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RESEARCH ARTICLE

Genetic diversity and differentiation of four goat lineages based on analysis of complete mtDNA d-loop

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Abstract The complete sequences of mtDNA D-loops from 362 individuals were analyzed in order to investigate the genetic diversity and differentiation of their lineages. The results indicated that all of the analyzed sequences were differentiated into four clear lineages (A, B, C, and D). Lineages C and D might originate from Lineages B and A, respectively. The genetic diversity of complete mtDNA D-loop of four lineages was very abundant. The 76 bp insertion and the 17 bp deletion were detected in the longest and the shortest sequences, respectively. The 76 bp insertion was a repeat like motif found in many other animals. Lineages C and D were differentiated into two subclades (C1 and C2) and (D1 and D2), respectively. Lineage C might originate from Asia, and Lineage D might originate from Fertile Crescent.

Keywords goat, mtDNA D-loop, lineages, origin, differentiation

Introduction

More than 10000 years ago, the transition of humans from hunting to manipulating the behaviors of certain animals led to the process of domestication (Naderi et al., 2007). The goat was one of the first domesticated animals in the world. The two wild species of *Capra aegagrus* (Bezoar) and *Capra falconeri* (Markhor) were suggested to be progenitors of the domestic goats by their morphological diversity (Takada et al., 1997; Zeder and Hesse, 2000). However, the origin of the domestic goat remained uncertain and controversial. Mitochondrial DNA (mtDNA) allowed maternal lineages to be followed and was less sensitive to introgression from wild species than nuclear DNA (Luikart et al., 2001; Bruford et al., 2003). Especially, the control region of mtDNA was used for describing genetic diversity and origin of domesticated species due to its constant rate.

Recent studies based on mtDNA sequences suggested that there were seven maternal lineages (A–G) in domestic goats. Luikart et al. (2001) partially sequenced the mtDNA hypervariable region (HVR) in 406 individuals from 88 breeds distributed across the world and defined lineages A, B, and C, of which Lineage A is the most diverse and widely distributed across all continents and corresponds to the initial domestication event, and Lineages B (detected in India, Malaysia, Mongolia, and Pakistan) and C (detected in Slovenia, Switzerland, and Mongolia) represent recent secondary expansions. Sultana et al. (2003) and Joshi et al. (2004) found a new low frequency lineage (D) in Pakistan and a new minority lineage (E) in India, respectively. Subsequently, Sardina et al. (2006) analyzed phylogenetic tree of Sicilian goats and revealed another new mtDNA lineage (F). Naderi et al. (2007) characterized the genetic diversity of domestic goats with 2430 individuals represented 1540 haplotypes for mtDNA HVR segment from all over the world and established a clear nomenclature of the goat maternal haplogroups (A, B, C, D, F, and G), in which five previously defined haplotypes and one new mitochondrial group (G) has been localized around the Fertile Crescent. Much attention has been paid on the study of mtDNA HVR due to its higher mutation rate. However, the analysis result of complete mtDNA D-loop might more exactly and scientifically reflect the genetic diversity of mtDNA in domestic goats. Meanwhile, the differentiation relationship among Lineages A, B, C, and D, especially the further differentiation of Lineages C and D is uncertain. Therefore, the complete sequences of mtDNA D-loop of 362 goats from Asian

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countries (China, Pakistan, Japan, Laos, and Korea), most of which, were analyzed in order to investigate the genetic diversity and differentiation of lineages.

Materials and methods

A total of 362 sequences with the complete sequence of mtDNA D-loop were obtained from GenBank (Table 1). All of the sequences were aligned using the ClustalW program implemented in BioEdit (Version 7.0.5). The phylogenetic tree based on the haplotypes was constructed using the neighbor–joining (NJ) method implemented by Mega 3.0 software (Kumar et al., 2004). DnaSP (Version 4.0) software was used to analyze the haplotype diversity (Hd), the average number of nucleotide differences (K) (Tajima, 1989), the nucleotide diversity (π), the polymorphic site (S), the singleton variable sites (SP), and the parsimony informative sites (PIP) for each goat lineage (Lynch and Crease, 1990). The Kimura2-paramter genetic distances among lineages and subclades were calculated by Mega 3.0 software in order to analyze the differentiation of lineages and subclades. Moreover, the Network 4.5 program was used for construction of reduced networks of Lineages C and D for world goats.

