Ungulate dietary traits and plasticity in zones of ecological transition inferred from late Pleistocene assemblages at Jou Puerta and Rexidora in the Cantabrian Region of northern Spain

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A B S T R A C T

The diet and habitats of Late Pleistocene ungulate taxa were analyzed in the caves of Jou Puerta and Rexidora (Marine Isotope Stage, MIS 3), in the Cantabrian Region of northern Spain, a zone of ecological transition between mainland Europe and Central-Southern Iberia. The two ungulate assemblages, which are composed mainly by cold-adapted species, were analyzed through tooth mesowear and microwear. The Jou Puerta community is dominated by the leaf browsers while at Rexidora the dominant taxa are grazers that suggest an open landscape with availability of grass, but also with significant presence of trees and/or forbs. Our results suggest an open landscape with presence of arboreal plant taxa during the coldest events of the MIS3. Concerning dietary plasticity, the diets for the cold-adapted woolly rhino and the reindeer in populations that lived in the southwestern boundary of their Eurasian distribution fit within the plasticity observed for other populations during the Pleistocene. It is proposed here that diet was not a limiting factor for the populations that inhabited the limit of their known range of distribution in the Cantabrian Region.

1. Introduction

During Late Pleistocene cold episodes, a mammal community known as the "Mammoth fauna" (Vereschagin and Baryshnikov, 1982) or "*Mammuthus-Coelodonta* faunal complex" (Kahlke, 1999, 2014) spread throughout middle and high latitudes of Eurasia. This faunal association was composed mainly by cold-adapted species, such as the woolly mammoth (*Mammuths primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*) and reindeer (*Rangifer tarandus*). During these cold periods, southern areas of Eurasia acted as glacial refuges for temperate-adapted species (Hewitt, 2000; Sommer and Nadachowski, 2006). Within this context, there can be also detected geographical areas of transitional character between those dominated by the mammoth fauna and the southern glacial refuges. A good example is the Cantabrian region (northwest Spain), which seems to have constituted a transitional area between mainland Europe and Central-Southern

Iberia (Álvarez-Lao and García, 2011a, 2012; Álvarez-Lao and Méndez, 2016). Particular faunal compositions of mixed character occurred here during the cold phases of the Late Pleistocene: cold adapted species as *M. primigenius*, *C. antiquitatis* and *R. tarandus*, typical inhabitants of steppe-like environments, occur as minor elements within mammal communities dominated by species of temperate environmental preferences, mainly *Cervus elaphus* (Álvarez-Lao and García, 2010, 2011b; Álvarez-Lao, 2014; Álvarez-Lao and Méndez, 2016). Even typical forest species as *Capreolus capreolus* and *Sus scrofa* can be detected into these same faunal associations. This particular faunal mixture between species of diverse environmental requirements, which can be detected in >40 assemblages of MIS 3-2 age from the Cantabrian Region (Álvarez-Lao and García, 2010, 2011b; Álvarez-Lao, 2014; Gómez-Olivencia et al., 2014), do not have modern analogues and, then, raises doubts about what type of landscape could accommodate all of them. Palynological analyses published from one of these sites (Rexidora Cave) suggest an open landscape, dominated by steppe plants, with

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presence of the arboreal plant taxa, including mesophilous species (Álvarez-Lao et al., 2015).

The study of the dietary traits of ungulate species, through various proxies such as stable isotopes or tooth wear analyses, yields an approach on the dietary traits and the available plant resources and, then, on the vegetal landscape at where one community lived (e.g., Bocherens et al., 1999; Ungar et al., 2012; Merceron et al., 2016). While some of the analyzed species as the steppe bison (*Bison priscus*) or the woolly rhinoceros (*C. antiquitatis*) are usually considered inhabitants of steppe-like environments, and others like the roe deer (*C. capreolus*) are typically linked to forests (Kurtén, 1968; Stuart, 1982; Guérin and Patou-Mathis, 1996), we consider that there is still much to know about the flexibility in feeding traits of these species, especially when they are under fluctuating environmental conditions (as those occurred during the MIS 3). Recent studies are detecting significant flexibility in diets in Pleistocene ungulates such as in bison (Rivals and Semprebon, 2011), red deer (Rivals and Lister, 2016), reindeer (Rivals and Semprebon, 2017) or Merck's rhinoceros (van Asperen and Kahlke, 2015) but dietary plasticity of many species is still poorly known, especially at the boundaries of their area of distribution.

The main goals of this study are (1) to infer the dietary traits of the ungulate species from late Pleistocene faunal communities from the Cantabrian Region, in order to get an approach of the available plant resources and, thus, of the vegetal landscape; and (2) to evaluate the dietary plasticity of some typical species of the mammoth fauna (as *C. antiquitatis* and *R. tarandus*) from populations that lived in the south-western boundary of their Eurasian distribution. For this purpose, we analyzed tooth mesowear and microwear of all ungulate species from two complete and abundant mammal assemblages of MIS 3 age from the Cantabrian Region, both discovered and excavated in the last few years: the caves of Jou Puerta and Rexidora.

