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ORIGINAL ARTICLE

A fine map for maternal lineage analysis by mitochondrial hypervariable region in 12 Chinese goat breeds

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ABSTRACT

As the fast pace of genomic research continues to identify mitochondrial lineages in animals, it has become apparent that many independent studies are needed to support a robust phylogenetic inference. The aim of this study was thus to further characterize the maternal lineage, proposed to originate in southwestern region of China, using a wider survey of diverse goat breeds in China. To this end, we sequenced the mitochondrial hypervariable region 1 (HVR1) of the mtDNA control region in 145 goats of 12 Chinese breeds. Phylogenetic analysis revealed that Chinese goats were classified into four distinct lineages (A, B, C and D) as previously reported. A Mantel test and the analysis of Analysis of Molecular Variance (ANOVA) indicated that there was not an obvious geographic structure among Chinese goat breeds. Population expansion analysis based on mismatch distribution and Fu's Fs statistic indicate that two expansion events in Chinese goats occurred respectively at about 11 and 29 mutational time units ago, revealing two star-like subclades in lineage B corresponding to two population expansion events. Moreover, lineage B sequences were presented only in the breeds of southwestern or surrounding regions of China. Multiple lines of evidence from this study and previous studies indicate that for Chinese goats mtDNA lineage B originated from the southwestern region of China.

Key words: *analysis of molecular variance, mitochondrial lineage, phylogeny, phylogeography, population expansion.*

INTRODUCTION

Archaeological evidence indicates that domestic goats (*Capra hircus*) were perhaps the first livestock species domesticated by humans around 10 000 years ago at the dawn of the Neolithic period in the Fertile Crescent region of the Near East (Porter & Tebbit 1996; Pringle 1998). Domestic goats have provided a full range of valuable products to human societies such as meat, milk, skin and fiber, and this livestock is thus of great economic importance particularly for developing countries like China. As such, goats are popularly known as the 'poor man's cows' (MacHugh & Bradley 2001). China raises the largest number of goats in the world including varieties of breeds. A total of 62 indigenous breeds have been characterized and documented in the Domestic Animal Diversity Information System (DAD-IS) of Food and Agriculture Organization of the United Nations (FAO 2007). However, there has been a serious concern that the goat diversity

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is shrinking rapidly, and some breeds are at the brink of extinction (Ma *et al.* 2002). From both views of evolution biology and conservation practice, there is a great demand for quantifying the amount of genetic diversities and for illuminating the phylogenetic origins of the Asian goat breeds at the molecular level. Firstly, genetic data at the molecular level can be instrumental for clarifying the ambiguities in the current taxonomic classification based on morphological and physiological data, which is deemed to be insufficient for determining relationships between breeds (Arranz *et al.* 1998). Secondly, recognizing historical patterns of genetic variation among the goat breeds is required to preserve evolutionary relationships during the conservation practice and to answer some fundamental questions regarding human domestication of the animals.

Yet, the origin of the domestic goats remains uncertain and controversial. It has been suggested that at least two wild species of the genus *Capra* have contributed to the gene pool of domestic goats (Mannen *et al.* 2001). Thanks to the use of mitochondrial DNA (mtDNA), recent worldwide studies (Luikart *et al.* 2001; Mannen & Tsuji *et al.* 2001; Sultana *et al.* 2003; Joshi *et al.* 2004; Chen *et al.* 2005) have allowed the identification of several maternal lineages that might be linked to different domestication events from the wild goat 'bezoar' (*Capra aegagrus*). Among various markers (e.g. microsatellites) useful for phylogenetic analysis (de Knijff 2000; Ma *et al.* 2006), mtDNA has been the most informative genomic markers for untangling the origins of domestic animals because of the unique characteristics of mtDNA, such as high copy number, lack of recombination, high substitution rate, and a maternal mode of inheritance (Ballard & Whitlock 2004).

