Journal of Human Evolution 211 (2026) 103797

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Reconstructing dietary preferences in the Middle Pleistocene Sima de los Huesos population: A molar macrowear perspective

Laura Martín-Francés [a, b, *], María Martinón-Torres [a, c], Marina Lozano [d, e], María Hernaiz-García [b, f], Juan Luis Arsuaga [g, h], José María Bermúdez de Castro [a], Luca Fiorenza [b]

[a] CENIEH (Centro Nacional de Investigación sobre la Evolución Humana), Paseo Sierra de Atapuerca, 3, 09002, Burgos, Spain
[b] Monash Biomedicine Discovery Institute, Department of Anatomy and Developmental Biology, Monash University, Melbourne, VIC, 3800, Australia
[c] Anthropology Department, University College London, 14 Tavinton St, London, WC1H 0BW, UK
[d] Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Edificio W3, Campus Sescelades URV, Zona Educacional, 4, 43007, Tarragona, Spain
[e] Departament d'Història i Història de l'Art, Universitat Rovira i Virgili (URV), Campus Catalunya Av. Catalunya, 35, 43002, Tarragona, Spain
[f] Laboratorio de Poblaciones del Pasado (LAPP), Facultad de Ciencias, Departamento de Biología, Universidad Autónoma de Madrid (UAM), Francisco Tomás y Valiente 7, 28049, Madrid, Spain
[g] Centro UCM-ISCIII de Evolución y Comportamiento Humanos, Avd. Monforte de Lemos, 5, Pabellón 14, 28029, Madrid, Spain
[h] Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, C. José Antonio Novais, 12, Ciudad Universitaria, 28040, Madrid, Spain

ARTICLE INFO

Article history:
Received 10 April 2025
Accepted 9 December 2025
Available online xxx

Keywords:
Maxillary molars
Occlusal fingerprint analysis
Paleodiet
Behavior
Paleoenvironment
Atapuerca

ABSTRACT

Molar macrowear analysis is a valuable tool for inferring dietary preferences in extinct hominins, ultimately aiding in the reconstruction of subsistence strategies and paleoenvironmental conditions. Radiometric studies suggest that the Middle Pleistocene population from the Atapuerca-Sima de los Huesos site likely lived during Marine Isotope Stage 12, one of the coldest global periods. In this study, we applied the occlusal fingerprint analysis method to maxillary M1s and M2s from this population to assess whether their macrowear patterns reflect these environmental conditions. Given the nature of the hominin accumulation and the limited availability of faunal, lithic, and pollen remains at the site, we rely on published data from the nearby Trinchera sites of Gran Dolina and Galería to reconstruct paleoecological conditions and subsistence strategies. Our occlusal fingerprint analysis results indicate that the Sima de los Huesos population had a mixed diet, consuming similar proportions of meat and plant foods. This dietary pattern does not align with expectations for a strictly cold environment, such as that of Marine Isotope Stage 12, but instead it suggests a diverse landscape, as supported by pollen, faunal, and isotopic evidence.

1. Introduction

The reconstruction of dietary habits in extinct hominin species is employed to infer subsistence strategies and to investigate their adaptive mechanisms to changing environmental conditions (e.g., Pérez-Pérez et al., 2003; Ungar et al., 2010; El Zaatari et al., 2011; Fiorenza et al., 2015, 2020). To do this, multiple lines of evidence are used, including faunal and pollen remains, dental stress indicators, isotopic values, dental calculus, and tooth wear (e.g., Cunha et al., 2004; Lev et al., 2005; Guatelli-Steinberg, 2004; Fiorenza et al., 2015; Hardy et al., 2017; Pérez-Pérez et al., 2017). Among these, dental macrowear has proven to be a reliable method for obtaining direct and long-term insights into food preferences in both past and modern human populations (e.g., Fiorenza et al., 2011a; Fiorenza et al., 2015; Fiorenza et al., 2018; Oxilia et al., 2018; Lee et al., 2021; Hernaiz-García et al., 2024a; Hernaiz-García et al., 2024b). In addition, macrowear may also result from behavioral factors, such as food processing or object manufacturing (e.g., Fiorenza et al., 2011b; Oxilia et al., 2018) or pathological conditions such as bruxism (Bronkhorst et al., 2024). Normal (nonpathologic) occlusal wear results primarily from two processes: attrition—tooth-to-tooth contact during food chewing—and abrasion—interaction between teeth and external materials (e.g., Butler, 1981; Hillson, 2003; Kaifu et al., 2003; Addy

* Corresponding author.
E-mail address: lauramartinfrancesmf@gmail.com (L. Martín-Francés).

https://doi.org/10.1016/j.jhevol.2025.103797

and Shellis, 2006; Kaidonis, 2008). Attrition during the chewing cycle produces flat, polished areas known as wear facets on the occlusal surface (e.g., Crompton and Hiiemae, 1970; Kay and Hiiemae, 1974; Hillson, 2003; Kaifu et al., 2003; Kullmer et al., 2009; Fiorenza et al., 2011a). The pattern of occlusal wear is influenced by food properties (e.g., texture and toughness), the distribution of pressure, as well as the individual direction of chewing (Kay and Hiiemae, 1974; Horio and Kawamura, 1989; Janis, 1990; Nakajima et al., 2001; Kullmer et al., 2009; Fiorenza et al., 2011a). The chewing cycle consists of two major movements. During phase I, the lower molars move superiorly and anteromedially producing a shearing action as they slide across the upper teeth, followed by a crushing motion at centric occlusion. Based on the location of the developing wear facets, phase I is further divided into lingual and buccal (Janis, 1990; Fiorenza et al., 2011a). In phase II, the molars move inferiorly and anteromedially out of the centric occlusion, generating grinding and crushing forces (Crompton and Hiiemae, 1970; Kay and Hiiemae, 1974; Kullmer et al., 2009; Fiorenza et al., 2011a). Each phase is associated with distinct wear facets, and comparative analyses across different species and populations have demonstrated that their development reflects dietary adaptation (e.g., Kullmer et al., 2009; Fiorenza, 2015). Kullmer et al. (2009) developed a reliable method, occlusal fingerprint analysis (OFA), to identify, digitize, and quantify individual wear facets. Studies using OFA have shown, for instance, that a greater proportion of lingual phase I facets in maxillary molars is associated with wider transverse movements of the mandible required to break down hard and abrasive plant materials. In contrast, individuals with higher meat consumption tend to show more pronounced buccal phase I facets, associated with vertical jaw movements and shearing forces (Fiorenza et al., 2011a, 2020). Moreover, dental macrowear also reflects ecogeographical dietary variation, often independent of both taxonomic affinities and species-specific morphological traits (e.g., Janis, 1990; Fiorenza et al., 2011a). Neanderthal (NEA) and early *Homo sapiens* groups living in Mediterranean evergreen environments with diverse food sources exhibit similar wear patterns, which are distinct from those populations living in steppe/coniferous forests, where diets were more restricted and meat based (Fiorenza et al., 2011a). Moreover, a distinct parameter of enamel wear, the inclination of the wear plane, has been used to infer changes in human subsistence strategies (e.g., Smith, 1984; Le Luyer et al., 2014; Fiorenza et al., 2018, 2020). Smith (1984) observed differences between hunter-gatherers, who exhibited flatter wear, and agriculturists, who showed more oblique wear, linking this variation to different food preparation techniques. Similarly, Fiorenza et al. (2018) compared wear inclination in Late Pleistocene specimens, including NEAs and anatomically modern humans, with that of modern hunter-gatherers (MHGs). They found that the Late Pleistocene group exhibited steeper wear angles than MHGs, which they attributed to differences in food preparation: Hunter-gatherer diets incorporated more dust and grit, producing flatter wear planes. Although wear inclination is inevitably influenced by environmental conditions, this does not appear to be the primary driver as various hunter-gatherer groups exhibited similar enamel wear angles despite differing ecogeographic contexts (e.g., Smith, 1984; Fiorenza et al., 2018, 2020).

