# *Patterns of Ethnic, Linguistic, and Geographic Heterogeneity of Palmar Interdigital Ridge Counts in the Indian Subcontinent*

B. MOHAN REDDY,[1] DARIO A. DEMARCHI,[2] S. BHARATI,[1] VIKRANT KUMAR,[1] AND MICHAEL H. CRAWFORD[3]

*Abstract* Published data on palmar interdigital ridge counts (a–b, b–c, and c–d) among 57 populations from the Indian subcontinent were analyzed with reference to ethnic, socioeconomic, linguistic, and geographic affiliations of the studied populations. The spatial autocorrelation analysis suggests significant correlation between dermatoglyphic and geographic distances. The congruence with the ethnic semblance of the groups is also apparent in the data, and, in fact, the multiresponse permutation procedure did suggest highly significant within-group homogeneity, confirming the biological validity of the social and ethnic criteria used in the analysis. The plots of populations on the first two principal components, accounting for 92% of the total variance, complement and support the results based on the other analyses, which show certain ethnic and geographic patterns. These findings can serve as baseline information for future studies on population variation in India, particularly studies based on molecular genetic markers, a trend that has already gained momentum.

The people of India exhibit a unique panorama of social, cultural, and ethnic diversity because of different waves of migration and other historical events. Anthropologists have solicited support from biological and archeological evidence to show that since prehistoric times people affiliated with different ethnic, cultural, and linguistic families have entered India and contributed to the present-day peopling of India. In each geographic and linguistic area the population is divided into a number of endogamous castes, tribes, and religious communities. Many of the castes are large and widely distributed, with further subdivisions, called subcastes, within them. These subcastes vary in size, mating patterns, and even adaptive strategies (Reddy, Sun et al. 2001). India abounds in such castes and subcastes in every region or linguistic area. Many of the subcastes have a

[1]Indian Statistical Institute, 203 Barrackpore Trunk Road, Calcutta 700 035, India.
[2]Departamento de Bioquímica Clínica, Facultad de Ciencias Químicas, Universidad Nacional de Córdoba, Córdoba 5000, Argentina.
[3]Department of Anthropology, University of Kansas, 622 Fraser Hall, Lawrence KS 66045.

*Human Biology,* April 2004, v. 76, no. 2, pp. 211–228.


KEY WORDS: PALMAR INTERDIGITAL RIDGE COUNTS, DERMATOGLYPHICS, PRINCIPAL COMPONENTS ANALYSIS, SPATIAL AUTOCORRELATION, INDIA

common origin, but other sociological phenomena, such as Sanskritization rather than genetic fission, were responsible for the existence of caste clusters (Karve and Malhotra 1968). This ubiquitous scenario in India provides unique opportunities to answer questions about the microevolutionary dynamics of the groups.

To understand microevolution and/or the pattern of variation among the populations, researchers have analyzed different sets of variables, such as anthropometrics, dermatoglyphics, and traditional genetic markers, although currently DNA markers are used for the same purpose. A number of studies have suggested high congruence between dermatoglyphic affinities and geographic and/or ethnohistorical patterns, particularly with reference to finger ridge counts (Jantz et al. 1982; Reddy and Reddy 1992; Krishnan and Reddy 1994) or finger pattern frequencies (Crawford and Duggirala 1992; Demarchi and Marcellino 1998), although other studies found better results from the analysis of palmar variables (Jantz and Chopra 1983; Reddy et al. 1988; Demarchi et al. 1997; Demarchi 2000).

Dermatoglyphic traits, in particular, quantitative finger and palmar interdigital ridge counts, are polygenic with moderate to high heritability. Dermatoglyphic traits are probably less amenable to selection (Van Valen 1963; Rogers and Harpending 1983; Blangero 1988; Loesch 1979; Loesch and Martin 1984; Loesch and Wolanski 1985) and stochastic processes of evolution (Rife 1954; Mavalwala and Hunt 1964) than genetic markers and anthropometric variables. Dermatoglyphic traits are thus expected to be phylogenetically more stable than other biological variables and may help to reconstruct biological human prehistory because they are more independent of evolutionary and environmental forces than other traits (Plato 1970; Rothhammer et al. 1977; Rudan 1978; Froechlich and Giles 1981a, 1981b). A classic example of the temporal stability of dermatoglyphic traits is the close resemblance between Jewish populations of different countries after 2,000 years of separation (Sachs and Bat-Miriams 1957). Contrary to these inferences, Babler (1978) demonstrated prenatal selection on dermatoglyphic patterns and Rogers and Harpending (1983) argued that quantitative traits are just as amenable to stochastic processes as single-gene traits.

Although numerous studies have focused on the pattern of dermatoglyphic variation in India, they are each based generally on a few endogamous groups and are dispersed over different regions. Only a handful of systematic and comprehensive studies have been undertaken at the regional (Reddy and Reddy 1992, 2001; Karmakar et al. 1996; Reddy et al. 2000) and national (Krishnan and Reddy 1994) levels. In the present study we attempted to collate published data on three interdigital ridge counts on both hands from 57 Indian populations; we subjected these data to comprehensive statistical analyses to elucidate patterns of variation with particular reference to geographic, ethnic, and linguistic affiliations. Although the current trend is to use molecular genetic markers for the purpose of gaining insights into population histories and relationships, we nevertheless hope that the results of our dermatoglyphic analyses can serve as a useful baseline for upcoming human genome diversity studies on Indian populations.

**Figure 1.** Map of India showing the geographic location of the 57 population samples included in the present study. The numbers correspond to the populations identified in Table 1.

## Materials and Methods

**Sample.** The study includes 57 populations: 8 populations from Nepal and Bhutan, 23 from Maharashtra, 11 from northern Indian, 5 from central India, 8 from southern India, and 2 from Andaman (Figure 1). Out of these 57 populations 12 are tribal groups and the remaining 45 are Hindu caste groups, which are further subdivided according to their social and/or ethnic affiliations (Table 1). The variables used in the analysis were the interdigital a–b, b–c, and c–d ridge counts for each hand, which correspond to the number of ridges between the palmar distal digital triradii a and b, b and c, and c and d, respectively. The name

**Table 1.** Mean Values of Palmar Interdigital Ridge Counts and Other Data for the 57 Populations (All Males) of the Indian Subcontinent

