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Inverted Y chromosome polymorphism in the Gujerati Muslim Indian population of South Africa

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Summary. An inverted Y chromosome has been found at a very high frequency in a Muslim Indian community living in the Johannesburg–Witwatersrand area of the Transvaal Province of South Africa: 8 of 141 (5.7%) retrospectively identified Indian males had an inv(Y)(p11.2q11.23) and all were of the Muslim faith. The inversion was found in 22 of 72 (30.5%) prospectively studied normal Muslim Indian males. All the carriers of the inversion were Gujarati-speakers whose families migrated to the Transvaal from the Gujerat Province of India during the first half of this century. The origins of the ancestors of the individuals with inv(Y) were traced to a small village, Kholvad, near the city of Surat, and some neighbouring villages. The polymorphic frequency of the inv(Y) has probably been produced through random genetic drift in a reproductively isolated community, maintained by strict endogamous marriage customs based on religious and linguistic affiliations. There was no indication that the inverted Y was associated with any reproductive disadvantages.

Introduction

Pericentric inversion of the Y chromosome [inv(Y)(p11q11)] was first documented in 1964 (Jacobs et al. 1964; Solomon et al. 1964). Subsequent reports have shown that this Y chromosome anomaly is familial (reviewed by Verma et al. 1982). An inverted Y has also been found, albeit infrequently, in various cytogenetic population studies (Table 1). The estimated incidence of inv(Y) based on these surveys is 0.6:1000 males.

During the course of routine diagnostic chromosome investigations on referred patients, an inverted Y chromosome was observed on several occasions. Nearly all of them were East Indians, despite the fact that only a small minority of the specimens processed in the laboratory came from Indian patients. A study was therefore initiated in order to: (1) confirm the impression that inv(Y) occurred in an unusually high frequency in South African Indians; (2) ascertain, by means of a prospective study, the incidence of an inv(Y) in healthy Indian males, living in the Johannesburg–Witwatersrand area of South Africa; (3) determine if inv(Y) is associated with infertility; and (4) explain the high frequency of this variant.

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The populations and methods

Retrospective study

The ethnic origins of all consecutively chromosomally investigated males with an XY constitution were recorded for the 8-year period, 1976–1983, during which 10 cases of inv(Y) were observed. Differences in the frequency of an inv(Y) between four different ethnic groups of the referred sample, were statistically analyzed by means of the χ^2 test.

Four ethnic groups were represented in the study: (a) whites (Caucasoids), the majority of whom were Afrikaners who originated from Holland, France, and Germany during the 17th and 18th centuries, and those of British extraction who migrated to South Africa during the 19th century (a minority of the whites were Ashkenazi Jews and other individuals were of Mediterranean origin); (b) blacks (Negroids) belonging to a number of different chiefdoms or "tribes", the majority of whom were Zulu (Nguni group) and Southern Sotho; (c) "coloureds", or individuals with a heterogeneous genetic constitution representing an admixture of Khoisan ("Bushman" and "Hottentot"), Negroid, and Caucasoid strains; (d) Indians who migrated to South Africa from diverse regions of India during the latter half of the 19th and the early 20th centuries.

Prospective study

The population sample consisted of 52 phenotypically normal, Muslim Indian, male volunteers, randomly selected from blood donors, adolescent schoolboys, and colleagues. The subjects were not known to be related to one another and after being recruited to the study, detailed questioning was undertaken in order to confirm that there was no known relationship between any of the 52 individuals. On giving their consent, they were asked to complete a questionnaire designed to give information on (a) family structure, including the number of siblings, number of father's siblings, and

number of children if married; (b) familial consanguinity; (c) religion and language of the individual and his antecedents; (d) region of India from which his father or his father's family originated.

Cytogenetic methods

Peripheral blood cultures were established by standard culture techniques. The morphology of the Y chromosome was determined by quinacrine (QFQ) and Giemsa (GTG) banding. The Y/18 and Y/20 ratios and centromeric indices of all retrospectively and prospectively studied cases with an inverted Y, were calculated to confirm visual impressions of the size and morphology of the inv(Y); the Y,18 and 20 chromosomes were measured from photographic enlargements of a minimum of five metaphases from each individual.

