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Genetic Diversity and Origin of Chinese Domestic Goats Revealed by Complete mtDNA D-loop Sequence Variation

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ABSTRACT : China has numerous native domestic goat breeds, but so far there has been no extensive study on genetic diversity, population demographic history, and origin of Chinese goats. To determine the origin and genetic diversity of Chinese goats, we analyzed the complete mtDNA D-loop sequences of 183 goats from 13 breeds. The haplotype diversity value found in each breed ranged from 0.9333 to 1.0000. The nucleotide diversity value ranged from 0.006337 to 0.025194. Our results showed that there were four mtDNA lineages (A, B, C and D), in which lineage A was predominant, lineage B was moderate, and lineages C and D were at low frequencies. Lineages C and D were observed only in the Tibetan breed. The results revealed multiple maternal origins of Chinese domestic goats. There was weaker geographical structuring in the 13 Chinese goat populations, which suggested that there existed high gene flow among goat populations caused by the extensive transportation of goats in the course of history. (**Key Words :** Chinese Domestic Goat, mtDNA, D-loop, Genetic Diversity, Origin)

INTRODUCTION

The domestic goat (*Capra hircus*) is the most adaptable and geographically widespread livestock species. Domestic goats provide a full range of useful products to human society (e.g., meat, milk, and fiber), and this makes the goat one of the most useful animals that humans have ever domesticated (Porter, 1996). The origin, genetic diversity, conservation, and sustainable utilization of this species have received close attention for a long time. Archaeological evidence indicates that the goat was one of the first animals to be domesticated by humans around 10,000 years ago at the dawn of the Neolithic period in the Fertile Crescent (Porter, 1996; Pringle, 1998), whereas some studies have suggested that an independent domestication in Pakistan gave rise to the Cashmere breeds (Porter, 1996). Goats played a central role in the Neolithic agricultural revolution and the spread of human civilization around the globe (Porter, 1996; Pringle, 1998; Zeder and Hesse, 2000). 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). However, the origin of the domestic goat remains uncertain and controversial, despite the archaeological evidence.

The examination of variations in the mitochondrial DNA (mtDNA) control region sequences has been shown to be very useful in elucidating the origin and diversification of domestic animals (Jeon et al., 2005; Sasazaki et al., 2006; Odahara et al., 2006). For instance, Luikart et al. (2001) carried out a worldwide survey of domestic goat mtDNA diversity and identified three major mtDNA lineages. Lineage A was 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. These three lineages were judged to have diverged over 200,000 years ago; this ancient divergence time and the different geographical localizations of the lineages suggested the likelihood of either multiple domestication events or the introgression of additional lineages after the original domestication. This initial survey provides a context for more detailed regional studies. Joshi et al. (2003) found additional lineages (lineage D and lineage E) in Indian goats.

China is a country especially rich in domestic goat breed resources as gene pool in the world. Previously our researchers took conformation traits, geographical distributions, ecological conditions and historical literature or cultural relics as the bases for classification. Chinese

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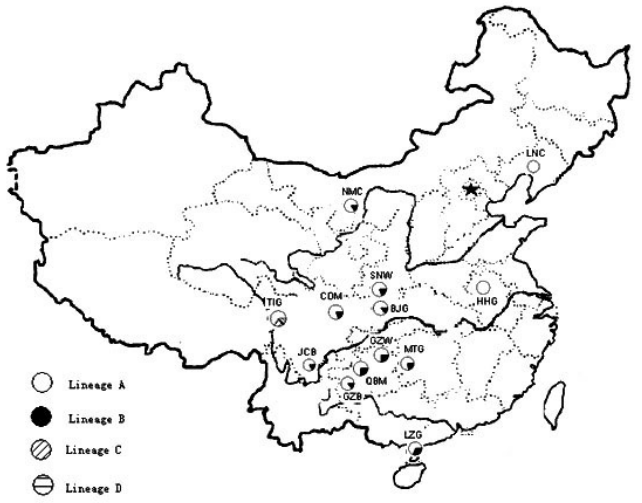

