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Uniparental (mtDNA, Y-chromosome) Polymorphisms in French Guiana and Two Related Populations – Implications for the Region's Colonization

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Running head: **mtDNA and Y-Chromosome Studies in French Guiana Indians**

Key words: genetic markers, Amerindian populations, French Guiana colonization

Summary

Blood samples collected in four Amerindian French Guiana populations (Palikur, Emerillon, Wayampi and Kali'na) in the early 1980's were screened for selected mtDNA and Y-chromosome length polymorphisms, and sequenced for the mtDNA hypervariable segment I (HVS-I). In addition, two other Amerindian populations (Apalaí and Matsiguenga) were examined for the same markers to establish the genetic relationships in the area. Strong dissimilarities were observed in the distribution of the founding Amerindian haplogroups and significant p-values were obtained from F_{ST} genetic distances. Interpopulation similarities occur mainly due to geography. The Palikur did not show obvious genetic similarity to the Matsiguenga, who speak the same language and live in a region from where they could have migrated to French Guiana. The African-origin admixture observed in the Kali'na is probably derived from historical contacts they had with the Bushinengue (Noir Marron), a group of escaped slaves who now have an independent life at a nearby region. The analysis raised significant clues about the Amerindian peoplement of the North-East Amazonian region.

Introduction

French Guiana is located on the Atlantic coast of South America, north of the mouth of the Amazon River. This French department is mostly covered by the Amazonian rainforest and is presently inhabited by five non-acculturated Native American populations whose members speak languages from three large families, Arawak (Palikur), Karib (Kali'na, Wayana), and Tupi-Guarani (Emerillon, Wayampi). The first groups arrived at the region in the first centuries of the present era occupying distinct places in the littoral and interior along the years; culturally they show a series of clear distinctions, both in relation to their material tools and social organization (Nimuendajú 1926; Grenand & Grenand 1985; Campbell 1997). Their genetic relationships have initially been examined by the study of several hemato-immunologic systems (Larrouy *et al*. 1964a,b; Daveau *et al*. 1975; Tchen *et al*. 1978a,b; 1981; Dugoujon *et al*. 1994). The results associated with those obtained for the Apalaí-Wayana, a neighboring Amerindian tribe living in the Brazilian state of Amapá (Salzano *et al*. 1988), have mainly revealed the genetic distinction between the hinterland Emerillon and the coastal Palikur, in accordance with archaeological, ethnological and contemporary demographic data (Mazières *et al*. 2007). These authors stressed the usefulness of DNA investigations to better understand French Guiana's early settlement. In particular, the Palikur remain one of the most enigmatic populations. Linguistic approaches placed the putative origin of this Maipurean-speaking group in as remote an area as the North-Central Peruvian region, from where speakers of the Maipurean branch of the Arawak family could have expanded 3,000 years ago (Urban 1992; Campbell 1997).

For more than two decades, Native American Indians have been widely examined for the mitochondrial DNA (mtDNA) and the nonrecombining portion of the Y-chromosome (NRY), two uniparental inherited genetic systems intensively screened in human populations (Horai *et al*. 1995; Ingman *et al*. 2000; Underhill *et al*. 2000, 2001). Problems related to the Amerindian populations relationships and their migration patterns were investigated (Torroni *et al*. 1992;

Horai *et al*. 1993; Merriwether *et al*. 1995; Underhill *et al*. 1996; Bonatto & Salzano 1997; Salzano 2002; Schurr & Sherry 2004). These and other studies showed that most of the Y-chromosome and mtDNA diversity fall into major haplogroups defined by specific single nucleotide polymorphisms (SNPs) and other types of markers (Wallace *et al*. 1985; Schurr *et al*. 1990; Bailliet *et al*. 1994; Forster *et al.* 1996; Underhill *et al*. 1996; Brown *et al*. 1998; Bergen *et al*. 1999; Bortolini*et al*. 2003; Jobling & Tyler -Smith 2003; Seielstad *et al*. 2003). In South America these studies have dealt with extinct and extant populations (Ribeiro-dos-Santos *et al*. 1996; Lalueza *et al*. 1997; Bert *et al*. 2001, 2004; Garcia-Bour*et al*. 2004; Moraga *et al*. 2005; Lewis *et al*. 2005; Marrero *et al*. 2007a; Torres *et al*. 2006). However, data derived from French Guiana are still nonexistent.

In the present work four native French Guiana populations (Palikur, Kali'na, Emerillon, Wayampi) were studied for three RFLP sites and a 9-bp deletion which are diagnostic for the major mtDNA haplogroups, as well as for the HVS-I region of the mtDNA; while the male fraction was also tested for eight NRY biallelic markers. They were compared using the same markers with the neighboring Brazilian Apalaí and the Peruvian Matsiguenga, a Maipurean-speaking tribe linguisticaly related to the French Guiana Palikur. The following questions were adressed: (1) are the genetic relationships mainly associated to geographic or linguistic factors? (2) by comparing the two Maipurean-speaking tribes, can genetics link the Palikur to the putative region from where they could have originated? (3) are the outside (non-Amerindian) influences mainly due to recent or past events? and (4) do the historical data agree with the genetic results? Which inferences can be drawn from the genetic data about French Guiana's Amerindian colonization?

