

Unique Genetic Structure of Y-chromosomal Lineage of the Moken from the Andaman Sea of Thailand

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<https://doi.org/10.12982/CMUJNS.2020.0066>

Received: January 12, 2020

Revised: May 1, 2020

Accepted: May 8, 2020

ABSTRACT

To investigate the genetic structure of the Y-chromosome of the Moken people living in the Andaman Sea area of Thailand, and to compare the genetic relationship between them and other groups on the mainland, as well as the islands Southeast Asia. This study analyzed 17 Y-chromosomal short tandem repeat (Y-STR) loci in 11 unrelated Moken males from Ranong Province of Thailand. The genomic DNA was extracted from buccal cells, and amplified using an AmpF ℓ STR Yfiler PCR Amplification Kit. We compared Y-STR genotypes with other populations from the Y Chromosome Haplotype Reference Database (YHRD) and constructed the multidimensional scaling (MDS) plot and the neighbor-joining tree (NJ), based on genetic distance R_{st} . Nine different haplotypes from 11 unrelated individuals were identified. The haplotype diversity was 0.9455 ± 0.066 , which was closer to other Southeast Asian populations. The genetic relationship results also showed the genetic differentiation of the Moken, without any significant differences among them, as well as some Austronesian (AN) groups from Malaysia and Sino-Tibetan (ST) groups from Taiwan. This study suggests that there was a unique genetic structure on the Y-chromosome of the Moken from the Andaman Sea, showing genetic relations with some AN and ST groups.

Keywords: Y chromosomal-STR, Genetic structure, Moken, Andaman Sea

INTRODUCTION

The Moken is one of the sea nomad groups, who inhabit the coastal area and islands of the Andaman Sea, in the southern part of Thailand, and are distributed up the coast of the Mergui Archipelago of Myanmar. The ancestors of the Moken people might have lived on the Southeast Asian (MSEA) mainland which is now Myanmar, and spread southwards to Malaysia (Hinshiranan, 1996). The alternative in hypothesis of the origin of the Moken is that they originated in the islands of Southeast Asia (ISEA) (Koechlin, 1967). However, genetic evidence, supports the hypothesis that the Moken originated within the coastal region of MSEA before migrating to ISEA (Dancause et al., 2009). Thus, the origins of the Moken are still debated.

Mitochondrial DNA (mtDNA) and Y-chromosomal DNA are two uniparental genetic markers, which are commonly used to reconstruct population history, and investigate the genetic relationship among populations, including the tracing of lineages of populations (Richards et al., 2000; Maca-Meyer et al., 2001; Y Chromosome Consortium, 2002; Jobling and Tyler, 2003; Barbieri et al., 2013). mtDNA is maternally inherited, while the Y-chromosome is a useful tool to study paternal ancestry, because it is passed down from father to son and the majority of its DNA lacks recombination (Y Chromosome Consortium, 2002; Jobling and Tyler, 2003; Santana et al., 2014). A previous study of the mtDNA variation of the Moken living in Phuket province of Thailand indicated a low mitochondrial diversity and distinct genetic structure from Austronesian speaking groups and the MSEA people (Lum et al., 1998). Another study of mtDNA variation of the Moken, who live in the Mergui Archipelago of Myanmar, reported the basal mtDNA lineage of the Moken; observed M21b2 and M46a (Dancause et al., 2009). A recent mtDNA study of the Moken from Chang Island suggested the signal of the influence of genetic drift. The identified mitochondrial lineages were M21b2, D4e1a, M46a and F1a1c1. The genetic relationship analysis suggested that the Moken on Chang Island shared common ancestors with the Moken people in the Mergui Archipelago and with some Austroasiatic speaking groups in MSEA. It also suggested that the Moken originated on the MSEA before migration to the islands (Seetaraso et al., 2019). However, the study of paternal lineage of the Moken people have not been studied.

In this study, we aim to investigate the genetic structure of Y-chromosomal DNA in the Moken people from Andaman Sea of Thailand and compare the genetic relationship between them and other published data. We examined the genotype 17 Y-chromosomal STR loci using AmpF ℓ STR Yfiler PCR Amplification Kit (Applied Biosystems, USA), from 11 Moken males. We found a unique genetic structure of Y-chromosomal lineage in the male Moken.

