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Contributed Paper

Genetic Structure of Khon Mueang Populations along a Historical Yuan Migration Route in Northern Thailand

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ABSTRACT

The genetic structure and diversity of the Khon Mueang, who constitute the majority of the current northern Thai populations, is poorly understood. In present study, 433 unrelated individuals from 10 Khon Mueang villages, located in different geographic areas along historical Yuan migration route, were analyzed using the mtDNA hypervariable region (HVR) 1 and 17 Y chromosome short tandem repeats (Y-STRs) as markers. The studied populations from the Chiang Mai-Lamphun basin showed the evidence of demographic expansion and gene flow process in this area. Genetic structure of the geographically diverse Khon Mueang was driven by geography, while genetic differentiation of Chiang Mai-Lamphun populations was shaped by genetic exchange with the neighbouring populations in the area. Contrasting patterns of mtDNA and Y chromosome variations, influenced by sex-bias rates of migration and admixture, suggests that male and female Khon Mueang do not have identical demographic histories.

Keywords: genetic structure, Khon Mueang, migration route, sex-bias.

1. INTRODUCTION

Within northern Thailand, the largest population is the Khon Mueang. Khon Muang is the word most commonly applied by the northern Thai people to themselves [1-2]. The term is more of a social and political category than a specific ethnic group. The greatest constituent part of the Khon Mueang is overwhelmingly the Yuan, but other ethnicities, including the local Mon-Khmer speaking populations and the other Tai populations have been genetically contributing to the Khon Mueang.

The ethnic Yuan founded the first Tai kingdom at Chiang Saen, presently the Chiang Rai province in Thailand, dating to the eighth century A.D. [3]. By the end of thirteenth

century A.D., they conquered the territory southward and settled at the present-day Chiang Mai and Lamphun provinces, then expanded their power further to Lampang [3-5]. Geography was one of the most important roles in selecting the location for Tai settlements. River plains surrounded by mountain peaks were chosen because of their agricultural advantage. Three geographically separate basins; the Chiang Rai, the Chiang Mai-Lamphun and the Lampang Basins, are areas along the historical Yuan migration route from Chiang Rai to Lampang provinces (Figure 1) [5].

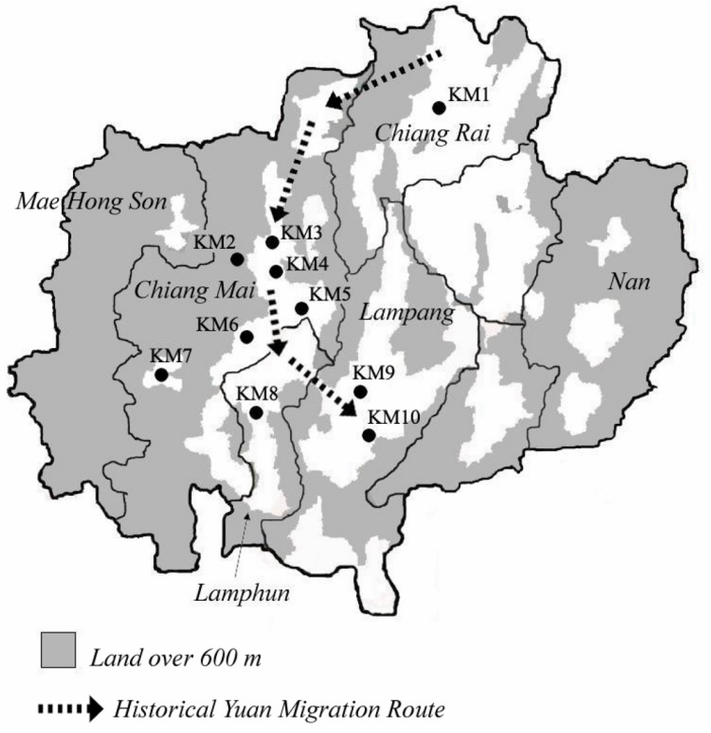

Figure 1. Geographic distribution of Khon Mueang populations (KM). See the meaning of population abbreviations in materials and methods.

Polymorphisms of mitochondrial DNA and the Y-chromosome, which are haploid and uni-parentally inherited, provide powerful tools for tracing ancestry as well as investigating the genetic structure and the evolutionary history of human populations [6-10]. Both markers can be employed to reconstruct different scenarios of demographic history, attributed to possible differential migration patterns [11-12] or other sex-bias demographic phenomena [13-17].

