GENETIC AND CRANIOMETRIC COMPARATIVE ANALYSIS OF THREE MEXICAN POPULATIONS

THESIS

Presented to the Graduate Council of
Texas State University-San Marcos
in Partial Fulfillment
of the Requirements

for the Degree

Master of ARTS

by

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San Marcos, Texas
August 2013

GENETIC AND CRANIOMETRIC COMPARATIVE ANALYSIS OF THREE MEXICAN POPULATIONS

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ACKNOWLEDGEMENTS

I would first like to thank my family for all of their support, both financially and emotionally, over my years in college. Without it, I would not be as successful as I am today. My parents, Karen and Duke Herrera, have always been there for me whenever I needed it, including all the times I frantically called them to talk about the next thing going wrong with my thesis. Their support has been invaluable. My sister, Sandy Bryant, helped me relax through it all with ice cream, cookies, understanding, and love. Alena Newland sent me encouraging pictures and texts, always letting me know she was thinking of me and supporting me. And Robbie Bryant helped me make the tough decisions about grad school and was emotionally supportive through the ups and downs grad school and life threw at me.

My friends have been there to listen to me complain about the craziness, but always made me feel better about whatever situation I was in. Alex Frye, I would like to thank you for the late night thesis/complain sessions, the emotional support even when I was overdoing it, all the million hamburger outings (which of course includes Dr.Pepper!), and simply being a supportive friend. Thank you to my bro Matt Elverson for helping through archaeology, keeping me on track with every deadline, and being there whenever I needed the support. Cristina Watson, thank you for always being understanding and willing to help me through whatever was going on, even when you didn't really have the time to do so. Leilani Case, good luck with the start of your new

family, and I'm going to miss our lunches in Austin. To the rest of my cohort, thank you for always being my friend and I wish everyone luck and happiness in the future.

A special thanks to Reswanul Khan for the technical support, with any computer program I was having to use. Without that, there is no telling what my analysis for my thesis would look like! Thank you also for listening and always trying to find a solution to my problems, even when there was no viable solution. It always let me know that you cared enough to try.

I would like to thank my advisor, Dr. Kate Spradley, for helping me with my thesis, even when the topic had to be changed at the last minute, and for guiding me through the numerous decisions that had to be made about grad school and my future career. Dr. Deborah Bolnick, thank you for the thoughtful edits to my thesis, always taking the time to talk with me, and the experience working in your lab. You helped me make my thesis the best that it could be. And thank you Dr. Hamilton for reading and editing my thesis. Your input was incredibly useful.

This manuscript was submitted on May 17, 2013.

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ABSTRACT

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Previous research has shown that craniometric data can serve as a proxy for molecular data (Relethford 2001, Roseman 2004) and that cranial shape is somewhat shaped by gene flow (Relethford 2004). Previous research on admixture frequencies suggests that complex population histories resulting from differential admixture account for the complex patterns of biological variation found throughout Mexico (Merriwether et al. 1997, Juárez-Cedillo et al. 2008). The purpose of this study is to test whether or not craniometric data show the same population patterns as molecular data and if so, can it be used to help reconstruct population history for archaeological groups in North and Central Mexico.

Craniometric data were obtained from the Sonora, Michoácan, and Tlanepantla groups, dating between AD 1200 and 1500 (Beekman and Christensen 2003) and curated at the American Museum of Natural History. Molecular data were obtained that best approximated the craniometric groups, including the Tarahumara, Purépecha, and the Otomi. Allele distributions forsix Y-linked short tandem repeats (STRs) in the Tarahumara and Purepécha populations were obtained from previously published data (Rangel-Villalobos et al. 2008). Allele distributions for the same six Y-linked STRs in the Otomi population were also studied (Barrot et al. 2007). Mitochondrial DNA (mtDNA) haplogroup frequencies from the same populations, Tarahumara, Purépecha, and Otomi, were used as well (Peñaloza-Espinosa et al. 2007). Distance matrices for the molecular data were obtained in the Kship program (Jantz, no date) and the craniometric distance matrix was obtained in Rmet (Relethford, 2003). Mantel tests were also performed. There were no statistically significant correlations found. Evidence for patrilocality was seen with the F_{ST} estimates and the distance matrices. When geography was considered, it was found that populations that were farthest away had the strongest similarity, except in the case of mtDNA, in which the most similar followed geographic distance.

CHAPTER I

INTRODUCTION

Research Statement

This current analysis is designed to answer one primary question: is it reasonable to assume that prehistoric craniometric data can approximate modern day molecular data and vice versa? Taking samples from pre-Hispanic populations dating to prior than 1492 AD is a useful approach to address questions concerning peopling of the New World. Pre-Hispanic groups in Mexico are specifically used in this analysis because the background and history of these populations are relatively well known. This means there is an understanding about how nearby populations interacted with each other and when, which is useful for interpreting the results. To answer the question of whether prehistoric craniometric data can approximate modern Y-chromosome DNA or mtDNA, and vice versa, craniometric data from pre-Hispanic groups in Mexico were used in combination with DNA (both mtDNA and Y-chromosome DNA) from modern Mexican groups where the population histories indicate interaction and/or geographic proximity.

This research may have important implications for peopling of the New World studies. If it can be shown that these two data types can be used as a proxy for each other, then the different patterns shown by the data types will need to be reconciled. More inclusive studies would have to be performed to get a better understanding of the whole picture, rather than just a part of it. If it cannot be shown that one data type can be used as

a proxy for the other, more work would need to be done to figure out which data type best represents the population history and the evolutionary processes occurring.

Background

There is a complicated relationship between cranial morphology and genetics. Some studies have shown that cranial morphology can provide information about the biological relationships among populations that is similar to that found using molecular data (Relethford 2001, Smith 2009). This is likely because natural selection, gene flow, and genetic drift are known to shape both cranial form and genetic diversity patterns in world-wide data sets (Relethford 2004, González-José et al. 2004, Weaver et al. 2007). Further, it has been demonstrated that using craniometrics in combination with molecular data, as well as archaeological and ethnohistorical information, yields a more complete picture of the biological history of a population (Varela and Cocilovo 2002).

Utilizing a combination of these different data types can aid studies of the peopling of the New World, which provide many different viewpoints on who came to the Americas, how many migrations occurred, what the population size was during the migrations, where the migrations were occurring, the time period of the migrations, etc. (Merriwether et al. 1994, Kitchen et al. 2008, Pitblado 2011). Many research articles do not incorporate different types of data, e.g. combining molecular data with craniometric data, or metric analysis compared to discrete traits. The current project utilizes two data types, craniometric and genetic data, from populations in Mexico. The craniometric data are from pre-Hispanic groups, while the genetic data are from modern individuals. The goal is to determine whether craniometric data can be used as a proxy for either Y-chromosome DNA or mtDNA, and vice versa. To do this, R and kinship matrices are

found, as well as F_{ST} estimates. Mantel tests were run between the data types and also with geographic distance. These populations are not expected to have strong correlations between data types due to the complicated history of the given populations. Knowing how well each data type reflects the patterns seen in the other can demonstrate how to best move forward with research, including research toward peopling of the New World. The following provides an overview as to what osteological evidence and molecular evidence concerning peopling of the New World demonstrates, followed by a discussion of the current project.

