Biological Affinities Between Migrant and Parental Populations of Fishermen on the East Coast of India

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Abstract We examined biological affinities between the migrant groups of fishermen in Puri and their parental counterparts using 3 sets of variables: genetic markers, anthropometric measurements, and quantitative dermatoglyphics. Results of both univariate and multivariate analyses suggest a significant migration effect, diversifying migrants from their parental populations, although the distance configurations based on each set of variables resemble each other. The migration effect is particularly remarkable for the anthropometric measurements. The plot of group centroids based on the discriminant analysis of the 7 populations depicts a clear segregation of migrants from the parental populations. Because of relatively large effective population sizes and short history of these populations in Puri, the role of genetic drift can be safely ruled out. However, a founder effect is a plausible reason for the observed differentiation of the migrants from their parental groups, especially given that certain rare variants that were not observed in the parental populations appear in the migrants. That the founders were a select group of fishermen with respect to body dimensions, not a random group, can be inferred from the occupational differences among the migrant groups, which in turn suggests phenotypic plasticity in the observed differentiation. Regression of mean phenotypic variance and heterozygosity on the distance from the centroid suggests a strong possibility of external gene flow into the migrant populations in Puri.

In a number of papers we have reported findings on the population structure (Reddy 1984) and biological composition (Reddy et al. 1987, 1988, 1989; Reddy 1990) of the migrant groups of fishermen living on the Puri coast of India. The migration history of these people suggests that they were drawn from about 100 villages distributed along the 400-km-long coast, south of Puri, starting from Ganjam District in Orissa and extending to the West Go-

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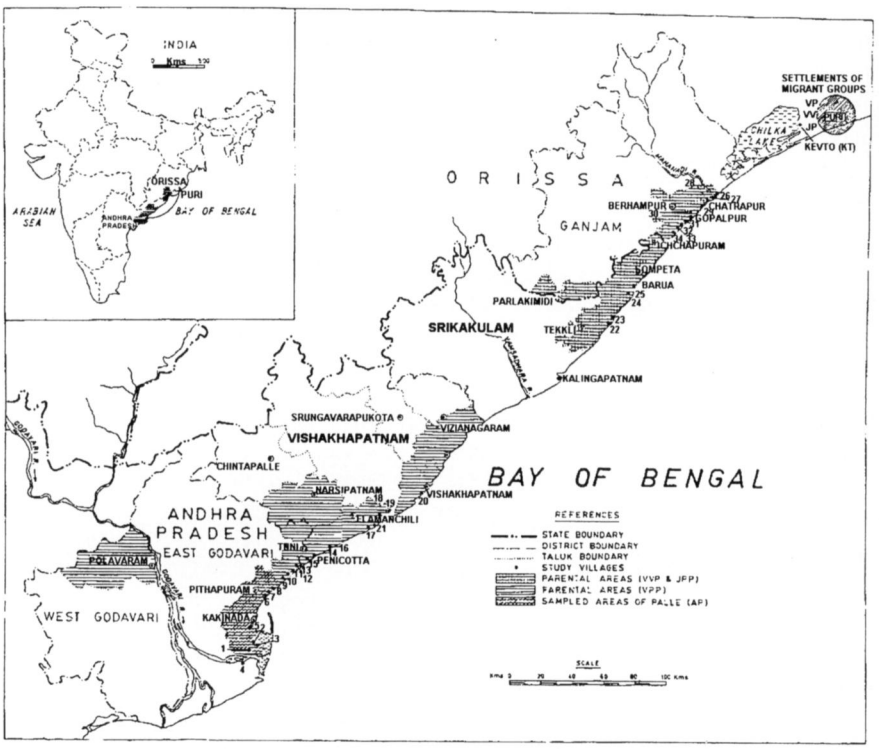

Figure 1. Geographic areas from which the Puri fishermen emigrated and the villages (numbered 1–34) from which the samples are drawn for their parental counterparts.

davari coast in Andhra Pradesh (Figure 1). They migrated to Puri at different points of time, have different caste affiliations, and form 3 endogamous groups: the Vadabalija of Penticotta (VP), the Vadabalija of Vadapeta (VV), and the Jalari of Puri (JP).

The 3 groups live in 4 different settlements in Puri. The population sizes of the VP, VV, and JP in Puri are estimated to be 8,000, 4,000, and 800, respectively. Although intermarriage between the VP and the VV (the 2 reproductive isolates of the same caste, Vadabalija) has been estimated to be only about 1% (12 of the 1,238 marriages), there has been no exchange of mates between members of the JP and those of the other 2 groups (Reddy 1984). However, all 3 groups claim to have a common origin (Rao 1980; Reddy 1981) and speak the same language, Telugu, which is spoken in the state of Andhra Pradesh. No case of caste exogamy, however, has been reported among them.

By analyzing different sets of variables—genetic markers, dermatoglyphics, and anthropometry—we found that the discrimination among the 3

groups is relatively higher for anthropometry compared with both quantitative dermatoglyphic variables and genetic markers. Furthermore, although the anthropometric affinities are consistent with the geographic pattern of the groups, the distance configurations based on dermatoglyphics and genetic markers suggest that the populations are marginally inclined to conform to ethnohistorical affiliations. However, the relative differences in the distances between pairs of populations are too small to reflect clearly any ethnic or geographic pattern. Therefore it was concluded that at the level of subcastes with a relatively recent history of separation, the groups differ little genetically and dermatoglyphically. Nevertheless, to resolve the relationship between ethnic affinity and genetic and biological pattern, we need to justify the assumption that the groups in Puri represent their parental stocks. This is pertinent especially because such migrations are usually not at random and because several investigators have observed that such offshoots are likely to have consisted of founders who differed in genetic composition from the parental populations (Birdsell 1950; Giles et al. 1966; Glass 1956; Roberts 1968). One way to resolve this problem is to examine whether the distance configurations of the Puri groups and of their parental counterparts mimic each other.

