Population Structure and Genetic Differentiation among 16 Tribal Populations of Central India

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Abstract Genetic polymorphisms for six blood groups, three red cell enzymes, three serum proteins, and hemoglobin were examined in sixteen central Indian tribal populations. Nine of the tribes belonged to Orissa, five to Madhya Pradesh, and two to Maharashtra. Eleven tribes spoke the Dravidian language, three Indo-Ayran, and two the language of the Austro-Asiatic families. The population structure of these tribal populations was analyzed at the inter- and intrastate and linguistic levels, using data for 13 genetic systems (38 alleles or haplotypes). Nine of the 13 loci showed significant heterogeneity in the 16 tribes, and the pattern of heterogeneity was also discernible in the different states and in the Dravidian-speaking tribes. As expected, the extent of genetic differentiation or gene diversity was the highest so far reported from central India. The mean F_{IS} and H_S for each locus in the different state, linguistic, and total tribal groups were consistently higher than the F_{ST} and G_{ST} values, respectively, showing that the genetic structure of each tribe is highly influenced by inbreeding. In a genetic affinity analysis by genetic distance the Indo-Aryan and Austro-Asiatic language groups showed little affinity with each other, although there was some tendency toward geographic affinity. The present analysis indicates that, in addition to genetic drift, gene flow, and selection, the genetic structure of the populations of central India is also highly influenced by sociocultural adaptation and inbreeding.

The central belt of India stretches from the state of West Bengal in the east to Maharashtra in the west, passing through the states of Orissa, Bihar, and Madhya Pradesh (Figure 1). From an ethnographic point of view central India has been the home of many autochthonous tribes living in virtually inaccessible hill and forest environments that inhibited gene flow among the tribal groups. Since early times the aboriginal tribal groups have been living in near

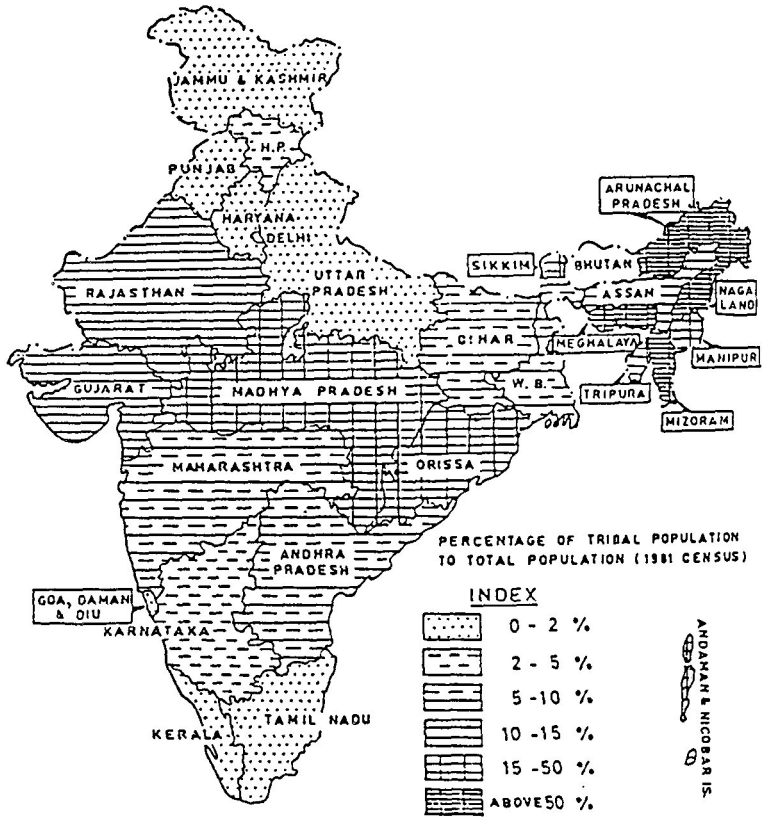


Figure 1. The three central Indian states (Orissa, Madhya Pradesh, and Maharashtra) from which the tribal populations were collected and the distribution of tribal populations in India.

isolation and have evolved their own morphogenetic characteristics in their respective ecological niches.

The numerical strength of the tribal populations in the states of India is shown in Figure 1. According to the 1981 census, in the 700 tribal populations there were approximately 52 million people, constituting 7.81% of the total population of India. The central region of India accounts for 63% of the entire tribal population of the country. Recently, Malhotra and Vasulu (1993) analyzed the size of 125 tribes of the central regions of India and observed that half of them are numerically small (size ranging from 1,000 to 25,000), whereas 22% of them have a population size greater than 100,000.

The tribes are by no means homogeneous in their history, language, culture, or social organization. There are tribal groups belonging to each of the four main linguistic families (Austro-Asiatic, Dravidian, Indo-European,

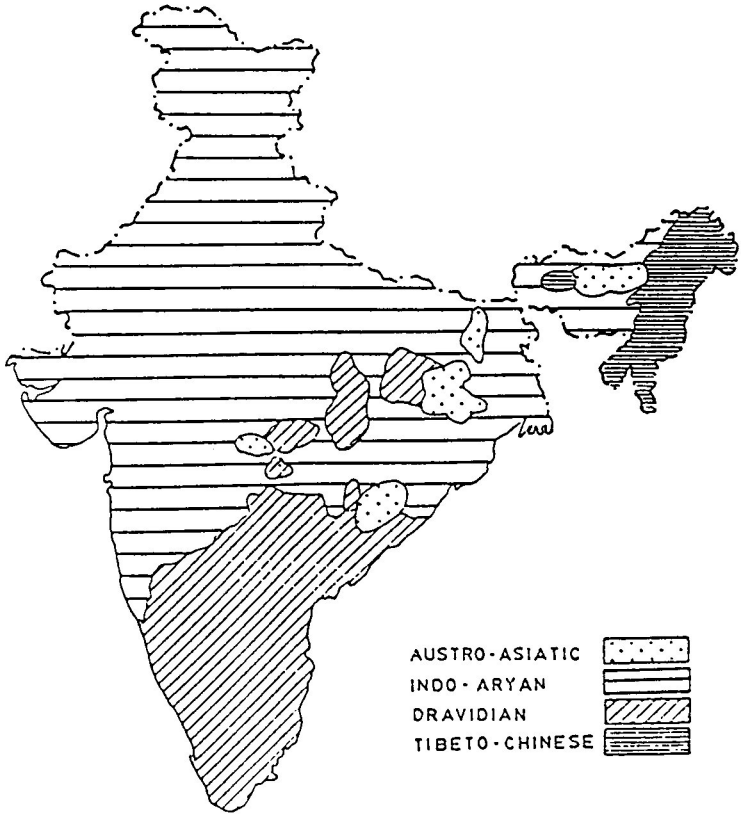


Figure 2. Geographic distribution of four language families in India.

and Tibeto-Burman); the Austro-Asiatic languages are spoken exclusively by tribal populations (Figure 2). In fact, in this relatively small central region, history has brought together numerous tribes belonging to all four language families. The Dravidian-speaking tribes of this region can be considered the descendants of the original inhabitants of India, who adopted Dravidian in preference to their original languages (Fuchs 1973).

Since the beginning of the twentieth century, several eminent scholars have provided definitive information on kinship organization, lifestyles, political organization, material culture, religion, and folklore of the tribes of central India (Russell and Hiralal 1916; Grigson 1938; Elwin 1954; Thusu and Jha 1969; Thusu 1977; Rakshit 1980). In the mid-twentieth century studies of the biological variation among the tribes of central India started with anthropometric and dermatoglyphic analyses (Ray 1958; Rakshit 1962; Tri-

pathy 1967; Ghosh 1978; Deka et al. 1991). The studies of genetic variables are relatively recent.

The earlier studies from the states of Orissa, Madhya Pradesh, and Maharashtra were limited to the distribution of blood groups. Sixteen tribal groups from Orissa, 20 from Madhya Pradesh, and 10 from Maharashtra have been studied for ABO blood groups (Sarkar et al. 1960; Das et al. 1962; Negi and Ahmed 1962; Kumar and Gandhi 1976; Deka 1977; Garg 1978; Mukherjee et al. 1979), and a few have been analyzed for MN and Rh blood groups (Negi and Ahmed 1962, 1963; Das et al. 1966). In the 1980s a more detailed analysis of some tribes for a number of serological and biochemical markers was carried out in Orissa (Reddy et al. 1982; Papiha et al. 1988), Madhya Pradesh (Papiha et al. 1978), and Maharashtra (Mukherjee et al. 1979). Further investigations concentrating on the hemoglobinopathies have been carried out in several tribal groups from Orissa (Das et al. 1967; Sharma et al. 1985), Madhya Pradesh (Kumar 1966; Negi 1967), and Maharashtra (Kate et al. 1978).

Most of the earlier studies were restricted to either a single tribe or a few genetic markers, and the later studies, using several single-gene systems on a few tribes of this region, were mainly descriptive rather than analytical. However, in three studies where data on some genetic systems were available, analyses of kinship and genetic differentiation were attempted (Chakraboty and Yee 1973; Rao et al. 1992; Mastana and Papiha 1994). Because of the inconsistency of the genetic data available from this region, systematic and rigorous analyses of the structure of the tribal groups or of their biological affinities could not be carried out. The present investigation aims at a more comprehensive analysis of genetic variation and structure and their geographic and linguistic components (within and between states and language families) covering 16 tribes from 3 states of central India (Maharashtra, Madhya Pradesh, and Orissa) using 13 genetic loci with 39 alleles.

