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Diversity at Three Tetrameric STR Loci in a Substructured Golla Caste Population of Southern Andhra Pradesh, in Comparison to Other Indian Populations

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KEY WORDS 3 STR loci; CSF1P0; TPOX; TH01; 7 Golla subgroups; Mongoloid populations; tribes; other castes; varied social hierarchy.

ABSTRACT Genomic diversity based on 3 STR loci, CSF1P0, TPOX and TH01 is studied among the 7 subpopulations of the pastoral caste, Golla, of southern Andhra Pradesh, India. The 169 blood samples analysed for the present study are drawn from 30 villages distributed in 9 taluks (administrative unit below the level of a district) of Chittor district, a culturally homogeneous area within which marriages generally took place. A comparative analysis of the G_{ST} values and the phylogenetic position of the Gollas vis-à-vis the other Indian populations was made based on the 3 STRs with 16 other Indian populations. There is consistent increase in the magnitude of G_{ST} value, reflecting the degree of differentiation/heterogeneity with increasing complexity of the Indian populations so far studied for these loci. The cluster of populations in the UPGMA diagrams portrays the underlying social, ethno-historical and geographical backgrounds of the Indian populations well, both at the local, regional and national levels. Not only are the Mongoloid populations clearly separated from the non-Mongoloid populations, lower castes from the upper and middle castes, but the local Golla populations from the extreme south are distinctly separated from the eastern as well as northern populations. Even the microgeographic variations within the Gollas seem to have been faithfully depicted. Overall, the results of the present study are consistent with those of our earlier study, based on a much larger sample and with more number of loci among the same set of populations.

INTRODUCTION

Indian subcontinent with its unique population structure based on the caste system and because of its variation considered a natural laboratory for population genetics research, hence the primary focus of such studies. Indian anthropology, therefore, has a long tradition of micro-evolutionary studies among its caste populations at the local, regional and national levels, using the traditional genetic markers as well as the quantitative and qualitative biological variables. Hundreds of populations have been studied in the quest for delineating the patterns of human variation in India. The most unique and fundamental to the Indian population structure is the existence of endogamous subcastes within many of these castes within any region or linguistic area. These subcastes are usually characterised by high degree of isolation, small effective population size, and high degree of inbreeding, the conditions that are both conducive and prerequisite for the process of rapid micro-differentiation. There are indications that, in most cases, these subcastes may have evolved from the common parental stock, involving different processes of fission (Basu 1969; Malhotra 1978a,b). However, given that the caste system is only about 3000 years old (Thapar 1977), the evolutionary history of these subpopulations might have been relatively short albeit it is at this level of Mendelian units that the forces of evolution basically operate. The resolving power of the traditional genetic markers and the quantitative biological variables used thus far to delineate patterns of microdifferentiation among such populations is considered to be low. However, with the identification of highly variable DNA markers, particularly the microsatellite loci, and with the development of rapid screening techniques, using PCR, the possibilities of understanding genetic structure and microdifferentiation accurately among the local subdivided populations have enormously brightened. Yet, the use of DNA markers in the study of human diversity in India in general (Mouton et al. 1995; Bamshad et al. 1996, 1998; Watkins et al. 1999; Mukherjee et

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al. 1999; Majumder et al. 1999; Bhattacharya et al. 1999; Clark et al. 2000) and particularly for the study of substructured caste populations, representing probably the most fundamental level of Mendelian units, has only just begun (Reddy et al. 2001a). Based on 13 hypervariable microsatellite loci (STRs) we have recently studied the patterns of genomic diversity and differentiation among the 7 subcastes of Golla of southern Andhra Pradesh and observed that these hypervariable loci offer useful insights into the population structure and evolutionary history of the concerned populations. We have also compared the patterns of variation in quantitative biological variables- anthropometry and dermatoglyphs- on the same set of subjects, in those populations to examine how well the molecular genetic markers portray population relationships when compared to the traditional biological variables (Reddy et al. 2001b). In the meantime, we have typed a subset of those samples for three STR loci for which comparative data were available on 16 other Indian populations. In the present paper we report findings on the pattern of genomic diversity based on the three STR loci among the 7 Golla subpopulations, on one hand, and the overall pattern based on 23 Indian populations on the other.