Genetic history of the Khon Mueang in northern Thailand has been less investigated. Therefore, in this study, the male and female gene pool of geographically diverse Khon Mueang along the historical Yuan migratory route were analyzed in order to 1) investigate the genetic diversity and genetic structure 2) evaluate if any geographic or demographic factors have shaped pattern of variation, and 3) examine the degree of concordance between mtDNA and Y-chromosome.

2. MATERIALS AND METHODS

2.1 DNA Samples and Extraction

Blood samples from 433 individuals (204 males and 229 females) from 10 Khon Mueang (KM) villages were collected with informed consent. The information, linguistic, village and personal history, were collected by interviewing. Nine villages reside along the migratory route in three different geographic areas: the Chiang Rai Basin (KM1), the Chiang Mai-Lamphun Basin (KM2-KM6 and KM8) and the Lampang Basin (KM9, KM10). Another village, which is not on the Yuan migratory route and situated in the different geographic region of the Mae Cham Basin, Chiang Mai province (KM7), was included in this study. Genomic DNA was extracted using the standard inorganic salting out method [18].

2.2 Y-STR Genotyping and mtDNA Sequencing

Male samples were genotyped at the following 17 Y-STR loci: DYS19, DYS388, DYS389a, DYS389b, DYS390, DYS391, DYS392, DYS393, DYS426, DYS434, DYS435, DYS436, DYS437, DYS439, DYS460, DYS461, Y-GATA-A10. All loci were amplified using fluorescent labelled primers (Applied Biosystems, USA) in 5 multiplex PCR modifying from previously described methods [19-21]. PCR products were separated by multi-capillary electrophoresis using the ABI 3100 genetic analyzer (Applied Biosystem, Foster City, CA). The results were analyzed by GeneMapper software v.3.7 (Applied Biosystem, Foster City, CA).

The mtDNA HVR-1 region in all samples were amplified using a published primer pair [17]. Sequencing of purified PCR products were performed, using the ABI 3730 DNA Analyzer (Applied Biosystem, Foster City, CA), employing a published set of primers [22-23] and the BigDye Terminator Cycle Sequencing Kit v3.1 (Applied Biosystem). The obtained 336-bp HVR-1 sequences (16048-16383) were edited, assembled and aligned with the revised Cambridge Reference Sequence [24] using SeqScape software v2.5 (Applied Biosystem, Foster City, CA). The HVR-1 sequences of all samples were submitted to GenBank (accession numbers HM633812–HM634244).

2.3 Statistical Analyses

Genetic diversity within population was measured as haplotype diversity (h) [25] using ARLEQUIN version 3.01 [26]. Numbers of shared haplotypes were determined for each of the 45 possible population pairs by a simple gene-count method. Nucleotide diversity (π), a raggedness index value (r), and neutrality estimators, Fu's Fs [27] and Tajima's D [28] from mtDNA sequence data were calculated using the same software program.

Association between demographic expansion parameter values: Fu's Fs statistic and Tajima's D values, and genetic diversities: haplotype and nucleotide diversities were investigated by regression analysis implemented in STATISTICA 7.0 software package.

Populations were grouped into 4 geographic regions (the Chiang Rai, the Chiang Mai-Lamphun, the Lampang and the Mae Cham Basins). Genetic variances at three hierarchical subdivisions: within individuals of population, among populations within a group, and among groups of populations, were performed by the AMOVA procedure [29]. The correlations between genetic and geographic distance matrices as well as between the Y chromosome and mtDNA genetic distance matrices were assessed by the Mantel test [30]. ARLEQUIN 3.1 software was used to compute AMOVA, and the Mantel test.

Pairwise genetic distances among studied populations based on sum of squared

difference (R_{st}) [31], and pairwise difference (F_{st}) for Y-STRs and mtDNA, respectively were calculated by ARLEQUIN 3.01. Significance levels for these values were adjusted according to the sequential Bonferroni correction [32]. The genetic distance matrix was then plotted in two dimensions by means of multidimensional scaling (MDS) using the commercially available STATISTICA 7.0 (StateSoft Software Ltd.).

