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Original investigations

Gm and Km allotypes in 74 Chinese populations: a hypothesis of the origin of the Chinese nation

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Summary. This paper reports the distribution of immunoglobulin Gm and Km allotypes in 74 Chinese geographical populations. These populations are derived from 24 nationalities comprising 96.6% of the total population of China. A total of 9,560 individuals were phenotyped for Gm(1,2,3,5,21) factors, and 9,611 were phenotyped for Km(1). Phylogenetic trees were constructed on the basis of Gm haplotype frequencies and genetic distances. The results of cluster analysis show the heterogeneity of the Chinese nation, and confirm the hypothesis that the modern Chinese nation originated from two distinct populations, one population originating in the Yellow River valley and the other originating in the Yangtze River valley during early neolithic times (3,000–7,000 years ago). Frequencies of the Gm haplotype of 74 Chinese populations were compared with those of 33 populations from major racial groups. The results suggest that during human evolution, the Negroid group and Caucasoid-Mongoloid group diverged first, followed by a divergence between the Caucasoid and Mongoloid. Interrace divergence is high in comparison with intrarace divergence. There appear to be two distinct subgroups of Mongoloid, northern and southern Mongoloid. The northern and southern Mongoloid have $Gm^{1;21}$ and $Gm^{1,3;5}$ haplotypes as race-associate markers, respectively. Furthermore, the Caucasian-associated haplotype $Gm^{3;5}$ was found in several of the minorities living in the northwest part of China. The presence of the $Gm^{3;5}$ haplotype is attributed to the Caucasians living in Central Asia throughout the Silk Road. The amount of Caucasian admixture has been estimated. In contrast to the Gm haplotype distribution, Km^1 gene frequencies showed a random distribution in the populations studied.

Introduction

Human immunoglobulin allotypes are known for IgG(Gm), IgA(Am), and IgE(Em) heavy chains and for type κ (Km) light chains. Currently, 18 Gm factors and 3 Km factors are well defined in three of four IgG subclasses and type κ light chains, respectively (van Loghem 1984). The close linkage of the heavy chain genes, located on chromosome 14, results in the inheritance of fixed combinations of the Gm factors as haplotypes. The Km allotypes are inherited independently of the Gm allotypes. The gene for Km has been shown to be on chromosome 2. Population and family studies show that the Gm haplotypes are very stable, and that crossing over is extremely rare. Gm allotypes are unique in that certain haplotypes are characteristic for a particular race or population and have different frequencies of occurence among various ethnic groups. This has made Gm a useful tool in anthropological studies, especially in the identification of ethnic groups and in the detection of gene flow from one population to another (Steinberg and Cook 1981).

China is a country of many nationalities. The Chinese nation consists of the Han nationality and 55 minorities. The 1981 survey recorded a populaltion of 1,031,882,551 (State Statistical Bureau of the People's Republic of China 1982). The Han nationality had a population of 936.7 million people, corresponding to 93.3% of the total population. The 55 minorities had a population of 67.2 million people, comprising only 6.7% of the total population.

The minorities, although small in number, inhabit 50% to 60% of the country's area. Most of the minority areas are located in border regions, which cover a larger area. Common borders are shared with the Soviet Union, Pakistan, Afghanistan, India, and eight other countries. Most of China's minorities have their own languages. Approximately half of the minorities have a written language of their own or share the written language of others.

To delineate the relationship between the Han nationality and China's minorities from a genetic point of view, Zhao et al. (1983, 1987) investigated the distribution of Gm alloytpes in 11 Chinese nationalities. Concurrently, Lee et al. (1988) studied the polymorphism of HLA antigens in 14 Chinese populations. On the basis of the distribution patterns of Gm haplotypes, Zhao et al. (1987) proposed the hypothesis that the origins of the contemporary Chinese nation might reside in both the Yellow River valley in north China and the Yangtze River in south China. The most likely boundary between northern and southern Chinese was drawn at a latitude of 30°N. HLA studies showed significant differences in HLA antigen frequencies between the northern and southern Han (Lee et al. 1988). To investigate this "north-south" hypothesis further, a comprehensive study of immunoglobulin allotypes of anthropological significance in 74 geographical populations from 24 Chinese nationalities was undertaken and is presented here.

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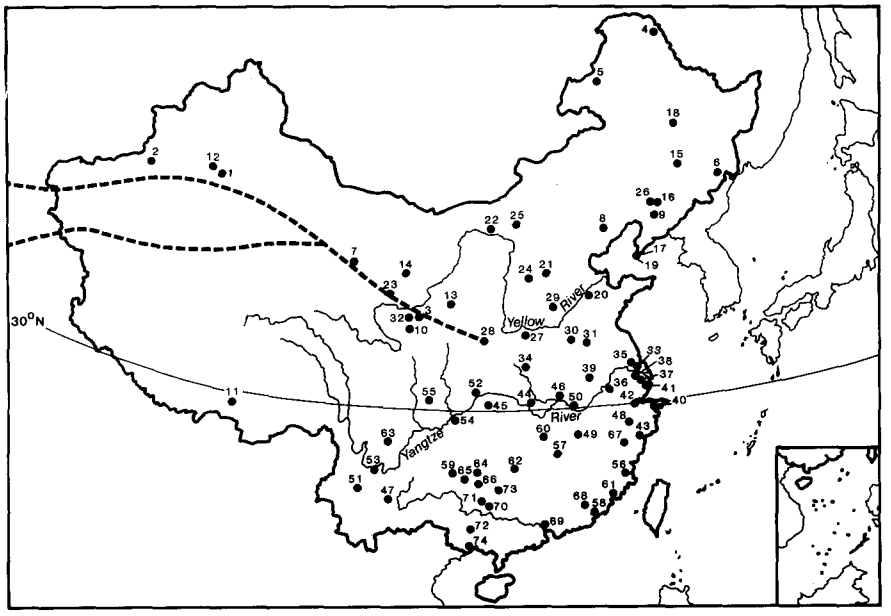

Fig. 1. Geographical distribution of 74 populations in China. *Black dots* indicate the locations sampled. Population numbers are the same as those used in Tables 2 and 3, and Figs. 2 and 3. The nationality, location and sample size of each population are listed in Table 3. *Dotted lines* indicate the route of the Silk Road (Chen 1987)

Materials and methods

Subjects

The subjects in this study were drawn from 74 geographical populations from 24 Chinese nationalities. These nationalities have a population of 996.6 million and comprise 96.6% of the total Chinese population. Of the 74 populations studied 44 were of Han nationality and the remaining 30 were derived from 23 minorities. The geographical distribution of the 74 populations is shown in Fig. 1. The families of all subjects had resided in the region for three generations without mixed marriage with other nationalities. A total of 9,560 subjects were typed for Gm; 9,611 subjects were typed for Km.

