

Congruence of genomic and ethnolinguistic affinities among five tribal populations of Madhya Pradesh (India)

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Abstract

The central Indian state of Madhya Pradesh is home to a large number of tribal populations of diverse linguistic and ethnic backgrounds. With a view to examining how well genomic affinities among tribal populations of this state correspond with their ethnic and linguistic affinities, we analysed DNA samples of individuals drawn from five tribes with diverse, but reasonably well-documented, ethnohistorical and linguistic backgrounds. Each DNA sample was scored at 16 biallelic DNA marker loci. On the basis of these data, genomic affinities among these populations were estimated. We have found an extremely good correspondence between the genomic and ethnolinguistic affinities.

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Introduction

Ethnic populations of India are culturally, morphologically, linguistically and genetically very diverse (Majumder 1998). Multiple waves of migration into India during prehistoric and historic times and the subsequent cultural differentiation resulting in strict rules governing mating practices are two of the major causes of the genomic diversity observed among contemporary ethnic groups of India. The tribal populations of India are accepted by anthropologists to be the autochthones. The total number of tribal groups is estimated to be about 450 (Singh 1992).

The central Indian state of Madhya Pradesh (MP) is inhabited by a large number of tribal groups, who are at different stages of modernization. Their occupations today range from hunting and gathering to white-collar jobs. Linguistically, the tribal populations of India speak dialects that belong to one of three language groups: Austro-Asiatic, Dravidian and Tibeto-Burman (Sino-Tibetan). Some large tribal groups (e.g. Bhil) speak a dialect that is classified by

many, but not all, as Indo-Aryan (Indo-European). The dialects of the tribal groups of MP represent the major language families present in India. It has been argued (Parpola 1975) that tribals belonging to different language families represent different genetic lineages. Therefore, it is of interest to study the genomic relationships among the tribal groups of this state who speak dialects belonging to different language families.

Materials and methods

Study populations and their ethnohistories: The earliest tribe of MP is the Austro-Asiatic-speaking Baiga tribe, while the Dravidian-speaking Gonds are geographically the most widespread and numerically very large. The Gonds seem to have highly influenced the Baigas. Inter-marriages between Gonds and Baigas appear to have been prevalent in historical times, although this practice has now been abandoned (Fuchs 1968). Gonds are said to have migrated from the southern regions of India and some anthropologists consider them as pre-Dravidian (Venkatachar 1935).

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We have studied five ethnic tribal populations from MP: (a) Muria and Halba, sampled in Bastar district, and (b) Kamar, Chinda Bhunjia and Chaukhtia Bhunjia sampled in Raipur district. The Murias are a numerically large ($\approx 100,000$) subtribe of the Gonds, inhabit only the Bastar district, and, as Elwin (1947) has stated, 'are the only civilized group among the other Gond subtribes of the same region'. They are highly endogamous but do not practise close inbreeding. The Kamars are a numerically small tribe ($\approx 13,000$) who primarily inhabit Raipur district and lead a very primitive lifestyle. They are known to be an offshoot of the Gonds (Russel and Hiralal 1916). Inbred marriages (such as a man marrying his father's sister's daughter) are permitted in this tribe. They speak Dravidian mixed with Halbi, a local Indo-European dialect. The Chinda Bhunjia and the Chaukhtia Bhunjia are numerically small (≈ 9500) subtribes of the larger Bhunjia tribe. The Chinda Bhunjias are considered to be an offshoot of the Austro-Asiatic-speaking Baiga, while the Chaukhtias are supposed to have arisen from admixture between the Gonds (maternal) and the Halbas (paternal) (Russel and Hiralal 1916). Both these tribes speak dialects that may be classified in the Indo-European language family (Shukla 1985), which appears to be due to acculturation with the Indo-European-speaking Halba, who number $\approx 60,000$ in Bastar district; the most modernized tribe of MP is Halba. They speak an Indo-European language. They have probably arisen from acculturation between some higher caste groups of Orissa (a neighbouring state) and some tribal people of MP. The Halbas deny any common ancestry with the Gonds.

