

9-24-2019

# Genetic Overview of the Maya Populations: Mitochondrial DNA Haplogroups

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## Recommended Citation

González-Oliver, Angélica; Pineda-Vázquez, Dircé; Garfias-Morales, Ernesto; De La Cruz-Laina, Isabel; Medrano-González, Luis; Márquez-Morfín, Lourdes; and Ortega-Muñoz, Allan, "Genetic Overview of the Maya Populations: Mitochondrial DNA Haplogroups" (2019). *Human Biology Open Access Pre-Prints*. 147.  
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## **Genetic Overview of the Maya Populations: Mitochondrial DNA Haplogroups**

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Short Title: Mitochondrial DNA Haplogroups of the Maya Populations

**KEY WORDS: MITOCHONDRIAL DNA, ANCIENT DNA, MITOCHONDRIAL HAPLOGROUPS, MAYA POPULATIONS**

## **Abstract**

We identified the mitochondrial DNA haplogroups A, B, C and D in 75 present-day Maya individuals, 24 Maya individuals of the colonial period and one pre-Columbian Maya individual from Quintana Roo, Mexico. We examined these data together with those of 21 Maya populations accounting for 647 present-day Maya individuals and 104 ancient Maya individuals. A demographic study based on the analysis of fertility and endogamy was carried out in two modern Maya populations to identify cultural factors that influence the mitochondrial haplogroup genetic diversity. Most present-day and ancient Maya populations show a distribution pattern of mitochondrial haplogroup frequencies A, C, B and D in decreasing order, with haplogroup D absent in several populations. Considering only modern Maya populations with at least 50 individuals analyzed, the present-day Tzotzil and Lacandon populations from Chiapas show the higher and lower genetic diversities, 0.706 and 0.025 respectively. Our results show small genetic differences between the Maya populations with exception of the present-day Tojolabal and Lacandon populations from Chiapas. The present-day Lacandon population from Chiapas is different to other Maya populations in showing almost only haplogroup A. This result suggests a long history of isolation and endogamy as well as a possible founder effect inside the Lacandonian rain-forest. The contemporary Tojolabal population is the only one with an unusual mitochondrial haplogroup pattern exhibiting a frequency of haplogroup B higher than A and the absence of haplogroup C. With a small sample size, the pre-Columbian Copan Maya show a high content of haplogroup C and a low frequency of haplogroup D. The genetic homogeneity of the Maya populations is indicative of a common origin and nearly continuous gene flow in the long-term within a general isolation of the whole group, conversely to the Nahua populations that had different origins. Our demographic study showed high fertility rates and high levels of endogamy

in the present-day Maya populations from Quintana Roo here analyzed that are consistent with their general low genetic diversity. We propose that the genetic similarity among ancient and present-day Maya populations persists due to a strong sense of social cohesion and identity that impacts their marriage practices maintaining this cultural group isolated. These factors have constrained gene flow inside the Maya region and impeded the differentiation among the Maya. Discernment of genetic differentiation within the peninsula is constrained by the lack of sampling documentation in the literature.

Pre-Columbian Mayan society was characterized by a highly developed social structure and productive technology. The population size fluctuated geographically and temporally with a tendency to increase in the cities. The Maya were divided in autonomous political entities, maintaining multiple networks through commerce, warfare, and migration that influenced their economic, cultural, and demographic development (Renfrew 1975; Schele and Freidel 1990; Folan et al. 2000; Sierra et al. 2014).

Evidence of far-reaching commerce, exchange of elite individuals through marriage, and non-elite population mobility suggests a degree of genetic flow among Mayan populations in the Classic period (Bishop 1994; Teufel 2001; Scherer 2007; Price et al. 2010, 2013). By the end of the Classic period, a population decrease occurred in several regions of the Mayan territory (Ford 1991; Folan et al. 2000); however, the northern and coastal regions of the Yucatán Peninsula maintained extensive commerce and cultural exchange with other Mesoamerican regions (Thompson 2003; Cobos 2004, 2013; Cucina et al. 2004, 2008, 2015). By the Late Postclassic period, the main urban centers of the Yucatán Peninsula participated in a complex system of political alliances and maintained commerce via the coastal region that positively influenced demographic development (Andrews 1976; Ortega et al. 2015).

The Spanish presence in the New World began in the sixteenth century. Approximately 250,000 Europeans, mostly men, migrated to the region currently known as Mexico during the entire colonial period; however, from the beginning, only a small number of European women migrated to New Spain. War, overwork, and diseases brought by Spaniards drastically reduced the native population. Depopulation in the Yucatán Peninsula is calculated to be in the range of 40 to 51% since post-Classic times; there was also a massive disappearance of localities along the eastern coast, in addition to the concentration of a wandering population in the Quintana Roo

jungle (Nalda 1994). Mayan survivors were resettled in the Yucatán Peninsula, Guatemala, Honduras, and El Salvador (Simon and Grube 2008). Europeans were mainly located in cities and along trade routes. After the rapid decline of the indigenous populations, the Spanish began to bring African slaves to Mesoamerica in the first decades of the conquest. Some 200,000 to 500,000 African slaves were introduced into New Spain over three centuries. The indigenous found refuge in the “*haciendas*”, where biological and cultural admixture occurred among indigenous people, Africans, and Europeans (Carmack 2007). However, the European and African admixture was contributed mostly by men, rendering little effect on the mitochondrial genome.

During the colonial period, several Mayan populations underwent a depopulation process due to relocation into “*republicas de indios*” (Bracamontes and Sosa 2001). In the 19th century, social unrest and long-standing problems in the tenure of land caused a caste war in the Yucatán that lasted more than half a century, affecting the social and demographic dynamics throughout the region (González 1970; Reed 1976). Notwithstanding, most Mayan groups maintained a degree of commercial, political, and cultural relations with segments of Mexican and foreign societies (Sullivan 1991). The Maya have continuously inhabited an approximately 400,000 km<sup>2</sup> area for nearly 5,000 years despite the severe impositions subjected upon them in the past five centuries after the Spanish conquest (Messmacher et al. 1986). At present, the Maya account for approximately nine million people. Mayan is the second most widely spoken indigenous language in Mexico, after Nahuatl (INEGI 2004; Ruz 2006). The Maya linguistic family includes approximately 30 languages that originated ca. 3000 years B.C. from an ancient language spoken in Western Guatemala (Campbell 1997, 2007). In the Yucatán Peninsula, the most widely spoken Mayan language is Yucatec, with 859,607 speakers of whom 177,979 inhabit the state of

Quintana Roo. Other Mayan languages are spoken in Chiapas state: 556,720 people speak Tzeltal; 487,898 Tzotzil; 251,209 Chol; 55,442 Tojolabal; and 988 Lacandon (INEGI 2015).

The economy of the Mayan people is based on agriculture, primarily maize; henequen is economically and socially important, but cultivated only in Yucatán state. Also important in their current economic system is the elaboration of handicrafts. Social organization in contemporary Mayan culture is similar to most rural regions in Mexico, based largely on the nuclear family that is in charge of the festivities related to birth, baptism, marriage, and death. Political organization is based on municipalities, often ruled by local “caciques” under the formal control of state governments (Redfield and Villa 1967; Wilk 1991; Scheffler 1992). At present, the Maya share their territory with urban Mexican Spanish speakers (usually called mestizos) and foreigners from Lebanon, China, and Korea, as well as other alien indigenous groups such as the Yaqui relocated from Northwest Mexico (Ruz 2006; Sierra 2007; Gurri 2010). Despite these social influences, Mayan populations have maintained their cohesion and identity largely by endogamic practices over their extensive and ecologically diverse territory, all the while faced with linguistic diversity and the presence of hostile groups throughout their history (Boremanse, 1983; Wilk 1991; Herrera et al. 2007).

Despite the abundance of historical and cultural information about Mayan populations, the study of their genetic variation to understand current population genetic structure as it relates to history is very recent (Merriwether et al. 1997; González-Oliver et al. 2001; Peñaloza et al. 2007; Sandoval et al. 2009; Ochoa-Lugo et al. 2017). The mitochondrial genome is maternally inherited; it does not recombine during meiosis and exhibits high mutation rates, making such variation useful in discerning maternal ancestral relationships (Molnar et al. 2002; Eshleman et al. 2003). The mitochondrial DNA (mtDNA) of present-day American indigenous groups



belongs to one of five maternal haplogroups—A, B, C, D, and X—distinguished by restriction fragment length polymorphisms (RFLPs) or, in the case of haplogroup B, by a nine base pair (bp) deletion (Torroni et al. 1992, 1993; Brown et al. 1998; Smith et al. 1999). These haplogroups can be used to analyze the genetic relationships between populations that share recent common ancestry related to the peopling of the Americas (Kemp et al. 2005; Mata-Míguez et al. 2012).

The modern Mesoamerican indigenous populations show high frequency of haplogroup A, low frequencies of haplogroups B, C, and D, and the absence of X (Torroni et al. 1994; Peñaloza et al. 2007; Sandoval et al. 2009; Kemp et al. 2010; Mata-Míguez et al. 2012). Studies on ancient DNA specimens of pre-Columbian Mayans from Xcaret and Quintana Roo (González-Oliver et al. 2001) and Aztecs from Tlatelolco (Kemp et al. 2005; De la Cruz et al. 2008), Mexico, suggest that this distribution pattern of haplogroup frequencies has long existed in the region (Kemp et al. 2005).

