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Mitochondrial DNA Variation of Tai Speaking Peoples in Northern Thailand

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ABSTRACT: The genetic structure and genetic affinity of Tai ethnic populations in northern Thailand has never been investigated, therefore their biological ancestor as well as their history is not clearly resolved. In this study, we examined the D-loop fragment of the mitochondrial DNA in 496 unrelated individuals belonging to 4 Tai ethnic groups from 10 villages: 4 Yuan, 4 Lue, 1 Yong and 1 Khuen. Based on a comparison of 522-bp sequences at the position 16048-16569, 195 distinct haplotypes defined by 130 polymorphic sites were distinguished. Of these, 154 types were unique to their respective populations, whereas 41 were shared by two or more populations. The studied Tai populations showed evidence of demographic expansion with corresponding estimated expansion times of more than 66,000 years before the present. During historical migration and settlement, intensive genetic drift and founder effects left their imprint as population differentiation. Genetic affinity among the populations was not consistent with their linguistic classification. The Yuan or Khon Muang in northern Thailand exhibited a close relationship to the Tai groups in South and Southeast China, which supported the immigrant hypothesis and their ancestor's origin. However, an admixture between the Khon Muang and the Lawa and Mon, the long existing populations of northern Thailand, needs to be investigated.

KEYWORDS: Mitochondrial DNA, D-loop region, sequence polymorphisms, nucleotide diversity, Tai

INTRODUCTION

The Tai people constitute the largest of many ethnic groups inhabiting northern Thailand. They are dispersed nearly all over the region but still retain their original cultural practices and speak their unique language, which belongs to the Tai-Kadai family. Although, their unique cultural practices are well-known, information on their genetic lineages and past ancestry has not been reported before. Close linguistic and cultural affinities between Tai peoples in northern Thailand and southern China suggested a hypothesis that the northern Thai may originally have migrated from southern or south-eastern China and moved southwards to the area of present northern Thailand [1]. This hypothesis was not supported by some archaeological and phenotypical evidence which revealed closer relationship between the Tai and the endogenous Mon-Khmer speaking peoples of northern Thailand [2, 3]. Until now, using different sources of evidence, a strong debate about the past history of Tai peoples in northern Thailand is still on going.

The present study aimed to use the mitochondrial DNA (mtDNA), an informative genetic marker due to its maternal uniparental inheritance pattern [4-6], to trace back biological ancestors, as well as to reconstruct the past history of four northern Thai populations - the Yuan, Lue, Yong, and Khuen. Their genetic structures and relationships with the nearby populations in northern Thailand and southern China were also investigated.

MATERIALS AND METHODS

Studied Populations

Studied populations were 496 unrelated volunteers from 10 villages, belonging to 4 ethnic groups: Yuan (YU), Lue (LU), Yong (YO) and Khuen (KH). The samples of the same ethnic group were selected from various geographic locations (Fig 1). Informed consent was obtained from each subject. Information on linguistic, cultural aspects, village and individual history was obtained by interviewing.

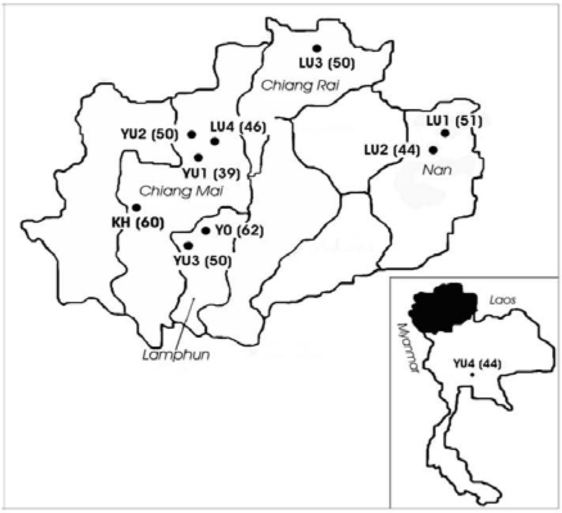

Fig 1. Geographic distribution of studied Tai populations and sample number (N). See the meaning of population abbreviations in Table 2's first column.

