

Selected Papers from the 3rd International Radiocarbon and Diet Conference, Oxford, 20-23 June 2023

#### CONFERENCE PAPER

# Correlation between dental microwear analysis and dietary habits of Neanderthal populations in the Iberian Peninsula

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Received: 03 October 2023; Revised: 26 February 2024; Accepted: 28 February 2024

Keywords: dental microwear; diet; Homo neanderthalensis; Iberian Peninsula

#### Abstract

The dietary habits of Neanderthals are considered an issue of great interest in the literature and have opened an important number of fruitful debates. Indeed, understanding diets can provide important information regarding issues of palaeoenvironmental reconstructions and subsistence strategies. In this respect, dental remains can play a vital role in the conducted efforts to reconstruct the palaeoecological niches securely and accurately since dental microwear analyses have precisely detected dietary patterns of the populations in the past. In this context, the Iberian Peninsula forms an interesting model for examining Neanderthal populations, their subsistence strategies, and adaptive skills. This study aims the examination of already published data in order to provide a holistic approach regarding the dietary habits of *H. neanderthalensis* populations in the Iberian Peninsula, along with the importance of the utilization of dental microwear analysis in the archaeological record.

# Introduction

The Iberian Peninsula is located in the southwestern part of the European continent and covers an extent of more than 583 km². The area is characterized by an abundance of geomorphological and environmental diversities, constituting a unique mosaic in every manifestation. Exhibiting sites such as Fuente Nueva 3, the Atapuerca sites, El Sidrón, and many more, it can be easily inferred that this specific geographical latitude played a major role in every aspect of human evolution from as early as the Early Pleistocene (Blain et al 2011; Espigares et al 2019). The abundance of well-dated sites and preserved remains regarding the lineage of *H. neanderthalensis* places the peninsula as a point of primary importance regarding hotly debated issues, such as the contacts between AMHs and Neanderthals (Yravedra et al 2015) and the temporal determination of the extinction of the latter, since it appears that the area functioned as a late refugium for the last populations of our closest ancestors (Zilhao 2000; 2006).

The dental microwear analysis is based on the detection of specific alterations on the enamel surface, which originate either from food consumption or by behavioral utilization of the teeth from the populations. These features, which are related to diet, mostly consist of striations and pits and are heavily dependent on several variables, such as the examined individual, the post-depositional processes, and the type of food, elements that can significantly disrupt the enamel profile (Espurz et al 2004). The possibility of intragroup variation regarding the microwear signatures has already been



exhibited in previous studies, exposing sexual and age separation with respect to masticatory activities (Pérez-Pérez et al 1994; Romero and de Juan 2007, for instance).

The first idea regarding the extraction of pieces of information to infer dietary habits from dental records is placed in the 1920s, when enamel striations were interpreted as indicators of chewing processes (Calandra et al 2019). However, it was only until the end of 1970s, that two pioneering works managed to provide a more stable methodological framework using scanning electron microscope on the occlusal views of mammalian teeth (Rensberger 1978; Walker et al 1978). During recent decades, technological development and the implementation of more enhanced microscopic applications have provided the opportunity to construct more stable methodologies and quantitative approaches. Nowadays, the most widespread methodology consists of examining the occlusal and buccal surfaces of the dental remains using a confocal microscope and a scanning electron microscope respectively, while at the same time, new types of microscopes are explored and utilized for the determination of dietary patterns, such as the digital microscope (Firmat et al 2010; Mihlbachler and Beatty 2012).

The microwear traces, which are produced during masticatory activities, such as pits and striations, can be detected on the occlusal and buccal surfaces of the dental remains, and occur from a variety of factors. Pits occur either when a particle is squeezed into the enamel surface (Mahoney 2006b), or as a consequence of acidic etching (King et al 1999), while the striations are the result of the tooth-food-tooth contact during the chewing cycle (Mills 1966). Regarding the latter, the quantification process predicts the delineation of the orientation of the observed striae on the enamel surface since studies have already depicted the importance of the comprehension of the jaw mechanics for the understanding of alimentary habits (Grine and Kay 1988; Williams et al 2009). Based on the proposed methodology by Lalueza Fox and Pérez-Pérez (1993), which enriched the existing framework of Puech et al (1980), the striations are attributed to four different orientations concerning their inclination, and more specifically are described either as horizontal (0°–22.5° or 157.5°–180°), disto-occlusal to mesio-cervical (22.5°–67.5°), vertical (67.5°–112.5°) or mesio-occlusal to disto-cervical (112.5°–157.5°).

The effect of non-alimentary activities on dental remains is revealed by the presence of striations, grooves, or chipping on the enamel surface. Explicitly, striations with characteristics of cut marks occur on the enamel tissue through the use of the mouth as a "third hand" for the stabilization of an object during the conduction of an activity, a practice, that has been identified in both the archaeological and ethnoarchaeological records (Lalueza Fox 1992; Lozano-Ruiz et al 2004). Grooves appear in the enamel surface in the morph of parallel striations (Frayer and Russell 1987), while their attribution to paramasticatory activities can be confirmed by the existence of polish within them, indicating tooth-picking behavior (Krueger and Ungar 2012). Finally, chipping on the dental tissue occurs through the process of holding or tearing different objects with the use of the alimentary apparatus (Fiorenza et al 2011a; Krueger 2015).

The dental features differ with respect to the view of the dental remain, since the examination of the buccal surfaces aims the detection of scratches, while the one of occlusal surfaces extracts information from scratches and pits. Raw meat is not hard enough to scratch dental enamel (Organ et al 2005). The microwear turnover, which can be attributed to the consumption of meat, can be better explained since the dried and though meat demands high chewing forces for a longer time, subsequently producing dental microwear. In some cases, individuals with a mainly based diet of meat show a high number of striations due to exogenous grit adhered to dental surfaces.

Furthermore, the use of grasses and plants in the diet is indicated by more worn facets with respect to the occlusal surfaces due to the abrasive composition of phytoliths, which is characterized by the existence of high levels of silica (Karriger et al 2016; Rodriguez-Rojas et al 2020). On buccal surfaces, this element can be recognized in the number and the orientation of scratches, since the specific part of the tooth is not directly exposed to the masticatory processes (Drtikolova Kaupova et al 2023). Important changes in the occlusal views regarding the tooth tissue can be attributed to tooth-to-tooth contact during the mastication process, as it has also been highlighted by experimental studies (Winkler et al 2020; Krueger et al 2021). Finally, microwear can also occur from the consumption of exogenous particles, such as sand, generic dirt, and ashes, which can be included in the food; this is the case mostly

when examining populations, which are placed in cold climates where the underground storage of meat is considered of vital importance for its long-term preservation (El-Zaatari 2008).

An important aspect for the undergone of dental microwear analysis is the production of replicas and the subsequent microscopic observations on the impression molds and casts. The production of the former is undergone with the use of silicone compound, while a study by Sawaura et al (2022) demonstrated that the most accurate result originates from the use of materials with medium viscosity, even though previous analyses have exhibited the importance of the use of compounds with low viscosities for the prevent of damage on the enamel and precise replications (Galbany et al 2006; Goodall et al 2015). For the latter, epoxy resins are the ones preferred due to their durable properties and their good possibilities regarding the production of precise imprints of the enamel surfaces of the tooth (Galbany et al 2004; Ungar et al 2019). Furthermore, the produced positives and negatives permit easy transportation among laboratories, providing convenience in the efforts for transmission and transfusion of knowledge in the scientific community. In the case of the examination of the buccal surface, the use of a conductive material such as a gold coat for the coverage and the subsequent non-exposure of the examined replica to the radiation of the scanning electron microscope prevents possible wear of the surface and loss of the archaeological information and permits a rational use of the SEM.

