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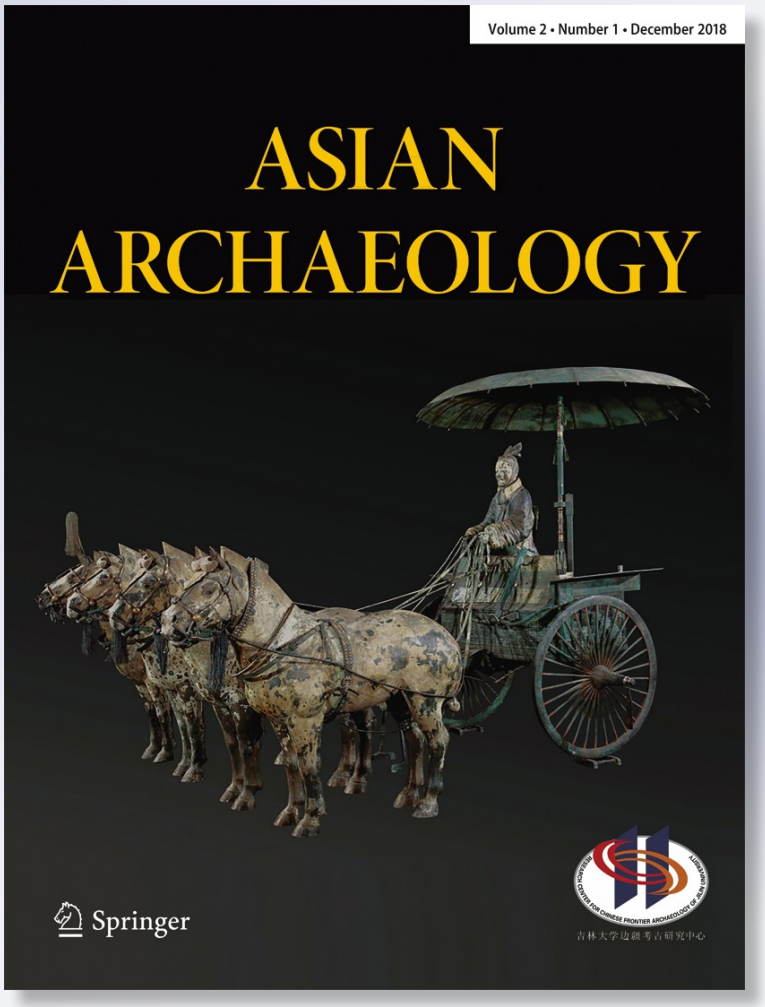

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ORIGINAL PAPER

New ancient DNA data on the origins and spread of sheep and cattle in northern China around 4000 BP

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Abstract

The time around 4000 BP marks a key stage from the Late Neolithic to the Early Bronze Age in China. During the time, sheep and cattle husbandry saw rapid development under the Qijia Culture in the Gansu-Qinghai region and also became more common in the Central Plains and Inner Mongolia. In this study, we performed ancient DNA analysis on sheep and cattle remains from four archaeological sites (Changning, Shimao, Taosi and Dashanqian) in northern China, and we obtained mtDNA D-loop fragments (overlapping 271 bp for sheep and overlapping 294 bp for cattle) from 22 of 26 sheep and 44 of 52 cattle remains. The mtDNA haplogroup data reveal that all the sheep DNA samples belong to sub-haplogroups A or B, and all the cattle DNA samples belong to haplogroup T3 or T4. The identification of these common haplogroups again confirms that the ancestors of these early sheep and cattle must have been introduced from outside China, likely from the Near East. The more detailed comparison of haplogroups also indicates potential intensified trade and cultural exchanges between different regions. Furthermore, this study also provides new ancient DNA data for better understanding the origins and spread of sheep and cattle in ancient China.

Keywords Sheep · Cattle · Ancient DNA · Mitochondrial DNA · Haplogroup · Origins and spread

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1 Introduction

Archaeological evidence indicates that sheep and cattle were all first domesticated somewhere in the Near East around 11,000 years ago and subsequently were introduced into Europe and Central Asia and East Asia (Zeder 2008). Northwest China, linking West and East, is believed to be an important transportation hub for introduction of Western domestic animals into the Central Plains of China. Zooarchaeological evidence found in Northwest China indicates that sheep and cattle arrived in the Gansu-Qinghai region during the Qijia 齐家 Culture period (4200 to 3600 BP), and further spread into the Central Plains (Flad et al. 2009; Yuan et al. 2007).

