USING MATCHED CRANIOMETRIC AND GENETIC DATA TO ASSESS THE POPULATION STRUCTURE OF TEXAS-MEXICO BORDER MIGRANTS

by

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A thesis submitted to the Graduate Council of
Texas State University in partial fulfillment
of the requirements for the degree of
Master of Arts
with a Major in Anthropology
August 2018

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ACKNOWLEDGEMENTS

I would like to thank Dr. Kate Spradley for her insights over the last two years that have shaped me into the scholar that I am today. Thank you for always having words of encouragement, sharing your data, and teaching me that sometimes you just have to say "c'est la vie" and keep moving forward. Dr. Lars Fehren-Schmitz, thank you for inspiring my interest in anthropological genetics as an undergraduate and for being a constant champion of my work since. Thank you for donating your resources because without your generosity this research would not have been possible. Dr. Nick Herrmann, thank you for your keen eye and for always encouraging me to think outside of the box. Conversations with you inspire me to try something new and look at my work in a different way. Working with the three of you to develop this research has been an incredibly rewarding experience. Because of you I managed to come out of my thesis still loving my topic and twice as passionate about this work!

Thank you to my parents for your unconditional love. You taught me that success takes hard work, failure, and the drive to try again. Thank you to my siblings for always making me laugh and keeping me humble. Thank you to my cohort and to my friends for endless adventures! You make my world brighter. The last two years have been quite the journey and it wouldn't have been the same without you. Finally, thank you to the Grady Early Foundation for providing funding that allowed me to travel to UC Santa Cruz and work with Dr. Fehren-Schmitz.

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ABSTRACT

Human population structure studies suggest that craniometric and genetic data demonstrate similar genetic distances within and between populations. However, few studies use craniometric and genetic data from the same individuals to conduct comparative analyses. Therefore, it is necessary to assess whether distance analysis methods deliver significant results when comparing craniometric and genetic data obtained from the same individuals. Using interlandmark distances (ILD) and short tandem repeats (STR) obtained from a sample of 32 Texas-Mexico migrants, this study investigates the within and between population variation of this unique data set.

Genetic distances, Procrustes plots, and Mantel tests were conducted to assess the correlation between ILD and STR data. Interindividual results suggest no significant correlation between ILD and STR data ($r = -0.01$, $p = 0.83$). Between population results demonstrate a moderate correlation between ILD and STR samples, but the relationship between distance matrices is not statistically significant ($r = 0.317$, $p = 0.239$). The results are discussed in the context of Texas-Mexico migrant population structure and the fit of matched ILD and STR data. This research is integral for not only understanding relationships within the given sample, but also for understanding the relationship between the craniometric and genetic data that biological anthropologists frequently utilize.

I. INTRODUCTION

Human population structure studies suggest that craniometric and molecular data demonstrate similar genetic distances between populations (Harvati and Weaver 2006; Relethford and Harpending 1994; Relethford 1994; Roseman 2004; Smith 2009; Smith et al. 2016; Strauss and Hubbe 2010; von Cramon-Taubadel 2009) However, few studies have the opportunity to use matched craniometric and genetic samples from the same individuals. While comparing similar populations can highlight general relationships, using truly matched data enhances our understanding of the relationships between individuals, populations, and data types. Deepening our understanding of these relationships is important in both a bioarchaeological context where skeletal remains are incomplete or DNA is unattainable, as well as in a forensic context where any skeletal or genetic information can aid in the identification process.

Humanitarian Crisis on the United States Border

The purpose of this research is to assess the population structure of Texas-Mexico border migrants, a heterogenous sample with Latin American origins, using matched molecular and craniometric data. For over a decade, deaths along the U.S.-Mexico border have steadily increased due to U.S. policy changes from the 1990s to present that are aimed at restricting undocumented migrants from easily entering the U.S. (Ackleson 2005; Anderson 2008; Anderson and Spradley 2016; Coleman 2005; Gocha et al. 2018). Increased border patrol efforts prevent migrants from using the safest, most easily accessible migration routes, funneling them to isolated and dangerous desert regions in

Arizona and south Texas (Cornelius 2001; Eschbach et al. 2003; Gocha et al. 2018; Guerette 2007).

With thousands of deaths along the Sonoran Desert sector of the border and numbers increasing each year along the Texas-Mexico border, there is a great need to contextualize who these people are, where they are coming from, and why they were willing to risk, and ultimately lose, their lives to enter the United States (Anderson and Spradley 2016; Gocha et al. 2018; Spradley 2016). Contrary to popular discourse within the U.S., the migrants crossing our borders are not a homogenous group (Ross et al. 2004; Spradley 2016; Spradley et al. 2008; Tise 2014). Migrants come from a variety of locations and cultural backgrounds both within and between geographic regions of origin. In Arizona, for example, border patrol apprehension statistics and identified remains suggest that many of the migrants crossing in the Sonoran Desert sector are from various regions of Mexico (Anderson 2008; Anderson and Spradley 2016; Spradley et al. 2016). In Texas, however, there is a greater diversity of people who originate throughout Central America including El Salvador, Honduras, Guatemala, Nicaragua, etc. (Gocha et al. 2018; Spradley 2016; Spradley et al. 2016).

Despite this wide variation in cultural and geographic backgrounds, Latin American populations migrating to the U.S. are often conflated into a general category of "Hispanic" due to shared population histories of Spanish colonialism and West African slavery (Ross et al. 2004; Sans 2000; Tise et al. 2014). In U.S. governmental rhetoric "Hispanic" is defined as any individual of "Cuban, Mexican, Puerto Rican, South or Central American, or other Spanish culture or origin regardless of race" (Ennis et al. 2011). Due to a lack of region specific information, this terminology crossed

governmental boundaries and is reflected in many early studies on Latin American populations. However, recent research on Latin American diversity recognizes that a term that encapsulates over a continent and a half of people conflates differential population histories by erasing the sociocultural, political, and economic contexts driving this mass migration. These studies have begun untangling the complex relationships between Latin American populations from a variety of perspectives including morphological (Hefner et al. 2015; Hurst 2012), metric (Gocha et al. 2017; Hughes et al. 2013; Spradley 2013; Spradley 2014; Spradley 2016; Spradley et al. 2008; Tise 2014; Tise et al. 2014), and genetic (Bonilla et al. 2004; Bryc et al. 2010; Klimentidis et al. 2009). Each study argues that relationships between populations labeled under the "Hispanic" nomenclature are patterned, therefore region-specific methods will better reflect the diversity of "Hispanic" populations.

