

Ancient DNA unveils population dynamics and integration in Pingcheng, the first Northern Wei capital established by the Tuoba Xianbei



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ABSTRACT

Pingcheng, the first capital of the Northern Wei dynasty, was also the first city in Chinese history established by a nomadic regime following Han Chinese cultural norms. To investigate the genetic history of its inhabitants, this study analyzed complete mitochondrial genomes from 145 ancient individuals excavated from three major cemeteries in Pingcheng. The results reveal a complex and diverse maternal genetic structure, dominated by high-frequency haplogroups characteristic of northern steppe populations, admixed with lineages from the Yellow River Basin, southern China, Xinjiang, and western Eurasia. The maternal gene pool underwent a recent and rapid expansion, accompanied by continuous gene flow from exogenous sources. Individuals from Pingcheng exhibit substantial genetic similarity and homogeneity with the Tuoba Xianbei, underscoring their foundational role in shaping the city's maternal genetic landscape. Additional maternal inputs from Yellow River populations—and more limited but direct connections with southern China, Xinjiang, and beyond—reflect a typical pattern of multi-ethnic integration. Notably, within-group analyses reveal a paradoxical pattern: distinct haplogroup-level structuring coexists with minimal sequence-level divergence. This suggests a temporal lag between admixture events and the emergence of statistically significant genetic differentiation, pointing to an ongoing process of multi-source integration and dynamic genetic reorganization. Moreover, the integration process varied across cemetery groups in direction, tempo, and intensity, shaped by interwoven factors including Tuoba traditions of incorporation, social hierarchy, cultural identity, and political governance. These findings highlight a dynamic model of population formation characterized by unity within diversity and harmony amidst differences. Together, these findings provide novel genetic insights into population dynamics in Pingcheng and offer a representative snapshot of the broader processes of ethnic amalgamation during early medieval China.

1. Introduction

The Northern Wei was the first dynasty in Chinese history established by a nomadic people, the Tuoba Xianbei, who entered and ruled the Central Plains. This dynasty made remarkable contributions in various domains such as politics, economy, and culture, laying a profound foundation for the prosperity of the subsequent Sui and Tang dynasties. Furthermore, it served as an inspiration for later dynasties established by minority groups, such as the Liao, Jin, Yuan, and Qing, thus holding a groundbreaking position in Chinese dynastic history (Li,

2014; Du, 2017). Pingcheng (present-day Datong 大同), located in present-day Datong, Shanxi Province, was the first capital city established by the Tuoba Xianbei following their conquest of the Central Plains. Developed under six successive emperors from Daowu (道武帝) to Xiaowen (孝文帝), the city featured a palace precinct of approximately 2 km², a 10-km outer wall, and a larger defensive perimeter extending to 16 km, forming a tripartite configuration of palace, city, and outer enclosure. Archaeological and textual sources attest to its substantial scale, sophisticated planning, and high population density.

The period during which Pingcheng served as the capital of the

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Northern Wei (398–494 CE) represents a crucial phase in the early development of the dynasty. Historians commonly refer to this era as the Pingcheng Period of the Northern Wei. Over the course of nearly a century, the Northern Wei Dynasty profoundly influenced the trajectory of Chinese history in multiple ways. Militarily, it brought an end to the prolonged turmoil and fragmentation in northern China following the Eastern Jin, achieving partial unification. Culturally, the Northern Wei Dynasty implemented large-scale Sinicization reforms, actively promoting the sinicization of the Xianbei and other nomadic peoples, while instituting significant policies to facilitate the exchange and transformation between nomadic and agrarian civilizations. Economically, it encouraged the growth of handicrafts, agriculture, and commerce, fostering substantial social and economic prosperity. Furthermore, the reopening of the Silk Road reestablished crucial channels of interaction between China and the West. Politically, the Northern Wei implemented inclusive and open policies toward ethnic groups, promoting large-scale population migrations to Pingcheng, thereby fostering interactions and integration between various ethnic groups (Wei, 1974).

Pingcheng served not only as the political center of the Northern Wei dynasty but also as the first capital in Chinese history constructed by a nomadic population drawing upon Han cultural and institutional models. Its urban layout and ceremonial architecture incorporated Han-style planning principles while integrating ritual elements specific to the Xianbei, such as the suburban heaven-sacrifice. Structures including the Jiaotiantan (Suburban Altar of Heaven 郊天坛) and Mingtang (Bright Hall 明堂) reflected this cultural synthesis between Han and Xianbei traditions. Although initiated by the Tuoba Xianbei, historical records indicate that more than one million individuals from diverse regions migrated to Pingcheng during this period. As a result, the city became the most densely populated urban center in northern China and a hub of demographic and cultural diversity (Su, 1996).

Archaeological research has further substantiated the pluralistic and integrative social landscape of the era in question. Most Northern Wei tombs unearthed in Datong date to the brief Pingcheng period, exhibiting a variety of burial forms. The cultural elements of these burials are marked by a complex, diverse, and integrative character (Shanxi Institute of Archaeology Datong Museum, 1992; Yin, 2004; Liu et al., 2006; Zhang et al., 2006). Funerary architecture and associated material culture suggest cultural heterogeneity, with burial practices indicative of differences in ethnic affiliation, social hierarchy, and economic status (Zhao, 2002; Ma and Li, 2010; Wei and Cui, 2020). Physical anthropological studies reveal the intricate physical characteristics of the Pingcheng population. Not only are there discernible differences in craniofacial morphology among different cemeteries, but variations also exist among individuals within the same cemetery. Although there are certain individuals exhibiting strong Europoid traits, the area's predominant racial composition remains closely aligned with the East Asian type within the Asian Mongoloid race, albeit with possible influences from other ethnic groups such as the Xianbei (Zhang and Ning, 1995; Han, 2005; Fan, 2020; Cui, 2021; P. Li, 2021; Ruan, 2022). Additionally, stable carbon and nitrogen isotope analysis indicates variations in the dietary structures of the Pingcheng population. One group exhibits low $\delta^{13}\text{C}$ values coupled with extremely high $\delta^{15}\text{N}$ values, while another shows very high $\delta^{13}\text{C}$ values, reflecting the presence of populations engaged in two distinct subsistence strategies: nomadic/hunting and agricultural economies (Zhang et al., 2015; Hou et al., 2017; Hou and Gu, 2018b; Zhou et al., 2022; Liu et al., 2022; Hou et al., 2023).

Current bioarchaeological research focuses primarily on physical anthropology and stable carbon and nitrogen isotope analysis. However, ancient DNA studies remain absent. Questions such as the genetic structure of the Pingcheng population, their origins, and their kinship with surrounding ancient populations, as well as whether genetic exchange occurred between different populations during the Pingcheng era and potential genetic changes of the Tuoba Xianbei after they entry into Pingcheng, remain at the forefront of academic inquiry. Mitochondrial DNA (mtDNA), due to its high copy number, strong resistance

to degradation, and strict matrilineal inheritance pattern (Lippold et al., 2014; Prüfer et al., 2014; Petr et al., 2020), serves as an ideal genetic marker for addressing these questions. Given that previous palaeogenomic studies of Xianbei populations have also mainly focused on the mitochondrial level, this research adopts the same approach to ensure effective comparison, analysis, and discussion.

We sampled 145 specimens from three distinct large burial cemeteries in Datong City, Shanxi Province. This represents the first large-scale matrilineal genetic study of ancient urban inhabitants in China and fills the gap in ancient DNA research for the Pingcheng area. This study provides a new matrilineal genetic perspective for exploring socio-cultural evolution, population migration, and ethnic integration in early medieval capitals.

2. Materials and methods

2.1. Archaeological site and sample collection

Samples were collected from the Huayu, Yuechengjinmaofu, and Yongtaiwanlu cemeteries in Datong, Shanxi Province, each situated at distinct locations within the city (Fig. 1). The grave goods display typical characteristics of the Northern Wei Pingcheng period. Detailed archaeological information on the three cemeteries is available in the Supplementary Materials. A total of 145 samples were collected: 35 from Huayu, 26 from Yuechengjinmaofu, and 84 from Yongtaiwanlu. The majority of the samples consisted of well-preserved, intact, and healthy teeth, with additional specimens including temporal bones and a small number of humeri, tibiae, and femora (Supplementary Table S1).

2.2. Extraction, library preparation, and sequencing of ancient DNA

For the ancient samples, the first step involved removing external contamination. This was achieved by using sterile cotton and disposable tweezers to clean any visible debris from the surface of the samples, followed by immersion in a 5 % sodium hypochlorite solution for 10 min. Next, the samples were placed in DEPC-treated water and repeatedly agitated using disposable tweezers (which were replaced frequently) for approximately 5 min. Afterward, the samples were transferred to 70 % ethanol and left for 5 min. Following the cleaning process, each side of the samples was uniformly exposed to UV light until they were completely dried. Finally, 50 mg of powdered material was carefully drilled from the samples using an appropriately sized dental drill.

The extraction of ancient DNA was performed according to the method described by Ning et al. (2019). In this process, the bone powder was combined with a prepared solution containing 0.5M EDTA, 0.25 mg/ml proteinase K, and 0.05 % Tween-20, and incubated at 37 °C for 24 h in a molecular hybridization oven to digest the bone powder. The resulting supernatant was collected and mixed with a binding buffer containing 5M guanidine hydrochloride, 40 % isopropanol, 0.05 % Tween-20, and 90 mM sodium acetate. The mixture was then transferred to a MinElute silica spin column (QIAGEN, Germany), washed twice with PE buffer (80 % ethanol), and the ancient DNA was eluted using 50 μl of TET buffer (1M Tris-HCl, pH 8.0, 0.5M EDTA, and 10 % Tween-20).

A double-stranded library (150 bp paired-end) was constructed following the protocol outlined by Dabney et al. (2013), with partial treatment using UDG-half (Rohland et al., 2015), to minimize sequencing biases due to uracil damage in ancient DNA. The library underwent subsequent shotgun sequencing on the Illumina HiSeq X Ten sequencing platform (Novogene, China).

2.3. Data processing and evaluation

First, ancient DNA sequencing data were processed using the EAGER pipeline v1.92.37 (Peltzer et al., 2016). Quality assessment was performed with FastQC (Andrews, 2010), followed by adapter removal

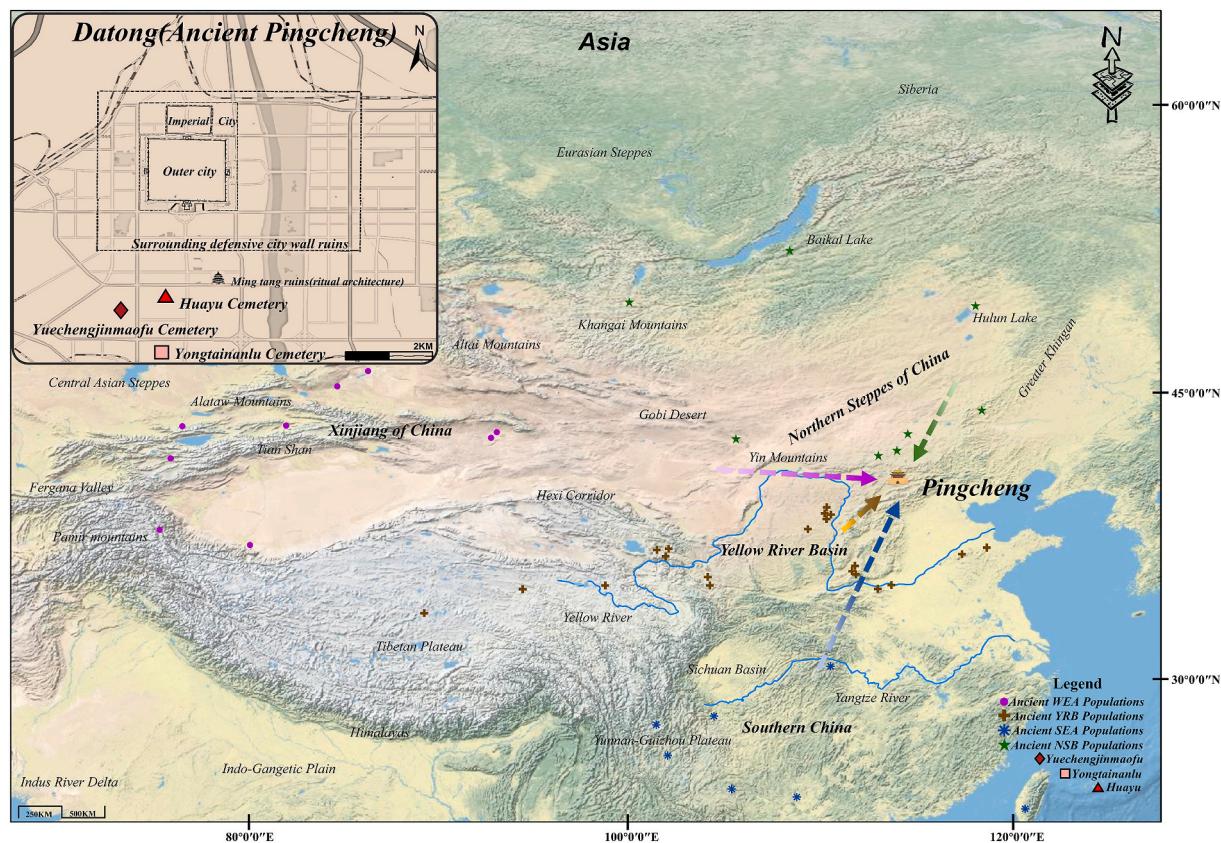


Fig. 1. Geographic distribution of sampling locations.

using AdapterRemoval v2.2.0 (Schubert et al., 2016), and merging of paired-end data. Next, the sequences were aligned to the human reference genome (hs37d5) using BWA v0.7.17-r1188. PCR duplicates were then removed using DeDup v0.12.8 (Peltzer et al., 2016). MapDamage v2.2 (Jónsson et al., 2013) was employed to assess the misincorporation patterns in ancient DNA. Finally, to reduce bias caused by deamination at the 3' and 5' ends of the ancient DNA, 20 base pairs were trimmed from both ends using BamUtils, a tool in the BamTools suite.

