Dietary inferences from dental microwear patterns in Chalcolithic populations from the Iberian Peninsula: the case of El Portalón de Cueva Mayor (Sierra de Atapuerca, Burgos, Spain) and El Alto de la Huesera (Álava, Spain)

Rebeca García-González[a*], Zuriñe Sánchez-Puente[a], Juan Luis Arsuaga[b,c] and José Miguel Carretero[a,b]

[a] Laboratorio de Evolución Humana. Departamento de Historia, Geografía y Comunicación. Facultad de Humanidades y Educación. Universidad de Burgos. Plaza Misael Bañuelos s/n. 09001. Burgos. Spain

[b]Centro UCM-ISCIII de Investigación sobre Evolución y Comportamiento Humanos, Avda. Monforte de Lemos, 5 (Pabellón 14), 28029 Madrid, Spain.

[c] Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, Ciudad Universitaria s/n, 28040 Madrid, Spain.

(*) corresponding author:

Rebeca García-González

Laboratorio de Evolución Humana. Dpto. de Historia, Geografía y Comunicación. Universidad de Burgos. Edificio I+D+i. Plaza Misael Bañuelos s/n. 09001 Burgos, Spain.

E-mail: mrgarcia@ubu.es

Tel: +34 947 25 93 24

Abstract

Dietary habits are inferred through dental microwear analysis in humans from two Chalcolithic sites located on the Iberian Northern Plateau: El Portalón de Cueva Mayor and El Alto de la Huesera. The pattern of dental microwear was established on the buccal surfaces of permanent and deciduous molars, on the bottom of facet 9 on the occlusal surface of lower molars and on the incisal surfaces of deciduous incisors. Our findings suggest that during the Chalcolithic the diet of populations from the Northern Plateau is less abrasive than that at the Mediterranean coast, due mainly to high meat consumption. The differences in diet are related to environmental factors, which are more appropriate for animal husbandry on the Northern Plateau. The consumption of meat is not equivalent in subadult and adult individuals from our samples located on the Northern Plateau. Younger individuals show a harder diet with less meat intake than older ones.

Keywords: Chalcolithic diet, Northern Plateau, age-related dietary habits.

1. Introduction

Diet reconstruction is an important class of analysis in archaeology since it is closely related to behavioral and ecological factors (Clutton-Brock and Harvey, 1977). These reconstructions have been attempted from different sources, including the archaeological record, isotope chemistry and dental microwear. Zooarchaeological and arqueobotanical studies provide us with a general framework regarding diet when this kind of record is abundant. Nevertheless, even in these cases, the interpretation of the relationship between archaeological remains and diet is not always straightforward (Grine, 2007). In any case, studies of this kind are necessary and can be discussed in light of the dietary information inferred from other sources. Among these sources, isotope and dental microwear analyses are the most used (Larsen, 1997). Dental microwear analyses have proven to be a useful technique in characterizing subsistence strategies in both prehistoric and recent humans (Bullington, 1991; Molleson and Jones, 1991; Molleson et al., 1993; Pérez-Pérez et al., 1994; Ungar and Spencer, 1999; Schmidt, 2001; Romero et al., 2004; Teruyuki, 2005; Mahoney, 2006a, 2006b, 2007, Galbany et al., 2008; Hogue and Melsheimer, 2008; Kruege and Ungar, 2009; Gamza and Irish, 2012; Romero et al., 2013; El-Zaatari and Hublin, 2014). These studies have highlighted a close relationship between changes in dental microwear patterns to shifts in technical foodstuff processes (Romero and De Juan, 2007; Salazar-García et al., 2016). Moreover, dental microwear analysis also has the potential to identify age-related changes, along with different infant-rearing practices, including the age at weaning and the age of acquisition of the adult diet. Thus, this study has two main goals. The first goal of this study is to make dietary inferences through microwear analysis in Chalcolithic individuals recovered from the two archaeological sites located on the Northern Plateau (Figure 1). This kind of analysis in the Iberian Peninsula has been mainly restricted to the Mediterranean coast (Romero et al, 2004; Romero and De Juan, 2007; Polo-Cerdá et al., 2007; Salazar-García 2009,2011,2014; Salazar-García et al., 2010, 2016; McCure et al., 2011). In contrast, these approaches are scarce in prehistoric populations from the interior of the Iberian Peninsula. Thus, the analysis of the dental microwear pattern of these two samples from the Northern Plateau and the comparison of these findings with those from the Mediterranean coast allow us to study the effect of the interaction between environmental and cultural factors on dental microwear patterns. The second goal addresses the difference in dietary habits between subadult and adult individuals from the Northern Plateau. Specifically, we focus on the weaning process.

2. Material

2.1. Archaeological samples

This study is based on the analysis of teeth from the Chalcolithic levels from two archaeological sites from the Northern Plateau (Figure 1): El Portalón de Cueva Mayor (Sierra de Atapuerca, Burgos) and El Alto de la Huesera.

[INSERT FIGURE 1 HERE]

El Portalón is a holocene archaeological site located in the current entrance of the Cueva Mayor-Cueva del Silo karst system at the Sierra de Atapuerca (Spain). This site is of particular interest due to its prolonged human occupations documented from the Upper Palaeolithic to historic times (Carretero et al., 2008). Its complex formation is the result of a combination of natural processes, domestic anthropogenic activities, farming and funerary ritual practices (Alday et al., 2011, Galindo-Pellicena et al., 2014, 2017a,b; Castilla et al., 2014; Pérez-Romero et al., 2017). The currently known stratigraphic sequence exceeds 10 m of potential and is divided into 11 stratigraphic units grouped into two sedimentary units (Carretero et al., 2008). There is a basal sedimentary unit from the Upper Pleistocene with abundant microfauna, though evidence of macrofauna and human presence is scarce. The second sedimentary unit comprises the Holocene and is divided into ten stratigraphic units (Carretero et al., 2008). The cultural affiliation of the Holocene units, based on material records and supported by 70 radio-chronological dates, provides evidence of occupations in the Middle Ages, the Roman Age, Iron Age I (Levels 0, 1, and 2), the Final, Middle, and Early Bronze Age (Levels 3/4, 5), the Chalcolithic (Levels 6, 7/8) and the Neolithic/Mesolithic (Level 9) (Carretero et al., 2008). The Chalcolithic stratigraphic units are divided into two phases: an Early Chalcolithic or Pre-bell beaker funerary context and a Final Chalcolithic or Campaniform phase, characterized by herding and habitat context. In the funerary context, a minimum of eight individuals were recovered from several altered primary burials with bones showing different levels of associated grave goods and faunal remains. A series of radiocarbon dates obtained from seeds, human and animal bones place these burials at the end of the fifth millennium BP. The domestic animals and ceramics suggest a complex and symbolic human-animal relationship (Pérez-Romero et al, 2017). Among the faunal remains recovered from this burial context that have been anatomically and taxonomically identified, ovicaprines are the most dominant group (41.65%), followed by *Bos taurus* (11.15%), *Sus domesticus* (7.82%), *Canis familiaris* (1.64%) and *Equus sp.* (0.9%) In addition to these species, hunted animals (*Cervus elaphus*, C*apreolus capreolus, Vulpes vuloes,* Leporidae indet and small carnivores) and very low percentages of fish and turtle shells have also been recovered (Galindo-Pellicena, 2014; Pérez-Romero et al., 2017). In the habitat context, the ovicaprines (67% of the faunal remains) are the most represented livestock, followed by bovids (28%) and pigs

