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Ancient genomes shed light on the genetic history of the Iron Age to historical central Xinjiang, northwest China

Haijun Li^{1*†}, Baitong Wang^{2†}, Xiaomin Yang^{2*†}, Xiaoyu Yang¹, Haifeng He³, Rui Wang³ and Chuan-Chao Wang^{4,5*}

Abstract

Background The genetic profile of the population in Xinjiang, northwest China, has been shaped by interregional movement and admixture since the Bronze Age. However, the detailed and intraregional population history of Xinjiang, especially central Xinjiang, has been unsolved due to uneven sample distribution.

Results Here, we reported the ancient genomes from 8 individuals between the Iron Age and the historical period in central Xinjiang. We observed an east–west admixed ancestry profile and a degree of genetic continuity between the Iron Age and historical central Xinjiang individuals. Furthermore, these central Xinjiang individuals harboured ancestry related to ancient farmers of the Yellow River. We also identified a temporal change of the Yellow River farmers-related ancestry in central Xinjiang, showing an increase the Yellow River affinity from Iron Age to Historical Era.

Conclusions The finding indicated that the genetic structure of the central Xinjiang population since the Iron Age could have resulted from immigration from northern China, which was attributed to geopolitical factors. Hence, our results indicated that the geopolitical change with the deepening of Central Plains' management has influenced the genetic profile of central Xinjiang.

Keywords Ancient DNA, central Xinjiang, Genetic profile, Population movement, Yellow River farmers

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Background

Xinjiang, geographically located in northwest China, has long been one of the major crossroads for trans-Eurasian exchanges of populations, cultures, technologies, agriculture, and languages. As suggested by archaeological findings, diverse cultural influences on Xinjiang varied by region and time [1–3]. Xinjiang has shared cultural connections with the Western Eurasian Steppe, Central Asia, Siberia, Northeast Asia, and East Asia since the Bronze Age (BA) [1, 2]. Recent paleogenomic studies of Xinjiang suggested that the genetic history of the BA Xinjiang was heavily marked by Western Eurasian Steppe-related, Northeast Asian, and Central Asian migrations, in addition to the local ancestry represented by Xiaohe people Tarim_EMBA [4–6].

Compared with the preceding BA, the Iron Age (IA; ~ 800 to 200 BCE) is marked by extensive population movements and cultural exchanges in Xinjiang [2, 4, 6]. On the one hand, nomadic groups raised from the Eurasian Steppe affected different regions of Xinjiang. One such group was the Scythians, an important confederation of several populations, such as the Tagar, Pazyryk, and Sakas [7-10]. The iron materials, black pottery, and wooden objects with animal patterns found in Xinjiang archaeological sites were linked to the Scythian culture [2]. On the other hand, the cultural influences from East Asia on Xinjiang were more profound and extensive than during BA [2, 3, 11]. The painted pottery culture from the Gansu and Qinghai (Gan-Qing) region of northern China spread westward into eastern Xinjiang and as far as southern Xinjiang [2, 12]. After 200 BCE, the centralized state in the Central Plains adopted a series of strategies to deepen its control over Xinjiang [13-15]. Paleogenomic studies demonstrated that the post-BA Xinjiang maintained the genetic profile identified in BA while also overseeing an increase in movement and admixture of Steppe, Central Asian, and East Asian populations [4, 6, 16]. Moreover, ancient DNA studies suggested that introducing Tocharian and Khotanese languages into Xinjiang might be associated with the population expansions of Early to Middle Bronze Age (EMBA) Steppe pastoralists Afanasievo and IA Sakas [6, 16]. Paleogenomic studies have presented data from ancient samples of northern and western Xinjiang [5, 6]. However, due to the scarcity of ancient genomic data of central Xinjiang, the complicated demographic changes of central Xinjiang over the cultural and technological transitions remain obscure. For example, the mechanisms of cultural exchanges from East Asia are still poorly investigated. Furthermore, it remains unclear whether the population interactions between Xinjiang and the Central Plains have fluctuated in response to the changing control exerted by the Central Plains over Xinjiang.

Here, we successfully retrieved ancient genomes from seven IA individuals from the Hejing Horgutu Hydropower Station Cemetery (the Horgutu Cemetery) and one ancient individual from the Badamu tomb group in the central area of Xinjiang. The Horgutu Cemetery was dated from the Late Bronze Age (LBA) to IA [17]. In general, the IA Chawuhu culture in central Xinjiang is regarded as one of the representatives of the painted pottery culture of the central reach of the southern Tianshan Mountains. The flow-coloured clay pot with one ear is characteristic of Chawuhu culture. The recovered pottery of the Horgutu Cemetery contains a flow-coloured clay pot with one ear. Therefore, the Horgutu Cemetery is believed to relate to the IA Chawuhu culture. The Badamu tomb group is a historical tomb in Turpan, central Xinjiang [18–21]. The tomb group exhibits multiple cultural features from East and Central Asia and Europe. Notable among these are Kaiyuan Tongbao, silk painting, pseudo-Roman gold coins, Sasanian silver coins, etc. The retrieval of human samples from the Horgutu Cemetery and Badamu tomb group provides materials to explore the genetic history of central Xinjiang and answer whether the spread of painted pottery culture or the strengthening of control over Xinjiang led to population movements.

