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The transition from hunting-gathering to agriculture in Nubia:
Dental evidence for and against selection, population continuity, and discontinuity

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Abstract

Some researchers posit population continuity between Late Palaeolithic hunter-gatherers of the late Pleistocene and Holocene agriculturalists from Lower (northern) Nubia, in northeast Africa. Substantial craniodental differences in these time-successive groups are suggested to result from *in situ* evolution. Specifically, these populations are considered a model example for subsistence-related selection worldwide in the transition to agriculture. Others question continuity, with findings indicating that the largely homogenous Holocene populations differ significantly from late Pleistocene Lower Nubians. If the latter are representative of the local populace, post-Pleistocene discontinuity is implied. So who was ancestral to the Holocene agriculturalists? Dental morphological analyses of 18 samples (1,075 individuals), including one dated to the 12th millennium BCE from Al Khiday, near the Upper Nubian border, may provide an answer. It is the first Late Palaeolithic sample (n=55) recovered within the region in ~50 years. Using the Arizona State University Dental Anthropology System to record traits and multivariate statistics to estimate biological affinities, Al Khiday is comparable to several Holocene samples, yet also highly divergent from contemporaneous Lower Nubians. Thus, population continuity is indicated after all, but with late Pleistocene Upper- rather than Lower Nubians as originally suggested—assuming dental traits are adequate proxies for aDNA.

1. Introduction

The hypothesis of population continuity in Nubia from the late Pleistocene through Holocene is >50 years old. Arguments against it began >40 years ago, and the back-and-forth continues. This is remarkable, considering that to many outside observers the subject would seem esoteric and the location obscure. However, the issue at the heart of this debate is of interest to many, entailing in a microcosm a core event in world history—the transition from hunting-gathering to agriculture [1-3]. Specifically, are marked morphometric changes in skulls and teeth of Nubian skeletal remains before and after this shift a textbook example of regional diet-related selection, or population discontinuity?

Ancestry between Late Palaeolithic (20,000-12,000+ BP [4-5]) Nubians of the late Pleistocene, and Meroitic (300 BCE-400 CE) through later populations was proposed by Greene [6-7] and others [8-10]. As a region, Nubia parallels the Nile River from the First Cataract at Aswan, Egypt, to the Blue and White Nile Rivers [11-13] near Khartoum, Sudan (between dashed lines in Fig. 1). It is then bisected into sub-regions, Lower (north) and Upper (south) Nubia [14]. The continuity hypothesis pertains generally to the former, particularly the area straddling the Egypt/Sudan border. It is from there that skeletal samples studied by continuity advocates were recovered, including Late Palaeolithic Wadi Halfa [three km southwest of Gebel Sahaba in Fig. 1]. Support for this hypothesis was provided in later studies [1,15-18]. Larsen [19:312] agreed, stating that "studies of craniofacial morphology, biological change, and population history" is suggestive of continuity.

[FIGURE 1 HERE]

Nonetheless, much of the evidence is based on dentitions, including ostensibly shared "rare cusp variants" in Late Palaeolithic and Meroitic samples [7:322]. The first hypothesis to explain the differences between hunter-gatherers and agriculturalists—from cranially robust with large morphologically complex teeth, to gracile with globular crania and smaller simpler dentitions—was proposed to result from dental-related selection. The former population was said to have experienced selective pressures favouring large teeth with incisor shovelling, extra cusps, and other complex occlusal features to resist crown wear from dietary grit [6]. With the advent of agriculture and higher-carbohydrate foods, Holocene populations were then said to have undergone reduction, to smaller, simpler caries-resistant teeth. This “caries selection hypothesis” involved the molars, where fewer cusps and simpler groove patterns [7:323,17,20] presumably provided reproductive benefits.

Next came the “masticatory-functional hypothesis” [8:502,9-10]. It posited that dental reduction was a side effect of changes to the craniofacial complex after transitioning to agriculture. In order of importance, the change from hunting-gathering yielded: a) reduction in masticatory muscle size, b) reduction in jaw growth for a less projecting midface, c) secondary changes to more globular crania and, d) smaller teeth and jaws, which decreased prognathism [8-9].

Focus then returned to teeth [1:513,18], which were said to be “under selective pressure to reduce in size to avoid the negative sequelae of dental crowding,” not caries. Explicitly, all teeth decreased in size. Then during the 5000-year progression from agriculture to intensive agriculture, only molars reduced in support of caries selection [1]. Others [16] agree concerning dental reduction, though in response to general stress among agriculturalists based on more developmental pathologies than hunter-gatherers. Beyond conference papers, research supporting Nubian continuity then lessened—until recently. In 2016 Galland and colleagues [3] revisited the topic, finding cranial geometric morphometric analyses in five samples, including Wadi Halfa, again support the masticatory-functional hypothesis (but see below).

Conversely, while it is known craniodental reduction occurred worldwide in the agricultural transition [2], the amount of change in Lower Nubians since the Pleistocene is striking. Armelagos et al. [17:1] noted “the reduction in facial morphology...is greater by several orders in magnitude than the reduction in general body size.” Such major change prompted Hillson [21:91] to remark “although [*in situ* evolution] is an attractive idea, there is doubt as to whether there would be an adequate number of generations to achieve it.” Later dental [22-27], cranial [28-29], and post-cranial [30] research supported this statement, finding Late Palaeolithic Lower Nubians too divergent from later Holocene peoples to be ancestral.

It should then follow that population discontinuity occurred after the Pleistocene [22-26]. In the yet-largest regional analyses of 12 Lower and Upper Nubian samples, including one from Late Palaeolithic Gebel Sahaba (n=49 individuals) and Tushka (n=18) (Fig. 1), such an occurrence took place in the Neolithic, before 4600-4000 BCE (i.e., Final Neolithic (Table 1) according to [31], or Middle Neolithic in [32]); homogeneity is then evident through the Christian period (CE 550-1350) [33]. However, as a contradictory hypothesis, discontinuity would assume Wadi Halfa and Gebel Sahaba/Tushka peoples were indigenous to the region to have had the potential to contribute genetically to subsequent peoples. A-Group and later agriculturalists would then have represented “an arrival of new people at the advent of the shift from hunting-gathering to farming,” in the “population influx” hypothesis of Galland et al. [3:7]; like the masticatory-functional hypothesis, the authors relate that it also aligns with their analyses. However, most later studies suggest the population represented by Late Palaeolithic (Lower) Nubians originated extra-regionally [22-26,28-30,33]. As above, research along these lines then waned—until recently [34]. Larsen [35] also amended his earlier remarks [19], acknowledging the potential for population discontinuity.

It thus seems that additional analyses are needed to move this debate along. However, new evidence is critical. In this study the first 'new' Late Palaeolithic regional sample in ~50 years, from Al Khiday (Fig. 1), is analysed. Using 36 nonmetric traits from the Arizona State University Dental Anthropology System (ASUDAS) [36], these remains are compared with those from Gebel Sahaba/Tushka and 16 Holocene Upper and Lower Nubian samples. Using the mean measure of divergence—a distance statistic with a significance test—inter-sample affinities will help detect the most likely population hypothesis. That said, succession from A-Group, and probably earlier Neolithic, through Christian populations is not disputed in any studies. The contention is if/when discontinuity occurred. Thus, focusing on the two Late Palaeolithic, plus three recently-recorded Neolithic samples (≤5600-4300 BCE), from Al Khiday, El Ghaba, and R12 (Table 1), may refine this potential timing.

Within this analytical framework, continuity vs. discontinuity is restated as statistical hypotheses: $H_{0:}$ there is no vs. H_A: there is a significant dental morphological difference between late Pleistocene and Nubian Holocene samples. Of course, it is the contribution of evidence from multiple fields that will convince researchers, but this approach should provide useful insight. These results will in turn have ramifications regarding craniodental changes in the agricultural transition. Again, do they result from selection that affected other populations worldwide, albeit to a lesser degree, or something else?

2. Materials and methods

Eighteen samples, associated with subsistence strategies ranging from hunting-gathering to intensive agriculture [18,31,37-38] are listed in Table 1. Because Gebel Sahaba/Tushka ('Gebel Sahaba' from here on) is "biologically indistinguishable" from the less dentally-complete Wadi Halfa sample [11:316,39-41 (Supplementary Note S1)], it is analysed in the latter's place. Detailed backgrounds are available in earlier articles [33,42-44], except the Al

Khiday Late Palaeolithic and Neolithic samples described here. Archaeological evidence is provided elsewhere [45-47], but in brief, the Al Khiday cemetery was used for >10,000 years by Late Palaeolithic through Meroitic populations. Radiocarbon dating of the mineralized Late Palaeolithic skeletons is problematic, like similar-aged Lower Nubian sites [40,48]. But recent indirect dating at Al Khiday supported a 12th millennium BCE association [49]. The Neolithic skeletons were also dated indirectly (5000-4300 BCE). A key discriminating factor is body position, with Late Palaeolithic extended and prone (Supplementary Fig. S1), and Neolithic burials flexed, as is common across Nubia.

