Admixture and Sexual Bias in the Population Settlement of La Réunion Island (Indian Ocean)

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ABSTRACT   La Réunion, one of the three Mascarene islands located in the Indian Ocean, remained devoid of inhabitants until it was first colonized by the French in the middle of the 17th century. The continuous flow of foreign-born slaves and immigrant workers from Africa, India, Southeast Asia, and China to work on coffee and sugar cane plantations led to the island becoming a melting pot of people of multiple ethnic origins. To establish the impact of the different incoming ethnic groups on the present Reunionese gene pool, we have sequenced both hypervariable regions I and II of the mitochondrial DNA molecule, the 9 bp COII/tRNA^{Lys} deletion, and four SNPs located in the coding region in a total of 41 samples of the general population, and a further 18 STRs and 35 SNPs on the Y chromosome in 26 of these samples. Our results show that there was a strong sexual bias (asymmetrical gene flow) in the peopling of La Réunion, where admixture events were mainly between male settlers and females from the incoming slave groups. Most of the Y-chromosome gene pool is of European/Middle Eastern ancestry (85%), whereas the mtDNA gene pool is mainly of Indian and East Asian ancestry (70%). The absence of genetic diversity within these two major components of the mtDNA gene pool suggests these populations may have witnessed strong founder effects during the colonization process. Am J Phys Anthropol 136:100–107, 2008.   ©2008 Wiley-Liss, Inc.

The Mascarene islands are a group of islands located in the Indian Ocean 690 km East of Madagascar, off the southeastern coast of Africa (Fig. 1). Also known as the Mascarenhas archipelago, named after its discoverer, the Portuguese navigator Pedro Mascarenhas, it is composed of three islands; Mauritius, Réunion and Rodrigues. Rodrigues is a dependency of Mauritius, and La Réunion is one of the six French overseas departments or *Départments d'Outre-Mer* (DOM).

The Mascarenhas archipelago remained desert islands for a long time, and although it was apparently already known to Arab merchants who sailed the Indian Ocean, it was not discovered until the 16th century by the Portuguese. From then onwards, the islands remained uninhabited until they were colonized by the French in the middle of the 17th century. With the arrival of the first few French settlers to La Réunion came an influx of African slaves (especially from East Africa and Madagascar) (Ostheimer, 1975; Lavaux, 1988) to work on coffee and sugar plantations. The import of slaves continued well into the middle of the 19th century, when slavery was finally abolished in 1848. It is thought that during this slave trade period more than 60,000 slaves were imported into La Réunion (Ostheimer, 1975; Lavaux, 1988). To fill in the vacancies left by the slaves, the European landowners then recruited thousands of indentured labourers mainly from India (especially Malabars),

Southeast Asia (especially Malays and Anamites), and China (Ostheimer 1975; Lavaux 1988). The continuous flow of foreign-born slaves and immigrant contracted labourers from diverse locations created a highly multicultural and multilingual population structure that with time has led to the island becoming a mosaic of people of multiple ethnic origins. Such is the case, that La Réunion has currently a largely admixed population of over 780,000 inhabitants (Institut National de la Statistique et des Études Économiques, INSEE, http://www.insee.fr) belonging to six main ethnic groups: the Malbars (or

Fig. 1. Map of La Réunion island.

