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Evaluating a dentin exposure proxy for wear rates estimations on mesolithic and neolithic populations from the near East and the Iberian Peninsula: A comparative analysis

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ABSTRACT

A new statistical proxy of analyzing dentin exposure rates of molar teeth, proposed as a reliable indicator for inter-population comparisons, was tested in relation to dietary habits and socioeconomic practices in ancient human populations from Mesolithic and Neolithic periods in the Near East and the Iberian Peninsula (Portugal and Spain) with distinct patterns of food production and ecological constraints. The comparisons of wear rates among groups provided distinct regressions models consistent with previous dietary hypotheses, independently from the age distribution of specimens within the samples. We found clear trends in wear rates among time-periods and socioeconomic practices. Dentine exposure rates between molar eruption ages showed higher values for the Mesolithic, mainly hunter-gatherer populations than the Neolithic, agriculturalist ones. The modern and contemporary samples showed the lowest wear rates, while the Natufian specimens showed dentin exposure rates more closely resembling the posterior Neolithic than the contemporaneous Mesolithic samples from the same geographical area. Overall, the 3D dentin exposure rates proxy allowed the comparison of archaeological, scarcely represented samples, offering clear insights into hypotheses testing in relation to dietary habits, lifestyle shifts through time, or ecological constraints in the transition from a predominantly hunting and gathering lifestyle to a settled, agriculture-based Neolithic society.

1. Introduction

Ecological constraints and socioeconomic practices have significantly influenced human diets, leading to variations in dental wear rates across past populations (Smith 1984, Oxilia et al. 2018). During the Natufian period in the Near East, a warm and stable climate enabled a diet heavily reliant on wild nuts, cereals and legumes, which included hard, minimally processed foods, potentially causing significant dental wear due to the abrasiveness of the grains (Mahoney 2006). The subsequent Neolithic revolution in the Levant brought about agricultural advancements and the domestication of plants and animals, leading to a more varied diet and softer foods (Shavit & Sharon 2023). The same dietary changes arrived to Europe later (Araus et al. 2024), eventually also reducing dental wear. In modern times, the evolution of food processing technologies, such as refined milling techniques and the introduction of processed and cooked foods, significantly decreased dental wear rates. Overall, ecological and climatic changes have driven shifts in diet and dental health, from the abrasive, unprocessed foods of early agricultural societies to the more refined and less wear-inducing diets of contemporary populations (Alday 2012; Pérez & Arribas 2013).

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2. Cultural and ecological transitions

2.1. The near East Natufian and Neolithic populations

The Natufian period in the Levant, ca. 13,000-9,600 BCE, occurred during a time of significant climatic instability at the end of the last Ice Age (Richter et al. 2017). As the climate warmed and ice sheets retreated after the Younger Dryas (10,900–9,700 BCE), the Levant featured dryer environments, with expanding oak (Quercus calliprinos) and pistachio (Pistacia lentiscus) woodlands and wild cereals like barley (Hordeum vulgare ssp. spontaneum) and emmer wheat (Triticum dicoccum), crucial to the Natufian diet (Henry 1989). The abundance of resources supported a semi-sedentary lifestyle, with communities likely moving seasonally to exploit different resources, leading to the development of more permanent settlements (Richter 2017; Weide et al. 2018). Abu Hureyra in modern-day Syria, although outside the Levant, provides a continuous record of human occupation from the Epipaleolithic (15,000-9,600 BCE) to the Pre-Pottery Neolithic (9,600-5,800 BCE) period (Smith et al. 2022). Initially, a seasonal settlement reliant on hunting gazelles (Gazella dorcas) and gathering wild cereals, the site reflects a broader transition to agriculture similar to the Levant. By 9,500 BCE, Abu Hureyra had evolved into a more permanent settlement with mud-brick houses and increasing reliance on domesticated crops and animals, indicating a shift from foraging to agriculture (Smith et al. 1984). The main domestic plants were emmer and einkorn wheat (Triticum monococcum), barley (Hordeum vulgare), peas (Pisum sativum), and lentils (Lens culinaris). Among animals species, sheep (Ovis aries), goat (Capra aegagrus hircus), and eventually cattle (Bos taurus) and pigs (Sus scrofa domesticus) were present. Climatic conditions at Abu Hureyra, like those in the Levant, became more stable and warmer post-Younger Dryas, promoting plant growth and animal life. The Euphrates River, enabling a diverse range of plant and animal resources, although less forested, sustained the region's semi-arid steppe environment. Both regions saw a shift towards semi-sedentary lifestyles and early plant domestication, laying the groundwork for agriculture (Bar-Yosef 1998; Smith et al. 2022).

In the Near East, the Neolithic Revolution marked a crucial shift to settled agricultural communities, driven by the more stable and warmer climate of the Holocene epoch around 9,600 BCE. Increased precipitation expanded vegetation zones, including grasslands and forests, which provided abundant food resources for early Neolithic communities. The Euphrates and Tigris river valleys offered fertile floodplains ideal for early agriculture, with wild crops gradually becoming the basis of cultivation. Alongside plant domestication, the period saw the full domestication of sheep, goats, and cattle, supporting the sedentary lifestyle of these communities. During the Pre-Pottery Neolithic B (PPNB) period in Syria (Akkermans 2004), large, permanent settlements with well-constructed buildings and communal spaces emerged, reflecting the shift to a more settled way of life. This transition brought significant social changes, including complex hierarchies, trade networks, and communal organization. The ability to store surplus food spurred population growth and larger communities. As agriculture became central, Neolithic communities modified the landscape through practices like forests clearing, irrigation, and terracing, which eventually led to environmental challenges, such as soil depletion and deforestation (Akkermans & Schwrtz 2003).

2.2. The Mesolithic to Neolithic transition in Europe

The transition from hunter-gatherer societies to agriculture in Europe shares some broad similarities with the Natufian–Neolithic transition in the Near East but also reveals key differences in climate, ecology, and cultural developments. Both regions experienced significant climatic changes, leading to warmer, more stable conditions that expanded forests and grasslands, increasing food availability. However, agriculture began much earlier in the Near East during the Natufian

period, transitioning into the Neolithic by 9,000 BCE. In contrast, Europe's Mesolithic period persisted longer, with agriculture emerging around 5,500 BCE in Iberia. This shift in Europe was gradual and less uniform, involving interactions between indigenous Mesolithic huntergatherers and incoming Neolithic farmers from the Near East (Bicho et al. 2017). While Natufian sites show early plant cultivation and permanent structures, Mesolithic European sites generally do not. Agriculture in the Near East involved local domestication, whereas in Europe, migrating Neolithic populations introduced it. Mesolithic adaptations in the Iberian Peninsula reflect diverse environmental contexts. The Portuguese sites of Sado and Muge relied heavily on riverine and estuarine resources (Bicho et al. 2010; Bicho et al., 2013), similar to how Natufian sites exploited the Levantine corridor's resources. These coastal and river estuary locations offered abundant aquatic resources like fish, shellfish, and waterfowl, supporting more permanent settlements. In contrast, the Mesolithic site of La Oliva in Spain, despite also having evidences of shell middens, focused more on terrestrial resources within a continental environment (Gibaja et al. 2017a). This area, characterized by a mosaic of forests and grasslands, supported game animals like red deer (Cervus elaphus) and wild boar (Sus scrofa), which were vital for subsistence, highlighting a more mobile, hunting-focused lifestyle (Cubas et al. 2016; Zilhão 2001).

Neolithic settlements in the Iberian Peninsula and the Near East share the broad transition from hunter-gatherer to agricultural communities but differ significantly due to distinct ecological contexts. Near Eastern Neolithic settlements, concentrated in the Fertile Crescent, benefited from a Mediterranean climate and the fertile alluvial soils of the Tigris and Euphrates rivers, ideal for crop cultivation. In contrast, the Iberian Peninsula featured varied topography and climates, from Mediterranean coastal areas to cooler, wetter interiors. Agriculture arrived in Iberia around 5,500-5,000 BCE, influenced by migrating Neolithic farmers. Iberia's ecological diversity led to regional variations in Neolithic adaptations, with coastal areas adopting farming more readily than the challenging interior landscapes. Unlike the irrigationbased agriculture of the Near East, Iberian farming was mostly rainfed, limiting agricultural scale in some regions. While Iberian Neolithic settlements were near fertile land or rivers, they did not reach the size and complexity of those in the Near East (Alday Ruiz 2012).

The diet of post-Neolithic populations in Western Europe was more complex and varied than that of Neolithic societies, involving significant dietary changes due to advances in agriculture, food processing, and external influences from trade and conquest. By the Early Medieval period, 6th–11th centuries CE, agriculture provided a highly diverse diet (McClatchie et al. 2015) that included various grains (wheat, barley, rye), vegetables (onions, garlic, leeks), and fruits (apples, pears), and continued consumption of meat, dairy, and eggs. Improved food processing techniques, such as using mills for finer flour, led to softer bread and more palatable foods, and preservation methods like salting, smoking, and drying allowed for food storage and contributed to a more refined diet compared to the coarser, harder textures of the Neolithic diets (Pérez & Arribas 2013).

