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Do nuclear DNA and dental nonmetric data produce similar reconstructions of regional population history? An example from modern coastal Kenya

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ABSTRACT

This study investigates whether variants in dental morphology and nuclear DNA provide similar patterns of intergroup affinity among regional populations using biological distance (biodistance) estimates. Many biodistance studies of archaeological populations use skeletal variants in lieu of ancient DNA, based on the widely accepted assumption of a strong correlation between phenetic- and genetic-based affinities. Within studies of dental morphology, this assumption has been well supported by research on a global scale but remains unconfirmed at a more geographically restricted scale.

Paired genetic (42 microsatellite loci) and dental (nine crown morphology traits) data were collected from 295 individuals among four contemporary Kenyan populations, two of which are known ethnically as "Swahili" and two as "Taita;" all have well-documented population histories. The results indicate that biodistances based on genetic data are correlated with those obtained from dental morphology. Specifically, both distance matrices indicate that the closest affinities are between population samples within each ethnic group. Both also identify greater divergence among samples from the different ethnic groups. However, for this particular study the genetic data may provide finer resolution at detecting overall among-population relationships.

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INTRODUCTION

For more than two centuries, biological anthropologists have used biodistance analysis to evaluate biological affinity among past human populations (Konigsberg, 2006). A cursory review of the current literature suggests that, while some biodistance studies use both skeletal and ancient DNA data (e.g., Corruccini et al., 2002), a proportionally higher number rely on skeletal variants alone (for a review see Buikstra et al., 1990). In recent years, variants in dental morphology have become a favored dataset because (Scott and Turner, 1997): 1) crown morphology is not altered, except by wear or pathology, after the period of crown formation, 2) dental variants are highly heritable (60 to 80%), and 3) dental variants vary widely in frequency across populations.

This study had two goals. The first was to determine the strength of the correlation between biodistance estimates based on dental morphology and those based on genetic, i.e., nuclear microsatellite, variants. As reviewed below, biodistance studies based on dental morphology have long been used effectively to differentiate among populations on a global scale. However, more specific (i.e., regional comparisons) are also common in bioarchaeological research based on dental morphology (e.g., Willermet et al., 2013; Ragsdale and Edgar, 2014; Irish et al., 2014). It is at this level that the present study provides a direct test of consistency between dental morphological and genetic data in estimating biodistance using paired biological data. The second goal was to determine how closely biodistance estimates from these two datasets match population histories established through historic, linguistic, and archaeological research within coastal Kenya. To accomplish the second goal, paired genetic and dental morphology data were collected from living populations whose histories have been widely studied (as detailed below).

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Previous studies comparing dental and genetic biodistance estimates

Biodistance studies use dental morphology to examine patterns of population history at a variety of geographic scales. Scott and Turner (1997) identify six geographic scales that, from specific to general, are: 1) individual, 2) family, 3) local (i.e., subsets of a single population), 4) regional (i.e., multiple populations spatially proximate to one another), 5) continental (i.e., among populations widely distributed across a particular continent), and 6) global (i.e., where populations across continents are compared to one another). It has long been assumed among dental morphologists studying biodistance that phenotypic variation reflects genetic variation (and vice versa), so that either dataset can be used to reconstruct a similar overall pattern of population history at all geographic scales (Scott and Turner, 1997). To a large extent this assumption has been supported at a global scale; Scott and Turner (1997) comprehensively reviewed studies from populations on nearly every continent showing a general agreement between biodistance measures based on genetic data and dental morphology. Their review built on the work of various researchers who defined many of the major dental complexes (e.g., Sundadont vs. Sinodont), cementing the notion that dental morphology or genetic variants, can be used to differentiate among global populations (e.g., Hanihara, 1968; Mayhall et al., 1982; Turner, 1983, 1986, 1990; Townsend et al., 1990; Irish, 1993, 2013; Hawkey 2004; Scott et al. 2013).

However, bioarchaeologists are more often interested in investigating relationships among past groups at more geographically limited scales than continental and global. Many regional studies examine populations within a single country (e.g., Guatelli-Steinberg et al., 2001), region of a country (e.g., Hubbard, 2012), or bordering countries (e.g., Ullinger et al., 2005). As noted by Buikstra et al. (1990), this more refined focus is common in the

bioarchaeological literature and is reflected in an array of more recent publications (e.g., see Blom et al., 1998; Irish, 2006; Coppa et al., 2007; Sołtysiak and Bialon., 2013; Willermet et al., 2013; Irish et al., 2014). Such regional studies often focus on understanding mobility patterns (e.g., McIlvaine et al., 2014), trading networks (Ragsdale and Edgar, 2014), and other social phenomena (e.g., see Knudson and Stojanowski, 2008). Though not systematically tested, it is has long-been assumed that there is also a general agreement between biodistance measures based on genetic data and dental morphology when examining these regional scale networks (Scott and Turner, 1997).