Osteological Data: Peopling of the New World

Osteological evidence for peopling of the New World can be found in numerous sites ranging from North America to South America, although many are controversial due to various dating techniques. Many of the ancient South American skulls show a closer relationship to modern Africans or Australians rather than current Native Americans or East Asians (Neves et al. 2007), suggesting a common ancestor exists between these groups. Jantz and Owsley (2001) found 10 out of 11 ancient North American crania to be closest morphologically to Europeans, Polynesians, or East Asians, but not contemporary Native Americans. This has led Jantz, Owsley, and others to support a theory of two migrations into the New World: a migration of an initial population followed later by a separate population. This second population migration occurred around the Pleistocene/Holocene transition and carried the traits of modern Native Americans. Studies of ancient South American sites, such as in the region of Lagoa Santa in central Brazil, also show that these skulls are distinct from modern Native Americans or East Asians, supporting a theory of multiple migrations (Neves et al. 2004, Neves and Hubbe

2005). These studies tend to support a migration occurring before 13,000 yrs before present (BP), but after 25,000 – 30,000 yrs BP, which seems to (mostly) be the consensus among anthropologists studying osteology of ancient North and South American populations.

Powell and Neves (1999) also show results consistent with multiple migrations when using craniometric data, including a separate migration from which the current Native Americans are derived. However, they recognized that their assumptions of "equal long-term effective size for all populations and limited diversity within the founding populations with subsequent "freezing" of ancient among-group variability through rapid demographic growth" were not completely realistic as it is not yet understood what the population structure was during this time period (Powell and Neves 1999:160). Also, the diversity of these ancient populations could be explained by different processes of population structuring. This may include genetic drift or demographic growth. When Powell and Neves (1999) controlled for the effects of genetic drift, the Paleoindian samples no longer classified as a distinct group separate from modern Native Americans. The fact that Paleoindian crania are morphologically different from modern Native Americans is not all that unusual. Hajime et al. (2009) found that ancient Japanese skulls compared to modern Japanese skulls show a lot of variation, suggesting phenotypic traits are highly variable. This variability is likely due to genetic drift and migration or gene flow. Also, *in situ* natural selection could have affected the phenotypic traits over time. Nakahashi (1993) also found ancient Japanese skulls to differ from modern skulls, probably due to the introduction of different allelesfrom other Asians. This provides evidence for the fact that ancient Paleoindians do not necessarily have to show the same

features as modern Native Americans, especially if there were multiple populations migrating to the New World. Current research should consider that other forces could have been at play, e.g. genetic drift, especially considering more than 10,000 years passed between the populations they are comparing.

Molecular Data: Peopling of the New World

Genetics can also be used to investigate peopling of the New World. MtDNA is an extranuclear genome that is only maternally inherited. The mutation rate of mtDNA is higher than for the nuclear genome, which allows for an easier distinction to be made between populations with a recently diverged haplogroup or haplotypes (Kemp et al. 2007, Kemp and Schurr 2010). MtDNA is also not strongly affected by natural selection (Kivisild et al. 2006) meaning it would more strongly reflect population history rather than selection (Kemp and Schurr 2010). Y-chromosome DNA is only passed through males and therefore only represents the male lineage. As with mtDNA, genetic drift more strongly affects the Y-chromosome compared to autosomal DNA. Combinations of mtDNA and Y-chromosome DNA, or other types of DNA, would provide a more complete picture in comparison to a single type being used. One reason for this is because certain types of DNA, such as mtDNA or Y-chromosome DNA, only show the female lineage or the male lineage.

There is a consensus among molecular anthropologists that initial migrations into the Americas contained five founding mtDNA haplogroups: A, B, C, D, and X, all making up the majority of the lineages in existing Native American populations. The major lineages include A2, B2, C1b, C1c, C1d, and D1. There are other less frequent sublineages, such as C4c, D2a, D3, and X2a, with the possibility of 15 or more founding

lineages in total (Reidla et al. 2003, Starikovskaya et al. 2005, Tamm et al. 2007, Perego et al. 2009, 2010, Malhi et al. 2010). It is also well understood that northeast Asia is the point of origin for the founding population, with southern Siberia and Mongolia frequently cited as the region of origin (Goebel et al. 2008, Ray et al. 2010).

Recent molecular analyses estimate the coalescence time to be between 15 and 18 kya (Tamm et al. 2007, Perego et al. 2009, 2010). While there is consensus about the timing of migrations into the New World, there is some debate on the number or types of migrations to the New World. The majority of current studies lean toward the idea of a bottleneck occurring due to a pause in the migration across Beringia, i.e. a point in time during which the migration of a group or groups temporarily stopped on Beringia, possibly stopping for thousands of years. The Beringian standstill has been supported by using autosomal DNA, X- or Y-chromosome DNA, mtDNA, ABO blood groups, or a combination thereof (Tamm et al. 2007, Kitchen et al. 2008, Fagundes et al. 2008a, Halverson and Bolnick 2008, Perego et al. 2009, Henn et al. 2009, Arnaiz-Villena et al. 2010). The Beringian standstill hypothesis is frequently accompanied by a theory of a single migration, or at least a single source population. A theory supporting multiple migrations into the New World is also frequently used (Schurr 2004, Volodko et al. 2008, Reich et al. 2012) rather than a single wave migration.

Diversity in the Americas has previously been shown to decrease as a function of distance, moving from North to South, when using mtDNA, X-chromosome DNA, Y-chromosome DNA, and autosomal DNA (Wang et al. 2007, Yang et al. 2010). This supports previous research indicating a decrease in diversity as distance from Africa increases (Wang et al. 2007, Yang et al. 2010). Many of these same studies (Wang et al.

2007, Yang et al. 2010) also show evidence toward a coastal migration into the Americas. Each of these, however, recognize that migration may not and probably did not solely consist of utilizing the coast, but rather a combination of inland and coastal routes. Coastal routes are also supported by computer simulations using mtDNA (Surovell 2003, Fix 2005).

Thus far, there has been contrasting genetic evidence concerning the ancient population structure within South America. Yang et al. (2010) demonstrates that the lowest within-group diversity is in the eastern region, the highest within-group diversity is in the Andean populations, with intermediate values in the northwestern region. This is supported by Tarazona-Santos et al. (2001), Pucciarelli et al. (2006), Rothhammer and Dillehay (2009) whom all use either X-chromosome DNA, Y-chromosome DNA, mtDNA, or a combination of these data types. These results combined with the results from Fu's F-test indicate bottlenecks occurred, or that there was a smaller effective size during expansion, in the eastern and northwestern regions of South America, while the Andean region and Mesoamerica experienced population expansion. The bottlenecks also probably occurred with a population contraction, as indicated by the higher F_{ST} estimates in the Y-chromosome DNA compared to mtDNA and the faster diversity equilibrium on the X-chromosome compared to autosomal DNA. These possible bottlenecks are further supported in Ray et al. (2003), Wange et al. (2007), Lewis (2010).

