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Abstract Historical records indicate that the Portuguese brought the African Siddis to Goa, India, as slaves about 500 years ago. Subsequently, the Siddis moved into the interior regions of the state of Karnataka, India, and have remained there ever since. Over time the Siddis have experienced considerable cultural changes because of their proximity to neighboring population groups. To understand the biological consequences of these changes, we studied the Siddis to determine the extent of genetic variation and the contributions from the African, European, and Indian ancestral populations. In the present study we typed the Siddis for 20 polymorphic serological, red cell, and *Alu* insertion-deletion loci. The overall pattern of phenotype (and genotype) distribution is in accordance with Hardy-Weinberg expectations. Considering the ethnohistorical records and the availability of secondary-source genetic data, we used two data sets in the analysis: one comprising eight serological and red cell enzyme markers with eight population groups and another comprising six *Alu* insertion-deletion markers with seven tribal groups of South India. The dendrograms generated from these two data sets on the basis of genetic distance analysis between the selected populations of African, European, and Indian descent reveals that the Siddis are closer to the Africans than they are to the South Indian populations. Genetic admixture analysis using a dihybrid model (19 loci) and a trihybrid model (10 loci and 8 loci) shows that the predominant influence comes from the Africans, a lesser contribution from the South Indians, and a slight contribution from the Portuguese. Thus the original composition of the African genes among the Siddis has been diluted to some extent by the contribution from southern Indian population groups. There is no nonrandom association of alleles among a set of 10 genetic marker systems considered in the present study. The demonstration of genetic homogeneity of the Siddis, despite their admixed origin, suggests the utility of this population for genetic and epidemiological studies.

The diversity of the Indian population is complex and wide ranging. The subdivision of the Indian population by region, language, religion, caste, tribe, and

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KEY WORDS: SIDDIS, AFRICANS, GENETIC DISTANCE, AVERAGE HETEROZYGOSITY, GENETIC ADMIXTURE, NONRANDOM ASSOCIATION, SEROLOGICAL MARKERS, RED BLOOD CELL MARKERS, *ALU* INSERTION-DELETION, SOUTH INDIA.

immigrant group provides an ample opportunity to study the magnitude of gene differentiation among the different groups. It has been estimated that the Indian national population is composed of 50,000–60,000 essentially endogamous subpopulations (Gadgil et al. 1998). In addition, gene flow through different waves of migration and characteristic cultural, linguistic, and demographic histories of each of these groups have produced a great reservoir of genetic diversity.

The Siddis are one of the distinct tribal groups from the state of Karnataka in southern India. Their ancestry can be traced back to east Africa. India experienced the first migratory wave of the Siddis during the 12th century. Historical records indicate the presence of two Siddi kingdoms, established around A.D. 1100 on the Western coast of India at Janjira and Jaffrabad (Bhattacharya 1969). Subsequently, the Portuguese brought the Siddis as slaves to India in the 16th and 17th centuries. Between 1680 and 1720, a number of Africans from Mozambique were brought to India. In 1690, John the Britto, a Portuguese missionary, came to Goa (a state on the western coast of India), accompanied by 200 Africans from Mozambique (Nevet 1981). Ever since their arrival in India, these Africans have settled in different parts of the coastal regions of western India (Banaji 1932; Bhattacharya 1969; Palakshappa 1976; Enthoven 1975).

It is worthwhile to state that the Siddis, who were brought as slaves by the Portuguese to Goa, escaped from the increasing atrocities of the colonizers and moved into the interior regions of the neighboring state of Karnataka in South India. Most of them are now settled in Uttara Kannada District (an administrative division) of the state of Karnataka. The total population of the Siddis (10,500) who reside in Uttara Kannada are primarily distributed in the towns of Sirsi, Mundagoda, Joida, Haliyala, Yellapura, and Ankola (Tribal Welfare Department 2002). In their somatoscopic features (broad nose, dark skin color, kinky hair, alveolar prognathism, etc.), the Siddis resemble Africans even today. The Siddis also show signs of the clan system that once existed among the Siddis of Africa. Some of their clan titles (e.g., Kua, Makua, and Makoba) are the names of African tribes. Although through the years the Siddis have adopted Christianity, Hinduism, and Islam, interreligion marital alliances are not infrequent.

Ethnohistorical records have revealed a long period of Portuguese and South Indian contact with the Siddis, and therefore biological affinities of the Siddis with them cannot be ruled out. The social and cultural ties of the Siddis to their immediate neighbors are so strong that they have become bilingual and speak Konkani, a language belonging to the Indo-European family of languages, and Kannada, a language belonging to the Dravidian group of languages, and have abandoned the Swahili family of languages to which they originally belonged. Considering the available ethnohistorical information on the Siddis, it appears that there is a considerable gene flow in their gene pool, not just from the Portuguese but from South Indians as well.

So far, only a few genetic studies have been conducted on the Siddis of Karnataka. Vijaykumar et al. (1987) found that the gene distance between the local community of Havig Brahmins and Ethiopians was greater than the distance

between the Havig Brahmins and the Siddis or that between the Siddis and Ethiopians. Ramana et al. (2001) showed gene flow among caste, tribe, and Siddi populations of South India by studying Y-chromosome SNP haplotypes. Watkins et al. (2005), studying the diversity and divergence among the tribal populations of India (with the Siddis as one of the population groups), found that the Siddis were closer to African groups than to other non-African groups in an unrooted neighboring family network of 35 populations.

However, available genetic studies on the Siddis of Karnataka are scattered, and no systematic efforts have been made to understand the extent of African, European, and Indian affinities with the Siddis and their contribution to the gene pool of the Siddis of Karnataka. Thus, considering the ethnohistorical records, in this study we assess the extent of heterogeneity of the genetic structure of the Siddis and also of selected populations of African, European, and Indian descent chosen on the basis of their historical, linguistic, and ethnic proximity to the Siddis.