The Qijia Culture was distributed in the upper Yellow River 黄河region of Gansu 甘肃 and eastern Qinghai 青海 provinces, and this geographic zone represents a boundary area between farming and herding on Qinghai-Tibet Plateau 青藏高原 and Loess Plateau 黄土高原 (Song 2009). More than 350 archaeological sites of the Qijia Culture have been discovered. Due to the recovery of a large quantity of associated small copperware items, the Qijia Culture is regarded as one of the earliest bronze

cultures in China (Zhang 1987). With the beginning of the global 4.2 ka BP cold event, Northwest China became much colder and drier during the Qijia Culture period than the earlier Majiayao 马家窑 Culture period (5300–4000 BP), and the local vegetation changed from forest to temperate grassland: this allowed for the rapid development of sheep and cattle husbandry in the Gansu-Qinghai region (Hou et al. 2009).

Meanwhile, sheep and cattle breeding also became more and more common in the Central Plains during the Late Longshan 龙山 Culture period (4200–4000 BP) and in Inner Mongolia during the Lower Xijiadian 夏家店 Culture period (4000–3500 BP). Strontium isotope analyses of sheep and cattle from the Wadian 瓦店 site (4300–3800 BP) in Henan 河南 Province and the Taosi 陶寺 site (4300–3900 BP) in Shanxi 山西 Province show that a small number of sheep and cattle may have been imported from other regions and not raised locally (Zhao et al. 2012; Zhao et al. 2011). All of these phenomena may reflect a wider range of trade and cultural exchange between regions.

In this study, we analyze ancient DNA sequences of sheep and cattle from four archaeological sites dating to around 4000 BP in order to characterize the genetic profiles of sheep and cattle in each site region and to understand the origins and spread of sheep and cattle in northern China overall, and thereby to assess trade and exchange between different regions of northern China.

2 Materials and methods

2.1 Description of archaeological sites and samples

Sheep and cattle samples were collected from four archaeological sites (Fig. 1): 1. the Changning 长宁 site in Qinghai Province; 2. the Taosi 陶寺 site in Shanxi Province; 3. the Dashanqian 大山前 site in Inner Mongolia; and 4. the Shimao 石峁 site in Shaanxi Province. The four archaeological sites are similar in age but belong to different regional archaeological cultures.

The Changning site belongs to the Qijia Culture in Northwest China, and is located about 3 km southwest of Changning village in Datong 大通 County, Qinghai Province. It is believed to be a farming site, and many domestic animal remains, such as goat, sheep, and cattle, were recovered from the site. Twenty-one cattle remains (lab code: CN1-CN21) and ten sheep remains (lab code: CNS1-CNS10) from the Changning site were included in this study.

The Taosi site is located at the western foot of Ta'er 塔儿 Mountain, about 7.5 km northeast of Xiangfen 襄汾 County, Shanxi Province. The site dates to the Late Longshan Culture period, arguably representing the emergence of Chinese civilization and the cultural development of the Xia 夏 Dynasty. Fifteen cattle remains (lab code: TSC1–15) and one sheep specimen (lab code: TS01) were selected for this study.

The Dashanqian site is situated in Dashanqian village, Yongfeng 永丰 Township, Harqin Banner 喀喇沁旗, in the southwestern Chifeng 赤峰 region of Inner Mongolia. This archaeological site belongs to the Lower Xiajiadian 夏家店 Culture (4000–3500 BP). In terms of physical geography, this particular site may also be considered to be in Northeast China (Fig. 1). Many artifacts related to agricultural production as well as sacrificial grains were recovered from the site. In addition, pigs are the most abundant animal remains from the site, followed by sheep and cattle. Studies of the site indicate a complex pattern of subsistence practices in which agriculture was dominant with hunting and animal husbandry (Wang 2007). Some evidence also

