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Polymorphism of intronic microsatellites in the *A-FABP* and *LEPR* genes and its association with productive traits in the pig*

A. Chmurzyńska[1], M. Maćkowski[1], M. Szydłowski[1], J. Melonek[1], M. Kamyczek[2], R. Eckert[3], M. Różycki[3] and M. Świtoński[1,4]

[1]*Department of Animal Genetics and Breeding, August Cieszkowski Agricultural University Wołyńska 33, 60-637 Poznań, Poland*
[2]*Experimental Station 64-122 Pawłowice, Poland*
[3]*National Research Institute of Animal Production 32-083 Balice, Poland*

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ABSTRACT

The adipocyte fatty acid-binding protein (*A-FABP*) and leptin receptor (*LEPR*) genes are candidate quantitative trait loci (QTLs) for fatness traits in the pig. In both genes polymorphic short tandem repeat (STR) sequences in intron 1 (*A-FABP*) and in intron 3 (*LEPR*) were revealed. The association studies between both polymorphisms and productive traits were performed in two breeds (Polish Large White and Polish Landrace) and one synthetic line (L990) of the pig. In the *A-FABP* ten and in the *LEPR* gene eight alleles were identified, and the polymorphic information content (PIC) values ranged from 0.713 to 0.749 and from 0.441 to 0.557, respectively. The associations with backfat thickness and intramuscular fat content were found. Since the observed relationships considering each gene were not concordant in all the studied populations, it was concluded that both genes are linked with an unknown QTL.

KEY WORDS: *A-FABP, LEPR,* microsatellite, QTL, pig, fatness

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[4] Corresponding author: e-mail: switonsk@jay.au.poznan.pl

INTRODUCTION

The adipocyte fatty acid-binding protein (*A-FABP*) and leptin receptor (*LEPR*) genes were suggested as possible candidate genes for fatness traits in the pig (Gerbens et al., 1998; Ovilo et al., 2002). Both genes are localized in chromosomal segments identified as the regions harbouring QTLs for such traits (deKoning et al., 1999; Malek et al., 2001).

A-FABP belongs to the family of 9 proteins, which are specifically expressed in many tissues, i.e. in: adipocytes (*A-FABP*), the liver (*L-FABP*), intestine (*I-FABP*), brain (*B-FABP*), heart and skeletal muscle (*H-FABP*). FABPs play an important role in the solubilization of fatty acids (FAs), the transport of FAs across the plasma membrane and within the cell, the modulation of activity of enzymes involved in FA metabolism, the protection of cell proteins against the detergent-like action of FAs (Vogel Hertzel and Bernlohr, 2000).

The gene structure of all the family members is identical and consists of four exons and three introns (Zimmerman and Veerkamp, 2002). The pig *A-FABP* gene polymorphism was first described by Gerbens et al. (1998). In the first intron three polymorphisms were found, namely a polymorphic microsatellite and two SNPs (single nucleotide polymorphisms), *C/T* and *A/G* substitutions occur within the microsatellite sequence. The second SNP can be genotyped by digestion with *BsmI* restriction enzyme.

Leptin and its receptor play an important role in energy homeostasis and body weight regulation (Friedman and Halaas, 1998). Restrained signal transduction in the leptin metabolic pathway results in morbid obesity (Zhang et al., 1994; Chen et al., 1996). Six isoforms of the leptin receptor protein were described: Ra, Rb, Rc, Rd, Re and Rf (Tartaglia et al., 1995). The long form of the leptin receptor (Rb) is the most competent form to activate signaling pathways within a cell. The whole genomic sequence of the porcine *LEPR* is yet not known. Comparing the coding sequence of the porcine *LEPR* gene with its human ortholog, it can be assumed that the porcine gene also consists of 20 exons (60-930 bp long) separated by 19 introns (0.16-90 kb long). Several SNPs were described in exons 4, 6, 9, 13, 14, 15, 16 and 20 (Ovilo et al., 2002). Moreover, it was found that the sequence (GenBank, accession number AF184172S1) contains a repetitive motif $(CA)_{13}CG(CA)_4$ in intron 3.