Plan of Study and Populations

Nine scheduled tribes were studied from the state of Orissa, five from Madhya Pradesh, and two from Maharashtra. Eleven tribes spoke Dravidian languages, whereas three tribes spoke languages of the Indo-Aryan family and two tribes spoke languages of the Austro-Asiatic family. The study was planned to examine the nature and extent of genetic variability, the genetic relationships, and differentiation among the tribes at both the linguistic and the geographic level. The name of each tribe, the area (and district) in which they lived and were sampled, information regarding their population size and linguistic affinity, and the number of individuals tested from each tribe are given in Table 1. A brief description of each tribe is given in what follows.

Table 1. Distribution of the 16 Investigated Tribal Populations in Orissa, Madhya Pradesh, and Maharashtra

State	*Area of Sample Collection*	*Population*	*Number of Population in District (1971 Census)*	*Number of Individuals Studied*	*Language Family*
Orissa	Kalahandi	Deshia Khond	114,644	110	Dravidian
		Raj Gond	123,778	107	Dravidian
		Savara	4,148	107	Austro-Asiatic
	Koraput	Gadaba	46,237	104	Austro-Asiatic
		Konda Dora	8,129	95	Dravidian
		Kuvi Khond	325,144	100	Dravidian
		Paroja	193,736	104	Dravidian
	Sambalpur	Binjhal	50,280	104	Indo-European
		Kisan	87,792	108	Austro-Asiatic
Madhya Pradesh	Bastar	Bhatra	71,095	105	Indo-European
		Dhurwa	858,654	86	Dravidian
		Halba	57,052	97	Indo-European
		Maria	NA	103	Dravidian
		Muria	NA	99	Dravidian
Maharashtra	Chandrapur	Maria Gond	203,905	116	Dravidian
		Raj Gond	NA	106	Dravidian

NA, not available.

Orissa. Binjhal is the name given to one tribe because of its nomadic nature. This tribe is not widely known in Orissa or in Madhya Pradesh. The Binjhal speak an Indo-European language with some admixture of the local Oriya dialect.

The Kisan are an Austro-Asiatic-speaking tribe who occupy the Chota Nagpur area (Madhya Pradesh, Bihar) as well as the Sambalpur District (Orissa). They are now mainly settled agriculturists. Their society is patrilineal and patrilocal. At present, they are critically responding to the changing living conditions.

The Savara are part of a tribal group of whom the greater portion is now found in the Orissa hills, adjacent Bihar, and eastern Madhya Pradesh. They are known under several other names (e.g., Sawara or Sabra). Culturally and linguistically they belong to the Mundari-speaking tribes and thus to the Austro-Asiatic language family. Without doubt the Savara can be regarded as one of the oldest autochthonous populations of central India.

The Bade Gadaba are one of the tribal groups who undoubtedly represent archaic elements in the population of peninsular India. Their traditional agricultural system is slash-and-burn cultivation on hill slopes and plow cultivation of permanent dry fields and on irrigated terraces suitable for the growing of wet rice. They speak an Austro-Asiatic language (Mundari). Some

of the cultural rituals of the Gadaba are also widespread in the Munda-speaking tribes and societies of south and southeast Asia.

The Konda Dora are part of the large Khond tribe. They belong to the plains section of the Khond. The Konda Dora are agriculturists and speak a Dravidian language.

The Kuvi Khond are also part of the large Khond tribe and belong to the plains section of it. The Kuvi Khond are agriculturists and speak a Dravidian language. Their physical appearance is similar to that of other Khond groups.

The Deshia Khond are a Dravidian-speaking tribe with a number of subdivisions that are genetically isolated from each other by social endogamy. The tribe can be divided into a hill section (relatively untouched by Hinduism) and a plains section, which adopted both the language and the religion of the Hindu peasants. The Deshia Khond practice a traditional type of agriculture; all Khond are keen hunters.

The Raj Gond constitute the largest and most widely spread Dravidian-speaking tribes of central India. They cover the hills from Orissa westward and northward, with a strong concentration in the Satpura mountains (south-western Madhya Pradesh) and north of them. The Gond are generally settled agriculturists and slash-and-burn cultivators. Among the Gond there are two aristocratic subsections, the Raj Gond and the Khatolia. The Raj Gond claim a higher rank because they form the land-holding section of the tribe.

The Jhoria Paroja are a small tribe mainly settled in Orissa. They are divided into several sections and are mostly agriculturists, but hunting and food gathering are also practiced. Their language belongs to the Dravidian language family.

Madhya Pradesh. The Bhatra are a group of settled agricultural tribes in the northeastern plains of the Bastar District of Madhya Pradesh. They do not speak any distinct tribal language but use an Indo-European language known as Bhatri, which appears to be a corrupt form of Halbi influenced by Oriya dialects. The Bhatra are divided into a number of subdivisions that behave as distinct endogamous groups. They claim their origin from the southern state of Andhra Pradesh.

The Dhurwa of Madhya Pradesh, who are also known as the Parja, are part of a Dravidian-speaking tribal population that is also found in Orissa. The Bastar Parja adopted the name Dhurwa in order to distinguish themselves from other Parja of Orissa; the main difference is that the Dhurwa do not eat meat and the Bastar Parja do. The Dhurwa are divided into several exogamous clans; cross-cousin marriage is commonly practiced.

The Halba are settled in large numbers all around the Bastar District of Madhya Pradesh. They claim independent status and disown any relation to the Gond. Socially, they are divided into two main endogamous sections, each with endogamous clans that are partly totemic. Cross-cousin marriage

is the rule among the Halba. They are an aboriginal tribe who have adopted Hinduism and an Indo-European language. Today they are mostly settled agriculturists.

The Maria tribal population belongs to the Gond group and is said to be one of the largest in this group. The Maria are divided into two sections: the Hill Maria and the Bison-horn Maria. The Hill Maria are least influenced by the outside world and have retained most of their original cultural and religious traditions and customs. They practice a primitive form of shifting cultivation and hunt and fish; their domesticated pigs, fowls, and goats provide additional food. The Bison-horn Maria, to which our sample belongs, live south of the Indravati River (southern part of the Bastar District). They are mainly food gatherers and live for most of the year on forest produce.

The Muria also belong to the Gond group and are one of the major tribal populations of the Bastar District. They speak a Dravidian language. On the basis of their cultural background and their geographic distribution, they can be divided into three subgroups: Raja Muria, Ghotul Muria, and Jhoria Muria. The Muria are prosperous and industrious cultivators and practice paddy cultivation. They have been described as so-called proto-Australoid and thus represent a remnant of the ancient populations of the Indian subcontinent. Their name is thought to mean aboriginal.

Maharashtra. The Maria Gond are also part of the large Gond group and live in the Bastar District and in the adjacent areas of Maharashtra. They speak a Dravidian language and are generally settled agriculturists and also slash-and-burn cultivators.

The Raj Gond sampled in the Gadchiroli District of Maharashtra belong ethnically to the Raj Gond of Orissa.

Materials and Methods

Blood samples from 1651 individuals (both sexes) belonging to the 16 tribal groups under study were obtained during a field survey in 1989. Blood cells and serum were separated in the field and transported at wet ice temperature as soon as possible to Calcutta. Blood group typing was done in the Anthropometry and Human Genetics Unit of the Indian Statistical Institute in Calcutta using the usual typing methods. Antisera (A, A1, B; M, N, S, s; C, c, D, E, e; FYA; K, k; DiA), produced by Ortho Diagnostic Neckargmünd (Germany), were used for blood grouping. Hemolysates for the typing of hemoglobin variants and red cell enzyme groups were prepared in Calcutta and kept frozen. Frozen hemolysates and serum samples were transported to the Department of Human Biology, University of Bremen (Germany), where the phenotypes of red cell enzymes (ACP, ESD, PGD, and HB) and subtypes of serum proteins (HP, GC, and PI) were determined according to the standard procedures of the laboratory (Walter et al. 1991, 1993).

Results

The allele frequencies of six blood group, three serum protein, and four red cell systems are given in Tables 2 and 3. The observed phenotypes have already been reported (Walter et al. 1991, 1993). Among the various blood group systems studied, no significant deviation from Hardy-Weinberg equilibrium occurred in the ABO blood groups, but deviation was observed in four tribal groups for the MNSs system (Deshia Khond, Paroja, Maria, and Muria), in three groups for Rh (Savara, Kisan, and Muria), in one group for PGD (Kuvi Khond), in one group for GC (Parjas), and in three groups for PI (Gadaba, Paroja, and Maria Gond). Also, several of these tribes showed deviation from Hardy-Weinberg equilibrium for the HB system (Binjhal, Kisan, Kuvi Gond, Paroja, Bhatra, and Dhurwa).

Interpretation of these deviations from equilibrium requires some caution. The small sample size and large number of tests carried out on the same set of samples may lead by chance to some apparently significant deviation. However, in several systems the observed frequency of homozygous phenotypes was greater than expected. Therefore it is possible that the mating pattern among the tribes may promote heterozygote deficiency.

