

History of Human Population Genetics of Central America

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ABSTRACT. To frame and evaluate contributions to the development of human population genetics studies in Central America we summarize, classify, and compare the most relevant literature published since the beginning of the twentieth century. The development of human population genetics in Central America is a continuation of studies of morphological variation. From the 1920s to 1960s, emphasis was placed on morphology and the biochemical differences of local indigenous populations. From the 1970s to the 1990s, new serological discoveries made microevolutionary studies possible among indigenous and Afro-Caribbean populations. The molecular genetics investigations that were initiated in the 1990s started a new era of the examination of novel evolutionary questions in the twenty-first century. During this period, use of a wide variety of informative markers enabled the unraveling of demographic histories of national and indigenous populations. Despite steady development of population genetics in Central America over the past century, differences exist in the quantity and quality of investigations in this geographic area. Costa Rica, Nicaragua, and Panama are the most frequently studied countries in comparison with Guatemala, Honduras, Belize, and El Salvador. It is hoped that future research improves this disparity.

RESUMEN. Con el propósito de organizar y evaluar las contribuciones de la genética de poblaciones en humanos en América Central, hemos clasificado, resumido, y comparado la literatura más relevante que se ha publicado sobre este tema desde inicios del siglo XX. El desarrollo de la genética de poblaciones en América Central deviene como la continuación de los estudios de variación morfológica y bioquímica que se desarrollaron entre las décadas de 1920 y 1960 sobre poblaciones indígenas locales. Entre las décadas de 1970 y 1990 los nuevos descubrimientos en los estudios serológicos dieron paso a la investigación microevolutiva entre poblaciones indígenas y afrocaribeñas. Las investigaciones en genética molecular que se iniciaron en la década de 1990 en América Central fueron la antesala para plantear en el siglo XXI nuevas preguntas sobre aspectos evolutivos. Durante este último período, se han utilizado una amplia variedad de marcadores informativos que han permitido revelar las historias demográficas de poblaciones nacionales e indígenas. No obstante, a pesar del rápido aumento de publicaciones en los últimos 15 años en América Central es notable la diferencia en la cantidad y la calidad de las investigaciones en esta área geográfica. Costa Rica, Nicaragua y Panamá son los países que cuentan con más investigaciones en comparación con Guatemala, Honduras, Belice y El Salvador. Se espera que futuras investigaciones corrijan esta disparidad.

RESUMO. Visando reconhecer e avaliar as contribuições ao desenvolvimento dos estudos de genética de populações humanas na América Central, fazemos um resumo, classificamos e comparamos a literatura mais pertinente publicada desde o início do século XX. O desenvolvimento da genética de populações humanas na América Central é uma continuação de estudos da variação morfológica e bioquímica das populações indígenas locais que foram desenvolvidas entre as décadas de 1920 e 1960. Entre 1970 e 1990, novos descobrimentos sorológicos fizeram possíveis estudos microevolutivos entre populações indígenas e afro-caribenhas. As pesquisas genético-moleculares que se iniciaram na década dos 90 na América Central iniciaram uma nova era de pesquisas com novas perguntas evolutivas no século 21. Durante este período, o uso de uma ampla variedade de marcadores informativos possibilitou deslindar as histórias demográficas de populações indígenas e nacionais.

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Contudo, apesar do desenvolvimento estável da genética de populações na América Central durante os últimos 15 anos, existem diferenças na quantidade e qualidade de pesquisas dentro desta área geográfica. Costa Rica, Nicarágua e Panamá são os países mais estudados em comparação a Guatemala, Honduras, Belize e El Salvador. Espera-se que futuros estudos corrijam esta disparidade.

INTRODUCTION

The Central American Isthmus, a swath of land between Mexico and Colombia bordered by the Caribbean Sea to the east and the Pacific Ocean to the west, consists of seven countries: Panama, Costa Rica, Nicaragua, El Salvador, Honduras, Guatemala, and Belize. This region has important implications for biogeography, oceanography, animal migration, and the colonization of North and South American plants, as well as the interaction and settlement of human populations since the late Pleistocene. The latter being an area of research that has fascinated generations of investigators over the last 100 years, since early classification studies of local ethnic groups by physical anthropologists and other specialists (Schultz 1926; Willey and Sabloff 1974; Janzen 1983; Webb 1997; Cooke 2005). Despite this early interest, research centered on evolutionary questions began late in relation to other regions of the Americas. The first investigations to emerge—descriptions and phenotypic comparisons of anthropometrics and biochemistry (ABO blood-system)—began in the first half of the twentieth century in most Central American countries. However, it was not until after the 1970s that a significant number of studies centering on the population genetics of indigenous groups in Costa Rica and Panama were initiated. Technological advances of the second half of the twentieth century, including polymerase chain reaction (PCR), DNA sequencing, and the speed and capacity of microprocessors (Jobling et al. 2014), opened new avenues in the 1980s for anthropological studies. These studies included research on evolutionary relationships between *Homo sapiens* and other hominins, modern human origins, migrations and major demographic expansions out of Africa, and micro evolutionary processes of small-geographic-scale populations. Further technological advances of the twenty-first century have made it possible to study variation across the genome with methods like microarray hybridization and next-generation sequencing (Jobling et al., 2003; Crawford, 2007).

The objective of population genetics is to describe the distribution of allele frequencies in order to explain evolutionary phenomena of populations; that is, reproductive groups that share a geographic space. Changes in gene frequencies are influenced by mutation, natural selection, genetic flow, and genetic drift (Hartl, 2000). In humans, population genetics contextualizes the non-random distribution of alleles caused by social practices and the effect of constructed niches (Fix, 1999; Laland et al., 2010). The effects of geographic isolation on the distribution of certain genes, the consequences of population admixture, and the possible effects on health are among some of the aspects that have

been studied by researchers in Central America. However, until now an all-inclusive genetic history of the human population of the region has not been attempted. The objective of this chapter is to comprehensively review the development of the field of population genetics in Central America from its inception during the mid-twentieth century to the present. However, there are limitations to our ability to present a panoramic view of Central American population genetics due to the fact that a disproportionate number of studies have been carried out in Costa Rica in comparison to other Central American countries. Additionally, we discuss only investigations based on those molecular markers commonly used for population genetics studies. Although other types of research provide alternative information on population dynamics (such as isonomy-based studies), they are not reviewed in this chapter.