Figure 1. Geographical and lineage distribution of the Chinese goat breeds sampled. Circle area is proportional to sample size. Breed abbreviations are as follows: BJG, Banjiao goat; CDM, Chengdu Ma goat; GZB, Guizhou Black goat; GZW, Guizhou White goat; HHG, Huanghuai goat; JCB, Jianchang Black goat; LNC, Liaoning Cashmere goat; LZG, Leizhou goat; MTG, Matou goat; NMC, Neimonggol Cashmere goat; QBM, Qianbei Ma goat; SNW, Shaannan White goat; TIG, Tibetan goat.

specialists, after thorough study and discussion, during their compilation of the book "Sheep and Goat Breeds in China" all agreed on dividing the local goats into 20 breeds (Tu, 1989). But we have little knowledge of the origin, migration, evolution and breed genetic status of Chinese indigenous goat breeds. Moreover, a previous analysis of Chinese goats was confined to a single study by Luikart et al. (2001) who used a limited number of samples (two individuals from two breeds). Few reports are available, however, on mtDNA D-loop sequence variation and origins of Chinese goat (Chen et al., 2005). There is, therefore, a need for an extensive study of Chinese goat breeds to understand their origin, divergence, and past migration patterns. Hence, we have undertaken the present investigation of 183 goats belonging to 13 different breeds from different geographical regions in China (Figure 1). We want to learn more about the genetic diversity of Chinese goats and to provide information for informed conservation of these genetic resources.

MATERIALS AND METHODS

Sample collection and DNA extraction

A total of 183 unrelated goat blood samples were collected from natural habitats (Figure 1). An effort was made to collect samples from unrelated individuals based on the information provided by farmers. Details of the breeds, and sample sizes are given in Table 1. Total genomic DNA was extracted from the samples by the standard phenol-chloroform extraction method. Sequences of the outgroup species (*Capra aegagrus* and *Capra falconeri*) were obtained from GenBank (Accession No. AB044305, AB110590, AB110591).

PCR amplification and sequencing

To amplify the D-loop region of goat mtDNA, a pair of primers was designed using the known goat mtDNA sequence (GenBank Accession No. NC005044). Primers were designed using the PrimerSelect package of the DNASTAR program. The primer sequences were as follows:

Forward 5'-CAGTCGAACATCCCTACATTATTATTGG-3'
and
reverse 5'-TTAGTCTTATTGATTTGGAGGGCGTTA-3'.

PCR amplifications were conducted in a 50 μl volume containing 5 μl of 10×reaction buffer, 1.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.2 μM each primer, 1.5 U *Taq* DNA

Table 1. Sampling and distribution of the mtDNA lineages of the Chinese goat breeds and their genetic diversity

Breeds	Sample size	Haplotype diversity ±SD	Nucleotide diversity ±SD	Lineage observed (%)
Banjiao goat	15	0.9333±0.0449	0.008467±0.004593	A(86.67%),B(13.33%)
Chengdu Ma goat	15	1.0000±0.0243	0.017956±0.004410	A(73.33%),B(26.67%)
Jianchang Black goat	12	1.0000±0.0340	0.015269±0.008208	A(83.33%),B(16.67%)
Guizhou Black goat	14	0.9890±0.0314	0.015883±0.008405	A(78.57%),B(21.43%)
Guizhou White goat	15	0.9905±0.0281	0.018265±0.009567	A(60.00%,B(40.00%)
Qianbei Ma goat	13	0.9615±0.0496	0.019004±0.010063	A(69.23%,B(30.77%)
Matou goat	14	0.9670±0.0437	0.017578±0.009290	A(71.43%),B(28.57%)
Shaannan White goat	15	0.9905±0.0281	0.016017±0.008426	A(73.33%),B(26.67%)
Huanghuai goat	14	1.0000±0.0270	0.007062±0.003900	A(100%)
Leizhou goat	13	0.9615±0.0496	0.017283±0.009189	A(53.85%),B(46.15%)
Neimonggol Cashmere goat	13	1.0000±0.0302	0.015712±0.008372	A(84.62%),B(15.38%)
Liaoning Cashmere goat	12	0.9697±0.0443	0.006337±0.003579	A(100%)
Tibetan goat	18	1.0000±0.0185	0.025194±0.012914	A(66.67%),B(5.55%), C(16.67%),D(11.11%)

