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Mitochondrial DNA Diversity of Saint Vincent and Trinidad and Its Implications for Caribbean Settlement History

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Abstract

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European colonization of the Americas had profound impacts on the indigenous peoples of the Caribbean Basin. The indigenous communities of Saint Vincent and the Grenadines and Trinidad and Tobago, two island nations of the Caribbean Lesser Antilles, endured a European colonial presence for just shy of 500 years. Today, analysis of mitochondrial DNA can help paint a better portrait of pre-Columbian indigenous peoples, including their settlement of the Caribbean Basin and their resistance to European colonialism. To further explore these issues, we conducted analysis of genetic variation in two indigenous communities, the Garifuna of Saint Vincent and the First Peoples' Community (FPC) of Trinidad. Benn Torres et al. (2015) published their analyses of 65 participants' samples from both St. Vincent and Trinidad, which were collected during the first of two research expeditions to the islands. For this paper, we analyzed an additional 83 participant samples that were collected during a subsequent research expedition to the region. The results of this study confirmed several trends observed by Benn Torres et al. (2015), namely, that the predominate haplogroups represented by Trinidadian and Vincentian samples are A2 and C1, and that these and other observed haplogroups corroborate historical events or periods. Haplogroups previously unseen in these populations, including indigenous haplogroups B2 and D1 and certain South Asian haplogroups, were also observed, thus adding genetic evidence of a complex history of migration to and admixture within the region. This work thus complements and extends earlier research on genetic diversity in the Lesser Antilles, as well as illuminates the resistance and survival of indigenous Caribbean peoples before, during, and after European colonization and the African Diaspora.

Keywords

mtDNA, population genetics, haplogroup, caribbean, saint vincent, genetics, lesser antilles

Disciplines

Anthropology

MITOCHONDRIAL DNA DIVERSITY OF SAINT VINCENT AND TRINIDAD AND ITS IMPLICATIONS FOR CARIBBEAN SETTLEMENT HISTORY

By

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ABSTRACT

European colonization of the Americas had profound impacts on the indigenous peoples of the Caribbean Basin. The indigenous communities of Saint Vincent and the Grenadines and Trinidad and Tobago, two island nations of the Caribbean Lesser Antilles, endured a European colonial presence for just shy of 500 years. Today, analysis of mitochondrial DNA can help paint a better portrait of pre-Columbian indigenous peoples, including their settlement of the Caribbean Basin and their resistance to European colonialism. To further explore these issues, we conducted analysis of genetic variation in two indigenous communities, the Garifuna of Saint Vincent and the First Peoples' Community (FPC) of Trinidad. Benn Torres et al. (2015) published their analyses of 65 participants' samples from both St. Vincent and Trinidad, which were collected during the first of two research expeditions to the islands. For this paper, we analyzed an additional 83 participant samples that were collected during a subsequent research expedition to the region. The results of this study confirmed several trends observed by Benn Torres et al. (2015), namely, that the predominate haplogroups represented by Trinidadian and Vincentian samples are A2 and C1, and that these and other observed haplogroups corroborate historical events or periods. Haplogroups previously unseen in these populations, including indigenous haplogroups B2 and D1 and certain South Asian haplogroups, were also observed, thus adding genetic evidence of a complex history of migration to and admixture within the region. This work thus complements and extends earlier research on genetic diversity in the Lesser Antilles, as well as illuminates the resistance and survival of indigenous Caribbean peoples before, during, and after European colonization and the African Diaspora.

HISTORICAL BACKGROUND

Geographic context. The Caribbean region is a vast sea of approximately 2.75 million km^2 (Fitzpatrick 2015) (Figure 1). The region has over 700 islands inhabited by over 42 million people (Benn Torres et al. 2015, 2; 2011/12 Census data). Many of the islands (though not all) can be divided into one of three broad categories: the Greater Antilles, which include Cuba, Hispaniola, Jamaica, Puerto Rico; the Lesser Antilles, which stretch from Grenada to the Virgin Islands; and the Bahamian Archipelago, which, though not part of the Antillean chain, was settled by Amerindians and so are grouped culturally with the Antilles (Fitzpatrick 2015). The tropical climate has contributed to the region's extraordinarily high level of biodiversity, which prehistoric peoples most certainly exploited (Boomert 2016, 5-6; Fitzpatrick 2015).

Pre-Columbian Caribbean settlement. Historically, archaeological and ancestry research in the Caribbean has focused very little on the Lesser Antilles, with more data emerging from studies in northern Caribbean regions (Fitzpatrick 2006, 397-398). As an example, there are only 116 reliable radiocarbon dates from Martinique to Trinidad, a region of more than 500 kilometers (Fitzpatrick 2006). Saint Vincent in particular has very few dated sites (Fitzpatrick 2006, 399). However, scholars have drawn from a diverse body of evidence to overcome this limitation and better understand human migration and dispersal in the region (Figure 1).

Trinidad was the first Caribbean island that was settled prehistorically, with archeological sites dating to 8000 to 7800 years BP (before present) (Boomert 2016, 15-24; Fitzpatrick 2015, 308). However, because Trinidad was connected to mainland South America in the early Holocene, its colonization history is not exactly the same as those of other Caribbean islands (Fitzpatrick 2015, 308). The earliest colonization of the Antilles, with sites on Cuba and Hispaniola, has been dated to 7000 and 5500 years BP, with people coming from somewhere in

coastal South America or possibly Mesoamerica (Fitzpatrick 2015, 308). Around 5500 to 3500 years BP, Puerto Rico and other islands in the northern Lesser Antilles, as well as Barbados in the south, appear to have been settled by peoples coming from South America (Fitzpatrick 2015, 324). The reason for this regional discontinuity is unclear (Fitzpatrick 2015, 324).

The next major population dispersal took place during the Early Ceramic Age (2500-1500 years BP) (Fitzpatrick 2015, 324-325). Saladoid peoples – named for the cultural complex with which they are associated – moved into Puerto Rico and the northern Lesser Antilles (Giovas & Fitzpatrick 2014, 573-574). Archaeological, archaeobotanical, and genetic evidence points to South America as their likely origin. By 2000 years BP, the Saladoid occupied all Lesser Antilles islands, with a few exceptions in the Grenadines that were not occupied by the Saladoid peoples until 1700 years BP (Fitzpatrick 2015, 324).

Around 1500-500 years BP, known as the Late Ceramic Age, the earlier peoples of the northern Caribbean began another period of dispersal (Hofman 2013, 5; Fitzpatrick 2015, 315). Around 1600-1500 years BP, peoples who initially settled the northern Caribbean – after a 1000-year 'pause' in Puerto Rico – appear to have diffused across the Greater Antilles, Bahamas, and Jamaica (Fitzpatrick 2015, 315; Hofman 2013, 7). Evidence of the fusion of cultural and technological complexes emerges, indicating cultural contact between migratory groups (Fitzpatrick 2015, 316). This cultural contact was foundational to the complex systems of trade, travel, and cultural exchange that defined indigenous societies in the region for centuries (Hofman 2013; Boomert 2016; Fitzpatrick 2016).

These millennia of population movement and cultural exchange culminated in the diverse groups that were present on Caribbean islands at the time of European arrival. These included the Taíno groups of Cuba, Hispaniola, and the Bahamas, with origins in South America and possibly

Mesoamerica, as well as the Carib groups of the Lesser Antilles, also of South American origins (Keegan et al. 2015, 1-8; Fitzpatrick 2015, 325).

Figure 1: Map of the Caribbean depicting population movement and ceramic style zones. Dates in bold denote the earliest known dates or date ranges for a given region. Source: Fitzpatrick (2015). Note that these routes may be uncertain, particularly the migration of archaic peoples from Mesoamerica to Cuba (7000-5500 BP), represented by the arrow to the far left of the map (a South American route is also possible).

Colonial contact

Colonial contact on St. Vincent. Beginning with Columbus' voyages to the Caribbean in the 1490s, European arrival and colonialism had a profound impact on indigenous peoples throughout the Americas, including in St. Vincent and Trinidad (Newman 2014). Initially, Europeans did not aggressively attempt settlement of St. Vincent, but in 1763, St. Vincent –

along with Grenada, Dominica, and Tobago – were ceded to the British after the end of the Seven Years' War with the French (Newman 2014). The British noted two 'stocks' of people on St. Vincent, or, as British politician William Young II wrote, "two nations of very different origins and pretensions" (Newman 2014, 110). The Yellow or Red Caribs were believed to the descendants of the region's original natives. The Black Caribs were deemed to be mixed-race descendants of African slaves, brought to the Americas through the Trans-Atlantic slave trade (Benn Torres et al. 2015, 17). The British believed that these Black Caribs intended to "destroy the Red Charaibs [sic]" (Newman 2014, 110).

Today, historians believe this distinction by the British, though loosely phenotypic, was falsified for political purposes. Because Vincentian Black Caribs occupied territory ideal for agricultural development, the British invented narratives of Black Carib inferiority and savagery to undermine indigenous claims to native land ownership (Newman 2014, 110; Kim 2013, 122). There is also strong historical evidence that the Europeans' divisions of indigenous Caribbean peoples were not at all reliably phenotypic; European colonizers who referred to groups of "Black Caribs" or "African Caribs" noted diverse "colour…and mixed complexion" (Newton 2014, 18). Europeans – keen to portray these Caribs as barbarians – attributed this to the Black Caribs tendency to murder indigenous men and rape indigenous women. Contemporary historians discredit these claims (Newton 2014, 18). Regardless, these narratives were used to justify the enslavement of indigenous Caribbean peoples, as the vast majority of indigenous peoples were eventually categorized as "Black Caribs" and thus denied rights (Kim 2013, 122; Newton 2014, 8).