[TABLE 1]

The aim is to use ASUDAS traits, many known to be highly heritable, h^2=0.60-0.93 [50-51], as proxies for ancient DNA (aDNA). Due to degradation from environmental heat [52-53], aDNA has not been recovered in the above samples. Thus, affinities from ASUDAS data were calculated using the mean measure of divergence (MMD) [54-55] to estimate genetic relatedness. In support, a Mantel correlation of 0.84 resulted between distance matrices from ASUDAS traits (MMD) and >350,000 single nucleotide polymorphisms (i.e., Hudson F_{st}) in 12 matched North and sub-Saharan African samples [56].

The 36 traits (Supplementary Table S1) were used in earlier affinity studies [22-23,33,55-58]. Recording entails using standardized examples of trait expressions on a rank-scale to address interobserver error [36]. The latter is not an issue here because all data were recorded by J.D.I. Other reasons for choosing these traits include minimal sexual dimorphism to allow sample pooling, preservation despite crown wear, and their conservative evolution is ideal for diachronic biodistance analyses [19,36].

The rank-scale data were first dichotomized into standard states of present and absent [36], to simplify presentation of trait frequencies and as required for the MMD [54-55,59-60].

As a benefit, dichotomization can increase h^2 [61]. The MMD calculates phenetic affinities, where lower values indicate greater similitude and vice versa. The formula corrects for low (≤0.05) or high (≥0.95) trait frequencies and small samples (n<10) [54,59]. To determine if samples differ significantly, MMDs are compared with their standard deviations (Sx), e.g., if MMD>2*Sx, the null hypothesis $S_1=S_2$ (S=sample) is rejected at the 0.025 level [54-55].

While the MMD is a robust statistic [55], trait editing is recommended to increase precision. Minimally contributory traits should be deleted [60]. Some are obvious, e.g., mandibular torus frequency is 0.00 across samples (Supplementary Table S1). Others are identified quantitatively, here using correspondence analysis (CA) to discern which traits vary least across samples in combination biplots [62-63]. Additional CA information is available elsewhere [33,58 (Supplementary Note S2)]. Further, traits highly correlated with others can cause unwanted differential weighting of underlying dimensions [54]. Therefore, Kendall's tau-*b* was used to identify those most often highly inter-correlated ($\tau_b \geq |0.5|$).

Finally, beyond MMD distance matrices, inter-sample variation can be visualized with multidimensional scaling (MDS). SPSS 26.0 Procedure Alscal produced spatial representations of the samples.

3. Results

The number of individuals and percentages expressing traits by sample reveal inter-sample uniformities, except Gebel Sahaba (Supplementary Table S1). The latter exhibits relatively high frequencies of mass-additive traits [33]. This is supported by an initial 36-trait MMD comparison. In the matrix (Supplementary Table S2) and 3D MDS plot (Supplementary Fig. S2), Gebel Sahaba differs significantly from all others (MMD=0.09-0.26), including Late Palaeolithic and Neolithic Al Khiday (0.12 and 0.17), plus the other new Neolithic samples from Upper Nubia (0.16 and 0.17).

Following editing, 15 traits were deleted (Supplementary Note S2, Table S3, Figs. S3-S4), leaving 21 (Supplementary Table S4). The new distance matrix (Supplementary Table S5) and MDS (Fig. 2) place Gebel Sahaba (GSA) even farther from the rest (MMD=0.14-0.44); affinities among the latter changed minimally, including the new Neolithic samples (AKN, GHB, R12). Al Khiday Late Palaeolithic (AKH) is close to Hierakonpolis C-Group (MMD=0.04), Al Khiday Neolithic (0.01), Neolithic Ghaba (0.06), Kerma Ancien/Moyen (0.02), Kerma Classique (0.01), and Napatan Tombos (0.04); these distances do not differ significantly (Supplementary Table S6). Of all samples, Late Palaeolithic Al Khiday is farthest from Final Neolithic Gebel Ramlah (MMD=0.19), Meroitic (0.17), and Gebel Sahaba (0.17). An improvement in MMD performance is supported by the MDS. Beyond Gebel Sahaba being farther from the remaining, more homogeneous samples, the latter reveal a Lower/Upper Nubian division indicative of a north-to-south cline in ASUDAS frequencies (below).

[FIGURE 2 HERE]

4. Discussion

Assuming phenetic affinities reflect genetic relatedness, Gebel Sahaba appears too divergent to be ancestral to succeeding Nubians—differing significantly based on 36 and 21 traits. Such findings were reported previously [22-30,33-34]. These same studies indicate the Gebel Sahaba/Tushka/Wadi Halfa population was not indigenous to Nubia or the region, instead showing affinities to sub-Saharan Africans, notably West Africa. This too is not new, and two earlier studies reported cranial similarities with sub-Saharan samples: West African Ashanti [41], and late Palaeolithic Ishango, Democratic Republic of the Congo [40, also see 64].

This is expediently illustrated in a 2D plot of 36-trait distances (Fig. 3) among Gebel Sahaba, Al Khiday, pooled Lower (LNU) and Upper (UNU) Holocene Nubian samples (from

Table 1), and 12 early Holocene through historic samples from West, Central, and East sub-Saharan Africa ([23-24,55,57], Supplementary Note S3, Table S7). Of interest, the Ashanti crania from [41] comprise the Ghana (GHA) sample near Gebel Sahaba. The latter's location shows it most akin to West Africans and three Central African samples, sharing traits common among subcontinental populations [57,65-66]. None of these distances differ significantly (Supplementary Table S7). Except Gebel Sahaba, inter-sample distances parallel geographic locations [also 23,55-56], where Dimension 1 approximates west-to-east, and Dimension 2, north-south,.

[FIGURE 3]

A sub-Saharan population in late Pleistocene Nubia should not be unexpected, given northward expansions of Sahelian vegetation and sub-Saharan fauna during Saharan 'green' periods; the most recent initiated 15,000 BP [67], before its maximum around 9000 BP [67-69]. It may seem surprising that these apparent migrants originated so far away, but many well-watered migration routes were available then [22,26,68]. In any event, information on biological distinctiveness and non-local derivation is not novel, as mentioned. Nevertheless, diachronic change in a continuous, geographically stable Lower Nubian population from the late Pleistocene onward is still proposed as a viable explanation [3].

What is new, however, is the 12th millennium Al Khiday sample. None of the crania have been reconstructed but they appear robust (Supplementary Figs. S5-S6), perhaps not unlike contemporaneous Lower Nubians, Northwest African Iberomaurusians [29], or Central African Ishango [64]. Odontometrics have also not been recorded, but all teeth appear much larger than more recent samples, again not unlike the above material [27]. Yet, compared to Gebel Sahaba, Al Khiday teeth are simpler like in Holocene Nubians (Supplementary Table S5; Fig. 2). In particular, distances with the Hierakonpolis C-Group and five Upper Nubian samples do not differ significantly. However, Al Khiday also expresses traits indicative of sub-Saharan origin [57,65-66 (Supplementary Note S3)], but like geographically proximate East Africans, and one Central African sample (Supplementary Note S3, Table S7, Fig. 3). Site location is a likely factor, as during humid periods it would literally have been in 'sub'-Saharan Africa. Of course, regardless of climate, the Nile and tributaries acted as north-south migration routes during the whole of prehistory. Evidence of exchange is seen by an increase in sub-Saharan-like traits between Lower and Upper Nubian Holocene samples (Fig. 2, Supplementary Table S1, Note S3).

On the above bases, selection did not account for craniodental changes between the Lower Nubian late Pleistocene and Holocene samples studied by continuity proponents. The Wadi Halfa/Gebel Sahaba/Tushka population, whether in residence for a few generations or a thousand years, contributed little, if anything, to the Holocene gene pool for *in situ* evolution to occur. However, a candidate ancestral population was present. While divergent from some, Late Palaeolithic Al Khiday is closer to all samples than Gebel Sahaba (Supplementary Table S5). From this population then, craniofacial reduction relative to the masticatory-functional hypothesis [8-9] cannot be ruled out, given indications of Al Khiday robusticity. Neither can selection for size reduction in all teeth following the Pleistocene [1,16,18]. But the lack of reduction in dental morphological complexity does not support *in situ* caries selection [7,20] in this Upper Nubian scenario.

In sum, the most parsimonious explanation is ancestors of Holocene agriculturalists were in Nubia—just not at Wadi Halfa, Gebel Sahaba, and Tushka. Though cultural diffusion with incorporation of non-local resources occurred [70-71], with perhaps some immigration, it is unnecessary to hypothesize a significant post-Pleistocene influx of agriculturalists. The results suggest most future Nubian agriculturalists were in residence the entire time, though previously in the guise of Neolithic agro-pastoralists and intensive collectors. It would seem likely that, soil deflation aside, more Late Palaeolithic skeletal remains akin to Al Khiday may yet be discovered, possibly including Lower Nubia. So, long term population continuity appears likely after all, perhaps including *in situ* selection for reduction in cranial robusticity, as well as dental size (only), during the transition from hunting-gathering to agriculture.