To further elucidate the heterogenous nature of Latin American populations and promote region-specific methods, the present study will investigate the population structure of Texas-Mexico border migrants. Because Texas-Mexico migrants come from a variety of regions within Latin America, this research asks whether population structure is patterned both within the sample, as well as between this sample and other populations with shared admixture and population histories.

Comparing Molecular and Craniometric Data

Researchers use a variety of methods to explore population relationships therefore it is important to ask whether different methods and types of data, such as craniometric and molecular data, follow similar population patterns. Early population structure studies

suggest that, overall, variation of human crania is geographically patterned and approximates population structures estimated from neutral genetic markers (Relethford 2001; Relethford 1994; Relethford 2002). These studies argue that under a neutral evolutionary model, geographically proximate populations experiencing gene flow share more neutral genetic information and tend to look more alike than geographically distant populations. This notion has since been challenged by researchers exploring whether the effect of microevolutionary processes and biomechanical stressors are significant enough to alter cranial structures and render the comparison of craniometric and molecular data obsolete (Harvati and Weaver 2006; Roseman 2004; Roseman and Weaver 2004; Smith 2009; von Cramon-Taubadel 2009).

Smith (2009) addresses the morphological expression of genetic structures by comparing three dimensional landmarks and short tandem repeat (STR) data from 14 similar population samples. Smith argues that the best morphological traits for craniometric and molecular comparison are traits evolving through genetic drift rather than environmentally selective pressures because they can be utilized reliably across populations. To assess the correlation between STR data and cranial landmark data, the author partitioned landmark data by cranial region (basicranium, temporal bone, upper face, mandible, upper jaw, vault, and all regions combined). She concludes that the basicranium, upper face, and all cranial regions combined have the greatest association between morphological and molecular data. Therefore, it is likely that the basicranium, upper face, and the overall cranium are most likely evolving through genetic drift. Martinez-Abadias et al. (2009) confirm this conclusion by arguing that that high

intercorrelation between cranial traits demonstrates strong heritability, particularly in the facial, neurocranial, and basicranial regions of the skull.

The effect of biomechanical stressors was tested by von Cramon-Taubadel (2009). This study investigates the "homiology hypothesis", a hypothesis that argues strain placed on cranial structures through biomechanical processes, such as mastication, significantly alter the cranial phenotype of populations. Using STR and three-dimensional landmark data from 12 similar populations, von Cramon-Taubadel (2009) investigates how closely related morphological mastication structures are to neutral genetic data. The author argues that while morphological variation in mastication structures between populations was significant, estimating population histories through this region of the skull is no less reliable than other more morphologically static regions. Therefore, because cranial morphological traits are significantly heritable and remain consistent across populations, it is possible to compare STR data with craniometric distance data despite phenotypic plasticity.

Additional studies exploring the relationship between craniometric and molecular data utilize different populations from different time frames, different genetic markers, different craniometric data, and different analytical methods (Harvati and Weaver 2006; Herrera et al. 2014; Perez et al. 2009; Relethford 2010; Roseman 2004; Roseman Charles 2016). Despite variation in the analysis methods and types of data utilized, most studies acknowledge that, in the absence of extreme cold environments, overall cranial variation between populations reflects expected genetic relationships (Harvati and Weaver 2006; Herrera et al. 2014; Martinez-Abadias et al. 2009; Relethford 2010; Roseman 2004; Smith 2009; Smith et al. 2016; von Cramon-Taubadel 2009). Therefore, there is

precedent for comparing the molecular and craniometric data of similar groups to assess the relationships between populations.

The comparison of matched craniometric and molecular data from the same individuals however has been much more difficult to obtain. In both bioarchaeological and forensic contexts, researchers struggle with issues such as differential preservation or the availability of either set of data. Therefore, samples from similar populations are often utilized in population structure analyses. While researchers do their best to match population data by region and time frame, it is unavoidable that using similar populations with different samples of people will introduce error (Harvati and Weaver 2006; Herrera et al. 2014; Roseman 2004). Only one study currently exists that investigates the relationships between individuals, populations, and data types using data from the same individuals.

Smith et al. (2016) collected three-dimensional cranial landmark and molecular data from a historic North American sample of 36 individuals. The authors utilized this truly matched sample to ask if molecular and cranial data provide similar genetic distances on local and global scales. They also explored how genetic distances vary when using full cranial morphology versus a partial set of 36 interlandmark distances (ILDs). Smith et al. (2016) observed no significant relationships in the interindividual genetic distances of overall crania and any mtDNA region. Conversely, they observed a low correlation between interindividual distances estimated from mtDNA region HVI and the neurocranium. There were no significant relationships, after a Bonferroni correction, between the genetic and reduced ILD data for between population analyses. However, when comparing landmark data that represents overall cranial morphology with genetic

data (including STRs, mtDNA regions HVI-III and CR, and the overall mtgenome) all between population analyses were significant.

These results suggest that when comparing individuals or using reduced ILD data sets that do not represent the full scope of cranial variation, relationships between matched genetic and cranial data are dissimilar. Furthermore, Smith et al. (2016) argue that when utilizing matched population samples, overall cranial morphology does approximate genetic relationships in between population analyses. Following this example, the present study explores whether similar results can be obtained when comparing genetic distances from the matched craniometric and STR data of 32 Texas-Mexico border migrants.

Research Objectives

The purpose of this research is two-fold:

1. Use matched short tandem repeat (STR) and interlandmark distance (ILD) data from Texas-Mexico border migrants to assess whether the interindividual and between population distances analyses of these data types follow similar patterns.
2. Compare genetic distances from both data types using parental proxy groups as well as other Latin American groups to better understand the population structure of the Texas-Mexico migrant population.

Exploring the relationships between individuals, populations, and data types will not only highlight population structure present in the Texas-Mexico migrant population. It will

also highlight the differences and similarities in population structure estimates provided by craniometric and molecular data obtained from the same individuals.

II. MATERIALS AND METHODS

Sample Background

The craniometric and STR data employed in this study were obtained from the remains of identified and unidentified Texas-Mexico border migrants housed at the Forensic Anthropology Center of Texas State (FACTS) in the Osteological Research and Processing Laboratory (ORPL). These individuals were exhumed from counties in South Texas as part of an ongoing effort to identify the remains of migrants who died while crossing the Texas-Mexico border. *Operation Identification* (*OpID*), the Texas-based identification project, has exhumed over 200 remains to date and identified 24 individuals thus far. Through the efforts of Principal Investigator Dr. Kate Spradley and a team of volunteers, the identification of these individuals moves forward steadily with 15 identifications in the last year alone.

