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Ungulates from Teixoneres Cave (Moià, Barcelona, Spain): Presence of cold-adapted elements in NE Iberia during the MIS 3

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ABSTRACT

The site of Teixoneres Cave (Barcelona, NE Spain) provided two ungulate associations of MIS 3 age, one of which (from unit III) include two cold-adapted species, *Coelodonta antiquitatis* (Blumenbach, 1799) and *Mammuthus primigenius* (Blumenbach, 1799), which are infrequent in the Iberian fossil record. The collection includes the first Iberian find of a *M. primigenius* dP^2, a rare dental element. This assemblage is relevant from chronological, biogeographical and palaeoecological aspects.

Age of this faunal association (44,210 to 33,060 cal ka BP) is slightly older than most of the other Late Pleistocene Iberian occurrences of *M. primigenius* and *C. antiquitatis*, providing interesting information on the spatiotemporal distribution of these species.

The presence of these two cold-adapted species in NE Iberia is of special biogeographical relevance since they are infrequent and poorly known in this region.

The faunal association of unit III was compared with other Iberian and Western European fossil assemblages that included *C. antiquitatis* and/or *M. primigenius*, by means of multivariate statistical analysis. The Teixoneres unit III assemblage reflects a faunal mixture in which temperate ungulate species are predominant and cold-adapted taxa are very scarce. This pattern is the same that can be observed in most of the Iberian analyzed assemblages and does not reflect the typical faunal composition of the Eurasian mammoth steppe, suggesting that that cold-adapted taxa only reached the Peninsula occasionally, during the coldest episodes of the Pleistocene, cohabiting with the local faunas instead of replacing them.

1. Introduction

Fossil record from Western Europe corresponding to the MIS 3, an episode marked by numerous fast and extreme climate oscillations (Barron and Pollard, 2002; Van Andel, 2002), revealed environmental diversity among different regions: North and middle latitude record shows a predominance of cold-adapted mammals (e.g. *Rangifer tarandus* Linnaeus, 1758, *Mammuthus primigenius* and *Coelodonta antiquitatis*), which are distinctive elements of the "mammoth fauna" (Vereschagin and Baryshnikov, 1982), during most of this episode (Delpech, 1983, 1984; Turner, 2000; Münzel and Conard, 2004a, 2004b; David et al., 2005; Schreve, 2006). By contrast, contemporary faunal assemblages from the Iberian Peninsula are mainly constituted by species of temperate environmental preferences, such as the red deer (*Cervus elaphus* Linnaeus, 1758), and also document the occurrence of other typically interglacial taxa like steppe rhino (*Stephanorhinus hemitoechus* Falconer, 1868) and fallow deer (*Dama dama* Linnaeus, 1758) (Álvarez-Lao and Méndez, 2016), suggesting that this southern area acted as glacial refuge for these species during MIS 3. However, while infrequent, cold adapted large mammals also occurred at Iberian assemblages during the MIS 3 (García and Arsuaga, 2003; Álvarez-Lao et al., 2009; Álvarez-Lao and García, 2010, 2011a, 2012; Álvarez-Lao, 2014). Moreover, the southernmost geographical occurrence in Europe of the woolly mammoth (*Mammuthus primigenius*), a typical cold-adapted mammal, was documented during MIS 3 at Padul peat bog, southern Iberia (Álvarez-Lao et al., 2009).

Northern Iberia seems to have constituted a transitional area between mainland Europe and Central-Southern Iberia during the MIS 3: while faunal assemblages are here dominated by interglacial species, cold-adapted elements are also relatively frequent (Álvarez-Lao and García, 2010). This was widely documented at the Cantabrian area (NW Iberia), where 15 from a total of 34 revised MIS 3 assemblages yielded cold-adapted taxa, although normally at very low abundances (Álvarez-Lao and Méndez, 2016). Fossil record from Catalonia (NE Iberia) is more scarce and poorly known, however, a similar pattern to

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the Cantabrian area can be observed: cold-adapted elements also occur during MIS 3, as was stated in the sites of Reclau Viver, Arbreda and Canyars (Maroto et al., 1996; Daura et al., 2013), within assemblages dominated by temperate faunas. Such faunal distribution is consistent with the geomorphologic context since the Iberian Peninsula is relatively isolated from continental Europe by the Pyrenees, which acted as a barrier limiting dispersals (Álvarez-Lao and García, 2011a). The cold-adapted species, which were abundant in southern France during the Late Pleistocene (Delpech, 1983), could only enter into the Iberian Peninsula through narrow passes placed west and east of the Pyrenees, to the Cantabrian area and Catalonia respectively (Álvarez-Lao and García, 2011a). Into this context, the ungulate assemblage of Teixoneres Cave, here first studied, provides a new evidence of this particular faunal complex of transitional character in NE Iberia.

The main aim of this work is to present a palaeontological comparative description of the ungulate fossils from Teixoneres Cave within a Western European perspective. In addition, the ecological composition of this ungulate assemblage is statistically analyzed along with a number of faunal associations including *C. antiquitatis* and/or *M. primigenius* from Western and Central Europe. Chronological and biogeographical aspects are also discussed.

2. Setting

Teixoneres Cave is an archaeological site located in the Northeast of the Iberian Peninsula (Moià, Barcelona) at an altitude of about 760 m a.s.l. (Fig. 1). The cave is developed in a Neogene limestone (called Collsuspina Formation) and has a size of approximate 30 m length with three distinct chambers (namely X, Y, and Z). The excavation leaded by a team from IPHES and the University Rovira I Virgili of Tarragona (JR, RB, FR) has focused mainly on the largest area of the cave (Chamber X). The sedimentary sequence is 8 m thick, in which 10 different stratigraphic units have been identified. Hitherto, the two main archaeological units located at the upper part of the stratigraphic sequence namely units II and III, have been excavated in extension. Units I and IV, are continuous speleothems that cover much of the surface of the cave and did not provide any archaeological material. U-series dates have confidently situated the stalagmite of unit I in MIS 2 (ca. 14–16 ka BP) and the stalagmite of unit IV in MIS 5c (average date of 100.3 ± 6.1 ka) (Tissoux et al., 2006). Recently published radiocarbon dates indicate a chronology attesting the human presence from beyond 51,000 ^{14}C BP to 44,210 cal BP for unit III and 44,210 to 33,060 cal BP for unit II (Talamo et al., 2016).

Taphonomic studies suggest a formation mainly characterized by the alternation of Neanderthal groups and large carnivores (hyenas and cave bears). The anthropogenic remains tend to be close to the main entrance while the carnivores have a stronger presence at the inner areas of the cave. Human activity is identified by the presence of burned bones, cut-marks and intentional bone breakage on large mammal remains, lithic tools and some hearths (Rosell et al., 2010, in press). The list of large mammals so far includes *Ursus spelaeus* (Rosenmuller, 1794), *Canis lupus* (Linnaeus, 1758), *Vulpes vulpes* (Linnaeus, 1758), *Lynx* sp. (Kerr, 1792), *Crocuta crocuta* (Erxleben, 1777), *Meles meles* (Linnaeus, 1758), *Cervus elaphus*, *Capreolus capreolus* (Linnaeus, 1758), Bovini cf. *Bos primigenius* (Bojanus, 1827), *Rupicapra pyrenaica* (Bonaparte, 1845), *Capra pyrenaica* (Schinz, 1838), *Sus scrofa* (Linnaeus, 1758), *Equus ferus* (Boddaert, 1785), *Equus hydruntinus* (Regalia, 1907), *Coelodonta antiquitatis* and *Mammuthus primigenius*. The lithic assemblage shows a diversity of materials and the combination of local raw materials (orthogonal and discoid debitage) with non-local materials (Levallois method) seem to support the hypothesis of high mobility of the Neanderthal groups in the territory (Rosell et al., in press).

3. Material and methods

The large mammal assemblage comprises 27,353 fossil remains (2697 in unit II and 24,656 in unit III). Most of the fossils are highly fragmented, consequently only 5.4% resulted identifiable (11.9% for unit II and 4.6% in unit III). The number of identified specimens for large mammals is of 1465 (323 in unit II and 1142 in unit III), of which 1263 belong to ungulates (257 in unit II and 1006 in unit III).

Fossils recovered from units II and III are well preserved but highly fragmented as quantified through the percentage of identified

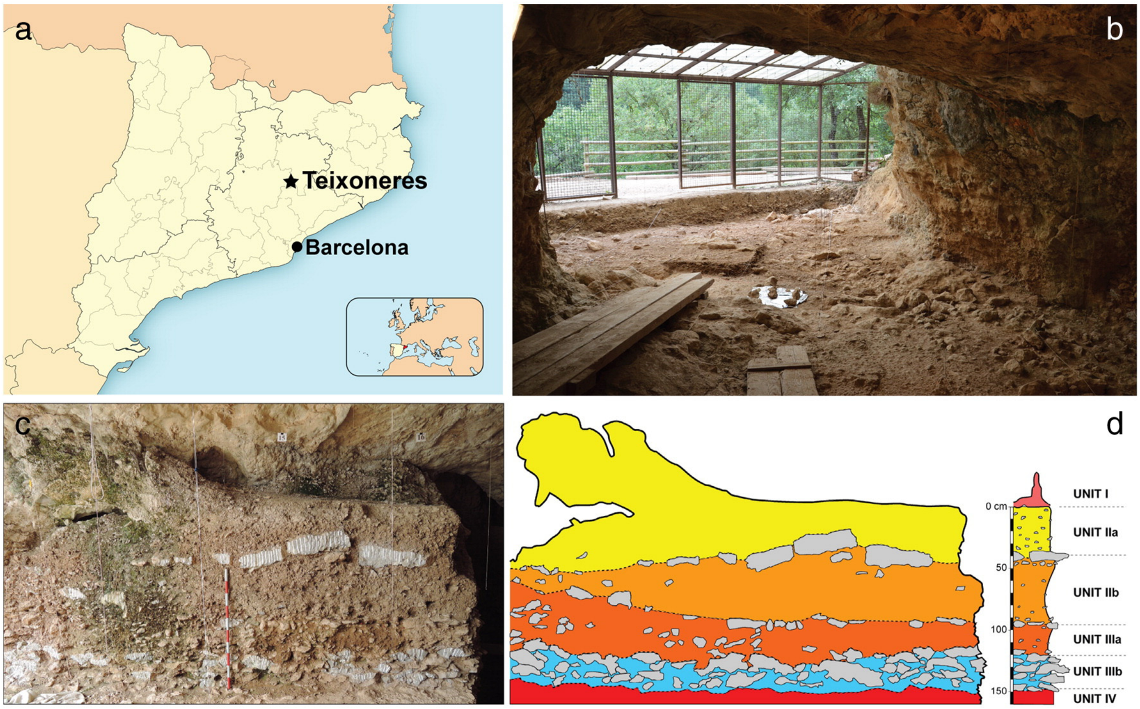


Fig. 1. Teixoneres Cave. (A) Location of the site. (B) View of the entrance of the cave from the inner area. (C) West stratigraphic profile. (D) Schematic drawing of the profile with the stratigraphical units I to IV.

specimens in the assemblage, especially in unit III. During field work all faunal remains larger than 2 cm are recovered following a system of Cartesian coordinates. Sediment is sieved (1 cm and 1 mm meshes) to recover elements (or fragments) smaller than 2 cm. All material has been analyzed for taxonomical and anatomical identifications, as well as for palaeontological and taphonomical studies.

Number of identified specimens (NISP) includes bones and teeth identified both at the anatomical and specific levels. Minimum number of individuals (MNI) was calculated from the teeth exclusively. Given the high fragmentation of bones, teeth have a higher percentage of identification and consequently provide the highest MNI. For each species, MNI was computed taking into account tooth position, laterality, age group (based on tooth eruption and wear).

