Yuan et al. *Zool. Res.* 2026, 47(3): 827−834
https://doi.org/10.24272/j.issn.2095-8137.2025.532
https://cstr.cn/32248.14.zr.2025.532

ZR | Zoological Research

Article Open Access

Traversing the ancient Overland Silk Road: Insights from domestic camel paleogenomics in Xi'an, China

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ABSTRACT

The ancient Overland Silk Road connected distant regions through commerce and movement, enabling large-scale dispersal of domesticated animals alongside goods. However, the evolutionary and demographic trajectories of domestic camels, vital transport animals within this trade network, remain poorly understood due to a scarcity of paleogenomic data. In the present study, complete mitochondrial genomes (mitogenomes) and low-coverage nuclear genomes were obtained from three *Camelus* specimens excavated in Xi'an, a major eastern hub of the ancient Overland Silk Road, with calibrated radiocarbon ages of approximately 2 300–2 000, 900–700, and 300–0 years before present (cal BP). Phylogenetic analyses identified two individuals as domestic Bactrian camels and one individual as an Arabian camel, yielding the first genetically validated Arabian camel bone remain reported from China. Maternal haplotypes showed limited phylogeographic partitioning, consistent with extensive human-mediated dispersal. Notably, admixture analysis provided potential evidence of ancient interspecific hybridization, with 7.3% Arabian-related ancestry detected in the ~2 300–2 000 cal BP domestic Bactrian camel and 45.1% domestic Bactrian-related ancestry in the ~900–700 cal BP Arabian camel. This bidirectional introgression pattern suggests intentional breeding and circulation of hybrid camels for trade caravans. Overall, these findings support a model in which the ancient Overland Silk Road acted as a genetic corridor, repeatedly reshaping the demographic history of domestic camels through sustained mobility and recurrent admixture.

Keywords: Domestic camel; Paleogenomics; Ancient Overland Silk Road; Hybridization; Migration

INTRODUCTION

The United Nations designated 2024 as the International Year of Camelids (IYC 2024) to strengthen global awareness of camelid diversity and the ecological and socioeconomic roles of these animals. Within Camelidae, the Old World comprises only three extant camel species, including the wild Bactrian camel (*Camelus ferus*), domestic Bactrian camel (*Camelus bactrianus*), and domestic Arabian camel (*Camelus dromedarius*). Camels are widely recognized for extreme-environment tolerance, although domestic Bactrian and Arabian camels occupy partially distinct climatic niches and landscapes (Habinger et al., 2020; Imamura et al., 2017; Wu et al., 2014). Arabian camels are primarily reared in hot arid deserts across Asia and Africa and exhibit exceptional heat tolerance, whereas domestic Bactrian camels are broadly distributed across higher-latitude arid regions of Central and East Asia and show pronounced cold tolerance (Almathen et al., 2016; Stanley et al., 1994; Vyas et al., 2015). Despite these differences, both domestic species coexist in several West and Central Asian countries, including Turkey, Iran, India, Afghanistan, and Kazakhstan (Burger et al., 2019; Çakırlar &Berthon, 2014; Imamura et al., 2017; Zarrin et al., 2020).

As vital transport animals along the ancient Overland Silk Road and Spice Route, domestic camels enabled cross-continental movement of people and commodities, supporting the exchange of technologies, economies, and cultural practices across Eurasia and Africa (Almathen et al., 2016; Burger, 2016; Ji et al., 2009; Lado et al., 2020; Potts, 2004).

Received: 02 December 2025; Accepted: 12 January 2026; Online: 13 January 2026

Foundation items: This work was supported by the National Natural Science Foundation of China (42472008, 42172027, 42494912)

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This history raises the possibility that long-distance trade could have repeatedly redistributed camel lineages and reshaped ancestry composition through recurrent movement and breeding. However, paleogenomic data remain substantially more limited for domestic camels than for other domesticated animals, such as horses, cattle, pigs, goats, and sheep (Alberto et al., 2018; Bai et al., 2025; Chen et al., 2023; Librado et al., 2024; Yang et al., 2024). Ancient DNA studies on Arabian camels have primarily relied on partial mitochondrial sequences, including archaeological samples from the Arabian Peninsula combined with modern data to infer domestication history and dispersal (Almathen et al., 2016). For domestic Bactrian camels, published evidence has been limited to a small number of partial mitochondrial fragments and a single complete mitochondrial genome (mitogenome) from archaeological remains (Chen et al., 2019; Trinks et al., 2012; You et al., 2014). Nuclear genomic data from ancient domestic camels remain especially scarce (Chen et al., 2019; Mohandesan et al., 2017), with both restricted sampling and reliance on mitochondrial DNA as a single molecular marker greatly constraining reconstruction of population history and limiting inference regarding the impact of ancient trade networks on genetic structure (Almathen et al., 2016; Orlando, 2016).

