

## Demography, genetic diversity, and population relationships among Argentinean Mapuche Indians

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### Abstract

Fertility, mortality and migration data from four Mapuche Indian communities located along a 215-km NE-SW linear area in the Province of Río Negro, Argentina, were collated with genetic information furnished by nine blood group systems and by mtDNA haplogroups. The demographic and genetic data indicated a clear dichotomy, which split the four populations into two groups of two. Differing degrees of non-Indian exchanges was probably the main determining factor for this separation. Total genetic variability was very similar in all groups, and the interpopulational variability accounted for only 10% of the total variability. A low prevalence of the Diego(a) antigen among the Mapuche was confirmed. The fact that significant genetic heterogeneity and population clusters were found in such a small territorial region attests to the sensitivity of demographic and genetic approaches in unraveling human history.

### INTRODUCTION

The Mapuche Indians have been the subject of several demographic and genetic studies, the first surveys dating back to the 1930s (reviewed in Haas *et al.*, 1985; Carnese *et al.*, 1996). Our investigations started in 1990, with studies of several communities in Río Negro Province, Argentina. The first investigation was conducted in Blancura Centro, and included demographic and genetic (blood groups, other blood protein loci) data (Carnese *et al.*, 1993, 1996). Other analyses involved the HLA system and mtDNA polymorphisms, surveyed in Anecón Grande, Cerro Policía and Aguada Guzmán (Ginther *et al.*, 1993; Baillet *et al.*, 1994). We made additional demographic and genetic studies of the latter three communities and compared the results with previous findings.

### SUBJECTS AND METHODS

The four localities are distributed in a NE-SW orientation, as follows: 1) Aguada Guzmán (68°57'W, 39°30'S) and 2) Cerro Policía (68°37'W, 39°10'S), both located in the Department of El Cuy, near the urban reference center of General Roca (165 km and 110 km, respectively), 3) Blancura Centro (69°20'W, 40°30'S), also in the Department of El Cuy and 4) Anecón Grande (70°22'W, 41°20'S), Department of 25 de Mayo (Figure 1). The latter two communities are more distant from General Roca (325 km and 200 km, respectively). The people of Blancura Centro and Anecón Grande do not share their habitat with mestizo groups, the settlement pattern being of the dispersed type

(Vapñarsky, 1983). The domestic units consist of nuclear and, in a few cases, extended families. In Cerro Policía and Aguada Guzmán, on the other hand, the settlement pattern is of the clustered type (Vapñarsky, 1983). Their villages are temporary sites in the movement towards urban centers (Caratini *et al.*, 1995), thus favoring contact with non-Indians.

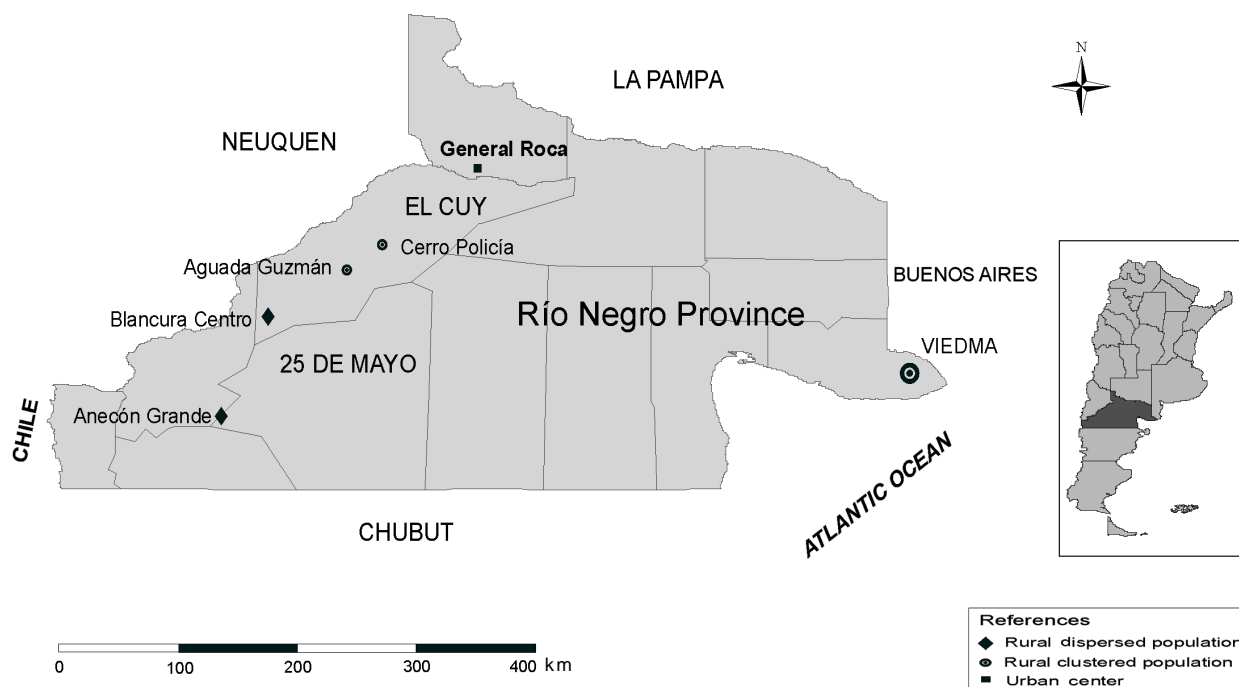
All localities are situated in a semi-desert region, the Patagonian steppe. The climate is cold and dry, with extreme temperatures ranging from -33° to +40°C. There is little rain; however, snow storms throughout the year bring water after melting. In the winter, the communities become isolated because of blocked roads.