The examination of the buccal surface aims the detection of wear patterns, which suggest feeding habits and dietary hints (Pinilla Perez et al 2011; Pérez-Pérez et al 2017). An important aspect regarding the buccal surface is the understanding of dietary patterns throughout the lifetime of the individual since this specific view is not exposed to non-masticatory activities (Alrousan 2016). In this case, the microscopic observation is being held with the utilization of a scanning electron microscope, while the methodology predicts the coverage of the replicas in gold-coating for the avoidance of any alternation of the original enamel surface during the examination process.

Dental microwear analyses on the occlusal surfaces of dental remains have proven to provide important insights regarding issues of dietary reconstructions on both extinct and extant human or mammal populations (Arman et al 2016; Bas et al 2021; El-Zaatari 2008, 2010). Since the occlusal surface of the tooth is heavily exposed to masticatory activities, an important level of wear can be observed on this specific surface (Grine 1986). At the beginning of the discipline, the analysis was performed using a scanning electron microscope (SEM); subsequently, the confocal microscope was introduced, which eventually replaced SEM for the examination of the occlusal surfaces since it provides the opportunity for the obtainment of 2D and 3D proxies of the enamel surface (DeSantis et al 2013). Based on the functional identifications of Maier and Schneck, the upper and lower molars of hominins are characterized by 13 corresponding pairs of facets on their occlusal surfaces (1981; 1982). Previous studies have aimed the understanding of the mechanical processes on occlusal surfaces, indicating that the most heavily affected parts are the facets 9 and 11 in the cases of both deciduous and permanent molars (Bas et al 2020; Mahoney 2006a).

The aim of this study is the examination of Neanderthal sites from the Iberian Peninsula, in which dental microwear analysis has been conducted, along with the explanation of general issues concerning the dental microwear methodologies (Figure 1).

# Materials and Methods

This research is based on bibliographic data, which pertain to operated dental microwear analyses with respect to neanderthal remains of the iberian record to date. For this reason, the described sites have been sorted based on their chronology, from the oldest site to the youngest one (Table 1).

The Devil's Tower site in the southern part of the Iberian Peninsula presents impressive findings with decisive paleoanthropological interest. More specifically, the discovery of human remains identified as Neanderthals in 1926 in the Gibraltarian karstic system, along with the extraction of ancient DNA from the fossils during the last years has placed the site in the spotlight and has created important debates regarding palaeoecological issues. However, the non-existence of scientific formalities and excavation

Table 1. Do	ntal microwear	analyses	applied of	on Neanderthal	populations of	of the Iberian	record
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Site	Dating	Examined dental remains	n	Reference
Devil's	130,000-30,000 BP	L dM <sub>1</sub> /R dM <sub>2</sub>	2	Lalueza Fox and
Tower				Pérez-Pérez 1993
Figueira	106,000-86,000 BP	$LP^4$	1	Egocheaga et al 2004
Brava				
Axlor	49,300 BP	L dPM <sup>4</sup> /L dI <sup>1</sup>	2	Estalrrich and Marin-
				Arroyo 2021
El Sidrón	49,000 BP	LM <sub>2</sub> /RM <sup>1</sup> /LM <sub>2</sub> /LM <sub>2</sub> /LM <sub>1</sub> /	8	Estalrrich et al 2017
		$LM_2/LM_1/RM^1$		
El Salt	47,200-45,200 BP	UPM	1	Pérez-Pérez et al 2003
Zafarraya	46,700 BP	Undetermined	3	Krueger et al 2017
Sima de las	43,000-40,000 BP	$RM_2/LM_1$	2	Pérez-Pérez et al 2017
Palomas				
Total			19	

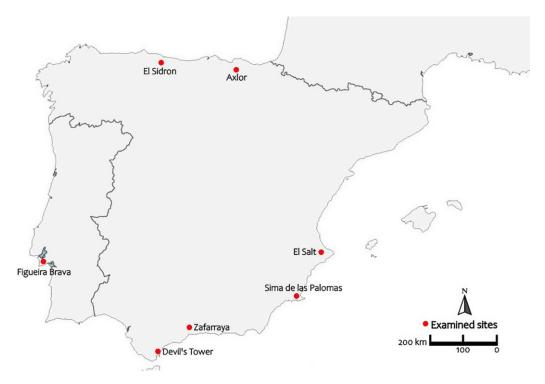


Figure 1. Geographic determination of the examined sites.

methods during the fieldwork has prevented a precise temporal specification of the findings, but a conventional one between 130 and 30 kya (Bokelmann et al 2019). The human remains at the site consist of a cranium and a mandible, which are attributed to a Neanderthal male child. Inside this context, the analysis of Lalueza-Fox and Pérez-Pérez (1993) focused on the buccal surfaces of the deciduous molars, aiming to extract pieces of information regarding dietary proxies.

Another Late Middle Pleistocene site with paleoanthropological interest attributed to Neanderthals, which includes dental remains as well, is Gruta da Figueira Brava on the eastern coast of the Peninsula. The site is dated between 106 and 86 kya and preserves an impressive record, which includes the

exploitation of marine resources (Nabais et al 2023; Zilhao et al 2020). Indeed, it appears that the location of the site on the coastline and its placement inside the Mediterranean vegetation contributed to the provision of all the decisive elements to the Neanderthal populations, which occupied the area. The dental remain of the site, which has undergone a dental microwear analysis is an LP<sup>4</sup>, while the microscopic observation focused on the buccal surface with the use of a scanning electron microscope (Egocheaga et al 2004).

Axlor Cave in the Cantabrian region has provided important insights regarding the subsistence strategies of Neanderthals, along with the development of the Mousterian knapping technocomplex (Garcia-Diez et al 2013). The Neanderthal occupation on the site appears in layers III and IV, with the latter to have been dated at >49,300 through the usage of new protocols for the extraction and the ultrafiltration of collagen from deer remains, which experienced anthropogenic modification (Gomez-Olivencia et al 2018). The human remains of Level IV have produced a debate regarding their attribution to a specific lineage, with Gonzalez-Urquijo et al (2021) supporting a clear taxonomical allocation on Neanderthals based on the understanding of the morphologies of the occlusal surfaces of the Axlor's dental remains and the sedimentary processes of the site. In this context, a study from Estalrrich and Marin-Arroyo (2021) focused on detecting patterns of enamel alternation using a digital microscope.

El Sidrón site has provided the scientific community with some of the most important human remains with respect to the lineage of *H. neanderthalensis* on a global scale. The site is located in the northern part of the Iberian Peninsula and is dated at ca. 49 kya through AMS dating method, thus providing the opportunity for the extraction of pieces of information just before the beginning of the end of Neanderthals (Rios et al 2019). Explicitly, the existence of anatomical anomalies in an important number of individuals indicates an alternation in the behavioral levels and subsistence strategies of Neanderthals just in the temporal point, when the arrival of AMHs in Europe is clearly documented (Hublin et al 2020; Slimak et al 2022). The study of Estalrrich et al (2017) included the analysis of the occlusal surfaces of the dental remains from 11 individuals and their subsequent microscopic observation with a confocal microscope.

El Salt site is located in the southeastern part of the Iberian Peninsula and is characterized by important findings for the understanding of the existence of Late Neanderthals. Explicitly, the site is placed between  $47.2 \pm 4.4$  and  $45.2 \pm 3.4$  kya through the TL dating method, while the dental record is comprised of six teeth (Garralda et al 2014). The recovery of human-modified faunal bones, a human coprolite, and a rich lithic record, which is associated with the human remains provides a rare opportunity for the undergone of a precise dietary reconstruction (Rampelli et al 2021; Sistiaga et al 2014). In this context, the study of Pérez-Pérez et al (2003) focused on the examination of the buccal surface of an upper premolar using a scanning electron microscope.