It is therefore important to ascertain how different biologically the migrant populations of Puri are from their parental stocks and how these differences are reflected in the observed distance configurations. It is with this objective that we collected the 3 sets of biological data on a representative sample from the parental populations. Here, we report the findings of the comparative analyses of these data among the migrant and parental populations and attempt to deduce the probable microevolutionary implications of the observed pattern of genetic and biological divergence between them.

Geographic Backgrounds of the Parental Populations and Sampling Strategy

The geographic areas from which the 3 groups of Puri fishermen migrated are depicted in Figure 1. The parental settlements of the VV and the JP overlap and are distributed northward, closer to Puri, and the parental villages of the VP are exclusively distributed southward; the 2 patches of distribution are separated by a distance of about 100 km. To adequately represent the heterogeneity of the parental populations, we collected samples from as many as 34 of about 100 villages, selected in such a way that they cover the entire coast from where the Puri fishermen were drawn (Figure 1). Furthermore, we took care that in each of the studied villages at least 1 subject from each surname was sampled; where more than 1 individual with a given surname was chosen, it was after ascertaining that there was no recognizable blood relationship between the subjects. The parental counterparts of the

3 Puri groups (VP, VV, and JP) are designated VPP, VVP, and JPP, respectively.

In addition to the 3 groups, a small number of families of Palle of Andhra Pradesh (AP) also live on the Puri coast, but they were not initially studied because of their small size. However, folk stories indicate that the AP are derived from the same original stock as the other groups of fishermen in Puri. They are predominantly distributed in the West Godavari District and extend marginally into the East Godavari District, overlapping the distribution of the VPP. In view of their supposed common origin, the AP were included for comparative analysis and to draw an overall configuration of the biological and genetic distances among the fishermen populations of these coastal areas.

Data and Methods

Data from the parental groups were collected during January–April 1987 in 2 field expeditions led by B.M. Reddy. During the first field trip, about 600 adult fishermen from the 4 groups were measured (by B.M. Reddy) for the same 9 anthropometric measurements as in the migrant groups (Reddy et al. 1987), and their finger and palm prints were taken using the ink and roller method (Cummins and Midlo 1961). Therefore we have anthropometric and dermatoglyphic data on the same set of subjects. Because of logistic problems, we could not collect blood samples during the first field trip; hence another field trip was undertaken during March–April 1987 to collect blood samples from about 430 fishermen, both males and females. However, this was an independent sample, although there was considerable overlap with the first group of subjects.

The results based on the genetic markers have already been published (Reddy et al. 1995), and readers may refer to that paper for details on the blood collection, methods of analysis, etc. The 10 loci that are common to both migrant and parental populations and hence used for the comparative analysis are *A1A2BO, MN,* Rh *D, ADA, AK, PGM, PGD, ACP, HP,* and *GC* (3 blood groups, 5 red cell enzymes, and 2 serum proteins). Two other loci were also studied: *ESD* in migrants and blood group *P* in the parental groups. Thus each populaion group had 11 loci typed.

Measurements of both the migrants and the parental populations were taken by the same investigator (B.M. Reddy), and therefore interinvestigator error is ruled out. Furthermore, to make the measurements comparable, B.M. Reddy took the measurements using the same protocol (Martin and Saller 1957) on both occasions. Similarly, finger and palm prints were scored by B.M. Reddy for 20 quantitative variables, using the same procedures (Cummins and Midlo 1961; Holt 1968), as outlined for the migrant populations. The anthropometric measurements were stature, sitting height, head length, head breadth, nasal height, nasal breadth, biacromial breadth, bicristal

Table 1. Sample Sizes of Different Data Sets for Different Populations

Population	*Anthropometrics*	*Dermatoglyphics*	*Genetic Markers*
Parental			
JPP	141	142	93
VVP	147	145	83
VPP	165	155	102
AP[a]	151	158	120
Migrant			
VP	208	160	121
VV	200	102	101
JP	65	132	77

a. Migrant counterpart for this population was not studied.

breadth, and chest girth; the quantitative dermatoglyphic variables were total finger ridge counts on 10 fingers and, for the right and left hands separately, total ulnar count, total radial count, total number of triradii on fingers, main line index, and a-b ridge count. The population-specific sample sizes for each set of variables are furnished in Table 1.

Results

Biological Affinities among the Parental Groups of Fishermen. Because we have published results based on genetic markers, we give only salient features here. For details readers may refer to the paper by Reddy et al. (1995). The 4 groups of parental populations did not show any new variant that is not specific to the other local populations. The heterogeneity of the allele frequency was statistically significant ($p < 0.01$) with a G_{ST} value of 1.95% from the 11 loci studied. However, the relative differences in the distances observed between different pairs of populations were small, and the distance configuration of the 3 parental populations is similar to that of their migrant counterparts.

Means and standard deviations and the univariate F ratios of the 9 anthropometric measurements and the 20 quantitative dermatoglyphic variables among the 4 parental groups are given in Tables 2 and 3. Although the univariate F ratios for the anthropometric measurements suggest that all the variables (except biacromial breadth and head breadth) show significant population heterogeneity ($p < 0.05$), only 6 of the 20 dermatoglyphic variables show such heterogeneity. Multiple discriminant analysis, however, suggests highly significant discrimination among the populations for both anthropometry (Wilks $\lambda = 0.742$, $F = 6.89$, d.f. = 17, 1,730; $p = 0.000$) and dermatoglyphics (Wilks $\lambda = 0.783$, $F = 2.29$, d.f. = 60, 1,606; $p = 0.0001$). The distance matrix (Table 4) and the plots of the group centroids on the 2

Table 2. Means ± Standard Deviations of the Anthropometric Variables for the 4 Parental Groups and *F* Values for Intergroup Heterogeneity