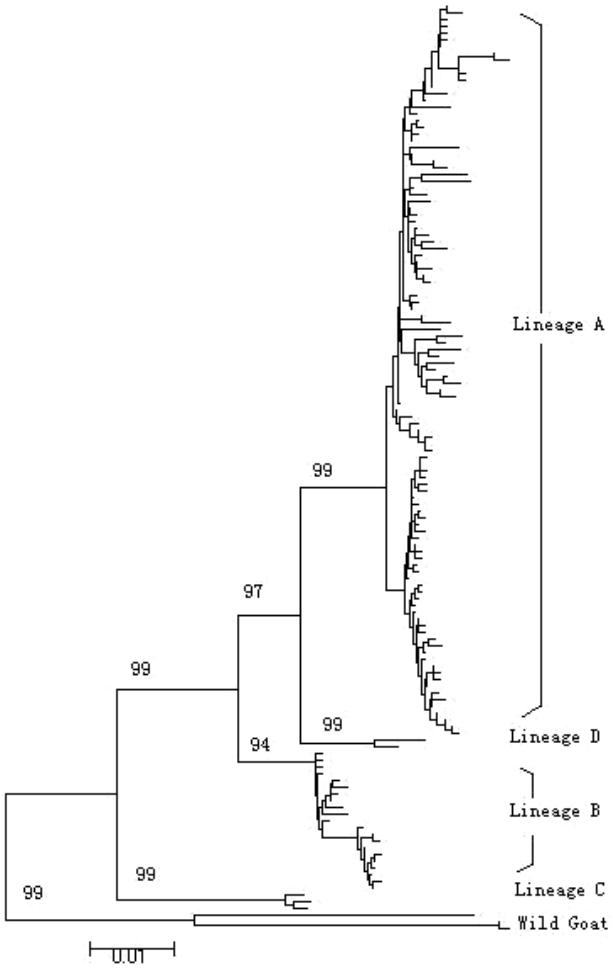

Figure 2. NJ tree of Chinese goat mtDNAs haplotypes and wild goat sequences. The bootstrap values of the main branches are shown in the figure.

polymerase (TaKaRa Biosystems), and approximately 30 ng genomic DNA. The PCR mixture underwent 3 min at 95°C, 35 cycles of 1 min at 94°C, 1 min at 66°C, and 1 min at 72°C, and 5 min at 72°C. PCR products were purified by using the Watson PCR Purification Kit (Watson BioTechnologies, Shanghai) according to the supplier's instructions. The complete D-loop sequence of the PCR product was obtained by using six internal primers. The internal primer sequences were as follows: GQF1: 5'-TACAATCAATACACTGGTCTT-3', GQR1: 5'-ATTACGT TTATGCTGGATT-3'; GQF2: 5'-ATAACGCGGACATACA GC-3', GQR2: 5'- AGAGTGGGCGATTTTAGGTGAGAT -3'; GQF3: 5'-GGGCCATCTCACCTAAAATC-3', GQR3: 5'-GGCTGGGACCAAACCTATG-3'. Sequencing was carried out from both ends of the PCR products using the ABI PRISM Big Dye Terminator v3.0 Ready Reaction Cycle Sequencing Kit in 5 μl volumes (Applied Biosystems). The cycling profile for the sequencing reaction consisted of 25 cycles of 96°C for 10 s, 50°C for 5 s, and 60°C for 4 min. Isopropanol-purified sequencing products were analyzed on the ABI PRISM 3700 DNA Analyzer (Applied Biosystems).