Cueva del Boquete de Zafarraya in the south of the Iberian Peninsula depicts decisive evidence regarding the late appearance of *H. neanderthalensis*. This specific site has been at the epicenter of important debates with respect to its temporal allocation; specifically, the first placement between 31 and 28 kya has been discarded with the use of new protocols and methodological approaches, such as the ultrafiltration of bone collagen for the minimization of the contamination factor (Mellars 2006). Nowadays, the site is placed at >46,700 BP for the Neanderthal occupation, exposing important difference with the preliminary dating (Wood et al 2013). The human remains consist of a mandible with clear Neanderthal morphologies based on a biometric analysis (Sanchez 1999), while the dental microwear analysis in a study from Krueger et al (2017) focused on the labial surfaces with the use of a white-light confocal microscope.

The Middle Palaeolithic site of Sima de las Palomas is dated between 43 and 40 thousand years BP and exhibits important lithic and faunal records, indicating an important presence of Neanderthals (Walker et al., 2008;). The excavation processes began during the '90s and revealed impressive findings, which are dated in a decisive temporal point for the understanding of the Middle to Upper Palaeolithic transition in the Iberian Peninsula. The human remains consist of a partial skull and skeletons, along with several isolated remains as an aftereffect of the unique formation processes of the site (Walker et al 2012; Zapata et al 2017). The extraction of pieces of information regarding dietary

Site	Observations	Diet	Reference
Devil's Tower	Predominance of vertical striations	Carnivorous	Lalueza Fox and
			Pérez-Pérez 1993
Figueira Brava	Existence of subvertical grooves	Mixed	Egocheaga et al 2004
Axlor	Indication of para-masticatory activities	Undetermined	Estalrrich and Marin-
	(chipped enamel)		Arroyo 2021
El Sidrón	Complex occlusal facets	Mixed	Estalrrich et al 2017
El Salt	Low number of striations	Carnivorous	Pérez-Pérez et al 2003
Zafarraya	High anisotropy level (epLsar)	Mixed	Krueger et al 2017
Sima de las	Long striations and low scratch density	Carnivorous	Pérez-Pérez et al 2017
Palomas			

**Table 2.** Determination of the alimentary habits of the Neanderthal populations based on the exhibited dental features

habits from dental remains has been gone through by Pérez-Pérez et al (2017) on an  $RM_2$  and an  $LM_1$  concerning the buccal surfaces.

The Neanderthal record of the Iberian Peninsula is comprised of several sites, which exhibit important interest regarding the dental remains, such as Bolomor Cave (Arsuaga et al 2012b), Mollet Cave (Maroto et al 2012), Cova Negra (Arsuaga et al 2007), Cueva del Camino (Arsuaga et al 2012a), among others. It is without a doubt that the appliance of dental microwear analysis on a further scale on Neanderthal dental remains from this specific geographic latitude could provide pieces of information of major importance regarding palaeoecological issues and palaeoenvironmental reconstructions.

#### Results

The reported results include analyses, which have been conducted on both the occlusal surfaces and the buccal ones of dental remains using the protocols for their examination with the use of a confocal microscope and a scanning electron microscope respectively (Table 2). In the case of the examination of the labial surfaces from the dental remains of Zafarraya site, the analysis was undergone with the use of a white-light Confocal Microscope, while the non-alimentary microwear traces of the dental remains of Axlor site were revealed with the use of a digital microscope.

The analysis of Lalueza-Fox and Pérez-Pérez (1993) exhibited that the diet of the Neanderthal male child from Devil's Tower can be characterized as a carnivorous one, based on the number and the direction of the striations in the buccal surface of the examined dental remain. Specifically, both examined deciduous molars exhibited the predominance of vertical striations on the buccal surfaces, along with a tendency towards lower values concerning the horizontal striations. When compared with data from the ethnoarchaeological record, the results indicate similarities with respect to the latter variable with groups of Fuegians and Inuit, while an important difference is observed in the number of striations and the level of wear (Lalueza-Fox and Pérez-Pérez, 1993). Previous studies on the dental remains of these groups have revealed mostly meat-based dietary habits, that can be explained by the unique environmental proxies, in which they are located (El Zaatari, 2010). In the case of Devil's Tower, the interpreted data are characterized by relative abrasive turnovers due to the intake of exogenous particles, which can be included in meat-based diets as described above.

In the case of Gruta da Figueira Brava, dental microwear analysis demonstrated the existence of interproximal grooves, which are the results of the appliance of heavy mastication forces during the chewing processes (Egocheaga et al 2004). Explicitly, the results indicated the inclusion of both meat and hard plants in the diets of the populations from the site due to the high frequency of subvertical grooves in the examined facet; inside this context, previous studies on the buccal surface of dental remains attributed to *H. neanderthalensis* have depicted the consumption of mixed diets, which can be

more readily apparent due to the existence of a noticeable level of wear on the buccal facet (Fiorenza et al 2011b).

Based on the microwear signatures, the dental remains of the populations from Axlor Cave are characterized by subvertical grooves, chipped enamel, and hints of tooth picking, which are alterations caused as an aftereffect of specific actions and consequently indicate behavioral processes (Estalrrich and Marin-Arroyo 2021). The alteration of the enamel due to non-alimentary activities has been documented from as early as the beginning of our lineage (Estalrrich et al 2020); concerning the Iberian Peninsula, behavioral traits have been extracted from the dental remains of the pre-Neanderthals from Sima de los Huesos (Lozano et al 2008; Lozano-Ruiz et al 2004), Cova Negra (Bermudez de Castro et al 1988), and Cova Forada (Lozano et al 2013) among others.

The occlusal dental microwear signatures of the El Sidrón site displayed the espousal of a mixed diet, which included the consumption of both meat and plants (Estalrrich et al 2017). More specifically, the occlusal surfaces of the molars of 11 individuals from the site are characterized by important levels of complexity, which couldn't occur from the intake of only meat proteins; these specific results confirm the study of Egocheaga et al (2004), who attribute the existence of interproximal grooves on the distal facet of a lower right M<sub>2</sub> from El Sidrón to the inclusion of hard plants in the diet among other foods. Moreover, when comparing the results with relevant data from the ethnoarchaeological record, important similarities can be observed between the examined materials and the results from the populations of Khoe-san and Chumash, thus suggesting mixed dietary habits. Interestingly, a study by Radini et al (2016) focused on the analysis of retrieved dental calculus from five individuals of El Sidrón and suggested a general familiarization with the use of vegetal remains for both para-alimentary and behavioral reasons.

The analysis of Pérez-Pérez et al (2003) demonstrated a low number of striations in the buccal surface of the upper premolar from El Salt, which is however bigger when compared with contemporaneous sites from OIS 3 and less than the ones from OIS 4. The former temporal point (OIS 3) is characterized as a generally warm event, which still includes both cold and warm intervals (Barron and Pollard 2002). Inside this context, the microwear signature from El Salt indicates the dependence on mostly meat-based diets, which comes as a response to the abundance of faunal remains for exploitation during this warm period principally. Indeed, the density of striations increases significantly when examining populations, who were placed in cold environmental contexts or inhabited cold geographical latitudes, since the consumption of meat overlaps with the use of hard roots or/and plants, as a response to the confined number of available faunal resources for exploitation (Rivals and Deniaux 2005).