Polymorphic microsatellites within these genes bring an opportunity to study the effect of both genes on productive traits in terms of linkage with causative mutation(s) or a direct influence of the microsatellites. Thus, our goal was to analyse associations between the microsatellites and productive traits in the pig.

MATERIAL AND METHODS

Two breeds, Polish Large White (PLW) and Polish Landrace (PL), and one synthetic line (L990) were analysed. L990 was created by crossing PLW, Duroc, Hampshire and three lines of Landrace. The animals were gilts fattened and slaughtered at a test station (Pawłowice, Poland). The sample consisted of full- and half-sib groups with the size of sire group ranging from 4 to 34. During the fattening period, from 25 to 100 kg liveweight, gilts were fed *ad libitum* with commercial mixed feed.

Nine fatness traits were considered: abdominal fat (AF) weight, intramuscular fat and seven measurements of backfat thickness (BF): over the shoulder, at the last rib, at the sacrum (point I, II, III), over *M. longissimus dorsi* and over the side of *M. longissimus dorsi*. Intramuscular fat content (IMF) was measured using the extraction system SOXTEC(R) AVANTI 2050 (Foss Tecator, Sweden). Four other traits analysed were: average daily gain (ADG), feed conversion ratio, lean meat content and loin eye area.

Altogether 190 animals were genotyped for the *A-FABP* microsatellite polymorphism in intron 1. The PCR primers according to Gerbens et al. (1998) (F: 5'GGG AAC TCT TGA AGT CTT TCT C, R: 5'GGT ACT TTC TGA TCT AAT GGT G) were used to amplify an approx. 250 bp fragment of the porcine *A-FABP* gene. The PCR reaction mixture (total of 20 μL) contained 100 ng of genomic DNA, 2 μL of 10 × PCR buffer (20mM Tris-HCl pH 8.0; 100 mM KCl; 0.5% Tween™20; 0.5% Igepal CA-630; 0.1mM EDTA), 10 pmol of each primer, 200 μM of dNTPs and 0.75U *Pfu* polymerase. The cycling profile was: 94°C for 3 min followed by 33 cycles of 94°C for 1 min; 59°C for 1 min, 72°C for 1 min and finally 72°C for 10 min. One homozygote sample was sequenced at the Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Warsaw (Poland).

The length of the microsatellite repeat - $(CA)_nCG(CA)_n$ - in intron 3 of the *LEPR* gene was determined for 562 animals. The PCR primers were designed on the sequence of exon 3 with flanking intronic fragments, available in GenBank (accession number AF184172) - F: 5'TCC TGG AAA ATG TCT GAA AT; R: 5'CAA CGG GAA CTC CTG TGT AT. The amounts of PCR reagents were identical as above. The amplification of the approx. 350 bp fragment was performed with the use of *Taq* polymerase. Thermal conditions included: denaturation at 94°C for 5 min, followed by 40 cycles of 94°C for 30 s, 56°C for 30 s and 72°C for 1 min, ended with final extension at 72°C for 10 min. In order to verify which of the two CA elements varies in the repeat number, samples of the two homozygotes (352 and 354 bp) were sequenced at the Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Warsaw (Poland).

Reverse primers for both fragments were fluorescently labelled, and the length of the PCR products was analysed in 6% denaturing polyacrylamide gel on an ALFexpress sequencer.

In order to exclude the *RYR1* gene effect, genotyping of the *RYR1* polymorphism in the analysed animals was performed, following the procedure described by Vogeli et al. (1994).

Association analyses were performed for each breed separately. Due to the high number of variants, the estimation was limited to the additive effects of alleles using multiple regression (Østergård et al., 1989). Beside the allelic effects, the initial model for a trait included fixed effects of the boar and genotype at RYR1 (for PL and L990), and the age at slaughter and the weight of carcass side as covariates. A model for intramuscular fat content included mean backfat thickness as the covariate. A significance level of P=0.25 was established as the maximum level for an effect to remain in the model. Rare variants (fewer than 10 copies found in a population) were lumped.

