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Identification of 14 new single nucleotide polymorphisms in the bovine *SLC27A1* gene and evaluation of their association with milk fat content

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The solute carrier family 27 member 1 (SLC27A1) is an integral membrane protein involved in the transport of long-chain fatty acids across the plasma membrane. This protein has been implicated in diet-induced obesity and is thought to be important in the control of energy homeostasis. In previous reports, our group described the isolation and characterization of the bovine *SLC27A1* gene. The bovine gene is organized in 13 exons spanning over more than 40 kb of genomic DNA and maps in BTA 7 where several quantitative trait loci for fat related traits have been described. Because of its key role in lipid metabolism and its genomic localization, in the present work the search for variability in the bovine *SLC27A1* gene was carried out with the aim of evaluating its potential association with milk fat content in dairy cattle. By sequencing analysis of all exons and flanking regions 14 new single nucleotide polymorphisms (SNPs) were identified: 1 in the promoter, 7 in introns and 6 in exons. Allele frequencies of all the SNPs were calculated by minisequencing analysis in two groups of Holstein-Friesian animals with highest and lowest milk-fat content estimated breeding values as well as in animals of two Spanish cattle breeds, Asturiana de los Valles and Menorquina. In the conditions assayed, no significant differences between Holstein-Friesian groups were found for any of the SNPs, suggesting that the *SLC27A1* gene may have a poor or null effect on milk fat content. In Asturiana and Menorquina breeds all the positions were polymorphic with the exception of SNPs 1 and 8 in which C allele was fixed in both of them.

Keywords: *SLC27A1* gene, milk fat, bovine.

Fat-related traits are of economic interest for both dairy and beef cattle production. Meat and milk nutritional and organoleptic characteristics are determined, at least in part, by the amount and quality of fat (Berner 1993; Wood et al. 2004). A certain amount of fat is necessary to improve meat flavour and tenderness whereas low fat content foods are preferred by consumers. On the other hand, milk fat content has also a very important effect on milk organoleptic and nutritional characteristics, just as on cheese production yield (Berner 1993; Lucey et al. 2003).

In recent years there has been a growing interest in the detection and characterization of markers associated with fat production traits in order to apply marker-assisted selection (MAS) which could improve them. To gain insight, investigations carried out in this field have identified several genes such as acyl-CoA:diacylglycerol acyltransferase (*DGAT1*) (Winter et al. 2002), leptin (Buchanan et al. 2002) or fatty acid synthase (*FASN*) (Roy et al. 2006) that are significantly associated with fat-related traits in cattle.

The solute carrier family 27 member 1 (SLC27A1) is the first described member of the fatty acid transport protein family (FATP) (Schaffer & Lodish 1994). These proteins are proposed to mediate long-chain fatty acids (LCFA) trafficking across the plasma membrane and so have the potential to regulate local and systemic LCFA concentrations and metabolism (Schaffer & Lodish, 1994; Kim et al. 2004; Wu et al. 2006; Gimeno, 2007).

SLC27A1 is expressed in tissues exhibiting rapid fatty acid metabolism such as heart, muscle and adipose tissues in different species (Hui et al. 1998; Martin et al. 2000; Ordovas et al. 2006). Adipocytes control flux of fatty acids (FA) to peripheral tissues by storing and hydrolysing

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Table 1. Set of primers used for PCR amplification. The sets 1, 2, 3, 5, 6, 7, 8, 9, 11 and 12 were used for PCR and sequencing of the *SLC27A1* exons. For each one the $MgCl_2$ concentration, annealing temperature and number of cycles used in PCR are indicated. The shaded primers were used for multiplex PCR and subsequent minisequencing reactions and the newly designed are in bold letters. The final concentration of each set in the multiplex PCR is indicated