Measurement	*JPP* (n = 141)	*VVP* (n = 147)	*VPP* (n = 165)	*AP* (n = 151)	*F*
Stature	1635.28 ± 58.75	1633.95 ± 56.91	1613.77 ± 57.54	1616.97 ± 56.36	5.78
Sitting height	832.91 ± 30.30	836.40 ± 31.88	824.78 ± 30.02	829.07 ± 28.86	4.24
Head length	186.17 ± 6.81	189.43 ± 6.14	189.99 ± 5.51	191.20 ± 6.64	17.01
Head breadth	143.60 ± 4.74	143.22 ± 4.75	143.84 ± 5.00	143.97 ± 5.00	0.69[a]
Nasal height	43.99 ± 3.28	44.42 ± 3.48	44.47 ± 3.34	45.07 ± 3.06	2.70
Nasal breadth	37.91 ± 2.46	38.17 ± 2.95	37.27 ± 2.92	37.54 ± 2.57	3.27
Biacromial breadth	375.55 ± 19.05	375.42 ± 18.27	374.24 ± 18.64	371.38 ± 15.08	1.76[a]
Bicristal breadth	261.16 ± 13.44	258.99 ± 12.39	259.59 ± 14.41	256.61 ± 12.80	2.96
Chest girth	880.46 ± 43.62	881.93 ± 42.73	871.06 ± 43.15	857.91 ± 40.88	10.00

a. Nonsignificant.

canonical variates (data not shown) suggest that, although the population configuration based on anthropometry conforms better to the geographic backgrounds for the migrant populations of Puri, there is no clear separation of groups according to ethnic or geographic affiliations and the populations are equidistant for dermatoglyphics. Thus the distance configurations of parental groups based on anthropometry and dermatoglyphics are also qualitatively similar to their migrant counterparts.

Overall, the correspondence between the distance matrices based on anthropometrics, dermatoglyphics, and genetic markers is not significant, as suggested by Mantel statistics (Table 5), in either the parental or the migrant populations. Furthermore, the correspondence between the distance matrices of parental and migrant populations is not significant in any of the 3 sets of variables. It should be kept in mind, however, that with so few populations and distances almost a perfect correlation would be required to reach statistically significant results.

The F_{ST} values (Table 6), as derived from the *R* matrix analysis (Harpending and Ward 1982; Relethford and Blangero 1990) suggest greater discrimination in anthropometric traits than in either dermatoglyphic traits or genetic markers, among which discrimination is much smaller. Genetic markers in turn show relatively larger discrimination compared with dermatoglyphics. However, although the extent of discrimination in body dimensions is threefold greater among the migrants compared with the parental groups, it is only marginally greater for genetic markers and of the same magnitude for dermatoglyphics.

Comparison Between Parental and Migrant Populations. Despite qualitative similarity in the population configurations of the migrant and parental populations, we cannot definitively conclude that the migrant populations of

Table 3. Means ± Standard Deviations of the 20 Quantitative Dermatoglyphic Variables in the Parental Groups and *F* Values for Intergroup Heterogeneity

Variables	*JPP* (n = 142)	*VVP* (n = 145)	*VPP* (n = 155)	*AP* (n = 158)	*F*
Finger ridge count					
R1	17.68 ± 4.91	17.37 ± 5.95	18.39 ± 5.13	19.01 ± 4.10	3.06[a]
R2	11.48 ± 6.17	12.39 ± 6.02	13.10 ± 5.28	12.52 ± 4.93	1.87
R3	12.94 ± 5.04	12.66 ± 5.52	13.60 ± 4.66	13.60 ± 4.20	1.69
R4	16.55 ± 5.43	15.88 ± 5.50	16.73 ± 4.95	15.97 ± 4.51	0.99
R5	13.57 ± 4.27	13.40 ± 4.81	14.54 ± 4.02	13.51 ± 4.12	1.95
L1	15.31 ± 5.39	16.12 ± 5.96	17.73 ± 5.25	17.30 ± 4.48	5.76[a]
L2	11.00 ± 6.36	11.64 ± 6.42	12.62 ± 5.36	12.32 ± 5.13	1.97
L3	13.91 ± 5.52	13.19 ± 6.05	14.53 ± 5.32	14.40 ± 4.81	1.99
L4	16.88 ± 5.44	16.17 ± 5.41	17.12 ± 4.60	16.31 ± 4.80	1.46
L5	13.61 ± 3.82	13.86 ± 4.49	14.96 ± 3.88	13.87 ± 3.86	2.45
Radial ridge count					
Right	68.99 ± 18.32	68.49 ± 22.11	73.61 ± 17.82	71.66 ± 15.51	2.34
Left	69.06 ± 20.35	69.30 ± 23.10	74.37 ± 18.56	71.87 ± 17.06	2.35
Ulnar ridge count					
Right	32.21 ± 26.56	32.49 ± 26.95	32.44 ± 25.82	27.21 ± 22.72	1.11
Left	23.95 ± 25.04	28.11 ± 24.69	27.90 ± 24.28	24.17 ± 21.63	0.90
Number of triradii of fingers					
Right	7.22 ± 1.82	7.19 ± 1.94	7.28 ± 1.69	7.00 ± 1.61	0.63
Left	6.68 ± 1.89	6.90 ± 1.97	7.00 ± 1.68	6.83 ± 1.64	0.51
Main line index					
Right	9.78 ± 1.79	10.04 ± 1.51	9.58 ± 1.67	9.42 ± 1.73	4.05[a]
Left	8.49 ± 1.71	9.04 ± 1.83	8.58 ± 1.80	8.18 ± 1.84	7.14[a]
a-b Ridge count					
Right	34.80 ± 5.75	35.04 ± 5.64	36.00 ± 4.95	37.44 ± 5.00	7.29[a]
Left	35.13 ± 5.26	36.59 ± 5.29	36.88 ± 5.01	38.03 ± 4.88	8.98[a]

a. Significant.

Puri are true representations of their parental sources. The qualitative similarity in distance configurations can result even when the migration is nonrandom or selective, causing biological compositions quite different from the parental populations but in such a way that it does not distort relative affinities

Table 4. Matrix of Mahalanobis D^2 Distances among the Parental Populations[a]

Parental Population	*JPP*	*VVP*	*VPP*	*AP*
JPP	0.0000	0.4291	1.0710	1.8148
VVP	0.9085	0.0000	0.6628	0.9529
VPP	0.4237	0.7491	0.0000	0.3681
AP	0.9596	0.5653	0.4955	0.0000

a. Values above the diagonal are anthropometric distances and those below the diagonal are dermatoglyphic distances.

