Diet of Neanderthals and early *Homo sapiens* from macrowear analysis of mandibular molars

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ABSTRACT

Neanderthal diet has been on the spotlight of paleoanthropological research for many years. The majority of studies that tried to reconstruct the diet of Neanderthals were based on the analysis of zooarchaeological remains, stable isotopes, dental calculus and dental microwear patterns. In the past few years, there have been a few studies that linked dental macrowear patterns of Neanderthals and modern humans to diet and cultural habits. However, they mostly focused on maxillary molars. Although mandibular molars have been widely used in microwear dietary research, little is known about their usage at the macroscopic scale to detect information about human subsistence strategies. In this study, we compare the macrowear patterns of Neanderthal (NEA), fossil *Homo sapiens* (FHS), modern hunter-gatherers (MHG), pastoralists, early farmers and Australian Aborigines from Yuendumu mandibular molars in order to assess their utility in collecting any possible information about dietary and cultural habits among diverse human groups. We use the occlusal fingerprint analysis method, a quantitative digital approach that has been successfully employed to reconstruct the diet of living non-human primates and past human populations. Our results show macrowear pattern differences between meat-eater MHG and EF groups. Moreover, while we did not find eco-geographical differences in the macrowear patterns of the fossil sample, we found statistically significant differences between NEA and FHS inhabiting steppe/coniferous forest. This latter result could be associated with the use of distinct technological complexes in these two species, which ultimately could have allowed modern humans to exploit natural resources in a different way compared to NEA.

1. Introduction

Dietary reconstructions are of major interest in the paleoanthropological field to unravel subsistence strategies that have led to the evolution of different human groups. Teeth are the first body structures involved in food processing due to the mechanical action of breaking the food down into smaller pieces, thus becoming key elements to investigate dietary habits (El-Zaatari, 2010, 2014; El-Zaatari et al., 2011, 2016; El-Zaatari and Hublin, 2014; Eshed et al., 2006; Fiorenza et al., 2011a, 2018, 2019, 2022; Frayer and Russell, 1987; Hardy et al., 2012; Henry et al., 2011; Salazar-García et al., 2013).

During mastication, tooth-tooth contacts produce attrition observable in the form of occlusal wear facets (Hillson, 2002). The masticatory cycle is composed by the successive Phase I and Phase II steps of the closing stroke of the chewing power stroke, which are separated by the centric occlusion situation (Kay and Hiiemae, 1974). Phase I facets are generally related to relatively steep angled shearing movements, which are characterized by the contact of occluding surface planes sliding parallel to each other during vertical motion. Well-developed Phase I in humans has been commonly linked to the consumption of tough and fibrous foods such as meat (Fiorenza et al., 2011a; Zink et al., 2014; Zink and Lieberman, 2016). Phase I facets develop over the buccal slopes of

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lower molar cusps and lingual aspect of maxillary cusps (Kay, 1975a, 1975b; Kay and Hiiemae, 1974). Phase II facets are associated to crushing and grinding activities, where the contacting surfaces come together with both a vertical and horizontal component (Kay, 1975a, 1975b; Kay and Hiiemae, 1974). Phase II facets develop along the occlusal basins and lingual slopes of lower molar cusps, and on the buccal slopes of maxillary molar cusps (Kay, 1975a, 1975b; Kay and Hiiemae, 1974), and they are generally associated with the intake of abrasive foodstuff (Krueger et al., 2008).

Studies based on the analysis of molar macrowear patterns have provided dietary information in great apes (Fiorenza and Benazzi, 2017; Fiorenza et al., 2022; Harty et al., 2022; Knight-Sadler and Fiorenza, 2017; Stuhlträger et al., 2021) and in human groups (Fiorenza, 2015; Fiorenza et al., 2011a, 2015, 2018, 2020). Specifically, Fiorenza et al. (2011a) analyzed the macrowear patterns of Neanderthals (NEA) and fossil *Homo sapiens* (FHS) maxillary molars finding an eco-geographic variation between groups living in cold and warm environments. They also found molar macrowear pattern differences between MHG populations with distinct diets: meat-eater populations exhibited larger Buccal Phase I facets, while mixed-diet groups showed more developed Lingual Phase I facets (Fiorenza et al., 2011a). The fossil groups from cold environments displayed macrowear patterns similar to meat-eater hunter-gatheres, while NEA and FHS from warmer environments had a molar macrowear patterns more similar to those of mixed-diet hunter-gatheres (Fiorenza et al., 2011a).

The use of maxillary molars has proven effective in detecting dietary signals, however there is limited knowledge regarding the applicability of mandibular molars in obtaining information about diet and cultural habits in ancient human populations. Oxilia et al. (2018) conducted a study analyzing macrowear patterns and tooth inclinations in Australian Aborigines from Yuendumu (Northern Territory) and found mirrored occlusal relationship between maxillary and mandibular molars. The lack of covariance between the upper and lower jaws suggests that these elements may be distinct but interconnected (Oxilia et al., 2018). Additionally, Oxilia and colleagues (2018, 2020, 2023) have identified various variables responsible for the development and alteration of wear patterns in lower M1s and lower M2s, including asymmetry and morphology, which may pose challenges in accurately interpreting the distribution of dental wear. This difficulty applies to both recent individuals and, more notably, fossil individuals, for whom information on their occlusal dynamics remains somewhat unclear. Having said that, the study of dental wear warrants further investigation and any research in this field can be valuable in elucidating the variables that contribute to alterations in the diverse development of occlusal patterns. The aim of this study is to explore if dietary variation can be detected also in samples of lower molars of different MHG, early farmers (EF), pastoralists (PAS) and Australian Aborigines from Yuendumu (AAY) groups with known dietary behavior, ultimately assessing the dietary ecology of NEA and FHS. We employ the well-established approach of occlusal fingerprint analysis (OFA) method (Fiorenza et al., 2010; Kullmer et al., 2009), allowing the quantification of dental macrowear patterns derived from the analysis of three-dimensional (3D) digital surface models of dental crowns.

Based on the results from previous studies (Fiorenza et al., 2011a, 2015, 2020), we do not expect to find taxonomic differences in macrowear between NEA and FHS, because the macrowear patterns of the mandibular molars should display an eco-geographic rather than a taxonomic signal. More specifically, we expect to find macrowear pattern similarities between fossil groups inhabiting cooler temperate environments such as that of meat-eater MHG, while FHS and NEA from warmer periods should display a macrowear patters more similar to those of hunter-gatheres with a mixed-diet.

