Anthropological Science 107 (3), 229-246, 1999

Population Genetic Studies on Nine Aboriginal Ethnic Groups of Taiwan. I. Red Cell Enzyme Systems

Feng Jin[1], Naruya Saitou[2], Takafumi Ishida[3], Cheih-Shan Sun[4], I-Hung Pan[5], Keiichi Omoto[6], and Satoshi Horai[7]

1 Laboratory for Human and Animal Genetic Studies, Institute of Genetics, Chinese Academy of Sciences, Beijing, China
2 Laboratory of Evolutionary Genetics, National Institute of Genetics, Mishima
3 Department of Biological Sciences, Graduate School of Science, University of Tokyo, Tokyo
4 Taidong Hospital, Taidong, Taiwan
5 Department of Bacteriology, College of Medicine, National Taiwan University, Taipei, Taiwan
6 International Research Center for Japanese Studies, Kyoto
7 Department of Biosystems Science, Graduate University for Advanced Studies, Hayama

(Submitted January 18, 1999; Review sent March 11, 1999; Accepted September 8, 1999)

Abstract Population genetic study of nine aboriginal ethnic groups of Taiwan (Ami, Atayal, Bunun, Paiwan, Puyuma, Rukai, Saisiat, Tsou, and Yami) was carried out. Twelve red cell enzymes (AcP, AK, CA1, CA2, EsD, GLO, GPT, GOT, LDH, MDH, PGD, and PGM1) were analyzed by isoelectric focusing method and starch gel electrophoretic method. Six loci (AcP, EsD, GLO, GPT, PGD, and PGM1) were polymorphic. Three alleles (*PGM1*6*, *GPT*6*, and *EsD*7*) were in relatively higher allele frequencies in Taiwan aboriginal populations, and we found homozygotes for those alleles. Phylogenetic relationship based on genetic distances among those ethnic groups more or less fit to their geographical distribution, but not to linguistic classification.

Keywords: Taiwan, Red cell enzyme polymorphism, Gaoshan, IEF Method

Introduction

Taiwan is an island of about 390 kilometers long and 140 kilometers wide, and is situated in the South China Sea between 22-25°N latitude and 120-122°E longitude. It lies 150 kilometers off the Southeastern Coast of Mainland China, and is separated from

Corresponding author: Satoshi Horai
Department of Biosystems Science, Graduate University for Advanced Studies, Hayama
Kanagawa, 240-0193, Japan
TEL: +81-468-58-1575 FAX: +81-468-58-1544 E-mail: horai@soken.ac.jp

Fujian Province by the Taiwan Strait. Southern and eastern neighbors of Taiwan are the Philippines Islands and the Japanese Ryukyu Islands.

About 400 years ago during the Ch'ing Dynasty, aboriginal people covered almost everywhere of the Taiwan Island. Those ethnic minorities were classified in several ways. They were called SHENG-FAN (raw savages), SHU-FAN (domesticated savages), SHAN-FAN (mountain savages), PINGPU-FAN (plains savages), YE-FAN (wild savages), and HUA-FAN (civilized savages) in the Ch'ing Dynasty period. At present, those natives are classified into two major groups, plains people (PING-PU) and mountain people (SHAN-PAO or GAO-SHAN) according to their geographical distribution. The plains people are composed of at least ten ethnic groups, namely Ketagalan, Kavalan, Luilang, Taokas, Pazeh, Papora, Babuza, Thao, Hoanya, and Siraya. Based on the language, cultural and geographical features, mountain people are divided into nine ethnic groups, namely Atayal, Saisiat, Bunun, Tsou, Paiwan, Rukai, Puyuma, Ami, and Yami. Puyuma and Ami occupy the eastern plain although they are called mountain people, and Yami live in the Lan Yu (Botel Tobago) Island. According to the census data of 1990, Ami were the largest (the population size was 129,200), followed by Atayal (78,957), Paiwan (60,434), and Bunun (38,267). Population sizes of other tribes were fairly less than the above four ethnic groups; 8,132, 8,007, 5,797, 4,335, and 4,194, for Puyuma, Rukai, Tsou, Yami, and Saisiat, respectively. Today, the aboriginal population of Gaoshan people is less than 2% of the total population of Taiwan.

Linguistically, aboriginal peoples of Taiwan belong to Atayalic, Tsouic, and Paiwanic branches of Austronesian subfamily of the Austric Language family (Table 1; based on Ruhlen, 1987). Plains residents are generally considered to be sinicized people who speak ten dialects of the Paiwanic branch. Mountain people use native, or non-sinicized languages.

The origin of the so-called aborigines of Taiwan has long been a question of anthropologists. There have been several hypotheses on the origin: they came from west, namely mainland China; or from south, namely the Philippines; or from some different sources. The western origin hypothesis is based on their custom of hair cropping and body tattooing, and worshiping snakes as their ancestors as well as the geographical location. Another theory says that their language and culture bear resemblance to the Malays from the Philippines and Borneo, therefore, they must have come from south. A third theory proposes that those minorities originated from a branch of ancient Baiyue ethnic group living along the coast of mainland China during stone age, and later, they were joined by immigrants from the Philippines, Borneo and Micronesia (Ma, 1989).

Many physical anthropological studies were carried out in the past. At the end of the 19th century and the beginning of the 20th century, Torii Ryuzo made a series of studies on culture and morphology of Taiwan natives (Torii, 1910, 1922). Chai (1967) conducted anthropological survey on the history and classification, population and family structure, anthroposcopic observations, anthropometric measurements, PTC taste sensitivity, blood pressure, dermatoglyphics and intelligence in eight ethnic groups.

Table 1 Linguistic classification of Taiwan ethnic groups within Austric (from Ruhlen, 1987)

Austric
- 1. Miao-Yao
- 2. Austroasiatic
- 3. Austro-Tai
  - A. Daic
  - B. Austranesian
    - 1. Atayalic: Atayal, Sedeq
    - 2. Tsouic
      - (1) Rukai
      - (2) Tsouic Proper
        - Northern: Tsou
        - Southern: Kanakanabu, Saaroa
    - 3. Paiwanic: Bunun, Paiwan, Puyuma, Saisiat, Ami
      - Sinicized: Kavalan, Pazeh, Thao, Ketangalan, Basay, Taokas, Papora, Babuza, Hoanya, Siraya
    - 4. Malayo-Polynesian
      - Western Malayo-Polynesian: Chamoro, Palauan, Yapese
      - Northern Philippines
        - a. Northern Luzon
        - b. Bashiic-Central Luzon-Northern Mindoro
          - I. Basiic: Yami
          - II: Central Luzon: Sinauna, Kapampangan
          - III.

Note. Underlined languages correspond to nine Aboriginal ethnic tribes of Taiwan examined in this study.

Genetic studies in Taiwan ethnic minorities started from examination of the ABO blood group (Kutsuna and Matsuyama, 1939; Chou, 1959). MNSs, P, Rh and other blood groups were studied by Huang (1964), Huang and Sheen (1966), and Ikemoto and others (1966), while acatalasemia, Gm, Inv allotypes, and Gc groups were studied by Takahara and others (1968) and Nakajima and Ohkura (1971). Nakajima and others (1967, 1971) studied ABO, MN, Lewis, Rh and other blood groups for several Taiwan aboriginal ethnic groups. Chen and others (1985) examined several blood groups, serum proteins and red cell enzymes in an Atayal (Toroko) population. Kobayashi and others (1992) studied the HLA-DR antigen distributions for Taiwan aborigines and Melton and others (1995) examined mitochondrial DNA 9bp deletion frequencies for those populations. However, no systematic studies have been carried out so far for all the nine mountain ethnic groups of Taiwan.