From the above accounts, it appears that the Murias and Kamars are ethnolinguistically the most close. The Chinda and Chaukhtia are subtribes of Bhunjia and are ethnically close. The Halbas, who speak an Indo-European dialect, are expected to be distinct from these two ethnolinguistic clusters of populations. The objective of this study was to test these ethnolinguistic expectations using genomic data.

Blood samples: Samples of 5–10 ml in EDTA were collected with consent from 220 unrelated individuals belonging to the five tribal groups mentioned above. These samples were transported in ice to the laboratory of the Anthropology and Human Genetics Unit, Indian Statistical Institute, Calcutta, where they were analysed.

Laboratory analysis: High-molecular-weight DNA was isolated from the blood samples by the salting out procedure (Miller et al. 1988). Each DNA sample was analysed for polymorphisms at 16 loci, of which nine were insertion/deletion polymorphisms (Indels) and the remaining seven were RFLPs. Primer sequences used for PCR amplification, their corresponding annealing temperatures, and restriction endonuclease digestion protocols are provided in table 1. The reaction mixture for all the amplification reactions contained 50–100 ng DNA, 25 ng of each primer, 200 μ M dNTP mix and 1.3 Units of *Taq* DNA polymerase in a total

of 10 μ l volume. PCR buffer made up of 10 mM Tris.Cl (pH 8.4), 50 mM KCl and 1.5 mM MgCl₂ (for two loci T2 and CYP1A, 1.0 mM MgCl₂) was used. For *Alu* mtNUC locus PCR cycling temperature protocol was 30 cycles \times (94^oC for 15 s, 63^oC for 1 min, 72^oC for 1 min). For ESR locus the cycling protocol was 30 cycles \times (94^oC for 30 s, 63^oC for 1 min, 72^oC for 1.5 min). For all other loci the cycling protocol was the same except for the annealing temperature, i.e. 30 cycles \times (94^oC for 1 min, x^o C (see table 1 for the value of x) for 1 min, 72^oC for 1 min).

Statistical analysis: Allele frequencies at each of these biallelic loci were estimated for each population by the maximum-likelihood method. Chi-squared tests of significance between the observed genotype frequencies and those expected under Hardy–Weinberg equilibrium were performed. Observed heterozygosities were estimated. The extent of genetic differentiation, G_{ST} , was estimated for individual loci (Nei 1973) and also for the pooled data. Genetic distances between populations were estimated using the D_A distance measure (Nei et al. 1983). An unrooted neighbour-joining tree (Saitou and Nei 1987) was constructed to identify affinities among the tribal populations.

Results

Allele frequencies and heterozygosities: Sample sizes and the + allele (insertion allele for the Indel loci and presence of the restriction site for the RFLP loci) frequencies are given in table 2; for the *Alu* CD4 locus, the – allele frequency is presented because the deletion allele is the human-specific allele. All the loci except *Alu* CD4 show high degrees of polymorphism. All populations at most loci show statistically nonsignificant differences of observed genotype frequencies and those expected under Hardy–Weinberg equilibrium (table 2). The heterozygosities at each locus and the average heterozygosities over all the loci for each of the study populations are given in table 3. All the five populations show high levels of diversity at most of the loci. The heterozygosities at the *Alu* CD4 locus are, however, low in all the populations. Diversity at loci *Alu* FX3B and NAT are also comparatively low. However, the average heterozygosities of the populations show considerable variation; 0.388 among Kamars to 0.457 among Chaukhtia Bhujias.

Genomic diversity between populations: Results of gene diversity analysis for individual loci and for all the loci taken together are presented in table 4. The total genomic diversity among the subpopulations is quite high, except that for the *Alu* CD4 locus. It is seen that most of this diversity is due to the diversity between individuals within the same population. This is reflected in the low estimated values of the coefficient of gene differentiation, G_{ST} , which for the pooled data set is 0.025. For four loci, *Alu* FX3B, ESR, LPL and ALB, the G_{ST} values are rather low (< 0.01).

