Electrophoretic Variants in Three Amerindian Tribes: The Baniwa, Kanamari, and Central Pano of Western Brazil

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ABSTRACT Data are presented on electrophoretic variants of 25 polypeptides found in the blood serum and erythrocytes, in 812 individuals from three Amerindian tribes, the Pano, the Baniwa, and the Kanamari. Two "private polymorphisms" were encountered, of PEPB in the Pano and CAII in the Baniwa. A single example of a different PEPB variant was encountered in the Baniwa, and two possible examples of an unstable variant of HGB A_2 in the Kanamari. In addition, the well-known A variant of ACP_1, the Duarte variant of GALT, the 2 variant of Hp and the 2 variant of PGM_1 occurred in polymorphic proportions in all three tribes, and the TF^{DChi} variant was present as a polymorphism in the Baniwa. These data have recently been incorporated into a treatment which concludes that the eight electrophoretically-defined "private polymorphisms" thus far encountered in Amerindian tribes can be explained by a mutation pressure of 0.7×10^{-5}/locus/generation on the assumption of neutrality of the phenotypes in question (Neel and Thompson, '78).

Most of the Amerindian tribes in close proximity of the great rivers of the Central Amazon Basin either disappeared shortly after contacts with the Old World were initiated, or, if they survived, underwent extensive admixture with neo-Brazilians. The central position of these tribes in South American geography renders them of especial interest for attempts to reconstruct the movements and biological interrelationships of the tribes of South America. In the summer of 1976 we were able to study representatives of four of these tribes (Central Pano, Kanamari, Baniwa, Ticuna) who, although relatively acculturated, are unusual in that they still have undergone little or no admixture with neo-Brazilians ($< \sim 1\%$, Neel, '78b; Gershowitz and Neel, '78). The primary objectives were (1) a variety of medical studies, (2) typings with respect to 13 polymorphic systems, with the ultimate goal of assigning these groups their place in a nexus of Amerindian relationships, and (3) by electrophoretic techniques, to determine the frequency of genetic variants of a series of polypeptides, in a continuing effort to define the genetic variation present at a representative series of loci in Amerindians.

In connection with this latter objective, one of the salient findings in previous studies of Amerindian tribes, by ourselves and others, has been the frequency of "private genetic polymorphisms," apparently unique alleles which within a single tribe or several adjacent tribes achieve gene frequencies well over 1% on the basis of a sample of some hundreds of persons. Thus far in a systematic application of *electrophoretic* techniques to an average of 25 proteins in ten tribes, we have encountered six examples of this phenomenon: $CRPL^{CAY1}$ (Salzano et al., '72; Tanis et al., '73; Neel,

'78b). $ALB^{YAN\,2}$ (Tanis et al., '74); $ESA_1^{D\,MAC\,1}$ (Neel et al., '77), $PEPA^{WAP\,1}$ (Tanis et al., '73; Neel et al., '77), ALB^{MAKU} (Tanis et al., '73; Neel et al., '77), and $LDH_B^{GUA\,1}$ (Tanis et al., '77). Given the kind of knowledge of the breeding structure and demography which we have developed on the basis of study of one unacculturated tribe, the Yanomama (Neel and Weiss, '75; Neel, '78a), it should on certain assumptions be possible to manipulate data of this type to derive insights into the duration of the tribal genetic isolation and the mutation rates/selective pressures consistent with the findings (Neel and Thompson, '78).

This report is restricted to the results of surveying representatives of the Baniwa, Kanamari, and Pano tribes, a total of 812 persons, with respect to electrophoretic variants of 25 polypeptides. The most noteworthy finding is the demonstration of two more private polymorphisms, one of peptidase B in the Pano and one of carbonic anhydrase II in the Baniwa.