| Population | Social–Ethnic Affiliation[a] | Latitude | Longitude | N | Right-Hand Ridge Count a–b | Right-Hand Ridge Count b–c | Right-Hand Ridge Count c–d | Left-Hand Ridge Count a–b | Left-Hand Ridge Count b–c | Left-Hand Ridge Count c–d | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Nepal and Bhutan | | | | | | | | | | | |
| 1. Kirantis | 5 | 28.0 | 84.0 | 34 | 39.09 | 26.91 | 34.82 | 38.97 | 25.63 | 36.13 | Woolley et al. (1984) |
| 2. Gurungs | 5 | 28.1 | 84.0 | 160 | 38.63 | 25.75 | 35.53 | 38.14 | 26.32 | 35.07 | Woolley et al. (1984) |
| 3. Mangars | 5 | 28.1 | 84.1 | 112 | 38.98 | 27.29 | 36.95 | 39.68 | 27.51 | 36.69 | Woolley et al. (1984) |
| 4. Shrestha Newars | 1 | 27.5 | 86.0 | 173 | 36.87 | 24.87 | 35.40 | 37.79 | 25.28 | 33.97 | Bhasin (1970, 1971) |
| 5. Gubhaju Newars | 1 | 27.6 | 85.8 | 39 | 35.41 | 24.97 | 34.03 | 37.49 | 24.79 | 33.03 | Bhasin (1970, 1971) |
| 6. Jyapu Newars | 1 | 27.5 | 85.6 | 82 | 36.77 | 24.97 | 35.58 | 38.02 | 26.11 | 34.64 | Bhasin (1970, 1971) |
| 7. Other Newars | 5 | 27.5 | 85.4 | 31 | 36.70 | 26.76 | 35.29 | 37.75 | 25.62 | 36.82 | Bhasin (1970, 1971) |
| 8. Bhutanese | 5 | 27.5 | 90.0 | 74 | 34.04 | 21.39 | 29.70 | 36.15 | 21.98 | 29.74 | Bhasin (1966) |
| Northern India | | | | | | | | | | | |
| 9. Kolis | 6 | 22.9 | 74.0 | 180 | 36.00 | 22.93 | 32.94 | 36.65 | 22.32 | 31.62 | Kshtriya (1987) |
| 10. Rajputs | 1 | 23.0 | 73.5 | 365 | 34.55 | 21.88 | 31.80 | 35.19 | 20.90 | 29.72 | Kshtriya (1987) |
| 11. Pangwalas | 3 | 32.5 | 76.4 | 189 | 33.64 | 22.51 | 33.49 | 34.58 | 22.25 | 31.94 | Bhasin et al. (1986) |
| 12. Brahmans (Chamba) | 1 | 32.5 | 76.0 | 83 | 32.35 | 20.43 | 31.14 | 34.35 | 20.09 | 29.38 | Bhasin et al. (1986) |
| 13. Rajputs (Chamba) | 1 | 33.0 | 76.2 | 191 | 33.83 | 23.08 | 32.72 | 34.69 | 22.72 | 30.81 | Bhasin et al. (1986) |
| 14. Schedule caste (Chamba) | 3 | 32.5 | 76.6 | 50 | 33.08 | 20.28 | 30.82 | 34.12 | 19.74 | 29.22 | Bhasin et al. (1986) |
| 15. Brahmans (Kangra) | 1 | 32.0 | 76.2 | 79 | 33.59 | 19.33 | 31.25 | 34.25 | 20.44 | 28.84 | Bhasin et al. (1986) |
| 16. Rajputs (Kangra) | 1 | 31.8 | 76.4 | 118 | 32.23 | 22.28 | 31.29 | 34.03 | 21.05 | 29.53 | Bhasin et al. (1986) |
| 17. Schedule caste (Kangra) | 3 | 31.8 | 76.0 | 19 | 30.00 | 17.17 | 29.67 | 30.05 | 17.78 | 26.22 | Bhasin et al. (1986) |
| 18. Hindu Gujhars | 2 | 30.9 | 76.7 | 92 | 34.17 | 23.34 | 29.36 | 34.17 | 23.34 | 29.36 | Balgir and Sharma (1986) |
| 19. Muslim Gujhars | 3 | 31.6 | 77.0 | 100 | 37.32 | 23.18 | 34.07 | 37.32 | 23.18 | 34.07 | Balgir and Sharma (1986) |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Central and Eastern India | | | | | | | | | | | |
| 20. Brahmans | 1 | 23.7 | 79.0 | 100 | 36.70 | 25.80 | 34.55 | 38.55 | 24.85 | 33.44 | Pateria (1976) |
| 21. Bhangi | 3 | 23.5 | 78.8 | 131 | 37.04 | 23.72 | 33.60 | 37.45 | 23.64 | 32.57 | Pateria (1976) |
| 22. Vadabalija (Pentikota) | 3 | 19.9 | 85.8 | 99 | 36.97 | 20.73 | 30.06 | 38.51 | 19.38 | 28.22 | Reddy et al. (1988) |
| 23. Vadabalija (Vadapeta) | 3 | 19.7 | 85.6 | 85 | 38.67 | 21.29 | 32.47 | 40.55 | 20.38 | 34.02 | Reddy et al. (1988) |
| 24. Jalari | 3 | 19.8 | 85.7 | 108 | 38.26 | 29.07 | 37.55 | 40.06 | 27.65 | 35.49 | Reddy et al. (1988) |
| Maharashtra (Western) | | | | | | | | | | | |
| 25. Patil | 4 | 18.0 | 76.2 | 92 | 33.79 | 20.73 | 33.18 | 35.19 | 20.68 | 32.03 | Malhotra et al. (1981) |
| 26. Chougule | 4 | 18.2 | 76.0 | 49 | 32.59 | 24.19 | 31.56 | 35.64 | 25.68 | 29.77 | Malhotra et al. (1981) |
| 27. Komti | 4 | 18.4 | 76.0 | 62 | 35.18 | 24.93 | 32.17 | 37.08 | 25.61 | 31.93 | Malhotra et al. (1981) |
| 28. Ahir | 4 | 20.7 | 75.5 | 267 | 33.91 | 20.60 | 29.81 | 36.46 | 19.30 | 26.21 | Karmakar et al. (1996) |
| 29. Dange | 4 | 17.5 | 73.6 | 173 | 32.61 | 19.66 | 28.94 | 34.53 | 18.31 | 25.94 | Karmakar et al. (1996) |
| 30. Gadhari Dhengar | 4 | 20.0 | 75.0 | 101 | 35.48 | 22.01 | 32.32 | 37.86 | 22.00 | 31.87 | Karmakar et al. (1996) |
| 31. Gadhari Nikhar | 4 | 20.3 | 75.1 | 85 | 35.54 | 23.15 | 30.81 | 38.21 | 23.11 | 30.00 | Karmakar et al. (1996) |
| 32. Hande | 4 | 17.5 | 75.1 | 85 | 32.06 | 20.88 | 30.89 | 34.30 | 20.11 | 27.26 | Karmakar et al. (1996) |
| 33. Hatkar | 4 | 17.7 | 74.9 | 537 | 35.96 | 23.43 | 33.39 | 38.01 | 22.13 | 30.17 | Karmakar et al. (1996) |
| 34. Kannade | 4 | 20.8 | 79.3 | 83 | 34.02 | 23.10 | 34.40 | 35.46 | 21.99 | 31.60 | Karmakar et al. (1996) |
| 35. Khatik | 4 | 18.6 | 74.1 | 160 | 34.92 | 19.89 | 30.19 | 35.51 | 20.69 | 29.56 | Karmakar et al. (1996) |
| 36. Khutekar | 4 | 19.4 | 76.1 | 420 | 33.65 | 20.51 | 30.72 | 34.87 | 19.61 | 28.11 | Karmakar et al. (1996) |
| 37. Kurmar | 4 | 20.0 | 79.7 | 83 | 33.37 | 23.01 | 32.01 | 35.60 | 22.07 | 29.30 | Karmakar et al. (1996) |
| 38. Ladshe | 4 | 21.1 | 79.3 | 102 | 36.70 | 24.93 | 33.64 | 39.04 | 24.23 | 30.48 | Karmakar et al. (1996) |
| 39. Mendhe | 4 | 16.9 | 74.5 | 166 | 33.22 | 21.44 | 29.09 | 34.87 | 20.14 | 25.31 | Karmakar et al. (1996) |

