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Eating through time: Understanding dietary practices across late prehistory in the northeastern Iberian Peninsula

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Abstract

Objective: This study seeks to contribute to the current understanding of dietary variation in the late Prehistory of the northeastern Iberian Peninsula by examining buccal dental microwear patterns alongside archeological data from the same populations.

Materials and Methods: Teeth from 84 adult individuals from eight distinct samples spanning the Middle-Late Neolithic to the Middle Bronze Age (Cova de l'Avi, Cova de Can Sadurní, Cova de la Guineu, Cova Foradada, Cova del Trader, Roc de les Orenetes, Cova del Gegant, Cova dels Galls Carboners) were analyzed using optical microscopy to examine buccal dental microwear patterns.

Results: The analysis did not reveal clear chronological contrasts in the dietary habits of these samples. Nevertheless, significant differences emerged among the samples, leading to their classification into two distinct sets based on the abrasiveness of the diet informed by the microwear patterns. These findings offer similarities and differences among samples in the Iberian Peninsula, shedding light on the diverse lifestyles of these individuals.

Discussion: Integrating our new results with other available proxies points to a multifaceted specialization in dietary patterns among these samples, influenced by factors such as habitat, resource selection, and available technology. By contextualizing the results within the broader context of the Iberian Peninsula, this research discerns shared characteristics and distinctive adaptations in the dietary practices and subsistence strategies of these groups. Ultimately, this study contributes to a deeper understanding of the intricate interplay between culture and environment in shaping human diets throughout late Prehistory.

KEYWORDS
dental microwear, Iberian Peninsula, paleodiet, prehistory, subsistence

1 | INTRODUCTION

The late Prehistory of the Iberian Peninsula (6th–2nd millennia BC) was a period of significant cultural dynamism and complexity characterized by a series of socio-cultural, technological, and demographic transformations with different regional expressions and rhythms. This diverse and changing historical and environmental context provides the perfect setting for investigating ancient dietary practices in the Iberian Peninsula.

In this context, paleodietary studies have shown a mixed dietary pattern characterized by the consumption of both agricultural and livestock products (Alt et al., 2016; Beck et al., 2018; Fernández-Crespo et al., 2021; Gluitz et al., 2023; McClure et al., 2011; Romero et al., 2004; Valdiosera et al., 2018; Villalba-Mouco et al., 2018; Viñas-Caron et al., 2022; Waterman et al., 2016). The importance attributed to one form of subsistence over the other varies depending on the region and climatic conditions (Díaz-Zorita Bonilla et al., 2019; Fontanals-Coll et al., 2016; García-González et al., 2018; Jones et al., 2019; López-Costas & Alexander, 2019; Riera et al., 2007). However, the complex economic systems of these populations make it challenging to characterize a predominant dietary pattern (Salazar-García et al., 2022).

Specifically, during the Late Neolithic to Chalcolithic transition, there was an intensification and specialization in food production, resulting in a relatively homogenized diet with less cereal varieties cultivated, focusing on cultivating naked wheat, naked barley, and legumes (Antolín, 2013; Antolín et al., 2015; Plasencia, 2016). This contributed to sustained demographic growth and the economic consolidation of these societies (Bernabeu Aubán & Orozco Köhler, 2014; Gibaja & Clop i García, 2012). From an economic perspective, this period is characterized by a significant interest in by-products, a phenomenon known as the "Secondary Products Revolution" (Sherratt, 1981). This revolution involves increased utilization of milk and its derivatives, manure, and wool (Francés-Negro et al., 2021; Garrido-Pena, 2005). However, subsistence still relied on both agriculture and livestock, varying according to regional and climatic factors (Díaz-Zorita Bonilla et al., 2019; Fontanals-Coll et al., 2016; García-González et al., 2018; Jones et al., 2019; Riera et al., 2007).

Subsequently, during the transition from the Chalcolithic to the Bronze Age, significant structural changes occurred with the intensification of production economies, the consolidation of social hierarchies, and the introduction of metal alloys (Blanco-González et al., 2018; Lillios, 2019; Soriano, 2013). These technological and social innovations led to large population movements and exchanges of genetic and cultural significance that potentially influenced the emergence of new food processing techniques (García-González et al., 2018; Olalde et al., 2019; Romero & De Juan, 2007). This gave rise to cases of dietary differences associated with status, age and sex (Díaz-Zorita Bonilla et al., 2019; García-González et al., 2018; Gluitz et al., 2023; Hernando, Willman, et al., 2020; Romero & De Juan, 2007; Waterman et al., 2016).

In this article, we focus on the study of dietary practices in the northeastern region of the Iberian Peninsula, an area that is particularly representative of these changes and transformations during late Prehistory, through dental microwear analysis. This technique has emerged as a valuable tool for understanding the physical and mechanical properties of consumed foods, providing a crucial line of evidence for the study of dietary practices (e.g., Grine, 1986; Hernando et al., 2021; Lalueza-Fox et al., 1996; Pérez-Pérez et al., 1994; Romero & De Juan, 2012). While dietary microwear accumulates on both the buccal and occlusal surfaces, there are notable distinctions related to the chewing cycle (Hernando, Willman, et al., 2022; Romero et al., 2012; Schmidt et al., 2019). In this study, we specifically focus on the buccal surfaces, which are known to undergo a more gradual turnover of enamel compared to the occlusal surface, thus reflecting dietary habits over a longer period of life (Pérez-Pérez et al., 1994; Romero et al., 2012; Romero & De Juan, 2007). Additionally, when integrated with other approaches that were already applied to the same archaeological sites, such as the study of oral pathologies, dental calculus and isotopic analyses, it offers a more comprehensive understanding of the diets and strategies adopted by these groups during these periods. This multiproxy approach allows us to delve deeper into the relationship between human groups and their environment, as well as to comprehend how these dietary dynamics contributed to the development of various subsistence strategies.

2 | MATERIAL

The sample included in this study comprises the teeth from 209 adult individuals belonging to eight groups spanning from the Middle-Late Neolithic to the Middle Bronze Age in the northeastern Iberian Peninsula (Figure 1, Table 1). It is important to note that while we initially analyzed the teeth of 209 individuals under the optical microscope, only 88 teeth exhibited preserved dental microwear patterns. For further details on the sites, please see the Data S2.

In these chronologies, it is common for human remains to be found in disarticulation due to the anthropogenic and natural disturbance processes that sometimes affect prehistoric collective burials sites (Moreno-Ibáñez et al., 2022). Consequently, in cases where