Gm and Km typing

Venous blood samples were collected and the sera stored at −20°C until ready for use. The Gm and Km typing reagents used in this study are listed in Table 1. All samples were tested for Gm(1, 2, 3, 5, 21) and Km(1) factors. Gm and Km typing were performed by the agglutination-inhibition test in glass tubes (van Loghem 1978). Typing of each sample was done in two dilutions, 1:10 and 1:30. Controls for the agglutination system were known positive and negative samples. Type O, R_1R_2 red cells were used. The reagents listed in Table 1 and reference samples were supplied by Professor R. Bütler of the Central Laboratory of the Swiss Red Cross Blood Transfusion Services.

Genetic analysis

Estimates of Gm haplotype frequencies were calculated using the method of maximum likelihood. Family studies indicated that the common Gm haplotypes in the Chinese nation were $Gm^{1,3;5}$, $Gm^{1;21}$, Gm^{1}, and $Gm^{1,2;21}$ (Zhao et al. 1985). An additional haplotype with a low frequency was $Gm^{3;5}$, found only in some minorities with $Gm^{3;5}$ phenotype (Zhao et al. 1983). The Km^1 gene frequency was calculated by the square root method. Genetic distances on the basis of Gm haplotype frequencies were computed using the formula of Nei (1972). Phylogenetic trees were constructed by unweighted pair-group clustering methods (Sneath and Sokal 1973). The Bernstein formula (Bernstein 1931; Cavalli-Sforza and Bodmer 1971) for determining the degree of racial admixture (m) in a hybrid population was applied, using the haplotype $Gm^{3;5}$ as a marker. The formula is $m = (P_H - P_B) / (P_A - P_B)$, where P_A is the frequency of $Gm^{3;5}$ haplotype in Caucasians,

Table 1. Reagents used to determine the Gm and Km allotypes[a]

Chain	Immunoglobulin allotype		Agglutinator	Coat
	Alphamerical	Numerical		
IgG1	G1m(a)	G1m(1)	Code 1.1 /Lot 02	Code 31/Lot 31
	(x)	(2)	Code 1.2 /Lot 9	Code 3.2 /Lot 24
	(f)	(3)	Code 1.4 /Lot 118	Code 3.4 /Lot 41
IgG3	G3m(b1)	G3m(5)	Code 1.5 /Lot 16	Code 3.5 /Lot 19
	(g)	(21)	Code 1.21/Lot 102.4	Code 3.21/Lot 30
κ	Km(1)	Km(1)	Code 2.1 /Lot 13.8	Code 3.2 /Lot 28.9

[a] Nomenclature from WHO Meeting on Human Immunoglobulin Allotypic Markers (1976). Only the numerical notation is used in this paper. Code and lot numbers are product names of the Central Laboratory of the Swiss Red Cross Blood Transfusion Services