(7%) (Galindo-Pellicena et al., 2013; Galindo-Pellicena, 2014; Galindo-Pellicena et al., 2017). In the case of the ovicaprine and bovids, their mortality profiles indicate that both young and elderly individuals were slaughtered (Galindo-Pellicena et al., 2013, Galindo-Pellicena et al., 2014; Galindo-Pellicena et al., 2017). About 50% of the ovicaprine bones show fire alteration and 90% of them show evidence of having been boiled, according to the criteria of Botella et al. (1999) (Galindo-Pellicena et al., 2014). Most of the fire-altered bovid (82.53%) and pig (92%) bones also show evidence of having been boiled (Galindo-Pellicena, 2014). Thus, we can assert that ovicaprines, bovids and pigs constitute the foundation of the food consumption for the inhabitants of El Portalón during both phases of the Chalcolithic (Pre-bell beaker and Campaniform) .

El Alto de la Huesera, located in Laguardia, Álava (Spain), is a dolmen formed by a chamber and corridor. A minimum of 106 individuals (29 subadults and 77 adults) (Fernández-Crespo, 2016) were interred in a primary burial during the Final Chalcolithic (Fernández- Eraso and Mujika, 2013). Neither faunal nor arqueobotanical remains have been recovered from this dolmen. Nonetheless, there is a close chronological and functional relationship between El Alto de la Huesera and some archaeological sites from Sierra de Cantabria (North of Spain). These sites are Peña Larga, Los Husos I and II and San Cristobal (Fernández-Eraso and Mujika, 2013). The relationship between these sites was that Chalcolithic people had their stables in Peña Larga, Los Husos I and II and San Cristobal and they are buried in El Alto de la Huesera (Fernández-Eraso and Mujika, 2013; Alonso-Eguiluz, 2012). The pollen study conducted on these sites shows that the environmental conditions were relatively dry during the Chalcolithic (Pérez-Díaz et al., 2010). Agriculture is detected through the presence of pollen and grasses, though the percentages are extremely low (above 1.5% in Peña Larga and around 3% in San Cristóbal) (Pérez-Díaz et al., 2010). The relatively high pollen percentages of *Chenopodiaceae*, *Plantago sp.* and *Urtica dioica*, along with some non-pollen palynomorphs, such as *Sordaria sp.* and *Sporormiella sp.,* suggest an intensification of the livestock during the Chalcolithic (Pérez-Día et al., 2010). Moreover, all these sites show levels of *fumier* (Fernández-Eraso, 2010). Levels of this kind are related to animal husbandry, since they are formed as a result of piling and burning the dung in order to reduce the volume and to eliminate parasites (Angelucci et al., 2009). The *fumiers* from these sites usually contain remains of bovids and ovicaprines (Fernández-Eraso, 2010). Thus, we would expect an economy mainly based on animal husbandry during the Chalcolithic in Cantabria.

2.2. Dental samples

In order to maximize the number of individuals analyzed, we performed the analysis of dental microwear on buccal, occlusal and incisal surfaces. Buccal microwear data from El Portalón were collected from a total of four teeth belonging to a minimum of 2 individuals. These teeth include two permanent lower right first molars, one deciduous lower right second molar and one permanent lower third molar (Table 1). From El Alto de la Huesera, we have analyzed the buccal surface from a total of six teeth belonging to six different individuals. Five of these teeth are permanent lower first molars (three from the left side and two from the right) and one is a deciduous lower second molar (Table 1).

[INSERT TABLE 1 HERE]

In the case of occlusal and incisal microwear, the data were limited to the El Portalón sample, since teeth from El Alto de la Huesera show dentine exposure over the entire occlusal surface. Data for occlusal microwear analysis were taken from the same two permanent molars from which buccal microwear was analyzed (Table 1). The sample for incisal microwear analysis consisted of six deciduous incisors belonging to a minimum of five individuals (Table 1).

The subadult individuals studied here were aged by assessing the stage of dental calcification and root formation (tooth mineralization). The mineralization stages of each tooth class were scored using the Moorrees et al. (1963) method. The age of attainment of the different mineralization stages were interpolated from tables provided by Smith (1991). When the sex of the individual under study was unknown, we calculated the mean of age of attainment for males and for females. For the deciduous teeth we followed the method of Liversidge and Molleson (2004).

The age at death in adult individuals was estimated following the standards developed by Lovejoy et al (1985) and Brothwell (1981). These methods are based on the rate and patterns of dental wear, which depend on several factors besides age (White et al., 2012). When these methods have been used to test different populations, a significant correlation between known age and tooth wear has been found (Lovejoy et al., 1985; Richards and Miller, 1991). Nonetheless, we are aware that pathology or use of the teeth as tools could accelerate the wear, leading to an overestimation of the age (Milner and Larsen, 1991).Thus, although we detected neither pathological signs nor evidence of using the teeth as a tool in the dental sample studied here, the age estimations for adults should be taken into account only as a gross approximation of the real age.

3. Methods

3.1. Imaging procedure

Teeth from El Portalón and La Huesera were imaged directly using an environmental scanning electron microscope (ESEM) JEOL JSM-6460LV in lower vacuum mode. The ESEM was used by García-González et al. (2015) when studying the El Mirón teeth, which indicates that the quality of images is sufficient to carry out a quantitative analysis based on dental microwear features.