The populations of the Indian subcontinent provide a wide range of A, B, and O gene frequencies, but the average frequencies are $*A1 = 0.163$, $*A2 = 0.025$, $*B = 0.238$, and $*O = 0.574$. The ABO gene frequencies of the tribal groups show narrow ranges around these averages ($*A1 = 0.135$–0.229, $*A2 = 0.012$–0.062, $*B = 0.165$–0.282, and $*O = 0.509$–0.606), and there is significant genetic heterogeneity among the 16 populations ($\chi^2 = 57.96$, d.f. $= 45$; $p < 0.05$). At the state level the nine populations of Orissa did not show any genetic heterogeneity, nor was there any significant variation between the two populations of Maharashtra. However, genetic heterogeneity in ABO among the five tribal groups of Madhya Pradesh was significant ($\chi^2 = 26.42$, d.f. $= 12$; $p < 0.01$). The examination by language showed no significant genetic heterogeneity among the 11 Dravidian- or the 3 Indo-Aryan-speaking tribes, but two Austro-Asiatic groups showed significant variation ($\chi^2 = 10.6$, d.f. $= 3$; $p < 0.025$).

The MNSs system was typed using four antisera; therefore haplotype frequencies were compared. In India the average frequencies of *MS*, *Ms*, *NS*, and *Ns* haplotypes were 0.198, 0.452, 0.092, and 0.260, respectively. The *MS* haplotype showed lower frequencies in the tribal populations (range, 0.086–0.160), and for this haplotype there was no genetic heterogeneity among the 16 populations ($\chi^2 = 14.6$, d.f. $= 15$; $p < 0.500$). However, the *Ms* and *Ns* haplotypes showed a wider range, and both these haplotypes showed significant heterogeneity among the 16 tribal groups (*Ms*: $\chi^2 = 45.4$, d.f. $= 15$, $p < 0.005$; *Ns*: $\chi^2 = 48.3$, d.f. $= 15$, $p < 0.005$). Overall, there is significant genetic diversity among the 16 groups ($\chi^2 = 468.7$, d.f. $= 40$; $p \leq 0.005$). The analysis showed significant diversity at the state level only

Table 2. Allele and Haplotype Frequencies of Blood Groups among 16 Tribes of Central India

Tribe	*Number Tested*	*p1*	*p2*	*q*	*MS*	*Ms*	*NS*	*Ns*	*CDE*	*CDe*	*Cde*	*cDE*	*cDe*	*cdE*	*cde*	*K*	*FY*A+*	*DI*A+*
Binjhal	104	0.1353	0.0229	0.2357	0.0984	0.3968	0.1131	0.3917	0.0131	0.6901	0.0492	0.0690	0.0422	0.0344	0.1020	0.0097	0.6202	0.0194
Deshia Khond	110	0.1648	0.0281	0.2329	0.1295	0.4622	0.0632	0.3451	0.0144	0.7113	0.0752	0.0981	0.0185	0.0000	0.0825	0.0137	0.6307	0.0137
Gadaba	104	0.1933	0.0122	0.2818	0.0892	0.4493	0.0893	0.3776	0.0124	0.7616	0.0000	0.0961	0.0182	0.0308	0.0809	0.0097	0.5957	0.0243
Kisan	108	0.1566	0.0225	0.2310	0.1284	0.3433	0.1216	0.4067	0.0167	0.7569	0.0000	0.0918	0.0000	0.0000	0.1346	0.0093	0.6151	0.0140
Konda Dora	95	0.1938	0.0271	0.2702	0.1335	0.5033	0.0875	0.2757	0.0065	0.7882	0.0000	0.0671	0.0584	0.0000	0.0798	0.0053	0.6161	0.0000
Kuvi Khond	100	0.1822	0.0187	0.2459	0.0925	0.4775	0.0826	0.3474	0.0055	0.8329	0.0000	0.0854	0.0762	0.0000	0.0000	0.0050	0.6127	0.0101
Paroja	104	0.2292	0.0592	0.1990	0.1019	0.4031	0.0961	0.3989	0.0000	0.8812	0.0000	0.0891	0.0000	0.0000	0.0297	0.0100	0.6412	0.0200
Raj Gond	107	0.2115	0.0122	0.2112	0.1168	0.3832	0.0954	0.4046	0.0117	0.7256	0.0271	0.0695	0.0574	0.0000	0.1087	0.0095	0.6498	0.0143
Savara	107	0.1572	0.0514	0.2385	0.0862	0.5034	0.1120	0.2984	0.0166	0.7892	0.0000	0.0757	0.1185	0.0000	0.0000	0.0094	0.6256	0.0189
Madhya Pradesh																		
Bhatra	105	0.1730	0.0355	0.2638	0.1160	0.4697	0.0745	0.3398	0.0174	0.7255	0.0000	0.0969	0.0294	0.0000	0.1308	0.0144	0.5976	0.0000
Dhurwa	86	0.1869	0.0596	0.1647	0.1476	0.4642	0.1171	0.2711	0.0262	0.8363	0.0000	0.0613	0.0762	0.0000	0.0000	0.0117	0.5554	0.0117
Halba	97	0.1390	0.0371	0.2215	0.1418	0.4613	0.1056	0.2913	0.0000	0.7738	0.0303	0.0567	0.0000	0.0000	0.1392	0.0104	0.5574	0.0000
Maria Gond	99	0.1716	0.0186	0.2218	0.0989	0.3960	0.1587	0.3464	0.0204	0.7881	0.0000	0.0595	0.0387	0.0000	0.0933	0.0102	0.6108	0.0000
Muria	103	0.1716	0.0624	0.1961	0.1601	0.5000	0.1069	0.2330	0.0286	0.6846	0.0732	0.0928	0.0000	0.0000	0.1208	0.0147	0.6313	0.0049
Maharashtra																		
Maria Gond	116	0.1445	0.0417	0.2706	0.1317	0.5580	0.0493	0.2610	0.0048	0.7718	0.0294	0.0857	0.0000	0.0000	0.1082	0.0130	0.5953	0.0130
Raj Gond	106	0.1938	0.0544	0.1925	0.1324	0.3629	0.0893	0.4154	0.0158	0.8207	0.0000	0.0707	0.0928	0.0000	0.0000	0.0143	0.6238	0.0095

Table 3. Allele Frequencies of Red Cell and Serum Protein Systems among 16 Tribal Groups of Central India

Tribe	*Number Tested*	*ACP*A*	*ACP*B*	*ESD*1*	*ESD*2*	*PGD*A*	*PGD*C*	*HB*A*	*HB*S*	*HP*1*	*HP*2*	*GC*1F*	*GC*1S*	*GC*2*	*GC*Var*	*PI*M1*	*PI*M2*	*PI*M3*
Orissa																		
Binjhal	97	0.2629	0.7371	0.6250	0.3750	0.9574	0.0426	0.9369	0.0631	0.0680	0.9320	0.2762	0.5381	0.1857	0.0000	0.5381	0.2809	0.1381
Deshia Khond	110	0.2455	0.7545	0.6239	0.3761	1.0000	0.0000	0.9579	0.0421	0.1574	0.8426	0.3853	0.4404	0.1743	0.0000	0.6095	0.2762	0.0952
Gadaba	104	0.1779	0.8221	0.6893	0.3107	0.9904	0.0096	0.9519	0.0481	0.1750	0.8250	0.3286	0.4476	0.2238	0.0000	0.6905	0.1952	0.0905
Kisan	106	0.1840	0.8160	0.6193	0.3807	1.0000	0.0000	0.9676	0.0324	0.1376	0.8624	0.2615	0.4954	0.2431	0.0000	0.5231	0.2546	0.2176
Konda Dora	89	0.1573	0.8427	0.6758	0.3242	1.0000	0.0000	0.9128	0.0872	0.1461	0.8539	0.3871	0.4892	0.1237	0.0000	0.5435	0.2989	0.0978
Kuvi Khond	103	0.2136	0.7864	0.6735	0.3265	0.9853	0.0147	0.9787	0.0213	0.1907	0.8093	0.3465	0.4356	0.2129	0.0050	0.5808	0.3081	0.1010
Paroja	91	0.2253	0.7747	0.6011	0.3989	0.9891	0.0109	0.9468	0.0532	0.2283	0.7717	0.3267	0.4554	0.2030	0.0149	0.6300	0.2550	0.0950
Raj Gond	101	0.2079	0.7921	0.6602	0.3398	0.9949	0.0051	0.9712	0.0288	0.0990	0.9010	0.1604	0.5849	0.2547	0.0000	0.5063	0.2371	0.2473
Savara	107	0.2243	0.7757	0.6262	0.3738	0.9952	0.0048	1.0000	0.0000	0.1449	0.8551	0.2569	0.5000	0.2431	0.0000	0.6557	0.1792	0.1321
Madhya Pradesh																		
Bhatra	104	0.2067	0.7933	0.6394	0.3606	0.8402	0.1598	0.9314	0.0686	0.1250	0.8750	0.2500	0.5385	0.2115	0.0000	0.5433	0.2596	0.1875
Dhurwa	78	0.2051	0.7949	0.6974	0.3026	0.9615	0.0385	0.9444	0.0556	0.0743	0.9257	0.2184	0.5747	0.2069	0.0000	0.6235	0.1882	0.1765
Halba	96	0.2396	0.7604	0.7344	0.2656	0.9933	0.0067	0.9192	0.0808	0.1300	0.8700	0.2222	0.5455	0.2323	0.0000	0.6162	0.2525	0.1313
Maria Gond	101	0.2178	0.7822	0.7500	0.2500	0.9505	0.0495	0.8777	0.1223	0.1311	0.8689	0.1618	0.6029	0.2353	0.0000	0.6323	0.2010	0.1618
Muria	105	0.2381	0.7619	0.6553	0.3447	0.9844	0.0156	0.9158	0.0842	0.9061	0.9039	0.2000	0.5952	0.2048	0.0000	0.5336	0.2308	0.2260
Maharashtra																		
Maria Gond	115	0.2391	0.7609	0.7097	0.2903	0.9224	0.0776	0.8628	0.1372	0.0804	0.9196	0.1681	0.6207	0.2112	0.0000	0.4741	0.3103	0.2070
Raj Gond	105	0.2905	0.7095	0.7552	0.2448	0.9764	0.0236	0.9461	0.0539	0.1068	0.8932	0.1571	0.5810	0.2571	0.0048	0.5524	0.2524	0.1857

in the 5 tribal groups of Madhya Pradesh and at the linguistic level only among the 11 Dravidian-speaking tribes.