RESULTS

In the three analysed pig groups ten microsatellite alleles of the *A-FABP* gene were identified (Table 1). The most common alleles in all the populations were those with the length of 251, 253 and 257 bp. The longest alleles 273, 277 and 279 bp, were found only in line 990. The values of the polymorphic information content (PIC) in the studied groups were: 0.749 (PLW), 0.728 (PL) and 0.713 (L990).

TABLE 1

The frequency of the *A-FABP* microsatellite alleles and the computed PIC values for three analysed pig groups

Pig breed[1]	n	PIC[2]	Allele length/ the number of CA repeat units									
			251 20	253 21	255 22	257 23	267 28	269 29	271 30	273 31	277 33	279 34
PLW	51	0.749	0.182	0.182	0.015	0.363	0.061	0.091	0.106	0.000	0.000	0.000
PL	33	0.728	0.176	0.343	0.000	0.216	0.010	0.069	0.186	0.000	0.000	0.000
L990	106	0.713	0.132	0.245	0.009	0.401	0.000	0.019	0.094	0.005	0.024	0.071

[1] PLW - Polish Large White, PL - Polish Landrace, L990 - synthetic line

[2] PIC - polymorphic information content

Including the effect of the *A-FABP* locus in the statistical model led to a significant reduction of the residual sum of squares for ADG in PLW (P=0.03) and backfat thickness (BF) (sacrum III) in PL (P=0.003). The results for the association between traits and distinct *A-FABP* microsatellite variants are given in Table 2. Five variants showed an association with some traits (under individual test error rate) depending on different breeds. None of the variants showed a consistent effect across the populations. Allele 253 bp was found to be associated with backfat thickness in PLW and PL. However, the distinct backfat thickness

TABLE 2

Additive effects of microsatellite alleles in the *A-FABP* gene (only statistically significant effects at P<0.05 are shown)

Trait	Allele				
	251 bp	253 bp	257 bp	271 bp	279 bp
PLW					
BF[1] (shoulder), cm		-0.18 ± 0.07*			
BF (sacrum II), cm		-0.07 ± 0.03*			
daily gain, g		-20.2 ± 8.6*			
PL					
BF(sacrum III), cm	-0.35 ± 0.09***	0.24 ± 0.06***			
IMF[2]	0.32 ± 0.14*				
feed conversion ratio			0.10 ± 0.05*		
meat content, %	1.12 ± 0.47*				
L990					
feed conversion ratio				-0.10 ± 0.05*	
loin eye area, cm^2					3.07 ± 1.08**

* P<0.05, ** P<0.01, *** P<0.001

[1] BF - backfat thickness

[2] IMF - intramuscular fat

measurement was found to be affected in each population. Moreover the effect was positive in PL (P=0.0007) and negative in PLW (P=0.015 and P=0.041). Interestingly, this allele was correlated with decreased ADG in PLW (P=0.025). In PL an allele 251 bp was associated with decreased BF at sacrum point III (P=0.008) and increased meat content (P=0.013). However, the same allele was associated with higher IMF (P=0.037). No associations have been found between *A-FABP* variants and fatness in L990. In this population the loin eye area was positively correlated with allele 279 bp (P=0.005).

Sequencing of *LEPR* gene fragments revealed that only first CA element shows variable length. In the analysed pig groups 8 alleles were identified (Table 3) and the allele frequencies were very similar in all the analysed pig groups. The two

TABLE 3

The frequency of the *LEPR* microsatellite alleles and the computed PIC values for three analysed pig groups

Pig breed	n	PIC	Allele length/ the number of CA repeat units							
			342 13	344 14	346 15	348 16	350 17	352 18	354 19	356 20
PLW	162	0.557	0.000	0.009	0.024	0.034	0.059	0.522	0.321	0.031
PL	180	0.441	0.003	0.017	0.039	0.022	0.078	0.722	0.097	0.022
L990	220	0.530	0.002	0.011	0.059	0.059	0.041	0.623	0.191	0.014

shortest alleles (342 bp and 344 bp) were very rare and the most common was 352 bp allele, with frequency ranging from 0.52 to 0.72. The PIC values were quite similar in the studied groups: 0.557 (PLW), 0.441 (PL) and 0.530 (L990).