In the present study, we analyzed mtDNA haplogroups in present-day and colonial Mayans as well as in one pre-Columbian individual from Quintana Roo, Mexico. We integrated this data with published mitochondrial haplogroup information of other present-day and ancient Mayan populations to evaluate the genetic diversity and differentiation among Mayan populations likely determined by historical, sociodemographic, and geographical factors. Furthermore, we elaborated upon a demographic analysis with present-day Mayans from two communities in Quintana Roo state to examine the influence of cultural factors such as marriage customs and their sense of cohesion and identity in the maintenance of mitochondrial haplogroup genetic patterns. If the modern Mayans exhibit an ancestral mitochondrial pattern, then it might

be sustained by the practice of marriage between members of the same or nearby communities and high fecundity rates for many generations.

## **Materials and Methods**

### *Samples.*

We initially visited municipal authorities and local communities to inform them of the research project with the assistance of bilingual translators. The field work to obtain the socio-demographic information was carried out in the communities of Santa María Poniente (19° 21'55.07" N; 88° 24'21.82" W), Laguna Kanah (19° 30'8.36" N; 88° 23'45.25" W) and Tulum (20° 12'41.65" N; 87° 27'54.71" W) in the municipalities of Felipe Carrillo Puerto and Tulum, Quintana Roo state, Mexico (Figure 1). A total of 124 randomly selected people were interviewed; from these, 75 adult individuals were selected that fulfilled the following inclusion criteria for the genetic study: recognized themselves as native Mayan; spoke and/or understood a Mayan language; were born locally from parents and grandparents from the same locality; practiced the customs and cultural traditions of the Maya and were not related through the maternal line.

Buccal swabs were obtained from the 75 selected individuals according to the ethical guidelines of the Helsinki Declaration established by UNESCO. All individuals gave informed consent and participated voluntarily in the research project.

A bone sample of an adult pre-Columbian Mayan individual from Xcaret archeological site, Quintana Roo (20° 34'51.91" N; 87° 7'11.17" W) was analyzed and added to the data of 24 Mayan individuals from the same site reported in a previous study (González-Oliver et al. 2001).

Bone remains (primarily ribs) from 24 Mayan individuals of the colonial period from the Xcaret archeological site, Quintana Roo, were also analyzed. These remains were excavated by María José Con in 1992 from a Spanish chapel built in the middle 16th century and active until the middle 17th century. A total of 136 male and female skeletons of different ages were recovered; the burial system followed a pattern similar to other colonial chapels according to the Catholic ritual imposed during the Spanish conquest (Márquez et al. 2002).

### ***Contamination Controls and DNA Extraction.***

Specific precautions were taken to minimize contamination and its occurrence was detected in order to ensure accurate assignment of haplogroups in the ancient samples, as reported in Shook et al. (2008) and Mata-Míguez et al. (2012). Sample preparation/cleaning, DNA extraction, and PCR reactions were performed in the ancient DNA laboratory at Facultad de Ciencias, UNAM, a physically isolated laboratory with double doors, restricted access, and head UV lights containing all of the equipment and reagents required specifically for ancient DNA research. The procedures in this laboratory were carried out in two dedicated laminar flow cabinets equipped with a 0.3 µm HEPA filter and UV radiation lamps (254 nm). One cabinet was used for sample surface decontamination and the other for DNA extraction and PCR reaction setup. The post-PCR laboratory was physically separate from the ancient DNA and modern DNA laboratories. These are cleaned regularly with Clorox bleach (10% sodium hypochlorite) and all procedures were carried out using new, sterilized, disposable tubes and filter pipette tips. All student movement between the aDNA and post-PCR laboratory were unidirectional every day. Other precautionary measures in the aDNA laboratory included wearing glasses and sterilized disposable coveralls, facemasks, and sterile hair and shoe covers. New surgical gloves were used

for each procedure and changed frequently. All reagents were molecular biology-grade and autoclaved ultrapure water was used (Gonzalez-Oliver et al. 2001). We ran controls to detect modern DNA contamination in the ancient samples using previously successful methods described in González-Oliver et al. (2001) and De la Cruz et al. (2008).

Bones were immersed in 6% sodium hypochlorite for 15 min, rinsed multiple times with sterilized ultrapure water, irradiated with 254 nm ultraviolet light (UV) for 10 min per side, then allowed to dry at 20 °C according to Shook et al. 2008 and Morales-Arce et al. 2017. We performed DNA extraction as described previously (González-Oliver et al. 2001) with slight modifications introduced by Kemp et al. (2005). A small sample fragment was ground to a fine powder and incubated with 1 ml of 5% sarkosyl, 0.5 M EDTA (pH 8.0), and proteinase K (10 mg/ml). At least two independent extractions were performed for each sample and the results were confirmed by multiple amplifications of each. Negative controls that included all reagents but no bone powder were carried out in parallel with the samples. Contemporary DNA was extracted from buccal swabs using a Qiagen QIAamp® DNA Blood Kit (Qiagen, Hilden, Germany) as described previously (González-Oliver et al. 2018) in the modern DNA laboratory.

The DNA extracted from 75 present-day Mayan and 25 ancient individuals was screened for the haplogroups A, B, C, and D using primers and PCR conditions described by Gonzalez-Oliver et al. (2018). The PCR amplifications were conducted in two Eppendorf Mastercycler® thermal cyclers (Eppendorf, Hamburg, Germany), one exclusively for the analysis of modern DNA and the other for ancient DNA. For haplogroup assignment in the ancient individuals, all four haplogroups were assessed in each individual.

***Statistical Analysis: Mitochondrial Haplogroup Frequencies.***

The mitochondrial haplogroup frequencies of the three Mayan populations examined in this study (pre-Columbian Xcaret, colonial Xcaret, and present-day Quintana Roo) were compared with 21 other ancient and present-day Mayan populations reported in the literature (Table 1). The genetic differentiation of the populations was examined using the Fisher's exact test available in RStudio 1.1.456 (RStudio 2018). We used Arlequin version 3.5.1.2. (Excoffier et al. 2005) to estimate haplogroup diversity ( $h$ ) based on the Tajima and Nei model (Tajima et al. 1984), genetic distance as pair-wise  $F_{ST}$  values, and the  $F_{ST}$  p values as well as their matrix of significance. Arlequin was also used to assess the temporal classification of Mayan populations as either ancient or present-day through an analysis of molecular variance (AMOVA). Populations with at least five sampled individuals were classified based on normalized haplogroup frequency data (correlations) by means of principal component analysis (PCA) using RStudio, 1.1.456. A weighted pair group method with arithmetic mean (WPGMA) dendrogram was constructed in R Statistical Software (R Core Team 2013) using the  $F_{ST}$  values.

### ***Demographic Analysis.***

A demographic study *in situ* to identify marriage customs and sense of cohesion and identity among modern Mayans was carried out in Laguna Kanah and Santa María Poniente in the Felipe Carrillo Puerto municipality; these are rural localities with low immigration accounting for a total population of 914 and 752 people, respectively (INEGI 2010). The Tulum locality was discarded from this study as an urban town with a total population of 18,233 people in 2010 and exhibiting high immigration related to the tourism industry in Tulum municipality (Daltabuit-Godás et al. 2006).

Two types of analysis were carried out to determine the integration of the Mayan communities from a demographic perspective. The reproductive histories of 95 women at least 10 years of age were analyzed. Forty-one women from Laguna Kanah and 54 from Santa María Poniente were interviewed to register their live born children to calculate specific fertility rates (SFR) by quinquennial group and total fertility rates (TFR) of the 1937–1969 and the 1979–2002 cohorts according to Livi-Bacci (1993). In the second analysis, a total of 368 individuals (186 from Laguna Kanah and 182 from Santa María Poniente) of both sexes, at least 10 years of age, were interviewed to obtain information about family formation and thereby to estimate endogamy percentages according to Otero (1990) and Kalmijn (1998).

## **Results**

### ***Mitochondrial DNA Haplogroup Frequencies and Genetic Diversity at Quintana Roo.***

The results of mitochondrial DNA haplogroup frequencies of the populations here analyzed (p-Xcaret, c-Xcat, and Q.R.1) showed the presence of only three haplogroups in pre-Columbian Xcaret with the following pattern: A (88%), C (8%), and B (4%); while in the present-day Maya from Quintana Roo, the four haplogroups are present with the following pattern: A (77%), C (11%), D (7%), and B (5%). These patterns are similar to colonial Xcaret: A (67%), C (17%), D (12%), and B (4%) (Figure 1, Table 1). The Fisher statistical test showed that these three populations are not significantly different ( $p > 0.05$ ; Table 2, Figure 1). Comparison of these three populations with other modern Mayan populations from Quintana Roo, Q.R.2 (Gorostiza et al. 2012) and Q.R.3 (González-Martín et al. 2015) showed that none of these samples are statistically different (Table 2).

Genetic diversity ( $h$ ) at Quintana Roo was higher in the pre-Columbian population of El Rey (p-Rey,  $h = 0.600$ ), the colonial Maya (c-Xcat,  $h = 0.533$ ), and the present-day Maya (Q.R.3,  $h = 0.537$ ) compared to the modern Maya (Q.R.1,  $h = 0.389$  and Q.R.2,  $h = 0.361$ ) and the pre-Columbian Maya (p-Xcaret,  $h = 0.227$ ). With the exception of the few samples gathered from El Rey, these differences do not seem to be related to sample size. The main difference in genetic diversity is in the content of haplogroup A, with lower values (60–67%) for the samples with higher diversity and larger values (77–88%) for the samples with lower diversity (Table 1, Figure 1). The high similarity among populations Q.R.1 and Q.R.2, could be due to the fact that both include individuals from Felipe Carrillo Puerto municipality and that Q.R.2 also includes individuals from the adjacent José María Morelos municipality. Conversely, Q.R.3 is different from both Q.R.1 and Q.R.2 populations; unfortunately, the authors (González-Martín et al. 2015) did not report the sampling localities of Q.R.3 to allow us to make further judgments.