In all communities, the demographic information was obtained by house visits with parallel clinical examinations (data not shown), as described in Carnese *et al.* (1996). Approximately 20 ml of blood was collected in sterile tubes with anticoagulant (ACD) from representative individuals of each community. The blood samples were sent by air mail on the same day to Buenos Aires, where they were processed in the Hematology and Hemotherapy Laboratory of the Clinical Hospital, University of Buenos Aires. Blood group typing was performed within 24-72 h of collection using standardized methods.

Allele frequencies for the ABO, MNS and Rh systems were obtained using the MAXLIK program of Reed and Schull (1968), while for the other blood groups, classic square root methods were used. Interethnic admixture was calculated using the ADMIX program (Chakraborty, 1975). The Mapuche population of Pedregoso, Chile (Etcheverry *et al.*, 1967) was considered as representative of the origi-

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**Figure 1** - Map of Río Negro Province, Argentina, showing the geographic location of the populations studied. The map of Argentina, bottom right, indicates the position of this province in the country.

nal Amerindian gene pool, while for the parental Spanish population the frequencies listed in Valls (1975) were used. The mtDNA data were obtained from previously published sources (Ginther *et al.*, 1993; Bailliet *et al.*, 1994). The demographic and protein results for Blancura Centro were taken from Carnese *et al.* (1996). Inter- and intrapopulation genetic variability and genetic distances were obtained following the methods of Nei (1973, 1978, 1986), Nei *et al.* (1983), and Nei and Roychoudhury (1993). The dendrogram was obtained by the neighbor-joining procedure (Saitou and Nei, 1987), using the DISPAN program (Ota, 1993).

## RESULTS

There was a clear dichotomy in types of marriage when the two localities with a more traditional way of life (Blancura Centro, Anecón Grande) were compared with the other two (Table I). Endogamy was higher (42-68% vs. 14%) and the proportion of interethnic unions lower (13-28% vs. 79-81%). In all populations, the sexes were evenly distributed among immigrants and emigrants. As expected, those who left their communities were young and were distributed among a vast array of localities. Interchange between the communities considered here was limited, with only one known case which involved a woman who migrated from Aguada Guzmán to Cerro Policía.

Fertility was high in three of the four populations (about 7-8 children per mother who completed reproduc-

tion), the exception being the number observed in Aguada Guzmán which was significantly lower than those at the other locations (Table II). The prevalence of premature deaths was not high (11-17%) for rural Third World populations. The index of opportunity for selection, which conveniently summarizes in a single number fertility and mortality data, was also not high (Table II). The differences observed were too small to be considered significant (Adams and Smouse, 1985).

The presence of the blood group alleles ABO\*A, ABO\*B, LU\*A and KELL\*K was associated with non-Indian antecedents (Table III). The relatively low prevalences of P\*1 and DI\*A, and the high incidence of RH\*RO were notable. The dichotomy observed in the demographic data was also present in these results, with the groupings Anecón Grande and Blancura Centro versus Cerro Policía and Aguada Guzmán showing much more intragroup than intergroup similarity.

