



Genetic structure of Shandong taurine cattle in Han Dynasty

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ABSTRACT

Shandong province, located in the Lower Yellow River, is one of the birthplaces of ancient Chinese civilization. In this region, domestic cattle were central to the development of agrarian society, serving not only as sources of meat and leather, but more importantly as indispensable draught animals for ploughing and transport. However, the genetic structure of these cattle and their relationships with surrounding populations remain largely unexplored. In this study, we sequenced 25 individuals from two Shandong sites dating to the late Dawenkou culture and the Han Dynasty, ultimately retaining one Han Dynasty genome (>70,000 SNPs) for downstream population genetic analysis. To begin with, mitochondrial genome analysis identified the Han Dynasty individual from Shandong as taurine cattle, predominantly belonging to haplogroup T3. Furthermore, it showed the closest genetic affinity to late Neolithic Shimao and ~2,500-year-old Bangga taurine cattle, suggesting close genetic connections among ancient Chinese taurine populations. Finally, we confirmed that contemporary taurine populations were mainly descended from ancient Chinese taurine cattle, with shared genetic components persisting over time. These results shed light on the spread and adaptation of ancient Chinese taurine cattle across the Yellow River Basin, highlighting their significant genetic contribution to modern taurine populations and their foundational role in early agricultural centers that underpinned the rise of Chinese civilization.

1. Introduction

In human history to date, only a few species of large animals have been domesticated, with cattle representing one of the most remarkable achievements of the Neolithic period (Diamond, 2002). As a vital component of early agricultural societies, cattle provided not only meat, dairy, and leather, but also essential labor for cultivation and transport, playing a crucial role in the development of human culture and civilization (Ebersbach, 2002). Both archaeological and genetic evidence strongly indicate that taurine and indicine cattle were independently domesticated from aurochs, with taurine cattle emerging in the Near East around 10,000 years before present (BP) (Ajmone-Marsan et al.,

2010) and indicine cattle in the Indus Valley approximately 8000 years BP (Verdugo, et al., 2019, Loftus, et al., 1994). Following domestication, these two lineages spread separately across the world, driven by human migrations (Felius, et al., 2014, Patel, 2009).

The introduction of domestic cattle in China not only greatly enriched people's meat resources but also spurred the development of animal sacrifice practices. Archaeological evidence suggests that the earliest undisputed domestic cattle remains in Northwest China were discovered at the Majiayao cultural layer (5,300–4,500 BP) of the Shizhao Village site (Lu, et al., 2017), as well as at the Qijia cultural layer (4,200–3,500 BP) at the sites of Qinweijia and Dahezhuang in Yongjing, and again at Shizhao Village in Tianshui, Gansu Province (Zhou, 1999).

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Moreover, the earliest known remains of taurine cattle in Northeast China were found at the Houtaoomuga site in Jilin Province, dating to approximately 5,500–5,300 BP (Cai, et al., 2018). Genetic evidence from mitochondrial genomes widely supports that Chinese taurine cattle originated from the Near East, with two primary migration routes: the Northwest and Northeast entrance routes (Dawei, et al., 2014, Zhang, et al., 2023). Shimao, a major Neolithic urban center known for its monumental architecture and complex society (Sun, et al., 2018), offers key genetic evidence for the early presence of domestic taurine cattle in northern China around 3,900 years BP (Chen, et al., 2018). Recent ancient DNA research from the Bangga site (~2,500 years BP), located near the modern agropastoral village of Bangga in the Yarlung River Valley on the southern Tibetan Plateau, supports the genetic legacy of the population's taurine cattle from Shimao to Bangga (Chen, et al., 2023a).

The Yellow River Basin in northern China was a key cradle of Neolithic culture and a vital center for early agricultural and livestock development (Zhao, 2011). Shandong was a crucial center of early Chinese civilization in the Lower Yellow River Basin. It played a significant role throughout key periods from prehistory to history, including the Dawenkou and Shandong Longshan cultures and the Shang, Zhou, and Han dynasties. During the Han Dynasty, Shandong entered a period of remarkable prosperity, characterized by advanced agricultural techniques, booming handicraft industries, population growth, urban development, and flourishing trade and cultural exchanges (Jianming, 2019, Qian and Huang, 2021, Gan, 2023, Shi, 2014). Genomic studies of ancient human populations have highlighted the strong genetic connections throughout the Yellow River Basin (Liu, et al., 2025, Du, et al., 2024), revealing patterns of migration and cultural exchange. The spread of agricultural practices, including cattle husbandry, appears to have been a key factor in the diffusion of populations and their genetic legacies across the basin. Despite this, very

limited zooarchaeological research has been conducted to date on domestic cattle in the Lower Yellow River Basin, leaving a significant gap in our understanding of their cultural and biological roles. In the Han Dynasty, domestic cattle were not only a major source of meat and secondary products but also played important ritual roles, particularly in sacrificial practices. Animal burial practices served as clear indicators of wealth and social hierarchy in ancient societies (Wang, et al., 2025). However, the genetic history and local development of taurine cattle in this region remain poorly understood. Systematic genomic research on ancient cattle from Shandong and surrounding areas is therefore essential to clarify their origins, dispersal, and long-term contributions to the evolution of East Asian taurine lineages.