All ancient DNA work was conducted in a clean laboratory specifically designed for ancient DNA research at the School of Archaeology, Jilin University, where strict contamination prevention protocols were followed for each experimental step. We used MapDamage v2.2 to analyze the damage patterns in the DNA data from the ancient samples, which all conformed to the typical damage characteristics of ancient DNA (Supplementary Table S1). To further assess contamination levels, we employed ContamMix v1.0 software (Fu et al., 2013), finding that the contamination rates across all libraries were extremely low (0–3.2 %), with the exception of one library (DYT 70), which had a contamination rate of 4.6 %, this library was excluded from subsequent analyses (Supplementary Table S1). Sequencing quality and mitochondrial coverage were calculated using Qualimap v2.2.1 (Okonechnikov et al., 2016), and data with a coverage greater than 1X were used for downstream analyses.

2.4. The sequencing results and sample grouping

After rigorous quality control, 30 samples with an average mitochondrial coverage of less than 1X were excluded, along with 4 individuals identified as close relatives and 1 individual with a contamination rate greater than 4 %. As a result, a total of 110 high-quality, complete mitochondrial genome datasets were obtained (Supplementary Table S1). To facilitate subsequent analysis and discussion, we designated all 110 newly acquired samples as PC_ALL, with

29 samples from the Huayu Cemetery labeled as PC_HY, 25 from the Yuechengjinmaofu Cemetery as PC_JMF, and 56 from the Yongtaihanlu Cemetery as PC_YTLN.

We also collected mitochondrial genome data from 1121 previously published ancient individuals across China and its surrounding regions (Supplementary Table S2). The ancient data were categorized into four major groups based on geographic regions: NSB, YRB, SEA, and WEA. WEA refers to Xinjiang, China, and regions further west, SEA encompasses Southern China (this study adopts the Qinling–Huaihe Line as the geographic boundary between northern and southern China) and areas further south, NSB includes the Northern Steppes of China and regions beyond, and YRB corresponds to the Yellow River Basin (Fig. 1).

2.5. Analysis of mitochondrial whole genome data

To comprehensively and deeply elucidate the genetic structure and genetic history of the Pingcheng population, this study conducts a systematic analysis at two levels: mitochondrial haplogroup frequency and whole mitochondrial genome sequence.

2.5.1. Analysis based on haplogroup frequency

Utilizing PhyloTree build 17 (Oven, 2015), we employed Haplogrep 2 (Weissensteiner et al., 2016) to determine the mitochondrial haplogroups of Pingcheng samples and used Haplogrep 3 (Schönherr et al., 2023) to calculate the frequencies of each haplogroup. Based on this, combined with haplogroup frequency data from other ancient populations, we performed a Principal Component Analysis (PCA) based on haplogroup frequencies using the “factoextra” and “FactoMineR” packages in R v4.4.1 (R Core Team, 2022), visualizing the results with the “ggplot2” package (Wickham, 2016).

2.5.2. Analysis based on whole mitochondrial genome sequence

We utilized DnaSP v6.12.03 (Rozas et al., 2017) to perform a series of

analyses and tests on the Pingcheng samples, including nucleotide diversity (π), haplotype diversity (Hd), Tajima's D, Fu's Fs, Fu and Li's D*/F*, and Achaz Y*. Subsequently, genetic distances (FST) between populations were calculated using the pairwise difference method in Arlequin v3.5.2.2 (Excoffier and Lischer, 2010), with a heatmap of FST values visualized using the pheatmap package in R. Molecular variance analysis (AMOVA) was also conducted using Arlequin software to further evaluate the intergroup molecular genetic variance among different Pingcheng burial sites. Both FST and AMOVA analyses were based on 10,000 permutation tests to obtain robust P-values.

Additionally, to capture subtle differences in population structure more effectively, we conducted a Discriminant Analysis of Principal Components (DAPC) based on the entire mitochondrial sequence using the "adegenet" package in R and visualized the results. DAPC, which does not rely on population genetics model assumptions (such as H-W equilibrium or mutation-drift balance), is particularly suited for structural analysis of non-recombining, maternally inherited data like mitochondrial DNA (Jombart et al., 2010). Compared to PCA, DAPC maximizes intergroup differences while minimizing intragroup differences, enhancing cluster recognition power. Especially when sample sizes are uneven or lineages are complex, its clustering results are more robust, providing important insights for identifying potential genetic structures.

Finally, we constructed Median-joining network and plotted network graphs using Arlequin, DnaSP, and PopART v1.7 (Leigh and Bryant, 2015) to further trace the sharing and differentiation of maternal lineages.

3. Result

3.1. The genetic complexity of the Pingcheng population

From the PC_ALL, we identified a total of 13 major haplogroups (A, B, C, D, F, G, H, M, N, R, U, Y, Z), which can be further subdivided into 81 distinct subhaplogroups. Among these subhaplogroups, several subtypes are relatively rare in ancient Chinese populations and may even be reported for the first time (e.g., Y1b1, U5b2a3, N11a1). This phylogenetic complexity, coupled with high Haplotype diversity (Hd = 0.877), suggests that the PC_ALL population harbored a complex maternal origin (Supplementary Tables S1 and S3).

Previous studies have shown that haplogroups A, C, D, and G are commonly found in high frequencies among present-day populations in

northern East Asia and North Asia (Kong et al., 2003; Tanaka et al., 2004; Derenko et al., 2010; Miao et al., 2021), whereas haplogroups B, M, and F are more prevalent in southern East Asia and Southeast Asia (Yao et al., 2002; Wei et al., 2024). A similar pattern is observed in ancient populations: haplogroup A appears more frequently among YRB populations (mean = 9.54 %, max = 25 %), while haplogroups C (mean = 27.03 %, max = 67.00 %) and D (mean = 44.19 %, max = 67.00 %) are predominant in NSB populations, exhibiting a decreasing north-to-south gradient along the NSB-YRB-SEA (Southeast Asia) trajectory. In contrast, haplogroups B, M, and F show a reverse trend, peaking in SEA populations (B: mean = 24.60 %, max = 39.00 %; M: mean = 23.51 %, max = 54.55 %; F: mean = 9.93 %, max = 20.00 %), and declining northward. Haplogroup G is most frequent among YRB populations (max = 37.50 %), followed by NSB (max = 20.00 %). Notably, haplogroups H and U reach their highest frequencies in western Eurasian (WEA) populations (H: max = 16.7 %; U: max = 13.3 %) (Fig. 2; Supplementary Table S4).

The major haplogroups in PC_ALL are those typically found in eastern Eurasia, including D (23.64 %; D4, D5), M (13.64 %; M7, M8, M9, M10, M11, M13), B (11.82 %; B4, B5), A (10.00 %; A5, A8, A15, A17), F (8.18 %; F1, F2, F3), C (8.18 %; C4, C5, C7), and G (5.45 %; G1, G2, G3). Together, these lineages account for 80.90 % of the maternal gene pool, forming the core of PC_ALL's mitochondrial structure. In addition, we identified a small number of haplogroups with western Eurasian origin (such as N1a3a, H6a1b, H2b, and U5b2a3) previously observed in Xinjiang, Central/West Asia, and Europe (Ning et al., 2021), suggesting a minor but detectable western Eurasian genetic influence in the PC_ALL population.

In PC_ALL, the combined frequency of haplogroups A, C, D, and G reaches 47.3 %, significantly exceeding that of B, M, and F (33.6 %) and of western Eurasian haplogroups such as H and U (approx. 5 %). This haplogroup profile aligns more closely with NSB and YRB populations, implying stronger historical interactions or shared ancestry with these groups, while showing limited similarity to SEA and WEA populations (Fig. 2; Supplementary Tables S1 and S4).

Although haplogroup frequency analysis provides a preliminary understanding of the maternal diversity and broad genetic affinities of the Pingcheng population, it offers limited resolution for uncovering fine-scale population structure, sequence-level variation, or complex demographic history. Therefore, we conducted a series of in-depth analyses based on complete mitochondrial genome sequences, focusing on sequence variation, diversity indices, genetic distances, and population

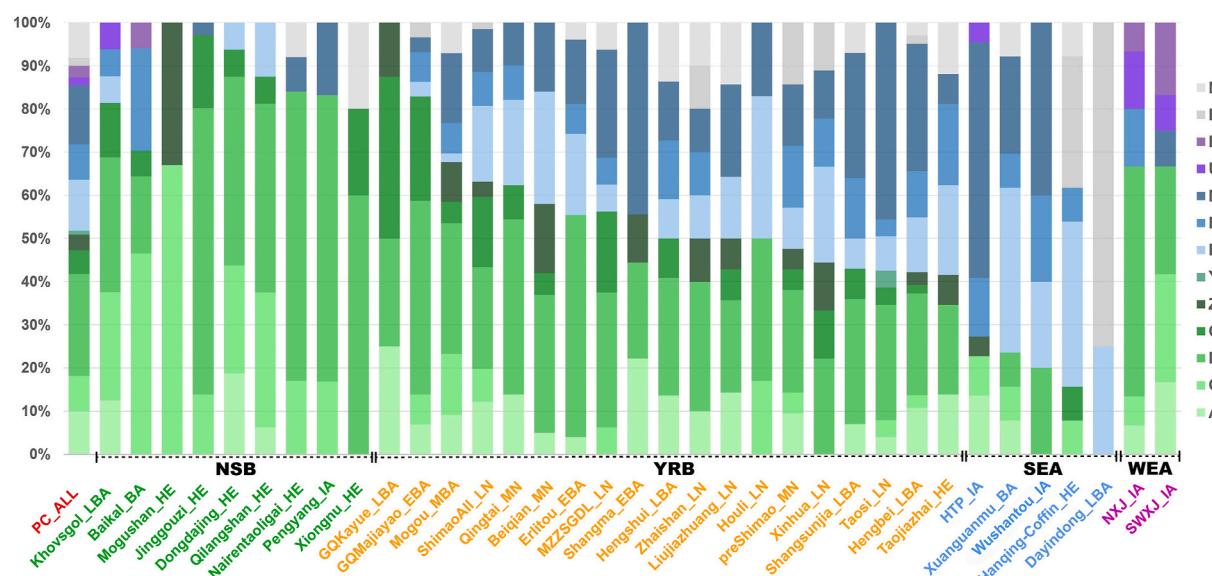


Fig. 2. Mitochondrial haplogroup frequencies among ancient populations.

structure to more comprehensively reconstruct the maternal genetic profile of Pingcheng.

Analysis revealed a relatively low nucleotide diversity ($\pi = 0.00162$) in PC_ALL, substantially below the expected mutation rate ($\theta = 0.00790$, $\pi/\theta \approx 0.205$). Both Tajima's D (-2.52 , $P < 0.001$) and Fu's Fs (-33.646) yielded significantly negative values, characteristic of recent population

expansion. This is further supported by the high haplotype diversity ($Hd = 0.877$) and the presence of diverse phylogenetic lineages, suggesting that the expansion was accompanied by the influx of multiple maternal sources. Additional neutrality tests, including Fu and Li's D^* (-4.98 , $P < 0.02$), F^* (-4.75 , $P < 0.02$), and Achaz's Y^* (-2.26), corroborate these findings (Supplementary Table S3).