Table 5. *r* Values from the Mantel Test of Matrix Correspondence[a]

	Anthropometrics	*Dermatoglyphics*	*Genetic Markers*
Anthropometrics	0.640	0.303	0.184
Dermatoglyphics	0.659	0.118	−0.029
Genetic markers	−0.427	0.400	−0.319

a. The *r* values forming the diagonal are for the correspondence between the parental and the migrant population matrices, whereas the values above the diagonal represent correspondence between distance matrices in the parental populations and the values below the diagonal represent correspondence between distance matrices in the migrant populations.

between the source populations. It is therefore necessary to compare each of the migrant populations with its parental counterpart so that the exact nature of the migration effect can be gauged.

Univariate Comparisons Between Migrant and Parental Populations. So far as genetic markers are concerned, we make the following brief observations [for details see Reddy et al. (1995)]: (1) All 3 migrant populations show significant departures from the parental sources in the gene frequency of *MN* and *HP*A* loci, whereas such departures are additionally seen for *GC* in the VV and for *AK* and *PGD* in the VP; (2) although the *A2* allele (*ABO*) is totally unrepresented in the VVP, suggesting an extremely low frequency, its frequency in the VV, the VVP's migrant counterpart, is 3%; (3) the *B* gene

Table 6. Estimates of $F_{ST} \pm$ Standard Error Indicating the Extent of Discrimination Based on Different Sets of Biological Variables[a]

Population Category[b]	*Anthropometrics*	*Dermatoglyphics*	*Genetic Markers*
Parental			
1	0.0248 ± 0.0033	0.0082 ± 0.0014	0.0098
2	0.0277 ± 0.0035	0.0097 ± 0.0015	
3	0.0181 ± 0.0025	0.0064 ± 0.0011	
Migrant			
1	0.0882 ± 0.0050	0.0084 ± 0.0011	0.0110
2	0.1359 ± 0.0071	0.0103 ± 0.0012	
3	0.0703 ± 0.0058	0.0055 ± 0.0009	

a. The average h^2 values used for computation of F_{ST} are considered close approximations to the population-specific values because they were derived from data on fishermen of the parental areas and others in the same locality.

b. 1, F_{ST} estimates derived by giving due weight to different populations sizes and using appropriate h^2 values (0.481 and 0.532 for anthropometrics and dermatoglyphics, respectively); 2, F_{ST} estimates using h^2's as specified in category 1 but assuming equal population size; 3, F_{ST} estimates assuming complete heritability and equal population sizes.

Table 7. Mean Differences (Parental − Migrant) Between Parental and Migrant Population Pairs for Different Anthropometric Measurements

	VPP		*VVP*		*JPP*	
Measurement	*Mean*	*t Value*	*Mean*	*t Value*	*Mean*	*t Value*
Stature	9.88	1.73	25.77	4.21[a]	17.11	2.17[a]
Sitting height	8.00	2.56[a]	19.03	5.63[a]	15.86	3.46[a]
Head length	1.52	2.39[a]	2.71	3.93[a]	1.62	1.40
Head breadth	−0.69	1.31	−0.76	1.49	0.86	1.20
Nasal height	−2.28	6.68[a]	−1.09	3.10[a]	−2.66	5.76[a]
Nasal breadth	0.47	1.62	0.93	3.03[a]	0.67	1.71
Biacromial breadth	−7.90	4.17[a]	6.21	3.22[a]	14.50	5.86[a]
Bicristal breadth	−9.03	5.78[a]	11.63	8.31[a]	18.93	9.71[a]
Chest girth	−4.66	1.02	23.69	4.78[a]	17.67	2.58[a]

a. Significant.

(*ABO*) is observed 7% less in frequency among both the VV and the JP compared with their parental populations (VVP and JPP); (4) some rare variants (*ADA*6, AK*3*) occur among migrants but not in the parental populations; and (5) the *ACP*C* allele either is absent or has a very low frequency in the parental groups, but it is observed with an average frequency of more than 5% among the migrants.

Anthropometry. The mean differences (parental − migrant) for each measurement and population are given in Table 7. In general, the migrant populations on average are shorter with relatively more brachycephaly and tend to have shorter and broader noses compared with their respective parental populations. On the other hand, the migrant VP had broader shoulders and larger waist and chest circumferences compared with the parental VPP. Interestingly, this pattern was reversed and differences were much larger for the VV and the JP in the sense that they had much less well built shoulders, waist, and chest compared not only with the parental VVP and JPP but also with their migrant neighbor, the VP. These differences were significant in 5 of the 9 body dimensions for the VPP, 6 for the JPP, and in all but 1 dimension for the VVP. The 2-way analysis of variance (ANOVA), in which population and migration are 2 independent factors, however, suggested that when population differences are removed, the migration effect becomes significant ($p < 0.01$) in all the measurements.

Dermatoglyphics. The pattern of migration effect seems somewhat different in the VP on the one hand and in the VV and the JP on the other (Table 8). Although there is a general decrease in finger ridge counts and other

Table 8. Mean Differences (Parental − Migrant) in Different Dermatoglyphic Variables

