



The role of climate change in the extinction of the last wild equids of Europe: Palaeoecology of *Equus ferus* and *Equus hydruntinus* during the Last Glacial Period

Flavia Strani^{a,b,*}, Daniel DeMiguel^{c,a,d}

^a Departamento de Ciencias de La Tierra, Universidad de Zaragoza, 50009 Zaragoza, Spain

^b Dipartimento di Scienze della Terra, Sapienza - Università di Roma, 00185 Rome, Italy

^c ARAID Foundation, Universidad de Zaragoza, 50009 Zaragoza, Spain

^d Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Spain

ARTICLE INFO

Keywords:

Palaeoenvironment
Equid Ecology
Dental mesowear
Dental microwear
Pleistocene
LGP

ABSTRACT

The last European wild equids —*Equus ferus* and *Equus hydruntinus*— were among the large mammals (or megafauna) that became extinct during the Late Quaternary Extinction Event disappearing from Europe during the Holocene. The role that the combined action of the major climatic changes of the Pleistocene/Holocene Transition and the human activities played in their extinction is not fully understood. The reduction of steppe-like biomes in Europe following the increase of mean global temperatures during the Holocene is usually regarded as the main event that triggered their disappearance, as both equids display typical morphological adaptations for open grasslands and grass eating. However, *E. ferus* and *E. hydruntinus* are found, often even co-occurring, in both warm and cold phases of the Late Pleistocene. Thus, the investigation of their niche occupation can help decipher whether their ecology and specialised dietary adaptations were the main reason of their decline following the early Holocene global warming. Here we investigate the feeding strategies of the two equids by studying their long- and short-term dietary adaptations through examination of their patterns of dental wear. As expected, dental mesowear points to a highly abrasive diet concordant with a grazing feeding behaviour for both *E. ferus* and *E. hydruntinus* which is consistent with their specialised morphological adaptations for open habitats. In contrast, dental microwear suggests a somewhat degree of plasticity in diets, as both species display microscopic features commonly recorded in modern mixed feeders. Such a flexibility may be the reason for which they could have persisted even when open grasslands were not the dominant landscape. Our findings provide a new line of evidence supporting the idea that human activities (e.g., competition with the first domestic forms brought from Eurasia and Africa) may have played a larger role in the extinction of some megafauna groups than climate change per se.

1. Introduction

The Late Quaternary Extinction (LQE) event led to the worldwide disappearance of several megafaunal mammal species (Koch and Barnosky, 2006). Multiple explanations have been proposed, suggesting that environmental changes at the end of the last Pleistocene glaciation, human activity, or a combination of both, played a crucial role in this loss of biodiversity (Barnosky et al., 2004; Koch and Barnosky, 2006; Faith and Surovell, 2009; Lyons et al., 2016). In the European continent, this extinction event did not occur uniformly due to the presence of several habitat refugia which allowed some large mammals (e.g., woolly

mammoths) to persist into the Holocene in fragmented or isolated populations (Guthrie, 2004). Among these, wild horses (*Equus ferus*) and the hydruntine or European wild ass (*Equus hydruntinus*) survived until the mid-late Holocene when they disappear from both fossil and archeological records (Boulbes and Van Asperen, 2019). The decline and eventual disappearance of these last wild equids in Europe is usually associated with the reduction of steppe biomes due to the development of warmer conditions after the Pleistocene/Holocene Transition, as well as to the arrival of domestic forms brought by human populations from Western Eurasia and Africa (Kimura et al., 2010; Crees and Turvey, 2014; Boulbes and Van Asperen, 2019; Librado et al., 2021).

* Corresponding author at: Departamento de Ciencias de La Tierra, Universidad de Zaragoza, 50009 Zaragoza, Spain.

E-mail address: flavia.strani@unizar.es (F. Strani).

<https://doi.org/10.1016/j.palaeo.2023.111564>

Received 13 March 2023; Received in revised form 11 April 2023; Accepted 11 April 2023

Available online 13 April 2023

0031-0182/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

According to palaeogenetic data (Bennett et al., 2017), *E. hydruntinus* became extinct in Europe during the Bronze Age while the tempo and mode of the extinction of *E. ferus* is still unclear with genetic data suggesting a substitution by domestic horses (*E. caballus*) which spread from Western Eurasian steppes around 2200–2000 BCE (Librado et al., 2021).

There are several hypotheses on the primary role of climate change or human activities (hunting, domestication, overkill) or both on the extinction of the European megafauna during the late Quaternary (Stuart, 2014). Due to morphological adaptations to live in open grasslands and grass eating (i.e., hypsodont dentition, cursorial locomotion), it is assumed that the raise in global mean temperatures after the Last Glacial Maximum with the subsequent reduction of dry and cold grasslands, was the main trigger leading to the extinction of wild equids (Boulbes and Van Asperen, 2019). Both *E. hydruntinus* and *E. ferus* are, however, consistently recorded (or even associated) in several Middle and Late Pleistocene localities also during warm interglacial phases (Rivals et al., 2009; Boulbes and Van Asperen, 2019; Sánchez-Hernández et al., 2020; Mecozzi and Strani, 2022). Understanding the palaeoecological adaptations of these equids and how they exploited available plant resources emerges, therefore, as crucial to shed light on the role played by climatic and environmental changes in their disappearance in Europe.

Dietary behaviour of fossil species can be inferred from different proxies; specifically dental wear patterns provide data on the direct effects of ingested items (e.g., food, dust, grit) produced over a long (mesowear) or short (microwear) period on tooth morphology (Fortelius and Solounias, 2000; Solounias and Semperebon, 2002). Both dental meso- and microwear patterns are thus strongly linked to feeding

preferences and can provide information on fossil taxa niche occupation.

The Late Pleistocene Iberian locality of La Carihuela (Granada, Spain) yielded a rich collection of *E. ferus* and *E. hydruntinus* fossil material dated during the Last Glacial Period (LGP) which is comprised of several dentognathic remains. By analysing dental wear patterns which records two different timeframes, it is possible to investigate whether these equids exhibited a pure grazing behaviour or, instead, displayed a more flexible diet which may have allowed them to adapt even to less favorable landscapes due to climatic shifts.

2. Material and methods

2.1. Carihuela Cave

Carihuela Cave is one of several caves located 45 km northeast of Granada (Andalusia, southern Spain) in the Píñar river valley (Fig. 1). The cave is comprised of six chambers which have been excavated since the 1950s (Spahni, 1955) unearthing a rich Late Pleistocene and Holocene archaeo-palaeontological collection consisting of lithic artifacts and fossil vertebrates (also recording human remains belonging to both Neanderthals and anatomically modern *Homo*) (García-Sánchez, 1960; Vega-Toscano et al., 1988). The cave has been divided into twelve Lithostratigraphic Units dated between 117 ± 41 ka and 1250 ± 60 years (Vega-Toscano et al., 1988; Fernández et al., 2007 and references therein) which have yielded several mammal remains, among which those of wild horses and hydruntines are especially abundant (Fernández et al., 2007; Samper Carro, 2010; Nacarino-Meneses et al., 2017).