Part of this narrative stemmed from a British fabrication regarding Black Carib origins. The Black Caribs, British colonizers claimed, were fugitive slaves who survived a shipwreck off

the coast and aggressively took over St. Vincent, reproducing with indigenous peoples (Kim 2013, 123). Contemporary historians believe the story is more complex. First, it is very likely that many of those initially designated by the British as "Black Caribs" were indigenous to the Caribbean long before European colonization (Kim 2013, 122-123). Second, those who possessed African ancestry did so as a result of complex interethnic alliances in the region, not because African ancestors aggressively conquered 'passive' indigenous peoples (Kim 2013, 122). Hence, "Black" Caribs likely emerged slowly and organically over a century as a result of intermarriage and interethnic alliances; had complex relationships with other St. Vincent groups; and exhibited strong attachments to Carib cultural tradition (Johnson 2007; Newman 2014, 131-133).

Vincentian Black Carib resistance to European colonizers eventually led to the First and Second Carib War (1772-73, 1795-97, respectively), after which the Black Caribs were forcibly deported to Balliceaux, an island near St. Vincent (Newton 2014, 5). After an epidemic killed almost half of those exiled, the survivors were relocated to Central America, and in particular, Roatán Island off the coast of Honduras (Newton 2014, 5; 15). Here, they forged a new cultural identity, they renamed themselves the Garifuna, and some eventually reestablished themselves in St. Vincent, as well, where many called themselves the Kalinago (Newton 2014, 15). Today, the Garifuna reside throughout Central America and St. Vincent, and some have immigrated to the United States. In St. Vincent, native communities are located in the north of the island, at Sandy Bay, Fancy, and Owia, and in the southwest of the island, at Grieggs Point, Rose Bank, and Rose Hall (Benn Torres et al. 2015, 4).

Colonial contact on Trinidad. Popular belief holds that, at the time of European arrival to Trinidad and Tobago, two broad indigenous groups existed in the Caribbean: the Caribs and

the Taíno (although many Europeans referred to the Taíno as Arawak). The Taíno were more common in the Greater Antilles and the Caribs dominated the Lesser Antilles (Boomert 2016).

Europeans initially associated Caribs with warfare and cannibalism, although the latter behavior is contested today; if cannibalism occurred, it was likely limited and ritualistic (Whitehead 1984). Nevertheless, Europeans used myths of exaggerated Carib brutality to justify their subjugation (Boomert 2016, 85; Whitehead 1984, 81). As the colonial presence in the region increased, Europeans began applying the term 'Carib' loosely and undiscerningly to any group deemed antithetical to European conquest – e.g., belligerent or aggressive (these divisions clearly resemble those utilized on Saint Vincent). The Amerindians of the Lesser Antilles, including those from Trinidad, were eventually identified as Caribs to suit European political and economic needs, which allowed Spanish colonizers to rationalize the enslavement of indigenous peoples beginning in 1503 (Boomert 2016, 85).

The real history of Trinidad's indigenous peoples is, like that of St. Vincent, more complex. At the time of Spanish European arrival in 1498, at least five distinct Amerindian groups existed in Trinidad, speaking languages belong to both the Arawak and Cariban language families. In the mid-17th century, some of Trinidad's 'Caribs' (as colonizers identified them) called themselves the Kali'nago, a derivation of Kali'na, used by indigenous peoples of the Guiana coastal zone and Venezuela (Boomert 2016, 63). Other Trinidadian indigenous groups spoke Cariban and also exhibited connections to the mainland (Boomert 2016, 63-64).

Through the 1500s, the Spanish enslaved many Amerindians, but their attempts at transforming Trinidad into a reliable supplier of indigenous slaves were thwarted largely as a result of fierce indigenous opposition (Boomert 2016, 88). Some Trinidadians fled the slave trade by emigrating to the Guiana coastal zone (Boomert 2016, 106). Spanish colonizers

remained in control of Trinidad until 1797, although French settlers had a substantial impact on Trinidadian culture and language (Trinidadian English Creole, for example, was influenced by the French language) (Révauger 2008, 187). In 1749, the Spanish established the Indian Mission of Arima in the north-central region of Trinidad, and indigenous peoples were consolidated into the Santa Rosa Mission (Benn Torres et al. 2015, 3). After the mission's dissolution in 1849, indigenous peoples remained, and in 1976, the Santa Rosa First Peoples' Community (FPC) was nationally recognized as an indigenous collective, comprised of the descendants of indigenous Caribbean peoples (Benn Torres et al. 2015, 3).

MITOCHONDRIAL DNA VARIATION

In addition to written, archaeological, and linguistic evidence, researchers have used genetic evidence to elucidate Caribbean history. For decades, mitochondrial DNA (mtDNA) has been used as a popular and effective marker of molecular diversity of both humans and animals (Galtier et al. 2009). Its usefulness to molecular anthropologists and other researchers stems from several traits of mtDNA itself: It is easy to amplify, as it appears in multiple copies in the cell; its gene content is strongly conserved; it exhibits clonal maternal inheritance; and it evolves close to neutrally at a stable and predictable rate (Galtier et al. 2009). While mitochondrial DNA has limitations, it remains a useful means of ancestral analysis, and it has provided researchers with a wealth of knowledge about human migration and dispersal (see, e.g., Medina-Martinez et al. 2009; Goedbloed et al. 2010).

More specifically, nucleotide sequences from the hypervariable segment of the noncoding control region, or the D-loop, are used to build phylogenetic networks for and

between human populations (Figure 2). Because of its rapid and predictably paced evolution, single-nucleotide polymorphisms (SNPs), or mutations, accumulate over time (Hernndstadt et al. 2002). This SNP 'clock' allows researchers to date human mtDNA, using, for example, a known HVSI mutation rate of 1.64273×10^{-7} per nucleotide per year and a known HSVII mutation rate of 2.29640×10^{-7} per nucleotide per year (Soares et al. 2009). These coalescence times are used frequently in research.

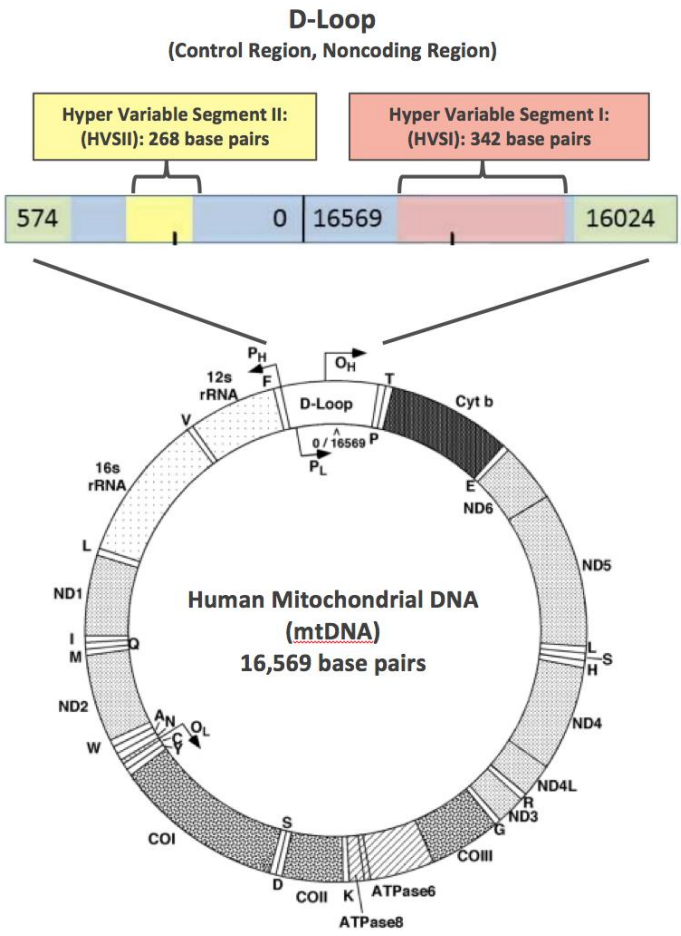


Figure 2: Diagram of human mtDNA. Modified from Jobling & Gill (2004).

Collectively, an individual's SNPs (i.e., linked set of nucleotide variants in a given region of DNA) is called a haplotype. Because mtDNA divergence levels reflect divergence through time (Galtier et al. 2009), clusters of haplotypes belong to haplogroups, or genetic clusters of

people who share a common maternal lineage. Haplogroups are denoted using uppercase letters and numbers – for example, A2 or L0 – to designate their identities and their locations in the broader phylogenetic tree of mtDNA (see van Oven & Kayser 2009).

Various haplogroups, both paternal and maternal, have corresponding geographic and temporal origins. As a result, human migration patterns can be traced around the globe by studying haplogroup patterns of distribution (Figure 3). Individuals of Native American ancestry typically belong to one of four haplogroups: A2, B2, C1, and D1. These four primary indigenous haplogroups are derived from ancestral Beringian populations, the earliest of which crossed into the Americas after the peak of the Last Glacial Maximum around 19,000 years ago (19 kya) (Achilli et al. 2008, 5-6). Other indigenous haplogroups have been identified, including X2a, though its distribution is restricted to a few Amerindian populations of northern North America (Achilli et al. 2008, 1). This is because X2a is believed to have entered the Americas through the ice-free corridor between the Laurentide and Cordilleran ice sheets, rather than along the Pacific coast (Kashani et al. 2012, 35).