### ***Principal Component Analysis (PCA).***

The three modern populations from Quintana Roo (Q.R.1, Q.R.2, and Q.R.3) appear highly similar, meanwhile the pre-Columbian Xcaret and colonial Xcaret appear slightly different; however, this difference is not significant at  $p \leq 0.05$  (Table 2, Figure 2). Conversely, in the PCA plot, the modern Yuc1 appear slightly different to modern Yuc2 and Yuc3 and the comparison of the three modern Mayan populations from Yucatán showed that Yuc1 is statistically different to Yuc2 and Yuc3 (Table 2). Unfortunately, sampling localities for Yuc2 and Yuc3 (Torróni et al. 1992; González-Martín et al. 2015) are not specified to make further inferences.

Broadly, the plot shows little difference between most Mayan populations, except for the modern Tojolabal from Chiapas and pre-Columbian Copán from Honduras that exhibit

substantial representation of haplogroups B and C, respectively (Figures 1-2). PCA indicates an apparent distinction between pre-Columbian and present-day populations, with colonial Xcaret being intermediate and closer to the modern populations (Figure 2).

The pre-Columbian populations appear subdivided into two groups, one of which includes Bonampak (p-Bon) and Xcaret (p-Xcaret) that overlap with the present-day Lacandon (Lac), the Chol, and the Yucatán sample Yuc1. All of these pre-Columbian and modern populations are distinctive in that they exhibit a higher representation (> 85%) of haplogroup A (Figures 1-2). The other group includes the remaining pre-Columbian populations that generally exhibit a higher content of haplogroups A and C. However, the number of individuals analyzed was small; therefore, this grouping could be an artifact resulting from sample size.

#### ***Weighted Pair-Group Method with Arithmetic Mean (WPGMA).***

The WPGMA dendrogram based on  $F_{ST}$  values exhibits two populations with the largest genetic distance: the modern Tojolabal and the pre-Columbian Copan (Figure 3, Supplementary Table S1-S2). The remaining populations are distributed into three clusters. Interestingly, the ancient and present-day Mayan populations from Quintana Roo (p-Xcaret, c-Xcat, Q.R.1, Q.R.2, and Q.R.3) are also distributed into three clusters. The colonial Maya is between two clusters, one of which contains only ancient populations and the other only modern populations. Yuc1 is in a different cluster from Yuc2 and Yuc3, in spite of their geographic proximity. The population Yuc1 appears closer to Q.R.1 and Q.R.2 (Figure 3, Tables 2, S1-S2), which can be explained by the fact that Yuc1 samples were collected in small localities from the Tizimin, Chamkon, and Chemax municipalities of Eastern Yucatán state close to Quintana Roo. Yuc2 and Yuc3 are



closer to Q.R.3; however, to understand these differences, it would be necessary to know the localities where Yuc2 and Yuc3 samples were collected.

### ***Analysis of Molecular Variance (AMOVA).***

We tested the apparent subdivision between the pre-Columbian and post-Columbian populations of the Maya through AMOVA. The largest and most significant variance (81.7%) was found within populations (Excoffier et al. 1992), 17.0% of variance was found among populations within groups, and only 1.3% of non-significant variance was identified among groups (Supplementary Table 3). These results suggest a genetic continuity between pre-Columbian and present-day populations.

### ***Demographic Study.***

The Mayan population from the two Quintana Roo localities here analyzed exhibits a high fertility rate (Table 3), particularly in the 20–29 year-old age range and for the 1937–1969 cohort that lived before the period after which contraception was available (Feldman et al. 2009; Juárez et al. 1989; Pullum et al. 1985). The 1970–2002 cohort also shows the higher fertility rate in the 20–29 age range, but with values lower than in the earlier cohort. The younger cohort also showed a tendency to experience final pregnancy at an earlier age of approximately 30–35 years. The global fertility rate for both localities was 5.13 children per woman in the 10–49 age range with the 1937–1969 cohort showing the highest global fertility rate of 6.31 children per woman compared to 3.00 children per woman for the 1970–2002 cohort.

The endogamy analysis showed that more than 70% of the individuals were born in their current locality and more than 90% were born in the same municipality (Supplementary Table

4). Considering the birthplace of married individuals, 59.6% had a couple from their own community (Santa María Poniente or Laguna Kanah) and 91.2% had a couple from their municipality (Felipe Carrillo Puerto) or from a close locality at the adjacent José María Morelos municipality. Consequently, our study indicates a high degree of endogamy in the present-day inhabitants of both localities. Our results also suggest that the modern Maya mostly inhabit the places where they were born and couple with members of their own community.

## **Discussion**

Ancestry informative markers, like mitochondrial haplogroups, have been widely used to compare populations at a continental scale; however, they are also informative of populations at a regional scale. Though the distribution pattern of haplogroup frequencies and the haplogroup diversity of populations are affected by sample size (Raff et al. 2011; Ragsdale et al. 2015), the actual haplogroup frequencies in a population are the result of other factors such as population growth rates, starting frequency of haplogroups in the region, population movements, endemic warfare, imperial expansion, the extensive admixture process that occurred during the past six centuries, drift, and other demographic processes. A similar pattern of haplogroup frequencies between populations might be due to shared common ancestry and/or admixture (Snow et al. 2011); however, it is not possible to distinguish between them based on haplogroup frequencies alone (Eshleman et al. 2003), which also makes the evaluation of drift more difficult (Kivisild 2015). Conversely, the study of mitochondrial haplotypes from ancient and modern populations allows for the identification of shared common ancestry from admixture (Raff et al. 2011; Snow et al. 2011; Ragsdale et al. 2015). The analysis of both ancient and modern populations that inhabited a defined geographic region serves as a means to distinguish genetic continuity or

discontinuity in that region and to understand demographic history. The haplogroup frequencies from Mesoamerican populations must be considered with caution when low sample sizes are analyzed. Lack of sampling representativity is expected to alter the haplogroup frequencies and heterogeneously overestimate genetic differentiation.

Although the frequency of mitochondrial haplogroups was influenced by the small sample size of some of the populations examined in this study, haplogroup A is clearly the most frequent in 18 out of 20 Mayan populations with at least five individuals analyzed. Usually, haplogroup A shows a high frequency in the range of 60 to 100% in modern populations with at least 50 individuals studied and in ancient populations with at least five. Conversely, haplogroup D shows the lowest frequency in present-day Mayan populations and it is absent in the majority of pre-Columbian populations.

After haplogroup A, haplogroup C is the most frequent in ancient and contemporary Mayans. Considering only present-day populations with at least 50 individuals analyzed, the majority exhibit mitochondrial haplogroups A and C, in this order, except Maya Campeche (Cam), Quintana Roo 3 (Q.R.3), Tojolabal (Toj), and Chiapas in which haplogroup B shows a higher frequency than C. The high frequency of haplogroup C in the ancient Maya from Copan, Honduras might be explained by the relatively high frequency of C in the Mayan populations and by the fact that the elite individuals analyzed by Merriwether et al. (1997) were probably consanguineously related. The presence of haplogroup C in modern Chol and Lacandon who inhabit isolated regions in Chiapas supports the ancient presence of C in this region.

Haplogroup B was absent in the pre-Columbian Mayans analyzed by Ochoa-Lugo et al. (2017); therefore, the authors proposed that the Mayan ancestors either did not carry this haplogroup or that it was lost by genetic drift. However, haplogroup B was detected in both pre-

Columbian and colonial Maya from Xcaret, Quintana Roo at 4%. These results show that haplogroup B is present at a low frequency in ancient Maya; consequently, in order to identify it, a larger number of individuals must be analyzed. Our results suggest that haplogroups A and C are predominant in Mayan populations. Conversely, other pre-Columbian populations from Teotihuacan, Estado de México (Álvarez-Sandoval et al. 2015), and colonial Mixtec from Teposcolula Yacundaa, Oaxaca (Warinner et al. 2012), as well as many modern populations from Central Mexico (González-Sobrino et al. 2016; González-Oliver et al. 2013, 2018) exhibit haplogroups A and B, in this order, as the most frequent.

Recently, the analysis of variations in autosomal single nucleotide polymorphisms (SNPs) suggested the presence of a “Mayan component” in Maya-speaking people from the Yucatán Peninsula and Chiapas, Mexico (Moreno-Estrada et al. 2014), as well as in Spanish-speaking people from Yucatán (Silva-Zolezzi et al. 2009). All of these results suggest that Mayan populations bear specific markers in the nuclear and mitochondrial genomes.

### ***Mitochondrial Haplogroups in Contemporary Mayan Populations from Chiapas.***

Two contemporary populations from Chiapas, Lacandon and Tojolabal, do not exhibit the common Mayan mitochondrial haplogroup pattern. The Lacandon (*hach winick*) show almost exclusively haplogroup A with 81 Lacandon individuals analyzed representing 13% of the 600 Lacandon (*hach t'an*) speakers (INEGI 2010). Therefore, the apparent absence of haplogroups B and D, as well as the low frequency of C, might be due to genetic drift resulting from small population size, isolation, and possibly non-random mating, all of which have likely increased such effects on haplogroup frequency.