With the purpose of study the faunal composition of the unit III from Teixoneres (the most complete and best represented), percentages of each species were analyzed in comparison with 33 other assemblages, which also include *M. primigenius* and/or *C. antiquitatis*, coming from Iberia and Western-Central Europe (see Section 6). The percentages of the different herbivore species in each assemblage have been calculated on the basis of NISP (Number of Identified Specimens). Following Lyman (2008), we consider this estimator of good reliability since no taphonomic bias is detected towards any of the species of each assemblage. Only assemblages with NISP larger than 100 have been considered for the analysis. In order to 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. Considering the high variation detected in 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).

Measurements taken on the fossils are given in millimeters and followed the standards of Von den Driesch (1976) for artiodactyls and equids, Guérin (1980) for *Coelodonta antiquitatis*, and Maschenko (2002) for *Mammuthus primigenius*. Morphometric data were compared with an extensive sample from Western Europe and Siberia, published by a number of authors specified in Section 4. The age at death in some of the species has been estimated on the basis of teeth wear following the criteria published by diverse authors indicated in Section 4.

All the material studied in this paper is curated at the *Institut Català de Paleoecologia Humana i Evolució Social* in Tarragona (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 is the most abundant species in the Teixoneres assemblage (Table 1), both in units II and III (comprising 42.18% and 59.34% of the ungulate remains, respectively). The sample (Fig. 2a–f) is very fragmented and the identifiable specimens are mainly teeth. Postcranial preserved elements include mainly compact bones as astragalus, phalanges, metapodials and some epiphyses of limb bones. Antler fragments were also recovered (Fig. 2f). All other elements are too fragmented to allow detailed descriptions and measurements.

All these elements correspond to a minimum of 36 individuals (9 in unit II and 27 in unit III), 5 of which are infantile, 8 juveniles, 19 adults and 4 old adults. Age at death has been estimated on the basis of teeth development and wear following the criteria of Brown and Chapman (1991).

Table 1
Composition of the Teixoneres faunal assemblages.

Taxa	Unit II			Unit III		
	NISP	% NISP	MNI	NISP	% NISP	MNI
Cervus elaphus	108	42.02	9	597	59.34	27
Capreolus capreolus	10	3.89	4	49	4.87	4
Bovini cf. *Bos primigenius*	26	10.11	5	61	6.06	5
Rupicapra pyrenaica	6	2.33	2	6	0.6	2
Capra pyrenaica	1	0.39	1	11	1.1	3
Sus scrofa	14	5.46	4	5	0.5	2
Equus ferus	32	12.4	4	129	12.82	12
Equus hydruntinus	12	4.67	4	64	6.36	7
Equus sp.	44	17.12		76	7.55	
Coelodonta antiquitatis	4	1.55	2	7	0.7	4
Mammuthus primigenius				1	0.1	1
Total	257	100	35	1006	100	67

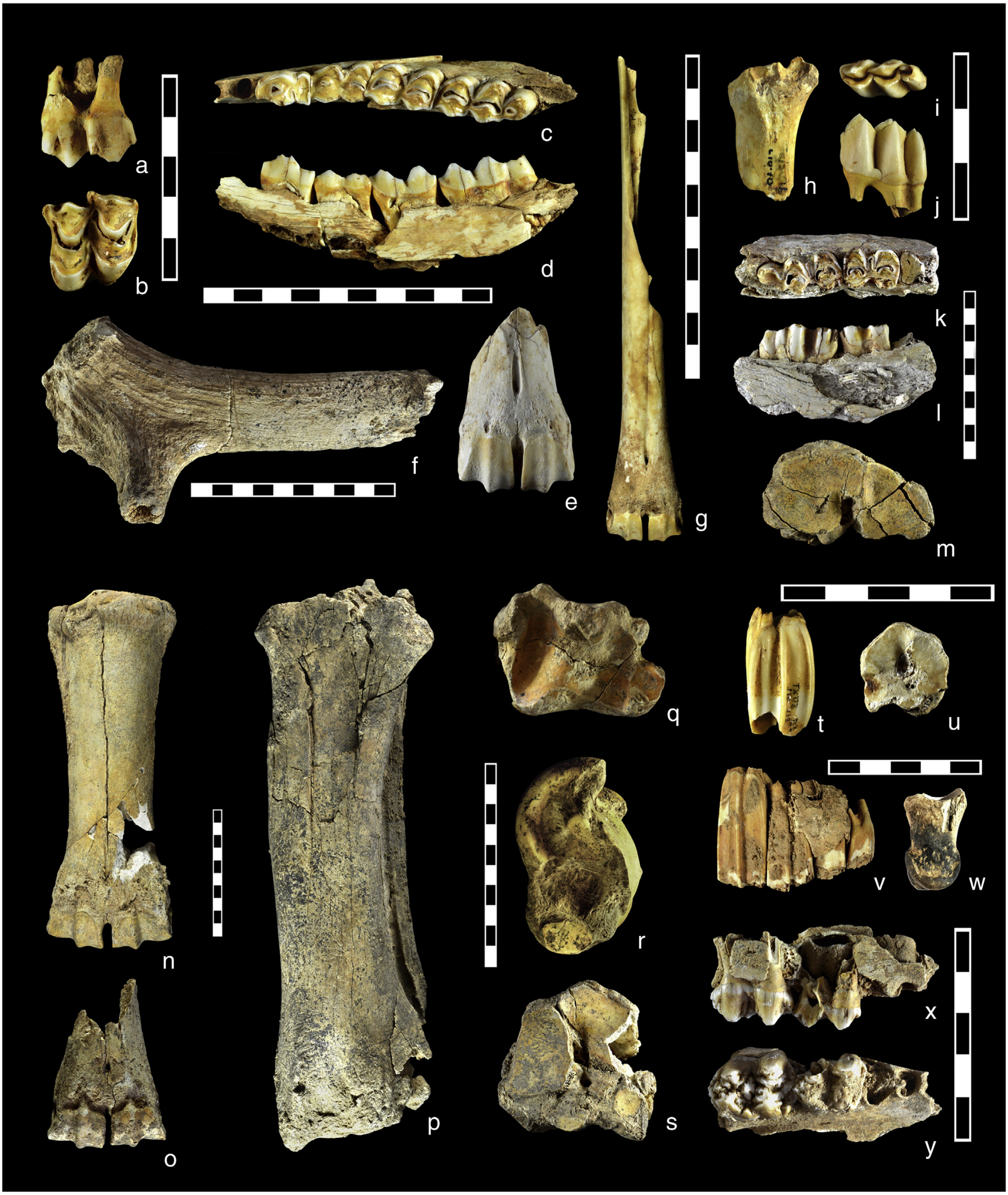
For morphometrical purposes we selected the M_3, a dental element which is not affected by attrition and is relatively numerous in the assemblage ($n = 4$, all coming from unit III). Most other molars were, to a greater or lesser extent, affected by interdental attrition, which can decrease their length considerably thus reducing their value for comparative purposes. Only few postcranial elements provided reliable measurements, so we also included the distal metacarpal ($n = 3$, all coming from unit III) and the distal tibia ($n = 2$, all coming from unit III) for comparative purposes, even assuming that they are very scarce and perhaps not representative enough for the whole sample. All these morphometric data were compared with a sample of Pleistocene red deer from Western Europe (Table 2). The size of the Teixoneres M_3 resulted visibly smaller than most other populations from cold stages (as Lezetxiki, Jou Puerta, Aitzbitarte IV, Urtiaga Morín or Las Caldas), but larger than populations from temperate stages (like Camino Cave, Cova Negra or Swanscombe). Postcraneal remains, although scarce, also showed a similar pattern (are smaller than most the comparison populations from cold stages). These morphometrical results were unexpected considering that red deer populations from Late Pleistocene cold stages (as is assumed for unit III, see Section 7) are normally larger in body size than those from temperate phases (Mariezkurrena and Altuna, 1989; Álvarez-Lao et al., 2013). Probably these results are not enough representative, considering that the available sample is low. However, it is interesting to emphasize that the largest M_3 of the sample (length = 34.5 mm) is similar to the largest specimens of other MIS 3 assemblages from the Cantabrian area, as Jou Puerta and Lezetiki (Table 2). Ungulate assemblages from cold episodes of the Mediterranean margin are not enough studied, so we cannot rule out the possibility that there were regional variations in body size for some species.

4.1.1.2. Capreolus capreolus (Linnaeus, 1758). Roe deer remains are scarce, comprising only 3.9% of the ungulate assemblage of unit II and 4.8% of unit III (Table 1). The sample is also very fragmented so only teeth and few postcranial elements (mostly phalanges, compact bones and few epiphyses of limb bones) were enough preserved (Fig. 2g–j).

All these elements correspond to a minimum of 8 individuals (4 in unit II and 4 in unit III), 3 of which are juveniles and 5 adults.

Measurements were compared with samples of fossil and recent roe deer from Iberian sites (Table 3), showing that body size of the Teixoneres specimens is not significantly different.

Capreolus is generally very poorly represented in Western European Pleistocene sites, as was also noted for British localities by Lister (1986) who suggested that there might be a general taphonomic bias against this species. Many assemblages from the Cantabrian area (NW Iberia) show the same pattern (Altuna, 1972; Castaños, 1986; Altuna and Mariezkurrena, 2000). The low percentage of this species at Teixoneres is also consistent with this trend.



The occurrence of roe deer in unit III of Teixoneres Cave is of high palaeoecologic interest because this species is very infrequent or lacking in assemblages associated to cold-adapted faunas from mainland Europe. However, co-occurrence of these allegedly incompatible taxa has been also stated in a number of MIS 3 assemblages from the Cantabrian area (Álvarez-Lao and Méndez, 2016), suggesting that this is a relatively common pattern in Northern Iberia.

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

Site		M_3 L	Mtc. DW	T. DW
Teixoneres III[a]	Mean (n)	30.7 (4)	41.8 (3)	49.8 (3)
	Min-max	28.4–34.5	40–43	45.7–52.55
Jou Puerta[b]	Mean (n)	32.1 (4)	46.42 (2)	54.7 (2)
	Min-max	30.15–34.3	46.55–46.3	54.3–55.1
Camino Cave[c]	Mean (n)	29.88 (11)	41.4 (5)	45.9 (2)
	Min-max	28.1–32.3	38.4–42.8	45–46.8
Cova Negra[d]	Mean (n)	30 (7)	36.2 (3)	43.9 (4)
	Min-max	25.2–32.8	34.6–37.9	41–48
Lezetxiki[e]	Mean (n)	32.26 (3)		57.25 (2)
	Min-max	28.2–34.6		57–57.5
Aitzbitatrte IV[e]	Mean (n)	34.6 (6)	47.73 (3)	54.56 (5)
	Min-max	31.5–36.1	45.1–51.1	50.5–59
Urtiaga D[e]	Mean (n)	34.8 (30)	45.2 (32)	55.5 (4)
	Min-max	30.1–38.1	38–51	53.5–59
Morín[f]	Mean (n)	35.27 (14)	43.13 (3)	52.4 (4)
	Min-max	31–39.5	40–45.7	49.1–55.1
Tito Bustillo[g]	Mean (n)	34.86 (13)	42.76 (15)	52.2 (6)
	Min-max	32–39	40–49	47.5–55
La Riera[h]	Mean (n)	33.2 (68)	43.95 (20)	54.57 (7)
	Min-max	30–39.5	40.5–48	52–58
Zatoya[i]	Mean (n)	32.12 (4)		
	Min-max	28–34.5		
Labeko Koba[j]	Mean (n)	32.93 (12)	48.59 (11)	54.4 (7)
	Min-max	31–35	44–51	50.5–60
La Paloma[k]	Mean (n)	34.29 (89)	42.67 (70)	50.8 (42)
	Min-max	29.5–39	38.5–50.5	45–57
Las Caldas[l]	Mean (n)	34.96 (3)		
	Min-max	33.5–36.8		
Liñares[m]	Mean (n)	33.3 (9)	42.3 (4)	51.47 (13)
	Min-max	29.8–35.4	40.9–43.1	46.46–56.5
Romain-la-Roche[n]	Mean (n)	31.8 (4)		
	Min-max	30–33.4		
Lazaret C II[o]	Mean (n)	34.5 (18)		
	Min-max	31.8–38.3		
Piégu[o]	Mean (n)	32.4 (10)		
	Min-max	29.3–37.4		
La Ferrassie[p]	Mean (n)	33.3 (7)		
	Min-max	31–37		
Vaufrey[q]	Mean (n)	32.2 (8)		
	Min-max	28.3–35.1		
Swanscombe[r]	Mean (n)	28 (3)		
	Min-max	27.8–28.3		
L'Arago[s]	Mean (n)	31 (16)	44.3 (6)	48.9 (3)
	Min-max	27–34	41.7–46.5	41.5–53.2
Mosbach[t]	Mean (n)	31.4 (23)		
	Min-max	29.7–34.9		
Voigtstedt[u]	Mean (n)	31.8 (5)		
	Min-max	31.3–33.6		

Mtc.: metacarpal; T.: Tibia; L: maximum length; DW: distal width.
[a] This study; [b] Álvarez-Lao (2014); [c] Álvarez-Lao et al. (2013); [d] Pérez Ripoll (1977); [e] Altuna (1972); [f] Altuna (1971); [g] Altuna (1976); [h] Altuna (1986); [i] Mariezkurrena and Altuna (1989); [j] Altuna and Mariezkurrena (2000); [k] Castaños (1980); [l] Soto and Meléndez (1981); [m] López González (2001); [n] Auguste (2010); [o] Liouville (2007); [p] Delpech (1984); q Delpech (1988); [r] Lister (1986); [s] Crégut (1979); [t] Kahlke (1960); [u] Kahlke (1965).