Up to now, seven maternal lineages (A, B, C, D, E, F and G) have been identified in domestic goats based on mtDNA data (Naderi *et al.* 2007). Luikart *et al.* (2001) sequenced part of the mtDNA hypervariable region 1 (HVR1) in 406 individuals from 44 countries throughout Europe, Asia, Africa, and the Middle Near East, and identified three major mtDNA lineages. Lineage A is the most common in all continents. Lineage B was found in the Indian subcontinent, Mongolia, and Southeast Asia. Lineage C was observed in a few samples from Mongolia, Switzerland, and Slovenia. Later, Sultana *et al.* (2003) found a new low frequency lineage (lineage D) in Pakistan. Chen *et al.* (Chen *et al.* 2005) also found lineage D in China. In 2004, Joshi *et al.* (Joshi *et al.* 2004) detected a new minority lineage (lineage E) in India. Recently, Naderi *et al.* (Naderi *et al.* 2007) constructed the neighbor-joining (NJ) tree of 2430 domestic goats from different countries demonstrating 6 highly divergent groups corresponding to different mitochondrial haplogroups called A, B, C, D, F and G, each having high haplotype diversity. The enormous level of diversity found among those lineages calls for more extensive and deeper surveys in order to clarify their genetic history and phylogeography among domestic goats.

Luikart *et al.* (2001) proposed that lineage B was likely to originate in Asia. Later, the support data for this proposal were obtained from different Asian countries (Mannen *et al.* 2001; Joshi *et al.* 2004; Chen *et al.* 2005). To determine whether the origin of lineage B was in eastern or southern Asia, Chen *et al.* (2005) compared the number of haplotypes and genetic diversity of sequence data from eastern and southern Asia, respectively. They found that the frequency of lineage B was higher in eastern Asia than in southern Asia, suggesting that lineage B might have arisen in eastern Asia. Liu *et al.* (2006) further analyzed lineage B in Chinese goats and found that mean mismatch numbers of differences for mtDNA lineage B were higher in Chinese goats than those of mixed goat population in five Asian countries (India, Pakistan, Mongolia, Malaysia, and Laos), indicating that mtDNA lineage B of goats probably originated from China.

Therefore, we performed a wider survey in this study aiming at precisely defining the phylogenetic structure for Chinese goats. We were particularly interested in further characterizing the mitochondrial lineage B for Chinese goats, proposed to originate in southwestern region of China and supported by two recent studies (Chen *et al.* 2005; Liu *et al.* 2006). Twelve Chinese native goat breeds were selected to sufficiently cover this target region and surrounding areas. One hundred and forty-five individuals from these breeds were sequenced at mitochondrial HVR1. Then, a comprehensive analysis of the collected molecular and geographic data was conducted to address the issues regarding genetic diversity, and distribution of mitochondrial lineages among Chinese goats.

MATERIALS AND METHODS

Sampling and DNA extraction

Goat ear tissue was collected from small remote villages belonging to 9 provinces or regions of China, for 145 goats from 12 indigenous Chinese breeds (Fig. 1). An effort was made to collect samples from unrelated individuals based on