Subjects And Methods

Population Samples, DNA Extraction and Typing

A total of 892 individuals from the six populations (Fig. 1) were previously sampled during the 1971-1985 missions led by two of us (G.L. and F.M.S.), as well as by E. B., under the auspices of the Centre National de la Recherche Scientifique (Centre d'Hémotypologie, Toulouse), Institut National de la Santé et de la Recherche Médicale (Paris) and the Universidade Federal do Rio Grande do Sul (Porto Alegre). Populations, sample collection and preservation were described in Salzano *et al*. (1988, 1997), Dugoujon *et al*. (1995), and reviewed in Mazières *et al*. (2007). Briefly, the bloods were refrigerated shortly after collection, and at the laboratory the red cells separated from the plasmas, the material tested, and afterwards stored at –20°C. During the French Guiana collections up to six-generation pedigrees were recorded. They indicated the presence of 347 maternal and 205 paternal unrelated lineages.

Genomic DNA from the Palikur, Kali'na, Emerillon, Wayampi and Matsiguenga samples was extracted from sera using the NucleoSpin Blood QuickPure kit (Macherey-Nagel) and the phenol-chloroform method coupled with the Cleanmix kit (Talent). The Apalaí DNA was obtained with the QIAmp DNA Minikit (Qiagen) from glycerolized red cells on which white cells were still adsorbed.

mtDNA and Y-chromosome Analyses

Fragments enclosing the *HaeIII* np663, 9bp-deletion, *HincII* np13259, and the *AluI* np5176 polymorphisms, which distinguish four (A-D) of the five major Amerindian mtDNA haplogroups (Torroni *et al*. 1992) were directly amplified using the polymerase chain reaction (PCR) with the following primers (Invitrogen): Haplogroup A, F570 (5'-CAACCAAACCCCAAAGACAC-3') and R741 (5'-ATGCTTGTCCCTTTTGATCG-3'); haplogroup B, F8223 (5'-CATGCCCATCGTCCTAGAAT-3') and R8383 (5'-TATGGTGGGCCATACGGTAG-3'); haplogroup C, F13229 (5'-CGCCCTTACACAAAATGACA-3') and R13353 (5'-GGACCCGGAGCACATAAATA-3'); haplogroup D : F5074 (5'-CCGTACAACCCTAACATAACCA-3') and R5219 (5'-

GAGAGGAGGGTGGATGGAAT-3'). Since there is abundant evidence that haplogroup X is present in North America only (Dornelles *et al.*2005) we did not try to test for it. The nu cleotide sequence of the first mtDNA hypervariable segment (HVS-I) was sequenced between nucleotide positions 16021 and 16422 of the Cambridge Reference Sequence (CRS; Anderson *et al*. 1981; Andrews *et al*. 1999) with the F16021 (5'-CTGTTCTTTCATGGGGAAGC-3') and R16422 (5'-ATTGATTTCACGGAGGATGG-3') primers.

Amplifications were carried out in a reaction mix containing 1x of buffer, 3mM of magnesium ions, 0.05mM of each dNTP, 0.2µM of each primer and 1.25 U of *Taq* polymerase. After an initial 10-minutes (min.) denaturation step, 35 cycles of amplification were performed. The temperature profile was 94°C for 1 min., 60°C for 1 min., 72 °C for 1:30 min., and a final extension step of 10 min at 72°C.

PCR products were digested with the appropriate endonucleases. The resulting fragments, as well as the PCR products containing the 9pb-deletion, were screened through electrophoresis on 3% NuSieve-Agarose (1:2) (Tebu-bio) gels stained with ethidium bromide. After purification of the HVS-I fragments with the QIAquick spin columns (Qiagen), both strands were sequenced using the BigDye™ terminator Cycle Sequencing Ready Reaction v1.1 (AB Applied Biosystems). The runs were carried out at Toulouse in an automatic ABI Prism 310 sequencer. The Apalaí samples were purified with the polyethylenoglycol (PEG) method and sequenced at Porto Alegre using the DYEnamic™ ET Dye terminator Cycle Sequencing kit, as required for the MegaBACE™ DNA Analysis System (Amersham Biosciences).

For the Y-chromosome eight biallelic markers (M3, M242, M9, 92R7, YAP, M2, RPS4Y_{711} and M19) were typed using the methods described in Bortolini *et al*. (2003) and Marrero *et al*. (2005). Haplogroups defined by these polymorphisms were named following the nomenclature suggested by the last Y Chromosome Consortium release (Jobling & Tyler-Smith, 2003). A designation such as Q* defines all chromosomes that do not possess the derived allele,

in this case describing all chromosomes in clade Q except those in Q3. Haplogroup Y* indicates the presence of the ancestral alleles for the eight markers investigated here.

