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Abstract

Located in the Eurasian heartland, Central Asia has played a major role in both the early spread of modern humans out of Africa and the more recent settlements of differentiated populations across Eurasia. A detailed knowledge of the peopling in this vast region would therefore greatly improve our understanding of range expansions, colonizations, and recurrent migrations, including the impact of the historical expansion of eastern nomadic groups that occurred in Central Asia. However, despite its presumable importance, little is known about the level and the distribution of genetic variation in this region. We genotyped 26 Indo-Iranian- and Turkic-speaking populations, belonging to six different ethnic groups, at 27 autosomal microsatellite loci. The analysis of genetic variation reveals that Central Asian diversity is mainly shaped by linguistic affiliation, with Turkic-speaking populations forming a cluster more closely related to East Asian populations and Indo-Iranian speakers forming a cluster closer to Western Eurasians. The scattered position of Uzbeks across Turkic- and Indo-Iranian speaking populations may reflect their origins from the union of different tribes. We propose that the complex genetic landscape of Central Asian populations results from the movements of eastern, Turkic-speaking groups during historical times, into a long lasting group of settled populations, which may be represented nowadays by Tajiks and Turkmen. Contrary to what is generally thought, our results suggest that the recurrent expansions of eastern nomadic groups did not result in the complete replacement of local populations but rather into partial admixture.

Introduction

The evolutionary history of modern humans has been characterized by range expansions, colonizations and recurrent migrations over the last 100,000 years.[1] Some regions of the world that have served as natural corridors between landmasses are of particular importance in the history of human migrations. Central Asia is probably at the crossroads of such migration routes.[1,2] Located in the Eurasian heartland, it encompasses a vast territory, limited to the east by the Pamir and Tien-Shan mountains, to the west by the Caspian Sea, to the north by the Russian taiga and to the south by the Iranian deserts and Afghan mountains. The role of Central Asia in both the early spread of modern humans out of Africa and the more recent settlement of differentiated populations[3] is not precisely known.[4-6] For example, it remains unclear whether this region harbored a Palaeolithic "maturation phase" of modern humans before giving rise to waves of migration resulting in colonization of the Eurasian continent[6] or whether it has served as a meeting place for previously differentiated Asian and European populations following their initial expansions.[3,7]

Central Asia entered the historical records about 1300 B.C., when Aryan tribes invaded the Iranian territory from what is nowadays Turkmenistan and established the Persian Empire in the 7th Century B.C.[8] A branch of those, the Scythians, described in ancient Chinese texts and in Herodotus' *Histories* as having European morphological traits and speaking Indo-Iranian languages, expanded north into the steppes. Thereafter, Central Asia was faced with multiple waves of Turkic migrations, although it is difficult to know precisely when these westward expansions began. Between the second and the first century B.C., Huns brought the East-Asian anthropological phenotype to Central Asia.[8] At the same period, the Chinese established a trade route (the Silk Road), which connected the Mediterranean Basin and Eastern Asia for more than 16 centuries. In the 13th century A.D. the Turco-Mongol Empire lead by Genghis Khan became the largest of all time, from Mongolia to the Black Sea.

All these movements of populations resulted in a considerable ethnic diversity in Central Asia, with Indo-Iranian speakers living as sedentary agriculturalists and Turkic speakers mainly living as traditionally nomadic herders.

Together with the ancient peopling of Central Asia, this intricate demographic history shaped patterns of genetic variability in a complex manner. Most previous studies, based on classical markers,[1] mitochondrial DNA (mtDNA)[3,9-13] or the non-recombining portion of the Y-chromosome (NRY),[6,14-16] have shown that genetic diversity in Central Asia is among the highest in Eurasia.[3,6,15] NRY studies suggest an early settlement of Central Asia by modern humans, followed by subsequent colonization waves in Eurasia,[6] while some mtDNA studies point to an admixed origin from previously differentiated Eastern and Western Eurasian populations.[11] Furthermore, a recent analysis of mtDNA data suggests east-to-west expansions waves across Eurasia.[14] However, inferring more accurately the impact of population movements, including the expansion of eastern nomadic groups, requires additional, fast-evolving molecular markers. Here we report on the first multilocus autosomal genetic survey of Central Asian populations. Twenty-six populations from six ethnic groups were genotyped at 27 autosomal unlinked microsatellite markers. We aimed to shed light on the genetic origins of Central Asian populations, and to investigate how the recurrent westward expansions of eastern nomadic groups during historical times have shaped the Central Asian genetic landscape.

Materials and methods

DNA samples

We sampled 767 men belonging to 26 populations from western Uzbekistan to eastern Kyrgyzstan (Table 1 and Figure 1) representative of the ethnological diversity in Central Asia: Tajiks, which are Indo-Iranian speakers (a branch of the Indo-European language family) and Kazakhs, Turkmen, Karakalpaks, Kyrgyz and Uzbeks, which are Turkic speakers (a branch of the Altaic language family). In two Uzbek populations from the Bukhara area (LUZa and LUZn), an extensive linguistic survey showed that individuals were bilingual, speaking both Tajik and Uzbek. Since their home language was Tajik (an Indo-Iranian language), we further classified these two populations into the Indo-Iranian group for subsequent analyses. We collected individuals unrelated for at least two generations back in time. All individuals gave informed consent for their participation in this study. Total genomic DNA was isolated from blood samples by a standard salting out procedure[17] followed by a phenol-chloroform extraction.[18]

Genotyping

We selected 27 microsatellite markers[19] from the set of 377 markers used in the worldwide study by Rosenberg *et al*.[20] The choice and description of markers, PCR and electrophoresis conditions are given in Ségurel *et al*.[19] We further genotyped 20 individuals from the HGDP-CEPH Human Genome Diversity Cell Line Panel[20-22] at the 27 microsatellite loci, in order to standardize the original Central Asian data presented here with the worldwide HGDP-CEPH data.