No assumptions are made about the identity of these unidentified individuals. Therefore, every bit of evidence, from personal effects to the biological profile, is considered before determining if an individual is a Texas-Mexico migrant (Anderson and Spradley 2016). Once it is determined that unidentified remains are likely migrants and a biological profile is established, *OpID* personnel input the information into *NamUs*, the National Missing and Unidentified Persons System, and collaborate with local and international NGOs to expand the reach of their identification efforts (Anderson and Spradley 2016; Gocha et al. 2018).

While personal effects and the biological profile can narrow a missing person list enough to establish a potential positive identification, *OpID* requires a positive DNA or

fingerprint match along with agreement between antemortem and postmortem findings to confirm identifications (Anderson and Spradley 2016). Furthermore, Texas law requires all genetic samples for unidentified remains to be submitted to a CODIS User Laboratory for sequencing and inclusion into CODIS, the Combined DNA Index System, where it will be compared with other samples within the United States (Anderson and Spradley 2016; Gocha et al. 2018). In compliance with Texas law, *OpID* submits a sample for all individuals to the University of North Texas Center for Human Identification (UNTCHI). Once UNTCHI has completed forensic DNA analysis, the samples are submitted to CODIS. However, because genetic profiles in CODIS are not cross-referenced with genetic profiles obtained through international agencies, *OpID* has collaborated with multiple institutions to obtain genetic profiles that can be compared against international databases and expedite the process of identification (Gocha et al. 2018). These institutions are Bode Cellmark Forensic Labs and the Human Paleogenomics Lab at University of California, Santa Cruz.

Texas-Mexico Migrant Data Description

The sample presented by this study consists of 32 individuals. These 32 individuals were selected for the availability of genetic profiles, as well as nearly complete craniometric profiles. Of those 32, 10 individuals have been identified. Their regions of origin include El Salvador, Mexico, Honduras, and Nicaragua (Table 1). The remaining 22 individuals are currently unidentified with unknown regions of origin. Additionally, the sample consists of 15 females and 17 males. The sex of all individuals was estimated as part of the biological profile and verified through genetic testing.

Table 1. Geographic origin and sex of identified and unidentified individuals

Geographic Origin	Sample Size	Female	Male
El Salvador	6	4	2
Mexico	2	0	2
Honduras	1	1	0
Nicaragua	1	0	1
Unknown	22	10	12
Total	32	15	17

ILD Data

The craniometric data utilized by this study were previously collected by *OpID* personnel as part of the forensic investigation that each set of skeletal remains undergoes. *OpID* personnel collected landmarks, as defined by Howells (1973), with a Microscribe digitizer and interlandmark distances (ILDs) were then derived through *3Skull.* To refrain from imputing missing values, the present study utilized 52 interlandmark distances in the analysis of this sample (Table 2).

Table 2. Interlandmark distances utilized in this study. See (Howells 1973) for definitions.

Abbr.	Measurement Name	Abbr.	Measurement Name
GOL	Glabello-occipital length	XML	Malar length, maximum
NOL	Nasion-occipital length	MLS	Malar subtense
BNL	Basion-nasion	WMH	Cheek height
BBH	Basion-bregma height	FRC	Frontal chord
XCB	Maximum cranial breadth	FRS	Frontal subtense
XFB	Maximum frontal breadth	FRF	Nasion-subtense fraction
ZYB	Bizygomatic breadth	PAC	Parietal chord
AUB	Biauricular breadth	PAS	Parietal subtense
ASB	Biasterionic breadth	PAF	Bregma-subtense fraction
BPL	Basion-prosthion length	OCC	Occiptial chord
NPH	Nasion-prosthion height	OCS	Occipital subtense
NLH	Nasal height	OCF	Lambda-subtense fraction
JUB	Bijugal breadth	FOL	Foramen magnum length
NLB	Nasal breadth	NAR	Nasion radius
MDH	Mastoid height	SSR	Subspinale radius
OBH	Orbit height	PRR	Prosthion radius
OBB	Orbit breadth	DKR	Dacryon radius
DKB	Interorbital breadth	ZOR	Zygoorbitale radius
WNB	Simotic chord	FMR	Frontomalare radius
ZMB	Bimaxillary breadth	EKR	Ectoconchion radius
SSS	Bimaxillary subtense	ZMR	Zygomaxillare radius
FMB	Bifrontal breadth	BRR	Bregma radius
NAS	Nasio-frontal subtense	VRR	Vertex radius
EKB	Biorbital breadth	LAR	Lambda radius
DKS	Dacryon subtense	OSR	Opisthion radius
IML	Malar length, inferior	BAR	Basion radius

STR Data

Because the migrant population in this study consists of active forensic cases, all destructive analyses must directly contribute to the identification potential and better understanding of Texas-Mexico migrants. Therefore, 15 short tandem repeat genetic markers were selected following standard identification procedures suggested by the United States Federal Bureau of Investigation (FBI) for CODIS (Table 3). Since 1997, the FBI has required 13 standardized loci for genetic identification (Butler 2006). However, to improve identification probabilities the FBI increased their recommendation to 20 standardized loci in January 2017 (Hares 2012). The sample utilized in this study includes individuals identified as early as 2011 whose genetic profiles only contain 15 loci. Therefore, to maximize sample size, 15 loci are included in the analysis of the present sample. A comparison of STR loci required by CODIS prior to 2017, post-2017, and those included in this study can be found in Table 3.

The genetic profiles used in this study were derived from three labs: Bode Cellmark Forensic labs, the University of North Texas Center for Human Identification (UNTCHI), and the Human Paleogenomics Lab at the University of California, Santa Cruz (Table 4). Seventeen samples were sequenced prior to this research by Bode and UNTCHI, whose standard operating procedures for genetic profiling are currently unknown. Thus, it is unclear whether some individuals' genotypes were homozygous or whether allelic dropout may have occurred during the sequencing process. Therefore, allele frequencies may not fully reflect the heterozygosity of the Texas-Mexico migrant sample and the results of this study come with some degree of uncertainty. The remaining 15 samples were sequenced by the principal investigator at the Human Paleogenomics

Lab. For allele frequencies, expected and observed heterozygosity measures, and Hardy-Weinberg equilibrium of all 32 samples please see Appendix A.

Table 3. STR loci used in this compared to CODIS requirements pre- and post-2017.