To understand the origin and further differentiation of Lineages C and D, 48 (C) and 24 (D) mtDNA HVR sequences (481 bp) from GenBank were collected. Lineage C includes AB110555, AB110559, AJ317834-40, AY155708, AY155877, AY156000, AY156009, AY424915, AY918059-60, AY961644, DQ188886, DQ188890, DQ188892, DQ089192, DQ089461, EF103513, EF103539, EF368314, EF368288, EF617786, EF618350, EF618347-49, EF618413-14, EF618486-91, EU035991, EU035998, EU036007, EU036014, EU036097, EU126791, and EU130770. Lineage D includes AB110587-9, AY155952, AY155964-5, DQ089350, DQ188888, DQ188893, EF103496, EF103519, EF103516, EF103529, EF103537, EF617701, EF618217-9, EU036025, EU036029, EU036032, EU036038, EU036055, EU036061, and EU130714.

Results

Genetic differentiation of complete mtDNA D-loop of goats

The phylogenetic tree showed four clear differentiated lineages, Lineages A, B, C, and D in 357 complete mtDNA

Table 1 The mtDNA D-loop sequences of different goat breeds from GenBank

source	breed	number	accession No.
Chinese indigenous goats	Tibet	27	AY860934-42, DQ188884-901
	Chengduma	24	DQ121506-20, AY860885-93
	Banjiao	20	DQ121491-505, AY860875-79
	Jianchang Black	17	AY860894-98, DQ188849-60
	Liaoning Cashmere	17	AY860909-13, DQ188861-70, DQ188902-03
	Guizhou White	15	DQ121535-49
	Shannan White	15	DQ121604-618
	Huanghuai	14	DQ121550-63
	Matou	14	DQ121577-90
	Nangjiang Yellow	14	AY860920-33
	Guizhou Black	14	DQ121521-34
	Leizhou	13	DQ121564-76
	Qianbeima	13	DQ121591-603
	NeiMeng Cashmere	13	DQ188871-83
	Lezhi Black	6	AY860914-19
	Chuandong White	5	AY860880-84
	Jintang	5	AY860899-903
	Jianyang Daer	5	AY860904-08
	Beichuan White	4	AY860871-4
Chinese introduced goats	Angora	8	AY853278-85
	Boer	6	AY853286-87, AY853292-95
	Nubian	6	AY853296-301
	Sannen dairy	4	AY853288-91

(*Continued*)

source	breed	number	accession No.
Pakistan	Patri	6	AB110557-9, AB162200-2
	Kohistani	5	AB110572-4, AB162208-9
	Pak Angora	5	AB110560-63, AB162203
	Tapri	5	AB110552-3, AB110589, AB162196-7
	Dera Din Panah	5	AB110580-2, AB162211-2
	Beetal	5	AB110585-88; AB162214
	Teddy	5	AB110554-6; AB162198-9
	Khurawsani	5	AB110575-78
	Lehri	4	AB110567-9; AB162205
	Long Hairy	4	AB110570-1; AB162206-7
	Nachi	4	AB110564-6; AB162204
	Barbari	3	AB110583-4; AB162213
	Punjab Random	3	AB162215-7
	Kamori	1	AB110579
	Lop-eared	1	AB004082
Korea	Indigenous	1	AB004080
Laos	Indigenous	10	AB044295-304
Japan	Sannen	1	AB004077
	Indigenous	2	AB004078-9
unknown	Dwarf	1	AB004081
	Goat genome	2	NC005044; AF533441
wild goats	Bezoar	1	AB004076
	Markhor	2	AB044305-6
	Sindh Ibex	2	AB110590-1

D-loop sequences of domestic goats in this study (Fig. 1), which was consistent with the results of the phylogenetic tree analyzed by mtDNA HVR sequences (Luikart et al., 2001; Sultana et al., 2003; Joshi et al., 2004; Chen et al., 2005; Fan et al., 2007). The haplotype of one wild goat (Bezoar) was clustered into Lineage A, while three haplotypes of two wild goats (Sindh, Ibex) and another two wild goats (Markhor) were clustered into an independent group showing far relationship with other lineages.

