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The Genetic Structure of a Tribal Population, the Yanomama Indians. XI. Gene Frequencies for 10 Blood Groups and the ABH-Le Secretor Traits in the Yanomama and Their Neighbors; The Uniqueness of the Tribe

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Thus far in the current series of papers documenting the results of our studies of the Yanomama, we have dealt primarily with microdifferentiation within the Yanomama, as expressed in terms of genetic markers, anthropometrics, or dermatoglyphics. However, the point has also been made that in comparison with 11 other tribes of Central and South America, the Yanomama (with the Guaymi) tend to be quite distinct genetically [1]. This fact, together with a number of cultural peculiarities, suggests a considerable period of relative isolation from other Indian tribes of Central and South America [2, 3]. Our interest in establishing this viewpoint is motivated by the conviction that if this is in fact the case, then the Yanomama provide unusual material for a variety of tests of genetic hypotheses.

In this paper we extend the earlier comparison of the Yanomama with other tribes. We first present the results of typings for seven polymorphic blood group systems (MNS, P, Rh, Duffy, Kidd, Diego, Lewis) and the H and Le secretor systems of saliva on 1,541 Indians from five "neighboring" tribes of Venezuela and northern Brazil (Yanomama, Makiritare, Macushi, Piaroa, and Wapishana). We also present data on the results of resampling four villages, at intervals of 1–3 years, which afford some insight into the reproducibility of gene frequency estimates for individual villages. These data will be used to derive empirical estimates of error for the genetic distance statistics used in previous studies.

The latter part of the paper is concerned with the genetic relationship of the Yanomama to 19 other South American tribes. Five of the 20 tribes will be characterized by the data in this paper and the preceding publication [4], while the data for the remaining 15 tribes has been abstracted from the literature. Four genetic statistics designed to explore the relationships and comparability of the Yanomama to other South American tribal populations will be employed. These are of two

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types. On the one hand, we are concerned with genetic relationship as defined either in terms of genetic distance or genetic identity. For these two analyses we will use the measures of Cavalli-Sforza and Edwards [5] and Nei [6], respectively, and derive an overall perspective of the total intertribal genetic relationships through the construction of dendrograms. We will also investigate the relationships between the geographical locations of the tribes and the deviations of the tribes from a multivariate genetic mean for all tribes, thus deriving contours of genetic relationship. On the other hand, we are concerned with the evolutionary potential of the Yanomama compared to other tribal populations. This we shall investigate by measures of genetic diversity, using both indices of "homozygosity" [6] and "information" [7] for the purpose. The combined analyses will serve to characterize the Yanomama both with respect to other tribal populations and to their evolutionary potential.

Materials and Methods

Populations

Blood samples were obtained from the inhabitants of 21 Yanomama villages, eight Makiritare villages, two Macushi villages, one Piaroa, and one Wapishana village, all not previously reported. The Yanomama constitute the largest tribe of the area, the others being neighbors to their northwest (Piaroa and Makiritare) and to their northeast (Macushi and Wapishana). The location of the villages and a description of their relationships can be found in a preceding paper in this series [4]. Layrisse and Wilbert [8] have summarized the results of previous typings of members of all five of these tribes; we will not combine these prior data with the present because of the problem of overlapping data sets.

Methods

The methods used were as previously described [9]. Most typings were performed on fresh specimens, in Caracas and in Ann Arbor. However, blood samples received in Ann Arbor in the summer of 1972 were immediately frozen in liquid nitrogen and not tested until October. Tests on the following villages were performed on the frozen-thawed specimens and done only once: 15O, 15QR, 26C and 27A.

All samples were typed in duplicate (except for those described above) with the following reagents: anti-A, B (group O), M, N, S, s, P_1, C, c, D, E, e, K, Fy^a, Jk^a, Le^a, Le^b, and Di^a. In addition, there were single typings on selected samples in Ann Arbor with the following reagents: anti-U, Vw, Hu, Mu + Ht, Mg, M^v, P + $P_1(Tj^a)$, f, k, Kp^a, Kp^b, Js^a, Fy^b, Di^b, and Wr^a. The anti-C reagent used was tested against selected R_zR_z (CCDEE) and R_zR_2 (CcDEE) blood samples to ensure the detection of C antigen and to obviate the mistyping of R_z phenotypes, a potential source of confusion in the typing of Indian populations [10]. A total of 300 saliva samples were tested for the ABH-Le secretor traits.

Gene frequencies have been calculated by a maximum-likelihood program (MAXLIK) for the IBM 1130, which assumes Hardy-Weinberg equilibrium. Results for the Rh system have been obtained assuming only four genes to be present, as discussed in Gershowitz et al. [11].

Results

In our previous publication of Yanomama gene frequency data, all specimens had been subjected to duplicate typings in different laboratories, and any discrepancies

resolved by repeat typings. Of the material included in this report, blood specimens from 137 Yanomama and 160 non-Yanomama were typed only once (in Ann Arbor) and from frozen specimens, at that. Estimates of the intralaboratory errors, for Ann Arbor only, were available from one set of duplicate typings on fresh specimens and another set of duplicate tests comparing the results of tests in fresh specimens to the tests on frozen blood specimens from the same individuals. Both sets of tests had been performed with anti-M, N, S, s (on S+ only), P, C, c, D, E, e, Fy^a, Jk^a, and Le^b. No discrepancies were detected among the 72 duplicates of fresh specimens but the fresh versus frozen comparison yielded the following frequencies of errors: s, 2.8%; e, 0.3%; Fy^a, 0.7%; Jk^a, 3.4%; and Le^b, 0.3%. No discrepancies were detected for the other reagents. The errors are sufficiently small and bidirectional that inclusion of the singly typed blood specimens in the data will not unduly bias the results.

Phenotypes and genotype frequencies for the systems characterized by polymorphisms are presented for the Yanomama (tables 1 and 2) and for the Makiritare, Piaroa, Macushi, and Wapishana (tables 3 and 4). Where less than 24 persons were sampled from a village, the results are entered under "Miscellaneous." Note that for both the Yanomama and Makiritare, the tables give summary columns combining previously reported data with those presented here. Numbers given for previous totals (both phenotype and gene frequencies) may not in all cases agree with the specific totals to be found in the reports cited because when revisits were made to some villages, old results were subtracted from the "previous" data column and the total data available for the village presented with new data. Gene frequencies are rounded to two or three significant figures, whichever was appropriate for the sample size.

Some of the reagents yielded uniform results. With respect to specific blood group systems, the number of individuals detected of each phenotype were as follows:

MN system: 38 U(+), 201 Vw(—), 264 Hu(—), 79 Mu + Ht(—), 500 Mg(—), and 786 M^v(—); only N(—) individuals were tested with anti-M^v.

P system: 247 P + P_1(+); only P_2 individuals were tested.

K system: 1,541 K(—); 79k(+), Kp(a — b+), Js(a—).

Wr system: 373 Wr(a—).

These findings confirm earlier results in the Yanomama [9] and Makiritare [11].

ABO. Only one non-O individual was detected in 1,541 tests on representatives of all five tribes. He was type A_1 and a member of one of the Macushi villages. These results bear out the earlier evidence [9, 11] for lack of admixture of the Yanomama and Makiritare with non-Indians and suggest little admixture for these villages of the other three tribes as well.

Rh. Since this is the largest series of blood samples from Indians to be tested for the true frequency of the R^z gene (*CDE*) by tests with anti-f, it is of some importance to present details of the tests and results. Of the 381 Yanomama R_1R_2 (CcDEe) samples reported in the grand total (table 1), none of the 113 R_1R_2 samples from villages 03LMN, Q, RS, T, U, W, and X were tested with anti-f, nor were 20 others scattered among several villages. Of the remaining 248 R_1R_2 samples

TABLE 1

BLOOD GROUP AND SECRETOR PHENOTYPES IN 15 ADDITIONAL YANOMAMA VILLAGES

SYSTEM AND PHENOTYPE	VILLAGE 08K 15M	08L 11P	11J	11K	11M	11S	11T	11U	11V	11X	11YZ	15H	15L	15O	15QR	Misc.	TOTAL	PREVIOUS TOTAL	GRAND TOTAL
MNSs:																			
MS	1	7	0	1	2	0	0	1	1	0	0	0	3	3	0	0	19	79	98
MSs	10	24	2	13	7	2	3	1	5	1	1	4	11	11	12	6	113	290	403
Ms	5	22	21	23	6	7	1	3	2	3	70	2	17	10	72	27	291	655	946
MNS	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	3	16	19
MNSs	6	13	13	1	6	5	3	4	6	5	24	11	9	0	7	16	129	298	427
MNs	37	18	11	7	4	14	10	11	10	22	17	14	29	0	21	51	276	745	1,021
NS	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	3	5	8
NSs	0	3	1	0	0	0	3	2	0	0	1	0	2	0	0	0	12	47	59
Ns	20	4	2	0	6	11	11	6	5	12	0	10	9	0	0	19	115	320	435
Total	80	91	51	46	31	39	32	28	29	43	114	41	80	24	113	119	961	2,455	3,416
P:																			
P_1	69	83	35	36	30	28	25	21	22	41	90	36	60	17	83	100	776	2,001	2,777
P_2	11	8	14	10	1	11	7	7	7	2	24	5	20	7	30	19	183	444	627
Total	80	91	49	46	31	39	32	28	29	43	114	41	80	24	113	119	959	2,445	3,404
Rh:																			
CDe	69	71	34	22	18	35	21	18	21	38	66	35	45	8	68	102	671	1,668	2,339
CcDe	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	52	54
CcDEe	2	5	5	5	2	0	5	3	2	0	3	6	27	7	22	10	104*	277†	381
CDEe	9	15	9	17	9	3	6	6	6	5	40	0	4	4	20	4	157	372	529
CcDE	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	2	6	21	27
CDE	0	0	2	1	1	0	0	1	0	0	4	0	1	0	0	0	10	31	41
cDE	0	0	0	0	0	0	0	0	0	0	1	0	3	3	3	1	11	26	37
cDEe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	6
cDe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Total	80	91	51	46	31	39	32	28	29	43	114	41	80	24	113	119	961	2,455	3,416