Data analysis

The sequences were edited by using the DNASTAR5.0 package (DNASTAR, Madison, WI). All sequences of mtDNA D-loop were aligned utilizing the ClustalX package (Thompson et al., 1997). Gaps in the aligned sequences were excluded from the following analyses. The polymorphisms in the analyzed segments, d_A distances (Corrected average pairwise difference between populations) and d_{XY} (Average number of pairwise differences between populations); mean number of pairwise differences (MNPD), and F_{st} (Nei, 1987) were obtained using the Arlequin 2.000 computer package (Schneider et al., 2000). The polymorphisms in the analyzed segments were exported by using MEGA2.1 (Kumar et al., 2001). A neighbor-joining (NJ) tree obtained by using the Kimura two-parameter model was first constructed based on the aligned sequences to identify possible phylogenetic clades with the aid of the MEGA 2.1 software package (Kumar et al., 2001). The Kimura two-parameter distances between haplotypes were calculated using MEGA 2.1 (Kumar et al., 2001) using a value for the alpha parameter of 0.29 (Luikart et al., 2001). Reduced median networks (Bandelt et al., 1995) were generated using the NETWORK 4.1 program (http://www.fluxustechnology.com/). The haplotype diversity (h) and nucleotide diversity (π) for the breeds and/or population samples were estimated by using the Arlequin 2.000 software (http://lgb.unige.ch/arlequin/; Schneider et al., 2000).

RESULTS

mtDNA variation and haplotype in Chinese domestic goats

We have examined 183 complete mtDNA D-loop sequences (Accession Nos. DQ121491-DQ121618, DQ18 8849-DQ188903) belonging to 13 different Chinese goat breeds representing different geographical regions of China, along with published wild goat sequences. Comparison of the 183 sequences revealed 135 different haplotypes with 144 polymorphic sites. Substantial heterogeneity in substitution rates among nucleotide sites was found when estimated under the Kimura two-parameter with gamma correction. This had also been observed for other mammals (Bradley et al., 1996; Luikart et al., 2001). The overall ratio of transitions: transversions (19.6:1) revealed a heavy transition bias in domestic goats similar to the 17:1 and 16.7 ratio*s* seen before (Luikart et al., 2001; Joshi et al., 2004 respectively). The haplotype diversity value found in each breed ranged from 0.9333 in the Banjiao to 1.0000 in the

