

Population structure and genetic differentiation among the substructured Vysya caste population in comparison to the other populations of Andhra Pradesh, India

N. LAKSHMI†, D. A. DEMARCHI‡, P. VEERRAJU† and T. V. RAO†

† Department of Human Genetics, Andhra University, Visakapatnam, India

‡ Departamento de Bioquímica Clínica, Facultad de Ciencias Químicas, Universidad Nacional de Córdoba, Córdoba, Argentina

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Summary. *Objectives.* The present paper focuses on the study of the patterns of genetic microdifferentiation among one of the substructured caste populations of Andhra Pradesh, namely Vysya, with reference to 17 other Telugu speaking populations from the same region of India.

Subjects and methods. A total of 302 individuals from the three Vysya subgroups (101 of Arya Vysya, 100 from Kalinga Vysya and 101 from Thrivarnika) were typed in 17 blood groups and protein polymorphisms. Nei's gene diversity analysis, as well as neighbour-joining tree and UPGMA cluster diagrams, derived from standard genetic distances, R-matrix analysis and a regression model for investigating the patterns of external gene flow and genetic drift due to isolation under the island model, were done at two levels: (1) considering only the three Vysya populations and (2) considering common loci among 20 populations of Andhra Pradesh.

Results: Seven of the 17 systems investigated were found to be monomorphic among all the three Vysya groups. The UPGMA tree and bidimensional scaling of the D^2 distances derived from R-matrix analysis show a very distinct cluster of Vysya populations. Application of the model of regression of average heterozygosity versus the distance of populations from the centroid shows the three Vysya populations placed as clear outliers above the theoretical regression line.

Conclusions: Different approaches employed in this study give support to the hypothesis of different origin and/or demographic story for the three Vysya groups compared with other populations of Andhra Pradesh.

1. Introduction

India is a land of enormous human genetic, cultural and linguistic diversity (Roychoudhury, Roy, Dey *et al.* 2000). India is subdivided by 20 major languages, hundreds of dialects, religion, almost innumerable castes and tribes, offering a unique opportunity for the study of the process of subdivision and their evolutionary consequences (Puppala and Crawford 1996). The social structure of the Indian population is governed by hierarchical caste system. In the Hindu caste system, each caste belongs to one of the five main classes/varnas, namely, Brahmins (priests), Kshatriya (warriors), Vyshya (business community), Sudra (rest of the castes) and Pancham (tribes). The caste structure is fairly rigid, and each caste remains as an endogamous unit, although the levels of endogamy vary substantially (Malhotra and Vasulu 1993). In India, there are nearly 5000 well-defined endogamous populations (Thangaraj, Ramana and Lalji Singh 1999). India is known for its unique population structure, which is characterized by subdivision of its population into a number of hierarchical caste, tribe and religious groups. These general features of population structure apply to each linguistic region of the country, while language forms a

strong barrier to gene flow between such regions even among the castes of same or similar hierarchy.

The State of Andhra Pradesh with its 70 million people, organized into several endogamous castes, tribes and religious groups, presents enormous variety of populations, sociocultural patterns and organization. These castes and tribes are also known to present extreme variation in size and nature of sub-structuring. Some of the major castes show number of endogamous subdivisions within them but with non-overlapping geographic distributions. Furthermore, populations of Andhra Pradesh are known to practise consanguineous marriages with high rates of village endogamy. This will lead to reduction in effective population size, creating breeding isolates within apparently single endogamous castes and subtribes. This will provide situations conducive for rapid genetic microdifferentiation among such populations. Therefore, study of such substructured populations along with the others may help in understanding the mechanisms behind the pattern of genetic variation observed in a particular region. The present paper focuses on the study of genetic microdifferentiation among one of the substructured caste populations of Andhra Pradesh, namely Vysya, with reference to 17 other populations from this Telugu-speaking Andhra Pradesh.

1.1. Population background

The Vysyas are third in rank among the four-fold Hindu caste hierarchy, next to Brahmins and Kshatriyas. There are three endogamous subcastes within them: the Arya Vysyas, the Kalinga Vysyas and the Thrivarnikas. These populations belong to a common stock, despite their separate caste identities and present sociocultural differentiation (Sherring 1881). Of the three, the Arya Vysyas are popularly known as Gavara Komatis in Andhra Pradesh and with different synonyms such as Agarwal, Bania, Gupta, Chetty, etc. in other provinces of the country (Gupta 1988). They are a community of traders and businessmen, strict vegetarians in food habits, practise consanguineous marriages and are distributed mostly in towns and cities. The Gavara Komati occupy the highest position in the social hierarchy of the trading communities, followed by Thrivarnikas, and Kalinga Komati, the latter being regarded as the lowest in the social scale.