MATERIAL AND METHODS

Studied populations

This study was approved by the Naresuan University Institutional Review Board (COA No. 0464/2017). Buccal samples were collected with informed consent from 11 unrelated male volunteers from Chang Island in the Ranong Province of Thailand (TH-MG) (Figure 1). The recruitment criteria for volunteers was unrelated men belonging to the Moken from Chang Island having at least two generations of ancestors, without any genetic admixed by other tribes. DNA was extracted from the buccal cells with the Gentra Puregene Buccal Cell Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocols. Sample DNA quantity and purity were determined by NanoDrop 2,000 UV-Vis Spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA). The Y-chromosomal STR data from 59 populations on the mainland as well as the islands of Southeast Asia (Table 1), were taken from the Y-chromosomal STR Haplotype Reference Database (YHRD; <http://www.yhrd.org/>) (Willuweit and Roewer, 2007) to then be compared with our results.

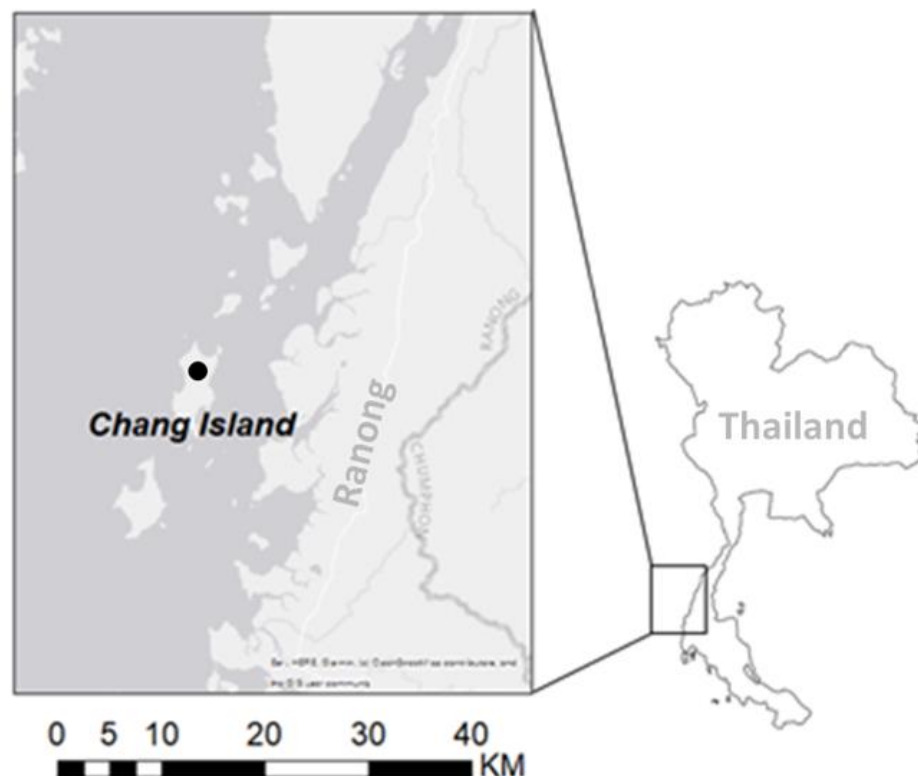


Figure 1. Map of sampling location of the Moken in Chang Island, Ranong Province of Thailand.

Table 1. General information about the current studied and other populations from the YHRD database.