The founding Y-chromosome haplogroups are still debated (Lell et al. 2002). Most evidence suggest that only two haplogroups, C and Q, are part of the original founding populations. Other haplogroups found are thought to be due to post-European contact (Zegura et al. 2004, Bolnick et al. 2006). A sublineage of the Q3-M242

haplogroup, Q3-M3, is the most commonly seen haplogroup in indigenous populations throughout the Americas, with its distribution supporting theories of a single source population containing Native American males migrating to the Americas (Zegura et al. 2004, Bolnick et al. 2006). The mutation that differentiates this haplogroup likely occurred during the migration to the Americas, or during the Beringian standstill (Kemp et al. 2007). This haplogroup is also found in Siberian populations, such as the Chukchi or Siberian Eskimos (Karafet et al. 1997, Kharkov et al. 2007).

Within Mexico in particular, Q3-M242 and Q3-M3 have been found in many indigenous populations, with a clear segregation between the populations containing these. This clear distinction has not been found in populations further south in Mesoamerica, and many populations within South America only have the Q3-M3 branch. These results support the idea that Mexico was a transitioning area, with only a single source population founding the regions south of Mexico. This critical role is what makes Mexico an important area of study for the peopling of the Americas (Sandoval et al. 2012).

Mexico

Using data from pre-Hispanic groups (prior to 1492) can help elucidate information about peopling of the New World. These groups date to before Europeans colonized the Americas, and therefore demonstrate less admixture than their modern counterparts. This makes them more representative of the founding populations of the New World. Using data from pre-Hispanic crania and comparing that data to modern molecular data can help us understand temporal differences between these time periods. However, it is possible that any observed differences may be due to using different data

types rather than time. It can also provide information about population differences, evolutionary patterns, and how closely population patterns mimic each other between data types.

The specific reference groups utilized in this analysis include populations from Sonora, Michoáca, and Tlanepantla, with a map provided in Figure 1. Many research articles have looked into the population structure and variation within these populations. For example, Rangel-Villalobos et al. (2008) used Y-chromosome STRs to assess genetic diversity in populations within Mexico. They found that Mexican Mestizos from western Mexico had a paternal ancestry primarily consisting of Europeans, followed by Amerindian and African. Northern Mexicans showed a similar patterning, but Mexicans from central Mexico were significantly less heterogeneous. From this, they conclude that two different evolutionary processes are present. Areas with a high migration rate (central Mexico) had a more homogeneous population structure, but areas that were more isolated with lower migration rates (western and northern Mexico) were more affected by other evolutionary forces. These include founder effect and/or genetic drift, and were subsequently more heterogeneous. Specifically, the Tarahumaras had a higher frequency of Y-chromosomes without the Q3 haplogroup. Haplogroup C was also present, a haplogroup that is also present in Europe, which can be explained by the Tarahumaras having a distinct Native American ancestry with European interaction. However, there are differences seen between autosomal DNA and the Y-chromosome DNA of the Purépechas population. This could be explained by preferentially mating with non-Purépechas women.

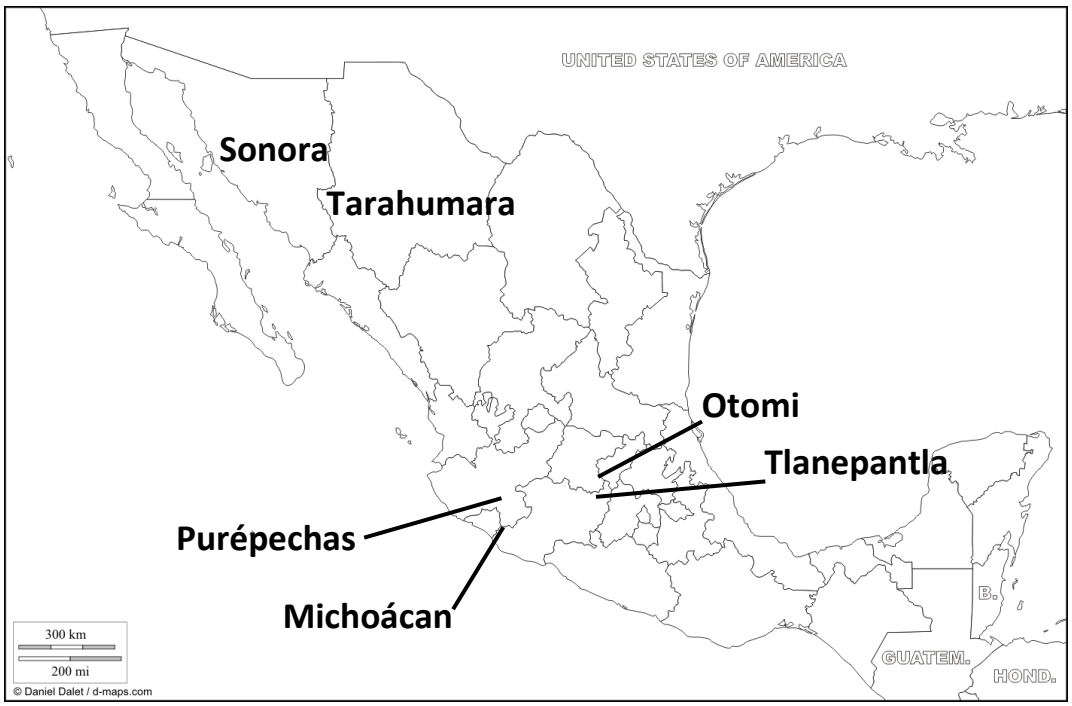

Figure 1: Map of Mexico displaying origin and distances between all populations used. Map obtained from http://d-maps.com/carte.php?num_car=4123&lang=en.

Peñaloza-Espinosa et al. (2007) investigates the population structure of 14 indigenous Mexican populations, three of which are the ones listed above. The Tarahumara did not have mtDNA haplogroup A, but they did contain B, C, and D. The Purépecha have low frequencies of haplogroups B, C, and D, possibly because they are relatively isolated. Many of these populations are known to have been conquered by the Aztecs before the Spanish arrived. Interestingly, several of the groups still speak Nahuatl, the language spoken by the dominant Aztec group, but not all contain genes typically associated with the Aztecs. Overall, these Mexican groups show mtDNA haplogroups associated with Europeans and Amerindians.