We have organized the literature chronologically to identify and synthesize three major trends in research: (a) studies on morphological traits focusing on human classification in Central America, (b) studies on microevolution and phylogenetic relationships based on blood group polymorphisms, and (c) studies on molecular genetics that highlight the population's genetic history and the impact of admixture.

TYPOLOGICAL CLASSIFICATIONS

Prior to the development of population genetics, research in Central America followed world historical trends, from the emphasis on classification and description of human types to modern studies based on genomics. These trends reflect shifts in the types of questions being investigated by researchers, developments in science and technology, and variations in the intellectual environment over time (Mielke et al., 2006).

In Central America, biological anthropologists, ethnographers, and archaeologists have long been interested in studying the history of human diversity in the region; however, pre-Columbian and post-Colonial population histories have been largely deduced by diffusionist models (e.g., Coe, 1960; Boudez, 1963; Haberland, 1981; Snarskis, 1984, 1992), or based on contentious ethnohistorical interpretations (e.g., Ibarra, 1990, 2011). The dearth of historical documentation in broad areas of Central America contribute to the difficulty of approximating important demographic events of the past (Baldi, 2013). The field of anthropological genetics in Central America has been central in understanding the causes of human variation, microevolution, and population history considering the insufficiency of other demographic and historical sources.

European exploration of uncharted geographical spaces in the sixteenth century, including Central America, encompassed not only descriptions of flora and fauna, but also of indigenous populations, their social organization, and their physical and behavioral characteristics (Mielke et al., 2006). These observations were based on the subjective, Hippocratic concept of “humors,” the temperament and external appearance associated with a

particular ethnic group. These early colonial demographic estimates and classification of Central American Amerindians were used as a means of military, political, economic, and social control. Human classification determined by visible morphological characteristics of the skin, the hair or the shape of the eyes began in Central America in the sixteenth century. Populations were geographically located and the number of the inhabitants recorded, along with causes of growth or decline—e.g., mortality, migrations, baptisms, marriages. After the sixteenth century, Europeans began documenting the great diversity of indigenous groups in Central America (Frazer, 1939). Their descriptions of “racial types,” despite the strong pejorative charge they convey, provide a general view of the demography, ethnic mosaic, languages, customs, and cultural practices of the region. The mix of different ethnic groups included Spaniards, Africans, and indigenous peoples that were further diversified by the new migratory influx to the region (Hall and Pérez-Brignoli, 2003). The delineation of the human geography (“local races”) continued in the nineteenth and early twentieth centuries, and they are depicted in works by a number of scholars in Costa Rica (e.g., Fernández-Guardia, 1921; Pittier, 1938; Lines, 1952); however, these classifications lacked scientific rigor and diachronic perspective of social and biological evolution.

The organization of this chapter is not meant to imply that trends in research are discrete. The overlapping nature of scientific discovery, a process illustrated by studies carried out during the twentieth and twenty-first centuries, has seen new scientific inquiries as well as the application of new technologies to research questions of the past.

PHYSICAL AND BIOCHEMICAL CLASSIFICATIONS

Before the discovery of blood-groups systems, protein, enzyme polymorphisms, and DNA analysis, anthropologists described human variation by using quantitative traits such as anthropometrics and dermatoglyphics (Relethford, 2007). In Central America, anthropometric studies were conducted by A. Schultz in 1924 among the Mayangna (Sumo) and Rama Amerindians in eastern Nicaragua (Schultz, 1926). Similar studies were undertaken by Aleš Hrdlička (1926) with the Guna (Kuna) of Panama, and by Laurencich de Minelli among the Boruca, the Guaymí, the Bribri, and the Cabécar groups in Costa Rica (Laurencich, 1966, 1968, 1974). Also, Ada D’Aloja developed demographic and anthropometric research between 1937 and 1939 among indigenous groups from Nicaragua, El Salvador, Honduras, and Guatemala (D’Aloja, 1939, 1940). These investigations relied mostly on typology based on the segregation of human groups according to their external (morphological) characteristics and their geographic location (Figure 1). In 1947 and 1949, T. D. Stewart (1947) recorded basic demographic information, blood samples, and dermatoglyphic data from four indigenous communities in Guatemala. Based on these dermatoglyphic data,

Newman (1960) found a biological division between the Maya of the North Highlands, the South Guatemalan Highlands, and the Yucatan Lowlands, differences which were interpreted to be the result of geographic isolation.

The discovery of blood groups in 1900 led to a shift in the typological paradigm. Rather than anthropometric methods, researchers began to focus on comparisons of Mendelian genetics based on ABO blood-system frequencies, particularly in the Americas (Neel and Salzano, 1964; Neel 1978; Crawford, 2001; Mielke et al., 2006). The assessment of Amerindian genetic variation was possible through the development of electrophoretic methods using primarily blood cell proteins and enzymes referred to as “classic genetic markers” which include ABO, Rhesus, MNS, and Duffy, among others (Crawford, 2007). Based on blood group frequencies, William Boyd (1950) proposed the distinctiveness of the Amerindians, and then blood cells were collected among indigenous groups across the Americas. Classical polymorphism was the first genetic system used for evaluating the origins of these populations, the number of migrations, and the chronology of events (Crawford, 2001). However, these types of studies began to emerge in Central America in the 1960s with Fuentes (1961) among the Guatuso in northern Costa Rica, and with A. Matson and J. Swanson, who compiled and systematized the distribution of blood antigens among indigenous populations from Guatemala, Belize, Honduras, Costa Rica, and Panama using different polymorphic systems (ABO, MNS, P, Diego, Duffy, Kell, haptoglobulins, transferrins, and hemoglobins) (Matson and Swanson, 1961, 1963, 1964, 1965a, 1965b).

Further studies attempted to understand the biological and cultural causes of variability in local indigenous populations, for example, those carried out by Gian Franco De Stefano and Jorge Jenkins among the Rama, Miskito, Mayangna, Subtiaba, and Ladino populations between 1969 and 1971 in Nicaragua (De Stefano and Jenkins, 1970–1971, 1972). Apart from the anthropometric, PTC testing, and serologic information collected in Nicaragua, De Stefano and his colleagues included in their analyses linguistic affiliation, history, geographical location, and demographic relationships among native and mestizo populations. Other studies based on fieldwork carried out between 1969 and 1972 highlight the importance of genetic and environmental components that have contributed to the phenotypic asymmetry of populations from Mexico and Belize (Baume and Crawford, 1980).

