocenosis en yacimientos del País Vasco con predominio de grandes carnívoros. Consideraciones sobre el yacimiento de Amalda. Actas de la 1a Reunión de Científicos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica. Zona Arqueológica, 13, pp. 214–228.

Altuna, J., Mariezkurrena, K., 2011. Estudio de los macromamíferos del yacimiento de Aitzbitarte III (excavación de la entrada). In: Altuna, J., Mariezkurrena, K., Ríos, J. (Eds.), Ocupaciones humanas en Aitzbitarte III (País Vasco) 33.600–18.400 BP (Zona de entrada a la cueva). Ekob, 5. Servicio Central de Publicaciones del Gobierno Vasco, San Sebastián, pp. 395–480.

Altuna, J., Mariezkurrena, K., Elorza, M., 2002. Arqueozoología de los niveles paleolíticos de Abauntz (Arraiz, Navarra). Saldvie. Estudios de Prehistoria y Arqueología, 2. Departamento de Ciencias de la Antigüedad, Universidad de Zaragoza, pp. 1–26.

Álvarez Laó, D.J., 2003. Macromamíferos fósiles del Pleistoceno de Asturias. Revisión bibliográfica y datos actuales. Naturalia Cantabricae, 2 11–23.

Álvarez-Lao, D.J., García, N., 2010. Chronological distribution of Pleistocene cold adapted large mammal faunas in the Iberian Peninsula. Quat. Int. 212, 120–128.

Álvarez-Lao, D.J., García, N., 2011a. Geographical distribution of Pleistocene cold adapted large mammal faunas in the Iberian Peninsula. Quat. Int. 233, 159–170.

Álvarez-Lao, D.J., García, N., 2011b. Southern dispersal and palaeoecological implications of woolly rhinoceros (Coelodonta antiquitatis): review of the Iberian occurrences. Quat. Sci. Rev. 30, 2002–2017.

Álvarez-Lao, D.J., García, N., 2012. Comparative revision of the Iberian woolly mammoth (Mammuthus primigenius) record into a European context. Quat. Sci. Rev. 32, 64–74.

Álvarez-Lao, D.J., García-García, N., 2006. A new site from the Spanish Middle Pleistocene with cold-resistant faunal elements: La Parte (Asturias, Spain). Quat. Int. 142 (143), 107–118.

Álvarez-Lao, D.J., Kahlke, R.-D., García, N., Mol, D., 2009. The Padul mammoth finds— on the southernmost record of Mammuthus primigenius in Europe and its southern spread during the Late Pleistocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 278, 57–70.

Álvarez-Lao, D.J., Arsuaga, J.L., Baquedano, E., Pérez-González, A., 2013. Last Interglacial (MIS 5) ungulate assemblage from the Central Iberian Peninsula: the Camino Cave (Pinilla del Valle, Madrid, Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 374, 327–337.

Arceredillo, D., Gómez-Olivencia, A., García-Pérez, A., 2011. Three statistical methods for sex determination in extant and fossil caprines: assessment of the Rupicapra long bones. J. Archaeol. Sci. 38, 2450–2460.

Arsuaga, P.M., Aguirre, E., 1979. Rinoceronte lanudo en la provincia de Madrid (Coelodonta antiquitatis Blumenbach). Bol. Real Soc. Esp. Hist. Nat. 77, 23–59.

Auguste, P., 2010. Les Cervidae (Mammalia, Cetartiodactyla) du gisement pléistocène moyen final de l'aven de Romain-la-Roche (Doubs, France). Rev. Paleobiol. Geneve 29 (2), 619–653.

Badoux, D., 1964. A mandible of the woolly rhinoceros, Coelodonta antiquitatis (Blumenbach, 1803), from the Wieringermeer, Netherlands. Säugetierkd. Mitt. 14 (3), 212–214.

Barron, E., Pollard, D., 2002. High-resolution climate simulations of oxygen isotope stage 3 in Europe. Quat. Res. 58, 296–309.