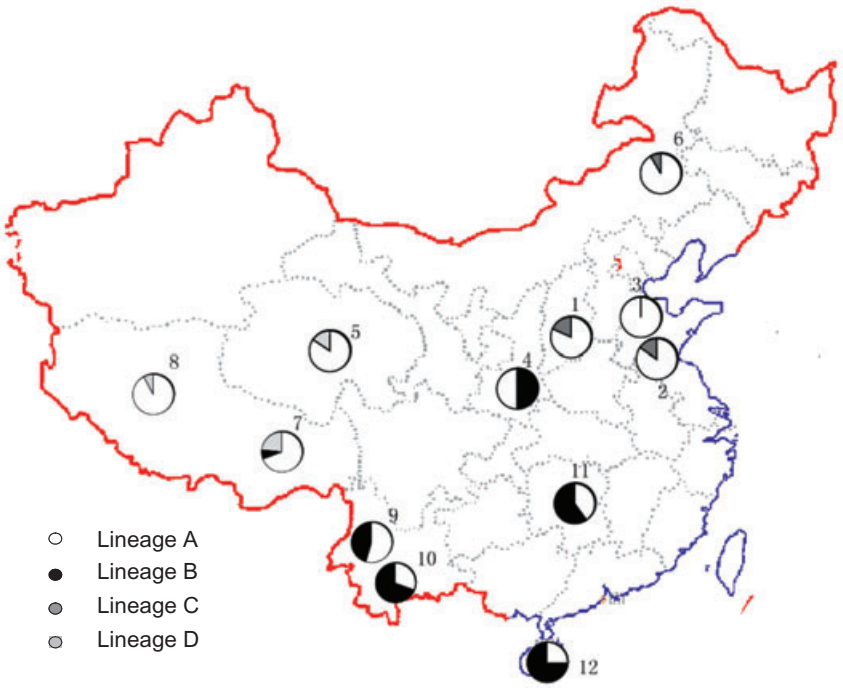

Figure 1 Geographical and lineage distributions of Chinese goat breeds.1–10 breed includes 11,13,12,12,13,12,13,13,11,13,10 and 12 individuals respectively.

Table 1 Location of goat breeds and their diversity

Map No.	Breed	Location	Sample size	Haplotype diversity (±SE)	Nucleotide diversity (±SE)
1	Taihang	Central region (Shanxi)	11	0.9455 ± 0.0659	0.0333 ± 0.0180
2	Laiwu Black	Eastern region (Shandong)	13	0.9872 ± 0.0354	0.0326 ± 0.0174
3	Lubei White	Eastern region (Shandong)	12	0.9697 ± 0.0443	0.0195 ± 0.0108
4	Shaanan White	Northern region (Shaanxi)	12	0.9697 ± 0.0443	0.0317 ± 0.0171
5	Tsaidam Cashmere	Northwestern region (Qinghai)	13	0.9615 ± 0.0496	0.0228 ± 0.0123
6	Ujumqin White Cashmere	Northeastern region (Inner Mogolia)	12	0.9848 ± 0.0403	0.0292 ± 0.0158
7	Langkazi	Northwestern region (Tibet)	13	0.9872 ± 0.0354	0.0290 ± 0.0155
8	Duoma	Northwestern region (Tibet)	13	0.9744 ± 0.0389	0.0255 ± 0.0138
9	Yunling Black	Southwestern region (Yunnan)	11	0.9818 ± 0.0463	0.0365 ± 0.0198
10	Maguan	Southwestern region (Yunnan)	13	0.9615 ± 0.0412	0.0308 ± 0.0165
11	Matou	Central region (Hunan)	10	0.9111 ± 0.0773	0.0300 ± 0.0166
12	Hainan Black	Southern region (Hainan)	12	0.9394 ± 0.0577	0.0350 ± 0.0188
	All breeds		145	0.9974 ± 0.0012	0.0331 ± 0.0163

the information provided by farmers. Goat ear tissue was stored at −70°C prior to DNA extraction. Total genomic DNA was extracted from ear tissue by a standard phenol-chloroform extraction method (Sambrook & Russell 2000). Details of the breeds, regions, and sample sizes are given in Table 1. Breeds of Shaanan White and Matou were also used in previous studies for Chinese goats (Chen *et al.* 2005; Liu *et al.* 2006).

DNA amplification and sequencing

Mitochondrial HVR1 of goats was amplified using the primers: forward 5′CATTACACCGCTCGCCTAC3′ and reverse 5′GGGCTGATTAGTCATTAGT3′, designed using the Premier 5.0 package and the known goat mtDNA sequence (Parma *et al.* 2003). PCR amplifications were carried out in 25 μL reaction mixtures including each primer (1 μL of a 10 μmol/L solution), dNTPs (1 μL of a 2.5 mmol/L solution), 2.5 μL of 10× buffer and 0.25 μL of 5 U/μL Taq DNA polymerase (Tiangen Biotech, Beijing, China). The PCR conditions were an initial denaturing step at 95°C for 5 min, followed by 33 amplification cycles (94°C for 30 s, 58.5°C for 30 s and 72°C for 30 s) and a final extension at 72°C for 10 min in a PTC200TM Programmable Thermal Controller (MJ Research Inc., Waltham, MA, USA). The PCR products were cloned into a pGEM–T easy vector (Promega Inc.,

Madison, WI, USA) according to the manufacturer's instructions. Positive clones were then sequenced by Shanghai Bioasia Co. (Shanghai, China). All sequences were deposited in GenBank (Accession Nos. EU035991-EU036135).

