

## TECHNICAL NOTE

# Allele frequencies and diversity parameters of 27 single nucleotide polymorphisms within and across goat breeds

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## Abstract

Single-nucleotide polymorphisms (SNPs) are useful markers for biodiversity assessment, linkage analysis, traceability and paternity testing. To date, there are no available SNPs for goat in the NCBI dbSNP database and only a few are reported in the literature. Within the European Union Econogene project, we characterized 27 SNPs in goats using a targeted-gene approach. Polymorphisms were identified in a panel of 16 unrelated individuals belonging to eight different goat breeds selected throughout Europe. Genotypes of 30 goats from each of the eight breeds were determined for all the SNPs characterized and diversity measures were estimated. The caprine SNPs described will be a useful complement to the available genome markers.

*Keywords:* gene diversity, goat, selection, single-nucleotide polymorphisms

*Received 24 February 2006; revision accepted 31 March 2006*

Ideal genetic markers for population and evolutionary studies should be abundant and distributed widely across the genome, whereas genotyping data must be comparable across laboratories with different scoring methods (Sunucks 2000). These requirements are fulfilled by the single-nucleotide polymorphisms (SNPs) (Brouillette *et al.* 2000; Sachidanandam *et al.* 2001; Shubutowski *et al.* 2001), which have been shown to be suitable for ecological and conservation studies (Vignal *et al.* 2002; Brumfield *et al.* 2003; Morin *et al.* 2004; Seddon *et al.* 2005), for estimation of parameters such as population history and for inference of relationships (Kuhner *et al.* 2000; Glaubitz *et al.* 2003). Furthermore, SNPs are cost-effective for high-throughput

and accurate linkage or association studies (Syvanen 2001; Vitalis *et al.* 2001; Vignal *et al.* 2002; Schlötterer 2004). However, in spite of these obvious advantages and their increasing use in human and model organism studies, SNPs have not been employed frequently in studies of nonmodel organisms, which is primarily due to a lack of availability.

Within the Econogene project, we have selected 23 genes involved in key metabolic pathways or potentially relevant for production traits. Primers were designed from goat sequences available at GenBank, or from sequences of related species also available at GenBank. Initially, a panel of 16 unrelated individuals belonging to eight goat breeds from different European regions were used for SNP discovery. This procedure permitted us to avoid ascertainment bias on our heterozygosity estimations by using samples that represented a wide geographical area and

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environments and thus representing the majority of the genetic variation of Goat's gene pool: German Alpine (Germany), Corsican (France), Verata (Spain), Greek goat (Greece), Grigia Molisana (Italy), Baladie (Egypt), Polish fawn improved goat (Polony), Brava (Portugal). The authenticity of the amplification was checked by BLAST searches. A requirement to accept an SNP as authentic (not a sequencing error) and sufficiently polymorphic was that at least two copies of the rarer allele be observed (out of the 32 chromosomes observed).

SNPs were identified in exons, introns and 5'- or 3'-flanking regions (Table 1). In four genes, two SNPs were identified. Of the 27 SNPs, 18 were transitions, eight were transversions and one was a deletion.

The SNPs were subsequently typed by polymerase chain reaction–restriction fragment length polymorphism (PCR–RFLP), PCR single-strand conformation polymorphism (SSCP), SnaPshot, or TaqMan via custom service (K-Bioscience). We genotyped 30 individuals from each of the eight breeds caring that at most only three individuals per farm were analysed. The program POWERMARKER (Liu & Muse 2001) was used to compute the frequencies of the rare allele, the expected heterozygosity ( $H_E$ ), the observed heterozygosity ( $H_O$ ) (Weir 1996), polymorphic information content (PIC) value (Botstein *et al.* 1980) and *F* statistics of genetic differentiation (Weir & Cockerham 1984) (Table 1), and the program GENECLASS2 (Piry *et al.* 2004) was used to provide allele frequencies, heterozygotes proportion and Nei's gene diversity for each breed (Table 2).

