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ORIGINAL ARTICLE

Genetic trail for the early migrations of Aisin Gioro, the imperial house of the Qing dynasty

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The House of Aisin Gioro, the imperial clan of Qing dynasty (1644–1911), affected the history of China and the formation of Manchu ethnicity greatly. However, owing to the lack of historical records and archeological evidences, the origin of the House of Aisin Gioro remains ambiguous. To clarify the origin of Aisin Gioro clan, we conducted whole Y-chromosome sequencing on three samples and Y-single-nucleotide polymorphism (Y-SNP) genotyping on other four samples beside those reported in previous work. We confirmed that the paternal lineage of the Aisin Gioro clan belongs to haplogroup C3b1a3a2-F8951, a brother branch of C3*-Star Cluster (currently named as C3b1a3a1-F3796, once linked to Genghis Khan), which is quite different from the predominant lineage C3c-M48 in other Tungusic-speaking populations. We also determined a series of unique Y-SNP markers for the Aisin Gioro clan. Diversity analyses of haplogroup C3b1a3a2-F8951 revealed the early migration of the ancestors of the Aisin Gioro clan from the middle reaches of Amur River to their later settlement in southeastern Manchuria. Hence, our results suggest that the Aisin Gioro clan may be descendants of ancient populations in Transbaikal region and closely related to origin of current Daur populations. Our research indicated that detailed research of stemma and deep sequencing of Y chromosomes are helpful to explore the prehistoric activities of populations lacking historical records and archeological evidences.

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INTRODUCTION

Peopling of Northeast China dated back to early Neolithic Age. A number of archeological cultures had been found in this region. According to the traditional opinion, the origin of Manchu ethnic group can be traced back to various ancient populations once living in this region, such as *Sushen*, *Yilou*, *Wuji*, *Mohe* and *Jurchen*.[1] By late Ming Dynasty (1368–1644), the Aisin Gioro clan of *Jianzhou Jurchen* tribe started to unify all other *Jurchen* tribes and contributed greatly to the formation of modern Manchu. Subsequently, they conquered the other parts of China and established the last empire of China—the Qing Dynasty (1644–1911).[2] It is generally accepted that the modern Manchu ethnic group are an admixture of ancient populations in Northeast part of China.[1]

However, the origin of the Aisin Gioro clan remains ambiguous. There have been three versions of the story (Figure 1). (1) An official book, *Manjusai da sekiyen-i kimcin bithe* (*Royal Researches on Manchu Origins*), was compiled from AD 1777 to record the activities of ancestors of all Manchu populations. In this book, the Aisin Gioro clan traced their origin to the Changbai Mountain region on the border between present China and North Korea.[3] (2) On the contrary, their claimed ancestor, Dudu Mentemu (or Möngke Temür), was the leader of Mongolian warring clans of Odoli, which moved from *Yilan Hala* castle to Tumen River region.[2] (3) Furthermore, the Aisin Gioro clan shared the same legend of ancestor with *Hūrha* tribe, a tribe living in the middle reaches of the Amur River.[4] Both Aisin Gioro clan and *Hūrha* tribe claimed *Bukūri Yongšon*, a mythical hero, to be their earliest ancestor. The difference between these three versions of records is yet to be clarified.

Previous researches of Y chromosome had provided some clues to the origin of Manchu and the Aisin Gioro clan. As a major ethnic group of Tungusic-speaking populations, Manchu was included in most researches about East Asia populations.[5,6] The high diversity of Y-chromosome haplogroup indicated that modern Manchu is an admixture of various ancient populations. However, haplogroup C3c-M48 (following the nomenclature of Karafet *et al.*[7]), the predominant lineage of other Tungusic-speaking populations,[8–10] contributes only s few percent in paternal gene pool of Manchu.[5,6] A Y-short tandem repeat (Y-STR) cluster under haplogroup C3c-M48, the 'Manchu cluster', was proposed to be the Y-chromosome profile of Giocangga, the most recent common ancestor (TMRCA) of the Royal branch of the Aisin Gioro clan.[11] In previous work, we tested several members of this clan and proposed that the lineage of this clan is haplogroup C3b1a3a*-M401(xF5483).[12] In this study, we genotyped the Y-single-nucleotide polymorphism (Y-SNP) and Y-STR of more samples from the Aisin Gioro family and carried out whole Y-chromosome sequencing of four samples, to explore the origin and

