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High Genetic Variation in Y Chromosome Patterns of the Mocoví Population

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Abstract

In numerically small ethnic groups, the loss of genetic variability in the Y chromosome is frequent, because this genomic compartment is often subjected to selective sweeps.

Despite its small size, the Mocoví population retains a significant amount of genetic variation in relation to other native communities, but their Y chromosome diversity is not known in depth. The aim of this study was to analyze the genetic variability of the Y chromosome in a sample of Mocoví males from Santa Fe province (Argentina). We genotyped 11 short tandem repeats (STRs) and two single nucleotide polymorphisms (SNPs): M3 and M346. The diversity observed was high, and the 25 haplotypes obtained were compared to the YHRD database, with 13 of them absent of that database. A comparison with previous data reported from other Gran Chaco native groups showed significant differences between the Mocoví and other populations of different ethnic origin. This result and other studies on molecular markers of the Mocoví prove that this ethnic group retains a high genetic diversity that clearly differentiate them from other Amerindian populations.

Keywords: Haplotypes; genetic diversity; STRs; M3; Amerindians.

Alta variación genética en los patrones del cromosoma Y de la población Mocoví

Resumen

La pérdida de variabilidad genética en el cromosoma Y es frecuente en grupos étnicos reducidos numéricamente, debido a que este cromosoma suele estar sometido a barridos selectivos. A pesar de ser pequeña, la población Mocoví conserva una cantidad significativa de variación genética en relación con otras comunidades nativas, pero su diversidad a nivel del cromosoma Y no se conoce en profundidad. El objetivo de este trabajo fue analizar la variabilidad genética del cromosoma Y en una muestra de varones Mocoví de la provincia de Santa Fe (Argentina). Se tipificaron 11 microsatélites (STRs) y dos marcadores bialélicos (SNPs): M3 y M346. La diversidad observada fue elevada, y los 25 haplotipos obtenidos se compararon con la base de datos YHRD, donde 13 de ellos estuvieron ausentes. Se realizó una comparación con datos publicados de otros grupos nativos de Gran Chaco, la cual mostró diferencias significativas entre los Mocoví y algunas comunidades de distinto origen étnico. Este estudio, junto con otros realizados sobre marcadores moleculares del pueblo Mocoví, demuestran que este grupo étnico conserva una alta diversidad, que los diferencia claramente de otras comunidades amerindias.

Palabras claves: Haplotipos; diversidad genética; STRs; M3; amerindios.

The first Spanish-Indian interbreeding took place in the sixteenth century, when the Spanish conquerors contacted the Native American communities. At that time, many natives resisted the Conquest and remained free in their territories for centuries, while others were

fully interbred, uniting ethnic and cultural aspects. The subsequent Indian massacres led to a significant reduction in the Amerindian gene pool throughout the Americas (de las Casas y Casaus 1995 [1552], Martínez Sarasola 1992). However, in some populations there is still considerable

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genetic variation, depending on the different biological and cultural processes that each community has suffered.

The Mocoví population (a Guaycurú language group) is a very small ethnic group that, despite its reduced number, retains a significant genetic variation in relation to other native communities. It has been described that this community has specific genetic characteristics for certain autosomal markers, highlighting the Mocoví identity among the multiplicity of ethnic groups currently living in Argentina (Catanesi et al. 2001, Catanesi et al. 2006; Turret et al. 1999). However, the scientific literature related to the genetic variation of this ethnic group is still scarce, and the variation on the Y chromosome is not known in detail.

The Y chromosome is of particular interest given that the variability in this genomic compartment is frequently subjected to strong selective sweeps, being even faster in numerically small ethnic groups. The Y chromosome is only paternally transmitted, and its genetic polymorphisms are transferred to all the sons, thus establishing a male line.

The Y-STR markers are still extensively used in population genetics and in many cases, these polymorphisms have allowed studying the source and geographical origin of human groups. On the other hand, among the Y-SNP markers, those polymorphisms that have arisen only once in the human history (non-redundant) allow drawing much older phylogenies than Y-STRs (Jobling and Tyler-

Smith 2003). Among them, the M3 (rs3894) marker consists of a C-T transition whose presence indicates that the Y chromosome belongs to subhaplogroup Q1a3a which is unique to Native Americans and widespread among them (Karafet et al. 2008; Underhill et al. 1996; Zegura et al. 2004).