Results

Ancient genome data production

We initially constructed double-stranded DNA libraries for ancient individuals from the teeth or petrous portions of the temporal bone. We screened 16 ancient individuals from central Xinjiang by shallow shotgun sequencing. We obtained 8 individuals with sufficient preservation of DNA ranging from 3.68 to 70.21% (Additional file 2: Table S1). All samples showed the characteristic postmortem damage patterns of ancient DNA (Additional file 1: Fig. S1). The libraries showed a low level of modern human contamination, < 2% for mitochondrial estimates of all individuals and < 5% for nuclear estimates of all males (Table S1). None of the individuals shared close kinship (Additional file 1: Fig. S2). The pseudo-haploid genotype was called on the 1240 k and Human Origin (HO) panels [22]. As a result, the eight ancient individuals covered 85,074-941,368 SNPs in the 1240 k panel and 44,522–480,931 SNPs on the HO panel. We then merged the new data with two reference datasets for further analysis. We primarily grouped ancient individuals for group-based analyses based on their date, archaeological context, and genetic profile, as PCA and ADMIXTURE analyses revealed.



Fig. 1 The genetic landscape of Hejing and Badamu individuals in ancient and present-day Eurasian contexts. **a** Sampling location. **b** Principal Component Analysis (PCA) of present-day Eurasians on which ancient individuals were projected. The west–east gradient of Eurasians along PC1 and the East Asian north–south cline along PC2 were visible. **c** Histograms of ADMIXTURE analysis (K=5; Fig. S3) for a subset of temporally preceding groups maximizing key genetic components

Overall genetic structure of ancient individuals from central Xinjiang

The PCA was first performed to explore the overall genetic structure of ancient individuals from central Xinjiang with various Eurasians (Fig. 1b). We observed distinct separations between East and West Eurasians and northern and southern East Asians. Our ancient Hejing Horgutu individuals fell on the West-East Eurasian genetic cline and separated into two clusters. One cluster shifted towards West Eurasians, and the other clustered with ancient northern and western Mongolia Plateau populations. The Badamu individual clustered with northern East Asians, especially ancient individuals from the Yellow River region. The genetic structure of our studied ancient individuals was recapitulated in model-based unsupervised ADMIXTURE analysis (Fig. 1c). When we assumed that five distinct ancestries constituted the involved Eurasian populations, the Hejing samples showed a similar East-West admixed genetic profile with Xinj_IA8_aEA and China_Xinjiang_EIA_Shirenzigou_1D. The uniparental lineages of Hejing also showed the admixed ancestry from eastern and western Eurasia (Additional file 2: Table S1). The dominant mtDNA of Hejing individuals were East-Eurasian-specific haplogroups D4 and G2a, and they also hosted haplogroups commonly found in modern and ancient West Eurasian populations, U5. The paternal Y chromosome of Hejing individuals included Q1a prevailing in North Asia and the EMBA Steppe-specific haplogroup R1b. The Badamu individual presented a genetic profile similar to the ancients from the upper-to-middle reaches of the Yellow River Basin (represented by YR_LN, YR_LBIA, and Upper_YR_IA), which coincided with the Y chromosome O2a2 found in the individual. Accounting for archaeological dates and genetic differences, we regrouped the Hejing individuals into two subgroups (Xinj_Hejing_ EIA and Xinj_Hejing_IA) for the follow-up analyses.



Fig. 2 The genetic affinity between Hejing individuals and Badamu to ancient Yellow River and West Liao River groups. **a** f_4 (Mbuti, 95 Reference populations; Xinj_Hejing_EIA, Xinj_Hejing_IA) result showed the significant genetic heterogeneity between. Dots in dark red or dark blue indicated |Z| > 3, dots in light red or light blue indicated 2 < |Z| < 3, grey dots indicated 0 < |Z| < 2. **b** f_4 (Mbuti, Reference populations; Xinj_Badamu_HE, Yellow River and West Liao River groups. Dots in dark red or dark blue indicated 2 < |Z| < 3, grey dots indicated 2 < |Z| < 3, grey dots indicated 0 < |Z| < 2.

