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Brief Communication

The Y-Chromosome C3* Star-Cluster Attributed to Genghis Khan's Descendants Is Present at High Frequency in the Kerey Clan from Kazakhstan

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Abstract To verify the possibility that the Y-chromosome C3* star-cluster attributed to Genghis Khan and his patrilineal descendants is relatively frequent in the Kereys, who are the dominant clan in Kazakhstan and in Central Asia as a whole, polymorphism of the Y-chromosome was studied in Kazakhs, represented mostly by members of the Kerey clan. The Kereys showed the highest frequency (76.5%) of individuals carrying the Y-chromosome variant known as C3* star-cluster ascribed to the descendants of Genghis Khan. C3* star-cluster haplotypes were found in two subclans, Abakh-Kereys and Ashmaily-Kereys, diverged about 20-22 generations ago according to the historical data. Median network of the Kerey star-cluster haplotypes at 17 STR loci displays a bipartite structure, with two subclusters defined by the only difference at the DYS448 locus. Noteworthy is a strong correspondence of these subclusters with the Kerey subclans affiliation. The data obtained suggest that the Kerey clan appears to be the largest known clan in the world descending from a common Y-chromosome ancestor. Possible ways of Genghis Khan's relationship to the Kereys are discussed.

A few years ago, Zerjal et al. (2003) identified a C3* Y-chromosome lineage frequent in Central Asia (about 8%). They suggested that this lineage originated in Mongolia about 1000 years ago, and it is carried by likely male-line descendants of Genghis Khan. Population screening revealed the highest frequencies of C3* star-cluster (more than 30%) in Kazakhs, Mongols, and Hazaras of Pakistan (Derenko et al. 2007; Zerjal et al. 2003;

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Zhong et al. 2010), while in Siberia the frequency of star-cluster varies from 18% in Altaian Kazakhs to less than 3% in Tuvinians and Altaians (Derenko et al. 2007; Dulik et al. 2011).

Recently discovered was that Kazakhs do not share a common paternal source (Dulik et al. 2011). Possibly, differences between sample sets of Kazakhs were mostly maintained by their tribal affiliations, because Kazakh society is characterized by a complex tribal structure (Dulik et al. 2011). However this possibility was not considered in previous studies of Y-chromosome variation in Kazakh populations (Chaix et al. 2007; Malyarchuk et al. 2010; Perez-Lezaun et al. 1999; Wells et al. 2001; Zerjal et al. 2002; Zhong et al. 2010; Zhong et al. 2011). Our preliminary unpublished data suggested that C3* star-cluster haplotypes are relatively frequent in the Kereys, who are the dominant clan in Kazakhstan and in Central Asia as a whole (Atwood 2004; Khoyt 2008). Therefore, to verify the possibility that C3* star-cluster is a genetic marker of the Kereys, we investigated the Y-chromosome profiles for 17 STR loci in Kazakhs living both in Kazakhstan and Russia and belonging to different tribes, mostly to the Kerey clan.

Materials and Methods

Samples. Samples of hair roots, a total of 57, were collected in males from different Kazakh tribes, including 51 members of the Kereys, with the ethical approval of the Forensic Medicine Institute (Bydgoszcz, Poland) and the Institute of Biological Problems of the North (Magadan, Russia). All biological samples were collected using informed consent. Genomic DNA was prepared by means of ExtraGene DNA Prep 200 kit (Laboratory Isogen, Moscow).

Y-Chromosome Polymorphism Typing. All DNA samples were analyzed at 17 STR loci (DYS19, DYS385a, DYS385b, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, DYS439, GATA-H4, DYS448, DYS456, DYS458, DYS635) using AmpFl-STRYFiler PCR Amplification kit (Applied Biosystems) according to the manufacturer's instructions. Products of amplification were analyzed on ABI 3100 and ABI 3130 Genetic Analyzers (Applied Biosystems). Electrophoresis results were analyzed by using Genscan v. 3.7 and Genotyper v. 3.7 software (Applied Biosystems).

To search for haplotypes belonging to C3*-paragroup, SNP markers defining the whole haplogroup C (RPS4Y $_{711}$) and its subgroups C1 (M8), C2 (M38), C3 (M217), C3a (M93), C3b (P39), C3c (M77), C3d (M407), C3e (P53.1), and C3f (P62) were assayed by using PCR primers summarized in Karafet et al. (2008) as described in Malyarchuk et al. (2010). Thus, C3* paragroup includes haplotypes which are outside of SNP-defined subgroups C3a-f.