The aim of this study was to compare the genetic diversity of the Mocoví with that observed in other ethnic groups from the Gran Chaco region. For this purpose, we analyzed the amount of variation in the Y chromosome on a Mocoví male sample, assuming a reduction in their variation due to historical processes and/or genetic drift.

Subjects and Methods

Twelve Y-chromosome markers were analyzed in a sample of 26 unrelated Mocoví males from Colonia Dolores, Santa Fe province, Argentina (Figure 1), including 11 Y-STRs and one Y-SNP. The STRs analyzed were DYS389 I, DYS389 II, DYS390, DYS391, DYS392, DYS393, DYS19, DYS437, DYS438, DYS385-a, DYS385-b, and the SNP M3. A second SNP, M346, was kindly genotyped by Dr. G. Bailliet in those individuals where the transition M3 C to T was not present, in order to confirm their non Amerindian origin.

The markers were manually genotyped using genomic DNA obtained from blood. After PCR-amplification, STR fragments were run in 6% denaturing polyacrylamide gels and visualized by silver staining. The SNP M3

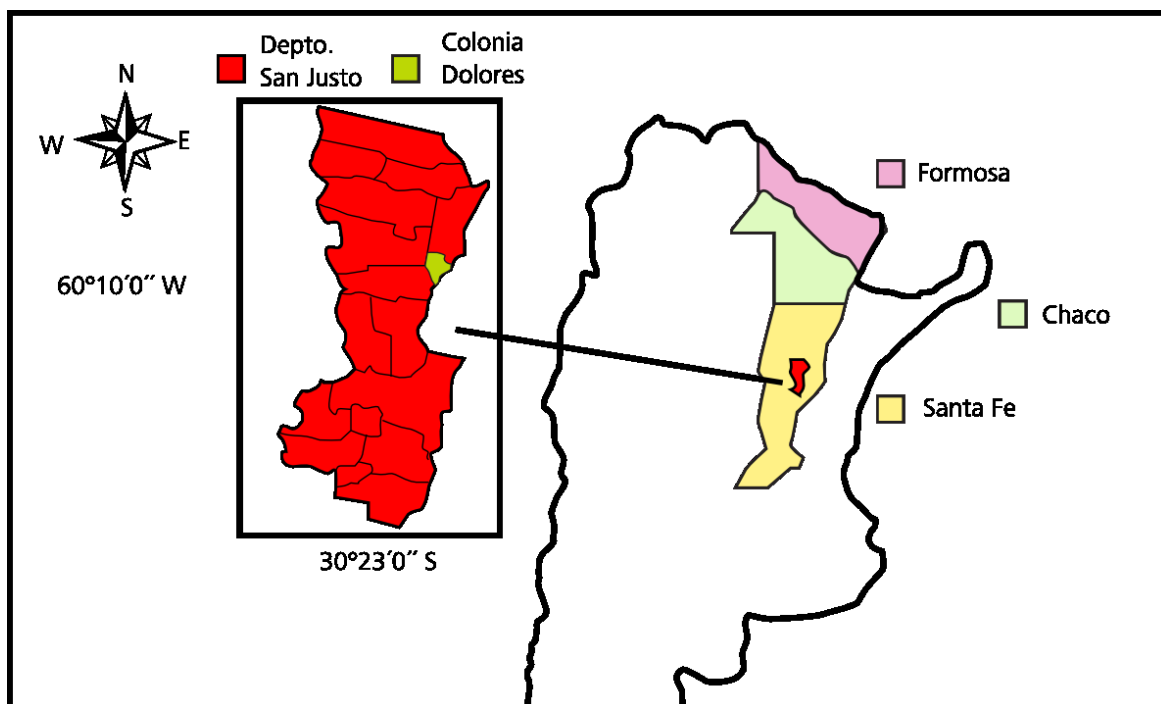


Figure 1. Geographic location of the Mocoví community analyzed, in Departamento San Justo, Santa Fe province. The provinces of Chaco and Formosa are also indicated, for comparing to data from Demarchi and Mitchell (2004) and Ramallo et al. (2009).

Figura 1. Ubicación geográfica de la comunidad Mocoví analizada (Departamento San Justo, Provincia de Santa Fé). También se señalan las provincias de Chaco y Formosa a los fines de comparar los datos de Demarchi y Mitchell (2004) y Ramallo et al. (2009).

was genotyped by direct sequencing of the fragment containing the transition C to T. The primers used for all the amplifications were published elsewhere (Kayser *et al.* 1997; Underhill *et al.* 1996). The alleles observed for the different markers were combined in each individual for constructing the haplotypes.