Data analyses

Genetic diversity

In each population and for each locus, we calculated the allelic richness (*AR*) using the rarefaction method proposed by El Mousadik *et al.*[23] with the software package FSTAT.[24] Unbiased estimates of expected heterozygosity (H_e)[25] were computed in each population for each locus with GENETIX.[26] Both *AR* and H_e estimates were averaged over loci in each population. We tested heterogeneity in both *AR* and H_e among populations using the Kruskal-Wallis test, with locus-specific estimates taken as replicate observations. Locus-specific allelic richness and expected heterozygosity were also estimated for populations pooled into Indo-Iranian- and Turkic-speaking groups, and averaged over loci within groups. We tested between-group differences in both *AR* and H_e using the Wilcoxon's signed-rank test, with locus-specific estimates taken as replicate observations. We further estimated *AR* and H_e for each locus over the pooled data from Central Asia and over the pooled data for Central/South Asia, East Asia, Europe and the Middle-East from the HGDP-CEPH Panel, and calculated the averages over loci within groups. We tested heterogeneity in both *AR* and H_e across the five groups of Eurasian populations using the Kruskal-Wallis test, taking locus-specific estimates as replicate observations. When significant differences among groups were found, we ran the Tukey range test to find which group statistics were significantly different from one another. All statistical analyses were performed with the software package JMP5.1 (SAS Institute Inc.). [27]

Genetic structure

Population differentiation (F_{ST}) was calculated overall and between pairs of Central Asian populations with GENEPOP 4.0.[28] Exact tests of differentiation were performed with FSTAT,[24] adjusting *p*-values with Bonferroni correction for multiple tests. We performed a correspondence analysis (CA) based on tables of allele counts using GENETIX.[26] The population structure was also inferred by means of a hierarchical analysis of molecular

153 variance (AMOVA[29]), with populations pooled into ethnic or linguistic groups. For ethnic
154 grouping, populations were pooled as Tajiks (TJA, TDS, TJT, TJK, TJR, TJN, TDU, TJE,
155 TJY and TJU), Karakalpaks (KKK and OTU), Kazakhs (KAZ and LKZ), Kyrgyz (KRA,
156 KRG, KRL, KRB, KRT and KRM), Uzbeks (UZA, UZB, LUZa, LUZn and UZT) and
157 Turkmen (TUR). For linguistic grouping, populations were pooled as Indo-Iranian speakers
158 (Tajiks and the two Uzbek populations LUZa and LUZn) and Turkic speakers (all other
159 populations). These analyses were performed with ARLEQUIN 3.11.[30] Isolation-by-distance
160 (IBD) was tested with GENEPOP 4.0.[28] We used PATHMATRIX[31] to compute the matrix of
161 effective geographical distances, based on a least-cost path algorithm. The least-cost
162 distances, which account for the cost of the movement through the slopes in the landscape,
163 were calculated from the digital elevation model GTOPO30 of the Earth Resources
164 Observation and Science (EROS) Center.
165
166 Clustering analyses
167 We performed a clustering analysis with STRUCTURE[32] on the Central Asian populations
168 together with all the Eurasian and African populations from the HGDP-CEPH Panel H952
169 corrected dataset.[33,34] We used the latest version of STRUCTURE[35] (version 2.3), which
170 allows structure to be detected at lower levels of divergence than the original model. Each
171 Markov chain was run for 10^6 steps, after a 10^5-step burn-in period. In each case, the results
172 were checked to ensure consistency over forty independent runs. Potential distinct modes
173 among the 40 runs were identified using the *Greedy* algorithm implemented in CLUMP[36]. We
174 varied the hypothetical number of clusters (K) from 1 to 8 for all analyses. All chains were
175 run using the F model for correlations of allele frequencies across clusters.[37]
176

177 Admixture analyses

178 The Central Asian genetic pool may be more than just the result of admixture from Eurasian
179 populations, but we were nonetheless interested in investigating the potential origins of
180 Central Asian populations among all Eurasian populations. We used LEADMIX[38] to calculate
181 maximum likelihood estimates (MLE) of the admixture proportions for each Central Asian
182 population. We ran the program independently for each of them, considering four putative
183 parental groups from the HGDP-CEPH Panel: Central/South Asia, East Asia, Europe and
184 Middle East. For the Central/South Asian group, we chose a pool of Balochi (n = 25) and
185 Makrani (n = 25) individuals, both populations being non-significantly differentiated (F_{ST} = -
186 0.002; exact test p = 0.34). We chose the Han Chinese (n = 44) for the East Asian parental
187 group, and we further considered a pool of French (n = 28), Bergamo (n = 13) and Tuscan (n
188 = 21) individuals for the European group, these three populations being non-significantly
189 differentiated (F_{ST} < -0.006; p > 0.42). Last, we chose the Palestinians (n = 46) for the Middle
190 Eastern group.[39]
191

Results

Genetic diversity

Average allelic richness and expected heterozygosity for each of the 26 Central Asian populations and across regions are given in Table 2. We found a significant difference in allelic richness (Kruskal-Wallis test, χ^2 = 105,29, d.f. = 25, $p < 0.0001$) and in expected heterozygosity (Kruskal-Wallis test, $\chi^2 = 67.98$, d.f. = 25, $p < 0.0001$) among populations. We found no significant difference in allelic richness between Indo-Iranian (*AR* = 13.8) and Turkic speakers *(AR* = 13.7, Wilcoxon signed rank test, $Z = -0.69$, $p = 0.49$), although the expected heterozygosity was significantly higher in Indo-Iranian as compared to Turkic speakers ($H_e = 0.818$ and $H_e = 0.787$, respectively, Wilcoxon signed rank test, $Z = -4.55$, $p < 0.0001$). We found a significant difference in allelic richness across Central Asia, Europe, Central/South Asia, Middle East and East Asia (Kruskal-Wallis test, $K = 36.46$, d.f. = 4, $p < 0.0001$), as well as in expected heterozygosity (Kruskal-Wallis test, $K = 52.94$, d.f. = 4, $p < 0.0001$). Yet, these differences were rather due to a lower heterozygosity in East Asia and also slightly higher allelic richness in Middle East (Tukey's test, $p < 0.0001$ for both *AR* and H_e). Central Asia therefore showed neither higher nor lower diversity than the rest of Eurasia.