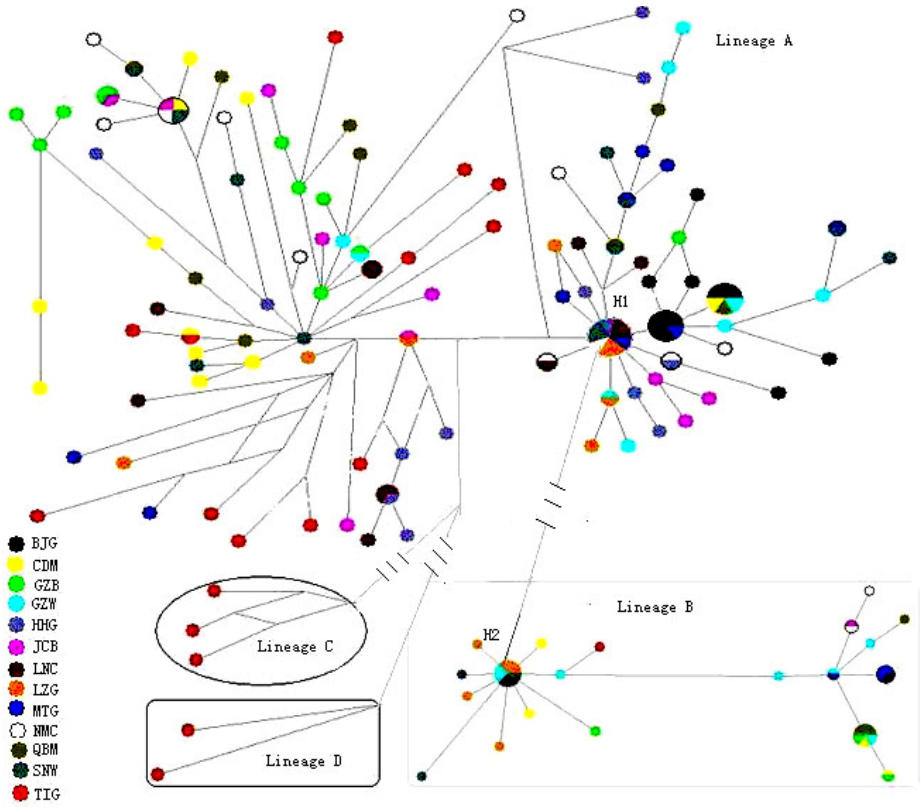

Figure 3. Reduced median network of Chinese goat mtDNAs. Circles represent haplotypes and have sizes proportional to frequencies.

Chengdu Ma, Jianchang Black, Huanghuai, Neimonggol Cashmere and Tibetan goat breed. The nucleotide diversity value ranged from 0.006337 in the Liaoning Cashmere goat to 0.025194 in the Tibetan goat (Table 1).

Phylogenetic tree of the haplotypes and network map of the major lineages in Chinese domestic goats

The 135 different haplotypes found in 183 individuals of Chinese domestic goats and three wild goat sequences were used to construct a NJ tree (Figure 2). The NJ tree showed four different mtDNA lineages, A, B, C and D in Chinese domestic goats according to the notation system of the lineage described by Luikart et al. (2001) and Joshi et al. (2004). The four distinct lineages could be interpreted as evidence for either four separate maternal origins from genetically distinct populations, or one origin from an extremely large population containing four highly divergent lineages. Our results further support the multiple maternal origins of domestic goats (Luikart et al., 2001; Joshi et al., 2004). The phylogenetic relationships among the four lineages in Chinese domestic goats were further demonstrated by the network presented in Figure 3.

Phylogenetic analysis and a reduced median network analysis revealed main two highly divergent goat mtDNA lineages A and B, including 109 and 21 haplotypes comprising 140 and 38 mtDNA samples, respectively (Figures 2 and 3). The frequency of lineage A and B was 76.50% and 20.77%, respectively. We also observed additional lineages C and D only in the Tibetan breed with three and two haplotype samples respectively (Figures 2, 3 and Table 1). These two lineages are present in China at low frequencies (1.64% and 1.09%). The network shows considerable diversity. The most predominant haplotype H1 in lineage A was represented nine times and was shared among six goat breeds (LZG, LNC, SNW, NMC, HHG and MTG). The most predominant haplotype H2 in lineage B was represented eight times and was shared among four goat breeds (LZG, GZW, BJG and SNW). H1 and H2 stood out at the center of the star-shaped network of lineage A and B respectively. Another two haplotypes occurred six times; one occurred five times; three occurred thrice; 12 were found twice; and 114 haplotypes were unique (Figure 3).

Population structure

To probe into the relationships among the 13 goat breeds, the estimates of nucleotide divergence between the 13 populations (Table 2) and the NJ tree derived from them (Figure 4) show the populations grouped into two clusters. The NJ tree showed that the Chinese domestic goat breeds from different geographical and cultural regions intermixed together. These results indicated weaker geographic structuring in the Chinese domestic goat breeds. In order to further study their geographical structures, AMOVA analysis was performed. AMOVA indicated that the