Analysis of sequence data

Six hundred and twenty-two base pairs from the mtDNA HVR1 region of 145 individuals of 12 Chinese goat breeds and four wild goats (accession nos AB044305–AB044306, AB110590–AB110591) were aligned using the Bioedit package (Hall 1999). Haplotype diversity and its standard error (SE), nucleotide diversity and its SE, Fu's Fs statistics (Fu 1997), neutrality test based on Tajima's D measure, mismatch distribution, ANOVA derived molecular variances, mean number pairwise differences, and population pairwise FST values were computed using ARLEQUIN version 3.0 (http://cmpg.unibe.ch/software/arlequin3/) (Excoffier & Schneider 2005). A Mantel test was also carried out using ARLEQUIN to evaluate the correlation between geographical distances (pairwise distances in kilometers between the production centers of the sampled breeds) and genetic distances measured using FST. The NJ tree was constructed using the program Mega 3.0 (Kumar *et al.* 2004), with a Kimura 2-parameter model and a bootstrap (number of replications = 1000) test. The MJ network was drawn using the program Network 4.2 (Bandelt *et al.* 1999) (http://www.fluxus-engineering.com/sharenet.htm). Population pairwise FST genetic distances were displayed in two dimensions via multidimensional scaling (MDS) analysis, using the SPSS 14.0 software package (http://www.spss.com/registration/premium/consol056.cfm?Demo_ID=37).

RESULTS

Analysis of the mitochondrial HVR1 region

We sequenced the mtDNA HVR1 region of 145 domestic goats (see Table 1 for collection locations), belonging to 12 different Chinese breeds that inhabit in different geographic regions (southwestern, southern, northwestern, northern, eastern and central regions) of China. The diverse areas were surveyed in order to precisely map mtDNA lineages. The 145 sequences gave 123 different haplotypes with 170 variable sites defined. Only one deletion of a base pair was detected, and all the remaining were polymorphisms including 64 singleton variable sites and 106 parsimony informative sites. The overall ratio of transitions versus transversions (32:1) revealed a heavy transition bias in domestic goats. Haplotype diversity values ranged from 0.9111 ± 0.0773 in Matou (central region) to 0.9872 ± 0.0354 in Laiwu Black (eastern region), and nucleotide diversity values from 0.0195 ± 0.0108 in Lubei White (eastern region) to 0.0365 ± 0.0198 in Yunling Black (southwestern region) (Table 1).

Phylogenetic analysis

Phylogenetic reconstruction of Chinese domestic goats was performed using the mtDNA HVR1 region sequences collected in this study and the published sequences of the wild goats. The phylogenetic tree constructed using NJ method is shown in Figure 2. The Chinese domestic goats were classified into four distinct lineages A, B, C and D, with 82, 26, 5 and 6 haplotypes corresponding to 98, 36, 5 and 6 individuals, respectively. In the further analysis, we combined 112 previously published sequences for Chinese domestic goats belonging to the mtDNA lineage B (Chen *et al.* 2005; Liu *et al.* 2006) with the 36 sequences in our data. The analysis revealed 49 haplotypes in the combined 148 sequences, and the phylogenetic relationships among these haplotypes are shown in an MJ network (Fig. 3).

A global ANOVA estimated that 96.96% ($P < 0.001$) of the variation was within breeds and 3.04% ($P < 0.001$) was among breeds. When all goat breeds were divided into three geographic groups (Northern China, Central China, and Southwestern and Southern China) only 0.15% ($P < 0.001$) of the genetic variation could be attributed to differences among regional groups. The results indicated that there was no obvious geographic structure among Chinese goat breeds (Table 2). The MDS plot of pairwise FST distances shows that the phylogenetic relationships among the breeds were not in perfect agreement with their geographic relationships. For instance, Duoma breed in Tibet plateau was closely related to a far geographically separated breed, Lubei White in northern mountains of Shandong province (Fig. 4). A Mantel test revealed that there was a negative correlation between the genetic measure (FST) and the geographical distance measure ($r = -0.31$, $P < 0.05$). The above evidence shows that the breeds from different geographic regions had frequent genetic communications. Some haplotypes were even shared by individuals of different breeds living in diverse geographic regions.

