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Tooth wear analyses track niche partitioning at Gerakarou, a 1.8 Ma old site from Greece

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ABSTRACT

The climatic instability of the Early Pleistocene induced regional paleoenvironmental changes, which impacted faunal composition and dynamics. It coincides with the *Homo* dispersal out of Africa. The role played by the Eastern Balkans in this dispersal is at the heart of current scientific debates. The rich fossil assemblage of Gerakarou-1 (2–1.8 Ma; northern Greece) can provide important insight into the environmental conditions of that time and area. In this study, we provide insights into the dietary habits of the herbivore guild of Gerakarou-1 at both short and long-term scales based on two complementary dental proxies, mesowear and microwear textures applied on 70 specimens and we infer the local paleoecology and paleoenvironment. As diet varies between and among populations within the same species, we conduct a population-level study, including a reference dataset of 144 extant individuals belonging to six populations of ruminants with well-known ecology. As we aim to contribute to the collective effort of the community to improve the mesowear methodology, we propose and discuss here the benefits of an alternative, quantitative Geometric Morphometric approach. We show that the occlusal relief, as calculated in the classical mesowear approach, is a variable of little relevance and that the quantitative approach allows better discrimination between dietary categories. By proposing for the first time a multi-scale and multi-proxies study of the entire herbivore guild at Gerakarou-1, we nuance and clarify the paleoecology and niche-partitioning of the ungulates from this site and improve past paleoenvironmental interpretations.

1. Introduction

In the Early Pleistocene of the Northern Hemisphere, alternating glacial and interglacial cycles led to a gradual global cooling and habitat opening (Bonifay and Brugal, 1996; Gibbard and Cohen, 2008; Kahlke et al., 2011; Lisiecki and Raymo, 2005). Large-scale global changes have impacts on local environments as they significantly affect floral and faunal assemblages, and thus ecological and biogeographical aspects (Kahlke et al., 2011 and references therein). This topic is of prime interest as the Early Pleistocene coincides with the dispersal of the genus *Homo* from Africa, as documented in the locality of Dmanisi, Georgia (1.85–1.77 Ma; Ferring et al., 2011). The diversity of habitats available during the dispersal of early humans throughout Europe is at the heart of the discussions (Bartolini-Lucenti et al., 2022; Spassov, 2016; van der Made and Mateos, 2010). Due to its location, Eastern Balkans may have played a crucial role in the early *Homo* dispersal into Europe (Harvati and Roksandic, 2017), although there are currently no known human fossil records in Europe before the Middle Pleistocene (Tourloukis and Karkanas, 2012). The Early Pleistocene site of Gerakarou-1 (Mygdonia Basin, Greece) is biochronologically estimated to be around 2–1.8 Ma (Konidaris et al., 2015), making it roughly contemporaneous with the first occurrence of the genus *Homo* out of Africa.

Being the most durable organs and thus best-preserved remains found in paleontological sites, teeth of herbivorous mammals are often used to infer paleoecology and paleoenvironmental conditions (Merceron et al., 2023). Here, we extract two dental proxies that constitute complementary temporal windows over the dietary habits of past ungulates (Davis and Pineda-Munoz, 2016). Numerous studies on wild

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extant populations with long-term records of ecological preferences (e.g. Berlioz et al., 2017; Kubo et al., 2017; Kubo and Fujita, 2021; Kubo and Yamada, 2014; Merceron et al., 2021) and controlled experimental settings (e.g. Louail et al., 2021; Winkler et al., 2020) have shown the relations between food properties and resulting dental microwear textures. Besides, molar mesowear is known to inform feeding habits on a much longer scale (Ackermans et al., 2020).

Here, by combining dental microwear texture analysis with a new protocol of molar mesowear analysis using geometric morphometrics, set up on a comparative dataset of extant species (Fig. 1), we analyze 70 specimens of five meso-herbivores from Gerakarou-1 to decipher dietary preferences, niche partitioning, and habitats available in this Early Pleistocene site.

