

再论 Y 染色体 C3* 星簇的起源从 成吉思汗改为蒙古尼伦家族

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摘要: C3* 星簇(C3* - ST)是世界上分布最广的人类父系 Y 染色体世系,也被认为是成吉思汗的 Y 染色体类型。然而,最近的研究却提供了关于这种假说的相反例证。为了阐明 C3* - ST 的起源以及其与成吉思汗和蒙古人的关联,我们对东部欧亚人群中的这一世系进行了综合研究。那些 C3* - ST 频率较高的人群只能追溯他们的共同祖先到蒙古尼伦部族。因而,关于 C3* - ST 与成吉思汗之间的联系并没有直接的证据。

关键词: 东部欧亚; Y 染色体; C3* 星簇; 蒙古尼伦; 成吉思汗

Reanalysis of Y-Chromosome C3* -Star Cluster Converted its Origin from Genghis Khan to Mongol Niru'un Clan

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Introduction

In recent decades, Y-chromosome has been proved to be a powerful tool to trace the paternal history of certain ethnic groups or clans. Y-chromosome haplogroup C3* - Star Cluster (in short, C3* - ST), firstly discovered by Zerjal *et al*¹, is one of the most famous paternal profile. This lineage was common among the peoples (about 8%) residing between the Yellow River and the Caspian Sea. The most recent common ancestor (TMRCA) of this lineage (700—1300 years ago) lived during the life time of Genghis Khan (A.D. 1162 - 1227) and the present distribution of this lineage matches with Genghis Khan's Mongol Empire. A possible descendant population of Genghis Khan, Hazara in Afghanistan, are frequently found with this paternal lineage. With these evidences, Genghis Khan or his close relatives were proposed to be the origin of this special Y-chromosome lineage.

However, as discussed in Zakharov *et al*², other researches about C3* - ST have oppugned the connection between this lineage and Genghis Khan.^{3,4,5} The highest frequencies of C3* - ST was found in two populations of Kazakhs (Kerey-Abakh and Kerey-Ashmaily, 89.3% and 55.0% respectively).⁵ Besides, the Y haplotype of a direct descendant of Genghis Khan, Batu-Mungke Dayan Khan (A.D. 1474 - 1517, ruler of North Yuan Khanate) was determined to be C3d through direct testing of his well-documented descendants.⁶ In this study, we genotyped and analyzed samples from a broader geographic scale to clarify the origin of C3* - ST and its connections with Genghis Khan and Mongol populations.

Materials and methods

Samples

Blood or saliva samples of 6,348 individuals from 74 populations in eastern Eurasia were collected from unrelated healthy males between 2005 and 2012. The donors signed informed consent in their languages to participate in the study. The ethics committee for biological researches at Fudan School of Life Sciences approved the study.

Molecular methods

Firstly, Y-chromosome marker M130 was the genotype to identify haplogroup C samples. The M130 - derived individuals were then subjected to further typing of 10

biallelic markers: C1 – M8, C2 – M38, C3 – M217, C3a – M93, C3b – P39, C3c – M48, C3d – M407, C3e – P53.1, C4 – M347 and C5 – M356. In the early stage of this project, these downstream markers were not tested in some populations. Seventeen STR loci of all DNA samples were genotyped using the AmpFlSTR® Yfiler™ PCR Amplification Kit (Applied Biosystems, CA, USA), including DYS19, DYS385a, DYS385b, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, DYS439, GATA – H4, DYS448, DYS456, DYS458, and DYS635. Products of amplification were analyzed on ABI 3730 and ABI 3130 Genetic Analyzers (Applied Biosystems). Electrophoresis results were analyzed by using Genscan v. 3.7 and Genotyper v. 3.7 (Applied Biosystems).