No information is available about the exact stratigraphic position of

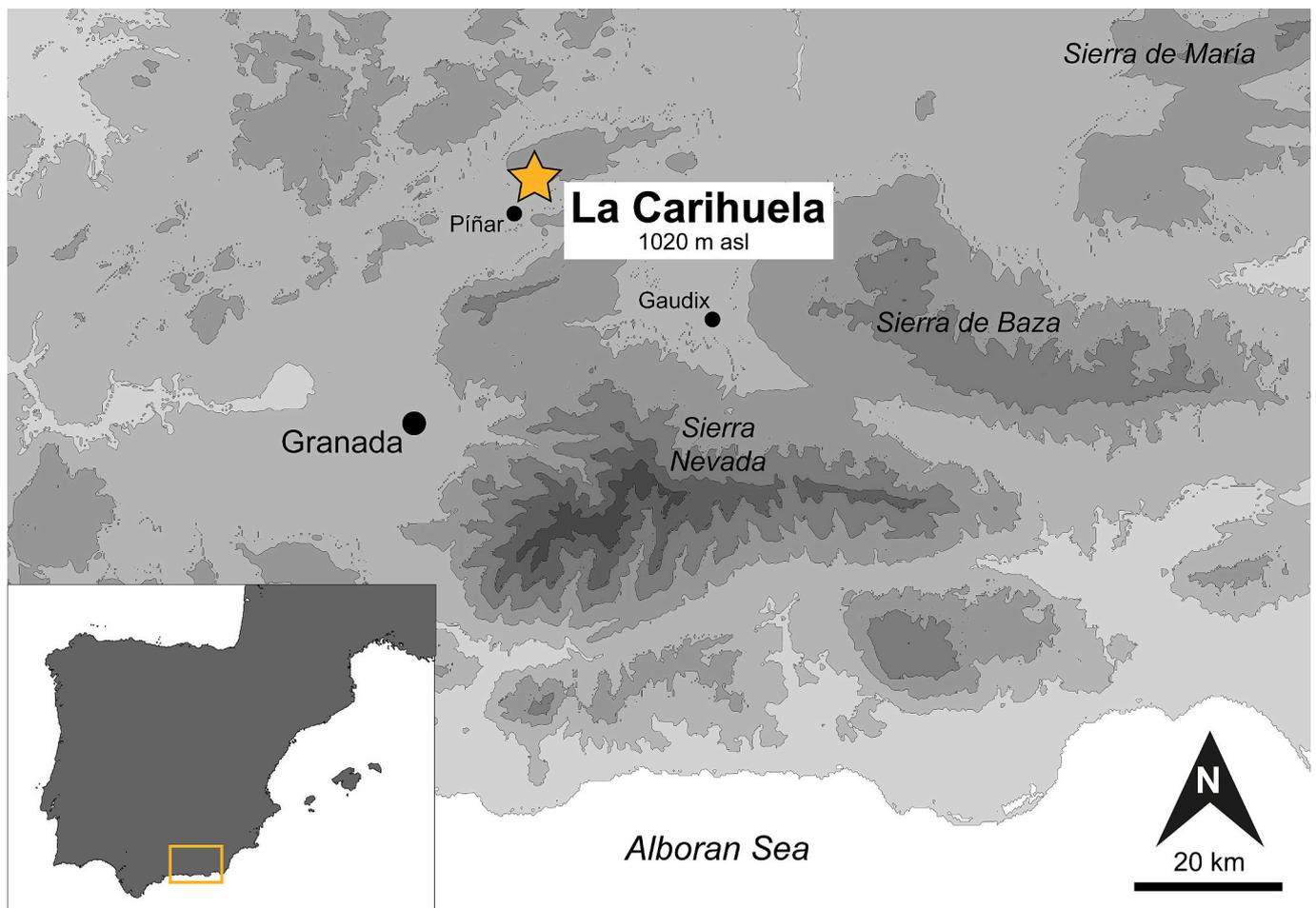


Fig. 1. La Carihuela geographical location (approximate coordinates: 37°26'56" N, 3°25'47" W). Map generated from contours.axismaps.com. Contour interval: 500 m.

the equid fossil material examined in the present study, however, Fernández et al. (2007) and Samper Carro (2010) report that the material of *E. ferus* (= *E. caballus* cf. *germanicus* in Fernández et al., 2007) and *E. hydruntinus* (Samper Carro, 2010) has been collected from Units X–VI, dated using thermoluminescence approaches approximately between 70 and 37 ka (Vega-Toscano et al., 1988; Fernández et al., 2007 and references therein) (Fig. 2). The material is currently stored at the Museum of the Institut Català de Paleontologia Miquel Crusafont (ICP, Sabadell).

2.2. Dental mesowear

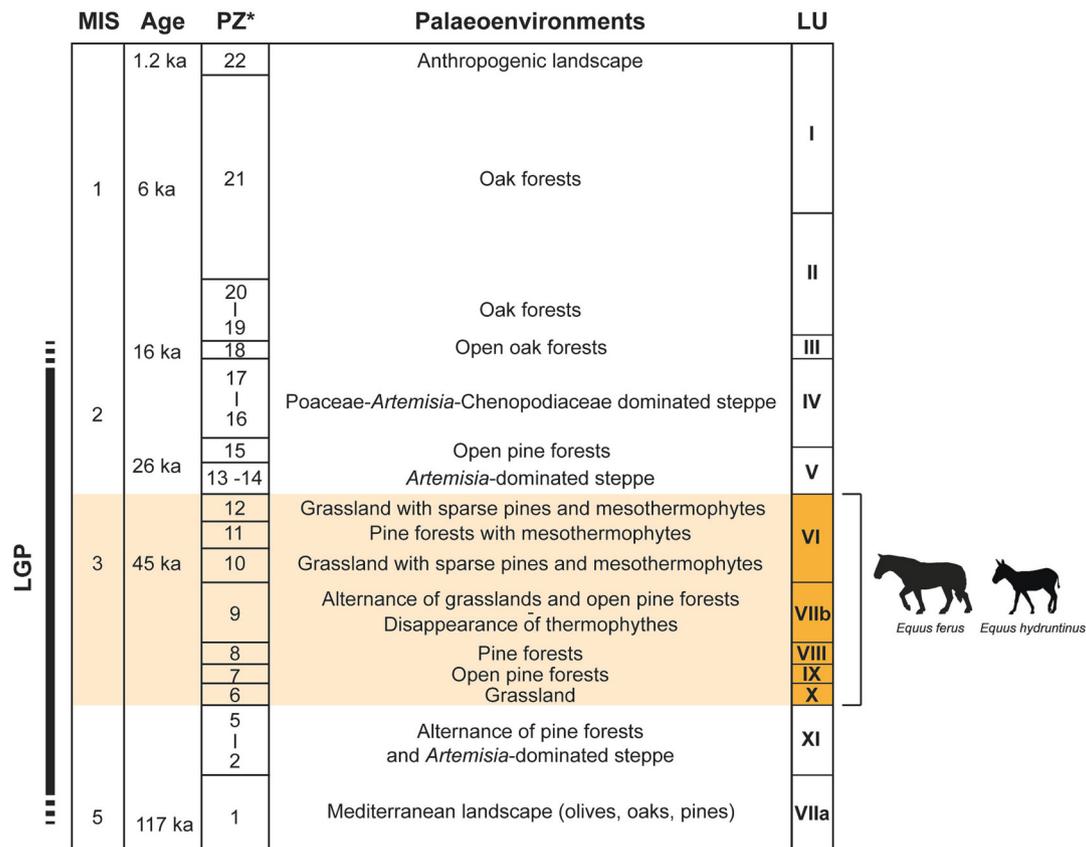
For herbivorous ungulates, dental mesowear is a direct signal of a species’s diet representing the cumulative effects of ingested items on the dental surface that are produced over a long period of time compared to the lifespan of the animal (years or months; Fortelius and Solounias, 2000; Strani et al., 2018a, 2018b, 2019a). Attrition (tooth-to-tooth contact) and abrasion (tooth-to-food contact) are the main factors that determine the tooth wear. High levels of attrition produce sharper cusps and a higher dental occlusal relief, while high levels of abrasion lead to blunter cusps and low occlusal relief. Modern ungulates which feed on soft plant resources (e.g., leaves, twigs, fruits, buds) usually display higher levels of attrition while grazing animals whose diet is comprised mostly of grasses, show a higher degree of abrasion due to abrasive silica contents present in monocotyledonous plants (phytoliths) (Fortelius and Solounias, 2000). The effects of other particles ingested while feeding at ground level (e.g., dust or grit) may also influence the tooth wear (Kaiser et al., 2009) although it has been observed that some ruminants are capable of “washing away” exogenous particles in the rumen and then

chewing on a “clean” bolus (Ackermans et al., 2018).

In this study, the traditional mesowear analysis originally limited to upper second molars (M2) described by Fortelius and Solounias (2000) was extended to the whole upper molar row (M1-M3) and to the upper fourth premolar (P4) following Kaiser and Solounias (2003) and DeMiguel et al. (2012). Occlusal relief (high or low) and cusp shape (sharp, rounded, or blunt) of the apex of the paracone or metacone were examined and converted to a single mesowear score (MWS) following the “mesowear ruler” developed for scoring dental mesowear on fossil equids by Mühlbachler et al. (2011). 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). Additionally, a “stage 7” is given to teeth with a convex cusp apex. Of a total of 117 teeth, 85 specimens were scored using this method (*Equus ferus* N = 72; *Equus hydruntinus* N = 13). Teeth belonging to either juvenile or old individuals were excluded from this analysis as mesowear is sensitive to the ontogenic age of the animals (Fortelius and Solounias, 2000). Raw mesowear data are provided as Supplementary Information (Table S1).

