*INTRATRIBAL GENETIC DIFFERENTIATION AMONG THE YANOMAMA INDIANS OF SOUTHERN VENEZUELA**

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Two interrelated problems currently dominate the field of human population genetics, namely, what is responsible for the maintenance of the many genetic polymorphisms being uncovered in human populations, and what is the significance of the rather wide differences being observed between ethnic groups in the frequency of specific genes in specific polymorphic systems. Although both of these problems have been on the genetic horizon for some years, and subject to considerable inquiry, the mounting tempo of discovery of new polymorphisms has now thrown them into a position of stark prominence.

Recent studies on 10 villages of the Yanomama (Waica) Indians appear to shed some additional light on the second of these two problems. These Indians are a very primitive and relatively unacculturated group found in southern Venezuela and adjacent portions of Brazil, occupying, roughly, the area between the equator and latitude 5°N and longitudes 63° and 66°W (descriptions in Zerries[1, 2] and Chagnon[3]). Their some 100–125 widely scattered villages range in size from about 40 to 250 inhabitants, the median size being about 75–80 people. The total tribal population is probably of the order of 10,000, modest by African and Melanesian standards, but quite large for a group of this cultural level in tropical South America. Their material culture inventory places them, roughly, on a par with such better-known groups as Copper Eskimos, Andamanese, and Chippewa Indians, all of whom are only slightly more advanced in culture content than the Bushmen of Africa, the Yahgan of Tierra del Fuego, and the Walbiri Aborigines of Australia (see Carneiro and Tobias[4]). Economically, however, the Yanomama differ from these hunting-collecting peoples in that they rely heavily on cultivated foods, particularly plantains, bananas, and several root crops. This economic pattern constitutes one of the puzzling features of their otherwise very primitive culture. Zerries[1] asserts that the tribe is currently in transition from a purely hunting and gathering economy to a purely horticultural one. Other evidence, however, suggests that they have relied heavily on cultivated food for at least four to five generations, and that they may in fact have cultivated some portion of their food for a much longer period.

Although the region in which these Indians live has been penetrated by a number of expeditions in the past 140 years, the first sustained contact with any Yanomama group was made in 1950 by James P. Barker of the New Tribes Mission, who moved into a village on the upper Orinoco River. Since 1957 a total of about a dozen villages in both Brazil and Venezuela have been permanently contacted by several missionary groups. The overwhelming number of villages have had no direct contact with outsiders yet and will probably remain isolated for a few years to come due to their location in the almost inaccessible headwaters of small rivers; these can only be reached by walking to them through dense jungle.