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Data availability

Nubian nonmetric data are listed in Supplementary Table S1. Nonmetric data for the 12 sub-Saharan African samples in Irish [23-24,55,57].

Competing interests

The authors declare no competing interests.

Authors' contributions

J.D.I. designed the research, sampled and analysed data, and wrote the paper with assistance from D.U. J.D.I and D.U. discussed results and agreed on the final manuscript. D.U. directed and excavated the Al Khiday cemetery.

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Figure legends

Figure 1. Locations of place names relative to samples in Table 1.

Figure 2. Three-dimensional MDS of 21-trait MMD distances among Nubian samples. Three-letter abbreviations from Table 1 and text. The MDS Kruskal's stress formula 1 value=0.151 and r^2=0.886.

Figure 3. Two-dimensional MDS of 36-trait MMD distances among Late Palaeolithic Gebel Sahaba (GSA) and Al Khiday (AKH), pooled Lower (LNU) and Upper (UNU) Holocene Nubian samples from present study, and 12 early Holocene and historic samples from West, Central, and East sub-Saharan Africa (details in Supplementary Note S3, Table S7). MDS Kruskal's stress formula 1=0.214 and r^2=0.787.

Supplementary Information for

The transition from hunting-gathering to agriculture in Nubia: Dental evidence for and against selection, population continuity, and discontinuity

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Supplementary Note S1: Wadi Halfa and Gebel Sahaba/Tushka

An obvious concern is to establish that Wadi Halfa, the sample used in population continuity arguments, represents the same Late Palaeolithic population from Gebel Sahaba and Tushka, generally used in population discontinuity studies and the present analysis (see main text). In support, all three sites relate to the same late Pleistocene horizon, originally dated >12,000-10,000 BCE (Wendorf, 1968; Strouhal, 1984). All have been said share the Qadan microlithic industry, initially thought to have spanned 11,950-6,400 BCE (Wendorf, Shiner, and Marks, 1965; Wendorf, 1968); this dating influenced the age assigned to Wadi Halfa, from the work of the site archaeologist, Saxe (1971:39), who suggested a date range of 11,000-8,000 BP as "guess dates" related to the, then uncompleted, lithic analyses (also see Greene et al., 1967). This range was erroneously listed as 11,000-8,000 BCE in Galland et al. (2016). The best estimate for the advent of the Qadan industry today is ~15,000 BP, or 17,000 cal BP (Schild and Wendorf, 2010; Usai, 2020), lasting perhaps for ca. two millennia. That said, given the range of difficulties in dating any of these sites (see Usai, 2020 for review), the best estimate for Wadi Halfa, Jebel Sahaba, and Tushka is likely >11,600 BP (Antoine et al., 2013). Wadi Halfa's location (not shown) is just 3 km southwest of Gebel Sahaba in Figure 1 of the main text, though Tushka is >70 km north. Craniometric data have long indicated one homogenous population (Anderson, 1968; Greene and Armelagos, 1972), with Strouhal (1984) advocating pooling of all crania into one sample.

Additional support for common ancestry is evident here from a mean measure of divergence (MMD) comparison of the small Wadi Halfa dental sample (n=30), recorded and data kindly provided by Prof. Chris Stojanowski (personal communication, 2017), with Gebel Sahaba/Tushka (n=67) recorded by the first author (JDI). From 35 ASUDAS traits, excluding missing LM1 C1-C2 crest data in Wadi Halfa, the phenetic distance is a very low 0.038, with *p*=0.671 to indicate no statistically significant difference between samples. That said, contra Strouhal's (1984) recommendation, pooling was not undertaken for this study out of caution. Many very small trait sample sizes (n=0-5) yield extreme Wadi Halfa frequencies relative to Gebel Sahaba/Tushka (Supplementary Table S1); more critical, interobserver error between Stojanowski and JDI in recording of ASUDAS traits has not been assessed. All 18 samples in the present study were recorded by JDI.

Supplementary Note S2: Trait editing for optimum performance of the MMD

The MMD yields acceptable results with traits that are invariant or minimally variant across samples, and/or highly inter-correlated (Irish, 2010). But for optimum performance such traits should be edited out (Harris and Sjøvold, 2004). Correspondence analysis identified the traits most important for sample variation, whereas Kendall's tau-*b* correlation coefficient revealed highly correlated trait pairs (Irish, 2005, 2006; 2010; also Materials and methods).

Correspondence analysis is like principal components analysis (PCA), but it factors discrete data comprising rows and columns of a contingency table. Data in the present study are derived from Supplementary Table S1. A chi-square distance matrix of the 36 traits is then submitted to PCA to produce a biplot combining rows and columns to help visualize association. Like PCA, the biplot's Dimension 1 axis corresponds to the first dimension and explains the most inertia (i.e., variation) of the chi-square value. The Dimension 2 and Dimension 3 axes are then orthogonal and explain less variation (Greenacre and Degos, 1977; Clausen, 1988; Benzécri, 1992; Phillips, 1995).

A summary CA table is provided in Supplementary Table S3. The significant χ^2-value of 3740.24 indicates that the row and column variables of the contingency table are related. A total of 17 interpretable dimensions are listed. Inertia and total inertia are presented in the second column. The bottom value reveals that 25.5% of the total variance is explained.

Finally, the proportion and cumulative inertia for each of the 17 dimensions is tabulated. The first three dimensions account for 47% of the variance explained by the actual model, as subsequently used for two separate 2D biplots.

The first biplot (Supplementary Fig. S3) locates the 18 samples relative to the 36 traits on the first two dimensions, accounting for 33.5% of the inertia. Some minor differences are evident, but the overall inter-sample relationships are similar to those in the MDS of the 36-trait MMD (Supplementary Fig. S2). The distribution indicates which traits are the most important, i.e., those near the extreme ends of each axis are the most responsible for driving the sample variation. For example, traits toward the top of the Dimension 2 axis are more frequently expressed in Gebel Sahaba (GSA) and Al Khiday (AKH), namely: 1 Winging UI1, 2 Labial Curvature UI1, 8 Bushman Canine UC, 20 Midline Diastema UI1, 26 Cusp Number LM1, 32 Tomes Root LP1, and Root Number LM1 (see Supplementary Table S1); the opposite is true for trait 17 Peg-Reduced UI2, near the bottom of the same axis. Traits in the centre of the main grouping in the graph contribute less to the sample variation. The same interpretive approach is followed for the second biplot (Supplementary Fig. S4), which includes Dimension 3 to account for the abovementioned 47% of inertia (Supplementary Table S3). On this basis, nine traits having the least impact on sample variation were deleted: 3 Palatine Torus, 7 Tuberculum Dentale UI2, 10 Hypocone UM2, 15 Root Number UP1, 18 Odontome P1-P2, 19 Congenital Absence UM3, 23 Mandibular Torus, 29 C1-C2 Crest LM1, and 36 Torsomolar Angle LM3 (see Supplementary Table S1).

After submitting the remaining 27 non-dichotomized rank-scale data to Kendall's tau-*b* correlation coefficient, six were found to be strongly intercorrelated ($\tau_b \geq |0.5|$) multiple times among all trait pairs (table available upon request). These include: 2 Labial Curvature UI1, 5 Double Shoveling UI1, 8 Bushman Canine UC, 11 Cusp 5 UM1, 28 Deflecting

Wrinkle LM1, and 30 Protostylid LM1 (Supplementary Table S1). Several include smaller sample sizes than the MMD Freeman and Tukey transformation is intended to handle, most notably Lower Nubian Pharaonic (PHA) and Upper Nubian Soleb (SOL) (Table 1), to further improve performance. The result of this editing process yielded 21 final traits for the second MMD analysis (Supplementary Table S4).

Supplementary Note S3: MMD comparison of Late Palaeolithic and pooled Holocene Nubian samples with 12 from West, Central, and East sub-Saharan Africa

This MMD comparison based on all 36 ASUDAS traits was conducted to summarize simply the findings of a link between the Lower Nubian Late Palaeolithic samples and sub-Saharan Africans as discussed in the main text (Irish and Turner, 1990; Irish, 1993, 1998a,b,c, 2000, 2005; Franciscus, 1995; Holliday, 1995, 2015; Groves and Thorne, 1999). The sub-Saharan samples (Irish, 1993, 1997, 1998a, 2010), were selected mainly for demonstrative purposes, to represent three major regions—West, Central, and East Africa, and temporal periods from prehistoric to historic (Supplementary Table S7). Late Palaeolithic Al Khiday and two pooled samples of Lower and Upper Holocene Nubians (compiled from the 16 samples in Table 1) were also included to assess their affinities on a continental scale.