The Lacandon inhabit the interior of the Chiapas rain-forest that acted as a geographic barrier for neighboring populations such as the Chol and Tzeltal (González Oliver et al. 2011). Conversely, small population size has favored endogamy. Marriage between relatives is allowed among the Lacandon and is a traditional custom of this group (Garay and Cobo 1975). These factors have been proposed to explain the low mtDNA genetic diversity in the Aleutian population from Alaska (Merriwether et al. 1995; Lorenz and Smith 1996; Rubicz et al. 2003, 2010).

The contemporary Tojolabal population shows an unusual mitochondrial haplogroup pattern with the absence of haplogroup C and higher frequency of B than A, whereas the neighboring populations such as the Tzeltal, Tzotzil, and Lacandon, exhibit high haplogroup A frequencies. The Tojolabal do not inhabit the innermost area of the jungle as do the Lacandon; they reside closer to urban towns in the Margaritas, Comitán, and Altamirano municipalities according to Cuadriello and Megchún (2006). Therefore, they have a greater geographic and social proximity to other surrounding populations and thus, greater probability of genetic admixture. Still, it is surprising to find a higher frequency of B than A and the complete absence of haplogroup C in the Tojolabal. Few populations show a higher frequency of haplogroup B than A as do the Mazahua from Central Mexico (Mizuno et al. 2014; Gonzalez-Oliver et al. 2018), the Cora and Huichol from Nayarit (Peñaloza et al. 2007; Kemp et al. 2010; González-Sobrino et al. 2016), and the Tarahumara from Chihuahua (Peñaloza et al. 2007; González-Sobrino et al. 2016). Information regarding the communities where the samples were collected and the inclusion criteria for the Tojolabal genetic study may help us to better understand these results.

### ***Mitochondrial Haplogroups in Contemporary Mayans from Yucatán.***

The modern Mayan population from Yucatán 1 (Yuc1) is significantly different from Yuc2 and Yuc3 and shows lower genetic diversity (0.274); this is probably due to the fact that individuals from Yuc1 belong to small and isolated localities. The isolation of Mayan localities in Yucatán state has been documented since 1930 (Redfield and Villa 1967); however, this situation has been changing with urbanization and the growth of the road network (Redfield 1970; Paré and Fraga 1994), making many indigenous people migrate to urban settlements that currently exhibit larger diversity of Amerindian mtDNA lineages in comparison with indigenous populations (González-Sobrino et al. 2016). The distinctiveness of sample Yuc1 with a high content of haplogroup A, similar to the Lacandon, supports a history of isolation and genetic drift.

### ***Mitochondrial Haplogroups in Ancient and Contemporary Mayans from Quintana Roo.***

The genetic diversity in Mayan populations from Xcaret was small during the pre-Columbian period; however, it increased in the colonial period while it decreased once again in the modern Mayan populations Q.R.1 and Q.R.2. but not in Q.R.3. Xcaret was an important Mayan settlement since the Classic period. It was a relevant commercial harbor that reached its maximum development during the post-Classic period and continued its maritime activity after the Spanish conquest (Con 2004; Márquez et al. 2002). During the colonial period, coastal Mayan populations experienced changes in lifestyle wherein an increase of settlements and population density occurred due to both Mayan and non-Mayan indigenous relocations at the beginning of this period (Márquez et al. 2006). These facts suggest gene flow between coastal Mayans with surrounding populations that arrived to the region. The subsequent decrease of genetic diversity in the present-day Mayan populations of Quintana Roo might be due to a long

period of isolation by armed conflicts during and after the colonial period (Reed 1976; Villalobos 2006; Bracamontes and Sosa 2004).

All colonial Mayan individuals analyzed in this study showed the presence of a Native American haplogroup. This result suggests that the Spanish and African presence in the region did not significantly influence the mitochondrial gene pool of the Maya, in agreement with the historical evidence of scarce migration of European women to the Mayan region (Borah 1954). The majority of Europeans were distributed in the colonial cities of Mexico and in smaller cities in central Mexico. To the southeast came a smaller number of Spaniards who settled in the cities, especially in Merida. The African presence in the Yucatán Peninsula was low due to the absence of mines and plantations. Spaniards interacted at varying degrees in different indigenous communities, with some populations experiencing less contact, as happened with Mayan populations (Caso, 2002).

The analysis of autosomal nuclear markers in 20 present-day Native populations from Mexico reflected Native American genetic ancestry within their genetic pool, despite the intense gene flow that occurred between populations during the colonial period that tended to homogenize their genetic structure (Moreno-Estrada et al. 2014).

The mitochondrial haplogroup frequencies in ancient and contemporary Mayans from Quintana Roo support a genetic continuity between Mayan populations from the Yucatán Peninsula, as proposed by González-Oliver et al. (2001, 2011, 2013) and also identified in other studies (González-Martín et al. 2015; Ochoa-Lugo et al. 2017). This genetic continuity is also supported by a specific “Mayan component” found in the nuclear genome of present-day Mayan populations (Moreno-Estrada et al. 2014).

### ***Mitochondrial Haplogroups in American Southwest and Mesoamerican Populations.***

The Cora and Huichol populations from Nayarit inhabiting regions between the geographic limit of Mesoamerica and the American Southwest showed a higher frequency of haplogroup B than A similar to the Tojolabal population; however, this similarity likely does not establish any genetic relationship. To clarify any genetic relationship, the detailed analysis of mitochondrial haplotypes will provide better evidence of genetic relationships between these populations than haplogroup frequency analysis alone. A study of mtDNA reported little genetic relationship between contemporary Mayans and the populations from North Mesoamerica (González-Martín et al. 2015).

The Mayan populations from the Yucatán Peninsula show few mitochondrial genetic differences among them in contrast with other populations from Mexico such as the Nahua, who are less-related genetically (González-Oliver et al. 2013). Another mtDNA study with modern Nahuatl populations revealed different origin as well as extensive admixture with the Spaniards (González-Sobrino et al. 2016). Conversely, homozygosity analysis to measure the genetic variation of present-day Mayan and Nahuatl populations showed that their genomes contain very low levels of homozygosity, indicating high variation at the nuclear level in both populations (Moreno-Estrada et al. 2014).

Generally, haplogroups A and B, in this order, are the most frequent in ancient and modern populations from Central Mexico (Sandoval et al., 2009; Kemp et al. 2005, 2010). However, haplogroup A is not always more frequent than B in this region; for example, the Mazahuan population from Estado de Mexico exhibits a lower frequency of haplogroup A than B (Mizuno et al. 2014; González-Oliver et al. 2018). Many Mayan populations exhibit a relatively high frequency of haplogroup C in the presence of a higher frequency of haplogroup A. Two



modern indigenous populations from Northern Mexico that inhabit the American Southwest cultural and geographical region, the Akimel O'otham from Sonora (Sandoval et al. 2009) and the Tarahumara from Chihuahua (Peñaloza et al. 2007; González-Sobrino et al. 2016), also exhibit high and intermediate frequencies of haplogroup C, respectively; however, in this case, it is accompanied by a high frequency of haplogroup B, similar to certain American Southwest populations (Kemp et al. 2010) that exhibit high frequencies of mitochondrial haplogroups B and C.

Haplogroup D is the least frequent or is absent in indigenous populations of the Otomanguean, Uto-Aztecan, and Mayan linguistic families (González-Oliver et al. 2013). Haplogroup X has only been identified in one Huichol individual from Nayarit and one Tarahumara from Chihuahua, Mexico (Peñaloza-Espinosa et al. 2007). This haplogroup has a restricted distribution among Amerindian populations of North America (Smith et al. 1999; Kemp et al. 2010), and Northern Mexico.

The distribution of the main haplogroups is not homogeneous in indigenous and urban populations. There is an apparent cline in which haplogroup B is more abundant toward the American Southwest, whereas haplogroup A is more abundant toward Southeast Mesoamerica (Kemp et al. 2010; González-Sobrino et al. 2016). The frequencies of mitochondrial haplogroups vary based on influences including evolutionary forces and local history, as well as economic, demographic, social, and cultural factors.

### ***Demographic Study.***

The global fertility rate of the two Mayan communities analyzed in this study (5.1 children per woman) is higher than the national fertility rate (2.2 children per woman) (CONAPO 2018) and

is similar to the rate of urban localities in countries with high fertility rates (Roser 2019). Despite recent sociodemographic changes in Mexico (CONAPO 2001, 20015), the Mayan populations examined maintain high fertility rates coupled with a remarkably high degree of endogamy (60%), whereas other Native American populations show a lower degree (up to 45%) of endogamous marriages (Kalmijn 1998). Although a decrease in endogamic processes in Mexico due to globalization was previously foreseen (Quilodrán 2008), such a decrease has not been detected in the Mayan communities of Quintana Roo. The high degree of endogamy detected in the Mayan communities is consistent with the low diversity values exhibited by modern Mayan populations Q.R.1 and Q.R.2.

