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Ancient sacrificial dog DNA reveals North–South interactions during the late Shang Dynasty in northern China

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ABSTRACT

During the Shang Dynasty in ancient China, dog domestication, dog consumption, and the utilization of dogs peaked. In this study, we analysed the mitochondrial DNA (mtDNA) of 36 dogs from the Zhoujiazhuang site in Hebei Province, China. We successfully obtained 21 high-quality complete mitochondrial genomes, revealing the maternal genetic structure of the dog population. The results revealed that the majority of dogs belonged to the A haplogroup (20/21), but they were further classified into different subhaplogroups. Through comparisons with other dogs from surrounding regions, we found that both northern Eurasia and southern East Asia dogs may have influenced the maternal genetic heritage of dogs in North China. This finding sheds light on the social context behind dog domestication, specifically the trade and exchanges between populations in the north and south.

1. Introduction

Dogs (*Canis lupus familiaris*), the first species to be domesticated by humans, were trained not only for practical roles such as guarding, assisting in hunting, and providing companionship, but they also held significant importance as offerings in funerary rituals and other ceremonial practices. This underscores their integral role in human cultural expressions. In China, the tradition of burying dogs alongside humans can be traced back to the Jiahu archaeological site in Wuyang, dating back to the Neolithic period (~8500BP) (Henan Provincial Institute of Cultural Heritage and Archaeology, 1999). During the Shang Dynasty, the ritual of dog sacrifice underwent a series of evolutionary stages, with its prevalence notably increasing in the late Shang period (~3000BP). The most representative sites are the Yinxu site in Anyang, Henan Province (The Anyang Archaeological Team, 1979), the Taixi site in Gaocheng, Hebei Province (Hebei Provincial Institute of Cultural Relics and Archaeology, 1985) and the Zhoujiazhuang site in this study. Previous studies (Dong, 2020; Guo, 2014; Liu, 2011, 2016) have explored aspects such as the sacrificial position of dogs, their functions, and the human–dog relationship. However, the genetic origins, domestication, and migratory processes of these dogs remain unclear.

Current research on ancient DNA (aDNA) concerning dogs primarily focuses on the origins and migration patterns of domestic dogs. Mitochondrial DNA (mtDNA) studies have been particularly instrumental in this discourse, suggesting that dogs may have originated in several regions, including Europe (Thalmann et al., 2013), East Eurasia (Zhang et al., 2024), Siberia (Da Silva Coelho et al., 2021; Perri et al., 2021), and Southern East Asia (Pang et al., 2009; Wang et al., 2016; Zhang et al., 2020). In addition to these findings, research on nuclear genomes and Y-chromosomes has identified two further centres of domestication in Central Asia and the Middle East (Gray et al., 2010; Shannon et al., 2015; Vonholdt et al., 2010) and has proposed the possibility of independent domestication events occurring in the eastern and western parts of Eurasia (Bergström et al., 2022; Frantz et al., 2016).

Moreover, studies have revealed genetic variations and migration patterns of domestic dogs across diverse geographical regions and historical periods (Ameen et al., 2019; Bergström et al., 2020; Feuerborn et al., 2021; Greig et al., 2018; Ollivier et al., 2018; Zhang et al., 2020, 2024), providing essential insights for a deeper understanding of the origins of domestic dogs and the intricate relationship between humans and canines. However, the population composition, origin, and migration pathways of domestic dogs in East Asia remain unclear, particularly during the Late Shang period, and the specific relationship between the Shang people and dogs has not been adequately elucidated. Therefore,

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conducting ancient DNA research on sacrificial dogs from the Late Shang period is essential.

The Zhoujiazhuang site, located in Luancheng County, Hebei Province, is a representative late Shang Dynasty aristocratic burial site in the northern Henan and southern Hebei regions of China. Through salvage excavations conducted from the end of 2019 to the end of 2020, a total of 23 tombs were discovered, 17 of which date back to the late Shang Dynasty. In these tombs, evidence of canine and human sacrifices was frequently observed, and there were evident hierarchical differences between the tombs. In particular, two larger tombs were situated in the central area of the cemetery, with the largest tomb covering an area of 20 square metres. The other medium-sized tombs were approximately 3 m in length, with widths exceeding 2 m and burial depths of about 6 m. In the eastern part of the cemetery, there were seven smaller tombs of similar specifications, with lengths ranging from 2.5 to 3 m, widths of approximately 1.5 m, and burial depths of around 6 m. These small tombs usually contained sacrifices of 1–3 dogs, but the richness of offerings was far lower than that of the tombs in the central and western areas (Fig. 1 B and C).

During the late Shang Dynasty in the northern Henan and southern Hebei regions of China, dog sacrifice was common in tombs. In this study, we analysed the mitochondrial genomes of 21 sacrificial dogs from the Zhoujiazhuang cemetery and conducted an in-depth investigation and discussion of these dogs.

2. Materials and methods

2.1. Sample Collections for DNA analyses

A total of 36 samples were obtained from the Zhoujiazhuang cemetery in Hebei Province, China (Fig. 1), for this study, all dating back to the late Bronze Age (~3000BP). These samples were from sacrificial dogs and were found in waist pits, second-tier platforms, and the backfills of various tombs (Table S1).

2.2. DNA extraction and Amplification

Before the ancient samples were processed, the preservation status of the samples was analysed qualitatively on the basis of burial conditions and external morphological features. First, the damaged and contaminated surface layers of the samples were removed via an electric grinding tool. The bone fragments were subsequently soaked in a 10 % hypochlorite solution for 10–20 min. Afterwards, the hypochlorite was washed away with water and ethanol, and the samples were air-dried under ultraviolet light. The bone powder of each sample was obtained via disposable drill bits. All the samples were processed in a dedicated aDNA laboratory within the Bioarchaeology Laboratory at Jilin University. The ancient DNA extraction was performed following the method described by Velsko (Velsko, 2020), and all samples were prepared as double-stranded libraries (Aron et al., 2020). Due to the poor preservation conditions of the samples, UDG treatment was not carried out.