	VPP		*VVP*		*JPP*	
Variable	*Difference*	*t Value*	*Difference*	*t Value*	*Difference*	*t Value*
Finger ridge count						
R1	−0.12	0.19	−0.89	1.06	−0.81	1.28
R2	1.27	2.01[a]	−1.33	1.69	−0.44	0.59
R3	0.23	0.44	−1.27	1.78	−0.04	0.06
R4	0.35	0.59	−1.19	1.66	−0.10	0.16
R5	0.69	1.27	−0.79	1.30	−0.27	0.48
L1	0.89	1.40	−0.60	0.73	−1.22	1.86
L2	1.55	2.38[a]	−2.15	2.68[a]	−0.67	0.86
L3	0.46	0.77	−1.55	2.04[a]	−0.54	0.77
L4	0.44	0.81	−1.29	1.78	−0.62	0.92
L5	0.78	1.69	−0.92	1.57	−0.69	1.32
Radial ridge count						
Right	2.22	1.04	−4.89	1.64	−1.40	0.56
Left	4.01	1.77	−5.18	1.70	−3.20	1.25
Ulnar ridge count						
Right	5.09	1.76	−4.20	1.22	−1.64	0.50
Left	0.55	0.20	−5.18	1.49	−4.38	1.39
Number of triradii of fingers						
Right	0.35	1.77	−0.19	0.80	−0.03	0.14
Left	0.16	0.80	−0.36	1.43	−0.32	1.46
Main line index						
Right	0.30	1.48	0.91	4.04[a]	1.19	4.30[a]
Left	0.79	3.50[a]	0.84	3.36[a]	0.96	4.10[a]
a-b Ridge count						
Right	−0.39	0.61	−3.33	4.38[a]	−3.58	5.32[a]
Left	−0.81	1.26	−3.51	4.83[a]	−4.91	7.88[a]

a. Significant.

quantitative measures in the VP, there is, in fact, a general increase in the other 2 migrant groups. However, the mean differences are significant only in the ridge counts of the right and left index fingers and in the left main line index for the VP. In the VV and the JP the mean differences are highly significant in the main line index and a-b ridge counts on both hands. In addition, marginally significant differences are observed in the mean ridge counts of the left index and third finger. The 2-way ANOVA suggested that when population differences are removed the migration effect becomes highly significant in the 4 palmar variables but in none of the 16 finger variables.

Overall Effect of Migration: Multivariate Analysis. The multivariate ANOVA with population and migration status as 2 factors suggested a highly significant ($p = 0.000$) overall migration effect in both anthropometric di-

Table 9. Multivariate ANOVA Results on the Effect of Migration as Reflected in Anthropometric and Dermatoglyphic Variables

Factor	*Wilks λ*	*F Value*[a]	*d.f.*
Anthropometrics			
Population	0.6621	23.20	18, 1,824
Migration	0.8005	25.25	9, 912
Population × migration	0.7886	12.77	18, 1,824
Dermatoglyphics			
Population	0.8915	3.15	40, 2,134
Migration	0.8685	8.08	20, 1,067
Population × migration	0.9280	2.03	40, 2,134

a. All F values are significant at $p = 0.000$.

mensions and dermatoglyphics (Table 9). The degree of population discrimination is also similarly significant after the migration effect is removed. On the other hand, the interaction term between population and migration is also significant, implying that the pattern of population heterogeneity is different in migrant and parental populations. Conversely, the interaction can also be inferred as the migration effect being significantly different in the 3 populations.

Pattern of Variation among All Groups: Combined Analysis. To visualize the relative positioning of the migrant and parental populations in the multivariate space, we performed a multiple discriminant analysis using data on both the migrant and parental populations. The multivariate test statistic (Wilks λ) suggests significant discrimination among the groups in both anthropometric (Wilks $\lambda = 0.4542$; $F = 16.8$; $p = 0.000$) and dermatoglyphic variables (Wilks $\lambda = 0.7141$, $F = 3.5$; $p = 0.0001$). The plots of group centroids not only suggest the greater dispersion of migrant populations among them compared with the parental populations but also depict a clear separation of each of the migrant populations from its parental source in both anthropometric and dermatoglyphic variables (Figure 2). That the migrant groups form a cluster separated from the parental groups who form a cluster themselves is also apparent from the principal coordinates analysis of the genetic distances (Figure 3). The distance matrices of these populations based on the 3 sets of variables (Table 10) are complementary to these observations; the average distance between the migrant and parental population pairs is systematically larger than the average interpopulation distance of either migrants or parental groups. The only exception to this is the average anthropometric distance of migrants. However, the cluster analysis of the distances results in 2 distinct clusters separating migrants from parental populations in all 3 sets.