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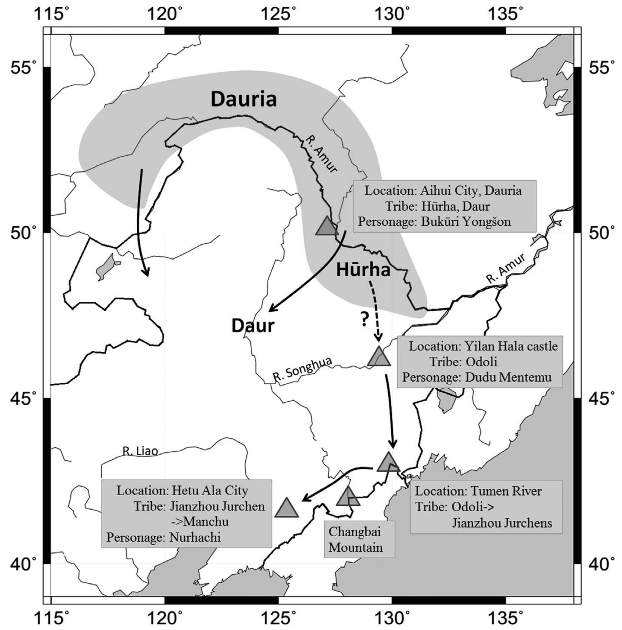

Figure 1 The possible early migration route of the ancestor of the Aisin Gioro clan.

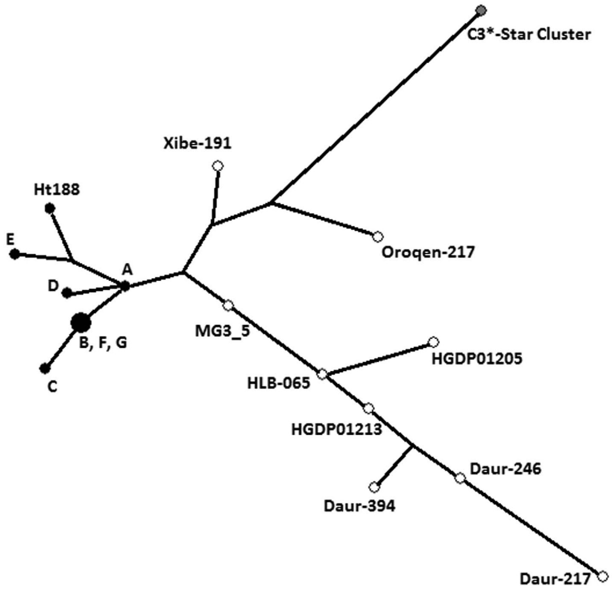

Figure 2 Y-STR network of 'C3b-Daur Clade' based on 15 Y-STRs (black for samples A–G from the Aisin Gioro clan and Manchu ht188 from Xinbin County). The center value of C3*-Star Cluster haplotype was used as an outgroup.

unique Y-SNP markers of this clan, as well as their contributions to the formation of Manchu ethnicity.

MATERIALS AND METHODS

Samples

Beside the three samples mentioned in previous work, blood samples were collected from other four members of the Aisin Gioro clan confirmed by their genealogy records. They were subsequently proved to be genetically linked to Aisin Gioro by Y-chromosomal STRs. The genealogy of these seven samples from the Aisin Gioro clan was shown in Supplementary Figure S1. To protect the privacy of the testees and their close relatives, we blocked the names of testees or the information of their near ancestry. The donors signed informed consent to participate in the study. The ethics committee for biological researches at the School of Life Sciences in Fudan University approved the study.

Molecular methods

First, we extracted the DNA of four samples and amplified 17 Y-STRs (DYS19, DYS389I/II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, DYS439, DYS448, DYS456, DYS458, DYS635, Y-GATA H4 and DYS385a/b) using Y-Filer Kit (Life Technologies, Carlsbad, CA, USA). For these four samples, we genotyped seven SNPs using Sanger sequencing, including M217, F1396, F3535, F3273, F5483/SK1074, M546 and M401. Primers of these markers had been reported.[12] We also collected available Y-STR haplotypes, which are close to the profiles of the Aisin Gioro clan ($DYS390=24$, $DYS393=14$ and $DYS635\geqslant 23$).[6,8,13–19] Y-STR network of C3 samples from this study and references (see Results) were drawn using Network 4.6.1.2 (Fluxus, Suffolk, UK), excluding the marker DYS385a/b. Next-generation sequencing technology was used to sequence the whole Y-chromosome of four samples, including sample A, B and C from the Aisin Gioro clan and HLB-065 from Buryats in Inner Mongolia of China. We used the whole protocol of sequencing and data analysis reported by Yan *et al.*[20] We followed the regulations proposed by the YCC (Yakima County Code) to construct the phylogenetic tree relevant to new mutations of the NRY region of the Y chromosome.[21]

