Recent Anthropological Genetic Study of Taiwan Indigenous Populations

CHEN Shu-Juo[1,2*], CHEN Yao-Fong[2,3*], YEH Jih-I[3*], HSU Mutsu[2]

(1.Department of Life Science, Tzu Chi University, Hualien, Taiwan; 2.Institute of Anthropology, Tzu Chi University, Hualien, Taiwan; 3.Institute of Genetics, Tzu Chi University, Hualien, Taiwan.)

Besides of cultural, linguistic, and physical characteristic comparisons, genetic tools have become one of the most powerful methods to study the relationships and migration pattern of human populations. The question about the dispersal of Austronesian has remained controversial among the papers studied by different discipline, but Taiwan indigenous populations always play the important role. In order to clarify the genetic relationship between the Taiwan indigenous populations and other populations among Southeast Asia and Oceania, we use three genetic markers: single nucleotide polymorphism of Y chromosome, microsatellite polymorphism of Y chromosome, and ΨGRK6 pseudogene sequences to get more information and postulate the possible dispersal pathway.

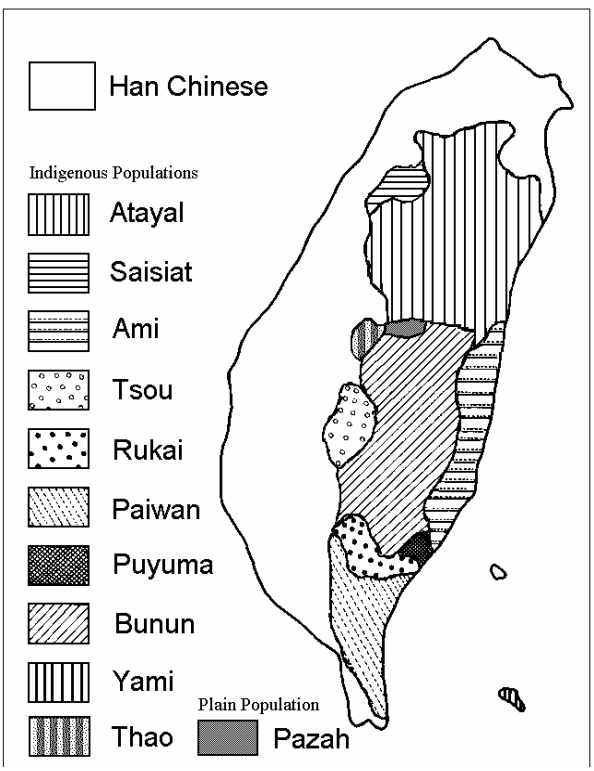

Fig. 1. Map showing the locations of the studied populations.

Single nucleotide polymorphism of Y chromosome

The question about the dispersal of Austronesian has remained controversial. Three popular hypotheses, The Express Train (Diamond 1988), The Entangled Bank (Terrell 1988), Eden in the East (Oppenheimer 1998), reveal quiet different dispersal patterns. Taiwan plays very important but different roles in these three hypotheses: The express train hypothesis indicated

*The three authors ahead contribute equally in this paper.

that ancient Austronesian rapid expanded from southern china, through Taiwan, and into Polynesia. It seems that Taiwan was the cradle of all the Austronesian. The entangled bank hypothesis indicated that Island Southeast Asian and western Melanesian populations have been continuously interacting, and rapid expanded into remote Oceania without the need for an intrusive Asian migration. It seems that Taiwan would be an end place of Austronesian dispersal. Eden in the East hypothesis indicated that the Austronesian languages originated in Sundaland. High degree of interaction among most languages had occurred after some floods, and Taiwan was being isolated at the extreme northern periphery and left out of the exchange.

The Y chromosome marker has greatly improved the resolution of the migratory patterns of modern humans (Jin and Su 2000; Ke et al. 2001). The biallelic markers or small deletions on the non-recombinant part of Y chromosome allow us to reconstruct the intact and highly informative haplotypes, which can be considered as alleles from a single locus that occurred in an ordered time series, might mark the footprint of a unique migration event. The absence of recombination of Y chromosome provides unambiguous lineages and a small effective population size, probably make Y chromosome the best genetic tool to study early human migrations.

