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## Article

# The Exceptional Presence of *Megaloceros giganteus* in North-Eastern Iberia and Its Palaeoecological Implications: The Case of Teixonerres Cave (Moià, Barcelona, Spain)

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**Abstract:** In this article we announce the discovery of the first remains of *Megaloceros giganteus* found in Catalonia (north-eastern Iberia) from the Late Pleistocene: a fragment of maxillary. Dated between 35,000 and 37,000 cal BP, it is also among the youngest occurrence of this taxon in the Iberian Peninsula, while its last known occurrence is dated to the Neolithic period. Through a comparison with the giant deer of the northern Pyrenees, we analyzed the herbivore guilds in which this taxon was associated to understand the context in which it was able to enter the Iberian Peninsula. By comparing its diet with those of specimens from Northern Europe, we detail the ecological adaptations of this taxon in this new environment. We suggest that *Megaloceros* accompanied the migrations of cold-adapted species by taking advantage of the opening of corridors on both sides of the Pyrenees during the coldest periods of the Late Pleistocene. The diet of the Iberian individuals, which is oriented towards abrasive plants, suggests an adaptation to a different ecological niche than that found in Northern European individuals. The northern Iberian Peninsula may have been an extreme in the geographical expansion of *M. giganteus*. More specimens will be needed in the future to establish the variability of the southern *Megaloceros* populations.

**Keywords:** cervids; Late Pleistocene; linear morphometry; dental microwear; biogeography



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## 1. Introduction

The giant deer, *Megaloceros giganteus* Blumenbach, 1799, is one of the most iconic fossil species in prehistory. It occupied Eurasia, where it appeared about 400,000 years ago [1], and is one of the megafauna species that disappeared during the Holocene. The last populations of *Megaloceros* have been found in Eastern Europe and Siberia and are dated around 7660 cal BP [2–4]. In Western Europe, the last populations have been confined to the North—Ireland, Scotland, Sweden, Germany and Denmark—and are dated between 13,900 and 12,800 cal BP [4].

Populations of giant deer also appear to have occupied South-western Europe outside the Mediterranean peninsulas throughout the Late Pleistocene until relatively recent times [5]. It is notably described in south-eastern France at Chinchon I (Vaucluse) around 12,000 BP [6,7] and south-western France at Tournal ensemble IV (Aude) around 16,605 cal BP [8]. Nevertheless, *Megaloceros* appears to have become extinct much earlier in the southernmost European peninsulas. In Late Pleistocene Greece, it has been described in very few sites that have not been dated precisely, all located in the northern part of the peninsula, such as Agios Geórgios or Angítis [9]. In Italy, the last representatives were found in the

North (Settepolesini, Emilia-Romagna) and date to ca. 29,044 cal BP [4]. In Spain, the last populations seem to have been confined to the North (Asturias, Cantabria and Basque Country), whose ecological conditions are more similar to south-western France than to the rest of the Iberian Peninsula [10]. Jou Puerta (Asturias), dated between 36,665 and 30,275 cal BP, is the site that has yielded the most recent specimen(s) [11]. Nonetheless, *M. giganteus* is only known through isolated individuals in Late Pleistocene Iberia.

The causes of the extinction of *Megaloceros* are still debated and vary from region to region. They have generally been attributed to climate change during the Pleistocene–Holocene transition and to anthropogenic pressure [12–14]. The latest research suggests that climate may have been the determining factor [4]. *Megaloceros* genetic diversity decreased suddenly from MIS 3 onwards until it reached a bottleneck during the Last Glacial Maximum (LGM), with the loss of many lineages [15]. Populations would have been very fragmented during this period. Later, they faced with the arrival of the Neolithic people [2,3]. Thus, a final human contribution to the extinction of *Megaloceros* cannot be excluded [4]. Prior to the Neolithic, local population extinctions are more likely related to competition for resources between *Megaloceros* and other cervids [16].

In this article, we present the discovery of the first *Megaloceros* fossil remains in the Late Pleistocene deposits of Teixoneres Cave in Catalonia (Spain). This species had never been described in this region at this period. Thus, while several populations were becoming extinct during the MIS 3 [15], others had expanded into new territories, a phenomenon that raises the question of the ecological requirements of *Megaloceros* that favoured its expansion into and its maintenance in new territories.

## 2. Materials and Methods

### 2.1. Teixoneres Cave

Teixoneres Cave is located near the village of Moià (Barcelona, Spain) and is part of the Toll Caves karst complex (Figure 1). It is located in the highlands (780 m above sea level), in a region connecting inner Catalonia and the Mediterranean coast, between the two main rivers, namely the Llobregat and the Ter [17].

The site has been excavated in the 1940s, the 1970s and then the 2000s. Since 2003, Teixoneres Cave has been excavated under the leadership of a team from the *Institut Català de Paleoeologia Humana i Evolució Social* (IPHES-CERCA) [18–21].

The cave has yielded a 6 m high sedimentary sequence in which eight stratigraphic units were identified and separated into sub-units [18,19,22]. The most recent archaeological unit, Unit II, has been radiocarbon dated to 44,210 to 33,060 cal BP on the basis of seven bones, all located in the main cave (chamber X). Unit II was separated into two subunits: IIa and IIb [23]. The analysis of three samples from unit IIa, which has yielded the remains of *Megaloceros*, give an age from 35,000 to 37,000 cal BP [24].

A considerable section of Unit II was excavated during the 1940s and 1970s excavations. The materials recovered during this fieldwork remain unknown [25]. The accessible material in Unit IIa comes from excavations carried out between 2006 and 2009. Until now, little work has been done on Unit IIa, which remains relatively unknown. This sub-unit has yielded the remains of six ungulate species apart from *Megaloceros*: *Bos primigenius* (Minimum number of individuals = 2), *Cervus elaphus* (MNI = 3), *Equus caballus* (MNI = 2), *Equus hydruntinus* (MNI = 1), *Coelodonta antiquitatis* (MNI = 1) and *Sus scrofa* (MNI = 1). Carnivores have also been found, including *Ursus spelaeus*, *Crocuta crocuta*, *Lynx* sp. and *Meles meles*. In addition, remains of *Hystrix* sp., *Oryctolagus cuniculus* and *Erinaceus europaeus* have been found. Finally, at least 10 birds and 14 small-vertebrate species are known in this sub-unit [25,26].





**Figure 1.** Geographical position of Teixoneres Cave and the sites discussed in this work. In blue: sites used in the biometric analysis; in white: sites used in the biogeographical analysis; in red: sites used in the dietary analysis. Circles: sites without *Megaloceros giganteus*; square: sites with *M. giganteus*. 1: Chinchon I; 2: Le Pignon; 3: L’Arquet; 4: La Calmette; 5: Cornille; 6: Barasses; 7: Observatoire; 8: Baume Goulon; 9: Baume des Peyrards; 10: Cavillon; 11: Enfants; 12: Prince; 13: Tournal; 14: Roc Traücat; 15: Pair non pair; 16: Camiac; 17: La Crouzade; 18: La Crouzade; 19: Belvis; 20: Salpêtrière; 21: Salpêtre de Pompignan; 22: L’Hortus; 23: Baumasse d’Antonègue; 24: Gazel; 25: Arbreda; 26: Canyars; 27: Cova del Gegant; 28: Abric Romaní; 29: La Rexidora; 30: El Castillo; 31: Labeko Koba; 32: Jou Puerta; 33: Covacho de Arenillas; 34: Lezika; 35: Lezetxiki; 36: Las Caldas; 37: Morin; 38: Urtiagako Leizea; 39: Moros de Gabasa; 40: Ermitons; 41: Fouvent; 42: Kent’s Cavern; 43: Netherlands; 44: Bruine Bank; 45: Siuren I; 46: Geißenklösterle; 47: Einhornhöhle; 48: Große Ofnet; 49: Wolfalhöhle.