TMRCA of the studied Y-STR haplotypes were estimated using Average Squared Distance (ASD[22–24]) and Bayesian analysis of trees with internal node generation (BATWING[6,25]) method. The genealogical mutation rate[26] and the evolutionary mutation rate[27] described previously were used for the age estimates both by the ASD method and BATWING. Generation time was set at 25 years.

RESULTS

Same as the other three samples reported previously, all four samples in this study belong to haplogroup C3b1a3a*-M401(xF5483). Y-STR haplotypes of these seven samples are similar to each other (Supplementary Table S1). Additionally, a series of Y-STR haplotypes that are close to the profiles of the Aisin Gioro clan were collected from other published researches (Supplementary Table S1). In total, we collected 17 haplotypes of 15 Y-STR to draw the Y-STR network (Figure 2). All seven samples from the Aisin Gioro clan and Manchu sample ht188 from Xinbin County clustered together on the left of the network, whereas other samples from Mongolian, Buryats, Oroqen and Daur compromised to another branch of Y-STR haplotypes in network.

Whole Y-chromosome sequences of Aisin Gioro samples and one Buryat sample (HLB-065) formed a brother branch (C3b1a3a2-F8951) beside C3b1a3a1-F3796 (previous C3*-Star Cluster) (Figure 3). Sequence data from Lippold *et al.*[15] indicated that their Oroqen sample HGDP01205 and Daur sample HGDP01213 also belong to this branch. Based on unpublished phylogenetic data from our lab, the names of all downstream clades of haplogroup C3-M217 were revised. Detailed information of newly discovered 29 Y-SNPs was listed in Supplementary Table S2. On the phylogenetic tree of C3b1a3a2-F8951, all three samples from the Aisin Gioro clan belong to a special sub-branch C3b1a3a2a-F14735 (Figure 3). Three other samples from Oroqen, Daur and Buryats belong to another sub-branch. This relationship corresponded to their location on the Y-STR network.

Time estimations can be used to determine when this particular lineage arose and possibly when the diffusion happened. We calculated TMRCA for all haplotypes with value on 17 Y-STR makers (ht1–ht17 in Supplementary Table S1). For haplotypes from published resources (Supplementary Table S1), the downstream haplogroups are not determined. However, all these haplotypes are extremely similar to those of Manchu, while different from the medium value of C3*-Star

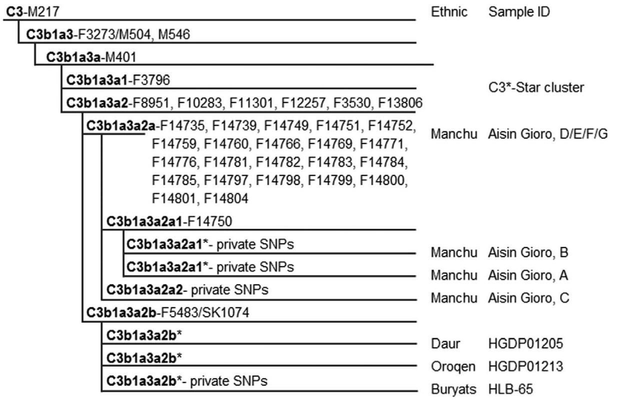

Figure 3 Phylogenetic tree of haplogroup C3b1a3a2-F8951 based on Y-SNP genotyping and sequencing data.

cluster haplotype (DYS390 = 25, DYS393 = 13 and DYS635 = 22, haplogroup C3b1a3a1-F3796) clearly. Therefore, we judge that all these haplotypes are haplogroup C3b1a3a2-F8951. In this research, we named this special haplotype cluster as 'C3b-Daur Clade'. The age of 'C3b-Daur Clade' calculated by the evolutionary rate is far beyond the history of Daur or of all Mongolic-speaking populations. On the contrary, the ASD estimations using genealogical rate (2260 ± 1198 years ago) is closer to the age when ancestor of Mongolic-speaking population, *Xian-Bei* tribe, appeared in the history of China (about 1900 years ago).[28] It had been proved that the 'evolutionary rate' is suitable for the estimation of paternal clades that emerged in the Paleolithic Age,[29] while 'genealogical rate' gives the best-fit estimation for historical lineage dating.[30] Therefore, we preferred the estimation based on 'genealogical rate' in this study.