Each Y-STR haplotype was confronted with the profiles comprised in the Y chromosome Haplotype Reference Database (YHRD) (<http://www.yhrd.org/>) which includes 42267 individuals from different regions of the world.

The haplotype diversity was estimated according to Melton *et al.* (1995). The gene diversity, the exact test for F_{ST} (number of different alleles), and the analysis of molecular variance AMOVA (by F_{ST} distance method)

were calculated using the program Arlequin 3.5 (<http://cmpg.unibe.ch/software/arlequin35>). For the latter calculation, we considered other ethnic groups from Gran Chaco previously published (Pilagá, Wichí, Toba) to perform comparisons among populations, and among groups of populations from a same province or, otherwise, from a same ethnic group (Demarchi and Mitchell 2004, Ramallo *et al.* 2009). When using data from Ramallo *et al.* (2009), we considered a geographic design separating the two Wichí samples (although both are from the same province) because local differences were reported in that paper.

An haplotype median-joining network was constructed using Network 4.6 (<http://www.fluxus-engineering.com/sharenet.htm>), applying a higher weight for the

	DYS 19	DYS 389 I	DYS 389 II	DYS 390	DYS 391	DYS 392	DYS 393	DYS 437	DYS 438	DYS 385a/b	M3
A	13	13	31	24	10	14	13	15	11	14/17	T
B	14	12	30	23	10	14	13	14	11	13/18	T
C	13	13	30	24	10	14	13	14	11	14/17	T
D	13	13	31	25	10	14	13	14	11	14/18	Nd
E	14	13	29	24	11	13	13	15	12	11/14	C
F	13	13	30	24	10	14	13	15	11	14/17	T
G	14	13	28	24	10	13	13	15	12	11/14	C
H	14	14	30	24	11	13	13	14	12	11/14	C
I	16	14	32	25	11	12	13	14	11	11/13/14	C
J	13	14	30	24	10	12	13	14	10	13/14	C
K	13	13	30	23	10	14	13	14	11	14/15	T
L	13	13	30	24	10	14	13	14	11	13/16	T
M	14	13	29	23	11	13	13	16	12	11/15	C
N	13	12	28	22	11	15	11	15	10	13/16	C
O	13	13	32	24	10	14	13	14	11	15/17	T
P	15	13	29	24	11	14	13	15	11	11/15	C
Q	14	13	29	24	11	13	14	15	12	11/15	C
R	14	12	28	22	10	12	14	16	10	13/15	C
S	14	13	30	23	11	13	13	15	12	11/15	T
T	15	13	28	24	10	13	14	15	12	11/14	C
U	14	13	31	23	10	15	13	15	11	15/17	T
V	13	13	30	24	10	14	13	14	11	15/15	T
X	13	13	30	24	11	15	12	14	11	13/14	T
Y	13	13	30	23	10	14	13	14	11	13/17	T
Z	14	14	30	24	12	13	14	15	12	12/13	Nd

Table 1. Y-Chromosome Haplotype Distribution in the Mocoví sample based on the SNP M3 and 11 Y-STRs (in bold, uncommon alleles). Nd: not genotyped. Haplotype M was the only one found in two individuals.

Tabla 1. Distribución de haplotipos del cromosoma Y en la muestra Mocoví basada en el marcador bialélico M3 y en 11 STRs (en negrita los alelos no comunes). Nd: sin genotipificar. El haplotipo M fue el único hallado en dos individuos.

transition C to T in the M3 marker (weight=50) than for the STRs (default weight=10). The markers included for the network construction were M3, DYS19, DYS389-I, DYS389-II, DYS390, DYS391, DYS392, DYS393, and DYS438. The STRs DYS437 and DYS385a/b were not included because we have not any Amerindian ancestral data available for comparison.

Results

A total of 25 different haplotypes were observed from the 26 unrelated individuals included in the analysis (Table 1), which represents a haplotype diversity of 99.69%. The M3-T transition was present in 52% of the haplotypes -12 out of 23 determined + 2 individuals which were not possible to determine (=Nd)-. Among the T haplotypes, 4 of them (identified as C, F, L, and V in Table 1) are coincident with the ancestral STR haplotype 0a described in Bianchi et al (1998), even when we extended the haplotype by including the allele DYS438-11 considered as ancestral, according to Demarchi and Mitchell (2004). Taking into account the possibility of an Amerindian origin for the Y-chromosomes carrying the M3-C variant, we genotyped them for the marker M346 in order to check if some of them belong to the paragroup Q1a3*, according to Bailliet et al. (2009). The results show that none of the M3-C individuals present the M346-T allele, thus allowing us to consider those haplotypes of non Amerindian origin.