MATERIALS AND METHODS

Population

The Golla is a great pastoral caste of Telugu people of Andhra Pradesh. Their traditional occupation has been tending sheep and cattle and selling milk, although many of them have now acquired lands and do agriculture as well. These people are distributed throughout Andhra Pradesh. People belonging to this tradition and occupation are also found in other parts of India, in different linguistic and geographical areas, known by different names and probably have different origins.

Extensive interviews with the elders of this community suggest existence of 12 endogamous subcastes within Gollas, although Thurston (1909) noted only nine such sects. This is probably because of the localised distribution of some of these subcastes, hence escaped the attention of the ethnographer. However, these people still retain their traditional patterns intact and maintain high degree of endogamy within the subcastes. The exchange of mates between the Golla subcastes has just started, and is still estimated to be <1%. As all other traditional populations of southern India, Gollas prefer consanguineous marriages and village endogamy, with marriage contacts usually restricted to a small radius. Therefore, we restricted our study to a culturally homogeneous area called Chittoor district in Andhra Pradesh and collected samples from all the subgroups found in that area. We found only seven subcastes in this area, including the Kurava whose position among the Gollas is currently disputed.

Blood Samples

The 317 blood samples were collected from 30 villages distributed among the 9 taluks of Chittor district in Andhra Pradesh. DNA was extracted from a subset of 169 individual buffy-coat spots using a standard method of DNA isolation (Organic method), and utilised for the present study. The isolated DNA was quantified on 1% Agarose Gel. The subgroup-wise sample sizes are given in table 1.

Amplification and Typing

The 3 STRs were analyzed in one multiplex PCR reaction for the loci CSF1PO, TH01 and TPOX. Twenty five to fifty nanograms of DNA was amplified in a total volume of 25 ml reaction mixture using commercially available kit (Promega Corporation, USA). The amplified product was separated on 6% denaturing polyacrylamide gels. Following electrophoresis, the gels were stained using a silver staining kit from Promega. The repeat sizes were determined with respect to the standard CTT Ladder supplied with the kit. Alleles at these loci have been designated by the size (in base pairs) of their PCR product and their corresponding repeat numbers. The studied tandem repeats are tetrameric with 4 base-pair increment between alleles, except for allele 9.3 of locus THO1which is one base pair shorter than allele 10. The CSF1PO, TPOX and THO1 have core repeat sequences AGAT, AATG and AATG, respectively, and their chromosomal locations are at 5q33.3-q34, 2p25.1-pter and 11p15.5.

For comparison, data on the 3 STR loci available for 16 other Indian populations (Mukherjee et al. 1999; Dutta and Kashyap 2000a, b;) representing different geographic regions, ethnic elements and socioeconomic strata- five Mongoloid populations (Kuki, Naga, Hmar, Meitei and Garo), besides Muslims from the north-east, five from West Bengal (Two independent Brahmin samples, Kayastha, Bagdi and Santal), three from Orissa (Tanti, Agharia and Gaud) and two from Uttar Pradesh (Chamar and Brahmin) were also compiled.

Statistical Analysis

Allele frequencies were computed using gene-counting method. The pair-wise genetic distances were computed using modified Cavalli-Sforza distance (D_A) of Nei et al. (1983). G_{ST} values and heterozygosities were computed and UPGMA trees were drawn using the NJBAFD program supplied by Dr. Takezaki.

RESULTS

Allelic Distributions

The allelic frequencies among the Golla subgroups at the three STR loci are given in table 1. At the CSF1P0 locus, a total of 7 alleles were observed, with repeat numbers ranging from 8 – 14. The repeat numbers 12, 10 and 11 are the three most predominant alleles. However, allele 12 occurs with highest frequency with a range of 0.425 – 0.650. Karnam is the only population that showed all the alleles. At the TPOX and the TH01, a total of 8 alleles are found among the Golla populations, the repeat numbers ranging from 6 – 13 and 5 - 11, respectively. At TPOX, the most predominant alleles- 11, 8 and 12 – are common to all the Golla populations, although alleles 9 and 10 are also found with moderate frequency in at least some of them. The frequency of the most predominant allele 11 varies between 0.175 in Puja and 0.565 in Punugu. At the TH01, all the 8 alleles are traced only in the Pokanati, while 7 of those were present in the Doddi, Karnam and Punugu populations. While allele 6 is most predominant, ranging from 0.187 in the Doddi to 0.400 among the Erra and Kurava, alleles 9 and 9.3 are found to be the other two predominant alleles. However, alleles 7 and 8 also occur with uniformly moderate frequency in each of the Golla populations. A comparison among the Indian populations suggest that the spectrum of allelic variation at each of the three