In China, historical documentation and zooarchaeological discoveries support a long history of domestic Bactrian camel husbandry (He et al., 1986; Zhang & Luo, 2014). Camel remains have been reported from early northern archaeological sites such as Zhukaigou (Ordos, Inner Mongolia) and Huoshaogou (Yumen, Gansu Province), dated to approximately 4 000 and 3 700 BP, respectively. Subsequent sites, including Shirenzigou (~2 300 BP) and Yuansha ancient city (~2 200 BP), yielded more abundant camel remains, consistent with increasing reliance on camel-based transport and husbandry (Huang, 1996; You et al., 2014). Xi'an, historically known as Chang'an, is located in the central Guanzhong Plain and served as a major eastern hub of the ancient Overland Silk Road. During the Han (202 BC–220 AD) and Tang (618–907 AD) dynasties, camel caravans frequently departed from Xi'an, traveling through Central Asia to West Asia and Europe, with reciprocal movement along the same corridors. *Camelus* remains recently unearthed from the Wei River floodplain in Gaoling district, Xi'an, provide a unique opportunity to evaluate how this long-distance trade network influenced the genetic structure of ancient camels, yet focused study of this assemblage has remained limited (Chen et al., 2019; Li & Li, 2023).

To address these knowledge gaps, complete mitogenomes and low-coverage nuclear genomes were generated from three *Camelus* remains excavated from the Wei River floodplain in Xi'an. These data were used to determine phylogenetic placement, infer genetic structure, estimate genetic diversity, and test for potential gene flow between domestic Bactrian and Arabian camels during historical periods. Overall, these findings provide new insights into the impact of ancient Overland Silk Road trade patterns on the evolutionary history of Old World domestic camels.

MATERIALS AND METHODS

Sampling

Three *Camelus* specimens were collected from the Wei River floodplain in Gaoling district, Xi'an city, Shaanxi Province, China (Figure 1). All three specimens comprised left forearm bones and exhibited remarkable morphological similarity to forearm bones of extant *Camelus* species (Lei et al., 2002). In adult camels, the forearm includes the radius and ulna, which are fused but retain several interosseous spaces (Lei et al., 2002; Wang & Xie, 1992). A notable morphological distinction between domestic Bactrian camel and Arabian camel involves the number of interosseous spaces, with the former possessing one additional interosseous space relative to the latter (Wang & Xie, 1992). Based on this criterion, SLT2 and SLT3 were provisionally assigned to domestic Bactrian camel, while SLT4 was provisionally assigned to Arabian camel. The specimens, currently housed in the Department of Geology, Northwest University, China, were sent to Beijing Normal University for accelerator mass spectrometry (AMS) radiocarbon dating. Results yielded ages of 130±25 BP (~300–0 cal BP), 2 135±25 BP (~2 300–2 000 cal BP), and 875±25 BP (~900–700 cal BP) for SLT2, SLT3, and SLT4, respectively. Calibration was performed in OxCal v.4.4.4 using the IntCal20 calibration curve (Reimer et al., 2020). Additional specimen information is provided in Supplementary Table S1.

Laboratory procedures

All steps prior to polymerase chain reaction (PCR) analysis were performed in dedicated ancient DNA facilities at China University of Geosciences (Wuhan), physically isolated from modern molecular laboratories. DNA extraction was performed as described in Dabney et al. (2013) with minor modifications. Bone powder was generated using a NAKANISHI drill, and DNA was extracted from approximately 50 mg of powder. Samples were incubated overnight in 1 mL of extraction buffer (0.45 mol/L EDTA, 0.25 mg/mL proteinase K) with gentle rotation at 37℃, followed by centrifugation at 7 000 r/min with a centrifugal radius of 12 cm for 10 min. DNA purification was performed using a MinElute PCR Purification Kit (Qiagen, Germany), with the final extract eluted in 30 μL of EB buffer. Double-stranded sequencing libraries were constructed from 20 μL of extract according to the protocols described by Meyer & Kircher (2010), incorporating modifications described in Xiao et al. (2023). Negative controls were included during both DNA extraction and library construction to monitor potential contamination. Libraries were finally subjected to shotgun sequencing on the Illumina NovaSeq 6000 platform (USA) to generate 2×150 bp paired-end reads.

