mtDNA Haplogroup Analysis of Black Brazilian and Sub-Saharan Populations: Implications for the Atlantic Slave Trade

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Abstract Seventy individuals from two African and four black Brazilian populations were studied for the first hypervariable segment of mtDNA. To delineate a more complete phylogeographic scenario of the African mtDNA haplogroups in Brazil and to provide additional information on the nature of the Atlantic slave trade, we analyzed our data together with previously published data. The results indicate different sources of African slaves for the four major Brazilian regions. In addition, the data revealed patterns that differ from those expected on the basis of historical registers, thus suggesting the role of ethnic sex differences in the slave trade.

From the 15th to the 19th century, 9 million sub-Saharan Africans were brought to the Americas as slaves; about 40% of them were probably brought to Brazil (Klein 2002). This forced migration had a tragic impact on some African societies and determined that part of the history of Africans began to be written outside Africa. At present, genetic studies of Brazilians and other New World descendents of Africans have provided data that have been used to rescue part of this particular history (Zago et al. 1992; Figueiredo et al. 1994; Bortolini et al. 1997, 1999, 2004; Silva et al. 1999; Salzano and Bortolini 2002). Some of these investigations used *HBB*S* haplotypes to define the origin of Africans that arrived in Brazil, because historical records about slavery contain many gaps (Zago et al. 1992; Figueiredo et al. 1994). In an extensive review, Salzano and Bortolini (2002) estimated that 61%, 34%, and 3% of the *HBB*S* haplotypes found in

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Brazil are of the Bantu, Benin, and Senegal types, respectively. These values are different from those observed in other New World countries, such as Venezuela, Cuba, and Jamaica, where the Benin haplotype is the most frequent.

More recently, however, lineage markers such as mtDNA have been used for this purpose. Alves-Silva et al. (2000) furnished an initial landscape of the phylogeography of African mtDNA haplogroups in Brazil. Together, haplogroups L3e and L1c constitute approximately 49% of the African fraction of sequences identified by Alves-Silva et al. (2000). Although these analyses have been limited so far by the lack of mtDNA data on important African slave sources to Brazil, such as Angola, Congo, and Mozambique, Alves-Silva et al. (2000) suggested that most of the mtDNA lineages of African ancestry in their Brazilian sample had an origin in central Africa, although a substantial number must have come from western Africa. Bandelt et al. (2001) evaluated the phylogeography of the L3e mtDNA haplogroup, which is omnipresent in Africa but virtually absent in Eurasia, and concluded that the distributions of haplogroup L3e in Brazil and in the Caribbean area still reflect the different African slave sources to the New World.

Salas et al. (2004a) compared the distribution of all the main mtDNA haplogroups and their derived lineages in Africa with available data from the Americas. They estimated that 65%, 41%, and 28% of mtDNA types found in South, North, and Central America, respectively, had a Central-West African origin. Earlier the same research group had identified a new African haplogroup (L3g), which is frequent in Tanzania and Kenya (Salas et al. 2002). The presence of haplogroup L3g in three Brazilians (among the 92 African mtDNA haplotypes that were characterized; Bortolini et al. 1997; Alves-Silva et al. 2000) was interpreted as either direct slave trade from eastern Africa to the New World or hitherto undetected gene flow from eastern Africa into western or southwestern Africa and then into the Americas. Bortolini et al. (2004) evaluated this proposal and, from the identification of L3g in several Cameroon ethnic groups, concluded that the Camaroonese L3g lineages originated from eastern Africa by transcontinental gene flow and that the L3g lineages in the Americas probably have their immediate origin in Cameroon or in neighboring regions and not in eastern Africa. On the basis of the extensive amount of new data that could be added to the L3g phylogeny, Salas et al. (2004b) corroborated this proposal.

