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Ancient genomes reveal the genetic history of domestic goats on the Qinghai-Xizang Plateau approximately 3 600 years ago

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ABSTRACT

The Qinghai-Xizang Plateau imposes severe environmental pressures that have driven extensive adaptive responses in both humans and animals. Among the domestic species that underpin high-altitude pastoral livelihoods, goats are of particular importance, yet their historical origins remain poorly resolved. In this study, ancient genomic data were generated from five goat remains recovered from the Lake Qinghai Basin and dated to approximately 3 600 years ago. After stringent authentication and filtering, three individuals with genomic coverages ranging from 0.152× to 1.45× were retained for subsequent population genetic analysis. These data revealed a close genetic affinity between ancient goats from the Lake Qinghai Basin and goat populations from West Eurasia. In contrast, most present-day Chinese goats predominantly carried ancestry related to Neolithic Iran. Notably, modern Dazu black goats (*Capra hircus*) were found to derive primarily from a lineage closely related to the ancient Lake Qinghai Basin goats, indicating marked genetic continuity across time. In addition, modern Alpas cashmere goats and Qinghai-Xizang goats carried approximately 4%–8% ancestry from the Lake Qinghai

Basin-related lineage. Collectively, these findings refine current understanding of early herd management on the Qinghai-Xizang Plateau and provide new insight into the genetic history and population formation of Chinese goats.

Keywords: Ancient DNA; Chinese goats; Genetic history; Lake Qinghai Basin; *PAPSS2*

INTRODUCTION

The Qinghai-Xizang Plateau, the highest and most extensive plateau on Earth, represents one of the most environmentally inhospitable regions occupied by human populations. Persistent cold, pronounced aridity, and reduced atmospheric pressure impose substantial constraints on subsistence and long-term habitation, making survival in this region exceptionally demanding (Qiu, 2008). Early Qinghai-Xizang populations underwent biological adaptation to these harsh conditions, yet enduring occupation of the plateau also depended on cultural strategies capable of securing stable food resources under severe ecological limitation (Ding et al., 2020; Jeong et al., 2014; Liu et al., 2022; Yang et al., 2017;

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Zhang et al., 2023). Previous studies have emphasized the importance of frost-tolerant barley cultivation in enabling sustained human presence on the Qinghai-Xizang Plateau and in promoting permanent settlement by approximately 3 600 years ago (Chen et al., 2015). Archaeological investigations have found evidence of successful barley cultivation at high elevations, although this practice appears to have been largely confined to relatively favorable warm valleys (D'Alpoim Guedes et al., 2014; Fu et al., 2000; Gao et al., 2021; Knörzer, 2000; Tang et al., 2021). How prehistoric communities maintained occupation across the broader expanse of the plateau, where agricultural potential was far more limited, remains an open question.

Restricted arable land across the Qinghai-Xizang Plateau highlights the central role of animal resources in regional subsistence systems. In this context, pastoralism, particularly the management and domestication of livestock, likely formed a critical foundation for human survival and mobility. Recent discoveries from numerous zooarchaeological sites across the plateau have expanded current understanding of prehistoric interactions between humans and animals (Chen et al., 2023; Lu et al., 2021; Wang et al., 2023b; Yang et al., 2024; Zhang et al., 2024). Archaeological evidence indicates that several major livestock taxa, including sheep (*Ovis aries*), taurine cattle (*Bos taurus*), and goats (*Capra hircus*), were first domesticated in different parts of Eurasia and subsequently dispersed into the interior of the Qinghai-Xizang Plateau during prehistory through processes linked to human migration and the spread of agricultural practices (Chen et al., 2023; Lu et al., 2021; Tang et al., 2023; Wang et al., 2023b; Zhang et al., 2024). In parallel, ancient genomic evidence has provided strong support for early management and domestication of yak, taurine cattle, and admixed forms (Chen et al., 2023), offering important insight into animal resource use among prehistoric high-altitude communities. Together, these findings indicate that mobile pastoralism and diverse agropastoral systems (Tashi et al., 2002) have underpinned continued human occupation in the higher and more environmentally challenging regions of the plateau.

Among domestic livestock on the Qinghai-Xizang Plateau, goats occupy an indispensable position in everyday subsistence and household economy (Wu et al., 2020). Their value is especially pronounced under the extreme ecological constraints of this high-altitude, resource-scarce environment (Goldstein & Beall, 1990; Silanikove, 2000). This importance reflects several complementary functions. Goat milk constitutes a major nutritional resource, particularly during winter, when food availability declines sharply (Hirata & Hirata, 2020). Goat meat further provides a reliable source of sustenance for pastoral communities in the highlands. Goat fiber, notably cashmere, provides an additional essential material resource by supporting thermal protection and clothing production in a region characterized by extreme cold (Miller, 2000). Furthermore, goat dung serves as an important fuel source, compensating for the scarcity of wood and other combustible materials in high-altitude landscapes (Wu et al., 2023). The capacity of goats to tolerate harsh, high-altitude terrain, cold conditions, and nutritionally sparse forage further underscores their suitability for the Qinghai-Xizang Plateau and helps explain their enduring importance in regional life.

Given the ecological and economic importance of goats, tracing the origin and early dispersal of this domestic species into the Qinghai-Xizang Plateau is essential for reconstructing

the emergence of high-altitude pastoralism. However, the chronology and underlying processes associated with the early history of goats on the plateau remain poorly understood. Recent paleogenomic research has shown that Neolithic goat populations around the Fertile Crescent were not genetically uniform but instead comprised three major regional groups (Daly et al., 2018): the Neolithic West (Anatolia and the Balkans), Neolithic East (Iran and Turkmenistan), and Neolithic Levant, each of which contributed differently to the genetic composition of present-day goat populations. Independent archaeological evidence based on skeletal morphology has suggested that domestic goats entered China from the Eurasian steppe by the early second millennium before the common era, coinciding with a period of climatic cooling and aridification in northern China that may have expanded open grazing environments and favored the spread of pastoralism (Liu & Chen, 2012). Studies of mitochondrial variation have identified four matrilineal lineages, A, B, C, and D, in ancient Chinese goats (Song et al., 2024), although inference from mitochondrial markers alone remains inherently limited because such data capture only a single genetic locus (Chen et al., 2005; Han et al., 2010). Broader genomic evidence has begun to clarify this history. Recent analysis of ancient DNA (aDNA) from nine archaeological sites in northern China, spanning 450 to 3 900 years ago, indicated that the common ancestor of ancient Chinese goats can be traced to Neolithic Iran in the eastern Fertile Crescent (Cai et al., 2020). Despite these advances, the genetic history of early goats associated with the Qinghai-Xizang Plateau has remained largely unexplored.

Goat bones recovered from the Dacang site in the Lake Qinghai Basin provide a direct window into early caprine history on the Qinghai-Xizang Plateau. Although these specimens date to around 3 600 years before present (BP), their origin and genetic composition remain unresolved (Qiu et al., 2023) (Figure 1A, B). Ancient DNA anchored by archaeological chronology can shed light on historical selection processes and offer direct evidence of the genomic dynamics experienced by populations. To address this question, genomic evidence from the Dacang goat specimens was analyzed together with published ancient and modern goat genomes to reconstruct the origin and genetic differentiation of early Qinghai-Xizang Plateau goats. This analysis refines current understanding of goat domestication and dispersal, reveals how early human societies adapted to the extreme environments of the Qinghai-Xizang Plateau, and provides a scientific framework for the conservation and sustainable utilization of modern livestock genetic resources.