Population differentiation

The 26 Central Asian populations were slightly but significantly differentiated ($F_{ST} = 0.015$, $CI_{99\%} = [0.011\text{-}0.018]$, $p < 0.01$). Pairwise F_{ST} estimates ranged from -0.004 to 0.056, with 205 out of 325 pairs of populations (i.e., 63.1%) being significantly differentiated after Bonferroni correction for multiple tests (see Supplementary Table 1). These significant estimates mainly corresponded to pairwise comparisons between one Turkic and one Indo-Iranian population, as well as to comparisons between two Indo-Iranian populations. The apportionment of genetic variation among linguistic or ethnic groups of populations (Table 3)

showed that more than 98% of the total variation lay within populations ($p < 0.0001$). Yet, both ethnicity and linguistic affiliation accounted significantly for the observed variation ($F_{CT} = 0.007$, $p < 0.0001$ and $F_{CT} = 0.011$, $p < 0.0001$, respectively). We found no evidence of isolation-by-distance within each of Turkic and Indo-Iranian group of populations ($p = 0.363$ and $p = 0.772$, respectively).

The correspondence analysis (CA) based on the table of allele counts in Central Asia separated Turkic- and Indo-Iranian-speaking populations on the first axis (Figure 2a). The first two factorial components (FC) accounted for 20.5 % of the total inertia. There were some exceptions, though: two Turkic-speaking populations, TUR and UZA, were clearly clustered with Indo-Iranian-speaking populations. Interestingly, the Uzbek populations (LUZa, LUZn, UZA and UZT) showed a scattered pattern on the CA which overlapped the Turkic-speaking and the Indo-Iranian-speaking groups of populations. The CA based on the table of allele counts in Eurasia placed Central Asian populations in an intermediate position between a group of European population, a group of Middle Eastern populations, a group of Central/South Asian populations, and a group of East Asian populations (Figure 2b). The first two factorial components accounted for 22.4 % of the total inertia. Turkic- and Indo-Iranian-speaking populations were separated on the first axis, with Turkic-speaking populations being closer to East Asian populations, and Indo-Iranian-speaking populations being closer to Central/South Asian, European and Middle Eastern populations. It is noteworthy that Central Asian and Central/South Asian populations were more scattered than any other group of populations in Eurasia (Figure 2b). Interestingly, the Hazaras from Pakistan, who claim to be direct male-line descendants of Genghis Khan,[40,41] as well as the Uygurs, clustered together with the Turkic-speaking populations of Central Asia.

Cluster analyses

Analyzing the Eurasian plus the African populations altogether, we found that the highest average posterior probability of the data (D), across 40 runs, was obtained for $K = 7$ putative clusters, with $\text{Log}[P(K = 7 \mid D)] = -167565.4$ (SD = 22.8), although the average posterior probability for $K = 6$ was only slightly lower, with $\text{Log}[P(K = 6 \mid D)] = -167653.8$ (SD = 10.6). The symmetric similarity coefficients computed with CLUMPP across independent runs were all larger than 0.99 for K varying from 2 to 5, and larger than 0.87 for $K = 6$, which suggests the absence of genuine multimodality across runs. As seen in Figure 3, at $K = 2$, we observed a clear east-west cline. Central Asia seemed to be intermediate between one cluster made of European, Middle Eastern, Central/South Asian and African populations on the one hand and one cluster of East Asian populations on the other hand, which is consistent with the CA (Figure 2b). There was no individual assigned exclusively to one cluster, with Turkic-speaking individuals having a higher membership coefficient in the East Asian cluster, and Indo-Iranian-speaking individuals having a higher membership coefficient in the cluster made of Europe, Middle East, Central/South Asia and Africa. At $K = 3$, the six African populations clustered together. At $K = 4$, the European and Middle Eastern populations clustered together, with Central/South Asian and Central Asian populations (mostly Indo-Iranian speakers) showing a small contribution from this European/Middle Eastern cluster (represented in green in Figure 3). At $K = 5$, the Turkic-speaking populations from Central Asia showed a large contribution from a fifth cluster (in orange in Figure 3). At $K = 6$, the Indo-Iranian speaking populations from Central Asia show a large contribution from a sixth cluster (in light blue in Figure 3). The two latter clusters were found almost exclusively in Central Asian populations. Most Turkic-speaking populations showed a contribution from the East Asian cluster (in red), and most Indo-Iranian populations showed a contribution from Europe and Middle East (in green). It is noteworthy that Uygur and Hazara populations showed the same pattern as the Turkic-speaking populations from Central Asia. At $K = 7$, all Eurasian populations (but

mostly Turkic-speaking populations) had a variable proportion of the new component. Yet, no run at $K = 7$ resulted in a new cluster of populations, as compared to $K = 6$, which is the reason why the output for $K = 7$ is not represented in Figure 3.

Admixture analyses

The maximum likelihood estimates (MLE) of admixture proportions obtained with LEADMIX for each Central Asian population are given in Figure 1 and Table 4. Most Turkic-speaking populations had a large East Asian ancestral contribution, which represented in general 49.5%, or more, of the total contribution. There were four notable exceptions, though, with the Turkmen (TUR) and three Uzbek populations (UZA, UZB and UZT) showing a lower contribution from East Asian populations (respectively, 27.2%, 28.6%, 28.1% and 28.7%). Indo-Iranian-speaking populations had a large western Eurasian contribution (Central/South Asia, Europe and Middle-East), which represented 72.7% to 94.5% of the total contribution, although the relative contributions from these three parental groups differ across Indo-Iranian-speaking populations. It is noteworthy that, in general, many geographically close populations that speak different languages showed contrasted admixture proportions (see, e.g., UZT and TJU in Table 4), which supports the idea that language is a major determinant of population differentiation in Central Asia.