**Table 1.** Continued.

| Population | Social–Ethnic Affiliation[a] | Latitude | Longitude | N | Right-Hand Ridge Count a–b | b–c | c–d | Left-Hand Ridge Count a–b | b–c | c–d | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 40. Sangar | 4 | 17.6 | 74.4 | 81 | 35.60 | 21.49 | 30.86 | 37.15 | 21.40 | 29.45 | Karmakar et al. (1996) |
| 41. Shegar | 4 | 18.7 | 74.5 | 82 | 31.66 | 20.95 | 31.33 | 34.20 | 20.10 | 27.45 | Karmakar et al. (1996) |
| 42. Telangi | 4 | 19.1 | 77.2 | 82 | 35.70 | 21.70 | 32.30 | 38.13 | 20.44 | 28.55 | Karmakar et al. (1996) |
| 43. Thellari | 4 | 21.0 | 74.8 | 110 | 36.75 | 22.21 | 32.52 | 38.23 | 20.27 | 29.64 | Karmakar et al. (1996) |
| 44. Unnikankan | 4 | 17.0 | 76.0 | 61 | 36.77 | 24.30 | 33.92 | 37.70 | 22.52 | 31.64 | Karmakar et al. (1996) |
| 45. Varhade | 4 | 21.1 | 78.7 | 73 | 35.75 | 22.86 | 33.74 | 37.99 | 22.07 | 30.62 | Karmakar et al. (1996) |
| 46. Zende | 4 | 17.1 | 75.0 | 106 | 35.09 | 23.04 | 30.25 | 37.46 | 20.84 | 27.01 | Karmakar et al. (1996) |
| 47. Zade | 4 | 20.5 | 79.0 | 70 | 32.71 | 21.86 | 31.24 | 34.57 | 19.75 | 29.45 | Karmakar et al. (1996) |
| Southern India | | | | | | | | | | | |
| 48. Koya Dora | 6 | 17.2 | 82.1 | 204 | 37.35 | 27.99 | 35.54 | 38.22 | 26.59 | 34.86 | Babu (1984) |
| 49. Yerukalas | 6 | 15.5 | 79.5 | 69 | 37.22 | 25.83 | 32.75 | 38.87 | 25.10 | 33.76 | Narhari and Reddy (1983) |
| 50. Vadabalijas | 3 | 17.9 | 83.3 | 107 | 34.38 | 26.20 | 35.61 | 35.19 | 27.42 | 36.95 | Babu and Jaikishan (1983) |
| 51. Kuruvikkarans | 6 | 15.0 | 79.0 | 75 | 37.52 | 24.80 | 35.08 | 40.08 | 25.97 | 33.88 | Narhari (1979) |
| 52. Izhavas/Illavans | 3 | 8.3 | 77.0 | 50 | 39.04 | 27.22 | 36.70 | 40.26 | 26.02 | 35.82 | Malhotra and Bhanu (1967) |
| 53. Hindu | 2 | 10.0 | 76.0 | 45 | 32.95 | 24.31 | 31.33 | 34.21 | 23.29 | 32.59 | Bhasin et al. (1980) |
| 54. Christians | 3 | 10.1 | 76.1 | 25 | 35.48 | 24.39 | 32.00 | 36.91 | 24.83 | 32.52 | Bhasin et al. (1980) |
| 55. Narikoravas | 6 | 13.8 | 79.5 | 121 | 36.64 | 23.71 | 34.24 | 38.39 | 23.31 | 33.35 | Deep Kumar and Ramachandriah (1991) |
| Andaman Islands | | | | | | | | | | | |
| 56. Onge (Negritos) | 7 | 11.1 | 93.0 | 47 | 40.87 | 26.09 | 35.00 | 42.15 | 26.82 | 36.50 | Sarkar (1991) |
| 57. Jarawa (Negritos) | 7 | 11.2 | 93.0 | 12 | 40.58 | 26.58 | 32.92 | 42.08 | 26.42 | 33.67 | Sarkar (1991) |

a. 1, Upper castes; 2, middle castes; 3, lower castes; 4, nomads; 5, Asian groups; 6, Australian groups; 7, African groups.

of each population, social or ethnic affiliation, geographic location in terms of latitude and longitude, sample size, and mean value for each of the interdigital ridge counts is given in Table 1, along with the published sources of the data.

The published data were predominantly from males; hence data on only male samples were used for the present study. Furthermore, the Indian studies in general and particularly those considered for the present study treated the b–c and c–d ridge counts as missing when the c triradius was absent. We find that such cases were uniformly excluded from the analyses when the three interdigital ridge counts were considered. Therefore the sample sizes given in Table 1 are for samples with each of the three interdigital ridge counts scored. Although the Indian castes were grouped by socioeconomic similarity, tribal groups were categorized on the basis of their physical features or characteristics as Asian, Australian, and African. The Asians represent the tribal populations of northeastern India, and the Australian category is represented by the tribal populations of the southern and central parts of India. The two tribal populations from the Andaman Islands represent the African category.

## Statistical Procedures

*Multiple Mantel Tests.* Association between dermatoglyphics (as measured by Euclidean distances computed from correspondence analysis scores), geography (computed as great circle distances), and linguistics (ordinal language distances between groups were computed based on hierarchical classification) were examined using the Mantel test (Mantel 1967). In addition, the Smouse–Long–Sokal test (Smouse et al. 1986) was used to produce partial and multiple matrix correlations. This method extends Mantel's statistic to three or more matrices and tests whether an association between matrix $A$ and $B$ is significant when one or more matrices $C, D, \ldots$ are held constant.

Ordinal language distances were obtained using a simple criterion: Distance between populations speaking the same language was scored as 1; distance between populations of the same linguistic family but speaking different languages was scored as 2; and distance between populations speaking languages of different linguistic families was scored as 3. The populations included in the present study fall into three broad language families, namely, Dravidian, Indo-European, and Tibeto-Burman, besides the unique language category of the Andaman Islanders.

*Multiresponse Permutation Procedure.* The multiresponse permutation procedure (MRPP) was used to test the significance of association between dermatoglyphic variation on the one hand and patterns of social–ethnic and geographic variation of the populations on the other (Mielke et al. 1981). The MRPP is a nonparametric procedure for testing the hypothesis of no differences among two or more groups of populations; it is equivalent to discriminant analysis or one-way analysis of variance (MANOVA) (McCune 1991). Because the probability value of an MRPP statistic is derived through a permutation argument, there are no distributional requirements on the data, such as multivariate normality and homogeneity of variances.

A permutation is a specific arrangement or assignment of all *N* objects (in this case population samples) to the specified groups (here grouped by ethnic and geographic affiliation). The null hypothesis for the MRPP states that all the possible permutations are equally likely. The test statistic indicates the extent of differentiation between groups. The observed $\delta$ (the average of the within-group distances) is compared to an expected $\delta$, which is calculated to represent the mean $\delta$ for all possible partitions of the data. Small values of $\delta$ indicate a tendency for clustering, whereas larger values of $\delta$ indicate a lack of clustering. The variance and skewness of $\delta$ are descriptors of the distribution of all possible values of $\delta$ corresponding to the possible partitions of the items. The probability value expresses the likelihood of obtaining a $\delta$ as extreme or more extreme than the observed $\delta$, given the distribution of all possible $\delta$ [for details, see Zimmerman et al. (1985)].

*Principal Components Analysis.* A principal components analysis was used to graphically represent the relationships among populations based on palmar ridge counts. This method is a general technique for reducing the dimensions of variability. This reduction technique looks for linear combinations of the original measurements that preserve as much of the variation as possible. The correlation matrix instead of the covariance matrix was preferred in deriving the principal component scores/eigenvectors.

*Spatial Autocorrelation.* Spatial autocorrelation analysis (Cliff and Ord 1973; Sokal and Oden 1978) of palmar dermatoglyphics was used to explore continental-scale patterns of population structure among the 57 populations of the Indian subcontinent. Longitude and latitude for each population were estimated from maps of the region. Spatial autocorrelation analysis and construction of correlograms were carried out using Moran's *I*, a product-moment coefficient. We used 18 distance classes, each with an interval of 125 km, because this is roughly the upper limit for mating distances.