2.3. Dental microwear

Food and other material consumed during the last few days prior to the death of an animal, leave microscopic patterns on tooth surfaces which are produced during the mastication process, recording the so-called “last supper effect” (Grine, 1986; Strani et al., 2018c). These microwear features were examined following the standard protocol developed by Solounias and Semprebon (2002). Teeth were cleaned with acetone and alcohol, moulded with high-resolution silicone (vinylpolysiloxane) and casts were created using clear epoxy resin. Casts



*from Fernández et al. (2007)

Fig. 2. Chronostratigraphy and lithostratigraphy of La Carihuela with correlated vegetation information (modified from Fernández et al., 2007). Highlighted: units where *Equus ferus* and *Equus hydruntinus* fossil remains have been recovered (from Fernández et al., 2007 and Samper Carro, 2010). Abbreviations: Lithostratigraphic Units (LU), Pollen Zones (PZ). Silhouette image of *E. ferus* by Flavia Strani, silhouette image of *E. hydruntinus* from PhyloPic.org (Public Domain).

were then examined with a stereomicroscope equipped with a camera (Leica S9i) under incident light to reveal microfeatures on the enamel. Specimens displaying badly preserved enamel, taphonomic distortions or major post-mortem alterations (e.g., fresh features made during the collecting or storing process) were excluded from the analysis following King et al. (1999) and Weber et al. (2021). Of a total of 117 teeth, 42 specimens (*Equus ferus* $N = 27$; *Equus hydruntinus* $N = 15$) were suitable for this analysis.

Upper molars (M1–M3) and fourth upper premolars (P4) were selected for this analysis as they are the ones more involved in the mastication process. Second upper molars (M2) were preferably selected. The anterior lingual blade of the paracone of upper cheek teeth and the posterior buccal blade of the protoconid of lower molars was preferably sampled. If badly preserved, other facets were selected. Following Solounias and Semprebón (2002), microwear features were observed at $35\times$ magnification (Fig. 3), quantified in a standard square area of 0.16 mm^2 and divided into five categories: small pits, large pits, fine scratches, coarse scratches, and gouges and also recording the presence of cross scratches. The IC Measure software (ver. 2.0.0.286; The Imaging Source Europe GmbH) was used to record microwear features.

Mean number of scratches and mean number of pits can be used to discriminate between herbivorous ungulates with a browsing (i.e., animals feeding mostly on ligneous plant parts, bushes, leaves, and fruits), grazing (i.e., animals feeding mostly on grasses), or mixed (i.e., animals feeding on both food types) diet (Solounias and Semprebón, 2002; DeMiguel et al., 2008; DeMiguel et al., 2010). The percentage of individuals with scratch numbers falling in a low scratch range (%0–17) has also been used to discriminate browsers, grazers, and mixed feeders

(Semprebón and Rivals, 2007). In extant ungulates, grazers have 0.0–22.2% of individuals with scratches between 0 and 17, mixed feeders have 20.9–70.0% of individuals with scratches between 0 and 17, and leaf-dominated browsers have 72.7–100.0% of individuals with scratches between 0 and 17 (Semprebón and Rivals, 2007). Scratch textures were also converted into a Scratch Width Score (SWS) to simplify representation of the data: '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. Individual scores for a sample were then averaged to get the SWS and compared to data of extant taxa (data from Rivals, 2012 and references therein). Raw microwear data are provided as Supplementary Information (Table S2).

2.4. Statistical analysis

Discriminant analyses were performed to examine the resolution of both mesowear and microwear variables applied to the fossil taxa. For the mesowear analysis, the percentages of high relief, rounded and blunt cusps were used as independent variables and two dietary (conservative and radical) classifications were used as grouping variables (Fortelius and Solounias, 2000). For microwear, 1) average number of pits, 2) average number of scratches, 3) percentage of individuals with predominantly fine scratches, 4) percentage of individuals with predominantly coarse scratches, 5) percentage of individuals with a mixture of fine and coarse scratches, 6) percentage of individuals with >4 large pits, 7) percentage of individuals with >4 cross scratches, and 8) the percentage of individuals displaying gouges, were selected as independent variables and dietary classifications of modern taxa (modified from

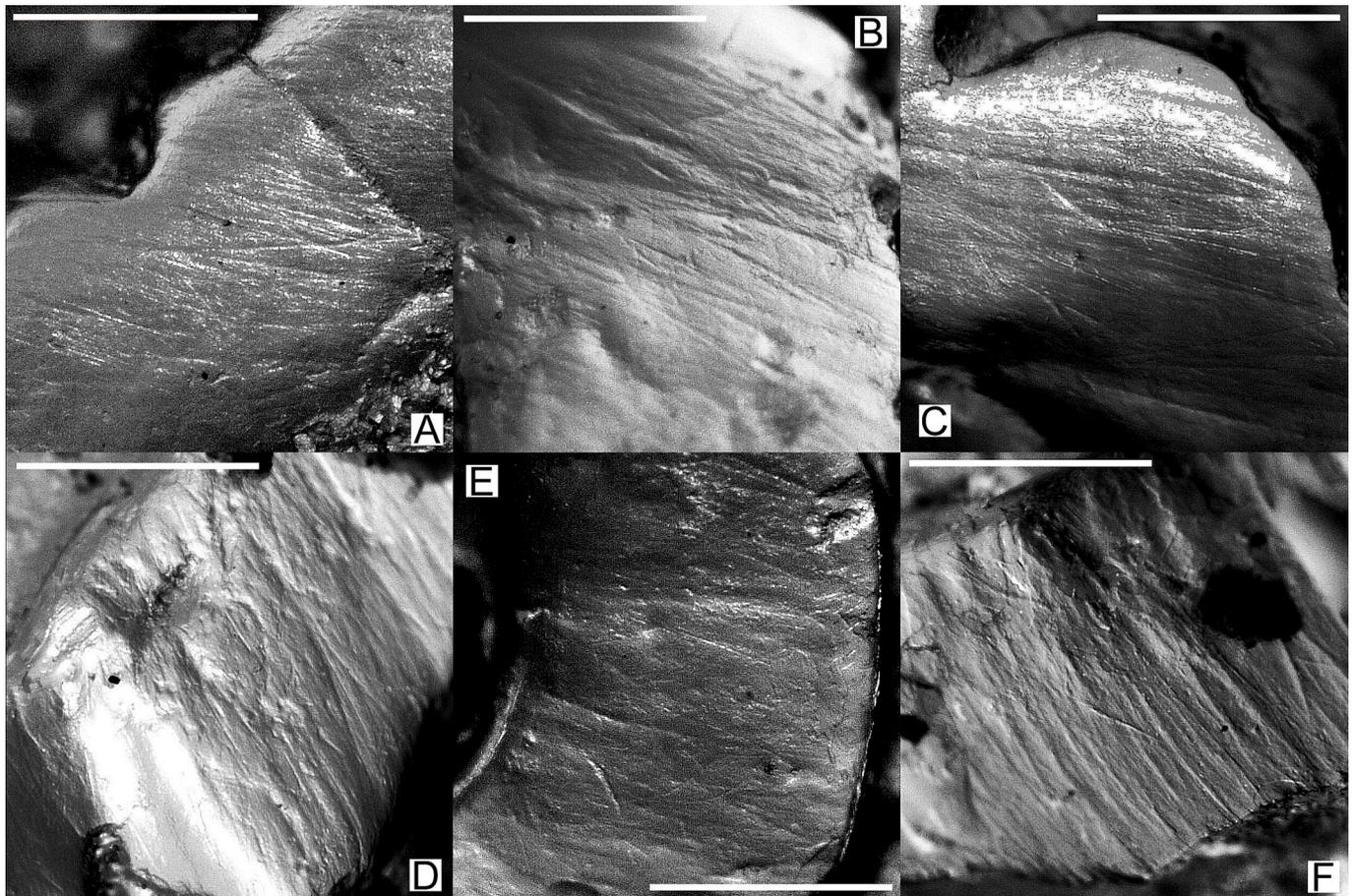


Fig. 3. Photomicrographs of enamel surfaces at $35\times$ magnification of selected teeth. *Equus ferus*: (A), specimen 54, left M1/M2; (B), specimen 77, right P4; and (C), specimen 59, right M1/M2. *Equus hydruntinus*: (D), specimen 10b, right M2; (E), specimen 11b, left M1/M2; and (F), specimen 7b, left M1/M2. Scale bars: 500 μm .

Solounias and Semprebon, 2002) were used as grouping variables. Analyses were performed using IBM SPSS Statistics 24.

