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From hunter-gatherers to food producers: New dental insights into the Nile Valley population history (Late Paleolithic–Neolithic)

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Abstract

Objectives: This study presents biological affinities between the last hunter-fisher-gatherers and first food-producing societies from the Nile Valley. We investigate odontometric and dental tissue proportion changes between these populations from the Middle Nile Valley and acknowledge the biological processes behind them.

Materials and Methods: Dental remains of 329 individuals from Nubia and Central Sudan that date from the Late Pleistocene to the mid-Holocene are studied. Using 3D imaging techniques, we investigated outer and inner metric aspects of upper central incisors, and first and second upper molars.

Results: Late Paleolithic and Mesolithic foragers display homogeneous crown dimensions, dental tissue proportions, and enamel thickness distribution. This contrasts with Neolithic trends for significant differences from earlier samples on inner and outer aspects. Finally, within the Neolithic sample differences are found between Nubian and Central Sudanese sites.

Discussion: Substantial dental variation appears to have occurred around 6000 BCE in the Nile Valley, coinciding with the emergence of food-producing societies in the

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region. Archeological and biological records suggest little differences in dietary habits and dental health during this transition. Furthermore, the substantial variations identified here would have happened in an extremely short time, a few centuries at most. This does not support in situ diet-related adaptation. Rather, we suggest these data are consistent with some level of population discontinuity between the Mesolithic and Neolithic samples considered here. Complex settlement processes could also explain the differences between Nubia and Central Sudan, and with previous results based on nonmetric traits.

KEYWORDS

crown dimensions, dental tissue proportions, Neolithic transition, population discontinuity, settlement processes

1 | INTRODUCTION

The early to mid-Holocene transition in the Nile Valley is characterized by dramatic climate changes. The monsoonal rains, which had been moistening the valley and Eastern Sahara since 8500 BCE, withdrew during the fifth millennium BCE (Kuper & Kröpelin, 2006; Pausata et al., 2020; Said, 1993). After three millennia of humid and habitable climate, the desert margins extended and only the river floodplains became suitable for human occupation. In this context of aridification of the "Green Sahara", a massive exodus toward the Nile occurred and the valley became the only access route between Northern and sub-Saharan Africa (Hoelzmann et al., 2001; Kuper & Kröpelin, 2006).

Significant cultural and behavioral changes occurred in response to this dramatic climate modification: the progressive regional transition to food production between the early sixth millennium bce and advent of the fifth millennium BCE, with the earliest dates in Southern Egypt/Northern Sudan and later ones in Central Sudan (Brass, 2013, 2018; Gautier, 2002; Honegger & Williams, 2015; Salvatori & Usai, 2019a, 2019b). This period witnessed the transition from hunting, fishing, and gathering to herding and cultivation. Archaeological, archaeobotanical, and archaeozoological data show evidence of a gradual conversion to food production until its full-fledged adoption along the Middle Nile during the fifth to mid-forth millennium BCE (Honegger, 2019; Honegger & Williams, 2015; Kuper & Kröpelin, 2006; Linseele, 2010, 2012; Monroe et al., 2023; Ryan et al., 2016; Salvatori & Usai, 2019a, 2019b). Evidence was found for Near Eastern/Levantine ancestry of the first domesticated animals (Decker et al., 2014; Edwards, 2007; Garcea, 2016; Garcea et al., 2016; Gifford-Gonzalez & Hanotte, 2011; Olivieri et al., 2015) and cereals (Neumann, 2005; Ryan et al., 2016; Salvatori & Usai, 2019b). This naturally raises the question of whether this near Eastern influence arrived in the Nile Valley through diffusion or some degree of migration after ca. 6000 BCE.

Transitioning to food production was a worldwide phenomenon, accompanied by reduction in craniofacial and dental dimensions (e.g., Brace et al., 1987; Le Luyer & Bayle, 2017; Pinhasi et al., 2008). It appears that such variation could result from the adoption of a new lifestyle and diet. Transitioning from foraging to food-production implied numerous and significant behavioral changes that could all have been involved in this craniofacial reduction and simplification. During the past decades, three morpho-functional adaptation models were hypothesized to describe, explain, and predict such dental variation in a context of Neolithic transition:

- Probable mutation effect (Brace, 1963; Brace & Mahler, 1971; Pinhasi et al., 2008): this model hypothesizes that in the absence of selective pressure, natural mutations will occur and lead to a reduction and simplification of dental morphology. It assumes that transitioning to a Neolithic lifestyle substantially changed dietary habits and led to a relaxation of selective pressure toward larger and more complex teeth. An overall reduction in all dental dimensions or homogeneous variation is expected.

- Increasing population density effect (Macchiarelli & Bondioli, 1986): this model suggests that a sedentary lifestyle (that may appear with Neolithic cultures) led to a dramatic decrease in health status and nutrition. This would have resulted in an overall reduction in body size, and therefore tooth size. An overall reduction of body size and of all dental dimensions, but also a significant poorer health status is expected in this model.

- Selective compromise effect (Calcagno & Gibson, 1991; Y'Edynak & Fleisch, 1983): it is assumed that individuals with larger teeth are more likely to suffer from caries and dental crowding, resulting in a selective pressure toward smaller teeth. However, abrasive diets that usually result from Neolithic cooking methods are assumed to result in selection for larger teeth with thicker enamel, to counter severe wear. This model suggests that dental reduction is the result of a compromise between these two selective pressures, resulting in overall dental reduction or uniform trends (e.g., in a tooth class) and overall enamel thickening.

These evolutionary models suggest that these changes could have led to either selective pressure on Neolithic populations toward smaller and simpler teeth to prevent caries and dental crowding; or conversely a diminution of the selective pressure toward larger and more

complex morphologies, allowing for derivation toward smaller and simpler teeth. Both mechanisms could be resulting in natural derivation toward simpler morphologies and smaller crown diameters.

The Nile Valley is no exception to these tendencies, with significant morphological modifications and reduction described between the Late Pleistocene to early Holocene hunter-gatherers and later food-producing populations (Anderson, 1968; Crevecoeur, 2008; Crevecoeur et al., 2009; Greene, 1972; Holliday, 2015; Irish, 2000, 2005, 2010; Irish & Usai, 2021; Shackelford, 2007). Still, the application of the morpho-functional adaption evolutionary models detailed above to the Middle Nile area is argued. As a matter of fact, debates on whether the morphological changes observed in the Nile Valley result from an in situ adaptation or rather population replacement have been on-going for almost half a century. The continuity hypothesis assumes that the adoption of food production in the Nile Valley did imply dramatic changes in dietary habits, which would have triggered any of the morpho-functional adaptation models and led to simpler and smaller masticatory apparatuses (Armelagos et al., 1989; Calcagno & Gibson, 1988; Carlson & Van Gerven, 1979; Galland et al., 2016; Greene, 1972; Greene et al., 1967). On the contrary, the discontinuity hypothesis argues that such a morphological shift is related to some population replacement, or at least a significant gene influx, during the transition to food production. In other words, it may suggest the arrival of new people alongside the introduction of food-production practices, domesticated animals, and cereals in the Nile Valley (Benoiston et al., 2018; Crevecoeur et al., 2023; Franciscus, 1995; Holliday, 2015; Irish, 2000, 2005, 2010).

The latest studies on outer dental morphology (Irish & Usai, 2021) and dental tissue proportions (Benoiston et al., 2018) have displayed even more complex results and hypotheses. Indeed, some Nubian Late Paleolithic and Mesolithic populations, such as those from Jebel Sahaba or El-Barga, show complex and large teeth and display very significant dissimilarities with Neolithic and later samples. The El-Barga Mesolithic individuals also appear to have different enamel thickness distribution from later Neolithic individuals in the UI1 and UM1. On the contrary, the Central Sudanese pre-Mesolithic assemblage from Al-Khiday (Dal Sasso et al., 2020; Usai et al., 2010) shows some level of affinities with later Neolithic and historic populations. These results highlight the complex settlement processes that might have happened during the Neolithic transition in the Nile Valley. As a matter of fact, they highlight the need for new data on samples dating to the transition, and the necessity of studying large-scale samples both in Nubia and Central Sudan.[i]

Recent excavations of early to mid-Holocene sites in Sudan, especially in the western part of Jebel Sabaloka at the sixth Nile cataract (Varadzinová, Varadzin, Brukner Havelková et al., 2022; Varadzinová, Varadzin, Crevecoeur, et al., 2022; Brukner Havelková et al., 2022; Varadzinová et al., 2023), provide plentiful and so far untested samples of human remains dating just prior to the Neolithic transition. These new data and analyses might be the key to explore and describe more precisely the morphological changes and dental reduction between the last hunter-fisher-gatherers and the first food-producers.

The use of dental data in biological affinities studies relies on their strong genetic control and limited environmental impact on morphological expression and size (Dempsey & Townsend, 2001; Kono et al., 2002; Potter & Nance, 1976; Scott & Turner, 1997; Stojanowski et al., 2018; Townsend et al., 2009). Outer (Irish et al., 2020; Stojanowski & Schillaci, 2006) and inner (Hlusko, 2016; Horvath et al., 2014; Martín-Francés et al., 2020) aspects of tooth crowns are demonstrated proxies for neutral genetic data and provide reliable insights into biological affinities. This study describes dental tissue proportions and crown dimensions of a large sample of human remains dated from the Late Pleistocene to mid-Holocene. With a continuous time span from the eighth to the fifth millennium BCE and dental remains originating from both Nubia and Central Sudan, this sample covers the Neolithic transition in a large area of the Nile Valley. This study will therefore address the following questions: (1) how distinct are Late Pleistocene, early Holocene and mid-Holocene populations, based on crown dimensions and dental tissue proportions? (2) If these differences are significant, could they be related to morpho-functional adaption resulting from new dietary habits? (3) If not, what can be the cause of such biological discontinuity? Biological characterization of these populations should therefore bring new insights into the understanding of the morphological shift and dental reduction reported around 8000 years ago.

