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Indentured Migration and Differential Gender Gene Flow: The Origin and Evolution of the East-Indian Community of Limón, Costa Rica

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ABSTRACT After the emancipation of African slaves in the Caribbean, the labor void left by out-migrating former slaves was filled by in-migrating indentured servants from prepartition India and China. In some areas of the Caribbean such as Trinidad, Suriname, and Guyana, the East-Indian migrants formed large communities. In this article, we report a study based on mtDNA and Y-chromosomal markers of a small East-Indian community from Limón, Costa Rica. The purpose of the project is to determine the place of origin in the Indian subcontinent of the ancestors of our group and the contributions to its gene pool through gene flow by members of other ethnic groups. Both Y-chromosome and mtDNA suggest that the Indo-Costa Ricans descend from migrants primarily from Central India. While both paternal and maternal markers indicate that this group is overwhelmingly of Indian origin, they also indicate that males and females of African, European, and Amerindian origin contributed to it differently. We discuss our results in the historical context of the virtual extinction of Amerindian Caribbean groups, the forced migration of African slaves to the Caribbean, and the gene flow between Amerindians, Europeans, East-Indians, and Africans that eventually produced the Caribbean's currently diverse gene pool. Am J Phys Anthropol 134:175–189, 2007.

Few geographical regions have experienced the degree of human population extinction and repopulation that the Caribbean has. This region has been witness to extinctions, massive population movements, and the subsequent formation of new groups. Migration and gene flow have been a constant force in the evolution of the Caribbean human gene pools.

A quarter century after the European invasion of the Caribbean, the native populations of the entire region were approaching extinction. Soon after the demise of the native Caribbean populations, the Europeans turned to African sources of labor so that by the 1700's the human landscape of the region was changed, and the great majority of humans in the Caribbean were born in Africa or descended from African slaves (Kline, 1978; Kipple and Ornelas, 1996; Crawford, 1998; Cook, 1998, 2002).

After the emancipation of slaves in the Caribbean (beginning in 1793 in Haiti, continuing in 1833 in the British colonies), many former slaves continued working in the same plantations they did as slaves, others left the plantations and established peasant villages. Starting in this period (1860's and 1870's), indentured workers were brought to the Caribbean from India, China, and to a lesser extent, from Europe (Vertovec, 2000). Indentured servants were brought to the New World with the promise of a free passage back home and a lump sum at the end of their contract. In this article, we refer to the people from the area that was prepartition India and now consists of India, Pakistan, Sri Lanka, and Bangladesh with the term East Indian for the sake of brevity and to distinguish them from West Indians.

Some of these indentured workers from the Indian subcontinent formed large communities in Trinidad, Suriname, and Guyana, dramatically changing the human genetic landscape of these regions. These three Indo-Caribbean communities in particular have received a great deal of attention from cultural anthropologists

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because the groups have been able to maintain their own religious practices and music, and have become important political actors in their countries (Klass, 1961; Speckmann, 1965; Angrosino, 1974; van der Veer and Vertovec, 1991; Vertovec, 1992, 1994, 2000; van der Veer, 1995). In contrast, there is a dearth in biological anthropology work among Indo-Caribbean groups. Indeed, we could find only a few citations on the population genetics of Indo-Caribbean groups (Carrington et al., 2002, 2003).

The Atlantic province of Limón Costa Rica was affected by the Caribbean population extinctions and movements described in the previous paragraph more than by those experienced by the country at large. Just like the rest of the Central American coast, Limón proved a privileged site for the expansion of malaria, which contributed to the decimation of Amerindian groups, forcing them to retreat to the highlands. Indeed, malaria was the main reason the Costa Rican Atlantic coast was not developed by the Spanish colonial government or by the young Costa Rican republic government through the seventeenth, eighteenth, and most of the nineteenth centuries. In the late 1800's however, the Costa Rican government started to build a railroad from the central part of the country to the Atlantic coast. Consequently, a large inflow of foreign workers, the large majority of whom were descendants of African slaves from Jamaica, migrated to the area. These workers came to work on the construction of the railroad line and a young banana industry, and permanently changed the ethnic composition and culture of Costa Rica (Harpelle, 1993; Purcell, 1993; Herzfeld, 2002). Just like the rest of the Caribbean, the Limón region also received immigrants from China and from India, who were part of the indentured servant migration of the 1860's and 1870's previously discussed. Although the Chinese and Afro-Limonense groups of Limón have received attention from anthropologists and others (Duncan, 1981; Purcell, 1993; Grillo-Rosanía, 2003; Madrigal, 2006), the presence of descendants of the East-Indian migrants has been ignored until recently by scholars. Indeed, when we first raised the issue of studying an Indo-Costa Rican group into which one of us (LM) had literally "bumped into", we were told by other anthropologists that the members of this community "had all died out". When the cultural anthropologist of our team (FO) first visited the community, she learned that the community was very much alive and selfconscious of its own ethnicity.

The purpose of this article is to report genetic evidence that may allow us i) to identify the region (s) of the Indian subcontinent from where the ancestors of our community immigrated and ii) to quantify the contribution of East Indian immigrants and other groups to the Indo-Costa Rican gene pool.

MATERIALS AND METHODS

The community and field work

The group we studied uses for itself, and is referred to by its neighbors by a name derived from an offensive term for people of the Indian subcontinent diaspora. Since in Limón this term does not have any pejorative connotations, we felt it was appropriate to use it in publications (for a more in-depth discussion see Madrigal et al., 2007). Thus, we refer to our community with the name they use with pride: the *Culís* of Costa Rica.

The *Culís* live in a small settlement called Westfalia, to the South of Puerto Limón (Fig. 1), although a family has relocated to the Costa Rican Central Valley, three more to the South of Westfalia, and a few to Puerto Limón. Westfalia itself has no more than 30 houses. Our best estimate is that there are fewer than 100 people who call themselves *Culí*, and this estimate includes the families in all of the locations mentioned above.

Since 2003, an international team of biological and cultural anthropologists from the University of South Florida and the Universidad de Costa Rica has been working with the community. This project was approved by the committee on bioethics of both universities. After 4 years of fieldwork with the community, the cultural anthropologist in our team (FO) is confident that she has collected the genealogies of all living members of the community. What is remarkable about the *Culí* families is that they can all be linked into one single pedigree, which we show in Figure 2. Our analysis of the community genealogies indicated that all living individuals descend in one way or another from a few initial founding couples, that migration continued through several generations, and that gene flow with non-*Culís* has been very common. Madrigal et al. (2007) discuss in detail the pedigree, the *Culí* culture in general, and their marriage patterns in particular.

Sampling for DNA extraction took place over two field seasons. In the first one, we collected hair follicles from forty-four participants (20 females and 24 males) and in the second one we collected buccal swaps from twenty-four individuals who had been sampled previously but whose hair follicles did not yield amplifiable Y-chromosome DNA. All families are represented in our sample, including members from Westfalia and the other places where *Culí* families have relocated. Based on the community's genealogy, we are confident that we have multiple copies of each and every one of the mitochondrial and the Y-chromosomal lines of the group.