This is the first extensive study of the Rh system in tribal populations of India, although Rh has been examined in particular samples. In the populations of the Indian subcontinent the average frequencies of various haplotypes are *CDE* = 0.012, *CDe* = 0.632, *Cde* = 0.021, *cDE* = 0.092, *cDe* = 0.056, *cdE* = 0.004, and *cde* = 0.177, and for each haplotype there is a wide range of variation. For central India the Rh haplotype frequencies were similar to the average values. Some haplotypes (*cdE*, *Cde*) were present in only a few tribes, whereas for other haplotypes, such as *cde*, the average value was lower than the Indian average. However, in the present samples the average frequencies of the various haplotypes were comparable to the overall average frequencies of India (*CDE* = 0.013, *CDe* = 0.771, *Cde* = 0.018, *cDE* = 0.079, *cDe* = 0.392, *cdE* = 0.004, *cde* = 0.076). All haplotypes except *CDe* and *cDE* showed significant genetic heterogeneity among the 16 tribal populations. Both at the state level and in the populations of the three different linguistic families the distribution of the Rh haplotypes showed significant genetic heterogeneity (Table 4).

The population of the Indian subcontinent shows a wide range of the *FY*A* gene frequency (0.136–1.000), and an earlier single study in the Bhil tribe from central India gave a mean *FY*A* frequency of 0.724 (Papiha et al. 1978). The 16 tribal groups studied here showed a slightly lower mean value of 0.611 and a much narrower range of *FY*A* gene frequency (0.555–0.649). Mean values in the different states and linguistic families are also close to each other.

The mean frequency of the *K* gene, 0.011 (range, 0.005–0.015), is typical of the Indian region. The Diego system is the least studied in India, and there is no previous report from central India. The *DI*A* gene was absent in the Konda Dora, Bhatra, Halba, and Maria tribes but was at high frequency in the Austro-Asiatic-speaking tribes. The mean frequency in the present 12 tribes (0.011) is similar to the overall mean *DI*A* frequency (0.014) for Indian populations.

The polymorphisms of red cell enzymes acid phosphatase (ACP), esterase D (ESD), and 6-phosphogluconate dehydrogenase (PGD) have been studied in various populations of the Indian subcontinent. For ACP the *ACP*C* allele is perhaps of recent origin in urban populations of India, an interpretation supported by its absence from all the tribal groups studied here and in most previous investigations. In the peoples of the Indian subcontinent the mean frequencies of the *ACP*B* and *ACP*A* alleles are 0.756 and 0.242, respectively. In the present study the *ACP*B* gene frequency ranges from 0.709 to 0.843, with a mean of 0.779, similar to the overall mean of Indian populations.

ESD has been less investigated in India. In the present study the *ESD*2* gene frequency ranged from 0.245 in the Raj Gond (Maharashtra) to 0.398

Table 4. Results of Locus-Specific Analysis of Heterogeneity on the Basis of State and Linguistic Level

	Orissa (9 Populations)			*Madhya Pradesh (5 Populations)*			*Maharashtra (2 Populations)*			*Dravidian (11 Populations)*			*Indo-Aryan (3 Populations)*			*Austro-Asiatic (2 Populations)*			*Total Tribes (16 Populations)*		
Locus	χ^2	*d.f.*	*p*	χ^2	*d.f.*	*p*	χ^2	*d.f.*	*p*	χ^2	*d.f.*	*p*	χ^2	*d.f.*	*p*	χ^2	*d.f.*	*p*	χ^2	*d.f.*	*p*
Blood Groups																					
A1A2BO	32.62	24	<0.250	26.42	12	<0.010	4.92	3	<0.900	39.91	30	<0.250	4.17	6	<0.750	10.62	3	<0.025	57.96	45	<0.05
MNSs	33.70	24	<0.100	19.08	12	<0.100	19.55	3	<0.005	75.27	30	<0.005	7.85	6	<0.250	3.45	3	<0.500	468.71	45	<0.005
Rh	196.43	48	<0.005	98.34	20	<0.005	52.12	5	<0.005	264.54	60	<0.005	38.97	12	<0.005	39.03	6	<0.005	91.52	90	<0.005
Kell	0.61	8	>0.995	0.31	4	<0.990	0.01	1	>0.900	2.12	10	>0.995	0.24	2	<0.900	0.00	1	>0.900	2.46	15	>0.995
Duffy	1.85	8	<0.995	3.55	4	<0.500	2.75	1	<0.100	5.14	10	<0.900	1.67	2	<0.500	0.40	1	<0.750	8.47	15	<0.950
Diego	28.69	8	<0.005	6.22	4	<0.005	0.12	1	<0.750	7.61	10	<0.750	7.90	2	<0.050	0.15	1	<0.750	17.62	15	<0.950
Red cell enzymes																					
ACP	10.69	8	<0.250	1.22	4	<0.900	1.49	1	<0.250	13.81	10	<0.250	1.78	2	<0.500	1.41	1	<0.250	18.67	15	<0.950
ESD	6.67	8	<0.500	8.87	4	<0.100	1.16	1	<0.500	22.84	10	<0.025	6.20	2	<0.050	1.87	1	<0.250	32.61	15	<0.010
PGD	47.29	8	<0.005	52.32	4	<0.005	6.58	1	<0.010	60.31	10	<0.005	0.86	2	<0.750	0.34	1	<0.750	178.66	15	<0.005
Hemoglobin	24.65	8	<0.005	6.18	4	<0.025	8.66	1	<0.005	49.18	10	<0.005	0.50	2	<0.900	10.06	1	<0.005	68.26	15	<0.005
Serum Proteins																					
HP	27.96	8	<0.005	4.34	4	<0.500	0.89	1	<0.500	12.16	10	<0.500	5.07	2	<0.100	0.70	1	<0.500	48.86	15	<0.005
GC	69.93	24	<0.005	8.77	8	<0.500	2.47	3	<0.500	125.78	30	<0.005	2.74	4	<0.750	2.67	2	<0.500	146.93	45	<0.005
PI	98.48	32	<0.005	25.24	20	<0.250	19.42	4	<0.005	136.01	60	<0.005	23.52	8	<0.005	4.96	4	<0.500	202.82	105	<0.005

in the Paroja (Orissa), with a mean of 0.329, slightly higher than the overall mean for Indian populations (0.271). The mean frequencies of the *ESD*2* gene in the three linguistic families were similar (0.323–0.342), but interstate differences were more prominent (Orissa, 0.356; Madhya Pradesh, 0.304; Maharashtra, 0.267).

Among Indian populations the *PGD*A* gene frequency ranges from 0.754 to 1.000. In the peoples of the Himalayan foothills or those with Asian affinity, lower *PGD*A* and higher *PGD*C* gene frequencies were observed. The mean frequency of the *PGD*A* gene in the 16 samples was 0.971, and the *PGD*C* gene frequency ranged from 0.000 to 0.078. These values are comparable to most of the populations so far studied from India.

At both the state and the linguistic level genetic heterogeneity for the ACP and ESD systems was not significant, but for the ESD system there was significant overall heterogeneity among the 16 tribes ($\chi^2 = 32.6$, d.f. = 15; $p < 0.01$). The tribal groups of each state and the 11 Dravidian-speaking groups all showed statistically significant heterogeneity for the PGD system.

For serum proteins three systems (HP, GC, and PI) were analyzed. The *HP*1* gene frequency in the 16 populations ranged from 0.068 to 0.228 (the highest and lowest values were found in the Orissa tribes). The nine populations of Orissa showed significant genetic heterogeneity for the HP system ($\chi^2 = 27.9$, d.f. = 8; $p < 0.005$). The *GC*1F* allele frequency showed a wide range (0.160–0.387), and, like the HP system, the nine populations of Orissa with their wide range of *GC*1F* allele frequencies, showed significant heterogeneity for the GC system ($\chi^2 = 69.9$, d.f. = 24; $p < 0.005$). This is the first comprehensive analysis of the PI system in tribal populations. There is a wider range of variation of the *PI*M3* allele frequency in Orissa than in Maharashtra and Madhya Pradesh, and this system showed significant genetic heterogeneity in the populations of Orissa ($\chi^2 = 98.48$, d.f. = 32; $p < 0.005$).

In the present study HbS is found in all tribes except the Savara of Orissa. The frequency of the *HB*S* gene varied from 0.021 in the Kuvi Khond to 0.137 in the Maria Gond. The homozygous phenotype (HB S,S) was present in all tribes except the Deshia Khond, Raj Gond, and Savara. There is a suggestion of a geographic cline of increasing frequency of the *HB*S* gene from east to west.