2 | MATERIALS AND METHODS

Nine samples dated from the Late Paleolithic to the Neolithic and located both in Nubia and Central Sudan are considered in this study (see Figure 1 and Table 1). These samples are among the most complete human remains assemblages for this period in the Nile Valley. They precisely cover the transition from foraging to food-production in a wide area, extending across almost all of modern day Sudan. Three time periods are represented in this sample: the Late Paleolithic, the Mesolithic, and the Neolithic. The former includes the site of Jebel Sahaba ("JS"; Wendorf, 1968; Zazzo, 2014; Crevecoeur et al., 2021) which has been the main pre-Neolithic comparative sample in most previous studies (e.g., Anderson, 1968; Crevecoeur, 2008; Crevecoeur et al., 2009, 2023; Galland et al., 2016; Holliday, 2015; Irish, 2000, 2005, 2010). The Mesolithic group involves remains from the previously studied Mesolithic assemblage from El-Barga in Nubia ("EBK_M"; Benoiston et al., 2018) and more recently excavated and directly dated remains from the sites of Sphinx ("SPX") and Fox Hill in the western part of Jebel Sabaloka (Varadzinová et al., 2023). However, considering the few direct dates available so far at Fox Hill (highlighting both Mesolithic and Neolithic occupations) and the complex organization of the burial ground at this site (Varadzinová, Varadzin, Brukner Havelková et al., 2022; Varadzinová, Varadzin, Crevecoeur, et al., 2022), only clearly identified or directly dated Mesolithic individuals are included in this study (Fox Hill ["FHM"]). Finally, the Neolithic sample includes remains from Neolithic El-Barga ("EBK_N"; Crevecoeur, 2012), Kadruka 1 ("KDK"; Benoiston et al., 2018) and Ghaba in Central Sudan ("GHB"; Irish & De
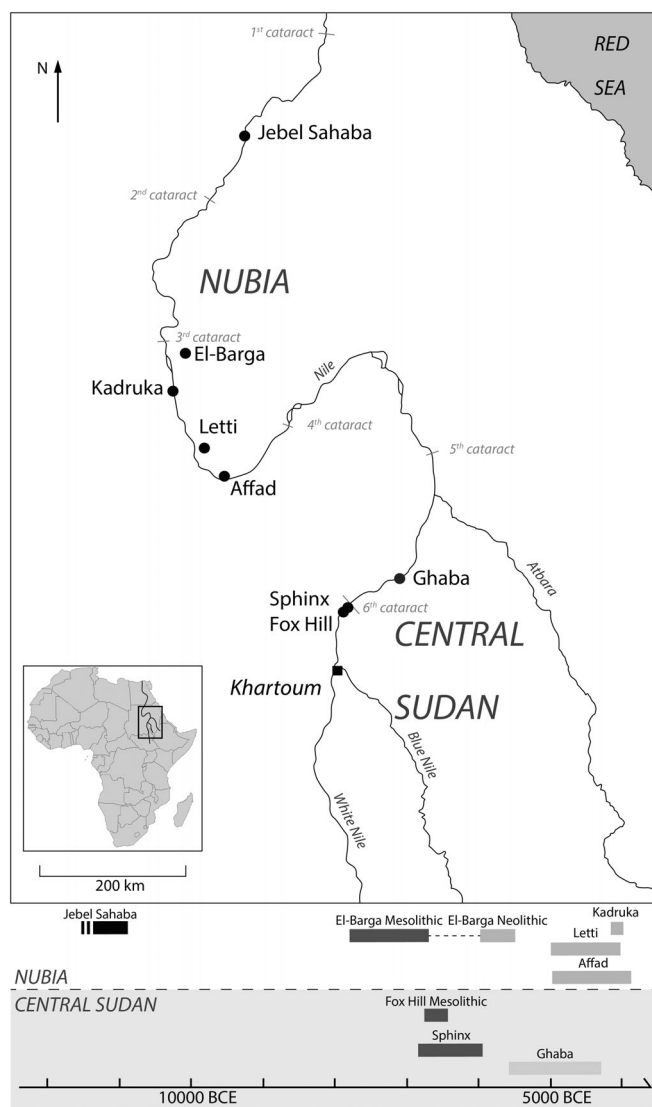
FIGURE 1 Location of the sites and samples used in this study. See Table 1 for details on the precise dating of the human remains assemblages.

Groote, 2016). Recently excavated and yet unpublished Neolithic remains from the Affad ("AFD") and Letti ("LTD") basins (Osypińska et al., 2020) were also included.

In total, this study analyses crown dimensions of 329 individuals (the entire dentition was considered, see Table S2 for tooth class details). Considering overall sample preservation, teeth with fewer wear, and to allow comparison with previous studies, we then focused on upper central incisors (n = 27), and upper first (n = 30) and second molars (n = 28) for an in-depth dental tissue proportion analysis (85 total teeth from 58 individuals, see Table 2).

2.1 | Outer crown dimensions

Buccolingual (BL) and mesiodistal (MD) crown diameters were recorded for all samples and all teeth following Bräuer (1988) and

using a digital caliper accurate to 0.01 mm. Teeth exhibiting substantial interproximal wear or damaged crowns were excluded from this study. To avoid duplicating the data unnecessarily and to have the most complete dataset possible, only left antimere measurements were considered here. When not available, the left antimere was substituted by the right antimere. Means of the BL and MD diameters of each tooth class (i.e., 32 measurements in total) were then computed for all samples separately.

Within-dentition crown dimension variations were monitored through tooth size apportionment (TSA) analysis developed by Hemphill (1991) and Harris (1997). This approach allows comparisons of whole dentitions, instead of each tooth individually (e.g., Hemphill, 2016; Irish et al., 2016; Romero et al., 2018). To minimize the effect of size that can substantially influence the results of TSA analyses (Irish & Kenyhercz, 2013), all 32 BL and MD measurements means were size-corrected for each sample separately following Darroch and Mosimann (1985) method. This consists of computing the geometric mean (the 32nd root of the product of the 32 mean measurements) per sample, and then dividing each mean measurement by their respective geometric mean. Principal component analysis (PCA) was computed on the correlation matrix of the 32 size-corrected mean crown dimensions. In order to better visualize the inter-sample relations, three-dimensional plots were computed on the first three principal components and hierarchical clustering analysis was performed on the size-corrected measurements using Ward's minimum variance agglomerative clustering. All statistical analyses were performed in R.

2.2 | Dental tissue proportions

Upper central incisors and first and second molars for which occlusal wear degree was less than Molnar (1971) grade 3 (small dentine patches) were selected for microtomographic acquisitions (μCT scans) and analysis of dental tissue proportions. Details on the acquisition devices are given in Table S1. The final volumes were reconstructed with an isotropic voxel size ranging from 16.01 to 42.00 μm. Using Avizo 9.5.0 (Thermo Fisher Scientific), a semi-automatic segmentation of the reconstructed images was performed, followed by manual corrections. According to Olejniczak's (2006) method, crowns were digitally separated from roots and dental tissue proportions were measured. These include the crown total volume (Vc), coronal enamel and coronal dentine volumes (Ve and Vd), percentage of the crown that is dentine and pulp (Vdp.Vc), enamel-dentine junction surface (Sedj), 3D average enamel thickness (AET), and 3D relative enamel thickness (RET)—a measurement independent of overall tooth size (Lockey et al., 2020; Martín-Francés et al., 2020; Olejniczak, Smith, et al., 2008; Olejniczak, Tafforeau, et al., 2008). Kruskal–Wallis tests were computed to assess any significant differences among all samples. Mann–Whitney U-tests were then used to identify which samples were significantly different. To have stronger statistical weight and avoid small sample-size bias, samples were pooled into larger geographically and chronologically coherent groups: Late

TABLE 1 Description of the samples used in this study.

Sample	Code	Site	Cultural affiliation	Date (d/i/c)[a]	Lifestyle	N	Archeological & chronological context	Dental analyses
Nubia								
Jebel Sahaba	JS	Jebel Sahaba / site 117	Late Paleolithic	16,650–11,450 BCE [d]	Hunter-fisher-gatherers	27	Wendorf, 1968; Zazzo, 2014	*Metrics and inner crown morphology: original data*
El-Barga Mesolithic	EBK_M	El-Barga, near Kerma	Mesolithic	7800–6700 BCE [i]	Hunter-fisher-gatherers	33	Honegger, 2005; Crevecoeur, 2012	UI1 and UM1: Benoiston et al., 2018; UM2: original data
El-Barga Neolithic	EBK_N	El-Barga, near Kerma	Early Neolithic	6000–5500 BCE [i]	Pastoralists and fishers	68	Honegger & Williams, 2015	
Kadruka	KDK	KDK1	Middle Neolithic	4200–4000 BCE [i]	Food-producers	26	Reinold, 2001	Original data
Affad	AFD	AFD 124, 127–130, 132, and 133	Middle Neolithic	5000–3900 BCE [i]	Food-producers	3	Osypińska et al., 2020	Original data
Letti	LTD	LTD2/B and LTD_Cluster1	Middle Neolithic	Fifth millennium BCE [c]	Food-producers	1	Yet unpublished	Original data
Central Sudan								
Sphinx	SPX	Jebel Sabaloka (West), SBK.W-60	Mesolithic	6800–5900 BCE [d]	Hunter-fisher-gatherers	44	Varadzinová et al., 2023; Brukner Havelková et al., 2022	Original data
Fox Hill Mesolithic	FHM	Jebel Sabaloka (West), SBK.W-20	Mesolithic	6700–6400 BCE [d]	Hunter-fisher-gatherers	8	Varadzinová, Varadzin, Brukner Havelková, et al., 2022; Varadzinová, Varadzin, Crevecoeur, et al., 2022	Original data
Ghaba	GHB	El-Ghaba	Early Neolithic	5600–4300 BCE [i]	Food-producers	119	Salvatori et al., 2016	Metrics: Irish & De Groote, 2016; Inner crown morphology: original data

[a,d]: direct radiocarbon dating on human remains (bones and/or teeth); [i]: indirect radiocarbon dating of the burials; and [c]: dating based on context.

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TABLE 2 Detailed sample of UI1, UM1, and UM2 used in the dental tissue proportions analysis.

Sample	UI1	UM1	UM2
Nubia			
JS	4	7	4
EBK_M	4	2	4
EBK_N	10	13	4
KDK	-	-	-
AFD	1	-	2
LTD	-	-	1
Central Sudan			
SPX	2	2	4
FHM	1	2	5
GHB	5	4	4

Abbreviations: AFD, Affad; EBK_M, Mesolithic El-Barga; EBK_N, Neolithic El-Barga; FHM, Mesolithic Fox Hill; GHB, Ghaba; JS, Jebel Sahaba; KDK, Kadruka; LTD, Letti; SPX, Sphinx.

Paleolithic (LP: JS), Nubian Mesolithic (MESON: EBK_M), Central Sudanese Mesolithic (MESOSC: SPX and FHM), Nubian Neolithic (NEON: EBK_N, AFD, and LTD), and Central Sudanese Neolithic (NEOSC: GHB). Kruskal–Wallis and Mann–Whitney tests were computed for these groups as well. All statistical analyses were performed in R.

To compare the enamel thickness distribution between samples, 3D surface models were computed for the outer enamel surface (OES) and enamel-dentine junction (EDJ) using constrained smoothing (Kupczik & Hublin, 2010). 3D enamel thickness maps were then computed as the distance between the OES and EDJ (Macchiarelli et al., 2008). The teeth of individuals that reflect the AET of LP, MESON, MESOSC, NEON and NEOSC samples were selected as mean representatives of their group.

3 | RESULTS

3.1 | Outer crown measurements

The raw mean MD and BL measurements for the whole dentition and all samples are displayed in Table S2, and size-corrected mean measurements are listed in Table S3. Considering the few teeth and lack of complete dentitions recovered from AFD and LTD, these samples were excluded from the odontometric analyses (they are however included in the dental tissue proportions analyses).

All 32 size-corrected measurements of the seven remaining samples were submitted to PCA. The three first components account for 74.83% of the total variance, their loadings and eigenvalues are listed in Table S4. The three-dimensional graphic representation of these components (Figure 2) and a Ward's dendrogram computed on the size-corrected measurements (Figure 3) both show clear distinction between the Neolithic samples (GHB, KDK, and EBK_N) and all forager samples (JS, SPX, EBK_M, and FHM). This distinction appears to

be mainly determined by the first two components of the PCA, with the Neolithic samples plotting in the negative values of PC1 and PC2, while the Mesolithic samples (EBK_M, FHM, and SPX) and Late Paleolithic JS are rather found in the positive values and/or near zero on each component. When considering the detailed loadings of each component, the Neolithic samples are characterized by high magnitude (>|0.5|) negative loadings on both component 1 and component 2, which relate to relatively large upper canines, upper first molars, and lower incisors. In the same way, these individuals appear to have relatively large MD dimension for UI1, UP1, UP2, LP2, and LM1, as well as BL diameters for the lower canines only. On the contrary, as EBK_M and FHM are mostly characterized by high magnitude positive loadings on component 1, they show relatively large upper third molars and lower second molars, and have relatively large MD dimensions for UI2 only and BL dimension for UP1, UM2, LP1, LP2, and LM3. Similarly, it appears that JS and SPX are characterized by high magnitude positive values on PC2 (i.e., relatively large BL dimension for upper incisors and LP1, and MD diameters for upper second molars).