The examination of the labial surfaces from Zafarraya exhibited the existence of a medium level of wear concerning the volumes of anisotropy (epLsar) and texture fill volume (Tfv) (Krueger et al 2017). The volume of anisotropy (epLsar) as a variable is laid in the understanding of the determination of the roughness in the respective surface of the dental remain (Scott et al 2005), while the texture fill volume (Tfv) quantifies the dental surface in square cuboids for the comprehension of different volumes (Scott et al 2006). Indeed, when comparing different sites and obtained values, it can be inferred that the samples of Zafarraya are placed in the general context of populations, which inhabited deciduous forests or woodlands, such as the ones of Krapina, Tabun, and Shanidar; the diets of these populations can be characterized as mixed, with the incorporation of both meat and plants in the alimentary process. In the case of Zafarraya, a significant anisotropy level (epLsar) indicates the consumption of foods with adherent endogenous or/and exogenous particles, which subsequently lead to more worn facets regarding the labial surfaces.

The analysis of the buccal surfaces of the molars from Sima de las Palomas suggested a low scratch density and longer striations of the buccal surfaces when compared with species, which inhabited the Iberian Peninsula during the Early and Middle Pleistocene, such as *H. antecessor* and *H. heidelbergensis* (Pérez-Pérez et al 2017). As described above, the analysis of the buccal surface can provide a general approach to the alimentary composition throughout the lifetime of an individual (Pérez-Pérez 2004). Inside this context, the results from Sima de las Palomas underline the consumption of processed foods from the Neanderthal population of the site, which lead to less worn facets on dental remains due to the use of fire and more developed lithic technocomplexes in the preparation of food.

#### Discussion

The majority of the described analyses include conducted examinations on the buccal surfaces of the dental remains using scanning electron microscopes, such as in the cases of Devil's Tower, Figueira Brava, El Salt, and Sima de las Palomas sites. Based on the results above, it can be easily extracted that the diets of Neanderthal populations of the Iberian Peninsula are totally correlated to the environmental context, in which they inhabited. However, concerning the relatively small number of examined Neanderthal sites of the Iberian Peninsula through dental microwear analysis, along with the scarce pieces of information regarding demographic dynamics on the majority of them, it should be clear that the described results reflect the dietary habits of the populations in the studied cases with the existing data up to date.

Neanderthal populations on sites, which are located in a coastal context or/and a low elevation, are characterized by relatively less worn facets, whose possible level of abrasiveness is justified by the intake of adherent particles to the meat, such as in the cases of Devil's Tower, and Zafarraya, since the coastal or nearly coastal environments imply the existence of sand. The effect of the ingestion of exogenous particles during the masticatory activity has been already highlighted by experimental studies on mammalian dental remains (Louail et al 2022; Uzunidis et al 2021). On the contrary, the inhabitation of sites, which were located in environments with the presence of deciduous forests or/ and woodlands, resulted in a bigger level of wear to the feeding apparatus due to the implementation of plants or/and hard roots in the alimentary processes, such as in the cases of Gruta da Figueira Brava, El Sidrón, and El Salt. Interestingly, when comparing the sites in chronological terms, a shift in the dietary patterns cannot be observed; this shift only occurs when considering the different palaeoecological placement of the sites, confirming the total correlation between the diets of the populations and the palaeoenvironmental context.

When comparing the dental microwear signatures between different sites from Europe and Western Eurasia, it can be easily understood that the Neanderthal behavior didn't change significantly with respect to different Marine Isotope Stages; on the contrary, the climatic fluctuations led to the adoption of different dietary habits, with the implementation of hard roots or/and plants in the cases of the cold-stepped environments (El Zaatari et al 2011). Indeed, dental microwear texture analysis on hunted ungulates has exhibited these differences in the palaeoecological statuses between MIS 5 and MIS 3, with the prevalence of more open environments and lower temperatures in the European continent (Berlioz et al 2023). Inside this context, it doesn't appear that the environmental conditions led to the gradual demise of the Neanderthal populations, which only occurred after the arrival of the AMHs (Timmermann 2020).

To obtain a holistic approach regarding the dietary habits of the populations of a site, the contextualization, and verification between the results of different types of analyses are required, imparting certainty regarding the archaeological interpretation. Inside this context, the low anisotropy levels on the dental remains of Vindija site, Croatia, indicate a mostly meat-based diet, which has been confirmed by the stable isotopic analysis from the site (Karriger et al 2016; Richards et al 2000). Specifically, the high values of  $\delta^{13}$ C on the Neanderthal remains of the site have suggested the intake of animal protein on a similar level with carnivores of the Croatian plateau, such as the Arctic fox and the Wolf. It is without consideration that the appliance of both dental microwear analysis and stable isotopic one on sites of the Iberian Peninsula can provide comprehensive approaches concerning the alimentary tendencies of Neanderthal populations, such as in the case of Moros de Gabasa site (Jaouen et al 2022).

In the last decades, the appliance of analyses on dental remains on a further scale has reversed the perception of the total dependence of Neanderthal populations on the consumption of meat in their diets (Binford 1981, 1984). These assumptions were based on the correlation between faunal remains on Neanderthal levels, indicating a wide and—in some cases—solely exploitation of faunal resources. However, studies on dental calculus have demonstrated the introduction of plants for alimentary purposes in Neanderthal populations from a wide range of geographical latitudes, from the Iberian Peninsula (El Sidrón) to Northern Europe (Spy I and II), and Western Asia (Shanidar III and Douara

Cave) (Akazawa 1987; Henry et al 2010; Radini et al 2016). The above statement was confirmed by a subsequent metagenomic analysis of the dental calculus from two individuals of the El Sidrón site, which exhibited the consumption of pine nuts (*Pinus koraiensis*), and forest moss (*Physcomitrella patens*), among others (Weyrich et al 2017), even though a study by Dickson et al (2017) attributed the presence of the latter (*Physcomitrella patens*) to contamination or taphonomic reasons. The described elements indicate the high cognitive level, which characterizes the populations of *H. neanderthalensis*, along with endured adaptive skills.

## **Conclusions**

From the described data above, it can be understood that the applied dental microwear analyses on dental remains of the Iberian Neanderthals have provided important insights regarding palaeoecological issues and have enhanced the scientific community with data regarding efforts of palaeoenvironmental reconstructions. Explicitly, the diets of the referred populations are characterized by a general consumption of meat, with an opportunistic implementation of plants and/or hard roots in the dietary habits in the cases of Figueira Brava, El Sidrón, and Zafarraya. The adoption of the exposed alimentary manners underlines the total correlation between the environmental context and the dietary habits of the populations, along with the behavioral complexity, which characterizes the Neanderthal populations of the Iberian record.

In general, the importance of dental microwear analysis in the discipline of Archaeology is laid in the understanding of one of the most vital elements for the survival and dominance of the genus *Homo* throughout our evolutionary line, which is the obtainment of pieces of information with respect to the subsistence strategies and dietary habits of extinct populations. It is without any consideration that technological development, along with the appliance of new means of research could provide more stable methodological frameworks, and quantitative approaches, and enhance our knowledge regarding the alimentary behaviors of populations of the past.

Acknowledgments. The authors are grateful to A. J. Timothy Jull, and Rachel Wood, along with the two anonymous reviewers for their contribution to the final form of the manuscript. This study was supported by the Spanish Government MICINN PID2021-122355NB-C32 and received financial support from the CERCA Programme/Generalitat de Catalunya, AGAUR agency, 2021 SGR 01239 and 2017 Research Groups. This research was supported by the Spanish Ministry of Science and Innovation through the "María de Maeztu" excellence accreditation (CEX2019-000945-M).

Declaration of Competing Interests. The authors declare no conflicts or competing interests.

# References

Akazawa T (1987) The ecology of the Middle Paleolithic occupation at Douara Cave. *Syria Bulletin of the University Museum* **29**, 5–66. University of Tokyo. DOI: http://www.um.utokyo.ac.jp/publishdb/Bulletin/no29/no29012.html.

