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Quantitative trait loci analysis of swine meat quality traits

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ABSTRACT: A QTL study was performed in large half-sib families to characterize the genetic background of variation in pork quality traits as well as to examine the possibilities of including QTL in a marker-assisted selection scheme. The quality traits included ultimate pH in LM and the semimembranosus, drip loss, and the Minolta color measurements L*, a*, and b* representing meat lightness, redness, and yellowness, respectively. The families consist of 3,883 progenies of 12 Duroc boars that were evaluated to identify the QTL. The linkage map consists of 462 SNP markers on 18 porcine autosomes. Quantitative trait loci were mapped using a linear mixed model with fixed factors (sire, sex, herd, month, sow age) and random factors (polygenic effect, QTL effects, and litter). Chromosome-wide and genome-wide significance thresholds were determined by Peipho’s approach, and 95% Bayes credibility intervals were estimated from a posterior distribution of the QTL position. In total, 31 QTL for the 6 meat quality traits were found to be significant at the 5% chromosome-wide level, among which 11 QTL were significant at the 5% genome-wide level and 5 of these were significant at the 0.1% genome-wide level. Segregation of the identified QTL in different families was also investigated. Most of the identified QTL segregated in 1 or 2 families. For the QTL affecting ultimate pH in LM and semimembranosus and L* and b* value on SSC6, the positions of the QTL and the shapes of the likelihood curves were almost the same. In addition, a strong correlation of the estimated effects of these QTL was found between the 4 traits, indicating that the same genes control these traits. A similar pattern was seen on SSC15 for the QTL affecting ultimate pH in the 2 muscles and drip loss. The results from this study will be helpful for fine mapping and identifying genes affecting meat quality traits, and tightly linked markers may be incorporated into marker-assisted selection programs.

Key words: linkage analysis, meat quality, pig, quantitative trait loci

INTRODUCTION

There is a growing interest from retail and consumer organizations in high-quality and healthy food and growing concerns about the well-being and health of pigs in production systems. Unlike growth traits and reproduction traits, such traits at present have no clear economic value to the farmer. In the case of meat quality there is no general consensus on definitions of good quality, and the perception of greatest quality varies from country to country and even within a country.

Consequently, the challenge of improving meat quality will be the ability to compose a set of standards of different quality traits that would satisfy different markets or groups of consumers.

Traditionally, selection in pigs has been mostly based on production traits like growth rate, feed conversion rate, and reproductive traits like litter size. Carcass traits with clear economic values, like relative meat content, have also been considered as important selection criteria. Genetic improvement of meat quality through traditional selective breeding is possible (Cameron, 1990; Larzul et al., 1997; Oksbjerg et al., 2004), but the required measurements are time-consuming and thus expensive regardless of whether sampling is performed on live animals or on carcasses. Further, such a selection will imply a relatively slow improvement of traits. Marker- or gene-assisted selection (MAS) represents
a possibly faster and less costly strategy to improve such traits (Meuwissen and Goddard, 1996). Identification of QTL is required for the MAS, and many QTL studies have been undertaken for a variety of traits (Quintanilla et al., 2002; Lee et al., 2003; Thomsen et al., 2004; Edwards et al., 2008). However, the information concerning QTL for meat quality is scarce, and in published studies the sizes of resource populations used have been relatively small.

The objective of this research was to conduct a genome scan using SNP markers to identify QTL affecting pork quality traits in a large commercial population.

**MATERIALS AND METHODS**

The pigs were raised at conventional farms and slaughtered at conventional slaughterhouses according to the regulations and rules for producing and slaughtering pigs in Denmark.

**Population and Phenotypic Measurements**

The study was conducted with 3,883 progeny of 12 purebred Duroc boars from Danish AI stations. Semen was kept at a temperature above 0°C and transported to the herd with the sows for use within 24 h. The sows were of different ages and selected from 3 ordinary production herds and were all crosses of Danish Landrace and Danish Large White. All piglets were born in the period from February 3, 2000, to March 18, 2001. After birth, each piglet was ear-tagged with an individual number, and within the first days after birth, the farmer recorded the BW of the individual piglets (PFII-60N, Tanaka Scale Works, Fukujimashindenhei, Japan).

Only litters with 8 or more piglets were included in the experiment. To reduce environmental disturbances, all pigs born in the same litter were kept together with their siblings from birth to slaughter. However, large litters with more piglets than the mother could feed were reduced by randomly omitting piglets from the litter and moving them to sows that were not included in the experiment. After this reduction no litters contained more than 15 piglets.