2. Material and methods

2.1. Sample

The sample in our study consists of 86 lower molars, of which 34 are NEA, 13 are FHS (which includes Middle and Upper Paleolithic specimens), and 39 are recent modern humans representing individuals living in various environments and with different subsistence strategies (Table 1). The grouping of fossil specimens follows the study of Fiorenza et al. (2011a), where they distinguished three eco-geographical categories considering: chronology, faunal and palynological information available in the literature, and European vegetation reconstruction (van Andel and Tzedakis, 1996). The three major eco-geographical groups representing specific environments are: deciduous woodland (DEW), Mediterranean evergreen (MED) and steppe/coniferous forest (SCF) (Supplementary Information (SI) Table S1). Within each biome, taxonomical division of the fossil sample has been made to test possible differences between NEA and FHS.

The modern human sample is divided into two groups: meat-eater MHG (7 Inuit, 4 Vancouver Islanders, 1 Fuegian), and mixed-diet group which, in turn, is subdivided into pastoralists (PAS) (n = 7), early farmers (EF) (n = 10) and Australian Aborigines from Yuendumu (AAY) (n = 10) (SI Table S2).

The Inuit specimens included comes from a heterogeneous distribution along Greenland. Due to the harsh climatological conditions, plant species are restricted to tundra mosses and lichens, reason why Inuit's diet is mainly based on animal proteins coming from fish, marine and terrestrial mammals, as well as some amount of vegetables when the environmental conditions are milder during springs and summers (Baarrengaard, 1949; Bertulli et al., 2013; Gotfredsen, 1997; Pedersen, 1947; Pedersen and Scott, 1951; Sinclair, 1953; Wright, 1939). They usually consume raw meat, although sometimes frozen, dried or underground storaged (Baarrengaard, 1949; Gotfredsen, 1997; Pedersen, 1947; Pedersen and Scott, 1951). Vancouver islander's subsistence strategy was mainly based on the exploitation of animal protein coming from fish, shellfish (crustaceans, molluscs), birds and sea mammals. However, the dietary regime was mainly composed by diverse species of salmon (Ames and Maschner, 1999; Tafuri et al., 2017), which they consume fresh, dried, smoked, and stored. Also, the molluscs were steamed and often smoked and preserved (Ames and Maschner, 1999). The only Fuegian individual of this study comes from Patagonia. Fuegian groups hunted on sea mammals, fish, birds, crustaceans and shellfish and also collected edible berries (Bridges, 1885). Although they consume some of the animal organs raw (heart, marrow, liver, blood, kidneys), the meat is invariably cooked, that of the ostrich being preferred. They covered the meat with hot stones, roast it on spits or sometimes boil it (Musters, 1872). Fuegians also used iron pots to fry out the grease or marrow and occasionally introduced vegetables into their diet (roots of a species of wild potato, spinach, and few other plants, when available) (Musters, 1872).

Hottentots were tribes of South African nomadic PAS who depended on the mobility of their flocks of domesticated animals (cattle, goat, sheep) according to the seasonal pasture availability (Bernard, 1992; Dyson-Hudson and Dyson-Hudson, 1980). Hottentot people lived in drier areas of savannah lands marked by high seasonality and variability in rainfall (Little, 1989). While PAS tended to consume food derived from their livestock and traded livestock products (Little, 1989), Hottentots rarely ate the flesh of their animals, being the milk, the main food obtained from them (Grosskopf, 1933). They mostly rely on game, insects and on a great variety of wild vegetable foods (Grosskopf, 1933). Their material culture was more complex compared to other African tribes and included utensils made chiefly of wood and of iron, later on, for the manufacturing of implements and weapons (Schapera, 1926).

The sample from Yuendumu was collected during a longitudinal study where researchers annually examined the dentition of Aborigine children an early adult between 1951 and 1971 (Brown et al., 2011).

Table 1

Sample considered in this study and associated diet. NEA = Neanderthals, FHS = fossil *Homo sapiens* (MP = Middle Paleolithic, UP = Upper Paleolithic), MHG = modern hunter-gatherer, PAS = Pastoralists, EF = Early farmers, AAY = Australian Aborigines from Yuendumu. M-E = meat-eater; M-D = mixed-diet.

Group	N	Specimen	Tooth	Diet
NEA	34	Krapina 1	M_2	
		Karpina 6	M_2	
		Krapina 10	M_2	
		Kaprina 53	M_2	
		Kaprina 54	M_2	
		Kaprina 55	M_1	
		Kaprina 57	M_1	
		Kaprina 58	M_2	
		Kaprina 59	M_2	
		Kaprina 77	M_1	
		Kaprina 79	M_1	
		Kaprina 80	M_1	
		Kaprina 81	M_1	
		Kaprina 86	M_2	
		Kaprina 168	M_1	
		Mountgaudier 5	M_1	
		Malarnaud 1	M_1	
		Tabun 1	M_2	
		Guattari 3	M_2	
		Subalyuk	M_2	
		Regourdou 1	M_2	
		La Quina 5	M_2	
		La Quina 9	M_2	
		Combre Greanal 1	M_1	
		Petit Puymoyen 1	M_2	
		Petit Puymoyen 3	M_1	
		Amud 1	M_2	
		Arcy 8	M_1	
		Arcy B9IV66	M_2	
		Vindija 206	M_1	
		Le Moustier 1	M_1	
		Spy 1	M_2	
		Spy 2	M_2	
		Saint Cesaire 1	M_2	
FHS	13	Skhul 6 (MP)	M_2	
		Qafzeh 7 (MP)	M_2	
		Qafzeh 9 (MP)	M_2	
		Qafzeh 11 (MP)	M_1	
		Qazzeh 15 (MP)	M_1	
		Qafzeh H27 (MP)	M_2	
		Tagliente (UP)	M_2	
		Oase 1 (UP)	M_2	
		Sungir 2 (UP)	M_1	
		Sungir 3 (UP)	M_1	
		Barma Grande 4 (UP)	M_2	
		Pataud 224 (UP)	M_1	
		Villabruna (UP)	M_2	
MHG	12	AM10854 (Inuit)	M_1	M-E
		FC826 (Inuit)	M_2	M-E
		FC831 (Inuit)	M_1	M-E
		FC833-2 (Inuit)	M_2	M-E
		FC833-3 (Inuit)	M_2	M-E
		FC835 (Inuit)	M_2	M-E
		FC857 (Inuit)	M_1	M-E
		BD1201 (V. Islanders)	M_1	M-E
		BD1204 (V. Islanders)	M_1	M-E
		FC848 (V. Islanders)	M_1	M-E
		FC855 (V. Islanders)	M_2	M-E
		NHMW15353 (Fuegians)	M_2	M-E
PAS	7	S4 (Hottentot)	M_1	M-D
		S5 (Hottentot)	M_2	M-D
		S6 (Hottentot)	M_2	M-D
		S16 (Hottentot)	M_2	M-D
		S17 (Hottentot)	M_2	M-D
		S18 (Hottentot)	M_2	M-D
		S19 (Hottentot)	M_2	M-D
EF	10	EM_H23 (Natufian)	M_1	M-D
		EM_H57 (Natufian)	M_1	M-D
		EM_H32 (Natufian)	M_2	M-D
		EM_H87_l (Natufian)	M_2	M-D
		EMH69 (Natufian)	M_2	M-D