Expected heterozygosity values ranged from 0.549 (MEG3) to 0.051 (IL2\_1) with a mean of 0.358; observed heterozygosity values from 0.475 (DES) to 0.040 (IL2\_1) with a mean of 0.290. Except one of the two SNPs in the interleukin-2 gene, all SNPs have a frequency of the rare allele higher than 5% over all breeds and are suitable for genetic analysis.  $F_{ST}$  values are variable within the range of 0.004–0.224, but suggest that breed differentiation by a panel of well-selected SNPs is feasible. The assignment of individuals performed by GENECLASS2 software, using the criterion of Paetkau *et al.* (1995), assuming default allelic frequency of 0.001 and a threshold of 0.05, allocated correctly 59.1% of the individuals using all loci and 61.5% excluding MSTNG-5 and PRP\_IN2 loci, less variable among populations. Assignment of groups of individuals under the same conditions using all loci resulted in 100% of corrected assignments. Biases can arise when transferring SNP markers across populations (Morin *et al.* 2004); if these markers are used to analyse non-European breeds, a potential limitation of ascertainment bias should be accounted for.

So far, only few SNPs in goats have been reported in the literature. This study may be a further step towards the exploitation of the vast potential of SNP-based typing within and across goat breeds for a variety of purposes.

Table 1 SNP genotyping and diversity parameters in goat genes

Locus	Name	Primers 5'-3' (forward/reverse)	Genotyping method	SNP	Location	Rare allele frequency	$N$	$H_E$	$H_O$	PIC	$F_{ST}$
ACVR2B	Activin receptor IIB	GCCTTCTGGATGTTACCGAC/ TCCTTCTGTCACTCTGGGC	TaqMan	U57707:g.824+102G>A	Exon 3	0.177	243	0.291	0.255	0.249	0.054
CAST	Calpastatin	AAAGAAGAGGATCGCAGG/ ATCAGAAGTGTCTGCTCCA	TaqMan	U66320:g.1019+345A>G	Intron 14	0.097	242	0.175	0.161	0.160	0.100
MEG3	Callipyge	TCCGAGCTCCAATAATCTTC/ TCCTTGACACGTAAGCATGG	SnaPshot	XM_872707:r.3218u>s	3' UTR+	0.074	237	0.549	0.414	0.459	0.117
CSN151_1	$\alpha$ S1-casein	TTCATAAAGTCTCAGAGGAG/ GGGTTGATAGCCTTGATGT	PCR-RFLP*	X56462:g.275delC	Exon 9	0.446	242	0.494	0.339	0.372	0.122
CSN151_2	$\alpha$ S1-casein	GGGAAAATACCCTGCAGAG/ AAATGGATGGCATTTGTTCTA	PCR-RFLP	AY687344:g.793A>G	5' UTR	0.349	235	0.454	0.281	0.351	0.224
CSN3	$\kappa$ -casein	GGTATCCTAGTTCATGGACTCAAT/ GTTGAAGTAACTTGGGCTGTGT	PCR-SSCP†	X60763:c.418G>A	Exon 4	0.246	238	0.371	0.349	0.302	0.019
CTSK	CathepsinK	TCTCACGGTTCCTACTGCTGCC/ ACTGGCCATGAACCACTTTGG	TaqMan	AY737515:g.180A>T	Intron 2	0.044	229	0.084	0.079	0.080	0.057
DES	Desmin	AGGAGATGATGAGTACCAGCC/ CTGACCACCACCAGACCCAT	TaqMan	AB011673:g.997+338G>A	Intron 5	0.400	240	0.480	0.475	0.365	0.069