Preventing Contamination and Artifacts

DNA extractions and PCR determinations were performed following a series of standard practices to avoid laboratory contamination. Negative controls consisting of mock extractions (sample omitted) and PCR blanks without DNA were used all along the testing procedures. To prevent the introduction of exogenous DNA, laboratory rooms were routinely ultraviolet (UV)-irradiated. Nucleic acid extractions, PCRs and post-PCR handling were performed in isolated work areas, using sterile equipment for each of them. The instruments were subjected to extensive rinsing in sterile μQH_2O. Aerosol-resistant barrier pipette tips were employed. All equipments, disposables, and reagents were UV-irradiated before use, and frequent bleaching of working surfaces was adopted. Finally, all researchers and laboratory staff were typed for the markers of study.

Stringent criteria were employed for authentication. As far as possible, related individuals were typed or sequenced. The genotypic results of their lineages were then validated after comparison with the genealogical data; only unrelated individuals, however, were included in the analysis. To ensure that no systematic artifacts were introduced in the course of the sequencing process that could have produced "phantom" mutations we applied the filtering process described by Bandelt *et al*. (2002). This analysis filters speedy transitions and thus scores weighty mutations only.

Genetic Analysis

The mtDNA and Y-chromosome haplogroups were assigned following published criteria (Torroni *et al*. 1992; Salas *et al.* 2002; Bandelt *et al*. 2003, Jobling & Tyler-Smith 2003). Haplogroup frequencies were calculated by counting. Genetic distances were obtained with the

DISPAN (Ota 1993) package. The distance employed was the modified Cavalli-Sforza D_A distance (Nei *et al*. 1983) since it has a more discriminatory power for closely related groups (Nei & Roychoudhury 1993; Nei & Takezaki 1996). The relationships among the populations were then displayed through neighbour-joining (NJ) trees (Saitou & Nei 1987) with the PHYLIP (Felsenstein 2002) software using D_A matrices as input files, and visualized with TREEVIEW (Page 1996).

HVS-I sequence evaluation was manually performed with the SEQUENCING ANALYSIS (ABI PRISM v.3.7) and CHROMAS v2.3 reading programs. Sequence alignment was accomplished using the BIOEDIT (Hall 1999) software. F_{ST} distances were calculated with the ARLEQUIN ver 3.1 (Excoffier *et al*. 2005) program, using the pairwise difference method. The reliability of the F_{ST}-based tree was tested by bootstrap replications, following Hedges (1992), considering each polymorphic site as a system.

Results

mtDNA Analysis

Three hundred of the 349 samples available (86%) have been successfully typed by both the RFLP and sequencing methods. Considering that the samples were collected at different times, under diverse field conditions, the indicated level of success should be considered favorably. Tables 1 and 2 summarize the mtDNA sequence variation observed among the six populations examined. Fifty-one polymorphic sites defining 56 haplotypes were observed. Almost all of them could be classified into the four major founding mtDNA haplogroups. A non-Amerindian, African mtDNA lineage (L2d2) was found in the Kali'na (haplotype n°56; it also shows mutations 16390 and 16399, not indicated in Table 1 because these sites do not vary among Amerindians). Only two major haplogroups were found in the Emerillon (A: 30%, B: 70%) and Palikur (B: 56%, D: 44%), while three or more were observed in the other four populations examined. Finally, only seven HVS-I haplotypes (n°s. 2, 15, 21, 27, 31, 44, and 49) were shared by the several populations.

The median joining network obtained with the 300 HVS-I sequences is displayed in Fig. 2. Four clusters can be visualized, corresponding to the B/B4 (left), A2/A4, D1, and C1 (right) haplogroups. The mutations leading to the different haplotypes are shown, together with their frequencies (as depicted by the sizes of the circles and their relative shading). The distinctiveness of the African lineage no. 56 is clearly observed, its connection with the network being mediated by seven mutations. Exclusive, relatively frequent Apalaí and Wayampi haplotypes occur in A2, A4 and D1, but not clear pattern appears in relation to the populations in which the other haplotypes occur.

Y-chromosome

Successful typing for the eight Y-chromosome markers was obtained for 179 of the 203 male samples tested. Y-haplogroup frequencies are presented in Table 3. Amerindian lineages Q* and Q3* are predominant, and the Emerillon, Wayampi, and Apalaí are monomorphic for Q3*. There is no previous report of the K* occurrence in Amerindians; this haplogroup is especially frequent in Asiatics (about 30%), but also occurs (generally in frequencies of less than 5%) in Europeans (Bortolini *et al.*2003). It is possible, therefore, that its pres ence in three of the six populations sampled may be due to non-Amerindian heritage. The sub-Saharian E3a lineage was found in the Kali'na (9.4%; who also presented evidence of African admixture in the mtDNA data) and Matsiguenga (3.2%).