DNA sequence data processing

Raw sequencing reads were processed by removing adapter sequences using Fastp v.0.23.3 (Chen et al., 2018) and discarding reads shorter than 30 bp prior to downstream analyses. To minimize potential biases from reference genome selection, the sequencing data were aligned to different camel reference genomes at both mitochondrial and nuclear levels. Trimmed reads were mapped independently to three mitochondrial reference genomes: domestic Bactrian camel (GenBank No. NC_009628.2), wild Bactrian camel (GenBank No. NC_009629.2), and Arabian camel (GenBank No. NC_009849.1). Alignments were performed using the "aln" algorithm in BWA v.0.7.15 (Li & Durbin, 2010) under default parameters. PCR duplicates were removed and alignments were sorted using the "sort" function in SAMtools v.1.9 (Li et al., 2009). Mitochondrial consensus sequences were generated in Geneious (https://www.geneious.com/), with a minimum sequencing depth of 3× and a base agreement threshold greater than 75% (Supplementary Table S1). Trimmed reads were also aligned to three nuclear

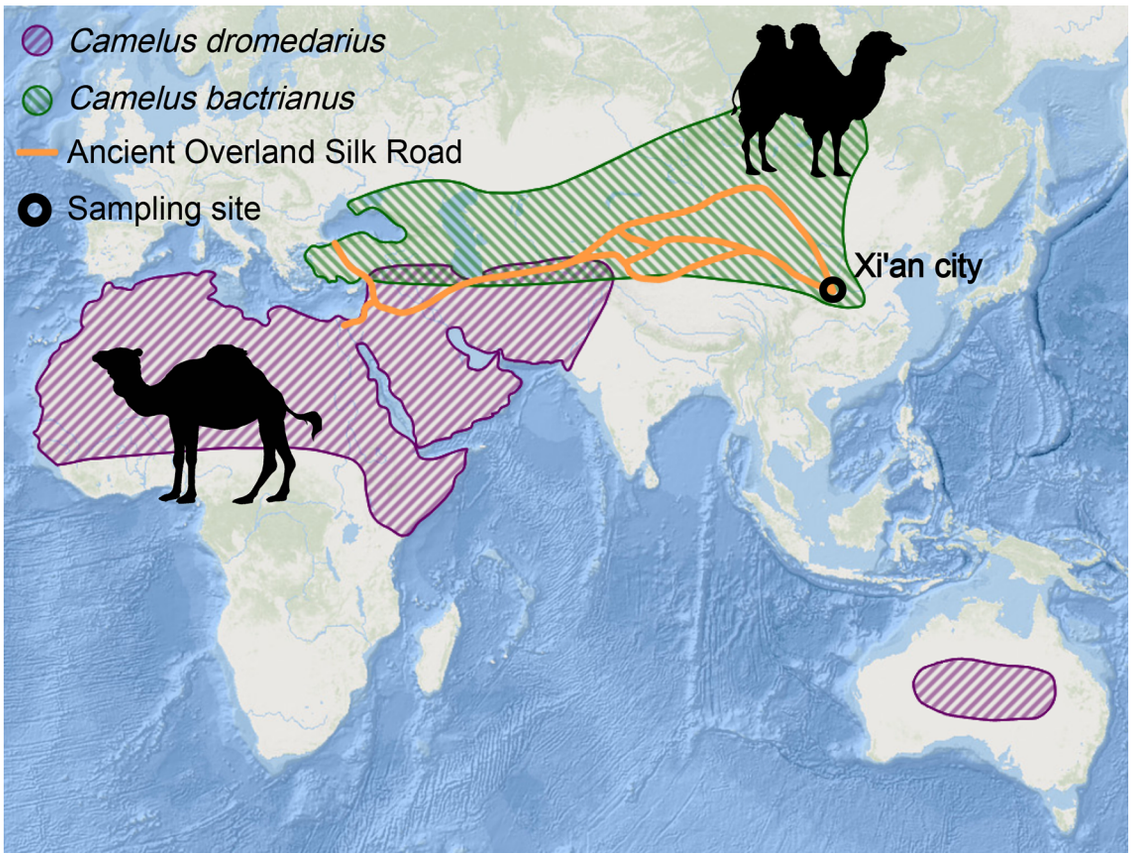

Figure 1 Sampling locality in Xi'an, ancient Overland Silk Road corridor, and geographic distribution of Old World domestic camels (Zarrin et al., 2020)

reference genomes: domestic Bactrian camel (GenBank No. GCF_000767855.1), wild Bactrian camel (GenBank No. GCF_009834535.1), and Arabian camel (GenBank No. GCF_036321535.1), following the same workflow described above. Mean genome-wide coverage was calculated using Qualimap v.2.2.1 (Okonechnikov et al., 2016), and ancient DNA damage patterns were assessed using MapDamage v.2.0 (Jónsson et al., 2013).

To comprehensively explore the evolutionary history of the analyzed specimens at the nuclear genome level, raw sequencing data were retrieved from NCBI for additional *Camelus* individuals, including 15 domestic Bactrian camels, nine wild Bactrian camels, and eight Arabian camels (Supplementary Table S2). All external datasets were processed using the same bioinformatic pipeline as described above.