3. RESULTS AND DISCUSSIONS

3.1 Genetic Diversity

A total of 193 distinct Y-STR haplotypes were observed in 204 males. Among observed haplotypes, 190 types are unique within populations whereas 3 were shared between two or more populations. Of the 190 unique haplotype, 6 were shared by two or more individuals within one group whereas the remaining 184 haplotypes belonged to each individual. There are 3 pairs of populations from the 45 possible pairs who shared haplotypes: KM2 and KM5, KM6 and KM7, and KM8 and KM10. Haplotype diversity ranges from 1.000 (KM1, KM3, KM4, KM5, and KM6) to 0.9890 ± 0.0314 (KM10) (Table 1). The overall haplotype diversitiy (*h*) for 10 populations was 0.9994±0.0006 which was in the same range as another published research on Thai populations (0.9996) [33].

MtDNA sequence analysis of 433 individuals showed the presence of 183 haplotypes, defined by 110 polymorphic sites. From the 183 observed haplotypes, 145 types were unique within populations, whereas 38 were shared by two or more populations. Among the unique haplotypes, 42 were shared by two or more individuals within one group, whereas the remaining 103 haplotypes belonged to one individual. Out of the 45 possible shared haplotype pairs, the highest number of shared haplotypes (7 haplotypes) was found between KM5 and KM9 but none were shared among three pairs of populations: KM2 and KM10, KM5 and KM10, and KM7

Table 1. Y-STR genetic diversity.

	KM1	KM2	KM3	KM4	KM5	KM6	KM7	KM8	KM9	KM10
No. of individuals	21	16	15	29	20	22	23	22	22	14
No. of haplotypes	21	15	15	29	20	22	21	20	20	13
Unique										
No.	21	14	15	29	19	21	20	19	20	12
Proportion	1.00	0.93	1.00	1.00	0.95	0.95	0.95	0.95	1.00	0.92
Single unique										
No.	21	14	15	29	19	21	18	17	19	11
Proportion	1.00	0.93	1.00	1.00	0.95	0.95	0.86	0.85	0.95	0.85
Multiple unique										
No.	0	0	0	0	0	0	2	2	1	1
Proportion	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10	0.05	0.08
Non-Unique										
No.	0	1	0	0	1	1	1	1	0	1
Proportion	0.00	0.07	0.00	0.00	0.05	0.05	0.05	0.05	0.00	0.08
Haplotype diversity *(h)*	1.0000	0.9917	1.0000	1.0000	1.0000	1.0000	0.9921	0.9913	0.9870	0.9890
SD	0.0147	0.0254	0.0243	0.0091	0.0158	0.0137	0.0154	0.0165	0.0201	0.0314

and KM10. Haplotype diversity varied from 0.9804±0.0085 (KM4) to 0.9218±0.023 (KM10) (Table 2). The total haplotype diversitiy of all populations was 0.9893± 0.0013, which was in the same range as other Tai populations [34]. Nucleotide diversity was in a narrow range from 0.0201±0.0107 (KM7) to 0.0248±0.0130 (KM6) (Table 1) and total nucleotide diversity of all 10 Khon Mueang villages (0.0223±0.0116) was similar to that of other northern Thai populations (0.0200±0.0110) in previous reports [34-35].

3.2 Population Expansion

The highly significant negative value of the Fu's *Fs* and the non significant negative value of Tajima's D (Table 2) were consistent with the predictions of demographic expansion in KM1, KM2, KM3, KM4, KM6 and KM8 [26-27]. The lower raggedness index (less than 0.03) as well as the unimodal mismatch distribution graph for these populations (data not shown) also provide congruent evidence for population growth and expansion [36]. Apparently, almost all populations residing in

Table 2. MtDNA genetic diversity and demographic parameters.