No.	Country	Population	Code	Linguistic family	Size (n)	Accession number	No.	Country	Population	Code	Linguistic family	Size (n)	Accession number
1	Thailand	Moken	TH-MG	AN	11	This study	31	Malaysia	MY-BY	Bidayuh	AN	113	YA003415
2	Thailand	Thai	TH-TH	TK	140	YA004250	32	Malaysia	MY-CH	Champa	AN	13	YA004033
3	Thailand	Central Thai	TH-CE	TK	256	YA003923	33	Malaysia	MY-IB	Iban	AN	103	YA003416
4	Thailand	Northern Thai	TH-NT	TK	15	YA004164	34	Malaysia	MY-JA	Jawa	AN	14	YA004039
5	Thailand	Padong	TH-PD	ST	13	YA004162	35	Malaysia	MY-KD	Kedah	AN	9	YA004035
6	Thailand	Pwo	TH-PW	ST	15	YA004168	36	Malaysia	MY-KL	Kelantan	AN	43	YA004038
7	Thailand	Shan	TH-SH	TK	12	YA004163	37	Malaysia	MY-KS	Kensiu	AA	16	YA004133
8	Thailand	Skaw	TH-SK	ST	24	YA004167	38	Malaysia	MY-LA	Lanoh	AA	11	YA004134
9	Thailand	Yong	TH-YO	TK	124	YA004161	39	Malaysia	MY-ME	Melanau	AN	104	YA003417
10	Bangladesh	BD-MA	Barma	ST	107	YA004285	40	Malaysia	Minang	MY-MI	AN	23	YA004036
11	Bangladesh	BD-RA	Rakhine	ST	110	YA004284	41	Malaysia	Northern Borneo	MY-NB	AN	51	YA003927
12	China	CN-HA	Han	ST	30	YA003866	42	Malaysia	Rawa	MY-RA	AN	11	YA004034
13	China	CN-FJH	Han	ST	124	YA004397	43	Malaysia	Semai	MY-SE	AA	18	YA004135
14	China	CN-FJS	She	ST	92	YA004031	44	Philippines	Filipino	PH-FP	AN	943	YA002895 YA003206 YA003892
15	China	CN-FZD	Danmin	ST	87	YA004488	45	Philippines	Manila	PH-MA	AN	64	YA003202
16	China	CN-FZS	She	ST	152	YA003747 YA004066 YA004066	46	Singapore	Malay	SG-ML	AN	556	YA004367 YA003272
17	China	CN-GDH	Han	ST	1623	YA004304 YA004330 YA004392	47	Taiwan	Ami	TW-AM	AN	86	YA003920 YA003961
18	China	CN-GXG	Gin	AA	161	YA004217	48	Taiwan	Atayal	TW-AT	AN	240	YA003524 YA003919 YA003964
19	China	CN-GXM	Miao	AA	186	YA004220	49	Taiwan	Bunan	TW-BU	AN	38	YA003918
20	China	CN-GXY	Yao	AA	138	YA004221	50	Taiwan	Han	TW-HA	ST	30	YA003963
21	China	CN-GXZ	Zhuang	TK	2913	YA003542 YA004006 YA004208 YA004222	51	Taiwan	Hakka	TW-HK	ST	22	YA003962
22	China	CN-SZH	Han	ST	136	YA004280	52	Taiwan	Paiwan	TW-PA	AN	237	YA003500 YA003915
23	China	CN-XBD	Dai	TK	92	YA003876 YA003877	53	Taiwan	Puyama	TW-PU	AN	15	YA003913
24	Indonesia	IN-BT	Batak	AN	100	YA003769	54	Taiwan	Rukai	TW-RU	AN	28	YA003916
25	Indonesia	IN-JA	Java	AN	137	YA003200 YA003770	55	Taiwan	Saisiat	TW-SA	AN	24	YA003914
26	Lao	LA-LT	Laotian	TK	45	YA003948	56	Taiwan	Tsou	TW-TS	AN	27	YA003912
27	Malaysia	MY-AC	Achen	AN	7	YA004032	57	Taiwan	Yami	TW-YA	AN	24	YA003911
28	Malaysia	MY-BJ	Banjar	AN	18	YA004040	58	Vietnam	Kinh	VN-KI	AA	123	YA003984
29	Malaysia	MY-BT	Bateq	AA	19	YA004131	59	Vietnam	Mong	VN-MO	AA	59	YA003985
30	Malaysia	MY-BU	Bugis	AN	15	YA004037	60	Vietnam	Tay	VN-TA	AA	21	YA003986

Note: BD: Bangladesh, CN: China, IN: Indonesia, MY: Malaysia, PH: Philippines, SG: Singapore, TH: Thailand, TW: Taiwan, VN: Vietnam.