At least two Giemsa or quinacrine-banded metaphases were fully analyzed from every subject prospectively studied, in order to exclude a stable, balanced karyotypic abnormality which could have health implications for their offspring or the offspring of family members.

Results

Retrospective study

A total of 5931 consecutively investigated males were reviewed for the presence of an inv(Y). Among 141 Indian cases, eight individuals showed an inverted Y; one of 3939 whites, one of 1593 blacks, and none of the 258 "coloured" males showed the inversion (Table 1). The difference in frequency of an inv(Y) between the Indian and the other ethnic groups was highly significant ($P \ll 0.0001$). The surnames of the eight Indian patients were different and they were not known to be related to one another, but they all belonged to the Muslim faith. The inherited nature of the inversion was shown in five Indian families and the one white family, but in the remainder, male relatives of index cases were not available for chromosome analysis.

Of the 10 index cases with an inv(Y), six were phenotypically normal males, including two diagnosed prenatally. The 9-year-old son of a woman with an X;18 translocation was said to be normal, despite having inherited the t(X;18) from his mother, in addition to the inv(Y) from his father; this boy has, however, not yet been personally examined. The three abnormal index cases all had different phenotypes, but only one had a phenotype consistent with a sex chromosome abnormality, namely hypogonadism. Unfortunately, his normal male family members could not be traced to determine if the inv(Y) was a normal familial variant.

Prospective study

An inverted Y chromosome was found in 15 of the 52 (29%) randomly ascertained Muslim Indian male subjects. Two very interesting correlations emerged from a consideration of language and area of origin in India. The 52 individuals were all Gujarati-speaking and their families had migrated to South Africa from the province of Gujerat, on the west coast of India, with the exception of one individual (carrying a normal Y), whose family came from Delhi, and all the families of subjects with an inv(Y) originated from the environs of the city of Surat in the province of Gujerat (Figs. 1, 2). No fewer than 9 of the 15 individuals with an inv(Y) were from the village of Kholvad, whereas only 2 of the 37 men with a normal Y were from this village (Table 2).

Table 1. Prevalence of inv(Y) in various populations (males only). (1) Cavalli et al. 1984; (2) Cohen et al. 1966; (3) Lubs and Ruddle 1971; (4) Patel et al. 1977; (5) Shapiro et al. 1984; (6) Verma et al. 1983; (7) Bochkov et al. 1974; (8) Friedrich and Nielsen 1973; (9) Funderburk et al. 1978; (10) Gerald and Walzer 1970; (11) Hamerton et al. 1975; (12) Jacobs et al. 1964; (13) Jacobs et al. 1971; (14) Jacobs et al. 1974; (15) Laurent et al. 1973; (16) Lin et al. 1976; (17) McIlree et al. 1966; (18) Nielsen and Rasmussen 1974; (19) Podugolnikova and Blumina 1983; (20) Price et al. 1976; (21) Sergovich et al. 1969; (22) Zeuthen and Nielsen 1973; (23) Hara et al. 1976; (24) Verma et al. 1982. Figures in parentheses denote incidence per thousand

Ethnic group	Proportion of cases with inv(Y)				References
	Present study[a]		Previous surveys		
Whites	1:3939	(0.25)	4:6605	(0.6)	1–6
Presumed Whites[b]			14:28,280	(0.49)	7–22
Hispanics			3:1343	(2.2)	5
Blacks	1:1593	(0.63)	0:2950	(0)	2–6, 23
East Indians	8:141	(56.7)*	1:90	(11.1)	2, 6, 24
"Asians"[c]			3:244	(12.3)	5
Japanese			0:47	(0)	1, 2
"Coloureds"	0:258	(0)			
"Others"			0:15	(0)	4
Total	10:5931	(1.7)	25:39,574	(0.63)	

[a] The four ethnic groups in the present study are defined in the text
[b] Ethnic groups are not specified, but presumed to be Caucasoids, from area of survey
[c] Ethnic origins of "Asians" not specified, apart from one Phillipino with an inv(Y)
* $P \ll 0.0001$

From the above findings, it was obvious that this rare chromosomal variant (Table 1) had reached a highly polymorphic frequency in the descendants of families from the village of Kholvad. To further test this supposition, blood samples were requested from 10 unrelated Muslim Indian, Gujarati-speaking males, specifically selected because their families originated from Kholvad. Another 10 samples were obtained from unrelated Muslim Indian, Gujarati-speaking men originating from Lajpur, a village very near Kholvad (Fig. 2).