MATERIALS AND METHODS

Blood samples were obtained from 41 randomly selected and unrelated individuals. Given the largely admixed nature of the population of La Réunion, where nearly half of the population is considered *métis* (Césari, 1999, doctoral thesis), defining the precise ethnic origin of an individual is sometimes problematic, most having several different ethnic groups in their genealogical line and identifying themselves with several groups, a phenomenon common in multiethnic societies (Yu-Sion, 2003). This is the case of the 41 samples used here, where the individuals themselves could not be precise about their exact ethnic origin. They did ensure, however, that they were Réunionese as far back as three generations (at least), with their grandparents (both maternal and paternal) and parents having been born in La Réunion. We have considered these samples to be representative of the general population of la Réunion. DNA was extracted using standard phenol-chloroform methods.
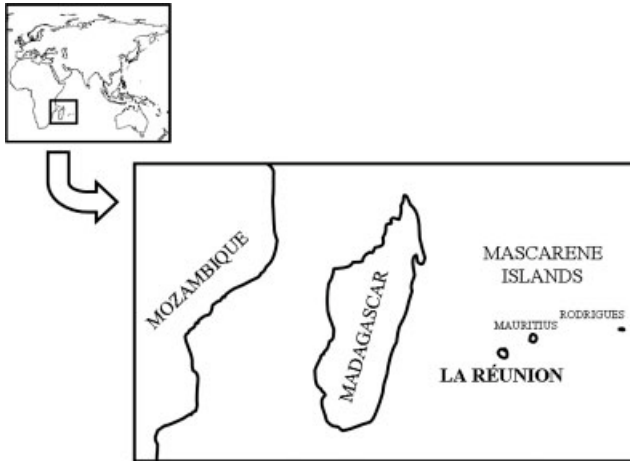
Malabars), descendents of Indian workers imported to La Réunion after the abolition of slavery; the Zarabes (derived from the French les Arabes, the Arabs), descendents of Muslim Indians imported at the end of the 19th century; the Chinois, descendents of the Chinese; the Zoreilles (derived from the French words les oreilles, the ears) descendents of the European settlers; the Caffres, the descendents of the African slaves, and the Creoles, the rest of the admixed population.

To our knowledge, there is no information on the genetic diversity present in the population of La Réunion. A few genetic studies have focused on Madagascar (Soodyall et al., 1995; Hewitt et al., 1996; Hurles et al., 2005), the Mascarenhas closest neighbouring island, which was originally settled from Indonesia according to linguistic and archaeological evidence (Dahl, 1951; Vérin and Wright, 1999). Using data on the beta-globin gene, Hewitt et al. (1996) showed that Malagasy individuals present a strong Central and East African component, specifically a Bantu component, together with a smaller Asian/Oceanic and European component. Using mitochondrial DNA, Soodyall et al. (1995) suggested that maternal lineages from Madagascar had a mixed African/Polynesian origin. This observation was later reinforced and elaborated further by Hurles et al. (2005), who using both mitochondrial and Y chromosome data, demonstrated an approximately equal African and Indonesian contribution to both paternal and maternal Malagasy lineages.

MtDNA and the Y chromosome are haploid (or uniparental) markers, inherited from the mother and the father, respectively. Both these types of DNA have a well-established phylogeography (geographic distribution of lineages) which makes them ideal tools for the tracing of both female and male ancestry. To provide information on the genetic origins of the population of La Réunion from both a maternal and paternal point of view, trying to identify the genetic footprints of the colonization process and subsequent admixture effects on the present gene pool, we have typed four SNPs in the coding region of the mitochondrial DNA molecule and sequenced both hypervariable regions (I and II) in 41 samples, and further investigated 26 of these samples (males) for 18 STRs and 35 SNPs on the Y chromosome.

Mitochondrial and Y-chromosome typing

For the mtDNA, both hypervariable regions, the 9-bp tandem repeat (CCCCCTCTA) of the COII/tRNA[Lys] intergenic region, and positions 10,400, 10,873, 12,308, and 12,705 in the coding region of the molecule (according to Anderson et al., 1981) were typed as previously described (Comas et al., 2004). Sequences from positions 16,024 to 16,391 and from 63 to 322 (according to (Anderson et al., 1981) were used in the present analysis. Previously published mtDNA data for several Asian and African populations were used for comparison purposes (Mountain et al., 1995; Horai et al., 1996; Kivisild et al., 1999; Lum and Cann, 2000; Richards et al., 2000; Bamshad et al., 2001; Fucharoen et al., 2001; Kivisild et al., 2002; Salas et al., 2002; Yao and Zhang, 2002; Hurles et al., 2005). HVR I sequences classified as European according to the well-established mtDNA phylogeography (Richards et al., 2000), were compared with a European database of sequences from 14,382 individuals collected from 68 published articles (Calafell, unpublished data). For the Y chromosome analysis, 35 biallelic markers and 18 microsatellite markers were typed. The binary markers defining major Y-chromosome haplogroups were genotyped as previously described by (Berniell-Lee et al., 2007). The STRs were amplified in the form of three previously described multiplex reactions: MSI multiplex DYS 19, DYS 388, DYS 390, DYS 391, DYS 392, DYS 393 (Bosch et al., 2002); CTS multiplex DYS 434, DYS 435, DYS 436, DYS 437, DYS 438, DYS 439 (Ayub et al., 2000) and EBF multiplex DYS 389 I, DYS 389 II, DYS 462, DYS 460, DYS 461, DYS 385 (Bosch et al., 2002). PCR cycling conditions for multiplex MSI were modified from Bosch et al. (2002) as follows: 95°C for 10 min; 10 cycles of 95°C for 1 min, 60–55°C for 1.5 min (−0.5°C per cycle), and 72°C for 1 min; 20 cycles of 95°C for 1 min, 55°C for 1 min, 72°C or 1 min; final extension of 72°C for 10 min.

