Early to Middle Holocene Hunter-Fisher-Gatherers from the Green Sahara (Gobero, Niger): Dental evidence for regional African affinities

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Abstract

Objectives. We assess patterns of dental morphological variation at the site of Gobero, located in central Niger, to test competing models of population history in northern Africa during the Holocene "Green Sahara" period. We test three competing models: East African Dispersal Model, Maghreb Dispersal Model, and Multisource Dispersal Model.

Materials and Methods. Data were collected on dental morphological variables using the Arizona State University Dental Anthropology system for two successive occupation phases at the Gobero site (Early and Middle Holocene). Using Mean Measure of Divergence statistics, these data were compared to Late Pleistocene, Early Holocene, and Middle Holocene sites from 22 premodern dental samples from the Maghreb, Nile Valley, and eastern, central and southern Africa. Results were visualized using MDS ordination. Analyses were run using a 35 trait and a 26 trait data matrix.

Results. The resulting inter-sample affinities suggest that time-successive Gobero populations are dentally indistinguishable, suggesting continuity of populations through time at the site despite significant climate deterioration. Both the Early and Middle Holocene samples at Gobero share dental affinities with Nile Valley populations, in particular the multicomponent Sudanese site of al-Khiday. However, both samples also show intermediate affinities with northern and sub-Saharan African populations.

Discussion. These results suggest that for most of the Holocene, an admixed population was present in the central Sahara with a primarily East African/Nile Valley origin. Nonetheless, as the climate deteriorated we cannot discount population interactions with northern African and sub-Saharan populations.

Keywords: Dental morphology; Hunter-fisher-gatherer; African Humid Period; Green Sahara; Niger; Gobero

1. Introduction

Understanding the great diasporas in human prehistory necessitates a synthesis of data from several fields including biological anthropology, the archaeological record, ancient and modern genomic data, linguistic analysis, the record of environmental settings, and the overarching climate history. Africa not only harbors the greatest range of human genetic diversity of any continent (Campbell and Tishkoff, 2008, 2010; Tishkoff et al., 2009), but the northern half was subject to significant climatic fluctuation following the withdrawal of the glaciers at the close of the Pleistocene (Armitage et al., 2015; Boisard et al., 2025; Drake and Breeze, 2016). The Sahara received considerably greater precipitation for approximately five millennia from 10,000 to 5,000 years ago (the African Humid Period; Adkins et al., 2006; Armstrong et al., 2023; de Menocal et al., 2000; Pausata et al., 2020; Schuster et al., 2009) and was repopulated by human populations after the hyper-arid occupational hiatus of the terminal Pleistocene (Cancellieri et al., 2016; Drake et al., 2011; Maley and Vernet, 2015; Petit-Maire, 1986, 1991; Petit-Maire et al., 1983). Understanding the dynamics of human migration during this period has been challenged by poor preservation (precluding aDNA recovery) and exceedingly small and isolated records of human burials. At one unique site in Niger in the central Sahara, called Gobero (Sereno et al., 2008), well preserved burials have been recovered that span the entirety of the African Humid Period that provide an unprecedented record of biological diversity for the region. Here, we assess the dental morphology of two time-successive samples at this one locale over several millennia to assess diachronic population change, both here and, by extension, across the greater central Sahara. We also compare the Gobero populations to Pleistocene and Holocene samples from the margins of the desert, and further surrounding regions, to consider possible source populations for the Holocene re-entry of the desert.

2. Late Pleistocene to Middle Holocene Ancient Saharans

Here we divide the population history of the central and southern Sahara into four successive phases: the MIS5-2/Aterian, “Ogolian hyper-arid”, “Initial amelioration”, and the African Humid Period. Understanding the long-term nature of human movement and occupation of northern Africa is key to the research framework we test here.

2.1. MIS5-2/Aterian (~150-30 kBP)

The Aterian is a Middle Stone Age tool technology and associated cultural complex found throughout much of northern Africa roughly corresponding with the beginning of MIS5 and continuing through the end of MIS2. This relatively long interval is characterized by episodic occupation by hunter-gatherers linked to desert adaptions and a distinctive toolkit (Wrinn and Rink, 2003; Garcea, 2004b, 2012, 2021, 2022; Bouzouggar et al., 2008; Barton et al., 2009, 2016; Dibble et al., 2013; Scerri, 2013; Scerri and Spinapolice, 2019; see also Drake and Breeze (2016) for a different interpretation of the adaptive focus). Although initially considered a terminal Pleistocene industry based on problematic radiometric dates, the Aterian is now understood to span ~150 to 30 kBP with intermittent occupations at most sites. Dates generally cluster early in the sequence, leaving a temporal gap from ~40 to 20 kBP in many areas (Garcea, 2004b; Scerri, 2013; Stoetzel et al., 2014). Haour (2003) and Clark (2008a) review the sparse, poorly dated Aterian record in Niger, which has not preserved any human remains. The apparent hiatus between Aterian and succeeding Epi-paleolithic sites in the Sahara is key to establishing that re-population from surrounding refugia must have occurred once the climate began to improve.

2.2 LGM/Ogolian hyper-arid (25-14.5 kBP)

A hyper-arid phase at the end of the Last Glacial Maximum, termed the Ogolian in western Africa (Chevrier et al., 2016; Collins et al., 2013; Coutros, 2019; Makaske et al., 2007), periodically generated dune fields in the southern Sahara starting ~20 to 25 kBP and continuing through the Younger Dryas (12.9 to 11.7 kBP). During the Ogolian hyper-arid, Niger and most of the present-day central and southern Sahara was devoid of human occupation (see Brooks et al., 2005; Haour, 2003). Repopulation would, therefore, be required to account for its occupants during the Holocene African Humid Period. This hyper-arid phase exacerbated conditions that may have existed since the end stages of Aterian occupation.

2.3 Initial amelioration (14.5-11.7 kBP)

A third phase is sometimes differentiated toward the end of the arid Late Pleistocene involving initial bursts of climatic amelioration prior to the African Humid Period (Haasan,1997; de Menocal et al., 2000; Gasse, 2000; Kuper and Kröpelin, 2006; Adkins et al., 2006; Drake et al., 2011). For some, the African Humid Period begins abruptly at ~14.5 kBP (de Menocal at al., 2000); for others a discrete warming event at ~11.7 kBP defines a clear boundary between the Pleistocene and Holocene, as marked by several biochemical indicators in ice cores (Walker et al., 2019). This initial amelioration may be associated with episodic occupation of certain locations by hunter-gatherers associated with distinctive tanged or shouldered projectile points (Ounan points; Barich, 2013; Cancellieri and di Lernia, 2014; Clark, 2008b; McDonald, 2004, 2020; Roset, 1987, 2000; Vernet et al., 2007). Ounan points were identified at several sites in Niger (reviewed by Clark, 1976, 2008; Roset et al., 1990) and a similar pre-pottery phase was reported in the Libyan Sahara (Cancellieri and di Lernia, 2014; di Lernia, 2022). However, no human remains have been found that can be associated with these populations; their biological contribution to succeeding African Humid Period populations is unknown but was likely minimal and sporadic based on assumed small population size reflected in ephemeral archaeological sites.

2.4 African Humid Period (Early and Middle Holocene, 11.7-4.2 kBP)

The African Humid Period (AHP) began roughly 11.7 kBP at the close of the Pleistocene. It continued through the Early Holocene (11.7-8.2 kBP), and ended at the close of Middle Holocene around 4.2 kBP (Ait Brahin et al., 2023; Walker et al., 2012, 2019), when the Sahara expanded to near its present geographical extent. At the onset, populations rapidly expanded into a Sahara devoid of human occupation, their origins linked via linguistics and archaeological evidence to various satellite refugia in the Maghreb to the north, the Nile and Rift Valleys to the east, and forested regions to the west and south (MacDonald, 1998; Blinkhorn et al., 2022). This repopulation appears to have occurred rapidly across much of northern Africa, with sites spanning from the Nile Valley to the Atlantic Coast (Senegal, Mauritania) (Petit-Maire et al. 1983; Roset 1987; Haaland, 1992, 1995, 1997, 2009; Haaland and Magid, 1995; Close 1995; Yellen, 1998). Most of the Sahara experienced a shorter arid spike around 8.2 kBP that anchors the boundary between the Early and Middle Holocene

(Walker et al., 2019). Out-migration and then in-migration may have occurred during this interval as well, influencing populations that flourished during the Middle Holocene (8.2-4.2 kBP). Any depopulation was short-lived, however (800-1,000 years), and in some regions there is no evidence for any depopulation at this time (cf., di Lernia, 2002). By 4.2 kBP, increasing aridity transformed much of the region into the desert we know today.

3. Migration models and major questions

3.1 Migration models

Three hypotheses have emerged to account for repopulation of the Sahara during the Early Holocene after a sustained period of aridity toward the end of the Late Pleistocene.

The first model, identified here as the "East Africa Dispersal model" (Fig. 1A), suggests a northward and westward migration from the Nile and Rift Valleys of eastern Africa to repopulate the center and then peripheral regions of the Sahara during the Holocene. It has historical origins in the work of Sutton (1974, 1977), who coined the term "Aqualithic" for a distinctive "aquatic way of life," which emerged across much of northern Africa, from the Rift Valley northward to the Nile Valley and eastward to the Atlantic coast of the Sahara (his "Middle Africa"). The overlap of barbed bone spear/harpoons, dotted wavy line ceramics and distribution of Nilo-Saharan languages is undeniable (Sutton, 1973, 1977; Drake et al., 2011; Blench, 2019; Ehret, 2019), despite some diversity of material culture inventories and adaptations that arose over time and through processes of regional diversification (Garcea, 1998; Jesse, 2002, 2003, 2010; Mohammed-Ali and Khabir, 2003; Holl, 2005; Clark and Gifford-Gonzalez, 2008; di Lernia, 2022). Of the two distinctive material artifacts commonly preserved at Aqualithic sites—bone barbed spear/harpoons and ceramics with a dotted wavy line motif—Sutton noted that the former appears to have arisen substantially earlier in the southern Rift Valley, a pattern that has withstood subsequent research (Yellen, 1998). On this basis, Sutton suggested that the origin of at least the spear/harpoon tradition, and possibly the peoples who came to reoccupy the central Sahara, may have come from the southern end of the Rift Valley—a pattern that maps well onto present-day Nilo-Saharan speakers (Sutton, 1977; Blench, 2014, 2019; Ehrens, 2019). Although pottery styles are also broadly similar across these regions, subsequent work has largely called the association between "people and pots" into question (Garcea, 1998; Jesse, 2002, 2003, 2010; Mohammed-Ali and Khabir, 2003; Holl, 2005; Clark and Gifford-Gonzalez, 2008; di Lernia, 2022). Furthermore, the earliest pottery in Africa was discovered at sites near Ounjougou, Mali (11.4-10.8 kBP; Huysecom et al., 2004, 2009), which is farther west and south than other early ceramics from the central and eastern Sahara and Nile Valley (Roset, 2000; Jesse, 2002, 2003, 2010). These earliest ceramics may suggest a south-to-north migration from the Sahel to the Sahara (Close, 1995; MacDonald 1998). Pottery, however, may have had multiple centers of origin, given the patchy availability of clay versus other materials such as bone (Jesse, 2010; Rotunno and Crema, 2025).

The second model, identified here as the "Maghreb Dispersal model" (Fig. 1B), argues that populations along the northern coast of Africa (Maghreb), who were long-term residents there, spread southward to colonize the Sahara when the climate ameliorated at the close of the Pleistocene. The historical origins of this hypothesis trace back to the work of Petit-Maire and Dutour, who documented end-Pleistocene and Early Holocene burials in the Maghreb and elsewhere (Petit-Maire and Dutour, 1987; Dutour, 1989a, 1989b, 1992, 1993, 1995, 1998; Dutour et al., 1994) that shared a similar skeletal morphotype termed “mechtoid”. Cranial features including a low, elongated calvarium and rectangular orbits and postcranial robusticity with a tall stature were considered diagnostic (Dutour, 1989a, b, 1992, 1993, 1995, 1998; Dutour et al., 1994; Petit-Maire and Dutour, 1987). Cultural practices such as incisor ablation are known at sites in the Late Pleistocene Maghreb before their appearance in the central Sahara during the Early Holocene, which may further suggest some connections between the two regions (Sereno et al., 2008; Stojanowski et al., 2014). This model is supported by analysis of two genomes from the Middle Holocene of southwestern Libya suggesting a connection between early pastoralist groups there and the Maghreb (Salem et al., 2025).

The third model, designated the “Multisource Dispersal model” (Fig. 1C), suggests that migrants repopulating the central Sahara during the terminal Pleistocene/Early Holocene came from multiple circum-Saharan areas, including northern Africa (Maghreb), sub-Saharan western and central Africa (Sahelian locales), and eastern Africa (Nile, Rift Valley) (D’Atanasio et al., 2023). These admixed populations persisted through the Middle Holocene after an interval of increased aridity around 8.2 kBP (Walker et al., 2019). This resulted in a pattern of linguistic distinctiveness in modern Saharan peoples (Blench, 2014, 2019; Ehrens, 2019) whose genomes suggest diverse circum-Saharan sources (D’Atanasio et al., 2023).

[FIGURE 1 HERE]

3.2 Major questions

Using dental morphological data from Gobero recorded in Early and Middle Holocene skeletons, as well as contemporaneous samples from across Africa, we assess the pattern of phenetic affinities to address two key questions:

(1) What source population(s) reoccupied the central Sahara at the beginning of the African Humid Period during the Early Holocene, and

(2) Were Early Holocene occupants of the central Sahara resilient to the 8.2 kBP aridity spike that impacted much of the Sahara, and if not, can a distinct source population be identified?

4. Gobero Site Complex

4.1 Gobero site complex and occupational phases

The Holocene archaeological site of Gobero (central Sahara, Niger, Fig. 2) preserves burials ranging across five millennia. Located approximately 60 km southwest of the Aïr Massif, Gobero was discovered in the year 2000 and initially described based on evidence garnered in two field seasons (i.e., 2005, 2006; Sereno et al., 2008). Five additional field seasons have since been undertaken (2011, 2012, 2018, 2019, 2022 by P.C.S.), increasing the number of excavated burials, artifacts, sediment horizons sampled, and radiometric dates obtained. Gobero is properly understood as a “site complex” rather than a single site, as it consists of paleodune habitations and burials, lake margin habitations with burials, and lakebed deposits preserving abundant fauna and artifacts. Its location east of the Lake Chad basin and south of the Aïr Massif situates Gobero in the cross-roads of both north-to-south and east-to-west historical movements of peoples.

[FIGURE 2 HERE]

A site chronology for Gobero has been outlined using optically stimulated luminescence dating of paleodune sand and radiocarbon dating of burials, fauna, material artifacts and lake sediments (Sereno et al., 2008). All dates are calBP using IntCal20 (Bronk Ramsey et al., 2023). Two successive occupational phases were dated to Early (9.6 kBP to 7.4 kBP) and Middle (6.6 kBP to 4.8 kBP) Holocene intervals initially associated with Kiffian and Tenerean cultural designations, respectively, previously defined at Adrar Bous in northern Niger (Clark et al., 1973; Clark and Gifford-Gonzalez, 2008). Whereas the gap separating these phases was initially thought to be approximately one millennium (Sereno et al., 2008), subsequent excavations by Sereno (from 2011 to 2022) produced additional dated materials to narrow this gap to around 800 years (7.4 kBP to 6.6 kBP). During this time the site complex, but not necessarily the broader region, was at least temporarily abandoned due to high water levels. This suggests the spring-fed waters of Gobero's paleolake might have mitigated, to some degree, the effects of the arid spike elsewhere in the Sahara around 8.2 kBP. Thus, it calls into question whether any population turnover occurred, something we directly test here.