Time-stamped ancient DNA data can help clarify historical selection processes and provide direct evidence of the genomic dynamics experienced by populations. To investigate the genetic structure of ancient cattle from the Shandong region and their potential connections with the Yellow River Basin, we sampled 25 ancient individuals from two archaeological sites in Shandong region, dating to the late Dawenkou period ($n = 24$) and the Han Dynasty ($n = 1$) (Fig. 1A). Due to poor DNA preservation, only the Han Dynasty individual yielded sufficient genome-wide data for analysis. Although limited in genomic representation, this individual provides a valuable case study for exploring cattle ancestry and domestication history in Shandong during the Han Dynasty. While not fully representative of the entire cattle population at the time, the genomic data offer preliminary insights into the genetic makeup of cattle in the Han Dynasty Shandong and their role in local agricultural practices.

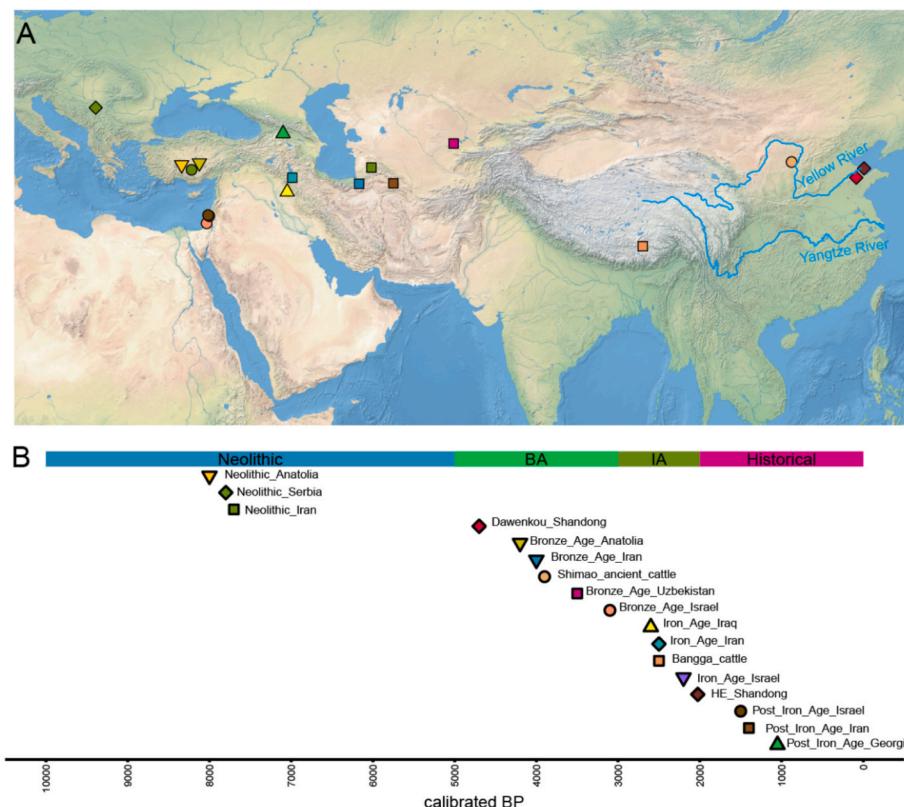


Fig. 1. Geographic location and dates of ancient individuals. (A) Geographical location of the newly sampled ancient Shandong sample, shown alongside previously published ancient individuals from across the world and archaeological sites in China. (B) Calibrated radiocarbon dates of ancient samples from Shandong. Important published samples from China and other regions worldwide are also presented.

2. Materials and methods

2.1. Modern cattle genotyping following a previously published dataset

We generated genotype data from several previously published studies (NCBI BioProject accessions: PRJNA379859, PRJNA833533, PRJNA720245) (Chen, et al., 2018, Chen, et al., 2022, Gao, et al., 2022). Low-quality bases and sequencing artifacts were removed using fastp (Chen, 2023), and the resulting clean reads were aligned to the cattle reference genome (ARS-UCD1.2, GCA_002263795.2) (Rosen, et al., 2020) using BWA-MEM (version 0.7.17) with default settings. The aligned BAM files were then sorted with SAMtools (v1.9) (Li and Durbin, 2010), and potential PCR duplicates were marked using Picard Tools (version 2.21.4). Variant calling was performed using the HaplotypeCaller module in GATK, with the “-ERC GVCF” option to generate GVCF files (McKenna, et al., 2010). After applying stringent quality control filters, a total of 4,825,034 common SNPs were retained for downstream analyses.

2.2. Archaeological background and radiocarbon dating of the studied sites

We collected 25 ancient samples from two archaeological sites in Linzi District of Shandong Province: the Xujia Village East Cemetery and the Huaixing Site. Specimens from the Xujia Village East Cemetery were recovered from burial contexts, while those from the Huaixing Site came from huikeng. Despite Shandong’s prominent role in early state development and agricultural history, zooarchaeological and genetic studies on domestic cattle from the region remain scarce. Thus, these remains offer rare and valuable insights into local cattle management strategies, subsistence practices, and the economic, ritual, and funerary significance of cattle in ancient Shandong. Approval for their use was curated by co-authors and obtained with permission from the respective provincial archaeology institutes or universities that managed the samples. Then, we randomly selected three cattle bone samples for radiocarbon dating, which were analyzed using a compact 0.5 MeV NEC Accelerator Mass Spectrometer at the Guangzhou Institute of Geochemistry, Chinese Academy of Sciences (Zhu, et al., 2015). All three radiocarbon dates were modelled in OxCal (Ramsey and Lee, 2013) using the IntCal20 (Reimer, et al., 2020) calibration curve.