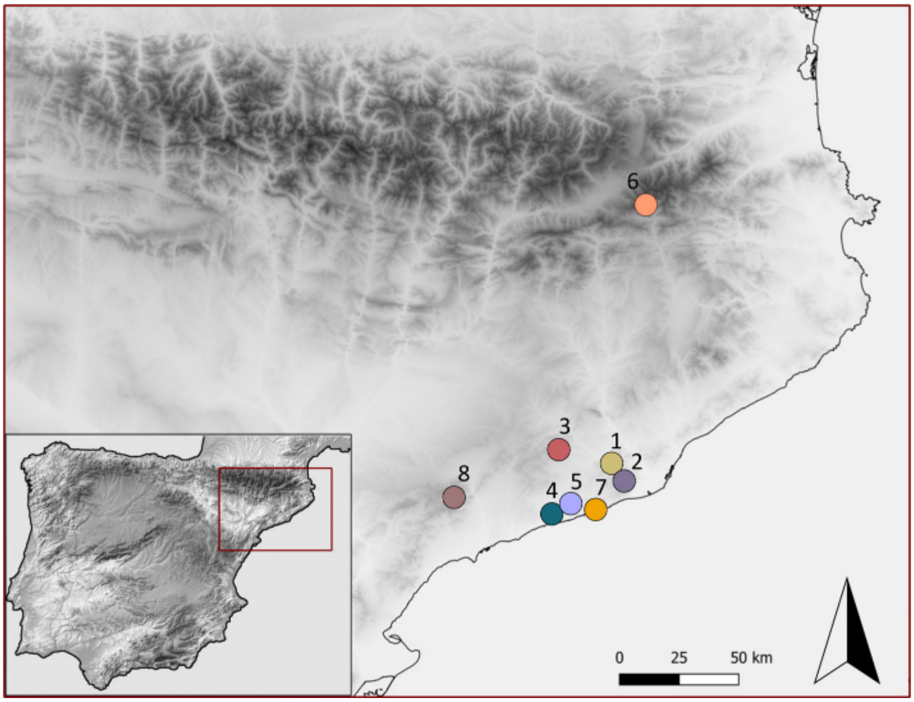

FIGURE 1 Digital elevation map and hillshade map showing the location of the sites employed in this study. Archeological sites: 1. Cova de l'Avi; 2. Cova de Can Sadurní; 3. Cova de la Guineu; 4. Cova Foradada; 5. Cova del Trader; 6. Roc de les Orenetes; 7. Cova del Gegant; 8. Cova dels Galls Carboners.

TABLE 1 Archeological sites, locations, chronology, MNI based on the dentition, and the final sample with preserved dental microwear of adult individuals.

Site	Location	Chronology	MNI	Preserved dental microwear sample
Cova de l'Avi	Vallirana, Barcelona	MN-LN	9	7 M2LL
Cova de Can Sadurní	Begues, Barcelona	LN-C	34	21 M1LR
Cova de la Guineu	Font-Rubí, Barcelona	LN-C	77	29 M2LL
Cova Foradada	Calafell, Tarragona	LN-C	8	5 P3LL
Cova del Trader	Cubelles, Barcelona	LN-C-BA	5	1 M3LR
Roc de les Orenetes	Queralbs, Girona	LC-EBA	51	4 M1LR, 5 M1LL, 4 M2LL, 2M2LR
Cova del Gegant	Sitges, Barcelona	MBA	19	1 P3LL, 1 P3LR, 1 P3UR, 1 P4UL, 1 M1LR, 1 M2LL
Cova dels Galls Carboners	Mont-ral, Tarragona	MBA	6	4 M2LR

Note: Nomenclature: Abbreviations for tooth types correspond to jaw (upper or lower: U or L), side (left or right: L or R), and position in the tooth row (third or fourth for premolar: (P3) or (P4) and first, second or third for molars: (M1) (M2) or (M3)). Chronology: MN-LN, Middle-Late Neolithic; LN-C, Late Neolithic-Chalcolithic; LN-C-BA, Late Neolithic-Chalcolithic-Bronze Age; LC-EBA, Late Chalcolithic-Early Bronze Age; MBA, Middle Bronze Age.

dental remains were not individually identified, a Minimum Number of Individuals (MNI) analysis was conducted based on the permanent dentition. Only one tooth per individual was selected, with a preference for lower molars (second and first molar) (Estebaranz et al., 2009; Lalueza-Fox et al., 1996; Pérez-Pérez et al., 1994). Previous research has demonstrated that there are no significant differences in the buccal microwear pattern based on tooth laterality (Estebaranz et al., 2009; Lalueza-Fox et al., 1996; Pérez-Pérez et al., 1994). Consequently, if neither of these two teeth exhibited a clear microwear pattern, the next prioritized was the lower second premolar, followed by the mandibular first premolar or the mandibular M3 in the absence of suitable options. In the case where there was no lower tooth, the selection process continued with the upper dentition. (Estebaranz et al., 2009; Gluitz et al., 2023; Lalueza-Fox et al., 1996; Pérez-Pérez et al., 1994). For further details on sample selection, please see the Data S2.

3 | METHODS

3.1 | Cleaning and casting procedures

Prior to microscopic analysis, the original teeth were cleaned with cotton swabs soaked in 99% acetone to remove any adhering dust or residues (Galbany et al., 2004). Whenever possible, the dental remains were observed directly under the microscope. However, in some cases (e.g., when the teeth were in situ in the jaws), high-resolution casts were made to facilitate manipulation under the microscope.

Polyvinylsiloxane (Coltène President Plus Jet regular body) was used to make two molds of each tooth. The second impression was selected to produce the high resolution casts (Epo-Tek 301, Epoxy Technology, Inc). Contrary to SEM analysis, observation under the optical microscope does not require to sputter coat the replica with a layer of gold, which is an expensive and time-consuming process (Hernando, Fernández-Marchena, et al., 2020).

3.2 | Buccal microwear analysis using the optical microscope (OM)

The dental remains were observed with a ZEISS Axioscope A1 optical microscope held in Institut Català de Paleoecologia Humana i Evolució Social (IPHES, Tarragona). The camera used with the OM was a 6.3 MP Color Blackfly S USB 3.0 camera, 1/1.8″, FLIR, and the software used to control image acquisition was Kivy Capture MIC Z.

Tooth orientation was standardized by keeping the occlusal side at the top. Micrographs were taken at 100× on the medial third of the buccal surfaces with a horizontal field of view of 1464 μm in keeping with the parameters established in Hernando, Fernández-Marchena, et al. (2020). The resulting images were processed with the Helicon Focus 5.3 image processing program (Plisson & Zotkina, 2015), using the pyramidal C-mount method, which eliminates common image distortions caused by highly reflective material such as dental enamel (Hernando, Fernández-Marchena, et al., 2020).

3.3 | Image processing and quantification

After image acquisition, the images were cropped to an area of 0.56 mm^2 (Pérez-Pérez et al., 1994). The total number of striations (TN), the average striation length (XT, in μm) and the orientation of each striation was recorded semi-automatically with the open-access software, ImageJ®.

Following the established methodology with the Scanning Electron Microscope (Pérez-Pérez et al., 1994; Pérez-Pérez et al., 2003), the orientation of each striation was classified in 45° intervals: horizontal (H) (0°–22.5°; 157.5°–180°), vertical (V) (67.5°–112.5°), mesiodistal (MD) (Lower Left Molar/Upper Right Molar [LL/UR]: 112.5°–157.5°; Upper Left Molar/Lower Right Molar [UL/LR]: 22.5°–67.5°); distomesial (DM) (Lower Left Molar/Upper Right Molar [LL/UR]: 22.5°–67.5°; Upper Left Molar/ Lower Right Molar [UL/LR]: 112.5°–157.5°). The last two depend on the side of the tooth and whether it is a mandibular or maxillary tooth. Two indexes were calculated: the number of horizontal striations/total number of striations (NH/TN) and the number of vertical striations/total number of striations (NV/TN) (Lalueza-Fox et al., 1996).

In addition, this study explores, for the first time, the maximum width of buccal striations (W). This variable has been used in other studies focusing on occlusal and incisal surfaces (García-González et al., 2015; Mahoney, 2007; Schmidt, 2001; Ungar, 1994), but it has been applied for the first time on buccal surfaces in this work. Therefore, from each micrograph the five widest striations were recorded (in μm) to obtain the mean value (see Data S1).