Phylogenetic reconstruction

The three newly generated mitogenomes were aligned with 180 published *Camelus* mitogenomes retrieved from GenBank using MAFFT v.7.490 (Katoh et al., 2002), with *Lama glama* included as an outgroup (Supplementary Table S2). Ambiguous and undetermined sites were excluded using BioEdit v.7.2.5 (Hall, 1999), yielding a final alignment of 16 526 bp. The best-fit nucleotide substitution model, HKY+G, was selected using jModelTest v.2.1 (Darriba et al., 2012). Phylogenetic placement of the ancient camels from Xi'an was evaluated using Bayesian inference implemented in BEAST v.1.10.4 (Drummond & Rambaut, 2007) based on complete mitogenomes from Camelidae (Supplementary Table S2, Dataset 1). Analyses assumed a strict molecular clock with a prior substitution rate of 1.232×10^{-6} substitutions/site/year (Almathen et al., 2016). Markov chain Monte Carlo (MCMC) runs comprised 8 000 000 iterations with sampling every 1 000 generations, and the first 10% of states were discarded as burn-in. Convergence and effective sample sizes (ESS) were assessed using Tracer v.1.7.2 (Rambaut et al., 2018), confirming ESS values exceeding 200 for posterior parameters. A maximum clade credibility (MCC) tree was summarized using TreeAnnotator v.1.8.3 (https://beast.community/treeannotator) and visualized in FigTree v.1.4.4 (http://tree.bio.ed.ac.uk/software/figtree).

Nuclear phylogenetic position was assessed using a neighbor-joining (NJ) tree constructed from 33 571 single nucleotide polymorphisms (SNPs) inferred in ANGSD v.0.941 (Korneliussen et al., 2014). The dataset included 15 domestic Bactrian camels, nine wild Bactrian camels, eight Arabian camels, and the three newly sequenced specimens (Supplementary Table S2, Dataset 2). Key parameters for SNP calling were set as follows: -doIBS 2 -doCov 1 -makeMatrix 1 -doCounts 1 -doMajorMinor 1 -GL 2 -minMinor 2 -minInd 5 -skiptriallelic 1 -uniqueonly 1 -howOften 1 000 -rmTrans 1 -minQ 30 -minMapQ 30. The resulting pairwise genetic distance matrix was used to build the NJ tree with the ape package in R.

Sex identification and population structure

Biological sex was inferred from the ratio of average read coverage on the X chromosome relative to chromosome 1, following Yuan et al. (2024). Due to the similarity in length between the X chromosome and chromosome 1 in *Camelus* species, samples with an X/Chr 1 rate close to 0.5 were classified as male, while those with a ratio approximating 1 were identified as female.

To investigate intraspecific nuclear genetic affinities among domestic Bactrian camels, principal component analysis

(PCA) was performed using 36 193 filtered SNPs inferred with ANGSD v.0.941 (Korneliussen et al., 2014). This analysis included 15 publicly available domestic Bactrian camel genomes from NCBI and two newly sequenced specimens (SLT2 and SLT3) (Supplementary Table S2, Dataset 2). SNP calling used the following parameters: -doGlf 2 -GL 2 -minMapQ 30 -minQ 30 -uniqueonly 1 -rmTrans 1 -skiptriallelic 1 -minInd 3 -doMajorMinor 1 -doMaf 1 -minmaf 0.01 -SNP_pval 1e-6. Ancestral population structure was then inferred with NGSadmix v.32 (Skotte et al., 2013) using the same SNP dataset. Analyses were conducted for *K* values ranging from 2 to 4, with 100 bootstrap replicates per *K* and different random seeds.

RESULTS

Genome reconstruction and sex determination

Mapping against multiple *Camelus* reference genomes at mitochondrial and nuclear levels showed that SLT2 and SLT3 achieved higher mean coverage when aligned to the domestic Bactrian camel genome, whereas SLT4 exhibited higher mean coverage when aligned to the Arabian camel reference (Supplementary Table S1). Three complete mitogenomes were successfully reconstructed (16 594–16 659 bp), with mean coverage ranging from 4.44× to 19.24×. Three low-coverage nuclear genomes were also generated, with mean coverage ranging from 0.09× to 0.14×. All samples showed elevated C>T substitution rates at the 5′ termini of sequencing reads (Supplementary Figure S1), consistent with typical ancient DNA damage patterns (Dabney et al., 2013).

Sex determination based on the X-to-chromosome 1 coverage ratio (X/Chr1) yielded values of 0.51 for SLT2, 0.43 for SLT3, and 0.99 for SLT4, indicating male sex for SLT2 and SLT3 and female sex for SLT4 (Supplementary Table S1).