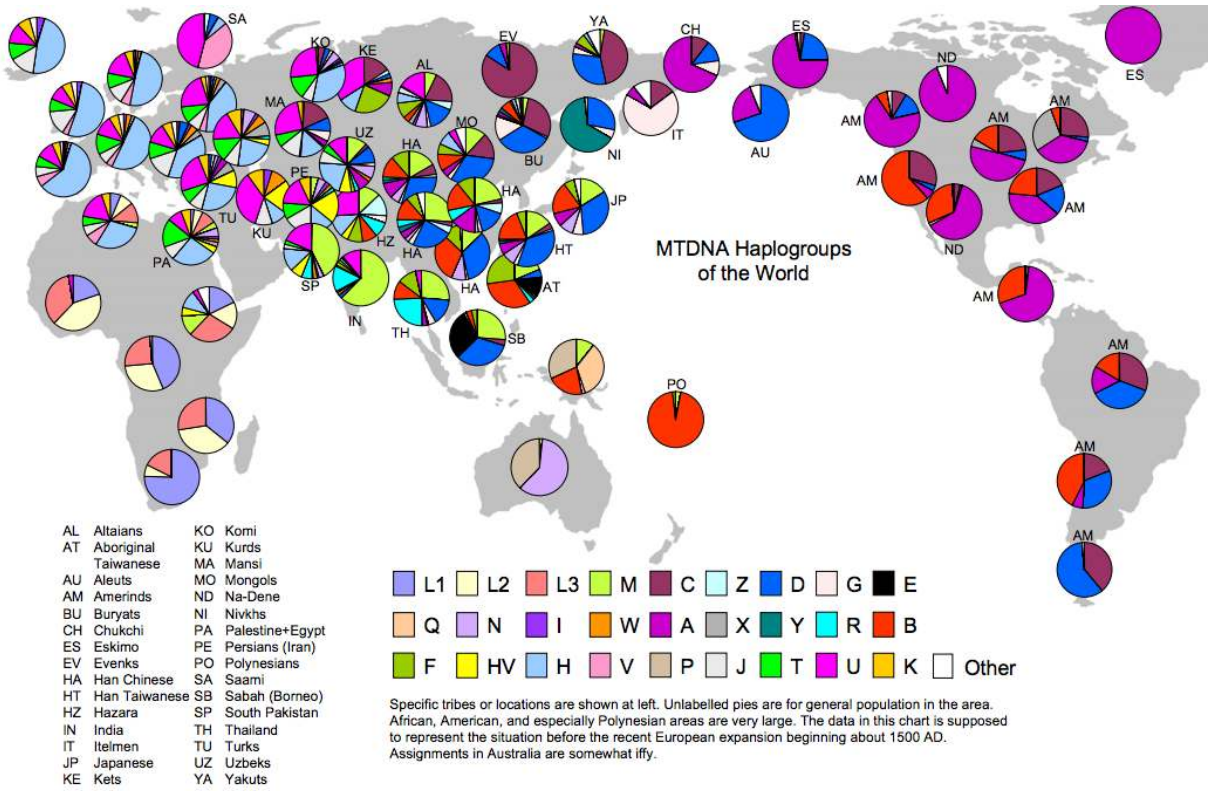


Figure 3: Simplified map portraying mtDNA haplogroups and their geographic correlates. Source: Transpacific Project Genetic Research.

METHODS OVERVIEW

Given the usefulness of mtDNA in elucidating the origins and diversity of a population, this project sought to analyze the mtDNA genetic diversity of the Vincentian Garifuna and Trinidadian First Peoples' Community (FPC). In addition, this project sought to compare this maternal genetic diversity with that of nearby populations of the Caribbean, South America, and Mesoamerica, incorporating prior genetic and historical research on the region. Statistical and phylogenetic analysis was applied, as well, to uncover potential genetic clusters in the broader circum-Caribbean region.

For Vincentian indigenous individuals, 14 participant samples from Sandy Bay or Kingstown and 46 participant samples from St. Vincent Community College or other indigenous communities were analyzed. For Trinidadian indigenous individuals, 23 participant samples were collected from members of the Santa Rosa First People's Community (FPC) in Arima. These sample sizes are relatively small, which reflects the small sizes of the indigenous communities from which they are drawn. However, the data were analyzed in conjunction with the 12 Trinidadians and 43 Vincentians from Benn Torres et al. (2015), thus raising the overall sample size from each community.

The samples analyzed for the purposes of this research paper were retrieved, stored, and studied with permission from the University of Pennsylvania IRB #8 and the University of Notre Dame IRB. Approval was also obtained prior to sample collection from the National Ethics Research Committee, Ministry of Health, Wellness and the Environment, St. Vincent and the Grenadines; the Ethics Committee, Government of the Republic of Trinidad and Tobago; and the Santa Rosa FPC and St. Vincent Garifuna Community. Each participant provided written informed consent (Benn Torres et al. 2015, 3). After consent, each participant provided a genetic

sample via buccal (inner cheek) swab and a documentation of known family history (Benn Torres et al. 2015, 3-4). Samples were stored in the University of Pennsylvania Molecular Anthropology Laboratory until analysis, which – for the samples assessed in this paper – took place between May and July of 2016.

For all samples, the HSV1 and HSV2 regions of the mtDNA control region (base pairs 16024 to 576) were amplified via standard Polymerase Chain Reaction (PCR). This was done to ensure that the entire control region could be sequenced. The following reagents and primers were mixed to make the reaction cocktail: 0.20 µl 15838FOR (forward primer), diluted from stock to 10 picomoles/µm; 0.20 µl 16552REV (reverse primer), diluted from stock to 10 picomoles/µm; 0.25 µl Deoxynucleotide triphosphates (dNTPs); 1.25 µl 10x TAQ buffer; 7.3 µl double distilled water (ddH2O); 0.75 µl magnesium chloride (MgCl2); 0.05 µl TAQ polymerase; and 0.5 µl pf a given DNA sample.

For the first round of sequencing, a segment of 714 base pairs (bp) of the HVSI was analyzed, as derived from the forward and reverse primers used (see above). For the second round of sequencing, a segment of 841 base pairs using the aforementioned method with primers16453FOR and 725REV. After amplification, the amount of viable PCR product was assessed using agarose gel electrophoresis. If viable, the PCR products were presequenced using 0.1 µl of Exonuclease I, 0.1 µl of thermosensitive Shrimp Alkaline Phosphatase (tSAP), and 1.9 µl of ddH2O per DNA sample. This step removes unincorporated primers and nucleotides, which can interfere with the sequencing process. The segments were then prepared for sequencing using 0.5 µl of BigDye® Terminator Pre-Mix v.3.1, 2 µl Big Dye buffer, and 3 µl of H20 per sample.

After this, the samples were purified, or removed of unincorporated BigDye terminators and salts, using 10 µl of BigDye® XTerminator™ and 45 µl of SAM™ solution per sample. Samples were sequenced at the University of Pennsylvania DNA Sequencing Facility.

Sequence Analysis

After sequencing, the results were read using Sequencher DNA Sequence Analysis Software, version 4.8, with comparison made to the Cambridge Reference Sequence (rCRS) (Andrews et al. 1999). Mutations were identified manually using Sequencher and confirmed by referring to both forward and reverse DNA strand readings. Mutations were identified and logged for their respective samples.

Each sample's haplotype – documented as the distinct set of mutations identified in each sample's mtDNA control region – was recorded, and haplogroups were assigned using the PhyloTree$_{mt}$ mtDNA Tree Build 17 (van Oven & Kayser 2009). Haplogroup assignments were rechecked independently by Dr. Theodore Schurr to confirm their accuracy.

Phylogenetic Analysis

After haplotypes and haplogroups were assigned to each sample, median-joining (MJ) phylogenetic networks of HVSI sequences were generated using Network 5.0.0.0 (Bandelt et al. 1999). This software allows researchers to reconstruct phylogenetic trees and branchings, infer ancestral types, and date variants. Haplotypes for all Trinidadians and Vincentians were used to generate the networks to increase the robustness of the results. Polymorphisms were weighted at 10 (the software's default weight value). Hypervariable mutations (e.g., at T16519C) were disregarded because of their commonness in all haplogroups, which tends to skew networks. Additionally, any mutation that appeared in two ancestral haplogroups was demarcated as two

separate mutations, each representing one of the two haplogroups. This distinction prevented unnecessary median vectors and links, and was used for T16325C and T16362C.

Statistical Analysis

To further elucidate the origins of the region's diversity, HVS1 haplotypes from other Caribbean and neighboring South American and Mesoamerican populations were analyzed using Arlequin 3.5.2.2 (Excoffier & Lischer 2010). Comparative data sources are outlined in Table 1.

Table 1: Comparative mtDNA HVS1 sequences used in this study.

Geographic region		**Source**
Caribbean	Cuba	Mendizabal et al. 2008
	Dominican Republic	Bryc et al. 2010; Oakley et al. 2017
	Puerto Rico	Fleskes (unpublished); Vilar 2014
Mesoamerica	El Salvador	Salas et al. 2009
	Mexico (Yucatec Maya)	González-Martín et al. 2015
South America	Venezuela	Lander et al. 2008
	Columbia	Bryc et al. 2010

To estimate population differentiation, AMOVA population comparisons and pairwise distance matrices were generated. Comparisons using F_{ST} genetic distances within and between populations were calculated based on the frequency of shared unique haplotypes in the Arlequin 3.5.2.2 program. These calculations were based on 100 permutations, with a significance level of 0.05. In order to better visualize the relative genetic distances among the indigenous groups, the F_{ST} estimates were used to create multidimensional scaling (MDS) plots using R and RStudio software (RStudio Team 2015).

RESULTS

Considering all mutations observed in the HVSI and HVSII regions among the Trinidad and St. Vincent samples, 125 of the 173 total haplotypes (125 St. Vincent samples and 48 Trinidad samples) were unique (see Appendix A). For both Trinidadian and Vincentian samples, the two most prominent indigenous haplogroups were A2 and C1. As previously mentioned, these haplogroups are derived from ancestral Beringian populations that dispersed across the Americas. As a result, they are common maternal lineages for Native American populations. The St. Vincent samples exhibited less overall diversity than the Trinidadian samples, with 8 major haplogroups represented compared to the Trinidadians' 12. This is despite the significantly smaller sample size of the Trinidadian FPC.