Genetic Heterogeneity. In each system tested there is a wide range of variation in allele frequencies. The extent of genetic diversity among the 16 tribal populations and among 11 Dravidian-speaking, 3 Indo-Aryan-speaking and 3 Austro-Asiatic-speaking tribal groups was examined using chi-square analysis (see Table 4). Nine of the 13 genetic systems (ABO, MNSs, Rh, ESD, PGD, HB, HP, GC, and PI) showed significant genetic diversity among the 16 tribal groups. The states varied considerably in intrastate heterogeneity. Significant heterogeneity was found in seven genetic systems among the tribes of Orissa (Rh, DI, PGD, HB, HP, GC, and PI), in five genetic systems in the

tribal groups of Madhya Pradesh (ABO, Rh, Di, PGD and HB), and in five genetic systems in Maharashtra (MNSs, Rh, PGD, HB, and PI). Three of the genetic systems (Rh, PGD, and HB) showed significant genetic heterogeneity in all three states investigated. In terms of number of systems, genetic heterogeneity is higher among the Dravidian speakers (MNSs, Rh, PGD, HB, GC, and PI) than in the populations belonging to the Indo-Aryan (Rh, DI, and PI) and Austro-Asiatic (Rh and HB) linguistic families. This may be due partly to the larger number of populations (11) belonging to the Dravidian family in this study. The Rh system showed significant heterogeneity in populations of all three linguistic families.

***F* Statistics.** The extent to which the mating structure of the tribal groups influences the maintenance of the variation was examined using Wright's (1951) fixation index (F), which is defined as

$$F = 1 - H_o/H_e, \tag{1}$$

where H_o is the observed number of heterozygotes in a diallelic system and H_e is the expected number of heterozygotes, assuming Hardy-Weinberg equilibrium. In other words, F can be viewed as a deviation from panmixia.

For a population that is divided into a large number of subpopulations, partitioning the total index into fixation indexes within and between subpopulations allows the effect of subdivision to be studied. Three indexes, F_{IT}, F_{IS}, and F_{ST}, are defined. F_{IT} and F_{IS} are coefficients of inbreeding and represent the probability of identity of alleles of individuals relative to the total population and relative to the subpopulation, respectively; F_{ST} is the probability of identity by descent between random alleles from each subpopulation relative to those of the total population. These three indexes reflect the nature of genetic differentiation within the total and individual subpopulations and between subpopulations and are related by

$$F_{ST} = (F_{IT} - F_{IS})/(1 - F_{IS}). \tag{2}$$

For all diallelic loci where the heterozygotes are discernible, values of F_{ST}, F_{IT}, and F_{IS} in the 3 state populations and in the 16 tribal groups are given in Table 5. For different loci the F_{IT} and F_{IS} estimates varied considerably both at the state level and for total tribal populations. For *Ss* and ESD the F_{IS} and F_{IT} values showed small negative values, suggesting little influence of these loci on genetic differentiation. *MN*, *Ee*, and HB loci exhibit the largest F_{IT} and F_{IS} values, indicating a possible excess of homozygotes at these loci because of either selection or nonrandom mating or both. The mean F_{IT} values both at the state level (Orissa, 0.199; Madhya Pradesh, 0.089; Maharashtra, 0.090) and in the total tribal groups (0.166) are quite large; this is mainly due to F_{IS} (Orissa, 0.178; Madhya Pradesh, 0.153; Maharashtra, 0.080; total tribes, 0.149) rather than to F_{ST} (Orissa, 0.015; Madhya Pradesh, 0.018; Maharashtra, 0.012; total tribes, 0.022), suggesting tendencies toward consanguineous mat-

Table 5. Comparison of a Set of *F* Statistics for 9 Codominant Alleles in 16 Tribal Groups of Orissa (OR), Madhya Pradesh (MP), and Maharashtra (MH)

	F_{ST}				F_{IT}				F_{IS}			
Locus	*OR*	*MP*	*MH*	*Total*	*OR*	*MP*	*MH*	*Total*	*OR*	*MP*	*MH*	*Total*
MN	0.0699	0.0055	0.0228	0.0461	0.4249	0.5741	0.2694	0.4919	0.3817	0.5717	0.2523	0.4674
Ss	0.0061	0.0044	0.0004	0.0069	0.1836	−0.0662	−0.2324	−0.0102	0.1787	−0.0662	−0.2329	−0.0168
Cc	0.0082	0.0091	0.0010	0.0080	0.0332	0.0002	−0.0430	0.0214	0.0253	−0.0093	−0.0451	0.0135
Ee	0.0149	0.0167	0.0008	0.0284	0.6894	0.0061	0.4319	0.5975	0.6847	0.4946	0.4315	0.5857
ACP	0.0060	0.0011	0.0037	0.0058	0.0494	0.0257	0.0472	0.0433	0.0437	0.0246	0.0437	0.0377
ESD	0.0040	0.0089	0.0020	0.0099	0.0485	0.0451	0.0125	−0.0086	−0.0527	0.0365	0.0105	−0.0187
PGD	0.0104	0.0587	0.0145	0.0595	0.0990	−0.0411	0.1257	0.0404	0.0895	0.1060	0.1128	−0.0180
HB	0.0150	0.0065	0.0196	0.0163	0.2622	0.1641	0.1047	0.2455	0.2510	0.1586	0.0868	0.2330
HP	0.0041	0.0515	0.0476	0.0158	0.0051	0.0991	0.0945	0.0697	0.0012	0.0636	0.0625	0.0547
Mean	0.0154	0.0180	0.0123	0.0218	0.1995	0.0897	0.0901	0.1657	0.1781	0.1533	0.0802	0.1487

Table 6. Comparison of F Statistics for 9 Codominant Alleles in 16 Tribal Groups of Three Linguistic Groups[a]

	F_{ST}			F_{IT}			F_{IS}		
Locus	*DR*	*IA*	*AA*	*DR*	*IA*	*AA*	*DR*	*IA*	*AA*
MN	0.0542	0.0066	0.0012	0.4761	0.3981	0.7613	0.4761	0.3941	0.7610
Ss	0.0048	0.0101	0.0016	−0.0701	0.2038	0.1957	−0.0752	0.1957	−0.0096
Cc	0.0011	0.0023	0.0014	0.0326	−0.0600	0.0861	0.0251	−0.0624	0.0849
Ee	0.0270	0.0495	0.0006	0.6261	0.5719	0.4808	0.6157	0.5497	0.4800
ACP	0.0064	0.0028	0.0037	0.0522	0.0264	0.0134	0.0461	0.0236	0.0090
ESD	0.0105	0.0104	0.0100	0.0100	−0.0387	−0.0496	0.0040	−0.1213	−0.1258
PGD	0.0238	0.0647	0.0139	0.1142	−0.0742	−0.0073	0.0926	−0.1485	−0.0215
HB	0.0213	0.0030	0.0213	0.1743	0.2736	0.1782	0.1563	0.2714	0.1603
HP	0.0184	0.0083	0.0015	0.0808	0.0843	−0.0089	0.0636	0.0766	−0.0104
Mean	0.0186	0.0175	0.0061	0.1662	0.1539	0.1833	0.1560	0.1309	0.1477

a. DR, Dravidian; IA, Indo-Aryan; AA, Austro-Asiatic.

ings, particularly in Orissa. All three linguistic families showed high F_{IT} and F_{IS} values (Table 6), whereas the highest F_{ST} value was observed for Dravidian speakers (0.019) and the lowest value was observed for Austro-Asiatic speakers (0.006). This large difference between these two linguistic families may be due to the small number of populations studied in the Austro-Asiatic group.

Gene Diversity. The F estimates were based on the diallelic loci, and for multiple alleles the relationship between F indexes does not hold. In its place Nei (1973) described the coefficient of gene differentiation (G_{ST}), which is identical in interpretation to F_{ST} and which Nei mentions as independent of pattern of selection, migration, mutation, and method of reproduction. If population differentiation occurs primarily by genetic drift in isolated or partially isolated populations, the F_{ST} or G_{ST} values would be expected to increase as the average geographic distance between population increased.

G_{ST} is a ratio of the extent of gene differentiation among populations (D_{ST}) to the extent of the total genetic variation in the entire population $H_T = D_{ST} + H_S$, where H_S is the intrapopulation heterozygosity. Therefore G_{ST} may be large even for a small value of D_{ST} if H_S is small. This situation can occur especially when a population goes through a bottleneck and splits into isolated subpopulations. Nei (1973) suggested that this type of bottleneck effect on G_{ST} can be detected by examining the absolute values of H_S and D_{ST} or D_M (the average minimum genetic distance among subpopulations). The ratio $G_{ST} = D_{ST}/H_T$ is called the coefficient of gene differentiation, the variance of which can be calculated using the equation given by Chakraborty (1974).

Table 7. Gene Diversity Analysis among the 16 Tribal Populations

Locus	H_T	H_S	G_{ST}
Blood Groups			
A1A2BO	0.6025	0.5991	0.0056
MNSs	0.6640	0.6558	0.0123
Rh	0.3922	0.3836	0.0219
Kell	0.0210	0.0209	0.0010
Duffy	0.4753	0.4741	0.0025
Diego	0.0286	0.0280	0.0210
Red cell enzymes			
ACP	0.3443	0.3423	0.0058
ESD	0.4415	0.4371	0.0100
PGD	0.0558	0.0526	0.0574
Hemoglobin	0.1221	0.1201	0.0164
Serum proteins			
HP	0.2272	0.2236	0.0158
GC	0.6110	0.5989	0.0198
PI	0.5801	0.5714	0.0150
Mean	0.3512	0.3467	0.0157
Variance	0.1752	0.1710	0.0032

G_{ST} was computed for the 16 populations on the basis of 13 polymorphic loci (Table 7). The total average gene diversity H_T was 35.1%, and the intrapopulation diversity H_S was 34.7%. The overall coefficient of gene differentiation was small in these populations ($G_{ST} = 0.0157 \pm 0.0566$). The variance of G_{ST} was 0.0032. The level of total heterozygosity H_T is highest in the MNSs loci and lowest in the Kell system under the assumption of Hardy-Weinberg equilibrium for the pooled data. Within populations the diversity H_S was largest at the MNSs loci and smallest at the Kell locus. The PGD locus yielded the highest G_{ST} value (0.0574) in the 16 tribal populations, just as with F_{ST}.

