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## Faunal dietary response to the Heinrich Event 4 in southwestern Europe

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### Abstract

The dietary traits of the ungulates from the Canyars assemblage (Late Pleistocene; Gavà, Barcelona, Spain) are analysed through tooth mesowear and microwear to study their feeding behaviour as well as the climatic conditions during the time of the arrival of the early modern Europeans in the northeast of the Iberian Peninsula. During the Heinrich Event 4 (HE4, between 39 and 40 kyr B.P.), the dietary adaptations of ungulates to grazing dominated the community, and included horses, as well as some red deer, aurochs, and ibex. Results show a rigorous climate, with the presence of grasslands capable of sustaining a high ungulate biomass. The composition of the Canyars ungulate community and its dietary adaptations clearly reveals some particularity of the HE4 in the northeast of the Iberian Peninsula. These open landscapes certainly favoured the migration routes of large mammals along the Mediterranean basin, and also favoured the dispersal of modern humans into the northeast of the Iberian Peninsula.

### Keywords:

Late Pleistocene; Paleodiet; Mesowear; Microwear; Ungulates; Terrasses de la Riera dels Canyars

## **1. Introduction**

Heinrich Event 4 (HE4) is a well-documented event in the North Atlantic Ocean cores (Cortijo et al., 1997) and adjacent territories (Sepulchre et al., 2007) that occurred between 39 and 40 kyr B.P. and was one of the most abrupt climate cooling stadials recorded in the Upper Pleistocene. According to Sánchez Goñi et al. (2002), significant climatic differences existed between the Mediterranean and the Atlantic margins of the Iberian Peninsula, with the Atlantic margin being more humid than the Mediterranean margin. For example, the estimated mean annual precipitation was 500 mm in the Atlantic and 200 mm in the Mediterranean (being 800 and 600 mm in present days) and the mean temperature of the coldest month was  $-1\text{ }^{\circ}\text{C}$  and  $-8\text{ }^{\circ}\text{C}$ , respectively ( $+5\text{ }^{\circ}\text{C}$  nowadays). Several approaches based on pollen analysis (d'Errico and Sánchez Goñi, 2003; Fletcher et al., 2010), and simulation models (Sepulchre et al., 2007) have been conducted to evaluate the terrestrial response to this drastic change in climatic conditions. In the Iberian Peninsula, Heinrich Event 4 corresponds to the time frame of the arrival of modern humans and the extinction of Neanderthals, which are one of the major topics in human evolution (Zilhão, 2009). Moreover, it is highly significant in the Iberian Peninsula, where Neanderthals seem to have persisted longer than elsewhere in western Europe (Zilhão, 2009). The role of climatic oscillations seems to be crucial in this process and several models based on climatic approaches have been conducted (Jiménez-Espejo et al., 2007; Sepulchre et al., 2007). However, paleoecological evidence from the terrestrial record are very scarce and imprecise in southern Europe, thus, most of the data about HE4 come from marine pollen records and simulation studies. This paper provides inferences regarding the dietary traits and habitat of large mammals from Terrasses de la Riera dels Canyars site based on tooth mesowear and microwear analyses in order to evaluate the faunal dietary response to the palaeoecological changes that occurred during HE4. Furthermore, this site, located on the Mediterranean coast of northeastern Iberia, is one of the few containing a stratigraphic layer accumulated over a short time interval coinciding with that estimated

for the HE4. The fossil vertebrate remains are abundant and provide important data for palaeoenvironmental reconstructions. We focus on two objectives: (1) to characterize the diet of the ungulates present in the assemblage from Canyars, and (2) to evaluate the implications for palaeoenvironmental reconstruction of HE4.

## **2. Terrasses de la Riera dels Canyars**

Terrasses de la Riera dels Canyars (henceforth, Canyars) ( $41^{\circ}17'46''$  N,  $01^{\circ}58'47''$ E) is located in the Garraf Massif, in the municipality of Gavà (20 km south of the city of Barcelona) (Fig. 1A–C). The locality is at an altitude of 27m a.s.l. and 3.5 km in land from the extant coastline.