Table 2. The distribution of Gm and Km phenotypes in 74 Chinese populations

Population no.[a]	Gm									Km[d] (1)+
	1,3;5	1;21	1	1,2;21	1,3;5,21	1,2,3;5,21	3;5	χ^{2c}	P	
1	46 (47.10)[b]	49 (43.46)	5 (5.03)	25 (31.72)	63 (67.39)	36 (28.44)	35 (35.86)	4.47	0.11	124
2	22 (21.18)	25 (23.55)	2 (2.53)	14 (14.35)	25 (26.99)	10 (9.61)	6 (5.78)	0.41	0.81	61
3	19 (19.97)	25 (24.86)	4 (3.57)	15 (16.09)	23 (22.57)	10 (8.79)	3 (3.15)	0.36	0.84	45
4	3 (3.64)	53 (53.57)	20 (19.52)	25 (24.94)	4 (3.26)	1 (1.07)	0	0.30	0.86	24
5	12 (12.51)	56 (57.35)	2 (1.73)	36 (35.16)	33 (31.31)	9 (9.94)	0	0.29	0.86	64
6	5 (6.95)	47 (47.66)	3 (2.16)	25 (25.83)	19 (17.31)	6 (5.08)	0	1.24	0.54	67
7	3 (3.02)	18 (18.14)	1 (0.98)	16 (15.89)	7 (6.84)	3 (3.12)	0	0.01	0.99	21
8	11 (10.77)	46 (46.43)	4 (4.06)	20 (19.43)	19 (18.69)	4 (4.61)	0	0.11	0.95	74
9	5 (6.18)	41 (43.19)	5 (4.20)	22 (20.87)	14 (11.34)	2 (3.23)	0	1.65	0.44	52
10	6 (7.45)	36 (38.81)	5 (4.00)	26 (24.55)	16 (12.57)	3 (4.61)	0	2.32	0.31	48
11	4 (3.25)	60 (59.28)	5 (5.47)	26 (26.16)	6 (7.01)	2 (1.83)	0	0.39	0.82	56
12	25 (24.46)	26 (25.70)	2 (2.22)	13 (12.77)	28 (28.61)	8 (8.25)	1 (0.99)	0.06	0.97	56
13	27 (27.87)	45 (42.87)	3 (2.94)	38 (40.68)	38 (39.72)	23 (19.90)	1 (1.03)	0.87	0.65	114
14	13 (14.31)	43 (44.37)	5 (4.28)	50 (49.81)	24 (22.00)	13 (13.22)	0	0.47	0.79	108
15	21 (21.59)	40 (39.01)	2 (1.92)	37 (38.40)	34 (34.71)	19 (17.38)	0	0.26	0.88	111
16	12 (14.68)	27 (28.15)	2 (1.14)	32 (33.25)	28 (25.26)	16 (14.52)	0	1.67	0.43	80
17	25 (28.33)	41 (41.03)	4 (2.91)	42 (44.82)	40 (38.22)	25 (21.68)	0	1.56	0.46	119
18	26 (27.32)	69 (69.00)	5 (4.53)	65 (66.06)	46 (45.32)	24 (22.77)	0	0.21	0.90	134
19	9 (10.74)	23 (21.84)	2 (1.52)	21 (23.46)	16 (16.32)	12 (9.11)	0	1.67	0.43	40
20	18 (19.72)	38 (38.47)	3 (2.38)	43 (44.01)	32 (30.61)	19 (17.81)	0	0.48	0.79	105
21	15 (14.72)	37 (36.20)	3 (3.20)	21 (21.49)	21 (21.93)	8 (7.46)	0	0.13	0.94	56
22	8 (7.81)	15 (16.35)	1 (0.93)	15 (13.62)	14 (12.71)	4 (5.58)	0	0.84	0.66	34
23	18 (18.86)	41 (41.95)	3 (2.61)	34 (33.86)	32 (30.56)	13 (13.16)	0	0.19	0.91	105
24	20 (19.68)	42 (42.77)	3 (3.04)	32 (31.04)	31 (30.39)	11 (12.08)	0	0.16	0.92	93
25	15 (17.22)	29 (30.02)	3 (2.13)	21 (21.96)	27 (24.76)	11 (9.91)	0	1.04	0.59	79
26	20 (22.28)	41 (41.59)	4 (3.13)	33 (34.37)	34 (32.20)	16 (14.44)	0	0.81	0.67	64
27	20 (23.36)	38 (39.04)	4 (2.76)	33 (34.89)	36 (33.14)	18 (15.81)	0	1.72	0.42	107
28	27 (26.55)	42 (42.51)	4 (4.11)	37 (36.17)	34 (33.71)	15 (15.95)	0	0.09	0.95	76
29	18 (19.56)	28 (25.48)	6 (5.66)	30 (33.41)	15 (16.92)	17 (12.97)	0	2.21	0.33	68
30	15 (16.66)	27 (29.14)	5 (4.01)	32 (31.48)	22 (19.10)	11 (11.61)	0	1.05	0.59	60
31	20 (19.21)	28 (28.21)	4 (4.31)	33 (32.16)	20 (20.12)	12 (12.98)	0	0.15	0.93	74
32	26 (25.99)	19 (19.67)	3 (2.92)	20 (19.41)	23 (22.34)	12 (12.68)	0	0.10	0.95	44
33	39 (38.04)	27 (26.26)	4 (4.48)	31 (30.78)	29 (30.19)	20 (20.25)	0	0.15	0.93	110
34	27 (26.66)	24 (22.03)	2 (2.36)	24 (25.43)	24 (26.20)	18 (16.32)	0	0.67	0.71	68
35	31 (33.82)	31 (30.99)	5 (3.95)	28 (30.50)	34 (32.62)	21 (18.11)	0	1.24	0.54	83
36	26 (26.47)	21 (20.50)	1 (0.94)	23 (23.89)	31 (31.25)	19 (17.95)	0	0.12	0.94	75
37	59 (62.40)	54 (58.42)	5 (3.59)	43 (42.10)	81 (74.47)	28 (29.01)	0	1.70	0.43	144
38	25 (24.37)	21 (20.41)	1 (1.23)	15 (14.96)	27 (27.98)	11 (11.04)	0	0.11	0.95	60
39	24 (23.19)	20 (19.03)	1 (1.34)	18 (18.14)	24 (25.46)	13 (12.84)	0	0.25	0.88	68
40	26 (26.75)	21 (20.55)	2 (1.82)	15 (16.09)	27 (27.03)	13 (11.77)	0	0.25	0.88	70
41	49 (47.72)	46 (44.40)	5 (5.68)	32 (32.28)	44 (46.23)	20 (19.68)	0	0.29	0.87	120
42	21 (21.24)	24 (24.23)	2 (1.90)	17 (17.00)	26 (25.63)	10 (9.99)	0	0.02	0.99	74
43	61 (60.31)	21 (19.49)	2 (2.40)	12 (12.65)	38 (39.88)	16 (15.27)	0	0.35	0.84	86
44	45 (45.82)	18 (18.24)	4 (3.65)	11 (11.59)	29 (28.36)	12 (11.35)	0	0.13	0.94	72
45	45 (43.65)	16 (16.46)	2 (2.40)	15 (13.30)	29 (29.27)	12 (13.92)	0	0.60	0.74	61
46	56 (52.40)	13 (12.36)	3 (4.73)	15 (11.92)	19 (21.10)	10 (13.48)	0	2.82	0.24	64
47	29 (30.39)	9 (9.88)	4 (3.25)	8 (8.61)	16 (14.56)	9 (8.31)	0	0.56	0.76	43
48	43 (44.16)	11 (10.20)	2 (1.75)	14 (15.84)	23 (23.27)	22 (19.79)	0	0.59	0.74	80
49	38 (39.85)	10 (9.79)	1 (0.63)	9 (11.02)	28 (27.09)	18 (15.62)	0	1.07	0.59	69
50	48 (50.43)	12 (12.48)	2 (1.30)	11 (12.99)	33 (31.12)	20 (17.69)	0	1.23	0.54	88
51	62 (65.33)	17 (16.83)	3 (2.07)	16 (19.43)	41 (39.37)	29 (24.97)	0	1.91	0.38	122
52	49 (51.30)	10 (11.45)	2 (1.22)	9 (10.03)	33 (30.18)	16 (14.82)	0	1.26	0.53	75
53	59 (59.34)	11 (9.93)	1 (1.05)	9 (10.28)	30 (30.89)	19 (17.51)	0	0.43	0.81	83
54	85 (84.48)	8 (7.42)	4 (4.34)	7 (6.91)	19 (19.75)	13 (13.10)	0	0.11	0.95	79
55	107 (109.73)	16 (14.98)	5 (4.08)	5 (8.82)	41 (40.57)	20 (15.82)	0	3.11	0.21	129
56	45 (45.67)	7 (7.46)	2 (1.70)	5 (5.30)	20 (19.21)	9 (8.66)	0	0.15	0.93	47
57	75 (76.67)	10 (9.81)	3 (2.45)	10 (11.92)	29 (28.39)	23 (20.76)	0	0.73	0.69	117
58	56 (55.97)	10 (8.38)	2 (2.25)	7 (8.36)	20 (21.59)	15 (13.45)	0	0.86	0.65	73
59	52 (53.66)	7 (9.10)	4 (3.01)	4 (3.93)	23 (20.23)	6 (6.08)	0	1.25	0.54	73
60	71 (71.73)	15 (13.67)	2 (1.93)	4 (5.92)	36 (36.82)	12 (9.92)	0	1.22	0.54	84
61	60 (60.57)	9 (9.27)	1 (0.83)	4 (4.35)	32 (31.36)	9 (8.62)	0	0.10	0.95	57
62	70 (71.78)	10 (9.47)	2 (1.53)	4 (6.33)	31 (30.48)	15 (12.40)	0	1.63	0.44	105
63	73 (75.87)	11 (11.20)	2 (1.24)	5 (7.79)	39 (37.02)	18 (14.88)	0	2.34	0.31	83
64	89 (88.77)	1 (1.09)	0 (0.06)	1 (0.68)	18 (18.09)	5 (5.36)	0	0.19	0.91	60

Table 2 (continued)

Population no.[a]	Gm									Km[d] (1)+
	1,3;5	1;21	1	1,2;21	1,3;5,21	1,2,3;5,21	3;5	χ^{2c}	P	
65	101 (101.17)	1 (1.68)	1 (0.84)	1 (0.62)	13 (12.29)	3 (3.40)	0	0.62	0.73	56
66	109 (108.72)	1 (0.51)	0 (0.15)	0 (0.08)	8 (8.62)	1 (0.92)	0	0.73	0.69	47
67	84 (84.29)	4 (3.81)	1 (0.94)	2 (2.49)	20 (20.02)	9 (8.46)	0	0.15	0.93	72
68	65 (65.50)	4 (4.25)	2 (1.75)	1 (1.36)	16 (15.51)	4 (3.62)	0	0.20	0.90	64
69	106 (105.56)	5 (4.75)	2 (2.23)	3 (2.69)	20 (20.44)	8 (8.33)	0	0.09	0.95	74
70	142 (142.80)	12 (13.03)	4 (3.57)	7 (7.00)	46 (44.60)	16 (16.00)	0	0.18	0.91	138
71	80 (80.08)	1 (0.79)	3 (2.96)	1 (1.32)	3 (3.19)	5 (4.66)	0	0.17	0.92	33
72	101 (100.81)	2 (1.72)	4 (4.16)	0 (0.00)	6 (6.31)	0 (0.00)	0	0.07	0.79	57
73	174 (175.52)	1 (2.93)	5 (3.84)	0 (0.37)	17 (14.71)	2 (1.62)	0	2.46	0.29	89
74	82 (82.35)	2 (2.46)	3 (2.74)	3 (3.05)	10 (9.46)	9 (8.95)	0	0.14	0.93	79