Table 1. Primer sequences, annealing temperatures, and restriction digestion protocols for the loci studied.

| Locus | Primer sequence | Annealing temp. (°C) | Restriction digestion protocol | Reference |
|---------------------|---|----------------------|---|-------------------------------------|
| <i>Alu</i> mtNUC | 5'-ACA AAG TCC AGG TTT CTA ACA G-3' 5'-AGT CTT GCT TAT TAC AAT GAT GG -3' | 63 | Not applicable | Zischler <i>et al.</i> 1995 |
| <i>Alu</i> ACE | 5'-CTG GAG ACC ACT CCC ATC CTT TCT-3' 5'-GAT GTG GCC ATC ACA TTC GTC AGA T- 3' | 58 | Not applicable | Stoneking <i>et al.</i> 1997 |
| <i>Alu</i> APO | 5'-AAG TGC TGT AGG CCA TTT AGA TTA G-3' 5'-AGT CTT CGA TGA CAG CGT ATA CAG A-3' | 50 | Not applicable | Stoneking <i>et al.</i> 1997 |
| <i>Alu</i> CD4 | 5'-AGG CCT TGT AGG GTT GGT CTG ATA-3' 5'-TGC AGC TGC TGA GTG AAA GAA CTG-3' | 58 | Not applicable | Edwards and Gibbs 1992 |
| <i>Alu</i> D1 | 5'-TGC TGA TGC CCA GGG TTA GTA AA-3' 5'-TTT CTG CTA TGC TCT TCC CTC TC-3' | 66 | Not applicable | Stoneking <i>et al.</i> 1997 |
| <i>Alu</i> FX3B | 5'-TCA ACT CCA TGA GAT TTT CAG AAG T -3' 5'-CTG GAA AAA ATG TAT TCA GGT GAG T-3' | 56 | Not applicable | Stoneking <i>et al.</i> 1997 |
| <i>Alu</i> TPA25 | 5'-GTA AGA GTT CCG TAA CAG GAC AGC T-3' 5'-CCC CAC CCT AGG AGA ACT TCT CTT T-3' | 58 | Not applicable | Stoneking <i>et al.</i> 1997 |
| <i>Alu</i> PV92 | 5'-AAC TGG GAA AAT TTG AAG AGA AAG T-3' 5'-TGA GTT CTC AAC TCC TGT GTG TTA G-3' | 54 | Not applicable | Stoneking <i>et al.</i> 1997 |
| <i>Alu</i> PLAT | 5'-GTG AAA AGC AAG GTC TAC CAG-3' 5'-GAC ACC GAG TTC ATC TTG AC-3' | 60 | Not applicable | Tishkoff <i>et al.</i> 1996 |
| ESR | 5'-CTG CCA CCC TAT CTG TAT C-3' 5'-CTC TGC CAC CCT GGC GTC-3' | 63 | 5 units of <i>PvuII</i> in appropriate buffer was added to the tube, incubated at 37°C for 2 h | Anderson <i>et al.</i> 1994 |
| NAT | 5'-GAC ATT GAA GCA TAT TTT GAA A-3' 5'-GAT GAA AGT ATT TGA TGT TTA-3' | 56 | 5 units of <i>KpnI</i> in appropriate buffer was added to the tube, incubated at 37°C for 2 h | Cascorbi <i>et al.</i> 1996 |
| CYP1A | 5'-CTG ACT GGC TTC AGC AAG TT-3' 5'-TAG GAG TCT TGT CTC ATG CCT-3' | 56 | 5 units of <i>MspI</i> in appropriate buffer was added to the tube, incubated at 37°C for 2 h | Hayashi <i>et al.</i> 1991 |
| PSCR | 5'-GGG TTC TAA AGG GAA GAA A-3' 5'-CCT AAC AGA GGT CAC AAG G-3' | 60 | 5 units of <i>TaqI</i> in appropriate buffer was added to the tube, incubated at 65°C for 2 h | Stinissen and Broeckhoven 1991 |
| T2 | 5'-CTG CAG CTT TTT CTC TAG GG-3' 5'-CGT CTG CTA CAA GTT CTG GCT T-3' | 65 | 5 units of <i>MspI</i> in appropriate buffer was added to the tube, incubated at 37°C for 2 h | Lynn Jorde (personal communication) |
| LPL | 5'-AGG CTT CAC TCA TCC GTG CCT CC-3' 5'-TTA TGC TGC TTT AGA CTC TTG TC-3' | 62 | 5 units of <i>PvuII</i> in appropriate buffer was added to the tube, incubated at 37°C for 2 h | Stepanov and Lemza 1993 |
| ALB | 5'-GTA GGT GGA CTT GGA GAA GG-3' 5'-GAT ATA CTT GGC AAG GTC C-3' | 63 | 5 units of <i>HaeIII</i> in appropriate buffer was added to the tube, incubated at 37°C for 2 h | Lynn Jorde (personal communication) |