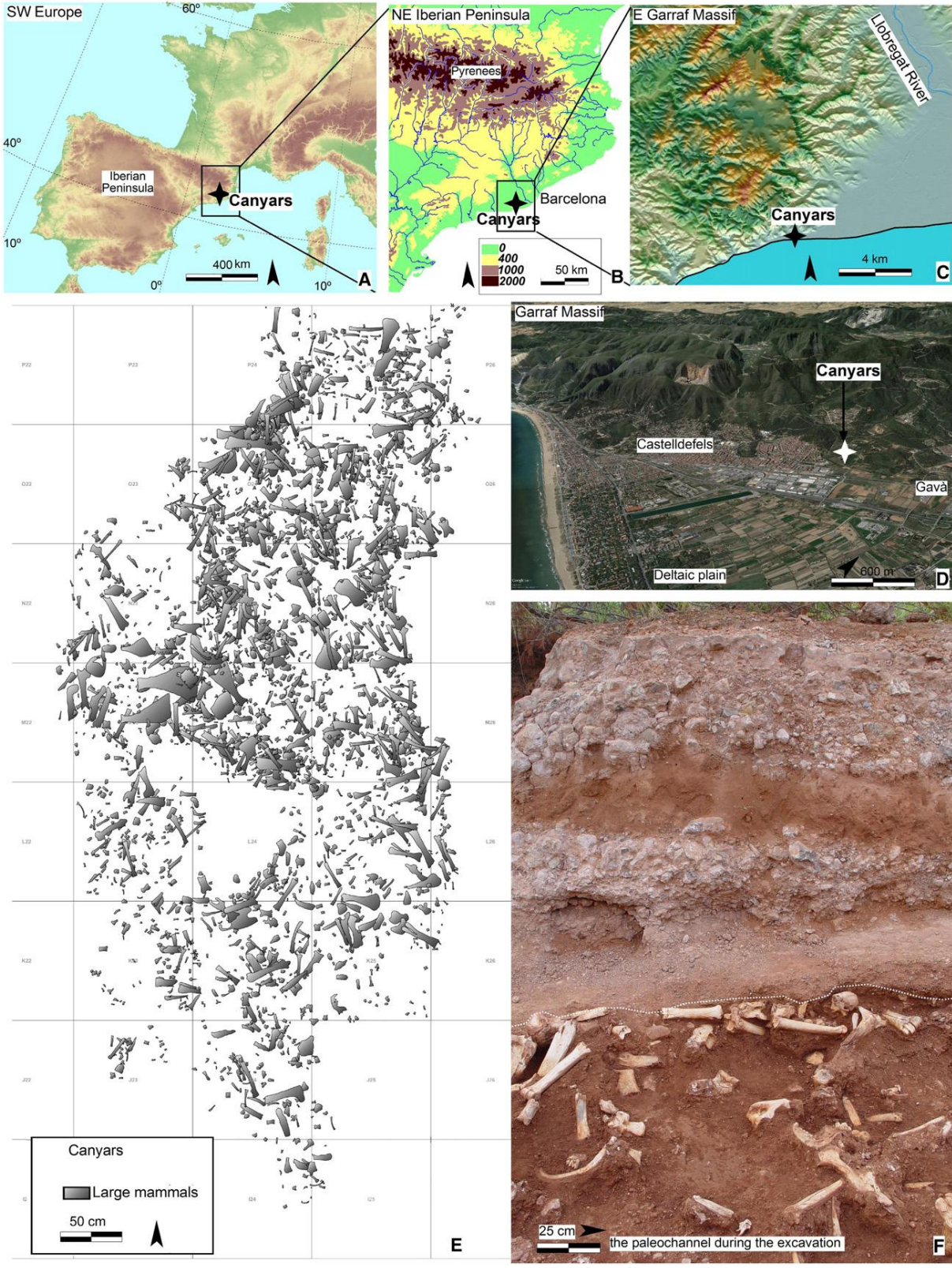


Fig. 1. A–C: Location of Terrasses de la Riera dels Canyars. D: Location of the site, view from the east. E: Distribution of the large mammal remains plotted against the excavation grid. F: Stratigraphic profile, at the base layer I.

The site corresponds to the terrace of the Canyars, a torrential stream, that formed part of fluvial terraces developed between the foot of the Garraf Massif and the Llobregat Delta that drained the slopes of the Garraf Massif into the beaches of the Mediterranean Sea (Fig. 1D). Canyars is located in an abandoned gravel pit, and was exposed during gravel quarrying activities. The locality was completely excavated during 2007, with the recovery of N5000 large mammal remains (Fig. 1E–F). The main area of the site was a surface of 12 × 6 m (Cala Arasa D). This is where the main paleochannel (~18 m<sup>2</sup>) was exposed and where most of the finds were located and these were contained in a single unit (layer I), dated to ~34.6 14C (~39.6 cal) kyr B.P. (Daura et al., 2013). This paleochannel was filled by a flash food event, that collected and preserved coeval elements (such as

ecofactual remains and lithics) and this site formation suggests a short-term accumulation for the remains, i.e. less than a millennium where bone and lithic surfaces were not altered by weathering or transport. Thus, Canyars ecofactual evidence serves as a proxy for determining synchronic diversity across the surroundings (Daura et al., 2013). The assemblage is mainly composed of large mammals (Table 1). The most abundant herbivores are the horses, mostly caballine horse (*Equus ferus*), followed by the large bovids (*Bos primigenius*), red deer (*Cervus elaphus*) and woolly rhinoceros (*Coelodonta antiquitatis*). Wild boar (*Sus scrofa*), ibex (*Capra pyrenaica*), and elephantids are present but with MNIs (Minimum Number of Individuals) of 1 in all cases. Among the carnivores, lynx (*Lynx pardinus*) and hyaena (*Crocuta crocuta*) are largely dominant. This large mammal fauna includes cold adapted taxa, such as the woolly rhinoceros (Daura et al., 2013). Other taxa, including small mammals (López-García et al., 2013), birds, and rabbits (Rosado-Méndez et al., 2015) are also recorded. Human presence is scarce and only documented by few stone-tools ascribed to the Upper Palaeolithic (Aurignacian) techno-complex.

Taphonomic analysis is still in process; however, some inferences can be drawn. For example, carnivores are the main biological agents responsible for the faunal accumulation at Canyars. The main carnivorous representative is the hyena, as determined by the presence of coprolites, the damage inflicted to ungulate bones and the hyena remains, with a high number of individuals (MNI= 13) and different skeletal portions preserved. The hyena is a bone collector and the mortality profile includes an

abundance of juveniles. These two facts suggest that Canyars was mainly a hyena den. The other relevant carnivore at the accumulation is the lynx, that also has a high number of individuals (MNI= 13)

and a good representation of the different body parts. Lynx could be mostly responsible for the accumulation of leporids (MNI = ~221) at the site (Rosado-Méndez et al., 2015) rather than for the accumulation of ungulates. The canids are represented by several individuals, such as the wolf (MNI=4) and the fox (MNI=3), but their role in the accumulation is unknown at the present state of our work. Finally, other carnivores are present in the assemblage by few skeletal elements and scarce individuals are present, such as other felids (lion, leopard and wildcat) and bears (Daura et al., 2013). The presence of these isolated remains together with scarce individuals could indicate a riverside thanatocoenosis, and therefore, should not be related to the accumulation of ungulates. Finally, the scarce human activities documented at the site are not relevant for large mammal accumulation, because no anthropogenic marks have been identified.