The Sima de los Huesos (SH) site (Fig. 1), part of the Cueva Mayor-Cueva del Silo cave system, is located approximately 500 meters from the entrance of Cueva Mayor, at the base of a 13-meter vertical shaft (Aranburu et al., 2017). The majority of hominin remains, along with a single hand axe (Carbonell and Mosquera, 2006), are concentrated in a small chamber (4 × 8 m) at the end of a ramp in Lithostratigraphic Unit 6 (LU-6) (Aranburu et al., 2017). The associated faunal assemblage is dominated by

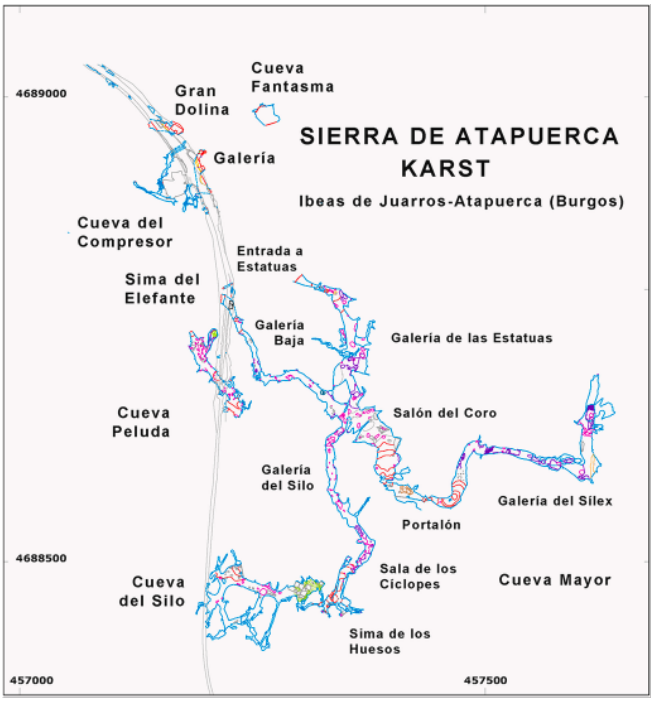

Figure 1. Map of the Sierra Atapuerca Karst with the localization of the SH site, as well as the nearby sites of Gran Dolina and Galería, situated in the Railroad Trench (modified from Ortega and Martín, 2022). SH = Sima de los Huesos. (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article.)

carnivores, with scarce presence of small mammals and the absence of ungulates (García and Arsuaga, 2011). Taphonomic and site formation studies concluded that the hominin accumulation represents an intentional single event, ruling out carnivorous activity and potentially indicating funerary behavior (Sala et al., 2014, 2015, 2024; Aranburu et al., 2017). Combining dating methods, including Single-grain thermally transferred optically stimulated luminescence (TT-OSL), OSL, and U-series, indicates that deposition of the hominin-bearing layer (LU-6) in the SH site occurred during the Marine Isotope Stage (MIS) 12, with a mean age of 448 ± 15 ka (Demuro et al., 2019). Marine core records from multiple locations suggest that this period was characterized by extreme global cooling, including within the Iberian Peninsula, leading to a marked expansion of semidesert vegetation (Voelker et al., 2010; Sánchez-Goñi et al., 2016; Demuro et al., 2019 and references therein; Rodríguez et al., 2021). However, despite this seemingly harsh conditions, palynological evidence from the SH site indicates more temperate conditions (García-Antón, 1987). Furthermore, previous attempts to define the dietary pattern of the SH population yielded contrasting results. While the isotopic data suggested a diet dominated by animal protein (García García et al., 2009), the microwear analysis revealed plant components in their diet (Pérez-Pérez et al., 1999, 2017).

Due to the unique characteristics of the hominin accumulation at SH, reconstructing the paleoecological context and subsistence strategies of this population remains particularly challenging. Therefore, to reconstruct with maximum accuracy the context of the SH population, the dietary information derived from the macrowear analysis will be integrated with other available proxies. For this purpose, we draw upon published data from the SH site as well as the nearby Trinchera sites of Gran Dolina (TD) and Galería, which provide valuable evidence of human activity, including Acheulean technology and faunal modification, as well

as environmental indicators, such as faunal and pollen remains (e.g., Falguères et al., 1999; Berger et al., 2008; Demuro et al., 2014; Ollé et al., 2016; Mosquera et al., 2024). Within this framework, we contextualize our discussion of the macrowear results in relation to previously published data on microwear and isotopes in SH sample (Pérez-Pérez et al., 1999, 2003; García et al., 2009; García and Arsuaga, 2011), together with chronological, technological, faunal, and pollen evidence from the three sites (e.g., García-Antón, 1987; García and Arsuaga, 2011; Rodríguez et al., 2011; Pérez-Pérez et al., 2017; Mosquera et al., 2024).

In this article, we reconstruct the dietary habits of SH individuals to test whether their macrowear pattern reflects the environmental conditions of the MIS 12. If this is the case, we expect to find a wear pattern similar to that of populations living in cold environments where animal protein is a primary food source (e.g., Fiorenza et al., 2011a, 2015). Alternatively, if the wear pattern suggests different environmental conditions, we will contextualize the subsistence strategy of this group by integrating the macrowear results into a broader ecological framework.

2. Materials

First, we excluded teeth showing signs of pathology and/or abnormal wear that could obscure the identification of occlusal wear facets. Second, because OFA cannot be applied to teeth with heavily worn crowns, where advanced wear stages (WSs) cause facet coalescence and hinder identification, we followed the exclusion criteria established by Fiorenza et al. (2011a). Accordingly, we selected only SH maxillary molars exhibiting slight to moderate wear (stages 2–3, as defined by Smith, 1984). The final SH sample comprises 16 maxillary molars (7 M^1s and 9 M^2s): 14 assigned to different individuals and 2 isolated (Table 1).

We used comparative samples from published studies including NEAs, fossil *H. sapiens*, and anatomically modern humans from different geographical regions and chronologies, all exhibiting WSs between 2 and 3 (Fiorenza et al., 2011c; Fiorenza and Kullmer, 2013). The grouping of these samples varied by analysis. (See Supplementary Online Material [SOM]; Tables S1 and S2 provide the full list with abbreviations used for the relative facet area and wear facet inclination analyses.) For the analysis of wear facet areas, we followed the categories mentioned by Fiorenza et al. (2011a, Table 6) based on ecogeographical contexts: Deciduous woodland (D), Mediterranean (M), and Steppe/Coniferous Forest (S/C). For the analysis of the facet inclination, we grouped the samples according to their technocomplexes following Fiorenza et al.'s classification (2018) including NEAs, Paleolithic *H. sapiens*, and MHGs. (See Table 1 from the study by Fiorenza et al., 2018 for a complete list of the specimens, localities and dating.)

Table 1
List of Sima de los Huesos (SH) maxillary molars used in this study including the tooth type, associated individual, and wear stage (following Smith, 1984).

Accession	Tooth	Individual	Wear stage	Wear facet	Inclination facet
AT-6584	M^1	15	3	Y	N
AT-26	M^1	13	2	Y	Y
AT-196	M^1	10	3	Y	N
AT-812	M^1	19	3	Y	N
AT-959	M^1	16	2	Y	Y
AT-2071	M^1	18	2	Y	Y
AT-3177	M^1	8	2	Y	Y
AT-817	M^2	3	2	Y	Y
AT-270	M^2	7	2	Y	Y
AT-15	M^2	8	1–2	Y	Y
AT-170	M^2	12	2	Y	Y
AT-822	M^2	17	2	Y	Y
AT-588	M^2	22	3	Y	N
AT-4336	M^2	28	2	Y	Y
AT-824	M^2	Isolated	2	Y	Y
AT-12	M^2	Isolated	2	Y	Y

3. Methods

3.1. μCT scanning and three-dimensional surface generation

We employed high-resolution μCT scans of SH molars to generate three-dimensional (3D) polygonal models. Scanning of the SH sample was carried out at Centro Nacional de Investigación sobre la Evolución Humana's Microscopy and Micro-Computed Tomography Laboratory using a Scanco Medical Micro-CT80 system, using the following parameters: 70 kV and 114 mA, 0.1 Al filter, and isometric voxel size ranging between 18 and 36 μm. Then, we uploaded the image stack in Amira v.2024.1 (Thermo Fisher Scientific Inc., Massachusetts, United States) and generated the 3D model using the Isosurface module. Finally, we save the model as an .stl file.

3.2. Occlusal fingerprint analysis

For the analysis of the tooth macrowear, we grouped the occlusal wear facets into three categories that correspond to distinct masticatory movements and the associated forces involved in food reduction, as well as the location of developing facets: buccal and lingual phase I and phase II facets (Kay and Hiiemae, 1974; Janis, 1990). We followed the well-established OFA method by Kullmer et al. (2009). This can be summarized into four steps: a. Model orientation, b. Wear facet identification, c. Measurement of the relative surface facet areas, and d. Measurement of the facet inclination. a. First, the 3D model is uploaded into the 3D metrology software PolyWorks® V. 12 (InnovMetric, Québec, Canada). Subsequently, we oriented the model by creating a reference Cartesian plane passing through the cervical line. b. We manually outlined the wear facets on the polygonal model (Fig. 2) according to Maier and Schneck (1981) classification, which was later modified by Kullmer et al. (2009). This consists of a maximum of 13 wear facets that we grouped according to the chewing cycle phases (Kay and Hiiemae, 1974; Maier and Schneck, 1981; Janis, 1990; Fiorenza et al., 2011a). In maxillary molars, phase I movement initially produces the buccal phase I facets (shown in blue in Fig. 2) during the shearing action. Facets 1, 1.1, and 3 form on the slopes of the paracone, followed by facets 2, 2.1, and 4 on the metacone. During the second part of the phase I movement, the crushing action produces the lingual facets 5, 5.1, 6, and 6.1 (shown green in Fig. 2) along the slopes of the protocone, as well as facets 7 and 8 on the hypocone. Finally, during phase II of the chewing cycle, facets 9, 10, 11, 12, and 13 (shown in red in Fig. 2) develop on the buccal slopes of the protocone and hypocone. We also outlined the worn areas around the cusp tips, known as tip-crush contacts (Gordon, 1984; Janis, 1990). These form during the initial puncture-crushing and do not involve tooth-to-tooth contact (Fiorenza et al., 2020). c. We measured the areas enclosed in the outlined region of each wear facet and tip-crush areas. Since wear facet areas are size dependent, with smaller teeth developing smaller wear facets than larger teeth, we employed the relative wear facet areas. These were calculated by dividing the areas of buccal and lingual phase I and phase II facets by the total occlusal wear area, which resulted from the sum of absolute area of each occlusal wear facet (Fiorenza et al., 2011a). d. We obtained the inclination values by calculating the angle between the intersection of the reference plane and the facet plane (Knight-Sadler and Fiorenza, 2017). We considered the average inclination plane