Population Relationships

Interpopulation genetic distances based on Y-chromosome and mtDNA haplogroups were calculated (data not shown) but this comparison is hampered by the lack of large variability at the Y-chromosome level. In this case the only point that could be stressed is the separation of the Palikur from the three other Guianese tribes that are monomorphic for Q3*. Table 4 presents the F_{ST} distances matrix based on the mtDNA HVS-I sequence variability. They varied from 0.11 (Apalaí-Wayampi) and 0.51 (Apalaí-Matsiguenga), but almost half (7 in 15) occur in the 0.11-0.19 interval. The derived relationships are displayed in the tree of Fig. 3. No clear north-south gradient is observed, but the littoral groups (Kali'na, Palikur) are near each other, as well as the southern Apalaí and Wayampi. Also, no clear relationships according to languages can be discerned. The two Karib (Apalaí, Kali'na), two Tupi-Guarani (Wayampi, Emerillon), and two Arawak (Palikur, Matsiguenga) are all separated in both mtDNA trees.

Genetic intrapopulation diversity

The Y-chromosome data is not appropriate for intrapopulation diversity comparisons because the variability is low and may be heavily influenced by non-Amerindian admixture. The mtDNA results, on the other hand, can be profitably considered for this purpose, and results of the analyses made are displayed in Table 5. The amount of diversity found in the present study show values that are generally within the range (with two exceptions) observed in a survey of other South Amerindians. The Kali'na, Wayampi and Apalai show values above the South Amerindian averages, the opposite occurring with the Emerillon and Matsiguenga; the Palikur show a mixed pattern.

Discussion

We can now examine the questions asked in the introduction in the light of the results obtained. In relation to the first, it is clear that geographic factors should have played a more important role than linguistic similarity in French Guiana, since the mtDNA relationships associated mainly the two littoral (Kali'na, Palikur) and two southern (Apalaí, Wayampi) tribes, who speak languages from different families (Karib, Tupi-Guarani).

The second question is concerned with the Arawak Maipurean-speaking tribes, Matsiguenga and Palikur. There has been several hypotheses in relation to the possible center of Maipurean dispersion. The Maipurean language cluster chronological depth is estimated in three thousand years, and Payne (1991) subdivided it in five groups, according to the location of the tribes which speak versions of it. Two of the five have representatives in north-central Peru, and Urban (1992) suggested that this area could represent the Maipurean center of dispersion. The Palikur of French Guiana represent the most extreme eastern speakers of this language, and we therefore decided to verify whether they could show any genetic resemblance with another

Peruvian Maipurean-speaking group. As was previously indicated the answer is negative, since they do not show any special type of similarity. At this juncture, Rostain's (1994) suggestion that the Palikur may be the Arawak descendants of people who developed the Aristé archeological complex in Amapá (northern Brazil) seems the most likely explanation, since the Aristé sites overlap the present Palikur distribution and the complex seems to represent an ancient center of population diversification.

Thirdly, the question of non-Amerindian influence can be addressed. The mtDNA results indicated only one non-Amerindian, African haplogroup, present in two Kali'na subjects, was detected. The Y-chromosome data, as expected for the asymmetrical mating patterns that characterized Colonial America (predominantly European-derived men with Amerindian- or African-derived women; Bortolini *et al.* 2004; Campos-Sánchez *et al.*2006; Marrero *et al.* 2007b) showed additional indications of admixture. In relation to the E3a* lineage findings, while the Matsiguenga result may derive from recent interbreeding, its presence in the Kali'na could be most easily explained by historical contacts they have had with the Bushinengue (Noir-Marron), an African- derived group which lives nearby, composed by escaped slaves who established a free, independent life at the mouth of the Maroni river (Price & Price 2004).

Historical and anthropological data have furnished a fairly good picture of French Guiana's Amerindian colonization (review in Grenand & Grenand 1985). Table 6 gives information about some selected results which may be correlated with the genetic findings reported here. The northern littoral populations (Kali'na, Palikur) were the first to enter the region, at 800-900 AD. The Tupi-Guarani colonization (Emerillon, Wayampi) occurred half-a-century later, and the two tribes may have followed different migration routes. The mtDNA results agree with this information by showing a good relationship between the Kali'na and Palikur, but clear differences between the Emerillon and Wayampi. As for the demographic-anthropological population estimates, the fact that all four tribes experimented strong population bottlenecks, the Kali'na and Palikur at the middle of the 19th century and the Emerillon and

Wayampi one hundred years afterwards, is reflected especially in the low haplotype mtDNA diversity found among the Emerillon (who experimented a very strong bottleneck, with a nadir number of 52). ~~and the Palikur.~~

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Figure 1 Partial maps of Peru and French Guiana showing the geographic location of the studied populations.