Maternal and nuclear phylogenetic trees

Phylogenetic placement of the newly reported *Camelus* remains was evaluated using a mitochondrial MCC tree reconstructed in BEAST v.1.10.4 and a nuclear NJ tree inferred in ANGSD v.0.941. Both mitochondrial and nuclear frameworks resolved three major Old World camel clades corresponding to domestic Bactrian camel, wild Bactrian camel, and Arabian camels, consistent with previous studies (Yuan et al., 2024). SLT2 and SLT3 clustered within the domestic Bactrian camel clade, while SLT4 grouped within Arabian camels (Figure 2).

Within domestic Bactrian camels, mitochondrial sequences were further partitioned into two lineages (B1 and B2) without clear geographical stratification. SLT2 and SLT3, along with a previously published Tang Dynasty individual from the same locality (SLT1, GenBank No. MW357598, ~1 290–1 180 cal BP) (Chen et al., 2019; Li & Li, 2023), fell within lineage B1. Arabian camels comprised two deeply divergent maternal lineages (A1 and A2). The newly sequenced SLT4 was assigned to lineage A1 and showed closer phylogenetic affinity to modern Middle Eastern Arabian camels (Figure 2A).

PCA and genetic structure analyses

PCA using 36 193 SNPs from domestic Bactrian camels revealed two well-separated clusters along the first principal component (PC1), which explained 39.81% of total genetic variation (Figure 3A). This nuclear partition was concordant with the two maternal lineages (B1 and B2) observed in the mitochondrial phylogeny (Figure 2A). SLT2 and SLT3 grouped within a single cluster, while the second cluster further separated into two subclusters along PC2, including one subcluster comprising four individuals from Iran (Figure 3A).

Ancestry inference using NGSadmix v.32 was conducted on the same dataset used for the nuclear phylogenetic analysis. At *K*=2, 3, and 4, SLT3 and SLT4 exhibited mixed ancestry components consistent with contributions from both domestic Bactrian and Arabian camel sources, whereas all modern individuals analyzed from both species, together with the younger SLT2 sample (~300–0 cal BP), displayed ancestry dominated by a single source (Figure 3B; Supplementary Figure S2). Specifically, SLT3, which phylogenetically clustered with domestic Bactrian camels, carried 7.3% Arabian ancestry. Conversely, SLT4, positioned within Arabian camels in both phylogenies, carried 45.1% domestic Bactrian camel ancestry (Figure 3B).

DISCUSSION

Molecular identification of *Camelus* remains from Xi'an

Species-level attribution of archaeological *Camelus* material based on morphology alone presents considerable challenges. Such specimens are often fragmentary, and extant *Camelus* taxa exhibit substantial intraspecific variation and interspecific overlap in diagnostic traits (Heintzman et al., 2015; Ji et al., 2009; Martini et al., 2018; Peters & von den Driesch, 1997). It is widely recognized that both domestic and wild Bactrian camels co-occurred in western and northern China during historical periods, further complicating osteological assignment in regions where both forms were plausible. Consequently, many reports, particularly from early archaeological records, conservatively assigned such specimens to "Bactrian camels", a classification supported by iconographic records that depicted two-humped camels in artwork and pottery figurines (Chen, 1991; He et al., 1986; Zhang & Luo, 2014).

Ancient DNA analysis has increasingly resolved taxonomic identity and biogeographic history across Camelidae (Almathen et al., 2016; Heintzman et al., 2015; Westbury et al., 2016; Yuan et al., 2024). In the present study, mitochondrial and nuclear evidence assigned SLT2 and SLT3 to domestic Bactrian camels (Figure 2A, B). Along with the previously reported SLT1 individual from the same locality (Chen et al., 2019), both Xi'an specimens fell within mitochondrial lineage B1 (Figure 2A), indicating shared maternal origin. Given that SLT3 was dated to ~2 300–2 000 cal BP, the presence of lineage B1 in northwestern China was supported by at least the early phase of ancient Overland Silk Road activity, near 2 150 BP (Mei, 2014), consistent with introduction from Central Asia during initial intensification of transregional exchange.

Paleogenomic evidence further identified SLT4 as an Arabian camel. Maternal phylogeny resolved two Arabian camel lineages (A1 and A2), consistent with previous studies (Almathen et al., 2016), and SLT4 clustered within the broadly distributed A1 lineage that included individuals sampled across Africa, Asia, Europe, and Australia (Figure 2A). Median-joining network analysis further revealed lower haplotype diversity among Arabian camels than among domestic Bactrian camels. SLT4 mapped to the central haplotype (Hap_1) and showed close genetic affinity to individuals drawn from multiple continents (Supplementary Figure S3A, B).