Materials and Methods

We collected 219 blood samples for the analysis of serological and red cell enzyme markers. The number of blood samples used for each marker varied because of laboratory constraints. For *MN*, Rh (*CcdEe*), and PTC tasting ability, 100 individuals were tested. For *Alu* (insertion-deletion) markers, 50 blood samples were collected. Here also, the results obtained on different *Alu* markers varied because of laboratory constraints. The numbers of samples typed for different polymorphic loci in the present investigation are listed in Table 1. The geographic location of the population under study is presented in Figure 1.

Informed consent was obtained from all subjects before blood collection. Unrelated individuals were chosen for the blood sample collection, and all the necessary precautions were taken.

For the blood grouping and the red cell enzyme markers, we collected about 1 ml of blood in an Eppendorf tube containing EDTA as an anticoagulant. For the DNA markers, we collected 5 ml of intravenous blood in vacutainers with ACD as an anticoagulant. The blood samples were analyzed for the following serological, red blood cell enzyme, and *Alu* (insertion-deletion) markers: *A1A2BO*, *MN*, Rh (*CcdEe*), *ABH*, PTC tasting ability, *ADA*, *AK1*, *ACP1*, *ESD*, *PGM1*, *PGM2*, *GLO1*, *GPI*, *HB*, *PV92*, *F13B*, *D1*, *ACE*, *PLAT*, and *APO*.

Blood group systems *A1A2BO*, Rh (*CcdEe*), and *MN* were typed according to the methods described by Race and Sanger (1975). PTC tasting ability test was performed following the method of Harris and Kalmus (1949).

Red blood cell enzymes were analyzed following the protocol for each marker. First, hemolysates were prepared and then typed biochemically for seven different polymorphic red blood cell enzymes and hemoglobin types, following standard horizontal electrophoretic techniques. Isozymes of erythrocyte enzymes esterase D (*ESD*) and phosphoglucomutase locus 1 (*PGM1*) were electrophoresed together on one agarose gel and stained in the same order (Wraxall and Stolorow

Table 1. Allele Frequencies Among the Siddis of Karnataka

Locus	*Number Tested*	*Allele*	*Frequency*
A1A2BO	219	*ABO*A1*	0.117
		*ABO*A2*	0.042
		*ABO*B*	0.194
		*ABO*O*	0.647
MN	100	*MN*M*	0.539
		*MN*N*	0.461
Rh (*CcdEe*)	100	*CDE*	0.0
		CDe	0.265
		CdE	0.153
		Cde	0.393
		cDE	0.0
		cDe	0.0
		cdE	0.0
		cde	0.189
ABH	100	*ABH*Se*	0.434
		*ABH*se*	0.566
PTC	100	*PTC*T*	0.590
		*PTC*t*	0.410
GLO1	163	*GLO1*1*	0.295
		*GLO1*2*	0.705
GPI	100	*GPI*1*	1.000
		*GPI*2*	0.0
		*GPI*3*	0.0
		*GPI*5*	0.0
		*GPI*8*	0.0
		*GPI*9*	0.0
ACP1	100	*ACP1*A*	0.212
		*ACP1*B*	0.788
		*ACP1*C*	0.0
ESD	218	*ESD*1*	0.890
		*ESD*2*	0.110
PGM1	217	*PGM1*1*	0.761
		*PGM1*2*	0.237
		*PGM1*3*	0.002
		*PGM1*7*	0.0
PGM2	217	*PGM2*1*	0.952
		*PGM2*A*	0.048
AK1	100	*AK1*1*	0.953
		*AK1*2*	0.047
ADA	218	*ADA*1*	0.940
		*ADA*2*	0.046
		*ADA*3*	0.014
HB	163	*HB*V*	0.003
		*HB*N*	0.997
PV92	42	+	0.222
		−	0.667
F13B	42	+	0.202
		−	0.798
D1	45	+	0.422
		−	0.578
APO	46	+	0.543
		−	0.457
ACE	42	+	0.333
		−	0.667
PLAT	48	+	0.365
		−	0.635

1986). The typing of phosphoglucomutase locus 2 (*PGM2*) was carried out along with *PGM1*. Similarly adenosine deaminase (*ADA*) and adenylate kinase locus 1 (*AK1*) enzymes were separated together on the same agarose gel and simultaneously stained, as described by Murch et al. (1986). The method of Wraxall and Emes (1976) was followed for typing red blood cell acid phosphatase locus 1 (*ACP1*), with agarose as a medium of separation. The mixed agarose/starch gel electrophoretic technique of Scott and Fowler (1982) was used for glyoxalase locus 1 (*GLO1*) typing. Variants for glucose phosphate isomerase (*GPI*) were screened following the method of Detter et al. (1968) with some modifications by Papiha and Chahal (1984). Hemoglobin (*HB*) variants (sickle cell) were studied in conjunction with *GLO1* typing, as described by Divall and Greenhalgh (1983).

DNA extraction from whole blood was carried out as described by Miller et al. (1988), and we followed standard protocols for typing each *Alu* insertion-deletion marker (Majumder et al. 1999).

Figure 1. Geographic location of the Siddis of Karnataka (Uttara Kannada District) in India.

The present-day Siddis are considered an admixed population. A number of population groups of African, European, and Indian descent have contributed in varying proportions to the contemporary Siddis. The available information on genetic data of these most likely contributory gene pools was obtained, and two data sets were chosen in light of the ethnohistorical background of the Siddis.

A detailed genetic structure analysis was performed, first on the basis of 8 population groups (Siddis, Marathas, Africans, Portuguese, and populations of Andhra Pradesh, Karnataka, Kerala, and Tamil Nadu) with 27 alleles controlled by 8 loci and, second, on the basis of 7 population groups (Siddis, Africans, Toda, Kurumba, Irula, Pallan, Kota) with 12 alleles controlled by 6 *Alu* insertion-deletion markers (see Appendixes 1 and 2).