THE TRIBES

Baniwa

At the time of first contact, the Rio Negro was lined with Arawak-speaking tribes from

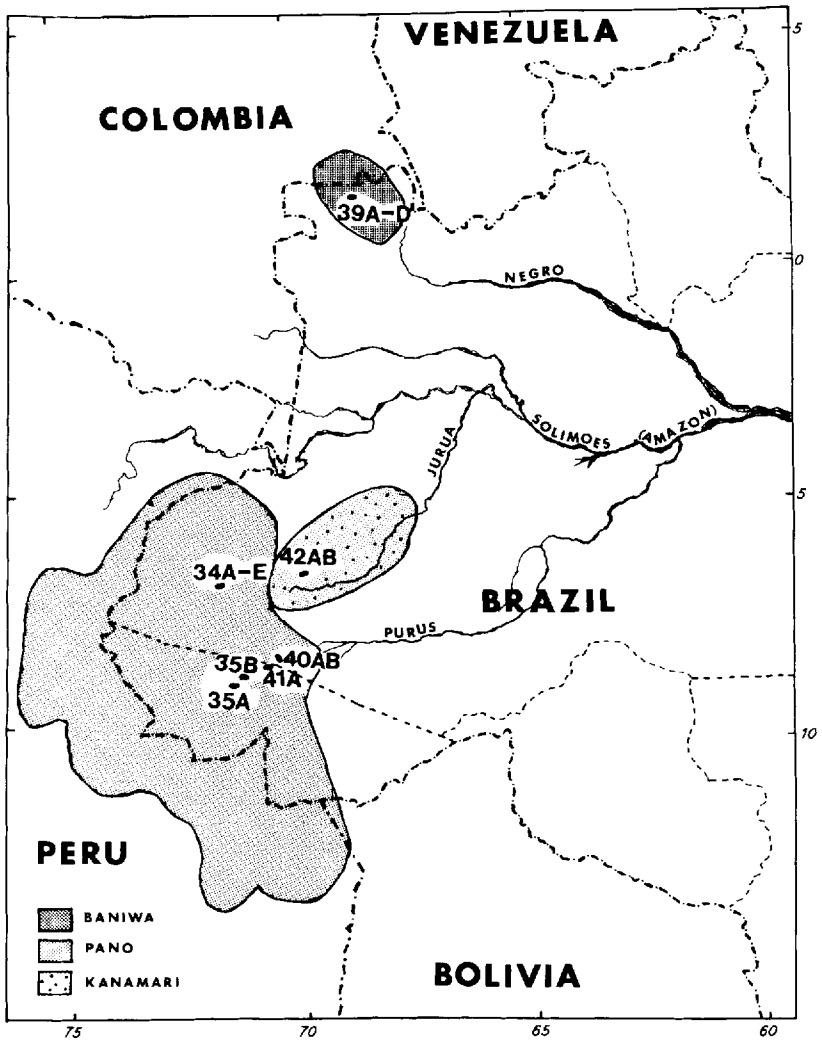

Fig. 1 Map indicating present location of tribes and villages sampled. Further identification in text.

its confluence with the Solimões to form the Amazon, to its headwaters in what is now Colombia. The Baniwa, who inhabit the area drained by the Içana River, a tributary of the Rio Negro in the extreme northwestern corner of Brazil and adjacent Colombia, are one of the very few of these tribes now extant. Classified as "in permanent contact" (but not "integrated") by Gama Malcher in 1964, we would now term them semi-acculturated. They are currently estimated to number some 1,500 persons, distributed among some 16 villages, in the area indicated in figure 1. They are organized into 20 exogamous, patrilineal clans; the preferred marriage is with a paternal cross-cousin. Ethnographic data will be found in Goldman ('48), Galvão ('59), Oliviera and Galvão ('73), and Noble ('62). This tribe was of particular interest to us as a representative of the western neighbors of the Yanomama, among whom a previously mentioned polymorphism of serum albumin had been encountered (Tanis et al., '74): would it have spread to the Baniwa? The present collections were carried out at a small station of the New Tribes Mission on the Upper Içana River, at latitude 1°33'N, longitude 68°44'W (cf. fig. 1). The sample was obtained from representatives from six villages who had gathered at the station as a result of advance word of our measles vaccination program.