2.3. Capture and sequencing of mtDNA

The commercial reagent kit, the TargetSeq One® Hyb & Wash Kit v2.0, provided by iGeneTech Corporation, was used for mitochondrial capture following the steps outlined in the user manual. PE150 paired-end sequencing on the Illumina platform was conducted at Novogene Corporation.

2.4. Sequencing data processing

Our study employed the PALEOMIX pipeline for sequencing data analysis (Schubert et al., 2014). First, Adapter Removal v2.2.0 (Schubert et al., 2016) was used to identify and remove adapter sequences, filter out reads shorter than 35 bp, discard bases with a quality score below 20, and merge the paired-end data. BWA v0.717 (Li, 2013) was used to align the data against the dog mitochondrial reference sequence (NC_002008) (Kim et al., 1998), and reads with a mapping quality below 25 were discarded. PCR duplicates were removed via the MarkDuplicates command from Picard v2.20.0 (Sacco et al., 2017). Regional variations were corrected via GATK v3.7.0 (McKenna et al., 2010). The base quality was recalibrated, and damaged reads were trimmed from both ends via MapDamage v2.2.1 (Jónsson et al., 2013). Sequencing quality and mitochondrial coverage were assessed via Qualimap v2.2.1 (Okonechnikov et al., 2016). Finally, ANGSD v0.931 (Korneliussen et al., 2014) was employed to extract mtDNA consensus sequences from samples with coverage of over 10,000 sites for downstream analysis.

2.5. Authenticity Criteria for aDNA

All the experiments were conducted in a dedicated ancient DNA laboratory that strictly adhered to protocols for preventing ancient DNA contamination. Pre-PCR and post-PCR experiments were carried out in separate buildings, and all materials and reagents used were of molecular biology grade (MB level). Typically, ancient DNA samples present a relatively high frequency of C > T mutations at the 5′ end. After the sequencing data were evaluated via MapDamage v2.2.1 (Jónsson et al., 2013), the observed damage patterns were consistent with those of

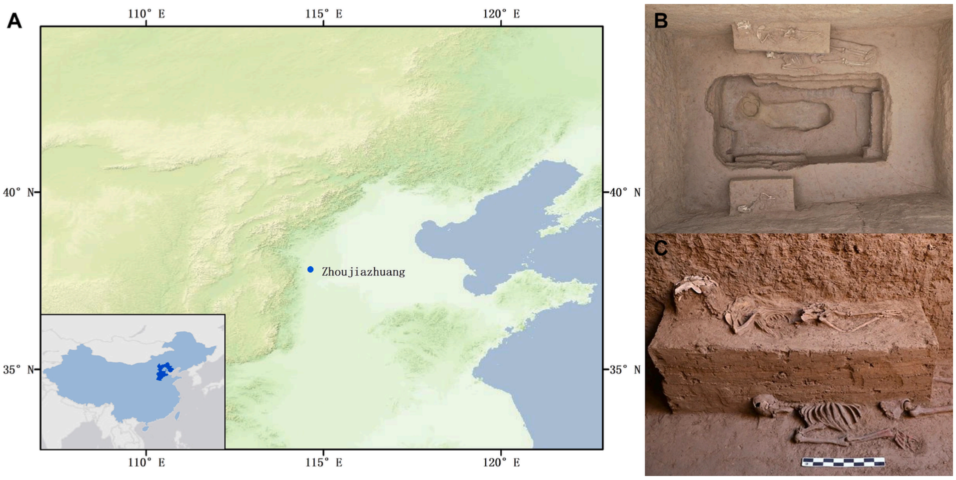

Fig. 1. (A) Map of Zhoujiazhuang site's geographical location. (B) Internal configuration of Tomb M5, indicating the positions of the sacrificed dogs within the burial structure. (C) Preservation status of the sacrificed dogs in Tomb M5.

ancient DNA, ensuring the authenticity and reliability of the ancient DNA data. Additionally, the approach proposed by Fu (Fu et al., 2013) was employed to evaluate all the data probabilistically, and a dataset of 477 modern dog samples was used to estimate the contamination rate of the ancient samples. The results revealed that the samples' contamination rates were less than 5 % (Table S1).

2.6. Sequence analysis

Approximately 1113 complete or nearly complete mitochondrial sequences were collected from the National Center for Biotechnology Information (NCBI) (Table S2) for comparative research. All sequences were aligned against the dog mtDNA reference sequence (NC_002008) (Kim et al., 1998) via MAFFT v7.520 (Katoh et al., 2019). The haplogroups were subsequently called via mitotoolpy-seq.py, a Python script available on Dometree (https://www.dometree.org) (Peng et al., 2015).

The sequences were divided into six regions: the first, second, and third codon positions, and the rRNA, tRNA, and control regions. The best model was determined via ModelTest-NG v0.1.6 (Darriba et al., 2020) via the Akaike information criterion (AIC) (Table S4). The grey wolf sequence NC_008093.1 was used as an outgroup. The phylogenetic tree was constructed via RAxML-NG v0.9.0 (Kozlov et al., 2019), and the resulting tree was visualized and enhanced using the iTOL tool (Letunic & Bork, 2021).