Component 3 accounts for 15.3% of the total variance and appears to only distinguish EBK_M individuals from the rest of the sample. This distinction appears to be related to EBK_M individuals having a relatively large BL dimension for upper canines and second premolars, and MD for lower canines and first premolars (high magnitude negative loadings on PC3). At the same time, these individuals would appear to have relatively small lower third molars and BL dimensions for UI1 only.

3.2 | Dental tissue proportions

Dental tissue measurements for each tooth type and all samples (LP, MESON, MESOSC, NEON, and NEOSC) are presented in Figure 4. Data for each sample (JS, EBK_M, SPX, FHM, GHB, EBK_N, AFD, and LTD) are displayed in Figure S1, with samples mean, standard deviation, and range in Table S5, and individual enamel thickness values in Tables S6–8. Results of Kruskal–Wallis tests and Mann–Whitney U-tests for the inter-sample comparisons are also presented in both figures. Enamel thickness maps for LP, MESON and MESOSC, and NEON and NEOSC samples are also displayed in Figures 5–7.

3.3 | Maxillary central incisors

Significant variations of dental tissue proportions are present between sites and groups for the UI1s (Figure 4a, Figure S1A). The most striking and singular pattern is expressed by the JS LP individuals. Although having significantly higher values of dentine volume and on average larger EDJ surface, with respect to the other comparative samples, they possess very similar enamel volume values to them. In the same way, JS individuals exhibit significantly higher percentages of dentine and pulp in the crown, especially compared to Nubian individuals (both MESON and NEON). As a consequence, the JS sample lies in the lowermost part of AET values, outside all other comparative

FIGURE 2 Three-dimensional plot of the first three components scores for tooth size apportionment on seven Nile Valley samples (see Table 1 for site abbreviations). Components variance: PC1 = 38.0%; PC2 = 22.8%; and PC3 = 15.3%. EBK_M, Mesolithic El-Barga; EBK_N, Neolithic El-Barga; FHM, Mesolithic Fox Hill; GHB, Ghaba; JS, Jebel Sahaba; KDK, Kadruka; SPX, Sphinx.
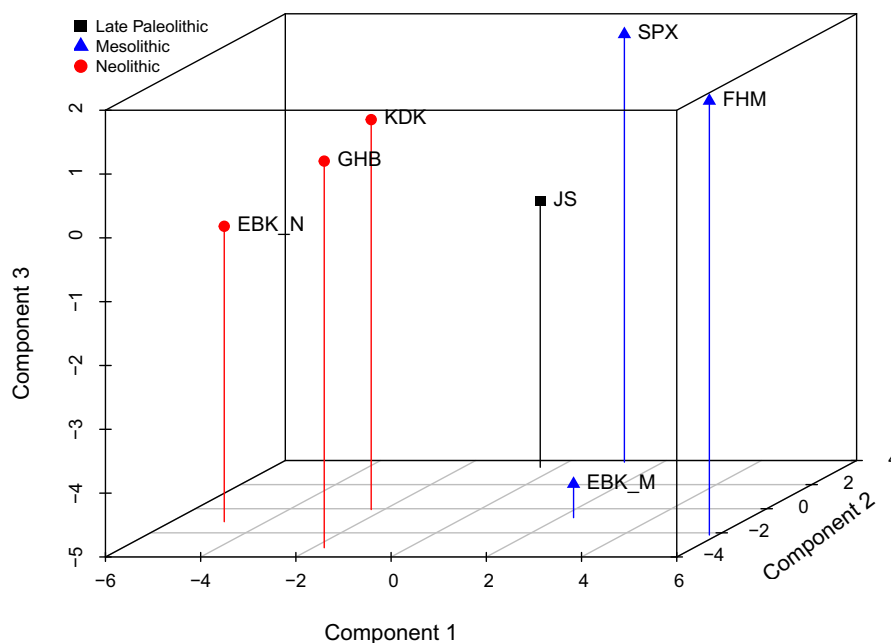
group variability, and has significantly lower RET than the others. Surprisingly, while the Mesolithic individuals from SPX) exhibit the strongest similarities in terms of crown dimensions, dentine volume, and EDJ surface value with JS, they align with the other Mesolithic site EBK_M regarding their average and RET (see Figure S1A). This might be due to the small sample size of Mesolithic individuals as, once regrouped in MESOSC and MESON, both align for all variables measured (Figure 4a). Interestingly, despite very low EDJ surface, crown, enamel, and dentine volumes, the only UI1 from FHM aligns with the other Mesolithic sites examined (EBK_M and SPX) in terms of average and RET. This relates to similar tissue proportions between all these sites. Finally, the Neolithic groups tend to have lower enamel thickness in comparison to the Mesolithic sample (mean RET values: MESON = 17.62; MESOSC = 16.51; NEON =15.63; and NEOSC = 15.17). This trend is mostly related to the size of Neolithic individual EDJ surface values, which are slightly higher than with most of the Mesolithic sites.

Enamel thickness distribution maps (Figure 5) show that, despite having significantly lower RET values, LP individuals display the same topography as Mesolithic groups (MESON and MESOSC). This consists of a major thickening of the buccal surface and occlusal part of the distal aspects of the crown. In comparison, Neolithic samples lack this reinforcement of the buccal surface. This might explain the relatively lower AET and RET values of these individuals compared to those of the hunter-gatherer groups. No difference appears between NEON and NEOSC samples.

3.4 | Maxillary first molars

The UM1s from JS individuals display on average high values of EDJ surface and dentine volume (Figure 4b), compared to the other samples. Still, these individuals tend to have lower enamel volume values
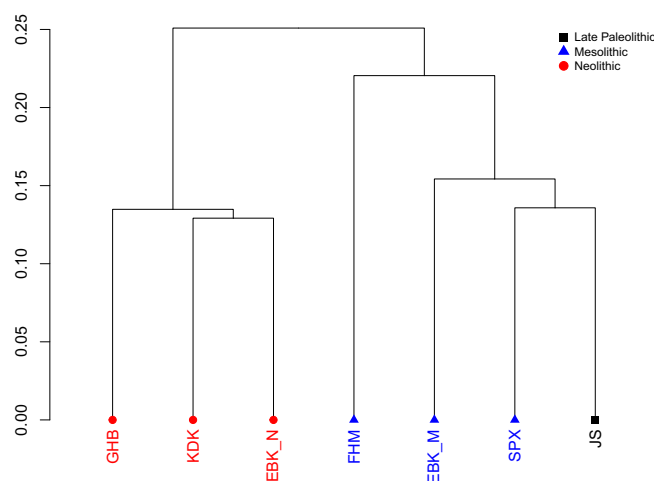

FIGURE 3 Ward's minimum variance agglomerative clustering dendrogram based on the size-corrected crown measurements of seven Nile Valley samples (see Table 1 for site abbreviations). EBK_M, Mesolithic El-Barga; EBK_N, Neolithic El-Barga; FHM, Mesolithic Fox Hill; GHB, Ghaba; JS, Jebel Sahaba; KDK, Kadruka; SPX, Sphinx.

with regard to those of dentine volume. This results in significantly higher Vdp.Vc values and lower average and RET values. The individuals from Mesolithic SPX display high crown and dentine volumes, aligning with JS variability and on average higher than EBK_M and FHM (see Figure S1B). However, having proportionally higher enamel volume values than all samples, SPX individuals show high average and RET values and align with all other Mesolithic samples. Variation is also noted at the regional scale (i.e., between MESON and MESOSC) for EDJ surface and dentine volume, with the Nubian individuals showing relatively lower values. Still, the mean AET (MESON = 1.57 mm; MESOSC = 1.42 mm) and RET values (MESON = 23.77; MESOSC = 21.35) are very similar between
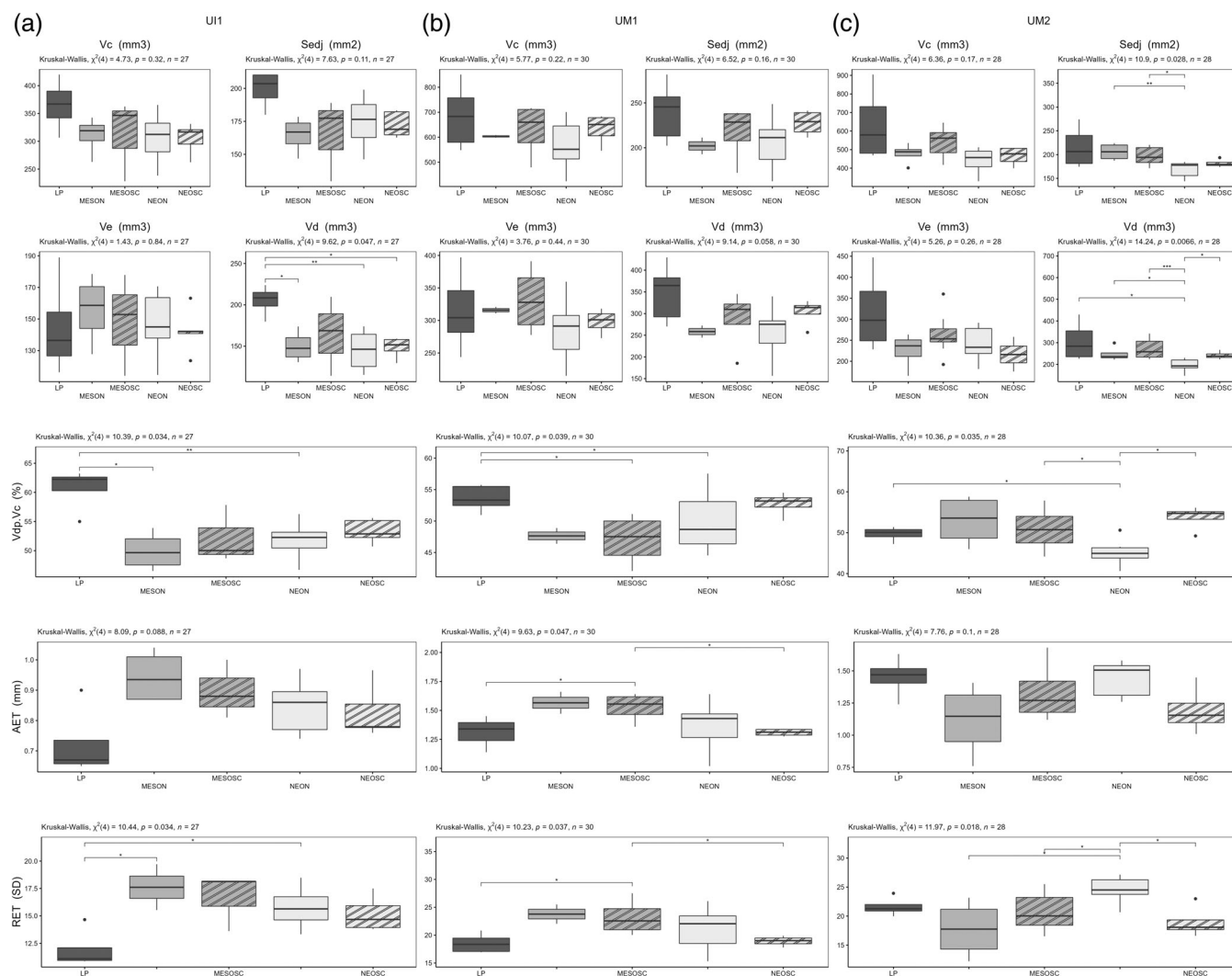
FIGURE 4 Dental tissue proportions for all tooth types and groups. Only significant Mann–Whitney tests results are shown ('*': $p < 0.05$; '**': $p < 0.01$; '***': $p < 0.001$; '****': $p > 0.0001$). See Table 1 for site abbreviations. AET, average enamel thickness; RET, relative enamel thickness; Sedj, enamel-dentine junction surface; Vc, crown volume; Ve, coronal enamel volume; Vd, coronal dentine volume; Vdp.Vc, percentage of the crown that is dentine and pulp.

groups. Finally, considering Neolithic groups NEON and NEOSC, Nubian individuals display on average low crown, dentine, and enamel volume values, compared with MESON individuals. Still, they tend to have greater percentage of dentine and pulp in the crown, with relatively lower enamel volume values than the Mesolithic samples, resulting in slightly lower mean average and RET (AET = 1.38 mm; RET = 21.26). Moreover, NEOSC individuals tend to have relatively higher EDJ surface and dentine volume values than NEON, while having similar enamel and crown volume values. This results in Vdp.Vc values similar to those of the LP population and significantly lower average and RETs, again closer to the variability observed in these LP individuals from JS.