Establishing families based on endogamous marriages is a practice maintained in Mayan populations for centuries, probably related to land possession (Restall, 2000). Although many Mayan people usually inhabit the place where they were born, at present many of them travel to nearby cities to work in the tourism industry; notwithstanding, they maintain their place of residence in their natal community and choose to couple mainly with members of their own community, keeping the traditional marriage customs of the group (Gaskins 2003). This custom of marriage between the Mayan communities throughout generations has maintained the distribution of mitochondrial haplogroups, which serves as a means of distinguishing groups in a defined region. The marriage customs identified in Santa María Poniente and Laguna Kanah, Quintana Roo, are probably common to many Mayan populations of the Yucatán Peninsula; this might contribute to the maintenance of an ancestral mitochondrial genetic pattern in most Mayan populations. As long as these traditional marriage customs continue to be practiced, the ancestral mitochondrial genetic pattern will be maintained.

The present and other demographic studies of the Mayan peninsula provide information of reproductive systems, population migration, cultural and social strategies for adaptation to a changing environment, as well as the demographic development of specific localities (Gurri 2010; Gurri and Ortega-Muñoz 2015). All of this information can be used by inhabitants of specific communities for the protection and practice of their own traditional customs and native languages in an increasingly complex social and political system. To the best of our knowledge, this is the first demographic study in native Mayan populations to involve mitochondrial genetic analysis.

## **Conclusions**

Our results show low mitochondrial genetic differentiation among most Mayan populations and support genetic continuity via maternal lines of inheritance with a common origin and a degree of continuous gene flow throughout their history.

The results of this study indicate high fertility rates and high levels of endogamy in present-day Mayan populations from Quintana Roo that are consistent with their low genetic diversity. We propose that the genetic similarity among ancient and present-day Mayan populations persists due to a strong sense of cohesion and identity that influences marriage practices that maintain their isolation. Gene flow has occurred mainly inside the Mayan region; even though a degree of gene flow with other neighboring non-Mayan populations could happen, it not a favored differentiation among the Maya.

Some Mayan populations exhibit large genetic differentiation that is likely related to geographical separation and social differences in culture and demography. In particular, the distinctive genetic differentiation of the indigenous Lacandon suggests a long history of isolation

and endogamy as well as a possible founder effect inside the Lacandonian rain-forest. The pattern of genetic differentiation within the peninsula cannot be further examined due to the lack of sampling documentation in the literature. The localities or communities where samples were collected must be specified to associate the genetic data with the demographic, historical, and cultural information. The proper documentation of the populations sampled in the publications will make various regional and large-scale studies more feasible in the future.

### **Acknowledgments**

We thank all the Maya people of Quintana Roo who voluntarily participated in this study. We are grateful to Mirna Ethel Canul Montañez, Karla González Cadeñanez and Javier Sánchez Llanes for their participation in the collection of the samples. We thank as well Miriam Jetzabel Bravo López for analysis one pre-Columbian individual. This study was supported by the grants PAPIIT. 2015, IN303415; 2017, IN403217, DGAPA. UNAM and Consejo Nacional de Ciencia y Tecnología. Proyecto Ciencia Básica, SEP-CONACyT, 2015. No. 252130.

*Received 7 March 2019; accepted 24 June 2019.*

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**Table 1. Haplogroup Frequencies from 24 Pre-Columbian (p), Colonial (c), and Present-Day Mayan Populations**

Population	Time period	Abbreviation <sup>a</sup>	(n)	A%	B%	C%	D%	<i>h</i> <sup>b</sup> +/- SD	Geographic location	References
Bonampak	580 - 800 AD	p-Bon	5	100.0	0.0	0.0	0.0	0.000 +/- 0.000	Bonampak, Chiapas	Ochoa-Lugo et al. 2017
Palenque	750 - 800 AD	p-Pal	9	55.6	0.0	33.3	11.1	0.639 +/- 0.126	Palenque, Chiapas	Ochoa-Lugo et al. 2017
<b>Xcaret</b>	<b>600 - 1521 AD</b>	<b>p-Xcaret</b>	<b>25</b>	<b>88.0</b>	<b>4.0</b>	<b>8.0</b>	<b>0.0</b>	<b>0.227 +/- 0.106</b>	<b>Xcaret, Quintana Roo</b>	<b>Gonzalez-Oliver et al. 2001; This study</b>
El Rey	1200 - 1500 AD	p-Rey	5	60.0	0.0	40.0	0.0	0.600 +/- 0.175	El Rey, Quintana Roo	Ochoa-Lugo et al. 2017
Comalcalco	700 - 900 AD	p-Com	8	50.0	0.0	37.5	12.5	0.679 +/- 0.122	Comalcalco, Tabasco	Ochoa-Lugo et al. 2017
Tenosique	700 - 900 AD	p-Ten	5	60.0	0.0	40.0	0.0	0.600 +/- 0.175	Tenosique, Tabasco	Ochoa-Lugo et al. 2017
Sueños de Oro	700 - 900 AD	p-Sue	2	0.0	0.0	50.0	50.0	NA	Sueños de Oro, Tabasco	Ochoa-Lugo et al. 2017
Calicanto	700 - 900 AD	p-Cal	1	100.0	0.0	0.0	0.0	NA	Calicanto, Jalapa, Tabasco	Ochoa-Lugo et al. 2017
Peje Lagarto	700 - 900 AD	p-Pej	1	0.0	0.0	100.0	0.0	NA	Peje Lagarto, Huimanguillo, Tabasco	Ochoa-Lugo et al. 2017
Xcambo	250 - 550 AD	p-Xca	2	100.0	0.0	0.0	0.0	NA	Xcambo, Yucatán	Ochoa-Lugo et al. 2017
Copán	700 - 1300 AD	p-Cop	9	0.0	0.0	88.9	11.1	0.222 +/- 0.166	Copán, Honduras	Merriwether et al. 1997
<b>Colonial</b>	<b>1550 - 1650 AD</b>	<b>c-Xcat</b>	<b>24</b>	<b>66.7</b>	<b>4.2</b>	<b>16.7</b>	<b>12.5</b>	<b>0.533 +/- 0.105</b>	<b>Xcaret, Quintana Roo</b>	<b>This study</b>
Campeche	Present-day	Cam	52	61.5	17.3	15.4	5.8	0.575 +/- 0.064	Campeche	Sandoval et al. 2009
Chol	Present-day	Chol	9	88.9	0.0	11.1	0.0	0.222 +/- 0.166	NA	Mizuno et al. 2017
Lacandon	Present-day	Lac	81	98.8	0.0	1.2	0.0	0.025 +/- 0.024	Chiapas	González Oliver et al. 2011

<b>Quintana Roo 1</b>	Present-day	<b>Q.R.1</b>	<b>75</b>	<b>77.3</b>	<b>5.3</b>	<b>10.7</b>	<b>6.7</b>	<b>0.389 +/- 0.067</b>	<b>Quintana Roo</b>	<b>This study</b>
Quintana Roo 2	Present-day	Q.R.2	44	79.5	6.8	9.1	4.5	0.361 +/- 0.088	Quintana Roo	Gorostiza et al. 2012
Quintana Roo 3	Present-day	Q.R.3	74	64.9	16.2	14.9	4.1	0.537 +/- 0.057	Quintana Roo	González-Martín et al. 2015
Tojolabal	Present-day	Toj	74	25.7	58.1	0.0	16.2	0.578 +/- 0.043	Chiapas	González-Martín et al. 2015
Tzeltal	Present-day	Tze	35	60.0	14.3	14.3	11.4	0.603 +/- 0.079	Chiapas	Peñaloza et al. 2007
Tzotzil	Present-day	Tzo	87	41.4	24.1	25.3	9.2	0.706 +/- 0.023	Chiapas	González-Martín et al. 2015
Yucatán 1	Present-day	Yuc1	125	84.8	4.8	8.0	2.4	0.274 +/- 0.051	Yucatán	González Oliver et al. 2011
Yucatán 2	Present-day	Yuc2	26	53.8	23.1	15.4	7.7	0.652 +/- 0.075	Yucatán	Schurr et al.1990; Torroni et al. 1992
Yucatán 3	Present-day	Yuc3	40	65.0	15.0	12.5	7.5	0.547 +/- 0.080	Yucatán	González-Martín et al. 2015

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Data generated for this study in bold.

<sup>a</sup>Abbreviations used in the Figures and Tables.

<sup>b</sup>Haplogroup diversity based in A, B, C and D, and the standard deviation (SD).

NA = Not available.