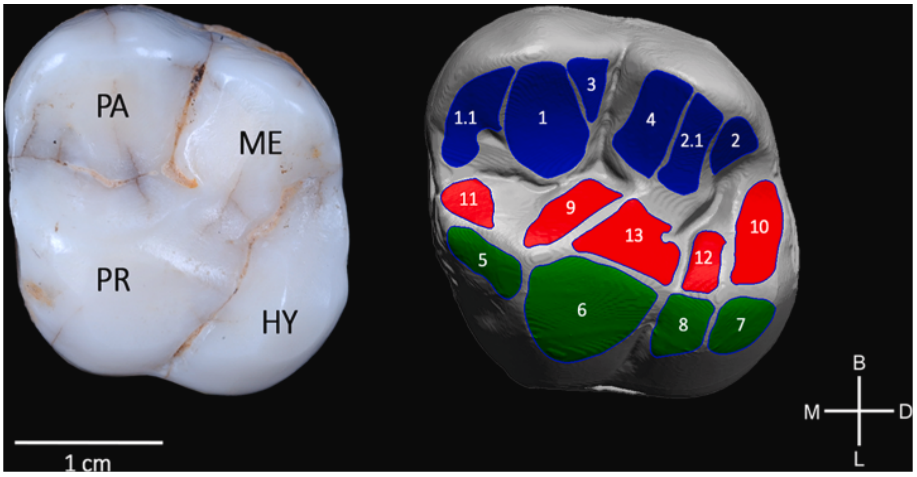

Figure 2. SH maxillary molar (left): specimen AT-3177 left M^1 (PR = protocone; PA = paracone; ME = metacone; HY = hypocone). Three-dimensional polygonal model of AT-3177 (right): occlusal wear facets identification grouped by chewing phases: buccal phase I facets (in blue): facets 1, 1.1, and 3 form on the slopes of the paracone, facets 2, 2.1, and 4 on the metacone; lingual phase I facets (in green) 5, 5.1, 6, and 6.1 on the slopes of the protocone and 7 and 8 on the hypocone; phase II facets (in red) 9, 10, 11, 12, and 13 form on the buccal slope of the protocone and hypocone. SH = Sima de los Huesos. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

for each phase group: buccal and lingual phase I and phase II (Fiorenza et al., 2018).

3.3. Statistical analysis

We calculated descriptive statistics for all measured variables including median, SD, and interquartile ranges. To investigate the relationship between the macrowear pattern of SH hominins and their dietary habits, we first conducted a one-way Permutational Multivariate Analysis of Variance (PERMANOVA) test, a non-parametric method that assesses significant differences between two or more groups, calculated directly from any asymmetric distance or dissimilarity matrix (Anderson, 2001). Statistical significance was determined with a permutation test of group membership (n = 9999). When significant differences were detected, we employed the Mann-Whitney U-test with Bonferroni correction to test for differences between SH and each of the ecogeographical groups for the buccal and lingual phase I and phase II facets. For illustrative purposes, we generated a ternary plot to depict the proportion of each of the three variables (buccal and lingual phase I and phase II facets), which sum to one, or 100%.

Since wear facet inclination correlates with the abrasiveness of diet and the masticatory load necessary for food processing (Fiorenza et al., 2018), we grouped the comparative sample based on their technocomplexes. Additionally, since inclination values are wear dependent and flatter surfaces develop as wear advances, we restricted the analysis to teeth with a wear score of 2 (Smith, 1984). To identify differences across all groups, we first employed the nonparametric Kruskal-Wallis test. When significant differences were observed, we applied the Mann-Whitney U-test with Bonferroni correction to test differences in the inclination of the chewing cycle facets between SH and the technocomplex groups.

Finally, we generated box and whisker plots to illustrate the distribution of relative area and inclination of buccal phase I, lingual phase I, and phase II across the analyzed groups. All statistical analyses were performed in Sigmaplot v.14.5 (Grafiti LLC, California, United States).

4. Results

4.1. Relative areas of chewing phases

The macrowear observed in SH sample is dominated by phase I buccal facets (41%), followed by phase II (32%) and lingual phase I facet (28%) areas (Table 2; Fig. 3a). If we analyze the distribution based on WSs (WS 1–2 vs. WS 3), we observe intragroup variability (Fig. 3b). The small sample size (WS 1–2 consist of 12 specimens and WS 3 only four specimens) limits the interpretation of the data. While the relative percentage of lingual phase I facets seems to remain stable with the advance of wear, the percentage of buccal phase I facets increases, while the phase II facets decrease in relation to the total occlusal wear area (Fig. 3b). If we group the SH sample based on molar class (M1 vs. M2), we observe that the proportion of lingual phase I facets decreases from the M1 to the M2 (Fig. 3c).

Compared to the three ecogeographical groups, the SH sample shows a low degree of variation in chewing cycle facets. In addition, the SH group falls within the overlapping region of the three ecogeographical groups (Fig. 4).

The distribution of individual values of the relative areas for the three phases shows intergroup variability (Fig. 5). Only buccal phase I is relatively evenly distributed across the samples, with lower SD values (Table 2), whereas both lingual phase I and phase II display greater variation across groups. The SH and the Deciduous woodland groups show a similar distribution of the chewing cycle facets, with a substantial overlap between them. In contrast, the Mediterranean and Steppe/Coniferous groups show greater variability, with no overlap in the distribution of chewing facets (Fig. 5).

Table 2
Descriptive statistics of relative facet area of the original sample from Sima de los Huesos (SH) and the comparative sample (data extracted from Fiorenza et al., 2011a) grouped into ecogeographical contexts.

Specimen	Group	N	Ecogeographical context groups	Descriptive statistics	Relative buccal PI	Relative lingual PI	Relative PII
AT-6584	SH-Early Neanderthal	1			43.18	35.20	21.62
AT-26		1			34.92	29.00	36.07
AT-196		1			44.28	27.88	27.84
AT-812		1			44.70	36.10	19.20
AT-959		1			36.54	25.59	37.87
AT-2071		1			34.70	37.10	28.20
AT-3177		1			41.50	28.95	29.55
AT-817		1			43.04	25.25	31.71
AT-270		1			43.63	16.36	40.01
AT-15		1			44.85	21.61	33.54
AT-170		1			43	22.99	34.01
AT-822		1			48.85	26.04	25.11
AT-588		1			48.66	33.07	18.27
AT-4336		1			35.65	21.72	42.63
AT-824		1			29.58	29.67	40.75
AT-12		1			41.43	25.47	33.10
				Mean	**41.16**	**27.62**	**31.22**
				SD	**5.38**	**5.73**	**7.52**
				Interquartile	**8.73**	**8.67**	**11.63**
	Neanderthals	13	D	Mean	**36.94**	**34.25**	**28.81**
				SD	**5.22**	**8.60**	**4.80**
				Interquartile	**6**	**6.36**	**7.45**
	Neanderthals and fossil *Homo sapiens*	11	M	Mean	**39.40**	**23.13**	**37.47**
				SD	**3.93**	**6.63**	**5.63**
				Interquartile	**5.27**	**9.75**	**6.69**
	Neanderthals and anatomically modern humans	11	S/C	Mean	**44.95**	**20.58**	**34.47**
				SD	**3.84**	**4.89**	**5.87**
				Interquartile	**5.87**	**4.44**	**12.27**

D = Deciduous woodland; M = Mediterranean; S/C = Steppe/Coniferous Forest.
Data are presented with mean, SD, and interquartile range in bold.

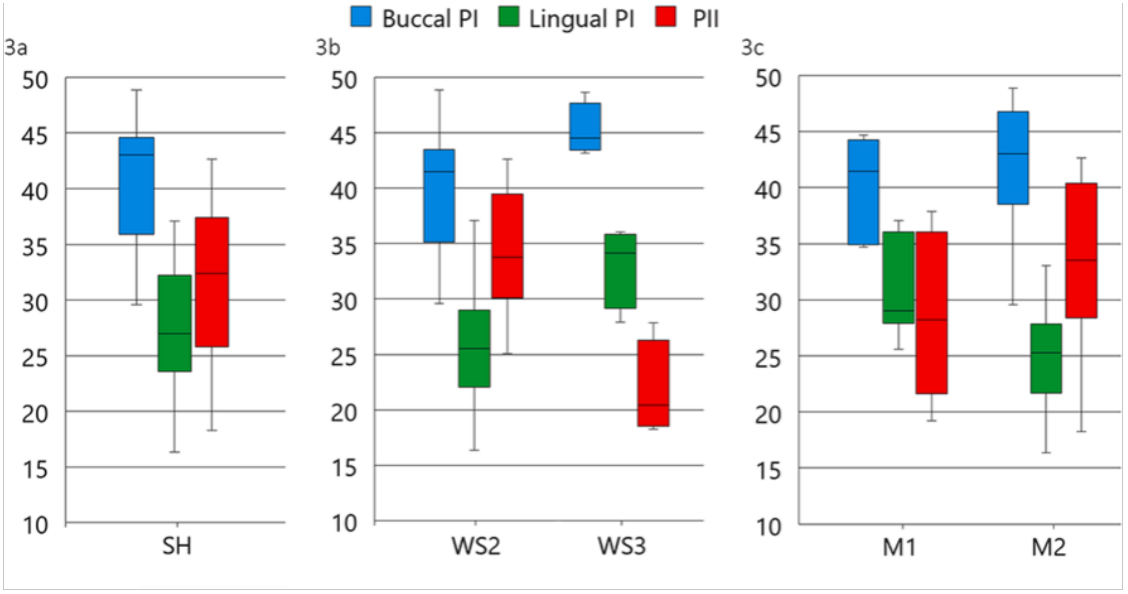

Figure 3. Box and whisker plot showing the distribution of the proportions of buccal phase I, lingual phase I, and phase II wear facets in the SH complete sample (3a) in SH by wear stage (3b) and on molar class (3c). SH = Sima de los Huesos; WS = wear stage. (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article.)