An inversion of the Y chromosome was found in 5 of the 10 men from Kholvad and 2 of the 10 men from Lajpur (Table 2). Thus, 22 of 72 prospectively studied Muslim Indian, Gujarati-speaking Indian males showed the inversion (30.5%), 14 of them originating from Kholvad, 3 from a nearby village, Lajpur and 5 from 3 other villages in the Surat area (Table 2, Fig. 2).

Half of the subjects (24 of 50 individuals with a normal Y and 12 of 22 subjects with an inverted Y) knew when their families had migrated to South Africa from India. None of the families of individuals with an inverted Y had migrated to South Africa before the turn of the century and some families had arrived in South Africa less than 50 years ago (Table 3). Therefore, the high frequency of this Y variant could not have been due to a single founder with an inverted Y, who happened to migrate to South Africa.

The numbers of offspring and their sex ratios in three generations of men with an inverted Y (4.1 offspring per man and

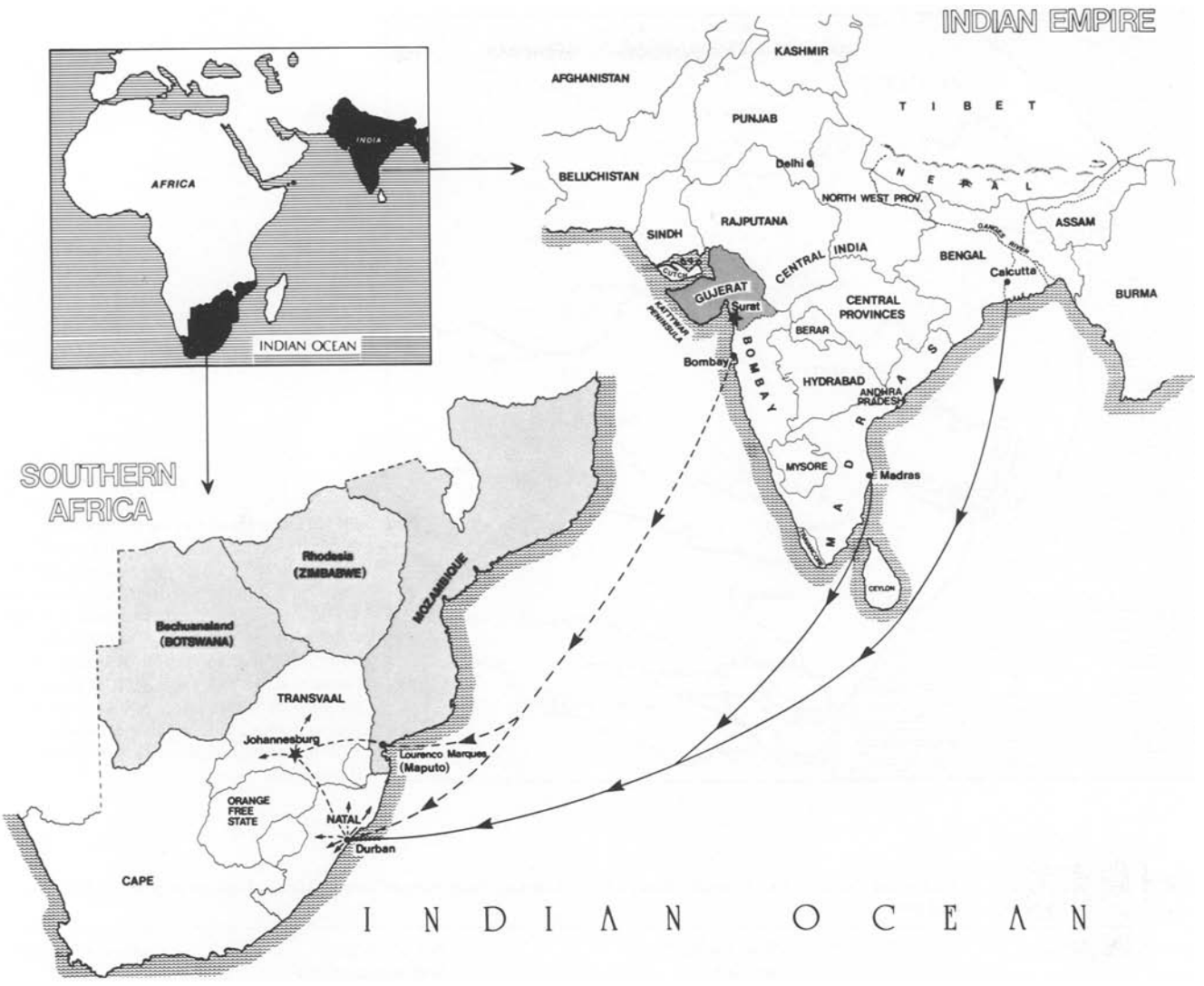

Fig. 1. Map of the Indian Empire from an atlas published in 1901 and a map of the four provinces of South Africa, after the formation of the Union of South Africa in 1910, showing the migration pathways of indentured Indians (→) and "free passenger" Indians (---→)

1.38 males:1 female) were not significantly different from those of men with a normal, acrocentric Y (4.4 offspring per man and a M:F ratio of 1.08:1) (Table 4). The mean ages of married index cases with an acrocentric Y (37.8 years) and an inv(Y) (39.4 years) were not significantly different ($P > 0.10$). Two men with an inverted Y had been married for 14 years and 28 years, respectively, but had no children and one man with a normal Y had been married for 10 years and had no offspring. (The reasons for this apparent infertility are not known.)