The haplotypes were assigned to the sequences using DnaSP v6.0 (Rozas et al., 2017), and the frequencies of different haplotypes were calculated via Arlequin v3.5.2.2 (Excoffier & Lischer, 2010). Additionally, nucleotide diversity was also computed with DnaSP v6.0 (Rozas et al., 2017). A median-joining network was subsequently constructed via PopART v1.7 (Leigh & Bryant, 2015). To further investigate the genetic diversity among different populations, principal component analysis (PCA) of the mitochondrial whole-genome sequences was performed via the "adegenet" R package (Jombart, 2008) in R v4.1.2 (R Core Team, 2022), and the results were visualized via ggplot2 (Wickham, 2016).

Furthermore, the Fst values were grouped and calculated via DnaSP v6.0, and the results were visualized via a heatmap via the "pheatmap" v1.0.12 R package (https://cran.rstudio.com/web/packages/pheatmap/pheatmap.pdf) in R v4.1.2 (R Core Team, 2022).

3. Results

3.1. Sequencing results and matrilineal haplotype ascription

In this study we used ancient DNA capture technology to analyse 36 samples from ancient dogs. A total of 21 high-quality mitochondrial whole-genome sequences were successfully obtained, with data coverage ranging from 1x to 90x (Table 1). The contamination rates were consistently low, ranging from 0.83 % to 5 % (Table S1). All ancient dog sequences in this study were deposited in GenBank of NCBI (https://www.ncbi.nlm.nih.gov/) under the accession numbers PQ073351-PQ073371.

The MitoToolpy tool (Peng et al., 2015) was used in conjunction with phylogenetic tree analysis to assign haplotypes to each sample (Table 1). The results revealed that the majority of dogs from the Zhoujiazhuang site belonged to haplotype A (n = 20), with only one sample belonging to haplotype C. Within haplotype A, the A2 subhaplotype (n = 9) was predominant, whereas the other subhaplotypes were A1 (n = 3), A3 (n = 2), A4′5 (n = 3), A5 (n = 2), and Unassigned A (n = 1) (Fig. 1A).

To further investigate the population composition of the Zhoujiazhuang site, we conducted haplotype frequency analysis on ancient samples from Africa, the Russian Far East (RFE), the Shaanxi region of China, South Asia (S_Asia), the Gansu–Qinghai region of China (W_China), Europe, the Middle East, New Zealand, Oceania, Siberia, and the Zhoujiazhuang site (ZJZ). Haplogroup A constitutes approximately 75 % of the global maternal lineage haplogroups in domestic dogs, with the highest maternal subhaplotype diversity observed in the Asian region (Zhang et al., 2020). The proportion of Haplogroup A dogs among the Zhoujiazhuang burial dogs reached as high as 90 %, similar to that reported for dogs from Shaanxi, the Gansu–Qinghai region, South Asia, New Zealand, and Oceania.

Table 1
Sequencing information of canine samples from the Zhoujiazhuang site.

Lab Code	Raw reads	Mapped reads	Endogenous DNA (%)	Mean coverage of mtDNA (X)	Haplotype
ZJZ01Dg	9,137,782	369,628	8.277	4.54x	A2b1
ZJZ02Dg	6,338,958	159,445	5.2	16.41x	A3
ZJZ03Dg	5,506,292	845,685	31.144	22.86x	A2b1
ZJZ04Dg	4,345,062	851,941	39.472	18.45x	A1
ZJZ05Dg	2,270,396	414,986	34.416	8.94x	C
ZJZ06Dg	331,832	22,021	12.868	2.02x	A5a
ZJZ07Dg	189,180	12,745	10.529	1.79x	A4′5
ZJZ09Dg	5,447,356	2,319,916	84.763	207.38x	A2b1
ZJZ15Dg	8,761,948	374,956	8.456	4.59x	A2
ZJZ17Dg	5,269,638	1,053,350	39.299	90.21x	A5a
ZJZ18Dg	800,754	146,963	36.028	7.88x	A4′5
ZJZ21Dg	8,679,400	7,861,807	87.906	3.26x	A3
ZJZ22Dg	8,486,535	7,607,955	88.2604	17.30x	A2a
ZJZ24Dg	2,690,772	993,652	69.205	23.03x	A2a
ZJZ25Dg	888,224	257,570	52.398	5.95x	A2b1
ZJZ26Dg	1,111,650	1,050,647	89.6404	10.05x	A2b1b
ZJZ29Dg	2,627,734	629,011	47.364	14.44x	A4′5
ZJZ33Dg	385,628	60,315	31.467	4.84x	A1
ZJZ34Dg	19,847,354	16,374,990	77.6314	29.69x	A1b
ZJZ35Dg	1,300,554	565,734	86.437	69.19x	A1′2′3
ZJZ36Dg	1,272,282	44,306	7.135	4.80x	A2a

Due to the unequal sample sizes, we calculated the nucleotide diversity (Pi) across different populations to address this issue. The results indicated that the dogs from the Zhoujiazhuang site exhibited the highest nucleotide diversity (Table 2).

The maternal subhaplotype and nucleotide diversity of the burial dogs at the Zhoujiazhuang site were found to be higher than those in other regions, indicating an atypical population composition at the site. Furthermore, the presence of ancient Chinese A1- and A3-type dogs suggests that the population at the Zhoujiazhuang site may have undergone distinct population migrations or exchanges in ancient times, leading to genetic structures that differ from those of other regions (Fig. 2).

3.2. Phylogenetic analysis

To further ascertain the nature of the ancient canine remains at the Zhoujiazhuang site and determine their genetic relationship with other canid species from different regions, a maximum likelihood tree was constructed using mitochondrial whole-genome sequences (Fig. 3).