Table 1: Comparative allele frequencies in the seven Golla populations at the three STR loci; the numbers in parentheses are the number of chromosomes typed

Locus	*Allele*	*Doddi (80)*	*Erra (40)*	*Karnam (64)*	*Pokanati (48)*	*Puja (40)*	*Punugu (46)*	*Kurava (20)*
CSF1PO	8	0	0	0.016	0.063	0	0	0
	9	0.075	0	0.031	0.021	0.075	0	0
	10	0.238	0.3	0.297	0.353	0.3	0.37	0.3
	11	0.125	0.1	0.125	0.063	0.15	0.109	0
	12	0.525	0.55	0.453	0.479	0.425	0.478	0.65
	13	0.037	0.05	0.062	0.021	0.05	0.043	0.05
	14	0	0.016	0	0	0	0	0
TPOX	6	0.012	0	0	0.021	0	0	0
	7	0.012	0	0	0	0.025	0.022	0
	8	0.25	0.225	0.281	0.312	0.225	0.13	0.2
	9	0.15	0.075	0.125	0.188	0.15	0.087	0.25
	10	0.076	0.2	0.094	0.125	0.15	0.13	0.05
	11	0.238	0.375	0.297	0.229	0.175	0.565	0.45
	12	0.25	0.125	0.203	0.125	0.275	0.065	0.05
	13	0.012	0	0	0	0	0	0
THO1	5	0	0	0	0.042	0	0	0
	6	0.187	0.4	0.297	0.229	0.3	0.391	0.4
	7	0.113	0.125	0.094	0.146	0.125	0.087	0
	8	0.138	0.125	0.171	0.208	0.2	0.13	0.1
	9	0.213	0.075	0.125	0.083	0.1	0.283	0.4
	9.3	0.162	0.175	0.203	0.083	0.25	0.065	0.05
	10	0.162	0.1	0.094	0.188	0.025	0.022	0.05
	11	0.025	0	0.016	0.021	0	0.022	0

STR loci seems to be somewhat different in the Mongoloid populations when compared to the other Indian populations in general and particularly when compared to the populations from outside West Bengal.

The values of probability for non-random association of alleles based on interclass correlation between loci are presented in table 2, which suggest that the correlation between the loci are not significant, hence the studied loci can be considered independent. Results based on three different tests for Hardy-Weinberg Equilibrium status (Table 3) suggest that each of the 7 populations are in equilibrium with reference to each of the three studied loci.

Average Heterozygosity and G_{ST} Values

Average population heterozygosity per locus along with the G_{ST} values that indicate the degree of differentiation among the Golla populations are furnished in table 4. The average heterozygosity which reflects within population heterogeneity is similar among 5 of the 7 Golla populations (Range, 0.72 - 0.77), while the Kurava and Punugu show relatively low values. Heterozygosity values at the CSF1P0 was lower (0.513 – 0.717) in comparison to the values obtained at the TPOX (0.649 – 0.818) and TH01 (0.700 – 0.849) loci. The coefficient of gene differentiation (G_{ST}) among the subpopulations is very low in case of the CSF1P0 (0.016), while it is relatively much higher at the other two loci (0.039 and 0.041). However, the average G_{ST} is moderate among Gollas (0.032 ± 0.0079). Table 5 presents comparative data on the average G_{ST} values for the Gollas and the other Indian regional population groups. The average G_{ST} is smallest for the Gollas at the lowest level of

Table 2: Pair-wise interclass correlation for non-random association of alleles between the studied loci