The consanguinity rates were the same in the families of the two groups of men: 6 of 22 men (27%) with an inv(Y) and 13 of 49 men (26.5%) with a normal Y. There were 20 different surnames among the 22 carriers of an inverted Y chromosome. The two sets of subjects with the same surnames had no knowledge of any family ties.

Cytogenetic findings

The morphology of the inverted Y was the same in all the individuals studied both retrospectively and prospectively. Based on the Q- and G-banding patterns (ISCN 1981) and centromeric index, the inversion was interpreted as inv(Y)(p11.2 q11.23) (Fig. 3). The centromeric index showed both intra- and inter-patient variation, depending on the degree of chromosomal contraction. The inter-patient index ranged from 41.36 to 46.04, with a mean of 44.13 ± 1.65.

The inverted Y chromosome appeared to be the same size in all the 8 retrospectively and 22 prospectively studied Indian individuals (Fig. 3) and the single white patient, but the aberrant Y of the black patient seemed smaller. This impression was confirmed by the Y/18 and Y/20 ratios which showed very little intra- and inter-patient variation among the Indians and the white man. In the 30 Indian individuals the Y/20 ratio ranged from 0.94 to 1.09, with a mean of 1.02 ± 0.03, and the Y/18 ratio ranged from 0.71 to 0.89 with a mean of 0.80 ± 0.05. The Y/20 and Y/18 ratios in the one black patient were 0.87 and 0.70, respectively. There were thus no significant differences between any of the Y/20 and Y/18 ratios found in the Indian cases. (These data are not presented here but are available on request.)