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

Site		M_3 L	Rad. PW	Mtc. DW	Ph.3 L
Teixoneres[a]	Mean (n)	16.55 (2)	27.4 (1)	24.2 (1)	25.86 (3)
	Min-max	16.5–16.6			24.8–27.3
Jou Puerta[b]	Mean (n)	17.2 (2)	27.67 (3)	23.15 (4)	28.3 (2)
	Min-max	16.29–18.11	27.3–28.25	22.28–23.9	27.1–29.5
Urtiaga[c]	Mean (n)	16.53 (24)	26.8 (1)	24.4 (13)	26.2 (7)
	Min-max	14.5–17.6		21.3–27.9	24.4–28.7
Marizulo[c]	Mean (n)	15.2 (1)	26.4 (1)		
Santimamiñe[d]	Mean (n)	16.05 (27)	29 (3)	24.06 (8)	27.02 (26)
	Min-max	14.2–17.6	27.5–31.5	23–25.5	24–29.5
La Riera[e]	Mean (n)	16.88 (8)		24 (2)	28.5 (1)
	Min-max	15.5–18		23.5–24.5	
Recent roe deer from NW Iberia[b]	Mean (n)	15.43 (3)			
	Min-max	15.1–15.77			

Rad.: radius; Mtc.: metacarpal; Ph.3: third phalange L: maximum length; DW: distal width; PW: proximal width.
[a] This study; [b] Álvarez-Lao (2014); [c] Altuna (1972); [d] Castaños (1984); [e] Altuna (1986).

4.1.2. Family Bovidae (Gray, 1821)

4.1.2.1. Bovini cf. Bos primigenius (Bojanus, 1827). Bovine remains comprise 10.15% of the ungulate assemblage of unit II and 6.06% of unit III (Table 1). The identifiable specimens are teeth and few postcranial elements (Fig. 2k–s), including one complete radius, three metacarpals and one metatarsal, belonging to a minimum of 10 individuals (5 in unit II and 5 in unit III), 1 of which is infantile, 4 juveniles, 4 adults and 1 old adult.

Regardless of the distinction between *Bos primigenius* and *Bison priscus* (Bojanus, 1827) is not always possible, several postcranial elements from the Teixoneres Cave assemblage are useful for systematical purposes. Descriptions of these elements are provided below.

A left radius (Fig. 2p) is fairly complete showing an interesting trait in the proximal end: the shape of the ulnar joint with the proximal posterior edge of the radius is deep and sharply pointed, which is accepted by Gee (1993) as a distinctive feature of *Bos*.

One well preserved right metacarpal (Fig. 2m-n) shows two features of systematic significance. In proximal view, the facet for the unciform is trapezoidal shaped that is characteristic of *Bos* and different of *Bison* (in which is more triangular shaped), following the criteria of Bibikova (1958) and Gee (1993). In anterior view, the lateral edges of the diaphysis are smoothly divergent towards the distal end (Fig. 2n–o), which is an indicative feature of *Bos* and different of *Bison* (whose diaphysis show a more abrupt shape towards the distal end, with distinct “shoulders”), following the criteria provided by Stampfli (1963) and Gee (1993).

One left tibia fragment preserved the distal epiphysis (Fig. 2q) showing both the anterior and posterior malleolar facets clearly confluent, which is considered by Gee (1993) as a reliable character for the identification of *Bos*.

One almost complete left astragalus (Fig. 2r) shows also interesting features: in the distal part of the posterior face, the nutrient foramen opens straight downwards and there is not a discernible flange around it. In addition, the lateral articular facet for the calcaneum is taller proximo-distally, not elongated. These two traits are more comparable to *Bos*, according to Gee (1993).

A left metatarsal proximal fragment (Fig. 2s) shows another interesting character of systematic significance: the two largest proximal facets (for the 2nd/3rd tarsal and the cubonavicular) are well separated

Fig. 2. Artiodactyla cranial and postcranial remains from Teixoneres. *Cervus elaphus*: left M^1 in labial (a) and occlusal (b) views (TX'11.IIIb.K15.90); right mandible with the series P_4–M_3 in occlusal (c) and lingual (d) views (TX'11.IIIb.K15.70 + 119); metacarpal distal fragment in anterior view (e) (TX11.IIIb.L10.204); shed antler fragment in lateral view (f) (TX12.IIIb.L23.13). *Capreolus capreolus*: right metacarpal in anterior view (g) (TX11.IIIb.K16.20); right radius proximal fragment in posterior view (h) (TX13.IIIb.L10.70); left M^3 in occlusal (i) and labial (j) views (TX13.IIIb.K11.49). Bovini cf. *Bos primigenius*: left mandible fragment with the series M_2-M_3 in occlusal (k) and lingual (l) views (TX10.IIIa.J15.80); right metacarpal in proximal (m) and anterior (n) views (TX12.IIIb.K23.6); metacarpal distal fragment in anterior view (o) (TX13.III.N26.13 + N27.1); left radius in anterior view (p) (TX13.IIIb.K24.1); left tibia in distal view (q) (TX12.IIIb.L24.28); left astragalus in lateral view (r) (TX12.IIIb.L23.12); left metatarsal in proximal view (s) (TX12.IIIb.L22.3). *Rupicapra pyrenaica*: left M^3 in labial view (t) (TX08.IIb.J15.115); right metatarsal in proximal view (u) (TX10.IIIa.L10.160). *Capra pyrenaica*: right maxillary with the series P^3–M^2 in labial view (v) (TX15.IIIb.M10.316 + 317 + 380); second phalange in lateral view (w) (TX12.IIIb.O10.107). *Sus scrofa*: right maxillary fragment with the series dP^4-M^1 in labial (x) and occlusal (y) views (TX09.IIb.K14.234). Scale bars are in cm.
Photos: SiobaGrande/IPHES.

Table 4
Selected comparative measurements on Bovini cranial and postcranial elements.

Site		M_3 L	Rad. PW	Mtc. L	Mtc. DW
Teixoneres[a]	Mean (n)	46.75 (2)	131.3 (1)	268 (1)	90.66 (3)
	Min-max	45.7–47.8			82.3–94.9
Jou Puerta[b]	Mean (n)	48 (1)			
Lezetxiki[c]	Mean (n)	45.5 (1)			
Leibar[c]	Mean (n)	38.75 (2)			
	Min-max	38.5–39			
Labeko Koba[d]	Mean (n)	46.47 (18)	101.4 (4)	238.6 (4)	78.9 (4)
	Min-max	38–53	97–109	221–259	71–92
Santimamiñe[e]	Mean (n)	41.94 (9)		172.5 (1)	74.8 (3)
	Min-max	37–52			50–93.5
Lumentxa[f]	Mean (n)	46 (1)		224.5 (1)	76.5 (1)
Bolinkoba[f]	Mean (n)	48 (2)			92 (1)
	Min-max	47–49			
Aitzbitarte III[g]	Mean (n)	44.5 (1)			
Habarra (*Bison priscus*)[h]	Mean (n)		110.6 (9)	229.1 (9)	82.06 (8)
	Min-max		96.5–122.5	217.5–239.5	73–90.5
Kiputz IX (*Bison priscus*)[i]	Mean (n)	48.4 (15)	106.6 (17)	236.9 (14)	87.9 (14)
	Min-max	45.5–52.5	96.5–117.5	217–254	70–101.5
Ilford (*Bos primigenius*)[j]	Mean (n)	48.7 (12)		257.43 (7)	92.76 (5)
	Min-max	45–53		248–269	86.4–95.3
Avetrana (*Bos primigenius*)[k]	Mean (n)			263.72 (11)	82.8 (12)
	Min-max			252–275	74.6–95.4
Atapuerca TG8-TG10 (*Bison* sp.)[l]	Mean (n)	40.9 (3)			
	Min-max	40.4–41.1			
Mestas de Con (*Bison* sp.)[m]	Mean (n)	40 (1)			
Paglicci Cave (*Bos primigenius*)[n]	Mean (n)	48.8 (21)			
	Min-max	46–52.8			
Mauer (*Bison schoetensacki*)[n]	Mean (n)	42.8 (24)	109.75 (4)	264 (2)	75 (2)
	Min-max	38.8–48	104–115	263–265	75–75
Isernia la Pineta (*Bison schoetensacki*)[n]	Mean (n)	43.1 (30)			
	Min-max	40–49			

Rad.: Radius; Mtc.: mecarpal; PW: proximal width; L: maximum length; DW: distal width.
[a] This study; [b] Álvarez-Lao (2014); [c] Altuna (1972); d Altuna and Mariezkurrena (2000); [e] Castaños (1984); [f] Castaños (1986); [g] Altuna and Mariezkurrena (2011); [h] Prat et al. (2003); [i] Castaños (2014); [j] Wright (2013); [k] Pandolfi et al. (2011); [l] Van der Made (1999); [m] Álvarez-Lao (2016); [n] Sala (1986).

anteriorly by a channel, which is also considered by Gee (1993) as a reliable character for *Bos*.

In sum, the described features strongly suggest that the bovine remains from Teixoneres Cave belong most probably to *Bos primigenius*.

For morphometrical purposes we selected the M_3 because, as above indicated for the red deer, is not affected by attrition. Among the few postcranial elements which provided reliable measurements, we selected the metacarpals because they are relatively numerous ($n = 3$, all coming from unit III), and the radius. The morphometric data were compared with a sample of Pleistocene bovines from Europe (Table 4). The size of the Teixoneres M_3 is larger than most other populations and similar to the specimens from Ilford and Pagglici Cave, both ascribed to *Bos primigenius*. Postcranial data follows the same pattern, with large metacarpals similar in size to those from Ilford and Avetrana, both classified as *Bos primigenius*. It seems that the large size of the bovines from Teixoneres also supports their ascription to *Bos primigenius*.

4.1.2.2. Rupicapra pyrenaica (Bonaparte, 1845). Chamois remains are rare, comprising only 2.3% of the ungulate assemblage of unit II and 0.6% of unit III (Table 1). Conserved elements include few teeth, phalanges and fragmented limb bones (Fig. 2t–u) corresponding to a minimum of 4 adult individuals (2 in unit II and 2 in unit III). The few measurable elements showed that body size of the Teixoneres specimens is similar from other Iberian Pleistocene chamois populations (Table 5).