3.2. Data collection

For the analysis of buccal microwear patterns, digitized micrographs were taken at a magnification of 100X. The number, length and angles of all scratches were measured manually using ImageJ software. For methodological standardization, these measurements were taken in a selected area of $0.56mm^2$ (Pérez-Pérez et al., 1999). Negative angles were transformed into positive ones, by adding 180º. All observed scratches were classified by categories of orientation: vertical (67.5º-112.5º), mesio-occlusal to distocervical (22.5º-67.5º for right teeth and 112.5º-157.5º for left teeth), disto-occlusal to mesio-cervical (112.5º-157.5º for right teeth and 22.5º-67.5º for left teeth) and horizontal (0º-22.5º and 157.5º-180º) (Pérez-Pérez et al., 1994, 1999). For each category, three summary variables were calculated (number, mean and standard deviation of the length). Additionally and, following the recommendations of Pérez-Pérez et al. (1994, 1999) and Lalueza et al. (1996), three indices were calculated: the number of vertical and horizontal scratches divided by the total number of striations (NV/NT and NH/NT) and the number of horizontal striations divided by the vertical ones (NH/NV).

For the analysis of occlusal and incisal microwear, these surfaces were imaged at 500X (Bullingotn, 1991 and Mahoney 2006 a,b,c). In the case of occlusal surfaces, we have specifically imaged the bottom of facet 9 (Mahoney 2006 a,b). Pits and scratches were measured and counted on both surfaces using the same software as was used for the buccal microwear analysis. A 4:1 ratio was chosen to distinguish between these two microwear features (Mahoney, 2006 a,b).The variables analyzed on the occlusal surface were the frequency or percentage of pits, as well as the mean length and width of pits and scratches (Mahoney, 2006a,b,c and Mahoney, 2007). On the incisal surface, we only counted the number of pits and scratches and calculated the ratio between these two microwear variables (Bullington, 1991).

3.3. Analysis and comparisons of microwear patterns

The small sample size available in this study for tooth type, surface analyzed and archaeological site precludes any statistical treatment. Thus, in order to obtain a chronological and geographical perspective of the dietary habits inferred from microwear patterns in the Chalcolithic populations under study, we used several comparative samples obtained from Pérez-Pérez et al. (1994), Romero and de Juan (2007) and Salazar-García et al. (2016). Most samples came from the sites located in the Iberian Peninsula and span a wide chronological period ranging from the Neolithic to the Medieval ages (Table 2). Among them, seven sites are located along the Mediterranean coastline and one is on the Northern Plateau (Figure 1).

[INSERT TABLE 2 HERE]

We are aware that there is a potentially high level of inter-observer error of the dental microwear analysis using scanning electron microscopy (SEM) methods (Grine et al., 2002). This high error rate basically depends on the decision of whether fine and short scratches should be counted or not. Thus, a direct comparison of microwear densities obtained by different authors should be performed with caution. For this reason, the comparisons performed in this study have relied on the overarching trend rather than on the magnitude of the data of the studied and comparative samples.

Dietary studies performed on the comparative samples are based on the analysis of buccal microwear and, thus, our comparative analysis is limited to this surface. Our results regarding occlusal microwear patterns are only considered to complement the dietary inferences obtained from buccal surfaces. The analyses carried out on buccal surfaces provide information about dietary habits over relatively long periods of time, while analyses performed on occlusal surfaces are able to reflect seasonality of food resource exploitation. In this sense, a recent study has demonstrated that the application of these two kinds of analyses in the same specimens offer consistent results and allow us to obtain more complete dietary conclusions (García-González et al., 2015).

The findings obtained from incisal surface are taken into account in order to establish some inferences about the weaning process and age-related dietary changes.

4. Results

4.1. Buccal microwear analysis

Descriptive statistics for dental microwear features collected from buccal surfaces of teeth from El Portalón and El Alto de la Huesera are provided in Table 3.

[INSERT TABLE 3 HERE]

The total number of striations on the buccal surface ranged from 61 to 195, with the third molar (M3) from El Portalón as the tooth with the highest number of striations followed by both deciduous second molars (dm2), one from each archaeological site included in this analysis (Table 3). The high number of scratches on the two dm2 may be due to structural differences between deciduous and permanent tooth enamel (Scott and Halcrow, 2017). Deciduous dental enamel is thinner and weaker than permanent enamel (Grine, 2005; Low et al., 2008; Mahoney et al, 2016). It could yield differences in the rate and pattern of microwear features formation independent of the food consumed (Scott and Halcrow, 2017). However, Mahoney et al. (2016) demonstrates that there were no statically significant differences in the pattern of formation of microwear features between deciduous and permanent teeth. Although the findings of Mahoney et al (2016) were obtained through dental microwear texture analysis on the occlusal surface of deciduous molars, they can be extrapolated into the present study with some caution. As we have mentioned above, there are differences in the pattern of formation and turnover of microwear features between occlusal and buccal surfaces. Nonetheless, Mahoney et al. (2006) tested the differences between some microwear texture values before and after deciduous and permanent teeth were experimentally abraded. These values affected neither the pattern of formation nor the rate of turnover. Thus, we can infer that there would be differences between these microwear texture values from deciduous enamel when compared to permanent. The microwear texture variables considered by Mahoney et al. (2016) were complexity and anisotropy, which can easily be related to microwear variables obtained through analysis of SEM images. Anisotropy measures the orientation of microwear over surface and can be related to the orientation of the scratches. Complexity is a measurement of the number of striations (Ungar et al., 2003; Scott et al. 2005). Thus, changes in the number and orientation of the striation are related to changes in complexity and anisotropy; in other words, high values of complexity and anisotropy reflect a high number of scratches with an orientation in the same direction. Based on this, a higher number of scratches in deciduous teeth than in permanent teeth cannot be explained exclusively by differences between the enamel structure of these two kinds of teeth. The most plausible explanation for the high number of striations on the two dm2 is the same reason behind the high frequency of scratches on permanent teeth. Following this reasoning, the high scratch densities on M3 and two dm2 may be due to the fact that the total number of scratches increases with the tooth age since eruption, given that the pattern of buccal microwear is a dynamic process with a cumulative effect throughout life (Pérez-Pérez et al., 1994). An increase in scratch density with the eruption age is observed in the teeth from El Portalón (Table 3). In these teeth, the older the eruption age, the higher the scratch density. Moreover, the comparison of the number of scratches between the dm2 and first molars (M1) of the same individual (ATP12-1420) also confirm this trend. The M1 shows a smaller striation density than the dm2 (Table 3), but the age of clinical eruption of these two teeth also differs. The dm2 usually is erupted around 2.5 years old, while for the M1, this occurs between 5.5 and 6.5 years of age (AlQahtani et al., 2010). This implies that the time elapsed between the eruption of dm2 and the death of the individual could be up to four years, while the period of time between the eruption of M1 and the death could only have lasted up to 1 year. Thus, the higher number of striations in dm2 than in M1 is due to a longer functional time.