2. Material and methods

2.1. Material

Gerakarou-1 is one of the 12 known fossil sites from the Mygdonia basin (Koufos and Kostopoulos, 2016), which covers the Lower Pleistocene (2.6–0.8 Ma; Gibbard and Head, 2009). Based on typical late Villafranchian faunal elements and more recent taxa, Gerakarou-1 is attributed to MNQ 18 (Koufos, 2001) before the Olduvai event (1.92–1.78 Ma; Cohen and Gibbard, 2022). In Gerakarou-1, almost 60% of the faunal assemblage comprises ungulates while carnivore species account for around 30% and rodents around 10% (Koufos, 2001).

Only adults with erupted UM3/lm3 were considered for the analyses. We excluded teeth at the severely worn stage or unworn. As the first molars are often too worn, and the third molars are frequently not worn enough, we work preferentially on the second molars. This is the tooth most studied in Dental Microwear Texture (DMT) studies, which facilitates inter-team comparisons. We analysed 70 molars belonging to *Equus altidens* (N = 8), *Antilope koufosi* (N = 3), *Gazella bouvrainae* (N = 30), *Croizetoceros ramosus gerakarensis* (hereafter *C. ramosus*; N = 26), and *Eucladoceros tegulensis* (N = 3) (Table S1). The few specimens of *Leptobos* cf. *etruscus* and an undetermined Bovidae were excluded. All fossil specimens are housed in the Museum of Geology, Paleontology, Palaeoanthropology (LGPUT) of the Aristotle University of Thessaloniki, Greece.

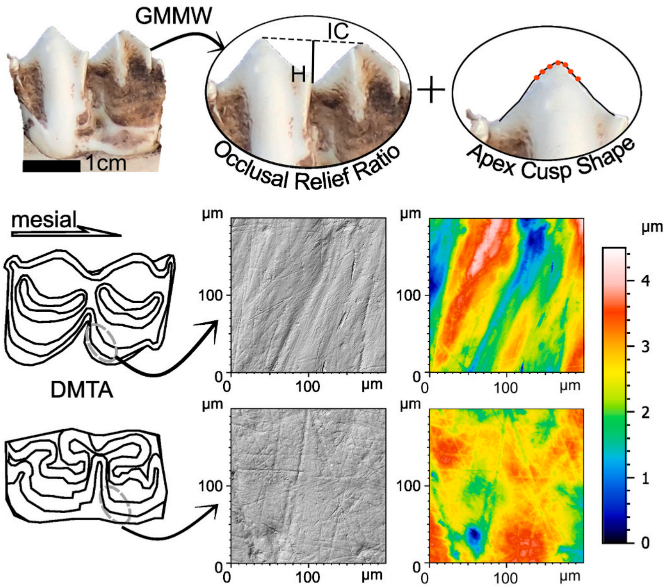

Fig. 1. Combination of long-term (Mesowear) and short-term (Microwear) approaches for palaeoecological inferences. Top of the figure: Geometric Morphometric MesoWear (GMMW) is based on the occlusal relief as a continuous variable and the apex cusp shape determined by an outline digitalized with 2-D landmarks and semi-landmarks. DMT (lower part): Dental microwear texture analysis allows the quantification of different texture parameters using 3D cloud points here represented as a photosimulation and a false-colour elevation map for the lower second molars of *Eucladoceros tegulensis* (GER 136; middle of the figure); and *Equus altidens* (GER 33; bottom of the figure).

As diet varies between populations within a species (Gebert and Verheyden-Tixier, 2001) depending on age, sex, physiological condition, and season, we conducted a population-level study. When considered among herbivore ungulates, phylogenetic relationships and masticatory movements are known to have little impact on the two dental proxies used in this study (Calandra and Merceron, 2016; DeSantis et al., 2018; Schulz et al., 2010). Therefore, in the absence of strict present-day representatives, our comparative material comprises 144 individuals from six European populations of extant species of ruminants (Table 1; Table S1) with well-known ecology, from biomes comparable with Early Pleistocene European landscapes. The sympatric *Ovis ammon* (N = 21), *Rupicapra rupicapra* (N = 19), *Cervus elaphus* (N = 19), and *Capreolus capreolus* (N = 18) samples come from the Bauges Natural Regional Park (French Alps; Redjadj et al., 2014). *Alces alces* (N = 28) are from the Biebrza marshes (Eastern Poland; Kuijper et al., 2016), and *Bos taurus* (N = 39) are from a Camargue sample (Rhône delta, France; Blaise, 2005; Duncan and D'Herbes, 1982). Previous dental microwear texture (DMT) studies have focused on these extant populations (Berlioz et al., 2022; Hermier et al., 2020; Merceron et al., 2021). All dental molds are stored at the PALEVOPRIM lab (University of Poitiers, France).