Polymorphism and genetic diversity of goat lineages

Length variation and base constitution of goat mtDNA D-loop

Comparisons of the 362 complete mtDNA D-loop sequences revealed that most sequences were 1212 or 1213 bp in length, but there was also length variation, showing that the length of the complete mtDNA D-loop sequences varied greatly in Pakistani goats, ranging from 1195 to 1288 bp. The longest length (1288 bp) was a long hairy breed (AB162206) due to an insertion (76 bp) of ATGTATATAGTACATTAAAC-

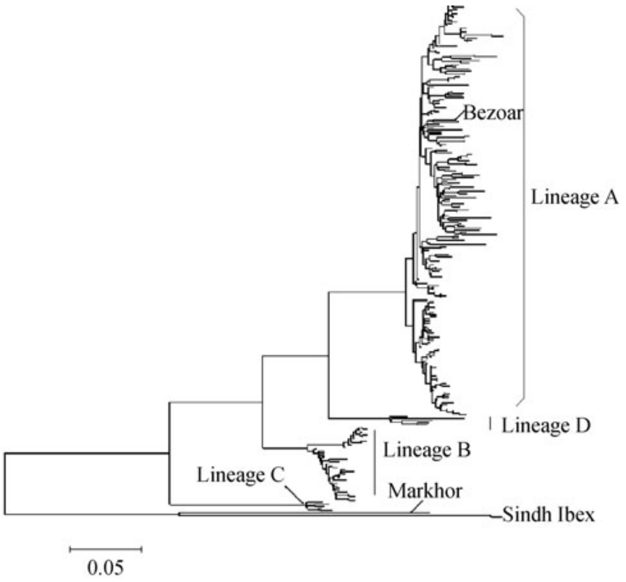

Figure 1 Neighbor-joining tree constructed with 255 haplotypes of goat mtDNA D-loop

GATTTTCCGCATGCATATTAAGTACGTACATAATAT-TAATGTAACAGGGACATAGT from 415 to 490 bp, which was the repeat-like motif from 491 to 566 bp. The shortest length (1195 bp) of AB162201, AB162207, AB162213, and AB110575 was due to a 17 bp deletion of CACA-CAAACGCCAACAC from 176 to 192 bp that existed in all other sequences. Another variation sequence (AB110569) was 1214 bp due to 9C nucleotides from 1068 to 1076 bp, whereas 7C or 8C nucleotides existed in the other sequences.

The complete mtDNA D-loop sequences in Chinese goats varied from 1212 to 1213 bp in 276 individuals. Comparisons of these sequences revealed 224 individuals with 1212 bp and 52 individuals with 1213 bp. A poly C was important for the mtDNA D-loop length variation due to 8C nucleotides from 1068 to 1075 always in 1213 bp and 7C nucleotides from 1068 to 1074 always in 1212 bp. Three Chinese introduced goats (Boer) were 1211 bp due to a base deletion at 520, where C or T was found in other individuals. The mtDNA D-loop length of the goats from Japan (3) and Laos (10) was also 1212 bp, and another one from Korea was 1213 bp due to an insertion T at 1209.

The average base composition of T, C, A, and G in the mtDNA D-loop was 28.9%, 25.8%, 31.1%, and 14.1%, respectively. The high A/T contents found in goat mtDNA D-loop were also described in sheep (Zhao et al., 2008), cattle (Li et al., 2008), mouse (Bibb et al., 1981), donkey (Xu et al., 1996), and whale (Arnason et al., 1991). However, the rich A/C contents were found in primates (Foran et al., 1988), seal (Arnason et al., 1993), and rabbit (Mignotte et al., 1990). This was attributed to the species-specific variations that existed in mtDNA D-loop among different mammalian species.