The temporal changes in the Hejing Horgutu Cemetery

To explore the genetic variation on the multi-century scaled Hejing Cemetery, we performed pairwise f_4 statistics in the form of f_4 (Mbuti, reference populations; Xinj_Hejing_EIA, Xinj_Hejing_IA) (Fig. 2a), where reference populations included 95 modern and ancient populations from Eurasians. We observed a significant genetic difference between Hejing subgroups. Xinj_Hejing_EIA shared more alleles with Western Eurasian Steppe pastoralists, Anatolia_N, and European populations who hosted ancestry related to Western Eurasian Steppe groups (Z < -2). While Xinj_Hejing_IA shared extra genetic affinity to ancient Northeast Asian (ANA) and ancient Yellow River groups compared with Xinj_Hejing_EIA (Z > 2).

We further quantified genetic affinities between Hejing samples and ancient Eurasians using f statistics. Outgroup- f_3 statistics in the form of f_3 (Xinj_Hejing_EIA/ Xinj_Hejing_IA, ancient Eurasians; Mbuti) showed that the Hejing Horgutu individuals shared the highest level of genetic drift with populations carrying elevated levels of Ancient North Eurasian (ANE) ancestry (Additional file 1: Fig. S4), such as the BA agropastoralists from the Tarim Basin (Tarim_EMBA), horse herders associated with the Botai culture from Kazakhstan. The genetic affinity was further confirmed with f_4 (Mbuti, Xinj_Hejing_EIA/Xinj_Hejing_IA; X, Y) (Additional file 1: Fig. S5). We observed significant f_4 values when X or Y was Tarim_EMBA or Botai (Additional file 2: Table S3). The outgroup f_3 statistics also showed the high allele sharing of Hejing samples with Western Steppe pastoralists or Xinjiang populations, such as Dzungarian_EBA and Xinj_BA3.

Hence, we used these ANE-related populations to model the Hejing individuals. To complement the ANE ancestry, we first included East Eurasians (Shamanka_EBA, Mongolia_N_North, DevilsCave_N, and Upper_YR_LN) and Western Steppe pastoralists or Central Asian Bactria–Margiana Archaeological Complex (BMAC) and Indus Periphery populations as possible ancestry sources (Additional file 2: Table S4a). Threeway admixture models worked in Hejing groups poorly (0.01 < p < 0.05), with a negative contribution from ANE-related populations. To explain the high genetic affinity to ANE, we used East Eurasian, Western Steppe



Fig. 3 Admixture proportion of central Xinjiang individuals estimated by *qpAdm*. Well-fitted modelling results for the Iron Age and historical central Xinjiang groups. Raw ancestry proportions, standard error estimates, and other feasible models for each group were provided in Tables S4, S6 and S7

pastoralists, and Central Asians as ancestral sources (Additional file 2: Table S4c). We found that only Xinj Hejing_EIA could be explained by the three-way models of East Eurasian+Western Steppe pastoralist+Central Aians when we added the ANE-related popultions into the outgroups. We interpreted this as reflecting the deep affinity to ANE rather than a direct contribution from ANE-related ancestry. To investigate the eastwest admixed profile of the Hejing groups, we used the three-way model based on the "base outgroup set" (Fig. 3 and Additional file 2: Table S4d). We observed that the Hejing groups derived their West Eurasian ancestry from the Middle and Late Bronze Age (MLBA) Western Steppe pastoralists (Andronovo and Sintashta, ~ 32–44%) and Central Asian-related populations (Turkmenistan_ Gonur_BA_2, ~ 34–58%). Both Ancient Northeast Asians (ANA)-related and Yellow River-related ancestry could explain the East Eurasian-related ancestry of Hejing groups. The East Eurasian-related ancestry ranged from 9 to 25% in different modellings. The DATES results suggested that the early west-east admixture event of the Hejing individuals occurred before 3000 BP (Additional file 2: Table S5). The temporal occurrence of admixture with Central Asian-related ancestry was slightly subsequent to that of the admixture with Western Stepperelated ancestry. A temporal gap existed between the admixture dates calculated for the two Hejing populations. However, this did not imply that only two admixture events occurred between 2300 and 3300 years ago. In general, actual admixture events may have been continuous, whereas the DATES software only estimates the average admixture time within the population.

Distal *qpAdm* modelling from pre-Iron Age sources indicated a dominant amount of West Eurasian and a minimum of East Eurasian-related ancestry in the Hejing individuals, whereas proximal modelling from post-Bronze Age sources in Hejing gave two types of alternative models representing two different periods. The alternative model indicated that Tianshan Sakas was sufficient to explain Xinj_Hejing_EIA (p=0.5192), while Xinj_Hejing_IA needed an additional ancestry from Upper_YR_IA (~11.2%) (Additional file 2: Table S4f). Furthermore, Xinj_Hejing_EIA could be modelled as the two-way admixture of Xinj_LBA1 and Tianshan_Sakas (p=0.0548) (Additional file 2: Table S4g). In conclusion, our Hejing Horgutu individuals could be equally modelled from Tianshan Sakas.