Considering enamel thickness topography (Figure 6), JS appears to have thin enamel on the occlusal aspect of molars, with the thickest area of enamel on the distal aspect of the hypocone. Still, it does not substantially differ from the Mesolithic groups as they all display homogeneously distributed enamel thickness. Only the occlusal and

distal parts of the hypocone cusp appear to be slightly thickened for these individuals too. Conversely, the Neolithic samples from both Nubia and Central Sudan exhibit significantly different distribution, with very thick enamel on both lingual cusps (hypocone and protocone) and especially on their lingual aspects. Slight variation is also noticeable between EBK_N and GHB sites, with the Central Sudanese individuals exhibiting a significant reinforcement on the buccal aspect of the crown that the Nubian teeth miss.

3.5 | Maxillary second molars

Considering second molar dental tissue proportions (Figure 4c), LP individuals tend to have relatively higher crown and enamel volumes than all others, while also having EDJ surface values similar to those of Mesolithic samples. Nevertheless, they display similar average and RET values with the other hunter-gatherer samples (only the AET

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FIGURE 5   Enamel thickness maps of upper central incisors in occlusal (O), mesial (M), distal (D), buccal (B) and lingual (L) views. Chromatic scale values in millimeter. JS: JS_13 (right incisor flipped); MESO (Nubia): EBK_T121; MESO (Central Sudan): SBK_W60_B44 (right incisor flipped); NEO (Nubia): EBK_T20; NEO (Central Sudan): GHB_G313.
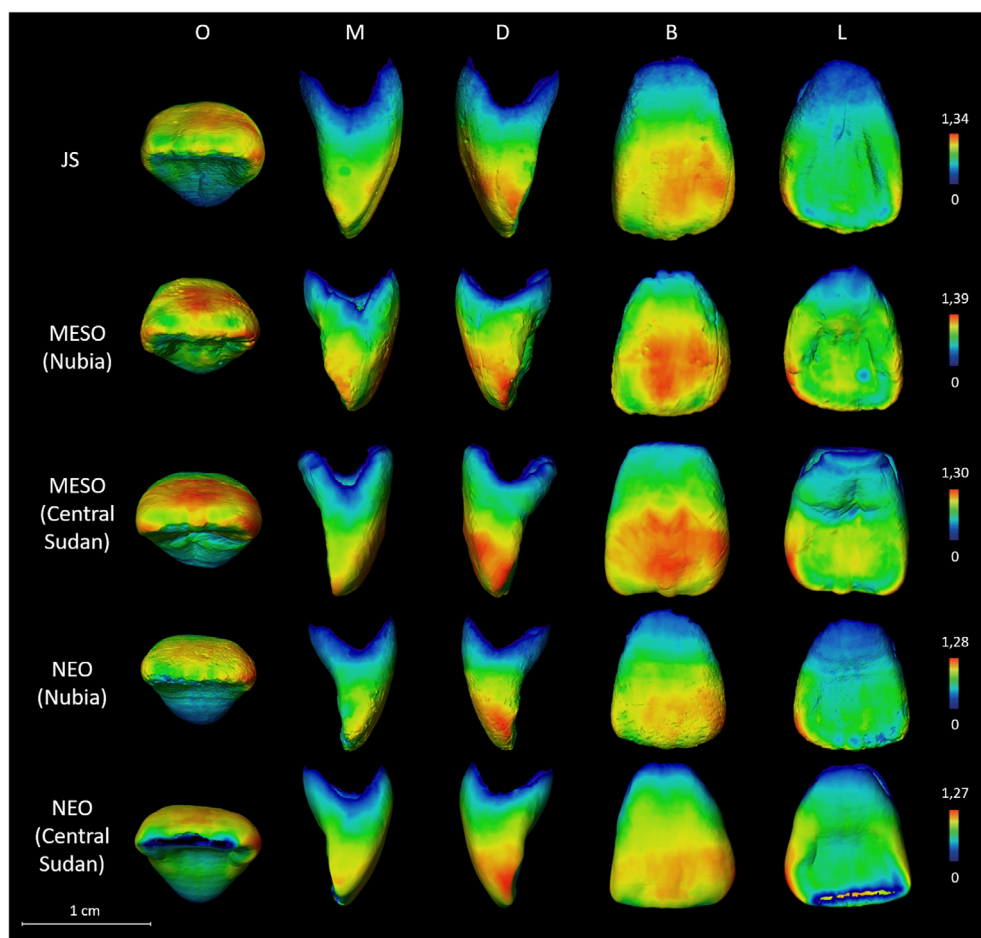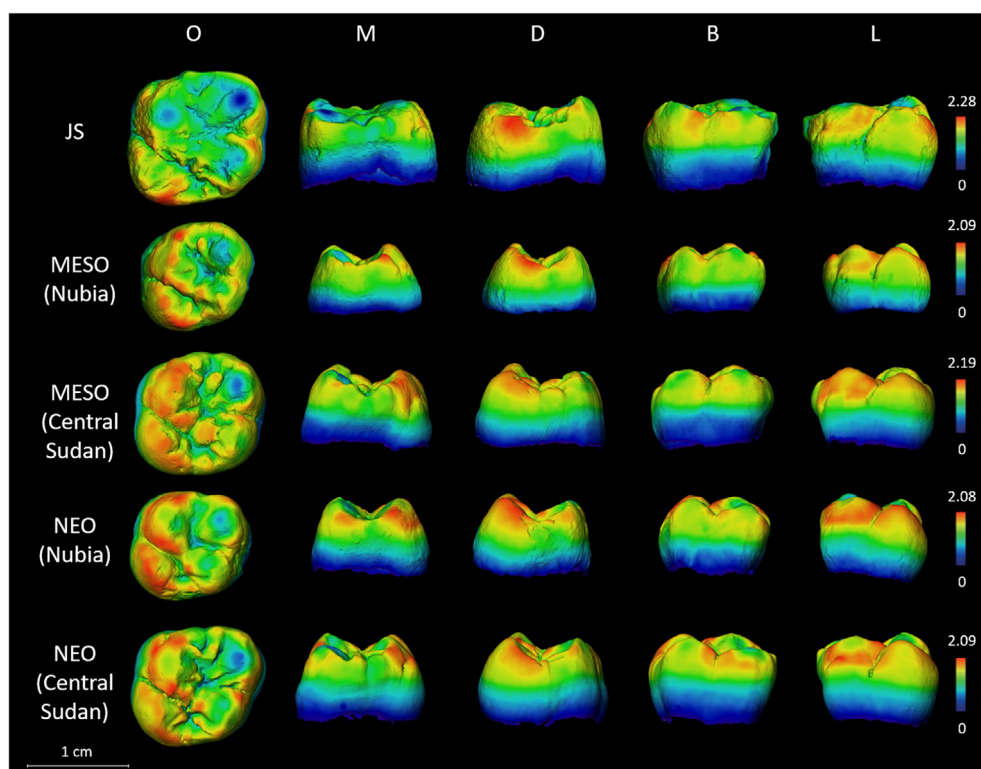
FIGURE 6   Enamel thickness maps of upper first molars in occlusal (O), mesial (M), distal (D), buccal (B) and lingual (L) views. Chromatic scale values in millimeter. JS: JS_24 (right molar flipped); MESO (Nubia): EBK_T140b (right molar flipped); MESO (Central Sudan): SBK_W60_B31 (right molar flipped); NEO (Nubia): EBK_T115; NEO (Central Sudan): GHB_G107.
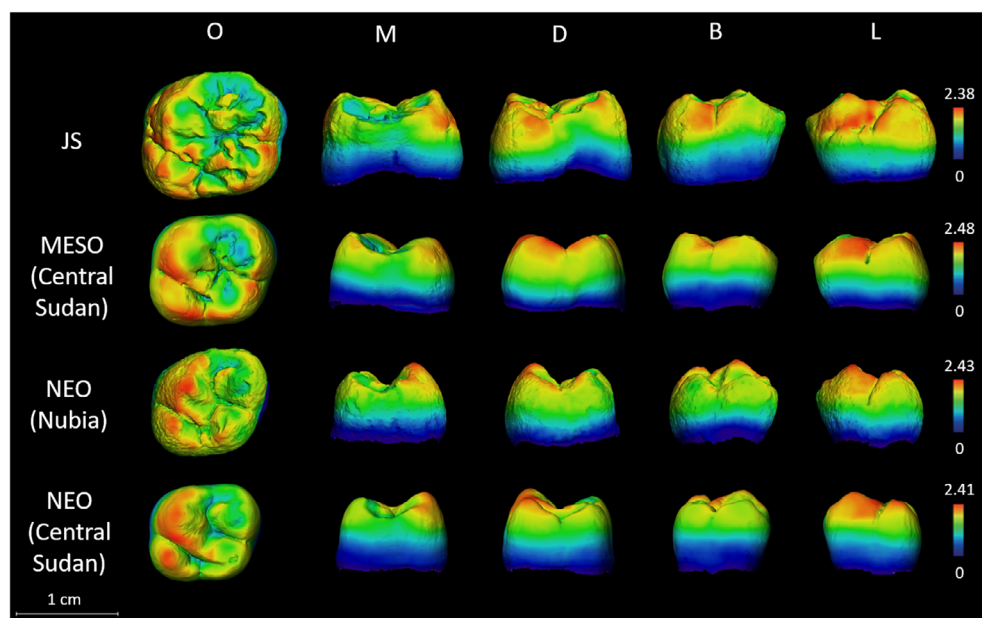
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FIGURE 7 Enamel thickness maps of upper second molars in occlusal (O), mesial (M), distal (D), buccal (B) and lingual (L) views. Chromatic scale values in millimeter. JS: JS_24 (right molar flipped); MESO (Central Sudan): SBK_W60_S6_LB1/15 (right molar flipped); NEO (Nubia): AFD_132_G1; NEO (Central Sudan): GHB_G91.

values are slightly higher for the JS population). Significant reductions in EDJ surface, dentine, and Vdp.Vc values appear between hunter-gatherer groups (LP, MESON, and MESOSC) and NEON. Still, there is little to no variation of enamel volume between these groups. This results in slightly higher AET and significantly higher RET (mean NEON RET = 24.62). Finally, although NEOSC individuals show crown volume and EDJ surface values close to the other Neolithic samples, they exhibit noticeably different patterns with respect to tissue proportions. In fact, these individuals tend to have lower enamel volumes than all other samples (LP, MESOSC, MESON and NEON), while at the same time having relatively high dentine volumes, similar to the hunter-gatherer samples. This difference in enamel/dentine proportion results in significantly higher Vdp.Vc, relatively lower AET, and significantly lower RET compared to NEON individuals. This places the NEOSC group in the lowermost part of Mesolithic variability.