DISCUSSION

In this research, all seven volunteers from the Aisin Gioro clan were determined to be C3b1a3a*-M401(xF5483). Their Y-STR haplotypes formed a special cluster deviated from the haplotype of other populations. Through the whole Y-chromosome sequencing of Aisin Gioro samples (A, B and C) and Buryat sample HLB-65, we determined 23 unique Y-SNP markers for the Aisin Gioro clan (see Figure 3 and Supplementary Table S2). Hence, we confirmed that the paternal lineage of the Aisin Gioro clan is C3b1a3a2a-F14735.

According to the results of the sequencing data, haplogroup C3b1a3a2-F8951 is a brother branch of C3b1a3a1-F3796 (previous 'C3*-Star cluster'), which was predominant in Mongolic-speaking populations. According to our investigation, all available samples of 'C3b-Daur Clade' belong to this haplogroup C3b1a3a2-F8951. Combining the published data, haplotypes of 'C3b-Daur Clade' were found from several ethnics from northeastern China and the flanking regions. Most of haplotypes of 'C3b-Daur Clade' came from Manchu and Daur populations (Supplementary Table S1). A few samples of this cluster found in Buryats, Mongolian, Oroqen, Ewenki and Xibe populations might have resulted from recent admixtures.

It is worth noting that the ASD estimations of 'C3b-Daur Clade' using genealogical rate (2260 ± 1198 years ago) is a little older than the age when the ancestor of all Mongolic-speaking population, *Xian-Bei* tribe, appeared in history records of China (~1900 years ago).[28] As shown in the revised phylogenetic tree of C3b1a3a-M401 (Figure 3), C3b-Daur Clade (C3b1a3a2-F8951) is the brother branch of C3b1a3a1-F3918, which cover other C3*-Star cluster haplotypes from other Mongolic-speaking populations.[14,31] When the *Xian-Bei* tribe appeared in history records of China, there had been many tribes under the name *Xian-Bei*.[32] These *Xian-Bei* tribes (and their close relative *Shi-Wei* tribes) scattered in a vast geographic region, ranging from West Liao River in the south to the upper reaches of Heilongjiang River (Amur River) in the north.[32] Thus, the diversification history of *Xian-Bei* tribes could be older than recorded (~1900 years ago). From a genetic perspective, it may take a long time for a newly emerging clade to become the predominant lineage in a population.[20] According to genetic data of modern population, paternal lineage of the C3*-Star Cluster (including C3b-Daur Clade and C3b1a3a2-F8951) are predominant in Daur and other Mongolic-speaking populations.[14] Therefore, we considered that the age of both C3b1a3a2-F8951 (C3b-Daur Clade) and C3b1a3a1-F3918 should be older than the age when *Xian-Bei* tribe appeared in history records of China (~1900 years ago). Therefore, the ASD estimations of 'C3b-Daur Clade' using genealogical rate (2260 ± 1198 years ago) might be closer to the history (Table 1). Tribe with the lineage 'C3b-Daur Clade' may be a important part of ancient *Xian-Bei* groups, while Daur population is the only survived descendants of them in modern age.

Table 1 TMRCAs and expansion times of C3b-Daur Clade

C3b-Daur Clade	N	*ASD*	*BATWING–TMRCA*		*BATWING–Expansion*	
		ρ ± σ	*Median*	*95% CI*	*Median*	*95% CI*
Evolutionary rate	17	8149 ± 5411	15405	9224–21 586	9629	3755–15 503
Genealogical rate	17	2260 ± 1198	3878	2718–5038	3982	2213–5751

Abbreviations: ASD, Average Squared Distance; BATWING, Bayesian analysis of trees with internal node generation; CI, confidence interval; TMRCA, the most recent common ancestor.