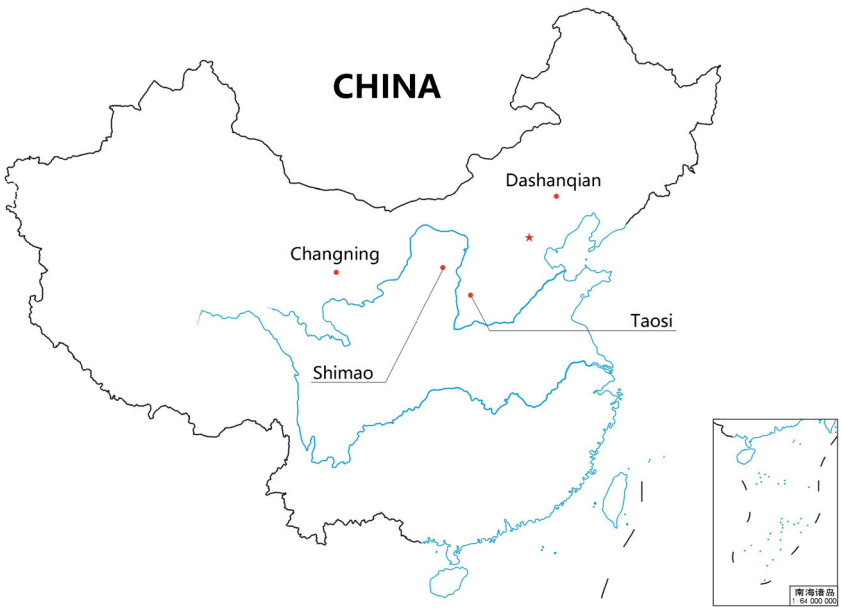

Fig. 1 Geographical locations of the four archaeological sites included in this study

indicates that domesticated animals could have been often used in sacrificial practices. Five cattle remains (lab code: DSQC1-DSQC5) and six sheep remains (lab code: DSQS1-DSQS6) were analyzed in this study.

The Shimao site is located in Gaojiapu 高家堡 Township, Shenmu 神木 County, Yulin 榆林 City, Shaanxi Province (Dai 1977). The Shimao site dates to the Middle and Late Longshan Culture and the early Xia periods (4300–3800 BP), according to radiocarbon dates and recovered artifacts. The Shimao site is the largest known walled site of this period in China and provides a unique window for understanding the formation of Chinese civilizations. Eleven cattle remains (lab code: SM01C-SM11C) and 9 sheep remains (lab code: SM12S-SM20S) were collected and analyzed for this study.

2.2 Sample preparation

The outer surface of the bone was removed to about 2–3 mm of depth with a dental drill (Strong 90, repeated three times) to eliminate surface contamination. Subsequently, teeth or bones were soaked in 10% bleach for 20 min, rinsed with ethanol and distilled water, and then UV-irradiated for 30 min on each side. Finally, the teeth and bones were powdered in liquid nitrogen using a 6850 Freezer Mill (SPEX CertiPrep, Methucen, NJ, USA), and approximately 200 mg of powder was collected and kept in a 15 mL centrifuge tube (at −20 °C).

2.3 DNA extraction, PCR amplification and sequencing

DNA was extracted according to established protocols (Yang et al. 1998). The primers were designed from the mtDNA references of cattle (V00654) and sheep (AF010406) to amplify mtDNA control region (D-loop) fragments (271 bp for sheep and 294 bp for cattle) (Table 1).

PCR amplifications were performed on the Mastercycler® Thermal Cycler (Eppendorf, Hamburg, Germany) in a 25 μL reaction volume containing 1 U TransStart™ TopTaq DNA (TransGen Biotech, China), 1× buffer, 0.2 mM dNTPs. 0.2 μM of each primer and 3 μL DNA sample.

PCR conditions were as follows: pre-denaturation at 95 °C for 5 min, 36 cycles of 92 °C for 1 min, 50–55 °C for 1 min, and 72 °C for 1 min, and a final elongation step of 72 °C for 10 min. PCR products were electrophorezed on 2% agarose gel (Biowest, Germany), then purified using QIAEX®II GEL Extraction Kit (QIAGen, Germany). Then, both strand sequencing reactions were carried out on an ABI PRISM® 310 Genetic Analyzer (Applied Biosystems, USA) using Dyeprimer Sequencing kit.

2.4 Contamination controls

In this study, all the experiments were carried out in a dedicated ancient DNA laboratory at Jilin University. Sample preparation, DNA extraction, and PCR amplification were performed in physically separated rooms equipped with positive pressure and air filtration. All researchers wear coverall laboratory coats with hood and facemasks. Gloves were frequently changed. Strict cleaning procedures were performed by regular treatment with DNA-OFF™ (Q.BIO gene, Germany) and UV light irradiation. DNA-free reagents and dedicated equipment were used, and extraction and amplification blanks were used to monitor potential contamination.