The results indicated the presence of three A1-type domestic dogs in total. ZJZ34Dg is monophyletic with A1b-type Siberian samples, whereas ZJZ04Dg and ZJZ33Dg are monophyletic with modern samples. A2-type domestic dogs can also be divided into two groups: A2a (ZJZ15Dg, ZJZ22Dg, ZJZ36Dg) and A2b (ZJZ01Dg, ZJZ03Dg, ZJZ09Dg, ZJZ25Dg, ZJZ26Dg) subtypes, both of which exhibit close genetic affinity to domestic dogs in the Yellow River and Yangtze River Basins in China. ZJZ02Dg and ZJZ21Dg are monophyletic together with the A3 subtype, which is predominantly distributed in modern China and Southeast Asia (Thailand). ZJZ07Dg and ZJZ18Dg are monophyletic with ancient Siberian samples in the A4′5 monophyly, whereas another sample identified as A4′5 (ZJZ29Dg) presented closer genetic similarity to samples from the A6 Qinghai Yangqu site and ancient Siberian samples. The A5 samples from Zhoujiazhuang (ZJZ17Dg, ZJZ06Dg) are monophyletic with modern Chinese samples and samples from two

Table 2
Analysis of nucleotide diversity across different populations.

Group	Number of sequences	Number of polymorphic sites (S)	Number of Haplotypes (h)	Haplotype diversity (Hd)	Nucleotide diversity (Pi)
Africa	5	52	4	0.900	0.00138
RFE	5	160	5	1.000	0.00500
Shaanxi	17	344	16	0.993	0.00435
S_Asia	4	105	4	1.000	0.00378
W_China	8	163	8	1.000	0.00299
Europe	26	269	24	0.994	0.00431
Middle East	6	126	6	1.000	0.00273
New Zealand	34	17	11	0.619	0.00009
Oceania	6	181	6	1.000	0.00456
Siberia	30	173	25	0.989	0.00216
Zhoujiazhuang	21	279	21	1.000	0.00611

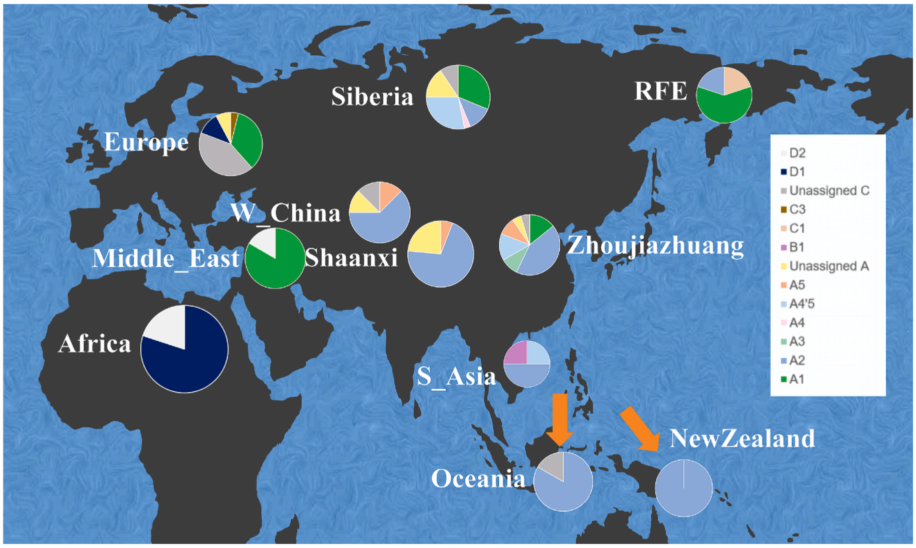

Fig. 2. Frequency distribution of various subhaplotypes across different regions illustrated through pie charts. The haplotype frequency analysis based on a total of 162 ancient samples, categorised as follows: Africa (n = 5), Russian Far East (RFE) (n = 5), Shaanxi region in China (n = 17), South Asia (n = 4), Gansu–Qinghai region in China (W_China) (n = 8), Europe (n = 26), Middle East (n = 6), New Zealand (n = 34), Oceania (n = 6), Siberia (n = 30), and Zhoujiazhuang (n = 21).

ancient sites in China's Yellow River and Yangtze River Basins. The undetermined A haplotype sample (ZJZ25Dg) is monophyletic with ancient samples from Shaanxi, China.

Additionally, the sample ZJZ05Dg discovered in the M1 waist pit belongs to the C haplogroup, which is similar to the haplogroup predominantly found in European dogs, suggesting a possible connection between them (Fig. 3).

3.3. Network construction

To analyse the relationships between domestic dogs from the Zhoujiazhuang site and other A-type domestic dogs, a comprehensive network diagram of the entire A haplogroup was constructed (Fig. S1). All the samples were divided into four groups: A2, A3, A4′5, and A5. The Zhoujiazhuang A4′5 dogs likely originated from Siberia and were associated with related populations (Ní Leathlobhair et al., 2018), whereas the Zhoujiazhuang A5 dogs likely contributed to the genetic makeup of modern A5 dogs in China (Pang et al., 2009).

To further elucidate the maternal genetic patterns of the two major subtypes (A1 and A2) at the Zhoujiazhuang site, intermediate network diagrams were constructed, comparing the Zhoujiazhuang dogs with ancient and modern related samples of A1 (Fig. S2) and A2 (Fig. 4) types, respectively. These diagrams reveal that some of the Zhoujiazhuang samples exhibit close genetic proximity to samples from southern China and Siberia.

The A2 haplogroup was divided into nine geographical groups: Russian Far East (RFE), Shaanxi in China (Shaanxi), South Asia (S_Asia), the Gansu–Qinghai region in China (W_China), the Middle East, New Zealand, Oceania, Siberia, and Zhoujiazhuang (Fig. 4). The results indicate that an ancient dog (TLS_6957) from Zhejiang Province is the central group (star-like expansion) in the A2a and A2b subhaplogroup networks, encompassing 119 dogs from Asia and Oceania, occupying a central position (Fig. 4). Therefore, it is possible that the ancestors of the Zhoujiazhuang A2 dogs are related to ancient dogs from the Tianluoshan site in Zhejiang Province (TLS_6957) and the populations associated with the ancestral A2 subhaplogroups.