n	Exon (Region)	Size (bp)	Forward	Reverse	$MgCl_2$ (mM)	Annealing T (°C)	PCR Cycles	[Multiplex PCR] (nM)
1	**1**(Promoter-In 1)	601	GCATTCCTGATCCCTAGCTG	CACAGGAAGCTCCACAGAGTC	1·5	60	40	150
2	**2** (In 1-In 2)	431	GGAACAGAGACTGTGTCGGG	GATCAGGCCCAGACTGCAC	1·5	60	35	120
3	**3** (In 2-In 3)	550	TCCTCTGCCCTCTCTGTGTG	GAAGCACCGTCTCCCTGC	1	60	40	—
4	**3 (Ex 3-In 3)**	**311**	**CAGCTGGATGCCTACTCCA**	**GAAGCACCGTCTCCCTGC**	—	—	—	150
5	**4** (Ex 3-Ex 5)	574	CTGCTCAACGTGAACCTGC	GGTCCCCGACGTGTAGATG	1	60	40	—
6	**5** (Ex 4-In 5)	400	GCAAGAGCCTGGTCAAGTTC	TGTGGGTTTTACCCAGTTGAG	1·5	58	35	75
7	**6–7** (In 5-In 7)	374	AACTCCCACGCTTTTCTCG	GGGTGGGAGGAGGGTAGG	0·5	56	40	—
8	**8** (In 7-In 8)	451	GAGGAAGGAGGTTGTTGGGT	GCAAGCTGTCAGGAAGGCT	1	60	40	210
9	**9** (In 8-In 9)	293	CAGGAGAGGCAAGGTGTCG	CAGCACTCAGGCTGTGCTG	1·5	58	35	—
10	**9–11 (Ex 9-Ex 11)**	**370**	**CCCAGCACAGCCTGAGTG**	**CCCAGAAGGCGACTTAGCAC**	—	—	—	100
11	**10–11** (Ex 9-In 11)	624	GTCAACGAGGACACCATGGA	CCTACCAGGGCACCTGTACC	2	60	40	—
12	**12** (In 11-In 12)	341	GGATAGGGCTGGAGGTCAGA	CAGGTTAGACCAGGCACAGG	1·5	60	35	75

triglycerides under hormonal control. Insulin regulates in part this process by promoting membrane translocation of intracellular SLC27A1 to the plasma membrane (Stahl et al. 2002; Wu et al. 2006) which suggests an important role for this protein in the control of energy homeostasis.

In addition to this important role in lipid metabolism, *SLC27A1* has been related also to traits such as diet-induced obesity (Wu et al. 2006). Moreover, a polymorphism in intron 8 has been associated with increased plasma triglyceride levels in man (Meirhaeghe et al. 2000) and elevated postprandial lipaemia and alterations in LDL particle size distribution (Gertow et al. 2003). In addition, expression of *SLC27A1* in heart caused lipotoxic cardiomyopathy in transgenic mice (Chiu et al. 2005).

In previous work our group reported the isolation and characterization of the bovine *SLC27A1* gene both structurally and functionally. In this way we established that it is organized in 13 exons extending over more than 40 kb of genomic DNA (Ordovas et al. 2006) and that the gene maps in BTA 7 (Ordovas et al. 2005) where several quantitative trait loci (QTL) for fat related traits have been found (Casas et al. 2003; Ron et al. 2004).

Since genetic variation in the *SLC27A1* gene may affect lipid metabolism, the present study was conducted to search for variability in the bovine gene and analyse its potential association with milk fat content in dairy cattle.

Materials and Methods

Sample collection

Two groups of samples were collected. The first consisted of 211 Holstein-Friesian animals with highest [tail H, $n=117$ estimated breeding values (EBV)=45·19, reliability=54%] and lowest [tail L, $n=94$ estimated breeding values (EBV)=−24·45, reliability=58%] milk fat yield. EBVs for milk fat yield were evaluated by the National Confederation of the Spanish Holstein-Friesian Associations (CONAFE). These animals were selected from 7631 cows from connected herds located in Aragon (a region in the north-east of Spain), with an EBV reliability >47%. Each tail was constituted by the 1% of the population with the animals having the most extreme EBVs. Table 3 shows the genetic parameters for milk fat yield of the whole Aragon Holstein-Friesian animals and the selected animals for high and low tails.