Locus	This Study	Pre-2017	Post-2017
CSF1PO	✓	✓	✓
D3S1358	✓	✓	✓
D5S818	✓	✓	✓
D7S820	✓	✓	✓
D8S1179	✓	✓	✓
D13S317	✓	✓	✓
D16S539	✓	✓	✓
D18S51	✓	✓	✓
D21S11	✓	✓	✓
FGA	✓	✓	✓
TH01	✓	✓	✓
TPOX	✓	✓	✓
vWA	✓	✓	✓
D1S1656			✓
D2S441			✓
D2S1338	✓		✓
D10S1248			✓
D12S391			✓
D19S433	✓		✓
D22S1045			✓

Table 4. Number of samples sequenced by each lab

Lab	Samples Analyzed
Bode Cellmark Forensic Lab	6
University of North Texas	11
Human Paleogenomics Lab	15
Total	32

Other Population Data

To assess the population structure of Texas-Mexico migrants and the fit of molecular and craniometric data, the matched migrant ILD and STR data were compared to the closely related ILD and STR data for five other populations (Table 5 & Table 6). These samples are South Central Mexico, Yucatan, American White, American Black, and Spain/Portugal. These groups were selected to explore whether between population analyses follow expected population structure patterns shaped by admixture frequencies and shared population histories.

Table 5. Populations used for ILD between population analyses

Population	Sample Size (M/F)	Source
South Central Mexico	67 (55/12)	Spradley (2013)
Yucatan	40 (27/13)	Spradley (2013)
American White	325 (223/102)	Forensic Data Bank
American Black	54 (36/18)	Forensic Data Bank
Portugal	133 (69/64)	Weisensee (2014)

Table 6. Populations used for STR between population analyses

Population	Sample Size	Source
South Central Mexico	622	Rubi-Castellanos et al. (2009a)
Yucatan	262	Rubi-Castellanos et al. (2009a)
American White	342	Steffen et al. (2017)
American Black	361	Steffen et al. (2017)
Spain	114	Coudray et al. (2007)

There are two Latin American groups for which closely related ILD and STR data could be obtained. The first sample, denoted as South Central Mexico, originates from

identified and unidentified border migrants from the Pima County Office of the Medical Examiner (PCOME) (Spradley 2013). The second Latin American ILD sample, denoted as Yucatan, originates from an indigenous Xoclán cemetery in the Yucatan region of Mexico (Spradley 2013). Latin American STR samples of Mexican mestizo origin were compiled from three regions of Mexico: Jalisco, Puebla, and Yucatan (Rubi-Castellanos et al. 2009a). For the purpose of this study, data from Jalisco and Puebla were combined to create a general South Central Mexico sample against which migrant ILD data could be compared. By comparing closely matched Latin American samples, the present study seeks to explore whether Texas-Mexico migrants included in this study are more closely related to Latin American groups with higher European admixture or groups with higher indigenous admixture.

In forensic anthropological analyses, the crania of border migrants often misclassify as American White or American Black due to shared admixture and a lack of region-specific data for "Hispanic" populations (Algee-Hewitt 2016; Dudzik and Jantz 2016; Spradley et al. 2008). Therefore, including ILD and STR samples for American White and American Black groups will assess whether this Texas-Mexico migrant sample is more closely related, genetically and phenotypically, to Latin American, American White, or American Black groups. Both the American White and American Black ILD and STR samples come from large databases that catalogue U.S. population data. The ILD samples are comprised of identified forensic cases from the Forensic Anthropology Data Bank (FDB) while the STR samples originate from the Revised NIST 1036 Population Dataset (Steffen et al. 2017).

Finally, the history of Spanish colonialism and West African slavery in Latin America created a unique population structure between three primary parental groups: European, Amerindian, and African (Bryc et al. 2010; Hughes et al. 2013; Rubi-Castellanos et al. 2009b; Salazar-Flores et al. 2015; Sans 2000). While the Latin American and American Black samples serve as a proxy for Amerindian and African admixture, it was necessary to obtain European parental proxy samples to assess whether European admixture is greater than Amerindian or African admixture in the Texas-Mexico migrant sample. A sample of ILDs from a modern Portuguese population and a sample of STRs from a modern Andalusian Spanish population were selected to act as European parental proxy groups because of the genetic contribution of Spain and Portugal to Latin American communities (Coudray et al. 2007; Weisensee 2014).

Statistical Analyses

ILD Analysis

Within Population Variation

The Texas-Mexico migrant population is heterogenous with documented origins throughout Central America. Therefore, it is necessary to determine whether there is discernable regional variation within the population by assessing how individuals within this sample of 32 individuals vary from one another.

To assess variation at the interindividual level, a Mahalanobis distance analysis was employed using the program DISPOP (Jantz n.d.). ILD measurements (Table 2) were input into DISPOP, which uses a reference sample to develop a covariance matrix against

which the individuals in the sample can be compared. The reference sample used to develop the covariance matrix included South Central Mexico, Yucatan, American White, American Black, and Portuguese samples. Using this covariance matrix, DISPOP also estimates the random expected distance (D) between individuals as outlined by Defrise-Gussenhoven (1967). For this study, if the distances between individuals are greater than 1.96 standard deviations from the expected distance, the individuals are considered significantly different from one another (Defrise-Gussenhoven 1967; Jantz and Owsley 2001; Spradley 2006).

Between Population Variation

Following the same distance analysis methods for within population variation, Mahalanobis distances were derived in DISPOP using ILD data from Texas-Mexico Migrants (*OpID*), South Central Mexico (SoCenMex), Yucatan, American White (AmWhite), American Black (AmBlack), and Portuguese (Portugal) samples (Table 5).

STR Analysis

Within Population Variation

Variation between individuals was also analyzed using genetic distances from short tandem repeat data. Genetic distances were calculated from STR data (Table 3) using GenAlEx 6.503, a statistical software add-on for Excel. To calculate genetic distances between individuals, GenAlEx uses a standardized F_{st}-statistic nested in a pairwise analysis of molecular variance (AMOVA-F_{st}) (Meirmans 2006; Peakall and Smouse 2012). The AMOVA- F_{st} first assesses the variation between individuals using a

sample specific variance covariance matrix produced through squared Euclidean distances. These distances are then standardized using Meirmans (2006) method of F_{st} standardization. Additionally, expected and observed heterozygosity and a Chi-Square test of Hardy-Weinberg equilibrium were calculated for each locus within the Texas-Mexico migrant sample. These statistical measures assessed the quality of the genetic data and whether missing alleles significantly altered the population structure of this sample.

Between Population Variation

Distances between populations were assessed using Wright's F_{st} isolation by distance method in GenAlEx 6.503 (Wright 1946; Wright 1965). F_{st} is a fixation index that measures the degree of genetic differentiation within a population by estimating expected heterozygosity (Ma et al. 2015). In recent years, the use of F_{st} in population differentiation studies has been challenged in favor of other methods of differentiation such as G_{st} or *D* (Ma et al. 2015; Meirmans and Hedrick 2011). However, no measure of genetic differentiation is without its limitations or assumptions. F_{st} was selected because heterozygosity measures do not exceed expectations and allele frequencies are consistent with random mating for all samples utilized in the analysis. Therefore, F_{st} is an appropriate measure of population differentiation (Meirmans and Hedrick 2011). F_{st} values were derived from STR data between Texas-Mexico Migrant (*OpID*), South Central Mexico (SoCenMex), Yucatan, American White (AmWhite), American Black (AmBlack), and Spanish (Spain) samples (Table 6).