MATERIALS AND METHODS

Modern goat genotyping based on previously published datasets

Genotype data for modern goats were generated from previously published studies (NCBI BioProject accession: PRJNA387635; Genome Sequence Archive: CRA004127) (Li et al., 2023; Zheng et al., 2020). Detailed sample information is provided in Supplementary Table S1. Low-quality bases and technical artifact sequences were removed using fastp, and the resulting high-quality reads were mapped to the goat reference genome assembly (ARS1, GCA_001704415.1) (Bickhart et al., 2017) using BWA-MEM v.0.7.17 with default parameters (Li & Durbin, 2010). BAM files were sorted with

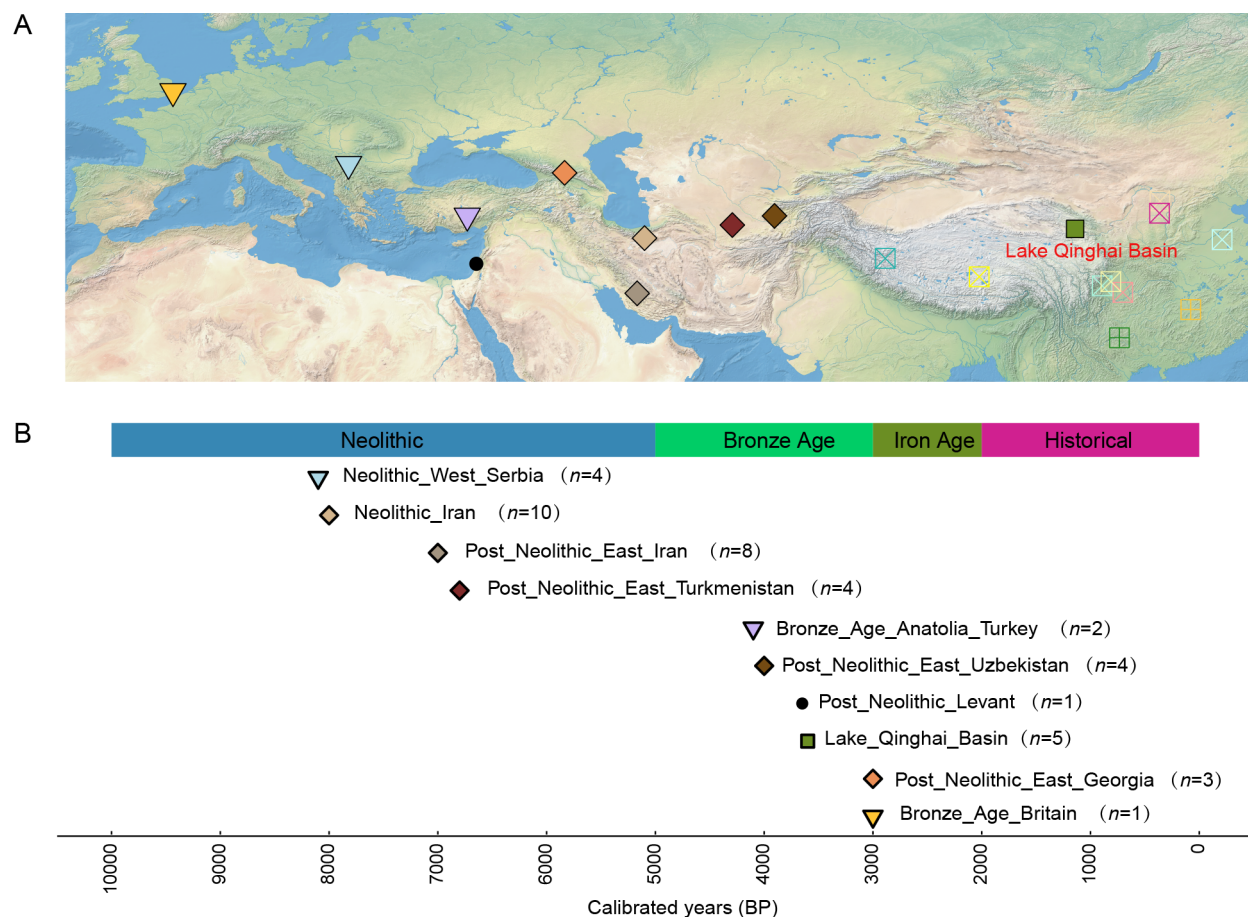


Figure 1 Geographic location and dates of ancient individuals

A: Geographic distribution of the newly analyzed ancient Lake Qinghai Basin samples together with published ancient individuals from regions surrounding the Fertile Crescent and present-day Chinese goats. B: Calibrated radiocarbon dates of ancient samples from the Lake Qinghai Basin, with key published ancient samples from the Fertile Crescent shown for comparison.

SAMtools v.1.9 and potential polymerase chain reaction (PCR) duplicates among mapped reads were identified with Picard Tools v.2.21.4. Variant calling was performed with HaplotypeCaller in GATK using the “-ERC GVCF” mode to generate GVCF files for single-nucleotide polymorphism (SNP) discovery. SNPs were retained only when all of the following criteria were met (McKenna et al., 2010): average sequencing depth ≥ 3 ; minor allele frequency (MAF) ≥ 0.05 ; missing rate ≤ 0.1 ; and biallelic status. After strict quality filtering, 1 200 112 common SNPs were retained for downstream analyses.

Archaeological background and sample information

Teeth and skeletal elements from five ancient goat specimens were collected from an archaeological site in the Lake Qinghai Basin (Qiu et al., 2023). All study procedures were reviewed and approved by the local archaeological institutions and the Institute of Earth Environment, Chinese Academy of Sciences. Among these samples, individual DC47_4HE was sequenced and directly dated by accelerator mass spectrometry (AMS) radiocarbon analysis to 3 480–3 580 years BP.

Ancient DNA extraction and library preparation

All laboratory procedures were conducted in the dedicated ancient DNA clean room at the Institute of Anthropology, Xiamen University. Animal remains were first cleaned using 75% ethanol and 10% sodium hypochlorite solution to remove surface dust and exogenous DNA contaminants, followed by

30 min of ultraviolet irradiation. Teeth were separated from the jaw using a blade saw, and approximately 100 mg of powder was obtained from tooth roots using dental drills. DNA extraction followed a modified protocol based on the method of (Rohland et al., 2018). Each sample was digested in 1 mL of lysis buffer containing 0.5 mmol/L EDTA (Sigma-Aldrich, USA) and 0.25 mg/mL Proteinase K (Qiagen, Germany) at 37°C and 300 rpm in a shaking incubator. DNA was then purified using a MinElute Kit (Qiagen, Germany) according to the manufacturer’s instructions. Double-stranded DNA libraries were prepared for all samples using a protocol based on the NEB Next Ultra II DNA Library Prep Kit (New England Biolabs) (Zhu et al., 2024). Sequencing of the resulting libraries was performed on the DNBSEQ-T7 platform (MGI Tech, China).