The average gene diversity over all loci was 57%. Some individuals presented alleles that are uncommon in other Amerindian ethnic groups: DYS393-11 (excepting in the Mbyá-Guarani, as in Sala et al. 2010), DYS19-16, and DYS391-12, thus generating a haplotype network with a wide dispersion (Figure 2). However, individuals having those alleles do not carry the M3-T nor the M346-T alleles and, therefore, have a non Amerindian origin.

One of the haplotypes showed a duplication that has been previously described in the YHRD for the bi-locus marker DYS385a-b, resulting in three alleles 11-13-14. Among the M3-T haplotypes, the most represented was the ancestral 0a (n=4), while the next better represented (n=2) shows only one mutational step from the 0a.

Until the date of submission of this work, 13 out of the 25 Y-STR haplotypes (Table 2) were not described in the database of the Y-STR profiles of YHRD (Release 35, December 30th 2010, consisting of 91601 haplotypes within 710 populations). The remaining 12 haplotype variants were observed in interbred populations, whereas half of them have also been described among Amerindians.

The AMOVA (Table 3) were performed separately for the data from Demarchi and Mitchell (2004) (Table 3-a), and for the data from Ramallo et al. (2009) (Table 3-b), because different Y-STR markers were available in each of those studies. All comparisons showed that the highest variance component was within populations, as expected. After grouping populations by their geographic locations, we found the lowest intergroup variance for the Mocoví sample (Santa Fe province), compared to the Toba+Wichí from Chaco province, and to the Toba+Wichí+Pilagá from Formosa province (Demarchi and Mitchell, 2004). On the contrary, the comparison to the data from Ramallo et al. (2009) showed high intergroup variance between Mocoví and the Wichí from different communities living in Formosa province. Table 4 details the F_{ST} values for pairwise comparisons between the Mocoví sample and the other Gran Chaco ethnic groups included in the analysis (Demarchi and Mitchell 2004, Ramallo et al. 2009).

Finally, we constructed a median-joining network

	Total	Amerindians	EskimoAleut	Mixed	Eurasians	Africans	Afro-Asians
YHRD	42267	397	272	5895	19494	1671	2073
C	5	2	-	3	-	-	-
D	2	-	-	2	-	-	-
E	467	7	2	168	274	14	2
F	2	1	-	1	-	-	-
G	11	2	-	3	5	1	-
H	64	-	-	41	23	-	-
K	2	-	-	2	-	-	-
L	1	-	-	1	-	-	-
Ñ	2	1	-	1	-	-	-
P	7	1	-	3	3	-	-
R	9	-	-	4	4	1	-
U	2	-	-	2	-	-	-

Table 2. Haplotype variants in the Mocoví sample also found in the YHRD database.

Tabla 2. Variantes haplotípicas en la muestra Mocoví hallados también en la base de datos YHRD.

	Among groups			Source of variation Among populations within groups			Within populations		
	Sum of squares	Variance components	% of variation	Sum of squares	Variance components	% of variation	Sum of squares	Variance components	% of variation
1	6.884	0.0533	3.85	5.478 *	0.0456	3.30	101.414**	128.373	92.85
2	8.565	0.0373	2.71	3.797 *	0.0536	3.90	101.414**	1.284	93.39

Table 3a. AMOVA analysis. Significant values are marked with asterisks (*: $p < 0.05$; **: $p < 0.005$). Analysis using data from Demarchi and Mitchell (2004); AMOVA designs: 1: geographical grouping; 2: ethnic grouping. References: 1: geographic grouping = Santa Fe province (Mocoví) vs Formosa province (Pilagá+Wichí+Toba) vs Chaco province (Wichí+Toba); 2: ethnic grouping = Mocoví (Santa Fe) vs Pilagá (Formosa+Chaco) vs Wichí (Formosa+Chaco) vs Toba (Formosa+Chaco).