The one-way PERMANOVA test (Table 3) did not identify significant differences between the SH group and any of the ecogeographical groups. We further conducted a Mann-Whitney test to compare the groups based on chewing cycle phases (buccal and lingual phase I and phase II facets). The results showed a significant difference only between the SH group and the Steppe/Coniferous group for lingual phase I facets (Table 4).

4.2. Wear facet inclination

Sima de los Huesos maxillary molars are characterized by steeper shearing wear facets (buccal and lingual phase I) than grinding (phase II) wear facets (Table 5; Fig. 6). In particular, buccal phase I facets show a slightly higher mean inclination (33°) than lingual phase I facets (32°). The SH population along with all

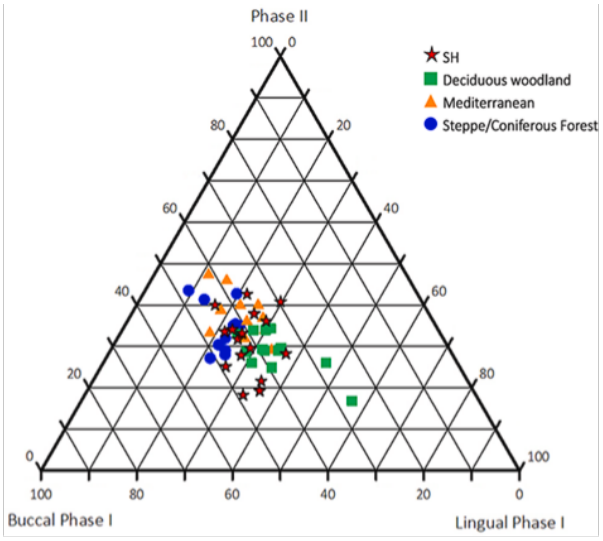

Figure 4. Ternary diagram of relative wear facet areas. The ternary diagram graphically depicts the proportions (%) of three variables (buccal phase I, lingual phase I, and phase II relative wear facet areas) as positions in an equilateral triangle. Each base of the triangle represents a proportion of 0%, while the vertices correspond to a proportion of 100%. Neanderthals and *Homo sapiens* are grouped into three different ecogeographical contexts (Fiorenza et al., 2011a). (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article.)

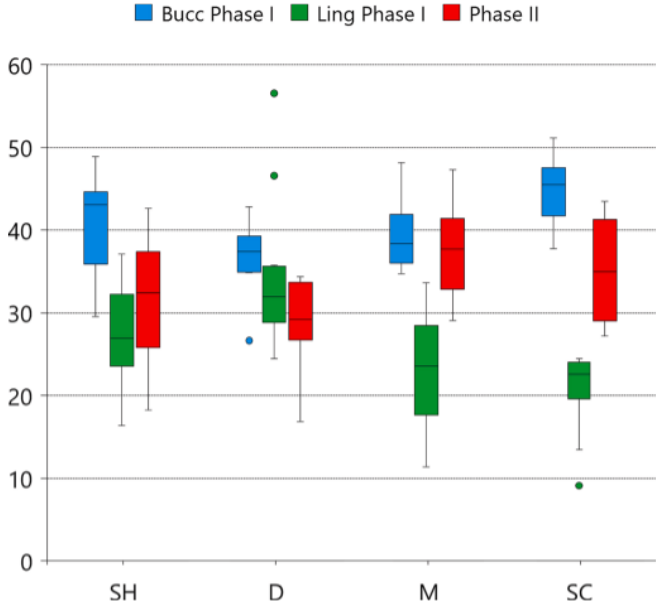

Figure 5. Box and whisker plot showing the distribution the proportions of all buccal phase I, lingual phase I, and phase II wear facets across the three analyzed groups (SH = Sima de los Huesos; D = Deciduous woodland; M = Mediterranean evergreen; S/C = Steppe/Coniferous Forest). (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article.)

groups from the comparative sample exhibit a similar pattern of facet inclination, with steeper wear on the shearing facets than on the grinding facets (Table 5; Fig. 6). Overall, the SH sample shows a lower range of variation in the distribution of the individual values of the complete sample. Among all comparative samples, the SH group only falls within the variation of the Paleolithic group, except for the buccal phase I facets (Fig. 6). Additionally, the SH individuals exhibit the steepest mean values for the shearing wear

Table 3
One-way Permutational Multivariate Analysis of Variance (PERMANOVA) (Bonferroni-corrected p values) test based on the relative areas (%) of buccal phase I facets, lingual phase I facets, and phase II facets of the Sima de lo Huesos (SH) sample and the comparative sample grouped into ecogeographical zones.

	SH	D	M	S/C
SH		0.1314	0.2208	0.0924
D	0.1314		**0.0042**	**0.0006**
M	0.2208	**0.0042**		0.3132
S/C	0.0924	**0.0006**	0.3132	

D = Deciduous woodland; M = Mediterranean; S/C= Steppe/Coniferous Forest. Values in bold indicate statistical significance ($p < 0.05$).

facets compared to the rest of the comparative sample, with marked differences in the buccal phase I facets. The SH mean value is 33°, whereas for all groups in the comparative sample, the mean value remains below 29°. This difference is reflected in the statistical results. The Kruskal-Wallis test identified significant differences between groups for two variables, the buccal and lingual phase I (Table 6). We then performed the Mann-Whitney test to compare wear inclination in each chewing facet between the SH population and the comparative sample (Table 7). The results indicate that the SH population statistically differs from all groups for the buccal phase I facets and also to the MHGs for the lingual phase I facets.

5. Discussion

The molar macrowear pattern observed in SH individuals, characterized by a similar proportion of phase II facets (31%) and lingual phase I facets (28%) in the maxillary molars, suggests that this population exploited both animal and plant foods. A higher percentage of buccal phase I facets, which are formed during the shearing phase of mastication, in maxillary molars are indicative of a diet with a substantial meat component. These facets develop through the processing of pliant and tough food items, such as meat (e.g., Janis, 1990; Fiorenza et al., 2011a). Conversely, a high proportion of lingual phase I facets reflects transverse mandibular movements (Kay and Hiiemae, 1974; Kay, 1975; Janis, 1990) related to the consumption of hard and abrasive foods, including roots, seeds, gums, and other plant materials (Fiorenza et al., 2011a; Fiorenza and Kullmer, 2015). Moreover, according to Kay (1975), food breakdowns during phase II, grinding, also results from the traverse movement of the hypoconid (the lower molar) across the surface of the upper molar. Moreover, an occlusal microwear analysis of phase II facets revealed more complex and anisotropic textures than in phase I facets, likely due to food abrasiveness (Krueger et al., 2008). In this context, and despite the ongoing debate regarding the functional significance of phase II (see articles by Hylander and Crompton, 1986; Hylander et al., 1987; Wall et al., 2006), it is plausible that the high percentage of phase II facets in SH specimens reflects the processing of plant materials, further supporting the contribution of plant resources to the SH population's diet.

Previous results on dietary proxies, including microwear analysis and isotopes ratios, provided a differing interpretation of this population's dietary preferences (Pérez-Pérez et al., 1999, 2003; García et al., 2009; García and Arsuaga, 2011). While microwear analysis indicates contribution of plant foods to the diet, the isotopic signal suggests a diet dominated by animal proteins. Nonetheless, these methods provide complementary rather than direct dietary composition. Buccal microwear documents long-term turnover but does not capture seasonal dietary variability. Moreover, it is influenced not only by the abrasiveness of the diet but

Table 4
Between-group comparison (Mann-Whitney test) of the relative areas (%) of the wear facets grouped according to chewing cycle phases (buccal phase I facets 1–4, lingual phase I facets 5–8, and phase II facets 9–13) of Sima de los Huesos (SH) and comparative sample grouped into ecogeographical zones.

	Lingual phase I				Buccal phase I				Phase II			
	SH	D	M	S/C	SH	D	M	S/C	SH	D	M	S/C
SH		0.294	0.656	**0.035**		0.243	1.000	0.609		1.000	0.179	1.000
D	0.294		**0.005**	**0.001**	0.243		1.000	**0.004**	1.000		**0.009**	0.212
M	0.656	**0.005**		1.000	1.000	1.000		0.052	0.179	**0.009**		1.000
S/C	**0.035**	**0.001**	1.000		0.609	**0.004**	0.052		1.000	**0.212**	1.000	

D = Deciduous woodland; M = Mediterranean; S/C = Steppe/Coniferous Forest.
Values in bold indicate statistical significance ($p < 0.05$).