The internal diversification of haplogroup C3b1a3a2-F8951 issues clue to the origin of the Aisin Gioro clan. As indicated by the phylogenic tree in Figure 3, separated branches, C3b1a3a2b-F5483/SK1074, were formed by three non-Manchu samples from Oroqen, Daur and Buryats. Meanwhile, 5 out of 39 haplotypes (12.8%) from the Daur population in Xue *et al.*[6] also shared the same Y-STR profile with 'C3b-Daur Clade'. As mentioned in the previous section, Hūrha tribe share the same legend with the Aisin Gioro clan, tracing their origin back to a mountain and a lake near the present Aihui City in the middle reaches of the Amur River. According to historic records, Aihui City was an important fortress in the south part of Dauria during the Qing Dynasty. During the seventeenth century, most Daur populations, together with Hūrha tribe and other Tungusic-speaking tribes, moved from the north bank to the south of Amur River. Therefore, we proposed that the close genetic relationship between Aisin Gioro clan and Daur population represented ancient common origin of these two groups. The internal differentiation of C3b1a3a2-F8951 is corresponding to the prehistory separation of ancestors of the Daur and Aisin Gioro clan.

The southward migration of Daur population during the seventeenth century was well recorded in the history book of the Qing Dynasty.[33] Daur population lives in the north beach of Heilongjiang River (Amur River) before the seventeenth century.[34] Owing to the invasion of Russian Cossacks after the four decades of the seventeenth century, Daur population moved southward to Nen River region gradually (Figure 1).[35] At the end of seventeenth century, most Daur populations had settled down in the south beach of Heilongjiang River (Amur River).[34]

On the contrary, the earliest origin location of the Aisin Gioro clan remains ambiguous. The later progresses of migration of the Aisin Gioro clan were well documented in history records of the Ming Dynasty and Qing Dynasty (Figure 1).[4,33,34] First, they moved southward from the *Yilan Hala* castle to Tumen River region near the Changbai Mountain at about the fourteenth century (Figure 1). They then moved westward from Tumen River region to the Liao River region where they establish the *Hetu Ala* City (Figure 1). Our genetic data help to provide some clues to reassess the earliest stage of migration of ancestors of the Aisin Gioro clan. The Aisin Gioro clan claimed that they share the same prehistoric ancestor, *Bukūri Yongšon*, a mythical hero, with *Hūrha* tribe who lived in the middle reaches of the Amur River.[4] The location of *Hūrha* tribe and the living place of *Bukūri Yongšon* were well documented in history records of the Qing Dynasty (Figure 1).[4] Even though the Aisin Gioro clan cannot remember when and why their ancestor left the middle reaches of the Amur River, our genetic data support the close connection between the Aisin Gioro clan and populations in this region. The memory about the Dudu Mentemu in *Yilan Hala* castle and Changbai Mountain near the Tumen River region in the legend of the Aisin Gioro clan may indicate that these two places were both important during the long-term migration of the clan. In summary, we proposed that the ancestors of the Aisin Gioro clan migrated from the middle reaches of the Amur River to their current settlements. Our genetic data support their close relationship with current Daur population, as claimed in the legend about their earliest ancestor Bukūri Yongšon, rather than the leader Dudu Mentemu of warring clan Odoli or Changbai Mountain region.

The formation of modern Manchu ethnicity is the direct result of historical activities of the Aisin Gioro clan.[4] The Aisin Gioro clan is the leader family of Jianzhou Jurchens, the precursor of modern Manchu population.[34] Our research confirmed that the paternal clade of the Aisin Gioro clan is not the predominant lineage (aka haplogroup C3c-M48) of other Tungusic-speaking populations.[10,18] After the rising of ancient Jurchen population, all other ancient populations in northeastern China disappeared in the history records of China.[34] Thus, population admixture and/or language replacement may have happened frequently during the rising of ancient Jurchen population. In modern Manchu ethinc group, the diversity of paternal lineage is much higher compared with other Tungusic-speaking populations.[6,10] Therefore, we conclude that the population admixture may have taken an important role during the formation of modern Manchu ethnicity.

In conclusion, our genetic evidences of C3b1a3a2-F8951 outline the dispersal and expansion patterns of this lineage in northeastern China clearly. We determined that haplogroup C3b1a3a2a-F14735 is the paternal lineage of the Aisin Gioro clan, the imperial house of the Qing Dynasty. This haplogroup is close to the lineage found in current Daur populations. Large-scale sequencing of Y chromosome discovered a series of unique Y-SNP markers of the Aisin Gioro clan and gave clue to the early migration of this clan. Meanwhile, more work of modern DNA analysis, as well as ancient DNA testing, are still necessary for understanding the history of the Aisin Gioro clan and Manchu ethnic. Our research indicated that detailed research of pedigree and large-scale sequencing of Y chromosome are helpful to explore the prehistoric activities of ancient populations lacking historical records and archeological evidences.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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