4.2 Gobero inhabitants

The Early Holocene phase lasted approximately 2,200 years, roughly contemporaneous with Kiffian hunter-fisher-gatherer sites at Adrar Bous about 400 km north (Fig. 2; see Smith, 2008a), Hassi el Abiod in Mali (Dutour, 1989a), al-Khiday in Sudan (Usai and Salvatori, 2019), and multiple sites near Lake Turkana (Robbins, 1974, 1980; Barthelme, 1985; Prendergast and Beyin, 2018). Most Early Holocene burials at Gobero were recovered from a single paleodune cemetery (G3, see Fig. S1) and exhibited dark (pyrolusite) staining from sustained submergence during a high lake stand sometime before the 8.2 kBP event. In addition to being taphonomically distinct, with rare exceptions most individuals were buried in a hyperflexed posture (supine or seated) (Fig. 3A; Sereno et al., 2008; Stojanowski, 2013). Craniofacially (Fig. 4A-C) these individuals have long, low cranial vaults and appear phenotypically similar to individuals from Late Pleistocene and Early Holocene Maghrebi sites, as well as Early and Middle Holocene Saharans from Mali and Mauritania (Sereno et al., 2008; Stojanowski, 2013). Postcrania tend to be robust with well-defined muscle markers and a tall stature. Lithic/bone tool inventories, isotopic analyses of human craniodental remains, and direct dating of the remains prior to any evidence of pastoralism in the Sahara all indicate these individuals were undoubtedly hunter-gatherers that persisted on a mix of aquatic resources, hunted terrestrial fauna and gathered plant foods (Sereno et al., 2008; Stojanowski and Knudson, 2014).

The Middle Holocene occupation is contemporaneous with Tenerean pastoral sites at Adrar Bous (Smith, 2008b) and elsewhere in the Sahara. These burials were predominantly light-colored skeletons that lack the dark staining caused by aqueous submergence, thus providing a relatively reliable dating marker that was confirmed with dozens of radiometric dates (Sereno et al., 2008) (Fig. 3C). Mottled- (Fig. 3B) and especially dark-stained individuals from the Middle Holocene are much rarer and, when present, were associated with different paleodune cemeteries (i.e., not G3, but G2, G5 and G8; see Fig. S1) generally peripherally located within the greater lake basin. Burial postures were more variable but overall exhibited less constricted body postures, with loosely flexed, side burials being the most common burial type (Fig. 3C). Craniofacially, the Middle Holocene occupants had higher, more rounded cranial vaults, smaller faces (Fig. 4D-F) and reduced postcranial robusticity.

The lifeways of the Middle Holocene occupants at Gobero have been debated in numerous papers (Sereno et al., 2008; Garcea, 2013; Stojanowski, 2018, 2019; Stojanowski and Carver, 2011; Stojanowski and Knudson, 2011, 2014; Sereno, 2021). The scarcity, or possible absence, of domesticated cattle at Gobero is a striking contrast to Adrar Bous and many other Saharan sites of Middle Holocene age that show clear evidence of pastoralism. From the diverse wild fauna in middens, *in situ* bone spear/harpoons dated to the Middle Holocene, patterns of oral health, and strontium isotope analysis, the Middle Holocene occupants appear to have been persistent hunter-fisher-gatherers. Their specific ecological concentration may have shifted due to climate change but generally remained focused on resource extraction (Sereno et al., 2008; Stojanowski and Knudson, 2014; Schmidt et al., 2019; Sereno, 2021; for extended discussion, see Stojanowski, 2019).

[FIGURES 3 and 4 HERE]

5. Comparative materials and methods

We compared dental data from the two Gobero temporal samples (Early Holocene, n=20 individuals, Middle Holocene, n=30) with 22 other African samples recorded by the second author. Twelve were recovered from North Africa and 10 from the subcontinent. They in turn are divided into sub-regions: Northwest Africa (Maghreb), Northeast Africa (Nile Valley region), sub-Saharan West Africa, sub-Saharan Central Africa, sub-Saharan East Africa, and sub-Saharan South Africa in all tables and figures. Other than an African origin, all were selected because they are the oldest available sites in the database that predate, postdate and, importantly, overlap with either the Early or Middle Holocene horizons at Gobero. Therefore, beyond assessing general phenetic relatedness of the two Gobero samples to other African populations, a temporal element was introduced to explore potential cross-continental ancestral linkages. All comparative samples predate the historic period to mitigate the confounding effects of markedly increased mobility and gene flow in historic times.

Summary data for each comparative sample, including approximate date by sub-epoch, are listed in Table 1, with locations in Fig. 5. About half the samples were recovered from specific archaeological sites, with many having relatively narrow date ranges [e.g., Taforalt (TAF), Badari (BAD), and Ngorongoro (NGO)]. The proveniences of the remainder vary from multiple site origins, including Gebel Sahaba (GSA) and the Kenya Holocene samples (KHL, KHE), to broader geographic areas, such as Capsian (CAP), A-Group (AGR), South Africa Holocene Early (SHE), and West Africa Holocene (WAH). The latter includes sites from different countries, Burkina Faso and Cameroon that, by standard regional breakdown (United Nations Statistics Division, 2024), are considered to be in West and Central Africa, respectively. However, dentally, western Cameroon populations group with West Africans (Irish, 1993, 1997). More detailed information is available in the supplementary online material (SOM Table S1). Many pooled samples also have broad date ranges—in several cases spanning multiple Holocene sub-epochs, i.e., CAP, WAH, KHE, and four of five South African samples: Holocene Middle South (SHMs), Matjes River (MAT), Holocene Early (SHE), and Holocene Middle West (SHMw). In the latter cases, where possible, samples were divided temporally into Early-Middle and Late Holocene to distinguish the more recent individuals who would have experienced notable admixture with Eurasian pastoralists in East Africa, and subsequently, East African pastoralists and Bantu-speaking farmers in South Africa (Irish et al., 2014; Skoglund et al., 2017; Wang et al., 2020). Though not desirable, such caveats are unavoidable based on the scarcity and often small sizes of ancient African samples—balanced against the aim of representing as much of the continent as possible for comparative analyses. As such, the results from these more heterogeneous samples should be interpreted with caution. Additional sample information is available elsewhere (M Leakey, 1966; L Leakey, 1970; de Maret, 1992; Irish, 2000, 2005, 2006; de Maret et al., 2001; Maes et al., 2004; Irish et al., 2014; Irish and Usai, 2021).

[TABLE 1 & FIGURE 5 HERE]

Thirty-six nonmetric crown, root, and intra-oral osseous traits in the Arizona State University Dental Anthropology System (ASUDAS) (list in SOM Table S2 and descriptions in Scott and Irish, 2017) were recorded. This entailed referencing a series of ASUDAS plaques and images depicting each trait's range of expression on either binary or, mostly, ordinal scales—indicating minimum, maximum, and intermediate grades. These traits were shown to be reliable proxies for neutral genetic variation and serve as markers of population history and structure (Rathmann et al., 2017, 2023; Rathmann and Reyes-Centeno, 2020). Indeed, Irish et al. (2020) found that phenetic distances from ASUDAS data are highly correlated, r_m=0.84, with genetic distances based on >350,000 single nucleotide polymorphisms in 12 matched sample pairs from Africa. These are the same dental traits in all prior studies by the second author (references in Irish 2005; Irish and Usai 2021). Their comparative analyses have been used successfully to address questions concerning population history across Africa (Irish, 1997, 1998, 2000, 2005; Irish and Konigsberg, 2007; Irish and Usai, 2021) and are particularly well suited for identifying North vs. sub-Saharan ancestry (Irish, 1997, 2013). The ASUDAS minimizes errors among observers, which is not an issue in this study because all data were collected by the second author. Other advantages of the traits include: 1) little or no sexual dimorphism to enable pooling of the sexes and inclusion of unsexed individuals in larger samples, 2) accurate recording despite some crown wear, and 3) their conservative evolution to facilitate diachronic comparisons (Scott and Irish, 2017).

To simplify tabular presentation of trait percentages, and as required for the most commonly used distance measures for nonmetric traits, e.g., Mahalanobis D^2 (Konigsberg, 1990; Konigsberg et al., 1993) and mean measure of divergence statistic (MMD) (Sjøvold, 1977; Irish, 2010), all non-binary trait data were dichotomized into standard states of present and absent (Scott and Irish 2017; Irish and Usai 2021). This approach reduces the range of variation in ordinal traits among samples (Harris, 2008), but dichotomized data have several advantages: 1) further reduction of any residual inter- or intra-observer error, 2) higher average heritability estimates—where one recent study found h^2 to be almost twice that of traits treated as continuous variables (Stojanowski et al., 2019) and, importantly, 3) avoidance of weighting bias from different grade numbers across ASUDAS traits, which range from two (e.g., C1-C2 crest, premolar odontome) to eight grades (UI2 shovelling, Carabelli's cusp).

The D^2 and MMD distance measures have proven to be highly concordant (see Irish, 2010 and Results below), but both have pros and cons in application. Thus, selection of the most suitable method is driven by the sample data and research strategy. The squared Euclidean-based D^2 has an advantage over the MMD (though see work-around in Irish, 2010) in studies of population structure when calculating an R-matrix of average kinship coefficients between and within *contemporaneous* samples (Konigsberg, 2006). Our diachronic study dissuades use of this approach. Some samples are separated by millennia (Table 1), as are individuals comprising several pooled samples [CAP, West Africa Holocene (WAH), KHL, KHE, SHE and South African Holocene SHMs and SHMw)]. As Relethford (2018:30) cautions, an R-matrix, and F_{ST} derived from it, should not be used if "computed from samples taken from a wide temporal range," as "the underlying population-genetic model is synchronic." Specifically, the model assumes that gene flow and genetic drift occur at one point in time among interbreeding populations (also see Relethford and Blangero, 1990; Relethford, 1991, 1997). Another D^2 advantage is that it adjusts for phenotypic between-trait correlations to avoid undue weight on suites of traits that co-occur (Konigsberg, 1990). With the MMD, problematic traits are edited out prior to analysis; this editing process (outlined below) was also found to improve D^2 performance, particularly the removal of traits with numerous missing data (Irish, 2010). On the other hand, the D^2, unlike the MMD, does not have a bias correction for small sample sizes—so it is not an unbiased estimator of population divergence, nor does it have a test of significance (Irish, 2010)—meaning it cannot be used to test hypotheses of population history. On these bases we chose the MMD as most appropriate for this model-free diachronic investigation.

The MMD yields inter-sample affinities, where higher values indicate phenetic dissimilarity and vice versa. The formula used here incorporates the Freeman and Tukey angular transformation (Green and Suchey, 1976) to correct for very low or high trait frequencies and small samples. To determine if samples differ significantly from one another, MMD distances are compared to their standard deviations to test the null hypothesis [Population 1 = Population 2], with rejection at a standard 0.05 alpha (details and references in Irish, 2010; Sołtysiak, 2011). The MMD is a robust statistic, shown to provide accurate results even when traits might be considered problematic (Irish, 2010). However, selective editing can yield finer grain resolution, by identifying traits with many missing data, minimal variation, and strong pairwise correlations. Following standard protocol (Irish and Guatelli-Steinberg, 2003), the first step is to remove traits of very small sample size [e.g., LP1 Tomes' root in Gobero Early Holocene sample GEH (see SOM Table S2)]. Second, traits fixed at 0% or 100% across samples are deleted to avoid adding uninformative information to the analysis that reduces inter-population variation. To further remove uninformative traits, principal components analysis (PCA) is used to identify traits with low PC loadings that are subsequently removed from MMD calculations. Finally, to ensure no residual trait inter-correlations, pairwise trait Kendall's tau-*b* correlation coefficients are calculated among the remaining traits with affected traits removed. Finally, beyond reviewing MMD distances among the samples, phenetic affinities can be more intuitively assessed visually. Here, we used interval-level multidimensional scaling (MDS) (Kruskal and Wish 1978). This method was accessed and imaged with SPSS 28.0.

5. Results

The present/absent breakpoints, percentages of presence, and number of observations for the full suite of 36 ASUDAS traits were tabulated for the 24 total samples (SOM Table S2). The large amount of frequency data dissuades simple visual interpretations, but overall trait homogeneity is evident between Gobero early (GEH) and middle (GMH), with some exceptions. This result is of interest given how distinctive individuals of the two occupation phases are craniometrically (Sereno et al., 2008); dental data instead suggest some degree of population continuity. Unfortunately, the sample size, particularly the early Holocene sample, is too small to draw meaningful inferences about some of the larger trait frequency differences (e.g., UI1 shoveling, UM1 cusp 5, LM2 groove pattern). We note, however, remarkable consistency through time in the frequency of several key traits associated with sub-Saharan populations (i.e., UP1 root number, UM2 root number, LM1 cusp 7, Bushman canine, LM2 root number, UM3 presence), with some disparity in other key traits, including UM1 Carabelli's cusp and LM2 Y-groove pattern.

5.1 Dental morphology 35 trait analysis

For an initial quantitative indication of biological relatedness, 35 of the traits, after removing LP1 Tomes' root (see above), were used to generate MMDs among samples. Results of the 35-trait analysis are presented in Table 2, showing distances between GEH and GMH (MMD=0.000, p=1.0), and between each of the Gobero occupations and the 22 comparative samples. Underlined MMD distances indicate a significant difference at $p \leq 0.05$. Mean MMD values were calculated within each comparative region to give a summary assessment of phenetic similarity between Gobero and these regional samples. GEH and GMH are both highly divergent from sub-Saharan South Africans represented by the large, mostly significant distances with means of 0.119 and 0.127, respectively. Both Gobero samples appear more similar to the remaining African samples, albeit with potential geographic patterns. That is, most distances do not significantly differ, but GEH is closer than GMH to samples from Northwest Africa (mean MMD 0.078 vs 0.096), Northeast Africa (0.016 vs 0.030), and sub-Saharan West Africa (0.000 vs 0.026); GMH is more similar to sub-Saharan Central (0.000 vs 0.027) and sub-Saharan East (0.003 vs 0.027) samples.

[TABLE 2 HERE]

This patterning is evident in the 3D MDS plot (Fig. 6). The two Gobero samples are centered between North Africans mostly grouped on the right and sub-Saharan Africans on the left side of the X-axis, with the southern African samples most distant. Though recovered in Northeast Africa, the Gebel Sahaba sample (GSA) is also distinct, toward the bottom left of the plot nearest the WAH sample. The placement is consistent with prior findings of sub-Saharan cranial (Franciscus, 1995; Groves and Thorne, 1999) and post-cranial (Holliday, 1995; 2015) affinities, specifically West African based on dental phenetic distances for this late Pleistocene group (Irish, 1993, 1997, 1998, 2000, 2005, Irish and Turner, 1992; Irish and Usai, 2021). A 2D configuration is easier to interpret, but its solution yielded an R^2 of 0.884 and a high stress of 0.172—values approaching what is considered a poor fit (Kruskal and Wish, 1978; Dugard et al., 2022). The 3D solution improved the R^2 and stress values to 0.915 and 0.124, respectively, but still indicate only a fair fit. The MDS plot should, therefore, only be used to interpret general relationships. For specific pairwise interpretations the MMD distances and sub-region means in Table 2 should be given higher priority.

[FIGURE 6 HERE]

5.2 Dental trait editing

The 35 traits were edited as described above for the next MMD analysis. Given the emphasis of our study, four additional root traits were removed due to very small sample sizes in one or both of the Gobero samples (SOM Table S2): UP1 root number, UM2 root number, LC root number, and LM2 root number, to leave 31 total. UI1 double shoveling was also removed due to a lack of variation across samples.