Table 1 Continued

Locus	Name	Primers 5'–3' (forward/reverse)	Genotyping method	SNP	Location	Rare allele frequency	N	H <sub>E</sub>	H <sub>O</sub>	PIC	F <sub>ST</sub>
HLA-DQA_1	MHC class II DQA gene	GAAGCCCAACAATGTTTGATAGTCA/ GGGGAAGAACAACAAGAGAGGCA	TaqMan	AY464654:g.156A>T‡	Exon 2	0.214	227	0.336	0.181	0.280	0.156
HLA-DQA_2	MHC class II DQA gene	GAAGCCCAACAATGTTTGATAGTCA/ GGGGAAGAACAACAAGAGAGGCA	TaqMan	AY464654:g.207A>G‡	Exon 2	0.213	195	0.335	0.118	0.279	0.081
HLA-DRB	MHC class II DRB gene	GGGGCTTCTGGACAGATACTT/ CGCTGCACAGTGAAACTCTC	TaqMan	AB008362:g.153A>G	Exon 2	0.235	168	0.360	0.327	0.295	0.058
FABP4	Fatty acid-binding protein 4	CTACGCGAGCCTGGATGATAAGATGGTGCT/ ATACAACGGAAATCAACCATAAAGAGAAAATC	TaqMan	X89244:g.409+59A>G	3' UTR	0.024	227	0.047	0.040	0.046	0.050
FN1	Fibronectin	CTGAACCCGGTAACGAAG/ CTCTGGGAATCTTCTCTGT	TaqMan	AY935993:g.221C>T	Intron 15	0.246	191	0.371	0.272	0.302	0.065
GDF9	Growth differentiation factor 9B	ACTCCGCTTCGTGTGTCAGC/ TACTCCCATTTGCCTCAATC	SNaPshot	AF236079:g.1145T>G	Exon 2	0.191	246	0.309	0.220	0.261	0.068
GHR	Growth hormone receptor	TATGCCAGGTAAGCGACAT/ ATTGAGTACGAGGCCCTGTG	TaqMan	AY292282:g.77C>T	Exon 10	0.431	224	0.490	0.433	0.370	0.090
IL2_1	Interleukin-2	CTTCTGTTTAATCAACAAATCT/ AACCTTGGGCATGTAGAAGT	PCR-RFLP	AF535145:g.88C>T	5' flanking	0.026	247	0.051	0.053	0.050	0.004
IL2_2	Interleukin-2	CACCTCATCTGAGGAGAAGAA/ CCAGCCACTATCTGAGTACTT	PCR-RFLP	AF535145:g.931G>T	Intron 2	0.239	243	0.363	0.313	0.297	0.148
IL4	Interleukin-4	TCACATTTGTCAGTGCAAAATAGAG/ TTTGGGGCAGCAAAGACGT	SNaPshot	U14131:g.900C>T	Exon 2	0.461	246	0.497	0.386	0.374	0.152
ITGB1	Integrin B1	GTCTGTACTACGGCAGCTC/ CGGTGTAGTTAGGGTTGCACT	TaqMan	AY787746:g.253G>T	Intron 8	0.268	231	0.393	0.381	0.316	0.055
LGB	β-lactoglobulin	ACTCTTGTGGGGTGACCTGT/ CCTCCCTGGTTCTGAAAGT	TaqMan	Z33881:g.6751A>G§	Exon 7	0.237	215	0.362	0.251	0.296	0.081
LIPE	Lipase	CGTTCCTGCAGACCACT/ CCTCAATCTCGGTGATATTC	TaqMan	AY935992:g.123A>C	Intron 3	0.366	220	0.464	0.414	0.356	0.046
MTNR1A	Melatonin	AGCTGTATAGCGGCACGAAT/ CCTGCCTGAAATTTTGGTTT	TaqMan	AF419334:g.421C>T¶	Exon 2	0.370	219	0.466	0.438	0.357	0.055
GDF8	Myostatin	CCCTCCCTTTACTGTCATCC/ ATCAAGCCCAAATCTCTCC	TaqMan	AY032689:g.2121A>G	Exon 3	0.058	216	0.109	0.088	0.103	-0.012
PRNP_1	Prionprotein	TGTGGCCATGTGGAGTGACGT/ CTGGGCTTGTCCACTGACTG	PCR-RFLP	X91999:g.145A>G	Exon 3	0.469	245	0.498	0.449	0.374	0.090
PRNP_2	Prionprotein	ATGATCTCAGCACCTACCTTG/ ATAAGAGGCCCTGCTCATGGCA	PCR-RFLP	DQ366112:g.144C>T	Intron 2	0.465	215	0.498	0.437	0.374	0.056
TLR4	Toll-like receptor 4	TTCAAGGGTTGCTGTCTCA/ CAGCACCTGAAGGCTAGAGAG	SNaPshot	AY297043:g.1414T>C	Exon 3	0.492	246	0.500	0.431	0.375	0.168
U80	Capra hircus microsatellite	AGTATCTTTTCTTGCATTTGTTTCC/ CACAGGGTTTCTGGTTGG	SNaPshot	U80588:g.201A>C	Microsatellite	0.191	246	0.309	0.252	0.261	0.043