Gene frequency data on the different populations were compiled from Mourant et al. (1976), Bhasin et al. (1992), Roychoudhury and Nei (1988), the *ALFRED* database (*ALFRED* 2008), and the studies by Vishwanathan et al. (2004) and Basu et al. (2003).

The allele frequency estimates for the 20 markers in the Siddis were computed using the maximum-likelihood method (Reed and Schull 1968). Genetic distances among the populations were computed using Nei's standard genetic distance (Nei 1972), and the standard errors (SE) were computed using Nei and Roychoudhury's (1974) method. To determine the significance of genetic distances among the different populations, the gene frequency data were compared pairwise using the chi-square statistic (Nei and Roychoudhury 1974). The distance matrix was then used to construct a phylogenetic tree based on the unweighted pair group method with arithmetic mean (UPGMA) (Nei 1987). We next performed a regression analysis of heterozygosity on genetic distance, as proposed by Harpending

Table 2. Chi-Square Test for Estimating Hardy-Weinberg Equilibrium for the Siddis of Karnataka

Locus	*Number Tested*	χ^2	*df*
A1A2BO	219	2.209	2
MN	100	8.400[a]	1
Rh	100	5.100	10
ADA	218	1.333	1
AK1	100	0.207	1
ACP1	100	1.390	1
ESD	218	0.061	1
PGM1	217	0.682	1
PGM2	217	0.332	1
GLO1	163	0.003	1
HB	163	0.003	1
PV92	42	0.054	1
F13B	42	16.490[a]	1
D1	45	3.311	1
APO	46	0.060	1
ACE	42	9.054[a]	1
PLAT	48	1.020	1

a. Significant at $p < 0.05$.

and Ward (1982). The regression equation was subjected to a test of significance, following the method of Snedecor and Cochran (1967). The percentage contributions from the ancestral populations to the hybrid population (the present-day Siddis) were estimated using the method of Chakraborty (1985, 1986). Finally, examination of nonrandom association of alleles at different genetic loci, using the methods of Brown et al. (1980) and Chakraborty (1981, 1984), was intended to show whether any individual effects of admixture remain in the current population, thus making it heterogeneous.

Results

Allele Frequencies. Table 1 shows the allele frequency distribution of 20 loci among the Siddis. The allele frequency estimates were used for the goodness-of-fit chi-square test to determine whether the phenotype and genotype frequencies in the Siddis depart from Hardy-Weinberg proportions (Table 2). The phenotype (and genotype) frequencies for most of the loci are in reasonable agreement with their respective Hardy-Weinberg expectations. The overall pattern of phenotype (genotype) distribution is in accordance with Hardy-Weinberg expectations.

Genetic Distance and Heterozygosity. The analysis was performed in two stages. First, we considered populations belonging to different southern states of India along with the Siddis, Africans, and Portuguese. Next, we considered the South Indian tribal populations with the Siddis and the Africans.

The allele frequencies of 27 alleles for 8 genetic loci in 8 populations are presented in Appendix 1. The genetic differences were estimated using Nei's standard genetic distance among all pairs of populations with their respective standard errors (Table 3). The average heterozygosity varied from 33.42% in the Africans to 44.27% in the Andhra Pradesh populations. The genetic distance shows no significant differentiation, as determined by the pairwise chi-square statistic. However, the dendrogram generated from the genetic distance matrix reveals an absorbing pattern of clustering. It can be seen that the Siddis and the Africans are close to each other, whereas the South Indian populations cluster together, separated by the Portuguese (Figure 2).

The allele frequencies of 12 alleles for 6 molecular markers in 7 population groups are presented in Appendix 2. Average heterozygosity and genetic distances among all pairs of populations together with their standard errors are presented in Table 4. The average heterozygosity varied from 35.24% in the Todas to 47.07% in the Irulas. The genetic distances do not reveal significant differentiation, as examined pairwise using the chi-square statistics (Table 4). Nevertheless, the dendrogram obtained from the genetic distance matrix (Figure 3) further strengthens earlier observations. Here, too, the Siddis and the Africans fall together, whereas all the South Indian tribal groups form a separate cluster.

In both data sets the pattern of average heterozygosity is similar, and the dendrograms for the two data sets reveal close similarities between the Siddis and the Africans on the one hand and the population groups of South India on the other.

Population Structure and Gene Flow. Harpending and Ward (1982) determined that the genetic distance of an island from the gene frequency centroid (the overall mean gene frequencies of the population) and the relative homozygosity of that island are linearly related, if exchange with populations outside the region is the same for each island. Considering this, we examined the regression of heterozygosity on distances from a centroid in six population groups, comprising the Siddis and their neighbors (Tamil Nadu, Andhra Pradesh, Karnataka, and Kerala), using eight genetic loci [*A1A2BO*, *MN*, Rh (*CcdEe*), *ACP1*, *ESD*, *PGM1*, *AK1*, and *PTC*] (Table 5), followed by a regression on six tribal groups (Irula, Kota, Kurumba, Toda, and Pallan and the Siddis) of South India, using 6 *Alu* insertion-deletion markers (*PV92*, *F13B*, *D1*, *APO*, *ACE*, and *PLAT*) (Table 6). The regression is consistent with linearity. An average heterozygosity of 43.32% in the pooled population does not differ significantly from the regression coefficient of 43.86% in the eight population groups. Similarly, in the six tribal groups the average heterozygosity of 46.17% in the pooled population does not differ significantly from the regression coefficient of 46.31%. Thus the results imply that the South Indian population groups and tribal groups are not overtly admixed, nor are they mostly isolated.