Apart from the inverted Y, a normal Giemsa or quinacrine banded karyotype was found in 71 of 72 subjects. One man

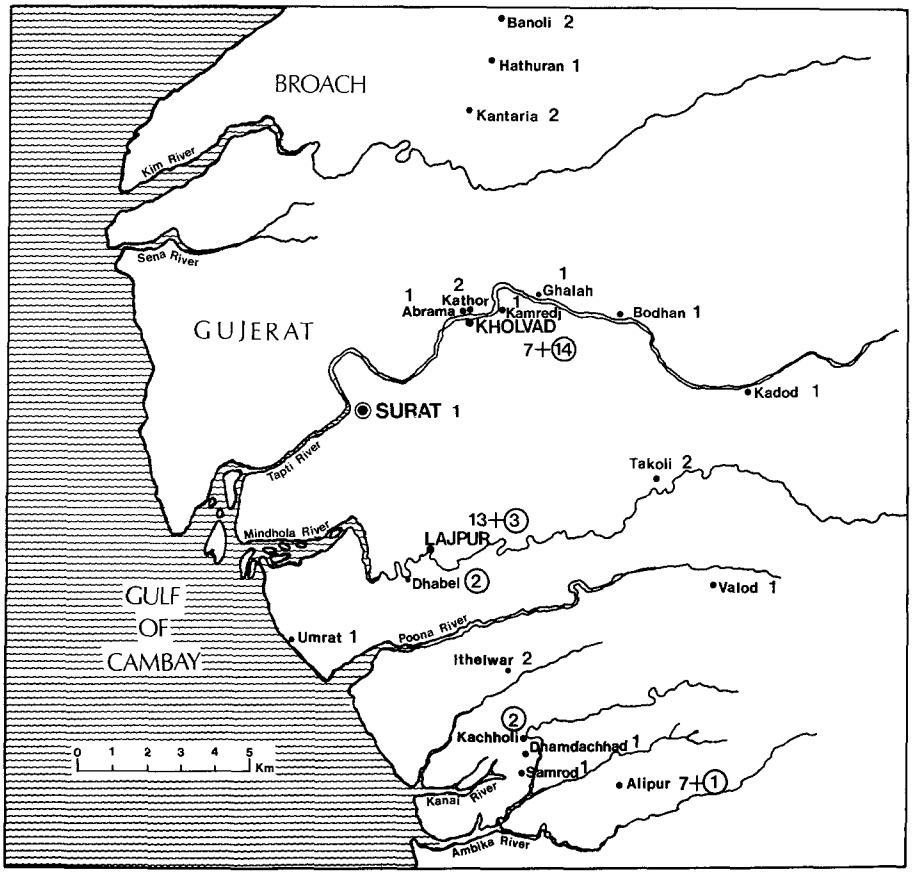

Fig. 2. Diagram of the Surat region of Gujerat, India, showing the villages of origin and the number of subjects studied from each village, possessing an acrocentric Y and an inverted Y chromosome *(circled)*. All the villages shown are within 40 km of Surat. One individual from Ahmedabad in North Gujerat and another from Delhi are not shown (adapted from a map of the Surat region drawn by R. N. Modi of Kholvad in 1959 and a map of the area from Bhana and Brain 1984)

Table 2. Incidence of inv(Y) in normal, Muslim Indian males living in the Johannesburg area of South Africa. Figures in parentheses denote incidence of inv(Y) per thousand males

Area of origin in India[a]	No. of subjects with inv(Y)		No. of subjects with acrocentric Y		Total no. of subjects	
Kholvad – Gujerat Province						
Random survey	9		2		11	
Selected from Kholvad	5	14 (667)	5	7	10	21
Lajpur – Gujerat Province						
Random survey	1		5		6	
Selected from Lajpur	2	3 (188)	8	13	10	16
Alipur – Gujerat Province						
Random survey		1 (125)		7		8
Other areas						
Random survey		4[b] (148)		23[c]		27
Total		22 (305)		50		72

[a] Kholvad, Lajpur, and Alipur are all villages in the Surat region of Gujerat (refer to the map, Fig. 2)
[b] Two from Khacholi and two from Dhabel, both villages in the Surat region of Gujerat
[c] Originating from 20 different areas, 19 of which are in Gujerat

with a normal Y was the carrier of a balanced Robertsonian translocation, karyotype 45,XY,−14,−21,+t(14q21q). He had a phenotypically normal son and there was no history of Down syndrome in his family. The subject was counselled and his family is being investigated to identify other "at-risk" family members.