**Table 2. Probability Values and Statistical Significance (+) of Fisher Test**

Abbreviation	p-Bon	p-Pal	<b>p-Xcaret</b>	p-Rey	p-Com	p-Ten	p-Sue	p-Cal	p-Pej	p-Xca	p-Cop	<b>c-Xcat</b>	Cam	Chol	Lac	<b>Q.R.1</b>	Q.R.2	Q.R.3	Toj	Tze	Tzo	Yuc1	Yuc2	Yuc3
p-Bon		+			+		+				+								+		+		+	
p-Pal	0.014										+				+				+			+		
<b>p-Xcaret</b>	<b>0.694</b>	<b>0.061</b>			+		+				+				+				+		+		+	
p-Rey	0.058	1.000	<b>0.272</b>								+				+				+					
p-Com	0.010	1.000	<b>0.042</b>	1.000							+				+				+			+		
p-Ten	0.058	1.000	<b>0.272</b>	1.000	1.000						+				+				+					
p-Sue	0.008	0.273	<b>0.028</b>	0.571	0.644	0.571									+			+	+			+		
p-Cal	1.000	1.000	<b>1.000</b>	1.000	1.000	1.000	1.000																	
p-Pej	0.067	0.500	<b>0.154</b>	1.000	1.000	1.000	1.000	1.000							+				+					
p-Xca	1.000	1.000	<b>1.000</b>	1.000	0.600	1.000	0.333	1.000	0.333		+													
p-Cop	<0.001	0.029	<b>&lt;0.001</b>	0.028	0.036	0.028	0.346	0.200	1.000	0.018		+	+	+	+	+	+	+	+	+	+	+	+	+
<b>c-Xcat</b>	<b>0.104</b>	<b>0.797</b>	<b>0.206</b>	<b>0.657</b>	<b>0.696</b>	<b>0.657</b>	<b>0.188</b>	<b>1.000</b>	<b>0.360</b>	<b>1.000</b>	<b>&lt;0.001</b>				+				+					
Cam	0.056	0.259	<b>0.122</b>	0.544	0.223	0.544	0.105	1.000	0.396	1.000	<0.001	<b>0.373</b>			+				+					
Chol	0.391	0.294	<b>1.000</b>	0.506	0.164	0.506	0.054	1.000	0.200	1.000	<0.001	<b>0.761</b>	0.666						+					
Lac	1.000	<0.001	<b>0.040</b>	0.008	<0.001	0.008	0.001	1.000	0.024	1.000	<0.001	<b>&lt;0.001</b>	<0.001	0.191		+	+	+	+	+	+	+	+	+
<b>Q.R.1</b>	<b>0.435</b>	<b>0.172</b>	<b>0.758</b>	<b>0.265</b>	<b>0.128</b>	<b>0.265</b>	<b>0.058</b>	<b>1.000</b>	<b>0.237</b>	<b>1.000</b>	<b>&lt;0.001</b>	<b>0.603</b>	<b>0.106</b>	<b>1.000</b>	<b>&lt;0.001</b>				+		+			
Q.R.2	0.568	0.151	<b>0.886</b>	0.231	0.090	0.231	0.053	1.000	0.222	1.000	<0.001	<b>0.487</b>	0.262	1.000	<0.001	<b>1.000</b>			+		+			
Q.R.3	0.085	0.179	<b>0.184</b>	0.474	0.131	0.474	0.036	1.000	0.360	1.000	<0.001	<b>0.237</b>	0.955	0.742	<0.001	<b>0.111</b>	0.330		+		+			
Toj	<0.001	<0.001	<b>&lt;0.001</b>	<0.001	<0.001	<0.001	0.005	0.427	0.013	0.097	<0.001	<b>&lt;0.001</b>	<0.001	<0.001	<0.001	<b>&lt;0.001</b>	<0.001	<0.001		+	+	+	+	+
Tze	0.053	0.542	<b>0.109</b>	0.612	0.446	0.612	0.180	1.000	0.417	1.000	<0.001	<b>0.718</b>	0.832	0.536	<0.001	<b>0.217</b>	0.279	0.540	<0.001			+		
Tzo	0.001	0.362	<b>0.001</b>	0.681	0.401	0.6810	0.108	1.000	0.584	0.581	<0.001	<b>0.055</b>	0.182	0.083	<0.001	<b>&lt;0.001</b>	<0.001	0.035	<0.001	0.242		+		
Yuc1	0.850	0.035	<b>1.000</b>	0.131	0.020	0.131	0.011	1.000	0.158	1.000	<0.001	<b>0.047</b>	0.004	0.778	0.006	<b>0.402</b>	0.746	0.007	<0.001	0.006	<0.001		+	+
Yuc2	0.019	0.360	<b>0.044</b>	0.544	0.294	0.544	0.114	1.000	0.259	1.000	<0.001	<b>0.294</b>	0.883	0.324	<0.001	<b>0.041</b>	0.104	0.654	<0.001	0.853	0.729	0.002		
Yuc3	0.114	0.276	<b>0.229</b>	0.524	0.208	0.524	0.098	1.000	0.366	1.000	<0.001	<b>0.548</b>	0.954	0.717	<0.001	<b>0.318</b>	0.518	0.904	<0.001	0.961	0.122	0.022	0.832	

Populations analyzed in this study are in bold.

Abbreviations were described on Table 1.

Significance level,  $p \leq 0.05$

**Table 3. Fertility Rates in Present-Day Maya Individuals from Quintana Roo**

Age interval (years)	Number of children born alive		Total
	Cohort		
	1937 - 1969	1970 - 2002	
10 - 14	5	1	6
15 - 19	39	21	60
20 - 24	67	32	99
25 - 29	66	33	99
30 - 34	52	10	62
35 - 39	26	1	27
40 - 44	13	0	13
45 - 49	3	0	3
Total	271	98	369

Age interval (years)	Age-specific fertility rates		Total
	Cohort		
	1937 - 1969	1970 - 2002	
10 - 14	0.02	0.00	0.01
15 - 19	0.18	0.10	0.14
20 - 24	0.31	0.18	0.25
25 - 29	0.31	0.21	0.27
30 - 34	0.24	0.09	0.19
35 - 39	0.12	0.01	0.09
40 - 44	0.06	0.00	0.05
45 - 49	0.02	0.00	0.02
Total fertility rate	6.31	3.00	5.13

**Supplementary Table S1. Values of Pair-wise Genetic Distances (Fst) between Populations with at Least Five Individuals**

Abbreviation	p-Bon	p-Pal	<b>p-Xcaret</b>	p-Rey	p-Com	p-Ten	p-Cop	<b>c-Xcat</b>	Cam	Chol	Lac	<b>Q.R.1</b>	<b>Q.R.2</b>	<b>Q.R.3</b>	Toj	Tze	Tzo	Yuc1	Yuc2	Yuc3
p-Bon	0.000																			
p-Pal	0.362	0.000																		
<b>p-Xcaret</b>	<b>0.020</b>	<b>0.168</b>	<b>0.000</b>																	
p-Rey	0.499	-0.164	<b>0.171</b>	0.000																
p-Com	0.431	-0.129	<b>0.228</b>	-0.166	0.000															
p-Ten	0.499	-0.164	<b>0.171</b>	-0.250	-0.166	0.000														
p-Cop	0.914	0.377	<b>0.757</b>	0.419	0.321	0.419	0.000													
<b>c-Xcat</b>	<b>0.148</b>	<b>-0.040</b>	<b>0.048</b>	<b>-0.053</b>	<b>-0.019</b>	<b>-0.053</b>	<b>0.498</b>	0.000												
Cam	0.151	-0.006	<b>0.069</b>	-0.029	0.010	-0.029	0.456	-0.009	0.000											
Chol	0.052	0.082	<b>-0.075</b>	0.078	0.133	0.078	0.753	0.001	0.038	0.000										
Lac	-0.036	0.645	<b>0.090</b>	0.735	0.708	0.735	0.954	0.331	0.278	0.143	0.000									
<b>Q.R.1</b>	<b>0.060</b>	<b>0.060</b>	<b>-0.003</b>	<b>0.046</b>	<b>0.104</b>	<b>0.046</b>	<b>0.611</b>	<b>-0.006</b>	<b>0.028</b>	<b>-0.036</b>	<b>0.125</b>	<b>0.000</b>								
<b>Q.R.2</b>	<b>0.053</b>	<b>0.081</b>	<b>-0.015</b>	<b>0.068</b>	<b>0.128</b>	<b>0.068</b>	<b>0.645</b>	<b>0.003</b>	<b>0.028</b>	<b>-0.046</b>	<b>0.136</b>	<b>-0.016</b>	<b>0.000</b>							
<b>Q.R.3</b>	<b>0.129</b>	<b>0.005</b>	<b>0.052</b>	<b>-0.021</b>	<b>0.027</b>	<b>-0.021</b>	<b>0.481</b>	<b>-0.007</b>	<b>-0.015</b>	<b>0.023</b>	<b>0.223</b>	<b>0.018</b>	<b>0.017</b>	<b>0.000</b>						
Toj	0.471	0.286	<b>0.412</b>	0.309	0.280	0.309	0.510	0.287	0.212	0.395	0.607	<b>0.364</b>	<b>0.359</b>	<b>0.240</b>	0.000					
Tze	0.163	-0.022	<b>0.078</b>	-0.033	-0.008	-0.033	0.448	-0.022	-0.020	0.040	0.328	<b>0.024</b>	<b>0.028</b>	<b>-0.014</b>	0.208	0.000				
Tzo	0.257	-0.000	<b>0.181</b>	-0.018	-0.010	-0.018	0.294	0.054	0.027	0.148	0.371	<b>0.134</b>	<b>0.135</b>	<b>0.045</b>	0.130	0.022	0.000			
Yuc1	0.025	0.174	<b>-0.021</b>	0.159	0.235	0.159	0.714	0.053	0.084	-0.052	0.062	<b>0.002</b>	<b>-0.009</b>	<b>0.063</b>	0.457	0.092	0.218	0.000		
Yuc2	0.225	-0.008	<b>0.127</b>	-0.024	-0.001	-0.024	0.423	0.006	-0.021	0.085	0.439	<b>0.067</b>	<b>0.068</b>	<b>-0.010</b>	0.145	-0.024	-0.006	0.153	0.000	
Yuc3	0.134	-0.000	<b>0.050</b>	-0.017	0.022	-0.017	0.494	-0.019	-0.020	0.018	0.273	<b>0.009</b>	<b>0.009</b>	<b>-0.018</b>	0.232	-0.024	0.042	0.060	-0.015	0.000

The present-day and ancient populations from Quintana Roo are indicated in bold.

