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Short Communication

Inferring the demographic history of Hexi Corridor over the past two millennia from ancient genomes

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The Hexi Corridor in northwest China has for millennia served as a crossroads for interactions between East Asia, Central Asia and lands further west, while also connecting the Chinese heartland and the northern Mongolian Steppe and Tibetan Plateau (TP) to the south (Fig. 1a). Previous studies have revealed the details of this cross-continental material and cultural transmission as early as the Bronze Age onwards. Materials and technologies exchanged along the ancient Silk Road included East Asian millets and painted pottery, West Asian wheat and barley, bronze metallurgy, domesticated sheep, horses, and cattle [1]. To date, paleogenomic studies have examined the genetic structure of the eastern Hexi Corridor [2] and neighboring populations, such as northern China [2], the Western Regions (present-day Xinjiang) [3], Tibetan Plateau [4] and Mongolia [5] for these formative Neolithic and Bronze Age periods. Uniparental or limited autosomal studies have shed some light on demographic interactions in the east[2], center[6] and far west[7] of the historical Hexi Corridor, and genome-wide single nucleotide polymorphisms (SNPs) studies revealed the genetic landscape of western-eastern admixture pattern of the present-day Hexi Corridor [8–10]. However, population dynamics in Hexi Corridor across a longer tranche of time has been gravely under-represented. To address the limitations above, we sampled and sequenced 30 ancient individuals across the Hexi Corridor (Fig. 1a, b and Table S1A online). We sampled 17 human individuals from the Heishuiguo site from the central Hexi Corridor, dating from the Western Han Dynasty (202 BC–8 AD) through the Eastern Han Dynasty (25–220 AD). From the western Hexi Corridor, we sampled 13 human individuals from the Foyemiaowan cemetery, dating from the Cao-Wei (220–265 AD) to the Tang dynasties (618–907 AD). To establish the chronology of our study, we relied on both archaeological and radiocarbon dating evidence. We list the detailed information of each sample in Table S1A (online).

We constructed double-stranded DNA libraries from teeth or petrous portions of the temporal bone for the studied individuals. We generated shotgun sequencing data that revealed high levels of DNA preservation with endogenous DNA contents ranging from 0.95% to 83.60% (28.79% on average) (Table S1A online). All samples showed characteristics of postmortem damage patterns (Fig. S1 online). The pseudo-haploid genotype was called on the 1240k (i.e., 1.24 million) SNP panel, resulting in 14,387 to 1,141,519 SNP sites (Table S1A online). Of the 30 Hexi Corridor individuals sequenced, we detected one second-degree kinship confirmed by three methods (Fig. S2 online), and we removed relatives with fewer SNP counts. Finally, we used 25 individuals with <3% contamination rates and >50,000 SNPs for population genetics analysis (Table S1A online).

To describe the genetic background of the individuals in our study, we initially performed principal component analysis (PCA) by projecting our ancient genomes onto the PCA space computed from present-day Eurasians (Fig. 1c and Fig. S3 online). Both Heishuiguo and Foyemiaowan people clustered neatly with ancients from geographically close Dacaozi (DCZ-M17IV, DCZ-M22IV, and DCZ-M21II) and middle-to-lower reaches of Yellow River Basin (represented by YR_LN and YR_LBIA) as well as present-day northern Han Chinese populations. Notably, the two Foyemiaowan individuals (G32712 and G40803) deviated from this YR-related cluster along PC1 with varying genetic affinity to western Eurasians, suggesting potential assimilation of the non-local ancestry. This result was recapitulated in model-based unsupervised ADMIXTURE (Fig. 1d). When we assumed that five distinct ancestries constituted the involved Eurasian populations, our time transect individuals presented a genetic profile similar to the Dacaozi and ancients from the middle-to-lower reaches of Yellow River Basin (represented by YR_LN and YR_LBIA), except G32712 and G40803 who displayed a high proportion of YR-related ancestry but also with a trace of pink component that was enriched in western Eurasians. Samples G32712 and G40803 were genetic outliers harboring a less common ancestry in the sampling area. Accounting for archaeological background, G32712 and G40803 were denoted as Foyemiaowan_Cao-Wei_o and Foyemiaowan_Tang_o, respectively. In the subsequent quantitative analysis, we analyzed outliers separately from Heishuiguo and other Foyemiaowan individuals.