Alrousan M (2016) Human dental buccal microwear and paleodiet reconstruction. Anthropologie 54(3), 305-315.

Arman SD, Ungar PS, Brown CA, DeSantis LRG, Schmidt C and Prideaux GJ (2016) Minimizing inter-microscope variability in dental microwear texture analysis. *IOP Science* **4**, 024007. DOI: 10.1088/2051-672X/4/2/024007.

Arsuaga JL, Baquedano E, Perez-Gonzalez A, Sala N, Quam RM, Rodriguez L, Garcia R, Garcia N, Alvarez-Lao DJ, Laplana C, Huguet R, Sevilla P, Maldonado E, Blain H-A, Ruiz-Zapata MB, Sala P, Gil-Garcia MJ, Uzquiano P, Pantoja A and Marquez B (2012a) Understanding the ancient habitats of the last-interglacial (late MIS 5) Neanderthals of central Iberia: Paleoenvironmental and taphonomic evidence from the Cueva del Camino (Spain) site. *Quaternary International* 275, 55–75. DOI: 10.1016/j.quaint.2012. 04.019.

Arsuaga JL, Peris JF, Gracia-Tellez A, Quam R, Carretero JM, Gonzalez VB, Blasco R, Cuartero F and Sanudo P (2012b) Fossil Human Remains from Bolomor Cave (Valencia, Spain). *Journal of Human Evolution* **62**, 629–639. DOI: 10.1016/j.jhevol. 2012.02.002.

Arsuaga JL, Villaverde V, Quam R, Martinez I, Carretero JM, Lorenzo C and Gracia A (2007) New Neanderthal remains from Cova Negra (Valencia, Spain) *Journal of Human Evolution* **52**, 31–58. DOI: 10.1016/j.jhevol.2006.07.011.

Barron E and Pollard D (2002) High-resolution climate simulations of Oxygen Isotope Stage 3 in Europe. *Quaternary Research* **58**, 296–309. DOI: 10.1006/qres.2002.2374.

- Bas M, Le Luyer M, Kanz F, Rebay-Salisbury K, Queffelec A, Souron A, Willman J and Bayle P (2020) Methodological implications of intra- and inter-facet microwear texture variation for human childhood paleo-dietary reconstruction: Insights from the deciduous molars of extant and medieval children from France *Journal of Archaeological Science: Reports* 31: 102284. DOI: https://doi.org/10.1016/j.jasrep.2020.102284.
- Bas M, Waltenberger L, Kurzmann C, Heimel P, Rebay-Salisbury K and Kanz F (2021) Quantification of dental macrowear using 3D occlusal surface topographic measurements in deciduous and permanent molars of children American Journal of Physical Anthropology 175(3), 701–711. DOI: https://doi.org/10.1002/ajpa.24289.
- Berlioz E, Capdepon E and Discamps E (2023) A long-term perspective on Neanderthal environment and subsistence: Insights from the dental microwear texture analysis of hunted ungulates at Combe-Grenal (Dordogne, France). *PLoS ONE* **18**(1), e0278395. DOI: https://doi.org/10.1371/journal.pone.0278395.
- Bermudez de Castro JM, Bromage T and Fernandez-Jalvo Y (1988) Buccal striations on fossil human anterior teeth: evidence of handedness in the middle and early Upper Pleistocene. *Journal of Human Evolution* 17, 403–412. DOI: https://doi.org/10.1016/0047-2484(88)90029-2.
- Binford LR (1981) Bones: Ancient Men and Modern Myths. New York: Academic Press.
- Binford LR (1984) The Faunal Remains from Klasies River Mouth. New York: Academic Press.
- Blain H-A, Bailon S, Agusti J, Martinez-Navarro B and Toro I (2011) Paleoenvironmental and paleoclimatic proxies to the Early Pleistocene hominids of Barranco León D and Fuente Nueva 3 (Granada, Spain) by means of their amphibian and reptile assemblages. *Quaternary International* **243**, 44–53. DOI: 10.1016/j.quaint.2010.12.031.
- Bokelmann L, Hajdinjak M, Peyregne S, Brace S, Essel E, de Filippo C, Glocke I, Grote S, Mafessoni F, Nagel S, Kelso J, Prufer K, Vernot B, Barnes I, Paabo S, Meyer M and Stringer C (2019) A genetic analysis of the Gibraltar Neanderthals. *PNAS* 116 (31), 15610–15615. DOI: www.pnas.org/cgi/doi/10.1073/pnas.1903984116.
- Calandra I, Pedergnana A, Gneisinger W and Marreiros J (2019) Why should traceology learn from dental microwear, and vice-versa? *Journal of Archaeological Science* 110, 105012. DOI: https://doi.org/10.1016/j.jas.2019.105012.
- DeSantis LRG, Scott JR, Schubert BW, Donohue SL, McCray BM, Van Stolk CA, Winburn AA, Greshko MA and O'Hara MC (2013) Direct Comparisons of 2D and 3D Dental Microwear Proxies in Extant Herbivorous and Carnivorous Mammals. *PLOS ONE* 8 (8), e71428. DOI: 10.1371/journal.pone.0071428.
- Dickson JH, Oeggl K and Stanton D (2017) "Forest Moss": no part of the European Neanderthal Diet Antiquity 91(359): e3. DOI: https://doi.org/10.15184/aqy.2017.165.
- Drtikolova Kaupova S, Jarosova I, Biskova J, Hrncir V, Kvetina P, Neugebauer-Maresch C, Pokutta DA, Ridky J, Vytlacil Z and Trampota F (2023) The diet of settled Neolithic farmers of east-central Europe: isotopic and dental microwear evidence. *Archaeological and Anthropological Sciences* **15**(21). DOI: https://doi.org/10.1007/s12520-023-01720-9.
- Egocheaga JE, Pérez-Pérez A, Rodriguez L, Galbany J, Martinez LM and Telles Antunes M (2004) New evidence and interpretation of subvertical grooves In Neandertal teeth from Cueva De Sidrón (Spain) and Figueira Brava (Portugal) *Anthropologie* **42**(1), 49–52.
- El-Zaatari S (2008) Occlusal molar microwear and the diets of the Ipiutak and Tigara populations (Point Hope) with comparisons to the Aleut and Arikara. *Journal of Archaeological Science* **35**:2517–2522. DOI: 10.1016/j.jas.2008.04.002.
- El-Zaatari S (2010) Occlusal microwear texture analysis and the diets of historical/ prehistoric hunter-gatherers. *International Journal of Osteoarchaeology* **20**, 67–87. DOI: 10.1002/oa.1027.
- El Zaatari S, Grine FE, Ungar PS and Hublin J-J (2011) Ecogeographic variation in Neandertal dietary habits: Evidence from occlusal molar microwear texture analysis. *Journal of Human Evolution* **61**, 411–424. DOI: 10.1016/j.jhevol.2011. 05.004.
- Espurz V, Pérez-Pérez A and Turbon D (2004) An approach to the studies of post-depositional processes affecting inter-proximal wear facets and buccal enamel surfaces in hominid teeth. *Anthropologie* **42**(1), 43–48.
- Estalrrich A, Alarcon JA and Rosas A (2020) Toothpicking in early Homo OH 62 from Olduvai Gorge (Tanzania): An indirect evidence of intensive meat consumption? *Journal of Human Evolution* **143**:102769. DOI: https://doi.org/10.1016/j.jhevol. 2020.102769.
- Estalrrich A, El Zaatari S and Rosas A (2017) Dietary reconstruction of the El Sidrón Neandertal familial group (Spain) in the context of other Neandertal and modern hunter-gatherer groups. A molar microwear texture analysis. *Journal of Human Evolution* **104**, 13–22. DOI: http://dx.doi.org/10.1016/j.jhevol.2016.12.003.
- Estalrrich A and Marin-Arroyo AB (2021) Evidence of habitual behavior from non-alimentary dental wear on deciduous teeth from the Middle and Upper Paleolithic Cantabrian region, Northern Spain. *Journal of Human Evolution* **158**, 103047. DOI: https://doi.org/10.1016/j.jhevol.2021.103047.
- Fiorenza L, Benazzi S and Kullmer O (2011a) Para-masticatory wear facets and their functional significance in hunter-gatherer maxillary molars. *Journal of Archaeological Science* **38**(9), 2182–2189. DOI: https://doi.org/10.1016/j.jas.2011.03.012.
- Fiorenza L, Benazzi S, Tausch J, Kullmer O, Bromage TG and Schrenk F (2011b) Molar macrowear reveals Neanderthal eco-geographic dietary variation. *PLOS ONE* **6**(3): e14769. DOI: 10.1371/journal.pone.0014769.
- Firmat C, Gomes Rodriguez H, Hutterer R, Rando JC, Alcover JA and Michaux J (2010) Diet of the extinct Lava mouse Malpaisomys insularis from the Canary Islands: insights from dental microwear. *Naturwissenschaften* 98, 33–37. DOI: https://doi.org/10.1007/s00114-010-0738-z.
- Frayer DW and Russell MD (1987) Artificial Grooves on the Krapina Neanderthal teeth. *American Journal of Physical Anthropology* **74**, 393–405. DOI: 10.1002/ajpa.1330740311.