2. Setting

Jou Puerta and Rexidora caves are two paleontological sites located in the Northwest of Iberia, northern Spain, 24 km apart. (Fig. 1), within an area with a high density of karstic cavities developed on extensive Carboniferous Limestone. > 45 fossiliferous caves have been discovered, to date, in this geographic area smaller than 30 km in length (Adán, 1997; Álvarez Lao, 2003; Álvarez-Lao, 2014). Both sites are associated to natural traps, providing unusually well preserved and abundant fossil assemblages (Álvarez-Lao, 2014; Álvarez-Lao et al., 2015). No human activity is detected at any of the sites and, consequently, no bias induced by humans in the faunal composition can be considered. This is very uncommon in assemblages from northwest Iberia, which normally are in connection with archaeological contexts, and provides special interest to these sites in order to study the faunal compositions. Both sites show a mixture of temperate and cold elements, which seems to be typical from Late Pleistocene cold stages in North Iberia, but does not reflect the typical faunal composition of the Eurasian mammoth steppe (Álvarez-Lao and García, 2011b, 2012; Álvarez-Lao et al., 2015, 2017).

2.1. Jou Puerta Cave

Jou Puerta Cave (Llanes, Asturias) was discovered in April 2011 under a collapse sinkhole during the excavation works for the construction of a highway. The fossils were recovered in two debris pyramids, composed mainly by clay and limestone blocks. The chaotic nature of the deposit does not allow definition of a stratigraphical sequence. Fossil remains were recovered during an intensive excavation campaign in the summer of 2011, a few weeks before the cave was destroyed by the works. The origin of the bone accumulation is related to a natural trap, so most of the fossils were unusually well preserved. An outstanding assemblage consisting of 1064 fossil remains was recovered and studied by Álvarez-Lao (2014). This assemblage comprises an interesting faunal complex, including 10 large-mammal species (ungulates are listed in Table 1), at which temperate taxa are predominant, but with a remarkable presence of cold elements, such as *Coelodonta antiquitatis* and *Mammuthus primigenius*. The fossils were dated between 36,655 to 30,275 cal yr B.P. (Álvarez-Lao, 2014), corresponding to the MIS 3.

2.2. Rexidora Cave

Rexidora Cave (Ribadesella, Asturias) was discovered in 2012 during the construction of a house. The origin of the cavity is also is related to a collapse sinkhole, which was filled up by limestone boulders and pebbles, and fossil bones, embedded in a matrix of silt and clay. The deposit shows a chaotic arrangement so it is not possible to define a general stratigraphical sequence. The recovered fossils are exception-
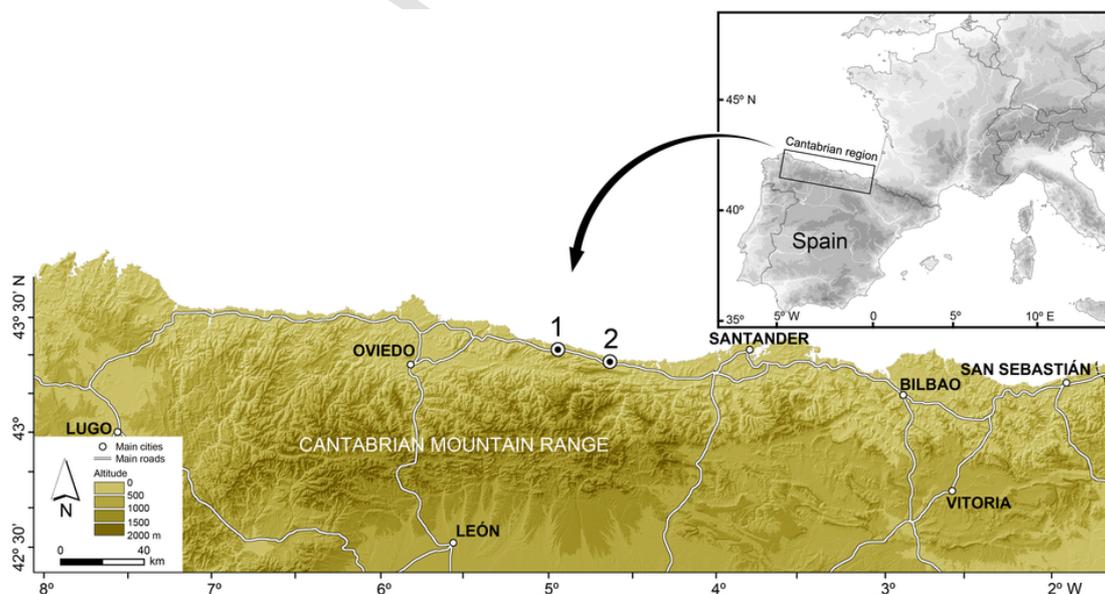

Fig. 1. Location of the studied sites: 1 = Rexidora Cave; 2 = Jou Puerta Cave.

Table 1
Composition of the Jou Puerta ungulate assemblage.

