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Three-dimensional cranial shape analyses and gene flow in North Africa during the Middle to Late Holocene

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ABSTRACT

Archaeological evidence shows that populations used to transverse the Sahara Desert throughout the Holocene despite the extreme temperatures and the rough physical terrain. The current paper examines whether the desert inhibited extended gene flow among populations by means of cranial morphology as captured by geometric morphometrics. The examined populations include the Garamantes, a group centered in Southwest Libya and largely controlling trans-Saharan trade, and various Egyptian, Tunisian and Sudanese groups dating to the Middle and Late Holocene. The results showed that most inter-population comparisons were statistically significant and therefore all populations appear more or less distant to each other. The Mahalanobis biodistance measure identified four clusters. The first consists of the Garamantes alone, the second includes the populations from Kerma and Gizeh, the third includes the Badari and Naqada, while the fourth consists of the samples from Algeria, Carthago, Soleb and Alexandria. Moreover, the distance of the Garamantes to their neighbors was significantly high and the population appeared to be an outlier. This is attributed to the location of the Garamantes at the core of the desert, indicating that, despite the archaeological evidence, the Sahara Desert posed important limitations to gene flow between the Garamantes and other North African populations.

Introduction

Recent research using non-metric cranial traits and focusing on the biological affinities of North African Late Holocene populations and the role of the Sahara Desert in the formation of these relationships has shown that the Central Sahara restricted population contacts (Nikita et al., 2012). The focus of that study was the Garamantes, a population that flourished in southwestern Libya, in the core of the Sahara Desert, approximately 3000 years ago and who controlled a significant portion of trans-Saharan trade. The biological affinities of the Garamantes to other North African populations, including Algerians, Carthagenians, Alexandrians, Gizeh, Kerma and Soleb, roughly contemporary to them, were examined by means of cranial non-metric traits using the Mean Measure of Divergence and Mahalanobis distance. The study identified three broad clusters among the populations. The first consisted of the Garamantes, the second included the Gizeh and Kerma, and the third comprised the Soleb, Alexandrians, Algerians and Carthagenians. The Garamantes appeared rather isolated possessing distant affinities to their neighbors. Overall, whenever the Sahara desert intervened among populations, their biodistances increased.

This result is reasonable given the hyper-arid climate and the harsh physical terrain of the desert; however, it appears to contradict the extensive archaeological evidence that suggests that the Sahara was always transversible, initially on foot and later by horses and camels (Mauny, 1978), and that North African populations had a long history of contact throughout the Holocene. More specifically, it is believed that, despite the harsh environment they occupied, the Garamantes had a pivotal role in a network linking the Mediterranean littoral, Egypt, the Maghreb, and sub-Saharan Africa (Liverani, 2000). Evidence of this includes large numbers of Roman artifacts (for example, glassware, fine ceramics, amphorae, cast bronze statues) in Garamantian contexts (Daniels, 1989; Mattingly, 2003a). The Garamantes also engaged in hostile encounters with the Romans in the late 1st century BC and 1st century AD, but the Roman expeditions later acquired a financial character (Mattingly, 2003b). The population was in contact with other North African groups too, as indicated by the adoption of Saharan funerary structures (e.g. keyhole monuments) by them (Mattingly, 2003c). Moreover, the knowhow for the Garamantian subterranean irrigation channels (*foggaras*) and medical practices, like trephinations, was most likely introduced from Egypt (Nikita et al., in press; Wilson, 2003). As a result of all these contacts, the Garamantes introduced important innovations in the Central Sahara, such as

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urbanism, irrigated agriculture, trans-Saharan trade, and the development of a hierarchical, probably slave-using society (Mattingly, 2006).

The above archaeological evidence for extensive contacts between the Garamantes and their neighbors can converge with the results from the analysis of cranial non-metric traits if we accept that population contacts took place mainly through trade networks which involved a subset of male merchants and local traders (Nikita et al., 2012). However, this conclusion also presumes that cranial non-metric traits are an accurate tool for studying population biodistances. In general, non-metric traits are believed to reflect an expression of genes that affect development and follow a non-Mendelian pattern of inheritance (Berry and Berry, 1967; Hauser and De Stefano, 1989; Ossenberg, 1984; Tyrrell, 2000). Many studies have demonstrated that the majority of these traits are under strong genetic control (Cheverud and Buikstra, 1981a,b, 1982; Saunders and Popovich, 1978). However, recent studies yielded low values of heritability for non-metric traits (Carson, 2006), which questions their use in biodistance analyses. Note also that for cranial traits, no standard protocol exists that defines where the threshold between presence and absence should be placed, an aspect that may have an important impact on the obtained results (Carson, 2006).