The results (Fig. 3, Supplementary Table S7) again reveal the similarity of Gebel Sahaba to West and some Central African samples as reported. All express similarly 11 traits common in sub-Saharan Africans relative to other world populations. These 11 include two that are notable by their absence or very low frequencies, 5 Double Shoveling UI1 and 14 Enamel Extension UM1, and nine of frequent occurrence, 8 Bushman Canine UC, 12 Carabelli's Trait UM1, 15 Root Number UP1, 16 Root Number UM2, 19 Congenital *Presence* UM3, 24 Groove Pattern LM2, 31 Cusp 7 LM1, 32 Tomes Root LP1, and 35 Root Number LM2; two additional high-frequency traits not often recorded in other world populations are 2 Labial Curvature UI1 and 20 Midline Diastema UI1. This trait pattern was initially referred to as the Sub-Saharan African Dental Complex (Irish, 1997, 1998d), before confirmatory research permitted use of the final term, Afridonty (Irish, 2013), following standard global nomenclature, including, Sinodonty, Sundadonty, Indodonty, and Eurodonty (Turner, 1985, 1987; Hawkey, 2004; Scott et al., 2013). However, Gebel Sahaba, the four West African, and three of four Central African samples also share similar frequencies of morphologically complex traits that are not common among populations throughout the remainder of the sub-continent: 1 Winging UI1, 9 Distal Accessory Ridge UC, 26 6-Cusped LM1, and 34 3-Rooted LM1. These four traits are particularly important for the distinct position of Gebel Sahaba in Figure 3.

The Al Khiday Late Palaeolithic sample also expresses trait frequencies indicative of Afridonty, with the exception of a comparatively low frequency for 24 Groove Pattern LM2. It additionally expresses relatively high frequencies of 2 Labial Curvature UI1 and 20 Midline Diastema UI1. It does not, however, evidence the additional complex traits to the same degree as Gebel Sahaba (Supplementary Table S1). Instead, Al Khiday is most akin to the neighbouring East African samples (Fig. 3, Supplementary Table S7) that, given the site's geographic location, is not unexpected. Both pooled Holocene samples, particularly Upper Nubia, also show phenetic similarities to the East Africans. This association is indicative of a north-south cline in trait frequencies, as discussed in the main text. Thus, Al Khiday is patently indigenous to greater northeast Africa, as are its Holocene successors in Nubia. The population of Gebel Sahaba/Tushka (and Wadi Halfa) apparently originated farther afield, and given the significant phenetic distances from subsequent Nubian samples, would have contributed little or nothing to them genetically.

Table S1. Thirty-six ASUDAS dental trait percentages (%) and number of individuals scored (n) for the 18 samples from Nubia

			Lower Nubia										Upper Nubia								
	Sample[1]		GSA	GRM	AGR	CGR	HCG	PHA	MER	XGR	CHR	/	AKH	AKN	GHB	R12	KAM	KMC	SOL	TOM	KUS
No.	Trait[2]																				
1	Winging UI1	%	29.63	0.00	2.56	6.12	0.00	3.33	12.82	5.71	7.69		0.00	0.00	0.00	0.00	6.25	5.36	8.33	4.88	4.17
	(+=ASU 1)[3]	n	27	36	39	49	29	30	39	35	26		11	16	8	18	32	56	24	41	48
2	Labial Curvature UI1	%	3.70	9.30	4.35	0.00	11.11	0.00	4.88	0.00	0.00		18.18	30.00	3.70	4.00	5.71	7.69	12.50	12.50	0.00
	(+=ASU 3-4)	n	27	43	23	19	18	5	41	18	13		22	20	27	25	35	13	8	16	32
3	Palatine Torus	%	12.00	0.00	0.00	0.00	0.00	0.00	10.71	10.20	8.82		0.00	0.00	0.00	7.69	7.14	1.82	10.34	2.33	3.13
	(+=ASU 2-3)	n	25	30	24	42	23	29	84	49	34		30	8	3	13	28	55	29	43	32
4	Shovelling UI1	%	45.83	46.15	15.79	10.53	25.00	25.00	38.89	25.00	8.33		21.05	0.00	5.00	0.00	46.67	22.22	11.11	14.29	26.92
	(+=ASU 2-6)	n	24	39	19	19	16	4	36	12	12		19	16	20	22	30	9	9	14	26
5	Double Shovelling UI1	%	4.35	4.65	0.00	0.00	0.00	0.00	4.55	6.67	15.38		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.70
	(+=ASU 2-6)	n	23	43	21	17	17	3	44	15	13		20	22	31	28	32	7	8	15	27
6	Interruption Groove UI2	%	16.00	20.00	4.35	25.00	0.00	20.00	36.17	40.00	26.67		16.67	15.38	10.00	21.05	15.38	9.09	30.77	18.18	26.09
	(+=ASU +)	n	25	35	23	20	10	5	47	15	15		24	13	20	19	26	11	13	11	23
7	Tuberculum Dentale UI2	%	38.89	52.78	13.04	35.00	27.27	20.00	40.48	42.86	21.43		34.78	15.38	22.22	26.32	61.54	8.33	25.00	27.27	50.00
	(+=ASU 2-6)	n	18	36	23	20	11	5	42	14	14		23	13	18	19	26	12	12	11	22
8	Bushman Canine UC	%	20.00	8.82	11.54	0.00	0.00	0.00	19.61	10.00	33.33		35.00	9.09	6.25	0.00	0.00	16.67	0.00	0.00	10.00
	(+=ASU 1-3)	n	20	34	26	26	11	8	51	20	12		20	11	32	19	30	18	11	11	20

9	Distal Acc. Ridge UC	%	88.89	44.44	33.33	12.50	11.11	50.00	30.95	21.43	22.22	21.43	10.00	40.00	35.29	20.83	18.18	0.00	0.00	42.86
	(+=ASU 2-5)	n	9	27	18	16	9	4	42	14	9	14	10	30	17	24	11	7	6	14
10	Hypocone UM2	%	94.12	93.62	73.68	76.09	90.48	83.33	78.48	85.71	72.73	72.73	80.00	92.19	93.75	84.85	91.67	78.95	92.59	87.88
	(+=ASU 3-5)	n	34	47	38	46	21	24	79	35	22	33	20	64	32	33	48	19	27	33
11	Cusp 5 UM1	%	33.33	17.24	12.00	40.00	37.50	16.67	10.94	21.21	25.00	0.00	5.56	13.33	8.70	30.00	24.14	14.29	9.09	28.57
	(+=ASU 2-5)	n	15	29	25	25	8	12	64	33	20	20	18	30	23	20	29	7	11	14
12	Carabelli's Trait UM1	%	42.86	85.29	73.08	75.00	54.55	71.43	43.10	50.00	56.25	31.58	35.29	27.78	73.91	70.59	38.71	0.00	53.85	45.00
	(+=ASU 3-7)	n	14	34	26	24	11	14	58	28	16	19	17	36	23	17	31	8	13	20
13	Parastyle UM3	%	0.00	2.56	0.00	2.50	0.00	4.35	0.00	4.00	0.00	4.55	0.00	0.00	0.00	6.06	5.41	0.00	5.00	0.00
	(+=ASU 2-5)	n	37	39	40	40	16	23	58	25	20	22	21	62	27	33	37	15	20	29
14	Enamel Extension UM1	%	0.00	2.63	0.00	2.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28.57	0.00	0.00	2.00	5.00	0.00	0.00
	(+=ASU 2-3)	n	36	38	40	43	11	27	89	45	24	15	16	7	24	19	50	20	23	32
15	Root Number UP1	%	72.73	69.05	72.41	82.98	84.21	72.00	53.85	70.73	73.08	85.71	83.33	35.71	82.61	63.16	80.39	69.23	78.26	57.14
	(+=ASU 2+)	n	33	42	29	47	19	25	78	41	26	21	12	14	23	38	51	13	46	49
16	Root Number UM2	%	72.97	66.67	77.78	86.67	69.23	84.21	81.67	90.32	100.00	90.48	92.86	83.33	92.00	80.00	90.24	90.91	78.79	61.54
	(+=ASU 3+)	n	37	39	27	30	13	19	60	31	24	21	14	24	25	35	41	11	33	39
17	Peg-Reduced UI2	%	2.94	6.25	4.76	0.00	3.70	11.11	1.85	4.76	0.00	0.00	0.00	0.00	0.00	4.65	1.59	0.00	2.22	0.00
	(+=ASU P or R)	n	34	48	42	56	27	36	54	42	31	41	21	33	31	43	63	24	45	54
18	Odontome P1-P2	%	0.00	0.00	0.00	5.26	4.35	0.00	0.00	0.00	0.00	6.90	0.00	1.22	0.00	2.94	0.00	0.00	9.68	2.63
	(+=ASU +)	n	11	33	36	38	23	21	82	31	19	29	21	82	23	34	41	12	31	38
19	Congenital Absence UM3	%	0.00	11.76	4.44	7.14	3.70	3.03	5.00	9.76	6.45	3.03	0.00	1.41	0.00	2.50	16.67	11.54	2.17	9.62
	(+=ASU -)	n	45	51	45	56	27	33	80	41	31	33	24	71	36	40	60	26	46	52

