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Bioassay of Kinship in a South American Indian Population

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INTRODUCTION

Extensive data concerning the Makiritare Indians, a relatively undisturbed tribe of southern Venezuela, have recently been published [1–5]. Eleven polymorphic systems were studied in each of seven villages, sampling between 57% and 94% of the residents. All blood typings were performed in duplicate, so that typing errors are likely to be rare. A history of the recent movements of these villages is reported, as well as some data on migration between villages. Using phenotypes for bioassay of kinship [6], we shall compare these observations with other indicators and predictors of kinship, examine isolation by distance, and interpret various topologies constructed from the kinship matrix, which contains all the information in the record about genetic differentiation.

Following Workman and Niswander [7], one could test the heterogeneity of gene frequencies among villages by χ^2 and, if significant, conclude that the gene pools are different. However, the value of such significance tests is questionable [8], since the null hypothesis corresponds to origin of the villages in the present generation by strictly random sampling. The past history of the villages and their very existence are formal disproof of this hypothesis. What we require is not a test of the significance of divergence, but an estimate of its extent.

Considering that the villages correspond more or less to the local breeding units, one could test for Hardy-Weinberg proportions within samples, but statistical tests of random mating in small samples are notoriously unreliable [9]. Random mating within villages therefore seems to us to be a reasonable approximation.

Tests of randomness of differentiation are also weak. In bioassay we are interested in the mean kinship for as many loci as can be studied, without assuming whether differentiation is random. Studies such as this one tend to concern regions and populations so small that genetic drift is likely to be much more important than diversifying selection.

BIOASSAY OF KINSHIP

A new method of bioassay of kinship has been developed by Morton et al. [6] which estimates kinship using information given by several genetic systems and

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should give better estimates of the coefficients of kinship between and within populations than do phenotype pairs. These estimates can be fitted to the function

$$\phi(d) = (1 - L)\, ae^{-bd} + L, \tag{1}$$

describing isolation by distance, where ae^{-bd} is the probability that two genes sampled randomly at distance d are identical by descent. This function is derived from the theory of Malécot [10–12] and simplified by taking the dimensionality parameter c equal to zero, which appears by experiment to be generally true at small and medium distances [13]. Malécot [14] has recently derived $c = 0$ for bidimensional isotropic migration between discrete populations when the effective systematic pressure exceeds stepping-stone migration.

A problem has to be solved at this point: to estimate any ϕ_{ij} between two villages with the information furnished by several genetic systems, we have to choose weights so that

$$\phi_{ij} = \sum_h W_{ijh}\, \phi_{ijh} / \sum_h W_{ijh}, \tag{2}$$

the sum extending over all systems. We take

$$W_{ijh} = N_{ih} N_{jh}\, [1 + W(k_h - 1)] / (N_{ih} + N_{jh}), \tag{3}$$

where N_{ih} and N_{jh} are sample sizes for the hth system, k_h is the contribution per individual to the information about $F = 0$ when gene frequencies are known exactly in a sample of phenotypes [15], and W is chosen to minimize the error variance in the least-squares fit to equation (1). For the Makiritare data we obtained $W = .17$.

The hybridity θ_{ij} between populations i and j is defined [6] as

$$\theta_{ij} = (\phi_{ii} + \phi_{jj} - 2\phi_{ij}) / (4 - \phi_{ii} - \phi_{jj} - 2\phi_{ij}). \tag{4}$$

While not a probability, this parameter is useful because in Malécot's theory for isolation by distance,

$$\theta(d) = a(1 - e^{-bd}) / [2 - a(1 + e^{-bd})]. \tag{5}$$

The expected value of $\theta(d)$ increases from zero within populations to an asymptote at large distances and so provides a reasonable measure of genetic differentiation. Least-squares estimates of a and b from equation (5) are expected to be consistent with those obtained from equation (1) when L is estimated simultaneously. Here L represents kinship at large distances within the tribe and so is a measure of the drift of contemporary gene frequencies from the founder population.