Three early studies that examined the degree of concordance between biodistance estimates based on both genetic and dental morphology data produced conflicting results. Sofaer et al. (1972) and Brewer-Carias et al. (1976) found a generally strong agreement, while Harris (1977) found that genetic and dental distances produced fundamentally different patterns of relationships among regional populations. Several patterns appear when the study design and sample composition of these three projects are compared; these differences could account for the disagreement between results.

First, the types of data used across the three studies differ. As noted by Sofaer et al., (1972) and Brewer-Carias et al. (1976) each dental trait exhibits a wide range of phenotypic expression, leaving the interpretation of each stage up to the observer; as such, these early interpretations were partially subjective based on the observers' selection of traits and rankings of trait expression. Subsequently, Turner et al. (1991) established a standard set of descriptions and scoring plaques that both specify which traits are most appropriate for studies of biological affinity and a standardized method for scoring varied trait expressions (known today as the ASUDAS). Further, it is not clear which types of DNA were compared (e.g., uniparental versus

biparental) in each study, which could account for the differences in results[1].

Second, while all three studies compare genetic and dental data from the same populations they do not appear to compare paired data from the same individuals; that is, the dental samples came from partially or completely different individuals than the genetic samples.[1] Harris (1977) explicitly states that some samples were paired while others were not, given that much of his dataset was pieced together from existing, published datasets. Neither Sofaer et al. (1972) nor Brewer-Carias et al. (1976) specify whether data were paired or unpaired; however, the two studies used genetic and dental morphology data collected during different field seasons, increasing the likelihood that not all participants were included for both datasets. It is still common and practical for bioarchaeologists to collect unpaired data, usually in the form of a larger sample of morphological markers and smaller subset of genetic data. However, given that genetic variation between human groups is low relative to within-group variation (e.g., see a review in Witherspoon et al., 2007), it is possible that such practices could result in sampling biases. Specifically, when comparing populations with the express purpose of assessing consistency between genetic and dental biodistance estimates, genetic and dental data should be derived from the same individuals. Otherwise, any differences in the biodistance estimates derived from genetic and dental morphology will at least partly reflect the different segments of the populations used for each dataset.

The present study is the only one known of regional-scale populations that: 1) uses standardized data collection techniques for dental morphology; 2) examines differences using genetic data spaced across the human genome (one to two loci from each autosomal chromosome); and 3) compares dental morphology and genetic data from the same individuals in a very localized region (southeastern, coastal Kenya). Based on the design of this study, we

initially hypothesized that there would be a strong correlation between the biodistance matrices based on genetic and dental morphology data.

Reconstructing coastal Kenyan population history

As noted, the second goal of this study was to further test whether obtained biodistance estimates were consistent with predicted relationships based on established population histories. The setting, Kenya's Coastal Province, covers 30,767 square miles (79,686 km) including the littoral coast and areas roughly 150 km inland (Kenya National Bureau of Statistics, Wundanyi Office). Participants for the study were recruited from four communities: Lamu (Northeast), Mombasa (East Central), Dawida (Southwest), and Kasigau (Southwest) (Fig. 1). A unique component of the project was the use of living,as opposed to archaeological samples, with documented population histories based on archaeological, linguistic, and historical datasets. This information, therefore, could provide an opportunity to develop predictions about the relationships among the four populations that, in turn, comprise two ethnic groups. One caveat is that these samples represent modern peoples whose population histories may reflect more modern gene flow, which is not fully considered in these hypothesized relationships.

The inhabitants of Lamu and Mombasa are known ethnically as "Swahili" or "Swahili-Arab," and represent communities within a larger urban mercantile population that has strong roots in Africa despite ongoing connections to coastal Arab groups (Nurse et al., 1985; Middleton, 1992, 2003; Chami, 1994; Chami and Msemwa, 1997; Abungu, 1998; Kusimba, 1999; Horton and Middleton, 2000; Kusimba and Kusimba, 2000; Spear, 2000). The inhabitants of Dawida and Kasigau are known ethnically as the "Taita," and are a rural agrarian population with few genetic contributions from outside East Africa (Merritt, 1975; Bravman, 1998; Batai et al., 2013). The Swahili and Taita are thought to have been part of a larger migration of Bantu-

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speaking populations out of western Africa as early as 800 BC (Nurse and Spear 1985; Ehret 1998, 2001; Salas et al., 2002). The Swahili arrived on the littoral coast as early as 100 BC (de Vere Allen, 1993; Chami, 1994; Abungu, 1998; Kusimba, 1999; Salas et al., 2002), eventually developing complex intraregional trading networks with hinterland coastal peoples such as the Oromo, Kamba, Taita, and Mijikenda (as these groups arrived in the area) and hundreds of years before the arrival of non-African traders (Chami, 1994; Chami and Msemwa, 1997; Abungu, 1998; Kusimba, 1999; Kusimba and Kusimba, 2000). Oral traditions and linguistic analyses suggest that the Taita arrived in the Tsavo region (where they reside today), around AD 1400 (~600 yrs BP) (Merritt, 1975; Spear, 1981; de Vere Allen, 1993; Bravman, 1998), though Bravman (1992) suggests an arrival as early as 1000 years BP.