Migration History

The **Yuan** or Yonok, who call themselves "Khon Muang", are a major population of Northern Thailand. According to an immigrant hypothesis, the Yuan moved southward from the area where now three countries, Myanmar, Laos, and Thailand, meet or somewhere further north, in the thirteenth century. They then conquered the native Mon-Khmer peoples along their southern migration route until they reached the present day northern Thailand[1]. Contradictory, it is stated in the endogenous hypothesis that the Khon Muang's ancestors were not the Tai from China, but the native Mon-Khmer peoples who were later, through an influence of Tai politics and culture, assimilated by the small group of Tai rulers [2, 7]. Due to limited archaeological and anthropological evidence, the geographic origin, biological ancestors and demographic history of Khon Muang are not clearly confirmed. Nowadays, 87.5% of Tai people in northern Thailand speak the Yuan's language. Its script had been used to write Buddhist sermons, inscriptions and the Bible for a long time, but only a few people can read it now[8].

The Yuan (YU1, 2, 3) settled in the Chiang Mai - Lamphun basin about 700 years ago. YU1 and YU2 reside in Chiang Mai province on the eastern and western banks of the Ping River, respectively, while YU3 live in Lamphun province. Another well-known Yuan group (YU-4), living in Saw Hai district, Saraburi province in central Thailand, is believed to be the direct descendent of the Yuan who used to occupy Chiang San city in northern Thailand. They migrated from the north to central Thailand in 1804 A.D. (about 200 years ago). These people still call themselves Yuan and speak the Yuan language.

The historical homeland of the **Lue** is Xishuangbanna, Yunnan, China, but now they are dispersed in some parts of southern China, Upper Myanmar, northern Laos and northern Thailand [8, 9]. The Lue or Xishuangbanna Dai in Yunnan is officially a group under Dai ethnicity. Two waves of Lue migration into northern Thailand occurred about 400 years ago (LU4) and 200-300 years ago, using two migratory routes - through Myanmar (LU3) and Laos (LU1 and 2). Lue people have their own unique dialect and costumes, in particular Nong Bua Lue village in Nan (LU2) is well known for its typical architecture and weaving.

The **Yong** are the local people of Yong City, which was founded in the thirteenth century in Chiang Tung, Shan State, Myanmar and was ruled by the Lue King[9]. Some scholars point out that the Yong might be the same ethnic group as the Lue [10]. A mass migration of Yong into Northern Thailand occurred in 1805 A.D., when King Kawila tried to rebuild Lamphun city. Until now, most Yong people live in Lamphun and still speak their own phonology, which is similar to Lue.

The **Khuen** are named after a river in their homeland, the Shan State, Myanmar[9]. In Thailand, Khuen people reside in Mae Wang and San Pha Tong districts, Chiang Mai. Khuen colloquialisms and script are closely related to Lue and Yong. These ethnic groups also consider their spoken dialects close to each other.

Blood Sampling and DNA Extraction

Five milliliters of peripheral blood was obtained from each individual, using a vacutainer coated with EDTA-anticoagulant. Total genomic DNA was extracted from whole blood sample according to a standard inorganic salting out protocol [11].

Mitochondrial DNA Sequencing

A D-loop HVRI fragment of mitochondrial DNA (mtDNA) was amplified by polymerase chain reaction (PCR) using a set of two primers: LHmt 430-CTGTTAAAAGTGCATACCGCC-410 and LLmt 15704-CTAAGCCAATCACTTTATTG-15723[12]. The notation of Anderson *et al* (1981)[13] was used for base numbering. PCR reactions were carried out under the following thermal cycle conditions: denaturation at 94°C for 1 min, primer annealing at 56°C for 1 min, and extension at 72°C for 1 min, for a total of 30 cycles. PCR product was purified for direct sequencing, using the BigDye Terminator Cycle Sequencing Kit v3.1 (Applied Biosystems) and ABI 3730 DNA Analyzer (Applied

Biosystems). The following oligonucleotide primers were used for sequencing [12, 14].

