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Detection of quantitative trait loci for meat quality in a commercial slaughter pig cross

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Abstract. The primary goal of this study was to localize quantitative trait loci (QTL) affecting meat quality traits in swine. In total, 42 traits were scored on 305 F_2 individuals from a commercial slaughter pig cross in Norway. F_1 and F_2 individuals were genotyped for 29 markers on Chromosomes (Chrs) 4, 6, and 7, since previous studies had revealed QTL affecting meat quality traits on these chromosomes. The most evident result was detection of a QTL affecting amount of intramuscular fat on Chr 6. The QTL might also influence tenderness, whereas no effect was observed for back-fat thickness. Additionally, suggestive evidence for QTL affecting other meat quality traits was found on Chr 4 and Chr 7.

Introduction

Traditionally, breeding programs in meat-producing animals have focused on growth rate and lean meat deposition. In pig breeding, fat reduction is surveyed by a selection for decreased backfat thickness (BFT), which also creates a reduction in intramuscular fat (IMF) content. The reduction in IMF is unwanted because of positive correlations with meat tenderness, juiciness, and taste (DeVol et al. 1988; Cameron 1990a). For the last years, other meat quality traits have also increasingly attracted more attention in pig breeding. Traits like pH, water-binding capacity (drip loss), protein traits (protein amount in muscle and amount of hydroxyprolin), sensory measurements, fatty acid composition, and color are all investigated for their possible positive effect on meat quality. Altogether the traits make a complex picture, where some correlations between traits are highly positive and others are highly negative (Cameron 1990a; Hovenier et al. 1992; Casteels et al. 1995).

Genetic improvement of IMF and other meat quality traits by selective breeding is often difficult and expensive because of measurement difficulties. Selection can only be exerted through indirect measurements in slaughtered relatives; this increases genetic lag and prediction error. Marker or gene-assisted selection has been suggested as a promising strategy for genetic improvement of such recording intensive traits (Meuwissen and Goddard 1996), and much focus is now on mapping individual loci controlling these traits (QTL). In swine, most of the experiments have been conducted in crosses between divergent populations, which typically produce larger genetic and phenotypic contrasts than within-population studies.

In this study, a search for QTL affecting meat quality traits was conducted in a cross consisting of individuals from the Duroc, Norwegian Landrace, and Yorkshire breeds. Markers for Chr 4, 6, and 7 were chosen for the initial study because previous work had revealed QTL affecting meat quality traits on these chromosomes (Clamp et al. 1992; Andersson et al. 1994; Renard et al. 1996; Rohrer and Keele 1998a, 1998b; Wang et al. 1998; de Koning et al. 1999; Ovilo et al. 2000; Gerbens et al. 2000).

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Materials and methods

Animals and phenotypic records. For each trait, 305 phenotypic records based on a commercial slaughter pig cross were available. The experiment was designed by mating five Duroc boars to five Norwegian Landrace sows in the parental generation, to produce five Landrace/Duroc boars (F_1). Each of the F_1 boars was mated to five Norwegian Slaughter Pig cross sows (50% Norwegian Landrace–50% Yorkshire) to produce F_2 individuals. Norwegian Landrace and Yorkshire (hereafter called white breeds) are considered to be breeds that are very similar in meat quality traits compared with Duroc (Cameron 1990b; Wood et al. 1996; Kolstad 2000). Using such a commercial cross for QTL mapping has two main advantages: 1) results from the study are of interest for the industry because the QTL can easily be implemented in the breeding program via marker-assisted selection (MAS) in the commercial stocks, and 2) the actual costs of the experiment are lower since the carcasses can be sold at relatively high prices in the market. The piglets were randomly chosen from each litter, with an emphasis on obtaining a 1:1 ratio of males to females. Each litter was placed in separate pens. Phenotypic data on 42 traits describing carcass characteristics, sensory observations (16 traits describing taste, smell, texture, and color), drip loss, fatty acid content, amount of intramuscular fat (IMF), protein in muscle, and connective tissue protein were collected on 305 F_2 individuals. All animals in the experiment were halothane negative. Males in the F_2 generation were castrated at 3–5 days of age.