Discussion

The extremely high frequency of an inversion of the Y chromosome in Muslim, Gujarati-speaking Indians residing in the Johannesburg–Witwatersrand area of the Transvaal Province of South Africa (Fig. 1), has been shown to be due to random

genetic drift. Indians first arrived in South Africa in 1860 from very diverse geographic and religious/cultural backgrounds. The various migrants had strong community identities, maintained by strict marriage customs, which permitted marriages only between members of the same community; first cousin marriages were common among the Muslims and certain Hindus. Intermarriage between geographically close but differing communal ancestral settlements, even if they were of the same faith, was rare (Mistry 1965). These villages of origin therefore formed isolates where a neutral variant (whether single gene or chromosomal) might well attain polymorphic frequencies. [This sense of community among the different religious/cultural Indian groups still prevails to a large extent in South Africa to-day, and there is very little intermarriage between different religious groups (Mistry 1965)].

The majority of immigrants were Hindus who had been indentured to work in the sugar-cane fields of Natal (Fig. 1), and a minority were Muslims who migrated as "free passengers". A disproportionate number of the Muslim, Indian immigrants were Gujarati speakers who came from the city of Surat and a cluster of small towns and villages near Surat, in the Province of Gujerat; the majority were from the villages of Kholvad and Kathor (Fig. 2) (Bhana and Brain 1984).

Many of these Muslim Indians subsequently settled in the present-day Transvaal Province of the Republic of South Africa from about 1880, having come either from Natal or directly to the Transvaal through the port of Lourenco Marques (now Maputo) in nearby Mozambique (Fig. 1) (Bhana and Brain 1984; Pachai 1971; Mistry 1965). The different migration patterns gave rise to the present distribution of Indians in South Africa. Although Muslim Indians constitute only about 20% of Indian South Africans, nearly 50% of Indians in the Johannesburg–Witwatersrand area are Muslims (South African Department of Statistics 1982; South African Department of foreign affairs and information 1984) accounting for the relatively large number of cases of inv(Y) encountered in our laboratory.

An inverted Y has previously been documented twice in Indian populations. Grace et al. (1972) investigated a large Indian family whose male members showed an inv(Y) through four generations. This Gujarati-speaking, Muslim family originally came to Natal from Kathor, which is in the Surat district (Fig. 2) (Dr. J. Grace, personal communication 1986). Verma et al. (1982) found an inv(Y) in one of 50 East Indians they studied in New York City for C- and Q-band polymorphisms, but the area of origin, religious faith, and language of origin of this subject and his family are not stated.

The uniform morphology of the inverted Y and the lack of any significant differences in the size and centromeric indices of the Y, is consistent with the postulated single origin of this variant, but is certainly not conclusive evidence for it.

Because of the polymorphic frequencies achieved by the inv(Y) in the descendants of the Muslim population of Kholvad and nearby villages, it is assumed that the carrier of an inverted Y is not at a reproductive disadvantage compared to a similar population with a normal, acrocentric Y. Comparison of the number of offspring sired by three generations of men with and without the inversion did not indicate any decrease in the fertility of bearers of the inverted Y, nor in the number of their male offspring (Table 4).

It is therefore concluded that this pericentric inversion of the Y is a phenotypically unexpressed variant, which can achieve a high frequency due to random genetic drift in a community, such as the one described here. One puzzling finding, which at first sight appeared to militate against this single origin theory, was that almost all the individuals with an inverted Y had different surnames. In a culture in which surnames are, like the Y chromosome, inherited through males, a common surname would have been expected. It was, however, customary in this Indian community until recently that a son took the middle name of his father as his surname.