[a] Numerical order of populations corresponds to the order listed in Table 3
[b] Numbers before parentheses are observed phenotype numbers. Numbers in parentheses are Hardy-Weinberg expected numbers
[c] Chi-square is presented for testing the goodness of Hardy-Weinberg fit. P values were computed by standard χ^2 goodness-of-fit test. Degree of freedom (df) = number of phenotype − number of haplotype
[d] Numbers under the Km (1)+ are observed phenotype numbers. Test for the goodness of fit for Km was not done as $df = 0$

P_B is the frequency of this haplotype in Mongoloid populations, and P_H is the frequency in the hybrid population.

Results

A total of seven Gm phenotypes were found in 74 populations (Table 2). The corresponding haplotypes for these phenotypes were $Gm^{1,3;5}$, $Gm^{1;21}$, Gm^{1}, $Gm^{1,2;21}$, and $Gm^{3;5}$. Several atypical phenotypes [Gm(1;5), Gm(1;5,21), and Gm(1,2,3;21)] with frequencies averaging less than 0.5% were observed, but are not included in this paper. For all populations, the distribution of Gm phenotypes was in accordance with Hardy-Weinberg equilibrium ($0.99 > P > 0.11$) as shown in Table 2.

On the basis of Gm haplotypes and computed genetic distances, the phylogenetic tree of the 74 populations studied was constructed (Fig. 2). These populations could be divided into two clusters, Yellow River origin and Yangtze River origin. The Yellow River cluster, populations no. 1–42, include Han living in northern China (no. 14, 15, 17, 18, 20, 21, 23, 24, 27–31, 33–42), Uygur (no. 1), Kazak (no. 2), Dongxiang (no. 3), Oroqen (no. 4), Mongol (no. 5, 22, 25), Korean (no. 6, 9, 16), Yugur (no. 7), Manchu (no. 8), Tibetan (no. 10, 11), Hui (no. 12, 13, 19), Xibo (no. 26), and Boan (no. 32). The Yangtze River cluster, populations no. 43–74, include Han living in southern China (no. 43, 44, 46–50, 52–62, 68–70), Tujia (no. 45), Bai (no. 51), Yi (no. 63), Miao (no. 64), Bouyei (no. 65), Shui (no. 66), She (no. 67), Mulao (no. 71), Zhuang (no. 72), Dong (no. 73), and Jing (no. 74).

The results show evidence of marked heterogeneity in the distribution of Gm phenotypes, with striking differences between the two clusters (Fig. 3). The Yellow River populations possess high frequencies of $Gm^{1;21}$ (0.28–0.56) and $Gm^{1,2;21}$ haplotypes (0.11–0.24). In contrast, the Yangtze River populations are characterized by a high frequency of $Gm^{1,3;5}$ (0.46–0.92), and low frequencies of $Gm^{1;21}$ (0.02–0.26) and $Gm^{1,2;21}$ (0.0–0.17) haplotypes. The geographical boundary between the two clusters is near the latitude of 30° N.

To measure the percentage of Caucasoid gene mixture, we have estimated m, the fraction of a given genetic marker contributed by a given racial group, using $Gm^{3;5}$ haplotype as a

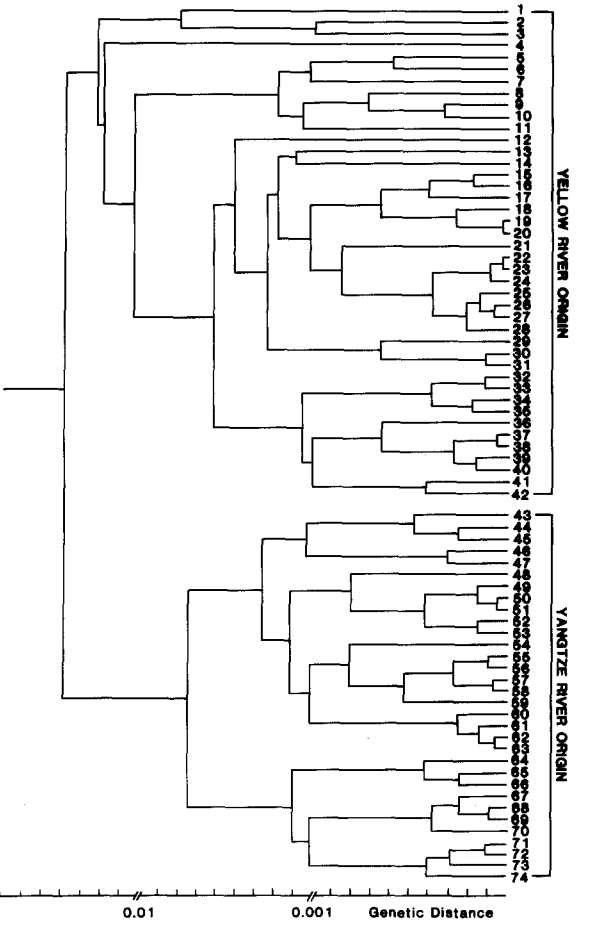

Fig. 2. Phylogenetic tree of 74 populations constructed by unweighted pair-group clustering method (Sneath and Sokal 1973). The genetic distances were calculated according to Nei (1972) on the basis of Gm haplotype frequency. The *numbers* on the right are the population numbers, which correspond to those in Tables 2 and 3. The 74 Chinese populations, independent of nationality, are divided into two clusters at the level of a genetic distance of 0.48. The geographical boundary between two clusters is near the latitude of 30° N

