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A Comparison of the Utility of Craniometric and Dental Morphological Data for Assessing Biodistance and Sex-Differential Migration in the Pacific Islands

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Abstract
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Genetic analysis of maternally-inherited mitochondrial DNA and the paternally-inherited Y-chromosome yield contrasting pictures of movement of peoples into the Pacific Islands. A possible explanation for this discrepancy is a matrilocal residency pattern practiced by early Pacific settlers, in which Melanesian men were brought into settler communities to intermarry with local women, yielding a higher intrapopulation variance and lower interpopulation variance exhibited in males compared to females. This research investigates the possibility of sex-differential migration in the Oceanic populations of Easter Island, Fiji, Guam, Mokapu, and New Britain through analysis of biodistance based on dental morphological trait frequencies and craniometric measures while simultaneously comparing the utility of these two different data types, dental non-metrics and continuous cranial measurements, to determine whether these two types of data can be usefully combined or utilized interchangeably to represent underlying genotypic variation. Using Mean Measure of Divergence and Mahalanobis distance, variation for these populations was modelled with Principal Coordinatess Analysis, Generalized Procrustes Analysis, Mantel tests, discriminant analysis, and K-means clustering. Overall, the dental data was not found to be consistently more variable between the sexes and populations than craniometric data, indicating that if craniometric measurements are smoothed out by environmental factors while dental morphology is more canalized, this effect is subtle for this region and these particular samples. Additionally, estimates of possible residence patterns were not in agreement between analyses, indicating that residency was likely only slightly unilocal if not ambilocal, depending on population. However, uneven sample sizes and the small number of populations available for study likely affected the ability to draw out conclusive inferences about the peopling of this vast and complex region.

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Chapter 1: Introduction

Human migrations throughout history can be traced through observations in the archaeological record, changes in language, melding and innovation in cultural practices, and in physical factors in humans themselves, including genes and the manifestation of the traits for which they code. When human groups have been separated for an extended period of time and gene flow between them restricted, or when inputs into this gene flow are varied, their genetic compositions will tend to become more different. On the other hand, when groups are close in proximity or contact for many generations, allowing for ample gene flow among them, they will tend to become more genetically similar. If groups are moving together as insular units, these genetic changes can be expected to be equivalent across both sexes, with males and females bearing similar genetic diversities and subsequently equally expressing physical traits. However, when migration is sex-differential, with one sex being more mobile in relation to the other more stationary sex, these traits can vary independently between the sexes in the same population. A cause for this phenomenon is post-marital residence pattern, a practice that dictates where a couple resides after marriage, either with the kin of the female or of the male. The stationary sex, who is living in close proximity to its relatives, tends to become more genetically similar over time to those in its population, and more genetically distinct from those outside of it. The mobile sex, who is migrating into a population in which it is not closely related to those living there, tends to be more genetically distinct from members of their same sex within the group, while maintaining a generally genetic homogeneity over all groups which are all likewise mobile. In a matrilocal post-marital residence pattern, females are the stationary sex while males are mobile, while in a patrilocal residence, the opposite pattern is true. The extended practice of a particular pattern over time can lead to differential patterns of gene flow and migration detected in genetic and physical variation between males and females. In the Pacific Islands, differential patterns of

haplotype diversity have been observed in males (in the paternally-inherited Y-chromosome) and females (in the maternally-inherited mitochondrial DNA) across the general route of migration through Melanesia from Southeast Asia and into Polynesia that have raised questions about the speed and level of indigenous admixture associated with eastward expansion (Redd et al 1995, Sykes et al 1995, Melton et al 1998, Hagelberg et al 1999, Kayser et al 2000, Kirch 2000, Lum and Cann 2000, Su et al 2000, Oppenheimer and Richards 2001, Underhill et al 2001, Hurles 2002, Kayser et al 2006, Matisoo-Smith 2007). The existence of sex-differential migration due to practice of particular post-marital residence in the Pacific during this expansion, which left females isolated as males took part in extended exploratory voyages, could explain the differences in genetic variation observed between the sexes.

When genetic evidence is not readily available for study or comparison of the variation between populations or sexes, other physical traits, such as skeletal or dental morphology, can be used as a proxy to do so. Under the same principle, genetically similar groups will exhibit similar physical traits, causing them to look alike, while genetically distant groups will appear physically distinct. This concept is the foundation of the field of biodistance, which attempts to reconstruct population history, assess ancestry, or elucidate patterns of social organization from evidence of relatedness among human populations (Buikstra et al 1990, Larsen 1997, Larsen 2002, Pietrusewsky 2014). In particular, variation in measurements of cranial size and shape as well as presence of non-metric skeletal and dental features between males and females have been utilized to exemplify overall genetic variation within and between populations, as mechanisms of heritability are well-known for such traits (Lane and Sublett 1972, Spence 1974, Konigsberg 1988, Stefan 1999, Schillaci and Stojanowski 2003, Tomczak and Powell 2003, Schillaci and

Stojanowski 2005, Stojanowski and Schillaci 2006, Hubbe et al 2009, Nystrom and Malcom 2010, Cook et al 2014).

Despite the fact that metric and non-metric features of the skeleton and dentition are known to be heritable, intervening factors of environment and nutrition differentially influence their manifestation and observability. The size and shape of the cranium is has been shown to be affected by external and non-biological forces, causing these traits to bear more similarity over individuals under like conditions, which may or may not be analogous to their underlying genetic variation (Hylander 1977, Carey and Steegman 1981, Beals et al 1983, Beals et al 1984, Havarti 2001, Wood and Lieberman 2001, Roseman 2004, Gonzalez-Jose et al 2005, Havarti and Weaver 2006). Non-metric features of dentition, however, are thought to escape this quandary. Dental morphology is highly heritable, selectively neutral, and not affected by remodeling due to environmental insult, allowing for variation in its expression to correspond more directly with the genetic variation underlying it (Saunders and Mayhall 1982, Powell 1993, Scott and Turner 1997). Additionally, dental traits are not sexual dimorphic, unlike cranial size and shape, so variation in males and females can be directly compared to elucidate their differential variation (Scott and Turner 1997).

This research utilizes both dental morphological features and craniometric measurements to examine variation of males and females in the Pacific Island populations of Easter Island, Fiji, Guam, Mokapu, and New Britain. By comparing the different levels of variation between the sexes, the goal is to explore whether sex-differential migration as the result of a particular post-marital residence pattern occurred during settlement of the Oceanic region, as well as how differences in these patterns between populations can elucidate which pattern was practiced during certain stages of the overall peopling of the Pacific, and what that implies about societal

behavior at those stages. The concurrent objective of this study is to investigate how craniometric measurements and dental morphological traits compare as evidence of variation in order to establish which feature is a closer approximate to underlying genetic variation, and whether these types of data can be useful used in combination to study patterns of biological distance.

If matrilocal post-marital residence was being practiced in the populations in this study, females will be more similar within each group and more distant between groups than males, while males will exhibit more similarity over all groups but will be more distinct within each group than females. If patrilocality was the more common practice, the opposite pattern will hold true. If an ambilocal residence pattern was occurring, in which couples live with either the male's or female's kin in approximately equal frequency, the levels of variation will not differ substantially between the sexes. Additionally, if dental morphological variation is a more accurate proxy to the underlying genetic variation in these populations compared to craniometric variation, implying that cranial size and shape are more heavily subject to environmental influences, variation based on cranial data will bear more overall similarity, as well as greater agreement between the sexes, than that based on dental data. Thus, two broad questions are approached in this study: How do the sexes compare between these populations, and can we elucidate residence pattern from this? And how do the data types compare, and can they usefully be combined to produce similar results?

Chapter 2: Literature Review

2.1. Migrations into the Pacific Islands: linguistic, archaeological and genetic evidence.

Oceania, or the Pacific Islands, is a vast zone encompassing thousands of islands extending from island Southeast Asia, east and south across the Pacific Ocean to cover an area of over 10,000 square kilometers. The unique layout of this region and its changing geography through deep time has contributed to it being the result of not only one of the world's most complex patterns of migration and colonization, but one of the latest as well. Periods of glaciation during the later Pleistocene tied up oceanic waters and lowered sea levels worldwide, allowing for exposure of the land masses of Sahul, constituting modern day New Guinea and Australia, and Sunda, which makes up the Malay Peninsula and Indonesian islands. The vast water barrier between, known as Wallacea, separated the two land masses, but was peppered by a number of continuous intervisible islands. This meant that movement from Sunda to Sahul required the use of water craft, but did not necessitate long or arduous seafaring journeys. Even with the later rising of sea levels and the breaking of these land masses into smaller islands, this "voyaging corridor" region provided an area of relatively smooth waters where navigational skill and sailing technology could be refined within the range of closely dispersed islands (Irwin 1992). With this, humans were able to initiate settlement of Near Oceania 42,000 to 60,000 years ago, where the earliest archaeological evidence of human activity in the Pacific was recovered (Groube et al 1986). By 28,000 to 35,000 BP, people had moved through Sahul and out to the Bismarck Archipelago and northern Solomon Islands. Occupation of Manus Island dates to 13,000BP (Frederickson et al 1993). This great time depth allowed for a high degree of linguistic, biological, and cultural diversity to accumulate in the area as movements occurred. Around 31,000 BP, sailing technology advanced to the point where humans were able to successfully breach the much wider waterway between the Solomon Islands and the

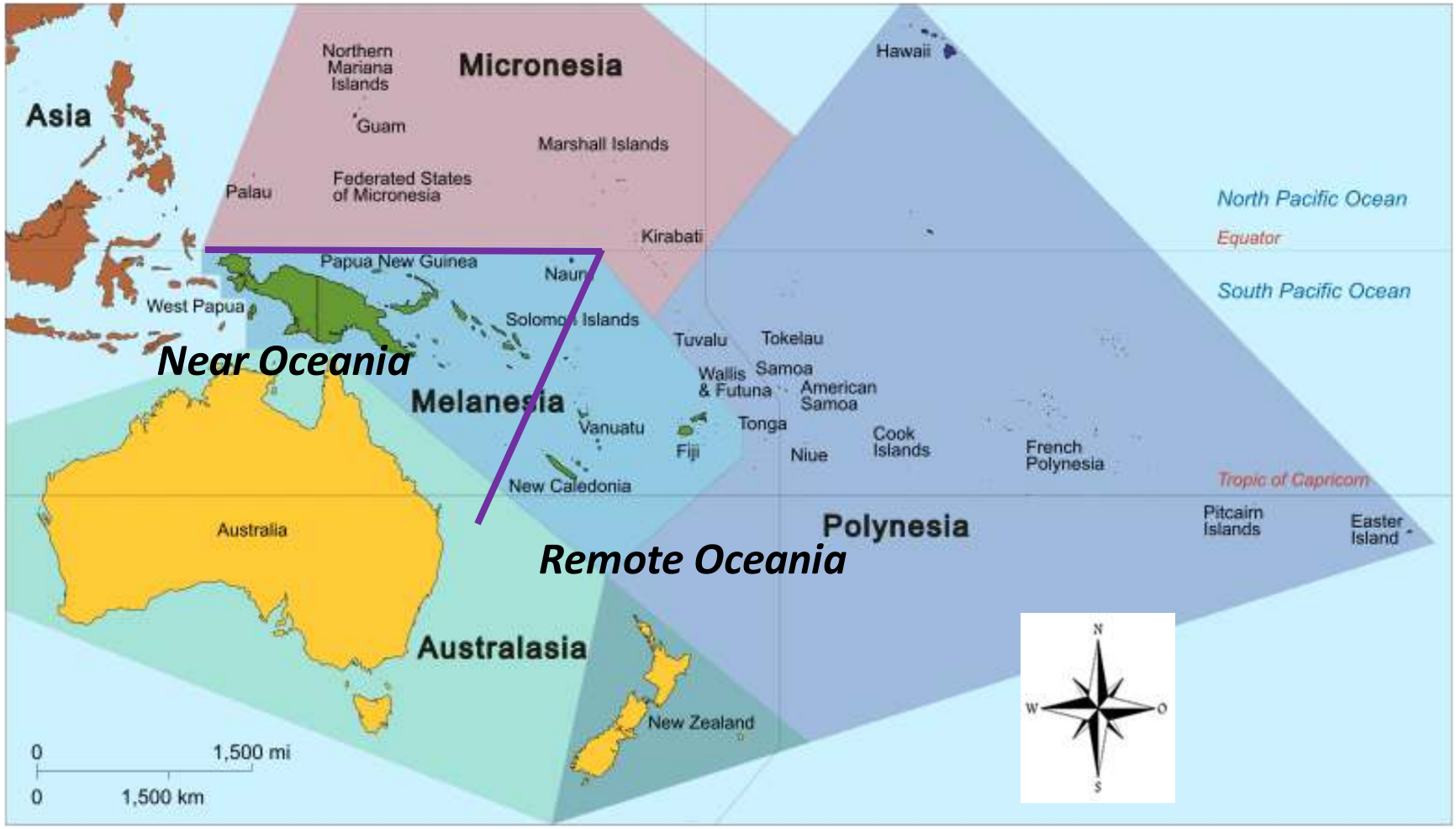

Figure 1: Map of Oceania. The purple line separates the regions of Near and Remote Oceania. *Source: https://upload.wikimedia.org/wikipedia/commons/thumb/5/54/Oceania_UN_Geoscheme_Regions.svg/800px-Oceania_UN_Geoscheme_Regions.svg.png*

arc of the Reef/Santa Cruz Islands, Vanuatu, and New Caledonia to begin colonizing Remote Oceania. The first archaeological evidence of occupation in this area is associated with the Lapita Cultural Complex, first appearing in the Bismarcks around 3500 BP. This suite of artifacts represents a distinct interruption in the archaeological record, and is comprised of unique dentate-stamped and red-slip decorated pottery as well as evidence of a village settlement pattern and a Neolithic subsistence economy encompassing a large range of plants and domesticated animals (Kirch 1997).

A number of competing theories debate the timeline of events associated with the Lapita intrusion, as well as the origins of this cultural complex. The Express Train to Polynesia model posits a rapid dispersal from Southeast Asia, particularly Taiwan, through Melanesia and into Polynesia with little to no interaction or admixture with indigenous populations along the way (Bellwood 1978, Diamond 1988, Blust 1999, Pawley and Ross 1993). The contrasting theory, known as the Slow Boat to the Bismarcks model, suggests that interactions did occur within the "voyaging nursery" region from 6000-3500 BP, allowing for ample admixture, before a sudden expansion into Remote Oceania around 3100BP (Hagelberg 1999, Kayser et al 2000, Underhill et al 2001). Green's (2003) Triple I model, along with Terrell's (1986) Entangled Bank, builds on this idea, explaining the appearance of Lapita as a complex combination of various processes, including the intrusion of new gene flow and cultural ideas, integration of these from the indigenous inhabitants of Melanesia, and the innovation of novel elements. Finally, the Bismarck Archipelago Indigenous Inhabitants model (Allen 1984) discounts any major migration as the source of Lapita, but instead claims that the culture was an indigenous development that occurred without any input from Southeast Asia.

Linguistic evidence, of which development is assumed to bear resemblance to biological development during migration, reveals a high level of diversity in the Papuan language family of the indigenous inhabitants of Near Oceania. This family, which includes the 12 very distinct language groups of the indigenous inhabitants of Near Oceania, reveals the great time depth of human occupation in the area. The arrival of Austronesian languages, specifically the Oceanic subgroup, is closely associated with the appearance of the Lapita Cultural Complex in Near Oceania. The Malayo-Polynesian subfamily of Austronesian is widely spoken from Madagascar to Easter Island, as well as throughout Southeast Asia, while the other nine Austronesian subfamilies are spoken exclusively by Taiwanese aboriginals. This suggests Taiwan as the homeland for the Austronesian language dispersal, and a rapid and stepwise spread of Malayo-Polynesian languages into Polynesia, via the Express Train model. Additionally, all Polynesian languages appear to be closely related and trace back to the Proto-Central-Pacific subgroup of Oceanic languages spoken by the original Lapita settlers of Fiji, Tonga, and Samoa (Kirch 2000, Kirch and Green 2001).

Once humans crossed into Near Oceania around 3200 to 2900 BP, colonization proceeded rapidly though Vanuatu at 3050 to 2950 BP, south to the Loyalty Islands and New Caledonia, and east across 1000 kilometers of relatively open water to Fiji, Tonga, and Samoa by 3000 AD (Anderson and Clark 1999, Green et al 2008). At this point, a 500-1000 year hiatus occurred during which long-distance exploration was halted to focus on improving technology of double-hulled outrigger canoes, horticultural production systems, and the transport of crop plants and domestic animals in order to facilitate expansion into the Polynesian triangle. Along with sweeping cultural innovations, this lengthy pause, along with a bottlenecking of the founder population once exploration resumed, resulted in a relative genetic homogeneity in Polynesian

settlers detectable to the present (Flint et al 1989, Martinson et al 1993, Harding and Clegg 1996). Beginning in the first millennia AD, purposeful exploratory voyages led to the swift settlement of the Cook Islands, Austral Islands, Mangreva, and Easter Island between 800 and 1000 AD, Hawaii by 800 AD, New Zealand by 1250-1300 AD, and Chatham Islands by 1500 AD (Kirch 1995, Athens 1997, Green and Wiesler 2002, Hogg et al 2003).

While the archaeology of Micronesia is less well known than that of Melanesia and Polynesia, the earliest dates for occupation in this region come from the Marianas Island chain around the same time as Lapita in the south but do not seem to be related. Explanations for this appearance include possible intrusion of an ancestral tradition from the Philippines or Southeast Asia or as a northern arm of a later Lapita expansion from the south (Kirch 1997, Kirch 2000). Linguistically, western Micronesia shares many traits with the Polynesian and Western-Malayo-Polynesia subgroup of Austronesian, which is more closely related to the languages of the Philippines and Indonesia, while the proto-Oceanic languages of the Caroline Islands, Marshall Islands, and Kiribati belong to a distinct Nuclear Micronesia subgroup (Bender and Wang 1985). This evidence supports a three-part sequence for the peopling of Micronesia: an expansion of Western-Malayo-Polynesian speakers in Palau and the Marianas Islands from island Southeast Asia; a northern extension of Lapita to the Caroline Islands from the Solomon Islands and Vanuatu linked to sea level changes that prevented colonization until 1AD; and settlement of Yap directly from the Bismarck Archipelago plus later contact with west and east islands (Ross 1996). Additionally, later westward backtracking to Melanesia, including Vanuatu, New Caledonia, and the Solomon Islands, occurred following initial migration into Micronesia (Kirch 2010).

Recent advances in ancient DNA recovery and genetic analysis has provided a bounty of information about the origins of Pacific Island populations and given clearer insights into the speed and level of interaction associated with dispersal throughout the region. Two specific traits in the mitochondrial genome have offered valuable information: a lineage characterized by a deletion of a 9 basepair repeat in the COII/tRNA intergenic region and a suite of three transition substitutions in the control region, known collectively as the Polynesian motif and occurring in 90-95% of Polynesian mtDNA (Melton et al 1998, Redd et al 1995, Skyes 1995). Presence of the deletion ranges from Madagascar to Easter Island, but is not found in the New Guinea highlands or Australia, and haplotype diversity decreases from Taiwan eastward into Indonesia, the Philippines, and Remote Oceania, suggesting an origin in East Asia and the occurrence of several bottleneck events during colonization (Skyes 1995, Betty et al 1996). Frequency of the deletion plus the motif is highest in east Polynesia and is also present in the Bismarck Archipelago, coastal New Guinea, the Solomon Islands, and central and eastern Micronesia, but is not found in Taiwan or the Philippines (Figure 2).

Figure 2: Distribution of mitochondrial DNA haplotype lineages in Oceania. From Kayser et al 2006.

This distribution, plus an estimated coalescence date of 9300 years ago, suggests that the full motif was present in Near Oceania prior to Lapita. Its immediate ancestral haplogroup has a similarly wide distribution but includes Taiwan, the Philippines, and China in addition to Indonesia, coastal New Guinea, and Remote Oceania, and has an earlier coalescence date of 13,000 years ago. This places its origins in Asia, and evidences a series of successive founder effects occurring during a swift expansion through Melanesia and into Polynesia as per the "Express Train Model", resulting in a relatively homogenous haplotype diversity in Remote Oceania (Sykes et al 1995, Oppenheimer and Richards 2001, Matisoo-Smith 2007).

The most common mtDNA lineages in Micronesia possess the deletion and 2 to 3 of the mutations associated with the motif, but also possess unique point mutations not associated with

those found in Polynesia. In the Marianas Islands, there is a low frequency of the Polynesian motif, differing from other Micronesian populations and consistent with settlement from the Philipines and Taiwan. Yap and Palau mtDNA genomes also suggest more direct interaction and gene flow with Southeast Asia and Near Oceania (Kirch 2000, Lum and Cann 2000).

While materally-inherited mtDNA in Polynesia is dominated by island Southeast Asian markers, the paternally-inherited Y chromosome tells a different story, suggesting ample admixture and input from indigenous populations as per the Slow Boat Model (Su et al 2000, Kayser et al 2000, Underhill et al 2001, Hurles et al 2002). Of the three main Y-haplotypes observed in Polynesia, the dominant one, DYS 390.3del/RPS4Y711T, decreases in frequency from mid-Polynesia to island Southeast Asia and is not seen in Southeast Asian or mainland Asian populations, suggesting its origin in Melanesia (Hagelberg et al 1999, Kayser et al 2000). The second haplotype, M122C/M9G, increases in frequency in this direction, pointing to a probable Asian origin and indicating that ancestors of modern-day Polynesians moved slowly through Melanesia, allowing for ample admixture (Kayser et al 2000) (Figure 3).

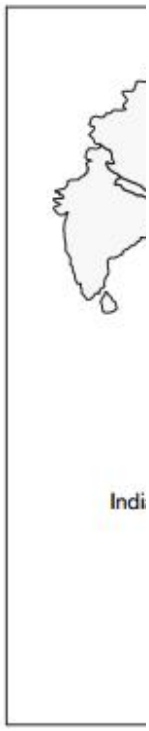

Figure 3: Distribution of Y-chromosome haplotype lineages in Oceania. From Kayser et al 2000.

The extensive voyaging and exchange networks of the Lapita, a maritime horticulturist people, would have easily facilitated such interactions (Hage and Marck 2003). Su et al (2000) failed to identify a Melanesian-specific haplotype in their Polynesian sample of Y-chromosome polymorphism distributions, yet observed all Polynesian, Micronesian and Taiwanese haplotypes in extant Southeast Asian populations, but no Taiwanese haplotypes in Micronesia or Polynesia. They postulated from this evidence that Southeast Asia was the genetic origin site for two independent migrations toward Taiwan and toward Polynesia through island Southeast Asia. Underhill et al (2001) showed that half of Maori and Polynesia males possessed the DYS390.3del, following Kayser et al (2000) as evidence of a Melanesian ancestry, but also found that the 9-basepair deletion of the mtDNA Polynesian motif present in 85% of Maori samples. Hurles et al (2002) observed from a combination of binary, microsatellite, and

minisatellite markers that most Micronesian and Polynesia Y-chromosome appear to originate from different source populations within Melanesia and eastern Indonesia.

It is clear that there is disagreement between the relatively constant higher haplotype diversity in the paternally-transmitted Y-chromosome and the gradual reduction in maternally-inherited mtDNA diversity observed west to east in the Pacific (Hagelberg 1999). Additionally, there is contrast between the predominance of Asian-derived mtDNA and the high frequency of Y-chromosome lineages of a Melanesian origin in Polynesian DNA (Hage and Marck 2003). Such a striking difference suggests an admixture bias toward Melanesian males, which could possibly be accounted for by a sex-differential migration pattern, the result of matrilocal residency and matrilineal descent in Lapita societies, resulting in more admixture of Asian migrants with Melanesian males than females (Hagelberg 1999, Hage and Marck 2003, Kayser et al 2006).

2.2. Post-marital residence pattern

Though post-marital residency manifests in a number of complex ways, the two unilocal patterns most commonly identified in the ethnographic literature are patrilocal residence, in which a married couple lives with the kin group or in the village of the husband, and matrilocal residence, where they reside with the wife's family or villages. Additionally, in societies practicing bilocal residence, couples live with either the male's or female's family, either by choice or necessity (Service 1962, Ember, Ember, and Peregrine 2007). Of the cultures studied worldwide to date, it has been reported that 50-70% are patrilocal, with the female migration rate eight times that of males (Divale 1974, Murdock 1967, Levinson and Malone 1980, Murdock 1981, Burton et al 1996, Seielstad et al 1998).

Agricultural societies are overwhelmingly patrilocal, likely due to a bias in favor of male land inheritance that leads to a tendency of males to reside where they are born (Wilkins and Marlowe 2006). This is observed in the archaeological record and ancient DNA, with reduction in male migration and an increase in female migration coinciding with the spread of agriculture (Linton 1936, Murdock 1949). Forager societies, however, tend to show a more balanced pattern of marital residence, with males performing bride-service during which they reside with the wife's kin early in the marriage, while the couple lives with the husband's kin later in life, or they change residencies seasonally or year-to-year, in ways that may or may not be influenced by the presence of kin (Marlowe 2004). Additionally, mobile forager societies do not grow crops or accumulate wealth, so there is not bias within these groups toward male inheritance or patrilocality (Marlowe 2000). In maritime societies in which subsistence and travel is water-dependent, males primarily are the ones taking to the waters (Walker and Hollimon 1989). During the Oceanic expansion, this also meant long-term exploratory voyages that resulted in extended absences of males from societies, leaving most day-to-day tasks within villages to females. Depending on the length of this absence, an increasingly matricentric orientation in the societies of such villages gave way to matrilocal residence pattern that would have profound genetic influence (Hage and Marck 2003).

While post-marital residence does not exclusively determine the manner of lineal descent or inheritance within a society, the two factors often coincide so that membership is often traced through the line of the non-migratory sex (Murdock 1967). In Murdock's (1949) "classic theory of kinship", social organization proceeds from changes in residence rules, which proceed from changes in descent rules resulting from changes in kinship terminology. Additionally, while residency often determines kin group membership, genetic patterns are more heavily influenced

by social norms regarding dispersal and individuals, rather than more abstract concepts of association and inheritance (Jordan et al 2009).

A variety of factors influence the manifestation of post-marital residence, including sexual division of labor, subsistence economy, and instance of warfare. Elements of social organization, such as residency, reflect the economic, social, and cultural conditions of a society; when changes in these underlying factors occur, residence patterns tend to be modified accordingly to accommodate the sex ratio or the relative importance of the societal contributions of each sex (Tomczak and Powell 2003). Additionally, individual cultures can perform multiple types of residence patterns, or shift their reliance on a certain type according to the varying needs of the population over time (Allen and Richardson 1971). In times of instability, such as depopulation or warfare, adopting an ambilocal residence pattern maximizes the benefit of living with and pooling the resources of consanguinal relations on either side (Service 1962).

Ember and Ember (1971) and Divale (1974) provide a model to predict whether residence is matrilocal or patrilocal in a society based on the type of warfare practiced (Figure 4). Where periodic internal warfare between neighboring communities is commonplace, patrilocality is favored because it keeps sons at home to provide a loyal and quickly mobilized fighting force in case of sudden attack. When warfare is primarily external with other more distant groups, having a reserve army is of less concern, and matrilocality tends to take over, especially when women do a majority of the primary subsistence work and are an asset to keep near home (Ember and Ember 1971, Divale 1974).

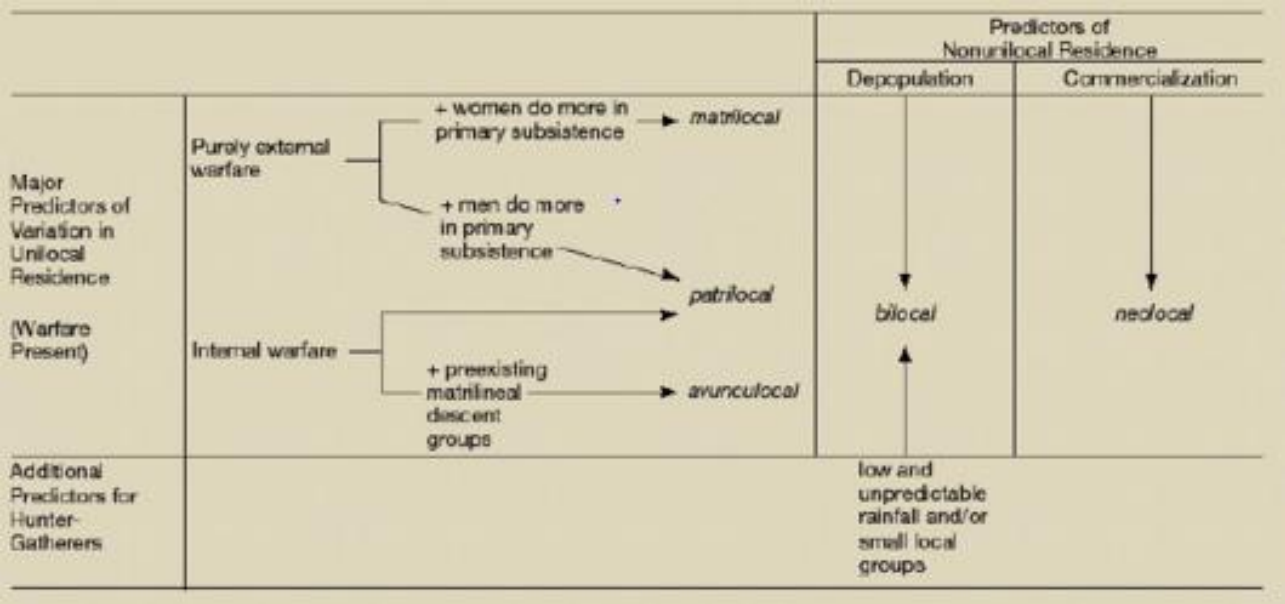

Figure 4: The main predictors of marital residence pattern. From Ember and Ember 1983.

Reconstructing post-marital residence patterns, whether through ethnographic, archaeological, by biological lines of evidence, provides insights into the social and economic relationships within a population. While the more variable rate of reproductive success in males favors patrilineal inheritance and leads to patrilocality as the default for most populations when the sex ratio is relatively even, when males are absent females tend to move into positions of dominance within the division of labor and become more significant in the subsistence economy (Helms 2004, Ember, Ember and Peregrine 2007). Conditions of prolonged male absence due to warfare, long-term voyaging, trade, or resource exploitation leaves an excess of females in the population, which will rely more heavily on females for management of common corporate interests and give way to a matricentric orientation in lineality and locality (Harris 1980, Harris 1985, Hart 2001). This allows for domestic life to continue without interruption when the sex ratio is skewed towards females. Ember and Ember (1971), however, do not cite a clear

relationship between postmarital residence and subsistence. A stronger relationship is thought to exist between migration, depopulation, and residence, matrilocality in particular. As societies expand into new areas, matrilocality is favored because it separates genetically-related males, or "fraternal interest groups", and thus minimizing internal warfare (Divale 1974). Levi-Strauss (1984) claims that matrilocality is apt to disappear when societies become isolated due to their inherent instabilities, resulting from conflicts between men over the control of their own and their sisters' children. Proto-Oceanic Lapita societies exemplified a set of such factors, evidenced through linguistic, archaeological, and genetic lines of evidence. Early Pacific settlers were a sophisticated maritime and horticultural society at the time of initial expansion through Near and Remote Oceania, beginning in the Bismarck Archipelago in 1500 BC (Kirch 2000). These people took part in an extensive network of voyaging and exchange, in which males, who were the primary facilitators of exploration and trade, were often absent from their kin groups for these purposes. The unimportance of paternity within the lexicon of Proto-Oceanic languages is also thought to evidence matricentric orientiation (Hage and Harary, 1996).