Percentages of the remaining 30 traits were then submitted to PCA. Eight components having eigenvalues of ≥ 1.0, accounting for 80.2% of the total variance, were retained (SOM Table S3). Only one trait had low loadings ($\leq|0.5|$) across all components, LM1 root number, which was removed from further analysis. Alternatively, traits with higher loadings are important in characterizing samples and driving the variation among them. A PCA scatterplot of the first three components (45.6% total variance) focusing on loadings $\geq|0.6|$ is presented in Fig. 7. On component 1, North African samples toward the right side are mostly characterized by higher percentages of UI2 interruption groove and UM1 Carabelli's cusps (see SOM Table S2), as previously reported (Irish 1998, 2000, 2005, 2006). Sub-Saharan samples (and GSA), particularly the South Africans, have fewer of these traits and higher occurrences of UI1 labial curvature, UC Bushman Canine, peg-reduced UI2, LM1 anterior fovea, LM2 Y-groove, five-cusped LM2, and LM1 cusp 7, as documented previously (Irish, 1997, 1998, 2013; Irish et al., 2014). Component 2 reflects higher percentages of UI1 winging, UI1 shoveling, UI2 tuberculum dentale, UC distal accessory ridge, six-cusped LM1, LM1 deflecting wrinkle, and LM1 protostylid in samples at the bottom of the plot, with the reverse for those at the top. Finally, along component 3 samples near the bottom of the Z-axis have higher UM2 hypocone and premolar odontome prevalence. Though set on a larger scale to highlight trait variation among samples, the *overall* patterning is, unsurprisingly, similar to the 35-trait MDS plot—with some relative movement of individual samples.

[FIGURE 7 HERE]

In the final editing step, high pairwise correlations of $\tau_b \geq |0.8|$ prompted the deletion of UI1 midline diastema, UI2 tuberculum dentale, and LM1 C1-C2 crest. This resulted in 26 traits (see SOM Table S2) for this MMD analysis.

5.3 Dental morphology 26 trait analysis

The MMD distances are provided in Table 3. The value between GEH and GMH increased but does not reach the level of a significant difference (MMD=0.058, p=0.266). Distances between Gobero and the comparative samples also increased, as indicated by mean MMD values for each sub-region. This change is not unexpected, as the removal of uninformative traits yields higher distances. Again, GEH and GMH are divergent from sub-Saharan South Africans based on mostly larger, significant distances with increased means, 0.144 and 0.146. Other changes include an increase in total significant differences, and GEH is now less similar to Northwest (mean MMD 0.141 vs 0.136) and Northeast Africans (0.067 vs 0.049) in comparison to distances for GMH. GEH is still more similar to the sub-Saharan West African sample (0.000 vs 0.038), while GMH remains closer to sub-Saharan Central (0.000 vs 0.067) and East African (0.009 vs 0.076) samples.

[TABLE 3 HERE]

The 26-trait 3D MDS solution indicates another fair fit (R^2=0.906, stress=0.134), so again, while good for discerning general patterns among all samples, specific interpretations should rely on the MMD distances. Not unexpectedly, the plot (Fig. 8) is largely analogous to the 35-trait configuration, as supported by a Mantel correlation between matrices of r_m=0.975 (p=0.000). As before, both GEH and GMH are positioned between North Africans on the right and sub-Saharan Africans on the left of the X-axis. Some minor shifting of comparative samples occurred, with the increase in separation of GEH and GMH. This parallels the PCA scatterplot, where GEH is located below GMH along the Y-axis based on a higher occurrence of UI1 shoveling (SOM Table S2) and, to a lesser extent, other traits evidencing large component 2 loadings [(UI2 tuberculum dentale, UC distal accessory ridge, LM1 deflecting wrinkle), SOM Table S2]. Otherwise, overall comparability in MDS and PCA results indicates the sample affinities are robust and not artifacts of the analytical procedure. In fact, parallel results (not shown) were obtained with the Mahalanobis distance statistic, supported by a strong correlation (r_m=0.931, p=0.000) between the 26-trait MMD and D^2 MMD matrices, and the latter's MDS solution (see SOM Fig. S1).

Consideration of the pattern of distances (Table 3) within an ancestor-descendant hypothesis testing framework provides more clarity. For GEH, which dates to between 9.6 kBP and 7.4 kBP, there are only four comparative samples that represent older, possibly ancestral populations (TAF, AFA, GSA, and AKH). Of note, GEH is significantly different from all of these samples except AKH (al-Khiday's Late Pleistocene component), which is located in the Nile Valley. It is interesting to note that GEH is still more similar to GMH than to AKH, again suggesting some degree of continuity through time at Gobero. For GMH, which dates to between 6.6 kBP and 4.8 kBP, we instead consider distances among its contemporaries (NW Africa: CAP; NE Africa: BAD, NAQ, GRM, AGR, R12, GHB, AKN; W. Africa: WAH, E. Africa: KHE). Interestingly, GMH is most similar to AKN (the Neolithic component at al-Khiday), followed by KHE and R12, sites located in East Africa and the Nile Valley, respectively. However, GMH is also not significantly different from sites in Northwest or West Africa, which is different from the pattern for GEH, and suggestive of a different and more inclusive pattern of affinity during the Middle Holocene.

[FIGURE 8 HERE]

Finally, because the South Africans are so distinct from the Gobero and other comparative samples—as visualized along the X-axes of PCA and MDS plots—it was decided to rerun analyses without them to focus on 'circum-Sahara' affinities. As such, the same 30 traits after initial editing were again submitted to PCA for the two Gobero and, now, 17 comparative samples. Eight components accounting for 82.4% of the total variance, were retained (SOM Table S4). Four traits with low loadings (≤|0.5|) across components were identified for removal: UI1 shoveling, UM1 cusp 5, UM3 congenital absence, and LM1 C1-C2 crest. Another PCA scatterplot (46.3% variance) was then created (Fig. 9).

[FIGURE 9 HERE]

Without the South African samples, the most variation is now between GSA and WAH on the left, and all others on the right of the X-axis. Again, focusing on loadings ≥|0.6|, six traits with higher frequencies in the former two samples are the main drivers: UI1 winging, UI2 tuberculum dentale, UC distal accessory ridge, LM1 anterior fovea, LM1 cusp number, and LM1 deflecting wrinkle (SOM Table S2). Samples toward the right generally have successively lower frequencies of these same traits, with most sharing a relatively elevated occurrence of rocker jaw (though with loading <|0.6|, SOM Table S4). Among the latter grouping of samples, those toward the top of the plot along the Y-Axis have more common sub-Saharan traits, including UI1 labial curvature and LM1 cusp 7, while those nearer the bottom are characterized by the UM2 Hypocone, UM1 Carabelli's trait, and LM1 protostylid. Along component 3, samples at the top of the Z-axis are more likely to have high frequencies of palatine torus and premolar odontomes, and vice versa. Lastly, pairwise correlations were identified, and one remaining trait prompted deletion, UI1 midline diastema. This left 25 traits (list in SOM Table S4) for the MMD analysis excluding the South African samples.

These distances are tabulated in Table 4. The value between GEH and GMH decreased to now indicate no difference (MMD=0.000, *p*=1.000). Distances between Gobero and the 17 comparative samples also mostly decreased, as implied by the mean sub-region MMDs. Regarding inter-region patterning, Gobero affinities to the Northwest samples remain relatively constant, i.e., divergent from late Pleistocene TAF and AFA, and close to CAP. The mean MMDs now show GEH to be more similar to Northeast Africans than GMH (0.016 vs 0.032), while both Gobero samples are similarly like samples in West, Central, and East Africa, with low, insignificant MMD values. Consideration of these data (Table 4) in an ancestor-descendant hypothesis testing framework is remarkably similar to the 25 trait analysis (Table 3). GMH is most similar to two Nile Valley sites (AKH, GRM) and KHE in East Africa, followed by WAH in West Africa. Of note again is that GMH is not significantly different from contemporaneous samples in Northwest Africa (CAP), although at a higher MMD.

[TABLE 4 HERE]

The fit of this 25-trait MDS solution is again fair (R^2=0.904, stress=0.138), so capable for visualizing overall patterning (Fig. 10) but with specific interpretations best left to the MMD distances and means. As before, GEH and GMH are positioned centrally among North and sub-Saharan African samples, least like Northeast GSA and Northwest AFA and TAF Late Pleistocene samples at opposite ends of the X-axis. With the South African samples removed, some shifting, like the PCA plot, clearly occurred between X- and Y-axes. However, overall concordance of post-Pleistocene relationships remains similar with, as stated, lower MMD distances.

[FIGURE 10 HERE]

6. Discussion

These inferences of population history from central Niger are consistent with models of Holocene Saharan prehistory based on independent lines of archaeological, linguistic, and biological anthropological evidence. Whereas an initial craniometric analysis (Sereno et al., 2008) aligned with the "mechtoid" model of Dutour and colleagues suggesting a Northwest African origin for central Saharan populations (Petit-Maire and Dutour, 1987; Dutour, 1989a, 1989b, 1992, 1993, 1995, 1998; Dutour et al., 1994), the dental results presented here are more consistent with aspects of the "East Africa Dispersal" model for the Early Holocene and the "Multisource Dispersal" model for the Middle Holocene (with qualifications). The first posits an expansion of populations from the Nile headwaters/eastern Africa westward during the Early Holocene (Sutton, 1974, 1977; Petit-Maire et al. 1983; Roset, 1987; Close 1995; Haaland, 1992, 1995, 1997, 2009; Haaland and Magid, 1995; Yellen, 1998). The second, based on the genetics of modern populations, identifies contributions from all peripheries of the Sahara. We discuss these results with respect to previous work at Gobero, inferences of Early Holocene population affinity, Middle Holocene population affinity, and ancient and modern DNA from North Africa.

6.1 Relationship to previous work at Gobero

Sereno et al. (2008) presented a prior analysis of population affinity at Gobero based on craniometric data that differs from the results presented here. That paper used published comparative data that was available to us (CMS, PCS) at the time, with results indicating similarity between Gobero Early Holocene (n=6) and Late Pleistocene and Holocene/Capsian populations in the Maghreb as well as contemporaneous Holocene samples from Mali and Mauritania. These latter samples had previously been studied by Dutour and colleagues and gave support to the Maghreb Dispersal model, as outlined in this paper. Sereno et al. (2008) further found that the Early and Middle Holocene (n=12) craniofacial profiles at Gobero were divergent, which suggested population discontinuity across the 8.2 kBP arid phase. Lacking a broader comparative sampling scheme, that paper did not offer an interpretation of from where the Middle Holocene population may have originated.

Dental analyses presented in this paper provide a different interpretation—Early Holocene linkages to the Nile valley/East Africa instead of the Maghreb, and population continuity through time based on small and insignificant MMD distances between GEH and GMH.

Regarding the former, we argue the results of the two papers are not directly comparable and therefore not necessarily contradictory. First, the sampling strategies are distinct. Sereno et al. (2008) did not include a Nile Valley or East African sample, or any of the sub-Saharan West, Central and South African samples in their analysis. While we also included the Maghrebi samples in the current paper, we did not include samples from Mali and Mauritania. Because distances are relative measures of population affinity, the lack of a Nile Valley/East African craniometric sample indicates there is no comparable consideration of the Maghreb Dispersal and East African Dispersal models in the Sereno et al. paper. In fact, with the exception of the Taforalt, Afalou, and Capsian composite samples, there is no overlap in geographic representation in the two papers. These papers, therefore, assess different hypotheses. Sereno et al. considered whether Gobero was similar to other so-called “mechtoid” samples from the Maghreb and western Sahara; it does not test whether Gobero is *more* similar to these samples than to those in the Nile Valley or East Africa, which the current paper explicitly considers.

Second, the Sereno et al. paper used Principal Components Analysis of a matrix of sample means and not individual level data (which is more typical in craniometric analysis). No statistical inferences were offered (i.e., no p-values) and the craniometric results were based on ordination of PCA loadings and pattern recognition. We note that the most comparable dental morphological results are those presented in Figs 7 and 9 in the current paper, both of which show *more* dissimilarity between GEH and GMH in comparison to the MDS ordinations based on MMD distances (Figs. 6, 8, 10). Therefore, regarding the issue of population continuity vs discontinuity, the results of the two papers may not be as different as they initially seem. Differences in sample size and the effects of outliers on a mean or frequency-based approach, especially considering the sample size differences in the two papers (cranial: GEH=6, GMH=12; dental: GEH=20, GMH=30), may also be driving the apparent disconnect in the results.

Finally, we note a divergence of dental and cranial data sets is not unusual in regional scale studies such as this (see Falk and Corruccini, 1982; Heathcote, 1990; Herrera et al., 2014; Hershkovitz et al., 1990; Rathmann et al., 2023). For example, a similar result was documented in northeastern Africa that figured prominently in a decades long debate about population continuity in the Nile Valley at sites contemporaneous with the occupational phases at Gobero (reviewed in Irish and Usai 2021). Likewise, Irish (2000) discusses the disconnect between cranial and dental signatures in the Taforalt and Afalou samples, which are craniometrically quite similar but dentally distinct. Such disconnects likely reflects the fact that craniometric data and dental morphological data are phenotypic proxies with different relationships to evolutionary history and population structure. Craniofacial size and shape, for example, are clearly linked to masticatory function (and by extension subsistence adaptation) and selective pressures regarding overall vault size and shape, facial and mandibular form, and morphological anatomical variation, which includes a climate signature (Evtev and Movsesian, 2015; Reyes-Centeno et al., 2016; von Cramon Taubadel, 2016). Dental data, on the other hand, are considered more evolutionarily conservative, linked primarily to neutral patterns of variation, and not subject to mechanical demands given their early age of formation and aplastic morphology throughout the life course (Hubbard et al., 2015; Irish et al., 2020; Rathmann and Reyes-Centeno, 2020; Rathmann et al., 2017, 2023; but see also Kimura et al., 2009, 2015; Park et al., 2012).

Nonetheless, the disconnect between cranial and dental results remains unresolved. As discussed below, we do not infer a wholesale transition in subsistence adaptation at Gobero making a functional explanation for craniofacial reduction incomplete. And despite significant climatic deterioration during the course of the region's use as a burial ground, it seems unlikely that this alone can account for the variation in craniofacial form over the short (in evolutionary terms) timespan we are sampling here.

6.2 Early Holocene population affinity

Our results for the Early Holocene suggest a connection between Gobero and Nile Valley populations. This result is consistent with the work of Drake et al. (2011) who synthesized elements of both the "Maghreb dispersal" and "East Africa Dispersal" models in their comprehensive review of early Saharan population history. Based on the distribution of Ounan points in the northern Sahara (Clark, 1976, 2008b; McDonald, 2004, 2020; Roset, 1987, 2000; Vernet et al., 2007) and the toolkit of the "Aqualithic" (bone spear/harpoons, bone fish hooks, dotted wavy line ceramics) to the south, they concluded that the "initial Holocene repopulation [was] carried out by two separate populations practicing two quite different resource exploitation strategies: 1) aquatic foraging using bone point and fishhook technology, and 2) savanna hunting using the bow and arrow" (Drake et al., 2011: 461). Thus, two technological innovations and subsequent population expansions are proposed. Of note, here, is the work of biological anthropologists in the western Sahara also documenting a biological connection (though not necessarily a direct migration) between the Maghreb and the populations of the southern and central western half of the Sahara (Petit-Maire and Dutour, 1987; Dutour, 1989a, 1989b, 1992, 1993, 1995, 1998; Dutour et al., 1994), thus supporting one element of the Drake et al. model. However, we believe the current paper is the first to document evidence for the second element of their model linked to the expansion of aquatic-adapted populations from eastern Africa.

Although Gobero does not preserve burial evidence from early putative "savanna hunting" groups before the arrival of "aquatic foraging" populations, evidence exists elsewhere in Niger for their presence (see discussion and debate in Clark, 1976, 2008b; Roset, 1987, 1995, 2000; Roset et al., 1990; Smith, 2008a). The particulars of these earliest occupants have been extensively discussed (see Riemer et al., 2004; Vernet et al., 2007; Cancellieri and di Lernia, 2014). Northern Niger was home to forager groups ~12 kBP, during the "initial amelioration" phase, who were using a macrolithic point technology. These poorly dated sites seem to be earlier than pottery-bearing sites and may have been disrupted by the Younger Dryas. There are no skeletal remains to assess population affinities of these ephemeral hunter-gatherer groups. Nonetheless, "Aqualithic fisherfolk'" may have migrated into a Sahara "already populated by a broad swath of diverse hunting-gathering peoples who show in some cases a direct lithic continuity with later ceramic-using traditions" (MacDonald, 1998:38). Our data suggest that if these two populations lived side-by-side there may have been little admixture between them (based on the significant differences between GEH and sites in the Maghreb).