Polymorphism and genetic diversity of goat lineages

Higher polymorphism and genetic diversity were found based on the analysis of complete sequences of mtDNA D-loop compared with those of mtDNA HVR. The comparison of 362 complete sequences of mtDNA D-loop of goats revealed 255 different haplotypes and higher haplotype diversity (0.993). The results of DnaSP analysis indicated that there were 948 invariable sites and 242 variable sites including 38 singleton variable sites and 204 parsimony informative sites in 1190 analyzed sites excluding sites with gaps (103). The nucleotide diversity (π) and the average number of nucleotide differences (K) for all sequences are 0.018 and 21.451, respectively. However, the comparison of mtDNA HVR (predominant length 481bp) with the same sequences only revealed 199 different haplotypes and relative lower haplotype diversity (0.988). There were 332 invariable sites and 146 variable sites including 23 singleton variable sites and 123 parsimony informative sites in 478 analyzed sites excluding sites with gaps (79). The nucleotide diversity (π) and the average number of nucleotide differences (K) for all sequences were 0.0335 and 16.034, respectively.

The genetic diversity of complete mtDNA D-loop for each lineage was listed in Table 2. Lineage A has the highest number of variable sites (148), singleton variable sites (53), and the parsimony informative sites (95), and Lineage D has the highest average number of nucleotide differences (12.4) and the highest nucleotide diversity (0.0102).

Further differentiation of Lineages C and D

There were 48 (Lineage C) and 24 (Lineage D) mtDNA HVR sequences (481 bp) from GenBank collected to gain an insight into further differentiation of Lineages C and D. The results of Network analysis revealed that the 48 mtDNA HVR (481 bp) sequences of Lineage C in Europe and Asia were classified into two central subclades (C1 and C2), of which C1 included 21 haplotypes representing 24 individuals all from Asia, and C2 included 16 haplotypes representing 24 individuals all from Europe (Fig. 2). Only one haplotype in C1 included two goats from Asia and Europe, respectively.

The results of Network analysis revealed that the 24 mtDNA HVR sequences (481 bp) of Lineage D in the world were also classified into two central subclades (D1 and D2), of which D1 included 12 haplotypes representing 15 individuals, and D2 included 9 haplotypes representing 9 individuals (Fig. 3). There was no correspondence between the geographic regions of origin and subclades. The 14 haplotypes representing 14 individuals from China and 3 haplotypes representing 3 individuals from Pakistan existed in both two subclades. Two haplotypes representing three individuals from Kyrgyzstan, one haplotype representing three individuals from India, and one haplotype representing one individual from Austria all belonged to D2.

Table 2 Genetic variability of goat mtDNAD-loop of different lineages

Lineage	diversity parameter							
	N	h	Hd	π	S	SP	PIP	K
Lineage A	258	194	0.9943	0.0090	148	53	95	10.71
Lineage B	70	36	0.9420	0.0047	42	18	24	5.725
Lineage C	5	5	1.0000	0.0048	11	4	7	5.8
Lineage D	5	5	1.0000	0.0102	27	19	8	12.4

Note: N is the number of individuals within Lineages, h is the Number of haplotypes, Hd is haplotype diversity, K is the average number of nucleotide differences, π is the nucleotide diversity, S is the number of polymorphic sites, SP is singleton variable sites, and PIP is parsimony informative sites.