Ancient DNA sequence data processing

Sequencing adapters were removed and paired-end reads were merged with AdapterRemoval v.2.3.1 (Schubert et al., 2016). The merged reads were mapped to the goat reference genome (ARS1, GCA_001704415.1) (Bickhart et al., 2017) using BWA v.0.7.17 samse (Li & Durbin, 2009) with parameters -l 1024 and -n 0.01. PCR duplicates were removed with Dedup v.0.12.3 (Peltzer et al., 2016). To reduce the influence of terminal deamination, six bases were trimmed from both ends of each read using trimBam in BamUtil v.1.0.14 (<https://github.com/statgen/bamUtil>) to avoid excess C→T and G→A transitions at read termini (Skoglund et al.,

2014). Alignment quality was filtered with mpileup in SAMtools using parameters -q30 and -Q30. Pseudo-haploid genotypes for the ancient samples were generated using the modern goat variation SNP dataset as a reference and the parameter -RandomHaploid in pileupCaller (<https://github.com/stschiff/sequenceTools>). The same analytical framework was applied to published ancient goat genome data.

Authentication of ancient DNA

Post-mortem damage patterns characteristic of ancient DNA were evaluated with MapDamage v.2.0 (Jónsson et al., 2013), which was also used to estimate 5' C→T and 3' G→A misincorporation frequencies (Supplementary Figure S1). Mitochondrial contamination in all individuals was assessed with Schmutzi based on deamination damage patterns (Renaud et al., 2015).

Genetic sex determination

Genetic sex of individuals was inferred by comparing sequence coverage of the X chromosome with that of the autosomes (Fu et al., 2016). As males carry a single X chromosome, X-chromosome coverage is expected to be approximately half of autosomal coverage in males and approximately equivalent to autosomal coverage in females.

Kinship detection

Genetic relatedness among ancient individuals was evaluated with IcmLkin (Lipatov et al., 2015). No pair of individuals showed relatedness closer than the third degree.

Principal component analysis (PCA)

PCA was carried out using smartpca implemented in EIGENSOFT (Patterson et al., 2006) with the parameters "lsqproject: YES" and "numoutlieriter: 0". Principal components (PCs) were calculated from modern populations, and ancient individuals were subsequently projected onto the first two PCs.

ADMIXTURE and phylogenetic analyses

Linkage disequilibrium pruning was conducted with PLINK v.1.9 (Chang et al., 2015) using the parameters "--indep-pairwise 200 25 0.2". Population structure was then inferred with ADMIXTURE v.1.3.0 (Alexander et al., 2009) in unsupervised mode using the parameters "-B 100 --cv -s time". A neighbor-joining tree was constructed from the genome-wide SNP dataset using MEGA based on a pairwise genetic distance matrix generated with PLINK v.1.9.

F-statistics and admixture modeling

To evaluate differential gene flow, f_4 statistics were calculated in the form $f_4(\text{bezoar}, A; B, C)$, which tests whether A shares greater affinity with B or C relative to the reciprocal comparison. QpDstat v.980 was used for f_4 statistics estimation with the parameter " $f_4\text{-mode: YES}$ " (Lawson et al., 2018; Peter, 2016). Outgroup f_3 analysis was performed with Qp3Pop v651 in the form $f_3(A, B; \text{bezoar})$ to quantify shared

genetic drift between A and B. Both programs were implemented in ADMIXTOOLS. $F_4\text{-ratio v.0.131}$ (Patterson et al., 2012) was used to estimate the proportion of related ancestry in target populations.

Phenotypic SNP analysis

A set of functionally important PAPSS2 mutations in present-day Qinghai-Xizang goats has been proposed to have contributed to adaptation to high-altitude environments, potentially through introgression from *Capra falconeri* (Li et al., 2022). The present analysis focused on a 10-SNP motif within PAPSS2 composed of transversion sites showing high allele-frequency differentiation between Qinghai-Xizang and low-altitude goats. This motif has been used to define the PAPSS2 haplotype commonly observed in Qinghai-Xizang goats. For each of the 10 candidate SNPs, the number of mapped reads at the corresponding genomic position was quantified using only high-confidence reads with a mapping quality ≥ 30 .

RESULTS

Ancient genome-wide data from the Lake Qinghai Basin

Genome-wide data were generated from ancient goat samples from the Qinghai-Xizang Plateau to investigate their genetic composition and population history, providing the first such dataset for this region. Calibrated radiocarbon dating placed these individuals to about 3 600 years before present. All five specimens were recovered from the Lake Qinghai Basin. Although the sample size was limited, it encompassed all individuals excavated from the study area, thus providing the most comprehensive picture of prehistoric goat husbandry on the Qinghai-Xizang Plateau achievable to date using genome-wide data. DNA was extracted from all five individuals and double-stranded DNA libraries were constructed, with sequencing coverage ranging from 0.0065-fold to 1.45-fold (Table 1; Supplementary Table S2). The authenticity of the ancient genomic data was supported by characteristic post-mortem damage patterns (Supplementary Figure S1). Genetic sex assessment identified one male and four females. Mitochondrial contamination estimates generated with Schmutzi were below 1% for all samples. To reduce the influence of terminal damage, 6 bp was trimmed from both ends of each read based on C>T and G>A misincorporation profiles. Mitochondrial genomes were first compared with published mtDNA hypervariable fragment data (Naderi et al., 2007), showing that the Lake Qinghai Basin goats belonged to haplogroup C. Pseudo-haploid genotypes were then generated for all five individuals using a modern goat SNP panel. After removing low-coverage samples, three unrelated ancient individuals (Supplementary Table S3), spanning 67 122–428 121 SNPs, were used for downstream analyses. These data were integrated with previously published modern and ancient goat genomes for population genetic analysis. Together, this dataset addresses a major gap in current

Table 1 Summary of ancient samples reported in this study

Sample	Label	Number of SNPs (Modern goat reference panel)	Coverage (%)	Genetic sex	5' C → T (%)	3' G → A (%)	mtDNA haplogroup
DC23	Lake Qinghai Basin	2 652	0.65	Male	4.27	4.26	C
DC27-HE	Lake Qinghai Basin	73 524	17.32	Female	9.56	8.37	C
DC40	Lake Qinghai Basin	67 122	15.24	Female	9.73	9.52	C
DC47_4HE	Lake Qinghai basin	428 121	145.55	Female	9.55	9.22	C
DC48-1	Lake Qinghai Basin	7 997	1.75	Female	6.14	6.07	C

understanding of early goat population formation on the Qinghai-Xizang Plateau and provides direct genetic evidence relevant to animal management by human communities during the period around 3 600 years BP, when permanent occupation of the plateau had already been established.

Overall genomic structure of Lake Qinghai Basin goats

To characterize the broad genomic affinities of the Lake Qinghai Basin goats, PCA was first performed by projecting ancient individuals onto axes defined by present-day goat populations. Modern goat populations formed three major genetic clusters corresponding to Asia-related (ASI), Europe-related (EUR), and Africa-related (AFR) groups, which occupied the three extremes of the distribution (Figure 2). Ancient individuals associated with the Neolithic East (Iran, Uzbekistan, Georgia, and Turkmenistan) were projected close to the cline defined by ASI-related populations. In contrast, ancient western individuals from Neolithic Serbia and Bronze Age Britain clustered near EUR-related populations, whereas ancient Neolithic Levant individuals projected closer to AFR populations. All Lake Qinghai Basin individuals clustered together and were clearly separated from both modern and ancient Asian goat groups. Notably, these individuals were closely aligned along the same genetic cline as modern and ancient domestic goats from western populations.