Data Analysis. Median joining networks of C3* STR-haplotypes were constructed using the Network 4.6 program (www.fluxus-engineering.com). For

the network construction, STR variants were weighted (with a weight assigned to a range of variance values) following the distribution of the number of mutations at character (Bandelt et al. 2000). The allele sizes for locus DYS389II were determined with the subtraction of DYS389I. In addition, loci DYS385a and DYS385b were excluded from all analyses due to the possibility of ambiguous assignment of the alleles to these loci.

The upper bound for divergence time of two groups of haplotypes was calculated as estimation of divergence time ($T_{\rm D}$) assuming STR variance in repeat number at the beginning of population subdivision ($V_{\rm o}$) equal to zero (Zhivotovsky 2001).

Results

In the present study, we studied Y-chromosome variability at 17 STR loci in 57 Kazakhs (Table 1). SNP typing and median network analysis of C3* STR haplotypes demonstrate that 70% of individuals studied belong to the Y-chromosome star-cluster within paragroup C3* (Table 2; Figure 1). However, our Kazakh sample is represented mostly by the Kereys, so 76.5% of them are carriers of haplotypes belonging to the C3* star-cluster (Table 2). Noteworthy is that frequency of this cluster is almost 90% in the Kerey-Abakh, whereas it is fairly less in the Kerey-Ashmaily (55%).

Phylogenetic analysis of the Kerey star-cluster haplotypes demonstrates that median network displays a bipartite structure, with two subclusters recognized (Figure 1). One of them is determined by the allele DYS448-22, and another one by the allele DYS448-23 (Figure 1; Table 3). Noteworthy is that a strong correspondence of these subclusters with the Kerey subclans affiliation exists. We found that all members of the Kereys-Abakh belong to the DYS448-23 subcluster, while all but one of the Kereys-Ashmaily belong to the DYS448-22 subcluster. According to the historical data, the split between these subclans occurred about 20-22 generations ago (Khalidullin 2005). The $T_{\rm D}$ of two groups of 15 STR haplotypes (except for DYS385a,b loci) found in the Kereys sub-clans demonstrates that $T_{\rm D}$ value equal to 630 \pm 190 years (or approximately 21 ± 6 generations) results when a mean of per-locus, per-generation mutation rate of 0.0033 and a 30-year generation time are used. Note that a similar value of mutation rate (0.00324) was calculated as optimal for 15 STR haplotypes by Busby et al. (2011), who have investigated the question on how average squared distance (ASD) estimates change within haplotype sets when using different combinations of Y-chromosome STRs. This mutation rate belongs to a class of so-called genealogical STR mutation rates revealed by direct observation in father/son pairs (Goedbloed et al. 2009; Kayser et al. 2000). Genealogical rates differ by about a factor of three from the evolutionary mutation rate based on microsatellite variation within Y-chromosome haplogroups in the populations with documented short-term histories (Zhivotovsky et al. 2004). Although genealogical rates are suggested to not consider the evolutionary consequences of population dynamics (Zhivotovsky et al. 2006),

Table 1. Y-Chromosome STR Haplotypes in Kazakhs^a

Clan/Subclan D)	DYS19 L	DYS385a	DYS385b	DYS3891	DYS38911	DYS390	DYS391	DYS392	DYS393	DYS437	DYS438	DYS439	DYS448	DYS456	DYS458	DYS635	$GATA_H4$
	16	12	13	13	16	25	10	11	13	14	10	10	22	15	18	21	11
	15	12	14	13	16	24	10	Ξ	13	14	Ξ	12	del	17	16	22	Ξ
	13	13	17	14	15	23	10	12	13	16	10	14	22	16	15	20	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	22	15	18	21	=
	16	12	13	13	16	25	10	Ξ	13	14	10	10	22	15	18	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	22	15	18	21	11
	41	12	13	13	16	23	10	41	13	14	10	10	19	15	17	25	=
	15	12	20	41	16	23	Ξ	Ξ	15	14	10	=	21	15	15	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	17	21	11
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	16	18	21	=
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	16	18	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	18	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	18	21	Ξ
	16	12	14	13	16	25	10	Ξ	13	14	10	10	23	15	17	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	18	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	18	21	=
	13	13	17	14	15	23	10	12	13	16	10	13	22	16	15	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	18	21	Ξ
	16	12	13	13	16	25	10	=	13	14	10	10	23	14	18	21	==
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	18	21	Ξ
	15	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	17	21	Ξ
	15	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	17	21	=
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	18	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	14	18	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	14	18	21	Ξ
	15	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	17	21	Ξ
	15	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	17	21	11
	15	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	17	21	==
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	18	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	18	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	24	15	18	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	18	21	Ξ
	16	12	13	13	16	25	10	Ξ	13	14	10	10	23	15	18	21	Ξ
	16	12	13	13	16	25	10	=	13	14	10	10	22	31	9	,	