Population expansion

The star-like phylogeny of Chinese goat lineage B in the MJ network (Fig. 3) is consistent with the finding from the population expansion analysis. The mismatch distributions (pairwise comparisons) of mtDNA have been widely used to explore such a demographic event (Slatkin & Hudson 1991; Rogers & Harpending 1992). A constant sized population is expected to show a ragged, multimodal distribution, while an expanding

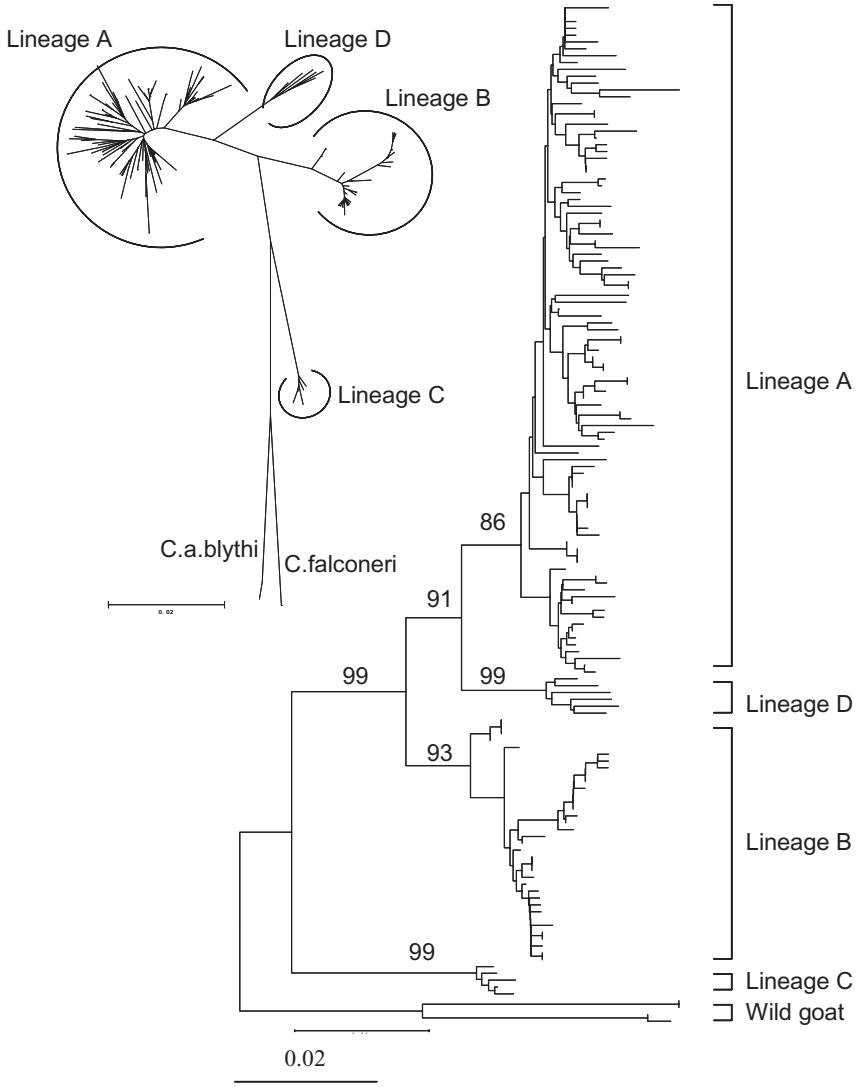

Figure 2 Neighbor-joining (NJ) tree constructed from Chinese goat mtDNA and two wild goat (C.a.blythi and C. falconeri) sequences. The numbers at the branches represent bootstrap values out of 1000 replications. The lineage A includes all the breeds. The lineage B includes Shaanan White, Langkazi, Yunling Black, Maguan, Matou and Hainan Black breeds. The lineage C includes Taihang, Laiwu Black and Ujumqin White breeds. The lineage D includes Tsaidam Cashmere, Langkazi and Duoma breeds.