In teeth from El Alto de La Huesera, however, there is no clear trend showing an increase in the total number of striations with an increased eruption age. From this site, teeth with a higher number of scratches (ADLH-4 and ADLH-12) have a difference in eruption ages of up to 6.5 years (Table 2). The total number of striations showed by these teeth is even higher than in those teeth belonging to fully adult individuals (Table 1 and Table 3). Interestingly, the scratch densities of M1 belonging to these fully adult individuals are close to the total striation density of the M1 belonging to the adolescent ADLH-10 (Table 1 and Table 3). Pérez-Pérez et al. (1994) have asserted that a definitive striation pattern is attained between 5-12 years from eruption. Based on the eruption age of ADLH-10 (6 years, Table 3) and the similarity in the total number of scratches present on that tooth and those of full adults, we can assert that this individual could have already attained the tooth striation pattern of the adult population. If this is true, the high number of striations shown by ADLH-12 with an age of 16 years could reflect inter-individual variability.

Regarding the scratch length, the high values for standard deviations are worth noting, which implies a high variability in the length of striations. The general trend indicated by teeth from El Portalón and El Alto de la Huesera is that the average length of the scratches increases with age, though some exceptions were found. The teeth that do not follow this rule are the M3 from El Portalón and the dm2 and one M1 (ADLH-50) from El Alto de la Huesera. The lower average length of the scratches on the M3 from El Portalón than on the other teeth from the same site is likely independent of the tooth type, since third molars are both morphologically and functionally similar to first molars (Pérez-Pérez et al., 1994). The average length of the striations for this M3, together with the ages estimated for it and the M1 from El Alto de la Huesera, seems to suggest that the length of the scratches increases with age in younger groups and then decreases in older groups (Pérez-Pérez et al. 1994).

In sum, the analysis of buccal microwear patterns in teeth from El Portalón and El Alto de la Huesera reveals that the striation pattern is related to both the age at death of the individuals and the period of time elapsed from the eruption of teeth. Thus, in order to obtain the appropriate framework of comparison, we perform different comparisons based on the age of the individuals. In this way, Figures 2-4 depict the buccal microwear length against buccal microwear density for dm2, M1 belonging to subadult individuals and teeth belonging to fully adult individuals.

[INSERT FIGURE2 HERE]

[INSERT FIGURE 3 HERE]

The dm2 scratch densities from El Portalón and El Alto de la Huesera are comparable to the medieval sample from La Olmeda compounded by 6-9 year old children (Figure 2). However, the two Chalcolithic dm2 are characterized by shorter scratches than the two age groups from La Olmeda. A similar pattern is observed when the M1s belonging to subadult individuals from El Alto de La Huesera are compared to equivalent age groups from La Olmeda (Figure 3). These Chalcolithic individuals show shorter scratches than medieval ones. However, the scratch density and average length of striations of ATP12-1420 fall well within the range of variation of medieval children between 6 and 10 years old. Thus, Chalcolithic individuals analyzed in this study resemble each other in that they have a density of scratches similar to medieval individuals who had an equivalent age at death; however, the individuals from El Alto de la Huesera show a distinct pattern, since the scratches are shorter on average.

[INSERT FIGURE 4 HERE]

In Figure 4 the buccal microwear variability among the analyzed Chalcolithic individuals is depicted, as well as the populations used for comparisons, when only the full adults are considered. In general, prehistoric populations from the Mediterranean coast of Iberian Peninsula show a higher number of striations the older the chronology of the site. Neolithic and Chalcolithic individuals are characterized by a higher number of shorter striations than Bronze (Figure 4). It implies that there is a reduction in the abrasiveness of the diet of individuals from older sites to younger ones over the course of prehistory. Interestingly, the Islamic individuals from Tossal de les Basses have the same number of scratches as the Neolithic sample. In contrast, medieval individuals from La Olmeda present one of the lowest values for the number of striations and the highest values for the length of the scratches. The contemporary sample from Villena and Later Roman individuals show a buccal microwear pattern characterized by few and short scratches. These findings suggest that there are differences in abrasive particles between the Mediterranean Islamic sample on the one hand, and the Medieval from La Olmeda, the Contemporary and the Later Roman individuals on the other. These differences could be due to changes in both food content and preparation methods between these samples. Individuals from El Alto de la Huesera have as few scratches as medieval individuals from La Olmeda and the contemporary sample from the Mediterranean coast. Molars from El Portalón show higher variability than those from El Alto de la Huesera. While ATP11-26-H14 resembles the molars from El Alto de la Huesera in the number and length of the striations, the number of striations found on ATP11-S304 is at the lower end of the Mediterranean Neolithic and Islamic range of variation.

In sum, the comparison of the buccal microwear variables reveals that both subadult and adult individuals from El Portalón and El Alto de la Huesera show a number of striations equivalent to that of medieval individuals from La Olmeda (Figures 2-4). The main difference between these two distinct chronological samples is that individuals from the Chalcolithic sites display shorter scratches than the medieval ones on average. Based on the number of striations, we can assert that the diet of Chalcolithic individuals from El Portalón and El Alto de la Huesera is as abrasive as that of the medieval sample from La Olmeda. The abrasiveness of the diet depends on both dietary and non-dietary factors. The medieval population of La Olmeda had a diet mostly based on cereals, which were processed by the grinding of seeds with stone mills.

4.1. Occlusal microwear analysis

The dental microwear variables taken from the occlusal surface of the two first molars from El Portalón are provided in Table 4.