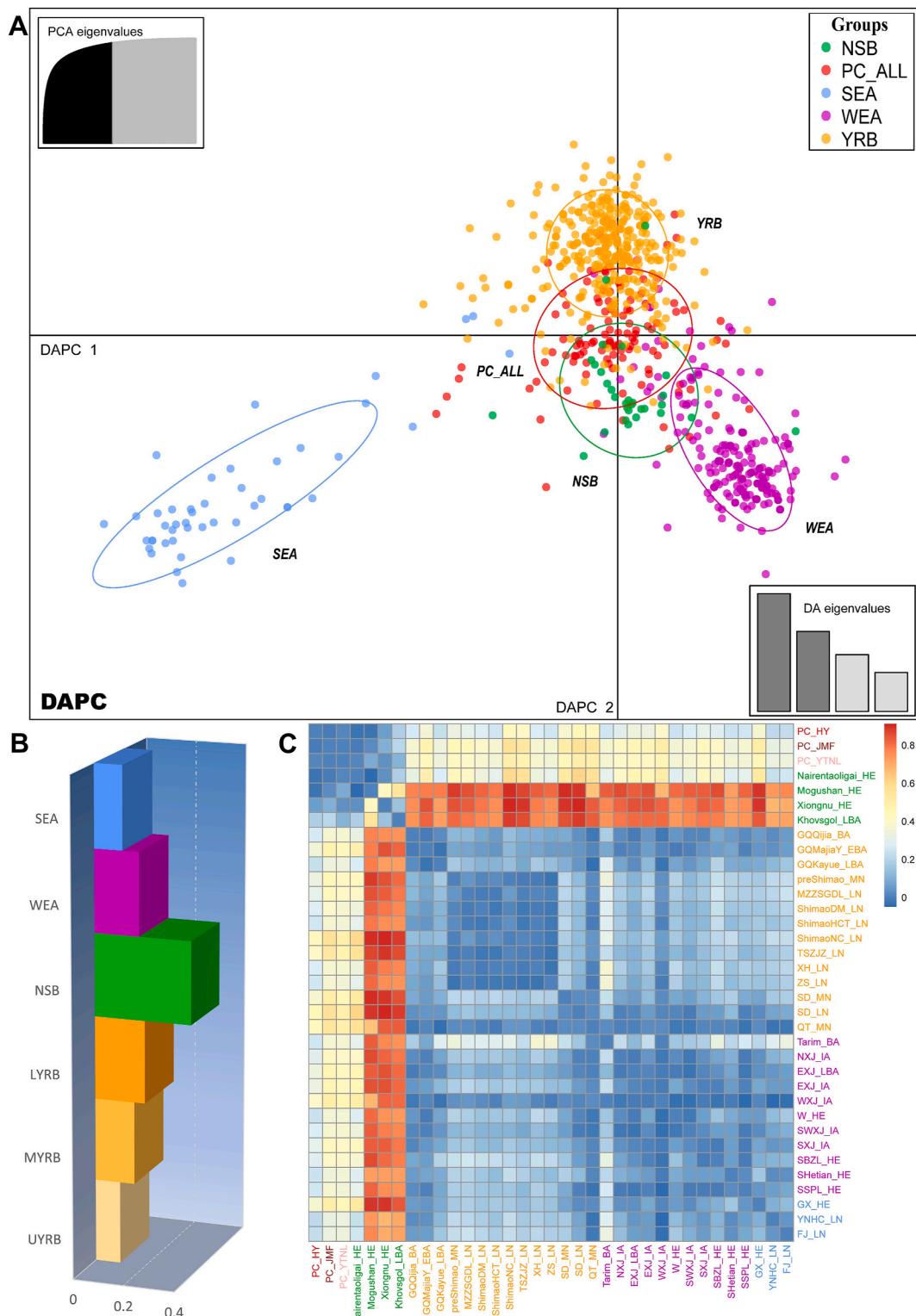


Fig. 3. (A) DAPC showing genetic differentiation between the Pingcheng population and other ancient groups; (B) The proportion of shared haplogroups between the Pingcheng population and the ancient groups relative to the total haplogroups in the ancient groups; (C) Heatmap of genetic distances (FST) between the Pingcheng population and other ancient populations.

Genetic Distance Analysis (FST) further clarify the genetic affinities of the Pingcheng populations. Genetic distances between PC_HY, PC_JMF, and PC_YTNL and NSB populations are the lowest (most FST <0.1, P > 0.05); moderate genetic differentiation is observed with YRB populations (most FST >0.24, P < 0.05); and significant differentiation is noted with both SEA (most FST >0.32, P < 0.05) and WEA populations (most FST >0.35, P < 0.05). These patterns are clearly illustrated in the FST heatmap (Fig. 3C; Supplementary Table S5).

DAPC based on complete mitochondrial sequences further confirms the genetic heterogeneity and structural admixture of PC_ALL. Individuals in PC_ALL are primarily distributed between NSB and YRB clusters, forming a genetic transition zone. Some individuals are even mutually embedded within NSB, YRB, and WEA clusters, indicating a degree of genetic permeability. In contrast, PC_ALL exhibits greater genetic distance from SEA populations, with only a few individuals extending toward this group. These spatial patterns align with previous analyses, and the presence of shared haplogroups between Pingcheng and multiple ancient populations suggests processes of maternal lineage convergence, admixture, and reshaping (Fig. 3A; Supplementary Tables S5–S9).

In sum, the maternal genetic structure of the Pingcheng population reveals a tri-layered complexity. First, in terms of haplogroup composition, PC_ALL exhibits high Haplotype diversity dominated by NSB-affiliated lineages, along with contributions from YRB, limited SEA input, and trace WEA proportion, which reflects geographically diverse maternal origins. Second, at the sequence diversity and population history level, low nucleotide diversity coupled with high haplotype diversity, a significantly lower π than θ , and consistently negative neutrality test results point to a recent population expansion accompanied by multi-source maternal influx. Third, in terms of inter-population relationships and structure, PC_ALL shows the closest affinity to NSB, followed by YRB, while being more genetically distinct from SEA and WEA populations. These features, as visualized in DAPC, indicate that Pingcheng functioned as a transitional zone at the confluence of multiple maternal genetic lineages.

3.2. The genetic affinities between the Pingcheng population and other ancient populations

3.2.1. Genetic affinities between Pingcheng and NSB populations

Haplogroup analysis revealed that haplogroup D occurred at the highest frequency in PC_ALL (23.64 %). Together with haplogroup C (8.18 %), these two lineages accounted for 31.82 % of the maternal gene pool. In NSB populations, particularly among those identified as Xianbei such as Naientaoligai_HE, Dongdajing_HE, and Qilangshan_HE, haplogroup D also showed the highest frequency (43.75–67 %), with the combined frequency of D and C reaching 68.75–84 %. This indicates a strong similarity in haplogroup composition between the Pingcheng and NSB populations, especially the Xianbei groups, suggesting a potential genetic connection through maternal lines (Fig. 2; Supplementary Table S4).

This interpretation is supported by genetic distance analysis. Among all comparative populations, Pingcheng populations (PC_HY, PC_JMF, and PC_YTNL) show the closest genetic affinity with NSB populations. Notably, their genetic distances with Tuoba Xianbei groups such as Mogushan_HE and Naientaoligai_HE are near zero (FST ≈ 0, P > 0.05), indicating substantial gene flow or a recent shared maternal ancestry. In addition, low genetic differentiation was observed with the historical Xiongnu population (FST <0.10, P > 0.05 with Xiongnu_HE), suggesting partial genetic exchange or a common northern steppe background. In contrast, comparisons with Bronze Age Mongolic populations such as Khovsgol_LBA show significantly greater differentiation (FST <0.20, P < 0.05), implying that the maternal ancestry of the Pingcheng population aligns more closely with historical-period NSB populations (Fig. 3C; Supplementary Table S5).

DAPC further supports this pattern. Individuals from PC_ALL largely

overlap with NSB populations, and some are embedded within them spatially. Multiple shared haplogroups were identified between Pingcheng and several NSB populations, including Naientaoligai_HE (Cai et al., 2023), Mogushan_HE (Ning et al., 2020), Xiongnu_HE (Damgaard et al., 2018), and Khovsgol_LBA (Jeong et al., 2018). These include A+152, A+152 + 16362, B5b1, C4a1a+195, C5d1, D4a1, D4c2b, D5a2a, G3a3, N9a1, and N9a2a. In the median-joining network, individuals from Pingcheng and Tuoba Xianbei frequently cluster within the same branches and differ by only a few mutations, such as in haplotypes C5, C5d1, and N9a1 as shown in the figure. This further highlights the close maternal genetic relationship between the two populations (Figs. 3A and 4; Supplementary Table S6).

Taken together, these results demonstrate that the Pingcheng population shares significant maternal genetic similarity and continuity with NSB populations, particularly the Tuoba Xianbei. This reflects substantial gene flow or a recent shared maternal ancestry between two groups.

3.2.2. Genetic affinities between Pingcheng and YRB populations

Genetic distance analysis indicates moderate differentiation between Pingcheng populations (PC_HY, PC_JMF, and PC_YTNL) and YRB populations. While the FST values are higher than those between Pingcheng and NSB populations, they are considerably lower than values observed for SEA and WEA populations. Furthermore, the genetic distance between the Pingcheng population and the YRB populations is smaller compared to the genetic distance between the NSB and YRB. The data further indicate that the genetic differentiation between the Pingcheng population and YRB groups decreases with chronological proximity. For instance, among the YRB populations subjected to genetic distance analysis, the most recent group, HTP_IA, exhibits the lowest genetic differentiation from the Pingcheng population (FST = 0.13–0.28, P < 0.05). Conversely, populations from earlier periods, such as GQMa-jiaY_EBA (FST >0.36, P ≈ 0), GQQijia_BA (FST >0.26, P ≈ 0), and GQKayue_LBA (FST >0.24, P ≈ 0), show significantly increased genetic differentiation. Although ancient data more contemporaneous with the Northern Wei Pingcheng period are unavailable for comparison, the aforementioned results suggest a certain degree of genetic connection between the Pingcheng population and populations from the Yellow River Basin. This connection appears to increase over time, indicating the possibility of limited gene flow between the Pingcheng population and more temporally proximate YRB populations (Supplementary Table S5).

The haplogroup composition shows that haplogroups B and M, which occur at high frequencies in YRB populations (averaging 30.5 %), are also well represented in the PC_ALL, accounting for a combined proportion of 25.46 %. Moreover, DAPC reveals a clear spatial overlap and interspersing between PC_ALL and YRB populations, further indicating the presence of maternal admixture between the two populations (Figs. 2, 3A and 3C; Supplementary Tables S4 and S7).

Shared haplotypes were detected between Pingcheng and ancient populations from the upper, middle, and lower Yellow River Basin. For the upper basin, GQMajiaY_EBA and GQKayue_LBA (Ding et al., 2020) share haplotypes A17, C4a1, D4i, F1b, R+16189, M9a1a, and G2a1g. Mid-YRB populations such as TSZJZ_LN, preShimao_MN, Shimao ALL LN, ZS_LN, and MZZLSGDL_LN (Xue et al., 2022) share B5b2a1, B5b1, B4c1a2, M8a2, M7c1a, M9a1a1c1a, M10a1a1b, M11c, and M11d. Lower-YRB groups including SD_MN, SD_LN, and QT_MN share B4a4, B5b1, M9a1a, M10a1b, and M11d (Miao et al., 2021; J. Liu et al., 2021).

The median-joining network analysis reveals that individuals from the Pingcheng population cluster with those from the YRB group in the intermediates constructed from haplotype aggregations based on sub-haplogroups of B and M (such as B5b2a1, B4a4, B4d1'2'3, M9a1a, and M10a1b), with relatively few differences in mutations between them (Fig. 5; Supplementary Table S7). This further supports the existence of a maternal genetic link between the Pingcheng population and ancient

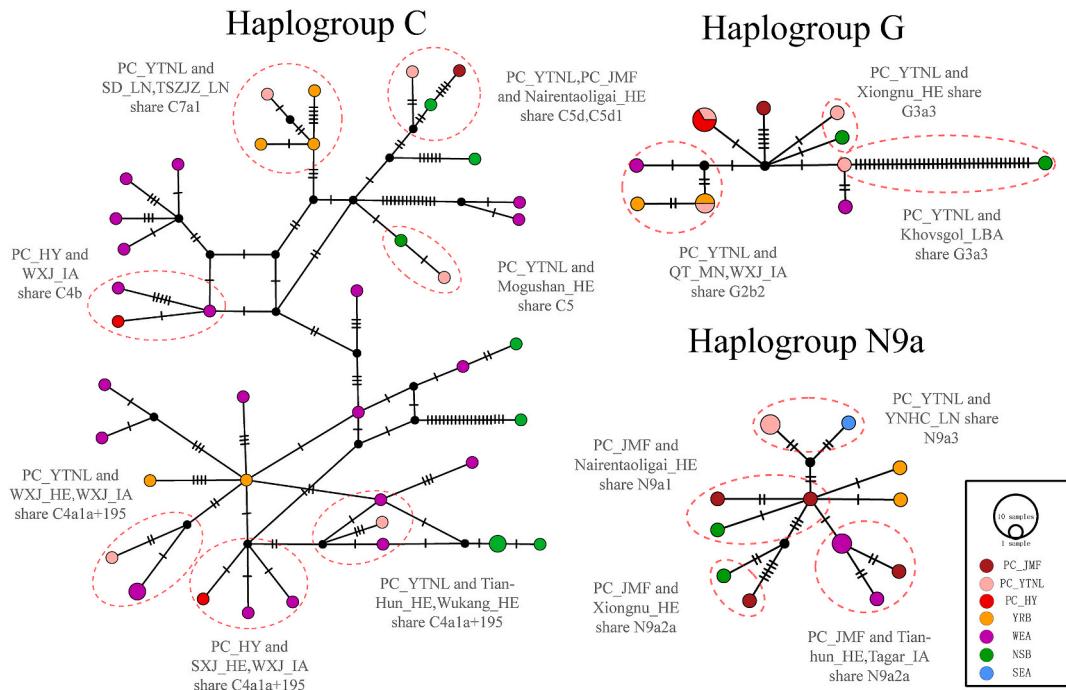


Fig. 4. Median-joining networks of haplogroups C, G and N9a.