We therefore collected blood samples of all the nine ethnic groups of Taiwan aborigines in field surveys conducted in 1990 and 1991. Two new genetic variants of ADA have been already reported (Jin and others, 1995) for those samples. Genetic

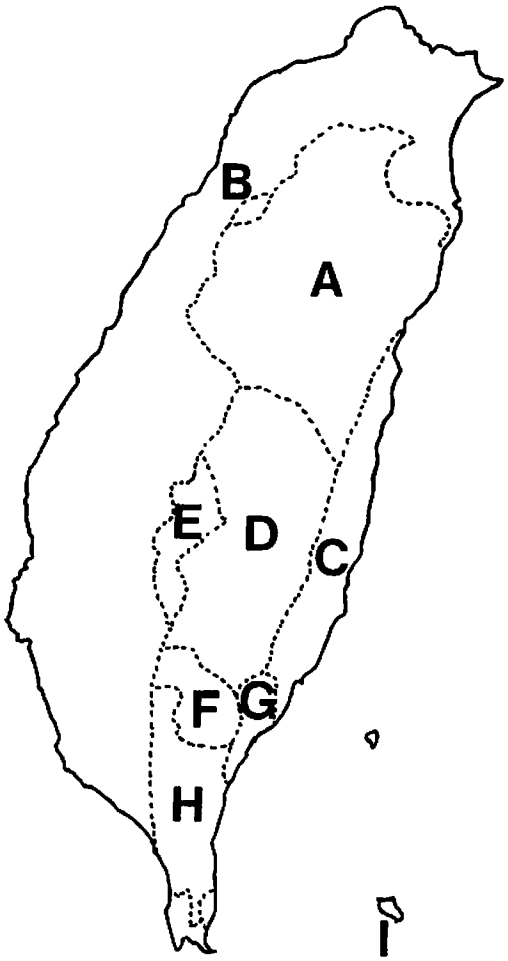

Figure 1 A map of Taiwan and distribution of sampling populations. A: Atayal, B: Saisiat, C: Ami, D: Bunun, E: Tsou, F: Rukai, G: Puyuma, H: Paiwan, and I: Yami.

polymorphisms of two plasma proteins were also reported (Umetsu and others, 1994, 1995), as well as examination of HTLV-I antigen (Ishida and others, 1993). We now produced extensive results on various genetic markers, and start to publish a series of papers regarding the genetic polymorphism of the nine ethnic groups of Taiwan. The present study is the first of this series, and we will present results of twelve red cell enzyme systems.

Materials and Methods

Nine non-sinicized ethnic groups, totaling 654 individuals, were studied. Blood samples were taken from different areas where those ethnic groups are distributed (Figure 1; see

also Figure 1 of Jin and others 1995). One hundred samples for Atayal were taken at Shuiyuan Village of Hualian; 63 samples for Saisiat were taken at Donghe Village of Nanzhuang; 79 samples for Tsou were collected at Dana Village of Wufeng (Dabang); 88 samples for Bunun were collected from the following sites: 41 at Jinping village, 46 at Chulai Village of Guanshan area, and one at Taitung; 72 subjects for Ami were collected at Longchang and Dulan Villages; 61 samples for Puyuma were collected at Lijia, Nanwang and Xiabinlang of Beinan; 53 samples for Rukai were collected at Danan and Dongxing Villages of Danan area; 60 samples for Paiwan were mainly taken at Xinyuan and very few from Paiwan and Taitung areas; 78 samples for Yami were obtained from high school students of five villages of Lanyu island, including Yeyou, Yeyin, Yureng, Hongtou, and Dongqing.

The following 12 red cell enzymes were analyzed: acid phosphatase (AcP), adenylate kinase (AK), carbonate anhydrase 1 (CA1), carbonate anhydrase 2 (CA2), esterase D (EsD), glutamate oxaloacetate transaminase (GOT), glutamate pyruvate transaminase (GPT), glyoxalase I (GLO), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), phosphogluconate dehydrogensae (PGD), and phosphoglucomutase 1 (PGM1).

Condensed erythrocytes were diluted into 1:1 with 0.05M dithiothreitol which enabled red cell enzymes stable for many times of freeze thawing. Starch gel electrophoresis (SGE) for EsD, AK, CA1, CA2, GLO, GOT, PGD, LDH, and MDH was performed on 150×260×6mm glass plate. We mainly followed methods of Harris and Hopkinson (1976). Four enzymes (AcP, EsD, GPT, and PGM1) were typed using the isoelectric focusing (IEF) method. Polyacrylamide gel for IEF was made by acrylamide-bis (21% and 1%, respectively) 2.25ml, DDW 6.60ml, saccharose 1.12g, and Pharmalyte (Pharmacia LKB) 0.6ml. Gel was polymerized by adding 0.08ml riboflavin (0.01%) and illuminated under fluorescent light. Method for enzyme staining was based on Harris and Hopkinson (1976) and Omoto (1980) with some modifications. For experimental procedures in detail, see Jin (1993).

Allele frequencies and average heterozygosities for Taiwan Aboriginal populations and genetic distances based on 13 red cell enzymes systems, including the data for ADA (Jin and others, 1995) were calculated. The standard distance (Nei, 1987) was used as genetic distance measure. Phylogenetic trees were constructed based on the unweighted pair-group method with arithmetic mean (UPGMA) (Sokal and Sneath, 1963) and the neighbor-joining (NJ) method (Saitou and Nei, 1987).

Results and Discussion

Distribution of phenotype frequencies and allele frequencies of the nine Taiwan ethnic groups examined in the present study are listed in Table 2 and Table 3, respectively. Six loci (AcP, EsD, GLO, GPT, PGD, and PGM1) were polymorphic, and results only for those polymorphic loci are presented in these tables. We will describe those polymorphic loci separately, followed by description of six monomorphic loci. Data reported without references are from the data book of Roychoudhury and Nei (1988).

Table 2 The phenotype distribution of 6 polymorphic red cell enzymes in nine Taiwan ethnic minorities