TABLE 1 (*Continued*)

System and Phenotype	Village																		
	08K 15M	08L 11P	IIJ	11K	11M	11S	11T	11U	11V	11X	11YZ	15H	15L	15O	15QR	Misc.	Total	Previous Total	Grand Total
Fy:																			
a+b—	10	8	38	12	4	3	13	2	4	2	28	24	46	...	...	23	217	633	850
a+b+	44	49	10	24	13	24	9	11	9	15	55	17	31	...	...	58	369	811	1,180
a—b+	26	33	3	10	14	12	10	15	16	26	31	0	3	...	...	32	231	313	544
Total	80	90	51	46	31	39	32	28	29	43	114	41	80	...	...	113	817	1,757	2,574
a+	...	...	...	...	...	...	...	...	...	...	...	...	...	23	89	5	117	577	674
a—	...	...	...	...	...	...	...	...	...	...	...	...	...	1	24	1	26	89	115
Total	...	...	...	...	...	...	...	...	...	...	...	...	...	24	113	6	143	646	789
Jk:																			
a+	62	75	41	39	26	31	25	21	26	38	67	15	52	19	65	73	675	1,923	2,598
a—	18	15	10	7	5	8	7	7	3	5	47	26	28	5	48	46	285	529	814
Total	80	90	51	46	31	39	32	28	29	43	114	41	80	24	113	119	960	2,452	3,412
Di:																			
a+b+	...	...	...	...	...	...	...	...	...	...	...	...	12	...	...	...	12	...	12
a+	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	12	12
a—	80	91	51	46	31	39	32	28	29	43	114	41	68	24	112	119	948	2,443	3,391
Total	80	91	51	46	31	39	32	28	29	43	114	41	80	24	112	119	960	2,455	3,415
Le:																			
a—b+	51	64	28	34	22	30	23	21	12	34	83	37	68	17	56	90	670	1,819	2,489
a—b—	29	27	23	12	9	9	9	7	17	9	31	4	12	7	57	29	291	630	921
Total	80	91	51	46	31	39	32	28	29	43	114	41	80	24	113	119	961	2,449	3,410
ABH secretor:																			
Secretor	67	69	...	...	22	...	...	...	...	...	...	...	...	...	...	...	158	1,635	1,793
Non-secretor	4	...	...	...	9	...	...	...	...	...	...	...	...	...	...	...	13	15	28‡
Total	71	69	...	...	31	...	...	...	...	...	...	...	...	...	...	...	171	1,650	1,821

* All were negative to anti-f.

† 144 were tested with anti-f; two were positive (see text).

‡ True H secretor status in doubt; see text.

TABLE 2

GENE FREQUENCIES OF POLYMORPHIC BLOOD GROUP SYSTEMS AND SECRETOR SYSTEMS AMONG YANOMAMA INDIAN VILLAGES

SYSTEM AND GENE	VILLAGE 08K 15M	08L 11P	11J	11K	11M	11S	11T	11U	11V	11X	11Y 11Z	15H	15L	15O	15Q 15R	Misc.	TOTAL	PREVIOUS TOTAL	GRAND TOTAL
MNSs:																			
MS	.12	.26	.03	.18	.27	.09	.10	.11	.22	.07	.01	.18	.16	.35	.06	.09	.129	.141	.138
Ms	.36	.49	.66	.72	.37	.38	.25	.34	.33	.34	.80	.27	.47	.65	.81	.47	.523	.491	.500
NS	.01	.03	.15	.02	.00	.00	.07	.05	.00	.00	.11	.00	.02	.00	.03	.00	.029	.029	.029
Ns	.51	.22	.16	.08	.36	.53	.58	.50	.45	.59	.08	.55	.35	.00	.10	.44	.319	.339	.333
P:																			
P^1	.63	.70	.47	.53	.82	.47	.53	.50	.51	.78	.54	.65	.50	.46	.48	.60	.563	.574	.571
Rh:																			
R^z	.06	.08	.14	.22	.18	.04	.09	.14	.10	.06	.21	.00	.04	.13	.09	.02	.095	.094	.094
R^1	.93	.89	.80	.72	.77	.95	.83	.80	.86	.94	.77	.93	.76	.56	.79	.92	.835	.821	.825
R^2	.01	.03	.06	.06	.03	.00	.08	.06	.04	.00	.02	.07	.20	.31	.12	.06	.069	.071	.071
R^0	.00	.00	.00	.00	.02	.01	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.001	.014	.010
Duffy:																			
Fy^a*	.40	.36	.84	.52	.34	.38	.55	.27	.29	.22	.49	...	.77	.80	.54	.47	.483	.591	.557
Fy^a†	.43	.39	.75	.53	.33	.46	.44	.27	.26	.22	.48	.79	.80	...	...	.46	.491	.591	.559
Kidd:																			
Jk^a	.53	.59	.56	.61	.60	.55	.53	.50	.68	.66	.36	.20	.41	.54	.35	.38	.455	.536	.512
Diego:																			
Di^a	0	0	0	0	0	0	0	0	0	0	0	0	.08	0	0	0	.006	.002	.004
Lewis:																			
Le‡	.40	.45	.33	.49	.46	.52	.47	.50	.23	.54	.48	.69	.61	.46	.29	.51	.450	.493	.480
Le§	.48	.45	...	...	.43	...	...	...	...	...	...	...	...	...	...	...	.46	.524	.518
Secretor:																			
Se‖	1.0	1.0	...	...	1.0	...	...	...	...	...	...	...	...	...	...	...	1.0	1.0	1.0

* Gene frequencies derived from two phenotypes, Fy(a+) and Fy(a—).

† Gene frequencies derived from three phenotypes.

‡ Gene frequencies derived from red cell phenotypes ($Le = 1 - \sqrt{\text{Le(a—b—)}/N}$).

§ Gene frequencies derived from secretor phenotypes ($Le = 1 - \sqrt{\text{lele}/N}$).

‖ See test for explanation of discrepancies.

which were tested with anti-f, two were found to be f+ and so shown to be from persons who were genotypically either R^z/R^0 (*CDE/cDe*) or R^z/r (*CDE/cde*). (A previous report [9] cites one sample as positive to anti-f in village 03F in a footnote to the table but incorrectly states in the text that three were f+. Subsequent retesting indicated that, in fact, only two f+ existed.) The only two phenotypically R_0 (ccDee) individuals (*cDe/cde* or *cDe/cDe*) detected among the 3,416 persons tested were from the same village (03F) as the two R_1R_2f+ (cCDEef) individuals, making it highly likely that, since Rh— Yanomama have never been found, the true genotype of these R_1R_2f+ individuals was R^zR^0 (*CDE/cDe*). In view of our continuing failure to demonstrate the Rh— phenotype and the fact that the four unusual phenotypes we have just described can be as well explained by the presence of the R^0 (*cDe*) as the *r* (*cde*) gene, we conclude that *r* is not present in the Yanomama.

Among the non-Yanomama R_1R_2 samples (table 3), 319 were tested with anti-f; only two Makiritare, from among the previously reported group [11], were positive and thus are of genotype R^z/R^0 *or* R^z/r.

Duffy. Gene frequencies for the Duffy system have been presented in two forms. Since all villages were tested with anti-Fy^a and only some with anti-Fy^b and since almost all published Indian gene frequencies which might be used in distance estimates have been based on tests with only anti-Fy^a, tables 2 and 4 report Fy gene frequencies on (1) the total material as determined from tests with anti-Fy^a with gene frequencies derived by the square-root method and (2) the subsample typed with both antisera, and gene frequencies determined by the gene-counting method.

Diego. Limited numbers of samples have been tested with both anti-Di^a and anti-Di^b: 126 Yanomama from villages 11F and 11HI [9]; 146 Makiritare from villages 10G and 10H [11]; and 146 Piaroa from village 12ABC (present report). Not one of the 418 Indian bloods was found to be negative to both reagents. All other tests with anti-Di^b were limited to specimens known to be Di(a+). We had previously noted the relative absence of Di^a from the Yanomama and documented that the presence of that gene in one Yanomama village (03X) is explained by Makiritare admixture [12]. Again, in the present series the occurrence of Di^a in a single Yanomama village (15L) is explained by a known history of admixture [13].

