

Niger-Congo Speaking Populations and the Formation of the Brazilian Gene Pool: mtDNA and Y-Chromosome Data

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ABSTRACT We analyzed sequence variation in the mitochondrial DNA (mtDNA) hypervariable segment I (HVS-I) from 201 Black individuals from two Brazilian cities (Rio de Janeiro and Porto Alegre), and compared these data with published information from 21 African populations. A subset of 187 males of the sample was also characterized for 30 Y-chromosome biallelic polymorphisms, and the data were compared with those from 48 African populations. The mtDNA data indicated that respectively 69% and 82% of the matrilineages found in Rio de Janeiro and Porto Alegre originated

from West-Central/Southeast Africa. These estimates are in close agreement with historical records which indicated that most of the Brazilian slaves who arrived in Rio de Janeiro were from West-Central Africa. In contrast to mtDNA, Y-chromosome haplogroup analysis did not allow discrimination between places of origin in West or West-Central Africa. Thus, when comparing these two major African regions, there seems to be higher genetic structure with mtDNA than with Y-chromosome data. *Am J Phys Anthropol* 133:000–000, 2007. © 2007 Wiley-Liss, Inc.

The massive forced African migration to the Americas that occurred from the 15th to the 19th centuries (involving not less than about 10 million persons) included Brazil in a fraction estimated as 40% (Klein, 2002). Most of these individuals were men, since it was supposed that they would be more able to support the hard work in the farms and mineral mines (Bergmann, 1977; Conrad, 1985). Additionally, the slave trade to the Middle East preferentially involved sub-Saharan women, and this resulted in a relatively reduced number of available slave women plus an increased price for them (Klein, 2002).

According to historical data (Klein, 2002), the Africans who were brought to Brazil as slaves originated mainly from two major geographical regions: (a) West-Central/Southeast Africa, that included basically areas represented by two former Portuguese colonies (Angola and Mozambique) and the Congo; and (b) West Africa, that covers all region at the northern of the Gulf of Guinea. Historical references are vague and normally cite that “gentile” from Guinea and Coast of Mina were brought to Brazil. Both terms were frequently used to refer to all region of slave traffic in West Africa (Bergmann, 1977; Klein, 2002). These two major areas have large dimensions and are populated by very distinct peoples and cultures. Most of them, however, are inhabited by speakers of languages belonging to the Niger-Congo linguistic subphylum (Greenberg, 1963; Ruhlen, 1987; Fig. 1). The Niger-Congo subphylum comprises the large Bantu branch, which includes about ~500 languages spoken in virtually all Central-South Africa, except for the area occupied by the Khoisan-speaking groups (Cavalli-Sforza et al., 1994).

The place of origin of the Bantu languages has been identified as most likely being between Cameroon and Nigeria (Newman, 1995). From there the Bantu expanded at the end of the Neolithic throughout sub-Saharan Africa (Murdock, 1959; Curtin et al., 1991; Phillipson, 1993; Cavalli-Sforza et al., 1994; Diamond and Bellwood, 2003; Plaza et al., 2004; Zhivotovsky et al., 2004; Rexová et al., 2006). In contrast, in the West African branch of the Niger-Congo subphylum, the native inhabitants speak several non-Bantu languages (Greenberg, 1963; Ruhlen, 1987; Cavalli-Sforza et al., 1994). Genetic studies have demonstrated that Niger-Congo speaking populations are more related to each other than to other Africans. These same investigations have also shown that Bantu speaking groups show a higher level of genetic homogeneity than do the non-Bantu populations (Cavalli-Sforza et al., 1994; Poloni et al., 1997;

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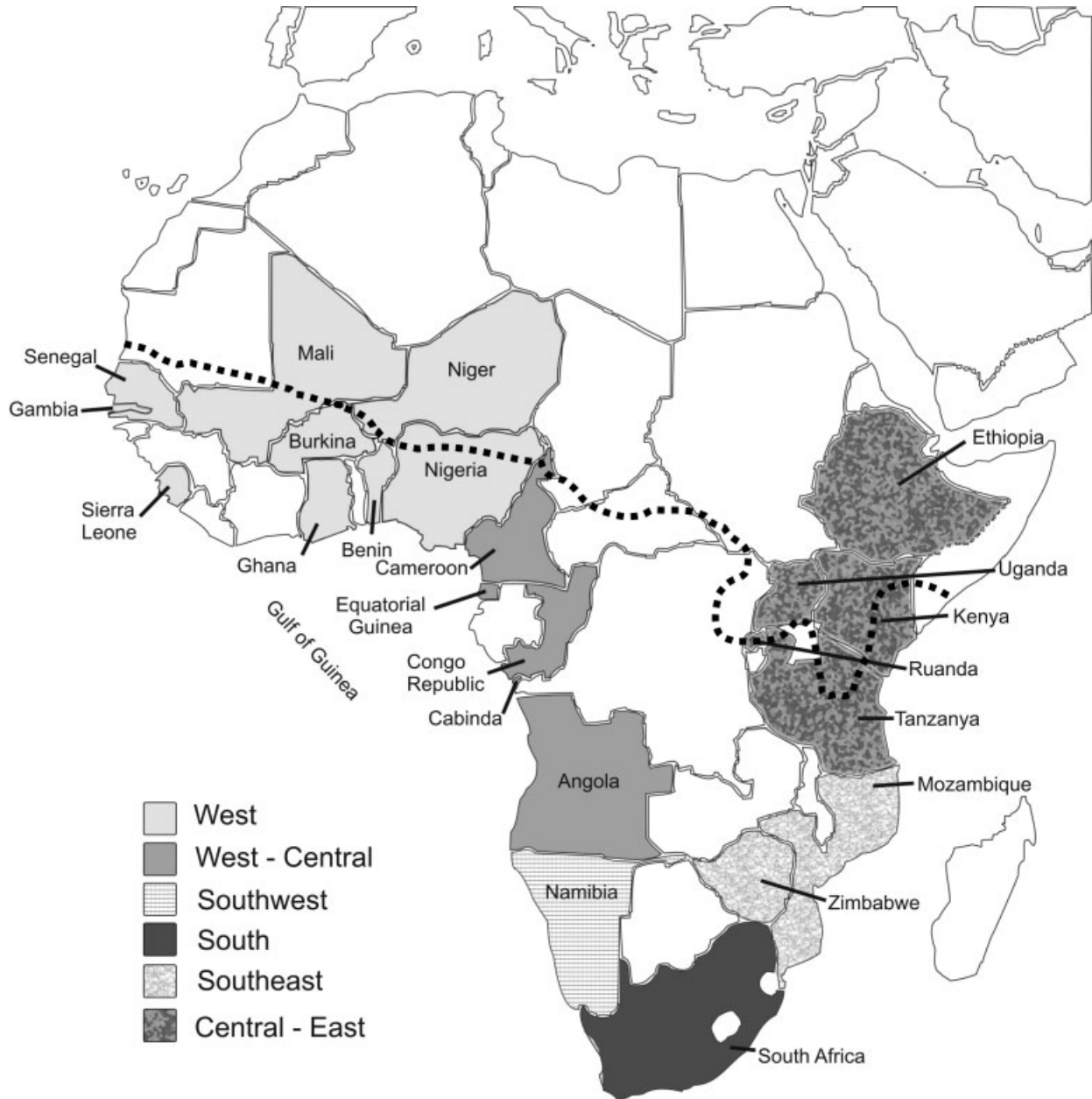