East Asian ancestry increased from the IA to the historical central Xinjiang

We also included two published individuals (XXKD_HE and XSQG_HE) [6] from the Bayinguoleng region, central Xinjiang, to explore the overall genetic structure of historical central Xinjiang. In PCA and ADMIXTURE results (Fig. 1), we found that the historical Badamu individual (Xinj_Badamu_HE) clustered with ancient groups of the Yellow River. The outgroup $-f_2$ statistics also showed the high genetic affinity of Xinj_Badamu_HE and ancient Yellow River and West Liao River populations, especially the middle reach of Yellow River groups represented by YR_LBIA and YR_LN (Additional file 1: Fig. S6). Moreover, the genetic homogeneity between Xinj Badamu HE and ancient populations of Yellow River and West Liao River was supported by non-significant f_4 (Mbuti, X; Xinj_Badamu_HE, Yellow River/West Liao River groups), negative f₄ (Mbuti, Xinj_Badamu_HE; X, Yellow River/ West Liao River groups), and pairwise-qpWave analysis (p > 0.05) (Fig. 2b, Additional file 1: Fig. S7 and Additional file 2: Table S6), except for Shimao_LN. To test the robustness of our one-way models using WLR_LN, WLR_BA, YR_LN, YR_LBIA, or Upper_YR_IA as a single source, we further added each of the reference populations identified in negative- f_4 (Mbuti, X; Xinj Badamu_HE, WLR_LN/WLR_BA/YR_LN/ YR_LBIA/ Upper_YR_IA) (Z < -2) to the outgroup list in *qpAdm* analysis (Additional file 2: Table S7). We found that all one-way models still fit well (p > 0.05). The genetic homogeneity between Xinj Badamu HE and ancient Yellow and West Liao River farmers was also further attested in a rotating qpAdm analysis (Additional file 2: Table S7). Hence, we inferred that Xinj_Badamu_HE was the nonadmixed descendants of the agricultural immigrants from northern China. Moreover, we found an increased East Asian genetic affinity in other historical central Xinjiang individuals. We first observed that XXKD_HE and XSQG_HE showed a higher affinity with ancient northern East Asians in outgroup- f_3 statistics (Additional file 1: Fig. S6), such as West Liao River populations, ancient groups in Mongolia Plateau, and ancient Xinjiang groups with higher affinity to East Asians. Compared to preceding central Xinjiang groups (i.e. Xinj_Hejing_IA), XXKD_HE and XSQG_HE shared more alleles with ancient East Asians than Xinj Hejing IA, as shown in the positive- f_4 (Mbuti, ancient East Asians; Xinj_Hejing_ IA, XXKD_HE/XSQG_HE) (Z > 2) (Additional file 1: Fig. S8). *QpAdm* results supported the increased East Asian affinity in historical central Xinjiang populations (Fig. 3 and Additional file 2: Table S8). Both XXKD_HE and XSQG_HE could be modelled as deriving most of their ancestry from groups related to the IA central Xinjiang populations (represented by Xinj_Hejing_EIA or Xinj_ Hejing IA, \sim 76–85%), and the remaining ancestry from ancient groups of Yellow River (represented by YR_LBIA and Upper YR IA, ~15-24%). In addition, the alternative two-way models of early Xiongnu_west or Tianshan_Sakas with YR_LBIA or Upper_YR_IA worked to historical central Xinjiang populations (p > 0.01).

Discussion

Archaeological findings from Xinjiang have suggested that the post-BA Xinjiang was a mixed confederation of West and East Eurasians [2]. Previous studies revealed the high mobility and admixture of the post-BA Xinjiang populations [4, 6, 23, 24]. The gene pool of the post-BA Xinjiang was shaped by various ancestries, including the local ancestry represented by Tarim EMBA1, as well as those related to Western Steppe pastoralists, Central Asians, ANA, and East Asians [6, 16]. However, the detailed genetic history of regional Xinjiang remains unknown, especially in the central Xinjiang area. In this study, we presented genome-wide data of 8 individuals dated to the IA and the historical period from central Xinjiang. Our data showed a west-east admixture pattern characterized by the genetic profile of the IA central Xinjiang individuals. They derived their West Eurasian ancestry from MLBA Western Steppe pastoralists (~32-44%) and Central Asian Indus Periphery (~34-58%), and the East Eurasian ancestry from ANA or Yellow River populations (~10-25%). Therefore, the results suggested that the incoming ancestry from the Western Steppe, Central Asia, and East Eurasia continue to shape the genetic makeup of the IA central Xinjiang populations. Additionally, by analyzing the historical central Xinjiang individuals, we found a degree of genetic continuity in the mixed ancestry of IA central Xinjiang. The historical central Xinjiang individuals could be modelled as having a majority of their ancestry from Xinj_Hejing_EIA or Xinj_Hejing_IA (~76-85%) and the rest from Yellow River groups (Upper_YR_IA or YR LBIA, ~15–24%).