Differences in mtDNA haplogroup distribution in three of the localities investigated were not marked in haplogroups A-D, with the exception of the high prevalence of D in Aguada Guzmán (Table IV). On the other hand, haplogroup E was not found in Anecón Grande, but was present in the other two locations.

Total genetic variability (Ht) was very similar in all groups (0.22 considering all of them together), and inter-population variability accounted for only 10% of this value. Most of the variability was due to MNSs (Ht: 0.62) and Rh (Ht: 0.61), while Kell (Ht: 0.004) appeared at the other ex-

**Table I** - Types of marriages and migration data for the *Argentinean Mapuche* populations studied.

Types of marriages and migration data	Localities							
	Blancura Centro*		Anecón Grande		Cerro Policía		Aguada Guzmán	
	N	%	N	%	N	%	N	%
<b>1. Classified by place of birth</b>								
Both partners from the same village	38	68	8	42	6	14	3	14
One partner from another population	14	25	8	42	9	22	7	32
Both partners from another population	4	7	3	16	27	64	10	54
Total number of marriages	56	100	19	100	44	100	20	100
Number of localities which contributed with immigrants	13	-	9	-	25	-	9	-
<b>2. Classified by ethnic group</b>								
Indian x Indian	49	87	13	72	7	19	4	21
Indian x mestizo	7	13	1	6	10	26	5	26
Mestizo x mestizo	-	-	4	22	21	55	10	53
Total	56	100	18	100	38	100	19	100
<b>3. Immigrants</b>								
Males	10	50	6	46	31	49	14	52
Females	10	50	7	54	32	51	13	48
<b>4. Emigrants</b>								
Males	20	40	24	51	38	59	19	63
Females	30	60	23	49	26	41	11	37
Born in the locality	43	86	43	91	51	80	28	93
Born elsewhere	7	14	4	9	13	20	2	7
Average age	26	-	24	-	30	-	24	-
Number of localities which received emigrants	19	-	16	-	20	-	9	-

\*Data from Carnese *et al.*, 1996. Total population sizes: Blancura Centro: 211; Anecón Grande: 74; Cerro Policía: 188; Aguada Guzmán: 108.

**Table II** - Fertility and mortality of the Indian populations studied.

Group analyzed	Locality	Number of women	Number of live births	Births/Family (mean $\pm$ SD)	Premature deaths (%)*
All families	Blancura Centro	42	225	5.3 $\pm$ 1.8	17
	Anecón Grande	18	111	6.1 $\pm$ 0.5	17
	Cerro Policía	38	206	5.4 $\pm$ 0.3	11
	Aguada Guzmán	22	106	4.8 $\pm$ 0.2	13
Completed families **	Blancura Centro	24	162	6.7 $\pm$ 3.1	
	Anecón Grande	12	94	7.8 $\pm$ 0.8	
	Cerro Policía	19	134	7.0 $\pm$ 0.8	
	Aguada Guzmán	12	46	3.8 $\pm$ 0.4	
Opportunity for selection ***		Im	If	If/ps	I
	Blancura Centro	0.20	0.22	0.26	0.46
	Anecón Grande	0.22	0.14	0.17	0.39
	Cerro Policía	0.11	0.25	0.28	0.39
Aguada Guzmán	0.11	0.47	0.54	0.63	

\*Before 15 years old. \*\*From females  $\geq$  40 years old. \*\*\*Im = pd/ps, where pd: premature deaths and ps: proportion surviving or (1-pd). If = Vf/x<sup>2</sup>, where Vf: variance in offspring number in completed sibships and x: mean number of livebirths per woman who completed reproduction. I: Im + If/ps: index of opportunity for selection (Crow, 1958).

treme. The dendrogram (Figure 2) which was constructed using the blood group and mtDNA data also clearly showed two clusters, one involving Anecón Grande and Blancura Centro, and the other Aguada Guzmán and Cerro Policía.