Piglets stayed with their mother until they were about 4 wk old. Thereafter, the litters were transferred to a pen in another stable where the first growth period after weaning was completed. To reduce the positive environmental effects of small litters, extra nonexperimental pigs were added. Thus, an equal density of animals during rearing was obtained for all litters.

After slaughter the carcasses were stored at 4°C. At 24 h postmortem, the pH was measured in the left LM at the last rib curvature and in the central part of semimembranosus (SM); we denote these 2 traits as pHLM and pHSM. At the same time two 2-cm-thick chops were excised from the right LM (longissimus dorsi) at the last rib curvature. One of the chops was used for determination of drip loss, and the other was used for color measurements.

Drip loss was measured according to the EZ-method of Rasmussen and Andersson (1996), and color measurements were made after blooming of the chop for 1 h at 8°C, using a Minolta Chroma Meter CR-300, with a D65 light source (Minolta Co., Osaka, Japan), calibrated against a white tile. The tristimulus parameters L*, a*, and b* (representing lightness, redness, and yellowness, respectively) were measured on 4 sites of each chop surface.

In this study 3,883 progeny have measurements of meat quality traits, and among those 3,595 individuals have no missing values of these traits. This study was part of a larger study where several different traits have been measured. In addition to meat quality traits, QTL studies on osteochondrosis traits (Christensen et al., 2010) and chronic pleuritis (Gregersen et al., 2010) have been published.

**Genotypes and Linkage Map**

The genetic map covers all 18 porcine autosomes and contains 462 SNP markers. The SNP markers were selected in porcine expressed sequence tags and were genotyped by TaqMan oligo-displacement assay (Assay-by-Design) or SNPlex Genotyping System (PE, Applied Biosystems, Carlsbad, CA) according to manufacturer’s protocols as described previously by Vingborg et al. (2009). Genome-wide mean entropy (Shannon, 1948) for the markers was 0.877 with SD of 0.123. The sex-average linkage maps were constructed using CRIMAP v. 2.50, an improved version of CRIMAP v. 2.4 (Green et al., 1990) developed by Maddox and Evans (J. Maddox, University of Melbourne, Melbourne, Australia, personal communication) and Kosambi’s mapping function. Pairwise linkage analysis was performed with the TWINPOINT function, and the critical threshold value was set as 55 logarithm of odds score. Then the BUILD option was used to determine the order of these markers of each linkage group; subsequently, the ALL option was used to determine the most likely position of markers in each linkage group, and finally the FLIPS option was used to ensure the correctness of the order. On the resulting linkage map, the number of markers on each chromosome varied from 6 to 57, and the average distance between markers was 3.94 cM (see Supplemental Table 1; http://jas.fass.org/content/vol88/issue9/). Further details of the linkage map including linkage to previously mapped microsatellite markers can be found in Vingborg et al. (2009).

**Statistical Analyses**

**Initial Genome Scan.** The genome scan was performed using variance component-based linkage analysis (Goldgar, 1990). The method involves the following 4 steps:

1) The alleles of each marker were phased and constructed with software GDQTL (Guldbrandtsen...
and Labouriau, 2006), taking the genotyping error at a 0.05 significance level into account.

2) For each chromosome, positions every 1 cM and also midpoints of all marker brackets along the chromosomes were considered as putative QTL positions. For every such position, probabilities of identity by descent (IBD) of pairs of haplotypes were calculated using the IBD program (Sorensen and Thomsen, 2003), and from this an IBD correlation matrix was constructed.

3) Log-likelihood ratios for testing the hypothesis of no segregating QTL were calculated for each position using the software DMU (Madsen and Jensen, 2002). In this step, variance components of the polygenic, QTL, and residual effects were estimated simultaneously.

4) For each chromosome, the positions on the chromosome and the corresponding log-likelihood ratios were plotted. Chromosome-wide and genome-wide critical threshold values for QTL detection were approximated using Piepho’s method (Piepho, 2001). The position of the peak of the log-likelihood ratio curve was taken as the QTL position.

The following model was used for the different meat quality traits:

\[ Y = Xb + Zu + Wv + Sc + e, \]  

where \( Y \) is the vector of phenotypes, \( b \) is a vector of fixed effects (including sire, sex, herd, month, sow-age), \( u \) is a vector of random additive polygenic effects of background loci, \( v \) is a vector of random effects due to the QTL, \( c \) is the vector of the other random effects (litter), and \( e \) is the vector of random residuals. The \( X \), \( Z \), \( W \), and \( S \) are incidence matrices for the effects of \( b \), \( u \), \( v \), and \( c \), respectively. The random effects were assumed to be normally distributed with mean zero and variances \( \sigma_u^2 \), \( \sigma_v^2 \), \( \sigma_c^2 \), and \( \sigma_e^2 \), respectively. In addition, \( u \) had the usual additive relationship matrix, and \( v \) had the IBD correlation matrix. The percentage of total variance accounted for by a given QTL was calculated from the estimated variance components.