Bonifay, M.-F., 1961. Les Rhinocéros a Narines Cloisonnées de L'Aven de Coulon (Gard). Bull. Mus. Anthrop. Préhist. Monaco 8, 135–175.

Borsuk Białynicka, M., 1973. Studies on the Pleistocene rhinoceros Coelodonta antiquitatis (Blumenbach). Palaeontol. Pol. 29, 1–95.

Bouchud, J., 1968. L'Abri du Facteur a Tursac (Dordogne) II. La faune et sa signification climatique. Gallia Préhist. 11 (1), 113–121.

Brown, W.A.B., Chapman, N.G., 1991. The dentition of red deer (Cervus elaphus): a scoring scheme to assess age from wear of the permanent molariform teeth. J. Zool. 224, 519–536.

Byrne, N., 1979. Le gisement de la Roche Cotard à Langeais: Bovidae. In: Marquet, J.-C. (Ed.), La Roche Cotard à Langeais. Publications du Laboratoire de Géologie de l'Université François Rabelais, Tours, pp. 64–79.

Cardoso, J.L., 1996. The large Upper-Pleistocene mammals in Portugal. A synthetic approach. Geobios 29 (2), 235–250.

Castaños, P., 1980. La Macrofauna de la Cueva de La Paloma. In: Hoyos Gómez, M., Martínez Navarrete, M.I. (Eds.), La Cueva de La Paloma. Soto de las Regueras (Asturias). Excavaciones Arqueológicas en España, 116, pp. 65–100.

Castaños, P., 1982. Estudio de los Macromamíferos del yacimiento de Cueto de La Mina. Bol. Inst. Estud. Asturianos 105 (106), 43–86.

Castaños, P., 1984. Estudio de los Macromamíferos de la cueva de Santimamiñe (Vizcaya). Kobie (Serie Paleoantropología y Ciencias Naturales), 14 235–318.

Castaños, P., 1986. Los Macromamíferos del Pleistoceno y Holoceno de Vizcaya. Faunas asociadas a los yacimientos arqueológicos. Unpublished PhD, Universidad del País Vasco.

Castaños, P., Murelaga, X., Bailon, S., Castaños, J., Saezde Lafuente, X., Suárez, O., 2009. Estudio de los vertebrados del yacimiento de Lezikako Koba (Kortezubi, Bizcaia). Kobie (Ser. Paleontol.) 28, 25–50.

Castaños, J., Castaños, P., Murelaga, X., Alonso-Olazabal, 2012. Kiputz IX: un conjunto singular de bisonte estepario (Bison priscus Bojanus, 1827) del Pleistoceno Superior de la Península Ibérica. Ameghiniana 49 (2), 247–261.

Clot, A., 1980. La grotte de la Carrière (Gerde, Hautes-Pyrénées). Stratigraphie et Paléontologie des Carnivores. Unpublished PhD. Université deToulouse.

Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl-Jensen, D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S., Steffensen, J.P., Sveinbjörnsdottir, A.E., Jouzel, J., Bond, G., 1993.

Evidence for general instability of past climate from a 250 kyr ice-core record. Nature 364, 218–220.

Delpech, F., 1983. Les faunes du Paléolithique Supérieur dans le Sud-Ouest de La France. Cahiers du Quaternaire, 6. Editions du Centre National de la Recherche Scientifique.

Delpech, F., 1984. Les ongulés en périgord et Nord-Ouest du Quercy durant le würm III. Chronoclimatologie, paléobiogéographie, palethnologie. Geobios 17, 531–548.

Delpech, F., 1988. Les grands mammifères, à l'exception des Ursidés. In: Rigaud, J.-P. (Ed.), La grotte Vaufrey à Cenac et Saint-Julien (Dordogne). Paléoenvironnements, chronologie, et activités humaines. Mémoire de la Société Préhistorique Française, Paris, pp. 213–289.