Tropical central Africa and the western African Sahel and coastal regions are usually not incorporated into discussions of the peopling of the Sahara during the early Holocene, largely because of the relatively poor archaeological record from these regions. Drake et al. (2011) give the region little consideration, for example. Nevertheless, terminal Pleistocene sites indicate a human presence in the coastal and subtropical portions of West Africa (Casey, 2003; Cerasoni et al., 2022; Chevrier et al., 2016; Ndiaye et al., 2023). In MacDonald's survey of competing hypotheses of Saharan prehistory, he concludes, "[at] some point after 12,000 BP these indigenous populations began an expansion northward….from the coast to as far north as Mali….and Burkina Faso" (MacDonald, 1998:40). While not quite as far north as Gobero, the geographical proximity and presumed climate model, wherein more tropically-adapted taxa are migrating north during periods of climatic amelioration, both suggest the possibility of migration from south-to-north. Unfortunately, we lack data to test this competing hypothesis. Iwo Eleru is the only burial from the Late Pleistocene of western Africa, and it lacks a usable dentition. However, craniometric analysis suggests it is distinct from most Late Pleistocene and Early Holocene African populations, including Gobero (Stojanowski, 2014).

6.3 Middle Holocene population affinity

During the Middle Holocene, our data support elements of both the East Africa Dispersal model (GMH shows primary affinity with AKH and other Nile Valley and East African contemporaries) and the Multisource Dispersal model (based on insignificant differences between GMH and sites in the Maghreb and West Africa). Results also suggest population continuity at Gobero (based on insignificant MMDs between GEH and GMH and both having closest affinity with the occupation phases at al-Khiday in the Nile Valley) within the context of a more expansive pattern of gene flow during the Middle Holocene that seems to have integrated much of northern Africa. However, it is important to note that the Middle Holocene comparisons include much broader time horizons, smaller sample sizes, and more aggregated samples. Therefore, it is more parsimonious to interpret the MMD distances with respect to gene flow rather than direct migration, which requires much tighter spatio-temporal control to interpret. Of course, the bulk analyses may be capturing the effects of *both* direct in-migration *and* more expansive gene flow due to increasing mobility, increasing population size, expanding trade networks, and more complex and variable social networks and structures. It is also instructive to consider how these results relate to the 8.2 kBP “event” that disrupted the longer-term pattern of increasing humidity and relatively stable populations that likely resulted in population movements away from certain areas and aggregation at others. Gobero’s persistent waters suggest it was an attractive location for several millennia until it was finally abandoned as the modern Saharan climate was established. As such, out-migration from the Sahara during hyper-arid intervals must also be considered as an element of the “Multisource Dispersal model.”

The Middle Holocene population that flourished at Gobero, unlike many contemporary Saharan sites dominated by cattle pastoralists, persisted as hunter-fisher-gatherers. Although pastoralism (Garcea, 2013) or a mixed-use landscape (Stojanowski and Carver, 2011; Stojanowski and Knudson, 2011, 2014; Stojanowski et al., 2014, 2015) were proposed for Middle Holocene occupants at Gobero, the preponderance of evidence supports the original interpretation of a persistent aquatic, lake-centered lifestyle (Sereno et al., 2008; Stojanowski, 2019; Sereno, 2021). Evidence includes the composition of middens, absence of securely identified cattle remains, presence of year-round fishing with *in situ* harpoons, persistence of a similar oral health profile, lack of change in mobility as inferred from strontium isotope analysis, and now dental morphology—indicating a broadly similar biological profile throughout the site’s occupation history. We note how remarkable the record of persistence hunter-gatherer activity is at Gobero considering the presence of numerous pastoralist populations in the central Sahara during the Middle Holocene (di Lernia, 2006, 2013; di Lernia and Manzi, 1998; di Lernia et al., 2013; Gifford-Gonzalez and Parham, 2008; Paris, 1984, 1990, 1992, 1995, 1996, 1997).

This persistent hunter-fisher-gatherer lifestyle is even more noteworthy given patterns of gene flow during the Middle Holocene that resulted in dental features indistinguishable from any surrounding population centers. Wholesale replacement from any single direction does not appear to have occurred, despite the rather sudden appearance of a decidedly distinct cranial shape, altered and enhanced burial practices, and changes in material culture—including a disc knife that remains the most distinctive lithic artifact in the central Sahara. Instead, these same mid-Holocene Saharans may have contributed to the dental profile of Sahelian and western African populations as they moved southward in response to Saharan aridification at about 4.2 kBP.

Indeed, ancient DNA recovered from the Middle to Late Holocene burials at Shum Laka, Cameroon, (Fig. 5, no. 13) supports the inference that early western Africans were not ancestral to Middle Holocene Saharan populations, but rather partly descended from them (Lipson et al., 2020). The genetic profiles at Shum Laka were interpreted as representing a highly fragmented population history in western Africa. Lipson et al. (2020:6) identified genetic signatures among *some* Shum Laka individuals that are shared with Saharan populations, suggesting they received “[g]ene flow from the north before 8000 BP . . . due to a short period of Saharan and Sahelian aridification.” This inference is also supported by ancient genomes from southwestern Libya (Salem et al., 2025). Although dental data lack the resolution of genome-level data, our results show a small, statistically insignificant MMD between the GMH sample and a small western African Holocene composite sample, which includes dentitions from Shum Laka. The aDNA from Shum Laka (Lipson et al., 2020), the morphometric discontinuity between Iwo Eleru and most modern human samples

(Stojanowski, 2014), and dental similarity between GMH and the West African Holocene composite sample all suggest western Africa was the recipient of Saharan gene flow during mid-Holocene arid intervals.

6.4 Ancient and modern DNA confirms subsistence mosaics in the Maghreb and Sahel

The record of aDNA research in northern Africa is growing and providing new insights into the complex population history of the region. Genome-level aDNA from individuals at ten sites in the Maghreb dating from the Late Pleistocene through Middle/Late Holocene documents: 1) isolation and continuity in forager populations between 15 and 7.5 kBP, 2) the arrival of Iberian agriculturalists at 7.5 kBP who lived alongside indigenous foragers for hundreds of years with limited gene flow (despite adoption of some local cultural practices), 3) unidirectional gene flow from foragers into *some* agricultural groups, but not vice versa, and 4) in-migration of pastoralists from the Near East who exchanged genes with local forager populations (van de Loosdrecht et al., 2018; Fregel et al., 2022; Simões et al., 2023; Lipson et al., 2025). The Late Pleistocene-Holocene of northwestern Africa, therefore, was a mosaic of foraging, agriculturalist, and pastoralist groups, often living side-by-side, and in some cases remaining genetically isolated from each other for centuries (also see Irish, 2000). Or, in other words, the aDNA record from the Maghreb reconstructs a population history which shows that “northern Africa featured both more heterogeneity and more continuity of autochthonous ancestry after the arrival of migrants and the adoption of new lifestyles… [in which] local hunter-gatherer populations remained more stable and resilient … during the approximately 8,200 years BP climatic cooling event… (Lipson et al., 2025: 6).” South of the Sahara, Wang et al. (2020) reported the recovery of 20 ancient samples from hunter-gatherer and pastoralist populations in Uganda, Botswana, Kenya, and the Democratic Republic of Congo. These data demonstrated an increasing temporal divergence among hunter-gatherers attributed to “resistance to interaction with incoming pastoralists of delayed-return foragers in aquatic environments” (Wang et al., 2020:1). Finally, a similar dynamic was documented by Lipson et al. (2020) at Shum Laka, Cameroon. Their observed divergence of Shum Laka individuals from contemporary Cameroonian hunter-gatherers and agriculturalist Bantu speakers suggests a similar degree of subsistence-based isolation of forager populations in a diverse economic landscape during the Middle and Late Holocene.

These results from ancient DNA are interesting in light of the results presented in this paper. At Gobero, we argue for similar degrees of long-term continuity of forager populations through a circa 5,000 year sequence that, no doubt, witnessed the arrival of pastoralism to this part of the Sahara (Gifford-Gonzalez and Parham, 2008). This makes Gobero an exceptional example of forager persistence in the midst of populations movements and in-migrations that largely favor the visibility of pastoralists on the landscape (e.g., at Adrar Bous (Gifford-Gonzalez and Parham, 2008; Iwelen (Paris, 1990), and in the Libyan Fezzan (di Lernia et al., 2013). As such, our results provide a central Saharan corollary to that documented in the Maghreb, Libya, western Africa (Cameroon) and central and eastern Africa (Uganda, Botswana, Kenya, and the Democratic Republic of Congo) in which long term stability of an autochthonous population is demonstrated, thus resulting in regional heterogeneity of subsistence adaptations. Indeed, numerous studies of modern DNA in the Sahel and Lake Chad basin have shown that subsistence economy affects population structure (Černý et al., 2011, 2017, 2020, 2022; Bučková et al., 2013; Nováčková et al., 2020; Priedhová et al., 2020; Kulichová et al., 2021; Diallo et al., 2022; Fortes-Lima et al., 2022, 2024). Therefore, it is no surprise that a resilient hunter-gatherer population might maintain a relatively distinct population structure over extended periods of time, while also receiving waves of migrants or gene flow over the course of 5,000 years of site use.

How the people of Gobero relate to the modern Tuareg (Berber/Imazighen) (cf., Ottoni et al., 2009, 2010, 2011 vs. Watson et al., 1996, 1997; Rando et al., 1998; González et al., 2006 vs. Cavalli-Sforza et al., 1994) and Fulani (Triska et al., 2015; Čižková et al., 2017; Kulichová et al., 2017; Vicente et al., 2019; Nováčková et al., 2020) pastoralist populations of Niger is unclear. Pereira et al.'s (2010) analysis of modern Tuareg DNA is consistent with the dental analyses of Gobero. They concluded that the aridification of the desert "could have entrapped Tuareg populations coming from northern Africa to the Sahel belt together with other pastoralists such as the Chadic speaking peoples from eastern Africa and Fulani nomads from western Africa . . . all populations arriving in the Sahel were further enriched by various admixtures of many other sub-Saharan lineages…" (Pereira et al., 2010: 921-922). Similarly, D'Atanasio et al. (2023) identified the non-sub-Saharan African component of the Fulani genome as having coalesced ~7 to 8 kBP somewhere in the central Sahara; their origins were traced to "unsampled ancient Green Saharan population(s)" (D'Atanasio et al., 2023:1), which they interpret as "possible Green Saharan cattle herders that moved westward in response to the changing climate and then mixed with local people" (D'Atanasio et al., 2023:6). Analogous work among other African Sahelian populations infers bidirectional movements that entailed gene flow, isolation, and selection (for malarial resistance and lactase persistence, in particular), which shaped localized gene pools constrained by arid phase cycling of the Sahara (Černý et al., 2011, 2017, 2020, 2022; Diallo et al., 2022; Fortes-Lima et al., 2022, 2024; Priehodová et al., 2020; Triska et al., 2015; Vicente et al., 2019). Nonetheless, we reiterate the possible disconnect between inferred resilient hunter-gatherers at Gobero, inferred population structure related to subsistence adaptation, and the singular emphasis on studying pastoralist populations in the modern-day Sahara. The gap between the terminus of Gobero's use and the modern Fulani and Tuareg is 4,500 years and our dental analysis, while suggestive, must be interpreted with caution.

7. Conclusions

This paper addressed two major questions about central Saharan population history at the central Saharan site of Gobero:

(1) What source population(s) reoccupied the central Sahara at the beginning of the African Humid Period during the Early Holocene, and

(2) Were Early Holocene occupants of the central Sahara resilient to the 8.2 kBP arid phase that impacted much of the Sahara, and if not, can a distinct source population be identified?

These questions were framed in terms of three models of population history: East Africa Dispersal model, Maghreb Dispersal model, and Multisource Dispersal model.

Time successive dental morphological data from Gobero yielded results that bear directly on the three models proposed for repopulation of the central Sahara during the Early and Middle Holocene. We favor an "East African Dispersal" model for the Early Holocene (Question 1), partial population continuity through time at Gobero (Question 2), and the "Multisource Dispersal" model during the Middle Holocene (Question 2) (Fig. 2). These results can be further enriched with additional sampling at Gobero, incorporation of additional comparative samples from across North Africa, and greater integration of phenotypic and genomic datasets.

Supplementary Online Material

Supplementary online material to this article can be found online at: TBD

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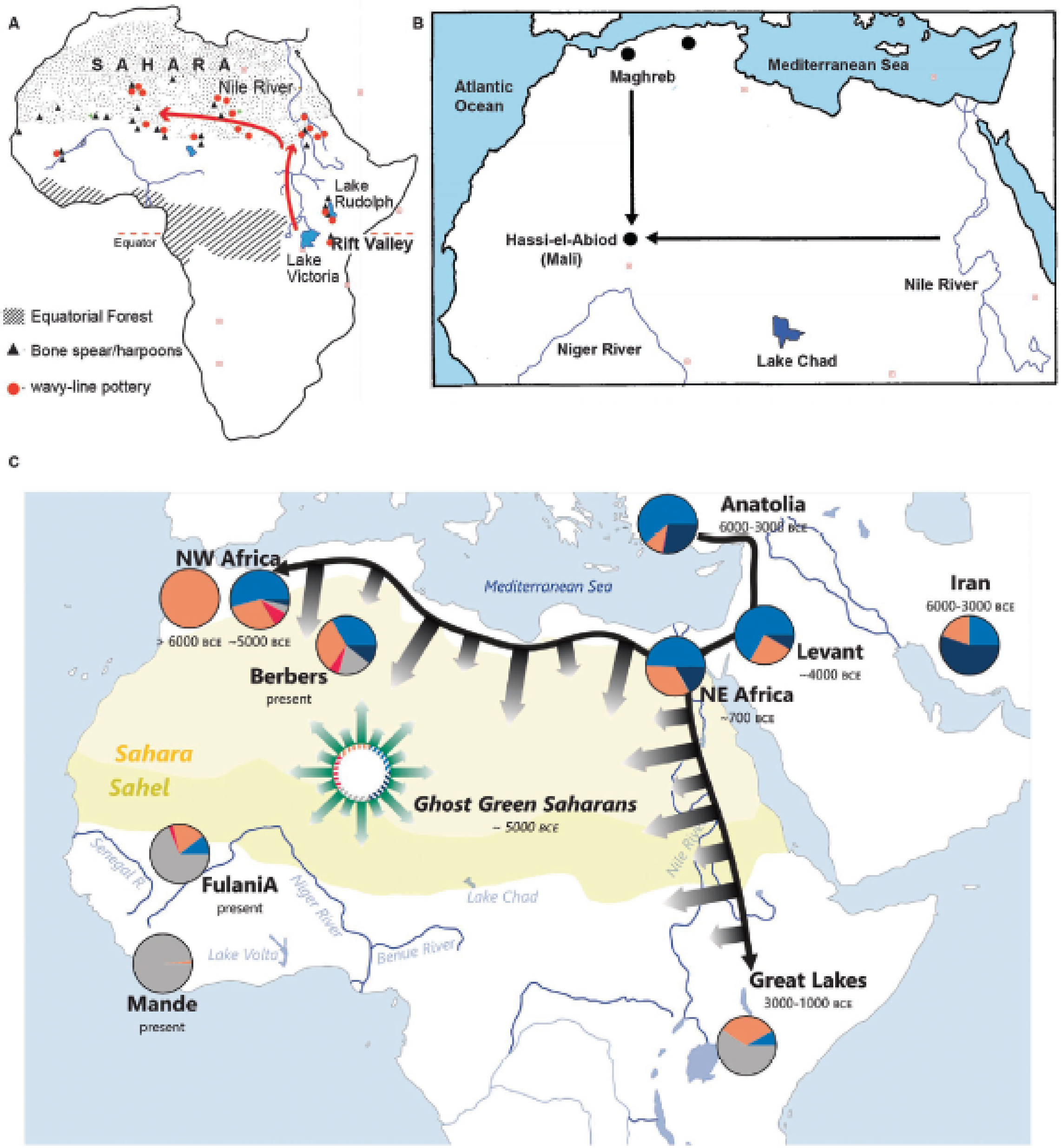


FIGURE 1 | Historical precedents of the three dispersal models defined in the present paper for reoccupation of the Sahara during the Early Holocene. (A) East Africa Dispersal model highlighting source populations in the Rift and Nile Valleys with historical precedent in the work of Sutton (after Sutton 1977: Figure 1, red arrow added following his text); (B) Maghreb Dispersal model highlighting source populations along the northern coast of Africa with historical precedent in the work of Dutour (after Dutour 1989a, 1989b, 1995). (C) Multisource Dispersal model highlighting circum-Saharan source populations based on recent genetic sampling (from D'Atanasio et al. 2023: Figure 4).