The Iron Age witnessed the emergence of Eurasian Steppe pastoralists, i.e., Scythians in the Western and Central Steppe and Xiongnu in the Eastern Steppe [25]. The Central Steppe served as a centre for the population expansion of multiple nomadic regimes. These events involved neighbouring Xinjiang and significantly influenced the population history of Xinjiang [26]. The archaeological findings, i.e., Subeixi culture from central Xinjiang and Zhagunluke culture from southern Xinjiang, showed close cultural connections with the Scythians [2, 27, 28]. In the study, our data showed that the IA and historical Xinjiang populations were equally modelled from Tianshan Sakas. We found that the Hejing individuals could be modelled as having~89-100% ancestry related to Tianshan Sakas (represented by Kyrgyzstan TianShanSaka) and ~11% ancestry related to the ancient group of Yellow River (Upper_YR_IA). Hence, the West Eurasian-related ancestry of the IA Hejing populations might be traced back to the genetic introduction of the Sakas, who possessed predominant ancestry from Western Steppe and Central Asian BMAC or Indus Periphery-related populations [7, 8]. Meanwhile, for the historical central Xinjiang individuals, the fitted models with the combination of Tianshan Sakas and ancient Yellow River groups were also acceptable (p > 0.01). Our results suggested that the southward movement of the Scythians influenced the gene pool of central Xinjiang populations. In addition, Xiongnu-related ancestry was also detected in the historical central Xinjiang individuals. The alternative models of earlyXiongnu_west and YR_LBIA or Upper_YR_IA provided fitted models for XXKD_HE and XSQG_HE. Hence, the surrogates of the IA Steppe ancestry coincided with the expansion of the Xiongnu into Xinjiang and the formation of the Hun-Scythians in the fourth to fifth century CE [7].

Cultural diffusion, economic exchanges and political policies can promote population migration. According to the archaeological findings of the Xinjiang region, the westward spread of the painted pottery of the Gan-Qing region impacted most areas of Xinjiang since IA [2, 3, 12, 29], and this cultural diffusion was also shown in the Hejing Cemetery [17]. As the IA central Xinjiang individuals possessed ancestry related to ancient farmers of the upper Yellow River, our results supported the co-diffusion model of expanding the painted pottery culture and populations of the Gan-Qing region to central Xinjiang. Furthermore, the management of Xinjiang and the Silk Road facilitated economic and demographic exchanges between the Central Plains and Xinjiang [11]. Archaeological and craniofacial studies have also attested to the close connection between the Central Plains and Xinjiang [30, 31]. For example, migrants from the Central Plains were observed in the Badamu tomb group [32]. In addition, the paleogenetic study at the Shichengzi site of Changji region of eastern Xinjiang has revealed the presence of immigrants from northern China in Xinjiang during the Han Dynasty [33]. Our results reaffirmed the migration from the Central Plains to Xinjiang. Furthermore, we observed the temporal changes of the ancestry related to Yellow River farmers in central Xinjiang. The later IA Hejing individuals had an elevated level of ancestry related to the Yellow River population compared to the early IA Hejing individuals. In comparison, the proportion of Yellow River farmers-related ancestry was higher in the historical central Xinjiang individuals than in the later IA Hejing individuals. We also identified the descendants of the farming migrants from the Yellow River or West Liao River in historical central Xinjiang. Our results suggested that an increasing genetic influence of northern China probably reflected the deepened connection between the Central Plains and Xinjiang. The centralized state in the Central Plains has adopted a series of strategies to deepen its control over Xinjiang since the Han Dynasty [14]. The political control included agricultural garrisons (tun tian) and the establishment of the Western Regions Frontier Command after the first century BC. The dynasties in the Central Plains after the Han Dynasty expanded the administration of Xinjiang by setting up the Anxi and Beiting Frontier Commands, Yizhou, Xizhou, and Tingzhou counties [13–15]. The strengthened control led to the migration and settlement of ancient Han from the Central Plains in Xinjiang. In conclusion, we found an increase in Yellow River-related ancestry over time in central Xinjiang. Our results supported that strengthened administration in Xinjiang promoted the genetic influence of the Central Plains on central Xinjiang.

