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Genetic variation in the Bribri and Cabecar Amerindians from Talamanca, Costa Rica

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Abstract: A screening of more than 40 loci was performed in the Bribri and Cabecar Amerindian populations of Talamanca in Southeastern Costa Rica. Some differences were found in the distribution (presence or absence) of the variants (some of them private) of the GOT, PEPA, RH, TF and TPI loci when the results reported here were compared with those of the Bribris and Cabecars that inhabit in the Pacific side of the country. Admixture with non-Indians was detected at the ABO, ADA, and G6PD loci. The proportion of polymorphic loci (P) found were 17.1 in the Bribris and 19.4 in the Cabecars; their average heterozygosities (H) estimates were 0.039 and 0.049 respectively. Fst values (0.019 in the Bribris and 0.056 in the Cabecars) seem to indicate that random events have played important roles in the divergence of the Cabecars. Low effective population sizes of the emigrant groups to the Pacific side and probable gene flow in the case of the Bribris, could be the causes of these differences.

Key words: Amerindians, genetic variation, polymorphic loci, heterozygosis, geographic variation.

The importance of studying Amerindian groups to understand some aspects of human evolution was pointed out by Neel and Salzano (1964); after that, a great deal of work was performed particularly in South America (Salzano & Callegari-Jacques 1988). In Lower Central America, systematic work began by 1979 with the study of the Costa Rican and Panamanian groups (Spielman *et al.* 1979, Barrantes *et al.* 1982, 1990).

The Bribris and Cabecars represent together more than fifty percent of the total Costa Rican Amerindian population that was estimated to be around 13000 by 1982 (Bozzoli 1986). These groups are found in the south of the country, on both sides of the Cordillera de Talamanca (Talamanca Mountain Range): nearly sixty percent in the Atlantic and the remaining in the Pacific (Bozzoli 1986), whose former settlers were immigrants from the southeastern (Atlantic) part of the country (Stone 1962). Genetic studies include a previous examination (Azofeifa 1987) of part of the same sample here reported, and a phylogenetic analysis of the Chibcha-speaking groups of Costa Rica and Panama (Barrantes *et al.* 1990). Here we present new information on nearly 40 genetic loci that show that their genetic structures are similar to those of other Amerindian groups of Lower Central America (Barrantes *et al.* 1990) and South America (Neel 1978, Salzano & Callegari-Jaques 1988), although the gene frequencies distributions as well as the presence of private variants at certain loci are distinctive within each group.

MATERIAL AND METHODS

Samples were collected during three trips to the field. The first two were to the Talamanca Indian Reservation that is located between the 9° 27' and 9° 40' N and between 82° 50' and 83° 7' W, at the localities of Amubri, on May, 1984 and Mojoncito, on February, 1985. The Bribris and Cabecars in these places are here referred as Talamancans. The third trip was to a place near the locality of Moravia in the Chirripo Indian Reservation, between the 9° 43' and 9° 54' N and between 83° 32' and 83° 36' W on February, 1986.

Blood was obtained, transported and processed as described elsewhere (Barrantes *et al.* 1982). The number of samples analysed, according to the declared ethnic group of the donors, is shown in Table 1. Differences in these figures are due to availability of reagents at the moment of the sampling and to damage of storing containers.

The ABO, Duffy, MN, RH and Ss blood group typings were performed by the saline tube test and following the antisera manufacturers' indications. The electrophoretic analyses were done using both polyacrylamide and starch gels. In polyacrylamide the following loci were screened: a. enzymes: adenosine deaminase (ADA) glucose phosphate isomerase (GPI), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (PGD) and triose phosphate isomerase (TPI); b.serum proteins: albumin (ALB), ceruloplasmin (CP), haptoglobin (HP) and transferrin (TF); c.hemoglobins: A (HBA) and A2 (HBA2) following the same methods employed by us in other works (Barrantes et al 1982, 1990, Barrantes, Azofeifa & Mata 1985). In starch gels the following enzymes were studied: acid phosphatase (ACP1), adenylate kinase (AK1), carbonic anhydrases 1 and 2 (CA1, CA2), NADH diaphorase (DIA1), esterases A, B, C and D (ESA, ESB, ESC, ESD), glutamate-oxaloacetate transaminase (GOT), isocitrate dehydrogenase (ICD), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), nucleoside phosphorilase (NP), peptidases A, B, C and D (PEPA, PEPB, PEPC, PEPD), phosphoglucomutases 1 and 2 (PGM1, PGM2) and superoxide dismutase (SOD) using the techniques described in Barrantes *et al.*, (1982 , 1990) and Harris and Hopkinson (1976). For glucose-6-phosphate dehydrogenase the methodology used was that detailed by Motulsky and Yoshida (1969) .

The allele frequency calculations were done by the gene counting method. The average heterozygosities (gene diversities) (Nei 1987) and proportions of polymorphic loci were estimated for the 35 (Bribris) and 36 (Cabecars) electrophoretically studied loci. The criterion we used for a polymorphic locus was that the frequency of its commonest allele does not exceed 0.99. To estimate the effect of population subdivision, Fst values, based on the observed and expected heterozygosities (Nei 1987), were calculated using 6 (Bribris) and 8 (Cabecars) polymorphic loci (the phenotype data on which these estimators were based could be sent on request). The variation detected with non-Indian alleles was not included in the estimations.