LEPR polymorphism explained a significant part of the BF variability (sacrum I) in PLW (P=0.045) and L990 (P=0.037). Results of the association analyses between traits and microsatellite variants are presented in Table 4. The effects of alleles were not consistent across the populations. In PLW backfat thickness was correlated with alleles 352 and 354 bp. None of the fatness traits have been found to be correlated with *LEPR* in PL. Strong evidence was found for the association between 350 bp variant and fatness in L990. This variant was associated with lower backfat thickness (3 measurements) (0.009<P<0.028), decreased weight of abdominal fat (P=0.03) and increased ADG (P=0.036) and feed conversion ratio (P=0.005). An antagonistic effect on the feed conversion ratio was found for 354 bp allele (P=0.002).

TABLE 4

Additive effects of microsatellite alleles in the *LEPR* gene (only statistically significant effects at P<0.05 are shown)

Trait	Allele			
	348 bp	350 bp	352 bp	354 bp
PLW				
BF[1] (sacrum I), cm			-0.08 ± 0.04*	
BF K1, cm				0.09 ± 0.04*
PL				
loin eye area, cm^2		0.75 ± 0.77*		
L990				
daily gain		24.4 ± 11.6*		
AF[2]	0.06 ± 0.03*	-0.05 ± 0.03*		
BF (back)		-0.15 ± 0.07*		
BF (sacrum I), cm		-0.20 ± 0.08**		
BF (K1), cm		-0.14 ± 0.06*		
feed conversion ratio		-0.14 ± 0.05**		0.11 ± 0.03**

* P<0.05, ** P<0.01

[1] BF - backfat thickness

[2] AF - abdominal fat

DISCUSSION

The porcine *A-FABP* gene was mapped between markers *S0001* (position 45cM) and *S0073* (position 75cM) (Marklund et al., 1993) on the porcine chromosome 4 (Gerbens et al., 1998). According to multipoint linkage analysis the marker and the

A-FABP gene order was more precisely defined: *S0001*-[9.9cM]-*A-FABP*-[10.1cM]-*S0217*, with the *A-FABP* gene position on 54 cM of Haldane map (Gerbens et al., 2000), in the region with suggestive QTL for intramuscular fat content (IMF) (de Koning et al., 1999; Rattink et al., 2000). On the pig chromosome 4 QTLs for growth and fat deposition were also mapped (Knott et al., 1998; Perez-Enciso et al., 2000; Malek et al., 2001; Cepica et al., 2003).

Results of the candidate gene approach concerning a possible effect of the *A-FABP* gene on BFT and IMF content were somewhat ambiguous. Gerbens et al. (1998) suggested that the *A-FABP* locus has a considerable effect on IMF content and growth in pigs. The 253 bp allele seemed to be beneficial when compared to 259 and 281 bp alleles. However, further analysis did not confirm this suggestion and in Meishan crossbred pigs no evidence for a significant *A-FABP* effect on IMF content was found (Gerbens et al., 2000). The authors explained the differences in the obtained results by the unequal number of the segregating alleles in these two experiments. For BFT, the two alleles (defined as A5 and A9) were associated with the higher trait value, but no QTL affecting BFT was found on the 4 chromosome. Nechtelberger et al. (2001) did not detect any association of the *A-FABP* gene variants with IMF. The candidate gene testing gave no reliable evidence of the direct influence of the studied *A-FABP* gene polymorphism on fatness traits in pigs.