In our comparative material, the population that is the most engaged in grazing is *Bos taurus* (Duncan and D'Herbes, 1982), and the most browsing is the moose *Alces alces* (Kuijper et al., 2016). The red deer *Cervus elaphus*, the chamois *Rupicapra rupicapra,* and the mouflon *Ovis ammon* are known to be mixed feeders (Gebert and Verheyden-Tixier, 2001; Marchand et al., 2013; Pérez-Barbería and Nores, 1994) while the roe deer *Capreolus capreolus* is a selective browser prone to select the most nutritive items (Tixier et al., 1997).

2.2. Methods

Regarding dental facets for DMT analysis, we followed recommendations by Ramdarshan et al. (2017): we focused on the mesio-lingual facet of the protocone on upper molars and the disto-labial facet of the protoconid on lower molars. For the upper teeth of equids, we adapted the location by molding the lingual facet of the protoloph. Cleaning and molding procedures are detailed here: https://zenodo.org/doi/10.5281/zenodo.7305566. For scanning with "Trident", the Leica DCM8 (Leica Microsystem) microscope of PALEVOPRIM Lab has been used; for pre-treating and analysing the data we used Leica MAP v. 8.2Sfrax software (Surfract, www.surfract.com), following procedures by Merceron et al. (2016) and in supplementary information therein; appendix A1). We applied Scale Sensitive Fractal Analysis and extracted complexity (Asfc), heterogeneity of complexity (HAsfc; nine cells), and anisotropy (epLsar, measured following the traditional method; Calandra et al., 2022; Scott et al., 2006). Whenever the sample size was large enough ($N \geq 5$; Table 1, Table S1), we also calculated inter-individual disparities for Asfc and epLsar (Disp-Asfc and Disp-epLsar, respectively) following Levene's equations (Plavcan and Cope, 2001; $\text{Disp-X} = \Sigma(|\ln(X_i) - (\text{Med}_{1- > n}(\ln(X_i))|)/n))$. This approach allows the assessment of inter-sample variation, which has interesting ecological implications in terms of diet breadth, social behaviours, and habitat use (Burgman et al., 2016; Merceron et al., 2021).

Regarding molar mesowear analysis, we followed the procedures by Rivals and Semprebon (2006). The coding of the occlusal relief (OR) and the apex shape (CS) generates a mesowear score (Ms) for each individual. A lower Ms corresponds to sharper cusps with higher relief, while a higher Ms indicates rounder and lower cusps. Our study is part of an ongoing collective effort to refine the link between mesowear and dietary ecology and improve the discriminatory power of the approach

Table 1

Summary statistics for the molar mesowear and dental microwear textures for both extant and extinct species (for populations with N>5). N: sample size; SE: standard error; SD: standard deviation; ORR: Occlusal Relief Ratio; ACS: Apex Cusp Shape using Geometric Morphometric Mesowear Method; Ms: Mesowear score (Rivals and Semprebon, 2006); Asfc: complexity; epLsar: anisotropy; Disp-Asfc: disparity of complexity; HAsfc: heterogeneity of complexity (9 cells). Regarding DMT, only variables displaying significant variations are shown.

