

Genes flow by the channels of culture: the genetic imprint of matrilocality in Ngazidja, Comoros Islands

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1	Genes flow by the channels of culture: the genetic imprint of matrilocality in
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23 Abstract

24 Post-marital residence of spouses is one of the architects of population genetic structure. In the present study, we tested how the uxori-matrilocality in Ngazidia, Comoros Islands, 25 has unequally channelled the dispersal of male and female gene diversity amongst the 26 27 villages. Using sequences of the hypervariable segment I of the mitochondrial DNA (mtDNA HVS-I) and seven Y-chromosome microsatellites (Y-STRs), we measured the 28 genetic variation and male-to-female ratios based on F_{ST} values and revealed a genetic 29 structure driven by male gene flow across villages but one. This genetic feature illustrates 30 the social place of residence of males and females which is inherited from the matrilocal 31 Bantu expansion. Exception is Bandamadji whose past military status made patrilocality 32 33 necessary.

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35 Keywords: Comoros, matrilocality, mtDNA, Y-STRs, gene diversity

36 Introduction

The Comoros Islands are an archipelago of four island, Ngazidja (Great Comoros), Nzduani (Anjouan), Mwali (Mohéli), and Mahore (Mayotte), located at the northern end of the Mozambique Channel in the Indian Ocean. Historical, social, religious, linguistic and genetic studies showed that the Comorian population arose from the encounter of East African Bantu metallurgists with Islamic Middle Eastern traders and to a lesser degree, with Austronesian people ¹⁻⁵.

The social structure in Comoros Islands results from the interactions between 43 Islam's laws and ancestral rites from East Africa, with a mix distribution of matrilineal 44 45 and patrilineal traits in various domains of social organization: kinship, inheritance of property, succession to titles, mode of residence, and detention of authority ^{2,6}. In the four 46 islands, the post-marital residence is largely uxori-matri-local: the husband resides with 47 48 his wife and the children (girls) marry in the place of their mother. Under African's costumes and Islam's laws, men are allowed to practice polygyny. However, in order to 49 rise its social position, a man has to realize his "great marriage" with a woman from his 50 own village. This specific union happens while he is able to assume the great expenses 51 needed for this unique event and in for his adult's life. Before, he may or has to conclude 52 53 others unions that are not necessarily with women from his own maternal village, called "little marriage". Men are thus considered as "itinerant" husbands moving from one to 54 other village and will have between two to five unions in their life. Meanwhile, for her 55 56 weeding the bride is given a house from her mother's family. The oldest maternal uncle looks after their education and the one of the children, but these rules are not applied if 57 the woman leaves the village. Furthermore, each Comorian individual and its social rights 58

are as a priority identified by his matriclan, called *hinya*. All these conditions create a real
economic pressure to stay in a village ^{2,6}.

Previous surveys in matri- and patrilocally structured populations have shown a contrasted pattern of within and between-population genetic variation when examined for male and female genetic markers ^{7,8}. To what extent the matrilocal and matrilineal social organization has left footprints in the genetic structure of the Great Comoros Island is of the topic of the present study. To this aim, we explored the uniparental genetic variation between five villages of Ngazidja in order to test to what extent matrilocality would have shaped the gene diversity in the island.

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69 Material and Methods

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After informed consent approval, we collected 86 male samples from five villages of Ngazidja: Bandamadji, Hahaya, Iconi, Male and Mitsoudje. We included only unrelated men for at least two generations back in time and recorded ethnological information including the name of the lineage village.

Samples were screened for seven Y-STRs (DYS389I, DYS389II, DYS19,
DYS390, DYS391, DYS392 and DYS393) (S1 Table) and sequenced for HVS-I (S2
File). Blood collection and lab methods are detailed in ⁹.

We first estimated the within-village gene diversity then tested the inter-village genetic structure with a measure of F_{ST} and R_{ST} genetic distances and amount of variance (AMOVA) ¹⁰. We also performed two median joining networks where we considered the HVS-I poly-C region according to ¹¹ and weighted the Y-STRs loci as a function of their variance ¹² after exclusion of DYS389I-II as recommended. Lastly, we measured the ratio

between effective numbers of male and female migrants per generation as described in ¹³ 83 and ¹⁴. In this approach, populations are in the island model, considered as stable, 84 mutation as negligible and allele frequencies are assumed to result mainly from 85 differences in migration rate and/or effective population size. Hence, the expected value 86 of genetic differences between populations, F_{ST} , is seen as a function of N and m, the 87 effective number of males or female and their migration rate, per generation: $F_{ST}^{(Y-STRs)}$ 88 = $1/(1+N_{male}m_{male})$ and $F_{ST}^{(mtDNA)} = 1/(1+N_{female}m_{female})$ for haploid systems. Hence, the 89 male-to-female ratio per generation $N_{male}m_{male} / N_{female}m_{female}$ were inferred from F_{ST} 90 values ¹³. 91

92

93 **Results**

Figure 1 depicts the genetic relationships amongst the five Comoros villages based 94 95 on female and male genetic markers. For HVS-I, genetic similarities link the Iconi with Bandamadji while Hayaya and Male stand at peripheral positions. As far as the Y-STRs 96 genetic variation is concerned, the Bandamadji village departs strongly from the four 97 remaining villages, separated with non-significant R_{ST} values. When compared on a 98 haplotype basis, networks mirror the gene diversity pattern showed in Table 1. Iconi, 99 100 Mitsoudje and Bandamadji encapsulate the highest HVS-I haplotype diversity with 101 numerous branches while most of the Hayaya and Male mtDNAs are included into one main profile. As far as Y-STRs are concerned, every village are spread over the nodes, 102 103 but Bandamadji which is represented by almost exclusively one profile. Networks also depict a higher pairwise differences (Pw) for HVS-I than for Y-STRs (mean Pw_{HVS-I} = 104 9.3; mean $Pw_{YSTRs} = 3.3$). Finally, one can notice twice more village-specific haplotypes 105 106 for HVS-I (n= 24) than for YSTRs (n= 12).