Table 5
Descriptive statistics of wear facet inclination of Sima de los Huesos (SH) and comparative sample grouped into technogroups with mean, median, SD, and interquartile range (IQR).

		Buccal phase I				Lingual phase I				Phase II			
Group	N	Mean	Median	SD	IQR	Mean	Median	SD	IQR	Mean	Median	SD	IQR
SH	12	**33.48**	**34.05**	**4.27**	**5.2**	**32.41**	**31.50**	**1.76**	**6.75**	**23.96**	**23.95**	**1.50**	**6.12**
NEA	20	28.95	31	4.90	7.35	32.37	32.55	5.11	8.6	17.30	22.45	6.38	8.58
PHS	14	23.85	25.15	5.37	8.40	30.55	31.15	8.92	13.6	24.92	23.50	8.70	15.75
MHG	11	20.13	18.80	3.63	6.60	22.01	22.00	8.38	17.50	20.36	20.20	4.68	3.2
AGR	7	25.38	26.50	6.58	9.3	30.98	31.20	10.79	14	25.19	26.70	8.39	14.2

NEA = Neanderthal; PHS = Paleolithic *Homo sapiens*; MHG = Modern hunter-gatherer; AGR = early farmers-Natufians.
Values in bold indicate original data, SH. Comparative sample data were extracted from the study by Fiorenza et al. (2011).

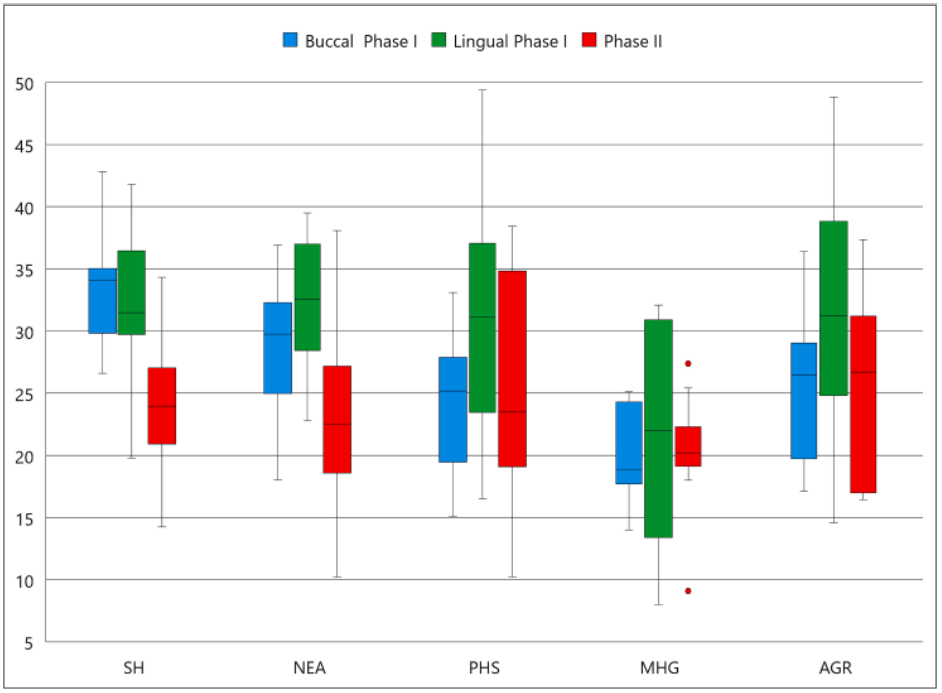

Figure 6. Box and whisker plot showing the inclination values of buccal phase I, lingual phase I, and phase II wear facets across the technocomplex groups (SH = Sima de los Huesos; NEA = Neanderthal; PHS = Paleolithic *Homo sapiens*; MHG = modern hunter-gatherer; AGR = agriculturalist). (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article.)

Table 6
Kruskal-Wallis test of wear facet inclination within complete sample, including Sima de los Huesos, Neanderthals, Paleolithic *Homo sapiens*, modern hunter-gatherers, and early farmers-Natufians.

	Buccal phase I					Lingual phase I					Phase II				
Source of variation	DF	SS	MS	F	P	DF	SS	MS	F	P	DF	SS	MS	F	P
Between groups	5	1271.92	254.38	10.50	**<0.001**	5	914.36	182.87	3.19	**0.013**	5	164.124	32.82	0.70	0.61
Residual	58	1404.89	24.22			58	3322.75	57.28			58	2686.02	46.31		
Total	63	2676.81				63	4237.11				63	2850.14			

DF = degree of freedom; SS = sum of squares; MD = mean square; F = F-statistic; P = p value.
Values in bold indicate statistical significance ($p < 0.05$).

Table 7
Between-group comparison (Mann-Whitney test) of wear facet inclinations grouped according to chewing cycle phases (buccal phase I, lingual phase I, and phase II) of Sima de los Huesos (SH) and comparative sample grouped into technogroups.

	Buccal phase I	Lingual phase I	Phase II
	SH	SH	SH
NEA	**0.02**	0.71	0.39
PHS	**0.001**	0.47	0.87
MHG	**0.001**	**0.006**	0.06
AGR	**0.02**	0.55	0.73

NEA = Neanderthal; PHS = Paleolithic *Homo sapiens*; MHG = modern hunter-gatherer; AGR = early farmers-Natufians.
Values in bold indicate statistical significance ($p < 0.05$).

also by exogenous abrasive particles introduced during food preparation methods (Pérez-Pérez et al., 1994; Romero et al., 2012). Additionally, there is evidence that ratios of nitrogen and carbon isotopes may underestimate the consumption of plant foods (e.g., Hedges and Reynard, 2007; Sponheimer and Lee-Thorp, 2007; Fontes-Villalba et al., 2013; Fiorenza et al., 2015). In this context, the macrowear evidence provides a more comprehensive perspective on the mixed feeding behavior of this population.

In relation to the ecogeographical signal, although the ternary diagram shows that the SH population falls within the overlapping area of the three comparative groups, it exhibits a tendency to overlap more with the group from temperate regions dominated by deciduous woodlands (Fig. 4). Additionally, the wear pattern distribution in the SH population closely resembles that of the deciduous ecogeographical group, with no statistical differences detected between these two groups. These distinguish the SH population from the Steppe/Coniferous and Mediterranean groups (Tables 2–4; Fig. 3a). Additionally, we observed intrapopulation variability in the proportion of phase I and II wear facets influenced by wear and dental class (Fig. 3b and 3c and SOM Table S3 and S4). We emphasize the small sample size ($n = 4$) for WS 3, which limits the interpretation of the results based on WSs. As such, we can only discuss possible causes rather than draw definitive conclusions. With this limitation in mind, a shift is apparent in the proportion of buccal phase I facets in relation to phase II facets. As dental wear progresses from WS 2 to 3, the proportion of buccal phase I continues to increase, while the proportion phase II decreases. This shift on wear distribution on the occlusal surface could respond to change in dietary habits over the individuals' lifespans. Assuming that wear advances with age (e.g., Brothwell, 1989; Mays et al., 2022), we speculate that higher meat consumption may result from either changing environmental conditions or increasing energetic demands. Previous studies have shown that the proportions of crushing, shearing, and grinding facets are not influenced by crown morphology (Janis, 1990; Fiorenza et al., 2011a). For instance, despite NEAs displaying a different first maxillary crown morphology compared to *H. sapiens*, the formation of wear facets does not reflect the cusp size difference between these two species (Fiorenza et al., 2011a). However, when examining SH molar classes, M^1 vs. M^2, we identified some differences in these trends. While the proportion of buccal phase I wear facets increases from the M^1 to M^2, the lingual phase I wear facets decrease in favor of phase II facets in the M^2 compared to the M^1. When analyzing the individual values of each of the wear facet (5–8) in lingual phase I, we observed that seven M2 molars lack either wear facet 7 or 8 and that two M2s are missing both wear facets. Wear facets 7 and 8 form in the hypocone, a cusp that, according to Martinón-Torres et al. (2012), undergoes a marked reduction in SH sample, being absent in 33.4% of the cases. Therefore, we propose that the lower proportion of lingual phase I wear facets in the M^2, than in the M^1 could respond to morphological constrains rather than dietary habits.

The analysis of the facet inclination revealed a significant difference in the inclination of the buccal phase I wear facets in the SH sample compared to the rest of the comparative sample. Moreover, the observed significant difference between SH and MHG groups for the lingual phase I facets further supports the interpretation of a less abrasive diet for the SH population. According to wear inclination analyses, molar wear angulation is strongly influenced by dietary abrasiveness and serves as an indicator of the amount of exogenous material, such as grit or sand, accidently ingested while eating. This parameter reflects food preparation practices better than dietary differences (e.g., Lucas et al., 2013; El Zaatari and Hublin, 2014; Le Luyer et al., 2014; Fiorenza et al., 2018, 2020). For instance, MHG populations that inadvertently incorporate abrasive particles in their diet through food preparation techniques (e.g., grinding stones, earth ovens, etc.) show flatter occlusal wear than other groups (Le Luyer et al., 2014; Fiorenza et al., 2020). Furthermore, microwear texture analysis detected changes in the Upper Paleolithic groups linked to material culture. Specifically, the pattern of microwear complexity, reflecting dietary abrasiveness, differentiated between Aurignacian and Gravettian groups from Magdalenian individuals, with the latter characterized by a more abrasive diet (El Zaatari and Hublin, 2014). Previous nonocclusal microwear analysis of the SH population revealed a lower density of scratches than earlier populations, such as Atapuerca-*Homo antecessor*, associated to Oldowan (Mode 1) culture, indicating a less abrasive diet. In this context, the steeper inclination of wear facets in the SH sample is consistent with these findings and likely reflects the absence of food-processing techniques that could have incorporated exogenous abrasive particles, like dust or grit, into their diet.