2.3. Dental wear and diet

Dental wear is a classical indicator of diet and lifestyle in ancient populations (Petraru et al. 2022), revealing insights into food consumption, preparation methods, and health of ancient communities (Molnar 1971; Molnar et al. 1983; Scott & Turner 1988), as well as nondietary activities (Lukacs & Pastor 1988). The study of molar wear is crucial in bioarchaeology, offering a window into human adaptation to environmental and climatic conditions (Smith 1984; Walker and Erlandson, 1986). Dental wear is also an age-dependent process (Maat, 2001), involves enamel and dentin removal due to mechanical actions driven by dietary abrasiveness (Kaifu et al. 2003; Hilson et al. 2005; Romero et al. 2019). This wear results from various mechanisms (Kaidonis 2008): attrition (tooth-to-tooth contact), abrasion (tooth-tofood contact with abrasive particles like silica phytoliths), and *erosion* (chemical demineralization) (Smith & Knight 1984). These processes vary depending on diet and chewing activities, creating distinct wear patterns (Kaidonis et al. 2012). Wear is not uniform across teeth, with variation influenced by tooth morphology, function, and eruption sequence, particularly in molars. Dental wear affects not just tooth conservation during lifetime but also life-history patterns, such as tooth loss and bone resorption (Hillson 1996; Hillson et al. 2005).

The dual nature of dental wear, being both age- and diet-dependent, as well as affected by extra-masticatory use (Walsh 2022), complicates the interpretation of occlusal dentin exposure rates, as these measures are influenced by the age distribution of archaeological samples (Molnar 1971; Górka et al. 2015; Vieira et al., 2015). In contrast, Yang et al. (2024) propose a 3D dentin exposure proxy, applied to Neolithic to Bronze Age Chinese populations, that allows inter-population comparisons independent of age distributions. The significance of this proxy lies in its applicability to samples with unknown age distributions.

The goal of this research is to test the 3D dentin exposure proxy's effectiveness in characterizing the shift from hunter-gatherer to agricultural practices in the Near East and Iberian Peninsula. The study aims to analyze regional discontinuities in dietary practices during the Mediterranean transition from forager to agriculture. A reliable measure of molar wear rates would help characterize dietary and lifestyle shifts accompanying the Neolithic revolution, using skeletal populations with distinct diets and socioeconomic practices from Epipaleolithic to Neolithic periods (Eshed et al. 2006).

3. Materials and methods

3.1. Study sample

We reviewed dental cast collections from Mesolithic and Neolithic populations in the Iberian Peninsula and the Near East (Fig. 1), housed at the *Universitat de Barcelona* (UB) and the *Universitat Autònoma de Barcelona* (UAB). These cast collections were gathered through research collaborations and projects on dental wear coordinated by Dr. A. Pérez-Pérez (UB) and Dr. M. E. Subirà (UAB). For comparative purposes, we also analyzed dental casts of two modern samples: an Early Medieval sample from Catalunya (Spain), 6–11th c. CE, and a contemporary skeletal collection from Coimbra (Portugal), 18–19th c. CE. This research was part of various national and international archaeological and anthropological projects led by Dr. S. Carrascal, Dr. A. Malgosa, and Dr. M. Molist from UAB; Dr. B. Chamel and Dr. E. Coqueugniot (*Maison de l'Orient et de la Méditerranée*, Lyon); and Dr. C. Umbelino (*Universidade de Coimbra*, Portugal).

The skeletal sample studied (Table 1) included 323 individuals (N_i) with 1,674 M teeth (Nt). We analyzed molar quadrant, irrespective of side (left or right) or jaw (maxilla or mandible). Molar quadrants with dental crown damage or pathologies like carious lesions were excluded, resulting in a final sample of 544 quadrants (N_a) with 930 M teeth (N_{at}). Selection criteria for including a molar quadrant followed Yang et al. (2024). A quadrant had to include a first molar with dentin exposure, with other molars either showing patches of dentin exposure or not yet erupted. Molars without dentin exposure were recorded as having zero exposure areas. Unidentifiable or missing molars (lost ante-mortem or post-mortem) were excluded. Due to poor preservation in some archaeological samples, analyzing multiple molar quadrant per individual increased the available sample size from 323 individuals to 544 quadrants, though it reduced the available molar sample from 1674 to 930. Final sample sizes varied by site, making site-specific comparisons impractical. Therefore, samples were grouped by geographic areas and periods, resulting in seven groups.

3.2. Portuguese Mesolithic

The Mesolithic sample from Portugal included 123 quadrants with

246 M teeth from two closely related shell middens, Sado and Muge, located on riverbanks and dating to the Mesolithic period (5,400–3,900 BCE) (Meiklejohn et al. 2009; Bicho et al. 2010; Bicho et al., 2013). The Sado Valley sample, originating from shell middens (Arapouco, Cabeço das Amoreiras, Cabeço do Pez), was initially excavated between 1960 and 1962 near Lisbon. However, this sample was limited (N_i = 10 individuals, N_q = 20 quadrants), with most quadrants (N_q = 14) coming from Cabeço do Pez. In contrast, the Muge Complex in the Tagus Valley (Cabeço da Amoreira, Cabeço da Arruda, Moita do Sebastiao) was better represented, with 103 quadrants, most of which came from Moita do Sebastiao (N_q = 79). Cabeço da Arruda was discovered in 1863 by Portuguese archaeologist Carlos Ribeiro, while the other two sites, Cabeço da Amoreira and Moita do Sebastião were identified one year later, in 1864.

3.3. Spanish Mesolithic

The Mesolithic sample from Spain included 28 quadrants with 54 M teeth. The El Collado in Oliva, Valencia (Spain), initially excavated between 1987 and 1988, dates to 6,630–6,250 BCE (Gibaja et al. 2015, 2017a). Fourteen burials were unearthed across a 143 m^2 area, yielding 21 quadrants with 40 M teeth. The site's dating has been debated (Hernández Pérez & Soler Mayor 1997; Bernabeu Aubán & Orozco Köhler 1991). The La Braña site, located in Valdelugueros, León (Spain), dates to 5,900–5,650 BCE (Vidal Encinas et al. 2010). Excavated by Vidal Encinas after its discovery in 2006, the site revealed two Mesolithic burials (LB-1 and LB-2) from the La Braña-Arintero Cave, providing 7 quadrants with 14 M teeth.

3.4. Spanish Middle Neolithic

The Spanish Middle Neolithic sample consists of 83 quadrants with 162 M teeth from eleven sites in Catalunya, northeast Spain, dating between 4,694 and 3,294 cal. BCE. Among these, 25 quadrants are from Puig d'en Roca (Maroto & Soler 2000), and 19 are from Sant Pau del Camp (Molist et al. 2012). The remaining Neolithic sites, with fewer individuals, included numerious sites: Can Gambús (Masclans 2017; Gibaja et al. 2017b), Mines de Gavà (Villalba et al. 1986; Bordas et al. 2009), Ca l'Estrada (Subirà et al. 2015), Camí de Can Grau (Pou et al. 1995), Can Roqueta II, 4,230–3750 cal. BCE (Oliva et al. 2008; Fontanals-Coll et al. 2015), Hort de Can Torras, 3607–3522 cal. BCE (Coll & Roig 2005; Fontanals-Coll et al. 2015), Pantà de Foix (Cebrià et al. 2013), Pla del Riu (Guitart 1987), and Segudet (Yáñez de Aldecoa 2003) (Table 1).

3.5. Near East Natufian / Epipaleolithic

Key Natufian sites in Israel include Mugharat El-Wad ($N_q = 16$), on Mount Carmel, dating from 11,000 to 8,730 cal. BCE (Weinstein-Evron 1991), and Me'arat Kebara ($N_q = 7$), dating from 12,550 to 11,050 cal. BCE (Arensburg & Belfer-Cohen 1998). The Shuqba Cave site ($N_q = 3$), in the West Bank, Palestine, dates from 12,500 to 9,500 cal. BCE, and was the first identified Natufian site showing the transition from mobile to sedentary lifestyles (Weinstein-Evron 2003). Tell Abu Hureyra ($N_q =$ 3), in Syria, dating from 11,500 to 10,500 cal. BCE, shows phases reflecting the shift from hunting and gathering to agriculture, though it is outside the core Natufian region (Akkermans & Schwartz 2003). Abu Hureyra, while not a Natufian site, is included for its parallel early agriculture development. The final Near East Natufian/Epipalaeolithic sample included 29 quadrants with 66 M teeth from these four sites.

3.6. Near East Pre-Pottery Neolithic B

The PPNB (Pre-Pottery Neolithic B) samples from Syria included 31 quadrants with 47 M teeth from four sites. Excavations at Dja'dé El Mughara ($N_q = 6$), dating from 8,800 to 8,000 cal. BCE, located in



Fig. 1. Geographic location of the Mesolithic and Neolithic sites studied in the Iberian Peninsula (top) and the Near East (bottom)-Natufian, Mesolithic and prepottery site locations indicated with a lithic tool, and Neolithic site locations shown with a pottery amphora.

