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Microsatellite DNA markers indicate three genetic lineages in East Asian indigenous goat populations

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Summary

The genetic differentiation and phylogenetic relationships of 18 indigenous goat populations from seven East Asian countries were analysed based on data obtained from 26 microsatellite DNA markers. The mean number of alleles (MNA) per population ranged from 2.5 to 7.6, with an average of 5.8. Genetic variability estimated from MNA and heterozygosity (H_E and H_O) were relatively low in coastal and island populations. A heterozygous deficiency within populations ($F_{IS} = 0.054$, $P < 0.001$) and total inbreeding ($F_{IT} = 0.181$, $P < 0.01$) were observed, and genetic differentiation in the populations (F_{ST}) was 13.4%. The results of Bayesian model-based clustering and a neighbour-joining tree based on Nei's genetic distance showed that Asian goat populations could be subdivided into at least the following three genetic clusters: East Asian, Southeast Asian and Mongolian. These results are in close accordance with conventional morphological and geographical classifications and migration history.

Keywords genetic distance, genetic diversity, indigenous goats, microsatellite (MS) markers.

Introduction

According to archaeological records, goats are believed to be the earliest domesticated ruminants in the Fertile Crescent region of West Asia, dating back approximately 10 000 years. Today, goats are well adapted to a variety of climatic conditions and have a wider geographical distribution than any other domestic animal. They are able to survive on marginal land, even in mountains and deserts or on plateaus and islands (Porter 1996). In 2009, there were approximately 868 million goats in the world, with the population having increased annually by 1.2-fold of the number measured in 2000. More than half of the goats in the world are reared in Asia (FAOSTAT, http://faostat.fao.org; Rischkowsky & Pilling 2007). The majority of these animals are domestic or local breeds that are not developed for commercial purposes. However, they have become well adapted to the environment in each country, including tolerating severe climatic stress (Porter 1996), reproduction under poor management conditions and adaptation to a variety of forage qualities. During this decade, the domestic breeds have attracted attention, as they are valuable genetic resources, with conservation of domestic animal diversity being essential to meet future needs (Scherf 2000). From an economic standpoint, some Asian countries recently have become concerned about their indigenous goat populations. For example, cashmere wool from indigenous goats is a major export product in Mongolia (Takahashi *et al.* 2008) and Black Bengal goats are an important source of income for small farmers, who constitute the majority of the population in Bangladesh (Faruque *et al.* 2010). In Thailand, creation of a new goat breed has begun by crossbreeding their indigenous breed with some exotic breeds (Suwit *et al.* 2010).

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Studies on the genetic diversity of domestic goats using a maternal mitochondrial DNA marker have been conducted over the last few years throughout the Asian continent and the Old World (Luikart *et al.* 2001; Joshi *et al.* 2004; Naderi *et al.* 2007). These studies concluded that the domestic goat showed a weak phylogeographic structure. Using European and Middle Eastern breeds, Cañón *et al.* (2006) studied genetic diversity using nuclear DNA microsatellite (MS) markers. Several studies using MS markers revealed important information on genetic diversity in some Asian goat populations, although each study was performed regionally or within a country, such as in Southeast Asia (Barker *et al.* 2001), China (Li *et al.* 2002; Li & Valentini 2004), India (Rout *et al.* 2008) or Mongolia (Takahashi *et al.* 2008).

In this study, we used MS markers to examine the genetic diversity and relationships among native Asian goat populations, ranging from Mongolia in the north to Indonesia in the south and from Bangladesh in the west to Japan in the east. The genetic specificity of each population becomes clear from genetic comparison between cross-border goat populations. This information may be valuable for maintaining diversity and genetic uniqueness of the genetic resource of each goat.

Materials and methods

Sample collection and microsatellite markers

Blood samples were collected from 450 goats that originated from seven countries [four East Asian (Japan, Korea, Taiwan and Mongolia), two Southeast Asian (the Philippines and Indonesia) and one South Asian (Bangladesh) countries; Table 1]. The number of individual populations per country ranged from 1 to 7, and the number of samples per population ranged from 20 to 30 unrelated animals within the original area of the population.