Conclusions

Our study reported the ancient genomes from 8 individuals dated to the Iron Age and the historical period from central Xinjiang to supplement the detailed genetic history of regional Xinjiang. We observed an east-west admixed ancestry profile with Western Steppe, Central Asian, and East Asian-related in IA Hejing. Meanwhile, the proximal admixture models with Xiongnu or Saka of IA and historical populations of central Xinjiang suggested that the expansion of the Xiongnu into Xinjiang and the formation of the Hun-Scythians could explain the source of West Eurasian-related ancestry. More importantly, our results identified the increasing Yellow River farmers-related ancestry in central Xinjiang from IA to historical period. This suggested that the spread of the farming culture of northern China with the population expansion and the deepening of Central Plains' control of Xinjiang has influenced the genetic history of central Xinjiang. However, we acknowledged certain limitations, including the insufficient sample size and inclusion of archaeological sites from central Xinjiang, which only gave us a glance at the temporal change of genetic history in a small area of Xinjiang. Future studies of longspanned ancient genomes across Xinjiang and the surrounding Gan-Qing region are necessary.

Methods

Archaeological information

Hejing Horgutu Hydropower Station Cemetery

Hejing Huoergu Hydropower Station Cemetery is located on the north bank of the Kaidu River, adjacent to Hejing County, Bayinguoleng region, central Xinjiang [17]. Systematic excavation was performed in 2021. The excavations contained 31 tombs, over 60 pieces of artefacts (including pottery, bronze and iron wares, and bone artefacts), faunal remains (including sheep and horses), and a residential structure remains. The stirrups were closely related to the Scythian culture. The tomb types consisted of stone chamber tombs with stone fences, larger-scaled cairn tombs, and

small-scaled cairn tombs; these tombs were radiocarbon dated by Lanzhou University. According to the results of radiocarbon date in the Carbon 14 Laboratory, Lanzhou University, stone chamber tombs with stone fences dated to the Late Bronze Age to the Early Iron Age (~2800 BP), the stone chamber tombs dated to the Early Iron Age (~2300-2500 BP), the lager-scaled and small-scaled cairn tombs dated to the Late Iron Age ($\sim 1900-2100$ BP) [17]. The earliest tombs are characterized by a flexed supine or flexed on-side position of a single person and fewer burial objects with copper knives or sheep vertebrae. The stone chamber tombs are characterized by individuals positioned in a supine posture with limbs and by secondary burials or multiple burials. The larger-scaled and small-scaled cairn tombs are characterized by extended supine positions, and the head of these tomb owners faces east; the main funerary objects are ironic objects and goat remains. The stone chamber tombs and potteries excavated from larger-scaled cairn tombs were regarded to correlate to the Chawuhu culture in Central Xinjiang.

Badamu tomb group

Badamu village is located in Turpan city, central Xinjiang. A vast number of tombs in Badamu village have been excavated since 2004. Subsequently, several salvage excavations and clean-ups were performed in 2005, 2007, 2008, 2021, and 2022, respectively [18-21]. The recovered tombs group dates back to the Spring and Autumn Period and the time from the late Qu Clan Gaochang Kingdom to the Tang Dynasty's Xizhou District, with the latter as its main body. Badamu was regarded as a multi-population settlement during the Gaochang Kingdom Period to the Tang Dynasty. The excavated tombs contained family burial tombs of Hushang ("胡商") and the ancient Central Plains Han. The skeletons used for ancient DNA analysis in this study came from the excavation conducted in 2021. The tombs of these individuals belonged to vertical cave tombs with partial chambers (M1) and earthen cave tombs with ramp passageways (M2-M8); most tombs belong to multiple burials with extended supine position, except for M8, buried one single person. The unearthed funerary objects include pottery, bronze mirrors and hairpins, coins with the legend "Gaochang Jili" and "Kaiyuan Tongbao", and sheep remains. In addition, an epitaph is found in M3, reading "fourth Yihe year" (around 617 AD). Based on the information, these tombs could be dated from the late Sui Dynasty to the Tang Dynasty.

Radiocarbon dating

We collected 1–4 g of bone per sample for radiocarbon dating. Of these individuals reported in this study, M2B from the Badamu site and M2 and M8 from Hejing Cemetery were directly dated using accelerator mass spectrometry (AMS) at Beta Analytic Testing Laboratory in Guangzhou, China. The resulting ¹⁴C dates were calibrated using OxCal v4.4 [34] and IntCal20 [35] calibration curves. The three individuals dated from the Iron Age to the Historical Period (2300–1309 cal. BP), consistent with spanning time estimated from archaeological stratigraphic layers and excavated grave goods.