Genomic affinities among populations: Pairwise genetic distances between the study populations were calculated from the allele frequencies using the D_A distance measure (Nei *et al.* 1983). An unrooted neighbour-joining tree was constructed from this distance matrix, which is depicted in figure 1. It is seen from this figure that the five study populations group themselves in three clusters: {Muria, Kamar}, {Chinda Bhunjia, Chaukhtia Bhunjia} and {Halba}.

Discussion

Human-specific insertion/deletion polymorphisms and the RFLP markers that have been used in this study are known to be selectively neutral in nature. Therefore, observed variations in the allele frequencies among populations are primarily due to random genetic drift or admixture. Since the study populations have generally remained endogamous,

Table 2. Allele frequencies and Hardy-Weinberg chi-square values at 16 biallelic loci in five populations of Madhya Pradesh.

| Locus | Population | | | | | | | | | | | | | | |
|------------------|------------|--------------|----------|----------|--------------|----------|----------|--------------|----------|----------------|--------------|----------|--------------------|--------------|----------|
| | Muria | | | Halba | | | Kamar | | | Chinda Bhunjia | | | Chaukhutia Bhunjia | | |
| | <i>n</i> | <i>p</i> (+) | χ^2 | <i>n</i> | <i>p</i> (+) | χ^2 | <i>n</i> | <i>p</i> (+) | χ^2 | <i>n</i> | <i>p</i> (+) | χ^2 | <i>n</i> | <i>p</i> (+) | χ^2 |
| <i>Alu</i> mtNUC | 49 | 0.388 | 0.145 | 48 | 0.625 | 0.592 | 54 | 0.463 | 0.609 | 25 | 0.420 | 0.113 | 39 | 0.513 | 0.027 |
| <i>Alu</i> APO | 49 | 0.714 | 3.864 | 47 | 0.691 | 5.803 | 57 | 0.649 | 3.008 | 27 | 0.481 | 10.780 | 37 | 0.622 | 0.043 |
| <i>Alu</i> ACE | 49 | 0.531 | 7.570 | 48 | 0.646 | 0.000 | 57 | 0.640 | 0.876 | 27 | 0.796 | 0.020 | 37 | 0.649 | 0.097 |
| <i>Alu</i> CD4 | 49 | 0.010 | 0.006 | 48 | 0.094 | 0.511 | 57 | 0.018 | 0.019 | 26 | 0.038 | 0.043 | 39 | 0.090 | 0.377 |
| <i>Alu</i> D1 | 49 | 0.347 | 7.210 | 48 | 0.427 | 3.096 | 57 | 0.342 | 9.840 | 25 | 0.620 | 8.280 | 38 | 0.289 | 9.080 |
| <i>Alu</i> FX3B | 49 | 0.786 | 2.212 | 48 | 0.698 | 0.817 | 57 | 0.746 | 1.392 | 26 | 0.731 | 9.660 | 38 | 0.750 | 0.105 |
| <i>Alu</i> TPA25 | 49 | 0.622 | 1.435 | 48 | 0.625 | 0.592 | 57 | 0.614 | 1.966 | 27 | 0.556 | 1.080 | 38 | 0.750 | 0.125 |