A neighbor-joining tree further clarified these relationships (Figure 3A). Lake Qinghai Basin individuals and Dazu black goats clustered together on a sub-branch, indicating a close genetic relationship. In addition, the Lake Qinghai Basin population showed strong genetic affinity with ancient western populations (Serbia, Britain, and Turkey) from the Neolithic and Bronze Age, while remaining clearly distinct from other Chinese goat populations and ASI-related groups. The

separation of Lake Qinghai Basin goats and Dazu black goats from Neolithic East populations and most other Chinese goats further suggests divergent population histories within Chinese domestic goats. Present-day Chinese goats were broadly divided into two sub-groups. Together, these results indicate that goats from the Lake Qinghai Basin, dated to approximately 3 600 years ago on the Qinghai-Xizang Plateau, were closely related to ancient western populations and to present-day Dazu black goats. This pattern was also recovered in unsupervised ADMIXTURE analysis (Supplementary Figure S2), in which the yellow ancestry component reached its highest proportion in the Lake Qinghai Basin goats and Dazu black goats. A consistent signal emerged from outgroup f_3 statistics, which measure shared genetic drift among populations. These results showed that Dazu black goats, the Lake Qinghai Basin population, and western groups shared closer genetic affinity with each other than with other populations (Figure 3B; Supplementary Figure S3). The close relationship between the Lake Qinghai Basin population and Dazu black goats indicates shared ancestry, whereas the clustering of Lake Qinghai Basin individuals with ancient Neolithic West populations points to a possible link between the Qinghai-Xizang Plateau and nomadic steppe populations.

Lake Qinghai Basin ancestry derived from western domestic goats

To clarify the population history and genetic affinities of the ancient Chinese Lake Qinghai Basin goats, f_4 statistics were used to perform symmetry tests comparing these individuals with three major Neolithic goat populations distributed around the domestication center. Results indicated that Lake Qinghai Basin goats shared significantly greater affinity with Neolithic

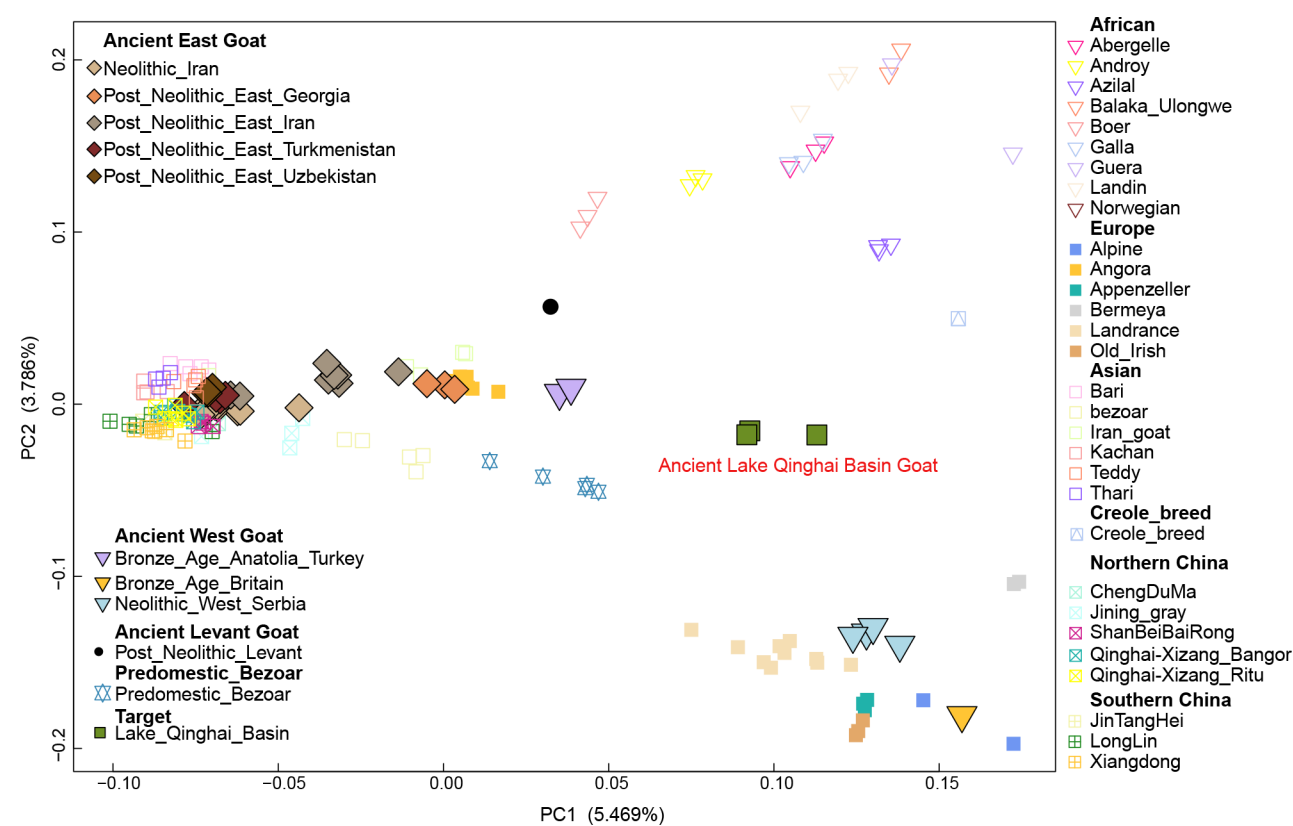


Figure 2 Principal component analysis (PCA) plot

PCA of globally distributed present-day goats, ancient Lake Qinghai Basin goats, and Neolithic goats from regions surrounding the Fertile Crescent.