Statistical Analysis

The proposed “Genghis Khan’s Y-profile” was C3* – ST (M217+, M93 –, P39 –, M48 –, M407 –, P53.1 –).^{3,4,5} To obtain a more comprehensive picture of this lineage, Y-chromosome haplogroup frequencies and Y-STR data of haplogroup C – M130 in 164 East Eurasia populations were collected from literature. Y-STR haplotype of C3* – ST were identified by the definition of the original paper, which contains mutation within one to three steps from a central haplotype with a set of Y-STR loci (DYS389I – DYS389b – DYS390 – DYS391 – DYS392 – DYS393 – DYS388 – DYS425 – DYS426 – DYS434 – DYS435 – DYS436 – DYS437 – DYS438 – DYS439, excluding DYS425 – DYS426 – DYS434 – DYS435 – DYS436 that were rarely used in other researches). The results were also confirmed by Y-STR Networks (Figure 1A). The Y-STR data were used to construct the median-joining network using the program NETWORK 4.6.0.0 (Fluxus Engineering).⁷ Frequencies of C3* – ST in populations were plotted onto a geographic map using Surfer 7.0 (Golden Software, Inc., CO, USA). Only those haplotypes with 15 Y-STR (excluding DYS385a/DYS385b from 17 Y-STRs) were used in further analysis. The average gene diversities and F_{st} values⁸ of populations with more than five C3* – ST samples were calculated based on 15 STR loci by Arlequin 3.11.⁹ Multi-dimensional scaling (MDS) plots were constructed using F_{st} values and SPSS (SPSS, Chicago, USA). Analysis of the molecular variations (AMOVA) was also done using Arlequin 3.11 software.

Coalescence Dating

The TMRCA (the most recent common ancestor) of C3* – ST were estimated using Average Squared Distance (ASD) and Bayesian analysis of trees with internal node generation (BATWING) method. ASD-based age estimations^{10,11,12} were computed with the assumption that Median haplotype is the founder haplotype. The age estimations were constructed employing Coalescence methods implemented in the program BATWING.¹³ This estimation was done assuming the population growth model with

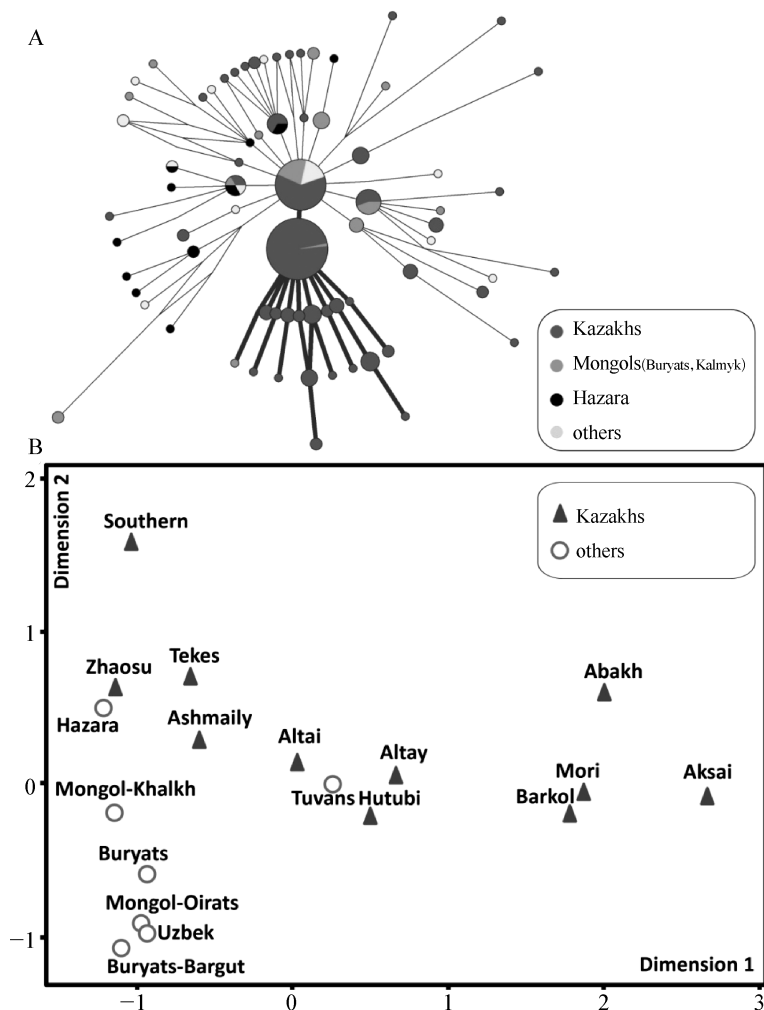


Figure 1 (A) Network of C3* - ST based on 15 Y-STRs; (B) MDS based on F_{st} of 15 Y-STRs among populations