The Purépechas speak a language called Purépecha. The language is currently only spoken by 28% of children in the Purépecha culture who now prefer to learn Spanish. In some villages though, Purépecha is still spoken by all family members. Spanish has now been spoken in the area for many centuries, but prior to contact with Spanish, Nahuatl and Otomi were spoken. The relationship of these languages to the Purépecha language is currently unknown (Chamoreau 2010).

The Otomi are a central Mexican group who speak Otomi. Before the Spanish conquest, Aztecs were well known enemies of the Otomi because the Otomies were the first group to make war against them. The Aztecs eventually won against the Otomi toward the end of the 14th century, causing the Otomi to flee east (including into Michoácan where the Purépecha population) and south. This also caused an increase in Nahuatl influence on the Otomi language.

The Tarahumara belong to the language family of Uto-Aztecan and live in a mountainous region in the state of Chihuahua, Mexico. Over the past few centuries, their land has been gradually reduced by the Europeans who came to the area. The Tarahumara had to leave the most fertile areas, which caused large changes to their economy. They had to incorporate practices from the Mestizos, such as raising cattle and sheep, and start participating in the larger Mexican economy. In spite of centuries of contact, the Tarahumara has retained much of their traditional way of life and remained relatively isolated (Paciotto 1996).

During the early 1500s, Diego de Guzman first invaded the area of Sonora, Mexico. This was soon followed by Cabeza de Vaca, Pedro Nadal and Juan de la Asuncion, Marcos de Niza, Coronado, and Ibarra. After the 1500s, many friars and other

explorers came to the region. Sonora still had many Native American populations in 1902 when Hrdlička visited. These groups consisted primarily of the Mayos, Yaquis, Opatas, Seris, Pimas, Papagos, and Yumas. The skeletal samples Hrdlička recovered from this region consisted of Native Americans belonging to the Opatas, Yaquis, Mayos, Seris, Pimas, and Papagos. The time period the samples came from are not listed (Hrdlička 1904).

Lumholtz excavated the Michoácan crania from a site called El Palacio near Zacápu, Michoácan. Zacápu used to be one of the larger pueblos in the areas, housing the Tarasco Native Americans. During the time when Lumholtz excavated the site, there were still a large number of Native Americans present, of which about half of the people still retained the customs and language of their culture (Lumholtz and Hrdlička 1898). The sample from Tlanepantla dates to a Pre-Columbian period of 1300 – 1500 AD. Little is known about the archaeology of the site because the excavators published very little information about the sites excavated in Northern Mexico. This particular population is known to have remained fairly isolated for a long period of time, and it is suspected that the colonization of the Spanish had little effect on their material culture (Christensen 1997).

Under the assumption that molecular data represents biological relatedness, we are testing whether craniometric data shows the same patterns. If this is the case, then craniometric data could be used in place of molecular data in some circumstances. One circumstance where this would be appropriate is in populations where the genetic data is highly admixed. The craniometric data in this case could provide a picture of the diversity and biological relationship prior to the advanced admixture.

Many studies concerning this topic use a range of ancient and modern material to perform statistical analyses (Santos et al. 1999, Neves et al. 2003, González-José et al. 2008). Sometimes a combination is used. However, there are a limited number of ancient skeletal specimens available. There are also relatively few ancient specimens where DNA has been taken, and it is much easier to get large quantities of data for a particular population if modern DNA is used. This leads researchers to use modern DNA and model the coalescent to analyze the relavent mutations (Kingman 1982a,b, Henn et al. 2009). Knowing how well modern DNA approximates ancient cranial morphology and vice versa for a given population is important to ensuring that the current methods used are meaningful.

CHAPTER II

MATERIALS & METHODS

Materials

Craniometric and molecular (mtDNA and Y-chromosome) data from populations in Mexico are used to aid in answering these questions. The craniometric data were obtained from populations in Sonora, Michoácan, and Tlanepantla, with locations shown in Figure 1 and having sample sizes of 15, 22, and 17 respectively. All data was collected by Dr. Kate Spradley at the American Museum of Natural History. This cranial series was part of an expedition carried out by Aleš Hrdlička, with the Michoácan sample collected by Lumholtz (Lumholtz and Hrdlička 1898, Lumholtz 1903). These crania are pre-Hispanic, with one group thought to be pre-Hispanic (pre-Spanish), dating between 1200 and 1500 AD (Beekman and Christensen 2003).

The molecular data were obtained from previously published data to best approximate the craniometric data, i.e. the data came from as similar of a population as possible. This includes populations from a similar geographic region with either a similar or a shared population history. It is important to note that while the craniometric data is pre-Hispanic, the molecular data is collected from modern individuals. The samples specifically came from the Tarahumara, Purépecha, and Otomi. The locations and geographic distances between these populations are shown in Figures 2 and 3. The Tarahumara were used to approximate Sonora because of their close proximity to one another. According to isolation by distance models, migration is limited by geographic distance. This creates a patterning of less genetic similarity in populations separated by a greater geographic distance and higher genetic similarity in populations in close

geographic proximity (Relethford 2004). It has been found that populations in Sonora speak the same language of the Tarahumaras, and there is a known interaction between these neighboring groups (Passin 1944, Felger and Yetman 2000). Therefore, Tarahumara was used to approximate the samples from Sonora. The Purépecha are the indigenous people of Michoácan, and were thus used to approximate the Michoácan samples. The Otomi were the approximation of Tlanepantla because of historical evidence of interbreeding and geographic location. From this point on, the terms "northern samples" will be used in place of Sonora or Tarahumara, "central samples" will be used instead of Otomi or Tlanepantla, and "eastern samples" will be used instead of Purépecha or Michoácan.