RESULTS

The allelic frequencies of the genetic systems at which variation was observed are shown in Table 1. Most of the loci analysed by electrophoresis were found to be monomorphic, what means in terms of P (proportion of polymorphic loci) 17.1% in the Bribris and 19.4% in the Cabecars. The average heterozygosities (H) obtained were 0,039 and 0.049 respectively. Racial admixture with non-Indians was evident at three loci: at the ABO blood group system, at the ADA enzyme locus and at the G6PD enzyme locus.

In general, three groupings can be made with the variant loci: a. those with alleles normally found in almost every studied population (Harris & Hopkinson 1976) and that present, basically, the same allele frequencies in the groups compared here; they are ACP1 and PGM1. b. Five loci, ESD, FY, HP, MN and Ss show variation with segregating alleles common to nearly all the human populations (Harris & Hopkinson 1976, Mestriner, Simoes & Salzano 1980, Bowman & Kurowsky 1982, Mourant 1983) but without a clear pattern among the groups compared in Table 1. c. A third group of loci shows a rather interesting variation that includes, besides the normal alleles, private variants restricted to Amerindian populations, or to others related to them. The notability of these loci comes from the presence or absence of a determined allele in the Bribri and Cabecar populations from the Pacific side of the Talamanca Mountain Range and the Bribri and Cabecar ones from its Atlantic side. They are GOT, PEPA (that shows, besides the normal, a low-activity variant allele, PEPA*2KUNA up to now detected only in the Chibcha-speaking groups of Lower Central America; Barrantes *et al.* 1990), RH, TF (that includes two variant alleles, D-China on TF*DCHI, an allele disttinctive of Mongoloids and Amerindians; Neel 1978; as well as D-Guaymi (TF*DGUA), that was first detected in a sample of Panamanian Guaymis; in Tanis, Neel & Torres de Arauz 1977) and TPI (where the private TPI*3BRI allele was ob-

TABLE 1

*Allelic frequencies for the systems that showed variation in the Bribri and Cabecar from the Atlantic of Costa Rica , and a comparison with those of other Costa Rican and Panamanian Amerindians**

		Atlantic	Pacific					
Locus	Allele	Br(123)	Ca(99)	Br(99)@	Ca(60)@	Gt(80)@	Te(63)@	Gy(770)
ABO	A1	0.004	-	-	-	-	-	
	A2	0.004	-	-	-	-	- (A+B)	0.002
	O	0.992	1.000	1.000	1.000	1.000	1.000	0.998
ACP1	A	0.131	0.077	0.131	0.075	0.084	0.103	0.057
	B	0.869	0.923	0.869	0.925	0.160	0.897 (+C)	0.811
	BGUA	-	-	-	-	-	-	0.132
ADA	1	1.000	0.990	1.000	1.000	1.000	1.000	1.000
	2	-	0.010	-	-	-	-	-
ESD	1	0.893	0.912	0.939	1.000	0.717	0.690	0.958
	2	0.107	0.088	0.061	-	0.283	0.310	0.042
FY	a	ND	0.931 (58)	0.641	0.808	0.526	0.373	0.478
	b	ND	0.069	0.359	0.192	0.474	0.627	0.522
GOT	1	ND	0.991 (57)	0.949	0.975	1.000	0.952	0.988
	2	ND	0.009	0.036	-	-	0.032	0.012
	3	ND	-	0.015	0.025	-	0.016	-
G6PD	A	0.009	-	-	-	-	-	-
	B	0.991	1.000	1.000	1.000	1.000	1.000	1.000
HP	1	0.516	0.321	0.383	0.525	0.410	0.661	0.545
	2	0.484	0.679	0.671	0.475	0.590	0.339	0.455
MN	M	ND	0.741 (58)	0.919	0.975	0.506	0.786	0.686
	N	ND	0.259	0.081	0.025	0.494	0.214	0.314
PEPA	N	1.000	0.760	1.000	1.000	0.699	0.794	1.000
	2KUNA	-	0.240	-	-	0.301	0.206	-
PGM1	1	0.984	0.897	0.924	0.908	0.964	0.921	0.947
	2	0.016	0.103	0.076	0.092	0.036	0.079	0.053
RH	0	0.079	0.052	0.030	0.200	0.050	0.032	0.023
	1	0.540	0.448	0.546	0.467	0.519	0.413	0.845
	2	0.357	0.490	0.424	0.333	0.418	0.547	0.132
	Z	0.024	0.010	-	-	0.013	0.008	-
Ss	S	ND	0.810 (58)	0.460	0.450	0.234	0.500	0.380
	s	ND	0.190	0.540	0.550	0.766	0.500	0.620
TF	C	0.837	0.747	0.853	0.966	1.000	0.794	0.945
	DCHI	0.163	0.016	-	-	-	0.206	0.055
	DGUA	-	0.237	0.147	0.034	-	-	-
TPI	1	0.952	0.974	1.000	1.000	0.976	1.000	1.000
	3BRI	0.048	0.026	-	-	0.024	-	-

Notes: Sample sizes indicated in brackets .
Br=Bribri, Ca=Cabecar, Gt=Guatuso, Te=Teribe, Gy=Guaymi, ND=no data.