The A1 haplogroup was also divided into seven groups based on geographical region: Russia, Mongolia, the Americas, Africa, Oceania, and Zhoujiazhuang A1 dogs (Fig. S2). The network diagram clearly separates the A1b and A1i subtypes, but the two A1i dogs from Zhoujiazhuang do not cluster with other A1i samples, making it difficult to determine whether these two samples contributed to the modern A1i type. Therefore, we conclude that these two samples do not belong to the A1i sub-haplotype. Due to the limited number of samples, we are unable to ascertain whether they represent a new sub-haplotype. Consequently, we provisionally classify the haplotypes of these two samples as A1. The Bronze Age steppe dog occupies a basal position within the A1b cluster. As this seems to imply, Ishkinino1 is a dog that belonged to a population that gave rise to A1b. Ishkinino1 is a member of the population from Russia, which was excavated from a Late Bronze Age site in the southern Urals of the Eurasian steppe belt known as Ishkinino. On this basis, it can be further speculated that the Zhoujiazhuang A1b dog (ZJZ34Dg) may

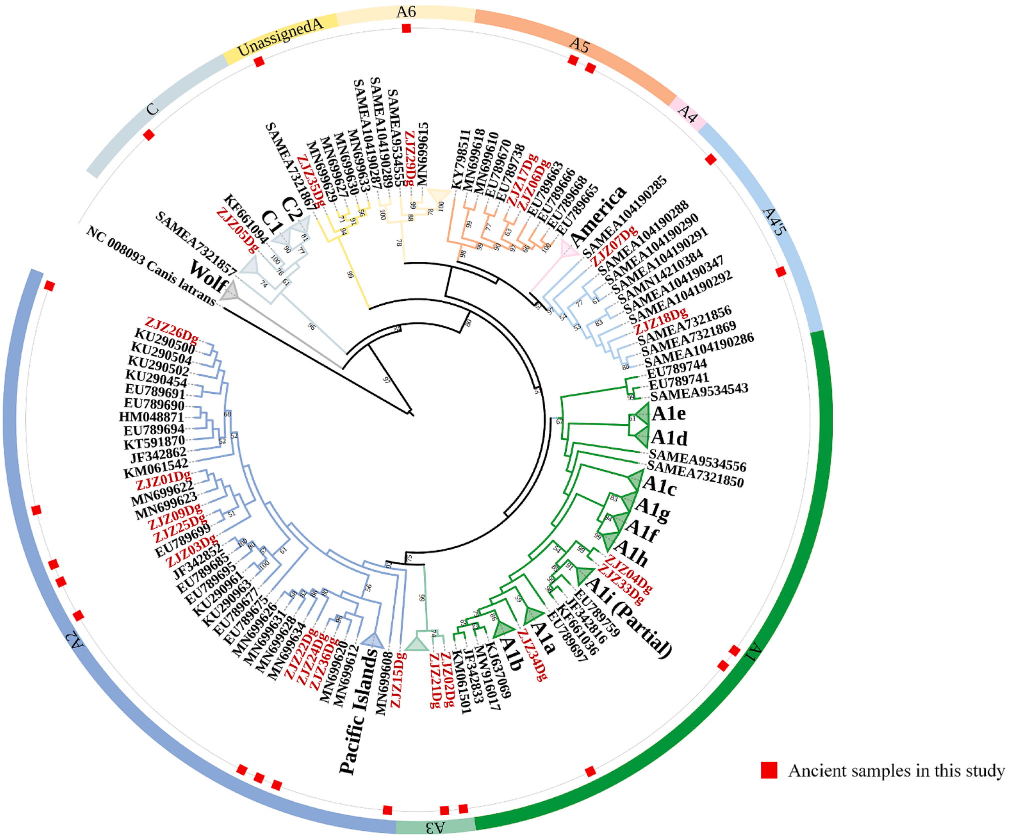

Fig. 3. Maximum likelihood tree constructed based on the whole mitochondrial genome. The clade that does not include samples from this study was collapsed.