Ancient DNA sequencing and pre-processing Ancient DNA extraction and sequencing

Ancient DNA was extracted from both teeth and bone samples from these remains following established protocols [36] at the ancient DNA clean room facilities of the Institute of Anthropology, Xiamen University. Double-stranded libraries were prepared using the NEBNext Ultra II DNA Library Prep Kit. In short, we collected 80-200 mg of bone powder, and the powder was incubated for 16 to 18 h (37 °C) in extraction buffer containing 0.5 M EDTA and 0.25 mg/mL proteinase K. DNA was purified and concentrated using a Qiagen MinElute/ Zymo reservoir apparatus. Subsequently, DNA extracts were constructed into double-stranded Illumina libraries using a blunt-end protocol with NEBNext DNA Library Prep Master kit, and libraries were double-indexed using PCR amplification with 15 cycles of amplifications, followed by AMPure XP Beads to purify DNA libraries. All libraries were sequenced using the DNBSEQ-T7 platform to produce pair-ends $(2 \times 150 \text{ bp})$.

Ancient DNA sequence data processing

We first performed AdapterRemoval v2.3.3 [37] to trim adapters, filter low-quality reads, and merge the pair-end sequence reads. The merged reads were mapped to the human reference genome (hs37d5) using BWA v0.7.17 [38] aln/samse alignment algorithm with the parameters "aln -l 1024 -n 0.01". PCR duplicates were removed by Dedup v0.12.8 software [39]. Based on the patterns of DNA misincorporation, we removed five bases from both ends of each read to reduce the number of wrong calls due to excess C->T and G->A transitions at the ends of the sequences using trimBam module of bamUtil v1.0.15 (https://github.com/statgen/bamUtil). Then, we generated pileup data using the samtools mpileup module, using bases with Phred-scale quality score>30 ("-Q30") on reads with Phred-scale mapping quality score > 30 ("-q30") from the BAM files. Finally, the pseudo-haploid genotypes were called by pileupCaller (https://github.com/stschiff/ sequenceTools) with "-randomHaploid" mode.

Data quality authentication

To estimate the amount of C to T deamination at the ends of the mapped fragments, we used mapDamage v2.0 [40] run on a subset of 200,000 reads using default

parameters. Exogenous human nuclear DNA contamination was estimated in males with enough coverage (>100 SNPs on the X chromosome) by assessing the X chromosome heterozygosity levels with ANGSD v0.910 [41], and mitochondrial DNA contamination of all libraries was calculated via the Schmutzi program [42]. No individuals were estimated to have >5% nuclear or mitochondrial DNA contamination. We included all individuals in downstream population genetic analyses.

Sex determination, uniparental haplotype assignment, and estimation of genetic relatedness

We used Rx and Ry methods to determine the biological sex of all ancient individuals [43, 44]. We called the mitochondrial consensus sequence from the Schmutzi output using the log2fasta script built in the Schmutzi package with parameter "-q 10". We then assigned the consensus sequence into haplogroup using the HaploGrep2 [45]. Y chromosome haplogroup for males was determined using all reads mapping to the Y chromosome with a minimum mapping quality and base calling quality of 30 (-q 30, -Q 30). The final Y haplogroup was identified by Yleaf software [46]. Haplogroup assignments are shown in Table S1. We used Relationship Estimation from Ancient DNA (READ) [47] and TKGWV2 [48] to evaluate the relatedness. We included high-quality samples (SNPs > 50,000) in the kinship testing. We used the pseudo-haploid genotype data calling from the 1240 K panel and excluded low-frequency variants (by plink maf 0.01); a total of 384,478 SNPs were included to perform READ analysis. In the tkwv2 analysis, we started from trimmed BAM files that removed deaminationbased misincorporations, ran the "bam2plink" model by default parameters, and ran the "plink2tkrelated" model.

Data compilation

We merged our data with previously published modern genotyped data and available ancient genomic data across the Eurasian continent [35], obtaining two datasets, namely the 1240 k dataset consisting of 1,233,011 overall SNPs and the HO dataset including 597,569 overall SNPs, separately.

Genetic population analysis

Population structure analyses

We applied the smartpca v16000 function implemented in the EIGENSOFT package (Patterson et al., 2006) to perform principal components analysis (PCA) on the HO dataset; the "lsqproject" option was used to project ancient individuals onto the pre-calculated components by modern individuals. We then applied ADMIXTURE v.1.3.0 [49] to conduct unsupervised cluster analyses testing K=2 to K=12 on a set of ancient and modern Eurasian populations based on the HO dataset. We pruned 300,346 variants in linkage disequilibrium using PLINK v.1.90 [50] with the option "–indep-pairwise 200 25 0.4" to prepare the final marker set for ADMIXTURE analysis. For ADMIXTURE analysis, we randomly sampled 15 individuals from a reference population with more than 15 individuals to reduce the computational burden. We ran ten replicates with random seeds for each K, and the lowest CV error was plotted.