Attempts to draw conclusions about residence based on artifact evidence have been mixed. Ember (1973) suggests that living floor area can be used to infer matrilocal versus patrilocal residence from conventional archaeological materials. Where the floor of the average house is greater than 600 square feet, residence is like to have been matrilocal, while patrilocality is assumed when floor space is smaller. The reasoning behind this model is Ember's assumption that sisters find it easier to live together than non-sisters if they are married to different men as in a matrilocal society, so groups of two or more married women living together would be commonplace and necessitate a larger house (1973). However, literature concerning living floor size in Oceanic, specifically Lapita, settlements describes structure size as less than 100 square

feet in size, and occupation of small caves as an often utilized option (Sheppard and Green 1991, Gathergole 2001, Nunn et al 2007). Allen and Richardson (1971) suggest that in matrilocal communities, "pottery and other items of material culture manufactured by female artisans would exhibit a nonrandom clustering of stylistic attributes" as a result of combinations of attributes being passed through the female line (pg 3). Marshall (1985) has described distinct sex differences in Lapita pottery design specifically, including simple motifs and tool kits for women that are distributed coastally, and complex elaboration requiring extensive tool kits for men that are distributed sporadically inland. However, Allen and Richardson (1971) also criticize the attempt to infer kinship and sexual division of labor based on assumedly sex-specific artifacts types, citing the many assumptions about adherence to design frameworks and the discrepancy between residence rules and actual practice as too speculative.

Relative levels of genetic diversity between males and females, examined either through the genes directly or through the frequency and distribution of phenotypic traits, can provide evidence for possible post-marital residency in a society, especially when ethnographic data is lacking. Spence noted in 1974:

> "Practices of marriage, descent, and residence act to channel people in consistent and non-random ways within a society, and so may be expected to have an effect upon the distribution of traits. Consequently irregularities in these distributions should reflect, and thus permit identification of, the features of social organization underlying them." (pg 265)

Nonetheless, the possibility of a lack of adherence to proscribed residence rules can make assumptions about residency erroneous if cultural norms and actual residence in practice do not correspond, even when utilizing a biological line of evidence, as per Allen and Richardson's

argument (1971). However, when ethnographic accounts are limited or absent, relative genetic diversities can provide a starting point for investigation of residency or other aspects of paleodemography, or can be utilized to demonstrate such discrepancies when used in conjunction with available ethnographic data.

Because the typical distance between the birthplace of the non-mobile sex and their offspring is smaller than that of the migratory sex and their respective offspring, over many generations of maintaining a matrilocal or patrilocal residency pattern in a given society, systematic changes in genetic diversity occur (Seielstad et al 1998, Pérez-Lezaun et al 1999, Jorde et al 2000, Wilkens and Marlowe 2006). In matrilocal societies, a high level of male Y-chromosome haplotype diversity and a low level of female mtDNA diversity occurs within groups, while between groups a higher level of mtDNA diversity and lower level of Y-chromosome diversity is observed. The opposite pattern is true of patrilocal populations. When utilizing variation in phenotypic traits, such as skeletal or dental morphology, as a proxy for genetic diversity, the same pattern holds: the more mobile sex, representing those who married into the group, will exhibit a higher within-groups variance and lower between-groups variance in trait frequency or measure, while the less mobile sex, representing those with whose family the couple resides, will have a lower within-groups variance and higher between-groups variance (Lane and Sublett 1972, Spence 1974, Konigsberg 1988, Konigsberg and Buikstra 1995).

This pattern is consistent with the observed haplotype diversity in Oceania. An expanding group with strong matrilineality and matrilocality would show a restricted and geographically specific origin of mtDNA but a diverse and widespread origin of Y-chromosome and nuclear DNA (Hage and Marck 2003, Hurles 2002). In a matrililocal society, wherein females are bringing in males from outside localities to marry, reside, and interbreed with, over

time females within-groups tend to become more genetically similarity to each other while becoming more distinct from females in other populations. Since males from unrelated outside groups are migrating to the females' villages, over several generations this will result in males that are more distinct from each other within each group, but relatively homogenous overall. Gene flow is restricted between populations for females, since they remain in the village of their birth, while occurring amply between populations for males, who actively migrate. In Polynesian lineages, the predominance of maternally-transmitted mtDNA of Asian origin, consistent with the Express Train model of rapid movement and limited admixture during colonization (Diamond 1988, Sykes et al 1995, Melton et al 2001), and paternally-transmitted Y-chromosome haplotypes of Melanesian origin, consistent with the Slow Boat model of ample interaction and admixture as settlers migrated (Hagelberg 1999, Kayser et al 2000, Underhill et al 2001), suggests a framework of matrilocality in Proto-Oceanic Lapita (Hage and Marck 2003, Hurles 2002, Kayser et al 2008).

The large discrepancy in Asian and Melanesian contributions to Polynesian haplotype diversity for mtDNA and Y-chromosomes likely exists as a remnant of a matrilocal post-marital residence pattern in Proto-Oceanic Lapita societies, stimulated by a prolonged male absence due to regular long-distance voyaging during expansion and resulting in sex-differential migration tendencies (Hage and Marck 2003, Kayser et al 2008). With the demise of these prolonged exploratory voyages as people became settled and consequently isolated, matrilocality and matrilineality likely waned and gave way to an ambilocal to patrilocal pattern with an occasionally matricentric orientation (Hage and Marck 2002, Hage and Marck 2003, Jordan et al 2009). This may also be true of the "pauses" in expansion that occurred prior to entry into the Philippines 4000-4500BP and prior to Remote Oceanic dispersal in 3500BP associated with the

Lapita Cultural Complex, in which patrilocality was repeatedly adopted as Austronesian-speakers moved across the Pacific (Diamond and Bellwood 2003, Green 2003, Hage and Marck 2003, Gray et al 2009, Jordan et al 2009).

2.3. Biodistance and investigation of social organization through skeletal remains

While variation in material culture may reveal elements that elucidate possible residence patterns or demography of a society, such variation may also result from interaction, exchange, and assimilation of populations that often coincide with genetic admixture (Parkington 1998, Tomczak and Powell 2003). Archaeological studies of residence pattern have focused on sex-specific artifact style and house size or form. Though longer, larger houses have been positively correlated with matrilocal societies, stylistic features and manufacture style of artifacts provide little more than an arbitrary relationship (Allen and Richardson 1971, Ember 1973, Hollinger 1995). Thus, human biological evidence, including skeletal and dental as well as biomolecular materials, provide the most direct confirmation of population variation, movement, and differences between sexes through inference from comparative within-sex intrasite variation in genetics and morphology and relative mobility of the sexes based on comparative biodistance (Lane and Sublett 1972, Konigsberg 1988, Parkington 1998, Schillaci and Stojanowski 2003). This is especially crucial when ethnographic accounts of social organization and behavior are unavailable. Additionally, investigating biological variation within a population genetics framework provides insight into biological relationships within as well as between populations (Hanihara 1992, 2005, 2008, Irish 1997, 1998, 2006, Neves et al 1999, Irish and Guatelli-Steinberg 2003, Sutter 2004, 2005) . Heritable morphological traits, including metric and non-metric characteristics of the skeleton and dentition, can also serve as a proxy for genetic

composition when biomolecular elements are not available or compromised by contamination or degradation, which remains a significant factor in ancient DNA analysis (Williams-Blangero and Blangero 1990, Hofreiter et al 2001, Pääbo et al 2004, Barnes 2015).

Biological distance, or biodistance, is a measure of the relatedness among human groups that are separated temporally or geographically in order to reconstruct population history, assess ancestry, or elucidate social organization (Buikstra et al 1990, Larsen 1997, Larsen 2002, Pietrusewsky 2014). Studies in biodistance rely on morphological variation or heritable physical traits as a proxy for variation in the underlying genetics responsible for their expression. Assuming that the phenotype is an accurate representation of the genotype, individuals that exhibit similar morphological characteristics, or are comparable in size and shape of physical traits, are assumed to share more genetic material in common with each other, and are thus more closely related than those who do not share these traits. The more closely related the individuals, the closer in time they shared a common ancestor, and the shorter the amount of time that they have been geographically or temporally, thus reproductively, isolated from each other, according to the assumption of isolation by distance (Wright 1943). Under this framework, measures of biodistance can be utilized to assess several facets of population history, including routes of migration, levels of admixture between various groups, or differential gene flow between sexes or other groups. Depending on the amount of a priori knowledge about the individuals and groups being assessed, factors such as social status, paternity or fecundity, and social organization can be examined in finer detail to investigate the interplay between culture and mating behaviors in a group.

Studies in biodistance assess the amount of variation present both within a defined group as well as between many such groups. The greater the number of generations that a group has

been endogamously mating with other members of its group, the more homogenous the variation in this group will be. Continued endogamy will cause this group to become increasing dissimilar with other groups with which it is not in networks of gene flow with, thus increasing variation between these groups. On the other hand, where exogamous mating, or mating with individuals outside of one's native group, is common, networks of gene flow between these groups are opened, and over time these groups will become increasingly similar to each other as variation between them decreases. This logic underlies the concept of tracking past migrations of human populations.

There are a number of ways of quantifying variation in studies of biodistance, but in studies of skeletal and dental morphology, two methods in particular, Smith's Mean Measure of Divergence and Mahalanobis distance have become the standards for describing distance from nominal and metric data, respectively. The Mean Measure of Divergence (MMD) is a dissimilarity measure – lower values indicate samples that are more similar, while higher values indicate greater phenetic distance between them (Edgar 2004, Harris and Sjøvold 2004, Irish 2010). This method has been used since the 1960's, and has since become the standard statistical technique for assessing biological affinities from dental morphological characteristics (Scott and Turner 1997, Edgar 2004). MMD was originally developed by C.A.B. Smith for use by M.S. Grewal (1962) in estimation of biological divergences across generations of sublines of the C57BL strain of laboratory mice based on 27 nonmetric skeletal traits. Berry and Berry (1967) were the first to apply the technique to assessment of human biological affinity in an examination of 30 nonmetric cranial traits in eight cranial samples. Since their original anthropological application, MMD has been popularized both in assessment of nonmetric cranial and dental traits in human groups for reconstruction of population movement and structure over

temporal and geographic space, and more recently in such analyses using frequencies of non-metric dental morphological characteristics (Berry Berry 1972, Berry 1974, Greene 1982, Turner 1984, Turner 1985, Turner 1986, Turner 1987, Irish and Turner 1990, Irish 1998a, Irish 1998b, Sciuli 1998, Donlon 2000, Hanihara et al 2003, Edgar 2004, Hallgrimsson et al 2004, Irish 2005, Sutter and Verano 2007).

There have been several variations of Smith's original formula published in attempts to improve or alter its performance, as well as several criticisms of these alterations (Harris and Sjøvold 2004, Irish 2010, Nikita 2015), but the basic formula that is most often utilized and agreed upon in anthropological applications is the following, first published by Constandse-Westermann (1972):

$$\text{MMD} = \frac{\sum_{k=1}^{r} (\theta_{ik} - \theta_{jk})^2 - (\frac{1}{n_{ik}} + \frac{1}{n_{jk}})}{r}$$

where the difference between samples *i* and *j* for the frequencies of trait *k* is squared (so that positive and negative differences do not cancel each other out), and the sum of the differences is divided by *r*, or the number of traits used in the equation, in order to generate an average difference between samples *i* and *j*. The correction term (second parenthetical term in the numerator) accounts for sampling fluctuations and is placed in the numerator in order to apply to each variable (samples sizes for *k*th trait will vary from trait to trait based on observability in the sample), not just to the summary value, as in Smith's original equation (Grewal 1962, Berry and Berry 1967, Harris and Sjøvold 2004).

There are several advantages of this statistic that make it suitable for use in studies of non-metric morphological traits, notably those that are scored on presence/absence. First, it is devised to deal with summaries of samples expressed as trait frequencies, so that dichotomous

data can be utilized. Data that is scored on an ordinal scale is converted to binary data scored on breakpoints, and separate matrices of the proportions of trait presence in the sample and trait frequencies per sample are the input data (Edgar 2004, Harris and Sjøvold 2004, Soltysiak 2011). Second, because it employs a summary score, incomplete specimens can be included in which not all traits are observed on all individuals, which is very often in the case in archaeological skeletal or dental samples (Irish 2010). Third, it can work with small sample sizes of less than 20 observations, which, again, is a common plight in fragmentary archaeological samples (Edgar 2004). Finally, MMD is fairly easy to compute, comparable among researchers, and intuitively interpretable as a measure a biological distance (Edgar 2004).

However, there also exist drawbacks. MMD can only be accurately applied when traits are independent, as intertrait correlations within group will falsely inflate its distance from other groups being analyzed, since they share the same informational content. A tetrachoric correlation matrix must be computer in order to identify correlated traits, which are subsequently eliminated from analysis. Use of frequencies for both of a set of correlated traits overloads the formula with statistically redundant information and should be removed prior to calculating MMD (Edgar 2004, Harris and Sjøvold 2004, Irish 2010, Nikita 2015). However, Constandese and Westermann (1972) claim that if the same suite of traits is utilized for all pairwise comparisons, insofar as such correlations are a species-wide phenomenon, the effect of redundancies can be viewed as constant across the study. Trait frequencies that are put into the MMD formula need to be carefully chosen not just on the basis of independence, but should vary sufficiently among groups while still being representative of them, as traits that are non-discriminatory across samples do not contribute effective information about the ability to differentiate among them (Irish 2010). Souza and Houghton (1977) suggest that only traits with frequencies of 5-95% be

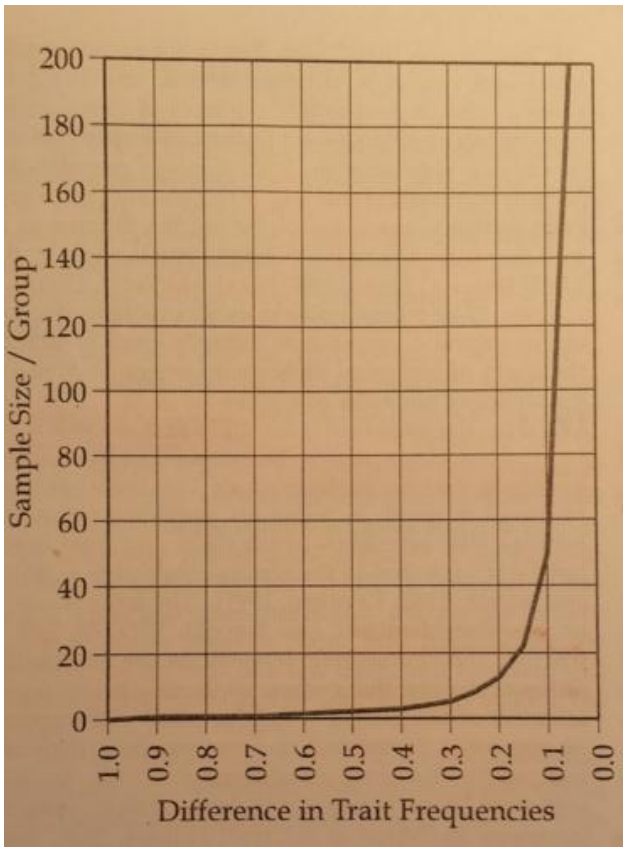

Figure 5: Graph showing where the difference in trait frequencies is equal to the correction term as a function of sample size for MMD. From Harris and Sjøvold 2004, pg. 89.

included, while other authors restrict this interval to 10-90%, and that frequencies should vary statistically significantly between at least one pair of the groups being evaluated (Tomczak and Powell 2003, Harris and Sjøvold 2004). However, MMD can handle a large number of traits commonly associated with dental morphological observation, unlike other comparable distance statistics, so the pruning of non-discriminatory traits is not thought to diminish the true level of distance represented by the MMD value (Scott and Turner 1997, Edgar 2004, Nikita 2015).

Negative MMD values are an issue in its calculation that represents "statistical artifacts" with "no biological meaning" (Irish 2010, pg 380). When sample sizes for a trait are small in one or both samples being compared, the correction term in the formula can be larger than the phenetic distance $(\Theta_{ik} - \Theta_{jk})^2$, leading to a zero or negative MMD that does not represent

similarity in trait frequencies but, rather, breakdown of the formula due to abnormally small sample size (Harris and Sjøvold 2004, Irish 2010). This relationship is shown in Figure 5, illustrating that a sample size of less than 20 will only yield a positive contribution to the MMD when trait frequencies differ by at least 15% (Harris and Sjøvold 2004). Methods suggested to deal with this issue include converting all negative MMD's to zero, raising all MMD's by the amount of the largest negative value, omitting all samples that generate negative MMD's, eliminating the correction factor from the MMD formula, or interpreting the values "as is" (Ossenberg et al 2006, Irish 2010, Nikita 2015).

Mahalanobis generalized distance was proposed by Mahalanobis in the context of his studies on Bengali anthropometrics in the mid-20th century, and has since been applied in inferences about interrelations about population origins, evolution, and relatedness that require a measure of divergence or distance between groups based on multiple variables (Mahalanobis 1930, Mahalanobis1936, Majumdar, Rao, and Mahalanobis 1958, McLachlan 1999). Because of the continuous, quantitative nature of craniometric data, Mahalanobis distance is commonly used in studies of distance based on cranial size and shape, and "remains the classic, if only realistic, measure of biological distance for analyzing metric data" (Reyment et al 1984, pg 11). Mahalanobis distance uses the squared Euclidean distance – essentially, an application of Euclidean distance to an analysis of more than two variables that takes into account the covariance structure of the data (Hammer et al 2001, Pietrusewsky 2008). It is computed by maximizing the difference between pairs of groups by maximizing the between-groups variance to the pooled within-group variance, involving an inversion of the pooled within-group variance-covariance matrix. The original variables are transformed into a new set of variables whose correlation with the remaining variables has been removed, and the resultant distance represents

the summed square difference between the transformed mean values of any two groups compared (Mahalanobis 1936, Pietrusewsky 2008). The equation is as follows:

$$d_{jk} = \sqrt{(x_j - x_k)^T S^{-1} (x_j - x_k)}$$

where *T* denotes a transposed matrix and S^{-1} denotes the inverted covariance matrix of *x* in each group. McLachlan (1999) offers the following intuitive description of the mathematical process:

There are 2 distinct populations *G1* and *G2*, *p* relevant characteristics, and *X* is a random vector that contains the characteristics measured on each individual in *G1* and *G2*. We are interested in summarizing the differences between *G1* and *G2,* with the assumption that vector *X* with *p* dimensions has the same variation about its mean within either group. The difference between the groups can be considered in terms of the difference between mean vectors of *X* in each group relative to the common within-group variation. If the variables in *X* are uncorrelated and scaled, then this corresponds to the squared Euclidean distance between the group mean vectors as a measure of difference between the groups – the presence of the inverse covariance matrix allows for the different scales on which the variables are measured and for correlations between variables (McLachlan 1999, pg 21-22).

The Mahalanobis distance possesses the properties especially useful in biodistance studies of morphological variation that it accounts for different variances in each direction, account for covariance between variables, and provides a way to measure distances that takes into account the scale of the data (Wiklin 2012). Several qualities of the measure have also been cited as both advantages and drawbacks of its utility, though they exist inevitably from the nature of the formula. First, Mahalanobis distance is useful only for variables measured on a metric scale. Koningsberg (1990) generated a version of the formula called the pseudo-Mahalanobis that allows for nominal data input, though this alteration also comes with its own set of critiques,

including its computational difficulty, need for multiple observations per individual, and limited applicability when analyzing traits with no correlation, the opposite problem encountered with MMD (Edgar 2004, Irish 2010). The need for a complete dataset for Mahalanobis and pseudo-Mahalanobis makes it inappropriate for application with datasets with missing observations, as is extremely common with dental morphological and metric studies and cranial non-metrics, though is less of an issue with craniometrics (Edgar 2004). Additionally, unlike MMD, Mahalanobis distance does not account for differences in sample sizes between populations since it utilizes z-scores as opposed to actual number of observations, which assumes that sample sizes are relatively similar among all groups being compared (Irish 2010).

In addition to extensive and thorough study of population composition and human migration patterns through DNA analysis, skeletal and dental remains have also been utilized in investigations of population structure and residence pattern. Lane and Sublett (1972) and Spence (1974) laid the groundwork for the utilization of osteological evidence in the reconstruction of residence pattern. Lane and Sublett (1972) claimed that due to the direct relationship between manifest traits and underlying biology, "to the degree that any social organizational feature corresponds to the biological referents of the kinship system, osteological data can be used to elucidate that feature" (pg 186). They developed a method to test for residence pattern that they applied to frequencies of non-metric cranial characteristics in a historic population from the Seneca reservation utilizing MMD and similarity matrices. Spence (1974) examined variance in non-metric traits of the skeleton and teeth by obtaining Triangular and Square Cumulative Similarity values as measures of within and between groups similarities in remains from a prehispanic urban center in Teotihuacán, Mexico.

Konigsberg (1987, 1988) applied a population genetics framework to the study of prehistoric postmarital residence from physical remains, providing a modified version of Wright's (1969) migration matrix method that decomposes measures of standardized genetic variance by sex. Using non-metric cranial data, he applied these components separately to assess the effect of residential patterns on the population genetic structure of males and females from several prehistoric west-central Illinois sites (1988). This method has been widely applied to both cranial (Stefan 1999, Schillaci and Stojanowski 2003, Schillaci and Stojanowski 2005, Stojanowski and Schillaci 2006, Hubbe et al 2009, Nystrom and Malcom 2010) and dental morphological data (Tomczak and Powell 2003, Cook et al 2014).

The ability to utilize the frequencies of and variance in the characteristics of physical remains as representative of the underlying genotype lies in the heritabilities of such traits, especially the size, shape, and morphological variants of the cranium and dentition. Cranial traits, including both metric measurements and non-metric trait variants, have been demonstrated to have average moderate heritabilities, allowing for genetic information to be retrieved through phenotypic traits determined to be at least partly determined by quantitative genetic loci. While the heritability and selective neutrality of cranial size and shape have been argued as justification for use of craniometrics as proxies for genetic variation (Sjøvold 1984, Devor 1987, Cheverud 1988, Sparks and Jantz 2002, Carson 2006, Sherwood et al 2008), developmental plasticity due to environmental stressors has been noted as a confounding factor in such studies (Coon et al 1950, Collard and Wood 2000, Relethford 2004, Nicholson and Harvati 2006, Harvati and Weaver 2006). Cavalli-Sforza and Bodmer (1971) caution that:

> "All anthropometric characteristics are usually genetically complex and always subject to environmental influences. Even when heritability is relatively high…it is always dangerous to use the character for comparative observations between [populations], because there can be unsuspected environmental effects." (pg 704)

The classic study in environmental modification of craniofacial morphology is Boas' 1912 study on American-born descendants of immigrants in the early 20th century. He demonstrated that the average cranial size of immigrants was significantly different than that of their descendants, and that these measures differed significantly between children born within ten years of their mother's arrival to the U.S. and those born more than ten years after (Boas, 1912). While Boas' results have been refuted and supported by physical anthropologists since publication (Sparks and Jantz 2002, Gravlee et al 2003, Jantz 2003), he did not deny the inheritance of cranial morphology, as they claim, but stated that over time differential environmental conditions, including nutritive improvement and exposure to industrialization, can act to alter their overall expression. Since then, morphological similarity between family members due to a common environment have been demonstrated (Susanne 1975, Byard et al 1985, Devor et al 1986, Kohn 1991), and Jantz himself claimed that the pattern and magnitude of craniofacial change in American blacks and whites over the past 125 years was "probably due to changes in growth of the cranial base due to improved environmental conditions" (Jantz 2001, pg 231).

Facial form, particularly nasal index and zygomatic height, have been linked to climatic adaptation, specifically in high-altitude regions with consistently low mean annual temperature (Carey and Steegman 1981, Roseman and Harpending 2004,Gonzalez-Jose et al 2005). Thermoregulatory adaptation in head shape has also been demonstrated in cranial and cephalic indices, endocranial volume, and the brain size relative to stature (Beals et al 1983, 1984). Dietary practices and differential mechanical load on masticatory muscles also influences the relative robusticity of the skull through differential development of muscle attachment sites (Hylander 1977, Wood and Lieberman 2001, Gonazlez-Jose 2005). These influences are not so

dramatic as to entirely overwhelm genetic signals of population difference, and the manifestation of cranial morphology is undeniably the result of a complex interplay between the factors of genetics and environment (Relethford 2004) – "no trait is influenced by genetics or environment alone, and no traits have heritabilities of 1.0 or 0.0" (Kohn 1991, pg 273). However, preservation of population history varies by cranial region. While the shape of the basocranium and temporal region are more genetically determined and evolutionarily conserved, the face and neurocranium are more sensitive to environment changes (Olson 1981, Harvati 2001, Havarti and Weaver 2006). Because of these post-translational modifications to the phenotype, such traits cannot be said to be directly representative of the underlying genotype.

Dental morphological characteristics, however, are the result of a highly integrated and strongly canalized developmental system (Saunders and Mayhall 1982, Scott and Turner 1997). The mechanisms guiding dental ontogeny are under tight genetic control, allowing development from formation to eruption to occur in a precise and predictable fashion. Genes control the rate, timing, and orientation of specific odontogenetic processes, including ameleoblast differentiation, formation of the enamel-dentine matrix, and mineralization, that ultimately result in the morphological phenotypes of the root and crown (Scott and Turner 1997). Because these processes initiate early in life, with formation of the deciduous dentition beginning in utero and that of the permanent dentition at 4 months of age, the form of the tooth is set early on. Additionally, teeth do not undergo continuous remodeling in response to environmental stress in the way that other bones of the body do. Although enamel hypoplasias and histological indicators of physiological perturbations can affect the appearance of enamel and dental microstructure, and play a major role in age determination and bioarchaeological analyses, non-metric traits of the cusp and root are not influenced by these processes (Scott and Turner 1988,

Powell 1995). Because of this, dental morphology provides an accurate reflection of its underlying genetic variation that is not obscured by uncontrolled environmental insults.

Early research into the mechanism of inheritance of discrete dental traits concluded that crown morphology was under simple Mendelian inheritance. Studies in the 1950's by Lasker (1950), Kraus (1951), and Tsuji (1958) found parent-offspring patterns consistence with simple autosomal codominant and dominant inheritance in shoveling, Carabelli's cusp, lower molar groove pattern, and cusp number, as well as several traits that were novel for such studies until more recently, including cusps 6 and 7, enamel extensions, and root variation. These initial findings led to the notion, exemplified by Turner (1967, 1969), that if dental trait frequencies could be reduced to gene frequencies, then population genetics models could be applied to this data in extinct and extant populations. In this model of simple dominant-recessive inheritance, absence of a trait represented a recessive homozygous genotype, while intermediate expression resulted from a heterozygous genotype and pronounced expression from a homozygous dominant one (Kraus 1951, Turner 1967, Turner 1969). These assumptions, however, required a substantial environmental influence or action of multiple loci on expression to smooth out the wide range of variation exhibited for the two genotypes for presence (Scott 2008).

Further investigations in the 1970's began to find exceptions to this model, including several instances of affected individuals resulting from crosses of unaffected parents in numbers not expected for a trait thought to be inherited as simple autosomal dominant (Goose and Lee 1971, Lee and Goose 1972, Portin and Alvesalo 1974, Hanihara 1975, Escobar et al 1976, Mizoguchi 1977). Along with the question of how to explain the wide range of variation in these traits, these results suggest that the pattern of inheritance was more multifactorial that strictly dominant-recessive. Grüneberg's (1952) model of quasicontinuous variation, originally

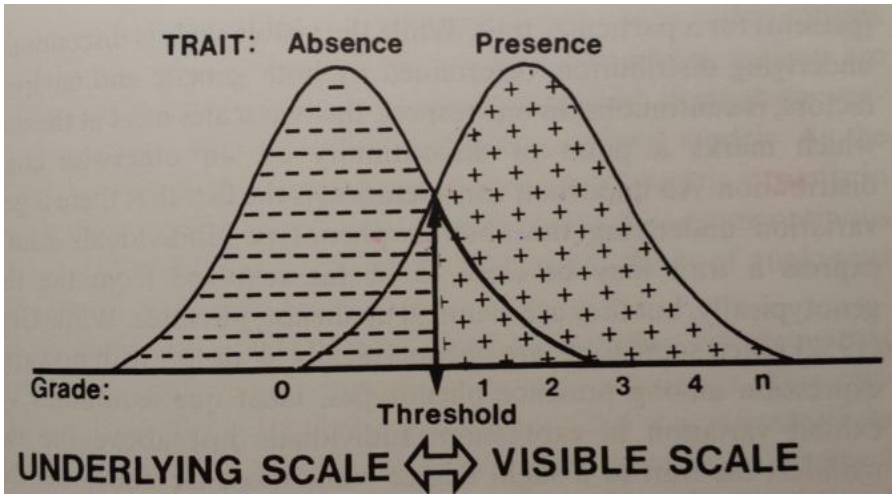

Figure 6: Model of quasicontinuous variation and threshold effect from Scott and Turner (1997). "Two overlapping normal distributions illustrate the continuous genetic basis of quasicontinuous traits. A threshold separates a visible scaling from an underlying scale. When an individual has a genotype to the right of the threshold, they present a visible phenotype that can be scored…depending on distance from the threshold. Individuals with genotypes below the threshold fail to exhibit any visible trait manifestation, but there is also genotypic variability underlying the absence phenotype depending on genotypic position relative to the threshold." (Scott and Turner 1997; pg 137).

established from large-scale breeding experiments on mice, seemed a parsimonious explanation for the nature and inheritance of dental traits. This model holds that some discontinuous traits can have continuous genotypic distributions with underlying and visible scales, manifesting as absence or presence of the trait, that are separated by a physiological threshold, so that inheritance is polygenic, with genes at multiple loci interacting to produce a final phenotype (Figure 6). Additionally, low-frequency traits have been found to follow segregation ratios more consistent with the expectations of recessive inheritance, while high-frequency traits more closely followed simple dominance patterns (Scott 1973, 1974, Scott and Turner 1997). This correlation between total trait frequency and degree of expression was further evidence for the concept of threshold dichotomies with complex modes of inheritance. Thus, characterizing populations by total trait frequencies for quasicontinuous traits, or frequencies defined by

Table 1: Heritability values for several dental morphological traits. Provided by Blanco and Chakraborty (1976), Harris (1977), Mizoguchi (1977), Townsend et al (1992, 2009), and Bockman et al (2010).

Maxillary Traits			**Mandibular Traits**		
Trait	***Tooth***	***h2***	***Trait***	***Tooth***	***h2***
Shoveling	I1, I2, C	0.3-0.9	Shoveling	I1, I2	0.3-0.9
Double shoveling	I1, I2	0.5-0.9	Congenital absence	I2, M3	0.7-0.9
Congenital absence	I2, M3	0.7-0.9	Premolar complexity	P3, P4	0.5
Tuberculum dentale	I1, I2, C	0.4-0.8	Cusp number	M1, M2, M3	0.6-0.8
Premolar accessory cusp	P3, P4	0.7	Deflecting wrinkle	M1	0.5
Tri-cusped premolar	P3, P4	0.7	Trigonid crest	M1, M2, M3	0.7
Metacone	M1, M2, M3	0.4-0.8	Protostylid	M1, M2, M3	0.5
Hypocone	M1, M2, M3	0.5-0.9	Cusp 5	M1, M2, M3	0.5
Cusp 5	M1, M2, M3	0.5-0.9	Cusp 6	M1, M2, M3	0.7
Carabelli's cusp	M1, M2, M3	0.5-0.9	Cusp 7	M1, M2, M3	0.7
Parastyle	P3	0.5			

breakpoints, captures the threshold separation point and specifies the entire continuous distribution of genotypic variation underlying variation in trait expression (Falconer 1960). Recent additional work by Townsend (2009, 2010) and Hughes and Townsend (2013) further investigated the influence of environment and epigenetics in conjunction with genetic transmission of dental morphology, adding the growing list of known heritabilities for various traits, seen in Table 1.

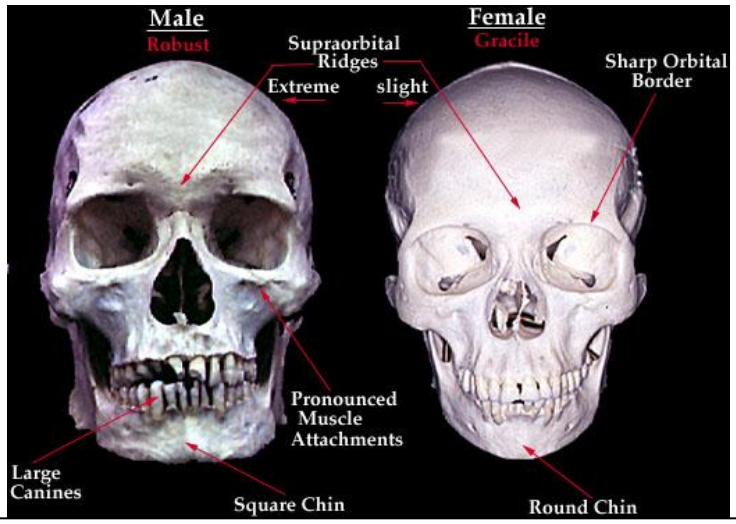

Figure 7: Male (left) versus female (right) cranial morphology and sexually dimorphic features. From Tercerie et al (2015).