N, number of genotyped animals; H<sub>E</sub>, expected heterozygosity of gene diversity; H<sub>O</sub>, observed heterozygosity; PIC, polymorphic information content; F<sub>ST</sub>, genetic differentiation parameters of breeds versus total. \*Ramunno *et al.* 2000; †Prinzenberg *et al.* 2005; ‡Amills *et al.* 2005; §Pena *et al.* 2000; ¶Migaud *et al.* 2002.

**Table 2** Allele frequencies, heterozygotes proportion and Nei's gene diversity (Nei 1987) for each locus and each breed

Loci	Populations								
	German alpine	Verata	Corsican	Greek goat	Grigia molisana	Baladie	Polish fawn imp. goat	Brava	Means
<b>ACVR2Ch353_SNP2</b>									
Frequencies A	0.774	0.933	0.8	0.717	0.919	0.677	0.817	0.95	0.823
Frequencies G	0.226	0.067	0.2	0.283	0.081	0.323	0.183	0.05	0.177
Heterozygotes proportion	0.387	0.133	0.333	0.5	0.161	0.065	0.367	0.1	0.256
<b>CALPA_ChRev345_SNP2</b>									
Frequencies A	0.081	0.333	0.052	0.033	0.032	0.032	0.083	0.133	0.098
Frequencies G	0.919	0.667	0.948	0.967	0.968	0.968	0.917	0.867	0.902
Heterozygotes proportion	0.161	0.4	0.103	0.067	0.065	0.065	0.167	0.267	0.162
<b>CALSNP385R</b>									
Frequencies C	0.435	0.29	0.274	0.306	0.677	0.341	0.4	0.233	0.37
Frequencies G	0.548	0.71	0.661	0.629	0.323	0.182	0.533	0.75	0.542
Frequencies T	0.016	0	0.065	0.065	0	0.477	0.067	0.017	0.088
Heterozygotes proportion	0.29	0.387	0.452	0.484	0.387	0.545	0.433	0.367	0.418
<b>CSN1_EX9</b>									
Frequencies delC	0.435	0.55	0.741	0.177	0.581	0.452	0.448	0.2	0.448
Frequencies wild	0.565	0.45	0.259	0.823	0.419	0.548	0.552	0.8	0.552
Heterozygotes proportion	0.419	0.5	0.172	0.097	0.774	0.452	0.276	0	0.336
<b>CSN1S1_5</b>									
Frequencies A	0.7	0.935	0.823	0.452	0.667	0.095	0.613	0.75	0.629
Frequencies G	0.3	0.065	0.177	0.548	0.333	0.905	0.387	0.25	0.371
Heterozygotes proportion	0.267	0.129	0.355	0.258	0.333	0.19	0.387	0.3	0.277
<b>CSN3_Ex4</b>									
Frequencies A	0.823	0.645	0.839	0.806	0.79	0.795	0.71	0.633	0.755