A very similar phenomenon was observed in a recent study from the USSR where a Yq− variant was detected in 20.8%

Table 3. Dates of familial migration from India to South Africa of 36 Muslim Indian males[a]

Years of migration	No. of families		
	Acrocentric Y ($N = 24$)	Inv(Y) ($N = 12$)	Total ($N = 36$)
1890–1899	3	0	3
1900–1909	3	2	5
1910–1919	7	2	9
1920–1929	3	4	7
1930–1939	6	2	8
1940–1949	2	2	4

[a] Data not available for 26 of 50 males with an acrocentric Y and 10 of 22 males with an inv(Y), but no Indians were resident in the Transvaal prior to 1882

Table 4. The number of offspring in 3 generations of 50 Muslim Indian subjects with an acrocentric Y and 22 subjects with an inverted Y

Generation	Acrocentric Y				Inv(Y)			
	No. of men	No. of offspring			No. of men	No. of offspring		
		Male	Female	Total		Male	Female	Total
I: Subjects' paternal grandfathers	41[a]	95	99	194	18[a]	47	35	82
II: Subjects' fathers	50	147	127	274	22	63	42	105
III: Married index cases	34[b]	46	41	87	18[c]	28	23	51
Total for 3 generations	125	288*	267	555**	58	138*	100	238**

[a] Data unavailable for nine grandfathers of subjects with an acrocentric Y and four grandfathers of subjects with an inverted Y
[b] One of 34 subjects was married for 10 years and had no children
[c] Two of 18 subjects were married for 28 years and 14 years respectively and had no children
* Sex ratio: $\chi^2_{[1]} = P > 0.05$; ** No. of offspring: $\chi^2_{[1]} = P > 0.05$

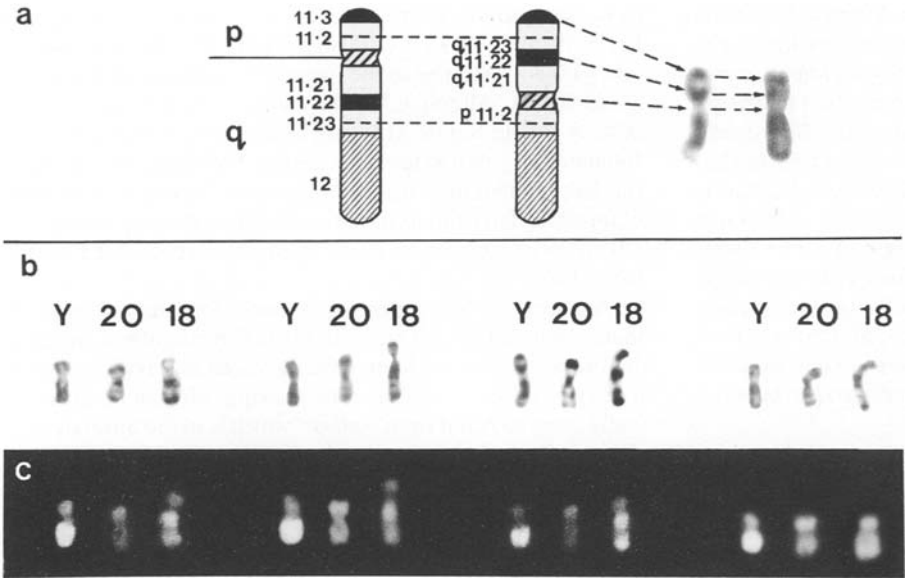

Fig. 3. a Diagrammatic representation of the Y chromosome breakpoints involved in the formation of the inverted Y, related to the GTG banded appearance of the inv(Y) in two Indian males. **b, c** G- and Q-banding patterns of the inv(Y) and its size compared to chromosomes 20 and 18 from the same cell, in eight Indian subjects

of 154 males studied from a small, indigenous, isolated community, the Khanty, living in West Siberia (Nazarenko and Puzyrev 1985). As was the case in the present study, many of the carriers had differing surnames which had arisen through historical and cultural circumstances. The genealogy of the Yq− carriers was traced through six generations and the authors concluded that the high frequency of the variant was due to a founder effect many centuries earlier (Nazarenko and Puzyrev 1985).

The tracing of such variants, whether single gene or chromosomal, can lead to useful demographic data on the historical, cultural, and geographic origins of particular communities such as the Muslim Indian population presently residing in the Johannesburg area of South Africa. In addition, the determination of the number of offspring of carriers of the inversion has provided useful information on the relevance to infertility of such anomalies.

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