The second group of samples included 101 unrelated animals belonging to two different Spanish breeds: a beef breed, Asturiana de los Valles ($n=50$) and a dairy breed, Menorquina ($n=51$).

Identification of variation

Screening for variation in the bovine *SLC27A1* gene was performed by PCR amplification and direct sequencing of most of the coding region in ten animals of each Holstein-Friesian, Asturiana de los Valles and Menorquina breeds. A set of primers was designed to amplify each exon (Table 1) using Primer Express software (Applied Biosystems) and the bovine genomic DNA sequence (GenBank Accesssion number AAFC03051286). All exons were amplified with the exception of exon 13 for which several sets of primers were tested but no amplification was obtained.

PCR amplification was performed in an ABI2700 thermocycler in 25 μl using 50 ng of bovine genomic DNA, standard PCR buffer, different amounts of $MgCl_2$ (Table 1), 100 μM each dNTP, 150 nM each primer and 1·25 U *Taq* DNA polymerase (Invitrogen). The PCR profile included an initial denaturation step of 95 °C for 5 min and a final extension step of 72 °C for 5 min. Cycling conditions were 95 °C for 30 s, specific annealing temperature for each set of primers (Table 1) for 30 s and 72 °C for 30 s for different number of cycles depending on the set of primers (Table 1). PCR products were enzymically purified with ExoSAP-IT

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Table 2. Extension primers for minisequencing genotyping. The number (*n*), name of the SNPs and the region of localization in the gene are indicated as well as the size, sequence, direction of the primer according to the sense coding sequence and the concentration in the 12X primer mix for each extension primer. The length of the 5′ poli-T tail used to modify the size of each primer is indicated in brackets

n	SNP	Gene Region	Size (bp)	Sequence	Sense/Antisense	12X Primer Mix (μM)
1	g.41534C>T	Promoter	79	(T_{61})TCTCATGGGGCCTGCTGT	Antisense	4
2	g.39900A>G	In 1	57	(T_{40})GGGCTTGAAGCAGGGAG	Sense	1·5
3	g.39834A>G	In 1	61	(T_{44})AGCTCGGCTCCCGCTT	Antisense	3
4	g.39768A>C	In 1	63	(T_{46})GAGAGCTCTGAGGCCGC	Antisense	3
5	g.14996C>G	Ex 3	36	(T_{15})CTTCGGAGGAGAGCTGGC	Sense	3
6	g.14791C>T	Ex 4	83	(T_{64})GAGATGTGGGGCCTGATGG	Sense	2
7	g.14589A>G	Ex 5	67	(T_{42})ATCGACTCTTCTACATCTACACGTC	Sense	2
8	g.14497C>T	In 5	71	(T_{53})CTCAACAAGAGCTGGGGC	Antisense	2
9	g.7502A>G	In 7	39	(T_{21})CTGAGGAGCCTCCAGCCC	Sense	50
10	g.7287C>T	Ex 8	41	(T_{23})GGAGTTCACGGAGCGCTT	Sense	1·5
11	g.5886C>T	Ex 10	45	(T_{24})GTTGATCTGACCCACGAGAAG	Antisense	0·5
12	g.5745A>G	In 10	49	(T_{29})CTGTCAGGTGTGCAGATCCC	Sense	0·5
13	g.5631C>G	Ex 11	53	(T_{35})ACGTCAGCGGAAGGTGTC	Antisense	3·5
14	g.4971A>G	In 12	75	(T_{55})CAGGTGGACACTACAGGTGC	Sense	2

(Amersham) according to manufacturer's instructions and bi-directionally sequenced.

Sequencing reactions were done in 5 μl using 1 μl of the BigDye Terminator V3.1 Cycle Sequencing Kit (Applied Biosystems), 250 nM each primer and 3–5 ng of PCR purified product. Samples were analysed in an ABI Prism 3130 Genetic Analyzer (Applied Biosystems). ClustalW multiple sequence alignment software (http://www.ebi.ac.uk/clustalw/) was used to analyse the sequences. Prediction of *cis* elements was done using the Patch software (http://www.gene-regulation.com/cgi-bin/pub/programs/patch/bin/patch.cgi).