Su et al. (2000) studied the distribution of Y-chromosome SNP haplotypes of Austronesian, and concluded that Taiwan is not the homeland of the other Austronesian groups. This conclusion contradicts the express train hypothesis and astonished lots of linguists (Gray & Jordan 2000). Several debates were erupted immediately and one of the valid criticisms is that the conclusion was based on only 58 samples of Taiwan, not sufficient enough to support the conclusions. More specifically: (1) the most common haplotypes of the world, H1 and H5, were not observed in Taiwan indigenous populations; (2) the Ami showed the haplotype H9 but the sample size is merely six. A study in a larger sample is therefore essential to either verify or falsify the conclusion that has been considered controversial.

We genotyped 183 unrelated male DNA samples, of which 23 were from Han Chinese, and 160 were from 10 Taiwan indigenous populations, and 1 plain Taiwan indigenous population. These 10 indigenous populations still retain their distinct languages, respectively, but the plain population has mixed with the Han Chinese population considerably, and as a result lost their linguistic and cultural distinctiveness. All donors were drawn after informed consent, and it was established that no donors were related by a family relationship of three degrees or closer. (Fig. 1 and Table1) For genotyping, an allelic-specific PCR assay was used for 19 Y-chromosome biallelic markers. PCR application protocols are given in Su et al. (Su et al. 1999).

Ten haplotypes were found in the sample of 183 Y chromosome in this study. In this study Ami samples revealed higher level of diversity than Su et al. (2000) but the diversity observed in Atayal is less. The differences between the two studies are significant in Atayal and Yami but not in Bunun, Paiwan, and Ami. One of the old lineages, H5, was absent in Su et al. (2000) but it was found in Bunun, Thao, and Pazah with low frequencies. The other old lineage H1 was not observed in this extended sample.

The most common haplotypes in Taiwan indigenous peoples are the two that were derived from M119, H9 and H10, with their combined frequencies ranging from 55% to 100%. This mutation has high frequencies in Southeast Asia but very rare in Oceanic populations except in Majuro. A single origin or a strong bottleneck event that led to a significant reduction of the other haplotypes can either explain this observation. Interestingly, the haplotypes derived from M122, H6, H7, H8 were found in Yami, Ami, Puyuma, Saisiat, Thao, and Pazah though with relatively low frequencies. Those haplotypes were only found in Atayal in the previous study with a much smaller sample size (Su et al. 2000). The presence of M122 can probably be attributed to the admixture with Han Chinese since it is the most frequent mutation found in the latter (54%, Su et al. 1999). Again, the high frequency of M122 in the Han Chinese (48%) in this study further supports this notion.

In this study, we showed that the Taiwan indigenous populations on one hand, and the Micronesians and Polynesians on the other, carry two different subsets of haplotypes found in the extant Southeast Asian populations. This is consistent with the earlier observation made by Su et al. (2000). With an extended sample from Taiwan indigenous populations, more haplotypes were observed than those by Su et al. (2000). Higher frequencies of M122 were observed when more populations were included in the study. This observations bare certain significance in the understanding of the origin of Austronesian since they happen to be the two haplotype groups that are shared among two major groups of the language family: Formosans and Malay-Polynesians. It is probably quite convincing to attribute the presence of M122 haplotypes (H6, H7, and H8) to the admixture with Han Chinese (Su et al. 1999, 2000).

The different subsets of haplotypes found in Taiwan indigenous populations and in Malay-Polynesians are confirmed in this study, which is the major evidence to the conclusion posed by Su et al. (2000). Furthermore, a difference observed between the two groups can also be explained by two distinctive bottleneck events besides the model invoking two independent migrations as suggested by Su et al. (2000). Therefore, The conclusion of this study strongly supports the Eden in the East hypothesis, partially supports the entangle bank hypothesis, and didn't support the express train hypothesis.

Table 1. SNP haplotype frequency of Y-chromosome in Asian and Oceanic populations