Sexual dimorphism, or the difference in anatomical appearance or size between males and females of the same species, are most pronounced in soft tissue areas and tissue type ratios, with more limited and but nevertheless notable differences in the human skeleton. This difference is described mainly by size and robusticity, which begins to manifest itself most observably at the onset of puberty. Males tend up to be approximately 10% larger in body size than females, with certain skeletal dimensions exhibiting a 20% increase (White, Black, and Folkens 2012). In addition, male skeletons tend to be more robust, a term describing the general increase in pronouncement and ruggedness of muscle attachments and topography of the skeleton. Though normal individual variation results in some overlap between size and robusticity between the sexes, especially when comparing between distantly related populations, elements of the skull remain one of the most useful traits in distinguishing males from females. Not only are male crania generally larger in size, but several distinct features of the crania are more marked in males, including the nuchal crest, mastoid process, supraorbital margin, glabella region, and mental eminence (Buikstra and Ubelaker 1994) (Figure 7). Because several landmarks used in craniometric measurements are located on these sexual dimorphic features, cranial dimensions of males will tend to measure larger than features, especially those of the cranial vault.

Sexual dimorphism in the human dentition is much less pronounced than in the rest of the skeleton, although some studies have shown slight correlations reliant on sex. Crown diameters have been shown to be slightly larger in males, most markedly in the canines at 6%, possibly as an evolutionary remnant of their importance in hunting and fighting in non-human primates, and least pronounced in the premolars (Garn et al 1964, 1966). This is not surprising, as there is a high positive correlation between body size and crown size amongst primates as a whole, though

less so within living humans (Gingerich 1977, Perzigian 1981). There is also evidence of slight sexual dimorphism in some non-metric traits of the dentition as well. Females have been shown to have a higher frequency of congenital absence and a lower frequency of supernumerary teeth than males (Brook 1984). The only crown trait that shows consistent dimorphism across diverse samples is the distal accessory ridge of the maxillary and mandibular canines, though higher frequencies of maxillary incisor shoveling have been exhibited in females in certain population-specific samples, including Asia and the Pacific Islands (Harris 1980, Scott et al 1983). A link has been suggested between these differences and genes on the sex chromosomes that are involved in various aspects of dental ontogeny that manifest in formation of these features, exemplified by abnormalities of the sex chromosomes that influence crown and root morphology (Lau et al 1989). Despite these slight differences in based on sex, when such differences are exhibited, they are inconsistent among samples and low in magnitude, and have not been shown to have a wide effect over all populations (Scott and Turner 1997). Male and female data are often pooled when examining population frequencies, or can be examined separately for variation due to other factors.

2.4. Craniometrics and dental morphology

Compared to craniometric measurements, dental morphological variants are better suited for analysis of kinship and social organization for several key reasons. First, dental traits are not significantly sexually dimorphic, so differences between trait frequencies are not due to sex, but to underlying genetic variation. Second, they are selectively neutral, so their frequencies are allowed to vary via drift and give insight into relatedness between populations and individuals (Turner 1985, 1987). Third, although both cranial and dental traits are under strong genetic

control, dental morphology is highly canalized and does not respond to environmental stress through remodeling, so the relationship between genotype and phenotype is not obscured by post-translational alterations in teeth (Powell 1995, Scott and Turner 1988). For these reasons, dental trait frequencies are a more direct and accurate reflection of the underlying genotype than that of craniometric measurements, and are thus better suited for kinship analysis and studies of relatedness.

Of the more than 100 different morphological dental variants that have been recognized in the human dentition, around 40 crown and root traits have been defined, standardized, and subjected to detailed analysis in an anthropological context (Scott and Turner 1997). There is no standard battery of traits use in morphological analysis, and those that are observable vary by the condition of the remains, the method of observation (in situ, loose, in the living or dead, casts, photography, etc), or the goal of the analysis. The traits observed can be described by presence vs absence, by degree of expression, by shape, number, or angle, or as a manifestation of several types of variation.

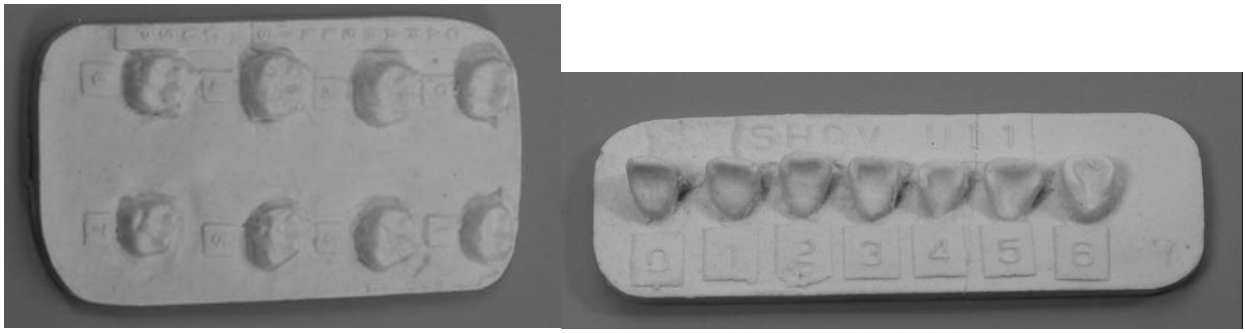

Figure 8: Examples of ASUDAS casts of graded expression for Carabelli's cusp (left) and UI1 shoveling (right).

The importance of having a standardized set of descriptions and scoring for non-metric dental traits was recognized early in dental anthropology as a field, in order to make studies of these features comparable and reproducible across different studies and researchers. With a general idea of the mode of inheritance and the mechanism of expression for these traits, the Arizona State University Dental Anthropology System (ASUDAS) was developed and published in 1991 (Turner, Nichol, and Scott 1991). This system built on the early work of Dahlberg (1956) and years of coordinated efforts among the students of Turner in the late 1970's to 1990's, resulting in observation standards, descriptions of graded expressions and scoring procedures, scoring sheets, and plaster reference plaques of 48 non-metric crown and root traits. Since its initial publication, the ASUDAS has become the worldwide standard for characterizing these traits and has allowed for greater concordance among studies of dental morphology. Recently, the Smithsonian Museum of Natural History developed a free data recording program for human skeletal material called Osteoware (Smithsonian Institution 2015). This software is modelled after both Buikstra and Ubelaker's *Standards* (1994) and the ASUDAS, and includes a dental morphology module that digitizes the trait descriptions, graded expressions, and scoring sheets of the standard ASUDAS.

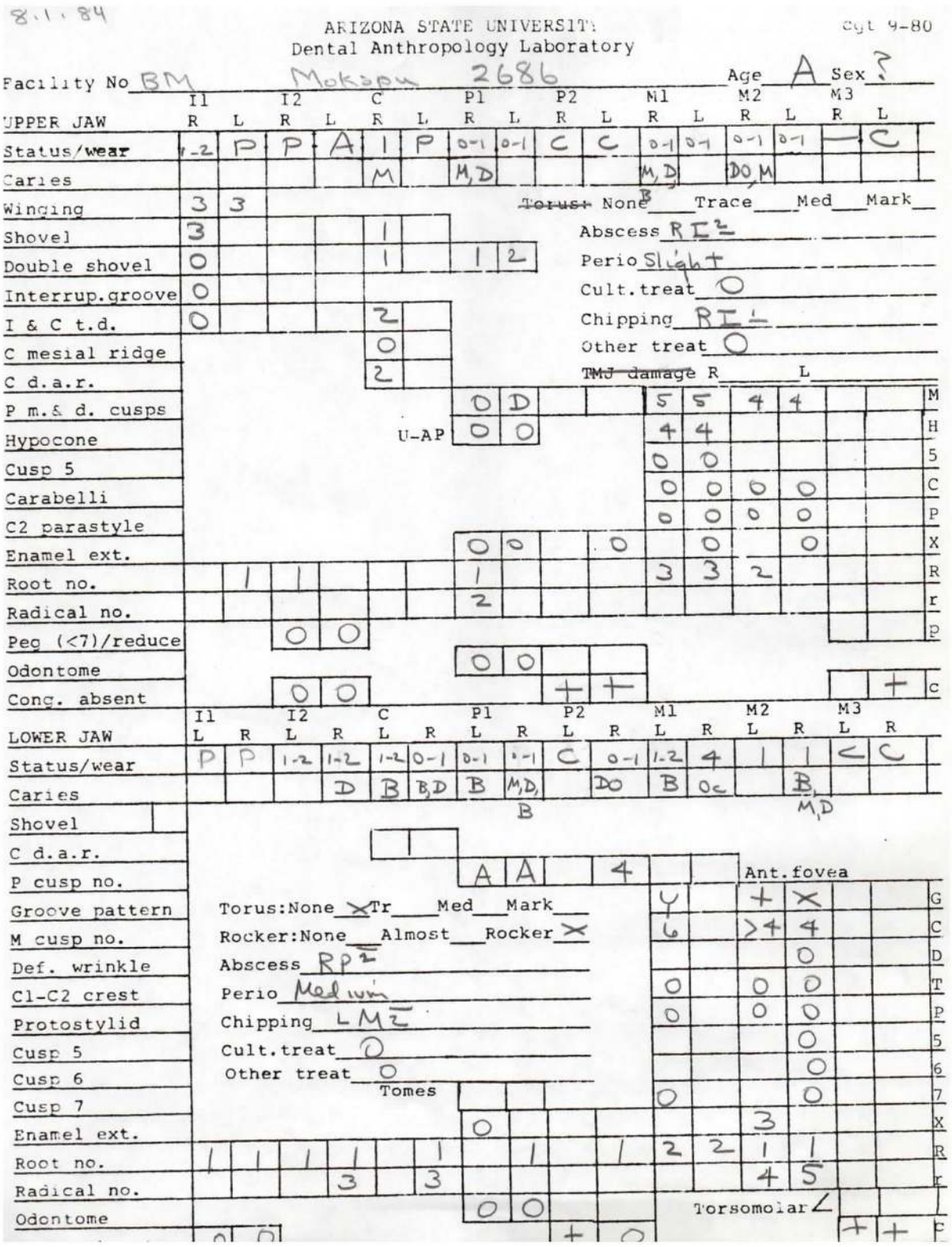

Figure 9: Example of ASUDAS score sheet. Scoring procedures and graded expression descriptions are found in Turner, Nichol and Scott (1991). From Turner data supplied by G.R. Scott.

Table 2 describes the traits analyzed in the ASUDAS. Further information on scoring procedures can be found in Turner, Nichol, and Scott (1991).

Table 2: Traits, affected teeth, and descriptions of traits analyzed in the ASUDAS (Turner, Nichol and Scott 1991).

Trait	***Affected teeth***	***Description***
Winging	UI1	Mesiolingual or distolingual rotation of one or both of the maxillary central incisors.
Shoveling	UI1, UI2, UC, LI1, LI2	Presence of lingual marginal ridges, giving the affected tooth a "shovel-like" appearance.
Labial convexity	UI1, UI2	Convexity of the labial surface when viewed from the occlusal aspect.
Double shoveling	UI1, UI2, UC, UP3, LI1, LI2	Presence of labial marginal ridges in addition to those on the lingual surface.
Interruption groove	UI1, UI2	Grooves that cross the cingulum and continue along the root. Can manifest on the either the mesiolingual or distolingual border, both borders, or in the medial area of the cingulum.
Tuberculum dentale	UI1, UI2, UC	Relief on the cingular region of the lingual surface, ranging from ridging to a cusp.
Canine mesial ridge	UC	Presence of a pronounced mesial ridge compared to the distal ridge, which can deflect distally to attach to the tuberculum dentale.
Canine distal accessory ridge	UC, LC	Ridge in the distolingual fossa between the apex and distolingual marginal ridge.
Premolar mesial and distal accessory cusps	UP3, UP4	Small accessory cusps at the mesial and/or distal ends of sagittal grooves.
Tricuspid molars/hypocone	UP3, UP4	Presence of third cusp equal in size to the normal lingual cusp.
Distosagittal ridge (Uto-Azetacan premolar)	UP3	Pronounced ridge from the apex of the buccal cusp extending to the distal occlusal border at or near the sagittal sulcus.
Metacone	UM1, UM2, UM3	Presence of distobuccal cusp (cusp 3).
Hypocone	UM1, UM2, UM3	Presence of distolingual cusp (cusp 4).
Cusp 5 (metaconule)	UM1, UM2, UM3	Presence of fifth cusp in distal fovea between metacone and hypocone.
Carabelli's cusp	UM1, UM2, UM3	Relief of the lingual surface of the mesiolingual cusp (protocone, cusp 1) ranging from a groove, pit, or Y-shaped depression to a free cusp.
Parastyle	UM1, UM2, UM3	Relief of buccal surface of mesiobuccal cusp (paracone or cusp 2) ranging from a pit to a free cusp.
Enamel extensions	UP3, UP4, UM1, UM2, UM3	Projections of enamel border in apical direction.
Premolar root number	UP3, UP4	Deviation from usual single root to 2 or 3 roots.

Upper molar root number	UM1, UM2, UM3	Variation from usual 3 roots to 1, 2, or 4 roots.
Radical number	All teeth	Developmental grooves which partition the cross-sectional area into two or more unseparated rootlike divisions.
Peg-shaped tooth	UI2, UM3	Reduction in size and loss of normal crown morphology.
Odontome	UP3, UP4, LP3, LP4	Pin-sized, spike-shaped enamel and dentin projection occurring on the premolar occlusal surface.
Congenital absence	UI2, LI1, UP4, LP4, UM3, LM3	Lack of any development of tooth, as described for adults.
Premolar lingual cusp variation	LP3, LP4	Variation in number of cusps from 1 to 3, which variable relative size of cusps.
Anterior fovea	LM1	Ridge and resulting groove on anterior occlusal surface connecting the message aspects of cusps 1 and 2.
Groove pattern	LM1, LM2, LM3	Variable contact of cusps on occlusal surface resulting in Y, +, or X-shapes grooves.
Lower molar cusp number	LM1, LM2, LM3	Variation in number of cusps from 1 to 5.
Deflecting wrinkle	LM1	Distal deflection of the medial ridge on cusp 2
Protostylid	LM1, LM2, LM3	Paramolar cusp on buccal surface of cusp 1.
Cusp 5	LM1, LM2, LM3	Presence of hypoconulid on distal occlusal aspect.
Cusp 6	LM1, LM2, LM3	Presence of entoconulid in distal fovea lingual to cusp 5.
Cusp 7	LM1, LM2, LM3	Presence of metaconulid in lingual groove between cusps 2 and 4.
Canine root number	LC	Presence of 1 or 2 roots.
Tome's root	LP3	Deep grooving of the mesial root surface, ranging from a developmental groove to two free roots.
Lower molar root number	LM1, LM2, LM3	Presence of 1 to 3 roots.
Torsomolar angle	LM3	Lingual or buccal rotation relative to line drawn through the middle of first and second molars.
Other features	***Description***	
Palatine torus	Linear exostosis along part or all of palatine suture.	
Mandibular torus	Nodular bony exostoses on lingual aspect of lower jaw in canine and premolar region.	
Rocker jaw	Curvature of the inferior surface of the horizontal ramus of the mandible.	
Tooth status	Presence/absence status and degree of attrition of all teeth.	
Caries	Presence of lesion with irregular border, discoloration, and necrotic dentin at lesion site that can easily be removed.	
Abscessing and periodontal disease	Localized or generalized alveolar bone loss correlated with soft tissue periodontal disease.	
Cultural treatment	Modification or removal of teeth (most often anterior) according to various cultural practices and customs.	
Crown chipping	Exfoliation or pressure chips in tooth crown.	

TMJ damage	Osteoarthritic damage of the articular surface of the temporomandibular joint (TMJ).
Other treatment	Any other tooth modification not listed under cultural treatment.

Like in observations of dental morphology, a standardized method of assessing cranial shape and size is imperative in order to make results comparable across different studies and observers. This is achieved through the use of craniometric measurements based on cranial landmarks, or specific sites on the cranium that serve as anchor points for a variety of these measurements. Many of these landmarks were defined by early anthropological scholars and have since been supplemented with additional points and manipulated as indices. Despite the ethical quandaries of early studies in craniometry that aimed to categorize individuals into discrete racial "types", describe their "degeneration" from a primordial type, or correlate variations in skull shape to differences in brain shape and function, such studies nonetheless generated considerable interest in research of human cranial variation that ultimately led to the development of a standardization of measurements, as well as a massive accumulation of data (Morton 1839, Nott and Gliddon 1854, Broca 1861, Blumenbach et al 1865, Coon 1962). Prior to the 1960's, single measurements or indices were usually evaluated independently, but the increasing availability and advancement of computers and multivariate statistical analysis has allowed for multiple measurements to be simultaneously examined. There are two types of landmark points: paired landmarks, which lie on either side of the midsagittal plane, and unpaired landmarks, which exist along the midsagittal plane. There are also three general types of cranial measurements based on these points: direct distances, measured from two set points on the cranium; maximum or minimum distances, which measure the chord between two arbitrary points that give the longest or shortest distance across a plane, such as maximum cranial length (abbreviated GOL); and length of a projection, such as that of the mastoid process (mastoid

length, abbreviated MDH). Additionally, volumetric measurements such as cranial capacity and curvilinear measurements can also be utilized to describe cranial size and shape.

Several software programs, including the previously described Osteoware and FORDISC (Ousley and Jantz 2005, Smithsonian Institution 2015), are available that digitize records of craniometric measurements and can make estimates of stature, sex, and ancestry using multivariate statistics such as stepwise discriminant function analysis. Table 3 describes the 82 craniometric measurements used in the Howells dataset (see *Samples* chapter), which include measurements typically utilized in craniometric analysis.

Table 3: Craniometric measurements utilized in the Howells' dataset. All measurements are described in Howells 1973, except for RFA, RPA, ROA, BSA, SBA, SLA, TBA, BRR, LAR, OSR, and BRA, which are described in Howells 1989.

Abbreviation	***Name***	***Description***
GOL	glabello-occipital length	Greatest length, from the glabellar region, in the median sagittal plane.
NOL	nasio-occipital length	Greatest cranial length in the median sagittal plane, measured from nasion.
BNL	basion-nasion length	Direct length between nasion and basion.
BBH	basion-bregma height	Distance from bregma to basion.
XCB	maximum cranial breadth	The maximum cranial breadth perpendicular to the median sagittal plane (above the supramastoid crests).
XFB	maximum frontal breadth	The maximum breadth at the coronal suture, perpendicular to the median plane.
STB	bistephanic breadth	Breadth between the intersections, on either side, of the coronal suture and the inferior temporal line.
ZYB	bizygomatic breadth	The maximum breadth across the zygomatic arches, wherever found, perpendicular to the median plane.
AUB	biauricular breadth	The least exterior breadth across the roots of the zygomatic processes, wherever found.
WCB	minimum cranial breadth	The breadth across the sphenoid at the base of the temporal fossa, at the infratemporal crests.
ASB	biasterionic breadth	Direct measurement from one asterion to the other.
BPL	basion-prosthion length	The facial length from prosthion to basion.
NPH	nasion-prosthion height	Upper facial height from nasion to prosthion.
NLH	nasal height	The average height from nasion to the lowest point on the border of the nasal aperture on either side.
OBH	orbit height (left)	The height between the upper and lower border of the left orbit, perpendicular to the lond axis of the orbit and bisecting it.

OBB	orbit breadth (left)	Breadth from ectocochion to dacryon, approximating the longitudinal axis which bisects the orbit into equal upper and lower parts.
JUB	bijugal breadth	The external breadth across the malars at the deepest points in the curvature between the frontal and temporal process of the malars.
NLB	nasal breadth	The distance between the anterior edges of the nasal aperture at its widest extent.
MAB	palate breadth	The greatest breadth across the alveolar borders, wherever found, perpendicular to the median plane.
MDH	mastoid height	The length of the mastoid process below, and perpendicular to, the eye-ear plane, in the vertical plane.
MDB	mastoid width	Width of the mastoid process at its base, through its transverse axis.
ZMB	bimaxillary breadth	The breadth across the maxillae, from one zygomaxillare anterior to the other.
SSS	zygomaxillary subtense	The projection or subtense from subspinale to the bimaxillary breadth.
FMB	bifrontal breadth	The breadth across the frontal bone between the most anterior points on the fronto-malare suture on either side.
NAS	nasio-frontal subtense	The subtense from nasion to the bifrontal breadth.
EKB	biorbital breadth	The breadth across the orbits from ectoconchion to ectoconchion.
DKS	dacryon subtense	The mean subtense from dacryon to the biorbital breadth.
DKB	interorbital breadth	The breadth across the nasal space from dacryon to dacryon.
NDS	naso-dacryal subtense	The subtense from the deepest point in the profile of the nasal bones to the interorbital breadth.
WNB	simotic chord	The minimum transverse breadth across the two nasal bones.
SIS	simotic subtense	The subtense from the nasal bridge to the simotic chord.
IML	malar length inferior	The direct distance from the zygomaxillare anterior to the lowest point of the zygo-temporal suture on the external surface.
XML	malar length maximum	Total direct length of the malar in a diagonal direction, from the lower end of the zygo-temporal suture on the lateral surface to zygoorbitale.
MLS	malar subtense	The maximum subtense from the convexity of the malar angle to the maximum length of the bone at the level of the zygomaticofacial foramen.
WMH	cheek height	The minimum distance from the lower border of the orbit to the lower margin of the maxilla, mesial to the masseter attachment.
SOS	supraorbital projection	The maximum projection of the supraorbital arch between the midline near glabella and the frontal bone just anterior to the temporal line.

GLS	glabella projection	The maximum projection of the midline profile between nasion and supraglabellare.
FOL	foramen magnum length	The length from basion to opisthion.
FRC	nasion-bregma chord	The frontal chord, or direct distance from nasion to bregma.
FRS	nasion-bregma subtense	The maximum subtense, at the highest point on the convexity of the frontal bone in the midplane, to the nasion-bregma chord.
FRF	nasion-subtense fraction	The distance along the nasion-bregma chord at nasion at which the nasion-bregma subtense falls.
PAC	bregma-lambda chord	The direct distance from bregma to lambda.
PAS	bregma-lambda subtense	The maximum subtense at the highest point on the convexity of the parietal bones in the midplane to the bregma-lambda chord.
PAF	bregma-subtense fraction	The distance along the bregma-lambda chord, from bregma, at which the bregma-lambda subtense falls.
OCC	lambda-opisthion chord	The direct distance from lambda to opisthion.
OCS	lambda-opisthion subtense	The maximum subtense at the most prominent point on the basic contour of the occipital bone in the midplane.
OCF	lambda-subtense fraction	The distance along the lambda-opisthion chord at lambda at which the lambda-opisthion subtense falls.
VRR	vertex radius	The perpendicular to the transmeatal axis from the most distant point on the parietals.
NAR	nasion radius	The perpendicular to the transmeatal axis from nasion.
SSR	supspinale radius	The perpendicular to the transmeatal axis from subspinale.
PRR	prosthion radius	The perpendicular to the transmeatal axis from prosthion.
DKR	dacryon radius	The perpendicular to the transmeatal axis from the left dacryon.
ZOR	zygoorbitale radius	The perpendicular to the transmeatal axis from the left zygoorbitale.
FMR	frontomalare radius	The perpendicular to the transmeatal axis from the left frontomalare anterior.
EKR	ectoconchio radius	The perpendicular to the transmeatal axis from the left ectoconchion.
ZMR	zygomaxillare radius	The perpendicular to the transmeatal axis from the left zygomaxillare anterior.
AVR	M1 alveolus radius	The perpendicular to the transmeatal axis from the most anterior point on the alveolus of the left first molar.
BRR	bregma radius	The perpendicular to the transmeatal axis from bregma.
LAR	lambda radius	The perpendicular to the transmeatal axis from lambda.
OSR	opisthion radius	The perpendicular to the transmeatal axis from opisthion.
BAR	basion radius	The perpendicular to the transmeatal axis from basion.
NAA	nasion angle, ba-pr	Of the facial triangle, the angle at nasion whose sides are basion-nasion and nasion-prosthion.
PRA	prosthion angle, na-ba	Of the facial triangle, the angle at prosthion whose sides are basion-prosthion and nasion-prosthion.

BAA	basion angle, na-pr	Of the facial triangle, the angle at basion whose sides are basion-nasion and basion-prosthion.
NBA	nasion angle, ba-br	The angle at nasion whose sides are basion-nasion and basion-bregma.
BBA	basion angle, na-br	The angle at basion whose sides are basion-nasion and basion-bregma.
BRA	bregma angle (basion-nasion)	The angle at bregma whose sides are basion-bregma height and nasion-bregma chord (the opposite side being basion-nasion).
SSA	zygomaxillare angle	The angle at subspinale whose two sides reach from this point to zygomaxillare anterior left and right.
NFA	nasio-frontal angle	The angle at nasion whose two sides reach from this point to frontomalare, left and right.
DKA	dacryal angle	The angle formed at dacryon by the orbital breadth from ectoconchion and the subtense from dacryon to biorbital breadth (left and right angles added).
NDA	naso-dacryal angle	The angle formed at the midline of the nasal bones, whose sides reach from this point to dacryon, left and right.
SIA	simotic angle	The angle at the midline of the nasal bones, at their narrowest point, whose sides reach to the end points of the minimum breadth of the nasal bones.
FRA	frontal angle	In the sagittal plane, the angle underlying the curvature of the frontal bone at its maximum height above the frontal chord.
PAA	parietal angle	In the sagittal plane, the angle underlying the curvature of the parietal bones along the sagittal suture, at its maximum height above the parietal chord.
OCA	occipital angle	In the sagittal plane, the angle underlying the curvature of the occipital bone at its maximum height above the occipital chord.
RFA	radio-frontal angle (nasion-bregma)	The angle at the transmeatal axis of which the opposite side is the frontal chord (FRC).
RPA	radio-parietal angle (bregma-lambda)	The angle at the transmeatal axis of which the opposite side is the parietal chord (PAC).
ROA	radio-occipital angle (lambda-opisthion)	The angle at the transmeatal axis of which the opposite side if the occipital chord (OCC).
BSA	basal angle (prosthion-opisthion)	The angle at the basion between the basion-prosthion and basion-opisthion (FOL) distances.
SBA	sub-bregma angle	The angle at bregma of the triangle nasion-bregma-lambda.
SLA	sub-lambda angle	The angle at lambda of the triangle bregma-lambda-opisthion.
TBA	trans-basal angle	The angle at basion subtended by the transverse axis.

Chapter 3: Materials and Methods

3.1 Samples

Five Pacific Island populations were chosen for study: Easter Island, Fiji, Guam, Mokapu, and New Britiain. This selection limited by the availability of dental data and choosing corresponding populations from available craniometric data. The locations of these populations is displayed in Figure 10.

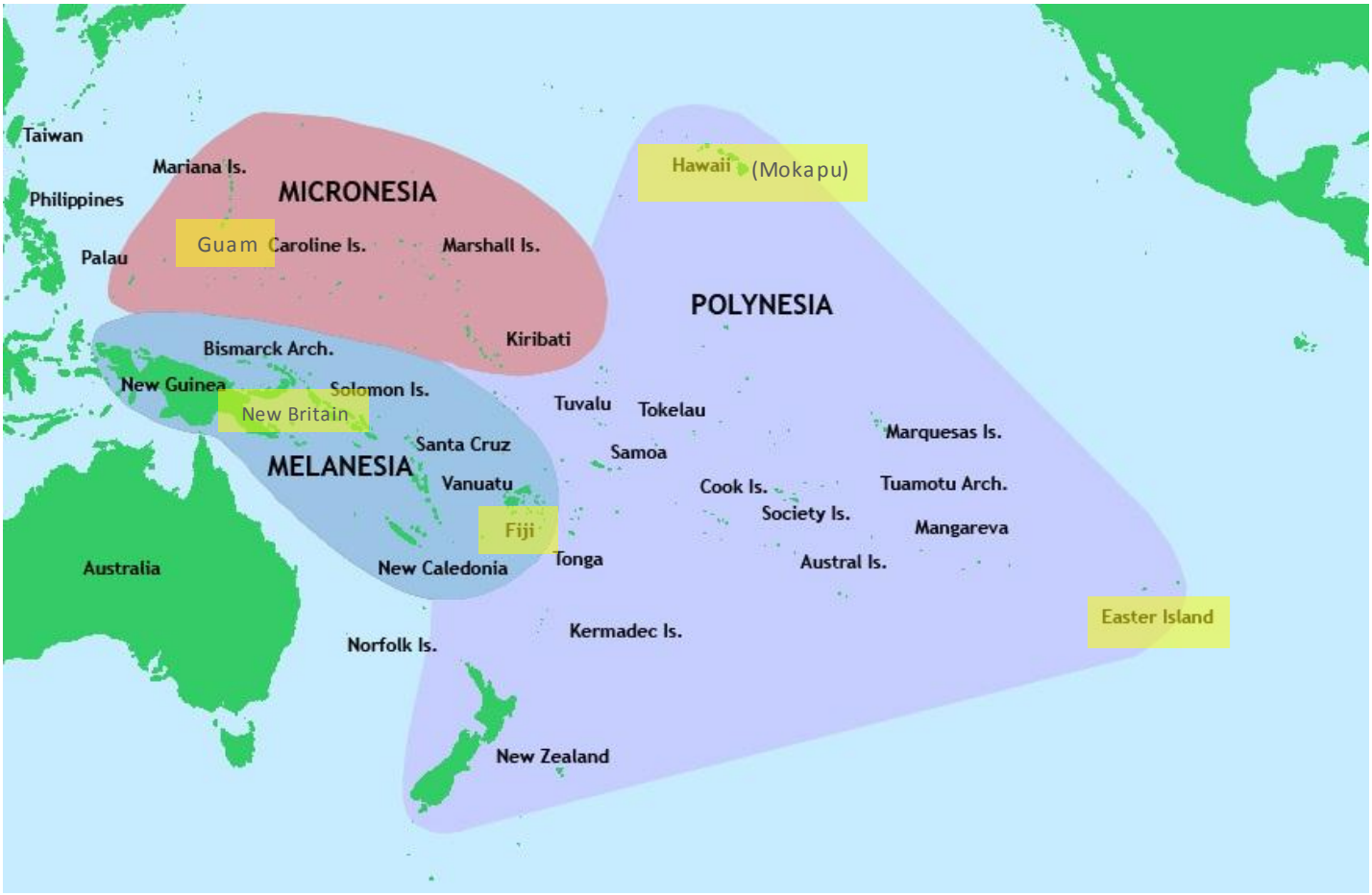

Figure 10: Map of the Pacific Islands with sample populations highlighted in yellow.

Table 4: Population descriptions, including locations of recovery and curation and approximate date. All information on dental data was included on the data sheets. All information on cranial data is found in Howells (1973, 1989, and 1995).