The current paper explores the biological affinities of North African populations dating to the Middle and Late Holocene by means of cranial shape variation as captured by three-dimensional morphometrics. Shape variation in the cranium of different human groups has been long identified as a powerful means for assessing population affinities and distances largely thought to multivariately reflect population history rather than adaptation (Howells, 1973, 1989; Lahr, 1996; Relethford, 1994; Roseman, 2004). In recent years, the development of geometric morphometrics has added recording and analytical sophistication to the study of craniometric variation, since '*geometric morphometrics focuses on the retention of geometric information throughout the analysis and provides efficient, statistically powerful tools that can readily relate abstract, multivariate results to the physical structure of the original specimens*' (González-José et al., 2008, p. 177). Thus the aim of the paper is to obtain a second, independent measure of gene flow across North African populations of the Middle to Late Holocene, and compare these to the results of the non-metric study. As in the previous paper, greater emphasis is placed on the biodistances of the Garamantes to their neighbors from Egypt, Sudan and Tunisia, since this population is geographically located at the desert core as well as at the center of the various trade networks.

Materials and methods

Materials

The populations under study are largely the same as in the non-metric traits study (Nikita et al., 2012). The nine North African populations analyzed for their biological affinities, including the Garamantes, are given in Table 1, their geographic location is depicted in Fig. 1 and their temporal and straight-line distances are shown in Table 2. Sub-adults were excluded, since their cranial morphology has not been fully shaped (Mays, 1998). Adults displaying poor preservation or diseases that could affect cranial shape were also excluded from the analysis. Sex and age were assessed following standard osteological methods (Buikstra and Ubelaker, 1994). Due to lack of availability, some sample sizes are relatively small. To avoid biases due to small sample sizes, only the statistically significant results were taken into account in the conclusions of the present study. In addition, the Algerians, which have the smallest sample size, were only included in the analyses for pooled sexes.

In brief, the Garamantes flourished in Southwest Libya, in the hyper-arid environment of the Sahara Desert, and are most likely the descendants of mobile Neolithic Pastoral Saharan communities

Table 1
Material used in the current study.

Population-origin	Symbol	Males	Females	Date	Country	Collection
Garamantes	GAR	11	13	900 BC–500 AD	Libya	Museum of Jarma (Libya)
Kerma	KER	45	88	2000–1550 BC	Sudan	Duckworth Lab. (Cambridge)
Soleb	SOL	10	17	1575–1380 BC	Sudan	Musée de l'Homme (Paris)
Gizeh	GIZ	85	63	664–343 BC	Egypt	Duckworth Lab. (Cambridge)
Alexandria	ALE	11	9	323 BC–330 AD	Egypt	Musée de l'Homme (Paris)
Naqada	NAQ	42	77	4000–3200 BC	Egypt	Duckworth Lab. (Cambridge)
el-Badari	BAD	15	19	4400–4000 BC	Egypt	Duckworth Lab. (Cambridge)
Carthage	CAR	12	8	751 BC–435 AD	Tunisia	Musée de l'Homme (Paris)
Algerians	ALG	5	8	1500 BC	Algeria	Musée de l'Homme (Paris)

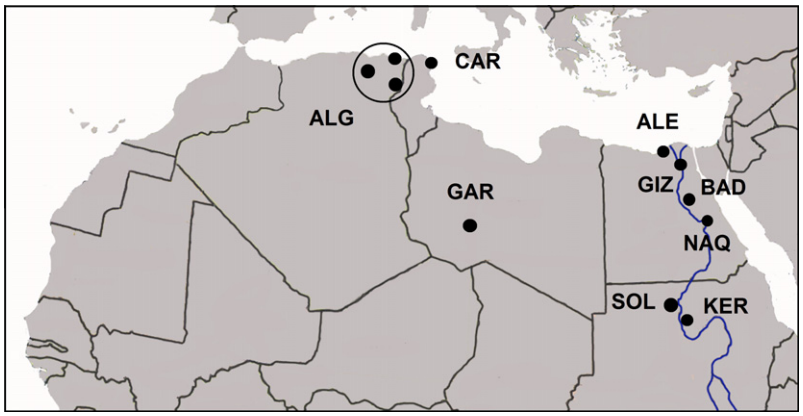

Fig. 1. Selected archaeological sites and populations within the study region. (ALG: Algerians, CAR: Carthagenians, GAR: Garamantes, ALE: Alexandrians, GIZ: Gizeh, BAD: Badari, NAQ: Naqada, SOL: Soleb, KER: Kerma).