## Results

**Principal Components Analysis.** The projection of populations with geographic and social–ethnic affiliations onto the first two eigenvectors derived from the analysis of six variables (interdigital ridge counts for both hands) and by using a correlation matrix (Table 2) is depicted in Figures 2 and 3, respectively. The first axis, which explains about 80% of the total variation, is a size component, where populations possessing a higher number of interdigital ridge counts are placed more to the right-hand side of the plot (Figure 2). Broadly, the first

**Table 2.** Correlation Matrix Between the Six Palmar Interdigital Ridge Count Variables

| | *Right a–b* | *Right b–c* | *Right c–d* | *Left a–b* | *Left b–c* |
|---|---|---|---|---|---|
| Right b–c | 0.6904 | | | | |
| Right c–d | 0.7025 | 0.8134 | | | |
| Left a–b | 0.9276 | 0.6550 | 0.6231 | | |
| Left b–c | 0.6298 | 0.9364 | 0.7967 | 0.5731 | |
| Left c–d | 0.7233 | 0.8209 | 0.8843 | 0.5992 | 0.8522 |

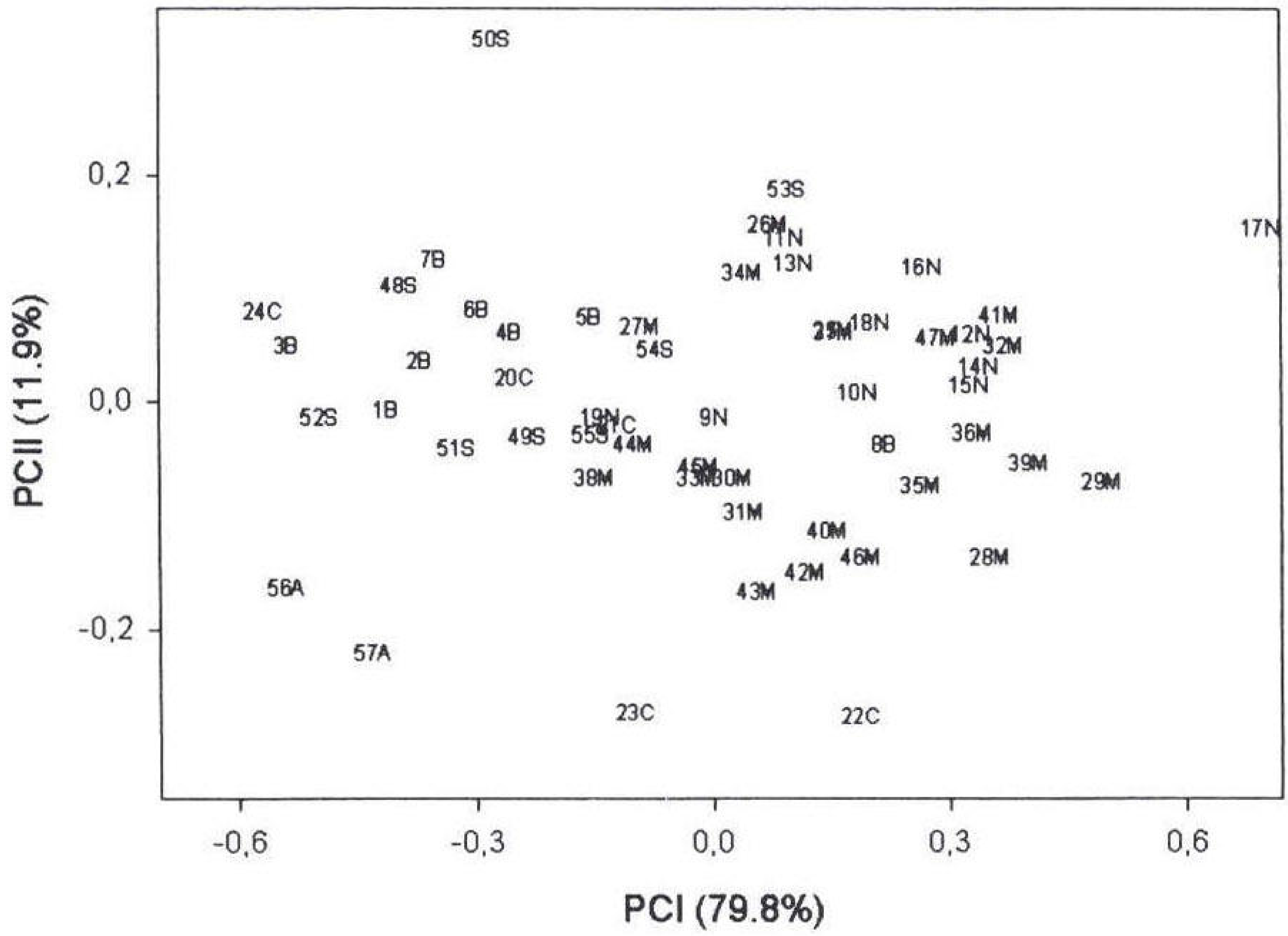


**Figure 2.** Projection of the Indian populations, identified by geographic region, on the first two principal components derived from the six interdigital ridge counts. The geographic regions are the following: B, Nepal and Bhutan; N, northern India; M, Maharashtra; C, central India; S, southern India; A, Andaman Islands. The numbers correspond to the populations identified in Table 1.

axis separates the northern and most of the Maharashtran groups from the rest of the populations, besides showing a greater proximity of the populations of each region (Figure 2). There is also some tendency of clustering within these broad geographic categories, consistent with their socioeconomic position. Furthermore, populations from Nepal and Bhutan have been placed relatively closely together on the left-hand side of this plot (Figure 2). Populations from central and southern India, which are ethnically heterogeneous, are scattered all around, and a couple of those are outliers (populations 23C, 22C, and 50S in Figure 2). The two primitive groups from the Andaman Islands are clear outliers, separated from the other populations on both the first and second axes. On the second axis,