Discussion

Central Asia in the heartland of Eurasia

We found a high level of autosomal genetic diversity in Central Asia, consistent with previous observations,[3,16] and similar in extent to other major regions in Eurasia (Table 2). Population differentiation among Central Asian populations was similar, or even stronger, than that measured among populations within other regions in Eurasia: the pairwise F_{ST} estimates ranged from -0.004 to 0.056 in Central Asia, a range which should be compared to that found in the European group [-0.011; 0.015], the Middle-Eastern group [0.008; 0.021], the Central/South Asian group [-0.002; 0.062] and in the East Asian group [-0.011; 0.046], based on the same set of 27 microsatellite loci as we used in our study. This pattern is also apparent in the correspondence analysis (Figure 2b), where Central Asian and Central/South Asian populations were more scattered than each of the East Asian, European and Middle-Eastern groups, which suggests a higher diversification within Central Asia and Central/South Asia. Most importantly, the observed diversity was mainly due to the differentiation into two main groups of populations (Figure 3): on the one hand, Indo-Iranian-speaking populations (which include Tajiks and three Uzbek populations) that are genetically closer to populations from Western Eurasia; on the other hand, Turkic-speaking populations (which include Karakalpaks, Kazakhs, Kyrgyz, and two other Uzbek populations) that are closer to Eastern Asian populations (with the exception of the Turkmen). This pattern was also apparent in the correspondence analysis (Figure 2b), and consistent with the significant differentiation of almost all pairwise comparisons between an Indo-Iranian-speaking and a Turkic-speaking population (Supplementary Table 1).

Although several studies have shown that geography is, in general, a better predictor of genetic differentiation than ethnicity and linguistics,[42,43] language affiliation appears as the most important factor explaining the distribution of genetic diversity in Central Asia (Table

311 3). We found indeed that, although most (98%) of the variation lay within Central Asian
312 populations ($p < 0.0001$), a significant part of the total variation (1.09%; $p < 0.0001$) lay
313 among linguistic groups, which provides an estimate of differentiation among groups equal to
314 $F_{CT} = 0.011$. For comparison purpose, the differentiation among Central/South Asia, East
315 Asia, Europe and Middle East was found to be $F_{CT} = 0.044$, with 94.1% of the total variation
316 found within populations ($p < 0.0001$) and 4.4% found among groups, based on the same set
317 of 27 microsatellite loci as we used in our study. We found no evidence of a correlation
318 between geography and genetics within each of the Indo-Iranian or Turkic groups of Central
319 Asian populations. For the Turkic-speaking populations, this may be explained by their recent
320 arrival in the region and/or their nomadic life-style. However, more striking is the fact that no
321 geographic pattern of genetic variation was found among sedentary Indo-Iranian speakers
322 either.

323

324 **Putative origins of Indo-Iranian- and Turkic-speaking populations**

325 The clustering analysis showed that most individuals from the Indo-Iranian-speaking
326 populations had large membership coefficients into two clusters (light blue and beige in
327 Figure 3) that were found mostly in these populations. Altogether, the significant pairwise F_{ST}
328 estimates between almost all pairs of Indo-Iranian-speaking populations (Supplementary
329 Table 1), the high level of diversity across Indo-Iranian populations (Table 2) and the variable
330 level of admixture from the putative parental populations (Table 4) seem consistent with the
331 premise that Indo-Iranian speakers are long term settled populations in the area. This latter
332 hypothesis is strongly supported by archaeological evidence.[44] Conversely, we found a lower
333 genetic differentiation among Turkic-speaking populations despite their wide geographic
334 distribution (Figure 1), which suggests a more recent common origin of these populations as
335 compared to Indo-Iranian-speaking populations, in consistence with historical records.

Our study further shed some light on the origins of the Turkic-speaking populations in Central Asia. The clustering analyses showed indeed that most individuals from the Turkic-speaking populations had large membership coefficients into one Central Asian cluster (in orange in Figure 3) and smaller membership coefficients into the East-Asian cluster (in red in Figure 3) thus confirming the result of Li *et al*[45] based on a small central Asian cluster for Uygur, Kazakh and Khanty. This pattern likely reflects the existence of an ancestral group of Turkic-speakers (orange cluster in Figure 3), which popular Turkic culture considers as originating from the Altai region. The East-Asian ancestry of Turkic-speaking populations (red cluster in Figure 3) may then correspond to the westward expansions of nomadic groups form East Asia during historical times.

The Westernized view of westward invasions usually emphasizes the extreme violence and cruelty of the hordes led by Attila the Hun (A.D. 406-453), or that from the Mongolian empire led by Genghis Khan. However, our results somehow challenge this view and rather suggest that these more recent expansions did not lead to the massacre and complete replacement of the locally settled populations but rather to partial admixture. We found almost no eastern ancestry in Indo-Iranian speaking populations (see Figure 3), which suggests that the group of people from which the current-day Tajik and Turkmen populations would be the descendants, did not suffer from the westward expansions of eastern nomadic groups. This is consistent with Zerjal *et al*'s study[16], which showed the absence of the "Genghis Khan lineage" in the Tajik and Turkmen populations they studied. Furthermore, the present finding that the partial admixture with eastern nomadic groups concerned almost exclusively the Turkic-speaking populations is consistent with the fact that Turks and Mongols share cultural traditions and life-style, which may have facilitated inter-groups marriages.

360 Our study also contradicts the claim that these westward invasions resulted in founder
361 effects.[16] The high level of autosomal diversity observed in all Turkic-speaking populations
362 (Table 2) contrasts indeed with the low level of Y-chromosome diversity found in some
363 populations of the region.[10,16] Our recent studies based on the analysis of uni-parental markers
364 in Central Asia already showed that the low level Y-chromosome diversity is only found in
365 the Turkic-speaking group[46], which may therefore be explained by the social organization of
366 Turkic-speaking populations, that is based on patrilineal descent groups.[10, 18]

367 Overall, our results are partly consistent with Comas et al.'s hypothesis[11] that Central
368 Asia has been a contact zone between two differentiated groups. Our study suggests that one
369 of these groups is a long lasting group of settled populations, now represented by Tajiks and
370 Turkmen, although the origin of this group is difficult to infer; the second of these groups is
371 likely to have a more recent origin, resulting from the movements of eastern nomadic Turkic-
372 speaking groups. Interestingly, we found almost no African ancestry in the genetic pool of
373 Central Asian population from clustering analyses (Figure 3). Yet, with the same level of
374 clustering, we found no African ancestry either in Europe or in East-Asia. Further work is
375 therefore required to infer the more ancient peopling of Central Asia, after the spread of
376 modern humans out of Africa.