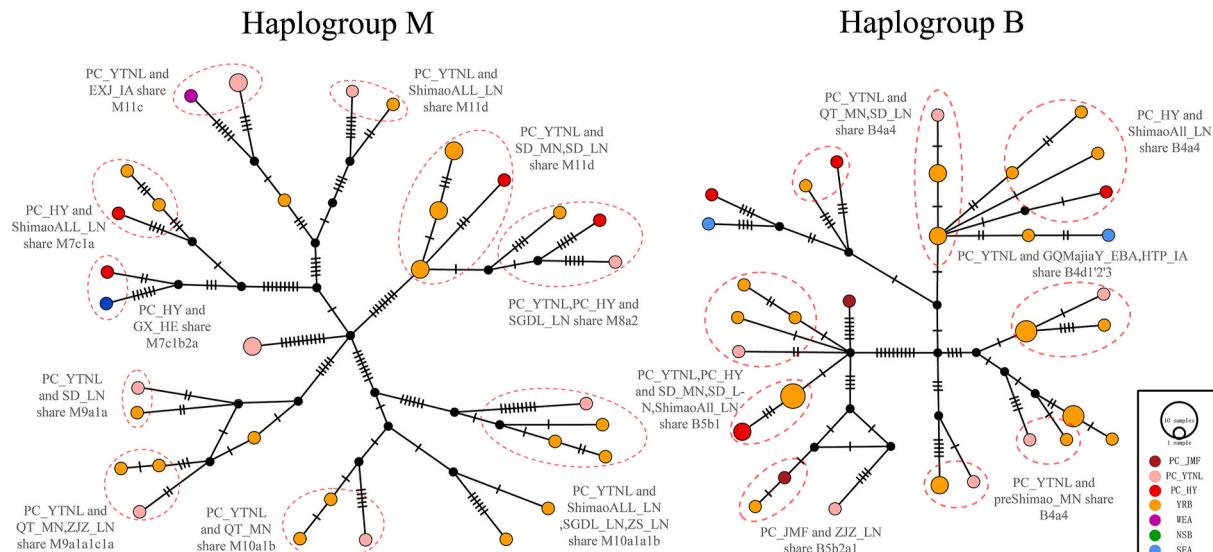


Fig. 5. Median-joining networks of haplogroups M and B.

populations from the Yellow River Basin.

In summary, while the Pingcheng population exhibits significant maternal genetic similarity and continuity with the Tuoba Xianbei, a certain proportion of YRB components can still be detected within its maternal gene pool. This suggests that, based on the NSB maternal genetic background centered around the Tuoba Xianbei, there is also a degree of genetic exchange with the Central Plain populations of the Yellow River Basin.

3.2.3. Genetic affinities between Pingcheng and WEA populations

Genetic distance analysis shows significant differentiation between Pingcheng populations (PC_HY, PC_JMF, and PC_YTNL) and WEA populations (most $F_{ST} > 0.35$, $P < 0.05$). Nonetheless, haplogroups of Western Eurasian origin, such as U and H, are present in PC_ALL, albeit at low frequencies. In DAPC analysis, PC_ALL individuals also exhibit

partial spatial overlap with WEA populations (Figs. 2, 3A and 3C; Supplementary Tables S4 and S5).

Multiple shared haplogroups were identified between Pingcheng and ancient populations from various regions and periods of WEA. These include Iron Age Xinjiang groups (SXJ_IA, NXJ_IA, EXJ_IA, WXJ_IA) with shared haplogroups A+152 + 16362, C4a1a+195, C4a1, C4b, D4i, D4c1b1, H2b, H6a1b, N1a3a, and Z4a1; historical-period Xinjiang groups (SXJ_HE, EXJ_HE, WXJ_HE) with A+152 + 16362, A8a1, C4a1a+195, M11c, G3a3, H2b, and H6a1b (Wang et al., 2021); and Central Asian groups such as TianHun_HE, TianSaka_IA, and Nomad_IA with C4a1a+195, D4j, D4b1, D4b1a2a1, F1b, N9a9, and HV. Even distant European populations such as BellBeaker_LN (Allentoft et al., 2015) share haplogroup U5b2a3 with Pingcheng. It is noteworthy that, in addition to sharing certain haplogroups with a steppe background (such as subhaplogroups of C and D), the median-joining network

analysis reveals that subhaplogroups of U and H (such as HV, H2b, H6a1b, U5b2a3) also reside in the same clade as the Pingcheng samples (Fig. 6; Supplementary Table S8), separated by only 1–2 genetic mutations.

These findings indicate that while the Pingcheng population predominantly exhibits maternal genetic backgrounds characteristic of the northern steppes, their gene pool still contains detectable maternal elements originating from WEA. This suggests a limited but direct maternal genetic exchange between the two populations.

3.2.4. Genetic affinities between Pingcheng and SEA populations

Genetic distance analysis indicates significant differentiation between Pingcheng (PC_HY, PC_JMF, and PC_YTNL) and SEA populations (most $FST > 0.32$, $P < 0.05$). DAPC results show that PC_ALL and SEA populations are largely separated in spatial distribution, with only a few Pingcheng individuals extending toward the SEA genetic space (Fig. 3A and C; Supplementary Tables S4 and S5).

Although the overall differentiation is clear, only a few individuals extend toward the SEA cluster in the DAPC analysis (Fig. 3A and C; Supplementary Tables S3 and S4). Nevertheless, we identified shared mitochondrial haplogroups, such as R+16189, F1c1a, F1b, F2e1, and F3a+207, between the Pingcheng population and several SEA populations, including NW_Yunnan, C_Yunnan, and GX_HE (Y. Liu et al., 2021; Wei et al., 2024). Moreover, in the subsequent median-joining network analysis, these haplotypes were also found to cluster together (Fig. 7; Supplementary Table S9).

These results indicate that the Pingcheng population also exhibits a certain degree of maternal genetic affinity with SEA populations.

3.3. The genetic differences and affinities within the Pingcheng population

To systematically reveal the maternal genetic structure and inter-group relationships among the populations from different cemeteries at Pingcheng, we conducted a comprehensive, multidimensional analysis of PC_HY, PC_JMF, and PC_YTNL.

In terms of haplogroup composition, PC_HY individuals predominantly carried haplogroups D (20.69 %), B (17.24 %), and M (13.79 %), with haplogroup B showing the highest frequency among all three groups. Haplogroups N and Y were absent in PC_HY, but haplogroups R (3.45 %) and U (6.90 %), which were not detected in the other two cemeteries, were present. Notably, haplogroups H and U are typically associated with WEA populations, and their combined frequency in PC_HY reached 10.34 %, far exceeding that of the other two cemeteries. This exhibits a relatively closer affinity between PC_HY and WEA

populations.

PC_JMF exhibited higher frequencies of haplogroups D (32.00 %), N (20.00 %), and Z (16.00 %), all of which were the highest among the three cemeteries. Haplogroups A, R, H, and U were not detected in PC_JMF, while haplogroup Y (4.00 %) was uniquely present. The frequency of haplogroup D was highest in PC_JMF, and the combined frequency of haplogroups C and D reached 40.91 %, significantly higher than in the other two cemeteries. Given that haplogroups C and D are highly prevalent in NSB populations, this pattern suggests a relatively close genetic relationship between PC_JMF and the NSB populations.

PC_YTNL was characterized by higher frequencies of haplogroups D (21.43 %), M (17.86 %), and A (16.07 %). Haplogroups R, U, Z, and Y were not detected, while haplogroups A and M appeared at much higher frequencies than in the other two cemeteries. Since haplogroups A and M are highly distributed in YRB populations, their elevated presence in PC_YTNL implies a relatively closer genetic connection with YRB populations.

Although all three Pingcheng cemeteries carried haplogroups B, C, D, F, G, and M, and haplogroup D had the highest frequency in each, there were still pronounced differences in their overall haplogroup compositions. Haplogroup correlation analysis indicated weak correlation coefficients among the three cemeteries, further suggesting distinct maternal contributions (Fig. 8A and B; Supplementary Tables S4 and S10).

PCA based on haplogroup frequencies further highlighted genetic differentiation among the cemetery populations. Ancient groups were broadly separated into four clusters, with those from nearby regions exhibiting similar genetic distributions. PC_HY, PC_JMF, and PC_YTNL were dispersed across the PCA space and did not cluster within any specific group. PC_HY was slightly displaced toward the upper right quadrant, influenced by haplogroups U and H, while PC_JMF shifted toward the lower left due to the influence of haplogroups N and Y. Overall, all three cemeteries were surrounded by NSB, YRB, and SEA populations, reflecting their complex maternal genetic composition and multiple original contributions (Fig. 9A; Supplementary Table S3).

To quantitatively assess whether the spatial differentiation observed in haplogroup frequencies was statistically significant, and to evaluate the relative contributions of within- and between-group genetic variation, we conducted population genetic differentiation analyses based on complete mitochondrial sequences. The results showed no significant genetic differentiation among the three cemeteries ($FST \approx 0$, $P > 0.05$), indicating either recent gene flow or a shared recent maternal ancestry. Analysis of molecular variance (AMOVA) further revealed that only 0.56 % of total genetic variance was attributable to differences among

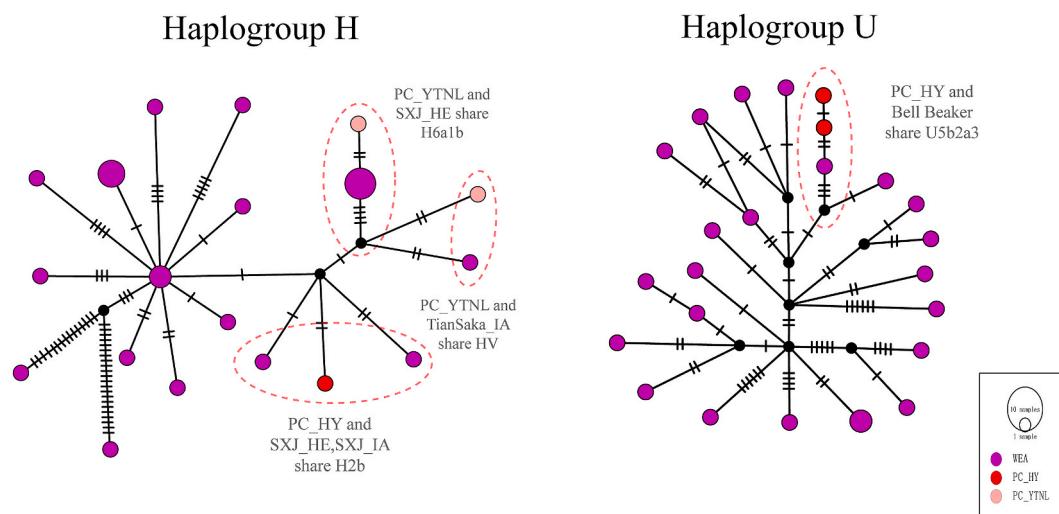


Fig. 6. Median-joining networks of haplogroups H and U.

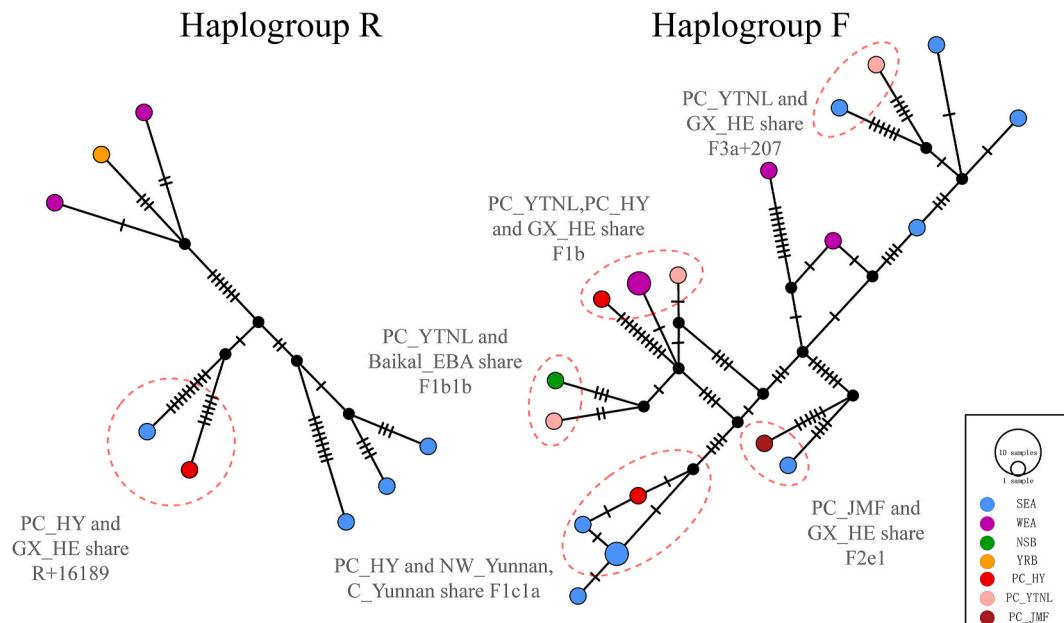


Fig. 7. Median-joining networks of haplogroups R and F.

the cemeteries, while 99.44 % was due to variation within groups, suggesting high levels of internal diversity and possible gene inflow, yet no statistically significant differentiation between different cemeteries (Fig. 3C; Supplementary Tables S5 and S11).