2.5 DNA data analysis

Sequences of the D-loop were aligned using the Clustal X 1.83 program to identify the position of nucleotide variation and mtDNA haplotypes.

3 Results and discussion

3.1 Ancient DNA analysis of sheep

Sheep (*Ovis aries*) are one of the earliest domesticated animals and play an important role in agriculture, economy, culture, and even religion in human history. Archaeological evidence suggests that sheep were first domesticated in the Near East. The Aşıklı Höyük site in Central Anatolia is suggested as the oldest domestication site (Stiner et al. 2014). The wild sheep (*Ovis gmelinii* anatolica) in Central Anatolia is considered to be the wild ancestor of the domestic sheep (Demirci et al. 2013).

Mitochondrial DNA has been widely used to explore the origins of domestic sheep. Five haplogroups (A-E) have been observed in modern sheep, and all of them are found in Near Eastern sheep. Haplogroups A and B are the most frequently observed haplogroups and are widely distributed across Asia and Europe, respectively (Hiendleder et al. 1998). Hapolgroup C is the third most common haplogroup (Guo et al. 2005; Pedrosa et al. 2005). Haplogroups E and D are rare, possibly resultant from sporadic interbreeding between wild sheep and domestic sheep (Meadows et al. 2006). A recent study suggests that all haplogroups originated from two maternally distinct ancestral *Ovis gmelinii* populations (Demirci et al. 2013).

Twenty-one ancient sheep sequences were successfully recovered from the 26 samples. Three samples, CNS2, CNS6 and CNS9, from the Changning site and two samples, SM16S and SM20S, from the Simao site failed to yield PCR products. According to sequence motifs of sheep mtDNA haplogroups, two haplogroup, A and B, were identified. Haplogroup A was dominant in the ancient sheep populations, with the highest

Table 1 PCR amplification primers and PCR amplicons

Species	Region	Primers	Primer sequence	Length (bp)
Cattle	16,022–16,315 (294 bp)	L16022	5′-GCCCCATGCATATAAGCAAG-3′	157 bp
		H16178	5′-CACGCGGCATGGTAATTAAG-3′	
		L16137	5′-TTCCTTACCATTAGATCACGAGC-3′	179 bp
		H16315	5′-GGAAAGAATGGACCGTTTTAGAT-3′	
Sheep	15,391–15,661 (271 bp)	L15391	5′-CCACTATCAACACCCAAAG-3’	144 bp
		H15534	5′-AAGTCCGTGTTGTATGTTTG-3’	
		L15496	5′-TTAAACTTGCTAAAACTCCCA-3’	166 bp
		H15661	5′-AATGTTATGTACTCGCTTAGCA-3’	

frequency of 86%, which is consistent with previous studies (Cai et al. 2011). It is clear that the maternal ancestors of these ancient sheep must be originally from the Near East, as suggested and demonstrated by many previous studies.

Through comparison with the reference sequence AF010406, five haplotypes H1-H5 could be easily identified (Table 2). Remarkably, haplotype H2 was the most common haplotype: it is shared by 16 individuals (73% of all the positive samples) from all archaeological sites. The results show that the peoples living in the different regions represented by the four northern China sites may have raised similar sheep breeds; the data also suggest that sheep husbandry was common throughout northern China during this period of time. In this study, the Changning, Shimao, and Taosi sites are located along Yellow River, from the upper to the middle reaches. The geographic distribution of haplotype H2 may well reflect the trend of the spread of sheep from West to East within China. Both haplogroup A and B are found in Northwest China and Northeast China during the same time period (ca. 4000 years ago), which may indicate the rapid spread of sheep from West to East.

Except for haplogroups A and B, the data failed to reveal any other haplogroups in these ancient sheep, which gives rise to the possibility that the other haplogroups such as C arrived into China in later times. In a previous study, haplogroup C was found at the Bancheng 板城 archaeological site in Inner Mongolia dating to 2500 BP (Han et al. 2009). Recent studies based on mitogenomic meta-analysis support there being two phases of migration in the history of Eastern Eurasian sheep (Lv et al. 2015).