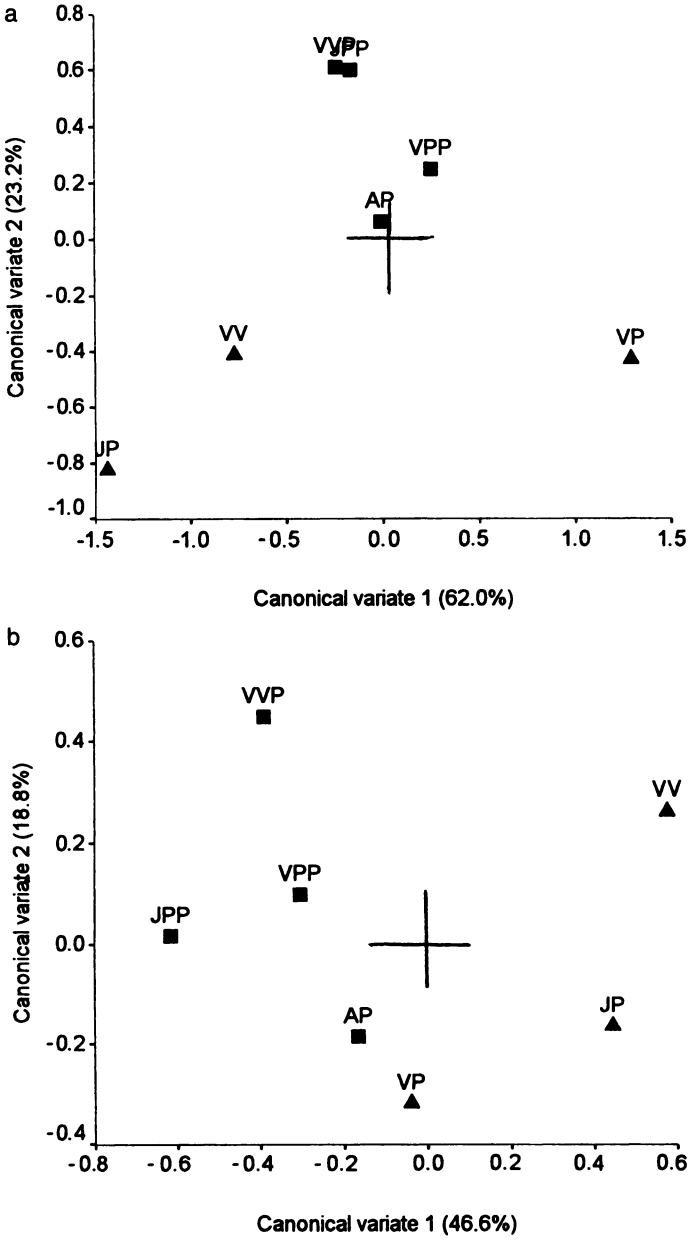

Figure 2. Plots of group centroids of the 7 fishermen groups (migrant and parental) based on the discriminant analysis of (a) the anthropometric measurements and (b) the quantitative dermatoglyphic variables. Triangles, migrants; squares, parental populations.

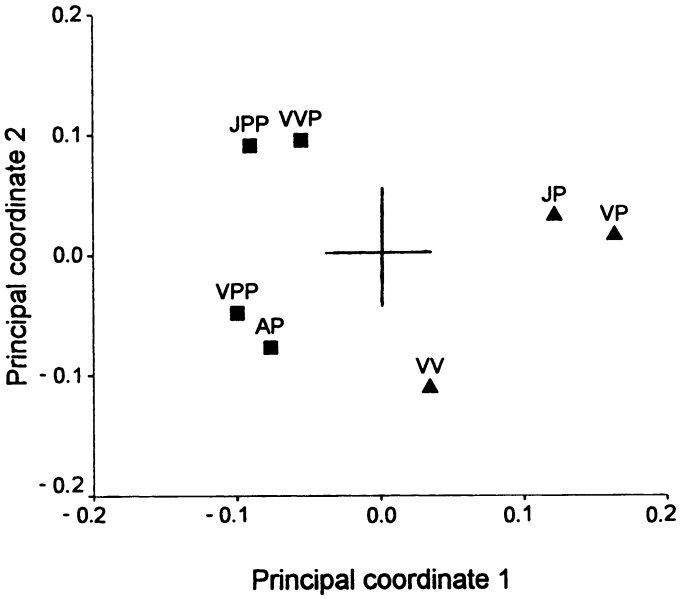

Figure 3. Plot of group centroids of the 7 fishermen groups (migrant and parental) based on the principal coordinate analysis of the genetic distance matrix. Triangles, migrants; squares, parental populations.

Discussion

From the analysis of the results it is apparent that the distance configuration of the parental populations is qualitatively similar to that of the migrant fishermen of Puri in each of the 3 sets of variables, and therefore the results validate the hypothesis that the distance configurations of the Puri populations reflect ethnohistorical or geographic affiliations. However, this need not necessarily suggest that the migrant populations are true biological representations of their parental groups. This is evident from the fact that there are significant differences between parental populations and their migrant counterparts in each of the 3 sets of variables. Both the univariate and the multivariate analyses of these differences clearly establish the migration effect as highly significant, although this differentiation was relatively marked for the anthropometric variables.

The earliest of the migrant groups in Puri is only 4 generations old; hence the role of genetic drift in the observed differentiation between the migrants and their parental counterparts can be safely ruled out. Furthermore, the effective population sizes of the 3 migrant groups are estimated to be 1,662, 944, and 238 for the VP, VV, and JP, respectively (Reddy 1984), with a coefficient of breeding isolation N_{em} (Lasker and Kaplan 1964) far above

Table 10. Distance Matrices of the Fishermen Populations Based on 3 Sets of Variables[a]

	VP	*VV*	*JP*	*VPP*	*VVP*	*JPP*	*AP*
Genetic markers[b]							
VP	0.0000						
VV	0.0731	0.0000					
JP	0.0444	0.0569	0.0000				
VPP	**0.0931**	0.0695	0.0855	0.0000			
VVP	0.0854	**0.0726**	0.0725	0.0652	0.0000		
JPP	0.0979	0.0772	**0.0727**	0.0586	0.0568	0.0000	
AP	0.0887	0.0599	0.0782	0.0522	0.0624	0.0615	0.0000
Anthropometrics[c]							
VP	0.0000						
VV	4.3386	0.0000					
JP	7.7353	1.0338	0.0000				
VPP	**1.7570**	1.6164	4.4245	0.0000			
VVP	3.4885	**1.4353**	3.6994	0.5579	0.0000		
JPP	3.3236	1.7089	**3.9020**	0.9164	0.3838	0.0000	
AP	2.5258	1.3769	3.4553	0.3275	0.7804	1.5423	0.0000
Dermatoglyphics[c]							
VP	0.0000						
VV	0.7864	0.0000					
JP	0.7499	0.5340	0.0000				
VPP	**0.5504**	1.0085	0.9886	0.0000			
VVP	0.8001	**1.0758**	1.3131	0.4123	0.0000		
JPP	0.8627	1.7185	**1.3248**	0.6650	0.5673	0.0000	
AP	0.4457	0.9584	0.7855	0.3371	0.7497	0.7751	0.0000

a. Bold values are distances between pairs of parental and migrant counterparts.
b. Edwards and Cavalli-Sforza (1972) distance.
c. Mahalanobis D^2.

50 (except for the JP, who have $N_{em} = 54$); thus random genetic drift does not seem to be a significant force in the genetic history of these populations. These observations, based on demographic evidence, are corroborated by a test of the mutation-drift hypothesis (Fuert et al. 1977); the expected variances of heterozygosities over 11 loci (Table 11) are about twice the observed value, and therefore the effect of drift can be safely negated. Furthermore, the effect of drift on quantitative polygenic traits such as anthropometrics or dermatoglyphics is expected to be negligible.