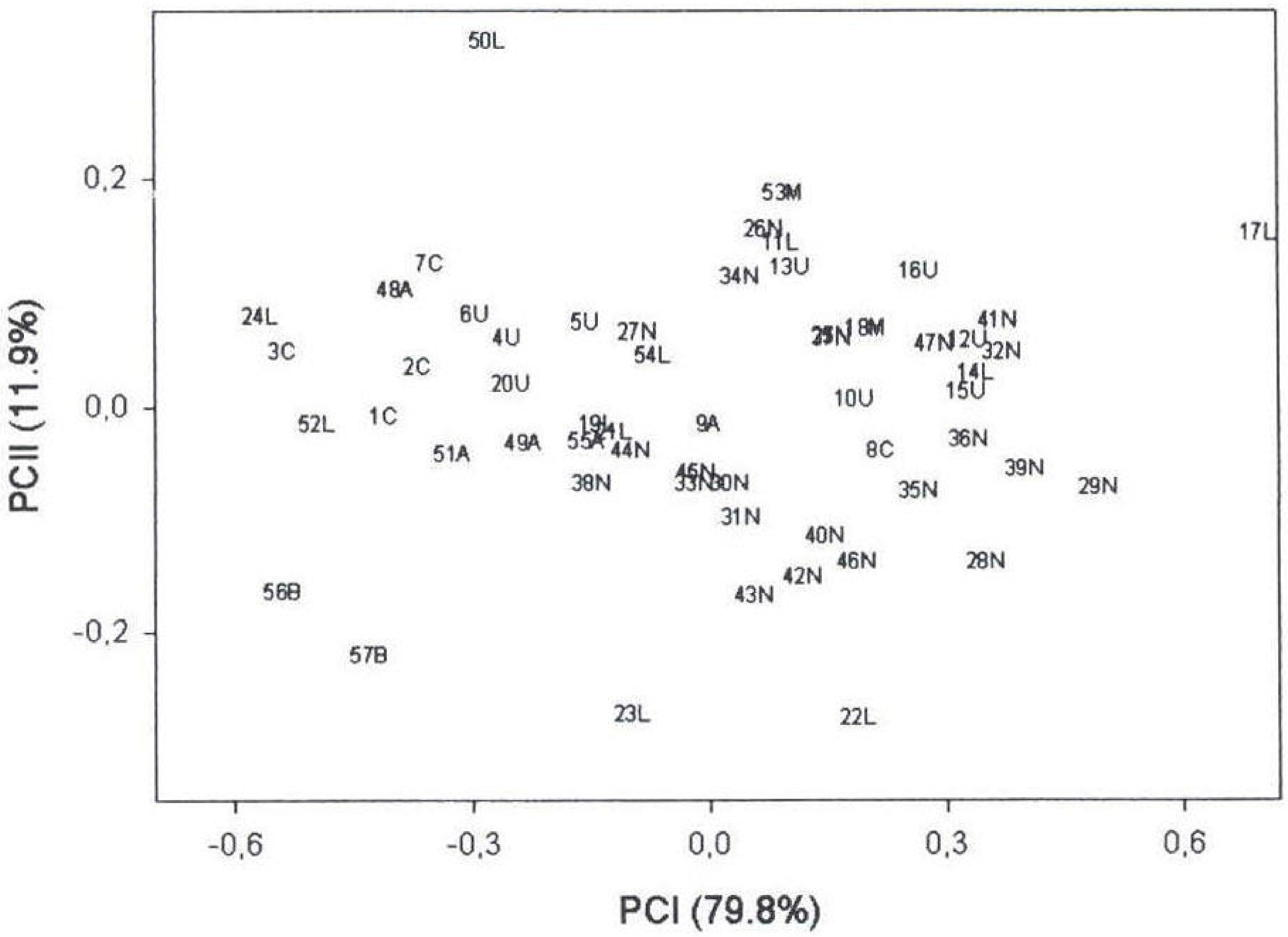


**Figure 3.** Projection of the Indian populations, identified by ethnic–social criteria, on the first two principal components derived from the six interdigital ridge counts. The ethnic–social groups are the following: U, upper castes; M, middle castes; L, lower castes; N, nomads; C, Asian groups; A, Australian groups; B, African groups. The numbers correspond to the populations identified in Table 1.

which accounts for 12% of the variation, positive scores represent high values for a–b ridge counts and negative scores correspond to high values for b–c and c–d scores. On this axis, except for the outliers, there is little differentiation; but most of the northern groups lie in the upper right quadrant of the scatterplot, whereas the Maharashtran groups lie in the lower half.

It is apparent in Figure 3 that there is tendency for proximity based on ethnic–social affiliation within homogeneous geographic regions, not generally across the regions. For example, the upper castes from northern India (populations 10U, 12U, 13U, 15U, and 16U), the Australian groups from southern India (populations 48A, 49A, 51A, and 55A), and the two African and Asian populations from the Andaman Islands (populations 56B and 57B) and Nepal and Bhutan (populations 1C, 2C, 3C, 7C) tend to be placed closer to each other. Thus the effects of geography and socioeconomic–ethnic effects appear somewhat confounding.

**MRPP.** The results of the MRPP, which are expected to qualitatively complement the multivariate plots from the principal components analysis, are summarized in Table 2. The MRPP analysis for the groups clustered by social and ethnic

**Table 3.** Results from the Multiresponse Permutation Procedure for Socioeconomic–Ethnic and Geographic Heterogeneity

| *Grouping Defined by* | *N* | *Mean Distance*[a] |
|---|---|---|
| Social–ethnic affiliation | | |
| Upper caste | 9 | 6.300 |
| Middle caste | 2 | 4.092 |
| Lower caste | 11 | 9.772 |
| Nomad | 23 | 5.457 |
| Asian group | 5 | 6.706 |
| Australian group | 5 | 4.634 |
| African group | 2 | 3.581 |
| Observed $\delta^{b}$ | | 6.347 (6.447) |
| Expected $\delta$ | | 7.696 (7.456) |
| Significance | | $p \leqslant 0.00001$ (0.001) |
| Major geographic region | | |
| Andaman Islands | 2 | 3.581 |
| Nepal and Bhutan | 8 | 5.835 |
| Northern India | 11 | 5.557 |
| Maharashtra | 23 | 5.457 |
| Central and eastern India | 5 | 8.327 |
| Southern India | 8 | 5.365 |
| Observed $\delta^{b}$ | | 5.703 (5.778) |
| Expected $\delta$ | | 7.696 (7.456) |
| Significance | | $p \leqslant 0.0000001$ (0.001) |

a. Values in parentheses are results obtained by excluding Andaman groups.
b. Average within-group distance.

affiliation reveals that the average distances observed between populations, within groups, are significantly lower ($p < 0.001$) than the distances expected for groups of populations randomly generated. A more detailed analysis shows a lack of clear clustering for the lower castes, because within-group distances were observed to be higher than the distance expected from a random distribution. However, within-group distances were observed to be lower than the distance expected from a random distribution for the upper and middle castes. The nomadic populations from Maharashtra and the ethnically defined groups (Asians, Australians, and Africans) also show clear within-group patterning, with distance values markedly lower than the expected values. The MRPP analysis for the groups clustered by major geographic regions yielded even higher values of significance for the clusters, and only one of the six clusters (central India) exhibited within-group distances higher than those expected for a random distribution of populations within the groups.

**Mantel Test and Multiple Correlations.** Table 3 provides the correlation values between pairs of dermatoglyphic, geographic, and linguistic distance matrices. The correlation values are moderate but statistically highly significant ($p = 0.001$) between the pairs of all the different matrices. However, the association between dermatoglyphics and geography ($r = 0.298$) seems slightly stronger

**Table 4.** Mantel Correlations of Dermatoglyphic (DERM), Geographic (GEOG), and Linguistic (LING) Distance Matrices[a]

| *Correlation* | *R* | $p^b$ |
|---|---|---|
| Correlations | | |
| DERM × GEOG | 0.298 (0212) | 0.001 (0.001) |
| DERM × LING | 0.194 (0.169) | 0.001 (0.001) |
| GEOG × LING | 0.448 (0.434) | 0.001 (0.001) |
| Partial correlations[c] | | |
| DERM × GEOG (LING) | 0.242 (0.156) | 0.001 (0.001) |
| DERM × LING (GEOG) | 0.088 (0.087) | 0.01 (0.01) |
| Multiple correlation[d] | | |
| DERM × GEOG, LING | 0.275 (0.228) | 0.001 (0.001) |

a. Values in parentheses are the values obtained after excluding the Andaman groups from the analyses.
b. Mantel test probabilities.
c. Partial correlations removing the influence of the matrix in parentheses.
d. Multiple correlation obtained through multiple regression of the dermatoglyphic distance matrix against both geographic and linguistic distance matrices.

than that between dermatoglyphics and linguistics ($r$ = 0.194). The high correlation observed between the geographic and linguistic distances ($r$ = 0.448) could be due to the fact that the linguistically similar groups are geographically clustered. That the partial correlation between the distance matrices of dermatoglyphics and geography is high, even after removing the effect of language, suggests that geography mediates the population structure significantly independently of the linguistic differences (partial $r$ = 0.242). On the other hand, the effect of language differences on the dermatoglyphic variation is small ($r$ = 0.088) but nevertheless significant when the effect of geography is held constant. The multiple correlation value between dermatoglyphics and the combined effects of geography and language is moderately high ($r$ = 0.275) and significant ($p$ = 0.001).

The Andaman and Nicobar Islands, although politically aligned with the Indian subcontinent, are not geographically contiguous with it, and the populations from this region speak somewhat unique languages compared with those on the Indian subcontinent. To verify whether these unique linguistic and geographic positions of the populations influenced the results of the Mantel correlations and other analyses, we reanalyzed the data by excluding those groups. Although there was a general reduction in the absolute values of the Mantel correlations, etc. (Tables 3 and 4), the results remained qualitatively similar.