Figure 2 Median joining network showing the relationships among the 56 mtDNA HVS-I haplotypes. The numbers represent the nucleotide position (-16000). Tranversions are indicated by letters after the numbers.

Figure 3 Neighbor joining tree obtained from pairwise differences between HVS-I haplotypes. Numbers are percentage bootstrap values based on 2,000 replications.

Table 1 HVS-I sequence variation in four French Guiana and two related populations[1]

	Nucleotide variable positions																																																		Hgp	Populations					
				1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3							
	5	9	9	1	2	2	4	4	5	6	6	7	7	8	8	8	8	0	1	2	2	3	5	5	5	5	6	6	6	6	7	7	8	9	9	9	9	9	9	9	0	1	1	2	2	4	5	5	5	6	6		Pal	Kal	Em	Wyp	Ap	Mts
	1	2	3	1	6	9	2	5	5	8	9	8	9	2	3	4	9	9	7	3	4	9	6	7	8	9	1	5	6	7	4	8	8	0	1	2	3	4	5	8	3	1	9	5	7	2	5	6	7	2	8							
CRS	A	T	T	C	T	G	C	G	A	C	C	T	C	A	A	C	T	T	T	C	T	C	C	C	A	C	C	A	C	C	G	C	T	C	C	C	A	C	C	T	G	T	G	T	C	T	C	T	T	T	T							
1	G	.	.	T	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	C	.	A2		2				
2	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	C	.	A2			9	5	11	
3	N	.	.	T	.	A	.	.	.	.	.	.	.	C	C	.	C	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	C	A	.	.	.	.	.	.	C	.	A2				4		
4	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	C	.	C	.	A2				13		
5	.	.	.	T	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	C	.	A2					7	
6	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	C	C	.	A2					7	
7	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	A	.	.	.	.	.	.	T	.	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	C	.	A2					12	
8	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	T	.	T	.	.	.	T	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	C	.	A2					1	
9	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	C	A	.	.	.	.	.	.	C	.	A2					1	
10	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	C	.	A4				3		
11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	C	C	.	A4					1	
12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	C	.	A4						1
13	.	.	.	.	.	.	.	.	.	.	.	.	.	C	C	.	C	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	C	.	A4						1

Table 1 (Cont.)

	Nucleotide variable positions																																																			Hgp	Populations					
				1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3							
	5	9	9	1	2	2	4	4	5	6	6	7	7	8	8	8	8	0	1	2	2	3	5	5	5	5	6	6	6	6	7	7	8	9	9	9	9	9	9	9	0	1	1	2	2	4	5	5	5	6	6		Pal	Kal	Em	Wyp	Ap	Mts
	1	2	3	1	6	9	2	5	5	8	9	8	9	2	3	4	9	9	7	3	4	9	6	7	8	9	1	5	6	7	4	8	8	0	1	2	3	4	5	8	3	1	9	5	7	2	5	6	7	2	8							
CRS	A	T	T	C	T	G	C	G	A	C	C	T	C	A	A	C	T	T	T	C	T	C	C	C	A	C	C	A	C	C	G	C	T	C	C	C	A	C	C	T	G	T	G	T	C	T	C	T	T	T	T							
14	N	.	.	.	.	.	.	.	.	.	.	.	.	C	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	B4	1					
15	.	.	.	.	.	.	.	.	.	.	.	.	.	C	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4	3	2				
16	N	.	.	.	.	.	.	.	.	.	T	.	.	C	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4		1				
17	.	C	.	.	.	.	.	.	.	.	.	.	.	C	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4					1	
18	.	.	.	.	.	.	.	.	.	.	.	.	.	C	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	B4						8
19	N	.	C	.	.	.	.	.	.	.	.	.	.	C	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	B4						1
20	N	.	.	.	.	.	.	.	.	.	.	C	.	.	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4	2					
21	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4	2	1	19			3
22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	B4	16					
23	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	C	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	B4	2					
24	N	N	N	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4	1					
25	.	C	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	A	.	.	.	.	.	.	.	.	B4		4				
26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4		1				
27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	C	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4			1	7		

Table 1 (Cont.)