The Kalinga Vysyas live in the old Kalinga country which extended roughly from Visakapatnam in Andhra Pradesh to contiguous areas in Orissa state. They are the second largest section of Vysyas, their number running into several thousands. Like the Arya Vysyas, Kalinga Vysyas are known for trade and business enterprise as their core activity. Interestingly, they are non-vegetarian by diet, but practise consanguineous marriages and worship deities belonging to both Vaishnavite and Saivite sects, like the Arya Vysyas do (Census of India 1981).

Thrivarnikas call themselves as Thrivarnika Vaishnavites. They claim that their community came into existence during 11th century AD at the time of greater Vaishnava reformer Sri Ramanujacharya. There is, however, a controversy regarding their origin. They follow Brahminical customs more scrupulously than others do, except that they are non-vegetarians by diet. The major economic resource for the Thrivarnikas is trade. Their principal occupation is business in gold, silver and glass. They consider themselves only next to Arya Vysyas in social hierarchy. Although economically affluent, most of them have only informal education. They are found mostly in big towns and cities in Andhra Pradesh, besides a large number of families in Chennai. Their number is said to be in the vicinity of about 15000 individuals.

The Thrivarnikas can be identified with their facial markings known as 'namam'. Their namam is U-shaped with white and red markings. They are strictly an endogamous group. They attribute that their religious creed is distinct and in no way similar with Komati. They differ remarkably with the Gavara Komati in the observance of various customary practices.

The 17 other Telugu-speaking populations for which comparative marker data were available on seven common polymorphic loci, represent wide socio-economic network of the region. These populations represent upper castes like Brahmins; middle-ranking castes such as Reddy, Kamma, Kapu; low-ranking castes such as Pattusali, Jalari, Bestha, Relli, etc.; traditionally untouchable scheduled castes such as Mala and Madiga; and tribal group such as Pardhi (Gopalam and Rao 1981, Naidu, Mohrenweiser and Neel 1985, K. P. Lakshmi, personal communication, Char, Lakshmi, Gopalam *et al.* 1989, S. Praveena, personal communication, Ramesh and Veeraju 1992, 1996a, b, 2001).

2. Subjects and methods

A total of 302 blood samples were collected from the unrelated adults of the three Vysya groups (101 of Arya Vysya, 100 from Kalinga Vysya and 101 from Thrivarnika) distributed in the three north coastal districts of Andhra Pradesh, namely Visakapatnam, Vizianagaram and Srikakulam. Subjects were chosen only from the respective three municipalities of those three districts, except for Kalinga Vysyas for whom the samples were also collected from Bobbili municipality of Vizianagaram district.

About 3 mL of blood was drawn by venepuncture using disposable syringe into sterile, labelled test tubes containing EDTA. The samples were stored in a thermocol box containing ice and transported to the laboratory on the same day. Plasma and cells were separated. Plasma was stored at -20°C until use. One drop of packed cells was taken to test A1A2BO and Rh (D) blood groups on the same day of collection. The remaining cells were haemolysed. The haemolysate was subjected to electrophoresis for G6PD and HB the next day as the G6PD enzyme is unstable. The remaining haemolysate was stored at -20°C until use.

Red cell enzymes were determined on starch and starch agarose gels. The methods opted for different systems were as follows: 6PGD, G6PD, LDH and MDH (Harris and Hopkinson 1978); ACP and ESD (Karp and Sutton 1967); PGM2 and SOD (Spencer, Hopkinson and Harris 1964); glyoxalase (Pflugshaupt, Scherz and Butler 1978); haemoglobin (Bhatia 1986). HP and CP were typed by disc gel electrophoresis (Clark 1964). Alb and Tf were typed by vertical polyacrylamide gel electrophoresis (Kitchin and Bearn 1966).