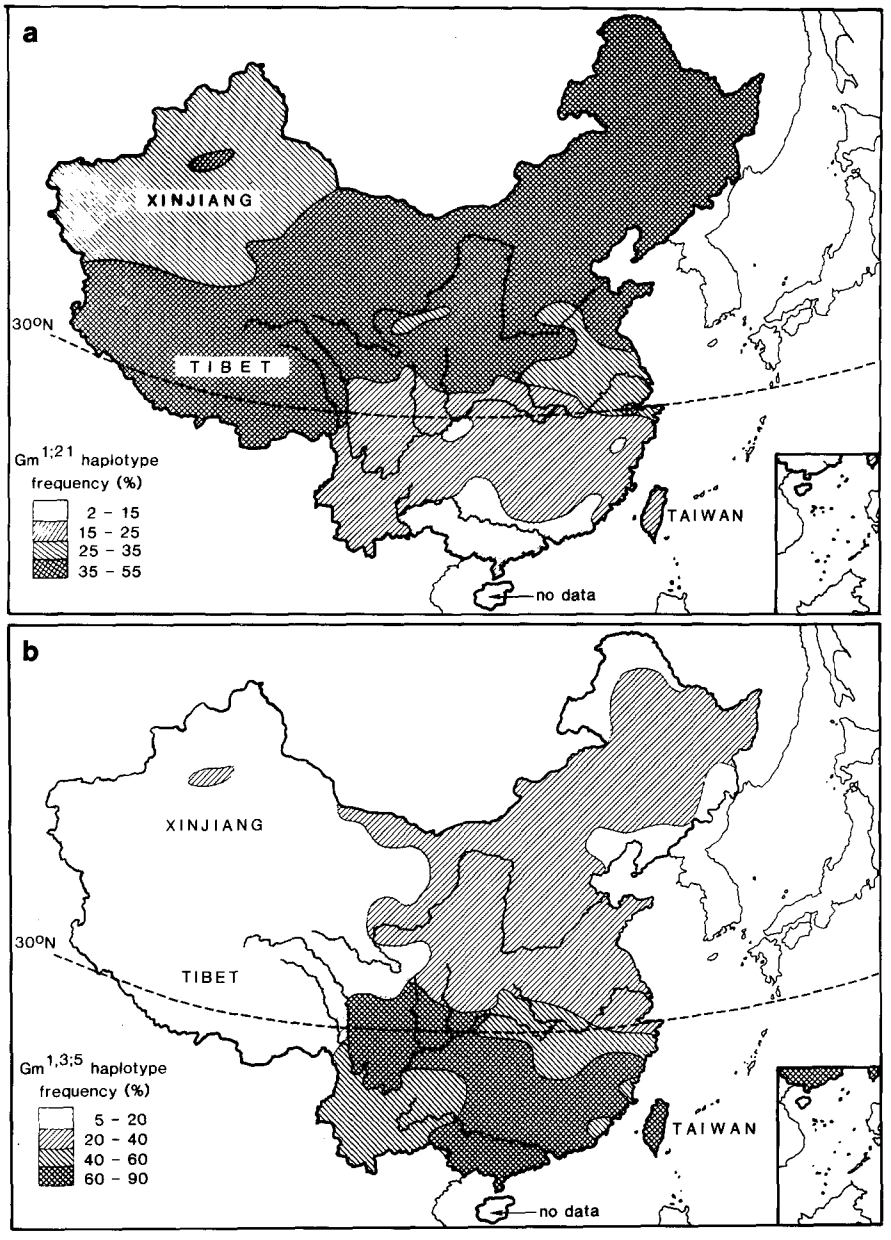

Fig. 3. Distribution of **a** $Gm^{1;21}$ and **b** $Gm^{1,3;5}$ haplotype. Taiwanese data are derived from Matsumoto (1982)

Table 3. Frequencies ($\times 10^{-4}$) of Gm haplotypes and Km^1 gene in 74 Chinese populations

Population			Gm						Km	
No.[a]	Nationality	Location	N[b]	1,3;5	1;2	1	1,2;21	3;5	N	Km^1
1	Uygur	Xinjiang	259	714	2,934	1,393	1,238	3,721	268	2,670
2	Kazak	Yinin	104	1,408	3,447	1,561	1,227	2,357	106	3,484
3	Dongxiang	Linxia	99	1,510	3,461	1,898	1,347	1,784	99	2,615
4	Oroqen	Shibazhan	106	383	4,013	4,291	1,313	0	106	1,205
5	Mongol	Hailar	148	2,020	5,236	1,082	1,662	0	148	2,466
6	Korean	Yanbian	105	1,511	5,453	1,436	1,600	0	105	3,984
7	Yugur	Sunan	48	1,460	4,883	1,428	2,229	0	48	2,500
8	Manchu	Qinlong	104	1,800	4,992	1,976	1,232	0	104	4,629
9	Korean	Liaoyang	89	1,242	5,126	2,171	1,461	0	91	3,453
10	Tibetan	Gannian	92	1,443	4,736	2,086	1,735	0	93	3,044
11	Tibetan	Lasha	103	605	5,624	2,305	1,466	0	103	3,245
12	Hui	Changji	103	2,739	3,739	1,468	1,079	975	104	3,206
13	Hui	Ninxia	175	2,201	3,821	1,295	1,914	769	174	4,128
14	Han	Wuwei	148	1,844	4,032	1,701	2,423	0	150	4,708
15	Han	Changchun	153	2,800	4,052	1,120	2,028	0	156	4,629

Table 3 (continued)