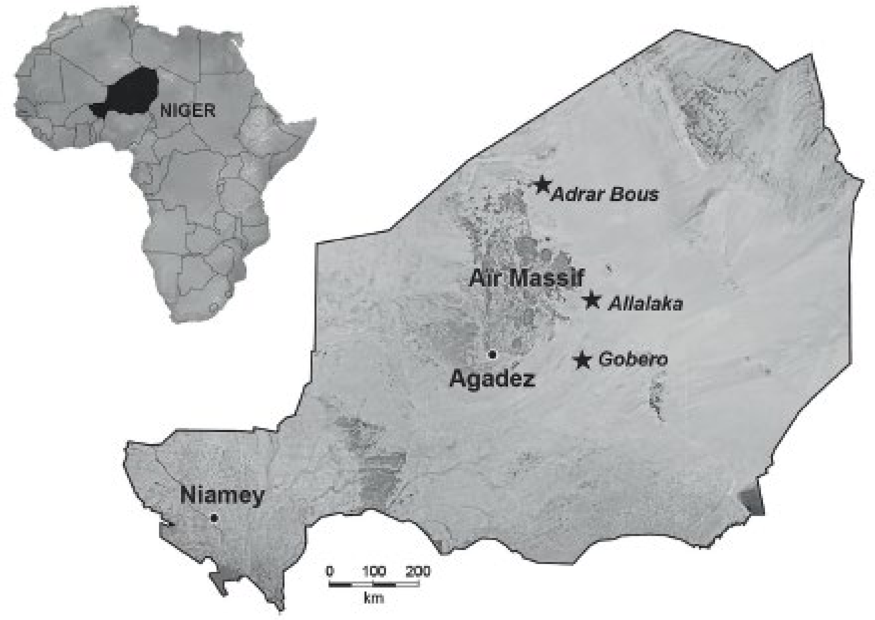


FIGURE 2 | Location of key archaeological sites on the east side of the Aïr Massif in central Niger.

FIGURE 3 | Representative early and Middle Holocene burials at Gobero. (A) Burial from the Early Holocene occupational phase (9456 BP, MNBH G3B8). (B) Earliest burial from the Middle Holocene occupational phase in top and bottom views, the latter showing a mud turtle carapace (6579 BP, MNBH G1B11). (C) One of the latest burials at Gobero from the Middle Holocene occupational phase (4828 BP, MNBH G1B2). Dates are calibrated and represent median values using IntCal 20. Scale bars equal 10 cm.

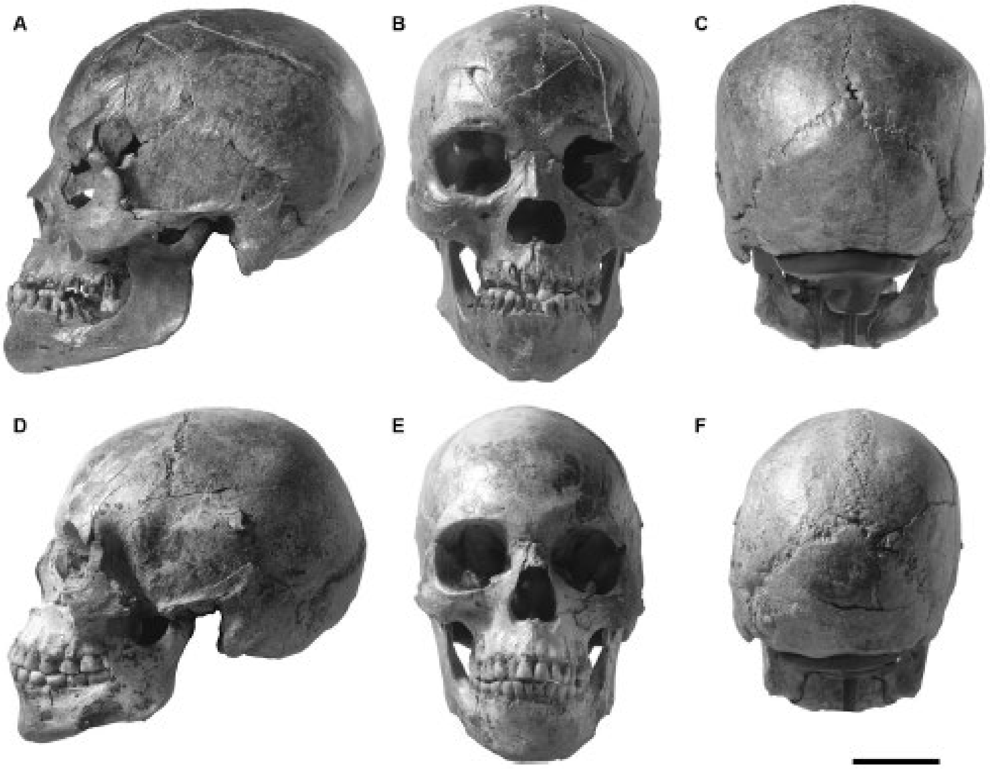


FIGURE 4 | Comparison of adult male skulls from successive occupational phases at Gobero in left lateral, anterior, and posterior views. (A–C) Early Holocene skull (MNBH G3B8). (D–F) Middle Holocene skull (MNBH G1B11). Scale bars equal 5 cm.

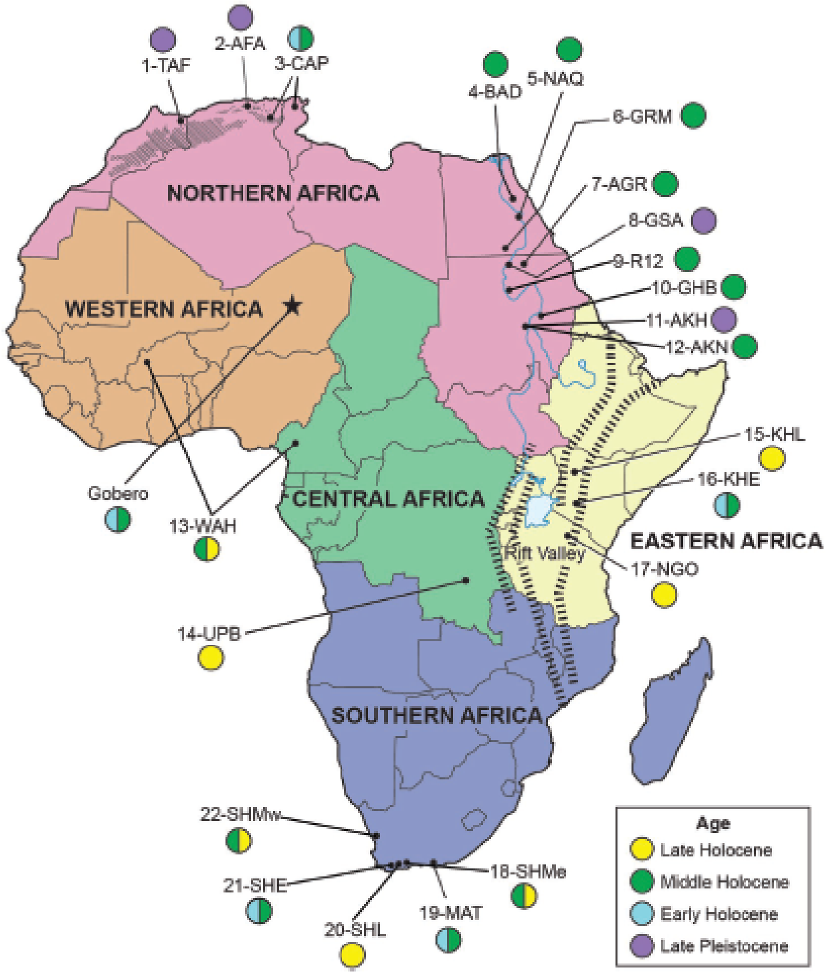


FIGURE 5 | Location of Gobero (star) is compared with 22 dental samples from five African regions. The age (subepoch) of each sample is indicated by color: Late Pleistocene (purple); Early Holocene (blue); Middle Holocene (green); Late Holocene (yellow). *Northwestern (Maghrebi):* 1-TAF (Taforalt); 2-AFA (Afalou-Bou Rhummel); 3-CAP (Capsian). *Northeastern (Nilotic):* 4-BAD (Badari); 5-NAQ (Naqada); 6-GRM (Gebel Ramlah); 7-AGR (Faras to Gamai); 8-GSA (Gebel Sahaba); 9-R12 (Kawa); 10-GHB (El Ghaba); 11-AKH (Al Khiday); 12-AKN (Al Khiday). *Central Africa:* 13-WAH (Shum Laka, Burkina Faso); 14-UPB (Upemban). *Eastern Africa:* 15-KHL (Lothagam, Njoro, Makalia); 16-KHE (Gambles Cave, Bromhead); 17-NGO (Ngorongoro Crater). *Southern Africa:* 18-SHMe (eastern); 19-MAT (Matjes River); 20-SHL (south coast); 21- SHE (west/south coast); 22-SHMw (western).

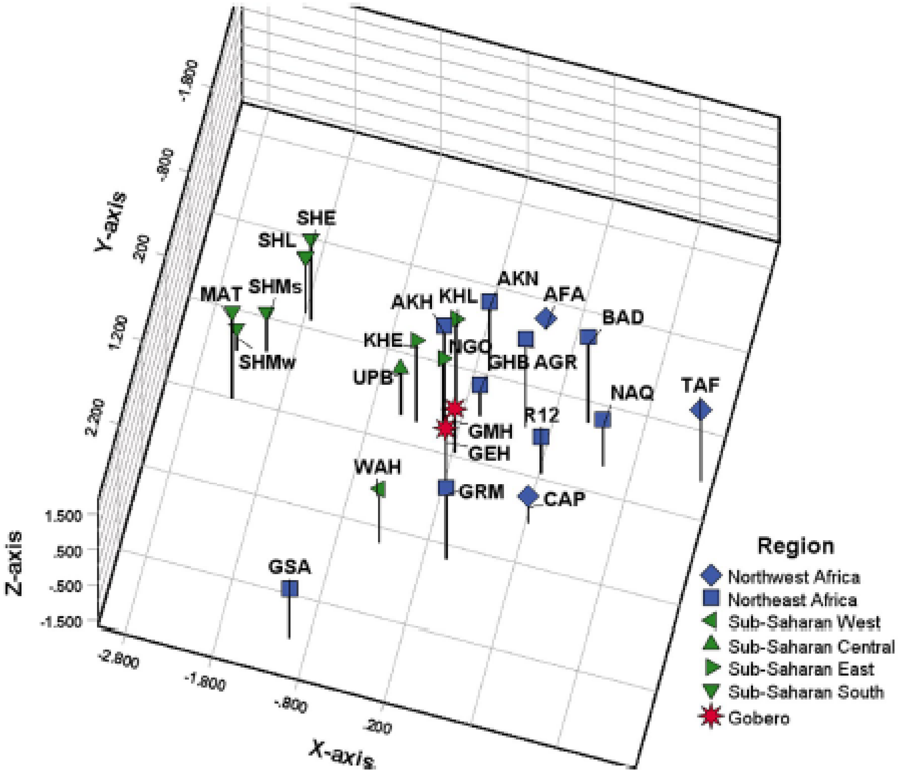


FIGURE 6 | Location in MDS three-dimensional space of Early and Middle Holocene samples from Gobero (red stars) compared to other African samples based on 35-trait MMD distances. Three-letter abbreviations are defined in Table 1 and Figure 5.

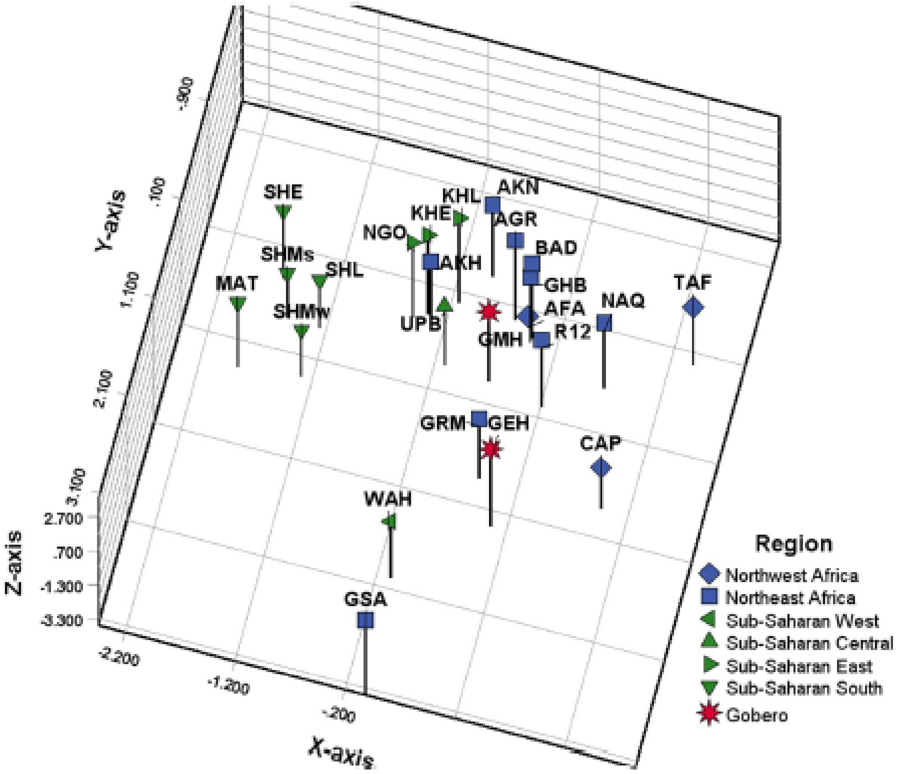


FIGURE 7 | Three-dimensional ordination of Early and Middle Holocene samples from Gobero (red stars) compared to other African samples based on Principal Components Analysis of 30 dental traits. Three-letter abbreviations are defined in Table 1 and Figure 5.