Fifty-three MS markers were tested, including 30 loci recommended by the International Society for Animal Genetics and FAO for evaluating goat genetic diversity (MoDAD marker set, Hoffman *et al.* 2004). Twenty-seven markers were excluded from further analyses, as described below. Of the 30 MoDAD markers, after repeat testing, four (*OarAE54*, *INRA063*, *SRCRSP15* and *DRBP1*) failed to amplify DNA fragments. Given the results of the Evens–Watterson test for marker neutrality, eight markers (OarFCB048, *SR-CRSP-9*, *SR-CRSP-5*, ILSTS087, *CSRD247*, *MCH2-DR*, *BM848* and *BM4621*) departed from neutrality ($P < 0.05$). Linkage disequilibrium between each pair of loci was estimated and resulted in exclusion of seven loci (*INRA023*, *SR-CRSP-7*, *SR-CRSP-3*, *SR-CRSP-24*, *SR-CRSP-25*, *SPS113* and *SR-CRSP-23*). To estimate the error rate of genotyping, 10% of the random samples were genotyped again and the results were compared with the original genotype (Pompanon *et al.* 2005). Eight loci (*IDVGA37*, *OarFCB11*, *ILSTS011*, *TGLA53*, *HUJ625*, *INRA081*, *IDVGA43* and *BM6444*) were estimated to have more than a 3% error rate in genotyping and were therefore excluded. The other 26 markers, listed in Table 2, were used in the statistical analyses.

The PCR amplification conditions have been described in a previous study (Dadi *et al.* 2008). Amplified fragments were separated using an ABI-PRISM 3100-Avant Genetic

Table 1 Diversity parameters in 18 Asian goat populations.

Country	Population	Abbreviation	*n*	TNA	MNA	AR	H_E	H_O	F_{IS}
Japan	Shiba	JS	30	66	2.54	2.30	0.302	0.312	−0.035
Korea	Southwest	KW	25	136	5.23	4.69	0.535	0.531	0.008
	Southeast	KE	25	95	3.65	3.30	0.388	0.334	0.143***
Taiwan	West	TW	20	136	5.23	5.06	0.615	0.563	0.087***
	East	TE	20	138	5.31	5.09	0.613	0.579	0.057*
Philippines	Luzon and Mindoro	PH	30	140	5.38	4.75	0.584	0.522	0.107***
Indonesia	Kambing Katjang Bali	IB	25	113	4.35	3.82	0.407	0.368	0.099***
	Kambing Katjang Java	IJ	30	125	4.81	4.26	0.502	0.419	0.168***
	Etawa	IE	25	139	5.35	4.89	0.598	0.553	0.077***
Bangladesh	Black Bengal	BB	30	165	6.35	5.52	0.601	0.578	0.039*
	Indian breed	BI	20	180	6.92	6.41	0.673	0.642	0.047*
Mongolia	Zavkhan Buural	MZ	25	182	7.00	6.39	0.698	0.664	0.050**
	Zalaajinst White	MW	25	184	7.08	6.44	0.695	0.660	0.051**
	Erchim Black	ME	24	195	7.50	6.77	0.715	0.697	0.026
	Ulgii Red	MU	24	190	7.31	6.61	0.687	0.681	0.009
	Bayandelger	MB	23	177	6.81	6.32	0.688	0.661	0.039*
	Dorgon	MD	24	197	7.58	6.89	0.715	0.707	0.012
	Sumber	MS	25	164	6.31	5.81	0.690	0.673	0.025

TNA, total number of alleles/population; MNA, mean number of alleles/locus; AR, allelic richness; H_E, heterozygosity estimates; H_O, heterozygosity observed; MS, microsatellite.
*$P < 0.05$;
**$P < 0.01$;
***$P < 0.001$.