Morphological studies were developed within the context of the research conducted by Barrantes and his colleagues on populations including the Bribri, Cabécar, and Guaymí from Costa Rica and Panama after the 1970s (Barrantes, 1993a). A number of these studies demonstrate the applicability of dermatoglyphics and dental morphology for inferring population structure at the tribal level (Brenes and Barrantes, 1983, 1986; Quesada and Barrantes, 1983, 1986, 1991; Segura-Wang and Barrantes, 2009).

These investigations, led by De Stefano, Crawford, and Barrantes, mark the transition between anthropometric studies and

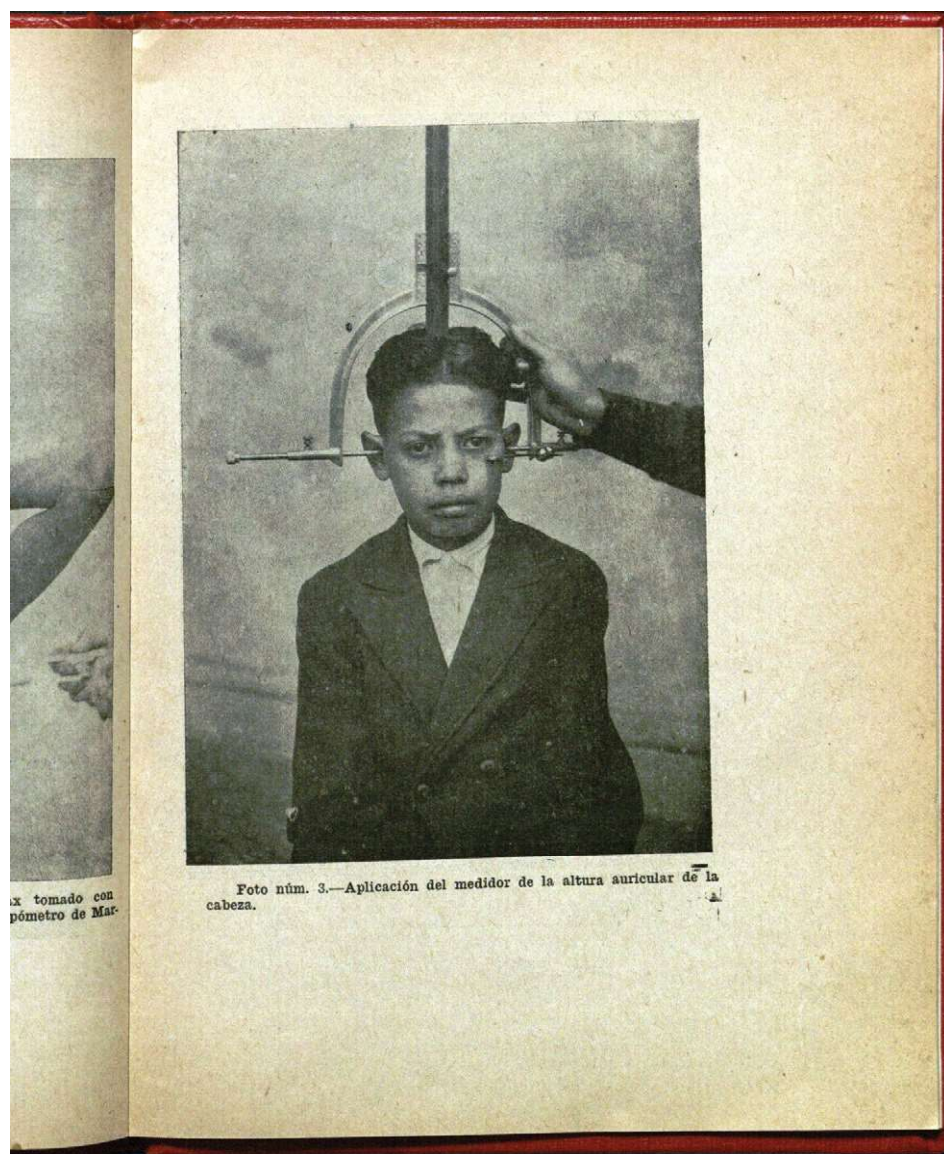


FIGURE 1. Page from a book typical of anthropometric studies among indigenous populations of the east coast of Nicaragua. Photograph taken by Ada D'Aloja (1939).

those that attempted to explain the microevolutionary consequences in Central American populations.

MICROEVOLUTIONARY STUDIES BASED ON CLASSICAL GENETIC POLYMORPHISMS

Innovations in biochemistry, genetics, and serology produced additional genetic markers, for example, those encoded in the human leukocyte antigens (HLA) or in immunoglobins (GM and KMs), which can yield insights on migration patterns and

evolution (Crawford, 2001). HLA markers have been used to compare populations, to better understand the history and structure of Chibchan populations in southern Central America (SCA: i.e., Nicaragua, Costa Rica, and Panama), to determine the origin of Maya, and to establish the ethnic profile of the Garifuna on the Caribbean coast of Central America (Dykes et al., 1981).

Based on HLA, Gómez-Casado et al. (2003) highlight the genetic particularity of the Maya of Guatemala in comparison with the Mesoamerican Zapotec, Mixe, and Mixtec Amerindians, and with the Arawaks, the first recorded inhabitants of the Caribbean Islands, as well as with Chibchan populations in Colombia (Kogi and Arsario). A second study based on HLA class

II alleles indicated that the Maya of Mexico and Guatemala are distinct populations (Vargas-Alarcón et al., 2011).

In Costa Rica and Panama, serological studies continued the research that James V. Neel had begun in the 1950s among the Xavante in Brazil and the Yanomamo in Venezuela (Neel and Salzano, 1964, 1967; Neel, 1978). Neel sought to understand which evolutionary forces shape the genetic structure of populations and how conditions that regulate survival and reproduction had changed from “pre-civilized” indigenous groups to modern populations (Neel, 1994). Fieldwork and the collection of demographic and ethnographic data were instrumental in testing such models in vivo (Ventura, 2003). The proposal by Fitch and Neel (1969) of the genetic relationship between the Guaymí from western Panama and the Yanomamo from southern Venezuela was a crucial advance in the understanding of the population structure and history of the indigenous groups in SCA. This hypothesis was later tested by Spielman et al. (1979) who did not find evidence of any such relationship, but instead discovered two new private polymorphisms (DH*BGUA and ACP*BGUA) among the Guaymí and the absence of albumins among the Yanomamo (Tanis et al., 1977). A subsequent study among the Guaymí including blood markers, anthropometrics, and linguistics, found substantial differences from the Yanomamo as well as indications of the early divergence of the two groups around 4000 years ago. This study was one of the first that combined genetics, linguistics, and anthropological methods in the study of human variation and evolution in Latin America (Crawford, 1979).

