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Genetic Relationships among Australian and Mongolian Fleece-bearing Goats

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ABSTRACT : Microsatellites (MS) are useful for quantifying genetic variation within and between populations and for describing the evolutionary relationships of closely related populations. The main objectives of this work were to estimate genetic parameters, measure genetic distances and reconstruct phylogenetic relationships between Australian Angora/Angora_Aus/ and Cashmere/Cashmere_Aus/ populations and three Mongolian Cashmere goat (Bayandelger/BD/, Zavkhan Buural/ZB/, and Gobi Gurvan Saikhan/GGS/) populations based on variation at fourteen MS loci. The level and pattern of observed and expected heterozygosity and polymorphic information content of the fourteen loci studied across the populations were quite similar and high. Except for *SRCRSP07*, all studied microsatellites were in Hardy-Weinberg Equilibrium ($p<0.001$). Moderate genetic variation (7.5%) was found between the five goat populations with 92.5% of total genetic variation attributable to diversity existing between the individuals within each population. The greatest Nei's genetic distances were found between the Angora and four Cashmere populations (0.201-0.276) and the lowest distances were between the Mongolian Cashmere goat populations (0.026-0.031). Compared with other Cashmere goat populations, the GGS (crossbred with Russian Don Goats) population had the smallest pairwise genetic distance from the Australian Angora population (0.192). According to a three-factorial correspondence analysis (CA), the three different Mongolian Cashmere populations could hardly be distinguished from each other. (**Key Words** : Population, Microsatellite Marker (MS), Hardy-Weinberg Equilibrium (HWE), Genetic Variation, Phylogenetic Relationships)

INTRODUCTION

The availability of thousands of molecular markers allows us to characterize the genetic structure of groups of individuals or populations. In particular, microsatellites (MS) are broadly used to describe the evolutionary relationships of closely related populations because of their highly polymorphic nature. The patterns and extent of genetic variation observed within and between populations could provide useful information concerning the genetic affinities and phylogenetic inference of domesticated animals. It is well known that evolutionary forces such as mutations, recombination, selection, genetic drift and gene flow influence and shape the genetic variation observed within and between populations.

A phylogeographic study based on mtDNA reported that the genetic differences among goat breeds sampled from Europe, Africa and Asia were small compared to the differences observed between cattle breeds (Luikart et al., 2001). Several studies on genetic structure and variation between different goat populations based on MS markers have been published, finding small to moderate genetic differentiation among goat populations (Barker et al., 2001; de Araújo et al., 2006). The relatively low level of genetic differentiation between goat populations could be related to extensive transportation of these animals in the past. The aims of this study were to estimate population genetic parameters such as allele frequency, heterozygosities, and polymorphic information content (*PIC*), deviations from Hardy-Weinberg equilibrium (HWE), genetic distances and F_{ST} statistic for five goat populations from Mongolia and Australia and to infer genetic variation within and between goat populations using these genetic parameters.

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MATERIALS AND METHODS

Resource populations

This study included genotype information from Australian Angora and Cashmere goats and three Mongolian Cashmere goat populations (Bayandelger, Zavkhan Buural, and Gobi Gurvan Saikhan). Australian

Table 1. Cycling parameters for PCR amplification

Step	Purpose	Temperature (°C)	I**		II**	
			Duration	Cycle No.	Duration	Cycle No.
1	Activation of enzyme	94	2.55 minutes	1	2 minutes	1
2	Denaturation	95	05 seconds	35	45 seconds	30
	Annealing	55-63*	30 seconds	35	45 seconds	30
	Elongation	72	30 seconds	35	60 seconds	30
3	Final extension	72	2.30 minutes	1	7 minutes	1
	Total period		1.27 h		1.57 h	

* Different annealing temperatures were used for different primer pairs.

** I duration and number of cycles was used for *LSCV44*, *INRABERN172*, *INRABERN185*, *INRA063*, *ILSTS029*, *ILSTS11*, *SRCRSP05*, *SRCRSP07*, *OarCP020*, and *TGLA53* primers and II duration and number of cycles was used for *RM096*, *OarCP73*, *BM1258* and *BM1818* primers.