Table 1 shows the female and male gene diversity indices in the five Comoros 107 villages. The main pattern is a higher male than female gene diversity as observed in 108 Hayaya, Male and Mistoudje. Exceptions are Iconi which shows similar values for both 109 uniparental markers, and overall Bandamadji which distinguishes with a higher mtDNA 110 111 than Y-STRs gene diversity. AMOVA points out that HVS-I presents 3.2-times more 112 genetic variation amongst villages than Y-STRs (respectively 15.32% and 4.74%), but less within-village variation (~0.9-fold, respectively 84.68% and 95.26%). Due to the 113 peculiar behaviour of Bandamadji above-mentioned, we ran an additional AMOVA 114 excluding this village. We noticed an strong increase of the contrasting patterns of within-115 116 and between-population genetic variation as seen from HVS-I and Y-STRs (Table 1), since the female genetic variation among populations reached almost 10-fold the male 117 one (17.08% and 1.74%). 118

Lastly, from the F_{ST} values we inferred the magnitude of male-to-female migration ratio per generation for each village and across villages (Table 1 and Figure 2). The main pattern is a male-to-female ratio above 1 in Ngazidja where the male gene flow ranges from 2.6 and 7.1 (mean ratio = 3.5) in four villages (Hayaya, Iconi, Male, and Mitsoudje). Exception is Bandamadji with a male-to-female ratio under 1 (ratio = 0.9), which could signify an equal or slightly more female than male gene flow.

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126 Discussion

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128 A great variety of human social organizations defined by rules of marriage, 129 residence, descent and mode of subsistence has been described worldwide¹⁵, which in 130 return can substantially impact the genetic diversity ^{7,8,16}. At the global scale, populations would be genetically more structured for male than for female genetic markers, mirroring sex-biased gene flows involving mostly women and thus, patrilocality ⁷. Nevertheless, matrilocality rules other societies (e.g.¹⁷) and in the Indian Ocean, the earliest inhabitants of the Comoros originated from the Shambara in East Africa, as the extension of the matrilineal belt that encompassed Africa Bantu which opens to the east since the 11th century ^{3,18}.

When examined for uniparental genetic systems, inter- and intra-village genetic diversity in Ngazidja indicate male-oriented gene flows amongst villages. Exception is Bandamadji which behaves as a patrilocal population. Oral and historical knowledge evokes that Bandamadji was the military basis of one of the great Comorian clan M'Dombozi, where men have sworn fidelity to their sultan Hachim ben Ahmed (died 1889) to stay to protect the city (¹⁹ and Kassim Papa, pers. com.).

143 Finally, the Comorian villages are organized according to the social space in which males and females participate distinctly, and the present data agree with the ethno-144 historical records ². Human gene diversity results mainly from demography, natural and 145 cultural selection. The present study evidences that amongst and within human 146 populations, genes also flow through the channels dug by culture. It especially illustrates 147 148 the positive collaboration between geneticists and anthropologists to search together how distribution maps of biological phenomena and cultural phenomena illuminate each other 149 20. 150

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Titles and legends to tables and figures

Table 1. Summary statistics of mtDNA and Y-STRs genetic variation within and between
five villages of Ngazidja. Pw: mean number of pairwise differences. Values in the
Ngazidja column were obtained from the AMOVA. Male-to-female ratio was inferred
from Ségurel et al. 2008.

238	Fig 1. Multidimensional Scaling of F_{ST} and R_{ST} genetic distances and haplotype networks
239	(NETWORK 5.0) for mtDNA HVS-I (left panel) and Y-STRs (right panel)
240	
241	Fig.2 Intensity of female and male gene flow amongst the five villages understudy. Width
242	of the tip of the arrows is proportional to $\log_{10}(F_{ST'}$ ratio). Grey: female/male ratio >1,
243	white: male/female ratio >1. Background map was taken from www.d-maps.com©.
244	
245	S1Table (.xlsx). Y-STRs haplotypes in five Comorian villages
246	
247	S2 File (.doc). HVS1 profiles in five Comorian villages
248	
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Genetic marker	Estimator	Bandamadji	Hahaya	Iconi	Male	Mitsoudje	Ngazidja
mtDNA	Sample size	11	20	17	18	11	77
	Gene diversity	0.946	0.742	0.985	0.699	0.927	0,864
	Pw	10.1	4.3	10.8	10.4	10.8	
	Mean F_{ST} with the other villages	0.108	0.220	0.071	0.150	0.098	0.136
Y-STRs	Sample size	9	16	22	22	17	86
	Gene diversity	0.722	0.942	0.952	0.987	0.971	0.953
	Pw	2.3	3.3	3.7	3.6	3.5	
	Mean $F_{\rm ST}$ with the other villages	0.114	0.043	0.018	0.062	0.032	0.048
	Mean male-to-female ratio	0.9	7.1	7.0	2.6	3.3	3.6