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Table 2 Number of alleles, range of allele size and results of *F*-statistics for each 26 loci across the 18 goat populations.

Locus	Chromosome[1]	Number of allele	Allele size	F_{IS}	F_{IT}	F_{ST}
BM3205	1	17	206–248	0.090***	0.178***	0.097***
TCRVB6	1	15	222–254	0.038	0.134***	0.099***
INRA040	2	19	210–290	0.066**	0.238***	0.185***
OarFCB20	2	13	78–116	0.149***	0.283***	0.158***
ILSTS029	3	11	146–176	0.005	0.109***	0.104***
MAF70	4	13	131–157	0.080**	0.201***	0.132***
ETH-10	5	6	201–215	0.131**	0.236***	0.120***
BM143	6	13	90–118	0.056	0.169***	0.120***
INRABERN192	7	10	171–195	0.083**	0.214***	0.139***
MCM527	7	11	150–170	0.017	0.166***	0.152***
ILSTS005	10	6	172–184	0.018	0.127***	0.111***
CSSM030	13	5	156–168	0.016	0.154***	0.141***
BM2934	14	14	78–116	0.070**	0.208***	0.149***
MAF065	15	16	108–152	0.035	0.188***	0.158***
HUJ614	16	10	149–181	−0.007	0.165***	0.171***
MAF209	17	4	89–101	0.059	0.419***	0.382***
INRABERN185	18	12	162–286	0.020	0.063**	0.044***
HAUT14	18	11	139–171	0.035	0.095***	0.062***
BM1818	23	14	244–272	0.035	0.158***	0.128***
P19(DYA)	23	14	172–204	0.066**	0.167***	0.109***
INRABERN172	26	12	231–257	0.051	0.215***	0.172***
CSSM043	27	11	226–256	0.051*	0.142***	0.097***
RM044	29	16	79–109	0.073***	0.202***	0.139***
SR-CRSP8	Unknown	13	211–241	0.017	0.141***	0.126***
OarCP34	Unknown	13	104–128	0.052*	0.161***	0.115***
SR-CRSP26	Unknown	12	121–147	0.063**	0.184***	0.129***
	All	311		0.054***	0.181***	0.134***

[1]From Vaiman *et al.* 1996 and GOATMAP DATABASE http://locus.jouy.inra.fr/cgi-bin/lgbc/mapping/common/intro2.pl?BASE=goat.
*$P < 0.05$,
**$P < 0.01$,
***$P < 0.001$.

Analyser (Applied Biosystems), and allele sizes relative to an internal size standard (GS400HD) were determined using GENEMAPPER™ 3.5 (Applied Biosystems).

Statistical analyses

Allele frequencies, mean number of alleles (MNA), and observed (H_O) and expected (H_E) heterozygosities were calculated for each population using the Microsatellite Toolkit (Park 2001). Allelic richness (AR) per population (i.e. the corrected mean allele number reflected in the standardised sample size) was calculated using FSTAT 2.9.3 (Goudet 2001). Wright's *F*-statistics [within-population inbreeding (F_{IS}), total inbreeding (F_{IT}) and among-population genetic differentiation (F_{ST})] for each locus and overall population and pairwise F_{ST} values were obtained from FSTAT using the variance-based method of Weir & Cockerham (1984). The significance values for pairwise F_{ST} were adjusted using the Bonferroni correction method. Deviation from the Hardy–Weinberg equilibrium (HWE) was determined using Fisher's exact test in GENEPOP version 4.0 (Rousset 2008). Unbiased estimates of exact *P*-values were obtained using the Markov Chain Monte Carlo (MCMC) algorithm (Guo & Thompson 1992). The linkage disequilibrium between each pair of loci was tested with GENEPOP. A neutrality test was performed to detect the selective pressure on a locus and exclude those loci under selective pressure using POPGENE 1.31 (Yeh *et al.* 1999).