[INSERT TABLE 4 HERE]

Based on these variables we can infer that the El Portalón molars have a low frequency of pits, which may reflect a relatively soft and tough diet (Schmidt, 2001; Mahoney, 2007). A diet mainly based on these foods requires more shearing than compressive forces during the chewing cycle, yielding small pits and long scratches on the occlusal surface (Gordon, 1982; Molleson et al., 1993; Mahoney, 2006 a,b). However, both molars from El Portalón show large pits. Although pitting and pit size seem to be inconsistent at first glance, it is important to note that the pit size is also related to the physical properties of the abrasive particles adhering to the food. Thus, in this case, differences in the pitting and pit size are due to different factors. The length of the scratches on two first molars is extremely variable (high SD), which implies that there are short and long scratches on these occlusal surfaces. The presence of long striations on the occlusal surface of first molars concurs with a low percentage of pits, since long scratches and few pits are associated with a chewing cycle in which shearing forces are predominant. Instead, the short scratches may reflect the chewing of soft foods, for which the lateral movements of the mandible can be less important (Luschei and Goodwin, 1974).

In sum, the occlusal microwear pattern on the first molars from El Portalón seems to indicate a diet mainly consisting of soft and tough foods with large abrasive particles adhered.

4.1. Incisal microwear analysis

[INSERT TABLE 5 HERE]

The microwear variables taken from the incisal surface in teeth from El Portalón are depicted in Table 5. With the exception of ATP12-65 and ATP10-H2, there is a downward trend in regard to the total incisal microwear features with both age and eruption age. Bullington (1991) reported a different trend in a sample of deciduous incisors and molars. He established that the total microwear feature frequency increases with both age and age from eruption, which he explained through changes in the diet.

Studies in primates have shown that high densities of total features on incisal surfaces may reflect a heavier use of incisors in the ingestion of foods (Ryan, 1981; Kelley, 1986, 1990; Ungar, 1990, 1994). If we were to extrapolate these findings into our results, it might show that younger individuals use more of the incisors, probably related to the normal mechanism of mastication and feeding processes of children. Basically, the process can be divided into four phases related to the eruption of deciduous teeth (Scott and Halcrow, 2017). The first phase begins between the ages of 6 and 8 months, when the deciduous incisor erupts. In this phase, vertical movements during mastication are predominant and the tongue drives the food bolus over incisors. Also during this phase, if the food bolus contains abrasive particles, it will abrade the incisal surface. The second phase begins when the first deciduous molar erupts (around 1.5 years old). In this second phase, chewing of the foods is carried out by the first deciduous molar through vertical movements of the jaw. In the third phase, the mastication cycle consists of both vertical and horizontal movements. This phase begins with the eruption of the second deciduous molars (at around 2 years of age). Starting at this time, first and second deciduous molars are responsible for the crushing and slicing of foods. Finally, starting at 3 years of age, the chewing cycle becomes similar to that of adults. Thus, younger individuals from El Portalón (those aged up to 18 months, see Table 5) would show higher density of total incisal microware features because their deciduous molars would not have played a role in mastication. The decrease in the number of striations and pits on the incisal surface as the age at death increased would reflect the beginning of the use of deciduous molars in mastication. Therefore, the age-related trend shown by incisors from El Portalón is easily explained by developmental changes. Nonetheless, all these incisors show high numbers of both pits and scratches, which may be related to a relatively hard diet in these young Chalcolithic individuals.

5. Discussion

The results obtained through dental microwear analysis on teeth from El Portalon and El Alto de la Huesera provide valuable information about two important topics: the age-related dietary habits in prehistoric populations and the effect of the interaction between environmental and cultural factors on the microwear pattern.

Regarding the effect of environmental factors on the dental microwear pattern, adult individuals from El Portalón and El Alto de la Huesera show a pattern of buccal microwear more similar to that found in medieval individuals from La Olmeda. Interestingly, the buccal microwear of adults from this medieval population is characterized by the lower density of shorter microwear features, indicative of a less abrasive diet than that of the other comparative samples, including historical counterparts from the Mediterranean coast (Figure 4). Since the abrasiveness of the diet depends on both dietary and non-dietary factors, such as the foodstuff technical processes (Romero and De Juan, 2007), we would expect to find differences between different chronological groups. Nonetheless, our findings suggest that differences in buccal microwear features also depend on geographical location. Thus, environmental factors, such as elevation, temperature and precipitation, could also be correlated with the buccal microwear pattern. The environmental conditions during the Chalcolithic in the Sierra de Atapuerca were relatively dry, with a decrease in the woodlands and nitrophilous taxa and a slight increase in xeric taxa (Martínez-Pillado et al., 2014). This could have led to higher intensification of animal husbandry to the detriment of agriculture. One of the uses of the cattle herd from El Portalón during the Chalcolithic, among others, was obtaining secondary products, such as milk and meat consumption (Galindo-Pellicena, 2014, 2017). Obviously, this does not mean that agriculture was not part of the economy during the Chalcolithic in the Sierra de Atapuerca, but we hypothesized that during this prehistoric period, livestock was preferred and probably more relevant. Regarding El Alto de la Huesera during the Chalcolithic period, the studies performed on the archaeological sites related to this dolmen also reveal an intensification of animal husbandry in this area during this period. Thus, differences between Chalcolithic groups from the Northern Plateau and those from the Mediterranean coast could be due to a higher intake of meat in the former than in the latter.

The consumption of meat can be inferred from buccal microwear patterns regarding the relative frequencies of vertical and horizontal scratches. In this sense, individuals from El Portalón and El Alto de la Huesera have a higher number of vertical striations than horizontal ones. In a study of different dietary groups, Lalueza et al. (1996) established that the group with a diet mainly based on meat had a higher relative frequency of vertical scratches than horizontal ones. Thus, if we extrapolate these findings into the present study, we can assert that the relative frequency of scratches by orientation found in the teeth from El Portalón and El Alto de la Huesera suggest a high intake of meat.

A high intake of meat could also be related to the occlusal microwear pattern found in first molars from El Portalón. Although it is more difficult to establish meat consumption through occlusal microwear patterns than it is to do through buccal microwear features (Mahoney, 2007), some conclusions can be drawn. The low frequency of pits present on the first molars from El Portalón can reflect a relatively soft and abrasive diet, requiring more shearing than compressive forces during the chewing cycle (Schmidt, 2001; Mahoney, 2007). A diet based on this kind of food yields long scratches, a length that reflects the amount of shearing needed to comminute the foods. However, the scratches on the first molars from El Portalón are short. When meat is tough enough to require significant shearing force to cut it during chewing, this yields longer scratches and can even result in forceful tooth-on-tooth contact, leading to bigger and more abundant pits. Therefore, the relatively high frequency of short scratches on the teeth from El Portalón could be related to the consumption of soft meat. Soft meat can possibly come from immature animals or from a technical process, such as boiling, which softens the food. The data compiled with respect to the management of domestic animals support this assertion. As we have mentioned above, most of the domestic faunal remains recovered from El Portalón show evidence of having been boiled (Galindo-Pellicena, 2014).

