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POPULATION GENETIC STUDY OF RED CELL ENZYME PHOSPHOGLUCOSE ISOMERASE IN INDIA

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Summary The distribution of red cell enzyme phosphoglucose isomerase was studied by starch gel electrophoresis in 27 different endogamous groups of India. Forty one electrophoretic variants belonging to four out of the nine known heterozygote types and one rare homozygous variant (PGI-3) were found. Comparison of the results with in India and certain other populations showed that PGI is certainly another useful genetic parameter for the study of population diversity in Asia.

Inherited variation of the enzyme phosphoglucose isomerase [PGI; α-D-glucose 6-phosphate ketol isomerase; EC 5.3.1.9] was initially described by Detter *et al.* (1968), the enzyme being referred to as phosphohexose isomerase. Since this discovery there have been reports of rare genetically determined variants or variants with low catalytic activities from various populations of the world (Baughan *et al.*, 1968; Fitch *et al.*, 1968; Paglia *et al.*, 1969; Shinoda, 1970; Tariverdian *et al.*, 1970; Welch 1971; Luan Eng and Welch, 1972; Sanpitak *et al.*, 1973; Nakashima *et al.*, 1973; Isacchi *et al.*, 1979), most of which concerns the sporadic occurrence of one or two of the nine heterozygotic types originally described in addition to the usual homozygous phenotype PGI-1. The exceptions are the heterozygous phenotypes PGI 3-1 and 4-1 which are of particular interest in Asiatic populations. In both the studies from London (Detter *et al.*, 1968; Welch, 1971) the Asiatic Indians showed an appreciable frequency of the variant PGI 3-1 and subsequent studies of indigenous samples confirmed that the PGI^3 allele attains polymorphic frequencies in certain populations of India. Indeed, the relatively high frequency of this allele led to the detection of the homozygous phenotype PGI-3 (Papiha *et al.*, 1974).

Ishimoto and Kuwata (1974) compiled the PGI studies in Japan and showed that in Japanese PGI 4-1 variant is more frequent than the other known heterozygous variants. This relatively high frequency of the PGI^4 allele in Japan consistent with the previous studies of Shinoda (1970), also led to the finding of a rare

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homozygous phenotype PGI-4 in the Nagasaki population of Kyushu. The PGI 3-1 variant was the second most frequent found in Japan.

More recent studies of India populations have also indicated frequencies of the PGI^8 and PGI^5 alleles greater than .01 as well as the PGI^3 allele (Papiha *et al.*, 1980; Ramesh *et al.*, 1980). The present study extends information on the incidence and distribution of PGI alleles in 27 different endogamous groups and assesses the importance of this system in the study of population diversity in India.

METHODS AND MATERIAL

As part of the genetic studies in Indian populations, 4,618 blood specimens collected in the last 10 years were studied for PGI types in the Department of Human Genetics, Newcastle upon Tyne. The results of 2,009 samples have already been published in several surveys (Papiha *et al.*, 1972, 1976, 1978, 1980, 1981; Papiha, 1974, 1979; Roberts *et al.*, 1980; Chahal *et al.*, 1982). The results on a further 2,609 subjects belonging to 27 different endogamous groups are reported here.

The hemolysates were phenotyped for PGI, using horizontal starch gel electrophoresis with Connaught hydrolysed starch. The bridge buffer consisted of 0.25 M Tris and 0.057 M citrate pH 8 and the gel buffer was 0.017 M Tris and 0.0023 M citrate pH 8. With Whatman No. 3. filter inserts, the electrophoresis was carried out at 10–12 V/cm for 5 hr at 4°C.

Staining was carried out using fructose 6-phosphate as substrate. Certain commercial preparations contain as an impurity sufficient glucose 6-phosphate to turn the stain dark purple before the PGI zones are developed. In this case fructose 6-phosphate was prepared by the hydrolysis of fructose 1,6-diphosphate with 1 N HCl. This solution is adjusted to pH 7 before use. Fructose 6-phosphate (disodium salt) now available from Boehringer with 99.8% purity serves a practicable substrate. Fourteen mg substrate, 8 mg NADP, 8 mg MTT and 8 mg PMS, 15 μl glucose 6-phosphate dehydrogenase (140 μ/ml) in Tris buffer pH 8 forms the staining mixture, which is overlaid with agar on the bottom half of the cathodal portion of the gel.