Kanamari

In the basins of the Juruá and Purus Rivers in southwestern Amazonas State, Brazil, there are three different populations referred to as Kanamari. They belong to three different linguistic groups. One, speaking Pano, is a subdivision of the Central Pano, whom we consider in the next section. One is a member of the Arawak-speaking tribes of the Upper Purus River. The third group, the object of our study, constitutes an independent tribe, whose language, Katukina, shows no close affiliation with the other languages of the area; Greenberg ('60) classified the language as a member of the Macro-Tucanovan family, the other components of which are Ticuna and Tucano. They are a small tribe, estimated to number about 800 persons living in 19 villages located in the area shown in figure 1, with a long history of contact with neo-Brazilians. Our studies were carried out at a station of the New Tribes Mission, at a location known as Tres Unidos, on the Mamoré Creek, a tributary of the Juruá River, some 25 air miles east of the town of Eirunepé. Approximate coordinates are 6°37'S, 69°32'W (cf. fig. 1). The sample was obtained from representatives of three villages, totaling about 130 persons, who had consolidated at this location following the establishment of the Mission Station, in 1967. The tribe, which has never been intensively studied ethnographically (characterized with a single paragraph in Métraux's ('48) treatment of the tribes of the Juruá-Purus basin), is now relatively acculturated, practicing subsistence agriculture.

Central Pano

These Indians are located in the extreme southwestern portion of Amazonas State and the western half of Acre State, Brazil, and in the adjacent portions of Peru. They are re-

TABLE 1

Data on the sampling of the Central Pano

Pano subdivision	Brazilian place name	Location	Comments	Our designation
Cashinawa	Cana Brava	8°7'S, 70°19'W	New Tribes Station (villages subdivided into Cana Brava and Paredão)	40 A,B
Jaminawa	Near Sete Estrelas	8°17'S, 71°34'W	Village 6 km down Jurúa River from Sete Estrelas	35 B
Marubo	Vida Nova	6°47'S, 72°8'W	New Tribes Station	34 A-E
Pano (Katukina)	Sete Estrelas	8°17'S, 71°34'W	New Tribes Station	35 A
	Morada Nova [1]	8°9'S, 70°21'W	Village 2 km up Embira River from Feijó	41A

[1] Morada Nova is in fact a "mixed" village recently established by Central Pano desiring proximity to the town of Feijó. Of 60 adults interviewed, 34 identified themselves as Katukina (Pano Proper), 10 as Cashinawa, 2 as Jaminawa, 5 as of mixed Pano ancestry, 1 as Kashinawa/neo-Brazilian, and 4 as Neo-Brazilian. None of the latter 5 was sampled.

TABLE 2

Cognate density (percentages) among four groups of the Central Pano

		Group		
		Marubo	Pano	Yaminawa
Group	Pano	91		
	Yaminawa	83	85	
	Kashinawa	87	84	90

ferred to by at least 15 different local names, each loosely considered a separate tribe. The approximate area they occupy is shown in figure 1. We sampled four different groups at five different locations, as shown in table 1. An analysis of cognate density on the basis of our modification of the Swadesh list of 200 items (Swadesh, '55) revealed the situation shown in table 2. This degree of mutual intelligibility is greater than that we encountered among the various subdivisions of the Yanomama (Spielman et al., '74), and is a principal reason why we consider these various groups as all samples from a single tribe. The total number of Pano is about 18,000 (Kensinger, personal communication). The social structure of the various areas is, in general, similar. For instance, the Marubo (34A-E) are organized into nine matrilineal clans named after animals. Marriage is clan exogamous, preferentially with a cross-cousin. Residence is in communal houses containing representatives of two or more clans. Pertinent common features of their culture at time of first contact were slash-and-burn agriculture depending heavily on sweet manioc and maize, the custom of each extended family occupying a single large house, and ritual endocannibalism and cremation of the dead. The principal sources of ethnographic data are Steward and Métraux ('48), Steward and Faron ('59) and Melatti and Melatti ('75). Coincident with the pressures of the Rubber Boom, a group of Cashinahua related to those we examined migrated to Peru, where they were studied by Johnston, Kensinger, and colleagues (cf. esp. Johnston et al., '68, '69).