 Table 1. (continued)

635 GATA_H4	111	11		10		111	11	11	11	11	11	11	1 12	0 11	11	1 12	11	0 12	2 12	0 11	3 12	5 11	:
8 DYS635	21	2	2	2	2	19	2	2	2	21	2	2	2	3	2	2	2	7	2.	3	2	5	
DYS458	18	15	18	18	18	18	17	18	18	18	19	19	18	15	17	17	20	20	17	15	18	17	
DYS456	15	16	15	15	15	15	15	15	15	15	15	16	15	16	18	17	16	15	15	16	14	15	
DYS448	22	22	22	20	22	22	22	22	22	22	22	22	23	22	del	20	19	20	19	22	18	18	
DYS439	10	13	10	Ξ	10	10	10	10	10	10	10	10	10	12	12	Ξ	Ξ	12	10	13	12	Ξ	
DYS438	10	10	10	10	10	10	10	10	10	10	10	10	10	10	Ξ	10	10	Ξ	10	10	10	Ξ	
DYS437	14	16	14	14	14	14	14	14	14	15	14	14	14	16	14	16	15	15	14	16	14	14	
DYS393	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13	14	12	12	14	13	13	14	
DYS392	11	12	Ξ	Ξ	Ξ	Ξ	Ξ	Ξ	Ξ	Ξ	Ξ	Ξ	Ξ	12	Ξ	10.2	Ξ	41	14	12	13	10	
DYS391	10	10	10	6	10	10	10	10	10	10	10	10	10	10	10	10	10	Ξ	10	10	10	10	
DYS390	25	23	25	24	25	25	25	25	25	25	56	25	25	23	24	23	24	23	23	23	25	23	
DYS389II	16	15	16	17	16	16	16	16	16	16	16	16	16	15	16	17	16	16	16	15	16	15	
DYS389I	13	14	13	14	13	13	14	13	13	13	13	13	14	14	13	12	13	12	14	14	12	14	
DYS385b	13	17	13	12	13	13	13	13	13	13	13	13	14	17	15	14	16	20	13	17	20	14	
DYS385a	12	13	12	12	12	12	12	12	12	12	12	12	12	13	12	13	13	13	11	13	12	13	
DYS19 1	16	13	16	15,16	16	15	16	16	16	16	16	16	16	13	15	15	14	14	14	13	13	15	
Clan/Subclan	Kerey/Ashmaily	Naiman	Tore/Kogadai																				
Sample Code	Gz1	Gz34	Gz35	Gz36	Gz56	Gz59	Gz60	Gz62	Gz64	Gz65	89Z9	Gz84	Gz85	Gz57	Gz58	Gz61	Gz63	99Z5	Cz67	69Z9	Gz55	Gz82	

a. C3* star-cluster haplotypes are shown in grey. "?" denotes unknown tribal affiliation and "del" means deletion.

Table 2. Frequency of the Y-Chromosome C3* Star-cluster in Kazakhs Based on the Present Study Data

Population	Sample Size	C3* Star-cluster Frequency (%)
Kazakhs	57	40 (70.2)
The Kereys, including:	51	39 (76.5)
The Kereys-Abakh	28	25 (89.3)
The Kereys-Ashmaily	20	11 (55.0)

seemingly genealogical rates could be used for age estimations of some phylogenetic subclusters, associated, for instance, with the influence of social selection (Zerjal et al. 2003).

Figure 2 demonstrates a fragment of the median network of C3* haplotypes based on the variability of 7 STR loci (DYS19, DYS389I, DYS389I, DYS390, DYS391, DYS392, DYS393), as a part of the reference data did not include other STR markers, in different populations of North Eurasia (Table 4), as well as in Kazakhs studied here. As seen, C3* star-cluster is present in different populations of Central and East Asia, but its highest frequencies are revealed in Kazakhs and Mongols (Table 4) as well as in the Kereys. Therefore, possibly the C3* star-cluster of Y-chromosome can be considered as a genetic marker of the Kerey clan.

Discussion

The Keraits, a people related to modern Kereys, inhabited the area of modern Mongolia along the Onon, Kherulen, Selenga, and Argun rivers. This area is considered as the motherland of the Keraits (Atwood 2004; Khoyt 2008).