	Dental		
	Curation location	**Recovered from**	**Date**
Easter Island	British Museum of Natural History, London; American Museum of Natural History, New York; Musee de l'Homme, Paris	Kotuu; Hotu Iti; Vaihou; La Perouse Bay	Historic or uncertain
Fiji	Simon Fraser University, Burnaby, British Columbia; Bernice P. Bishop Museum, Honolulu; British Museum of Natural History, London; Musee de l'Homme, Paris; University of California, Berkley; Smithsonian Institution, Washington D.C.	Rotuma; Thikombia Island; Levuka Ovalau; Cicia Island; Lebanka; Obalaou; Vita Levu; Kantava; Levuka; Rivua River, Oba Saou; Kambara Island; Buca, Vanualevu.	Prehistoric to historic
Guam	Bernice P. Bishop Museum, Honolulu; California State University, Los Angeles; Musee de l'Homme, Paris	Talaque; Dano Island; Eapu; Apotguan; Tumon; Agana; Piti; Tarague	Prehistoric (3435 BP) to historic
Mokapu	Bernice P. Bishop Museum, Honolulu	Mokapu, Oahu, Hawaii	Prehistoric
New Britain	American Museum of Natural History, New York, Smithsonian Institution, Washington D.C.	Ralum; Gazelle Peninsula;	Recent
	Craniometric		
	Curation location	**Recovered from**	**Date**
Easter Island	Musee de l'Homme, Paris; British Museum of Natural History, London; Naurhistorisches Museum, Vienna; Peabody Museum, Harvard University; Canterbury Museum, Christchurch, New Zealand	Collected from La Perouse Bay in northeast Easter Island and Vaihu in southern Easter Island (Paris collection)	Middle to Late Periods (1110-1868 AD)[1]
Fiji	Part of Howells' TEST series, comprised of small numbered examples from populations outside of his main study populations, but possibly related to them. Not collected systematically, but gathered opportunistically from the various institutions housing Howells' main study populations. Recovery locations not noted by Howells.		Not noted by Howells[6]
Guam	Bernice P. Bishop Museum, Honolulu	Collected by Hornbostel in the 1920's from latte sites along Tumon Beach, Tumon Bay in western Guam[2]	1100 AD[4]
Mokapu	Bernice P. Bishop Museum, Honolulu	Collected from burial plots along north shore of Mokapu Peninsula, Oahu, Hawaii[3]	1400-1790 AD[5]
Tolai	American Museum of Natural History, New York	Collected from Northeast Gazelle Peninsula, New Guinea islands	Approximately 1600 AD[4]

[1]Murill 1968, [2]Graves and Moore 1985, [3]Pietrusewky 1971, [4]Howells 1989, [5]Howells 1973, [6]Howells 1995

3.1.1. Turner data (dental)

All dental data was gathered by Christy G. Turner II between 1977 and 1984, and utilized in various combinations in a number of publications on the Pacific during his career (Turner 1983b, 1985c, 1986b, 1990b, Turner and Scott 1977, among many others). The dataset was provided by G. Richard Scott of the University of Nevada Reno, a former student of Turner who has been handling his data since Turner's death in 2013. The data consists of 847 individuals (Table 5) scored on 57 non-metric morphological traits in the maxillary and mandibular dentition (Table 7) according ASUDAS scoring standards (see Turner, Nichol, and Scott 1991). Though Turner collected non-metric dental data for several Pacific Island populations, the data available for this study consisted of Easter Island, Fiji, Guam, Mokapu, and New Britain. Sex estimation and approximate age were provided for each individual. Further sample description is provided in Table 4.

Table 5: Total number of individuals scored from Turner data.

	Male	*Male?*	*Sex indeterminate*	*Female?*	*Female*	***Total***
Easter Island	89	21	31	14	25	**180**
Fiji	25	5	23	1	3	**57**
Guam	81	29	72	13	28	**223**
Mokapu	26	97	47	28	49	**247**
New Britain	68	24	4	10	34	**140**
Total	**289**	**176**	**177**	**66**	**139**	**847**

3.1.2. Howells data (craniometrics)

All craniometric data was obtained from the William W. Howells Craniometric Data set, which is freely available online to the public (at http://web.utk.edu/~auerbach/HOWL.htm). The set consists of craniometric measurements taken from 2,524 human crania from 28 worldwide populations, in addition to 524 "test" crania, compiled between 1965 and 1980 from which

Howells analyzed and published in three monographs (1973, 1989, and 1995). The populations included for this analysis were chosen into order to match the analogous populations of available dental data, totaling 370 individuals (see Table 6). These include Easter Island, Fiji, Guam, Mokapu, and Tolai (aboriginal New Britain). Further sample description is provided in Table 3. The 82 measurements are described in Table 3. Sex estimation and provenance information is also provided by Howells.

Table 6: Total number of individuals scored from Howells data.

	Male	*Female*	*Total*
Easter Island	48	37	85
Fiji	6	2	8
Guam	32	27	59
Mokapu	54	53	107
New Britain	57	54	111
Total	**197**	**173**	**370**

3.2. Methods

3.2.1. Preprocessing

Input Data from Score Sheets

Scores for dental non-metric traits were gathered from the ASUDAS score sheets completed by Turner (Figure 9) and input into an Excel spreadsheet for the traits listed in Table 6. Also noted were the facility where the specimen was held and recorded, the individual specimen number, and sex. While all teeth were scored by Turner for crown and root traits, an individual count method was employed, in which all crown and root traits are recorded, except for when individuals are scored for a trait in both antimeres, in which case only the antimere with the highest grade of expression is used to characterize the individual (Scott 2008). This procedure relies on the notion that the more pronounced phenotype best reflects the genetic potential of the underlying genotype (Scott and Turner 1997, Scott 2008). Two versions of the

ASUDAS score sheets were utilized in this dataset, from 1977 and 1980. On the earlier sheets, all traits presented in Table 6 were scored with the exception of Uto-Azetecan premolar, metacone, and congenital absence in the maxillary teeth, and anterior fovea, Tome's root, torsomolar angle, and congenital absence in the mandibular teeth. In order to pool the 1977 and 1980 data, these traits were treated as not observed for the specimens scored with the earlier sheets. The total number of scored individuals is indicated in Table 5.

Table 7: Traits recorded from ASUDAS score sheets

Maxillary		**Mandibular**	
Trait	***Tooth***	***Trait***	***Tooth***
Winging	I1	Shovel	I1
Shovel	I1, I2, C	Canine distal accessory ridge	C
Double shovel	I1, I2, C, P3, P4	Premolar cusp number	P3, P4
Interruption groove	I1, I2	Anterior fovea	M1
Tuberculum dentale	I1, I2, C	Molar groove pattern	M1, M2, M3
Canine mesial ridge	C	Molar cusp number	M1, M2, M3
Canine distal accessory ridge	C	Deflecting wrinkle	M1, M2, M3
Premolar mesial and distal accessory cusps	P3, P4	Distal trigonid crest	M1, M2, M3
Uto-Aztecan premolar	P3, P4	Protostylid	M1, M2, M3
Metacone	M1, M2, M3	Cusp 5	M1, M2, M3
Hypocone	M1, M2, M3	Cusp 6	M1, M2, M3
Cusp 5	M1, M2, M3	Cusp 7	M1, M2, M3
Carabelli's cusp	M1, M2, M3	Tomes' root	P3
Cusp 2 parastyle	M1, M2, M3	Enamel extensions	P3, P4, M1, M2, M3
Enamel extension	P3, P4, M1, M2, M3	Root number	I1, I2, C, P3, P4, M1, M2, M3
Root number	I1, I2, C, P3, P4, M1, M2, M3	Odontome	P3, P4
Peg tooth/reduction	I2, M3	Radical number	I1, I2, C, P3, P4, M1, M2, M3
Odontome	P3, P4	Torsomolar angle	M3
Congenital absence	I2, P3, M3	Congenital absence	I1, P4, M3
Radical number	I1, I2, C, P3, P4, M1, M2, M3		

Trait Pruning

Definite males (Male) and probable males (Male?), as well as definite females (Female) and probable females (Female?) were pooled into male and female groups, while all sex

indeterminate individuals were eliminated from any further analysis. The total number of individuals following this pooling and elimination is noted in Table 8.

Table 8: Total number of individuals from Turner data following pooling of definite and probable males and females and elimination of sex indeterminate individuals.

	Male	*Female*	***Total***
Easter Island	110	39	**149**
Fiji	30	4	**34**
Guam	110	41	**151**
Mokapu	123	77	**200**
New Britain	92	44	**136**
Total	**465**	**205**	**670**

Scores for the remaining individuals were dichotomized based on published breakpoints into categories of present (1) or absent (0). Breakpoints are described in Table 9.

Table 9: Breakpoints, taken from Turner 1985, 1987, 1992; Haeussler et al 1989; Irish 1993, 1997; and Scott and Turner 2000.

Maxillary		***Score***	
Trait	**Tooth**	**0 (Absent)**	**1 (Present)**
Winging	I1	0, 2-4	1
Shovel	I1	0-2	3-7
	I2	0	1-7
	C	0-1	2-7
Double shovel	I1, I2	0	1-6
Peg-shaped	I2, M3	0	1
Interruption groove	I1, I2	0	1-4
Congenital absence	I2, M3	0	1
Tuberculum dentale	I1, I2, C	0-1	2-6
Canine mesial ridge	C	0	1-3
Canine distal accessory ridge	C	0-1	2-5
Premolar mesial and distal accessory cusps	P3, P4	0	1
Metacone	M1, M2, M3	0-4	5-6
Hypocone	M1	0-4	5-6
	M2, M3	0-1	2-6
Cusp 5	M1, M2, M3	0	1-5
Carabelli's cusp	M1, M2, M3	0	1-7
Cusp 2 Parastyle	M1, M2, M3	0	1-6
Enamel extension	P3, P4, M1, M2, M3	0	1-3
Root number	I1, I2, C, P3, P4	1	2-3

	M1, M2, M3	1-2	3-4
Radical number	I1, I2, C, P3, P4, M1, M2, M3	1	2-8
Odontome	P3, P4	0	1
Mandibular		***Score***	
Trait	**Tooth**	**0 (Absent)**	**1 (Present)**
Shovel	I1, I2	0	1-7
Congenital absence	I1, P3, M3	0	1
Canine distal accessory ridge	C	0	1-5
Premolar cusp number	P3	0-3	4-9
	P4	0-2	3-9
Anterior fovea	M1	0-1	2-4
Molar groove pattern	M1, M2, M3	Y	+, X, X & Y, X & +, Y & +
Molar cusp number	M1	4-5	6
	M2	4	5-6
	M3	3	4-6
Deflecting wrinkle	M1	0	1-3
Distal trigonid crest	M1, M2, M3	0	1
Protostylid	M1, M2, M3	0	1-7
Cusp 5	M1, M2, M3	0	1-5
Cusp 6	M1, M2, M3	0	1-5
Cusp 7	M1, M2, M3	0	1-4
Tomes' root	P3	0-3	4-5
Enamel extensions	P3, P4, M1, M2, M3	0	1-3
Root number	I1, I2, C, P3, P4	1	2-3
	M1, M2, M3	1	2-3
Radical number	I1, I2, C, P3, P4, M1, M2, M3	1	2-8
Torsomolar angle	M3	0 degrees	>0 degrees
Odontome	P3, P4	0	1

Percent frequencies of observed traits were determined for each trait and each population. Any traits with high or low frequencies for all populations observed (<0.10 or >0.90) were eliminated from further analysis (Harris and Sjøvold 2004). A Pearson correlation test in R was performed on the remaining traits and any traits with a correlation value of 0.7-0.9 (Table 10) were also eliminated (Tomczak and Powell 2003). Finally, any trait in which more than one population had a frequency of 0 or 1 were eliminated. In order to make males and females

comparable, any trait that was still present at this point in one sex but eliminated in the other was also eliminated, yielding a set of traits that is identical between the sexes. Table 11 shows the traits remaining after these pruning steps that were used in the final analyses. These are the traits that best reflect variation within and between the sexes and the populations used in this study.

Table 10: Correlated traits eliminated from both sexes.		
Males		
Traits		***Correlation***
Molar cusp number, LM1	Cusp 6, LM1	0.9
Molar cusp number, LM2	Cusp 5, LM2	0.9
Double shoveling, UP3	Double shoveling, UC	0.7
Torsomolar angle, LM3		NA
Females		
Traits		***Correlation***
Molar cusp number, LM1	Cusp 6, LM1	0.9
Molar cusp number, LM2	Cusp 5, LM2	0.9
Molar cusp number, LM3	Distal trigonid crest, LM1	0.7
Cusp 5, LM1		NA

Table 11: Traits remaining after trait pruning.			
Maxillary (n = 11)		**Mandibular (n = 18)**	
Trait	***Tooth***	***Trait***	***Tooth***
Tuberculum dentale	C	Shovel	I1
Canine distal accessory ridge	C	Premolar cusp number	P3, P4
Metacone	M1	Anterior fovea	M1
Hypocone	M2, M3	Molar groove pattern	M1, M2, M3
Cusp 5	M1, M2, M3	Deflecting wrinkle	M1
Carabelli's cusp	M1	Cusp 2 protostylid	M1, M2, M3
Enamel extension	M1, M2	Cusp 5	M3
		Cusp 6	M2, M3
		Enamel extension	M1, M2
		Congenital absence	M3

3.2.2 Statistical Analysis

MMD

MMD distances were obtained in R from dental trait frequencies and observed counts of the final traits in Table 11 using a modified script from Soltysiak (2011). This was done separately for males and females as well as for a single group of the sexes pooled. The formula utilized an Anscombe transformation to stabilize variance, thus reducing the degree of distortion in sample variance due to its nonlinear association with trait frequency. This transformation has been shown to perform better than alternative frequency transformations (Harris and Sjøvold 2004), such as Smith's original arcsine transformation (Grewal 1962), and is the default option in Soltysiak's script (2011). The adjustment factor for any correction for sample size (i.e. Freeman & Tukey, Grewal, etc.) overwhelmed the relatively small sample sizes of these samples, resulting in a negative MMD values. For this reason, the formula was uncorrected for sample size (Harris and Sjøvold 2004, Soltysiak 2011). The formula was also adjusted for use of trait frequencies in the form of proportions (0-1) as opposed to percentage (0-100).

Mahalanobis Distance

Mahalanobis distances were obtained in PAST (Hammer et al 2001) from craniometric measurements separately for males, females, and the sexes pooled. All traits were utilized. Distances were obtained for all individuals for each sex, then averaged over each pairing within the matrix to obtain a single distance value for each comparison. For example, distances between all Easter Island males and all Fiji males were averaged to give a mean Mahalanobis distance between Easter Island and Fiji males. The values of the diagonal of the resultant matrices were noted as measures of average intrapopulation variance. The diagonal was converted to zero for all further analysis of interpopulation variance.

Principal Coordinates Analysis

Principal coordinates analysis models the relationships between populations by displaying the higher-dimensional structure of a distance matrix into a lower-dimensional space, allowing for visual interpretation of distances. Principal coordinates analysis was performed in PAST for MMD and Mahalanobis distance matrices for males and females separately and for sexes pooled, with Euclidean distance designated as the similarity index for the MMD distances and Mahalanobis distance for the Mahalanobis. Eigenvalues and percent variance captured by each axes are presented in Table 16, and coordinates for axes 1 through 4 are presented in Table 17. Plots of axes 1 and 2 were generated for all analyses, as well as 3D plots of axes 1 through 3 using the Landmarks 3D option for the Mahalanobis.

Generalized Procrustes Analysis

Generalized Procrustes Analysis gives insights into the magnitude of differences between sexes and between data types by providing a consensus that equally captures the variation of the two groups being looked at into a single statistic, and analyzing the efficiency with which it was able to force such an agreement. Principle coordinates for MMD and Mahalanobis matrices for each sex and for all individuals were obtained in PAST. Generalized Procrustes Analysis (GPA) was performed in Excel XLStat using the Commandeur method on the coordinates from the first two axes of principle coordinates analysis (see Table 17) to generate consensus configurations of the data (Addinsoft 2015). The groups combined are presented in Table 12. Agreement statistics (Rc), scaling factors, and relative contributions of each type of transformation (scaling, rotation, translation) for each consensus configuration were obtained. Residual variance and variance by

configuration and dimension were obtained and modelled as bar charts. The consensus coordinates were plotted by configuration and by population for each consensus.

Table 12: Groups combined via Generalized Procrustes Analysis.
Male Cranial + Female Cranial
Male Dental + Female Dental
Female Dental + Female Cranial
Male Dental + Male Cranial

Mantel Tests

Mantel tests offer another way to compare datasets, specifically matrices of identical or differing measures, in order to determine how well they correlate with each other and how significantly. Mantel tests were performed in PAST to compare MMD and Mahalanobis distance measures between the groups in Table 13 as well as the coordinates of the consensus configurations for male dental/cranial data and female dental/cranial data obtained from Generalized Procrustes Analysis. All tests were run on the distance matrices, with the exception of the consensus configurations, which were run on the object coordinates of the consensus. Euclidean distance was used as the similarity measure for the MMD matrices, while Mahalanobis distance was used for the Mahalanobis matrices. Tests were run five times at 10,000 permutations, and p-values (uncorrelated, one-tailed) were averaged over the five runs.

Table 13: Comparisons utilized for Mantel tests. MMD values represent distances among groups based on dental non-metric data. Mahalanobis values represent distances among groups based on craniometric data.	
Male MMD vs Female MMD	Compare sexes
Male Mahalanobis vs Female Mahalanobis	
Consensus Configurations for Male MMD/Mahalanobis vs Female MMD/Mahalanobis	
Male MMD vs Male Mahalanobis	Compare dental non-metrics and craniometrics
Female MMD vs Female Mahalanobis	
Pooled sexes MMD vs Pooled sexes Mahalanobis	

Determinant Analysis

Determinant analysis helps to elucidate differential mobility of the sexes by comparing their relative variances, and can be examined separately for each data type to see how their results compare. Where the equation is greater than one, males are more mobile than females, and the residence pattern can be assumed to be matrilocal. When the equation equals less than 1, females are the more mobile sex, and patrilocality is assumed. In order to prevent a singular covariance matrix with a determinant of zero, which occurs when the number of variables is equal to or greater than the number of observations, covariance matrices and their respective determinants were obtained for the first 10 axes generated from principal components analysis for each population separately by sex. The natural log of the ratio of male to female determinants for each population was calculated. Where this value is greater than 1, it is assumed that males are more mobile relative to females and a matrilocal residence pattern was practiced. Where this value is less than 1, females are assumed to be more mobile relative to males as the result of a patrilocal residence pattern. Determinant analysis was performed separately for both the dental and craniometric data. Generation of covariance matrices and determinants as well as all calculations for determinant analysis were performed in Excel. Because of the small sample size for Fiji females (n=2) in the craniometric data, PCA could not be performed, so mobility of Fijian sexes based on craniometric measurements could not be analyzed.

K-means Clustering

K-means analysis is a clustering method that partitions similar individuals into a specified number of sets. The way in which individuals are divided and the relative size of the clusters between populations can be compared to make inferences about components of gene flow and subsequent migratory routes. K-means clustering assignments were generated for 4 clusters for

each sex over all populations, as well as for all individuals for both the dental non-metric and craniometric data. These clustering assignments were input into Excel to generate pivot tables and subsequent pivot charts in 100% stacked style. The order of the bars within the pivot charts were manipulated to give a clearer visualization of population groupings.

Chapter 4: Results

Distance Matrices

Table 14: Mean Measure of Divergence (MMD) distance matrices for dental non-metric scores for males, females, and pooled sexes.

Male

	Easter Island	*Fiji*	*Guam*	*Mokapu*	*New Britain*
Easter Island	0				
Fiji	0.244762	0			
Guam	0.341039	0.183125	0		
Mokapu	0.134372	0.122376	0.169681	0	
New Britain	0.541123	0.350469	0.283626	0.311238	0

Female

	Easter Island	*Fiji*	*Guam*	*Mokapu*	*New Britain*
Easter Island	0				
Fiji	0.563286	0			
Guam	0.232979	0.465558	0		
Mokapu	0.145668	0.38711	0.141147	0	
New Britain	0.488152	0.23959	0.301724	0.278399	0

Pooled Sexes

	Easter Island	*Fiji*	*Guam*	*Mokapu*	*New Britain*
Easter Island	0				
Fiji	0.246162	0			
Guam	0.275585	0.183513	0		
Mokapu	0.122233	0.171541	0.14436	0	
New Britain	0.526486	0.343899	0.279556	0.293093	0

The MMD matrix (Table 14) displays the Mean Measure of Divergence values between populations based on dental non-metric scores for males and females separately and for the sexes pooled. According to the MMD distances, New Britain and Easter Island are the most distant populations overall when looking at the pooled sexes (0.526486), and are more distant in the males (0.541123) than the females (0.488152). Mokapu and Easter Island are the least distant populations in the pooled sample (0.122233), and are the second closest distance for both males

(0.134372) and females (0.145668). Mokapu, Guam, and Easter Island display the least distance between them for both males and females, with more similarity between Mokapu/Guam and Guam/Easter Island for females and between Mokapu and Easter Island for males.

Fiji/Guam and Fiji/Mokapu represent two of the greatest distances represented by the female samples, while these same groups represent two of the smallest distances represented by males. Likewise, Fiji/New Britain and Guam/Easter Island are relatively similar compared to all other distances for females, while the same groups are more distant in males.

Comparing male to female distances by population, female values are higher than respective male values between Easter Island and Fiji, Easter Island and Mokapu, Guam and Fiji, and Guam and New Britain. Males values are higher than females for distances between Easter Island and Guam, Easter Island and New Britain, Fiji and New Britain, Mokapu and Guam, and Mokapu and New Britain.

Table 15: Mahalanobis distance matrices for craniometric measurements for males, females, and pooled sexes.					
Males					
	Easter Island	***Fiji***	***Guam***	***Mokapu***	***New Britain***
Easter Island	0				
Fiji	1.45654	0			
Guam	1.39902	1.46828	0		
Mokapu	1.3969	1.46649	1.4078	0	
New Britain	1.41212	1.47237	1.42166	1.42192	0
Females					
	Easter Island	***Fiji***	***Guam***	***Mokapu***	***New Britain***
Easter Island	0				
Fiji	1.39288	0			
Guam	1.43064	1.39444	0		
Mokapu	1.41613	1.37619	1.41796	0	
New Britain	1.41837	1.37703	1.42178	1.40744	0
Pooled Sexes					
	Easter Island	***Fiji***	***Guam***	***Mokapu***	***New Britain***
Easter Island	0				
Fiji	1.46584	0			
Guam	1.41825	1.46282	0		
Mokapu	1.41385	1.45942	1.40825	0	
New Britain	1.41591	1.45277	1.41047	1.40767	0

In the Mahalanobis distances for the pooled sexes, Fiji and Easter Island are the most distant (1.46583), though Fiji and Guam are nearly equally as distant (1.46282). These distances are higher in males (1.45654 and 1.46828) than females (1.39298 and 1.39444) for both comparisons. Mokapu/New Britain and Mokapu/Guam display the most similar relationships in the pooled sample (1.40767 and 1.40825), while these distances are both higher in males (1.42192 and 1.4078) than females (1.40744 and 1.41806).

Distances between Easter Island, Guam, and Mokapu are among the highest in the female samples, while these same comparisons are the lowest among the male distances. The most distant and most similar populations within each sex oppose each other, with distances between Fiji and all other populations displaying the highest distances in males and the lowest distances in the females. Males are also slightly more distant than females in comparisons of Easter Island/New Britain and New Britain/Guam, though these values are essentially equal (1.41212/1.41837 and 1.42166/1.42178).

Principle Coordinates Analysis

Table 16: Eigenvalues and percent variance captured on axes 1-4 from principal coordinates analysis based on distance matrices.

Male MMD			**Male Mahalanobis**		
Axis	***Eigenvalue***	***% variance***	***Axis***	***Eigenvalue***	***% variance***
1	0.35641	70.327	***1***	1.6402	47.3
2	0.10248	20.222	***2***	1.0838	31.255
3	0.02865	5.6527	***3***	0.63587	18.337
4	0.01925	3.7982	***4***	0.10779	3.1085
Female MMD			**Female Mahalanobis**		
Axis	***Eigenvalue***	***% variance***	***Axis***	***Eigenvalue***	***% variance***
1	0.5918	79.345	***1***	1.2628	36.678
2	0.10356	13.885	***2***	1.2398	27.513
3	0.02579	3.4571	***3***	0.85104	22.189
4	0.02471	3.3131	***4***	0.35689	13.619
All MMD			**All Mahalanobis**		
Axis	***Eigenvalue***	***% variance***	***Axis***	***Eigenvalue***	***% variance***
1	0.32521	71.026	***1***	1.5483	52.106
2	0.07486	16.35	***2***	0.87703	29.514
3	0.03954	8.636	***3***	0.38359	12.909
4	0.01826	3.9879	***4***	0.16258	5.4711

Table 17: Coordinates for axes 1-4 from principal coordinates analysis based on distance matrices.									
Male MMD					**Female MMD**				
	Axis 1	***Axis 2***	***Axis 3***	***Axis 4***		***Axis 1***	***Axis 2***	***Axis 3***	***Axis 4***
Easter Island	-0.32017	0.20954	0.042264	-0.02039	***Easter Island***	-0.38582	-0.18712	0.017848	-0.06995
Fiji	-0.08755	-0.11565	-0.0892	-0.08442	***Fiji***	0.5039	-0.15728	-0.03347	0.046802
Guam	0.085426	-0.15446	0.12477	-0.00801	***Guam***	-0.21549	0.12646	-0.12048	0.010104
Mokapu	-0.14463	-0.06848	-0.05136	0.10778	***Mokapu***	-0.21383	0.063841	0.08489	0.099905
New Britain	0.46693	0.12905	-0.02648	0.005043	***New Britain***	0.31123	0.1541	0.051217	-0.08686
Male Mahalanobis					**Female Mahalanobis**				
	Axis 1	***Axis 2***	***Axis 3***	***Axis 4***		***Axis 1***	***Axis 2***	***Axis 3***	***Axis 4***
Easter Island	-0.58189	0.53171	0.2298	-0.16405	***Easter Island***	0.00589	-0.65362	-0.54615	-0.016171
Fiji	0.007639	-0.78869	0.36824	-0.03715	***Fiji***	-0.22154	0.46542	-0.13167	-0.50867
Guam	0.61873	-0.04274	-0.48897	-0.1427	***Guam***	-0.84082	0.046691	0.22872	0.31485
Mokapu	0.65516	0.40711	0.26361	0.17252	***Mokapu***	0.61478	0.48367	-0.18492	0.34308
New Britain	-0.69964	-0.10739	-0.37267	0.17139	***New Britain***	0.4417	-0.34216	0.63401	-0.13309
Both Sexes MMD					**Both Sexes Mahalanobis**				
	Axis 1	***Axis 2***	***Axis 3***	***Axis 4***		***Axis 1***	***Axis 2***	***Axis 3***	***Axis 4***
Easter Island	-0.3013	0.18064	-0.0106	0.038732	***Easter Island***	0.36162	-0.40433	-0.33413	-0.19674
Fiji	-0.05932	-0.10621	-0.15638	-0.01914	***Fiji***	-0.33614	-0.60582	0.22379	0.17011
Guam	0.022748	-0.13951	0.077279	0.084106	***Guam***	-0.60172	0.4015	-0.326	0.13084
Mokapu	-0.12544	-0.03592	0.094753	-0.09625	***Mokapu***	0.91121	0.31139	0.1172	0.13814
New Britain	0.46331	0.101	-0.00506	-0.00745	***New Britain***	-0.33497	0.29726	0.31915	-0.24234

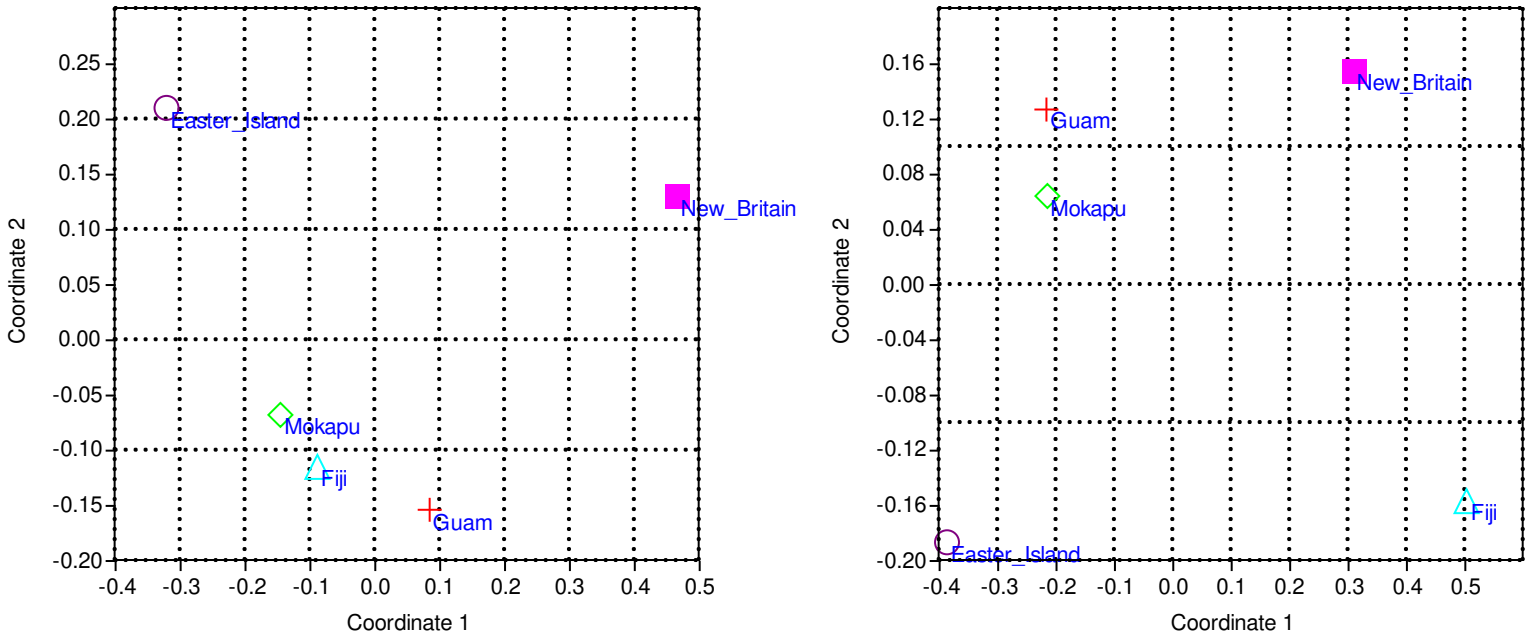

Figure 11: Principal coordinates plots for males (left) and females (right) based on distance matrices (MMD) obtained from dental non-metric scores.

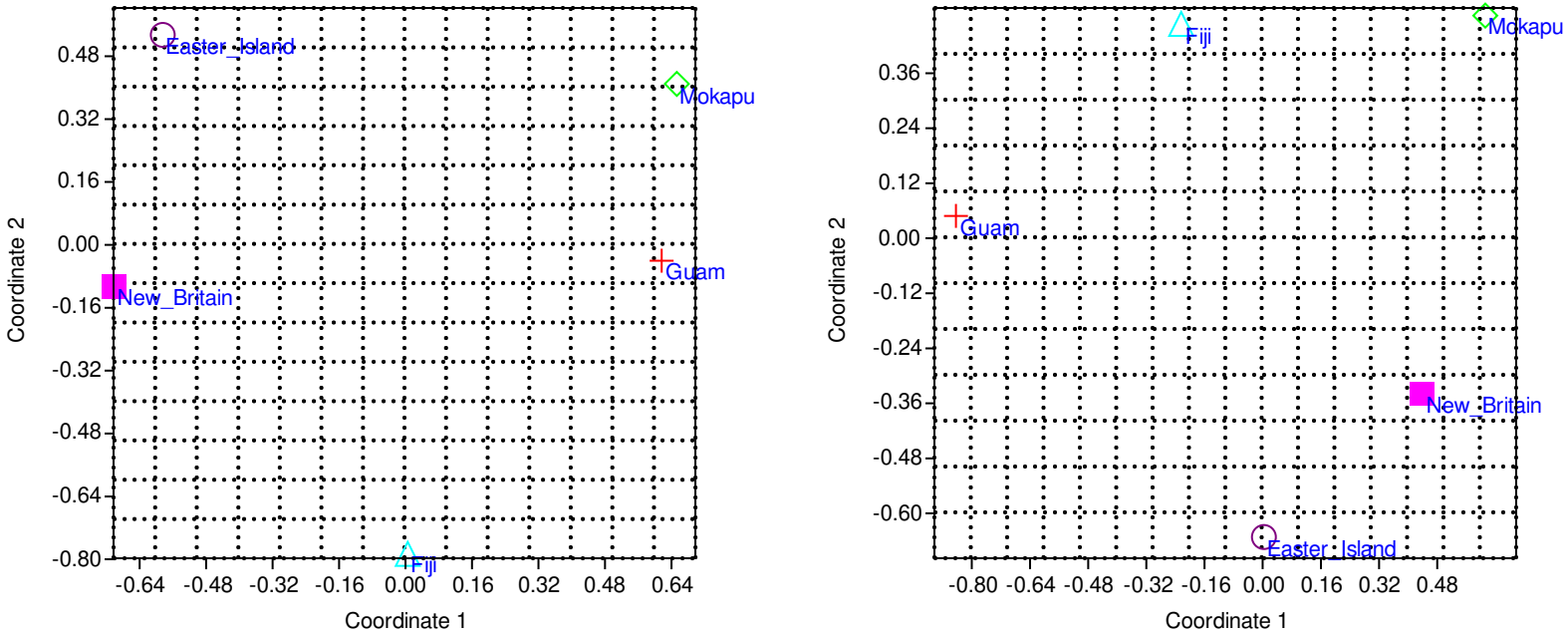

Figure 12: Principal coordinates plots for males (left) and females (right) based on distance matrices (Mahalanobis) obtained from craniometric measurements.