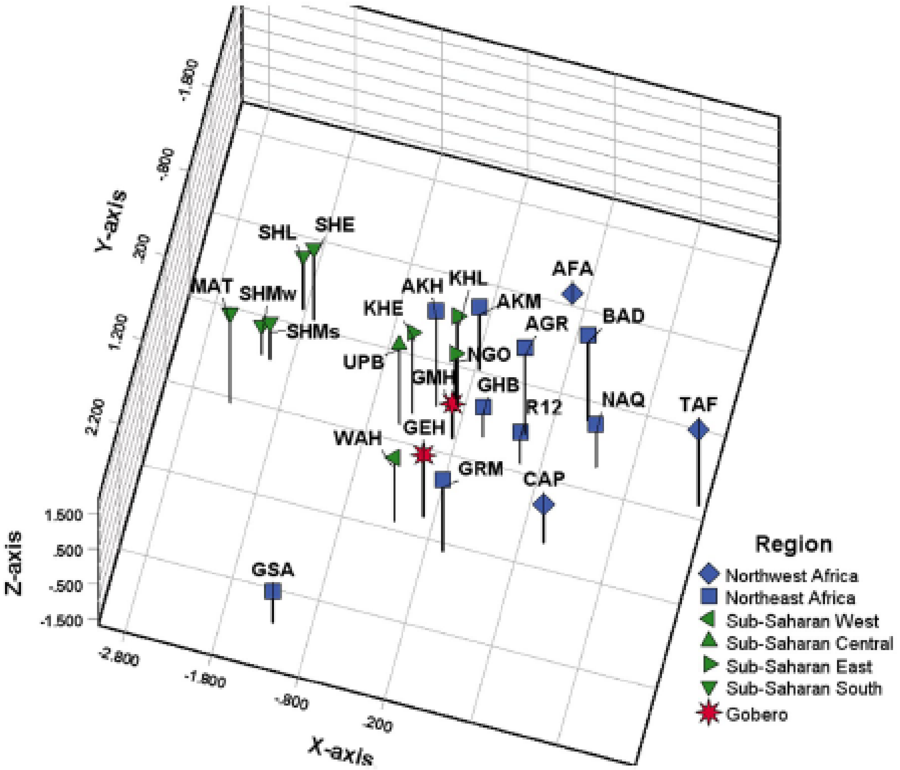


FIGURE 8 | Location in MDS three-dimensional space of Early and Middle Holocene samples from Gobero (red stars) compared to other African samples based on 26-trait MMD distances. Three-letter abbreviations are defined in Table 1 and Figure 5.

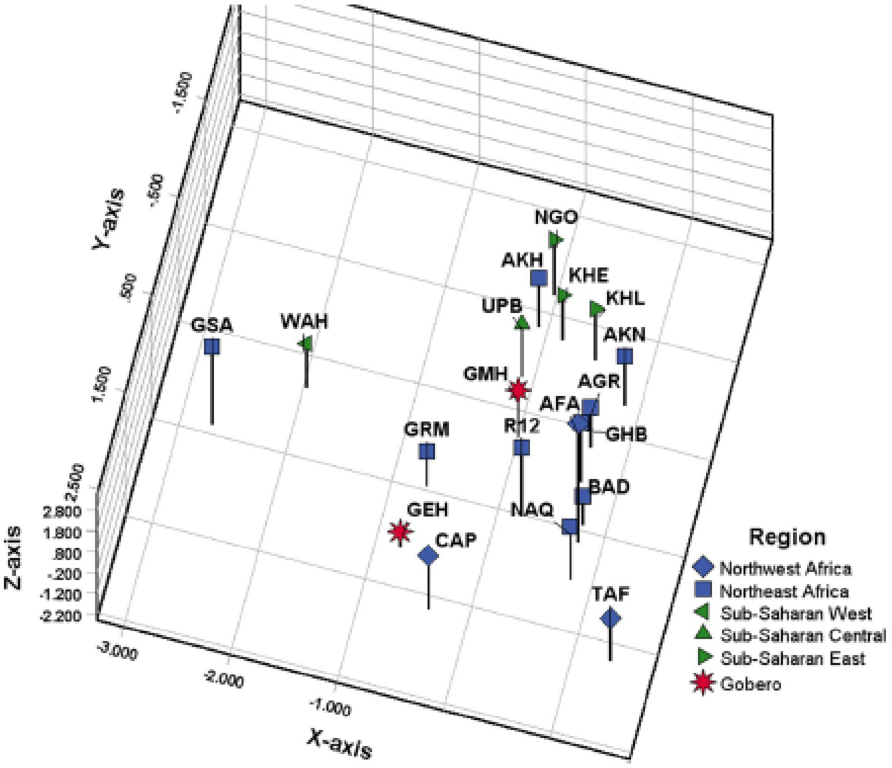


FIGURE 9 | Three-dimensional ordination of Early and Middle Holocene samples from Gobero (red stars) compared to other African samples (i.e., excluding those from southern Africa) based on Principal Components Analysis of 30 dental traits. Three-letter abbreviations are defined in Table 1 and Figure 5.

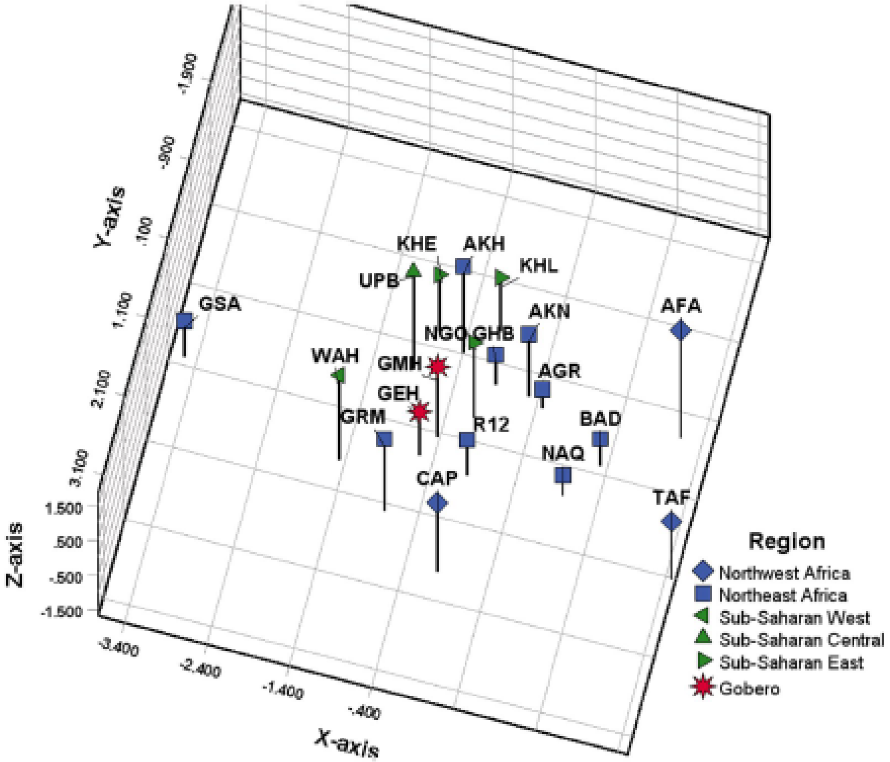


FIGURE 10 | Location in MDS three-dimensional space of Early and Middle Holocene samples from Gobero (red stars) compared to other African samples (i.e., excluding those from southern Africa) based on 25-trait MMD distances. Three-letter abbreviations are defined in Table 1 and Figure 5.

Table 1. The 22 premodern dental samples used in the present study for comparison to Gobero early and middle Holocene samples.

Sample	Site(s)/Region of Origin	Cultural Affiliation	Sub-epoch	Date	No.	Curation
Northwest Africa (Maghreb)						
1-Taforalt (TAF)[1]	Taforalt, Morocco	Iberomaurusian; Late Paleolithic	Late Pleistocene	16750 BP+	42	IPH
2-Afalou-Bou Rhummel (AFA)	Afalou, Algeria	Iberomaurusian; Late Paleolithic	Late Pleistocene	13120-11450 BP	48	IPH[2]
3-Capsian (CAP)	Algeria; Tunisia	Capsian; Mesolithic, Neolithic	Early-Mid Holocene	8500-5000 BP	22	UM, IPH
Northeast Africa (Nile Valley)						
4-Badari (BAD)	Badari, Egypt	Predynastic Egyptian	Middle Holocene	6350-5950 BP	40	CAM
5-Naqada (NAQ)	Naqada, Egypt	Predynastic Egyptian	Middle Holocene	5950-5150 BP	65	CAM
6-Gebel Ramlah (GRM)	Gebel Ramlah, Egypt	Neolithic	Middle Holocene	6550-6350 BP	82	GRM
7-A-Group (AGR)	Faras to Gamai, Sudan	A-Group Nubian	Middle Holocene	4950 BP+	52	PAN
8-Gebel Sahaba (GSA)[3]	Gebel Sahaba, Sudan; Tushka, Egypt	Qadan, Late Paleolithic	Late Pleistocene	>11600 BP	67	BM
9-R12 (R12)	Kawa, Sudan	Neolithic	Middle Holocene	7250-6250 BP	50	BM
10-El Ghaba (GHB)	Near Khartoum, Sudan	Neolithic	Middle Holocene	7550-6250 BP	119	LJMU
11-Al Khiday (AKH)	Al Khiday, Sudan	Late Paleolithic	Late Pleistocene	~14-13000 BP	55	UP
12-Al Khiday (AKN)	Al Khiday, Sudan	Neolithic	Middle Holocene	6950-6250 BP	28	UP
Sub-Saharan West						
13-West Africa Holocene (WAH)	Shum Laka, Cameroon; Burkina Faso	Mid-Late Holocene	Mid-Late Holocene	5000-800 BP	23	ISB[4]
Sub-Saharan Central						
14-Upemban (UPB)	Upemba Valley, Dem Rep of Congo	Kisalian, Kabambian	Late Holocene	1360-620 BP	56	UBB, ISB
Sub-Saharan East						
15-Kenya Holocene Late (KHL)	Lothagam, Njoro, Makalia, Kenya	Forager/Pastoralist	Late Holocene	2950 -550 BP	69	NMK
16-Kenya Holocene Early (KHE)	Gambles Cave, Bromhead, Kenya	Forager	Early-Mid Holocene	9000-6000 BP	80	NMK
17-Ngorongoro (NGO)	Ngorongoro Crater, Tanzania	Stone Bowl	Late Holocene	~2650 BP	28	CAM
Sub-Saharan South[5]						
18-So. Africa Hol. Middle South (SHMs)	South Coast, South Africa	Forager/Pastoralist	Mid-Late Holocene[6]	>4000-2000 BP	42	NMB, SAM, UCT
19-Matjes River (MAT)	Plettenberg Bay, South Africa	Forager	Early-Mid Holocene	9600-2200 BP	51	NMB
20-So. Africa Holocene Late (SHL)	South Coast, South Africa	Pastoralist/Forager	Late Holocene	<2000 BP	85	SAM, UCT
21-So. Africa Holocene Early (SHE)	West/South Coasts, South Africa	Forager	Early-Mid Holocene	12000-4000 BP	40	NMB, SAM, UCT
22-So. Africa Hol. Middle West (SHMw)	Western South Africa	Forager/Pastoralist	Mid-Late Holocene	>4000-2000 BP	73	SAM, UCT

[1] Sample three-letter abbreviations used in tables and figures.

[2] BM=British Museum; CAM=Cambridge University; GRM=Gebel Ramlah site, Egypt; IPH=Institut de Paléontologie Humaine; ISB=Institut royal des Sciences naturelles de Belgique; LJMU=Liverpool John Moores University; NMB=National Museum in Bloemfontein; NMK=National Museums of Kenya; PAN=Panum Institute; SAM=Iziko (South African) Museum; UBB=Université de Bruxelles, Belgique; UCT=University of Cape Town, Department of Human Biology; UM=University of Minnesota; UP=University of Padova.

[3] The Gebel Sahaba (GSA) sample was recovered from Egypt and Sudan (Nubia) in Northeast Africa, but prior research (e.g., Irish and Usai, 2021) indicates sub-Saharan West African population affinity.

[4] The Shum Laka material is at ISB. That from Burkina Faso was repatriated from another institution.

[5] Only data in dentitions recorded by Irish from Irish et al. (2014) were used in the present study.

[6] Epoch attribution based on dating approach in South African archaeology.

Table 2. MMD distances based on 35 ASUDAS traits among the Gobero early (GEH), middle Holocene (GMH) and 22 comparative dental samples by African region.[1]

GEH	0.000	GMH
	Northwest Africa	
0.097	1-TAF	0.161
0.136[2]	2-AFA	0.094
0.000	3-CAP	0.032
0.078	Mean MMD	0.096
	Northeast Africa	
0.024	4-BAD	0.088
0.000	5-NAQ	0.054
0.000	6-GRM	0.045
0.017	7-AGR	0.027
0.060	8-GSA[3]	0.154
0.000	9-R12	0.000
0.055	10-GHB	0.029
0.015	11-AKH	0.000
0.017	12-AKN	0.000
0.016	Mean MMD	0.030
	Sub-Saharan West	
0.000	13-WAH	0.026
	Sub-Saharan Central	
0.027	14-UPB	0.000
	Sub-Saharan East	
0.036	15-KHL	0.009
0.018	16-KHE	0.000
0.028	17-NGO	0.000
0.027	Mean MMD	0.003
	Sub-Saharan South	
0.136	18-SHMs	0.087
0.067	19-MAT	0.170
0.100	20-SHL	0.095
0.125	21-SHE	0.107
0.169	22-SHMw	0.176
0.119	Mean MMD	0.127

[1] See main text and Table 1 for sample number and other information.

[2] Underlined values are significantly different from GEH and GMH at *p*≤0.05.

[3] GSA not included in mean MMD for this region due to West African affinity. See Table 1.

Table 3. MMD distances based on 26 ASUDAS traits among the Gobero early (GEH), middle Holocene (GMH) and 22 comparative dental samples by African region.[1]

GEH	0.058	GMH
	Northwest Africa	
0.156[2]	1-TAF	0.206
0.252	2-AFA	0.166
0.013	3-CAP	0.035
0.141	Mean MMD	0.136
	Northeast Africa	
0.095	4-BAD	0.126
0.057	5-NAQ	0.079
0.000	6-GRM	0.045
0.066	7-AGR	0.057
0.119	8-GSA[3]	0.221
0.061	9-R12	0.017
0.079	10-GHB	0.030
0.079	11-AKH	0.039
0.097	12-AKN	0.000
0.067	Mean MMD	0.049
	Sub-Saharan West	
0.000	13-WAH	0.038
	Sub-Saharan Central	
0.067	14-UPB	0.000
	Sub-Saharan East	
0.074	15-KHL	0.021
0.077	16-KHE	0.004
0.077	17-NGO	0.003
0.076	Mean MMD	0.009
	Sub-Saharan South	
0.159	18-SHMs	0.090
0.111	19-MAT	0.251
0.143	20-SHL	0.126
0.144	21-SHE	0.119
0.161	22-SHMw	0.143
0.144	Mean MMD	0.146

[1] See main text and Table 1 for sample number and other information.

[2] Underlined values are significantly different from GEH and GMH at $p \leq 0.05$.

[3] GSA not included in mean MMD for this region due to West African affinity. See Table 1.