SNP genotyping by primer extension assay

SNP genotyping was carried out by minisequencing (Pastinen et al. 1996) analysis using SNaPshot chemistry (Applied Biosystems). To optimize the multiplex PCR of fragments containing all SNPs, new sets of primers were designed when necesssary (Table 1). Multiplex PCRs were carried out in 5 μl using the Multiplex PCR Kit (QIAGEN) according to the manufacturer's instructions, the concentrations of primers showed in Table 1 and 15 ng of genomic DNA as template. The PCR profile included an initial denaturation step of 95 °C for 15 min and a final extension step of 72 °C for 5 min. Cycling conditions consisted of 40 cycles of 95 °C for 30 s, 60 °C for 1 min and 72 °C for 30 s. Multiplex PCR was enzymically purified with ExoSAP-IT (Amersham) as previously described.

Minisequencing reactions were done using 0·5 μl of SnaPshot Multiplex Kit (Applied Biosystems), 1 μl of purified PCR and 0·5 μl of the 12X extension primer mix (Table 2) in a final volume of 6 μl. Reactions were then purified with 1 unit of Shrimp Alkaline Phosphatase (SAP) (Sigma) according to the manufacturer's instructions. Minisequencing products (1 μl) were mixed with 10 μl of Hi-Di™ formamide and 0·25 μl of GeneScan-120LIZ size standard (Applied Biosystems) and analysed in an ABI Prism 3130 Genetic Analyzer (Applied Biosystems).

Data analysis

Allelic frequencies were calculated by direct counting in both groups of samples. In the analysis of the potential association with milk fat content in Holstein-Friesian animals, the allele frequency comparison was tested using binomial contrast of proportions using χ^2 test. To take into account multiple testing, the Bonferroni correction was applied. A comparison-wise error rate, or type I error *P* value was calculated using standard statistical procedures ($P<0·05$).

Results and Discussion

Using the sets of primers shown in Table 1, we searched for variability in the bovine *SLC27A1* gene by PCR amplification and direct sequencing of all exons and flanking introns in animals from different breeds. Overall, we examined ∼4 kb of genomic DNA of which 47·5% corresponded to exonic regions. In this way we identified 14 SNPs (Fig. 1). One of them was in the promoter region (SNP 1), seven in intronic regions (SNPs 2, 3, 4, 8, 9, 12 and 14) and the other six in coding exons (SNPs 5, 6, 7, 10, 11 and 13). This gives one polymorphic position every 268 and 323 nucleotides sequenced in intronic and exonic regions respectively. The SNPs were annotated in the reference sequence used for the search of variability taking into consideration that the *SLC27A1* gene is coded in the complementary sense (Table 2 and Fig. 1).

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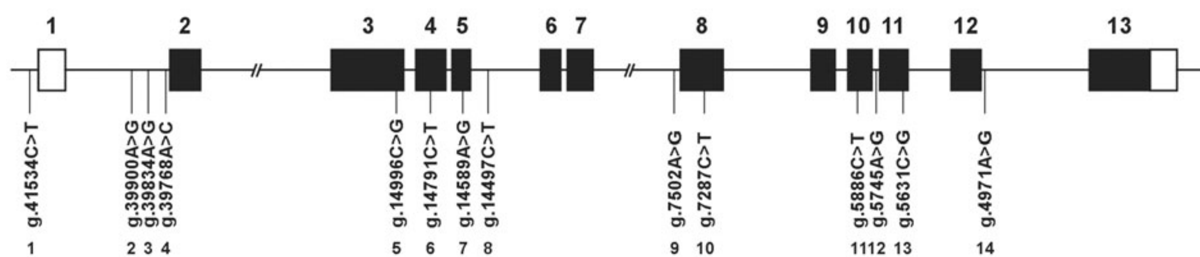

Fig. 1. Newly identified SNPs in the bovine *SLC27A1* gene by sequencing all the exons and flanking introns. Each SNP was assigned to its position in the reference sequence (AAFC03051286) taking into consideration that the gene is coded in the complementary sense. Also a correlative number was given to each of them.