During the formation of Unit IIa, the cave was used mainly by carnivores, although short visits from human groups have been also identified. These human occupations have been detected mainly by the presence of lithic artefacts, which are technologically similar to the Middle Palaeolithic technocomplexes of the region [27]. From an archaeospatial point of view, two main areas have been identified in the cave: the inner and the porch of the



main entrance. Most of the accumulation of bone remains inside the cave is associated with carnivore activities, while the porch, where the *Megaloceros* remains were found, is related to human activities [20,22].

Pollen, isotope and micro-faunal analyses have been carried out on this unit to reconstruct the environment. Unit IIa corresponds to a stable period marked by a cool climate with heavy precipitation [28]. The environment must have been closed because tree pollen exceeds 65% of the spectrum [24] but at least seasonally open since the red deer fed on grass at their time of death according to dental microwear [29].

The collection from Teixoneres Cave is stored in the IPHES-CERCA in Tarragona, Spain.

## 2.2. Methods

We employed several proxies from palaeontological and dental wear approaches to describe the *Megaloceros* of Teixoneres and to place it in its ecological context. We compared this specimen to different fossil series listed in Table 1. We performed all the statistical analyses with R version 4.2–RStudio version 4.1.3 using the package FactoMineR [30].

**Table 1.** Summary of the archaeological/paleontological sites used in this work with their geographical positions, date, type of analysis they were used for: linear morphometry (LM), biogeography and dental wear (DW) and the references of the original works.

Site	Location	Date	Analysis	References
Chinchon I l. 13	France	MIS 2	Biogeography	[7]
Le Pignon	France	MIS 2	Biogeography	[31]
L'Arquet	France	MIS 3	Biogeography	[32]
La Calmette	France	MIS 4-3	Biogeography	[33]
Cornille	France	MIS 2	Biogeography	[34]
Barasses I. 2-3	France	MIS 3	Biogeography	[35]
Observatoire I.4	France	MIS 4	Biogeography	[36]
Baume Goulon	France	MIS 2	Biogeography	[37]
Baume des Peyrards I. c-d	France	MIS 4	Biogeography	[35]
Cavillon Foyer II	France	MIS 4	Biogeography	[38]
Enfants coupe 7	France	MIS 3	Biogeography	[38]
Prince foyer B	France	MIS 4	Biogeography	[38]
Tournal ens. II	France	MIS 3	Biogeography, LM	[8]
Tournal ens. IV	France	MIS 2	Biogeography, LM	[8]
Roc Traücat	France	MIS 4-2	Biogeography	[39]
Pair non pair	France	MIS 3	Biogeography, LM	[5,39]
Camiac	France	MIS 3	Biogeography, LM	[4,40]
La Crouzade C.7	France	MIS 3	Biogeography	[41,42]
La Crouzade C.8	France	MIS 3	Biogeography	[41,42]
Belvis I. 7	France	MIS 3	Biogeography	[43]
Salpêtrière I. 3	France	MIS 2	Biogeography	[44]
Salpêtre de Pompignan	France	MIS 4-3	Biogeography	[33]
L'Hortus	France	MIS 3	Biogeography	[33]
Baumasse d'Antonègue	France	MIS 3	Biogeography	[33]
Gazel I. 7-8	France	MIS 2	Biogeography	[43]
<b>Teixoneres</b>	<b>Spain</b>	<b>MIS 3</b>	<b>Biogeography, LM, DW</b>	<b>This work</b>
Arbreda I. H	Spain	MIS 3	Biogeography	[45]
Canyars	Spain	MIS 4	Biogeography	[46]
Cova del Gegant I. 1	Spain	MIS 3	Biogeography	[47]
Abric Romaní	Spain	MIS 3	Biogeography	[48]
La Rexidora	Spain	MIS 3	Biogeography, DW	[49,50]
El Castillo I. 20	Spain	MIS 3	Biogeography	[4,51]
El Castillo I. 14	Spain	MIS 3	Biogeography	[4,51]

Table 1. Cont.

Site	Location	Date	Analysis	References
Labeko Koba I. IX superior	Spain	MIS 3	Biogeography	[4,52]
Jou Puerta	Spain	MIS 3	Biogeography	[11,50]
Covacho de Arenillas I. II	Spain	MIS 3	Biogeography	[53]
Lezika	Spain	Unknown	Biogeography	[54]
Lezetxiki I. IIIa	Spain	MIS 2	Biogeography	[55]
Las Caldas I. VII	Spain	MIS 2	Biogeography	[56]
Morin	Spain	MIS 3	Biogeography	[57]
Urtiagako Leizea	Spain	Unknown	Biogeography	[57]
Moros de Gabasa	Spain	MIS 3	Biogeography	[58]
Ermitons	Spain	MIS 3	Biogeography	[59]
Italy	Italy	Unknown	LM	Raven, 1935 in [60]
Fouvent	France	MIS 3	LM	[61]
Kent's Cavern	England	MIS 3	DW	[62]
Netherlands	Netherlands	MIS 3	DW	[63]
Bruine Bank	North Sea	MIS 3	DW	[63]
Siuren I	Crimea	MIS 3	DW	[64]
Geißenklösterle	Germany	MIS 3	DW	[65]
Einhornhöhle	Germany	MIS 3	DW	[65]
Große Ofnet	Germany	MIS 3	DW	[65]
Wolfthalhöhle	Germany	MIS 3	DW	[65]

### 2.2.1. Linear Morphometry and Biogeography

In this work, we refer to each tooth by its initials—uppercase for upper teeth and lowercase for lower teeth—followed by its number in the tooth row (e.g., P4 means the upper fourth premolar).

We measured the *Megaloceros* maxilla with a digital caliper. We determined the width and length of each tooth and the length between M3 and M1 at the base of the crown to allow comparisons between individuals from different age classes. Morphological descriptions are based on the criteria described by Lister et al. [66].

To contextualise the conditions of the passage of *Megaloceros* south of the Pyrenees, we compared the composition of faunal assemblages from southern France and Spain in the Late Pleistocene. We compared the presence and co-occurrence of 16 species of herbivorous ungulates with *Megaloceros* from 43 assemblages (25 in France and 18 in Spain) by using multiple correspondence analysis (MCA). MCA is a statistical approach which analyses the relationship patterns between more than two categorical dependent variables [67]. The MCA permits the representation of the structure by presenting complex relationships in a two-dimensional Euclidean space [68]. The position of the variables on the graph represents the relationship between them in the building of the dataset representation, in this case, the faunal compositions of various sites from Late Pleistocene North of Spain and South of France. We based our analysis on the presence/absence of herbivorous ungulate species (1) to consider as many deposits as possible, some of which are published without a minimum number of individuals or remains per taxon; (2) to ensure we did not artificially reduce the impact of *Megaloceros*, which is never abundantly represented, in the statistical analysis and (3) to avoid normalised the dataset since the scale differences were negligible. Thus, MCA appeared to be appropriate to deal with categorical data. *Megaloceros* sp. is plotted as an illustrative variable in order to observe its position compared with other herbivores without influencing the analysis.

### 2.2.2. Dental Wear Analysis

To identify the ecological niche occupied by *Megaloceros* from Teixoneres, we carried out a microwear dental study to reconstruct its diet. The mesowear analysis had to be discarded due to the advanced wear of the maxillary dentition.