Table 1 (*continued*)

Group	N	Specimen	Tooth	Diet
		FA_H1 (Natufian)	M_2	M-D
		FA_H26 (Natufian)	M_2	M-D
		FA_H43 (Natufian)	M_2	M-D
		FAH8 (Natufian)	M_2	M-D
		HAY_H11 (Natufian)	M_2	M-D
AAY	10	183	M_1	M-D
		243	M_1	M-D
		247	M_1	M-D
		251	M_1	M-D
		288	M_1	M-D
		294	M_1	M-D
		305	M_1	M-D
		307	M_1	M-D
		549	M_1	M-D
		634	M_1	M-D

This is one of the most studied dental collections in the world consisting of family history information, radiographs, measurements and 1717 dental casts belonging to 446 individuals (Brown et al., 2011). While between 1951 and 1960 researchers were mainly concerned about dental features, general body measurements and the assessment of the skeletal maturation were introduced from 1961 in order to obtain an integrative understanding of the craniofacial growth and development of the jaws and dentition in this population (Brown et al., 2011). During the 1960s, AAY from the Northern Territory were at an early stage of transition from a hunting and gathering activity to a more settled existence with contacts with Europeans (Brown et al., 2011). Before settling at Yuendumu, older Aboriginal individuals would have been exposed to western food in their working places while the younger Aboriginal people, who were born and raised at Yuendumu, were exposed to both coarse native foods and wester aliments (Brown et al., 2011). The dietary trend of AAY led to the intake of a wide range of food including also tough foodstuff which, along with the use of teeth as tools, allows a great development of dental wear in this population (Barrett, 1958, 1977; Brown et al., 2011; Helm, 1979). While many plants were eaten fresh and raw by the people from Yuendumu, flesh foods received a minimum cooking either on an open fire or in a crude earth oven of hot sands and ashes (Brown, 1985). Seeds were stone-grinded to a flour which was mixed with water to form a thick paste that was cooked over hot ashes (Brown, 1985).

The lifestyle of Natufians significantly differs from the traditional hunter-gatherer societies (Bar-Yosef, 2011; Bowles and Choi, 2013). During the terminal period of the Pleistocene and at the beginning of the Holocene the Levant individuals experienced significant social changes that gave rise to the "preagricultural revolution" (Henry, 1985). This is the frame that characterized the moment of the Natufians' societies appearance (14,000–10,000 years ago). Associated to sedentarism and with an intense exploitation of resources, Natufians have been considered as EF (Bar-Yosef, 2011; Bowles and Choi, 2013). Their groups settled in large sites (~700 m^2) placing their hamlets between grasslands and wooden slopes of the Mediterranean hill zone, which enabled them to seasonally make the most of the resource available (Henry, 1985). The sharp use of camps by EF has been proved by the finding of yield specialized tool kits and artefacts related to plant processing techniques, such as querns, grinding slabs, mullers, pestles, mortars or sickle gloss (Belfer-Cohen, 1991; Henry, 1985; Maher et al., 2012; Rosenberg et al., 2021).

The sample analyzed in this study contains slightly worn first (M_1) and second (M_2) permanent molars, ranging between wear stages 2–3 (according to Smith, 1984). In more advance wear stages facets start to merge together, thus making them difficult to identify (Fiorenza et al., 2010).

2.2. Occlusal fingerprint analysis (OFA)

OFA method (Fiorenza et al., 2010; Kullmer et al., 2009) application requires three-dimensional (3D) digital reconstructions of dental surfaces. Original dentition and high-resolution dental replicas were molded using a light viscosity polyvinylsiloxane silicone, ProvilH Novo Light C.D.2 (Heraeus Kulzer GmbH). The negative replicas were filled using a special gypsum (Everest® Rock, KaVo), with non-reflective properties and ideal for 3D scanning (Fiorenza et al., 2009). 3D digital surface models were generated using a 55 mm resolution white-light scanning system (smartSCAN 3D, Breuckmann GmbH). Collection and alignment of the scan-data point clouds and generation of surface meshes was carried out using optoCAT software (Breuckmann, GmbH).

Wear facets were identified a segmented on the molar occlusal 3D surface models following the terminology of Maier and Schneck (1981), who described 13 pairs of facets in hominin molars. Afterwards, the facets were grouped by power stroke phases (Kay and Hiiemae, 1974; Janis, 1990) (Fig. 1): Lingual Phase I (facets 1, 2, 3 and 4), Buccal Phase I (facets 5, 6, 7 and 8) and Phase II (facets 9, 10, 11, 12 and 13). The post-processing of the 3D surface scans was carried out in PolyWorks® V12.1 (InnovMetric Software Inc.), a 3D model editing software package. Orientation of the digital models and wear facet quantification were performed using the IMEdit module of PolyWorks® V12.1 by the manual delineation and posterior insertion of each facet into the 3D model (Ulhaas et al., 2004, 2007) for the final area measurement. The wear facet area values for each chewing cycle phase group were summed and divided by the total occlusal wear area (the total occlusal wear area was calculated as the sum of the absolute area of each occlusal facet).