Color is used in Brazil as an equivalent to "race" and is based on a subjective phenotypic evaluation (Parra et al. 2003). In contrast to the situation in the United States, in Brazil the emphasis is on physical appearance rather than ancestry. The Brazilian Institute of Geography and Statistics (IBGE) has adopted the criterion of classification of individuals according to the following categories: white (in Portuguese, *branco*), black (*preto*), brown (*pardo*), yellow (*amarelo*), and Amerindian (*Indígena*). Accordingly, in Brazil as a whole, 90 million, 10 million, and 65 million of the people were identified as white, black, and brown, respectively; the remaining 5 million people are distributed between the two other categories (IBGE Census 2000; available at http://www.ibge.gov.br). However,

according to Telles (2003), two other major systems, beyond that adopted by the IBGE, are associated with "racial classification": (1) The popular discourse, which uses a large and variable nomenclature, includes several ambiguous terms, such as mulatto; and (2) the political discourse of the black organized social movements lumps together as "black" all the variations, such as black, brown, and mulatto. More recently, the expression *Afro-descendant* has been incorporated into this ethnic semantics (Pena and Bortolini 2004). Pena and Bortolini (2004) estimated that 148 million Brazilians present more than 10% African nuclear genome ancestry and that at least 89 million individuals have mtDNA lineages of African origin. This illustrates the extent of admixture in Brazil and corroborates the suggestion that color and other phenotypic traits can be poor predictors of genomic ancestry (Parra et al. 2003). These results also strengthen the opinion that classification of individuals within a population is always difficult and subject to error, whatever the basis for the "ethnic" or "racial" classification. In this paper we use the word *black* to refer to any person (or population) identified and/or self-identified with some term that reports African ancestry according to physical appearance.

Here, we provide information about the distribution of the mtDNA haplogroups in three rural and one urban Brazilian black communities and in two Bantu populations from Africa (Cameroon and Democratic Republic of Congo). Our data from African populations furnish information about an until now largely uncharacterized region, which is known as the birthplace of and an important route for the major Bantu expansion. The importance of Cameroon and Congo as sources of slaves to Brazil is also well known. In addition, we analyzed our data with respect to other recently published data, including data from Angola and Mozambique, and provide new considerations about the nature of the Atlantic slave trade to Brazil.

Materials and Methods

Population Samples and DNA Extraction. The African samples were obtained from 20 Bantu-speaking subjects living in two African countries: (1) the Democratic Republic of Congo (formerly Zaire) (samples from 10 individuals were collected in Lubumbashi city, in Shaba province); and (2) Cameroon (samples from 10 individuals were collected in Yaoundé city from the Boulou, Bamileke, Bene, Eton, Nweh, Sonaga, and Etongo ethnic groups).

The black Brazilian samples consist of 30 individuals from 3 rural communities: (1) Cametá ($N = 10$; 2°3′ S, 59°55′ W), in the region of the lower Tocantins River, state of Pará, northern Brazil; (2) Trombetas ($N = 10$; 1°8′–1°46′ S, 55°51′–57° W), at the margins of the Trombetas and Cuminá rivers, state of Pará, northern Brazil; and (3) Cajueiro ($N = 10$; 2°25′ S, 44°20′ W), located in the county of Alcantara, state of Maranhão, northeastern Brazil. These rural black communities are recognized as *quilombos*, because their founders were probably

fugitive slaves. One urban sample was also investigated. This sample was obtained from 20 individuals living in Ribeirão Preto (20°10′ S, 40°75′ W), located in the northern part of the state of São Paulo. Additional information about these populations can be obtained from Bortolini et al. (1999, 2004) and Silva et al. (1999).

DNA extraction from whole blood was performed according to the method of Lahiri and Nurnberger (1991).

mtDNA Amplification and Sequencing. The nucleotide sequence of the first mtDNA hypervariable segment (HVS-I) was directly amplified using the polymerase chain reaction (PCR) with the primers and PCR protocol described by Ward et al. (1991). Reaction products were then purified and sequenced according to the conditions described or referenced by Bortolini et al. (1997). For all samples both strands of DNA were sequenced.

Genetic Analysis. Nucleotide positions 16020 to 16365 were considered for the analysis. To evaluate whether artifacts were generated (phantom mutations) during the sequencing process, we applied the method described by Bandelt et al. (2002). The first analysis filtered out all speedy transitions and thus scored weighty mutations only. After filtering for speedy transitions, we constructed a network of sequences with the program Network 3.1 (available at http://www.fluxus-engineering.com) using a median-joining algorithm (Bandelt et al. 1995, 1999). Weight networks showing perfect star tree patterns are expected when the data are potentially free of phantom mutations.