Tabla 3a. Análisis AMOVA. Los valores significativos se marcan con asteriscos (*: $p < 0.05$; **: $p < 0.005$). Análisis utilizando datos de Demarchi y Mitchell (2004); Diseño de AMOVA: 1, agrupamiento geográfico; 2: agrupamiento étnico. Referencias: 1: agrupamiento geográfico = Santa Fe (Mocoví) vs Formosa (Pilagá+Wichí+Toba) vs Chaco (Wichí+Toba); 2: agrupamiento étnico = Mocoví (Santa Fe) vs Pilagá (Formosa+Chaco) vs Wichí (Formosa+Chaco) vs Toba (Formosa+Chaco).

considering all the haplotypes (Figure 2-a), and a second one including only M3-T individuals (Figure 2-b). The latter shows that some intermediate haplotypes were absent from the sampling.

Discussion and conclusions

Our findings demonstrate that the Mocoví Y-chromosomes still remain highly variable. Particularly, some of the M3-T haplotypes we found in this Mocoví community have not been observed in other Amerindian groups. According to this, a considerable amount of haplotype variability was not acquired by gene flow, but it is originary of this ethnic group.

The AMOVA analysis shows different aspects when comparing with the data from Demarchi and Mitchell (2004) and from Ramallo *et al.* (2009). In the first group of comparisons we cannot emphasize any divergence between the Mocoví and other ethnic groups from the Gran Chaco, apparently due to the high differences between Wichí and Toba living in the same province. The divergence among groups increases when we cluster the data from Demarchi and Mitchell (2004) by ethnic origin. On the other hand, the analysis including data from Ramallo *et al.* (2009) shows a high divergence between

both Wichí groups analyzed in that work and our Mocoví sample. Moreover, the most significant F_{ST} values in the pairwise comparisons are those found between the Mocoví and the populations analyzed by Ramallo *et al.* (2009). It is interesting to find the highest F_{ST} value in the comparison between the Mocoví and the Wichí from Laguna Yema (12.5%), two populations very distant not only from a geographic point of view, but also because their different linguistic origin. Another high F_{ST} value was found between the Mocoví and Toba from Chaco province (Demarchi and Mitchell 2004); this value could be interpreted as divergence due to genetic drift.

With regard to the M3 transition, we found an intermediate representation of the derived allele (T), in comparison to data from other Amerindian populations (Pena *et al.* 1995; Santos *et al.* 1999; Underhill *et al.* 1996). The ancestral haplotype 0a, extended with DYS438, was the most well represented, and conformed part of the central torso in the network of M3-T haplotypes.

Other STR markers located on autosomal chromosomes also present higher diversity values in the Mocoví in comparison to other indigenous communities, particularly the Chorote, Wichí, Mapuche, and Tehuelche from Argentina, the Ayoreo from Paraguay and the Huilliche

	Among groups			Source of variation Among populations within groups			Within populations		
	Sum of squares	Variance components	% of variation	Sum of squares	Variance components	% of variation	Sum of squares	Variance components	% of variation
1	9.112	0.1157	7.70	-	-	-	114.005	1.373	92.23
2	7.723	0.1786	11.50	1.389	0.0005	0.04	114.005**	1.373	88.46

Table 3b. AMOVA analysis. Significant values are marked with asterisks (*: $p < 0.05$; **: $p < 0.005$). Analysis using data from Ramallo *et al.* (2009); AMOVA designs: 1: geographical grouping; 2: ethnic grouping. References: 1: geographic grouping = Colonia Dolores (Mocoví) vs Ingeniero Juárez (Wichí) vs Laguna Yema (Wichí); 2: ethnic grouping = Mocoví (Colonia Dolores) vs Wichí (Ingeniero Juárez+Laguna Yema)

Tabla 3b. Análisis AMOVA. Los valores significativos se marcan con asteriscos (*: $p < 0.05$; **: $p < 0.005$). Análisis utilizando datos de Ramallo *et al.* (2009); Diseño de AMOVA: 1, agrupamiento geográfico; 2: agrupamiento étnico. Referencias: 1: agrupamiento geográfico = Colonia Dolores (Mocoví) vs Ingeniero Juárez (Wichí) vs Laguna Yema (Wichí); 2: agrupamiento étnico = Mocoví (Colonia Dolores) vs Wichí (Ingeniero Juárez+Laguna Yema)

Pairwise comparison	Fst value	Reference
Mocoví – Wichí Formosa	0.07416*	Demarchi and Mitchell (2004)
Mocoví - Wichí Chaco	0.03488	Demarchi and Mitchell (2004)
Mocoví - Wichí Ing. Juárez	0.07033**	Ramallo et al. (2009)
Mocoví - Wichí Lag. Yema	0.12589**	Ramallo et al. (2009)
Mocoví - Toba Formosa	0.04796	Demarchi and Mitchell (2004)
Mocoví - Toba Chaco	0.11939*	Demarchi and Mitchell (2004)
Mocoví - Pilagá	0.03027	Demarchi and Mitchell (2004)

Table 4. F_{st} comparisons between pairs of populations. Significant values are marked with asterisks (*: $p < 0.05$; **: $p < 0.005$).