		Haplotypes														
Populations	N	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H14	H16	H17
Southeast Asia																
Tujia*	10	10				20	30	10		20			10			
Yao*	20	35		15		10	15	15				20				
Dong*	10	20					10		20	20	10	20				
Yi*	14			14.3		42.9	21.4		7.1			14.3				
She*	11	18.2				9.1	18.2	27.3	18.2			9.1				
Li*	11								9.1	27.3		54.5	9.1			
Zhuang*	28	3.6		3.6	7.1	3.6	3.6		25	17.9		25	10.7			
North Thai*	20		20				5		30			20	20	5		
Northeast Thai*	20				5	5	5	5		5	5	45	20	5		
So*	5	20	20						40				20			
Cambodian*	26	3.8		3.8	11.5	11.5	3.8		15.4	3.8	3.8	23.1	11.5	3.8	3.8	
Orang Asli*	17					23.5	5.9	5.9				64.7				
Malay*	27				3.7	18.5	33.3		22.2	3.7	14.8	3.7				
Batak*	18	5.6			5.6	11.1	11.1	16.7		22.2		27.8				
Javanese*	11	9.1			9.1	27.3	9.1			18.2	9.1	18.2				
Kota Kinabalu*	19	10.5				5.3	10.5			31.6	10.5	26.3		5.3		
Taiwan																
Bunun*	9									11.1	66.7		22.2			
Bunun**[a]	17					5.9				17.6	58.8		17.6			
Atayal*	24						29.2	4.2	4.2	54.2	8.3					
Atayal**[b]	22						4.5			95.5						
Yami*	8									25		75				
Yami**[b]	7							14.3		71.4	14.3					
Paiwan*	11								18.2	54.5	27.3					
Paiwan**[a]	22								9.1	63.6	27.3					
Ami*	6									100						
Ami**[a]	19							31.6	5.3	36.8	26.3					
Puyuma**	11							9.1		72.7	9.1			9.1		
Tsou**	18							5.6		88.9	5.6					
Rukai**	11									81.8	18.2					
Saisiat**	11							27.3		45.5	9.1	9.1	9.1			
Thao**	11					9.1		9.1		72.7	9.1					
Pazah**	11					18.2		27.3		18.2	36.4					
Han Chinese**	23			4.3		26.1		47.8		17.4	4.3					
Melanesia																
Bankes & Torres*	6	33.3				33.3	16.7									16.7
Maewo*	10					60	20									20
Santo*	4					100										
Nasioi Melanesian*	3															100
New Guinea*	90	15.5			2.2	43.3										38.9
Micronesia																
Truk*	17	5.9				64.7	5.9		5.9					5.9		11.8
Majuro*	9				11.1	66.7					22.2					
Kiribati*	11						63.6		9.1				27.3			
Guam*	6	16.7	16.7			33.3	33.3									
Palau*	13	7.7			7.7	61.5	23.1									
Phonpei*	10	30				70										
Nauru*	7					28.6	71.4									
Polynesia																
Kapingamarangi*	10	30				70										
Tonga*	1						100									
Samoan*	29	48.3				6.9	41.4							3.5		

*Data published in Su et al. (2000)

** Data studied in this research

a: The different distribution between * & ** of the same population is non-significant

b: The different distribution between * & ** of the same population is significant

Microsatellite polymorphism of Y chromosome

Microsatellites are sequences composed of runs of repeat units 2-5 bp in length. The role of microsatellites in population genetic study lies in their high mutation rates, so that they very greatly in copy number between individuals between and within populations. Several microsatellites among Taiwan indigenous populations have been studied (Chu et al.1998; Wei et al. 1999), except the microsatellites of Y chromosome. As the same merit with the SNP study of Y chromosome, the microsatellites of Y chromosome may reveal more useful information of human dispersal than any other microsatellites.

The DNA samples collected from 216 unrelated Taiwan aboriginal males. They were 21 Ami, 16 Atayal, 32 Bunun, 51 Paiwan, 14 Puyuma, 33 Rukai, 14 Saisiat and 35 Tsou. Six Y chromosome microsatellites were typed in this study: DYS19, DYS388, DYS389, DYS390, DYS391, and DYS 393, and the genotype method followed the protocol of Kittles et al. (1999) The allele frequency distribution of the six Y chromosomes microsatellites are shown in Table 2. Tsou, Bunun, and Atayal reveal highly genetic homogenous, and show quiet different distribution than other populations in DYS19 and DYS389. We postulate these three populations migrated to Taiwan early than other populations, stayed in the area isolated, and encountered great bottleneck effects indispensably. Ami, Saisiat, Paiwan, Puyuma, Rukai reveal genetic heterogeneous in all the six loci. We postulate these five populations may migrated to Taiwan later but contacted with each other frequently, or mixtured with the Han Chinese occasionally in the recent centuries.

The variation of six loci generates 56 different haplotypes in total 200 individuals, but only 13 out of the 56 are shared among populations. These shared haplotypes and the distributions are shown in Table 3. Haplotype H12 reveals in all the eight populations, and it may be one of the ancestral haplotypes by parsimony arrangement. Haplotypes H1, H13, H14, H15, H16, H18, H19, H25, and H44 were possible all derived from H12 by one or two mutations. H39 may be another ancestral haplotype for Taiwan indigenous people, since it was three mutations varied from H12.