Taxa	NISP	MNI
Cervus elaphus	395	11
Megaloceros giganteus	8	1
Capreolus capreolus	101	4
Rupicapra pyrenaica	117	5
Capra pyrenaica	77	3
cf. *Bison priscus*	159	4
Equus ferus	4	1
Coelodonta antiquitatis	105	3
Mammuthus primigenius	4	1
Total	970	33

ally well preserved and lack any evidence of human or carnivore activity, suggesting that the cave was also in connection with a natural trap. The location of the deposit within a sinkhole supports this idea. Ongoing excavations, directed by one of the authors (DAL), provided up to date nearly 700 fossil remains corresponding to seven large mammal species (ungulates are detailed in Table 2). While the predominant species in the fossil assemblage is the steppe bison (*Bison priscus*), cold-adapted taxa like *Coelodonta antiquitatis* and *Rangifer tarandus* also occur. A preliminary study of the large-mammal fossils, pollen and geomorphology of this site was published by Álvarez-Lao et al. (2015). The fossil assemblage was dated between 44,515 to 37,640 cal yr B.P. (Álvarez-Lao et al., 2015), also corresponding to the MIS 3.

3. Materials and methods

3.1. Material

The material studied includes all dental remains excavated at Jou Puerta in 2011 and Rexidora from 2012 to 2017. The fossil material is stored at the Geology Department, University of Oviedo, Spain. All upper and lower molars available were sampled, molded, and casted for tooth wear analyses (Jou Puerta, n = 24; Rexidora, n = 22). These include 2 upper and 2 lower premolars, 6 upper and 6 lower first molars, 13 upper and 11 lower first molars, and 4 upper and 3 lower first molars.

The occlusal surface of each specimen was cleaned using 96% alcohol. The surface was molded using high-resolution silicone (vinylpolysiloxane) and casts were created using clear epoxy resin. All casts were carefully screened under the stereomicroscope. Those with badly preserved enamel or taphonomic defects (features with unusual morphology and size, or fresh features made during the collecting process or during storage) were removed from the analysis, following King et al. (1999). Molds and casts are stored in the microwear cast collection at IPHES (Tarragona).

3.2. Tooth mesowear analysis

Mesowear analysis is a method of categorizing the gross dental wear of ungulate molars by evaluating the relief and sharpness of cusp apices in ways that are correlated with the relative amounts of attritive

Table 2
Composition of the Rexidora Cave ungulate assemblage.

Taxa	NISP	MNI
Coelodonta antiquitatis	57	5
Bison priscus	395	8
Cervus elaphus	48	4
Rangifer tarandus	10	3
Megaloceros giganteus	5	1
Total	515	21

and abrasive dental wear (Fortelius and Solounias, 2000). Mesowear is scored macroscopically from the buccal side of upper molars, preferably the paracone of the M2. A diet with low levels of abrasion maintains sharpened apices on the buccal cusps as the tooth wears. In contrast, high levels of abrasion, associated with a diet of siliceous grass, results in more rounded and blunted buccal cusp apices. Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices, are omitted from mesowear analysis. Cusp sharpness is sensitive to ontogenetic age among young individuals (which have not yet developed substantial wear facets) and among dentally senescent individuals. However, for intermediate age groups, mesowear is found to be less sensitive to age and more strongly related to diet (Rivals et al., 2007) and therefore suitable for dietary reconstruction.

In this study, the standardized method (mesowear 'ruler') introduced by Mihlbachler et al. (2011) is employed. The method is based on seven cusp categories, ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). The average value of the mesowear data from a single sample of fossil dentitions corresponds to the 'mesowear score' or MWS (Mihlbachler et al., 2011). Dental mesowear analysis was conducted by a single experienced researcher to reduce inter-observer error, corresponding to the recommendations of Loffredo and DeSantis (2014).

3.3. Tooth microwear analysis

Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following the examination protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). The low-magnification microwear technique has been questioned in relation to repeatability and inter-observer error (DeSantis et al., 2013; Mihlbachler et al., 2012). Such problems may arise when observers are not properly trained in the microwear method or when comparing data that were collected by different researchers. To avoid this problem, in the present study all the data were collected by a single experienced observer (FR). Both premolars and molars were used because intertooth variation in microwear patterns is not significant. Both premolars and molars provide consistent data for dietary studies in Artiodactyla and Perissodactyla (Rivals et al., 2015; Xafis et al., 2017).

The transparent epoxy casts were observed under incident light with a Zeiss Stemi 2000C stereomicroscope at 35× magnification, using the refractive properties of the transparent cast to reveal microfeatures on the enamel. Microwear scars (i.e., elongated scratches and rounded pits) were quantified on the paracone of the upper teeth or the protoconid of the lower teeth in a square area of 0.16 mm^2 using an ocular reticule. We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004), which basically distinguishes pits and scratches. Pits are microwear scars that are circular or sub-circular in outline and thus have approximately similar widths and lengths, while scratches are elongated microfeatures that are not merely longer than they are wide, but have straight, parallel sides.

The presence of some other features is recorded qualitatively. Cross scratches are oriented approximately perpendicularly to the majority of scratches observed on the enamel (Solounias and Semprebon, 2002). Gouges are features which have ragged, irregular edges and are much larger (approximately 2–3 times as large) and deeper than large pits. They are relatively dark features with low refractivity. The presence or absence of these features in a microscope field was recorded.