(i) *Profound impact of historically-documented military expansion from Central Plains on the gene pool of the historical Hexi Corridor populations.* To explore potential genetic variation on a multi-century spatiotemporal scale in the historical period Hexi Corridor, we performed pairwise f_4 statistics in the form of $f_4(\text{Yoruba}, X; \text{historical period Hexi Corridor subgroups } i, \text{ historical period Hexi Corridor subgroup } j)$, where X included ancient Eurasian lineages, i and j were any pairs of Heishuiguo/Foyemiaowan/Dacaozi populations grouped by geography and dynasty (Fig. S4 online). We observed non-significant f_4 values with $|Z\text{-scores}| < 3$ when using diverse Eurasians as population X , suggesting minimal genetic heterogeneity across Hexi Corridor in the historical era. In pairwise $qpWave$ analysis (Fig. S5b online), genetic differentiation among each pair of the Heishuiguo/Foyemiaowan/Dacaozi groups was also indistinguishable ($P > 0.01$). These findings suggested little or no genetic impact on the gene pool of Hexi Corridor from other lineages, especially diverse western Eurasian-related ancestries—despite large spatial and temporal variation among analyzed historical period Hexi Corridor groups.

We further quantified genetic affinities between Heishuiguo, Foyemiaowan, Dacaozi groups and ancient western and eastern Eurasians using f statistics. Outgroup- f_3 statistics (Fig. S5a online) supported the idea of a strong genetic link between the historical period Hexi Corridor and ancient northern East Asians, especially ancients harboring YR-related ancestry. We then performed f_4 (Yoruba, X ; historical period Hexi Corridor subgroups, ancient northern East Asians) where X included ancient Eurasian lineages (Fig. S6 online) and $qpWave$ tests to examine whether YR and

historical period Hexi Corridor populations consistently derived from a single genetic source (Fig. S5b and Table S2A online). We detected genetic differentiation between the Neolithic Hexi Corridor-related ancestry represented by Late Neolithic Qijia culture-related people (Upper_YR_LN) and historical period Hexi Corridor people, as inferred from the significant negative f_4 values (Z -scores < -3) in f_4 (Yoruba, ancient Southern Chinese; historical period Hexi Corridor subgroups, Upper_YR_LN). However, ancient farmers from middle-to-lower reaches of the Yellow River represented by WLR_LN, YR_LBIA, and YR_LN were relatively genetically homogenous with all historical period Hexi Corridor subgroups, given the lack of significant f_4 values ($|Z$ -scores > 3). Our 1-way *qpWave* modeling on the 1240k dataset also supported the idea that all historical period Hexi Corridor subgroups could be non-admixed descendants of WLR_LN, YR_LBIA, or YR_LN (Fig. S5b and Table S2A online). To test the robustness of our 1-way models using WLR_LN, YR_LBIA or YR_LN as single sources, we further added each of the populations identified in f_4 (Yoruba, X ; historical period Hexi Corridor subgroups, WLR_LN/YR_LBIA/YR_LN) (Fig. S6 online) who shared slightly more alleles (Z -scores < -2) with historical period Hexi Corridor populations to the outgroup list in *qpAdm* analysis (Table S2B online). We observed that all of the 1-way YR_LBIA/WLR_LN/YR_LN models still fit well, even with the inclusion of these additional outgroups (Table S2B online). Besides, an alternative 2-way *qpAdm* model (Fig. 2a, b and Table S2C online) suggested that Heishuiguo (pooled populations of Heishuiguo subgroups), Foyemiaowan (pooled populations of Foyemiaowan subgroups), Dacaozi, YR_LBIA, and YR_LN had similar proportions of YR-related ancestry from the Yangshao culture (YR_MN) and Coastal Southern East Asian-related ancestry from present-day Austronesian speakers Amis (Table S2C online, $P=0.7408$, χ^2 test). These results indicated that the YR_LBIA/YR_LN-related ancestry sufficiently explains the genetic profile of historical Hexi Corridor groups.