Y-STR genotyping

All samples were genotyped for 17 Y-chromosomal STR loci (DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS385a/b, DYS438, DYS439, DYS437, DYS448, DYS456, DYS458, DYS635, and Y-GATA H4) with the AmpF ℓ STR Yfiler PCR Amplification Kit, according to

the manufacturer's recommendations. Amplification reactions were performed using a GeneAmp PCR System 9700: these products were analyzed in an ABI 3130 sequencer (Applied Biosystems). Genotyping designations were based on a comparison with allelic ladders in the AmpF ℓ STR Yfiler PCR Amplification Kit, along with GeneMapper ID-X software (Applied Biosystems).

Statistical analyses

The allele and haplotype frequencies were counted directly, and then compared. Each of the haplotypes were found with the YHRD database. Gene diversity (GD) of the 17 Y-chromosomal STR loci and haplotype diversity (h) (Nei, 1987), were calculated using the ARLEQUIN software package v. 3.5.2.2 (Bern, Switzerland) (Excoffier and Lischer, 2010). We also compared haplotype diversity between the Moken and other MSEA and ISEA populations, according to four language families: Austronesian (AN), Austroasiatic (AA), Tai-Kadai (TK), and Sino-Tibetan (ST) from previous studies (Trejaut et al., 2014; Brunelli et al., 2017; RahayuKarmilla et al., 2018).

To ascertain the genetic relationship among populations, we compared the 17 Y-chromosomal STR loci with the published data of 59 Southeast Asian populations, belonging to four linguistic categories (AN, AA, TK, and ST) in the YHRD database (Table 1). The genetic distance (R_{st}) between pairs of the population and their statistical significance using 10,000 permutations, were estimated by AMOVA and MDS tools of the YHRD. The genetic distance was plotted in two dimensions by means of a multidimensional scaling (MDS) plot, using the XLSTAT statistical software demo version (Addinsoft, Paris, France). A neighbor-joining (NJ) tree was constructed using the MEGA-X (Kumar et al., 2018).

RESULTS

Allele frequencies, gene diversities, and haplotype diversity

Given 11 unrelated Moken men, they were analyzed for allele frequency distributions and gene diversities of the 17 Y-chromosomal STR loci (Table 2). A total of 54 alleles from 17 Y-chromosomal STR loci were identified with the corresponding allele frequencies, ranking from 0.0909 to 0.9091. The DYS448 is the highest polymorphic STR locus (7 alleles), and showed the highest gene diversity ($GD = 0.9091$), whereas the lowest polymorphic STR locus was DYS391 (2 alleles and $GD = 0.1818$).

Among 11 males, there are nine haplotypes (Table 3), out of which eight were single unique, and one (HAP03) was multiple unique. The haplotype diversity was found to be 0.9455 ± 0.066 . When we compared the haplotypes of the Moken with other people from the YHRD database, we found that one haplotype (HAP08) exactly matched that of the ST people from China.

The haplotype diversity of the Moken was close to the values from various comparative populations (Trejaut et al, 2014; Brunelli et al, 2017; RahayuKarmilla et al; 2018) (Figure 2).