Domingo, M.S., Alberdi, M.T., Sánchez, B., Cerceño, E., 2005. La fauna cuaternaria de la Cornisa Cantábrica en las colecciones del Museo Nacional de Ciencias Naturales. Munibe (Antropol.-Arkeol.) 57 (1), 325–350.

Driesch, A. von den, 1976. A guide to measurement of animal bones from archaeological sites. Peabody Mus. Nat. 1, 1–137.

Drucker, D., Bocherens, H., Cleyet-Merle, J.-J., Madelaine, S., Mariotti, A., 2000. Implications paléoenvironnementales de l'étude isotopique (^{13}C, ^{15}N) de la faune des grands mammifères des Jamblancs (Dordogne, France). Paléo 12, 127–140.

Fernández Rodríguez, 2000. Los Macromamíferos en los yacimientos arqueológicos del Noroeste Peninsular. Un estudio económico. Unpublished PhD. Universidad de Santiago de Compostela.

Fosse, P., 1997. Variabilite des assemblages osseux créés par l'hyène des cavernes. Paléo 9, 15–54.

Friant, M., 1961. Le Rhinoceros (Tichorhinus) antiquitatis Blum. Recherches anatomiques sur la tête osseuse et la dentition. I: la tête osseuse. Ann. Soc. Géol. Nord 81, 157–166.

Frison, G.C., 1978. Animal population studies and cultural inference. Plains Anthropol. 23, 44–52.

Frison, G.C., Wilson, M., Wilson, D.J., 1976. Fossil bison and artifacts from an early altithermal period arroyo trap in Wyoming. Am. Antiq. 41, 28–57.

Fuentes Vidarte, C., 1980. Estudio de la fauna de El Pendo. In: González Echegaray, J. (Ed.), El yacimiento de la cueva de "El Pendo" (Excavaciones 1953–57). Biblioteca Praehistórica Hispana, 17. CSIC (Consejo Superior de Investigaciones Científicas, Madrid, pp. 215–237.

Gautier, A., 1995. The faunal remains of Trou Magrite (Namur Province, Belgium). In: Otte, M., Strauss, L.G., Otte, M., Strauss, L.G. (Eds.), Le Trou Magrite, Fouilles 1991–1992, pp. 137–158.

Gee, H., 1993. The distinction between postcranial bones of Bos primigenius Bojanus, 1827 and Bison priscus Bojanus, 1827 from the British Pleistocene and the taxonomic status of Bos and Bison. J. Quat. Sci. 8, 79–92.

Geist, V., 1999. Deer of the World: Their Evolution, Behaviour, and Ecology. Swan-Hill Press, Shrewsbury.

Gould, S.J., 1974. The origin and function of 'bizarre' structures: antler size and skull size in the 'Irish Elk', Megaloceros giganteus. Evolution 28, 191–220.

Grootes, P.M., Stuiver, M., 1997. Oxigen 18/16 variability in Greenland snow and ice with 10^{-3}- to 10^5-year time resolution. J. Geophys. Res. 102, 26,455–26,470.

Guérin, C., 1980. Les Rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène Supérieur en Europe occidentale. Comparaison avec les espèces actuelles. Quatrième Partie. Le carrefour du Pléistocène moyen et supérieur. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon, 79(3), pp. 785–1185.

Guthrie, R.D., 1982. Mammals of the mammoth steppe as paleoenviromental indicators. In: Hopkins, D.M., Matthews Jr., J.V., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia, Academic Press, New York, pp. 307–326.

Guthrie, R.D., 1990. Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe. The University of Chicago Press 1–323.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics software package for education and data analysis. Palaeontol. Electron. 4 (1) (9 pp.).

Harlé, E., 1912. Ensayo de una lista de mamíferos y aves del cuaternario conocidos hasta ahora en la Península Ibérica. Bol. Inst. Geol. Esp. 12 (2ª serie), 135–162.

Hillman-Smith, A.K.K., Owen-Smith, N., Anderson, J.L., Hall-Martin, A.J., Selaladi, J.P., 1986. Age estimation of the White rhinoceros (Ceratotherium simum). J. Zool. 210, 355–379.