population shows a smooth, unimodal distribution. Fu's Fs statistic (Fu 1997) depicting the probability of having a number of alleles greater or equal to the observed number in a sample, drawn from a stationary population, provides a sensitive test for a population expansion event. We applied the two types of analysis to our data. Two smooth, bimodal distributions separated by a large time interval were identified as shown in Figure 5. The mismatch distribution for the complete dataset of all Chinese goat breeds shows two major peaks at positions 11 and 29, respectively, being similar to the peaks of 12 and 28 identified previously (Chen *et al.* 2005). These data indicate that two expansion events in Chinese goats occurred respectively at about 11 and 29 mutational time units ago. Thus, it is not surprising that both the neutrality test (Tajima's $D = -1.07$, $P < 0.05$) and Fu's Fs statistics (-23.83, $P < 0.05$) revealed a significant departure from the neutrality assumption. The evolution story for lineage B is of particular interest. We thus performed further mismatch distribution analysis for mtDNA lineages A (as comparison) and B. The results shown in Figure 5 clearly indicate that lineage B suffered two recent demographic expansions.

Estimation of divergence time

The unweighted mean pair-wise differences were 11.9. Using a calibration of five or seven million years for the sheep–goat split derived from fossil records (Savage & Russell 1983; Carroll 1987) and the method

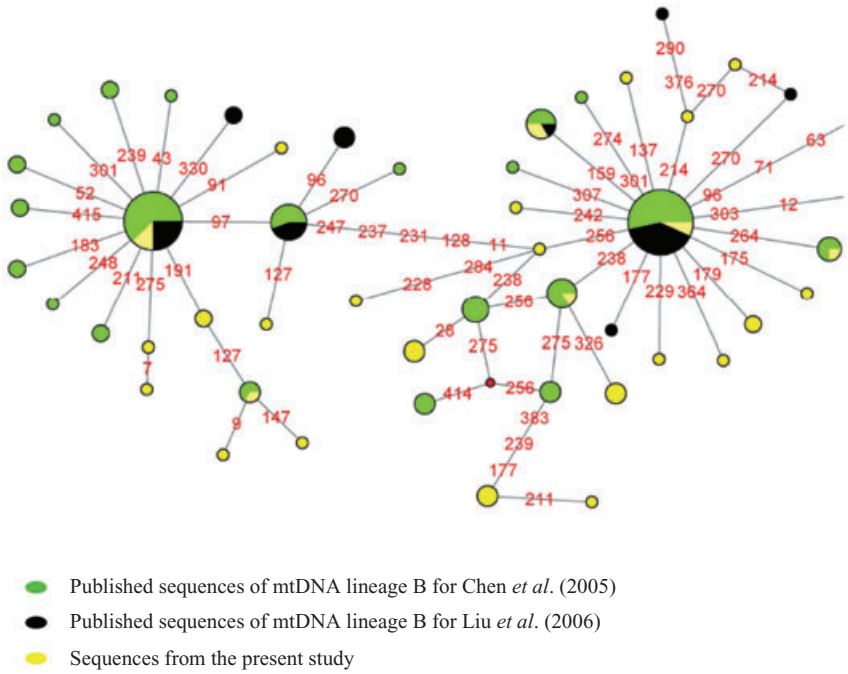

Figure 3 Median-joining (MJ) network showing genetic relationships among Chinese goat haplotypes for mtDNA HVR1 lineage B. The size of the circle is proportional to haplotype frequency. Mutational differences are shown on lines.

Table 2 The hierarchical components of mtDNA variation computed under AMOVA framework

Source of variation	Percentage of variation	
	No Grouping	Three Groups
Among groups		0.15
Among breeds	3.04	2.95
Within breeds	96.96	96.91