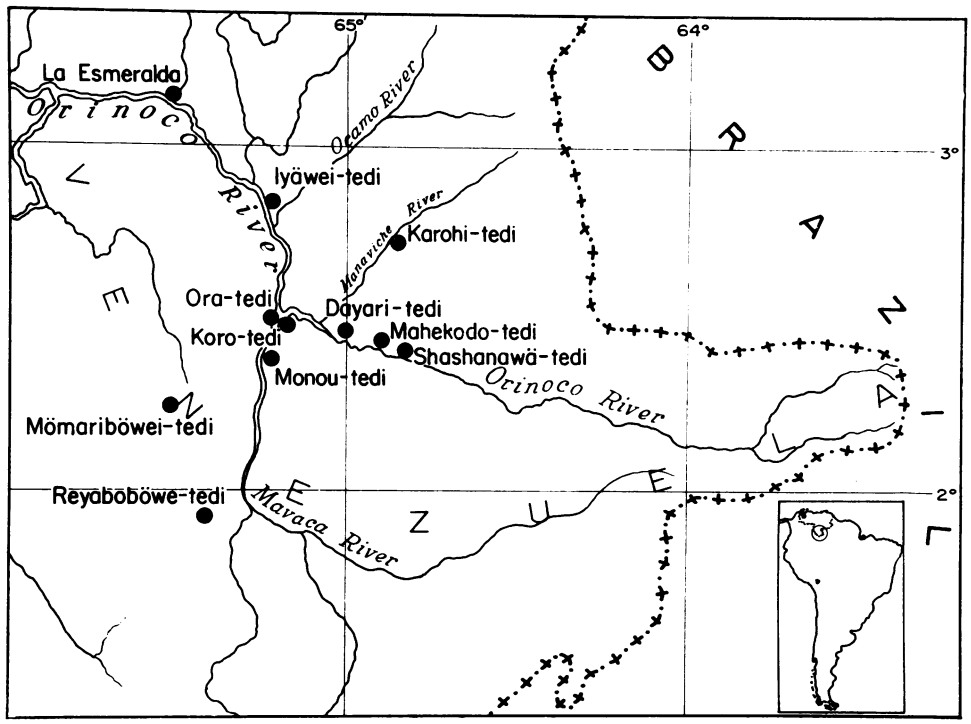

FIG. 1.—The location of the 10 Yanomama villages from which blood specimens were obtained.

The location of the villages studied is shown in Figure 1. As best as it can be determined, these villages are related to one another as follows. The villages of Ora-tedi (A), Koro-tedi (B), and Monou-tedi (C) are derived from what was last a single village about 1954. The villages of Mömariböwei-tedi (D) and Reyabobö-we-tedi (H) were last a single village in 1960. The villages of Mahekodo-tedi (E), Shashanawä-tedi (F), and Dayari-tedi (I) were last a single village about 1956; Karohi-tedi (G) apparently separated some years earlier from the group that gave rise to the preceding three villages. Finally, Iyäwei-tedi (J) is thought to have had a common origin with the A-B-C complex some four generations previously. At the time of our study, Iyäwei-tedi had an influx of visitors from a neighboring village (Toroba-tedi), a group living some 30 miles up the Ocamo River. We have included the results on the samples from this village with the Iyäwei-tedi, but are not yet sure of the relations of the two villages. The fissioning of villages described above corresponds to a pattern encountered in previous studies of the Xavante Indians of the Brazilian Mato Grosso[5-7] but is accentuated in the Yanomama, perhaps because they appear to be an expanding population.[3]

As one aspect of a multidisciplinary study, blood specimens were obtained from 568 members of these 10 villages in the course of field work in January–February, 1966. The number of inhabitants of each village and the number of specimens classified for certain systems are shown in Table 1. All blood specimens were typed in duplicate at the University of Michigan and the Instituto Venezolano de Investigaciones Científicas with respect to the following eight systems: ABO, MNSs,

TABLE

GENE FREQUENCIES OBSERVED

Genetic system	No. tested	Allele in system	A(85)	B(51)
			(79)	(43)
Rh*	567	CDe (R^1)	0.80	0.86
		CDE (R^z)	0.09	0.05
		cDE (R^2)	0.11	0.09
		cDe R°	0.00	0.00
		cDe, cde } R° or r	0.00	0.00
			(79)	(43)
MNSs	567	*MS*	0.04	0.06
		Ms	0.60	0.49
		NS	0.08	0.00
		Ns	0.28	0.45
			(78)	(43)
Duffy	485	Fy^a	0.63	0.68
			(79)	(43)
P	565	*P*	0.63	0.60
			(78)	(43)
Kidd	565	Jk^a	0.43	0.39
			(22)	(19)
Erythrocyte phosphoglucomutase 1	299	PGM^1	0.84	0.92
			(53)	(32)
Erythrocyte acid phosphatase	324	B	1.0	1.0
			(53)	(18)
6-Phosphogluconic dehydrogenase	283	A	1.0	1.0
			(76)	(43)
Group component (*Gc*)	555	Gc^1	0.92	0.97
			(71)	(43)
(*Lp*)	381	Lp^a	0.0	0.0
			(69)	(29)
(*Ag*)	395	Ag^a	0.01	0.09
			(55)	(39)
Haptoglobins	422	Hp^1	0.92	0.96
			(65)	(36)
Transferrins	429	Tf^c	1.00	1.00
			(70)	(37)
ABH-secretor	274	*Se*	0.88	1.00
			(70)	(37)
Lewis-secretor	274	*Le*	0.68	0.77

Each village is designated by a letter; a brief description of the villages is given in the text. The estimated number in the village is given in the parentheses after the village designation; the number actually examined with respect to any specific systems is indicated separately for each system.