In addition, scratch textures were assessed using the scratch width score (SWS) which is obtained by giving a score of '0' to a tooth with predominantly fine scratches, '1' to one with a mixture of fine and coarse types of textures, and '2' to one with predominantly coarse

scratches. Individual scores for a sample of teeth are then averaged to get the SWS.

4. Results

The tooth microwear pattern is very well preserved at the two caves, even its preservation is higher at Jou Puerta (95.8% of teeth with microwear well preserved, n = 23) than at Rexidora (86.4%, n = 19). Nevertheless, due to differences in the representation of the species, sample size is small for many taxa we analyzed.

The mesowear and microwear results for each taxa from Jou Puerta and Rexidora (mean and standard deviation when n ≥ 3) are reported in Table 3. The raw data have been published in Mendeley Data (Rivals, 2017) and are available at: http://dx.doi.org/10.17632/6j848p7szd.1.

4.1. Tooth mesowear

Coelodonta antiquitatis has the highest mesowear scores among all ungulates analyzed in the two sites (Fig. 2). At Jou Puerta only one specimen could be scored for mesowear, but the value fits within the range of values observed at Rexidora (MWS values of 4 and 5). Such values plot among the extant grazers. In comparison to extant Perissodactyla, the mesowear values of the two samples of *C. antiquitatis* are similar to those reported by Fortelius and Solounias (2000) for the white rhino, *Ceratotherium simum* (CS on Fig. 2) or the plains zebra, *Equus quagga* (EB on Fig. 2).

Equus ferus is only represented with a single lower premolar which could not be used for tooth mesowear analysis.

Cervus elaphus is represented by a significant number of specimens at Jou Puerta (N = 9) and provides a MWS value of 1.44. At Rexidora, only 1 specimen could be sampled for mesowear, but its MWS fits within the range of variation of the values from Jou Puerta (MWS = 0 to 3). Such values plot among the extant leaf browsers and browse-dominated mixed feeders (Fig. 2). The two fossil samples plot near the values of the modern red deer from Europe (CEE on Fig. 2) with a MWS = 1.73 (Rivals et al., 2010) but plot above the population from Canada (MWS = 1.05; CEC on Fig. 2) sampled by Fortelius and Solounias (2000).

Megaloceros giganteus is represented by a single specimen from Rexidora. The low mesowear score (MWS = 1) place this individual among the extant browsers but this result should be taken with caution because only one specimen is analyzed here and may certainly not the full variability that existed in the population.

Capreolus capreolus is represented by a small sample (N = 3) from Jou Puerta. It is the lowest mesowear value observed this this study (MWS = 0.67; Table 1). It plots with values similar to extant leaf browsers and browse-dominated mixed feeders (Fig. 2). Interestingly, it has a value very similar to the extant roe deer (MWS = 0.74; OL on Fig. 2).

Rangifer tarandus is represented by only two specimens from Rexidora. Its mesowear score plots among the mixed feeders (Fig. 2). In comparison from extant populations of *Rangifer tarandus*, it is similar to the caribou from Prince of Wales and Baffin Islands (two populations belonging to *Rangifer tarandus groenlandicus*), with MWS of 2.44 and 2.61, respectively (Rivals and Semprebon, 2017).

Bison priscus is well represented at Rexidora (n = 9) but has a low sample size at Jou Puerta (cf. *B. priscus*; n = 2). However the two mesowear values reported for Jou Puerta fit within the range of values observed at Rexidora. The two samples plot among the extant grass-dominated mixed feeders and the extant grazers. The values for the fossil samples are in between the extant European bison, *Bison bonasus* (BBO), a grazer, and the wood bison from Canada, *Bison bison athabascae* (BBA), a mixed feeder, but way below the extant North American plains bison (*Bison bison bison*) a pure grazer with the highest mesowear score (BBB on Fig. 2).

Capra pyrenaica is only represented with 3 specimens from Jou Puerta. The mesowear value (MWS = 1.33) plots among the extant leaf browsers and browse-dominated mixed feeders (Fig. 2). The value is very similar to the MWS reported for the extant *Capra pyrenaica* (MWS = 1.30; CP on Fig. 2) but above *Capra ibex* (CI on Fig. 2) and below *Capra caucasica* (CC on Fig. 2).

Rupicapra pyrenaica, as *Capra pyrenaica*, is only represented with 3 specimens from Jou Puerta and its mesowear value (MWS = 1.67) plots among the extant leaf browsers and browse-dominated mixed feeders (Fig. 2). The value is slightly higher than for the extant *Rupicapra rupicapra* (RA on Fig. 2). Unfortunately, there is no mesowear data available for the extant *Rupicapra pyrenaica*.

Table 3
Summary of mesowear and microwear data for the fossil ungulates from Jou Puerta and Rexidora.