Estimates of kinship for each pair of villages are reported in table 1 using 11 polymorphic systems: Hp, Rh, Acp, Gc, PGM_1, MNSs, Le, Fy, Jk, P, and Di. There is good agreement with migration history. The pairs BD-C and G-HI with a high intermarriage rate have high kinship; A-F with a common history have a similarly high value; and the pairs A-C and C-F, of distant origin, have low kinship. Estimates tend to be negative for pairs of villages at large distances, which are less closely

TABLE 1

THE KINSHIP MATRIX FOR SEVEN VILLAGES FROM BIOASSAY OF 11 SYSTEMS

	A	BD	C	E	F	G	HI
A	.0600	—.0091	—.0592	—.0104	.0122	.0069	—.0094
BD	...	.0090	.0204	—.0010	—.0028	—.0165	—.0101
C	...	...	.1061	—.0019	—.0328	—.0348	—.0054
E	...	...	...	.0087	.0011	—.0012	—.0021
F	...	...	...	...	.0762	—.0194	—.0243
G	...	...	...	...	...	.0380	.0197
HI	...	...	...	...	...	...	.0232

related than random villages. The results may be summarized by two coefficients: ***random kinship,*** defined by

$$\phi_R \equiv \sum_{i,j} N_i N_j \phi_{ij} / \sum_{i,j} N_i N_j, \tag{6}$$

where

$$N_i = \sum_h N_{ih} W_h,$$

and ***mean kinship*** within villages,

$$\phi_0 \equiv \sum_i W_{ii} \phi_{ii} / \Sigma W_{ii}. \tag{7}$$

We obtain $\phi_R = -.0009$ and $\phi_0 = .0350$. Note that ϕ_R is close to $-1/2\Sigma N_i$, as expected in sampling without replacement. The mean kinship within villages relative to panmixia in the array of seven villages is $(\phi_0 - \phi_R)/(1 - \phi_R) = .0359 \doteq \phi_0$.

Estimates of hybridity from equation (4) are given in table 2, together with genetic distances computed by Ward and Neel [4]. The genetic distances have been divided by $26 - 11 = 15$, the number of independent alleles, so as to make them comparable with hybridity apart from errors of estimate [6]. There is gross

TABLE 2

COMPARISON OF HYBRIDITY (UPPER TRIMAT) WITH GENETIC DISTANCE (LOWER TRIMAT)

	A	BD	C	E	F	G	HI
A	...	.0230	.0733	.0243	.0301	.0223	.0267
BD	.0278	...	.0208	.0050	.0233	.0201	.0131
C	.0458	.0221	...	.0323	.0632	.0552	.0372
E	.0288	.0160	.0293	...	.0212	.0124	.0091
F	.0319	.0324	.0452	.0307	...	.0386	.0374
G	.0269	.0240	.0369	.0189	.0333	...	.0054
HI	.0323	.0223	.0311	.0203	.0323	.0161	...

NOTE.—Genetic distances from table 2 of Ward and Neel [4] were divided by 15, the difference between 26 alleles and 11 loci.

similarity between the two indices, with highest differentiation for the pairs A-C and C-F and least differentiation for BD-E and G-HI, as expected from historical relationship and migrations.

Estimates of kinship and hybridity as a function of distance are given in table 3, where

$$\phi(d) = \Sigma W_{ij} \phi_{ij}/\Sigma W_{ij}, \qquad (|i - j|) = d,$$

$$\theta(d) = \Sigma W_{ij} \theta_{ij}/\Sigma W_{ij},$$

and $d = 0$ is taken for pairs from the same village. The value of L is —.0096, which is the kinship of villages at large distance. Estimates from kinship and hybridity are consistent for the Malécot parameters a (.0458, .0534) and b (.0435, .0400). Essentially the same estimates are obtained by equating the limit of large distance to any value between 25 and 140 km.

TABLE 3

DECREASE OF KINSHIP WITH DISTANCE FOR SEVEN VILLAGES

Distance Class (Km)	Class Value	Weight	$\phi(d)$
0	0	2,855	.0350
0-25	12.5	360	.0204
25-40	32.5	930	.0077
40-70	55.0	900	—.0154
70-100	85.0	785	—.0269
100-140	120.0	675	—.0004
140-195	167.5	1,799	—.0153
195-245	220.0	2,310	—.0039

Source	a	σ_a	b	σ_b	L	σ_L	Residual Variance
$\phi(d)$	.0458	.0075	.0435	.0266	—.0108	.0047	.1148
$\theta(d)$	.0534	.0097	.0400	.0424	...	...	.1313
$\phi(d)$, with $L = 0$	.0352	.0074	.0691	.0761	0	...	.1606
$\phi(d)$, with $L_d > 25$	.0438	.0058	.0475	.0261	—.0087	...	.0997
$\phi(d)$, with $L_d > 70$	.0454	.0057	.0443	.0221	—.0104	...	.0957
$\phi(d)$, with $L_d > 140$	.0439	.0058	.0472	.0256	—.0089	...	.0991