Kahlke, R.-D., 1999. The History of the Origin, Evolution and Dispersal of the Late Pleistocene Mammuthus–Coelodonta Faunal Complex in Eurasia (Large Mammals). Fenske Companies, Rapid City.

Kahlke, R.-D., 2013. The origin of Eurasian Mammoth Faunas (Mammuthus–Coelodonta Faunal Complex). Quat. Sci. Rev. http://dx.doi.org/10.1016/j.quascirev.2013.01.012 (in press).

Koken, E., 1885. Über Fossile Säuger aus China. Palaeontol. Abh. 3, 31–114.

Kurtén, B., 1968. Pleistocene Mammals of Europe. Weidenfeld & Nicolson, London.

Le Tensorer, J.-M., 1998. Le Paléolithique en Suisse. Collection Des Origines, Série "Préhistoire d'Europe"Nº 5. Grenoble.

Liouville, M., 2007. Variabilité du Cerf élaphe (Cervus elaphus Linné 1758) au cours du Pléistocène moyen et supérieur en Europe occidentale: approches morphométrique, paléoécologique et cynégétique. Unpublished PhD, Muséum National d'Histoire Naturelle, Paris.

Lister, A.M., 1986. New results on deer from swanscombe, and the stratigraphical significance of deer in the middle and upper Pleistocene of Europe. J. Archaeol. Sci. 13, 319–338.

Lorenzana, S., 1982. La fauna Cuaternaria del yacimiento del Peñón de Malverde (Llera, Grado). Unpublished MSc. Universidad de Oviedo

Lovari, S., Scala, C., 1980. Revision of Rupicapra genus L. A statistical re-evaluation of Couturier's data on the morphometry of six chamois subspecies. Bol. Zool. 47, 113–124.

Lyman, R.L., 1994. Relative abundances of skeletal specimens and taphonomic analysis of vertebrate remains. Palaios 9, 288–298.

Mariezkurrena, K., 1983. Contribución al conocimiento del desarrollo de la dentición y el esqueleto postcraneal de Cervus elaphus. Munibe (Antropol.-Arkeol.) 35, 149–202.

Mariezkurrena, K., Altuna, J., 1983. Biometría y dimorfismo sexual en el esqueleto de Cervus elaphus würmiense, postwürmiense y actual del Cantábrico. Munibe (Antropol.-Arkeol.) 35, 203–246.

Mariezkurrena, K., Altuna, J., 1989. Análisis arqueozoológico de de los Macromamíferos del yacimiento de Zatoya. In: Barandiarán, I., Cava, A. (Eds.), El Yacimiento prehistórico de Zatoya (Navarra). Trabajos de Arqueología Navarra, 8, pp. 237–266.

Mariezkurrena-Gastearena, K., 2011. Hallazgos de macromamíferos poco frecuentes en yacimientos arqueológicos y paleontológicos del Pleistoceno de la Región Cantábrica. Kobie (Paleoantropología) 30, 83–110.

Maroto, J., Soler, N., Fulloa, J.M., 1996. Cultural change between Middle and Upper Palaeolithic in Catalonia. In: Carbonell, E., Vaquero, M. (Eds.), The last Neanderthals, the first anatomically modern humans: a tale about the human diversity, pp. 219–250.

Martínez, E., 1980. Mapa Geológico de España E. 1:50.000, Hoja 32 - Llanes. Instituto Geológico y Minero de España, Madrid.

Maschenko, E.N., 2002. Individual development, biology and evolution of the Woolly Mammoth. Cranium 19, 4–120.

Münzel, S.C., Conard, N.J., 2004a. Cave bear hunting in the Hohle Fels, a cave site in the Ach Valley, Swabian Jura. Rev. Paléobiol. Genève 23 (2), 877–885.