Regarding dietary changes with age, the analysis of the microwear on buccal surfaces of teeth from El Portalón shows that the buccal microwear pattern is accumulated throughout life in this population, and subadult individuals attain the characteristic striation pattern of the population in ages older than seven years (Figures 2-4). It could imply a similar diet in adult and subadult individuals from this Chalcolithic site.

However, the analysis of microwear on incisal surfaces that belong to subadult individuals reveals a pattern characterized by numerous pits and scratches. This finding suggests that the diet of subadult individuals was harder than that of the adults. This might suggest, therefore, that meat consumption intensified after a certain age in this society. This assertion is confirmed by findings obtained from teeth found in El Alto de la Huesera. A shift in dietary habits with age in this population has been established by

Fernández-Crespo and Schulting (2017). These authors analyzed the stable carbon and nitrogen isotope in teeth from El Alto de la Huesera, along with those from other mortuary monuments and caves from north-central Spain. Although the main goal of this paper was to establish differences in the burial location and treatment based on stable isotopes, they also claimed that, when data are combined from all sites, there is a clear upward trend in the values of 15N with age. This increase in 15N values may be attributable to skeletal growth, but could also be because of differences in diet due to a high meat intake.

Finally, the analysis of incisal microwear in deciduous teeth from El Portalón provides some insights about the weaning process. Weaning implies the introduction of supplemental foods besides maternal milk into the infant diet and it mainly depends on the availability of soft foods (Bullington, 1991). In traditional societies, this process occurs during the first year of life. The age of some individuals from El Portalón fall within this range, but the high frequency of pits and scratches on these teeth suggests that, during weaning, supplemental foods were hard enough to lead to these numerous microwear characteristics in this population.

6. Conclusions

In sum, findings obtained through occlusal and buccal dental microwear analysis on teeth from El Portalón and El Alto de La Huesera suggest a mixed diet but one with a high rate of meat intake. Since the meat is unlikely to be hard enough to cause numerous microwear features (Mahoney, 2007), it could be related to the less abrasive diet in Chalcolithic populations from the Northern Plateau than what was consumed by their counterparts from the Mediterranean coast.

In contrast with the archaeological sites from the Northern Plateau, sites from the Mediterranean coast are located on a wetland. Accordingly, a difference in food resources must be responsible for the observed differences between the Mediterranean site and the Northern Plateau sites in regard to microwear features.

7. Acknowledgements

We thank our colleagues from the Laboratorio de Evolución Humana, Centro UCM-ISCIII sobre Evolución y Comportamiento Humanos and the El Portalón research team for their help during field seasons and for their useful comments and critical review of the manuscript. The authors received financial support from the Ministerio de Economía y Competitividad, Spain (project CGL2015-65387-C3-2-P, MINECO-FEDER). Excavations in El Portalón are funded by the Junta de Castilla y León and Fundación Atapuerca.

References

AlQahtani SJ, Hector MP, Liversidge HM (2010) Brief communication: the London atlas of human tooth development and eruption. Am J Phys Anthropol 142:481-490.

Alday A, Pérez-Romero A, Carretero JM, Galindo-Pellicena MA, Adán G and Arsuaga JL (2015) Proofs of long distance relations between central Europe and inland Iberian Peninsula during Neolithic and Bronze Age. Evidences from the material culture of the site of El Portalón (Sierra de Atapuerca, Burgos, Spain). Advances in Anthropol 5: 249-309.

Alonso-Eguíluz M (2012) Estudio de los fitolitos en conjuntos de la Prehistoria reciente en la Sierra de Cantabria. El caso de los niveles de redil de San Cristóbal (Laguardia, Álava) CKQ 2:1–14.

Angelucci DE, Boschian G, Fontanals M, Pedroti A, Vergés JM. (2009) Shepherds and karst: the use of caves and rock-shelters in the Mediterranean region during the Neolithic. World archaeology 41:191–214

Brothwell DR (1981) Digging up bones: the excavation, treatment, and study of human skeletal remains. Cornell University Press. Nueva York.

Botella M, Alemán I and Jiménez SA (1999). *Los huesos humanos. Manipulación y alteraciones.* Eds. Bellaterra. Barcelona.

Bullington J (1991) Deciduous dental microwear of prehistoric juveniles from the lower Illinois River valley. Am J Phys Anthropol 84:59–73.

Carretero JM, Ortega AI, Juez L, Pérez-González A, Arsuaga, JL, Pérez R, Ortega, MC, (2008) A late pleistocene-early Holocene archaeological sequence of portalón de Cueva mayor (Sierra de atapuerca, burgos, Spain). Munibe 59:67–80.

Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. Journal of Zoology 183:1–39

El Zaatari S, Hublin JJ (2014) Diet of Upper Paleolithic Modern Humans: evidence from microwear texture analysis. Am J Phys Anthropol 153:570-581.

Fernández-Crespo T, de-la-Rúa C (2016) Demographic differences between funerary caves and megalithic graves of northern Spanish Late Neolithic/Early Chalcolithic. Am J Phys Anthropol 160:284–297.

Fernández-Crespo T, Schulting RJ (2017) Living different lives: Early social differentiation identified through linking mortuary and isotopic variability in Late Neolithic/ Early Chalcolithic north-central Spain. Plos One 12:1-19.

Fernández-Eraso JF (2010) La actividad pecuaria en la Rioja Alavesa durante la Prehistoria Reciente. Cuadernos de Arqueología de la Universidad de Navarra 18:159–171

Fernández-Eraso J, Mujika-Alustiza JA (2013) La estación megalítica de La Rioja alavesa: cronología, orígenes y ciclos de utilización/The megalithic station of the Rioja Alavesa: chronology, origins and utilisation cycles. Zephyrus 71:89.

Galbany J, Garriga N. Majoral Salich N, Coll Monteagudo R, Fluxá J. (2008) Microdesgaste y patología dental en la población de la Edad de Bronce de "Mar i Muntanya" (Alella, Barcelona). Rev Esp Antrop Fís 28:25–36.

Galindo-Pellicena M.A (2014) Estudio de la macrofauna de los niveles holocenos del yacimiento de El Portalón (sierra de Atapuerca, Burgos) Dissertation. University Complutense of Madrid (Unpublished thesis).