**Supplementary Table S2. Probability Values of *Fst* and Statistical Matrix for 20 Mayan Populations with at Least Five Individuals**

Abbreviation	p-Bon	p-Pal	p-Xcaret	p-Rey	p-Com	p-Ten	p-Cop	c-Xcat	Cam	Chol	Lac	Q.R.1	Q.R.2	Q.R.3	Toj	Tze	Tzo	Yuc1	Yuc2	Yuc3
p-Bon		+		+	+	+	+	+	+					+	+	+	+		+	+
p-Pal	0.009		+					+			+				+			+		
<b>p-Xcaret</b>	0.333	0.018			+			+	+		+				+		+		+	
p-Rey	0.045	0.991	0.063					+			+				+					
p-Com	<0.001	0.991	0.027	0.991				+			+	+	+		+			+		
p-Ten	0.045	0.991	0.108	0.991	0.991			+			+				+					
p-Cop	<0.001	<0.001	<0.001	0.036	0.027	0.009		+	+	+	+	+	+	+	+	+	+	+	+	+
<b>c-Xcat</b>	0.0180	0.676	<b>0.171</b>	0.576	0.532	0.667	<0.001				+				+		+			
Cam	0.018	0.477	0.009	0.496	0.324	0.450	<0.001	0.586			+				+		+	+		
Chol	0.441	0.225	0.991	0.586	0.108	0.594	<0.001	0.387	0.189						+		+			
Lac	0.991	<0.001	0.045	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.234		+	+	+	+	+	+	+	+	+
<b>Q.R.1</b>	0.108	0.162	<b>0.504</b>	0.153	0.027	0.108	<0.001	<b>0.540</b>	0.081	0.739	<0.001				+		+		+	
<b>Q.R.2</b>	0.126	0.090	<b>0.685</b>	0.162	0.018	0.180	<0.001	<b>0.351</b>	0.072	0.838	<0.001	<b>0.900</b>			+		+		+	
<b>Q.R.3</b>	0.036	0.369	<b>0.054</b>	0.504	0.243	0.468	<0.001	<b>0.568</b>	0.946	0.306	<0.001	<b>0.081</b>	<b>0.135</b>		+		+	+		
Toj	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001		+	+	+	+	+
Tze	0.009	0.504	0.063	0.568	0.486	0.559	<0.001	0.793	0.865	0.315	<0.001	0.090	0.117	0.775	<0.001			+		
Tzo	<0.001	0.369	<0.001	0.568	0.504	0.468	<0.001	0.009	0.036	0.018	<0.001	<0.001	<0.001	<0.001	<0.001	0.081		+		+
Yuc1	0.216	<0.001	0.946	0.090	0.009	0.072	<0.001	0.054	<0.001	0.991	<0.001	0.297	0.631	<0.001	<0.001	0.009	<0.001		+	+
Yuc2	<0.001	0.369	<0.001	0.586	0.387	0.622	<0.001	0.369	0.838	0.090	<0.001	<0.001	0.036	0.577	<0.001	0.748	0.405	<0.001		
Yuc3	0.009	0.297	0.072	0.496	0.324	0.522	<0.001	0.667	0.973	0.297	<0.001	0.198	0.189	0.964	<0.001	0.928	0.027	0.018	0.667	

Number of permutations: 110.

+ symbol indicates statistical significance at level  $p \leq 0.05$ .



**Supplementary Table S3. Analysis of Molecular Variance with 1023 Permutations**

Groups	Variation level	Variation percentage	Fixation index	p value
<p><b>pre-Columbian</b> (p-Bon, p-Pal, p-Xcaret, p-Rey, p-Com, p-Ten, p-Cop)</p> <p><b>vs</b></p> <p><b>Present-day</b> (Cam, Chol, Lac, Q.R.1, Q.R.2, Q.R.3, Toj, Tze, Tzo, Yuc1, Yuc2, Yuc3)</p>	Within populations	81.7	0.183	<0.001
	Among populations within groups	17.0	0.173	<0.001
	Among groups	1.3	0.013	0.236

Significance level  $p \leq 0.05$

**Supplementary Table S4. Origins Localities of the Maya Individuals Interviewed for the Endogamy Analysis**

<b>Place of birth</b>	<b>Locality</b>	<b>State/Country</b>	<b>Laguna Kanah % (n)</b>	<b>Santa María Poniente % (n)</b>
Belice, Belice	Unknown	Belice	0.54 (1)	-
Chan Santa Cruz	Felipe Carrillo Puerto	Quintana Roo	0.54 (1)	1.10 (2)
Chan Chen Chuc	Felipe Carrillo Puerto	Quintana Roo	-	0.55 (1)
Chanchen	Felipe Carrillo Puerto	Quintana Roo	0.54 (1)	0.55 (1)
Chanka De Repente	Felipe Carrillo Puerto	Quintana Roo	-	1.10 (2)
Chetumal	Othón P. Blanco	Quintana Roo	1.08 (2)	-
Chiapas	Unknown	Chiapas	0.54 (1)	-
Chunchumil	Maxcanú	Yucatán	0.54 (1)	-
Chunhuas	Felipe Carrillo Puerto	Quintana Roo	2.69 (5)	-
Chunhuhub	José María Morelos	Quintana Roo	0.54 (1)	-
Dzula	Felipe Carrillo Puerto	Quintana Roo	3.23 (6)	-
Felipe Carrillo Puerto	Felipe Carrillo Puerto	Quintana Roo	3.76 (7)	2.20 (4)
Ix-Mul	Chikindzonot	Yucatán	0.54 (1)	-
Laguna Kanah	Felipe Carrillo Puerto	Quintana Roo	75.81 (141)	1.10 (2)
Naranjal Poniente	Felipe Carrillo Puerto	Quintana Roo	0.54 (1)	1.10 (2)
Playa del Carmen	Solidaridad	Quintana Roo	1.08 (2)	-
Santa María Poniente	Felipe Carrillo Puerto	Quintana Roo	-	89.56 (163)
Señor	Felipe Carrillo Puerto	Quintana Roo	0.54 (1)	-
Tecomate	Francisco Z. Mena	Puebla	0.54 (1)	-
Tepich	Felipe Carrillo Puerto	Quintana Roo	0.54 (1)	-
Trapich	Unknown	Unknown	-	0.55 (1)
Tizimín	Tizimín	Yucatán	0.54 (1)	-
Tulum	Tulum	Quintana Roo	-	0.55 (1)
X-Hazil Sur	Felipe Carrillo Puerto	Quintana Roo	-	0.55 (1)
X-Muluc	Felipe Carrillo Puerto	Quintana Roo	2.15 (4)	-
X-Piehl	Felipe Carrillo Puerto	Quintana Roo	0.54 (1)	-
Yoactun	Felipe Carrillo Puerto	Quintana Roo	2.15 (4)	-
Yodzonot	Felipe Carrillo Puerto	Quintana Roo	-	0.55 (1)
Not available	Not available	Not available	1.08 (2)	0.55 (1)
Total			100.00 (186)	100 (182)

Figure 1.