It can be assumed that in case of the direct influence of the microsatellite length the effect should be detectable and similar in all the analysed pig groups. This was not observed in our studies. Thus, we suggest that our results reflect linkage between the studied polymorphisms and an unknown polymorphic QTL, possibly localized outside the *A-FABP* gene. The most likely, the 253 bp allele of PLW breed segregates with one allele of the QTL, which gives a negative effect on BTF.

The porcine *LEPR* gene was localized on 6q33-q35 (Ernst et al., 1997), the region where suggestive QTLs for BFT and IMF were mapped as well (de Koning et al., 1999; Malek et al., 2001). More precisely the region of QTL localization was assigned between markers *S0228* and *Sw1881*, in close vicinity of the *LEPR* gene locus by Ovilo et al. (2002). *LEPR* was tested as a candidate gene, although the analysed mutation (an *Hpa*II restriction site in the fourth intron) did not seem to be the causative one. However, the significant association of the alleles with backfat thickness and intramuscular fat content was suggested (Ovilo et al., 2002).

In our studies the microsatellite polymorphism of the *LEPR* gene was tested for the first time, as a marker of the productive traits in pigs. The associations of the most frequent alleles (352 and 354 bp) with unknown QTLs giving a strong effect on fatness traits were detected mainly in the 990 line. For example, abdominal and intramuscular fat mass is positively correlated with the 352 bp allele. Because of the complex structure of the *LEPR* gene, which so far has

been poorly recognized, the role of the *LEPR* gene in fatness trait determination requires further investigations.

Our results do not support a major role of the *A-FABP* and *LEPR* gene polymorphisms on the IMF and BFT phenotypic variation, but confirm that in chromosomes 4 and 6 - in the vicinity of *A-FABP* and *LEPR* - a QTL(s) for fatness traits are localized. Knott et al. (1998) postulated two possible candidate genes located in the homologous regions on human chromosomes - the β-3-adrenegic receptor gene (*ADRB3*) and *ATP1B1* one. However, the *A-FABP* gene in the human and the mouse is a part of a cluster group, which includes also other members of the FABP family. One can anticipate that also in the pig genome this cluster exists. Thus, in the vicinity of the *A-FABP* gene may be localized loci of the *mP2, FABP9* and *FABP5* genes and a common regulatory element could be responsible for the expression of the genes influencing fatness traits.

On the distal part of the 6 pig chromosome several genes involved in lipid metabolism are localized, for example *H-FABP* (Gerbens et al., 1997) and *JAK1* (Kuiper et al., 2003), but their precise position is unknown. The distance between *LEPR* and *JAK1* (Janus kinase 1) loci on the human chromosome is very small (approx. 0.6cM). Thus, the *JAK1* gene can be proposed as a candidate QTL.

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STRESZCZENIE

Polimorfizm mikrosatelitarny w intronach genów *A-FABP* i *LEPR* świni oraz ich związek z cechami produkcyjnymi

Geny adipocytarnego białka wiążącego kwasy tłuszczowe (*A-FABP*) i receptora leptyny (*LEPR*) są potencjalnymi QTL (ang. quantitative trait loci) dla cech otłuszczenia świni. W obydwóch tych genach stwierdzono występowanie intronowych polimorficznych sekwencji mikrosatelitarnych (*A-FABP* – intron 1, *LEPR* – intron 3). Związek pomiędzy polimorfizmem tych genów a cechami produkcyjnymi badano na świniach dwóch ras (wielka biała polska i polska biała zwisłoucha) oraz jednej linii syntetycznej (L990). Zidentyfikowano 10 alleli genu *A-FABP* i 8 alleli genu *LEPR*, a wyliczone wartości PIC mieściły się odpowiednio w przedziałach od 0,713 do 0,749 oraz od 0,441 do 0,557. Wykazano związek polimorfizmu genów z grubością słoniny i zawartością tłuszczu międzymięśniowego. Ze względu na to, że otrzymane zależności nie wystąpiły we wszystkich badanych rasach i linii świń, sugeruje się że geny *A-FABP i LEPR* są sprzężone z nieznanymi QTL.