Population			Gm						Km	
No.[a]	Nationality	Location	N^b	1,3;5	1;2	1	1,2;21	3;5	N	Km[1]
16	Korean	Shenyang	117	2,689	4,015	988	2,308	0	117	4,376
17	Han	Dalian	177	2,918	3,700	1,283	2,099	0	177	4,276
18	Han	Harbin	235	2,293	4,206	1,388	2,113	0	238	3,390
19	Hui	Dalian	83	2,489	3,951	1,355	2,205	0	83	2,802
20	Han	Jinan	153	2,553	3,919	1,248	2,280	0	153	4,399
21	Han	Shijiazhuang	105	2,385	4,379	1,747	1,489	0	107	3,096
22	Mongol	Baotou	57	2,637	4,228	1,278	1,857	0	57	3,648
23	Han	Xinin	141	2,542	4,262	1,360	1,836	0	141	4,947
24	Han	Taiyan	139	2,564	4,262	1,479	1,695	0	139	4,247
25	Mongol	Huhehaote	106	2,855	4,090	1,418	1,637	0	106	4,953
26	Xibo	Shenyang	148	2,690	4,044	1,453	1,813	0	148	2,466
27	Han	Luyang	149	2,826	3,935	1,361	1,878	0	150	4,646
28	Han	Xian	159	2,784	3,807	1,608	1,801	0	159	2,775
29	Han	Anyang	114	2,475	2,999	2,228	2,298	0	114	3,648
30	Han	Shangqiu	112	2,404	3,548	1,892	2,156	0	112	3,186
31	Han	Xuzhou	117	2,565	3,353	1,919	2,163	0	118	3,894
32	Baoan	Ganshu	103	3,614	3,000	1,683	1,703	0	103	2,432
33	Han	Nantong	150	3,596	2,798	1,728	1,878	0	150	4,836
34	Han	Nanyang	119	3,530	3,118	1,409	1,943	0	119	3,453
35	Han	Rugao	150	3,394	3,203	1,624	1,779	0	150	3,317
36	Han	Wuhu	121	3,880	3,329	880	1,911	0	121	3,714
37	Han	Taichang	270	3,790	3,639	1,154	1,417	0	273	3,126
38	Han	Changshu	100	3,950	3,542	1,110	1,398	0	100	3,675
39	Han	Hefei	100	3,795	3,355	1,158	1,692	0	100	4,343
40	Han	Ninbe	104	3,919	3,316	1,321	1443	0	104	4,282
41	Han	Shanghai	196	3,517	3,353	1,702	1,428	0	200	3,675
42	Han	Xiaoshan	100	3,432	3,734	1,378	1,456	0	100	4,901
43	Han	Wenzhou	150	5,201	2,556	1,264	979	0	150	3,468
44	Han	Sashi	119	4,696	2,537	1,751	1,016	0	119	3,715
45	Tujia	Ensi	119	4,802	2,561	1,419	1,218	0	119	3,019
46	Han	Wuhan	116	4,999	1,819	2,019	1,163	0	116	3,305
47	Han	Kumming	75	4,617	2,103	2,080	1,200	0	75	3,468
48	Han	Jinhua	115	5,084	1,989	1,234	1,692	0	115	4,483
49	Han	Nanchang	104	5,459	2,386	779	1,376	0	104	4,199
50	Han	Huangshi	126	5,391	2,291	1,016	1,302	0	126	4,508
51	Bai	Dali	168	5,223	2,243	1,111	1,423	0	168	4,767
52	Han	Wanxian	119	5,632	2,252	1,011	1,105	0	119	3,919
53	Han	Panzhihua	129	5,940	2,016	902	1,142	0	129	4,028
54	Han	Chongquing	136	6,294	1,154	1,787	765	0	136	3,526
55	Han	Chendu	194	6,209	1,684	1,450	657	0	200	4,042
56	Han	Fuzhou	88	5,947	1,836	1,390	827	0	89	3,130
57	Han	Yichuen	150	5,985	1,581	1,278	1,156	0	150	5,310
58	Han	Santou	110	5,846	1,679	1,430	1,046	0	110	4,200
59	Han	Guiyang	96	5,913	1,782	1,770	535	0	95	5,188
60	Han	Changsha	140	6,078	2,163	1,176	583	0	140	3,675
61	Han	Xiamen	115	6,455	2,112	852	581	0	115	2,898
62	Han	Shaoyang	132	6,376	1,810	1,077	737	0	135	5,286
63	Yi	Xichang	148	6,303	1,984	916	797	0	148	3,373
64	Miao	Taijiang	114	8,751	907	74	268	0	114	3,118
65	Bouyei	Duyun	120	8,382	611	838	169	0	120	2,697
66	Shui	Sandu	119	9,211	393	354	42	0	119	2,222
67	She	Jingning	120	7,544	1,106	883	467	0	120	3,675
68	Han	Meixian	92	7,171	1,176	1,379	274	0	92	4,483
69	Han	Guangzhou	144	7,409	958	1,243	390	0	144	3,028
70	Han	Liuzhou	227	6,776	1,450	1,254	520	0	234	3,595
71	Mulao	Luocheng	93	7,666	224	1,783	327	0	93	1,968
72	Zhuang	Nannin	113	7,719	362	1,919	0	0	115	2,898
73	Dong	Guangxi	199	8,105	456	1,389	50	0	199	2,565
74	Jing	Fangchen	109	7,249	598	1,586	567	0	109	4,754

[a] Population numbers are the same as those used in this paper
[b] Number tested

marker. A pooled frequency of $Gm^{3;5}$ haplotype in European Caucasian populations (P_A) is approximately 0.70 (Johnson et al. 1977). The frequency of this haplotype in Mongoloid populations (P_B) is almost 0.0 in multiple studies (Johnson et al. 1977; Steinberg and Cook 1981; Matsumoto et al. 1982; Zhao et al. 1983; de Lange et al. 1985). Therefore, it is reasonable to assume that the $Gm^{3;5}$ haplotype in the four Chinese minorities originated from contact with Caucasian populations. According to the above formula, $m = P_H/0.7$, using frequencies in Table 3, m is determined to be 0.53 in Uygur, 0.34 in Kazak, 0.25 in Dongxiang, 0.14 in Hui living in Changji, and 0.11 in Hui living in Ninxia.

In the subjects sampled, the Km^1 gene frequencies range from 0.12 to 0.53 (Table 3). The overall distribution of Km^1 gene frequencies appears to be random.

Discussion

Han is the major Chinese nationality, comprising approximately 93.3% of the total population. According to the distribution of Gm haplotypes, the Han nationality can be divided into two clusters (Fig. 2). The phylogenetic tree clearly indicates that the Han nationality is not a homogeneous population. In fact, the heterogeneity of the Han can be traced back to the Xia tribe (Xia Dynasty, 2205 B.C. – 1766 B.C.), which inhabited primarily the Yellow River region. Over thousands of years, the Chinese minorities have been absorbed and integrated into the major nationality of the Han (Chen 1987). From physical anthropology studies, the heterogeneity of the Han nationality is evident. Northern Chinese are taller with longer facial features than their shorter counterparts in the south, who have rounder facial features (Wang 1986).

The phylogenetic tree (Fig. 2) demonstrates that the distribution of Gm haplotypes of the minorities residing in the northern part of China are similar to those of the northern Han nationality. Likewise, the minorities residing in the south also belong to the same cluster as the southern Han. In other words, the genetic differences between the northern and southern Han are greater than the differences between the Han nationality and the minorities. This reinforces the distinction between nationality and race. A nationality is a group of people with the same language, custom, culture, and religion. On the other hand, race is based on biological traits. Genetic traits should continue to be inherited despite the regrouping, segregation, or difference in development of an ethnic culture. Indeed, the Han nationality and the other 55 minorities of China all belong to the Mongoloid race.

It has been proposed that the Chinese Han originally resided in the Yellow River area and then integrated with other minorities into the largest nationality in China (Jian 1983). Our studies show that the Han nationality is not a homogeneous population. Cluster analysis of 24 nationalities indicates that there are two distinct clusters, southern and northern. These results are consistent with our earlier hypothesis (Zhao et al. 1987; Lee et al. 1988) that the Chinese nation originated from the Yellow River valley (north) and the Yangzte River valley (south).

Cluster analysis of the 74 populations shows a parallel relationship between geographical distance and genetic differentiation. Certain nationalities that are close geographically are separated by small genetic distance. This pattern suggests that migration and admixture of genes have been limited by the natural boundaries of mountain ranges and rivers. For instance, the Tibetans of Tibet inhabit an area southwest of China, but belong to the Yellow River cluster (Fig. 2). An explanation is that the Hengduan Mountains separate the Yangtze River from Tibet. The northern population from the Yellow River would have found it easier to migrate into Tibet, whereas southern groups would have been hindered by this mountain range. Furthermore, the physical characteristics of the Tibetan people are basically similar to those of the minorities and of the Han nationality living in the provinces of northwestern and northern China (Zhang 1985).