Site	Species		MESOWEAR		MICROWEAR						
			n	MWS	n	NP	NS	%LP	%G	SWS	%XS
Jou Puerta Cave	*Coelodonta antiquitatis*	M	1	5.00	3	12.67	25.00	0	0	1	33.3
	Equus ferus	M	–	–	1	16.50	24.50	0	0	1	0
	Cervus elaphus	M	9	1.44	9	29.89	10.50	100	55.6	1.6	0
		SD		0.88		7.59	1.41				
	Capreolus capreolus	M	3	0.67	3	16.00	11.33	0	0	1	0
		SD		0.58		1.80	1.53				
	cf. *Bison priscus*	M	2	2.50	1	23.00	22.00	0	0	1	0
	Capra pyrenaica	M	3	1.33	3	33.17	16.83	100	33.3	1	0
		SD		0.58		2.36	0.76				
	Rupicapra pyrenaica	M	3	1.67	3	27.17	15.17	100	0	1	0
		SD		0.58		2.02	0.58				
Rexidora Cave	*Coelodonta antiquitatis*	M	3	4.67	5	25.30	24.00	0	0	1	0
		SD		0.58		3.27	2.60				
	Cervus elaphus	M	1	2.00	2	20.00	15.25	0	0	1	0.5
	Megaloceros giganteus	M	1	1.00	1	24.50	20.50	0	0	1	0
	Rangifer tarandus	M	2	2.5	2	21.5	22.25	50	0	1.5	0
	Bison priscus	M	12	2.75	9	28.94	22.28	88.9	33.3	1.2	44.4
		SD		0.75		3.98	1.698				

Abbreviations: n = number of specimens; MWS = mesowear score; NP = average number of pits; NS = average number of scratches; %LP = percentage of specimens with large pits; %G = percentage of specimens with gouges; SWS = scratch width score; %XS = percentage of specimens with cross scratches; SD = standard deviation.
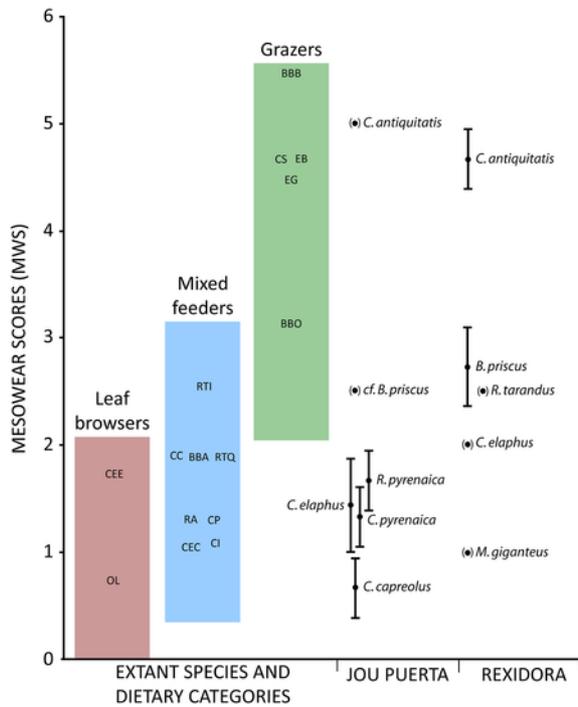
Fig. 2. Mesowear scores of the fossil samples from Jou Puerta and Rexidora in comparison to extant ungulates (data from Fortelius and Solounias (2000), Rivals et al. (2010, 2013, 2014, 2015) and Rivals and Takatsuki (2015)). List of abbreviations for the extant ungulates: Grazers: BBB = *Bison bison bison*, BBO = *Bison bonasus*, CS = *Ceratotherium simum*, EB = *Equus quagga*, EG = *Equus grevyi*. Leaf browsers: CEE = *Cervus elaphus elaphus*, OL = *Capreolus capreolus*. Mixed feeders: BBA = *Bison bison athabascae*, CC = *Capra caucasica*, CEC = *Cervus elaphus canadensis*, CI = *Capra ibex*, CP = *Capra pyrenaica*, RA = *Rupicapra rupicapra*, RTI = *Rangifer tarandus* from Prince of Wales and Baffin Islands, RTQ = *Rangifer tarandus* from Qamanirjuaq.

4.2. Tooth microwear

Coelodonta antiquitatis provided very similar number of scratches at Jou Puerta and Rexidora, indicating diet on the same type of vegetation (Table 1). Based on the number of scratches and the absence of large pits, gouges and cross scratches, the two samples fit with the extant grazers. The two samples plot within the confidence ellipse of the extant grazers but the sample from Rexidora has a higher number of pits than at Jou Puerta (Fig. 3). This certainly is related to the presence of dust or grit on the leaves of the vegetation consumed (Semprebon and Rivals, 2007). Compared to our fossil samples, in extant rhinos the number of pits is usually higher than what we observed such as in the white rhinoceros, *Ceratotherium simum* (NP = 95.9; Rivals et al., 2010) or the black rhinoceros, *Diceros bicornis* (NP = 88.6; Solounias and Semprebon, 2002).

Equus ferus is represented by a single specimen from Jou Puerta. The result should be taken with caution because it may not reflect the values of the whole population. It plots among the extant grazers, with values close to the extant zebras, *Equus quagga* (EB) and *Equus grevyi* (EG on Fig. 3).