The Central Pano came into extensive contact with neo-Brazilians in the Seventeenth Century. Today the degree of acculturation of the various subgroups is quite variable. Gama Malcher in 1964 classified most groups as "integrated" but several still only had "sporadic contact." Since then all groups have established permanent contacts with missions or

TABLE 3

Systems in which genetic polymorphisms of widespread occurrence were encountered

	r_p					Tf				ACP				PGM_1				GALT				
	1	1-2	2	Σ	HP^2	0[1]	C	C-D$_{Chi}$	Σ	Tf^C	A	AB	B	Σ	ACP_1^B	1	1-2	2	Σ	PGM_1	1	1+D	D	Σ	GALT[1]
Baniwa	104	183	90	377	0.519	–	365	12	377	0.984	6	43	328	377	0.927	256	109	12	377	0.824	373	3	1	377	0.993
Kanamari	59	37	4	100	0.775	–	100	–	100	1.0	3	25	72	100	0.845	55	32	13	100	0.710	97	2	1	100	0.980
Pano																									
34A-E	47	54	11	112	0.661	–	112	–	112	1.0	2	21	89	112	0.888	53	54	5	112	0.714	106	6	–	112	0.973
35A,41A	27	34	14	75	0.587	12	87	–	87	1.0	1	7	79	87	0.948	72	15	–	87	0.914	87	–	–	87	1.0
35B	19	19	4	42	0.679	6	48	–	48	1.0	–	–	48	48	1.0	48	–	–	48	1.0	48	–	–	48	1.0
40AB	44	36	6	86	0.721	2	88	–	88	1.0	1	5	82	88	0.960	87	1	–	88	0.994	86	2	–	88	0.989
Pano total	137	143	35	315	0.662	20	335	–	335	1.0	4	33	298	335	0.939	260	70	5	335	0.881	327	8	–	335	0.988

[1] No activity.

government posts. Among the groups we studied, the Marubo are still culturally intact and relatively unacculturated but the other groups are now living much as the Brazilian of the interior.

METHODOLOGY

Blood samples were collected in Becton-Dickinson vacutainers containing 2 ml of acid-citrate-dextrose anticoagulant and chilled as soon as possible, usually within 12 hours of collection. The samples were shipped with ice to Ann Arbor where the plasma and washed packed cells were stored at −80°C or in liquid N_2 until typing. Samples were normally processed for storage within seven days of collection.

The following erythrocyte proteins were studied in this laboratory: acid phosphatase-1 (ACP_1), adenosine deaminase (ADA), adenylate kinase-1 (AK), carbonic anhydrase-I (CAI), carbonic anhydrase II (CAII), galactose-1-phosphate uridyltransferase (GALT), hemoglobin A_1 (Hb_α and Hb_β), hemoglobin A_2 (HB_α and HB_δ), isocitrate dehydrogenase (ICD_S) lactate dehydrogenase (LDH_A and LDH_B), malate dehydrogenase (MDH_S), nucleoside phosphorylase (NP), peptidase A (PEPA) peptidase B (PEPB), phosphoglucomutase-1 (PGM_1), phosphoglucomutase-2 (PGM_2), phosphogluconate dehydrogenase (PGD), phosphoglucose isomerase (PHI) and triosephosphate isomerase (TPI). Four serum proteins, albumin (ALB), ceruloplasmin (CP), haptoglobin (HP) and transferrin (TF), were also studied. In addition, esterases (A and D) were examined in the laboratory of Mestriner; the results will be reported elsewhere. All of the electrophoretic methods were as previously described (Tanis et al., '73; Neel et al., '76, '77).

RESULTS

In recent years, with the continuing penetration of neo-Brazilians into these tribal areas, some intermarriages with non-Indians have occurred. Although it was expedient to sample them in the field, the neo-Brazilians contracting these marriages and their offspring have been excluded from the tabulations. After these exclusions, the number of persons examined, each for all 25 of the systems listed above, were as follows: Baniwa, 377; Kanamari, 100; and Pano, 335 (Cashinawa, '88; Jaminawa, 48; Marubo, 112; Pano, 87). A total of 812 persons was examined, resulting in 40,600 locus determinations. Except for the findings noted in table 3 (common polymorphisms) and table 4 (private polymorphisms and rare variants) all individuals were of standard phenotypes. The findings will be described under three headings:

Common polymorphisms

Well known polymorphisms of five loci (*ACP_1, GALT, HP, PGM_1*, and *TF*) were detected in various of the tribes. Phenotype and gene frequencies for these polymorphisms are presented in table 3. The following points are of interest: (1) The Pano villages exhibited the range of intratribal variation with respect to the *ACP_1, GALT, HP,* and *PGM_1* polymorphisms which is characteristic of Amerindians, although the Jaminawa (35 B) are unusual in lacking three of these four polymorphisms. (2) The tribal values with respect to these four polymorphisms were within the range characterizing Amerindians, with the exception of the Duarte allele of GALT, which in all three tribes was less common than has been the case in most tribes studied to date (Neel et al., '77; Tanis et al., '77). (3) A TF variant with mobility similar to the D_{Chi} variant when examined by either starch or polyacrylamide gel electrophoresis (fig. 2a) was encountered in one of the three tribes, the Baniwa, with an allelic frequency of 0.016.

TABLE 4

Systems in which only private variants were identified

Tribe/protein		CA II	HGBδ	PEP B
		2BAN1		
	Variants	37BAN1/+	0	1BAN1/+
Baniwa	Total typed	377	377	377
	Variants	0	2KAN1/+(?)	0
Kanamari	Total typed	100	100	100
	Variants	1CAII2/+	0	16PAN1/+
Pano	Total typed	335	335	335

The D_{Chi} variant has been reported in several Amerindian tribes (Arends and Gallango, '64; Tanis et al., '77).

Private polymorphisms

Previously undescribed variants of CAII and PEPB occurred in polymorphic frequency in the Baniwa and Pano tribes, respectively. The CAII variant in the Baniwa was identified electrophoretically by a slightly slower migration than the normal CAII enzyme (CAII 1). It also stained less intensely than CAII 1 when the fluorescein diacetate substrate was used (fig. 2c). The mobility and staining intensity were also different from the CAII 2 variant which most commonly occurs in Negroes (fig. 2c). Although the variant enzyme had different staining characteristics than normally observed for CA it was inhibited by acetazolamide (Diamox). This inhibitor is specific for CA and has no effect on esterase staining (Tashian and Carter, '76). Thus the possibility that the activity was due to a new esterase variant was excluded. The reduced staining intensity of the variant band relative to the normal band was still observed after the hemolysate was extracted with $CHCl_3$-MEOH to remove the hemoglobin (procedure of Tashian and Carter, '76). The CA in the $CHCl_3$-MEOH extracted sample can be localized following starch gel electrophoresis with the protein stain, nigrosin. The intensities of the two CAII bands (normal and variant) were similar after nigrosin staining, indicating similar amounts of protein (fig. 2d). This would indicate that the specific activity of the CAII BAN-1 variant is less than the specific activity of either CAII 1 or CAII 2. Additional characterization of the variant enzyme continues.

The variant was detected in 39 of the 377 Baniwa; two of the 39 exhibited no CAII activity in the normal position and are presumed homozygotes. Thus the frequency of the $CAII^{BAN\text{-}1}$ allele is 0.054. The pedigree of an illustrative family is shown in figure 3b.

As noted in the description of the tribes, in view of the proximity of the Baniwa to the Yanomama (cf. figs. 1 and 2 in Neel et al., '72), we were interested in the question of whether the $ALB^{YAN\text{-}2}$ polymorphism would be encountered in the Baniwa. It was not. The discovery of the CAII BAN-1 polymorphism in the Baniwa obviously created a new opportunity to seek evidence for genetic exchange between these two tribes. Accordingly, some 194 individuals from four Yanomama villages (11 G, 11 HI, 11 YZ and 15 QR—see fig. 2, Tanis et al., '74 for village locations) located on the southwest edge of the Yanomama territory were screened for the presence of the CAII BAN-1 variant. No affected individuals were identified. The D_{Chi} variant of Tf was also not detected in the Yanomama. Thus the evidence continues to accumulate for a relative paucity of intertribal migration.