SeqLmt-A 15897-GTATAAACTAATACACCAGTCTTGT-15921
SeqLmt-B 15979-ACCATTAGCACCCAAAGCTA-15998
SeqLmt-C 16203-AGCAAGTACAGCAATCAACC-16222
SeqHmt-D 16420-TGATTTCACGGAGGATGGT-16402
SeqHmt-E 100-CAGCGTCTCGCAATGCTATCGCGTG-76

The 522 bp sequences of mtDNA HVRI at the position 16048-16569 were assembled and aligned with the Cambridge Reference Sequence [15] using SeqScape software v2.0 and DNASP v4.0.

Data Analyses

The ARLEQUIN v2.0 package [16] of software for population genetics data was used to calculate haplotype and nucleotide diversity values. The demographic expansions of pooled Yuan, pooled Lue and pooled all samples were traced, using two different approaches. First, the distributions of the number of pairwise differences between sequences within populations or mismatch distribution were computed [17]. This method was based on an infinite-site model and assumed that an expansion occurred sometime in the past from a small stationary population to a large stationary population. Second, Fu's *Fs* statistic [18], which is particularly sensitive to population growth, was calculated. It is based on the probability of having a number of alleles greater than or equal to the observed number in a sample drawn from a stationary population. Significantly, a large negative *Fs* value is evidence of population expansion. The level of significance of *Fs* was tested with a coalescent simulation program, as implemented in ARLEQUIN.

In order to evaluate the genetic affinity among populations, our study populations were compared to other Tai, Mon-Khmer and Tibeto-Burman speaking populations (Table 1). A multidimensional scaling (MDS) of all chosen samples was performed by STATISTICA (StateSoft Software, Ltd.), based on pairwise different genetic distances. Since the mtDNA length from the selected data sources was unequal, only a minimal length of 336 bp (nucleotide positions 16048-16383) was employed for the analysis.

RESULTS AND DISCUSSION

Diversity Indices and Demographic Parameters

MtDNA HVRI nucleotide sequences of 522 bp were examined in 496 individuals from 4 Tai-speaking populations in northern Thailand. There were 195 distinct haplotypes, defined by 130 polymorphic sites. Among the observed haplotypes, 154 types were unique within the populations, whereas 41 were shared by 230 individuals (46.37% of total samples) between two or more populations. Of the 154 unique haplotypes, 50 were shared by two or more individuals within one group (162 individuals, 32.66% of total samples), whereas the remaining 104 haplotypes belonged to one individual. The percentages of population-specific haplotypes were relatively low in LU4 from Chiang Mai (26.3%), while the percentages in other populations were higher, ranging from 50.0 to 67.7% (Table 2). Moreover, deletions were observed at nucleotide

Table 1. Population sources and related information.

Population	Code	Locations	No. of samples	Language subfamily, family	Reference
Dai-1	DA1	Yunnan, China	21	Tai, Tai-Kadai	Qian *et al.* (2001)[19]
Dai-2	DA2	Yunnan, China	38	Tai, Tai-Kadai	Yao *et al.* (2002a)[20]
Lao Song	LS	Supanburi, Central Thailand	25	Tai, Tai-Kadai	Fucharoen *et al.* (2001)[14]
Phuthai	PH	Mukdahan, Northeast Thailand	25	Tai, Tai-Kadai	Fucharoen *et al.* (2001)[14]
Thai-1	TH1	North Thailand	32	Tai, Tai-Kadai	Yao *et al.* (2002a)[20]
Thai-2	TH2	Chiang Mai, North Thailand	30	Tai, Tai-Kadai	Fucharoen *et al.* (2001)[14]
Thai-3	TH3	Khon Kaen, Northeast Thailand	44	Tai, Tai-Kadai	Fucharoen *et al.* (2001)[14]
Zhuang	ZH	Guang Xi, China	83	Tai, Tai-Kadai	Yao *et al.* (2002a)[20]
Blang-1	BL1	Chiang Rai, North Thailand	38	Mon-Khmer, Austro-Asiatic	unpublished data
Blang-2	BL2	Chiang Rai, North Thailand	45	Mon-Khmer, Austro-Asiatic	unpublished data
Chong	CH	Chantaburi, East Thailand	25	Mon-Khmer, Austro-Asiatic	Fucharoen *et al.* (2001)[14]
Paluang	PA	Chiang Mai, North Thailand	51	Mon-Khmer, Austro-Asiatic	unpublished data
Wa	WA1	Yunnan, China	22	Mon-Khmer, Austro-Asiatic	Qian *et al.* (2001)[19]
Wa	WA2	Yunnan, China	36	Mon-Khmer, Austro-Asiatic	Yao and Zhang (2002b)[21]
Akha	AK	North Thailand	91	Tibeto-Burman, Sino-Tibetan	Oota *et al.* (2001)[22]
Karen (red)	KA1	North Thailand	39	Tibeto-Burman, Sino-Tibetan	Oota *et al.* (2001)[22]
Karen (white)	KA2	North Thailand	40	Tibeto-Burman, Sino-Tibetan	Oota *et al.* (2001)[22]
Lisu-1	LI1	Chiang Rai, North Thailand	53	Tibeto-Burman, Sino-Tibetan	Oota *et al.* (2001)[22]
Lisu-2	LI2	Mae Hong Son, North Thailand	42	Tibeto-Burman, Sino-Tibetan	Oota *et al.* (2001)[22]
Lisu-3	LI3	Chiang Mai, North Thailand	25	Tibeto-Burman, Sino-Tibetan	Fucharoen *et al.* (2001)[14]
Mussur-1	MU1	Chiang Mai, North Thailand	21	Tibeto-Burman, Sino-Tibetan	Fucharoen *et al.* (2001)[14]
Mussur-2	MU2	North Thailand	39	Tibeto-Burman, Sino-Tibetan	Oota *et al.* (2001)[22]