Comparing ILD and STR Distances

Within Population

One of the purposes of this research is to assess whether craniometric data and molecular data obtained from the same individuals estimates similar relationships between individuals. To answer this question the distance matrices described above were compared using a Mantel test. These distance matrices are comparable because the Mahalanobis distance and the AMOVA- F_{st} are standardized measures derived from squared Euclidean distances. The Mantel test standardizes the distance matrices and uses a correlation to assess the strength of their relationship. A Spearman's rank correlation was selected because it does not assume normality or a linear relationship between two variables (Hauke and Kossowski 2011). Using this method, a Mantel statistic was produced in XLSTAT, a statistical software add-on for Excel, to assess how strong the relationship between the two distance matrices is and whether that relationship is statistically significant at $p < 0.05$. Next, a generalized Procrustes analysis (GPA) was conducted to visualize the relationships between the distance matrices. The generalized Procrustes converts the distances on each matrix into eigenvectors using a least squares analysis.

Between Population

To compare population relationships across ILD and STR data and assess the relationship between Texas-Mexico migrants, parent proxy groups, and Latin American groups, genetic distances were compared following the within population comparison guidelines. A Spearman's rank Mantel test with 10,000 permutations and GPA was

conducted in XLSTAT to assess the correlations between these two data sets and visualize population relationships.

III. RESULTS

ILD Results

Within Population

Mahalanobis distance results are presented in Table 7. Expected distance, mean distance, standard deviation, and the significance sectioning point are included in this table. All significant distances are in bold. The Defrise-Gussenhoven random expected distance is 10.15 whereas the mean distance of this sample is 9.98. This indicates that while the sample is relatively homogenous, a few outlying relationships may be pulling the overall mean distance higher than expected. Only three individuals, 6, 10 and 23, vary significantly from other individuals within the sample consistently. All three of these individuals are currently unidentified. Finally, there does not appear to be any consistent patterning between individuals with known regions of origin. Individuals 1, 2, 3, 4, 7, and 26 are identified with El Salvadorian origin, but do not consistently exhibit lower Mahalanobis distances. Individuals 19 and 20 are identified with Mexican origin with a relatively low distance of 8.92. Please see Appendix B for a list of which numbers correspond with which *OpID* case numbers and geographic regions of origin.

Table 7. Interindividual Mahalanobis distances. Significant values are in bold.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	0																															
2	10.95	0																														
3	8.70	8.65	0																													
4	**12.44**	11.12	10.83	0																												
5	10.09	10.20	9.22	9.96	0																											
6	**12.95**	10.33	**12.15**	**13.02**	10.83	0																										
7	11.12	6.68	8.26	10.87	9.71	10.59	0																									
8	8.65	9.12	7.43	11.01	10.08	**12.46**	9.83	0																								
9	9.79	10.34	10.45	11.29	9.63	11.08	11.19	10.83	0																							
10	11.41	**13.23**	11.30	**13.00**	**12.12**	**15.80**	**12.73**	**12.96**	11.99	0																						
11	9.07	8.07	8.41	10.53	10.09	**12.46**	8.26	8.93	9.42	11.43	0																					
12	10.20	9.97	9.07	11.46	9.21	11.01	9.70	10.36	9.32	11.63	9.83	0																				
13	10.29	8.46	8.22	9.86	8.39	10.29	8.08	8.11	10.30	11.86	8.43	9.41	0																			
14	12.06	10.81	9.68	11.33	10.96	**12.90**	10.58	11.92	10.51	**12.55**	10.13	11.02	10.03	0																		
15	9.84	9.61	8.47	10.79	7.21	**12.15**	9.48	8.85	9.44	9.51	8.05	8.64	8.26	10.46	0																	
16	11.21	10.52	11.09	11.63	9.31	11.08	10.73	11.20	10.53	**13.13**	10.78	10.03	9.75	9.08	8.45	0																
17	9.79	9.36	7.02	12.05	9.44	**12.36**	9.16	9.17	10.93	**12.74**	9.14	9.03	9.27	11.11	8.90	11.36	0															
18	**12.27**	10.64	10.72	11.85	8.78	**12.24**	9.33	10.76	11.01	12.07	10.08	9.84	9.31	11.71	8.25	10.36	10.82	0														
19	9.81	9.14	7.35	11.19	9.84	**12.53**	7.30	9.20	11.82	10.93	8.66	9.99	7.97	9.89	8.13	9.94	8.97	9.62	0													
20	9.21	8.90	8.02	9.75	8.65	11.02	9.40	7.69	8.82	11.41	7.87	8.92	7.85	9.67	6.94	8.86	7.16	9.76	8.92	0												
21	10.42	8.11	8.38	9.79	9.47	10.05	8.29	8.15	9.62	**12.26**	8.85	8.69	7.17	10.48	9.60	10.79	8.49	9.88	9.25	7.05	0											
22	9.35	9.83	9.73	**12.48**	8.92	11.67	9.71	8.88	10.56	**12.31**	9.77	9.90	8.96	11.96	9.34	11.35	9.04	9.42	9.32	8.96	8.73	0										
23	**13.73**	**12.19**	11.64	**12.97**	12.06	**14.42**	**13.07**	**12.70**	**12.73**	**14.86**	**12.96**	11.84	11.09	11.52	11.96	**12.52**	**12.31**	**13.63**	**13.02**	11.42	11.48	**14.85**	0									
24	10.06	8.65	8.59	11.19	9.25	11.39	8.93	9.35	9.92	**12.26**	9.59	9.09	9.18	10.90	8.91	10.49	8.75	10.72	8.70	8.79	8.44	9.43	10.54	0								
25	8.25	10.38	7.80	**12.29**	9.02	11.98	9.75	8.32	9.52	10.80	9.41	9.57	8.67	11.46	7.97	10.45	8.05	10.17	8.70	8.19	8.92	9.32	**12.94**	8.80	0							
26	9.76	9.80	9.36	**12.17**	10.60	12.02	10.25	9.68	10.64	11.44	11.22	10.99	10.23	11.88	10.71	11.56	10.68	**12.38**	9.96	9.58	10.03	10.06	**13.31**	10.25	9.51	0						
27	10.91	10.47	10.02	11.72	9.74	10.10	9.65	10.03	10.76	**13.04**	10.00	8.88	9.36	10.76	9.76	9.68	9.80	9.82	10.08	7.93	8.35	9.97	**12.84**	10.02	9.33	10.90	0					
28	9.32	9.92	9.05	**12.28**	8.32	10.81	10.08	10.07	10.03	11.29	10.29	7.91	8.08	11.92	8.83	10.33	9.03	10.10	9.39	8.69	9.13	9.28	11.63	9.68	8.11	9.61	10.15	0				
29	10.81	8.81	8.38	10.97	9.35	10.80	7.44	10.02	10.51	11.15	8.68	9.12	7.91	10.48	7.56	9.45	9.50	9.89	8.25	8.42	8.66	10.16	12.06	9.00	8.34	10.35	9.08	8.71	0			
30	9.76	9.34	7.70	11.75	9.39	**12.77**	8.89	9.01	9.29	11.28	8.38	9.14	8.54	11.28	7.03	10.13	8.70	8.91	7.64	8.40	9.06	9.53	**12.13**	8.67	7.67	10.22	10.42	7.73	8.73	0		
31	8.65	9.45	7.64	11.89	8.33	11.84	8.31	8.40	9.83	10.34	8.23	8.64	7.41	9.90	6.78	9.98	7.33	9.66	6.86	7.33	8.55	9.01	**12.30**	9.19	6.97	9.77	9.35	8.11	8.23	7.34	0	
32	9.75	10.32	8.87	**12.31**	8.69	10.51	9.00	10.12	10.70	11.96	11.01	9.51	9.37	11.92	9.45	11.07	8.43	9.25	10.12	9.28	9.08	9.16	**13.27**	8.46	7.95	9.98	9.22	9.19	8.43	9.55	8.80	0