Considering the unique characteristics of the SH accumulation and in order to contextualize our findings within the paleonvironmental framework of Atapuerca as accurately as possible, we discuss additional proxies such as dating, pollen, faunal remains, and lithic industry not only of the SH site but also of the nearby Galería and Gran Dolina sites. We focused on levels GIII–II from Galería and level TD10 from Gran Dolina since their chronological estimates overlap with the current SH dating. The combination of several dating methods provides an age range for Galería's Unit GIIa between 500 and 313 ± 14 (via SG TT-OSL and pIR-IR; Demuro et al., 2014; ESR/U-series estimates Falguères et al., 2013; and TL/IRSL ages Berger et al., 2008), although it is important to note that the maximum age is considered less reliable according to Demuro et al. (2014). In addition, TD10 has been dated to approximately 420–340 ka using similar methods (Falguères et al., 1999; Berger et al., 2008), though caution is warranted regarding TL/IRSL results (Demuro et al., 2014).

Pollen from SH shows the presence of conifers (*Pinus*), mesic trees (deciduous *Quercus*, *Betula*, and *Fagus*), and Mediterranean taxa (evergreen *Quercus)* (García-Antón, 1987). The pollen record corresponding to TD10.4 and TD10.3 (lower levels) reflects an increase of Poaceae at the expense of Mediterranean and mesic species, suggesting more open landscapes, although the persistence of mesic trees indicates that environmental conditions were not particularly harsh. No pollen or spores have been recovered from the GIII subunits of Galería (Rodríguez et al., 2011). Isotopic data from faunal teeth in Galería, units GII and GIII, and TD10 support the predominance of C3 vegetation characteristic of an open woodland environment (García et al., 2009). The presence of diverse fauna, including ungulates (e.g., *Dama clactoniana*, *Cervus elaphus priscus*, *Equus ferus*), carnivores (e.g., *Ursus deningeri*, *Homotherium*), and herpetofauna, further suggests a dynamic mosaic landscape with both open and wooded areas (e.g., Blain

et al., 2008; García and Arsuaga, 2011; Rodríguez et al., 2011; Mosquera et al., 2024).

The Acheulean tradition (mode II) is well represented in these sites from ~500 ka onward (Ollé et al., 2016). Technological similarities across Galería, Gran Dolina, and SH suggest a shared behavioral repertoire among early NEAs. Galería, likely a natural trap, shows evidence of carcass exploitation, while TD10 presents a more complex subsistence pattern. Lower levels (TD10.3 and TD10.4) reflect brief occupations, based on the scarcity of faunal remains with cut marks and the spatial distribution of lithics and faunal remains, whereas the faunal remains and lithic assemblages of the upper levels (TD10.2 and TD10.1) indicate regular hunting and base-camp-like activities (e.g., Blasco et al., 2013; García-Medrano et al., 2015; Rodríguez-Hidalgo et al., 2017). These patterns suggest that increasing behavioral complexity, rather than climatic pressure, drove the technological change during the Middle Pleistocene (e.g., Rodríguez et al., 2011; Blasco et al., 2013; Ollé et al., 2013; Ollé et al., 2016; Rodríguez-Hidalgo et al., 2017).

The results of the macrowear analysis indicate a roughly equal dietary contribution of both animal and plant foods for the SH population, in contrast to the isotopic analyses, which suggest a diet primarily based on animal proteins (García García et al., 2009). Furthermore, the evidence for a mixed diet supports the interpretation of an environment dominated by woodland, contrasting with the harsh conditions associated with MIS 12, as also indicated by pollen, isotopic, faunal, and lithic data. Finally, the steep inclination of the wear facets indicates low degree of abrasiveness in SH diet, suggesting that the SH population likely did not employ food preservation or preparation techniques, in agreement with microwear results (Pérez-Pérez et al., 1999, 2017).

6. Conclusions

According to chronological data, SH population likely lived during the MIS 12, one of the coldest periods globally, which led to an expansion of semidesert vegetation across the Iberian Peninsula (Demuro et al., 2019). In this study, we analyzed for the first time the macrowear pattern of SH population to assess whether it reflects such environmental conditions. Our results indicate that SH individuals relied on a mixed diet with similar proportions of both animal and plant products, in disagreement with isotopic results that suggested an animal-protein diet. This dietary pattern does not reflect a strictly cold or resource-limited environment but rather suggests the exploitation of a diverse landscape as supported by pollen, fauna, and isotopic evidence.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We acknowledge all members of the Atapuerca research and archaeological team for their valuable contributions. We sincerely thank Dr. Palmaria Saladié (IPHES) and Dr. Andreu Ollé (IPHES) for their valuable insights and constructive feedback. The authors gratefully thank the curators and institutions which allowed us to study comparative and fossil specimens: Almut Hoffmann (Museum fur Vor-und Fruhgeschichte, Berlin, Germany), Maria Teschler Nicola (Naturhistorisches Museum Wien, Vienna, Austria), Marta Dŏckalová (Moravské Zemské Muzeum, Anthropos Institute, Brno, Czech Republic), Bence Viola (Department of Anthropology, University of Vienna, Austria), Yoel Rak (Department of Anatomy and Anthropology, University of Tel Aviv, Israel), FabioParenti (Istituto Italiano di Paleontologia Umana, Rome, Italy), Chris Stringer and Rob Kruszynski (Natural History Museum of London, England), Angiolo del Lucchese (Museo Preistorico dei Balzi Rossi, Ventimiglia, Italy), and Erik Trinkaus (Department of Physical Anthropology at Washington University in Saint Louis, USA). We also would like to thank Christine Hemm for her help in surface scanning the original and cast dentition included in this sample.

This work is supported by the Horizon Program-Marie Sklodowska-Curie Actions of the EU Ninth programme (2021–2027) under the HORIZON-MSCA-2021-PF-01-Project: 101060482; the Spanish Ministry of Science and Innovation and European Regional Development Fund "ERDF A way of making Europe" (projects PID2021-122355NB-C31, PID2021-122355NB-C32, PID2021-22355NB-C33). Fieldwork is supported by the Junta de Castilla y León and the Fundación Atapuerca. L. M-. F. receives funding from the EU-Horizon Program-Marie Sklodowska-Curie Actions of the EU Ninth programme (2021–2027) under the HORIZON-MSCA-2021-PF-01-Project: 101060482. M. M-. T. receives funding from The Leakey Foundation through the personal support of D. Crook. M. H-. G. received funding from the Biomedicine Discovery Scholarship (Monash University) and project SI4/PJI/2024-00104 (Universidad Autónoma de Madrid and the Comunidad de Madrid). The Sima de los Huesos dental remains were scanned at the Microscopy and Micro-Computed Tomography laboratory of the CENIEH-ICTS with the support of the staff.

Author contributions

Laura Martín-Francés: Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **María Martinón-Torres:** Writing – review & editing, Project administration, Investigation, Funding acquisition. **Marina Lozano:** Writing – review & editing, Methodology, Investigation. **María Hernaiz-García:** Writing – review & editing, Methodology, Investigation. **Juan Luis Arsuaga:** Writing – review & editing, Resources, Investigation, Funding acquisition, Data curation. **José María Bermúdez de Castro:** Writing – review & editing, Resources, Investigation, Funding acquisition. **Luca Fiorenza:** Writing – review & editing, Validation, Software, Resources, Methodology, Investigation, Conceptualization.

Supplementary Online Material

Supplementary Online Material related to this article can be found at https://doi.org/10.1016/j.jhevol.2025.103797.

References

Addy, M., Shellis, R.P., 2006. Interaction between attrition, abrasion and erosion in tooth wear. In: Lussi, A. (Ed.), Dental Erosion. From Diagnosis to Therapy. Karger, Basel, pp. 17–31.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

Aranburu, A., Arsuaga, J.L., Sala, N., 2017. The stratigraphy of the Sima de los Huesos (Atapuerca, Spain) and implications for the origin of the fossil hominin accumulation. Quat. Int. 433, 5–21.

Berger, G.W., Pérez-González, A., Carbonell, E., Arsuaga, J.L., Bermúdez de Castro, J. M., Ku, T.L., 2008. Luminescence chronology of cave sediments at the Atapuerca paleoanthropological site, Spain. J. Hum. Evol. 55, 300–331.

Blain, H.-A., Bailon, S., Cuenca-Bescós, G., 2008. The Early–Middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca, Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 261, 177–192.

Blasco, R., Rosell, J., Domínguez-Rodrigo, M., Lozano, S., Pastó, I., Riba, D., Vaquero, M., Peris, J.F., Arsuaga, J.L., de Castro, J.M.B., Carbonell, E., 2013.