The analysis of the promoter sequence where SNP 1 is located predicted different *cis* elements depending on the allele. For example, when C allele was present GATA-1 or GATA-6 elements were predicted while GR or En-1 elements were predicted with T allele. In any case, none of them have been involved in the control of *SLC27A1* gene expression in other species. However, given the big repercussion that the SNP 1 could have over the whole gene expression, further studies such as band shift assay should be carried out to determine the real transcription factor binding activity of the region including the SNP.

Intronic polymorphisms are mainly A>G transitions (71%) while exonic polymorphism are mainly C>T transitions (60%). Exonic SNPs are in the third 3′ nucleotide of the codons, all of them constituting silent (synonymous) SNPs. So, with the exception of the SNP of the promoter, all the variation identified is intronic or synonymous. Nevertheless, although both are assumed to be not functional, there are SNPs that can affect intronic elements of regulation (Van Laere et al. 2003), consensus sequences of splicing (Aretz et al. 2004), the mRNA stability (Capon et al. 2004) or the co-translational folding of the protein (Komar et al. 1999). For example, an intronic regulatory polymorphism in the *IGF2* gene causes a major QTL effect on muscle growth in pigs (Van Laere et al. 2003) and a synonymous SNP changes the protein activity of the MDR1 protein by altering the co-translational folding of the protein (Kimchi-Sarfaty et al. 2007). In this regard, SNPs 7 and 13 are in codons of amino acids included in the functional motifs 1 and 2 of the protein respectively. Motif 1 is essential for the transport function of the protein since mutation within it abolishes its function (Stuhlsatz-Krouper et al. 1998; Stuhlsatz-Krouper et al. 1999). On the other hand, motif 2 has been proposed as a fatty acid binding motif (Black et al. 1997; Hui et al. 1998). So, if the fact that synonymous substitutions can affect the co-translational folding of the protein is taken into consideration (Kimchi-Sarfaty et al. 2007; Komar et al. 1999), the SNPs 7 and 13 located within the functional motifs of the protein might exert a variation in the protein activity.

Once the variation was identified, a single reaction genotyping procedure based on primer extension analysis was developed. Firstly, the conditions for amplifying in a multiple reaction the fragments containing all the SNPs were established (Table 1). Then, extension primers for each polymorphism were designed (in the sense or antisense direction of the coding sequence) and the conditions for each primer in the multiple minisequencing reaction were defined (Table 2). As result, a fast and reliable method to genotype simultaneously the 14 SNPs of an individual was obtained.

The expression pattern of the *SLC27A1* gene has been studied in different tissues and species including cattle (Hui et al. 1998; Martin et al. 2000; Ordovas et al. 2006) but no data exist for the expression profile of this gene in the bovine mammary gland. In this regard, our group has preliminary evidence demonstrating that the bovine *SLC27A1* gene is expressed in mammary gland (data not shown).

The potential association of the *SLC27A1* gene with milk fat content was evaluated by estimation of the allele frequencies in two tails of Holstein-Friesian animals with extreme EBVs for this trait (Fig. 2). All the SNPs, with the exception of SNP 11 and SNP 12, presented mean frequencies higher than 5% of the minor allele. Analysis of the data obtained showed no significant differences between groups for any of them (Fig. 1). These results could indicate that the *SLC27A1* gene was not associated with milk fat content. Taking into account several considerations as the distance between tails of the EBV's distribution (each one contains the 1% of the animals with the most extremes EBVs and, so, the 98% of the initial population of 7631 individuals was rejected), the large size of the sample (n=211) and the use of a commercial population (in which the use of the same sires is not done and consanguinity is systematically avoided) any strong association should have been detected if it had existed. In effect, this approach allowed us to describe recently the association of two fatty acid synthase (*FASN*) polymorphisms with milk fat content in dairy cattle (Roy et al. 2006).