2.1. Statistical methods

Gene frequencies were calculated by gene counting, except for ABO, and Rh (D), for which maximum likelihood estimates were calculated using the program MAXIM. A chi-square goodness-of-fit test was used to test the fit of the observed genotype frequencies to those expected under Hardy-Weinberg equilibrium. Nei's gene diversity analysis (Nei 1973) as well as neighbour-joining and UPGMA cluster diagrams, derived from standard genetic distances (Nei 1972), were accomplished by using NJBAFD program, supplied by Dr N. Takezaki. These analyses were done at two levels: (1) considering only the three Vysya populations and the 12 polymorphic

genetic loci and (2) considering seven common loci among 20 populations of Andhra Pradesh.

2.2. *R*-matrix analysis and the regression model of Harpending and Ward (1982)

D^2 distances derived from *R*-matrix analysis (Harpending and Jenkins 1973) were employed for multidimensional scaling (MDS) (Kruskal 1964), collapsing into two dimensions on which the 20 populations are projected to gauge the genetic affinities. MDS scaling was accomplished using the NTSYS 1.8 package (Rohlf 1993).

For gaining insights into the patterns of external gene flow and genetic drift due to isolation under the island model, we employed the Harpending and Ward (1982) regression model. The model predicts that the average heterozygosity of the population (H_i) should be equal to the overall mean heterozygosity of the entire population (in this case, a group of populations from Andhra Pradesh with common recent origin) H_T , multiplied by $(1 - r_{ii})$, where r_{ii} is the genetic distance from gene frequency centroid. If gene flow from outside the region varies in amount from population to population, this linear relationship no longer holds. Isolated groups will be less heterozygous than the linear prediction, hence lie below the theoretical regression line, whereas populations receiving more gene flow from outside will be more heterozygous and lie above the line. Thus, the outliers above and below the theoretical regression line may give some insights into the population structure.

3. Results

3.1. Genetic polymorphism and differentiation in the substructured Vysya

Out of the 17 loci tested, 10 were polymorphic in at least one of the three Vysya groups. The allelic frequency of the 10 polymorphic loci is presented in table 1. LDH, MDH, PGM2, SOD, HB, CP and ALB were found to be monomorphic among all the three Vysya groups. Several deviations from Hardy-Weinberg equilibrium reach statistical significance because of an excess of homozygotes: among the Arya for the PGM1 system ($p < 0.05$), among the Kalinga for the ACP and GLO ($p < 0.01$), and among the Thrivarnikas for the ESD ($p < 0.05$). The South Indian populations, especially those from Andhra, are known for the practice of consanguineous marriages, amongst the highest in the world (Sanghvi 1966, Cavalli-Sforza and Bodmer 1971). Therefore, the observed excess of homozygotes for several systems in the present context may be attributable to inbreeding.

With reference to the polymorphic loci, the following salient features emerge in comparison to the other Telugu-speaking populations studied earlier (Lakshmi, unpublished results):

- (1) While allele A could not be traced among the Thrivarnikas, it is observed with negligible frequency among the other two groups.
- (2) The 6PGD*C allele is completely absent in Thrivarnikas.
- (3) G6PD deficiency is observed only among the Kalinga Vysyas but with highest frequency (8%) compared with any other population from Andhra Pradesh.

The results of the gene diversity analysis for the Vysyas are presented in table 2. It is apparent that the levels of within group diversity are very low for the studied loci, particularly for 6PGD, G6PD, and TF. The largest proportion of variation (about 0.50) is observed at the ESD, PTC, GLO and ACP1 loci. Arya Vysyas tend to show slightly higher heterozygosity at most of the loci compared with the other two populations, which is reflected in the average heterozygosity as well.

Table 1. Allelic frequencies at 10 polymorphic loci among the three Vysya groups from coastal Andhra Pradesh.

Locus	Allele	Arya	Kalinga	Thrivarnika
ABO	A1	0.0303	0.0050	0.0000
	A2	0.0104	0.0050	0.0000
	B	0.1926	0.1690	0.2357
	O	0.7667	0.8210	0.7643
Rh	D	0.8593	0.9000	0.9005
	d	0.1407	0.1000	0.0995
ACP	ACP*A	0.2600	0.2228	0.3850
	ACP*B	0.6800	0.7446	0.5700
	ACP*C	0.0600	0.0326	0.0450
ESD	ESD*1	0.4839	0.6605	0.5500
	ESD*2	0.5161	0.3395	0.4500
6PGD	6PGD*A	0.9850	0.9900	1.0000
	6PGD*C	0.0150	0.0100	0.0000
GLO	GLO*1	0.4780	0.4350	0.3958
	GLO*2	0.5220	0.5650	0.6042
PGM1	PGM1*1	0.6000	0.7806	0.7680
	PGM1*2	0.4000	0.2194	0.2268
	PGM1*3	0.0000	0.0000	0.0052
HP	HP*1	0.1414	0.2525	0.2050
	HP*2	0.8586	0.7474	0.7950
TF	TF*B	0.0000	0.0050	0.0000
	TF*C	0.9900	0.9800	1.0000
	TF*D	0.0100	0.0150	0.0000
G6PD	B	1.0000	0.9184	1.0000
	b	0.0000	0.0816	0.0000