Even though these populations all had H12, but we can't postulate they were from one origin because the H12 distribution of each population was not matched. Otherwise, Atayal, Bunun, and Tsou reveal specific haplotype distribution on H14, H16, H19, and H39 based on the specific distribution of some alleles (199, 203 of DYS192; 252, 256 of DYS389). Furthermore, the relationship of these populations was very complicate by the heterogeneous and numerical haplotype distribution.

Table 2. Allele frequency of six Y-chromosome microsatellites in Taiwan indigenous populations

Locus DYS19		Allele				Locus DYS388		Allele			
Populations	N	191	195	199	203	Populations	N	122	125	128	131
Bunun	29	3.5	17.2	65.5	13.8	Bunun	30	0	0	96.7	3.3
Atayal	16	0	100	0	0	Atayal	16	0	0	100	0
Paiwan	50	8	50	24	18	Paiwan	50	10	0	90	0
Ami	21	0	61.9	28.6	9.5	Ami	20	0	0	60	40
Puyuma	13	15.4	61.6	15.4	7.7	Puyuma	13	7.7	0	92.3	0
Tsou	33	0	9.1	18.2	72.7	Tsou	32	0	0	100	0
Rukai	33	3	75.8	15.2	6.1	Rukai	31	0	0	96.8	3.2
Saisiat	13	23.1	46.2	30.8	0	Saisiat	14	21.4	0	78.6	0
Locus DYS389		Allele				Locus DYS390		Allele				
Populations	N	248	252	256		Populations	N	209	213	217	221	225
Bunun	30	16.7	80	3.3		Bunun	32	25	59.4	15.6	0	0
Atayal	15	6.7	40	53.3		Atayal	16	0	100	0	0	0
Paiwan	51	90.2	9.8	0		Paiwan	51	0	82.4	9.8	0	7.8
Ami	21	71.4	28.6	0		Ami	21	9.5	42.9	42.9	4.8	0
Puyuma	14	92.9	7.1	0		Puyuma	14	7.1	85.7	0	7.1	0
Tsou	35	2.9	94.3	2.9		Tsou	35	5.7	88.6	5.7	0	0
Rukai	33	84.8	15.2	0		Rukai	33	25	59.4	15.6	0	0
Saisiat	14	71.4	21.4	7.1		Saisiat	14	0	64.3	21.4	14.3	0
Locus DYS391		Allele				Locus DYS 393		Allele				
Populations	N	280	284	288	292	Populations	N	118	122	126	130	
Bunun	32	0	62.5	37.5	0	Bunun	30	3.3	76.7	20	0	
Atayal	15	0	93.3	6.7	0	Atayal	16	0	100	0	0	
Paiwan	51	23.5	58.8	17.7	0	Paiwan	49	16.3	81.6	2	0	
Ami	21	0	57.1	38.1	4.8	Ami	21	9.5	57.2	33.3	0	
Puyuma	14	14.3	78.6	7.1	0	Puyuma	14	28.6	50	21.4	0	
Tsou	35	0	91.4	8.6	0	Tsou	35	29	97.1	0	0	
Rukai	32	9.4	65.6	25	0	Rukai	33	3	90.9	3	3	
Saisiat	13	0	61.5	30.8	7.7	Saisiat	14	35.7	50	14.3	0	

Table 3. Haplotype distribution of six Y-chromosome microsatellites in Taiwan indigenous populations*,

DYS	H1	H12	H13	H14	H15	H16	H18	H19	H25	H39	H44	Other	
391	280	284	284	284	284	284	284	284	284	288	288		
390	213	213	213	213	213	213	213	213	217	209	213		
388	128	128	128	128	128	128	128	128	128	128	128		
393	122	122	122	122	122	122	122	122	122	122	122		
19	195	195	195	195	199	199	203	203	195	199	195		
389	248	248	252	256	248	252	248	252	248	252	252		No.Total
Bunun		2	2			6				5		14	29
Atayal		1	4	8							1		14
Paiwan	11	10			7		5		2			14	49
Ami		2	1		2		1			1	1	12	20
Puyuma	2	3			1		1					6	13
Tsou		1				2		22		1	1	5	32
Rukai	3	6	1		3	1	2		3	1	2	8	30
Saisiat		4			1							8	13
Haplo. Total	16	29	8	8	14	9	9	22	5	8	5	67	200

*** H12** has the highest frequency in the Taiwan indigenous populations. The allele in **bold and gray** letter indicates the difference with H12. H1, H13, H15 and H25 were possibly derived from H12. H14, H16 and H44 were possibly derived from H13. H19 was possibly derived from H16. H18 was possibly derived from H15.