3. Results

3.1. Dental mesowear

The *Equus ferus* mesowear pattern is characterized by a predominance of low occlusal relief (79.2%) and rounded cusps (70.8%), though a few specimens display also sharp (19.4%) or blunt cusps (9.7%) (Table 1). *Equus hydruntinus* displays a similar pattern (%L = 69.2; %R = 69.2), but contrary to that observed in *E. ferus*, none of the specimens exhibit blunt cusps and there is a higher incidence of sharp cusps (30.8%) (Table 1). Both patterns result in a relatively high score (MWS = 3.5 for *E. ferus* and 3.0 for *E. hydruntinus*) (Table 1) which points to a predominance of abrasion over attrition in the wear process that is consistent with grazing diets. Few individuals display a combination of low occlusal relief and sharp cusps (%L + S = 15.3 for *E. ferus* and 15.4 for *E. hydruntinus*) (Table 1) a mesowear signal correlated with a diet based on grasses but also including a component of open environment browse such as aridity-resistant shrubs (Fortelius and Solounias, 2000). These results are in agreement with the discriminant analysis, which provides a dietary discrimination of 74.1% of extant taxa correctly classified according to both classifications (68.5% and 74.1%, respectively, in cross-validation). Also, bivariate diagrams show that both *E. ferus* and *E. hydruntinus* are classified as grazers (Table 1; Fig. 4).

3.2. Dental microwear

Both *E. ferus* and *E. hydruntinus* display a high number of scratches (*E. ferus* AS = 29.9; *E. hydruntinus* AS = 25.9; Table 1), concordant with the consumption of a high amount of abrasive items. The average numbers of scratches and pits are consistent with those observed in extant ungulates with a diet characterized by a high intake of grasses (grazers and grass-dominated mixed feeders) (Fig. 5). Only two

specimens of each taxon show <17 scratches (*E. ferus* %0–17 = 3.7; *E. hydruntinus* %0–17 = 6.7; Table 1). Scratches are predominantly fine (*E. ferus* SWS = 0.1; *E. hydruntinus* SWS = 0.2; Table 1) with similar lengths in both taxa (*E. hydruntinus* Average SL = 121.1 μm; *E. ferus* Average SL = 126.9 μm; Table S2). Coarse scratches are generally longer than fine ones (Table S2) and *E. ferus* displays a higher percentage of cross scratches than *E. hydruntinus* (%XS = 63 and 47 respectively; Table 1). Pits are generally small (*E. ferus* Average PS = 59 μm; *E. hydruntinus* Average PS = 64.3; Table S2) although a higher percentage of individuals displaying large pits is recorded in *E. hydruntinus* if compared with *E. ferus* (%LP = 20 and 3.7 respectively; Table 1). Gouges are recorded in few individuals (*E. ferus* %G = 11.1; *E. hydruntinus* %G = 13.3; Table 1).

While these microwear patterns point to a somewhat high abrasive diet, the marked predominance of fine textured scratches is seldom observed in modern grazing ungulates which instead display a predominance of coarser scratches especially in those species which feed mostly on C4 grasses (Solounias and Semprebon, 2002). Abundant fine scratches are recorded in some modern mixed feeders which feed on C3 grasses such as the Sumatran serow *Capricornis sumatraensis*, the wapiti *Cervus canadensis*, the takin *Budorcas taxicolor* or in the llama *Lama glama* who inhabits non-forested areas and feeds in alpine grasslands (Solounias and Semprebon, 2002).

Discriminant analysis performed using microwear variables classifies *E. ferus* and *E. hydruntinus* as a seasonal and a meal-by-meal mixed feeder, respectively (72.2% correctly classified modern taxa, 47.7% in cross-validation; Table 1, Fig. 6). When extant seasonal and non-seasonal mixed feeders are grouped together in a single dietary category (named as mixed feeder), both fossils are classified as mixed feeders (77.3% correctly classified modern taxa, 61.4% in cross-validation; Table 1, Fig. 6).

Table 1
Summary of dental mesowear and microwear analysis.

Taxon		Mesowear								Predicted Diet	
		N	%High	%Low	%Sharp	%Round	%Blunt	%L + S	MWS	CONS	RAD
<i>Equus ferus</i>	Mean	72	20.8	79.2	19.4	70.8	9.7	15.3	3.5	Grazer	Grazer
	SD								1.5		
	CV								0.4		
<i>Equus hydruntinus</i>	Mean	13	30.8	69.2	30.8	69.2	0.0	15.4	3.0	Grazer	Grazer
	SD								1.6		
	CV								0.5		

Taxon		Microwear											Predicted Diet	
		N	AP	AS	%LP	%G	%XS	%0–17	SWS	%FS (0 SWS)	%MS (1 SWS)	%CS (2 SWS)	Type	Type*
<i>Equus ferus</i>	Mean	27	12.9	29.9	3.7	11.1	63.0	3.7	0.1	92.6	7.4	0.0	Seasonal Mixed Feeder	Mixed Feeder
	SD		5.8	7.3										
	CV		0.5	0.2										
<i>Equus hydruntinus</i>	Mean	15	17.5	25.9	20.0	13.3	46.7	6.7	0.2	80.0	20.0	0.0	Meal-by-Meal Mixed Feeder	Mixed Feeder
	SD		8.6	7.1										
	CV		0.5	0.3										

Abbreviations (mesowear): number of specimens measured (N); percentage of specimens with high (%High) and low (%Low) occlusal relief; percentage of specimens with sharp (%Sharp), rounded (%Rounded) and blunt (%Blunt) cusps; percentage of individuals with low occlusal relief and sharp cusps (%L + S); mesowear score (MWS); standar deviation (SD); coefficient of variation (CV). Predicted diets according to a conservative (CONS) and radical (RAD) mesowear classification.

Abbreviations (microwear): average number of pits (AP); average number of scratches (AS); percentage of individuals with >4 large pits (%LP); percentage of individuals with gouges (%G); percentage of individuals with >4 cross scratches (%XS); scratches width score (SWS); percentage of specimens with between 0 and 17 scratches (%0–17); percentage of individuals with predominantly fine scratches (%FS); percentage of individuals with a mix of fine and coarse scratches (%MS); percentage of individuals with predominantly coarse scratches (%CS).

* Extant seasonal and non-seasonal mixed feeders are grouped together in a single dietary category “mixed feeders”.

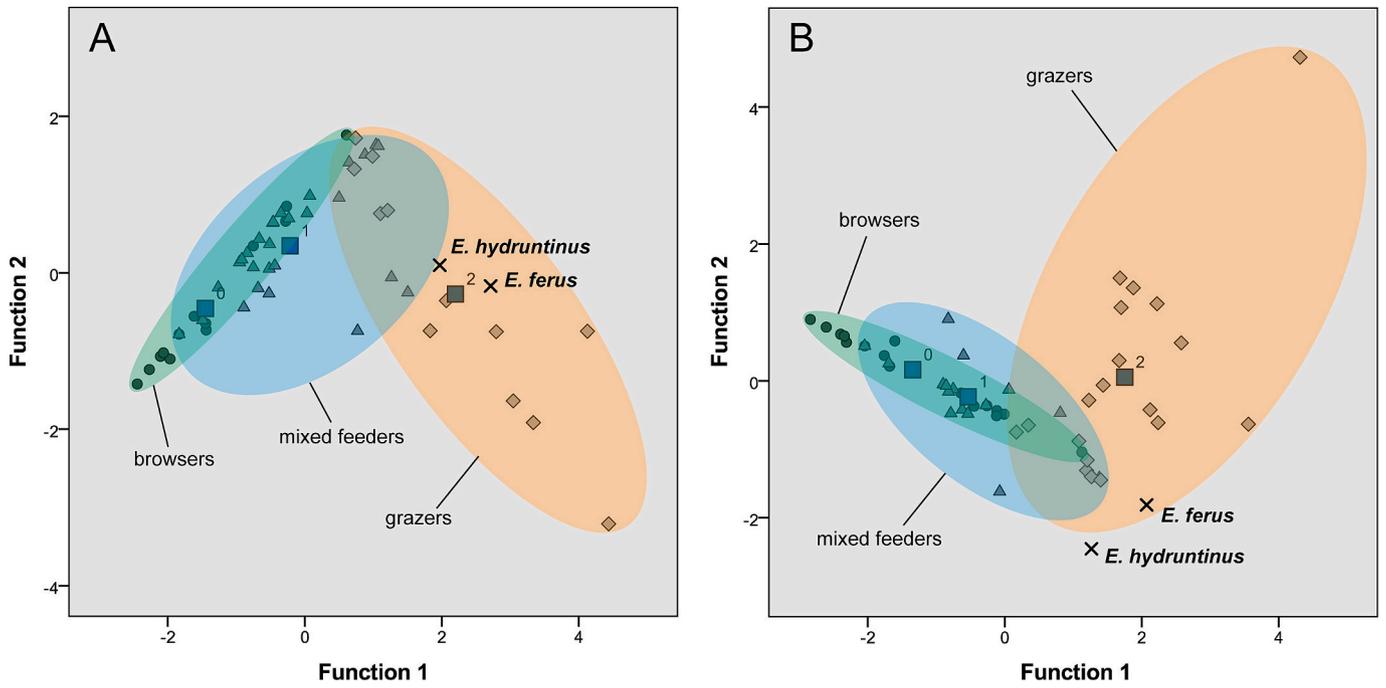


Fig. 4. Bivariate diagrams based on discriminant analysis performed with mesowear data: (A), conservative classification; (B), radical classification. Group centroids: browsers (0); mixed feeders (1); and grazers (2). Extant ungulates data from Fortelius and Solounias (2000).