**Spatial Autocorrelation.** We examined the form of geographic patterning of the dermatoglyphic variation and tried to identify the kind of spatial processes implicated. Results of the spatial autocorrelation analysis for palmar interdigital ridge counts (both hands pooled) are summarized in Table 5. Spatial correlograms for the a–b, b–c, and c–d interdigital ridge counts are shown in Figure 4. The horizontal axis measures geographic distance between populations (in kilometers), and the vertical axis shows the standardized ($z$-score) value of Moran's $I$ at each spatial lag. Moran's $I$ values are plotted at the upper distance limit for the lags.

**Table 5.** Spatial Autocorrelation (Moran's *I*) Results for Palmar Interdigital Ridge Counts Among the Indian Populations: Both Hands Pooled

| *Spatial Lag* | *km* | *Number of Pairs* | *a–b Ridge Count* | | *b–c Ridge Count* | | *c–d Ridge Count* | |
|---|---|---|---|---|---|---|---|---|
| | | | *I* | *P*[a] | *I* | *P* | *I* | *P* |
| 1 | 131 | 88 | 0.568 | 0.000 | 0.302 | 0.000 | 0.464 | 0.000 |
| 2 | 256 | 89 | 0.250 | 0.003 | 0.314 | 0.000 | 0.609 | 0.000 |
| 3 | 404 | 88 | − 0.035 | 0.429 | 0.175 | 0.020 | 0.308 | 0.000 |
| 4 | 531 | 89 | 0.007 | 0.397 | 0.092 | 0.124 | 0.036 | 0.290 |
| 5 | 632 | 89 | − 0.132 | 0.118 | − 0.117 | 0.147 | − 0.106 | 0.180 |
| 6 | 762 | 88 | − 0.087 | 0.240 | − 0.008 | 0.458 | − 0.114 | 0.164 |
| 7 | 868 | 89 | 0.072 | 0.175 | − 0.050 | 0.368 | − 0.120 | 0.145 |
| 8 | 960 | 89 | − 0.005 | 0.446 | − 0.446 | 0.000 | − 0.296 | 0.002 |
| 9 | 1,049 | 88 | − 0.352 | 0.000 | − 0.440 | 0.000 | − 0.423 | 0.000 |
| 10 | 1,180 | 89 | − 0.148 | 0.091 | 0.004 | 0.410 | − 0.024 | 0.477 |
| 11 | 1,267 | 89 | 0.061 | 0.213 | 0.008 | 0.394 | − 0.205 | 0.030 |
| 12 | 1,357 | 88 | − 0.047 | 0.383 | 0.128 | 0.068 | − 0.077 | 0.279 |
| 13 | 1,473 | 89 | 0.118 | 0.083 | 0.044 | 0.262 | 0.016 | 0.366 |
| 14 | 1,560 | 89 | 0.223 | 0.007 | 0.067 | 0.193 | − 0.011 | 0.473 |
| 15 | 1,655 | 88 | 0.059 | 0.216 | − 0.014 | 0.483 | − 0.209 | 0.027 |
| 16 | 1,810 | 89 | 0.019 | 0.351 | − 0.060 | 0.329 | 0.005 | 0.408 |
| 17 | 2,127 | 89 | − 0.217 | 0.011 | − 0.049 | 0.358 | 0.031 | 0.288 |
| 18 | 2,981 | 89 | − 0.674 | 0.000 | − 0.269 | 0.002 | − 0.204 | 0.017 |
| Total | | 1,596 | | 0.000 | | 0.000 | | 0.000 |

a. Significance of Bonferroni approximation.

Several salient features emerge from Figure 4. First, there is a high degree of similarity in the plots for the three ridge count measures. All three correlograms illustrate a general trend of monotonic decline in the level of spatial autocorrelation: from large positive values at the smallest spatial lags, followed by a sharp decline to the large negative values in the intermediate distances. This is followed by a zigzag pattern of the distribution of Moran's *I*, around the value of 0, until the last distance lag, which shows by far the lowest *I* value. Yet, overall, all three variables show this pattern to be statistically significant. The plots of these variables can be considered to represent the first law of geography, that is, "Everything is related to everything else but near things are more related than distant things." This pattern is consistent with Reddy, Demarchi et al.'s (2001) study, based on anthropometric and genetic markers, of 20 populations of the Dhangar caste cluster distributed throughout the state of Maharashtra in India. This suggests that these biological systems exhibit strong patterns over short distances but are not spatially patterned monotonically over large distances.

## Discussion

The results of the four analytical procedures to understand the pattern of variation in palmar interdigital ridge counts among the Indian populations are complementary. Broadly, both the principal components analysis and the Mantel

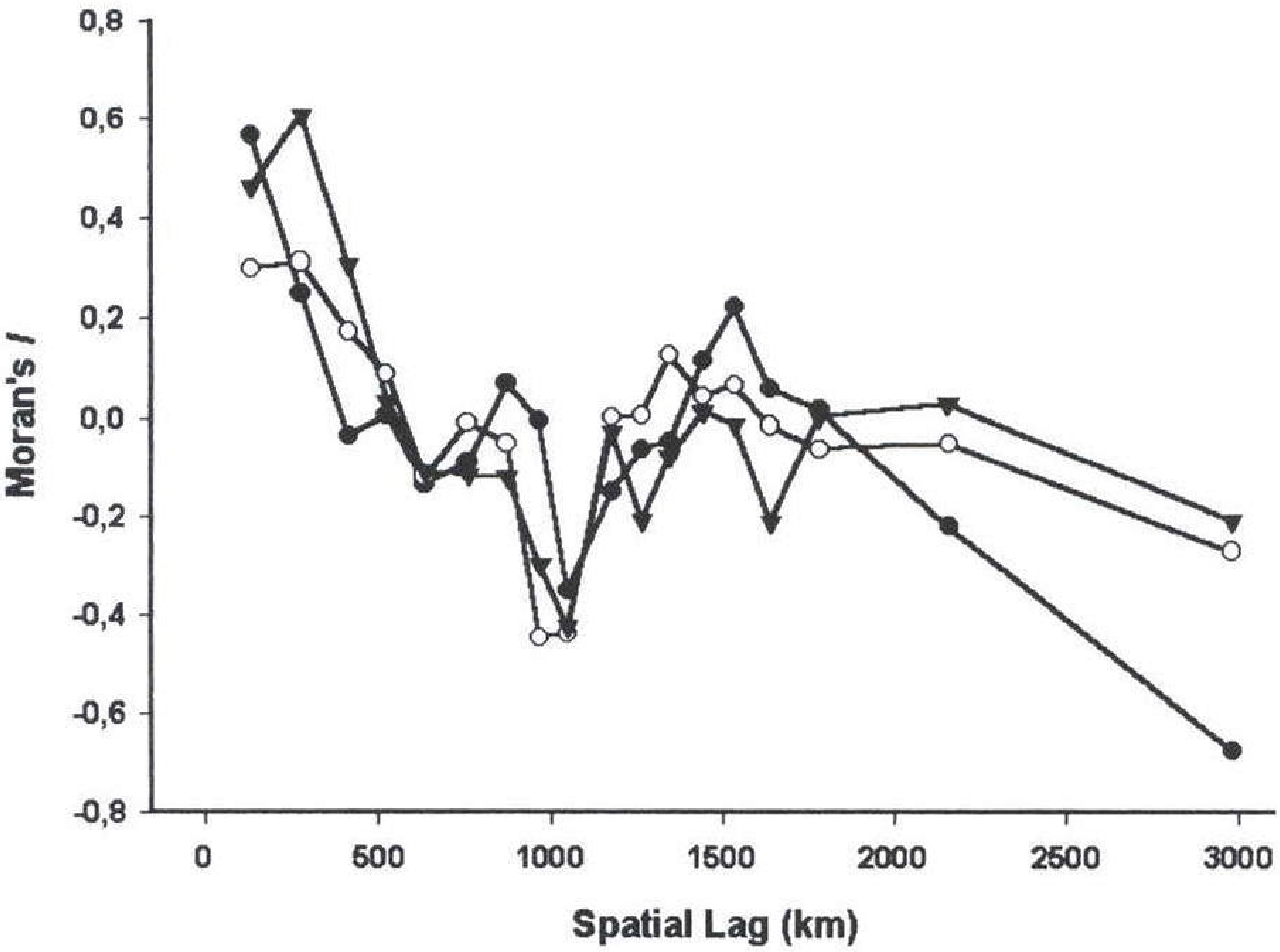


**Figure 4.** Plot of Moran's *I* against the geographic distances between the pairs of 57 Indian populations for the three interdigital ridge counts (filled circles = a–b; open circles = b–c; and triangles = c–d).