Genetic analysis

mtDNA. DNA was extracted following standard procedures. A total of forty-four *Culí* participants were typed for Hypervariable Sequence I (HVSI) and, when necessary for phylogenetic purpose, Hypervariable Sequence II (HVSII) of mtDNA. Polymerase Chain Reaction (PCR) amplification was carried out for 30 cycles by adding 5 ng DNA in a 25 μl final volume with 1 U Taq DNA polymerase (Promega Corporation, Madison) and 0.25 μM of the primers HVSI L15997 and H16401. PCR reactions were purified using ExoSAP-IT (United States Biochemical Corporation, Cleveland) and the amplified products were sequenced with the Big Dye Terminator Cycle Sequencing Ready Reaction kit version 1.1 (Applied Biosystems, Foster City, CA). Sequences were separated by capillary electrophoresis on ABI PRISM 3730 (Applied Biosystems, Foster City) automatic sequencer. Each sample was sequenced for both forward and reverse strands to avoid errors or artifacts in mtDNA sequencing. Sequences were aligned using DNA Alignment software (Fluxus Technology Ltd. 2005) with respect to the revised Cambridge Reference Sequence (rCRS) (Andrews et al., 1999). The ambiguous sequences were independently confirmed by PCR and sequencing in two different laboratories. All individuals were typed for three Restriction Fragment Length Polymorphism (RFLP) sites diagnostic for the four mtDNA macrohaplogroups (Hg) that encompass all the variability in Africa, Eurasia, and America: +3592HpaI HgL1/L2; −3592HpaI HgL3; +10397AluI HgM; +10871MnlI HgN. The individuals were then typed

Fig. 1. A map of Costa Rica showing the location of Puerto Limon. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

using a hierarchical approach for eight RFLP sites that define African, Amerindian, and Indian haplogroups: −5176AluI HgMD; +2349MboI HgL3e; +16389HinfI HgL2; +13803HaeIII HgL2a; +12308HinfI HgU; −12282AluI HgR6; +663HaeIII HgA; COII/tRNAlys 9-bp deletion HgB. RFLP analysis of the mtDNA coding region was performed by PCR using primers and conditions described elsewhere (Chen et al., 1995; Torroni et al., 1996; Metspalu et al., 2004). Digestions were carried out according to the conditions specified by the manufacturer (Fermentas International Inc, Burlington, Canada). The resulting fragments were resolved by electrophoresis in NuSieve plus SeaKem Agarose gels (Cambrex Bio Science Inc., Rockland, ME) and were visualized by UV-induced fluorescence after ethidium bromide staining. Our haplogroup classification follows Bandelt et al. (2003), Salas et al. (2004), Kong et al. (2006), and Palanichamy et al. (2004).

The sources of published HVSI sequence data used for comparison with the sequences obtained in our group are shown in the supplementary data section of the article. These data come from thirty-one populations from Central and South America (1,600 individuals), fifty-six from sub-Saharan Africa (3,600 individuals), sixty-two from India (2,500 individuals), and forty-eight from Eurasia (3,881 individuals).

Y-chromosome. A subsample of 24 male individuals was analyzed for the presence of 20 Y-Single Nucleotide Polymorphism (SNPs) markers, which allow one to distinguish between African, Native American, Indian, and European Y chromosome haplogroups (Thomas et al., 2000; Underhill et al., 2000; Pereira et al., 2002). SRY10831, M2/sY81, 92R7/M45, M3/DYS199, M9, 12f2, M173, and the insertion polymorphism M145/YAP were typed by using RFLPs as previously described (Rosser et al.,

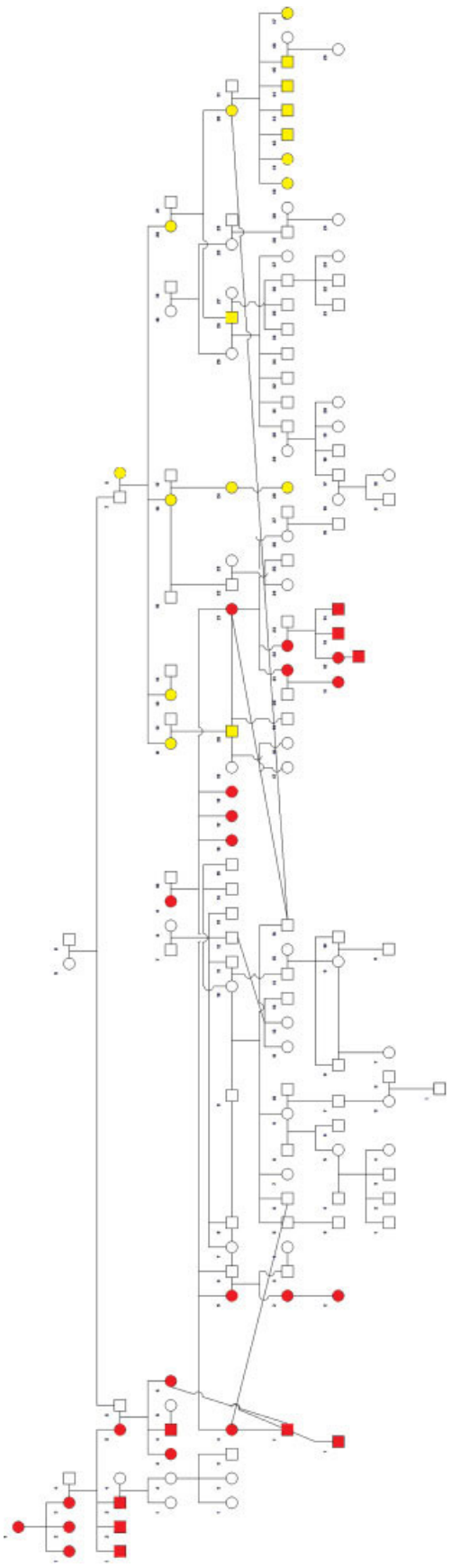

Fig. 2. The pedigree of the community showing three mtDNA lineages of East-Indian origin. In red (dark gray), two identical haplotypes of haplogroup M and in yellow (light gray) haplogroup R6. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

Fig. 3. Phylogenetic relationships and frequencies of the Y-chromosome binary haplogroups. In bold, the Y-haplogroups found in Indo-Costa Rica sample.

2000; Underhill et al., 2000). M42 and M60 were typed using primers and conditions described by Underhill et al. (2000) and digested with the enzymes AluI and MboI following the conditions specified by the manufacturer (Fermentas International Inc, Burlington, Canada). The resulting fragments were resolved by electrophoresis in NuSieve plus SeaKem Agarose gels (Cambrex Bio Science Inc., Rockland, ME) and visualized by UV-induced fluorescence after ethidium bromide staining. M52, M124, M130, and M242 were typed by use of allele-specific PCR (Wells et al., 2001; Seielstad et al., 2003). M34, M81, M78, M35, M96, and M123 were typed by means of a multiplex PCR, followed by a single base extension reaction using the SNaPshot multiplex kit, as described by Brion et al. (2004). The SNPs typed and their phylogenetic relationships are shown in Figure 3. We used the nomenclature system recommended by the Y Chromosome Consortium (YCC 2002) (Jobling and Tyler-Smith, 2003). To estimate haplotype variation within the haplogroups defined by binary polymorphisms, all individuals were also typed at Y-STR loci, by means of the PowerPlex Y System (Promega Corporation, Madison) which allows coamplification and detection of 12 Y-STR loci: DYS19, DYS385a/b, DYS389I/II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, and DYS439 (Ayub et al., 2000).