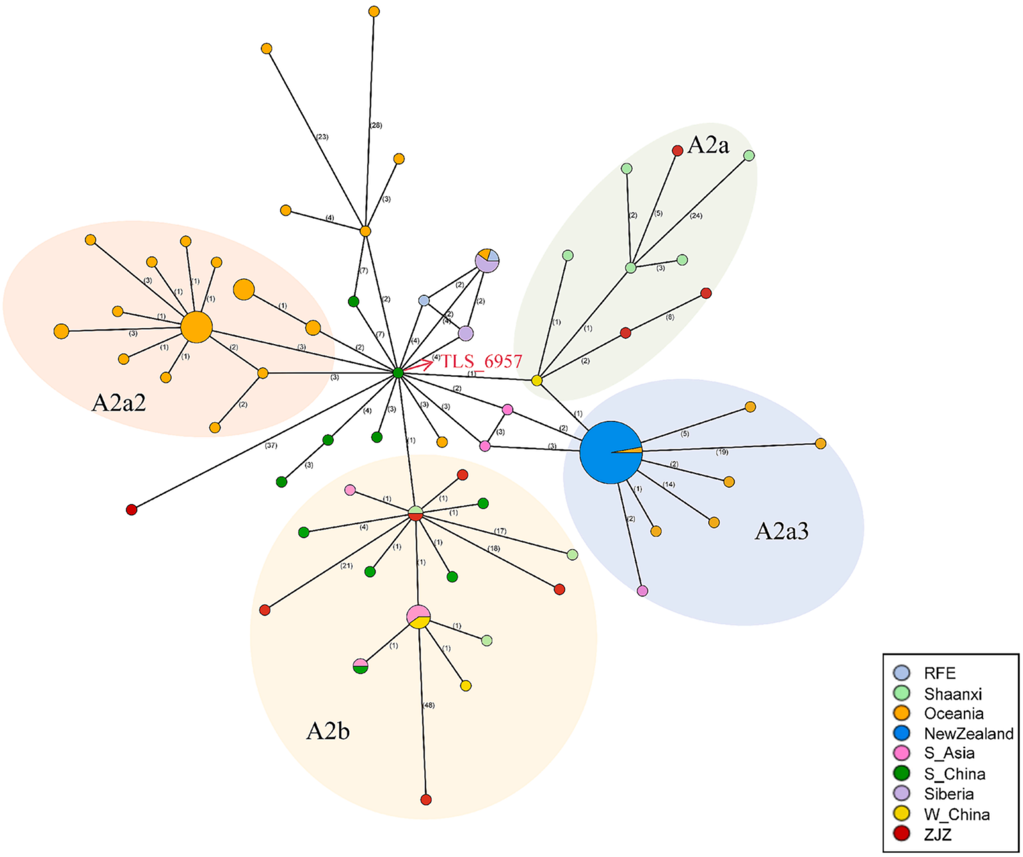

Fig. 4. Median-joining network map of mitochondrial DNA in domestic dogs, derived from ancient A2 dogs.

have been influenced by the Bronze Age steppe region in Russia.

3.4. Fst genetic distance

To further analyse the population structure and genetic differences between the Zhoujiazhuang dogs and ancient canine populations from other regions, genetic distance calculations were performed using mitochondrial whole genome data from 164 samples (Table S2).

The results indicate that our samples have relatively low genetic differentiation with samples from the Russian Far East (RFE), European Neolithic (SA), Oceania, and Siberian Bronze Age (Siberia3k). However, they exhibit greater genetic differentiation with samples from northern China (Shaanxi) and western China (W_China). Due to the limited number of samples from southern China, the relationship between the Zhoujiazhuang samples and those from southern China remains unclear at present (Fig. 5).

4. Discussion

4.1. Revealing the population dynamics of canids in the late Shang period in China

In the published ancient samples from the Yangtze and Yellow River Basins (YYRB) in China, the A1 haplogroup has not been found, whereas three individuals with the A1 haplogroup were discovered at the Zhoujiazhuang burial site, accounting for 14.3 % of the total population. In the YYRB samples, the A2 haplotype predominates, but in modern confirmed domesticated samples, the proportion of A1-type dogs exceeds half. Previous studies suggested that major replacement has occurred in the past 2000 years, with A1 haplotype dogs replacing the A2 haplogroup in the YYRB region, as modern dogs found in the northern regions of the Yangtze River mainly belong to the A1 haplogroup and rarely to the A2 haplogroup (Zhang et al., 2020). However, the discovery of three A1-type individuals at the Zhoujiazhuang site during the late Bronze Age suggests that this replacement may have started earlier.

The study revealed that the Zhoujiazhuang burial site, as a higher-ranking noble tomb group during the Chinese Bronze Age, presented a more diverse range of dog haplotypes, surpassing even other site populations of dogs (Fig. 2, Table 2). While the presence of a greater variety of haplotypes and genetic diversity can serve as evidence of domestication centres in studies on the origin of domestic dogs (Pang et al., 2009), the importance of migration and exchange should not be overlooked. Therefore, we believe that the maternal genetic diversity of domestic dogs observed at the Zhoujiazhuang burial site is more likely a result of frequent interactions among contemporary human populations. Population migration and exchange often accompany the diffusion of culture, technology, and genes, playing crucial roles in developing and maintaining genetic diversity in domestic dogs.

4.2. The maternal lineage of the Zhoujiazhuang canine

Through our previous analysis, we can reasonably infer that the Zhoujiazhuang dogs appears to have two distinct sources of ancestry: the Eurasian Steppe and Southern China. This deliberate separation in discussing the breed's maternal origins is not merely a methodological choice but a necessary approach to fully appreciate the intricate tapestry of genetic and cultural influences that have shaped this breed. Each region presents its own unique environmental conditions, breeding practices, and historical contexts, which have played a pivotal role in the development of specific traits and behaviours within the Zhoujiazhuang dog. By undertaking independent investigations into these two sources, we can further elucidate the influence of distinct regions on the Zhoujiazhuang site, as well as the historical migrations and interactions of human populations in those areas during that period.