Five days after slaughtering, at a live weight of 108–115 kg, the chilled carcass weights were recorded and backfat measurements were taken between 4^{th} and 5^{th} rib. Chemical properties and sensory measurements were taken on samples from the longissimus dorsi muscle on fresh (non-frozen) meat. pH was measured directly in the muscle by standard methods, and IMF was determined by the Foss-Let method (Woodward et al. 1976). Fatty acid composition was analyzed by gas-liquid chromatography as described by Whittington et al. (1986). Driploss was measured in meat samples of constant size, weighed before and after incubation at 4°C for at least 48 h in plastic bags according to Honikel (1985). For sensory measurements, the loin was sliced into 2-cm-thick chops. The chops were vacuum-packed the same day, stored at 4°C for 5–6 days, and put into an 80°C water bath for 1 h before tasting. The vacuum packing is utilized to save all the flavor inside and around the meat until the panelist opens the bag to evaluate the sample. The samples were evaluated by a trained taste panel of 10 assessors, who scored each chop for the following attributes: tenderness, juiciness, hardness, intensity smell, meat smell, subacid smell, rank pig smell, rancid smell, off smell, intensity taste, meat taste, pig taste, rancid taste, off taste, acidic taste, whiteness (on a cut). Additionally, fat was sliced from each chop and scored for smell. The fat slices were vacuum-packed separately from the meat and served together with the meat. The traits measured on fat samples were intensity smell, meat smell, subacid smell, rank pig smell, rancid smell, and off smell. The sensory

Table 1. Mapping of QTL affecting meat quality traits in a Duroc × Norwegian Landrace backcross.

Chr	Trait	cM[a]	PN[b]	PC[c]	CI (cM)[d]
4	Fatty acid C17:0	94	0.003	0.015	84–104
	Subacid smell	46	0.002	0.015	27–65
		84	0.002	0.014	78–90
	Intensity taste	65	0.007	0.043	53–77
	BFT	97	0.003	0.020	88–106
6	IMF[e]	79	<0.000001	0.0008	72–86
	Intensity smell	92	0.008	0.043	87–97
	Meat%	63	0.003	0.019	56–70
7	Intensity smell—fat	40	0.011	0.015	34–46

[a] Approximate QTL position in cM from the first marker in the linkage map.
[b] Nominal P-value.
[c] Chromosomewise significance level based on 2000 permutations.
[d] CI = Confidence Interval based on 1000 simulation repetitions.
[e] PC based on 10,000 permutations.

traits were measured on a scale from 1 (no intensity) to 9 (distinct intensity).

Genotyping and map construction. Microsatellites on Chr 4, 6, and 7 were selected from the USMARC Genome Database (2000) based on position, ease of scoring, and number of alleles. Additionally, a microsatellite in the adipose fatty acid binding protein (A-FABP) was included in the study (Gerbens et al. 1998). Microsatellite markers were amplified by using PCR as described by Våge et al. (2000), and fragment lengths were determined upon electrophoresis on 6% denaturating polyacrylamide gels in an ABI-373 sequencer (ABI, Perkin Elmer, Foster City, Calif.). Marker map was constructed by using the CRIMAP package (Green et al. 1990).

Statistical analysis. Only a few experiments have previously been undertaken for many of the meat quality traits included in this study. In order to get better insight into the characteristics of recorded traits, preliminary analysis of phenotypic data, ignoring the molecular information, was performed. Initially, phenotypic correlations between traits were calculated. Moreover, as methods used for QTL mapping assume a normal distribution of phenotypes, their frequency distributions were visually checked for especially extreme departures from normality. Furthermore, a sequence of linear regression models was fitted to the data in order to identify whether sex and slaughter weight have a significant effect on the observed phenotypic variation. Differences in goodness of fit between particular models were assessed by using the likelihood ratio test with a number of degrees of freedom corresponding to the difference in the number of parameters. Based on model comparison, instead of raw phenotypic data, trait values corrected for sire, dam, and eventually for sex or slaughter weight were used for QTL mapping. Exceptionally, BFT values were corrected for slaughter weight although it showed no significant effect on its phenotypic variation. The SAS package (SAS, 1996) was used to perform all the above analyses. For QTL mapping, the interval mapping method (Lander and Botstein 1989) was applied by using the QTL-cartographer package (Basten et al. 1994). The likelihood ratio test statistic was used as a testing criterion:

$$\lambda = -2ln\frac{L(\hat{\beta}_0)}{L(\hat{\beta}_1)} \sim \chi^2$$

where, $L(\hat{\beta}_0)$ and $L(\hat{\beta}_1)$ are the maximum values of a likelihood function underlying a statistical model under the null hypothesis (H_0: q = 0) and under no restrictions, respectively. The customary procedure in estimating the most probable QTL position is to derive a so-called likelihood profile, i.e., to calculate λ for a grid of molecular map locations along the chromosome considered. Apart from the maximum likelihood estimate of a QTL position, 95% confidence intervals are calculated (Table 1), based on the numerical approximation of the variance of an estimated QTL position, as proposed by Meyer and Hill (1992). For the highest value of the test statistic, we report chromosome-wise significance levels. These are based on an empirical distribution of the λ, derived from permuting values of vector *Y* among individuals 2000 times (for IMF, 10,000 times) each time picking the highest value of λ for the chromosome (Churchill and Doerge 1994). Additionally, genomewise significance values (P_{genome}) were obtained according to de Koning et al. (1999) as follows: $P_{genome} = 1 - (1 - P_{chromosome})^c$, where c is the number of porcine chromosomes (c = 19). In order to quantify credibility of the QTL mapping results, power of mapping various QTL effects was calculated specific to our data, i.e., based on the particular family design, numbers of individuals, phenotypic variation of IMF, and available marker information on Chr 6; 1000 simulation repetitions and type I error of 5% were assumed.

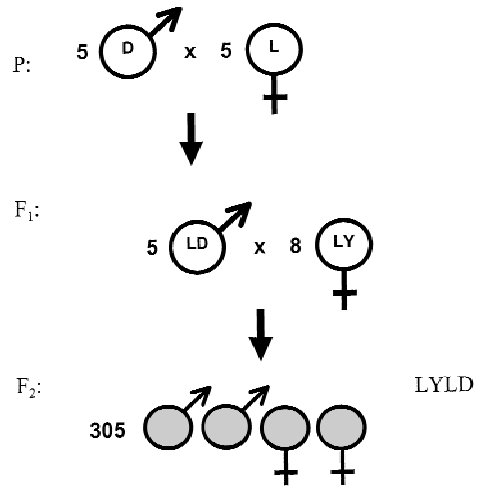

Fig. 1. Design for the Norwegian resource population. Three generations of pigs (P, F_1, and F_2) from three different breeds were used; Duroc (D), Norwegian Landrace (L), and Yorkshire (Y).

Results

The linkage maps in this study (see Figs. 2, 3, and 4) are in agreement with other studies, with the same marker order and similar distances between markers (Walling et al. 1998; USMARC Genome Database 2000).

All of the available traits, for which frequency distribution did not show extreme departures from normality, were subjected to QTL mapping. The most convincing result in the analyses was evidence for a QTL affecting IMF content on Chr 6 (Fig. 3), for which the genomewise significance level of 0.015 was obtained. The highest probability of QTL position was found to be between markers *SW1823* and *S0003*, 74–79 cM from the first marker at the chromosome. In order to gain statistical credibility for this putative QTL, the methods of Haley and Knott (1992) and of Zeng (1994) were additionally applied to the data, resulting in genomewise thresholds of 0.00019 and 0.054, respectively for the same QTL position (detailed results are available upon request). Power of localizing a QTL responsible for IMF calculated based on the available data set was 0.34, 0.43, 0.57, and 0.70 (assuming 5% type I error), for additive QTL effects of 0.3, 0.5, 0.7, and 0.9 respectively. The same QTL may also influence meat tenderness, as indicated by the likelihood profile, but this result does not reach the 5% chromosomewise significance level. No effect of the QTL was observed for BFT (Fig. 3).

Suggestive evidence for a QTL affecting fatty acid C17:0 (heptadecanoic acid) and BFT was found between markers *S0214* and *SW445* on Chr 4 (Fig. 2). An almost identical shape of the graphs for the two traits may indicate that it is the same QTL affecting the two traits. Furthermore, suggestive QTLs were found for subacid smell and intensity taste on the same chromosome (Fig. 2). On Chr 7 a QTL for intensity smell in fat was found with the most likely position between markers TNFB and S0102 (Fig. 4). A summary of QTL results is presented in Table 1.