The sources of published data which were used for comparison with the sequences obtained in our group on seven Y-STRs (DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393) from 25 populations from Africa (1,592 individuals), 13 from Europe (1,700 individuals), 28 from Central and South America (2,560 individuals), and 21 populations from Eastern Eurasia (2,880 individuals) are shown in the supplementary data section. Additional pairwise comparisons were made with six Indian populations (615 individuals) (Kivisild et al., 2003; Cordaux et al., 2004b; Das et al., 2002, 2004; Banerjee et al., 2005; Mitchell et al., 2006), not all typed for all the 7 Y-STRs.

Statistical and admixture analyses

Parameters of within-population (haplotype diversity and mean number of pairwise comparisons, MNPD) and between population diversity were estimated by means of the software package Arlequin, version 3.01 (Excoffier et al., 2005). Haplotype diversity was calculated according to Nei (1987). A median-joining network (Bandelt et al., 1999) of the Y-STR haplotypes belonging to HgH was constructed using the Network 4.1.1.2 program (Fluxus Technology Ltd). Indian and Pakistan Y-STR data were from Sengupta et al. (2006). Y-STRs were weighted according to their repeat number variances so that higher weights were assigned to the least variable loci. The RM and MJ algorithms (reduction threshold = 1; $\varepsilon = 0$) were applied sequentially to reduce high dimensional reticulations within the network. Admixture estimates were obtained with ADMIX 2.0 (Dupanloup and Bertorelle, 2001). The software estimates from allele frequencies the relative contribution to a hybrid population of any number of parental populations. The admixture rates were estimated either from allele-frequency differences between populations or also considering in the calculations the molecular differences between alleles. In the former case, the admixture contributions correspond to conventional admixture rates (Dupanloup and Bertorelle, 2001). The estimates were independently obtained for mtDNA and Y chromosome data using haplogroup frequencies of four potential parental populations, namely Central/South America, the Indian subcontinent, West Africa, and Western Europe (the source of published data are given in the supplementary section).

RESULTS

mtDNA haplogroup diversity

The frequencies and the HVSI sequences of the mtDNA haplogroups found in the *Culí* sample are reported in Table 1. We obtained 17 haplotypes showing 31 polymorphic sites, with a gene diversity of 0.9218 ± 0.0182. This value is higher than that of Central Native American populations (Costa-Rica, Huetar, Kuna, Ngoebe), as expected in admixed populations (Table 2). This high intrapopulation heterogeneity as compared to the other Central America populations is confirmed by the high MNPD value (Table 2).

The *Culí* mtDNA gene pool is characterized by the presence of Native American (A2, B4), African (L2a, L2, L3e2b), and Eastern Eurasian (M*, MD, M2b, R6, U2a) haplogroups. The four Native American haplotypes belong one to haplogroup A2 and three to haplogroup B4 (Bandelt et al., 2003). To better characterize the A2 individual, we typed the HVSII sequence. The presence of the diagnostic motif 16,111/146/153 and of a 6 bp deletion of nps 106–111 associated with 16,360 transition, which have been detected in Central America populations (Santos et al., 1994; Merriwether et al., 1995), confirmed that this A haplotype is undoubtedly a Native American haplotype. Indeed, it is shared with a Boruca individual from Central America (Torroni et al., 1993).

In contrast, the attribution of the B4 haplotypes to subhaplogroup B2 that is typical of Native Americans is relatively uncertain, since no diagnostic HVSII motifs have been associated with this subhaplogroup (Bandelt et al., 2003). In addition, the haplotype CR011 has also been found in East-Eurasian populations (Yao et al.,

TABLE 1. mtDNA HVSI sequences and haplogroup frequencies in the Culí *sample*

Haplotypes	HVSI (HVSII)	RFLPs											HG	Freq
		+3592 HpaI	+10397 AluI	+10871 MnlI	+2349 MboI	+16389 HinfI	+13803 HaeIII	+12308 HinfI	−12282 AluI	9 BP DEL	−5176 AluI	+663 HaeIII		
CR037	111 124 223 290 319 360 362 (106-111 del, 146, 153, 235, 263, 309.2C, 315.1C)	−	−	+						D		+	A2	1
CR011	189 217	−	−	+						D			B4	1
CR019	183C 189 217	−	−	+						D				2
CR050	183C 189 217 309	−	−	+						D				1
CR042	114 223 278 318 390	+	−			+							L2	2
CR044	223 264 278 390	+	−			+								2
CR009	189 223 278 294 309 311 319 390	+	−	−	−	+	+						L2a	1
CR012	223 278 286 294 309 390	+	−	−	−	+	+							1
CR103A	223 278 290 294 309 390	+				+	+							5
CR0A	172 183C 189 223 320				+								L3e2b	3
CR001	192 223 271 316 362	−	+	−	−						−		MD	8
CR005	051 183C 189 223 316 355A	−	+	−						N	+		M*	4
CR027	183C 189 209 223 278	−	+							N	+			1
CR036	189 209 223 278	−	+							N	+			1
CR055	167iC 172 183C 189 223 274 319 320	−	+	−							+		M2b	1
CR015	114G 129 362	−	−	+				−	−				R6	6
CR016	051 206C 230 304 311	−	−	+				+	+				U2a	4
Total														*44*

2002a,b). Nevertheless, haplotypes CR011 and CR019 are largely shared with other Central and South American Native populations (Shields et al., 1993; Torroni et al., 1993; Santos et al., 1994; Batista et al., 1995; Kolman et al., 1995; Ward et al., 1996; Alves-Silva et al., 2000; Carvajal-Carmona et al., 2000; Green et al., 2000; Moraga et al., 2000; Fuselli et al., 2003; Bert et al., 2004; Bonilla et al., 2004; Salas et al., 2005), and the B haplotype CR050 is only one step derivative from CR019. Therefore, the attribution of these three haplotypes to Native American B2 lineages seems to be the most likely.

The African haplogroups represented in the *Culí* sample are L2, L2a, and L3e2b. Only the haplotype belonging to L3e2b has been observed in a New World population of African descent (Salas et al., 2005), while the other haplotypes are shared with West African populations, in particular with Guinea Bissau, Cabo Verde, and Sao Tomè (Mateu et al., 1997; Brehm et al., 2002; Rosa et al., 2004; Trovoada et al., 2004).

We found three haplogroups of likely Indian origin: M, U2a, and R6. The *Culí* haplotypes belonging to Hg M could be divided in three lineages: M*, MD, and M2b. The MD haplogroup could be found both in Asian and Native American populations, but Native American haplotypes belonging to MD can be distinguished from Asians by the presence of the 16,325 mutation (Bandelt et al., 2003). The haplotypes found in our *Culí* sample do not present this mutation and hence may be tentatively assigned to Indian lineages. M* and D lineages have been found widespread in the entire Indian subcontinent, but both M* and D *Culí* haplotypes have not been found to be shared with Indian or Eastern Eurasian populations, even if haplotype CR005 is a one step derivative from two individuals from West Bengal (Roychoudhury et al., 2001). This is not surprising since these haplogroups have a high genetic variability, and a large number of new and unique M haplotypes are frequently revealed in studies involving different parts of India (Metspalu et al., 2004; Kong et al., 2006; Sahoo and Kashyap, 2006). In contrast, the M2b haplotype has a restricted geographical distribution, since it has been found only in six Mukri individuals from Karnataka (Central/SW India) (Metspalu et al., 2004).