Fig. 1. Map of Africa. The dotted line approximately delimits the northern border of the area occupied by Niger-Congo speakers according to Greenberg (1963) and Ruhlen (1987). Within this large region, of course, languages from other families are also spoken. The regions/countries considered in the present analysis are identified by different shading.

Cruciani et al., 2002; Salas et al., 2002, 2005; Wood et al., 2005).

Because historical records on slavery contain many gaps, genetic studies with South Americans of African descent have been used to trace the ancestry of Niger-Congo speakers back into Africa. Salzano and Bortolini (2002) showed that 61%, 34%, and 3% of the $Hb\beta^S$ haplotypes found in Brazil as a whole are of the types named Bantu (or Central African Republic-CAR), Benin, and Senegal, respectively. These results are in good agreement with the historical sources which indicate that ~68% and ~32% of the African slaves were brought from West-Central/Southeast and West Africa, respectively (Klein, 2002).

Recently, lineage markers [mitochondrial DNA (mtDNA) and the nonrecombining portion of the Y-chromosome] have been used to try to unravel the history of human populations, since they are uniparentally transmitted, and escape recombination. These markers allow the reconstruction of unequivocal haplotype phylogenies, which can be related to geographic distributions, in an approach known as phylogeography (Avise, 2000).

Alves-Silva et al. (2000) reported an initial landscape about the phylogeography of the African mtDNA haplogroups in Brazil as a whole. Haplogroups L3e and L1c together constituted approximately 49% of the African fraction of mtDNAs analyzed by these authors. These results suggested that the majority of the mtDNA line-

ages of African ancestry in their Brazilian sample would have an origin in West-Central Africa, with a minor contribution from the Southeast, although a substantial number could also have come from West Africa through non-Bantu speaking carriers.

Salas et al. (2004) estimated for the first time the quantitative contribution of the different African regions to the formation of the New World mtDNA gene pool. According to their estimate, 65% of the types found in South America would have a West-Central African origin, its complementary value indicating a West African contribution. These numbers are particularly different from those obtained for Central America (41% West-Central, 59% West), and North America (28% West-Central, 72% West), in agreement with the historical data of these regions (Curtin, 1969; Thomas, 1998). Using the same kind of approach but substantially more data, Salas et al. (2005) estimated that >55% of the U.S. mtDNA lineages have a West African ancestry, with <41% coming from West-Central or Southwestern Africa, results which are close to the historical record (McMillin, 2004).

However, the most recent investigation of mtDNA-HVS-I variation in Brazilian populations has yielded discrepancies between the patterns obtained with the mtDNA haplogroup distributions and the historical sources (Silva et al., 2006). These findings raised the suggestion of a possible geographical gender-specific difference, with a proportionally larger number of West-African men than that of women compulsorily migrating to Brazil (Silva et al., 2006). The authors mentioned that only research with Y-chromosome markers could provide a more complete picture about this and other questions related to the Atlantic slave trade to Brazil.

Several studies of Y-chromosome phylogeographical landscape in Africa are now available (Cruciani et al., 2004, Luis et al., 2004, Beleza et al., 2005, Wood et al., 2005), but up to now no investigation has evaluated the same set of markers in males from the three Americas.

Here we provided information about the distribution of the mtDNA and Y-chromosome haplogroups in two Brazilian Black populations, and compared these results with those published for populations of several African regions. Two major questions were asked: (a) Do the proportion of African ancestry differs when maternal and paternal inheritance is considered? and (b) Can these two sets of data furnish information about possible regions of origin of the African slaves who arrived in Brazil?

SUBJECTS AND METHODS

Populations

After appropriate informed consent, samples of 201 individuals classified as Black according to their physical appearance and originating from two Brazilian cities, Rio de Janeiro ($N = 94$), the capital of Rio de Janeiro state, and Porto Alegre ($N = 107$) the capital of Rio Grande do Sul, the southernmost state of Brazil were studied. Rio de Janeiro, plus the northeastern cities of Salvador (state of Bahia) and Recife (state of Pernambuco) were the most important ports of arrival of slaves in Brazil. From these centers these persons would be distributed to the other provinces. For example, according to historical data, 88% of the Rio Grande do Sul slave population was brought from Rio de Janeiro, with the complementary number of slaves being brought from

other Brazilian provinces and Uruguay, not directly from Africa (Maestri-Filho, 1993; Berute, 2006).

mtDNA

The nucleotide sequence of the first hypervariable segment (HVS-I) of 201 individuals was amplified and sequenced according to conditions described in Marrero et al. (2005). Both strands of DNA were sequenced.

The information provided by HVS-I was used to classify the lineages into haplogroups according to Salas et al. (2002, 2004), with two exceptions: (a) Haplogroup L3g shares motifs, within HVS-I and HVS-II and at positions 769 and 1018 with L4a. This information led Kivisild et al. (2004) to suggest that L3g is actually a sister cluster of L4a; therefore, they proposed to rename it L4g. (b) Haplogroup L1e has been recently redefined as L5a because it occupies an intermediate phylogenetic position between L1 and L2/L3 major haplogroups (Shen et al., 2004).

Although the hierarchical relation between the human mtDNA lineages is well known, the terminology to define them remains confusing. Haplogroup, clade, subhaplogroup, and subclade are words frequently used as synonymous. In this paper, to facilitate reading and comprehension, the term haplogroup will be used to define the major lineages (L0, L1, L2, L3, L4, L5, etc.), as well as their derivations (L2a, L3e, L2a1, L3e1, etc.).