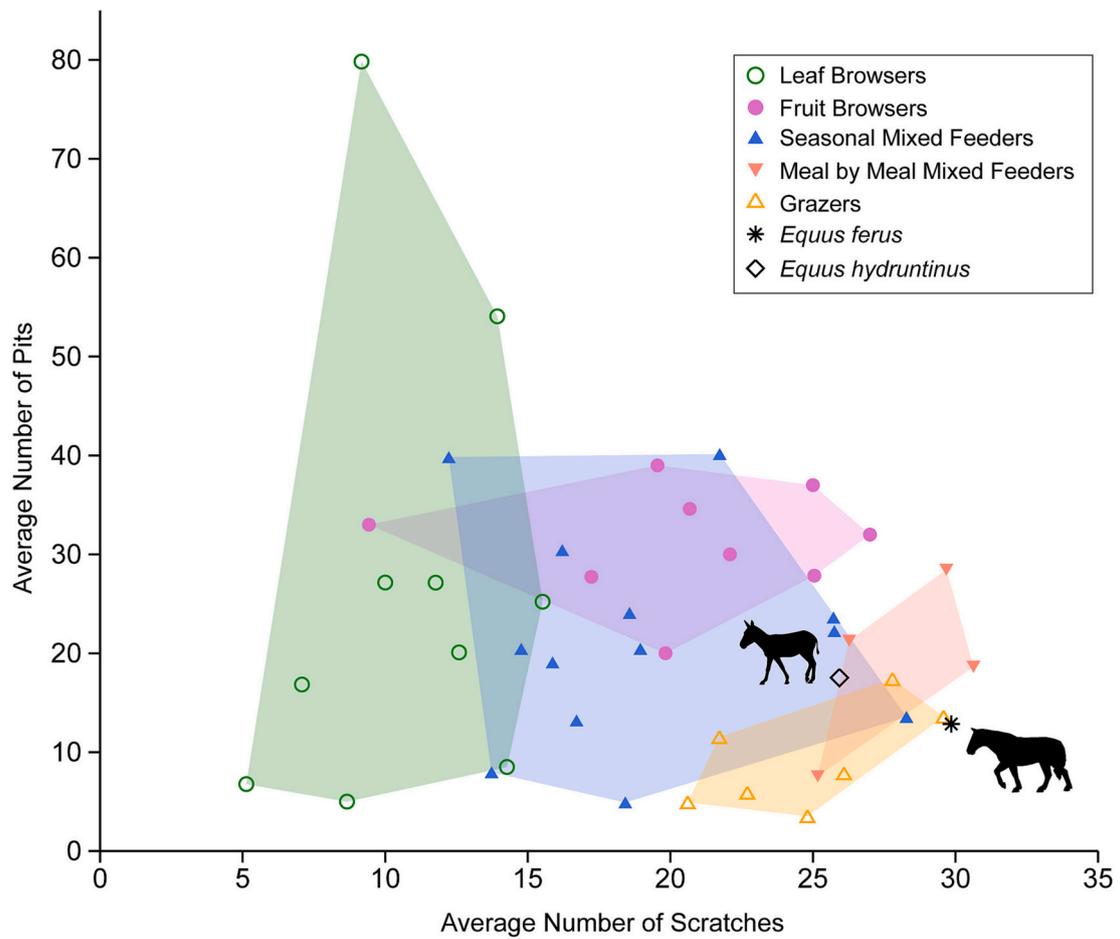


Fig. 5. Bivariate plot of the average number of pits versus average number of scratches in extant ungulates (data modified from Solounias and Semperebon, 2002) and fossil equids from La Carihuela. Silhouette image of *E. ferus* by Flavia Strani, silhouette image of *E. hydruntinus* from PhyloPic.org (Public Domain).

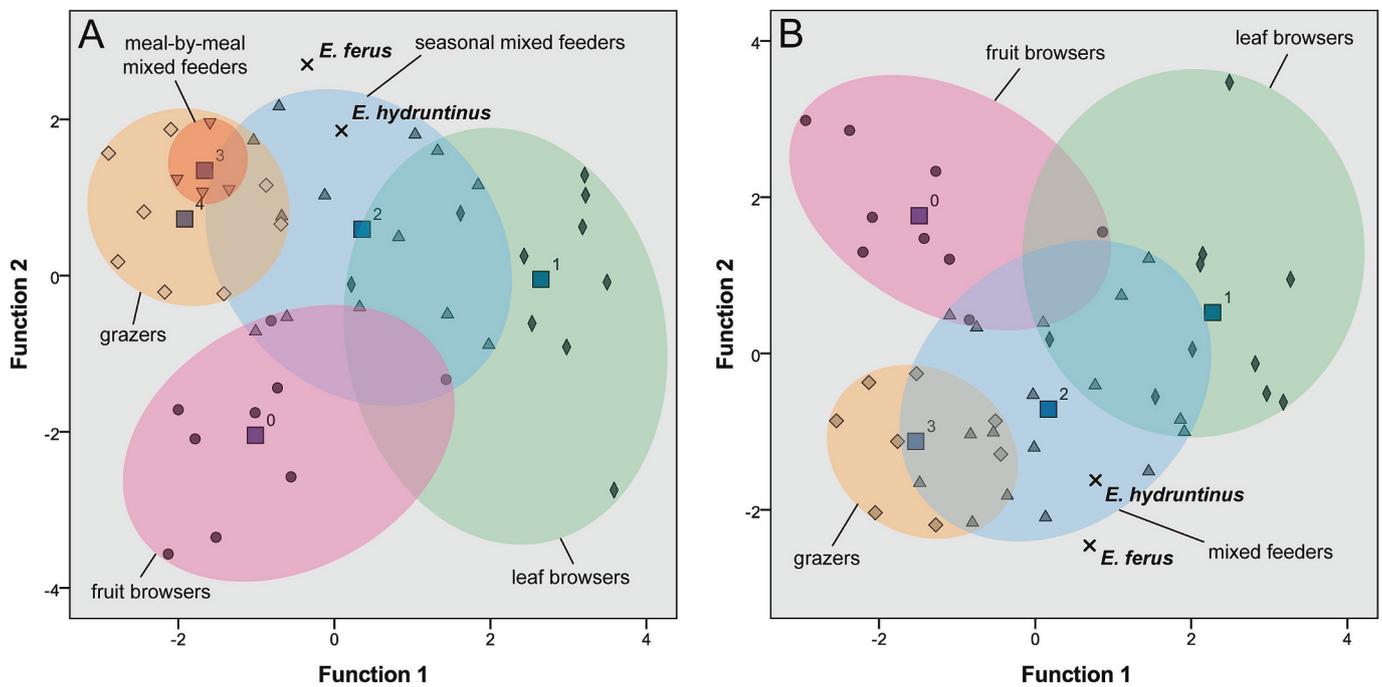


Fig. 6. Bivariate diagrams based on discriminant analysis performed with microwear data. (A), classification using extant ungulates dietary types as grouping variables: fruit browsers (0); leaf browsers (1); seasonal mixed feeders (2); meal-by-meal mixed feeders (3); and grazers (4). (B), classification grouping extant seasonal and non-seasonal mixed feeders in a single dietary category (mixed feeders): fruit browsers (0); leaf browsers (1); mixed feeders (2); and grazers (3). Square symbol indicates group centroids. Extant ungulates data from Solounias and Sempredon (2002).

Table 2

Summary table of dietary adaptations of *E. ferus* and *E. hydruntinus* from selected Late Pleistocene European localities.