| Taxa                           | MNI | MNI% | Base of estimate |
|--------------------------------|-----|------|------------------|
| Artiodactyla                   |     |      |                  |
| <i>Bos primigenius</i>         | 18  | 30   | Metapodials      |
| <i>Capra pyrenaica</i>         | 1   | 2    | Dentition        |
| <i>Cervus elaphus</i>          | 7   | 11   | Metapodials      |
| <i>Sus scrofa</i>              | 1   | 2    | Dentition        |
| Perissodactyla                 |     |      |                  |
| <i>Coelodonta antiquitatis</i> | 2   | 3    | Astragali        |
| <i>Equus ferus</i>             | 27  | 44   | Metapodials      |
| <i>Equus hydruntinus</i>       | 4   | 7    | Metapodials      |
| Proboscidea                    |     |      |                  |
| <i>Cf. Mammuthus sp.</i>       | 1   | 2    | Postcrania       |
| Total                          | 61  | 100  |                  |

Table 1 Canyars herbivores and omnivores and their Minimum Number of Individuals (MNI) from Daura et al. (2013).

### 3. Material and methods

Dental specimens were studied through tooth mesowear and microwear analyses to assess dietary traits of herbivorous mammals. The two techniques provide dietary information on two different timescales: mesowear averages the diet over a few months (Fortelius and Solounias, 2000), while microwear reveals the diet in the last days of an animal's life (Grine, 1986). The remains analysed here were recovered during the 2007 field season at Canyars. All available upper and lower M2 were selected and molded, i.e. a total of 64 specimens. We sampled a number of teeth higher than the minimum number of individuals (MNI) based on teeth to maximize sample size after exclusion of the specimens belonging to the same individual and those not suitable because of taphonomic reasons.

### **3.1. Tooth mesowear**

Mesowear analysis, first introduced by Fortelius and Solounias (2000), 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 and abrasive dental wear. Mesowear is scored macroscopically from the buccal side of upper molars, preferably the paracone of M2 (Fortelius and Solounias, 2000). A diet with low levels of abrasion (high attrition) maintains sharpened apices on the buccal cusps as the tooth wears. In contrast, high levels of abrasion, associated with a diet of siliceous grass and/or a high rate of soil or dust particle, ingestion results in more rounded and blunted buccal cusp apices. However, recent work based on empirical results showed that mesowear is more likely to reflect grazing in particular rather than ingesting soil or dust (e.g., Kaiser et al. 2013, Kubo and Yamada 2014, Saarinen and Lister 2016). Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices are omitted from mesowear analyses. Cusp sharpness is sensitive to ontogenetic age among young individuals (who have not yet developed substantial wear facets) and among dentally senescent individuals. However, for intermediate age groups, which typically include the majority of individuals in a fossil collection, mesowear was found to be less sensitive to age and more strongly related to diet (Rivals et al., 2007a) and therefore suitable for dietary reconstruction. In this study, the standardized method (mesowear 'ruler') introduced by Muhlbachler et al. (2011) and modified by Rivals et al. (2013) is employed (Fig. 2). The method is based on seven cusp types (numbered from 0 to 6), 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 corresponds to the mesowear score (MWS) (Muhlbachler et al., 2011). For mesowear analysis, a total of 43 teeth were suitable: *Equus ferus* N = 26, *Bos primigenius* N = 9, *Cervus elaphus* N = 7, and *Capra pyrenaica* N=1.

### 3.2. Tooth microwear

Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following the cleansing, molding, casting, and examination protocol developed by

Solounias and Semprebon (2002) and Semprebon et al. (2004). In short, the occlusal surface of each specimen was cleaned using acetone and then 96% alcohol. The surface was molded using high-resolution silicone (vinylpolysiloxane) and casts were created using clear epoxy resin. All specimens molded 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). 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 in a square area of 0.16 mm<sup>2</sup> using an ocular reticule. We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004) as follows (Fig. 3A–D): pits (small and large pits, puncture pits), scratches (fine, coarse, hypercoarse), and gouges. 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. Large pits are deeper, less refractive (always dark), generally at least about twice the diameter of small pits, and often have less regular outlines than do small pits. Gouges are features which have ragged, irregular edges and are much larger (approximately 2–3 times as large)

and deeper than large pits. Cross scratches are oriented somewhat perpendicularly to the majority of scratches observed on tooth enamel (Solounias and Semprebon, 2002). In addition, scratch textures were assessed as being either fine (i.e., narrow scratches that appear relatively shallow and have low refractivity), coarse (i.e., wide scratches that are also relatively deep but have high refractivity (relatively shiny)), or a mixture per tooth surface reflecting the most common pattern seen on the two areas where counts were made. The scratch width score (SWS) is obtained by giving a score of '0' to teeth with predominantly fine scratches per tooth surface, '1' to those with a mixture of fine and coarse types of textures, and '2' to those with predominantly coarse scratches (Rivals et al., 2007b). Individual scores for a sample were then averaged to get the SWS. Scratches and pits were counted in two areas on the paracone of the upper molars or the protoconid of the lower molars. The results were compared with a database constructed from extant ungulate taxa (Solounias and Semprebon, 2002). Using average scratch and pit data, it is possible to discriminate between the dietary