Y-chromosome markers

The male fraction of our sample ($N = 187$) was studied for thirty biallelic Y-chromosome polymorphisms (92R7, M9, M3, M19, M242, RPSY711, M17, M173, SRY2627, PN2, M2, M174, M145, M33, M35, M75, M58, M191, M149, M116.2, M10, M78, M154, M155, M281, M123, M81, M213, M60, V6) using hierarchical strategies plus RFLP and mini-sequencing methods as described in Bortolini et al. (2003) and developed by Carvalho and Pena (2005), respectively. These markers define the major European, Amerindian, and African haplogroups, but identify especially well subtypes of the haplogroup E, the most common and widespread Y chromosome in Africa.

The haplogroup nomenclature adopted is that proposed by the last Y-chromosome Consortium release (Jobling and Tyler-Smith, 2003). Here also the term haplogroup will be used to define the major lineages (E, etc.), as well as their derivations (E1, E2, E3, E3a, E3a7, etc.).

Data analyses

The mtDNA sequences were checked manually, validated with the help of the CHROMAS LITE 2.0 program (www.technelysum.com.au) and aligned with the revised Reference Sequence (rCRS; Andrews et al., 1999) using the BIOEDIT software (Hall, 1999). Since artifacts ("phantom mutations") can be introduced during the sequencing and editing process, we applied the filtering procedure described by Bandelt et al. (2002) and used criteria like those of Yao et al. (2004) to check for the quality of the sequences. After filtering a network of sequences was constructed with the NETWORK 4.1.1.2 program (www.fluxus-engineering.com) using the median-joining algorithm. Weight networks showing perfect star tree patterns are expected when the data are potentially free of phantom mutations. However, other criteria as phylogenetic analysis in comparisons with closely

TABLE 1. Major sub-Saharan African mtDNA haplogroups and their distributions in two Brazilian and 21 African populations

Brazil ^a		Africa ^b																					
Haplogroups		West-Central							Niger-Congo speakers							West							Afro-Asiatic speakers
POA	R _J	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
L0							0.022																
L0a												0.125	0.033				0.018						
L0a1	0.059	0.071	0.045	0.111	0.068	0.023	0.022	0.006	0.006	0.200	0.051	0.033	0.033	0.024	0.027	0.054	0.018	0.018	0.033	0.015	0.051		
L0a2	0.048	0.068	0.111	0.029	0.111	0.066	0.067	0.129	0.097	0.100	0.102	0.125	0.135	0.024	0.210	0.163	0.178	0.205	0.133	0.015	0.103		0.067
L0d								0.064	0.177														
L0d1									0.038														
L0d2									0.013														
L1b	0.047	0.095	0.045						0.003														
L1b1									0.006														
L1c									0.006														
L1c1	0.070	0.048	0.045	0.028	0.111	0.098	0.067	0.111	0.003														
L1c2	0.059	0.071	0.093	0.111	0.126	0.088	0.133	0.032	0.019														
L1c3	0.047	0.023	0.028	0.010	0.010	0.023	0.022	0.165	0.013														
L2																							
L2a-α1									0.006														
L2a-α2									0.006														
L2a-α3									0.010														
L2a1a	0.047	0.059	0.068						0.091														
L2a1b									0.129														
L2a1-β1	0.120	0.117	0.023	0.222	0.010	0.066	0.044		0.031														
L2a1-β2	0.012	0.012	0.045					0.064	0.010														
L2a1-β3	0.023	0.023	0.068						0.013														
L2b	0.070	0.024	0.045	0.028	0.010	0.023	0.022	0.032	0.013														
L2b1																							
L2c																							
L2c1									0.006														
L2c2									0.010														
L2d1																							
L2d2																							
L3	0.012	0.012							0.013														
L3b	0.023	0.036	0.023						0.025														
L3b1	0.023								0.032														
L3b2	0.023								0.032														
L3d	0.012	0.024	0.023						0.025														
L3d1	0.023	0.012	0.023						0.038														
L3d2																							
L3d3																							
L3e1	0.059	0.024	0.068	0.083	0.039	0.023	0.022	0.064	0.003														
L3e1a	0.059	0.012	0.045						0.028														
L3e1b									0.039														
L3e1c									0.028														
L3e2	0.023	0.023	0.250	0.111	0.078	0.044	0.129	0.010	0.003														
L3e2b	0.023								0.028														
L3e3	0.047	0.071	0.068	0.028	0.020	0.066	0.022	0.038	0.003														
L3e4									0.038														
L3f	0.036	0.024	0.023	0.334	0.137	0.023	0.067	0.025	0.038														

(continued)

TABLE 1. (Continued)

Brazil ^a		Africa ^b										Afro-Asiatic speakers										
Haplogroups		West-Central					Southeast			Niger-Congo speakers					West							
POA	RJ	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
L3f1	0.047	0.024							0.010									0.056				
L3g (L4g)	0.036	0.045			0.010	0.023												0.018		0.046		0.060
L5a1 (L1e)		0.023																				

POA: Porto Alegre, N=85; RJ:Rio de Janeiro, N=84. The numbers correspond to the following African populations: 1 - Angola, N=44, Plaza et al. (2004); 2 - Bubi, N=36 (Equatorial Guinea) Mateu et al. (1997); 3 - Fang, N=9 (Equatorial Guinea), Pinto et al. (1996); 4 - Cabinda, N=101 (Cabinda, former Portuguese protectorate), Beleza et al. (2005); 5 - Bakaka, N=44 (Cameroun), Coia et al. (2005); 6 - Bassa, N=45 (Cameroun), Coia et al. (2005); 7 - Fulbe, N=31 (Cameroun), Coia et al. (2005); 8 - Mozambique, N=307, Salas et al. (2002); 9 - Kanuri, N=10 (Niger, Nigeria), Watson et al. (1997); 10 - Fulbe, N=39 (Nigeria, Niger, Benin, Cameroun, Burkina Faso), Watson et al. (1997); 11 - Songhai, N=8 (Nigeria, Niger, Mali), Watson et al. (1997); 12 - Yoruba, N=30 (Nigeria), Watson et al. (1997); 13 - Senegalese, N=42 (Senegal), Rando et al. (1998); 14 - Serer, N=19 (Senegal), Rando et al. (1998); 15 - Wolof, N=37 (Senegal), Rando et al. (1998); 16 - Mandenka, N=112 (Senegal), Graven et al. (1995); 17 - Mende, N=54 (Sierra Leone), Jackson et al. (2005); 18 - Loko, N=30 (Sierra Leone), Jackson et al. (2005); 19 - Limba, N=65 (Sierra Leone), Jackson et al. (2005); 20 - Temne, N=117 (Sierra Leone), Jackson et al. (2005); 21 - Hausa, N=15 (Niger, Nigeria), Watson et al. (1997).

related sequences from other databases must be observed to guarantee the quality of the data (Yao et al., 2004).