Table 2. Locus-wise and population diversity estimates along with the average values.

Locus	Within-group diversity			Nei's diversity estimates		
	Arya	Kalinga	Thrivarnika	H_T	H_S	GST
ABO	0.377	0.298	0.362	0.346	0.344	0.005
Rh	0.243	0.181	0.180	0.201	0.200	0.004
ACP	0.469	0.397	0.527	0.472	0.462	0.021
ESD	0.502	0.451	0.497	0.492	0.481	0.022
6PGD	0.030	0.020	0.000	0.017	0.016	0.005
GLO	0.502	0.494	0.481	0.492	0.490	0.005
PGM1	0.482	0.344	0.361	0.408	0.394	0.034
HP	0.244	0.379	0.328	0.320	0.315	0.013
TF	0.020	0.040	0.000	0.020	0.020	0.006
G6PD	0.000	0.151	0.000	0.053	0.050	0.056
Average	0.287	0.276	0.274	0.282	0.277	0.017

Decomposition of the total diversity (H_T) into within (H_S) and between ($H_T - H_S$) components (GST) suggests that only about 1.7% of the total diversity is due to differences between populations while the rest is between individuals within populations.

Nei's (1972) standard genetic distances between pairs of Vysya populations suggest relatively greater differentiation of the Kalinga Vysyas from Arya Vysyas

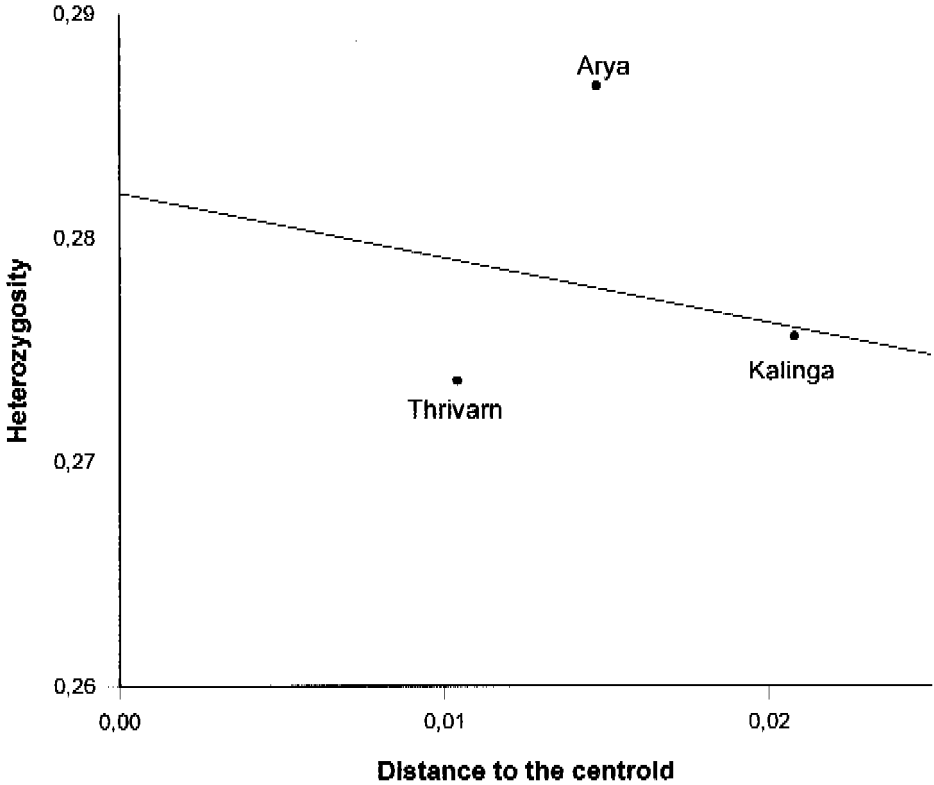


Figure 1. Regression of average heterozygosity on the gene frequency centroid of the three Vysya populations, based on 10 polymorphic loci.