Angora and Cashmere goats were drawn from separate commercial herds of each breed. The Angora herd initially comprised 250-300 does of mixed Australian, Texan and South African blood which was upgraded to a minimum of 87% South African blood. Australian Cashmere goats were drawn from a single Cashmere goat herd. The herd was established in 1985 and bucks and does were sourced from a wide variety of sources over the years including Kinross, the WA group breeding scheme, Noel Waters, Bess Vickers, Fred Brown and Northumbria. Animals from three other Cashmere goat populations (Bayandelger/BD/, Zavkhan buural/ZB/, and Gobi Gurvan Saikhan/GGS/) were included in this study for phylogenetic comparison. These animals were randomly sampled from different herds in the experimental stations of the Institute of Animal Husbandry (IAH) in Ulaanbaatar and its branch in southern region of Mongolia. Around 350 goats of each BD and ZB goat strains were originally shifted from the Eastern and North-Western regions of Mongolia to the experimental station of the IAH in 1996 and 1998, respectively.

Microsatellite genotype analysis

DNA of animals of these populations was extracted from blood and ear punch samples according to the phenol/chloroform extraction protocol described by Sambrook et al. (1989). In total, fourteen microsatellite markers (Tables 2 and 3) were used in genotyping analysis from the "goat map" website: http://dga.jouy.inra.fr/cgi-bin/lgbc/carte.pl?BASE=goat&NOM=schibler_1998.

PCRs were conducted in 4 μl reagent volumes containing ~10 ng genomic DNA. Optimization of PCR conditions was carried out by changing the concentrations of $MgCl_2$ (1.5-4.5 mM) and 4dNTP's (62.5 μM, 80.0 μM and 100.0 μM). 4dNTP's in PCR reagent volumes were prepared with a 1 (dATP):10 (dGTP, dCTP and dTTP) ratio because a lower concentration of dATP helps for more efficient incorporation of ^{33}Pα-dATP. For running PCR, two different durations and numbers of thermal cycles were used for the different primers based on PCR optimization (Table 1).

Visualization of PCR products was done using gel electrophoresis and autoradiography. 5 μl of 500 fmol plasmid dsDNA template (pGEM®-3Zf(+) control DNA) was used to prepare the sequencing ladders for sizing PCR products (Promega, 2001). PCR products and the four sequencing ladders (adenine (A), cytosine (C), guanine (G), and thymine (T)) were loaded on a 6% polyacrylamide gel electrophoresis. After completion of electrophoresis, the gel was exposed to BioMax® or X-Omat K autoradiography (Kodak) film for 18-72 h depending on the activity of the ^{33}Pα-dATP used. The absolute length of the PCR product (sizes of two alleles per each animal or a sample) was determined by visual comparisons with the sequencing bands or ladders, which were observed as four lanes of sequenced nucleotide in the middle of the film.

In total, 1,118 goats representing five goat populations were screened for their genotypes at fourteen MS loci. The total number of genotypes studied was 15,652. From these, 15,614 genotypes were identified. The sample size of each population varied from 47 to 548 across populations (Tables 2 and 3).

Population genetic parameter analysis

In order to describe the genetic variation within and amongst studied goat populations, the allele frequency, observed and expected heterozygosities of each locus, and the amount of polymorphism (*PIC*) at a single locus were calculated using ARLEQUIN program (Schneider et al., 2000). Departures from the Hardy-Weinberg equilibrium were detected using the GENEPOP program (Raymond and Rousset, 1995), which implemented the modified version of the Markov-chain random walk algorithm described by Guo and Thompson (1992) and used a method analogous to Fisher's exact test. The calculation was carried out on genotypic data of all individuals of each population with Markov chain of 100 batches of 1,000 iterations. The calculation of HWE was based on allele frequencies. If a population deviated from HWE, a score test (U-test) (Rousset and Raymond, 1995) was then performed to examine whether the observation was caused by excess or

Table 2. Number of animals studied, number of observed microsatellite alleles, observed and expected heterozygosity and deviation from Hardy-Weinberg Equilibrium (HWE) on each locus for two Australian goat breeds