Table 2. Genetic diversities of studied populations.

Ethnic Group	Code	Location	No. of samples	No. of haplotypes	No. of unique haplotyes[a]	Haplotypic Diversity	Nucleotide diversity
Yuan 1	YU1	Chiang Mai	39	26	13 (50%)	0.9690±0.0145	0.0151±0.0080
Yuan 2	YU2	Chiang Mai	50	31	21 (67.7%)	0.9755±0.0093	0.0159±0.0083
Yuan 3	YU3	Lamphun	50	28	17 (60.7%)	0.9657±0.0116	0.0154±0.0081
Yuan 4	YU4	Saraburi	44	22	10 (45.5%)	0.9503±0.0149	0.0197±0.0102
Lue 1	LU1	Nan	51	23	12 (52.2%)	0.9153±0.0274	0.0136±0.0072
Lue 2	LU2	Nan	44	14	7 (50%)	0.8784±0.0257	0.0150±0.0079
Lue 3	LU3	Chiang Rai	50	40	22 (55%)	0.9902±0.0062	0.0155± 0.0081
Lue 4	LU4	Chiang Mai	46	19	5 (26.3%)	0.9324±0.0197	0.0136±0.0072
Yong	YO	Lamphun	62	31	20 (64.5%)	0.9651±0.0088	0.0156±0.0081
Khuen	KH	Chiang Mai	60	31	20 (64.5%)	0.9672±0.0096	0.0168±0.0087
Pooled Yuan			183	95		0.9880±0.0019	0.0173± 0.0088
Pooled Lue			191	79		0.9759±0.0037	0.0150±0.0078
Total			496	195		0.9909±0.0009	0.0163±0.0084

[a] haplotypes that are unique to their respective populations (not shared with other populations).

positions 16166 and 16298.

Haplotype diversity (h) at the sequence type level varied in the studied populations, ranging from 0.8784±0.0257 in LU2 to 0.9902±0.0062 in LU3. Total diversity of the 10 Tai populations was 0.9909±0.0009, which was within the same range as most other East and Southeast Asian populations [20]. At the nucleotide level, the diversity of the studied populations was in the range of 0.0136±0.0072 (LU2 and LU3) to 0.0197±0.0102 (YU4). The nucleotide diversity of all populations (0.0163±0.0084) was similar to that of Thai populations in northern Thailand (0.020±0.011) [21].

The mismatch analyses of pooled samples showed a unimodal distribution, which is characteristic of a population that has undergone large-scale expansion (Fig 2) [23]. The same evidence was also found in pooled Yuan and pooled Lue populations. The large negative significant *Fs* values ($P<0.01$) agreed well with a demographic model as inferred from the mismatch distribution. The negative values of *Fs*, which differ significantly from zero, indicate demographic expansion in the studied populations [18].