H and Le systems. We have previously concluded that 15 instances wherein Yanomama had been typed as H nonsecretors were probably the result of technical error and suggested that the gene resulting in H nonsecretor (*se*) was absent from the Yanomama [9]. The reasoning employed previously leads us to reject the validity of 13 additional typings of H nonsecretors, which, given the distribution of H and Le secretors and nonsecretors among all other persons tested, is a very unlikely event ($\chi^2 = 29.9$, 1 df). Among 1,821 Yanomama saliva samples tested, the distribution of Le secretion among the 28 H nonsecretors is 24 Le nonsecretors and four Le secretors, while among 1,793 H secretors, the distribution is 1,393 Le secretors and 400 Le nonsecretors.

A more rigorous test of the basis for the nonrandom distribution of the H-Le double nonsecretors can be performed by restricting the analysis only to those

TABLE 3

BLOOD GROUP AND SECRETOR PHENOTYPES IN FOUR TRIBES NEIGHBORING THE YANOMAMA

SYSTEM AND PHENOTYPE	MAKIRITARE										PIAROA	MACUSHI			WAPISHANA
	10L	10M	10N	10P	10Q	10S	Misc.	Total	Previous Total	Grand Total	12ABC	26AB	26C	Total	27A
ABO:															
O	22	27	31	35	24	26	20	185	539	724	146	89	97	186	62
A_1	...	...	...	...	...	...	...	...	...	...	...	...	1	1	...
MNSs:															
MS	3	2	1	...	2	1	1	10	58	68	17	1	1	2	4
MSs	9	9	11	8	6	5	9	57	130	187	66	15	14	29	14
Ms	2	2	6	10	1	6	3	30	94	124	41	34	49	83	10
MNS	2	2	...	...	1	1	2	8	51	59	...	2	1	3	...
MNSs	3	9	3	5	8	8	2	38	111	149	11	8	9	17	12
MNs	1	2	7	9	5	2	3	29	50	79	10	23	23	46	18
NS	...	...	1	...	...	2	...	3	11	14	...	...	...	...	...
NSs	2	1	...	2	...	...	...	5	19	24	...	1	...	1	1
Ns	...	...	2	1	1	1	...	5	14	19	1	5	1	6	3
Total	22	27	31	35	24	26	20	185	538	723	146	89	98	187	62
P:															
P_1	17	21	13	21	22	15	13	122	370	492	127	70	91	161	45
P_2	5	6	18	14	2	11	7	63	168	231	19	19	7	26	17
Total	22	27	31	35	24	26	20	185	538	723	146	89	98	187	62
Rh:															
CDe	4	2	5	4	1	6	1	23	83	106	27	31	49	80	22
CcDe	...	...	1	4	1	...	1	7	16	23	1	...	4	4	3
CcDEe	8	13	11	13	6	9	10	70*	248†	318	55*	40*	39*	79*	27*
CDEe	...	...	1	...	...	...	2	3	10	13	...	3	2	5	...
CcDE	...	...	...	...	4	1	1	6	6	12	...	...	...	...	...
cDE	10	12	13	11	10	10	5	71	155	226	52	15	3	18	9
cDEe	...	...	...	3	2	...	...	5	21	26	9	...	1	1	1
Total	22	27	31	35	24	26	20	185	539	724	144	89	98	187	62
Fy:															
a+b−	9	17	9	7	10	14	15	81	206	287	...	23	...	23	...
a+b+	11	10	16	23	13	11	5	89	158	247	...	46	...	46	...
a−b+	2	...	6	5	1	1	...	15	28	43	...	20	...	20	...

TABLE 3 (*Continued*)

System and Phenotype	Makiritare										Piaroa	Macushi			Wapishana
	10L	10M	10N	10P	10Q	10S	Misc.	Total	Previous Total	Grand Total	12ABC	26AB	26C	Total	27A
a+	...	...	...	...	...	...	...	...	140	140	125	...	91	91	59
a—	...	...	...	...	...	...	...	...	7	7	21	...	7	7	3
Total	22	27	31	35	24	26	20	185	539	724	146	89	98	187	62
Jk:															
a+	11	10	13	18	18	16	10	96	287	383	76	50	66	116	52
a—	11	17	18	17	6	10	10	89	250	339	70	39	32	71	10
Total	22	27	31	35	24	26	20	185	537	722	146	89	98	187	62
Di:															
a+b—	2	2	...	2	...	4	3	13	6	19	5	3	...	3	1
a+b+	6	7	8	17	11	2	4	55	29	84	27	11	...	11	20
a—b+	14	18	23	16	13	20	13	117	111	228	114	75	...	75	41
a+	...	...	...	...	...	...	...	...	153	153	...	...	27	27	...
a—	...	...	...	...	...	...	...	...	240	240	...	...	71	71	...
Total	22	27	31	35	24	26	20	185	539	724	146	89	98	187	62
Le:															
a—b+	18	19	19	28	17	17	11	129	363	492	95	63	73	136	48
a—b—	4	8	12	7	7	9	9	56	176	232	48	26	25	51	14
a+b—	...	...	...	...	...	...	...	...	...	...	3	...	...	...	...
Total	22	27	31	35	24	26	20	185	539	724	146	89	98	187	62
ABH secretor:															
Secretor	...	...	...	...	...	...	11	11	464	475	113	...	...	...	...
Nonsecretor	...	...	...	...	...	...	...	...	...	...	5	...	...	...	...
Total	...	...	...	...	...	...	11	11	464	475	118	...	...	...	...
Le secretor:															
Secretor	...	...	...	...	...	...	7	7	325	332	79	...	...	...	...
Nonsecretor	...	...	...	...	...	...	4	4	139	143	39	...	...	...	...
Total	...	...	...	...	...	...	11	11	464	475	118	...	...	...	...

* All were negative to anti-f.

† 160 genotyped by pedigree as R^1/R^2. Of 88 tested with anti-f, two were positive.

TABLE 4

GENE FREQUENCIES OF POLYMORPHIC BLOOD GROUP SYSTEMS AND SECRETOR SYSTEMS AMONG FOUR TRIBES NEIGHBORING THE YANOMAMA

SYSTEM AND GENE	MAKIRITARE										PIAROA	MACUSHI			WAPISHANA
	10L	10M	10N	10P	10Q	10S	Misc.	Total	Previous Total	Grand Total	12ABC	26AB	26C	Total	27A
MNSs:															
MS	.42	.36	.24	.15	.38	.17	.35	.29	.320	.310	.38	.13	.10	.12	.27
Ms	.35	.36	.50	.57	.28	.50	.48	.44	.401	.412	.54	.61	.72	.67	.42
NS	.13	.14	.05	.07	.04	.23	.07	.10	.145	.134	0	.04	.03	.03	.02
Ns	.10	.14	.21	.21	.30	.10	.10	.17	.134	.144	.08	.22	.15	.18	.29
P:															
P^1	.52	.53	.24	.37	.71	.35	.41	.42	.441	.435	.64	.54	.73	.63	.48
Rh:															
R^z	.00	.00	.02	.00	.09	.02	.08	.03	.015	.018	.00	.02	.01	.02	.00
R^1	.36	.31	.37	.36	.18	.40	.37	.34	.408	.390	.38	.59	.73	.66	.60
R^2	.64	.69	.59	.54	.66	.58	.52	.60	.542	.558	.58	.39	.23	.31	.37
R^0	.00	.11	.02	.10	.07	.00	.03	.03	.035	.034	.04	.00	.03	.01	.03
Duffy:															
Fy^{a*} ...	.70	...	.56	.62	.80	.80	...	.72	.745	.737	.62	.53	.73	.62	.78
$Fy^{a\dagger}$ ...	.66	.81	.55	.53	.69	.75	.87	.68	.727	.711	...	.52	...	...	...
Kidd:															
Jk^a	.29	.21	.24	.30	.50	.38	.29	.31	.318	.315	.31	.34	.43	.38	.60
Diego:															
$Di^{a\ddagger}$ ...	.23	.20	.12	.30	.23	.19	.24	.22	.193	.196	...	.08	.15	.12	...
$Di^{a\S}$ ...	.20	.18	.14	.23	.26	.12	.19	.20	.140	.184	.13	.10	...	...	.18
Lewis:															
Le‖	.57	.46	.38	.55	.46	.41	.33	.45	.429	.434	.43	.46	.49	.48	.52
Le#	...	...	...	...	...	...	.40	.40	.453	.451	.43	...	...	...	...
Secretor:															
Se	...	...	...	...	...	...	1.0	1.0	1.0	1.0	.79	...	...	...	...

* Gene frequencies derived from two phenotypes, Fy(a+) and Fy(a—).
† Gene frequencies derived from three phenotypes.
‡ Gene frequencies derived from two phenotypes, Di(a+) and Di(a—).
§ Gene frequencies derived from three phenotypes.
‖ Gene frequencies derived from red cell phenotypes ($Le = 1 - \sqrt{\text{Le(a—b—)}/N}$).
Gene frequencies derived from secretor phenotypes ($Le = 1 - \sqrt{\text{lele}/N}$).

villages wherein the H nonsecretors were detected, on the theory that the nonsecretor (*se*) gene does, in fact, exist in them. We exclude, however, 12 H nonsecretor individuals whose red cell type was Le(a—b+) and thus presumed to be the H secretors and two H nonsecretors who were not blood typed. The distribution among the eight villages is, then, as follows: among H secretors, there are 401 Le secretors and 73 Le nonsecretors; among H nonsecretors, there are one Le secretor and 13 Le nonsecretors. The improbability of this distribution ($\chi^2 = 56$, 1 df) suggests that the findings are due to technical error and leads us to the conclusion that the H nonsecretor gene (*se*) is absent from the Yanomama.