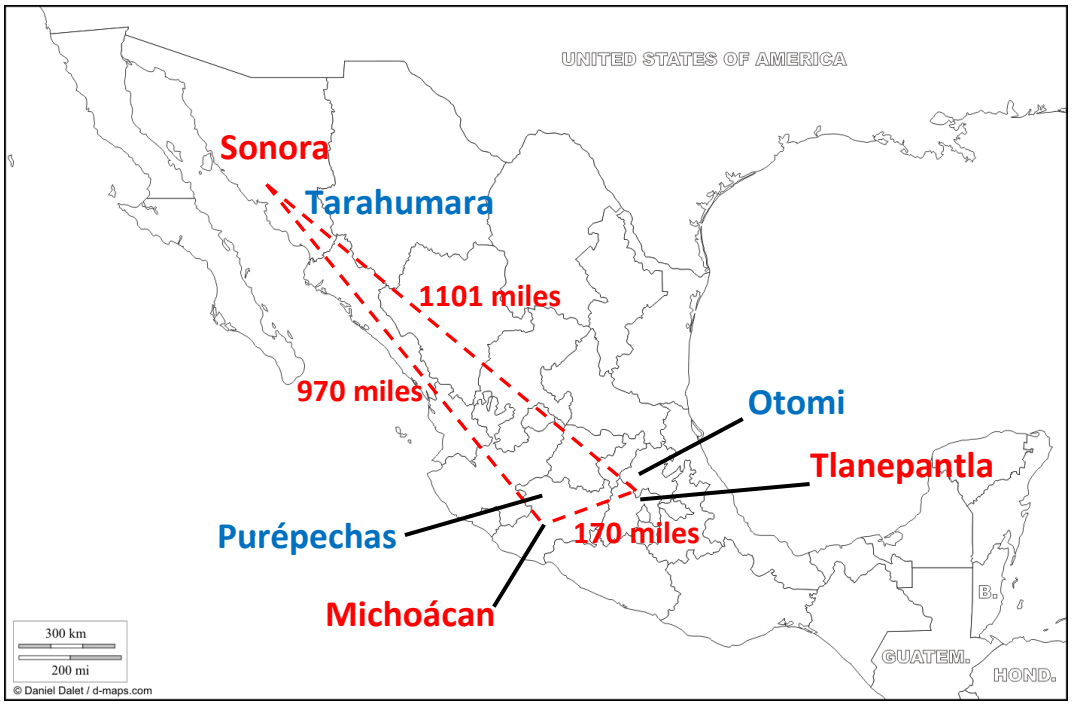

Figure 2: Map of Mexico displaying origin and distances between craniometric data. Red represents pre-Hispanic craniometric data and blue represents modern DNA data. Map obtained from http://d-maps.com/carte.php?num_car=4123&lang=en.

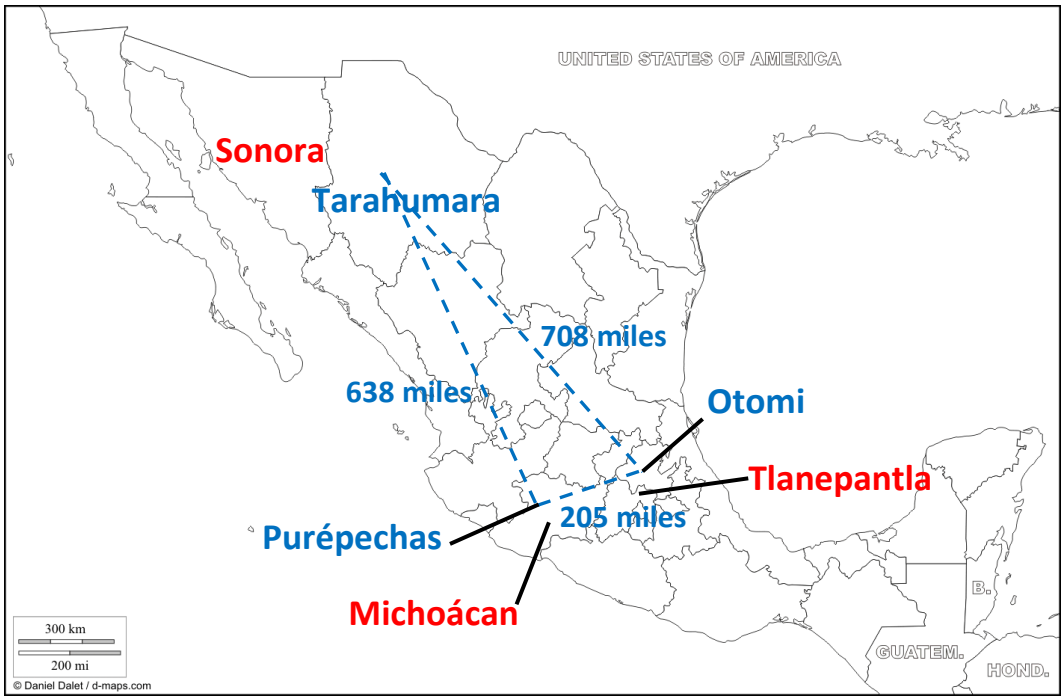

Figure 3: Map of Mexico displaying origin and distances between genetic data. Red represents pre-Hispanic craniometric data and blue represents modern DNA data. Map obtained from http://d-maps.com/carte.php?num_car=4123&lang=en.

Allele distributions, or distributions of various forms of the same gene, of six Y-linked short tandem repeats (STRs) were obtained. I utilized the populations Tarahumara, Purépecha, and Otomi. All data was retrieved from previously published data (Barrot et al. 2007, Rangel-Villalobos et al. 2008). All allele frequencies and a list of the specific alleles used are provided in Table 1. The sample sizes of each of these populations are 20, 16, and 41 respectively.

MtDNA haplogroups help define the major branches of the mitochondrial genome and are commonly used to illuminate evidence on the number and age of migrations. Data on mtDNA haplogroups A1, A2, B1, B2, C1, C2, D1, D2, and X2 were obtained for the Purépecha, Tarahumara, and Otomi from Peñaloza-Espinosa et al. (2007). Table 2

shows the haplogroup frequencies for each population. The sample sizes of each population used are 53, 37, and 35 respectively.

Table 1: The Y-chromosome alleles and frequencies used in the analysis. All frequencies from previously published data (Barrot et al. 2007, Rangel-Villalobos et al. 2008). Sample size is also listed.

Y-Chromosome Alleles			
	Tarahumara	**Purépecha**	**Otomi**
DYS19-13	0.800	0.813	0.756
DYS19-14	0.100	0.188	0.195
DYS19-15	0.050	0.000	0.024
DYS19-16	0.050	0.000	0.024
DYS389I-9	0.300	0.375	0.000
DYS389I-10	0.300	0.500	0.000
DYS389I-11	0.400	0.125	0.000
DYS389I-12	0.000	0.000	0244
DYS389I-13	0.000	0.000	0.512
DYS389I-14	0.000	0.000	0.244
DYS390-22	0.000	0.000	0.024
DYS390-23	0.400	0.125	0.293
DYS390-24	0.600	0.375	0.366
DYS390-25	0.000	0.375	0.317
DYS390-26	0.000	0.125	0.000
DYS391-8	0.000	0.000	0.024
DYS391-9	0.100	0.313	0.048
DYS391-10	0.600	0.563	0.707
DYS391-11	0.300	0.125	0.221
DYS392-11	0.000	0.000	0.122
DYS392-12	0.150	0.313	0.000
DYS392-13	0.450	0.438	0.366
DYS392-14	0.350	0.188	0.146
DYS392-15	0.500	0.063	0.073
DYS392-16	0.000	0.000	0.293
DYS393-12	0.200	0.000	0.048
DYS393-13	0.800	0.812	0.537
DYS393-14	0.000	0.000	0.415
DYS393-15	0.000	0.188	0.000
Sample Size	20	16	41

Table 2: The mtDNAhaplogroup frequencies listed by population (Peñaloza-Espinosa et al. (2007). Sample size is also listed.