Genetic Admixture and Genetic Structure. Genetic admixture estimates, obtained on the basis of 32 serological and red blood cell enzyme alleles [*A1A2BO*, *MN*, Rh (*CcdEe*), *PTC*, *GLO1*, *ACP1*, *ESD*, *PGM1*, *AK1*, and *ADA*) and fitting

Table 3. Standard Genetic Distances, Average Heterozygosity, and Chi-Square Values Among the Siddis, South Indians, Africans, and Portuguese[a]

Population	*Siddis*	*Karnataka*	*Andhra Pradesh*	*Tamil Nadu*	*Kerala*	*Maratha*	*Africa*	*Portuguese*
Siddis	40.37 ± 7.10	7.11	3.63	24.65	6.45	2.41	0.85	3.17
Karnataka	0.47 ± 0.36	42.93 ± 5.05	0.73	1.19	0.77	0.51	4.02	2.43
Andhra Pradesh	0.38 ± 0.27	0.20 ± 0.08	44.27 ± 5.42	0.38	0.47	0.19	2.82	2.59
Tamil Nadu	0.56 ± 0.40	0.21 ± 0.12	0.06 ± 0.03	41.73 ± 4.68	0.16	0.54	4.07	3.36
Kerala	0.50 ± 0.40	0.21 ± 0.14	0.12 ± 0.06	0.04 ± 0.02	39.59 ± 4.06	0.35	3.15	2.45
Maratha	0.45 ± 0.34	0.13 ± 0.07	0.04 ± 0.02	0.02 ± 0.01	0.06 ± 0.02	43.14 ± 5.29	4.66	2.13
Africa	0.11 ± 0.05	0.91 ± 0.63	0.73 ± 0.51	1.02 ± 0.73	0.93 ± 0.73	0.88 ± 0.64	33.42 ± 7.25	4.20
Portuguese	0.53 ± 0.38	0.60 ± 0.30	0.50 ± 0.29	0.54 ± 0.30	0.50 ± 0.29	0.43 ± 0.24	0.88 ± 0.62	43.60 ± 6.13

a. Values on the diagonal are the average heterozygosities expressed in percentage; below the diagonal are standard genetic distances in 10^{-1} codon differences per locus, and above the diagonal are chi-square values (polymorphic loci) with 19 df, $p > 0.05$.

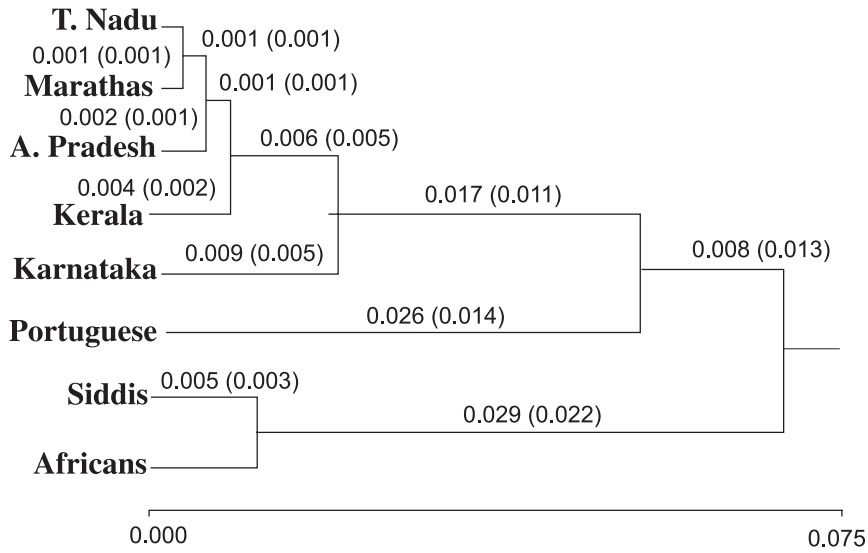

Figure 2. Genetic relationships of the Siddis with the South Indian, African, and Portuguese study populations (27 alleles controlled by 8 loci). Values given in parentheses are the standard errors of the branch lengths.

a trihybrid model using the ancestral frequencies shown in Appendix 3, are presented in Table 7. The Africans, South Indians, and Portuguese are considered parental populations for the Siddis. The major contribution comes from the Africans (59.46%) followed by South Indians (28.41%) and the Portuguese (12.13%). The trihybrid model was also used for the analysis with eight serological and red blood cell enzyme markers [*A1A2BO*, *MN*, Rh (*CcdEe*), *PTC*, *ACP1*, *ESD*, *PGM1*, *AK1*], and we found that there is not much difference in terms of the contribution from the putative ancestral population to the Siddis (Table 7).

Furthermore, we also used a dihybrid model (Table 7), considering the Africans and the South Indians as parental groups of the hybrid Siddis, and the computations of admixture estimates were based on 52 serological, red blood cell enzyme, and *Alu* insertion-deletion alleles [*A1A2BO*, *MN*, Rh (*CcdEe*), *ABH*, *GLO1*, *GPI*, *ACP1*, *ESD*, *PGM1*, *PGM2*, *AK1*, *ADA*, *PTC*, *PLAT*, *ACE*, *APO*, *PV92*, *F13B*, and *D1*). In this model, the African and South Indian contributions are 71.65% and 28.35%, respectively. Thus the Siddis appear to be a hybrid population with African, South Indian, and Portuguese admixture, with a dominant contribution from the Africans followed by the South Indians and a small Portuguese contribution.