Roisenberg and Morton [16] used published data to bioassay kinship by phenotype pairs, which have been shown by Harpending [17] and Morton [18] to underestimate kinship within localities by about one-third. When we correct for this, their estimates become $a = .0379 \pm .0096$ and $b = .0032 \pm .0016$. These are substantially below the Makiritare values. As Roisenberg and Morton note: "There may have been a tendency to sample large villages preferentially, which would tend to underestimate *a* and *b*." Imaizumi and Morton [19] observed a striking difference in the Malécot parameters for New Guinea when attention was focused on isolated areas, excluding towns. Observing rather small values of *a* and *b* from prefectural samples in Japan, Imaizumi and Morton [20] cautioned that "future studies of population structure should be careful not to lump small communities into larger regions, since most migration is over small distances." As might be expected, the method of sampling is of critical importance in bioassay of kinship, and the Malécot parameters necessarily apply only to the populations of which the samples are representative.

Fitch and Neel [21] selected 12 "tribes" sampled extensively but presumably nonrandomly. In fact, no investigator of South American Indian populations has claimed to have sampled villages at random within tribes. The concept of tribe is itself imprecise, and in some cases corresponds to what are conventionally considered linguistic groups. These sampling problems sharply limit the utility of Wright's hierarchical model, which in this context we may express as $\phi_T = \phi_0 + (1 - \phi_0)\phi_V$, where ϕ_T is the kinship of two random Makiritare from the same village, relative to South American Indians as a whole; ϕ_0 is the conditional kinship relative to the seven village samples; and ϕ_V is the kinship of two Makiritare taken at random from the pool of the seven villages, relative to South American Indians.

We have just estimated $\phi_0 = .0359$. The mean kinship of the seven villages relative to the 13 tribes is estimated in table 4 as .0635, which we may take as

TABLE 4

KINSHIP (UPPER TRIMAT) AND HYBRIDITY (LOWER TRIMAT) FOR 13 TRIBES FROM BIOASSAY WITH SIX SYSTEMS

	Ay	Ck	Cy	Cu	Gu	Ji	Pe
Aymara (Ay)	.0541	.0096	.0144	—.0047	—.0149	—.0067	—.0032
Cakchiquel (Ck)	.0135	.0149	—.0024	—.0001	.0121	—.0003	—.0050
Cayapa (Cy)	.0188	.0169	.0453	—.0001	—.0298	.0031	.0004
Cuna (Cu)	.0208	.0100	.0193	.0234	.0204	—.0039	.0037
Guaymi (Gu)	.0547	.0298	.0561	.0293	.1168	.0177	—.0290
Jivaro (Ji)	.0245	.0114	.0169	.0166	.0288	.0272	—.0213
Pemon (Pe)	.0219	.0133	.0182	.0117	.0523	.0243	.0268
Quechua (Qu)	.0127	.0101	.0146	.0176	.0381	.0128	.0154
Shipibo (Sh)	.0867	.0616	.0855	.0955	.1362	.0799	.0607
Xavante (Xa)	.0372	.0170	.0296	.0137	.0368	.0110	.0170
Yanomama (Ya) ...	.0369	.0265	.0257	.0356	.0499	.0352	.0366
Yupa (Yu)	.0599	.0366	.0265	.0214	.0556	.0250	.0249
Makiritare (Ma) ...	.0229	.0173	.0415	.0222	.0565	.0280	.0193

ϕ_V on the assumption that the tribes are representative of South American Indians. Therefore, the mean kinship of two Makiritare from the same village is $\phi_T = .0971$. Tribal affiliation is estimated to account for $.0635/.0971 = .65$ of the differentiation of villages among South American Indians. This value is of course subject to many reservations because of nonrandom sampling, but it supports and provides some quantification to the conjecture of Salzano et al. [22] that "regardless of the situation at any one moment, over a time span of a relatively few generations, the entire tribe probably may be regarded as the breeding unit."