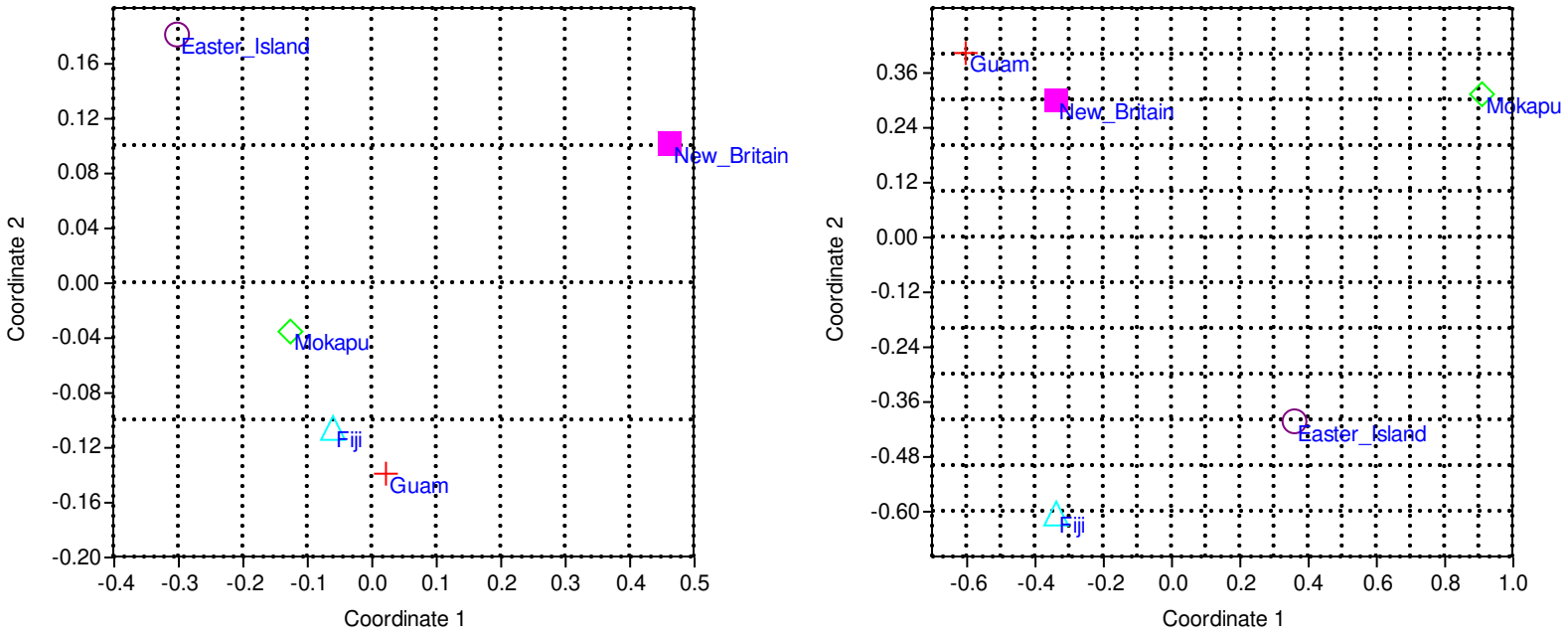

Figure 13: Principal coordinates plots for both sexes based on MMD (left) and Mahalanobis (right) distance matrices for dental non-metric scores and craniometric measurements.

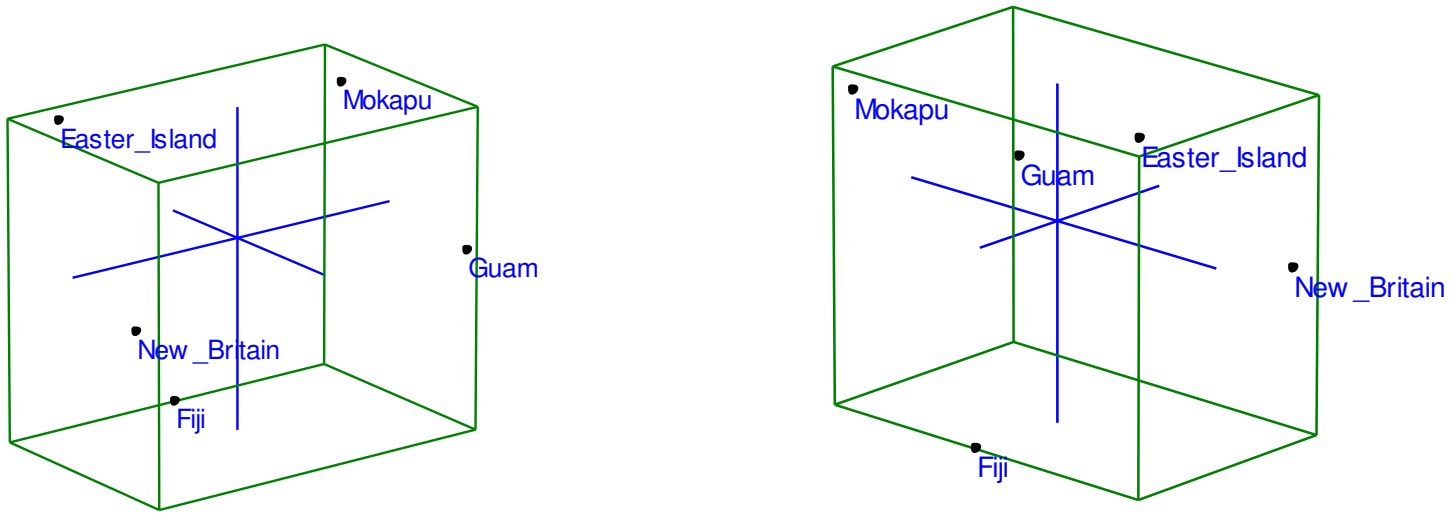

Figure 14: 3D plot of principal coordinates axes 1-3 for males based on Mahalanobis distance matrix for craniometric measurements, rotated along y-axis for better visualization in three dimensions.

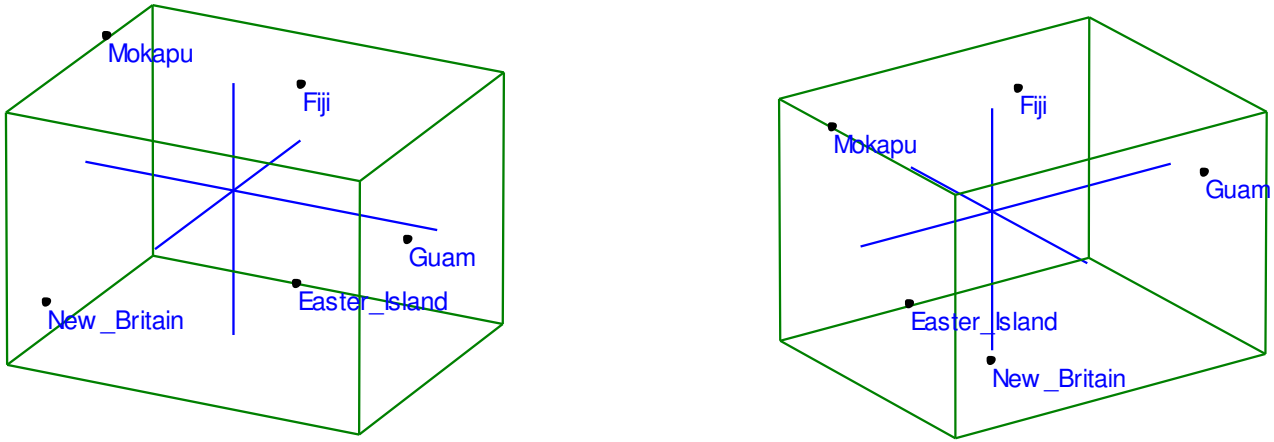

Figure 15: 3D plot of principal coordinates axes 1-3 for females based on Mahalanobis distance matrix for craniometric measurements, rotated along y-axis for better visualization in three dimensions.

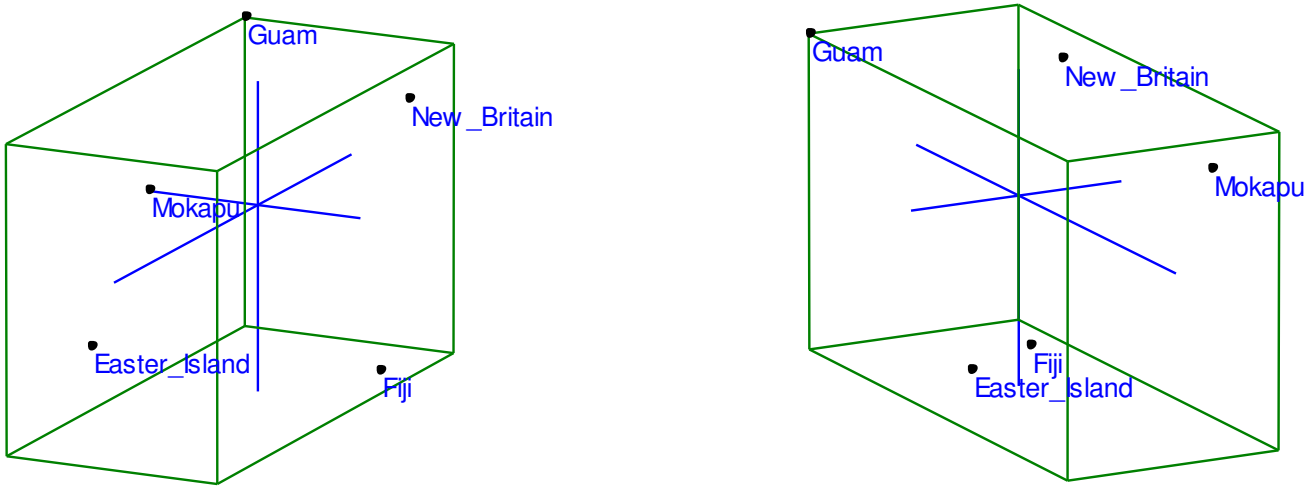

Figure 16: 3D plot of principal coordinates axes 1-3 for both sexes based on Mahalanobis distance matrix for craniometric measurements, rotated along y-axis for better visualization in three dimensions.

Plots of the axes 1 and 2 obtained from principal coordinates analysis on the distance matrices are displayed for MMD and Mahalanobis distances for males, females (Figures 11 and 12) and sexes pooled (Figure 13). Three-dimensional plots for axes 1-3 of the Mahalanobis distances are also displayed (Figures 14-16).

For the MMD plots of the males and females separated, Fiji is isolated in the females, but clusters with Mokapu and Guam in the males. New Britain clusters with Mokapu and Guam in the females but is isolated in the males, while Guam also plots slightly further from Mokapu in the males than the females. For the Mahalanobis distance plots of males and females, all populations plot far from each other and similarly in both sexes, with the exception of Mokapu and Guam, which plot closer for males than females. Comparing the pooled sexes for the MMD and Mahalanobis plots, Mokapu and Fiji. Comparing the pooled sexes for the MMD and Mahalanobis distance plots, Mokapu, Guam, and Fiji cluster in the MMD plot, while these populations are far separated in the Mahalanobis plot, and New Britain plots close to Guam in the Mahalanobis plot and far from all other populations in the MMD plot. The addition of axes 3 in the 3D plots of the Mahalanobis do not drastically alter the relationships already apparent in the 2D plot, with the exception of slightly drawing out distance between the cluster of Mokapu and Guam in the plot of pooled sexes.

Generalized Procrustes Analysis

Table 18: Agreement statistics (Rc) for Generalized Procrustes Analysis consensus configurations.	
Data Combined	***Agreement Statistic (Rc)***
Male Cranial/Female Cranial	0.755
Male Dental/Female Dental	0.757
Female Dental/Female Cranial	0.806
Male Dental/Male Cranial	0.809

Rc values provided for GPA corresponds to the proportion of original variance explained by the consensus configuration, measured from 0-1. A high Rc value indicates that the consensus configuration found an good level of agreement between the two datasets combined. An Rc above .7 is considered to have significantly reduced the variation between the original coordinates. All consensus configurations were significant based on the agreement statistic, with the combinations of data types having slightly higher agreement (0.809 and 0.806 for males and females, respectively) than the combinations of sexes (0.755 and 0.757 for cranial and dental data, respectively).

Table 19: Relative contribution of each transformation to evolution of consensus configuration.			
Coordinates Combined	***Source***	***Fisher's F***	***Probability***
Male Cranial + Female Cranial	*Scaling*	0.002	0.964
	Rotation	8.550	0.026
	Translation	0.000	1.000
Male Dental + Female Dental	*Scaling*	0.135	0.726
	Rotation	1.673	0.243
	Translation	0.000	1.000
Female Dental + Female Cranial	*Scaling*	2.771	0.147
	Rotation	7.866	0.031
	Translation	0.000	1.000
Male Dental + Male Cranial	*Scaling*	3.983	0.093
	Rotation	5.376	0.060
	Translation	0.000	1.000

The Fisher's F statistic for each transformation represents a ratio of the variances before and after transformation, and indicates the relative contribution of the types of transformation to the evolution of the consensus configuration for each comparison (Addinsoft 2015). The probability values indicate which transformation was more efficient in terms of reduction of the total variability. For all consensuses, rotation was the most efficient transformation, and was significant ($p < 0.05$) for all comparisons except Male Dental + Male Cranial. Translation did not contribute to the consensus in any of the comparisons.

Table 20: Residual variance by population for each consensus confirmation.				
	Male Cranial/Female Cranial	***Male Dental/Female Dental***	***Female Dental/Female Cranial***	***Male Dental/Male Cranial***
Easter Island	0.004	0.007	0.101	0.176
Fiji	0.016	0.098	0.327	0.301
Guam	0.000	0.090	0.161	0.336
Mokapu	0.000	0.034	0.290	0.079
New Britain	0.004	0.052	0.046	0.014

R

Residual variance refers to the variance that is left unexplained after the consensus, and identifies for which populations the GPA has been the most efficient (Addinsoft 2015). Lower values indicate that the consensus explains more of the variance in the original data for that population,

and higher values indicate that the GPA has been less efficient and that actual population variance is farther from the consensus.

Table 21: Scaling factors for each configuration.	
Object	***Factor***
Male Cranial	1.013
Female Cranial	0.987
Male Dental	1.121
Female Dental	0.911
Female Dental	1.850
Female Cranial	0.765
Male Dental	2.275
Male Cranial	0.744

Scaling factors represent the magnitude of weighting applied to each object to compensate for differences in the data points for each (Addinsoft 2015). A scaling factor of less than one indicates that the corresponding object encompasses a wider scale relative to the object it is being compared to, while a scaling factor greater than one describes a narrower scale. Scaling factors were wider for males compared to females, and for dental data compared to cranial data. There was a smaller difference between scaling factors for consensuses across sexes than across data types, especially for males.

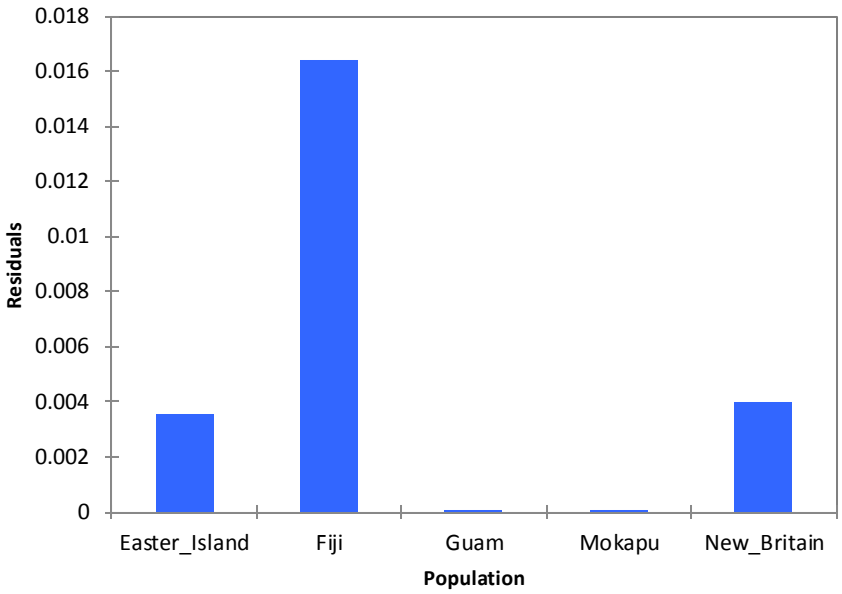

Figure 17: Residuals by population for Male Cranial/Female Cranial consensus configuration

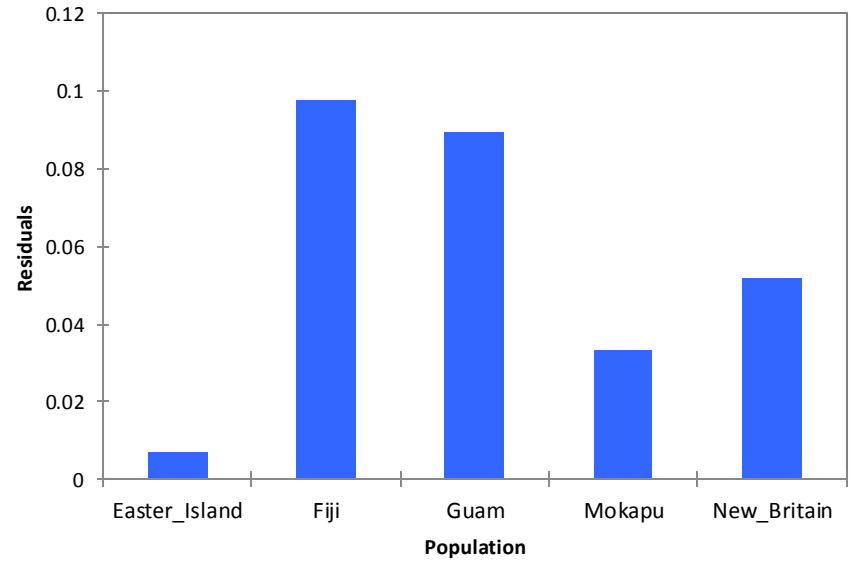

Figure 18: Residuals by population for Male Dental/Female Dental consensus configuration

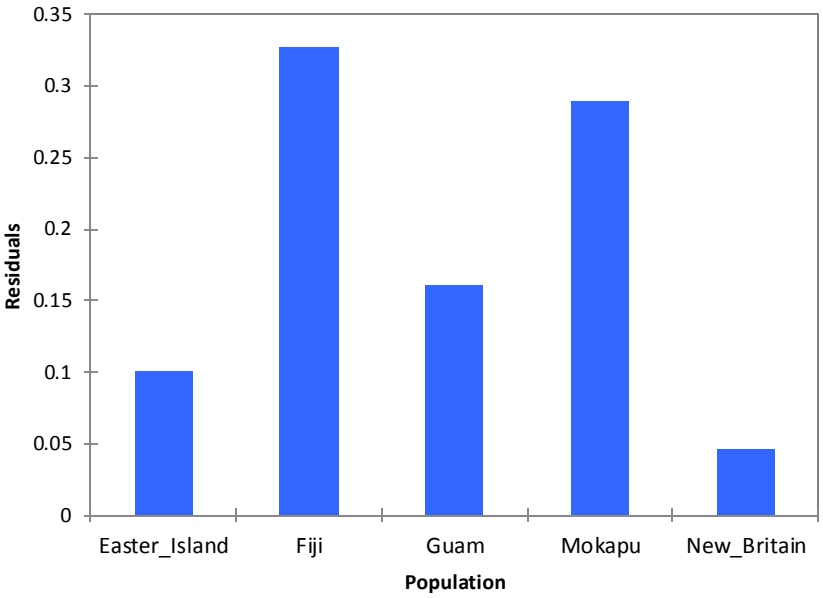

Figure 19: Residuals by population for Female Dental/Female Cranial consensus configuration.

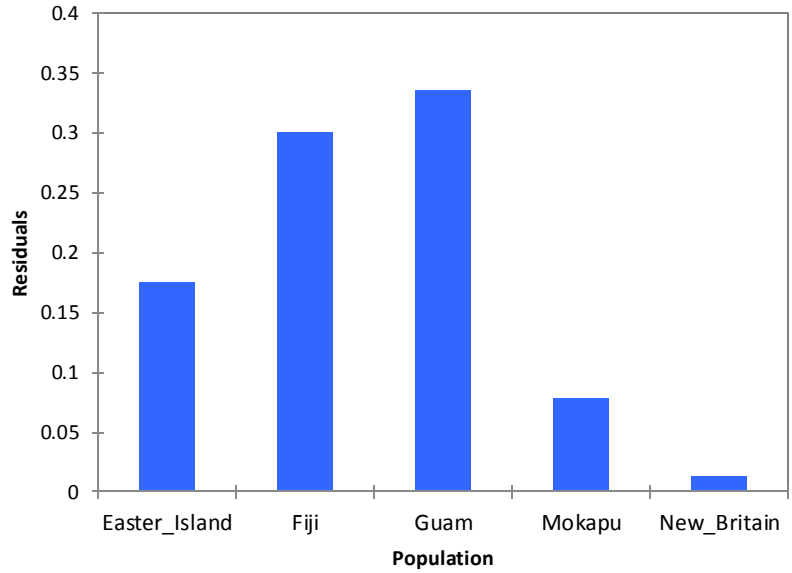

Figure 20: Residuals by population for Male Dental/Male Cranial consensus configuration.

In combining the cranial data for males and females (Figure 17), Guam and Mokapu had no residual variance leftover after the consensus, indicating that the consensus entirely accounts for the variance between these two populations. Fiji had the highest residual value, indicating that much less of the variation in this population is captured by the consensus. For the dental data consensus (Figure 18), all residuals were higher than the cranial data consensus. Fiji and Guam had the least amount of variation accounted for by the consensus, while Easter Island had the most. Residual values were overall much higher in the consensuses of data types by sex (Table 20). Though the residual for New Britain remained low (0.014 in males and 0.046 in females), the high residuals in the other populations indicate a lesser amount of variance captured by the consensus. Male consensus by data type was greater than that of females for Fiji, Mokapu, and New Britain, while Guam was twice as low.

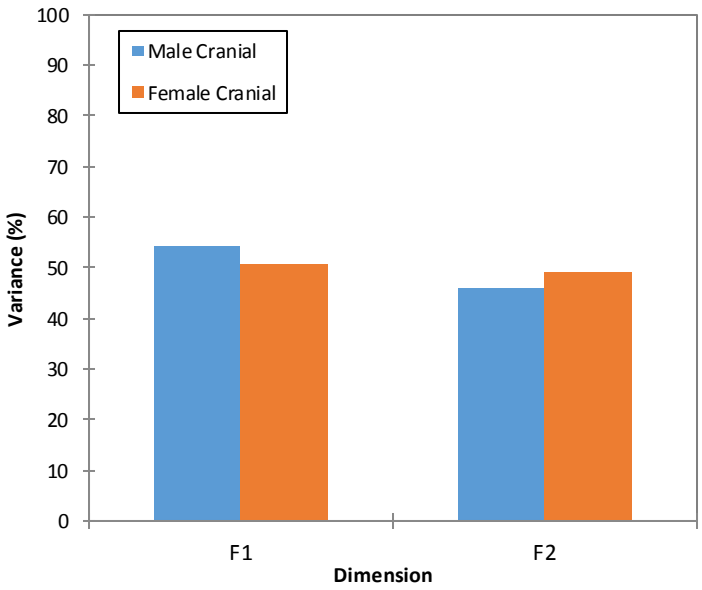

Figure 21: Variance by configuration and by factor for Male Cranial/Female Cranial consensus configuration.

Table 22: Variance and correlations for Male Cranial/Female Cranial consensus configuration

Variance by configuration and by factor (%):		
Configuration	***F1***	***F2***
Male Cranial	54.219	45.781
Female Cranial	50.744	49.256
Correlations between dimensions in the initial consensus configuration and the factors:		
	F1	***F2***
Var1	-0.036	0.191
Var2	-0.599	0.798

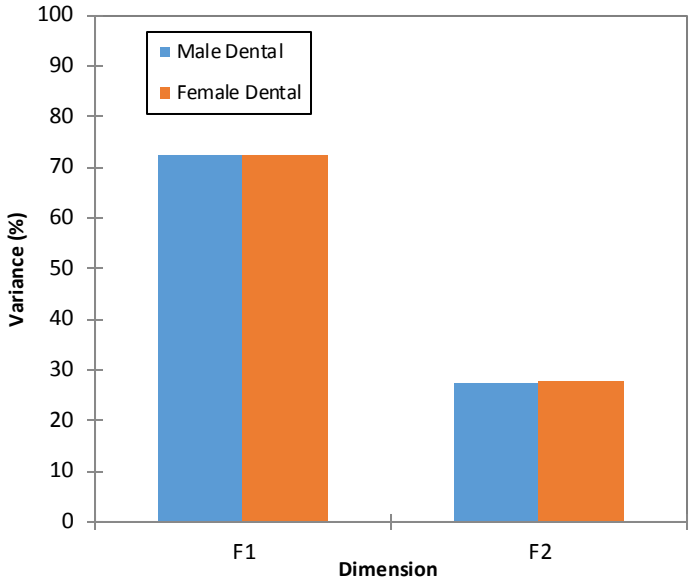

Figure 22: Variance by configuration and by factor for Male Dental/Female Dental consensus configuration.

Table 23: Variance and correlations for Male Dental/Female Dental consensus configuration.

Variance by configuration and by factor (%):		
Configuration	***F1***	***F2***
Male Dental	72.475	27.525
Female Dental	72.366	27.634
Correlations between dimensions in the initial consensus configuration and the factors:		
	F1	***F2***
Var1	0.982	-0.074
Var2	0.254	0.950

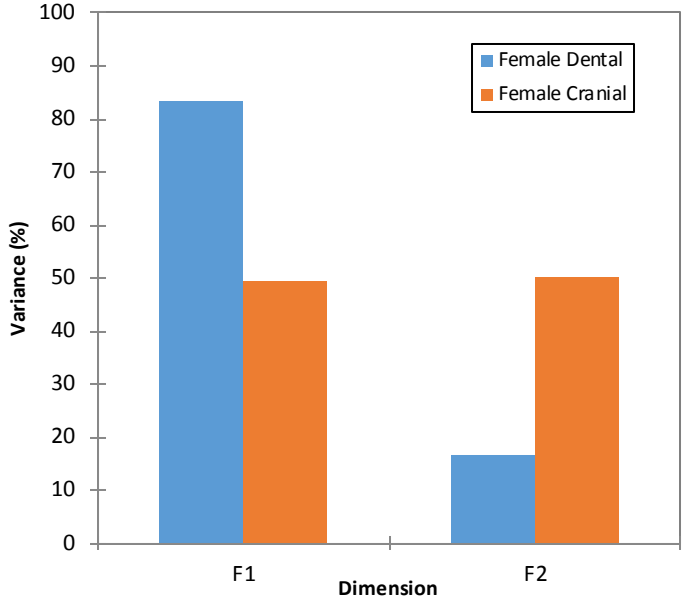

Figure 23: Variance by configuration and by factor for Female Dental/Female Cranial consensus configuration.

Table 24: Variance and correlations for Female Dental/Female Cranial consensus configuration.

Variance by configuration and by factor (%):		
Configuration	***F1***	***F2***
Female Dental	83.376	16.624
Female Cranial	49.618	50.382
Correlations between dimensions in the initial consensus configuration and the factors:		
	F1	***F2***
Var1	0.460	-0.764
Var2	-0.919	-0.095

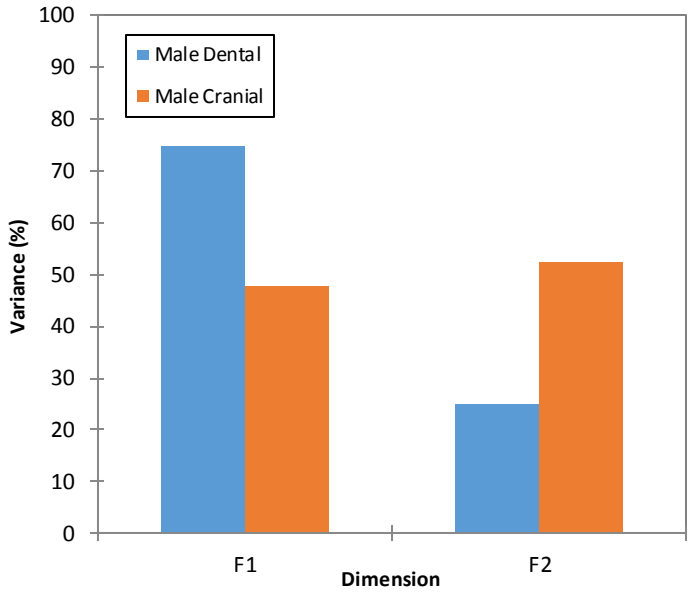

Figure 24: Variance by configuration and by factor for Male Dental/Male Cranial consensus configuration.

Table 25: Variance and correlations for Male Dental/Male Cranial consensus configuration.

Variance by configuration and by factor (%):		
Configuration	***F1***	***F2***
Male Dental	75.019	24.981
Male Cranial	47.621	52.379
Correlations between dimensions in the initial consensus configuration and the factors:		
	F1	***F2***
Var1	0.176	0.925
Var2	0.902	-0.094

The percentages of variance corresponding to each axis that is divided between each configuration in the consensus are modeled by bar charts. For the cranial data consensus, variance was divided nearly equally between each configuration (males and females), and each axis corresponds to nearly to same amount of variance (Figure 21, Table 22). Variance in the dental consensus falls more heavily onto the first axis (F1), but both axes for equal amounts of variance between males and females (Figure 22, Table 23). The consensuses of dental and cranial data by sex show much less equality (Figures 23-24, Tables 24-25). For both males and females, the first axes accounts for most of the variance, while the axes for the cranial data are nearly equal (Tables 24-25).

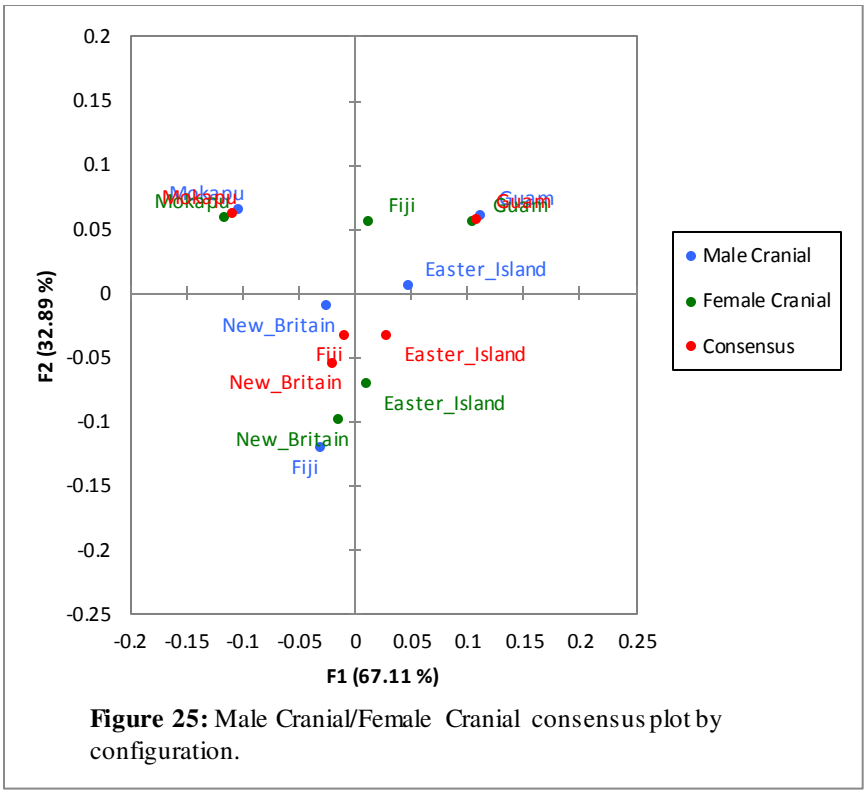

Figure 25: Male Cranial/Female Cranial consensus plot by configuration.