- Galbany J, Estebaranz F, Martinez LM, Romero A, de Juan J, Turbon D and Pérez-Pérez A (2006) Comparative analysis of dental enamel polyvinylsiloxane impression and polyurethane casting methods for SEM research. *Microscopy Research and Technique* **69**, 246–252. DOI: 10.1002/jemt.20296.
- Galbany J, Martinez LM and Pérez-Pérez A (2004) Tooth replication techniques, sem imaging and microwear analysis in primates: methodological obstacles *Anthropologie* **42**(1), 5–12.
- Garcia-Diez M, Ochoa Fraile B and Barandiaran Maestu I (2013) Neanderthal graphic behavior: The Pecked Pebble from Axlor Rockshelter. *Journal of Anthropological Research* 69(3), 397–410. DOI: 10.3998/jar.0521004.0069.307.
- Garralda MD, Galvan B, Hernandez CM, Mallol C, Gomez JA and Maureille B (2014) Neanderthals from El Salt (Alcoy, Spain) in the context of the latest Middle Palaeolithic populations from the southeast of the Iberian Peninsula. *Journal of Human Evolution* **75**, 1–15. DOI: https://doi.org/10.1016/j.jhevol.2014.02.019.
- Gomez-Olivencia A, Sala N, Nunez-Lahuerta C, Sanchis A, Alregi M and Rios-Garaizar J (2018) First data of Neandertal bird and carnivore exploitation in the Cantabrian Region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula) Scientific Reports 8, 10551. DOI: 10.1038/s41598-018-28377-y.
- Gonzalez-Urquijo J, Bailey SE and Lazuen T (2021) Axlor's level IV human remains are convincingly Neanderthals: A reply to Gómez-Olivencia et al American Journal of Physical Anthropology 176(4), 553–558. DOI: 10.1002/ajpa.24252.
- Goodall RH, Darras LP and Purnell MA (2015) Accuracy and precision of silicon based impression media for quantitative areal texture analysis. *Nature Scientific Reports* 5, 10800. DOI: 10.1038/srep10800.
- Grine FE (1986) Dental evidence for dietary differences in Australopithecus and Paranthropus: a quantitative analysis of permanent molar microwear *Journal of Human Evolution* **15**(8), 783–822. DOI: https://doi.org/10.1016/S0047-2484(86)80010-0.
- Grine FE and Kay RF (1988) Early hominid diets from quantitative image analysis of dental microwear *Nature* 33, 765–768. DOI: https://doi.org/10.1038/333765a0.
- Henry AG, Brooks AS and Piperno DR (2010) Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *PNAS* **108**(2), 486–491. DOI: www.pnas.org/cgi/doi/10.1073/pnas.1016868108.
- Hublin J-J, Sirakov N, Aldeias V, Bailey S, Bard E, Delvigne V, Endarova E, Fagault Y, Fewlass H, Hajdinjak M, Kromer B, Krumov I, Marreiros J, Martisius NL, Paskulin L, Sinet-Mathiot V, Meyer M, Paabo S, Popov V, Rezek Z, Sirakova S, Skinner MM, Smith GM, Spasov R, Talamo S, Tuna T, Wacker L, Welker F, Wilcke A, Zahariev N, McPherron SP and Tsanova T (2020) Initial Upper Palaeolithic Homo sapiens from Bacho Kiro Cave, Bulgaria. *Nature* 581, 299–315. DOI: https://doi.org/10.1038/s41586-020-2259-z.
- Jaouen K, Villalba-Mouco V, Smith GM, Trost M, Leichliter J, Luedecke T, Mejean P, Mandrou S, Chmeleff J, Guiserix D, Bourgon N, Blasco F, Mendes Cardoso J, Duquenoy C, Moubtahij Z, Salazar Garcia DC, Richards M, Tuetken T, Hublin J-J, Utrilla P and Montes L (2022) A Neandertal dietary conundrum: Insights provided by tooth enamel Zn isotopes from Gabasa, Spain. PNAS 119 (43), e2109315119. DOI: https://doi.org/10.1073/pnas.2109315119.
- Karriger WM, Schmidt CW and Smith FH (2016) Dental microwear texture analysis of Croatian Neandertal molars. Paleoanthropology 172–184. DOI: 10.4207/PA.2016.ART102.
- King T, Andrews P and Boz B (1999) Effect of taphonomic processes on dental microwear. *American Journal of Physical Anthropology* **108**(3), 359–373. DOI: https://doi.org/10.1002/(SICI)1096-8644(199903)108:3<359::AID-AJPA10>3.0.
- Krueger KL (2015) Reconstructing diet and behavior in bioarchaeological groups using incisor microwear texture analysis. Journal of Archaeological Sciences: Reports 1:29–37. DOI: http://dx.doi.org/10.1016/j.jasrep.2014.10.002.
- Krueger KL, Chwa E, Peterson AS, Willman JC, Fok A, van Heel B, Heo Y, Weston M and DeLong R (2021) Technical note: Artificial resynthesis technology for the experimental formation of dental microwear textures. *American Journal of Physical Anthropology* 176(4), 703–712. DOI: https://doi.org/10.1002/ajpa.24395.
- Krueger KL and Ungar PS (2012) Anterior dental microwear texture analysis of the Krapina Neandertals. *Central European Journal of Geosciences* **4**, 651–662. DOI: https://doi.org/10.2478/s13533-012-0111-1.
- Krueger KL, Ungar PS, Guatelli-Steinberg, Jublin J-J, Pérez-Pérez A, Trinkaus E and Willman JC (2017) Anterior dental microwear textures show habitat-driven variability in Neandertal behavior. *Journal of Human Evolution* **105**, 13–23. DOI: http://dx.doi.org/10.1016/j.jhevol.2017.01.004.
- Lalueza Fox C (1992) Information obtained from the microscopic examination of cultural striations in human dentition. *International Journal of Osteoarchaeology* **2**(2), 155–169. DOI: https://doi.org/10.1002/oa.1390020207.
- Lalueza Fox C and Pérez-Pérez A (1993) The diet of the Neanderthal Child Gibraltar 2 (Devil's Tower) through the study of the vestibular striation pattern. *Journal of Human Evolution* 24, 29–41.
- Louail M, Caner L, Neaux D, Ortiz K, Locatelli Y and Cucchi T (2022) Identifying the impact of soil digestion on dental microwear textures using a wild boar experimental model. *Journal of Archaeological Method and Theory* 30, 855–875. DOI: https://doi.org/ 10.1007/s10816-022-09574-6.
- Lozano-Ruiz M, Bermudez de Castro JM, Martinon-Torres M and Sarmiento S (2004) Cutmarks on fossil human anterior teeth of the Sima de los Huesos Site (Atapuerca, Spain). *Journal of Archaeological Science* **31**, 1127–1135. DOI: 10.1016/j.jas.2004. 02.005.
- Lozano M, Bermúdez de Castro JM, Carbonell E and Arsuaga JL (2008) Non-masticatory uses of anterior teeth of Sima de los Huesos individuals (Sierra de Atapuerca, Spain). *Journal of Human Evolution* 55, 713–728. https://doi.org/10.1016/j.jhevol. 2008.04.007.