exponential growth from an initially constant-size population. Mutational priors were as previously proposed.¹⁴ The genealogical mutation rate and the evolutionary mutation rate described previously were used for the age estimates both by ASD method and BATWING.^{15,16} Generation time was set at 25 years. A total of 1.5 million Markov chain Monte Carlo (MCMC) samples were collected per run in BATWING and the first 0.5 million were discarded as burn-ins.

Results

Among 2266 samples of C - M130+ in 238 populations throughout eastern Eurasia, 701 samples with 588 haplotypes were identified as C3* - ST. Only 385 haplotypes from 420 samples have been typed 15 Y-STR data, and were used in our further analysis. C3* - ST comprised a special group of Y-STR haplotypes in network, which was still

distinctly separated from other known branches under C3, such as C3c, C3d (Figure 1A). Y-STR networks based on 9 markers and 15 markers show a star-like expansion of this lineage.

The high frequencies of C3* - ST were observed in several Kazakh populations from Southeast Kazakhstan and Northwest China, followed by Mongolian, Buryat-Bargut and Uzbeks. Totally, there are 17 populations who have more than 25% C3* - ST and 13 of them are Kazakhs. 7 populations have more than 50% C3* - ST and all of them are Kazakhs. According to sampling information, all these Kazakh samples were collected in the Great Jüz of Kazakhs or Kazakh-Kerey population. This scene suggests that C3* - ST is a dominant component of paternal gene pool in these populations. On the contrary, C3* - ST is absent or found at very low frequencies among Altaics population. The only two exceptions are Hazara and one Han population from Hailar, Inner Mongolia, China. Hazara is a Persian-speaking population who has a Mongol origin. Han population lives together with Mongolian and Buryat-Bargut in Hulunbuir grassland. Hence a nearby admixture is highly possible.

The highest Y-STR diversity was observed in Kazakhs-Altay, Mongolian, Buryat, and Hazara. In contrast, other Kazakh populations and one Uzbek display relative low diversity. The STR diversity pattern shows a reverse tendency with the frequency distribution of this lineage. In the MDS plot (Figure 1B), Mongolian, Buryat, Kalmyk, and Uzbek cluster together in the upper left. This is consistent with the history records about their common origin. Interestingly, Kazakh populations scatter widely on the MDS plot in the lower right. When all Kazakhs were grouped together to run AMOVA, variation within populations is larger than among groups. These results indicated that all these Kazakh populations have high frequencies but low diversity of C3* - ST, and they are distinct from each other. In oral history of Kazakhs, one tribe is usually traced back to one single paternal ancestor. These descriptions may not be true for all tribes. But the genetic variation of the lineage we studied here agreed with these records to a certain degree. Combining with history records, all genetic scenes here suggest a probable East Mongolian origin, and then a westward migration of C3* - ST together with continuous founder effects.

The estimation of TMRCA and expansion time can aid in determining when this particular lineage arose and possibly when the diffusion happened. As showed in Y-STR network, a special branch with DYS448=23 (defined as C3* - ST α , Figure 1A) emerged in Kazakh-Kerey-Abkh population. C3* - ST α showed a similar star like expansion as C3* - ST. Therefore calculations were carried out for both of them. The TMRCA based on ASD method using the genealogical rate provided a good fit between genetics and history records (Table 1).