Enamel thickness maps show little variation between LP and MESOSC samples (Figure 7). All these individuals display homogeneously distributed enamel with the thickest area around the crown. This significantly differs from the topographies observed in Neolithic samples, which show the thickest enamel on the lingual cusps and overall thin enamel on the distal and buccal surfaces (especially Central Sudanese GHB individuals). Despite significant differences in terms of dental tissue proportions, no clear topographic variation appears between Nubian and Central Sudanese samples. Finally, considering the occlusal wear stages on EBK_M individuals (stages 2–3 based on Molnar (1971)), no enamel thickness map was computed for this sample.

4 | DISCUSSION

The outer and inner aspects of dental crown dimensions studied here highlight numerous variations and differences between sites and especially between Mesolithic and Neolithic individuals. This supports the results of several previous studies (Benoiston et al., 2018; Crevecoeur et al., 2023; Irish, 2005) that showed significant changes in cranial and crown outer morphology, dimensions, and enamel thickness between hunter-gatherer and food-producing populations from the Nile Valley.

Tooth size apportionment analysis and dental tissue proportions show significant affinities between all MESON and MESOSC samples (FHM, SPX, and EBK_M) and the LP site of Jebel Sahaba. JS and SPX individuals appear to share significant similarities both on outer and inner aspects. Conversely, tooth crown measurements display substantial variations between Neolithic groups and earlier samples in tooth apportionment within the dentition.

Similar patterns are noted in the enamel thickness distribution. Jebel Sahaba and Mesolithic samples all display homogeneous distribution, even though the LP individuals stand out by having significantly lower RET values for upper central incisors and first molars. When compared with the earlier samples, Neolithic individuals show significant variation in dental tissue proportions and enamel thickness distribution. Topographies specific to the foraging and to the food-producing populations were found: a significant enamel thickening of the buccal aspect of the Late Paleolithic and Mesolithic upper first incisors and homogeneously distributed enamel thickness in their first and second upper molars; a significant thickening of the lingual cusps (hypocone and protocone) of the Neolithic molars and relatively thin enamel on the buccal aspect of their first upper incisors.

Finally, upper second molars dental tissue proportions showed significant variation between Central Sudanese Neolithic GHB and other Nubian Neolithic samples (EBK_N, AFD, and LTD). Still, little variation in enamel thickness distribution was found between these groups, except for an enamel thickening on the buccal aspect of GHB upper first molars that Nubian individuals lack.

Tooth crown morphology and dimensions are determined by multiple controls, such as genetic, epigenetic, and environmental factors

(Dempsey & Townsend, 2001; Grine, 2005; Kono et al., 2002; Townsend et al., 2009). Twin studies highlighted the high heritability of crown outer measurements (MD and BL diameters), with minimal influence from epigenetic and environmental factors for maxillary teeth and BL dimensions (Dempsey & Townsend, 2001; Potter & Nance, 1976; Townsend et al., 2009). Interpretation of enamel thickness and enamel distribution are more debated, as there might be greater influence of diet-related functional aspects (Constantino et al., 2009; Hlusko et al., 2004; Horvath et al., 2014; Le Luyer & Bayle, 2017). Although the pressure of diet on enamel cap morphology is significant for comparisons at the genus level, studies on modern humans showed relatively low influence of it and high underlying genetic control (Grine, 2005; Kono et al., 2002). Previous studies also highlighted some level of sexual dimorphism in dental tissue proportions (e.g., Smith, Olejniczak, Reid, Ferrell & Hublin, 2006; Sorenti et al., 2019; Fernée et al., 2020). Considering that only few sex estimations are available for the individuals studied here, as a result of medium-to-poor preservation of the remains, enamel thickness measurements presented here do not account for possible influence of sex. Still, comparison with the results of TSA and enamel distribution suggests most probably minor influence of biological sex on the signal recorded for dental tissue proportion as very similar results and differences are monitored for each analysis. In summary, all proxies studied here appear to be under high genetic control and only slightly influenced by epigenetic factors, therefore providing reliable insights into biological relatedness estimates and micro-evolution analyses. Still, to assess the potential effect of the diet on the enamel thickness and distribution variation, thorough discussion of this issue is provided further below.

4.1 | Jebel Sahaba: A unique population?

Previous studies on dental nonmetric traits (Irish, 2000, 2005; Irish & Usai, 2021), but also cranial (Anderson, 1968; Crevecoeur, 2008; Crevecoeur et al., 2009, 2023; Greene, 1972) and postcranial (Holliday, 2015; Shackelford, 2007) evidence described Jebel Sahaba as an outlier in the later biological diversity spectrum of the Nile Valley, mostly in comparison with Neolithic and later populations. On the contrary, with high frequencies of mass-additive nonmetric traits (e.g., UI1 shoveling, LM1 entoconulid, UM1 enamel extension), affinities were rather found between the Late Pleistocene individuals and historic sub-Saharan populations (Holliday, 2015; Irish, 2000, 2005; Irish & Usai, 2021). The new data presented here also provide further example of the significant differences, in both outer and inner dental aspects, displayed between the JS population and Neolithic samples from the Nile Valley. However, major similarities were highlighted between JS and Mesolithic groups (EBK_M, FHM, and especially SPX). The only major difference between JS and later hunter-gatherers that this study highlighted is that the LP population displayed significantly lower RET values for both upper central incisors and upper first molars. As detailed above, this results from the very high dentine volume, EDJ surface, and Vdp.Vc values compared with the enamel

volumes of these individuals. Interestingly, despite clear crown volume and outer BL and mesiodistal diameter reduction (Table S2) between JS and the Mesolithic groups (EBK_M, SPX, and FHM), little to no variation in enamel volume is recorded. Therefore, it would seem that the decrease in tooth size and crown volume between the Late Paleolithic individuals and Mesolithic samples was substantially driven by a decrease of absolute dentine volume. Variations of dentine volume preferentially to enamel volume in a context of dental reduction are not surprising, and has already been documented (e.g., Grine, 2002, 2005; Olejniczak, Smith, et al., 2008). Therefore, these differences in enamel thickness between the JS population and the other hunter-gatherer groups might rather be related to overall dental reduction than clear biological differences.

We suggest that the overall homogeneity, between Jebel Sahaba and early Holocene populations, but also between the Mesolithic samples, indicates biological proximity between hunter-gatherer groups from the Late Pleistocene through the early Holocene. In fact, despite substantial cultural and behavioral differences between these populations, there seems to be clear biological affinities between the Late Paleolithic JS and the Mesolithic groups studied here across Sudan. However, results of nonmetric traits analysis (Irish & Usai, 2021) on the pre-Mesolithic individuals from Al-Khiday in Central Sudan highlighted significant morphological differences with JS.

These few disparities between pre-Mesolithic Al-Khiday and those between the samples in this study (e.g., EBK_M individuals showing some differences in TSA) should be acknowledged as they might provide further insights in the complexity of the pre-Neolithic population of the Nile Valley. These local variations, with apparent overall homogeneity, might actually reflect and result from the earlier population dynamics and history of the Nile Valley. In fact, previous studies on Late Pleistocene North-eastern African population substructure in the Late Pleistocene highlighted fragmented and phenotypically diverging subgroups (see Crevecoeur et al., 2023). Some aspects of this very complex population substructure might have lasted until the early Holocene, and impacted the phenotypes of samples under study here.

4.2 | The Neolithic transition: Population continuity versus discontinuity

Several significant differences were highlighted between hunter-fisher-gatherer and food-producer samples. Some support previous observations on outer crown dimensions, but also significant changes in dental tissue proportions and enamel thickness distribution of upper central incisors and first molars (Benoiston et al., 2018). The results from this study acknowledge even more complex dental changes between the Late Pleistocene to early Holocene groups and the mid-Holocene populations. Several morpho-functional adaptation models (probable mutation effect: Brace, 1963; Brace & Mahler, 1971; increasing population density effect: Macchiarelli & Bondioli, 1986; and selective compromise effect: Calcagno & Gibson, 1988) were hypothesized to describe, explain, and predict

such dental morphological shift and size variation in a worldwide context of the Neolithic transition. All of these models are based on the hypothesis of a dramatic change in dietary habits that would have accompanied the transition to food production. This new diet is assumed to be much softer, as a result of the introduction of pottery and new cooking habits, but also much more abrasive, as the introduction of grinding stones would have led to significant consumption of stone grit from the grinders. This would have resulted in an overall reduction and simplification of the teeth. These models also suggest that significantly poorer (dental) health status and more severe dental wear are also assumed to result from this new lifestyle.

These scenarios might have been true for some regions (e.g., Southern Levant; Pinhasi et al., 2008), but archaeological data from the Nile Valley do not seem to support such a shift in diet. As a matter of fact, hunter-gatherer populations in Africa did use and produce pottery as early as the 10th millennium BCE (Huysecom, 2020), with the earliest attestations along the Nile in the early ninth millennium BCE (Garcea et al., 2020; Varadzinová et al., 2023) and numerous grinding stones, suggested to have been used for food preparation, were also excavated from Mesolithic sites along the Nile (Řídký et al., 2022; Ryan et al., 2016; Salvatori et al., 2018; Usai, 2014). In this regard, it appears that cooking habits did not substantially vary between early and mid-Holocene Nile Valley peoples. In fact, the Neolithic diet only differed from the Mesolithic one by the introduction of domesticated cereals (wheat and barley) and animals (cattle, sheep, and goats; Salvatori & Usai, 2019b).

These new food resources, and especially cereals, could indeed represent a higher risk of abrasion (higher intake of phytoliths; Xia et al., 2015; Rodriguez-Rojas et al., 2020) or of caries (higher intake of carbohydrates; Navia, 1994; Caselitz, 1998; Reich et al., 1999). However, we suggest this would not have significantly impacted dental health of the Neolithic populations. This is supported by the prevalence of tooth wear and caries in Neolithic samples (e.g., 1.7% prevalence of carious lesions for GHB and minor to medium occlusal wear; Irish & De Groote, 2016) that is in several instances lower than in hunter-gatherer samples (e.g., Mesolithic SPX individuals display medium to very severe wear degrees with cupped or half-cupped profiles; Brukner Havelková et al., 2022). The latter assumption is also supported by the homogeneity of all Neolithic samples, and because this adoption of food-producing practices occurred very gradually and heterogeneously throughout the Nile Valley (see Monroe et al., 2023).

This heterogeneity of subsistence strategies is reflected within our sample with Neolithic El-Barga. Of interest, faunal remains from this site mainly include Nilotic resources and possible domesticated animals, with no evidence of domesticated plants (Linseele, 2012), suggesting these individuals would have had a similar diet to hunter-gatherers. Still, no variation in dental health is found between EBK_N and later cereal-consuming populations in our sample (e.g., AFD, GHB, or KDK), even though marked change in diet occurred between samples (Irish & De Groote, 2016; Maines, 2019; Osypińska et al., 2020; Ryan et al., 2016; Salvatori & Usai, 2019a, 2019b). This finding does not support the hypothesis of decreasing dental health accompanying the introduction of domesticated plants in the food-producing diet. In

the same way, homogeneity in dental data on both inner and outer aspects among all Nubian Neolithic samples, despite significant subsistence strategy differences, does not suggest diet-related change.