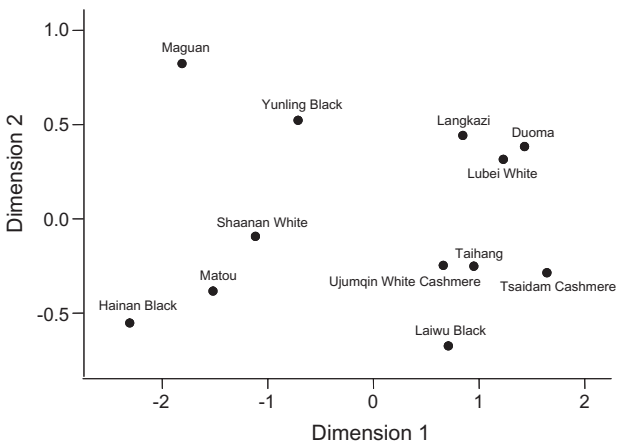

Figure 4 Multidimensional scaling plot of pairwise FST values between 12 China goat breeds. Dimension 1 and 2 means a two space dimensions.

of Tamura and Nei (1993) for molecular dating of the human mtDNA hypervariable region TMRCA (Time to Most Recent Common Ancestor) by comparison with the chimpanzee counterpart, the mutation rate was estimated to be $1.75–2.45 \times 10^{-5}$. The age of the TMRCA of the four Chinese domestic goat mtDNA lineages was dated back to roughly 242 790 to 339 900 years. This time is higher than the domestication time for goats (10 000 years ago) estimated by Zeder and Hesse (2000).

DISCUSSION

The origin of modern domestic livestock has been extensively investigated, and evidence of profound maternal diversity has been seen in many domesticated animals (Guo *et al.* 2005; Larson *et al.* 2005; Fernandez *et al.* 2006; Lei *et al.* 2006; Luis *et al.* 2006; Meadows *et al.* 2007). In this study, we conducted a comprehensive phylogenetic analysis in order to precisely define the genetic origins of Chinese goats. The NJ tree constructed with 145 sequences of Chinese native goats and four wild goats as controls clearly shows that Chinese domestic goats were divided into four distinct mtDNA lineages (A, B, C and D). Lineage A was found in all breeds; lineage B was presented in some regional breeds (Shaanan White, Langkazi,

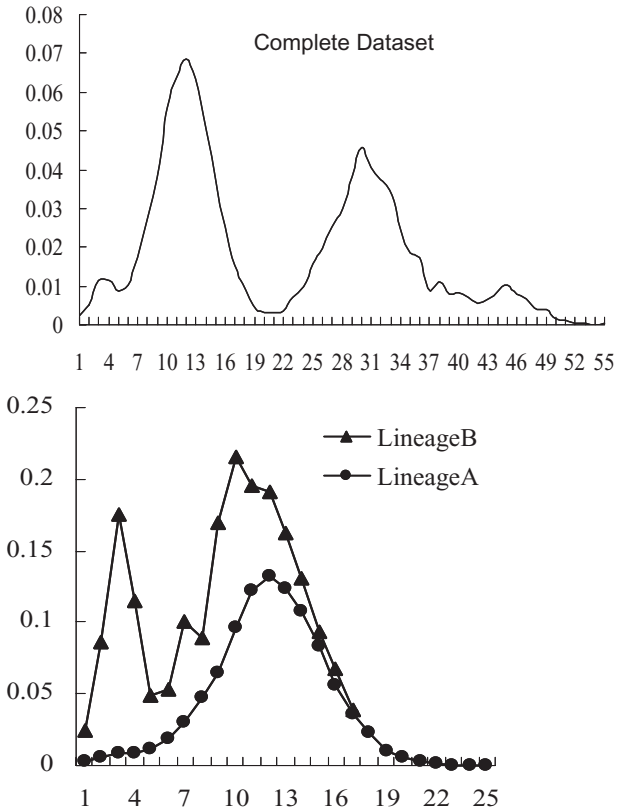

Figure 5 Mismatch distribution constructed using sequences collected in the study. X axes represent pairwise differences, Y axes represent relative frequency.

Yunling Black, Maguan, Matou and Hainan Black), all belonging to southwestern or surrounding regions; lineage C was found in Taihang, Laiwu Black and Ujumqin White Cashmere breed; and lineage D was found in the Langkazi, Tsaidam Cashmere and Duoma breed, suggesting that this lineage is unique to the breeds on the Tibet plateau. This study also showed that substantial diversity existed within Chinese domestic goats, and this finding was consistent with multiple genetic goat origins identified (Luikart *et al.* 2001), and also suggests that goat domestication might take place independently in different regions of the world. The MDS plot of pairwise FST distances displayed a weak phylogeographic relation among Chinese goat breeds, and this result may largely be attributed to the high gene flows accompanying historical human migrations in the regions or achieved through trade and commerce.