Table 1. TMRCA and Expansion Times of C3* - ST (years)

Hg	ASD		BATWING - TMRCA		BATWING - Expansion	
	N	$\rho \pm \sigma$	Median	95% C.I.	Median	95% C.I.
Evolutionary rate						
C3* - ST	420	3996 \pm 2788	7288	[7160 - 7946]	5215	[5020 - 5774]
C3* - ST α	227	1902 \pm 1273	6143	[3260 - 12722]	4748	[2107 - 11147]
Genealogical Rate						
C3* - ST	420	1330 \pm 1074	2218	[2052 - 2383]	3340	[3211 - 3470]
C3* - ST α	227	492 \pm 222	1526	[826 - 2969]	2090	[474 - 6327]

C3* - ST is the dominant East Eurasia component in several modern populations, such as Nogay, Keneges and Dulat. All of them can trace back to Mongol Niru'un clan arising about 1100 years ago (see details in Discussion section). On the other hand, oral epics of Kazakhs showed that Kerey-Abkh has a relative recent origin.^{17,18} They split from Kerey-Ashmaily or the Great Jüz after the foundation of Kazakh Khanate at A.D. 1456 (about 500 years ago). The TMRCA of C3* - ST and C3* - ST α based on ASD method (256 - 2404 and 270 - 714 years ago respectively) is extremely close to these records. Estimates based on the “evolutionary” mutation rate fall far outside the range of the respective historical dates (Table 1). Ages of the above clusters based on evolutionary and genealogical rates using BATWING were similar to those indicated by ASD method. Expansion time of both C3* - ST and C3* - ST α given by BATWING are older than the TMRCA of these lineages. These counterintuitive results can be explained by the unique history of these lineages. Mongol populations scattered widely after the rapid conquest of the Mongol Empire. Before that, the Mongol Niru'un clan — the core of Mongol populations — had also underwent an explosive growth. They multiplied from three single male ancestors to more than twenty tribes within about 260 years (Figure 2). This situation is again the pre-assumption in BATWING that the population grow exponentially from an initially constant-size population. Therefore it is possible that the Y-profile remain the same haplotype even through the population size had been growing in several times in a short period. Due to the same reason, it is considered that the TMRCA based on ASD method is more confident than that of BATWING.

Discussion

According to Rashid Al-din¹⁹, all the Mongol people were divided into two sub-tribes. One was the Darlakin Mongol tribe and the other was the Niru'un Mongol tribe. The Darlakin Mongol referred to the commonality of the Mongol people, while the Niru'un Mongol (means “The pure Mongol”) was believed to be the descendants of Alan

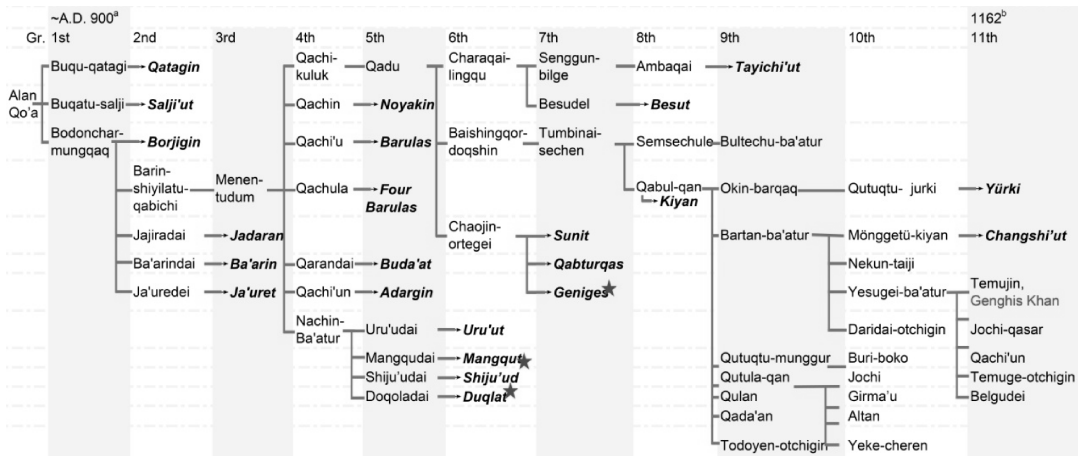


Figure 2 Pedigree of the Niru'un Mongol.^{19,20} Clan names were listed in **italic bold** after its founder. Red pentacle presented the three clans with Y-chromosome data. Gr. = Generation, a = approximate activity age of three sons of Alan Qo'a, b=the year Genghis Khan was born