Frequencies G	0.177	0.355	0.161	0.194	0.21	0.205	0.29	0.367	0.245
Heterozygotes proportion	0.355	0.452	0.323	0.258	0.29	0.227	0.452	0.4	0.345
<b>CTSK-G-2</b>									
Frequencies A	0.065	0	0	0.037	0.052	0	0.173	0.033	0.045
Frequencies T	0.935	1	1	0.963	0.948	1	0.827	0.967	0.955
Heterozygotes proportion	0.129	0	0	0.074	0.103	0	0.269	0.067	0.08
<b>DESMIN_Ch315_SNP1</b>									
Frequencies A	0.468	0.467	0.267	0.45	0.268	0.177	0.55	0.55	0.4
Frequencies G	0.532	0.533	0.733	0.55	0.732	0.823	0.45	0.45	0.6
Heterozygotes proportion	0.484	0.533	0.4	0.433	0.464	0.355	0.567	0.567	0.475
<b>DQA_Ch156_SNP1</b>									
Frequencies A	0.967	0.466	0.759	0.897	0.946	0.893	0.672	0.685	0.786
Frequencies T	0.033	0.534	0.241	0.103	0.054	0.107	0.328	0.315	0.214
Heterozygotes proportion	0.067	0.379	0.185	0.138	0.107	0.071	0.31	0.185	0.18
<b>DQA_Ch207_SNP2</b>									
Frequencies A	0.111	0.238	0.06	0.431	0.24	0.288	0.024	0.262	0.207
Frequencies G	0.889	0.762	0.94	0.569	0.76	0.712	0.976	0.738	0.793
Heterozygotes proportion	0.074	0	0.04	0.241	0.24	0.192	0.048	0.048	0.11
<b>DRB-G-3</b>									
Frequencies A	0.407	0.079	0.222	0.194	0.25	0.094	0.364	0.115	0.216
Frequencies G	0.593	0.921	0.778	0.806	0.75	0.906	0.636	0.885	0.784
Heterozygotes proportion	0.519	0.158	0.296	0.056	0.346	0.188	0.636	0.231	0.304
<b>FABP4_Ch1_SNP1</b>									
Frequencies A	0.968	0.983	1	1	1	0.984	1	0.883	0.977
Frequencies G	0.032	0.017	0	0	0	0.016	0	0.117	0.023
Heterozygotes proportion	0.065	0.033	0	0	0	0.032	0	0.167	0.037
<b>FN1</b>									
Frequencies C	0.286	0.341	0.08	0.36	0.341	0.357	0.188	0.042	0.249
Frequencies T	0.714	0.659	0.92	0.64	0.659	0.643	0.813	0.958	0.751
Heterozygotes proportion	0.214	0.318	0.16	0.4	0.409	0.333	0.292	0.083	0.276
<b>GDFSNP452R</b>									
Frequencies G	0.032	0.242	0.194	0.113	0.339	0.048	0.317	0.25	0.192
Frequencies T	0.968	0.758	0.806	0.887	0.661	0.952	0.683	0.75	0.808
Heterozygotes proportion	0.065	0.161	0.194	0.161	0.355	0.097	0.433	0.3	0.221