Confirmation might be sought in calculations of the inbreeding coefficient from pedigrees, assuming this to approximate mean kinship within a village. Makiritare data are not available, but Salzano et al. [22] obtained .004 for the Xavantes and .005 for the Caingang, results which led the investigators to suggest that the mean inbreeding coefficient in complete pedigrees might be in the range of .02–.03, not far below our estimate of $\phi_0 = .0359$ and in quite reasonable agreement, since the Makiritare villages appear smaller and more isolated, although perhaps of shorter duration. The fraction of kinship actually ascertained through pedigrees is discouragingly small, and with the small migration rates of contemporary Makiritare, it is not possible to obtain convergence by a method to extrapolate from incomplete data to the total coefficient of inbreeding [23].

TOPOLOGY OF KINSHIP

To summarize information on relationship between villages furnished by kinship and hybridity matrices, we resort to eigenvectorial and tree representations.

TABLE 4 (*Continued*)

	Qu	Sh	Xa	Ya	Yu	Ma
Aymara (Ay)	.0113	—.0079	—.0305	—.0019	—.0452	.0106
Cakchiquel (Ck)	.0005	—.0101	—.0100	.0058	—.0168	.0031
Cayapa (Cy)	.0087	—.0275	—.0201	.0274	.0143	—.0282
Cuna (Cu)	—.0126	—.0523	.0027	—.0088	.0175	—.0006
Guaymi (Gu)	.0027	—.0977	.0029	.0171	—.0078	—.0208
Jivaro (Ji)	.0029	—.0199	.0086	—.0003	.0095	—.0099
Pemon (Pe)	—.0044	.0228	—.0039	—.0064	.0092	.0064
Quechua (Qu)	.0213	.0153	—.0135	.0078	—.0296	—.0040
Shipibo (Sh)	.0673	.2118	.0216	—.0524	—.0496	.0662
Xavante (Xa)	.0215	.0624	.0338	—.0353	.0248	.0198
Yanomama (Ya)	.0266	.1162	.0538	.1052	.0161	—.0740
Yupa (Yu)	.0445	.1101	.0187	.0403	.0909	—.0349
Makiritare (Ma)	.0236	.0470	.0145	.0801	.0555	.0635

Kinship and cognates constitute similarity matrices to which can be associated a representation of the populations in multidimensional space such that the interdistances reflect those similarities. Orthogonal transformation of a kinship or cognates matrix after centroid adjustment gives a set of independent vectors for which it can be shown [24] that the pair associated with the largest eigenvalues in absolute value gives the best two-dimensional representation of those distances.

These two-dimensional representations can be plotted simultaneously with geography after rotation to maximum congruence [24]. The norms of the two configurations are taken as equal, and the rotation leaves invariant the norms as well as the interdistances. Goodness of fit is measured by Carroll's measure of disagreement, C_p, which is the ratio of the minimum distance between configurations to the norm. The smaller the C_p, the better is the fit. This representation measures deviations from an isotropic model of exchanges. Figure 1 shows such a representation for the Makiritare villages. Despite recent population movements, there is a clear relation between kinship and current geographic location.

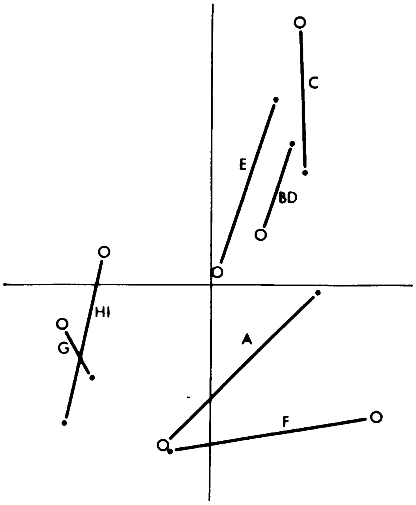

FIG. 1.—Eigenvectorial representation of kinship in Makiritare villages after rotation to maximum congruence with geography. Dot = geographic location; circle = genetic location.