Münzel, S.C., Conard, N.J., 2004b. Change and continuity in subsistence during the Middle and Upper Palaeolithic in the Ach Valley of Swabia (South-west Germany). Int. J. Osteoarchaeol. 14, 225–243.

Nascetti, G., Lovari, S., Lanfranchi, P., Berducou, C., Mattiucci, S., Rossi, L., Bullini, L., 1985. Revision of Rupicapra genus. III. Electrophoretic studies demonstrating species distinction of chamois populations of the Alps from those of the Apennines and Pyrenees. In: Lovari, S. (Ed.), The Biology and Management of Mountain Ungulates. Croom Helm, London, pp. 56–62.

Niven, L.B., 2007. From carcass to cave: large mammal exploitation during the Aurignacian at Vogelherd, Germany. J. Hum. Evol. 53, 362–382.

Niven, L.B., Hill, M.G., 1998. Season of bison mortality at three plains archaic kill sites in Wyoming. Plains Anthropol. 43, 5–26.

O'regan, H.J., Turner, A., Wilkinson, D.D., 2002. European Quaternary refugia: a factor in large carnivore extinction? J. Quat. Sci. 17, 789–795.

Obermaier, H., 1916. El Hombre fósil. Comisión de investigaciones Paleontológicas y Prehistóricas, 9. Comisión de Investigaciones Paleontológicas y Prehistóricas, Madrid 1–398.

Pathou-Mathis, M., 2005. Comportement de subsistance des Néandertaliens du niveau châtelperronien de Saint-Césaire (Charente-Maritime). Munibe (Antropol.-Arkeol.) 57 (1), 197–204.

Pérez Ripoll, M., 1977. Los mamíferos del yacimiento musteriense de Cova Negra (Játiva, Valencia). Serie de Trabajos Varios, 53. Servicio de Investigación Prehistórica, Diputación Provincial de Valencia 1–147.

Pérez, T., Albornoz, J., Domínguez, A., 2002. Phylogeography of chamois (Rupicapra spp.) inferred from microsatellites. Mol. Phylogenet. Evol. 25, 524–534.

Pérez, T., Hammer, S.E., Albornoz, J., Domínguez, A., 2011. Y-chromosome phylogeny in the evolutionary net of chamois (genus Rupicapra). BMC Evol. Biol. 11, 272.

Piperno, M., Giacobini, G., 1991. A taphonomic study of the paleosurface of Guattari Cave (Monte Circeo, Latina, Italy). Quat. Nova 1, 143–161.

Prat, F., Delpech, F., Cancel, N., Guadelli, J.L., Slott-Moller, R., 2003. Le Bison des steppes, Bison priscus Bojanus, 1827, de la grotte d'Habarra à Arudy (Pyrénées-Atlantiques). Paléo 15, 1–102.

Raynal, J.P., Guadelli, J.L., Paquereau, M.M., Daugas, J.P., 1989. A propos de l'interstade Wurmien dans le Massif Central: le gisement de Theillat a Sanssat, Allier. l'Anthropologie 93 (1), 293–298.

Rodríguez, F., Pérez, T., Hammer, S.E., Albornoz, J., Domínguez, A., 2010. Integrating phylogeographic patterns of microsatellite and mtDNA divergence to infer the evolutionary history of chamois (genus Rupicapra). BMC Evol. Biol. 10, 222.

Scala, C., Lovari, S., 1984. Revision of Rupicapra genus. II. A skull and horn statistical comparison of Rupicapra rupicapra ornata and Rupicapra rupicapra pyrenaica chamois. Bol. Zool. 51, 285–294.

Scheer, A., 2001. The utilisation of mammoth remains as raw material and its importance for the Gravettian people of the German Danube. In: Cavarreta, G., Giola, P., Mussi, M., Palombo, M.R. (Eds.), La Terra degli Elefanti/The World of Elephants. Proceedings of the 1st International Congress, Rome, 16–20 October 2001, pp. 455–459.