Table 2 Continued

Loci	Populations								
	German alpine	Verata	Corsican	Greek goat	Grigia molisana	Baladie	Polish fawn imp. goat	Brava	Means
<b>GHR-G-1a</b>									
Frequencies C	0.645	0.638	0.37	0.517	0.5	0.897	0.481	0.444	0.561
Frequencies T	0.355	0.362	0.63	0.483	0.5	0.103	0.519	0.556	0.439
Heterozygotes proportion	0.452	0.586	0.391	0.433	0.5	0.138	0.444	0.519	0.433
<b>IL2_5p</b>									
Frequencies C	0.048	0	0.032	0.048	0	0.032	0.048	0	0.026
Frequencies T	0.952	1	0.968	0.952	1	0.968	0.952	1	0.974
Heterozygotes proportion	0.097	0	0.065	0.097	0	0.065	0.097	0	0.052
<b>IL2_In2</b>									
Frequencies G	0.806	0.855	0.9	0.871	0.903	0.586	0.417	0.733	0.759
Frequencies T	0.194	0.145	0.1	0.129	0.097	0.414	0.583	0.267	0.241
Heterozygotes proportion	0.387	0.29	0.2	0.258	0.129	0.207	0.5	0.533	0.313
<b>IL4SNP119R</b>									
Frequencies C	0.29	0.661	0.629	0.484	0.645	0.887	0.4	0.3	0.537
Frequencies T	0.71	0.339	0.371	0.516	0.355	0.113	0.6	0.7	0.463
Heterozygotes proportion	0.387	0.419	0.419	0.387	0.452	0.161	0.4	0.467	0.387
<b>ITGB1-G-2</b>									
Frequencies G	0.194	0.4	0.397	0.267	0.379	0.065	0.155	0.25	0.263
Frequencies T	0.806	0.6	0.603	0.733	0.621	0.935	0.845	0.75	0.737
Heterozygotes proportion	0.387	0.467	0.448	0.467	0.414	0.13	0.31	0.367	0.374
<b>Lact-G-1</b>									
Frequencies A	0.107	0.192	0.306	0.167	0.518	0.25	0.103	0.25	0.237
Frequencies G	0.893	0.808	0.694	0.833	0.482	0.75	0.897	0.75	0.763
Heterozygotes proportion	0.214	0.231	0.226	0.333	0.393	0.167	0.207	0.214	0.248
<b>LIPE-G-1</b>									
Frequencies A	0.786	0.556	0.661	0.423	0.534	0.674	0.776	0.648	0.632
Frequencies C	0.214	0.444	0.339	0.577	0.466	0.326	0.224	0.352	0.368
Heterozygotes proportion	0.357	0.519	0.355	0.462	0.517	0.13	0.448	0.481	0.409
<b>mel-G-1</b>									
Frequencies C	0.554	0.648	0.435	0.667	0.722	0.87	0.534	0.685	0.639
Frequencies T	0.446	0.352	0.565	0.333	0.278	0.13	0.466	0.315	0.361
Heterozygotes proportion	0.321	0.407	0.613	0.519	0.407	0.261	0.517	0.407	0.432
<b>MSTNG-5</b>									
Frequencies A	0.952	0.967	0.931	0.897	0.964	0.935	0.933	0.969	0.943
Frequencies G	0.048	0.033	0.069	0.103	0.036	0.065	0.067	0.031	0.057
Heterozygotes proportion	0.032	0.067	0.069	0.138	0.071	0.13	0.133	0.063	0.088
<b>PRP_EX3</b>									
Frequencies A	0.661	0.452	0.387	0.419	0.452	0.194	0.724	0.483	0.471
Frequencies G	0.339	0.548	0.613	0.581	0.548	0.806	0.276	0.517	0.529
Heterozygotes proportion	0.484	0.516	0.581	0.516	0.581	0.258	0.345	0.3	0.448
<b>PRP_IN2</b>									
Frequencies C	0.597	0.45	0.357	0.389	0.333	0.341	0.722	0.467	0.457
Frequencies T	0.403	0.55	0.643	0.611	0.667	0.659	0.278	0.533	0.543
Heterozygotes proportion	0.548	0.5	0.524	0.481	0.37	0.5	0.333	0.267	0.441
<b>TL4SNP214R</b>									
Frequencies C	0.258	0.613	0.452	0.484	0.306	0.742	0.35	0.867	0.509
Frequencies T	0.742	0.387	0.548	0.516	0.694	0.258	0.65	0.133	0.491
Heterozygotes proportion	0.452	0.323	0.581	0.387	0.613	0.516	0.367	0.2	0.43
<b>U80SNP129F</b>									
Frequencies A	0.645	0.855	0.871	0.887	0.839	0.661	0.85	0.867	0.809
Frequencies C	0.355	0.145	0.129	0.113	0.161	0.339	0.15	0.133	0.191
Heterozygotes proportion	0.387	0.29	0.258	0.226	0.258	0.097	0.3	0.2	0.252
<b>All loci</b>									
Mean heterozygotes proportion	0.296	0.304	0.287	0.292	0.324	0.206	0.335	0.263	
Heterozygotes proportion standard deviation	0.161	0.187	0.182	0.169	0.197	0.152	0.155	0.168	

## Acknowledgements

This work was partially supported by the EU Econogene contract QLK5-CT-2001-02461. Major objectives of the project and a list of participants can be found on the website <http://lasig.epfl.ch/projets/Econogene>. We would like to thank all the farmers who kindly provided the material.

The content of the publication does not represent necessarily the views of the Commission or its services.

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