377 We found that the Uzbek populations were scattered across Turkic- and Indo-Iranian
378 speaking populations (Figure 2b). Some Uzbek populations (LUZa, LUZn, UZA) were closer
379 to Indo-Iranian speaking populations, while other populations (UZB, UZT) clearly clustered
380 with Turkic-speaking populations. This is consistent with the fact that Uzbek populations
381 include the 17th century Uzbeks, which were nomadic herders before they sedentarized
382 around the 16th Century,[10] and the former Chagatai Turk groups who were already settled in
383 Uzbekistan.[47] Uzbeks therefore result from the union of different tribes, some of recent origin

clustering with Turkic-speaking populations, and some tracing back to Chagatai Turks who were strongly admixed with Iranian dwellers of Central Asia.

Evidence for linguistic replacements

We found two presumable cases of linguistic replacements in Central Asia. The Turkic-speaking populations, TUR (Turkmen) and UZA (Uzbek) were found to cluster together with Indo-Iranian-speaking populations (Figure 2). The Uzbek population UZA, a currently Turkic-speaking population, is indeed genetically more similar to Indo-Iranian speakers, which suggests a linguistic shift in this population. Concerning the Turkmen, their genetic similarity with Tajiks (see also Table 4) is consistent with the hypothesis that they may be the present-day descendants of populations established over long periods of time. The indigenous cultural history of the Turkmen in Turkmenistan can indeed be dated back to 10,000 years B.C. and similarities between the cultures and technologies found in the archaeological record suggest that this region has been continually occupied since 6,000 B.C. A recent linguistic replacement in the TUR population would then explain the observed pattern of a Turkic-speaking population clustering with Indo-Iranian speakers.

A Central Asian origin of the Hazaras?

Our study confirms the results of Li *et al.*'s study[48] that cluster the Hazara population with Central Asian populations, rather than Mongolian populations, which is consistent with ethnological studies.[49] Our results further extend these findings, since we show that the Hazaras are closer to Turkic-speaking populations from Central-Asia, than to East-Asian or Indo-Iranian populations.

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Figure legends

Figure 1 Geographic location of the 26 Central Asian populations sampled. Linguistic affiliation, as well as admixture proportions from putative parental origins (Central/South Asia, East Asia, Europe and Middle East) are also indicated. See Table 1 for acronyms.

Figure 2 Correspondence analysis (CA) based on the table of allele counts in Central Asia (**a**). The first two factorial components (FC) are represented, and their relative contribution to the total inertia are indicated. Colors indicate language affiliation; blue: Indo-Iranian speakers; orange: Turkic speakers. CA based on the table of allele counts in Eurasian populations (**b**). Colors represent major geographic regions; purple: Europe; grey: Middle East; green: Central/South Asia; red: East Asia.

Figure 3 Population structure inferred from microsatellite data using the software package STRUCTURE. *K* represents the number of putative clusters. Each individual is represented by a vertical line, divided into up to *K* colored segments, each of which represents the individual's estimated membership fraction to that cluster. Each output represents the matrix of membership coefficients averaged over 40 independent runs with CLUMPP. The data consisted in 767 individuals from 26 Central Asian populations genotyped at 27 microsatellite loci, plus 869 individuals from 44 African and Eurasian populations from the HGDP-CEPH Human Genome Diversity Cell Line Panel. See Table 1 for acronyms.

Table 1 Description of the 26 Central Asian studied populations

Sampled populations (area)	Acronym	Location	Language family	Long.	Lat.	*n*
Tajiks (Samarkand)	TJA	Uzbekistan / Tajikistan border	Indo-Iranian	**39.54**	**66.89**	31
Tajiks (Samarkand)	TJU	Uzbekistan / Tajikistan border	Indo-Iranian	**39.50**	**67.27**	29
Tajiks (Ferghana)	TJR	Tajikistan / Kyrgyzstan border	Indo-Iranian	**40.36**	**71.28**	29
Tajiks (Ferghana)	TJK	Tajikistan / Kyrgyzstan border	Indo-Iranian	**40.25**	**71.87**	26
Tajiks (Gharm)	TJE	Northern Tajikistan	Indo-Iranian	**39.12**	**70.67**	25
Tajiks (Gharm)	TJN	Northern Tajikistan	Indo-Iranian	**38.09**	**68.81**	24
Tajiks (Gharm)	TJT	Northern Tajikistan	Indo-Iranian	**39.11**	**70.86**	25
Tajiks (Penjikent)	TDS	Uzbekistan / Tajikistan border	Indo-Iranian	**39.28**	**67.81**	25
Tajiks (Penjikent)	TDU	Uzbekistan / Tajikistan border	Indo-Iranian	**39.44**	**68.26**	25
Tajiks (Yagnobs from Dushanbe)	TJY	Western Tajikistan	Indo-Iranian	**38.57**	**68.78**	25
Uzbeks (Ferghana)	UZA	Uzbekistan / Kyrgyzstan border	Turkic	**40.77**	**72.31**	25
Uzbeks (Penjikent)	UZT	Northern Tajikistan	Turkic	**39.49**	**67.54**	25
Uzbeks (Bukhara)	LUZn	Central Uzbekistan	Indo-Iranian	**39.70**	**64.38**	20
Uzbeks (Bukhara)	LUZa	Central Uzbekistan	Indo-Iranian	**39.73**	**64.27**	20