2.3. Statistical analysis

The heterogeneous characteristic of the sample regarding chronology and geography prevents from classifying the fossil specimens into large groups. The use of a small sample size does not allow the assumption of a normal distribution (Hammer and Harper, 2006). Therefore, a general explorative analysis of each variable is provided in the form of medians and standard deviations (SD) to avoid sensitivity towards extreme values. The statistical analysis was conducted through non-parametric tests. A Permutation Multivariate Analysis of Variance (PERMANOVA) is a multivariate test commonly used in studies with small sample and large number of features (Tang et al., 2016), not restricted by distributional assumptions and that accommodates

heterogeneity of within-group dispersions (Anderson, 2014). The pairwise one-way PERMANOVA tests between all group pairs were based on the relative areas (%) of the three groups: Buccal Phase I, Lingual Phase I and Phase II. The wear facet proportions were represented in a ternary plot, where each variable is place in the apex of the triangle, of which each segment displays values ranging from 1 to 100%. The sample plot within the triangle in the form of a cloud of points. The pairwise one-way PERMANOVA tests was used to assess differences between the MH and fossil samples and also between NEA and FHS belonging to the SCF and DEW ecosystems. When statistically significant differences were obtained, we tested the magnitude of the differences beyond their significance by calculating the effect sizes and the 95% confidence intervals (Cohen, 1988). The statistical analyses were conducted in SPSS Statistics v28 and the ternary plot were generated using the software PAST v4 (PAlaeontological STatistics) (Hammer and Harper, 2006).

In order to test the potential variability introduced by the usage of both M_1s and M_2s, we compared the two tooth types by using the NEA sample from Krapina (SI, Table 3). Because the individuals recovered from Krapina belong to the same geographic region and from same chronological period, we can more accurately investigate if morphological variation between M_1s and M_2s influences wear facet development. We did not find any statistically significant differences between both tooth classes (one-way PERMANOVA: $p = 0.69$), confirming, thus, that relative wear facet areas of first and second mandibular molars can be considered together, as also suggested for maxillary molars (Fiorenza et al., 2011a).

Table 2
Descriptive statistics of relative facets area (in %) including median and standard deviation (SD) within the meat-eater modern hunter-gatherer (MHG) and mixed-diet groups: pastoralists (PAS), early farmers (EF), Australian Aborigines from Yuendumu (AAY).

Group	N	Buccal Phase I		Lingual Phase I		Phase II	
		Median	SD	Median	SD	Median	SD
MHG	12	39.79	8.33	29.52	5.76	31.07	7.88
PAS	7	33.75	4.76	35.9	3.78	32	5.29
EF	10	19.85	14.89	38.48	9.34	37.8	10.99
AAY	10	30.8	10.05	36.25	7.05	33.28	8.56

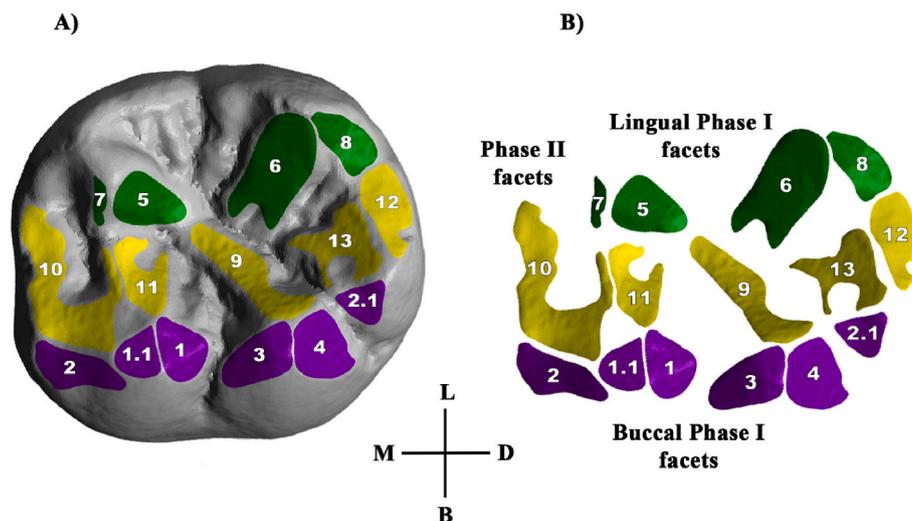**A)**   **B)**

Fig. 1. Occlusal wear pattern of the NEA first left lower molar Krapina 81. 3D model (A) and the identified wear facets (B) divided into Buccal Phase I facets (purple), Phase II facets (yellow), and Lingual Phase I facets (green). Numbering based on Kullmer et al. (2009). Orientation: buccal (B), mesial (M), lingual (L), distal (D). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Descriptive statistics of relative wear facets areas (in %) within the fossil Biome groups.

Group	N	Buccal Phase I		Lingual Phase I		Phase II	
		Median	SD	Median	SD	Median	SD
DEW	18	34.28	13.18	29.35	9.02	33.77	10.21
MED	9	29.55	13.59	31.39	8.34	32.75	10.56
SCF	21	33.68	10.19	37.55	6.63	28.78	7.91

3. Results

3.1. Phase I and phase II facet distribution in MHG, PAS, EF and AAY

The wear pattern follows distinct trends in the different groups utilized in this study (Table 2). Buccal Phase I facets are the most developed in the meat-eater group (40%), who also exhibit less pronounced Phase II facets (31%) and Lingual Phase I facets (29%). PAS individuals display an evenly distributed macrowear pattern. The Lingual Phase I facets represent the 36% of the total wear, followed by a 34% of Lingual Phase I facets and a 32% of the Phase II facets. In the case of EF, Lingual Phase I and Phase II facets exhibit the greatest values with a similar percentage (39% and 38% respectively), followed by Buccal Phase I facets which are the least developed (20%). EF show the highest variation, especially in Buccal Phase I facets (SD = 14.89) and in Phase II facets (SD = 10.99) (Table 2). Finally, AAY are characterized by great Lingual Phase I facets (36%), followed by less pronounced Phase II facets (33%) and Buccal Phase I facets (31%).