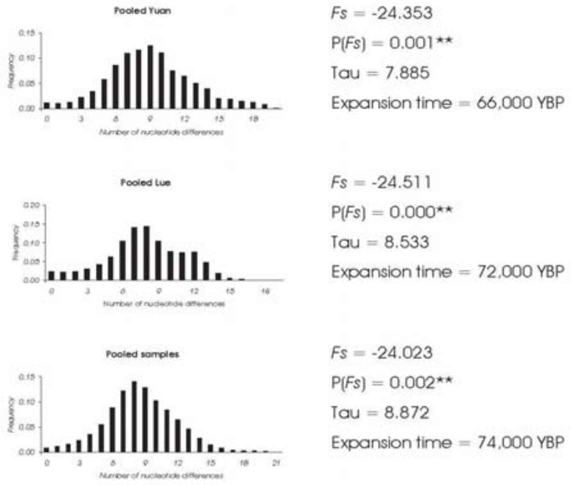

Fig 2. Mismatch distribution and Fu's *Fs* statistic with their P values. The expansion time (YBP) was estimated from the Tau value (t), assuming the divergent rate to be 33% site/million years.

The Tau value (t), which reflects locations of the mismatch distribution crest, provides a rough estimation of the time when rapid population expansion started [17]. The tau values of pooled Yuan, pooled Lue, and a pool of all samples range from 7.88 to 8.87, which correspond to an estimated expansion time of 66,000 to 74,000 years before present (YBP), assuming a mutation rate of 1.65×10^{-7} per bp per year or 33% divergence per million years and a generation of 20 years [24] (Table 2).

As previously reported, most human populations all over the world show significant signs of Pleistocene expansion. The earliest expansion times are found in East Africa (Turkana, 110,000 YBP). The average expansion times are slightly earlier in Asia and Oceania (72,000 YBP) than in sub-Saharan Africa (70,000 YBP), America (57,000 YBP), and in Europe, the Middle East, and India (42,000 YBP) [25]. Our result also reflects an ancient imprint of the Pleistocene expansion in Tai populations and agrees with the previous expansion estimate for the Dai, Thai and Zhuang, which occurred more than 66,000 YBP; earlier than for the East Asian population (60,000 YBP) [20].

Relationship among Populations

On the basis of pairwise difference distance, a multidimentional distribution plot of the 10 studied populations as well as the selectively published Tai, Mon-Khmer and Tibeto-Burman speaking populations, were constructed to investigate their relationships (Fig 3). The Tai and Mon-Khmer speaking groups from northern Thailand and the Dai from southern China were compared, in order to determine the Khon Muang's ancestors. The selective Tibeto-Burman speaking populations were used as the more distant out-group. They are hill-tribes who residing in northern Thailand and practicing the endogamous tradition.

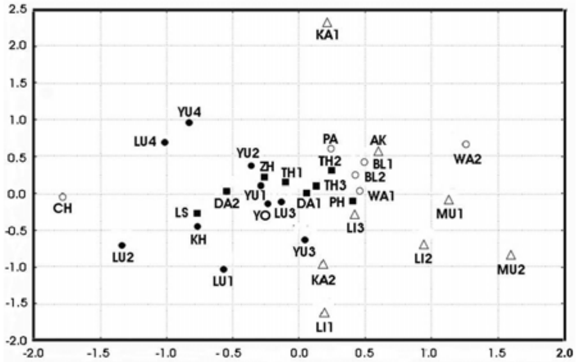

Fig 3. Multidimensional scaling scatter plot based on the pairwise distance matrix (● studied Tai, ■ published Tai, o Mon-Khmer, △ Tibeto-Burman). See the meaning of population abbreviations in Table 1 and 2's first column.