Modern Arabian camels are primarily distributed in the Horn of Africa, the Middle East, Pakistan, India, and arid regions of

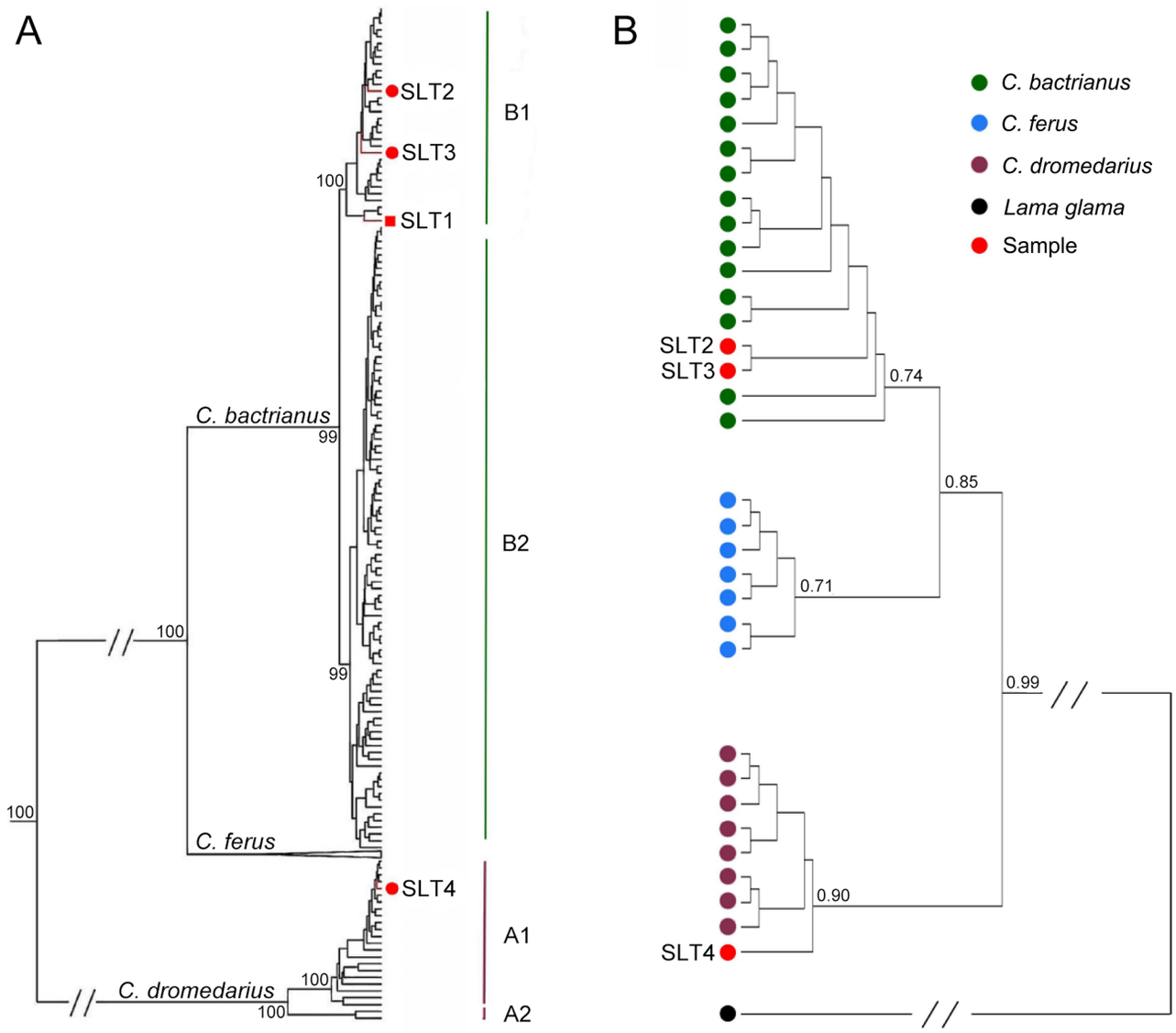

Figure 2 Phylogenetic relationships among extant *Camelus* species and ancient Xi'an specimens

A: Maximum clade credibility (MCC) tree inferred from a 16 526 bp alignment of complete mitogenomes. B: Neighbor-joining tree inferred from 33 571 nuclear single nucleotide polymorphisms (SNPs). *Lama glama* was used as an outgroup. SLT1 from Xi'an was previously reported by Chen et al. (2019).

North and West Africa (Zarrin et al., 2020). Archaeological documentation in China has been sparse, with only a small number of ceramic figurines from the Han and Tang dynasties in Shaanxi and Henan provinces tentatively interpreted as representations of this taxon (Mei, 2014). SLT4 therefore provides the first archaeologically derived bone remain in China genetically confirmed as an Arabian camel, highlighting the utility of ancient DNA for resolving *Camelus* taxonomic identity in contexts where osteological criteria alone remain equivocal.