The ternary plot shows overlapping values for the meat-eater MHG, PAS and AAY groups and a more distinct pattern for the EF (Fig. 2). This is also confirmed by one-way PERMANOVA test, which corroborates the statistically significant differences between the meat-eater MHG group and the EF ($p = 0.02$) (effect size described into SI Table 5). No statistically significant differences have been found between meat-eater MHG
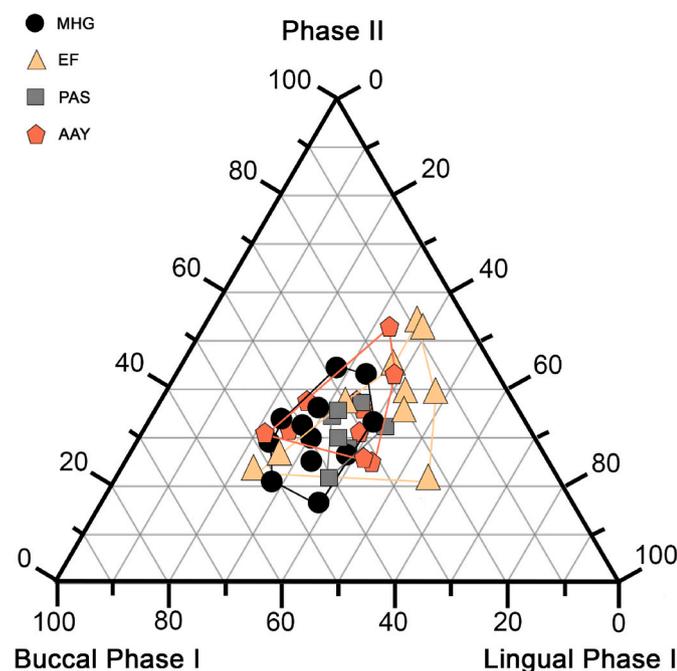
and PAS ($p = 0.09$), neither between meat-eater MHG and AAY ($p = 0.09$). Likewise, PAS and EF show no statistically significant difference ($p = 0.20$), as well as PAS and AAY group ($p = 0.60$) and EF and AAY ($p = 0.36$).

3.2. Phase I and phase II facet distribution in NEA and FHS

Overall, Buccal Phase I facets are the most developed facets in DEW and SCF (34% in both groups), and reduced in MED (30%) (Table 3). Lingual Phase I facets exhibit the greatest values in SCF (38%), followed by MED (31%) and by DEW (30%). Finally, Phase II facets are more developed in DEW and MED (33% in both groups), and reduced in SCF (29%) (Table 3).

Taxonomical differences have been found between the wear patterns of NEA and FHS belonging to the SCF group (one-way PERMANOVA: $p = 0.005$) (effect size described into SI Table 5), while no statistically significant differences were found between the species from the Mediterranean environments (one-way PERMANOVA: $p = 0.78$). While NEA of SCF are characterized by a 37% of Buccal Phase I facets, 36% of Lingual Phase I facets and 29% of Phase II facets, the wear patterns of the FHS specimens from the same environment exhibit 44% of Lingual Phase I facets, 32% of Phase II facets and 24% of Buccal Phase I facets (SI, Table 2, Figs. 1, Fig. 2).

The ternary plot shows some overlapping between the three biome groups in the central region, but the SCF group plots towards the Lingual Phase I vertex of the triangle, while the DEW group spreads out towards the Buccal Phase I and Phase II regions (Fig. 3). This is also shown by the one-way PERMANOVA test, which provides non-significant p-values for the comparisons between SCF and MED groups ($p = 0.41$), SCF and DEW groups ($p = 0.07$) and between MED and DEW groups ($p = 0.81$).

3.3. Comparison between MHG, PAS, EF, AAY and biome-specific fossil groups

Statistically significant differences are found between NEA and FHS

Fig. 2. Ternary diagram of relative wear facet areas in the modern human sample: meat-eater modern hunter-gatherers (MHG), Pastoralists (PAS), early farmers (EF) and Australian Aborigines from Yuendumu (AAY). The ternary diagram illustrates the proportion (%) of the three studied variables (Buccal Phase I, Lingual Phase I and Phase II) in a triangle where each phase grades from 0% to 100% of the total occlusal wear.
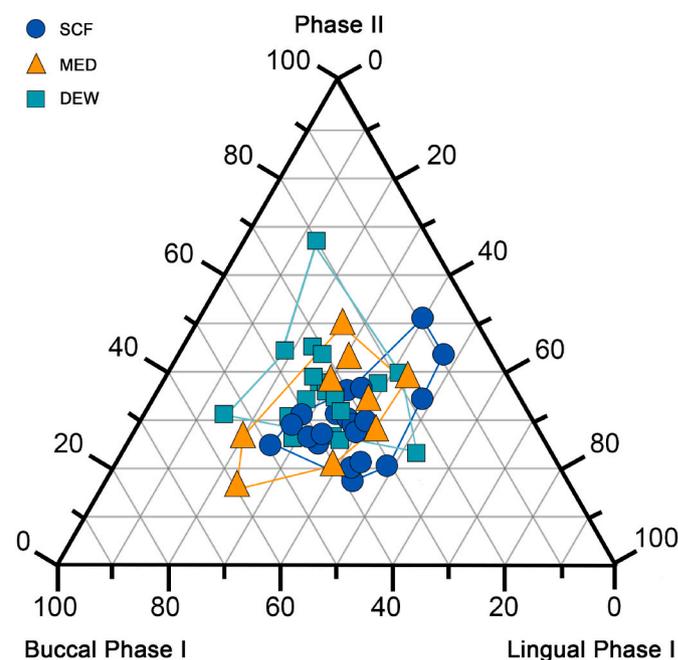

Fig. 3. Ternary diagram of relative wear facet areas in the fossil sample grouped in eco-geographical contexts: deciduous woodland (DEW), Mediterranean evergreen (MED) and steppe/coniferous forest (SCF). The ternary diagram illustrates the proportion (%) of the three studied variables (Buccal Phase I, Lingual Phase I and Phase II) in a triangle where each phase grades from 0% to 100% of the total occlusal wear.

from deciduous woodlands ecosystems and EF (one-way PERMANOVA: $p = 0.02$) (effect size described into SI Table 5). None of the other comparisons between the Pleistocene hominins inhabiting steppe/coniferous forests and Mediterranean ecosystems reveal differences when compared to the modern human sample (Table 4).

4. Discussion

4.1. Occlusal macrowear patterns in relation to diet

The examination of the mandibular molar occlusal macrowear provides important dietary signals. The present study shows significant differences between hunter-gatherer and EF populations.