| <i>Alu</i> PV92 | 49 | 0.520 | 2.375 | 48 | 0.563 | 1.131 | 56 | 0.554 | 4.312 | 27 | 0.407 | 1.396 | 34 | 0.412 | 0.294 |
| <i>Alu</i> PLAT | 48 | 0.625 | 1.113 | 47 | 0.574 | 0.812 | 57 | 0.535 | 0.029 | 27 | 0.556 | 1.080 | 35 | 0.729 | 0.245 |
| ESR | 49 | 0.520 | 0.980 | 48 | 0.563 | 1.131 | 57 | 0.500 | 0.468 | 26 | 0.596 | 1.021 | 36 | 0.611 | 1.189 |
| NAT | 49 | 0.847 | 0.882 | 48 | 0.750 | 0.592 | 57 | 0.877 | 1.965 | 25 | 0.700 | 0.510 | 37 | 0.581 | 1.036 |
| CYP1A | 47 | 0.532 | 2.507 | 46 | 0.435 | 0.728 | 56 | 0.598 | 0.000 | 25 | 0.600 | 0.694 | 31 | 0.532 | 1.650 |
| PSCR | 49 | 0.286 | 0.490 | 48 | 0.365 | 3.887 | 57 | 0.228 | 0.528 | 25 | 0.180 | 1.205 | 38 | 0.263 | 1.864 |
| T2 | 49 | 0.480 | 0.980 | 48 | 0.521 | 1.043 | 55 | 0.655 | 2.342 | 25 | 0.380 | 0.268 | 38 | 0.289 | 2.975 |
| LPL | 49 | 0.551 | 0.694 | 48 | 0.583 | 0.157 | 57 | 0.640 | 0.431 | 27 | 0.630 | 0.060 | 39 | 0.526 | 5.880 |
| ALB | 49 | 0.510 | 1.007 | 48 | 0.594 | 0.304 | 54 | 0.454 | 1.070 | 26 | 0.500 | 0.154 | 35 | 0.514 | 2.330 |

Table 3. Observed heterozygosities at 16 biallelic loci and pooled heterozygosity in five population groups of Madhya Pradesh.

| Locus | Population | | | | |
|-----------------------|------------|-------|-------|----------------|--------------------|
| | Muria | Halba | Kamar | Chinda Bhunjia | Chaukhutia Bhunjia |
| <i>Alu</i> mtNUC | 0.449 | 0.417 | 0.444 | 0.520 | 0.513 |
| <i>Alu</i> APO | 0.245 | 0.277 | 0.351 | 0.815 | 0.486 |
| <i>Alu</i> ACE | 0.694 | 0.458 | 0.404 | 0.333 | 0.432 |
| <i>Alu</i> CD4 | 0.020 | 0.188 | 0.035 | 0.077 | 0.179 |
| <i>Alu</i> D1 | 0.286 | 0.354 | 0.263 | 0.200 | 0.211 |
| <i>Alu</i> FX3B | 0.265 | 0.479 | 0.439 | 0.154 | 0.447 |
| <i>Alu</i> TPA25 | 0.551 | 0.417 | 0.386 | 0.593 | 0.395 |
| <i>Alu</i> PV92 | 0.429 | 0.417 | 0.357 | 0.593 | 0.529 |
| <i>Alu</i> PLAT | 0.542 | 0.553 | 0.509 | 0.593 | 0.429 |
| ESR | 0.429 | 0.417 | 0.544 | 0.577 | 0.389 |
| NAT | 0.224 | 0.333 | 0.175 | 0.360 | 0.405 |
| CYP1A | 0.383 | 0.435 | 0.482 | 0.400 | 0.613 |
| PSCR | 0.449 | 0.313 | 0.386 | 0.360 | 0.474 |
| T2 | 0.429 | 0.583 | 0.545 | 0.520 | 0.526 |
| LPL | 0.531 | 0.458 | 0.474 | 0.444 | 0.692 |
| ALB | 0.571 | 0.521 | 0.426 | 0.538 | 0.629 |
| Pooled heterozygosity | 0.406 | 0.414 | 0.388 | 0.445 | 0.457 |