Locus	Chromo-some No	Australian goats												
		Angora_Aus							Cashmere_Aus					
		Individuals	Alleles	H_o	H_e	*PIC*	HWE (p value)	Allele size (bp)	Individuals	Alleles	H_o	H_e	*PIC*	HWE (p value)	Allele size (bp)
OarFCB020	2	426	7	0.564	0.580	0.537	0.428	96-108	542	6	0.730	0.743	0.699	0.105	96-108
ILSTS029	3	428	8	0.754	0.754	0.720	0.351	154-186	548	13	0.644	0.641	0.603	0.265	154-186
SRCRSP07	6	428	4	0.543	0.581	0.504	0.001*	123-129	548	5	0.428	0.455	0.405	0.106	123-135
RM096	11	428	10	0.853	0.807	0.782	0.326	100-120	544	9	0.822	0.786	0.761	0.460	100-120
LSCV44	11	428	9	0.785	0.766	0.730	0.874	112-132	547	11	0.746	0.740	0.708	0.329	112-134
ILSTS11	14	427	5	0.779	0.764	0.726	0.452	268-280	547	8	0.756	0.736	0.699	0.225	268-282
TGLA53	16	427	7	0.793	0.799	0.768	0.160	117-143	541	10	0.822	0.807	0.783	0.296	115-139
INRA063	18	428	4	0.743	0.704	0.653	0.303	164-170	548	5	0.664	0.650	0.600	0.671	164-172
INRABERN185	18	428	3	0.481	0.449	0.403	0.263	266-282	547	7	0.567	0.556	0.516	0.785	266-284
SRCRSP05	21	427	9	0.768	0.742	0.712	0.104	160-180	548	11	0.852	0.850	0.834	0.940	160-180
OarCP73	23	426	13	0.849	0.846	0.827	0.113	160-210	547	13	0.801	0.803	0.775	0.028*	158-228
BM1258	23	427	9	0.888	0.857	0.840	0.363	102-126	548	10	0.843	0.841	0.821	0.202	102-128
BM1818	23	427	9	0.819	0.792	0.758	0.215	250-266	544	8	0.673	0.663	0.636	0.644	250-266
INRABERN172	26	428	8	0.785	0.754	0.711	0.417	232-252	548	7	0.684	0.666	0.610	0.315	232-246
MNA			7.50	0.743	0.728	0.691				8.79	0.717	0.710	0.710		
Total genotypes					5.983							7.647			

* Significant deviations from HWE ($p<0.05$); MNA = Mean number of alleles; H_o = Observed heterozygosity; H_e = Expected heterozygosity; *PIC* = Polymorphic information content.

Table 3. Number of observed microsatellite alleles, observed and expected heterozygosity and deviation from Hardy-Weinberg equilibrium on each locus for three Mongolian goat populations

Locus	Mongolian goat populations																
	GGS (47*)						ZB (47*)						BD (48*)				
	Alleles	H_o	H_e	*PIC*	HWE (p value)	Allele size (bp)	Alleles	H_o	H_e	*PIC*	HWE (p value)	Allele size (bp)	Alleles	H_o	H_e	*PIC*	HWE (p value)	Allele size (bp)
OarFCB020	9	0.702	0.730	0.687	0.762	82-110	7	0.660	0.759	0.717	0.157	96-124	6	0.723	0.740	0.686	0.634	96-124
ILSTS029	9	0.617	0.678	0.644	0.200	154-186	10	0.553	0.608	0.579	0.099	154-182	7	0.563	0.487	0.451	0.977	154-182
SRCRSP07	5	0.596	0.492	0.453	0.526	119-129	6	0.511	0.499	0.454	0.402	123-133	5	0.563	0.535	0.494	0.278	119-129
RM096	12	0.745	0.810	0.778	0.395	100-122	10	0.702	0.784	0.751	0.353	100-124	9	0.875	0.800	0.764	0.797	98-126
LSCV44	11	0.957	0.847	0.819	0.893	112-134	12	0.936	0.892	0.872	0.505	112-134	9	0.938	0.821	0.790	0.609	112-130
ILSTS11	9	0.702	0.741	0.701	0.538	260-282	9	0.809	0.757	0.709	0.057	262-284	9	0.750	0.741	0.687	0.986	260-282
TGLA53	11	0.723	0.700	0.666	0.687	117-141	7	0.617	0.713	0.673	0.274	117-131	9	0.813	0.797	0.763	0.749	117-139
INRA063	5	0.739	0.714	0.652	0.827	164-172	5	0.766	0.712	0.655	0.111	164-172	5	0.702	0.672	0.628	0.738	164-172
INRABERN185	5	0.340	0.353	0.332	0.630	256-282	6	0.426	0.412	0.383	0.102	266-282	5	0.479	0.439	0.399	0.626	256-282
SRCRSP05	11	0.894	0.855	0.830	0.865	160-182	10	0.702	0.736	0.708	0.481	158-180	11	0.688	0.754	0.715	0.881	158-180
OarCP73	21	0.872	0.904	0.886	0.101	154-210	18	0.851	0.921	0.905	0.048**	154-216	17	0.854	0.902	0.885	0.121	154-242
BM1258	8	0.915	0.826	0.794	0.535	102-130	12	0.936	0.869	0.845	0.170	102-136	11	0.813	0.866	0.841	0.711	102-128
BM1818	11	0.891	0.863	0.838	0.034**	250-270	9	0.830	0.805	0.777	0.344	252-268	10	0.750	0.790	0.756	0.263	250-270
INRABERN172	7	0.723	0.760	0.713	0.345	236-250	6	0.660	0.704	0.650	0.612	236-246	7	0.813	0.782	0.743	0.687	236-252
MNA	9.57	0.744	0.734	0.699			9.07	0.711	0.727	0.691			8.57	0.737	0.723	0.686		
Total genotypes				656						658						670		

* Number of individuals.