* Does not include all the variant loci found in the groups from outside Talamanca and Chirripo.

@ Frequencies calculated from the gene counts reported by Barrantes et al. (1990). The frequencies of the Guaymis are from Barrantes *et al.*, (1982).

served). This variant (Figure 1) that was first found in the Cabecars of Talari (Barrantes *et al.* 1990) is characterized by its particular staining (activity) pattern rather than by an altered mobility of any specific band, and seems to be restricted, with the exception of the Guatusos, to the Talamancan groups.

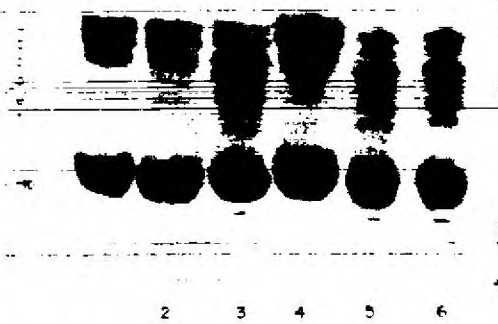

Figure 1 . Electrophoretic patterns of the TPI 1,1 (normal), lanes 1, 2 and 4, and TPI 1, 3 BRI, lanes 3, 5 and 6 after a PAGE (7% acrylamide , pH 8.5). Note the stronger activity of bands a , b and c in the normal and of bands c , d , e and f in the heterozygote with the variant.

Fst values were 0.019 in the Bribri and 0.056 in the Cabecar.

DISCUSSION

The genetic structures of the Bribri and Cabecar populations of Talamanca are very similar to those of other Amerindian populations (Barrantes *et al.* 1982, 1990, Neel 1978) as can be seen from the high proportion of monomorphic loci, the low values of average heterozygosities (H) as well as for the presence of at least one private polymorphism, the TPI*3BRI and the PEPA*2KUNA alleles, in both groups considered here. As expected, differences in gene frequencies were observed between the groups, particularly if we take into account their estimated time of divergence, that ranges, according to lexicostatistical and genetic analyses, from 600 to 1500 years (Barrantes *et al.* 1990, Bozzoli, 1979, Constenla 1985, Vargas 1986).

An early observation (Azofeifa 1987) detected differences between the Bribris of Talamanca and the Bribris of Salitre, and between the Cabecars of Talamanca and the Cabecars of Ujarras. They were evident when we first compared most of our data with those of Matson and his group (Matson & Swanson 1965, Matson *et al.* 1965) which served as a source for the Pacific side populations. These desimilarities are now confirmed when we use our group's data from Cabagra and Ujarras (Barrantes *et al.* 1990). In this latter case more loci were compared, which were sampled and analysed using the same methodologies. The differences are specially clear at the PEPA, TF, TPI and RH loci. Similar differences were found when the dermatoglyphic patterns of these populations were compared (Quesada , M. & R. Barrantes, in preparation).

The Fst va s of both groups suggest that different evol nary determinants may have affected them, nging the Cabecars to diverge more between em than the Bribris. The random effect that results from subdivision, seems to have played a main role in the Cabecars ; low effective population sizes of the emigrant groups could explain this. Another important factor that could account for the dissimilarities observed, particularly in the Bribris, is admixture with the Cabecars and other indian groups (Borucas, Teribes). This has not been documented in the past, but detected by demographic information (Azofeifa 1987, Barrantes & Azofeifa 1983). Admixture with non-Indians was also inferred due to the resullts of certain loci. Despite the exclusion of bearers of non-Indian markers, an absolute depuration of the sample can never be guaranteed.

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RESUMEN

Se analizaron más de 40 loci de las poblaciones amerindias bribri y cabécar de Talamanca, del sureste de Costa Rica . Se encontraron algunas diferencias en la distribución (presencia o ausencia) de las variantes, algunas de ellas privadas, de los loci de la GOT, la PEPA, el RH, la

TF y la TPI, al compararse nuestros resultados con los descritos para las poblaciones bribris y cabécares de la región del Pacífico Sur del país. Se encontró mezcla con no indígenas por intermedio de los loci del ABO, de la ADA y de la G6PD. Los valores de la proporción de loci polimórficos (P) hallados fueron 17.1 en los bribris y 19.4 en los cabécares; las estimaciones de heterocigosis media (H) fueron 0.039 y 0.049 respectivamente. Los valores de Fst obtenidos (0.019 en los bribris y 0.056 en los cabécares) sugieren que eventos aleatorios han sido más importantes en la divergencia de los cabécares entre sí . Tamaños efectivos pequeños de los grupos emigrantes al lado del Pacífico y flujo génico, en el caso de los bribris, pueden ser las causas de estas diferencias.

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