Among the studied Tai groups, the results showed that populations within the same ethnic group did not cluster together, especially the Lue. All four Lue populations did not show close genetic relatedness, although some of them (LU1 and LU2) were from the same province. Historically, Yong and Lue had closed linguistic affinity, but the genetic affinity found in the present study did not correspond to linguistic evidence. The Yong was closest to LU3 from Chiang Rai, but did not cluster with other Lue populations. The two Yuan populations from Chiang Mai (YU1 and YU2) were closely related, but did not group with Yuan from Lamphun (YU3). The Yuan from Saraburi (YU4) was separated from Yuan in northern Thailand. This probably reflected differences in migration history and geographic location. The relatively large genetic distances among some studied Tai samples - LU1, LU2, LU4 and YU4, which were scattered from the rest of Tai speaking groups, reflected the low female migration rate and founder effect episodes within these populations. After small population migrated out of their homeland, at different times via different routes, intense genetic drift changed their genetic structure. Consequently, each of these villages became genetically unique, despite the same ancestral ethnic name usage.

Classically, language was used as an important criterion to distinguish human relationships in terms of linguistic affinity. Languages of the same group must have originated in one area and distributed to be the local languages in several places. The shared features of languages in one group can be due to shared ancestors. Therefore, close genetic relationshipa are expected among the populations that use closely related languages. When the Mon-Khmer and Tibeto-Burman speaking populations from the northern part of Thailand and Yunnan province of China and the studied Tai populations were analyzed for the genetic affinity, populations of the same language family were not grouped together. The MDS plot showed that most of Tai populations appear in the left half and the Tibeto-Burman on the right, while Mon-Khmer occupied the place between the first two groups (Fig 3). The Mon-Khmer speaking populations except the Chong (CH) seem to be more closely related to Tai populations. Even though our selected Mon-Khmer samples did not share any of the ancient civilization of northern Thailand with the Tai peoples as Lawa and Mon did, they appeared to share a closer genetic relationship with the Tai peoples than did the Tibeto-Burman populations.

Focusing on the majority of northern Thai peoples, the Yuan or Khon Muang, an interesting pattern is found, in which the Yuan from Chiang Mai (YU1 and YU2) and Zhuang from Guang Xi, China, are closely related. The Dai from South China (DA1 and DA2) also show some relationship to these two groups of Yuan. This observation tends to support the immigrant hypothesis that one of the Khon Muang's ancestors may be the Tai groups from South or Southeast China. Although the closed genetic affinity between Khon Muang and Tai groups in China can be revealed in this study, a clear relationship between Khon Muang and the endogenous Mon-Khmer groups cannot be found out.

There are another two groups of Mon-Khmer speaking populations that have long lived in northern Thailand, the Lawa and the Mon who might share the gene pool with the Khon Muang. Unfortunately, there is no such genetic data set available. In order to clarify this relationship, genetic data of the Lawa and the Mon are needed. If the Khon Muang showed close genetic relatedness to both mentioned populations, the potential of admixture processes might be the reason. The fact that contact among different ethnic groups occurred during the time of Tai migration, which led to the admixture processes, cannot be ignored. Cultural and commercial contacts among the groups inevitably led to inter-cultural and inter-ethnicity blending. To determine whether the present day Khon Muang might be the result of admixture processes between Tai and Mon-Khmer populations would require further investigation.

CONCLUSION

Using an informative mtDNA marker, the genetic structure of four Tai speaking peoples in northern Thailand and their relationship with the nearby populations in northern Thailand and southern China areas could be revealed. The population dispersion suggested that the genetic structure of each village was generated by a founder effect episode. Genetic drift and low female migration rates have left a genetic imprint on their current unique gene pool, despite the same ancestral ethnic name usage. Genetic clustering of Tai, Mon-Khmer and Tibeto-Burman groups, as revealed by mtDNA HVRI sequences, did not correlate well with linguistic classification. The Yuan or Khon Muang in northern Thailand exhibited a close relationship to the Tai group in South and Southeast China, which supported the immigrant hypothesis of their ancestors. However, more genetic data of the endogenous Mon-Khmer ethnic groups is needed to reconstruct a clear history of the Tai, as well as their biological ancestor.

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ELECTRONIC-DATABASE INFORMATION

Accession numbers and URL for data presented herein are as follows:

GenBank, http://www.ncbi.nlm.nih.gov/Genbank/ [accession numbers DQ900051-DQ900546]

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