A set of specific expected relationships among the four populations were proposed (as summarized in Table 1) based on a large collection of archaeological, linguistic, and ethnohistorical evidence as well as Wright's (1943) concept of isolation by distance.[2] These predicted relationships rely primarily on the caveat that both datasets reflect long-term interactions among populations in the region, not a recent snapshot of interaction among the four groups.

First, we expected that populations from the same ethnic group (e.g., Dawida and Kasigau) would be more similar to each other (and hence, produce a smaller biodistance) than populations from different ethnic groups (e.g., Mombasa and Dawida). Though the Taita and Swahili may only have "diverged" 2000 years ago, Kasigau and Dawida (also known as the "Taita Hills") are far from Lamu (~ 450 km) and Mombasa (~ 150 km) and separated by a fairly harsh, dry environment (Wright, 2005). However, it is unclear whether Dawida and Kasigau would be more similar than Mombasa and Lamu. Lamu and Mombasa are a greater distance

apart than Kasigau and Dawida, though the Taita Hills have been described as "islands" dotting the plains (Merritt, 1975; Bravman, 1998) with most participants living in the same villages since birth. In contrast, participants from Mombasa frequently reported being born in Lamu (and vice versa), suggesting more mobility between these coastal locations despite their greater distance. Based on isolation by distance alone, it was therefore predicted that Dawida and Kasigau would be more similar.

Second, we anticipated that the two Taita populations (Dawida and Kasigau) would be more similar biologically to the sample from Mombasa than from Lamu, with Mombasa more akin to Kasigau than Dawida. This expectation is based on archaeological evidence indicating that between AD 1000 and 1500, trade between the interior and coast thrived – with Mombasa operating as the major port out of which caravans ventured into areas such as the Taita Hills (Kusimba et al., 2007). Archaeologists believe that Swahili caravans developed extensive "fictive kin" networks with neighboring coastal communities ("undugu wa chale"), such as the Taita; struggling communities would thus have had places to go and people to rely on during times of famine, drought, and/or conflict (Kusimba and Kusimba, 2001, 2005; Wright, 2005), something prevalent between AD 1600 and 1800 (Merritt, 1975; Kusimba and Kusimba, 2000). Further, according to missionaries' journals and oral histories, the primary stopping point for water, food, and trade items was situated in and around "Mount Kasigau" (Kusimba and Kusimba, 2000), suggesting that Kasigau might have had closer ties to Mombasa than Dawida.

Third, we expected to observe the largest biodistances between Lamu and the two Taita locations, with a small probability that Lamu would be more like Kasigau than Dawida. These last two predictions are based solely on Wright's (1943) concept of isolation by distance and a lack of evidence that Lamu and Taita populations came into direct contact. Due to direct contact

between Mombasa and Kasigau traders (and ongoing contact between Mombasa and Lamu), it was further predicted that there might be a slightly higher chance of the Kasigau sample sharing greater similarities with Lamu, though again, the level of *recent* genetic contact among all groups has not been taken into consideration.

MATERIALS

Sample composition and characteristics

Impressions of permanent dental crowns and saliva samples were collected from 400 unrelated adults (18+ years of age). Willing participants were given an oral exam prior to sample collection, and individuals exhibiting poor oral and dental health, including infection and/ or missing, worn (to the point that a particular morphological feature was obscured or missing), or broken teeth, were excluded from the study. These steps were taken to ensure a high quality dental sample as well as to protect participants from pain and discomfort. Of the original 400 participants, only 295 paired dental and genetic samples were analyzed. Three individuals did not complete both sample collections, 12 were later found to be related (sharing a grandparent or closer), and the remaining 92 were excluded, either due to poor setting of the dental impressions or absence of discernible DNA (mostly due to contaminants that inhibited the PCR process).

A questionnaire was used to collect information on place of birth, current residence, and ethnicity of participants and family members including siblings, parents, and grandparents, ethnic identity (Taita or Swahili/Swahili-Arab) of participants and their parents, and the sex and age of participants. Roughly equal numbers of male and female participants were selected to reduce potential effects of sexual dimorphism, though age was not controlled because the only age-related impact on morphology is the level of dental attrition, which was evaluated during the oral exam. Ethnicity, though more difficult to account for, was determined based on the ethnicity

of the participant and the ethnicity of the participant's father. Table 2 presents the sample composition by location, ethnicity, and sex.