Uzbeks (Karakalpakia)	UZB	Western Uzbekistan	Turkic	**43.04**	**58.84**	35
Karakalpaks (Qongrat from Karakalpakia)	KKK	Western Uzbekistan	Turkic	**43.77**	**59.02**	45
Karakalpaks (On Tört Uruw from Karakalpakia)	OTU	Western Uzbekistan	Turkic	**42.94**	**59.78**	45
Kazaks (Karakalpakia)	KAZ	Western Uzbekistan	Turkic	**43.04**	**58.84**	49
Kazaks (Bukhara)	LKZ	Central Uzbekistan	Turkic	**40.08**	**63.56**	25
Kyrgyz (Andijan)	KRA	Uzbekistan / Kyrgyzstan border	Turkic	**40.77**	**72.31**	45
Kyrgyz (Narin)	KRG	Eastern Kyrgyzstan	Turkic	**41.60**	**75.80**	18
Kyrgyz (Narin)	KRM	Eastern Kyrgyzstan	Turkic	**41.45**	**76.22**	21
Kyrgyz (Narin)	KRL	Eastern Kyrgyzstan	Turkic	**41.36**	**75.50**	22
Kyrgyz (Narin)	KRB	Eastern Kyrgyzstan	Turkic	**41.25**	**76.00**	24
Kyrgyz (Issyk Kul)	KRT	Eastern Kyrgyzstan	Turkic	**42.16**	**77.57**	37
Turkmen (Karakalpakia)	TUR	Western Uzbekistan	Turkic	**41.55**	**60.63**	47

Long., longitude; Lat., latitude. *n*, sample size.

Table 2 Genetic diversity in the studied populations and in Eurasia

World Area	Population	AR	H_e
Central Asia	KAZ	7.9	0.784
Central Asia	KKK	7.8	0.782
Central Asia	KRA	7.5	0.769
Central Asia	KRB	7.3	0.757
Central Asia	KRG	7.7	0.779
Central Asia	KRL	7.8	0.778
Central Asia	KRM	7.6	0.752
Central Asia	KRT	7.7	0.761
Central Asia	LKZ	7.8	0.778
Central Asia	LUZa	8.3	0.817
Central Asia	LUZn	8.6	0.821
Central Asia	OTU	8.0	0.784
Central Asia	TDS	7.7	0.784
Central Asia	TDU	7.9	0.805
Central Asia	TJA	8.0	0.806
Central Asia	TJE	8.4	0.814
Central Asia	TJK	8.6	0.820
Central Asia	TJN	8.4	0.811
Central Asia	TJR	8.6	0.812
Central Asia	TJT	8.5	0.812
Central Asia	TJU	8.5	0.811
Central Asia	TJY	7.9	0.799
Central Asia	TUR	8.5	0.812

Central Asia	UZA	9.0	0.817
Central Asia	UZB	8.5	0.774
Central Asia	UZT	8.4	0.795
Central Asia (pooled populations)		12.58	0.803
Central/South Asia		12.66	0.819
East Asia		11.4	0.705
Europe		11.83	0.808
Middle East		13.17	0.827

AR, allelic richness; H_e, expected heterozygosity. *AR* was calculated using a common sample size of $n = 13$ diploid individuals for the Central Asian samples, and a common samples size of $n = 123$ diploid individuals for the regional samples. These sample sizes correspond to the smallest number of genes sampled at a locus, including missing data.

Table 3 AMOVA of the 26 Central Asian studied populations

Grouping	Source of variation	Percentage of variation	F_{ST}	F_{SC}	F_{CT}
Linguistic affiliation	Among groups	1.09			0.010***
	Among populations within groups	0.91		0.009***	
	Within populations	98.0	0.020***		
Ethnicity	Among groups	0.69			0.007***
	Among populations within groups	0.91		0.009***	
	Within populations	98.39	0.016***		

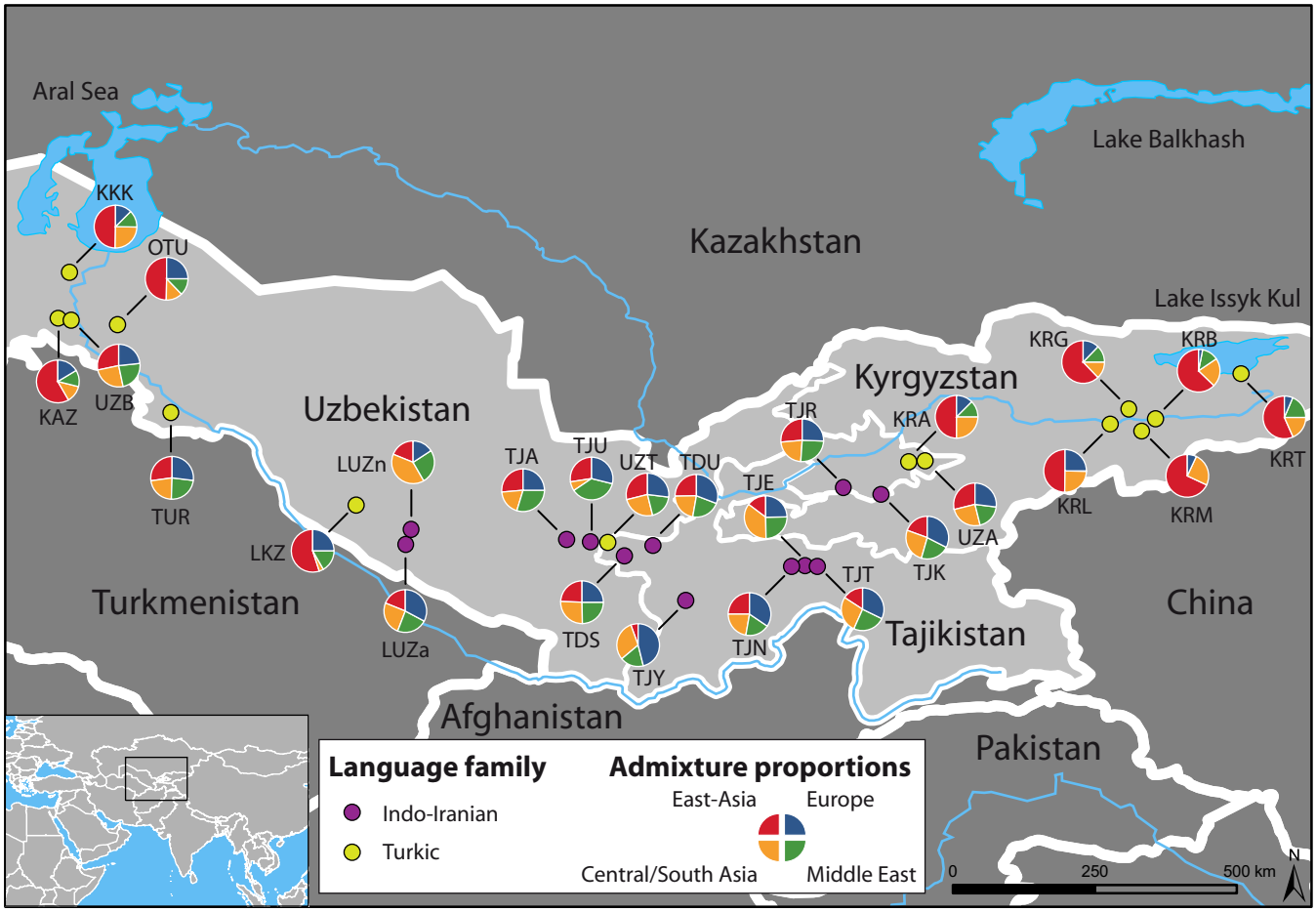
*$p < 0.01$, **$p < 0.001$, ***$p < 0.0001$.