St. Vincent. Among the Vincentian Garifuna, approximately 30% of participants had an indigenous mtDNA haplogroup, while significantly over half (68%) had an African haplogroup (see Figure 4). Haplogroup L2 and L3 represented 50% of the samples' haplotypes at 32% and 18%, respectively. Two samples had European haplotypes (U5b2a1a2 and H2).

Trinidad. Among the Trinidadian FPC participants, over half (51%) had indigenous mtDNA haplogroups, while 31.1% of the samples had African haplogroups (see Figure 5). Among the African haplogroups, L2 and L3 were represented relatively evenly (12% and 13%, respectively), with L1 less common. 13% of individuals belonged to mtDNA haplogroup M33, a common haplogroup in Southeast Asia. While haplogroups A2 and C1 were well-represented, one individual also belonged to haplogroup B2 and one individual belonged to haplogroup D1. Thus, all four of the major indigenous haplogroups are represented in the Trinidadian population to varying percentage degrees. As aforementioned, the Trinidadian samples exhibited greater overall diversity than the St. Vincent samples. This greater diversity confirms the observations of

Benn Torres et al.' (2015). Trinidad also had a number of haplotypes that were observed neither in the samples analyzed by Benn Torres et al. (2015) nor in samples from St. Vincent. These haplotypes – including M10a1b, M35b, K, and U6a1a – will be assessed in this paper's Discussions section.

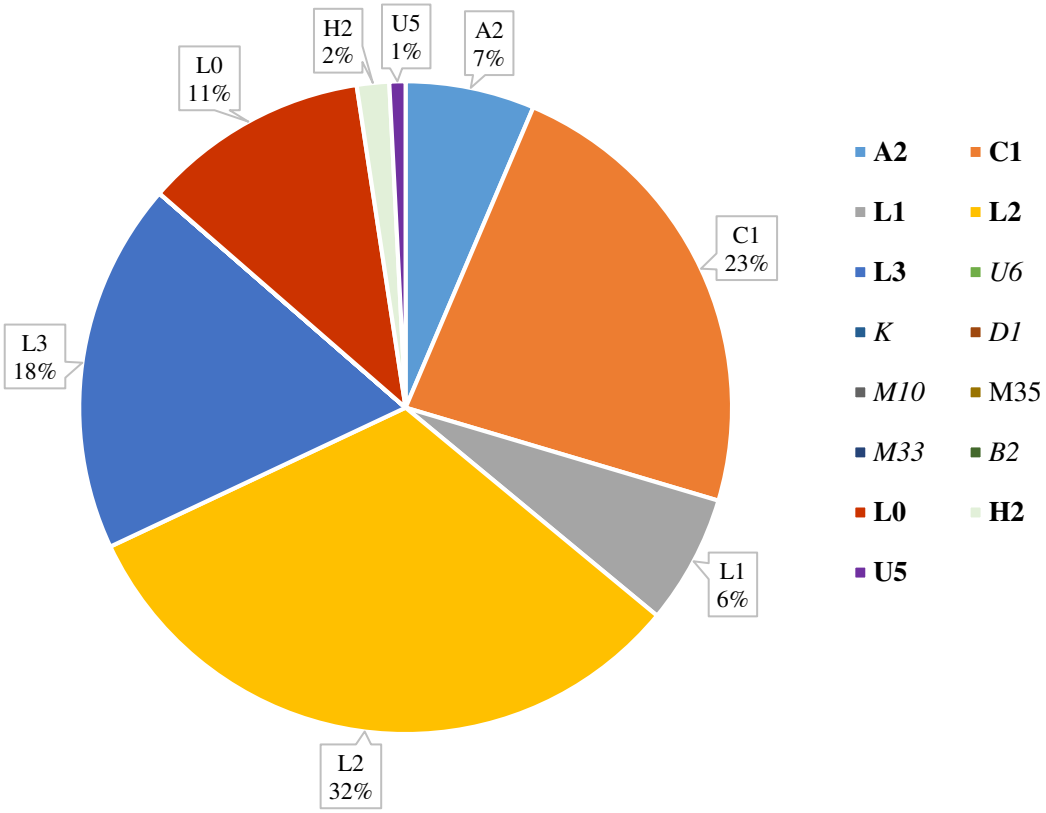


Figure 4: mtDNA haplogroup distribution of St. Vincent Garifuna (125 samples). Italicized haplogroups do not appear in St. Vincent samples, but do appear in Trinidadian FPC samples.

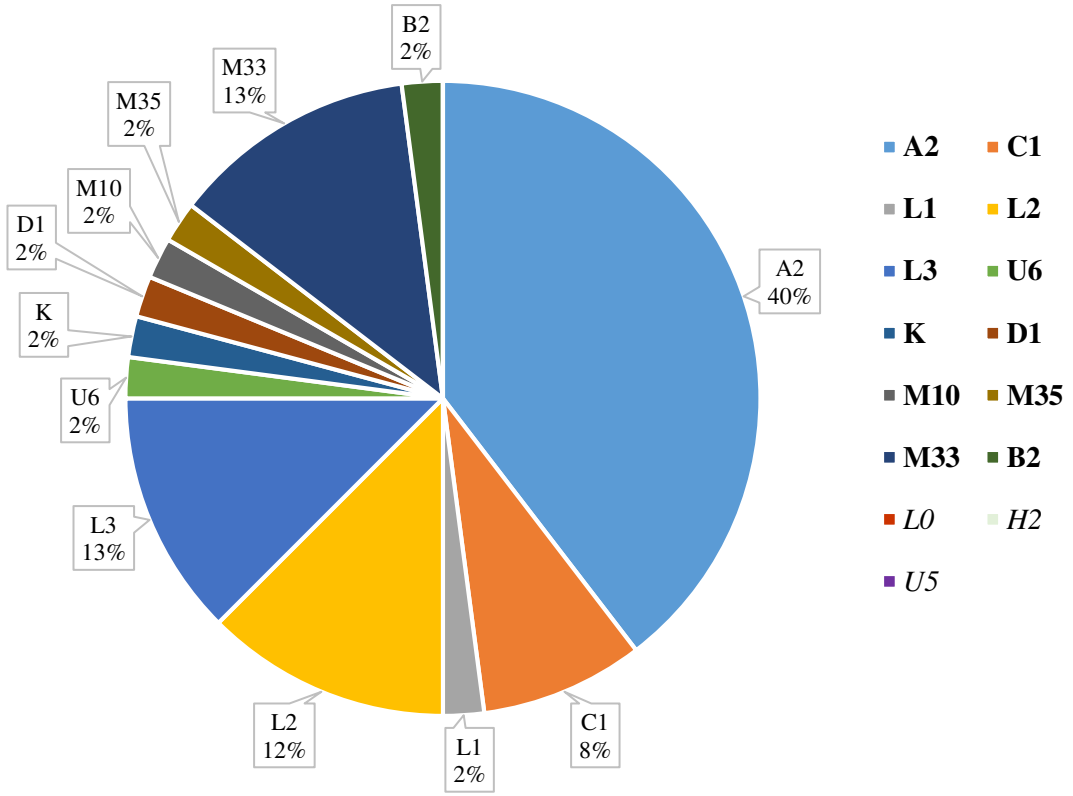


Figure 5: mtDNA haplogroup distribution of Trinidadian FPC (45 samples). Italicized haplogroups do not appear in Trinidad samples, but do appear in St. Vincent Garifuna samples.

Phylogenetic network results

The phylogenetic network of all indigenous Trinidadian and Vincentian haplogroups displays the diversity among each major haplogroup, although also reflecting Trinidad's greater relative diversity (see Figures 6-8). Haplogroup A2 contains the greatest diversity, with five distinct haplotypes, four of which represent haplotypes present only in the Trinidadians. Haplogroup C1 is the second most diverse, with four major haplotypes represented. There is only one B2 haplotype and one D1 haplotype, both coming from Trinidad. There were only two missing intermediate nodes in the networks, indicating a relatively complete set of data (Figure 6). Interestingly, the Trinidadian and Vincentian populations do not share any haplotypes, with one exception: one Trinidadian shared a C1 haplotype with a large number of Vincentians. This

trend – seen in Benn Torres et al. (2015) as well – is surprising, given the islands' close proximity to one another (the islands are less than 200 apart).

The separate phylogenetic networks for Trinidadian FPC (Figure 7) and Vincentian Garifuna (Figure 8) present the clearest visualization of the former's greater diversity, as indicated by the presence of secondary branches among both haplogroups A2 and C1.