Allele frequency estimation in Asturiana de los Valles and Menorquina breeds (Fig. 2) showed that all the

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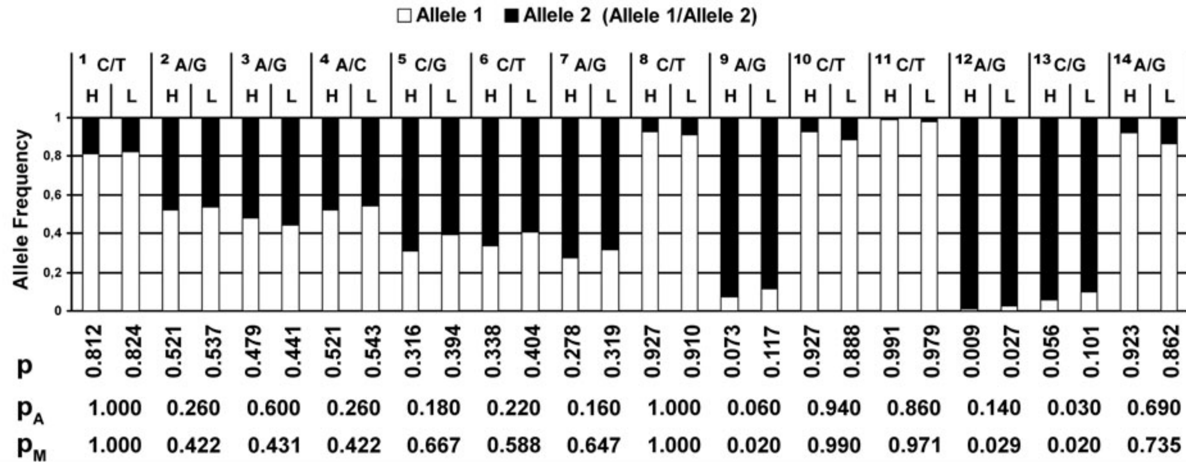

Fig. 2. Allele frequencies of the *SLC27A1* SNPs (numbered from 1 to 14 according to Fig. 1) in the tails of Holstein-Friesian animals with highest (H) and lowest (L) EBV for milk fat content. For each SNP, bars correspond to frequencies of allele 1 (white) and allele 2 (black). Also the value of allele 1 frequency (p) is indicated below for the high and low Holstein-Friesian groups and the Asturiana de los Valles (p_A) and Menorquina (p_M) breeds.

Table 3. Mean, SD and range of the EBVs (maximun and minimum) for milk fat yield (kg) in the Holstein-Friesian population and in the animals of the high and low tails of the milk fat content EBV's distribution

Population	Mean	SD	Maximum	Minimun
Aragon Holstein-Friesian (*n*=7631)	13·67	14·58	63	−53
High and Low tail (*n*=211)	14·17	35·35	63	−53
High tail (*n*=117)	45·19	5·53	63	39
Low tail (*n*=94)	−24·45	8·08	−17	−53

positions were polymorphic with the exception of SNP 1 and SNP 8 which presented the allele C fixated in both of them. Major allele frequency differences between breeds were observed for SNPs 2–7 while the rest of the SNPs presented more similar frequencies. This trend seemed to be maintained also in Holstein-Friesian groups.

Taken overall, the results suggested that the *SLC27A1* gene could have a poor effect on milk fat content, or so small as not to be detected in this study. However, further studies should be carried out to analyse in depth the role of the bovine *SLC27A1* gene in milk fat content. Indeed, it could also be studied as a candidate gene for other fat-related traits. In this regard, the newly identified SNPs and the genotyping method that we report here provide a very useful tool for such studies.

In addition, although no significant association of the *SLC27A1* gene with milk fat content was found, the present results provide new data relevant to dairy science because this is the first time that this fatty acid transporter has been studied in relation to milk traits in cattle or in any other species.

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