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Table 1

Samples studied from Mesolithic and Neolithic periods in the Iberian Peninsula (Portugal, Spain) and the Near East (Syria, Israel, West Bank Palestine). Site names, chronology, geographic location, and repositories (Rep.) of the cast collection (UB, UAB) are indicated. Numbers of the individuals analyzed (N_i), molar teeth available (N_t), molar quadrants selected (N_q), and teeth studied in the selected quadrants (N_{qt}) are provided.

Chronology	$\mathbf{N_i}$	Nt	$\mathbf{N}_{\mathbf{q}}$	$\mathbf{N}_{\mathbf{qt}}$
1. Portugal Mesolithic	67	314	123	246
Sado, 5000 BCE	10	54	20	40
Arapouco	2	8	3	6
Cabeço das Amoreiras	1	3	1	1
Cabeço do Pez	5	37	14	29
Sado	2	6	2	4
Muge, 5400–3900	57	260	103	206
Cabeço da Amoreira	3	11	4	8
Cabeço da Arruda	17	85	34	57
Moita do Sebastiao	37	172	79	141
2. Spain Mesolithic	14	78	28	54
El Collado, Valencia, 6630-6250 BCE	12	58	21	40
La Braña León, 5900–5650 BCE	2	20	7	14
3. Spain Middle Neolithic (Catalunya)	49	251	83	162
Ca l'Estrada, 4694–4491 BCE	1	6	2	4
Camí Can Grau, 3800–3500 BCE	2	12	4	8
Can Gambús-1, 3766-3356 BCE; CG-2, 3200-23300 BCE	5	18	6	14
Can Roqueta, 4310–4220 BCE	3	24	8	17
Horts de Can Torras, 3698–3620 BCE	3	27	9	17
Mines de Gavà, 3400–2360 BCE	1	3	1	2
Pantà de Foix, 3620–3294 BCE	2	6	2	3
Pla del Riu, 4038–3640. BCE	2	12	4	9
Puig d'en Roca, 4045–3642 BCE	9	75	25	44
Segudet, 4320–4050 BCE	1	9	3	6
Sant Pau del Camp, 4250–3700 BCE	20	59	19	38
4. Near East Natufian / Epipaleolithic	24	68	29	66
Tell Abu Hureyra, Syria, 11500–10500 cal. BCE	3	6	3	6
Mugharat El-Wad, Israel, 11000–8730 cal. BCE	13	40	16	40
Me'arat Kebara, Israel, 12550–11050 cal. BCE	6	16	7	14
Shuqba, West Bank Palestine 12500–9500 cal. BCE	2	6	3	6
5. Near East PPNB Neolithic (Syria)	31	47	31	47
Dja'dé el Mughara, 8800–8000 cal. BCE	6	14	6	14
Tell Aswad, 8700–7500 cal. BCE	5	9	5	9
Tell Halula, 7800–6300 cal. BCE	4	5	4	5
Tell Ramad, 7230–6800 cal. BCE	16	19	16	19
6. Spain Early Medieval, Accés Est Casserres, Catalunya, V-XI ACE	52	295	126	188
7. Coimbra Portugal contemporary, XIX-XX ACE	86	621	123	167
	323	1674	544	930

northern Syria on the Euphrates River's eastern bank, revealed evidence of wild plant use, hunting, and early cereal cultivation (Coqueugniot 2000, 2011). Tell Ramad site, dating from 7,230 to 6,800 cal. BCE (Ferembach 1969) is the most represented site ($N_a = 16$), situated near the Diyala River in eastern Iraq. It revealed early agriculture, including domesticated two-row barley (Hordeum vulgare) and einkorn wheat (Triticum monococcum), alongside circular mudbrick structures, storage pits, and distinct pottery, making the transition to settled agricultural communities. Tell Aswad ($N_q = 5$), dating from 8,700 to 7,500 cal. BCE (Stordeur 2003; Stordeur & Abbès, 2002), located 30 km northeast of Damascus, Syria, uncovered circular mudbrick houses, storage pits, and artifacts such as stone tools and pottery. It is notable for its early evidence of domesticated emmer wheat (Triticum dicoccum) and barley. Tell Halula ($N_q = 4$), dating from 7,800 to 6,300 cal. BCE (Aurenche 2005; Estebaranz-Sánchez et al., 2007), in the middle Euphrates valley, Syria, is one of the largest known Neolithic sites. Excavations, led by Dr. Miquel Molist revealed early agricultural practices, domestication plants like wheat, barley, and flax (Linum usitatissum), and domesticated animals including cattle, sheep, and goats (Akkermans 2004). Despite the extensive human remains uncovered (Estebaranz-Sánchez et al., 2007), very few quadrants were preserved.

3.7. Spanish Early Medieval and Portuguese contemporary comparative samples

The Spain Early Medieval site of *Accés Est Casserres* (Berguedà, Catalunya, Spain), dating from the 6th to the 11th century CE, served as a comparative collection. This period encompasses the arrival of the Visigoths and the conflicts between the Franks and the Muslims (Carrascal 2021). By 2021, 211 individuals from 184 burials had been documented at this site, and the sample analyzed included 126 quadrants with 188 M teeth. A modern sample was sourced from the Portuguese Coimbra International Exchange Collection, dating from the 18th to 19th centuries (Cunha & Wasterlain 2007). Housed at the University of Coimbra, this collection constitutes of skulls with documented sex and age at death, making it invaluable for anthropological and forensic research, including comparative skeletal anatomy, pathology, population genetics, and forensic anthropology; Yang et al. (2024) previously examined the molar dentin exposure of the lower dentition in this sample. The current study extends that analysis to include the upper dentition; the final sample consisted of 123 quadrants with 167 M teeth of 86 individuals, with evenly represented age groups ranging from 6 to 90 years old.

3.8. Sample processing and analysis

Prior to this research, we had already molded the molar quadrants using ColténeTM Affinis regular body (UB) and 3MTM light-body polyvinylsiloxane (UAB) materials, adhering to standardized protocols (Galbany et al. 2006). High-resolution casts of the complete dental crowns in each molar quadrant were made using polyurethane Feropur PR55 (FerocaTM, Spain). The dental casts were digitized with a 3D EinScan SP scanner (ShinningTM) from occlusal, buccal, and lingual views, using *non-texture* mode with eight captures per scan at 45° angles.



Fig. 2. 3D point-cloud meshes (bleu) of selected specimens from the archaeological sites analyzed; the measured dentin exposure surfaces are shown in red. All specimens correspond to lower, left quadrants: upper row, 1. Arapouco 1A P4-M3; 2. Cabeço do Pez 62518 P3-M3; 3. Cabeço d'Arruda 81.19.103 I1-M3; 4. El Collado 20.14 I1-M3; 5. La Braña 2 P4-M3; 6. Puig d'en Roca 14 I1-M3; 7. Can Gambús 137 P4-M3; lower row, 8. El Wad 153 P4-M3; 9. Abu Hureyra 11 P3-M3; 10. Dja'dé 77 M1-M3; 11. Accés Est Casserres 88 P4-M3; 12. Accés Est Casserres 22 P4-M3; 13. Coimbra 370 P3-M3; 14. Coimbra 433 P3-M3. The meshes are not all at identical scales. The red colored surfaces show dentin-exposed areas on the occlusal surfaces of the molar teeth indicaive of the measured surfaces with the Shinning software.

The 24 scans were then automatically fused into a single point-cloud mesh model, with a slightly smoothing filter applied to remove outliers. The meshes were exported in polygon (.ply) and ASCII object (.obj) file formats.

Dentin exposure areas (in mm^2) were measured directly from the 3D meshes (Fig. 2) using the Shinning software's *measure* mode. The software automatically calculated the total dentin exposed area (D) for each tooth by summing the surfaces of all defined patches on the occlusal plane. For molars without dentin exposure or those not yet erupted, D was recorded as zero. Additionally, for each molar, we calculated the sum of the dentin exposure areas of all characterized molars in the quadrant, denoted as $S = D_{M1} + D_{M2} + D_{M3}$. Quadrants with unmeasurable dentin exposure were excluded from the analysis. This method ensured that all M1 teeth included in the study exhibited some degree of dentin exposure ($D_{M1} > 0$), while M2 and M3 could have zero exposure if no dentin was exposed or the tooth had not yet erupted (Yang et al., 2024).

3.9. Statistical approach

We tested various regression models (Linear, Quadratic, Compound, Power) to determine which best predicted the overall dentine exposure area (S) from the dentin exposure (D) of each molar. The slope (*b*) of each regression indicated the rate of S accumulation as D increase, while the intercept (*a*) represented the S value when D was zero. The coefficient of determination (\mathbb{R}^2) was used to assess the precision of the models, indicating the percentage of total variance explained. The ANOVA F statistic and its significance (*P*) were employed to compare the models.

The slope comparisons between samples and groups were conducted using a *t*-test (Equation (1), with degrees of freedom (*d.f.*) equal to $n_1 + n_2$ -4. The *P* value was derived from the two-tail *t* distribution, computed as P = T.DIST.2 T(t, d.f.) in MS-EXCEL.

$$t = \frac{ABS(b_1 - b_2)}{\sqrt{SE_{b1}^2 + SE_{b2}^2}}$$
(1)

Slope comparisons were made by molar between mandibular and maxillary quadrants within each group, and between groups for the combined samples of upper and lower molars. All statistical analyses were performed using IBM SPSS v. 27 (licensed to UB), with the significance level set at $\alpha < 0.05$.