Table 8 shows the gene diversity partitioned among the populations of Orissa, Madhya Pradesh, and Maharashtra. G_{ST} depends on the number of populations considered, as mentioned by Nei (1973, 1975). Nei (1986) redefined G_{ST} as G'_{ST}, in which $G'_{ST} = D_M/H_S + D_M$, where D_M is $rD_{ST}/(r - 1)$. Here r denotes the number of subpopulations examined. D_M is a measure of absolute gene differentiation. The levels of total heterozygosity H_T varied among the populations of the three states, with Madhya Pradesh showing the highest H_T value (0.3507), H_S value (0.3476), and G_{ST} value (0.0111). These high values can be attributed to population differentiation compared with populations of the other two states. Between-population differences were at low levels among populations of Maharashtra (0.0073) compared with Orissa (0.0096). Subsequently, the values obtained in the measure of gene diversity

Table 8. Gene Diversity among the Tribes of Orissa, Madhya Pradesh, and Maharashtra

	Orissa			*Madhya Pradesh*			*Maharashtra*		
Locus	H_T	H_S	G_{ST}	H_T	H_S	G_{ST}	H_T	H_S	G_{ST}
Blood groups									
A1A2BO	0.6048	0.6014	0.0056	0.5932	0.5909	0.0039	0.6116	0.6093	0.0038
MNSs	0.6598	0.6537	0.0092	0.6719	0.6677	0.0063	0.6513	0.6354	0.0244
Rh	0.3926	0.3844	0.0213	0.4042	0.3961	0.0200	0.3544	0.3485	0.0166
Kell	0.0180	0.0180	0.0006	0.0243	0.0243	0.0007	0.0268	0.0268	0.0007
Duffy	0.4697	0.4691	0.0013	0.4836	0.4818	0.0037	0.4760	0.4756	0.0008
Diego	0.0296	0.0294	0.0068	0.0066	0.0066	0.0064	0.0221	0.0221	0.0009
Red cell enzymes									
ACP	0.3330	0.3310	0.0060	0.3449	0.3445	0.0012	0.3894	0.3880	0.0036
ESD	0.4586	0.4568	0.0038	0.4237	0.4199	0.0090	0.3919	0.3911	0.0020
PGD	0.0192	0.0190	0.0104	0.1022	0.0962	0.0587	0.0961	0.0947	0.0146
Hemoglobin	0.0801	0.0789	0.0150	0.1511	0.1501	0.0066	0.1729	0.1693	0.0208
Serum proteins									
HP	0.2546	0.2506	0.0157	0.1978	0.1968	0.0025	0.1697	0.1695	0.0012
GC	0.6276	0.6192	0.0134	0.5837	0.5783	0.0139	0.5577	0.5567	0.0018
PI	0.5731	0.5646	0.0152	0.5723	0.5661	0.0108	0.6188	0.6163	0.0040
Mean	0.3477	0.3443	0.0096	0.3507	0.3476	0.0111	0.3491	0.3464	0.0073
G'_{ST}			0.0109			0.0119			0.0153

were found to vary also at the locus level. Out of six blood group loci or gene clusters studied, at least four loci (ABO, MNSs, Rh, and FY) exhibited high levels of heterozygosity, and out of three enzyme and three protein loci two enzyme loci (ACP and ESD) and two protein loci (GC and PI) also revealed high levels of heterozygosity to varying degrees in all three subset populations.

G'_{ST} values were also computed when populations of each of the three states were analyzed separately (see Table 8). The overall G'_{ST} value in the Maharashtra population was higher (0.0153) than that in the population of Orissa (0.0109) or Madhya Pradesh (0.0119). In the present study G_{ST} was found to be inversely related to geographic distance; for example, populations in Orissa are sparsely distributed and cover a wider geographic area than the populations of Madhya Pradesh and Maharashtra. Populations of Orissa showed lower G_{ST} values than the populations of Madhya Pradesh and Maharashtra.

The gene diversity results for the populations classified according to linguistic affiliation are set out in Table 9. The average total heterozygosity H_T level was highest (0.3589) among the Indo-Aryan-speaking populations. The Dravidian- and Austro-Asiatic-speaking populations showed values of 0.3491 and 0.3397, respectively. Consequently, within-population diversity H_S was higher in the Indo-Aryan group (0.3384), but between-population

Table 9. Gene Diversity among the Dravidian, Indo-Aryan and Austro-Asiatic Groups

	Dravidian			*Indo-Aryan*			*Austro-Asiatic*		
Locus	H_T	H_S	G_{ST}	H_T	H_S	G_{ST}	H_T	H_S	G_{ST}
Blood groups									
A1A2BO	0.6038	0.6009	0.0048	0.5877	0.5822	0.0094	0.6167	0.6151	0.0026
MNSs	0.6724	0.6574	0.0223	0.6668	0.6609	0.0088	0.6416	0.6391	0.0039
Rh	0.3777	0.3682	0.0252	0.4450	0.4422	0.0063	0.3846	0.3799	0.0122
Kell	0.0210	0.0208	0.0105	0.0227	0.0226	0.0009	0.0190	0.0189	0.0001
Duffy	0.4728	0.4718	0.0021	0.4832	0.4818	0.0029	0.4755	0.4753	0.0004
Diego	0.0200	0.0172	0.1414	0.0129	0.0127	0.0154	0.0423	0.0422	0.0005
Red cell enzymes									
ACP	0.3436	0.3414	0.0064	0.3610	0.3600	0.0028	0.3213	0.3201	0.0037
ESD	0.4390	0.4344	0.0105	0.4447	0.4401	0.0103	0.4502	0.4484	0.0040
PGD	0.0419	0.0409	0.0239	0.1297	0.1213	0.0648	0.0143	0.0142	0.0014
Hemoglobin	0.1221	0.1195	0.0213	0.1316	0.1314	0.0015	0.0470	0.0458	0.0255
Serum proteins									
HP	0.2286	0.2244	0.0184	0.1922	0.1906	0.0083	0.2688	0.2684	0.0015
GC	0.6062	0.5922	0.0231	0.6014	0.6005	0.0015	0.6353	0.6332	0.0033
PI	0.5888	0.5813	0.0127	0.5865	0.5841	0.0041	0.4991	0.4981	0.0020
Mean	0.3491	0.3439	0.0248	0.3589	0.3562	0.0105	0.3397	0.3384	0.0047
G'_{ST}			0.0163			0.0155			0.0076

heterozygosity (D_{ST}) was higher in the Dravidian group (0.0052) than in the Indo-Aryan (0.0027) or Austro-Asiatic group (0.0013). It seems that populations included in the Dravidian linguistic group represent more isolated groups compared with those included in the other two linguistic groups. This assumes further significance because the highest G_{ST} value (0.0248) or G'_{ST} value (0.0163) was observed among the Dravidian-speaking group compared with the other two linguistic groups (Indo-Aryans, $G_{ST} = 0.0105$, $G'_{ST} = 0.0155$; Austro-Asiatic, $G_{ST} = 0.0047$, $G'_{ST} = 0.0076$).

Genetic Distance. Another measure of genetic differentiation among the tribal groups of the different states that may point out their relationship along the evolutionary scale is genetic distance. Of the various methods available, that of Harpending and Jenkins (1973) was used here. The allele frequencies were converted to the normalized kinship matrix R. The R matrix provides the mean squared standard deviation of gene frequency from the population mean (r_{ii}) in each tribal group and the average covariance of gene frequencies relative to the mean (r_{ij}) in each pair of tribal groups. The r_{ij} element of the R matrix is

$$r_{ij} = \frac{1}{k} \sum \frac{(p_{ik} - \bar{p}_k)(p_{jk} - \bar{p}_k)}{\bar{p}_k(1 - \bar{p}_k)}, \tag{3}$$

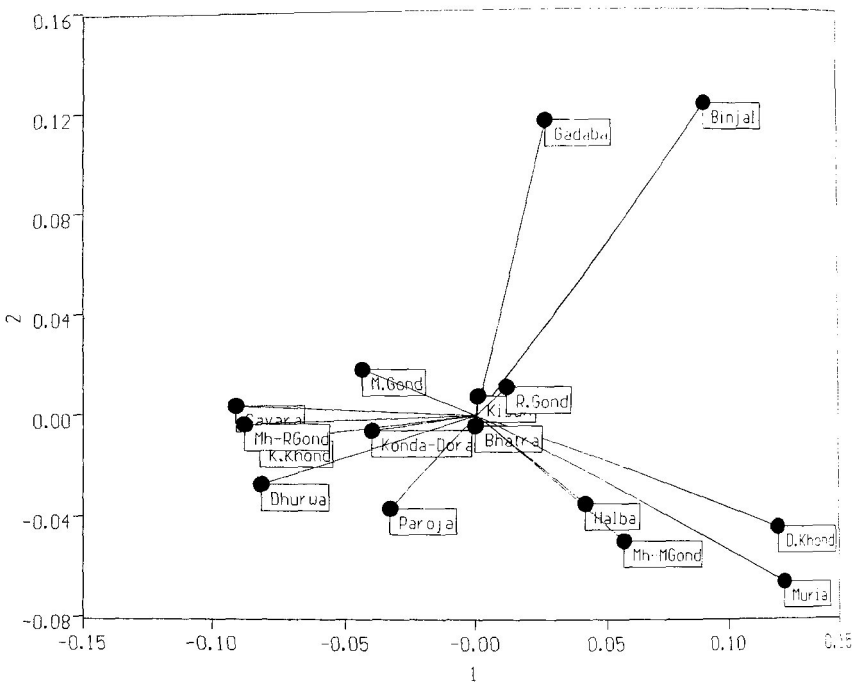


Figure 3. Genetic relationships among 16 tribal populations of central India shown by plot of the first and second eigenvectors of the R matrix.