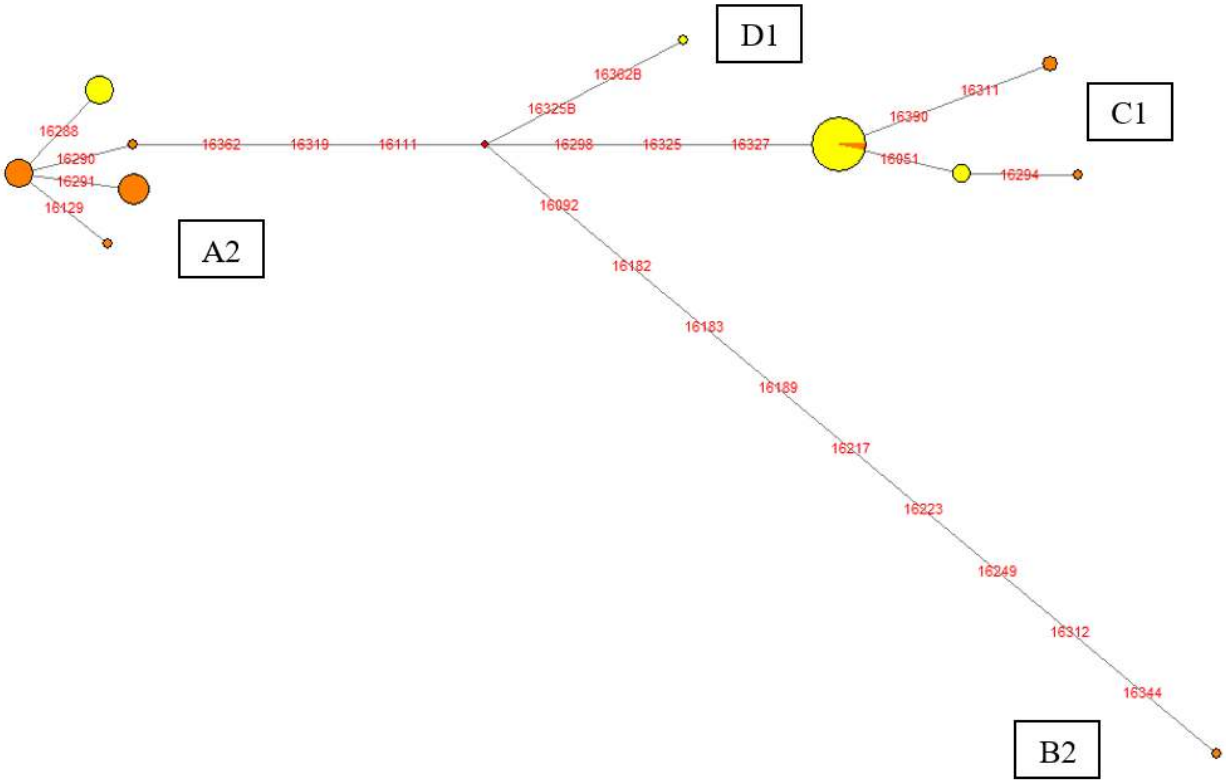


Figure 6: Phylogenetic HVS1 network of all Trinidadian and St. Vincentian indigenous haplotypes. Boxed letters refer to major haplogroups. The orange color represents mtDNA samples drawn from Trinidadian FPC, while the yellow color represents mtDNA samples from Vincentian Garifuna.

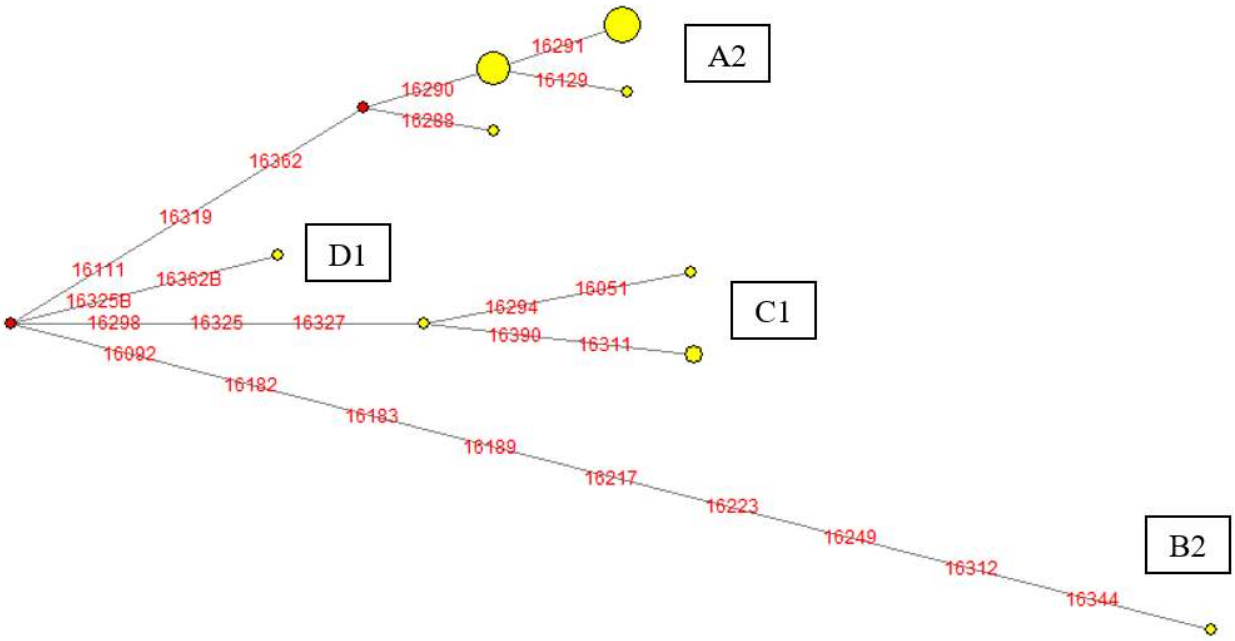


Figure 7: Phylogenetic HVS1 network of all indigenous Trinidadian haplotypes. Boxed letters refer to major haplogroups.

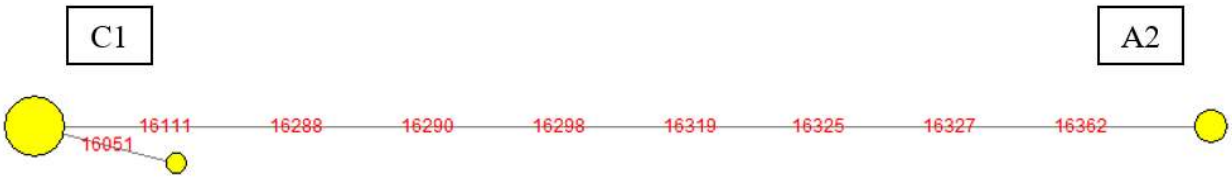


Figure 8: Phylogenetic HVS1 network of all indigenous St. Vincentian haplotypes. Boxed letters refer to major haplogroups.

F_{ST} and MDS plot results

Table 2: F_{ST} population pairwise distances among South American, Mesoamerican, and Caribbean peoples with haplogroup **A2**. Abbreviations are as follows: DR = Dominican Republic, PR = Puerto Rico, VEN = Venezuela, CUB = Cuba, ELSAV = El Salvador, MAYA = Maya (Yucatec), SVG = St. Vincent, and TRI = Trinidad.

	DR	**PR**	**VEN**	**CUB**	**ELSAV**	**MAYA**	**SVG**	**TRI**
DR	0							
PR	0.05026	0						
VEN	0.00853	0.03345	0					
CUB	0.29355	0.33937	0.31971	0				
ELSAV	0.04179	0.06284	0.03651	0.30959	0			
MAYA	0.03235	0.06657	0.04075	0.23774	0.0204	0		
SVG	0.53781	0.52537	0.63183	0.53017	0.49792	0.4092	0	
TRI	0.45633	0.45498	0.52301	0.49981	0.42519	0.34878	0.62297	0

Table 3: F_{ST} population pairwise distances among South American, Mesoamerican, and Caribbean peoples with haplogroup **C1.** Abbreviations are as follows: DR = Dominican Republic, PR = Puerto Rico, VEN = Venezuela, CUB = Cuba, ELSAV = El Salvador, MAYA = Maya (Yucatec), SVG = St. Vincent, and TRI = Trinidad.

	DR	**PR**	**VEN**	**SVG**	**COL**	**TRI**
DR	0					
PR	0.27231	0				
VEN	0.13739	0.17815	0			
SVG	0.24416	0.11927	0.18047	0		
COL	0.11482	0.11468	0.07306	0.29494	0	
TRI	0.11111	0.27694	0.10324	0.56899	0.05251	0

The F_{ST} population pairwise distances and the MDS plot for haplogroup A2 corroborate observations by Benn Torres et al. (2015) that the Trinidadians are genetically distant from comparator populations (Table 4). The Vincentian Garifuna clustered more closely with the comparator populations from Central and South America. Other Caribbean populations (Cuban, Dominican, and Salvadorian) clustered near the top center of the MDS plot. Interestingly, the MDS plot for haplogroup C1 suggests that the indigenous Caribbean populations are somewhat distant from each other, separated by the Venezuelan and Columbian C1 populations (Table 5).

Beyond this, there were no easily discernible clusters on the C1 MDS plot, as all populations appeared somewhat distant. Note, however, that Mesoamerican samples were not used for C1.

Table 4: A MDS plot of F_{ST} estimates for haplogroup **A2,** based on mtDNA HVS1 sequences for indigenous Caribbean and comparative populations. Purple = Mesoamerica; blue = Caribbean; green = South America.