RESULTS

The distribution of phenotypes and gene frequencies in the populations now studied, and from reported surveys from India, is given in Table 1. In a total of 8,002 subjects studied from India 80 variants of type 3-1 were found, giving an overall incidence of 1%. The second most frequent variant is PGI 5-1, the 17 cases found indicating a phenotypic incidence of approximately 1 in 500. Unlike PGI 3-1, which is distributed over all the endogamous groups, the distribution of PGI 5-1 shows affiliation to particular ethnic groups.

a) The PGI^2 allele

The initial PGI 2-1 variant was found in a Thai individual (Detter *et al.*, 1968). Omoto and Blake (1972) described a similar variant in a Chinese of Singapore. In the present investigation no variant of type 2-1 was found, but there are reports of one example in each of the nontribal groups of Andhra and a frequency of the PGI^2 allele of 1.2% from Christians of Kerala (Ramesh *et al.*, 1979, 1980; Saha *et al.*, 1976). This suggests localisation of the allele to specific populations of south India.

b) The PGI^3 allele

Among Indian populations so far 49 occurrences of the variant PGI 3-1 have been reported, and the present investigation adds a further 31 bringing the total to eighty. As regards its overall distribution the lack of the PGI^3 allele among certain samples where a considerable number of subjects has been studied such as Kanets in Himachal Pradesh and the south Indian tribes Kolam and Chenchu suggest a genuine absence of PGI^3 allele from these populations, whereas in all the other population samples lack of the allele could well be due to small sample size. In India the PGI^3 allele frequency ranges from .02–3.4%, and 14 populations show clear polymorphic frequencies (>1%).

In a semi-urban population from central India, Papiha *et al.* (1974) described the rare homozygous variant PGI-3 (genotype PGI^3/PGI^3) in addition to the usual PGI-1, and regular codominant inheritance was demonstrated by family study. In the present investigation another PGI-3 homozygote was found in a Mahajan Agarwal of Punjab (Fig. 1). This group has the highest frequency of the PGI^3 allele so far reported in the world (3.4%).

c) The PGI^5 allele

PGI 5-1 was originally described as a Furopean variant but its occurrence in India was described initially in north India by Blake *et al.* (1971) and later in west-

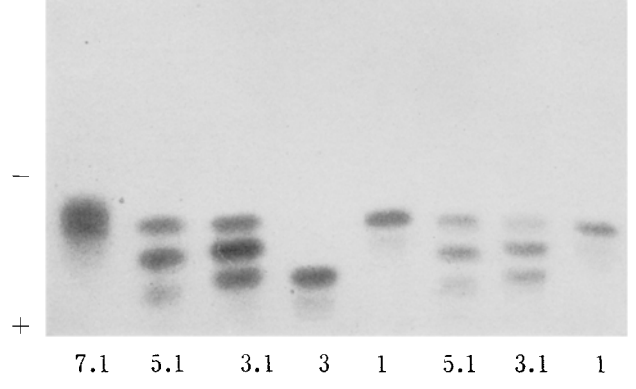

Fig. 1. Electrophoretic variants of enzyme phosphoglucose isomerase.

Table 1. Phosphoglucose isomerase (PGI) variants and gene frequencies in indigenous populations of India.