## DISCUSSION

The demographic pattern observed in these communities was typical of rural New World populations, and did

not differ markedly from those observed in other Amerindian populations which adopt the same way of life (Salzano and Callegari-Jacques, 1988). The low number of children per completed family in Aguada Guzmán suggests or indicates that non-Indian fertility control measures are presently being taken in this community, with other factors, such as excessive prenatal losses, being unlikely explanations. The indices of opportunity for natural selection were of the same order of magnitude as those observed in Argentinean

**Table III** - Blood group allele frequencies in the Indian populations studied.

Alleles	Populations and allele frequencies			
	Anecón Grande (N = 61)	Blancura Centro* (N = 95)	Cerro Policía (N = 82)	Aguada Guzmán (N = 57)
ABO*O	0.932	0.951	0.837	0.842
ABO*A	0.050	0.043	0.102	0.148
ABO*B	0.017	0.005	0.060	0.010
FY*A	0.638	0.709	0.534	0.438
JK*A	0.317	0.347	0.458	0.239
DI*A	0.025	0.032	0.000	0.017
P*1	0.249**	0.246	0.251	0.251
LU*A	0.031**	0.032	0.029	0.031**
KELL*K	0.000	0.000	0.000	0.009
RH*RZ	0.041	0.029	0.012	0.009
RH*R1	0.475	0.518	0.439	0.535
RH*R2	0.385	0.339	0.365	0.386
RH*RO	0.098	0.113	0.183	0.070
L*MS	0.071	0.058	0.113	0.109
L*Ms	0.537	0.568	0.412	0.399
L*NS	0.054	0.016	0.082	0.075
L*Ns	0.337	0.358	0.393	0.416

\*Data from Carnese *et al.* (1993, 1996). \*\*Information not available. Average of three other frequencies. The estimates of non-Indian admixture based on these frequencies were as follows: Anecón Grande, 7%; Blancura Centro, 6%; Cerro Policía, 12%; Aguada Guzmán, 13%. Total heterozygosity by locus was as follows, ABO: 0.20; Duffy: 0.49; Kidd: 0.47; Diego: 0.04; P: 0.40; Lutheran: 0.06; Kell: 0.004; Rh: 0.61; MNSs: 0.62.

**Table IV** - mtDNA haplogroups (%) in the Indian populations studied.\*

mtDNA haplogroup	Anecón Grande**	Cerro Policía***	Aguada Guzmán***
A	15	4	6
B	38	35	28
C	21	27	19
D	26	15	44
E	0	19	3
No.	39	26	32

\*Since this information was not available for Blancura Centro, averages of the frequencies obtained in the three other populations were used to allow the inclusion of these results in the calculation of genetic distances and construction of the dendrogram. \*\*Data from Ginther *et al.* (1993). \*\*\*Data from Baillet *et al.* (1994), where the results from the two localities were presented as a whole. No., Number of individuals studied.

Toba populations (Fortín Lavalle: 0.66; Villa Iapi: 0.42) (Palatnik, 1973; Carnese and Caratini, 1992).

Spatial analysis indicated heterogeneity for several blood group loci, with significant differences occurring in relation to ABO, MNSs and Duffy. However, this heterogeneity did not follow a regular geographical pattern, reflecting instead the dichotomy indicated earlier, which was probably related to the degree of non-Indian influence more than any other factor.

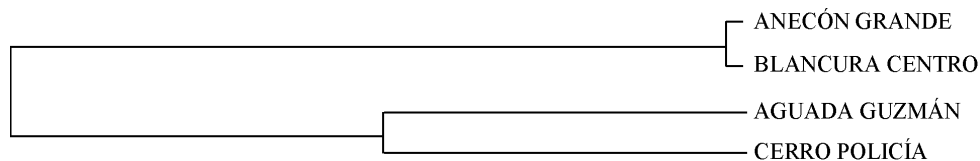
The low prevalences of P\*1 and DI\*A, and high prevalence of RH\*RO were significantly different from South American Indian averages (Salzano and Callegari-Jacques, 1988). Previous studies involving some or all of these markers have been performed in Mapuche Indians

from Chile by Sandoval and Henckel (1954), Witkop and Gaiser (1960), Etcheverry *et al.* (1967), and Matson *et al.* (1967), and from Argentina by Matson *et al.* (1969) and Haas *et al.* (1985). Null or low frequencies of DI\*A were observed in five Mapuche populations of the two countries, indicating that this may be a distinctive trait of this tribe. Although variable prevalences of P\*1 and RH\*RO were obtained in these same groups, no generalization about them is possible at the moment.

The high frequencies of RH\*RO seen in this study may be explained by admixture with African-derived persons. We previously suggested this possibility in relation to Blancura Centro (Carnese *et al.*, 1993). Studies with serum proteins, the hemoglobin gene, and Y chromosome DNA markers (Weidle de Araujo *et al.*, 1995; Kaufman *et al.*, 1998; Bianchi *et al.*, 1997) seem to confirm this hypothesis. Ethnohistorical investigations need to be performed to identify the sources of these African markers.