		Extant Species						Fossil Species		
		B. taurus	*R. rupicapra*	*O. ammon*	*C. elaphus*	*C. capreolus*	*A. alces*	*G. bouvrainae*	*C. ramosus*	*E. altidens*
Variables	N	39	19	21	19	18	28	30	26	8
ORR	Mean	0.59	0.56	0.46	0.44	0.39	0.33	0.32	0.33	0.12
	SE	0.02	0.03	0.02	0.01	0.02	0.01	0.02	0.02	0.02
	SD	0.12	0.11	0.08	0.04	0.08	0.07	0.09	0.09	0.05
ACS (PC1)	Mean	0.06	−0.01	0.02	−0.04	−0.01	−0.05	−0.03	−0.01	0.12
	SE	0.01	0.02	0.02	0.02	0.03	0.01	0.02	0.02	0.03
	SD	0.09	0.09	0.11	0.07	0.11	0.07	0.10	0.10	0.07
Ms	Mean	0.92	0.89	0.81	0.84	0.72	0.57	0.87	0.92	2.25
	SE	0.04	0.07	0.09	0.09	0.11	0.10	0.17	0.12	0.25
	SD	0.27	0.32	0.40	0.37	0.46	0.50	0.94	0.63	0.71
Asfc	Mean	1.59	1.85	2.04	1.38	2.61	4.63	2.01	1.33	0.96
	SE	0.16	0.23	0.19	0.14	0.59	0.72	0.20	0.13	0.11
	SD	0.99	1.00	0.89	0.60	2.49	3.82	1.11	0.65	0.30
epLsar	Mean	5.29	4.29	3.80	5.89	6.05	1.87	4.51	6.39	3.88
	SE	0.34	0.43	0.57	0.62	0.55	0.24	0.34	0.44	0.63
	SD	2.11	1.88	2.61	2.72	2.34	1.25	1.84	2.25	1.78
Disp-Asfc	Mean	0.21	0.23	0.25	0.19	0.43	0.39	0.27	0.21	0.14
	SE	0.04	0.05	0.04	0.03	0.09	0.07	0.04	0.03	0.02
	SD	0.24	0.21	0.16	0.15	0.38	0.35	0.20	0.16	0.06
HAsfc	Mean	0.41	0.39	0.33	0.58	0.36	0.69	0.41	0.34	0.24
	SE	0.05	0.05	0.02	0.12	0.03	0.07	0.02	0.03	0.02
	SD	0.28	0.24	0.11	0.50	0.14	0.39	0.13	0.17	0.07

(Ackermans, 2020; Alifieri et al., 2021, 2022; Mihlbachler et al., 2023). This is why we also proposed a Geometric Morphometric MesoWear method (GMMW). We photographed the dental rows of all specimens, focusing preferentially on second molars (UM2/lm2; Table S1), using an Olympus TG-3 and a Nikon D5200 digital cameras and a professional photographic table equipped with a graduated arm and lighting. For the upper molars, the picture was taken on the labial side, and for the lower molars, on the lingual side. We favored the right molars, but, when these were unusable, we photographed the left ones, and mirrored the picture along the X-axis. We orientated the samples by placing them on foam pads, so that the walls of the molars were perfectly perpendicular to the camera lens. Each photo was taken with the same scale and the same distance between the lens and the specimen. We then digitally computed the Occlusal Relief Ratio (ORR; corresponding to H/IC, as illustrated in Fig. 1) with tpsDig (v. 2.32; Rohlf, 2021). The Apex Cusp Shape (ACS; Fig. 1) is digitalized by 40 2-D semi-landmarks from the mesial to the distal side of the anterior cusp (or posterior whenever the anterior was damaged; Table S1) with TpsUtil (v 1.78; Rohlf, 2021). Then we selected the upper-25% semi-landmarks reflecting the shape of the apex of the cusp and performed generalized least squares procrustes superimpositions with MorphoJ (v 107a; Klingenberg, 2011) to remove scale, rotation, and translation differences and work in the same morphological space (Kendall, 1977; Slice, 2007; Webster and Sheets, 2010).

Then, we generated an eco-dietary space by conducting a Principal Component Analysis on extant specimens. In this PCA, we secondarily included the fossil specimens, using PC scores from the PCA on extant. Analyses focus on PC1, which determines the Apex Cusp Shape (56.93% of the variance; Figs. 1 and 2, Table S3, Fig. S1).

After rank-transformations (Conover and Iman, 1981), we performed one-way ANOVAs (Table S2) to determine whether the DMT and GMMW significantly varied, followed by Tukey (HSD) and Fisher (LSD) post-hoc tests to identify inter-group significative differences (Table 2).

3. Results

3.1. Dental microwear texture analysis

The ANOVA detected significant differences in complexity, disparity of complexity, heterogeneity of complexity, and anisotropy (Table S2). Among extant populations, *Alces alces* differs from all other extant species in having a higher complexity and lower anisotropy (Tables 1 and 2, Fig. 2). It also has a higher heterogeneity of complexity than all species, but *C. elaphus*. *A. alces* also has a higher disparity of complexity than *B. taurus* and *C. elaphus*. *Alces alces* differs significantly from *C. capreolus* in having higher complexity, heterogeneity of complexity, and lower anisotropy. However, these cervids share a high inter-individual disparity of complexity (Table 1) compared to the other extant ruminants. *O. ammon*, *R. rupicapra,* and *C. elaphus*, known as mixed feeders, and *B. taurus*, known as grazer, all show significant differences with *A. alces*. It is worth noting that there are no significant differences between *R. rupicapra* and *B. taurus* and that *C. elaphus* has the lowest complexity among all the extant species (Tables 1 and 2, Fig. 2).