2.3. Ancient DNA extraction and library preparation

All samples were processed in the dedicated ancient DNA clean room at the Institute of Anthropology, Xiamen University. Animal remains were first cleaned with 75 % ethanol and 10 % sodium hypochlorite to remove surface contaminants, followed by 30 min of ultraviolet light exposure. Using a blade saw, the teeth were separated from the jaws, and approximately 100 mg of powder was drilled from the tooth roots. DNA was extracted using a modified protocol based on Rohland’s method (Rohland, et al., 2018), with 1 mL of lysis buffer (0.5 mM EDTA and 0.25 mg/mL Proteinase K) used to digest the powder at 37 °C and 300 rpm. The resulting DNA was purified with the MinElute PCR Purification Kit (Qiagen, Germany) following the manufacturer’s instructions. Double-stranded DNA libraries were prepared for all samples using the NEBNext Ultra II DNA Library Prep Kit (New England Biolabs) (Zhu, et al., 2024).

2.4. Ancient DNA sequence data processing

We used AdapterRemoval v2.3.1 to trim the sequencing adapters and merged the paired-end reads into a single sequence (Schubert, et al., 2016). The merged reads were then mapped onto the cattle reference genome (ARS-UCD1.2, GCA_002263795.2) (Rosen, et al., 2020) using BWA v0.7.17 samse (Li and Durbin, 2009), with parameters -l 1024 and -n 0.01. Dedup v0.12.3 (Peltzer, et al., 2016) was used to remove the

PCR duplicates. Then, we clipped 5 bases from both ends of each read to avoid excess C->T and G-> A transitions at the ends of the sequences, using trimBam implemented in BamUtil v1.0.14 (<https://github.com/statgen/bamUtil>) (Jun, et al., 2015). We filtered alignment quality using mpileup implemented in samtools with parameters -q10 and -Q10. Pseudo-haploid calls for out samples were generated using the dataset of modern cattle variation SNPs as reference and parameter –Random-Haploid in pileupCaller (<https://github.com/stschiff/sequenceTools>). For more detailed information, please refer to Supplementary Table 1. At the same time, we used the method described above to analyze published ancient cattle genome data. See Supplementary Table 2 for published ancient cattle genomes used in downstream analysis.

2.5. Authentication of ancient DNA and assessment of genetic sex

MapDamage2.0 (Jónsson, et al., 2013) was used to detect the post-mortem pattern of ancient DNA and to estimate 5' C->T and 3' G->A misincorporation rates. We estimated the genetic sex of individuals by comparing the genome coverage of the X chromosomes with that of autosomes (Fu, et al., 2016). Since males have only one copy of X, the coverage on the X should be half of that on autosomes and roughly equal in females.

2.6. Principal component analysis

We performed principal component analysis (PCA) using smartpca v16000 with default parameters, setting lsqproject: YES (Patterson, et al., 2006). The PCA was calculated based on modern cattle populations, and ancient individuals were subsequently projected onto the first two principal components.

2.7. ADMIXTURE and phylogenetic analysis

After pruning for linkage disequilibrium in PLINK v1.90 (Chang, et al., 2015) using the parameters –indep-pairwise 200 25 0.4 (Peter, 2016a, Lawson, et al., 2018), we conducted an unsupervised admixture analysis with ADMIXTURE v1.3.0 (Alexander, et al., 2009). Fivefold cross-validation was performed for each value of K, with the number of ancestral populations ranging from 2 to 10. Additionally, a neighbor-joining tree was constructed using MEGA (Kumar, et al., 2018), based on a pairwise genetic distance matrix generated from the whole-genome SNP dataset using PLINK v1.90.

2.8. F-statistics

We calculated f_4 statistics in the form of $f_4(Bos grunniens, A; B, C)$ to explore the additional gene flow between A and B/C relative to C/B. QpDstat v980 was performed to calculate the f_4 statistics using parameter f_4 -mode: YES (Patterson, et al., 2012, Peter, 2016b). Qp3Pop v651 was implemented to calculate the outgroup- f_3 analysis. We calculated outgroup- f_3 statistics in the form of $f_3(A, B; Bos grunniens)$ to measure the shared genetic drift between A and B. Both software programs are implemented in ADMIXTOOLS (Patterson, et al., 2012).

3. Results

3.1. Ancient genome-wide data from the Shandong Province

We generated genome-wide data from 25 ancient individuals sampled from 2 sites in the Shandong region. Calibrated carbon dating placed these individuals between 2,025 and 4,795 years BP, covering the late Dawenkou cultural period and Han Dynasty (Fig. 1B). DNA extraction and double-stranded library preparation were conducted for all 25 individuals, resulting in genome-wide coverage ranging from $0.0005 \times$ to $0.0248 \times$ (Table 1 and S1). Samples were filtered through several steps. The authenticity of ancient genome-wide data was verified

Table 1
Summary of ancient sample reported in this study.