One author (RH) was responsible for measuring all observed microwear. In order to evaluate intra-observer consistency (Galbany et al., 2005), three micrographs were selected and counted three times on different days (see Data S3 [Table S1]).

3.4 | Open data repository

In an effort to create a reference data- and image-set for future research and to ensure transparency, the complete raw database has been made available in an open repository together with all the archeological sample micrographs obtained with the OM and the micrograph with the counted striations (see link: 10.5281/zenodo.10372048).

3.5 | Interpretation of microwear variables

The total number of striations (TN) is one of the most crucial variables and provides information on the abrasiveness of the diet. This abrasiveness is directly related to the physical and mechanical properties of the consumed foods (Grine, 1986; Lalueza-Fox et al., 1996; Pérez-Pérez et al., 1994). Chewing foods that are more abrasive than enamel, such as cereals (due to their phytoliths), tends to result in higher TN values (Daegling et al., 2016; Gügel et al., 2001; Rodriguez-Rojas et al., 2020; Xia et al., 2015). Additionally, high abrasiveness can be attributed to the inclusion of extrinsic particles in food due to different processing strategies. For example, milling can introduce mineral particles into food from the disaggregation of rocks during the process (Molleson et al., 1993; Romero et al., 2012; Teaford et al., 2001; Teaford & Lytle, 1996). Therefore, the interpretation of TN values should take into consideration not only the characteristics of the foods consumed, but also the processing methods employed by the groups under study.

The maximum width of buccal striations (W) serves as an indicator of food hardness, revealing the presence of coarse particles that give rise to striations of greater width, while narrower striations are associated with highly processed foods (García-González et al., 2015; Mahoney, 2007; Schmidt, 2001). Lastly, the length of the striations (XT) is influenced not only by the hardness of the foods but also by the direction and dynamics exerted by the oral muscles during chewing (Pérez-Pérez et al., 1994). Longer XT are related to products that require a longer time to chew, such as tough foods that require a shearing movement during chewing (Pérez-Pérez et al., 1994).

4 | RESULTS

From the 209 individuals analyzed, buccal dental microwear was well preserved on 88 permanent teeth (44% of the total number). The detailed list of buccal microwear data by individual can be found in

TABLE 2 Descriptive statistics for buccal microwear variables by group (CA, Cova de l'Avi; CS, Cova de Can Sadurní; GN, Cova de la Guineu; FO, Cova Foradada; RO, Roc de les Orenetes; CG, Cova del Gegant; GC, Cova dels Galls Carboners).

Variable		CA	CS	GN	FO	RO	CG	GC
TN	Mean	135.8	104.2	125.8	121	97.2	114.2	95.3
	Median	141	104	122	128	96	117.5	94.5
	IQR	117–149	97–111.5	113–138	109–129.5	94–104	101.5–101.8	86.5–104.8
	SE	6.9	2.2	2.9	5.5	1.7	4.2	4.9
	SD	18.3	10	16	12.4	6.4	10.3	9.8
	CV	13.5	9.6	12.7	10.2	6.6	9.1	10.3
XT	Mean	228.3	241.22	231.91	221.1	260.3	198.1	232.6
	Median	232.66	241.9	225.1	227.90	265	196.7	236.6
	IQR	215.3–244.7	221–263.5	215.5–245.8	201.9–236.9	238.5–271.5	168.6–230.8	215–246.2
	SE	7.4	5.8	4.6	8.8	6.3	14.7	8.7
	SD	19.7	26.6	24.5	19.6	24.3	36.1	17.3
	CV	8.6	11	10.6	8.9	9	18.2	7.44
NV/TN	Mean	0.6	0.5	0.5	0.6	0.5	0.5	0.5
	Median	0.6	0.5	0.5	0.52	0.5	0.5	0.5
	IQR	0.5–0.7	0.4–0.6	0.4–0.6	0.5–0.7	0.5–0.6	0.4–0.6	0.4–0.6
	SE	0.03	0.02	0.02	0.05	0.02	0.03	0.05
	SD	0.09	0.10	0.11	0.10	0.09	0.08	0.09
	CV	16.3	20	22.4	18.2	17	17	19.14
NH/TN	Mean	0.1	0.1	0.1	0.1	0.1	0.10	0.2
	Median	0.1	0.12	0.1	0.1	0.1	0.10	0.1
	IQR	0.1–0.14	0.06–0.15	0.07–0.13	0.03–0.11	0.05–0.13	0.06–0.14	0.14–0.16
	SE	0.02	0.01	0.01	0.02	0.01	0.02	0.01
	SD	0.04	0.05	0.05	0.04	0.05	0.04	0.02
	CV	36.4	45.5	50	57.1	55.6	40	13.3
W	Mean	9.6	7.1	6.9	8.5	4.5	14.8	7.2
	Median	9.4	7.1	6.40	8.5	4.6	12.4	7.6
	IQR	8.7–10.3	6–8.5	5.8–7.8	7.4–9.6	3.5–5.3	8.9–21.1	5.1–8.8
	SE	0.4	0.4	0.3	0.6	0.3	2.9	1.1
	SD	1.2	1.7	1.7	1.4	1.1	7.2	2.1
	CV	11.9	24.1	23.9	15.9	23.5	48.8	29.28

Abbreviations: TN, total number of striations; XT, length of striations (in μm); W, the maximum width of the buccal striation (in μm); NH/TN, horizontal index; NV/TN, vertical index. CV, coefficient of variation; IQR, interquartile range; SD, standard deviation; SE, standard error).

the Data S3 (Table S2). The inevitable reduction in the sample size is a typical consequence of various taphonomic factors. Teeth with severe evidence of post-mortem damage were excluded from the analysis (Correia et al., 2020; Hernando, Fernández-Marchena, et al., 2020; Hernando, Willman, et al., 2022; Krueger, 2016; Teaford, 2007).

The descriptive statistics for the buccal dental microwear variables of each sample are summarized in Table 2. All statistical analyses were conducted with R studio, using the packages dplyr, ggplot2, gridExtra, ggpubr, ggsci, grid, and FSA (Auguie et al., 2017; Kassambara, 2020; Ogle et al., 2022; R Core Team, 2020; Wickham, 2016; Wickham et al., 2020; Xiao, 2018). First, a Shapiro–Wilk test was done which indicated a deviation from normal distribution (see Data S3 [Table S3]). This, together with the sample size of each sample, required the use of non-parametric statistics. We therefore chose the Kruskal-Wallis test for comparison among samples. When comparing buccal microwear variables across samples, we observed statistically significant differences between samples in the total number of striations, striation length, and the maximum striation width (TN; Kruskal-Wallis: $X2 = 50.5$, $p = 3.74e\text{-}09$; XT; Kruskal-Wallis: $X2 = 20.6$, $p = 0.003$; W; Kruskal-Wallis: $X2 = 45.3$, $p = 4.096e\text{-}08$) (Figure 2). In contrast, no statistically significant differences were found among samples for the vertical and horizontal indexes (NV/TN; Kruskal-Wallis: $X2 = 4.9$, $p = 0.547$; NH/TN; Kruskal-Wallis: $X2 = 8.2$, $p = 0.226$) (See Data S3 [Figure S1]).