Loci	*Two Sided Probability*						
	Doddi	*Erra*	*Karnam*	*Kuruva*	*Puja*	*Pokanati*	*Punugu*
TPOX /HUMTHO1	0.752	0.665	0.621	0.899	0.299	0.312	0.466
CSF1PO/HUMTHO1	0.079	0.328	0.826	1.000	1.000	0.304	0.923
CSF1PO/ TPOX	0.952	0.192	0.665	0.410	0.494	0.764	0.228

Table 3: The p-values based on different tests for the status of Hardy Weinberg Equilibrium at the three STR loci in the 7 Golla populations

Locus	*Doddi*	*Erra*	*Karnam*	*Kuruva*	*Puja*	*Pokanati*	*Punugu*
CSF1PO							
HWE Test	0.341	0.129	0.912	0.571	0.981	0.193	0.824
Likelihood Ratio Test	0.229	0.466	0.850	0.422	0.443	0.227	0.259
Exact Test	0.313	0.529	0.951	0.627	0.394	0.102	0.422
TPOX							
HWE Test	0.481	0.939	0.409	0.532	0.115	0.810	0.147
Likelihood Ratio Test	0.545	0.201	0.411	0.776	0.410	0.220	0.300
Exact Test	0.890	0.309	0.510	0.622	0.215	0.213	0.599
THO1							
HWE Test	0.428	0.732	0.412	0.167	0.988	0.430	0.226
Likelihood Ratio Test	0.665	0.334	0.445	0.557	0.123	0.449	0.500
Exact Test	0.513	0.131	0.327	0.487	0.096	0.248	0.611

P<0.050 suggests deviation from the HWE.

Table 4: Average heterozygosity per locus and the G_{ST} values

Locus	*Doddi*	*Erra*	*Karnam*	*Pokanati*	*Puja*	*Punugu*	*Kurava*	G_{ST}
CSF1PO	0.653	0.610	0.697	0.651	0.717	0.635	0.513	0.016
TPOX	0.800	0.767	0.779	0.800	0.818	0.649	0.726	0.041
THO1	0.845	0.782	0.821	0.849	0.801	0.754	0.700	0.039
Average	0.766	0.720	0.765	0.767	0.779	0.679	0.646	0.032

var=0.000063 se=0.007930

Table 5: Locus-wise and average G_{ST} values among the Indian population groups from different regions and complexity

Population	*CSF1P0*	*TPOX*	*THO1*	*Average G_{ST} ± S.E.*
Gollas	0.016	0.041	0.039	0.032 ± 0.008
N.E & Bengal (WB)	0.032	0.085	0.033	0.050 ± 0.018
Gollas, N.E & WB	0.045	0.084	0.056	0.061 ± 0.012
8 Indian groups	0.060	0.019	0.062	0.047 ± 0.014
All Indian Groups	0.060	0.067	0.067	0.065 ± 0.002

N. E = North East

Table 6: Pair-wise genetic distances (D_A) based on the 3 STR loci between the seven Golla populations

Population	*1*	*2*	*3*	*4*	*5*	*6*
Doddi	-					
Erra	0.051	-				
Karnam	0.022	0.025	-			
Pokanati	0.043	0.051	0.034	-		
Puja	0.032	0.041	0.024	0.065	-	
Punugu	0.069	0.038	0.052	0.084	0.073	-
Kurava	0.108	0.088	0.095	0.116	0.133	0.059

population hierarchy and the G_{ST} for the other groups, broadly speaking, follow the trend of increase with the increasing complexity of populations- geographic, socioeconomic and ethnic heterogeneity- and range from 0.032 among the Gollas to 0.067 when all the Indian populations studied were considered together.

The UPGMA tree constructed for Golla subpopulations, using the D_A distances (Table 6), is presented in figure 1. The UPGMA tree suggests a relatively earlier separation, hence the distinctiveness, of Kurava population whose position among the Gollas is disputed. The relatively earlier separation of Punugu from the rest of Golla subpopulations is also depicted. The clustering of the remaining 5 Golla populations is consistent with the microgeographic affiliations; for example, the Doddi, Puja and Karnam distributed in the western parts of the district tend to cluster together although the Pokanati and Erra, distributed in the eastern region do not form a compact cluster.