The information provided by HVS-I was used to classify the lineages into haplogroups, according to Salas et al. (2002, 2004a). However, studies of the coding regions have revealed novel parsimony, informative polymorphisms, or previously unidentified splits in the inner branches of the mtDNA phylogeny. Considering this recent information, Kivisild et al. (2004) defined new haplogroups that extend the framework of the existing classification scheme. For example, 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 haplogroup L3g is actually a sister cluster of haplogroup L4a and therefore to propose that L3g be renamed L4g. Haplogroup L1e, previously characterized on the basis of HVS-I motifs (Salas et al. 2002), has been recently redefined as L5a because it occupies an intermediate phylogenetic position between the L1 and L2′L3 major haplogroups (Shen et al. 2004).

Although the hierarchical relation among the human mtDNA lineages is well known, the terminology to define them remains confusing. *Haplogroup*, *clade*, *subhaplogroup*, and *subclade* are words frequently used synonymously. In this paper the term *major haplogroup* is used to define the major lineages (A, B, C, D, J, L0, L1, L2, L3, L4, L5, etc.), whereas *haplogroup* is used to identify their first derivations (L2a, L2b, L3e, etc.). *Subclade* and *subhaplogroup* are used

equally to define any derived lineage from the haplogroups (L2a1, L1c1, L3e1, L3e2, etc.).

Because most sub-Saharan mtDNA haplogroups are not region specific, we estimated the parental contributions using the haplogroup frequencies and Long's (1991) least-squares method.

Results and Discussion

The networks obtained for the HVS-I weighty variation showed perfect star tree configurations, indicating that our HVS-I data sets are potentially free of phantom mutations.

Table 1 shows the mtDNA lineages and the haplogroups or subhaplogroups identified in our black Brazilian and African samples. The higher non-African fraction was observed in Cametá, because 60% of sequences can be associated with the major Amerindian haplogroups A, B, C, and D. The large Amerindian component in Cametá is not surprising, because the community is located in the Amazonian region. The native American component was also detected in Cajueiro and Trombetas but in lower proportions (30% and 10%, respectively). No European mtDNA sequence was observed in these populations. These results probably reflect the introduction of native American women into the *quilombos*, particularly during the slavery era, because the number of men who escaped was larger than the number of women who escaped.

European presence was detected only in the urban sample of Ribeirão Preto, but in low frequency (5%; major haplogroup J). A more significant presence of non-African lineages would be expected in the urban black Brazilian population; for instance, Bortolini et al. (1997) estimated that 17% of the mtDNA sequences in their urban black sample had an Amerindian or European origin. However, we had selected the Ribeirão Preto urban sample so that it would include only individuals who did not report any nonblack ancestry (Silva et al. 1999).

The African sequences show large diversity, with several haplogroups or subhaplogroups normally found in the sub-Saharan region detected; all these sequences could be assigned to the major African haplogroups L0, L1, L2, L3, and L4 (Salas et al. 2002, 2004a; Bortolini et al. 2004; Kivisild et al. 2004; Plaza et al. 2004). The subclade L2a1 is unique and was found in all four black Brazilian populations. Haplogroup L4g (formerly L3g), which has been the target of recent analyses (Bortolini et al. 2004; Salas et al. 2004b), is present in Trombetas. This last result indicates that the distribution of haplogroup L4g is not restricted to the southern and southeastern regions of Brazil (Bortolini et al. 1997, 2004; Alves-Silva et al. 2000). Both subclades L4g1 and L4g2 (Salas et al. 2004b) are found in Brazil, with subclade L4g2 showing a higher frequency (75% of the Brazilian L4g sequences).

Table 1. mtDNA Haplogroups and Lineages in Black Brazilian and African Populations