 f_3 and f_4 -statistics All the f-statistics were performed using the ADMIXTOOLS package [51] on the 1240 k dataset. We run outgroup f_3 -statistics in the forms f_3 (Test, X; Mbuti) for the Badamu, Hejing, and other historical Central Xjing groups as Test. The f_4 -statistics in the form of f_4 (Mbuti, X; Y, Z) with Mbuti as an outgroup and parameter "f4mode: YES" were run, significantly positive f_4 -statistics indicate that X shares more alleles with Z than Y, while significantly negative f_4 -statistics indicate that X shares more alleles with Y than Z (*Z*-score > 3, *Z*-score < -3, respectively). For f_3 -statistics, we considered only the results with the number of overlapped SNPs > 50,000.

qpWave analysis

QpWave built in the ADMIXTOOLS package [51] was used to test whether the Badamu individual and ancient Yellow River's populations were genetically homogenous to a set of outgroups using the parameter "allsnps: YES". We used the outgroup set to investigate the genetic affinity, including Mbuti, Yana_UP, Kostenki14, Italy_North_Villabruna_HG, Iran_GanjDareh_N, Anatolia_N, AR19K, Liangdao2, Shanong_EN, AR_EN, Mongolia_N_North, Taiwan_Hanben.

qpAdm modelling

To estimate the admixture proportions for Hejing and published central Xinjiang populations, we used *qpAdm* [51] with the option "allsnps: YES" and modelled in two strategies following: (i) the combination method where we separated our potential sources into three groups and modelled our target as the combination of one to three ancestral populations from different groups; (ii) the competition approach that is using a set of base outgroups and putting Tarim_EMBA1, Tarim_EMBA2, Botai_EN in the outgroup set, to identify the contribution of ANE. Base outgroups including: Mbuti, Yana_UP, Kostenki14, Italy_ North_Villabruna_HG, Iran_GanjDareh_N, Anatolia_N, AR19K, Liangdao2, Shanong_EN. As qpWave is integrated into qpAdm, the nested p values in the log files indicate the optimal rank of the model. This means that if the *p*-value for the nested model is above 0.05, the model will be discarded. The *qpAdm* analyses of Xinj Badamu HE were performed by the other outgroup list, similar to the qpWave analysis. To provide robust models, we conducted a rotating *qpAdm* analysis and added each of the reference populations identified in the negative- f_4 (Mbuti, X; Xinj_Badamu_HE, WLR_LN/WLR_BA/YR_LN/ YR_LBIA/Upper_YR_IA) (Z < - 2) to the outgroup list.

Time of admixture

We used the DATES (Distribution of Ancestry Tracts of Evolutionary Signals) [52] method on the 1240 k dataset to estimate the admixture time of Hejing groups. For this analysis, the option "binsize: 0.001, maxdis: 1, runmode: 1, mincout:1, qbin: 10 and lovalfit: 0.45" was used in the parameter file for running DATES. To convert the DATES output to years BP, we took the mean value of admixture dates (in generation), multiplied this by a generation average time of 29 years, and added it to the range of the dates of the samples. The dates of the samples were inferred based on the archaeological information and radiocarbon date of the tombs.

Abbreviations

mtDNA	Mitochondrial DNA
SNPs	Single nucleotide polymorphisms
HO	Human Origin
PCA	Principal components analysis
Xinj	Xinjiang
Gan-Qing	Gansu and Qinghai region
YR	Yellow River
WLR	West Liao River
aEA	East Asia-affinity
LN	Late Neolithic Age
BA	Bronze Age
EBA	Early Bronze Age
EMBA	Early and Middle Bronze Age
LBA	Late Bronze Age
IA	Iron Age
EIA	Early Iron Age
LBIA	Late Bronze Age and Iron Age
HE	Historical Era
BMAC	Bactria–Margiana Archaeological Complex
MLBA	Middle and Late Bronze Age
XXKD	Xikakandasayi
XSQG	Xianshuiquangucheng
ANA	Ancient North Asians
ANE	Ancient North Eurasian

Supplementary Information

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Supplementary Material 1.
Supplementary Material 2.
Supplementary Material 3.
Supplementary Material 4.
Supplementary Material 5.
Supplementary Material 6.
Supplementary Material 7.
Supplementary Material 8.
Supplementary Material 9.
Supplementary Material 10.
Supplementary Material 11.

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Authors' contributions

Haijun Li and Chuan-Chao Wang designed the study. Haijun Li and Xiaoyu Yang conducted field surveys and sample collection. Baitong Wang, Xiaomin Yang, and Haifeng He completed the experiments. Xiaomin Yang and Rui Wang analyzed the data and designed the figures. Xiaomin Yang and Chuan-Chao Wang wrote the manuscript in consultation with all authors. All authors discussed the results and commented on the manuscript.

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Data availability

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 HRA009813, following the regulations of the Human Genetic Resources Administration of China (HGRAC).

Declarations

Ethics approval and consent to participate

The procedures related to human subjects were approved by the Medical Ethical Committee of Xiamen University (XDYX202412K88).

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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