In this regard, it seems that the morpho-functional adaptation models do not fit the archaeological context of the Nile Valley or the novel data presented here; we do not discern any substantial change in dietary habits, worsening dental health, nor additional tooth size apportionment variations and enamel thickness changes during the Neolithic period and intensification of food-producing practices. Moreover, we need to acknowledge that all dental variations highlighted in this study would have to have happened in an extremely short time. Yet, only seven centuries separate the Mesolithic from Neolithic samples considered here in Nubia and 200 years at most for those in Central Sudan. Within the entire collection studied here, samples from both periods overlap chronologically (SPX and EBK_N, see Table 1). In this regard, it appears the variation highlighted here occurred much faster than elsewhere in the world (e.g., Brace et al., 1987; Pinhasi et al., 2008). We suggest that such a rapid shift in dental dimensions and enamel thickness distribution could not have happened through an in situ adaptation or evolutionary process, even within the context of a transition to food production. Conversely, we suggest this is consistent with some measure of biological discontinuity between early Holocene and later Neolithic groups. In other words, this suggests the Jebel Sahaba and Mesolithic populations studied here did not—or very little—contribute genetically to later Neolithic populations included in this study. Nevertheless, the contribution of some pre-transition groups to Neolithic populations should not be entirely ruled out, as the latest study on dental nonmetric traits highlighted some affinities and morphological proximities between pre-Mesolithic Al-Khiday (Central Sudan) and later samples associated with food-production (Irish & Usai, 2021). In this regard, it would appear that the Al-Khiday pre-Mesolithic population contributed, to some extent, to later population phenotypes and might be ancestral. Still, to date, no other hunter-fisher-gatherer population from the Nile Valley has shown affinities with later food-producers from the region, and the Al-Khiday contribution to Neolithic populations could be a unique phenomenon. Thus, we suggest that significant gene flow likely accompanied the arrival of domesticated plants and animals during and after the sixth millennium BCE. Still, some isolated and local events of admixture might have happened with pre-transition hunter-gatherers (like the people from Al-Khiday) contributing some aspects of their phenotypes to later populations.

4.3 | Regional diversity during the Neolithic period?

Beyond overall homogeneity with other Neolithic samples, Ghaba individuals tend to have distinctive features and characteristics on both outer and inner aspects (see above). These variations are of lesser significance than those highlighted between hunter-gatherers and Neolithic individuals but are nevertheless specific to this Central Sudanese sample. We should acknowledge some micro-regional

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morphological and metric variation between Neolithic Nubia and Central Sudan. Previous studies of dental nonmetric traits (Irish, 2005, 2010; Irish & Usai, 2021) highlighted the existence of a North–South cline throughout Nubia, distinguishing samples from Upper and Lower Nubia. The same phenomenon might be evident here between (Upper) Nubia and Central Sudan. This would suggest that, despite overall uniform and shared morphology, crown size, and enamel thickness, Neolithic groups locally varied and acquired specific dental features. Such regional diversity can result from many complex processes, including genetic drift, admixture with other/earlier groups, and isolation, among others. Further investigations on additional sites and new samples from Central Sudan and/or Nubia are needed to validate these hypotheses and better understand this diversity.

5 | CONCLUSION

The recent excavations of early to mid-Holocene cemeteries in the Nile Valley provided novel data on the biological profiles of these populations. The study of outer and inner aspects of the tooth crown highlighted significant changes in crown size and tissue proportions between the last hunter-fisher-gatherers and first food-producers. This includes variation in the tooth size apportionment, differences in the dental tissue volumes and enamel thickness, and changes in the enamel thickness distribution. Considering that such shifts occurred in an extremely short time (a few centuries at most), we suggest that significant biological discontinuity happened during the Neolithic transition. The first evidence of complex and varying settlement processes along the Nile River were also identified, distinguishing Nubian from Central Sudanese individuals. More in-depth analyses of the EDJ shape will promote finer-grained characterization of the morphological variation highlighted here. It will also allow a better understanding of the factors contributing to the variation in crown diameters, tissue proportions and dental nonmetric traits, as well as a better understanding of the micro-regional specificities in the Neolithic populations.

AUTHOR CONTRIBUTIONS

Nicolas Martin: Conceptualization (equal); formal analysis (lead); funding acquisition (supporting); investigation (equal); methodology (lead); writing – original draft (lead); writing – review and editing (equal). **Adrien Thibeault:** Formal analysis (supporting); methodology (supporting); writing – review and editing (equal). **Lenka Varadzinová:** Data curation (equal); funding acquisition (equal); writing – review and editing (equal). **Stanley H. Ambrose:** Writing – review and editing (equal). **Daniel Antoine:** Data curation (equal); writing – review and editing (equal). **Petra Brukner Havelková:** Data curation (equal); funding acquisition (equal); writing – review and editing (equal). **Matthieu Honegger:** Data curation (equal); writing – review and editing (equal). **Joel D. Irish:** Data curation (equal); writing – review and editing (equal). **Piotr Osypiński:** Data curation (equal); funding acquisition (equal); writing – review and editing (equal). **Donatella Usai:** Data curation (equal); writing – review and editing (equal). **Nicolas**

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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ENDNOTE

[i] In this study we refer to Nubia as the region between the 1st and 5th cataract of the Nile and Central Sudan as the area south of the 5th cataract. Some other authors consider Nubia to extend from the 1st cataract of the Nile to the confluence of the White and Blue Nile rivers, near Khartoum in Sudan (Adams, 1977; Williams & Emberling, 2021).

REFERENCES

Adams, W. Y. (1977). *Nubia: Corridor to Africa*. Allen Lane.

Anderson, J. E. (1968). Late Paleolithic skeletal remains from Nubia. In F. Wendorf (Ed.), *Prehistory of Nubia* (pp. 996–1040), Fort Burgwin Research Center, Inc.

Crevecoeur, I., Matu, M., Dias-Meirinho, M., Bayle, P., & Pearson, O. (2023). Paleoanthropology and population processes since the MIS 3 in north-east Africa, a regional synthesis. In Lesur, et al. (Eds.), *Du Big dry à l'Holocène en Afrique de l'est et au-delà*. Bulletins de la Société Préhistorique Française.

Armelagos, G. J., Van Gerven, D. P., Goodman, A. H., & Calcagno, J. M. (1989). Post-Pleistocene facial reduction, biomechanics and selection against morphologically complex teeth: A rejoinder to macchiarelli and bondioli. *Human Evolution*, 4(1), 1–7. https://doi.org/10.1007/BF02436415

Benoiston, A.-S., Bayle, P., & Crevecoeur, I. (2018). Biological affinity of the Mesolithic and Neolithic populations from El-Barga, Sudan: The dental remains. In *Nubian archeology in the 21st century* 1st-6th September 2014 (pp. 805–817). Peeters Publishers.

Brace, C. L. (1963). Structural reduction in evolution. *The American Naturalist*, 97(892), 39–49. https://doi.org/10.1086/282252

Brace, C. L., & Mahler, P. E. (1971). Post-Pleistocene changes in the human dentition. *American Journal of Physical Anthropology*, 34(2), 191–203. https://doi.org/10.1002/ajpa.1330340205

Brace, C. L., Rosenberg, K. R., & Hunt, K. D. (1987). Gradual change in human tooth size in the late Pleistocene and post-Pleistocene. *Evolution*, 41(4), 705–720. https://doi.org/10.1111/j.1558-5646.1987.tb05847.x

Brass, M. (2013). *Revisiting a hoary chestnut: The nature of early cattle domestication in North-East Africa*. SAHARA.

Brass, M. (2018). Early north African cattle domestication and its ecological setting: A reassessment. *Journal of World Prehistory*, 31(1), 81–115. https://doi.org/10.1007/s10963-017-9112-9

Brukner Havelková, P., Crevecoeur, I., Villotte, S., Veleminský, P., Varadzin, L., & Varadzinová, L. (2022). Palaeodemography and palaeopathology of Khartoum Mesolithic skeletal remains from Jebel Sabaloka in central Sudan: First insights from the site of sphinx. *Journal of the National Museum (Prague), Natural History Series*, 191(1), 65–82. https://doi.org/10.37520/jnmpnhs.2022.006

Bräuer, G. (1988). Osteometrie. In R. Knussmann (Ed.), *Anthropologie, Handbuch der vergleichenden Biologie des Menschen. Zugleich 4. Auflage des Lehrbuchs der Anthropologie begründet von R. Martin. Band I/1. Wesen und Methoden der Anthropologie* (pp. 160–223). Stuttgart.

Calcagno, J. M., & Gibson, K. R. (1988). Human dental reduction: Natural selection or the probable mutation effect. *American Journal of Physical Anthropology*, 77(4), 505–517. https://doi.org/10.1002/ajpa.1330770411

Calcagno, J. M., & Gibson, K. R. (1991). Selective compromise: Evolutionary trends and mechanisms in hominid tooth size. In M. A. Kelley & C. S. Larsen (Eds.), *Advances in dental anthropology* (pp. 59–76). Wiley-Liss.

Carlson, D. S., & Van Gerven, D. P. (1979). Diffusion, biological determinism, and biocultural adaptation in the Nubian corridor. *American Anthropologist*, 81(3), 561–580. https://doi.org/10.1525/aa.1979.81.3.02a00030

Caselitz, P. (1998). Caries—Ancient plague of humankind. In K. W. Alt, F. W. Rösing, & M. Teschler-Nicola (Eds.), *Dental anthropology* (pp. 203–226). Springer Vienna. https://doi.org/10.1007/978-3-7091-7496-8_12

Constantino, P. J., Lucas, P. W., Lee, J. J.-W., & Lawn, B. R. (2009). The influence of fallback foods on great ape tooth enamel. *American Journal of Physical Anthropology*, 140(4), 653–660. https://doi.org/10.1002/ajpa.21096

Crevecoeur, I. (2008). *Etude anthropologique du squelette du Paléolithique supérieur de Nazlet Khater 2 (Egypte): Apport à la compréhension de la variabilité passée des hommes modernes*. Leuven University Press. https://doi.org/10.2307/j.ctt9qdwcx

Crevecoeur, I. (2012). First anthropological insights on the early Holocene funerary assemblages from El-Barga. *Documents de la Mission Archéologique Suisse au Soudan*, 4, 19–28.

Crevecoeur, I., Dias-Meirinho, M.-H., Zazzo, A., Antoine, D., & Bon, F. (2021). New insights on interpersonal violence in the late Pleistocene based on the Nile Valley cemetery of Jebel Sahaba. *Scientific Reports*, 11(1), 9991. https://doi.org/10.1038/s41598-021-89386-y

Crevecoeur, I., Rougier, H., Grine, F., & Froment, A. (2009). Modern human cranial diversity in the late Pleistocene of Africa and Eurasia: Evidence from Nazlet Khater, Peștera cu Oase, and Hofmeyr. *American Journal of Physical Anthropology*, 140(2), 347–358. https://doi.org/10.1002/ajpa.21080

Dal Sasso, G., Artioli, G., Maritan, L., & Angelini, I. (2020). A microscopic view of ancient bones: Archaeometry and taphonomy of human remains from Al-Khiday (Central Sudan). In D. Usai, S. Tuzzato, & M. Vidale (Eds.), *Tales of three worlds-archaeology and beyond: Asia, Italy, Africa. A tribute to Sandro Salvatori* (pp. 234–249). Archaeopress.