* There were five specimens which were negative to five anti-c sera but which also reacted negatively or very weakly to anti-C serum from several sources (Ortho, Spectra, BGL, Dade, and CBDS). These

Duffy, P, Kidd, Lutheran, Diego, and Kell. In addition, there were single determinations of seven serum protein traits (haptoglobins, group specific component (*Gc*), transferrins, ceruloplasmin, albumin, and the lipoprotein groups *Lp* and *Ag*), and, for smaller numbers of specimens, of seven erythrocyte enzyme groups (glucose-6-phosphate dehydrogenase, 6-phosphogluconic dehydrogenase, acid phosphatase, phosphoglucomutase$_2$, carbonic anhydrase, adenylate kinase, A-esterases). Salivas were examined for secretion of both the H and Lewis substances (*Se* and *Le* traits). Hemoglobin was subjected to electrophoresis. The methods employed in the participating laboratories were those currently standard and have been listed and/or described elsewhere.[5, 8–11] Of the sera, 22.6 per cent were ahaptoglobinemic, quite possibly due to endemic *Pl. falciparum* and *vivax* malaria, and so could not be typed for this trait. All specimens were blood type O, Kell negative, and Lutheran a-negative, b-positive; there is thus no evidence of non-Indian admixture. No specimen positive for the Diego antigen was encountered, suggesting little admix-

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IN 10 YANOMAMA VILLAGES

Village							
C(66)	D(85)	E(93)	F(62)	G(53)	H(77)	I(73)	J(145)
(59)	(76)	(60)	(34)	(34)	(52)	(50)	(80)
0.77	0.83	0.76	0.59	0.75	0.77	0.85	0.79
0.17	0.16	0.12	0.24	0.21	0.23	0.14	0.11
0.06	0.01	0.11	0.03	0.00	0.00	0.00	0.11
0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
0.00	0.00	0.02	0.12	0.04	0.00	0.01	0.00
(59)	(76)	(60)	(34)	(34)	(52)	(50)	(80)
0.00	0.02	0.05	0.24	0.04	0.09	0.05	0.21
0.63	0.77	0.50	0.47	0.58	0.65	0.67	0.64
0.10	0.07	0.02	0.00	0.03	0.11	0.10	0.05
0.27	0.14	0.43	0.29	0.35	0.15	0.18	0.10
(59)	(76)	(59)	(34)	(34)	(52)	(50)	
0.77	0.58	0.67	0.74	0.62	0.60	0.60	
(59)	(76)	(59)	(33)	(34)	(52)	(50)	(80)
0.53	0.34	0.51	0.26	0.49	0.38	0.53	0.70
(59)	(76)	(59)	(34)	(34)	(52)	(50)	(80)
0.57	0.84	0.40	0.36	0.43	0.80	0.38	0.75
(26)	(18)	(53)†	(21)	(24)	(40)	(38)	(77)
0.96	1.00	0.99	0.95	0.92	0.91	0.89	0.95
(28)	(34)	(30)	(15)	(17)	(21)	(26)	(68)
1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.93
(30)	(28)	(30)	(17)	(17)	(26)	(26)	(39)
1.0	1.0	1.0	1.0	0.97	1.0	1.0	1.0
(55)	(76)	(59)	(34)	(34)	(52)	(50)	(76)
0.97	0.95	0.93	0.97	0.97	0.74	0.95	0.88
(46)	(55)	(39)	(24)	(27)	(51)	(50)	(68)
0.0	0.18	0.0	0.02	0.04	0.05	0.0	0.10
(36)	(65)	(31)	(24)	(28)	(39)	(15)	(59)
0.01	0.12	0.05	0.11	0.07	0.22	0.0	0.04
(36)	(32)	(48)	(29)	(24)	(45)	(41)	(73)
0.82	0.73	0.95	0.83	0.94	0.68	0.90	0.73
(46)	(72)	(29)	(24)	(28)	(37)	(26)	(66)
1.00	1.00	0.98‡	1.00	1.00	1.00	0.98‡	1.00
(47)	(71)				(49)		
1.00	1.00	—	—	—	0.86	—	—
(47)	(71)				(49)		
0.40	0.56	—	—	—	0.53	—	—

specimens were all D-positive, E-positive, e-negative. Pending confirmation and extension of this observation, we have scored them as R_1R_1 but recognize that they may represent a new Rh phenotype.

† Five specimens in village E exhibited an abnormal phosphoglucomutase band in the presence of normal patterns for phosphoglucomutase 1 and 2.