3.10. Dentin exposure rates

As described by Yang et al. (2024), we used the regression model intercepts to estimate the wear rates of each molar quadrant during the intervals between the onsets of dentin exposure for each molar. Molar eruption ages for modern *Homo sapiens* were taken from Ash & Nelson (2003)—5.5 years for M1, 11.5 years for M2, and 18.5 years for M3—to compute the lengths of the M1–M2 juvenile interval (6 years) and an M2–M3 subadult interval (7 years). While variations in molar eruption ages exist (Gilmore & Grote, 2012), these differences are of little relevance if the intervals between eruption ages remain consistent across modern humans populations. Therefore, we applied the same intervals across all samples: 6 years (5.5 to 11.5 years) for the juvenile interval,

Table 2

Basic statistic of 3D dentin exposure by site. Dentin exposure by site and tooth type (M1, M2, M3) for the combined samples of upper and lower quadrants. N: sample size; mean: average of the 3D dentin exposure (D) in *mm*²; s.d.: standard deviation of D.

		M1		M2				М3	
Site	Ν	mean	s.d.	N	mean	s.d.	Ν	mean	s.d.
Accés Est Casserres	112	17.891	17.974	54	13.431	15.745	22	10.990	10.413
Arapouco	2	33.395	18.901	2	31.530	9.687	2	7.910	4.285
Ca l'Estrada	2	20.200	4.186	2	3.370	1.810	_	_	_
Cabeço da Arruda	31	35.181	25.961	19	26.671	21.622	7	26.420	27.962
Cabeço das Amoreiras	5	42.016	28.349	2	45.580	3.239	2	2.434	0.245
Cabeço do Pez	14	34.645	21.697	11	15.656	11.184	4	9.505	14.305
Camí Can Grau	4	22.170	6.668	3	1.213	0.199	1	0.680	_
Can Gambús 1 & 2	6	31.161	25.889	5	20.812	19.324	3	7.340	3.027
Can Roqueta	8	36.127	19.602	7	4.403	3.255	2	1.555	0.686
Coimbra	123	6.890	9.312	38	3.953	5.312	6	3.216	3.006
Dja'dé el Mughara	6	74.590	7.345	6	54.237	15.889	2	12.175	9.907
El Collado	21	30.434	28.670	14	17.452	19.006	5	8.894	6.635
Horts de Can Torras	9	17.490	14.221	5	5.866	5.453	3	2.480	1.621
La Braña	7	40.500	13.727	5	10.238	12.065	2	0.643	0.067
Me'arat Kebara	7	8.623	4.462	5	1.886	1.882	2	1.425	0.488
Mines de Gavà	1	30.530	-	1	2.860	-	_	-	-
Moita do Sebastiao	70	39.226	18.979	58	13.540	12.084	13	5.539	8.790
Mugharat el-Wad	16	39.125	15.926	16	17.164	15.095	8	10.954	8.552
Pantà de Foix	2	8.940	3.606	1	3.160	_	_	-	_
Pla del Riu	4	31.898	24.874	3	30.393	26.693	2	8.685	0.700
Puig d'en Roca	25	17.130	9.795	16	6.455	3.981.	3	4.053	5.072
Sado (unspecified)	2	28.880	5.869	2	4.555	0.276	_		
Sant Pau del Camp	19	25.241	17.331	14	6.359	7.055	5	2.198	1.348
Segudet	3	27.810	5.080	3	6.160	3.475	_	-	-
Shuqba	3	62.750	36.426	3	37.240	24.819	_		_
Tell Abu Hureyra	3	28.807	22.211	3	4.946	3.957	_	-	-
Tell Aswad	5	26.088	22.788	3	12.067	9.001	1	4.420	-
Tell Halula	4	9.910	6.448	1	3.150	_	_	_	-
Tell Ramad	16	10.821	10.676	3	1.200	0.641	-	-	-

and 7 years (11.5 to 18.5 years) for the subadult interval, acknowledging that the M3 may erupt later in present-day humans.

Yang et al. (2024) computed two dentin exposure rates for these intervals: a direct wear measure, calculated as $(S_1 - S_2)/t$ in $mm^2/year$, and a relative dentin exposure rate (r) as shown in Equation (2). This per-one rate, representing growth (r > 0) or decay (r < 0) of S, was calculated per month rate, with t being the number of years in the age interval and n the number of intervals within a year (n = 12 for monthly calculations). Equation (2) derives from equation (3), the continuous compound growth rate function.

$$r = \frac{\ln(S_1) - \ln(S_0)}{nt} \tag{2}$$

$$\mathbf{S}_1 = \mathbf{S}_0 e^{-mt} \tag{3}$$

Although non-continuous, compounded exponential growth is commonly used in social sciences to estimating storage and investment benefits (Connolly et al. 2001; Hember et al. 2012), it tends to underestimate future value of exponential growing variable (Almenberg & Gerdes 2012). Alternatively, a continuous exponential growth trend, defined as $S_1 = S_0 e^{rt}$, where S_1 accrues based solely on *r* (the exponential growth rate) and *t* (the time interval length in years), better reflects continuous processes like dentin exposure accumulation (Shimojo et al.

2010; Han et al. 2014). In evolutionary ecology, this continuous compounded function has been extensively studied (Weis et al. 2000; Pandey et al, 2017). The overall dentin exposure (S) growth follows this continuous model, with the wear rate (r) representing a percent increase in dentin exposure, expected to decreases with age.

4. Results

The basic statistics (sample size, mean, and standard deviation) for the 3D dentin exposure area (D, in mm^2) by site are shown in Table 2. We did not compare dentin exposure areas among sites due to the heterogeneity and small sizes of most samples, making meaningful comparison impossible. Additionally, the average D values by site are heavily influenced by unknown age distribution within each sample. Since D increases with older age distributions, average values are not informative. This applies to the average D values of the seven groups considered (Table 3). Although these groups had large sample sizes, D did not follow a Normal distribution in any group (K-S test, P < 0.001), which is expected when the age distribution is highly heterogeneous, samples sizes are small, or the variable is age dependent. Sample sizes ranged from 28 (Spanish Mesolithic) to 124 (Portuguese Mesolithic) for M1, from 13 (Near East Neolithic) to 98 (Portugal Mesolithic) for M2, and from 3 (Near East Neolithic) to 28 (Portugal Mesolithic) for M3. As expected,

Basic statistic of the 3D dentin exposure by group. Dentin exposure by periods tooth type (M1, M2, M3) for the combined samples of upper and lower quadrants. N: sample size; mean: average of the 3D dentin exposure (D) in *mm*²; s.d.: standard deviation of D.

		M1			M2		M3			
Sample group	Ν	mean	s.d.	Ν	mean	s.d.	Ν	mean	s.d.	
1. Portugal Mesolithic	124	37.549	21.256	94	17.315	15.706	28	11.273	17.718	
2. Spain Mesolithic	28	32.950	25.893	19	15.553	17.432	7	6.537	6.749	
3. Spain Middle Neolithic	83	23.250	16.117	60	8.043	10.711	19	3.883	3.387	
4. Near East Natufian	29	33.139	23.170	27	15.208	16.889	10	9.048	8.547	
5. Near East PPNB Neolithic	31	25.508	27.726	13	28.336	27.519	3	9.590	8.314	

sample sizes decreased from M1 to M3, as the later-erupting molars (M2 and M3) are less frequently observed. Additionally, not all molar quadrants showed dentin exposure on M2, and especially on M3, further reducing sample sizes due to methodological constraints in molar selection. In all groups and teeth examined, except for the Near East PPNB Neolithic M2, the average 3D dentin exposure area of M1 was greater than that of M2, and M2 was greater than M3, consistent with the sixvears offset of molar eruption ages. Despite these limitations, both Mesolithic groups from Portugal and Spain, as well as the Natufian sample, showed higher average D values for M1 than the Neolithic samples from both geographic zones, as well as the Medieval Catalan and the contemporaneous Coimbra samples, which had the lowest average D values. However, this trend was not observed for M2 or M3. Such comparisons are not informative due to the unknown age distribution of the samples, given the age-dependent nature of dentin exposure.

4.1. Regression models by jaws

The sample sizes for the upper quadrants were smaller than for the lower ones, likely due to differences in bone preservation and recovery at the sites, as we studied all available remains, except for the Coimbra sample, where we selected a representative subset (see methods). The

linear regression model lnS = lna + blnD (*Power* function) for both maxillary bones by groups showed significant associations (P < 0.05) between logarithmic transformed variables ln D and ln S for all molars, explaining a large proportion of total variance (R^2) , although less so when the sample sizes were small (Table 4). These models tested the hypothesis of equality of the regression slopes (b) between the upper and lower quadrants, yielding non-significant P-values for most comparisons by tooth type—15 of the 19 comparisons made. Some comparisons could not be made due to the small sample sizes for Near East Neolithic M2 (N = 1) and M3 (N = 0). Significant differences in slope (*b*) between upper and lower jaw teeth were found for the Spain Neolithic M1 sample (P =0.036, $N_U = 34$, $N_L = 49$, $\delta = 0.082$, the absolute difference between slopes); the Portugal Mesolithic M3 sample (P = 0.034, $N_U = 7$, $N_L = 21$, $\delta = 0.164$); and the Coimbra contemporaneous M3 sample (P = 0.031, $N_U = 2$, $N_L = 4$, $\delta = 1.459$), the smallest sample. Based on these results, we combined the upper and lower quadrants to create larger samples for population comparisons.