Darroch, J. N., & Mosimann, J. E. (1985). Canonical and principal components of shape. *Biometrika*, 72(2), 241–252. https://doi.org/10.1093/biomet/72.2.241

Decker, J. E., McKay, S. D., Rolf, M. M., Kim, J., Molina Alcalá, A., Sonstegard, T. S., Hanotte, O., Götherström, A., Seabury, C. M., Praharani, L., Babar, M. E., de Almeida Regitano, L. C., Yildiz, M. A., Heaton, M. P., Liu, W.-S., Lei, C.-Z., Reecy, J. M., Saif-Ur-Rehman, M., Schnabel, R. D., & Taylor, J. F. (2014). Worldwide patterns of ancestry, divergence, and admixture in domesticated cattle. *PLoS Genetics*, 10(3), e1004254. https://doi.org/10.1371/journal.pgen.1004254

Dempsey, P. J., & Townsend, G. C. (2001). Genetic and environmental contributions to variation in human tooth size. *Heredity*, 86, 685–693.

Edwards, D. N. (2007). The archaeology of Sudan and Nubia. *Annual Review of Anthropology*, 36(1), 211–228. https://doi.org/10.1146/annurev.anthro.36.081406.094305

Fernée, C., Zakrzewski, S., & Robson Brown, K. (2020). Dimorphism in dental tissues: Sex differences in archaeological individuals for multiple tooth types. *American Journal of Physical Anthropology*, 175(1), 106–127. https://doi.org/10.1002/ajpa.24174

Franciscus, R. G. (1995). *Later Pleistocene nasofacial variation in Western Eurasia and Africa and modern human origins*. University of New Mexico.

Galland, M., Van Gerven, D. P., Von Cramon-Taubadel, N., & Pinhasi, R. (2016). 11,000 years of craniofacial and mandibular variation in lower Nubia. *Scientific Reports*, 6(1), 31040. https://doi.org/10.1038/srep31040

Garcea, E. A. A. (2016). Multi-stage dispersal of southwest Asian domestic livestock and the path of pastoralism in the middle Nile Valley. *Quaternary International*, 412, 54–64. https://doi.org/10.1016/j.quaint.2016.01.026

Garcea, E. A. A., D'Ercole, G., Sterba, J. H., Dunne, J., Manning, K., Gillard, T., Evershed, R. P., Varadzin, L., & Varadzinova, L. (2020). Technological variability in foragers' pottery productions at the early-mid Holocene site of sphinx, western part of Jebel Sabaloka, Sudan.

Quaternary International, *555*, 110–125. https://doi.org/10.1016/j.quaint.2020.01.020

Garcea, E. A. A., Karul, N., & D'Ercole, G. (2016). Southwest Asian domestic animals and plants in Africa: Routes, timing and cultural implications. *Quaternary International*, *412*, 1–10. https://doi.org/10.1016/j.quaint.2016.09.002

Gautier, A. (2002). The evidence for the earliest livestock in North Africa: Or adventures with large Bovids, Ovicaprids, dogs and pigs. In F. A. Hassan (Ed.), *Droughts, food and culture* (pp. 195–207). Kluwer Academic Publishers. https://doi.org/10.1007/0-306-47547-2_12

Gifford-Gonzalez, D., & Hanotte, O. (2011). Domesticating animals in Africa: Implications of genetic and archaeological findings. *Journal of World Prehistory*, *24*(1), 1–23. https://doi.org/10.1007/s10963-010-9042-2

Greene, D. L. (1972). Dental anthropology of early Egypt and Nubia. *Journal of Human Evolution*, *1*(3), 315–324. https://doi.org/10.1016/0047-2484(72)90067-X

Greene, D. L., Ewing, G. H., & Armelagos, G. J. (1967). Dentition of a mesolithic population from Wadi Halfa, Sudan. *American Journal of Physical Anthropology*, *27*(1), 41–55. https://doi.org/10.1002/ajpa.1330270107

Grine, F. E. (2002). Scaling of tooth enamel thickness, and molar crown size reduction in modern humans. *South African Journal of Science*, *98*(9), 503–509.

Grine, F. E. (2005). Enamel thickness of deciduous and permanent molars in modern Homo sapiens. *American Journal of Physical Anthropology*, *126*(1), 14–31. https://doi.org/10.1002/ajpa.10277

Harris, E. F. (1997). A strategy for comparing odontometrics among groups. *Dental Anthropology*, *12*, 1–6.

Hemphill, B. E. (1991). *Tooth size apportionment among contemporary Indians: An analysis of caste, language, and geography*. Ph.D. dissertation. University of Oregon.

Hemphill, B. E. (2016). Assessing odontometric variation among populations. In J. D. Irish & G. R. Scott (Eds.), *A companion to dental anthropology* (pp. 311–336). Wiley-Blackwell.

Hlusko, L. J. (2016). Elucidating the evolution of hominid dentition in the age of phenomics, modularity, and quantitative genetics. *Annals of Anatomy—Anatomischer Anzeiger*, *203*, 3–11. https://doi.org/10.1016/j.aanat.2015.05.001

Hlusko, L. J., Suwa, G., Kono, R. T., & Mahaney, M. C. (2004). Genetics and the evolution of primate enamel thickness: A baboon model. *American Journal of Physical Anthropology*, *124*(3), 223–233. https://doi.org/10.1002/ajpa.10353

Hoelzmann, P., Keding, B., Berke, H., Kröpelin, S., & Kruse, H.-J. (2001). Environmental change and archaeology: Lake evolution and human occupation in the eastern Sahara during the Holocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *169*(3–4), 193–217. https://doi.org/10.1016/S0031-0182(01)00211-5

Holliday, T. W. (2015). Population affinities of the Jebel Sahaba skeletal sample: Limb proportion evidence: Jebel Sahaba limb proportions. *International Journal of Osteoarchaeology*, *25*(4), 466–476. https://doi.org/10.1002/oa.2315

Honegger, M. (2005). El-Barga: Un site clé pour la compréhension du Mésolithique et du début du Néolithique en Nubie. *Revue de Paléobiologie*, *10*, 95–104.

Honegger, M. (2019). The Holocene prehistory of upper Nubia until the rise of the Kerma kingdom. In D. Raue (Ed.), *Handbook of ancient Nubia* (pp. 217–238). De Gruyter. https://doi.org/10.1515/9783110420388-011

Honegger, M., & Williams, M. (2015). Human occupations and environmental changes in the Nile Valley during the Holocene: The case of Kerma in upper Nubia (northern Sudan). *Quaternary Science Reviews*, *130*, 141–154. https://doi.org/10.1016/j.quascirev.2015.06.031

Horvath, J. E., Ramachandran, G. L., Fedrigo, O., Nielsen, W. J., Babbitt, C. C., St. Clair, E. M., Pfefferle, L. W., Jernvall, J.,

Wray, G. A., & Wall, C. E. (2014). Genetic comparisons yield insight into the evolution of enamel thickness during human evolution. *Journal of Human Evolution*, *73*, 75–87. https://doi.org/10.1016/j.jhevol.2014.01.005

Huysecom, E. (2020). The first emergence of ceramic production in Africa. In *Oxford research encyclopedia of anthropology*. Oxford University Press. https://doi.org/10.1093/acrefore/9780190854584.013.66

Irish, J. D. (2000). The Iberomaurusian enigma: North African progenitor or dead end? *Journal of Human Evolution*, *39*(4), 393–410. https://doi.org/10.1006/jhev.2000.0430

Irish, J. D. (2005). Population continuity vs. discontinuity revisited: Dental affinities among late Paleolithic through Christian-era Nubians. *American Journal of Physical Anthropology*, *128*(3), 520–535. https://doi.org/10.1002/ajpa.20109

Irish, J. D. (2010). The mean measure of divergence: Its utility in model-free and model-bound analyses relative to the Mahalanobis D(2) distance for nonmetric traits. *American Journal of Human Biology*, *22*(3), 378–395. https://doi.org/10.1002/ajhb.21010

Irish, J. D., & De Groote, I. (2016). The human skeletal remains from Ghaba: A physical anthropological assessment. In S. Salvatori, D. Usai, & Y. Lecointe (Eds.), *Ghaba: An early Neolithic cemetery in Central Sudan* (Vol. 1). Africa Magna.

Irish, J. D., & Kenyhercz, M. W. (2013). Size does matter: Variation in tooth size apportionment among major regional north and sub-Saharan African populations. *Dental Anthropology Journal*, *26*(3), 38–44. https://doi.org/10.26575/daj.v26i3.50

Irish, J. D., & Usai, D. (2021). The transition from hunting–gathering to agriculture in Nubia: Dental evidence for and against selection, population continuity and discontinuity. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1952), 20210969. https://doi.org/10.1098/rspb.2021.0969

Irish, J. D., Hemphill, B. E., De Ruiter, D. J., & Berger, L. R. (2016). The apportionment of tooth size and its implications in *Australopithecus sediba* versus other Plio-pleistocene and recent African hominins. *American Journal of Physical Anthropology*, *161*(3), 398–413. https://doi.org/10.1002/ajpa.23039

Irish, J. D., Morez, A., Girdland Flink, L., Phillips, E. L. W., & Scott, G. R. (2020). Do dental nonmetric traits actually work as proxies for neutral genomic data? Some answers from continental- and global-level analyses. *American Journal of Physical Anthropology*, *172*(3), 347–375. https://doi.org/10.1002/ajpa.24052

Kono, R. T., Suwa, G., & Tanijiri, T. (2002). A three-dimensional analysis of enamel distribution patterns in human permanent first molars. *Archives of Oral Biology*, *47*(12), 867–875. https://doi.org/10.1016/S0003-9969(02)00151-6

Kupczik, K., & Hublin, J.-J. (2010). Mandibular molar root morphology in Neanderthals and late Pleistocene and recent *Homo sapiens*. *Journal of Human Evolution*, *59*(5), 525–541. https://doi.org/10.1016/j.jhevol.2010.05.009

Kuper, R., & Kröpelin, S. (2006). Climate-controlled Holocene occupation in the Sahara: Motor of Africa's evolution. *Science*, *313*(5788), 803–807. https://doi.org/10.1126/science.1130989

Le Luyer, M., & Bayle, P. (2017). Microevolution of outer and inner structures of upper molars in late Pleistocene and early Holocene humans. *Comptes Rendus Palevol*, *16*(5–6), 632–644. https://doi.org/10.1016/j.crpv.2016.11.009

Linseele, V. (2010). Did specialized pastoralism develop differently in Africa than in the near east? An example from the west African Sahel. *Journal of World Prehistory*, *23*(2), 43–77. https://doi.org/10.1007/s10963-010-9033-3

Linseele, V. (2012). Animal remains from the early Holocene sequence at Wadi El-Arab. *Kerma*, *4*, 16–18.

Lockey, A. L., Alemseged, Z., Hublin, J.-J., & Skinner, M. M. (2020). Maxillary molar enamel thickness of Plio-Pleistocene hominins. *Journal of*

Human Evolution, 142, 102731. https://doi.org/10.1016/j.jhevol.2019.102731

Macchiarelli, R., & Bondioli, L. (1986). Post-pleistocene reductions in human dental structure: A reappraisal in terms of increasing population density. *Human Evolution*, 1(5), 405–417. https://doi.org/10.1007/BF02436617

Macchiarelli, R., Bondioli, L., & Mazurier, A. (2008). Virtual dentitions: Touching the hidden evidence. In J. D. Irish & G. C. Nelson (Eds.), *Technique and application in dental anthropology* (pp. 426–448). Cambridge University Press. https://doi.org/10.1017/CBO9780511542442.018

Maines, E. (2019). *Diversité biologique et archéologique de la mort: Une approche populationnelle et culturelle du Néolothique soudanais (Haute-Nubie) (PhD thesis)*. Université Paris 1. Panthéon-Sorbonne.