To further examine potential genetic structures, we conducted a Discriminant Analysis of Principal Components (DAPC) based on the complete mitochondrial DNA sequences. This analysis aims to maximize differences between groups while minimizing within-group variability, thereby enhancing the identification of population structures. The DAPC results indicate that although there is overlap in the discriminant space between PC_HY, PC_JMF, and PC_YTNL, they can still be effectively distinguished (Fig. 10). These findings suggest that while the three cemetery populations lack statistically significant genetic differentiation, there are still detectable subtle variations in their genetic structures.

Median-joining network analysis further supports this view. Although no haplotypes were shared by all three cemeteries, several shared lineages were observed between pairs. Specifically, haplotypes D4c2b and D4e2 were shared between PC_HY and PC_JMF, while A+152 + 16362, B4a4, B5b1, C4a1a+195, D4, G2a5, and F1b were shared between PC_HY and PC_YTNL. Median-joining network analysis showed that in some haplotypes, such as B5b1, D4, D4c2b, and G2a5, samples from different cemeteries clustered within the same branches, indicating shared lineages or gene flow between different cemeteries. In contrast, for haplotypes such as A+152 + 16362, B4a4, C4a1a+195, D4e2, and F1b, individuals from different cemeteries appeared on separate branches, reflecting subgroup-specific maternal contributions (Fig. 11; Supplementary Table S12).

In summary, PC_HY, PC_JMF, and PC_YTNL exhibit both recognizable haplogroup structural differences in maternal inheritance and high intra-population diversity. These differences are identifiable in both PCA and DAPC analyses. However, the overall level of genetic differentiation among the three different cemeteries remains low, as statistical significance in genetic differentiation was not detected in FST and AMOVA analyses. The coexistence of "structural difference" and "low differentiation" provides crucial insights into understanding the mechanisms and dynamic processes of maternal genetic integration in the Pingcheng population. Further discussion on this topic will be presented in the following sections.

4. Discussion

4.1. The complex origins and background of the Pingcheng population

4.1.1. Political expansions: genetic substrate from the Northern Steppe

Multiple lines of evidence, including haplogroup composition, Genetic distance analysis, and Median-joining network based approaches, indicate that the Pingcheng population is genetically closest to the NSB populations among all ancient populations. In particular, they show a marked similarity in genetic structure and high genetic continuity with the Tuoba Xianbei, and also exhibit relatively small genetic distances from the Xiongnu (most FST < 0.1, P > 0.05).

According to historical records, the Tuoba Xianbei originated from the "Great Xianbei Mountains" and lived primarily by fishing and hunting, forming relatively primitive kinship-based tribes. Around the first century CE, Tuyin led a southward migration to the "Great Marsh" (present-day Hulunbuir region 大泽), but the group came under Xiongnu dominance due to the latter's regional strength. In the mid-second century, Jifen continued the southward movement. Following the Eastern Han's defeat of the Xiongnu, Jifen led the Tuoba Xianbei to migrate into the "former lands of the Xiongnu" (now south-central Inner Mongolia). By the mid-third century, Tuoba Liwei moved the group to Shengle (present-day Inner Mongolia Horinger), where they gradually consolidated steppe forces and formed a tribal confederation centered on the Tuoba Xianbei. In the early fourth century, Tuoba Shiyijian established the state of Dai in Shengle. By the end of the fourth century, Tuoba Gui (拓跋珪) renamed the state to Wei, moved the capital to Pingcheng, and proclaimed himself emperor, thus founding the Northern Wei dynasty and initiating the transformation from a steppe polity to a Central Plains empire (Wei, 1974).

Bioarchaeological research provides genetic support for this historical trajectory. Published ancient DNA studies demonstrate that the Tuoba Xianbei in south-central Inner Mongolia (NRG_Xianbei_1750BP) shared genetic similarities and strong affinities with early Xianbei individuals from Hulunbuir (AR_Xianbei_1850BP) and Neolithic populations (AR_LN and AR_EN) in the Amur River basin (Ning et al., 2020). These groups also experienced gene flow with surrounding populations, particularly receiving limited genetic incorporation of Han Chinese in the Central Plains (Cai et al., 2023). Relevant anthropological studies indicate that the Tuoba Xianbei from south-central Inner Mongolia were

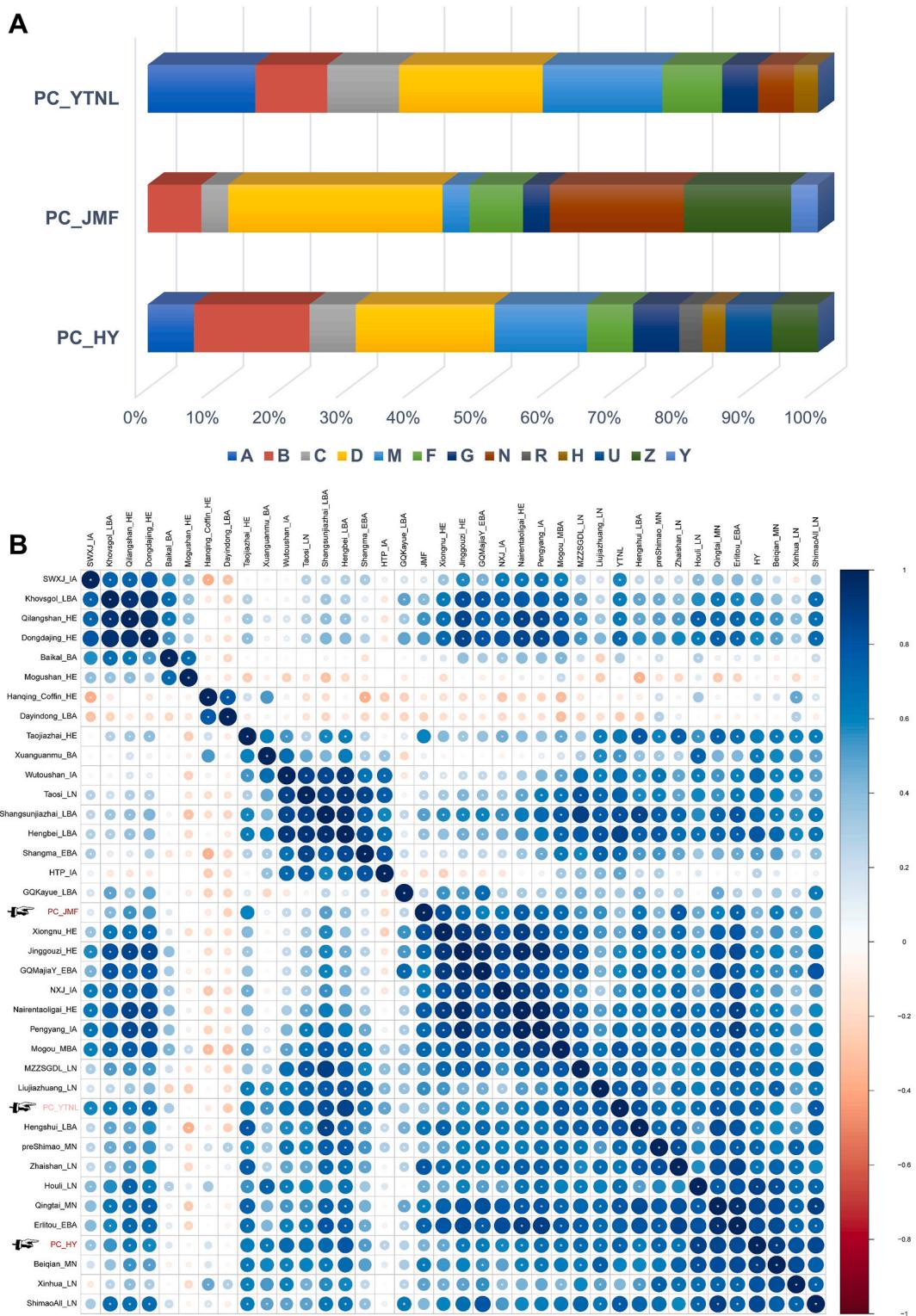


Fig. 8. (A) Haplotype frequency; (B) The haplotype correlation heatmap of PC_HY, PC_JMF, and PC_YTNL.

closely related to those in Hulunbuir, with cranial morphology predominantly consistent with the North East Asian subtype of the Mongoloid group,. However, some individuals show increased cranial height, narrower faces, and decreased facial flatness, reflecting noticeable influence from the East Asian subtype of the Mongoloid group, as represented by Han Chinese populations.

Although physical anthropology and stable isotope research have been conducted in Pingcheng, ancient DNA data had long been lacking,

leaving the post-migration genetic dynamics of the Tuoba Xianbei unclear. The present study fills this gap and shows that the Pingcheng population is genetically highly similar to Tuoba Xianbei populations from south-central Inner Mongolia, such as Nairentaoligai_HE, Qilangshan_HE, and Dongdajing_HE. Haplotype D was most frequent, and together with haplotype C accounted for 31.82 %. No statistically significant sequence-level differentiation was observed between these populations, indicating strong genetic homogeneity ($F_{ST} \approx 0$, $P > 0.05$)

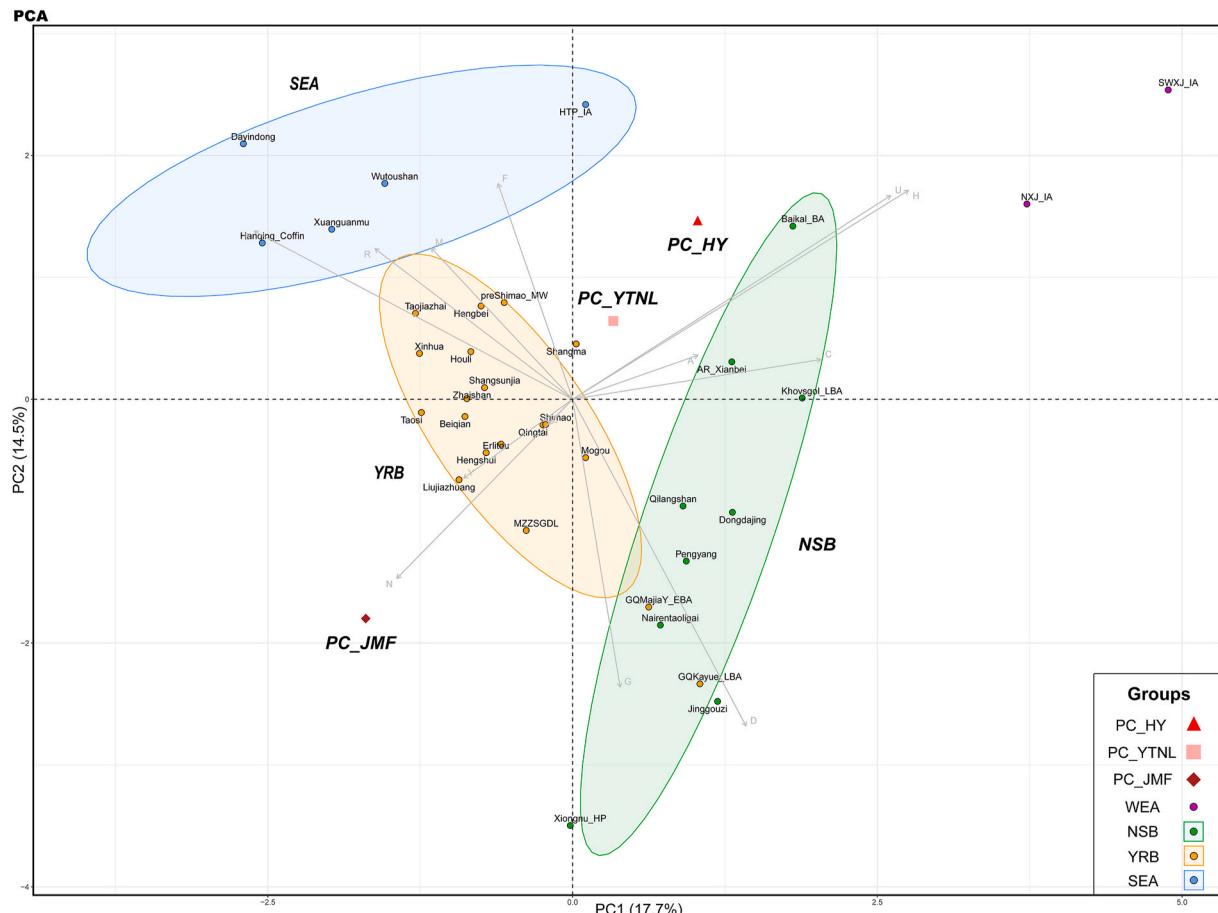


Fig. 9. Principal component analysis (PCA) based on mitochondrial haplogroup frequencies.

with Nairentaoligai_HE and Mogushan_HE). In addition, multiple haplotypes were found to be shared between Pingcheng and Nairentaoligai_HE. Specifically, PC_YTNL shares C5d and D4; PC_JMF shares N9a1, C5d1, and D4c2b; PC_HY shares D4, D4a1, and D4c2b. Moreover, PC_YTNL also shares haplotype C5 with Mogushan_HE from the Hulunbuir region (Figs. 2, 3A and 3C, 4; Supplementary Tables S4–S6). These close genetic ties are further supported by median-joining network results (e.g., C5, C5d1). Such patterns reflect the genetic continuity associated with the southward and westward migration of the Tuoba Xianbei and their eventual settlement of Pingcheng. They provide strong genetic support for the historical narrative and underscore the Tuoba Xianbei's foundational contribution to the maternal gene pool in Pingcheng.