Genetic relationships among individuals and populations were estimated by constructing neighbour-joining (NJ) trees using the shared allele distance (D_{AS}) between individuals (Jin & Chakraborty 1994) and pairwise D_A distances (Nei *et al.* 1983), with 1000 bootstraps being implemented in POPULATIONS 1.2.30 (Langella 1999). The generated trees were visualised using NJPLOT and UNROOTED (Perrière & Gouy 1996).

The population structure and degree of admixture were inferred using Bayesian model-based clustering of multilocus genotypes to obtain the number of parental populations (*K*) for a given sample with STRUCTURE 2.3.1 (Pritchard *et al.* 2000). The admixture proportions of individual samples were estimated and assigned a *K* value. To obtain a representative value of *K* for data modelling, we performed 20 independent runs for each value from 1 to 23 with burn-in and MCMC iterations of 30 000 and 50 000 each with default settings and an admixture model, followed by ΔK statistics (Evanno *et al.* 2005). The results of independent runs were aligned using CLUMPP version 1.1.2 (Jakobsson & Rosenberg 2007) and visualised using DISTRUCT version 1.1 (Rosenberg 2004).

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Results

Genetic diversity

The 26 markers listed in Table 2 amplified 311 alleles that ranged from four alleles at MS *MAF209* to 19 alleles at *INRA040*, with an average of 12 alleles per locus. The genetic variability quantified as MNA, AR, H_E and H_O for each goat population is presented in Table 1. The lowest MNA was 2.54 in the Japanese Shiba population, and the highest was 7.58 in the Mongolian Dorgon. AR based on 16 individuals per population ranged from 2.30 in Shiba to 6.89 in Dorgon. The estimated H_E per population ranged from 0.302 in Shiba to 0.715 in Erchim Black and Dorgon. H_O ranged from 0.312 in Shiba to 0.707 in Dorgon. H_E was comparatively high in the Mongolian and Indian populations. Relatively low genetic variability ($H_E < 0.6$) was observed in populations from Indonesia, the Philippines, and Korea. The Indonesian Etawa, a crossbreed between native Kambing Katjang and exotic Indian Jamnapari (Porter 1996), showed higher genetic variation than the original native populations. H_O was lower than H_E in all the populations studied, except Shiba. Deviation from HWE was statistically significant ($P < 0.05$) for 53 out of 468 locus–population combinations (Table S1). Ten populations (Korean east, Taiwan west, Philippines, Indonesian Bali, Java, Etawa, Bangladeshi Black Bengal, Mongolian Zavkhan Buural, Zalaajinst White and Bayandelger) showed significant deviations from HWE ($P < 0.05$).

Genetic differentiation and relationships among populations

The mean estimates of *F*-statistics obtained by jack-knifing over 26 loci are as follows: $F_{IS} = 0.054 \pm 0.007$, $F_{IT} = 0.181 \pm 0.009$ and $F_{ST} = 0.134 \pm 0.007$ (Table 2). The overall F_{IS} value was low, but highly significant ($P < 0.001$). This was most likely due to non-random mating within populations. Twelve loci significantly ($P < 0.05$) contributed to the F_{IS} estimate, and all loci influenced F_{IT} ($P < 0.01$). F_{IS} for the populations showed a significant deficit of heterozygotes in 12 populations, ranging from 0.039 in Mongolian Bayandelgel to 0.168 in Indonesian Java (Table 1). As shown in Table 1, the lowest genetic variation was observed in Shiba goats, possibly because of their small population size in Japan. Currently, Shiba goats are used as laboratory animals only at a few research stations in Japan. For F_{IS}, one to seven loci contributed significantly to heterozygous deficiency in all the populations (Table S1). On the other hand, one to two loci showed significant excess of heterozygotes in some goat populations.

All pairwise F_{ST} values were significantly different, with the exception of pairs between some Mongolian populations ($P > 0.05$) (Table 3). The pairwise F_{ST} values were comparatively low for within-country populations, except those for Indonesian Etawa. Although geographical distances between goat populations are greater in Mongolia than in other countries, the F_{ST} values in Mongolian populations were notably lower than those of other countries. As reported previously, this result may indicate a high level of gene flow among Mongolian populations (Takahashi *et al.* 2008). In between-country relationships, the F_{ST} values between Indian and Mongolian populations were low, ranging from 0.067 to 0.081 (Table 3).