Estimates of geographic parental contributions considering our mtDNA and Y-SNP data were calculated using the weighted least square method (Long, 1991) performed with the ADMIX program, kindly made available by Dr. J.C. Long. The relationships among the populations were examined using the D_A distance and the neighbor-joining method (Nei et al., 1983; Saitou and Nei, 1987; Nei and Roychoudhoury, 1993). The trees were visualized using the TreeView program (Page, 1996), version 1.6.6 (<http://taxonomy.zoology.gla.ac.uk/rod/rod.html>). Analyses of molecular variance (AMOVA), implemented in the Arlequin program (Excoffier et al., 2005), version 3.01 (<http://cmpg.unibe.ch/software/arlequin3/>), were performed to test the hypothesis of differentiation between population groups of particular interest observed in the phylogenetic trees.

RESULTS
mtDNA

The networks obtained for the HVS-I weighty variation showed perfect star trees. Associated with other criteria (see Subjects and methods), they indicate that our HVS-I data sets are potentially free of artifacts (data not shown).

About 90% and 79% of the mtDNA sequences found in Blacks from Rio de Janeiro and Porto Alegre, respectively, are estimated as having an African origin, and they are listed in Table A1 (Appendix). The remaining sequences were identified with haplogroups of European (2% and 6%, respectively) or Amerindian (8% and 15%) origin (data not shown). Table 1 presents the mtDNA haplogroup distributions for the two Brazilian Black samples and for 21 African populations. About 70% of the haplogroups present in these African groups can also be seen in Brazil, while all haplogroups observed in these two Brazilian Black samples can be found in Africa. Table 1 also shows that there are similarities of haplogroup frequencies between the West and West-Central regions of Africa in comparison with other major regions of the continent (Salas et al., 2005), probably reflecting genetic similarity within the Niger-Congo linguistic subphylum. However, some haplogroups are present only in West-Central and/or Southeast Africa (L3e1a, L5a1, L0d, L0d1, L0d2), whereas others seem to be exclusive of West Africa (L2c1, L2d2, L3b1). Many haplogroups show striking differences in their distributions. For example, the cumulative frequency of L1b1 in the West (12.3%) is about 7 times higher than that found in West-Central/Southeast Africa (1.7%). Ancient or more recent (but not less complex) demographic events have been related to these particular mtDNA haplogroup distributions across Africa (Salas et al., 2002).

Of special interest is the presence of haplogroup L0d1 in Rio de Janeiro. This and other related haplogroups (L0d, L0d2) are characteristic of southern African Khoisan-speaking groups, but are also present in Mozambique, probably due to admixture between Khoisan women and Bantu Southeast men (Salas et al., 2002). The sequence observed in Rio de Janeiro is the same as that described by Salas et al. (2002) in Mozambique, suggesting that the occurrence of L0d1 in Brazil is probably due to the direct slave trade from this former African Portuguese colony to Brazil.

TA1
T1

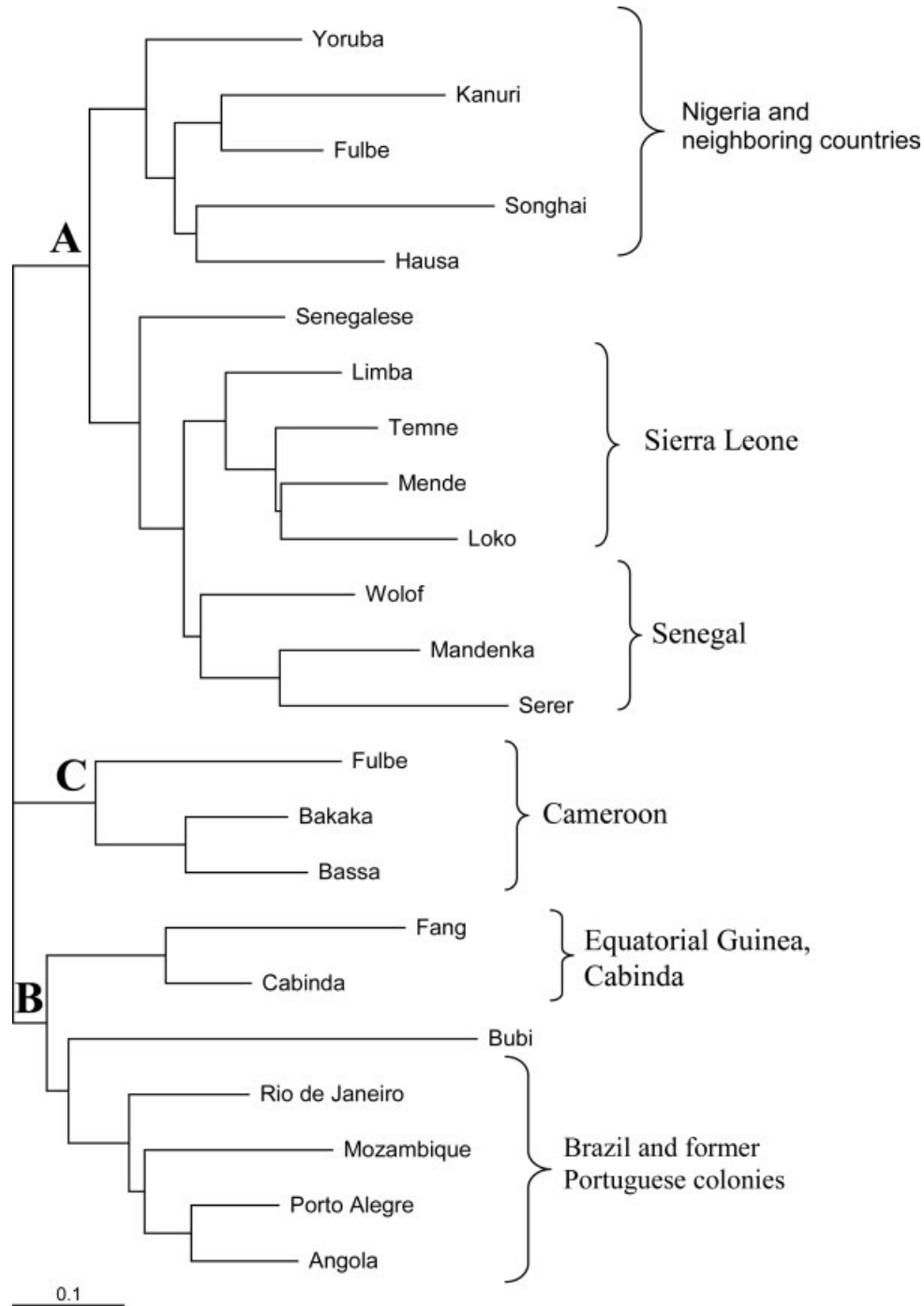


Fig. 2. Unrooted tree based on the mtDNA haplogroup distributions presented in Table 1. **A:** Western non-Bantu cluster; **B:** West-Central/Southeastern Bantu cluster; **C:** Cameroon populations.