Figure 2 gives for the same data a tree representation, which is here based on phenetic similarity rather than on an attempt to reconstruct a phylogeny. The clustering method used for our program ARBOR averages the two populations with the smallest pairwise hybridity and reduces the matrix by replacing the hybridity coefficients involving those populations with their weighted mean. Weights are generally unity but may be population or sample size. At any step, the weight attributed to a new cluster is the sum of the weights of the contained groups, and so the corresponding hybridity is the mean between two random individuals from different clusters, the sampling being proportional or uniform, according to the weighting

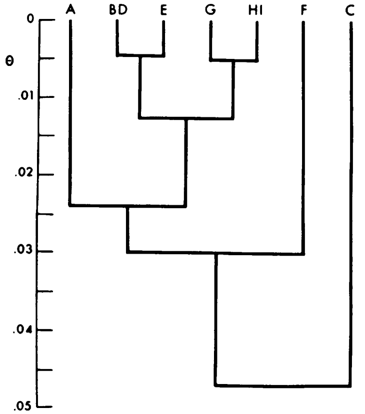

FIG. 2.—Dendrogram of Makiritare villages ($R = .798$)

system used. The goodness of fit of these representations can be measured by the correlation between observed and predicted values.

Using the 12 tribes selected by Fitch and Neel [21] and the pooled data on the Makiritare, eigenvectorial representation (fig. 3) and a dendrogram with equal weights (fig. 4) describe the similarities between tribes: Aymara (Ay), Cakchiquel (Ck), Cayapa (Cy), Cuna (Cu), Guaymi (Gu), Jivaro (Ji), Pemon (Pe), Quechua (Qu), Shipibo (Sh), Xavante (Xa), Yanomama (Ya), Yupa (Yu), and Makiritare (Ma). Although the cophenetic correlation is rather high (.85) and highest with equal weights, sample weights give a different representation. Moreover, neither can be explained in terms of geographical proximity or linguistic relationship, and so we do not attempt to interpret the phenetic dendrogram as a phyletic cladogram.

DISCUSSION

Pedigree data to compare with kinship bioassay have not been published for the Makiritare. Experience with other South American Indians suggests that the frac-

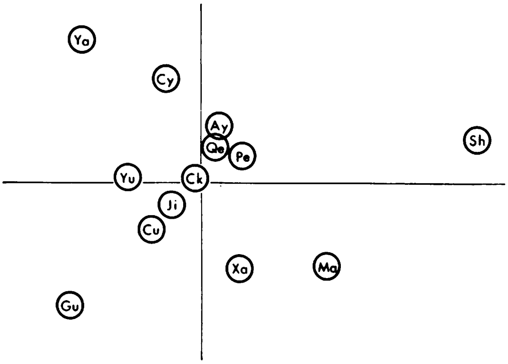

FIG. 3.—Eigenvectorial representation of kinship in American Indian tribes. $R = .88$; $f(\lambda) = .61$.

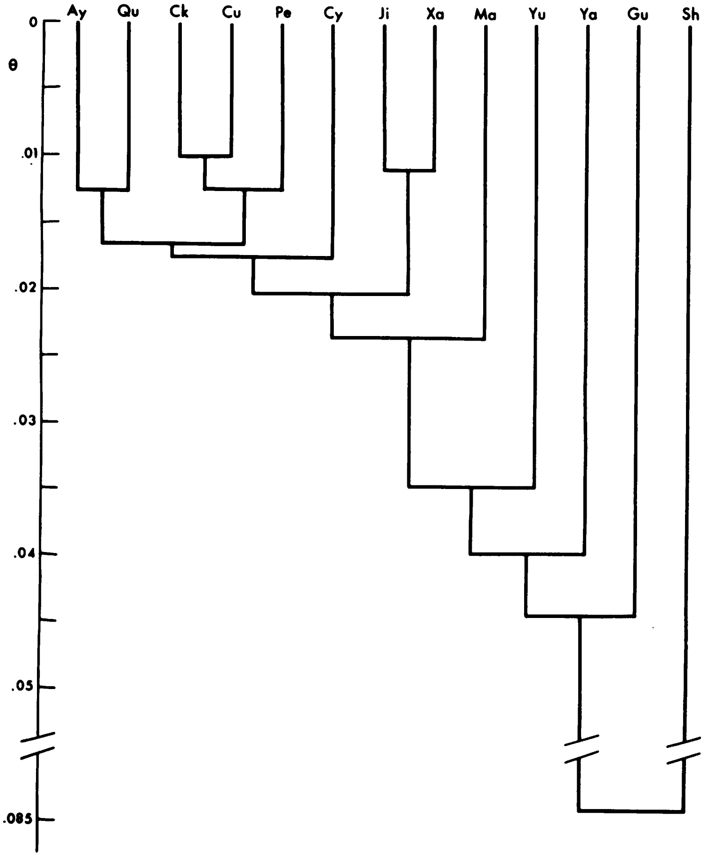

FIG. 4.—Dendrogram of Indian tribes ($R = .855$)

tion of inbreeding which can be ascertained through pedigree data is too small for reliable extrapolation to total inbreeding [22].