An NJ tree based on D_A was used to portray the degree of genetic relationships among goat populations (Fig. 1). The tree divided Asian goats into three clusters: Southeast Asia, East Asia and Mongolia. The East Asian cluster was divided into sub-clusters of Japan–Korea and Taiwan. As indicated in Fig. S1, the NJ tree based on D_{AS} showed that, with few exceptions, each individual animal was clustered to its population of origin.

Graphical displays of the results from the STRUCTURE analysis are presented in Fig. 2. The STRUCTURE analysis did not clearly return genetic clusters with maximum likelihood (ln Pr $[G|K]$) and reached a plateau beyond $K = 7$. The ΔK values obtained were 16.8 at $K = 2$, 328.8 at $K = 3$, 2.4 at $K = 4$, 23.5 at $K = 5$, 1.8 at $K = 6$ and 1.8 at $K = 7$. At $K = 2$, there was a transition from the North Asian population (yellow) to the South Asian population (blue) (Fig. 2). At $K = 3$, the ΔK value reached a maximum and the East Asian cluster (red) was separated. At $K = 3$, the Japan (red), Indonesia–Philippine (blue) and Mongolia (yellow) populations showed three distinct clusters, whereas the Taiwanese and Bangladeshi populations showed an admixture pattern with a Mongolian cluster, which showed low-level population differentiation. At $K = 5$, no admixture clusters were observed for within-country populations; the five clusters were Japanese–Korea, Taiwan, Philippine–Indonesia, Bangladesh–India and Mongolia. Generally, the clustering pattern observed in the STRUCTURE analysis was similar to the classification of the NJ tree based on D_A.

Discussion

In this study, we estimated the genetic diversification of the extensive Asian indigenous goat populations using MS DNA markers. Our data showed that the genetic variation estimated by MNA and AR in within-country populations of Asian goats was lower than that of European breeds, which was 5.2–9.1 MNAs, with an average of 7.1 and 6.1–7.9 AR values (Cañón *et al.* 2006). Genetic variation was comparatively high in Asian inland populations (Mongolian and Indian goats) and low in populations that ranged from Southeast Asian islands and the southeastern or eastern edge of the continent (Black Bengal in Bangladesh, Kambing Katjang in Indonesia and Philippine and Korean goats).

Table 3 Pairwise F_{ST} values (upper diagonal) and D_A genetic distances (lower diagonal) between 18 goat populations.