(0.011) as well as from Thrivarnikas (0.008), whereas the lowest distance is found between these two populations (0.006).

The results of application of Harpending and Ward (1982) regression model to the genetic data (figure 1) suggest that the Arya Vysya with a relatively greater heterozygosity is placed above the theoretical line as an outlier, suggesting above average gene flow from outside the Vysyas whereas the other two populations lie below but relatively closer to the line. However, the distance from the centroid for the Kalinga Vysyas is somewhat higher than for the other two groups, suggesting probably larger effect of stochastic processes.

3.2. Genetic differentiation of Vysyas with reference to other Telugu-speaking populations

The comparative data on 7 of the 12 loci earlier studied for 17 other populations from this region were used for comparative analysis along with the Vysyas. Nei's (1973) gene diversity analysis performed separately for the three Vysyas and for all the 20 groups suggest a relatively lower degree of differentiation in the local Vysya populations ($G_{ST} = 0.011 \pm 0.003$) when compared with the populations of the region as a whole ($G_{ST} = 0.018 \pm 0.002$), consistent with the hierarchy of populations involved.

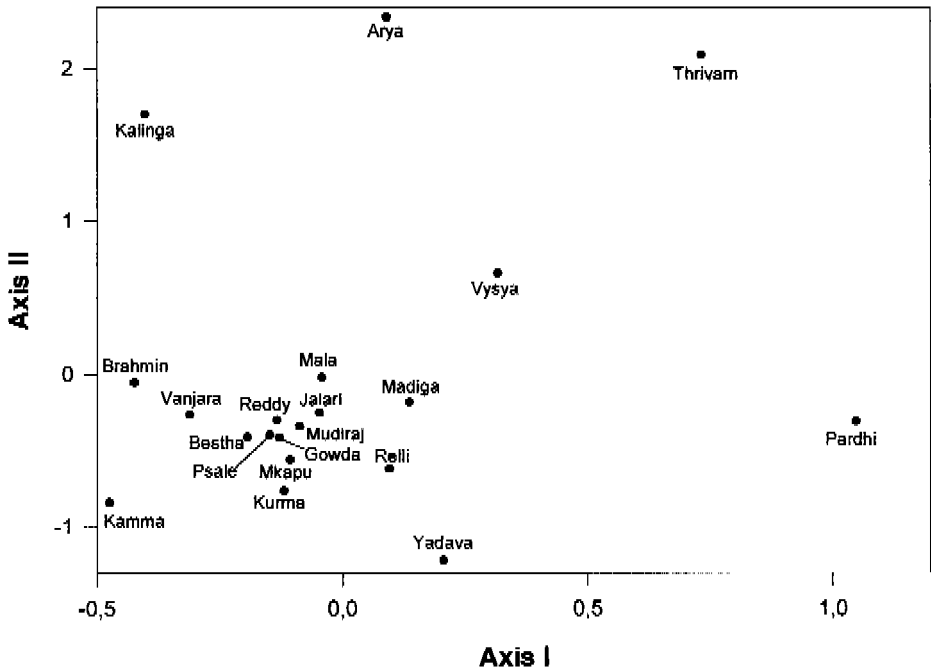


Figure 2. Projection of 20 Telugu populations onto the two-dimensional space based on multidimensional scaling of the D^2 values obtained from R-matrix analysis of seven loci.

In order to gauge the genetic affinities of the Vysyas to other populations in the region R-matrix analysis of Harpending and Jenkins (1973) and the genetic distances D^2 obtained from this analysis were subjected to the multidimensional scaling (Kruskal 1964). After 49 iterations, a stress of 0.114 was achieved which is, according to Kruskal's criteria, good and interrelations among populations can adequately be reduced to two dimensions. The population relationships thus obtained are depicted in figure 2. From this diagram it can be seen that the Vysya populations are clearly differentiated from the rest of Telugu-speaking populations, most of whom are placed closely together with few exceptions. While the Pardhi is distinctly placed, far removed from all other groups, the middle-ranking Yadava and Kamma also lie outside this compact cluster. However, the UPGMA (figure 3) tree constructed based on the Nei's standard distances among the 20 groups suggest much more rational and clear clusters of populations that are broadly consistent with known ethnohistorical and social backgrounds. For example, not only are the four Vysya groups forming a distinct cluster, separated from all other groups, but also others like Pardhi and Brahmin, the scheduled castes Mala and Madiga, the lower castes Vanjara, Bestha and Kurma and others like Pattusale, Reddy and Jalari, Gowda, Munnuru Kapu and Mudiraj each form as rational subclusters.