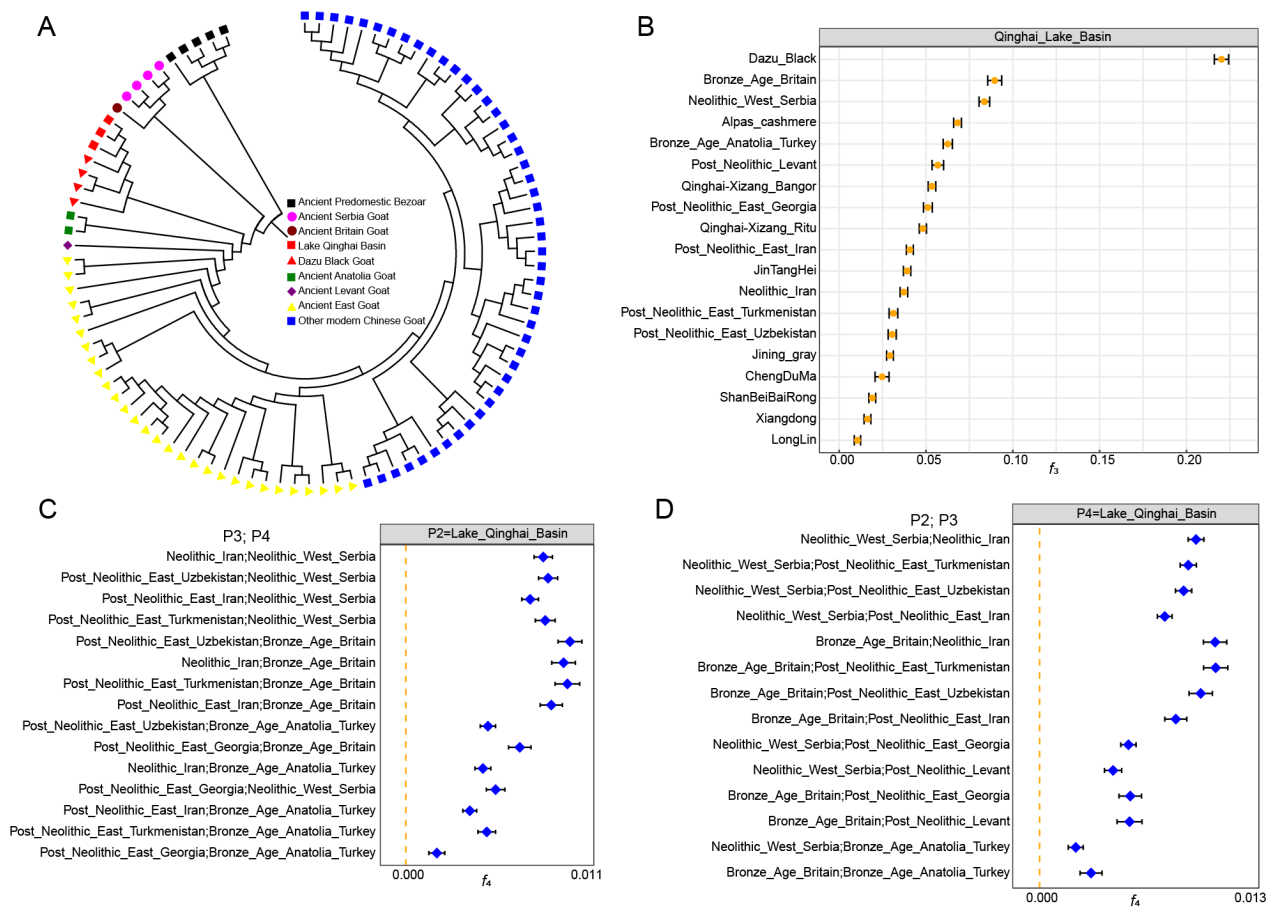


Figure 3 Genomic structure of ancient Lake Qinghai Basin goats

A: Neighbor-joining (NJ) tree including present-day Chinese goats, ancient Lake Qinghai Basin goats, and ancient goats from regions surrounding the Fertile Crescent. B: Outgroup f_3 statistics measuring genetic affinity involving ancient Lake Qinghai Basin goats. C: f_4 statistics in the form $f_4(\text{bezoar, Lake_Qinghai_basin; Neolithic East group, Neolithic West group})$, showing close genetic affinity between Lake Qinghai Basin goats and western populations. D: f_4 statistics in the form $f_4(\text{bezoar, Bronze_Age_Britain/Neolithic_West_Serbia; other Neolithic ancient goat population, Lake_Qinghai_basin})$, showing a close genetic relationship with Lake Qinghai Basin goats. Additional details are provided in Supplementary Tables S4 and S7.

West populations than with Neolithic East populations (Figure 3C), with Z-scores for $f_4(\text{bezoar, Lake_Qinghai_basin; Neolithic East, Neolithic West})$ ranging from 3.887 to 14.955 (Supplementary Table S4). Additional asymmetry tests comparing Lake Qinghai Basin goats with Neolithic West and Levant populations further demonstrated closer genetic affinity with Neolithic West populations than with Neolithic Levant populations (Supplementary Figure S4), with Z-scores for $f_4(\text{bezoar, Lake_Qinghai_basin; Post_Neolithic_Levant, Bronze_Age_Anatolia_Turkey/Neolithic_West_Serbia/Bronze_Age_Britain})$ ranging from 0.598 to 6.709 (Supplementary Table S5). These results were further supported by f_4 analyses placing the Lake Qinghai Basin goats within the western branch of domestic goats from the Fertile Crescent. Stronger allele sharing was also detected between the Lake Qinghai Basin samples and Bronze_Age_Britain and Neolithic_West_Serbia than between the Lake Qinghai Basin samples and Bronze_Age_Anatolia_Turkey (Supplementary Figure S5), with Z-scores for $f_4(\text{bezoar, Lake_Qinghai_basin; Bronze_Age_Anatolia_Turkey, Bronze_Age_Britain/Neolithic_West_Serbia})$ ranging from 7.305 to 7.522 (Supplementary Table S6). Consistent with this pattern, Bronze_Age_Britain and Neolithic_West_Serbia populations exhibited the strongest genetic affinity with the Lake Qinghai Basin population among the tested groups (Figure 3D), with Z-

scores for $f_4(\text{bezoar, Bronze_Age_Britain/Neolithic_West_Serbia; X, Lake_Qinghai_basin})$ ranging from 4.692 to 19.785 (Supplementary Table S7). Together, these results indicate that the newly sampled ancient goats from the Qinghai-Xizang Plateau represent an East Asian branch derived from Neolithic western goat populations. This pattern suggests that the Lake Qinghai Basin population inherited a substantial portion of its genetic legacy from western populations, potentially through dispersal linked to steppe expansions.

The distinctive *PAPSS2* haplotype identified in present-day Qinghai-Xizang goats has been proposed to contribute to their adaptation to high-altitude environments and may have entered domestic goat populations through introgression from *Capra falconeri* (Li et al., 2022). This haplotype has not been detected in lowland goat populations. Despite limited sequence coverage across this genomic region, the highly differentiated 10-SNP transversion motif defining the *PAPSS2* haplotype was examined in the Lake Qinghai Basin individuals. Surprisingly, none of these ancient goats carried the high-altitude adaptive *PAPSS2* allele (Supplementary Table S8). This result suggests that the Lake Qinghai Basin goats may represent an early domestic population that had already reached the plateau before the adaptive *PAPSS2*-derived alleles became established. Taken together, these findings demonstrate that domestic goats derived from

western Fertile Crescent populations had reached the Qinghai-Xizang Plateau by no later than around 3 600 years ago, coinciding with the emergence of animal husbandry in highland regions during the same timeframe.

West- and East-related ancestry shaped the gene pool of present-day goat populations

To investigate the genetic formation of present-day goat populations in China, $f_4(\text{bezoar, present-day Chinese goats; Lake_Qinghai_basin, Neolithic East Group})$ was used to evaluate relative genetic affinity between modern Chinese goats and Neolithic goat populations distributed around the Fertile Crescent. This analysis revealed two distinct patterns among contemporary Chinese goats. First, most present-day Chinese goat populations, with the exception of Dazu black

goats, showed the strongest genetic affinity with Neolithic East populations (Figure 4A), with f_4 -statistic Z-scores ranging from -1.126 to 28.125 when the Neolithic East Group was represented by Neolithic_Iran, Post_Neolithic_East_Georgia, Post_Neolithic_East_Iran, Post_Neolithic_East_Uzbekistan, or Post_Neolithic_East_Turkmenistan (Supplementary Table S9). Second, Dazu black goats showed a pronounced genetic affinity with Lake Qinghai Basin populations (Figure 4A), with f_4 -statistic Z-scores ranging from -48.789 to -40.556 (Supplementary Table S9). This relationship was further supported by the consistently negative results for $f_4(\text{bezoar, Dazu_Black_Goat; Lake_Qinghai_basin, Neolithic_West_Serbia/Post_Neolithic_Levant/Bronze_Age_Britain/Bronze_Age_Anatolia_Turkey})$ (Supplementary Figure S6; Supplementary Table S10). Together, these results indicate