categories of browser (i.e., eating woody and non-woody dicotyledonous plants) versus grazer (i.e., eating grass). Mixed feeding ungulates can best be separated from browsers or grazers by calculating the percentage of individuals in a population with scratch numbers that fall between 0 and 17 scratches in the 0.16 mm<sup>2</sup> area (%0–17) (Semprebon and Rivals, 2007). Thus, for extant ungulates, the percentages of individuals in the low-scratch range are generally as follows: grazers with 0.0–22.2% of scratches between 0 and 17; mixed feeders with 20.9–70.0% of scratches between 0 and 17; and leaf browsers with 72.7–100.0% of scratches between 0 and 17 (Semprebon and Rivals, 2007). A total of 43 tooth surfaces resulted suitable for microwear analysis: *Equus ferus* N = 26, *Bos primigenius* N=8, *Cervus elaphus* N = 8, and *Coelodonta antiquitatis* N=1.

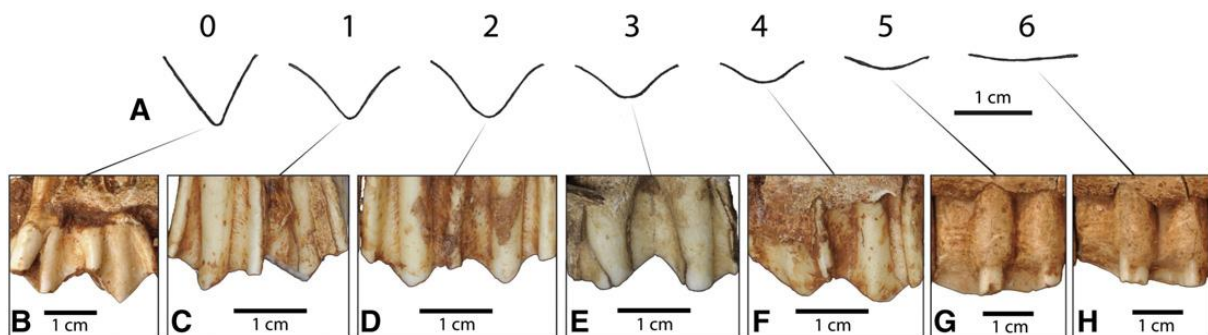


Fig. 2. A: Scale used to assess mesowear scores considering two variables: cusp relief and cusp shape (modified from Rivals et al., 2013). B–H: Examples of cusps corresponding to mesowear scores of 1 to 3 on upper molars of *Cervus elaphus* (B = Upper M2 Site Inventory # 3180), *Bos primigenius* (C = Upper M1 Site Inventory # 1908, D = Upper M2 Site Inventory # 1908, E=UpperM1 Site Inventory # 3446, F=Upper M3 Site Inventory # 1908), and *Equus ferus* (G=Upper M1 Site Inventory # 849, H=UpperM2 Site Inventory # 849).