POPULATION	ATAYAL	SAISIAT	TSOU	BUNUN	AMI	PUYUMA	RUKAI	PAIWAN	YAMI
Phenotype	Obs. (Exp.)	Obs. (Exp.)	Obs. (Exp.)	Obs. (Exp.)	Obs. (Exp.)	Obs. (Exp.)	Obs. (Exp.)	Obs. (Exp.)	Obs. (Exp.)
AcP:									
A	0 (0.16)	1 (1.15)	5 (5.32)	2 (0.92)	5 (4.01)	5 (2.77)	5 (4.53)	0 (0.60)	2 (1.70)
AB	8 (7.68)	15 (14.71)	31 (30.36)	14 (16.16)	24 (25.97)	16 (20.46)	21 (21.93)	12 (10.80)	19 (19.61)
B	92 (92.16)	47 (47.15)	43 (43.32)	72 (70.92)	43 (42.01)	40 (37.77)	27 (26.53)	48 (48.60)	57 (56.70)
Total	100 (100.00)	63 (63.00)	79 (79.00)	88 (88.00)	72 (72.00)	61 (61.00)	53 (53.00)	60 (60.00)	78 (78.00)
Chi-Square	0.17 (DF=1)	0.02 (DF=1)	0.03 (DF=1)	1.57 (DF=1)	0.41 (DF=1)	2.89 (DF=1)	0.09 (DF=1)	0.74 (DF=1)	0.07 (DF=1)
EsD:									
1	30 (33.06)	33 (32.86)	51 (49.45)	27 (29.56)	33 (35.42)	18 (17.32)	16 (16.98)	13 (16.02)	48 (48.49)
1-2	55 (48.87)	24 (23.11)	20 (22.15)	48 (42.89)	31 (27.35)	22 (26.11)	20 (20.94)	30 (25.83)	27 (26.02)
2	15 (18.06)	4 (4.06)	3 (2.48)	13 (15.56)	4 (5.28)	13 (9.84)	8 (6.46)	9 (10.42)	3 (3.49)
1-7	0 (0.00)	1 (2.17)	3 (3.96)	0 (0.00)	4 (2.81)	7 (4.26)	8 (5.09)	6 (4.13)	0 (0.00)
2-7	0 (0.00)	0 (0.76)	2 (0.89)	0 (0.00)	0 (1.08)	1 (3.21)	1 (3.14)	2 (3.33)	0 (0.00)
7	0 (0.00)	1 (0.04)	0 (0.08)	0 (0.00)	0 (0.06)	0 (0.26)	0 (0.38)	0 (0.27)	0 (0.00)
Total	100 (100.00)	63 (63.00)	79 (79.00)	88 (88.00)	72 (72.00)	61 (61.00)	53 (53.00)	60 (60.00)	78 (78.00)
Chi-square	1.57 (DF=1)	0.15 (DF=3)	2.07 (DF=3)	1.25 (DF=1)	2.60 (DF=3)	5.23 (DF=3)	3.96 (DF=3)	3.07 (DF=3)	0.11 (DF=1)
GLO:									
1	2 (3.06)	4 (3.81)	5 (6.13)	0 (1.25)	5 (5.01)	0 (1.81)	1 (1.21)	2 (3.27)	0 (0.01)
1-2	31 (28.87)	23 (23.37)	34 (31.75)	21 (18.49)	28 (27.97)	21 (17.39)	14 (13.58)	24 (21.47)	2 (1.97)
2	67 (68.06)	36 (35.81)	40 (41.13)	67 (68.25)	39 (39.01)	40 (41.81)	38 (38.21)	34 (35.27)	76 (76.01)
Total	100 (100.00)	63 (63.00)	79 (79.00)	88 (88.00)	72 (72.00)	61 (61.00)	53 (53.00)	60 (60.00)	78 (78.00)
Chi-square	0.54 (DF=1)	0.01 (DF=1)	0.39 (DF=1)	1.61 (DF=1)	0.00 (DF=1)	2.63 (DF=1)	0.04 (DF=1)	0.83 (DF=1)	0.01 (DF=1)
GPT:									
1	2 (1.44)	1 (1.02)	3 (2.85)	3 (3.09)	9 (8.00)	4 (3.45)	4 (2.08)	7 (3.75)	7 (11.54)
1-2	20 (19.08)	11 (12.44)	24 (24.30)	27 (26.81)	30 (32.00)	21 (22.11)	13 (16.84)	16 (22.50)	38 (30.38)
2	61 (63.20)	40 (38.11)	52 (51.85)	58 (58.09)	33 (32.00)	36 (35.45)	36 (34.08)	37 (33.75)	17 (20.00)
1-6	0 (2.04)	3 (1.52)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	8 (6.54)
2-6	17 (13.52)	7 (9.33)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	7 (8.61)
6	0 (0.72)	1 (0.57)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.93)
Total	100 (100.00)	63 (63.00)	79 (79.00)	88 (88.00)	72 (72.00)	61 (61.00)	53 (53.00)	60 (60.00)	78 (78.00)
Chi-square	4.00 (DF=3)	2.59 (DF=3)	0.01 (DF=1)	0.00 (DF=1)	0.28 (DF=1)	0.15 (DF=1)	2.75 (DF=1)	5.00 (DF=1)	4.77 (DF=3)
PGD:									
A	75 (73.96)	56 (56.19)	46 (43.32)	61 (59.73)	62 (62.35)	50 (50.50)	36 (36.53)	41 (40.84)	53 (51.70)
A-C	22 (24.08)	7 (6.61)	25 (30.36)	23 (25.54)	10 (9.31)	11 (10.01)	16 (14.94)	17 (17.32)	21 (23.61)
C	3 (1.96)	0 (0.19)	8 (5.32)	4 (2.73)	0 (0.35)	0 (0.50)	1 (1.53)	2 (1.84)	4 (2.70)
Total	100 (100.00)	63 (63.00)	79 (79.00)	88 (88.00)	72 (72.00)	61 (61.00)	53 (53.00)	60 (60.00)	78 (78.00)
Chi-Square	0.74 (DF=1)	0.21 (DF=1)	2.46 (DF=1)	0.87 (DF=1)	0.40 (DF=1)	0.59 (DF=1)	0.26 (DF=1)	0.02 (DF=1)	0.95 (DF=1)
PGM1:									
1-	0 (3.06)	1 (0.32)	1 (1.53)	0 (1.92)	0 (0.89)	3 (1.48)	1 (0.68)	0 (0.50)	3 (5.65)
1+/1-	32 (25.37)	7 (7.21)	12 (11.56)	20 (16.99)	13 (10.00)	9 (10.28)	3 (5.32)	5 (5.32)	24 (22.35)
1+	50 (52.56)	39 (40.48)	20 (21.80)	37 (37.57)	24 (28.12)	19 (17.85)	12 (10.42)	14 (14.02)	23 (22.08)
2-/1-	1 (2.97)	0 (1.07)	1 (2.51)	5 (4.14)	2 (1.44)	2 (1.87)	5 (3.28)	0 (0.92)	10 (7.27)
2-/1+	12 (12.33)	15 (12.02)	10 (9.46)	17 (18.30)	8 (8.12)	6 (6.49)	11 (12.86)	6 (4.83)	11 (14.37)
2-	2 (0.72)	0 (0.89)	3 (1.03)	2 (2.23)	0 (0.59)	0 (0.59)	4 (3.97)	0 (0.42)	3 (2.34)
2+/1-	2 (0.52)	0 (0.07)	7 (4.87)	1 (0.74)	1 (2.67)	2 (2.34)	2 (1.36)	6 (3.48)	2 (0.81)
2+/1+	1 (2.18)	1 (0.80)	21 (18.39)	3 (3.27)	21 (15.00)	7 (8.11)	4 (5.32)	16 (18.37)	1 (1.60)
2+/2-	0 (0.25)	0 (0.12)	1 (3.99)	1 (0.80)	2 (2.17)	3 (1.48)	5 (3.28)	4 (3.17)	0 (0.52)
2+	0 (0.02)	0 (0.00)	3 (3.88)	0 (0.07)	0 (2.00)	1 (0.92)	0 (0.68)	6 (6.02)	0 (0.03)
6/1-	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.30)	0 (0.11)	0 (1.56)	0 (0.68)	0 (0.28)	0 (0.27)
6/1+	0 (0.00)	0 (0.00)	0 (0.00)	1 (1.31)	0 (0.62)	6 (5.41)	5 (2.66)	3 (1.45)	1 (0.53)
6/2-	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.32)	1 (0.09)	1 (0.98)	0 (1.64)	0 (0.25)	0 (0.17)
6/2+	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.06)	0 (0.17)	1 (1.23)	1 (0.68)	0 (0.95)	0 (0.02)
6	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.01)	0 (0.00)	1 (0.41)	0 (0.17)	0 (0.04)	0 (0.00)
Total	100 (100.00)	63 (63.00)	79 (79.00)	88 (88.00)	72 (72.00)	61 (61.00)	53 (53.00)	60 (60.00)	78 (78.00)
Chi-Square	3.28 (DF=3)	4.43 (DF=6)	8.82 (DF=6)	4.89 (DF=10)	5.41 (DF=4)	6.73 (DF=10)	9.47 (DF=10)	7.64 (DF=10)	6.81 (DF=10)