Previous ancient genomic studies have revealed prehistoric genetic differences between the Hexi Corridor and neighboring regions, including western Mongolia to the north [5] (Fig. S12 online), Tibetan Plateau to the south [4] (Fig. S13 online), the Western Regions to the west [3], and Central Plains to the east [2] (Fig. 2a and Table S2D online). In the Central Plains, YR_LN and YR_LBIA harbored a similar ratio of YR_MN (~90%–93%) to coastal southern East Asian-related ancestry (represented by Amis, ~7%–10%). In the Western Regions (present-day Xinjiang), local Xiaohu culture-related ancestry (represented by Tarim_EMBA1), eastern Eurasian-related ancestry (represented by Shamanka_EBA), and diverse western Eurasian-related ancestries were detected in the gene pool of Bronze Age populations with high genetic diversity [3,11]. Western Mongolia exhibited a dynamic population history with admixture between diverse western and eastern Eurasian ancestries [5,10] (Fig. S12 online). On the Tibetan Plateau, both present-day and ancient individuals were primarily of Early Ancient Tibetan ancestry (represented by Yushu2.8k from northeast TP, Chamdo2.8k_1 from southeast TP, and Lubrak from southwest TP), with contributions from ancient northern East Asians and an unknown deeply diverged lineage [4] (Fig. S13 online). In the eastern Hexi Corridor, Late Neolithic Qijia culture-related Di-Qiang people (represented by Upper_YR_LN) were a mixture of ~64%–66% Neolithic YR farmers (represented by YR_MN) and ~34%–36% ancient Northeast Asian (ANA) (represented by AR_EN and

Ulaanzuukh_SlabGrave) under our *qpAdm* modeling. In our study (Fig. 2b), we discovered that historical era Dacaozi (3 individuals) from the eastern Hexi Corridor, Heishuiguo (13 individuals) from the central Hexi Corridor, most Foyemiaowan individuals (10 individuals of 12) from the western Hexi Corridor and half of the Shichengzi [12] individuals (2 individuals of 4, denoted as Shichengzi_1) from eastern Xinjiang exhibited a relative genetic homogeneity, suggesting the presence of a relatively uniform genetic pool across the historical period Hexi Corridor, extending as far west as eastern Xinjiang. These individuals could be modeled as a non-admixed descendent of the Late Neolithic and Bronze Age people from the middle-to-lower reaches of the Yellow River (YR_LN and YR_LBIA) rather than the Neolithic Hexi Corridor-related ancestry represented by Upper_YR_LN. The data strongly indicated at least one major genetic shift in the Hexi Corridor between the Neolithic Age and the Han Dynasty. We argue that, based on our analysis of the genetic evidence under the parsimonious models (i.e., preferred the models with fewer source populations over more complicated models), the probability was higher that these historical periods Hexi Corridor people were migrants from the middle-to-lower YR basin as opposed to descendants of the local Neolithic population with the additional gene flow.

We cannot pinpoint the exact time of this ancestry shift due to a gap in our time transects in Hexi Corridor. Multiple lines of evidence suggested that the relatively unified YR-related gene pool presented by Heishuiguo/Foyemiaowan/Dacaozi was most likely underpinned by the rapid expansion of the Han Empire with large-scale agricultural garrisons established in the northwest during the Han Dynasty. First, Xiongnu people occupied the Hexi Corridor before 121 BC in the Western Han Dynasty according to the historical records; Xiongnu from the eastern Eurasian steppe and our historical Hexi Corridor time series (all overlapped or postdating Western Han Dynasty) did show distinguishable genetic profiles. Second, the Central Plains was the most likely geographic origin of historical Hexi Corridor-related ancestry; WLR_LN/YR_LN/YR_LBIA-related genetic profile remained at least until 1550–50 BC (represented by YR_LBIA) that largely overlapped with the Western Han Dynasty. Third, Heishuiguo, Dacaozi, Shichengzi, and Foyemiaowan sites were located in Zhangye County, Jincheng County (金城郡), Shule City (疏勒城) and Dunhuang County, respectively, which were critical Han Dynasty garrisons in their own right [13]. Historical documents and bamboo slips described the migration of population from more than 20 counties in the Yellow River Basin to Hexi Corridor counties as a means of strengthening regional administration and control, a relatively small population stationed at Shule city responsible for the security of northern route Silk Road [14]. Based on the multidisciplinary evidence available, we can reasonably infer a connection between the expansion of the ancient Han Empire and the YR-related ancestry found in our historical Hexi Corridor time transects. Our genomic results supported the idea of rapid military expansion accompanied by large-scale immigration, resulting in the spread of middle-to-lower Yellow River farmer-related lineages throughout the historical period Hexi Corridor as far west as eastern Xinjiang. This serves as a prime example of migration facilitated by the ancient empire's expansion. It is important to note that the expansion of ancient empires can result in genetic changes not only in the conquered