20	Midline Diastema UI1	%	12.50	10.81	5.88	0.00	3.85	3.03	8.70	3.57	0.00	11.11	0.00	0.00	0.00	2.63	3.33	0.00	4.88	8.51
	(+ 0.5 mm)	n	24	37	34	52	26	33	23	28	23	9	16	9	19	38	60	25	41	47
21	Lingual Cusp LP2	%	46.67	29.63	57.14	51.72	56.25	50.00	64.00	66.67	58.33	56.00	35.29	63.79	72.41	54.17	77.27	22.22	68.18	57.14
	(+=ASU 3-9)	n	15	27	35	29	16	8	50	18	12	25	17	58	29	24	22	9	22	28
22	Anterior Fovea LM1	%	69.23	50.00	20.00	81.25	40.00	0.00	40.00	57.89	33.33	46.15	50.00	37.04	47.37	45.45	43.75	40.00	12.50	58.33
	(+=ASU 2-4)	n	13	20	15	16	10	2	35	19	9	13	10	27	19	11	16	5	8	12
23	Mandibular Torus	%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(+=ASU 2-3)	n	47	47	43	50	31	24	81	52	39	38	22	10	28	46	60	31	49	52
24	Groove Pattern LM2	%	62.50	63.64	63.41	50.00	50.00	25.00	10.53	28.95	33.33	37.50	68.18	45.45	42.86	45.71	41.30	52.94	22.86	45.45
	(+=ASU Y)	n	32	44	41	46	24	16	76	38	18	32	22	77	35	35	46	17	35	44
25	Rocker Jaw	%	0.00	18.18	5.88	27.27	15.15	11.11	21.95	13.21	25.64	0.00	5.88	20.00	0.00	2.38	5.26	10.71	2.08	18.18
	(+=ASU 1-2)	n	45	44	34	44	33	18	82	53	39	37	17	5	21	42	57	28	48	44
26	Cusp Number LM1	%	31.25	12.12	3.13	5.71	5.88	0.00	6.94	5.71	9.09	5.00	5.56	2.17	13.79	15.79	0.00	0.00	0.00	5.71
	(+=ASU 6+)	n	32	33	32	35	17	9	72	35	11	20	18	46	29	19	28	8	15	35
27	Cusp Number LM2	%	94.59	78.38	32.14	56.25	47.37	25.00	33.33	33.33	33.33	64.29	45.00	64.06	50.00	54.55	41.18	26.67	50.00	51.61
	(+=ASU 5+)	n	37	37	28	32	19	16	75	33	18	28	20	64	28	22	34	15	26	31
28	Deflecting Wrinkle LM1	%	30.77	31.82	12.00	36.36	38.46	50.00	7.02	11.11	0.00	19.05	16.67	11.43	7.14	11.76	11.11	0.00	0.00	20.69
	(+=ASU 2-3)	n	13	22	25	22	13	6	57	27	8	21	18	35	28	17	27	4	9	29
29	C1-C2 Crest LM1	%	0.00	0.00	0.00	0.00	0.00	0.00	4.92	0.00	0.00	0.00	0.00	0.00	3.85	0.00	0.00	0.00	0.00	3.57
	(+=ASU +)	n	16	27	26	26	13	8	61	28	8	20	17	37	26	17	27	4	9	28
30	Protostylid LM1	%	0.00	6.06	0.00	9.68	5.56	14.29	2.90	0.00	0.00	0.00	0.00	0.00	3.13	5.26	0.00	0.00	0.00	3.13
	(+=ASU 2-6)	n	24	33	34	31	18	7	69	40	14	20	20	42	32	19	26	7	8	32

31	Cusp 7 LM1	%	9.68	6.82	7.14	11.63	12.50	0.00	3.53	14.58	0.00	25.00	8.33	14.81	20.00	13.79	17.14	0.00	8.33	14.23
	(+=ASU 2-4)	n	31	44	42	43	24	12	85	48	17	32	24	54	40	29	35	17	24	42
32	Tome's Root LP1	%	52.38	9.30	15.38	19.57	19.35	8.70	6.00	2.86	17.24	70.00	33.33	9.52	16.67	34.15	25.00	10.53	20.41	13.46
	(+=ASU 3-5)	n	21	43	26	46	31	23	50	35	29	10	12	21	24	41	52	19	49	52
33	Root Number LC	%	0.00	3.92	2.63	8.16	6.06	4.17	1.54	0.00	0.00	0.00	5.56	2.63	3.13	0.00	1.92	5.56	4.26	1.82
	(+=ASU 2+)	n	17	51	38	49	33	24	65	43	33	25	18	38	32	47	52	18	47	55
34	Root Number LM1	%	6.67	0.00	2.70	2.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.25	0.00	2.04	0.00	3.13	2.08
	(+=ASU 3+)	n	45	50	37	39	23	15	45	29	17	29	17	44	32	38	49	16	32	48
35	Root Number LM2	%	83.72	82.00	84.62	91.18	92.31	91.67	89.58	92.00	89.47	81.25	90.91	88.89	96.55	84.21	94.00	80.00	80.49	88.89
	(+=ASU 2+)	n	43	50	26	34	26	12	48	25	19	16	11	36	29	38	50	20	41	45
36	Torsomolar Angle LM3	%	7.69	7.69	4.88	4.76	14.29	0.00	16.67	16.67	11.11	6.06	4.55	0.00	6.25	7.69	15.69	5.26	11.11	4.35
	(+=ASU +)	n	39	52	41	42	28	20	60	30	18	33	22	57	32	39	51	19	45	46

[1]GSA=Gebel Sahaba, GRM=Gebel Ramlah, AGR=A-Group, CGR=C-Group, HCG=Hierakonpolis C-Group, PHA=Pharaonic, MER=Meroitic, XGR=X-group, CHR=Christian, AKH=Al Khiday Late Palaeolithic, AKN=Al Khiday Neolithic, GHB=Ghaba, R12=R12 site, KAM=Kerma Ancien/Moyen, KMC=Kerma Classique, TOM=Tombos, SOL=Soleb, KUS=Kush. See text for details.

[2]ASUDAS traits defined in Scott and Irish (2017).

[3]ASU rank-scale trait breakpoints from Irish (1993, 1997, 1998a,b, 2005, 2006) and Scott and Irish (2017). See text.

Table S2. Symmetrical MMD distance matrix for the 18 samples from Nubia based on 36 dental traits

	GSA	GRM	AGR	CGR	HCG	PHA	MER	XGR	CHR	AKH	AKN	GHB	R12	KAM	KMC	SOL	TOM	KUS
GSA[1,2]	0	**0.106**	**0.168**	**0.189**	**0.140**	**0.162**	**0.200**	**0.171**	**0.187**	**0.121**	**0.171**	**0.172**	**0.164**	**0.091**	**0.161**	**0.256**	**0.231**	**0.082**
GRM	**0.106**[3]	0	0.068	0.071	0.021	0.013	0.126	0.081	0.126	**0.131**	0.105	0.107	0.123	0.033	0.117	0.168	0.119	0.024
AGR	**0.168**	0.068	0	0.075	0.000	0.000	0.074	0.042	0.015	**0.064**	0.000	0.039	0.022	0.041	0.001	0.063	0.009	0.032
CGR	**0.189**	0.071	0.075	0	0.000	0.029	0.132	0.043	0.064	**0.135**	0.040	0.088	0.051	0.038	0.062	0.083	0.080	0.023
HCG	**0.140**	0.021	0.000	0.000	0	0.000	0.081	0.027	0.057	**0.060**	0.000	0.035	0.028	0.000	0.000	0.032	0.000	0.000
PHA	**0.162**	0.013	0.000	0.029	0.000	0	0.013	0.001	0.006	**0.096**	0.035	0.035	0.026	0.006	0.015	0.049	0.000	0.000
MER	**0.200**	0.126	0.074	0.132	0.081	0.013	0	0.000	0.000	**0.123**	0.107	0.080	0.103	0.068	0.055	0.051	0.049	0.023
XGR	**0.171**	0.081	0.042	0.043	0.027	0.001	0.000	0	0.000	**0.096**	0.057	0.056	0.034	0.019	0.000	0.025	0.021	0.000
CHR	**0.187**	0.126	0.015	0.064	0.057	0.006	0.000	0.000	0	**0.082**	0.015	0.050	0.039	0.065	0.000	0.010	0.030	0.030
AKH	**0.121**	**0.131**	**0.064**	**0.135**	**0.060**	**0.096**	**0.123**	**0.096**	**0.082**	**0**	**0.000**	**0.102**	**0.084**	**0.063**	**0.026**	**0.091**	**0.037**	**0.082**
AKN	**0.171**	0.105	0.000	0.040	0.000	0.035	0.107	0.057	0.015	**0.000**	0	0.020	0.000	0.059	0.000	0.000	0.005	0.058
GHB	**0.172**	0.107	0.039	0.088	0.035	0.035	0.080	0.056	0.050	**0.102**	0.020	0	0.045	0.080	0.034	0.024	0.052	0.019
R12	**0.164**	0.123	0.022	0.051	0.028	0.026	0.103	0.034	0.039	**0.084**	0.000	0.045	0	0.041	0.029	0.093	0.009	0.049
KAM	**0.091**	0.033	0.041	0.038	0.000	0.006	0.068	0.019	0.065	**0.063**	0.059	0.080	0.041	0	0.046	0.074	0.012	0.008
KMC	**0.161**	0.117	0.001	0.062	0.000	0.015	0.055	0.000	0.000	**0.026**	0.000	0.034	0.029	0.046	0	0.021	0.000	0.028
SOL	**0.256**	0.168	0.063	0.083	0.032	0.049	0.051	0.025	0.010	**0.091**	0.000	0.024	0.093	0.074	0.021	0	0.000	0.050
TOM	**0.231**	0.119	0.009	0.080	0.000	0.000	0.049	0.021	0.030	**0.037**	0.005	0.052	0.009	0.012	0.000	0.000	0	0.053
KUS	**0.082**	0.024	0.032	0.023	0.000	0.000	0.023	0.000	0.030	**0.082**	0.058	0.019	0.049	0.008	0.028	0.050	0.053	0