The R6 clade is an Indian specific sublineage of haplogroup R characterized by the HVSI motif 16,129–16,362. The *Culí* haplotype belonging to R6 is a one-step derivative from the ancestral motif and has been found also in one individual from Pakistan (Quintana-Murci et al., 2004). Haplogroup U is frequent in the Indian population and nearly 50% of the Indian U lineages belong to the Indian specific subhaplogroup U2 (Metspalu et al., 2004). The *Culí* haplotype assigned to U2a has been previously found in five individuals, all from the Northern area of prepartition India: three from Uttar Pradesh (N India, Kivisild et al., 1999; Metspalu et al., 2004), one from Rajastan (Metspalu et al., 2004), and one from Pakistan (Quintana-Murci et al., 2004).

In summary, the Native American lineages represent only 11.4% of the *Culí* mtDNAs, a value substantively lower than that observed in other Costa Rican populations (Table 3). It is also important to note the absence of European specific lineages, which have been found at high frequencies in some Central and South American populations (Table 3). The major components of the *Culí* mtDNA gene pool are African and Indian lineages. The former are present at frequencies of 31.8%, a relatively

TABLE 2. Gene diversity indices in some Native American populations

Pop	*n*	Geographic region	Countries	Haplotype diversity	SD	Mean number of pairwise	SD	Reference
N. Amer	25	North America	USA	0.9733	0.0223	6.7129	3.2754	Torroni et al. (1993)
Cheyenne	39	North America	USA	0.9730	0.0121	7.8338	3.7254	Kittles et al. (1999)
Eskimo	49	North America	Alaska	0.9141	0.0302	3.4640	1.7984	Shields et al. (1993)
Haida	42	North America	USA	0.6992	0.0617	2.6740	1.4530	Ward et al. (1993)
Pima	44	North America	USA	0.9408	0.0209	7.3680	3.5128	Kittles et al. (1999)
Yakima	42	North America	USA	0.8931	0.0317	5.3489	2.6327	Shields et al. (1993)
Costa-Rica	58	Central America	Costa-Rica	0.8693	0.0290	4.7994	2.3784	Carvajal-Carmona et al. (2003)
Limon	44	Central America	Costa-Rica	0.9218	0.0182	7.1567	3.4206	Present study
LimonAF	14			0.8352	0.0704	4.6679	2.4335	
LimonIN	25			0.8133	0.0411	6.7073	3.2729	
LimonNA	5			0.7000	0.2184	4.5167	2.6694	
Huetar	27	Central America	Costa-Rica	0.7094	0.0701	3.2385	1.7231	Santos et al. (1994)
Kuna	63	Central America	Panama	0.5699	0.0593	3.6248	1.8621	Batista et al. (1995)
Ngoebe	46	Central America	Panama	0.5237	0.0692	3.9868	2.0307	Kolman et al. (1995)
SAmerTorr	13	South America		1.0000	0.0302	6.2839	3.1890	Torroni et al. (1993)
Antioquia	84	South America	Colombia	0.8560	0.0272	5.7456	2.7784	Carvajal-Carmona et al. (2003)
Arequipa	22	South America	Perù	0.9307	0.0463	5.2848	2.6539	Fuselli et al. (2003)
Brazilian	246	South America	Brazil	0.9843	0.0040	7.9513	3.7088	Alves-Silva et al. (2000)
Gaviao	28	South America	Brazil	0.8624	0.0266	4.6256	2.3391	Ward et al. (1996)
Xavante	24	South America	Brazil	0.6848	0.0517	3.3875	1.7970	Ward et al. (1996)
Zoro	29	South America	Brazil	0.7586	0.0661	4.1896	2.1431	Ward et al. (1996)
Guahibo	59	South America	Venezuela	0.8106	0.0283	5.5665	2.7122	Vona et al. (2005)
Mapuche 2	34	South America	Chile	0.8378	0.0456	6.1374	2.9924	Moraga et al. (2000)
Movima	12	South America	Bolivia	0.8939	0.0777	3.1144	1.7366	Bert et al. (2004)
Moxo	27	South America	Bolivia	0.9772	0.0171	6.8075	3.3087	Bert et al. (2004)
Pehuenche	24	South America	Chile	0.9022	0.0462	6.4596	3.1676	Moraga et al. (2000)
San Martin	22	South America	Perù	0.9394	0.0367	5.7529	2.8629	Fuselli et al. (2003)
Tacuarembo	24	South America	Uruguay	0.9928	0.0144	7.5765	3.6636	Bonilla et al. (2004)
Tayacaja	61	South America	Perù	0.9678	0.0144	6.6681	3.1900	Fuselli et al. (2003)
Yaghan	15	South America	Chile	0.8857	0.0501	5.8624	2.9675	Moraga et al. (2000)
Yanomama	100	South America	Brazil	0.8702	0.0307	3.9572	2.0147	Easton et al. (1996)
Yuracare	15	South America	Bolivia	0.9429	0.0403	6.7628	3.3770	Bert et al. (2004)

TABLE 3. Frequencies of continent specific mtDNA haplogroups in some Central and South America populations

		Native American		African		European		Indian		
	Total	*n*	%	*n*	%	*n*	%	*n*	%	Reference
Mexico	223	199	89.10	10	4.50	12	5.38	0	0.00	Green et al. (2000)
Garifunas	44	7	15.91	37	84.09	0	0.00	0	0.00	Salas et al. (2005)
Costa Rica	59	49	83.00	nd	nd	nd	nd	nd	nd	Carvajal-Carmona et al. (2003)
Limón	44	5	11.36	14	31.82	0	0.00	25	56.82	Present study
Puerto Rico	800	489	61.30	220	27.20	91	11.50	0	0.00	Martinez-Cruzado et al. (2005)
Chocó	49	8	16.33	41	83.67	0	0.00	0	0.00	Salas et al. (2005)
Antioquia	113	102	90.00	nd	nd	nd	nd	nd	nd	Carvajal-Carmona et al. (2003)
Colombia	230	96	41.74	58	25.22	61	26.52	0	0.00	Rodas et al. (2003)
Brazil	247	81	33.00	69	28.00	96	38.87	0	0.00	Alves-Silva et al. (2000)

nd, Not determined.

high value if compared with that observed in New World groups with the exception of Afro-Colombians from Choco and Garifunas from Honduras. The highest contribution to the *Culí* mtDNA gene pool is due to Indian lineages with a frequency of 56.8%. These lineages have not been revealed in other Central or South American population, with the exception of some sporadic occurrence (Alves-Silva et al., 2000). Moreover, the low number of haplotypes (one in the case of haplogroups U2a, R6 and MD) belonging to each Indian lineage points out to a strong founder effect, evident also for the Native American and African components.

Figure 2 shows the descendants of three women who brought East Indian haplotypes to the community, two of whom have the same haplotype belonging to haplogroup M, although they arrived in the community at different times. Each haplogroup is denoted by a different color. The figure illustrates that most of the individuals who have East-Indian lineages descend from a few women.

Y-chromosome

The frequency distribution of Y-Hgs for the Indo-Costa Rica population is given in Figure 3, and the Y-STR haplotypes are shown in Table 4. Six haplogroups (E3a-M2, E3b-M35, E3b3a-M34, R1-M173, H-M52, Y*) have been detected within our sample, five of them representing a continent-specific lineage.