While the macrowear patterns of hunter-gatherer mandibular molars show somehow similar dental wear percentages to those observed in maxillary molars, such as greater Buccal Phase I facets in the meat-eater MHG group and larger Lingual Phase I facets in the mixed-diet groups, we could not find any significant differences between the two major dietary groups. Moreover, differently from the results obtained in a previous study carried out in maxillary molars (Fiorenza et al., 2011a), our results indicate a relevant presence of Buccal Phase I facets in PAS and AAY in an evenly distributed macrowear pattern, even if the development of Lingual Phase I facets is predominant.

Oxilia et al. (2018) observed that while the macrowear patterns of upper and lower molars of AAY overlap, there were some differences between Buccal Phase I and Lingual Phase I facets of antagonistic molars. They found larger Buccal Phase I facets in upper molars, and more developed Phase II and Lingual Phase I facets in the lower molars. The results of our study seem to confirm this trend. It is possible that differences in the occlusal anatomy would lead to distinct ranges of motion (Kullmer et al., 2009), making it feasible to assume that different morphological configurations would have allowed unequal wear patterns development. This could make it difficult to detect differences in diet but only showing divergence when harder particles, coming from food processing techniques, come into play. The complex occlusal anatomy of lower molars, characterized by a higher number of grooves compared to their counterparts (Hillson, 2002), may facilitate the opportunity for exogenous particles to get entrapped (Mair et al., 1996; Mair, 1999). This, together with sliding movements of the lower molars' cusps against their quiescent antagonistic (Kay, 1975a, 1975b; Kay and Hiiemae, 1974) could favour the enlargement of the wear facets on the occlusal surface of lower molars in presence of grit.

The PAS and the AAY belonged to transitional group from hunter-gatherer to a more settled lifestyle (Bernard, 1992; Brown et al., 2011; Dyson-Hudson and Dyson-Hudson, 1980). This could be the reason behind the lack of differences between these two groups with the meat-eater MHG and with the EF. However, it is interesting to note that the AAY and EF followed a similar pattern where Lingual Phase I facets are the most developed, followed by the Phase II facets and by Buccal Phase I facets. However, EF show almost equal proportions of Lingual Phase I and Phase II facets while, in the case of the AAY, there is a noticeable difference between Lingual Phase I facets and Phase II facet development. According to their lifestyle, both human groups were incorporating abrasive elements into the food (Brown et al., 2011;

Mahoney, 2006). However, the exogenous materials coming from the food processing techniques were mainly attached to different aliments. EF highly processed plants by the use of pestles and mortars (Belfer-Cohen, 1991; Henry, 1985; Maher et al., 2012; Rosenberg et al., 2021). AAY preferred the consumption of fresh vegetables and processed the meat in ground ovens (Brown, 1985). Hua et al. (2020) findings suggested that the exogenous abrasive particles inflict greater damage over the dental tissues when attached to vegetable foodstuff rather than meat. Consequently, the increased intake of plant-based food prepared with stone tools by EF could have increased the development of Phase II facets in this human group (Eshed et al., 2006; Krueger et al., 2008). Phase II facets develop in the occlusal basins and cuspal lingual slopes of the lower molars (Kay, 1975a, 1975b; Kay and Hiiemae, 1974). These are the areas where the food and its attached external particles are interposed between the functional surfaces of molars during grinding movements (Kay, 1975a, 1975b; Kay and Hiiemae, 1974). Krueger et al. (2008) associated the greater microwear complexity and anisotropy in Phase II facets with the presence of abrasive particles. Thus, this could also explain why PAS, whose material culture was mainly made of wood (Schapera, 1926) and therefore reduced the number of exogenous particles coming from food preparation techniques, are the ones exhibiting the less Phase II facet development within the mixed-diet groups.

The differences between EF and the MHG groups are significant for the meat-eater MHG group (Fuegians, Inuit and Vancouver Islanders) and not significant when we compare EF with the other mixed-diet groups (PAS and AAY). This result could reflect the dietary regimes characterizing these groups, considering that EF, PAS and AAY had a diet consisting of plant and animal foods (Brown, 1985; Henry, 1985). The statistically significant difference found between EF and the meat-eater MHG could be mainly associated to their distinct subsistence strategy. While the hunter-gatherer took advantage of the natural resources available in their surroundings, the gradual adoption of food production by EF determined the main diet for those populations (Bar-Yosef, 2011; Bowles and Choi, 2013).

This could also be supported by the findings of Oxilia et al. (2023) who found a correlation between dental wear and enamel thickness, which has been commonly thought to provide resistance to attrition (Macho and Spears, 1999; Molnar and Gantt, 1977; Pampush et al., 2013). In their study, Oxilia et al. (2023) analyzed the enamel thickness of lower molars based on the masticatory phases in a sample of Neolithic, Eneolithic and Bronze populations. Curiously, enamel placed over the Phase II and Lingual Phase I was thicker in Neolithic individuals and the pattern reverses towards more recent groups, where Buccal Phase I region increases its enamel thickness (Oxilia et al., 2023). This correlates with higher rates of macrowear giving an idea of the possible adaptative response of enamel to changing functional demands (Oxilia et al., 2023). The fact that EF present a higher development of Lingual Phase I and Phase II facets could be in concordance with previous research that found the crushing/grinding molar facets of MHG exhibit a great complexity, which has been frequently linked to the presence of a high number of abrasive particles into the food (El-Zaatari, 2010; El-Zaatari, 2014). Thus, the transition from hunter-gatherer societies to Neolithic full-scale agriculture and animal husbandry initiated during the Natufian times (Guerrero and Naji, 2008) could have determined macrowear pattern changes along with dental adaptations to emergent processing techniques (Belfer-Cohen, 1991; Henry, 1985; Maher et al., 2012; Oxilia et al., 2023; Rosenberg et al., 2021).

4.2. Eco-geographical variation between NEA and FHS

In Fiorenza et al. (2011a) study of upper molars, statistically significant differences were found between fossil specimens inhabiting different ecosystems, while no taxonomical difference between the wear pattern of NEA and FHS occupying similar environments were found. The present results on lower molars do not show an eco-geographic divergence, but they do describe differences between individuals of

Table 4
Pairwise comparison between fossil Biome groups, meat-eater modern hunter-gatherer (MHG), pastoralists (PAS), early farmers (EF), and Australian Aborigines from Yuendumu (AAY). One-way PERMANOVA based on relative areas (%) of Buccal Phase I facets, Lingual Phase I facets and Phase II facets. Significant p-values (<0.05) are highlighted in bold.