Microwear is considered to record the diet over the last days to months of an individual's life [69–71]. Our microwear analysis study followed the protocol established by Solounias and Semprebon [72] and Semprebon et al. [73]. We cleaned the occlusal surface of the tooth using acetone followed by 96% ethanol. Then, we moulded the surface with a high-resolution silicone (vinylpolysiloxane) and made casts using clear epoxy resin. We then observed the transparent casts with a stereomicroscope at 35× magnification. We restricted observations to a standard surface of 0.16 mm<sup>2</sup> (using an ocular reticule) localized on the lingual sides of the protocone and metaconule of the M2.

Micro-traces, scratches and pits, in particular, are left on the occlusal surfaces during mastication [74]. The variability in the density of these traces due to the presence of phytoliths in the plants is indicative of various diets: grazer, mixed feeder and browser. We observed various features following the classification of Solounias and Semprebon [72] and Semprebon et al. [73]: pits (small and large), scratches (fine, coarse and hypercoarse) and gouges. We calculated the scratch width score (SWS) with a score of '0' for teeth with predominantly fine scratches per tooth surface, '1' for those with mixed fine and coarse scratches on the tooth surface, and '2' for those with predominantly coarse scratches.

We compared the diet of *Megaloceros* from Teixoneres Cave with nine of the MIS 3 populations that were studied through dental wear analysis. Beside Teixoneres, only the diet of one other specimen was published in the Iberian Peninsula: La Raxidora [50]. Several populations are known in Germany: Geißenklösterle, Einhornhöhle, Große Ofnet, Wolftalhöhle [65], in the Netherlands and in the North Sea (Netherlands and Bruine Bank [63]). Two others were published in Britain (Kent's cavern [62]) and Crimea (Siuren I [64]).

### 3. Results

#### 3.1. Morphometric Description of the Teixoneres *Megaloceros Giganteus* Maxillary

The Teixoneres specimen is a fragment of a maxilla with teeth from P4 to M3 and corresponds to an old individual. The teeth are very abraded and partly broken, especially on the lingual side. Nevertheless, some morphological characters remain observable. The metacone on the M3 is elongated and the root behind is concave. In addition, the occlusal surface of P4 is symmetric and the internal fold is triangular. Finally, there is a buccal cingulum on M1, M2 and P4. There may be one on M3 but it is too worn to say (Figure 2).

From a metric point of view, the dimensions of the Teixoneres giant deer teeth are slightly smaller than those of sub-contemporary counterparts from north of the Pyrenees, in particular from those from Pair-non-Pair (Table 2). The numbers of teeth, however, both in Teixoneres and in the comparative samples, severely limit comparisons. Nevertheless, these dimensions are significant, particularly the width at the base of the crown, which distinguishes it very well from the red deer.

**Table 2.** Measurements of the teeth of the *Megaloceros* from Teixoneres compared to other sub-contemporary series. Details and references about other sites can be found in Table 1. All the measurements have been taken at the base of the crown and are expressed in millimetres. L = length; w = width.

Site		P4_L	P4_w	M1_L	M1_w	M2_L	M2_w	M3_L	M3_w	M1-M3_L
Teixoneres_IIa	n	1		1	1	1	1	1	1	1
	m	17.4		22.3	31.77	24.7	30.9	27.51	27.54	77
TournaI ens. II	n	3	3	2	2	3	3	3	3	
	m	19.1	24.2	25	30.3	28.2	31.7	30.2	29.5	
	min	19	24	25	30	28	31.5	30	29.5	
	max	19.2	24.5	25	30.5	28.5	32	30.5	29.5	
Pair-non-Pair	n	12	12	2	2	5	5	9	9	
	m	18.7	26.1	26.3	34.5	28.6	33.9	29.8	30.5	
	s	0.6	2			0.7	0.9	1.8	1.4	
	min	18	22	26	34.5	28	33	27.5	28	
	max	19.5	27	26.5	34.5	29	35	32.5	32.5	



Table 2. Cont.

Site		P4_L	P4_w	M1_L	M1_w	M2_L	M2_w	M3_L	M3_w	M1-M3_L
Camiac	n	1	2			2	1			
	m	19.5	25.8			27.7	32.8			
	min		25			27.3				
	max		26.5			27.7				
Italy	n	1	1	1	1	1	1	1	1	1
	m	19	24	28.5	28	31	30	29	27	84.5
Fouvent	n			1	1	4	4	2	2	
	m			28	33	28	29.4	34	27.3	
	min					26	27	33	25	
	max					31	32	35	29.5	
Teixoneres_Ila and b <i>Cervus elaphus</i>	n	2	2	3	3	2	2	3	2	
	m	14.61	18.43	18.99	21.43	22.22	24.08	22.32	24.81	
	s	0.65	1.32	2.32	4.04	2.32	1.78	1.05	1.04	
	min	14.15	17.5	16.46	16.8	20.58	22.82	21.5	24.07	
	max	15.07	19.36	21	24.25	23.86	25.34	23.5	25.54	