The historical development of the Tuoba Xianbei is, in essence, a process of continuous migration and interaction with diverse populations. As early as their settlement in the "Great Marsh," they began integrating with the Xiongnu and other groups (Du, 2017). Burial artifacts from this period, including weapons, horse gear, and animal-shaped bronze ornaments, exhibit clear Xiongnu stylistic influences (Su, 1977). Among steppe populations, only the Xiongnu and Tuoba Xianbei are known to have practiced mirror-breaking rituals (Ma, 2015). After occupying the former Xiongnu lands, the Tuoba integrated over 100000 Xiongnu tribespeople (匈奴余種留者尚有十餘萬落，皆自號鮮卑) and absorbed other nomadic groups (Fan, 1965). The state of Dai functioned as a tribal alliance led by the Tuoba Xianbei, comprising the "Ten Imperial Clans," the "Inner Immigrant Clans," and the "Peripheral Clans," which included branches of the Xianbei, the Xiongnu, Gaoche, Rouran, Wuhuan, and other smaller nomadic tribes (He, 2001; Wei, 1974). After the capital was moved to Pingcheng and imperial status was established, these groups settled in the central region and constituted

the political and demographic foundation of the Pingcheng court.

The Tuoba Xianbei's early experience of integration with the Xiongnu and other steppe groups, along with the tribal alliance model developed during the state of Dai, laid the ideological, institutional, and social groundwork for later multiethnic integration in Pingcheng. Evidence from FST, AMOVA, nucleotide diversity, and neutrality tests indicates that while all Pingcheng cemetery populations share the closest maternal genetic affinity with the Tuoba Xianbei, there is no statistically significant genetic differentiation among the cemeteries ($FST \approx 0$, $P > 0.05$). At the same time, these populations exhibit high internal genetic diversity and signals of exogenous gene flow ($Hd > 0.97$, $Vb = 99.44\%$). Analyses of haplogroup composition, DAPC, and network structure reveal varying degrees of maternal genetic connection between Pingcheng populations and populations from the YRB, WEA, and SEA. For example, PC_HY shows affinity with WEA populations. Despite overall genetic homogeneity, minor but detectable differences exist, including the presence of distinctive maternal lineages such as HV, Y1b1, and U5b2a3.

In summary, the Tuoba Xianbei not only laid the foundation for the Pingcheng population at the level of matrilineal genetics, but also continued the previous tradition of openness, inclusiveness, and integration, providing the conceptual, institutional, and social groundwork for the subsequent influx of diverse populations.

4.1.2. Forced migrations: genetic contributions from the Yellow River Basin and the south

Multiple lines of evidence, including haplogroup composition, FST values, sequence-based DAPC, and median-joining network analysis, indicate that the Pingcheng population, while primarily shaped by a maternal genetic background from the Northern Steppe centered on the

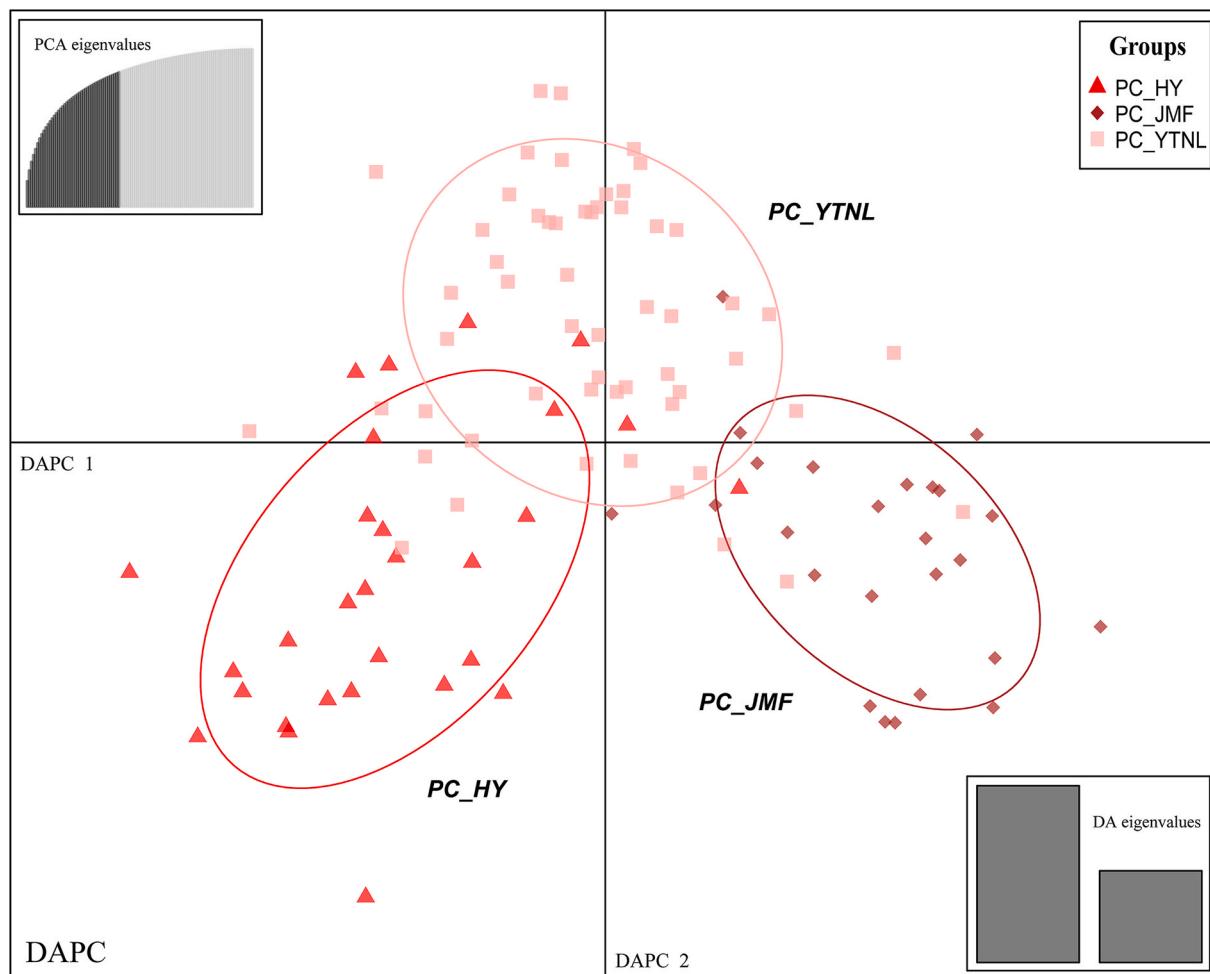


Fig. 10. Discriminant analysis of principal components (DAPC) illustrating the genetic differentiation among PC_HY, PC_JMF, and PC_YTNL based on complete mitochondrial DNA sequences.

Xianbei, also experienced gene flow from YRB populations. Based on historical records and archaeological evidence, we hypothesize that these genetic links are closely related to the large-scale forced migrations implemented by the Northern Wei during its unification of northern China (五方之民, 輻輳京邑) (Wei, 1974). These population movements not only had profound socio-political implications but also left clear genetic imprints.

First, we observe a genetic affinity between the Pingcheng population and populations from the upper Yellow River, such as GQMajiaY_EBA, GQKayue_LBA, and HTP_IA. The GQMajiaY_EBA and GQKayue_LBA represent the Majiayao and Kayue cultures respectively, both of which played important roles in shaping the prehistoric cultural sequence in the upper YRB (Shi, 1962; Xu, 2002). Geographically, this region occupies a strategic position at the intersection of the Central Plains, the Eurasian Steppe, and Xinjiang, and has historically witnessed frequent population movements and ethnic integration. During the Sixteen Kingdoms period, a number of short-lived regimes—including Western Qin, Southern Liang, Northern Liang, and Xia—rose to power in the upper YRB (Yang and Ma, 2009).

As these regimes were successively conquered by the Northern Wei, large numbers of their inhabitants were forcibly relocated to Pingcheng, which explains the close genetic connection observed between the Pingcheng population and populations from the upper YRB. According to historical records, in the third year of the Shiguang era, more than ten thousand households were relocated from the Xia capital (始光三年, 徙萬餘家而還, 426 CE), Tongwan City, to Pingcheng; in the fourth year, several thousand individuals from the Qin and Yong (始光三年, 秦雍人士

數千人, 427 CE) regions were captured and likewise sent to Pingcheng. In the first year of the Taiyan era, the government ordered the relocation of residents from Pingliang to the capital (太延元年, 詔平涼民徙在京師, 435 CE). In the fifth year of the same era, over 200,000 individuals were registered in Guzang City (太延五年, 收姑臧城內戶口二十餘, 439 CE), several thousand households were seized during the campaign against Ledu (太延五年, 討樂都, 掠數千家而還, 439 CE), and more than 30,000 households from Liangzhou (太延五年, 徙涼州民三萬餘家, 439 CE) were relocated to the capital (Wei, 1974). Notably, some of the relocated aristocratic families later formed powerful regional political factions—such as the Hexi, Hedong, and Guanlong groups—that wielded considerable political influence during the Northern Wei, as well as in the Sui and Tang dynasties (Zhang, 1995).

Second, we identified genetic connections between the Pingcheng population and several populations from the middle reaches of the YRB, including TSZJZ_LN, preShimao_MN, Shimao_ALL_LN, ZS_LN, and MZZLSGDL_LN. Shimao_ALL_LN is associated with the Shimao culture, while preShimao_MN belongs to the Yangshao culture. Shimao_ALL and preShimao_MN exhibit a close genetic affinity with each other and with neighboring populations (ZS and MZZLSGDL). These populations originated from the local Neolithic Yangshao culture of Shaanxi and show the closest genetic affinity with the Taosi culture population (TSZJZ) in Shanxi. Furthermore, these populations display significant genetic continuity with early, later, and even modern populations in the region, reflecting a degree of genetic persistence (Xue et al., 2022).

As early as the Dai regime period, the Tuoba Xianbei had integrated factions from the central and southern regions of Inner Mongolia and

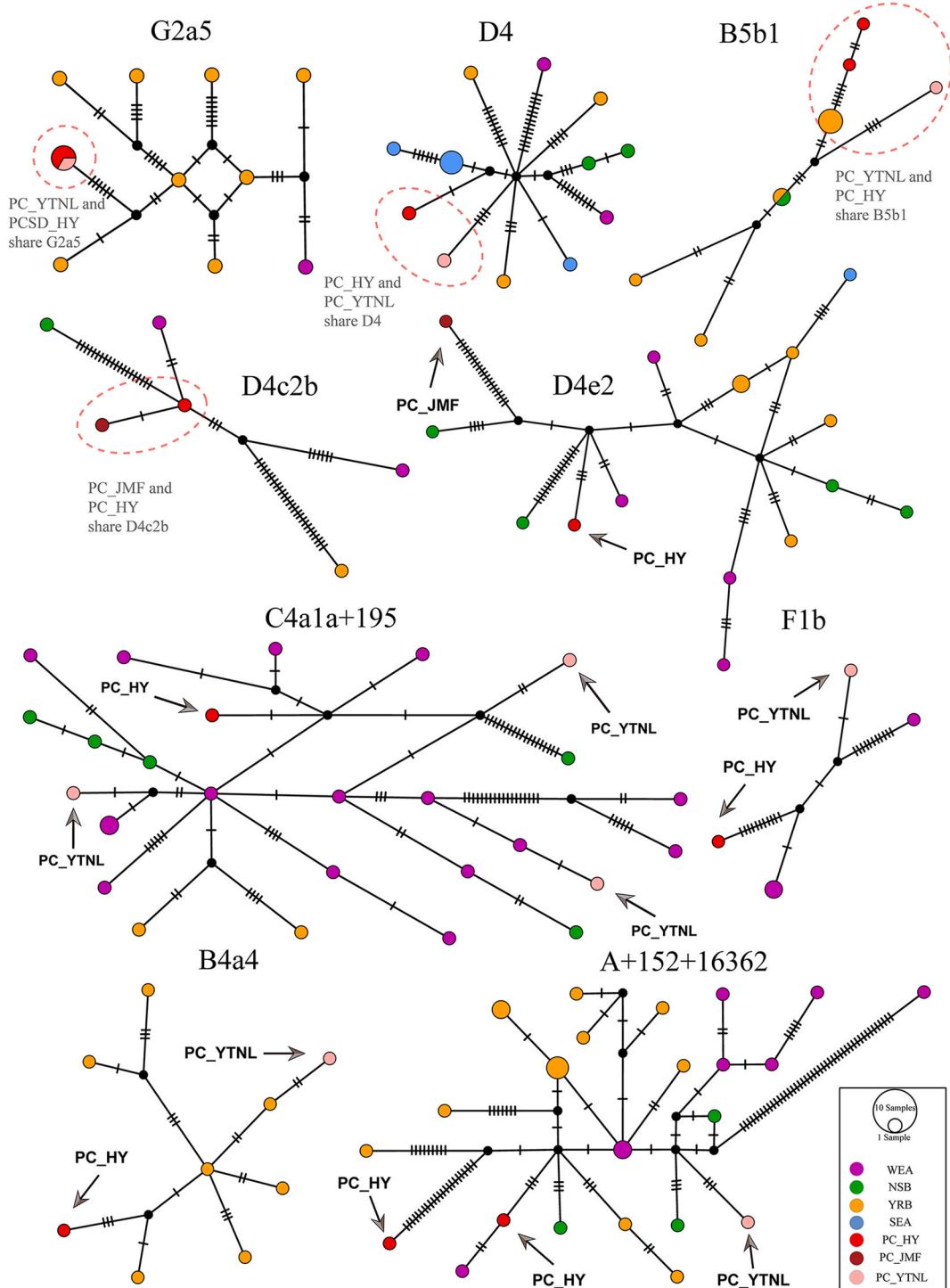


Fig. 11. Median-joining networks of mitochondrial haplotypes A+152 + 16362, B4a4, B5b1, C4a1a+195, D4, D4c2b, D4e2, G2a5, and F1b.

northern Shanxi (Xu, 1993). After founding the Northern Wei, they expanded into the Shanxi and Shaanxi regions through a series of successful campaigns against Later Qin, Later Yan, and Xia, and relocated populations to the capital in the fifth year of Tianxing (天興五年, 徙後秦民眾于京師, 402 CE) and the first year of Tianchi (天賜元年, 獲三千餘口, 404 CE) (Wei, 1974). Consequently, populations from the middle reaches of the YRB in Shanxi and Shaanxi made a certain contribution to the genetic makeup of the Pingcheng population.