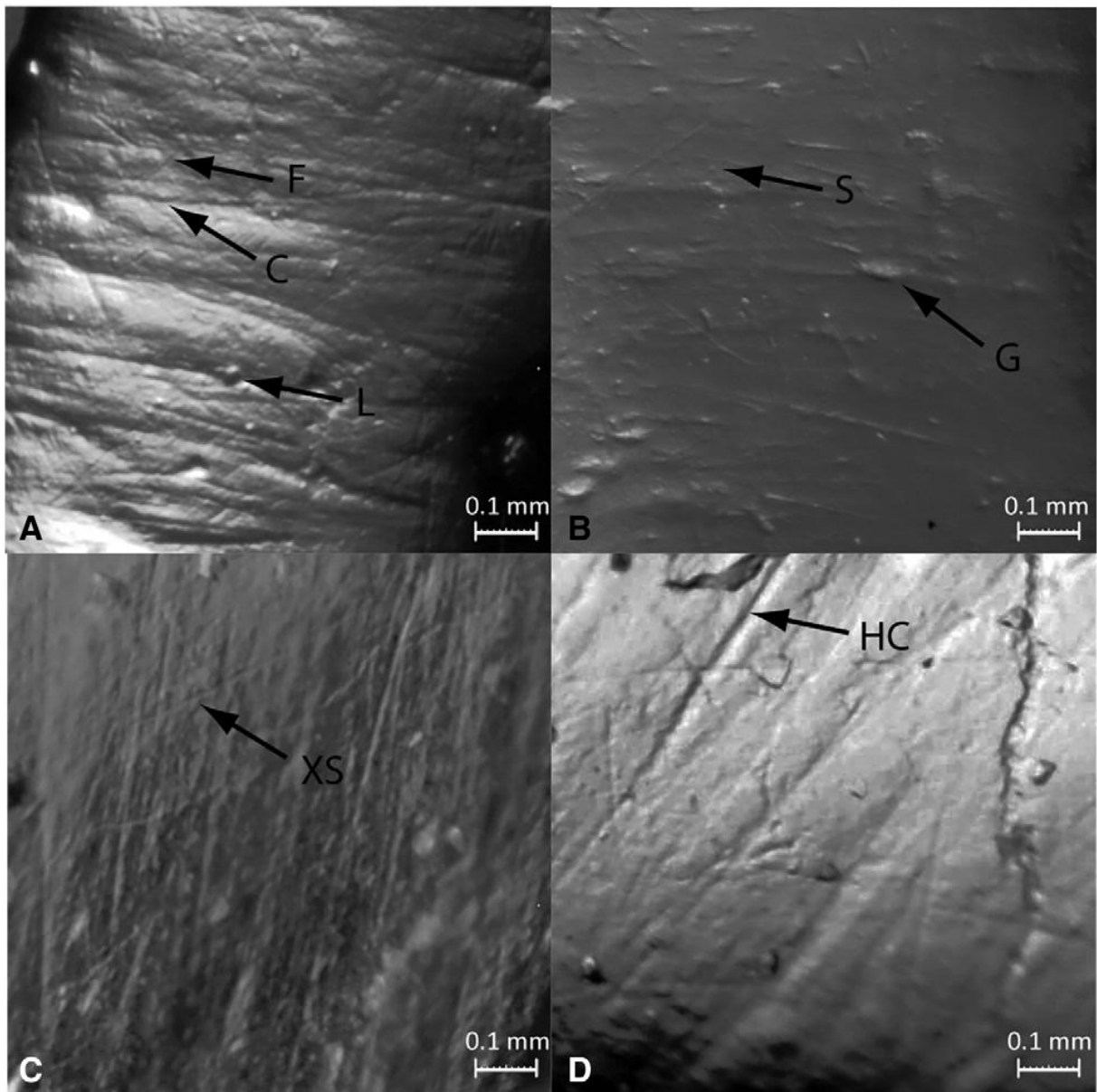


Fig. 3. Photomicrographs of selected fossil ungulate tooth enamel surfaces (35× magnification) from Terrasses de la Riera dels Canyars. (A) *Equus ferus* (Site Inventory # 5259) with fine and coarse scratches, (B) *Cervus elaphus* (Site Inventory # 825), (C) *Bos primigenius* (Site Inventory # 2619e) with mostly fine scratches, (D) *Coelodonta antiquitatis* (Site Inventory # 3979) with mostly coarse scratches. Scale bar = 0.1 mm. Scratches: fine (F), coarse (C), hypercoarse (HC), cross scratches (XS); Pits: small (S), large (L); Gouge (G).

#### 4. Results

From the five species analysed through tooth mesowear and microwear, three provided samples large enough to infer conclusions about the dietary traits (Table 2). The horse, *Equus ferus*, displays the highest mesowear value (MWS = 5.35), as well as the highest number of scratches (NS = 22.63)

and the lowest %0–17 (7.69%) (Fig. 3A). The two proxies indicate a grazing signal (Figs. 4 and 5), i.e. a diet based on highly abrasive plants. The values observed on the fossil horse indicate a stronger grazing signal

than in extant equids like the Plains zebra (*E. quagga*) or Grevy's zebra (*E. grevyi*) (Fig. 4).

The red deer, *Cervus elaphus*, has a low mesowear score (MWS = 1.57) with a variability spanning the values reported for extant mixed feeders, leaf browsers, and the lower range of the grazers (Fig. 4A). It indicates a mixed feeding diet which varies depending on the availability of vegetal resources in the environment. The microwear pattern (Fig. 3B), with a low number of scratches (NS = 14.25) and a high %0–17 (87.5%), suggest dietary habits based on browse at the time of death. Both mesowear and microwear signals are very similar to those of the extant red deer (Fig. 4). The aurochs, *Bos primigenius*, has an intermediate mesowear score (MWS = 2.67) with a variability (SD) spanning the values reported

for extant mixed feeders and the lower range of the grazers (Fig. 4). The microwear pattern, shows the lowest number of scratches (NS = 11.5) and the highest %0–17 (100%), suggests leaf browsing traits at

the time of death (Figs. 3C and 5). Interestingly there is no overlap in the microwear values for the red

deer and the aurochs. Both fall among the extant leaf browsers, but their numbers of pits and scratches differ significantly (Fig. 5). The red deer has slightly more scratches than the aurochs, but also definitely more pits. The red deer is also characterized by more proportion of large pits and gouges, and wider scratches (higher SWS) (Table 2). This would indicate the consumption of dust or grit present on the leaves in dry conditions (Semprebon and Rivals, 2007) or the consumption of bark from small branches and twigs. Despite the same mesowear signal, *Bos primigenius* and *Cervus elaphus* might not have been competitors and they might have consumed different kinds of food resources. The last two species, the woolly rhino *Coelodonta antiquitatis* and the Spanish ibex *Capra pyrenaica* are only represented with samples from a single individual (Table 2). The two individuals might be mixed feeders, but the sample size is too small to allow for a definite conclusion to be made regarding their dietary traits.

For a better interpretation of the distribution of individuals' data among the community, we took into account the MNI for the largest samples that provided definite dietary interpretations i.e. horse, red deer, aurochs. We used the mesowear results because they are less sensitive to seasonal shifts than microwear (Rivals and Semprebon, 2006). Considering each specimen and grouping individuals of each species according to their general dietary traits (Table 3) we determined that 69.0% of the community of ungulates is made of grazers, 28.6% of mixed feeders, and only 2.4% of browsers.