AcP

Only two common alleles, *AcP1*A* and *AcP1*B*, were recognized through the IEF method. Observed values were in good agreement with those expected (Table 2). Allele frequencies of *AcP1*A* are very different from population to population, ranging from 4% to near 30% (Table 3). Percentages of *AcP1*A* of other neighboring populations including southern Chinese minorities (Zhao, 1985), Japanese, Korean, and Filipinos vary from 10% to 31%. The Atayal ethnic group has the lowest *AcP1*A* frequency, only 4%, and so far it is also the lowest record in East Eurasian (Asians; see Saitou [1995] for use of major human population cluster names in this paper). Allele *AcP1*C* is absent in most East Eurasian populations, and no *AcP1*C* was found in this study. Another genetic polymorphism study (Windhof and Walter, 1983) suggested that this allele is polymorphic in Filipinos with frequency of 2.4%. Allele *AcP1*C* was also found in Hui ethnic group of north-western China (Xu and Du, 1984) and Malays in Singapore (Blake and others, 1973) with only one case in more than 200 samples. On the other hand, frequency of *AcP1*C* is not so low in many West Eurasian (European) populations.

Table 3 Allele frequencies of six polymorphic red cell enzymes in nine Taiwan Aboriginal populations

Population	AcP		EsD			GLO	
	*AcP*A*	*AcP*B*	*EsD*1*	*EsD*2*	*EsD*7*	*GLO*1*	*GLO*2*
ATAYAL	0.0400	0.9600	0.5750	0.4250	-	0.1750	0.8250
SAISIAT	0.1349	0.8651	0.7222	0.2540	0.0238	0.2460	0.7540
TSOU	0.2595	0.7405	0.7911	0.1772	0.0317	0.2785	0.7215
BUNUN	0.1023	0.8977	0.5796	0.4204	0.0000	0.1193	0.8807
AMI	0.2361	0.7639	0.7014	0.2708	0.0278	0.2639	0.7361
PUYUMA	0.2131	0.7869	0.5328	0.4016	0.0656	0.1721	0.8279
RUKAI	0.2925	0.7075	0.5660	0.3491	0.0849	0.1509	0.8491
PAIWAN	0.1000	0.9000	0.5167	0.4167	0.0666	0.2333	0.7667
YAMI	0.1474	0.8526	0.7885	0.2115	-	0.0128	0.9872

Population	GPT			PGD		PGM1				
	*GPT*1*	*GPT*2*	*GPT*6*	*PGD*A*	*PGD*C*	*PGM*1-*	*PGM*1+*	*PGM*2-*	*PGM*2+*	*PGM*6*
ATAYAL	0.1200	0.7950	0.0850	0.8600	0.1400	0.1750	0.7250	0.0850	0.0150	-
SAISIAT	0.1270	0.7778	0.0952	0.9444	0.0556	0.0714	0.8016	0.1191	0.0079	-
TSOU	0.1899	0.8101	-	0.7405	0.2595	0.1393	0.5253	0.1139	0.2215	-
BUNUN	0.1875	0.8125	-	0.8239	0.1761	0.1477	0.6534	0.1591	0.0284	0.0114
AMI	0.3333	0.6667	-	0.9306	0.0694	0.1111	0.6250	0.0903	0.1667	0.0069
PUYUMA	0.2377	0.7623	-	0.9098	0.0902	0.1557	0.5410	0.0984	0.1229	0.0820
RUKAI	0.1981	0.8019	-	0.8302	0.1698	0.1132	0.4434	0.2736	0.1132	0.0566
PAIWAN	0.2500	0.7500	-	0.8250	0.1750	0.0917	0.4833	0.0833	0.3167	0.0250
YAMI	0.3846	0.5064	0.1090	0.8141	0.1859	0.2692	0.5321	0.1731	0.0192	0.0064

EsD

All samples were examined by both SGE and IEF for EsD. Three common alleles, *EsD*1*, *EsD*2*, and *EsD*7*, were found, which gave rise to six phenotypes, EsD 1-1, EsD 2-1, EsD 2-2, EsD 7-1, EsD 7-2, and EsD 7-7 (Table 2). EsD 7 is a rare variant in elsewhere but this variant was found in all the Taiwan ethnic groups except Atayal, Bunun, and Yami. In Puyuma, Paiwan and Rukai of Southern Taiwan, the frequency of *EsD*7* was as high as about 7-8% (Table 3). Atayal and Bunun are distributed in north-central Taiwan, and their *EsD* allele frequencies are quite similar with each other. Interestingly, both populations lack *EsD*7*. This allele was found as a heterozygote in Yamaguchi Prefecture of Japan (Yuasa and others, 1985). The present study also indicated that the conventional starch-gel electrophoresis is capable but difficult in distinguishing of EsD 7 from EsD 1 isozyme. Probably because of this difficulty, this allele has not been recognized in some population studies including Southern Chinese and Southeast Asians in which the conventional electrophoretic method was used. We suppose that this allele should be common in South-Eastern Asian populations. A further detailed study on neighboring populations is necessary, from which we will be able to have more insights into where this allele came from and how it distributed in other places.

Another study (Chen and others, 1985) on Toroko-aborigines, a branch of Atayal, showed the frequency of about 32% of *EsD*2*, 10 points less than the present result for Atayal. In East Eurasian, frequency of *EsD*2* is generally more than 30%. In southern Chinese minorities and Han Chinese, *EsD*2* frequencies vary from 36% to 42% (Zhao, 1985). Guangzhou Han people and Hainan Li ethnic group have the highest *EsD*2* frequencies, with 48% and 45%, respectively (Li and others, 1989; Omoto and others, 1993). In Japanese, *EsD*2* ranged from 34% to 43%, while Ainu people in Hokkaido has the lowest frequency of less than 32%. However, frequencies of *EsD*2* tend to gradually increase from northern to southern Japan; in Yamaguchi it is 39% (Yuasa and others, 1985), but it reaches at about 43% in Amami Island (Omoto and others, 1975a, 1975b). Among populations of Philippines, Ifugao has highest *EsD*2* frequency, 42.8%, while Visayan, Tagalog, and Filipino are in a range from 27.1% to 30.8% (Omoto and others, 1978; Windhof and Walter, 1983).

GLO

Three common GLO phenotypes, GLO 1-1, GLO 2-1, and GLO 2-2 were observed. Both observed and expected values were in good agreement (Table 2). In the present sample, *GLO*2* was the most common allele in this system (Table 3). In Taiwan ethnic groups, distribution of *GLO*1* allele frequency is rather different from each other. Tsou possess the highest, 28%; and then Ami, 26%; Rukai and Bunun have relatively lower frequencies, 15 and 12%, respectively. In Yami, compared with other Taiwan ethnic groups, *GLO*1* frequency was extremely low, only 1%. The present study indicated that the GLO allele distribution in Taiwan native people is very different from population to population. It is interesting to note that allele frequency of *GLO*1* in East Eurasian is

usually in the range of 10% - 25%. In this sense, Taiwan aborigines are very special with a wide range of allele frequency for *GLO*1*.