[1]GSA=Gebel Sahaba, GRM=Gebel Ramlah, AGR=A-Group, CGR=C-Group, HCG=Hierakonpolis C-Group, PHA=Pharaonic, MER=Meroitic, XGR=X-group, CHR=Christian, AKH=Al Khiday Late Palaeolithic, AKN=Al Khiday Neolithic, GHB=Ghaba, R12=R12 site, KAM=Kerma Ancien/Moyen, KMC=Kerma Classique, TOM=Tombos, SOL=Soleb, KUS=Kush (see main text for details).

[2]GSA and AKH distances in bold face to facilitate comparison.

[3]Underlined MMD distances indicate significant difference at the ≤0.05 level.

Table S3. Correspondence analysis summary table for the 36 traits

Dimension	Inertia (Eigenvalue)	Chi square	Sig.	Proportion of inertia accounted for	Cumulative inertia
1	.046			.181	.181
2	.039			.153	.335
3	.034			.134	.469
4	.033			.129	.598
5	.018			.072	.671
6	.016			.063	.733
7	.014			.057	.790
8	.012			.048	.838
9	.010			.039	.877
10	.008			.032	.909
11	.007			.029	.938
12	.005			.021	.959
13	.004			.015	.974
14	.003			.011	.984
15	.002			.008	.992
16	.001			.005	.997
17	.001			.003	1.000
Total	**.255**	**3740.240**	**.000**[1]	**1.000**	**1.000**

[1]595 degrees of freedom

Table S4. Final ASUDAS traits for 21-trait MMD analysis among the 18 Nubian samples

Maxillary Traits	Mandibular Traits
Winging UI1	Lingual Cusp LP2
Palatine Torus	Anterior Fovea LM1
Shoveling UI1	Groove Pattern LM2
Interruption Groove UI2	Rocker Jaw
Distal Acc. Ridge UC	Cusp Number LM1
Carabelli’s Trait UM1	Cusp Number LM2
Parastyle UM3	Cusp 7 LM1
Root Number UM2	Tomes’ Root LP1
Peg-Reduced UI2	Root Number LC
Midline Diastema UI1	Root Number LM1
	Root Number LM2

Table S5. Symmetrical MMD distance matrix for the 18 samples from Nubia based on 21 dental traits

	GSA	GRM	AGR	CGR	HCG	PHA	MER	XGR	CHR	AKH	AKN	GHB	R12	KAM	KMC	SOL	TOM	KUS
GSA[1,2]	0	**0.190**	**0.278**	**0.306**	**0.263**	**0.308**	**0.321**	**0.309**	**0.315**	**0.169**	**0.283**	**0.228**	**0.265**	**0.144**	**0.268**	**0.440**	**0.376**	**0.158**
GRM	**0.190**[3]	0	0.074	0.100	0.050	0.054	0.181	0.136	0.160	**0.185**	0.147	0.114	0.173	0.054	0.169	0.303	0.179	0.050
AGR	**0.278**	0.074	0	0.089	0.000	0.000	0.118	0.075	0.037	**0.102**	0.021	0.020	0.042	0.030	0.019	0.161	0.025	0.034
CGR	**0.306**	0.100	0.089	0	0.021	0.105	0.136	0.046	0.032	**0.124**	0.007	0.046	0.053	0.064	0.053	0.152	0.099	0.033
HCG	**0.263**	0.050	0.000	0.021	0	0.000	0.082	0.039	0.038	**0.041**	0.000	0.000	0.051	0.000	0.000	0.096	0.000	0.000
PHA	**0.308**	0.054	0.000	0.105	0.000	0	0.000	0.001	0.000	**0.126**	0.073	0.017	0.064	0.022	0.011	0.129	0.000	0.020
MER	**0.321**	0.181	0.118	0.136	0.082	0.000	0	0.000	0.014	**0.174**	0.157	0.056	0.147	0.086	0.066	0.116	0.069	0.032
XGR	**0.309**	0.136	0.075	0.046	0.039	0.001	0.000	0	0.000	**0.117**	0.066	0.018	0.048	0.030	0.002	0.082	0.039	0.004
CHR	**0.315**	0.160	0.037	0.032	0.038	0.000	0.014	0.000	0	**0.107**	0.000	0.000	0.023	0.046	0.016	0.047	0.032	0.043
AKH	**0.169**	**0.185**	**0.102**	**0.124**	**0.041**	**0.126**	**0.174**	**0.117**	**0.107**	0	**0.014**	**0.061**	**0.094**	**0.018**	**0.007**	**0.152**	**0.043**	**0.070**
AKN	**0.283**	0.147	0.021	0.007	0.000	0.073	0.157	0.066	0.000	**0.014**	0	0.000	0.008	0.056	0.006	0.000	0.035	0.039
GHB	**0.228**	0.114	0.020	0.046	0.000	0.017	0.056	0.018	0.000	**0.061**	0.000	0	0.020	0.069	0.000	0.054	0.036	0.000
R12	**0.265**	0.173	0.042	0.053	0.051	0.064	0.147	0.048	0.023	**0.094**	0.008	0.020	0	0.066	0.033	0.212	0.063	0.059
KAM	**0.144**	0.054	0.030	0.064	0.000	0.022	0.086	0.030	0.046	**0.018**	0.056	0.069	0.066	0	0.014	0.167	0.031	0.025
KMC	**0.268**	0.169	0.019	0.053	0.000	0.011	0.066	0.002	0.016	**0.007**	0.006	0.000	0.033	0.014	0	0.084	0.000	0.016
SOL	**0.440**	0.303	0.161	0.152	0.096	0.129	0.116	0.082	0.047	**0.152**	0.000	0.054	0.212	0.167	0.084	0	0.079	0.112
TOM	**0.376**	0.179	0.025	0.099	0.000	0.000	0.069	0.039	0.032	**0.043**	0.035	0.036	0.063	0.031	0.000	0.079	0	0.070
KUS	**0.158**	0.050	0.034	0.033	0.000	0.020	0.032	0.004	0.043	**0.070**	0.039	0.000	0.059	0.025	0.016	0.112	0.070	0

[1]GSA=Gebel Sahaba, GRM=Gebel Ramlah, AGR=A-Group, CGR=C-Group, HCG=Hierakonpolis C-Group, PHA=Pharaonic, MER=Meroitic, XGR=X-group, CHR=Christian, AKH=Al Khiday Late Palaeolithic, AKN=Al Khiday Neolithic, GHB=Ghaba, R12=R12 site, KAM=Kerma Ancien/Moyen, KMC=Kerma Classique, TOM=Tombos, SOL=Soleb, KUS=Kush (see main text for details).

[2]GSA and AKH distances in bold face to facilitate comparison.

[3]Underlined MMD distances indicate significant difference at the ≤0.05 level. Actual *p*-values presented in Supplementary Table S6.