| Taxon                          |    | Mesowear |      | Microwear |       |       |      |      |      |     |      |       |
|--------------------------------|----|----------|------|-----------|-------|-------|------|------|------|-----|------|-------|
|                                |    | N        | MWS  | N         | NP    | NS    | %LP  | %XS  | SWS  | %G  | %HC  | %0-17 |
| <i>Equus ferus</i>             | M  | 26       | 5.35 | 26        | 16.75 | 22.63 | 19.2 | 96.2 | 0.92 | 3.8 | 0    | 7.7   |
|                                | SD |          | 0.63 |           | 3.89  | 3.64  |      |      |      |     |      |       |
|                                | CV |          | 0.12 |           | 0.23  | 0.16  |      |      |      |     |      |       |
| <i>Cervus elaphus</i>          | M  | 7        | 1.57 | 8         | 34.31 | 14.25 | 0.4  | 25   | 1.25 | 25  | 0    | 87.5  |
|                                | SD |          | 1.27 |           | 6.79  | 2.55  |      |      |      |     |      |       |
|                                | CV |          | 0.81 |           | 0.20  | 0.18  |      |      |      |     |      |       |
| <i>Bos primigenius</i>         | M  | 9        | 2.67 | 8         | 23.38 | 11.50 | 0    | 100  | 0.88 | 100 | 12.5 | 100   |
|                                | SD |          | 0.71 |           | 2.88  | 2.63  |      |      |      |     |      |       |
|                                | CV |          | 0.27 |           | 0.12  | 0.23  |      |      |      |     |      |       |
| <i>Capra pyrenaica</i>         |    | 1        | 2    |           |       |       |      |      |      |     |      |       |
| <i>Coelodonta antiquitatis</i> |    |          |      | 1         | 24    | 19    | 0    | 100  | 1    | 100 | 0    |       |

Table 2 Summary of mesowear and microwear data for the fossil ungulates from Canyars. 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; %HC = percentage of specimens with hypercoarse scratches; %0-17= percentage of specimens with 17 or less scratches per counting area. M = average; SD= standard deviation; CV= coefficient of variation.

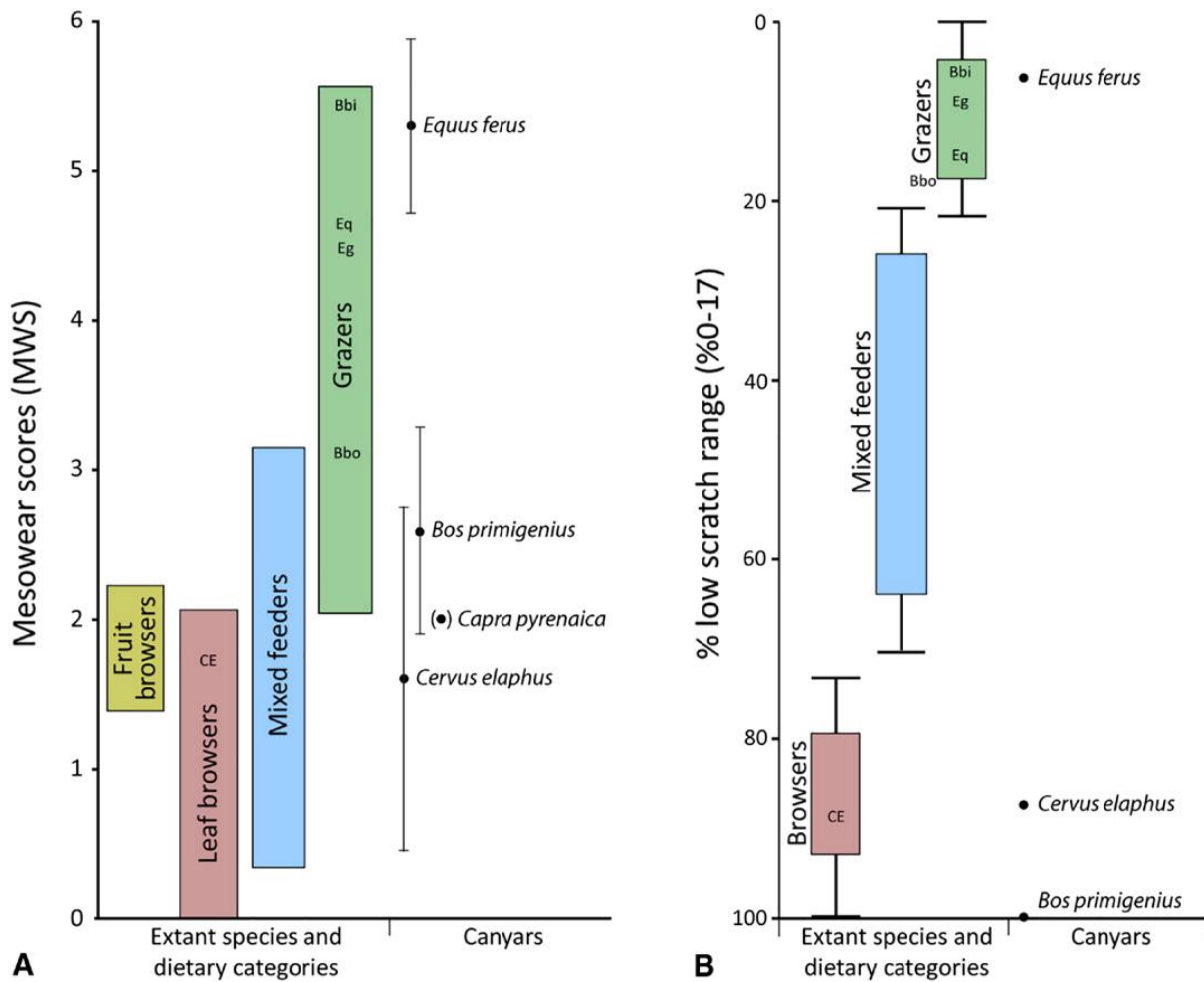


Fig. 4. Mesowear (A) and microwear (B) results for the ungulates fromCanyars (this study) and extant ungulates (fromFortelius and Solounias (2000), Solounias and Semprebon (2002), Rivals et al. (2010, 2014)). Abbreviations for extant ungulates: Bbi=Bison bison; Bbo=Bison bonasus; CE=Cervus elaphus; Eq=Equus quagga; Eg=Equus grevyi. Error bars correspond to standard deviation ( $\pm 1$  S.D.) for the fossil samples.