The differences in gene frequencies between the two clusters of Chinese populations were found not only in Gm but also in other genetic markers, such as blood groups and HLA (Table 4). The HLA system is the most polymorphic genetic system in man. Variations in the frequencies of various HLA specificities within and between various ethnic groups provide information useful in the characterization of these ethnic groups. Table 4 shows that the southern Chinese have higher frequencies of HLA-A11 and B15 antigens and of the A2-Bw46, A11-B15, and A11-B40 haplotypes. The frequencies of these HLA specificities in southern Chinese were about twice those of northern Chinese. In contrast, the northern Chinese have higher frequencies of HLA-A1, B8, and B12 antigens and the A1-B37 and A3-B40 haplotypes. Recently, HLA-A, B, C, and DR antigens were determined in a study of 2,441 individuals from 14 Chinese populations. The results indicate that the Han nationality can be divided into two distinct groups based on significant differences in HLA antigen fre-

Table 4. Frequencies of some genetic markers in southern and northern Chinese[a]

Locus	Gene or haplotype	Southerner	Northerner
ABO	A	0.280	0.1986
	B	0.1819	0.2331
	O	0.6101	0.5683
MN	M	0.6533	0.5013
	N	0.3467	0.4987
Rh	cde	0.0067	0.0380
	CDe	0.7284	0.5901
	cDE	0.1416	0.2417
GLO	GLO^1	0.1213	0.1750
	GLO^2	0.8787	0.8250
HLA	A1	0.0166	0.0603
	A11	0.3019	0.1598
	A30	0.0110	0.0439
	B8	0.0079	0.0143
	B12	0.0095	0.0472
	B15	0.1303	0.0931
	A1, B37	0.0009	0.0132
	A2, Bw46	0.0527	0.0249
	A3, B40	0.0003	0.0114
	A11, B15	0.0691	0.0294
	A11, B40	0.0623	0.0268

[a] Data are derived from Zhao (1987). The total numbers tested were 326,460 for ABO; 20,962 for MN; 15,938 for Rh; 1,371 for GLO; and 1,835 for HLA

Table 5. Gm haplotype frequencies of some populations selected for comparison with those reported in this paper[a]

No.	Population (location)	Gm haplotype frequency ($\times 10^{-3}$)							
		1,3;5	1;21	1	1,2;21	3;5	1,17;5	1,17;5,6	1,17;5,6,14
75	Mazanderanian (Iran)	26	143	85	7	738	0	0	0
76	Gilanian (Iran)	18	150	88	17	726	0	0	0
77	Uralian (Ural USSR)	0	279	29	85	608	0	0	0
78	Finn (Finland)	0	273	0	143	584	0	0	0
79	English (Britain)	0	229	0	119	652	0	0	0
80	Athabascan (Alaska, USA)	56	468	143	333	0	0	0	0
81	Eskimo (Alaska, USA)	52	683	254	11	0	0	0	0
82	Koryak (Kamchatka, USSR)	31	714	200	55	0	0	0	0
83	Yakut (Yakutskaja, USSR)	94	552	267	87	0	0	0	0
84	Ainu (Hokkaido, Japan)	43	571	252	134	0	0	0	0
85	Japanese (Mainland, Japan)	129	450	261	159	0	0	0	0
86	Buriat (South Burtskaja, USSR)	111	492	272	125	0	0	0	0
87	Buriat (North Buratskaja, USSR)	58	473	307	162	0	0	0	0
88	Japanese (Okinawa, Japan)	83	434	262	221	0	0	0	0
89	Korean (Cheju Island, Korea)	87	483	231	199	0	0	0	0
90	Pima (Arizona, USA)	26	910	6	57	0	0	0	0
91	Quechuan (Andes, Peru)	26	865	16	93	0	0	0	0
92	Machiguenga (Amazon, Peru)	4	735	4	257	0	0	0	0
93	Tibetan (Xizhang, China)	61	650	130	159	0	0	0	0
94	Mongol (Mongolia)	238	431	229	102	0	0	0	0
95	Taiwanese (Taiwan, China)	643	222	47	87	0	0	0	0
96	Kazadan (Borneo)	973	15	0	12	0	0	0	0
97	Thai (Thailand)	899	44	15	42	0	0	0	0
98	Negrito (Luzon)	759	136	0	100	0	0	0	0
99	Indonesian (Java)	751	127	5	116	0	0	0	0
100	Indonesian (Celebes)	766	156	0	78	0	0	0	0
101	Gooshan (Taiwan, China)	762	194	2	42	0	0	0	0
102	Negrito (Mindanao)	672	120	0	208	0	0	0	0
103	Keneba (Gambia)	0	1	35	0	0	793	167	4
104	Kuambi (Southwest Africa)	0	1	0	0	0	773	143	83
105	Tonga (Zambia)	0	1	50	0	0	633	248	69
106	Tonga (Mocambique)	0	1	65	0	0	648	124	162
107	Xhosa (South Africa)	7	105	254	0	0	442	83	108

[a] Data in the above table are derived from Johnson et al. (1977) and Matsumoto et al. (1982). Populations 75–79 are Causasoid; 80–102 are Mongoloid; and 103–107 are Negroid

quencies between southern and northern Han (Lee et al. 1988).

Although we propose the Yellow River valley and the Yangtze River valley as the original sites of Chinese ancestors, the exact time and locations have not been determined. Data from paleoanthropology and archaeology trace the Chinese in these areas back to neolithic times (3000–7000 years ago). Wu and Zhang (1985) studied 17 metric traits of neolithic skulls from China and divided the skulls into three groups, i.e., south China group, eastern subgroup of north China, and western subgroup of north China. Chen (1986) compared eleven physical characteristics between neolithic man and later paleolithic man. He concluded that "the neolithic man in China can be divided into two large groups: northern China group and southern China group." Wang (1986) studied the cranial metric traits of Chinese neolithic and modern inhabitants. He found that in both neolithic and recent times, northern Chinese have had higher upper facial height, orbital height, and nasal height than southern Chinese. Using Gm and HLA genetic markers, our studies agreed well with the distinction between northern and southern Chinese found in paleoanthropology and archaeology.

In search of the relationship between the Chinese nation and major racial groups, a phylogenetic tree was constructed on the basis of Gm haplotype frequencies of 107 populations listed in Tables 2 and 5 (Fig. 4). Populations 1–74 are Chinese populations typed for Gm in this current investigation. Populations 75–107 are derived from previous Gm allotype studies (Johnson et al. 1977; Matsumoto 1982). At the level of a genetic distance of 1.62, these populations were clustered in three major groups corresponding to Caucasoid, Mongoloid, and Negroid (Fig. 4). At the level of a genetic distance of 0.71 the Mongoloid group was divided into two subgroups, north and south.