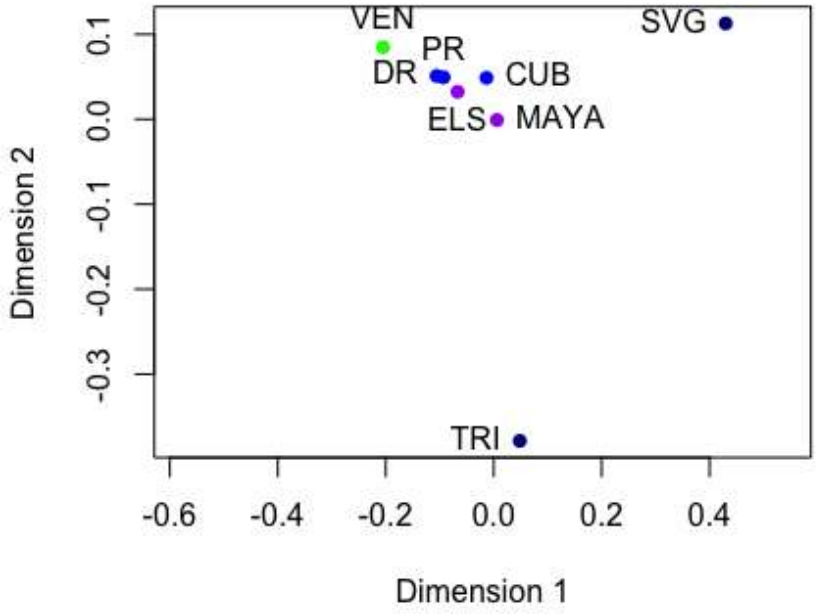
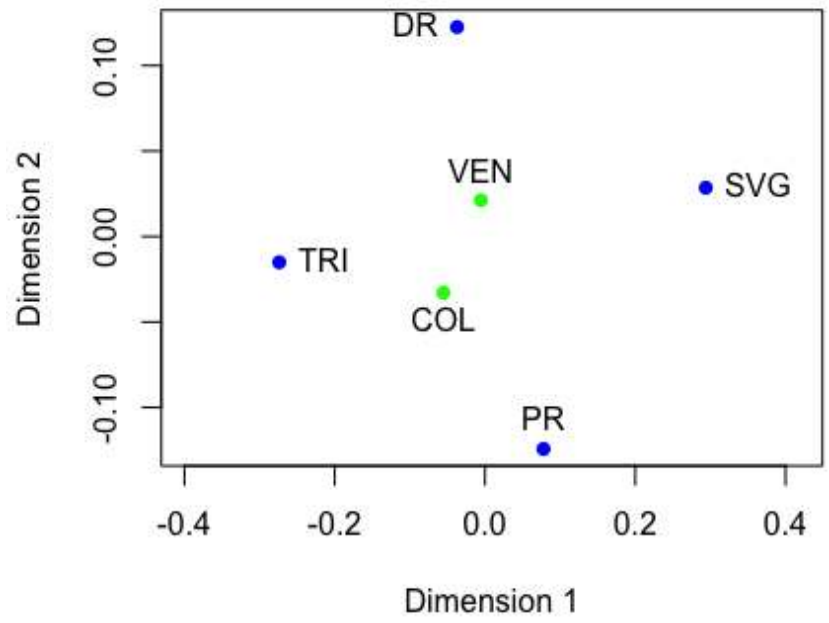


Table 5: A MDS plot of F_{ST} estimates for haplogroup **C1,** based on mtDNA HVS1 sequences for indigenous Caribbean and comparative populations. Blue = Caribbean; green = South America.



AMOVA results

For haplogroup A2, the percentage of variation within and among populations was 86.32% and 13.68%, respectively (Table 6). For haplogroup C1, the percentage of variation within populations and among populations was 82.04% and 17.96%, respectively (Table 7). For both haplogroups, these results from the AMOVA test suggest that significantly more diversity exists within the populations, as compared to diversity between the populations. This corroborates evidence that only a small fraction of the total variance in allele frequencies come from between-population differences, which has been observed over decades of research (Witherspoon et al. 2007). Interestingly, statistical analysis also revealed that neither Vincentian nor Trinidadian samples share haplotypes with comparator populations, although all the other populations that were assessed share at least several haplotypes with one another.

Table 6: AMOVA results for A2 haplotype comparisons between and among Vincentian Garifuna, Trinidadian FPC, and comparator populations.

Source of Variation	**d.f.**	**Sum of squares**	**Variance components**	**Percentage of variation**
Among populations	5	73.208	0.18856	13.68
Within populations	451	536.391	1.18934	86.32
Total	456	609.6	1.3779	

Table 7: AMOVA results for C1 haplotype comparisons between and among Vincentian Garifuna, Trinidadian FPC, and comparator populations.

Source of variation	**d.f.**	**Sum of squares**	**Variance components**	**Percentage of variation**
Among populations	5	24.56	0.18999	17.96
Within populations	156	135.366	0.86773	82.04
Total	161	159.926	1.05772	

DISCUSSION

The distribution of haplogroup frequencies of the Vincentian Garifuna and Trinidadian FPC was relatively consistent with results from Torres et al. (2015). Trinidadian FPC had a greater percentage of indigenous samples, and among indigenous samples from both populations, the Trinidadian FPC had more A2 than C1 haplotypes. The vice versa was true for the Vincentian Garifuna.

The results raise a number of questions about pre-Columbian indigenous populations in the Caribbean and the effects of colonization on St. Vincent and Trinidad. One question concerns possible explanations of the greater percentage of indigenous haplotypes observed among the Trinidadian FPC, compared to the St. Vincent Garifuna. This difference may derive from differences in the islands' colonial histories. Contemporary historians believe that, during the colonial era, indigenous St. Vincentians developed complex interethnic alliances with African or African-descended people, as part of a strategy of indigenous resistance to European colonial pressures (Kim 2013). By 1668, African slaves were being imported in large numbers to St. Vincent, and indigenous Caribs began to affiliate and assimilate with them to fortify their abilities to resist their colonizers (Kim 2013).

Additionally, St. Vincent's colonial history was more rife with violent conflict than was Trinidad's, with the First and Second Carib War (1772-73, 1795-96) eventually culminating in the relocation of Black Caribs – the ancestors of modern-day Garifuna – to Central America (Kim 2013, 118). The impacts of this exile were profound, with close to half of those relocated dying (Kim 2013, 118). As far more Africans were imported into the region than existed Caribs during this era, it is not surprising that Vincentians exhibit a higher percentage of African haplotypes.

The Trinidadian samples may also show more indigenous haplotypes partially as a result of Capuchin missions in Spanish Trinidad, the establishment of which began in earnest in 1686 (Boomert 2016, 131). Though intended to Hispanicize and convert indigenous Trinidadians, these missions also allowed indigenous populations to survive during Spanish colonialism, and even attracted indigenous refugees from other regions in the Lesser Antilles (Boomert 2016, 131-142).

Another question concerns the haplogroup frequencies of indigenous haplogroups between St. Vincent and Trinidad, as the frequency of C1 is higher – and A2 lower – for St. Vincent individuals. The vice versa is true for Trinidadians. There are at least two possible explanations for this difference in frequencies. First, it could be the result of different populations that initially settled the region in one of several migratory waves (Benn Torres et al. 2015, 15). If correct, this model may corroborate existing theory about the histories of Trinidad and St. Vincent: the former is believed to have been settled initially by populations emerging from coastal South America, while the latter is believed to have been settled by Saladoid peoples from South or Central America (see Fitzpatrick 2015). Second, the haplogroup disparity could be the result of genetic drift. Genetic drift, along with mutation and recombination, produces the gametes on which natural selection can act; if there is no selective pressure, then allele frequencies in any given population change only by genetic drift and mutation (Masel 2011, R837). Because mtDNA variants segregate remarkably quickly between generations, genetic markers in isolated populations (e.g., in St. Vincent versus Trinidad) can potentially diverge over a short period of time (Jenuth et al. 1996, 146). Both of these possibilities may also explain, at least in part, why the Trinidadians and Vincentians sampled for this study share only one haplotype, despite the islands' close proximity.

The distribution of African haplotypes also has probative value for understanding the history of Caribbean colonization with African slaves. The novel Vincentian and Trinidadian samples corroborate trends seen with the samples analyzed in Benn Torres et al. (2015). More specifically, haplogroup L2 was the most commonly observed African haplogroup within the Vincentians, whereas L2 and L3 were the most common African haplogroups among the Trinidadians. Between 1500 and 1850, more than 12 million African slaves were forcibly taken to the Americas, with the vast majority coming from West and West-Central Africa (Schroeder et al. 2015, 3669). Citing Stefflova et al. (2011), Benn Torres et al. (2015, 17) note that "within Afro-Caribbean populations 46% of their African ancestry could be traced back to the Guinea Bissau, Mali, Senegal and Sierra Leone regions, 29% to the region encompassing Niger, Nigeria, and Cameroon, and 25% to Angola."

Moreover, Stefflova et al. (2011) notes that mtDNA variation among African-descended Caribbean peoples may reflect the unique colonial histories on each island. While both islands had extensive British colonial histories, St. Vincent was also influenced by slaves brought by French settlers, while Trinidad was more influenced by slaves brought by the Spanish. It is possible that the different frequencies of various L haplogroups between the Vincentians and Trinidadians stem from different African populations utilized by Europeans for slaves. For example, French settlers retrieved many African slaves from Senegambia, which has a higher percentage of L2 haplogroups than Bight of Benin, Bight of Biafra, and West-Central Africa (Harich et al. 2010, 11-12; Stefflova 2011, 5; Lovejoy 2007).

Beyond these questions, this study's results also corroborate evidence that supports various theories of migration. The percentage variation between indigenous haplogroups on the two islands adds credence to the theory that St. Vincent and Trinidad experienced different

prehistoric settlement patterns, with Trinidad settled earliest as a result of its connection to mainland South America (see Fitzpatrick 2015; Benn Torres et al. 2015). For haplogroup A2, the genetic distance of the Trinidadian FPC from comparator populations, including the Vincentian Garifuna, corroborates existing evidence of Trinidad's unique and early settlement history. This supports existing evidence that Trinidad was settled first around 8000 to 7800 BP, in the earliest migratory wave to the Caribbean region (Fitzpatrick 2015, 308). The implications for the statistical analysis of haplogroup C1 is less clear, as the MDS plot lacks easily discernible clusters.

The results also support the theory – backed by archaeological, archaeobotanical, and other evidence – that many Caribbean islands experienced several migratory waves in which older inhabitants were replaced and/or assimilated into new populations (Benn Torres et al. 2015, 16). However, for both haplogroups A2 and C1, Benn Torres et al. (2015, 15) did not find clear evidence for genetic relationships between Mesoamerican and Antillean populations. While the sample sizes for the Vincentian Garifuna and Trinidadian FPC were nearly doubled by this analysis, evidence for genetic relationships with Mesoamerica is still lacking.

Moreover, the presence of haplogroup M33 in the Trinidadians confirms written and genetic evidence that an influx of East Asian, and particularly Indian, indentured laborers in the mid-1800s contributed to the mitochondrial DNA in Trinidad (see Brereton 2007). This will be discussed in the next section.

Eurasian and East Asian haplotypes. There were a number of unusual haplotypes that appeared in the samples, particularly among samples from the Trinidadian FPC community. These haplotypes will be discussed individually.