3.2 Ancient DNA analysis of cattle

Cattle have had a close association with development of human cultures and civilizations, providing food such as meat, milk, and fat and secondary products such as hides for clothing, as well as traction, such as for pulling plows in agricultural activities. According to archaeological and genetic evidence, wild aurochs (*Bos primigenius*) in the Near East were first domesticated about 10,500 BP (Helmer et al. 2005) and later in the Indus Valley about 8500 BP (Ajmone-Marsan et al. 2010), leading to two types of domestic cattle: the humpless

Table 2 Variation positions and mtDNA haplogroups of sheep

Haplotypes	Variable Positions													Samples	Haplogroups
	1	1	1	1	1	1	1	1	1	1	1	1	1		
	5	5	5	5	5	5	5	5	5	5	5	5	5		
	4	4	4	4	5	5	5	5	5	6	6	6	6		
	5	5	6	8	1	4	8	8	9	2	3	3	3		
	0	9	4	4	3	7	3	6	7	2	5	8	9		
AF010406	G	C	T	G	C	G	C	A	T	T	A	C	A	Reference sequence	
H1	C	T	.	A	.	A	T	.	C	.	G	T	G	CNS3	A
H2	.	T	.	A	.	A	T	.	C	.	G	T	G	TS01, CNS1,CNS4,CNS5,CNS7,CNS8,CNS10 SM12S,SM13S,SM14S,SM15S,SM17S DSQS1,DSQS2,DSQS4,DSQS5	A
H3	.	T	.	A	.	A	T	.	C	C	G	T	G	DSQS3	A
H4	.	.	.	.	.	.	.	.	.	.	.	.	.	SM18S,SM19S	B
H5	.	.	.	.	.	.	.	G	.	.	.	.	.	DSQS6	B

Dot (·) denotes identical with the reference sequence(AF010406)

taurine cattle (*Bos taurus*) and the humped zebu cattle (*Bos indicus*), respectively.

Mitochondrial DNA analyses indicate that almost all modern taurine cattle belong to macro-haplogroup T, which consists of six sub-haplogroups: T*, T1, T2, T3, T4, and T5 (Achilli et al. 2008; Mannen et al. 2004; Troy et al. 2001). The six taurine sub-haplogroups show a distinctive geographical distribution pattern: T3 predominates in Europe, and along with T, T2 comprises almost all Near Eastern variations; T1 is dominant in Africa, while T4 is typical of East Asian breeds. Genetic studies support the Near Eastern origin of T, T2, and T3, and the possibility of an additional domestication event in Africa for T1. T4 was once thought to have originated independently in East Asia, but the idea was rejected based on a more thorough analysis (Achilli et al. 2008). Based on mtDNA genomic data, some studies suggest that the macro-haplogroup T could have originated from a small number of cattle in the Near East (Bollongino et al. 2012).

In this study, ancient DNA was successfully recovered from 44 of the 52 cattle samples. Eight samples (CN9, CN15, CN16, CN21, TSC9, TSC13, DSQ5, and SM02C) failed to yield PCR products. The 44 ancient cattle DNA sequences reveal 10 variable positions when compared with the reference sequence V00654. All the substitutions were transitions and could be grouped into 9 different haplotypes (H1–H9, Table 3). Based on DNA sequence analysis, all of the ancient cattle samples analyzed belong to taurine cattle (not zebu cattle). Two haplogroups, T3 and T4, could be identified, with T3 as the dominant haplogroup (86%); some other haplogroups, such as T2, were not found in this study.

As with the sheep, our data confirm that the maternal ancestors of ancient Chinese cattle were originally from outside China, eventually traceable to the Near East. Previous studies indicate that haplogroup T2 could be found in some later archaeological sites in China, such as the Xiaohe 小河 cemetery (3900–3600 BP) in Xinjiang Uygur Autonomous Region and the Erlitou 二里头 site (3750–3500 BP) in Henan, and the Dashanqian site (Upper Xiajiadian Culture, 3000–2300 BP) (Cai et al. 2014). The dates of the appearance of T2 in ancient China seem to be later than those of T3 and T4, suggesting that T2, T3 and T4 might have been introduced into China at different times.