Martín-Francés, L., Martinón-Torres, M., Martínez de Pinillos, M., García-Campos, C., Zanolli, C., Bayle, P., Modesto-Mata, M., Arsuaga, J. L., & Bermúdez de Castro, J. M. (2020). Crown tissue proportions and enamel thickness distribution in the middle Pleistocene hominin molars from Sima de los Huesos (SH) population (Atapuerca, Spain). *PLoS One*, 15(6), e0233281. https://doi.org/10.1371/journal.pone.0233281

Molnar, S. (1971). Human tooth wear, tooth function and cultural variability. *American Journal of Physical Anthropology*, 34(2), 175–189. https://doi.org/10.1002/ajpa.1330340204

Monroe, S., Smith, S. T., & McClure, S. B. (2023). Pastoralism, hunting, and coexistence: Domesticated and wild bovids in Neolithic Sudan. *International Journal of Osteoarchaeology*, 33(3), 517–531. https://doi.org/10.1002/oa.3223

Navia, J. (1994). Carbohydrates and dental health. *The American Journal of Clinical Nutrition*, 59(3), 719S–727S. https://doi.org/10.1093/ajcn/59.3.719S

Neumann, K. (2005). The romance of farming: Plant cultivation and domestication in Africa. In A. B. Stahl (Ed.), *African archaeology: A critical introduction* (pp. 249–275). Blackwell Pub.

Olejniczak, A. J. (2006). *Micro-computed tomography of primate molars*. Stony Brook University.

Olejniczak, A. J., Smith, T. M., Feeney, R. N. M., Macchiarelli, R., Mazurier, A., Bondioli, L., Rosas, A., Fortea, J., de la Rasilla, M., Garcia-Tabernero, A., Radovcić, J., Skinner, M. M., Toussaint, M., & Hublin, J.-J. (2008). Dental tissue proportions and enamel thickness in Neandertal and modern human molars. *Journal of Human Evolution*, 55(1), 12–23. https://doi.org/10.1016/j.jhevol.2007.11.004

Olejniczak, A. J., Tafforeau, P., Feeney, R. N. M., & Martin, L. B. (2008). Three-dimensional primate molar enamel thickness. *Journal of Human Evolution*, 54(2), 187–195. https://doi.org/10.1016/j.jhevol.2007.09.014

Olivieri, A., Gandini, F., Achilli, A., Fichera, A., Rizzi, E., Bonfiglio, S., Battaglia, V., Brandini, S., De Gaetano, A., El-Beltagi, A., Lancioni, H., Agha, S., Semino, O., Ferretti, L., & Torroni, A. (2015). Mitogenomes from Egyptian cattle breeds: New clues on the origin of haplogroup Q and the early spread of Bos taurus from the near east. *PLoS One*, 10(10), e0141170. https://doi.org/10.1371/journal.pone.0141170

Osypińska, M., Osypiński, P., Chłodnicki, M., Kuc, M., Wiktorowicz, P., & Ryndziewicz, R. (2020). The PalaeoAffad project and the prehistory of the middle Nile. *Archaeologia Polona*, 58, 79–97. https://doi.org/10.23858/APa58.2020.005

Pausata, F. S. R., Gaetani, M., Messori, G., Berg, A., Maia De Souza, D., Sage, R. F., & deMenocal, P. B. (2020). The greening of the Sahara: Past changes and future implications. *One Earth*, 2(3), 235–250. https://doi.org/10.1016/j.oneear.2020.03.002

Pinhasi, R., Eshed, V., & Shaw, P. (2008). Evolutionary changes in the masticatory complex following the transition to farming in the southern Levant. *American Journal of Physical Anthropology*, 135(2), 136–148. https://doi.org/10.1002/ajpa.20715

Potter, R. H., & Nance, W. E. (1976). A twin study of dental dimension. I. Discordance, asymmetry, and mirror imagery. *American Journal of Physical Anthropology*, 44(3), 391–395. https://doi.org/10.1002/ajpa.1330440303

Reich, E., Lussi, A., & Newbrun, E. (1999). Caries-risk assessment. *International Dental Journal*, 49(1), 15–26. https://doi.org/10.1111/j.1875-595X.1999.tb00503.x

Reinold, J. (2001). Kadruka and the Neolithic in the northern Dongola reach. *Sudan & Nubia*, 5, 2–10.

Řídký, J., Varadzin, L., & Varadzinová, L. (2022). An introduction to the study of (late) prehistoric ground stone artefacts in the Western part of Jebel Sabaloka in Central Sudan. *Pamatky Archeologicke*, 113, 5–44. https://doi.org/10.35686/PA2022.1

Rodriguez-Rojas, F., Borrero-Lopez, O., Constantino, P. J., Henry, A. G., & Lawn, B. R. (2020). Phytoliths can cause tooth wear. *Journal of the Royal Society Interface*, 17(172), 20200613. https://doi.org/10.1098/rsif.2020.0613

Romero, A., Ramirez-Rozzi, F. V., & Pérez-Pérez, A. (2018). Dental size variability in central African pygmy hunter-gatherers and bantu-speaking farmers. *American Journal of Physical Anthropology*, 166(3), 671–681. https://doi.org/10.1002/ajpa.23458

Ryan, P., Out, W. A., García-Granero, J. J., Madella, M., & Usai, D. (2016). Plant microremains from the white deposits and skeletons of Ghaba and R12 cemeteries. Identification and implications. In S. Salvatori, D. Usai, & Y. Lecointe (Eds.), *Ghaba: An early Neolithic cemetery in Central Sudan* (Vol. 1). Africa Magna.

Said, R. (1993). *The River Nile*. Elsevier. https://doi.org/10.1016/C2009-0-11234-5

Salvatori, S., & Usai, D. (2019a). The Mesolithic and Neolithic in Sudan. In D. Raue (Ed.), *Handbook of ancient Nubia* (pp. 171–194). De Gruyter. https://doi.org/10.1515/9783110420388-009

Salvatori, S., & Usai, D. (2019b). The Neolithic and 'pastoralism' along the Nile: A dissenting view. *Journal of World Prehistory*, 32(3), 251–285. https://doi.org/10.1007/s10963-019-09132-1

Salvatori, S., Usai, D., & Lecointe, Y. (Eds.). (2016). *GHABA: An early Neolithic cemetery in central Sudan*. Africa Magna.

Salvatori, S., Usai, D., & Zerboni, A. (2018). New evidence from the prehistoric sites at Al Khiday and Al Jamrab, Central Sudan. *Desert and the Nile. Prehistory of the Nile Basin and the Sahara. Papers in Honour of Fred Wendorf*, 71–94.

Scott, G. R., & Turner, C. G. (1997). *The anthropology of modern human teeth: Dental morphology and its variation in recent human populations*. Cambridge University Press.

Shackelford, L. L. (2007). Regional variation in the postcranial robusticity of late upper Paleolithic humans. *American Journal of Physical Anthropology*, 133(1), 655–668. https://doi.org/10.1002/ajpa.20567

Smith, T. M., Olejniczak, A. J., Reid, D. J., Ferrell, R. J., & Hublin, J. J. (2006). Modern human molar enamel thickness and enamel-dentine junction shape. *Archives of oral biology*, 51(11), 974–995. https://doi.org/10.1016/j.archoralbio.2006.04.012

Sorenti, M., Martinón-Torres, M., Martín-Francés, L., & Perea-Pérez, B. (2019). Sexual dimorphism of dental tissues in modern human mandibular molars. *American Journal of Physical Anthropology*, 169(2), 332–340. https://doi.org/10.1002/ajpa.23822

Stojanowski, C. M., & Schillaci, M. A. (2006). Phenotypic approaches for understanding patterns of intracemetery biological variation. *American Journal of Physical Anthropology*, 131(S43), 49–88. https://doi.org/10.1002/ajpa.20517

Stojanowski, C. M., Paul, K. S., Seidel, A. C., Duncan, W. N., & Guatelli-Steinberg, D. (2018). Quantitative genetic analyses of postcanine morphological crown variation. *American Journal of Physical Anthropology*, 168(3), 606–631. https://doi.org/10.1002/ajpa.23778

Townsend, G., Hughes, T., Luciano, M., Bockmann, M., & Brook, A. (2009). Genetic and environmental influences on human dental variation: A

critical evaluation of studies involving twins. *Archives of Oral Biology*, *54*, S45–S51. https://doi.org/10.1016/j.archoralbio.2008.06.009

Usai, D. (2014). *The fourth cataract and beyond. Proceedings of the 12th International Conference for Nubian Studies*. Leuven-Paris-Walpole: Peters (pp. 31–44).

Usai, D., Salvatori, S., Iacumin, P., Matteo, A. D., Jakob, T., & Zerboni, A. (2010). Excavating a unique pre-Mesolithic cemetery in central Sudan. *Antiquity*, *84*(323), 323.

Varadzinová, L., Varadzin, L., & Ambrose, S. H. (2023). New radiocarbon dates for postglacial reoccupation of the Sudanese Nile. *Quaternary Science Reviews*, *303*, 107953. https://doi.org/10.1016/j.quascirev.2023.107953

Varadzinová, L., Varadzin, L., Brukner Havelková, P., Crevecoeur, I., & Garcea, E. A. A. (2022). Archaeology of Holocene hunter-gatherers at the sixth Nile cataract, central Sudan. *Bulletin d'Archéologie Marocaine*, *27*, 101–118.

Varadzinová, L., Varadzin, L., Crevecoeur, I., Kaputska, K., & McCool, J.-P. (2022). Excavations at the prehistoric site of Fox Hill in the western part of Jebel Sabaloka (2017–2018). *Sudan & Nubia*, *26*, 160–181. https://doi.org/10.32028/9781803274096-160-181

Wendorf, F. (1968). Site 117: A Nubian final Paleolithic graveyard near Jebel Sahaba, Sudan. In F. Wendorf (Ed.), *Prehistory of Nubia* (pp. 954–995). Fort Burgwin Research Center, Inc.

Williams, B. B., & Emberling, G. (2021). Nubia, a brief introduction. In G. Emberling & B. B. Williams (Eds.), *The Oxford handbook of ancient Nubia*. Oxford Academic. https://doi.org/10.1093/oxfordhb/9780190496272.013.1

Xia, J., Zheng, J., Huang, D., Tian, Z. R., Chen, L., Zhou, Z., Ungar, P. S., & Qian, L. (2015). New model to explain tooth wear with implications for microwear formation and diet reconstruction. *Proceedings of the National Academy of Sciences*, *112*(34), 10669–10672. https://doi.org/10.1073/pnas.1509491112

Y'Edynak, G., & Fleisch, S. (1983). Microevolution and biological adaptability in the transition from food-collecting to food-producing in the Iron Gates of Yugoslavia. *Journal of Human Evolution*, *12*(3), 279–296. https://doi.org/10.1016/S0047-2484(83)80150-X

Zazzo, A. (2014). Bone and enamel carbonate diagenesis: A radiocarbon prospective. *Palaeo*, *3*, 168–178.

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