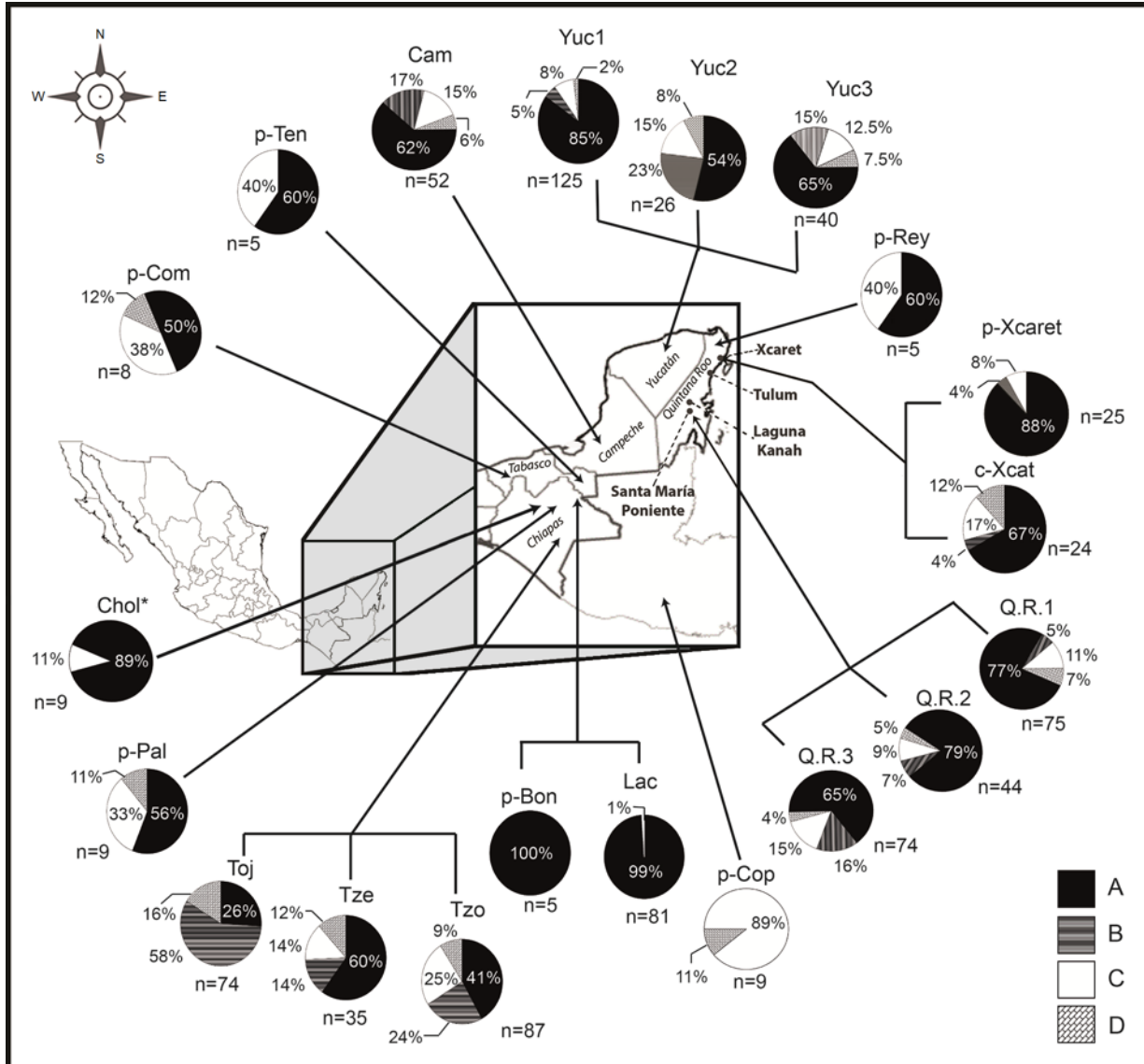
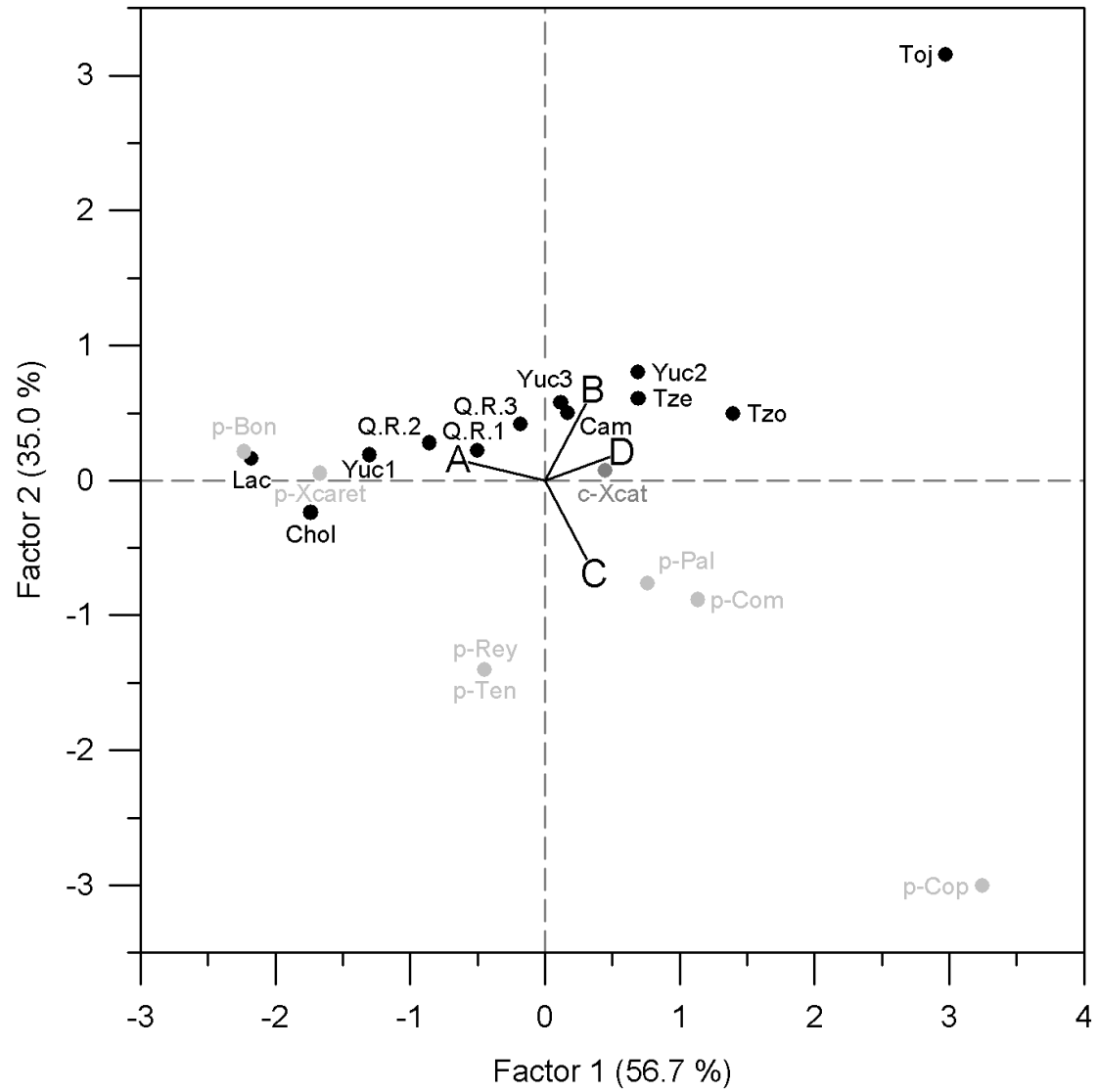
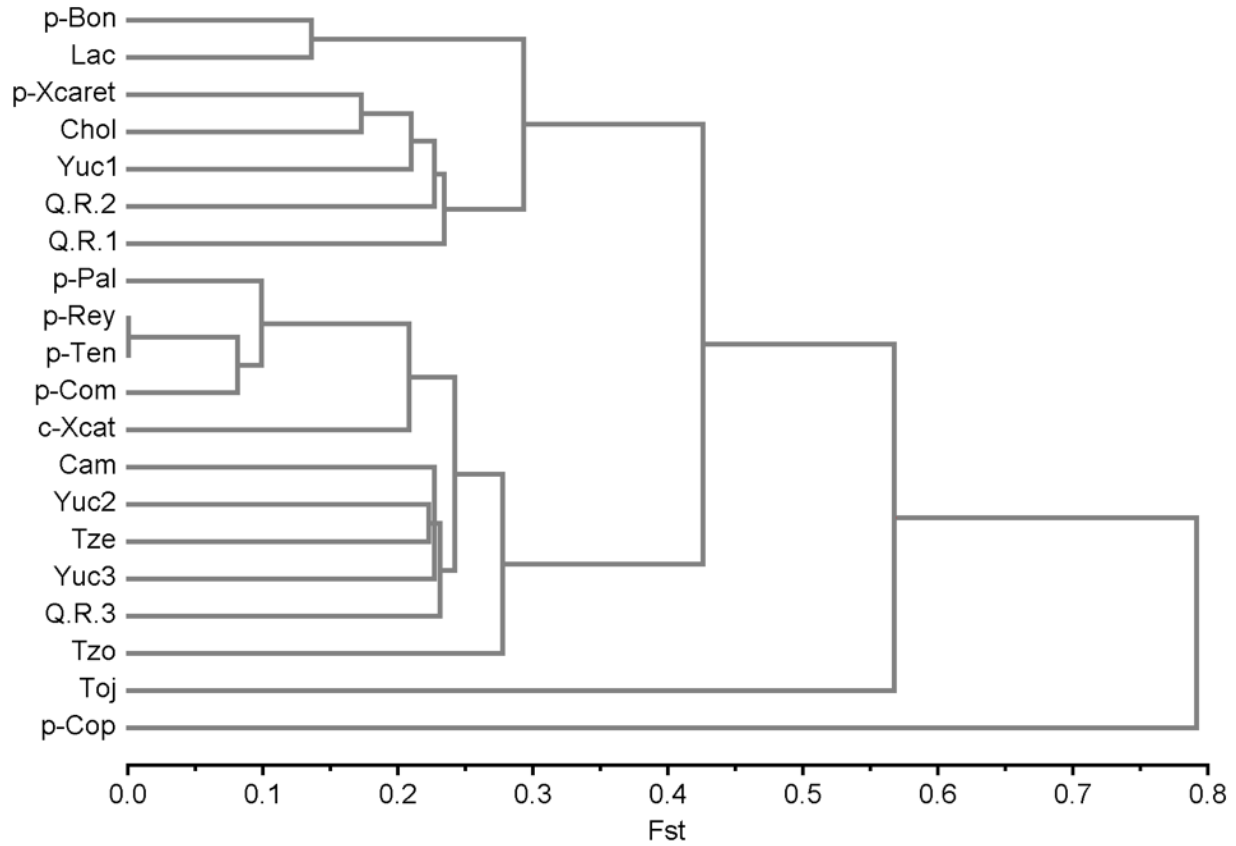


Figure 2.



**Figure 3.**



## Figure Captions

**Figure 1.** Map shows the mitochondrial haplogroup frequencies and approximate geographic locations of 20 pre-Columbian (p), colonial (c) and present-day Mayan populations.

Abbreviations are defined in Table 1. Original source of the Chol\* population data does not indicate geographic location; we assume it is from Chiapas. The map also shows the localities of ancient and present-day Maya analyzed in this study.

**Figure 2.** Principal component analysis based on mitochondrial haplogroup frequencies of 20 Maya populations. Pre-Columbian populations are indicated in light gray, the colonial population is indicated in dark gray, and present-day populations as well as haplogroup vectors are indicated in black.

**Figure 3.** Weighted pair group method with arithmetic mean dendrogram based on pair-wise genetic distance values ( $F_{st}$ ) between populations with at least five individuals sampled.