The question as to whether the mtDNA haplogroup E was present in the parental groups which colonized America is still unanswered. The absence of haplogroup E in Anecón Grande, which has an estimated non-Indian admixture of 7%, and the presence in Cerro Policía and Aguada Guzmán (calculated admixture rates of 12 and 13%, respectively) suggest that its presence reflects non-Indian gene flow. However, a close examination of the genealogies of carriers of this haplogroup revealed no indications of interethnic exchange, at least in recent generations.

In conclusion, we found significant genetic heterogeneity in a set of four populations of the same tribal origin established in an area whose linear limits do not ex-



**Figure 2** - Dendrogram of the Mapuche populations studied, obtained using Nei's (1973) standard genetic distances and the neighbor-joining method.

ceed 215 km. The clear clustering of these populations into groups of two attests to the sensitivity of the demographic and genetic approaches used to detect even small differences that may be important in studies of human diversification.

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#### RESUMO

Dados relativos a fertilidade, mortalidade e migração de quatro comunidades de índios Mapuche localizadas em uma área linear na direção nordeste-sudoeste com 215 km de extensão na Província de Río Negro, Argentina, foram associados com a informação genética fornecida por nove sistemas de grupos sanguíneos e os haplogrupos do DNA mitocondrial. Ambos os tipos de informação apontam claramente para uma dicotomia, as quatro populações sendo divididas em grupos de duas. O principal fator responsável por esta separação é provavelmente graus diferentes de mistura com não-índios. A variabilidade genética total foi muito similar em todos os grupos, aquela entre populações sendo de apenas 10% deste valor. Foi confirmada a baixa prevalência do antígeno Diego(a) entre os Mapuche. O fato de que heterogeneidade genética significativa e conjuntos populacionais diversos foram observados em uma região territorial tão pequena demonstra a sensibilidade dos enfoques demográfico e genético no esclarecimento da história humana.

#### REFERENCES

**Adams, J.** and **Smouse, P.E.** (1985). Genetic consequences of demographic changes in human populations. In: *Diseases of Complex Etiology in Small Population* (Chakraborty, R. and Szathmary, E.J.E., eds.). Alan R. Liss, New York, pp. 283-299.