Population and location	Number tested	PGI phenotypes								PGI gene frequencies							Reference
		1-1	2-1	3-1	3-3	5-1	7-1	8 1	9-1	*PGI*^{1}	*PGI*^{2}	*PGI*^{3}	*PGI*^{5}	*PGI*^{7}	*PGI*^{8}	*PGI*^{9}	
NORTH INDIA																	
Himachal Pradesh																	
Brahmin	105	105	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	present study
Chowdhury	111	110	—	1	—	—	—	—	—	0.995	—	0.005	—	—	—	—	present study
Gaddi Rajput	96	94	—	2	—	—	—	—	—	0.990	—	0.010	—	—	—	—	present study
Chamar	48	48	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	present study
Nepali	87	82	—	1	—	3	1	—	—	0.971	—	0.006	0.017	0.006	—	—	present study
Kanet	166	162	—	—	—	—	—	4	—	0.988	—	—	—	—	0.012	—	Papiha *et al.*, 1980
Koli	61	60	—	1	—	—	—	—	—	0.992	—	0.008	—	—	—	—	Papiha *et al.*, 1980
Gaddi Brahmin	39	38	—	1	—	—	—	—	—	0.987	—	0.013	—	—	—	—	Chahal *et al.* ,1982
Gaddi Rajput (Bharmour)	69	64	—	4	—	—	—	1	—	0.963	—	0.029	—	—	—	0.007	Chahal *et al.*, 1982
Gaddi Rajput (Chuwari)	63	63	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	present study
Gaddi Rajput (Palampur)	145	145	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Chahal *et al.*, 1982
Rajput (Churah)	120	115	—	5	—	—	—	—	—	0.979	—	0.021	—	—	—	—	present study
Rajput (Chuwari)	168	167	—	1	—	—	—	—	—	0.997	—	0.003	—	—	—	—	present study
Tibetan (immigrants)	115	113	—	—	—	—	—	—	2	0.991	—	—	—	—	—	0.009	present study
Punjab & Delhi																	
Jat Sikh	78	78	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	present study
Ramdasia Sikh	76	76	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	present study
Mahajan Agarwal	104	98	—	5	1	—	—	—	—	0.966	—	0.034	—	—	—	—	present study
Arora	71	70	—	1	—	—	—	—	—	0.993	—	0.007	—	—	—	—	Blake *et al.*, 1971
Brahmin	61	60	—	1	—	—	—	—	—	0.992	—	0.008	—	—	—	—	Blake *et al.*, 1971
Khatri	78	77	—	1	—	—	—	—	—	0.994	—	0.006	—	—	—	—	Blake *et al.*, 1971
Rajput	41	40	—	—	—	1	—	—	—	0.988	—	—	0.012	—	—	—	Blake *et al.*, 1971
Vaish	63	63	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Blake *et al.*, 1971
Scheduled Castes	83	79	—	3	—	—	—	—	1	0.976	—	0.018	—	—	—	0.006	Blake *et al.*, 1971
Punjabis	100	99	—	1	—	—	—	—	—	0.995	—	0.005	—	—	—	—	Papiha *et al.*, 1972

Jat Sikh (Bhatinda)	145	144	—	1	—	—	—	—	—	0.997	—	0.003	—	—	—	—	present study
Haryanvies	112	111	—	1	—	—	—	—	—	0.995	—	0.005	—	—	—	—	Papiha *et al.*, 1976
Muslims	117	113	—	3	—	—	—	—	1	0.983	—	0.013	—	—	—	0.004	Papiha *et al.*, 1976
Uttar Pradesh																	
Hindu	182	178	—	3	—	1	—	—	—	0.989	—	0.008	0.003	—	—	—	present study
Muslim	105	104	—	1	—	—	—	—	—	0.995	—	0.005	—	—	—	—	present study
Rajasthan																	
Paliwal Brahmin	57	57	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	present study
Rajput	80	77	—	2	—	—	1	—	—	0.981	—	0.013	—	0.006	—	—	present study
Oswal Mahajan	94	93	—	1	—	—	—	—	—	0.995	—	0.005	—	—	—	—	present study
Bhil Tribe	42	41	—	—	—	—	1	—	—	0.988	—	—	—	0.012	—	—	present study
Meghwal	73	73	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	present study
Meena Tribe	76	74	—	—	—	—	2	—	—	0.987	—	—	—	0.013	—	—	present study
CENTRAL INDIA																	
Madhya Pradesh																	
Hindu	174	170	—	3	1	—	—	—	—	0.986	—	0.014	—	—	—	—	Papiha, 1974
Muslim	164	163	—	1	—	—	—	—	—	0.997	—	0.003	—	—	—	—	Papiha, 1974
Bhil	143	141	—	2	—	—	—	—	—	0.993	—	0.007	—	—	—	—	Papiha *et al.*, 1978
WEST INDIA																	
Gujarat																	
Vania Soni (Saurashtra)	100	99	—	1	—	—	—	—	—	0.995	—	0.005	—	—	—	—	Undevia *et al.*, 1978
Vania Soni (Gaujarat)	83	80	—	3	—	—	—	—	—	0.982	—	0.018	—	—	—	—	Undevia *et al.*, 1978
Vania Soni (Surat)	82	81	—	—	—	1	—	—	—	0.994	—	—	0.006	—	—	—	Undevia *et al.*, 1978
Ghanchi	56	56	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Papiha *et al.*, 1981
Kunbi	116	112	—	3	—	—	—	—	1	0.983	—	0.013	—	—	—	0.004	Papiha *et al.*, 1981
Anvil	49	49	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Papiha *et al.*, 1981
Muslim	61	61	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Papiha *et al.*, 1981
EAST INDIA																	
Orissa																	
Langia Soura	110	108	—	2	—	—	—	—	—	0.991	—	0.009	—	—	—	—	present study
Khond	115	115	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	present study
Orriya	125	124	—	—	—	—	1	—	—	0.996	—	—	—	0.004	—	—	present study