Using the haplogroup distributions presented in Table 1, we constructed a tree which shows three well-defined clusters (Fig. 2). One of them (A) groups all West Africans; another (B) clusters the West-Central/Southeast African with the two Brazilian Black populations. Note the proximity of the latter with the two former Portugal colonies, Angola and Mozambique. A third, intermediate and more restricted cluster (C), is represented by three populations from Cameroon (Bassa, Bakaka, and Fulbe).

Cameroon is geographically located in the probable center of spread of the Bantu languages and is positioned exactly between Western and Western-Central African regions. As a consequence it contains both Bantu (Bakaka and Bassa) and non-Bantu (Fulbe) speaking populations. Figure 2 also suggests a genetic differentiation within the Niger-Congo subphylum, separating the West-Central/Southeast Bantu speakers (Fang, Cabinda, Bubi, Angola, Mozambique) from the Western non-Bantu

TABLE 2. Distributions (in %) of the B*, D* and E* Y-chromosome haplogroups in two Brazilian and twenty-one African populations^a

Population (country)	Haplogroup ^b																						
	E3* (PN2)	E3a* (M2)	E3a1 (M58)	E3a2 (M116.2)	E3a3 (M149)	E3a4 (M154)	E3a5 (M155)	E3a6 (M10)	E3a7 (M191)	E1* (M33)	E2* (M75)	E3b* (M35)	E3b1* (M78)	E3b2* (M81)	E3b3 (M123)	E3b4 (M281)	E-V6 ^c (M145)	YAP (xDE)	D* (xE)	B* (M60)	Others		
Porto Alegre (Brazil)	57	16							9													3	64
Rio de Janeiro (Brazil)	130	33	1						12	2	2	2	2	2	1							1	44
Niger-Congo speakers																							
<i>West</i>																							
Mossi (Burkina Faso)	49	2	68						22		4	2				ND	ND					2	
Rimaibe (Burkina Faso)	37	3	52	5					8	5	27					ND	ND						
Fulbe (Burkina Faso)	20	90								10						ND	ND						
Fon (Benin)	100	38		ND	ND	ND	ND		57		5					ND	ND						
<i>West-Central</i>																							
Fulbe (Cameroon)	17	6								53						ND	ND						41
Ewondo (Cameroon)	29	66							21							ND	ND					10	3
Fali (Cameroon)	39	26							33							ND	ND					18	23
Tali (Cameroon)	15	46						7	20	20						ND	ND					12	7
Mixed Adamawa (Cameroon)	18	17						11								ND	ND					4	60
Bakaka (Cameroon)	12	67				8			25							ND	ND						
Bamileke (Cameroon)	48	25				15			56							ND	ND					4	
Bamileke (Cameroon)	85	59		ND	ND	ND	ND		41							ND	ND						
Bantu (Cameroon)	14	57		ND	ND	ND	ND		21							ND	ND					22	
<i>Central-East</i>																							
Bantu (Kenya)	29	21		ND	ND	ND	ND		31		17	14				ND	ND					3	14
Wairak (Tanzania)	43	21		ND	ND	ND	ND	2	19		2	37				ND	ND					19	
Hutu (Ruanda)	69	22	10	ND	ND	ND	ND		51		8	3				ND	ND					6	
Tutsi (Ruanda)	94	32		ND	ND	ND	ND		48		4	1				ND	ND					15	
Nilo-Saharan speakers																							
<i>West-Central</i>																							
Mixed-Nilo-Saharan (Cameroon)	9	11							22		11					ND	ND					22	34
<i>Afro-Asiatic-Speakers</i>																							
<i>West-Central</i>																							
Mixed-Chadic (Cameroon)	15	7							7			7				ND	ND					7	72
Daba (Cameroon)	18	28								22		6				ND	ND					44	
Ouldeme (Cameroon)	21															ND	ND					5	95

^a The African data were compiled from Cruciani et al. (2002) and Luis et al. (2004). ND = not determined (marker was not investigated).

^b Nomenclature according to The International Y-Chromosome Consortium revised by Jobling and Tyler-Smith (2003).

^c This haplogroup showed frequencies ranging from 4% to 17% in populations from Kenya and Ethiopia (Cruciani et al., 2004).

TABLE 3. Distributions (in %) of the B* and E* Y-chromosome haplogroups in two Brazilian and in 48 African populations^c

Population (country)	N	Haplogroup ^b									
		E3* (xE3a)	E3a* (xE3a7)	E3a7 (M191)	E1* (M33)	E2* (M75)	E3b* (xE3b1,xE3b2)	E3b1* (M78)	E3b2* (M81)	B* (M60)	Others
Porto Alegre (Brazil)	57		16	9	2	2	3	3	2	3	64
Rio de Janeiro (Brazil)	130		34	12	2	2	4	1	1	1	44
Niger-Congo speakers											
<i>West</i>											
Wolof (Gambia/Senegal)	34	3	68		12	3	6		6	3	2
Mandinka (Gambia/Senegal)	39	3	79		3					3	7
Ewe (Ghana)	30		73	23							1
Ga (Ghana)	29		62	34	3						1
Fante (Ghana)	32	3	44	41	3		3				6
Fon (Benin)	100		38	57							
Mossi (Burkina Faso)	49	2	68	22		5	2			2	
Rimaibe (Burkina Faso)	37	3	57	8	5	4					
Fulbe-I (Burkina Faso)	20		90		10	27					
<i>West-Central</i>											
Mixed-Adamawa (Cameroon)	18		28							12	60
Fali (Cameroon)	39		26	33						18	23
Tali (Cameroon)	15		53	20	20						7
Fulbe-II (Cameroon)	17	6			53						41
Tupuri (Cameroon)	21									11	89
Ewondo (Cameroon)	29		66	21						10	3
Bakaka-I (Cameroon)	12		75	25							
Bakaka-II (Cameroon)	17		47	53						4	
Bamileke-I (Cameroon)	48		40	56							
Bamileke-II (Cameroon)	85		59	41							
Bantu (Cameroon)	14		57	21							22
Bassa (Cameroon)	11		55	36							9
Ngumba (Cameroon)	31		39	32		6				23	
Nande (Democratic Republic of Congo)	18		33	37							30
Hema (Democratic Republic of Congo)	18		17	11		39					5
Cabinda (Democratic Republic of Congo)	74		46	32	ND	ND	28		ND	9	13
<i>Central-East</i>											
Bantu (Kenya)	29		21	31	17	14				3	14
Wairak (Tanzania)	43		22	19	2	37					20
Hutu (Ruanda)	69		32	51	8	3					6
Tutsi (Ruanda)	94		32	48	4	1					15
Ganda (Uganda)	26		31	46	16						7
<i>Southwest</i>											
Herero (Namibia)	24		38	33							29
Ambo (Namibia)	22	5	50	32	5	5					3
<i>Southeast</i>											
Shona (Zimbabwe)	49		51	37	2					10	
<i>South</i>											
Sotho-Tswana (South Africa)	28	4	36	21	4	7				18	10
Zulu (South Africa)	29	3	34	21	21					17	4
Xhosa (South Africa)	80	4	34	20	28	5				5	4
Nilo-Saharan speakers											
<i>West-Central</i>											
Mixed (Cameroon)	9		11	22	11					22	34