Nonrandom Association Among Genetic Loci. It is well known that the mixture of populations with disparate allele frequencies can produce nonrandom

Table 4. Standard Genetic Distances, Average Heterozygosity, and Chi-Square Values Among the Siddis, the Tribes of South India, Africans, and Portuguese[a]

Population	*Siddis*	*Irula*	*Kota*	*Kurumba*	*Toda*	*Pallan*	*Africans*
Siddis	44.77 ± 2.60	2.23	3.40	3.43	3.35	2.61	1.24
Irula	1.38 ± 0.69	47.07 ± 1.91	0.70	0.44	2.18	0.78	1.59
Kota	2.19 ± 1.38	0.34 ± 0.12	40.37 ± 4.18	1.22	1.29	0.60	1.66
Kurumba	2.37 ± 0.84	0.23 ± 0.20	0.75 ± 0.47	42.87 ± 2.74	3.00	1.03	2.79
Toda	1.76 ± 1.13	1.20 ± 0.39	0.57 ± 0.24	1.86 ± 0.56	35.24 ± 7.58	0.69	0.82
Pallan	1.59 ± 0.78	0.44 ± 0.27	0.32 ± 0.19	0.63 ± 0.21	0.28 ± 0.10	42.75 ± 3.37	1.05
Africa	0.08 ± 0.08	1.84 ± 0.72	2.50 ± 1.57	2.96 ± 0.92	1.51 ± 1.18	1.63 ± 0.92	39.95 ± 2.79

a. Values on the diagonal are the average heterozygosities expressed in percentage; below the diagonal are the standard genetic distances in 10^{-1} codon differences per locus, and above the diagonal are chi-square values (polymorphic loci) with 6 df.

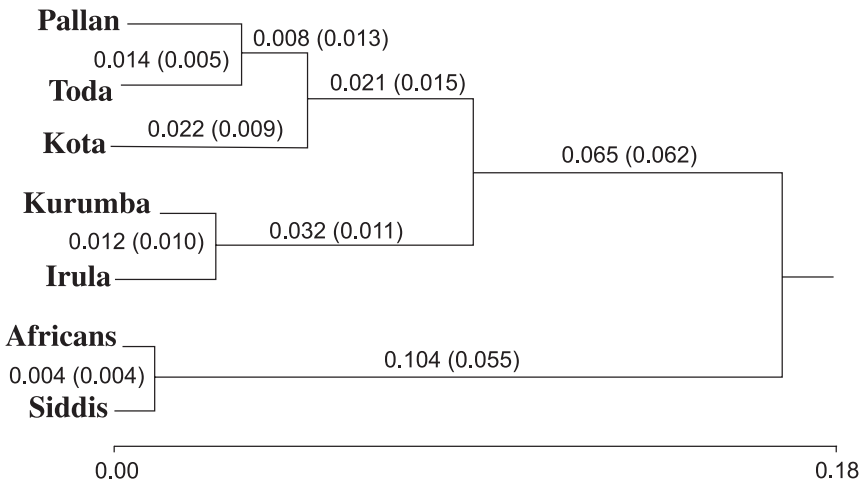

Figure 3. Genetic relationships of the Siddis with the tribes of South India, Africans, and Portuguese (12 alleles controlled by 6 *Alu* insertion-deletion markers). Values given in parentheses are the standard errors of the branch lengths.

association of alleles at two or more unlinked loci (Li 1955; Nei and Li 1973; Chakraborty and Weiss 1988). By using the procedure suggested by Brown et al. (1980), we defined a multilocus genotype for each individual using the available genotype data on each individual. With respect to the 10 loci (*A1A2BO*, *GLO1*, *ABH*, *PTC*, *ACP*, *ESD*, *PGM1*, *PGM2*, *AK1*, and *ADA*), the number of loci was determined for which each of 100 individuals was heterozygous. Comparing the observed distribution with that expected, under the assumption of random

Table 5. Average Heterozygosity (H_i) and Genetic Distances from the Centroid (r_{ii}) Among the Siddis and the Populations of South India on the Basis of Eight Serological and Red Blood Cell Loci[a]

Population	$r_{ii} \pm SE$	$H_i \pm SE$
Tamil Nadu	0.0049 ± 0.0014	0.4172 ± 0.0468
Maratha	0.0046 ± 0.0013	0.4307 ± 0.0528
Andhra Pradesh	0.0035 ± 0.0017	0.4426 ± 0.0542
Kerala	0.0197 ± 0.0123	0.3955 ± 0.0406
Karnataka	0.0418 ± 0.0127	0.4287 ± 0.0505
Siddis	0.2161 ± 0.1657	0.4012 ± 0.0703

Regression analysis: $H_i = b(1 - r_{ii})$; H_i plotted against $1 - r_{ii}$ through the origins has $t = 3.4952$, 4 df, $p > 0.05$.

Regression coefficient through origin: $b = 0.4386 \pm 0.0316$; $H = 0.4332 \pm 0.0495$.

a. *A1A2BO*, *MN*, Rh (*CcdEe*), *ACP1*, *ESD*, *PGM1*, *AK1*, *PTC*.

Table 6. Average Heterozygosity (H_i) and Genetic Distances from the Centroid (r_{ii}) Among the Siddis and the Tribes of South India on the Basis of Six *Alu* Insertion-Deletion Markers[a]

Population	$r_{ii} \pm SE$	$H_i \pm SE$
Irula	0.0534 ± 0.0244	0.4660 ± 0.0189
Kota	0.0729 ± 0.0333	0.3992 ± 0.0413
Kurumba	0.1253 ± 0.0485	0.4247 ± 0.0271
Toda	0.1387 ± 0.0458	0.3488 ± 0.0751
Siddis	0.3333 ± 0.2021	0.3897 ± 0.0779
Pallans	0.0235 ± 0.0109	0.4253 ± 0.0335

Regression analysis: $H_i = b(1 - r_{ii})$; H_i plotted against $1 - r_{ii}$ through the origin has $t = 1.9057$, 4 df, $p > 0.05$.

Regression coefficient through origin: $b = 0.4631 \pm 0.0486$.