Ancient human-mediated interspecific hybridization in domestic camels

Interspecific admixture has recurred throughout the evolutionary history of *Camelus* (Yuan et al., 2024). Although domestic Bactrian and Arabian camels have occupied largely distinct geographic ranges, long-term co-management in parts of Central and West Asia has created repeated opportunities for contact and crossbreeding (Dioli, 2020; Potts, 2004). In contrast to many other camelid species, hybridization between these two domestic species has frequently reflected deliberate human intervention, as hybrids have been reported to outperform parental types in load-carrying capacity and tolerance across heterogeneous environments (Amandykova et al., 2023; Burger et al., 2019; Dioli, 2020; Potts, 2004). Archaeological evidence has suggested that this practice extended back at least to the early first millennium BC (Potts, 2004), although the precise timing of its first occurrence remains unresolved.

Admixture analysis provided direct support for ancient hybridization between domestic camel species. The domestic Bactrian camel individual SLT3 (~2 300–2 000 cal BP) carried ~7.3% Arabian ancestry, whereas the Arabian camel individual SLT4 (~900–700 cal BP) carried ~45.1% domestic Bactrian ancestry, consistent with bidirectional introgression during historical periods (Figure 3B). This genomic signal aligned with zooarchaeological interpretation that camel management along Asian caravan routes shifted over time from reliance on domestic Bactrian camels toward a preference for more robust hybrids, particularly along the Overland Silk Road (Peters & von den Driesch, 1997).

Notably, SLT3 and SLT4 exhibited stronger interspecific

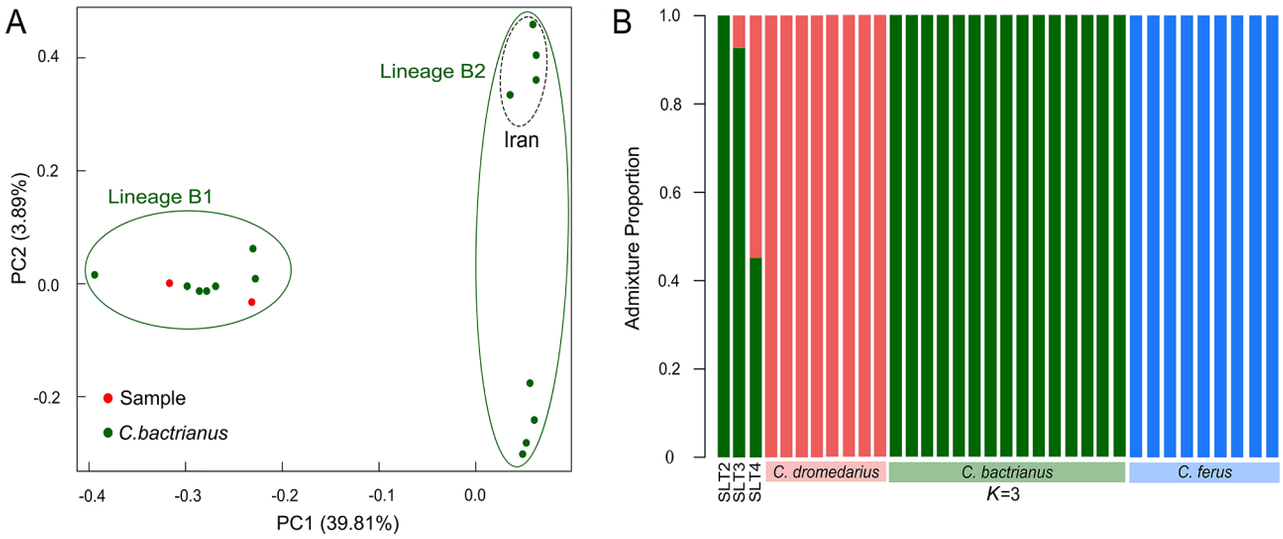

Figure 3 Nuclear population structure and admixture signals in domestic Bactrian camels and *Camelus* comparative datasets

A: Nuclear population structure of domestic Bactrian camels. B: Admixture profiles of the ancient Xi'an specimens and modern *Camelus* individuals retrieved from NCBI.

ancestry components than the modern individuals analyzed in this study (Figure 3B; Supplementary Figure S2). This pattern may be explained by several historical and demographic factors. Declining dependence on camels with expansion of maritime trade and subsequent adoption of mechanized transportation systems likely led to a sharp reduction in camel abundance and the collapse of long-distance caravan trade (Sala, 2017). Contraction of husbandry into geographically constrained desert systems would have limited opportunities for interspecific contact, while repeated backcrossing within non-admixed herds may have progressively diluted introgressed genomic segments. However, incomplete representation of contemporary diversity also remains a plausible explanation, and limited modern sampling may have reduced power to detect hybrid ancestry if introgression persisted at low frequency or in unsampled regions.