The northern Mongoloid cluster includes northern Chinese (populations 4–42, 93), Athabascan (USA no. 80), Eskimo (USA no. 81), Pima (USA no. 90), Japanese (no. 84, 85, 88), Korean (no. 89), Mongolian (no. 94), minorities in the Asian area of the USSR (no. 82, 83, 86, 87), and Peru (no. 91, 92). The southern Mongoloid cluster includes southern Chinese (no. 43–74, 95, 101), Thai (no. 97), Indonesians (no. 96, 99, 100), and Filipinos (no. 98, 102).

The northern Mongoloid group is associated with the racial haplotype $Gm^{1;21}$, while the southern Mongoloid group has the racial haplotype $Gm^{1,3;5}$. According to haplotype distribution, one can hypothesize that the northern Paleomongoloid populations distributed to Korea and Japan. They may have also crossed the Bering Land Bridge into America as forerun-

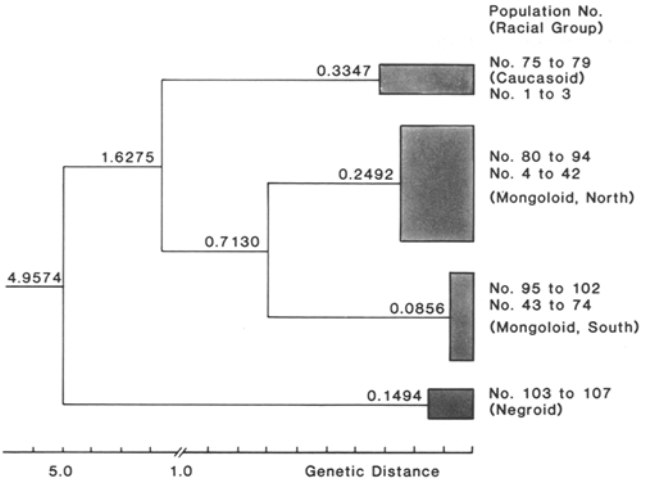

Fig. 4. Profilogram of phylogenetic tree constructed by the unweighted pair-group clustering method (Sneath and Sokal 1973) using Nei's genetic distance (Nei 1972) on the basis of Gm haplotype frequency. Only a short summary of the dendrogram and four main clusters are given. Each check indicates a cluster. The population numbers are the same as those used in this paper. Populations 1–74 are present data; 75–107 are derived from Johnson et al. (1977) and Matsumoto (1982). Populations 75–79 are Caucasoid; 80–102 are Mongoloid; and 103–107 are Negroid. The Mongoloid populations analyzed here can be divided into two groups, north and south

ners to the American Indians. American Indians have a high frequency of $Gm^{1;21}$ haplotype (0.7–0.9). This interpretation agrees with the hypothesis of Williams et al. (1985) that Native Americans originated from northeastern Asia. Southern Mongoloid populations spread into Taiwan, the Philippines, and Indonesia. Southeastern Asians have a high frequency of the $Gm^{1,3;5}$ haplotype (0.7–0.9). As a result of admixture and migration between northern and southern Paleomongoloid populations of China, the frequencies of these distinct racial haplotypes are not as high in current Chinese populations as in the American Indian or the Southeast Asian aborigine.

The time of differentiation of the Mongoloid race into north and south subgroups is not clear. Based on the temporal and morphological sequence of early man in China and his geographical locations, Lin (1987) proposed that early man in China was restricted to an area south of the Yangtze River in the Early Pleistocene (0.7–1.8 million B.P.), and then dispersed to the Qinling Mountain and south of the Yellow River in the early Middle Pleistocene (0.1–0.7 million B.P.). Later, Peking man spread further north of the Yellow River and arrived at a latitude of 40° N, the northern limit of *Homo erectus* so far found in China.

Unexpectedly, three Chinese populations (Uygur, Kazak, and Dongxiang) were clustered together with populations of Finnish, English, Iranian, and Uralian of the USSR. The $Gm^{3;5}$ phenotype was found in four Chinese minorities living in the northwest region of China (Uygur, Kazak, Dongxiang, and Hui). The corresponding genotype of $Gm^{3;5}$ phenotype is homozygous for the haplotype $Gm^{3;5}$, which has been characterized as a Caucasoid haplotype. Therefore, the presence of the $Gm^{3;5}$ phenotype among these populations appears to be the result of admixture from Caucasoid-derived populations. The amount of Caucasian admixture among Uygur, Kazak, and Dongxiang was equal to or greater than 25%. This would explain the clustering of these three populations in the Caucasian group (Fig. 4).

The source of the $Gm^{3;5}$ haplotype in the Chinese populations above can be attributed to Caucasian traders along the Silk Road trade route in ancient China. As early as the Han Dynasty (206 B.C. – 220 A.D.) and on into the Tang Dynasty (618 A.D. – 907 A.D.), China's trade with western countries was developed primarily through the Silk Road (Jian 1983). The Silk Road started from the current city of Xian (capital of the Han and Tang dynasties, no. 28 in Fig. 1), continued westward through Gansu and Xinjiang provinces (Fig. 3), through Samarkand (USSR), Faizabad (Afghanistan), Baghdad (Iraq), and Antalya (Turkey), and finally ended at the Mediterranean Sea (Chen 1987). Over the Silk Road, many trade caravans of Persians, Arabs, and traders from Central Asia entered China, with some traders residing within China (Jian 1983). A recent archaeological discovery was made of six skulls from an ancient cemetery (2,000 B.C.) at Loulan in Xinjiang (Han 1986). Morphological observation and measurements revealed that five of the skulls have Caucasoid characteristics and one skull is a Mongoloid cranium. It was suggested that the ethnic group of Loulan did non consist of a single race. Geographically, the populations of Uygur (no. 1), Kazak (no. 2), Dongxiang (no. 3), and Hui (no. 12, 13) are located along the route of the Silk Road (Fig. 1). One may conclude that the most probable source of the $Gm^{3;5}$ haplotype is by way of the Silk Road.

In conclusion, the model proposed for the separation of the original Mongoloid race into northern and southern subgroups using Gm as a genetic marker is a contribution to the ongoing debate of the origins of man. Genetic distance analysis for protein loci, mtDNA (Cann et al. 1987), and beta-globin gene cluster (Wainscoat et al. 1986) suggests that there was a primary division of human populations into an African and an Eurasian group.

Gm studies agree with the above observation as illustrated in Fig. 4, which shows a close relationship between the Caucasoid and Mongoloid groups. On the other hand, human phylogenetic trees based on blood groups (Cavalli-Sforza and Edwards 1963) and HLA (Piazza et al. 1975; Zhao et al. 1984) indicate a major division between Mongoloid and the Caucasoid-Negroid. The difference in genetic markers used in the investigations above may account for the different theories of divergence between the races. A more distinct racially associated genetic marker will reveal clearer distinctions between different groups. The use of a common specification as a genetic marker will lead to dilution of significant differences between groups. In all the above studies using the genetic markers Gm and DNA polymorphism, a separation between African and non-African patterns is clear. To substantiate the theory that man originated in Africa, further work in both the fields of paleoanthropology and genetics is needed (Stringer and Andrews 1988).

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