		Africans		*Black Brazilians*			
Haplogroup	*HVS-I (16000+)*	*Congo*	*Cameroon*	*Cajueiro*	*Cametá*	*Ribeirão Preto*	*Trombetas*
African							
L0a1	129 148 168 171 172 187 188G 189 223 230 256A 278 291 311 320	1					
L0a1	129 148 168 172 187 188G 189 223 230 311 320			2			
L0a1	129 148 168 172 187 188G 189 223 230 278 293 311 320					2	
L1b	126 187 189 193 213 223 264 278 293 311					1	
L1b	111 126 187 189 223 239 270 278 287 293 311		1				
L1c1	129 163 187 189 209 223 278 293 294 298 311 360		1				
L1c1	086 129 187 189 223 241 278 291 293 294 311 360					1	
L1c1	038 187 189 223 278 293 294 311 360					1	
L1c2	093 129 187 189 223 265C 278 286G 294 311 358G 360	1					
L1c2	129 145 187 189 213 223 265C 278 286G 294 311 360	1				1	
L1c2	129 187 189 223 234 265C 278 286G 294 311 360					1	
L1c2	129 187 189 223 265C 278 286G 294 311 359 360					1	
L1c2	129 187 189 223 265C 278 286G 294 311 343T 360			1			
L1c2	187 189 223 265C 278 286G 294 311 343T 360			1			
L2a	111A 223 234 249 278 294 295					1	
L2a	223 234 235C 249 278 294 295	1					
L2a	095G 096G 223 234 249 278 294 295	1					
L2a1	223 278 294 309		1			1	
L2a1	223 225 234 278 294 309						1

L2a1	223 278 291 294 309 360					1	
L2a1	042 086 092 223 278 294 309 356					1	
L2a1	223 278 294 309 363						1
L2a1	189 223 278 294 363						1
L2a1	131 189 223 278 294 309 363						1
L2a1	189 223 278 294 309				1		
L2a1	189 192 223 278 294 309			1	2		
L2b	114A 129 213 223 278 354	1					
L2b	093 129 167 189 278 300 311 354				1		
L2c	223 278						2
L3b	124 189 223 278 362						1
L3b	145 223 278 362	1					
L3d	069 124 192 223 242					1	
L3d	124 223 266 319					1	
L3d1	111 124 223						1
L3e1	223 327	1					
L3e1	223 260 327	1					
L3e1	126 169 180 223 255 327		1				
L3e1a	185 223 327					2	
L3e1a	185 209 223 327					1	
L3e4	051 223 264			1			
L3e2b	172 223 278 320		1				
L3e2b	172 223 311 320	1					
L3e2b	223 234 311 320		1				

Table 1. (Continued)

		Africans		*Black Brazilians*			
Haplogroup	*HVS-I (16000+)*	*Congo*	*Cameroon*	*Cajueiro*	*Cametá*	*Ribeirão Preto*	*Trombetas*
L3e2b	172 189 223 320					1	
L3e2b	164 172 189 320			1			
L3f	209 223 311					1	
L3f	148 209 223 311		1				
L3f1	129 209 223 292 311		1				
L3f1	111 209 218 223 292 311		1				
L4g1	051 114 189 192 223 293T 311 316 355 360		1				
L4g2	093G 223 287A 293T 301 311 355 362						1
Amerindian							
A	126 223 278 290 319 362				1		
A	111 223 290 319 362						1
B[a]	217				1		
C	051 093 223 298 325 327				1		
C	179 223 298 325 327				1		
C	223 298 325 327 354				1		
C	129 223 294 298 325 327 360			1			
C	223 298 311 325 327			1			
C	126 223 298 325 327			1			
D	223 293 325 362				1		
European							
J	069 126					1	
Total		10	10	10	10	20	10

a. CoII/tRNA^{Lys} 9-bp deletion was also detected in this sample, beyond the transition 16217C → T, which characterizes Amerindian haplogroup B. The 9-bp deletion has been described in several other backgrounds, including the African haplogroup L0a2 (Bortolini et al. 1999).

Twelve mtDNA haplogroups were identified in the two Bantu populations. Only two subclades are shared: L3e1 and L3e2. This result shows important differences between the Bantu from Congo and those from Cameroon, but caution is necessary because this result can also reflect sampling, as the number of individuals investigated is low.

Table 1 shows that in Ribeirão Preto two L1c2 and L2a1 sequences are the same as two other sequences observed in Congo and Cameroon, respectively. Among the black Brazilian populations, only Cametá and Cajueiro shared one identical L2a1 sequence.

To better understand the phylogeographic scenarios of the mtDNA sub-Saharan haplogroups and their respective subclades found in Brazil, we grouped our data with data obtained by Bortolini et al. (1997) and Alves-Silva et al. (2000), according to the origin of the sampled individuals into four main geographic regions of country: north, northeast, southeast, and south. Table 2 shows these distributions and the estimates considering three major sub-Saharan groups: West-Central Bantu, East Bantu, and West Africa.