Samples	Label	Number of SNPs Modern cattle variation SNPs	Coverage	Date (cal years BP)
H1	Dawenkou_Shandong	11,680	0.49 %	4795- 4785 ^a
H10	Dawenkou_Shandong	12,590	0.56 %	4795- 4785 ^a
H11	Dawenkou_Shandong	19,170	0.90 %	4795- 4785 ^a
H12	Dawenkou_Shandong	23,039	1.00 %	4785 ± 30 BP
H13	Dawenkou_Shandong	15,965	0.71 %	4795- 4785 ^a
H14	Dawenkou_Shandong	6610	0.27 %	4795- 4785 ^a
H15	Dawenkou_Shandong	17,917	0.81 %	4795- 4785 ^a
H16	Dawenkou_Shandong	7130	0.30 %	4795- 4785 ^a
H17	Dawenkou_Shandong	1192	0.05 %	4795- 4785 ^a
H18	Dawenkou_Shandong	22,070	1.05 %	4795- 4785 ^a
H19	Dawenkou_Shandong	19,582	0.87 %	4795- 4785 ^a
H2	Dawenkou_Shandong	14,657	0.61 %	4795- 4785 ^a
H20	HE_Shandong	72,979	2.48 %	2025 ± 20 BP
H21	Dawenkou_Shandong	13,276	0.60 %	4795- 4785 ^a
H23	Dawenkou_Shandong	26,314	1.34 %	4795 ± 30 BP
H24	Dawenkou_Shandong	14,254	0.63 %	4795- 4785 ^a
H25	Dawenkou_Shandong	19,291	0.89 %	4795- 4785 ^a
H26	Dawenkou_Shandong	5916	0.25 %	4795- 4785 ^a
H27	Dawenkou_Shandong	5671	0.23 %	4795- 4785 ^a
H3	Dawenkou_Shandong	15,309	0.68 %	4795- 4785 ^a
H4	Dawenkou_Shandong	21,980	0.97 %	4795- 4785 ^a
H5	Dawenkou_Shandong	18,020	0.80 %	4795- 4785 ^a
H6	Dawenkou_Shandong	23,706	1.10 %	4795- 4785 ^a
H7	Dawenkou_Shandong	18,557	0.80 %	4795- 4785 ^a
H8	Dawenkou_Shandong	7587	0.31 %	4795- 4785 ^a

^a We note that this sample was not directly radiocarbon dated. The date used here was based on archaeological context.

by identifying the presence of post-mortem patterns of ancient DNA (**Fig. S1**). To minimize the impact of post-mortem damage on genotyping, 5 bp were trimmed from each end of the reads. Then, pseudo-haploid calls for 25 individuals were generated using a modern cattle variation SNP panel. Specifically, historical era individual from Shandong (HE_Shandong) with at least 70,000 SNPs was retained for downstream population genetic analyses, and individuals from the late Dawenkou cultural period with lower coverage (< 27,000 SNPs) were removed from downstream analyses. The mitogenome of the historical era individual was compared with published data on mtDNA hyper-variable fragments (Chen, et al., 2023a, Zhang, et al., 2021), and its mitochondrial DNA falls within the domestic taurine cattle haplogroup T3. Biological sex determination identified the individual from the Han Dynasty as male. We merged our data with previously published modern and ancient cattle genome datasets for further population genetic analysis. This dataset represents the first collection of ancient cattle

genomes from the Shandong region, highlighting the role of livestock in sustaining agricultural economies and cultural practices in antiquity.

3.2. Characterization of the genetic profile of Shandong taurine cattle from the Han Dynasty

In this study, we initially conducted principal-component analysis (PCA) to examine the overall genomic structure of the ancient Shandong taurine in the Han Dynasty. We project ancient individuals onto axes computed using the present-day cattle population. The PCA result showed modern cattle populations formed several major genetic clusters (**Fig. 2A**): Eurasian taurine, Chinese taurine, Chinese indicine, and Indian indicine. We found that the Shandong taurine cattle from the historical era, along with the previously reported ~3,900-year-old Shimao and ~2,500-year-old Bangga taurine cattle (Chen, et al., 2018, Chen, et al., 2023a), clustered together and located close to the genetic cline of ancient populations worldwide. We also observed the genetic substructure of other ancient taurine individuals worldwide, which were clustered into distinct major geographical groups (Serbia, Anatolia, Iran, Georgia, and Israel). This genetic structure aligns with the findings of a previous study (Verdugo, et al., 2019).

Next, we constructed a Neighbor-Joining (NJ) tree (**Fig. 2B** and **Fig. S2**). In the NJ phylogenetic tree, ancient Shandong cattle in the historical era fell within the same branch as the ancient Shimao and Bangga taurine cattle. Similarly, unsupervised ADMIXTURE analyses displayed that Shandong historical individuals shared genetic compositions similar to ancient Shimao and Bangga taurine cattle (**Fig. S3**). To further investigate the genetic relationships among ancient Shandong taurine, other ancient, and present-day cattle, we calculated the out-group f_3 statistic from whole-genome sequences to assess their shared genetic drift (**Fig. S4**). This analysis was corroborated by the PCA and NJ results, which revealed that ancient Shandong taurine cattle were highly similar to the Shimao cattle from Shaanxi Province, China and the Bangga cattle from the Tibetan Plateau. These results indicated that the Shandong historical individual was related to the ancient Shimao and Bangga taurine cattle, suggesting a shared genetic ancestry.

3.3. Strong genetic connections among ancient HE_Shandong, Shimao, and Bangga taurine cattle

The Yellow River Basin is one of the cradles of Chinese civilization. Recent ancient human genomic studies indicate that agricultural populations across the Yellow River Basin share a common ancestry (Du, et al., 2024, Xiong, et al., 2024, Ma, et al., 2025). As a key commensal species shaped through human domestication, the genetic relationships between ancient cattle from Shandong and surrounding populations remain largely unexplored. To gain insights into the genetic relationships and population history of Shandong historical individual, we then applied the quantitative f_4 statistic in the format of $f_4(Bos grunniens, HE_Shandong; Shimao_ancient_cattle/Bangga_cattle, References populations)$ to compare the genomic profiles of the Shandong populations with those of the late Neolithic Shimao populations in northern China and the ~2,500-year-old Bangga populations on the Tibetan Plateau. This analysis was conducted using a reference set comprising 14 representative ancient populations worldwide. Interestingly, the Shandong historical individual in this study, HE_Shandong (~2,025 years BP), showed genetic affinities with both ancient Shimao and Bangga taurine cattle populations (**Fig. 3A**), evidenced by Z scores of f_4 ranging from -25.194 to 1.9352 (**Table S3**). Likewise, the negative results of f_4 (*Bos grunniens, Shimao_ancient_cattle/Bangga_cattle; HE_Shandong, References populations*) confirm this genetic affinity (**Fig. S5** and **Table S4**). Our results reveal a close genetic relationship among the historical Shandong individual from the Lower Yellow River Basin, the Shimao taurine cattle from the middle Yellow River Basin, and the Bangga taurine cattle from the Tibetan Plateau. The observed genetic affinity indicates a shared genetic component among these populations