Recent chamois populations are ascribed to two species on the basis of morphological and behavioral characters: *R. rupicapra* (Linnaeus, 1758), from Central and Eastern Europe, and *R. pyrenaica*, from the Iberian Peninsula (Lovari and Scala, 1980; Scala and Lovari, 1984; Nascetti et al., 1985; Pérez et al., 2002). Although the remains from Teixoneres are insufficient as to get an accurate taxonomical ascription, the divergence time between *R. rupicapra* and *R. pyrenaica* has been estimated on the basis of genetic distance (Rodríguez et al., 2010; Pérez et al., 2011). Different methods provided different ages for this divergence: 1.7 ma, based in molecular clock methods (Rodríguez et al., 2010), and 655 ka, based on phylogenetic analyses of the Y-chromosome (Pérez et al., 2011). These genetic results imply that Late Pleistocene fossil chamois from the Iberian Peninsula should be included in the species *R. pyrenaica*.

The occurrence of this species provides also an interesting palaeoenvironmental information (see Section 7), indicating presence of rocky mountain areas in the surroundings.

4.1.2.3. Capra pyrenaica (Schinz, 1838). The ibex is an infrequent species in the assemblage, comprising only 0.4% of the ungulates of unit II and 1.1% of unit III (Table 1).

Preserved elements include teeth and very fragmented and scarce postcranial remains, belonging to a minimum of 4 individuals (1 in unit II and 3 in unit III), 2 of which are infantile, 1 juvenile and 1 adult. Unfortunately, none of the teeth are useful for comparative analyses since there are not any preserved last molar (M_3 or M^3) and all other pieces could be affected by attrition, not providing reliable measurements. The single well preserved postcranial element is a second phalange (Fig. 2v–w), whose measurements were compared with other Iberian populations (Table 5). There is a high variability in the comparison sample, most likely due to it includes a mixing of second phalanges from the forelimb and from the hind limb. The specimen of Teixoneres is close to the largest values, which suggests that it corresponded to a hind leg.

Table 5
Selected comparative measurements on *Rupicapra pyrenaica* and *Capra pyrenaica* cranial and postcranial elements.

Site		*R. pyrenaica*		*C. pyrenaica*	
		M^3 L	Mtt. PW	Ph.2 L	Ph.2 PW
Teixoneres[a]	Mean (n)	14.6 (1)	21.7 (1)	32.9 (1)	18.5 (1)
Jou Puerta[b]	Mean (n)	15 (3)	20.86 (5)	34.17 (1)	18.25 (1)
	Min-max	14.4–15.7	20–22.4		
Naranco[b, c]	Mean (n)	14.66 (3)	21.8 (10)		
	Min-max	14.3–15.2	21.05–23.1		
El Conde[c]	Mean (n)	13.55 (6)			
	Min-max	12.9–14			
Malverde[d]	Mean (n)		21.45 (6)		
	Min-max		20–23.3		
Ekain[e]	Mean (n)		22.66 (3)		
	Min-max		22–23.4		
Valdegoba[f]	Mean (n)		22.6 (16)		
	Min-max		20.6–26.6		
Lumentxa[g]	Mean (n)		20.4 (3)	31.6 (6)	13.43 (6)
	Min-max		18.9–23	24.5–39	12.6–15.2
Santimamiñe[g]	Mean (n)		22.5 (1)	28.9 (8)	14.83 (8)
	Min-max			25.5–33	13.6–16.8
Atxuri[g]	Mean (n)			30.8 (13)	16.9 (15)
	Min-max			26–44	14.4–19.4
Bolinkoba[g]	Mean (n)			28.22 (34)	15.8 (36)
	Min-max			24.6–33	13.2–20.5
Urratxa III[g]	Mean (n)			30.12 (8)	15.9 (11)
	Min-max			28.5–31.5	13–17.8
La Riera[h]	Mean (n)			29.35 (7)	15.8 (7)
	Min-max			26–32	13.5–17.7

Mtt.: metatarsal; Ph.2: second phalange; L.: maximum length; PW: proximal width.
[a] This study; [b] Álvarez-Lao (2014); [c] Álvarez-Lao (unpublished data); [d] Lorenzana (1982); [e] Altuna and Mariezkurrena (1984); [f] Arceredillo et al. (2011); [g] Castaños (1984); [h] Altuna (1986).

Presence of this species into the assemblage is also indicative of rocky mountain areas in the vicinity of the site.

4.1.3. Family Suidae (Gray, 1821)

4.1.3.1. Sus scrofa (Linnaeus, 1758). Wild boar remains comprise 5.5% of the ungulates of unit II and 0.5% of unit III (Table 1) and consist mainly of dentition (Fig. 2x–y), while postcranial elements are limited and fragmented. These remains correspond to a minimum of 6 individuals (4 in unit II and 2 in unit III), 1 of which is infantile, 2 juveniles, 2 adults and 1 old adult. The sample is insufficient to allow comparative studies. The presence of this species in the assemblage is of palaeoenvironmental interest (see Section 7), indicating presence of forested areas near the site.

4.2. Order Perissodactyla (Owen, 1848)

4.2.1. Family Equidae (Gray, 1821)

Equids are relatively frequent in the Teixoneres assemblage, comprising 36.4% of the ungulates in unit II and 26.7% in unit III. It was possible to identify two different equid species: *E. ferus* and *E. hydruntinus*. In addition, there is a substantial quantity of equid remains which, due to the high degree of fragmentation, was not possible to be ascribed to a single species, so they are designated as *Equus* sp. (Table 1).

4.2.1.1. Equus ferus (Boddaert, 1785). Horses constitute 12.5% of the ungulates of unit II and 12.82% of unit III (Table 1). The identified material entails mainly of teeth (Fig. 3a–b), while postcranial elements are very rare and badly preserved, consisting mainly in phalanges and metapodial fragments. These remains correspond to a minimum of 16 individuals (4 in unit II and 12 in unit III), 1 of which is infantile, 5 juveniles, 8 adults and 2 old adults.

The morphology of the upper dentition is typical of the caballine equids, with a large protocone, concave surfaces between styles, intense folding in the enamel of the fossettes and a well-developed caballine fold. In the lower cheek teeth, the lingual valley shows the distinctive "caballine" u-shaped morphology (Eisenmann, 1991; Maldonado, 1996).

For comparative purposes we selected the upper molars M^{1-2} because they are the most frequent elements and, therefore, the most representative. Postcranial elements are not considered since they are so scarce and fragmentary. These data were compared with a sample of Pleistocene horses from Western Europe (Table 6). The size of the Teixoneres specimens is very similar to other populations of similar age from northern Iberia (as Cueto de La Mina, Santimamiñe and Labeko Koba), slightly larger than other Late Pleistocene populations from central and southern Iberia (like Camino Cave, Cueva del Buho and Carihuela), and smaller than Middle Pleistocene specimens (from Mosbach and Arago).

4.2.1.2. Equus hydruntinus (Regalia, 1907). Remains ascribed to *E. hydruntinus* constitute 4.7% of the ungulates of unit II and 6.4% of unit III (Table 1). They comprise almost exclusively teeth (Fig. 3c–d), with very few postcranial elements (mainly phalanges), corresponding to a minimum of 11 individuals (4 in unit II and 7 in unit III), 2 of which are juveniles, 7 adults and 2 old adults.

Morphologically the upper dentition shows distinctive features of this species, with a short protocone, flattened surfaces between styles and low folding in the enamel of the fossettes. The caballine fold is normally absent or, when it is present, much reduced. In the lower cheek teeth, the lingual valley shows the distinctive "stenonian" v-shaped morphology (Eisenmann and Patou, 1980; Maldonado, 1996; Boulbes, 2009).

For comparative studies we also selected the upper molars M^{1-2} because, as for the case of *E. ferus*, they are the most frequent elements. Their size is visibly smaller than the *E. ferus* sample (Table 6). These data were compared with a sample of *E. hydruntinus* from Iberia and France (Table 6). The size of the Teixoneres sample is slightly larger than the other Iberian populations and more similar of those from southern France. The protocone length is among the highest values of the comparison samples, which could agree with Prat (1968), who proposed that specimens from the second half of the Late Pleistocene had largest protocones than older populations.

4.2.2. Family Rhinocerotidae (Owen, 1845)

Rhinoceros dental remains were recovered at both units II and III. Two of the specimens from unit III and one from unit II were enough preserved as to be classified to species level as *Coelodonta antiquitatis*. All other rhinoceros remains from both units are assumed to belong to this same species (Table 1).

4.2.2.1. Coelodonta antiquitatis (Blumenbach, 1799). The woolly rhinoceros sample was represented by 11 teeth fragments, comprising 1.5% of the ungulates from unit II and 0.7% of the unit III (Table 1). Only three of the fragments are taxonomically identifiable and can be ascribed to *C. antiquitatis*. These dental remains correspond to a minimum of six individuals (two from unit II and four from unit III): one very young calf, one young, three adults and one old adult.

One left dP^2 (Fig. 3i–j) is relatively well preserved, showing taxonomically interesting morphologic features: the mediofosette is well developed and totally closed; the arrangement of the protoloph draws a low angle with the ectoloph; the enamel surface is rough. All these are diagnostic traits of *Coelodonta antiquitatis*. Although this specimen is slightly incomplete, the conserved size (Table 7) indicates that the specimen is noticeably smaller than all the P^2 sample from Western Europe published by Guérin (1980), and more similar to the dP^2 measurements provided by the same author (Table 7). The crown length is greater than the width, which is other typical feature of dP^2 and different of P^2. The low height of the crown fits into the range of the dP^2, and is far under the minimum values of the P^2 provided by Guérin (1980). In addition, the enamel is very thin, which is also a typical feature of

Fig. 3. Perissodactyla and Proboscidea dental remains from Teixoneres. *Equus ferus*: right M^1 in occlusal view (a) (TX08.IIb.L18.40); left M$_1$ in occlusal view (b) (TX11.IIIb.Q9.21). *Equus hydruntinus*: left M^3 in occlusal view (c) (TX09.IIIa.O10.341); left M$_3$ in occlusal view (d) (TX08.IIIa.O11.158). *Coelodonta antiquitatis*: left P^3 in occlusal (e) and posterior (f) views (TX09.IIIa.K12.376); right M$_3$ in lingual (g) and occlusal (h) views (TX16.IIb.P15.9); left dP^2 in occlusal (i) and lingual (j) views (TX10.IIIa.J13.34). *Mammuthus primigenius*: dP^2 in labial (k), lingual (l), and occlusal (m) views (TX10.IIIa.O8.289). Scale bars are in cm.
Photos: SiobaGrande/IPHES.

deciduous dentition. The crown wear is very slight, suggesting an ontogenetic age ranging between 4 and 12 months, by analogy with living African white rhinoceroses (*Ceratotherium simum* Burchell, 1817), following Hillman-Smith et al. (1986).

A right M$_3$ (Fig. 3g-h) is very well preserved, showing interesting features of systematic significance: the enamel is thick and rough; the metalophid has a clear constriction in the middle part, which is visible in occlusal view (Fig. 3h). All these are typical features of *C. antiquitatis*. Its size falls within the range of this species, close to the average values (Table 7). The crown shows an advanced wear, suggesting an ontogenetic age of approximately 25–32 years, following Hillman-Smith et al. (1986).

The other specimen is a premolar remnant, which probably belonged to a P^3 (Fig. 3e–f), showing very heavy wear. Despite this extreme wearing stage, the low angle of the protoloph with respect to the ectoloph, suggests that this specimen is more comparable to *Coelodonta* than to *Stephanorhinus*. The crown preserves about 1 cm in height. The occlusal surface is almost completely composed by dentine, only remaining one small patch of enamel corresponding to the lingual valley. The length of the crown is markedly low respect to the width (Table 7), indicating an advanced interdental attrition. These features suggest that this specimen belonged to an old aged individual, whose ontogenetic age can be estimated in between 30 and 38 years, following Hillman-Smith et al. (1986).

In addition to these specimens, a fragment of a lower deciduous tooth which could well correspond to the same individual that the described dP^2, was also recovered. Apart from these dental elements, no postcranial remains of rhinoceros have been identified in the assemblage.

Presence of this species at the assemblage is of high palaeoenvironmental significance, indicating cold and dry conditions, as is discussed later in Section 7.