Discussion

Analysis of experimental crosses of different breeds, lines, or populations provides informative data sets enabling insight into the

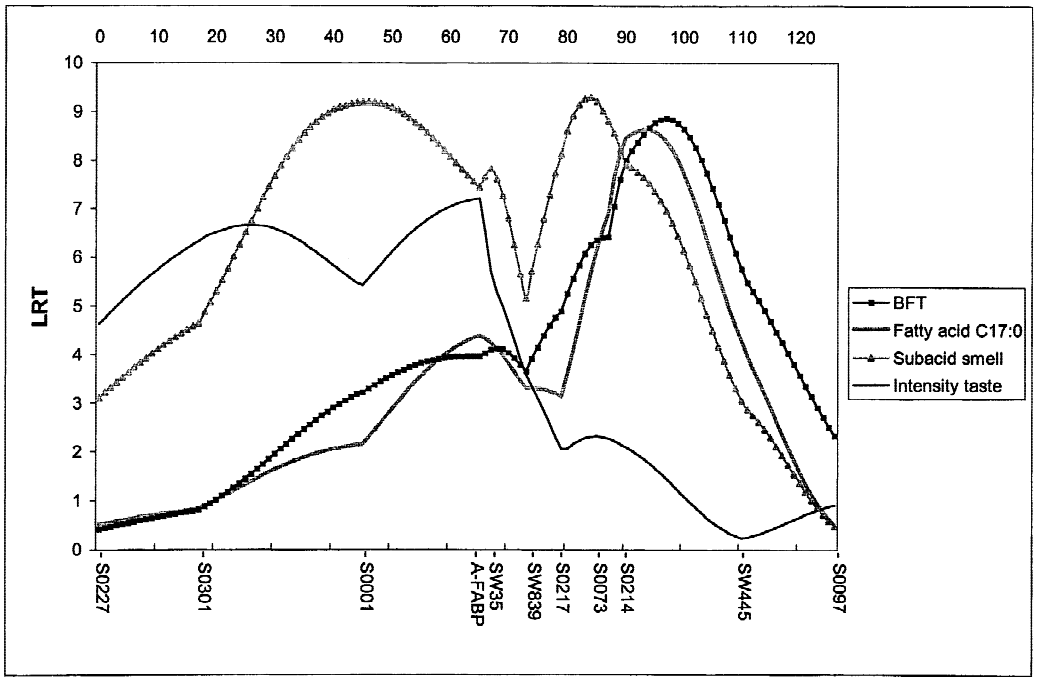

Fig. 2. Likelihood profiles (LRT) for QTLs on porcine Chr 4, affecting BFT, fatty acid C17:0, subacid smell, and intensity taste.

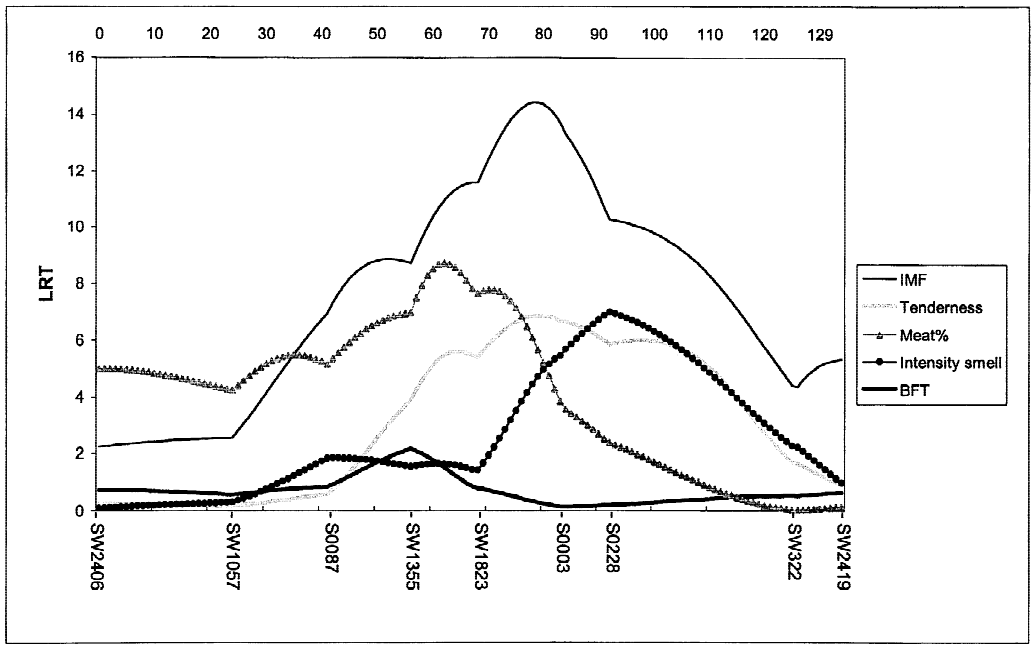

Fig. 3. Likelihood profiles (LRT) for QTLs on porcine Chr 6, affecting IMF, tenderness, meat%, subacid smell, and BFT.