We performed post hoc Dunn tests with the Holm's adjustment in order to identify any significant differences between samples (Table 3). Finally, a Principal Component Analysis (PCA) on the covariance matrix was used to identify differences or similarities between the different samples based on the dental microwear variables that showed statistically significant differences (TN, W and XT). The first two principal components (PC1, PC2) explained 75.62% of the total sample variation (Table 4, Figure 3). There was overlap among samples; however, three samples (Cova de Can Sadurní, Cova dels Galls Carboners and Roc de les Orenetes) display low PC1 values with clearly differentiated trends, with a 95% confidence interval of the mean, from the other samples (Cova de l'Avi, Cova de la Guineu, Cova Foradada and Cova del Gegant) which display high PC1 values. Meanwhile, on the PC2 axis, we found that all of the groups overlapped except Cova del Gegant, which exhibited the most different central trend (Figure 3).

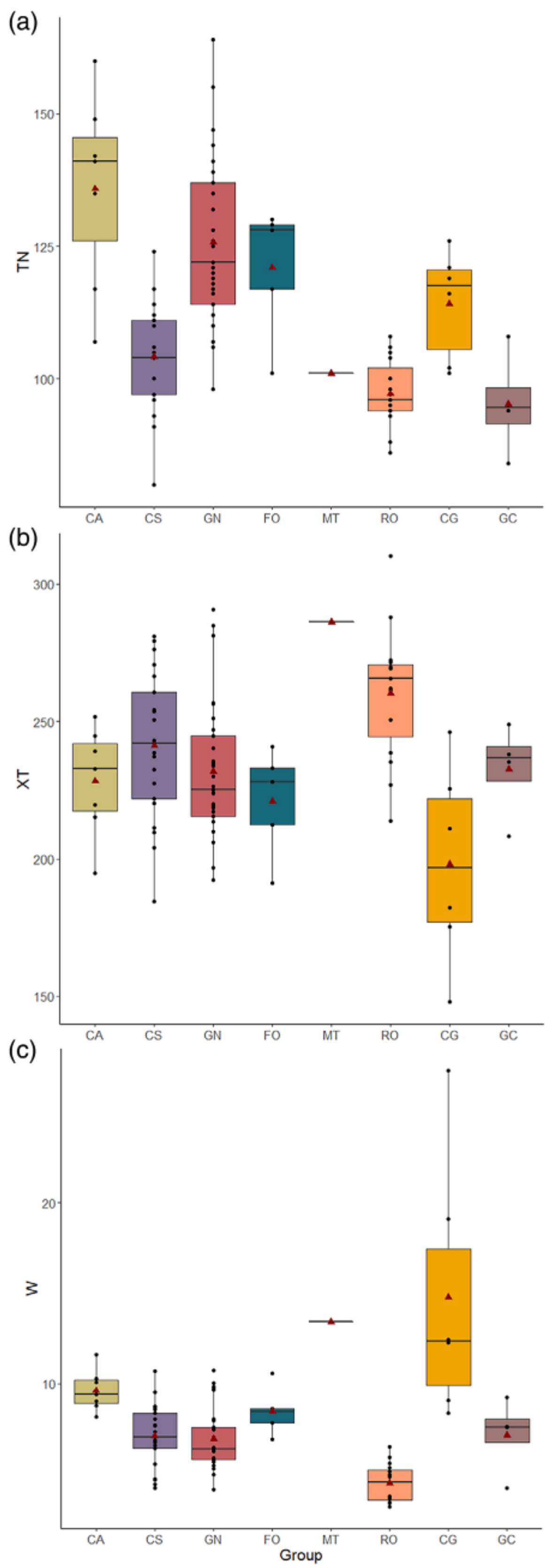

FIGURE 2 Boxplot showing (a) the total number (TN); (b) the length (XT, in μm) and (c) the maximum width of buccal striations (W, in μm) of buccal striations by group. Red triangles show the means; middle horizontal lines represent the medians. The length of the whiskers correspond to +/− 1.5*IQR. Group: CA, Cova de l'Avi; CS, Cova de Can Sadurní; GN, Cova de la Guineu; FO, Cova Foradada; MT, Cova del Trader; RO, Roc de les Orenetes; CG, Cova del Gegant; GC, Cova dels Galls Carboners.

5 | DISCUSSION

5.1 | Characterization of the diet of NE Iberian samples

To better understand the characterization of the diet and subsistence strategies of NE Iberian samples, additional approaches have been incorporated to offer a comprehensive perspective of their dietary choices (Table 5).

Through various studies on human dental microwear, a diachronic transition has been observed from the Late Neolithic to the Middle Bronze Age in food processing strategies towards more refined and processed diets (García-González et al., 2018; Gluitz et al., 2023; Hernando, Willman, et al., 2020; Polo-Cerdá et al., 2007; Romero & De Juan, 2007). The increased use of ceramic cooking utensils had an impact on the physical composition of food, resulting in a softer diet that reduced bite force and subsequently led to changes in microwear patterns (Bullington, 1991; Molleson et al., 1993; Schmidt et al., 2015; Schmidt et al., 2019). In our study, no clear chronological distinction could be made in the dietary pattern of these samples based upon their microwear patterns. However, the archeological groups separated into two microwear sets with statistically significant differences between them. One set comprises individuals from Cova de l'Avi, Cova de la Guineu, Cova Foradada, and Cova del Gegant, while the other set consists of specimens from Roc de les Orenetes, Cova de Can Sadurní, and Cova dels Galls Carboners. The results highlight TN as the most explanatory variable. Among the set with a higher number of striations, individuals from Cova de l'Avi exhibited significantly higher means (Table 2; Figure 2), suggesting an abrasive diet, as evidenced by their elevated levels of macrowear (Daura et al., 2015). In addition, a lower caries rate (2.6%) was observed in this group (Daura et al., 2015), as a highly abrasive diet results in a relatively rapid occlusal macrowear ratio, which prevents plaque adhesion on dental

TABLE 3 Dunn post hoc test with Holm's adjustment for multiple comparisons of the total number of striations (TN), the length (XT) and the maximum width of buccal striations (W) variable between groups (CA, Cova de l'Avi; CS, Cova de Can Sadurní; GN, Cova de la Guineu; FO, Cova Foradada; RO, Roc de les Orenetes; CG, Cova del Gegant; GC, Cova dels Galls Carboners).

TN	CA	CG	CS	FO	GC	GN
CG	1.000	X				
CS	0.005*	1.000	X			
FO	1.000	1.000	0.397	X		
GC	0.008*	0.529	1.000	0.176	X	
GN	1.000	1.000	2.04e-13*	1.000	0.011	X
RO	3.72e-45*	0.167	1.000	0.030*	0.912	2.89e-26*
XT	CA	CG	CS	FO	GC	GN
CG	1.000	X				
CS	1.000	0.156	X			
FO	1.000	1.000	1.000	X		
GC	1.000	1.000	1.000	1.000	X	
GN	0.922	1.000	1.000	1.000	1.000	X
RO	0.316	0.002*	1.000	0.149	1.000	0.022*
W	CA	CG	CS	FO	GC	GN
CG	1.000	X				
CS	0.165	0.054	X			
FO	1.000	1.000	1.000	X		
GC	0.851	0.490	0.942	1.000	X	
GN	0.047*	0.014*	1.000	0.936	1.000	X
RO	6.15e-06*	1.69e-06*	0.003*	0.003*	0.256	0.009*

*There is a significant difference ($\alpha = 0.05$) between groups.

TABLE 4 Principle component analysis eigenvalues and factor loadings.

Factors	Eigenvalue	% variance	% cumulative variance
PC1	1.384	46.16	46.16
PC2	0.883	29.46	75.62
PC3	0.731	24.37	100

surfaces, thus reducing the likelihood of caries (Esclaressan et al., 2009; Lunt, 1974; Maat & Van der Velde, 1987).