These works heeded new comparative studies on indigenous groups of similar linguistic phyla. The work of Barrantes et al. (1982) is the first attempt to establish the intra-population variation between two Guaymí communities from Costa Rica (Limoncito and Abrojo) and their relationship with other Chibchan-speaking populations from SCA and northern South America. This study proposed the relationship of three geographically separated groups: Central American, northern South American, and Chocoan-speaking populations. Most of the indigenous Chibchan-speaking populations cluster together (Figure 2). Subsequent analyses of three systems—blood group, plasma proteins, and erythrocyte proteins—were conducted by Barrantes using a combination of newly gathered data and previously published sources, Barrantes (1993b) proposed that kin structure migration and the fission and fusion of villages were responsible for the population structure of the Guaymí from Panama and Costa Rica.

Nevertheless, using a bigger sample size of 22 Chibchan-Paezan populations from Colombia and Central America and 25 polymorphisms, Layrisse et al. (1995) did not find clear phylogenetic relationships among these populations. Baldi (2013), using data from literature, tested the hypothesis of the genetic relationship among Chibchan-speaking populations from Central America and Colombia by analyzing 22 alleles of seven blood group systems of 24 populations (MNSs, P, Kidd, Diego, Rhesus, ABO, and Duffy). The results indicated spatial association among Chibchan populations from Central and South America

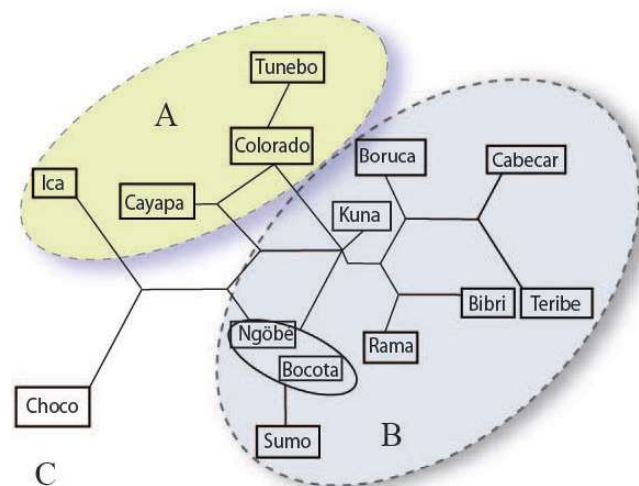


FIGURE 2. Minimum string network showing genetic relationships among South American Chibchan Populations (A), Central American Chibchan populations (except Sumo) (B), and a Chocoan-speaking population (C). Diagram modified from Barrantes et al., (1982).

and demonstrated that heterozygosity values and distance from the centroid (*r_{ii}*) indicate that most Chibchans presented lower genetic heterozygosity than other non-Chibchan populations from Central America.

Subsequent publications (Barrantes et al., 1990; Thompson et al., 1992; Bieber et al., 1996; Barrantes 1998; Azoifeifa et al., 1998, 2001) proposed that the genetic structure of Chibchan speakers of SCA was likely the result of kinship, environmental conditions, and geographic isolation. The combination of these factors generated higher frequencies of transferrins D-Chi, the 6PGD allele, and the absence of the Diego A* allele (DiA*), as well as other rare, regionally restricted polymorphic variants. In accordance with these observations, the authors of the studies mentioned above concluded that the genetic differentiation of Chibchan populations in SCA underpins an in situ development of Chibchan-speaking populations and their divergence around 7000 B.P. (years before present).

Despite their importance in studies of population genetics, classical genetic markers provide only a gross approximation of the complexity and the genetic history of Central American indigenous populations. However, they paved the way for later studies of greater evolutionary resolution such as investigations of molecular markers. In addition, microevolutionary studies based on blood polymorphisms provided the foundation for the hypothesis of the coevolution of culture and genetics in the Isthmo-Colombian Cultural Area (ICCA) which is occupied predominantly by Chibchan speakers and includes northern Colombia, Panama, Costa Rica, Caribbean Nicaragua, and portions of

eastern Honduras (Constenla, 1991; Barrantes, 1993b; Cooke and Ranere, 1992; Fonseca, 1998; Hoopes and Fonseca, 2003).

MOLECULAR POLYMORPHISMS

Unlike the indirect investigation of biochemical markers such as protein and enzyme polymorphisms that are influenced by natural selection (Destro-Bisol et al., 2010), four principal discoveries have permitted the direct study of the DNA molecule in the last forty years. Restriction enzymes make it possible to cleave strands of DNA in specific positions; DNA hybridization techniques facilitate the comparison of different species through the similarity or difference of their nucleotide constitution; PCR creates “copies” of DNA sequences in geometric progression; and automated DNA sequencing permits the rapid characterization of the human genome (Rubicz et al., 2007). These inventions established the genetic variability and worldwide phylogenetic relationships among and within human populations by facilitating the study of several DNA polymorphisms, the non-recombining portion of the Y-chromosome (NRY), and autosomal DNA (Bhasin and Walter, 2007). In addition to mitochondrial DNA (mtDNA) and the NRY, autosomal DNA data provide the combined history of males and females due to the chromosomal reshuffling through generations. These three systems are commonly used today for the study of the genetic history of isolated populations and of national gene pools in Central America.

Studies of Central American mtDNA polymorphisms consist of the sequence of hypervariable sections 1 and 2 (HVS-I and HVS-II) of the mtDNA control region, whole genome sequences, and the analysis of restriction fragment length polymorphisms (RFLPs), which facilitates the study of haplogroups—groups of related haplotypes that share a common ancestor and are correlated by cultural affiliation, language family, and geographic location (O’Rourke et al., 2000). The RFLPs are used to characterize single nucleotide polymorphisms (SNPs) that define the major haplogroups present in America (A, B, C, D, and X) inherited through the maternal side (Rubicz et al., 2007). Additional resolution of the mtDNA haplogroups, assisted by full genome sequences, has led to the classification of 15 founder subclades (<http://www.phylotree.org/>). From the paternal side, two deep clades are present in Amerindian populations: C and Q (O’Rourke and Raff, 2010).