Looking at the fossil samples, *Equus altidens* differs from all extant species in having lower complexity (except *C. elaphus*) and lower heterogeneity of complexity (except *O. ammon;* Tables 1 and 2, Fig. 2). It also differs in having a lower anisotropy than *C. elaphus* and *C. capreolus* and a lower disparity of complexity than *C. capreolus* and *A. alces*. *Gazella bouvrainae* has a higher complexity than *B. taurus* and *C. elaphus*. It has lower anisotropy than *C. capreolus* and *C. elaphus* but higher than *A. alces*. *Gazella bouvrainae* differs from *R. rupicapra* and *O. ammon* in having a higher heterogeneity of complexity (but lower than that of *A. alces*). *Croizetoceros ramosus* has significantly lower complexity than *A. alces*, *C. capreolus*, and *O. ammon* and lower heterogeneity of complexity than *C. capreolus* and *A. alces*. All but one of the *Antilope koufosi* and *Eucladoceros tegulensis* (Fig. 2) plot far from *A. alces*. However, the low sample size (N = 3 in both cases) for these two species forbids us to apply statistical tests and discuss further the differences with extant species.

3.2. Molar mesowear analysis

The occlusal relief (OR), one of the two variables used to calculate the mesowear score (Ms), is high for 100% of the individuals used as a reference, and for 78% of the fossil individuals (Table S1). The extant *A. alces* has the lowest mesowear score (Ms; Table 1, Fig. S2), and *B. taurus* the highest (Table 1; Fig. S2). Other species plot between these