4.2. Regression models by groups

For the combined jaw quadrants, the four models tested (*Linear*, *Quadratic*, *Compound*, *Power*) showed highly significant regressions between D and S in most groups and molars (Table 5). The *Linear* model did

Table 4

Slope comparisons between upper and lower quadrants. X: maxillary quadrants; M: mandibular quadrants. N: sample size; \mathbb{R}^2 : coefficient of determination (percentage of total variance explained by the regression model); In *a*: intercept of the model; *b*; slope of the linear regression; \mathbf{e}_b : standard error of the regression model); Let \mathbf{h}_1 : the slope $(\mathbf{h}_0: b = 0)$. δ : difference between the slopes compared; \mathbf{e}_δ : standard error of the difference between the slopes compared; \mathbf{t}_δ : statistic of the comparison; $\mathbf{P}\delta$: probability of significance of the difference of the difference between slopes ($\mathbf{H}_0: b_1 = b_2$). $\alpha = 0.05$.

Sample	Tooth	Jaw	Ν	R ²	ln a	b	e _b	δ	\mathbf{e}_{δ}	t_{δ}	P_{δ}
Near East Natufian	M1	U	7	0.990	0.006	1.078	0.070	0.056	0.096	0.582	0.566
		L	22	0.968	-0.110	1.134	0.066				
	M2	U	6	0.781	2.464	0.505	0.202	0.068	0.212	0.321	0.751
		L	21	0.902	2.561	0.573	0.063				
	M3	U	2	1.000	2.624	0.412	0	-0.057	0.106	0.523	0.626
		L	8	0.799	3.678	0.355	0.109				
Near East Neolithic	M1	U	8	0.995	-0.104	1.078	0.044	0.028	0.054	0.520	0.607
		L	23	0.992	-0.700	1.106	0.031				
	M2	U	1								
		L	12	0.901	2.336	0.624	0.095				
	M3	U	_								
		L	3	0.707	3.443	0.618	0.618				
Spain Mesolithic	M1	U	14	0.990	0.068	1.021	0.043	0.100	0.079	1.269	0.216
		L	14	0.980	-0.120	1.121	0.066				
	M2	U	6	0.267	3.010	0.251	0.452	0.131	0.464	0.282	0.782
		L	13	0.734	3.206	0.382	0.106				
	M3	U	2	1.000	3.885	0.199	0	0.022	0.203	0.108	0.921
		L	5	0.450	4.130	0.177	0.203				
Spain Neolithic	M1	U	34	0.991	-0.012	1.051	0.024	0.082	0.038	2.134	0.036
		L	49	0.984	-0.199	1.133	0.030				
	M2	U	22	0.664	2.771	0.419	0.106	0.053	0.115	0.462	0.626
		L	38	0.871	2.770	0.472	0.044				
	M3	U	5	0.438	3.702	0.200	0.333	0.142	0.344	0.413	0.685
		L	14	0.758	3.738	0.342	0.085				
Spain Medieval	M1	U	41	0.991	-0.058	1.076	0.023	0.052	0.032	1.634	0.105
		L	71	0.987	-0.096	1.128	0.022				
	M2	U	13	0.941	2.121	0.684	0.074	-0.121	0.083	1.455	0.152
		L	41	0.920	2.455	0.563	0.038				
	M3	U	3	0.997	3.278	0.590	0.043	-0.134	0.095	1.407	0.171
		L	19	0.793	3.248	0.456	0.085				
Portugal Mesolithic	M1	U	55	0.982	-0.088	1.096	0.029	0.046	0.049	0.931	0.354
		L	69	0.961	-0.220	1.142	0.040				
	M2	U	40	0.770	3.028	0.404	0.054	0.058	0.068	0.848	0.399
		L	54	0.833	2.917	0.462	0.042				
	M3	U	7	0.950	3.759	0.370	0.054	-0.164	0.073	2.249	0.034
		L	21	0.694	4.256	0.206	0.049				
Portugal Coimbra	M1	U	56	0.973	0.113	0.997	0.032	0.053	0.041	1.285	0.201
		L	67	0.980	0.043	1.050	0.026				
	M2	U	17	0.420	1.908	0.664	0.371	0.167	0.395	0.423	0.675
		L	21	0.807	1.622	0.811	0.136				
	M3	U	2	1.000	2.724	-0.749	0.000	1.459	0.264	5.527	0.031
		L	4	0.885	2.568	0.710	0.264				

Table 5

Regression models between S and D by group and tooth type. N: sample size; R^2 : coefficient of determination (percentage of total variance explained by the model); *P*: significance of the regression model (H_0 : b = 0). The non-significant *P*-values are shown in bold, as well as the highest R^2 values by tooth type.

		Linear		Qua	dratic	Com	pound	Рс	ower
Group	Ν	R ²	Р	R ²	Р	R ²	Р	R ²	Р
Portugal N	Iesolithic								
M1	124	0.771	< 0.001	0.800	< 0.001	0.759	< 0.001	0.948	< 0.001
M2	94	0.813	< 0.001	0.827	< 0.001	0.630	< 0.001	0.660	< 0.001
M3	28	0.732	< 0.001	0.732	< 0.001	0.494	< 0.001	0.559	< 0.001
Spain Mes	olithic								
M1	28	0.880	< 0.001	0.883	< 0.001	0.823	< 0.001	0.975	< 0.001
M2	19	0.685	< 0.001	0.692	< 0.001	0.406	0.003	0.410	0.003
M3	7	0.179	0.344	0.180	0.673	0.255	0.248	0.345	0.165
Spain Mid	dle Neolithic								
M1	83	0.887	< 0.001	0.902	< 0.001	0.804	< 0.001	0.973	< 0.001
M2	60	0.818	< 0.001	0.832	< 0.001	0.530	< 0.001	0.675	< 0.001
M3	19	0.589	< 0.001	0.606	< 0.001	0.556	< 0.001	0.582	< 0.001
Near East	Natufian								
M1	29	0.864	< 0.001	0.864	< 0.001	0.826	< 0.001	0.959	< 0.001
M2	27	0.903	< 0.001	0.924	< 0.001	0.647	< 0.001	0.811	< 0.001
M3	10	0.655	< 0.001	0.751	0.008	0.526	0.018	0.679	0.003
Near East	PPNB Neolithic								
M1	31	0.952	< 0.001	0.981	< 0.001	0.799	< 0.001	0.985	< 0.001
M2	13	0.970	< 0.001	0.978	< 0.001	0.763	< 0.001	0.825	< 0.001
M3	3	0.559	0.463	1.000	< 0.001	0.447	0.534	0.500	0.500
Spain Earl	y Medieval								
M1	112	0.900	< 0.001	0.917	< 0.001	0.761	< 0.001	0.976	< 0.001
M2	54	0.889	< 0.001	0.893	< 0.001	0.688	< 0.001	0.851	< 0.001
M3	22	0.444	< 0.001	0.568	< 0.001	0.368	0.003	0.644	< 0.001
Portugal C	Coimbra								
M1	123	0.835	< 0.001	0.845	< 0.001	0.59	< 0.001	0.955	< 0.001
M2	38	0.640	< 0.001	0.658	< 0.001	0.446	< 0.001	0.514	< 0.001
M3	6	0.683	< 0.001	0.694	0.005	0.518	0.008	0.631	0.059

not show a significant association for the Spain Mesolithic M3 sample (N = 7, *P* = 0.344) and the Near East PPNB Neolithic M3 samples (N = 3, *P* = 0.673). The *Quadratic* model was not significant only for the Spanish Mesolithic sample (N = 7, *P* = 0.165). Finally, the *Power* regression model was not significant for the Near East PPNB Neolithic M3 sample (N = 3, *P* = 0.500), the Spanish Mesolithic M3 (N = 7, *P* = 0.344) sample, and the Portuguese Coimbra contemporaneous M3 samples (N = 6, *P* = 0.059). All the non-significant associations affected the M3 molar, which had the smallest sample sizes. The highest coefficients of determination (R²) by group and tooth type were observed in 12 (57.1%) of the 21 M analyzed for the *Quadratic* model, 8 (38.1%) for the

Power model, 2 (9.5 %) for the *Compound* model, and 1 (4.8 %) for the *Linear* model. All the M1 teeth showed greater R^2 values for the *Power* model, while the other molars closely followed a *Quadratic* model, except in two cases. These may reflect the differing rates of dentin exposure of the second and third molars, as shown by Yang et al. (2024). For comparative purposes and since all the *Power* associations for M2 were also highly significant, we adopted our previous approach (Yang et al., 2024) and centered subsequent analyses on the *Power* model. The dispersion ranges of the coefficients of determination (R^2) for the *Power* models were [0.955, 0.985] for M1, [0.410, 0.851] for M2, and [0.345, 0.679] for M3. The percentage of total variance explained by the model

Linear models of the *Power* regression equations by group and tooth type for the combined jaw sample. In *a*: intercept of the linear model for D = 0; $a = e^{ln a}$, e_a : standard error of the intercept; t_i : Student t statistic for ln a = 0; P_i : significance probability for the intercept; *b*: slope of the linear regression model; e_b : standard error of the slope; t_s : Student t statistic for b = 0; P_s : significance probability for the slope.