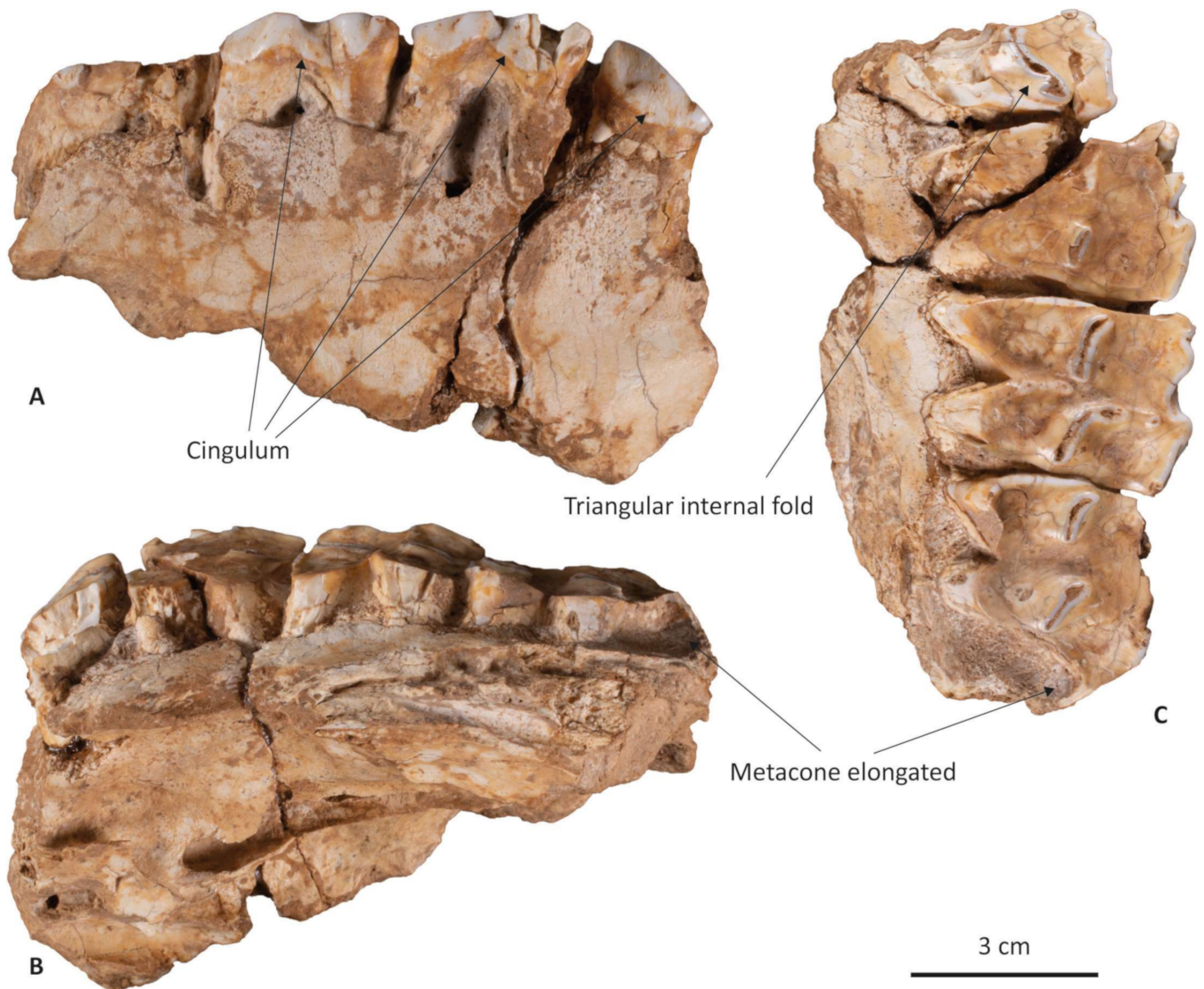


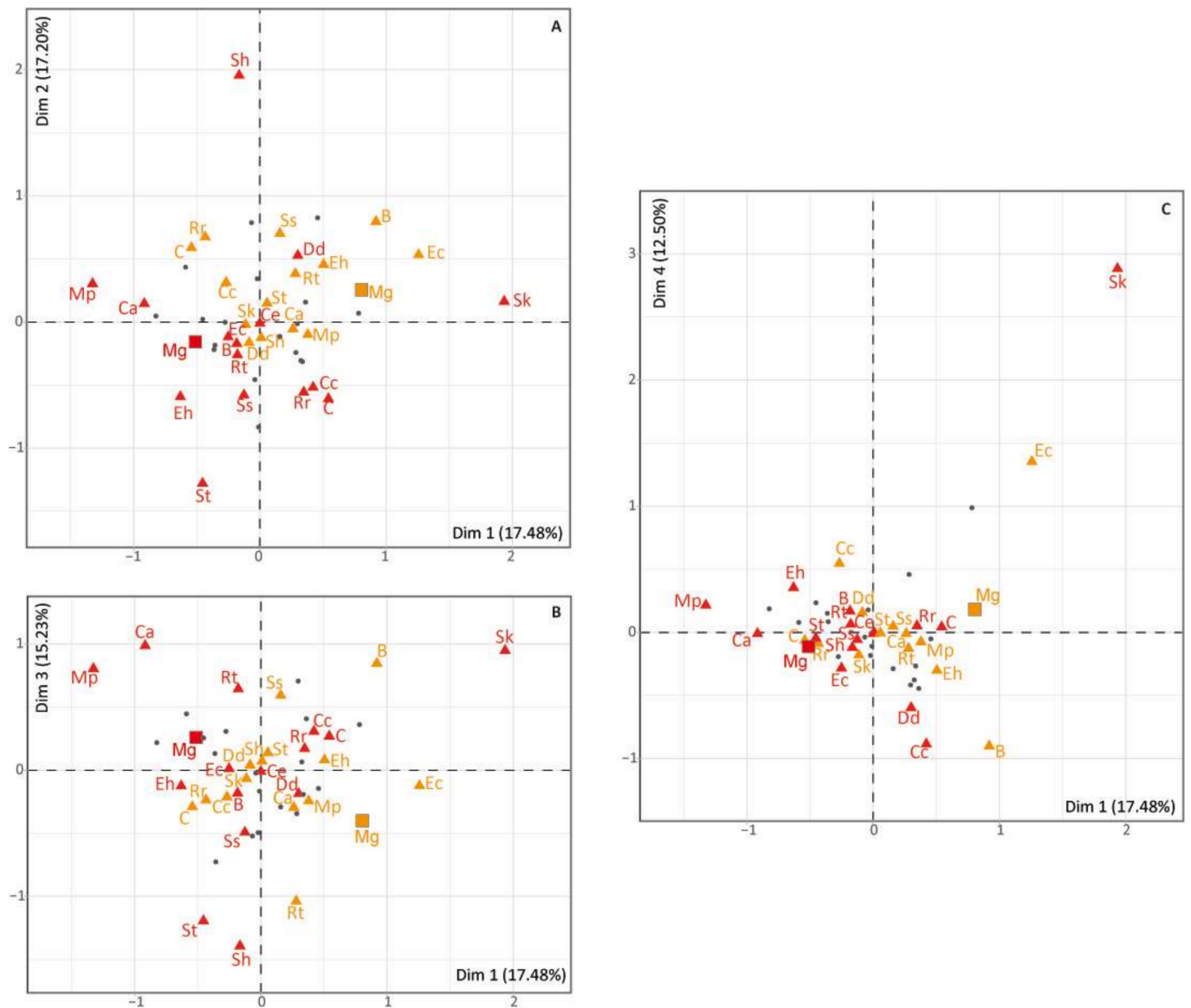
Figure 2. Illustration of the *Megaloceros* maxillary n°TX-06-Ila-M10-18 from Teixoneres Cave. (A) jugal view; (B) lingual view; (C) occlusal view. Photo: Maria Dolors Guillén.

### 3.2. Co-Occurrence of *Megaloceros* with other Herbivores North and South of the Pyrenees

North of the Pyrenees is where *Megaloceros* was often present during the Late Pleistocene. It is preferentially associated with some taxa and tended to avoid others (Table 3). On the first four axes of the MCA (Figure 3), *Megaloceros* is most commonly present with *Mammuthus primigenius*, *Coelodonta antiquitatis*, large bovids (*Bos primigenius* and/or *Bison priscus*), *Equus caballus* and *Rangifer tarandus*. It tends to be absent when *Rupicapra rupicapra*, *Capra* sp. (*Capra ibex* or *Capra pyrenaica*), *Capreolus capreolus* and, especially, *Stephanorhinus kirchbergensis* are present.

**Table 3.** Presence (1) and absence (0) of herbivores taxa north and south of the Pyrenees Late Pleistocene (MIS 4-2) sites. C = *Capra* sp. (*Capra ibex* or *Capra pyrenaica*); Ca = *Coelodonta antiquitatis*; Cc = *Capreolus capreolus*; Ce = *Cervus elaphus*; B = bovids (*Bos* and/or *Bison*); Dd = *Dama dama*; Ec = *Equus caballus*; Eh = *Equus hydruntinus*; Mg = *Megaloceros giganteus*; Mp = *Mammuthus primigenius*; Rr = *Rupicapra rupicapra*; Rt = *Rangifer tarandus*; Sh = *Stephanorhinus hemitoechus*; Sk = *Stephanorhinus kirchbergensis*; Ss = *Sus scrofa*; St = *Saiga tatarica*. Details and references for the sites are given in Table 1.