	KM1	**KM2**	**KM3**	**KM4**	**KM5**	**KM6**	**KM7**	**KM8**	**KM9**	**KM10**
No. of individuals	50	41	36	52	43	45	46	45	45	30
No. of haplotypes	31	25	22	36	22	29	21	26	25	12
Unique										
No.	14	14	12	26	11	19	14	17	12	6
Proportion	0.45	0.56	0.55	0.72	0.50	0.66	0.67	0.65	0.48	0.50
Single unique										
No.	13	7	8	22	6	18	10	11	8	0
Proportion	0.42	0.28	0.36	0.61	0.27	0.62	0.48	0.42	0.32	0.00
Multiple unique										
No.	1	7	4	4	5	1	4	6	4	6
Proportion	0.03	0.28	0.18	0.11	0.23	0.03	0.19	0.23	0.16	0.50
Non-Unique										
No.	17	11	10	10	11	10	7	9	13	6
Proportion	0.55	0.44	0.45	0.28	0.50	0.34	0.33	0.35	0.52	0.50
haplotype diversity (*h*)	0.9674	0.9744	0.9667	0.9804	0.9336	0.9535	0.9343	0.9606	0.9323	0.9218
SD	0.0121	0.0103	0.0141	0.0085	0.0222	0.0193	0.0201	0.0143	0.028	0.023
nucleotide diversity (π)	0.0202	0.0220	0.0204	0.0220	0.0203	0.0248	0.0201	0.0205	0.0210	0.0234
SD	0.0108	0.0117	0.0109	0.0116	0.0109	0.013	0.0107	0.0109	0.0112	0.0125
Raggedness value[1]	**0.0174**	**0.0137**	0.032	**0.00841**	**0.0251**	**0.0266**	**0.0098**	**0.01305**	**0.01905**	**0.0289**
Raggedness *P*-value	0.05	0	0.85	0.25	0	0	0.7	0.6	0.05	0
Fu's Fs statistic	**-15.29**	**-8.62**	**-7.208**	**-21.68**	-5.426	**-11.18**	-4.0869	**-9.451**	-7.924	0.8108
P(Fs)[2]	0.001	0.002	0.009	0	0.043	0	0.102	0.005	0.01	0.656
Tajima's D	-1.1491	-1.0516	-1.2779	-1.2768	-1.091	-0.8999	-0.8206	-1.1092	-0.7866	-0.2646
P (Tajima's D)	0.116	0.134	0.081	0.089	0.129	0.195	0.227	0.129	0.235	0.456

[1] Raggedness value lower than 0.03 for bold letter

[2] *P*-values highly significant for bold letter ($P<0.01$).

the Chiang Mai-Lamphun Basin had a demographic expansion signature.

Significant correlations ($P < 0.01$) between population expansion parameters (the Fu's Fs and Tajima's D values) and haplotype diversity (h) ($r = 0.7892$ and $r = 0.7931$ for Fu's Fs versus h and Tajima's D versus h, respectively), but no correlation ($P > 0.01$) between these parameters and nucleotide diversity (π) were observed ($r = 0.0042$ and $r = 0.4537$ for Fu's Fs versus π and Tajima's D versus π, respectively). It is worthy to note that, the demographic expansion parameters were correlated with haplotype diversity, which is largely affected by genetic drift and/or gene flow processes, but it is not correlated with nucleotide diversity, which is corresponding to an average age of population. These results suggest that Khon Mueang populations experienced recent expansion and had gene flow among them within the same geographic region after their migration and settlement at the end of thirteenth century A.D..

3.3 Association between genetics and geography

The proportion of genetic variation distributed within and between different geography among Khon Mueang groups was assessed by AMOVA (Table 3). When the population constituted a single group, inter-population differences were rather higher for the Y-chromosome (6.96%) compared to mtDNA (4.53%), indicating that the male gene pool is more diverse than the female gene pool. When populations are grouped according to geography, the statistically significant Φ statistics ($P < 0.05$) of the Y chromosome is also higher than mtDNA ($\Phi_{ct} = 0.0506$ and 0.0157 for Y-chromosome and mtDNA, respectively). To test the underlying cause of association between genetic *versus* geographic variation reflecting genetic exchange of genes between adjacent populations [37], we performed Mantel tests. The result revealed an absence correlation ($P > 0.01$) between genetic variation and geography ($r = 0.2500$ and $r = 0.0950$ for Y-STR and mtDNA, respectively).

The AMOVA results indicate that geography influences the genetic structure of Khon Mueang in different basins, but the Mantel test revealed that the Khon Mueang gene pool was not correlated with geographic distance. It seems likely that genetic divergence of Khon Mueang in different geographic areas was driven by geographic factor while genetic differentiation of Khon Mueang, especially in the Chiang Mai Lamphun basin,

Table 3. AMOVA results.

		Within population		Among populations		Among groups	
	No. of groups	**Variance (%)**	**Φ_{st}**	**Variance (%)**	**Φ_{sc}**	**Variance (%)**	**Φ_{ct}**
Y-STR All samples	1	93.04	**0.0696**	6.98			
Geography	4	91.36	**0.0864**	3.58	**0.0377**	5.06	**0.0506**
mtDNA All samples	1	95.47	**0.0453**	4.53			
Geography	4	94.94	**0.0507**	3.49	**0.0355**	1.57	**0.0157**

P-values statistically significant for bold letter ($P<0.05$).

was shaped by extensive gene flow among populations within this area. The Φ statistics as well as correlation between genetics and geography which is stronger for the Y chromosome than for the mtDNA in this study, suggest that men and women did not have identical demographic histories.