(continued)

TABLE 3. (Continued)

Population (country)	N	Haplogroup ^b																		
		E3* (xE3a)	E3a* (xE3a7)	E3a7 (M191)	E1* (M33)	E2* (M75)	E3b* (xE3b1,xE3b2)	E3b1* (M78)	E3b2* (M81)	B* (M60)	Others									
<i>Central-East</i>																				
Massai (Kenya)	26		12	4		35						15			8					26
Luo (Kenya)	9		22	44											22					12
<i>Afro-Asiatic speakers</i>																				
<i>West-Central</i>																				
Mixed-Chadic (Cameroon)	15		7	7											7					79
Podokwo (Cameroon)	19																			95
Mandara (Cameroon)	28		11	4	7							5			4					74
Uldeme (Cameroon)	13																			69
Ouldeme (Cameroon)	21																			95
Daba (Cameroon)	18		28		22							6			5					44
<i>Central-East</i>																				
Amhara (Ethiopia)	18	6				11						33								50
Mixed Semitic (Ethiopia)	20	10				20					35									35
Oromo (Ethiopia)	9	11				11					22									56

ND = not determined (marker was not investigated).
^aThe African population data were compiled from Cruciani et al. (2002), Luis et al. (2004), Wood et al. (2005), and Belezra et al. (2005).
^bNomenclature according to the International Y-Chromosome Consortium revised by Jobling and Tyler-Smith (2003).

speakers (Yoruba, Kanuri, Fulbe, Shongai, Senegalese, Limba, Temne, Mende, Loko, Wolof, Mandenka, Serer).

Using an AMOVA we tested the hypothesis of differentiation between these two major geographical groups (excluding the Brazilian samples). The value obtained, although low, is significant: $\Phi_{CT} = 0.025, P < 10^{-4}$.

Y-chromosome biallelic markers

Table 2 shows that 56% and 36% of the Y-chromosomes from Rio de Janeiro and Porto Alegre respectively have an African origin. All the other Y-chromosomes (44%) found in Rio de Janeiro have a probable European origin, while for Porto Alegre 5% and 59% have a probable Amerindian and European origins, respectively (data not shown).

E3a* is the most frequent African chromosome found in our Brazilian sample, followed by E3a7. With the exception of E3b2, all African haplogroup E chromosomes found in Brazil are also present in sub-Saharan Africans. E3b2 has been described in high frequencies in North African populations, particularly among the Berber (Cruciani et al., 2002; Luis et al., 2004; Semino et al., 2004). However, the presence of the E3b2 chromosome in Brazil is most likely related to Iberian men, since typical Berber Y-chromosomes have been reported in Portuguese/Spanish populations. The existence of a common genetic background between Berbers and Iberians probably reflects the genetic impact of the Islamic occupation of the Iberian Peninsula for 7 centuries (Carvalho-Silva et al., 2001; Lucotte et al., 2001; Bortolini et al., 2004b; Cruciani et al., 2004; Semino et al., 2004; Gonçalves et al., 2005).

Since few African populations have been studied with the same set of Y-SNPs used here, we assembled the haplogroups according to a hierarchical strategy. This procedure allowed the comparison of our results with those from 48 African populations, including 36 Niger-Congo speaking groups (Table 3). Afterwards, this information was used to obtain a distance matrix and a neighbor-joining tree (Fig. 3), which shows a clear split separating the Niger-Congo speakers (cluster B) from the other Africans (Afro-Asiatic and Nilo-Saharan speakers; cluster A). But there are some exceptions (the Masai and Luo from Kenya clustered together with Niger-Congo speakers, whereas Mixed-Adamawa, Fulbe-Cameroon, and Tupuri grouped with the Afro-Asiatic speakers). The two Black Brazilian populations are closely related to each other and with the Niger-Congo speaking-populations. The Niger-Congo cluster, however, does not show internal structure in accordance with geography or language, a pattern which differs from that observed with mtDNA. The same tendency was observed when just Niger-Congo populations were considered in the analysis (data not shown).

Using the populations from West and West-Central/Southeast Africa given in Table 3 (excluding those from Cameroon, see comment above) we obtained a value of $\Phi_{CT} = 0.006; P > 5\%$, i.e., no Y-chromosome differentiation between West-Central/Southeast (Bantu) and West (non-Bantu) men.

Admixture analysis

The two major population groups observed in our mtDNA phylogenetic tree (West-Central/Southeast Bantu speakers and Western non-Bantu speakers),