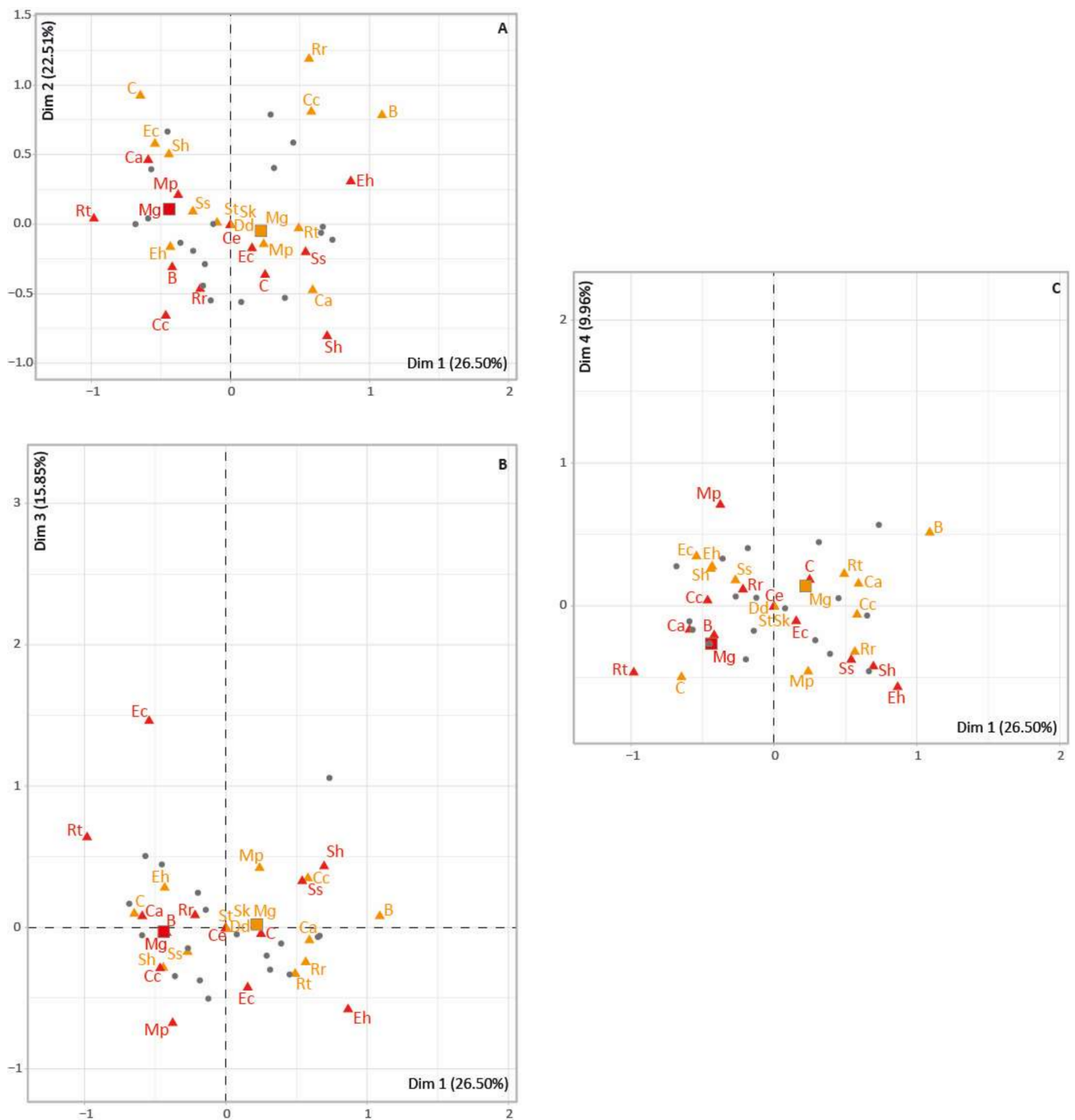
Site	Mp	Sh	Sk	Ca	B	Eh	Ec	Ce	Dd	Cc	Rt	Ss	C	Rr	St	Mg
Chinchon I l. 13	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	1
Le Pignon	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
L'Arquet	1	0	0	0	1	1	1	1	1	1	1	0	0	1	0	1
La Calmette	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0	1
Cornille	0	0	0	0	1	1	1	1	0	0	0	1	0	0	1	1
Barasses I. 2-3	0	0	0	1	0	0	1	1	0	1	1	0	1	1	0	1
Observatoire I.4	0	0	1	0	1	0	0	1	0	0	1	0	1	1	0	0
Baume Goulon	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	0
Baume des Peyrards I. c-d	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	0
Cavillon Foyer II	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0
Enfants coupe 7	0	0	0	0	1	0	1	1	0	1	0	1	0	1	0	0
Prince foyer B	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	0
Tournal ens. II	0	0	0	0	1	1	1	1	0	0	1	1	1	1	0	1
Tournal ens. IV	0	0	0	1	1	1	1	1	0	0	1	1	1	0	0	1
Roc Traucat	1	0	0	1	1	0	1	1	0	0	1	0	0	0	0	1
Pair non pair	1	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1
Camiac	1	0	0	1	1	1	1	1	0	0	1	1	0	0	0	1
La Cruzade C.7	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1
La Cruzade C.8	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	1
Belvis I. 7	0	0	0	0	1	0	1	1	0	1	1	0	1	1	0	0
Salpêtrière I. 3	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0
Salpêtre de Pompignan	0	0	0	0	1	1	1	1	0	1	1	0	1	1	0	0
L'Hortus	0	0	1	0	1	1	1	1	0	1	0	0	1	0	0	0
Baumasse d'Antonègue	0	1	0	0	0	1	1	1	0	0	1	0	1	0	0	0
Gazel I. 7-8	0	0	0	0	1	0	1	1	0	0	1	1	1	1	0	0
<b>Teixoneres IIa</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>
Arbreda I. H	1	0	0	0	1	1	1	1	0	1	0	0	0	1	0	0
Canyars	1	0	0	1	0	1	1	1	0	0	0	1	1	0	0	0
Cova del Gegant I. 1	0	1	0	0	1	1	1	1	0	0	0	1	1	0	0	0
Abric Romaní	0	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0
Rexidora	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1
El Castillo I. 20	0	1	0	0	1	0	1	1	0	1	1	0	1	1	0	1
El Castillo I. 14	0	1	0	0	1	0	1	1	0	1	0	0	1	1	0	1
Labeko Koba I. IX superior	1	0	0	1	1	0	1	1	0	1	1	1	0	1	0	1
Jou Puerta	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1
Covacho de Arentillas I. II	0	0	0	1	1	0	1	1	0	1	0	0	1	1	0	0
Lezika	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0
Lezetxiki I. IIIa	0	1	0	1	1	0	1	1	0	1	1	1	1	1	0	0
Las Caldas I. VII	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
Morin	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0
Urriagako Leizea	1	0	0	1	1	0	0	1	0	1	1	0	1	1	0	0
Moros de Gabasa	0	1	0	0	1	1	1	1	0	1	0	1	1	1	0	0
Ermitons	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0



**Figure 3.** Multiple correspondence analysis of the co-occurrence of herbivore species in the southern France Late Pleistocene. C = *Capra* sp. (*Capra ibex* or *Capra pyrenaica*); Ca = *Coelodonta antiquitatis*; Cc = *Capreolus capreolus*; Ce = *Cervus elaphus*; B = bovids (*Bos* and/or *Bison*); Dd = *Dama dama*; Ec = *Equus caballus*; Eh = *Equus hydruntinus*; Mg = *Megaloceros giganteus*; Mp = *Mammuthus primigenius*; Rr = *Rupicapra rupicapra*; Rt = *Rangifer tarandus*; Sh = *Stephanorhinus hemitoechus*; Sk = *Stephanorhinus kirchbergensis*; Ss = *Sus scrofa*; St = *Saiga tatarica*. Triangle = active variables; square = illustrative variables; circles = archaeological/paleontological sites. Red = presence; yellow = absence. (A) axis 1 (17.48%) × axis 2 (17.20%); (B) axis 1 (17.48%) × axis 3 (15.23%); (C) axis 1 (17.48%) × axis 4 (12.50%).