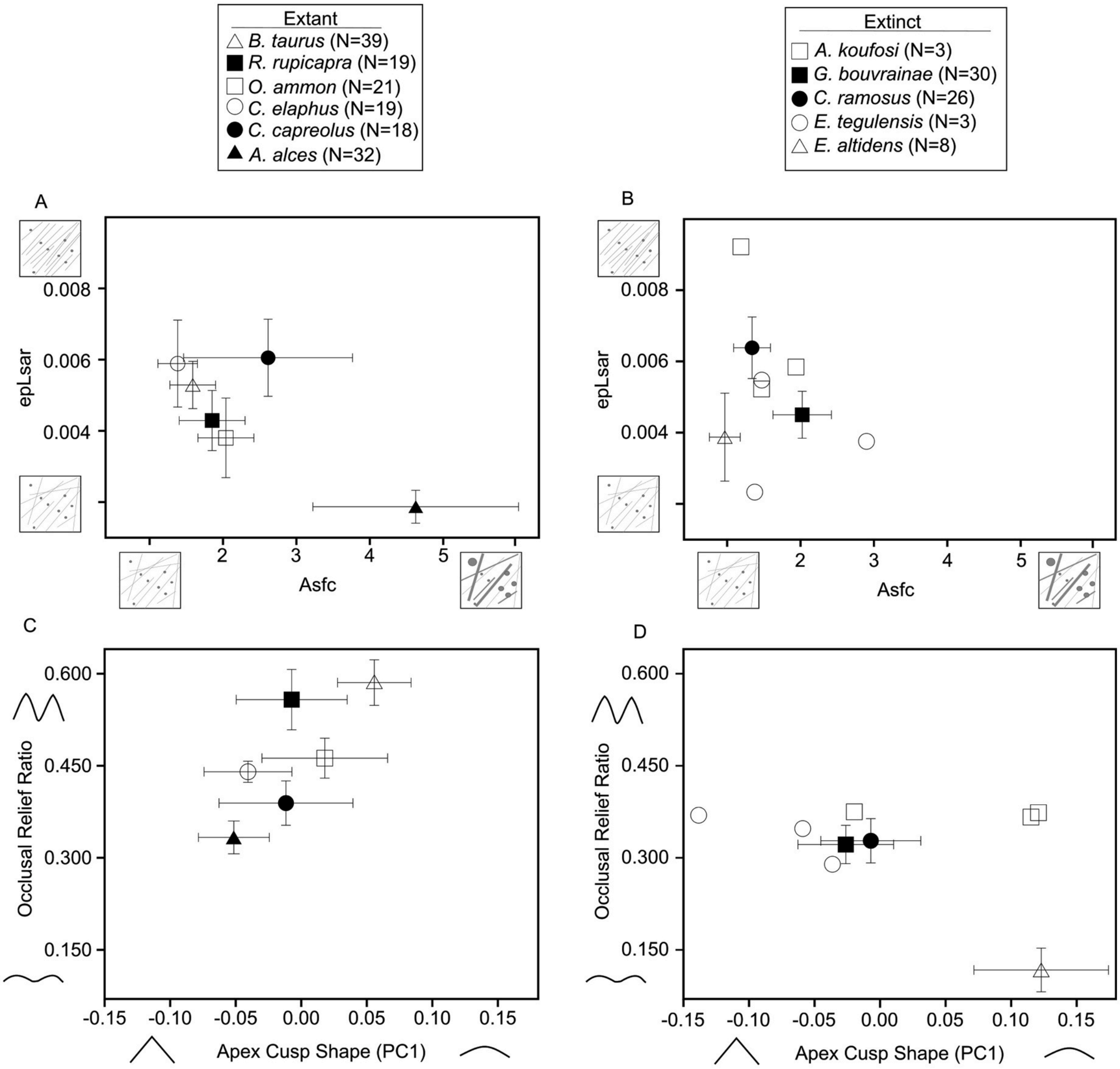

Fig. 2. Microwear and Mesowear results for extant and extinct populations. Mean and confidence interval of the mean at 95% of anisotropy (epLsar) and complexity (Asfc, A and B) and of occlusal relief ratio (ORR) and apex cusp shape calculated with the GMMW approach (PC1, C and D) for extant and extinct species.

Table 2

Results of post hoc tests for between samples differences. Significant differences supported by Fisher's Least Significant Difference tests (LSD), which are underlined when these differences are also supported by Tukey's Honestly Significant Difference tests (HSD). Analyses were done only whenever N ≥ 5 specimens.

	Extant Species						Fossil Species		
	B. taurus	*R. rupicapra*	*O. ammon*	*C. elaphus*	*C. capreolus*	*A. alces*	*G. bouvrainae*	*C. ramosus*	*E. altidens*
B. taurus	/		Asfc epLsar	HAsfc	Disp-Asfc	Asfc epLsar Disp-Asfc HAsfc	Asfc		Asfc HAsfc
R. rupicapra	ACS	/		epLsar HAsfc	epLsar	Asfc epLsar HAsfc		epLsar	Asfc HAsfc
O. ammon	ORR	ORR	/	Asfc epLsar HAsfc	epLsar	Asfc epLsar HAsfc	HAsfc	Asfc epLsar	Asfc
C. elaphus	ORR ACS	ORR	ACS	/	Disp-Asfc HAsfc	Asfc epLsar Disp-Asfc	Asfc epLsar	HAsfc	epLsar HAsfc
C. capreolus	ORR ACS	ORR	ORR	ORR	/	Asfc epLsar HAsfc	epLsar	Asfc	Asfc epLsar Disp-Asfc HAsfc
A. alces	ORR ACS	ORR	ORR ACS	ORR	ORR	/	Asfc epLsar HAsfc	Asfc epLsar HAsfc	Asfc epLsar Disp-Asfc HAsfc
G. bouvrainae	ORR ACS	ORR	ORR	ORR	ORR		/	Asfc HAsfc epLsar	Asfc HAsfc
C. ramosus	ORR ACS	ORR	ORR	ORR	ORR	ACS		/	epLsar
E. altidens	ORR	ORR ACS	ORR ACS	ORR ACS	ORR ACS	ORR ACS	ORR ACS	ORR ACS	/

two end-members with significant overlap. When it comes to fossils, the mesowear score of *Equus altidens* is the only one that is different from all extant and extinct ruminants in having the highest values (Tables 1 and S4, Fig. S2).