** Significant deviations from HWE ($p<0.05$); MNA = Mean number of alleles; H_o = Observed heterozygosity; H_e = Expected heterozygosity; *PIC* = Polymorphic information content.

deficit of heterozygote individuals. *F* coefficients (F_{IS} and F_{ST}) were used to estimate the amount of genetic variation within and between the five goat populations, respectively. Estimates of *F* coefficients, their standard deviation and confidence intervals were calculated using the GENEPOP. Genetic distances (Nei, 1978) between populations and their standard errors were measured using the DISPAN program (Ota, 1993). Allele frequencies were used to generate the genetic distance matrix for each pair of populations. A matrix of these genetic distances is used to construct neighbor-joining phylogeny for these five populations. Neighbour-Joining (NJ) tree was constructed using the MEGA program (Kumar et al., 1993-2005). Using the DISPAN, the reliability of the NJ tree obtained was examined by a bootstrap test with 1000 replicate resamplings of loci with replacement (Efron, 1982; Felsenstein, 1985).

RESULTS

Genetic variation within populations

The total number of detectable alleles in the fourteen studied loci was 105 and 123 for Australian Angora and Cashmere goats, whereas it was 137, 127, and 120 for Mongolian GGS, ZB and BD populations, respectively (Tables 2 and 3). Australian Angora goats thus had the lowest number of alleles, averaging 7.50 per locus (mean number of alleles, MNA). In the studied Cashmere populations, MNA ranged from 8.57 to 9.57. This shows that the Angora population is less diverse than the Cashmere populations.

Population-specific alleles (private alleles) were observed among all studied populations but their

Table 4. Sizes of the private alleles (bp) with the corresponding allele frequencies

Marker	Angora_Aus	Cashmere_Aus	GGS_Mon	ZB_Mon	BD_Mon
RM096					126:0.042
ILSTS11				262:0.021	
TGLA53		115:0.119			133:0.031
INRABERN185		284:0.077			
OarCP73			188:0.021	212:0.021	242:0.042
BM1258	120:0.186		130:0.021		
INRABERN172				248:0.042	

Numbers before colon indicates the allele size (in base pairs), whereas numbers after colon represents the frequency of the particular allele.

frequencies within populations never exceeded 19% (Table 4). Such private alleles were found at eleven loci. The number of private alleles was higher in all four Cashmere populations (2-3 alleles) than in the Angora_Aus population (1 allele). Interestingly, the Angora population contains a private allele (120 at locus *BM1258*) with a high frequency (18.6%). Also, allele 115 at locus *TGLA53* with 11.9% frequency was specific to the Cashmere_Aus population (Table 4). The remaining private alleles across the populations had low frequencies.

Deviations from HWE at the studied loci were tested for all five populations (Tables 2 and 3). Out of a total seventy tests, only four cases showed statistically significant deviations from HWE ($p<0.05$). One of these four significant deviations was found in locus *BM1818* in the GGS population and two were observed in locus *OarCP73* in the Cashmere_Aus and ZB populations. The remaining one was found in locus *SRCRSP07*.

All five studied goat populations displayed a quite similar and high mean observed heterozygosity (H_o), ranging from 0.711 for the ZB population to 0.744 for GGS (Tables 2 and 3). Compared with H_o, the mean estimated gene diversity (H_e) the studied loci was slightly lower and it ranged from 0.710 for the Cashmere_Aus population to 0.734 for the GGS population. Regarding either heterozygote deficiency or heterozygote excess (Rousset and Raymond, 1995) the *f*-statistic was used to test for statistically significant differences between the observed and the expected frequencies of heterozygotes. As shown in Table 5, five negative f values (locus *SRCRSP07* in GGS, *RM096* in both Australian populations, *LSCV44* in BD and *BM1258* in Angora_Aus populations) indicated significant excess of heterozygotes ($p<0.01$) or higher level of heterozygosity than that expected from HWE. A significant deficit of heterozygotes ($p<0.01$) was observed at loci *OarFCB20* in Cashmere_Aus, *SRCRSP07* in Angora_Aus, and *OarCP73* and *BM1818* in BD populations (significant positive f values as shown in Table 5).