Group	Tooth	N	ln a	а	ea	ta	Pa	b	e_b	t _b	P _b
Portugal Mesolithic	M1	124	-0.143	0.867	0.082	-1.738	0.085	1.117	0.024	47.373	<0.001
	M2	94	2.964	19.375	0.086	34.412	<0.001	0.439	0.033	13.368	<0.001
	M3	28	4.139	62.740	0.086	47.955	<0.000	0.247	0.043	5.73	<0.000
Spain Mesolithic	M1	28	-0.016	0.984	0.107	-0.151	0.881	1.077	0.034	32.154	<0.001
	M2	19	3.087	21.911	0.272	11.362	<0.001	0.390	0.114	3.435	0.003
	M3	7	4.039	56.770	0.216	18.719	<0.001	0.198	0.122	1.625	0.165
Spain Neolithic	M1	83	-0.121	0.886	0.061	-1.996	0.049	1.100	0.020	54.041	<0.001
	M2	60	2.757	15.753	0.078	35.442	<0.001	0.463	0.042	10.968	<0.001
	M3	19	3.712	40.936	0.096	38.657	<0.001	0.349	0.072	4.870	<0.001
Near East Natufian	M1	29	-0.086	0.918	0.148	-0.579	0.568	1.125	0.045	25.001	<0.001
	M2	27	2.513	12.342	0.135	18.673	<0.001	0.580	0.056	10.364	<0.001
	M3	10	3.182	24.095	0.261	12.193	<0.001	0.537	0.131	4.110	<0.003
Near East Neolithic	M1	31	-0.086	0.918	0.073	-1.176	0.249	1.103	0.026	43.126	<0.001
	M2	13	2.335	10.329	0.256	9.124	<0.001	0.626	0.087	7.210	<0.001
	M3	3	3.443	31.281	1.317	2.614	0.233	0.618	0.618	0.999	0.500
Spain Early Medieval	M1	112	-0.082	0.921	0.043	-1.895	0.061	1.109	0.017	66.900	<0.001
	M2	54	2.365	10.644	0.079	29.990	<0.001	0.599	0.035	17.246	<0.001
	M3	22	3.263	26.128	0.173	18.835	<0.001	0.473	0.079	6.010	<0.001
Portugal Coimbra	M1	123	0.080	1.083	0.035	2.278	0.024	1.027	0.020	50.852	<0.001
	M2	38	1.792	6.001	0.153	11.686	<0.001	0.735	0.119	6.173	<0.001
	M3	6	2.545	12.743	0.297	8.563	0.001	0.657	0.251	2.618	0.059



Fig. 3. Linear regression $\ln S = \ln a + b \ln D$ by molar types and by groups. The intercepts $a_i (mm^2)$ and slopes (*b*) are indicated, as well as the w_1 (juvenile 5.5-11.5 years) and w_2 (subadult 11.5-18.5 years) wear rates (mm^2 /month).

decreased from M1 to M3 in all groups, corresponding with the decreasing samples sizes from M1 to M3.

The slopes of the regression models for all the groups decrease from M1 to M3 (Table 6). The decrease in slopes from M1 to M2 was highly significant ($P \le 0.017$) across all groups, while the decrease from M2 to M3 was only significant for the Portuguese Mesolithic sample. This suggests that, regardless of the statistical model used, S accrues at different rates depending on how many molars contribute to the overall dentin exposure. This is consistent with the fact that the regression models for the three molars eventually intersect (Fig. 3), reaching the same D value and thus equally contributing to S. If the regression models did not cross, it would suggest that S accrued at a constant rate, independent of how many molars contributed to the overall dentin exposure, which is unlikely given the results obtained. All the intercepts (ln *a*) by group of the *Power* regression models for M1 were negative ($\ln a < 0$), as at the onset of dentin exposure, when S approaches 1 mm^2 , $\ln a$ may take negative values (S < 1)—except for the Coimbra sample (ln a = 0.080). A negative ln-transformed intercept is consistent with S being nil (no dentin exposure) before the onset of dentin exposure for this tooth. The intercepts for M1 did not significantly differ from zero, except in the Spanish Neolithic (N = 83, P = 0.049) and Portuguese Coimbra (N = 123, P = 0.024) samples. For M2 and M3, the intercepts significantly differed from zero in all groups except for the Near East Neolithic M3 (N = 3, P = 0.233), the smallest sample. The dispersion ranges of the intercepts were [-0.143, 0.080] for M1, [1.792, 3.087] for M2, and [2.545, 4.139] for M3. In all samples, the intercept for M1 was smaller than for M2, and this was smaller than for M3, reflecting the progressive nature of dentin exposure and the sequential eruption of molars.

4.3. Dentin exposure rates by groups

The magnitude of the differences in intercept values (a, mm^2) between consecutive molars depends on the dentin exposure rates for the population considered. A larger difference in $a_{M2} - a_{M1}$ indicates greater dentin exposure rates during a given age interval, while a smaller difference suggests lower rates. All seven groups followed the pattern a_{M2} – $a_{M1} < a_{M3} - a_{M2}$, even though the subadult interval was longer (7 years) than the juvenile one (6 years). This resulted in higher wear rates $(mm^2/$ year) during the subadult period than during the juvenile period ($w_2 >$ w1), except in the Near East Natufian sample, which showed similar wear rates for both periods (Table 7). This suggests that dentin exposure (S) does not accrue at a continuous rate over time but increases as molars erupt and come into occlusion. However, the percentage contribution to S of each molar decreases over time as dentin exposure accumulates (r2 < r₁). Although this may seem contradictory, it simply reflects that the percentage contribution of each molar's D value becomes smaller as the overall S value increases, which is uninformative about whether D remains constant, grows, or decreases over time.

The Portuguese and Spanish Mesolithic samples had the largest percentage contributions to S over the entire age interval (w_3) , at 2.74 and 2.60 % per month, respectively, followed by the Neolithic samples and then the Natufian (Table 7). The Spanish Early Medieval sample

showed w values similar to, though slightly higher than, those of the Natufian, while the modern Coimbra sample had much lower rates (Fig. 2). These results suggest that Mesolithic populations had higher dentin exposure rates than both the earlier Natufian and the later Neolithic populations in both geographic areas. In particular, the Portuguese Mesolithic sample had the highest wear rates during the combined interval (w_3), at 4.76 mm^2 /year, followed by the Spanish Mesolithic sample at 4.29 mm^2 /year. Both groups had higher w values in the subadult period than in the juvenile one. The Neolithic samples showed lower dentine exposure rates for the combined period, with $3.08 \text{ } mm^2$ /year for Spain and $2.34 \text{ } mm^2$ /year for the Near East. The other samples had even lower rates: 1.94 mm²/year for the Spanish Early Medieval, $1.78 \text{ }mm^2$ /year for the Near East Natufian, and $0.90 \text{ }mm^2$ /year for Coimbra, the most recent sample, while the Early Medieval sample had wear rates similar to those of earlier Neolithic samples. In the Near East, the Natufian and Neolithic samples clearly differed: during the juvenile period, the Natufian specimens wore their molars somewhat faster that the Near East Neolithic but slower than the Spanish Neolithic sample, while in the subadult period, the Neolithic specimens wore their molars at faster rates than the Natufian (Fig. 4).

For the juvenile age interval, the Portuguese and Spanish Mesolithic samples showed similar dentin exposure rates, though the Portuguese Mesolithic had a higher wear rate during the subadult period (Fig. 4). The Spanish Mesolithic specimens had greater wear rates than the Spanish Neolithic ones in both age intervals, and these, in turn, had greater wear rates than the Near East Neolithic sample. The Natufian sample had lower wear rate values than the Neolithic ones, closely resembling the Early Medieval sample. The modern Coimbra sample had the lowest wear rate values in both age intervals.

Overall, the observed wear rates suggest that the Natufian's mixed diet, which relied heavily on hunting and gathering, resulted in lower wear rates than those seen during the Mesolithic period, which relied on hunting and gathering, and the Neolithic period, more dependent on agriculture. The dentin exposure rates indicate that the Natufian population does not fit neatly into either the Mesolithic or the Neolithic categories in terms of molar use related to food chewing or other masticatory activities. Additionally, while the Spanish and Portuguese Mesolithic samples both had high wear rates in both age periods, they differed in that the Portuguese Mesolithic had higher wear rates during the *juvenile* period. Finally, the Neolithic samples from Spain and the Near East had similar wear rates, with slightly higher values in the Spanish sample in the *juvenile* period (Fig. 4).