The low frequency of Le(a+) individuals among American Indians and Eskimos (summarized by Salzano [14]) testifies to the generally high frequency of the H secretor (*Se*) gene in American aboriginal populations. The total absence of the Le(a+) red cell phenotype from the relatively uncontacted Yanomama, Makiritare, Macushi, and Wapishana leads to the conclusion that the *Se* gene has been fixed in these populations, thus confirming the conclusion which had already been reached in the Yanomama and Makiritare from the corresponding phenotypes in saliva.

Analysis

Is there intratribal heterogeneity in allele dispersion?

The genetic heterogeneity of the Yanomama villages may be measured by the standardized variance $\sigma^2/\bar{p}(1-\bar{p})$, the F_{ST} statistic of Wright [15]. In a previous analysis of 37 Yanomama villages [16], while there was evidence for considerable intervillage genetic heterogeneity, we found no evidence to suggest that any locus was significantly different from the others in the degree of variability, as measured by the F_{ST} statistic. In order to confirm this for the new total data set of the Yanomama (all publications to date), we utilized Lewontin and Krakauer's test of the heterogeneity of observed F_{ST} values [17]. For the 47 Yanomama villages with sample size over 30, we derived F_{ST} values for 17 alleles as follows: *MS*, .095; *Ms*, .122; *NS*, .041; *Ns*, .111; R^z, .071; R^1, .067; R^2, .081; R^0, .063; *P*, .071; Fy^a, .070; Jk^a, .072; Le^a, .041; Di^a, .078; Hp^1, .069; Gc^1, .066; PGM^1, .038; Ph^A, .080; mean, .073. The variance of these 17 F_{ST} values was not significantly greater than that expected under the assumption that the underlying distribution of village gene frequencies was binomial. If the underlying distribution of gene frequencies were more dispersed than binomial (due to inclusion of related individuals in village samples), then the test criterion used would be somewhat conservative. However, considering the previous results of this type of analysis [16, 17], it is unlikely, even if allowance could be made for this, that a demonstrably significant result would obtain. Hence, as far as the Yanomama are concerned, we feel confident in asserting that there is no evidence that differential selective forces are influencing the dispersion of allelic frequencies at these 11 loci.

How good is the reproducibility of village gene frequency estimates, and what are the errors of estimate for genetic distances?

The applicability of specific gene frequency estimates to calculations such as genetic distances will be limited by two sources of error: (1) typing errors and (2)

sampling errors. The first source of error has usually been controlled by duplicate typings in independent laboratories and appears to be insignificant in these studies. The magnitude of the second source of error, sampling error, for the estimation of village gene frequencies and the calculation of genetic distances was empirically gauged by resampling four villages and comparing the results of the original samples with the resampled situations. Three of the new samples (11F, 15J, 15DEF) resembled the original samples in that they contained 70%–85% of the total village population, while the fourth sample (11LQ) comprised a much smaller fraction. Comparison of the resulting gene frequencies (blood groups, table 5; other loci, [4, table 6]) indicates that the sampling procedure of this project does not appreciably distort the estimation of allelic frequencies. Of the 36 comparisons, only eight differed by more than .05.

TABLE 5

COMPARISON OF GENE FREQUENCIES OBTAINED FOR SIX POLYMORPHIC SYSTEMS BY REPEAT VISITS TO FOUR VILLAGES

System and Gene	Village 1		Village 2		Village 3		Village 4	
	Old* 03E	New 11F	Old* 03I	New 15J	Old* 03J	New 11LQ	Old* 08XY	New 15DEF
MNSs:								
MS	.05	.07	.06	.10	.27	.24	.29	.28
Ms	.50	.50	.66	.65	.62	.67	.29	.29
NS	.02	0	.08	.10	.03	0	0	0
Ns	.43	.43	.20	.15	.08	.09	.42	.43
No. subjects	60	50	50	48	62	27	120	98
P:								
P^1	.51	.51	.53	.51	.75	.67	.63	.71
No. subjects	59	50	50	49	62	27	120	98
Rh:								
R^z	.13	.15	.14	.17	.07	.07	0	0
R^1	.75	.74	.85	.83	.81	.82	.92	.94
R^2	.10	.10	0	0	.12	.11	.03	.03
R^0	.02	.01	.01	0	0	0	.05	.04
No. subjects	60	50	50	46	62	27	91	98
Duffy:								
Fy^a	.67	.76	.61	.62	.41	.42	.53	.58
No. subjects	60	50	50	49	11	27	120	98
Kidd:								
Jk^a	.42	.42	.38	.35	.75	.49	.54	.57
No. subjects	59	50	50	49	62	27	120	98
Lewis:								
Le	.59	.58	.51	.55	.59	.53	.52	.51
No. subjects	59	50	50	49	59	27	120	98

* Gene frequencies taken from [9].

However, sampling error does appear to exert a more profound effect at the level of calculating genetic distances and in the subsequent estimation of phenetic relationships. This is in part due to the sensitivity of the distance measure (the chord approximation of Cavalli-Sforza and Edwards [18]) to gene frequency discrepancies outside the range .05–.95 and partly to the accumulation of small differences among many loci. Two distance matrices, one for the original set of villages and one for the resampled set, were calculated from the 11 loci polymorphic in the Yanomama (26 alleles); these are presented in table 6. The average difference in the corresponding entries is .089 units; the deviation of each comparison about the joint mean was averaged over the six entries to give an "average standard deviation" of .063 units. As this is approximately 14% of the overall mean distance of .456 units, we shall assume that for our studies on the Yanomama the standard error that should be attached to each pairwise distance as a consequence of sampling error is of the order of 14% of that distance. This appears to be a more realistic estimate of the magnitude of sampling error than an estimate of a standard error based on the interlocus variability for each pairwise distance. This latter approach (which for the original samples involved a standard error of .087 about a mean of .122 units and for the repeat samples, .092 about a mean of .103 units) is essentially a measure of the stochastic events influencing gene frequencies in these small demes and its magnitude (80%–90% of the mean) an indication of the imprecision of single locus estimates of genetic distance. We consider the effect of this and other errors on the estimation of phenetic relationships in the discussion.

TABLE 6

COMPARISON OF ORIGINAL GENETIC DISTANCES BETWEEN FOUR YANOMAMA VILLAGES WITH GENETIC DISTANCES RESULTING FROM RESAMPLING

Village	1	2	3	4
1	...	.309	.565	.389
2	.416	...	.563	.479
3	.432	.419	...	.530
4	.403	.523	.440	...

NOTE.—Upper triangular matrix = genetic distance between original samples; lower triangular matrix = genetic distance between resampled villages.

WHAT IS THE RELATIONSHIP OF THE YANOMAMA TO OTHER SOUTH AMERICAN TRIBES, AND THESE TRIBES TO ONE ANOTHER?

We now turn to an analysis of the genetic relationships of the Yanomama to other South American tribes utilizing all available genetic data. (In this instance only six loci could be used due to the lack of extensive genetic typing of tribal populations in South America.) In several previous publications we have commented on the cultural, linguistic, and genetic differences between the Yanomama and other adequately studied South American tribes [1, 2]. Now we investigate in greater

detail whether the Yanomama form a genetic isolate, readily distinguishable from other South American tribal populations. The 12 tribes previously studied were at the time the only tribes that met the following criteria: (1) less than 5% admixture, as determined by ABO typing; (2) data available for six genetic loci (Rh, MNSs, Kidd, Duffy, Diego, and haptoglobin systems); and (3) adequate sample size (200). However, only one of the 12 tribes (Pemon) was geographically close to the Yanomama. Thus the reported genetic isolation of the Yanomama may have been due in part to an accident of sampling. Now we have gene frequency data for four additional tribes located in the same geographical area as the Yanomama (Macushi, Makiritare, Piaroa, Wapishana). In addition, four more distant tribes may now be included in an intertribal analysis, bringing the total to 20 tribes. These four tribes are: (1) the Cashinahua, a Panoan speaking tribe of the eastern montaña of Peru and Brazil [19, 20]; (2) the Cayapo, a Gê speaking group of the northern Mato Grosso of Brazil [21, 22]; (3) the Trio; and (4) the Wajana. The latter two are Carib-speaking tribes of Surinam and Brazil who share many elements of language and culture [23]. The allelic frequencies for these last two tribes, as determined by R. A. Geerdink and L. E. Nijenhuis, have been kindly communicated to us by Dr. Geerdink.

The criteria for inclusion in the study are as before, except that both the Wapishana (sample of 62) and the Macushi (sample of 187) fail to meet the criterion of 200 typed individuals. Because of their close proximity to the Yanomama, the temptation to include these preliminary results in the analysis was irresistible. However, since the genetic distance between villages of a single tribe may be as much as 85% of intertribal distances [24], the results concerning these two tribes may subsequently become altered by more extensive sampling.

Measures of Relationship

The genetic relationship of the Yanomama to the other 19 tribes is considered with reference to two slightly different but conceptually related statistics—genetic distance and genetic identity.