- Baillet, G., Rothhammer, F., Carnese, F.R., Bravi, C.M. and Bianchi, N.O.** (1994). Founder mitochondrial haplotypes in Amerindian populations. *Am. J. Hum. Genet.* 54: 27-33.
- Bianchi, N.O., Bailliet, G., Bravi, C., Carnese, F.R., Rothhammer, F., Martínez-Marignac, V. and Pena, S.** (1997). Origin of Amerindian Y-chromosomes as inferred by the analysis of six polymorphic markers. *Am. J. Phys. Anthropol.* 102: 79-89.
- Caratini, A.L., Ingold, L., Crognier, E. and Carnese, F.R.** (1995). Demografía genética de la población mapuche de Villa Obrera, Río Negro. *Rev. Arg. Antrop. Biol.* 1: 57-68.
- Carnese, F.R. and Caratini, A.L.** (1992). Demografía genética de una población toba de Villa Iapi, Quilmes, Prov. de Buenos Aires. *Emia* 36/37: 9-28.
- Carnese, F.R., Goicoechea, A.S., Rey, J., Niborsky, R.C., Kohan, A.I. and Arrayago, A.M.** (1993). Grupos sanguíneos en una población mapuche de Blancura Centro, Prov. de Río Negro, Argentina. *Bol. Soc. Esp. Antrop. Biol.* 14: 31-39.
- Carnese, F.R., Caratini, A.L., Goicoechea, A.S., Weimer, T.A., Franco, M.H.L.P., Hutz, M.H. and Salzano, F.M.** (1996). Demography and blood genetics of Argentinian Mapuche Indians. *Int. J. Anthropol.* 11: 31-40.
- Chakraborty, R.** (1975). Estimation of race admixture. A new method. *Am. J. Phys. Anthropol.* 42: 507-512.
- Crow, J.F.** (1958). Some possibilities for measuring selection intensities in man. *Hum. Biol.* 30: 1-13.
- Etcheverry, R., Guzmán, C., Hille, A., Nagel, R., Covarrubias, E., Regonesi, C., Miranda, M. and Durán, N.** (1967). Investigación de grupos sanguíneos y otros caracteres genéticos sanguíneos en indígenas de Chile. I: en atacameños y mapuches. *Rev. Med. Chile* 95: 599-604.
- Ginther, C., Corach, D., Penacino, A., Rey, J.A., Carnese, F.R., Hutz, M.H., Anderson, A., Just, J., Salzano, F.M. and King, M.C.** (1993). Genetic variation among the Mapuche Indians from the Patagonian region of Argentina: mitochondrial DNA sequence variation and allele frequencies of several nuclear genes. In: *DNA Fingerprinting: State of the Science* (Pena, S.D.J., Chakraborty, R.M., Epplen, J.T. and Jeffrey, A.J., eds). Birkhauser Verlag, Basel, pp. 211-219.
- Haas, E.J.C., Salzano, F.M., Araujo, H.A., Grossman, F., Barbetti, A., Weimer, T.A., Franco, M.H.L.P., Verruno, L., Nasif, O., Morales, V.H. and Arienti, R.** (1985). HLA antigens and other genetic markers in the Mapuche Indians of Argentina. *Hum. Hered.* 35: 306-313.
- Kaufman, L., Carnese, F.R., Goicoechea, A.S., Dejean, C.B., Salzano, F.M. and Hutz, M.H.** (1998). Beta-globin gene cluster haplotypes in the Mapuche Indians of Argentina. *Genet. Mol. Biol.* 21: 435-437.
- Matson, G.A., Sutton, H.E., Etcheverry, R., Swanson, J. and Robinson, A.** (1967). Distribution of hereditary blood groups among Indians in South America. IV. In Chile. *Am. J. Phys. Anthropol.* 27: 157-193.
- Matson, G.A., Sutton, H.E., Swanson, J. and Robinson, A.** (1969). Distribution of hereditary blood groups among Indians in South America. VII. In Argentina. *Am. J. Phys. Anthropol.* 30: 61-83.
- Nei, M.** (1973). Analysis of gene diversity in subdivided populations. *Proc. Natl. Acad. Sci. USA* 70: 3321-3332.
- Nei, M.** (1978). Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89: 583-590.
- Nei, M.** (1986). Definition and estimation of fixation indices. *Evolution* 40: 643-645.
- Nei, M. and Roychoudhury, A.K.** (1993). Evolutionary relationships of human populations on a global scale. *Mol. Biol. Evol.* 10: 927-943.
- Nei, M., Tajima, F. and Tateno, Y.** (1983). Accuracy of estimated phylogenetic trees from molecular data. *J. Mol. Evol.* 19: 927-943.
- Ota, T.** (1993). *DISPAN: Genetic Distance and Phylogenetic Analysis Uni-*

- versity Park: Institute of Molecular and Evolutionary Genetics. The Pennsylvania State University, University Park, PA, USA.
- Palatnik, M.** (1973). Demografía: parámetros de implicancia genética. In: *Simposio sobre Genética de la Población Toba del Chaco Argentino* (Palatnik, M., ed.). Fundación Miguel Lillo, Tucumán, pp. 8-21.
- Reed, T.E. and Schull, W.J.** (1968). A general maximum likelihood estimation program. *Am. J. Hum. Genet.* 20: 579-580.
- Saitou, N. and Nei, M.** (1987). The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* 4: 406-425.
- Salzano, F.M. and Callegari-Jacques, S.M.** (1988). *South American Indians. A Case Study in Evolution*. Clarendon Press, Oxford.
- Sandoval, L. and Henckel, C.** (1954). The ABO, MNS, and Rh-Hr blood groups of the Mapuche Indians of Cautin Province, Chile. *Hum. Biol.* 26: 324-329.
- Valls, A.** (1975). Seroantropología de la población española. *Rev. Univ. Compl.* 24: 111-139.
- Vapñarsky, C.A.** (1983). *Pueblos del Norte de la Patagonia 1779-1957*. Centro de Estudios Urbanos y Regionales, Buenos Aires.
- Weidle de Araujo, E., Ghinzelli, A.C., Franco, M.H., Carnese, F.R. and Salzano, F.M.** (1995). Polimorfismos protéicos em indios Mapuche da Argentina. *Rev. Bras. Genét.* 18 (Suppl.): 335.
- Witkop Jr., C.J. and Gaiser, J.** (1960). *Genetic Blood Studies. A Report by the Interdepartmental Committee on Nutrition for National Defense*. National Institutes of Health, Bethesda, pp. 317-320.

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