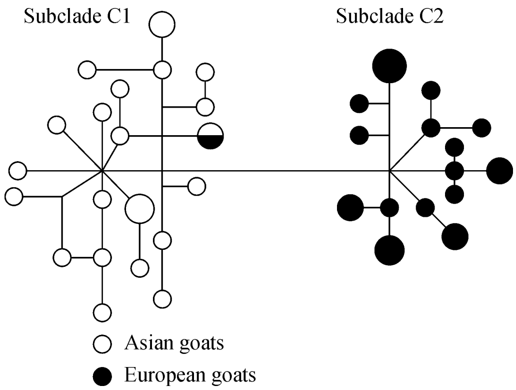

Figure 2 Network analysis of mtDNA HVR lineage C in world goat breeds

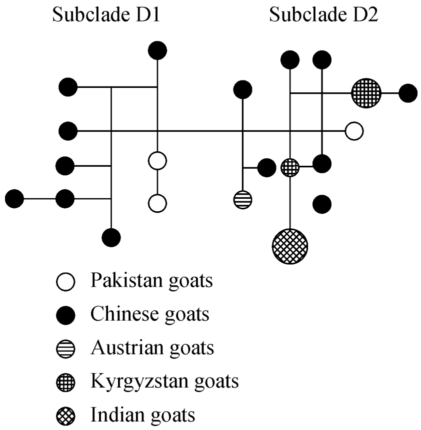

Figure 3 Network analysis of mtDNA HVR lineage D in world goat breeds

Discussion

Genetic diversity of goat mtDNA D-loop

The comparison of 362 sequences of complete mtDNA D-loop and mtDNA HVR revealed 255 and 199 different haplotypes, respectively. The results of DnaSP analysis indicated that there was an obvious difference of genetic diversity between complete mtDNA D-loop and mtDNA HVR in goats. Higher haplotype diversity was found in complete sequences of mtDNA D-loop compared with that of mtDNA HVR. The nucleotide diversity (π = 0.018) of complete mtDNA D-loop for all sequences was lower than that of mtDNA HVR (π = 0.0335), but the average number of nucleotide differences (K = 21.451) of complete mtDNA D-loop was higher than that (K = 16.034) of mtDNA HVR. The obvious difference of genetic diversity implied that the complete mtDNA D-loop might more exactly and scientifically reflect the genetic diversity of mtDNA in goats.

The haplotype diversity of four lineages (0.942–1) was basically accorded with those from other reports (Chen et al., 2005); however, there were obvious differences of the nucleotide diversity (π) and the average number of nucleotide differences (K) among four lineages. There were higher differences of π (0.009 and 0.0047) and K (10.71 and 5.725) between two main lineages A and B, showing that there was obvious differentiation between Lineages A and B. While Lineages A and D had little differences of π (0.009 and 0.0102) and K (10.71 and 12.4), and Lineages B and C had similar π (0.0047 and 0.0048) and K (5.725 and 5.8), showing that the lower genetic differentiation existed between Lineages A and D and Lineages B and C.

Variations of 76 bp insertion and 17 bp deletion

The 76 bp insertion belonging to mtDNA HVR was the repeat-like motif from 491 to 566 bp from one Pakistani goat (AB162206), which was also observed in two Pakistani goats by Luikart et al. (2001). The repeat-like motif was a general feature of mtDNA D-loop in diverse groups of other animals, for example, in cats (Lopez et al., 1996), tree frogs (Yang et al., 1994), and protozoans (Morin and Cech, 1986). In most species, only one copy of the motif was detected, while some species had commonly more than one copy, for example, four copies in sheep (Hiendleder et al., 1998), three in cats (Lopez et al., 1996), one to seven in donkeys (Xu et al., 1996), two to nine in bats (Wilkinson et al., 1997), fourteen to twenty-nine in pigs (Ghivizzani et al., 1993), and two to twenty-nine in horses (Xu and Arnason, 1994). The goat 76 bp insertion sequence marked homology (86%) with the 75 bp tandem repeat of domestic sheep. Li et al. (2006) once analyzed the 75 bp tandem repeat sequence to investigate the origin and differentiation of Chinese indigenous sheep breeds, whether the 76 bp repeat-like motif of goat mtDNA D-loop was related to the origin and differentiation of goats needs to be further investigated. Furthermore, the copy motif contained termination-associated sequences (Doda et al., 1981; Clayton, 1992), which were predicted to form thermodynamically stable secondary clover-leaf like structures and probably influence the rate of mtDNA replication. These similarities led to the possible interpretation of the phenomenon of convergent evolution (Saccone et al., 1991; Wilkinson and Chapman, 1991). Therefore, the structure and function of 76 bp insertion of goat also need to be further investigated.

The 17 bp deletion of CACACAAACGCCAACAC from 176 bp to 192 bp was less focused on due to its location of non-HVR. The 17 bp deletion and the 76 bp insertion of domestic goats were both detected in Pakistani goat breeds, showing that Pakistani goat breeds might differ from other goat breeds.