The individuals from Cova de la Guineu exhibited a similar pattern to those from Cova de l'Avi, characterized by high striation values. Previous isotopic analyses have suggested that these individuals had a mixed diet (Villalba-Mouco et al., 2018). Consequently, the high abrasiveness observed in the diet of these individuals cannot be attributed to a specific foodstuff, such as for example a main intake of cereals. Instead, it is more likely associated with the inclusion of extrinsic particles resulting from processing methods, such as grit from millstones or environmental contamination by particles like soil, ash, or dust (Polo-Cerdá et al., 2007; Romero et al., 2013). This assumption is supported by the dental microwear texture analysis conducted on the occlusal surface of the teeth of the same individuals from Cova de la Guineu, which also indicates a highly abrasive diet, as evidenced by the higher complexities (Asfc) (Hernando, Willman, et al., 2022). Notably, significant differences were observed in the maximum width of the striations (W) in the Cova de la Guineu samples, which exhibited finer striations (see Figures 2d, 4d and Table 3). This result is interesting because it revealed a very abrasive microwear pattern formed by very fine striations, suggesting a processing method that added a substantial quantity of small extrinsic particles to the food. These particles may have originated from environmental sources or from the raw materials of the millstone. In this case, Cova de la Guineu functioned only as a burial cave (Oms et al., 2016), so there are no associated millstones. However, some settlement sites from the Catalan Pre-Coastal Range—Mas d'en Boixos and Cinc Ponts—have yielded abundant millstones made of granite and sandstone (Bouso et al., 2004; Esteve et al., 2012), both rich in quartz and known to leave particles from the disaggregation of the rock during milling. These particles, when mixed with food, lead to a significant accumulation of fine striations on the dental enamel. In other words, prolonged processing with millstones would diminish the size of these extrinsic particles but would not eliminate them, resulting in finer striations. This hypothesis could be supported by the high prevalence of caries observed (13.1%), higher than Cova Foradada but lower than Can Sadurní and Cova dels Galls Carboners (Table 5; Data S2). This could be attributed to how these foods were processed. Cereals and other plant-products consumed with soft and sticky textures, such as porridge are highly cariogenic because their texture means they adhere to dental fissures and interproximal surfaces, causing cavities.

Similarly, the teeth of the individuals from Cova Foradada are characterized by a high number of striations, indicating an abrasive diet. The high frequency of caries (9.8%) in this group (Moreno-Ibáñez, 2023) points to the consumption of high carbohydrate

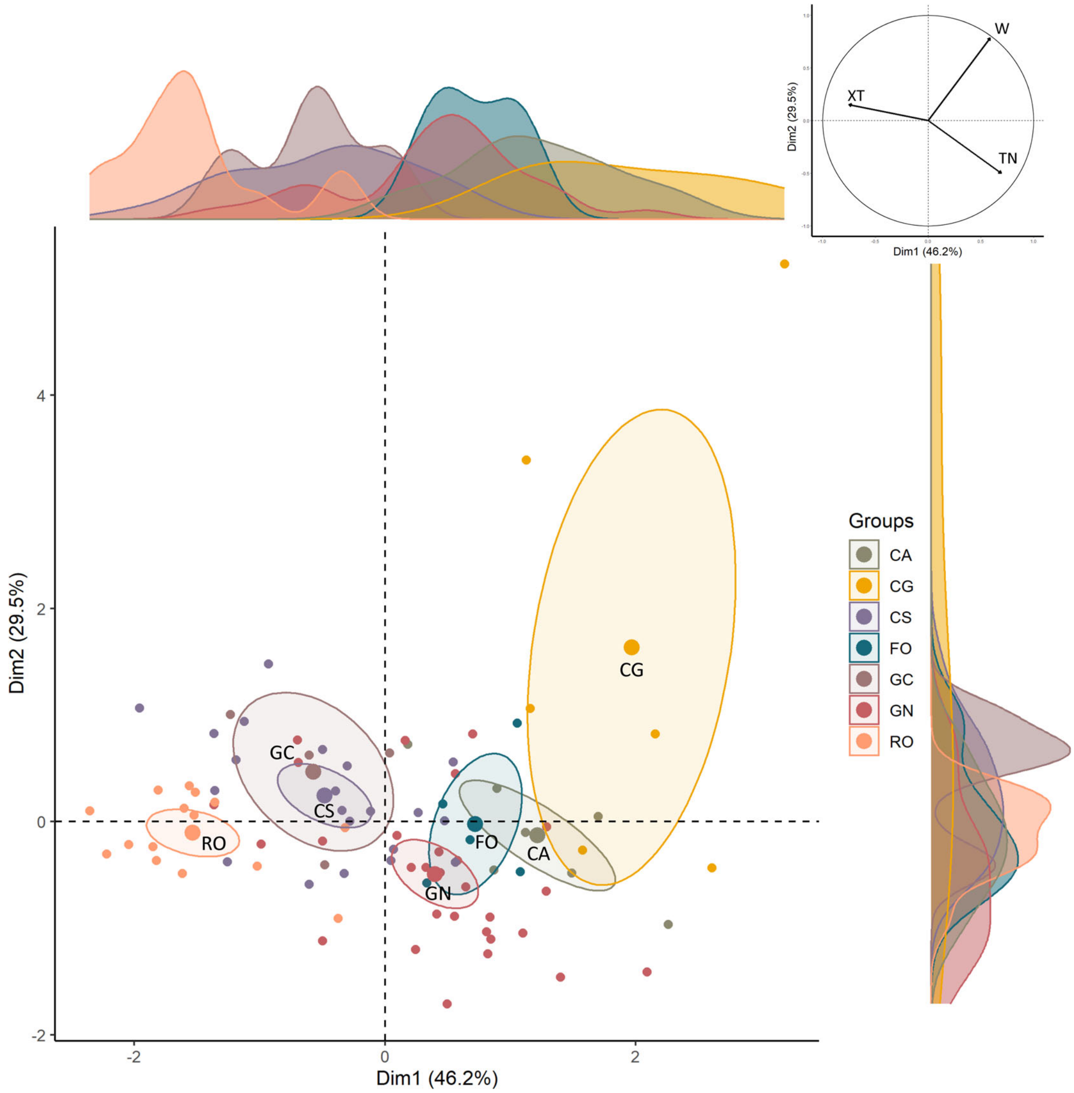

FIGURE 3 Principal component analysis representing variables with significant differences (TN, XT, W) for different groups. On the top of the PCA plot, we displayed density plots of PC1 and PC2 pooled by sites. Component 1 explains 46.2% of the variance, while component 2 explains 29.5% of the variance. The ellipses show the 95% confidence interval. Group: CA, Cova de l'Avi; CS, Cova de Can Sadurní; GN, Cova de la Guineu; FO, Cova Foradada; RO, Roc de les Orenetes; CG, Cova del Gegant; GC, Cova dels Galls Carboners.

foodstuff, such as cereals (Featherstone, 2008; Forshaw, 2014; Hillson, 1996), which is consistent with an abrasive microwear pattern. However, it is important to note that the representativeness of this group for dental microwear is limited, since the final sample was reduced to five individuals due to enamel loss caused by postdepositional damage. Further studies from different perspectives, such as dental calculus information or isotopic analysis, would be needed to corroborate this hypothesis.