An increasing number of mtDNA, Y-chromosome, and autosomal genetic studies in SCA have attempted to achieve two main goals: first, to understand the evolutionary implications of the peopling of Central America in a local and a broader continental context; and second, to look at history of the genetic admixture within national gene pools.

CHIBCHAN STUDIES IN SOUTHERN CENTRAL AMERICA

To test whether the *in situ* microevolutionary hypothesis, previously proposed by Barrantes and others, or the continued

gene flow across cultural areas explains most of the genetic history and population structure of Chibchan-speaking populations in SCA, recent research has been based on different levels of genetic resolution.

The first attempt to test the hypothesis of the early tribalization and microevolution of Chibchan populations from Panama and Costa Rica estimated their separation from other linguistic families early in the Holocene based on mtDNA (Torroni et al., 1994). A subsequent examination of the haplotype diversity of the Ngöbé from Panama (Kolman et al., 1995) detected lower diversity values at the HVS-I and II regions and a population expansion around 6800 B.P. Low levels of genetic diversity were also reported among the Guna from western Panama, and the Huetar from Costa Rica indicating that Chibchan-speaking populations experienced a population bottleneck around 10,000 B.P. (Batista et al., 1995, 1998; Kolman et al., 1995).

While examining the genetic variability of the Huetar from the Central Valley of Costa Rica, Santos et al. (1994) discovered a distinctive 6-bp deletion in the mtDNA HVS-II region between nucleotide pairs (np) 106 and 111. This mutation, named the “Huetar deletion,” corresponds with the *MspI* site loss at nucleotide position 104 within the haplogroup A2 that appears in some Chibchan-speaking populations of Central America, including the Teribe, Bribrí, Cabécar, Boruca, Guaymí (Ngöbé and Buglé), Guna (Torroni et al., 1993, 1994; Santos and Barrantes, 1994a, 1994b; Santos et al., 1994), and Chorotega, an Oto-Manguean-speaking population (analysis in progress by this chapter’s authors). The Huetar deletion was defined as the mitochondrial A2af lineage and is also present in high frequency among contemporary Panamanians and across SCA (Perego et al., 2012).

Kolman and Bermingham (1997) carried out the first study that contrasted the mtDNA (HVS-I and HVS-II), nuclear, and Y-chromosome genetic markers of two Chocó-speaking populations from eastern Panama—the Emberá and Wounan—and two Chibchan-speaking populations—the Guna and Ngöbé. Contrary to previous studies, the authors concluded that patterns among the Chocoans differ from the reduced diversity found in other Chibchan populations.

A number of recent studies have attempted to understand the genetic structure and diaspora of Chibchan speakers from Central and South America. Melton et al. (2007) examined the hypothesis of biological relationships between Chibchan populations of SCA and northern Colombia. This study found a low haplotype diversity and reduced heterozygosity among Chibchans likely caused by population drift. Furthermore, the absence of shared mtDNA haplotypes indicates an early split from an ancient stock during the Pleistocene/Holocene transition. The human diaspora from Central America to northern South America (based on mtDNA) might have occurred between 14,000 and 8,000 B.P. coupled with a shift in subsistence from hunting and gathering to horticulture. After this episode, Chibchan populations remained geographically isolated between SCA and northern South America. The transition to the Holocene facilitated the exploitation of and adaptation to a variety of microenvironments,

allowing for sedentarism and relative genetic homogeneity due to reduced genetic flow from other regions. According to this model, population growth in the Central American isthmus inhibited subsequent migrations from the north and might have induced northern South American populations to move further south. This study also found a genetic relationship in the distant past with Mayan populations from Central America. This possible relationship provides a more complex scenario than the in situ microevolutionary hypothesis proposed by the Barrantes group (Barrantes et al., 1990) due to its higher molecular resolution in comparison with blood polymorphisms.

Subsequent studies examined Y-chromosome and mtDNA variation in five populations (Rama from Nicaragua and Huetar, Maleku, and Guaymí from Costa Rica) to look at the evolutionary history and genetic relationships of the Chibchan speakers and their neighboring populations (Melton, 2008; Baldi, 2013; Melton et al., 2013). Deep phylogenetic relationships found at the mtDNA level indicate that central and northern South American Chibchans share a number of haplotypes or are separated by only one mutational step. Similar relationships were found with other Mesoamerican populations, while divergence from South American and Andean groups was indicated. In addition, coalescent dates based on haplogroup A2 suggest that the separation of Chibchans from founding Paleoindian populations occurred early in the Holocene followed by their geographical isolation (Melton, 2008; Baldi, 2013).

Chibchan populations characterized by their low mtDNA diversity due to genetic drift contrast with the recent flow of males of African and Euro-Asiatic origin. Also, the NRY shows little ancestral differentiation between Mesoamerican, Chibchan, and Chocoan populations (Melton et al. 2013) and unclear population structure from the paternal side (Ruiz-Narvaez et al., 2005; Ascunce et al., 2008).

These studies demonstrate that compared to the Y-chromosome, mitochondria was less impacted by demographic processes after European colonization in the sixteenth century. The population structure inferred by the mitochondria is consistent with recent studies of autosomal microsatellites that show a relative lack of differentiation between Mesoamerican and Andean populations and a close relationship between Chibchans from eastern South America and SCA. Further studies are needed to clarify whether these relationships were caused by ancient or more recent population events (Wang et al., 2007).

Contrary to the previous scenario, Reich and associates proposed that Chibchan speakers from SCA experienced a reverse gene flow to Central America after the initial peopling of South America (Reich et al., 2012). The continued gene flow hypothesis states that most of the genetic history in this region is explained by a back migration and subsequent gene flow across the Caribbean coast of Central America (Moreno-Estrada et al., 2013). Therefore, this hypothesis entails the absence of cultural and biological continuity and a relative isolation of Chibchan populations. This proposal is backed by the implementation of large scale genotyping microarray using autosomal markers, and it implies that

Chibchan speakers of SCA are not the direct descendants of the late Pleistocene hunter-gatherers that inhabited the region, contradicting the region's cultural history (Cooke et al., 2013).

Future genetic and genomic studies of extant and extinct populations will elucidate the population history of Central American indigenous groups on a local and continental level. Ancient DNA (aDNA) is an important tool for understanding regional migration history, including the interactions and dispersal of populations in the remote past (Raff et al., 2011).