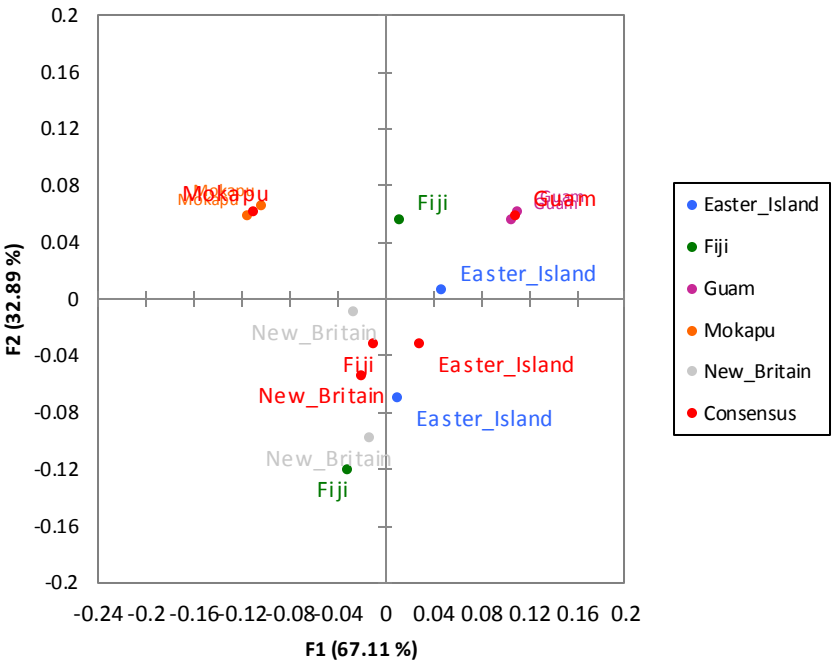

Figure 26: Male Cranial/Female Cranial consensus plot by population.

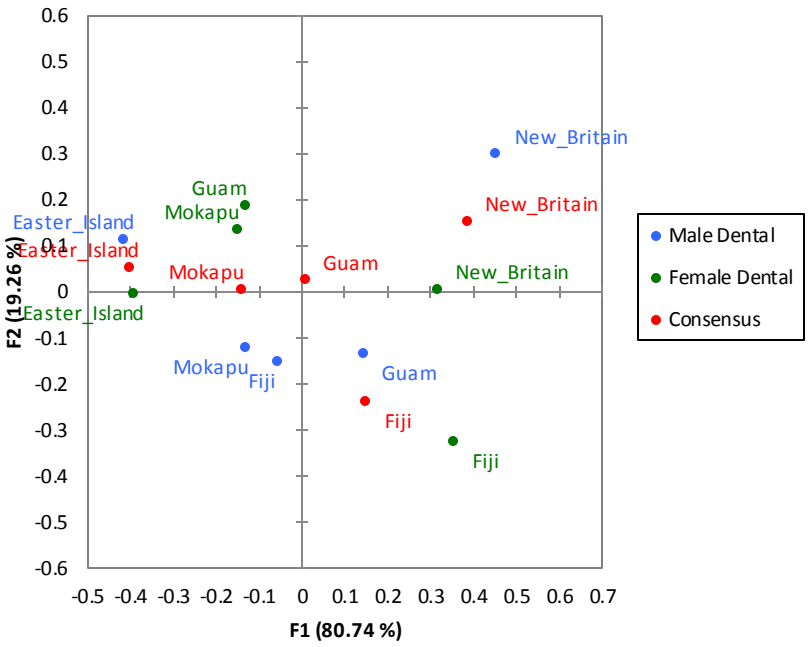

Figure 27: Male Dental/Female Dental consensus plot by configuration.

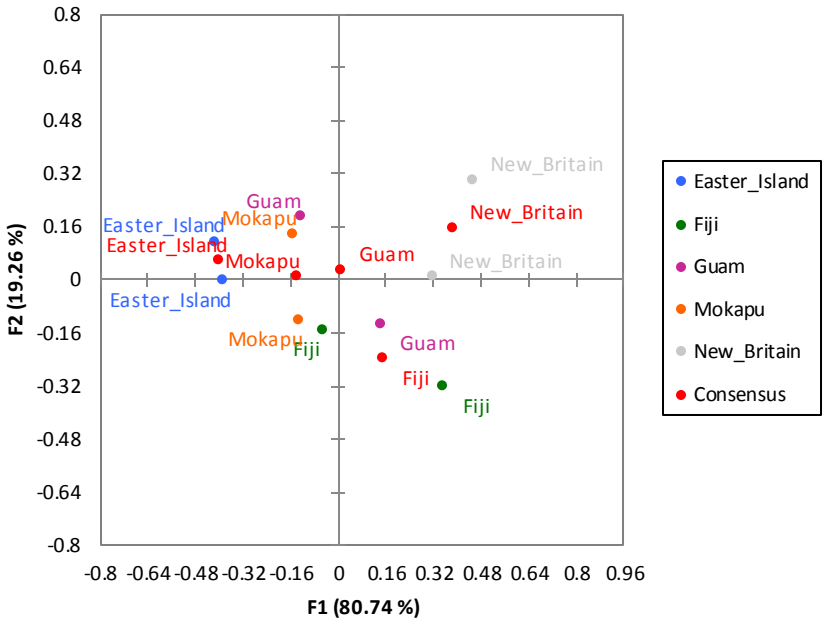

Figure 28: Male Dental/Female Dental consensus plot by population.

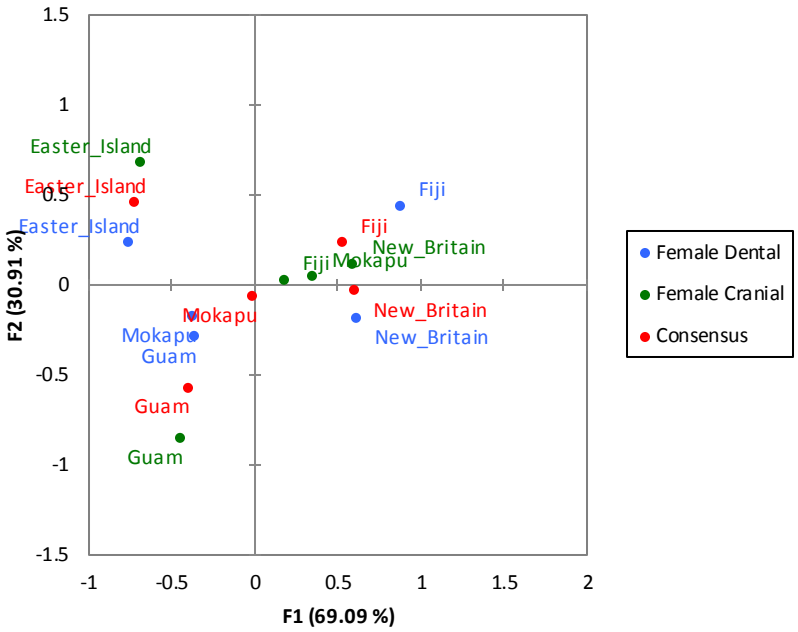

Figure 29: Female Dental/Female Cranial consensus plot by configuration.

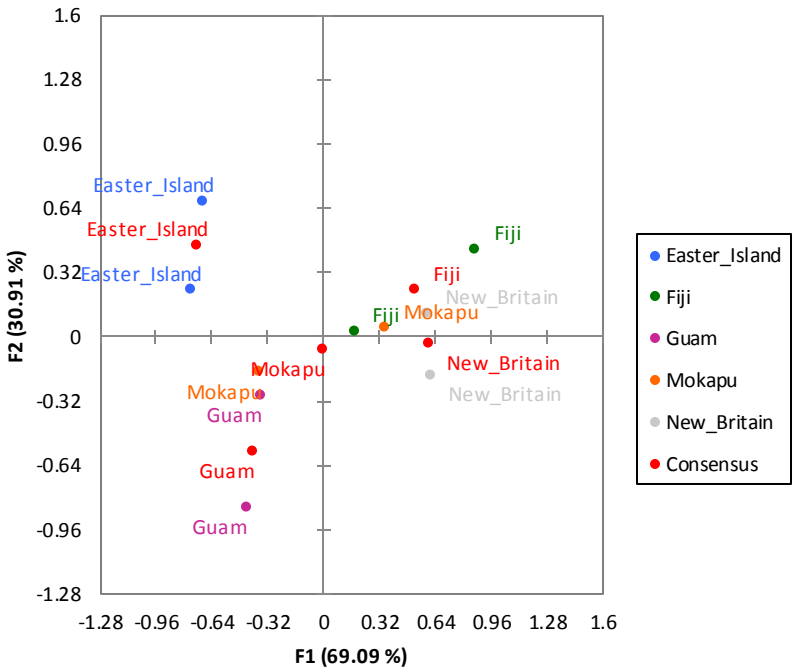

Figure 30: Female Dental/Female Cranial consensus plot by population.

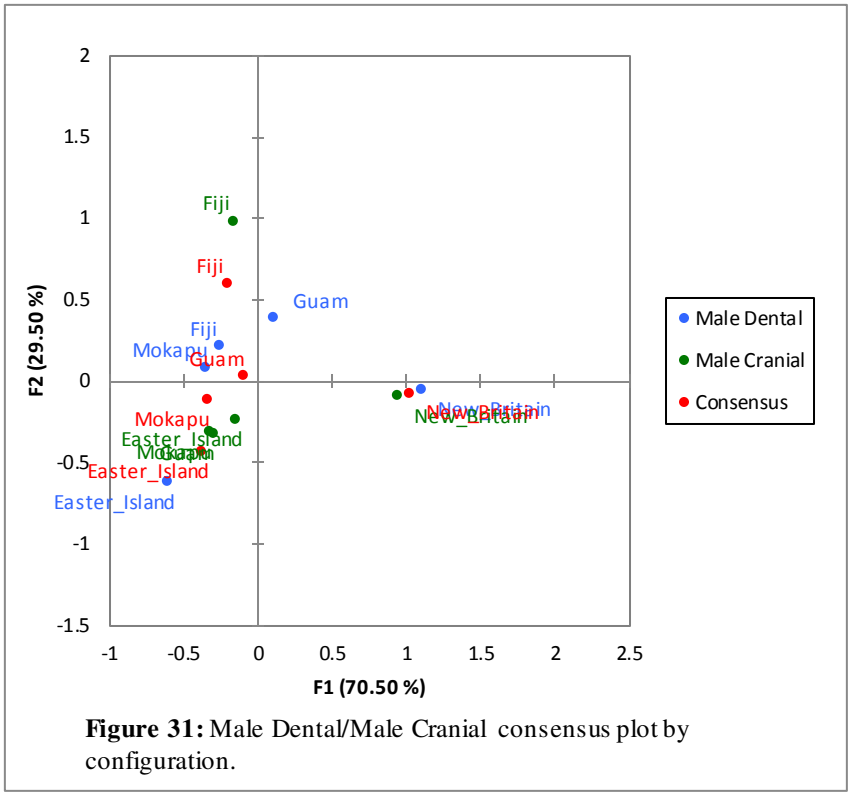

Figure 31: Male Dental/Male Cranial consensus plot by configuration.

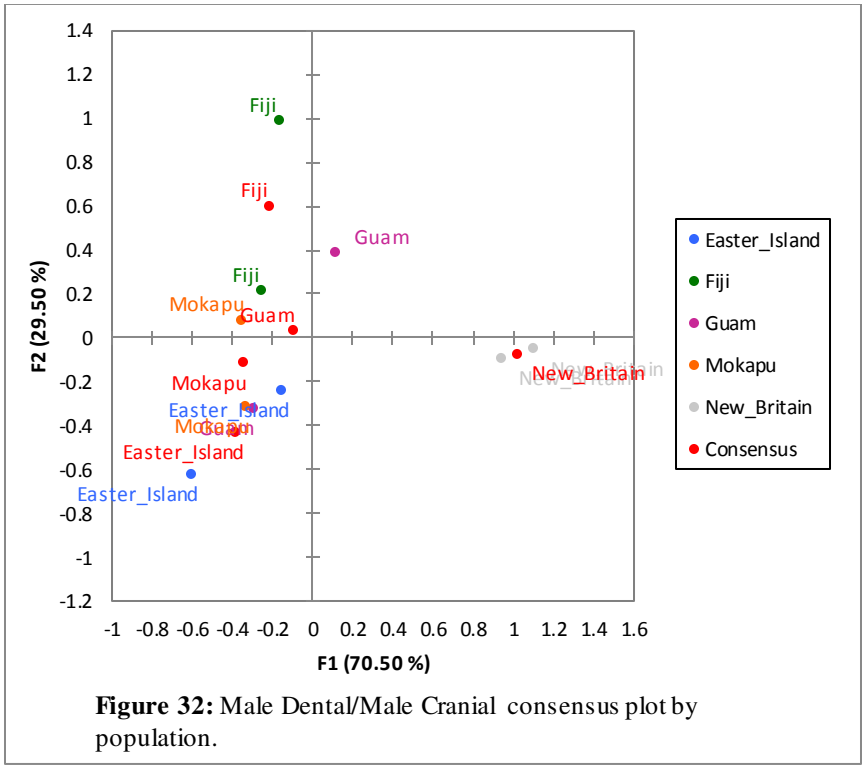

Figure 32: Male Dental/Male Cranial consensus plot by population.

The plots of the consensus coordinates provide a visual representation of how the consensus configurations compare to the original coordinates by configuration and by population. For the cranial consensus (Figures 25-26), both plots show nearly overlapping points for Guam and Mokapu, indicating that there was minimal variance between these populations for males and females to begin with and that the consensus configuration shows a high level of agreement between the sexes. Fiji males and females, however, plot far apart, indicating that the original data was quite different between the sexes and that the consensus captures less of the variance. Though the dental consensus (Figures 27-28) indicates less agreement overall, there is lesser variance and a better consensus for Easter Island and Mokapu than the other populations in this comparison. Combining the data types by sex (Figures 29 and 30 for Females, figures 31 and 32 for Males) appears to be moderately successful, with all original coordinates and respective consensus coordinates plotting relatively close, thought New Britain plots more closely for the males than the females.

Mantel Tests

Table 26: R values (correlation) and p-values (significance, one-tailed) for Mantel tests on MMD (dental) and Mahalanobis (cranial) distance matrices. Similarity measures were Euclidean for MMD matrices and Mahalanobis for Mahalanobis. P-values were averaged over five runs at 10,000 permutations. *Mantel tests performed on object coordinates for the consensus configurations from Generalized Procrustes Analysis.		
Comparison	***R***	***p-value***
Male Dental vs Female Dental	-0.01113	0.46932
Male Cranial vs Female Cranial	-0.345	0.93308
Male Dental vs Male Cranial	-0.06579	0.6166
Female Dental va Female Cranial	-0.4808	0.90774
Pooled sexes Dental vs Pooled sexes Cranial	-0.3615	0.84038
Consensus Configurations for Male Dental/Cranial vs Female Dental/Cranial*	-0.0696	0.58524

Comparisons of cranial data, females, and pooled sexes yielded negative correlations, while those of the dental data, males, and consensus configurations were close to zero. However, all p-values are not significant at a 0.05-level, so the null hypothesis of no relationship cannot be rejected.

Determinant Analysis

Table 27: Results of determinant analysis for dental non-metric scores and craniometric measurements, where the equation equals the natural log of the ratio of the determinants of the covariance matrices (obtained from the first 10 PC's from principal components analysis on each population by sex) for males and females. Because of the small sample size for Fiji females (n=2) in the craniometric data, PCA could not be performed, so mobility of Fijian sexes based on craniometric measurements could not be analyzed.

Dental non-metric scores

Population	Male determinant	Female determinant	ln(|Cov♂| / |Cov♀|)	Mobile sex	Residence pattern
Easter Island	4.95E-13	5.44E-16	6.813649	Males	Matrilocal
Fiji	5.25E-10	4.5E-35	57.71792	Males	Matrilocal
Guam	7.33E-08	3.57E-06	-3.88681	Females	Patrilocal
Mokapu	2.04E-07	8.82E-07	-1.4659	Females	Patrilocal
New Britain	2.61E-07	1.07E-06	-1.41399	Females	Patrilocal

Craniometric measurements

Population	Male determinant	Female determinant	ln(|Cov♂| / |Cov♀|)	Mobile sex	Residence pattern
Easter Island	1.85E+19	3.31E+18	1.719285	Males	Matrilocal
Fiji*	6.72E+11	**Female sample size insufficient*			
Guam	3.45E+19	5.09E+18	1.914813	Males	Matrilocal
Mokapu	1.93E+19	1.35E+19	0.359865	Females	Patrilocal
New Britain	1.27E+19	3.83E+18	1.199137	Males	Matrilocal

For the dental data, the equation was greater than one for Easter Island and Fiji, signifying that males were the mobile sex for these populations, while Guam, Mokapu, and New Britain were less than one, indicating that females were more mobile. The craniometric data showed that Easter Island, Guam, and New Britain were likely matrilocal, while Mokapu was patrilocal. The small sample size of Fiji females in the craniometric data (n=2) prevented determinant analysis from being performed, and mobility for the sexes in Fiji based on craniometrics could not be established.

K-means Clustering

Table 28: K-means clustering assignments for males for 4 clusters for dental non-metric scores.					
	1	***2***	***3***	***4***	**Grand Total**
Easter Island	96	6	1	7	*110*
Fiji	23	5	1	2	*31*
Guam	48	43	8	11	*110*
Mokapu	83	22	8	10	*123*
New Britain	13	24	41	14	*92*
Grand Total	**263**	**100**	**59**	**44**	**466**

Table 29: K-means clustering assignments for females for 4 clusters for dental non-metric scores.					
	1	***2***	***3***	***4***	**Grand Total**
Easter Island	2	8	2	27	*39*
Fiji	0	2	0	2	*4*
Guam	13	4	9	15	*41*
Mokapu	6	32	15	24	*77*
New Britain	17	7	10	10	*44*
Grand Total	**38**	**53**	**36**	**78**	**205**

Table 30: K-means clustering assignments for sexes pooled for 4 clusters for dental non-metric scores.					
	1	***2***	***3***	***4***	**Grand Total**
Easter Island	9	33	101	3	*149*
Fiji	2	7	21	5	*35*
Guam	4	19	70	58	*151*
Mokapu	34	57	68	41	*200*
New Britain	7	16	37	76	*136*
Grand Total	**56**	**132**	**297**	**186**	**671**

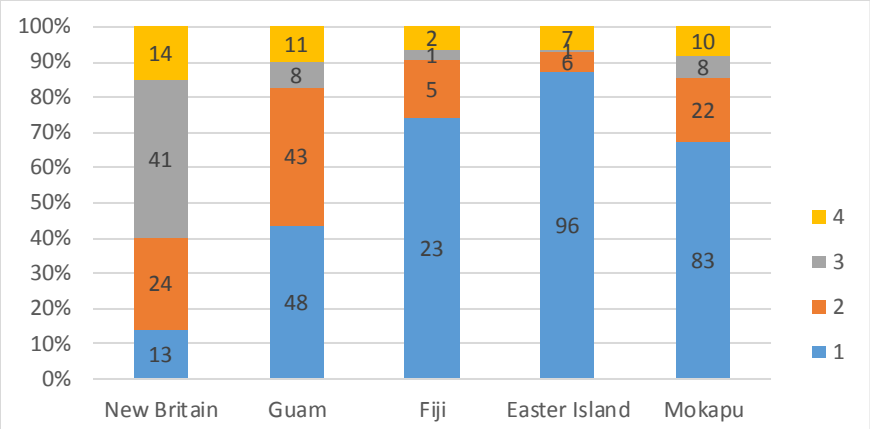

Figure 33: K-means clustering for Male Dental.

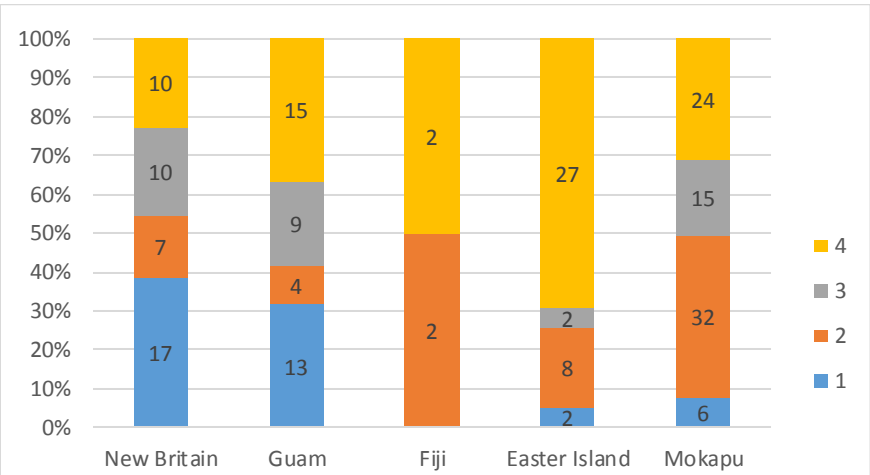

Figure 34: K-means clustering for Female Dental.

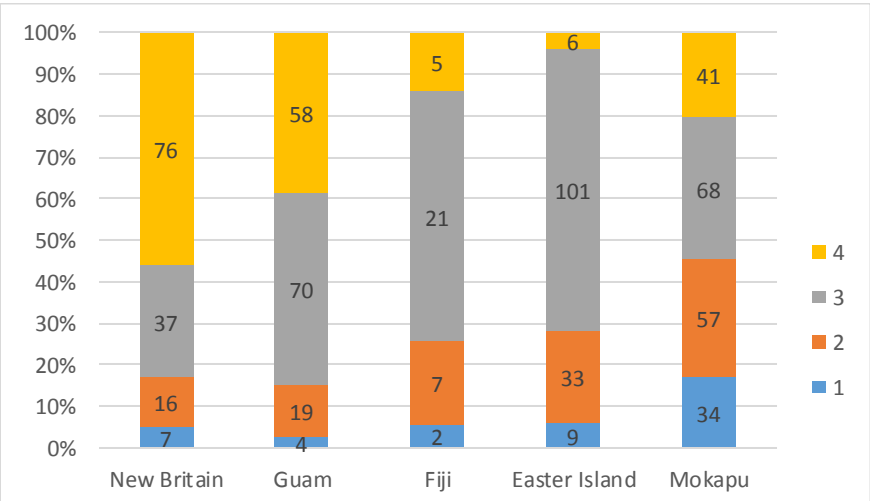

Figure 35: K-means clustering for Sexes Pooled Dental.

Table 31: K-means clustering assignments for males for 4 clusters for craniometric measurements.					
	1	***2***	***3***	***4***	**Grand Total**
Easter Island	28	7	10	3	*48*
Fiji	3	1	1	1	*6*
Guam	2	5	21	4	*32*
Mokapu	5	23	25	1	*54*
New Britain	8	1	2	46	*57*
Grand Total	**46**	**37**	**59**	**55**	**197**

Table 32: K-means clustering assignments for females for 4 clusters for craniometric measurements.					
	1	***2***	***3***	***4***	**Grand Total**
Easter Island	5	17	7	8	*37*
Fiji	0	1	0	1	*2*
Guam	1	10	2	14	*27*
Mokapu	8	27	8	10	*53*
New Britain	35	0	11	8	*54*
Grand Total	**49**	**55**	**28**	**41**	**173**

Table 33: K-means clustering assignments for sexes pooled for 4 clusters for craniometric measurements.					
	1	***2***	***3***	***4***	**Grand Total**
Easter Island	30	19	11	25	*85*
Fiji	2	5	0	1	*8*
Guam	24	4	6	25	*59*
Mokapu	41	13	17	36	*107*
New Britain	4	40	46	21	*111*
Grand Total	**101**	**81**	**80**	**108**	**370**

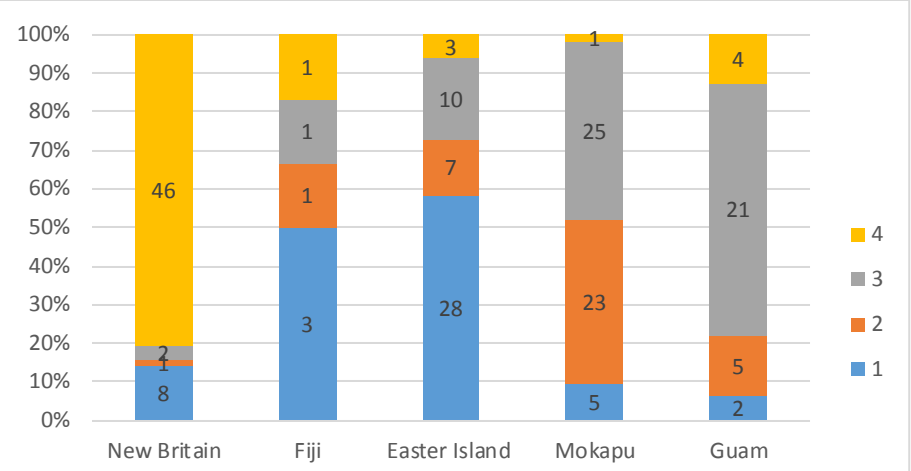

Figure 36: K-means clustering for Male Craniometrics.

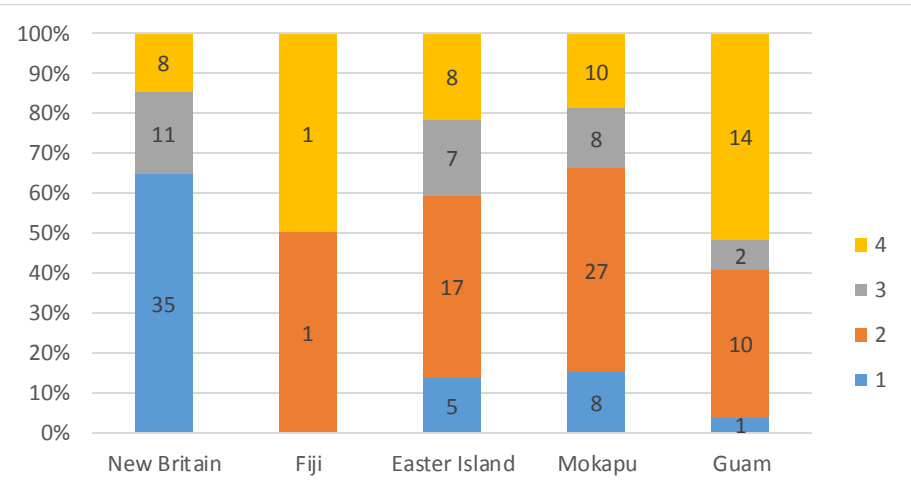

Figure 37: K-means clustering for Female Craniometrics.

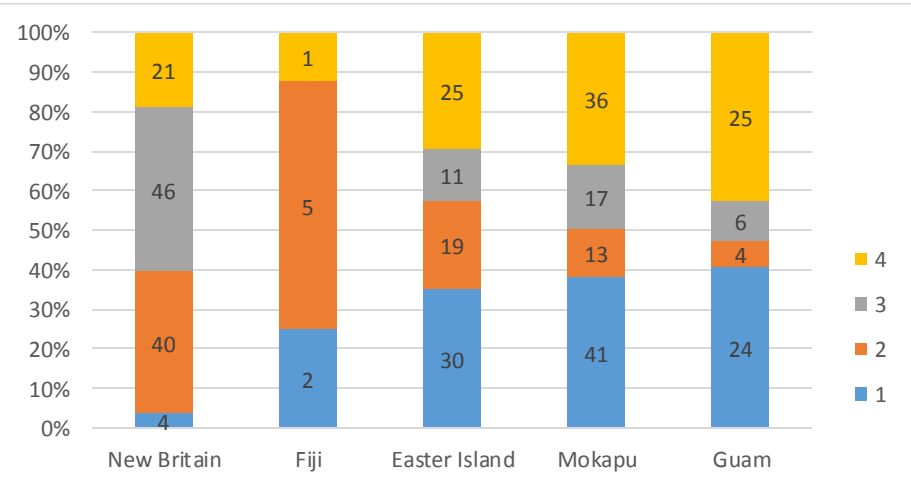

Figure 38: K-means clustering for Sexes Pooled Craniometrics.

K-means clustering assignments are displayed in Tables 28-33. Clusters 1, 2, and possibly 4 (female dental) likely represent a Melanesian component of gene flow, while clusters 3 (dental) and 4 (male cranial) likely represent an Asian component. Individuals are spread more evenly between clusters in females (Figures 34 and 37), and clustering patterns are overall more similar in the cranial (Figures 36-38) than dental data (Figures 33-35).

Chapter 5: Discussion

The two issues of focus in this research are comparing sexes, in order to identify differential patterns of variance as a result of sex-differential migration due to residency pattern, and comparing data types, in order to determine if craniometric measurements and dental morphological variation provided comparable results in analyses of biodistance and to assess their respective uses as proxies for genetic variation in studies of migration and social organization. Where gene flow is restricted between populations due to isolation by distance or a lack of migration, individuals within these groups will tend to become more genetically similar to those within their group, leading to more genetic distinction between separated groups (Wright 1943, Konisberg 1988). This effect is amplified by the effects of genetic drift, which tends to act as a potent factor in small and isolated island populations such as those of the Pacific Islands, especially Remote Oceania. The opposite mechanism, increased migration and gene flow between populations, causes genetic homogeneity throughout these populations to increase with many generations, while individuals within subpopulations are likely to be more distinct from others within that subpopulation. In this case, the potency of genetic drift is lessened due because a larger population is being taken into account. Sex-differential migration causes an unbalanced ratio in the level of gene flow between males and females, resulting in the between-groups variances decreasing while the within-groups variances increase for the more migratory sex the longer such a pattern of migration continues. In a patrilocal society, the migratory sex is female, while males are more migratory in a matrilocal society.

When the issue of sex-differential variance is looked at from an evolutionary perspective, as in population-wide change over time, the traits being utilized must be both heritable and sex-linked. This is because an autosomal allele present with equal frequency in males and female

parents will therefore experience an average of the parental frequencies in offspring, making any comparison of frequencies between the sexes over many generations difficult to draw out without sex-linked traits (Wilkens and Marlowe 2006). However, an analysis such as the present study escapes this conundrum because of the assumptions of unilocal residence, and thus becomes an issue of sampling rather than evolutionary change. Under a matrilocal framework, at the time that males and females are adults, it is assumed that any female adults present in the population are in-group and closely related to the other females there, while any adult males are migrants, as the males from the population of interest have migrated to a different group. Thus, regardless of whether the individuals in question are offspring of in-group females and migrant males, in which autosomal traits could be assumed to be recombined and averaged, adult females will be more closely related than adult males who have migrated in from several different groups and will not be closely related to each other or the females in the group.

There are two broad questions approached with this analysis that will be discussed separately: How do the sexes compare between these populations, and can we elucidate residence pattern? And how do the data types compare, and can they usefully be combined to produce similar results?

5.1. Comparing Sexes

The MMD and Mahalanobis distance matrices displayed differences between the sexes as to distances between populations, but in opposing ways. In the MMD matrix (Table 14), distances were higher overall for males than females, except for all distances with Fiji, in which females showed greater distance than males. This would indicate a higher level of migration in

females compared to males and a more patricentric orientation in residence pattern in all populations, except Fiji, which characterizes a pattern of greater male migration and a matrilocal pattern. The Mahalanobis distance matrix (Table 15) displays an opposite pattern, in which distances between populations are greater overall for females than males, except for Fiji, which shows greater distances for males. However, because of the small and irregular nature of the Fiji samples for both males in females in both the cranial and dental data, it is difficult to say that this dramatic level of variation is representative of the population at large, or represents a concentration of phenotypic anomaly in the few individuals sampled. Additionally, distances between Easter Island and Mokapu are comparatively close in magnitude between females and males in the MMD, while Easter Island and New Britain are similarly close in the Mahalanobis, while distances between Mokapu and Guam as well as New Britain are Guam are close in both matrices.