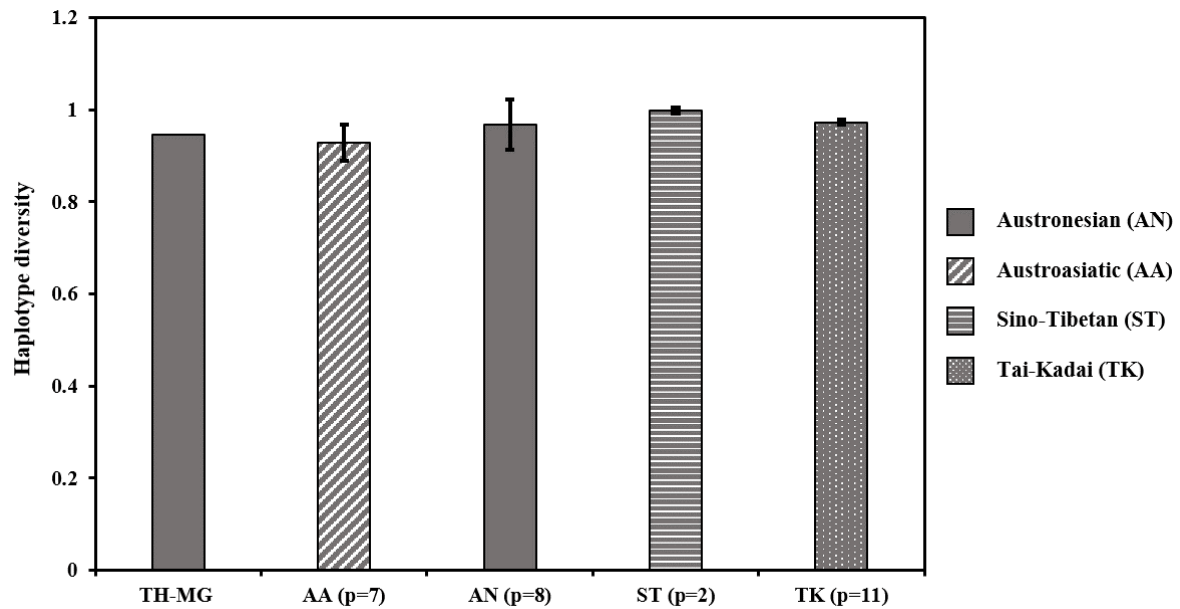


Figure 2. Comparison of haplotype diversity between the Moken and other Southeast Asian people. The error bars show range of haplotype diversity within linguistic family. (p = the number of populations).

Table 2. Allele frequencies and gene diversities of the 17 Y-chromosomal STR loci of the Moken

Allele	DYS19	DYS389I	DYS389II	DYS390	DYS391	DYS392	DYS393	DYS437	DYS438	DYS439	DYS448	DYS456	DYS458	DYS635	YGATA H4	Genotype	DYS385
9									0.4545							11, 16	0.1111
10					0.9091				0.2727							12, 12	0.1111
11		0.0909			0.0909	0.0909			0.2727	0.4545					0.4545	13, 15	0.2222
12		0.1818				0.0909	0.3636			0.2727					0.4545	13, 20	0.1111
13		0.2727				0.4545	0.6364			0.2727					0.0909	13, 21	0.2222
14	0.7273	0.4545				0.3636		0.3636								14, 19	0.2222
15	0.2727							0.4545			0.2727	0.7273					
16								0.1818			0.1818	0.0909	0.2727				
17												0.1818	0.2727				
18											0.1818		0.1818				
19											0.0909			0.2727			
20											0.0909		0.1818	0.4545			
21				0.2727							0.0909		0.0909	0.1818			
22				0.4545							0.0909						
23				0.2727										0.0909			
27			0.0909														
28			0.1818														
29			0.0909														
30			0.4545														
32			0.1818														
GD	0.4364	0.7454	0.7818	0.7091	0.1818	0.7091	0.5091	0.6910	0.7091	0.7091	0.9091	0.4727	0.8546	0.7636	0.6367	-	0.9020

Note: GD: gene diversity

Table 3. Y-chromosome haplotype distribution of the Moken, based on the 17 Y-chromosomal STR loci.

Haplotype	DYS19	DYS385a	DYS385b	DYS389I	DYS390II	DYS390	DYS391	DYS392	DYS393	DYS437	DYS438	DYS439	DYS448	DYS456	DYS458	DYS635	GATA-4	Frequency
HAP01	15	11	16	12	28	21	10	11	12	14	10	11	21	15	18	23	13	0.0909
HAP02	15	13	20	11	27	23	10	13	12	15	10	12	22	16	17	21	12	0.0909
HAP03	14	14	19	14	30	22	10	14	13	14	9	11	15	15	16	19	11	0.2727
HAP04	14	13	21	13	30	22	11	13	13	15	9	12	16	15	17	20	11	0.0909
HAP05	14	13	21	13	30	22	10	13	13	15	9	12	16	15	17	21	11	0.0909
HAP06	15	12	12	13	29	23	10	12	12	15	10	11	19	15	20	20	12	0.0909
HAP07	14	13	15	14	32	21	10	13	13	16	11	13	18	17	20	20	12	0.0909
HAP08	14	14	19	12	28	23	10	14	12	15	11	13	20	15	18	20	12	0.0909
HAP09	14	13	15	14	32	21	10	13	13	16	11	13	18	17	21	20	12	0.0909

Genetic relationship among populations

The genetic distance (R_{st}) among the population indicated that the Moken population (TH-MG) was not significantly different from the Acheh (MY-AC), the Champa (MY-CH), and the Minang (MY-MI) people from Malaysia, who speak the AN language, along with the ST-speaking Hakka (TW-HK) from Taiwan.