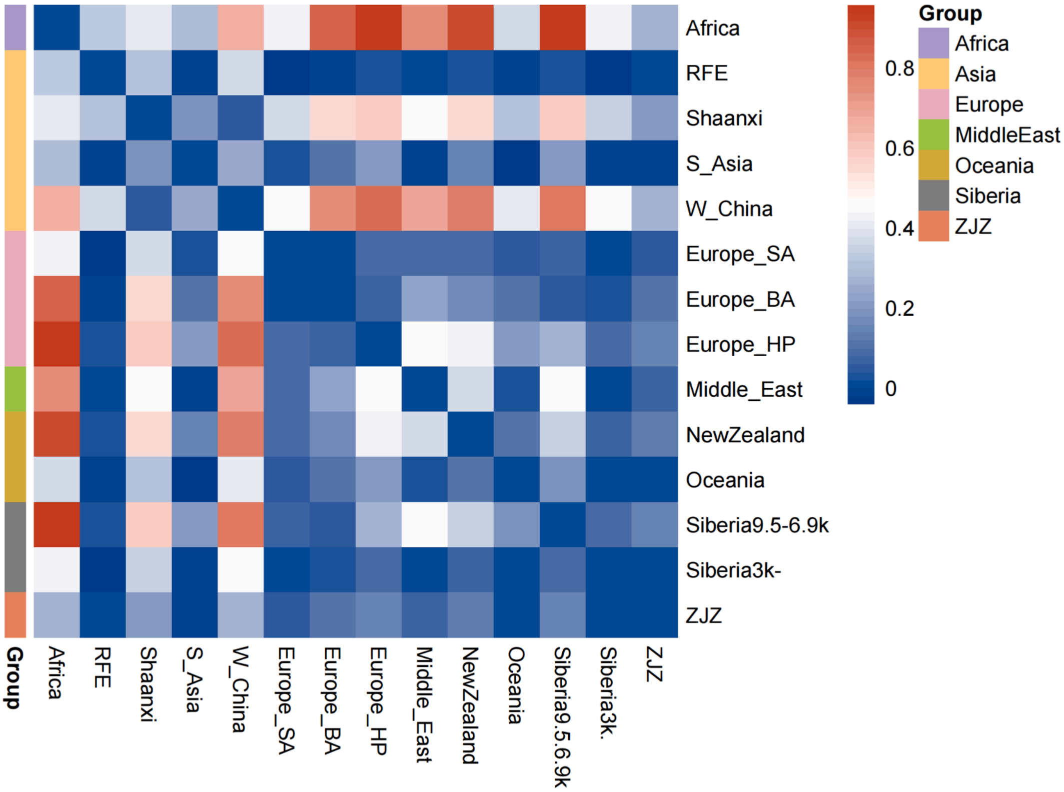

Fig. 5. The calculation of genetic distance involved a total of 164 ancient samples, comprising 21 samples from this study, as well as samples from Africa (n = 5), Asia (n = 35), Europe (n = 27), the Middle East (n = 6), Oceania (n = 40), and Siberia (n = 30). Darker shades of blue represent smaller Fst values, indicating closer genetic distances, while darker shades of red signify greater genetic distances.

4.2.1. Contributions from the Eurasian steppe

In 3000 BCE, the Eurasian steppe transitioned into the Bronze Age, which Russian scholars divided into three periods: early, middle, and late (3000–2500 BCE, 2500–1800 BCE and 1800–1000 BCE, respectively), corresponding to waves of migration in the late 4th, middle-3rd, and early 2nd millennium BCE, respectively (Christian, 2018). This period was characterized by the development of animal husbandry, expansion towards the central and eastern grasslands, the emergence of urban centres in southern Central Asia, and exchanges between different systems. Pastoral cultures, with their mobility, militarization, and rapid movement capabilities, were able to occupy large areas and triggered multiple waves of migration (Allentoft et al., 2015; de Barros Damgaard et al., 2018; Haak et al., 2015; Mathieson et al., 2015; Olalde et al., 2018). By the late Bronze Age, evidence from excavated artefacts indicates clear interactions between the Eurasian steppe region and the Anyang region in China (Christian, 2018). Metallurgical archaeological research has shown that the Karasuk culture spread eastwards for 3500 km, from the Sayan Mountains to Xinjiang to Mongolia to North China to the Liao River to Eastern Liaoning Province, whereas another route led south to the Loess Plateau of western Shanxi and northern Shaanxi and eventually reached the late Shang Dynasty capital, Anyang (Chernykh, 1992, 2008, 2011). These published archaeological studies provide further evidence of the interactions between the Eurasian steppe populations and the settled agricultural communities in China during that period.

According to historical sources (Christian, 2018) and archaeological research (Parzinger, 2006; J. Yang & Shao, 2015) there was likely interaction between the northern regions of China and the Eurasian steppe during the late Bronze Age, possibly through population movements or warfare. Although there are some controversies in archaeological studies of this region, the exchange between these two areas is closely associated with the Eurasian steppe population. As indicated by Fst genetic distance analysis, the dogs found at the Zhoujiazhuang site share a greater affinity with those from Siberia than with those from Shaanxi and the Gansu–Qinghai region of China (Fig. 5). Additionally, according to the phylogenetic tree (Fig. 3) and network construction (Fig. S1, S2), we suggest that dogs belonging to A1 and A4′5 from the Zhoujiazhuang cemetery may have connections with ancient dogs from Siberia.

Research has revealed that European Mesolithic samples and Siberian A4′5 samples predate the Zhoujiazhuang site, whereas Russian Bronze Age samples are closer in age to the Zhoujiazhuang site. Furthermore, a whole-genome study of Russian Bronze Age steppe dogs suggested that their ancestors can be modelled as approximately 40 % from the Arctic (represented by Zhokhov Island dogs) and 60 % from the Near East (represented by Iranian and Levantine ancient dogs), with no East Asian lineage (Feuerborn et al., 2021). Considering that the A1 haplotype is distributed mainly in the Eurasian steppe region, and with input from the intermediary network graphs (Fig. S1, Fig. S2), we speculate that the A1 and A4′5 haplotype dogs from the Zhoujiazhuang site likely originated from the Eurasian steppe region, with a transmission route more closely related to the northern Eurasian continent. C-type dogs from the Zhoujiazhuang site are also more likely to have been introduced from Europe through this transmission route.

Furthermore, the research by Zhang et al. (Zhang et al., 2024) highlights the genetic characteristics of East Asian dogs during the Late Shang period, indicating significant influence from Eurasian Steppe populations. This period represents a crucial nexus of cultural exchange in East Asia. Findings suggest that, approximately 4,000 years ago, maternal lineages from western Eurasia began to impact East Asian dog populations, with a notable increase in this influence after 3,000 years ago. While direct studies on Late Shang dogs from Hebei are limited, archaeological evidence from nearby regions and the genetic patterns identified in the aforementioned study support the hypothesis that dogs from the Zhoujiazhuang site were likely shaped by genetic exchanges with Eurasian Steppe populations. This influence may be evident in the distribution of mitochondrial DNA haplotypes and other genetic traits (Fig. 3, S1, S2).