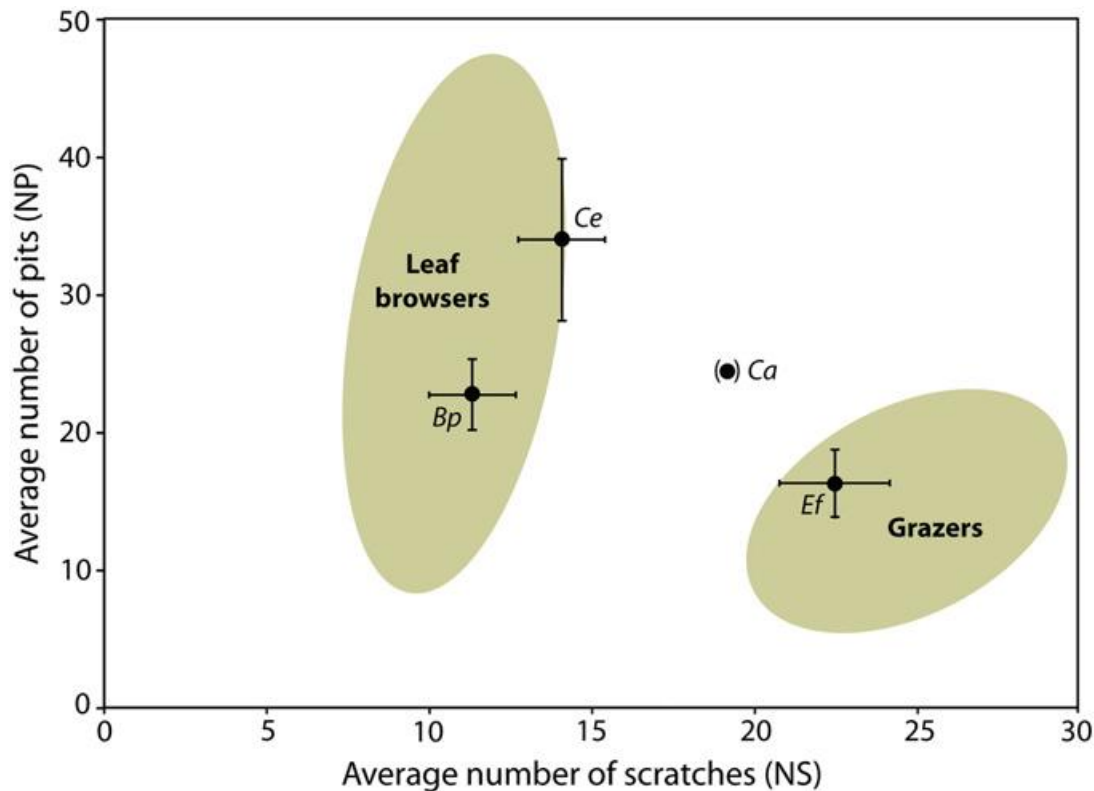


Fig. 5. Bivariate plot of the average numbers of pits and scratches in the fossil ungulates from Canyars. Error bars correspond to standard deviation ( $\pm 1$  S.D.) for the fossil samples. Plain ellipses correspond to the Gaussian confidence ellipses ( $p = 0.95$ ) on the centroid for the extant leaf browsers (B) and grazers (G) from Solounias and Semprebon (2002). Abbreviations: Bp = Bos primigenius; Ca=Coelodonta antiquitatis; Ce=Cervus elaphus; Ef = Equus ferus.

## 5. Discussion

### 5.1. Dietary traits of the Canyars ungulates

Based on the chronological approach and several taphonomical aspects, the site formation process and the burial of the Canyars assemblage was probably rapid (Daura et al., 2013). According to this result,

palaeobotanical evidence and faunal spectrum should both represent synchronic variation across the landscape rather than diachronic change in local conditions. Thus, the dental wear signal recorded on the teeth of the Canyars ungulates provides a good opportunity to evaluate the paleoenvironmental context and the faunal dietary changes during the HE4 in southwestern Europe. Tooth mesowear shows that the most abundant taxon in the assemblage, the horse, is likely a grazer. The aurochs show less grazing than horses and mesowear and microwear values reported are relatively lower. The red deer show mixed feeding traits. Although *Capra pyrenaica* is only represented by one sample, it is notable that their mixed feeding traits are closer to the red deer and are at the limit between the pure browsers and grazers. The composition of the ungulate community analysed (MNI = 42) shows a dominance of grazers which represent 69% of the ungulates (MNI = 29) present. The mixed feeders, (i.e., forms that alternate between grazing and browsing), correspond to 28.6% of the assemblage (NMI=12). Finally, the leaf browsers represent only 2.4% of the assemblage (NMI = 1). Thus, based on the dental wear results, the environment of the site was most likely mainly an open landscape. By contrast, nowadays the region occupies the meso- and thermo-Mediterranean environment, composed mainly of the Mediterranean maquis shrubland, with a high density of evergreen shrubs, and forests with sclerophyll vegetation to endure the dry season. A remarkable change in diet is shown by microwear results. Except