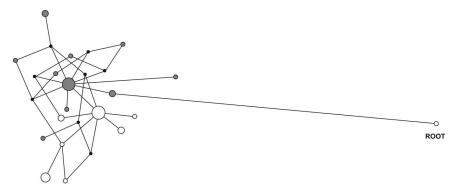


Figure 1. Median joining network of the Y-chromosome C3* star-cluster haplotypes based on 15 STR loci in the Kereys. Each circle represents a haplotype, defined by a combination of STR markers. Circle size is shown proportional to haplotype frequency and the smallest circle represents one haplotype. The lines between circles represent mutational distance, the shortest distance being a single mutational step. ROOT is the outgroup C3c-haplotype used for the network rooting. Haplotypes found in the Kereys-Abakh and the Kereys-Ashmaily are shown in white and grey, respectively. Median vectors are indicated by black points.

Table 3. Structure of Founder Haplotypes in the Y-Chromosome C3* Subclusters Defined by Different Variants of DYS448 Locus

	Haplotype (loci order: DYS19, DYS385a, DYS385b, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, DYS439, DYS448 , DYS456,
Subcluster	DYS458, DYS635, GATA-H4)
DYS448-22 DYS448-23	16-12-13-13-16-25-10-11-13-14-10-10- 22 -15-18-21-11 16-12-13-13-16-25-10-11-13-14-10-10- 23 -15-18-21-11

During the period of Mongolian tribe consolidation into one state ruled by Temujin (later Genghis Khan), the Keraits were led by Toghrul (Wang Khan) (Man 2004). In alliance with the Keraits, Genghis Khan destroyed the Naimans, and then redirected all the force against his former ally. Not all the Keraits were included in the Genghis Khan's empire—some of them were killed, some fled to the Altai, Central Asia, and the Irtysh and Volga rivers regions.

Consequently, after defeat, a part of the Keraits was disseminated among Turkic peoples and tribes. They were gradually assimilated, preserving a Turkicized form of the ethnonym "Kerait" as Kerey, Kiray, Karait, Giray, Ghirai, and so on. The Keraits were involved as a main element in the ethnogenesis of many Turkic peoples, such as Crimean Tatars, Karachays, Nogays, Bashkirs, Kazakhs, Uzbeks, Kyrgyz, Altaians, and Tatars (Khoyt 2008). Before the conquest of the Keraits by Genghis Khan, they were a powerful tribe in northern Mongolia and had a highly developed culture. They had a writing system and were Nestorian Christians (Moffett 1992). As one can assume, the Kerait descendants formed a large Kazakh clan of Kereys, which, as noted above, is divided into two subclans (Khalidullin 2005). The Kereys-Abakh live in Mongolia, China, Altai, and eastern regions of Kazakhstan Republic. As estimated, about 1.5 millions of Kazakhs live in China, and 20% of them belong to the Kereys and Naimans (Sadovskaya 2001). The Kereys-Ashmaily live in northern Kazakhstan and also in the Omsk, Tyumen, Kurgan, and Chelyabinsk regions of the Russian Federation.

The data reported above, taken together with the known arguments in favor of the possible Genghis Khan's descent of Y-chromosome C3* star-cluster (Zerjal et al. 2003), allow us to suggest two hypotheses.

- (1) The star-cluster is not directly related to the descendants of Genghis Khan, but rather is associated with the Kerait clan members. Mongol conquest with the participation of the Keraits as special Khan's military forces allowed them to disseminate the Kerait-specific Y-chromosomes in the vast area inhabited by various peoples.
- (2) Genghis Khan by himself belonged to the Keraits. This is supported by the following historical evidence (Khalidullin 2005; Man 2004). The Keraits inhabited the banks of the Onon River, where the camp of Genghis Khan's father Yesukhei was located. Yesukhei was declared as a blood brother of the Keraits' Khan Toghrul (Wang Khan). Toghrul then declared Genghis Khan his son-inlaw. Fraternization of the Genghis Khan family with the Keraits' Khan suggests