Ancient camels from Xi'an traversing the ancient Overland Silk Road

The ancient Overland Silk Road functioned as a major land corridor linking Asia with Europe and sustained large-scale movement of people and commodities across Eurasia. Zooarchaeological surveys of camel assemblages from multiple Overland Silk Road sites have demonstrated a central role for camels in transport and trade (Qi, 2004; Taylor et al., 2018). Persistent caravan movement along this route likely generated substantial gene flow among camel populations distributed across connected regions, with long-range translocation repeatedly reshaping ancestry patterns and profoundly influencing genetic evolution over time. Previous genetic studies have reported the absence of a clear phylogeographic structure in modern domestic Bactrian camels across broad geographic sampling (Chen et al., 2019; Ming et al., 2017). A similar pattern has been reported for Arabian camels, with neither modern nor ancient populations showing strong geographic genetic structuring (Almathen et al., 2016). This lack of clear phylogeographic signals in both ancient and modern domestic camels has therefore been widely interpreted as a consequence of sustained long-distance exchange and associated animal mobility during historical periods (Lado et al., 2020; Orlando, 2016; Satyanarayana et al., 2022).

Within China, camel remains from early archaeological sites are relatively uncommon. However, camel-related records increased markedly during the Han Dynasty (202 BC), coinciding with the formal opening of the ancient Overland Silk Road and intensification of transregional exchange documented in both historical texts and archaeological materials (He et al., 1986). The SLT3 specimen, excavated in Xi'an and dated to ~2 300–2 000 cal BP, fell within this pivotal period. Notably, SLT3 carried 7.3% Arabian-related ancestry (Figure 3B). Given that the natural range overlap of the two domestic species lies far to the west of Xi'an, the most parsimonious explanation is that this individual was introduced into China from West or Central Asia via the ancient Overland Silk Road. In parallel, SLT2 and SLT3, together with the previously reported Tang Dynasty specimen SLT1 from the same locality, clustered within mitochondrial lineage B1. This finding supports the inference that reduced phylogeographic structuring in domestic Bactrian camels traced back at least to the Tang Dynasty, reflecting sustained human-mediated dispersal.

As noted earlier, Arabian camel records remain relatively limited in China (Mei, 2014). In this study, the radiocarbon age of SLT4 (~900–700 cal BP) corresponds to the Song Dynasty (960–1 127 AD), a period that encompassed progressive reorientation of exchange toward maritime routes during the Tang-Song transition. Although the Maritime Silk Road reached high prominence during the Song Dynasty, overland connectivity persisted despite an overall decline in continental traffic (Lu & Su, 2016; Zhang et al., 2020). Under this historical context, episodic introduction of Arabian camels from Central or West Asia into Xi'an remained plausible, with SLT4 representing a genomic trace of late-stage transcontinental movement. Subsequent expansion of modern transportation likely eliminated remaining economic dependence on camel caravans, contributing to the collapse of long-distance caravan systems and closing a period in which camel-mediated mobility structured connectivity across Eurasia.

CONCLUSIONS

In the present study, complete mitogenomes and low-coverage nuclear genomes from *Camelus* remains excavated

in Xi'an were analyzed to resolve phylogenetic placement, reconstruct historical migrations, and evaluate potential gene flow among camel lineages. The results supported historical admixture between domestic Bactrian and Arabian camels, with patterns consistent with bidirectional introgression and deliberate production of hybrids for caravan transport along the ancient Overland Silk Road. These findings further indicated that this transcontinental route likely served as a genetic corridor, facilitating the repeated translocation and admixture of domestic camel populations. Expanded paleogenomic sampling across additional archaeological contexts and time intervals will be required to refine migration trajectories of domestic camels along the ancient Overland Silk Road and to quantify the contribution of camel mobility to connectivity within historical trade networks.

DATA AVAILABILITY

The sequencing data reported in this paper have been deposited in the NCBI database under BioProjectID PRJNA1371764, GSA database (https://ngdc.cncb.ac.cn/gsa/) (PRJCA061206), and Science Data Bank (doi: 10.57760/sciencedb.j00139.00273).

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

J.X.Y., X.L.L., and G.L.S. designed this study. H.J.G., K.X., and J.L. collected the samples. K.X. performed the morphological analyses. D.Q.Y., S.W.S., M.M.Z., C.D., Y.Z., L.Y.Z., and X.L.S. performed the DNA experiments. D.Q.Y. performed data processing and analyses. B.X. and J.M.H. guided the experiments and bioinformatics analyses. J.X.Y., G.L.S., D.Q.Y., and K.X. wrote the paper. X.L.L., B.X., and J.M.H. revised the manuscript. All authors read and approved the final version of the manuscript.

ACKNOWLEDGMENTS

We thank Professor Yun-Xiang Zhang and Professor Yong-Xiang Li (Northwest University, China) for help during this research.

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