Expected Distance (D) = 10.15
Mean Distance = 9.98
SD = 1.52
D > 12.11 are significant, significant values in bold

Between Population

The between population Mahalanobis distance matrix is presented in Table 8. The greatest distances occur between American White and Yucatan, American Black and Yucatan, and Portugal and Yucatan. Texas-Mexico migrants (*OpID*) are most similar to the South Central Mexican and Yucatan groups.

Table 8. Between population Mahalanobis distances.

	OpID	AmWhite	AmBlack	Yucatan	Portugal	SoCenMex
OpID	0					
AmWhite	12.4839	0				
AmBlack	18.6476	15.8388	0			
Yucatan	9.9531	25.5383	31.2265	0		
Portugal	15.0002	9.8316	20.8565	26.7703	0	
SoCenMex	6.855	14.9255	23.5856	9.2859	19.6557	0

STR Results

Within Population

The results for the genetic distance analysis are presented in Table 9. The interindividual genetic distances are generally high, but fairly consistent throughout the sample. No individual varies consistently from all other individuals in the sample. Allele frequencies, measures of heterozygosity, and Hardy-Weinberg equilibrium measures for each loci in the sample are presented in Appendix A. Generally, observed heterozygosity is close to expected heterozygosity measures. Finally, the *p*-values for Hardy-Weinberg equilibrium indicate that there are no significant deviations from the assumption of random mating in any loci.

Table 9. Interindividual AMOVA-F_{st} genetic distances.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	0																															
2	20	0																														
3	23	19	0																													
4	27	20	25	0																												
5	30	28	29	28	0																											
6	30	28	30	29	25	0																										
7	28	26	26	30	39	32	0																									
8	26	26	26	27	33	31	17	0																								
9	23	18	18	19	22	22	24	22	0																							
10	25	23	22	22	18	17	24	26	19	0																						
11	27	21	23	21	28	21	25	20	18	20	0																					
12	23	21	25	26	27	20	25	24	19	19	19	0																				
13	24	24	25	26	25	16	25	27	26	14	23	21	0																			
14	25	21	21	21	24	27	21	19	19	18	19	24	23	0																		
15	24	25	24	29	27	21	28	25	23	23	19	21	22	23	0																	
16	25	27	29	27	29	19	29	24	23	22	20	19	24	25	20	0																
17	20	23	24	27	29	28	23	22	24	22	26	23	19	20	29	23	0															
18	39	37	33	37	40	28	25	30	27	28	28	29	28	31	30	27	29	0														
19	21	22	20	22	27	23	19	23	22	18	23	23	21	24	24	21	23	24	0													
20	28	20	24	20	28	23	24	25	20	20	18	21	21	21	24	20	25	25	20	0												
21	24	25	22	24	25	26	25	21	20	17	20	23	20	23	20	22	26	32	19	24	0											
22	22	23	25	25	29	24	25	22	22	24	21	20	26	23	26	25	24	29	20	17	21	0										
23	25	25	21	25	29	26	25	21	21	23	16	16	23	24	23	22	24	33	21	21	18	21	0									
24	22	19	22	22	29	29	27	27	22	18	25	20	22	23	31	24	18	33	22	19	26	23	23	0								
25	30	26	27	31	25	20	23	26	24	18	24	23	18	27	21	21	21	20	19	21	22	25	25	26	0							
26	21	22	23	20	27	22	26	22	18	17	19	19	23	21	26	20	25	32	23	19	22	18	22	21	25	0						
27	26	21	26	22	25	19	29	24	20	20	21	19	23	22	27	17	23	20	20	18	20	18	24	19	21	18	0					
28	25	18	19	23	27	23	28	25	19	20	18	19	22	26	21	19	25	30	19	19	24	22	20	19	21	21	21	0				
29	26	23	22	22	20	22	28	20	18	16	19	20	21	21	19	22	27	31	22	19	18	22	20	22	22	22	20	15	0			
30	30	27	24	25	30	19	30	27	17	20	19	21	24	25	23	27	27	26	21	24	20	23	24	27	24	21	23	25	24	0		
31	24	20	24	20	30	25	29	25	20	23	22	19	27	20	24	21	26	38	21	24	20	21	21	23	31	19	22	22	23	23	0	
32	23	18	20	20	26	22	26	21	19	20	15	21	21	21	22	22	21	28	19	23	19	21	20	18	26	21	19	15	18	20	17	0

Between Population

The between population F_{st} distance matrix is presented in Table 10. The greatest distances occur between Texas-Mexico migrants (*OpID*) and American White, Texas-Mexico migrants (*OpID*) and American Black, and Texas-Mexico migrants (*OpID*) and Spain. Texas-Mexico migrants are most similar to the South Central Mexican and Yucatan groups.

Table 10. Between population F_{st} distance matrix.