Average heterozygosity in pooled population: $H = 0.4617 \pm 0.0173$.

a. *PLAT*, *ACE*, *APO*, *PV92*, *F13B*, and *D1*.

association of alleles at different loci using Chakraborty's (1981) algorithm, we found that the observed distribution is in fair agreement with the expected distribution (goodness-of-fit $\chi^2 = 3.404$, 9 df, $p > 0.05$) (Table 8). Because the expected distribution involves the observed data at least partly (locus-specific observed heterozygosity values), there are some technical difficulties for determining the degrees of freedom of the goodness-of-fit statistic, detailed by Chakraborty (1984). However, Brown et al. (1980) showed that the expectations of mean and variance of the number of heterozygous loci can be written as functions of locus-specific heterozygosities under the assumption of random association of alleles, and the 95% confidence limit of the observed variance of the number of heterozygous loci can also be calculated. In the Siddis the mean number of heterozygous loci is 3.8 and the variance is 2.16. Their expected values (under random association) are

Table 7. Contribution of African, South Indian, and Portuguese Gene Pools to the Contemporary Siddis of Karnataka

	Contribution of Parental Group (%)		
Hybrid Group: Siddis	*Africans*	*South Indians*	*Portuguese*
Trihybrid model[a]	59.46 ± 1.77	28.41 ± 4.38	12.13 ± 3.96
	56.75 ± 3.34[c]	28.06 ± 9.15	15.19 ± 8.52
Dihybrid model[b]	71.65 ± 4.58	28.35 ± 4.58	

a. Estimates are based on 10 polymorphic loci: *A1A2BO*, *MN*, Rh (*CcdEe*), *PTC*, *GLO1*, *ACP1*, *ESD*, *PGM1*, *AK1*, and *ADA*.

b. Estimates are based on 19 polymorphic loci: *A1A2BO*, *MN*, Rh (*CcdEe*), *ABH*, *GLO1*, *GPI*, *ACP1*, *ESD*, *PGM1*, *PGM2*, *AK1*, *ADA*, *PTC*, *PLAT*, *ACE*, *APO*, *PV92*, *F13B*, and *D1*.

c. Estimates are based on the eight polymorphic loci as mentioned in Appendix 1 [*A1A2BO*, *MN*, Rh (*CcdEe*), *PTC*, *ACP1*, *ESD*, *PGM1*, *AK1*].

Table 8. Observed and Expected Distributions of the Number of Heterozygous Loci in the Siddis

	Number of Individuals	
Number of Heterozygous Loci[a]	*Observed*	*Expected*
0–2	5	4.30
3	17	13.54
4	20	25.33
5	25	27.92
6	20	18.90
7	10	7.85
8–10	3	2.16
Total	100	100.00
Mean	3.80	4.76
Variance	2.16	1.87

Goodness-of-fit $\chi^2 = 3.404$, 9 df, $p > 0.05$.
95% confidence interval for variance (1.373, 2.372).
a. *A1A2BO*, *GLO1*, *ABH*, *PTC*, *ACP*, *ESD*, *PGM1*, *PGM2*, *AK1*, and *ADA*.

4.76 and 1.87, respectively. The 95% confidence limits range of the variance is 1.373–2.372. Clearly, these values provide no evidence of nonrandom association of alleles among the 10 polymorphic loci in this population.

Discussion

The results obtained from the genetic analysis of the Siddis demonstrate a distribution pattern close to that found in the African population. Furthermore, the frequency of the Atkinson variant (4.8%) of the *PGM2* system in the Siddis is high, a finding that is common in African groups. Other variables, such as the nasal index (94.14 ± 6.02) and cephalic index (75.55 ± 4.25), among the Siddis are similar to their characteristic distribution in east African populations (Taylor 1946). Similarly, in their somatoscopic characteristics, such as dark skin color, kinky hair, and alveolar prognathism, the Siddis can be associated with African ancestry.

The results of the genetic distance analysis between selected populations of African, European, and Indian descent do not indicate significant differentiation. However, the dendrogram generated on the basis of the genetic distance analysis invariably reveals that the Siddis are closer to the Africans, followed by their affinities with South Indian populations. The admixture results are largely consistent with the historical past and cultural and linguistic attributes of the Siddis. A few studies undertaken on the Siddis (Vijaykumar et al. 1987; Ramana et al. 2001; Watkin et al. 2005) indicate the African affinities and also the significant influence of the neighboring populations on them. The results obtained in the present investigation indicate 59.46%, 28.41%, and 12.13% contributions from the Africans, South Indians, and Portuguese, respectively.

Genetic admixture analysis shows that the predominant influence comes from the Africans, a lesser contribution from the South Indians, and a slight contribution from the Portuguese.

Furthermore, the Siddis of Karnataka, who were first brought as slaves by the Portuguese about 500 years ago, may have received and exchanged a considerable amount of genes with the populations of southern India. There seems to have been some infiltration of genes into the gene pool of the Siddis from the Portuguese of European descent as well. In fact, it appears that the original pool of African genes among the Siddis has been diluted to some extent by the long-standing contribution (over 500 years) of the population groups of southern India.

The history of admixture is old enough to have brought the Siddis' gene pool to Hardy-Weinberg equilibrium. There is no nonrandom association of alleles among the genetic marker systems considered in the present study, despite the fact that the population is of admixed origin. The multilocus heterozygosity distribution also supports the inference of genetic homogeneity of the Siddis of Karnataka of southern India. The demonstration of genetic homogeneity of the Siddis, despite their admixed origin, suggests the utility of this population for genetic epidemiological studies.