3.4 Population Affinity

Genetic distances, based on the R_{st} from Y-STR, are shown in the upper triangle of Table 4, while F_{st} from the mtDNA sequences are shown in the lower triangle. Paternally and maternally genetic relationships were represented in the MDS plots (Figure 2 and 3, repectively). The results, exhibiting different genetic patterns between males and females, might be influenced by a sex-bias demographic process. It is also supported by the absence of correlation between mtDNA and the Y chromosome genetic distance matrices (r = 0.112, P = 0.232) obtained from the Mantel test.

Paternal genetic homogeneity of the studied populations, except for the significantly differentiated populations from Mae Cham (KM7) and Lampang (KM9), might be explained by recent male migration along the route. Based on historical sources, after the eighteen century A.D. of Yuan civilization in northern Thailand, the demographic movement had occurred several times as a result of war and trade which was predominantly operated by males. The unique genetic structures in paternal lineage of KM7 and KM9 could be minimally caused by the recent migration and/or strong genetic admixture with other genetic sources living around. The paternal gene pool of KM7 might be shaped by the hill-tribes who living around Mae Cham basin, while the KM9 were mixed with the native Mon who ruled the region, presently the Lampang province, between 750-1,300 A.D. [3-5].

In the MDS plot (Figure 3), apart from a cluster of populations in the Chiang Mai-Lamphun basin (KM2-KM6 and KM8), the populations from Chiang Rai (KM1), Mae Cham (KM7), and one in Lampang (KM9) formed a distinct cluster, while another Lampang population (KM10) was distantly away from those two clusters. Maternal genetic

Table 4. Pairwise genetic distances among studied populations based on R_{st} (below diagonal) and F_{st} (above diagonal).

	KM1	KM2	KM3	KM4	KM5	KM6	KM7	KM8	KM9	KM10
KM1		**0.0650**	**0.0499**	**0.0554**	**0.0635**	**0.0662**	0.0101	**0.0405**	0.0025	**0.0713**
KM2	-0.0023		0.0222	0.0108	0.0156	**0.0416**	**0.0861**	**0.0296**	**0.0538**	**0.0602**
KM3	-0.0104	0.0139		0.0389	0.0232	**0.0664**	**0.0705**	0.0204	**0.0431**	**0.0672**
KM4	-0.0031	0.0135	0.0025		0.0298	0.0162	**0.0741**	**0.0390**	**0.0468**	**0.0519**
KM5	0.0195	-0.0041	0.0116	-0.0135		**0.0456**	**0.0596**	0.0269	**0.0355**	**0.0401**
KM6	**0.0731**	0.0347	0.0465	0.0503	0.0268		**0.0744**	**0.0510**	**0.0488**	**0.0641**
KM7	**0.1444**	**0.1337**	**0.1587**	**0.1966**	**0.1985**	**0.0927**		**0.0581**	0.0092	**0.0499**
KM8	0.0539	0.0561	0.0513	**0.0979**	0.0719	0.0189	0.0265		**0.0367**	**0.0709**
KM9	**0.1539**	**0.1220**	**0.1647**	**0.1974**	**0.1797**	0.0753	0.0364	0.0294		**0.0491**
KM10	0.0584	0.0274	0.0665	0.0711	0.0441	-0.0202	0.0625	-0.0307	0.0066	

P-values statistically significant after Bonferroni method for bold values (P<0.001)