GPT

A total of 6 phenotypes, GPT 1-1, GPT 2-1, GPT 2-2, GPT 6-1, GPT 6-2, and GPT 6-6 in Taiwan ethnic groups have been revealed by IEF, indicating the occurrence of three alleles: *GPT*1*, *GPT*2*, and *GPT*6*. Observed and expected values were in good agreement except for Paiwan (Table 2). A total of 60 individuals were examined for Paiwan, and the result showed that the observed value for heterozygote GPT 2-1 was somewhat less than that of expected. The results demonstrated that the *GPT*2* frequencies in Taiwan natives are in a range from 51% to 81%, or 77% in average. Except that of Yami (50.6%), all of the other eight ethnic groups have the highest *GPT*2* frequency compared with previously studied populations in the world (Roychoudhury and Nei, 1988).

The *GPT*6* has also been found in southern Han Chinese and minorities, overseas Chinese, Japanese, Malays, the Philippine populations and New Guineans, mostly with frequency no more than 1%, and just 3% in Ifugao of the Philippines (Chen and others, 1972; Omoto and others, 1978; Long and others, 1986). The distribution of GPT genes in Eurasia and America indicated an obvious gradient following change of latitude, that is, from north to south, *GPT*2* allele increasing from 30-40% to 70-80%. Negrito of the Philippines has the highest *GPT*2* frequency (86%). In southern Chinese minorities, the *GPT*2* allele frequency is generally higher than that of *GPT*1*; while in most Han Chinese and northern minorities, oppositely, the frequency of *GPT*1* is higher than that of *GPT*2*. In Japan, the frequency of *GPT*2* shows a clinal increase from north to south, 40% in Tokyo to 52% in Okinawa.

PGD

Two common PGD alleles, *PGD*A* and *PGD*C* were revealed by the SGE method. Observed and expected values were in a good agreement (Table 2). The results indicated that the distribution of *PGD*C* frequency in the nine ethnic groups is quite different from each other (Table 3). The *PGD*C* allele frequency distribution in southern Chinese minorities, Japanese, the Philippine populations, and some south-east Asian groups demonstrated that this allele frequency is generally not higher than 2% to 8% with very few exceptions. Population studies in East Eurasians revealed an extremely high *PGD* C* allele frequency in Bhutanese, with 23% (Roychoudhury and Nei, 1988). In southern China, Hainan Miao ethnic group showed an extreme example, with 22% *PGD*C* (Roychoudhury and Nei, 1988). Available data indicated that so far only few populations have been found to have the allele frequency more than 10%, they are Mongolians and Koreans in Northern China (Goedde and others, 1984). People in Yaeyama of Japan have the allele frequency of *PGD*C* ranging from 10% to 13% (Omoto, 1980). Compared with published *PGD*C* distribution data, the Tsous in the present study has the highest

frequency in the world so far.

PGM1

Five common alleles, *PGM1*1+*, *PGM1*1-*, *PGM1*2+*, *PGM1*2-* and *PGM1*6* (a rare allele in elsewhere except Taiwan), which produce 14 phenotypes have been observed in the nine Taiwan aboriginal populations, and the observed and the expected values of the phenotypes of six ethnic groups were more or less in a good agreement (Table 2). The chi-square value for Atayal was slightly large, probably because the observed numbers of PGM1 1-/1+ phenotypes are somewhat larger than that of expected. Generally speaking, *PGM1*1+* is the commonest in all of the nine ethnic groups, its allele frequency ranging from 44% to 80%; while the *PGM1*2+* is in the range from 8-27%. In most Asian populations, frequencies of four common subtypes are in the following order: *PGM1*1+* > *PGM1*2+* > *PGM1*1-* > *PGM1*2-*. However, the order of these four subtypes in nine Taiwan ethnic groups (in average) is: *PGM1*1+* > *PGM1*1-* > *PGM1*2-* > *PGM1*2+*.

Allele *PGM1*6* was found in Bunun, Ami, Puyuma, Rukai, Paiwan, and Yami. Puyuma possess the highest allele frequency in *PGM1*6*, more than 8%, and one *PGM1*6* homozygote has been found in this population. Population genetic studies in Chinese Han majority and ethnic minorities (Zhao, 1985) also indicated that *PGM1*6* allele is very common in many ethnic groups (Li and others, 1989) and Southern Han Chinese (Zhou and Du, 1988); in Miao and Tujia of Hunan Province, that allele is as high as about 6% and 3%, respectively; another Miao in Hainan Island bear more than 6.5% of *PGM1*6* (Jin and others, unpublished data; Omoto and others, 1993). Investigations of Asia-Pacific populations also indicated that *PGM1*6* exists in Thai and Indian though its frequency was not high. A population study (Lin-Chu and others, 1991) on Taiwan Han-Chinese from Guangdong and Fujian provinces revealed that *PGM1*6* (they called it *PGM1*W21*) exist in those immigrants.

Lie-Injo and others (1968) studied Chinese in U.S.A. and residents of Kuala Lumpur, Malaysia, and Indonesian by using SGE, and they guessed that *PGM1*6* came from an area in China where the allele was more prevalent. In a study of PGM1 in 20 Chinese populations, Li and others (1989) used both the IEF and SGE methods, by which they proved that *PGM1*6* widely distributed in Chinese populations. Summing up above results, it could be considered that allele *PGM1*6* most likely originated from central or southern China, which is now mostly covered by ethnic minorities. So far, population studies in Asian and rest of world demonstrated that Puyuma in Taiwan possess highest *PGM1*6* allele frequency. Furthermore, this allele will draw our special attention if it is a south-east Asian genetic marker.

MONOMORPHIC LOCI

In the present investigation, AK, CA1, CA2, GOT, LDH, and MDH were typed by using conventional starch gel electrophoresis (SGE). Those loci were monomorphic in all nine ethnic groups.

In the AK system, all the nine Taiwan ethnic groups bear identical type, *AK*1*, and this result corresponds with the AK gene distribution in Asia. Genetic studies in China indicated that *AK*2* allele is very rare in this country. It has relatively high frequencies in descendants of West Eurasian and East Eurasian mixtures, like Uygur and Tajik ethnic groups in Xinjiang, possessing 4 to 6% of *AK*2*. In northern China, only Mongolian has been proved to have this allele but the frequency is no more than 1%. As it was expected, this allele is absent in southern Chinese ethnic groups except Bai and Hani in the Yunnan Province. Only one individual in each of these two ethnic groups with phenotype AK 2-1 was found in more than 200 individuals (Li and others, 1989). In Korean, *AK*2* is only 0.74% (Saha and Tay, 1992). In the Philippines, although Negritos possess 7% of *AK*2*, the other three populations showed monomorphic distribution of the AK 1-1 phenotype (Omoto and others, 1978).

Population genetic studies on CA1 revealed that this locus is monomorphic in most populations in the world. However it is found to be highly polymorphic in Mamanwa of the Philippines (Omoto and others, 1981) with 34% of heterozygotes. In Malaysia, Indonesia and Australian Aborigines, rare alleles were found at the polymorphic level (Blake 1978, 1979; Blake and Spargo, 1986), and a CA1 rare variant was also found in Japanese (Ueda and others, 1977), though the frequency is extremely low (0.05%). Polymorphism of CA2 gene so far has been found only in African populations. Three phenotypes, CA2 1, CA2 2-1, and CA2 2, which are attributed to two common alleles *CA2*1* and *CA2*2* have been observed, and the frequency of *CA2*2* is in ranging from 4.6% to 19.4% in African populations (Harris and Hopkinson, 1976).