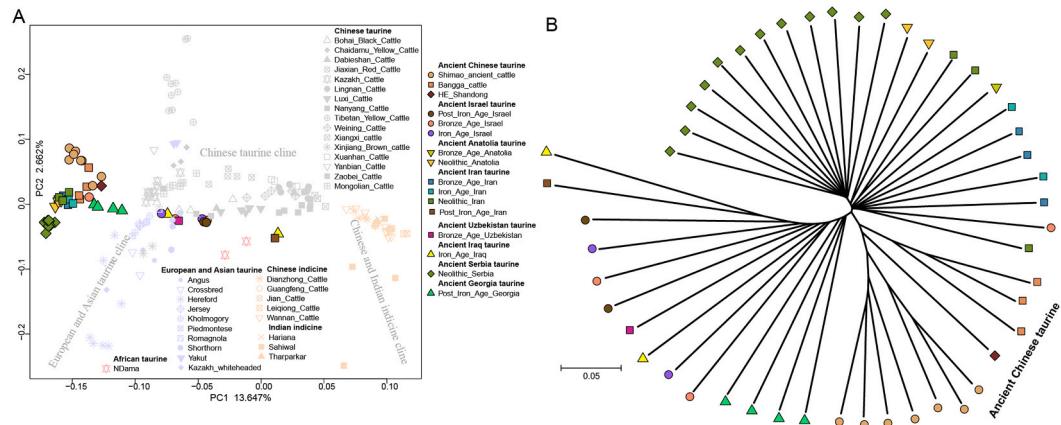


Fig. 2. General genetic structure of Shandong taurine cattle from the historical era. (A) Principal-component analysis (PCA) plot of ancient and present-day cattle. (B) Neighbor-Joining tree including ancient Chinese taurine cattle and representative ancient individuals worldwide.