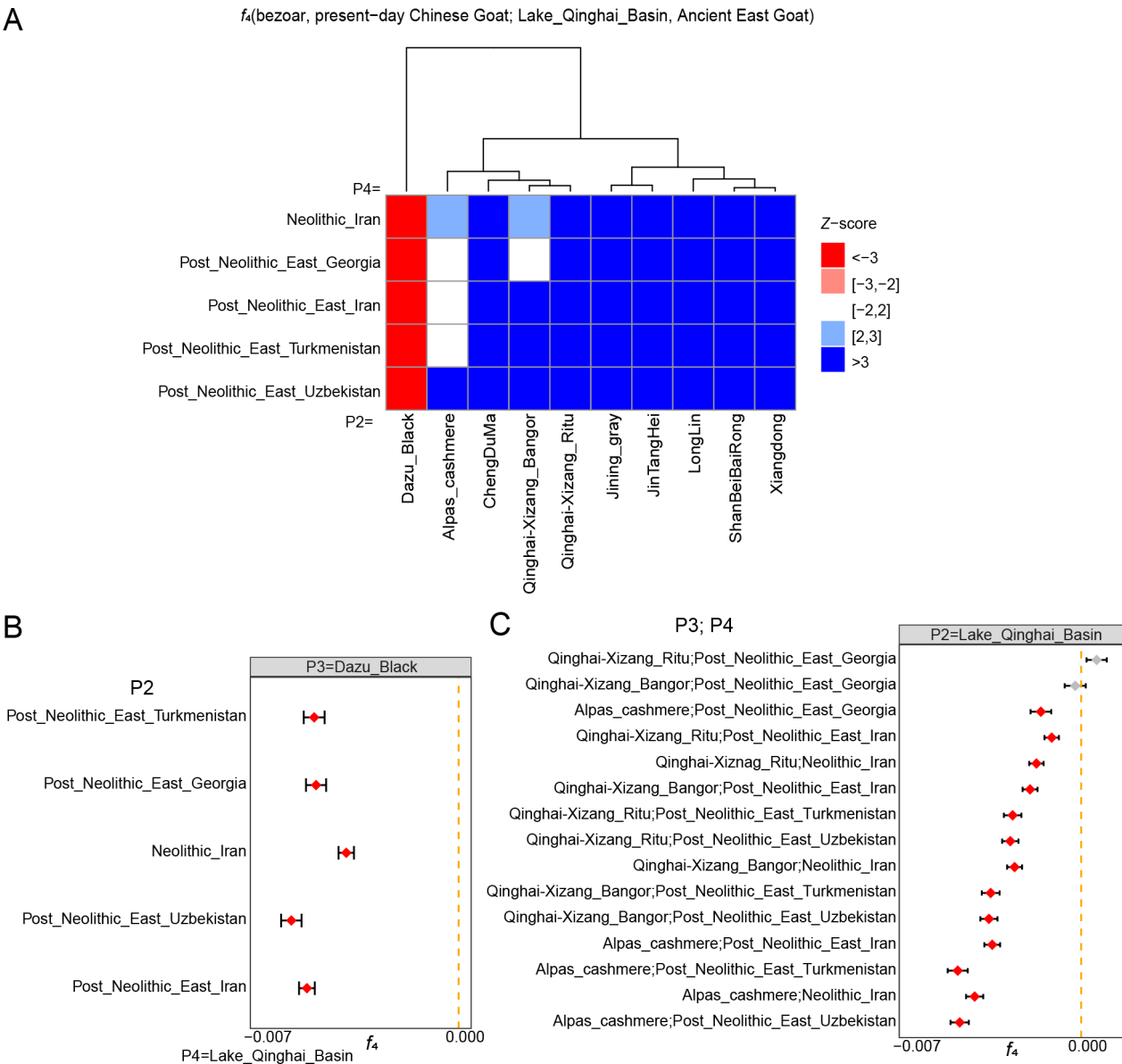


Figure 4 Genetic origin of present-day Chinese goats

A: Heatmap of $f_4(\text{bezoar, present-day Chinese goats; Lake_Qinghai_basin, Neolithic East Group})$, showing differential genetic affinity and revealing two distinct ancestry patterns among present-day Chinese goats. B: f_4 statistics in the form $f_4(\text{bezoar, Neolithic East Group; Dazu_Black_Goat, Lake_Qinghai_basin})$, showing that Dazu black goats exhibit closer genetic affinity with Neolithic East populations than with Lake Qinghai Basin populations. C: f_4 statistics in the form $f_4(\text{bezoar, Lake_Qinghai_basin; Alpas_cashmere/Qinghai-Xizang_Bangor/Qinghai-Xizang_Ritu, Neolithic East Group})$, showing that present-day Qinghai-Xizang goats and Alpas cashmere goats exhibit closer genetic affinity with Lake Qinghai Basin goats than with Neolithic East populations.

that the genomic composition of present-day goats was shaped by ancestry components associated with both western and eastern populations. In addition, Dazu black goats showed greater affinity with Neolithic East populations than did the Lake Qinghai Basin goats, as indicated by $f_4(\text{bezoar}, \text{Neolithic East Group}; \text{Dazu_Black_Goat}, \text{Lake_Qinghai_basin})$, with Z-scores ranging from -19.262 to -13.863 (Figure 4B; Supplementary Table S11). Beyond this pattern, present-day Qinghai-Xizang goats and Alpas cashmere goats from Ordos City, Inner Mongolia, also showed greater affinity with the Lake Qinghai Basin population relative to the Neolithic East group, as detected through $f_4(\text{bezoar}, \text{Lake_Qinghai_basin}; \text{Alpas_cashmere/Qinghai-Xizang_Bangor/Qinghai-Xizang_Ritu}, \text{Neolithic East Group})$, with Z-scores ranging from -13.277 to 1.53 (Figure 4C; Supplementary Table S12). These results highlight the influence of Lake Qinghai Basin-related ancestry ($\sim 3\,600$ years old) on both modern Qinghai-Xizang goats and Alpas cashmere goats in northern China.

To further quantify this contribution, goat populations associated with Neolithic Iran and the Lake Qinghai Basin were used as source populations to model admixture proportions in present-day goats. Notably, f_4 -ratio analysis revealed that modern Qinghai-Xizang goats and Alpas cashmere goats could be modeled as deriving 92%–96% of their ancestry from Iran-related sources, with the remaining proportion derived from Lake Qinghai Basin-related ancestry (Figure 5; Supplementary Table S13). Accordingly, modern Qinghai-Xizang goat populations retained approximately 7%–8% ancestry related to the Lake Qinghai Basin. Dazu black goats were successfully modeled as a mixture of 44% Iran-related ancestry and 56% Lake Qinghai Basin-related ancestry in the same analysis (Figure 5; Supplementary Table

S13). These results indicate that Lake Qinghai Basin-related ancestry has persisted in China and now constitutes a major component of the genomic background of Dazu black goats. Collectively, these analyses provide genomic insight into present-day goats from the Qinghai-Xizang Plateau and northern China, reveal evidence of admixture among different ancestral lineages, and support the existence of two diffusion pathways that contributed to the formation of modern Chinese goat populations.