The teeth of the individuals from Cova del Gegant exhibit a peculiar striation pattern characterized by very wide striations (W), indicative of a hard diet that includes large particles (Mahoney, 2007; Schmidt, 2001; Ungar, 1994) (see Figure 4c). These particles may come from the food itself—that is, hard foods that require fracturing during chewing—or from extrinsic environmental particles that contaminated the food during the preparation process. Additionally, these individuals were found to have higher values of TN than contemporaneous Middle Bronze Age group (Cova del Galls Carboners). Previous studies on oral pathologies indicated a diet that could be related to a carbohydrate intake (Daura et al., 2017). It is important to note that this group displays high intragroup variability in W and XT. However, it was observed that all individuals exhibited wide striations, suggesting a consistent pattern of dental microwear within the group despite individual variations.

In contrast, individuals from Cova de Can Sadurní exhibit significant differences in TN compared to their contemporaneous groups, resembling more closely the recent groups characterized by a lower number of striations. These values could be attributed to a highly processed diet, which may also include the consumption of foods that are softer than tooth enamel, such as meat and its secondary products (Hua et al., 2015; Organ et al., 2005; Romero et al., 2013). In this

TABLE 5 Detailed comparison between the dental microwear data collected in this study and previously published dietary information from different proxies for the analyzed archeological sites. The asterisks (*) in the table indicate the frequency of each proxy, with * representing 'scarce,' ** representing 'moderate,' and *** indicating 'abundant'.

	Buccal dental microwear		Caries		Stable isotopes		Dental calculus		Buccal DMTA		Dental macrowear	
Site	Data	Interpretation	Data	Sources	Data	Sources	Data	Sources	Data	Sources	Data	Source
Cova de l'Avi	***TN	Abrasive diet	*	Daura et al. (2015)							***	Daura et al. (2015)
Cova de Can Sadurní	*TN	Soft diet	***	Roca (2012)	Mixed diet	Alvarado (2017)	***	Roca (2012)				
Cova de la Guineu	***TN *W	Abrasive diet	***	Lozano report, in this study	Mixed diet	Villalba-Mouco et al. (2018)			****Asfc*	Hernando, Willman, et al. (2022)		
Cova Foradada	**TN **W	Abrasive diet	**	Moreno-Ibáñez (2023)								
Cova del Trader	**XT **W	Abrasive diet	**	Morales et al. (2023)			***	Morales et al. (2023)				
Roc de les Orenetes	*TN *W ***XT	Soft diet	*	Moreno-Ibáñez (2023)			**	Moreno-Ibáñez (2023)			**	Moreno-Ibáñez (2023)
Cova del Gegant	***W	Hard diet										
Cova dels Galls Carboners	*TN	Soft diet or highly processed food	***	Lozano report, in this study			*	Lozano report, in this study			*	Lozano report, in this study

Abbreviation: Asfc, Complexity; DMTA, dental microwear texture analysis.

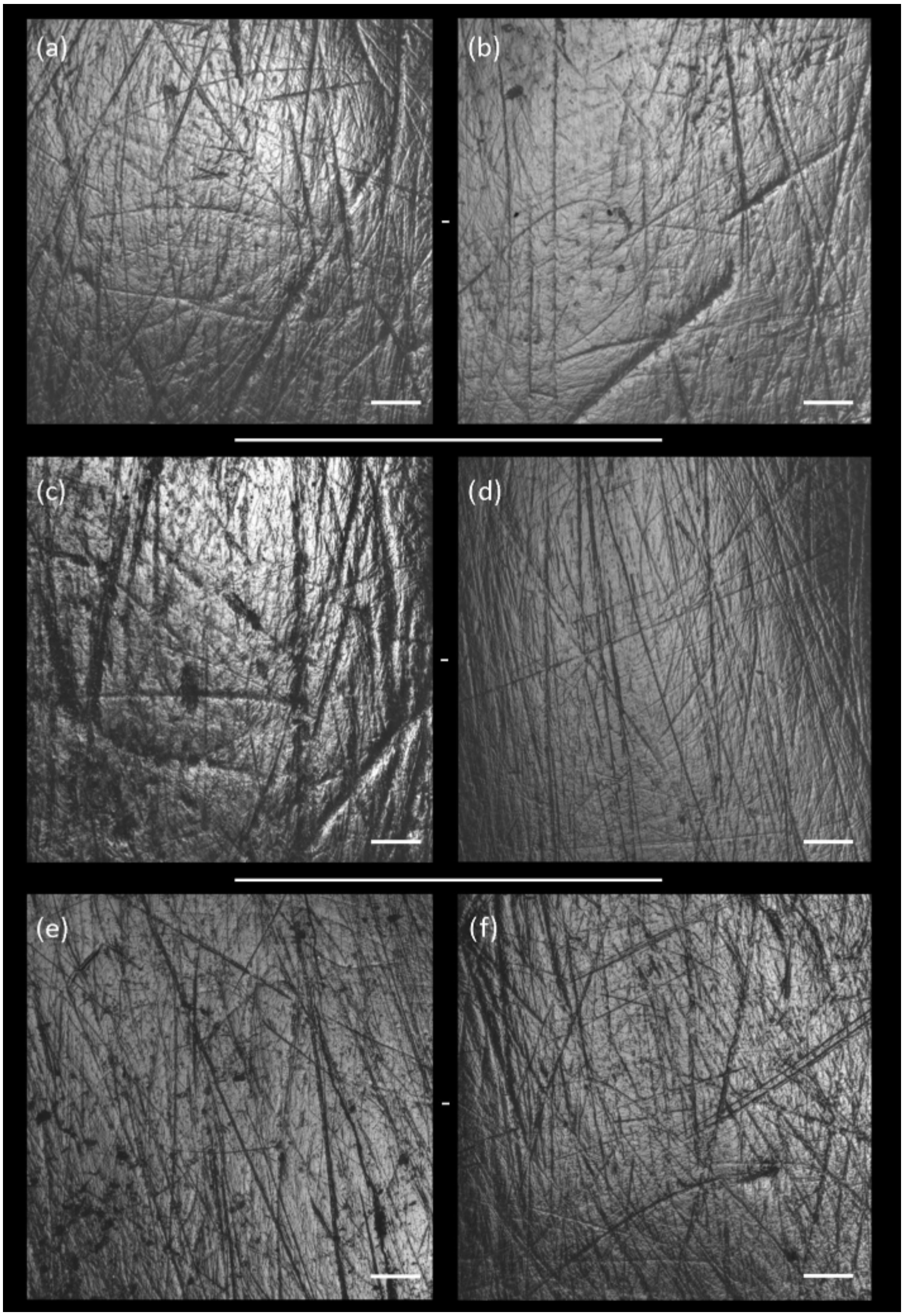

FIGURE 4 Dental microwear images showing differences between surfaces. (a) Cova de l'Avi individual with high number of striations (TN = 149); (b) Cova dels Galls Carboners individual with low number of striations (TN = 108); (c) Cova del Gegant individual high maximum width of buccal striations (W = 27.29); (d) Cova de la Guineu individual with low maximum width of buccal striations (W = 6.28); (e) Roc de les Orenetes individual with short length of striations (XT = 269.44); (f) Cova de Can Sadurní individual with long length of striations (XT = 276.34). Scale: 100 μm.

regard, several food processing techniques can reduce a food's hardness, including the use of pottery or improved food grinding techniques that introduced less grit into the diet (Polo-Cerdá et al., 2007; Romero et al., 2013; Schmidt et al., 2015; Schmidt et al., 2019; Teaford & Lytle, 1996). The isotopic analysis of $\delta^{13}C$ and $\delta^{15}N$ in these individuals revealed a mixed diet characterized by the high consumption of animal protein and freshwater resources, as well as a significant dependence on agricultural products (Alvarado, 2017). Moreover, studies of dental pathologies found high levels of caries (16.8%) and dental calculus, which was associated with a carbohydrate-rich diet (Roca, 2012). Taking into account the mixed diet proposed by previous studies, our results suggest that food processing techniques used by this group were more refined than those of the other groups analyzed.