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Appendix 1. Allele Frequencies for Eight Loci Among the Siddis, South Indians, Africans, and Portuguese[a]

Allele	*Siddis*	*Karnataka*	*Andhra Pradesh*	*Tamil Nadu*	*Kerala*	*Maratha*	*Africa*	*Portuguese*
*ABO*A1*	0.117	0.142	0.148	0.133	0.137	0.205	0.118	0.263
*ABO*A2*	0.042	0.037	0.033	0.024	0.025	0.034	0.066	0.097
*ABO*B*	0.194	0.152	0.225	0.245	0.187	0.193	0.140	0.052
*ABO*O*	0.647	0.669	0.594	0.598	0.651	0.568	0.676	0.588
*MN*M*	0.539	0.510	0.627	0.677	0.688	0.610	0.615	0.654
*MN*N*	0.461	0.490	0.373	0.323	0.312	0.390	0.385	0.346
CDE	0.000	0.000	0.019	0.012	0.005	0.012	0.000	0.000
CDe	0.265	0.458	0.557	0.667	0.692	0.596	0.135	0.328
CdE	0.153	0.000	0.008	0.000	0.000	0.000	0.072	0.000
Cde	0.393	0.006	0.083	0.004	0.009	0.012	0.580	0.000
cDE	0.000	0.062	0.084	0.100	0.070	0.091	0.000	0.094
cDe	0.000	0.279	0.097	0.048	0.028	0.077	0.010	0.036
cdE	0.000	0.032	0.015	0.000	0.000	0.014	0.003	0.000
cde	0.189	0.163	0.137	0.169	0.196	0.198	0.264	0.542
*ACP*A*	0.212	0.206	0.221	0.246	0.210	0.238	0.070	0.358
*ACP*B*	0.788	0.794	0.777	0.753	0.789	0.761	0.930	0.522
*ACP*C*	0.000	0.000	0.002	0.001	0.001	0.001	0.000	0.120
*ESD*1*	0.890	0.808	0.665	0.726	0.844	0.738	0.893	0.826
*ESD*2*	0.110	0.192	0.335	0.274	0.156	0.262	0.107	0.174
*PGM1*1*	0.761	0.687	0.699	0.668	0.665	0.701	0.800	0.699
*PGM1*2*	0.237	0.313	0.301	0.332	0.335	0.299	0.170	0.301
*PGM1*3*	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000
*PGM1*7*	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000
*AK1*1*	0.953	0.873	0.925	0.932	0.884	0.931	0.994	0.953
*AK1*2*	0.047	0.127	0.075	0.068	0.116	0.069	0.006	0.047
*PTC*T*	0.590	0.345	0.496	0.403	0.425	0.410	0.687	0.590
*PTC*t*	0.410	0.655	0.504	0.597	0.575	0.590	0.313	0.410

a. References for the secondary-source data are as follows: South Indian populations, Bhasin et al. (1992) and Roychoudhury and Nei (1988); African and Portuguese populations, Mourant et al. (1976) and Roychoudhury and Nei (1988).

Appendix 2. Allele Frequencies of Six *Alu* Insertion-Deletion Loci Among the Siddis, the Tribes of South India, and Africans[a]

Locus	*Allele*	*Siddis*	*Irula*	*Kota*	*Kurumba*	*Toda*	*Pallan*	*Africans*
PV92	+	0.333	0.449	0.300	0.713	0.255	0.560	0.316
	−	0.667	0.551	0.700	0.287	0.745	0.440	0.684
F13B	+	0.202	0.640	0.878	0.694	0.806	0.650	0.162
	−	0.798	0.360	0.122	0.306	0.194	0.350	0.838
D1	+	0.422	0.600	0.589	0.528	0.300	0.837	0.372
	−	0.578	0.400	0.411	0.472	0.700	0.163	0.628
APO	+	0.543	0.570	0.767	0.583	1.000	0.440	0.727
	−	0.457	0.430	0.233	0.417	0.000	0.560	0.273
ACE	+	0.333	0.750	0.622	0.806	0.469	0.720	0.316
	−	0.667	0.250	0.378	0.194	0.531	0.280	0.684
PLAT	+	0.365	0.550	0.659	0.704	0.406	0.320	0.267
	−	0.635	0.450	0.341	0.296	0.594	0.680	0.733

a. References for the secondary-source data are as follows: Africa, *ALFRED* database (*ALFRED* 2008); Pallan, Basu et al. (2003); Kota, Kurumba, Irula, and Toda, Vishwanathan et al. (2004).

Appendix 3. Allele Frequencies of Serological and Red Blood Cell Enzyme Loci Among the Siddis and Selected Population Groups[a]

Locus	*Allele and n*[b]	*Siddis*	*South India*	*Karnataka*	*Andhra Pradesh*	*Tamil Nadu*	*Kerala*	*Maratha*	*Africa*	*Portuguese*
A1A2BO	*n*	219	13,017	750	7,001	4,209	1,057	8,880	1,536	118
	*ABO*A1*	0.117	0.140	0.142	0.148	0.133	0.137	0.205	0.118	0.263
	*ABO*A2*	0.042	0.029	0.037	0.033	0.024	0.025	0.034	0.066	0.097
	*ABO*B*	0.194	0.202	0.152	0.225	0.245	0.187	0.193	0.140	0.052
	*ABO*O*	0.647	0.629	0.669	0.594	0.598	0.651	0.568	0.676	0.588
MN	*n*	100	8,225	478	2,839	3,224	1,684	348	1,245	114
	*MN*M*	0.539	0.625	0.510	0.627	0.677	0.688	0.610	0.615	0.654
	*NM*N*	0.461	0.375	0.490	0.373	0.323	0.312	0.390	0.385	0.346
Rh	*n*	100	5,843	578	1,847	2,855	563	98	1,184	116
	CDE	0.000	0.009	0.000	0.019	0.012	0.005	0.012	0.000	0.000
	CDe	0.265	0.593	0.458	0.557	0.667	0.692	0.596	0.135	0.328
	CdE	0.153	0.002	0.000	0.008	0.000	0.000	0.000	0.072	0.000
	Cde	0.393	0.025	0.006	0.083	0.004	0.009	0.012	0.580	0.000
	cDE	0.000	0.079	0.062	0.084	0.100	0.070	0.091	0.000	0.094
	cDe	0.000	0.113	0.279	0.097	0.048	0.028	0.077	0.010	0.036
	cdE	0.000	0.012	0.032	0.015	0.000	0.000	0.014	0.003	0.000
	cde	0.189	0.167	0.163	0.137	0.169	0.196	0.198	0.200	0.542
ABH	*n*	100	7,237	–	2,749	2,810	1,678	201	375	–
	*ABH*Se*	0.434	0.498	–	0.572	0.549	0.372	0.595	0.546	–
	*ABH*se*	0.566	0.502	–	0.428	0.451	0.628	0.405	0.454	–
PTC	*n*	100	11,195	429	7,007	2,739	1,020	395	1,069	564
	*PTC*T*	0.590	0.417	0.345	0.496	0.403	0.425	0.410	0.687	0.590
	*PTC*t*	0.410	0.583	0.655	0.504	0.597	0.575	0.590	0.313	0.410
GLO1	*n*	163	3,938	–	3,784	154	–	479	1,754	631
	*GLO1*1*	0.295	0.248	–	0.273	0.233	–	0.250	0.334	0.426
	*GLO1*2*	0.705	0.752	–	0.727	0.767	–	0.750	0.666	0.574