3.3 Importation and integration of sheep and cattle into ancient China

The analysis of the ancient DNA of sheep and cattle remains from the four archaeological sites studied here confirms the notion that early ancient domesticated sheep and cattle were

Table 3 Variable positions and mtDNA haplogroups of cattle

Haplotype	Variable positions										Lab code	Haplogroup
	1	1	1	1	1	1	1	1	1	1		
	6	6	6	6	6	6	6	6	6	6		
	0	0	0	0	1	1	1	1	2	3		
	4	5	5	9	1	1	2	4	6	0		
	2	0	5	3	3	9	6	1	0	2		
V00654	T	C	T	G	T	T	T	T	C	G		
H1	.	.	C	.	.	.		.	.	.	TSC3,TSC6,TSC7,TSC10,TSC12 SM06C CN5,CN8,CN14, CN17,CN19 DSQC3	T3
H2	.	.	.	.	.	C		.	.	.	TSC1,TSC2,TSC4,TSC8,TSC11 CN1,CN3,CN4,CN6, CN7, CN10, CN11, CN12, CN13, CN18, CN20, DSQC4 SM01C,SM05C,SM08C,SM09C,SM11C	T3
H3	.	T	.	.	.	C	.	.	.	.	CN2	T3
H4	.	.	C	.	.	.	C	.	.	.	SM03C	T3
H5	.	.	.	.	C	C	.	.	T	.	TSC15	T3
H6	.	.	.	A	.	.	.	.	.	.	TSC14	T3
H7	C	.	.	A	.	.	.	.	.	A	DSQC1,DSQC2	T4
H8	C	.	.	A	.	.	.	.	.	.	SM04C, SM07C, SM10C	T4
H9	C	.	.	A	.	.	.	C	.	.	TSC5	T4

Dot (·) denotes identical with the reference sequence(V00654)

introduced into China. This study provides no evidence that can support independent domestications locally in China. However, the broad distribution of these four archaeological sites, ranging from Northwest China and the Central Plains to Northeast China, indicate that those imported sheep and cattle were quickly adopted throughout northern China. It is also interesting to notice that the haplotype composition of the sheep and cattle in these different regions are similar, also suggesting that the sheep and cattle might have spread from one region to another quickly.

It is clear that the importation or introduction of both sheep and cattle each did not occur as a one-time event. The presence of two major haplogroups for each species (A and B in sheep and T3 and T4 in cattle) suggests multiple or continuous events. Furthermore, Haplogroup C in sheep and haplogroup T2 in cattle, which are detected from later archaeological sites, must have been imported into ancient China in separate events from the earlier introductions suggested here, indicating continued or intensified trade, exchange, and interaction between regions inside and outside China. For example, outside China, some studies suggest that the Proto-Indo-Europeans who lived in the vast Steppe lands north of the Black Sea might have had multiple waves of migration from their homeland into Central and South Asia and the Altai region (Shao 2009). The first major wave of migration started sometime around 5500–4500 BP and the second wave of migration around 4000–3500 BP: such migrations of human populations could prove to be effective in facilitating trade and exchange of not only artifacts but also domesticated animal and plant species.

Some debate remains over the entrance route of sheep and cattle into ancient China. At this stage, as suggested by many researchers, another route via Northeast China cannot be ruled out (Cai et al. 2018; Zhao 2015.). Although we have samples from four archaeological sites from Northwest, Central Plain and Northeast China, their relatively late ages and the relatively small sample size do not allow us to effectively trace the movements or spread of the imported sheep and cattle. While our data clearly support the Northwest entrance route, we still cannot reject the other possibility of the Northeast entrance route. That being said, there are no major questions over the existence of the Northwest entrance route, and in fact it, this route continued to be used and later developed into the well-known Silk Road. All archaeological evidence points to the likelihood that the Northwest entrance route was first in use during the Qijia Culture, and the Changning site, included in this study, is one such Qijia Culture site.

It is important to highlight the need to increase the sample size from Qijia Culture sites to more efficiently estimate the compositions of the initial haplogroups and haplotypes of both sheep and cattle in order to better trace the patterns of spread for the introduction of these animals into other parts of ancient China.

4 Conclusion

In this study, we performed mtDNA analysis on samples of ancient sheep and cattle from four archaeological sites in Northwest China, the Central Plains, and Northeast China, to understand the origins and spread of ancient sheep and cattle around 4000 BP. First, our results demonstrate that the maternal ancestors of these ancient Chinese sheep and cattle originated from outside China, and the mtDNA haplogroup analyses trace all of these ancient DNA samples to the haplogroups from the Near East essentially. Second, different mtDNA haplogroups of sheep and cattle were introduced into ancient China via different spread events during several different prehistoric periods. Third, haplotype analysis indicate the existence of extensive trade and culture exchange between the Gansu-Qinghai region and the Central Plains and Inner Mongolia around 4000 BP.

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