genetics controlling the traits of interest. Duroc and white breeds were chosen for the QTL study because they are shown to differ considerably in contents of BFT, IMF, and other meat quality traits (Cameron 1990b; Wood et al. 1996; Kolstad 2000). Gomez-Raya and Sehested (1999) investigated the power for commercial cross-experimental designs with incomplete linkage disequilibrium. Their results show that, depending on heritability and QTL effect, we can expect over 70% of power on the 5% type I error rate. Power estimates calculated specifically for the data of this study are lower than those of Gomez-Raya and Sehested (1999), owing to a difference in marker informativeness and assumed QTL effects between these two studies.

The most convincing result in this study is the evidence of QTL for IMF between markers *SW1823* and *S0003* on Chr 6. The mapping of a QTL for IMF in this part of the chromosome is highly supported by recent studies in other populations (Gerbens et al. 1999, 2000; de Koning et al. 1999; Óvilo et al. 2000). Gerbens et al. (1999) used the candidate gene approach and found significant associations between polymorphisms in the heart fatty-acid binding protein (H-FABP) and IMF in Duroc pigs. Significant effects were also detected for BFT. Recently, H-FABP was mapped to marker interval *SW316–S0003* (Gerbens et al. 2000), which is almost identical to the marker interval bracketing the most likely QTL position in our study. Two studies analyzing data from a cross between Meishan and Dutch Large White and Landrace lines (de Koning et al. 1999; Gerbens et al. 2000) detected a

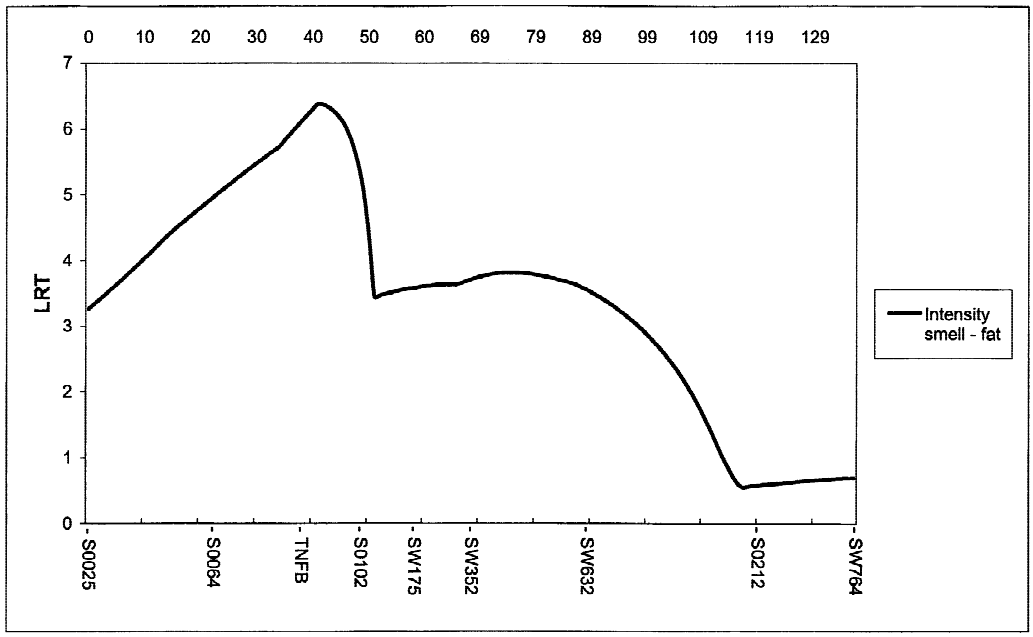

Fig. 4. Likelihood profiles (LRT) for QTL on porcine Chr 7, affecting intensity smell—fat.

QTL affecting IMF approximately 50 cM telomeric of H-FABP (Gerbens et al. 2000). In the same studies, suggestive evidence for QTL affecting BFT was found at the end of the chromosome. Recently it has also been suggested that the QTL affecting IMF is expressed only paternally (de Koning et al. 2000). If this turns out to be true in our population as well, it will highly affect the number of positional candidate genes for the QTL. Also Óvilo et al. (2000) found a QTL affecting both IMF and BFT at the end of Chr 6 in an Iberian × Landrace cross. The most likely position of this QTL was telomeric to marker *S0228*, close to marker *SW1881*.