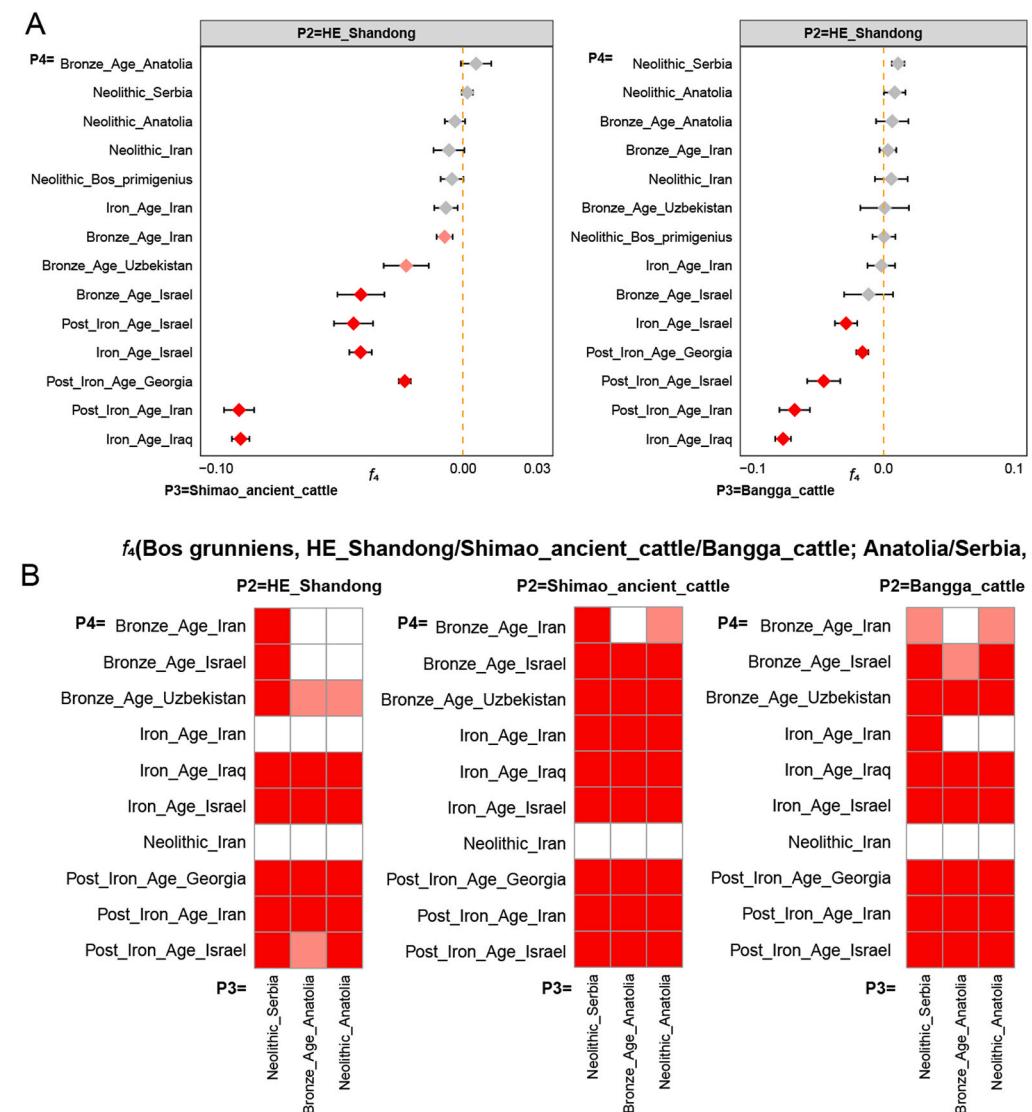


Fig. 3. The genetic relationships of among ancient Chinese taurine cattle. (A) f_4 -statistics test in the form of $f_4(Bos grunniens, HE_Shandong; Shimao_ancient_cattle/Bangga_cattle; Anatolia/Serbia, X)$ shows that HE_Shandong shares close genetic affinity with both Shimao_ancient_cattle and Bangga_cattle. (B) Heatmap of f_4 -statistics illustrating genetic affinities among ancient Chinese taurine cattle and ancient individuals worldwide. $|Z| \geq 3$ indicated by deep red or blue, $3 > |Z| \geq 2$ indicated in light red or blue.

and underscores their contribution to the genetic structure of ancient Chinese taurine cattle. We further investigated the genetic affinities between ancient Chinese taurine cattle and other ancient populations from the Neolithic to the Iron Age. We found suggestive evidence that taurine cattle from the HE Shandong, Shimao, and Bangga shared more alleles with populations from Anatolia and Serbia (including Neolithic_Serbia, Neolithic_Anatolia, and Bronze_Anatolia) (Fig. 3B), evidenced by Z scores of f_4 (*Bos grunniens*, HE_Shandong/Shimao_ancient_cattle/Bangga_cattle; Anatolia/Serbia, X) ranging from -47.038 to 1.94 (Table S5). In this analysis, X refers to the populations from Iran, Israel, Uzbekistan, Iraq, and Georgia. We then utilised quantitative f_4 in the format of f_4 (*Bos grunniens*, HE_Shandong/Shimao_ancient_cattle/Bangga_cattle; Neolithic_Anatolia/Bronze_Age_Anatolia, Neolithic_Serbia), which showed no difference in the genetic affinity of ancient Chinese taurine populations to ancient Anatolia and Serbia (Table S6). In summary, the similar genetic profiles observed among HE_Shandong, Shimao, and Bangga taurine cattle reflect close genetic connections among ancient taurine populations across different regions of China, underscoring their collective role in shaping the genetic landscape of indigenous Chinese cattle.

3.4. The contribution of ancient Chinese taurine cattle to contemporary taurine populations

To further determine the origin of present-day Chinese cattle, we then used f_4 statistics to measure the genetic affinities among all Chinese cattle and the ancient populations worldwide. We found that contemporary Chinese taurine cattle (Chen, et al., 2018, Chen, et al., 2022) showed the closest genetic affinity with HE Shandong and Shimao, with Z scores of f_4 (*Bos grunniens*, present-day Chinese taurine cattle; Israel/ Israel/ Georgia/Iraq/ Iran Group, HE_Shandong/Shimao_ancient_cattle) ranging from -1.016 to 45.375 (Table S7). Meanwhile, compared with present-day Eurasian taurine cattle, present-day Chinese taurine cattle also show a stronger genetic affinity with HE Shandong and Shimao populations, as evidenced by Z-scores of f_4 (*Bos grunniens*, present-day Chinese taurine cattle; present-day Eurasian taurine, HE_Shandong/Shimao_ancient_cattle) ranging from 0.690 to 44.131 (Table S8). In general, both ancient and contemporary Chinese taurine cattle exhibit the highest level of allele sharing (Fig. 4A). These results confirmed that modern Chinese taurine cattle were mainly descended from ancient Chinese taurine cattle. Notably, modern Chinese indicine group shared an excess affinity with modern Indian