regions but also within the empire itself. This phenomenon has been observed in other parts of the world, including Europe and the Americas [15–17].

(ii) *The first genetic evidence for East-West admixture was observed in Dunhuang, the far western Hexi Corridor.* We quantified the genetic profile of two outliers, Foyemiaowan_Cao-Wei_o and Foyemiaowan_Tang_o, initially identified in the qualitative analysis (i.e., PCA and ADMIXTURE). In outgroup- f_3 statistics, outliers shared the highest genetic drift with other historical period Hexi Corridor subgroups (Fig. S7a online). Thus, we used Foyemiaowan/Heishuiguo/Dacaozi as the first proximal East Asian-related source for outliers. The non-significant values shown in the f_4 (Yoruba, Foyemiaowan outliers; ANA, historical period Hexi Corridor) (Fig. S7b online) suggested outliers showed similar levels of shared genetic drift with ANA and Heishuiguo/Foyemiaowan/Dacaozi. Thus, we included the ANA-related groups (represented by Ulaanzuukh_SlabGrave for its large sample size) as the second surrogate of an East Asian-related source. Significant negative f_4 values in f_4 (Yoruba, ancient western Eurasians; Foyemiaowan outliers, Foyemiaowan/Heishuiguo/Dacaozi/ANA) validated those outliers harbored western Eurasians-related ancestry (Fig. S7c online); each element of western Eurasians identified from this f_4 who sharing more derived alleles with Foyemiaowan outliers were used as the third candidate source. Across all plausible 2-way and 3-way *qpAdm* models based on autosomal data, we found that Foyemiaowan_Cao-Wei_o and Foyemiaowan_Tang_o were best described as the 2-way mixture of ancestry related to locally established historical period Hexi Corridor (~50% and ~70%, respectively) and presumably incoming western Eurasian representatives, no need for additional ANA-related ancestry (Fig. S8a, and Tables S3A and S3D online). To determine the admixture dates, we used DATES, which applies to ancient DNA from single individuals. When we used the Foyemiaowan/Heishuiguo/Dacaozi and western Eurasian-related ancestry as sources in the well-fitted *qpAdm* models, we estimated that 10 out of 11 and 40 out of 41 admixture events occurred approximately 10–20 and 5–10 generations before the death of Foyemiaowan_Cao-Wei_o and Foyemiaowan_Tang_o. These dates aligned closely with the Warring States period (475/403–221 BC) to the Western Han Dynasty (220 BC–8 AD) and the Eastern Jin (317–420 AD) to the Tang Dynasty (618–907 AD), respectively (Fig. S8b and Table S3E online). The admixture dates of Foyemiaowan_Cao-Wei_o and Foyemiaowan_Tang_o coincided with the Historical era, particularly the period following the reclaiming of the Hexi Corridor and the establishment of the ancient Silk Road by the Han Empire. These findings emphasize the significant role played by the Silk Road in facilitating genetic exchanges between East and West.

This is the earliest western Eurasian-related ancestry in the easternmost part of modern-day China. We found that a two-way mixture of diverse western lineages and Heishuiguo/Foyemiaowan/Dacaozi approximated well with the outliers, although each pair of western Eurasian-related surrogates had distinguishable genetic profile via pairwise *qpWave* analysis through our selected outgroups (Fig. S9 online). Thus, we cannot determine which kinds of western Eurasian-related ancestry shaped the gene pool of Foyemiaowan outliers. However, we