Genetic distance. Genetic distance between tribes is based on the statistic originally proposed by Bhattacharyya [25], using the stereographic projection of Edwards [26] to achieve a Euclidean measure. That is,

$$D_{ij}^2 = 8\left(1 - \sum_{k=1}^{K} \sqrt{p_{ik}p_{jk}}\right) \Big/ \left(1 + \sum_{k=1}^{K} \sqrt{p_{ik}/K}\right)\left(1 + \sum_{k=1}^{K} \sqrt{p_{jk}/K}\right),$$

for a locus with K alleles. Distances are combined over loci by Pythagoras's theorem. We continue to use this type of distance representation rather than alternative forms, both to ensure compatibility with our earlier results using the chord approximation and because alternative measures are not likely to yield any marked improvements in the analysis of these data [27].

Genetic identity. This statistic, as developed by Nei [6], is conceptually related to Malecot's coefficient of kinship between individuals and measures the probability

that alleles drawn at random from each of two populations are identical. If mating is random and if selection is absent and mutations are unique nonrecurrent events, the measure is analogous to Wright's coefficient of relationship. For a pair of populations, the probability of identity for two alleles randomly chosen from one of the populations is given by

$$J_{ii} = \sum_{k=1}^{K} p_{ik}^2, \qquad J_{jj} = \sum_{k=1}^{K} p_{jk}^2.$$

The probability of identity for a pair of alleles that are drawn at random, one from each population, is given by

$$J_{ij} = \sum_{k=1}^{K} p_{ij} p_{jk}.$$

The normalized identity of alleles at this locus for the two populations is defined as $I_{ij} = J_{ij}/\sqrt{J_{ii}J_{jj}}$. The *average* genetic identity between the two populations is defined as $\bar{I}_{ij} = \bar{J}_{ij}/\sqrt{\bar{J}_{ii}\bar{J}_{jj}}$, where $\bar{J}_{ii}$, $\bar{J}_{jj}$, *and* $\bar{J}_{ij}$ are the respective arithmetic means of the J_{ii}, J_{jj}, and J_{ij} for each locus. The statistic can also be used to compute the average number of allele substitutions between the two populations by letting $D = -\ln I$, where D represents the average number of allele substitutions [6].

Genetic Relationships of 20 Central and South American Tribes

In table 7 we present the pairwise genetic distances as the upper triangular matrix and the normalized genetic identity between populations as the lower triangular matrix. We first consider the results obtained for Nei's measure of *genetic identity*. For the 20 tribes analyzed, the average normalized genetic identity is .948 with a range from 0.839 (Guaymí-Shipibo) to .991 (Cayapo-Trio). Thus at one end of the scale, for the six loci in this analysis, the Cayapo and Trio have 99% of their genomes in common and at the other the Guaymí and Shipibo have only 84% of their genomes in common. On the average, the proportion of genes that are common to any pair of South American tribes is 95%. Since the results in table 7 are obtained solely from six polymorphic loci, the actual figure for the whole genome can be expected to be much higher. The Yanomama (and the Guaymí) display a smaller degree of genetic affinity with other tribes than the average, the Yanomama affinity values ranging from .854 (Makiritare) to .965 (Quechua), about a mean of .925. However, the Yanomama do not differ significantly from the other 19 tribes with respect to their degree of shared genetic identity: all mean tribal values fall within 2 SD of the overall average value of .948.

Next we turn to a consideration of the *stereographic genetic distances* displayed in the upper matrix of table 7. The average intertribal pairwise distance is .409; the values ranging from .176 (Cayapo-Trio) to .712 (Guaymí-Shipibo). The Yanomama, who are the closest to the Guaymí (.406) and furthest from the Shipibo (.695), have an average genetic distance from all other tribes of .526—a tribally

TABLE 7

GENETIC DISTANCE AND GENETIC IDENTITY ($\times 10^3$) BETWEEN 20 SOUTH AMERICAN INDIAN TRIBES, BASED ON SIX LOCI

Tribe	Tribal Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Aymara	1	...	287	335	349	264	393	562	424	353	359	438	377	341	414	310	424	358	400	554	495
Cakchiquel	2	975	...	478	323	269	235	403	379	327	267	337	432	303	390	297	347	331	260	443	343
Cashinahua	3	976	954	...	503	359	546	704	521	497	413	527	500	478	466	332	470	439	507	549	538
Cayapa	4	958	978	953	...	346	298	484	331	442	311	373	378	241	540	418	360	415	373	476	364
Cayapo	5	980	982	977	973	...	329	546	422	321	301	378	396	289	274	176	349	257	240	563	362
Cuna	6	926	973	900	961	958	...	350	420	373	257	313	477	347	505	339	341	387	245	456	252
Guaymí	7	886	951	853	907	907	951	...	510	604	430	512	598	437	712	556	596	587	453	406	456
Jivaro	8	960	980	950	973	968	941	941	...	395	329	430	235	316	575	517	329	509	423	506	486
Makiritare	9	963	965	927	933	977	956	897	938	...	339	394	356	434	370	399	284	400	330	666	506
Macushi	10	949	984	948	965	978	977	952	966	951	...	246	378	291	490	339	325	446	323	430	345
Pemon	11	944	978	940	968	976	983	930	941	949	985	...	517	338	518	397	388	486	411	511	395
Piaroa	12	974	968	951	945	971	921	911	982	964	953	918	...	361	555	527	403	529	441	655	575
Quechua	13	968	986	960	978	978	946	944	984	937	976	964	966	...	479	385	427	403	361	479	417
Shipibo	14	951	944	955	934	975	900	839	929	958	920	930	941	943	...	308	427	256	352	695	513
Trio	15	970	978	973	972	991	967	901	948	963	976	986	940	967	760	...	386	240	301	516	346
Wapishana	16	938	963	934	981	972	968	886	956	955	954	965	936	946	946	971	...	357	314	538	367
Wajana	17	958	965	946	976	974	944	885	952	952	935	953	937	964	971	974	975	...	295	555	401
Xavante	18	930	973	914	959	969	982	947	967	966	972	964	954	953	931	958	978	953	...	532	265
Yanomama	19	904	954	918	955	921	926	945	958	854	951	942	898	965	864	925	914	913	924	...	418
Yupa	20	878	940	890	957	929	968	909	929	892	953	961	881	919	870	939	968	917	965	944	...

NOTE.—Upper triangular matrix contains values for the "stereographic" distance between pairs of tribes; lower triangular matrix contains values for Nei's measure of genetic identity between pairs of tribes.

specific average only exceeded by the average figure for the Guaymí (.567). The results of the genetic distance analysis thus approximate the results of genetic identity, although not exactly, as can be seen by comparing the upper and lower triangular matrices of table 7. The result most germane to this study is that the Yanomama (and the Guaymí) are noticeably distinct from the other tribal populations in terms of their genetic relationship, thus confirming a relationship noted earlier [1].

Dendrograms as a Representation of These Relationships

The overall genetic relationships of the 20 tribes can be examined without reference to geography by the construction of dendrograms. To this end, we display two dendrograms derived from the matrices of pairwise genetic distances (fig. 1) and

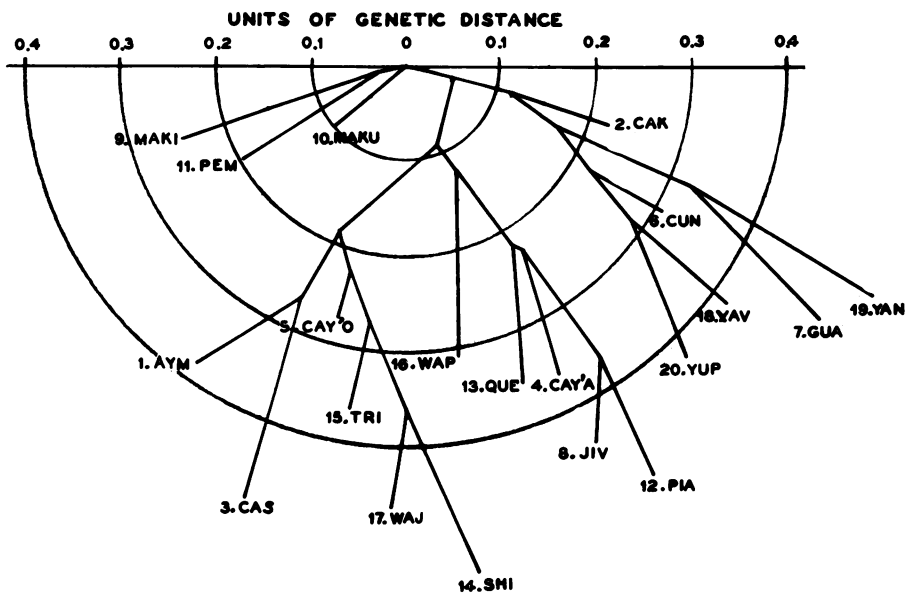

FIG. 1.—Genetic network for 20 South American tribes drawn to scale on polar graph paper. Units of genetic distance are measured along radii and are derived from the chord approximation (see text).