ΨGRK6 pseudogene sequences

Many of the commonly studied DNA sequences are regulatory or coding sequences of functional genes. The functionality will influence the substitution rate of the sequences for environmental adaptation. Only genes known to have no function are most likely to be free from the selection pressure and therefore have more uniform rate of change. Because it is not limited in the form of change that these sequences can take, there sequences are expected to have a higher than average rate of change. Pseudogenes come very close to have the desired property of no physiological function. They have accumulated mutations that knocked out the function of the gene over evolutionary times. They will no longer be selected once when they have lost their function.

ΨGRK6 is a pseudogene of G protein-coupled receptor kinases 6 (Gagnon and Benovic 1997). Forty unrelated individuals were sequenced theΨGRK6 pseudogene: They were 6 Han, 7 Ami, 3 Bunun, 3 Puyuma, 3 Rukai, 6 Saisiat, 11 Paiwan, and 1 Papua New Guinea. Seventeen polymorphic sites were found in this 1.5 kb fragment of the ΨGRK6 pseudogene. This frequency of single nucleotide polymorphism (SNP) in this region is about 10 times higher than that reported in the human genome draft sequence. Five polymorphic sites (330, 665, 1126, 1151,1332) construct at least two major haplotypes (A, H)(Table 4). The distribution of these two haplotypes is similar for all the sampled populations. The pooled data suggests that there is strong linkage disequilibrium of SNPs in this segment.

It is not surprising that linkage disequilibrium exists over a short distance of genome DNA, but surprising the similar patterns among all populations. We can postulate the two main different haplotypes revealed in all the populations mean the admixture have occurred frequently between indigenous populations or between indigenous people and Han Chinese. The sample size is too small to draw any solid conclusion about genealogical history of these populations and needs to be extended. Our expectation that the pseudogene sequences have higher rate of change and therefore more polymorphic is supported by theΨGRK6 gene sequence analysis. Whether this is generally true for pseudogenes or a peculiarity of theΨGRK6 gene will be known once we have results from other pseudogenes.

Table 4. The mutation sites of ΨGRK6 pseudogene among different populations

No.	Haplo.	70	122	208	330	426	433	444	51	558	655	112	1151	1166	1259	1331	1332
Ami001	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Ami002	B	A	A	T	TT	C	G	T	G	T	A	T	C	A	T	T	C
Ami003	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Ami004	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Ami005	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Ami006	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Ami007	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Paiwan001	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Paiwan002	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Paiwan003	C	A	A	T	T	C	A	T	G	T	G	T	C	A	C	T	C
Paiwan004	L	A	A	T	TT	C	A	T	G	T	G	C	T	A	T	T	G
Paiwan005	D	A	A	T	T	T	A	T	G	T	G	T	C	A	T	T	C
Paiwan006	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Paiwan007	E	A	A	T	T	C	A	T	G	T	A	T	C	A	T	T	C
Paiwan008	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Paiwan009	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Paiwan010	F	A	A	T	TT	C	A	T	G	T	A	T	C	A	T	T	C
Paiwan011	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Saisiat001	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Saisiat002	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Saisiat003	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Saisiat004	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Saisiat005	G	A	A	T	T	C	A	T	A	T	G	T	C	A	T	T	C
Saisiat006	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Rukai001	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Rukai002	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Rukai003	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Bunun001	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Bunun002	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Bunun003	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Puyuma001	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Puyuma002	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Puyuma003	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Papua001	A	A	A	T	TT	C	A	T	G	T	A	C	T	A	T	T	G
Han001	I	G	G	T	TT	C	A	C	G	C	A	C	T	A	T	T	G
Han002	J	A	A	G	TT	C	A	T	G	T	A	C	T	A	T	T	G
Han003	K	A	A	T	TT	C	A	T	G	T	A	C	T	G	T	C	G
Han004	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Han005	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C
Han006	H	A	A	T	T	C	A	T	G	T	G	T	C	A	T	T	C

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