also noticed that models with western Eurasian-related people who harbored high proportions of Bronze Age western steppe herders (WSH)-related ancestry (represented by Afanasievo and Sintashta) tended to fit well with the model. However, the wide geographical distribution of WSH-related ancestry, including Xinjiang (such as Xinj_BA5_oSte), eastern Eurasian Steppe (such as Chandman_IA), Inner Asia (such as Russia_Andronovo), and western Eurasian Steppe (such as Russia_EBA_Yamnaya_Samara) made it impossible to determine the geographic origins of the western Eurasian-related source. Additionally, our analysis does not support Dulan_o, an outlier individual from the ancient Tubo empire who possessed approximately 55% ANA and 45% WSH-related ancestry [18], as the western Eurasian-related source of ancestry in the Foyemiaowan outliers. To some degree, observed mixed East Eurasian–west Eurasian ancestry is unsurprising given Dunhuang’s international importance from the Han Dynasty to the Tang Dynasty, experiencing the arrival of merchants from further west and the introduction of Buddhism during these centuries. Their activities were materially immortalized in the Dunhuang Grottes art and thousands of documents in multiple languages unearthed at Dunhuang caves [19].

Surprisingly, results showed an increased proportion of western Eurasian-related ancestry on the X chromosome compared to autosomes in both Foyemiaowan_Cao-Wei_o and Foyemiaowan_Tang_o (Fig. S8c and Table S3C online). These outlier individuals exhibited a prominent female bias for western Eurasian-related ancestry. Interestingly, a similar pattern was observed in the Khitan and Mongol empires [5]. However, a lack of archaeological and ancient DNA studies on the sociocultural patterns (e.g., patrilocality or matrilocality; polygamy or polyandry) in the historical Hexi Corridor hindered our ability to explain the female-biased admixture with western Eurasian-related ancestry. However, historical documents, excavated epitaphs, and Tang poetry [20] indicate that marriages between Han males and non-Han females were common. Silk Road prosperity, furthermore, not only facilitated economic and cultural exchange between East and West but also contributed to the growth of transnational population movements. Fragments of the household registers of Tang Dingxing (唐定兴等户残卷) among other Dunhuang documents record instances of people keeping servants from the Western Regions [21]. This practice may have played a significant role in the marriage between Han males and non-Han females.

(iii) *Western Eurasians account for ~5%–20% of the gene pool of present-day Hexi Corridor ethnic groups.* To quantify the genetic contribution of historical period Hexi Corridor-related lineages to present-day ethnic groups residing in the Hexi Corridor, we reanalyzed published genome-wide SNP data of present-day Gansu Han Chinese [8], Altaic-speaking Yugur, Baoan and Dongxiang [9,10], who are indigenous in Gansu Province. In 2-way *qpAdm* modeling, we found that Gansu ethnic groups possessed ~80%–95% historical period Hexi Corridor-related ancestry (represented by Heishuiguo/Foyemiaowan/Dacaozi) and ~5%–20% western Eurasian-related ancestry (Fig. 2c), while no significant sex-biased admixture pattern was observed within our limited resolution (Fig. S10a–c, and Tables S4A–C and S5A–C online). According to our analysis

using present-day Han Chinese/Korean and Europeans/Inner Asians as sources (Fig. S10d, and Tables S4D and S5D online), the admixture events for present-day Gansu ethnic groups, estimated through ALDER, were dated to approximately 600–1000 years before the present, corresponding to the Song and Yuan dynasties (960–1368 AD).

During this period, the Mongol Empire rapidly expanded and formed a vast empire across Eurasia. This expansion played a critical role in the culture and genetic admixture of Eurasia. An increasing number of caravans arrived in China from Europe, the Arabian Peninsula, North Africa, and the east coast of Africa [22]. Additionally, Mongols conscripted legions of soldiers and craftsmen from Central Asia and Western Asia were included in three Western expeditions launched by Genghis Khan (1162–1227 AD), Ögedei Khan (1186–1241 AD), and Möngke Khan (1209–1259 AD) during 1219–1260 AD. These expeditions included regions such as Otrar, Jend, Khojend, and Samarqand. The group, known as the Hashar (斡军), later followed the khan in assaults on the Western Xia around modern-day Ningxia. Hezhou (河州), located in modern-day southern Gansu, subsequently became an important Mongol army garrison. It is possible that a large number of Central Asian and Western Asian individuals permanently settled in the region after these events [23]. The Yuan government is also documented to have relocated a significant quantity of military and civilians from the Western Regions into the Hexi Corridor for land reclamation purposes [24]. These migrations likely had an impact on the genetic composition of the present-day Hexi Corridor. Importantly, unlike the female-biased western Eurasian admixture events found in earlier historical Dunhuang, no significant sex-biased admixture pattern was identified in the present-day Hexi Corridor population.