Taxa	Locality	Country	Diet				
			Mesowear	Reference	Microwear	SWS	Reference
<i>Equus ferus</i>	Gough's Cave	UK	grazer	Saarinen et al. (2016)	grazer		Rivals and Lister (2016)
<i>Equus ferus</i>	Kent's Cavern	UK	grazer	Saarinen et al. (2016)	grazer		Rivals and Lister (2016)
<i>Equus ferus</i>	La Carihuella	Spain	grazer	this study	mixed feeder	0.1	this study
<i>Equus hydruntinus</i>	La Carihuella	Spain	grazer	this study	mixed feeder	0.2	this study
<i>Equus ferus</i>	Canyars	Spain	grazer	Rivals et al. (2017)	grazer	0.92	Rivals et al. (2017)
<i>Equus ferus</i>	Arbreda I	Spain	grazer	Sánchez-Hernández et al. (2020)	grazer	0.5	Sánchez-Hernández et al. (2020)
<i>Equus ferus</i>	Teixoneres Cave IIIa	Spain	grazer	Sánchez-Hernández et al. (2020)	grazer	0.55	Sánchez-Hernández et al. (2020)
<i>Equus ferus</i>	Teixoneres Cave IIIb	Spain	grazer	Sánchez-Hernández et al. (2020)	grazer	0.55	Sánchez-Hernández et al. (2020)
<i>Equus hydruntinus</i>	Teixoneres Cave IIIa	Spain	grazer	Sánchez-Hernández et al. (2020)	grazer	0.63	Sánchez-Hernández et al. (2020)
<i>Equus hydruntinus</i>	Teixoneres Cave IIIb	Spain	grazer	Sánchez-Hernández et al. (2020)	mixed feeder	0.64	Sánchez-Hernández et al. (2020)
<i>Equus ferus</i>	Salzgitter Lebenstedt	Germany	grass dom-mixed feeder	Rivals et al. (2009)	browser	1.1	Rivals et al. (2009)
<i>Equus ferus</i>	Abric Romaní KLM	Spain	grazer	Rivals et al. (2009)	grazer	1.1–2.0–0.0	Rivals et al. (2009)
<i>Equus hydruntinus</i>	Emine Bair Khosar Cave	Ukraine	grazer	Cirilli et al. (2022)			
<i>Equus ferus</i>	Aufhausener höhle	Germany	grazer	Saarinen et al. (2016)			
<i>Equus ferus</i>	Portel-Ouest F	France	grazer	Rivals et al. (2009)	mixed feeder	1.1	Rivals et al. (2009)
<i>Equus hydruntinus</i>	Kabazi II	Ukraine	grazer	Ramírez-Pedraza et al. (2020)	grazer	1.2	Ramírez-Pedraza et al. (2020)
<i>Equus ferus</i>	Villa Seckendorff	Germany	grazer	Saarinen et al. (2016)			
<i>Equus hydruntinus</i>	Villa Seckendorff	Germany	grazer	Cirilli et al. (2022)			
<i>Equus ferus</i>	Wallertheim F	Germany	grass dom-mixed feeder	Rivals et al. (2009)	grass dom-mixed feeder	0.5	Rivals et al. (2009)
<i>Equus ferus</i>	Payre D	France	grazer	Rivals et al. (2009)	mixed feeder	1.1	Rivals et al. (2009)
<i>Equus ferus</i>	Taubach	Germany	grazer	Saarinen et al. (2016)	browser	1	Rivals et al. (2009)

4. Discussion

4.1. Diet of *E. ferus* and *E. hydruntinus* from La Carihuela and comparison with species from other Late Pleistocene sites in Europe

Both *E. ferus* and *E. hydruntinus* from La Carihuela display a long-term grazing behaviour, in agreement with that observed in *Equus* populations from other Late Pleistocene localities across (Southern, Western and Central) Europe (from MIS 5 to MIS 2) (Rivals et al., 2009; Sánchez-Hernández et al., 2020; Cirilli et al., 2022) (Table 2), and with their well-known (morphological) adaptations (such as cursorial limbs, long metapodials, hypsodont cheek teeth, lophodont occlusal patterns, etc.) for open habitats (MacFadden, 2005; Cirilli et al., 2022).

Regarding short-term feeding behaviour, apparently both equids were able to also exploit plant resources other than grasses. While the high frequency of scratches and the low number of pits are consistent with a diet characterized by high levels of abrasion, the predominance of finely textured features are unusual for a strict grazing behaviour. Modern grazers (as well as bark eaters and fruit browsers) tend in fact to display coarse scratches (Solounias and Semprebon, 2002), while fine scratches are commonly observed in some extant ungulates displaying intermediate diets (Solounias and Semprebon, 2002), such as the four-horned antelope *Tetracerus quadricornis* (considered a grazer in Solounias and Semprebon, 2002, although dietary studies by Kunwar et al., 2016 on living populations point to a mixed diet).

Interestingly, this finding is not recorded in *E. ferus* and *E. hydruntinus* from other Late Pleistocene Iberian localities, which mostly display a SWS value above 0.5 (Rivals et al., 2009; Sánchez-Hernández et al., 2020). A less abrasive short-term feeding behaviour in *E. ferus* is recorded in other Late Pleistocene European localities, where microwear patterns points to a mixed (at Portel-Ouest and Payre in France and Wallertheim in Germany during MIS 5e-d and MIS 4) or even browsing (at Taubach and Salzgitter Lebenstedt in Germany during MIS 5e and MIS 3) diet (Rivals et al., 2009) (Table 2). Individuals ascribed to *E. cf. ferus* from another Iberian locality, the Middle Pleistocene Vallparadis Estació layer EVT3, also display microwear patterns which are consistent with a mixed feeding behaviour (Strani et al., 2019b), although this interpretation should be tentatively taken as the sample consists of only two specimens. The available data for *E. hydruntinus* from other European sites suggests that this equid usually displayed a grazing feeding behaviour although microwear patterns consistent with a less abrasive diet are recorded at Teixoneres Cave during the MIS 3 (Sánchez-Hernández et al., 2020).

The discrepancy between mesowear and microwear results indicates that while both wild horses and hydruntines were well adapted to feed on grasses, they could have displayed also a certain degree of flexibility in their dietary behaviour when necessary, in order to consume less abrasive plant resources.

Finely textured scratches have been observed by Solounias and Semprebon (2002) in taxa which feed on high altitude habitats where C3 grasses grow or which eat less abrasive fresh or wet grasses. La Carihuela cave is located at 1020 m above sea level (Fernández et al., 2007) close to the Baetic System mountain ranges of Sierra Nevada, Sierra de Baza and Sierra de María (Fig. 1). Thus, the abundance of fine scratches may be also a result of the fact that both equids fed on C3 grasses in mountainous areas.

Among modern wild (or feral) equids, Przewalski horses (*Equus przewalskii*) and kulans (*Equus hemionus kulan*) from Central Eurasia live in steppe-biomes in habitat and climatic conditions that are comparable to those recorded in most European regions during the glacial phases of the LGP. In Przewalski horses and kulan populations with overlapping home ranges, it has been observed that time-differentiation of area usage allowed the two species to live in sympatric conditions, with major overlapping (>60% of shared home range) occurring only during spring and kulans showing higher mobility than Przewalski horses (Bahloul et al., 2001). Similar niche partitioning mechanisms may had been

employed by sympatric *E. ferus* and *E. hydruntinus* populations at least during the most arid phases of the LGP, feeding on the same resources at different times of the day and with *E. hydruntinus* exploiting a larger area compared to *E. ferus*.

4.2. The role of climatic changes and habitat alterations in the extinction of wild equids in Europe

The reduction of steppe-like biomes in Europe following the warming phase at the beginning of the Holocene is considered the main factor that led to the extinction of *E. ferus* and *E. hydruntinus* in the continent (Boulbes and Van Asperen, 2019). Results from the La Carihuela sample as well as from other European localities, however, indicate that despite the fact that wild equids possessed marked adaptations for open grasslands feeding primarily on grass, they could adapt to feed also on other types of plant resources displaying a certain dietary flexibility whether or not cold, dry, open habitats were the predominant element of the European landscapes. *E. ferus* even displayed a short-term browsing behaviour during MIS 5e (Rivals et al., 2009), one of the warmest interglacials of the Pleistocene characterized by global mean temperatures comparable to projections for the current climate change, and wetter conditions than during the Holocene in Central Europe (Rohling et al., 2007; Dabkowski and Limondin-Lozouet, 2021).

Pollen records for the Lithostratigraphic Units X–VI of La Carihuela which yielded *E. ferus* and *E. hydruntinus* fossil remains, point to an alternation between pine forests (*Pinus*-dominated open or closed woodland) and grasslands (Fernández et al., 2007) (Fig. 2). The absence of oaks (*Quercus*) and deciduous trees across Units X–VI indicate generally cold climatic settings although the record of mesothermophytes in Unit VI suggests warmer conditions around 40 ka (Fernández et al., 2007). The lack of information on the exact stratigraphic provenance of the examined sample does not allow us to correlate the studied material with a specific vegetation phase, however it appears that *E. ferus* and *E. hydruntinus* from La Carihuela could successfully feed on the same resources and avoid competitive displacement despite these repeated fluctuations between forest- and grassland-dominated landscapes. It is possible that the mixed feeding short-term diet recorded is due to a sample consisting of specimens that may come from different units and thus lived under different climatic conditions.