Figure 4 depicts relationship between mean per locus heterozygosity and the distance from the centroid (r_{ii}) of the 20 populations of Andhra Pradesh. Here again, the three Vysya groups are placed as clear outliers above the theoretical regression line and quite distant from the centroid, suggesting both the effects of gene flow from outside and of the stochastic processes due to subsequent isolation. On the other hand, Munnuru Kapu, Relli, Kurma, Kamma and Yadava can be

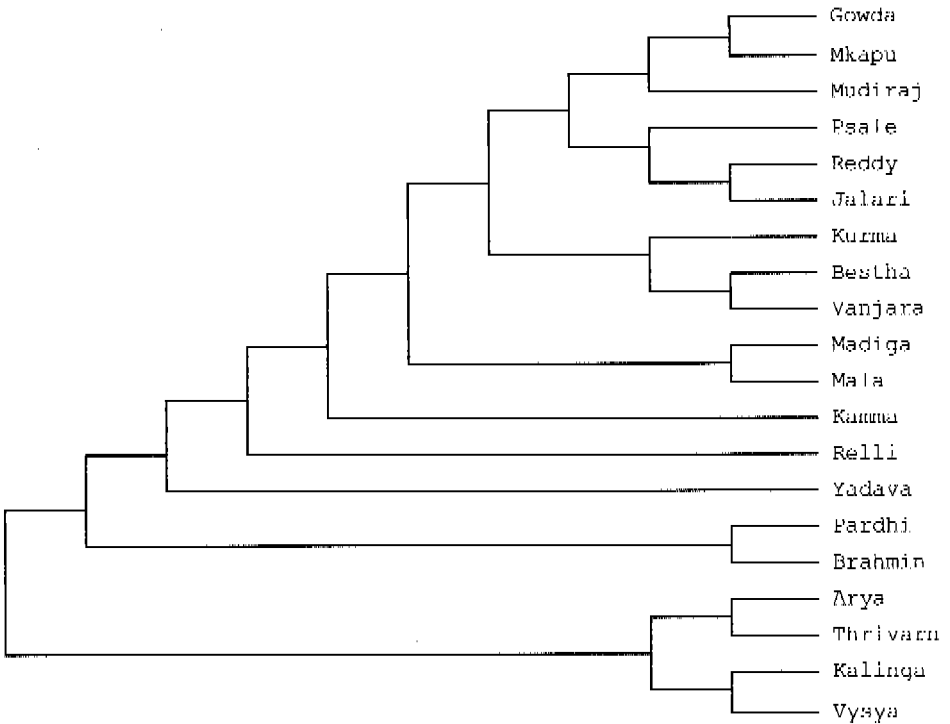


Figure 3. UPGMA tree based on Nei's standard genetic distances between pairs of 20 Telugu populations.

considered as outliers in the increasing order of magnitude below the theoretical regression line. Most of these groups are, however, placed relatively closer to the centroid, suggesting greater isolation but probably recent history of these groups. Among the remaining groups placed above the line, the scheduled castes Madiga and Mala and the lower caste Jalari are placed themselves somewhat farther from the line, suggesting above average external gene flow. However, these groups are placed close to the centroid, suggesting relatively less differentiation.

4. Discussion

India offers innumerable but unique situations for pursuing research in population structure and micro-genetic differentiation. The Vysyas of the present study are the local representatives of one of the five varnas of the Hindu caste system, but diverged and evolved in the course of time into independent endogamous subcastes, the basic units within which evolution must have taken place for a number of generations. The extent of differentiation as revealed by the G_{ST} value is small (0.018) but nevertheless relatively higher than the magnitude observed for populations with similar hierarchy of substructure. For example, Reddy and Chopra (1999), studying 10 traditional blood group, red cell enzyme and serum protein loci, observed G_{ST} values somewhat lower (about 1.1%) among the subgroups of fishermen from coastal areas of Andhra Pradesh and Orissa. However, the G_{ST} value is considerably less when compared with that based on all the Telugu-speaking groups (0.0203). This may reflect the history of subdivision of these clusters of groups. However, what