Genetic polymorphisms of soluble enzyme GOT are relatively rare and have been primarily described in certain East Eurasian populations. In addition to the common allele *GOT*1*, two different electrophoretically identifiable alleles were reported (Chen and Giblett, 1971; Ishimoto and Kuwata, 1974; Teng and others, 1978; Scott and Wright, 1978). However, in this study, distribution of GOT in all the individuals of the nine Taiwan ethnic groups showed the identical type, GOT 1. GOT typing was mostly omitted in genetic studies on Chinese minority populations, since it was simply considered to be a monomorphic genetic locus in most of Han-Chinese majorities and ethnic minorities. Genetic study on four populations of the Philippines (Omoto and others, 1978) revealed that there is no genetic variant in Negrito and Ifugao; but in Tagalog and Visayan, *GOT*2* allele appeared with 1.25% and 0.42%, respectively. Chen and Giblett (1971) found that GOT 2 existed in Han-Chinese of Taiwan, American Japanese, and Filipino.

LDH variants are so far all rare except in India where frequency of *LDH* "Calcutta 1" heterozygotes may be as high as 2% (Das and others, 1972). Rare variants were also found in some Southeast Asian populations like Malay, Indonesian, Filipino, and overseas Chinese with low frequencies (Blake and others, 1973; Breguet and others, 1982; Omoto and others, 1978).

Population studies indicated that in south and east Asia, MDH variant was observed only 7 out of more than 4000 individuals in Hiroshima and Nagasaki of Japan (Ueda and

others, 1977). But some other variants occurred in Melanesian of Oceania with somewhat high frequencies ranging from 2.4% to 1.7% (Leakey and others, 1972; Gajdusek and others, 1978; Mourant and others, 1981, 1982). In West Eurasian and African, genetic variants of the soluble MDH are generally considered to be absent.

GENETIC DISTANCE ANALYSIS

Standard genetic distances were computed based on 13 red cell enzyme genetic loci including data for ADA (Jin and others, 1995), as shown in Table 4. Dendrograms for nine Taiwan ethnic groups were constructed through two different methods: UPGMA and the neighbor-joining method (Figures 2A and 2B, respectively). Altough UPGMA is known to produce erroneous tree topologies more often than other distance matrix methods (for example, Saitou and Nei, 1987), relationship of human populations are usually quite complex and UPGMA phenograms are sometimes useful for presenting overall distance relationship. Therefore, we present both UPGMA and NJ dendrograms in the followings. Because only 13 loci were used for estimating genetic distances between populations, we did not use bootstrap methods, which requires large number of samples.

The UPGMA dendrogram revealed that Atayal and Bunun are the most closely related to each other, followed by the Puyuma and Rukai pair. These two pairs are further clustered with Saisiat and Paiwan, respectively (Figure 2A). The Atayal-Bunun-Saisiat cluster can be called the Northern cluster, because these three populations are distributed in the northern Taiwan, while the Puyuma-Rukai-Paiwan cluster may be called the Southeast cluster according to their geographical distribution (Figure 1). These two clusters are also conspicuous for the NJ dendrogram (Figure 2B). It is also interesting to note that Yami is quite apart from the remaining populations in the both dendrograms. However, other clusterings are not consistent between the UPGMA and the NJ dendrograms; Ami and Tsou are clustered in the NJ dendrogram, while Ami is clustered with the Southern cluster in the UPGMA dendrogram. In any case, those dendrograms more or less fit with the geographical distribution of the nine Taiwan aboriginal populations. However, those

Table 4 Standard genetic distances (lower diagonal) and average heterozygosities (diagonal)

Puyuma	0.1912								
Paiwan	0.0051	0.2063							
Ami	0.0056	0.0085	0.2011						
Bunun	0.0040	0.0081	0.0105	0.1622					
Rukai	0.0036	0.0094	0.0100	0.0070	0.2033				
Yami	0.0151	0.0221	0.0148	0.0134	0.0162	0.1671			
Atayal	0.0066	0.0101	0.0124	0.0018	0.0131	0.0175	0.1518		
Tsou	0.0109	0.0120	0.0085	0.0128	0.0088	0.0180	0.0162	0.1950	
Saisiat	0.0092	0.0152	0.0069	0.0073	0.0144	0.0190	0.0053	0.0125	0.1542
	Puyuma	Paiwan	Ami	Bunun	Rukai	Yami	Atayal	Tsou	Saisiat

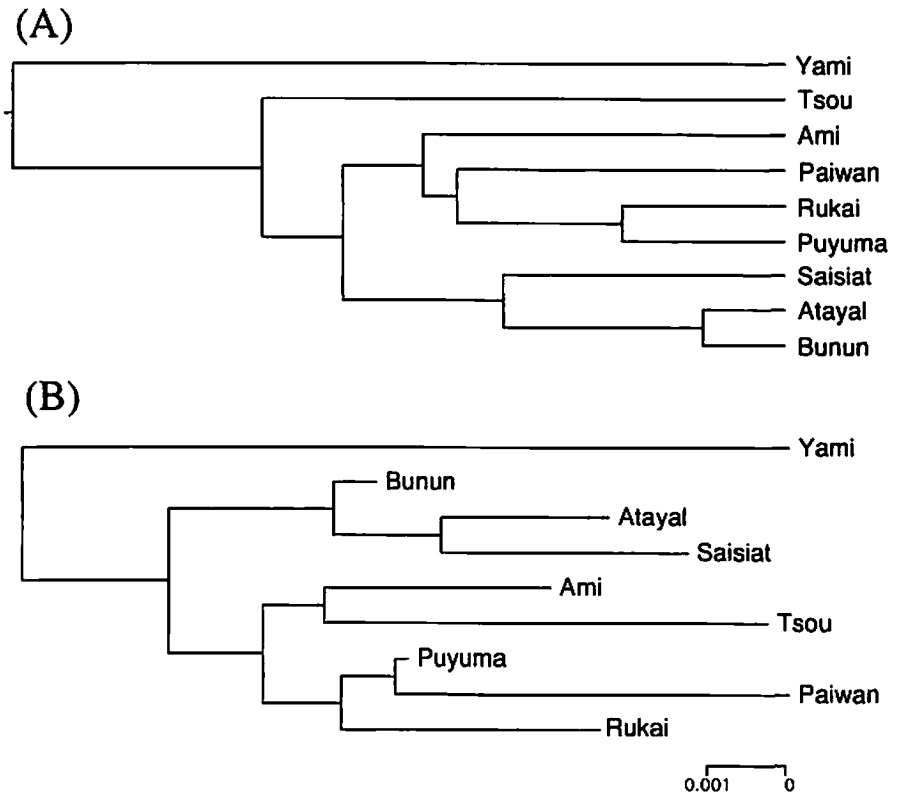

Figure 2 (A) A UPGMA dendrogram for nine Taiwan ethnic groups based on the distance matrix of Table 4. (B) An NJ dendrogram for nine Taiwan ethnic groups based on the distance matrix of Table 4.

are not in accordance with the language classification (Table 1). A more detailed phylogenetic analyses combining all the genetic markers (red cell enzymes, blood groups, and serum proteins) will be published elsewhere.