Learning by heart: Cultural patterns in the faunal processing sequence during the Middle Pleistocene. PLoS One 8, e55863.
Brothwell, D.R., 1989. The relationship of tooth wear to ageing. In: Işcan, M.Y. (Ed.), Age Markers in the Human Skeleton. Charles C Thomas, Springfield.
Bronkhorst, H., Kalaykova, S., Huysmans, M.-C., Loomans, B., Pereira-Cenci, T., 2024. Tooth wear and bruxism: A scoping review. J. Dent. 145, 104983.
Butler, P., 1981. Dentition in function. In: Osborn, J.W. (Ed.), Dental Anatomy and Embryology. Blackwell Oxford, p. 333.
Carbonell, E., Mosquera, M., 2006. The emergence of a symbolic behaviour: The sepulchral pit of Sima de los Huesos, Sierra de Atapuerca, Burgos, Spain. C. R. Palevol 5, 155–160.
Crompton, A.W., Hiiemae, K., 1970. Molar occlusion and mandibular movements during occlusion in the American opossum, *Didelphis marsupialis* L. Zool. J. Linn. Soc. 49, 21–47.
Cunha, E., Rozzi, F.R., Bermúdez De Castro, J.M., Martinón-Torres, M., Wasterlain, S. N., Sarmiento, S., 2004. Enamel hypoplasias and physiological stress in the Sima de los Huesos Middle Pleistocene hominins. Am. J. Phys. Anthropol. 125, 220–231.
Demuro, M., Arnold, L.J., Aranburu, A., Sala, N., Arsuaga, J.-L., 2019. New bracketing luminescence ages constrain the Sima de los Huesos hominin fossils (Atapuerca, Spain) to MIS 12. J. Hum. Evol. 131, 76–95.
Demuro, M., Arnold, L.J., Parés, J.M., Pérez-González, A., Ortega, A.I., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2014. New luminescence ages for the galería complex archaeological site: Resolving chronological uncertainties on the Acheulean record of the Sierra de Atapuerca, Northern Spain. PLoS One 9, e110169.
El Zaatari, S., Grine, F.E., Ungar, P.S., Hublin, J.-J., 2011. Ecogeographic variation in Neandertal dietary habits: Evidence from occlusal molar microwear texture analysis. J. Hum. Evol. 61, 411–424.
El Zaatari, S., Hublin, J.-J., 2014. Diet of upper paleolithic modern humans: Evidence from microwear texture analysis. Am. J. Phys. Anthropol. 153, 570–581.
Falguères, C., Bahain, J.-J., Bischoff, J.L., Pérez-González, A., Ortega, A.I., Ollé, A., Quiles, A., Ghaleb, B., Moreno, D., Dolo, J.-M., Shao, Q., Vallverdú, J., Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.L., 2013. Combined ESR/U-series chronology of Acheulian hominid-bearing layers at Trinchera Galería site, Atapuerca, Spain. J. Hum. Evol. 65, 168–184.
Falguères, C., Bahain, J.-J., Yokoyama, Y., Arsuaga, J.L., Bermudez de Castro, J.M., Carbonell, E., Bischoff, J.L., Dolo, J.-M., 1999. Earliest humans in Europe: The age of TD6 Gran Dolina, Atapuerca, Spain. J. Hum. Evol. 37, 343–352.
Fiorenza, L., 2015. Reconstructing diet and behaviour of Neanderthals from Central Italy through dental macrowear analysis. J. Anthropol. Sci. 93, 119–133.
Fiorenza, L., Benazzi, S., Estalrrich, A., Kullmer, O., 2020. Diet and cultural diversity in Neanderthals and modern humans from dental macrowear analyses. In: Schmidt, C.W., Watson, J.T. (Eds.), Dental Wear in Evolutionary and Biocultural Contexts. Academic Press, pp. 39–72.
Fiorenza, L., Benazzi, S., Henry, A.G., Salazar-García, D.C., Blasco, R., Picin, A., Wroe, S., Kullmer, O., 2015. To meat or not to meat? New perspectives on Neanderthal ecology. Am. J. Phys. Anthropol. 156, 43–71.
Fiorenza, L., Benazzi, S., Oxilia, G., Kullmer, O., 2018. Functional relationship between dental macrowear and diet in Late Pleistocene and recent modern human populations. Int. J. Osteoarchaeol. 28, 153–161.
Fiorenza, L., Benazzi, S., Tausch, J., Kullmer, O., Bromage, T.G., Schrenk, F., 2011a. Molar Macrowear Reveals Neanderthal Eco-Geographic Dietary Variation. PLoS One 6.
Fiorenza, L., Benazzi, S., Kullmer, O., 2011b. Para-masticatory wear facets and their functional significance in hunter–gatherer maxillary molars. J. Archaeol. Sci. 38, 2182–2189.
Fiorenza, L., Benazzi, S., Viola, B., Kullmer, O., Schrenk, F., 2011c. Relationship Between Cusp Size and Occlusal Wear Pattern in Neanderthal and *Homo sapiens* First Maxillary Molars. Anat. Rec. 294, 453–461.
Fiorenza, L., Kullmer, O., 2013. Dental wear and cultural behavior in Middle Paleolithic humans from the Near East. Am. J. Phys. Anthropol. 152, 107–117.
Fiorenza, L., Kullmer, O., 2015. Dental wear patterns in early modern humans from Skhul and Qafzeh: A response to Sarig and Tillier. HOMO 66, 414–419.
Fontes-Villalba, M., Carrera-Bastos, P., Cordain, L., 2013. African hominin stable isotopic data do not necessarily indicate grass consumption. Proc. Natl. Acad. Sci. U.S.A. 110, E4055.
García-Antón, M.D., 1987. Estudio polínico preliminar de los yacimientos de la Sierra de Atapuerca (Burgos). In: Aguirre, E., Carbonell, E., Bermúdez de Castro, J.M. (Eds.), El Hombre fósil de Ibeas y el Pleistoceno de la Sierra de Atapuerca, I. Junta de Castilla y León, Consejería de Cultura y Bienestar Social, Soria, pp. 55–59.
García-Medrano, P., Ollé, A., Mosquera, M., Cáceres, I., Carbonell, E., 2015. The nature of technological changes: The Middle Pleistocene stone tool assemblages from Galería and Gran Dolina-subunit TD10.1 (Atapuerca, Spain). Quat. Int. 368, 92–111.
García García, N., Feranec, R.S., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2009. Isotopic analysis of the ecology of herbivores and carnivores from the Middle Pleistocene deposits of the Sierra De Atapuerca, northern Spain. J. Archaeol. Sci. 36, 1142–1151.
García, N., Arsuaga, J.L., 2011. The Sima de los Huesos (Burgos, northern Spain): Palaeoenvironment and habitats of *Homo heidelbergensis* during the Middle Pleistocene. Quat. Sci. Rev. 30, 1413–1419.
Gordon, K.D., 1984. Orientation of occlusal contacts in the chimpanzee, *Pan troglodytes* verus, deduced from scanning electron microscopic analysis of dental microwear patterns. Arch. Oral Biol. 29, 783–787.
Guatelli-Steinberg, D., 2004. Analysis and significance of linear enamel hypoplasia in Plio-Pleistocene hominins. Am. J. Phys. Anthropol. 123, 199–215.
Hardy, K., Radini, A., Buckley, S., Blasco, R., Copeland, L., Burjachs, F., Girbal, J., Yll, R., Carbonell, E., Bermúdez de Castro, J.M., 2017. Diet and environment 1.2 million years ago revealed through analysis of dental calculus from Europe's oldest hominin at Sima del Elefante, Spain. Naturwissenschaften 104, 2.
Hedges, R.E.M., Reynard, L.M., 2007. Nitrogen isotopes and the trophic level of humans in archaeology. J. Archaeol. Sci. 34, 1240–1251.
Hernaiz-García, M., Oxilia, G., Benazzi, S., Sarig, R., Fu, J., Kullmer, O., Fiorenza, L., 2024a. Diet of Neanderthals and early *Homo sapiens* from macrowear analysis of mandibular molars. J. Archaeol. Sci. 164, 105950.
Hernaiz-García, M., Zanolli, C., Martín-Francés, L., Mazurier, A., Benazzi, S., Sarig, R., Fu, J., Kullmer, O., Fiorenza, L., 2024b. Masticatory habits of the adult Neanderthal individual BD 1 from La Chaise-de-Vouthon (France). Am. J. Biol. Anthropol., e24926
Hillson, S., 2003. Dental Anthropology. Cambridge University Press, Cambridge.
Horio, T., Kawamura, Y., 1989. Effects of texture of food on chewing patterns in the human subject. J. Oral Rehabil. 16, 177–183.
Hylander, W.L., Crompton, A.W., 1986. Jaw movements and patterns of mandibular bone strain during mastication in the monkey *Macaca fascicularis*. Arch. Oral Biol. 31, 841–848.
Hylander, W.L., Johnson, K.R., Crompton, A.W., 1987. Loading patterns and jaw movements during mastication in *Macaca fascicularis*: A bone-strain, electromyographic, and cineradiographic analysis. Am. J. Phys. Anthropol. 72, 287–314.
Janis, C.M., 1990. The correlation between diet and dental wear in herbivorous mammals, and its relationship to the determination of diets of extinct species. In: Boucot, A.J. (Ed.), Evolutionary Paleobiology of Behavior and Coevolution. Elsevier Scienc, Amsterdam, pp. 241–259.
Kaidonis, J.A., 2008. Tooth wear: The view of the anthropologist. Clin. Oral Invest. 12, S21–S26.
Kaifu, Y., Kasai, K., Townsend, G.C., Richards, L.C., 2003. Tooth wear and the "design" of the human dentition: A perspective from evolutionary medicine. Yearbk. Phys. Anthropol. 46, 47–61.
Kay, R.F., 1975. The functional adaptations of primate molar teeth. Am. J. Phys. Anthropol. 43, 195–215.
Kay, R.F., Hiiemae, K.M., 1974. Jaw movement and tooth use in recent and fossil primates. Am. J. Phys. Anthropol. 40, 227–256.
Knight-Sadler, J., Fiorenza, L., 2017. Tooth Wear Inclination in Great Ape Molars. Folia Primatol. 88, 223–236.
Krueger, K.L., Scott, J.R., Kay, R.F., Ungar, P.S., 2008. Technical note: Dental microwear textures of "Phase I" and "Phase II" facets. Am. J. Phys. Anthropol. 137, 485–490.
Kullmer, O., Benazzi, S., Fiorenza, L., Schulz, D., Bacso, S., Winzen, O., 2009. Technical note: Occlusal fingerprint analysis: Quantification of tooth wear pattern. Am. J. Phys. Anthropol. 139, 600–605.
Le Luyer, M., Rottier, S., Bayle, P., 2014. Brief communication: Comparative patterns of enamel thickness topography and oblique molar wear in two early neolithic and medieval population samples. Am. J. Phys. Anthropol. 155, 162–172.
Lee, J., Fung, S., Yong, R., Ranjitkar, S., Kaidonis, J., Evans, A.R., Fiorenza, L., 2021. Tooth wear development in the Australian Aboriginal dentition from Yuendumu: A longitudinal study. PLoS One 16, e0254151.
Lev, E., Kislev, M.E., Bar-Yosef, O., 2005. Mousterian vegetal food in Kebara Cave, Mt. Carmel. J. Archaeol. Sci. 32, 475–484.
Lucas, P.W., Omar, R., Al-Fadhalah, K., Almusallam, A.S., Henry, A.G., Michael, S., Thai, L.A., Watzke, J., Strait, D.S., Atkins, A.G., 2013. Mechanisms and causes of wear in tooth enamel: Implications for hominin diets. J. Royal Soc. Interface 10.
Maier, W., Schneck, G., 1981. Konstruktionsmorphologische Untersuchungen am Gebiß der hominoiden Primaten. Z. Morphol. Anthropol. 72, 127–169.
Martinón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Prado-Simón, L., Arsuaga, J.L., 2012. Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). J. Hum. Evol. 62, 7–58.
Mays, S., Zakrzewski, S., Field, S., 2022. The relationship between dental wear and age at death in British archaeological human skeletal remains: A re-evaluation of the 'Brothwell chart'. J. Archaeol. Sci.: Rep. 46, 103707.
Mosquera, M., Ollé, A., Saladié, P., Arroyo, A., Asryan, L., Bargalló, A., de Lombera-Hermida, A., Fernández-Marchena, J.L., García-Medrano, P., Lombao, D., Rodríguez-Hidalgo, A., Soto, M., Vallverdú, J., Arteaga-Brieba, A., Villalobos, J., Yeşilova, G.-C., Carbonell, E., 2024. Intriguing Occupations at Gran Dolina (Atapuerca, Spain): the Acheulean Subunits TD10.3 and TD10.4. J. Paleol. Archaeol. 7, 6.
Nakajima, J., Hideshima, M., Takahashi, M., Taniguchi, H., Ohyama, T., 2001. Masticatory mandibular movements for different foods textures related to onomatopoetic words. J. Med. Dent. Sci. 48, 121–129.
Ollé, A., Mosquera, M., Rodríguez-Álvarez, X.P., García-Medrano, P., Barsky, D., de Lombera-Hermida, A., Carbonell, E., 2016. The Acheulean from Atapuerca: Three steps forward, one step back. Quat. Int. 411, 316–328.
Ollé, A., Mosquera, M., Rodríguez, X.P., de Lombera-Hermida, A., García-Antón, M. D., García-Medrano, P., Peña, L., Menéndez, L., Navazo, M., Terradillos, M., Bargalló, A., Márquez, B., Sala, R., Carbonell, E., 2013. The Early and Middle