Group	MHG	PAS	EF	AAY
DEW	0.97	0.45	**0.02**	0.25
MED	0.73	0.81	0.15	0.59
SCF	0.06	0.76	0.06	0.21

NEA and FHS inhabiting the steppe/coniferous forest environment. In the study of Fiorenza et al. (2011a), the fossil sample belonging to the steppe/coniferous forest was associated with larger Buccal Phase I facet areas, resembling the wear patterns of meat-eater MHG group. We find greater values of Lingual Phase I facets for the NEA and FHS of steppe/coniferous forests. However, when we split the steppe/coniferous forest group into NEA and FHS, we observed statistically significant difference between the two species, as also noticed by Oxilia et al. (2020, 2023). The FHS display the greatest values for the Lingual Phase I facets in a pattern characterized by Lingual Phase I > Phase II > Buccal Phase I trend, compared to the pattern of NEA of Buccal Phase I > Lingual Phase I > Phase II tendency.

The chronology of almost the totality of fossil specimens assigned to the steppe/coniferous forest in this study places them during the Marine Isotope Stage 3 (MIS 3). MIS 3 (60-25 ka) (Huntley and Alan, 2003; van Andel and Davies, 2003), which was an interstadial period within the Last Glacial characterized by its climatic instability (Imbrie et al., 1984). Some studies have highlighted the importance of vegetable consumption during harsh environmental conditions in the Middle-Upper Palaeolithic (Hardy, 2010; Henry et al., 2011; Karriger et al., 2016; Mason et al., 1994; Pérez-Pérez et al., 2003; Williams et al., 2019, 2021, 2022). It has been suggested that Pleistocene populations heavily relied on the consumption of underground storage organs (USO) such as roots and bulbs, rich in carbohydrates and that were available year-round, helping them to meet the nutritional needs, especially during cold periods of time (Fiorenza et al., 2015). Hence, the presence of greater Lingual Phase I facets in the fossil sample associated to steppe/coniferous forest could be partially explained by the higher consumption of USO available in that ecosystem. Yet, it does not explain the difference in the wear pattern of NEA and FHS inhabiting the same steppe/coniferous forest ecosystem.

There are several opinions on how ecogeographic variability could have affected NEA's diet. While the studies of El-Zaatari et al., (2011, 2016) pointed at a higher consumption of plants with the increase in tree cover, Williams et al., (2019, 2021) found that MIS 3 NEA individuals inhabiting cold and arid environments (Spy I or Kůlna 1) also had diets largely based on coarse dietary items. This is also corroborated by the findings of phytoliths and starch grains in dental calculus of Spy I and Spy II (Henry et al., 2011). Krapina NEA, who have been associated to wooded ecosystems during MIS 5e (Rink et al., 1995; van Andel and Tzedakis, 1996), have also been linked to a high meat consumption, similar to that of Vindija NEA (Karriger et al., 2016), who habited steppe/coniferous environments during MIS 3 (Devièse et al., 2017; van Andel and Tzedakis, 1996). Thus, the broad dietary spectrum of NEA under varying environmental conditions make it difficult to assess the difference we found between their macrowear pattern and that of FHS from SCF only under the scope of diet, thus considering also processing techniques as another important factor around wear development (Smith, 1984; Watson, 2008). The FHS inhabiting SCF are related to the technologies from Aurignacian, typically taken as the spread moment of FHS during the Upper Paleolithic in Europe (Bailey et al., 2009; Bosinski, 2013; Conard and Richter, 2011; Fiore et al., 2001; Mussi et al., 2006; Nespoulet et al., 2013; Valletta et al., 2016). On the other hand, the FHS specimens from MED ecosystem are assigned to the Middle Paleolithic Mousterian stone tool industry (Shea and Bar-Yosef, 2005; Wolpoff, 1989), the same used by NEA (Hardy, 2004; Gravina and Discamps, 2015; Mellars, 2004; Patou-Mathis et al., 2018; Rocca et al., 2017; Trinkaus et al., 1999). Previous studies found correlation between the microwear pattern and the technological complex for Upper Palaeolithic modern humans, reaching to the interpretation that these human groups were able to culturally get over environmental constraints (El-Zaarati et al., 2016; El-Zaatari and Hublin, 2014). In fact, stone artefacts for plant processing have been considered by some as key elements in the development of Upper Paleolithic societies (Haws 2004; Stiner 2001, 2013) and the finding of starch grains, phytoliths and plant tissue fragments in their surfaces corroborate plant processing activities in Europe during Upper Paleolithic (Aranguren et al., 2007; Guan et al.,

2014; Revedin et al., 2015; Stepanova, 2020). Thus, considering that stone tools used for food processing could leave abrasive particles into the aliments (Bourdior and Mioche, 2000; El-Zaatari, 2008; Gügel et al., 2001; Kaidonis, 2008; Luke and Lucas, 1983; Lucas et al., 2013; Molnar, 1972; Organ et al., 2005; Rabinowicz and Mutis, 1965) and that facets linked to grinding processing movements are the most affected by wear when embedded exogenous particulates are present in the food (Krueger et al., 2008), our results could indicate that NEA and FHS from SCF during MIS 3 were exploiting natural resources differently. This could be reinforced by the fact that no differences have been found between NEA and FHS from MED environment, probably due to their shared used of Mousterian technocomplex.

The lack of statistically significant difference between NEA and FHS from SCF in Fiorenza and collaborators' study (2011a) could be linked to the reduce sample size (four NEA and five FHS) in comparison to this study (fourteen NEA and seven FHS). Moreover, the upper molars of SCF sample utilized by Fiorenza et al. (2011a) were mostly first molars, whereas a homogeneous set of first and second lower molar is considered in the present research. Although the morphological traits of both upper and lower first molars of FHS are broadly similar to that of NEA, the upper and lower second molars of FHS are characterised by a crown simplification compared to those of NEA (Bailey, 2006). Albeit no relationship between cusp height and macrowear pattern distribution has been previously reported (Fiorenza et al., 2011b), up to date and to our knowledge, there are no studies aiming to assess the effect of cusp number on the distribution of dental wear. Considering that it could be a variability factor, the fact that the current study employs both first and second molars for the SCF fossil groups could have revealed differences in the macrowear patterns. Previous studies have suggested that crown morphology, as well as the asymmetry of the masticatory systems, could be potential elements affecting the macrowear pattern distribution (Oxilia et al., 2018, 2020, 2023). However, we did not find any significant difference between first and second mandibular molars in the NEA from Krapina. Due to sample size limitations we could not test if there are any wear pattern differences between first and second molars in the other human groups considered in this study. Consequently, future studies could look at the anatomical aspect of the molar crowns of NEA and FHS by using a larger sample size.