The multidimensional scaling (MDS) plot revealed that the Moken (TH-MG) were separated from other populations, reflecting some degree of differentiation and unique genetic structure. The TK- and ST-speaking groups were clustered together in the center of the plot, indicating their close genetic relationship. The AA- and AN-speaking groups were scattered around the plot indicating genetic heterogeneity. However, eight aboriginal Taiwanese (TW-AM, TW-AT, TW-PA, TW-PU, TW-RK, TW-SA, TW-TS, and TW-YA) were dispersed in the lower right quadrant of the plot, reflecting their divergence (Figure 3).

The NJ tree showed five clusters of population: the Moken population (TH-MG) was not clustered with their linguistic relatives (clusters 3, 4, and 5), but were rather close to the ST group cluster (cluster 1). TK groups were located in cluster 2, while the AA-speaking groups were scattered throughout the tree (Figure 4).

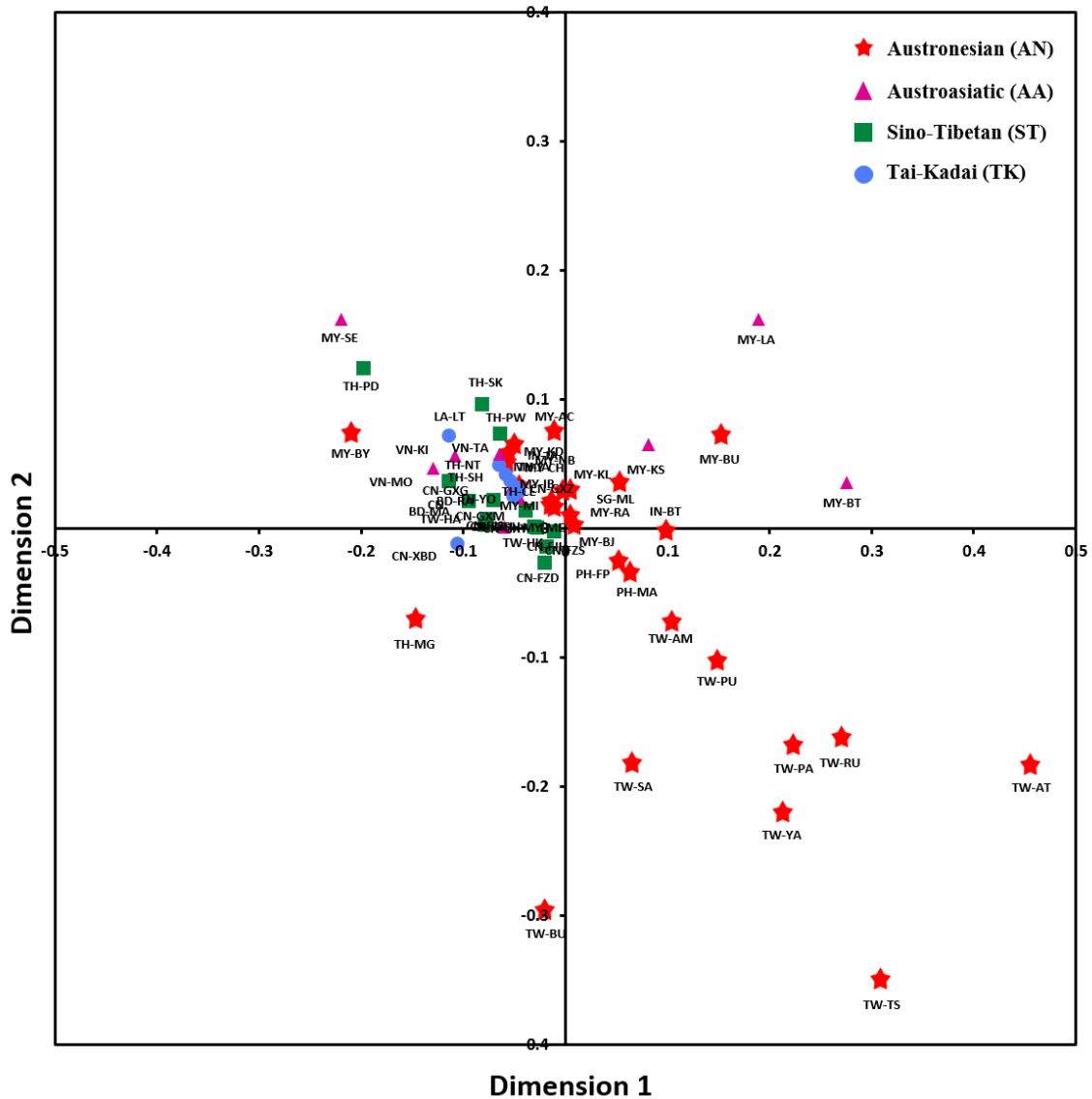


Figure 3. Multidimensional scaling (MDS) plot based on R_{st} values for 60 populations. Red star, purple triangle, green square and blue circle symbols indicate Austronesian, Austroasiatic, Sino-Tibetan and Tai-Kadai populations, respectively (See abbreviations of populations in Table 1). The stress value is 0.188.