- Lozano M, Subira ME, Aparicio J, Lorenzo C and Gomez-Merino G (2013) Toothpicking and Periodontal Disease in a Neanderthal Specimen from Cova Forada' Site (Valencia, Spain). PLoS ONE 8(10), e76852. DOI: 10.1371/journal.pone. 0076852.
- Mahoney P (2006a) Dental microwear from Natufian hunter-gatherers and Early Neolithic farmers: Comparisons within and between samples. *American Journal of Physical Anthropology* **130**, 308–319. DOI: 10.1002/ajpa.20311.
- Mahoney P (2006b) Microwear and morphology: Functional relationships between human dental microwear and the mandible. *Journal of Human Evolution* **50**, 452–459. DOI: 10.1016/j.jhevol.2005.11.003.
- Maier W and Schneck G (1981) Konstruktionsmorphologische Untersuchungen am Gebiß der hominoiden Primaten Zeitschrift für Morphologie und *Anthropologie* **72**(2), 127–169.
- Maier W and Schneck G (1982) Functional morphology of hominoid dentitions. *Journal of Human Evolution* **11** (8), 693–696. DOI: https://doi.org/10.1016/S0047-2484(82)80057-2.
- Maroto J, Julia R, Lopez-Garcia JM and Blain H-A (2012) Chronological and environmental context of the Middle Pleistocene human tooth from Mollet Cave (Serinyà, NE Iberian Peninsula). *Journal of Human Evolution* 62, 655–663. DOI: https://doi. org/10.1016/j.jhevol.2012.01.009.
- Mellars P (2006) A new radiocarbon revolution and the dispersal of modern humans in Eurasia. *Nature Reviews* **439**, 931–935. DOI: 10.1038/nature04521.
- Mihlbachler MC and Beatty BL (2012) Magnification and resolution in dental microwear analysis using light microscopy. *Palaeontologia Electronica* **15**(2), 15.3.25A. DOI: https://doi.org/10.26879/317.
- Mills JRE (1966) The functional occlusion of the teeth of Insectivora. *Zoological Journal of the Linnean Society* **46** (308):1–25. DOI: https://doi.org/10.1111/j.1096-3642.1966.tb00081.x.
- Nabais M, Dupont C and Zilhao J (2023) The exploitation of crabs by Last Interglacial Iberian Neanderthals: The evidence from Gruta da Figueira Brava (Portugal). Frontiers in Environmental Archaeology 2:1097815. DOI: 10.3389/fearc.2023.1097815.
- Organ JM, Ruff CB, Teaford MF and Nisbett RA (2005) Do mandibular cross-sectional properties and dental microwear give similar dietary signals? *Yearbook of Biological Anthropology* **130**(4), 501–507. DOI: https://doi.org/10.1002/ajpa.20377.
- Patrocinio Espigares M, Palmqvist P, Guerra-Merchan A, Ros-Montoya S, Garcia-Aguilar J, Rodriguez-Gomez G, Serrano FJ and Martinez-Navarro B (2019) The earliest cut marks of Europe: a discussion on hominin subsistence patterns in the Orce sites (Baza basin, SE Spain). *Nature Scientific Reports* 9, 15408. DOI: https://doi.org/10.1038/s41598-019-51957-5
- Pérez-Pérez A (2004) Why Buccal Microwear? Anthropologie 42(1):1-4.
- Pérez-Pérez A, Espurz V, Bermudez de Castro JM, de Lumley MA and Turbon D (2003) Non-occlusal dental microwear variability in a sample of Middle and Late Pleistocene human populations from Europe and the Near East. *Journal of Human Evolution* 44, 497–513. DOI: 10.1016/S0047-2484(03)00030-7.
- Pérez-Pérez A, Lalueza C and Turbon D (1994) Intraindividual and intragroup variability of buccal tooth striation pattern. Yearbook of Biological Anthropology 94(2), 175–187. DOI: https://doi.org/10.1002/ajpa.1330940203.
- Pérez-Pérez A, Lozano M, Romero A, Martinez LM, Galbany J, Pinilla B, Estebaranz-Sanchez F, Bermudez de Castro JM, Carbonell E and Arsuaga JL (2017) The diet of the first Europeans from Atapuerca. *Nature Scientific Reports* 7, 43319. DOI: 10.1038/srep43319.
- Pinilla Perez B, Romero A and Pérez-Pérez A (2011) Age-related variability in buccal dental-microwear in Middle and Upper Pleistocene human populations. *Anthropological Review* **74**, 25–37. DOI: 10.2478/v10044-010-0005-0.
- Puech P-F, Albertini H and Mills NTW (1980) Dental destruction in Broken-Hill Man. *Journal of Human Evolution* **9**(1), 33–39. DOI: https://doi.org/10.1016/0047-2484(80)90039-1.
- Radini A, Buckley S, Rosas A, Estalrrich A, de la Rasilla M and Hardy K (2016) Neanderthals, trees and dental calculus: new evidence from El Sidrón. Antiquity 90, 290–301. DOI: 10.15184/aqy.2016.21.
- Rampelli, Turroni S, Mallol C, Hernandez C, Galvan B, Sistiaga A, Biagi E, Astolfi A, Brigidi P, Benazzi S, Lewis Jr CM, Warinner C, Hofman CA, Schnorr SL and Candela M (2021) Components of a Neanderthal gut microbiome recovered from fecal sediments from El Salt. *Communications Biology* 4, 169. DOI: https://doi.org/10.1038/s42003-021-01689-y.
- Rensberger JM (1978) Scanning electron microscopy of wear and occlusal events in some small herbivores In Butler PM and Joysey KA (eds), *Development, Function and Evolution of Teeth.* New York: Academic Press, 415–438.
- Richards MP, Pettitt PB, Trinkaus E, Smith FH, Paunovic M and Karavanic I (2000) Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes. *PNAS* **97**(13), 7663–7666. DOI: 10.1073/pnas.120178997.
- Rios L, Kivell TL, Lalueza-Fox C, Estalrrich A, Garcia-Tabernero A, Huguet R, Quintino Y, de la Rasilla M and Rosas A (2019) Skeletal anomalies in the Neandertal family of El Sidrón (Spain) support a role of inbreeding in Neandertal Extinction. *Nature Scientific Reports* 9:1697. DOI: https://doi.org/10.1038/s41598-019-38571-1.
- Rivals F and Deniaux B (2005) Investigation of human hunting seasonality through dental microwear analysis of two Caprinae in late Pleistocene localities in Southern France. *Journal of Archaeological Science* 32(11), 1603–1612. DOI: https://doi.org/10.1016/j. jas.2005.04.014.
- Rodriguez-Rojas F, Borrero-Lopez O, Constantino PJ, Henry AG and Lawn BR (2020) Phytoliths can cause tooth wear. *Journal of the Royal Society Interface* 17: 20200613. DOI: https://doi.org/10.1098/rsif.2020.0613.
- Romero A and de Juan J (2007) Intra- and interpopulation human buccal tooth surface microwear analysis: inferences about diet and formation processes. *Anthropologie* **45**, 61–70.
- Sanchez F (1999) Comparative biometrical study of the Mousterian mandible from Cueva del Boquete de Zafarraya (Mfilaga, Spain). *Human Evolution* **14**(1–2), 125–138.