4.2.2. Influences from southern China

Research has shown that Australian dingoes, New Guinea singing dogs, and ancient Polynesian dogs all originated from East Asian dog breeds (Freedman et al., 2014; Greig et al., 2015, 2018; Oskarsson et al., 2012; Savolainen et al., 2004). Precolonial Pacific dogs are likely derived from the Yangtze and Yellow River Basins in China, spread through mainland Southeast Asia, and then reach Pacific islands associated with Lapita culture through Indonesia (Zhang et al., 2020). The Fst genetic distance analysis revealed that the dogs from the Zhoujiazhuang cemetery are closer to populations in the southern Pacific islands (Fig. 5). Therefore, we speculate that another group belonging to the A2 haplogroup in Zhoujiazhuang may also originate from the YYRB region, which is consistent with the results obtained from the network graph and phylogenetic tree (Fig. 3, Fig. 4).

Previous genetic studies on prehistoric populations in northern and southern East Asia have shown an increase in northern influence in the southern East Asian region compared with the early Neolithic period (Yang et al., 2020). The spread of northern East Asian ancestry has resulted in a bidirectional admixture, to the extent that most modern East Asians are a mixture of northern and southern East Asian ancestry. Most human migrations that have shaped the genetic patterns in modern East Asia likely occurred after the Neolithic period (Yang et al., 2020). The Zhoujiazhuang site dates back to the late Bronze Age, and thus far, only the A2 haplogroup has been found in ancient data from southern East Asia. However, the A1 haplogroup has a high frequency in modern samples, indicating a strong influence of northern regions on modern A1 dogs. Considering the bidirectional mixing scenario and the results of the DNA analyses conducted in this study, it is plausible to assert that haplogroup A2 was present in Northeast Asia during the late Bronze Age.

Based on the available evidence, we propose that by at least the late Bronze Age, the northern region of China may have been significantly influenced by interactions with both the Eurasian steppe and southern China. However, the two A3 haplotypes identified in this study were not found in ancient samples. Our study has yet to confirm the origins of the haplotype or draw conclusions regarding their local domestication. Although we can speculate on the general sources of the Zhoujiazhuang samples, owing to suboptimal sample preservation, we are unable to determine the genomic composition through whole-genome analysis. However, it is undeniable that as early as the late Bronze Age, populations on the Eurasian continent were already engaging in frequent exchanges, and these exchanges likely facilitated the migration and spread of domestic dogs.

5. Conclusions

The northern region of China was an important area during the late Bronze Age, and the Zhoujiazhuang cemetery was a late Shang Dynasty aristocratic burial site. We found two haplogroups, A and C, among the dog haplotypes at this site, with the A haplogroup showing multiple subtypes. Among the contemporary sites from the same period, Zhoujiazhuang presented the highest haplotype frequency diversity, indicating complex population composition and suggesting frequent interactions between the local population and people from other regions during migration or military activities. Additionally, the presence of sacrificial dogs in almost every burial at Zhoujiazhuang, along with the observed genetic diversity, may imply close interaction and communication between humans and dogs during the late Bronze Age. This could be attributed to the important roles that dogs play in hunting, herding, and guarding, among other aspects of human life.

The A1 subhaplogroup found in the dogs from Zhoujiazhuang represented a low proportion of published ancient Chinese samples but a relatively high proportion of modern Chinese samples. Researchers have hypothesised that a population replacement event occurred in the past

2000 years (Zhang et al., 2020). However, given the population structure of the dogs at the Zhoujiazhuang site, this replacement may have started even earlier.

In summary, the canine population at the Zhoujiazhuang site has at least two origins: the Eurasian Steppe and the East Asian southern region. This indicates that extensive interactions were already occurring across the Eurasian continent during the late Bronze Age. In the early 1st millennium BCE, significant changes occurred in the Eurasian Steppe region regarding technology, social structure, and ideology. The emergence of nomadic lifestyles marked the beginning of a new era, and for the following thousands of years, steppe civilizations were predominantly based on pastoral economies. By approximately the 7th century BCE, the entire Eurasian Steppe region had been occupied by nomadic populations (Yang et al., 2016). The canines at the Zhoujiazhuang site largely reflect the influence of early nomadic populations on the surrounding sedentary societies.

The Zhoujiazhuang burial site is located in Hebei Province and is in close proximity to the Yinxu site in Anyang, Henan Province. The artefacts at the Zhoujiazhuang site are similar to those from the second and third phases of the Yinxu site. According to our research findings, the A2 haplogroup of canines at Zhoujiazhuang likely originated from the southern region. As northern China's political and cultural centre during the late Shang period, the Yinxu site is reasonably speculated to have served as a pivotal hub for these exchanges. Furthermore, due to the poor preservation of ancient samples, we are unable to obtain nuclear genomic data suitable for analysis. Although we have successfully acquired mitochondrial whole genome data through capture methods, our understanding is limited to the matrilineal origins of these samples. With the continued advancement of experimental and analytical techniques, it is anticipated that whole genome data will provide us with further insights in the future.

CRediT authorship contribution statement

Wenqi Wei: Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation, Conceptualization. **Xingcheng Wang:** Writing – review & editing, Validation, Software, Investigation, Data curation, Conceptualization. **Wenyan Li:** Resources, Investigation. **Wei Chen:** Resources, Investigation. **Dawei Cai:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition.

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 data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2025.105008.

Data availability

All ancient dog sequences in this study were deposited in GenBank of NCBI (https://www.ncbi.nlm.nih.gov/)under the accession numbers PQ073351-PQ073371.

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