We tried to construct a migration matrix from the data reported by Ward and Neel [4]. Unfortunately, the sizes and migration patterns of regional samples of Makiritare and Yanomama are unknown. The long-range migration rate based on two mestizo children in 1,322 is so small as to compel the inference that either the observed villages are of very short duration or long-range migration was greater in the past, since otherwise at the observed population sizes the bioassayed kinship would be higher. The reported long-range pressure is so small that approach to equilibrium is exceedingly slow, and so no equilibrium condition can be assumed. When adequate data are available, it will be interesting to compare the kinship bioassay with prediction from migration, as has been done for Oceanic populations [25]. Ward and Neel [4] calculate a function of the migration matrix which they call an index of genetic isolation. It differs from the migration matrix by giving no predictions of kinship.

The phenotype bioassay estimate of mean kinship within Makiritare villages relative to panmixia in the array is .036 relative to the contemporary array, .046 relative to founders of the villages, and .097 relative to all South American Indians. Individuals in the same village are about as closely related as first cousins in an indefinitely large, panmictic population. Similar results have been obtained for Micronesia [25] and Melanesia [26].

Of the three representations attempted for the Makiritare villages, the eigenvectorial representation gives the highest correlation between observed and "summarized" values. Both the eigenvectorial representation and the dendrogram attest to the relatedness of BD to E and G to HI, the four villages clustering with a mean hybridity of .01, while A, F, and C are more distant. However, these two representations fail to show the close recent relationship between BD and C. Since interpretation of the dendrogram involves hybridization, which is formally excluded by a cladogram, it is meaningless to interpret the dendrogram as a branching process.

The eigenvectorial and dendrogram representations of the relationships between the 13 tribes of Central and South America cannot be explained by geographic proximity or common linguistic affiliation. Besides errors of estimates, the rarity of exchanges between these tribes and their origin from small numbers of founders suggest that most of the distances measured by hybridity reflect random evolution, making phylogenetic interpretation specious. Similarity even of neighboring tribes is so slight, as indicated by inspection of table 4, that there simply is not enough information in the six polymorphic systems to construct a reliable phylogeny, even if a model of fission without subsequent hybridization had any biological meaning.

Fitch and Neel [21] embraced a phylogenetic interpretation with more enthusiasm. They were struck by the similarity of Guaymi and Yanomama, which does not appear in our estimate of kinship or hybridity (table 4) or in the eigenvectorial representation (fig. 3). Their inference that Yanomama are separated by one fission from Guaymi and by five fissions from Jivaro is not open to discussion, since the fissions are entirely hypothetical, ignore the population exchanges which are an essential part of microevolution, and receive no support from linguistic, cultural, or ethnohistorical evidence. We are in complete agreement with the convention of numerical taxonomy [27] that the assumption of a cladogram is only useful as an hypothesis to be tested against other evidence, which is available for the seven villages whose history is short, but totally lacking for the 13 tribes.

SUMMARY

At the present state of the evidence, kinship in South American Indians cannot be predicted reliably from pedigrees or migration. However, kinship bioassay is applicable. For seven Makiritare villages studied by Ward and Neel, the mean kinship within a village is .036 relative to the contemporary array, .046 relative to founders, and .097 relative to other South American Indians. Estimates of the Malécot parameters for isolation by distance are consistent for kinship and hybridity. There is a rapid decline of kinship with geographic distance within the tribe ($b = .04/\text{km}$). Various representations of these data reflect recent history and

migration of the villages, but the same representations of 13 tribes have, as might be anticipated, no demonstrable relation to phylogeny.

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Symposium on Drugs and the Unborn Child

A Symposium on Drugs and the Unborn Child will be held at the Commodore Hotel in New York City March 15–16, 1973. The purpose of the 2-day session is to provide a forum where pediatricians, obstetricians, pharmacologists, and scientists actively working in the field of human development can meet to discuss recent advances and unsolved problems in fetal pharmacology.

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