test suggest patterning of the population structure based on geography, social–ethnic, and/or language affiliation, although not as clearly as one would have liked to be able to assign palmar dermatoglyphic features to specific geographic regions or social–ethnic or linguistic groups. Nevertheless, the effect of geography on dermatoglyphic variation seems more pervasive, given that the Mantel correlation remains highly significant even after nullifying the effect of linguistic differences.

Likewise, the MRPP analysis also suggests statistically significant patterns, implying biological validity of the assigned groupings of populations based on geographic and/or sociocultural and ethnic criteria. For example, the relatively close positioning of the Dhangar groups of Maharashtra is both geographically and ethnically consistent, because they belong to a homogeneous occupational group constituting a caste cluster. Similarly, although it is apparent that there is no clear pattern of social subclustering within the northern Indian groups, the clustering of these groups is evident. It may be pertinent to note here that Reddy and Reddy (1992) observed that, because of the relatively greater evolutionary stability of dermatoglyphic traits, the short-term differences that could be expected among caste groups of the same geographic and linguistic region might not be reflected.

The other regional groups, such as the Nepalese and tribes from the Andaman Islands, are differentiated from other regional groups, consistent with their distinct geographic positions. The absence of compact clustering of central and southern Indian populations might be due to the relatively greater linguistic and geographic heterogeneity of the populations constituting these groups. For example, in the southern Indian groups, four distinct languages can be found; this is also the case in the central and eastern Indian groups. The most important observation is the fact that there was no tendency for populations to cluster based on ethnic–social affiliation across the geographic regions. The population configurations are consistent with geographic rather than ethnic criteria observed in other studies based on other biological variables (Reddy et al. 2000; Reddy, Dutta et al. 2001; Reddy, Sun et al. 2001), including DNA polymorphisms (Dutta et al. 2002; Reddy, Demarchi et al. 2001; Reddy, Dutta et al. 2001; Reddy, Sun et al. 2001; Roychaudhury et al. 2001). This suggests diverse origins of the ethnic and caste groups from different linguistic or geographic regions.

The results of the autocorrelation reflect the unique feature of Indian population structure that the gene flow is restricted by the geography, that is, isolation by distance with reference to a single caste. Marital movement within a caste is traditionally restricted to small distances. Between the castes the gene flow is restricted by social norms (endogamy rule), even when the castes inhabit a single village. Overall, the lack of spatial structure in these dermatoglyphic variables is consistent with Indian population structure, in which numerous endogamous groups coexist, albeit as islands, with no or negligible gene flow between them. Therefore it is not surprising that the monotonic decline expected under the model of contiguous diffusion of genes is not evident in the Indian data. Another reason for the lack of clear spatial patterning may be the limited number of samples representing the Indian subcontinent and the disjoint nature of their distribution. Given that the samples were drawn from secondary sources, there was no way to surmount this shortcoming.

Overall, the palmar interdigital ridge counts were useful to clearly portray population affinities based on broad geographic affiliations of the groups. However, within a geographic or linguistic region, the ethnic–social affinities of the populations are depicted only subtly by these variables. The ethnic–social affinities of populations across linguistic or geographic regions are not reflected. The results of spatial autocorrelation for the palmar dermatoglyphics reiterate patterns observed earlier for other biological variables, such as anthropometric measurements and genetic markers, even on a relatively much reduced geographic scale (Reddy, Demarchi et al. 2001).

*Acknowledgments* D.A. Demarchi is a career member of the Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina (CONICET). We thank the anonymous reviewers for their valuable suggestions, which helped to improve the presentation of the results.

*Received 22 January 2003; final revision received 22 December 2003.*

## Literature Cited

Babler, W.J. 1978. Prenatal selection and dermatoglyphic patterns. *Am. J. Phys. Anthropol.* 48:21–28.

Babu, M.S. 1984. A quantitative study of palmar interdigital areas among Koya Doras. *Ind. J. Phys. Anthropol. Hum. Genet.* 10:68–72.

Babu, M.S., and G. Jaikishan. 1983. Finger and palmar dermatoglyphics of Vadabalijas of coastal AP. In *Human Biology: Recent Advances,* I.J.S. Bansal, ed. New Delhi: Today & Tomorrow's Printers & Publishers, v. 2, 189–198.

Balgir, R.S., and J.C. Sharma. 1986. Dermatoglyphic studies among the two breeding isolates of Ghujars of northwestern India. *Am. J. Phys. Anthropol.* 71:467–476.

Bhasin, M.K. 1966. The interdigital intervals a–b, b–c, c–d, and a–d ridge counts in palmar dermatoglyphics of the Bhutanese. *Anthropologist* 13:81–88.

Bhasin, M.K. 1970. Group differences among Newars of Nepal for palmar interdigital areas. *Hum. Hered.* 21:604–608.

Bhasin, M.K. 1971. A note on group differences among Newars of Nepal for palmar interdigital areas. In *Hautleisten und Krankheiten,* W. Hirsch, ed. Berlin: Ernst-Reuter-Gesellschaft, 273–278.

Bhasin, M.K., S.L. Malik, M.S. Grewal et al. 1980. Effect of natural background radiation on dermatoglyphic traits. *Acta Anthropogenet.* 4(122):1–27.

Bhasin, M.K., I.P. Singh, H. Walter et al. 1986. Genetic studies of Pangwalas transhuman and settled Gaddis: Palmar dermatoglyphics. *Ind. J. Anthropol. Hum. Genet.* 12(1):9–28.

Blangero, J. 1988. The selective neutrality of dermatoglyphic variation. *Int. J. Anthropol.* 3:289–299.

Cliff, A.D., P. Haggett, K.J. Ord et al. 1975. *Elements of Spatial Structure: A Quantitative Approach.* Cambridge: Cambridge University Press.

Cliff, A.D., and J.K. Ord. 1973. *Spatial Autocorrelation.* London: Pion.

Crawford, M.H., and R. Duggirala. 1992. Digital dermatoglyphic patterns of Eskimo and Amerindian populations: Relationships between geographic, dermatoglyphic, genetic, and linguistic distances. *Hum. Biol.* 64:683–704.

Deep Kumar, V.S., and T. Ramachandriah. 1991. Palmar dermatoglyphics of the three Negrito tribes of Andaman Islands, India. In *Dermatoglyphics Today,* B.M. Reddy, S.B. Roy, and B.N. Sarkar, eds. Calcutta: Indian Institute of Biosocial Research and Development, Anthropological Survey of India, and Indian Statistical Institute, 343–355.

Demarchi, D.A. 2000. Variation in palmar quantitative dermatoglyphics among Argentinian aboriginal populations. *Homo* 51:19–29.

Demarchi, D.A., A. Giordano, and A.J. Marcellino. 1997. Dermatoglyphics in Araucanian Indians from Patagonia and multivariate comparisons with other Argentinian indigenous populations. *Hum. Biol.* 69:227–239.