GPI	*n*	100	3,719	–	2,284	549	958	346	145	–
	*GPI*1*	1.000	0.996	–	0.994	1.000	0.994	0.989	0.999	–
	*GPI*2*	0.000	0.001	–	0.001	0.000	0.001	0.011	0.001	–
	*GPI*3*	0.000	0.002	–	0.002	0.000	0.005	0.000	0.000	–
	*GPI*5*	0.000	0.001	–	0.002	0.000	0.000	0.000	0.000	–
	*GPI*8*	0.000	0.000	–	0.000	0.000	0.000	0.000	0.000	–
	*GPI*9*	0.000	0.000	–	0.001	0.000	0.000	0.000	0.000	–
ACP1	*n*	100	8,558	468	5,510	1,630	950	924	443	116
	*ACP1*A*	0.212	0.220	0.206	0.221	0.246	0.210	0.238	0.070	0.358
	*ACP1*B*	0.788	0.778	0.794	0.777	0.753	0.789	0.761	0.930	0.522
	*ACP1*C*	0.000	0.002	0.000	0.002	0.001	0.001	0.001	0.000	0.120
ESD	*n*	218	6,219	293	5,113	701	112	911	964	778
	*ESD*1*	0.890	0.761	0.808	0.665	0.726	0.844	0.738	0.893	0.826
	*ESD*2*	0.110	0.239	0.192	0.335	0.274	0.156	0.262	0.107	0.174
PGM1	*n*	217	5,428	231	2,857	1,360	980	816	220	743
	*PGM1*1*	0.761	0.679	0.687	0.699	0.668	0.665	0.701	0.800	0.699
	*PGM1*2*	0.237	0.321	0.313	0.301	0.332	0.335	0.299	0.170	0.301
	*PGM1*3*	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	*PGM1*7*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000
PGM2	*n*	217	5,400	–	3,060	1,360	980	561	145	–
	*PGM2*1*	0.952	1.000	–	1.000	1.000	1.000	1.000	0.980	–
	*PGM2*A*	0.048	0.000	–	0.000	0.000	0.000	0.000	0.020	–
AK1	*n*	100	5,493	173	2,662	1,661	997	692	267	118
	*AK1*1*	0.953	0.903	0.873	0.925	0.932	0.884	0.931	0.994	0.953
	*AK1*2*	0.047	0.097	0.127	0.075	0.068	0.116	0.069	0.006	0.047
ADA	*n*	218	1,010	41	847	–	122	–	85	690
	*ADA*1*	0.940	0.889	0.866	0.901	–	0.857	–	0.940	0.932
	*ADA*2*	0.046	0.111	0.134	0.099	–	0.143	–	0.060	0.068
	*ADA*3*	0.014	0.000	0.000	0.000	–	0.000	–	0.000	0.000
HB	*n*	162	25,996	2,548	10,364	8,764	4,320	450	449	–
	HBV	0.003	0.065	0.048	0.062	0.097	0.051	0.000	–	–
	HBN	0.997	0.935	0.952	0.938	0.903	0.949	1.000	–	–

Appendix 3. *Continued*

Locus	*Allele and n*[b]	*Siddis*	*South India*	*Karnataka*	*Andhra Pradesh*	*Tamil Nadu*	*Kerala*	*Maratha*	*Africa*	*Portuguese*
PLAT	*n*	48	1,794	–	–	–	–	–	498	–
	+	0.365	0.600	–	–	–	–	–	0.267	–
	−	0.635	0.400	–	–	–	–	–	0.733	–
ACE	*n*	42	1,659	–	–	–	–	–	216	–
	+	0.333	0.612	–	–	–	–	–	0.316	–
	−	0.667	0.388	–	–	–	–	–	0.684	–
APO	*n*	46	1,796	–	–	–	–	–	312	–
	+	0.543	0.775	–	–	–	–	–	0.727	–
	−	0.457	0.225	–	–	–	–	–	0.273	–
PV92	*n*	42	1,769	–	–	–	–	–	312	–
	+	0.333	0.479	–	–	–	–	–	0.316	–
	−	0.667	0.521	–	–	–	–	–	0.684	–
F13B	*n*	42	1,107	–	–	–	–	–	152	–
	+	0.202	0.645	–	–	–	–	–	0.162	–
	−	0.798	0.355	–	–	–	–	–	0.838	–
D1	*n*	45	1,099	–	–	–	–	–	152	–
	+	0.422	0.393	–	–	–	–	–	0.372	–
	−	0.578	0.607	–	–	–	–	–	0.628	–

a. References for the secondary-source data are as follows: South Indian populations, Bhasin et al. (1992), Roychoudhury and Nei (1988), and *ALFRED* database (*ALFRED* 2008); African and Portuguese populations, Mourant et al. (1976), Roychoudhury and Nei (1988), and *ALFRED* Database (*ALFRED* 2008).

b. *n* denotes the sample sizes for the different population groups.