similarities of allele frequency profiles of the populations are a reflection of their common ancestry.

All the five populations in this study are from the central Indian state of Madhya Pradesh. The study populations have been selected from their primary regions of habitat. Muria and Halba have been sampled in Bastar and the other three populations have been sampled in Raipur.

There is significantly greater inter-individual variation within each study population than between the populations. The extent of population differentiation is rather low ($G_{ST} = 0.025$), probably indicating ancestral commonalities of the populations, which are not deep-rooted. The genomic affinities among the study populations indicate that

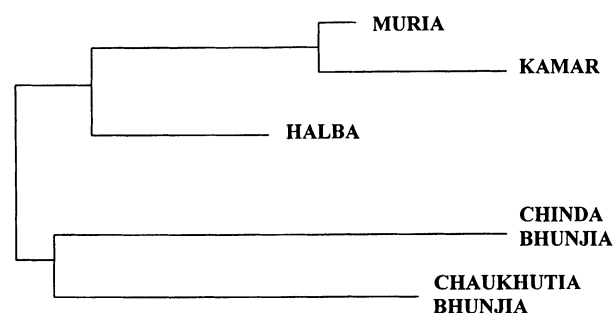


Figure 1. Unrooted neighbour-joining tree depicting genomic relationships among five population groups of Madhya Pradesh.

Table 4. Results of gene diversity analysis for individual loci and for all loci jointly considered.

| Locus | H_T | H_S | G_{ST} |
|------------------|-------|-------|----------|
| <i>Alu</i> mtNUC | 0.499 | 0.486 | 0.028 |
| <i>Alu</i> APO | 0.465 | 0.452 | 0.029 |
| <i>Alu</i> ACE | 0.454 | 0.439 | 0.031 |
| <i>Alu</i> CD4 | 0.095 | 0.092 | 0.027 |
| <i>Alu</i> D1 | 0.482 | 0.455 | 0.056 |
| <i>Alu</i> FX3B | 0.383 | 0.381 | 0.004 |
| <i>Alu</i> TPA25 | 0.464 | 0.456 | 0.017 |
| <i>Alu</i> PV92 | 0.500 | 0.491 | 0.019 |
| <i>Alu</i> PLAT | 0.478 | 0.469 | 0.020 |
| ESR | 0.493 | 0.490 | 0.007 |
| NAT | 0.374 | 0.351 | 0.061 |
| CYP1A | 0.497 | 0.490 | 0.015 |
| PSCR | 0.389 | 0.381 | 0.020 |
| T2 | 0.498 | 0.466 | 0.062 |
| LPL | 0.485 | 0.481 | 0.008 |
| ALB | 0.500 | 0.496 | 0.008 |
| All loci | 0.441 | 0.430 | 0.025 |

the Muria and Kamar are close to each other. From ethnohistorical accounts it is known that both these groups are descendants of the Dravidian-speaking Gonds. The two subtribes of the Bhunjias, Chinda and Chaukhutia, are also genetically close to each other. The Halbas are genetically distinct from these two clusters of populations. The Halbas are an Indo-European-speaking tribe of MP and do not share any common ancestry with the Gonds. Therefore, it is clear that genomic affinities among these populations of Madhya Pradesh correspond closely with their ethnohistorical and linguistic affinities.

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