It is also interesting to note that while the macrowear patterns of EF differs significantly (or close to) with those of human fossil groups inhabiting cold and temperate environments, it resembles more those of NEA and FHS living along Mediterranean costliness during warmer periods of time. This is also observable when comparing the AAY wear pattern to that of Mediterranean fossils. This could be due to the intake of plant and animal foods, as also indicated by lack of statistically significant difference with the mixed-diet hunter gatherers, but also by both living in arid and sandy environments (Fiorenza et al., 2018).

From the results of this study, it seems unlikely that the dietary diversity of FHS would have conferred a selective advantage over NEA by increasing their reproductive success (Hockett and Haws, 2003, 2009; O'Connell, 2006). The similarities in the macrowear values for NEA and FHS belonging to DEW and MED ecosystems that we found offer a new argument in favour of a varied diet for both human groups. Far from the traditional perception of NEA focusing their subsistence on large mammal exploitation (Bocherens et al., 2005; Richards and Trinkaus, 2009), these human groups would have been able to exploit a great variety of food resources available in their diverse ecological contexts (Hardy et al., 2012; Henry et al., 2011; Naito et al., 2016; Salazar-García et al., 2013, 2018, 2021).

Finally, it is important to highlight some limitations in this current study. Exploring the dental wear patterns of upper and lower molars taken from the same individual and from different populations will shed light into the potentially asymmetrical relationship between wear of antagonistic teeth and its variation among different human populations (Oxilia et al., 2018). Moreover, because of inter-individual differences between first and second lower molars in modern humans (Hlusko,

2002), studies counting on a wider sample of a single molar type would decrease the variability to better classify the possible factors triggering the wear pattern development. In relation to this, and following the study of Fiorenza et al. (2011b), where the relation between cusp height and dental wear was ruled out for upper molars, a similar study for lower molars would be beneficial to better understand the chewing cycle mechanism. Another important aspect to consider is that the use of large comparative groups with known diets and known cultural habits permits to obtain a better characterization of the dental macrowear patterns of past human populations. However, creating a robust comparative sample can be limited by the access to the collection or by the requirements imposed by the methodology (in this case whole crown preservation and moderate level of wear). The comparative modern human sample of this study is relatively small and heterogeneous. In addition, detailed information about the location of some individuals is often missing. For these reasons, our conclusions should be taken with caution. Counting on larger, homogeneous and exhaustively documented comparative sample would allow to create groups of enough individuals from the same chronology, surviving under the same climatic conditions, exploiting similar food resources dependent on the same ecological diversity and that were organized in the same economic systems. This would allow a precise relationship between diet, macrowear and cultural habits. Moreover, due to current limitations in the OFA method, which is restricted to the use of slightly to moderately worn teeth, we could not investigate if wear pattern differences associated to diet can be detected in individuals characterized by heavy occlusal wear. It would be interesting to examine how molar macrowear patterns change according to the level of wear (Fiorenza et al., 2023).

In relation to the fossil sample, their fragmentary nature does not allow us to create larger groups from the same chronological period. Although this problem is difficult to overcome when dealing with fossil remains, it constitutes a variability factor that needs to be considered. It is also important to note that this methodology is not effective in distinguishing dietary diversity within the same food type. Macrowear analyses cannot differentiate between the intake of marine and terrestrial animals, neither between large and small preys (Fiorenza et al., 2015). Moreover, the human tooth micro- and macrowear patterns are significantly influenced by the food processing techniques (El-Zaatari, 2008; Fiorenza et al., 2018; Molnar, 1972; Watson et al., 2013), because they alter the physical and textural properties of foods. Therefore, the combination of the results coming from macrowear studies along with those obtained from isotopic and dental calculus analyses, and together with dietary and ecological data derived with other methods (Fiorenza et al., 2015) would provide a better understanding of past human population's diet.

5. Conclusions

Our study has shown that the examination of macrowear patterns of mandibular molars can be used to distinguish populations characterized by broader dietary differences such as hunter-gatherers and early farmers. However, we were not able to detect dietary differences at a finer scale in the modern hunter-gatherer group. In the same way, we did not find eco-geographic differences in the fossil sample. On the other hand, Neanderthals and early *Homo sapiens* inhabiting the steppe/coniferous forest environment differ in their macrowear patterns. It is possible that these groups used the food resources in a different way, probably because of their different lithic industry. This interpretation is further reinforced by the lack of difference found between Neanderthals and early *Homo sapiens* from the Mediterranean environment, since both groups are associated with the Mousterian lithic technology. Also differences in occlusion conditions influenced by crown morphology and the asymmetry of the masticatory apparatus could be behind the divergence of the macrowear patterns in different human groups. In addition to this, the analysis of a wider, single molar type of restricted wear stage sample would be recommendable in order to better assess the utility of lower molars to provide information about diet and cultural living strategies. More individuals of the same chronology and from the same geographical distribution would assist in the understanding of specific dietary adaptations, considering that Neanderthals lived in Eurasia in a moment of great climatic variations, which most likely affected their survival strategies.

Data availability statement

Most of the 3D models of the specimens used in this study are available at 10.17632/g8p46cw7j4.1. Access to the Australian Aboriginal sample is more restricted and interested researchers should contact Luca Fiorenza, who created all the 3D models (email address).

CRediT authorship contribution statement

María Hernaiz-García: Formal analysis, Methodology, Writing – original draft. **Gregorio Oxilia:** Formal analysis, Methodology, Writing – review & editing. **Stefano Benazzi:** Writing – review & editing. **Rachel Sarig:** Writing – review & editing. **Jing Fu:** Writing – review & editing. **Ottmar Kullmer:** Writing – review & editing. **Luca Fiorenza:** Conceptualization, Funding acquisition, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

There are no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2024.105950.

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