Trinidad

Subhaplogroup M10a has its highest frequency among Tibetans and is seen in the Gallong (Galo) tribe of central Eastern Himalaya, residing today in what is now the northeast Indian state of Arunachal Pradesh (Chandrasekar et al. 2009, 6). The haplogroup M10a1b has also been detected in mtDNA samples from two language groups in Thailand and Laos, where researchers generated a Bayesian estimate of coalescence time of 1478 years (with a 95% confidence interval of 48-4574 years) (Kutanan et al. 2017, 92). It has been found in Koreans and mainland Japanese, as well (Chandrasekar et al. 2009, 6). As Benn Torres et al. (2015) noted, the presence of East Asian haplotypes may not be surprising because, after Trinidadian Emancipation in 1838, former slaves left plantations, and the labor void was filled by East Asian indentured laborers (15). However, given M10a1b's high frequency in Thailand and Laos, it is possible that indentured servants may have come from populations historically residing east of India.

Like M10a, M35b is an Indian subhaplogroup that is dispersed widely inside the Indian subcontinent, appearing in groups from Nepal to South India (Fornarino et al. 2009, 8). Interestingly, it is also believed to be a founder lineage of Roma in various Slavonic groups (Chandrasekar et al. 2009, 3). The presence of this lineage, like M10a, probably reflects the nation's history of East Asian indentured labor.

Haplogroup K is primarily a western Eurasian lineage. It is found throughout the Middle East and in approximately 10% of Europeans (Quintana-Murci et al. 2004, 829). It is particularly prevalent in certain populations, such as the Ashkenazi Jewish, 32% of whom belong to haplogroup K (Behar et al. 2004, 358). This haplogroup likely exemplifies admixture between European colonizers and indigenous Caribbean peoples.

Both haplogroups B2 and D1 are rarely found in contemporary Caribbean populations, and this observations holds true for ancient Lesser Antillean samples (Benn Torres et al. 2015, 14). Haplogroups B2 and D1 were not detected in the Vincentian and Trinidadian samples analyzed by Benn Torres et al. (2015), although one D1 haplotype and one B2 haplotype were identified in this sample set, both from Trinidad. D1 and B2 haplotypes have been identified in the Caribbean in prior research, albeit rarely (Benn Torres et al. 2015, 14). However, the fact that both these haplogroups appeared in Trinidad and not in St. Vincent, despite the latter's larger sample size, is interesting. It is possible this distribution reflects Trinidad's close proximity to South America, as well as Trinidad's longer settlement history, with coastal indigenous peoples crossing into Trinidad while it was connected to the mainland. It may also reflect historical evidence that Trinidad served as a refuge for indigenous peoples from mainland South America during the colonial era (Boomert 2016, 131-142).

Haplogroup U6 shows major distribution in East and, especially, North Africa, in the region commonly known as the Maghreb (Secher et al. 2014, 1). U6 was carried to southern Europe beginning in the Neolithic, after which European colonization brought various U6 lineages to the Americas (Secher et al. 2014, 1). U6a1a is identified as a European U6 sub-clade, appearing most prominently in southernmost European regions, particularly the Iberian Peninsula (Secher et al. 2014, 5). Thus, the presence of this haplotype is likely evidence of European colonization, and in particular, Spanish colonization of Trinidad, which Saint Vincent did not experience.

St. Vincent

One individual had haplotype U5b2a1a2. Haplogroup subcluster U5b2a is distributed in central Europe, with Malyarchuk et al. (2010) finding a large number of U5b samples in Poland,

Slovakia, and the Czech Republic. It is also found in northern Europe, including the British Isles and Scandinavia (Achilli et al. 2005, 883). This lineage, like U6a1a, reflects European and indigenous Caribbean admixture during colonization.

Haplogroup H is found in a high percentage (40-50%) of Europeans, with substantial numbers found also in the Near East and the Caucasus (Pereira et al. 2005, 19). Haplogroup H2, along with H6, are common in Eastern Europe and the Caucasus (Pereira et al. 2005, 21). This, along with U6a1a and U5b2a1a2, reflects European colonizers' presence on St. Vincent.

CONCLUSION

For many centuries, the story of Caribbean peoples was written by, for, and about the Europeans who 'discovered' the Americas, and who viewed indigenous Caribbean peoples as a roadblock to power or as potential economic assets through slave labor (Newton 2014, 9). A central tenet to this narrative is that European arrival led to indigenous disappearance (Newton 2014, 13; Kim 2013, 119). While it is true that a large number of Amerindians were killed by Old World diseases or European conflict with native populations, many indigenous peoples survived, a testament to their remarkable resiliency (Kim 2013, 119-120). Contemporary historians, archaeologists, anthropologists, and other researchers have attempted to rewrite the history of Caribbean peoples, and genetic data has the potential to provide concrete evidence of indigenous continuity.

To that end, this study aimed to build on existing scholarship surrounding the genetic evidence of the peopling of the Caribbean Basin. In this study, mtDNA from the Trinidad FPC and St. Vincent Garifuna was analyzed. Both the Trinidadian FPC and the St. Vincent Garifuna

exhibited indigenous mtDNA haplogroups, representing all four of the major founding indigenous haplogroups – A2, B2, C1, and D1. In St. Vincent, C1 was most prevalent, while A2 was most prevalent in Trinidad. B2 and D1 appeared only once each in the Trinidadians; this low frequency corroborates a larger distribution trend seen in the Caribbean (Benn Torres et al. 2015, 14). This study also identified haplogroups previously unseen in these populations, including ones associated with India and other East Asian regions. The haplotypes identified in this study were assessed in the larger framework of historical scholarship about the region and its people.

Overall, the results – including the unequal frequencies of A2 and C1 haplogroups and the lack of shared haplotypes – substantiate Torres et al. (2015, 17), who suggested that while some shared ancestry between indigenous Caribbean communities is likely, "each has become genetically differentiated from the others through genetic drift, separate migration events or stochastic lineage loss."

These data represent a critical step toward a more complete understanding of the migratory histories of St. Vincent, Trinidad, the rest of the Caribbean, and neighboring South America. In the future, comparative analyses between the haplotypes assessed in this paper and those from neighboring regions should be conducted, particularly because small sample sizes affected previous results (see Benn Torres et al. 2015, 21; Fitzpatrick 2006). This analysis should also be extended to Y-chromosome data, particularly because interesting patterns have emerged in prior research regarding the prevalence of indigenous haplogroups in mitochondrial (maternal) DNA versus Y-chromosome (paternal) DNA. When both mtDNA and Y-chromosome data, and perhaps autosomal DNA, can be compiled from across the circum-Caribbean region, additional comparative and statistical analyses – including F_{st}, which measures population differentiation – will further elucidate the complex indigenous migration histories of the Caribbean.

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CONTRIBUTIONS

T.G.S. designed the project and T.R.M. conducted laboratory analyses, with the instruction and assistance of T.G.S. T.R.M. wrote this manuscript, with review by T.G.S.

GENETIC TOOLS

Arlequin: http://cmpg.unibe.ch/software/arlequin35/

MITOMAP: http://www.mitomap.org/MITOMAP

Network: http://www.fluxus-engineering.com/sharenet.htm

PhyloTree: http://www.phylotree.org/

RStudio: https://www.rstudio.com/

APPENDIX

Appendix A: Haplotypes from all Trinidad FPC and St. Vincent Garifuna samples collected during several research expeditions (125 samples from St. Vincent, 48 samples from Trinidad).

Haplogroup	SVG	TRI	(np 16024-16569)
A2	1	0	C16111T-C16223T-T16288C-C16290T-G16319A-T16362C
A2	1	0	C16111T-C16223T-T16288C-C16290T-G16319A-T16362C
A2	2	0	C16111T-C16223T-T16288C-C16290T-G16319A-T16362C
A2	1	0	C16111T-C16223T-T16288C-C16290T-G16319A-T16362C
A2	1	0	C16111T-C16223T-T16288C-C16290T-G16319A-T16362C
A2	1	0	C16111T-C16223T-T16288C-C16290T-G16319A-T16362C
A2	1	0	C16111T-C16223T-T16288C-C16290T-G16319A-T16362C
A2	0	4	C16111T-C16223T-C16290T-C16291T-G16319A-T16362C
A2	0	2	C16111T-C16223T-C16290T-G16319A-T16362C
A2	0	1	C16111T-C16223T-C16290T-G16319A-T16362C-T16519C
A2	0	1	C16111T-C16223T-C16290T-C16291T-G16319A-T16362C
A2	0	1	C16111T-C16223T-C16290T-C16291T-G16319A-T16362C
A2	0	2	C16111T-C16223T-C16290T-C16291T-G16319A-T16362C
A2	0	1	C16111T-C16223T-C16290T-G16319A-T16362C-T16519C
A2	0	1	C16111T-G16129A-C16223T-C16290T-G16319A-T16362C
A2	0	1	C16111T-C16223T-C16290T-C16291T-G16319A-T16362C
A2	0	2	C16111T-C16223T-C16290T-G16319A-T16362C-T16519C
A2	0	1	C16111T-C16223T-C16290T-G16319A-T16362C-T16519C
A2	0	1	C16111T-C16223T-C16290T-G16319A-T16362C
A2	0	1	C16111T-C16223T-C16290T-G16319A-T16362C
C1	4	0	C16223T-T16298C-T16325C-C16327T-T16519C
C1	11	0	C16223T-T16298C-T16325C-C16327T-T16519C
C1c5	1	0	C16223T-T16298C-T16325C-C16327T-T16519C
C1	1	0	C16223T-T16298C-T16325C-C16327T
C1	4	0	C16223T-T16298C-T16325C-C16327T
C1	4	0	C16223T-T16298C-T16325C-C16327T
C1	1	0	C16223T-T16298C-T16325C-C16327T
C1	0	2	C16223T-T16298C-T6311C-T16325C-C16327T-G16390A-T16519C
C1d	2	0	A16051G-C16223T-T16298C-T16325C-C16327T-T16519C
C1d	0	1	A16051G-C16223T-C16294T-T16298C-T16325C-C16327T
C1d	1	0	A16051G-C16223T-T16298C-T16325C-C16327T-T16519C