This leaves us with 2 other plausible alternative factors that might explain the observed biological differentiation: external gene flow and a founder effect. Some earlier studies (Crawford 1975; Crawford et al. 1976) have suggested greater external gene flow (e.g., among the Tlaxcaltecans) into migrants compared with resident groups. Although the formal exchange of mates between fishermen and the neighboring Oriya populations is totally absent, the possibility of unrecognizable gene flow from external sources cannot be ruled out. The fishermen settlements of Puri are a hub of economic activity,

Table 11. Mean and Observed and Expected Variances of Heterozygosities of the 11 Loci Studied in the 3 Migrant Populations of Fishermen

	VP	*VV*	*JPP*
Average heterozygosity (H)	0.3200	0.3140	0.3010
Variance of H (observed)	0.0248	0.0234	0.0266
Variance of H (expected)	0.0508	0.0507	0.0505

especially during the fishing season, and involve a large number and variety of nonfishermen. The customary laws of these fishermen allow divorce and remarriage, and the norms governing sexual behavior seem to be somewhat favorable to the possibility of gene flow. Conjecturally, at least, one cannot ignore gene flow as also being responsible for observed differentiation, especially because of the appearance of some rare variants in the migrants that are not found in their respective parental groups. It is not known, however, if the surrounding populations possess these rare variants, because none of those populations have been studied genetically. The magnitude of the effect of external gene flow is more difficult to visualize and/or to estimate for the quantitative dermatoglyphic features and the anthropometrics.

The model of Harpending and Ward (1982) for genetic markers and its extension to quantitative traits by Relethford and Blangero (1990) offer some useful insights in this respect. Both groups have, in fact, found encouraging results in their application of these models in several case studies. One indicator that they found useful in examining the problem of gene flow was the regression of average heterozygosity on the genetic distance from the centroid. As per their model, the average heterozygosity of the ith population (H_i) should be equal to the overall mean heterozygosity of the entire population, H_T (in this case, all fishing groups) multiplied by $(1 - r_{ii})$, where r_{ii} is the genetic distance of a particular population from the centroid. If the gene flow from outside the region varies in amount from population to population, this linear relationship no longer holds. Isolated populations will be less heterozygous than the linear prediction, whereas populations receiving more gene flow from outside will be more heterozygous. The theory indicates that we might gain some insight by examining outliers.

The results of the application of Harpending and Ward's (1982) and Relethford and Blangero's (1990) models to our data are presented in Figures 4 and 5 for the 3 sets of variables. Overall, from Figures 4 and 5 it emerges unmistakably that it is the migrant populations that fall above the regression line, indicating a greater degree of heterozygosity, and the parental populations that are generally placed below the regression line, indicating relatively more isolation, hence less heterozygosity. For the anthropometric measurements, although the VP and the JP are close together and are outliers above the regression line, the remaining populations lie just below the regression line, with the AP lying somewhat farthest away of all. For the der-

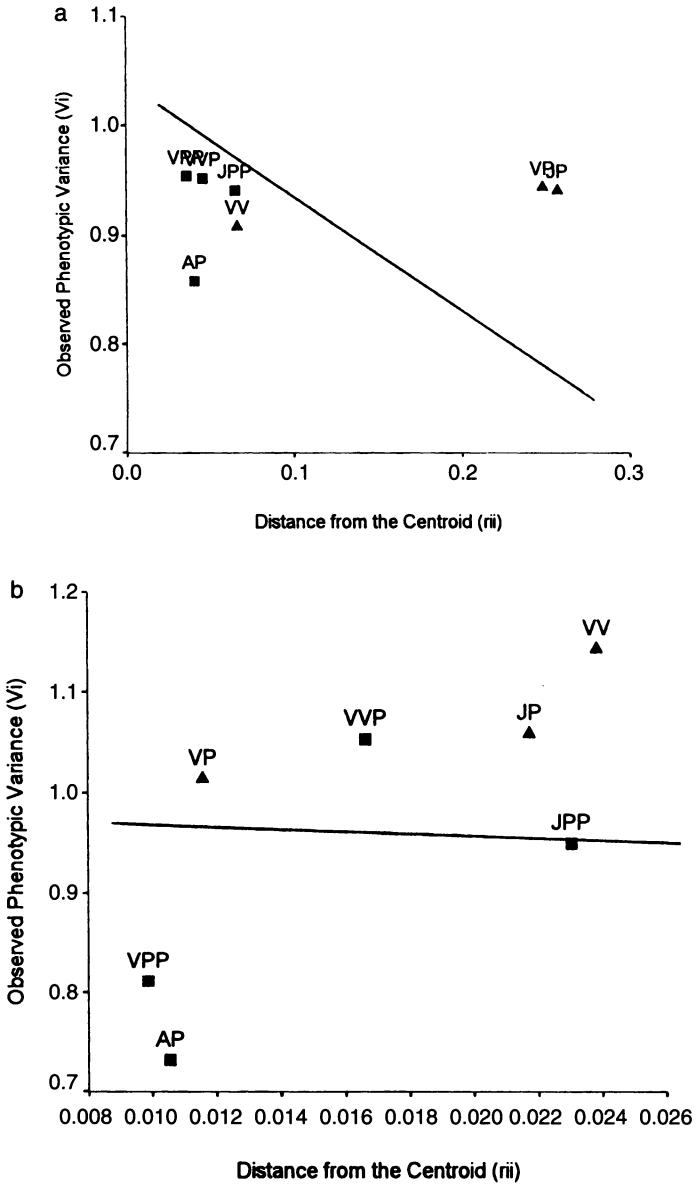

Figure 4. Plots of observed mean phenotypic variance versus (a) anthropometric distance and (b) dermatoglyphic distance from the centroid of the 7 fishermen groups and the theoretical regression line. Triangles, migrants; squares, parental populations.