Statistical analyses

MtDNA sequence diversity and Y chromosome haplotype diversity (h) (Nei, 1987) and mean number of pair-

TABLE 1. *Mitochondrial DNA lineages in La Réunion*

Haplogroup	N	10,400	10,873	12,308	12,705	HVRI sequence[a]	HVRII sequence[b]
African							
L1b1	1	C	A	T	C	111 126 187 189 223 239 270 278 293 311	73 146 151 152 182 185T 189 247
L2a1	1	C	A	T	C	092 223 278 294 309 390	73 146 152 195
L3b	1	C	A	T	C	093 223 278 362	73
L3e1	1	C	A	T	C	093 223 311 327	73 150 185 189
Indian							
M2	10	T	A	T	C	086 148 223 259 278 319	73 150 200
M6	3	T	A	T	C	223 231 311 356 362	73
U2i	4	C	G	C	T	051 206C 230 311	73
U2i	1	C	G	C	T	051 93A 154 206C 230 311	73 309.1 309.2
East Asian							
E1	8	T	A	T	C	221 223 291 362 390	73 309.1
D5a	1	T	A	T	C	164 182C 183C 189 223 266 362	73 150 207 309.1 309.2
M7c	1	T	A	T	C	223 295 362	73 146 199 309.1
F	1	C	A	C	T	266 278 304 309 356	73 152
European/Middle East							
U2e	3	C	G	C	T	051 129C 179 182C 183C 189 362	73 114 152 217 310
U2e	1	C	G	C	T	051 93 129C 179 182C 183C 189 362	73 114 152 217 310
T1	1	C	A	C	T	126 163 186 189 294	64 73 152 195 309.1
J	1	C	A	C	T	069 126	73 295
H	1	C	A	C	T	183 311	CRS
I	1	C	A	T	T	93 129 223 311 355 391	73 199 204 250 309.1

Position numbers according to the CRS (Anderson et al., 1981). Unless indicated, substitutions are transitions.
[a] Position numbers are given without the prefix "16."
[b] Insertion of one or two cytosines are indicated by ".1" and ".2," respectively. All sequences have 263G and 315.1.

wise differences (π) (Tajima, 1993) were computed using Arlequin v2.0 software (Schneider et al., 2000). The total number of mtDNA sequence types and of Y haplotypes, together with their frequency within each lineage, was determined by a simple counting scheme. The weighted intralineage mean pair-wise difference estimator (WIMP), which measures within haplogroup diversity, was calculated according to Hurles et al. (2002).

RESULTS

Maternal lineages in La Réunion island

A total of 18 different HVS-I/II sequences were found among the 41 Reunionese samples (Table 1). These were classified into a total of 16 mtDNA haplogroups whose ancestry has been phylogeographically established according to previously published data (Richards et al., 2000; Kivisild et al., 2002; Salas et al., 2002). The 9 bp deletion, a useful marker to trace migrations out of southeast Asia and the Pacific (Redd et al., 1995) and which is independently found in several African populations (Soodyall et al., 1996), was not found in the present sample set.