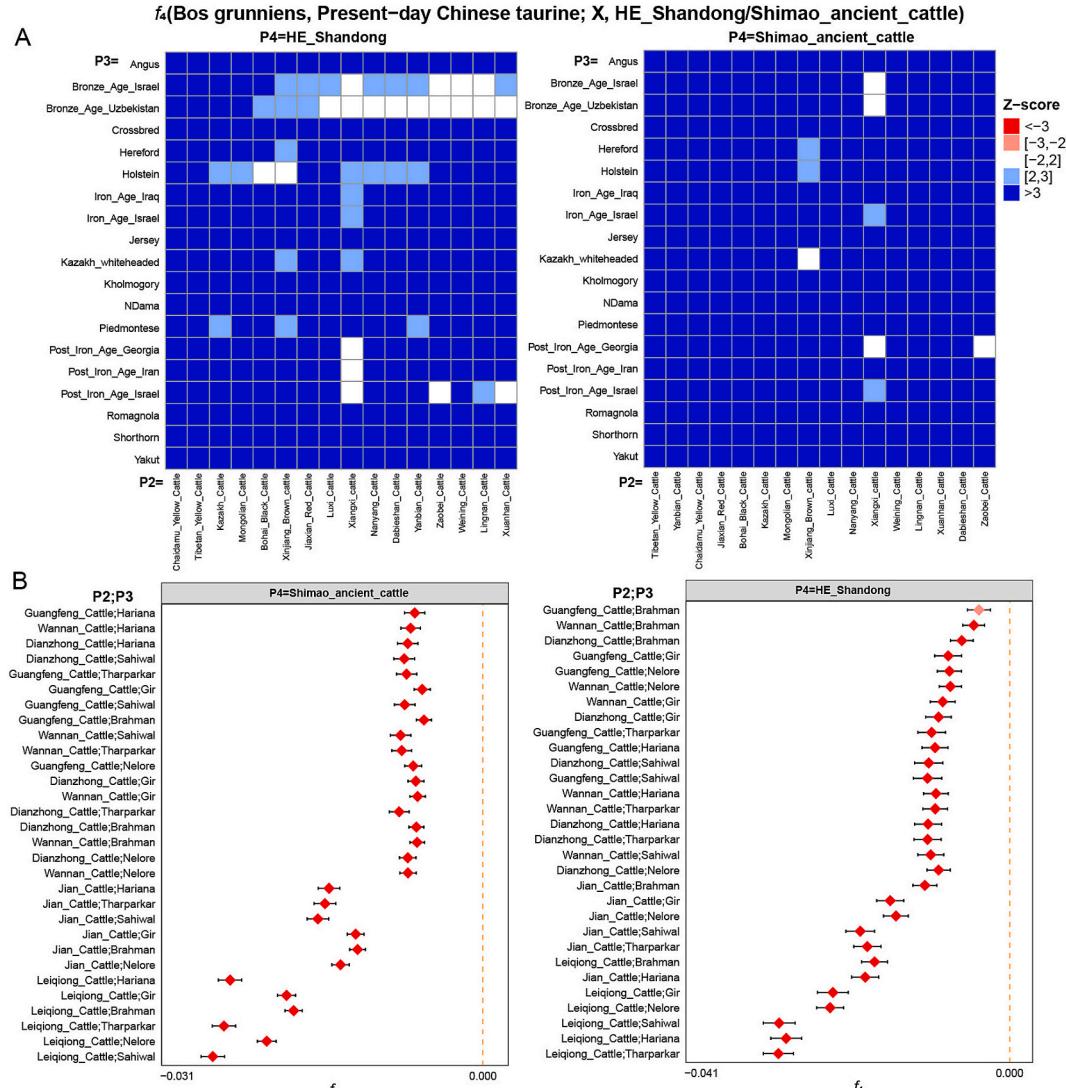


Fig. 4. f_4 -statistics plots show the genetic affinity of contemporary cattle populations. (A) f_4 -statistics test in the form of f_4 (*Bos grunniens*, present-day Chinese taurine cattle; HE_Shandong/Shimao_ancient_cattle, reference populations) indicating the close genetic profiles between modern and ancient Chinese taurine cattle. (B) f_4 -statistics test in the form of f_4 (*Bos grunniens*, present-day Chinese indicine; present-day Indian indicine, HE_Shandong/Shimao_ancient_cattle) indicating the close genetic profiles between Chinese and Indian indicine cattle.

indicine groups (Chen, et al., 2023b) compared to HE Shandong and Shimao (Fig. 4B), evidenced by the Z-score of f_4 (*Bos grunniens*, present-day Chinese indicine; present-day Indian indicine, HE Shandong/Shimao_ancient_cattle) ranging from $-23.051 < Z < -2.649$ (Table S9). In present-day Chinese cattle populations, we observed two genetically distinct ancestral lineages, derived from taurine and indicine cattle, reflecting their divergent domestication processes and migration trajectories. Modern taurine cattle populations are genetically closest to ancient Chinese taurine cattle, highlighting the long-term influence of both human management and environmental adaptation in shaping cattle genomes over millennia.

4. Discussion

Cattle, one of the six key livestock species in Chinese history, played an increasingly important role in ancient agrarian societies. This study collects cattle specimens from two archaeological sites in Shandong Province, dating to the late Dawenkou period and the Han Dynasty, with an estimated age range of 4,795 to 2,025 years BP. Due to the extremely low coverage of the late Dawenkou period samples, only the Shandong historical individual was included in downstream analyses. The Han Dynasty marked a mature phase in the development of animal husbandry in ancient China, supported by a flourishing millet-based agricultural economy and increasingly sophisticated livestock management (Liao, et al., 2022, Zhou, 2016). Cattle were integral not only as a source of meat but more critically ploughing, transportation, and other essential agricultural activities. Cattle remains found in tombs, highlighting their significant social and ritual roles. Genetic sexing identified the Han Dynasty cattle individual as male, consistent with the common practice of including male animals as grave goods. This practice aligns with traditional Chinese burial customs and is further supported by evidence from other animal burial studies. For example, burials of male horses in chariot pits are frequently observed in Qin Dynasty tombs (Li, et al., 2022), reflecting similar ritual preferences. Therefore, the cattle remains recovered from the Han Dynasty tomb offer valuable insights into the social structure, agricultural practices, and burial customs of the period.

We subsequently reconstructed the genetic profile of the Han Dynasty individual from Shandong. To date, ancient DNA studies of Chinese domestic cattle remain limited, with reported data primarily from the late Neolithic Shimao site in the middle Yellow River region and the Tibetan Plateau (Chen, et al., 2018, Chen, et al., 2023a). Here, we report the earliest genome-wide data from ancient cattle sample recovered in Shandong region, located in the lower reaches of the Yellow River Basin. Firstly, based on mitogenome analysis, the historical individuals from Shandong exhibited a maternal lineage profile similar to ancient populations from Shimao and Bangga, all belonging to haplogroup T3. Haplogroup T3 has a dominating founder effect in ancient Chinese taurine cattle (Zhang, et al., 2023, Zhang, et al., 2021). Previous studies of both modern and ancient DNA indicate that T3 originated in the Near East during the Neolithic period (Troy, et al., 2001, Edwards, et al., 2007). These findings strongly support the hypothesis that Chinese domestic taurine cattle ultimately trace their origins to the Near East. Building on this, nuclear genome analysis revealed that the genetic profile of the Shandong historical individual was similar to the late Neolithic populations of the middle Yellow River Basin (Shimao) and ~2,500-year-old Bangga taurine cattle. A previous study has shown that the ~2,500-year-old Bangga taurine cattle genomes from the Tibetan plateau displayed the Shimao-related genetic profile. Meanwhile, both archaeological and genetic evidence suggest that millet-farming populations in the Yellow River Basin shared a common ancestry and expanded widely across the region (Du, et al., 2024, Xiong, et al., 2024, Ma, et al., 2025). As a key domesticated companion species, taurine cattle likely dispersed alongside these human populations, facilitating their spread throughout the Yellow River cultural sphere. Taken together, we further propose a hypothesis that the late Neolithic Shimao-related taurine ancestry expanded into regions such as the Lower Yellow