METHODS

Sample collection and preparation

Participants were recruited through the assistance of local community leaders over a five-month period and included healthy adults with a fully erupted, permanent dentition. Roughly equal numbers of males and females were recruited to limit potential sex bias in the sample. Consenting participants were first interviewed using a genealogical survey to evaluate whether two or more relatives (defined as people sharing a grandparent, aunt/uncle, cousin, parent, or sibling) were enrolled in the study. Next, an oral examination was completed to assess whether sufficient teeth were present, dental attrition was low, and participants had good oral health. Participants passing the inspection had a dental impression taken using a two-part polyvinyl siloxane (PVS) system (Coltène-Whaledent "AFFINIS" super soft putty and regular body wash), though it was later determined that the PVS putty, alone, was sufficient to obtain a high resolution, dimensionally stable impression. Lastly, participants were asked to spit into a collection tube (DNA Genotek 2 mL "Oragene" system) to obtain a buccal tissue sample. Saliva collection kits were used because the materials are stable at room temperature (a buffer/preservative is used), easy to transport, and the collection method is non-invasive (Rylander-Rudqvist et al., 2006; Hansen et al., 2007). On average, each 2 mL sample can produce around 100 μg of DNA (Birnboim, 2004).

A total of 400 dental casts were made from impressions using a gypsum-based dental casting material (Modern Materials "Denstone" Type II, golden color). A detailed dental casting protocol is provided in Appendix A of Hubbard (2012). DNA was purified and extracted from

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500 mL saliva samples using standard protocols, suspended in 100 μL of distilled water, and frozen for transport. A detailed extraction and purification protocol is provided in Appendix B of Hubbard (2012).

Genetic data collection and analysis

A total of 351 DNA samples were sent to a commercial genetics lab (Prevention Genetics) for PCR amplification and microsatellite genotyping (49 of the original 400 samples did not yield sufficient quantities of DNA). Fifty microsatellite loci from the Marshfield Panel, a subset of the Human Genome Diversity Cell Line, were sampled. The Marshfield Panel is a selection of 377 microsatellite loci that have been identified as useful in ascertaining population differences (Rosenberg, 2002). Because the panel does not specify standard African-focused microsatellite marker sets or number of required markers, 50 loci were selected at random across equally-spaced intervals of the human genome to both minimize selection bias and maximize coverage of the genome. Genetic frequency data, heterozygosity, pairwise and global F_{ST} values, and STRUCTURE estimates for the sampled loci can be found in Hubbard (2012). These data show that sufficient diversity was present to warrant the use of these genetic loci in differentiating population history among the four sampled populations. Genetic samples from researchers working in the lab were sent to Prevention Genetics to control for contamination - none was found.

Goldstein et al.'s (1995) delta-mu squared (Ddm) distance was used to calculate genetic distance because the statistic is designed for use with microsatellite data following a stepwise mutation model and can account for the effects of genetic drift. Ddm was calculated using MSAT version 2.0 (with a bootstrapped model), an executable program designed by Dieringer and Schlotterer (2003) to calculate various genetic distance measures. Following standard data

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editing procedures, genetic loci with more than 10% missing data, loci in Hardy-Weinberg disequilibrium within a single population, loci that did not properly amplify during the PCR process, and loci or individuals that had high numbers of PCR dropouts were excluded from the study. Only 42 of the original 50 sampled loci were retained (Table 3).

Dental data collection and analysis

The first author recorded 30 permanent dental crown traits outlined in the Arizona State University Dental Anthropology System (ASUDAS) using the 351 dental casts for which there were paired genetic data. This widely adopted, standardized data collection system uses a set of reference plaques with written descriptions (Turner et al., 1991) to record variation in the dental traits most commonly observed in human populations worldwide. Each trait is recorded for a focal tooth using a ranked system designed to capture the range of variation (e.g., pit, furrow, cusp). Dental traits vary in a quasicontinuous manner, meaning that they can vary in expression while also having a threshold at which that trait is considered "present." Breakpoints established by Turner (1987) and Irish (2005) were used to transform the ranked data into dichotomized presence (i.e., 1) and absence (0) scores. Before collecting the final dataset, an intra-observer error test was conducted on 30 dentitions (maxillary and mandibular casts) for both the ranked and dichotomized data using gamma and kappa tests, respectively.

Editing dental morphology datasets differs depending on the biodistance statistic being used. Within anthropology a number of biodistance measures have been developed for analyzing morphological variation in the dentition including Pearson's (1926) Coefficient of Racial Likeness, Penrose's (1954) shape distance, Gower's (1971) distance, the Mean Measure of Divergence (MMD) (Grewal, 1962), and Konigsberg's (1990) pseudo-Mahalanobis D^2 (pseudo-

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D^2). Though there has great debate over the efficacy of various measures, a study by Irish (2010) documents that most measures provide comparable estimates.

The pseudo-D^2 statistic was used in the present study and calculated using an executable program by Konigsberg (1990). A benefit of the pseudo-D^2 statistic is that it accounts for trait intercorrelation and weights correlated traits (rather than removing them from the sample). Correlations are determined using a tetrachoric correlation matrix, which cannot be calculated when individuals or traits have large numbers of missing values. Though no standards exist for how best to identify the number or specific traits to remove, the present study employed the following method. The 30 dental traits were run through the program and those with the largest number of missing values were removed until a tetrachoric correlation matrix was produced. After editing the dental dataset, only nine traits remained (Table 4), which provides a good indication of the general state of individual dental completeness in these four groups.