These relationships evidence a more equal level of gene flow for males and females, and may represent two possible scenarios: areas where a matrilocal or patrilocal residency is giving way to the opposite pattern and is in a state of transition, or where a more ambilocal residency is taking place, allowing equivalent movement of both sexes. Matrilocality, which was often adopted during times of extended male absence due to warfare, extended trips for hunting or resource accumulation, or, as was typically the case during Oceanic expansion, long-term exploratory voyages, tended to give way to ambilocal and eventually patrilocal residency once groups became settled and relatively isolated for an extended period of time (Hage and Marck 2002, 2003, Jordan et al 2009). However, where shifts have occurred more recently, given the recent time of settlement, especially in far east Polynesia, the time lapse since this change hasn't been long enough to show a definitive skew towards one sex (Bolnick et al 2006, Gunnarsdóttir

et al 2011, Kolipakum et al 2011). Furthermore, ambilocality has the benefit of allowing for couples to reside with the spouse's family with more needed or resources or to pool the resources of both of their respective families in times of instability, including early periods of settlement, depopulation events, or warfare (Ember and Ember 1971).

The large distance between Easter Island and New Britain for both sexes in the MMD distances makes sense when looking at the general migration pattern into the Pacific, especially into Remote Oceania. Peoples moved from island Southeast Asia into New Guinea and through the smaller islands of Melanesia to Fiji, where there was a distinct 500-1000 year pause before migration into the wide waters of Polynesia resumed. When it did, migration from this threshold between Near and Remote Oceania was "star-like", with people moving north, eventually to Mokapu, and east, eventually reaching Easter Island (Friedlander 2008). Migrants in the Mokapu region also moved into Micronesia, where back-migration into Melanesia likely occurred. Within this scheme, Easter Island becomes the most genetically isolated from populations in Melanesia, as it is the furthest geographically displaced and not in any networks of gene flow via back-migration. Additionally, the "pause" in Fiji and the occurrence of repeated founder's effects as people moved across the wide expanse of the Polynesian triangle had led to a high level of genetic homogeneity in the peoples that ended up settling Easter Island (Spriggs and Anderson 1993, Houghton 1996, Hurles et al 2002, Kirch 2010). This pattern explains why distances between New Britain and Mokapu as well as New Britain and Guam are also large, considering that Mokapu and Guam, settled either contemporaneously or after Easter Island, are far displaced from New Britain both temporally and along the route of migration, though possible subsequent back-migration with New Britain through Micronesia is a possibility and would slightly decrease these distances (Matisoo-Smith et al 2004). The route of migration also elucidates why Easter

Island and Mokapu are similar, considering that the only population in this study that the peoples of Easter Island were sharing any genes with post-settlement was Mokapu.

Comparing the Principal coordinates plots from males and females in the dental data (Figure 11), three differences are observed. First, Fiji is far displaced from all populations in the females, but clusters with Mokapu and Guam in the males, suggesting increased male gene flow between these populations and possible matrilocality. Second, New Britain is distant from the other groups in males while it plots slightly nearer to Mokapu and Guam for females. Third, Guam plots slightly farther from Mokapu in males while it closer to Mokapu in females. The PCo plots from craniometric data show a wide distance between all populations with no obvious clustering for both sexes. Mokapu and Guam plot more closely in males while plotting far apart in females, again suggesting increased male gene flow compared to females, with Fiji plotting closer to Mokapu in the females, possibly indicating more female gene flow between Mokapu and Fiji than that of males (Figure 12).

Again, because of the anomalous nature of the extremely small sample size for Fiji in all comparisons (sex and data type), its differential placement between males and females must be approached with caution, as it likely does not represent a realistic level of variation for this population. However, if accurate, the difference in the positioning of Fiji between males and females, especially clear in the dental dataset, is characteristic of matrilocality in Fiji, with a distinction between populations in females and an analogous lack of distance in males. With Mokapu and Guam plotting close to Fiji in males, this suggests that these two populations were in a network of gene exchange with males migrating between these populations to marry in with local women. However, this pattern is not picked up for Fiji in the craniometric PCo plot, with Fiji actually plotting closer to Mokapu than in the females than the males, which may be a

further product the anomalous nature of the Fijian samples in either or both of the datasets. The close grouping of Mokapu and Guam is visible across both data types for males, with these two populations also plotting closely in females based on dental data, but separating in the PCo based on craniometric data (Figures 11 and 12). While the differential spacing of these populations in the craniometric data suggests an increased male gene flow between them compared to female gene flow and thus a matrilocal pattern, there is still enough distance in both instances to consider a existence of an ambilocal residence pattern between them, with equal migration of both sexes, or of a society in transition from a unilocal to an ambilocal pattern or vice versa. Likewise, New Britain plots closer to Mokapu and Guam in the female dental plot but far from all others in the males, possibly indicative of patrilocality in New Britain or a continuation of this style of practice as settlement progressed across Remote Oceania, but plots similarly far from these two in the craniometric plots. Differences between data types will be explored in the next section.

It is important to note the difference in eigenvalues and percent-variance captured for the PCo analyses of the MMD and Mahalanobis distance matrices. In all three analyses of the dental/MMD data (male, female, and sexes pooled), the majority of the variance among the samples is captured on the first two axes, with at least 90% explained by the combination of axes 1 and 2 (Table 16). This means that the plots of these coordinates in a two-dimensional plane displays most of the variation within the dataset and thus gives an accurate visual depiction of the distances between populations. In the PCo analysis for the Mahalanobis distance matrix, axes 1 and 2 capture approximately 70% of the variation in the data, thus a two-dimensional plot of these axes excludes up a third of the total variation. In order to more comprehensively model the variance within the cranial data and possibly draw out more differences between the sexes

that could be hidden without the third axis, three-dimensional plots were utilized to visualize the variation across more than two axes in male and female craniometrics (Figures 14-16). Doing so drew out a separation between Mokapu and Guam along the additional axis in the males, while this cluster was maintained in the females. New Britain and Easter Island appeared closer with the addition of axis three in the males, as did Easter Island to Mokapu and New Britain to Guam in the females. Fiji, however, maintained a large distance from all other populations along all axes in both sexes. However, these considerations do little to change the overall pattern that was already apparent with axes 1 and 2, and the relationships between populations that are close or more distant are maintained between the two types of plots.

5.2. Comparing data types

Comparison of the MMD and Mahalanobis distance matrices is a comparison of the distances between populations based on dental data, versus those distances based on cranial data. The most notable difference between these two matrices is that the range of distances in the Mahalanobis (Table 15) is more restricted than in the MMD (Table 14), both in each sex over both data types and in the pooled sexes between the two. Although distances from Fiji remain relatively large, those of the populations with more stable samples are all within a 0.02 range. Though the differences between male and female distances within the Mahalanobis matrix, with female distances generally slightly larger than male distances, theoretically indicate presence of a matricentric migration and residence pattern, the differences are too small to rule out an ambilocal residency as the source. Though this "flattening affect" can partially be accounted for by the nature of Mahalanobis distance, this reduction in distance may also be indicative of a

reduction in variation in craniometric measurements overall, over both the populations of study and the sexes.

Because of the canalized nature and lack of remodeling in response to environmental factors in dental morphological traits, the variation in phenotypic expression is expected to mirror that of the underlying genotypes. However, because cranial size and shape remodel in the presence of environmental insult, the underlying variation in the genes that impact these traits can be masked by a heavy environmental influence, smoothing out the variation within populations, as well as between those in similar environmental conditions. This pattern could account for the wider range of distances observed in the MMD based on dental traits relative to those in the Mahalanobis matrix based on craniometric measurements, drawing out the variation in the dental samples and smoothing it in the cranial data. Also important to note is the possibility of purposeful cranial deformation as factor in cranial shape in these populations. Literature on cranial modification in Oceania is limited, with the only evidence coming from New Britain (Blackwood and Danby 1955), while the practice has also been reported in Philippine (Suzuki et al 1993) and prehistoric Australian samples (Anton and Weinstein 1999). Because of the limited evidence of intentional cranial modification in this region, it is not considered to have a notable effect on the cranial sample in this study.

PCo plots of each sex individually (Figures 11 and 12), as well as the sexes pooled (Figure 13), were also compared across data types. While all populations were spread far apart from each other in the plot for males based on craniometrics, Mokapu, Fiji, and Guam form a cluster in the dental plot, with Easter Island and New Britain spaced far apart and far from the cluster. A clustering of Mokapu and Guam is observed in the dental plots for females, although not in the cranial plot. New Britain and Easter Island females plot close to each other in the

craniometric plot and far apart in the dental, while Fiji remains distantly isolated in the dental and placed between Mokapu and Guam in the cranial. Looking at PCo plots of all individuals not decomposed by sex, the two clusters observable between the data types manifest opposingly:

Mokapu, Guam, and Fiji clearly cluster in the dental data, while these populations are widely separated in the craniometric plot, and New Britain and Guam plot close to each other in the craniometric data while they maintain distance in the dental. Overall, PCo plots of Mahalanobis distances display a wide spread between all populations in both sexes, while the plots of MMD distances are slightly more constricted, thus drawing out a minor clustering pattern.

5.3. Comparing both sexes and data types

Four combinations of data were utilized in the Generalized Procrustes Analysis: male cranial + female cranial and male dental + female dental to determine how well the sexes could combine within each data type; female dental + female cranial and male dental + male cranial to determine how well the data types could be combined within each sex. The Rc values, which indicate the proportion of original variance explained by the consensus, are high for all comparisons (Rc> 0.7), indicating that the consensus found a good level of agreement between the datasets that were combined (Table 18). The data types combine slightly better within each sex than the sexes combine within each data type, but the data types combine the sexes equally well, as do the sexes combining the data types. Analysis of the residual variance leftover after each consensus, however, shows that more variance was left unexplained after combining data within sexes that combining sexes within data types, indicating that the agreement had to leave out some variation in order to force the consensus (Table 20, Figures 17-20). The very small

residual variance combined with a high Rc agreement statistic for the male cranial/female cranial and male dental/female dental consensuses show that there was not a lot of variation between the sexes, allowing the datasets to easily and informatively be combined. In addition, the smaller residuals in the cranial consensus further indicate that the cranial data shows a reduced level of overall variation compared to the dental data. The differences between data are further exemplified by the fact that more residual variance was leftover when combining data types across sexes than combine within data types. A greater difference in scaling factors between the groups in the consensuses of sexes across data types also indicates that they were more difficult to combine than sexes within data types (Table 21). Furthermore, there was twice the residual variance for the combined data in males than females in the Guam sample, while the Mokapu and New Britain samples had nearly three times the residual variance in females than males, indicating there was a lot more variation, which could not be captured by the consensus, for these sexes than in the opposite sex. Similar to the PCo axes, variance was nearly equally captured between sexes and between factors for the cranial data in all consensuses, while the variance in the dental data was concentrated in the first factor (Table 22-25). Additionally, males and females were represented equally across both factors in the male dental/female dental consensus, with, again, more variance captured by the first factor.

All comparisons for the Mantel tests (Table 26) were negatively correlated, which the correlation between dental and cranial data in the females being the largest in magnitude at -0.4808, indicating the greatest amount of similarity between them out of all comparisons tested. The comparison between male and female dental data, male dental and male cranial data, and the consensus configurations from Generalized Procrustes Analysis yielded correlation values close to zero, indicating that there is no correlation, and thus greater variation, between the data in the

two sets in each comparison. Overall, the lack of correlation in the dental data over the sexes compared to the negative correlation between the sexes in the cranial data suggests a slightly less variation in the cranial data and greater variation, and thus no correlation, in the dental data. A similar relationship in the males over both data types (close to zero) and females over both dental and cranial data (negative correlation). However, the average p-values are not significant at the 0.05 level, so the null hypothesis that there is no relationship between the variables cannot be rejected.

The results of the Mantel test for the Male Cranial/Female Cranial, Female Dental/Female Cranial, and Pooled Sexes Dental/Pooled Sexes Dental yielded decently negative correlation values, yet had highly insignificant p-values (Table 26). Thought intuitively contradictory, there are several possible explanations for this unique result. First, the relationships between the populations could be similar (and opposing, because of the negative correlation) in both matrices, but the magnitude of the differences between the populations based on the two distances are so large that the relationships cannot be considered significant. However, this does not seem to be the case for the particular comparisons in which this result was produced. Second, and more likely the case here, the small number of populations being compared here only allows for a small number of permutations to be calculated, less than the PAST default of 5000 and the 10,000 permutations utilized in this study. The redundancy produced the permutations because of this may also have contributed to the non-significant p-value.

Determinant analysis (Table 27) helps to elucidate differential mobility of the sexes by comparing their relative variances, and can be examined separately for each data type to see how their results compare. Where the equation is greater than one, males are more mobile than

females, and the residence pattern can be assumed to be matrilocal. When the equation equals less than 1, females are the more mobile sex, and patrilocality is assumed. For analysis of the dental data, the matrilocal pattern holds true for Easter Island and Fiji, while Guam, Mokapu, and New Britain appear to be patrilocal. The cranial data yields matrilocality in all populations except Mokapu. It must be noted that because of the small sample size of Fiji females in this data set, determinant analysis was mathematically impossible for this population, so mobility of the sexes in Fiji could not be assessed from the craniometric data. Similarly, the ratio produced from determinant analysis of the dental data was extremely high, nearly ten times the value of the next greatest ratio. These extremes are likely a product of the small sample sizes for this population, causing the equation to behave in a way that is uninformative for this analysis. What is notable from determinant analysis is that the dental and cranial data do not agree. Although Easter Island is matrilocal in both data sets, the ratio is much more heavily skewed towards males in the dental data (6.814) than in the cranial (1.719). Likewise, the patrilocal pattern evidenced in Mokapu for the cranial data is close to double that of the dental data. Additionally, the range of determinants for each sex is far more constricted in the cranial (Fiji males excluded) compared to the dental data, and is similarly much closer between the sexes. This is further evidence for a less variable cranial sample and more apparent variation in the dental sample.

K-means analysis is a clustering method that partitions similar individuals into a specified number of sets (4 in this analysis) (Tables 28-33). The way in which individuals are divided and the relative size of the clusters between populations can be compared to make inferences about components of gene flow and subsequent migratory routes. For both dental and cranial datasets, individuals are spread more evenly between the clusters in females (Figures 34 and 37) than males (Figures 33 and 36), most markedly in Easter Island and Mokapu, indicating that there is

more variation within these populations for females than males, though this effect is to a lesser degree in the cranial data. Additionally, between populations within each sex, there is a greater difference in partitioning between clusters in males than females. The difference in clustering patterns are overall more similar between the sexes in the cranial than the dental data.

As far as drawing out components of gene flow from the K-means clustering, a few inferences can be made, but are obscured by general similarity in cluster size, especially in the cranial data, as well as the difficulty in assigning Fiji females, considering their small sample sizes. Cluster 1 and cluster 2 (perhaps cluster 4 in the female dental assignments) likely represent a Melanesian component of gene flow; it is present in New Britain, increases in magnitude in Fiji, and dominates Easter Island. This is in line with the notion of subsequent bottleneck effects with migration across Polynesia, with a homogenization of genetic variance apparent by the time populations reach Easter Island. Additionally, clusters 3 (dental) and 4 (cranial males) show an opposing pattern, with high levels in New Britain and Fiji and a low representation in Easter Island, likely indicative of an Asian component of gene flow that dissipates as the Melanesian component takes over as populations move east, though this component could not definitively be drawn out in the female craniometric data. Both components appear and start to increase again in Mokapu and Guam, indicating a possible reconnection of gene flow with Melanesian and Asian populations as people moved back north into Micronesia. However, all of these indications of directions of gene flow are subtle, and especially considering the erratic nature of the Fiji samples in these analyses and the lack of representation of populations in central Polynesia or eastern Micronesia, these inferences should be approached with caution.

5.4. Limitations

There were several assumptions that had to be made in order to conduct this research, and numerous limitations that must be considered when analyzing the results of this data. I will address these limitations below.

Interobserver error and error due to inexperience were reduced through use of these particular datasets. Observations were made entirely by the credited individuals (Turner and Howells), who are considered masters in their field and with their scoring and measuring methods. However, because intraobserver error could not be evaluated for these datasets, the possibility of idiosyncratic measurement or scoring error cannot be eliminated.

While the cranial and dental data came from the same populations with similar provenances, it is not known that they were measured from the same individuals. Therefore, incongruence between the datasets may be partially due to variation between individuals rather than solely due to variation between dental and cranial features within individuals. Additionally, the sample dates provided were wide and nonspecific, ie "1400-1790 AD" or "historic", if they are known at all. The temporal discrepancy between samples could add variation that is representative of the difference in time of death between individuals, rather than exemplifying population differences or discrepancies between dental and cranial data. Similarly, the ages provided for were nonspecific, although all individuals included in the study were described as "adult". Though cranial form and tooth crown development are assumed to be fully formed by this time, it is possible that young or elderly adults could measure smaller in cranial size. While status/wear was noted on the ASUDAS score sheets for all present teeth, heavy wear (grade 1+) can greatly obscure the observability of crown features, so that traits that are present in the genotype are not observable in the phenotype and are thus falsely unaccounted for. Heavy wear

is more likely to be present in older individuals. Furthermore, estimations of sex for unknown individuals is assumed to be correct, while it is widely accounted that individual variation resulting in "robust" females and "gracile" males can skew sex estimation. There were a number of individuals in the dental data assessed as "possible male/female" (ie M? or F?) that were subsequently pooled with "probable male/females" (M and F, see Table 5) in order to increase sample sizes. These questionable remains were assumed to actually represent male and female individuals, but could possibly have been assessed as the incorrect sex due to idiosyncratic variation.

Table 34: Percent composition of cranial and dental datasets by sex and population.

Cranial

	M	***% of males***	***F***	***% of females***	***Total***	***% of total***	**% of total sample by sex**	
Easter Island	48	**24.4**	37	**21.4**	85	**23.0**		
Fiji	6	**3.0**	2	**1.2**	8	**2.2**	***Males***	53.2
Guam	32	**16.2**	27	**15.6**	59	**15.9**	***Females***	46.8
Mokapu	54	**27.4**	53	**30.6**	107	**28.9**		
New Britain	57	**28.9**	54	**31.2**	111	**30.0**		
	197		**173**		**370**			

Dental

	M	***% of males***	***F***	***% of females***	***Total***	***% of total***	**% of total sample by sex**	
Easter Island	110	**23.7**	39	**19.0**	149	*22.2*		
Fiji	30	**6.5**	4	**2.0**	34	*5.1*	***Males***	69.4
Guam	110	**23.7**	41	**20.0**	151	*22.5*	***Females***	30.6
Mokapu	123	**26.5**	77	**37.6**	200	*29.9*		
New Britain	92	**19.8**	44	**21.5**	136	*20.3*		
	465		**205**		**670**			

Differences in sample size could also have spuriously skewed statistical analyses (Table 33). While the ratio of males to females represented in the craniometric dataset was nearly equal (53% and 46% of the total sample, respectively), there were more than double the number of males to females in the dental dataset, with 69% of the sample comprised of males and 31% of females. When considering how the populations break down by sex, the populations are more equally represented in both the male cranial and dental data, while the female data is more lopsided, which approximately 60% of the individuals represented coming from the Mokapu and New Britain samples in both datasets. The most glaring discrepancy in sample size is the enormous difference in individuals represented by Fiji compared to the other populations over both sexes and in both datasets. Fiji males and females make up just 3% and 1.2%, respectively, of the cranial data, and 6.5% and 2% of the dental data. The notable differences exemplified by Fiji populations in the analysis must be approached with extreme caution, taking into account the minor amount of the overall data that they represent. While these differences may denote actual population-wide differences between Fiji and the other samples, it is just as likely that these individuals may represent outliers in this population and are not representative of the variation in the overall population.

In order to have a dataset best reflected the variation within and between sexes as well as populations, many dental traits were eliminated from analysis to yield a trait list that was uncorrelated, not sexually dimorphic, and comparable between males and females (see Table 11). Though this final trait list is assumed to best represent the variation present in these populations, any loss of traits is loss of variation. Additionally, any teeth that were not present were not scored, representing a large number of missing values within the dental dataset. Though

these missing values were accounted via pairwise and imputative deletion in the statistical analysis, variation is nonetheless lost. Also, statistical manipulations, including those made to account for missing values and removal of the correction factor for MMD analysis, were necessary to force the statistics to run, but are also possible sources of error in the final results.

The osteological paradox is a limitation that applies not just to this study in particular, but to all bioarchaeological studies in which conclusions are attempted to be drawn about the entirety of a population from a subset of individuals from that population (Wood et al 1992, Cohen et al 1994, Wright and Yoder 2003). Research design and subsequent analysis is built within a framework that assumes that the subset is statistically representative of the whole, and that variation that presents itself in the population will manifest itself proportionally at a smaller scale in the sample. This assumption, while necessary to extract any sort of meaning from limited archaeological samples, must be taken into consideration when attempting to make wide sweeping remarks about past populations. A variety of factors limit the number and type of individuals recovered from an archaeological site, including but not limited to age, health, cause of death, mortuary ritual, climate and environment, method of survey and excavation employed, and which area is chosen to excavate and to what spatial extent. Additionally, the remains that eventually end up curated in collection facilities often meet certain criteria that eliminate a portion of the total recovered sample, and which of these individuals are chosen to be included in studies or for measurement are further reduced by completeness and ability to accurately estimate sex and age if unknown. The resulting sample may or may not be statistically representative of the population as a whole. This is an issue that no doubt needs to be taken into account here.

Finally, this study was conducted based on a very small number of populations. Though populations of study represent the geographical extremes of the Pacific Island region, and thus encapsulate the continuum of variation represent within, an enormous geographical area was not represented in this study.

5.5. Future Research

Three specific elements would greatly aid future research in a study of this nature. First, increasing representation of the vast Pacific Island region by including larger sample sizes and a greater number of populations would expand and clarify the results obtained here. The cultural and migratory patterns of this region are extremely complex; with a more complete picture of the variation representing it, more robust inferences could be made about the history that molded it. Having data from populations within central Polynesia as well as eastern Micronesia would better elucidate gradations of variation occurring along migration routes that resulted in the extremes exemplified by their endpoints. Additionally, data from Southeast Asia would give greater insight on gene flow coming from this region as well as the relative speed of movement and amount of admixture that occurred during expansion into the Pacific.

Second, in order to better compare the interplay between the relative variation represented by dental morphology, craniometrics, and genetics as well as the utility of employing these data separately or in conjunction, it is necessary to have data sets that are known to have come from the same individuals. Being able to compare how these traits differ within the individual, rather than relying on representative samples, gives a more direct answer as to how they covary. Additionally, utilizing contemporaneous samples would eliminate spurious variation due to temporal incongruence.

Finally, having genetic data would allow for further exploration of the utility of physical features such as dental morphology and craniometrics as proxies for underlying genetic variation. Additionally, this would clarify which manifest features more directly correspond to their underlying genotypes, and which are more heavily influenced by environmental factors.

Conclusion

This research aimed to utilize variance in dental morphological traits and craniometric measurements to assess how males and females compare to each other, in order to elucidate possible residence pattern, and how well dental non-metric and craniometric data compare, in order to determine whether these two types of data can be usefully combined or interchangeably used as a proxy for underlying genetic variation between the populations. Overall, both the sexes and the populations of study differed more in the dental than the cranial data based on MMD and Mahalanobis distance matrices, suggesting that dental morphology is more closely representative of genotypic variation, while variation in cranial measurements is smoothed out by environmental components. Though further analysis via principal coordinates analysis and Mantel tests suggest that such differences are subtle and comparable over both data types, data was able to be adequately combined across sexes and data types through Generalized Procrustes Analysis. Analyses gave differing and often contradictory results as to which sex was more mobile, suggesting that any sex-differential migration in this region was likely subtle and that residency was closer to an ambilocal than unilocal pattern. Nevertheless, uneven sample sizes and sparse representation of this complex region give only a small insight into what is likely a multifaceted picture of migration into and throughout the Pacific Islands. This research would be greatly aided by a more comprehensive assortment of samples from a greater number of Oceanic populations and contemporaneous individuals as well as data from all three lines of evidence: genetic, dental, and craniometric.

Bibliography

AddinSoft. 2015. XLStat. https://www.xlstat.com/en/

Allen, J. 1984. In search of the Lapita Homeland. *Journal of Pacific History*. 19: 186-201.

Allen, William L. and James B. Richardson. 1971. The reconstruction of kinship from archaeological data: the concepts, the methods, and the feasibility. *American Antiquity*. 36(1): 41-53.

Anderson, A. and G. Clark. 1999. The age of Lapita settlements in Fiji. *Archaeology of Oceania*. 34: 31-39.

Anton, Susan C. and Karen J. Weinstein. 1999. Artificial cranial deformation and fossil Australians revisted. *Journal of Human Evolution*. 36(2): 195-209.

Athens JS. 1997. Hawaiian native lowland vegetation in prehistory. In P.V. Kirch ad T.L. Hunt (eds). *Historical Ecology in the Pacific Islands: Prehistoric Environmental and Landscape Change*. pp. 248–70. New Haven: Yale University Press.

Beals, K.L. et al. 1983. Climate and the evolution of brachycephalization. *American Journal of Physical Anthropology*. 62:425-437.

Beals, K.L. et al. 1984. Brain size, cranial morphology, climate, and time machines. *Current Anthropology*. 25: 301-330.

Bellwood, P. 1978. *Man's Conquest of the Pacific*. Auckland: Collins Press.

Bender, B.W. and Wang, J.W. 1985. The status of Proto-Micronesian. In *Austronesian Linguistics at the 15th Pacific Science Congress. Pacific Linguistics C-88*. Canberra: Australian National University. pg. 53-92.

Berry, A.C. 1974. The use of non-metrical variations of the cranium in the study of Scandinavian population movements. *American Journal of Physical Anthropology*. 40: 345-358.

Berry, A.C. and R.J. Berry. 1967. Epigenetic variation in the human cranium. *Journal of Anatomy*. 101: 361-379.

Berry, A.C. and R.J. Berry. 1972. Origins and relationships of the ancient Egyptians. Based on a study of non-metrical variations in the skull. *Journal of Human Evolution*. 1: 199-208.

Betty, D.A. et al. 1996. Multiple independent origins of the COII/tRNA^{Lys} intergenic 9-bp mtDNA deletion in aboriginal Australians. *American Journal of Human Genetics*. 58: 428-433.

Blackwell, Beatrice and P.M. Danby. 1955. A study of artificial cranial deformation in New Britain. *The Journal of the Royal Anthropological Institute of Great Britain and Ireland*. 85(1/2): 173-191.

Blumenbach, J.F. et al. 1865. *The anthropological treatises of Johann Friedrich Blumenbach*. London: Longman, Green, Longman, Roberts and Green.

Blust, R. 1999. Subgrouping, circularity and extinction: some issues in Austronesian comparative linguistics. In *Selected papers from the eighth international conference on Austronesian linguistics*. Taipei: Academia Sinica. 1:31-94.

Boas, Franz. 1912. Changes in the bodily form of descendants of immigrants. *American Anthropologist*.14(3):530-562.

Bolnick, D.A. et al. 2006. Asymmetric male and female genetic histories among Native Americans from Eastern North America. *Molecular Biology and Evolution*. 23: 2161.

Broca, Paul. 1861. Sur le principe des localisations cérébrales. *Bulletin de la Société d"Anthropologie* 2: 190–204.

Brook, A.H. 1984. A unifying aetiological explanation for anomalies of human tooth number and size. *Archives of Oral Biology*. 29: 373-378.

Brown, T.A. and I.M. Barnes. 2015. Current and future applications of ancient DNA in quaternary science. *Journal of Quaternary Science*. 30(2): 144-153.

Buikstra, J.E. et al 1990. Skeletal biological distance studies in American physical anthropology: recent trends. *American Journal of Physical Anthropology*. 82: 1-7.

Burton, M.L. et al. 1996. Regions based on social structure. *Current Anthropology*. *37*(1): 87-123.

Byard, P.J. et al. 1985. Path analysis of family resemblance for cranio-facial traits in Andhra Pradesh nuclear families and twins. *Annals of Human Biology*. 12: 305-314.

Carey, James W. and A.T. Steegman. 1981. Human nasal protrusion, latitude, and climate. *American Journal of Physical Anthropology*. 56(3):313-319.

Carson, Ann. 2006. Maximum-likelihood variance components of heritabilities of cranial non-metric traits. *Human Biology*. 78(4): 383-402.

Cavalli-Sforza, L.L. and W. Bodmer. 1971. *Human Population Genetics*. San Francisco: Free-man.

Chevarud, James M. 1988. A comparison of genetic and phenotypic correlations. *Evolution*. 42(5): 958-968.

Cohen, Mark Nathan et al. 1994. The osteological paradox considered. *Current Anthropology*. 35(5): 629-637.

Collard, M. and B. Wood. 2000. How reliable are human phylogenetic hypotheses? *Proceedings of the National Academy of Sciences of the United States*. 97: 5003-5006.

Constandse-Westermann, T.S. 1972. *Coefficients of biological distance*. The Netherlands: Oosterhout N.B.

Cook, Robert A. and B. Scott Aubry. 2014. Aggregation, interregional interaction, and postmarital residence patterning: a study of biological variation in the late prehistoric Middle Ohio Valley. *American Journal of Physical Anthropology*. 154: 270-278.

Coon, C.S. et al. 1950. *Races: a study of the problems of race formation in man*. Springfield: Charles C. Thomas.

Coon, C.S. 1962. *The origin of races*. London: Alfred A. Knopf, Inc.

Dahlberg, A.A. 1956. *Materials for the establishment of standards for classification of tooth characteristics, attributes, and techniques in morphological studies of the dentition*. University of Chicago: Zoller Laboratory of Dental Anthropology.

Devor, E.J. et al. 1986. Transmissiable and nontransmissible components of anthropometric variation in the Alexanderwohl Mennonites: II. Resolution by path analysis. *American Journal of Physical Anthropology*. 69: 83-92.

Devor, E.J., 1987. Transmission of human craniofacial dimensions. *Journal of Craniofacial Genetics and Developmental Biology*. *7*(2): 95-106.

Diamond, Jared. 1988. Express train to Polynesia. *Nature*. 336:307-308.

Diamond, J. and Bellwood, P. 2003. Farmers and their languages: the first expansions. *Science*. 300(5619): 597-603.

Divale, William Tulio. 1974. Migration, External Warfare, and Matrilocal Residence. Behavior Science Research. 9(2): 75-133.

Donlon, D.A. 2000. The value of infracranial nonmetric variation in studies of modern Homo sapiens: an Australian focus. *American Journal of Physical Anthropology*. 113: 349-368.

Edgar, Heather J.H. 2004. Dentitions, distance, and difficulty: a comparison of two statistical techniques for dental morphological data. *Dental Anthropology*. 17(2): 55-62.

Ember, M. 1973. An archaeological indicator of matrilocal versus patrilocal residence. *American Antiquity*. 38(2): 177-182.

Ember, M. and C.R. Ember. 1971. The conditions favoring matrilocal versus patrilocal residence. *American Anthropologist*. 73: 571-594.

Ember, M. and C.R. Ember. 1983. *Marriage, family, and kinship: comparative studies of social organization*. New Haven: HRAF Press.

Ember, C.R., M. Ember and P.N. Peregrine. 2007. *Anthropology*. 12th ed. Upper Saddle River: Prentice Hall.

Escobar, V. et al. 1976. The inheritance of bilateral rotation of maxillary central incisors. *American Journal of Physical Anthropology*. 45: 109-116.

Falconer, D.S. 1960. *Introduction to Quantitative Genetics*. New York: The Ronald Press Company.

Flint, J. et al. 1989. Population bottlenecks in Polynesia revealed by minisatellites. *Human Genetics*. 83: 257-263.

Frederickson, C. et al. 1993. Pamwak rockshelter: a Pleistocene site on Manus Island, Papua New Guinea. In: Smith et al (eds). *Sahul in Review: Pleistocene Archaeology in Australia, New Guinea, and Island Melanesia*. Canberra: Department of Prehistory at Australia National University. Pg. 37-59.

Friedlaender, J.S. et al. 2008. The genetic structure of Pacific islanders. *PLOS Genetics*. 4:1–18.

Garn, S.M. et al. 1964. Sex difference in tooth size. *Journal of Dental Research*. 43: 306.

Garn, S.M. et al. 1966. Sexual dimorphism is buccolingual tooth diameter. *Journal of Dental Research*. 45: 1819.

Gathercole, P. 2001. Progress on Polynesia. *Antiquity*. 75(289): 639-641.