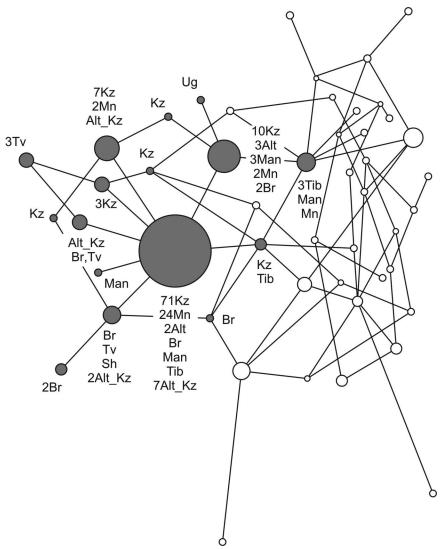


Figure 2. Fragment of the median joining network of C3* haplotypes showing position of the central star-cluster haplotype 16-13-16-25-10-11-13 and its one- and two-step derivatives (for 7 STR loci: DYS19-DYS389I-DYS389I-DYS390-DYS391-DYS392-DYS393). Each circle represents a haplotype defined by a combination of STR markers. Haplotypes belonging to C3* star-cluster are shown in grey. Circle size is proportional to haplotype frequency, and the smallest circle represents one haplotype. The lines between circles represent mutational distance, the shortest distance being a single mutational step. Populations coded as: Kz=Kazakhs, Alt Kz=Altaian Kazakhs, Mn=Mongols, Alt=Altaians, Br=Buryats, Man=Manchu, Tib=Tibetans, Ug=Uyghurs, Tv=Tuvinians, Sh=Shors.

Table 4. Frequency of the Y-Chromosome C3* Star-cluster in Different Populations of Northern Eurasia

Populations	N	C3* Star-cluster (%)	Reference
Kazakhs (from Xingjiang, China)	53	40 (75.5) ^a	Zhong et al. 2011
Kazakhs (from Kazakhstan)	181	73 (40.3) ^b	YHRD data (www.yhrd.org)
Altaian Kazakhs	36	$3(8.3)^{c}$	Derenko et al. 2007
Altaian Kazakhs	119	21 (17.6) ^c	Dulik et al. 2011
Mongols (from Mongolia)	46	16 (34.8) ^c	Derenko et al. 2007
Mongols (from Mongolia)	60	11 (18.3) ^b	YHRD data (www.yhrd.org)
Mongols (Khalkh)	84	14 (16.7) ^b	YHRD data (www.yhrd.org)
Mongols (from Inner Mongolia, China)	22	5 (22.7) ^a	Zhong et al. 2011
Altaians	89	$3(3.4)^{c}$	Derenko et al. 2007
Teleuts	44	0_{c}	Derenko et al. 2007
Khakassians	64	0^{c}	Derenko et al. 2007
Shors	38	0^{c}	Derenko et al. 2007
Todjins	26	0_{c}	Derenko et al. 2007
Tuvinians	108	$2(1.9)^{c}$	Derenko et al. 2007
Yakuts	10	0^{c}	Derenko et al. 2007
Sojots	28	0_{c}	Derenko et al. 2007
Nogays	29	4 (13.8) ^c	Derenko et al. 2007
Buryats	217	5 (2.3)°	Derenko et al. 2007
Khamnigans	51	0^{c}	Derenko et al. 2007
Kalmyks	91	$1(1.1)^{c}$	Derenko et al. 2007
Evenks	41	0^{c}	Derenko et al. 2007
Evens	63	0_{c}	Derenko et al. 2007
Koreans	52	0^{c}	Derenko et al. 2007
Koryaks	39	0^{c}	Derenko et al. 2007
Tibetans	222	5 (2.3) ^a	Zhong et al. 2011
Manchu	109	$7(6.4)^{a}$	Zhong et al. 2011
Uyghurs	187	6 (3.2) ^a	Zhong et al. 2011

a. Frequency of star-cluster was estimated based on results of the median network analysis of 7-loci STR haplotypes (DYS19-DYS389I-DYS389I-DYS390-DYS391-DYS392-DYS393).

that a real blood relationship, though probably not approved officially, existed between them.

One can hardly verify these hypotheses based on currently available data. However, our study demonstrates that the Y-chromosome C3* star-cluster, early ascribed to Genghis Khan, is a genetic marker of the Kerey clan, which consequently appears to be the largest known in the world clan descending from a common male ancestor.

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b. Frequency of star-cluster was estimated based on frequencies of the central star-cluster STR haplotype 16-12-13-13-16-25-10-11-13 for 9 loci (DYS19-DYS385a-DYS385b-DYS389I-DYS389II-DYS390-DYS391-DYS392-DYS393) and its one-step derivatives revealed in the YHRD 3.0 database (www.yhrd.org; release 37 built at 21 June 2011; 97575 haplotypes within 739 world populations).

c. Frequency of star-cluster was estimated based on results of the median network analysis of 12-loci STR haplotypes (DYS19-DYS385a-DYS385b-DYS389I-DYS389I-DYS390-DYS391-DYS392-DYS393-DYS437-DYS438-DYS439).

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