Comparison of biodistance matrices

Two approaches were used to determine the agreement between distance matrices based on these different data types. First, the correlation between the genetic and dental distance matrices were assessed using both Pearson's and Mantel's "r" tests (Dutilleul et al., 2000). Associated *p*-values were used to determine whether the correlation was significant at the 0.05 level. Second, principal coordinate values were calculated and plotted. Distance values within a single matrix must be compared, given that they are unitless. In general, a smaller biodistance between two samples reflects close biological affinity, while a larger biodistance reflects dissimilarity. Because it is not possible to compare differences in the raw values between two distance matrices, principal coordinate analysis is often used to visualize the relationship.

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RESULTS

Table 5 presents the biodistance values for each of the sample comparisons, ordered from largest expected values (top) to smallest expected values (bottom). Both the Mantel and Pearson tests produced a correlation of 0.50, though neither value was significant at a 0.05 level (Pearson's p=0.31; Mantel's p=0.21). Further, we predicted that distance values between sample pairs would exhibit the following pattern from largest to smallest: Dawida-Lamu, Kasigau-Lamu, Dawida-Mombasa, Kasigau-Mombasa, Mombasa-Lamu, and Dawida-Kasigau. The two smallest pseudo-D^2 distances were observed between Dawida and Kasigau (0.332) and between Mombasa and Lamu (0.362). Likewise, the smallest Ddm distances were observed between the two Taita (0.139) and two Swahili (0.186) samples. Thus, both the genetic and dental data identified close affinities between sampled populations from the <u>same</u> ethnic group.

Similarly, both data sets yielded greater distances among samples from the different ethnic groups. However, the biodistance values based on genetic data suggest a closer affinity between the sample from Mombasa and the two Taita samples (0.541 and 0.365) than between Lamu and the same two Taita samples (1.265 and 0.900); those based on dental data suggest an overall closer relationship between Dawida and the two Swahili samples (0.615 and 0.557) than between Kasigau and the same Swahili samples (0.779 and 0.836). As such, the calculated pairwise genetic distances for samples from different ethnic groups matched the predictions exactly, while those obtained from dental morphology data did not.

Figure 2 is a plot of sample scores obtained from the principal coordinate analysis (PCO) for the genetic distances overlaid by the scores based on dental morphology. The first principal coordinate (x-axis) explains around 65 percent of the variation in the sample for both genetic and dental distances; both plots clearly distinguish between the Swahili and Taita samples along this

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axis. The second principal coordinate (y-axis) explains the remaining variation (plus or minus a few percentage points) and reflects the differences between samples from different ethnic groups. The genetic PCO plot shows a closer biological affinity between Kasigau and Mombasa and between Dawida and Lamu; the plot based on dental morphology (pseudo-D^2) places Kasigau as an outlier. Still, the same general pattern is produced from both datasets; though there are variations regarding location within the clusters on the extreme left and right sides, the two Taita samples appear nearest one another, and distinct from the Swahili, and vice versa.

DISCUSSION

The results of this study provide a complex yet informative view into the relationship between biological distance estimates based on genetic data and those based on dental morphology data. The first goal of this study was to determine whether these two datasets provided analogous representations of population histories among the four regional populations sampled. A moderate to strong positive, though non-significant, correlation between genetic and dental biodistance matrices was observed (see Cohen, 1988 for correlation strength measures). Since the number of variables (in this case, six pairwise distance values) can affect p-values, a second method for analyzing similarities between these matrices was to plot principal coordinate scores from genetic and dental data to visualize the relative positions (and by proxy, relationships) among samples (Figure 2). This plot indicates that the genetic and dental distances produce a similar overall pattern, but give somewhat different pictures of detailed relationships among the four samples. Within the plot, the two Swahili samples cluster together and are distinct from the Taita. The major difference appears to be that the genetic data identify a greater affinity between Mombasa and the two Taita samples, while the dental data identify a closer affinity between Dawida and the two Swahili samples. Thus, we conclude that both genetic and

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dental morphology data are sensitive to differences between the Taita and Swahili samples (between ethnic groups), but provide a different overall picture of the relationships among samples from different ethnic groups.