Different from other reports, the QTL in our study seems to specifically affect IMF, and not BFT. It should also be noted that the QTL is mapped more centromeric than the most likely QTL positions in the other studies. Our mapping of QTL to marker interval *SW316–S0003* suggests that H-FABP is a very good positional candidate for the QTL. The fact that the QTL in our study affects IMF and not BFT also reflects the biological function of H-FABP. It has been shown that H-FABP is mainly expressed in cardiac and skeletal muscle cells, whereas no expression is found in subcutaneous adipocytes (Heuckeroth et al. 1987). H-FABP is involved in fatty acid transport from the cell membrane to the intracellular sites of fatty acid utilization (Veerkamp and Maatman 1995).

Another positional candidate gene for the QTL is the melanocortin-receptor 5 (MC5R), mapped close to marker *S0059* in swine (Kim et al. 2000) and located between markers *S0003* and *SW1823* (http://www.genome.iastate.edu/maps). MC5R is expressed mainly in brain and adipose tissue (Chagnon et al. 1997a), both relevant tissues for the control of adiposity. Targeted disruption of the MC5R produced mice with a decreased production of sebaceous lipids (Chen et al. 1997), and MC5R polymorphisms have previously shown linkage with fat mass in humans (Chagnon et al. 1997a, 1997b). Phosphogluconate dehydrogenase (PGD) and fucosidase alpha (FUCA1) are genes mapped close to marker *SW1823* (http://www.genome.iastate.edu/maps) and considered as candidate genes as well. Polymorphisms within the *PGD* gene have previously been associated with muscle firmness in pigs (Clamp et al. 1992).

The optimum range of IMF content for meat acceptability has been suggested to be 2–3% (Bejerholm and Barton-Gade 1986; DeVol et al. 1988). The IMF content in our research population was below this level, with an average of 1.68%. Because the QTL on Chr 6 specifically affects IMF content, and not BFT, it may have a potential use in MAS to increase the amount of IMF without simultaneously getting a higher unwanted BFT content. Our results show a possible positive effect of the same QTL on tenderness (Fig. 3), which actualizes its use in MAS. The confidence interval for IMF is not overlapping with the confidence intervals for meat% and intensity smell (Table 1 and Fig. 3), which indicates that different QTL are affecting these traits. This is of practical importance since meat% is strongly negatively correlated with IMF, but is considered as an important economic trait in several commercial slaughter pig populations.

The other traits analyzed did not show clear evidence for a QTL on Chrs 4, 6, or 7, but the rather limited power of the study implies that only QTL with fairly large effects were expected to reach statistical significance. Thus, QTL with more moderate effect considered not significant in this study may be corroborated by an increase in the sample size or may possibly be confirmed in other studies. Except for IMF, the most consistent result was detection of a QTL affecting fatty acid C17:0 on Chr 4. Methods of Haley and Knott (1992) and Zeng (1994) were used for comparison, and all methods show the same QTL with similar chromosomewise significance (data not shown). Moreover, a similar result was obtained when using a mixed model approach (Szyda et al. 2000). To our knowledge, no QTL for C17:0 has previously been detected in swine. Several studies have indicated a relationship between fatty acid composition of longissimus dorsi muscle and eating quality of pork (Cameron and Enser 1991; Cameron et al. 2000), but the fatty acid C17:0 has not been specifically investigated. The amount of saturated fatty acids has generally been correlated with contents of BFT and IMF (Cameron et al. 2000). It is thus of interest that we find suggestive evidence for a QTL affecting BFT in the same region as for C17:0 on Chr 4 (Table 1 and Fig. 2).

Finally, suggestive evidence for QTL affecting intensity smell: fat was detected close to the marker *S0102* on Chr 7, harboring the porcine histocompatibility complex (MHC). Interestingly, a previous study revealed a major QTL for androstenone level associated with boar taint in the region of MCH (Milan et al. 1998).

Furthermore, the activity of malic enzyme, a lipogenic enzyme in muscle, has been shown to be associated with the MHC complex on porcine Chr 7 (Renard et al. 1996).

In summary, this study reports evidence for a QTL affecting IMF on porcine Chr 6. The QTL also seems to affect meat tenderness, while QTLs for intensity smell and meat% are located in approximately the same chromosome region but with non-overlapping confidence intervals. No effect of the QTL was found on BFT, something that actualizes its use in MAS.

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