	Populations		
Haplogroup	**Tarahumara**	**Purépecha**	**Otomi**
A1	0.057	0.243	0.086
A2	0.038	0.324	0.514
B1	0.358	0.054	0.143
B2	0.057	0.162	0.057
C1	0.113	0.054	0.086
C2	0.264	0.108	0.029
D1	0.019	0.000	0.057
D2	0.075	0.054	0.029
X2	0.019	0.000	0.000
Sample size	53	37	35

Methods

The allele and haplogroup frequencies for the Tarahumara, Purépecha, and Otomi were put into matrix form. These matrices were then run in the program Kship (Jantz, n.d.). This provided a genetic distance matrix, eigenvalues, eigenvectors, and F_{ST} values for both mtDNA and the Y-chromosome data based on allele frequencies. The available cranial measurements and individuals were systematically eliminated until all missing values in the data were gone. The remaining data were then standardized by sex for each population. A list of the cranial measurements used in this analysis is provided in Table 3.

Table 3: The cranial measurements used in the analysis

Abbreviated Measurement	Description
BNL	Basion-nasion length
BBH	Basion-bregma height
XCB	Bi-parietal breadth
WFB	Minimum temporal frontal lines
AUB	Biauriculare breadth
NLH	Nasal height
NLB	Nasal breadth
WMH	Cheek height
FRC	Frontal chord
FRS	Frontal subtense
PAC	Bregma-lambda
PAS	Parietal subtense
NAR	Auriculare-nasion
ZOR	Zygoorbitale radius
FMR	Frontomalare radius
EKR	Ectoconchion radius
ZMR	Zygomaxilare radius
BRR	Bregma radius
VRR	Vertex radius
LAR	Auriculare-lambda
BAR	Auriculare-basion

The standardized measurements were run through Rmet (Relethford, not dated), a program that analyzes craniometric data and performs an R matrix analysis discussed in detail in Relethford and Blangero (1990), Relethford (1996), and Relethford et al. (1997). The program provides an output with a principle components analysis, the R matrix (also called a variance-covariance matrix), the D^2matrix, and F_{ST} values. The R matrix analysis is described in Relethford and Harpending (1995). The heritability was changed from the default value of 1.00 to 0.55, the value previously published research has shown to be most accurate (Devor 1987, Gravlee et al. 2003) before the data were run.

Rmet also provided a Principal Component Analysis (PCA) of the R matrix. A Principal Component Analysis changes the coordinate system of a matrix by performing a linear transformation. Specifically, this transformation places the maximum amount of

variation from any projection along the first coordinate, the second highest variation on the second coordinate, etc. A graph was also provided that showed the first two eigenvectors, scaled by the square root of the eigenvalues. This analysis takes correlated information and transforms it into linearly uncorrelated information. The transformation specifically transforms in a way that maximizes the variance. Using this analysis allows the researcher to know if the data (in this case populations) are different enough to be uniquely distinguishable (Wold 1987). Similar to the PCA, a graph of the eigenvectors of the R and kinship matrices is provided. These vectors are not scaled and transformed, like the PCA would do. This also allows us to know if the populations are distinct from each other in each data type.

Mantel tests were also performed using the R and kinship matrices. This test finds the correlation between two matrices, so three tests were performed to test for correlations between all combinations of data types, the craniometric and Y-chromosome DNA, craniometric and mtDNA, and Y-chromosome and mtDNA. Mantel tests were also performed between each data type and their corresponding geographic distance. These distances are the same as those shown in Figures 2 and 3. This part of the analysis allows us to not only examine the possible correlations between the data types, but also the correlations the populations within each data type have with their unique geography.

CHAPTER III

RESULTS

The Principal Component Analysis graph derived from craniometric data is provided in Figure 4. Each population is separated from each other on the graph. There are two non-zero eigenvalues: 0.1036 and 0.0510. The first eigenvalue accounts for 67% of the total variation and the second eigenvalue accounts for 33% of the total variation, with the two cumulatively accounting for the total 100% of the variation. The first axis separates the northern sample from the central sample with the eastern sample intermediate. The eastern sample is separated from the other groups on the second axis.

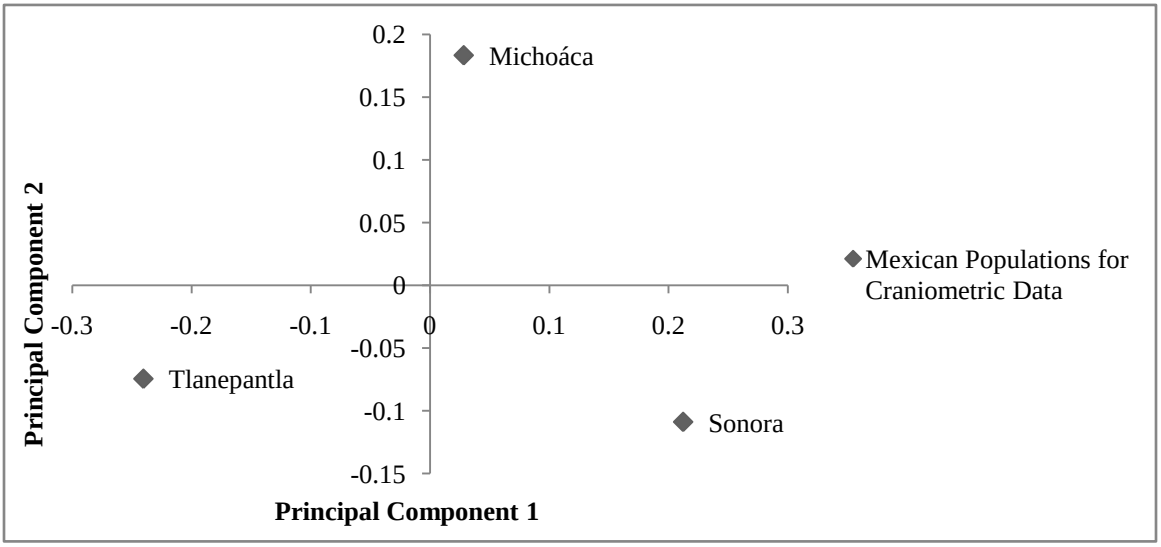

Figure 4: Principal Component graph of pre-Hispanic craniometric data

The obtained distance matrices from the three data sets are shown in Tables 4, 5 and 6. The three different data sets provide small genetic distances between the three groups. The distance matrices for Y-chromosome and craniometric data demonstrate the highest similarities in the northern and eastern samples. Next are the northern and central samples, with the eastern and central samples being the least similar. The mitochondrial DNA show that the central and eastern samples are most strongly similar, followed by the northern and eastern samples. The least similar are the northern and central sample groups. Lastly, craniometrics show the strongest similarities between the eastern and northern samples, followed by the eastern and central samples, and then the northern and central samples.