L0	1	0	G16129A-C16148T-C16168T-T16172C-C16187T-C16188G-T16189C-C16223T-A16230G-T16311C-C16320T-T16519C
L0	1	0	G16129A-C16148T-C16168T-T16172C-C16187T-C16188G-T16189C-C16223T-A16230G-T16311C-C16320T
L0	8	0	G16129A-C16148T-C16168T-T16172C-T16187C-16188G-T16189C-C16223T-A16230G-C16278T-A16293G-T16311C-C16320T
L0	1	0	G16129A-C16148T-C16168T-T16172C-T16187C-16188G-T16189C-C16223T-A16230G-C16278T-A16293G-T16311C-C16320T
L0a1b	2	0	G16129A-C16148T-C16168T-T16172C-C16187T-C16188G-T16189C-C16223T-A16230G-C16278T-A16293G-T16311C-C16320T-T16519C
L0	1	0	T16093C-G16129A-T16172C-C16184T-C16187T-T16189C-C16223T-C16261T-C16278T-C16290T-T16311C-C16360T-T16519C
L1	1	0	T16154C-C16187T-T16189C-C16223T-A16265C-C16278T-C16286G-C16294T-T16311C-C16360T
L1	1	0	T16126C-C16187T-T16189C-C16223T-C16294T-C16270T-C16278T-A16293G-T16311C
L1b2	1	0	T16126C-C16187T-T16189C-C16223T-C16264T-C16270T-C16278T-A16293G-T16311C-T16519C
L1b1a2	1	0	T16126C-C16187T-T16189C-C16223T-C16264T-C16270T-C16278T-T16311C-T16519C
L1c1	1	0	A16038G-T16086C-G16129A-C16187T-T16189C-C16223T-C16278T-A16284G-A16293G-C16294T-T16311C-C16360T
L1b1a10	1	0	T16126C-C16167T-C16187T-T16189C-C16223T-C16264T-C16270T-C16278T-T16311C-T16519C
L1b1a10	1	0	T16126C-C16187T-16189C-C16223T-C16264T-C16270T-C16278T-T16311C-T16519C
L1b1a2	1	0	T16126C-C16184T-C16187T-T16189C-C16223T-C16264T-C16270T-C16278T-A16278T-A16293G-T16311C-T16519C
L1c1b1	0	1	T16086C-G16129A-C16187T-T16189C-C16223T-A16241G-C16278T-C16291T-C16294T-T16311C-C16360T-T16519C
L2	1	0	T16093C-C16223T-C16264T-C16278T-G16390A-T16519C
L2	1	0	C16114A-G16219A-A16212G-G16213A-C16223T-C16278T-G16390A
L2b	0	1	C16114A-G16129A-A16212G-G16213A-C16223T-C16278T-G16390A
L2b1a	2	0	C16114A-G16129A-G16213T-C16223T-C16278T-C16355T-T16362C-G16390A
L2	1	0	C16114A-G16129A-T16189C-C16192T-C16223T-C16278T-C16290T-C16294T-T16362C-G16390A
L2c	5	0	C16223T-C16278T-T16311C-G16390A-T16519C
L2	1	0	C16223T-C16278T-C16294T-A16309G-T16368C-G16390A-T16519C
L2	1	0	C16223T-C16278T-C16294T-A16309G-T16368C-G16390A-T16519C
L2	1	0	C16223T-C16278T-C16286T-C16294T-A16309G-C16320T-G16390A
L2	1	0	C16223T-C16278T-C16294T-A16309G-T16368C-G16390A
L2	1	0	C16223T-C16278T-C16294T-A16309G-T16368C-G16390A
L2	1	0	C16223T-C16278T-C16294T-A16309G-T16398C-G16390A-T16519C
L2	1	0	T16189C-C16192T-C16223T-C16278T-C16294T-A16309G-G16390A-T16519C
L2a1a	1	0	T16189C-C16192T-C16223T-C16278T-C16294T-A16309G-G16390A-T16519C

L2	1	0	T16189C-C16192T-C16223T-C16278T-C16294T-A16309G-G16390A-T16519C
L2	1	0	C16223T-C16278T-C16294T-A16309G-T16398C-G16390A
L2	1	0	T16093C-C16223T-C16278T-C16291T-C1294T-A16309G-T16325C-G16390A-T16519C
L2	0	1	C16223T-C16278T-C16294T-A16309G-C16360T-G16390A
L2	0	1	T16093C-C16223T-C16264T-C16278T-G16390A
L2a1	1	0	C16223T-C16278T-C16294T-A16309G-G16390A-T16519C
L2	0	1	C16223T-C16278T-C16294T-A16309G-G16390A-T16519C
L2	0	1	C16223T-C16278T-C16294T-A16309G-G16390A-T16519C
L2	1	1	C16223T-C16278T-C16294T-A16309G-G16390A-T16519C
L2	1	0	C16223T-C16278T-C16294T-G16390A-T16519C
L2a1	1	0	A16183C-T16189C-C16192T-C16223T-C16278T-C16294T-A16300G-A16309G-G16390A-T16519C
L2a1	1	0	C16223T-C16278T-C16294T-A16309G-G16390A-T16519C
L2a1a	2	0	A16183C-16193.1C-T16189C-C16223T-C16278T-C16294T-A16309G-G16390A
L2a1a	1	0	T16189C-C16192T-C16223T-C16278T-C16294T-A16309G
L2a1	1	0	C16223T-C16278T-C16294T-A16309G-T16368C-G16390A-T16519C
L2	1	0	C16223T-C16279T-T16311C-G16390A
L2	1	0	C16223T-C16278T-T16362C-G16519C
L2c1	1	0	C16147T-C16223T-C16261T-C16278T-A16318G-G16390A
L2a1b2	1	0	T16189C-C16192T-C16223T-C16278T-C16294T-A16309G-G16390A-T16519C
L2a1a2	1	0	C16223T-16254G-C16278T-C16286T-C16294T-A16309G-G16390A-T16519C
L2a1b2	1	0	G16129A-T16189C-C16192T-C16223T-C16278T-C16294T-A16309G-G16390A
L2c	1	0	T16189C-C16223T-C16278T-G16390A
L2c	1	0	C16223T-C16278T-T16362C-G16390A
L2c2b	1	0	C16223T-C16264T-C16278T-G16390A-T16519C
L2c2	1	0	C16223T-C16264T-C16278T-G16390C
L3f1b1a1	1	0	G16129A-T16209C-C16223T-C16292T-C16295T-T16311C-T16519C
L3	1	0	C16223T-C16278T-T16362C
L3	1	0	T16124C-C16223T-C16278T-C16327T-T16362C
L3b1a5	1	0	T16124C-C16150T-C16223T-C16278T-T16362C-T16519C
L3b1a5	1	0	T16124C-C16223T-C16278T-T16362C-T16519C
L3	1	0	T16124C-C16223T
L3	1	0	C16223T-C16278T-T16362C-T16519C
L3	1	0	T16126C-T16172C-A16182C-T16189C-C16223T-C16320T
L3	1	0	C16223T-C16320T-T16362C-T16519C
L3	1	0	C16176T-C16223T-T16311C-C16327T

L3e1d	1	0	C16176T-C16223T-T16311C-C16327T-T16362C
L3e3	1	0	C16223T-A16265T-C16291T-C16301T-T16519C
L3	1	0	C16223T
L3	1	0	C16223T-C16320T-A16399G
L3	1	0	C16223T-C16320T-A16399G-T16519C
L3	0	1	T16124C-C16223T-G16319A
L3	0	1	T16172C-C16223T-A16265T-T16519C
L3	1	0	C16179Cd-C16223T-A16302G-T16325C-T16519C
L3e2a1b1	1	0	C16223T-C16278T-C16320T-A16399G-T16519C
L3e2a1b1	0	1	C16223T-C16320T-A16399G-T16519C
L3	1	0	T16189C-16193.1C-C16223T-C16278T-C16294T-T16362C-G16390A
L3	1	0	T16189C-16193.1C-16193.2C-T16356C-T16362C-T16519C
L3e4a	1	0	A16051G-T16189C-16193.1C-16193.2C-C16223T-C16264T-G16319A-T16519C
L3e3	1	0	T16093G-C16223T-A16265T-T16519C
L3	1	0	T16124C-A16166G-C16223T
L3	0	1	C16185T-C16223T-T16311C-C16327T-T16519C
L3b	1	0	A16051G-T16189C-C16223T-C16234T-C16278T-T16362C-T16519C
L3K1	0	1	C16223T-TC16355T
M33	0	2	C16169T-T16172C-C16223T-T16288C-C16295T
M33	0	2	C16169T-T16172C-C16223T-T16288C-C16295T-T16519C
M33a2	0	1	C16169T-T16172C-C16223T-T16288C-C16295T-T16519C
M33A2	0	1	C16169T-T16172C-C16223T-T16288C-C16295T-T16519C
M10a1b	0	1	A16066G-C16223T-T16311C
M35b	0	1	C16223T-T16304C-T16519C
H2	1	0	G16319A-T16519C
K	0	1	T16224C-T16311C-T16519C
B2b3a	0	1	T16092C-A16182C-A16183C-T16189C-T16217C-T16249C-A16312G-C16344T
D1	0	1	C16223T-T16325C-T16362C
U5b2a1a2	1	0	C16239T-A16269G-T16311C
U6a1a	0	1	T16172C-A16183C-T16189C-16193.1C-A16219G-C16278T

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