Pleistocene technological record from Sierra de Atapuerca (Burgos, Spain). Quat. Int. 295, 138–167.
Ortega, A.I., Martín, M.Á., 2022. Hypogenic origin of the Sierra de Atapuerca Karst (Burgos). In: 14th Eurospeleo Forum and XI Congreso Español de Espeleología, Burgos, pp. 46–49.
Oxilia, G., Bortolini, E., Martini, S., Papini, A., Boggioni, M., Buti, L., Figus, C., Sorrentino, R., Townsend, G., Kaidonis, J., Fiorenza, L., Cristiani, E., Kullmer, O., Moggi-Cecchi, J., Benazzi, S., 2018. The physiological linkage between molar inclination and dental macrowear pattern. Am. J. Phys. Anthropol. 166, 941–951.
Pérez-Pérez, A., Bermúdez De Castro, J.M., Arsuaga, J.L., 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., Espurz, V., Bermúdez de Castro, J.M., de Lumley, M.A., Turbón, D., 2003. Non-occlusal dental microwear variability in a sample of Middle and Late Pleistocene human populations from Europe and the Near East. J. Hum. Evol. 44, 497–513.
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-Pérez, A., Lozano, M., Romero, A., Martínez, L.M., Galbany, J., Pinilla, B., Estebaranz-Sánchez, F., Bermúdez de Castro, J.M., Carbonell, E., Arsuaga, J.L., 2017. The diet of the first Europeans from Atapuerca. Sci. Rep. 7, 43319.
Rodríguez-Hidalgo, A., Saladié, P., Ollé, A., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2017. Human predatory behavior and the social implications of communal hunting based on evidence from the TD10.2 bison bone bed at Gran Dolina (Atapuerca, Spain). J. Hum. Evol. 105, 89–122.
Rodríguez, J., Willmes, C., Mateos, A., 2021. Shivering in the Pleistocene. Human adaptations to cold exposure in Western Europe from MIS 14 to MIS 11. J. Hum. Evol. 153, 102966.
Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., Van der Made, J., Pérez González, A., Blain, H.A., Expósito, I., López-García, J.M., García Antón, M., Allué, E., Cáceres, I., Huguet, R., Mosquera, M., Ollé, A., Rosell, J., Parés, J.M., Rodríguez, X.P., Díez, C., Rofes, J., Sala, R., Saladié, P., Vallverdú, J., Bennasar, M. L., Blasco, R., Bermúdez de Castro, J.M., Carbonell, E., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quat. Sci. Rev. 30, 1396–1412.
Romero, A., Galbany, J., De Juan, J., Pérez-Pérez, A., 2012. Brief communication: Short- and long-term in vivo human buccal–dental microwear turnover. Am. J. Phys. Anthropol. 148, 467–472.
Sala, N., Arsuaga, J.L., Martínez, I., Gracia-Téllez, A., 2014. Carnivore activity in the Sima de los Huesos (Atapuerca, Spain) hominin sample. Quat. Sci. Rev. 97, 71–83.
Sala, N., Arsuaga, J.L., Pantoja-Pérez, A., Pablos, A., Martínez, I., Quam, R.M., Gómez-Olivencia, A., Bermúdez de Castro, J.M., Carbonell, E., 2015. Lethal Interpersonal Violence in the Middle Pleistocene. PLoS One 10, e0126589.
Sala, N., Pantoja-Pérez, A., Gracia, A., Arsuaga, J.L., 2024. Taphonomic-forensic analysis of the hominin skulls from the Sima de los Huesos. Anat. Rec. 307, 2259–2277.
Sánchez Goñi, M.F., Llave, E., Oliveira, D., Naughton, F., Desprat, S., Ducassou, E., Hodell, D.A., Hernández-Molina, F.J., 2016. Climate changes in south western Iberia and Mediterranean Outflow variations during two contrasting cycles of the last 1Myrs: MIS 31–MIS 30 and MIS 12–MIS 11. Global Planet. Change 136, 18–29.
Smith, B.H., 1984. Patterns of molar wear in hunter–gatherers and agriculturalists. Wiley Subscription Services, Inc., A Wiley Company, pp. 39–56.
Sponheimer, M., Lee-Thorp, J.A., 2007. Hominin palaeodiets: The contribution of stable isotopes. In: Henke, W., Tattersall, I. (Eds.), Handbook of Paleoanthropology. Springer-Verlag, Berlin, pp. 555–586.
Ungar, P.S., Scott, R.S., Grine, F.E., Teaford, M.F., 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. Phil. Trans. Biol. Sci. 365, 3345–3354.
Voelker, A.H.L., Rodrigues, T., Billups, K., Oppo, D., McManus, J., Stein, R., Hefter, J., Grimalt, J.O., 2010. Variations in mid-latitude North Atlantic surface water properties during the mid-Brunhes (MIS 9–14) and their implications for the thermohaline circulation. Clim. Past 6, 531–552.
Wall, C.E., Vinyard, C.J., Johnson, K.R., Williams, S.H., Hylander, W.L., 2006. Phase II jaw movements and masseter muscle activity during chewing in *Papio anubis*. Am. J. Phys. Anthropol. 129, 215–224.