genetic identity (fig. 2). Figure 1 is presented in such a way as to allow a ready comparison with the earlier trees for 12 South American tribes [1]. The initial procedure for constructing this tree follows Cavalli-Sforza and Edwards [18], that is, construction of a set of pairwise genetic distances in Euclidean space using the *chord approximation* and combining distances over loci by Pythagoras's theorem. The resulting matrix is very similar to the stereographic distances of the upper triangular matrix of table 7. We use chord distances in this context to ensure maximum comparability with the earlier treatment [1]. An initial topology was then generated by using an iterative hierarchical splitting technique [28]. However, once the best

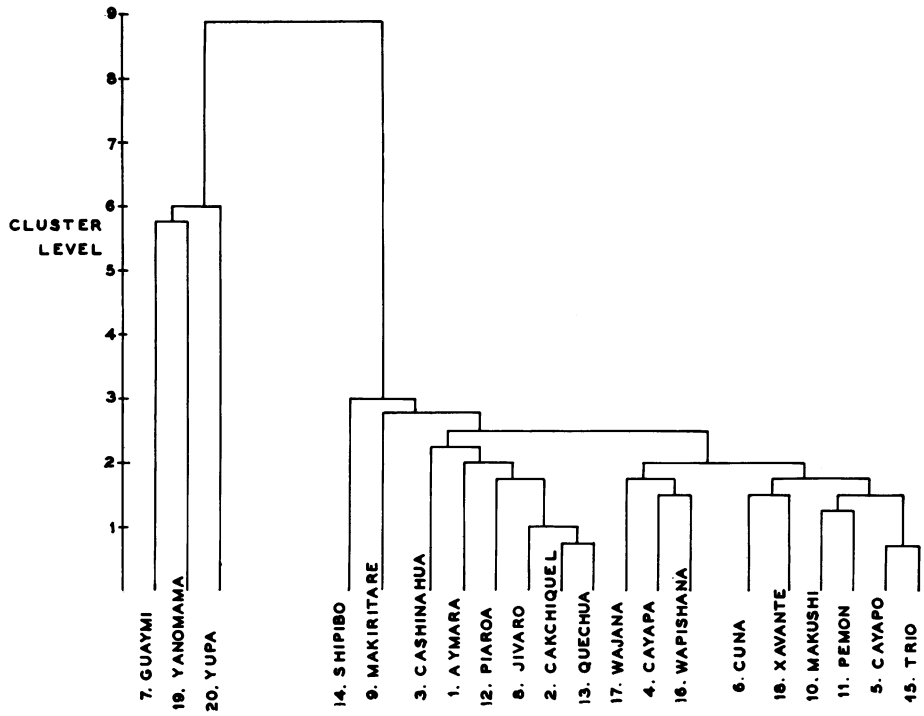

FIG. 2.—Dendrogram for 20 South American tribes derived by the median weighted centroid agglomerative method (see text).

"cluster tree" had been obtained by this technique, the minimum length configuration was found for that topology only, without making any attempt to find topologies with smaller lengths. The resulting topology, drawn to scale on polar coordinates, is shown in figure 1. The most appropriate comparison is with figure 4a of Fitch and Neel [1]. While comparison of trees containing different sets of elements will inevitably be difficult to evaluate [29], a comparison of our figure 1 and figure 4a of Fitch and Neel [1] indicates that the addition of eight more tribes to the analysis has done little to disrupt the pattern of intertribal genetic relationships originally revealed by this method.

An alternative method of displaying the phenetic relationships of the 20 tribes. utilizing genetic information, was used to construct the dendrogram in figure 2. The dissimilarity coefficient used in this analysis is derived from the matrix of genetic identities in table 7 by using the transformation $D_{ij} = -\ln I_{ij}$. The resulting "gene substitution" distances were used to form a tree by an agglomerative clustering process using the "median" method of Lance and Williams [30] which tends to conserve the original space. Hierarchic nonoverlapping clusters are produced in sequential fashion by joining clusters when the distance between their centroids is a minimum. Merging branches are weighted equally regardless of the number of populations they carry; hence populations joining at a higher level of clustering have

greater weight than populations joining at a lower level. The unequal sample sizes and nonrepresentative set of tribes in the analyses cause us to prefer this technique rather than an unweighted technique [31].

The difference between the two topologies gives ample indication of the extent to which the ***method*** of estimating phenetic relationships from a dissimilarity matrix may influence the form of the result. Without any phylogenetic implication, we briefly describe here the dendrogram in figure 2 and will take up the difference between these contrasting analyses in the discussion. The three tribes, Guaymí, Yanomama, and Yupa, that separate out of the highest level of clustering (lowest level of linkage) can be interpreted as "independent" or isolated populations. The genetic distinctiveness of the Yanomama and Guaymí is a recurrent theme of this paper, while the Yupa, despite their Carib affiliations, appear to have had a long tradition of isolation in the Sierra de Perijá in northern Venezuela [8]. At the next level of linkage the separation out of the Makiritare and Shipibo implies that both these tribes appear to be rather distinct from their immediate geographic neighbors, although not to the same extent as the Yanomama (see below). Whether this can be attributed to a relatively high degree of isolation or other factors awaits the acquisition of further data. The remaining 15 tribes are then separated into two major groups, each of which, with one exception, consists of populations inhabiting the same general geographic region. Five tribes associated with the Andean chain (Cashinahua, Aymara, Jivaro, Cakchiquel, and Quechua), together with the Piaroa, comprise the first group. The nine remaining tribes which, with the exception of the Cayapa, inhabit the eastern "lowland" area of South America belong to Arawak, Carib, and Gê linguistic stocks and might be expected to share genetic associations in light of the extensive population movements in this area during the past millenium. One interpretation of figure 2 is thus consistent with the bulk of information that we have on this small sample of South American tribes.

Lack of Correspondence between Geographic Proximity and Genetic Relationship to the Yanomama

Given that the Yanomama are genetically distinct from the other tribal populations, there are several ways in which this may have occurred. On the one hand, they might have become genetically distinct in situ, surrounded by the tribes who presently live there. In that case the Yanomama might be expected to show a closer genetic relationship to their immediate tribal neighbors than with more distant tribes. On the other hand, either the Yanomama *or* their tribal neighbors might be relatively recent intruders into the region, in which case there will be little difference between neighboring and distant tribes with respect to their genetic relationship to the Yanomama.

In table 8, we have compared both the normalized genetic identity and stereographic genetic distance between the Yanomama and three groups of tribes: neighboring, regional, and distant. Five tribes can be regarded as neighbors to the Yanomama either because some degree of gene flow is known to have occurred (Makiritare) or because it may potentially occur (Macushi, Pemon, Piaroa, Wapi-

TABLE 8

GENETIC IDENTITY AND GENETIC DISTANCE BETWEEN THE YANOMAMA AND 19 OTHER SOUTH AMERICAN TRIBES GROUPED INTO THREE GEOGRAPHICAL CLASSES.

Neighboring Tribes		Regional Tribes		Distant Tribes	
Normalized Genetic Identity (Mean .925)					
Macushi	.951	Macushi	.951	Quechua	.965
Pemon	.942	Yupa	.944	Jivaro	.958
Wapishana	.914	Pemon	.942	Cayapa	.955
Piaroa	.898	Trio	.925	Cakchiquel	.954
Makiritare	.854	Wapishana	.914	Guaymí	.945
Mean	.912	Wajana	.913	Cuna	.926
		Piaroa	.898	Xavante	.924
		Makiritare	.854	Cayapo	.921
		Mean	.918	Cashinahua	.918
				Aymara	.904
				Shipibo	.864
				Mean	.934
Stereographic Genetic Distance (Mean .526)					
Macushi	.430	Yupa	.418	Guaymí	.406
Pemon	.511	Macushi	.430	Cakchiquel	.443
Wapishana	.538	Pemon	.511	Cuna	.456
Piaroa	.655	Trio	.516	Cayapa	.476
Makiritare	.666	Wapishana	.538	Quechua	.479
Mean	.560	Wajana	.555	Jivaro	.506
		Piaroa	.655	Xavante	.532
		Makiritare	.666	Cashinahua	.549
		Mean	.538	Aymara	.554
				Cayapo	.563
				Shipibo	.695
				Mean	.514

NOTE.—Tribes listed in order of decreasing genetic affinity from the Yanomama. Values from table 7.

shana). The eight regional tribes include the five neighboring tribes together with the more distant Trio and Wajana (Carib tribes of Surinam) and the Yupa (a Carib tribe of northern Venezuela). The 11 remaining tribes which are classed as distant are, in order of geographic proximity to the Yanomama: Shipibo, Cashinahua, Cayapa, Jivaro, and Quecha (all of northeastern South America); the Cuna and Guaymí of Panama; the Cayapo of the Brazilian Mato Grosso; the Aymara of Bolivia; the Xavante of the Brazilian Mato Grosso; and finally the Cakchiquel of Guatemala.

Table 8 reveals that the mean genetic identity with the Yanomama is slightly greater for the 11 distant tribes (93%) than for either the eight regional tribes (92%) or the five neighboring tribes (91%). Similarly the average pairwise genetic distance from the Yanomama is greater for both the neighboring tribes (.560) and regional tribes (.538) than for the distant tribes (.515). Hence, at least in terms of their genetic relationships, the Yanomama cannot be regarded as possessing any close affinity with the tribes with which they may be presumed to have come in contact during the past 300–600 years.

A closer analysis of the distribution of values among the three geographically defined tribal groups reveals two points of interest.