Tabla 4. Comparación de F_{st} entre pares de poblaciones. Los valores significativos se marcan con asteriscos (*: $p < 0.05$; **: $p < 0.005$).

from Chile (Catanesi et al. 2001; Turret et al. 2000). Moreover, five STRs located on the X chromosome also show greater variability in the Mocoví than in other native communities (Catanesi et al. 2007), consistently with our current findings in the Y chromosome.

The loss of variability on the Y chromosome by means of selective sweeps is frequent in numerically small groups. Historically, the Mocoví population was gradually dispersed, persecuted and killed, and, in addition,

suffered the burden caused by diseases that led to their reduction. However, the Y chromosome of Mocoví people is still highly variable as seen in its haplotypic and allelic variabilities (including uncommon alleles), and it is also distinct from other native ethnic groups of South American Gran Chaco region, as shown in F_{st} values and AMOVA analysis.

Although we cannot exclude some amount of Y-chromosome variability coming from an external source, the haplotype richness observed in the Y chromosome of the Mocoví allows us to conclude that this ethnic group retains a high genetic variability, and still presents characteristics that differentiate Mocoví from other Amerindian communities, as well as from other populations of the world.

La Plata, June 22nd, 2011

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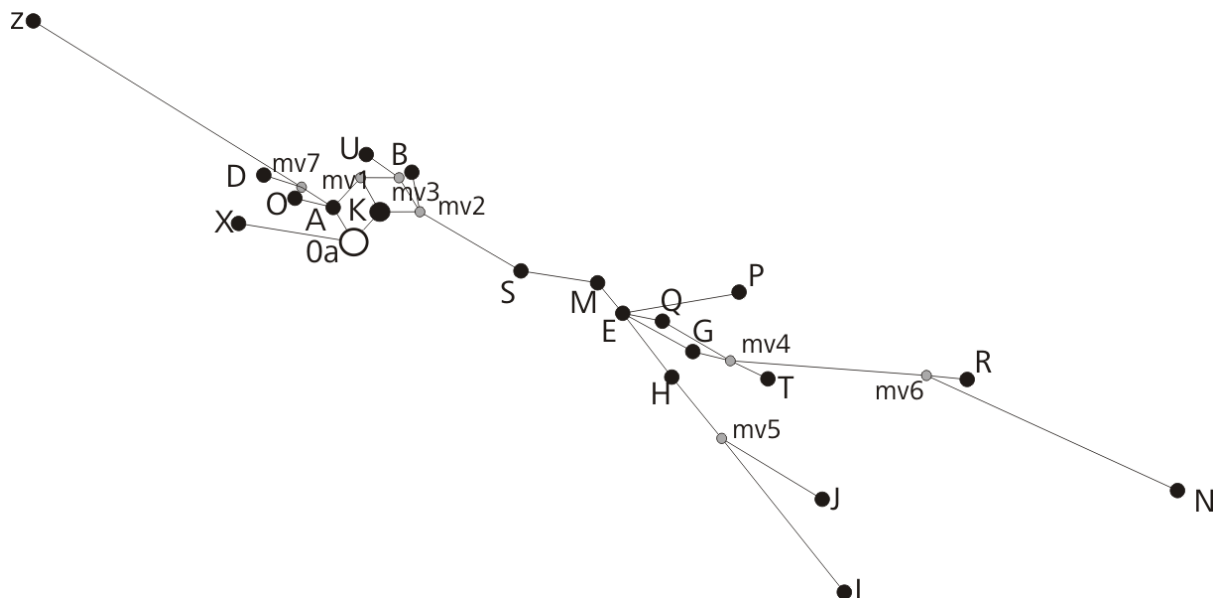


Figure 2a: Haplotype network constructed with Network 4.6. Considering all the haplotypes. The grey dots indicate the median vectors.