9 **Table 4** Maximum-likelihood estimates of admixture proportions in the 26 Central Asian populations

		Putative parental group			
Population	Ethnic group	Europe	Middle East	Central/South Asia	East Asia
KAZ	**Kazakh**	0.166	0.125	0.126	0.583
LKZ	**Kazakh**	0.252	0.166	0.033	0.549
KKK	**Karakalpak**	0.126	0.127	0.250	0.497
OTU	**Karakalpak**	0.250	0.128	0.125	0.497
KRA	**Kyrgyz**	0.125	0.126	0.250	0.499
KRB	**Kyrgyz**	0.031	0.125	0.218	0.625
KRG	**Kyrgyz**	0.124	0.126	0.129	0.621
KRL	**Kyrgyz**	0.250	0.004	0.250	0.495
KRM	**Kyrgyz**	0.072	0.000	0.250	0.678
KRT	**Kyrgyz**	0.066	0.184	0.184	0.566
TUR	**Turkmen**	0.271	0.236	0.221	0.272
UZA	**Uzbek**	0.271	0.192	0.250	0.286

UZB	**Uzbek**	0.235	0.234	0.250	0.281
UZT	**Uzbek**	0.271	0.192	0.250	0.287
LUZa	**Uzbek**	0.330	0.229	0.254	0.187
LUZn	**Uzbek**	0.160	0.257	0.395	0.188
TDS	**Tajik**	0.250	0.249	0.258	0.242
TDU	**Tajik**	0.310	0.219	0.220	0.251
TJA	**Tajik**	0.250	0.298	0.190	0.262
TJE	**Tajik**	0.250	0.248	0.358	0.145
TJK	**Tajik**	0.327	0.219	0.260	0.194
TJN	**Tajik**	0.345	0.184	0.221	0.250
TJR	**Tajik**	0.256	0.256	0.226	0.262
TJT	**Tajik**	0.324	0.244	0.274	0.158
TJU	**Tajik**	0.290	0.366	0.071	0.273
TJY	**Tajik**	0.462	0.179	0.303	0.055

Shaded cells correspond to Turkic-speaking populations, and non-shaded cells to Indo-Iranian-speakers.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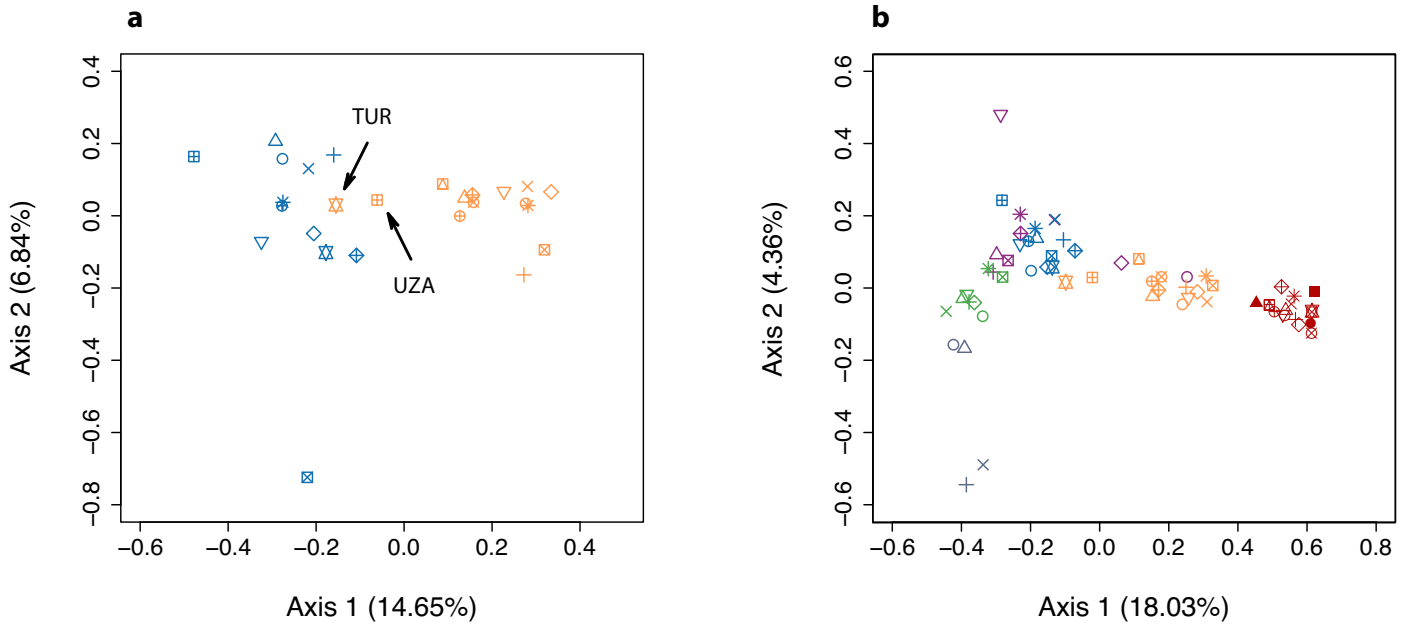