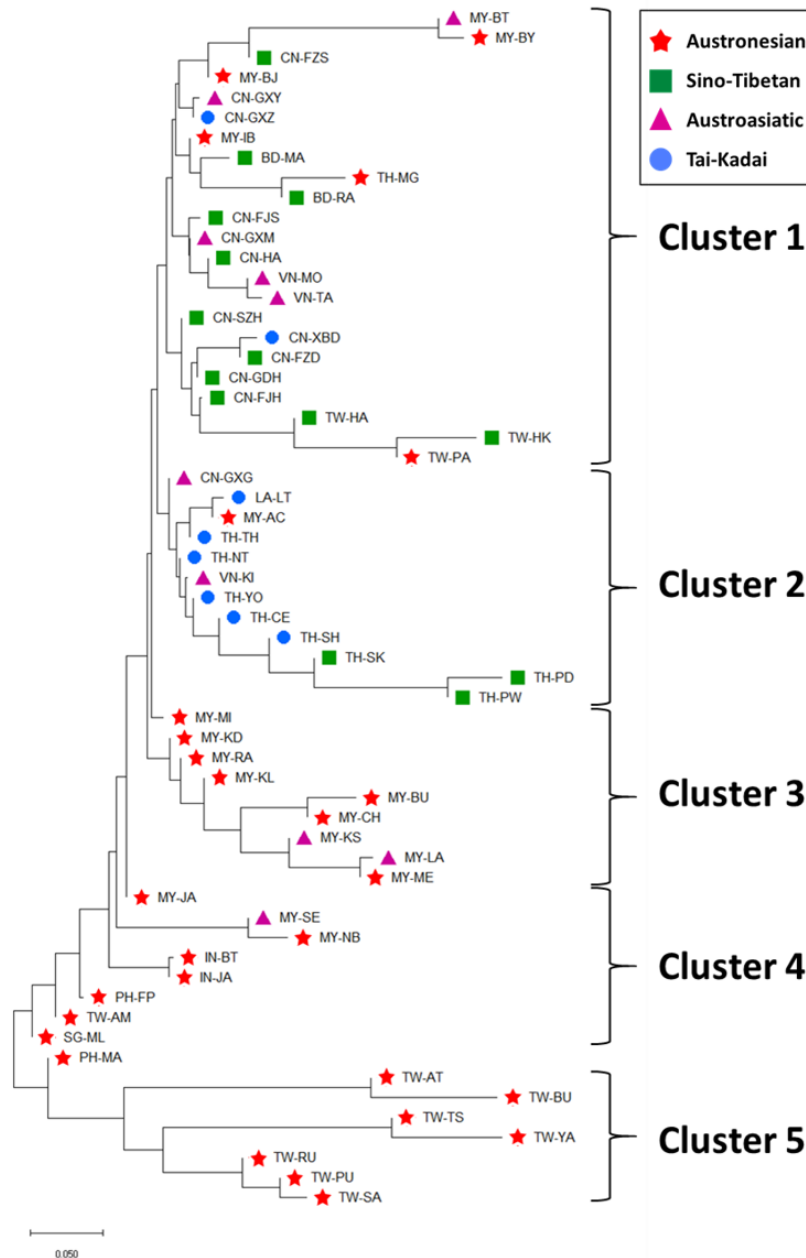


Figure 4. Neighbor-joining (NJ) tree constructed from the R_{st} values among 60 populations. Red star, purple triangle, green square and blue circle symbols indicate Austronesian, Austroasiatic, Sino-Tibetan and Tai-Kadai population, respectively (See abbreviations of populations in Table 1).

DISCUSSION

This study investigated the genetic structure of 17 Y-chromosome STR loci in 11 Moken males living on Chang Island, originally from Ranong Province, Thailand. The Moken are a group of sea nomads living in the Andaman Sea area who speak a local language, which is classified as an AN-language family. The

results show that there are nine haplotypes, with high haplotype diversity (0.9455 ± 0.066), which is close to other Southeast Asian people from previous studies (Trejaut et al., 2014; Brunelli et al., 2017; RahayuKarmilla et al., 2018). The AmpF ℓ STR Yfiler PCR Amplification Kit have been used to analyze the Y-chromosome in various populations (Grskovic et al., 2010; Santana et al., 2014). When the identified haplotypes in the Moken were compared with those available from the YHRD database, one was found to match a sample from the Han in China who speak ST languages, thus suggesting that the male Moken may have a genetic relationship with them. This is consistent with other reports about ancestors of the present-day AN population or “Proto-Austronesian speakers,” originating in the area that is now Southeast China (Diamond and Bellwood, 2003; Hwa et al., 2010; Wu et al., 2013).

The genetic relationships between Moken males and those from 59 other Southeast Asian groups showed that the Moken were distantly related to other Austronesian groups, but they tend to relate to certain AN groups in Malaysia and ST groups in Taiwan (Figure 3). The NJ tree suggested that Moken males are distinct from other Austronesian groups; however, they are in a linguistically-mixed cluster, consisting mainly of the ST population (Figure 4). These results show that the Moken male exhibited genetic relationships with both the AN and ST groups, while at the same time, Moken males possess their own unique genetic structure.