Table S6. Symmetrical significance matrix (p-values) of MMD distances for the 18 samples from Nubia based on 21 dental traits

	GSA	GRM	AGR	CGR	HCG	PHA	MER	XGR	CHR	AKH	AKN	GHB	R12	KAM	KMC	SOL	TOM	KUS
GSA[1]	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GRM	0.00	1	0.00	0.00	0.07	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01
AGR	0.00	0.00	1	0.00	1.00	1.00	0.00	0.00	0.23	0.00	0.52	0.60	0.09	0.20	0.43	0.00	0.41	0.13
CGR	0.00	0.00	0.00	1	0.47	0.07	0.00	0.05	0.28	0.00	0.83	0.21	0.03	0.01	0.03	0.00	0.00	0.13
HCG	0.00	0.07	1.00	0.47	1	1.00	0.00	0.22	0.32	0.24	1.00	1.00	0.12	1.00	1.00	0.04	1.00	1.00
PHA	0.00	0.32	1.00	0.07	1.00	1	1.00	0.99	1.00	0.04	0.26	0.79	0.27	0.70	0.85	0.08	1.00	0.72
MER	0.00	0.00	0.00	0.00	0.00	1.00	1	1.00	0.59	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.01	0.07
XGR	0.00	0.00	0.00	0.05	0.22	0.99	1.00	1	1.00	0.00	0.05	0.63	0.06	0.22	0.94	0.04	0.22	0.88
CHR	0.00	0.00	0.23	0.28	0.32	1.00	0.59	1.00	1	0.00	1.00	1.00	0.47	0.14	0.63	0.32	0.40	0.16
AKH	0.00	0.00	0.00	0.00	0.24	0.04	0.00	0.00	0.00	1	0.73	0.15	0.00	0.53	0.83	0.00	0.22	0.01
AKN	0.00	0.00	0.52	0.83	1.00	0.26	0.00	0.05	1.00	0.73	1	1.00	0.83	0.09	0.87	1.00	0.37	0.23
GHB	0.00	0.00	0.60	0.21	1.00	0.79	0.10	0.63	1.00	0.15	1.00	1	0.63	0.07	1.00	0.26	0.38	1.00
R12	0.00	0.00	0.09	0.03	0.12	0.27	0.00	0.06	0.47	0.00	0.83	0.63	1	0.01	0.21	0.00	0.05	0.02
KAM	0.00	0.01	0.20	0.01	1.00	0.70	0.00	0.22	0.14	0.53	0.09	0.07	0.01	1	0.58	0.00	0.32	0.28
KMC	0.00	0.00	0.43	0.03	1.00	0.85	0.00	0.94	0.63	0.83	0.87	1.00	0.21	0.58	1	0.04	1.00	0.51
SOL	0.00	0.00	0.00	0.00	0.04	0.08	0.00	0.04	0.32	0.00	1.00	0.26	0.00	0.00	0.04	1	0.09	0.00
TOM	0.00	0.00	0.41	0.00	1.00	1.00	0.01	0.22	0.40	0.22	0.37	0.38	0.05	0.32	1.00	0.09	1	0.02
KUS	0.00	0.01	0.13	0.13	1.00	0.72	0.07	0.88	0.16	0.01	0.23	1.00	0.02	0.28	0.51	0.00	0.02	1

[1]GSA=Gebel Sahaba, GRM=Gebel Ramlah, AGR=A-Group, CGR=C-Group, HCG=Hierakonpolis C-Group, PHA=Pharaonic, MER=Meroitic, XGR=X-group, CHR=Christian, AKH=Al Khiday Late Palaeolithic, AKN=Al Khiday Neolithic, GHB=Ghaba, R12=R12 site, KAM=Kerma Ancien/Moyen, KMC=Kerma Classique, TOM=Tombos, SOL=Soleb, KUS=Kush (see text for details).

Table S7. Sub-Saharan sample summary and MMD distances with Late Palaeolithic Gebel Sahaba and Al Khiday for 36 dental traits

Sub-Saharan Sample[1]	Date	Region	GSA MMD	*p*-value	AKH MMD	*p*-value
Ghana (GHA)	19th century	Sub-Saharan West	0.040	0.50	0.199	0.00
Nigeria-Cameroon (NIC)	19th century	Sub-Saharan West	0.006	0.79	0.084	0.00
Togo-Benin (TOB)	19th century	Sub-Saharan West	0.005	0.84	0.063	0.01
West Africa Holocene (WAH)	5000-500 BCE	Sub-Saharan West	0.012	0.71	0.073	0.03
Congo (CON)	19th century	Sub-Saharan Central	0.008	0.85	0.071	0.08
Dem. Rep. Congo Bas Iron Age (DBI)	~0-1500 CE	Sub-Saharan Central	0.035	0.40	0.003	0.94
Gabon (GAB)	19th-20th century	Sub-Saharan Central	0.023	0.41	0.072	0.01
Upemba Valley (UPB)	680-1335 CE	Sub-Saharan Central	0.140[2]	0.00	0.086	0.00
Ethiopia (ETH)	19th century	Sub-Saharan East	0.118	0.00	0.032	0.32
Kenya (KEN)	19th century	Sub-Saharan East	0.101	0.00	0.047	0.04
Kenya Holocene (KHO)	1000 BCE-1400 CE	Sub-Saharan East	0.127	0.00	0.062	0.00
Somalia (SOM)	19th-20th century	Sub-Saharan East	0.133	0.00	0.081	0.00

[1]Sample details in Supplementary Note S3

[2]Underlined values are significant at level indicated by the *p*-value

Figure S1. Late Palaeolithic burial showing prone, extended body position indicative of this period at Al Khiday. Photo CSSeS.

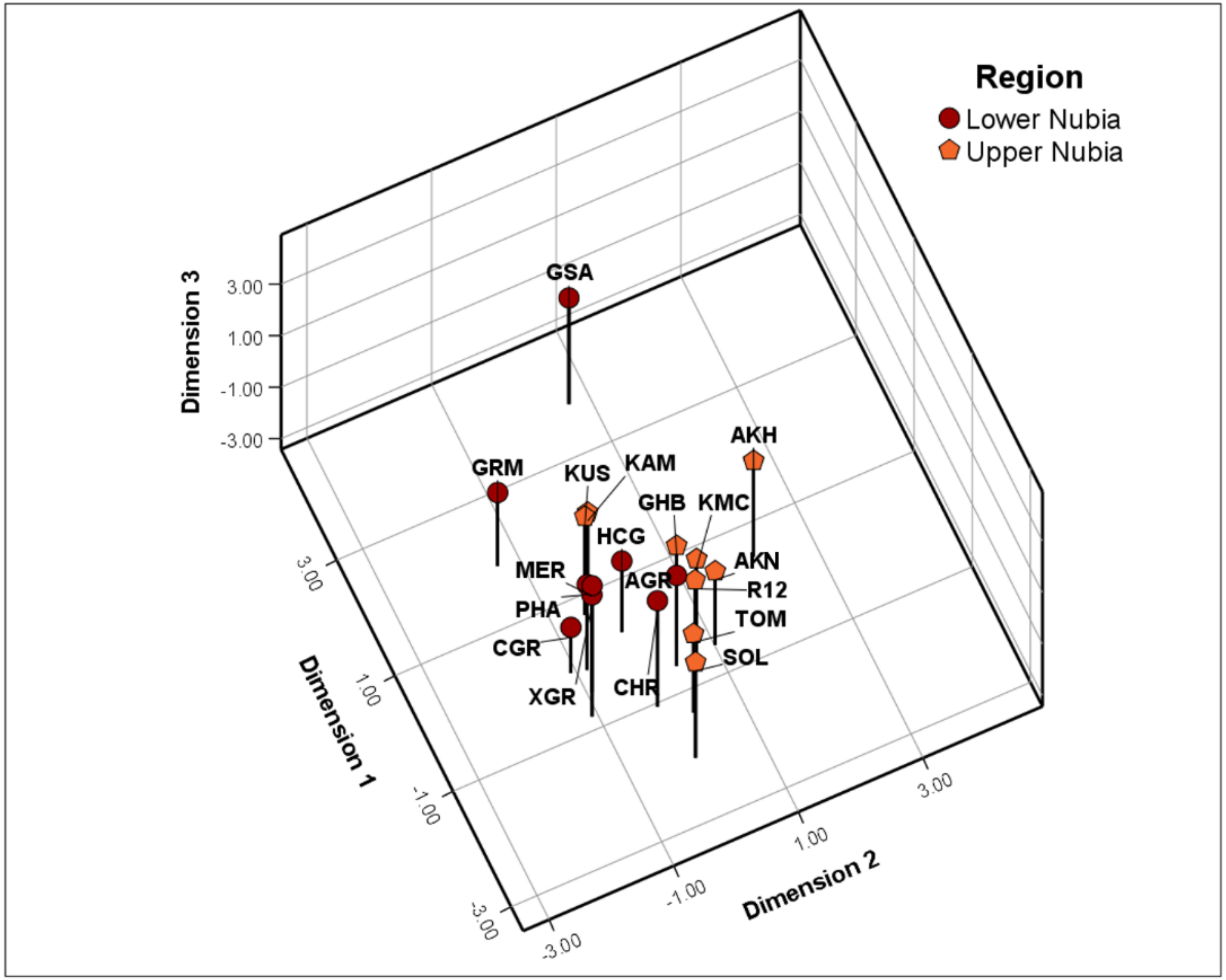

Figure S2. Three-dimensional MDS of 36-trait MMD distances among Nubian samples from Table S2. Three-letter abbreviations defined in Table 1. The MDS solution of the MMD matrix yields a Kruskal's stress formula 1 value of 0.147 and r^2 of 0.884. See main text for details.