The overall pattern of *PIC* values concords with values of heterozygosity (Tables 2 and 3). *PIC* values were high for all studied loci except for the loci that showed low values of either H_e or H_o. The range of the mean *PIC* across all loci was between 0.686 for the BD population and 0.710 for the Cashmere_Aus population.

Genetic variation between populations

Genetic differentiation of the studied populations (Table 6) was investigated by comparing mean values of the F_{ST} statistic using Weir and Cockerham's methodology (Weir and Cockerham, 1984). The results of F_{ST} statistic analysis

Table 5. Inbreeding coefficients (F_{IS}) in the studied goat populations for 14 microsatellite loci

Locus	Population									
	Angora_Aus		Cashmere_Aus		GGS_Mon		ZB_Mon		BD_Mon	
	Indiv.	f	Indiv.	f	Indiv.	f	Indiv.	f	Indiv.	f
OarFCB020	426	0.029	542	0.017**	47	0.038	47	0.132	47	0.022
ILSTS029	428	0.000	548	0.006	47	0.091	47	0.091	48	-0.157
SRCRSP07	428	0.133**"	548	0.061	47	-0.213*	47	-0.024	48	-0.052
RM096	428	-0.057*	546	-0.044*	47	0.082	47	0.105	48	-0.095
LSCV44	428	-0.024	547	-0.007	47	-0.132	47	-0.050	48	-0.143*
ILSTS11	427	-0.021	547	-0.027	47	0.053	47	-0.069	48	-0.012
TGLA53	427	0.007	541	-0.019	47	-0.034	47	0.135	48	-0.020
INRA063	428	-0.056	548	-0.022	46	-0.036	47	-0.076	47	-0.045
INRABERN185	428	-0.071	547	-0.019	47	0.037	47	-0.033	48	-0.092
SRCRSP05	427	-0.035	548	-0.002	47	-0.045	47	0.047	48	0.088
OarCP73	426	-0.004	547	0.003	47	0.036	47	0.077	48	0.054**
BM1258	427	-0.036*	548	-0.003	47	-0.109	47	-0.078	48	0.062
BM1818	427	-0.035	544	-0.016	46	-0.034	47	-0.031	48	0.052**
INRABERN172	428	-0.041	548	-0.028	47	0.049	47	0.064	48	-0.040

* Significant excess (-) of heterozygotes ($p<0.01$); ** Significant deficiency (+) of heterozygotes ($p<0.01$); Indiv. = Number of individual animals.

Table 6. Population differentiation coefficients (F_{ST}) for all pairwise combinations of Australian and Mongolian goat populations

	Cashmere_Aus	GGS_Mon	ZB_Mon	BD_Mon
Angora_Aus	0.087	0.061	0.081	0.064
Cashmere_Aus		0.048	0.053	0.044
GGS_Mon			0.011	0.012
ZB_Mon				0.009

Table 7. Coefficient of gene differentiation (F_{ST}) for the fourteen microsatellite loci applied in the studied goat populations

Markers	Total number of alleles	F_{ST} in all Mongolian Cashmere goat populations	F_{ST} in all Cashmere goat populations studied	F_{ST} in all Cashmere and Angora goat populations
OarFCB020	10	0.003	0.036	0.075
ILSTS029	14	0.013	0.049	0.054
SRCRSP07	8	0.003	0.028	0.052
RM096	15	0.000	0.044	0.093
LSCV44	12	0.015	0.074	0.114
ILSTS11	11	0.017	0.051	0.035
TGLA53	14	0.005	0.023	0.060
INRA063	5	0.015	0.012	0.011
INRABERN185	9	0.001	0.043	0.060
SRCRSP05	13	0.023	0.067	0.070
OarCP73	27	0.010	0.046	0.099
BM1258	15	0.009	0.041	0.052
BM1818	11	0.020	0.055	0.158
INRABERN172	10	0.007	0.050	0.083
All loci	174	0.011	0.045	0.075
Standard deviation		0.002	0.004	0.011
Confidence interval		0.0073-0.0148	0.0371-0.0532	0.0552-0.0950

show greater differentiation of the Angora goat from the four Cashmere goat populations than between any of the Cashmere populations. This indicates genetic distinction of the Angora goat population. The lowest F_{ST} values were found between Mongolian Cashmere goat populations. Australian Cashmere goats displayed a greater genetic differentiation from Angora goats (0.087) than Mongolian Cashmere goats (0.061-0.081). Another way to assess genetic differentiation using F_{ST} statistics is grouping the studied populations according to their known origins (Table 7). The average F_{ST} for grouping of all five populations across all loci was 0.075, indicating a moderate level of genetic differentiation between the five populations. This means that 7.5% of total genetic variation can be explained by the difference between the five populations. In other words, only 7.5% of the total number of shared alleles has been lost since the populations separated. The grouping of three Mongolian Cashmere goat populations displayed the lowest mean F_{ST} values (0.011), reflecting a high degree of genetic similarity among them. After adding the Cashmere_Aus population to the Mongolian Cashmere group, the differences between all four Cashmere goat populations accounted for 4.4% of the total genetic variation.