When considering the occlusal relief ratio as a continuous variable (ORR; Tables 1 and 2, Fig. 2), it occurs that *A. alces* has the lowest relief and *B. taurus* the highest. Other species plot between them (Fig. 2). The post-hoc test shows that *A. alces* differs from other extant species (but marginally with *C. capreolus*) in having a significantly lower occlusal relief ratio (Tables 1 and 2; Fig. 2). *Capreolus capreolus* also differs from *B. taurus*, *R. rupicapra*, *O. ammon* and marginally from *C. elaphus* in having a significantly lower occlusal relief ratio (Tables 1 and 2; Fig. 2). *Cervus elaphus* has a significantly lower occlusal relief ratio than *B. taurus* and marginally lower than *R. rupicapra*. *Ovis ammon* also has a lower occlusal relief ratio than *B. taurus*.

The Apex Cusp Shape (Table S3; Fig. S1) significantly varies along the PC1, explaining 56.93 % of the variance. PC2 does not reflect mesowear but is rather related to cusp inclination (mesial or distal) and explains 32.32% of the variance (Table S3; Fig. S1). *Bos taurus* significantly differs from all species but *O. ammon* in having higher values evidencing more rounded cusp apexes (PC1, Tables 1 and 2; Fig. 2). *Ovis ammon* also differs from *C. elaphus* and *A. alces* in having higher PC1, meaning rounder cusps (Tables 1 and 2; Fig. 2). PC1 of the Model PCA based on extant populations and setting our interpretive eco-dietary space explains 58.78% of the variance for the fossil dataset (Table S3). When considering the occlusal relief ratio, equids show the lowest value, significantly different from all extant and extinct ruminants. *Equus altidens* displays the highest coordinates along PC1 (Fig. 2, Table 1), being not different from *B. taurus*. The occlusal relief ratio of *G. bouvrainae* and *C. ramosus* are similar to the ones of *A. alces* and *C. capreolus.* They show significant differences in occlusal relief ratio with the three extant bovids and *C. elaphus.* Their coordinates along PC1 have lower values than *B. taurus*, confirming sharper cusps. *Eucladoceros tegulensis* and *A. koufosi* have occlusal relief ratio similar to *A. alces*. *Eucladoceros tegulensis* displays low values along the PC1 supporting sharp cusps, while two of the three specimens of *A. koufosi* have high values, the third one plotting near the mean values for the three extant cervids (Fig. 2).

4. Discussion

Molar mesowear bears a long-term dietary signal, at least on a yearly scale (Ackermans, 2020). In our study, the occlusal relief on mandibular cheek teeth of mid-latitude C_3 plant-eating ruminants does not discriminate between extant populations well-known to forage on different resources (OR; Tables S1 and S4). This finding can be generalized to a larger geographical scale since data from a recent study show similar results (Mihlbachler et al., 2023). The cusp shape is by then the only parameter that significantly contributes to the mesowear scores (Ms). It results that, in our study, all six extant ruminants share low mesowear scores, overlapping with the ranges of extant browsers, mixed feeders, and C_3 grazers in the comparative datasets from Fortelius and Solounias (2000; Fig. S2). In addition to the need for improving the measurement variables, such results highlight the need to set up *ad hoc* comparative models considering the fine-scale ecology. Indeed, large datasets built with species represented by few individuals occupying different biomes dispersed at different latitudes and sampled at different years, or even decades, might be, at best, non-adapted and, at worst, a source of misinterpretation regarding dietary habits (Fortelius and Solounias, 2000; Mihlbachler et al., 2023).

We calculated an occlusal relief ratio and modeled Apex Cusp Shape to overcome these limitations, thus treating these variables as continuous. They significantly discriminate extant populations. It is worth noting that the highest occlusal relief ratio is not found for browsing species but for *Bos taurus*, the most grazing species of our extant dataset, challenging the traditional view of a positive correlation between low occlusal relief and the consumption of monocots. One could interpret the low occlusal relief ratio of the two most browsing species (*Alces alces* and *Capreolus capreolus*) as the result of a diet rich in lignin components, requiring a higher chewing stroke to comminute these food items. That said, the Apex Cusp Shape results are consistent with former studies (Solounias and Semprebon, 2002): sharper apexes were found for browsing species and blunter apexes for grazing ones. The molar mesowear (GMMW) proposed here clearly shows better dietary discrimination.