Population	JS	KW	KE	TW	TE	PH	IB	IJ	IE	BB	BI	MZ	MW	ME	MU	MB	MD	MS
Japan																		
JS		0.263	0.339	0.251	0.293	0.331	0.439	0.372	0.305	0.304	0.272	0.261	0.260	0.276	0.277	0.285	0.279	0.298
Korea																		
KW	0.232		0.060	0.122	0.142	0.152	0.261	0.226	0.140	0.162	0.141	0.104	0.102	0.111	0.126	0.124	0.107	0.119
KE	0.255	0.091		0.205	0.229	0.222	0.343	0.308	0.224	0.244	0.230	0.190	0.186	0.200	0.212	0.219	0.196	0.208
Taiwan																		
TW	0.264	0.160	0.225		0.046	0.131	0.230	0.171	0.124	0.108	0.091	0.096	0.084	0.091	0.098	0.109	0.098	0.092
TE	0.289	0.180	0.253	0.079		0.154	0.262	0.201	0.153	0.119	0.123	0.108	0.103	0.097	0.114	0.120	0.106	0.104
Philippin																		
PH	0.321	0.204	0.236	0.199	0.214		0.143	0.103	0.113	0.121	0.131	0.132	0.133	0.121	0.145	0.152	0.124	0.125
Indonesia																		
IB	0.370	0.270	0.297	0.265	0.298	0.171		0.096	0.170	0.192	0.223	0.237	0.254	0.240	0.261	0.258	0.243	0.225
IJ	0.331	0.259	0.304	0.221	0.265	0.139	0.110		0.121	0.137	0.171	0.187	0.183	0.186	0.197	0.201	0.185	0.177
IE	0.305	0.196	0.247	0.202	0.236	0.150	0.175	0.142		0.101	0.074	0.106	0.117	0.111	0.124	0.119	0.120	0.103
Bangladesh																		
BB	0.321	0.236	0.290	0.211	0.213	0.144	0.205	0.168	0.137		0.080	0.097	0.104	0.086	0.102	0.106	0.095	0.105
BI	0.325	0.208	0.274	0.179	0.210	0.165	0.247	0.210	0.112	0.125		0.068	0.081	0.067	0.075	0.080	0.073	0.080
Mongolia																		
MZ	0.305	0.170	0.242	0.176	0.182	0.190	0.292	0.252	0.174	0.175	0.130		0.037	0.029^{NS}	0.025^{NS}	0.037	0.030	0.042
MW	0.316	0.177	0.236	0.172	0.187	0.188	0.315	0.250	0.183	0.178	0.138	0.088		0.035	0.034	0.047	0.037	0.046
ME	0.323	0.181	0.251	0.171	0.177	0.174	0.288	0.246	0.164	0.154	0.118	0.075	0.090		0.028^{NS}	0.040	0.027^{NS}	0.041
MU	0.331	0.190	0.270	0.174	0.203	0.211	0.327	0.267	0.192	0.185	0.138	0.072	0.087	0.080		0.034^{NS}	0.036	0.048
MB	0.339	0.193	0.276	0.186	0.209	0.218	0.319	0.264	0.183	0.188	0.138	0.086	0.097	0.097	0.073		0.043	0.061
MD	0.335	0.175	0.256	0.191	0.194	0.188	0.311	0.269	0.193	0.169	0.134	0.081	0.092	0.076	0.097	0.099		0.052
MS	0.348	0.179	0.247	0.171	0.177	0.168	0.272	0.234	0.171	0.179	0.143	0.102	0.111	0.099	0.120	0.118	0.116	

The population abbreviations are shown in Table 1.
MS, microsatellite; NS, all *P*-values applied to pairwise F_{ST} were significant at $P < 0.05$ except those with NS for non-significant.

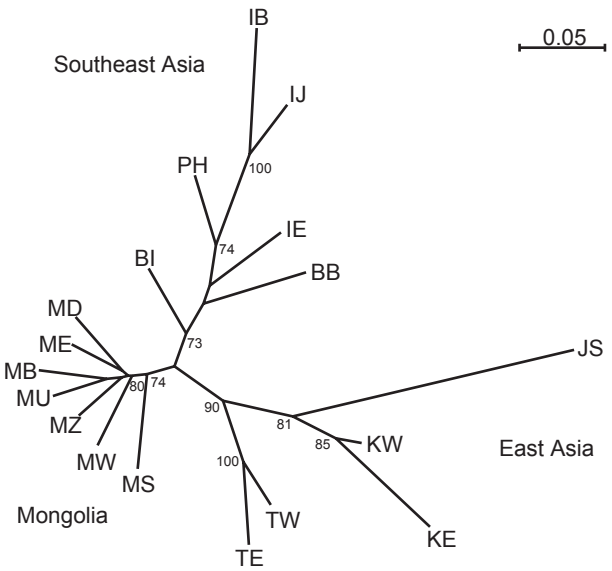

Figure 1 Neighbour-joining (NJ) tree of 18 goat populations from seven Asian countries, based on Nei's genetic distance (D_A). The population abbreviations are shown in Table 1. The numbers on the nodes indicate the bootstrap values (%) obtained from 1000 replications.