	Nucleotide variable positions																																																			Hgp	Populations					
				1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3							
	5	9	9	1	2	2	4	4	5	6	6	7	7	8	8	8	8	0	1	2	2	3	5	5	5	5	6	6	6	6	7	7	8	9	9	9	9	9	9	9	0	1	1	2	2	4	5	5	5	6	6		Pal	Kal	Em	Wyp	Ap	Mts
	1	2	3	1	6	9	2	5	5	8	9	8	9	2	3	4	9	9	7	3	4	9	6	7	8	9	1	5	6	7	4	8	8	0	1	2	3	4	5	8	3	1	9	5	7	2	5	6	7	2	8							
CRS	A	T	T	C	T	G	C	G	A	C	C	T	C	A	A	C	T	T	T	C	T	C	C	C	A	C	C	A	C	C	G	C	T	C	C	C	A	C	C	T	G	T	G	T	C	T	C	T	T	T	T							
28	N	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	B4			1			
29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	C	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4						4
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31	N	.	.	.	.	A	.	.	.	.	.	.	.	.	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4				4		16
32	N	.	.	.	.	A	.	.	.	T	.	.	.	.	C	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4						1
33	N	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B4						1
34	N	N	N	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B		1				
35	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	T	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	B		2				
36	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	T	.	.	.	.	.	.	C1					2	
37	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	C	T	.	.	.	.	.	.	C1		3				
38	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	C	T	.	.	.	.	.	.	C1		4				
39	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	C	T	.	.	.	.	.	.	C1		4				
40	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	C	.	.	.	C	T	.	.	.	.	.	.	C1					15	
41	G	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	C	T	.	.	.	.	.	.	C1					1	

Table 1 (Cont.)

	Nucleotide variable positions																																																			Hgp	Populations					
	51	92	93	111	126	129	142	145	155	168	169	178	179	182	183	184	189	209	217	223	224	239	256	257	258	259	261	265	266	267	274	278	288	290	291	292	293	294	295	298	303	311	319	325	327	342	355	356	357	362	368		Pal	Kal	Em	Wyp	Ap	Mts
CRS	A	T	T	C	T	G	C	G	A	C	C	T	C	A	A	C	T	T	T	C	T	C	C	C	A	C	C	A	C	C	G	C	T	C	C	C	A	C	C	T	G	T	G	T	C	T	C	T	T	T	T							
42	G	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	C	T	.	.	.	.	.	.	C1					3	
43	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	C	.	.	.	C	T	.	.	.	.	C	.	C1					9	
44	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	C	.	D1	11	1				
45	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	C	.	D1	1					
46	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	C	.	D1				8		
47	G	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	C	.	D1	9					
48	N	.	.	.	.	.	T	.	.	.	.	.	T	.	.	.	C	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	C	.	D1				1		
49	.	.	.	.	.	.	T	.	.	.	.	.	T	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	C	.	.	.	.	.	C	.	D1		1		1	27	
50	.	.	.	.	.	.	T	.	.	.	.	.	T	.	.	.	C	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	C	.	.	.	.	.	C	.	D1				5		
51	N	.	.	.	.	.	T	.	G	.	.	.	T	.	.	.	C	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	C	.	.	.	.	.	C	.	D1				1		
52	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	C	.	D1				1		
53	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	G	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	C	.	D1						1
54	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	C	.	D1					1	
55	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	.	.	C	.	D1					3	
56	.	.	.	A	.	.	.	A	.	.	.	.	.	.	.	T	C	.	.	T	.	T	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	L2d2		2				

Table 1 (Cont.)

Note: [1]Nucleotide positions are numbered after 16,000, following the Cambridge Reference Sequence (Anderson *et al.* 1981; Andrews *et al.* 1999). Haplogroup (Hgp) assignation according to Bandelt *et al.* (2003). Populations: Pal: Palikur; Kal: Kali'na; Em: Emerillon; Wyp: Wayampi; Ap. Apalaí; Mts: Matsiguenga. N: Not determined.

Table 2 mtDNA haplogroup frequencies (%) in four French Guiana and two related populations

Populations	N[1]	Haplogroups						
		A2	A4	B2	B4	C1	D1	L2d2
Palikur	48				56.2		43.8	
Emerillon	30	30.0			70.0			
Kali'na	29	6.9		10.4	31.0	37.9	6.9	6.9
Wayampi	53	41.5	5.7		20.7		32.1	
Apalaí	102	38.2	1.0		1.0	29.4	30.4	
Matsiguenga	38		5.3		92.1		2.6	

Note: [1]N: Number of individuals studied; [2]The HVS-I markers alone are not sufficient for subhaplogroup assignment.

Table 3 Y-chromosome haplogroup frequencies (%) in four French Guiana and two related populations

Populations	N[1]	Haplogroups								
		Q3a	Q3*	Q*	P*	K*	C*	E3a*	DE*	Y*
Palikur	35		91.4	2.9		5.7				
Emerillon	9		100							
Kali'na	21		81			4.8		9.4		4.8
Wayampi	38		100							
Apalaí	48		100							
Matsiguenga	28		80.7	9.7		3.2		3.2		3.2

Note: [1]N: Number of individuals studied.

Table 4 F_{ST} distances matrix based on the mtDNA HVS-I sequence variability[1]

	Palikur	Emerillon	Kali'na	Wayampi	Apalaí	Matsiguenga
Palikur						
Emerillon	0.15349					
Kali'na	0.13189	0.14991				
Wayampi	0.20324	0.18076	0.15186			
Apalaí	0.31340	0.34974	0.20315	0.11077		
Matsiguenga	0.26139	0.18964	0.28641	0.38321	0.51551	

Note: [1]All distances are statistically significant at the 5% level.