Nevertheless, obtained results suggest that Late Pleistocene wild equids could in fact adapt to warmer and more humid conditions, and that while environmental changes certainly affected their distribution “setting the stage” for their eventual extinction (e.g., locking them in habitat refugia such as the Iberian Peninsula; Schmitt and Varga, 2012), probably the arrival of and competition with domestic forms and other livestock, may have actually triggered and led to the disappearance of wild equids in Europe as observed between modern Przewalski’s horses and free-ranging domestic ungulates (Sietse et al., 2009).

5. Conclusions

The role that major climatic changes and human activity played in the extinction of the last European wild equids during the Pleistocene/Holocene Transition is not well understood. We report for the first time a dietary reconstruction of *E. ferus* and *E. hydruntinus* from the Late Pleistocene locality of La Carihuela (Iberian Peninsula), providing information on the niche partitioning that these equids exhibited in southern Europe during the LGP. Dental mesowear and microwear indicate that both wild horses and hydruntines occupied the same niche sharing similar long- and short-term adaptations as grazers that could periodically shift their diet to also include less abrasive plant resources. This, albeit limited in time, dietary flexibility is also recorded in other Late Pleistocene European localities suggesting that both wild equids were capable of adapting to the reduction of steppe-like biomes. Holocene climatic changes may thus have not been the main trigger of their

disappearance. Human activity, specifically the spreading of domestic horses and donkeys from Eurasia may have played a larger role in the extinction of wild equids in the continent competing with them for the same resources. We also highlight the importance of a comprehensive microwear analysis when reconstructing the diet of fossil ungulates including both quantitative (number of features) and qualitative (feature's texture) information to discriminate between feeding behaviours.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2023.111564>.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Flavia Strani reports financial support was provided by Italian Paleontological Society. The corresponding author (FS) and co-author (DDM) previously served as Reviewers for Palaeogeography, Palaeoclimatology, Palaeoecology.

Data availability

Raw data are provided as Supplementary Material

Acknowledgments

This research was funded by “Borsa di Studio SPI 2020” granted by the Italian Paleontological Society to F.S. This work is part of project PID2020-116220GB-I00 funded by MCIN/AEI/10.13039/501100011033/, with funding also by the Government of Aragon (ref. E33_20R). F.S. is a “Juan de la Cierva Formación” fellow (ref. FJC2020-042982-I) funded by the Agencia Estatal de Investigación of the Spanish Ministry of Science and Innovation (MCIN / AEI / 10.13039 / 501100011033) and the European Union “NextGenerationEU / PRTR” program. Authors thank Editor-in-Chief H.J. Falcon-Lang and two anonymous reviewers for their comments that greatly improved the quality of the manuscript.

References

- Ackermans, N., Winkler, D., Schulz-Kornas, E., Kaiser, T., Müller, D., Kircher, P., Hummel, J., Clauss, M., Hatt, J., 2018. Controlled feeding experiments with diets of different abrasiveness reveal slow development of mesowear signal in goats (*Capra aegagrus hircus*). *J. Exp. Biol.* 221 (21).
- Bahloul, K., Pereladova, O.B., Soldatova, N., Fisenko, G., Sidorenko, E., Sempér, A.J., 2001. Social organization and dispersion of introduced kulans (*Equus hemionus kulan*) and Przewalski horses (*Equus przewalski*) in the Bukhara Reserve, Uzbekistan. *J. Arid Environ.* 47, 309–323. <https://doi.org/10.1006/jare.2000.0714>.
- Barnosky, A., Koch, P.L., Feranec, R.S., Wing, S.L., Shabel, A.B., 2004. Assessing the causes of late Pleistocene extinctions on the continents. *Science* 306, 70–75.
- Bennett, E.A., Champlot, S., Peters, J., Arbuckle, B.S., Guimaraes, S., Pruvost, M., Bar-David, S., Davis, S.J.M., Gautier, M., Kaczensky, P., Kuehn, R., Mashkour, M., Morales-Muñiz, A., Pucher, E., Tournepiche, J.-F., Uerpmann, H.-P., Bălăşescu, A., Germonpré, M., Gündem, C.Y., Hemami, M.-R., 2017. Taming the late Quaternary phylogeography of the Eurasian wild ass through ancient and modern DNA. *PLOS ONE* 12, e0174216. <https://doi.org/10.1371/journal.pone.0174216>.
- Boulbes, N., Van Asperen, E.N., 2019. Biostratigraphy and palaeoecology of European Equus. *Front. Ecol. Evol.* 7, 301.
- Cirilli, O., Machado, H., Arroyo-Cabrales, J., Barrón-Ortiz, C.I., Davis, E., Jass, C.N., Jukar, A.M., Landry, Z., Marín-Leyva, A.H., Pandolfi, L., Pushkina, D., Rook, L., Saarinne, J., Scott, E., Semperebon, G., Strani, F., Villavicencio, N.A., Kaya, F., Bernor, R.L., 2022. Evolution of the Family Equidae, Subfamily Equinae, in North, Central and South America, Eurasia and Africa during the Plio-Pleistocene. *Biology* 11, 1258. <https://doi.org/10.3390/biology11091258>.
- Crees, J.J., Turvey, S.T., 2014. Holocene extinction dynamics of *Equus hydruntinus*, a late-surviving European megafaunal mammal. *Quat. Sci. Rev.* 91, 16–29. <https://doi.org/10.1016/j.quascirev.2014.03.003>.
- Dabkowski, J., Limondin-Lozouet, N., 2021. Comparison of temperature and humidity during MIS 11 and MIS 5e interglacials with the Holocene using stable isotopes in tufa deposits from northern France. *Quat. Res.* 107, 147–158. <https://doi.org/10.1017/qua.2021.66>.
- DeMiguel, D., Fortelius, M., Azanza, B., Morales, J., 2008. Ancestral feeding state of ruminants reconsidered: earliest grazing adaptation claims a mixed condition for Cervidae. *BMC Evol. Biol.* 8, 13. <https://doi.org/10.1186/1471-2148-8-13>.
- DeMiguel, D., Azanza, B., Morales, J., 2010. Trophic flexibility within the oldest Cervidae lineage to persist through the Miocene Climatic Optimum. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 289, 81–92. <https://doi.org/10.1016/j.palaeo.2010.02.010>.
- DeMiguel, D., Quirarte, V., Azanza, B., Montoya, P., Morales, J., 2012. Dietary behaviour and competition for vegetal resources in two early Miocene pecoran ruminants from Central Spain. *Geodiversitas* 34, 425–443. <https://doi.org/10.5252/g2012n2a10>.
- Faith, J.T., Surovell, T.A., 2009. Synchronous extinction of North America's Pleistocene mammals. *Proc. Natl. Acad. Sci. U. S. A.* 106, 20641–20645.
- Fernández, S., Fuentes, N., Carrión, J.S., González-Sampériz, P., Montoya, E., Gil, G., Vega-Toscano, G., Riquelme, J.A., 2007. The holocene and Upper Pleistocene pollen sequence of Carihuela Cave, Southern Spain. *Geobios* 40 (1), 75–90.
- García-Sánchez, M., 1960. Restos humanos del Paleolítico Medio y Superior y del Neolítico de Píñar (Granada). *Trabajos Inst. Bernardino Sahagún Antropol. Etnol.* 15, 17–72.
- Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *J. Hum. Evol.* 15, 783–822.
- Kaiser, T.M., Solounias, N., 2003. Extending the tooth mesowear method to extinct and extant equids. *Geodiversitas* 25 (2), 321–345.
- Guthrie, R., 2004. Radiocarbon evidence of mid-Holocene mammoths stranded on an Alaskan Bering Sea island. *Nature* 429, 746–749. <https://doi.org/10.1038/nature02612>.
- Kaiser, T.M., Brasch, J., Castell, J.C., Schulz, E., Clauss, M., 2009. Tooth wear in captive wild ruminant species differs from that of free-ranging conspecifics. *Mamm. Biol.* 74 (6), 425–437.
- Kimura, B., Marshall, F.B., Chen, S., Rosenbom, S., Moehlmann, P.D., Tuross, N., Sabin, R. C., Peters, J., Barich, B., Yohannes, H., Kebede, F., Teclai, R., Beja-Pereira, A., Mulligan, C.J., 2010. Ancient DNA from Nubian and Somali wild ass provides insights into donkey ancestry and domestication. *Proc. Royal Soc. B.* 278, 50–57. <https://doi.org/10.1098/rspb.2010.0708>.
- King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. *Am. J. Phys. Anthropol.* 108, 359–373.
- Koch, P., Barnosky, A., 2006. Late Quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Evol. Syst.* 37, 215–250.
- Kunwar, A., Gaire, R., Pokharel, K.P., Baral, S., Thapa, T.B., 2016. Diet of the Four-horned Antelope *Tetracerus quadricornis* (De Blainville, 1816) in the Churia Hills of Nepal. *J. Threat. Taxa.* 8, 8745. <https://doi.org/10.11609/jott.1818.8.5.8745-8755>.
- Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *Am. Mus. Novit.* 3301, 1–35.
- Librado, P., Khan, N., Fages, A., Kusliy, M.A., Suchan, T., Tonasso-Calvière, L., Schiavinato, S., Alioglu, D., Fromentier, A., Perdereau, A., Aury, J.-M., Gaunitz, C., Chauvey, L., Seguin-Orlando, A., Der Sarkissian, C., Southon, J., Shapiro, B., Tishkin, A.A., Kovalev, A.A., Alquraishi, S., 2021. The origins and spread of domestic horses from the Western Eurasian steppes. *Nature* 598, 634–640. <https://doi.org/10.1038/s41586-021-04018-9>.
- Lyons, S.K., Miller, J.H., Fraser, D., Smith, F.A., Boyer, A., Lindsey, E., Mychajliw, A.M., 2016. The changing role of mammal life histories in Late Quaternary extinction vulnerability on continents and islands. *Biol. Lett.* 12.
- MacFadden, B.J., 2005. Fossil Horses-evidence for Evolution. *Science* 307, 1728–1730. <https://doi.org/10.1126/science.1105458>.
- Mecozzi, B., Strani, F., 2022. Equids from the late middle pleistocene to early holocene of the Apulia Peninsula (southern Italy): Reassessment of their taxonomy and biochronology. *Geodiversitas* 44 (2).
- Mihlbachler, M., Rivals, F., Solounias, N., Semperebon, G., 2011. Dietary change and evolution of horses in North America. *Science* 331 (6021), 1178–1181.
- Nacarino-Meneses, C., Jordana, X., Orlandi-Oliveras, G., Köhler, M., 2017. Reconstructing molar growth from enamel histology in extant and extinct Equus. *Sci. Rep.* 7 (1).
- Ramírez-Pedraza, I., Rivals, F., Uthmeier, T., Chabai, V., 2020. Palaeoenvironmental and seasonal context of the late Middle and early Upper Palaeolithic occupations in Crimea: an approach using dental wear patterns in ungulates. *Archaeol. Anthropol. Sci.* 12. <https://doi.org/10.1007/s12520-020-01217-9>.
- Rivals, F., Schulz, E., Kaiser, T.M., 2009. Late and middle Pleistocene ungulates dietary diversity in Western Europe indicate variations of Neanderthal paleoenvironments through time and space. *Quat. Sci. Rev.* 28, 3388–3400. <https://doi.org/10.1016/j.quascirev.2009.09.004>.
- Rivals, F., 2012. Ungulate feeding ecology and middle Pleistocene paleoenvironments at Hundsheim and Deutsch-Altenburg 1 (eastern Austria). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 317–318, 27–31.
- Rivals, F., Lister, A.M., 2016. Dietary flexibility and niche partitioning of large herbivores through the Pleistocene of Britain. *Quat. Sci. Rev.* 146, 116–133.
- Rivals, F., Uzunidis, A., Sanz, M., Daura, J., 2017. Faunal dietary response to the Heinrich Event 4 in southwestern Europe. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 473, 123–130. <https://doi.org/10.1016/j.palaeo.2017.02.033>.
- Rohling, E.J., Grant, K., Hemleben, Ch., Siddall, M., Hoogakker, B.A.A., Bolshaw, M., Kucera, M., 2007. High rates of sea-level rise during the last interglacial period. *Nat. Geosci.* 1, 38–42. <https://doi.org/10.1038/ngeo.2007.28>.
- Samper Carro, S.C., 2010. Caracterización sistemática de los équidos de La Carihuela (Píñar, Granada). In: Moreno-Azanza, M., Díaz-Martínez, I., Gasca, J.M., Melero-Rubio, M., Rabal-Garcés, R., Sauqué, V. (Eds.), *Cidaris*, número 30, VIII Encuentro de Jóvenes Investigadores en Paleontología, volumen de actas, pp. 283–291.
- Sánchez-Hernández, C., Gourichon, L., Soler, J., Soler, N., Blasco, R., Rosell, J., Rivals, F., 2020. Dietary traits of ungulates in northeastern Iberian Peninsula: did these