River Basin and the Tibetan Plateau. Our ancient DNA analysis reveals a clear pattern of close genetic affinity and interregional connections among taurine cattle from HE Shandong in the Lower Yellow River region, Shimao in the middle Yellow River region, and Bangga on the Tibetan Plateau. These findings suggest that ancient taurine cattle populations across different regions of China were not isolated but maintained close genetic connections, likely shaped by regional exchanges, herd movements, and human-mediated interactions across diverse cultural and ecological settings.

In the present-day Chinese cattle populations, we observed that two distinct ancestral lineages have shaped the genetic landscape of modern cattle. Based on current data resolution, modern Chinese taurine cattle show the highest level of allele sharing with ancient Chinese taurine cattle, compared to other ancient and modern populations. This pattern indicates that ancient Chinese cattle made a major genetic contribution to the gene pool of modern populations. Although future excavations and ancient DNA sampling will undoubtedly increase variability, some level of continuity has been established. In contrast, Chinese indicine cattle share the closest genetic affinity with Indian indicine cattle, indicating a shared ancestry and historical gene flow between the two groups. Adapted to thrive in warm climates of 15–27 °C, indicine cattle have long dominated the ecological and agricultural landscapes of South and Southeast Asia (Chen, et al., 2010). Archaeological evidence indicates that indicine cattle were initially introduced into South China from their domestication centers (Higham, 1996). This is consistent with recent studies on the uniparental dispersal of indicine cattle, which have mapped the phylogeographic patterns and migration routes of global indicine populations. Genetic evidence also supports South Asia as the domestication center of indicine cattle, which spread to southern China along the coastal regions of Southeast Asia around 3,500 years ago (Chen, et al., 2023c). These lines of evidence collectively suggest that Chinese indicine cattle likely originated from or were influenced by indicine populations from South Asia. This genetic divergence between the two ancestral lineages is also reflected in the geographic distribution patterns: the northern Chinese breeds originate from taurine cattle, while southern breeds derive from indicine cattle (Zhang, et al., 2015, Gao, et al., 2017). These two distinct ancestries not only enhance the genetic diversity of Chinese cattle but also highlight China's pivotal role as a crossroads in the prehistoric migration and evolution of domestic animals across Asia.

We also noted that the genomic data available for ancient Chinese taurine cattle are still very limited, and thus may not fully represent the full genetic diversity in China. Additional ancient genomic data from earlier periods or other archaeological sites are still required to gain a more comprehensive understanding of the complex genetic history of Chinese cattle and to further elucidate China's pivotal role in the domestication, migration, and diversification of cattle across Asia.

5. Conclusions

In this study, we sequenced 25 individuals from two Shandong sites dating to the late Dawenkou culture and the Han Dynasty. Due to the low coverage of the Late Dawenkou samples, only the Han Dynasty individual was retained for downstream population genetic analyses. The genetic profile of the Shandong individual from the Han Dynasty revealed the closest affinity to late Neolithic Shimao and ~2,500-year-old Bangga taurine cattle, reflecting strong genetic connections among these ancient taurine populations. Moreover, modern taurine cattle populations are genetically closest to ancient Chinese taurine cattle, emphasizing the lasting genetic influence of these ancient populations. These results highlight the close genetic relationships of ancient Chinese taurine populations and emphasize their important role in shaping the genetic landscape of contemporary taurine cattle. However, our study's conclusions are based on a limited sample size, further research with expanded sampling across diverse archaeological sites is essential to fully reconstruct the genomic formation and population dynamics of

taurine cattle.

CRediT authorship contribution statement

Tianyou Bai: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Haifeng He:** Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation. **Qu Shen:** Writing – review & editing, Investigation. **Yu Xu:** Methodology, Investigation. **Le Tao:** Investigation. **Kongyang Zhu:** Investigation. **Rui Wang:** Investigation. **Jiajing Zheng:** Investigation. **Yilan Liu:** Investigation. **Xiaolu Mao:** Investigation. **Xiaomin Yang:** Investigation. **Hao Ma:** Investigation. **Yanying Peng:** Investigation. **Tanfeng Shi:** Investigation. **Xiaokun Wang:** Resources, Project administration, Investigation. **Jinguo Zan:** Resources, Project administration, Investigation. **Zhigang Wu:** Resources, Project administration, Investigation. **Chuan-Chao Wang:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The 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 material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jasrep.2025.105401>.

Data availability

All data essential for evaluating the conclusions of this study are included in the main text and the [Supplementary Materials](#). Alignment files (BAM format) are available at the Genome Warehouse in National Genomics Data Center, Beijing Institute of Genomics (China National Center for Bioinformation), Chinese Academy of Sciences, under accession number PRJCA046277 (<https://ngdc.cncb.ac.cn/gsa>).

Data will be made available on request.

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