The HgE haplotypes can be assigned to three sister clades E3a-M2, E3b-M35, and E3b3a-M34 that account for 25, 12.5, and 4.17% of the samples respectively. E3a-M2 and E3b-M35 clades are widespread in African populations and they are present at high frequencies also in individuals of African ancestry from the New World (Carvalho-Silva et al., 2001; Bortolini et al., 2002; Lell et al., 2002). Two of the five Indo-Costa Rican E3a-M2 haplotypes are shared with Central and South America populations, specifically El Salvador (Lovo et al., 2004), Antioquia (Builes et al., 2005; Gaviria et al., 2005),

TABLE 4. Y-chromosome STRs haplotypes in the Culí sample

	STRs											
Samples	DYS19	DYS385	DYS389I	DYS389II	DYS390	DYS391	DYS392	DYS393	DYS437	DYS438	DYS439	HG
CR004	15	16–18	13	33	21	10	11	13	14	11	12	E3a
CR015	15	16–18	13	30	21	10	11	13	14	11	12	
CR044	16	18–18	13	30	21	10	8	15	14	11	12	
CR055	17	18–18	11	31	21	10	11	14	14	11	12	
CR054	17	18–18	13	31	21	10	11	14	14	11	12	
CR005	17	18–18	13	31	21	10	11	14	14	11	12	
CR013	15	13–16	12	29	22	10	11	13	16	9	13	E3b
CR042	13	14–14	12	30	25	9	11	13	14	10	10	
CR047	14	14–18	12	28	25	10	11	13	14	11	12	
CR021	13	16–17	13	31	24	10	11	13	14	10	12	E3b3a
CR025	14	11–14	13	30	24	10	13	13	15	13	12	R1*
CR104A	14	11–14	13	30	24	10	13	13	15	13	12	
CR011	14	15–17	12	29	22	10	11	12	14	9	11	H
CR012	14	15–17	12	29	22	10	11	12	14	9	11	
CR016	14	15–17	12	29	22	10	11	12	14	9	11	
CR017	14	15–17	12	29	22	10	11	12	14	9	11	
CR018	14	15–17	12	29	22	10	11	12	14	9	11	
CR048	14	15–17	12	29	22	10	11	12	14	9	11	
CR050	14	15–17	12	29	22	10	11	12	14	9	11	
CR063	14	15–17	12	29	22	10	11	12	14	9	11	
CR0A	14	15–17	12	29	21	10	11	12	14	9	11	
CR34A	14	15–17	12	29	22	10	11	12	14	9	11	
CR052	16	14–15	12	28	22	10	12	14	16	11	11	Y(xCDEHJK)
CR053	16	14–15	12	29	22	10	12	14	16	11	11	

Choco (Yunis et al., 2005), and Brazil (deSousa-Goes et al., 2005), but they have also been found in African populations, mainly from the western regions such as Equatorial Guinea (Arroyo-Pardo et al., 2005) and Guinea Bissau (Rosa et al., 2004). Two E3b-M35 haplotypes have been found in western and south-eastern African populations (Guinea Bissau, Rosa et al., 2006; Mozambique, Alves et al., 2003; Pereira et al., 2002), and one of them has also been reported in South-American populations, specifically Choco (Yunis et al., 2005), Brazil (deSousa-Goes et al., 2005), and Argentina (Fondevila et al., 2003). Inversely, the E3b3a-M34 haplotype is shared with North-African and Spanish populations (Brandt-Casadevall et al., 2003; Fondevila et al., 2003; Martin et al., 2004; Cherni et al., 2005) and with South American individuals from Colombia, where a predominance of Y-chromosome of European ancestry has been observed (Carvajal-Carmona et al., 2000, 2003; Bedoya et al., 2006).

Two Indo-Costa Rica individuals belong to R1-M173, a lineage present in Europe, and, at low frequencies, in Native American populations and in Asia (Lell et al., 2002; Hammer et al., 2006; Xue et al., 2006). Therefore it would be hard to assess the genetic ancestry of these individuals. Nevertheless, comparisons with Asian, European, and Native American populations revealed that the Y-STR haplotype of R1-M173 Indo-Costa Rican samples is widely shared with Europeans and Latin and North Americans, with a number of haplotypes being one step neighbors from the Indo-Costa Rica R1-M173 haplotypes (YHRD, Y Chromosome Haplotype Reference Database). Only sporadic occurrences have been observed in Asian populations. Thus, this result can be interpreted as suggesting a European origin of the Y chromosomes for these two individuals.

Lineage H1-M52 accounts for 41.67% of the Indo-Costa Rica samples. This haplogroup is of indigenous Indian origin (Cordaux et al., 2004a), with higher frequencies in north-eastern Indian regions (Sengupta et al., 2006). Nine out of ten H1-M52 individuals show the same STR haplotype, whereas the other is a one-step neighbor, thus suggesting a strong founder effect. Although these two haplotypes were not detected in a sample of 1,341 chromosomes from different Indian regions (Kivisild et al., 2003; Das et al., 2004; Mitchell et al., 2006; Sahoo and Kashyap, 2006; Sahoo et al., 2006; Sengupta et al., 2006), they are one-step neighbors from one South Indian individual (Sengupta et al., 2006) and three steps derivatives from the modal haplotype (Fig. 5).

Finally, two Indo-Costa Rica individuals (8.33%) belong to the Y* (YxCDEHJK) haplogroup. The Y* lineage has been observed in populations from Colombia and Costa Rica (Carvajal-Carmona et al., 2003), with frequencies close to European populations. The two individuals are one step neighbor, and a search in the YHRD revealed the presence of one individual from Northern Portugal with the same CR052 haplotype. Then, it seems likely that these two Indo-Costa Rica individuals share a common European origin.

Figure 4 shows that all nine individuals with the H1-M52 STR haplotype descend from a single man (shown in red). In contrast, the men who carry the HgE haplotypes descend from different "founding fathers", that is, men who migrated into the community (shown in blue). Therefore, the genetic data validate what the pedigree indicates, namely, that the population descends from a few founding individuals from India and that it received many immigrants, most likely Afro-Limonenses.

When compared with those of other Central and South America populations (Table 5), our Indo-Costa Rica sample shows higher frequencies of African (E3a-M2 and E3b-M35) lineages and a dramatically lower frequencies of native American lineages (P-M45 and Q-M3). On the contrary, lineages of Indian origin (H1-M52), virtually absent in other New World populations, have very high frequencies, suggesting a strong contribution to the Indo-Costa Rica population. Nevertheless, Y-chromosome microsatellite haplotype diversity is lower than in other