The cophenetic correlation of 0.766 suggests that the dendrogram is a fair representation of the genetic distance.

The eigenvector plot drawn from the R matrix and the dendrogram plot of the distance matrix confirm that the tribes of the same linguistic families within the same states do not show close affinities. To some extent geographically close tribes of different linguistic groups showed greater affinity. The values of r_{ii}, the principal diagonal element of the R matrix, indicate the degree of isolation characteristic of a particular subgroup. The highest value was found for the oldest population of the region—Binjhal (0.026)—whereas the lowest value was found for the Bhatra population of Madhya Pradesh (0.004).

The mean diagonal value of the R matrix provides another estimate of genetic differentiation, R_{ST}, theoretically equivalent to F_{ST} or G_{ST}. The R_{ST} value for the 16 tribal populations was 0.0128, which is slightly lower than the G_{ST} value and much lower than the F_{ST} value.

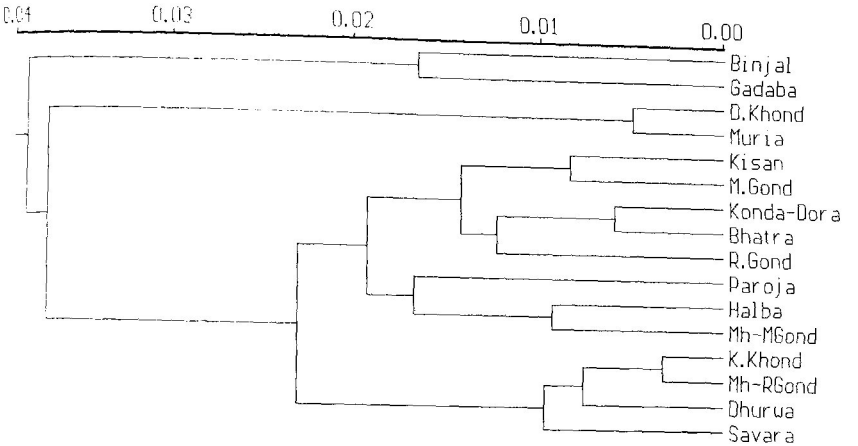


Figure 4. Dendrogram depicting relationships among 16 tribal populations of Orissa, Madhya Pradesh, and Maharashtra.

Discussion

This study is the first extensive investigation of the tribal populations of India in which the pattern of genetic heterogeneity and the genetic structure in a number of tribal groups of central India have been studied. The comparison of the allele and haplotype frequencies suggests that for most of the investigated genetic systems the average frequencies for the tribal groups are comparable with those reported for populations of the Indian subcontinent. However, there was considerable variation among the 16 tribal groups. Nine of the 13 loci showed significant heterogeneity in the 16 tribal groups, and similar patterns of heterogeneity also were discernible in different state populations and in the Dravidian-speaking tribes. Highly significant intertribal differences were noted for the *ABO*A2* allele and for the *Ms*, *Ns*, *cde*, *Cde*, *cdE*, *cDe*, and *CDe* haplotypes. The lack of some of these haplotypes in certain populations may be due to drift or a founder effect.

The *DI*A* frequency suggests gene flow among the tribes. The highest frequency of *DI*A* was found in the Austro-Asiatic-speaking Gadaba and Savara populations. *DI*A* was present in some populations but was absent in two Dravidian- and Indo-Aryan-speaking populations. The most likely explanation for this situation is that the Austro-Asiatic speakers, whose ancestors probably came to central India in prehistoric times, brought this allele with them and later through the process of admixture spread it into the populations speaking Dravidian and Indo-Aryan languages. However, confirmation of gene flow among these tribal groups needs further systematic study.

There was a wide range of *FY*A* gene frequencies in Indian populations but a lesser degree of variation (55–65%) in the tribal groups. From the known

where p_{ik} and p_{jk} are the frequencies of allele k in populations i and j and $\bar{p}_k$ is the mean frequency of allele k in all populations.

The values below the diagonal in Table 10 provide the kinship matrix of the 16 populations. Both weighted (by sample size) and unweighted matrices were computed; except for some populations there was no major difference between the two matrices, so the unweighted matrix is used in our discussion. The higher positive values, for example, between the Gadaba and the Binjhal (0.014) and between the Deshia Khond and the Muria (0.019), indicate greater affinity between these tribes. The low negative or low positive values, for example, between the Savara and the Raj Gond (0.001) or between the Halba and the Raj Gond (-0.001), show intermediate affinity. The lowest negative values, for example, between the Maharashtra Raj Gond and the Muria (-0.009), show the least affinity between these groups.

The multidimensional R matrix, reduced to a two-dimensional eigenvector plot, helps to visualize more clearly the genetic relations of the various groups (Figure 3). The first eigenvector is useful in differentiating a cluster of four groups (Maharashtra Raj Gond, Madhya Pradesh Dhurwa, and Orissa Kuvi Khond and Savara) and two pairs of tribal groups (Maharashtra Maria Gond and Madhya Pradesh Halba; Orissa Deshia Khond and Madhya Pradesh Muria). The second eigenvector helps to clearly differentiate a pair of populations of Orissa (Binjhal and Gadaba), whereas the remaining populations form a central cluster.

A Euclidian measure of genetic distance (d^2) was obtained directly from the uncorrected R matrix:

$$d^2 = r_{ii} + r_{ij} - 2r_{ij}. \tag{4}$$

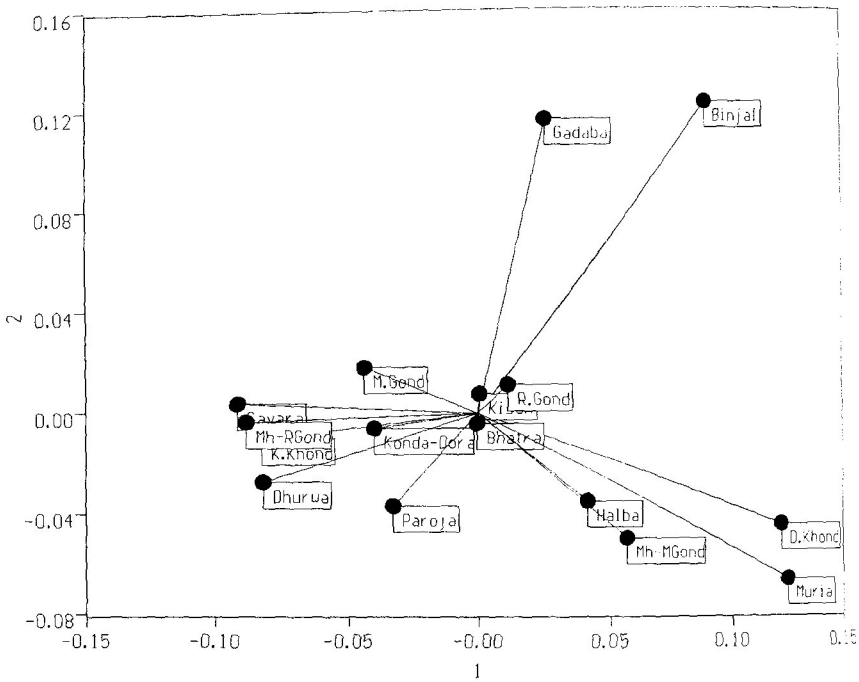
The values above the diagonal in Table 10 are the genetic distances between the tribes. The largest and the lowest distances were observed between tribes of Orissa: Paroja and Binjhal (0.058) and Konda Dora and Kuvi Khond (0.010), respectively. The Maria Gond of Maharashtra showed considerable distance (0.039) from the Raj Gond of Maharashtra. Other populations of Madhya Pradesh and Orissa varied considerably in genetic distance from one another.

The dendrogram in Figure 4 summarizes the affinity among the 16 populations obtained using the unweighted pair group method with arithmetic mean (UPGMA). The earliest differentiated were the Binjhal and Gadaba populations of Orissa, both being autochthonous groups in this region but belonging to different linguistic families. Another early differentiating population was the Raj Gond of Orissa. In the center of the dendrogram are three clusters: (1) Deshia Khond, Muria, Maria Gond (Maharastra), and Halba; (2) Kisan, Maria Gond, and Konda Dora; (3) Kuvi Khond, Savara, Dhurwa, Raj Gond (Maharashtra), Paroja, and Bhatra. The populations of Madhya Pradesh and Maharashtra are well scattered in these clusters; so is the group of populations belonging to the Indo-Aryan and Austro-Asiatic language families.