Comparing with mainland Chinese minorities, Japanese, and Korean, genetic distances among nine Taiwan ethnic groups are very large from each other (data not shown), although they have very close geographic distances. In contrast, populations like Northern Chinese, Japanese, and Korean have very close genetic relationship with each other. We therefore have reason to believe that these ethnic groups in Taiwan might have derived from various mother populations in the ancient time. However, this conjecture must be tested by comparing those Taiwan populations with surrounding ones.

Acknowledgments

Authors thank Gaoshan people of Taiwan who donated us their blood. This study was supported by Ministry of Education, Science, Sports and Culture (Japan) Grants-in-Aid

for Scientific Research (International Scientific Research Program) to S.H. and Grants-in-Aid for Scientific Research on Priority Areas ('Prehistoric Mongoloid Dispersal' and 'Origin of Japanese and Japanese Culture') to S. H. and N. S.

REFERENCES

Blake N.M., McDermid E.M., Kirk R.L., Ong Y.W., and Simons M.J. (1973) The distribution of red cell enzyme groups among Chinese and Malays in Singapore. Singapore Medical Journal, vol. 14, pp. 2-8.

Blake N.M. (1978) Genetic variants of carbonic anhydrase in the Asian-Pacific area. Annals of Human Biology, vol. 5, pp. 557-568.

Blake N.M. (1979) Genetic variation of red cell enzyme systems in Australian Aboriginal populations. Occasional Papers in Human Biology (Australian Institute of Aboriginal studies, Canberra), vol. 2, pp. 39-82.

Blake N.M. and Spargo R.M. (1986) Population genetic studies in the Kimberley of Western Australia. Human Heredity, vol. 36, pp. 286-298.

Breguet G., Ney R., Kirk R.L., and Blake N.M. (1982) Genetic survey of an isolated community in Bali, Indonesia. II. hemoglobin types and red cell isozymes. Human Heredity, vol. 32, pp. 308-317.

Chai C.K. (1967) Taiwan Aborigines: A Genetic Study of Tribal variations. Harvard University Press, Cambridge.

Chen S.H. and Giblett E.R. (1971) Genetic variation of soluble glutamic-oxaloacetic transaminase in man. American Journal of Human Genetics, vol. 23, pp. 419-424.

Chen S.H., Giblett E.R., Anderson J.E., and Fossum B.L.G. (1972) Genetics of glutamic-pyruvic transaminase: Its inheritance, common and rare variants, population distribution and differences in catalytic activity. Annals of Human Genetics, vol. 35, pp. 401-409.

Chen K.H., Cann H., Chen T.C., Van West B., and Cavalli-Sforza L. (1985) Genetic markers of an aboriginal Taiwanese population. American Journal of Physical Anthropology, vol. 66, pp. 327-337.

Chou P.L. (1959) A study on the blood groups of Paiwan tribe in Mu-Tan district. Pin-Tung prefecture, Formosa. Zinruigaku Kenkyu, vol. 6, pp. 127-132.

Das S.R., Mukhejee B.N., Das S.K., and Malhotra K.C. (1972) Four types of genetic variants of LDH in India. Human Heredity, vol. 22, pp. 264-270.

Gajdusek D.C., Leyshon W.C., Kirk R.L., Blake N.M., Keats B., and McDermid E.M. (1978) Genetic differentiation among populations in Western New Guinea. American Journal of Physical Anthropology, vol. 48, pp. 47-64.

Goedde H.W., Benkmann H.G., Kriese L., Bogdanski P., Du R., Chen L., Cui M., Yuan Y., Xu J., Li S., and Wang Y. (1984) Population genetic studies in three Chinese minorities. American Journal of Physical Anthropology, vol. 64, pp. 277-284.

Harris H. and Hopkinson D.A. (1976) Handbook of enzyme electrophoresis in human genetics. North-Holland Company, Amsterdam, Oxford American Elsevier Pub. co.

Inc., New York.

Huang M.C. (1964) Studies on the distribution of Rh blood types among various racial tribes in Formosa. Japanese Journal of Medicine, vol. 18, pp. 135-142.

Huang M.C. and Sheen N.L. (1966) Studies on the distribution of blood types among various racial tribes in Formosa. 11th Pacific Science Congress, Tokyo.

Ikemoto S., Ming C.T., Haruyama N., and Furumata T. (1966) Blood group frequencies in the Ami tribe (Formosa). Proceedings of Japan Academy, vol. 1942, pp. 173-177.

Ishimoto G. and Kuwata M. (1974) Studies on human glutamic-oxaloacetic transaminase variation, including enzyme patterns in some non-human primates. Japanese Journal of Human Genetics, vol. 18, pp. 364-372.

Ishida T., Pan I.-H., Horai S., Saitou N., and Sun C.-S. (1993) Seroepidemiological survey of Human T-lymphotropic retrovirus among indigenous populations in Taiwan. International Journal of Epidemiology, vol. 22, pp. 927-930.

Jin F. (1993) Genetic study of native Taiwan populations based on the investigation of red cell enzyme genetic markers. Ph.D. thesis, Graduate School of Science, University of Tokyo.

Jin F., Saitou N., Ishida T., Sun C.-S., Pan I.-H., Omoto K., and Horai T. (1995) Genetic polymorphism of ADA in Taiwan Aboriginal populations: New ADA variant detected by isoelectric focusing method. Anthropological Science, vol. 103, pp. 227-234.

Kobayashi K., Atoh M., Suzuki H., Ohshima K., Young C.D., Huang K.Y., Zou Y.H., and Sekiguchi S. (1992) A study of HLA distribution among Taiwan aborigines. In Tsuji K., Aizawa M., and Sasazuki T. eds., "HLA 1991", Oxford University Press, Oxford, pp.679-680.

Kutsuna M. and Matuyama M. (1939) On the blood groups of the Taiwan aboriginal tribes. Journal of Taiwan Medical Association, vol. 38, pp. 1153-1178.

Leakey T.E.B., Coward A.R., Warlow A., and Mourant A.E. (1972) The distribution in human populations of electrophoretic variants of cytoplasmic malate dehydrogenase. Human Heredity, vol. 22, pp. 542-551.

Li B., Huang L., Zhou J., and Qiu N. (1989) Distributions and Gene Frequencies of PGM1 Subtype EsD, GLO1, AK, ADA and 6-PGD in 20 Races of China. Acta Genetica Sinica, vol. 16, pp. 151-158.

Lie-Injo L.E., Lopez C.G., and Poey-Oey H.G. (1968) Erythrocyte and Leukocyte Phosphoglucomutase in Chinese. American Journal of Human Genetics, vol. 20, pp. 101-106.

Lin-Chu M., Loo J.H., and Hayward M.A. (1991) Phosphoglucomutase-1 Polymorphism among Chinese in Taiwan. Human Heredity, vol. 41, pp. 22-25.

Long J.C., Naidu J.M., Mohrenweiser H.W., Gershowits H., Johnson P.L., Wood J.W., and Smouse P.E. (1986) Genetic characterization of Gainj and Kalam speaking peoples of Papua New Guinea. American Journal of Physical Anthropology, vol. 70, pp. 75-96.

Ma Y. (1989) China's Minority Nationalities. FL Press, Beijing.

Melton T., Peterson R., Redd A.J., Saha N., Sofro A.S., Martinson J., and Stoneking M.

(1995) Polynesian genetic affinities with Southeast Asian populations as identified by mtDNA analysis. American Journal of Human Genetics, vol. 57, pp. 403-414.