In general terms, most of the groups analyzed in this study exhibit a certain degree of intrapopulation variability. Therefore, a single individual, such as in the case of Cova del Trader, is not indicative of a specific type of diet, beyond being included within the mixed diet typical of these communities in the late Prehistory.

Regarding the variables TN, XT, and W, the individuals from Roc de les Orenetes exhibited the most significant differences compared to the other groups. As previously stated, these individuals together with Cova de Can Sadurní, and Cova dels Galls Carboners, exhibit fewer striations than other groups (Figure 2). This is indicative of a soft diet resulting from food preparation practices that reduce the hardness of the foodstuff, such as boiling with pottery or refined grinding, as noted by Schmidt (2001, 2019, 2015). Alternatively, these results could be attributable to the characteristics of the types of food consumed (Hua et al., 2015; Lalueza-Fox et al., 1996; Romero et al., 2012; Schmidt et al., 2019) or secondary products. Paleopathological studies are currently being conducted on these individuals and have revealed a high degree of periodontal disease, associated with a high frequency of dental calculus along with a low prevalence of caries (1.8%) (Moreno-Ibáñez, 2023; Moreno-Ibáñez et al., 2024). This indicates high consumption of animal protein or secondary products (Campillo, 2001; Humphrey et al., 2014; Keenleyside, 2008).

Meat is typically softer than dental enamel, which results in lower and finer striation frequencies than plant-based foods (Hua et al., 2015; Lalueza-Fox et al., 1996; Romero et al., 2012). However, meats that are 'tender' due to their origin from immature animals or prior processing to transform their physical properties require reduced masticatory effort (García-González et al., 2018; Organ et al., 2005). In contrast, meats that are 'tough' or minimally processed require significant masticatory effort and a high shear force during chewing in order to cut through them (El-Zaatari, 2010; Krueger et al., 2021). This results in longer striations (XT) on the buccal surfaces (García-González et al., 2018; Pérez-Pérez et al., 1994), as observed in the case of Roc de les Orenetes individuals, who exhibit significant differences compared to the other groups (Figure 2b). The information from the dental microwear coupled with the documentation of oral pathologies lead us to suggest a diet with a high degree of dependence on the consumption of "tough" meat, complemented by processed agricultural products. We propose a subsistence economy for the Roc de les Orenetes individuals based primarily on meat or secondary products, with plant-based foods being less prominent in their diet. Future isotopic studies could complement this hypothesis to determine the types of foods consumed.

Finally, the individuals from Cova dels Galls Carboners have a lower number of striations (Figure 4b). In addition, studies on the oral pathologies of these individuals currently being carried out reveal a high frequency of caries (17.8%) along with low levels of dental macrowear, affecting both adults and children (see Data S2). This is indicative of a diet high in cariogenic foods. Within the mixed diet expected for these Middle Bronze Age populations, these individuals would have had a high degree of refinement in food processing and cooking techniques, allowing for the consumption of foods such as porridges, which are less abrasive and would explain the high frequency of caries, low macrowear values and low number of striations.

5.2 | Contextualizing the dietary practices of these farming and livestock groups in the Iberian Peninsula context

Paleodietary reconstructions of late Prehistory groups in the Iberian Peninsula point to a mixed dietary pattern, including cereals and protein intake (Alt et al., 2016; Beck et al., 2018; Fernández-Crespo et al., 2021, Fernández-Crespo et al., 2016; García-González et al., 2018; Gluitz et al., 2023; Hernando, Cano, et al., 2022, Hernando, Willman, et al., 2020; Lillios et al., 2010; Lozano et al., 2022; McClure et al., 2011; Romero and De Juan, 2007; Valdiosera et al., 2018; Villalba-Mouco et al., 2018; Viñas-Caron et al., 2022). However, it is important to note that, while generally maintaining mixed dietary practices, these groups have been found to have differing degrees of dietary specialization (Díaz-Zorita Bonilla et al., 2019; Fontanals-Coll et al., 2016; Jones et al., 2019; López-Costas & Alexander, 2019; Waterman et al., 2014).

Within the context of the mixed diets expected among these late Prehistory groups, our findings highlight several multicausal dietary specializations. As discussed below, these dietary patterns were primarily influenced by factors such as their habitat, voluntary resource selection, the availability of material culture and technology, and to some extent, the chronological and cultural context. These outcomes underscore the complex and diverse nature of dietary practices in these groups, shaped by a multitude of factors that guided their food preferences and consumption patterns.

The evidence found at the Roc de les Orenetes site suggest that the diverse subsistence economies of these groups may have been heavily influenced by the habitat as it is situated in the Catalan Pre-Pyrenees, representing a high-altitude mountain site (Ramírez-Pedraza et al., 2020). Our dental microwear analysis, along with preliminary documentation of oral and metabolic pathologies (Moreno-Ibáñez, 2023), suggests a diet with a heavy reliance on meat consumption. These studies showed not only a low prevalence of caries (1.8%) and antemortem tooth loss (only one individual) but also specific cases of *cribra orbitalia* and porotic hyperostosis. Among the most common causes of these metabolic disorders are the iron, vitamin C or vitamin D deficiency (Walker et al., 2009). In the case of the Roc de les Orenetes individuals, the paleopathological evidence points to a possible vitamin C deficiency, which could potentially be linked to the predominant consumption of meat (Moreno-Ibáñez, 2023).

While there are ongoing debates regarding subsistence economies in high mountain regions during prehistory, specifically between more settled agricultural economies and transhumant pastoralism (Antolín et al., 2018; Gassiot et al., 2014; Montes et al., 2016; Remolins et al., 2016; Rojo-Guerra et al., 2013; Rojo-Guerra et al., 2015), elevated areas with harsher climatic conditions are often interpreted as seasonal camps with specific uses, frequently associated with a pastoral economy (Laborda et al., 2017; Montes et al., 2016; Oms et al., 2009; Rojo-Guerra et al., 2013). Examples of sites of this type include Cueva de los Cristales (Chalcolithic, 1320 meters above sea level, Huesca) and Cueva Drólica (Bell Beaker-Chalcolithic, at 1200 meters above sea level, Huesca). It has been suggested that the groups documented at these sites did not permanently reside in the mountains but rather made recurring visits (Villalba-Mouco et al., 2020) as they relied on transhumant pastoral practices (Laborda et al., 2017; Montes et al., 2016). Similarly, this pattern of seasonality has been observed at Cova Colomera, a contemporaneous Early Bronze Age site located in the Pre-Pyrenees of Lleida (Oms et al., 2009).

Although there are currently not enough data to propose a precise model of settlement and economic management for the Roc de les Orenetes group, we propose a subsistence economy based on regular meat consumption or secondary products, potentially linked to high-altitude pastoral practices. This pastoral economy is also suggested in Cova de Els Trocs (at an elevation of 1564 meters in Bisaurri, Huesca) with earlier chronologies (Early Neolithic) (Tejedor-Rodríguez et al., 2021). However, this does not exclude the possibility that cereals or other plant resources played a secondary role in their diet. Pastoralism could have been combined with the exploitation of high-altitude or valley pastures, as observed in other high-mountain communities such as Feixa del Moro (at 1335 meters above sea level in Juberri, Andorra) with Middle Neolithic chronologies (Fontanals-Coll, 2015, p. 203; Remolins et al., 2016). Similarly, strontium isotope analysis of individuals from Cueva de los Cristales indicates a territorial mobility pattern that has been associated with transhumance between high mountain areas and the valley, where both practices could have been developed (Villalba-Mouco et al., 2020).