Central America is the region where the fewest number of published studies have been carried out when compared with the rest of the continent, and thus additional aDNA investigations are necessary to understand the initial colonization of the isthmus and the level of genetic continuity of the local populations. Additionally, aDNA studies provide reference points necessary to critically evaluate demographic models and to propose alternative hypotheses for the dispersal of populations in the Americas (Raff et al., 2011). Caribbean Central America was initially colonized by ~13,000 B.P. (Chatters et al., 2014), and Mayan populations in Copan, Honduras (750–1300 B.P.), present high frequencies of haplogroup C, which is relatively low in contemporary Mayan populations from Central America (Merriwether et al., 1997).

This is not to say that there have not been repeated attempts to study aDNA in pre-Colombian populations in Costa Rica, Nicaragua, and Panama. The first of these investigations was attempted by N. Baldi in 2004 with a sample provided by Richard Cook (Smithsonian Tropical Research Institute in Panama) from the Juan Diaz archaeological site (1600–1900 B.P.) under the tutelage of Dr. Dennis O'Rourke at the aDNA laboratory of the University of Utah. Unfortunately, the DNA was so degraded that it could not be amplified. Researchers await advances in extraction methods based on next generation sequencing that may make it possible in the near future to recuperate highly degraded DNA from the tropical regions of Central America (Templeton et al., 2013; Wade, 2015).

SOUTHERN MESOAMERICA AND THE CARIBBEAN COAST OF CENTRAL AMERICA

This section is organized in three major trends of genetic studies that have been carried out on the Caribbean coast of Central America and southern Mesoamerica: (a) descriptive studies on admixture of the national populations of Central American countries, (b) studies of the origin of the Mayan populations of Guatemala, and (c) studies of migration and microevolution of Afro Caribbean populations in Honduras, Belize, Nicaragua, and Costa Rica.

Admixture Studies in Central America

Knowledge of the Amerindian genetic component gleaned from mtDNA, autosomic markers, and NRY has also served to estimate the level of admixture in Central American populations and for forensic applications in El Salvador (Martínez-Jarreta et

al., 2004, 2005; Lovo-Gómez et al., 2007a), Belize (Flores et al., 2014), Costa Rica (Rodríguez et al., 2007), Nicaragua (Núñez et al., 2010, 2012; Vargas-Díaz et al., 2011), Honduras with a national pool population, and the Garifuna (Matamoros et al., 2004, 2008, 2009; Herrera-Paz et al., 2008). In the elaboration of these reports, between 6 and 18 autosomal and Y-STRs (Y-chromosome short tandem repeats) of Central American populations were screened with the idea of creating a database for forensic and parental testing applications.

Other investigations have centered on understanding the grade of admixture within each country or indigenous subpopulation, for example, in El Salvador the indigenous populations of Conchagua, San Alejo, Izalco, and Panchimalco show significant statistical differences compared to metropolitan samples (Lovo-Gómez et al., 2007b).

A study by Núñez et al. (2010) in Nicaragua utilized the mitochondrial control region (HVS-I and HVS-II) and STRs of the Y-chromosome of 165 mestizos and found that the Native American contribution to present-day Nicaraguans accounts for most of the maternal lineages (~90%), whereas the majority of Nicaraguan Y-haplogroups show a Spanish contribution of 69%, followed by 20.3% African, and 10.6% Amerindian. The biparental contribution was studied with a base in 6 autosomal loci by Morera (2006), who was able to estimate that the Nicaraguan population was made up of 47% European, 37% indigenous, and 16% African descent. However, studies carried out in Panama with better resolution and sample size utilized complete mitochondrial sequences and determined that 83% of the mitochondria in the Panamanian genetic pool was of American origin, 14% of African origin, and 2% European (Perego et al., 2012).

The majority of studies reporting the genetic structure and admixture in Central America have been carried out in Costa Rica using a variety of markers. The first analysis of the entire country was accomplished using classical markers (Morera et al. 2001). Subsequent investigations used STRs and mtDNA sequences (Campos-Sánchez et al., 2006), SNPs and Ancestral Informative Markers (AIMs) (Wang et al., 2008, Segura-Wang et al., 2010, Campos-Sánchez et al., 2013). The results obtained regarding ancestry were similar, showing 50% European ancestry, 30% Amerindian, and 10% African in central provinces, with a larger presence of Amerindian and African origins in coastal regions. Additionally, Campos-Sánchez et al. (2013) reported an Asian component of 5–10% in the population, originating with migrations from China to Costa Rica during the last 150 years.

The aforementioned studies provide evidence that Central American gene pools are composed of widely varied groups including Native American, European, African, and other populations, and indicate that admixture can be contributed primarily to European males reproducing with indigenous women.

Mayas from Southern Mesoamerica

Other studies have focused on understanding the history of the Maya of Mesoamerica and their relationship with other

indigenous populations in the area. The Maya are a group of populations extending from southern Mexico, Guatemala, Belize, northern and western Honduras, and El Salvador that share a common linguistic family of approximately 30 languages (Carmack, 1994).

At this time, few investigations based on molecular markers have focused on understanding the relationship between the Maya and other Mesoamerican populations. In a study based on polymorphic Alu insertions (PAI), Herrera et al. (2007) found that the Yucateco from Mexico and the Kakchikel and K'iche from Guatemala are not genetically homogenous. Another study using autosomal STRs found that the Huastec are significantly divergent and that substructures exist among the Poqomchi', Yucatec, Ch'orti', and K'iche (Ibarra-Rivera et al., 2008). This incongruity was also manifested in two separate HLA studies as was pointed out earlier in this chapter (Gómez-Casado et al., 2003, Vargas-Alarcón et al., 2011). To test this hypothesis, Justice (2011) examined the mtDNA and NRY of the Mayan Poqomchi' and Ch'orti' from Guatemala and compared them to other Latin American Indigenous populations, arriving at the conclusion that the Maya as a whole share a common history and a close genetic relationship, although some populations are more divergent than others, such as the K'iche. In addition, the Maya are considered biologically distinct from Chibchan and other Mesoamerican and South American populations.

Central American Caribbean

Two populations inhabiting the Caribbean coast of Central America are of interest in population genetics: the Garifuna, a community with strong African admixture, and the Indo-Limonense population ("Culíes"). Both populations are historically tied to the slave trade and labor migrations that shaped the human genetic diversity of the region.