Cervus elaphus is well represented at Jou Puerta (n = 9) but sample size is very small at Rexidora (n = 2). Moreover, the microwear values of the two specimens from Rexidora do not fit within the range of values reported for Jou Puerta, neither in the number pits nor in the number of scratches. Anyway, the two samples plot among the extant leaf browsers, but with higher numbers of pits compared to the extant red deer (CEE on Fig. 3).
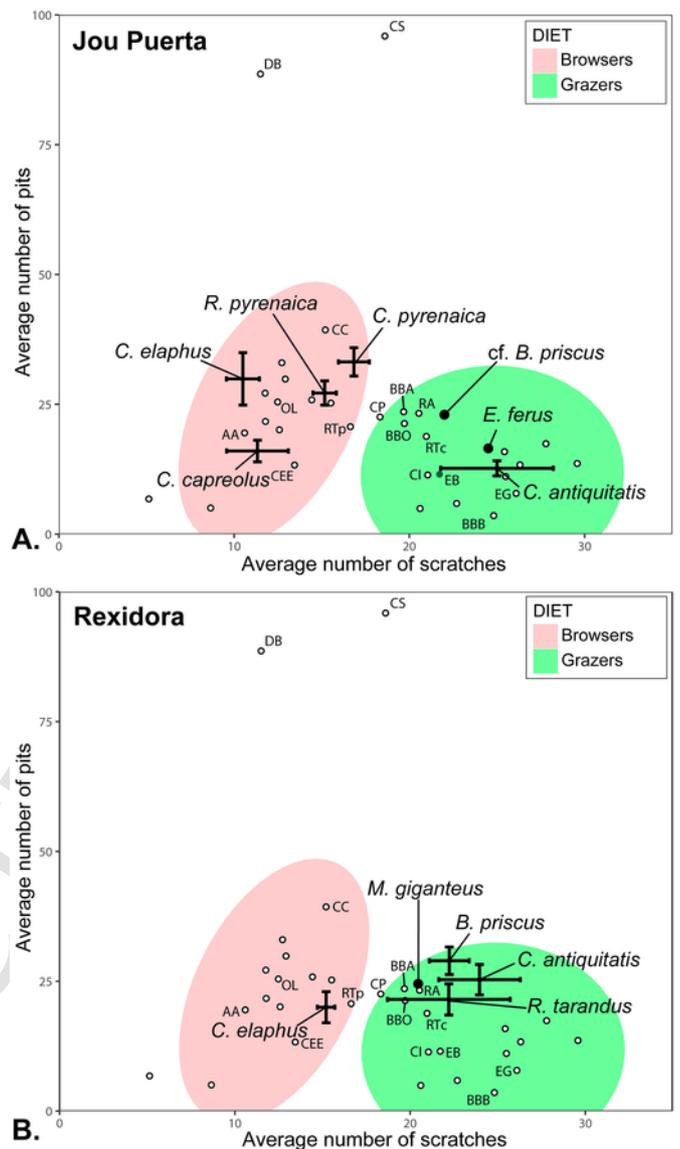

Fig. 3. Bivariate plots of the average numbers of pits and scratches for the ungulates from Jou Puerta (A) and Rexidora (B) represented by black dots. Bars correspond to standard error of the mean (SEM) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses (p = 0.95) on the centroid for the modern leaf browsers and grazers based data from Solounias and Semprebon (2002), Rivals et al. (2010, 2013, 2014, 2015) and Rivals and Takatsuki (2015). White dots represent the extant species used to draw the confidence ellipses. List of abbreviations for the extant ungulates: Grazers: BBB = *Bison bison bison*, BBO = *Bison bonasus*, CS = *Ceratotherium simum*, EB = *Equus quagga*, EG = *Equus grevyi*. Leaf browsers: AA = *Alces alces*, CEE = *Cervus elaphus*, DB = *Diceros bicornis*, OL = *Capreolus capreolus*. Mixed feeders: BBA = *Bison bison athabascae*, CC = *Capra caucasica*, CI = *Capra ibex*, RA = *Rupicapra rupicapra*, RTp = *Rangifer tarandus* from Prince of Wales Island, RTc = *Rangifer tarandus* from Cornwallis Island.

Megaloceros giganteus is represented with a single specimen from Rexidora. It plots in inside the confidence ellipse of the extant grazers, suggesting a grass-dominated diet at the time of death.

Capreolus capreolus is present only at Jou Puerta (n = 3). It plots among the extant leaf browsers, in between the red deer (CEE) and the moose, *Alces alces* (AA on Fig. 3). The extant roe deer (OL on Fig. 3) has a similar value for the number of scratches but higher number of pits than the fossil sample.

Rangifer tarandus, present at Rexidora (n = 2), plots in the confidence ellipses for extant grazers (Fig. 3). In *Rangifer*, the tooth microwear pattern is better interpreted using the scratch/pit ratio (Rivals and Semprebon, 2017). At Rexidora, the ratio NS/NP = 1.04 and fits in

between the ratio reported by Rivals and Semprebon (2017) for the extant caribou populations of Pearyi caribou (*Rangifer tarandus pearyi*) from Prince of Wales Island and Cornwallis Island in Canada (RTp and RTc on Fig. 3, respectively). The value observed at Rexidora would indicate the consumption of lichen.