South of the Pyrenees, where its presence is more exceptional, *Megaloceros* is usually associated with *M. primigenius*, *C. antiquitatis*, *R. tarandus* and large bovids (Table 3; Figure 4). However, it is rarely found with *S. scrofa*, *Capra* sp. and *Stephanorhinus hemitoechus*. *M. giganteus* does not appear as an extreme on the axes of the MCA in either analysis.





**Figure 4.** Multiple correspondence analysis of the co-occurrence of herbivores species in the northern Spain Late Pleistocene. C = *Capra* sp. (*Capra ibex* or *Capra pyrenaica*); Ca = *Coelodonta antiquitatis*; Cc = *Capreolus capreolus*; Ce = *Cervus elaphus*; B = bovids (*Bos* and/or *Bison*); Dd = *Dama dama*; Ec = *Equus caballus*; Eh = *Equus hydruntinus*; Mg = *Megaloceros giganteus*; Mp = *Mammuthus primigenius*; Rr = *Rupicapra rupicapra*; Rt = *Rangifer tarandus*; Sh = *Stephanorhinus hemitoechus*; Sk = *Stephanorhinus kirchbergensis*; Ss = *Sus scrofa*; St = *Saiga tatarica*. Triangle = active variables; square = illustrative variables; circles = archaeological/paleontological sites. Red = presence; yellow = absence. (A) axis 1 (25.04%)  $\times$  axis 2 (20.65%); (B) axis 1 (25.04%)  $\times$  axis 3 (17.21%); (C) axis 1 (25.04%)  $\times$  axis 4 (10.73%).

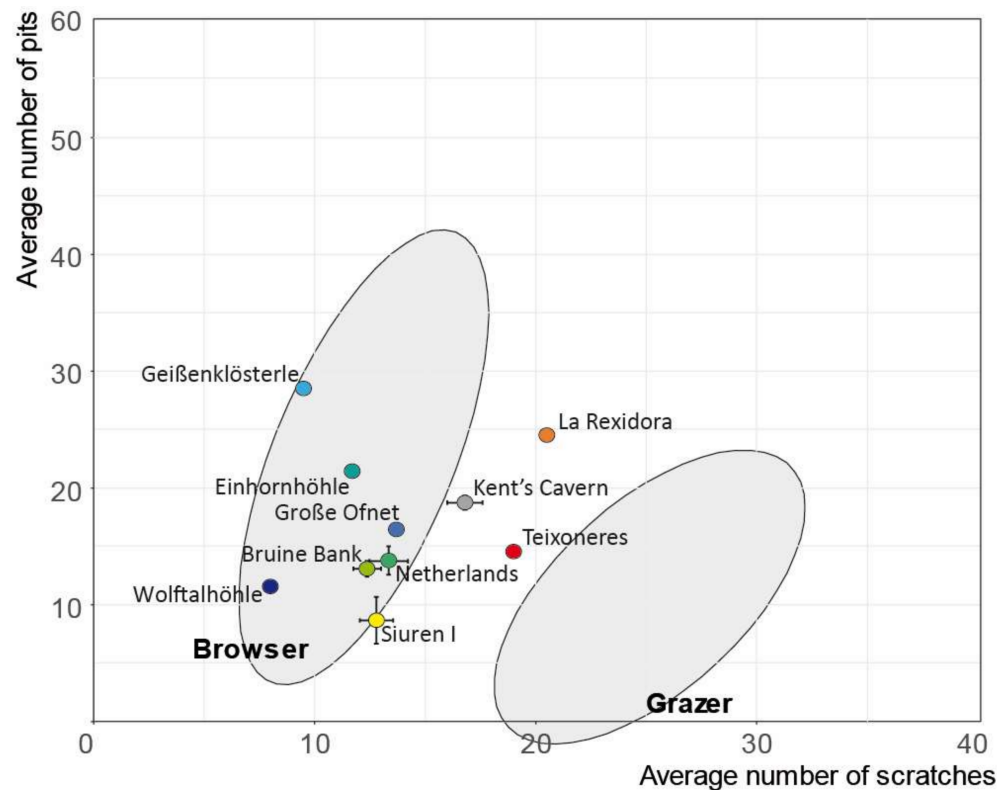
### 3.3. *Megaloceros* Dietary Habits

The cusps of the *Megaloceros* maxilla from Teixoneres are very abraded by age and do not reflect the animal's diet. Thus, mesowear was not conducted and, we only analysed its feeding habits at the level of dental microwear, representing the diet during its last days of life. We compared the feeding habits of the Teixoneres individual with that of Iberian, German, Dutch, British and Crimean populations from MIS 3 (Table 4).

**Table 4.** Summary of dental microwear data of *Megaloceros giganteus* and other herbivores from Unit Ila of Teixoneres Cave. Data of European *M. giganteus* from MIS 3 are also given (data from [50,62–65], see Table 1). Abbreviations: n = number of specimens; NP = mean number of pits; NS = mean number of scratches; %LP = percentage of specimens with large pits; %G = percentage of specimens with gouges; SWS = scratch width score; %HC = percentage of specimens with hyper coarse scratches; %XS = percentage of specimens with cross scratches; m = mean; sd = standard deviation.

Site		Microwear						
		n	NP	NS	%LP	%G	SWS	%HC
<b>Teixoneres unit Ila</b>								
<i>Megaloceros giganteus</i>		1	14.5	19	0	0	0	0
<i>Bos primigenius</i>		1	14	16.5	0	0	0	100
<i>Cervus elaphus</i>	m	4	9	25	0	0	0.25	100
	sd		7.22	3.24			0.5	
<i>Coelodonta antiquitatis</i>		1	3.5	20.5	0	0	0	100
<i>Equus caballus</i>	m	5	12.7	28.4	0	0	0	100
	sd		7.69	3.45			0	
<i>Equus hydruntinus</i>		1	3	19	0	0	1	0
<b>Rexidora</b>		1	24.5	20.5	0	0	1	0
<b>Kent's Cavern</b>	m	18	18.7	16.8	55.6	27.8	1.1	33.3
	sd		0.6	0.8				
<b>Siuren I</b>	m	4	8.6	12.8	73.3	0	1.1	0
	sd		2.01	0.75				
<b>Netherlands</b>		12	13.9	13.4	75	37.5	1.4	43.8
<b>Bruine bank</b>		28	13.6	13	78.6	39.3	1.4	53.6
<b>Geißenklösterle</b>		1	28.5	9.5			2	
<b>Große Ofnet</b>		10	16.4	13.7	100	20	1	30
<b>Einhornhöhle</b>		3	21.4	11.7	100	0	1.2	0
<b>Wolftalhöhle</b>		1	11.5	8			2	

Most of the populations, especially the ones from Germany, Netherlands and Crimea are characterized by a reduce number of scratches (Figure 5). They have a greater variability in the number of pits with almost 30 in Geißenklösterle and only 8.6 in Siuren I. They fall within the dietary space of the extant leaf browsers. They are also characterized by a high number of large pits and a high SW index (Table 4). The populations from Britain and Iberia are distinguished by a greater number of scratches that put them between the variability of the browsers and the grazers (Figure 5). While the giant deer from Kent's cavern display like the ones from Netherlands, Germany, and Crimea a high number of large pits and a high SW score, the individuals from La Rexidora and Teixoneres display thin scratches and no large pits.



**Figure 5.** Bivariate plot of the number of pits and scratches of European *Megaloceros giganteus* from MIS 3. Germany: Geißenklösterle, Einhornhöhle, Große Ofnet, Wolfstalhöhle [65], Netherlands and North Sea: Netherlands and Bruine Bank [63], Britain: Kent's cavern [62], Crimea: Siuren I [64] and Spain: La Rexidora [50] and Teixoneres (this work). The ellipses correspond to the Gaussian confidence ellipse ( $p = 0.95$ ) on the centroids of extant grazers and browsers published by [72].