Figura 2a: Red de haplotipos construidas con Network 4.6, considerando todos los haplotipos. Los puntos grises indican los haplotipos hipotéticos no hallados en este estudio vectores de la mediana.

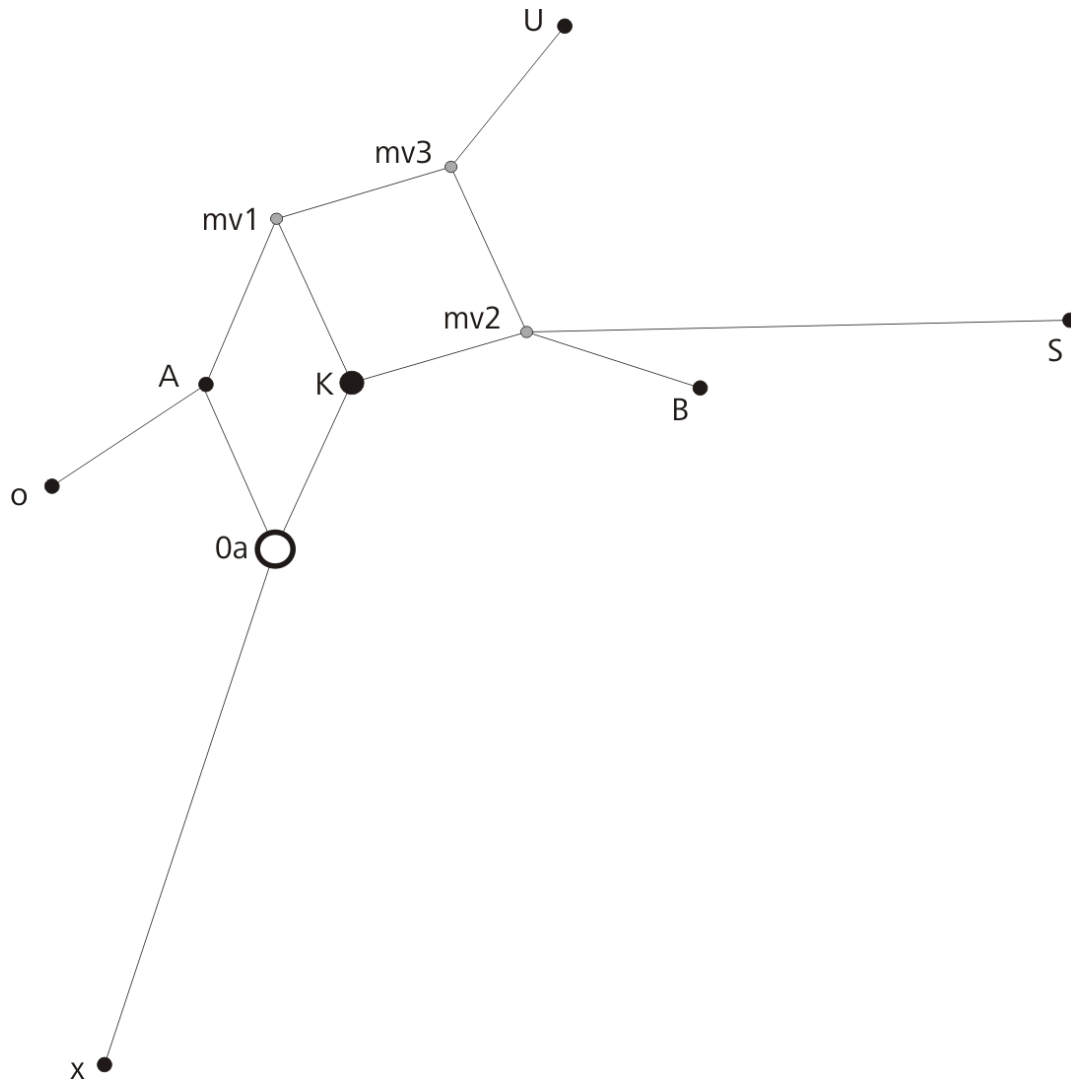


Figure 2b: Haplotype network constructed with Network 4.6 including only M3-T haplotypes. The grey dots indicate the median vectors.

Figura 2b: Red de haplotipos construidas con el programa Network 4.6 incluyendo solo los haplotipos M3-T. Los puntos grises indican los haplotipos hipotéticos no hallados en este estudio vectores de la mediana.

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