- Sawaura R, Kimura Y and Kubo MO (2022) Accuracy of dental microwear impressions by physical properties of silicone materials. *Frontiers in Ecology and Evolution* **10**: 975283. DOI: 10.3389/fevo.2022.975283.
- Scott RS, Ungar PS, Bergstrom TS, Brown CA, Childs BE, Teaford MF and Walker A (2006) Dental microwear texture analysis: technical considerations. *Journal of Human Evolution* **51**, 339–349. DOI: 10.1016/j.jhevol.2006.04.006.
- Scott RS, Ungar PS, Bergstrom TS, Brown CA, Grine FE, Teaford MF and Walker A (2005) Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436(4), 693–695. DOI: https://doi.org/10.1038/nature03822.
- Sistiaga A, Mallol C, Galvan B, Summons RE (2014) The Neanderthal meal: A new perspective using faecal biomarkers. *PLOS ONE* **9**(6), e101045. DOI: 10.1371/journal.pone.0101045.
- Slimak L, Zanolli C, Higham T, Frouin M, Schwenninger J-L, Arnold LJ, Demuro M, Douka K, Mercier N, Guerin G, Valladas H, Yvorra P, Giraud Y, Seguin-Orlando A, Orlando L, Lewis JE, Muth X, Camus H, Vandevelde S, Buckley M, Mallol C, Stringer C, Metz L (2022) Modern human incursion into Neanderthal territories 54,000 years ago at Mandrin, France. *Science Advances* 8, 1–16. DOI: 10.1126/sciadv.abj9496.
- Timmermann A (2020) Quantifying the potential causes of Neanderthal extinction: Abrupt climate change versus competition and interbreeding. *Quaternary Science Reviews* **238**, 106331. DOI: https://doi.org/10.1016/j.quascirev.2020.106331.
- Ungar PS, Livengood SV, Crittenden AN (2019) Dental microwear of living Hadza foragers. American Journal of Physical Anthropology 169(2), 356–367. DOI: 10.1002/ajpa.23836.
- Uzunidis A, Pineda A, Jiménez Manchón S, Xafis A, Ollivier V, Rivals F (2021) The impact of sediment abrasion on tooth microwear analysis: an experimental study. Archaeological and Anthropological Sciences 13:134. DOI: https://doi.org/10. 1007/s12520-021-01382-5.
- Walker MJ, Gilbert J, Lopez MV, Lombardi AV, Pérez-Pérez A, Zapata J, Ortega J, Higham T, Pike A, Schwenninger J-L, Zilhao J, Trinkaus E (2008) Late Neandertals in southeastern Iberia: Sima de las Palomas del Cabezo Gordo, Murcia, Spain. PNAS 105(52), 20631–20636.
- Walker A, Hoeck HN, Perez L (1978) Microwear of mammalian teeth as an indicator of diet. Science 201, 908–910.
- Walker MJ, Lopez-Martinez MV, Ortega-Rodriganez J, Haber-Uriarte M, Lopez-Jimenez A, Aviles-Fernandez A, Polo-Camacho JL, Campillo-Boj M, Garcia-Torres J, Carrion Garcia JS, San Nicolas-del Toro M, Rodriguez-Estrella T (2012) The excavation of buried articulated Neanderthal skeletons at Sima de las Palomas (Murcia, SE Spain). Quaternary International 259, 7–21.
- Weyrich LS, Duchene S, Soubrier J, Arriola L, Llamas B, Breen J, Morris AG, Alt KW, Caramelli D, Dresely V, Farrell M, Farrer AG, Francken M, Gully N, Haak W, Hardy K, Harvati K, Held P, Holmes EC, Kaidonis J, Lalueza-Fox C, de la Rasilla M, Rosas A, Semal P, Soltysiak A, Townsend G, Usai D, Wahl J, Huson DH, Dobney K, Cooper A (2017) Neanderthal behaviour, diet, and disease inferred from ancient DNA in dental calculus. *Nature* **544**, 357–361. DOI: https://doi.org/10.1038/nature21674.
- Williams VS, Barrett PM and Purnell MA (2009) Quantitative analysis of dental microwear in hadrosaurid dinosaurs, and the implications for hypotheses of jaw mechanics and feeding. PNAS 106 (27): 11194–11199. DOI: www.pnas.orgcgidoi10. 1073pnas.0812631106.
- Winkler DE, Schulz-Kornas E, Kaiser TM, Codron D, Leichliter J, Hummel J, Martin LF, Clauss M, Tutken T (2020) The turnover of dental microwear texture: Testing the" last supper" effect in small mammals in a controlled feeding experiment. *Palaeogeography, Palaeoclimatology, Palaeoecology* **557**, 109930. DOI: https://doi.org/10.1016/j.palaeo.2020.109930.
- Wood RE, Barroso-Ruiz C, Caparros M, Jorda Pardo JF, Galvan Santos B, Higham TFG (2013) Radiocarbon dating casts doubt on the late chronology of the Middle to Upper Palaeolithic transition in southern Iberia. PNAS 110(8): 2781–2786. DOI: https://doi.org/10. 1073/pnas.1207656110.
- Yravedra-Sainz de los Terreros J, Gomez-Castanedo A, Aramendi-Picado J, Montes-Barquin R, Sanguino-Gonzalez J (2015) Neanderthal and Homo sapiens subsistence strategies in the Cantabrian region of northern Spain. *Archaeological and Anthropological Science*. DOI: 10.1007/s12520-015-0253-4.
- Zapata J, Bayle P, Lombardi AV, Pérez-Pérez A, Trinkaus E (2017) The Palomas dental remains: Preservation, wear, and morphology. In Trinkaus E and Walker MJ (eds), The People of Palomas. Neanderthals from the Sima de las Palomas del Cabezo Gordo, Southeastern Spain. Texas AandM University Press, 52–88.
- Zilhao J (2000) The Ebro Frontier: A Model for the Late Extinction of Iberian Neanderthals. In Stringer C, Barton RNE and Finlayson C (eds), *Neanderthals on the Edge: 150th Anniversary Conference of the Forbes' Quarry Discovery*. Oxford: Oxbow Books, 111–121.
- Zilhao J (2006) Neanderthals and moderns mixed, and it matters. Evolutionary Anthropology 15, 183–195. DOI: https://doi.org/10.1002/evan.20110.
- Zilhao J, Angelucci DE, Araujo Igreja M, Arnold LJ, Badal E, Callapez P, Cardoso JL, d' Errico F, Daura J, Demuro M, Deschamps M, Dupont C, Gabriel S, Hoffmann DL, Legoinha P, Matias H, Monge Soares AM, Nabais M, Portela P, Queffelec A, Rodrigues F, Souto P (2020) Last Interglacial Neanderthals as fisher-hunter-gatherers. *Science* 367, eaaz7943. DOI: http://dx.doi.org/10.1126/science.aaz7943.
- **Cite this article:** Strimenopoulos A and Lozano M. Correlation between dental microwear analysis and dietary habits of Neanderthal populations in the Iberian Peninsula. *Radiocarbon*. https://doi.org/10.1017/RDC.2024.53