Quo'a, Genghis Khan belonged to Kiyān clan, one clan of Niru'un tribe (Figure 2). Combining the data from published researches, C3* - ST were found in several modern populations who can be traced back to Mongol Niru'un clan.

Manghit

Manghit was also called Manghuds and Mangqut. According to history records, Manghit was derived from the Niru'un Mongols.^{19,20,21} They moved westward together with Jochi's armies and lived in the Golden Horde (the Mongol empire in Central Asia and Northeast of Europe, 1219 A.D. - 1502 A.D.). They extensively involved in the political activities of the Khanates.^{19,21} At the beginning, they followed Nogai Khan (d.1299) to establish their own semi-independent horde from the Golden Horde in Sarai. Then, they supported their own commander Edigu (1352 - 1419) to found Nogai Horde or Manghit Horde in the 14th-15th century.²¹ Their descendants called themselves Nogay and lived in the plains of northern Caucasus and the Crimea since 17th century. Another group of them moved southward as a part of Uzbeks and finally established the Manghit Dynasty to rule the Emirate of Bukhara in Transoxania in 1785.²² Descendants of them became parts of modern Uzbeks and Karakalpak population.²³

Most of the C3 samples in Nogay belong to C3* - ST.^{2,24} In addition, the only one sample of Manghit tribe in Uzbekistan reported by Sabitov *et al*²⁵ also belongs to the above lineage. Among Qarasyraq clan of Manghit tribe reported by Chaix *et al* 2007²⁶, 11 out of 14 haplotypes possess the same Y-STR profile as C3* - ST. These data indicated that they shared a common ancestor.

Keneges

According to history records, Keneges was also derived from the Niru'un Mongol. As one of four thousand "original" Mongol troops that Genghis Khan bequeathed as auxiliary of Jochi, Keneges (Led by ҚУТАНОМ КЕНЕГЕСОМ) came in Jochi Ulus (The Golden Horde) in the early 13th century.^{19,20,21} After the collapse of The Golden Horde, Manghit and Keneges moved southward as a part of Uzbeks and then became a part of modern Uzbeks and Karakalpak population.^{23,27}

All the three C3 samples in Keneges reported by Sabitov *et al*²⁵ belong to C3* - ST. Another sample was predicted as G2a-P15 according to its special Y-STR profile. G2a is now predominant in Caucasian populations²⁸ and hence can be considered as indigenous mixture after Keneges' settlement in the Golden Horde.

Dulat

Dulat, aka Duqlat or Dughlat, were also derived from the Niru'un Mongols.^{19,20,27} Dulat was one of four thousand "original" Mongol troops that Genghis Khan bequeathed as auxiliary of Chagatai and eventually settled in the area comprising the Ulus of Chagatai Khan.¹⁹ During the last age of Moghulistan, which was also called the Eastern Chagatai Khanate, many Mongol-origin tribes joined the new-born Kazakh Khanate, like Husin, Jalair and Duqlat. Later, they became Uysun, Zhalair and Dulat tribe as a part of the Great Jüz (aka Senior Juz) in modern Kazakh populations.^{27,29}

Within four C3 samples in Dulat tribe, three of them belong to C3* - ST.³⁰ High frequency of C3* - ST was also found in other three sampling places within the area of the Great Jüz in southeast part of Kazakhstan. This lineage was also dominant in our samples at Zhaosu County located in the nomadic region of Alban (one tribe of the Great Jüz).