Schreve, D., 2006. The taphonomy of a Middle Devensian (MIS 3) vertebrate assemblage from Lynford, Norfolk, UK, and its implications for Middle Palaeolithic subsistence strategies. J. Quat. Sci. 21 (5), 543–556.

Shrader, A.M., Owen-Smith, N., 2002. The role of companionship in the dispersal of white rhinoceroses (Ceratotherium simum). Behav. Ecol. Sociobiol. 52, 255–261.

Slott-Moller, R., 1988. Contribution a l'étude paléontologique d'un gisement préhistorique: l'exemple du Roc de Marcamps (Gironde). Institut du Quaternaire, Université de Bordeaux I.

Soto, E., Meléndez, G., 1981. Fauna de la Cueva de Las Caldas. Cueva de Las Caldas. S. Juan de Priorio (Oviedo). Excavaciones Arqueológicas en España, 115 259–268.

Soto, E., Sesé, C., 1991. Restos de grandes Mamíferos del Pleistoceno del Arenero del Arroyo del Culebro (Getafe, Madrid). Estudios de Prehistoria y Arqueología Madrileñas, 7 7–27.

Stampfli, H.R., 1963. 18. Wisent, Bison bonasus (Linné) 1758, Ur, Bos primigenius Bojanus, 1827, und Hausrind, Bos taurus (Linné), 1758. In: Boessneck, J., Jéquier, J.-P., Stampfli, H.R. (Eds.), Seeberg Burgäschisee-Süd. Teil 3. Die Tierreste. Acta Bernensia, Beiträge zur prähistorischen, klassischen und jüngeren Archäologie II, pp. 117–196.

Stiner, 1991. The Guattari faunas then and now. Quat. Nova 1, 163–192.

Takahashi, K., Wei, G., Uno, H., Yoneda, M., Jin, C., Sun, C., Zhang, S., Zhong, B., 2007. AMS 14C chronology of the world's southernmost woolly mammoth (Mammuthus primigenius Blum.). Quat. Sci. Rev. 26, 954–957.

Teobald, N., Szymanek, C., 1963. Le crâne de Rhinoceros à narines cloisonnées des grottes de Rigney (Doubs). Annales Scientifiques de l'Université de Besançon (S. 2) 17, 97–113.

Todd, L.C., Hofman, J.L., Schultz, C.B., 1990. Seasonality of the Scottsbluff and Lipscomb Bison Bonebeds: implications for Modeling Paleoindian Subsistence. Am. Antiq. 55, 813–827.

Turner, A., 2000. The Paviland mammalian fauna. In: Aldhouse-Green, S. (Ed.), Paviland Cave and the "Red Lady": A Definitive Report. Western Academic and Specialist Press Limited, Bristol, pp. 133–140.

Ukraintseva, V.V., 1993. Vegetation Cover and Environment of the "Mammoth Epoch" in Siberia. The Mammoth Site of Hot Springs, South Dakota 1–309.

van Andel, T.H., 2002. The climate and landscape of the Middle Part of the Weichselian Glaciation in Europe: the Stage 3 Project. Quat. Res. 57, 2–8.

Vega del Sella, Conde de la, 1916. Paleolítico de Cueto de La Mina (Asturias). Comisión de Investigaciones Paleontológicas y Prehistóricas.

Vega del Sella, Conde de la, 1930. Las cuevas de La Riera y Balmori (Asturias). Comisión de Investigaciones Paleontológicas y Prehistóricas, 38 1–116.

Vereschagin, N.K., Baryshnikov, G.F., 1982. Paleoecology of the mammoth fauna in the Eurasian Arctic. In: Hopkins, D.M., Matthews Jr., J.V., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia. Academic Press, New York, pp. 267–279.

West, R.G., 2000. Plant Life of the Quaternary Cold Stages. Evidence from the British Isles. Cambridge University Press, Cambridge.

Yravedra Sáinz de los Terreros, J., 2006. Acumulaciones biológicas en yacimientos arqueológicos: Amalda VII y Esquilleu III–IV. Trab. Prehist. 63 (2), 55–78.