Gingerich, P.D. 1977. Correlation of tooth size and body size in living hominoid primates, with a note on relative brain size in Aegyptopithecus and Proconsul. *American Journal of Physical Anthropology*. 47(3):395-398.

González-José, Rolando et al. 2005. Functional-cranial approach to the influence of economic strategy on skull morphology. 2005. *American Journal of Physical Anthropology*. 128(4): 757-771.

Goose, D.H. and G.T.R. Lee. 1971. The mode of inheritance of Carabelli's trait. *Human Biology*. 43: 64-69.

Graves M.W. and D.R. Moore. 1985. *Tumon Bay area overview: cultural and historical resources*. Prepared for Department of Parks and Recreation, Agana, Guam, by Micronesian Area Research Center and Department of Anthropology, University of Guam, Mangilao.

Gravlee, Clarence C. et al. 2003. Boas's "Chandes in Bodily Form": the immigrant study, cranial plasticity, and Boas's physical anthropology. *American Anthropologist*. 105(2): 326-332.

Gray, R.D. et al. 2009. Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science*. 323(5913):479-483.

Greene, D.L. 1982. Discrete dental variations and biological distances of Nubian populations. *American Journal of Physical Anthropology*. 58: 75-79.

Green, R.C. 2003. The Lapita horizon and traditions – Signatures for one set of oceanic migrations. In Sand, C. (ed). *Pacific Archaeology: Assessments and Anniversary of the First Lapita Excavation (July 1952)*. Le cahiers de l'Archeologie en Nouvelle-Caledonie, Vol. 15. Nourmea, New Calcedonia.

Green, R.C. et al. 2008. The reconstructed and absolute dating of SE-SZ-8 Lapita site on Nendö, Santa Cruz, Solomon Islands. *Archaeology of Oceania*. 43: 49-61.

Green, R.C. and M.I. Weisler. 2002. The Managarevan sequence and dating of the geographic expansion in Southeast Polynesia. *Asian Perspective*. 41: 213-241.

Grewal, M.S. 1962. The rate of genetic divergence in the C57BL strain of mice. *Genetic Research*. 3: 226-237.

Groube, L.M. et al. 1986. A 40,000 year-old human occupation site at Huan Peninsula, Papua New Guinea. *Nature*. 324: 453-455.

Grüneberg, H. 1952. Genetical studies on the skeleton of the mouse. IV. Quasi-continuous variations. *Journal of Genetics*. 51: 95-114.

Gunnarsdóttir, E. et al. 2011. Larger mitochondrial DNA than Y-chromosome differences between matrilocal and patrilocal groups from Sumatra. *Nature Communications*. 2: 228.

Haeussler, A.M. et al. 1989. Morphological and metrical comparison of San and Central Sotho dentitions from southern Africa. *American Journal of Physical Anthropology*. 78(1):115-122.

Hage, P. and F. Harary. 1996. *Island networks*. Cambridge: Cambridge University Press.

Hage, P. and J. Marck. 2003. Matrilineality and the Melanesian origin of Polynesian Y chromosomes. *Current Anthropology*. 44(5):121-127.

Hagelberg, E. et al. 1999. Molecular genetic evidence from the human settlement of the Pacific: analysis of mitochondrial DNA, Y chromosome and HLA markers. *Philosophical Transactions of the Royal Society of London, Series B*. 354: 141-152.

Hallgrimsson, D. et al. 2004. Composition of the founding population of Iceland: biological distance and morphological variation in early historic Atlantic Europe. *American Journal of Physical Anthropology*. 124: 257-274.

Hammer, et al. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica http://palaeo-electronica.org. Internet.
http://palaeo-electronica.org/2001_1/past/past.pdf.

Hanihara, K. et al. 1975. Family studies of the shovel trait in the maxillary central incisor. *Journal of the Anthropological Society of Nippon*. 83(1): 107-112.

Hanihara, T. 1992. Dental and cranial affinities among populations of East Asia and the Pacific: the basic populations in East Asia, IV. *American Journal of Physical Anthropology*. 88(2): 163-182.

Hanihara, T. 2008. Morphological variation of major human populations based on nonmetric dental traits. *American Journal of Physical Anthropology*. 136(2): 169-182.

Hanihara, T. et al. 2003. Characterization of biological diversity through analysis of discrete cranial traits. *American Journal of Physical Anthropology*. 121: 241-251.

Hanihara, T. and Hajime Ishida. 2005. Metric dental variation of major human populations. *American Journal of Physical Anthropology*. 128(2): 287-298.

Harding, R.M. and J.B. Clegg. 1996. Molecular population genetic studies of the island peoples of the South Pacific. *American Journal of Human Biology*. 8: 587-597.

Harris, Edward F. and Torstein Sjøvold. 2004. Calculation of Smith's Mean Measure of Divergence for Intergroup comparisons using nonmetric data. *Dental Anthropology*. 17(3): 83-93.

Harris, E.F. 1980. Sex differences in lingual marginal ridging on the human maxillary central incisor. *American Journal of Physical Anthropology*. 52: 541-548.

Harris, M. 1980. *Cultural materialism*. New York: Random House.

Harris, M. 1985. *Culture, people, and nature*. 4th ed. New York: Random House.

Hart, J.P., 2001. Maize, matrilocality, migration, and northern Iroquoian evolution. *Journal of Archaeological Method and Theory*. 8(2):151-182.

Harvati, K. 2001. *The Neanderthal problem: 3-D geometric morphometric models of cranial shape variation within and among species*. Unpublished dissertation. City University of New York, New York.

Harvati, K. 2003. Quantitative analysis of Neanderthal temporal bone morphology using three-dimensional geometric morphometrics. *American Journal of Physical Anthropology*. 120: 323-338.

Harvati, K. and Timothy D. Weaver. 2006. Human cranial anatomy and the differential preservation of population history and climate signatures. *The Anatomical Record Part A*. 288A: 1225-1233.

Helms, Mary W. 2004. Miskito: Adaptations to colonial empires, past and present. In C.R. Ember, M. Ember, and P.N. Peregrine (eds). *Portraits of Culture: New Directions in Anthropology*. Upper Saddle River: Prentice Hall.

Hofreiter, M. et al. 2001. Ancient DNA. *Nature Reviews Genetics*. 2(5): 353-359.

Hogg, A.G. et al. 2003. A wiggle-match date for Polynesian settlement of New Zealand. *Antiquity*. 77: 116-125.

Hollinger, R.E. 1995. Residence patterns and Oneota cultural dynamics. In Green, W. (ed). *Oneota Archaeology: Past, Present, and Future*. Report 20, Office of the State Archaeologist. Iowa City: University of Iowa. pg. 141-174.

Houghton, P. 1996. *People of the Great Ocean: Aspects of Human Biology of the Early Pacific*. Cambridge: Cambridge University Press.

Howells, W.W. 1973. Cranial Variation in Man: A Study by Multivariate Analysis of Patterns of Difference Among Recent Human Populations. Cambridge: Harvard University.

Howells, W.W. 1989. Skull Shapes and the Map. *Papers of the Peabody Museum of Archaeology and Ethnology*. Cambridge: Harvard University.

Howells, W.W. 1995. Skull Shapes and the Map: Who's Who in Skulls. *Papers of the Peabody Museum of Archaeology and Ethnology*. Cambridge: Harvard University.

Hubbe, M., Hanihara, T. and Harvati, K. 2009. Climate signatures in the morphological differentiation of worldwide modern human populations. *The Anatomical Record*. 292(11):1720-1733.

Hughes, Toby E. and Grant C. Townsend. 2013. Three twin and family studies of human dental crown morphology: genetic, epigenetic, and environmental determinants of the modern human dentition. *Anthropological Perspectives on Tooth Morphology: Genetics, Evolution, and Variation*. 66: 31.

Hurles, M.E. et al 2002. Y chromosomal evidence for the origins of Oceanic-speaking peoples. *Genetics*. 160: 289-303.

Hylander, W.L. 1977. The adaptive significance of Eskimo craniofacial morphology. In: A.A. Dahlberg and T.M. Graber (eds). *Orofacial Growth and Development*. Chicago: Mouton. Pg. 129-170.

Irish, Joel D. 1993. *Biological Affinities of Late Pleistocene Through Modern African Aboriginal Populations: The Dental Evidence*. PhD dissertation. Arizona State University, Tempe.

Irish, Joel D. 1997. Characteristic high-and low-frequency dental traits in sub-Saharan African populations. *American Journal of Physical Anthropology*. 102(4):455-467.

Irish, Joel D. 1998a. Dental morphological affinities of late Pleistocene through recent sub-Saharan and North African peoples. *Bulletins et memoires de la Societe d'Anthropologie de Paris.* 10: 237-272.

Irish, Joel D. 1998b. Dental morphological indications of population discontinuity and Egyptian gene flow in post-Paleolithic Nubia. In Lukas, J.R. (ed). *Human dental development, morphology, and pathology: a tribute to Albert A. Dahlberg*. University of Oregon Anthropological Papers 54. Eugene: University of Oregon Press. pg. 155-172.

Irish, Joel D. 1998c. Ancestral dental traits in recent Sub-Saharan Africans and the origins of modern humans. *Journal of Human Evolution*. 34(1): 81-98.

Irish, Joel D. 2005. Population continuity versus discontinuity revisited: dental affinities among late Paleolithic through Christian era Nubians. *American Journal of Physical Anthropology*. 128: 520-535.

Irish, Joel D. 2006. Who were the ancient Egyptians? Dental affinities among Neolithic through postdynastic peoples. *American Journal of Physical Anthropology*. 129(4): 529-543.

Irish, Joel D. 2010. The Mean Measure of Divergence: its utility in model-free and model-bound analyses relative to the Mahalanobis D^2 distance for nonmetric traits. *American Journal of Human Biology*. 22: 378-395.

Irish, Joel D. and C.G. Turner II. 1990. West African dental affinity of late Pleistocene Nubians: peopling of the Eurafrican-South Asian triangle II. *Homo*. 41: 42-53.

Irish, Joel D. and Debbie Guatelli-Steinberg. 2003. Ancient teeth and modern human origins: an expanded comparison of African Plio-Pleistocene and recent world dental samples. *Journal of Human Evolution*. 45(2): 113-144.

Irwin, G. 1992. *The Prehistoric Exploration and Colonization of the Pacific*. Cambridge: Cambridge University Press.

Jantz, R.L. 2001. Cranial change in Americans: 1850–1975. *Journal of Forensic Science*. 46(4): 784-787.

Jantz, R.L. 2003. The anthropometric legacy of Franz Boas. *Economics & Human Biology*. 1(2):277-284.

Jantz, R.L. and S.D. Ousley. 2005. FORDISC 3.1 Personal Computer Forensic Discriminant Functions. University of Tennessee Knoxville. http://fac.utk.edu/fordisc.html

Jordan, F.M. et al. 2009. Matrilocal residence is ancestral in Austronesian societies. *Proceedings of the Royal Society*. 10(1098): 1-8.

Jorde, L.B., et al. 2000. The distribution of human genetic diversity: a comparison of mitochondrial, autosomal, and Y-chromosome data. *The American Journal of Human Genetics*. 66(3): 979-988.

Kayser, M. et al. 2000. Melanesian origin of Polynesian Y chromosomes. *Current Biology*. 10:1237-1246.

Kayser, M. et al. 2006. Melanesian and Asian origins of Polynesians: mtDNA and Y chromosome gradients across the Pacific. *Molecular Biology and Evolution*. 23:2243-2244.

Kayser, M. et al. 2008. Genome-wide analysis indicates more Asian than Melanesian ancestry of Polynesians. *The American Journal of Human Genetics*. 82(1): 194-198.

Kirch P.V. 1995. The Lapita culture of western Melanesia in the context of Austronesian origins and dispersals. In P. Li (ed). *Austronesian Studies Relating to Taiwan*. Taipei: Acad. Sin. pp. 255–294.

Kirch, P.V. 1997. *The Lapita Peoples: Ancestors of the Oceanic World.* Oxford: Blackwell Publishing.

Kirch, P.V. 2000. *On the Road of the Winds: An Archaeological History of the Pacific Islands Before European Contact*. Berkeley: University of California Press.

Kirch, P.V. 2010. Peopling of the Pacific: A Holistic Anthropological Perspective. *Annual Review of Anthropology*. 39:131-148.

Kirch, P.V. and R.C. Green. 2001. *Hawaiki, Ancestral Polynesia: An Essay in Historical Anthropology*. Cambridge: Cambridge University Press.

Kohn, L.A.P. 1991. The role of genetics in craniofacial morphology and growth. *Annual Review of Anthropology*. 20: 261-278.

Kolipakam, V. et al. 2011. Modelling sex-biased migration in the Pacific. In *7th International Society for Applied Biological Conference on Forensic, Anthropologic and Medical Genetics*. Zagreb, Croatia.

Konigsberg, L. W. 1987. Population Genetics Models for Interpreting Prehistoric Intra-Cemetery Biological Variation. Unpublished Ph.D. dissertation, Northwestern University.

Konigsberg, L.W. 1988. Migration Models of Prehistoric Postmarital Residence. *American Journal of Physical Anthropology*. 77:471-482.

Konigsberg, L.W. 1990. Analysis of prehistoric biological variation under a model of isolation by geographic and temporal distance. *Human Biology*. 62: 49-70.

Konigsberg, L.W. and J.E. Buikstra. 1995. Regional Approaches to the Investigations of Past Human Biocultural Structure. In *Regional Approaches to Mortuary Analysis*. Edited by L.A. Beck. New York: Plenum Press.

Kraus, B.S. 1951. Carabelli's anomaly of the maxillary molar teeth. *American Journal of Human Genetics*. 3: 348-355.

Lane, R.A and Sublett A. 1972. The osteology of social organization. *American Antiquity*. 37:186-201.

Larsen, C.S. 1997. *Bioarchaeology: Interpreting Behavior for the Human Skeleton*. Cambridge: Cambridge University Press.

Larsen, C.S. 2002. Bioarchaeology: the lives and lifestyles of past people. *Journal of Archaeological Research*. 10(2): 119-165.

Lasker, G.W. 1950. Genetic analysis of racial traits of the teeth. *Cold Spring Harbor Symposium on Quantitative Biology*. 15: 191-203.

Lau, E.C. et al. 1989. Human and mouse amelogenin gene loci are on the sex chromosomes. *Genomics*. 4: 162-168.

Lee, G.T.R. and D.H. Goose. 1972. The inheritance of dental traits in a Chinese population in the United Kingdom. *Journal of Medical Genetics*. 9: 336-339.

Lévi-Strauss, Claude. 1984. *Anthropology and myth: lectures, 1951-1982*. Oxford: Blackwell.

Levinson, D. and M.J. Malone. 1980. *Toward explaining human culture: a critical review of the findings of worldwide cross-cultural studies*. New Haven: HRAF Press.

Linton, R. 1936. The study of man. New York: Appleton.

Lum, J.K. and R.L. Cann. 2000. mtDNA lineage analyses: origins and migrations of Micronesians and Polynesians. *American Journal of Physical Anthropology*. 113: 151-168.

Mahalanobis, P.C. 1930. On tests and measures of group divergence I. Theoretical formulae. *Journal of the Proceedings of the Asiatic Society of Bengal*. 26: 541-588.

Mahalanobis, P.C. 1936. On generalized distance in statistics. *Proceedings of the National Institute of Sciences of India*. 2(1): 49-55.

Majumdar, D.N., Rao, C.R. and Mahalanobis, P.C. 1958. Bengal anthropometric survey, 1945: A statistical study. *Sankhyā: The Indian Journal of Statistics (1933-1960)*. 19(3/4): 201-408.

Marlowe, F.W. 2000. Paternal investment and the human mating system. *Behavioral Processes*. 51:45-61.

Marlowe, F.W. 2004. Marital residence among foragers. *Current Anthropology*. 45: 277-284.

Marshall, Yvonne. 1985. Who made the Lapita pots? A case study in gender archaeology. *The Journal of Polynesian Society*. 94(3): 205-233.

Martinson, J.J. et al. 1993. Demographic reductions and genetic bottlenecks in humans: minisatellite allele distributions in Oceania. *Human Genetics*. 91: 445-450.

Matisoo-Smith, E. and J.H. Robins. 2004. Origins and dispersals of Pacific peoples: evidence from mtDNA phylogenies of the Pacific rat. *Proceedings of the National Academy of Science of the United States*. 101:9167–72.

Matisoo-Smith, Michael. 2007. The Peopling of Oceania. In Crawford, M. (ed). *Anthropological Genetics: Theory, Methods, and Applications*. Cambridge: Cambridge University Press.

McLachlan, G.J. 1999. Mahalanobis Distance. *Resonance*. 20-26.

Melton, T. et al. 1998. Polynesian genetic affinities with Southeast Asian populations identified by mtDNA analysis. *American Journal of Human Genetics*. 57: 403-414.

Mizoguchi, Yuji. 1977. Genetic variability of permanent tooth crowns as ascertained from twin data. *Journal of the Anthropological Society of Nippon*. 85(4): 301-309.

Morton, S.G. 1839. *Crania Americana: or, a comparative view of the skulls of various aboriginal nations of North and South America: to which is prefixed an essay on the varieties of the human species*. Phildelphia: J. Dobson.

Murdock, G.P. 1949. *Social Structure*. New York: Macmillan.

Murdock, G.P. 1967. Ethnographic atlas: a summary. *Ethnology*. 6: 109-236.

Murdock, G.P. 1981. *Atlas of world cultures*. Pittsburgh: University of Pittsburgh Press.

Murrill, R.I. 1968. *Cranial and postcranial skeletal remains from Easter Island*. Twin Cities: University of Minnesota Press.

Neves, Walter A. et al. 1999. Extra-continental morphological affinities of Palli Aike, southern Chile. *Interciencia Caracas*. 24: 258-263.

Nott, J.C. and Gliddon, G.R., 1854. *Types of Mankind Or Ethnological Researches, Based Upon the Ancient Monuments, Paintings, Sculptures, and Crania of Races, and Upon Their Natural, Geographical, Philological, and Biblical History*. London: Trubner.

Nunn, P.D. et al. 2007. The Lapita occupation at Naitabale, Moturiki Island, central Fiji. *Asian Perspectives*. 96-132.

Nystrom, Kenneth C. and Christine M. Malcom. Sex-specific phenotypic variability and social organization in the Chiribaya of southern Peru. *Latin American Antiquity*. 21(4):375-397.

Nicholson, E. and K. Harvati. 2006. Quantitative analysis of human mandibular shape using three dimensional geometric morphometrics. *American Journal of Physical Anthropology*. 131: 368-383.

Nikita, E., 2015. A critical review of the mean measure of divergence and Mahalanobis distances using artificial data and new approaches to the estimation of biodistances employing nonmetric traits. *American Journal of Physical Anthropology*. 157(2):284-294.

Olson, T.R. 1981. Basicranial morphology od the extant hominoids and Pliocene hominids: the new material from the Hadar Formation, Ethiopia and its significance in early human evolution and taxonomy. In: Stringer, C.B. (ed). *Aspects of Human Evolution*. London: Taylor and Francis.

Oppenheimer, Stephan and Martin Richards. 2001. Fast trains, slow boats, and the ancestry of the Polynesian islanders. *Science Progress*. 84(3): 157-181.

Ossenberg N.S. et al. 2006. Ethnogenesis and craniofacial change in Japan from the perspective of nonmetric traits. *Anthropological Science*. 114: 99-115.

Pääbo, S. et al. 2004. Genetic analyses from ancient DNA. *Annual Review of Genetics*. 38: 645-679.

Pawley, A. and M. Ross. 1993. Austronesian historical, linguistic, and cultural history. *Annual Reviews in Anthropology*. 22:425-459.

Parkington, J. 1998. Resolving the past: gender in the Stone Age archaeological record on the Western Cape. In Kent, S (ed). *Gender in African Prehistoy*. Walnut Creek: AltaMira Press. pg. 25-37.

Pérez-Lezaun, A. et al. 1999. Sex-specific migration patterns in Central Asian populations, revealed by analysis of Y-chromosome short tandem repeats and mtDNA. *The American Journal of Human Genetics*. 65(1): 208-219.

Perzigian, A.J. 1981. Allometric analysis of dental variation in a human population. *American Journal of Physical Anthropology*. 54(3):341-345.

Pietrusewsky, Michael. 2008. Metric analysis of skeletal remains: methods and applications. In M.A. Katzenberg and S.R. Saunders (eds). *Biological Anthropology of the Human Skeleton*. Hoboken: Wiley and Sons.

Pietrusewsky, M. 2014. Biological distance in bioarchaeology and human osteology. In: C. Smith (ed). *Encyclopedia of Global Archaeology*. New York: Springer.

Portin, P. and L. Alvesalo. 1974. The inheritance of shovel shape in maxillary central incisors. *American Journal of Physical Anthropology*. 41: 59-62.

Powell, J.F. 1993. Dental evidence for the peopling of the New World: some methodological considerations. *Human Biology*. 65: 799-815.

Powell, J.F. 1995. *Dental variation and biological affinity among middle Holocene human populations in North America*. Unpublished dissertation. Texas A&M University, College Station.

Redd, A.J. et al. 1995. Evolutionary history of the COII/tRNA^{Lys} intergenic 9 base pair deletion in human mitochondrial DNAs from the Pacific. *Molecular Biology and Evolution*. 12: 604-615.

Relethford, J.H. 2004. Boas and beyond: migration and craniometric variation. *American Journal of Human Biology*.*16*(4):379-386.

Reyment, R.A. et al. 1984. *Multivariate Morphometrics*. 2nd ed. New York: Academic Press.

Roseman, Charles C. and Henry C. Harpending. 2004. Detecting interregionally diversifying natural selection on modern human cranial form by using matches molecular and morphometric data. *Proceedings of the National Academy of Sciences of the United States of America*. 101(35): 12824-12829.

Ross MD. 1996. Is Yapese oceanic? In B. Nothofer (ed). *Reconstruction, Classification, Description: Festschrift in Honor of Isidore Dyen*. Hamburg: Abera Verlag Meyer. pg. 121–66.

Saunders, S.R. and J.T. Mayhall. 1982. Developmental patterns of human dental morphological traits. *Archives of Oral Biology*. 27: 45-49.

Scott, G. Richard and Christy G. Turner II. 1997. *The anthropology of modern human teeth: dental morphology and its variation in recent human populations*. Cambridge: Cambridge University Press.

Schillaci, M.A. and Stojanowski, C.M. 2003. Postmarital residence and biological variation at Pueblo Bonito. *American Journal of Physical Anthropology*. *120*(1): 1-15.

Schillaci, M.A. and Stojanowski, C.M. 2005. Craniometric variation and population history of the prehistoric Tewa. *American Journal of Physical Anthropology*. 126(4): 404-412.

Sciulli, P.W. 1998. Evolution of the dentition in prehistoric Ohio Valley Native Americans: II. Morphology of the deciduous dentition. *American Journal of Physical Anthropology*. 106: 189-205.

Scott, G.R. 1973. *Dental morphology: a genetic study of American white families and variation in living Southwest Indians*. PhD dissertation. Arizona State University, Tempe.

Scott, G.R. 1974. A general model of inheritance for nonmetrical tooth crown characterisitics. *American Journal of Physical Anthropology*. 41: 503.

Scott, G.R. et al. 1983. The dental morphology of Pima Indians. *American Journal of Physical Anthropology*. 61: 13-31.

Scott, G.R. 2008. Dental morphology. In M.A. Katzenberg and S.R. Saunders (eds). *Biological Anthropology of the Human Skeleton*. Hoboken: Wiley and Sons.

Scott, G.R. and C.G. Turner II. 1988. Dental anthropology. *Annual Review of Anthropology*. 17: 99-126.

Scott, G.R. and C.G. Turner II. 2000. *The anthropology of modern human teeth: dental morphology and its variation in recent human populations*. Vol. 20. Cambridge: Cambridge University Press.

Seielstad, M.T. et al. 1998. Genetic evidence for a higher female migration rate in humans. *Nature Genetics*. 20(3): 278-280.

Seielstad, M.T., E. Minch, and L.L. Cavalli-Sforza. 1998. Genetic evidence for a higher female migration rate in humans. *Nature Genetics*. 20(3):278-280.

Service, Elman R. 1962. *Primitive Social Organization: An Evolutionary Perspective*. New York: Random House.

Sheppard, P.J. and Green, R.C. 1991. Spatial analysis of the Nenumbo (SE-RF-2) Lapita site, Solomon Islands. *Archaeology in Oceania*. 26(3): 89-101.

Sherwood, Richard J. et al. 2008. Quantitative genetics of modern human cranial variation. *Journal of Human Evolution*. 54: 909-914.

Sjøvold, T. 1984. A report on the heritability of some cranial measurements and non-metric traits. In *Multivariate Statistical Methods in Physical Anthropology*. Netherlands: Springer.

Smithsonian Institution. 2015. *Osteoware*. http://osteoware.si.edu/

Soltysiak, Arkadiusz. 2011. Technical note: an R script for Smith's Mean Measure of Divergence. *Bioarchaeology of the Near East*. 5: 41-44.

de Souza, P. and P. Houghton. 1977. The mean measure of divergence and the use of non-metric data in the estimation of biological distances. *Journal of Archaeological Science*. 4: 163-169.

Sparks, Corey S. and Richard L. Jantz. 2002. A reassessment of human cranial plasticity: Boas revisited. *Proceedings of the National Academy of Sciences of the United States*. 99(23): 14363-14639.

Spence, M.W. 1974. Residential practices and the distribution of skeletal traits in Teotihuachan, Mexico. *Man*. 9:262-273.

Spriggs, M.J.T. and A. Anderson. 1993. Late colonization of East Polynesia. *Antiquity*. 67:200–217.

Stefan, Vincent H. 1999. Craniometric variation and homogeneity in prehistoric/protohistoric Rapa Nui (Easter Island) regional populations. *American Journal of Physical Anthropology*. 110: 407-419.

Stojanowski, C.M. and Schillaci, M.A. 2006. Phenotypic approaches for understanding patterns of intracemetery biological variation. *American Journal of Physical Anthropology*. 131(S43): 49-88.

Su, B. et al. 2000. Polynesian origins: insights from the Y-chromosome. *Proceedings of the National Academy of Science, USA*. 97:8225-8228.

Susanne, C. 1975. Genetic and environmental influences on morphological characteristics. *Annals of Human Biology*. 2: 279-287.

Sutter, R.C. 2005. The prehistoric peopling of South America as inferred from epigenetic dental traits. *Andean Past*. 7: 183-217.

Sutter, R.C. and Lisa Mertz. 2004. Nonmetric cranial variation and prehistoric biocultural change in the Azapa Valley, Chile. *American Journal of Physical Anthropology*. 123(2): 130-145.

Sutter, R.C. and J.W. Verano. 2007. Biodistance analysis of the Moche sacrificial victims from Huaca de la Luna plaza 3C: matrix method test of their origins. *American Journal of Physical Anthropology*. 132: 193-206.

Suzuki, Hisashi et al. 1993. Craniofacial measurement of artificially deformed skulls from the Philippines. *Anthropological Science*. 101(1): 111-127.

Sykes, B. et al. 1995. The origins of the Polynesians: in interpretation from mitochondrial lineage analysis. *American Journal of Human Genetics*. 57:1463-1475.

Terrell J. 1986. *Prehistory in the Pacific Islands*. Cambridge: Cambridge Univ. Pres

Tomczak, Paula D. and Joseph F. Powell. 2003. Postmarital Residence Practices in the Windover Population: Sex-based Dental Variation as an Indicator of Patrilocality. *American Antiquity*. 68(1):93-108. *Archives of Oral Biology*. 54: 45-51.

Townsend, Grant et al. 2009. Genetic and environmental influences on human dental variation: a critical evaluation of studies involving twins.

Turner, C.G. II. 1967. Dental genetics and microevolution in prehistoric and living Koniag Eskimo. *Journal of Dental Research*. 46: 911-917.

Turner, C.G. II. 1969. Microevolutionary interpretations from the dentition. *American Journal of Physical Anthropology*. 30: 421-426.

Turner, C.G. II. 1981. Root number deamination in maxillary first premolars for modern human population. *American Journal of Physical Anthropology*. 54: 59-62.

Turner, C.G. II. 1983. Sinodonty and Sundadonty: a dental anthropological view of Mongoloid microevolution, origin, and dispersal into the Pacific basin, Siberia, and Americas. In R.S. Vasilievsky (ed). *Late Pleistocene and Early Holocene Cultural Connections of Asia and America*. Novosibirsk: USSR Academy of Sciences.

Turner, C.G. II. 1984. Advances in the dental search for Native American origins. *Acta Anthropogenetica*. 8: 23-78.

Turner, C.G. II. 1985a. Expression count: a method for calculating morphological dental trait frequencies by using adjustable weighting coefficients. *American Journal of Physical Anthropology*. 68: 236-268.

Turner, C.G. II. 1985b. The modern human dispersal event: the eastern frontier. Review of Out of Asia: Peopling of the Pacific. R.L. Kirk and E.J.E. Szathmary. *Quarterly Review of Archaeology*. 6:8-10.

Turner, C.G. II. 1986. Dentochronological separation estimates for Pacific Rim populations. *Science*. 232: 1140-1142.

Turner, C.G. II. 1987. Late Pleistocene and Holocene population history of East Asia based on dental variation. *American Journal of Physical Anthropology*. 73: 305-322.

Turner, C.G. II. 1990a. Major features of Sundadonty and Sinodonty, including suggestions about East Asian microevolution, population history, and late Pleistocene relationships with Australian aboriginals. *American Journal of Physical Anthropology*. 82: 295-317.

Turner, C.G. II. 1990b. Origin and affinity of the prehistoric people of Guam: a dental anthropological assessment. In R.L. Hunter-Anderson (ed). *Recent Advances in Micronesian Archaeology, Micronesian supplement, No. 2*. Mangilao: University of Guam Press.

Turner, C.G. II. and G.R. Scott. 1977. Dentition of Easter Islanders. In A.A. Dahlberg and T.M. Graber (eds). *Orofacial Growth and Development*. The Hague: Mouton Publishers.

Turner, C.G. II., C.R. Nichol, G.R. Scott. 1991. Scoring procedures for key morphological traits of the permanent dentition: the Arizona State Dental Anthropology System. In Kelley, M.A. and C.S. Larsen (eds). *Advances in Dental Anthropology*. Wiley-Liss.

Tsuji, T. 1958. Incidence and inheritance of the Carabelli's cusp in a Japanese population. *Japanese Journal of Human Genetics*. 3: 21-31.

Ubelaker, D.H. and J.E. Buikstra. 1994. Standards for data collection from human skeletal remains. In *Proceeding of a Seminar at The Field Muséum of Naturai History Organized by Jonathan Haas, Arkansas Archeological Survey Research Series*.

Underhill, P.A. et al. 2001. Maori origins, Y-chromosome haplotypes and implications for human history in the Pacific. *Human Mutation*. 17:271-280.

Walker, P.L. and S.E. Hollimon. 1989. Changes in osteoarthritis associated with the development of a maritime economy among southern California Indians. *International Journal of Anthropology*. 4(3): 171-183.

White, T.D., M.T. Black, P.A. Folkens. 2011. *Human Osteology*. London: Academic Press.

Wiklin, Rick. 2012. *Statistical Programming with SAS/IML Software*. Cary, NC: SAS Books.

Wilkins, J.F. and Marlowe, F.W. 2006. Sex-biased migration in humans: what should we expect from genetic data?. *Bioessays*. 28(3):290-300.

Williams-Blangero, S. and J. Blangero. 1990. Effects of population structure on within-group variation in the Jirels of Nepal. *Human Biology*.131-146.

Wood, B. and D.E. Lieberman. 2001. Craniodental variation in Paranthropus boisei: a developmental and functional perspective. *American Journal of Physical Anthropology*. 116: 13-25.

Wood, J.W. et al. 1992. Hazard models for human population biology. *American Journal of Physical Anthropology*. 35(15): 43-87.

Wright, L.E. and C.J. Yoder. 2003. Recent progress in bioarchaeology: approaches to the osteological paradox. *Journal of Archaeological Research*. 11(1):43-70.

Wright, Sewall. 1943. Isolation by distance. *Genetics*. 28(2): 114.

Wright, Sewall. 1969. *Evolution and the genetic of populations: Vol. 2: The theory of gene frequencies*. Chicago: University of Chicago Press.