4.3. Order Proboscidea (Illiger, 1811)

4.3.1. Family Elephantidae (Gray, 1821)

4.3.1.1. Mammuthus primigenius (Blumenbach, 1799). The woolly mammoth yielded a single fossil, constituting the 0.11% of the assemblage from unit III. The specimen is an upper dP^2, a very unusual dental element into the fossil assemblages, which is only present during nearly the first year of the individual's life.

The morphology of the mammoth dP^2, the first generation tooth, differs from the teeth of subsequent generations: the crown has three or four plates, all of them formed simultaneously, which are not divided into lobes, and the roots number is limited, from 2 to 3 in the upper teeth (Maschenko, 2002; Maschenko and Kalmykov, 2009). In addition, dP^2 has a completely formed alveolus, with ossified walls and complete interalveolar septum which is not resorbed when the tooth is replaced, while in subsequent teeth the intertooth septum is incomplete and is gradually resorbed during the replacement by the subsequent tooth (Maschenko and Kalmykov, 2009).

The specimen of Teixoneres (Fig. 3k–m) has four full plates with cement partially filling the interplate gaps. The roots number is unknown because they are not preserved. Measurements are indicated in Table 8 in comparison with other specimens from Siberia and Russian Plain, and plotted in Fig. 4. Morphologic and morphometric features of the specimen from Teixoneres strongly suggests that it corresponds to the

Table 6
Selected comparative measurements on *Equus ferus* and *Equus hydruntinus* upper molars.

Site		*E. ferus*			*E. hydruntinus*		
		M^1–M^2 L	M^1–M^2 W	M^1–M^2 Lpr	M^1–M^2 L	M^1–M^2 W	M^1–M^2 Lpr
Teixoneres[a]	Mean (n)	26.6 (14)	24.8 (13)	12.8 (14)	23.3 (16)	23.3 (16)	10.9 (15)
	Min-max	23–30.5	20.7–27.2	10.9–14.7	20.6–25.6	21–25.5	7.7–13.1
Cueto de La Mina[b]	Mean (n)	26.85 (21)	25.44 (17)	12.72 (20)			
	Min-max	24–29.5	21.5–28.5	10.4–14.7			
Santimamiñe[c]	Mean (n)	26.67 (8)	26.03 (8)	13.3 (8)			
	Min-max	25–27.9	25.4–26.9	11.2–15.4			
Labeko Koba[d]	Mean (n)	25.3 (33)	26.05 (33)	13.8 (33)			
	Min-max	22.4–31	23.5–29	11.5–16.6			
Mosbach[e]	Mean (n)	28.5 (27)		14.5 (27)			
Arago[e]	Mean (n)	28.8 (42)		15.1 (42)			
Ehringsdorf[e]	Mean (n)	29 (27)		15.1 (28)			
Suard[e]	Mean (n)	27.9 (26)		15.3 (26)			
Taubach[e]	Mean (n)	27.4 (23)		14.7 (22)			
Combe Grenal 12–15[e]	Mean (n)	26.1 (40)		14 (41)			
La Quina B3–C3[e]	Mean (n)	25.8 (28)		14.1 (28)			
Arcy (RGS) [e]	Mean (n)	25.9 (88)		14 (88)			
Jaurens[e]	Mean (n)	25.1 (37)		13.5 (37)			
Camiac[e]	Mean (n)	25.8 (33)		13.8 (33)			
Camino Cave (Pinilla del Valle)[f]	Mean (n)	24.6 (43)	26.1 (43)	13 (43)			
	Min-max	23–27.6	24–29	11–15.5			
Valdegoba[f]	Mean (n)	23.2 (20)	24 (20)	12.1 (20)	21.4 (4)	21.8 (4)	10.6 (4)
	Min-max	22–25.2	23–26.8	10–14.3	21.1–21.7	21.5–22.4	10.5–10.7
Cueva del Buho[f]	Mean (n)	24 (21)	25 (21)	12.5 (21)	20.9 (12)	21.2 (12)	9.3 (12)
	Min-max	23–27.4	23–29	11–14.3	20–22.3	20–23.7	8.6–10
Carihuela[f]	Mean (n)	24.2 (80)	24.8 (80)	13.25 (80)	20.5 (17)	21.4 (17)	9 (17)
	Min-max	22–26.3	22.5–29	11.5–15	19.4–22	20.5–22.2	8.2–10.4
Pair-non-Pair D[g]	Mean (n)				22.3 (4)	20.7 (4)	11.4 (4)
Lunel-Viel[g]	Mean (n)				21.7 (35)	20.5 (35)	8.4 (35)
Marzal 2[g]	Mean (n)				22.7 (11)	21.3 (11)	8.8 (11)
Crouzade[g]	Mean (n)				22 (7)	21.7 (7)	10.4 (7)
Balauzière[g]	Mean (n)				25.6 (6)	21.8 (6)	9.3 (6)
Valorgues[g]	Mean (n)				23 (2)	20.5 (2)	10.2 (2)

L: maximum length; W: maximum width; Lpr: length of the protocone.
[a] This study; [b] Castaños (1982); [c] Castaños (1986); [d] Altuna and Mariezkurrena (2000); [e] Eisenmann (1991); [f] Maldonado (1996); [g] Boulbes (2009).

species *Mammuthus primigenius*, according to descriptions provided by Maschenko (2002), Maschenko and Kalmykov (2009) and Tong and Chen (2016). The possibility that this specimen belongs to the straight-tusked elephant (*Palaeoloxodon antiquus*), which is the other European elephantid species contemporary to the Teixoneres assemblage, seems unlikely since known dP^2 of this species (which are quite rare in the fossil record) have only 2 or 3 full plates and 2 talons (Tong and Chen, 2016), and are larger in crown length than this specimen (Fig. 4).

The occlusal crown wear is slight. Following Maschenko (2002), dP^2 crown wear begins approximately at one month of individual life in woolly mammoth. Moreover, wearing state of this specimen is comparable to that of the Lyuba mammoth calf, whose age at death was estimated on about 30–35 days (Rountrey et al., 2012), so is reasonable to assume a similar time at death for the Teixoneres individual.

Table 7
Selected comparative measurements on *Coelodonta antiquitatis* teeth.

Site		L	W	H
Teixoneres dP^2		24.9[b]	22.5[b]	26.9[b]
Teixoneres P^3		27.5	38.2[b]	
Teixoneres M_3		48.9	32.3	
dP^2 European sites[a]	Mean (n)	30.52 (27)	29.35 (31)	26.29 (7)
	Min-max	28–33	26–32.5	25–33.5
P^2 European sites[a]	Mean (n)	32.13 (26)	34.43 (29)	43.39 (19)
	Min-max	25–37	27.5–42	32.5–53
P^3 European sites[a]	Mean (n)	38.28 (56)	42.06 (57)	57.21 (35)
	Min-max	33–43	35–47.5	44–68
M_3 European sites[a]	Mean (n)	51.58 (40)	29.9 (34)	
	Min-max	43–63	26–36	

L: crown length; W: crown width; H: crown height.
[a] Guérin (1980).
[b] This specimen is somewhat eroded, so the actual measurements must be slightly larger.

Occurrence of this other cold-adapted species is also of high environmental relevance, as is discussed in Section 7.

5. Chronologic and biogeographical framework

5.1. Chronological context

The fossil assemblages of Teixoneres were dated from beyond 51,000 ^{14}C BP to 44,210 cal BP (unit III) and from 44,210 to 33,060 cal BP (unit II) (Talamo et al., 2016), both corresponding to the MIS 3, 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 is considered of global significance (Dansgaard et al., 1993; Grootes and Stuiver, 1997). From a palaeoecologic point of view, unit III shows a special interest due to the occurrence of the cold

Table 8
Measurements of *M. primigenius* dP^2 from Teixoneres and other localities.

Site		L	W
Teixoneres[a]		16.3	13.6
Russian Plain[b]	Mean (n)	16.7 (13)	14.4 (13)
	Min-Max	15–20.5	11.5–17
Berelekh (East Siberia)[c]	Min-Max	14.3–18	13.5–17.8

L: crown length; W: crown width.
[a] This study; [b] Maschenko (2002); [c] Maschenko et al. (2006).

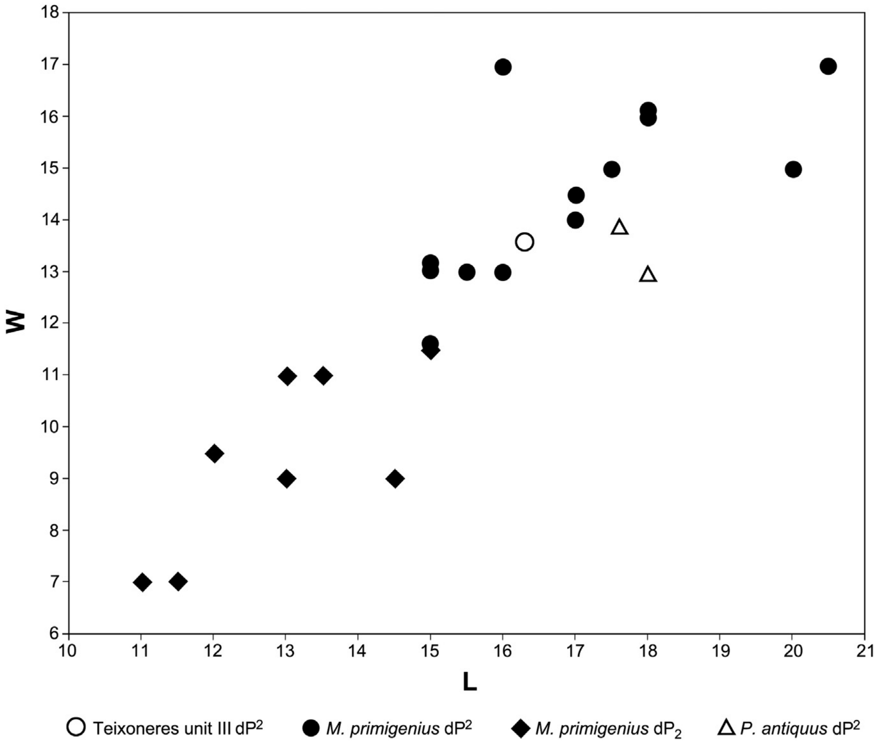


Fig. 4. Bivariate plot of *Mammuthus primigenius* and *Palaeoloxodon antiquus* dP^2 and dP_2 measurements L (crown length) and W (crown width). Data from Maschenko (2002) and Tong and Chen (2016). Measurements are in mm.

adapted taxa *Mammuthus primigenius* and *Coelodonta antiquitatis*. The ungulate association of unit II, while is significantly smaller than the one of unit III, also included a cold-adapted species, *C. antiquitatis*.