Black Caribs, known as Garifuna (or Garinagu), currently inhabit the Caribbean coast of Central America from Belize to Nicaragua (Gullick, 1976). The Garifuna are the result of admixture of three distinct groups: enslaved Africans brought to the new world by Europeans, Native American Caribs who are the descendants of Arawaks, and Europeans (Crawford et al., 1981). Records indicate that in 1665, English slave ships sailing from the West Indies wrecked off the coast of the island of St. Vincent. A great number of the shipwrecked sailors and slaves swam ashore where a number intermarried with indigenous Caribs living on the island. The new population admixed, incorporating indigenous traditions, such as the preparation and consumption of bitter manioc, with African traditions, particularly the musical traditions of drumming and dancing. By the end of the eighteenth century, some 2,500 Garifuna were transplanted by the Spanish army to the island of Roatan (Crawford, 2001). As the population expanded, the Garifuna spread to the coast of Honduras in 1832, and later to more than 54 villages along the coast of Central America. Some estimates suggest that there are over 200,000 Garifuna living in present-day Central

America (Paz-Bailey et al., 2009; Herrera-Paz et al., 2010). The expansion of the Garifuna on the Caribbean coast is considered one of the most salient examples of biocultural adaptation in the New World, due to the fact that this hybrid population has the highest birthrate of any population in the Americas, with an average of 10.9 children per woman, despite an endemic malaria epidemic. The population structure of the Garifuna is a product of a series of fusions and fissions of their gene pool (Brennan, 1983; Crawford, 2001). It is probable that one of the factors contributing to the success of bio-cultural adaptation has been the sickle-cell gene which occurs at a rate higher than expected for natural selection (Firschein, 1961; Crawford, 1983).

Although Crawford (1984) led a successful program of biocultural investigation among the Garifuna in Central America between 1975 and 1976, little is known of the impact of the African and indigenous components in the genetic composition of the Garifuna of Honduras and of other populations of the American Caribbean beyond blood-group polymorphisms. In the last decade, several studies with high genetic resolution have been carried out to better understand the population dynamics, structure, and phylogenetic relationships of the populations across the Caribbean. For example, Monsalve and Hagelberg (1997), using mtDNA samples from Garifunas in Belize, determined that nearly 100% of individuals presented African lineage. Later, Salas et al. (2005) estimated that the mitochondria of Afro-descendent Colombian Choco and Garifuna of Honduras was 16% Native American and 86% African. Similarly, Herrera-Paz et al. (2010) studied the allele frequencies of autosomal STRs in Honduran Garifuna and, like Salas et al. (2005), concluded that this population presented signatures of the founder effect in its low levels of genetic variability when compared to other world populations.

A comprehensive study of the Indo-Limonense, a population that originated in Central India but relocated to the province of Limon, Costa Rica as indentured servants, was carried out by Lorena Madrigal and associates (Madrigal et al., 2012). Through an analysis of mtDNA and the Y chromosome, the team confirmed the Indian origins of the population and quantified the effect of genetic flow and admixture over time (Castrì et al., 2007). In addition to other components of the population structure, they evaluated inbreeding and marriage patterns (Madrigal et al., 2007, 2011). After a century in the Atlantic region, the Indo-Limonense show a distinct level of genetic mixture and integration with the mestizo population and the Caribbean Afro-Costa Rican population.

CONCLUSION

The study of genetics of Central American populations has passed through three historical periods. The first, from the 1920s to the 1960s, based descriptions of human variation on quantitative physical traits; anthropometric measurements were made and genetic variation was measured using classical markers of

local indigenous groups. This phase is characterized by description and by the absence of scientific queries about indigenous populations in accordance with the paradigm of fixed racial traits, which was common among physical anthropologists during the first half of the twentieth century (Armélagos and Van Gerven, 2003).

During the second historical period, which stretched from the 1970s to the 1990s, studies led by Barrantes in Costa Rica and Panama, Crawford on the Caribbean coast of Honduras, Guatemala, and Belize, and De Stefano in Nicaragua increased attention to the cultural, demographic, and environmental variables responsible for indigenous and Afro-Caribbean population structure. Their research programs, carried out among the indigenous populations of southern Central America and the Garifuna, substituted statistical methods for typological methods as tools for testing hypotheses and included fieldwork to collect biological specimens, as well as biomedical, demographic, and ethnographic information. By deepening the knowledge of genetic structures and genetic flow that result from inter-ethnic contact, these pioneering contributions allowed for better interpretation of biological variation and highlighted the distribution of gene frequencies and private polymorphisms of Chibchan-speaking populations in Central America. This makes it possible for researchers to assess the genetic structures of these groups and to propose the model of in situ microevolution. Meanwhile, investigations with the Garifuna of the central and northern Caribbean coast of the isthmus provided information regarding the evolutionary consequences of migration, such as genetic flow between populations with different geographic origins. The selective pressures of the malarial environment, high fertility rate, and sociocultural adaptations enabled the Garifuna to successfully colonize the coast of Central America and expand in record numbers.

The third historical phase, which began in earnest during the 1990s and continues today, is marked by the incorporation of techniques and methods from the field of molecular biology, which allow a higher grade of genetic resolution and direct scrutiny of polymorphisms. This permits researchers to test new and old hypotheses, to approximate the genetic structure and history of indigenous populations inhabiting various cultural areas, and to establish the level of gene flow among populations. Current research emphasizes the complexity of demographic processes in the region, which are seen as a product of historical and social development. Despite technological advances, unresolved questions remain about central aspects in the field, for example, whether (a) dispersion and aggregation in situ or (b) genetic flow from outside Central America is responsible for the majority of the genetic history and structure of Chibchan-speaking populations. Doubtless, further investigation in the region will resolve this incongruity of theories, as has occurred in the more commonly studied areas of North and South America.