In order to gauge the phylogenetic relationships among the Indian populations, the D_A distances were computed between all the 23 populations and the UPGMA tree was constructed (Fig. 2). It is remarkable to note that the ethnic, socioeconomic and geographic backgrounds of the populations are all depicted clearly in the way the populations cluster among them. Altogether, five major and distinct clusters of populations can be seen from the UPGMA diagram, constituting (1) the lower castes, represented by Chamar from UP, Tanti from Orissa and Bagdi from West Bengal, to which the three upper caste – Brahmin and Kayastha from West Bengal and Brahmin from UP- together join as a sub-cluster; (2) the Mongoloid populations from the northeastern region consisting four tribes- Kuki, Hmar, Naga, and Garo- and a caste group called Meitei, (3) Upper and middle castes from the Eastern region, constituting one of the two Brahmin samples from Bengal, the middle ranking Gaud and Agharia from Orissa, (4) the six of the 7 Golla subpopulations, representing by far the most closely related group of populations and (5) the Santals, Kurava and a Muslim population from Manipur appear as a distinct outer elements in the cluster separated from almost all other groups, with relatively long branches.

DISCUSSION

The present study portrays ethnohistorical

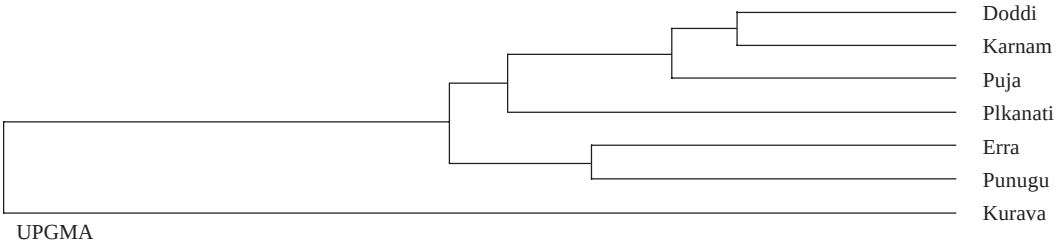

Fig. 1. UPGMA tree constructed using the DA distances between the 7 Golla subpopulations