1. The Makiritare, with whom the Yanomama appear to have had the most extensive degree of recent contact—some amount of gene flow probably occurred over 130 years ago [32] and has certainly occurred within the last 80 years [12, 33]—are the tribe with whom the Yanomama have the smallest amount of genetic identity (85%). With a distance of .666 units, the Yanomama are also the most distant tribe from the Makiritare (and only the Shipibo with a distance of .695 are more distant from the Yanomama). Hence, despite the documented gene flow that has occurred between these two neighboring tribes over several generations, the tribal gene frequencies for these six loci have remained remarkably distinct.

2. The three tribes (Quechua, Jivaro, Cayapa) that display the greatest degree of normalized genetic identity with the Yanomama (96%) are all located in the same general region of northwestern South America (see fig. 3). A possible interpretation is that the Yanomama may have originally migrated from that region.

Thus, there is no evidence that the Yanomama and their current tribal neighbors evolved together in situ, with the Yanomama becoming progressively isolated. Instead it appears that the Yanomama have had rather different origins than the other tribes of the Guyana shield. Which of the two groups, the Yanomama or their neighbors, is the more recent intruder into the area is a question that awaits the acquisition of cultural and archaeological rather than genetic data. However, in view of the large-scale movements of both Arawak and Carib groups in the immediate pre-Columbian period, a case can be made for considering the Yanomama as the more autochthonous population. Their intrusion into Carib tribal areas during the past century might then be properly considered a consequence of population expansion rather than immigration from a different area.

Geographic Location and Distribution of Genetic Distance

In the context of this paper it would be of interest to represent the information contained in the matrix of genetic distances in a manner that took into account the geographical location of each tribe. One method would be to plot two of the major eigenvectors and compare the congruence of the resulting genetic map with the real geographic locations. Alternatively, the distance of each tribe from the weighted mean of all the tribes can be substituted for the vector, that value assigned to the geographic location of the tribe, and the resulting distribution of values analyzed. We have chosen the latter method since it avoids the somewhat arbitrary choice of eigenvectors and because we wish to see if the total set of genetic relationships can be manipulated into a regular geographic pattern.

For each tribe, the root mean square (RMS) distance to the centroid of the hyperspace (defined as the vector of unweighted mean gene frequencies) was calculated using the stereographic approximation. This yields a single value for each tribe (table 9). This value was then assigned to the geographic location of that tribe, and the existence of a geographic pattern was gauged by drawing contour lines around these points (figure 3). The contour lines have been drawn to incorporate

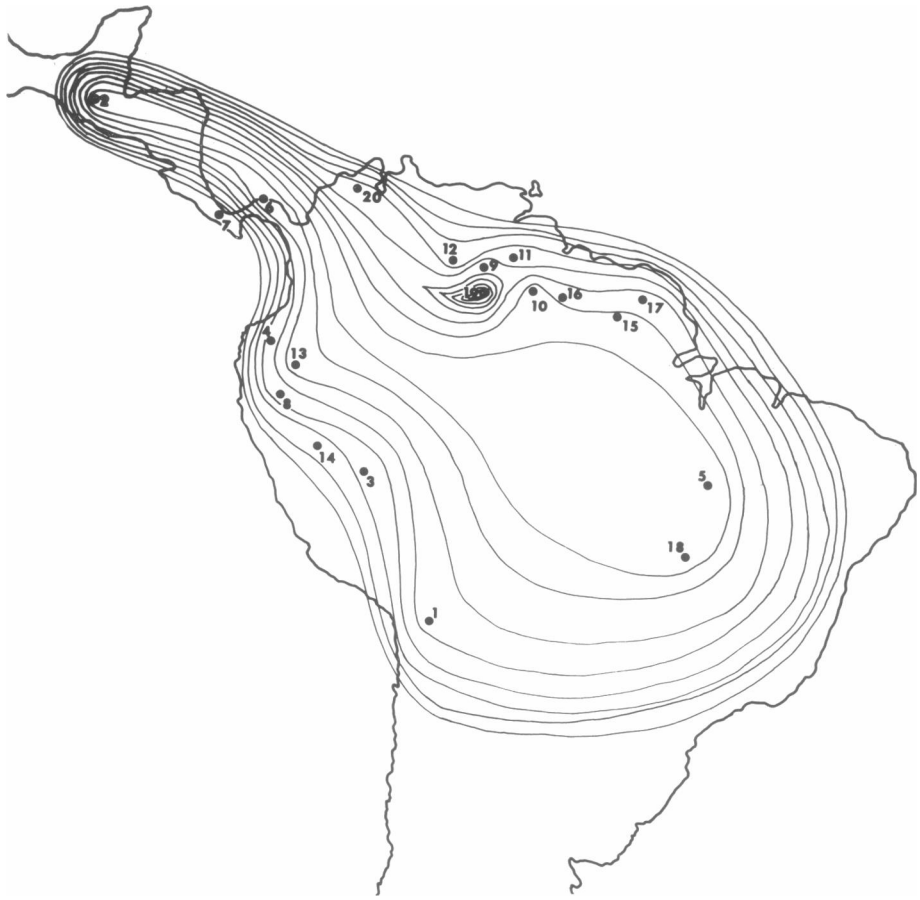

FIG. 3.—Geographic location of the 20 South American tribes and contours indicating deviation from the tribal average or centroid. The units of deviation are measured in the stereographic approximation for genetic distance (see text).

the major continental outline into the design, with the lowest contour (surrounding tribes 2, 5, 18) starting at .205 units and incrementing at intervals of .030 units thereafter. Where necessary in the interests of clarity, obvious liberties have been taken with the geography of the situation. The contours have also been smoothed by hand to give the impression of a uniform topography resulting from the scatter of 20 spot heights. Inspection of this rendition of the matrix of genetic distances reveals two points of interest with respect to the geographical structure inherent in table 7.

1. A general tendency for the genetic distance of a tribe from the centroid to be correlated with its geographic distance from a central "corridor" running from Meso-America to the Mato Grosso of Brazil. This is in part due to the assumption of a common center in the middle of the continent—hence the "corridor" uniting the Cakchiquel of Guatemala with the Cayapo and Xavante of the Mato Grosso. It is also partly due to the limited number of data points since incorporation of ad-

TABLE 9

GENETIC DISTANCE OF EACH TRIBE FROM TRIBAL AVERAGE (RMS STEREOGRAPHIC DISTANCE) AND MEASURES OF GENETIC DIVERSITY FOR 20 SOUTH AMERICAN TRIBES

TRIBE	DISTANCE FROM CENTROID (RMS)	MEASURE OF DIVERSITY	
		Homozygosity	Information
Aymara	.277	.594	0.941
Cakchiquel	.177	.556	1.035
Cashinahua	.376	.553	1.009
Cayapa	.297	.591	0.903
Cayapo	.178	.514	1.102
Cuna	.241	.590	0.983
Guaymí	.450	.645	0.830
Jivaro	.315	.556	1.003
Makiritare	.282	.524	1.091
Macushi	.215	.564	0.981
Pemon	.306	.548	1.026
Piaroa	.369	.562	0.952
Quechua	.263	.583	0.953
Shipibo	.339	.483	1.193
Trio	.223	.524	1.105
Wapishana	.243	.513	1.116
Wajana	.262	.528	1.109
Xavante	.204	.503	1.127
Yanomama	.438	.632	0.858
Yupa	.296	.553	1.033

NOTE.—See text for definitions.

ditional tribes into the analysis could well cause a significant alteration from the regular pattern displayed here.

2. The Yanomama are the only tribe that does not fit readily into the regular pattern of contours and which must be displayed as a graphic salient in the even flow of contours around the continent. This striking departure of the Yanomama from the general pattern of relationships uniting the other tribes is yet one more indication of their genetic distribution as an independent population.

We emphasize the provisional nature of this representation. Twenty points is inadequate to define a relationship of this complexity with any assurance! That such a regularity may exist is presented as a hypothesis to be tested in further work. There will obviously be future modifications in the contour lines. For example, no effort has been made to project below the twenty-fifth parallel because there are no data available.

HOW DOES THE RELATIVE GENETIC DIVERSITY OF THE YANOMAMA COMPARE WITH THAT OF OTHER TRIBES?

In attempting to assess the evolutionary potential of populations in terms of their genetic attributes, some measure of genetic diversity seems most relevant. If measures of genetic diversity are devised so that an increase in the number of alleles, K, and the approach of allelic frequencies to $1/K$ both cause an increase in the

measure, then a population with mean gene frequencies giving a high value can be considered to have a greater evolutionary potential than a population with a low value—at least in respect to the overall degree of fixation—irrespective of whether selection pressures or stochastic events are of prime importance. As the Yanomama are distinct from other South American tribes in terms of their genetic relationships, it becomes germane to investigate whether they are equally distinctive in terms of genetic diversity and, if so, whether they are appreciably more or less diverse than the average tribe. To measure genetic diversity we employ two statistics as follows.

Index of Genetic Homozygosity

This measure, which indicates the approach to fixation of a population, is derived for a single locus with K *alleles* as follows:

$$J = \sum_{k=1}^{K} p_k^2.$$

The values are averaged for all loci to give a single measure indicative of the average genetic diversity contained within the population [6].