The study of microsatellites and SNPs markers across the genome has made it possible to determine the geographic identity of the admixture in Central America and to quantify the genetic contribution of indigenous groups to a country's population as

TABLE 1. Contributions to human population studies (genetics and morphological variation) during the twentieth and the beginning of the twenty-first century in Central America based on 117 scientific publications.^a

Decade	Belize	Guatemala	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	Total references
1920–1930	0	1	1	1	2	0	1	6
1931–1940	0	1	1	1	1	0	0	4
1941–1950	0	0	0	0	0	0	0	0
1951–1960	0	3	0	0	0	0	0	3
1961–1970	0	1	0	2	3	4	1	11
1971–1980	1	0	0	0	6	2	2	11
1981–1990	2	2	0	2	1	7	3	17
1991–2000	1	0	0	1	1	9	7	19
2001–2010	0	6	7	6	3	23	8	53
2011–2015	2	4	0	0	7	6	2	21
Total references	6	18	9	13	24	51	24	145
(%)	(4%)	(12.5%)	(6%)	(9%)	(17%)	(35%)	(16.5%)	

^aThis table shows 145 scientific references contained within 117 peer reviewed articles, book and book chapters, Ph.D. dissertations on investigations into human morphological variation, classical and molecular markers, genetic epidemiology, isonomy, and DNA forensics. Some investigations include more than one country. **BELIZE:** Baume and Crawford, 1980; Dykes et al. 1981; Crawford, 1984; Monsalve and Hagelberg, 1997; Phillips-Krawcsak, 2012; Flores et al., 2014. **GUATEMALA:** D'Aloja, 1939, 1940; Matson and Swanson, 1959; Newman, 1960; Sutton et al., 1960; Matson, 1963; Crawford et al., 1981; Crawford, 1984; Gómez-Casado et al., 2003; Zegura, 2003; Herrera et al., 2007; Wang et al., 2007, 2008; Ibarra-Rivera et al., 2008; Justice, 2011; Vargas-Alarcón et al., 2011; Martínez-González et al., 2012; Reich et al., 2012. **EL SALVADOR:** D'Aloja, 1939, 1940; Martínez-Jarreta et al., 2004, 2005; Saul et al., 2004; Lovo-Gómez et al., 2007a, 2007b; Salas et al., 2009; Monterrosa et al., 2010. **HONDURAS:** D'Aloja, 1939, 1940; Firschein, 1961; Matson and Swanson, 1964; Brennan, 1983; Crawford, 1984; Merriwether et al., 1997; Matamoros et al., 2004, 2008, 2009; Salas et al., 2005; Herrera-Paz et al., 2008, 2010. **NICARAGUA:** Shultz, 1926; D'Aloja, 1939, 1940; Matson and Swanson, 1963; De Stefano, 1970–1971, 1973; De Stefano and Jenkins, 1970–1971, 1972, 1972–1973, 1974, 1976; De Stefano et al., 1979; Roberts and De Stefano, 1986; Azofeifa et al., 1998; Morera, 2006; Melton, 2008; Núñez et al., 2010, 2012, 2013; Núñez, 2011; Vargas-Díaz et al., 2011; Baldi, 2013; Melton et al., 2013; Baldi et al., 2014. **COSTA RICA:** Fuentes, 1961; Matson and Swanson, 1965a; Laurencich, 1966, 1968, 1974; Spielman et al., 1979; Barrantes and Azofeifa, 1981; Barrantes et al., 1982, 1990; Brenes and Barrantes, 1983; Quesada and Barrantes, 1983, 1986, 1991; Barrantes, 1988, 1993a, 1993b; Torroni et al., 1993, 1994; Santos and Barrantes, 1994a, 1994b; Santos et al., 1994; Bieber et al., 1996; Barrantes and Morera, 1999; Azofeifa et al., 2001; Madrigal et al., 2001, 2007, 2012; Morera et al., 2003; Zegura, 2003; Mathews et al., 2004; Morera and Barrantes, 2004; Ruiz-Narvaez et al., 2005, 2010; Campos-Sánchez et al., 2006, 2013; Herzberg et al., 2006; Castri et al., 2007; McInnes et al., 2007; Melton et al., 2007; Rodríguez et al., 2007; Wang et al., 2007, 2008; Lewis and Long, 2008; Melton, 2008; Jasinska et al., 2009; Segura-Wang and Barrantes, 2009; Segura-Wang et al., 2010; Wang et al., 2010; Amorim et al., 2011; Reich et al., 2012; Melton et al., 2013; Céspedes-Garro et al., 2014. **PANAMA:** Hrdlička, 1926; Matson and Swanson, 1965b; Tanis et al., 1977; Spielman et al., 1979; Barrantes et al., 1982, 1990; Barrantes, 1988, 1993a, 1993b; Torroni et al., 1993, 1994; Batista et al., 1995; Kolman et al., 1995; Bieber et al., 1996; Kolman and Bermingham, 1997; Zegura, 2003; Ruiz-Narvaez et al., 2005; Castro et al., 2007; Melton et al., 2007; Wang et al., 2007, 2008; Ascunce et al., 2008; Lewis and Long, 2008; Perego et al., 2012; Reich et al., 2012.

a whole—a contribution that varies due to the historical processes unique to each nation. These new research possibilities have revitalized interest in subpopulations that had previously been subsumed in national populations: the migratory history of groups like the Indo-Limonense, the tripartite ethnicity of the Garifuna, and the oriental component of the Costa Rican population are all recent areas of anthropological, sociological, and demographic interest. In the near future, these studies of genetic diversity of Central American populations have a great potential to enhance, through admixture mapping, our understanding of the genetic bases of complex traits, which in turn could contribute to the identification of genes that influence diseases and genetic disorders (Zhu et al., 2004).

Despite these areas of strength in Central American investigations, additional research is needed. Table 1 shows that the majority of studies combining morphological variation and

human population genetics from the 1920s through 2015 have been carried out in Costa Rica (35%), followed by Nicaragua and Panama (34%), leading to a disparity of population studies from the other four countries of Central America (31%). According to 145 country references in 117 peer-reviewed journals, chapters in books, and Ph.D. dissertations between 1920 and 1970, 17% of the publications were based on morphological and biochemical variation of indigenous populations. Between 1971 and 2000, most of the research (47%) focused on microevolutionary studies in indigenous and Afro-Caribbean populations using classical genetic markers and genetic polymorphisms. Interestingly in the last 14 years (2001–2015) the amount of research has increased by 51% compared to previous decades. This surge in research includes a wide variety of areas of interest, for example admixture studies, demographic approximations based on isonomy and genealogical studies, migration, and disease.

In contrast to investigation programs carried out before the 1990s, when contextual information was routinely collected along with biological samples for each population of interest (e.g., medical, demographic, ethnographic, and geographic data), to echo the criticism of Thompson et al. (1992), the fundamental problem in current Central American sample collection is its paucity of anthropological background and its implicit assumption that with enough genetic data, evolutionary reconstructions are possible. In fact, genetic data make more sense when analyzed alongside demographic, geographic, and sociocultural information collected in the field. Fortunately, in recent years there has been recognition of the importance of cultural niches and social practices as factors that drive evolution, phenomena that have been approximated by our multidisciplinary and multinational research program in Central America where the ethnographic context of the populations is central to our investigations.

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