Uysun and Kerey in Kazakhs

Highest frequencies of C3* - ST were observed in both Southeast Kazakhstan (the Great Jüz) and Kazakh-Kerey. Kazakh Khanate was established by a group of population that were separated from Uzbek Horde (late period of the Golden Horde). We found that C3* - ST is also dominant part of C3 in Uzbeks. After the joining of several tribes from Eastern Chagatai Khanate, they were called the Great Jüz (also the Uysun Jüz).^{27,29} Regarding the origin of Kerey tribe in Kazakh, several genealogical legends about conflict with each other give no well-resolved conclusion.^{17,18} One legend said that that Kerey-Ashmaily is the descendant of forefather Kerey and Kerey-Abakh is the descendant of the Great Jüz. The other legend said Kerey-Ashmaily originated from one of the three sons of the mythical forefather of Kazakhs. And Kerey-Abakh was derived from Kerey-Ashmaily. In this study, the most frequent haplotype in Kerey-Abkh (C3* - ST α), has only one step mutation from the central haplotype of C3* - ST. Therefore it is possible that C3* - ST α was derived from the C3* - ST in either Kerey-Ashmaily or the Great

Jüz. More evidences are needed to clarify these two hypotheses about the origin of Kerey-Abakh.

Hazara

According to history records, the Hazara are the descendants of Genghis Khan's soldiers, not male-line descendants of Genghis Khan himself. In Zerjal *et al*¹, Hazara people were considered as direct descendants of Genghis Khan and hence became a strong evidence for their conclusion. However, the original material cited by Zerjal *et al*¹ described that the Hazara were derived from ten military detachments sent by Genghis Khan.³¹ According to the available history records, those military detachments, 20,000 soldiers totally, were only ordinary people of Mongol tribe. There is no evidence that they were direct descendants of Genghis Khan, whose descendants had been well-documented at that era.^{19,20}

Heritage of Niru'un Mongol

According to history records, Manghit, Keneges and Dulat can be traced back clearly to Niru'un Mongol. At the time of Genghis Khan, the population of Niru'un Mongol (the Pure Mongols) had multiplied and they divided into more than twenty tribes (Figure 2). Before and after the foundation of the Mongol Empire, people of Niru'un Mongol were the core components of the Khanate's upper classes and provided most of soldiers and generals of army. Participating in the conquest of Genghis Khan, they scattered and settled in all regions comprising the empire from East Asia to Northeast Europe. As discussed above, Manghit, Keneges, Dulat, and Hazara are all descendants of the armies sent to different regions of the Mongol Empire by Genghis Khan. Haplotype of C3* - ST from Manghit, Keneges and Dulat only represents one of the several branches under this lineage. The early records of the Niru'un Mongol started from 1,100 years ago (A.D.900, Figure 2, 27, 28), which is slightly younger than the age of C3* - ST (256 - 2404 years ago). It is quite possible that the direct ancestor of this lineage and their relatives had already lived on the Mongolia grassland for hundreds of year before one branch of their descendants had been recorded as "The Niru'un Mongol".

On the other hand, no evidence was found to support the previous proposition that this lineage has direct connections with Genghis Khan himself. Since Genghis Khan himself is a member of Niru'un clan, it is possible that this Great Conqueror carried the same Y-STR profile. Although, according to descriptions in all researches (including this study), none of donors who carry C3* - ST can traced their genealogical tree to Genghis Khan. Also, none of self-claimed direct descendants of Genghis Khan had been proved to be C3* - ST. As showed in Batbayar *et al*⁶, a direct descendant of Genghis Khan, Dayan Khan's haplotype, was determined to be a different Y-chromosome haplogroup (C3d).

In conclusion, our genetic evidences of C3* - ST outline a clear picture about the dispersal and expansion patterns of this lineage throughout the steppe zone of Eurasia in last millennium. C3* - ST is proposed to be a predominant paternal profile in the Niru'un Mongol, where Genghis Khan's paternal family came from. However, direct genotyping of his well-documented male-line descendants from a wider geographic region is needed to get a solid conclusion about the Y-chromosome of Genghis Khan himself in the future.

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Appendix

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