The second variant in polymorphic proportions, in the Pano, was an electrophoretic variant of PEPB with a mobility slightly slower than the previously reported PEPB 2. This behavior was identical in the tris-maleate buffer system of Lewis and Harris ('67) (fig. 2b) and the tris-phosphate system of Harris and Hopkinson ('76). The substrate specificity of the variant enzyme was identical to the normal B isoenzyme, i.e., the normal and variant enzyme stained with equal intensity when Leu-Gly-Gly, Phe-Leu, Phe-Tyr and Leu-Leu-Leu were utilized as substrate. No bands migrating with the electrophoretic mobility of normal or variant PEPB were noted when substrates specific for PEPA, PEPC or PEPD were utilized. The electrophoretic pattern was unaffected when the sample was incubated in the presence of 5 mM dithiothreitol. No variation was noted in the electrophoretic mobility of PEPA, PEPC or PEPD in the affected individuals. An illustrative pedigree is presented in figure 3a. The pattern is of codominant inheritance of an allele we designate $PEPB^{2\,PAN\text{-}1}$. The frequency of the $PEPB^{2\,PAN\text{-}1}$ allele in the Pano was 0.023 although the distribution among the four groups was not uniform. The variant was not detected in the Cashinawa (40A,B) or in the Pano (Katukina) located at Morada Nova (41A). Only 2 of 48 individuals from the Jaminawa (35B) were affected; an allele frequency of 0.021. The allele frequency was 0.045 in the Marubo (34A-E) and 0.048 in the Sete Estrelas Pano (35A).

Rare variants

Three rare variants were encountered, involving three different systems. The findings are given in table 4; a brief characterization of each follows.

HGB

A suspected $HGBA_2$ variant was detected in the Kanamari. On the original starch gel, the staining intensity of the variant band was equal to the staining intensity of the band in