Finally, we identified genetic connections between the Pingcheng population and the SD_MN, SD_LN, and QT_MN populations from the lower YRB. QT_MN originates from the Qingtai site in Henan and

belongs to the Yangshao culture. QT_MN shows close matrilineal connections with SD_MN and SD_LN (especially the Longshan culture populations) (Miao et al., 2021). SD_MN and SD_LN represent populations from various sites in Shandong (Beiqian, Chengziya, Tonglin, Houli, Liujiazhuang), spanning cultures from Dawenkou, Longshan, Shang, and Zhou periods (J. Liu et al., 2021). Although the matrilineal genetic structure in Shandong became increasingly diverse from the Longshan culture onward, it retained some degree of matrilineal continuity. For instance, the Liujiazhuang population shares 59.40 % of haplogroups with the modern Shandong population (J. Liu et al., 2021).

During this time, Shandong and Henan belonged to the Yanzhou (兗

州), Qizhou (齐州), and Qingzhou (青州) regions within the Six Prefectures (六州) of Later Yan (Wu, 2005; Yan, 2017). In the first year of Tianxing (天興元年, 徒六州民吏及徒何高麗雜夷, 398 CE) and the third year of Huangxing (皇興三年, 徒青齊人, 469 CE), the Northern Wei relocated the officials and civilians from Later Yan's Six Prefectures, as well as people from Qing and Qi regions, to the capital (Wei, 1974). These groups, including the prominent clans of Henan and scholar-official clans of Qing and Qi, later became influential regional political forces within the Northern Wei state (Wei, 2005). Therefore, the matrilineal links between the Pingcheng population and those in the lower YRB likely originate from these migrations.

Not only were northern populations forcibly relocated to Pingcheng on a large scale, but southern populations were no exception. According to historical records, during the Northern Wei's military campaigns against the Southern Dynasties, more than 30,000 individuals were relocated to the capital in the fifth year of the Taihe era (太和五年, 俘獲三萬餘口, 481 CE) (Wei, 1974). This partially explains the observed genetic affinity between the Pingcheng and SEA populations. But the Northern Wei government required these relocated individuals must be buried in Sangqian (桑乾) after their deaths (Li, 1974). Sangqian, located east of the present-day county seat of Ying County in Shanxi Province, is far from Datong. Therefore, it is unlikely that there were populations in the tombs of Pingcheng who migrated from the Southern Dynasties.

Despite significant genetic differentiation between Pingcheng and SEA populations as indicated by FST and DAPC analyses, we identify shared haplogroups between Pingcheng individuals and populations such as NW_Yunnan, C_Yunnan, and GX_HE. Some Pingcheng individuals also cluster with these SEA populations in Median-joining network analyses. This suggests that limited gene flow may have occurred. NW_Yunnan and C_Yunnan are located in Yunnan, and GX_HE in Guangxi. During the Southern and Northern Dynasties period, much of southern China was governed by the Southern Dynasties (Liu Song and Southern Qi) (Hu, 2009). Due to the prolonged confrontation between the northern and southern regimes, direct contact between them was limited, aside from occasional diplomatic missions. Most interactions occurred through the Tea-Horse trade (Chen, 2004; Ge, 2002). The Tea-Horse Road, centered on Yunnan, Tibet, and Sichuan, extended into the Central Plains, South Asia, and Southeast Asia, facilitating trade primarily in tea, horses, and salt. This ancient trade route played a vital role in promoting exchanges between the Central Plains, Tibet, and various southern ethnic groups (Shi, 2002; Zhang, 2006). We thus speculate that the genetic affinity between the Pingcheng and SEA populations is more likely attributable to interactions facilitated by this network.

4.1.3. Spontaneous migrations: genetic impacts of the Silk Road

It is noteworthy that the origin of the Pingcheng population was not solely due to the forced migration imposed by the ruling authorities but also included spontaneous movements of people. Although there exists significant genetic differentiation between the Pingcheng population and WEA population, analyses such as haplogroup composition, DAPC, and Median-joining network analysis suggest a direct yet limited maternal genetic connection between the two populations. However, there are no explicit historical records indicating that the Northern Wei government ever relocated Western Eurasian populations to Pingcheng. Based on multidisciplinary evidence, we infer that such maternal genetic links are likely associated with the frequent movement of people along the Silk Road.

We identified widespread genetic affinities between the Pingcheng population and numerous populations from Xinjiang, spanning both the Iron Age (SXJ_IA, NXJ_IA, EXJ_IA, and WXJ_IA) and historical periods (SXJ_HE, EXJ_HE, and WXJ_HE). As early as the period of the Tanshihuai Xianbei tribal alliance, the Xianbei had contact with populations in Xinjiang. Historical records indicate that the influence of the Western Xianbei had already extended to the Western Regions (Chen, 1982), they

also engaged in trade with the Hu (胡) merchants (Wang, 2014), before the Tuoba Xianbei established the Northern Wei. After the establishment of the Northern Wei, the conquest of the "Southern Liang" reopened the Silk Road, and the Northern Wei government established administrative positions such as the Xiyu Changshi (西域长使, chief of the Western Regions) and the Wuji General (戊己校尉) to manage and govern the Western Regions (Wei, 1974). Subsequently, through intermittent military campaigns against the Rouran and small states in the Western Regions (including Gaochang, Shanshan, Kucha, Yanqi, Khotan, and Zhaiyi), the Northern Wei ensured the smooth functioning of the Silk Road (Ma, 1995). Although there are no definitive historical records indicating that the Northern Wei government relocated populations from the Western Regions to Pingcheng, a large number of Western Region merchants traveled to Pingcheng to engage in trade as the Silk Road was reopened and prospered (Li, 2007; Wang, 2014; Zhang, 2015).

In fact, Pingcheng was not only home to merchants from the Western Regions but also teemed with a considerable number of foreigners from Central Asia, West Asia, and even Europe (Wei, 1974; Shi, 2007; Lü, 2012). Ancient DNA studies have shown that the Silk Road, which passed through Xinjiang, played a pivotal role in facilitating population migration across the Eurasian continent (Hansen, 2015). Serving as a bridge between East and West, Xinjiang had already established connections with Central and West Asia through the Inner Asian Mountain Corridor during the Bronze Age, and further linked with East Asia via the Hexi Corridor (Long et al., 2018; Y. Li, 2021). During the Iron Age, all populations in Xinjiang exhibited genetic connections with Turan populations from Central and West Asia. Notably, the presence of the Turan-specific haplogroup HV suggests that populations may have migrated from Turan into Xinjiang via the Inner Asian Mountain Corridor. The genetic structure observed during historical periods appears largely consistent with that of the Iron Age, indicating a degree of genetic continuity (Macaulay et al., 1999; Wang et al., 2021).

We also found genetic evidence of a connection between the Pingcheng population and Central Asian populations such as TianHun_HE, TianSaka_IA, and Nomad_IA, including specific haplogroups like HV. Additionally, in the DAPC analysis, we observed clear interpenetration between the PC_ALL and WEA populations, suggesting that people might have further migrated to Pingcheng along the Silk Road.

According to statistics, during the Pingcheng period, the Northern Wei maintained diplomatic relations with over 50 countries, including those in the Western Regions, Central Asia, South Asia, West Asia, and even Europe, engaging in more than 100 official interactions (Wei, 1974). Notably, they even had multiple official interactions with the Pulan (普嵐國, The Eastern Roman Empire) (Shi, 2007). Moreover, we identified that the Pingcheng population shared the rare haplogroup U5b2a3 with individuals from the Bell Beaker culture in Germany, with only two mutation distances in the Median-joining network, providing genetic evidence for historical records. This corroborates Pingcheng's role as a central hub at the eastern end of the Silk Road, highlighting the extensive range of cultural difintegration and genetic exchange.

In addition to envoys and merchants, a significant number of foreign artisans, monks, and performers also came to Pingcheng. Exotic cultures exerted a profound influence on the popular culture of Pingcheng, particularly in music, dance, painting, sculpture, and decorative motifs, as vividly demonstrated in the Yungang Grottoes. The architectural structure, mural styles, and Buddhist sculptures of the Yungang Grottoes reflect the artistic influences of Gandhara in India, the Sasanian Empire in Persia, and Hellenistic Greece. In terms of decorative patterns, designs such as the honeysuckle motif and the pearl roundel—originating from Central and Western Asia—were widely adopted. Musical and dance scenes carved in the grottoes frequently depict exotic instruments such as the Qiang flute and vertical konghou harp (Zhang, 2005; Zhang et al., 2005; Zhao, 2007; Wang, 2008).

According to historical records, tens of thousands of foreigners—from the Pamir Plateau to the Roman Empire—came to Northern Wei (自葱嶺以西, 至於大秦, 百國千城, 莫不歡附), where many purchased

property, settled, and even chose to naturalize as citizens out of admiration for Northern Wei culture (因而宅者,不可勝數,附化之民,萬有餘家) (Wei, 1974; Yang, 1978). Archaeological excavations in Datong have uncovered numerous artifacts with Central Asian stylistic elements, including gold and silverware, gilt bronze vessels, and glassware. Additionally, silver coins from the Sasanian Empire and even gold coins from the Roman Empire have been discovered (Xia, 1983; Wang, 2005, 2014). Physical anthropologists have also identified skeletal remains exhibiting distinct Europoid features (P. Li, 2021).

In summary, we systematically explored the maternal genetic connections between the Pingcheng population and various regional groups, including NSB, YRB, WEA, and SEA, from three dimensions: the political expansion of the Tuoba Xianbei, the forced migration of the ruling authorities, and spontaneous population movements within the context of the Silk Road. Through multidisciplinary cross-analysis, we not only revealed that the Tuoba Xianbei laid the foundation for the Pingcheng population at the maternal genetic level but also identified multiple matrilineal components from the Yellow River basin and beyond. This provides direct DNA evidence for the large-scale population movements during Pingcheng period of the Northern Wei.

4.2. The driving forces behind population interactions

The Tuoba Xianbei's enduring tradition of integration not only laid the foundation for the genetic openness and diversity of the Pingcheng population but also provided an ideological impetus for the sustained influx and integration of multi-source populations. However, the complex and heterogeneous maternal gene pool of the Pingcheng population did not originate from a single event; rather, it reflects a dynamic process that was phased, continuous, and intertwined. In addition to ideological influence, this process was also shaped by geographical location, state policies, and economic structures.

4.2.1. Institutional regulation: integration of pastoral and agricultural populations

The collision and integration of nomadic and agrarian civilizations have been a crucial theme throughout the historical process of China, particularly exemplified by the Northern Wei Dynasty established by the Tuoba Xianbei. During their southward and westward migrations, the Tuoba Xianbei realized early on that an agricultural economy offered greater population carrying capacity and organizational advantages compared to the traditional nomadic economy. Once they established dominance in Pingcheng, the environment proved unsuitable for traditional pastoral practices. Consequently, they implemented a series of policies to encourage a transition from a pastoral to an agrarian economy among the nomadic tribes.

Firstly, through the policy of “離散諸部,分土定居” they disbanded tribal organizations, distributed land around Pingcheng to various nomadic tribes, and prohibited unrestricted migration. This policy fostered contact and interaction between nomadic and agricultural communities and, by requiring a settled lifestyle, encouraged nomadic tribes to engage in agricultural production. Secondly, the “計口授田” policy was implemented to help those who had migrated from the Yellow River region to quickly resume agricultural practices by distributing land based on household size. Lastly, by implementing the “勸課農桑” policy, they motivated and urged various ethnic groups to participate in agricultural production, and further promoted the transition to farming and the development of the agricultural economy (Wei, 1974).

Archaeological evidence demonstrates that the transformation has been highly effective. Millet, broomcorn millet, and economic crops such as jujubes and walnuts have been identified among burial goods in ceramic vessels. Additionally, large quantities of carbonized millet remains were recovered from the Northern Wei imperial granary site at Caochangcheng in Datong. Stable carbon and nitrogen isotope analyses further indicate the expansion of agricultural activity in Pingcheng, alongside a decline in pastoralism. However, agriculture had not yet

achieved absolute dominance as the primary subsistence strategy during the Pingcheng era (Zhang et al., 2015; Hou et al., 2017; Hou and Gu, 2018b; Zhou et al., 2022; Liu et al., 2022; Hou et al., 2023).