- Neanderthal preys show adaptive behaviour to local habitats during the Middle Palaeolithic? *Quat. Int.* 557, 47–62. <https://doi.org/10.1016/j.quaint.2020.01.008>.
- Saarinen, J., Eronen, J., Fortelius, M., Seppä, H., Lister, A.M., 2016. Patterns of diet and body mass of large ungulates from the Pleistocene of Western Europe, and their relation to vegetation. *Palaeontol. Electron.* 19.3.32A, 1–58.
- Schmitt, T., Varga, Z., 2012. Extra-Mediterranean refugia: the rule and not the exception? *Front. Zool.* 9, 22. <https://doi.org/10.1186/1742-9994-9-22>.
- Semprebon, G.M., Rivals, F., 2007. Was grass more prevalent in the pronghorn past? An assessment of the dietary adaptations of Miocene to recent Antilocapridae (Mammalia: Artiodactyla). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 253, 332–347.
- Sietses, D.J., Faupin, G., de Boer, W.F., de Jong, C.B., Henkens, R.J.H.G., Usukhjargal, D., Batbaatar, T., 2009. Resource partitioning between large herbivores in Hustai National Park, Mongolia. *Mamm. Biol.* 74, 381–393. <https://doi.org/10.1016/j.mambio.2009.04.001>.
- Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *Am. Mus. Novit.* 3366, 1–49.
- Spahni, J.C., 1955. Vestiges néanderthaliens de Pñnar. *Bull. l'Assoc. Française L'étude Q.* 52, 540–548.
- Strani, F., DeMiguel, D., Sardella, R., Bellucci, L., 2018a. Resource and niche differentiation mechanisms by sympatric early Pleistocene ungulates: the case study of Coste San Giacomo. *Quat. Int.* 481, 157–163. <https://doi.org/10.1016/j.quaint.2017.08.064>.
- Strani, F., DeMiguel, D., Bellucci, L., Sardella, R., 2018b. Dietary response of early Pleistocene ungulate communities to the climate oscillations of the Gelasian/Calabrian transition in Central Italy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 499, 102–111. <https://doi.org/10.1016/j.palaeo.2018.03.021>.
- Strani, F., Profico, A., Manzi, G., Pushkina, D., Raia, P., Sardella, R., DeMiguel, D., 2018c. MicroWearR: a new R package for dental microwear analysis. *Ecol. Evol.* 8, 7022–7030. <https://doi.org/10.1002/ece3.4222>.
- Strani, F., Pushkina, D., Bocherens, H., Bellucci, L., Sardella, R., DeMiguel, D., 2019a. Dietary adaptations of early and Middle Pleistocene equids from the Anagni Basin (Frosinone, Central Italy). *Front. Ecol. Evol.* 7 <https://doi.org/10.3389/fevo.2019.00176>.
- Strani, F., DeMiguel, D., Alba, D.M., Moyà-Solà, S., Bellucci, L., Sardella, R., Madurell-Malapeira, J., 2019b. The effects of the “0.9 Ma event” on the Mediterranean ecosystems during the Early-Middle Pleistocene transition as revealed by dental wear patterns of fossil ungulates. *Quat. Sci. Rev.* 210, 80–89. <https://doi.org/10.1016/j.quascirev.2019.02.027>.
- Stuart, A.J., 2014. Late Quaternary megafaunal extinctions on the continents: a short review. *Geol. J.* 50, 338–363. <https://doi.org/10.1002/gj.2633>.
- Vega-Toscano, L.G., Hoyos, M., Ruiz-Bustos, A., Laville, H., 1988. La séquence de la grotte de la Carhuela (Pñnar, Grenade): chronostratigraphie et paléocologie du Pléistocène Supérieur au Sud de la Péninsule Ibérique. In: Otte, M. (Ed.), *L'Homme de Néandertal, L'Environnement*, vol. 2. ERAUL, Liège, pp. 169–180.
- Weber, K., Winkler, D.E., Schulz-Kornas, E., Kaiser, T.M., Tütken, T., 2021. The good, the bad and the ugly – a visual guide for common post-mortem wear patterns in vertebrate teeth. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 578, 110577.