	OpID	AmWhite	AmBlack	Yucatan	Spain	SoCenMex
OpID	0					
AmWhite	0.039	0				
AmBlack	0.042	0.019	0			
Yucatan	0.03	0.027	0.037	0		
Spain	0.042	0.004	0.019	0.032	0	
SoCenMex	0.03	0.02	0.031	0.004	0.024	0

Comparing Craniometric and Genetic Distances Results

Within Population

The Mantel test results and Procrustes plot of within population variation are presented in Figure 1. The Spearman's rank Mantel correlation is r = -0.01, p = 0.83. This indicates that there is little to no overlap between matched ILD and STR data when comparing individuals within the population and the relationship is not statistically significant ($p > 0.05$). The only individuals whose ILD and STR data plot closely to each other are 14 and 20. Finally, there does not appear to be any consistent patterning for the ILD and STR data of individuals with known regions of origin.

Figure 1. Procrustes plot of matched Texas-Mexico migrant data.

Between Population

The Mantel test results and Procrustes plot of between population variation are presented in Figure 2. The Spearman's rank Mantel correlation is r = 0.317, p = 0.239. This indicates there is a moderate correlation between ILD and STR samples, but the relationships between the distance matrices are not statistically significant (p > 0.05). However, both data types show similar information for population relationships.

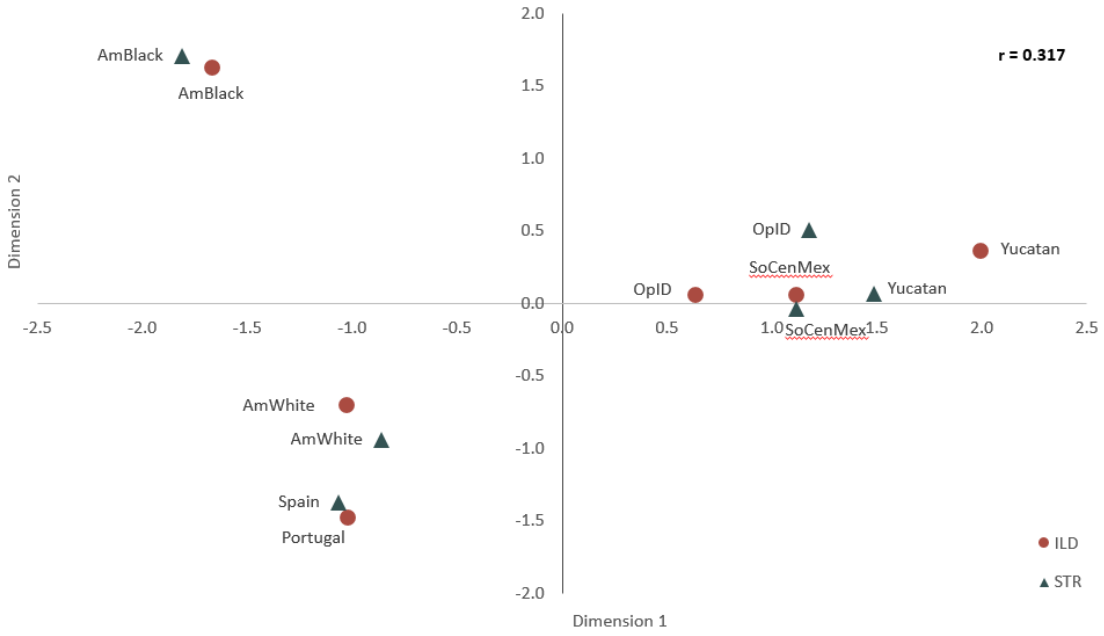

Figure 2. Between population Procrustes plot.

IV. DISCUSSION

Variation in the population structure estimates of cranial morphology and neutral genetic information reflect the complex interactions between heritability and environmental influences. The results of this study demonstrate that *within* population distances are variable across craniometric and molecular data and do not share similar population structure estimates for the Texas-Mexico migrant sample. In contrast, *between* population distances have a moderate correlation, and reflect similar population structure estimates across data types despite a nonsignificant *p*-value. Therefore, the present study concludes that there is concordance between the genetic distances for craniometric and STR data.

Using Matched Data to Assess Population Structure

The purpose of this research is two-fold: explore the population structure of Texas-Mexico migrants and assess whether population distance analyses for matched ILDs and STRs follow similar patterns.

In assessing the population structure of Texas-Mexico migrants through within population distance analyses, there is no clear clustering of individuals in the ILD data, STR data, or across data types (Figure 1). The eleven identified individuals with known regions of origin do not appear to cluster closely with each other or other unidentified individuals. While it is well documented that differences within populations are expected to be greater than differences between populations (Relethford 1994; Roseman and Weaver 2004), the lack of clustering in each data set is most likely a product of the small

sample size. A sample of 32 individuals with wide variation in regions of geographic origin may not be large enough to highlight shared relationships between people.

Furthermore, the results of the present study are similar to Smith et al. (2016), the only other study to utilize matched cranial and molecular data from the same individuals. Like Smith et al. (2016), the present study finds that the relationships within a population are not mirrored across matched ILD and molecular data. Potential explanations for the lack of concordance in interindividual distance analyses remain unclear because differences in the interindividual relationships could be due to several factors. For example, individuals may exhibit greater variation on the individual level in ways that mask shared phenotypic and genetic patterns. Future research that utilizes more matched genetic and cranial data from the same individuals with known geographic origin may provide further insight into the lack of shared interindividual patterning observed in this study and Smith et al. (2016).

Between population distance analyses demonstrate concordance between the ILD and STR data despite a low correlation and non-significant *p*-value ($r = 0.317$, $p = 0.239$). The Procrustes plot demonstrates that the ILD and STR data for American Black, American White, Spanish/Portuguese, and South Central Mexican groups plot closely to each other (Figure 2). However, there is greater spread between the ILD and STR data for the Texas-Mexico migrant and Yucatan groups that may account for the low correlation and non-significant *p*-values. Despite the greater spread, the relationships are similar. There are a few potential explanations for the population structure differences observed in these data types.

First, the Texas-Mexico migrant genetic sample has missing allelic data because it was unclear whether some individuals were homozygous or allelic drop out occurred during the sequencing process. Following a conservative approach, unclear alleles were treated as missing data. This missing data did not significantly alter Hardy-Weinberg equilibrium or expected heterozygosity for loci, but it may have altered the agreement between craniometric and molecular population structure estimates. Additionally, the small sample size may amplify differences between these data types.

Second, the Yucatan ILD and STR samples are not directly analogous with one another. The ILD Yucatan sample utilized in this analysis is from a documented Xoclán cemetery with high indigenous admixture (Spradley 2013). Conversely, the STR Yucatan sample is documented as Mexican Mestizo, a term that differentiates Mexican populations with higher European admixture (Rubi-Castellanos et al. 2009a). The differences in admixture between these two samples may account for the differences observed in the ILD and STR population structure estimates for the Yucatan samples.