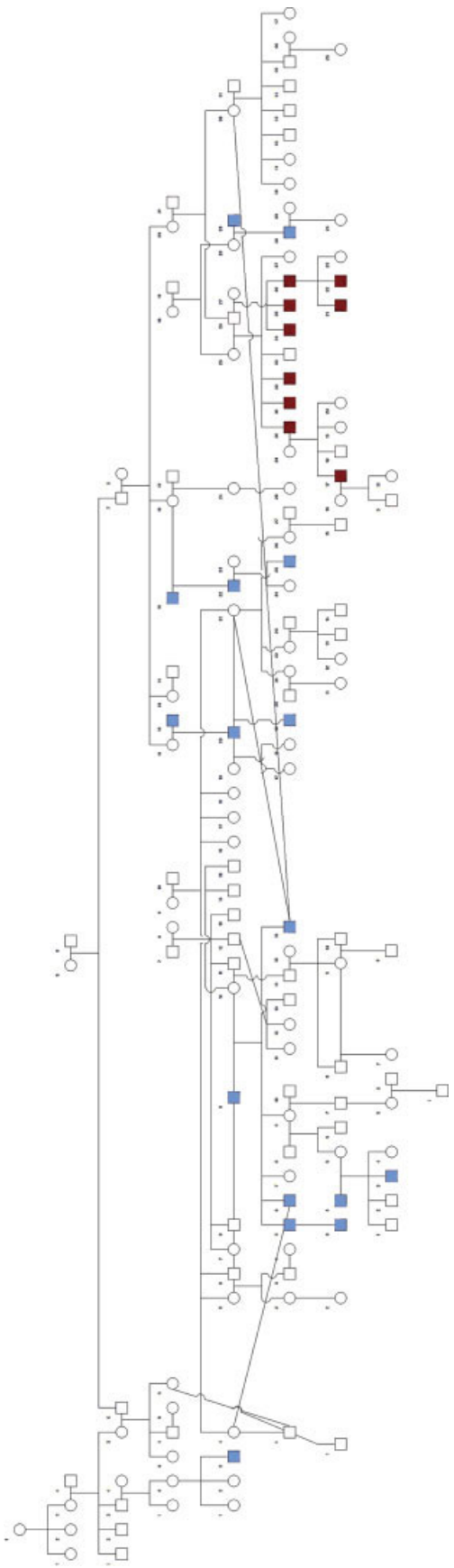

Fig. 4. The pedigree of the community shown in blue (gray) E3a (African-origin), and in red (black) H1-M52 (East-Indian origin) Y-haplotype lineages. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

Native American population, with a dramatic reduction of diversity when considering the Indian fraction separately (Table 6). The presence of at least two (R1-M173 and E3b3a), and probably three (Y*) lineages of possibly European origin, and the absence of Native American lineages is noteworthy, in contrast with the mtDNA data where no European haplogroup was observed, and Native American lineages represent 11.36% of the gene pool.

Admixture analysis

The haplotype frequencies in the potential sources of mtDNA and Y chromosomes were approximated by using the available data on four populations namely Central/South America, Western Africa, India, and Western Europe. The first tests showed negative admixture rates for European and Native Americans for mtDNA and the Y chromosome, respectively. Therefore, further analyses were performed using only three parental populations for both markers. The relative contributions to the maternal and paternal gene pool of the *Culí* sample are shown in Table 7. The estimated Indian contribution, when considering the Indian population as a whole, is high, and only slightly different from the admixture estimates obtained using the continent-specific haplogroup frequencies. We also estimated admixture rates considering the tribal and the caste populations separately; the estimated contributions from Indian caste populations were similar to the Indian tribal contributions. These values were only slightly different when the analysis was performed without taking into account the molecular differences between alleles, which is not surprising, given the large differences between the haplotypes characterizing the potential parental populations.

To better understand the role of different Indian regions in the migration wave to Central America, the admixture analysis was then performed using the haplogroup frequencies of the Indian provinces pooled in five geographic regions: North, Northeast, West, Central, and South. The highest contributions were obtained with Central Indian provinces and then with the Northern region for mtDNA and with the Southern region for the Y-chromosome. The genetic distances based on mtDNA and Y chromosome haplogroup frequencies (Table 8) between the Limón sample and each Indian region indicate closer relationships with the Central and North Indian region for mtDNA and with Central/South/West regions for the Y-chromosome.

In conclusion, the admixture estimates based on maternal and paternal markers reveal that the *Culí* population had different maternal and paternal contributions to its overwhelmingly Central Indian core. Whereas the mtDNA gene pool demonstrates a contribution from Amerindian and African sources, it lacks a European component. In sharp contrast, the Y chromosomal gene pool lacks Amerindian markers, has a substantial African component, and a moderate European contribution.

DISCUSSION

In this paper, we report results of an on-going biocultural investigation with a recently described Indo-Costa Rican population (Madrigal et al., 2007). The group was keenly interested in participating in the genetic aspect

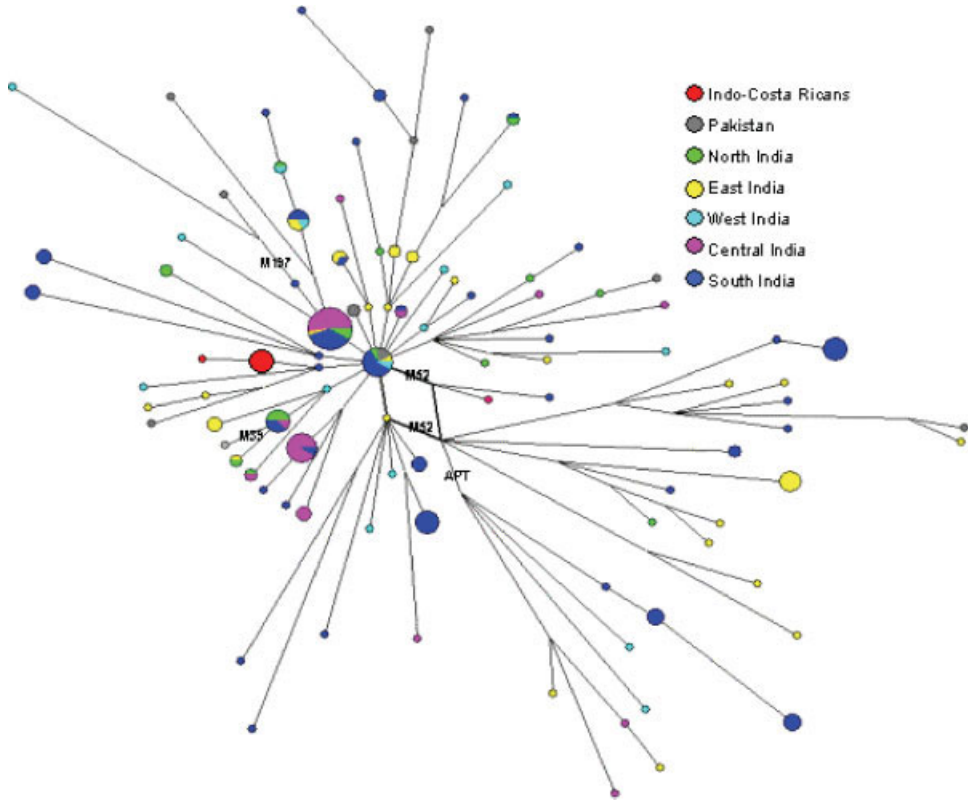

Fig. 5. Median-joining network of Y-STR haplotypes belonging to haplogroupH in Indo-CostaRican, India, and Pakistan samples. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

TABLE 5. Frequencies of Y-chromosome lineages in some Central and South America populations

		P-M45		DE		Y(xDEQ)		H1-M52		
	Total	*n*	%	*n*	%	*n*	%	*n*	%	Reference
Mexico	29	27	93.10	2	6.90					Lell et al. (2002)
C. America	60	56	93.33			4	6.67			Lell et al. (2002)
Panama	15	12	80.00			3	20.00			Ruiz-Narvaez et al. (2005)
Costa Rica	78	59	75.64			19	24.36			Ruiz-Narvaez et al. (2005)
Costa Rica	60	30	50.00	7	11.67	23	38.33			Carvajal-Carmona et al. (2003)
Limón	24			10	41.67	4	16.67	10	41.67	Present study
Antioquia	80	48	60.00	6	7.50	26	32.50			Carvajal-Carmona et al. (2003)
Oriente	92	69	75.00	5	5.43	18	19.57			Bedoya et al. (2006)
Colombia	102	92	90.20	4	3.92	6	5.88			Bortolini et al. (2003)
Brazil	200	108	54.00	57	28.50	35	17.50			Carvalho-Silva et al. (2006)

of the project, as it wished to know where in prepartition India (or even if) their ancestors came from. Thus, our study fills an important gap in the anthropological study of the Caribbean region, but most importantly, it is a service to the community itself.