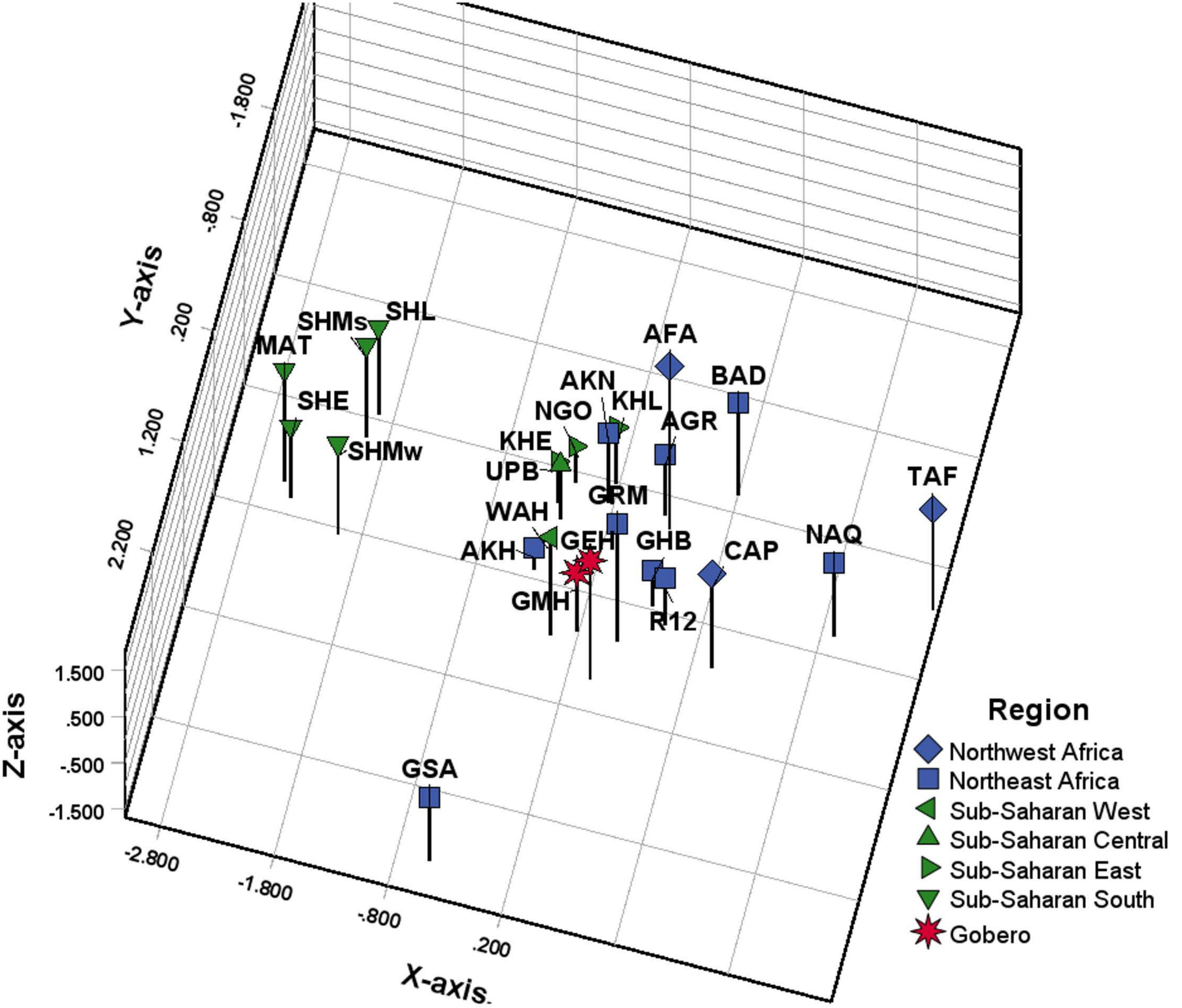
Table 4. MMD distances based on 25 ASUDAS traits among the Gobero early (GEH), middle Holocene (GMH) and 17 comparative dental samples by African region.[1]

GEH	0.000	GMH
	Northwest Africa	
0.153[2]	1-TAF	0.168
0.230	2-AFA	0.121
0.000	3-CAP	0.025
0.128	Mean MMD	0.105
	Northeast Africa	
0.058	4-BAD	0.103
0.024	5-NAQ	0.057
0.000	6-GRM	0.000
0.028	7-AGR	0.041
0.122	8-GSA[3]	0.136
0.000	9-R12	0.011
0.019	10-GHB	0.020
0.000	11-AKH	0.025
0.000	12-AKN	0.000
0.016	Mean MMD	0.032
	Sub-Saharan West	
0.000	13-WAH	0.001
	Sub-Saharan Central	
0.009	14-UPB	0.000
	Sub-Saharan East	
0.025	15-KHL	0.002
0.015	16-KHE	0.000
0.007	17-NGO	0.000
0.016	Mean MMD	0.000

[1] See main text and Table 1 for sample number and other information.

[2] Underlined values are significantly different from GEH and GMH at $p \leq 0.05$.

[3] GSA not included in mean MMD for this region due to West African dental affinity. See Table 1.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-.800
.200
1.200
2.200
Z-axis
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.500
-.500
-1.500
X-axis
-2.800
-1.800
-.800
.200
SHL
SHMs
MAT
SHE
SHMw
AFA
BAD
AKN
KHL
NGO
AGR
KHE
UPB
GRM
TAF
WAH
GEH
GHB
CAP
NAQ
AKH
GMH
R12
GSA
Region
◆ Northwest Africa
■ Northeast Africa
◀ Sub-Saharan West
▲ Sub-Saharan Central
▶ Sub-Saharan East
▼ Sub-Saharan South
✶ Gobero

Table S1.Origin locations of the 22 comparative dental samples used in the present study

Sample	Archaeological Site(s) and Regions/Countries of Origin
Northwest Africa (Maghreb)	
1-Taforalt (TAF)[1]	Taforalt, Morocco
2-Afalou-Bou Rhummel (AFA)	Afalou-Bou Rhummel, Algeria
3-Capsian (CAP)	Abri des Aiquades, Aïn Dokkara,Aïn Misteheyia,Bazancourt Marne, Grotte des Hyènes, Kef Zoura D, Mechta el-Arbi, Mechta-Chateaudun, Tebessa, Oum Ettiour, Algeria and Tunisia
Northeast Africa (Nile Valley)	
4-Badari (BAD)	Badari, Egypt
5-Naqada (NAQ)	Naqada, Egypt
6-Gebel Ramlah (GRM)	Gebel Ramlah, Egypt
7-A-Group (AGR)	Multiple locales in Faras to Gamai region, Sudan
8-Gebel Sahaba (GSA)[3]	Gebel Sahaba, Tushka, Sudan and Egypt
9-R12 (R12)	R12 (at Kawa), Sudan
10-El Ghaba (GHB)	Ghaba, Sudan
11-Al Khiday (AKH)	Al Khiday, Sudan
12-Al Khiday (AKN)	Al Khiday, Sudan
Sub-Saharan West	
13-West Africa Holocene (WAH)	Shum Laka, Cameroon; Mouhoun Bend, Burkina Faso
Sub-Saharan Central	
14-Upemban (UPB)	Kamilamba, Katoto, Kikulu, Malemba-Nkulu, Sanga in Upemba Valley, Dem Rep of Congo
Sub-Saharan East	
15-Kenya Holocene Late (KHL)	Homa Shell Mound, Hyrax Hill, Makalia, Nakuru, Njoro River Cave, Willey's Kopje, Kenya
16-Kenya Holocene Early (KHE)	Bromhead's Site, Gambles Cave II, Lothagam, Kenya
17-Ngorongoro (NGO)	Ngorongoro Crater, Tanzania
Sub-Saharan South	
18-So. Africa Hol. Middle East (SHMs)	Multiple sites, including Buffel's Bay, Drury's Cave, Glentyre, Great Brak River Cave, Llandudno, Matjes River Rockshelter, Plettenberg Bay,Robberg Cave, South Coast, South Africa
19-Matjes River (MAT)	Matjes River Rockshelter, Plettenberg Bay, South Coast, South Africa
20-So. Africa Holocene Late (SHL)	Multiple sites, including Coburn, Eland's Bay,Koffiefontein,Knusna, Llandudno,Melkbosstrand, Plettenberg Bay, West/South Coast, South Africa
21-So. Africa Holocene Early (SHE)	Multiple sites, including Elands Bay, Hout Bay, Fishhoek, Knysna Heads, Oakhurst Rockshelter, Robberg Cave, Still Bay, on West/South Coasts, South Africa
22-So. Africa Hol. Middle West (SHMw)	Multiple sites, including Blaauwberg, Elands Bay, Kommetjie, Llandudno, Melkbosstrand, Melkbosch, Snuifklip, Stompneusbaai, Vlammikvlei, West Coast, South Africa

[1] Sample three-letter abbreviations used in all tables and figures.

Table S2. Percentages and numbers of individuals scored for 36 ASUDAS traits in the two Gobero and 22 comparative dental samples.[1]

TRAIT /		Gobero		Northwest Africa			Northeast Africa									S-S West	S-S Cent	Sub-Saharan East			Sub-Saharan South[3]				
GRADES PRESENT		**GEH**	**GMH**	**TAF**	**AFA**	**CAP**	**BAD**	**NAQ**	**GRM**	**AGR**	**GSA[2]**	**R12**	**GHB**	**AKH**	**AKN**	**WAH**	**UPB**	**KHL**	**KHE**	**NGO**	**SHMs**	**MAT**	**SHL**	**SHE**	**SHMw**
Winging UI1	%	0.00	6.67	0.00	0.00	0.00	5.56	6.00	0.00	2.56	29.63	0.00	0.00	0.00	0.00	12.50	0.00	2.94	0.00	0.00	3.33	3.23	1.54	4.00	10.91
(+=ASU 1)	n	8	15	11	6	5	36	50	36	39	27	18	8	11	16	8	11	34	36	4	30	31	65	25	55
Labial Curvature UI1	%	27.27	20.00	14.29	0.00	25.00	50.00	12.50	45.45	43.48	51.85	36.00	22.22	63.64	55.00	38.89	37.93	42.86	44.83	41.18	50.00	88.89	65.38	80.00	62.50
(+=ASU 2-4)	n	11	15	7	3	4	20	8	44	23	27	25	27	22	20	18	29	28	29	17	24	18	26	15	32
Palatine Torus	%	0.00	0.00	0.00	13.79	0.00	5.56	0.00	0.00	0.00	12.00	7.69	0.00	0.00	0.00	0.00	0.00	6.06	0.00	0.00	19.35	6.67	20.55	3.85	16.95
(+=ASU 2-3)	n	5	8	17	29	10	36	50	30	24	25	13	3	30	8	4	28	33	31	2	31	30	73	26	59
Shoveling UI1	%	50.00	0.00	40.00	0.00	0.00	25.00	14.29	45.00	15.79	45.83	0.00	5.00	21.05	0.00	28.57	8.00	18.52	4.17	6.25	5.88	44.44	6.67	22.22	10.00
(+=ASU 2-6)	n	10	14	5	3	5	16	7	40	19	24	22	20	19	16	14	25	27	24	16	17	9	15	9	20
Double Shoveling UI1[4]	%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.55	0.00	4.35	0.00	0.00	0.00	0.00	5.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.13
(+=ASU 2-6)	n	10	16	4	3	5	16	7	44	21	23	28	31	20	22	17	28	28	26	17	24	16	31	13	32
Interruption Groove UI2	%	0.00	12.50	57.14	43.75	60.00	10.00	9.09	22.22	4.35	16.00	21.05	10.00	16.67	15.38	8.33	12.90	3.57	6.90	27.27	0.00	0.00	4.35	0.00	3.70
(+=ASU +)	n	7	16	14	16	5	20	11	36	23	25	19	20	24	13	12	31	28	29	11	13	14	23	10	27
Tuberculum Dentale UI2[4]	%	28.57	22.22	7.69	41.67	60.00	36.36	27.27	54.05	13.04	38.89	26.32	22.22	34.78	15.38	75.00	41.38	28.57	34.48	27.27	8.33	21.43	23.53	22.22	40.91
(+=ASU 2-6)	n	7	18	13	12	5	22	11	37	23	18	19	18	23	13	12	29	28	29	11	12	14	17	9	22
Bushman Canine UC	%	11.11	11.76	0.00	9.09	22.22	0.00	0.00	11.43	11.54	20.00	0.00	6.25	35.00	9.09	20.00	12.50	3.70	9.38	27.78	42.86	53.33	33.33	55.56	33.33
(+=ASU 1-3)	n	9	17	11	11	9	22	22	35	26	20	19	32	20	11	15	32	27	32	18	14	15	12	9	21
Distal Accessory Ridge UC	%	33.33	26.67	20.00	0.00	42.86	12.50	15.00	46.43	33.33	88.89	35.29	40.00	21.43	10.00	54.55	35.71	32.00	36.00	23.53	10.00	23.08	0.00	0.00	28.57
(+=ASU 2-5)	n	9	15	5	7	7	16	20	28	18	9	17	30	14	10	11	28	25	25	17	10	13	8	3	21
Hypocone UM2	%	100.00	77.78	100.00	96.88	100.00	86.67	90.91	93.75	73.68	94.12	93.75	92.19	72.73	80.00	93.33	85.37	68.09	73.81	84.21	93.55	100.00	98.21	91.67	95.83
(+=ASU 3-5)	n	9	18	20	32	10	30	44	48	38	34	32	64	33	20	15	41	47	42	19	31	27	56	24	48
Cusp 5 UM1	%	50.00	0.00	10.00	50.00	30.00	10.00	17.50	16.67	12.00	33.33	8.70	13.33	0.00	5.56	41.67	11.11	8.00	16.67	7.69	33.33	52.17	26.92	28.57	48.00
(+=ASU 2-5)	n	8	11	10	10	10	20	40	30	25	15	23	30	20	18	12	27	25	36	13	18	23	26	14	25
Carabelli's Trait UM1	%	88.89	66.67	71.43	36.36	100.00	64.71	68.42	88.57	73.08	50.00	73.91	33.33	42.11	41.18	72.73	33.33	46.15	52.63	38.46	22.22	32.00	36.46	18.18	30.77
(+=ASU 2-7)	n	9	12	7	11	6	17	38	35	26	14	23	36	19	17	11	33	26	38	13	18	25	26	11	26
Parastyle UM3	%	0.00	0.00	0.00	3.23	0.00	0.00	0.00	2.50	0.00	0.00	0.00	0.00	4.55	0.00	8.33	6.06	0.00	0.00	0.00	0.00	0.00	2.22	0.00	0.00
(+=ASU 1-5)	n	7	13	18	31	9	23	28	40	40	37	27	62	22	21	12	33	46	39	15	17	17	45	18	25
Enamel Extension UM1	%	0.00	0.00	0.00	0.00	0.00	6.45	15.22	7.89	5.00	58.33	4.17	28.57	0.00	0.00	0.00	0.00	0.00	3.57	0.00	2.86	0.00	0.00	0.00	0.00
(+=ASU 1-3)	n	8	17	21	30	13	31	46	38	40	36	24	7	15	16	16	36	20	28	9	35	24	54	26	54
Root Number UP1[4]	%	100.00	87.50	62.50	55.56	33.33	70.59	76.09	69.05	72.41	72.73	82.61	35.71	85.71	83.33	50.00	61.11	63.33	75.00	75.00	33.33	56.67	53.23	33.33	16.67
(+=ASU 2+)	n	2	8	16	27	12	17	46	42	29	33	23	14	21	12	10	18	30	12	8	30	30	62	27	42
Root Number UM2[4]	%	100.00	100.00	62.50	87.50	85.71	80.00	73.53	66.67	77.78	72.97	92.00	83.33	90.48	92.86	100.00	76.00	68.00	75.00	77.78	66.67	81.82	76.92	78.95	54.17
(+=ASU 3+)	n	3	6	16	16	7	15	34	39	27	37	25	24	21	14	7	25	25	20	9	18	22	39	19	24
Peg-Reduced UI2	%	0.00	4.76	0.00	0.00	0.00	10.26	0.00	6.12	4.76	2.94	0.00	0.00	0.00	0.00	6.25	0.00	0.00	4.55	0.00	5.41	14.63	1.47	17.24	6.90
(+=ASU P or R)	n	10	21	27	33	10	39	60	49	42	34	31	33	41	21	16	35	43	44	12	37	41	68	29	58
Odontome P1-P2	%	0.00	0.00	0.00	22.22	0.00	0.00	0.00	2.94	0.00	0.00	0.00	1.22	6.90	0.00	5.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(+=ASU +)	n	10	20	10	9	12	31	49	34	36	11	23	82	29	21	17	50	60	51	21	25	36	53	21	40