T3

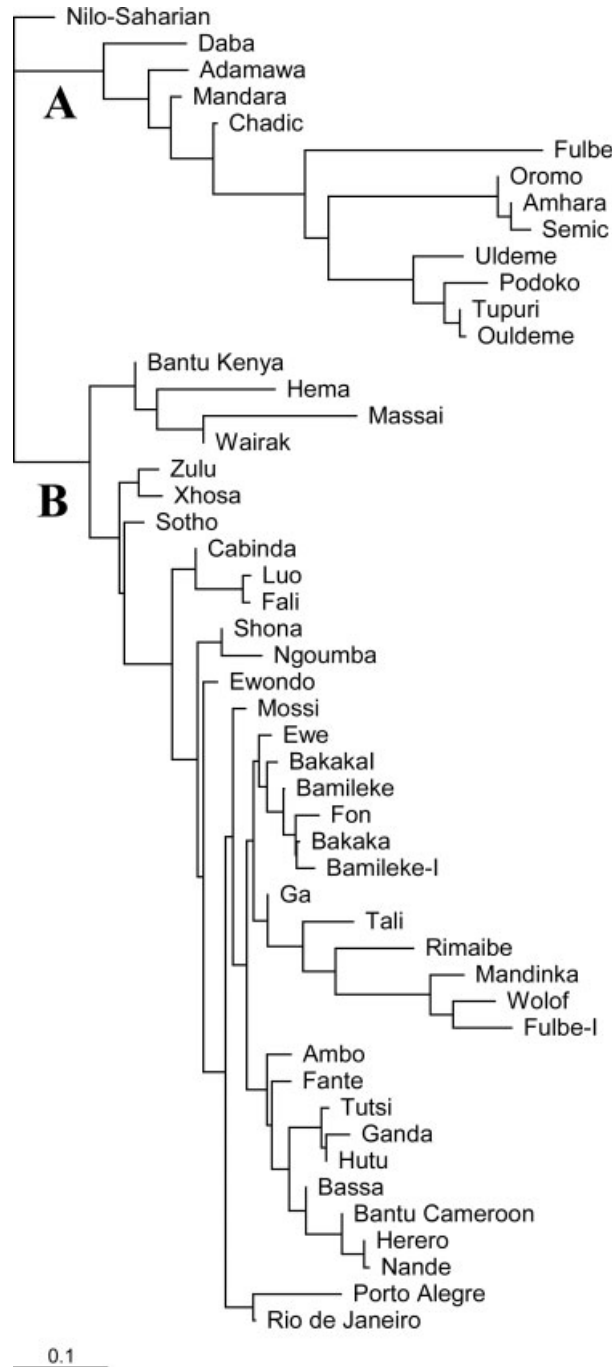


Fig. 3. Unrooted tree based on Y-SNP haplogroup distributions presented in Table 3. Since all “other” haplogroups in Rio de Janeiro and Porto Alegre had an European or Amerindian origin, this category was excluded of the analyses for these two populations. **A:** Afro-Asiatic speaker cluster; **B:** Niger-Congo speaker cluster.

which showed significant differences in their mtDNA haplogroup distributions, were used as parental stocks in the admixture analysis, using the data presented in Table 1 and a least squares approximation. The West-Central and Southeast African maternal contribution was majority (69% for Rio de Janeiro; 82% for Porto Alegre), whereas the complementary numbers can be attributable to the West African contribution (Table 4). These

admixture values are very similar to those suggested by the historical records. These findings could reflect the absence of major geographic gender-specific differences in the Atlantic slave trade (as mentioned in the introduction) in disagreement with another data set (Silva et al., 2006). Although sampling error cannot be discarded, the discrepancy between the two studies may be due to the different African sources that supplied slaves to the several Brazilian regions, and/or to different patterns of the slave trade for each of them.

DISCUSSION

As expected, estimates of the African contribution to the Black Brazilian mtDNA gene pool (79–90%) are larger than those obtained for populations identified as White in the different Brazilian regions, where the proportion of African mtDNA lineages ranged from 0% to 44% (Alves-Silva et al., 2000; Marrero et al., 2005). From these results a picture emerges, that the contemporary Brazilian population presents the most important reservoir of African mtDNA lineages out of Africa. It has been estimated that at least 90 million persons in Brazil, independently of their physical appearance, show mtDNAs of sub-Saharan African origin (Pena and Bortolini, 2004). This particularity allowed inferences not only about the probable mtDNA lineage composition of populations from African regions hitherto not studied (Alves-Silva et al., 2000), but also about possible evolutionary and demographic events mediated by women, which should have occurred in Africa (Bortolini et al., 2004a).

On the other hand, some demographic and historical circumstances related to Brazil’s colonization determined that the first Brazilians arose mostly by the union between Portuguese males and Amerindian or African females (Bortolini et al., 1997; Carvalho-Silva et al., 2001; Salzano and Bortolini, 2002). These asymmetrical matings determined that most of the Y-chromosomes of contemporary Brazilian populations have an European origin. The present results indicated that, although the proportion of the typical African chromosomes in the Black samples (36–56%) are much higher than those

TABLE 4. Origin of Africans (in %) who arrived in Rio Grande do Sul and Rio de Janeiro at the time of the slave trade considering genetic and historical sources

	West-Central and Southeast Africa ^a	West Africa ^b
Porto Alegre (POA)		
mtDNA ^c	82 ± 14	18 ± 14
Historical ^d	~80	~20
Rio de Janeiro		
mtDNA ^c	69 ± 13	31 ± 13
Historical ^e	~70	~30

^a Major geographical regions characterized by the presence of people who speak languages identified with the Bantu branch, Niger-Congo subphylum. Two important previous Portuguese colonies were located in this region: Angola and Mozambique.

^b Major geographical region characterized by the presence of people who speak languages identified with several non-Bantu linguistic groups of the Niger-Congo subphylum (except Hausa).

^c Some sub-clades with low frequencies in the derived populations (RJ and POA) were grouped in their respective haplogroups.

^d According to estimates presented by Klein (2002).

^e According to Maestri-Filho (1993).

obtained for Brazilian populations identified as White (0 to ~5%; Carvalho-Silva et al., 2001; Abe-Sandes et al., 2004; Marrero et al., 2005), the amount of Y-chromosomes of European origin is striking.

Our mtDNA results basically confirmed the historical evidence that the main source of African migration to Brazil originated from West-Central and Southeast Africa. These results could be obtained because there are clear mtDNA geographic or language structures within Africa, particularly considering the Niger-Congo cluster. The same was not true; however, for the Y-SNP data, due to lack of clear African Y-chromosome patterns of distribution. Cruciani et al. (2002) suggested that the absence of Y-chromosome differentiation in Africa could be due to relatively recent range expansion(s). E3a* chromosomes could have been already present along the Western region and then spread to South Africa through the Bantu expansion. This haplogroup was also observed in high frequencies among hunter-gatherer populations, like the Biaka/Mbuti and Khoisan-speaking people, probably due to admixture between Bantu-speaking men and Biaka/Mbuti/Khoisan women. The M191 mutation, which defines haplogroup E3a7, probably arose in West-Central Africa. A later demic expansion should have brought E3a7 chromosomes from West-Central to Western Africa (Cruciani et al., 2002). Studies with Y-SNPs associated with the fast-evolving Y microsatellite loci (STRs) revealed that the STR variation is structured within SNP-haplogroups. However, this variation is also not well correlated with geography (Scozzari et al., 1999; Cruciani et al., 2002). These results reinforce the idea that the present differences between HVS-I mtDNA and Y-SNP data is not an artifact related to different mutation rates.