Despite these limitations, genetic distances estimated for both data types match expected distances based on population histories and an isolation by distance model. As expected, the American Black samples exhibit the greatest distance from all other groups, the American White and Spanish or Portuguese samples are more closely related, and the Latin American samples cluster together. Of the Latin American samples, the Texas-Mexico migrant ILD and STR data are more closely related to ILD data from South Central Mexico and STR data from South Central Mexico and Yucatan. Additionally, the Yucatan ILD sample, with the highest Amerindian admixture, exhibits the greatest distance from Texas-Mexico migrants of all Latin American samples. Therefore, it is

evident that, in this analysis, the Texas-Mexico migrant sample exhibits the closest association to Latin American groups with higher European admixture.

However, without further investigation into other Latin American groups little can be said in this study to further elucidate the heterogenous nature of Texas-Mexico migrants. The complexity of these results further demonstrates the necessity for more Latin American specific population structure studies, particularly in the context of matched ILD and STR research. Moving forward, exploring how population relationships are shaped by shared phenotypic and genetic traits in a more localized context will allow researchers to better understand hereditary and environmental influences on population structure.

The results of this study are in concordance with the expectations of previous literature that suggests overall cranial variation is in agreement with genetic distances estimated by molecular data (Harvati and Weaver 2006; Herrera et al. 2014; Martinez-Abadias et al. 2009; Relethford 2010; Roseman 2004; Smith 2009; Smith et al. 2016; von Cramon-Taubadel 2009). Matched ILD and STR research is integral for understanding how populations are structured because it does not approximate the relationships between individuals or populations using different samples from similar populations. Instead, this research is a true representation of this samples' phenotypic and genetic relationships to each other as well as other populations.

V. CONCLUSION

Matched craniometric and molecular data, taken from the same individuals, is the next step toward clarifying the influences on and relationships between the skeletal structures and genetic markers we use to understand populations. This type of research has important implications in both bioarchaeological and forensic contexts because there are many instances in which genetic and/or skeletal data may be incomplete or not available at all. The research presented here engages with matched data in the context of the humanitarian crisis on the U.S.-Mexico border because every case of unidentified remains is different and forensic investigators must utilize everything at their disposal to aid in identification. While forensic DNA typing may help identify individuals whose information is already present genetic databases like CODIS, the estimation of geographic origin from craniometric data allows forensic investigators to target their identification efforts more efficiently for individuals not yet represented in missing persons databases. Therefore, whether craniometric data follows similar population structure patterns as molecular data has important implications for the identification of migrants who come from a variety of Latin American regions.

The present study can conclude that the ILD and STR data for this Texas-Mexico migrant sample has the closest association to Latin American groups with higher European admixture, but much exploration remains for how groups vary when analyses are focused on region-specific Latin American population structure. Furthermore, the more that research compares genetic and skeletal data in a region-specific context, the more holistic understanding anthropologists will have of the hereditary and

environmental influences that shape shared phenotypic and genetic traits utilized in the identification of unidentified remains.

APPENDIX SECTION

Page

APPENDIX A: ALLELE FREQUENCIES AND DATA QUALITY MEASURES

Allele	D8S1179	D21S11	D7S820	CSF1PO	D3S1358	TH01	D13S317	D16S539	D2S1338	D19S433	vWA	TPOX	D18S51	D5S818	FGA
6				0.026		0.391									
7						0.326								0.056	
8			0.094			0.043	0.080					0.370			
9			0.031	0.026		0.239	0.140	0.212		0.024		0.087		0.111	
10	0.154		0.406	0.263			0.100	0.173				0.043	0.029	0.056	
11	0.077		0.250	0.342			0.200	0.269				0.261		0.389	
12	0.154		0.219	0.316			0.220	0.269		0.143		0.239	0.088	0.278	
13	0.385			0.026			0.120	0.077		0.333			0.147	0.111	
14	0.115				0.115		0.100			0.190	0.071		0.206		
15	0.115				0.423		0.040			0.143	0.119		0.118		
16					0.250				0.024	0.167	0.333		0.118		
17					0.173				0.143		0.238		0.118		
18					0.038				0.071		0.190		0.029		0.021
19									0.143		0.024		0.059		0.125
20									0.167				0.029		0.042
21									0.024		0.024		0.029		0.063
22									0.143				0.029		0.083
23									0.214						0.229
24									0.024						0.146
25									0.048						0.125
26															0.104
27		0.019													0.042
28		0.192													0.021
29		0.154													
30		0.173													
31		0.231													
32		0.154													
33		0.058													
34		0.019													
N	26	26	16	19	26	23	25	26	21	21	21	23	17	27	24
Ho	0.923	1.000	0.938	0.895	0.846	0.826	1.000	0.962	0.857	0.952	0.905	0.957	1.000	0.852	0.917
He	0.772	0.828	0.715	0.712	0.714	0.681	0.850	0.774	0.856	0.783	0.776	0.729	0.879	0.741	0.869
p	0.607	0.859	0.502	0.813	0.182	0.301	0.842	0.465	0.361	0.556	0.933	0.080	0.960	0.340	0.143

N: sample size for each locus; Ho: observed heterozygosity; He: expected heterozygosity; *p* : Hardy-Weinberg equilibrium

APPENDIX B: CASE NUMBER AND GEOGRAPHIC ORIGIN FOR TEXAS-MEXICO MIGRANT SAMPLE

Number	Case Number	Geographic Origin
1	ME13-528	El Salvador
2	ME14-208	El Salvador
3	ME14-511	El Salvador
4	ME15-183	El Salvador
5	OpID 0367	Unknown
6	OpID 0368	Unknown
7	OpID 0373	El Salvador
8	OpID 0379	Unknown
9	OpID 0381	Unknown
10	OpID 0383	Unknown
11	OpID 0384	Unknown
12	OpID 0385	Unknown
13	OpID 0390	Unknown
14	OpID 0391-A	Unknown
15	OpID 0392	Unknown
16	OpID 0395	Unknown
17	OpID 0399	Unknown
18	OpID 0400	Unknown
19	OpID 0401-D	Mexico
20	OpID 0401-E	Mexico
21	OpID 0412	Unknown
22	OpID 0416	Unknown
23	OpID 0423	Unknown
24	OpID 0425	Honduras
25	OpID 0429	Unknown
26	OpID 0439	El Salvador
27	OpID 0446	Unknown
28	OpID 0448	Unknown
29	OpID 0487	Unknown
30	OpID 0508	Unknown
31	OpID 0601	Nicaragua
32	OpID 0634	Unknown

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