Haplogroups L2c and L1b are the most common among the West Africans (19% and 17%, respectively), but both have low frequencies among the Central-West and East Bantu speakers. Haplogroups L3b and L3d are also mainly found in West Africans. On the other hand, subclades L0a1 and L0a2 can be considered reliable Bantu markers, because they are not found in West Africans (in Africa the COII/$tRNA^{lys}$ 9-bp deletion has been associated with subclade L0a2; Soodyal et al 1996; Bortolini et al. 1999; Kivisild et al. 2004; Plaza et al. 2004). The phylogeography of subclades L0a1 and L0a2 in Africa has been associated with the Bantu expansion from the Cameroon plateau, 3,500 years ago (Cavalli-Sforza et al. 1994; Salas et al. 2002; Plaza et al. 2004).

The origin of haplogroup L1c was postulated to be in Central Africa toward the Atlantic coast with a reasonable diffusion to the east (Salas et al. 2002). The virtual absence of this haplogroup and of its subclades, L1c1, L1c2, and L1c3, in West Africans makes them reliable Bantu markers. Haplogroup L3e is the most widespread, frequent, and ancient of the L3 haplogroups, comprising most of the L3 subtypes in sub-Saharan Africa (Salas et al. 2002). Subclade L3e1 is common among Central-West (11%) and East Bantu (9%) speakers, but it is rare in non-Bantus from West Africa; subclade L3e2 is found with a significant frequency only among the Central-West Bantus (12%).

Additional haplogroups and subhaplogroups are rare, and others are amply distributed in both Bantu and non-Bantu speakers. For example, haplogroup L2a is the most frequent and widespread mtDNA cluster in Africa (nearly one-fourth of all natives types; Salas et al. 2002). Subclade L2a1 has a similar distribution among Central-West Bantus (16%) and West Africans (15%), but in East Bantus its frequency is twice as high (34%). A West African origin of subclade L2a1 has been postulated, and its phylogeographic picture is also compatible with the earliest demographic Bantu dispersal (Pereira et al. 2001; Salas et al. 2002; Plaza et al. 2004).

Table 2. Sub-Saharan mtDNA Haplogroups and Their Distributions (%)[a] in Four Brazilian Regions and in Bantu and Non-Bantu-Speaking Populations

	Africa[b]			*Brazil*[c]				
Haplogroup or Subclade	*Central-West Bantu (111)*	*East Bantu (416)*	*West Africa (348)*	*Southeast (51)*	*South (28)*	*Northeast (33)*	*North (19)*	*Total (131)*
L0a		<1	1					
L0a1	4	10		6	14	19		10
L0a2	7	15		2	4			2
L0d		5						
L1b	4	1	17	4	4	3		3
L1c	4	<1						
L1c1	4	2	1	16			10	8
L1c2	6	2		8	14	12		9
L1c3	2	1						
L2	4	2	5	10	11	6		8
L2a1	16	34	15	8		18	40	13
L2b	4	1	6	2	7		10	4
L2c		1	19	4			10	3
L2d	6	1	2					
L3		1						
L3b	2	3	12		7		5	2
L3d	1	5	9	4	7	6	5	5
L3e1	11	9	1	14		21	11	
L3e2	12	1	5	12	24	9	10	14
L3e3	4	3	1	4			5	2
L3e4		<1	2			3		1
L3f	5	2	4	2	4	3		2
L4g	3			4	4		5	3
L5a	1	<1						

a. Total number of individuals studied is shown in parentheses.

b. West-Central Bantu: Mbundu and Bakongo (Angola) (Plaza et al. 2004); Bubi and Fang (Guinea Equatorial) (Salas et al. 2002); Congolese (Democratic Republic of Congo) (present study); and Bamileke, Bene, Eton, Nweh, Sonaga, and Etongo (Cameroon) (present study). East Bantu: Yao, Tonga, Shangaan, Chopi, Chwabo, Lomwe, Makonde, Makhuwa, Ndau, Nguni, Nyungwe, Nyanja, Ronga, Shona, Sena, and Tswa (Mozambique) (Salas et al. 2002); and other nondefined Bantu-speaking people from Mozambique (Pereira et al. 2001). West Africa: Hausa, Kanuri, Fulbe, Songhai, Yoruba, Senegalese, Serer, Wolof, and Mandenka (from Nigeria, Niger, Benin, Cameroon, Burkina Faso, and Senegal) (Salas et al. 2002).