Most of the Reunionese sequences fell into Indian and East Asian haplogroups (44 and 27%, respectively), with fewer sequences falling into European/Middle Eastern and African haplogroups (19 and 10%, respectively) (Fig. 2a). The lineages of Indian ancestry found in La Réunion are M2, M6, and U2i, M2 and M6 been exclusive to India (Rajkumar et al., 2005). The mtDNA sequence associated with lineage M6 is found in three Lobana individuals from the Indian region of Punjab, and the two haplotypes associated with haplogroup U2i are found in one Lambadi individual from Andhra Pradesh and one Bogsa from Uttar Pradesh, and two individuals from Andhra Pradesh, respectively.
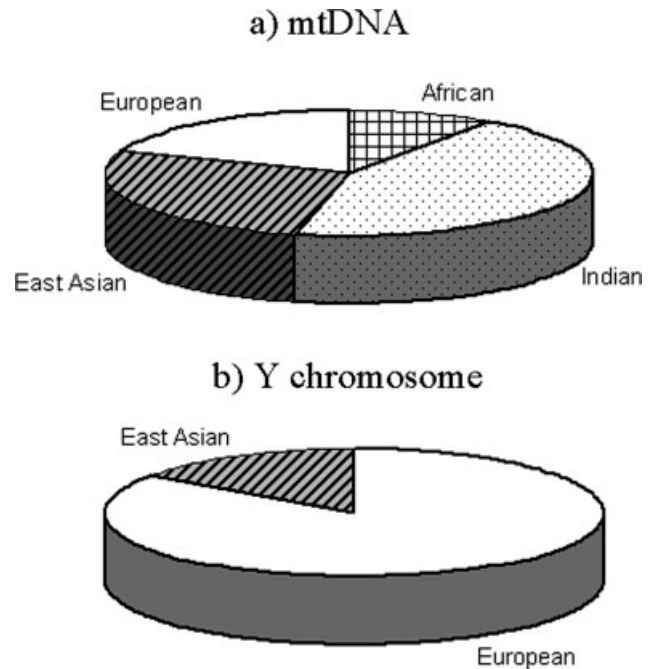

Fig. 2. Pie charts showing the frequencies of mtDNA (**a**) and Y chromosome (**b**) components. White areas represent the European/Middle Eastern component; striped areas represent the East Asian component; checked areas represent the African component, and dotted areas represent the Indian component.

The lineages of East Asian ancestry are E1, D5a, M7c, and F. The sequences associated with these haplogroups were compared with a set of previously published East Asian sequences (Horai et al., 1996; Lum and Cann,

TABLE 2. Y-chromosome lineages in La Réunion

Haplogroup	N	DYS 19	DYS 385[a]	DYS 388	DYS 389I	DYS 389II	DYS 390	DYS 391	DYS 392	DYS 393	DYS 434	DYS 435	DYS 436	DYS 437	DYS 438	DYS 439	DYS 462	DYS 460	DYS 461
European/Middle East																			
G	2	15	14/15	12	12	29	22	10	11	14	11	12	12	16	11	11	12	11	11
I	2	16	14/14	14	12	28	22	10	11	13	11	11	12	16	10	12	12	12	10
E3b3	1	13	15/17	12	12	30	23	10	11	13	11	11	12	14	10	12	11	13	11
R1b	1	14	11/14	12	12	28	24	11	13	13	11	11	12	15	12	12	11	12	11
R1b	1	14	11/14	12	12	28	24	11	14	13	11	11	12	15	12	12	11	12	11
R1b	1	14	11/14	12	13	28	24	10	10	13	11	11	12	14	13	10	11	12	10
R1b	1	14	11/14	12	13	29	24	11	12	10	11	11	12	15	12	12	11	12	11
R1b	1	14	12/14	12	13	29	23	11	11	13	11	11	12	15	12	12	11	12	11
R1b	4	14	11/14	12	13	29	24	10	13	14	11	11	12	16	12	11	12	12	11
R1b	1	15	11/14	12	13	30	24	10	13	13	11	11	12	15	12	13	11	12	11
R1b	1	14	11/14	12	13	29	24	11	12	13	11	11	12	15	12	11	11	13	11
R1b	1	14	11/14	12	13	29	24	10	13	13	11	11	12	15	12	13	11	12	10
R1b	3	14	11/14	12	14	30	23	11	13	13	11	11	12	15	12	12	12	13	11
R1b	1	14	11/14	10	14	30	23	11	13	13	11	11	12	15	12	12	12	13	11
R1b	1	14	11/14	10	13	30	23	11	13	13	11	11	12	15	12	12	12	12	11
East Asian																			
R1a	1	16	12/14	12	13	31	25	10	11	13	11	11	12	14	11	11	11	11	11
O3	2	16	13/20	12	12	29	25	9	13	12	11	12	12	14	10	11	12	13	10
O3	1	15	12/19	12	13	32	23	11	12	12	11	12	12	14	10	12	12	12	9

Haplogroups are named according to the Y Chromosome Consortium Nomenclature (YCC 2002). Microsatellite alleles are named according to the number of repeats following the YHRD STR database nomenclature.
[a] Alleles for this microsatellite already constitute a haplotype due to the duplicated nature of this STR locus.