Bison priscus is represented by a single specimen at Jou Puerta, but its microwear values fits within the range of the larger sample from Rexidora (n = 9). The two samples plot among the extant grazers, closer to the extant wood bison (BBA) and the European bison (BBO) than to the plains bison (BBB) which has significantly lower number of pits (Fig. 3).

Capra pyrenaica and *Rupicapra pyrenaica* from Jou Puerta plot among the extant leaf browsers, both with relatively high number of scratches. *C. pyrenaica* is mostly similar to the extant *Capra caucasica* (CC) but *R. pyrenaica* is very similar to its extant relative (RA on Fig. 3).

5. Discussion

5.1. Variability in dietary traits and vegetation

The dietary traits of the ungulates at Jou Puerta and Rexidora cover the full dietary spectrum from pure leaf browsers (Caprinae and most cervids) to pure grazers (bison, horse and woolly rhino). In this context of cold environmental conditions in the northern part of the Iberian Peninsula (Álvarez-Lao, 2014; Álvarez-Lao et al., 2015), all dietary niches are occupied which indicates availability of a large diversity of resources that could include browse (such as trees, shrubs and dicots) and grass.

At Jou Puerta, the number of browsing species (n = 4) is slightly higher than the number of grazing taxa (n = 3), while at Rexidora most species are grazers (n = 4), except the red deer (Table 4). However this proportion using the number of species does not reflect the proportion of individuals belonging to each species. This may induce a biased especially when the proportion of individuals is different among the sites, which is the case for Jou Puerta and Rexidora (Table 4). To cope with this issue, Rivals et al. (2016) suggested to take into account the minimum number of individuals (MNI) for each species to calculate the proportion of browsers vs. grazers. When the MNI is considered, at Jou Puerta, the ungulate community is dominated by the leaf browsers (75.8%) while at Rexidora they only represent 19%. For Jou Puerta, this proportion would suggest that most of the ungulates were feeding on browse such as trees, shrubs, or herbaceous plants. For Rexidora, this suggests an open landscape with availability of grass, but also with significant presence of trees and/or forbs. The presence of shrubs could probably be discarded as the pollen record did not record any evidence of shrub taxa (Álvarez-Lao et al., 2015).

At Rexidora the higher number of pit in *C. antiquitatis* in comparison to the sample from Jou Puerta suggest drier environmental conditions with presence of pits related to the ingestion of dust or grit on the leaves (Semprebon and Rivals, 2007). This scenario is supported by the pollen data at Rexidora which suggest a very open landscape under

Table 4
Proportion of browsers and grazers at Jou Puerta and Rexidora based on the number of species and the minimum number of individuals (MNI).

	Number of species		MNI	
	Jou Puerta	Rexidora	Jou Puerta	Rexidora
Grazers	42.9%	80%	24.2%	81.0%
	(n = 3)	(n = 4)	(n = 8)	(n = 17)
Browsers	57.1%	20%	75.8%	19.0%
	(n = 4)	(n = 1)	(n = 25)	(n = 4)

cold and dry conditions. The results obtained for species that occur at the two localities are very similar. Considering that the two localities are chronologically different, Jou Puerta was dated from 34 to 32 cal kyr B.P., and Rexidora from 37 to 44 cal kyr B.P., they could reflect the same environmental conditions during different cold pulsations of the MIS 3. The cold taxa form the Rexidora assemblage could be correlated to the Heinrich Event H5, while those from Jou Puerta to one of the cold pulsations from the Heinrich Events H3 to H4.

At Jou Puerta four species (out of 7) are leaf browsers. Mesowear suggest similar general diets at the annual scale, especially among *C. elaphus*, *C. pyrenaica*, and *R. pyrenaica* where the mesowear scores are overlapping. However, the microwear values do not overlap among these species, suggesting the use of different plants or plants parts at the time of death. At Rexidora, there is a significant overlap in the microwear values among the grazers. This suggests that *C. antiquitatis*, *M. giganteus*, *R. tarandus*, and *B. priscus* had similar diets at the time of death.

At Jou Puerta and Rexidora, the mesowear values are spread out across all the dietary categories, from pure browsers with low abrasive diet (*C. capreolus* from Jou Puerta) to pure grazers with highly abrasive diets (*C. antiquitatis*). However, microwear values show more differences and variability among the samples from Jou Puerta than Rexidora. This is indicating more diversity in diet for the ungulates from Jou Puerta at the time of death.

At the two localities, there is a general agreement between the results from mesowear and microwear analyses. We did not observe any clear discrepancy between the mesowear and microwear results. The slight variations like those observed for the giant deer or the red deer, for example, could be due either (1) to the effect of small sample size which can affect the mesowear or the microwear values, or both, or (2) to differences between the average annual diet (as reflected by mesowear) and the diet at the time of death (as revealed by microwear). It is most likely that such small variations are related to sample size. However, for most species the agreement between the two proxies indicates that microwear recorded the diet through all season and consequently that animals certainly died all year around. An accumulation of the remains all year around fits with the paleontological context of the localities, where the probability that animals accidentally fall is the same through the year.