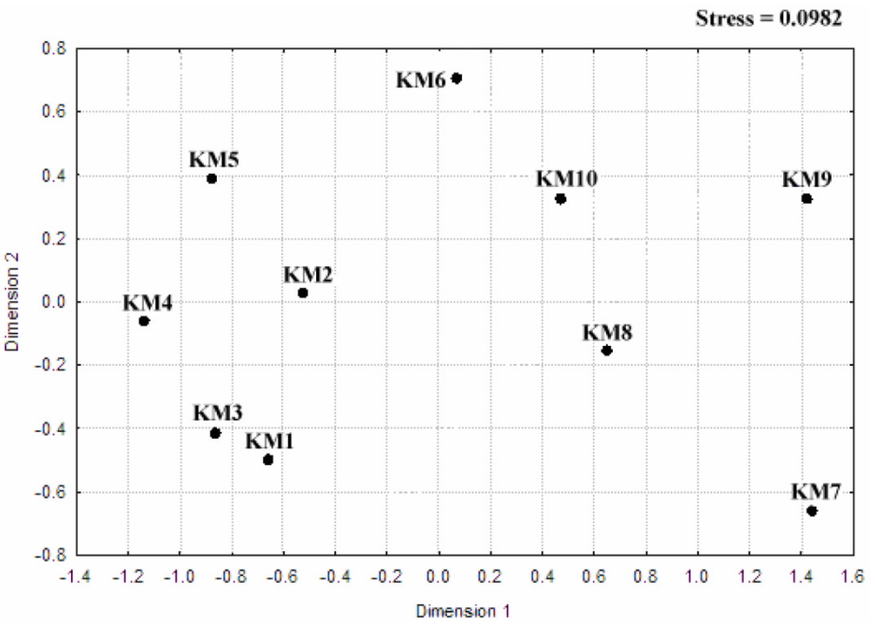

Figure 2. Multidimensional scaling scatter plot of studied populations based on R_{st} distance from Y-STR. See the meaning of population abbreviations in materials and methods.

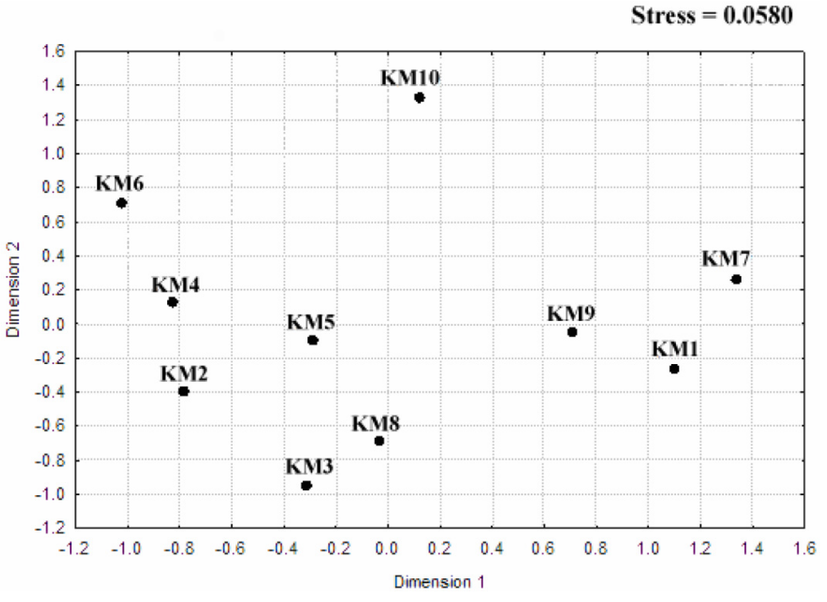

Figure 3. Multidimensional scaling scatter plot of studied populations based on F_{st} distance from mtDNA. See the meaning of population abbreviations in materials and methods.

similarity of Khon Mueang populations from Chiang Rai, Mae Cham, and Lampang is suggested by a shared common genetic legacy since the Yuan migration in the eighteen century A.D. [3-5]. After that, they might be less affected by gene flow process, unlike Khon Mueang in the Chiang Mai-Lamphun basin. Although KM10 were located in Lampang province, historically, they migrated from the city of Chiang Saen, located in present-day Chiang Rai province 200 years ago. Maternally genetic differentiation of them might be reflected by the low female migration rate and founder effect episodes.

In the present study, results obtained by multiple analyses were consistent and can be concluded that the Khon Mueang in Chiang Mai-Lamphun basin are closely related, reflecting a high gene flow within this area. The Chiang Mai-Lamphun basin used to be the center of several ancient civilizations [5]. Thus, the extensive genetic exchange among various populations led to a close genetic affinity among Khon Mueang in this region, which showed significant genetic differences from other Khon Mueang populations.

4. CONCLUSIONS

The analysis of mtDNA and Y-chromosome variations in this study provided insights into the genetic structure of present day Khon Mueang. Our data substantiate that the genetic structure of the Khon Mueang paternal lineage differs from that of the maternal lineage. These could have been caused by sex-bias demographic processes such as migration and admixture. Factors of geography and extensive gene flow among populations play an important role in shaping genetic differentiation of geographically diverse Khon Mueang groups, especially in the Chiang Mai Lamphun basin.

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