Table 10. *R* Matrix (below Diagonal) and Distance Matrix (above Diagonal) for 16 Populations of Central India

Tribe	*Binjhal*	*Deshia Khond*	*Gadaba*	*Kisan*	*Konda Dora*	*Kuvi Khond*	*Paroja*	*Raj Gond*	*Savara*	*Bhatra*	*Dhurwa*	*Halba*	*Maria Gond*	*Muria*	*Maharashtra Maria Gond*	*Maharashtra Raj Gond*
Binjhal	**0.126**	0.032	0.017	0.041	0.043	0.049	0.058	0.029	0.053	0.039	0.056	0.036	0.041	0.038	0.045	0.050
Deshia Khond	0.007	**0.019**	0.046	0.034	0.034	0.045	0.043	0.020	0.052	0.026	0.050	0.018	0.044	0.005	0.017	0.048
Gadaba	0.014	−0.004	**0.018**	0.024	0.024	0.035	0.032	0.032	0.042	0.019	0.043	0.029	0.030	0.056	0.029	0.041
Kisan	−0.003	−0.003	0.002	**0.009**	0.018	0.021	0.016	0.014	0.038	0.009	0.026	0.012	0.008	0.036	0.025	0.023
Konda Dora	−0.006	−0.005	−0.000	−0.002	**0.005**	0.010	0.018	0.014	0.010	0.066	0.014	0.014	0.015	0.042	0.014	0.013
Kuvi Khond	−0.007	−0.008	−0.004	−0.002	0.002	**0.009**	0.012	0.022	0.009	0.018	0.008	0.023	0.017	0.052	0.029	0.003
Paroja	−0.009	−0.006	−0.001	0.003	0.000	0.005	**0.012**	0.033	0.035	0.020	0.022	0.014	0.021	0.043	0.020	0.023
Raj Gond	0.003	0.003	−0.003	0.001	−0.001	−0.003	−0.006	**0.008**	0.022	0.011	0.024	0.017	0.015	0.029	0.026	0.016
Savara	−0.005	−0.009	−0.004	−0.037	0.005	0.008	−0.004	0.001	**0.016**	0.020	0.011	0.038	0.021	0.057	0.039	0.010
Bhatra	−0.004	−0.001	0.002	0.002	0.002	−0.002	−0.002	0.001	0.000	**0.004**	0.020	0.012	0.016	0.030	0.010	0.019
Dhurwa	−0.008	−0.009	−0.006	−0.003	0.002	0.007	0.001	−0.002	0.009	−0.001	**0.012**	0.024	0.016	0.046	0.034	0.007
Halba	−0.001	0.004	−0.002	0.002	−0.001	−0.004	0.002	−0.001	−0.006	−0.001	−0.002	**0.007**	0.017	0.018	0.009	0.029
Maria Gond	−0.003	−0.008	−0.001	0.005	0.000	0.001	0.001	0.001	0.002	−0.001	0.003	−0.000	**0.010**	0.044	0.035	0.018
Muria	0.006	0.019	−0.007	−0.002	−0.007	−0.010	−0.004	0.001	−0.009	−0.001	−0.005	0.006	−0.006	**0.023**	0.020	0.053
Maria Gond (Maharashtra)	−0.004	0.007	0.000	−0.002	0.002	−0.004	0.002	−0.003	−0.005	0.003	−0.005	0.004	−0.007	0.007	**0.012**	0.039
Raj Gond (Maharashtra)	−0.006	−0.008	−0.005	−0.001	0.002	0.009	0.001	0.002	0.009	−0.002	0.009	−0.005	0.002	−0.009	−0.008	**0.012**

R_{ST} = 0.01276.



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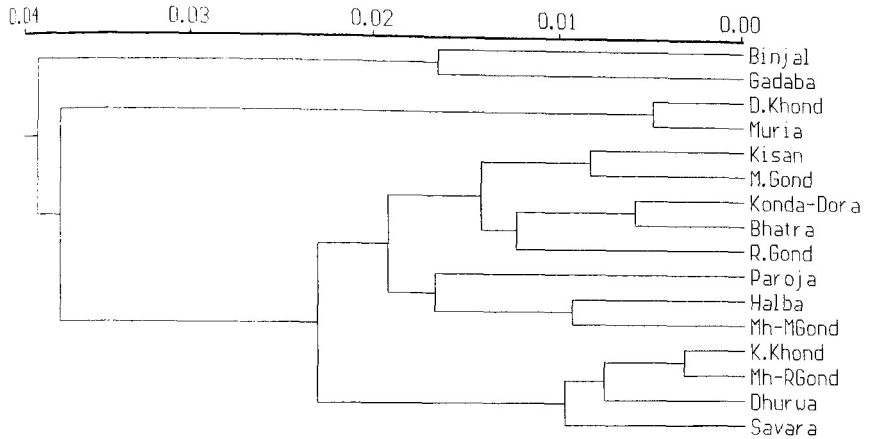

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There was a wide range of *FY*A* gene frequencies in Indian populations but a lesser degree of variation (55–65%) in the tribal groups. From the known

association of this system and particularly the FY phenotype with protection against malaria, this close range of FY gene frequency suggests the uniform operation of natural selection in this holoendemic malarial region of central India (Miller et al. 1976). The variance of allele frequency observed for the ESD, GC, and PI systems was relatively high, suggesting the converse, that there was either no or only locally varying selection by these alleles across the 16 populations.

The spatial patterning of certain genetic systems that was observed may reflect adaptation to a corresponding environmental variable. The distribution of the *HB*S* and *HP*1* allele frequencies showed that when *HB*S* is depressed, the *HP*1* allele is elevated. Whether the frequency clines of these two alleles at different loci represent gene flow across the region or provide a compensatory selective mechanism against malaria needs further investigation.

At both the state and the linguistic level there is sufficient genetic variability and differentiation among various tribal groups to allow the detection of a slight excess of homozygosity in the 16 tribal populations of central India. The estimates of genetic differentiation or gene diversity (F_{ST} or G_{ST}) based on our samples varied considerably from locus to locus, but the mean genetic differentiation of the 16 tribes was the highest so far reported from central India. This estimate is equivalent to the overall F_{ST} estimate for Indian populations (Papiha 1996) but is lower than the estimate for the Dhangar caste group (0.0438) in western India (Chakraborty et al. 1977) and nine tribal groups of southern India (Sirajuddin et al. 1994). In India the estimate of F_{ST} (the effect of population subdivision) varies considerably, perhaps because of the variable number of loci or populations involved in the different analyses. However, it is generally believed that the inclusion of tribal populations tends to elevate F_{ST} values. The present estimates from tribal populations of different states suggest that the groups exhibit F_{ST} values similar to other regional or caste groups.

The mean estimates of F_{IS} (coefficient of inbreeding within subgroups) and H_S (diversity in subpopulations) for each locus in state, linguistic, and total tribal groups were consistently higher than the F_{ST} or G_{ST} values, and these estimates were nearly equal to F_{IT} or H_T. However, the present values of F_{IS} and F_{IT} were considerably higher than the previously reported estimates from any state, tribal, or regional population (Papiha et al. 1982, 1984; Mastana and Papiha 1994). Although some of these variations may be due to the sample size, number, and geographic distance between populations and variables tested, the present analysis strongly suggests that the infrastructure of these populations is highly influenced by the local inbreeding within each tribal population. These results are also supported by the elevated coefficients of inbreeding in these tribal populations. For autosomal genes the coefficient of inbreeding ranged from 0.001 in the Binjhal to 0.029 among the Maria Gond, with an average for the 16 tribes of 0.014 (Chaudhuri 1993).

The other approach used to study the intertribal variability of genetic affinity was genetic distance. In the dendrogram (Figure 4) populations speaking Indo-Aryan or Austro-Asiatic languages showed little affinity with each other and they were widely spread in different clusters. However, there was some geographic affinity between different populations. The indigenous groups of Orissa, the Binjhal (Indo-Aryan speakers) and the Gabada (Austro-Asiatic speakers), showed close affinity and formed one clearly differentiated cluster, whereas the Raj Gond of Orissa seemed dissimilar to the remaining populations. The analysis of the central three clusters also demonstrated that the genetic affinities, rather than linguistic affinity, between the different tribal groups correlated better with geographic proximity. A small inverse relationship ($r = -0.1287$) was observed between genetic distance and average heterozygosity; this relationship may be due to a bottleneck effect, as suggested by Livshits and Nei (1990). This increase of genetic distance resulting from a bottleneck is due to the reduction in heterozygosity in one or both populations. Similar patterns of relationships in the Indian populations have also been reported by Roychoudhury (1982).

The lack of genetic relationship based on the linguistic data is intriguing. It may be explained by the considerable cultural and linguistic evidence that a number of Austro-Asiatic speakers gave up their languages in favor of Dravidian languages; several Dravidian-speaking tribes did adopt Indo-Aryan languages (Rakshit 1980). In the present study, therefore, it is not surprising to find that the Binjhal of Orissa, who speak an Indo-Aryan language, were previously Austro-Asiatic speakers and show a greater genetic affinity with the Austro-Asiatic-speaking Gadaba.

In conclusion, the genetic evidence of 39 alleles indicates a striking genetic heterogeneity in the 16 tribal populations of central India. This genetic diversity appears at both the geographic and the linguistic level. Genetic differentiation in these populations indicates that the genetic affinity correlates better with geographic proximity. In addition to genetic drift, gene flow, and selection, the genetic structure of the populations of central India is highly influenced by sociocultural adaptation and inbreeding.

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