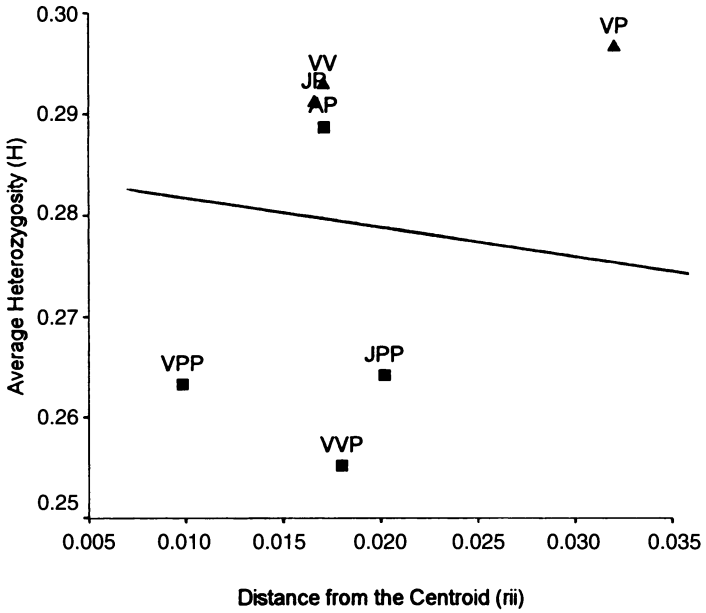

Figure 5. Average heterozygosity versus genetic distance of the 7 fishermen groups from the gene frequency centroid. Triangles, migrants; squares, parental populations.

matoglyphic traits, although the migrant VV and JP lie above the regression line, the parental VPP and AP lie below the regression line as outliers. The remaining 3 groups all lie above but close to the regression line. For the genetic markers (Figure 4c) the migrant and parental populations are clearly placed above and below the regression line and are somewhat removed from the vicinity of the line, suggesting a clear possibility of external gene flow into migrants and a greater degree of isolation of the parental populations.

We noted earlier that the establishment of a population by relatively few founders can more easily account for enhancement of gene frequency variation between new and old populations than random fluctuations in the populations of reasonable size (Cavalli-Sforza 1963). We think that in the Puri situation a founder effect in the composition of migrant populations, implying a selective, nonrandom migration of individuals or families, is also probable. However, we do not know the number of founders who came to Puri initially and established populations, although the available information suggests that the founders were certainly few in number. Given this scenario, it is difficult to visualize what would have guided the selective sample of those initial migrants, who brought with them gene pools or biological compositions that were significantly different from their source populations, especially in the cases of genetic markers and dermatoglyphics, whose func-

tional relevance for the groups under study is not known or even adequately understood otherwise.

Certain plausible explanations, however, seem to be in order for the body dimensions when one considers the occupational and migrational backgrounds of the Puri fishermen. Although the migrants of each population are relatively shorter, are somewhat brachycephalic, and had shorter and broader noses compared with their parental counterparts, there are certain differences among the groups with reference to the breadth measurements (biacromial breadth, bicristal breadth, and chest girth), which reflect body build. The migrant VP have significantly larger means for these 3 dimensions, indicating strong body build, whereas the VV and the JP have much smaller means, indicating weaker body build, compared with their respective parental populations.

The migration histories of Puri fishermen suggest that the founders of the VP initially arrived around 1950 because of the serious and extended drought conditions prevalent at that time in their parental areas, which acted as a strong push factor. The founders were forced to explore a new and productive niche not only for fishing but also for marketing their fish. In fact, these people had experimented with a couple of other places before finally reaching Puri. Such an adventurous mission to totally unknown areas probably needed people who the group of founders as a whole thought would be able to stand the test, through their past experience and acquaintance with their fellow fishermen. The people with a robust body composition, as noted in the VP migrants, probably had been more successful or suitable fishermen and hence constituted the group of founders.

On the other hand, although the VV and the JP are also reported to have migrated for economic reasons, no strong push factor was cited, except that the temple town of Puri has been a big religious and tourist attraction. Many of these fishermen engage in subsidiary occupations and earn money by helping tourists and pilgrims in sea bathing, by selling certain petty items of ornamental nature (such as beads and coral), and by working in hotels and as rickshaw pullers. It may not be surprising that the migrants might have constituted people who could not cope with the vagaries of sea fishing expeditions and the demanding physical exertion needed to operate the nonmechanized boats by the active fishermen in the parental areas. Although the stronger and more successful VP fishermen migrated to Puri, the less well built and less successful fishermen probably did so for the other 2 groups, probably because of qualitatively different push and pull factors that prompted the initial migrations. Strengthening these conjectures is the fact that the boats of the VP are about 3 times larger than those of the VV and the JP in Puri. Although most VP men and women actively engage in fishing and other related activities and go much farther out to sea, the members of the other 2 groups fish in shallow waters with fishing expeditions of much shorter duration. The VV and JP fishermen in fact acknowledge that the VP are much more expert in

fishing and that they cannot compete with them. This has also led to an occupational shift for many VV and JP fishermen into nonfishing activities. The foregoing observations seem plausible, especially because not only are there no differences in boat size in their parental areas but also there are no significant mean differences in body dimensions, particularly the 3 breadth measurements that showed highly significant differences among the Puri groups.

Given this discussion and implicit in the occupational differences among the Puri groups is the probable role of phenotypic plasticity that could have been equally responsible for the observed differentiation of the migrant groups. Such a phenomenon has been recorded in other situations, for example, among Algonquian-speaking Amerindian populations (Jantz and Meadows 1995). The difference in the direction of selective migration coupled with phenotypic plasticity might have accentuated the anthropometric distances between the migrant populations of Puri.

In conclusion, the roles of external gene flow and founder effects may have been important in an intricate way in diversifying the migrants from their parental counterparts, with an additional contribution of phenotypic plasticity for the body dimensions. However, the change in biological composition of the migrants is such that it has not affected the configuration of interpopulation distances in Puri vis-à-vis their parental groups. Their distance configurations resemble the pattern of their parental populations. It is, however, tempting to invoke the possible role of founder effects in further diversifying the gene pools of the splinter groups in Puri in future generations, especially given that 2 of the 3 groups (VV and JP) are small in size and that the cultural norms and resource competition in the new habitat promote reproductive barriers more effectively between the migrant groups.

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