An F_{ST} estimate is the ratio of among-group variation to the total variation. Therefore, a higher F_{ST} estimate demonstrates that there is higher variation within the group being studied. The F_{ST} values for each group are listed in Table 7. Each data set suggests a different pattern of similarity among the groups. The F_{ST} estimates for each group also vary, with the highest value belonging to the Y-chromosome data.

Table 4: Distance matrix derived in Kship for Y-chromosome data

	Northern	**Eastern**
Northern	0.000	
Eastern	0.243	0.000
Central	0.363	0.390

Table 5: Distance matrix derived in Kship for mtDNA data

	Northern	**Eastern**
Northern	0.000	
Eastern	0.201	0.000
Central	0.233	0.087

Table 6: Distance matrix derived for craniometric data

	Northern	**Eastern**
Northern	0.000	
Eastern	0.119	0.000
Central	0.206	0.139

Table 7: F_{ST} values for each data type

	F_{ST}
Y-chromosome	0.123
MtDNA	0.059
Craniometric	0.040

Along with the distance matrices, R matrices and kinship matrices were also computed. The R matrix or kinship matrix is also known as the variance-covariance matrix. The eigenvectors of the R matrix and kinship matrices were graphed, with the graph shown in Figure 5. This graph displays the relationship of the given data types without altering the shape or size of the distances between the points. Also, the points representing the same data type are directly comparable. As long as each point on the

graph representing the different data types is not overlapping, this would indicate that each sample set is linearly independent from the others. As shown in Figure 4, each point from each data type is separate and not overlapping any of the others. Therefore, each sample set from within each data type is representing an independent population.

A Mantel test was performed between each data type. The Mantel test finds correlations between two symmetric matrices and tests the null hypothesis that the matrices are not correlated. In this instance, the R or kinship matrices from each data type was used, with the p-values and normalized Mantel statistic reported in Table 8. All the p-values reported are substantially higher than 0.05 and therefore the genetic distance matrices are not correlated with each other or with the craniometric distance matrix. Mantel tests were also performed between each data type and their corresponding geographic distance. These p-values, listed in Table 9, are also substantially higher than 0.05 and therefore the null hypotheses cannot be rejected.

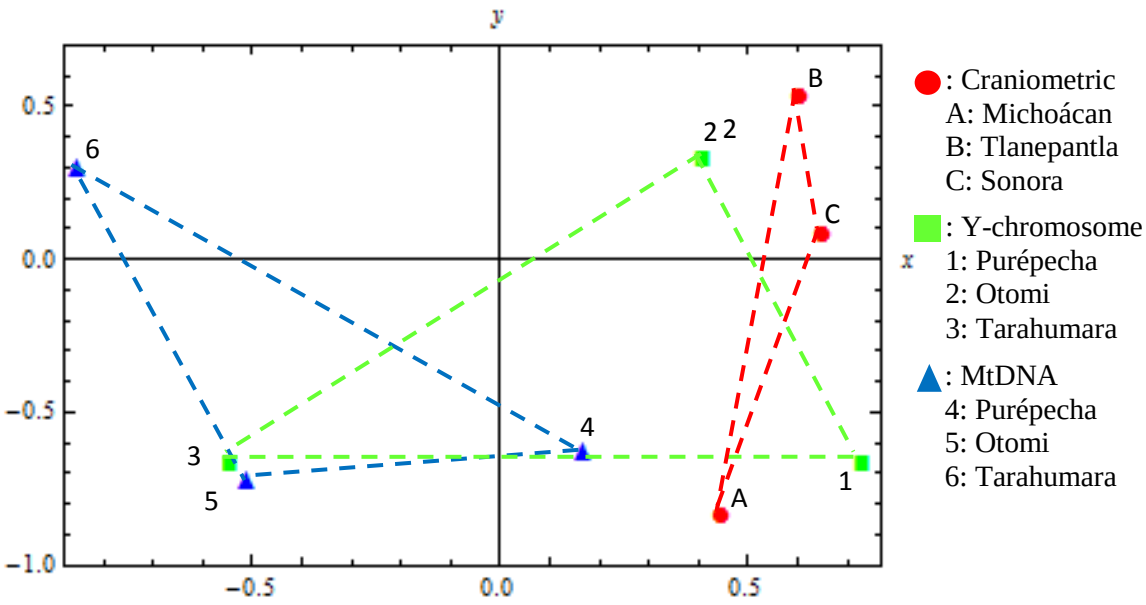

Figure 5: Graph of eigenvectors from R matrix and kinship matrices

Table 8: P-values and normalized Mantel statistic from all Mantel tests performed between data types

	P-values	Normalized Mantel statistic
Craniometric data and y-chromosome DNA	0.3449	0.5409
Craniometric data and mtDNA	0.4977	0.4902
Y-chromosome DNA and mtDNA	0.5019	-0.4629

Table 9: P-values and normalized Mantel statistic from all Mantel tests performed with geographic distance

	P-values	Normalized Mantel statistic
Craniometric data and geographic distance	0.5065	0.4193
Y-chromosome DNA and geographic distance	0.3378	-0.5381
mtDNA and geographic distance	0.1662	0.9967

CHAPTER IV

DISCUSSION

The PCA graph (Figure 4) demonstrates that there are differences between the three craniometric population samples, indicating that the samples obtained did actually come from different populations. If the population samples were too similar they would not be representative of different populations and that would bias the results. Similarly, the graph of the eigenvectors (Figure 5) from the R and kinship matrices also show a strong distinction between the populations when each data set is viewed separately. Again, this is important to establish because it means that each sample set within each data type is distinct and adequately represents each population. Each sample set is not a linear combination of any other sample set from within that data type.

The differences seen in the F_{ST} estimates are not likely explained by mutation rates, as this should not strongly affect the apportionment of within vs. among group genetic diversity (Excoffier and Hamilton 2003, Nasidze et al. 2004). There are a few possibilities to explain the higher Fst value for the Y-chromosome data. One possibility is patrilocality, which would lead to higher Y-chromosome differentiation compared to mtDNA (Oota et al. 2001, Bolnick et al. 2006). This patterning has been found in Mexico before (Herren 1992, Merriwether et al. 1997). A second possibility is the high mutation rate and high drift rate of the Y-chromosome, which could lead to higher variation (Jorde et al. 2000) when occurring concurrently with small effective population size of males, possibly due to patrilocality. Of course, both of these could be occurring concurrently.

The distance matrices for the Y-chromosome DNA and mtDNA each demonstrate a different relationship between the various populations. The Tarahumara and Purépecha show the strongest similarities using the Y-chromosome, with the geographic distance between them being 638 miles (Figure 3), but mtDNA suggests that the Purépecha and Otomi are most similar. The geographic distance between these is only 205 miles. The Purépecha and Otomi exhibit the least similar Y-chromosome allele frequencies, even though these are the closest geographically. Therefore, male and female gene flow appears to be different between these three populations. Female gene flow is more strongly correlated with geography than male gene flow is, suggesting that populations that are closer together are connected by female migration or gene flow. Different factors seem to be affecting male gene flow, as populations that are further away have the strongest correlation.