‡ In both villages E and I, a single specimen was found to have a slowly migrating fraction which, however, migrated more rapidly than *Tf* D_{chi}.

ture in this region between this tribe and some of the surrounding tribes with relatively high frequencies of the Diego antigen (distribution reviewed in Layrisse and Wilbert[12]). There was uniformity with respect to the following systems: erythrocyte glucose-6-phosphate dehydrogenase (all type B), phosphoglucomutase$_2$ (all type 1), adenylate kinase (all type 1), carbonic anhydrase and A-esterases (normal patterns), serum ceruloplasmin (all normal), albumin (all normal), and hemoglobin (all type A).

The variation in the other systems, expressed in terms of gene frequencies obtained in the usual manner, is also shown in Table 1. A later publication will present detailed data on phenotype frequencies and the nature of the alleles in each system (other than those indicated in the table). We have previously pointed out with respect to the Xavante Indians of the Brazilian Mato Grosso, a population of this same type, that although villages fail to meet the conditions for a Hardy-Weinberg equilibrium distribution of gene frequencies, nevertheless there is, for

"gene-counting" systems (*C-c* and *E-e* of the Rh system, *M-N* and *S-s* of the *MNSs* system, *Hp*-1 and *Hp*-2 of the *Hp* system, and *Gc*-1 and *Gc*-2 of the *Gc* system), a satisfactory approximation to Hardy-Weinberg genotypic proportions.[5, 8] This is also true for the Yanomama. Accordingly, we have felt justified in employing procedures that assume Hardy-Weinberg equilibrium in estimating gene frequencies.

It is apparent that there are some very striking differences between villages. Among these are the following: With respect to the erythrocytic antigens, all systems except the Duffy exhibit wide variations. Thus, the R^1 allele varies in frequency from 0.59 to 0.86, and the R^2 from 0.00 to 0.11 in frequency. R° (and/or r) is rare or missing in all villages. In the *MNSs* system, the *MS* gene varies from 0.00 to 0.24, and *Ns* from 0.10 to 0.45. The Fy^a allele is relatively stable, but the *P* allele varies from 0.26 to 0.70 and the Jk^a allele from 0.36 to 0.84.

With respect to the serum proteins and erythrocyte enzymes, for four systems (erythrocyte acid phosphatase, 6-phosphogluconic dehydrogenase, the transferrins, and *Lp* groups), only one allele was present in most of the ten villages, with one to five villages showing the presence of the second allele. With respect to the remaining systems, the PGM^1 allele ranged from 0.84 to 1.00 (and in one village five individuals showed a new *PGM* phenotype), the Gc^1 allele ranged from 0.74 to 0.97, the Ag^a from 0.01 to 0.22, and the Hp^1 from 0.68 to 0.96. Although on inspection there are some rather interesting similarities between the more closely related villages, the type of "cluster analysis" which permits an unbiased statement has been reserved for a later publication. The statistical tests which are customarily applied to the significance of differences between groups are here invalid. Thus, if we consider the individual village as the "universe" of interest, the observations are more akin to an enumerative than a sampling procedure; specimens were obtained from 568 of an estimated population of 790 for the ten villages combined (71.9%). Furthermore, many of the villages can be dissected into four or five extended lineages. Accordingly, because of the biological relationships between villagers, the individuals included in the sample are not "genetically unrelated events." In circumstances such as this it has often been customary to work with "apparently unrelated persons," but pedigree data are so inadequate at this cultural level that this approach begs the issue. We will content ourselves with simply directing attention to some of the more striking findings, without applying statistical tests. It should be emphasized at this juncture that in the present context we are not especially interested in whether villages differ "significantly" in gene frequencies, but rather in what, at any instant in time, is the genetic structure which a tribe presents to the action of evolutionary forces.

Blood specimens have been obtained from the Yanomama on one previous occasion.[13] These specimens, 142 in number, were drawn in six villages, four of them corresponding to vi lages included in this sample. Because of the tendency of the Yanomama to use assumed names, it is impossible to be certain of the precise amount of overlap between the present and the preceding sample. There is in general good agreement between the mean gene frequencies of the previous sample and those to be obtained by pooling the present results; the numbers for individual villages in the previous study are too small for a meaningful comparison. The agreement between the results of the two studies (despite wide village differences)

indicates the wisdom of sampling multiple villages in this type of investigation. Conversely, if only two or three villages had been sampled in the present study, it is obvious that the estimate of tribal gene frequencies could be highly colored by the particular villages selected for study.