2000; Fucharoen et al., 2001; Yao and Zhang, 2002). So far, haplogroup E1 has only been found in Southeast Asia (Ballinger et al., 1992; Kivisild et al., 2002). The classification of the haplotype associated with this haplogroup in our study, present in eight individuals, was somewhat problematic when only the variation for the control region was taken into account. For this reason, positions 7,598 and 10,384 of the coding region were analyzed by direct sequencing before it could be successfully classified. Although this sequence was not found in the East Asian samples used for comparison, it was found in four Malagasy individuals (Hurles et al., 2005). The Reunionese sequence associated with the East Asian haplogroup M7c was not found in mainland Asia (except for a Thai individual). It was found in the islands of Borneo, Java, and Philippines, and in three Malagasy individuals (Hurles et al., 2005). Haplogroup F is widespread in continental Asia and common in East Asia. No matches were found for the Reunionese sequence associated with this haplogroup.

The European/Middle Eastern mtDNA lineages found are U2e, T1, J, H, and I. These haplogroups are scattered across Europe and are found at high frequencies, without a clearly defined pattern (Richards et al., 2000). The sequences associated with haplogroups T1 and J in La Réunion are widespread in Europe, Southwest Asia, and Northwest Africa. No matches were found for the sequences associated with haplogroups U2e, H, and I.

The few lineages of African ancestry found in La Réunion belong to haplogroups L1b1, L2a1, L3b, and L3e1, all of which are L lineages widespread throughout Africa. The sequences associated with these haplogroups were compared with data compiled by Salas et al. (2002). The L1b1 and L2a1 sequences found in La Réunion were found in one Fang and one Bubi individual from Equatorial Guinea (West Central Africa), respectively. The sequence associated with haplogroup L3b was found in four Fulbe and two Senegalese individuals, and nine Malagasy individuals (Hurles et al., 2005).

The mtDNA sequence diversity value obtained for La Réunion (0.896 ± 0.030) is low compared with other African populations (Salas et al., 2002), whereas the average number of pairwise differences is high (mean pairwise for the HVRI = 8.03). This could be explained by the admixture of sequences from different haplogroups with low diversity as shown by the low weighted intralineage mean pairwise difference (WIMP = 0.20 (Hurles et al., 2002)).

Paternal lineages in La Réunion

The 26 male samples from La Réunion were classified into 6 different haplogroups on the Y chromosome phylogeny (Y Chromosome Consortium, 2002) (Table 2). Most of the samples fell into European/Middle Eastern haplogroups (85%), with fewer samples falling into East Asian haplogroups (15%) (Fig. 2b). No traces of African or Indian haplogroups (such A, B, E1, E2, E3a or C, F, H, L, J2 respectively) were found in this sample set of La Réunion. However, the highest frequency (F) of whatever unobserved haplogroup in a population can be estimated as $1 - e^{-FN} = 0.95$, with a 95% probability, according to the Poisson distribution. In this way, given our sample size of 26 males (N), if African or Indian haplogroups were to be present in the Réunion, we would expect them at a maximum frequency of 11.5%.

The lineages of European ancestry are haplogroups R1b and I. Haplogroup R1b, the most frequent haplogroup in the Réunion sample, is the most common Y-haplogroup in Western Europe (Semino et al., 2000) and haplogroup I is widely spread across Europe (Rootsi et al., 2004). Interestingly, haplogroup R1b has also been found in one individual from Madagascar, and in four individuals from several population groups within Island Southeast Asia (one individual in the population of Banjarmasin, and three individuals in the population of Kota Kinabalu (Hurles et al., 2005)). The Middle Eastern component of La Réunion is represented by haplogroup

E3b3. This haplogroup, only present in only one individual of our sample set, is highly frequent in the Middle East and Northeast Africa (Luis et al., 2004).

The lineage of East Asian ancestry found in La Réunion is O3, highly common in East Asia, especially in China (Shi et al., 2005) and Polynesia (Kayser et al., 2006). Interestingly, Hurles et al. (2005) also found traces of this haplogroup in 58 individuals from several populations of Island Southeast Asia, but not in Madagascar.