DISCUSSION

Genetic affinity of Qinghai-Xizang Plateau goats dating to 3 600 years BP: Insights into western Fertile Crescent ancestry

Ancient goat genomic data from the Qinghai-Xizang Plateau, dating to approximately 3 600 years BP, provide important new evidence for resolving the population history and genetic differentiation of goats in China. Paleogenomic analyses integrating phylogenetic reconstruction based on higher-coverage samples with PCA, outgroup f_3 statistics, and f_4 statistics across ancient and present-day goat datasets revealed a coherent pattern of ancestry. The 3 600-year-old Qinghai-Xizang Plateau goats showed close genetic affinity with present-day Dazu black goats from Dazu County, Chongqing, indicating persistence of Lake Qinghai Basin-related ancestry from the Bronze Age to modern populations. Comparison with the three major Neolithic goat populations surrounding the domestication center further showed that ancient Qinghai-Xizang Plateau goats were more closely related to western Fertile Crescent goats than to populations from other regions (Daly et al., 2018), indicating that a

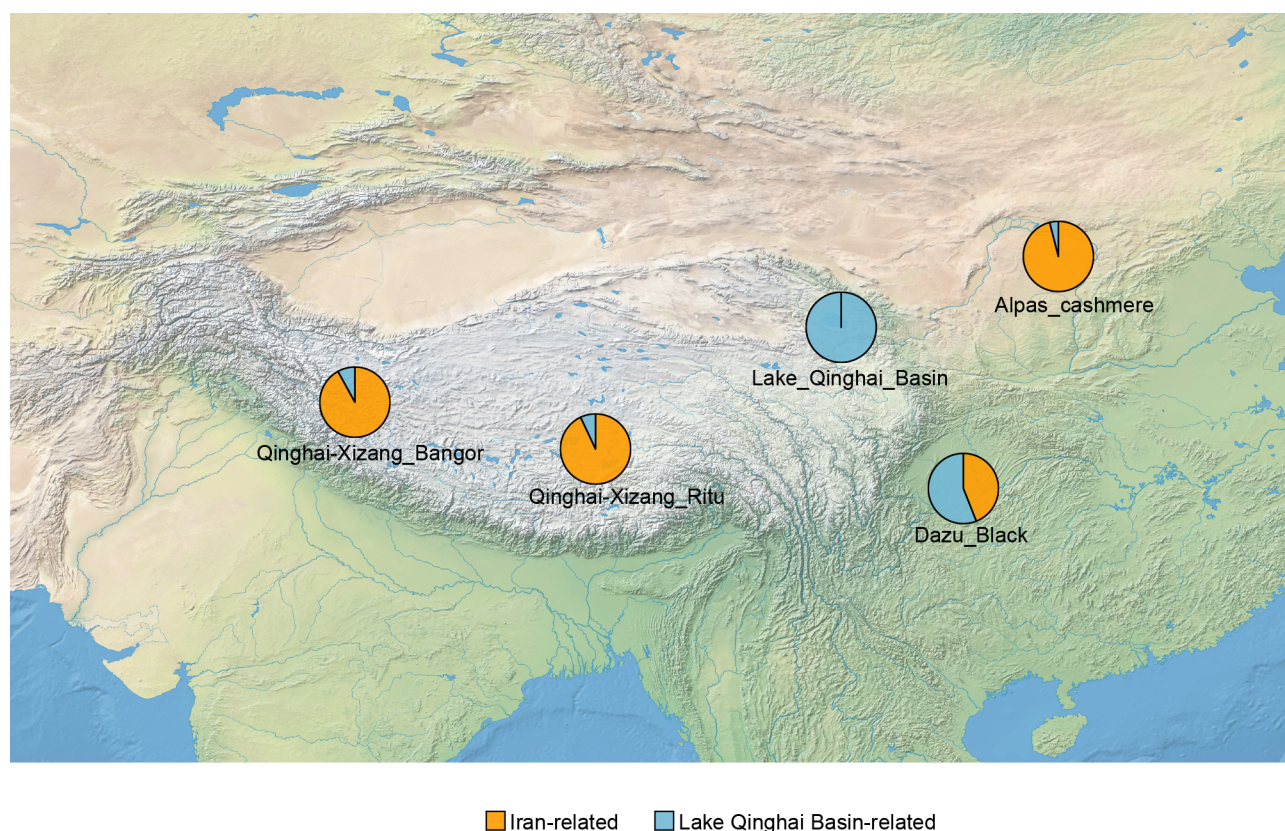


Figure 5 Admixture proportions of present-day Chinese goats

Ancestry proportions estimated for present-day Qinghai-Xizang goats and Alpas cashmere goats using f_4 -ratio analysis.

substantial component of early Chinese goat ancestry derived from Neolithic populations of the western Fertile Crescent. Within ancient goat populations from different periods of the western Fertile Crescent, the Qinghai-Xizang Plateau goats showed greater genetic affinity with Neolithic West Serbia and Bronze Age Britain populations than with individuals from Bronze Age Anatolia. From a maternal lineage perspective, all ancient individuals from the Lake Qinghai Basin belonged to mitochondrial haplogroup C. This haplogroup has been identified in both European and Asian goat populations (Deniskova et al., 2020; Yi et al., 2022), consistent with a broad Eurasian distribution. The mitochondrial profiles of the Lake Qinghai Basin individuals resembled those of western populations, further suggesting potential genetic connections or shared ancestral origins. Taken together, these findings support the inference that the Qinghai-Xizang Plateau goat population descended from a lineage that diverged from western Fertile Crescent populations during the interval between the Neolithic and Bronze Age. This pattern is consistent with west-to-east goat dispersal alongside the expansion of western steppe cultural traditions and broader Eurasian pastoralist networks, with the Eurasian steppes serving as a crucial corridor for human migrations and for the transfer of livestock and agricultural practices (Jeong et al., 2020; Liu et al., 2024; Wang et al., 2019).

Legacy of pastoralism: Supporting prehistoric occupation of the Qinghai-Xizang Plateau highlands

Recent paleogenomic evidence has placed goat domestication within the Neolithic period (Daly et al., 2018). Comparative analysis integrating genome-wide ancient DNA from the Lake Qinghai Basin with genomic data from ancient and present-day goats showed that domestic goats were already being managed by high-altitude herding communities on the Qinghai-Xizang Plateau approximately 3 600 years ago. These data provide the earliest direct genomic evidence currently available for domestic goats on the plateau. At the current level of genomic resolution, the *PAPSS2* haplotype associated with *Capra falconeri* introgression and high-altitude adaptation in present-day Qinghai-Xizang goats (Li et al., 2022) was absent in these ancient plateau individuals, despite occurring at high frequency in modern Qinghai-Xizang goat populations. This pattern suggests that the Lake Qinghai Basin goats represented an early wave of domestic goat introduction to the plateau and that the adaptive *PAPSS2* haplotype rose to prominence later in plateau populations, although the timing of its initial entry into ancient plateau populations remains unknown.