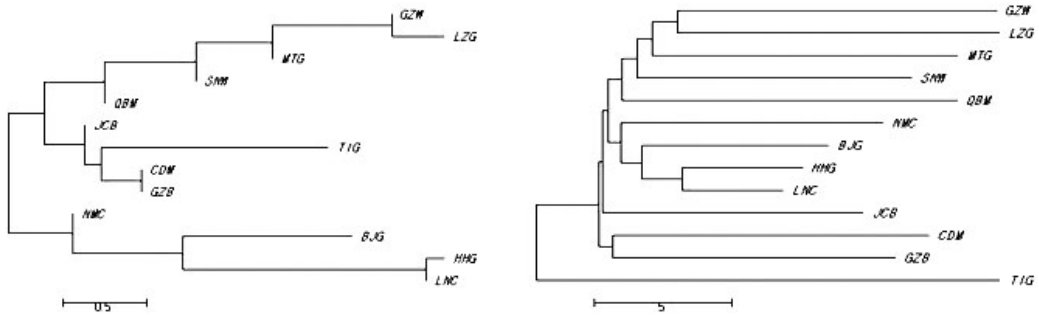

Figure 4. NJ trees for 13 Chinese goat breeds, based on nucleotide divergence (d_A) between populations, with negative divergence estimates set to zero(left) and average number of nucleotide substitutions between populations(d_{XY})(right). A scale bar for branch lengths is shown.

Table 2. Matrix of d_A distances (Corrected average pairwise difference between populations; below diagonal) and d_{xy} (Average number of pairwise differences between populations; above diagonal) among 13 Chinese goat breeds

	BJG	CDM	GZB	GZW	HHG	LZG	MTG	QBM	SNW	JCB	LNC	NMC	TIG
BJG		21.9996	20.7694	20.8914	12.6208	21.3032	18.7118	21.3031	16.9862	18.2056	12.1355	17.4629	28.1136
CDM	4.1405		22.0617	26.1779	20.4782	25.6368	25.7472	24.3240	23.5105	21.912	19.7944	22.5738	31.5747
GZB	4.2597	-0.9101		26.059	18.5198	25.7439	25.2089	23.5658	22.8638	20.3508	17.5563	21.2077	30.0509
GZW	2.7050	1.5295	2.7603		23.5481	23.678	23.7377	25.0275	23.2890	24.8142	22.7114	24.7723	34.1501
HHG	2.4933	3.8885	3.2795	6.6311		23.5930	20.0493	21.2439	17.9800	15.8599	8.0713	15.9713	25.1486
LZG	3.8245	1.696	3.1524	-0.5901	7.3837		24.4879	25.5528	22.819	24.9173	22.7265	25.0794	33.7646
MTG	0.9341	1.5074	2.3185	-0.8294	3.541	0.6284		24.5647	22.2905	23.055	19.4696	22.9101	32.6939
QBM	2.608	-0.8334	-0.2422	-0.457	3.8179	0.7757	-0.5114		23.5393	22.6961	20.4869	23.1233	32.4411
SNW	0.4948	0.5569	1.2596	0.0081	2.7579	0.2462	-0.5818	-0.2505		21.3647	17.2854	21.0946	30.9808
JCB	2.2105	-0.5454	-0.7570	2.0296	1.1342	2.8404	0.6791	0.5974	0.2751		15.2533	19.7077	29.0414
LNC	2.4742	3.6709	2.7822	6.2606	-0.3208	6.9833	3.4274	3.5272	2.5295	0.9936		15.4295	24.6028
NMC	1.2078	-0.1435	-0.1603	1.7277	0.9854	2.7424	0.2741	-0.4303	-0.2551	-1.1456	0.9099		29.8543
TIG	4.7043	1.7033	1.5288	3.9513	3.0086	4.2735	2.9038	1.7334	2.477	1.0339	2.9290	1.5866	

Table 3. AMOVA analysis of Chinese domestic goat breeds based on mtDNA variation

Source of variation	Percentage of variation		
	No grouping	Grouping based on d_A	Grouping based on d_{XY}
Among groups	7.87	0.07	6.07
Among breeds (within groups)		7.83	6.31
Within breeds	92.13	92.10	87.62

grouping based on d_{XY} was more reasonable than that based on d_A (Table 3). These results are in accord with the known history and geographical origins of these breeds. The Tibetan goat breed lives on the Northwest plateau, and their reproduction is mainly limited to this area. The results of AMOVA further demonstrated weaker geographical structuring in Chinese domestic goat breeds.