The standard genetic distance measure (Nei, 1978) revealed reliable genetic relationships between the five populations (Table 8). The greatest distances were observed between the Angora and four Cashmere populations (0.201-0.276); the shortest distances were between the Mongolian Cashmere goat populations (0.026-0.031). Compared with other Cashmere goat populations, the GGS (crossbred) population had the smallest pairwise genetic distance with Angora population (0.192). The comparisons between Australian Cashmere and Mongolian Cashmere goat populations indicated that ZB population displayed the highest pairwise distance with Australian Cashmere goats (0.150). As expected, the pairwise genetic distance between two Mongolian goat breed, ZB and BD, was the shortest

Table 8. Pairwise genetic distance (Nei, 1978) among the studied goat populations

	Angora_Aus	Cashmere_Aus	GGS_Mon	ZB_Mon	BD_Mon
Angora_Aus		0.080	0.050	0.064	0.044
Cashmere_Aus	0.276		0.032	0.038	0.029
GGS_Mon	0.192	0.136		0.012	0.010
ZB_Mon	0.270	0.150	0.030		0.009
BD_Mon	0.201	0.122	0.031	0.026	

Genetic distances (below diagonal) and standard errors (above diagonal).

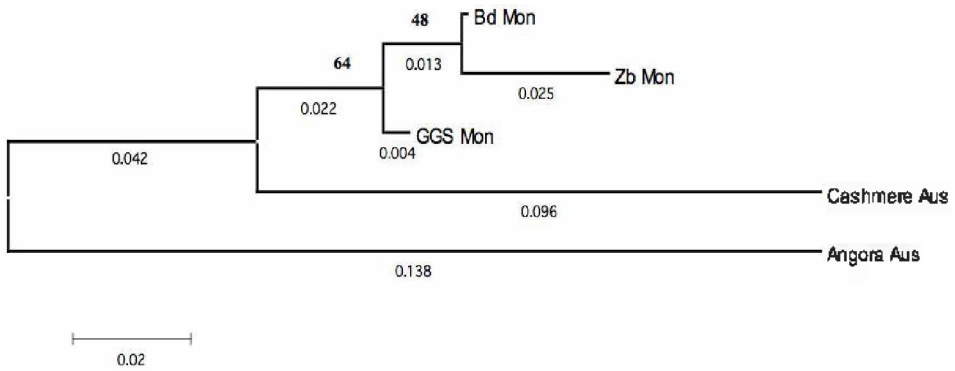

Figure 1. Neighbour-Joining dendogram showing the genetic relationship among the studied goat populations. The bold numbers represent the bootstrap values (% of 1,000 trees) whereas the numbers below each branch indicate the branch length in units of genetic distance.

-0.026 (Table 8). The standard errors of genetic distances between the studied populations were rather small.

Figure 1 shows a neighbour-joining tree illustrating that two native Mongolian populations are clustered in the same branch, which is closely related to the crossbred population (GGS), and then to the Australian Cashmere population. The Angora forms a branch alone, which was distinct from the four Cashmere populations. Separation between Angora and Cashmere populations as well as between Australian Cashmere and Mongolian Cashmere populations is strongly supported by bootstrap probability (100%, not shown on the tree). However, the divergence between Mongolian Cashmere goat populations was not strong (~48%), thus indicating a degree of admixture among these three populations. These results corroborate well with our data (F_{ST} values) showing that the Australian Angora and Cashmere populations belong to different and less related populations, with the Australian Cashmere more closely related to the three Mongolian Cashmere populations. The three Mongolian populations were the most similar or closely related populations among the five studied goat populations. This is in agreement with information about the origin and history of the populations.