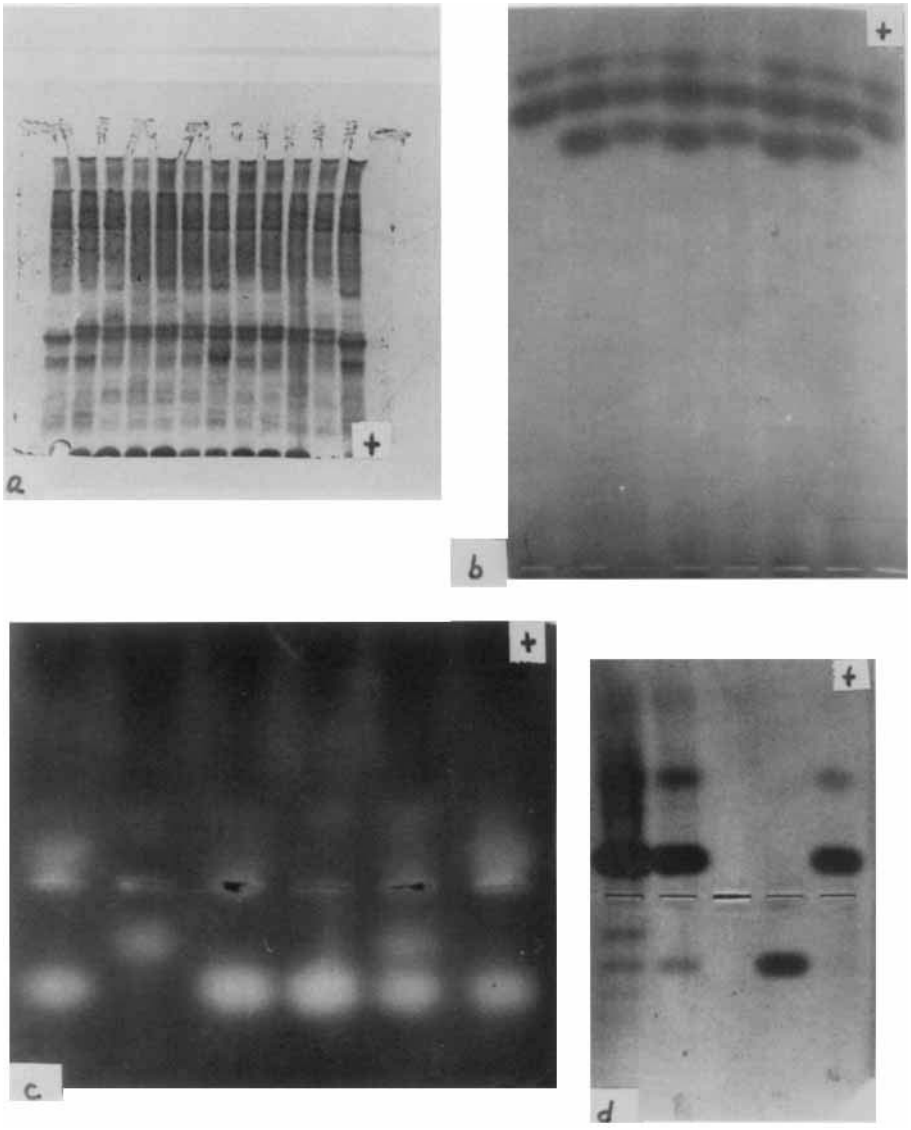

Fig. 2 Electrophoretic pattern of several variants.

a Transferrin: Wells 1 and 8 type C, wells 2 and 7 CD_{Chi} from Piaroa, wells 3 and 8 CD_{Chi} from Guaymi, wells 4 and 10 CD_{Chi} standard, wells 5, 9 and 11 samples from 3 different Baniwa individuals identified as CD_{Chi}, well 6 CD_{Gua}.

b Peptidase B: Wells 1 and 8 type 1, wells 2, 4 and 6 type 1-PAN-1, wells 3 and 7 type 1-2, well 5 type 1-BAN-1.

c Carbonic Anhydrase II — Activity stain: Wells 1 and 6 type 1-2, well 2 type BAN-1, wells 3 and 4 type 1, well 5 type 1-BAN-1.

d Carbonic Anhydrase — protein stain: Well 1 CAII type 1-BAN-1, well 2 type 1, well 3 purified CAII type 1, well 4 purified CAI type 1. Samples in wells 1 and 2 were not purified, thus CAI and some residual hemoglobin are also present and stained.

the A_2 position; this latter in turn was approximately one half of normal. No alteration in banding pattern or staining intensity was observed in the HbA_1 region, from which we infer that this is a δ-chain variant. This observation could not be repeated. On cellulose acetate electrophoresis, freshly prepared hemolysates from packed cells stored in N_2 reproducibly exhibited in addition to the normal $HGBA_2$ band, a *pair* of abnormal hemoglobin bands cathodal to the normal position of $HGBA_2$; as the hemolysate ages these disappear and a precipitate is seen at the origin. One of the three children of the propositus regularly exhibited similar findings with cellulose acetate electrophoresis, but no abnormality has been seen with starch gel electrophoresis. The presence of an unstable variant of $HGBA_2$ is suspected but clearly unproved. Unfortunately, circumstances preclude obtaining the confirmation sample that a finding such as this requires.

PEPB

A PEPB variant was detected in a single individual in the Baniwa (fig. 2d). The variant had an electrophoretic mobility identical in both the tris maleate system (Lewis and Harris, '67) and tris/phosphate system (Harris and Hopkinson, '76) with a variant seen in this laboratory in Caucasian populations, which variant we assume to be the PEPB 2 variant described by Lewis and Harris ('67). Because the ABO and Gm genetic systems reveal no evidence of non-Indian admixture for the Baniwa (Gershowitz, personal communication), this variant is not felt to have been introduced and the allele has been designated *PEPB*$^{2\,BAN\text{-}1}$.

CAII

A CAII variant which on direct comparison exhibited an electrophoretic mobility identical with the CAII 2 variant which occurs in polymorphic frequencies in Negroes was detected in one individual in the Panoan Jaminawa. The ABO system reveals no evidence of non-Indian admixture with the tribe, but the Gm groups suggest a 0.003 Negro component (Gershowitz and Neel, '78). Accordingly, this was not designated as a new variant.