A second goal of the project was to determine if either dataset (Table 5) provided a representative picture of expected relationships among the four samples (Table 1). When ordered from largest to smallest, the genetic distances follow the predicted pattern based on known population history (i.e., samples from the same ethnic group were more similar, those from different ethnic groups were least similar, and Mombasa shared an overall closer affinity to the Taita samples). While the dental distances show samples from the same ethnic group as most similar, a stronger affinity between Dawida and the two Swahili samples is also observed. Therefore, the genetic data best reflect the long-term history of the four populations. These findings do not contradict observations by Scott and Turner (1997) that dental morphological data are most effective at higher geographic scales of study, particularly global and continental. However, the present study compares samples at a regional, or even local scale (i.e., ethnic groups), given the very geographically restricted region in which the four populations live. This is not to say that dental comparisons at regional (e.g., Willermet et al., 2013; Ragsdale and Edgar, 2014; Irish et al., 2014) and local (Stojanowski and Schillaci 2006; Pilloud and Larsen 2011; Stojanowski, Johnson and Duncan 2013) geographic scales cannot successfully reconstruct documented population relationships elsewhere; rather, the findings presented here provide a cautionary tale and suggest that comprehensive tests among regional populations are needed.

Overall, this study provides a glimpse into the impacts and challenges of determining appropriate datasets to investigate population history at these more specific scales. However, there are some methodological limitations that, when taken into account, further enrich this

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picture. First, this study utilized nuclear microsatellite data paired with dental crown morphology data to ensure that differences in biodistance matrices reflected variation among populations, not differences between the collected genetic and dental samples. While this strategy allowed for the comparison of variation among the same individuals in each sample, it is still possible that these individuals do not fully represent population variation. Second, only nine of 30 dental traits remained after data editing, while 42 of 50 microsatellite loci were retained. The differences in biodistances could be explained by the many loci versus few dental traits, in that the latter may not capture adequate variation. Berry (1976) was among the first to propose that dental traits were polygenic, suggesting that each trait might be controlled by a minimum of 10 genetic loci (though the last postulate has not been validated). At present, specific genes controlling the varied expressions of all ASUDAS dental traits are unknown, and the potential for overlap in genes controlling for (or affecting) different traits is likely (Jernvall and Jung, 2000). Third, the positive match between the ranked genetic distance values and predicted biodistance rankings does not confirm that genetic data of all types are better suited than dental morphology data for biodistance studies. Among aDNA studies of past populations, mitochondrial markers are often favored because of a higher repeat number (see Pääbo et al., 2004 for full review). However, Williams et al. (2002) found that nuclear DNA produced a pattern of biodistances consistent with known Yanomamo population history, while mitochondrial DNA did not. Furthermore, Relethford (2007) warned that degradation in aDNA often can lead to studies examining a single locus, giving a potentially skewed view of affinity among samples. Finally, it is possible that one or more of our predicted relationships are faulty, though all are consistent with archaeological, linguistic, and historical data. Likewise, it is currently not possible to determine what temporal

scale is captured by each dataset. For example, could dental distances reflect short-term, recent population history differences while the genetic distances reflect long-term history?

While this study examines living groups, it provides important applications to the bioarchaeological study of past populations. Two recent publications also examine the agreement between paired genetic and morphological data using archaeological samples. First, Ricaut et al. (2010) examined mixed cranial and dental morphology samples to estimate <u>kinship</u> within a single site, while Herrera et al. (2014) examined cranial metric and morphological variation to understand population history at a <u>regional</u> level. Both acknowledge the value of skeletal variants in bioarchaeological studies at these geographic scales. Ricaut et al. (2010) found that combined morphological data provided good resolution in identifying pairs of kin within a Mongolian necropolis, although genetic findings detected double the number. In the second study, Herrera et al. (2014) compared Y-chromosome, mtDNA, cranial metric, and cranial morphology data in samples from the Bering Strait region; they found that craniometric distances were correlated with mtDNA, while distances based on cranial morphology were correlated with those from Y-chromosome variants. Viewed as a whole, two lessons can be learned from the present and previous studies: 1) additional work needs to be undertaken to determine which skeletal and genetic data are best suited to answer particular research questions (Herrera et al., 2014; present study); and 2) care should be taken when formulating very fine scale interpretations of population history from skeletal data (Ricaut et al., 2010; present study; also Scott and Turner, 1997).

CONCLUSIONS

This study examined the ability of nuclear microsatellite and dental morphology data to detect biologically informative differences among recent, geographically constrained regional and local Kenyan populations using biological distance analysis. Of existing studies comparing dental morphology with genetic variants, the present study is the first to use genetic and dental data from the same individuals, thus making it possible to directly assess the agreement between these two data sources in biodistance estimates. What is considered a moderate to strong positive, though non-significant correlation was found between genetic and dental distance matrices. Furthermore, comparisons of ranked distance values and principal coordinate plots of overall relationships among the four populations suggest that both genetic and dental morphology datasets are capable of identifying known ethnic differences. Overall, these findings suggest that nuclear microsatellite data should provide good resolution in other studies exploring fine scale population histories among regional and local groups. Dental morphology data may (or may not) do so among very proximate groups; however, additional testing using a full suite of dental traits and larger samples is necessary to resolve this latter issue. Future research will focus on incorporating additional dental traits as well as biodistance estimates based on mtDNA from the same populations to determine if these data provide a population history comparable to that produced by nuclear microsatellites.