The chronology of unit III, with most of the dates ranging from 46.2 to 43.4 cal ka BP (Talamo et al., 2016), is of special interest because is somewhat older than the majority of other Late Pleistocene occurrences

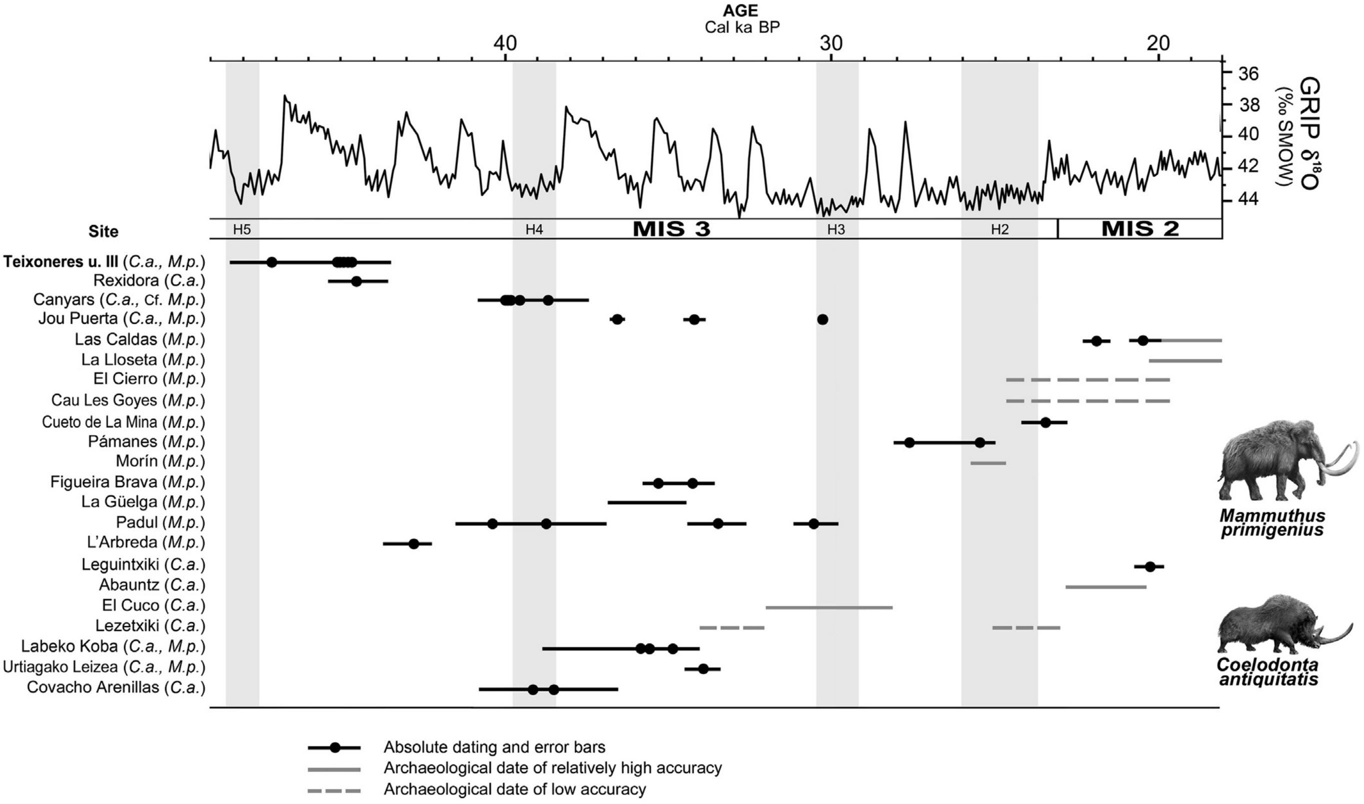


Fig. 5. Calibrated radiocarbon dates from Teixoneres unit III and other Iberian assemblages with *Coelodonta antiquitatis* (*C.a.*) and/or *Mammuthus primigenius* (*M.p.*), compared with the GRIP palaeoclimatic oxygen curve.
Modified from Álvarez-Lao and García (2010, 2012).

of these species (Fig. 5). Only other two of the compared Iberian sites yielded a similar age: the Rexidora cave (Asturias, NW Iberia), with a *C. antiquitatis* assemblage dated to 44.5 cal ka BP (Álvarez-Lao et al., 2015); and Arbreda cave (Gerona, NE Iberia), which provided a *M. primigenius* molar fragment dated to 42.8 cal ka BP (Galobart et al., 1996; Álvarez-Lao and García, 2010). These three sites represent the oldest dated evidences of these cold-adapted species during the MIS 3 in the Iberian record. We cannot exclude the possibility of previous entrances of these faunas into the Iberian territory during the Late Pleistocene, but the lack of suitable findings and the difficulty of dating older deposits (out of the range of the ^{14}C dating method) prevents a greater accuracy.

The MIS 3 is the episode when the greatest concentration of occurrences of these cold-adapted species is documented in the Iberian Peninsula (Fig. 5), most of them from the Cantabrian area (NW Iberia), but also others in NE, Centre and S Iberia. (Álvarez-Lao and García, 2010, 2011b, 2012; Álvarez-Lao, 2014). This episode is also of special interest since the maximum registered southern spread of *M. primigenius* occurred then both in Europe (in Padul, Spain, Álvarez-Lao et al., 2009) as in Asia (Beidasha River, China, Takahashi et al., 2007), which could reflects that cold climatic oscillations of MIS 3 may have been very intense.

5.2. Biogeographical context: cold adapted faunas in NE Iberia.

From a biogeographical perspective, Teixoneres Cave is of high relevance because its location in Catalonia (NE Iberia), where evidences of cold-adapted faunas are not abundant. The distribution of the *M. primigenius* and *C. antiquitatis* Iberian occurrences is not homogenous: the greatest concentration is documented in the Cantabrian area (NW Iberia), while only a minor part of them is located in NE Iberia and a few more are found in Central and Southern Iberia (Álvarez-Lao and García, 2011a). This distribution is consistent with the orography because the Iberian Peninsula is relatively isolated from continental Europe by a natural barrier, the Pyrenees, which limited dispersal of faunas. Cold-adapted species, which were abundant in southern France during the Late Pleistocene (Delpech, 1983), could only get into the Iberian Peninsula through narrow corridors placed west (Cantabrian area) and east (Catalonia) of the Pyrenees (Rivals and Blasco, 2008; Álvarez-Lao and García, 2011a).

Evidences of these cold-adapted taxa in NE Iberia, while they are not abundant, are reported in the sites listed below.

- In Arbreda cave (Gerona), *M. primigenius* remains were recovered at level H, dated to 42.8 cal ka BP (Galobart et al., 1996; Álvarez-Lao and García, 2010), corresponding to MIS 3 and close to the age of Teixoneres unit III. Additionally, other cold adapted taxa as the reindeer (*Rangifer tarandus*) and the muskox (*Ovibos moschatus* Zimmermann, 1780) have been recovered in Solutrean levels of this cave, dated to 20.7 and 21.2 cal ka BP (Galobart et al., 1996; Álvarez-Lao and García, 2010).
- Cau de Les Goges cave (Gerona) provided *M. primigenius* fossils in association with a Solutrean context, whose age can be estimated from around 25 to 20 ka BP (Obermaier, 1925; Álvarez-Lao and García, 2010).
- At Clot de Llop site (Gerona) several *M. primigenius* dental remains were recovered out of any archaeologic context (Harlé, 1912), so their chronology is unknown.
- In Cova del Toll (Barcelona), which is very close to Teixoneres Cave, several remains of *C. antiquitatis* were recovered during the old excavations from 1950's (Thomas and Villalta de, 1957; Álvarez-Lao and García, 2010, 2012). Unfortunately, the chronology of this find is unknown.
- From Arenys de Mar. (Barcelona), a well preserved *C. antiquitatis* skull was discovered during road works (Harlé, 1920; Álvarez-Lao and García, 2011b). Due to the absence of archaeological context and absolute dates, the age of this notable specimen is unknown.
- Riera dels Canyars site (Barcelona), yielded an abundant fossil assemblage including *C. antiquitatis* and Proboscidea cf. *M. primigenius*, dated to ~39.5 cal ka BP (Daura et al., 2013), also corresponding to the MIS 3.
- In addition, there are other sites from NE Iberia at where other cold-adapted ungulate species were recovered. *R. tarandus* remains are reported from Bora Gran d'en Carreres (dated to 11.7 cal ka BP), Reclau Viver (in Solutrean context), Mollet I (in Mousterian context) and in Can Rubau, along with *O. moschatus* (in Mousterian context) (Harlé, 1912; Altuna, 1994; Galobart et al., 1996; Álvarez-Lao and García, 2010). Even as the Aurignacian and Mousterian cited contexts lacks absolute dates, they could well correspond also to the MIS 3.

6. The faunal composition of unit III: comparative revision within a Western European perspective

6.1. Palaeoecological context

The occurrence of *M. primigenius* and *C. antiquitatis*, two typical elements of the "mammoth fauna" (Vereschagin and Baryshnikov, 1982) or "*Mammuthus-Coelodonta* faunal complex" (Kahlke, 1999, 2014), in Iberian sites is of special relevance since they are infrequent species in such southern area. Woolly mammoth fossils have been documented at other 27 Iberian sites and woolly rhinoceros remains were recognized in other 26 Iberian sites (Álvarez-Lao and García, 2011b, 2012; Daura et al., 2013; Álvarez-Lao, 2014; Álvarez-Lao et al., 2015). However, the Iberian fossil assemblages containing these two cold-adapted elements do not show the typical faunal composition of the Eurasian mammoth fauna (Álvarez-Lao and García, 2011b, 2012). Most of these Iberian occurrences come from the Cantabrian area, which hosted a transitional faunal assemblage between the northern cold faunas and the southern temperate faunas (Álvarez-Lao and Méndez, 2016). Iberian assemblages with *M. primigenius* and *C. antiquitatis* are generally dominated by species associated to temperate environments, particularly *Cervus elaphus*, as is the case of the unit III of Teixoneres (Table 1). By contrast, contemporary faunal associations from Central and Western Europe, where the mammoth fauna was fully established, were dominated by cold-adapted taxa, especially *R. tarandus*, while species of temperate preferences were scant or totally lacking (Álvarez-Lao and Méndez, 2016). The particular conditions of these Iberian faunal associations are here statistically analyzed into a Western European context in order to understand the ecological limitations of these cold-adapted elements.

6.2. Analysis of the faunal composition

For a comparative study of the faunal composition of Teixoneres unit III, percentages of each species were analyzed along with 33 other assemblages also including *M. primigenius* and/or *C. antiquitatis*, coming from Iberia and Western-Central Europe (Table 9), by means of a correspondence analysis (see Section 3 for methodological details).

The correspondence analysis showed a close association between sites with similar relative abundances of herbivore taxa, indicated by the eigenvalues and inertia values (see Fig. 6 caption). A clear separation between Iberian and Western-Central European faunal associations is identified (Fig. 6), with almost all Iberian sites (black dots) placed on the left part of the graph, associated with a high abundance of red deer and presence of *Stephanorhinus hemitoechus* (only at one site). The assemblage from unit III of Teixoneres, indicated by the unfilled circle, clustered with the other Iberian sites, displaying the same pattern of faunal composition. All other localities, indicated by unfilled squares, come from Western-Central Europe. Sites in the central part of the graph, clearly separated from the Iberian sample, are characterized by a high abundance of *Equus ferus*, *Coelodonta antiquitatis*, *Megaloceros giganteus* (Blumenbach, 1799) and bovines (*Bison priscus*/*Bos*

Table 9
Percentages of ungulate taxa at Teixoneres unit III 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.f.*	*E.h.*	*C.a.*	*S.h.*	*M.p.*		
Teixoneres unit III	Spain	0	64.2	0	5.26	1.2	0.64	0	6.56	0	0.53	13.9	6.9	0.75	0	0.11	930	(1)
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	(2)
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	(3)
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	(4)
Lezika	Spain	0.32	44.6	0	0	0	6.9	0	0.3	0	0	0	0	47.8	0	0	305	(5)
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	(6)
Las Caldas VII	Spain	0	79.5	0	0	12.3	0	0	0	0	0	7.4	0	0	0	0.8	122	(7)
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	(8)
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	(9)
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	(10)
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	(11)
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	(12)
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	(13)
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	20,992	(14)
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	(14)
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	(14)
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	(14)
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	(14)
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	(14)
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	(14)
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	(15)
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	(16)
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	(17)
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	(18)
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	(19)
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	(20)
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	(21)
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	(22)
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	(22)
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	(23)
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	(24)
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	(25)
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	(26)
Lynford	G. Britain	5.4	0	0	0	0	0	0	0.3	0	0	0.4	0	1.01	0	92.8	1347	(27)

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.*-Bovini indet.; *O.m.-Ovibos moschatus*; *S.s.-Sus scrofa*; *E.f.-Equus ferus*; *E.h.-Equus hydruntinus*; *C.a.-Coelodonta antiquitatis*; *S.h.-Stephanorhinus hemitoechus*; *M.p.-Mammuthus primigenius*.