When testing the significance of the differences in slopes and intercepts of the regressions among groups by tooth (Table 8), several significant (P < 0.05) differences were observed, most notably with the modern Coimbra sample, whose M1 slope significantly differed from all other samples. Coimbra had the smallest M1 slope (Table 6) and greatly reduced dentin exposure rates (Table 7). The M1 intercepts of Coimbra also significantly differed from all the other samples. For M2, the Coimbra slope only differed significantly from those of the two Mesolithic (Portugal and Spain) and the Spanish Neolithic samples, as did the intercepts, except for the Near East Neolithic. M3 comparisons showed

Comparisons of slopes and wear rates among the groups considered. The t-tests compare the slopes of M1, M2 and M3 for the combined maxillary bones. The dentin exposure rates of %/month and mm^2 /year refer to the molar eruption intervals M1-M2 (r_{1-2} , w_{1-2}), M2-M3 (r_{2-3} , w_{2-3}), and M1-M3 (r_{1-3} , w_{1-3}).

	$b_{\mathrm{M1}} \leftrightarrow b_{\mathrm{M2}}$		b _{M2} ·	$\leftrightarrow b_{M3}$	%/month				mm ² /year		
Group	<i>t</i> _{M1-2}	P _{M1-2}	t _{M2-3}	P _{M2-3}	r_1	<i>r</i> ₂	r_3	<i>w</i> ₁	w ₂	δ_{j-i}	w ₃
1. Portugal Mesolithic	16.62	0.000	3.54	0.001	4.32	1.40	2.74	3.08	6.19	3.10	4.76
2. Spain Mesolithic	5.77	0.000	1.15	0.263	4.31	1.13	2.60	3.49	4.98	1.49	4.29
3. Spain Neolithic	13.69	0.000	1.37	0.176	4.00	1.14	2.46	2.48	3.60	1.12	3.08
4. Near East Natufian	7.59	0.000	0.30	0.765	3.61	0.80	2.09	1.90	1.68	-0.22	1.78
5. Near East Neolithic	5.25	0.000	0.09	0.931	3.36	1.32	2.26	1.57	2.99	1.42	2.34
6. Spain Early Medieval	13.11	0.000	1.46	0.149	3.40	1.07	2.14	1.62	2.21	0.59	1.94
7. Portugal Coimbra	2.42	0.017	0.28	0.780	2.38	0.90	1.58	0.82	0.96	0.14	0.90



Fig. 4. Bivaried plot of the wear rates (*mm*²/year) for the juvenile (w1, X-axis) and the subadult (w2, Y-axis) age-intervals of all the groups studied (names shown in the plot).

Comparison of the slopes of the linear models among the groups considered. Tests (*t*-test) for the null hypotheses $H_0: b_i = b_j$ (upper diagonal matrix) and $H_0: a_i = a_j$. (lower diagonal matrix). The shaded areas indicate the comparisons of Coimbra and the Early Medieval groups with the rest of the samples. The significant *P*-values are shown in bold ($P \le 0.05$).

b		P-N	P-MES		Coimbra		S-MES		S-NEO		S-MED		NE-NEO		Natufian	
ln a		t	Р	t	Р	t	Р	t	Р	t	Р	t	Р	t	Р	
P-MES	M1	-	_	2.881	0.004	0.961	0.338	0.544	0.587	0.272	0.786	0.396	0.693	0.157	0.876	
	M2			2.397	0.018	0.413	0.681	0.449	0.654	3.326	0.001	2.010	0.047	2.169	0.032	
	M3			1.610	0.118	0.379	0.707	1.216	0.231	2.513	0.016	0.599	0.554	2.103	0.043	
Coimbra	M1	2.501	0.013		-	1.268	0.207	2.581	0.011	3.124	0.002	2.317	0.022	1.990	0.048	
	M2	6.678	0.000			2.094	0.041	2.155	0.034	1.096	0.276	2.155	0.034	1.179	0.243	
	M3	7.409	0.000			1.645	0.134	1.180	0.251	0.699	0.491	1.180	0.251	0.424	0.679	
S-MES	M1	0.942	0.348	0.853	0.395		-	0.583	0.561	0.842	0.401	0.607	0.546	0.851	0.399	
	M2	0.431	0.667	4.150	0.000			0.601	0.550	1.753	0.084	1.646	0.111	1.496	0.142	
	M3	0.430	0.670	5.541	0.000			1.066	0.298	1.892	0.070	0.667	0.530	1.894	0.081	
S-NEO	M1	0.215	0.830	2.858	0.005	0853	0.396		_	0.343	0.732	0.091	0.927	0.508	0.613	
	M2	1.783	0.077	5.619	0.000	1.166	0.247			2.453	0.016	1.680	0.098	1.657	0.101	
	M3	3.313	0.002	5.656	0.000	1.383	0.180			1.160	0.253	0.432	0.671	1.258	0.220	
S-MED	M1	0.659	0.511	2.922	0.004	0.572	0.568	0.523	0.602	-	-	0.193	0.847	0.333	0.740	
	M2	5.126	0.000	3.328	0.001	2.549	0.013	3.531	0.001			0.288	0.774	0.288	0.774	
	M3	4.534	0.000	3.424	0.002	2.804	0.010	2.269	0.029			0.233	0.818	0.418	0.679	
NE-NEO	M1	0.519	0.604	2.050	0.042	0.540	0.591	0.368	0.714	0.047	0.962			0.423	0.674	
	M2	2.329	0.022	1.821	0.075	2.013	0.054	1.577	0.119	0.112	0.911	-		0.445	0.659	
	M3	0.527	0.602	0.891	0.392	0.447	0.671	0.204	0.841	0.136	0.893			0.128	0.901	
Natufian	M1	0.337	0.737	1.092	0.277	0.383	0.703	0.219	0.827	0.026	0.979	0.000	1.000	-	-	
	M2	2.818	0.006	3.534	0.001	1.890	0.066	1.565	0.121	0.946	0.347	0.615	0.542			
	M3	2.618	0.013	2.629	0.017	2.530	0.025	1.906	0.068	0.259	0.798	0.194	0.850			

fewer significant differences; for the slope, Coimbra only differed from the Portuguese Mesolithic, while for the intercept, it differed from all the samples except the Near East Neolithic. On the other hand, the M1 slope and intercept of the Early Medieval Catalan sample only differed significantly from Coimbra, indicating that the Early Medieval sample more closely resembled the other samples than Coimbra. For M2, significant differences in both slope and intercept were observed between the Portugal Mesolithic and both the Natufian and Near East Neolithic samples. Finally, the M3 intercepts significantly differed between the Portugal Neolithic and both the Natufian and the Spanish Neolithic samples, though the slope only significantly differed from the Natufian. No other significant differences in slopes were detected. Overall, the Mesolithic samples had significantly high dentine exposure rates, particularly the Portugal Mesolithic, followed by the Spanish Mesolithic and Neolithic samples, with no significant differences between the two Neolithic samples.

5. Discussion

The Natufian culture (circa 12,500-9,500 BCE) is notable for its semi-sedentary lifestyle, advanced stone tool technology, and the early plant and animal domestication in the Levant, particularly Israel, Palestine, and Lebanon (Weinstein-Evron 1991, 2009). Patricia Smith analyzed dental attrition in the Natufian in the early 1970 s (Smith 1972). She noted that the age-attrition correlation is the major component of tooth wear. However, the limited accuracy of age estimations for adults with rapid attrition rates "may bias the findings considerably". Therefore, it is crucial to have samples of known age, a condition rarely met with skeletal material from early sites. Alternatively, attrition gradients within individual specimens, such as differences between molar eruption ages, can be used for intergroup comparisons (Smith, 1972). Smith employed a 5-point wear score for measuring attrition, but only scores 1 (enamel faceting), 2 (dentin exposure), and 3 (secondary dentin exposure) were used. Her findings showed a similar correlation coefficient between M1 and M2 at the Natufian sites of Eynan (r = 0.80) and El Wad (r = 0.82), but significantly different correlation at Kebara (r =0.70, P < 0.01). This difference persisted when examining M2 and M3 pairs, with r = 0.51 at Kebara, 0.86 at El Wad and 0.84 at Eynan. These results indicated that the attrition gradients at El Wad and Eynan were very similar but differed from Kebara, suggesting a diet of different consistency at Kebara. Eshed et al. (2006) supported Smith's conclusion that the low rate of attrition at Kebara Cave is typical of a hunting-based population consuming non-abrasive foods within the framework of a hunting/gathering economy (with a possible increased reliance on grains), as opposed to El Wad and Eynan, whose more severe attrition suggested a more abrasive diet. Smith et al. (1984) later confirmed that the attrition rate varied among Natufian groups, being most severe at El Wad and Eynan and least severe at Kebara and Hayonim Cave. Natufian hunter-gatherers in northern Israel exploited a diverse range of animal and plant foods from both sedentary and more mobile settlements (Bar-Yosef 1998), while Early Neolithic people practiced a hunting-farming economy from increasingly sedentary settlements (Garfinkel 1987). Despite the expectation that the removal of plant seed coats would reduce phytoliths, enamel pits were significantly larger among farmers than hunter-gatherers, and scratches were wider among farmers than hunter-gatherers, suggesting that the diet became harder during the Neolithic period, likely due to reliance on stone-ground plant foods containing grit particles harder than enamel (Mahoney 2006).