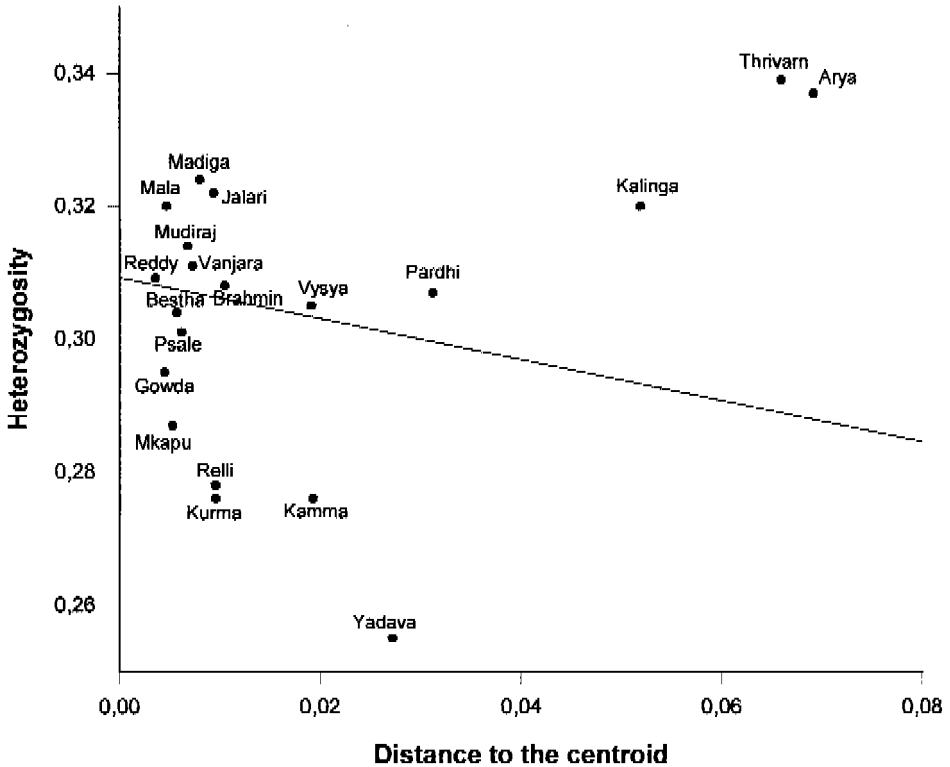


Figure 4. Regression plot of average heterozygosity versus the distance from gene frequency centroid of the 20 Telugu populations and the theoretical regression line.

is more remarkable and worth noting is the fact that these three Vysya groups form a very distinct cluster and diverged from the other local groups much earlier (figure 3). This may also reflect probably different origin and settlement of these groups in this area as compared with the other groups. It may be pertinent to note here that in a separate study based on finger dermatoglyphic variables among the major caste groups of Andhra Pradesh, Reddy and Reddy (1992) observed Vysyas, both male and female samples independently, to have clearly diverged from the other groups. There are other clusters in this tree that are consistent with the socio-economic affiliations of the groups which may lend further support to the genetic reality in the clustering pattern. The Vysya groups depend mostly on trade and commerce thus restricted mostly to urban locales with compact group identities and solidarity and with the least possibilities for genetic interaction with other groups. This may have given rise to smaller breeding isolates and greater genetic isolation with possibilities for rapid genetic differentiation, although their position above the theoretical line, as outliers, in the regression plot of heterozygosity versus r_{ii} does not bear testimony to this. That they are far removed from the centroid in the regression plot nevertheless lends support to surmise if they did not really have had a different origin or history compared with other populations of Andhra Pradesh.

What would be the probable explanation for a higher degree of heterozygosity observed among the Vysyas, given that their overall population size is much smaller than many other groups used in this plot? One possibility could be that these

populations are mostly based on urban habitats with greater possibilities for mobility even to distant areas, thus were able to manage larger effective population sizes compared with most other groups. Although large in the overall population size, it is known that the marriage contacts are limited to very small distances. Therefore, at the operational level the effective sizes must have been much smaller in most of these groups. This, instead of the routine interpretation of greater than average levels of external gene flow into the Vysyas, might have been responsible for the observed position of Vysyas in the regression plot. The other plausible explanation could be that since they have been diverged considerably from other Telugu-speaking groups with a possibility of distinct origin and migration into this area, the founding populations might have been from very heterogeneous sources. This is not an unlikely proposition given their occupational pattern.