Table 1. (Continued)

Population and location	Number tested	PGI phenotypes								PGI gene frequencies							Reference
		1-1	2-1	3-1	3-3	5-1	7-1	8-1	9-1	*PGI*^{1}	*PGI*^{2}	*PGI*^{3}	*PGI*^{5}	*PGI*^{7}	*PGI*^{8}	*PGI*^{9}	
SOUTH INDIA																	
Andhra Pradesh																	
Hindu	211	210	—	1	—	—	—	—	—	0.998	—	0.002	—	—	—	—	Roberts *et al.*, 1980
Muslim	86	86	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Roberts *et al.*, 1980
Lambadi	59	59	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Roberts *et al.*, 1980
Savara	132	132	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Rao *et al.*, 1978
Jatapu	157	155	—	2	—	—	—	—	—	0.994	—	0.006	—	—	—	—	Rao *et al.*, 1978
Kolam (Utnur)	168	167	1	—	—	—	—	—	—	0.997	0.003	—	—	—	—	—	Ramesh *et al.*, 1979
Kolam (Asifbad)	50	50	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Ramesh *et al.*, 1979
Chenchu (Mahbubragar)	139	127	1	—	—	11	—	—	—	0.957	0.004	—	0.040	—	—	—	Ramesh *et al.*, 1980
Chenchu (Kurnool)	64	64	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Ramesh *et al.*, 1980
Rajgonds	134	133	—	1	—	—	—	—	—	0.996	—	0.004	—	—	—	—	Blake *et al.*, 1981
Pardhans	100	100	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Blake *et al.*, 1981
Koya	159	153	—	6	—	—	—	—	—	0.981	—	0.019	—	—	—	—	Blake *et al.*, 1981
Konda Reddi	92	92	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Blake *et al.*, 1981
Sugali	61	61	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Blake *et al.*, 1981
Yerukula	40	40	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Blake *et al.*, 1981
Koya (Khammam)	234	228	—	6	—	—	—	—	—	0.987	—	0.013	—	—	—	—	present study
Kerala																	
Kadar	213	213	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Saha *et al.*, 1974
Malayali Keralites	81	81	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Papiha, 1979
Brahmin	60	57	—	3	—	—	—	—	—	0.975	—	0.025	—	—	—	—	Saha *et al.*, 1976
Nayar	142	141	—	1	—	—	—	—	—	0.996	—	0.004	—	—	—	—	Saha *et al.*, 1976
Izhava	68	68	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Saha *et al.*, 1976
Scheduled Castes	49	49	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Saha *et al.*, 1976
Muslim	125	120	—	5	—	—	—	—	—	0.980	—	0.020	—	—	—	—	Saha *et al.*, 1976
Christian	161	157	4	—	—	—	—	—	—	0.987	0.012	—	—	—	—	—	Saha *et al.*, 1976
Malayarayan	59	59	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Saha *et al.*, 1976
Tamilnadu																	
Kota	549	549	—	—	—	—	—	—	—	1.000	—	—	—	—	—	—	Ghosh *et al.*, 1977

ern India. Till today 17 PGI 5-1 variants have been reported in the Indian populations. Eleven of these variants were recorded in a single south Indian tribe, the Chenchu of Mahbubnagar in the state of Andhra Pradesh, giving the highest reported PGI^5 allele frequency (4%). Four variants of PGI 5-1 similar to that described by Omoto and Blake (1972) from the western highlands of New Guinea have been added by the present investigation (Fig. 1). Three of these variants were found in a single population, a group of Nepali, of Mongoloid affinities, who had migrated to and settled in the state of Himachal Pradesh, giving a PGI^5 allele frequency in Nepali of 1.5%. The other population described with the PGI 5-1 variant is that of Japan (Shinoda, 1970), again of Mongoloid affinity. Although the PGI^5 allele was initially described in western populations, its distribution shows that the occurrence of this allele is more characteristic of the populations of the eastern hemisphere.