Demarchi, D.A., and A.J. Marcellino. 1998. Dermatoglyphic relationships among South Amerindian populations. *Hum. Biol.* 70:579–596.

Dutta, R., B.M. Reddy, P. Chattopadhyay et al. 2002. Patterns of genetic diversity at the 9 forensically approved STR loci among the Indian populations. *Hum. Biol.* 74:33–49.

Froechlich, J.W., and E. Giles. 1981a. A multivariate approach to fingerprints variation in Papua New Guinea: Implications for prehistory. *Am. J. Phys. Anthropol.* 54:73–91.

Froechlich, J.W., and E. Giles. 1981b. A multivariate approach to fingerprints variation in Papua New Guinea: Perspective on the evolutionary stability of dermatoglyphic markers. *Am. J. Phys. Anthropol.* 54:93–106.

Jantz, R.L., and V.P. Chopra. 1983. A comparison of dermatoglyphic methodologies in population studies. *Am. J. Phys. Anthropol.* 60:61–67.

Jantz, R.L., C. Hawkinson, H. Brehme et al. 1982. Finger ridge count variation among various sub-Saharan African groups. *Am. J. Phys. Anthropol.* 57:311–321.

Karmakar, B., T.S. Vasulu, K.C. Malhotra et al. 1996. Variation in palmar interdigital ridge counts among 20 Dhangar castes of Maharashtra, India. *Anthropol. Anz.* 54:239–253.

Karve, I., and K.C. Malhotra. 1968. A biological comparison of eight endogamous groups of the same rank. *Curr. Anthropol.* 9:109–124.

Krishnan, T., and B.M. Reddy. 1994. Geographical and ethnic variability of finger ridge counts: Biplots of male and female Indian samples. *Ann. Hum. Biol.* 21:155–169.

Kshtriya, G.K. 1987. Palmar ridge count variation in two Gujrati populations. *Ind. J. Phys. Anthropol. Hum. Genet.* 13(2):149–154.

Loesch, D.Z. 1979. Dermatoglyphic distances: Selected topics. In *Dermatoglyphics Fifty Years Later,* W. Wertelecki and C.C. Plato, eds. New York: Alan R. Liss, 225–248.

Loesch, D.Z., and N.G. Martin. 1984. Finger ridge patterns and tactile sensitivity. *Ann. Hum. Biol.* 11:113–124.

Loesch, D.Z., and N. Wolanski. 1985. Dermal ridge patterns and fertility in a Polish rural sample. *Ann. Hum. Biol.* 12:463–477.

Malhotra, K.C., and B.V. Bhanu. 1967. A note on the A–B ridge counts in palmar dermatoglyphics of the Izhavas of Kerala. *Eastern Anthropol.* 20:257–262.

Malhotra, K.C., M. Vijay Kumar, and B. Karmakar. 1981. Palmar dermatoglyphics in three nomadic Mendelian isolates. *Man in India* 61:143–167.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Res.* 27:209–220.

Mavalwala, J., and E.E. Hunt Jr. 1964. Finger and palm prints of the Micronesians of Yap. *Z. Morphol. Anthropol.* 55:11–23.

McCune, B. 1991. *Multivariate Analysis on the PC-ORD System.* Corvallis: Department of General Science, Oregon State University.

Mielke, P., K. Berry, P. Brockwell et al. 1981. A class of nonparametric tests based on multiresponse permutation procedures. *Biometrika* 68:720–724.

Narhari, S. 1979. Palmar ridge counts among the Nakkalas of Andhra Pradesh. *J. Ind. Anthropol. Soc.* 14:265–268.

Narhari, S., and A.P. Reddy. 1983. Palmar ridge counts among the Yerukalas of AP. In *Human Biology: Recent Advances,* I.J.S. Bansal, ed. New Delhi: Today & Tomorrow's Printers & Publishers, v. 2, 329–336.

Pateria, H.N. 1976. Palmar ridge count among Brahman and Bhangi of Saugar (MP, India). *Ind. J. Anthropol. Hum. Genet.* 2:215–220.

Plato, C.C. 1970. Dermatoglyphics and flexion creases on the Cypriots. *Am. J. Phys. Anthropol.* 38:421–438.

Reddy, B.M., V.P. Chopra, B. Karmakar et al. 1988. Quantitative palmar dermatoglyphics and assessment of population affinities: Data from marine fisherman of Puri. *Anthropol. Anz.* 46:235–244.

Reddy, B.M., V.P. Chopra, B. Karmakar et al. 2000. Population structure and the patterns of dermatoglyphic variation in northwest India. *Am. J. Hum. Biol.* 12:315–326.

Reddy, B.M., A.D. Demarchi, and K.C. Malhotra. 2001. Pattern of variation in a caste cluster of Dhangars of Maharashtra, India. *Coll. Anthropol.* 25:425– 442.

Reddy, B.M, R. Dutta, B.T. Langstieh et al. 2001. Diversity at the three tetrameric STR loci in a substructured Golla caste population of southern Andhra Pradesh in comparison to other Indian populations. *Int. J. Hum. Genet.* 1:101–108.

Reddy, B.M., and P.C. Reddy. 1992. Dermatoglyphic affinities among the Telugu populations with contrasting ethnohistorical backgrounds. *Am. J. Hum. Biol.* 4:669–682.

Reddy, B.M., and P.C. Reddy. 2001. Population structure and the patterns of dermatoglyphic variation in Andhra Pradesh, India. *Int. J. Hum. Genet.* 1:203–209.

Reddy, B.M., G. Sun, R.L. Javier et al. 2001. Genomic diversity at the 13 STR loci among the 7 subcastes of the substructured Golla population of southern Andhra Pradesh, India. *Hum. Biol.* 73:175–190.

Rife, D.C. 1954. Dermatoglyphics as ethnic criteria. *Am. J. Hum. Genet.* 6:319–327.

Rogers, A., and H.C. Harpending. 1983. Population structure and quantitative characters. *Genetics* 105:985–1,002.

Rothhammer, F., R. Chakraborty, and E. Llop. 1977. A collection of gene and dermatoglyphic diversity at various levels of population differentiation. *Am. J. Phys. Anthropol.* 46:51–59.

Roychaudhury, S., S. Roy, B. Dey et al. 2001. Fundamental genomic unity of ethnic India is revealed by analysis of mitochondrial DNA. *Curr. Sci.* 79:1,182–1,192.

Rudan, P. 1978. Biological structure of Istrian population: Study of distances by anthropometric traits, dermatoglyphic properties, and blood group gene frequency. *Coll. Anthropol.* 2:53–58.

Sachs, L., and M. Bat-Miriams. 1957. The genetics of Jewish populations in Israel. *Am. J. Hum. Genet.* 9:117–126.

Sarkar, B.N. 1991. Palmar dermatoglyphics of the three Negrito tribes of Andaman Islands, India. In *Dermatoglyphics Today,* B.M. Reddy, S.B. Roy, and B.N. Sarkar, eds. Calcutta: Indian Institute of Biosocial Research and Development, Anthropological Survey of India, and Indian Statistical Institute, 419–430.

Smouse, P.E, J.C. Long, and R.R. Sokal. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Syst. Zool.* 35:627–632.

Sokal, R.R., and N.L Oden. 1978. Spatial autocorrelation in biology. 1. Methodology. *Biol. J. Linnean Soc.* 10:119–228.

Van Valen, L. 1963. Selection in natural populations: Human fingerprints. *Nature* 200:1,237–1,238.

Woolley, V., R.L.H. Dennis, and E. Sunderland. 1984. A dermatoglyphic study of the Ghrungs, Mangars, and Kirantis of Nepal. *Hum. Hered.* 34:141–147.

Zimmerman, G., H. Goetz, and P. Mielke. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology* 66:606–611.