The average F_{ST} of the breeds studied was 0.13, higher than that of the European breeds, which had a mean value of 0.07 (Cañón *et al.* 2006). The Indonesian Kambing Katjang and Japanese populations showed higher pairwise F_{ST} values than the mean, suggesting that the two populations showed higher genetic differentiation than other populations. The islands of Indonesia and Japan are located farthest from the goat domestication centre of West Asia, and it is most likely a reason for their high genetic differentiation.

A subdivision of the Asian goat populations containing at least three clusters was observed commonly in the NJ tree based on D_A and STRUCTURE model-based clustering of Southeast Asian, East Asian and Mongolian clusters. The populations that were assigned admixture clusters in STRUCTURE clustering at $K = 3$ were the Taiwanese and Bangladeshi populations. When assigned to their specific clusters at $K = 5$, these two populations showed low-level population differentiation based on D_A and F_{ST} values. Nozawa (1991) classified goats around the world into three categories or types based mainly on morphology and history of domestic goat migration: Bezoar, Savannah and Nubian types. The Bezoar type is the most general or unspecialized type, with erect ears and a straight and unraised nose bridge, the Savannah type with twisted horns is adapted to dry environments, and the Nubian type is the milk goat with drooping ears and an accipitrine nose. According to Devendra & Nozawa (1976), dispersion of these three types across Asia from the domestication centre occurred chronologically in the above order through two main routes. First, the Bezoar-type, and second, the Savannah-type goats migrated via the Silk Road. Finally, the Nubian-type goat, which had descended from the Savannah type, migrated through the Khybar Pass to the Indian subcontinent (Devendra & Nozawa 1976).

Comparison of the classifications of the MS markers used in this study showed that the East Asian cluster corresponded morphologically to the Bezoar type and the Mongolian cluster corresponded to the Savannah type. The STRUCTURE clustering results showed that some Indian and Taiwanese contained the same portion of the Mongolian cluster. Taiwanese goats are the direct descendants of the goats indigenous to southern China, Guangdong and Fujian, which were introduced by immigrants in the seventeenth century (Porter 1996). Therefore, it is believed that the Savannah type reached Mongolia with a genetic influence from the Indian subcontinent and China. The Indian population analysed in this paper corresponded morphologically to the Nubian type and was categorized as in the same cluster as the Black Bengal and Kambing Katjang, the Southeast Asian dwarf goats, with a 73% bootstrap value by an NJ tree on genetic distance (D_A). The Philippines was the northernmost country for distribution of the Southeast clustered goats, and genetically different goats were found in the neighbouring island of Taiwan.

The results of MS DNA markers in genetic subdivisions of East Asian indigenous goats were consistent with the migration history of goats and also with morphological and geographical classifications. This study provides valuable information on the genetic structure of Asian indigenous goats for future genetic improvement and conservation programmes in each country. Appropriate goat-breeding programmes are required to maintain the genetic uniqueness of each population and to minimize inbreeding as well as unnecessary gene flow among populations.

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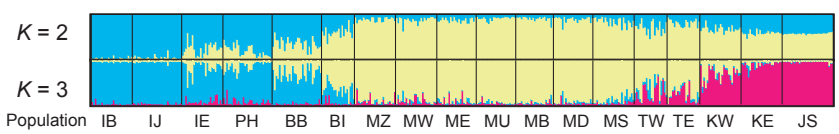

Figure 2 Model-based clustering of 18 Asian goat populations assuming $K = 2$ and 3. The population abbreviations are shown in Table 1. K is the number of assumed clusters. Individuals are represented by a vertical bar divided into estimated proportions of K colours.

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Supporting information

Additional supporting information may be found in the online version of this article.

Figure S1 Unrooted NJ tree of individual goats constructed by D_{AS}. The tree shows that each individual clustered to its population of origin, with the exception of the Mongolian population. The seven Mongolian indigenous populations formed one Mongolian cluster.

Table S1 F_{IS} for each locus in 18 Asian goat populations.

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