c. Southeast: White, brown, and black Brazilians (Alves-Silva et al. 2000; present study). South: White, brown, and black Brazilians (Alves-Silva et al. 2000; Bortolini et al. 1997). Northeast: White, brown, and black Brazilians (Alves-Silva et al. 2000; Bortolini et al. 1997; present study). North: White, brown, and black Brazilians (Alves-Silva et al. 2000; present study).

Most of the African haplogroups within L0–L5 are present in at least one of the four Brazilian regions. Exceptions are represented by haplogroups L0a (frequency in East Bantu, <1%; West Africa, 1%), L0d (East Bantu, 5%), L1c (Central-West Bantu, 4%; East Bantu, <1%), L5 (Central-West Bantu, 1%; East Bantu, <1%), and L3 (East Bantu, 1%). However, the pattern of sub-Saharan mtDNA type distributions is clearly different in the four main geographic Brazilian regions. For example, subclade L2a1 was detected in three Brazilian regions; distributions range from 8% in the southeast to 40% in the north, but curiously subclade L2a1 does not appear in the southern region. In contrast, subclade L0a1, which can be taken as an East Bantu marker, apparently is not present in the northern region. Subclade L1c1 shows substantial frequencies in the southeastern (16%) and northern (10%) regions, but it is absent in the southern and northeastern mtDNA pools, whereas haplogroup L3b, with a predominantly West African distribution, is present only in the southern (7%) and northern (5%) populations. Although sampling errors cannot be ruled out, it is possible that our results reflect the different African sources that supplied slaves to the Brazilian regions. There are, however, some differences between the patterns revealed by our results and those expected on the basis of the historical register (Klein 2002), and these differences deserve consideration.

Because of geographic proximity and other factors, the northeastern and northern regions of Brazil received the largest number of West Africans who were forcibly moved to Brazil during the Atlantic slave trade. Interestingly, the typical West African markers—haplogroups L1b, L2c, and L3b (together they represent about 50% of the mtDNA haplogroups observed in region)—have a relatively low distribution frequency in the northeastern and northern regions (L1b + L2c + L3b = 3% and 15%, respectively). Several hypotheses could explain these last results: (1) Early (when laws prohibited the direct slave trade from Africa) and recent internal migrations between Brazilian regions camouflaged the original phylogeographic landscape; (2) the West Africa group of Senegalese (≅70% of 348 sequences shown in Table 1), particularly the Mandenka, who did not come to Brazil in higher numbers than other groups (such as the Yoruba, who have been less studied), is overrepresented; (3) there are ethnic sex-specific differences in the Atlantic slave trade, so that more West African men than women would have been brought to Brazil.

Finally, Table 3 provides a general view of the origins of the Africans who came to Brazil. The numbers show that West-Central Africa provided most of the African slaves to Brazil, as the historical sources indicate. However, the differences observed between the West-Central Bantu and the West African contributions (80% and 65%, respectively, according to historical data, and 15% and 30%, respectively, according to mtDNA data) reinforce scenario 3 suggested in the previous paragraph. Only additional studies using geography-specific African Y-chromosome haplogroups (Cruciani et al. 2004) can provide a more complete picture of the origin of African slaves and can answer other questions related to the Atlantic slave trade to Brazil.

Table 3. Origin of Slaves (%) Who Arrived in Brazil During the Atlantic Slave Trade Considering Genetic (mtDNA) and Historical Sources

Source	*Central-West Bantu*	*East Bantu*	*West Africans*
mtDNA[a]	80 ± 1.3	5 ± 1.5	15 ± 8.9
Historical[b]	≅65	≅5	≅30

a. Because most sub-Saharan mtDNA haplogroups and subhaplogroups are not geography specific, the estimates of the African contributions were obtained using the frequencies presented in Table 2 and Long's (1991) least-squares method.

b. Values obtained according to data presented by Klein (2002).

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