#### 4. Discussion

##### 4.1. Taxonomic Attribution of the Teixoneres *Megaloceros* Specimen

While the specimen from Teixoneres is very damaged, we were able to observe several characteristics typical of the genus *Megaloceros*. Besides the expression of buccal cingulum on all the teeth, most of the criteria are located on the P4 and the M3. The triangular internal fold on the P4, the elongation of the metacone of the M3 and its concave root were described as features of *Megaloceros* [66]. In addition, the size of the teeth of the Teixoneres specimen falls within the variability of other *Megaloceros* population and exceeds the size of the contemporaneous red deer teeth. These morphometric characters allow to attribute without doubt to *Megaloceros giganteus*, the specimen of Teixoneres.

Several sub-species were described in the *Megaloceros* lineage. Especially, several authors have suggested to distinguish *Megaloceros giganteus ruffii* and *Megaloceros giganteus giganteus* [75–80].

*M. giganteus ruffii* was first described as an archaic form of *Megaloceros giganteus giganteus* present in Eastern Europe and Northern Asia during the Mindel-Riss and Riss [81,82]. More recently, this form has been recognised up to MIS 3 in Eastern Europe and Asia [76,79,80,83] but also in Western Europe, notably in England (Cowthrop) and Germany (Worms) [77]. In addition, Croitor et al. [76] have linked *M. giganteus ruffii* to the robust form described by van der Made [84] in Germany and the short-sized form described by Lister [1] in Western Europe, both for the early Late Pleistocene. In this scenario, *Megaloceros giganteus giganteus* would have replaced *M. g. ruffii* from the end of the MIS 3 up to its extinction. Other authors, however, refer only to *Megaloceros giganteus* and refute the existence of geographical or chronological sub-species [1,66].



In Teixoneres, the fossil remains of *Megaloceros* is limited to one bone and do not permit a possible sub-specific attribution. Pending on new findings, we suggest to keep its attribution at the specific level: *Megaloceros giganteus*.

#### 4.2. Did *Megaloceros* Avoid/Cohabit with the Same Herbivore Species North and South of the Pyrenees?

The comparison of the herbivore assemblages accompanying *M. giganteus* north and south of the Pyrenees did not show any major differences between the two geographical areas. During the Late Pleistocene, giant deer most often accompanied *M. primigenius*, *C. antiquitatis*, *R. tarandus* and large bovines (*Bos* or *Bison*) on both sides of the Pyrenees. It thus, mainly accompanied taxa that are considered characteristic to rather cold and/or open environments belonging to the *Mammuthus-Coelodonta* complex defined by Kahlke [85,86] or to the 'mammoth steppe' defined by Guthrie [87]. Since the faunal spectra accompanying the giant deer in the South of France and in the Iberian Peninsula were very similar, the arrival of *Megaloceros* south of the Pyrenees may have occurred at times when the ecological conditions in the areas north and south of the Pyrenees were rather analogous. Cold-adapted large herbivores are rare in the Iberian Peninsula, and their dispersal often corresponds to the coldest and driest time of the Late Pleistocene, notably MIS 3 and 2 [10,49]. At these times, sites in the northern Pyrenees are often dominated by cold-adapted taxa such as reindeer or bison, whereas sites on the Iberian Peninsula often show a mixture of cold and temperate-adapted taxa [10,17]. In Teixoneres Cave Unit IIa, *Megaloceros* was found associated with *B. primigenius*, *C. elaphus*, *E. caballus*, *E. hydruntinus* and *C. antiquitatis*. The mixture of temperate and cold-adapted taxa, and among them the giant deer from Teixoneres could reveal the ecotone position of the site, at the transition between the *Mammuthus-Coelodonta* complex in the North and the temperate refugium of the peninsula. In Teixoneres, the climate was cool and relatively humid and the environment was dominated by forest (arboreal pollen: 65%) with the presence of open areas [24,26,28,29]. This mosaic landscape will have been sufficient to allow the maintenance of several guilds of herbivorous ungulates, meeting especially the ecological requirements of both *Megaloceros* and *Coelodonta*.

The analysis of herbivore assemblages has also allowed us to highlight the taxa that least often accompanied giant deer. North of the Pyrenees, these taxa are *Capreolus capreolus*, *R. rupicapra*, *Capra* sp. and *S. kirchbergensis*. South of the Pyrenees, they are *S. scrofa*, *Capra* sp. and *S. hemitoechus*. Thus, in both areas, *Megaloceros* tended to be minimally present in the company of the taxa most closely associated with forest environments, *S. scrofa* and *C. capreolus*. This observation is consistent with previous ones that observed that pre-LGM *M. giganteus* is absent in the most densely forested biomes [4] favoured by *S. scrofa* and *C. capreolus*.

Moreover, in both areas, it is rarely found in association with the alpine taxa, *Capra* sp. and *R. rupicapra*. Due to the proportions of its limb bones, *M. giganteus* should have been rather adapted to plains or slightly hilly terrain [80] and should have avoided high mountains or steep relief, which makes cohabitation with Caprinae relatively rarer.

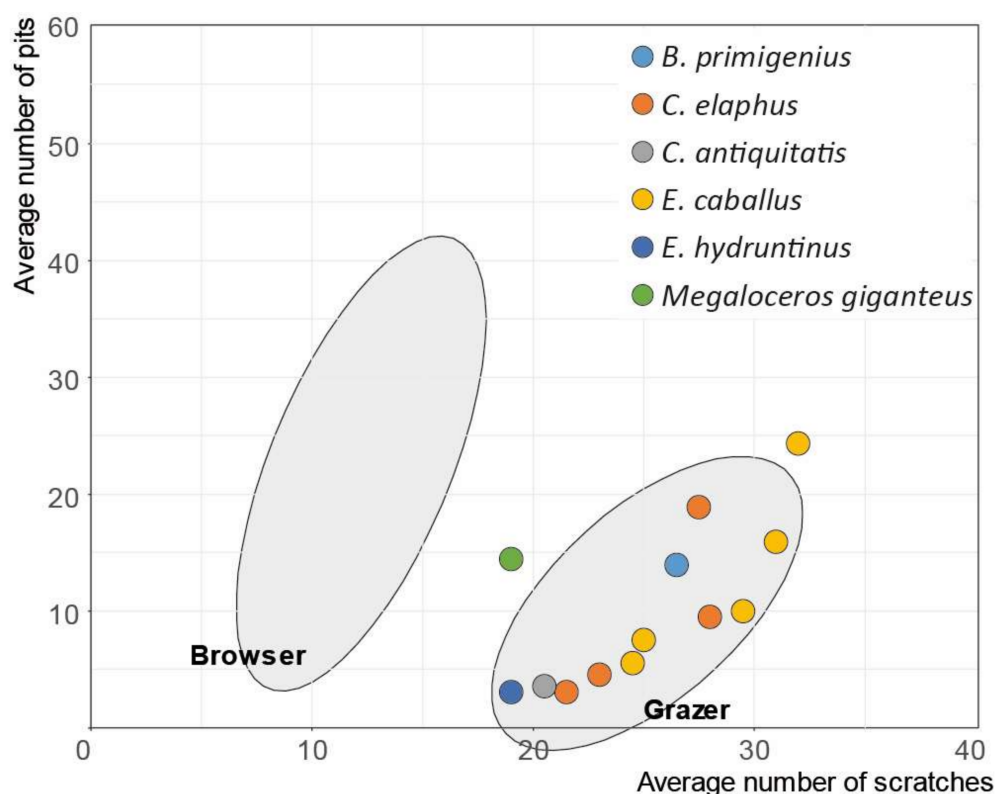
It is also interesting to note that the giant deer is rarely associated with *S. kirchbergensis* north of the Pyrenees and with *S. hemitoechus* south of the Pyrenees.