DISCUSSION

Genetic diversity of Chinese domestic goats

There are rich genetic resources of domestic goats in China. Tu et al. (1988) suggested that there are 20 goat breeds and many local goat populations in China. Due to their diverse geographical distributions, the native goat breeds have different characteristics. In this paper, we determined the complete mtDNA D-loop sequence variations in 13 breeds or populations from China. The focus of this study was to learn more about the origin and genetic diversity of goats in China. Our results were not consistent with those from previous studies based on mtDNA RFLP (Li et al., 1999; Jia et al., 1999). Haplotype diversity and nucleotide diversity of mtDNA are the important indices for assessing population polymorphisms and genetic differentiations. When the values of haplotype diversity and nucleotide diversity of mtDNA are bigger, the population polymorphism is higher. Li et al. (1999) revealed that the average nucleotide diversity of mtDNA RFLP was 0.0487% in 18 Chinese native goat breeds, suggesting the low genetic diversity and differentiation level in Chinese goats. Jia et al. (1999) indicated that the average nucleotide diversity of mtDNA RFLP was 0.0687% in four Guizhou goat breeds. The haplotype diversity and nucleotide diversity of mtDNA D-loop in 13 Chinese native

goat breeds were 0.9333-1.0000 and 0.006337-0.025194, respectively, revealing abundant genetic diversity in Chinese native goat breeds. The reason is the difference between the two methods.

Restriction endonucleases only recognize specific sites of the mtDNA molecule in mtDNA RFLP analysis rather than indicating every nucleotide site like nucleotide sequencing. Recently, Chen et al. (2005) determined a 481 bp fragment of the first hypervariable region of mtDNA D-loop region from 368 individuals representing 18 indigenous Chinese goat breeds. The level of haplotype diversity of 18 goat breeds (0.7121-0.9804) by Chen et al. (2005) is lower than that of 13 goat breeds (0.9333-1.0000) in our study, but the level of nucleotide diversity of 18 goat breeds (0.0159-0.0490) by Chen et al. (2005) is higher than that of 13 goat breeds (0.006337-0.025194) in our study. The reason is probably that the samples of every breed are higher than that of our study, thus finding more than two lineages in per breed with high nucleotide diversity.

The origin and genetic differentiation of Chinese goats

The phylogenetic tree shows that four clearly differentiated lineages, lineage A, B, C and D were observed in 183 animals from the 13 Chinese goat breeds analyzed in this study (Figures 2 and 3). This indicated four major maternal origins in Chinese goats. Our results are not the same as those of Li et al. (1999) and Jia et al. (1999) who found two mtDNA lineages in Chinese goats. Luikart et al. (2001) analyzed a hypervariable sequence (481 bp) of the mtDNA D-loop from 406 goats representing 88 breeds distributed in 44 countries (including two samples from two Chinese goat breeds) across the world. Their results revealed three highly divergent goat mtDNA lineages (A, B and C), with the Chinese goat breeds being in lineage A. Evidently, the small sample of Chinese goats resulted in only lineage A being found in the results of Luikart et al. (2001). Joshi et al. (2004) revealed the presence of five lineages in Indian goats. The four highly divergent lineages (A, B, C and D) which we detected in Chinese goat breeds in our study are nearly consistent with those of Indian goats (Joshi et al., 2004), and completely consistent with those of Chinese 18 goat breeds (Chen et al., 2005). Lineage A was found in all Chinese goat breeds while lineage B was found in all Chinese goat breeds except the Liaoning Cashmere goat breed and Huanghuai goat breed. Lineages C and D were found only in the Tibetan goat breed indicating a special population. One of reasons is that Tibet is close to India which has abundant multiple maternal origins for goats. In history, there may have high gene flow between Indian and Tibetan goat populations. It is reasonable that goats have often been transported for commercial trade or during migratory and exploratory movements of humans (Luikart et al., 2001).

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