The relationship of four lineages

Lineages C and D of the domestic goats were minority mtDNA lineages, which were identified by previous studies based on the analysis of mtDNA HVR (Luikart et al., 2001;

Sultana et al., 2003; Joshi et al., 2004; Chen et al., 2005; Fan et al., 2007). Lineage C presented low frequency in China (1.3%, Chen et al., 2005, and 4.1%, Fan et al., 2007), Pakistan (4.5%, Sultana et al., 2003), India (4.0%, Joshi et al., 2004), and Spain (5.0%, Azor et al., 2005). Lineage D was rare and observed in China with the frequency of 0.7% (Chen et al., 2005) and 4.1% (Fan et al., 2007), and the frequency of 6.4% and 0.5% in Pakistan (Sultana et al., 2003) and India (Joshi et al., 2004), respectively. Until now, there are no reports on the origin and differentiation of Lineages C and D due to the restricting of region and quantity. In this paper, the proportion of haplotypes of Lineages C and D were both 1.98%, which also proved that Lineages C and D were minority mtDNA lineage.

It was shown that Lineage D was close related to Lineage A, and Lineage C was close related to Lineage B (Fig. 1). The smallest genetic distance (0.153) and little differences of π (0.009 and 0.0102) and K (10.71 and 12.4) of complete mtDNA D-loop between Lineages A and D implied that Lineage D might come of Lineage A, which was basically in accordance with Naderi et al. (2007). The clear nomenclature of the goat maternal haplogroups was established by mtDNA HVR, and the haplogroup A and D had the closest relationship from the Neighbor-joining tree of the 2430 domestic goats (Naderi et al., 2007). The smaller genetic distance and little differences of π (0.0047 and 0.0048) and K (5.725 and 5.8) of complete mtDNA D-loop between Lineages B and C implied that Lineage C might come of Lineage B, which was not in accordance with Naderi et al. (2007). The different results might be due to the limited range of the samples of Lineages B and C.

The origin of Lineages C and D

Lineage C might originate from Lineage B in Asia. Luikart et al. (2001) initially detected Lineage C of goat mtDNA HVR in Slovenia, Switzerland, and Mongolia, which was also found in Teddy and Patri goat breeds in Pakistan (Sultana et al., 2003), and in Xinjiang and Tibetan goat breeds in China (Chen et al., 2005). However, it is difficult to explain the origin of Lineage C due to small samples. The Kimura2-paramter genetic distance between C1 and C2 is 0.013, which is obviously smaller than the genetic distance among lineages (0.153–0.296). The little difference of K (5.725 and 5.8) and π (0.0047 and 0.0048) of complete mtDNA D-loop between Lineages B and C reveals that their differentiation is low and the smaller Kimura2-paramter genetic distances (0.248), which all showed that Lineage C has close relationship with Lineage B. The network analysis in this paper revealed that the 48 mtDNA HVR sequences were classified into two central subclades (C1 and C2), of which subclade C1 included 21 haplotypes representing 24 samples all from Asia, and subclade C2 included 16 haplotypes representing 24 samples all from Europe (Fig. 2). The further differentiation study of Lineage C showed that the further differentiation of Lineage C was similar with Lineage B. Liu et al. (2006) examined 50 mtDNA HVR (481 bp) sequences of Lineage B from six Asian goats, which were classified into two subclades and considered that Lineage B was likely to originate from China. Therefore, Lineage C also might originate from Asia. On the other hand, the genetic loci from a center of origin were expected to retain more ancestral variation and show higher haplotype and nucleotide diversity, with lineage pruning through successive colonization events leading to a reduction in derived populations(Troy et al., 2001; Savolainen et al., 2002). It could also be inferred that Lineage C probably originated from Asia due to the higher genetic diversity (K = 5.359 and π = 0.0112) of subclade of Lineage C from Asian goats and the lower genetic diversity (K = 4.638 and π = 0.009) from European goats. The similar event was detected in the differentiation of Lineage B by Li et al. (2006).

The smallest genetic distance (0.153) and little differences of π (0.009 and 0.0102) and K (10.71 and 12.4) of complete mtDNA D-loop between Lineages A and D all revealed that Lineage D has close relationship with Lineage A. Moreover, further differentiation study of Lineage D showed that the further differentiation of Lineage D was similar with Lineage A. The results of Network analysis revealed that the 24 mtDNA HVR sequences of Lineage D in the world were classified into subclade D1 and D2, and there was no correspondence between the geographic regions and the subclades (Fig. 3). The distribution of Lineage D of world goats was similar with Lineage A, which was the most diverse and widely distributed in the world. Therefore, Lineage D might originate from Fertile Crescent as well as Lineage A.

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