These results also suggest that these groups are patrilocal. Patrilocality would lead to higher Y-chromosome differentiation between the populations, or higher F_{ST} values, which are shown in my results. The mtDNA would have lower differentiation between populations, and a lower F_{ST} value because men are not migrating as much as the women, which is also seen in my results (Oota et al. 2001, Bolnick et al. 2006).

The results of the three Mantel tests performed between the data types are listed in Table 8. All p-values indicate that each data type is not correlated with any other data type. This means that the craniometric data used in this analysis cannot act as a proxy for the molecular data, or vice versa, using these data sets. Table 9 shows the results from the Mantel tests done incorporating geographic distance. The p-values indicate that none of the data types are correlated with geographic distance. This means that the populations

are not correlated as a function of distance, i.e. the most genetically different populations are the not the populations that are geographically the furthest away, except for the mtDNA.

The craniometric data demonstrate the strongest similarity between the northern and the eastern samples. These two groups occupy a mountainous region, while the central samples live in a valley. Therefore, the topography of the area may play a role in the similarities seen. Further analysis incorporating elevation instead of just geographic distance may aid in understanding the relationships shown by the distance matrices. The results of these analyses agree to some extent with other research where cranial morphology is compared to DNA. One example is from Perez et al. (2007), where populations from Tierra del Fuego are discussed. These authors used mtDNA and Y-chromosome DNA and found evidence supporting theories that these populations are descended from a pre-Asian descent group rather than Amerindians, as suggested by cranial morphology. They also found differences in their results based on the region of the cranium being studied. The facial region agreed with the mtDNA haplogroup frequencies. Therefore, the same mechanism that results in the differing haplogroup frequencies may also account for the differences seen in the facial region. These results suggested that forces other than genetic drift may be acting on these populations.

Limitations

There are several possible reasons for to explain the results from the Mantel test done between data types. One reason is that the craniometric data are from pre-Hispanic populations, while the molecular data are from modern populations. Each data type therefore represents a different temporal period and too many evolutionary changes may

have occurred in this span of time for the data to be correlated. Another reason is that the data are not from the same populations. They are from similar populations with shared population histories, but this is a limitation in the study. If the exact populations for each data type were present, correlations might have been found. The craniometric data also did not all come from one population, but rather a combination of different local groups, as discussed in the Materials section. This could cause some of these discrepancies. Another possibility is that craniometric data and genetic data are shaped by different evolutionary forces. Cranial shape is recognized to be shaped by natural selection (Roseman 2004, Harvati and Weaver 2006), but the mtDNA and Y-chromosome DNA might be more strongly influenced by other forces, such as genetic drift or gene flow.

The differences seen between the different data types (mtDNA, y-chromosome, and craniometrics) may suggest that different evolutionary forces have been acting on each DNA set and cranial morphology. These forces may include genetic drift, natural selection, and gene flow. Further, if the same evolutionary forces were acting on populations from different data types, the forces appeared to have affected each data type in a different way. Given how stochastically genetic drift behaves (Weaver 2012), this is likely the driving force acting on some of these populations, but natural selection and gene flow cannot be ruled out and most likely additionally affected these populations.

Possible reasons to explain the results from the Mantel test between data type and geographic distance would be that some of the populations furthest apart have more of a shared population history than the ones closest together, there is a more recent common ancestor between the ones farthest away versus the ones that are closest, or there is gene flow between them. Given that different populations have invaded these regions over

time (for example, the Aztecs invaded the region occupied by the Otomi), forcible migrations have occurred and likely brought about contact between some of these groups. This most likely would have resulted in gene flow, to some degree.

Future Directions

In this study, the different regions of the crania were not analyzed separately in terms of being compared against the molecular data. Using our methods to look at these relationships will help illuminate the extent to which genetic drift, gene flow, or natural selection are acting on these particular populations, as exemplified in Perez et al. (2007) discussed above. Knowing what region of the skull is more controlled by either X- or Y-chromosome DNA, autosomal DNA, or mtDNA would allow researchers to more adequately structure their research questions and analyses. Rather than using the measurements from the entire cranium, only the regions known to be more influenced by a particular type of DNA would be used as a proxy for that particular type.

Performing a similar analysis on crania from the same time period as the molecular data should be done. Part of the discrepancy seen in this analysis could explained by having data from different time periods. Without utilizing data from the same time period, the full relationship between craniometric data and DNA cannot be understood. To address another problem with this analysis, data should be collected from the same populations within Mexico. Performing the analysis on the exact populations might change the results.

CONCLUSION

Based on the samples used in these analyses, present day molecular data does not exhibit the same population patterns as craniometric data for pre-Hispanic groups. The Y-chromosome, mtDNA, and craniometrics are not shown to be correlated. This demonstrates that craniometrics cannot be used as a proxy for molecular evidence, and vice versa, in some situations. These situations may include ones where the samples are coming from different temporal periods, although further confirmation of this is necessary.

When finding correlations using geographic distance I show that there is no correlation between the populations and geographic distance. This means that the relationships between the populations are not straight-forward and supports the claim that genetic similarity cannot be purely estimated based on geography alone. Interestingly, the populations that were the closest together, the eastern and the central samples, do not have any large geographic barrier between them, such as mountains or a large body of water. This kind of geographic isolation is a typical reason for a lack of genetic similarity in nearby populations. A likely reason to explain the lack of genetic similarity is that the populations used are known to have a complicated population history with numerous invasions by different cultures and groups of people, so the lack of geographic correlation is likely due to cultural practices and migration due to invasion.

Each of these populations appear to have different evolutionary forces acting on each the mtDNA, Y-chromosome DNA, and craniometric data. Given the stochasticity of

genetic drift, this is likely affecting at least one of the data types given that none of them are correlated. However, given that each population had been invaded by various populations, gene flow cannot be ruled out, as well as natural selection. If the same forces have been acting on the different data types, they appear to have been acting on them in different ways.

Further studies will provide more conclusive evidence for how well craniometrics and molecular (Y-chromosome and mtDNA) data serve as proxies for each other in worldwide populations. The ideal situation would be a case where the population has a well-understood history. Successful applications of this method for other groups would show that craniometrics can be used as a proxy for molecular data under other situations. Studies utilizing larger sample sizes should also be done to ensure that the samples are representative of the population as a whole.

In conclusion, this paper is unable to provide concrete evidence about whether craniometrics can be used as a proxy for molecular data, and vice versa. There does not appear to be concordance in the data in the present population groups, but more conclusive results may be found if either ancient DNA was used in comparison with the pre-Hispanic craniometrics, or if modern craniometrics was used with the current DNA data. These results support the discrepancies seen in studies relating to peopling of the New World. More work should be done to gauge which data more accurately predict the populational relationships and evolutionary processes seen in world-wide populations.

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