We acknowledge the small size of our sample, but note that if the entire population of *Culís* is less than 100 people, our initial sample of forty-four individuals included close to half of the population and our second subsample of 24 males included about a quarter of the group. It is hard to imagine that genetically unrelated individuals may have escaped sampling, thus leading us to underestimate the genetic diversity of the *Culí* population. Indeed, it is remarkable that there are 17 mtDNA haplotypes in the sample, and 16 females with no ancestors in the pedigree (Fig. 2). In the same manner, there are 14 Y-chromosomal STR haplotypes, and 17 "founding fathers" in the pedigree (two of whom were brothers and presumably had identical Y chromosomes). This suggests that if anything, we have missed a "founding mother" but not her genetic contribution, and that two of the "founding fathers" brought identical Y-chromosomal markers.

We used standard procedures to type mtDNA and Y-chromosomal markers. We were interested in determining not only the place in India from where the ancestors of the community migrated, but also the importance of gene flow with non-*Culís* in the evolution of the Indo-Costa Rican gene pool. Thus, we computed admixture measures to estimate the contribution of other ethnic groups to the *Culí* community. We wish to note that when we compute admixture estimates we do not subscribe to a racial view of human variation (Risch, 2006) but are focusing on the very small proportion of human variation that is different among groups and can throw light on the geographical origin of a marker (Barbujani,

TABLE 6. Haplotype diversity indices calculated from 7 Y-STRs in some Native American populations

	n	Geographic region	Countries	Haplotype diversity	*SD*	Reference
Maya	7	Central	Mexico	1.0000	*0.0764*	Bianchi et al. (1998)
El Salvador	120	Central	El Salvador	0.9927	*0.0032*	Lovo et al. (2004)
Culís	24	Central	Costa Rica	0.8587	*0.0657*	Present study
Limon AF	9			0.9444	*0.0702*	
Limon EU	5			0.9000	*0.1610*	
Limon IN	10			0.2000	*0.1541*	
Antioquia	777	Central	Colombia	0.9883	*0.0013*	Builes et al. (2005)
Cartagena	173	Central	Colombia	0.9895	*0.0036*	Builes et al. (2005)
Chocó	134	Central	Colombia	0.9909	*0.0025*	Yunis et al. (2005)
CaucMestizo	137	Central	Colombia	0.9879	*0.0044*	Yunis et al. (2005)
AntioquiaG	400	Central	Colombia	0.9793	*0.0035*	Gaviria et al. (2005)
Chimila	5	Central	Colombia	0.8000	*0.1640*	Bianchi et al. (1998)
Afro-Ecuador	9	South	Ecuador	0.7222	*0.1592*	Bravi et al. (2000)
Perú	79	South	Perù	0.9893	*0.0049*	Iannacone et al. (2005)
BrazilG	198	South	Brazil	0.9930	*0.0019*	Grattapaglia et al. (2005)
BrazilD	126	South	Brazil	0.9886	*0.0039*	de Souza et al. (2005)
Suriname	54	South	Suriname	0.9951	*0.0045*	Kayser et al. (2001)
Paraguay	10	South	Paraguay	0.8889	*0.0754*	Bianchi et al. (1998)
Afro-Uruguay	4	South		1.0000	*0.1768*	Bravi et al. (2000)
Wichi	13	South	Argentina	0.9872	*0.0354*	Bianchi et al. (1998)
Chorote	23	South	Argentina	0.9684	*0.0224*	Bianchi et al. (1998)
Córdoba	100	South	Argentina	0.9832	*0.0065*	Fondevila et al. (2003)
Buenos Aires	100	South	Argentina	0.9877	*0.0051*	Kayser et al. (2001)
La Plata	22	South	Argentina	0.9394	*0.0367*	Bravi et al. (2000)
Tehuelche	6	South	Argentina	1.0000	*0.0962*	Bianchi et al. (1998)
Mapuche	5	South	Argentina	1.0000	*0.1265*	Bianchi et al. (1998)
Native S. Amer	46	South		0.9826	*0.0089*	Kayser et al. (2001)

LimonAF, African haplotypes; LimonEU, European haplotypes; LimonIN, Indian haplotypes.

2005). Because there is more variation within than among human groups, when we say that a marker has only been found in a particular region of India, we do not mean that the marker is inexistent someplace else.

Madrigal et al. (2007) noted that the *Culís* avoided close kin marriage, a pattern found in Northern/Central non-tribal Indian Hindu communities. They proposed that this cultural trait suggested that the ancestors of the *Culís* migrated from these regions in prepartition India. In addition, Madrigal et al. indicated that the gene flow with non-*Culís* involved primarily males of the Afro-Limonense community and proposed that the Y chromosomal markers of the *Culí* community would have a greater African component than would the mtDNA markers. We find support for both propositions.

The genetic data indicate that the primary ancestral population of the *Culís* is from the Indian subcontinent, mostly from the Central area of India. Interestingly, whereas the mtDNA suggests a Central/Northern Indian origin, the Y-chromosome markers suggest a Central/South/West Indian origin of the ancestors. These results support the study participant's reports that some ancestors migrated not as married couples, but as single individuals who married other indentured servants in the New World. It is also possible that the ancestors came from different areas of India because they migrated at different times. The arrival of new individuals into the community at different times is indeed supported by the pedigree.

Although the maternal and paternal markers both agree on the overwhelmingly Indian origin of the community, they paint a very different picture of its evolution by gene flow. Whereas the *Culí* mtDNA gene pool has a substantial African component (31.82%) and a minor Amerindian component (11.36%), lacking evidence of European admixture, the Y-chromosome gene pool lacks any Amerindian marker, while having a large African (37.5%) and a moderate European component (20.8%). We do not know if the Amerindian markers were a result of gene flow with local Costa Rican Amerindians or if they came to the *Culí* population via the Afro-Limonenses who married in with the *Culís*, whose ancestors might have mated with Amerindian Jamaican or Costa Rican women. However, the most likely explanation is that the Amerindian markers were brought by Afro-Limonenses, given that most individuals who married in the community had English names. Local Amerindians, in contrast with Afro-Limonenses, usually have Spanish names.

At the same time, the absence of European mtDNA markers suggests that gene flow with the Spanish-speaking Limonense community and of African slaves with European females in Jamaica was either nonexistent, or left no traces to the present time. Our community's pedigree certainly supports this first point, as Spanish names enter into the pedigree only in the last two generations. Additionaly, the paucity of European females in the plantations of the Caribbean is a well-known fact. Thus, it is very unlikely that European females in Jamaica would have contributed to the mtDNA gene pool of the slaves.