Index of Genetic Information

This latter measure, the Shannon-Weaver measure of information, is defined as

$$H = -\sum_{k=1}^{K} p_k \log_2 p_k.$$

Given its use in ecology as a measure of community diversity, it is also a suitable measure for genetic diversity [7].

In table 9 we present the results of these two measures for the 20 tribes. Inspection reveals that the average homozygosity based on the six polymorphic loci ranges from .483 (Shipibo) to .645 (Guaymí), with a mean of .555. The Yanomama, with a value of .632, are considerably more homozygous than the other tribes and are, with the Guaymí, outliers in the distribution of homozygosity values. The index of genetic information indicates the same trend with respect to genetic diversity. The Shipibo, with a value of 1.193, represent the tribe with the greatest level of genetic diversity while the Guaymí are least diverse with a value of 0.830. The Yanomama value of 0.858 falls rather close to the Guaymí value and well below the tribal average of 1.017.

This range in diversity values between tribes is somewhat greater than that found between Bushman and urban colored populations in southern Africa [34]. Whether this apparent difference reflects a real biological distinction between the populations of these two continents or whether it is a function of the smaller number of polymorphic loci selected for our study is an intriguing question awaiting the acquisition of further data. However, relative to the other South American tribes, both measures employed in this study identify the Yanomama (along with the Guaymí)

as possessing appreciably less genetic diversity than the tribal average. This greater degree of "homozygosity" for the Yanomama implies a relatively long period of isolation for the tribe with reduced opportunity for intertribal gene flow, in corroboration of the results of the analyses of genetic relationship.

Discussion

Although many points have been raised by the data in this paper, we will limit the discussion to the two which bear on tribal evolution.

Essential Isolation of the Yanomama from Other Indian Tribes for a Considerable Period of Time

We have previously suggested [2] on the basis of cultural [35, 36], linguistic [13], and genetic data [1] that the Yanomama must be viewed as having been in relative isolation, for a considerable period of time, from all other Indian tribes adequately studied to date. The results of this study serve to strengthen that conclusion. The Yanomama (along with the Guaymí) are strikingly distinct from the other 18 tribes as measured by Genetic Distance or Nei's Measure of Genetic Identity. They also display considerably less genetic diversity, whether measured by an Index of Genetic Homozygosity or an Index of Genetic Information. It is of obvious interest to attempt to estimate the period of time in which these differences have arisen. An upper limit to the length of time the Yanomama could have been separated from the other tribes of South America, on the assumption that the ancestors of all tribes entered South America within a reasonably brief time span, is given by the oldest radiocarbon dates from human habitation sites in northern South America, 10,000–20,000 B.P. [37]. Another approach, which in theory provides an independent estimate of the point of divergence from all tribes, utilizes glottochronology. Here the data are both scanty and conflicting. Spielman et al. [3] estimate that the most different Yanomama sublanguages have been differentiating for a period of 600–1,200 years. Comparison of other languages with that of the Yanomama yields ambiguous information. The most similar language is Shipibo with 26% cognates yielding a time depth of 1,600–3,300 years. Yet this tribe is the most distinct genetically from the Yanomama; it is uncertain which of the pieces of evidence is most reliable. The other language comparisons yield estimates of 4,000–5,000 years. An extension of the glottochronological data is another target for future research. If the present preliminary findings are sustained, they suggest that the isolation of the Yanomama may extend back into the last 30% of the Indians' time in South America.

Biological Relationships of Central and South American Tribes with One Another

So far we have analyzed the genetic relationships of the 20 tribes in the phenetic sense only. We now wish to consider the possible historical interpretations that might be placed on these descriptions of the extant genetic relationships of these tribal populations. Inspection of the two dendrograms in figures 1 and 2 indicates that

neither is very satisfactory when viewed as a phylogeny. Three lines of reasoning present themselves.

1. Methods estimating phylogenetic relationships are based on the assumption of a continuous and monotonic distribution of genetic relationships over time. Major population units may be sufficiently large and isolated for these assumptions to hold, while tribal village populations which *do* violate the assumptions may have split sufficiently frequently without subsequent fusion for a phylogenetic interpretation of the dendrograms to hold [30, 38]. Tribal populations which may have undergone both extensive fissioning *and* extensive fusions may very well not be amenable to such phylogenetic interpretations.

2. Unrelated tribes may be "forced" into associations by the analysis simply because this rather small sample of tribes does not permit the alternative solutions that might obtain if considerably more tribes were in the analysis.

3. Representation of the phenetic relationship between populations by a dendrogram is only one *estimate* (albeit one which satisfies some optimality criteria), and radically different topologies with quite different phylogenetic interpretations may be only slightly suboptimal in terms of the criterion used. Since the precise reconstruction of a set of genetic relationships is, like any other approach, fallible, strategic considerations suggest inspecting some arbitrary fraction of the best dendrograms to see which fits best with the other available information. An approach which may have much in its favor as more data become available is to limit the dendrogram type of analysis to the number of tribes permitting a *convenient* examination of all possible relationships. Representations based on different types of biological data (anthropometrics, genetic markers) can first be searched for the several that fit the biological evidence best, and then these examined in the light of linguistic and cultural data. By working with overlapping sets one can gradually construct the most consistent total picture.

Earlier we demonstrated the effect of sampling error on the estimation of genetic relationships between Yanomama villages. This in turn leads to some distortions in the estimation of intervillage phenetic relationships (e.g., principal components, dendrograms, etc.) as evidenced by table 6, where the differences in ranking for the corresponding entries for each set of samples resulted in somewhat different estimates of phenetic relationships. While we hesitate to generalize from such a small set of repeat observations, the sampling error may be sufficiently large that the estimated relationships between Yanomama villages should be interpreted with some caution, especially where villages are represented by proportionally small samples. In this connection, we remind the reader that there are a variety of other sources of error in estimating relationships from such characteristics as blood types, anthropometrics, or dermatoglyphics [39]. Nevertheless, it is also apparent that for some sets of villages the phenetic (and descent) relationships do appear to be adequately estimated [33, 38, 39]; whether this results from a serendipitous choice of populations together with robust estimation procedures is a question that warrants further study. To the extent that tribal populations are likely to be even more cursorily sampled and characterized by unrepresentative gene frequencies than are

Yanomama villages, the distortions of phenetic (and descent) relationships will be exacerbated. We conclude that realistic estimates of relationships between tribal populations are extremely dependent on the existence of an extensive body of representative biological data for each tribe.

The isocline type of representation should be viewed as a supplement rather than a substitute for other approaches. It will not lead to unambiguous interpretations. Thus, when one views these isoclines with no regard to the topography of South America, two very different interpretations come to mind. One interpretation is that the overall distribution of gene frequencies in these tribal populations is simply due to the average effects of migration and relative isolation over a long period of time. Hence tribes in the center of the distribution will tend to receive more migrants and accordingly deviate less from the overall mean. This interpretation suggests that the initial patterns of gene frequency distributions due to such factors as colonization and the fission-fusion process eventually become obliterated.

The second interpretation is that these patterns are relics of the original pattern of colonization of South America. If so, three alternative colonization patterns can be postulated. One envisions a primary migratory thrust around the northern foothills of the Andes, in Colombia, with increasing diversification as man moved out from this corridor. Another sees the original intruders as splitting into two streams in Colombia, one following the Atlantic and the other the Pacific Coast, with reconstitution of the "original" gene pool when offshoots of these two streams met in central South America. Both of these explanations overlook the barrier to migration created by the Andes: the Aymara, Cayapa, and Quechua tribes are west of the Andes. The third pattern, and the one we favor, visualizes the peopling of South America in three streams, two following the coasts and one directed centrally. There then ensued a process of intertribal exchange, most extensive in the central region of South America, which most nearly erased the results of this diversification in central South America. No matter which of these explanations proves correct, the Yanomama stand as an enigma. The present data are so scanty that any further speculation seems premature. There are at least another 20 tribes in South America which can be brought into the context of both of the types of analysis which have been pursued. Hopefully, the finer delineation they will permit, together with linguistic and cultural data, will lead to an improved understanding of human evolution in South America and, by example, elsewhere.

Summary

In this paper we present the results of blood group typings for a total of 33 villages distributed among five South American Indian tribes—Yanomama (21 villages), Makiritare (eight villages), Macushi (two villages), Piaroa (one village), and Wapishana (one village). These new results for the Yanomama and Makiritare tribes have been combined with those previously reported to allow a better appreciation of the distribution of allelic frequencies in the tribes.

The relationship of the Yanomama to other South American Indian tribes is investigated using data on six polymorphic loci (Rh, MNS, Fy, Jk, Di, Hp). By use

of four genetic measures (two of genetic relationship and two of genetic diversity), we demonstrate that the Yanomama are genetically unique among a sample of 20 South American tribes. In addition, the Yanomama show somewhat less genetic diversity for the six loci analyzed than the average South American tribe. Taken together, these results indicate a rather long period of isolation for the population antecedent to the Yanomama—perhaps since the time of entry of man into the South American continent. The pattern of genetic relationships and genetic diversity for the 20 tribes is consistent with the hypothesis that evolution in South America proceeded by a process of fission-fusion leading to isolation of subpopulations with subsequent genetic differentiation as a consequence of population isolation. The uniqueness of the Yanomama appears to stem entirely from such a process, there being no evidence of any selective differential for the loci analyzed.

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