A three-factorial correspondence analysis using GENETIX program (Belkhir et al., 1996) was performed to study the degree of differentiation between all individuals of the five goat populations. Figure 2 is a graphical representation of this analysis based on allele frequencies of 14 MS markers in a three-dimensional space. The first two factors (axes 1 and 2) accounted for 58% and 30% of total variation respectively and clearly distinguished the Angora_Aus, Cashmere_Aus and the Mongolian Cashmere goats, seen as three separate blocks (Figure 2). On the other hand, the three different Mongolian Cashmere populations can hardly be distinguished from each other. They are mixed and present as groupings belonging to one population rather than being three separate populations. The Mongolian goats appear closer to the Cashmere_Aus population.

DISCUSSION

The number and range of described alleles in the fourteen loci differed considerably for each population. From the mean number of alleles per locus, it can be said that the four studied Cashmere populations (8.57-9.57 alleles/locus) are more diverse than the Angora_Aus population (7.50 alleles). Compared with the five populations in this study, twelve Chinese goat populations had lower mean number of alleles, ranging from 5.24 to 7.77 (Li et al., 2002). However, the mean number of alleles could be different depending on nature of MS markers studied and populations concerned.

The presence of private or population-specific alleles could underline the divergence between populations depending on their allele frequency. Generally a high frequency of private alleles reflects a low level of gene flow between populations. The frequency of private alleles in subpopulations decreases with increase of rate of migration. Angora_Aus and Cashmere_Aus populations presented at least one private allele (allele 120 on *BM1258* and 115 on *TGLA53*, respectively) with a reasonably high frequency, indicating a low level of gene flow between these two populations. The existence of such population-specific alleles with high frequency can be explained in two ways. Firstly, the new alleles (private alleles) could appear after a goat lineage split into Angora and Cashmere and further split. Secondly, some populations may have lost these alleles during their evolution.

In four cases, statistically significant deviations from

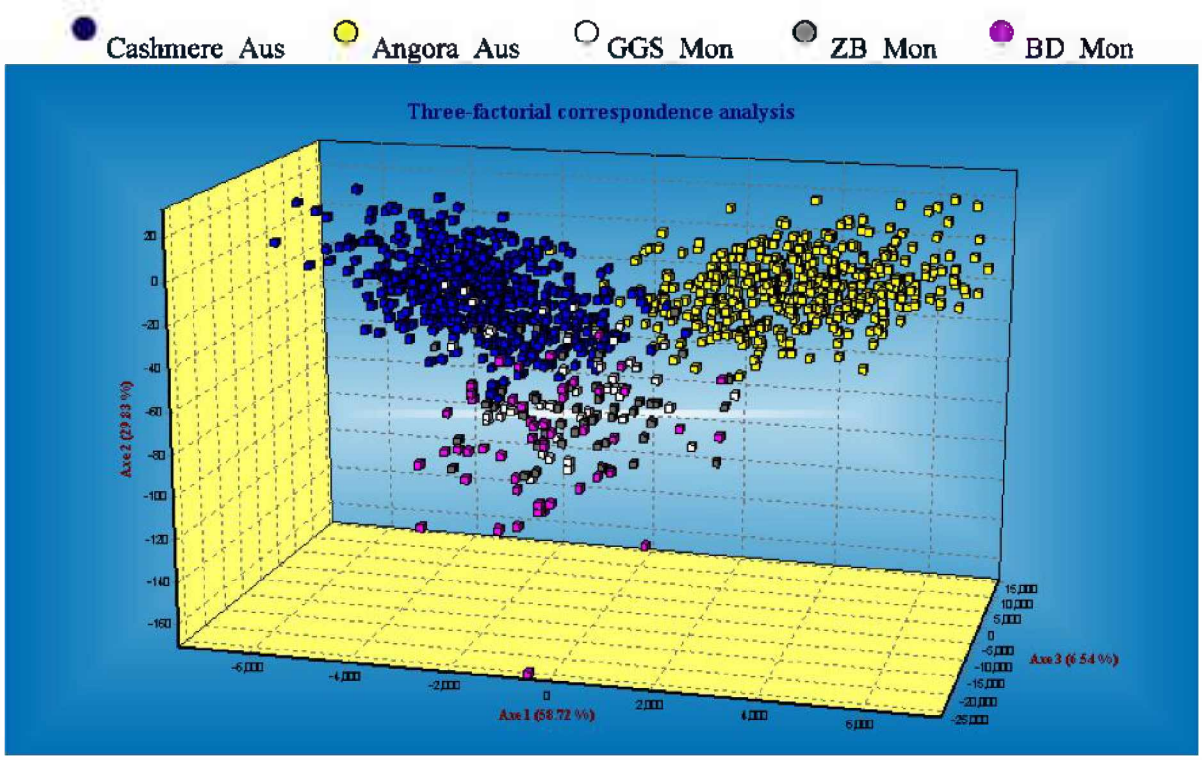

Figure 2. Correspondence analysis of allele frequencies from fourteen MS loci based on the genotypes of all individuals representing the five goat populations.