In contrast, it is well known that European males frequently produced offspring with their African slaves, thus contributing Y-chromosomal markers to the Afro-Jamaican ancestors of the Afro-Limonense community. Therefore, it is not surprising to find both European and African Y-chromosomal markers in the *Culí* group, whose pedigree shows more males than females of English names (and presumably of Jamaican descent) marrying into the community. These males probably brought the European as well as the African paternal markers to the *Culí* community. We also detected in our community some African haplotypes previously unreported in any New World African-derived population,

TABLE 7. Admixture estimates in Culís

	Central America				West Africa				India				Europe			
	mtDNA		Y chromosome		mtDNA		Y chromosome		mtDNA		Y chromosome		mtDNA		Y chromosome	
	m	*SD*	*m*	*SD*	*m*	*SD*	*m*	*SD*	*m*	*SD*	*m*	*SD*	*m*	*SD*	*m*	*SD*
	0.1136		0.0000		0.3182		0.3750		0.5682		0.4167		0.0000		0.2083	
India	**0.2469**	***0.0820***			**0.3949**	***0.0883***	**0.4037**	***0.1580***	**0.3582**	***0.1082***	**0.5120**	***0.1827***			**0.0843**	***0.1877***
	0.2015	*0.0644*			0.4414	*0.0811*	0.4907	*0.1559*	0.3570	*0.0809*	0.6745	*0.1775*			−0.1652	*0.0819*
India tribe	**0.2666**	***0.0819***			**0.4029**	***0.0864***	**0.3996**	***0.1599***	**0.3305**	***0.1045***	**0.5329**	***0.1515***			**0.0675**	***0.1532***
	0.2163	*0.0647*			0.4547	*0.0792*	0.5102	*0.1480*	0.3290	*0.0782*	0.5758	*0.1522*			−0.0860	*0.0902*
India caste	**0.2308**	***0.0806***			**0.3901**	***0.0874***	**0.4425**	***0.1534***	**0.3791**	***0.1082***	**0.4247**	***0.2203***			**0.1328**	***0.2422***
	0.1894	*0.0633*			0.4283	*0.0814*	0.5261	*0.1495*	0.3823	*0.0818*	0.6905	*0.1974*			−0.2166	*0.0970*
North India	**0.0964**	***0.1160***			**0.3773**	***0.0897***	**0.4907**	***0.1493***	**0.5263**	***0.1496***	**0.3361**	***0.1799***			**0.1731**	***0.2139***
	0.1472	*0.0785*			0.3176	*0.0961*	0.6529	*0.1266*	0.5352	*0.1087*	0.4084	*0.1547*			−0.0613	*0.1211*
North East India	**0.2172**	***0.1184***			**0.3995**	***0.0877***	**0.4890**	***0.1443***	**0.3833**	***0.1445***	**0.3448**	***0.0921***			**0.1662**	***0.1230***
	0.1712	*0.0906*			0.4089	*0.0877*	0.6236	*0.1249*	0.4199	*0.1198*	0.2829	*0.0764*			0.0935	*0.0827*
West India	**0.1389**	***0.1185***			**0.3781**	***0.0894***	**0.3933**	***0.1559***	**0.4830**	***0.1506***	**0.4655**	***0.1801***			**0.1412**	***0.1934***
	0.1180	*0.0822*			0.3617	*0.0933*	0.4976	*0.1451*	0.5203	*0.1171*	0.7627	*0.1833*			−0.2602	*0.1019*
Central India	**0.0881**	***0.1261***			**0.3620**	***0.0888***	**0.3930**	***0.1622***	**0.5499**	***0.1563***	**0.6450**	***0.1746***			**−0.0379**	***0.1629***
	0.0529	*0.1024*			0.3418	*0.0976*	0.4973	*0.1500*	0.6053	*0.1317*	0.7016	*0.1750*			−0.1989	*0.1013*
South India	**0.2205**	***0.1078***			**0.3912**	***0.0866***	**0.3869**	***0.1592***	**0.3882**	***0.1315***	**0.5714**	***0.1808***			**0.0417**	***0.1711***
	0.1547	*0.0865*			0.4118	*0.0843*	0.4702	*0.1599*	0.4334	*0.1097*	0.6780	*0.1813*			−0.1482	*0.0783*

In the first line the admixture rates estimated on the basis of continent-specific haplogroups frequencies.
In the first column were reported the different Indian groups or regional subgroups used as parentals for each estimates, in the following columns the estimates relative to each parental populations.
Boldface represents the rates obtained considering the molecular differences between alleles.
The Indian regions with the highest estimated contributions are underlined.*m*, admixture rate; SD, standard deviation.

TABLE 8. Genetic distances based on mtDNA and Y-chromosome haplogroup frequencies between Indo-Costa Ricans and different Indian regions

	mtDNA	Y chromosome
North	0.0668	0.2101
North East	0.1957	0.2672
West	0.1009	0.0880
Central	0.0475	0.0896
South	0.2148	0.0727

which is not surprising, given the diverse origin of African slaves brought to the New World.

Our results, together with those of previous researchers, strongly indicate that human populations which arise as a result of admixture do not necessarily include paternal and maternal representatives of the parental groups. Rather, whereas a parental population may supply males, another parental population may supply females. In the wider context of the evolution of Latin American living populations, our results confirm previous studies of African-derived and "Mestizo" populations in the Caribbean and Latin America, which indicate that whereas male Amerindians were largely eliminated upon the invasion of the Europeans, female Amerindians were kept as wives of European and African males. Similar results have been found in Afro-Uruguayan (Bravi et al., 1997) and Afro-Brazilian samples (Bortolini et al., 1997a,b; Abe-Sandes et al., 2004). In the same manner, the presence of European paternal, but not maternal markers in Afro-Jamaican groups indicates that male Europeans contributed to the formation of the Afro-Jamaican gene pool, whereas female Europeans did not (Parra et al., 1998). These studies indicate that gene flow in humans may be gender-mediated, and that the precise historical context in which the gene flow took place must be taken into consideration.

Just like gene flow has been a major force in the evolution of the *Culí* gene pool, so has genetic drift. Intrapopulation diversity, calculated as haplotype diversity for mtDNA and the Y chromosome, shows a clear reduction of diversity. Such reduction is a probable consequence of the founder effect, which is strong in female lineages and even stronger in male Indian lineages. Indeed, in the case of mtDNA, three women contributed their East-Indian mtDNA to a large proportion of the community. In the case of Y-chromosomal lineages, the most common Indian haplotype in the community is found in the descendants of one man.

If anything, the story of the *Culís* is a mirror of the story of many Caribbean communities. This group is part of massive migrations of indentured servants who filled the void left by the out-migration of former African slaves. In their new land, the *Culís* maintained a strict avoidance of close-kin marriage and married with their neighbors, who descended from Afro-Jamaican workers, and whose ancestors were forcefully brought to the Caribbean by the European powers. The evolution of the *Culí* gene pool cannot be considered separately from that of Afro-Caribbean communities that received mtDNA markers from Amerindian but not from European females and Y-chromosomal markers from European but not Amerindian males.

CONCLUSIONS

In the *Culí* gene pool, we can see slavery and indentured servitude resulting in mass migration, the disappearance of Amerindian males but the use of Amerindian females as wives to the invading males and their slaves, the virtual absence of European females in the plantation and their nonexistent contribution to the mtDNA slave gene pool, the-matter-of fact gene flow of European males into the slave Y-chromosomal gene pool, and the gene flow of Afro-Limonenses into the *Culí* community—a gene flow that brought not only African and European paternal markers, but also Amerindian maternal markers.

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