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FOOTNOTES

[1] Brewer-Carias et al. (1976) note that 11 genetic markers were analyzed from an unpublished work, while Sofaer et al. (1972) and Harris (1977) note that serological data were used but do not describe the number of or specific variants examined. As such, the genetic data used are not clearly specified.

[2] Wright's concept of isolation by distance postulates that populations in close proximity are expected to share greater biological similarity than those at a great distance.

FIGURE LEGENDS

Figure 1: Map of Kenya's coastal province noting locations of the study populations.

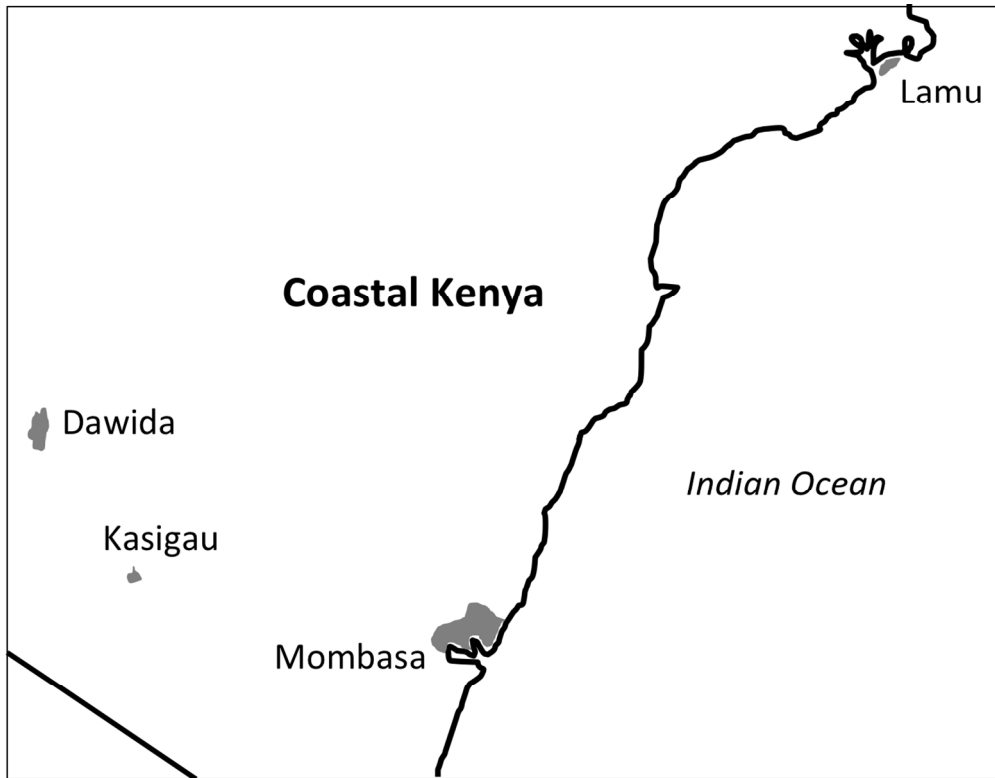Figure 2: Principal coordinate plot of Ddm (circle) and pseudo-D^2 (triangle) distances.

Figure 1: Map of Kenya's coastal province noting locations of the study populations.
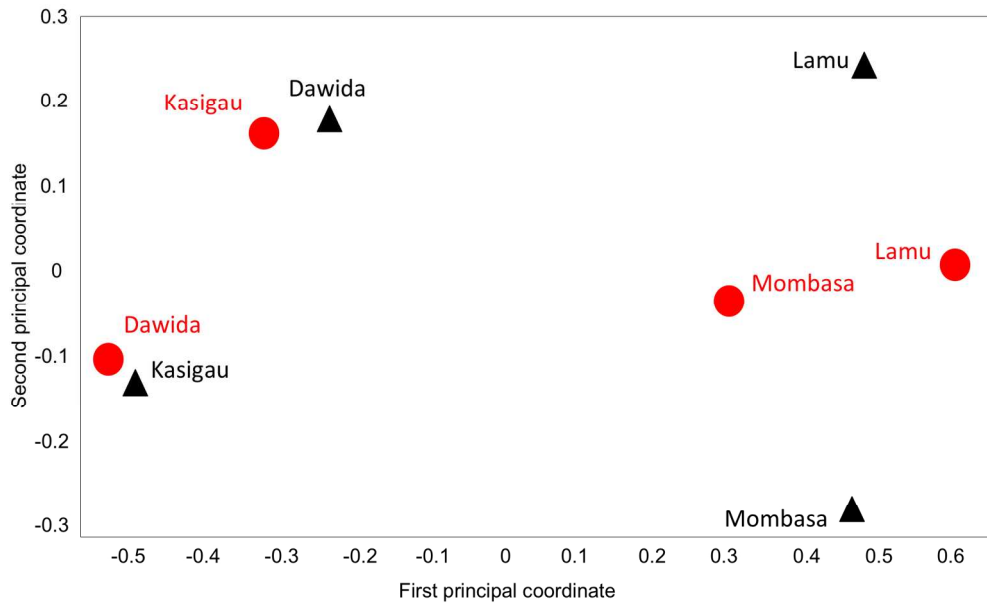512x397mm (72 x 72 DPI)