The absence of known ages at death for most skeletal remains complicates dental wear studies, making an age-independent measure of dental wear necessary (Elgart 2010; Molnar et al. 1983; Rose & Ungar 1998; Scott 1979; Smith 1972). Traditionally, wear rates comparisons across populations have utilized the principal axis technique (Benfer & Edwards 1991; Scott 1979). This method assesses wear on M1 when M2 erupts and on M2 when M3 erupts. Assuming a constant wear rate during these known-age intervals, the slope of the regression model between the wear scores of the two molars indicates the wear rate, with a steeper slope implying a high rate (Scott 1979). In this study, we employ this technique, incorporating the proxy by Yang et al. (2024) to examine changes in overall 3D dentin exposure area (S) within fixed age intervals (*juvenile* and *subadult*) based on molar eruption ages. Wear rates, both in mm^2 /year (w) and % per month (r), were calculated for these intervals and compared across populations. The innovation of this procedure lies in using the overall 3D dentin exposure area of the three molars (S) rather than a single molar. We used the intercepts from the regression models of each molar to derive the dentin exposure area of M1 at the onset of M2 dentin exposure and the combined dentin exposure area of M1 and M2 at the onset of M3 dentin exposure.

We show that regression models by tooth type were highly significant across the intervals considered. During the juvenile interval, M1 was the sole contributor to S, while both M1 and M2 contributed during the subsequent subadult interval. Wear rates increased during the subadult period compared to the juvenile one in all samples except Coimbra and the Near East Natufian, which exhibited the lowest dentin exposure rates, with the Portuguese Mesolithic sample showing the greatest increase. This likely reflects either a shift in food processing (Deter 2009), diet composition (Godinho et al. 2023), or a broader range of foods, including more abrasive items (Romero et al. 2012), as the three molars come into occlusion. Consequently, the overall accrual of dentin exposure was curvilinear rather than linear. S best fitted a Power model for D by molar type, indicating a non-constant rate of dentin exposure accumulation within a molar quadrant (Yang et al. 2024). We observed the same wear pattern in the present research for M1 across all seven groups considered. However, for M2 or M3, the Quadratic function explained the highest percentage of variance, likely due to smaller sample sizes of rear molars. Despite variations in R² values, all functions were highly significant.

The overall wear rates were similar during the Portuguese Mesolithic $(4.76 mm^2/\text{year})$, characterized by a high intake of seafood (as indicated by the numerous shellmiddens in the sites), and the Spanish Mesolithic $(4.29 mm^2/\text{year})$, not so intensively associated to shellmiddens. These wear rates were comparable to those reported for the Chinese Neolithic to Bronze Age population at Houtaomuga $(4.66 mm^2/\text{year})$ and Jiayi $(3.69 mm^2/\text{year})$ (Yang et al., 2024), which inhabited cold, arid environments. However, the high wear rates observed in the Mesolithic populations do not suggest similar environmental conditions to those of the Chinese populations during the transition from the Late Neolithic (5500–3200 BCE) to the Early Iron Age (2700 BCE–1781 ACE) (Wang 2018; Yang et al. 2024). Instead, these rates reflect the heavy loads, highly demanding, and poorly processed diets typical of the European Mesolithic.

The Mesolithic Concheiros in Portugal were seasonal settlements located in the estuaries of the Muge valley and the Sado River near Lisbon. Muge (Roche, 1972a: pp. 135-137; Lentacker 1986) and Sado (Arias et al. 2021) provided evidence of both marine and terrestrial animal food consumption. The faunal assemblages at Muge included various species, with cockles (Cerastoderma edule), peppery furrow shell (Scrobicularia plana), rabbits (Oryctolagus cuniculus), wild boar (Sus scrofa), and red deer (Cervus elaphus) being the most abundant. The Spanish Mesolithic site of El Collado (Gibaja et al. 2015, 2017a) also contained shell middens similar to those found at the Portugal sites, but shell consumption might have been less significant there than at Muge and Sado, indicating a greater reliance on terrestrial foods (Garcia-Guixé et al. 2006). The wear rate during the subadult interval was smaller in the Spanish Mesolithic sample (3.49 mm²/year) compared to the Portuguese Mesolithic sample (6.19 mm^2 /year), suggesting a more abrasive subadult diet in the latter, although the differences were not significant. This trend in food resource exploitation could be attributed to the seasonality of hunting and gathering activities or to lower mollusk production in the Mediterranean compared to the Atlantic region.

There is a consensus that abrasives foods were consumed by Neolithic populations (Mahoney 2006), with plant phytoliths and grit

from plant-grinding stone tools being primarily responsible for the variations observed between hunter-gatherers and early farmers. Accordingly, our findings show higher wear rates in the PPNB Neolithic (2.34 mm^2 /year) compared to the Natufian (1.78 mm^2 /year), likely due to the consumption of abrasives from various sources, such as contaminant grit, less processed foods, mineral-rich shells, or dry fish, which accelerated enamel and dentin wear (Alrousan et al. 2013; Yang et al. 2024).

In the Iberian Peninsula, Middle Neolithic populations were agriculture-based settlers consuming cultivated plants and livestock (Price 2000; Alday 2012), whereas Mesolithic populations were huntergatherers with temporary settlements in marine estuaries (Bicho et al. 2017). However, the lower wear rates observed in the Neolithic populations compared to Mesolithic ones suggest a less abrasive or processed diet in the Neolithic populations, despite the use of stone mills, which likely introduced abrasive particles into the foods, especially cereals. The Spanish Neolithic sample had a lower wear rate $(3.08 \text{ mm}^2/$ year) than the Spanish Mesolithic populations (4.29 mm^2 /year). Similarly, the Near East PPNB Neolithic samples exhibited a low wear rate $(2.34 \text{ }mm^2/\text{year})$, indicating a less abrasive diet in the Near East. Neolithic populations during the PPNB period were fully settled, with developed crops and livestock (Mahoney 2006), whereas the Natufian period was characterized by nomadic hunter-gatherers. The first domesticated crops appeared in the Early PPNB period, between 8,700 and 8,200 BCE (Nesbitt 2002). The results suggest that the Natufian lifestyle was associated with softer diets compared to the Neolithic PPNB period.

The transition to a Neolithic lifestyle, marked by full sedentarization, animal domestication, and increased reliance on edible plant remains (Galili et al. 1993; Garfinkel 1987) such as emmer wheat and pulses, indicates a greater emphasis on farmed foods. The use of stone tools for grinding may have maximized the nutritional value of these foods, potentially leading to overexploited local cultivable land (Wright 1993; Düring 2010). However, wear rates during the Neolithic were lower than those observed in Mesolithic populations. Although no Late Neolithic sites were included in this study, an increase in wear rates compared to the Middle Neolithic samples would be expected due to the increasing reliance on plant-grinding tools, shown to be responsible for microwear formation (Mahoney, 2006).

The diet of the Early Medieval Casserres population was highly variable, consisting of a significant proportion of meat, abrasive plant foods like cereals and dried fruits, minimally processed complex carbohydrates, and low intake of simple sugars (Carrascal 2021). We observed similar dentin exposure rates in the Natufian and PPNB Neolithic samples, indicating a highly varied and highly processed but low-abrasive diet, though dietary practices may not have been uniform across medieval populations. In contrast, the recent Portuguese collection from Coimbra exhibited the lowest wear rates among all the samples studied, suggesting a diet with much less abrasive potential. Most individuals documented at Coimbra cemetery were from lower socioeconomic classes, whose diet primarily consisted of low-quality foods such as combread, dried vegetables, potatoes, some fish (usually sardines or salted cod), and bacon (Correia 1951; Cuesta-Torralvo et al., 2021). These foods, combined with their methods of processing and chewing, had low abrasive potential, leading to minimal dentin exposure rates.

In conclusion, the dentin exposure results derived from the regression model proxy provide a robust indicator of dietary shifts from the Mesolithic to the Neolithic, closely aligning with the expected patterns associated with the transition to agriculture and sedentary life. The molar dentin exposure rates clearly illustrate the dietary changes, particularly the increased consumption of carbohydrates, including ground grains and cereals, which led to a decrease in dentin exposure rates in Neolithic samples compared to the more abrasive diets of Mesolithic hunter-gatherers, who relied heavily on hunting, gathering, and shellfish. Importantly, we made these comparisons despite the absence of known age distributions within the samples, yet the computed wear rates remained consistent with the expected dietary patterns and food preparation techniques of each period. This approach underscores the utility of the wear rate indicators derived from regression models of molar dentin exposure, offering a valuable tool for understanding the dietary and lifestyle changes in ancient populations.

Credit authorship contribution statement

Susana Carrascal: Writing – original draft, Resources, Investigation, Formal analysis. Ferran Estebaranz-Sánchez: Resources, Investigation. Albert E. Dyowe-Roig: Investigation. Shiyu Yang: Resources, Investigation. Claudia Umbelino: Writing – review & editing, Resources, Investigation, Funding acquisition. Bérénice Chamel: Resources. Miquel Molist: Resources. María Eulàlia Subirà: Resources, Investigation. Alejandro Pérez-Pérez: Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. Laura M. Martínez: Resouces, Investigation, Writing, Project administration.

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Declaration of competing interest

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Appendix A. Supplementary data

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Data availability

Data will be made available on request.

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