5.2. Dietary plasticity of the cold-adapted species

Dietary plasticity is one of the mechanisms for ungulates to broaden their dietary niche when facing a reduction in resource availability to be able to consume other type of resources. When comparing our results on the fossil species from Jou Puerta and Rexidora to data published for their extant relatives, for most species we observe many similarities in the dietary categories. Even if the ungulate communities from the two localities do not have any modern analogues, we did not identify any diet that would fall outside the range of variation usually observed.

Diets for the cold-adapted *C. antiquitatis* and *R. tarandus* from populations that lived in the south-western boundary of their Eurasian distribution fit within the plasticity observed for other populations during the Pleistocene.

For *C. antiquitatis* the comparison is difficult due to the lack of data for that species in southern Europe. However, in the context of northern Europe, a grazing behavior for *C. antiquitatis* was reported for assemblages from the North Sea (Rivals et al., 2010) and England (Rivals and Lister, 2016). The samples from Jou Puerta and Rexidora fit within the range of variation of these samples.

In the case of *R. tarandus*, which can be compared to its modern relatives, the diet is similar to populations from Canada which are mixed feeders including browse, grass, and lichens. The comparison of *R.*

tarandus from Rexidora was done with other Pleistocene populations from Western Europe (data from Rivals and Semprebon, 2017). Regarding the mesowear values (Fig. 4A), the sample from Rexidora plots near the sample from Portel-Ouest, a Late Pleistocene (MIS 4-3) locality from the northern side of the Pyrenees (Ariège, France). Moreover it plots in the middle of the values reported for populations from Southern Europe. Regarding microwear (Scratch/Pit ratio), the sample from Rexidora plots in between the values for Kent's Cavern (UK) and Portel-Ouest (France) at the boundary of the values for localities from southern and northern Europe (Fig. 4B). Through both proxies, mesowear and microwear, the reindeer from Rexidora has values intermediate to those available for northern and southern Europe. Even if the *R. tarandus* from Rexidora is at the southernmost limit of its distribution range, its diet is not different to what is known for that species during the Pleistocene. The dietary plasticity of the reindeer permitted to adapt to the specific cold conditions from the north of the Iberian Peninsula during the Pleistocene.

6. Conclusions

Tooth wear analysis, as well as the pollen record (at Rexidora), indicate an open landscape in the Cantabrian region during the coldest events of the MIS3. However, the presence of arboreal plant taxa was also significant and supported by the dietary traits of the red deer, roe deer, wild goat and chamois, in particular at Jou Puerta, but also by the pollen record at Rexidora. This supports the Cantabrian area as a zone of ecological transition. The typical species of the mammoth fauna (such as *C. antiquitatis* and *R. tarandus*) from Jou Puerta and Rexidora show diets that fit within the range of variation of other extinct and extant populations. It is suggested here that diet was not a limiting factor for the populations, which inhabit the limit of their known range of distribution in an ecological transition area. The diets of the populations analyzed in this study were not significantly different to those of other Pleistocene populations in Western Europe. Dietary plasticity is thus a crucial mechanism for ungulates to cope to specific environmental conditions in their distribution area.
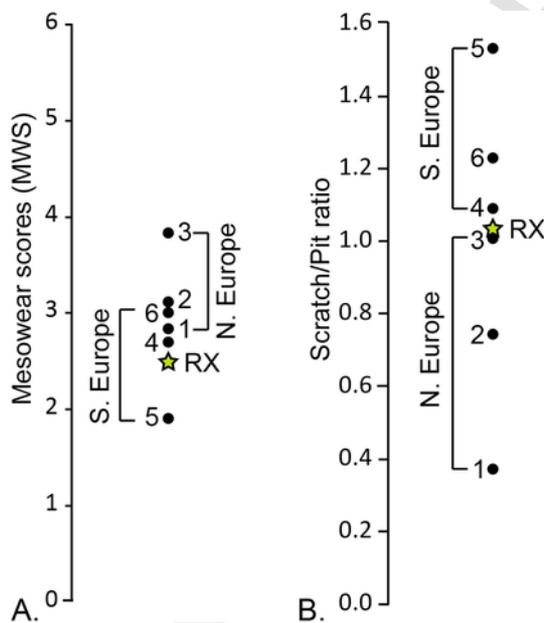

Fig. 4. Mesowear scores (A) and Scratch/Pit ratio (B) for the *Rangifer tarandus* from Rexidora (RX) in comparison to Pleistocene reindeer populations from Western Europe (Modified from Rivals and Semprebon, 2017). Origin of the samples: 1 = Salzgitter Lebenstedt, Germany; 2 = Brown Bank, North Sea; 3 = Kent's Cavern, UK; 4 = Portel-Ouest, France; 5 and 6 = Caune de l'Arago, France (MIS 14 and 12, respectively).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2018.03.024.

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