Figure 2: Principal coordinate plot of Ddm (circle) and pseudo-D2 (triangle) distances.
679x407mm (72 x 72 DPI)

Table 1: Predicted relationships among pairs of populations, ranked from largest to smallest biodistance

Predicted distances	Population comparisons[a]
Largest	dawida - LAMU
-----	kasigau - LAMU
----	MOMBASA - dawida
---	MOMBASA - kasigau
--	MOMBASA – LAMU
Smallest	dawida - kasigau

[a] Populations in CAPS are ethnically Swahili, populations in lowercase are ethnically Taita; comparisons are ordered according to predicted relationships among the four populations.

Table 2: Sample composition

Location	Ethnicity	Females	Males	Combined
Mombasa	Swahili	39	23	62
Lamu	Swahili	29	29	58
Dawida	Taita	39	39	78
Kasigau	Taita	45	52	97
	TOTAL	152	143	295

Table 3: List of the 42 microsatellite loci used in the present study

	Marker Name	Locus Name	Chromosome	Repeat Type
1	D1S3669	GATA29A05P	1	Tetra
2	D1S1627	ATA25E07M	1	Tri
3	D1S3462	ATA29C07L	1	Tri
4	D2S1400	GGAA20G10M	2	Tetra
5	D2S1328	GATA27A12	2	Tetra
6	D2S2968	GATA178G09M	2	Tetra
7	D3S3038	GATA73D01	3	Tetra
8	D3S4523	ATA34G06	3	Tri
9	D3S2398	GATA6G12	3	Tetra
10	D4S2397	ATA27C07P	4	Tri
11	D4S2368	GATA27G03	4	Tetra
12	D5S2845	GATA134B03	5	Tetra
13	D6S1277	GATA81B01	6	Tetra
14	D7S2846	GATA31A10	7	Tetra
15	D7S1799	GATA23F05	7	Tetra
16	D8S1048	UT7129L	8	Tetra
17	D8S1108	GATA50D10	8	Tetra
18	D9S1121	GATA87E02N	9	Tetra
19	D9S2157	ATA59H06Z	9	Tri
20	D10S1426	GATA73E11	10	Tetra
21	D10S1230	ATA29C03	10	Tri
22	D11S1993	ATA1B07	11	Tri
23	D11S1998	GATA23E06L	11	Tetra
24	D12S297	UT5029	12	Tetra
25	D12S2078	GATA32F05	12	Tetra
26	D13S787	GATA23C03P	13	Tetra
27	D13S779	ATA26D07	13	Tri
28	D14S599	ATA29G03Z	14	Tri
29	D14S1434	GATA168F06	14	Tetra
30	D15S659	GATA63A03N	15	Tetra
31	D16S2624	GATA81D12M	16	Tetra
32	D17S974	GATA8C04	17	Tetra
33	D17S1290	GATA49C09N	17	Tetra
34	D18S542	GATA11A06	18	Tetra
35	D18S1357	ATA7D07	18	Tri
36	D19S586	GATA23B01N	19	Tetra
37	D19S246	Mfd232	19	Tetra
38	D20S1143	GATA129B03N	20	Tetra
39	D20S164	UT1772	20	Tetra
40	D21S1437	GGAA3C07	21	Tetra
41	D21S1446	GATA70B08	21	Tetra
42	D22S689	GATA21F03	22	Tetra

Table 4: List of the nine dental traits used in the present study

Dental traits	Focal tooth	Breakpoint
Tuberculum dentale	Maxillary lateral incisor	+ =ASU 2-6
Distal accessory ridge	Maxillary canine	+ = ASU 2-5
Accessory cusps	Maxillary first premolar	+ = ASU +
Accessory cusps	Maxillary second premolar	+ = ASU +
Carabelli's cusp	Maxillary first molar	+ = ASU 2-7
Lingual cusp number	Mandibular second premolar	+ = ASU 2-9
Anterior fovea	Mandibular first molar	+ = ASU 2-4
Protostylid	Mandibular first molar	+ = ASU 1-6
Cusp number	Mandibular second molar	+ = ASU 5

Table 5: Biological distances based on nuclear microsatellite (Ddm) and dental morphology (pseudo-D^2).

Population comparisons[a]	Genetic (Ddm)	Dental (pseudo-D^2)
dawida - LAMU	1.265	0.615
kasigau - LAMU	0.900	0.779
MOMBASA - dawida	0.541	0.557
MOMBASA - kasigau	0.365	0.836
MOMBASA - LAMU	0.186	0.362
dawida - kasigau	0.139	0.332

[a] Populations in CAPS are ethnically Swahili, populations in lowercase are ethnically Taita; comparisons are ordered according to predicted relationships among the four populations.