Sources: (1): This paper; (2): Álvarez-Lao (2014); (3): Castaños (1982); (4): Castaños, pers. com. (2006); (5): Castaños et al. (2009); (6): Altuna (1972); (7): Soto and Meléndez (1981); (8): Altuna (1971); (9): Altuna and Mariezkurrena (2010); (10): Altuna and Mariezkurrena (2000); (11): Maroto et al. (1996); (12): Cardoso (1996); (13): Drucker et al. (2000); (14): Delpech (1984); (15): Bouchud (1968); (16): Raynal et al. (1989); (17): Fosse (1997); (18): Patou-Mathis (2005); (19): Yravedra Sáinz de Los Terreros (2006); (20): Le Tensorer (1998); (21): Münzel and Conard (2004a); (22): Münzel and Conard (2004b); (23): Scheer (2001); (24): Niven (2007); (25): Gautier (1995); (26): Turner (2000); (27): Schreve (2006).

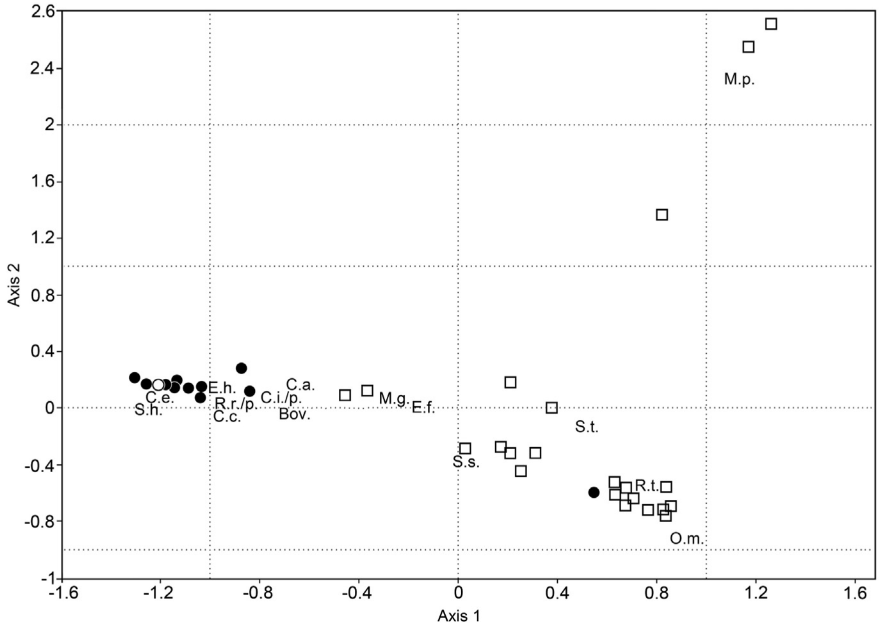


Fig. 6. Biplot of the two first axes extracted by the correspondence analysis (CA). Four main factors were extracted by the CA, with eigenvalues of 0.70, 0.62, 0.38, and 0.27 which explained 27.67%, 24.62%, 14.99% and 10.92% of the inertia in the data, respectively. Teixoneres unit III is indicated by the unfilled circle, other Iberian sites are indicated by black dots, Central-Western European assemblages are represented by unfilled squares. Taxa abbreviations as in the caption of Table 9.

primigenius). At the middle-right section of the graph the assemblages are associated with a high abundance of strictly cold-adapted taxa such as *Rangifer tarandus*, and the presence of *Saiga tatarica* (Linnaeus, 1766) and *Ovibos moschatus*. Only one Iberian site (Urtiagako Leizea) is placed on this area and separated from the rest of the Iberian localities. Three sites placed on the upper right quadrant of the graph, clearly apart from the remaining sites, are characterized by high abundances of *M. primigenius*.

6.3. Palaeoecologic interpretation

The faunal association from Teixoneres unit III show clear similarities with other Iberian assemblages where *M. primigenius* and *C. antiquitatis* occur, but is significantly different from contemporary ones from Western-Central Europe. Overall, Iberian assemblages are mostly composed by species indicative of temperate environments as *C. elaphus*, while cold taxa such as *Rangifer tarandus* are very infrequent. On the other hand, the analyzed assemblages from Western-Central Europe are mainly composed by of cold-adapted taxa, with *R. tarandus* as the dominant species in most cases, whereas temperate species are scarce or lacking at these sites; by instance, *C. elaphus* is a rare species here, with percentages below 2% at almost all cases. One single Iberian assemblage, Urtiagako Leizea, shows a similar faunal composition to the Western-Central European localities, with high percentages of *R. tarandus* (Altuna, 1984; Altuna and Mariezkurrena, 2010).

A particularity observed in unit III of Teixoneres as well as in other sites from NE Iberia where cold-adapted taxa occur, as Arbreda, Riera dels Canyars and Mollet, is the presence of the small equid *Equus hydruntinus* (Galobart et al., 1996; Daura et al., 2013). This species, which seems to have been frequent in the Mediterranean margin during the Late Pleistocene, was not detected in any of the analyzed sites from the Cantabrian area (NW Iberia). A possible explanation could be related to the orography: the Cantabrian area is a mountainous region, which could explain the absence of suitable lowland landscape for *E. hydruntinus* (Burke et al., 2003) and, by contrast, the abundance of rocky-adapted species like *R. pyrenaica* (Kurtén, 1968; Guérin and Patou-Mathis, 1996).

In sum, at unit III of Teixoneres, like in most of the Iberian analyzed assemblages, elements of the mammoth fauna occur within a faunal context dominated by temperate-adapted species. This singular faunal association does not reflect the typical composition of the "Eurasian mammoth fauna" or "*Mammuthus-Coelodonta* faunal complex", as was described by Guthrie (1982), Vereschagin and Baryshnikov (1982) and Kahlke (1999, 2014). This mixture of temperate and cold elements suggests that the cold-adapted taxa reached the Iberian Peninsula only occasionally, probably during the coldest episodes of the Late Pleistocene, and coexisted with the local faunas instead of replace it, as was proposed by Álvarez-Lao and García (2011b, 2012).

7. Palaeoenvironmental context inferred by the ungulate associations

The ungulate associations of Teixoneres Cave suggest an environmental complex composed of different ecosystems.

Equids, as a whole (including *E. ferus*, *E. hydruntinus* and *E.* sp.), are relatively abundant ungulates both in unit II (where they reach together 34.36% of the ungulates) and in unit III (comprising 26.71%), indicating herbaceous open grasslands (Kurtén, 1968; Burke et al., 2003). Moreover, the presence in unit III of *M. primigenius* and *C. antiquitatis* (this last also present in unit II), two typical species of the steppe-tundra or "Mammoth Steppe" (Guthrie, 1982, 1990), also an herbaceous ecosystem, is consistent with this landscape.

On the other hand, the most abundant species in both units is *C. elaphus* (reaching 42.18% of the ungulates of unit II and 59.34% of unit III). While this is a flexible species in its palaeoclimatic parameters, the high abundance suggests the presence of forested areas in the vicinity of the site, which is not incompatible with the "Mammoth Steppe" (Ukraintseva, 1993). In addition, occurrence of *C. capreolus* and *S. scrofa*, also supports the presence of tree-covered areas.

This landscape is consistent with the open forest conditions previously suggested for the Teixoneres assemblage, inferred by pollen, charcoal, small vertebrates and large-mammal dental wear analyses (López-García et al., 2012).

In addition, there are two species indicative of rocky mountain areas in the surroundings: *Rupicapra pyrenaica* and *Capra pyrenaica*. The location of the cave, at an altitude of about 760 m a.s.l. and into mountainous surroundings with altitudes of about 1000 m in the near vicinity, is consistent with the occurrence of these alpine species.

The climatic conditions inferred by the ungulate association are not fully consistent with previous studies: occurrence *C. antiquitatis* and *M. primigenius* at unit III is a clear indicative of cold and arid environment, which contrast with the relatively temperate and humid conditions inferred by other multidisciplinary approaches (López-García et al., 2012) for this assemblage. Interestingly, in this previous study, climatic conditions attributed to unit II are cold and dry, which is consistent with the occurrence of some remains of *C. antiquitatis* at this faunal association.

8. Conclusions

Teixoneres Cave provided two remarkable ungulate associations, especially the one from unit III which comprises *Coelodonta antiquitatis* and *Mammuthus primigenius*, two cold-adapted species that are infrequent in Iberian sites. The faunal assemblage of unit III includes a *M. primigenius* upper dP^2, a very rare dental element which is here first documented in the Iberian record. This specimen shows slight occlusal crown wear suggesting an individual age of death of around one month. Anatomically this dP^2 is very similar to other specimens from Siberia and the Russian Plain.

From a chronological point of view, both units correspond to the MIS 3, a period characterized by strong and brief climatic oscillations, including very cold events. The assemblage of unit III is of special interest since it constitutes one of the oldest dated evidences of *M. primigenius* and *C. antiquitatis* from the Iberian Late Pleistocene record. Biogeographically, the occurrence of *M. primigenius* and *C. antiquitatis* in NE Iberia is of singular relevance because these cold-adapted species are rare and poorly known in this region, yielding relevant information on the palaeoenvironmental conditions of this geographical area during the MIS 3.

From a palaeoecological perspective, the ungulate association of unit III was predominantly composed of temperate-adapted species, where *Cervus elaphus* was the most abundant taxon while *M. primigenius* and *C. antiquitatis* were very rare. This particular faunal composition is also observed in most of the Iberian assemblages where cold-adapted taxa occur, mainly coming from the Cantabrian area (NW Iberia), and contrasts with contemporary Western-Central European ungulate associations at which cold-adapted taxa, especially *Rangifer tarandus*, were predominant. As a peculiarity, the small equid *Equus hydruntinus* co-occur with the cold-adapted species at all the analyzed assemblages from NE Iberia, including Teixoneres unit III, while it was not detected in any of the analyzed sites from the Cantabrian area.

The mixture of temperate and cold elements observed in Teixoneres unit III, as well as in most of the analyzed Iberian assemblages, does not reflect the typical composition of the Eurasian mammoth fauna, providing an interesting view on the palaeoecology of *M. primigenius* and *C. antiquitatis* in the south-western border of its Palearctic distribution. Moreover, it supports the idea that these species only reached the Iberian Peninsula occasionally, during the Pleistocene coldest episodes, cohabiting with the local faunas instead of replacing them.

The ungulate assemblage from Teixoneres unit III indicate cold and arid environmental conditions and a diverse landscape complex, with steppe-like environments, open forested areas and rocky mountains in the surroundings of the site.

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References

Altuna, J., 1971. Los mamíferos del yacimiento prehistórico de Morín (Santander). In: González Echegaray, J., Freeman, L.G. (Eds.), Cueva Morín. Excavaciones 1966–68 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 (Antropologia-Arkeologia). 24, pp. 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). Boletín del Instituto De Estudios Asturianos, pp. 149–194.

Altuna, J., 1984. Primer hallazgo de mamut (*Mammuthus primigenius* Blumenbach) en el País Vasco Meridional. Munibe (Antropología-Arkeologia). 36, pp. 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 Gatrherer Adaptations in Northern Spain. Anthropological Papers 36. University of Arizona, pp. 237–274.

Altuna, J., 1994. Los Macromamíferos durante el Solutrense de la Península Ibérica. Férvedes. 1, pp. 47–55.

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 Vascos, Serie B 1, San Sebastián, pp. 211–280.

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, Vitoria, pp. 395–480.

Álvarez-Lao, D.J., 2014. The Jou Puerta cave (Asturias, NW Spain): a MIS 3 large mammal assemblage with mixture of cold and temperate elements. Palaeogeogr. Palaeoclimatol. Palaeoecol. 393, 1–19.

Álvarez-Lao, D.J., 2016. Middle Pleistocene large-mammal faunas from North Iberia: palaeobiogeographical and palaeoecological implications. Boreas 45, 191–206.

Álvarez-Lao, D.J., García, N., 2010. Chronological distribution of Pleistocene coldadapted 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., Méndez, M., 2016. Latitudinal gradients and indicator species in ungulate paleoassemblages during the MIS 3 in W Europe. Palaeogeogr. Palaeoclimatol. Palaeoecol. 449, 455–462.