Similarly, the Cova del Gegant group could have been influenced by its geographical setting, as the cave is in a coastal cliff. Diets that require higher bite pressures, such as those including large extrinsic particles, tend to create dental microwear features with wide and deep dental microwear features (Calandra et al., 2012; Schmidt, 2001; Schmidt et al., 2020; Ungar, 2015). Several studies have noted that coastal environments lead to increased diet abrasiveness (El-Zaatari, 2010; Mahoney, 2007; Schmidt et al., 2020). This is primarily due to the presence of sand particles in the food, which significantly heightens the abrasiveness of ingested items. Studies of the sedimentology of Cova del Gegant and adjacent areas have shown that during the Late Holocene, sediments were characterized by limestone and calcite sands with significant disintegration and high quantities of quartz grains (Daura et al., 2021). The wide striations observed in the teeth of the Cova del Gegant individuals are consistent with the idea of mixed diets, influenced by food processing and contamination by extrinsic particles in the environment. Moreover, extensive exchange networks were well established over considerable distances (Odriozola et al., 2017), allowing for the observation of different cultural and symbolic behaviors (Odriozola et al., 2019). This variability in cultural practices and symbolism may be reflected in the observed dietary patterns, suggesting distinct ways of life.

Turning back to the multicausal dietary specialization, another factor to consider is the voluntary choice of resources, where the chronological factor may have also played a role. This is exemplified by the case of the Cova de l'Avi (Middle-Late Neolithic) and Cova de Can Sadurní (Late Neolithic-Chalcolithic) sites, both situated in the same geographical area of the Garraf Massif (less than 10 kilometers apart). These groups were settled in close proximity to one another yet exhibited significantly divergent dietary regimes. While the Cova de l'Avi group had a mixed diet with the substantial inclusion of extrinsic particles resulting from food processing, at Cova de Can Sadurní, highly refined pre-processing of food can be inferred with distinctive characteristics that set it apart from other contemporaneous groups. This is relevant because dental morphology studies have suggested that the individuals from Cova de Can Sadurní could be a closed group with limited interactions to other groups (Gamarra et al., 2022; Pascual et al., 2018). This isolation may have led to distinct technological and cultural specializations in food processing for each group.

A pattern of groups inhabiting the same region with similar chronologies but different subsistence economies has also been documented in other areas of the northeastern Iberian Peninsula. A nearby example can be found in the Penedès region at the Middle Neolithic sites of Pujolet de Moja (Vilafranca del Penedès, Barcelona) and Hort d'en Grimau (Castellví de la Marca, Barcelona), located less than 11 kilometers apart. Isotopic analysis has revealed that individuals from Pujolet de Moja exhibited a dietary pattern more centered on pastoralism, while the community at Hort d'en Grimau was primarily characterized by agricultural activities. These findings reflect a group's deliberate choice of resources to exploit and its specialization in a specific subsistence activity (Fontanals-Coll et al., 2016).

However, we cannot rule out a difference in dietary patterns. This could also be attributed to a chronological factor, as Cova del Avi dates to the Middle to Late Neolithic period, while Can Sadurni dates to the Late Neolithic to Chalcolithic period.

5.3 | Caveats of dental microwear analysis in late prehistory human samples and perspectives

Despite our results and interpretations, some considerations should be addressed when working with human dental microwear. It is important to consider that the economic-cultural context of the Late Prehistory is complex which causes challenges when inferring the diets of past groups whose subsistence practices overlapped in spite of subtle differences in acquisition, preparation and consumption of food (Schmidt et al., 2019). Additionally, one of the major uncertainties in many bioarchaeological studies when analyzing collective burials in the late Prehistory is the inherent possibility of the presence of different burial phases, which could lead to significant variability within these assemblages. Although one possible solution would be obtaining direct radiocarbon dates for each individual, this is not always economically feasible or possible due to the disarticulation of the assemblages. While it is important to have this consideration in mind when extrapolating the results obtained to dietary interpretation, as it could be one of the factors conditioning the internal variability of each group, the results presented in this study have shown, and quantitatively corroborated, significant intergroup differences, as well as consistent and overall unique trends within each buried assemblage.

Finally, from a methodological perspective, it has been demonstrated that optical microscopy is a consistent and user-friendly method that provides good image resolution together with a series of economic and technical advantages for conducting these studies (Hernando, Fernández-Marchena, et al., 2020). However, it is essential to consider that this method is semiautomatic and comes with its intrinsic limitations. In this regard, the use of Dental Microwear

Texture Analysis (DMTA), although economically less accessible, offers a range of automated quantification possibilities that are relevant in the study of recent prehistoric groups, both on occlusal and buccal surfaces (Hernando, Willman, et al., 2022; Schmidt et al., 2019). Additionally, fractal analyses (SSFA) or the compilation of ISO parameters could allow for the exploration of other possibilities, such as more detailed topography and morphometry of the striations on the buccal surface.

6 | CONCLUSION

In conclusion, the diverse subsistence patterns among the Middle-Late Neolithic to Middle Bronze Age groups in the northeastern Iberian Peninsula are influenced by distinct dietary specializations within each group. These dietary practices evolved and become specialized in response to cultural, environmental, economic, and technological components specific to each group. Therefore, this study demonstrates that the integration of dental microwear with other proxies hold significant potential for detecting changes in the subsistence economies that frame the identity of a group.

AUTHOR CONTRIBUTIONS

R. Hernando: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); visualization (lead); writing – original draft (lead). **M. Á. Moreno-Ibáñez:** Funding acquisition (equal); writing – review and editing (equal). **E. Carbonell:** Funding acquisition (equal); writing – review and editing (equal). **A. Cebrià:** Funding acquisition (equal); writing – review and editing (equal). **J. Daura:** Funding acquisition (equal); writing – review and editing (equal). **C. Díez-Canseco:** Funding acquisition (equal); writing – review and editing (equal). **M. Edo:** Funding acquisition (equal); writing – review and editing (equal). **J. M. Fullola:** Funding acquisition (equal); writing – review and editing (equal). **J. I. Morales:** Funding acquisition (equal); writing – review and editing (equal). **F. X. Oms:** Funding acquisition (equal); writing – review and editing (equal). **I. Ramírez-Pedraza:** Funding acquisition (equal); writing – review and editing (equal). **M. Sanz:** Funding acquisition (equal); writing – review and editing (equal). **M. E. Subirá:** Funding acquisition (equal); writing – review and editing (equal). **C. Tornero:** Funding acquisition (equal); writing – review and editing (equal). **J. M. Vergès:** Funding acquisition (equal); writing – review and editing (equal). **M. Lozano:** Conceptualization (equal); formal analysis (equal); funding acquisition (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at https://onlinelibrary.wiley.com/doi/full/10.1002/ajpa.24950.

DATA AVAILABILITY STATEMENT

All data generated in this study is available in the "Supplementary Material, Methodology and Results" and in an Open Access Repository (10.5281/zenodo.10372048).

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SUPPORTING INFORMATION

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