d) The PGI^7, PGI^8 and PGI^9 alleles

The electrophoretic mobility of the proteins of alleles PGI^7, PGI^8 and PGI^9 places them cathodally to the normal PGI^1 (Fig. 1). Six variants of type PGI 7-1 were found in the present study. Four of these phenotypes were found in the state of Rajasthan (3 in tribal populations and 1 in an urban group of Rajput). One phenotype each was encountered in a Nepali and an Orriya sample from the states of Himachal Pradesh and Orissa, respectively.

The variant PGI 8-1 was initially described in a Chinese individual from London. No variant of this type was found in the present samples but in our previous studies five such variants were reported from Kanet and Gaddi populations of Himachal Pradesh (Papiha *et al.*, 1980; Chahal *et al.*, 1982). The highest frequency of the PGI^8 allele (1.2%) occurred in Kanets living near the Indo-Tibetan border who show considerable Mongoloid admixture (Papiha *et al.*, 1980).

PGI 9-1 is a slightly slower variant than PGI 8-1. Three PGI 9-1 variants have already been described from the north-western states of Delhi and Gujarat (Blake *et al.*, 1971, Papiha *et al.*, 1976, 1978). In the present study two more variants were found in Tibetan immigrants from the state of Himachal Pradesh.

DISCUSSION

This electrophoretic investigation of PGI has shown the presence of four out of the nine known heterozygous phenotypes and one rare homozygous phenotype within the geographical region of India, occurring in a further 43 heterozygotes and one homozygote similar to those previously reported. These increased numbers allow a better appreciation of the frequencies and distribution of the PGI alleles. The population of Kanet in the northwest state of Himachal Pradesh, the south Indian tribe of Chenchu from Mahbubnagar, and Christians of Kerala have polymorphic frequencies of the PGI^8, PGI^5, and PGI^2 alleles, respectively. Otherwise, the PGI^2,

PGI^5, *PGI*^{7}, *PGI*^{8}, and *PGI*^{9} alleles are in general rare and of only sporadic occurrence in the various endogamous groups of India. The distribution of the fast alleles *PGI*^{7}, *PGI*^{8} and *PGI*^{9} not only suggests that their presence is restricted to the north-west states of India but also indicates that their occurrence characterizes the Mongoloids and populations with Mongoloid admixture such as the Kanets and some tribal populations of India. In their overall distributions these five rare alleles add considerably to the genetic diversity among the various ethnic groups of India.

The incidence and distribution of the *PGI*^{3} allele in India also shows another interesting feature. The allele frequency exceeds 1% in a larger number of populations in north west India than in south India. The present investigation also confirms the observation of Omoto and Blake (1972). The *PGI*^{3} allele is present in Mongoloids or populations with Mongoloid admixture, but its frequency is far lower than in the populations with Caucasoid or Dravidian affinities. The consistent distribution and wide spread occurrence of the *PGI*^{3} allele may be attributable to the kinetic stability of protein synthesis (Tilley *et al.*, 1974) which in the particular regional, social and biological environments may confer a selective advantage. One of the social factors which increases homoygosity is a high degree of inbreeding in certain endogamous groups of India and this confers the occurrence of the otherwise rare homozygous phenotype PGI-3, identified in this study for the second time, in this case in the Mahajan Agarwal group of Punjab.

In conclusion, the data presented in this paper clearly indicate the interest attaching to the investigation of the genetic loci controlling the isozymic variation of PGI. It is another useful indication of genetic diversity in populations of the Indian sub-continent, and the problems that this reveals, namely why do some alleles occur at polymorphic frequencies in some populations and not others will provide a fruitful topic of inquiry for some time to come.

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