Galindo-Pellicena M, Carretero J., Arsuaga JL (2013) La gestión de Ovis aries y Capra hircus en los niveles calcolítico y bronce del yacimiento de El Portalón (Atapuerca, Burgos). Actas de las III Jornadas de jóvenes investigadores del valle del Duero: 83-100.

Galindo-Pellicena, M. A., Carretero, J. M. y Arsuaga, J. L. (2014) Primary or secondary products? The nature of *Ovis* and *Capra* exploitation within the Bronze Age levels at Portalón (Atapuerca hill, Burgos, Spain) In: Greenfield HJ (Eds.) The Archaeology of Animal Secondary Products Exploitation in Eurasia: from Europe to China. Oxbow Press, Oxford, pp 103-128

Galindo-Pellicena MA, Martín-Francés L, Gracia A, De Gaspar I, Arsuaga JL, Carretero JM (2017a) Evidences of the use of cattle as draught animals in Chalcolithic of El Portalón (Sierra de Atapuerca, Burgos) Quat Int 438:1-10.

Gamza T, Irish J (2012) A comparison of archaeological and dental evidence to determine diet at a predynastic egyptian site. Int J Osteoarchaeol 22:398–408.

García-González R, Carretero JM, Richards MP, Rodríguez L, Quam R (2015) Dietary inferences through dental microwear and isotope analyses of the Lower Magdalenian individual from El Mirón Cave (Cantabria, Spain). J Archaeol Sci 60:28–38.

Gordon KD. 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. Am J Phys Anthropol 59:195–215.

Grine FE, Ungar PS, Teaford MF (2002) Error rates in dental microwear quantification using scanning electron microscopy. Scanning 24:144–153.

Grine FE (2005) Enamel thickness of deciduous and permanent molars in modern Homo sapiens. Am J Phys Anthropol 126:14–31.

Grine FE (2007) Dentition and Diet: Introduction. In: Bailey SE and Hublin JJ (ed) Dental Perspectives on Human Evolution. Springer, Dordrecht, pp 291-302.

Hogue SH, Melsheimer R (2008) Integrating dental microwear and isotopic analyses to understand dietary change in east-central Mississippi. J Archaeol Sci 35:228-238

Kelley JJ (1986) Paleobiology of Miocene Hominoids. PhD dissertation, Yale University.

Kelley J (1990) Incisor microwear and diet in three species of Colobus. Folia Primatologica 55:73–84

Krueger KL, Ungar PS (2009) Incisor microwear textures of five bioarcheological groups. Int J Osteoarchaeol 20:549-560.

Lalueza C, Péréz-Perez A, Turbón D (1996) Dietary inferences through buccal microwear analysis of Middle and Upper Pleistocene human fossils. Am J Phys Anthropol 100:367–387.

Larsen CS (1997) Bioarchaeology: Interpreting Behavior Fromthe Human Skeleton. Cambridge University Press, Cambridge.

Liversidge HM, Molleson T (2004) Variation in crown and root formation and eruption of human deciduous teeth.Am J Phys Anthropol 123:172–180.

Lovejoy CO, Meindl RS, Mensforth RP, Barton TJ (1985) Multifactorial determination of skeletal age at death: a method and blind tests of its accuracy. Am J Phy. Anthropol 68:1–14.

Luschei ES, Goodwin GM (1974) Patterns of mandibular movement and jaw muscle activity during mastication in the monkey. J of Neurophysiology 37:954–966.

Mahoney P (2006a) Dental microwear from Natufian hunter-gatherers and early Neolithic farmers: Comparisons within and between samples. Am J Phys Anthropol 130:308–319.

Mahoney, P (2006b) Brief communication: intertooth and intrafacet dental microwear variation in an archaeological sample of modern humans from the Jordan Valley. Am J Phys Anthropol 129, 39–44.

Mahoney, P (2006c) Microwear and morphology: functional relationships between human dental microwear and the mandible. J Hum Evol 50:452–459.

Mahoney P (2007) Human dental microwear from Ohalo II (22,500–23,500 cal BP), Southern Levant.Am J Phys Anthropol 132:489–500.

Mahoney P, Schmidt CW, Deter C, et al (2016) Deciduous enamel 3D microwear texture analysis as an indicator of childhood diet in medieval Canterbury, England. J Archaeol Sci 66:128–136

Martínez-Pillado V, Aranburu A, Arsuaga JL, Ruiz-Zapata B, Gil-Garcías MJ, Stoll H, Yusta I, Iriarte I, Carretero JM, Edwards L, Cheng H (2014) Upper Pleistocene and Holocene palaeoenvironmental records in Cueva Mayor karst (Atapuerca, Spain) from different proxies: speleothem crystal fabrics, palynology, and archaeology. Int J Speleolog 43:1-14.

McClure S, García-Puchol O, Roca C, Culleton B, Kennett D (2011) Osteological and paleodietary investigation of burials from Cova la Pastora, Alicante, Spain J Archaeol Sci 38:420–428.

Milner GR, Larsen CS (1991) Teeth as artifacts of human behavior: Intentional mutilation and accidental modification. In: Kelley Ma, Larsen CS (Eds.) Advances in dental anthropol, pp: 357-378. New York.

Molleson T, Jones K (1991) Dental evidence for dietary change at Abu Hureyra. J Archaeol Sci 18: 525-539.

Molleson T, Jones K, Jones S (1993) Dietary change and the effects of food preparation on microwear patterns in the Late Neolithic of Abu Hureyra, northern Syria. J Hum Evol 24: 455-468.

Moorrees CF, Fanning EA, Hunt Jr EE (1963) Age variation of formation stages for ten permanent teeth. J Dental Res 42:1490–1502.

Pérez Díaz S, Ruiz Alonso M, López Sáez JA, Zapata Peña L (2010) Dinámica vegetal y antropización en la Sierra de Cantabria (Álava) desde el Neolítico a la Edad del Bronce. Polen 20:25–40

Pérez-Pérez A, Bermúdez de Castro JM, Arsuaga JL (1999) Nonocclusal dental microwear analysis of 300,000-year-old Homo heilderbergensis Teeth from Sima de los Huesos (Sierra de Atapuerca, Spain). Am J Phys Anthropol 108:433–457.

Pérez-Pérez A, Lalueza C, Turbón D (1994) Intraindividual and intragroup variability of buccal tooth striation pattern. Am J Phys Anthropol 94:175–187.