Combined molar mesowear and dental microwear textures provide complementary long-term and short-term signals offering a more comprehensive view into the paleoecology of species and populations. The analysis of the herbivore guild of the Greek faunal assemblage of Gerakarou-1 emphasizes food preferences and ecological niche partitioning. *Gazella bouvrainae* had a mixed-feeding diet similar to modern *R. rupicapra* and *O. ammon,* as the similar short-term DMT (complexity and anisotropy) and long-term Apex Cusp Shape of the three species demonstrate. *Croizeroceros ramosus* likely fed on resources more similar to that of the population of the extant *C. elaphus*. This small-size extinct deer likely consumed less lignified tissues and more herbaceous vegetation than *G. bouvrainae* as it displays higher texture anisotropy than *G. bouvrainae. Equus altidens* composed the third most important sample in the Gerakarou-1 community. Its diet was mainly based on herbaceous vegetation, as indicated by its Apex Cusp Shape and microwear values. The two other species investigated in this study, *E. tegulensis* and *A. koufosi,* are inadequately represented, so making interpretations is limited. However, we can pinpoint that the molar mesowear depicts *E. tegulensis* as a browser while the microwear texture supports mixed feeders. Observing contrasting results between the two approaches is not inconsistent: mesowear reflects an average diet, while microwear texture provides information on the last few weeks of the animal's life. On the other hand, *A. koufosi* was more engaged in grazing.

Considering that a taphocenosis does not represent a biocenosis, but an undetermined portion of it (Soligo and Andrews, 2005) and that the extinct species composing the taphocenosis might have originated from different habitats in the surrounding of the site (Merceron et al., 2021), the dietary reconstruction of the herbivorous species draws a more accurate picture of the habitat availabilities at a local scale. Our results exclude the occurrence of wooded landscapes, as none of the species were browsers. They all include a significant proportion of herbaceous resources, whose the development would have been severely restricted by a dense tree canopy. Indeed, *E. tegulensis* is the only species that could be classified as a mixed-feeding ruminant engaged in browsing (Berlioz et al., 2018). While the feeding habits of the ruminants support the presence of open habitats with woody vegetation present either as patches or shrub/bushland, the feeding habits of the equid support that it occupied the habitats providing the most abundant herbaceous resources. By proposing for the first time a multi-scale study of the entire herbivore guild at Gerakarou-1, we enhance and clarify previous paleoenvironmental interpretations, whether based on the faunal assemblage (Kahlke et al., 2011) or exclusively on the study of the ecology of Gerakarou-1 deer (Berlioz, 2017; Berlioz et al., 2018).

5. Conclusions

The present study investigates the feeding habits of the guild of the meso-herbivores found at Gerakarou-1, an Early Pleistocene faunal assemblage in northern Greece. The combination of dental microwear texture analysis and an improved version of molar mesowear analysis using geometric morphometry first applied on reference extant populations with known differences in diet, enables us to take a further look into the paleoecology, niche partitioning, and paleoenvironment of the ungulates from this site. *Equus altidens* is the most grazing species from this assemblage. The other species, all ruminants, were mixed feeders, with *Eucladeros tegulensis* most likely the most engaged in browsing. Our results support the presence of open habitats with a low abundance of woody patches or shrub/bushlands. Gerakarou-1 is one of the oldest sites in the Mygdonian basin. With a succession of sedimentary formations, including several fossil sites (Konidaris et al., 2015; Kostopoulos et al., 2023; Koufos, 2001), the Mygdonian basin provides a unique opportunity to decipher fine-scale changes in the ecological niches of the meso-herbivores based on complementary dental proxies, as a bridge to assess environmental variations throughout Early Pleistocene times.

The study also shows the need to continue improving the mesowear tool, particularly by increasing repeatability and moving towards a more effective quantitative (but still affordable and easy to use) approach.

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Author contributions

GM and DSK conceptualized the study in the framework of the master thesis of EA. EB-, GM, and DSK trained EA and supervised her work. EA and AG sampled the specimens. EA conducted all analyses and interpreted the results under the supervision of EB and GM. EA, GM, and EB wrote the manuscript. All co-authors collaborated on reviewing and editing the manuscript. All co-authors agreed to the published version of the manuscript.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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