A comparison of the Y-chromosomal STR data analyses to the control region in mtDNA data analyses of the same group of Moken (Seetaraso et al., 2019), revealed the difference between their paternal and maternal lineage. Their mitochondrial lineage is close to not only AN, but also to the AA people. As a contradiction, the Y-chromosomal lineage of the Moken is closely related to other AN groups, including a few to ST groups. From this point of view, there are contrasting genetic structures and patterns of female and male lineage in the Moken from Chang Island, Ranong Province. This might result from different microevolutionary forces in male and female lineages. Sex-biased demographic histories of males and females have been reported in previous studies of the Southeast Asian island populations (Kayser et al., 2008; Tumonggor et al., 2013), reflecting an unequal and complex population.

This is one of the studies focusing on the genetic structure of Y-chromosome STR in the Moken of Ranong Province from Thailand. The Moken show a paternal genetic pattern that is unique, but closer to the Austronesian groups of Malaysia and the ST group of Taiwan. These may share a common ancestry, or they may have mixed with them. This study is limited, in that no information on the Y-chromosomal single nucleotide polymorphism (Y-SNP) is included. Further investigation of SNPs will be necessary to identify the origin of the Moken and also that of other Sea Nomadic groups, i.e., the Urak Lawoi and Moken.

ACKNOWLEDGEMENTS

We would like to thank all volunteers and participants who donated their biological samples. This study was funded by Naresuan University (Grant No. R2561B029 and R2562B085). JK acknowledged partially supports by Chiang Mai University, Thailand.

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