We note that we only considered a single pulse-like admixture. Actual population admixture may have been a continuous process. The simplified model used in this study would result in a more recent admixture time in linkage disequilibrium (LD)-based estimations. In other words, the initiation of the period of frequent West and East Eurasian contacts mentioned above may precede the Song and Yuan, suggesting the establishment of the Silk Road had promoted bidirectional genetic and cultural exchanges between the East and the West long before the expansion of the Mongol Empire.

In our study, we investigated the population of the Hexi Corridor over the past two millennia. We have offered new perspectives on the constitution of population groups in separate historical periods. We observed that the historical Hexi Corridor population was genetically nearly identical to ancient farmers from the middle-to-lower reaches of the Yellow River. We found the first evidence of female-biased western Eurasian admixture in ancient China at the westernmost point of the Hexi Corridor—Dunhuang, following the Han Dynasty opening up of the Western Regions,

a key event in the development of the ancient Silk Road. The present-day Hexi Corridor population tends to exhibit a predominantly historical Hexi Corridor ancestry, with approximately ~5%–20% of genetic makeup being of western Eurasian origin. This is likely related to regional prosperity along the Silk Road following the expansion of the Mongol Empire. These results provide new insights into the demography of the ancestral Hexi Corridor population and extend our understanding of the exchange and integration between eastern and western populations and cultures.

Conflict of interest

The authors declare that they have no conflict of interest.

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Author contributions

Li Jin, Chuan-Chao Wang, and Shaoqing Wen conceived and supervised the project. Guoke Chen, Yishi Yang, and Hui Wang provided the materials and resources. Guoke Chen and Yishi Yang performed the archaeological data analysis. Jianxue Xiong and Panxin Du performed the wet laboratory work. Rui Wang and Chuan-Chao Wang analysed the genetic data and prepared the figures. Minmin Ma performed the radiocarbon dating of ancient samples. Jianxue Xiong, Rui

Wang, Shaoqing Wen, Edward Allen, and Chuan-Chao Wang wrote and edited the manuscript. All authors contributed to the article and approved the final version for submission.

Data availability

The DNA sequences reported in this paper have been deposited in the Genome Sequence Archive in the National Genomics Data Center (GSA) under accession HRA004375.

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Figure Legends

Fig. 1. Geographic locations, time periods, and the genetic profile of historical period Hexi Corridor individuals. (a) The geographic map showed the locations of the Heishuiguo and Foyemiaowan sites, the two new archaeological sites analyzed in this study. The orange shade indicated the geographic scope of Hexi Corridor. The four counties in Hexi Corridor were indicated in gray dots: Dunhuang, Jiuquan, Zhangye, and Wuwei. (b) The timeline displayed the ages of 30 newly reported ancient individuals based on the relics excavated. Heishuiguo individuals were estimated to date from the Western Han to Eastern Han periods; Foyemiaowan individuals were estimated to date from the Cao-Wei to the Tang Dynasties. The x -axis shows the time span of the corresponding dynasty based on the historical records. (c) Principal component analysis (PCA). The ancient individuals were projected onto the top 2 PCs calculated from present-day Eurasians. The present-day populations were shown in light grey circles. (d) The ancestral composition of Eurasian individuals inferred by ADMIXTURE for $K=5$ (lowest cross-validation error).

Fig. 2. Genetic changes in Hexi Corridor from Neolithic to present. Well-fitted *qpAdm*-based modeling results based on the autosomes for grouped-based population genetics analyses for prehistoric periods (a), historical periods (b), and present-day (c). Orange shading indicated the geographic scope of Hexi Corridor. Horizontal bars represented ± 1 standard error (SE). Raw ancestry proportions and standard error estimates are provided in Table S2D (online).



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