Haplogroups R1a and G were also found in La Réunion. Because these haplogroups are not specific to any geographic location, but rather frequent in several, we tried to pinpoint the most likely geographic origin of the haplotypes associated with these haplogroups. For this, a Y-haplotype search was performed on the world-wide Y Chromosome Haplotype Reference Database (YHRD) on http://ystr.charite.de. Although haplogroup G has been shown to be more frequent in the Middle East and the Caucasus than in Europe (Semino et al., 2000; King and Underhill, 2002; Goff and Athey, 2006), and R1a more frequent in Europe (Semino et al., 2000; Behar et al., 2003; Pericic et al., 2005) than in Central and South Asia (Wells et al., 2001; Nasidze et al., 2004), the YHRD search showed that in this case, the Reunionese sample belonging to haplogroup R1a showed a more Asian Y-haplotype profile rather than a European one (having been found once in a sample set of 186 individuals from Singapore and two one-step neighbours in individuals from China, Bhutan, and Nepal in a total set of 70 populations with 7,628 haplotypes), and that the two G samples showed a more European Y-haplotype profile than an Asian one (two of its one-step neighbours having been found in several European populations). Haplogroup R1a was also found in one sample from Madagascar, and in four samples from several Island Southeast Asian populations (Hurles et al., 2005), reinforcing the most-likely Asian ancestry of the R1a sample.

The average Y-haplotype diversity in La Réunion was high (0.975 ± 0.021), with no haplotypes being shared among haplogroups, and each one being unique, except for haplogroup R1b, where several haplotypes were found more than once (haplotype diversity for R1b = 0.941 ± 0.043). The average number of pair-wise differences was 9.462 ± 4.487, and the value for the WIMP diversity estimator (Hurles et al., 2002) was 5.43.

DISCUSSION

La Réunion is a relatively "young" population, in the sense that it remained devoid of inhabitants until the 17th century. If according to historical records no "indigenous" population originally lived on the island, with no traces of earlier settlement having ever been found (Ostheimer, 1975; Lavaux, 1988), the current Reunionese gene pool should be derived uniquely from the colonizing populations (namely Europeans) and the populations employed to carry out the colonization (mainly Africans, Indians and East Asians). A mixed ancestry of Asian and African origin has already been suggested in La Réunion by the presence and transmission of typically Asian and African Gm alleles and IgG immunoglobulin haplotypes (Dugoujon et al., unpublished data). The mtDNA and Y chromosome lineage composition found in this study further expands this observation, where apart from Asian and African lineages, European/Middle Eastern and Indian lineages have also been found. However, the distribution patterns of these lineages for both markers show that these ancestral populations did not contribute equally to the admixture process, with up to 85% of the Y chromosome being of European/Middle Eastern origin, as opposed to only 19% of the mtDNA. Furthermore, we have also seen asymmetries in the contributions of the different incoming population groups to both these pools, having found mtDNA lineages of Indian (44%), East Asian (27%), and African ancestry (10%), and only lineages of East Asian ancestry (15%) for the Y chromosome. Also, the impact of the different ethnic groups on the Réunion gene pool is more visible for the mtDNA than for the Y chromosome, not only in terms of the number of groups that have contributed to both pools, but also, in the fact that some of these groups seem to have specifically influenced one marker more than the other (the differences in the proportions of the lineages for mtDNA and Y chromosome DNA showed to be statistically significant in a chi-squared test, $\chi^2 = 26.60$, d.f. $= 2$, $P < 0.05$). Indian lineages, for example, that are completely absent for the Y chromosome, are the most frequent for mtDNA. And East Asian lineages, which are the second most frequent lineages for the mtDNA are only found at low frequencies for the Y chromosome. All these results point towards a strong sexual bias (or asymmetrical gene flow) in the peopling process of La Réunion, where the interethnic crosses taking place were mainly between male European colonizers and female imported workers (primarily of Indian ancestry).

A male-biased European admixture of this kind, which has previously been described in several other Oceanic islands (Hurles et al., 1998; Underhill et al., 2001; Hurles et al., 2002), was most probably due to the social organization of the colonization process. Although we do not have as much information available on the Indian Ocean slave trade as we do on the Atlantic slave trade (Drescher and Engerman, 1998; Finkelman and Miller, 1998), which has been studied in great detail, we do know that there was a strong gender imbalance among the slaves/workers, where there was an asymetrical import of men versus women. Because slaves were primarily imported in La Réunion for the arduous work on the sugar cane and coffee plantations, practically all the slaves introduced were men and only a few women. Restrictions in the movement of male slaves (i.e. interned in camps), without easy access to the few slave women, would limit reproductive levels among these populations. Likewise, the extremely harsh living and working conditions on the plantations in La Réunion (without any access to medical systems) would further reduce these levels, making it a struggle to survive and elevating mortality rates among slave/worker men. At the same time, the import of slave females by male European colonizers would increase slave female lineages and colonizer male lineages. A popular legend claims this to be the case for the first dozen or so French adventurers that agreed to go to La Réunion and soon imported women from Goa (Singhvi et al., 2000).