Discussion.—The possible significance of these findings to the question of the meaning of genetic differences between larger ethnic groups lies in what might be termed the population dynamics of the American Indian. Elsewhere, on the basis of detailed studies of another relatively unacculturated group, the Xavante Indians of the Brazilian Mato Grosso, we have developed what we term a "fission-fusion" model of an Indian population.[5, 7, 14] Periodically, as tension accumulates within the small "villages" which constitute the primary organizational unit of tribal populations with hunting–gathering–simple agriculture economies, there occur "fissions," in consequence of which a fragment of perhaps 40–60 persons splits off from a given village. This fragment has been observed in whole or part either (1) to form a new village, (2) to join another village, or (3) to rejoin the original village after a suitable "cooling-off" period. Presumably, if it travels far enough away from the sphere of influence of the original tribe, it may also become the nucleus for a new tribe. It must be emphasized that inasmuch as the actual origin of a new tribe has never been properly documented, and probably now never will be, this is conjecture on our part. It may be that equally often in the past a group of two or three related villages allied because of external pressures has either wandered away from the main body of the tribe or has been split off by warfare and has come to form the nucleus of a new tribe. Furthermore, we are not suggesting that this "new" tribe matures in complete isolation—there are undoubtedly continuing contacts of various types. But we do insist that this is the most plausible and important first step in the process.

Among the Xavante, these "fission" fragments were found to be very nonrandom samples of the village gene pool, consisting to a large extent of kinsmen and their wives;[5, 6] in a polygynous society, a man's several wives may be sisters or other relatives. The Yanomama have been observed to have essentially the same fission-fusion structure as the Xavante;[3] a more detailed description is in preparation. Thus, the group of 40–60 persons who split off to form a new village would represent less than half—perhaps only a quarter—that many independent genomes. With so small a genetic sample, a new village may, because of the lineal (kinship) organizational principle, differ markedly in its genetic composition from the parent village. We term this the "lineal effect." It may be regarded as a type of "founder effect," but presents aspects which have not been included in most discussions of the latter.

A possible supplementary interpretation of the present findings would be that the Yanomama result from the relatively recent coalition of several tribes. There is no evidence in favor of this suggestion. Moreover, the variation with which we are confronted cannot readily be visualized in terms of discrete tribal components.

Although there have been previous findings of genetic diversification within Indian tribes (reviewed in Neel and Salzano[7]), in no instance has it been as great as in this case. However, the other groups in which this observation has been made have either been reservation populations, or if not on reservations, have almost always had their freedom of movement curtailed in other ways. It is apparent that

the Yanomama are the best approximation to what one might expect in an expanding Indian tribe in pre-Colombian times thus far studied in this depth.

The archeological record suggests that once the ancestor of the Indian entered the Americas, his spread throughout the continent was relatively rapid, occurring in perhaps no more than 10,000 years. If population units propagated as observed in the Xavante and Yanomama Indians, and if the degree of internal differentiation in the very first "tribes" approaches that of the Yanomama today, the possible role of socially structured stochastic elements (i.e., the lineal effect) in genetic diversification is obvious.

More specifically, the suggestion which stems from these observations is that among the American Indian, gene frequencies were apt to be very different from those of the parent tribe at the time the initial steps toward a new tribe were taken, with subsequent migration between tribes and normalizing selection tending to restore the original frequencies (if these were at equilibrium values) at the same time that genetic drift was operating as a dispersive force. These initial differences stemmed in part from the fact that a relatively small sample (of an already small sample) was involved, but, to an extent not previously adequately emphasized, also from the social structure of primitive man. This model is rather different from several alternatives, such as the possibility that a new tribe was based on a random sampling of some hypothetical gene pool in a reasonable approximation to equilibrium, after which drift contended with migration and selection in determining the tribal gene frequencies. The demonstration may have a significance that extends beyond the explanation of genetic differences between Indian tribes when it is recalled that early human populations were few in number and may have dispersed over large areas in a relatively brief period.

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