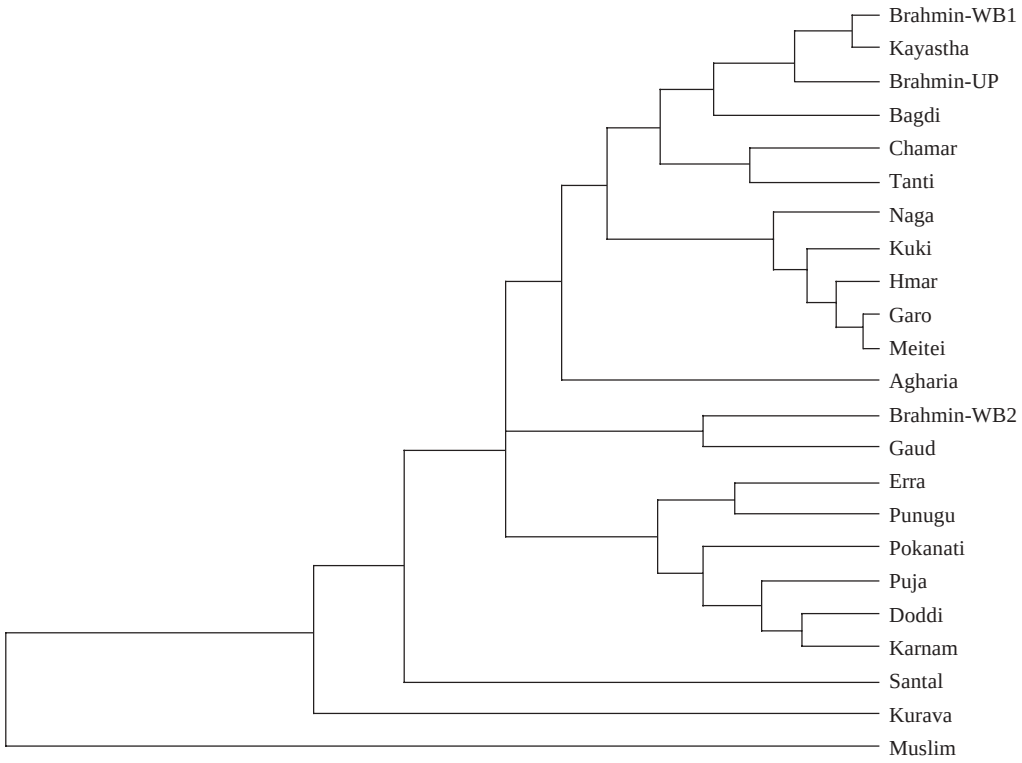

Fig. 2. UPGMA tree constructed using the DA distances based on 3 STR loci among the 23 Indian populations

relationships and the process of micro-differentiation among the local subdivided Golla populations rather well, although based on only three STR loci (Fig. 1). For example, that the Kurava had a different origin or was separated from the parental source of the remaining Golla populations much earlier is clearly depicted in the UPGMA tree. Similarly, the possibility of earlier separation of the Punugu and a parental population of the remaining Golla subgroups is also indicated, truly conforming to the hypothesis proposed in our earlier study which was based on 13 STR loci and larger number of samples (Reddy et al. 2001a). This may suggest the genetic reality in the inferred pattern of historical relationships among the studied populations.

The average G_{ST} value (0.032) is larger than that observed for traditional markers among the Indian populations which is only about 0.015. Further, it is interesting to note that average G_{ST} of the Gollas at a lowest level of population substructure is smallest when compared to the other population groups from other regions (Table 5), and that when all the 23 Indian population groups studied, representing the greatest heterogeneity, were analysed shows the largest G_{ST} value. This is consistent with the genetic pattern expected. This consistency is also extended to the degree of differentiation at different loci in the sense that Gollas and the other groups of populations show the same trend in each of the three STR loci. Even the pattern of allelic variation bears the stamp of ethno-specific patterns; for example, the Mongoloid populations along with certain groups of Bengal with a possibility of admixture with the former show a slightly different pattern in the alleles that are most predominant compared to the caste populations from other regions, at each of the three loci.

Now, how far and how well has the studied loci reflected the genetic, ethno-historical and

geographical heterogeneity represented by the Indian populations included here for comparative study? Overall, it may be said that the clustering pattern in the UPGMA diagram is consistent with the above backgrounds of the Indian populations. Not only are the Mongoloid populations clearly separated from the non-Mongoloid populations, lower castes from the upper and middle castes, but the local Golla populations from the extreme south are also distinctly separated from the eastern as well as northern populations. Even the microgeographic variations within the Gollas seem to have been faithfully depicted. Furthermore, when we construct UPGMA tree (not presented) including the Caucasian, Hispanic and African Americans and the Mongoloid Chinese samples together with the Indian populations, the American groups cluster together, separated from the Indians, whereas the Chinese sample integrates itself into the Mongoloid cluster from north-eastern India. Despite the inherent ethnic differences, the three American populations have been living together for long time and there had also been considerable amount of genetic exchange between them, hence the observed pattern of clustering together in the present context is in order. What is, however, not expected is the behaviour of the two independent Brahmin samples from West Bengal who align with two different clusters. Where as the Brahmin sample studied by Dutta and Kashyap (2000 b) along with Kayastha, the other upper caste sample from Bengal and Brahmins from UP form a cluster, the other Bengali Brahmin sample (Mukherjee et al. 1999) align with the two middle caste groups from Orissa. One may note that Brahmin is a very heterogeneous group comprising within them a number of subgroups and the samples were drawn independently from different locales by the two groups of investigators, hence represent probably different genetic compositions. The other reason could be the vastly different sample size, as Dutta and Kashyap (2000 b) sample is many-fold larger than the other. Nevertheless, in conclusion, we may say that the microevolutionary studies based on the molecular genetic markers, in general, and particularly those based on hyper variable DNA markers are useful in depicting population genetic relationships at different levels of hierarchy. Given the scope for proliferation of such studies among Indian populations there is hope for more precise understanding of the patterns of human variation in India.

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