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Address for correspondence: Dr Darío A. Demarchi, Departamento de Bioquímica Clínica, Facultad de Ciencias Químicas, Ciudad Universitaria, Córdoba 5000, Argentina. Email: ddemarchi@com.uncor.edu

Zusammenfassung. Ziel: Der vorliegende Artikel konzentriert sich auf die Untersuchung des Musters genetischer Mikrodifferenzierung innerhalb einer der substrukturierten Kastenbevölkerungen von Andhra Pradesh (der Vysya), im Vergleich mit 17 anderen Telugu sprechenden Bevölkerungen der gleichen Region Indiens.

Material und Methode: Bei insgesamt 302 Individuen der drei Vysya-Untergruppen (101 der Arya Vysya, 100 der Kalinga Vysya und 101 der Thrivarnika) wurden 17 Blutgruppen und Proteinpolymorphismen typisiert. Nei's Genverteilungsanalyse, Neighbour-Joining Tree und UPGMA Clusterdiagramme, erstellt aus durchschnittlichen genetischen Abständen, R-Matrix-Analysen und ein Regressionsmodell zur Untersuchung der Muster des externen Genflusses und des genetischen Drifts (zurückzuführen auf Isolation durch Inselmodell), wurden in zwei Stufen durchgeführt: (1) unter Berücksichtigung der drei Vysya-Populationen allein und (2) unter Berücksichtigung allgemeiner Loci innerhalb der 20 Populationen von Andhra Pradesh.

Ergebnisse: Sieben der 17 untersuchten Systeme wurden als monomorph in allen drei Vysya-Gruppen festgestellt. Der UPGMA-Stammbaum und das bidimensionale Diagramm der D^2 Abstände, abgeleitet aus der R-Matrix-Analyse, zeigen einen unterschiedlichen Cluster der Vysya-Populationen. Die Anwendung des Regressionsmodells der mittleren Heterozygotie im Vergleich zur Distanz der Bevölkerungen aus den Centroiden zeigt eine deutliche Platzierung der drei Vysya-Bevölkerungen oberhalb der theoretischen Regressionsgeraden.

Schlussfolgerung: Die verschiedenen in dieser Studie angewandten Methoden unterstützen die Hypothese vom unterschiedlichen Ursprung und/oder der demographischen Geschichte der drei Vysya-Gruppen im Vergleich mit anderen Bevölkerungen von Andhra Pradesh.

Résumé. Objectif: Cet article étudie le processus de micro différenciation génétique des Vysya, l'une des sous castes des populations de l'Andhra Pradesh, avec référence à 17 autres populations de la même région de l'Inde, parlant le Telugu.

Sujets et méthodes: 302 individus appartenant aux trois sous castes Vysya (101 Arya Vysya, 100 Kalinga Vysya et 101 thrivarnika) ont été typés pour 17 groupes sanguins et polymorphismes des protéines. Une analyse de diversité génétique de Nei ainsi que des configurations d'associations de voisinage et des diagrammes d'agrégation UPGMA extraits de distances génétiques standard, des analyses de matrices - R et un modèle de régression pour explorer les modalités de flux génique externe et de dérive génétique provoquée par l'isolement de type insulaire ont été effectués à deux niveaux: (1) considérant seulement les trois populations Vysya et (2) en englobant tous les loci présents dans 20 populations de l'Andhra Pradesh.

Résultats: On a trouvé que 7 des 17 systèmes explorés étaient monomorphes dans les trois groupes Vysya. Le dendrogramme UPGMA et l'échelonnement bidimensionnel des distances D^2 extraites de l'analyse de la matrice-R montrent une agrégation très marquée des trois populations Vysya. L'application d'un modèle de régression de l'hétérozygoté moyenne sur la distance des populations à partir du centroïde, indique que les trois populations Vysya sont nettement en-dehors et au-dessus de la ligne de régression théorique.

Conclusion: Les diverses approches utilisées dans cette étude appuient l'hypothèse d'une origine distincte et ou d'une histoire démographique particulière des trois groupes Vysya par rapport aux autres populations de l'Andhra Pradesh.