Table 5 Mitochondrial DNA diversity measurements (haplogroups and HVS-I sequences) in the populations studied here compared to other South Amerindians[1]

Populations	No. indiv.	Diversity parameters				
		H	k	D (SE)	P_w	π (SE)
Palikur	48	0.503	10	0.808 (0.034)	4.9	0.015 (0.008)
Emerillon	30	0.434	4	0.524 (0.074)	3.3	0.010 (0.006)
Kali'na	29	0.695	14	0.938 (0.021)	7.4	0.023 (0.012)
Wayampi	53	0.640	12	0.882 (0.022)	5.9	0.020 (0.011)
Apalaí	102	0.681	16	0.872 (0.017)	6.1	0.019 (0.010)
Matsiguenga	38	0.234	11	0.777 (0.054)	2.6	0.008 (0.005)
South Amerindians[2]	986					
Minimum	-	0.165	3	0.204	1.1	0.003
Average	-	0.511	14	0.767	4.3	0.013
Maximum	-	0.756	42	0.968	6.5	0.018

Notes: [1]The numbers of individuals studied for H (haplogroup heterozygosity) were slightly different from those given in the table: Wayampi, 54; Apalaí, 103; Matsiguenga, 40. k: number of haplotypes; D: haplotype diversity; P_w: number of differences between pairs of haplotypes; π: nucleotide diversity; [2]Included 26 population samples, but the values shown are only for 13 tribal samples with at least 30 individuals tested. Tribes with extreme values were the Aché, with uniformly low indices (Schmitt *et al.* 2004); and the Cayapa with high H, P_w and π (Rickards *et al.* 1999); Yanomama, with high k (Easton *et al.* 1996); and Mapuche, with high D (Ginther *et al.* 1993).

Table 6 Historical and linguistic data about the French Guiana and one neighboring tribes

Characteristic	Kali'na	Palikur	Emerillon	Wayampi	Apalaí
Language	Karib	Arawak	Tupi-Guarani	Tupi-Guarani	Karib
Date of colonization of present territory (AD)	900	800	1400	1400	1890
Origin	Amazon headwaters	Amazon headwaters	Tapajós headwaters	Amazon headwaters	Paru de Leste river
Population estimates					
First, Number	5,500	4,000	400	6,000	3,000
Year	1604	1604	1767	1824	1790
Nadir, Number	250	220	52	212	280
Year	1848	1840	1953	1947	1890
Recent, Number	1,550	866	218	910	415
Year	1978	1998	1985	1994	1998

Note: Sources: Grenand & Grenand (1979); Salzano *et al.* (1988); Campbell (1997); Ricardo (2000); http://www.pegue.com/indio/palikur.htm.