The policy-driven livelihood transformation not only advanced agricultural development but also narrowed the social gap between nomadic and farming communities at both institutional and practical levels. Previous research indicates that the NSB populations were primarily engaged in a pastoral economy based on the herding of herbivorous livestock such as cattle and sheep, with the Tuoba Xianbei group serving as a typical representative of this nomadic society. In contrast, the YRB populations practiced an agricultural economy focused mainly on the cultivation of millet, with the Han-dominated agrarian population of the Central Plains serving as a representative example (Dong et al., 2022). Our study provides genetic evidence for agricultural development and the interaction between nomadic and agrarian populations during the Pingcheng period. DAPC analyses reveal that the PC_ALL occupy a transitional space between the NSB and YRB clusters. Further analyses of haplogroup structure, FST, and Median-joining network indicate that, despite their dominant maternal heritage from the Tuoba Xianbei, the Pingcheng population also exhibits genetic exchange with YRB populations.

These findings suggest that the Northern Wei's institutional policies not only facilitated economic transformation but also promoted the integration of pastoral and agricultural communities. This process ultimately left discernible maternal genetic signatures within the Pingcheng population.

4.2.2. Economic Drivers: The underrepresented commercial populations

Beyond institutional regulation, commercial activity played a more subtle yet indispensable role in facilitating widespread population movement and cultural exchange. Our results indicate that the Pingcheng population shares limited but direct maternal genetic links with WEA and SEA populations. Based on historical and archaeological evidence, we suggest that such long-distance genetic connections are likely associated with population movements along the Silk Road and the Tea-Horse Road. These gene flows underscore Pingcheng's status as a pivotal node within transregional trade networks and highlight the important role of commerce in fostering population interactions.

Although successive Chinese dynasties generally pursued policies that prioritized agriculture over commerce, the Northern Wei took an open, inclusive, and supportive stance toward commerce (also artisanal) industries (Li, 1974), leading to an unprecedentedly prosperous commercial sector in Pingcheng. Hua Mulan, a figure widely praised, admired, and recognized around the world, lived during the Northern Wei Dynasty. The lines from *The Song of Mulan*, “In the eastern market, she bought a fine steed; in the western, a saddle and pad. In the southern market, a bridle; in the northern, a long whip she had,” vividly capture the bustling prosperity of the markets during that time. Historical records also indicate a large marketplace in Pingcheng: “south of the Imperial City, surrounded by numerous large and small markets, with larger ones hosting 400–500 vendors and smaller ones accommodating 60–70 merchants” (郭城繞宮城南,悉築為坊,坊開巷,坊大者容四五百家,小者六七十家) (Xiao, 2000). These materials have realistically depicted the multi-centered, large-scale, and multi-ethnic mixed neighborhood space within Pingcheng.

Yet the role of commerce and merchant groups has been largely overlooked in prior studies. Due to their inherently mobile nature, merchant populations demonstrated high levels of adaptability, cultural plasticity, and intergroup communicative capacity. Often serving as bridges across cultural boundaries, such as in trade missions, these individuals facilitated exchange between otherwise isolated communities. As nomadic and agricultural populations settled and resumed production in Pingcheng, the need for efficient redistribution of goods grew. Trade thus played a key role in coordinating diverse economic models and became essential for broader social integration. Accordingly, Pingcheng was not merely a site of pastoral-agricultural convergence but also

a key node in an expansive trade network involving multiple ethnic groups. Though merchants likely did not form the demographic majority, their frequent migration, settlement, and intermarriage contributed to the broader integration of multi-source populations, leaving behind sparse yet detectable maternal genetic traces.

In conclusion, following their occupation of Pingcheng, the Tuoba Xianbei were confronted with profound transformations in both environmental and governance contexts. To achieve the transition from a steppe polity to a centralized dynastic regime, they required a stable economic foundation and institutional mechanisms to support social restructuring. Within this transformation, the sustained mobility of diverse populations played a pivotal role in enhancing both productive capacity and institutional adaptability.

Notably, these movements also entailed the exchange, disintegration, and reconfiguration of cultural, ideological, institutional, and organizational structures. Such interactions gradually blurred ethnic boundaries and facilitated intergroup gene flow, culminating in the formation of the highly diverse maternal genetic landscape of the Pingcheng population.

4.3. The dynamic integration pattern of Pingcheng

Our analyses reveal marked differences among the PC_HY, PC_JMF, and PC_YTNL cemeteries in terms of haplogroup composition, haplogroup frequency-based PCA, and DAPC based on complete mitochondrial sequences. However, population-level analyses using full mitochondrial genomes (FST and AMOVA) did not detect statistically significant genetic differentiation. This apparent contradiction—structural divergence at the haplogroup level alongside minimal sequence-level differentiation—likely reflects a genetic signature characteristic of an ongoing admixture process.

As demonstrated above, no significant genetic divergence exists among the three cemeteries, all of which display genetic affinity with Xianbei groups. This is evidenced by overall maternal genetic homogeneity and continuity. At the same time, the maternal gene pool of the Pingcheng population shows signs of recent, rapid expansion accompanied by continuous influx from multiple maternal sources. Independent diversity indices and neutrality tests for each cemetery support this trend. All three cemeteries exhibit high haplotype diversity ($H_d > 0.97$), with consistently negative values for Tajima's D and Fu's Fs (Tajima's D: PC_HY = -1.85, PC_JMF = -1.40, PC_YTNL = -2.66; Fu's Fs: PC_HY = -16.67, PC_JMF = -3.77, PC_YTNL = -48.57), indicating recent demographic expansion with the input of diverse maternal lineages. Moreover, their haplogroup compositions differ, with evidence of unique maternal inputs in each cemetery (e.g., haplogroup U in PC_HY and haplogroup Y in PC_JMF).

These findings suggest that, despite a shared maternal genetic background, the Pingcheng cemeteries experienced ongoing gene flow—both among themselves and with recently introduced maternal lineages. This process involved lineage influx, maternal expansion, and complex demographic dynamics. The discrepancy between haplogroup-level variation and overall sequence homogeneity likely reflects a time lag between admixture events and the accumulation of sequence-level divergence. As Pingcheng was a newly established and short-lived capital (less than a century), insufficient time had passed for differentiation to manifest statistically. Given frequent gene flow, limited generational turnover, and the presence of diverse maternal inputs, the maternal genetic landscape remained in flux—lineages had merged, but not yet diverged at the sequence level. The result is a transitional genetic profile indicative of a population in the midst of dynamic integration.

Thus, the Pingcheng population represents a case of multi-source genetic recombination shaped by ongoing maternal admixture. This genetic pattern aligns closely with the historical context of Pingcheng—its foundation under the Northern Wei dynasty, its frontier location in the agro-pastoral ecotone, and its role as a hub of large-scale migration and interethnic contact.

In addition, our results indicate variation in the direction and extent of admixture among the three cemeteries. Analyses of haplogroup composition, DAPC, and median-joining networks reveal differing maternal affinities with populations from the YRB and WEA. Each cemetery contains distinct signatures of maternal introgression. For instance, PC_HY harbors a combined 10.34 % of haplogroups H and U, with haplogroup U (e.g., U5b2a3) exclusively present, suggesting closer genetic ties with WEA populations. FST analysis further supports this, as PC_HY shows lower genetic distance to WEA (most $FST > 0.24$, $P < 0.05$) compared to PC_JMF and PC_YTNL (most $FST > 0.35$, $P < 0.05$). By contrast, PC_JMF exhibits the highest frequency of haplogroup D among the three cemeteries, with C and D together accounting for 40.91 %, reflecting a stronger genetic legacy from northern steppe populations. Although Tajima's D for PC_JMF is negative, it is not statistically significant ($P > 0.10$), and other metrics suggest only mild population expansion—markedly different from the other two cemeteries.

Archaeological studies indicate that Pingcheng's burial distribution followed hierarchically organized spatial principles influenced by both Xianbei customs, which emphasized westward burial, and Han traditions, which prioritized a north-south axis aligned with social rank (Cao, 2016). Differences in social status, political affiliation, and cultural identity among cemetery groups may have influenced their respective integration trajectories and degrees of admixture with external populations, leaving distinct signatures in their genetic structure. This pattern of “unity within diversity” exemplifies the dynamics of early admixture: traditional ethnic identities and social boundaries continued to shape interaction, yet co-residence and sustained contact gradually blurred those boundaries, fostering cultural and genetic integration. Our results provide the first mitochondrial-level evidence of a potential association between social hierarchy and genetic structure in early medieval northern China.

As a contact zone for diverse populations, Pingcheng functioned as a crucible of admixture, where the direction, pace, and depth of integration varied across groups. The process was neither singular nor linear but was shaped by the Tuoba Xianbei's integrationist traditions, social stratification, state institutions, governance strategies, and identity negotiation mechanisms. Different groups followed distinct pathways toward social incorporation and genetic admixture. The “Pingcheng model” offers a representative case of China's “Second Great Ethnic Integration” during the early medieval period, when historically divided ethnic groups converged into a more unified and pluralistic society (Sun, 2003). It provides a temporally and spatially specific lens for understanding the mechanisms of population integration in early medieval China.

5. Conclusion

This study presents the first large-scale matrilineal genetic dataset of residents in an ancient Chinese capital, based on complete mitochondrial genome sequences from three major cemeteries in Pingcheng during the Northern Wei period. The results shed light on the maternal genetic composition, population origins, and mechanisms of admixture in Pingcheng, leading to the following key conclusions.

1 Matrilineal Genetic Structure:

The Pingcheng population exhibited a complex and diverse maternal genetic landscape. Haplotype diversity was high, with the gene pool dominated by lineages commonly found in the northern steppe zone of China, alongside maternal components from the Yellow River Basin, southern China, and regions west of Xinjiang. This pattern reflects the genetic profile of a metropolitan population shaped by large-scale demographic aggregation.

2 Population Genetic History:

The maternal gene pool of Pingcheng underwent rapid recent expansion, accompanied by sustained inputs of exogenous lineages, forming a typical pattern of multiethnic admixture. Genetically, the Pingcheng population is most closely related to the Tuoba Xianbei, displaying substantial maternal homogeneity and affinity, which highlights the foundational role of the Tuoba Xianbei in shaping Pingcheng's maternal genetic structure. Furthermore, genetic continuity between Pingcheng and Tuoba Xianbei groups from south-central Inner Mongolia and the Hulunbuir region provides molecular support for the Tuoba Xianbei's southward and westward migration, culminating in the establishment of Pingcheng as the capital.

On top of the Tuoba Xianbei genetic foundation, the presence of maternal lineages from the Yellow River Basin likely reflects the genetic impact of large-scale population movements during the Northern Wei's unification of northern China. In addition, limited but direct maternal links with populations from southern China, Xinjiang, and regions further west may indicate population mobility along the Silk Road and the Tea-Horse Road, underscoring Pingcheng's role as a strategic eastern hub in the Eurasian exchange network.

3 Mechanisms of Population Admixture:

The Tuoba Xianbei's longstanding tradition of ethnic integration not only fostered the open and inclusive genetic profile of Pingcheng but also ideologically promoted the sustained influx of diverse populations. National integration policies accelerated the convergence of northern steppe and Central Plains agrarian groups, while economic incentives facilitated the participation of commercial groups in the broader admixture process.

A striking feature of the Pingcheng population is the coexistence of pronounced structural divergence at the haplogroup level and low differentiation at the sequence level, suggesting a temporal lag between admixture events and observable genetic divergence. This pattern is indicative of an ongoing process of multi-source integration and dynamic recombination. Differences in social hierarchy, political affiliation, and cultural identity among the cemeteries may have influenced the trajectories and intensity of admixture with external populations, leaving distinct genetic signals in each group.

As a "melting pot" of diverse populations, Pingcheng exhibited admixture processes that varied in direction, tempo, and degree. This provides a vivid snapshot of the dynamic and transitional stage of genetic integration during fifth-century China. The findings offer important empirical evidence for understanding the demographic mechanisms that contributed to the evolution of Huaxia civilization in the early medieval period. It should be noted, however, that this study reflects only the maternal dimension of genetic structure. Future research incorporating paternal and autosomal genomic data will be essential for achieving a more comprehensive understanding of admixture patterns and population history in Pingcheng.

CRediT authorship contribution statement

Hexun Cui: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Xiaogang Hou:** Resources, Investigation. **Xiaojing Lü:** Resources, Investigation. **Xiaoting Jing:** Resources, Investigation. **Youyang Qu:** Data curation. **Jiashuo Zhang:** Data curation. **Pengzhen Li:** Investigation. **Dawei Cai:** Writing – review & editing, Supervision, Software, Resources, Project administration, Funding acquisition.

Data availability statement

The datasets presented in this study can be found in online repositories. The name of the repository and the accession number are provided below: The Genbase at the National Genomics Data Center, with the accession number [PRJCA033322](https://ngdc.cn/PRJCA033322) (accessible at <https://ngdc.cn/PRJCA033322>)

cb.ac.cn/genbase/.

Declaration of competing interest

All authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jas.2025.106341>.

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