Central Asia (Indo-Iranian language)

- LUZa
- LUZn
- TDS
- TDU
- TJA
- TJE
- TJK
- TJN
- TJR
- TJT
- TJU
- TJY

Central Asia (Turkic language)

- KAZ
- KKK
- KRA
- KRB
- KRG
- KRL
- KRM
- KRT
- LKZ
- OTU
- TUR
- UZA
- UZB
- UZT

Central/South Asia

- Uygur
- Balochi
- Brahui
- Burusho
- Hazara
- Kalash
- Makrani
- Pathan
- Sindhi

Europe

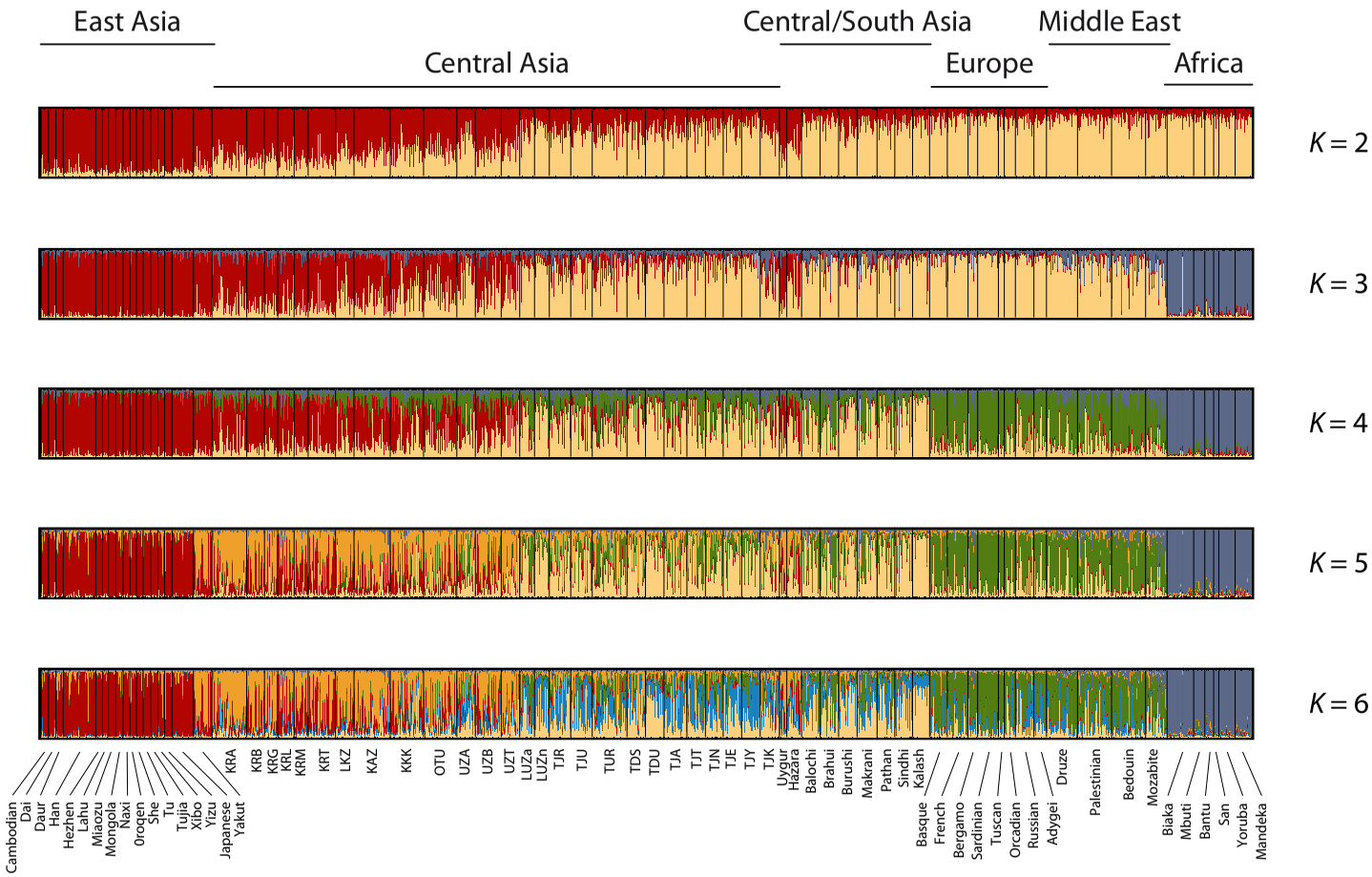
- Basque
- French
- Bergamo
- Sardinian
- Tuscan
- Orcadian
- Russian
- Adygei

Middle East

- Druze
- Palestinian
- Bedouin
- Mozabite

East Asia

- Cambodian
- Dai
- Daur
- Han
- Hezhen
- Lahu
- Miaozu
- Mongola
- Naxi
- Oroqen
- She
- Tu
- Tujia
- Xibo
- Yizu
- Japanese
- Yakut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Han
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Mongola
Naxi
Orogen
She
Tu
Tujia
Xibo
Yizu
Japanese
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LKZ
KAZ
KKK
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UZB
UZT
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Bantu
San
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