#### 4.3. *Megaloceros* Dietary Niches from North to South

General lifetime feeding habits of *M. giganteus* from MIS 3 according to dental mesowear or isotopic studies show a browse-dominated diet, from strictly browser to a mixed feeder in Northern and Eastern Europe, including Germany [65,88], France [89], Ukraine [64] and the North Sea [90]. In La Raxidora from the Iberian Peninsula, mesowear analysis show a browse dominated [50] diet included in the variability of the other European populations.

In Teixoneres, life-time trend dietary habits were not possible to assess due to the significant wear of the specimen teeth. Thus, we have only addressed time-at-the-death dietary habits that are strongly impacted by seasonal changes. *M. giganteus* shows the same

feeding characteristics as the other herbivores from the same level of Teixoneres: all five species focussed on grass, with strict grazing to a mixed-feeding grass-dominated diet at the time of their death (Figure 6). While in general, the landscape around Teixoneres may have been forested [24], the absence of browsers could indicate that browsing was inaccessible/non-existent at certain times of the year or that these species favoured open and herbaceous environments. Thus, in Teixoneres, *M. giganteus* probably adapted its dietary habits to a monocot-rich period.



**Figure 6.** Bivariate plot of the number of pits and scratches of *Megaloceros giganteus* from Teixoneres Unit IIa with the other herbivores from the same unit: *B. primigenius*, *C. elaphus*, *C. antiquitatis*, *E. caballus* and *E. hydruntinus*. The ellipses correspond to the Gaussian confidence ellipse ( $p = 0.95$ ) on the centroids of extant grazers and browsers published by [72].

At their time of death (Figure 5), MIS 3 *M. giganteus* show feeding habits that differ from browser in Germany, the Netherlands, the North Sea and Crimea [63–65], while population from England [62] and the Iberian Peninsula [50] are mixed-feeders. The diet of the Iberian individuals differs from all the other ones by an absence of large pits and a weak SW score (Table 4). In Kent’s cavern, the moderate number of pits and scratches associated with a high percentage of teeth with large pits and a general mixed scratch texture can be interpreted as a feeding on a mixture of short dicot and monocot herbs [62]. In La Raxidora and Teixoneres, the dental microwear data can indicate a leaf-feeding behaviour complemented with the consumption of tall monocot grasses.

Like others [65,89,91], this study highlights the capacity of *M. giganteus* to include dicots and monocots in its diet. Northern and Southern European specimens microwear data indicate distinct habits in plant selection. While, at least, British giant deer may have feed on dicots and monocots plants, Iberian ones (La Raxidora, Teixoneres) fed on a mixture of leaves and grass. The two only-known Iberian *M. giganteus* show then, extreme dietary patterns included within the variability of the feeding habits known for European *M. giganteus* at this period.

#### 4.4. Synthesis: Which Conditions Favoured the *Megaloceros* Incursions into the Iberian Peninsula?

*M. giganteus* is a poorly represented and often scarce species, suggesting that it is generally a rare taxon [1,92]. Although its range was extensive during the Late Pleistocene, it is known only from rare occurrences in the Iberian Peninsula. All the sites reported so far are in the northwest, in Asturias, Cantabria or the Basque Country [93]. The Teixoneres specimen is the first occurrence of this taxon in the Late Pleistocene so far east on the peninsula in a Mediterranean rather than an Atlantic context. Dated between 35,000 to 37,000 cal BP, it is currently among the youngest *M. giganteus* fossil of the Iberian Peninsula.

A comparison of herbivore guilds north and south of the Pyrenees shows similar trends between the two geographical areas. Thus, the arrival of the giant deer in the peninsula must have coincided with periods that are favourable for the ecology of species that depend on rather cold and open environments such as *C. antiquitatis* or *R. tarandus*. Nevertheless, *M. giganteus* cannot be considered a typical member of the ‘mammoth steppe’ fauna [4] because it could regularly occur in temperate areas of Mediterranean Europe without being accompanied by *M. primigenius* or *C. antiquitatis* [94]. Moreover, in the MCA analysis (Figures 3 and 4), the giant deer is positioned close to the centre of the axes, indicating that it is rather flexible and never strictly associated with one species or another. The migration periods of cold species in the Iberian Peninsula also coincide with a drop in sea level and the opening of a passage to the west of the Pyrenees Mountain range and a much narrower one to the east [95]. Given that *M. giganteus* tends to be rarely associated with alpine species and its locomotor adaptations adapted to flat or slightly hilly terrain [80], it is highly likely that the Pyrenees constituted an impassable geographical barrier for this species. Only during cold periods and when accompanying species adapted to this climate should it have been possible for *M. giganteus* to cross into the peninsula.

The environments occupied by *M. giganteus* are most often open habitats where it mainly feeds on browse [16,65,90,96]. In Teixoneres, the habitat is mostly forested [24]. At least at the time of its death, however, this individual had a grass-dominated mixed-feeding diet as did the other Iberian specimen from La Raxidora [50], probably composed by a mixture of leaves and grass. Thus, at least at one time of the year both populations did not have access to browsing either due to the composition and seasonal changes of the plant biome or due to competition with other herbivores for the same resources. During MIS 3, the vast majority of European *M. giganteus* focused on soft plants and very few populations show very different behaviour. Thus, although included in the general variability of the species, Iberian specimens stand out for their more pronounced seasonal consumption of grasses. More specimens will be needed in the future to test these hypotheses but, although *M. giganteus* is a flexible species [65], the environments of Northern Spain may correspond to the limits of the expression of their ecological tolerance.

## 5. Conclusions

This study presents the first discovery of a Late Pleistocene fossil of *M. giganteus* in the eastern Iberian Peninsula. Discovered in Unit IIa of Teixoneres Cave (35,000 to 37,000 cal BP), the maxillary fragment belongs to an old adult. Based on this fossil and analyses of published data, the conditions of the incursions of the giant deer into the Iberian Peninsula have been discussed. North of the Pyrenees, *M. giganteus* was regularly found in association with the cold species that it seems to have followed south of the Pyrenees during the coldest and driest periods of the Late Pleistocene. It must have favoured similar environments to those preferred by the ‘mammoth steppe’ fauna. Moreover, the Pyrenees must have constituted a natural barrier for the giant deer in particular. These periods also correspond to the opening up of corridors on both sides of the Pyrenees, which must have allowed it to pass to the South. Although *M. giganteus* was able to find environments suitable for its ecology south of the Pyrenees, the evidence we presented suggests it had to adapt its behaviour and consume grass more regularly than its counterparts in northern and eastern Europe. It is possible that this habitat did not allow great expansion of the populations and that the north-western and north-eastern portions of the Iberian Peninsula

constitute some of the limits of its maximum range. In any case, the specimen recovered from Teixoneres Cave represents an exceptional finding, and more individuals will be required to discuss the role played by the giant deer in the ecosystems of Southern Europe during the Late Pleistocene.

**Author Contributions:** A.U. collected the data; designed and conducted the research; wrote the main manuscript; and prepared all the figures, tables, and supplementary information. F.R. is part of the leading team at the Teixoneres Cave excavation and participated in the research design. A.R., R.B. and J.R. are part of the leading team at the Teixoneres Cave excavation. All authors have read and agreed to the published version of the manuscript.

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