The star-like phylogeny of Chinese goat lineage B identified in this study implicates that lineage B had two population expansions, starting at about 2 and 9 mutational time units ago, respectively. Nevertheless, it can not exclude the possibility of introduction of some *de novo* haplotypes into these breeds from external sources. In the studies of Chen *et al.* (2005) and Liu *et al.* (2006), most samples were collected from the central, southwestern and southern regions of China and lineage B was presented in almost all breeds. And as such, their studies are limited in precisely defining the geographic location for the mtDNA lineage B for Chinese goats. To make up for this weakness, we extended the sampling regions in this study. Among the goat breeds collected, 36 lineage B sequences was found only from the breeds in the central, southwestern and southern regions of China (Shaanan White, Langkazi, Yunling Black, Maguan, Matou and Hainan Black). It is likely that this lineage in the breeds of central (Shaanan White and Matou) or southern (Hainan Black) regions was derived from the same ancient domestication center, southwestern region of China or nearby countries. The present study provided evidence to the proposal that the ancient south western mountain area of China is a domestication center for Chinese goats (Sieh 1985). Overall, multiple lines of evidence accumulated in a series of studies [i.e. (Chen *et al.* 2005; Liu *et al.* 2006) and this study] suggest that mtDNA lineage B of goats either originated from the southwestern region of China or brought to this region from nearby countries through commerce and trade in very ancient time. Nevertheless, further independent replication studies for sampling more diverse regions and breeds as well as analysis of paternal Y chromosome could be used to consolidate the finding.

Conclusion

Based on analysis of the mitochondrial HVR1 of 12 Chinese breeds covering vast area of China, we have addressed the issues regarding genetic diversity, and distributions of mitochondrial lineages found in Chinese goats, thus adding further knowledge about goat mtDNA polymorphism to the previous studies (Chen *et al.* 2005; Liu *et al.* 2006). This analysis revealed four lineages (A, B, C, and D) and considerable diversity existing in Chinese domestic goats. Multiple studies conducted so far support the proposal that for Chinese goats, mtDNA lineage B originated from the southwestern region of China or from nearby countries. Nevertheless, prior to translation of this finding to more practical setting (e.g. in conservation genetics), many independent studies for sampling

more diverse regions and breeds in nearby countries in particular are needed to consolidate the phylogenetic inference. Also, we should recognize several weaknesses of the study. First, numerous papers have revealed that modern phylogeographic patterns are often not even remotely mirrored by the patterns revealed from sampling ancient populations (e.g. Hofreiter *et al.* 2004; Shapiro *et al.* 2004; Leonard *et al.* 2005; Larson *et al.* 2007; Valdiosera *et al.* 2007). Thus, whether the relatively high frequency of mtDNA lineage B in the southeastern China itself implicates an initial ancient domestication center remains controversial. The opponents argued that the wild ancestor of the domestic goats (i.e. the bezoar *Capra aegagrus*) has not been found in this area (Naderi *et al.* 2007). Overall, in order to fully resolve the issues, perhaps increasing number of independent studies like the present one are required to sample more breeds and areas including wild goat species for uncovering the true evolution story for the domesticated goats. Secondly, we should recognize the limitation of mtDNA when used for phylogenetic analysis that only information from maternal lineage was analyzed. To make up the gap, paternally derived Y chromosome can be used in future studies. Surveys of variation in the non-recombining portion of this chromosome have been immensely valuable in complementing and adding to the picture of mammalian evolution (de Knijff 2000). Finally, autosomes should not be neglected, although they are more likely influenced by evolutionary forces. Studies of microsatellites in cattle have shown that highly polymorphic diploid markers can also shed light on recent population dynamics and reveal the fine grain of admixture between divergent populations (MacHugh *et al.* 1997; Loftus *et al.* 1999).

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