Congenital Absence UM3	%	0.00	4.55	4.55	2.94	16.67	8.57	3.70	11.54	4.44	0.00	0.00	1.41	3.03	0.00	0.00	5.00	1.72	0.00	0.00	11.76	5.88	3.90	6.45	11.48
(+=ASU -)	n	10	22	22	34	12	35	54	52	45	45	36	71	33	24	13	40	58	53	18	34	34	77	31	61
Midline Diastema UI1[4]	%	0.00	13.33	0.00	0.00	0.00	5.26	0.00	10.81	5.88	12.50	0.00	0.00	11.11	0.00	16.67	0.00	10.00	9.09	33.33	8.82	12.50	7.25	17.86	5.17
(+≥0.5 mm)	n	8	15	13	6	5	38	52	37	34	24	19	9	9	16	6	10	30	33	3	34	32	69	28	58
Lingual Cusp LP2	%	77.78	80.00	35.71	88.89	84.62	79.17	95.65	64.29	80.00	93.33	93.10	84.48	80.00	76.47	46.15	62.16	59.26	64.86	78.95	85.71	58.33	79.41	92.86	100.00
(+=ASU 2-9)	n	9	15	14	18	13	24	23	28	35	15	29	58	25	17	13	37	54	37	19	14	24	34	14	31
Anterior Fovea LM1	%	66.67	54.55	8.33	0.00	45.45	9.09	18.75	47.62	20.00	69.23	47.37	37.04	46.15	50.00	73.33	81.82	48.15	63.16	53.33	81.25	71.43	71.43	75.00	65.22
(+=ASU 2-4)	n	6	11	12	11	11	11	16	21	15	13	19	27	13	10	15	22	27	38	15	16	21	14	8	23
Mandibular Torus	%	0.00	0.00	0.00	0.00	0.00	0.00	1.72	2.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.54	4.48	0.00	3.23	4.44	0.00	0.00	1.89
(+=ASU 2-3)	n	10	20	25	27	19	40	58	47	43	47	28	10	38	22	11	39	52	67	13	31	45	66	28	53
Groove Pattern LM2	%	30.00	66.67	34.78	78.57	41.18	35.29	45.83	64.44	63.41	62.50	42.86	45.45	37.50	68.18	56.25	71.79	62.30	65.57	77.27	82.14	64.52	75.00	59.09	78.26
(+=ASU Y)	n	10	18	23	28	17	34	48	45	41	32	35	77	32	22	16	39	61	61	22	28	31	56	22	46
Rocker Jaw	%	0.00	10.53	29.17	14.29	17.65	10.26	24.07	18.18	5.88	0.00	0.00	20.00	0.00	5.88	0.00	11.76	17.39	7.14	10.00	16.67	2.27	7.69	0.00	3.70
(+=ASU 1-2)	n	9	19	24	28	17	39	54	44	34	45	21	5	37	17	9	34	46	56	10	30	44	65	26	54
Cusp Number LM1	%	10.00	11.11	13.33	11.76	17.65	0.00	7.89	11.76	3.13	31.25	13.79	2.17	5.00	5.56	18.75	3.03	4.76	3.77	10.00	8.70	6.90	0.00	0.00	0.00
(+=ASU 6+)	n	10	18	15	17	17	24	38	34	32	32	29	46	20	18	16	33	42	53	20	23	29	36	13	34
Cusp Number LM2	%	60.00	87.50	10.53	76.00	38.89	19.05	27.78	78.95	32.14	94.59	50.00	64.06	64.29	45.00	66.67	77.14	66.07	78.85	38.10	100.00	96.43	97.92	100.00	100.00
(+=ASU 5+)	n	10	16	19	25	18	21	36	38	28	37	28	64	28	20	12	35	56	52	21	26	28	48	17	44
Deflecting Wrinkle LM1	%	55.56	21.43	0.00	0.00	20.00	9.52	15.15	34.78	12.00	30.77	7.14	11.43	19.05	16.67	38.46	20.00	16.22	12.77	31.25	22.22	20.00	16.67	11.11	21.74
(+=ASU 2-3)	n	9	14	11	13	10	21	33	23	25	13	28	35	21	18	13	25	37	47	16	18	20	18	9	23
C1-C2 Crest LM1[4]	%	14.29	0.00	0.00	0.00	0.00	9.52	3.03	0.00	0.00	0.00	3.85	0.00	0.00	0.00	0.00	0.00	0.00	2.04	0.00	0.00	0.00	0.00	0.00	3.85
(+=ASU +)	n	7	12	8	5	9	21	33	28	26	16	26	37	20	17	12	27	38	49	16	17	22	18	10	26
Protostylid LM1	%	33.33	40.00	30.77	10.53	53.33	12.50	22.22	29.41	2.94	29.17	21.88	14.29	15.00	5.00	43.75	28.13	9.52	9.09	5.26	26.32	6.06	5.26	9.09	8.33
(+=ASU 1-6)	n	6	15	13	19	15	24	36	34	34	24	32	42	20	20	16	32	42	55	19	19	33	19	11	24
Cusp 7 LM1	%	8.33	5.00	3.85	15.38	16.67	13.33	10.87	6.82	7.14	9.68	20.00	14.81	25.00	8.33	22.22	19.44	21.43	23.33	30.00	36.00	28.13	17.39	30.00	12.82
(+=ASU 2-4)	n	12	20	26	26	18	30	46	44	42	31	40	54	32	24	18	36	42	60	20	25	32	46	20	39
Tome's Root LP1[4]	%		50.00	0.00	21.05	0.00	5.56	10.71	9.30	15.38	52.38	16.67	9.52	70.00	33.33	9.09	7.41	19.05	15.00	36.36	4.35	23.08	11.86	23.53	2.33
(+=ASU 3-5)	n		4	18	19	15	18	56	43	26	21	24	21	10	12	11	27	21	20	11	23	39	59	17	43
Root Number LC[4]	%	0.00	0.00	0.00	0.00	0.00	4.17	5.08	3.92	2.63	0.00	3.13	2.63	0.00	5.56	0.00	0.00	2.50	2.86	0.00	0.00	0.00	0.00	0.00	2.17
(+=ASU 2+)	n	3	11	19	19	12	24	59	51	38	17	32	38	25	18	11	34	40	35	14	26	38	58	21	46
Root Number LM1[4]	%	0.00	0.00	0.00	0.00	5.88	0.00	5.13	0.00	2.70	6.67	6.25	0.00	0.00	0.00	0.00	0.00	3.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(+=ASU 3+)	n	5	7	22	12	17	19	39	51	37	45	32	44	29	17	15	25	32	28	7	16	28	42	14	26
Root Number LM2[4]	%	100.00	100.00	75.00	100.00	85.71	75.00	86.11	82.00	84.62	83.72	96.55	88.89	81.25	90.91	100.00	100.00	89.66	95.45	100.00	90.00	100.00	87.50	71.43	93.55
(+=ASU 2+)	n	2	4	16	8	14	16	36	50	26	43	29	36	16	11	7	14	29	22	10	20	29	48	14	31
Torsomolar Angle LM3	%	0.00	7.14	4.17	0.00	23.08	5.88	2.17	7.69	4.88	7.69	6.25	0.00	6.06	4.55	0.00	9.68	7.55	10.34	33.33	5.00	7.41	11.67	3.85	2.33
(+=ASU +)	n	7	14	24	22	13	34	46	52	41	39	32	57	33	22	12	31	53	58	12	20	27	60	26	43

[1] The Gobero samples are detailed in the Materials and Methods main text, with comparative sample background information summarized in Table 1. See the latter for meaning of sample abbreviations.

[2] The Gebel Sahaba (GSA) sample was recovered from Egypt and Sudan (Nubia) in Northeast Africa, but prior research reveals sub-Saharan West African population affinity (see Irish and Usai, 2021 for details).

[3] Only data recorded by Irish from Irish et al. (2014) were used in the present study.

[4] The 10 traits not used in the final 26-trait MMD analysis. See Results section for details.

Table S3. Component loadings, eigenvalues, and variance explained for 30 traits (after initial editing[1]) for the 24 samples.

Trait	Comp 1	Comp 2	Comp 3	Comp 4	Comp 5	Comp 6	Comp 7	Comp 8
Winging UI1	-0.139	**0.723**	0.096	-0.363	0.252	-0.186	0.188	-0.134
Labial Curvature UI1	**-0.803**[2]	0.088	0.289	-0.004	-0.097	0.184	0.044	-0.164
Palatine Torus	**-0.515**	0.102	**-0.505**	-0.486	0.073	0.050	0.042	0.131
Shoveling UI1	0.024	**0.545**	0.280	0.032	-0.470	0.027	0.442	-0.241
Interruption Groove UI2	**0.654**	-0.035	-0.455	0.231	0.270	0.247	0.066	-0.273
Tuberculum Dentale UI2	0.154	**0.569**	-0.274	0.452	0.008	-0.124	-0.121	0.151
Bushman Canine UC	**-0.827**	0.159	-0.202	0.113	-0.006	0.295	-0.056	-0.193
Distal Accessory Ridge UC	0.238	**0.776**	0.298	0.036	0.290	-0.100	0.122	0.113
Hypocone UM2	0.079	0.437	**-0.560**	-0.174	-0.342	0.340	0.036	-0.182
Cusp 5 UM1	-0.310	**0.501**	**-0.513**	-0.153	-0.383	0.030	0.062	0.052
Carabelli's Trait UM1	**0.749**	0.334	0.152	0.172	-0.207	0.239	-0.093	0.089
Parastyle UM3	-0.048	0.244	-0.291	**0.639**	-0.086	**-0.510**	-0.050	0.034
Enamel Extension UM1	0.139	**0.527**	0.171	**-0.535**	0.369	-0.189	0.176	-0.152
Peg-Reduced UI2	**-0.584**	0.099	0.098	-0.037	-0.334	0.207	0.314	-0.313
Odontome P1-P2	0.076	-0.070	**-0.707**	0.133	-0.019	**-0.540**	-0.006	-0.162
Congenital Absence UM3	-0.060	0.008	-0.414	0.016	-0.104	**0.710**	0.144	0.147
Midline Diastema UI1	**-0.509**	0.149	0.286	0.399	0.329	0.063	-0.008	-0.365
Lingual Cusp LP2	-0.116	0.027	-0.198	**-0.670**	0.220	0.065	**-0.570**	0.028
Anterior Fovea LM1	**-0.683**	0.431	0.165	0.210	0.047	0.104	-0.172	0.297
Mandibular Torus	-0.262	-0.152	0.241	0.023	0.119	0.053	**0.513**	**0.573**
Groove Pattern LM2	**-0.616**	-0.090	-0.313	0.043	0.425	-0.119	0.068	0.186
Rocker Jaw	**0.506**	-0.371	-0.248	0.024	0.156	0.276	0.455	0.221
Cusp Number LM1	0.342	**0.755**	-0.147	0.029	0.356	-0.007	0.081	-0.147

Cusp Number LM2	**-0.765**	0.313	-0.234	-0.072	0.062	-0.134	0.070	0.256
Deflecting Wrinkle LM1	-0.179	**0.653**	0.208	0.262	-0.228	0.058	-0.311	0.234
C1-C2 Crest LM1	0.200	0.133	0.228	-0.278	**-0.688**	0.061	-0.374	0.120
Protostylid LM1	0.498	**0.576**	-0.164	0.299	-0.022	0.224	-0.010	0.213
Cusp 7 LM1	**-0.637**	-0.110	-0.059	0.280	0.204	0.123	-0.083	-0.003
Root Number LM1[3]	0.398	0.363	0.106	-0.404	0.459	0.191	-0.076	0.102
Torsomolar Angle LM3	-0.033	-0.026	0.106	0.378	**0.547**	**0.537**	-0.289	-0.137
Eigenvalue	6.190	4.662	2.822	2.720	2.614	2.080	1.612	1.344
Variance (%)	20.635	15.540	9.406	9.066	8.714	6.934	5.374	4.482
Total Variance	20.635	36.174	45.581	54.647	63.360	70.294	75.669	80.150

[1] See the main text for trait editing process.

[2] Boldface numbers indicate strong PC loadings (i.e., ≥|0.5|) to retain traits.

[3] The one out of 30 remaining traits deleted due to low PC loadings. See main text for details.

Table S4. Component loadings, eigenvalues, and variance explained for 30 traits (after initial editing[1]) for the 19 samples from northern Africa.

Trait	Comp 1	Comp 2	Comp 3	Comp 4	Comp 5	Comp 6	Comp 7	Comp 8
Winging UI1	**-0.715**[2]	0.098	0.194	-0.455	0.086	0.246	0.176	-0.133
Labial Curvature UI1	-0.323	**-0.590**	-0.378	-0.186	0.131	-0.019	0.316	0.017
Palatine Torus	-0.163	0.152	**0.710**	-0.383	-0.143	-0.001	0.237	0.223
Shoveling UI1[3]	-0.462	0.339	-0.404	-0.166	-0.241	0.244	0.061	-0.241
Interruption Groove UI2	0.178	0.489	0.388	**0.525**	0.391	0.014	0.047	-0.175
Tuberculum Dentale UI2	**-0.638**	0.089	0.095	**0.533**	-0.130	0.069	0.197	0.400
Bushman Canine UC	**-0.531**	-0.395	0.077	0.433	0.204	-0.297	0.127	-0.236
Distal Accessory Ridge UC	**-0.846**	0.059	-0.055	-0.210	0.251	0.224	-0.131	0.021
Hypocone UM2	-0.234	**0.823**	0.150	0.192	-0.074	-0.175	-0.102	-0.178
Cusp 5 UM1[3]	-0.469	0.473	0.278	0.127	-0.448	-0.187	-0.069	0.128
Carabelli's Trait UM1	-0.197	**0.658**	-0.497	0.168	0.149	-0.032	0.130	0.245
Parastyle UM3	-0.372	-0.210	0.117	**0.565**	-0.484	0.140	0.016	-0.006
Enamel Extension UM1	-0.474	0.163	0.275	**-0.639**	0.198	0.148	0.028	-0.203
Peg-Reduced UI2	-0.227	-0.017	-0.349	-0.069	-0.191	0.373	**0.718**	0.094
Odontome P1-P2	0.041	0.050	**0.701**	0.332	**-0.531**	-0.047	0.214	0.020
Congenital Absence UM3[3]	0.097	0.456	-0.153	0.452	0.365	0.185	0.348	0.271
Midline Diastema UI1	-0.395	**-0.575**	-0.046	0.182	0.257	0.046	0.254	-0.218
Lingual Cusp LP2	-0.027	0.084	0.369	-0.435	0.202	**-0.588**	0.204	0.151
Anterior Fovea LM1	**-0.692**	-0.406	-0.249	0.083	0.046	-0.079	-0.437	0.080
Mandibular Torus	0.126	-0.328	-0.062	-0.169	0.058	0.434	-0.260	**0.608**
Groove Pattern LM2	-0.087	**-0.548**	0.493	0.114	0.035	0.278	-0.005	-0.043
Rocker Jaw	**0.559**	0.373	0.082	0.200	0.257	0.477	-0.185	-0.026

Cusp Number LM1	**-0.730**	0.405	0.327	-0.006	0.248	0.049	-0.056	-0.147
Cusp Number LM2	**-0.581**	-0.325	0.317	-0.040	-0.244	0.186	-0.238	0.155
Deflecting Wrinkle LM1	**-0.717**	-0.050	-0.445	0.107	-0.137	-0.222	-0.172	-0.056
C1-C2 Crest LM1[3]	-0.001	0.320	-0.494	-0.280	-0.397	-0.491	0.085	0.178
Protostylid LM1	**-0.511**	**0.576**	-0.171	0.399	0.119	0.085	-0.208	0.076
Cusp 7 LM1	-0.120	**-0.614**	0.184	0.321	0.095	-0.322	-0.018	0.304
Root Number LM1[3]	-0.255	0.344	0.232	-0.399	**0.559**	-0.129	-0.055	0.386
Torsomolar Angle LM3	-0.078	-0.285	-0.006	0.362	**0.752**	-0.230	0.099	0.000
Eigenvalue	5.733	4.851	3.310	3.290	2.709	1.903	1.533	1.381
Variance (%)	19.111	16.171	11.032	10.966	9.030	6.344	5.111	4.604
Total Variance	19.111	35.282	46.314	57.281	66.311	72.655	77.766	82.370

[1] See the main text for trait editing process, here with the South African samples not included.

[2] Boldface numbers indicate strong PC loadings (i.e., ≥|0.5|) to retain traits.

[3] The four of 30 remaining traits deleted due to low PC loadings. See main text for details.