The sources of the lineages we have found in La Réunion are in agreement with the colonization history of the island. The Y chromosome European lineages are most likely derived from the European males who colonized the island. However, given that haplogroup R1b has also been found in several populations within Island Southeast Asia and one individual from Madagascar,

areas which have also witnessed considerable migration from Europe, some of these lineages could have also been brought to La Réunion by slave individuals from these locations. The Indian lineages are most probably derived from the Indian labourers recruited to fill in the vacancies left by the freed slaves. African and East Asian mtDNA lineages are most likely derived from Malagasy individuals taken to La Réunion, with most of the sequences associated with African haplogroups being found in Madagascar, and all the sequences associated with East Asian haplogroups being found in Madagascar and in individuals from Southeast Asian islands. Malagasy individuals have been shown to have a dual Indonesian and African ancestry, result of the settlement of Madagascar by Indonesians via Southern India and of Africans via East Africa. It is highly likely, therefore, that the East Asian and African lineages found in La Réunion derive from the numerous Malagasy slaves imported into the island to work on the sugar and coffee plantations. Several sequences belonging to African-derived haplogroups were not found in Madagascar, but were found in West Central Africa. These lineages, therefore, could be the result of the import of slaves by the French from their respective colonies in this area. East Asian Y chromosome lineages most probably also have a Malagasy origin, as both East Asian haplogroups found in La Réunion were also found in several individuals from Island Southeast Asia. The fact that they were not found in Madagascar could be due to the low sample size (37 individuals) of the study (Hurles et al., 2005). However, haplogroup O3, was also found in China, indicating that this lineage could also have been introduced into La Réunion by Chinese workers imported later on to fill in the vacuum created by the emancipation of the slaves after the ban on the practice of slavery.

The analysis of the genetic diversity for both mtDNA and Y chromosome shows that La Réunion follows the general trend in human populations of Y chromosome diversity being higher than mtDNA (Seielstad et al., 1998). In this case, the main reason for this is the total lack of diversity within the two most frequent mtDNA haplogroups; haplogroup M2 and E1, where all 10 and 8 individuals respectively bear the same haplotype. The most plausible explanation for this strong reduction in diversity is the possible occurrence of founder effects, and in consequence to strong genetic drift due to a reduced population size, a phenomenon known to be common in the colonization of new territories (Forster and Matsumura, 2005). Founder effects are accentuated if the immigration of the incoming ethnic groups is kinship structured, as can occur in populations strongly guided by cultural practices within the community, language or group, where strict endogamic rules are generally applied. The previously mentioned asymmetrical import of men versus women during the slave trade period in La Réunion could have led to founder effects mainly taking place within the mtDNA gene pool of this population.

Founder effects, therefore, together with several historical and/or socio-cultural factors could have shaped the genetic diversity present in the current Reunionese gene pool. It would be interesting to carry out a microgeographic study of each of the six different ethnic groups in La Réunion, in order to ascertain whether the genetic diversity observed in our sample set (e.g. the reduced diversity observed in Indian and Asian mtDNA

pools) extrapolates to these populations in general in La Réunion, or whether it is partly due to the sample size in our study. We must also bear in mind that the admixture proportions here estimated need not reflect the true distributions during the colonization, and that they too might be sample-size dependent.

The results obtained in this study of the general population of La Réunion have shown that the genetic composition of the island nowadays is a true reflection of its colonization and subsequent admixture, where a sexual bias in the peopling of the island resulted in the Y chromosome gene pool being mainly of European ancestry (derived from European individuals colonizing the island), and the mtDNA pool a mixture of lineages of mainly Indian, East Asian and African ancestry (derived mainly from Indian and Malagasy slaves imported into the island to work on sugar and coffee plantations). La Réunion is a good example of how the social organization of a colonization event can impact the levels and patterns of genetic diversity in newly established populations.

LITERATURE CITED

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