A first important implication of these findings is that E3a* should be interpreted as a Niger-Congo marker. Although the presence of E3a* in Central to South Africa can be associated with the Bantu expansion, this chromosome may have existed for at least ~11,000 years before the spread of the carriers of the Bantu languages (Scozzari et al., 1999). Probably E3a* was the most

common chromosome in West Africa at the time of the Niger-Congo language emergence. A second implication is that these demic expansions in Africa, including the Bantu dispersion, probably did not involve a higher migration rate of Niger-Congo speaking women than men, but maybe the opposite, or at least the same female/male migration rate.

CONCLUSIONS

New World African-derived populations furnish important information about past events. When historical sources are lacking or deficient (for instance, on December 14, 1890, Brazilian's then Minister of Finances, Rui Barbosa, issued a decree ordering the burning of all documents related to slavery) genetic data can be used to clarify some of the uncertainties.

The present work was designed to answer specific questions, one related to the pattern of interethnic unions that occurred in the past, and the second about possible sources of origin of the Africans who were forcibly transported to Brazil. The results indicated a clear presence of European Y-chromosomes in Black persons, as well as confirmation, through the mtDNA findings, of historical data which placed West-Central and Southeast Africa as the main places from which such people came to Brazil. The lack of clear Y-chromosome prevalence patterns within Africa, however, prevents the ascertainment of the role played by possible gender differences which could have occurred in the slave traffic.

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APPENDIX

TABLE A1. List of the mtDNA haplogroups and haplotypes observed in Rio de Janeiro (RJ) and/or Porto Alegre (POA)

Haplotype	Haplogroup	HVS1 Mutations ^a	RJ	POA
1	L0a1	129 148 168 172 187 188G 189 223 230 278 311 320	1	1
2	L0a1	129 148 168 172 187 188G 189 223 230 278 293 311 320	3	3
3	L0a1	093 129 148 168 172 187 188G 189 223 230 278 293 311 320	2	
4	L0a2	148 172 187 188A 189 223 230 311 320	1	
5	L0a2	148 172 187 188G 189 223 230 311 320	3	
6	L0d1	129 187 189 223 230 239 243 294 311	1	
7	L0a1a	093 129 148 168 172 187 188A 189 223 230 278 293 311 320		1
8	L1b	111 126 187 189 223 264 270 278 293 311	1	
9	L1b	126 187 189 223 264 270 278 293 311	2	2
10	L1b	126 148 187 189 223 264 270 278 311	1	
11	L1b	126 187 189 223 264 270 278 311	4	2
12	L1c	129 187 189 223 278 294 311 360	1	
13	L1c	129 187 189 223 261 278 311 360	1	
14	L1c	129 187 189 223 274 278 287 294 311 320 360	1	
15	L1c	129 187 189 223 278 294 311 355 360 362	1	
16	L1c1	129 187 189 223 278 293 294 311 360	2	2
17	L1c1	129 187 189 223 274 278 293 294 311 360	1	
18	L1c1	093 129 187 189 223 263 278 293 294 311 360	1	1
19	L1c1	129 163 187 189 209 223 278 293 294 311 360		2
20	L1c1	093 129 187 189 223 278 293 294 311 360		1

(continued)

TABLE A1. (Continued)

Haplotype	Haplogroup	HVS1 Mutations ^a	RJ	POA
21	L1c2	129 187 189 223 265C 278 286G 294 311 320 360	3	
22	L1c2	129 187 189 223 265C 278 286G 294 311 355 360	1	
23	L1c2	129 187 189 223 265C 278 286G 294 311 360	1	3
24	L1c2	129 145 187 189 223 234 265C 278 286G 294 311 360	1	
25	L1c2	129 187 189 223 265C 278 286A 294 311 320 360		1
26	L1c2	129 187 189 213 223 234 265C 278 286G 294 311 360		1
27	L1c3	129 189 215 223 278 294 311 360		3
28	L1c3	129 189 215 223 278 294 311 354 360		1
29	L2a α1	223 234 249 278 294	2	
30	L2a1 β1	223 278 294 309	2	2
31	L2a1 β1	193 213 223 239 278 294 309	1	
32	L2a1 β1	093 223 256 278 292 294 309	1	
33	L2a1 β1	223 256 278 294 309	2	1
34	L2a1 β1	093 223 256 278 294 309	4	2
35	L2a1 β1	223 278 291 294 309		1
36	L2a1 β1	129 223 278 294 309		2
37	L2a1 β1	092 223 278 294 309		2
38	L2a1 β2	189 193 223 245 278 294 309	1	
39	L2a1 β2	189 223 278 294 309		1
40	L2a1 β3	189 192 223 278 294 309		2
41	L2a1a	092 223 278 286 294 309	2	
42	L2a1a	223 278 286 294 309	3	4
43	L2b	114A 129 213 223 278 354	2	1
44	L2b	114A 129 213 223 274 278		3
45	L2b	114A 223 264 274 278		1
46	L2b	223 264 274 278		1
47	L2b1	114A 129 213 223 278 355 362	3	
48	L2b1	114A 129 213 223 278 311 362	1	
49	L2c	223 264 278	2	
50	L3	223	1	1
51	L3b	124 223 278 362	1	2
52	L3b	124 145 223 278 362	2	
53	L3b1	223 278 294 362		2
54	L3b2	124 223 278 311 362		2
55	L3d	124 223 319	2	
56	L3d	124 223 278 290 292 312 362		1
57	L3d1	124 223	1	
58	L3d1	124 145 223 278 290 319 362		1
59	L3d1	124 223 278 290 319 362		1
60	L3d2	124 223 256	4	
61	L3e1	223 327	1	4
62	L3e1	176 223 327	1	1
63	L3e1a	185 223 327	1	1
64	L3e1a	185 223 311 327		2
65	L3e1a	185 209 223 327		2
66	L3e1b	223 325D 327	1	
67	L3e2	093 192 223 320		1
68	L3e2	192 223 320		1
69	L3e2b	172 189 223 320		2
70	L3e3	223 265T	3	2
71	L3e3	223 265T 355	1	
72	L3e3	223 265T 316	1	
73	L3e3	223 265T 288	1	
74	L3e3	189 223 265T		2
75	L3f	209 223 311	2	2
76	L3f	192 209 223 311		1
77	L3f1	129 209 223 292 295 311	1	2
78	L3f1	093 129 209 223 292 295 311	1	
79	L3f1	209 223 292 311		2
80	L3g	093 223 287 293T 301 311 355 362		2
81	L3g	093 223 293T 301 311 355 362		1
Total			84	85

^a The nucleotide positions (less 16,000) considered for the analyses were from 16051 to 16384. Sequences were aligned with the revised reference sequence (Andrews et al., 1999).

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