HWE were observed for these five populations. From the results of the *f*-statistic, the reason for significant deviations from HWE on loci *BM1818* in GGS and *SRCRSP07* in Angora_Aus was due to deficiency of heterozygotes at these two loci. Based on likelihood parentage analysis, the heterozygote deficiency at *SRCRSP07* in Angora_Aus was probably associated with the presence of a null allele. Surprisingly, the extremely variable locus *OarCP73* demonstrated p-values (deviations from HWE test) close to significance across all populations. This might be caused by the presence of many alleles with low frequencies. Low frequencies of alleles can lead to spurious rejection of the null hypothesis (Zapata et al., 2001). To avoid this we also examined the deviations from HWE in the data set, which included only alleles with frequencies >3%. With such data p-values for deviations from HWE in this locus generally increased for each population. However, a significant deviation ($p = 0.0476$) at *OarCP73* still remained in the Cash_Aus population even after excluding 6 alleles with frequency <3%. Therefore, beside low-frequency alleles, other factors might also cause the deviations from HWE in this locus. On the other hand, the observed significant deviations from HWE could be simply due to chance if we set a strict threshold for Multiple test (e.g. $p<0.05$ with the sequential Bonferroni correction).

The level and pattern of observed and expected heterozygosity and polymorphic information content at the fourteen loci studied across the populations were high, indicating a high power of these markers for this population genetic study. A similar amount of heterozygosity and *PIC* was observed by other researchers working with Chinese indigenous (Li et al., 2002) and Mongolian Cashmere goat and Angora (Turkey) goat populations (Luikart et al., 1999). A slightly lower variability was observed in Swiss goat breeds as well as in two feral (Creole and Bezoar) goat species (Saitbekova et al., 1999).

The level of the F_{ST} values reflects the level of divergence among the populations. The mean F_{ST} value (0.075) for all the five populations demonstrates that only 7.5% of total genetic variation is attributable to differences between the populations. Such limited differentiation between the Australian and Mongolian goat breeds is not very surprising if we consider previous findings in literature. For example, Luikart et al. (2001) using mtDNA diversity analysis found that around 10.7% of the total genetic variation was explained by a difference between goat breeds from different continents (Europe, Africa, Asia and Middle and Near East) and also they noted that mithochondrial DNA types found in Mongolian goat samples were represented in all three domestic goat lineages. Furthermore, Mannen et al. (2004) found in their mitochondrial analysis that 20% of Mongolian cattle carried *B. indicus* mitochondrial haplotypes whereas Japanesee and Korean

cattle carried only *B. taurus* haplotype. They postulated that this may have been due to the import of zebu and other cattle during the Mongol Empire era with subsequent crossing with native taurine cattle. Compared with cattle, goats are small portable animals and have been transported widely for food supply and trading purposes from one place to another by land or sea. Therefore widespread transportation and dispersal may be a factor contributing to lower than expected genetic diversity between some goat populations.

The results of pairwise F_{ST} values as well as genetic distances between the studied populations indicated that the Angora goats are genetically distinct from the Cashmere goat populations. However the magnitude of the difference between Angora and Cashmere populations was small for animals of different breeds. This may be true for all Australian Cashmere goat populations as crossbreeding with Angoras was commonly used in the early establishment of cashmere-bearing goats. The Australian Cashmere goat population showed slightly higher pairwise F_{ST} values and larger genetic distance from the Angora population, than did the Mongolian Cashmere goat populations, suggesting that the Mongolian Cashmere goats had a genetic link with Angora goats in the past. Russian Pri-Don and Gorno-Altai goats, which produce mohair, were brought in Mongolia in 1954 and 1970s, respectively, and were used in crossbreeding programs to improve the productivity of the Mongolian native goats in southern and south-western regions of Mongolia. Therefore, admixture or gene flow at some degrees may have occurred between crossbred goat populations and Mongolian native goat populations. Within the studied Mongolian Cashmere goat populations, a high level of polymorphism existed between individuals within populations (about 99%), but not between populations, which indicates a high rate of gene flow between these populations. As additional proof, according to the correspondence analysis, the three Mongolian goat populations appeared as a single population (Figure 2). Similar observations (negligible genetic difference) were made by Naymsamba (2003) in studies of genetic relationships among eight native Mongolian goat populations based on 33 biochemical genetic markers.

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