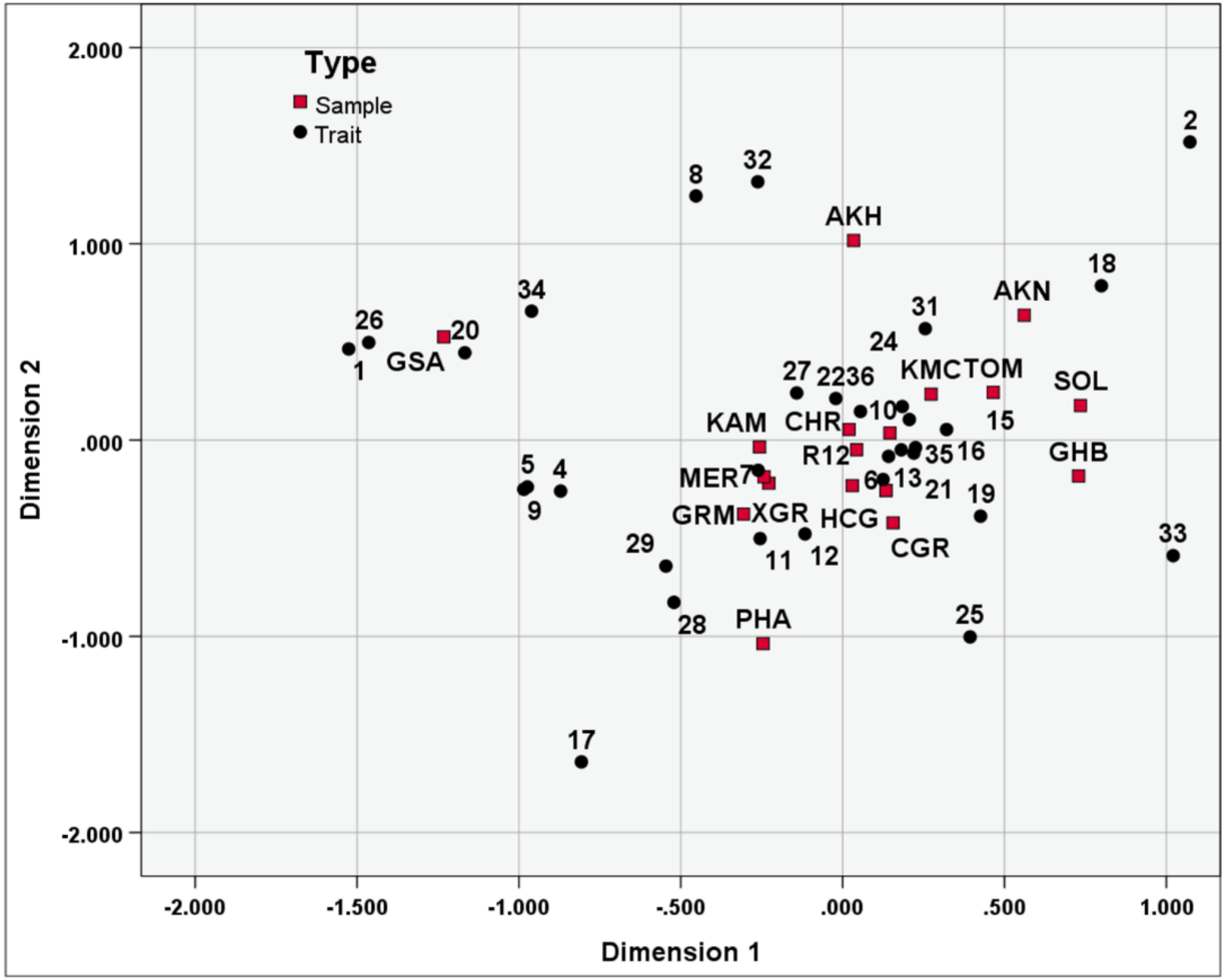

Figure S3. Correspondence analysis biplot for first two dimensions (33.5% of the inertia; see Table S3), showing relative locations of the Nubian samples (red squares; three-letter abbreviations from Table 1 in main text) and ASUDAS traits (black circles; numbers correspond to trait number in Table S1). See Supplementary Note S2 for interpretation.

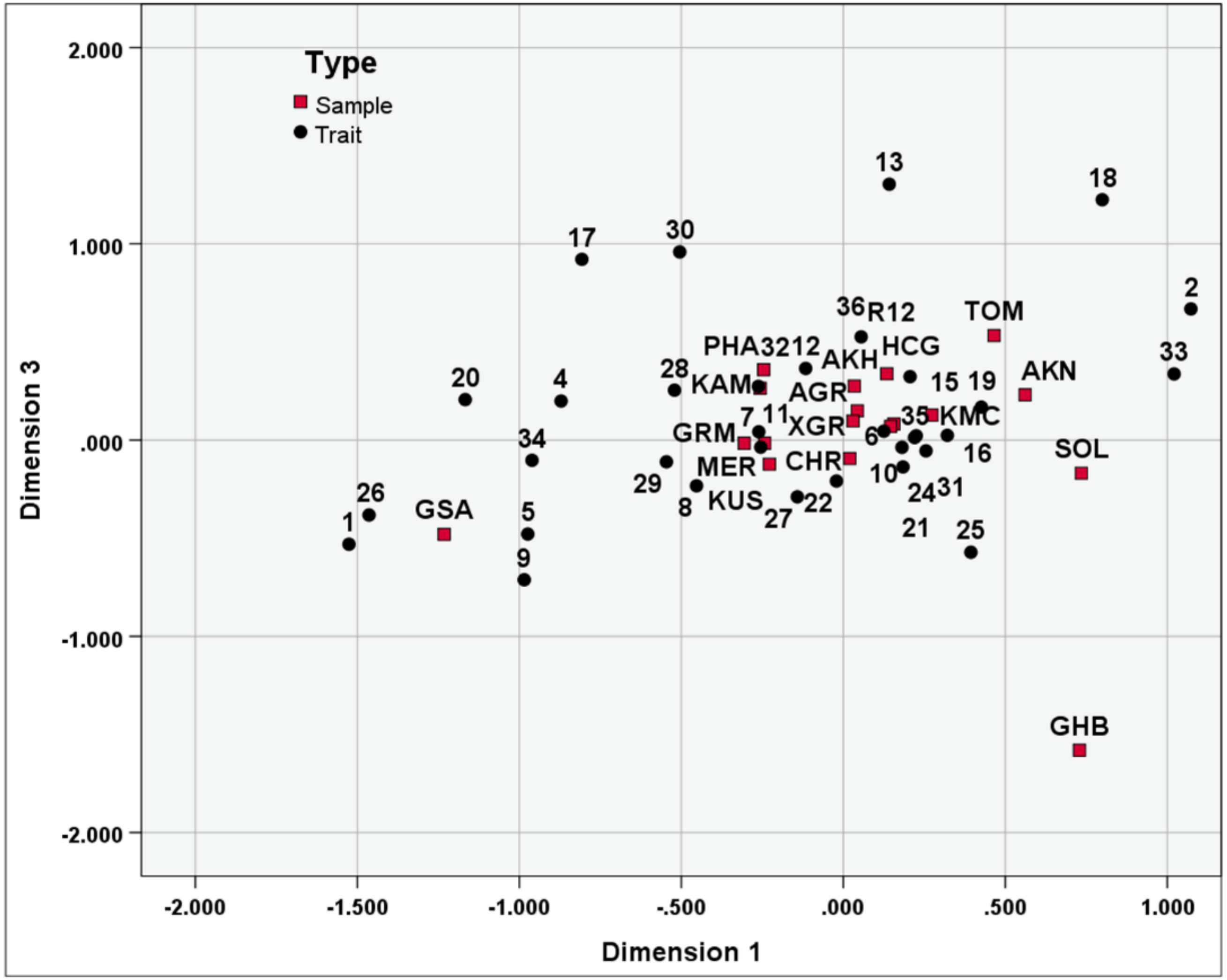

Figure S4. Correspondence analysis biplot for first and third dimensions (all three account for 46.9% of the inertia; see Table S3), showing relative locations of the Nubian samples (red squares; three-letter abbreviations from Table 1 in main text) and ASUDAS traits (black circles; numbers correspond to trait number in Table S1). See Supplementary Note S2 for interpretation.

Figure S5. Right side of Late Palaeolithic skull from Al Khiday *in situ*. This and other crania of this period at the site possess broad ascending rami of the mandible, gonial eversion (here obscured by matrix), a long, low cranial vault, large mastoid processes, and a massive nuchal crest, indicative of robusticity related to heavy musculature. See the text for details. Photo CSSeS.

Figure S6. Posterior view of same Late Palaeolithic male skull from Al Khiday as Figure S5. See the text for details. Photo CSSeS.

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