DISCUSSION

The most noteworthy finding in this report is the demonstration of two more electrophoretic "private polymorphisms" in Amerindian tribes, involving PEPB in the Pano and CAII in the Baniwa. This brings to eight the number of such polymorphisms encountered in a study of 13 tribes with respect to an average of 25 proteins (N.B.—the Kanamari were not included in the summary of Neel, '78b). In addition, we encountered a single example of a variant PEPB in the Baniwa, and two possible examples of an unstable variant of HGB A_2 in the Kanamari; in view of the lack of evidence of non-Indian admixture for these two tribes, we view the two variants as autochthonous.

The occurrence of this number of private polymorphisms in Amerindian tribes natural-

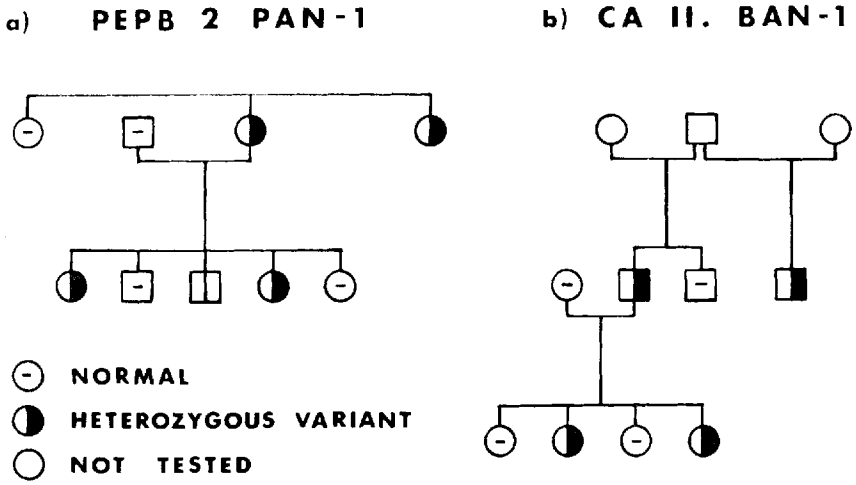

Fig. 3 Illustrative pedigrees of variants identified during study. a PEPB PAN-1. b CAII BAN-1.

ly leads to speculation concerning their maintenance by selective forces. Elsewhere we have demonstrated that in a situation where there is a marked degree of tribal isolation, with the passage of time a high proportion of the neutral variants which are not lost by chance may be expected to assume polymorphic proportions (Thompson and Neel, '78). In the situation as currently defined for South American Indians, the findings are consistent with neutrality of the mutant-bearing phenotypes and a mutation rate for electrophoretic variants of 0.7×10^{-5}/locus/generation (Neel and Thompson, '78). This estimate of the mutation rate may be biased downwards by failure to detect all the private polymorphisms in the tribes under consideration. For instance, despite the fact that we have sampled the Pano in four different locations, the Western Pano are untouched, and our sample is only 1.9% of the estimated 18,000 Pano. Be that as it may, the findings to date can be explained by mutation pressure consistent with current estimates of mutation rates in man, without the necessity to postulate the action of positive selection. Should the variants on the average be to some extent deleterious, then a higher mutation rate is necessary to account for the existence of these polymorphisms.

The second noteworthy finding of this paper is its supplementation of the previous evidence, based on the restricted distribution of the private polymorphisms, for a relative lack of gene flow between the Indian tribes of the Amazon and Orinoco basins. The available evidence suggests that in pre-Columbian times, the Yanomama and Baniwa appear to have been separated by the Arawak-speaking Bare, now reduced to a few remnant villages on or near the Rio Negro (Loukotka, '68). This tribe has yet to be studied for variants of the systems surveyed in this paper. Pending such studies, which would greatly improve the ability to make detailed statements, we point out that intertribal movements in that area have not been sufficient to introduce the $CA\,II^{BAN\text{-}1}$ or the TF^{DChi} variants of the Baniwa into the Yanomama, nor the $ALB^{YAN\text{-}2}$ variant of the Yanomama into the Baniwa. Thus the case is strengthened for regarding the tribe as the basic unit of Amerindian populations.

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