Genetic sex determination identified four females among the five analyzed individuals, a pattern that may reflect deliberate herd management, potentially involving preferential retention of females for breeding. Previous research has shown that cultivation of frost-tolerant barley was a major adaptive development that supported more sustained human habitation on the Qinghai-Xizang Plateau and contributed to permanent occupation by about 3 600 years ago (Chen et al., 2015). The ancient DNA evidence presented here indicates that domestic goats formed part of an agropastoral system that has remained poorly documented at the genomic level and that permitted early herding communities to establish permanent settlements in the extreme environments of the Qinghai-Xizang Plateau. The combined use of animal husbandry and barley cultivation would have enabled far more effective

exploitation of high-altitude resources than earlier subsistence strategies (d'Alpoim Guedes, 2015) and was likely central to prehistoric demographic expansion across the plateau. This mixed production system, integrating livestock with barley and possible millet agriculture, marked the emergence of a diversified agropastoral economy on the Qinghai-Xizang Plateau (Chen et al., 2015; Wang et al., 2023a). Such a system offered both mobility and resilience, maximizing use of the limited environmental resources while establishing a subsistence framework that in many respects continues to the present day. Although these findings provide novel genomic insight into early goat pastoralism on the Qinghai-Xizang Plateau, limited sample size and restricted spatiotemporal coverage constrain broader inferences regarding population structure and adaptive history. Future ancient DNA studies incorporating wider geographic and chronological sampling will be essential for a more complete reconstruction of their evolutionary history.

Two ancestral sources of Chinese goats: Predominant contribution from the eastern lineage

Present-day Chinese goats exhibited two distinct ancestral patterns. At the broadest level, contemporary Chinese goat populations could be divided into two principal clades: Dazu black goats and other modern Chinese goats. Admixture analysis together with outgroup f_3 and f_4 statistics revealed marked genetic heterogeneity between Dazu black goats and other present-day Chinese goat populations. Genomic evidence revealed that Dazu black goats, like the ancient Lake Qinghai Basin goats, shared close genetic affinity with ancient western populations. As an indigenous genetic resource in Southwest China (Zhao et al., 2019), Dazu black goats have previously been recognized as genetically distinct from surrounding goat populations (Yang, 2006). This pattern suggests that the ancestors of both Dazu black goats and the 3 600-year-old Qinghai-Xizang Plateau goats derived from western lineages, most probably originating from populations carrying western Fertile Crescent ancestry. In contrast, all other major present-day Chinese goat populations showed the closest genetic affinity to Neolithic populations from the eastern Fertile Crescent. These results indicate that the genomic background of modern Chinese goats was primarily shaped by ancestry derived from the eastern Fertile Crescent. This interpretation is consistent with previous studies showing that both ancient and modern Chinese goats from the late Neolithic to the Iron Age shared close genetic affinity with Neolithic populations from the eastern Fertile Crescent, supporting an origin associated with the Neolithic East (Asadollahpour Nanaei et al., 2023; Cai et al., 2020; Daly et al., 2018).

Two dispersal routes may have contributed to the formation of Chinese goat lineages (Supplementary Figure S7). The eastern route, passing through the Inner Asian Mountain Corridor, likely functioned as a pivotal conduit for cultural and biotic exchange during the late Neolithic to Bronze Age, facilitating eastward movement of domesticated animals and cultivated crops into Central Asia and northwestern China (Frachetti et al., 2017; Miller et al., 2016; Stevens et al., 2016). Gene flow associated with eastern ancestry appears to have played the dominant role in shaping the genetic profile of most present-day goat populations in China. In contrast, the western route, associated with the eastward extension of steppe pastoralists (Vigne, 2015; Wilkin et al., 2020), possibly

introduced western Eurasian-related ancestry into the eastern Eurasian steppe and northern China via the trans-Eurasian corridor, thereby contributing to the ancestry of both early Qinghai-Xizang Plateau goats and modern Dazu black goats. These early migrations long predated the Silk Road, although later networks may have further extended the legacy of these goat populations across vast geographic distances. Together, these two routes shaped the genomic landscape of Chinese goats and intersected with the emergence and expansion of pastoralism in ancient China. Through this interplay goats became deeply integrated into both nomadic and settled societies across China, substantially enriching the region's agricultural and cultural heritage.

Genomic footprint of ancient Lake Qinghai Basin-related ancestry in present-day Chinese goats

Genome-wide data from ancient specimens revealed that two distinct ancestral lineages contributed to present-day Chinese goat populations. Among modern northern Chinese goats, including Qinghai-Xizang goats and Alpas cashmere goats from Ordos, Inner Mongolia, an additional ancestry component related to the ancient Lake Qinghai Basin was detected. Notably, symmetric f_4 statistics further showed a close relationship between Dazu black goats and the approximately 3 600-year-old goats from the Lake Qinghai Basin. At the same time, evidence of gene flow from Neolithic eastern ancestries into Dazu black goats was also identified. Accordingly, Dazu black goats were modeled as deriving from two ancestral sources, namely Lake Qinghai Basin-related ancestry and Neolithic Iran-related ancestry. From a genomic perspective, these results supported admixture between Lake Qinghai Basin-related ancestry and Neolithic East-related ancestry. More specifically, all modern Qinghai-Xizang goat populations and Alpas cashmere goats could be explained by a two-way admixture model in which 92%–96% of ancestry derived from Neolithic Iran-related populations and the remaining proportion derived from a Lake Qinghai Basin-related lineage. The detection of approximately 7%–8% Lake Qinghai Basin-related ancestry in modern Qinghai-Xizang goats, including Qinghai-Xizang_Ritu and Qinghai-Xizang_Bangor, further indicates that this lineage exerted a broader genetic influence across goat populations of the Qinghai-Xizang Plateau. In contrast, Dazu black goats were modeled as deriving 56% of their ancestry from Lake Qinghai Basin-related sources and 44% from Neolithic Iran-related lineages. These results identify the approximately 3 600-year-old Lake Qinghai Basin population as the primary genetic source of modern Dazu black goats and demonstrate long-term continuity of this ancestry in Chinese goat populations. This persistent genomic signal underscores the importance of the Lake Qinghai Basin as a key region of livestock dispersal and genetic exchange in the evolutionary history of Chinese goats.

In conclusion, comparative analysis of ancient and present-day goat genomes on a broad geographic scale revealed that goats from the Lake Qinghai Basin, dating to around 3 600 BP, descended primarily from Neolithic goat populations of the western Fertile Crescent. Modern Chinese goats were shaped by two distinct ancestral lineages associated with the eastern and western Fertile Crescent, with the eastern lineage playing a dominant role. The approximately 3 600-year-old Qinghai-Xizang Plateau-related lineage formed the primary ancestral component of modern Dazu black goats. Moreover, Alpas

cashmere goats and modern Qinghai-Xizang goats retained an estimated 4%–8% ancestry related to the Lake Qinghai Basin lineage. These findings clarify the genetic origin and differentiation of Chinese goats and provide new insight into the dispersal routes and ancestral structure that shaped their present-day diversity.

DATA AVAILABILITY

Alignment files (BAM format) obtained in this study were uploaded to the Science Data Bank (SDB, Data DOI: 10.57760/sciencedb.j00139.00251), Genome Sequence Archive (GSA, accession number PRJCA045603), and National Center for Biotechnology Information database (NCBI, BioProjectID PRJNA1328209).

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

C.C.W., P.X.S., Y.H.Q., and J.Z. designed the project, supervised the research, and integrated resources. J.Z. provided the archaeological materials. P.X.S., H.W., and Y.H.Q. assembled the archaeological materials and performed dating. H.F.H., L.T., and L.M.Q. performed the ancient DNA extraction and library preparation. T.Y.B. performed all analyses related to population genetics under the supervision of K.Y.Z., Y.X., R.W., J.J.Z., and L.T. T.Y.B. prepared all figures and supplementary materials. X.M.Y., Q.S., and H.M. were involved in project discussion and design. C.C.W., P.X.S., T.Y.B., and H.F.H. wrote the manuscript. All authors read and approved the final version of the manuscript.

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