Mourant A.E., Tills D., Kopec A.C., Warlow A., Teesdale P., Booth P.B., and Hornabrook R.W. (1981) Red cell antigen, serum protein, and red cell enzyme polymorphisms in inhabitants of Jimi valley, Western Highlands New Guinea. Human Genetics, vol. 59, pp. 77-80.

Mourant A.E., Tills D., Kopec A.C., Warlow A., Teesdale P., Booth P.B., and Hornabrook R.W. (1982) Red cell antigen, serum protein and red cell enzyme polymorphisms in Eastern Highlanders of New Guinea. Human Heredity, vol. 32, pp. 374-384.

Nakajima H., Ohkura K., Sheen Y.Z., Chow Z.S., Lee S.P., Orita Y., and Masuda Y. (1967) The distributions of ABO, MN, Q Lewis and Rh blood groups in Taiwan. Japanese Journal of Human Genetics, vol. 11, pp. 244-251.

Nakajima H. and Ohkura K. (1971) The distribution of several serological and biochemical traits in East Asia. III. The distributions of gamma globulin (Gm[1], Gm[2], Gm[5] and Inv[1] and Gc groups in Taiwan and Ryukyu. Human Heredity, vol. 21, pp. 362-370.

Nakajima H., Ohkura K., Huang M.C., Saito R., and Seto T. (1971) The distribution of several serological and biochemical traits in East Asia. IV. The distribution of the blood groups in the Taiwanese mountain aborigines. Japanese Journal of Human Genetics, vol. 16, pp. 57-68.

Nei M. (1987) Molecular Evolutionary Genetics. Columbia University Press, New York.

Omoto K. (1980) Genetic polymorphism of red cell enzymes. In Miwa S. ed., Basic and Clinic of Red Cell Enzyme, Kagaku-Hyoronsha, Tokyo, pp. 286-303.

Omoto K., Aoki K., and Harada S. (1975a) Polymorphism of esterase D in some population groups in Japan. Human Heredity, vol. 25, pp. 378-381.

Omoto K., Ishimoto G., Harada S., and Misawa S. (1975b) The distribution of genetic markers in blood samples from Okinawa, the Ryukyus II. The distribution of several red cell enzyme types in Ishigaki Island. Journal of Anthropological Society of Nippon, vol. 83, pp. 253-260.

Omoto K., Misawa S., Harada S., Sumpaico J.S., Medado P.M., and Ogonuki H. (1978) Population Genetic Studies of the Philippine Negritos. I. A Pilot Survey of Red Cell Enzyme and Serum Protein Groups. American Journal of Human Genetics, vol. 30, pp. 190-201.

Omoto K., Ueda S., Goriki K., Takahasi N., Misawa S., and Pagaran I.G. (1981) Population genetic studies of the Philippine Negritos. III. Identification of the carbonic anhydrase-1 variant with CA1 Guam. American Journal of Human Genetics, vol. 33, pp. 105-111.

Omoto K., Hirai M., Jin F., Misawa S., Washio K., Tokunaga K., Yamazaki K., Saitou N., Du C., Lu B., Luo Z., Zeng Z., Xu J., Zhao H., Zhang Z., Wei X., Niu K., Hao L., and Du R. (1993) Population genetic study in Hainan Island, China. I. Distribution of blood genetic markers. Anthropological Science, Vol. 101, pp. 1-24.

Roychoudhury A.K. and Nei M. (1988) Human polymorphic genes world distribution.

Oxford University Press, Oxford.

Ruhlen M. (1987) A Guide to the World's Languages. Vol. 1: Classification. Stanford University Press, Stanford.

Saha N. and Tay J.S.H. (1992) Origin of the Koreans: a population genetic study. American Journal of Physical Anthropology, vol. 88, pp. 27-36.

Saitou N. (1995) A genetic affinity analysis of human populations. Human Evolution, vol. 10, pp. 17-33.

Saitou N. and Nei M. (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. Molecular Biology and Evolution, vol. 4, pp. 406-425.

Scott E.M. and Wright R.C. (1978) Polymorphism of red cell enzymes in Alaskan ethnic groups. Annals of Human Genetics, vol. 41, pp. 341-346.

Sokal R.R. and Sneath P.H.A. (1963) Principles of Numerical Taxonomy. Freeman, San Francisco.

Takahara S., Ogura Y., Orita Y., Masuda Y., Saito R., Seto T., Mitani Y., Kuroda Y., Okamoto K., and Sheen Y.Z. (1968) Field survey for acatalasemic gene among the population in Formosa. Journal of Okayama Medical Association, vol. 80, pp. 1275-1280.

Teng Y.S., Tan S.G., Lopez C.G., Ng T., and Lie-Injo L.E. (1978) Genetic markers in Malaysians: Variants of soluble and mitochondrial glutamic oxaloacetic transaminase and salivary and pancreatic amylase, phosphoglucomutase III and saliva esterase polymorphisms. Human Genetics, vol. 41, pp. 347-354.

Torii R. (1910) Etudes anthropologiques: Les aborigenes de Formose (2e fascicule) (in French). Journal for College of Science, Tokyo Imperial University, vol. 32, pp. 1-75.

Torii R. (1922) Etudes anthropologiques: Les Aborigenes de Formose (2e fascicule). 1. Caracteres Physiques: Une tribu Yami (in French). Tokyo Imperial University, Tokyo.

Ueda N., Satoh C., Tanis R.J., Ferrell R.E., Kishimoto S., Neel J.V., Hamilton H.B., and Baba K. (1977) The frequency in Japanese of genetic variants of 22 proteins. II. Carbonic anhydrase I and II, lactate dehydrogenase, malate dehydrogenase, nucleoside phosphorylase, triose phosphate isomerase, hemoglobin A and hemoglobin A2. Annals of Human Genetics, vol. 41, pp. 43-52.

Umetsu K., Yuasa I., Suzuki T., Sun C.-S., Pan I-H., Ishida T., Saitou N., and Horai S. (1994) Polymorphisms of complement component I and C1R subcomponent of C1 in 9 aboriginal Taiwanese populations. Human Biology, vol. 66, pp. 339-348.

Umetsu K., Yuasa I., Harada A., Suzuki T., Pan I-H., Ishida T., Saitou N., and Horai S. (1995) Orosomucoid phenotyping with monoclonal antibodies: polymorphic occurrence of ORM1*Q0 in aboriginal Taiwanese populations. Human Heredity, vol. 45, pp. 181-185.

Windhof O. and Walter H. (1983) Blood group, serum protein and red cell enzyme polymorphisms in Filipinos. Human Heredity, vol. 33, pp. 357-364.

Xu J. and Du R. (1984) The genetic investigation of red cell acid phosphatase in Dong, Hui, and Bai ethnic groups. A R I G A S. 1984, p. 57.

Yuasa I., Tamaki N., Suenaga K., Ito K., Inoue T., and Okada K. (1985) Reliable phenotyping of esterase D by low voltage isoelectric focusing: Evidence for the new variant ESD Yamaguchi. Electrophoresis, vol. 6, pp. 588-592.

Zhao H. (1985) Population genetic studies of ethnic minorities in China (in Chinese). Master thesis, Institute of Genetics, Chinese Academy of Science.

Zhou M. and Du C. (1988) Genetic Polymorphism of Human Red Cell Phosphoglucomutase-1 Subtypes in Chinese. Acta Genetica Sinica, vol. 15, pp. 68-73.

Handling editor: Laurent Excoffier