the horse, with values corresponding to grazing traits, the aurochs and the red deer show leaf browsing habits at the time before their death. This difference between the interpretation of the meso- and microwear results could be related to seasonality in feeding behaviour (Sánchez-Hernández et al., 2016). Furthermore, the leaf-browsing component observed in the red deer and to a lesser extent in aurochs requires the presence of trees or bushes in some areas near the site. The vegetation data available for this site (Daura et al., 2013) shows an abundant supply of heath and grassland communities, but arboreal taxa, such as *Pinus sylvestris* and other mesophilous taxa related to riparian areas are also present. However, a seasonality component is shown by the pollen trapped within the coprolites, with the dominance of two taxa, (1) an arboreal coverage of *Pinus sylvestris* and (2) the non-arboreal pollen of *Artemisia*. According to these data, as well as the dental wear, a seasonal mixed feeding habit could be suggested for aurochs based on the biomass of leaves, i.e., pine leaves are not a supply resource for aurochs and other plant taxa with edible leaves are scarce in the pollen record (e.g., *Quercus* or *Acer*). Such feeding seasonality has also been documented in historical times when aurochs were shown to be mainly grazers, but switched to leaf consumers during autumn-winter (Van

Vuure, 2002). Moreover, this dietary response suggests that the death of aurochs and red deer occurred during the same season. In general, the habitats dominated by large bovids and equids provide a high ungulate biomass, such as in the Canyars assemblage where these two species

represent 74% of the MNI for ungulate taxa. Thus, following Discamps (2014) and based on MNI values (Table 1),

we estimated the ungulate biomass index for the Canyars assemblage. The Canyars ungulate biomass index = 0.8. This value is closer to the index for actual grasslands (index = 1) with a biomass higher than

3 ton/km<sup>2</sup>, than to the value for forest and tundra biomes (index = 0) with a biomass lower than 1 ton/km<sup>2</sup>. This implies a vegetation capable of supporting and feeding large herbivores, and the cold-adapted fauna documented at the site such as woolly rhinoceros and possibly mammoth.

|                        | Leaf browsers | Mixed feeders | Grazers |
|------------------------|---------------|---------------|---------|
| <i>Equus ferus</i>     |               |               | 26      |
| <i>Cervus elaphus</i>  | 1             | 5             | 1       |
| <i>Bos primigenius</i> |               | 7             | 2       |
| Total                  | 1             | 12            | 29      |
|                        | 2.4%          | 28.6%         | 69.0%   |

Table 3 Distribution of the individuals among the three dietary categories according tomesowear analysis.

## 5.2. Implications for HE4 palaeoenvironmental reconstruction

Nowadays, the palaeoenvironmental conditions and the landmass in this area are not enough to sustain a biocenosis similar to the Canyars assemblage. The extant vegetation is composed mainly by Mediterranean maquis and evergreen trees. The littoral plain area to the Llobregat River is reduced (45 km<sup>2</sup>) and is limited to the north by the Garraf Massif and to the south by the sea, at ~3.5 km from the Canyars site. The conditions required by the Canyars faunal assemblage were only possible because of the climatic conditions during the Last Glacial period and mainly reinforced by Heinrich Event cycles. During this period, the sea-level fluctuations of the Mediterranean sea (Rabineau et al., 2006) and the sea topography (Marina, 2010) caused the emergence of a littoral platform of b10 km from the site with an elevation of b100m – creating a most favourable geographical setting. Today this littoral area is covered by Mediterranean vegetation but the results from our dental wear analysis imply that during HE4, the coastal landmass was mainly covered by grasslands where most of the ungulates were feeding. This type of vegetation implies harsh conditions and low values of annual precipitation. This is in agreement with the data from a study of small vertebrates (Daura et al., 2013; López-García et al., 2013) which indicates precipitation of about 99mm and a mean temperature of -6 °C (coldest month). It is also reinforced by the presence of E.

hydruntinus which is adapted to semi-arid conditions (Burke et al., 2003). However, the seasonal changes in feeding for the aurochs on shrublands and leaves points also to the presence of mesophile and deciduous trees, suggesting relative humidity, maybe restricted to the riparian areas, and signalling also a temperate component.

This is supported by the reconstruction of the paleovegetation which shows the presence of arboreal taxa, such as *Pinus sylvestris* and other mesophilous taxa (Daura et al., 2013). Thus, the biotope existing in the lowlands of the northeastern part of the Iberian Peninsula during the HE4 was characterized by a rigorous climate with arid conditions and with open-meadows, heaths and a secondary presence of trees, mainly deciduous, capable of feeding the high ungulate biomass shown in Canyars.

## **6. Conclusions**

The dietary traits of the ungulates observed in the Canyars assemblage are relevant for illustrating their feeding behaviour as well as the likely climatic conditions during the time of the arrival of the early

modern Europeans in the northeast of the Iberian Peninsula. A rigorous climate is noticeable, with the presence of grasslands capable of sustaining a high ungulate biomass. It is striking that dietary adaptations to grazing dominate the ungulate community, including the totality of horses and some of the red deer, aurochs, and ibex. This is because aurochs in the HE4 of this area demonstrate a dietary response to seasonal changes in vegetation, i.e. a decrease in foraging on grass or an increase of the ungulate's density leading to resource partitioning and feeding on other resources, such as leaves or woody vegetation. The paleoenvironmental data derived from this study denotes open meadows, as shown by the dietary traits of the ungulates resulting in a harsh and cold climate representative of the HE4. However, a secondary presence of mesophilous and deciduous trees with humid requirements

is evidenced by the dietary change denoted by the aurochs indicating a temperate component for this biome. The humidity requirements of these trees and vegetation could be restricted to the riparian areas. The composition of the Canyars ungulate community and its dietary adaptations clearly reveals some particularity of the HE4 in the northeast of the Iberian Peninsula.

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