Pérez-Romero A, Iriarte E, Galindo-Pellicena MA, García-González R, Rodríguez L, Castilla M, Francés-Negro M, Santos E, Valdiosera C, Arsuaga JL, Alday A, Carretero JM (2017) An unusual Pre-bell beaker copper age cave burial context from El Portal_on de Cueva Mayor site (Sierra de Atapuerca, Burgos). Quat Int 433:142-155

Richards LC, Miller SLJ (1991) Relationships between age and dental attrition in Australian Aboriginals. Am J Phys Anthropol 84:159–164.

Romero A, Martínez-Ruíz N, De Juan J (2004) Non-occlusal dental microwear in a bronze-age human sample from East Spain. Anthropologie 42:65-70.

Romero A, De Juan J (2007) Intra-and inter-population human buccal tooth surface microwear analysis: inferences about diet and formation processes. Anthropologie 45:61-70.

Romero A, Ramírez-Rozzi FV, De Juan J, Pérez-Pérez A (2013) Diet-related buccal dental microwear patterns in Central African pygmy foragers and bantu-speaking farmer and pastoralist populations. Plos One 8(12): e84804.

Ryan AS (1981) Anterior dental microwear and its relationship to diet and feeding behavior in three african primates (Pan troglodytes troglodytes, Gorilla gorilla gorilla and Papio hamadryas). Primates 22:533–550

Salazar-García DC (2009) Estudio de la dieta en la población neolítica de Costamar. Resultados preliminares de análisis de isótopos estables de carbono y nitrógeno. In: Flors Ureña E (Ed.) Evolución del paisaje antrópico desde la prehistoria hasta el medioevo. Servicio de Investigaciones Arqueológicas y Prehistóricas. Diputación de Castellón, Castellón, pp 411–418.

Salazar-García DC (2011) Patrón de dieta en la población púnica de Can Marines (Ibiza) a través del análisis de isótopos estables (C y N) en colágeno óseo. Saguntum 43: 95–102.

Salazar-García DC (2014) Estudio de la dieta en la población de Cova dels Diablets mitjançant anàlisi d'isòtops estables del carboni i del nitrogen en col·làgen ossi. Resultats preliminars. In: Aguilella Arzo G, Roman in Monroig D, García Borja P (Eds.) Prehistòria a la Serra d'Irta. Diputació de Castelló, Castellón, pp 67–78.

Salazar-García DC, Vives-Ferrándiz J, Fuller B, Richards MP (2010) Alimentación estimada de la población del Castellet de Bernabé (ss. V-III a.C.) mediante el uso de ratios de isótopos estables de C y N. Saguntum 9:313–322.

Salazar-García DC, Romero A, García-Borja P, Subirá ME, Richards MP (2016) A combined dietary approach using isotope and dental buccal-microwear analysis of human remains from the Neolithic, Roman and Medieval periods from the archaeological site of Tossal de les Basses (Alicante, Spain). J Archaeol Sci: Reports.

Schmidt CW (2001) Dental microwear evidence for a dietary shift between two nonmaize-reliant prehistoric human populations from Indiana.Am J Phys Anthropol 114:139–145.

Scott RM, Halcrow SE (2017) Investigating weaning using dental microwear analysis: A review. J Archaeol Sci: Reports 11:1–11

Scott RS, Ungar PS, Bergstrom TS, et al (2005) Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436:693–695

Smith BH (1991) Standards of human tooth formation and dental age assessment.Wiley-Liss Inc. New Jersey.

Teruyuki, H (2005) Regional differences of dental microwear on the occlusal surface of an M2 from Neolithic Japan: a case study. Dent Anthropol 18:61-64.

Ungar PS (1990) Incisor microwear and feeding behavior in Alouatta seniculus and Cebus olivaceus. Am J of Primatology 20:43–50

Ungar PS (1994) Incisor microwear of Sumatran anthropoid primates. Am J Phys Anthropol 94:339–363

Ungar PS, Spencer MA (1999) Incisor microwear, diet, and tooth use in three amerindian populations. Am J Phys Anthropol 109: 387-396.

Ungar PS, Brown CA, Bergstrom TS, Walker A (2003) Quantification of Dental Microwear by Tandem Scanning Confocal Microscopy and Scale-Sensitive Fractal Analyses. Scanning 25:185–193

White TD, Black MT, Folkens PA (2011) Human osteology.Academic press.

Figure legends

Figure 1. Archaeological sites from the Iberian Peninsula mentioned in the text and whose data are used.

1:El Portalón. 2: Alto de la Huesera. 3: La Olmeda. 4: Tossal de les Basses. 5: Villena.

Tossal de les Basses include sites with chronologies from Neolithic to Medieval ages

In Villena, the following archaeological sites are located: Losina, Cabeza Redondo and Molinico.

Figure 2. Density of striations of buccal-microwear (NT) plotted versus length of striations (XT, µm) on dm2 from El Portalón, El Alto de la Huesera and La Olmeda (Pérez-Pérez et al., 1994).

Filled triangles: teeth from El Portalón; filled squares: teeth from El Alto de La Huesera; filled circles: teeth from la Olmeda. Errors bars denote ± 1 SD.

Figure 3. Density of striations of buccal microwear (NT) plotted versus length of striations (XT, µm) on first molars belonging to subadult individuals from El Portalón, El Alto de la Huesera and La Olmeda (Pérez-Pérez et al., 1994).

Filled triangles: teeth from El Portalón; filled squares: teeth from El Alto de La Huesera; filled circles: teeth from la Olmeda. Errors bars denote ± 1 SD.

Figure 4. Density of striations of buccal microwear (NT) plotted versus length of striations (XT, µm) on molars belonging to adult individuals from El Portalón, El Alto de la Huesera and comparative samples

Filled triangles: El Portalón; filled squares: El Alto de La Huesera; filled circles: la Olmeda (Pérez-Pérez et al., 1994), open square: Mediterranean Chalcolithics (Romero and De Juan, 2007), diamond: Mediterranean Bronze Age (Romero and De Juan, 2007), arrow: Mediterranean Islamic (Romero and De Juan, 2007), open diamond: modern sample (Romero and De Juan, 2007). Open triangle: Neolithic (Salazar-García et al., 2016), star: Roman (Salazar-García et al., 2016), open circle: Medieval (Salazar-García, 2016). Errors bars denote ± 1 SD.