Figure 1

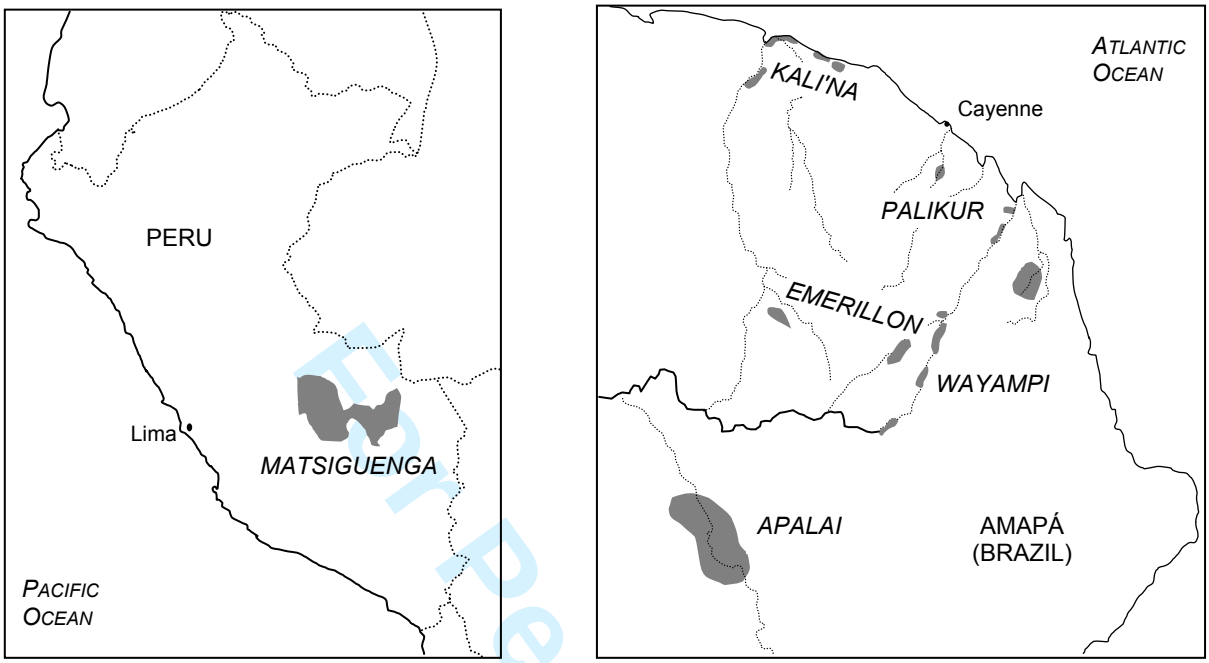

Figure 2

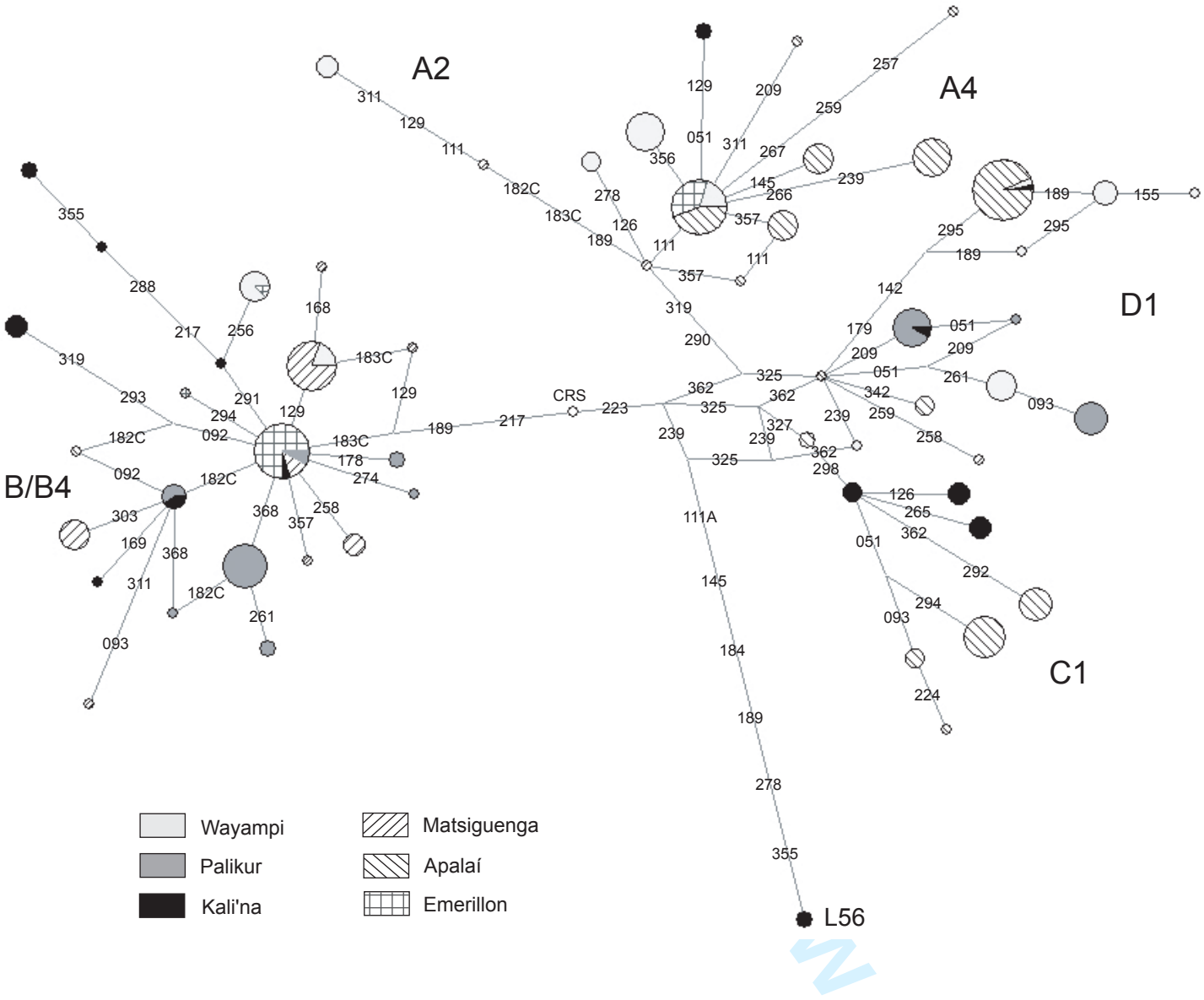
A2
A4
D1
C1
B/B4
L56
CRS
Wayampi
Palikur
Kali'na
Matsiguenga
Apalaí
Emerillon

Figure 3