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.

Álvarez-Lao, D.J., Ruiz-Zapata, M.B., Gil-García, M.J., Ballesteros, D., Jiménez-Sánchez, M., 2015. Palaeoenvironmental research at Rexidora Cave: new evidence of cold and dry conditions in NW Iberia during MIS 3. Quat. Int. 379, 35–46.

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.

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

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

Bibikova, V.I., 1958. Some distinguishing features in the bones of the genera *Bisron* and *Bos*. Bull. Mosk. Obschtschestwa isp. prirody, NS Otdel Biol. 63 (6), 23–35.

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

Boulbes, N., 2009. Étude comparée de la denture d'*Equus hydruntinus* (Mammalia, Perissodactyla) dans le Sud-Est de la France. Implications biogéographiques et biostratigraphiques. Quaternaire 20 (4), 449–465.

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.

Burke, A., Eisenmann, V., Ambler, G.K., 2003. The systematic position of *Equus hydruntinus*, an extinct species of Pleistocene equid. Quat. Res. 59, 459–469.

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. Boletín del Instituto De Estudios Asturianos. 105/106, pp. 43–86.

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

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

Castaños, J., 2014. Grandes faunas esteparias del Cantábrico oriental. Estudio isotópico y paleontológico de los macrovertebrados del Pleistoceno superior de Kiputz IX (Mutriku, Gipuzkoa). (Unpublished Ph.D.). Universidad del País Vasco (354 pp).

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

Crégut, E., 1979. La faune de mammifères du Pléistocène moyen de la Caune de l'Arago à Tautavel (Pyrénées-Orientales). Travaux du laboratoire de Paléontologie humaine et de Préhistoire de Marseille. 3, pp. 1–381.

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.

Daura, J., Sanz, M., García, N., Allué, E., Vaquero, M., Fierro, E., Carrión, J.S., López-García, J.M., Blain, H.A., Sánchez-Marco, A., Valls, C., Albert, R.M., Fornós, J.J., Julià, R., Fullola, J.M., Zilhão, J., 2013. Terrasses de la Riera dels Canyars (Gavà, Barcelona): the landscape of Heinrich Stadial 4 north of the “Ebro frontier” and implications for modern human dispersal into Iberia. Quat. Sci. Rev. 60, 26–48.

David, F., Connet, N., Girard, M., Miskovsky, J.-C., Mourer-Chauvire, C., Roblin-Jouve, A., 2005. Les niveaux du paléolithique supérieur à la grotte du Bison (Arcy-sur-Cure, yonne): Couches A à D. Revue archéologique de l'Est. 54 pp. 5–50.

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.

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.

Eisenmann, V., 1991. Les chevaux quaternaires Européens (Mammalia, Perissodactyla). Taille, typologie, biostratigraphie et taxonomie. Geobios 24, 747–759.

Eisenmann, V., Patou, M., 1980. La faune de la grotte de Félines-Termenès (Aude). Résultats préliminaires et étude détaillée des restes d'*Equus hydruntinus* (Mammalia, Perissodactyla). l'Anthropologie 84 (4), 633–649.

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

Galobart, A., Maroto, J., Ros, X., 1996. Las faunas cuaternarias de mamíferos de la cuenca de Banyoles-Besalú (Girona). Revista Española de Paleontología Extraordinary number, pp. 248–255.

García, N., Arsuaga, J.L., 2003. Last Glaciation cold-adapted faunas in the Iberian Peninsula. In: Reumer, J.W.F., De Vos, J., Mol, D. (Eds.), Advances in Mammoth Research (Proceedings of the Second International Mammoth Conference, Rotterdam, May 16–20 1999). Deinsea. 9, pp. 159–169.

Gautier, A., 1995. The faunal remains of Trou Magrite (Namur Province, Belgium). In: 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.

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 Rhinóceros (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.

Guérin, C., Patou-Mathis, M., 1996. Les Grands Mammifères Plio-Pléistocènes d'Europe. Masson.

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, pp. 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. Boletín del Instituto Geológico de España 12, 2ª serie, pp. 135–162.

Harlé, E., 1920. Restes d'Eléphant et de Rhinocéros trouvés récemment dans le Quaternaire de la Catalogne. Butlletí de l'Institució Catalana d'Història Natural. 20(2), pp. 40–43.

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, H.-D., 1960. Die Cerviden-Reste aus den altpleistozänen Sanden von Mosbach (Biebrich-Wiesbaden), teil 1, Die Gewerhe, Gehorne und Gebisse. Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin. 7, pp. 1–75.

Kahlke, H.-D., 1965. Die Cerviden-Reste aus den Tonen von Voigtstedt in Thüringen. Palaöntogische Abhandlungen, A. 2, pp. 381–426.

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., 2014. The origin of Eurasian mammoth faunas (*Mammuthus–Coelodonta* faunal complex). Quat. Sci. Rev. 96, 32–49.

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 cynégetique. (Unpublished Ph.D.). 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.

López González, F., 2001. Biogeografía y dinámica de la fauna de macromamíferos pleistocenos de Galicia: El yacimiento de Liñares. (Unpublished Ph.D.). Universidad de La Coruña.

López-García, J.M., Blain, H.-A., Burjachs, F., Ballesteros, A., Allué, E., Cuevas-Ruiz, G.E., Rivals, F., Blasco, R., Morales, J.I., Rodriguez Hidalgo, A., Carbonell, E., Serrat, D., Rosell, J., 2012. A multidisciplinary approach to reconstructing the chronology and environment of southwestern European Neanderthals: the contribution of Teixoneres cave (Moià, Barcelona, Spain). Quat. Sci. Rev. 43, 33–44.

Lorenzana, S., 1982. La fauna Cuaternaria del yacimiento del Peñón de Malverde (Llera, Grado). (Unpublished MSc.). Departamento de Geología, 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. Bolletino di Zoologia. 47, pp. 113–124.

Lyman, R.L., 2008. Quantitative Paleozoology. Cambridge University Press.

Maldonado, E., 1996. Revisión de los équidos del Pleistoceno Medio y Superior de España. (Unpulished Ph.D.). Universidad Complutense de Madrid.

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.

Maroto, J., Soler, N., Fullola, 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.

Maschenko, E.N., 2002. Individual development, biology and evolution of the woolly mammoth. Cranium. 19, pp. 4–120.

Maschenko, E.N., Kalmykov, N.P., 2009. Homology of the Elephantid dentition in the context of elephants (Mammalia, Proboscidea) evolution. Dokl. Biol. Sci. 425, 157–159.

Maschenko, E.N., Gablina, S.S., Tesakov, A.S., Simakova, A.N., 2006. The Sevsk woolly mammoth (*Mammuthus primigenius*) site in Russia: taphonomic, biological and behavioral interpretations. Quat. Int. 142–143, 147–165.

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. 23 (2), 877–885 Genève.

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.

Obermaier, H., 1925. El Hombre fósil. Comisión de investigaciones Paleontológicas y Prehistóricas 9, Madrid, pp. 1–398.

Pandolfi, L., Petronio, C., Salari, L., 2011. *Bos primigenius* Bojanus, 1827 from the Early Late Pleistocene deposit of Avetrana (southern Italy) and the variation in size of the species in Southern Europe: preliminary report. J. Geophys. Res. 2011, 1–11.

Patou-Mathis, M., 2005. Comportement de subsistance des Néandertaliens du niveau châtelperronien de Saint-Césaire (Charente-Maritime). Munibe (Antropologia-Arkeologia). 57(1), pp. 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, pp. 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.

Prat, F., 1968. Recherches sur les Equidés pléistocènes de France. (Unpublished Ph.D.). Université de Bordeaux.

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.

Rivals, F., Blasco, R., 2008. Presence of *Hemitragus* aff. *cedrensis* (Mammalia, Bovidae) in the Iberian Peninsula: biochronological and biogeographical implications of its discovery at Bolomor Cave (Valencia, Spain). C.R. Palevol 7, 391–399.

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.

Rosell, J., Blasco, R., Rivals, F., Chacón, M.G., Menéndez, L., Morales, J.I., Rodríguez-Hidalgo, A., Cebrià, A., Carbonell, E., Serrat, D., 2010. A stop along the way: the role of Neanderthal groups at level III of Teixoneres Cave (Moià, Barcelona, Spain). Quaternaire 21, 139–154.

Rosell, J., Blasco, R., Rivals, F., Chacón, M.G., Arilla, M., Camarós, E., Rufá, A., Sánchez-Hernández, C., Picin, A., Andrés, M., Blain, H.-A., López-García, J.M., Iriarte, E., Cebriá, A., 2015. A resilient landscape at Teixoneres Cave (MIS 3; Moià, Barcelona, Spain): The Neanderthals as disrupting agent. Quat. Int. http://dx.doi.org/10.1016/j.quaint.2015.11.077 (in press).

Rountrey, A.N., Fisher, D.C., Tikhonov, A.N., Kosintsev, P.A., Lazarev, P.A., Boeskorov, G., Buigues, B., 2012. Early tooth development, gestation, and season of birth in mammoths. Quat. Int. 255, 196–205.

Sala, B., 1986. *Bison schoetensacki* Freud. from Isernia la Pineta (early Mid-Pleistocene-Italy) and revision of the European species of *Bison*. Palaeontographia Italica 74, 113–170.

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. Bollettino Di Zoologia. 51, pp. 285–294.

Scheer, A., 2001. In: Cavarreta, G., Giola, P., Mussi, M., Palombo, M.R. (Eds.), The utilisation of mammoth remains as raw material and its importance for the Gravettian people of the German Danube. 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.

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, pp. 259–268.

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.

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.

Talamo, S., Blasco, R., Rivals, F., Picin, A., Chacón, M.G., Iriarte, E., López-García, J.M., Blain, H.-A., Arilla, M., Rufà, A., Sánchez-Hernández, C., Andrés, M., Camarós, E., Ballesteros, A., Cebrià, A., Rosell, J., Hublin, J.-J., 2016. The radiocarbon approach to Neanderthals in a carnivore den site: a well-defined chronology for Teixoneres Cave (Moià, Barcelona, Spain). Radiocarbon 58, 247–265.

Thomas, J.M., Villalta de, J.F., 1957. Le ruisseau souterrain du "Toll". Livret guidedes excursions B2-B3. INQUA. V Congrès International, Madrid, Barcelona, pp. 11–25.

Tissoux, H., Falguères, C., Bahain, J.-J., Rosell, I., Ardèvol, J., Cebria, A., Carbonell, E., Serrat, D., 2006. Datation par les séries de l'Uranium des occupations moustériennes de la Grotte des Teixoneres (Moia, Province de Barcelone, Espagne). Quaternaire 17 (1), 27–33.

Tong, H.-W., Chen, X., 2016. On newborn calf skulls of Early Pleistocene *Mammuthus trogontherii* from Shanshenmiaozui in Nihewan Basin, China. Quat. Int. 406, 57–69.

Turner, A., 2000. The Paviland mammalian fauna. In: Aldhouse-Green, S. (Ed.), Paviland Cave and the "Red Lady": A Definitive Report. Western Academic & 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, pp. 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.

Van der Made, J., 1999. Artiodactyla del yacimiento mesopleistoceno de Galería (Sierra de Atapuerca). In: Carbonell, E., Rosas, A., Diez, C. (Eds.), Ocupaciones humanas y paleoecología del yacimiento de Galería. Junta de Castilla y León, Valladolid, pp. 143–167.

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.

Von den Driesch, A., 1976. A guide to measurement of animal bones from archaeological sites. Peabody Museum Bulletin. 1, pp. 1–137.

Wright, E., 2013. The History of the European Aurochs (*Bos primigenius*) from the Middle Pleistocene to Its Extinction: An Archaeological Investigation of Its Evolution, Morphological Variability and Response to Human Exploitation. (Unpublished Ph.D.). Department of Archaeology, University of Sheffield.

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