**Two-QTL Model.** When a likelihood ratio curve had 2 or more peaks exceeding the chromosome-wide threshold, models with 2 QTL were investigated. All pairs of QTL positions in a \( 1 \times 1 \) cM grid were investigated, and the pair with the largest value of the likelihood ratio was taken as the best 2-QTL model. If the likelihood ratio test of the best 2-QTL model vs. the best 1-QTL model was not significant (\( P > 0.05 \)), the position from the best 1-QTL model was taken as the QTL position, and otherwise the 2 positions from the best 2-QTL model were taken as the QTL positions.

**QTL Segregation.** The QTL analysis was performed within each half-sib sire family using model (1) for every position where a QTL was detected for the specific trait. Families with minus 2 times the log-likelihood ratio (LR) greater than 3.84 were considered to be segregating for the specific QTL.

**Credibility Interval.** The 95% Bayesian credibility intervals (Sen and Churchill, 2001) were calculated from the approximate posterior distribution for the QTL position (Manichaikul et al., 2006).

**RESULTS**

**QTL Analysis**

Descriptive statistics of traits are listed in Table 1. The significance threshold values differed between trait and chromosome combinations, but were on average 6.52, 9.62, and 14.12 at the chromosome-wide 5, 1, and 0.1% level, respectively, and 12.69, 15.89, and 20.46 at the genome-wide 5, 1, and 0.1% significance level, respectively.

In total, 31 QTL affecting meat quality traits were detected at the 5% chromosome-wide level (see Table 2), among which 11 QTL were significant at the 5% genome-wide level and among these 5 were also significant at the 0.1% genome-wide level. These 31 QTL consisted of 3 QTL with pHLM, 3 QTL with pHSM, 5 QTL associated with drip loss, 8 QTL with L*; 8 QTL with a*, and 4 QTL with b*. The detected QTL were distributed on most of the chromosomes, but no QTL were detected on SSC10, SSC12, SSC16, SSC17, and SSC18.

**pH Value.** Five among 6 QTL affecting pH value were significant at the 5% genome-wide significance level. Three QTL affected pHSM and 3 QTL affected pHLM, and among those identical QTL positions were seen for pHSM and pHLM on SSC6 and SSC15, indicating that ultimate pH in the 2 muscles are regulated by the same genes on these 2 chromosomes. The percentages of phenotypic variance explained by these

<table>
<thead>
<tr>
<th>Trait value in LM</th>
<th>Abbreviation</th>
<th>Number</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH value in LM</td>
<td>pHLM</td>
<td>3,684</td>
<td>5.47</td>
<td>0.13</td>
<td>5.11</td>
<td>6.39</td>
</tr>
<tr>
<td>pH value in SM</td>
<td>pHSM</td>
<td>3,749</td>
<td>5.55</td>
<td>0.15</td>
<td>5.16</td>
<td>6.48</td>
</tr>
<tr>
<td>L̄DRIP</td>
<td>DRIP</td>
<td>3,782</td>
<td>3.62</td>
<td>2.07</td>
<td>0.00</td>
<td>15.32</td>
</tr>
<tr>
<td>Minolta L*</td>
<td>L*</td>
<td>3,826</td>
<td>53.45</td>
<td>3.05</td>
<td>38.04</td>
<td>65.27</td>
</tr>
<tr>
<td>Minolta a*</td>
<td>a*</td>
<td>3,826</td>
<td>6.14</td>
<td>1.09</td>
<td>2.63</td>
<td>10.90</td>
</tr>
<tr>
<td>Minolta b*</td>
<td>b*</td>
<td>3,826</td>
<td>5.18</td>
<td>1.13</td>
<td>1.18</td>
<td>9.40</td>
</tr>
</tbody>
</table>

1SM = semimembranosus.
QTL were large (e.g., the QTL associated with pHSM on SSC15 explained more than 10% of the phenotypic variance). As seen in Table 2, SSC6 and SSC15 had multiple QTL, which were significant at the genome-wide 5% level and located at nearby positions for different traits. These chromosomes were therefore chosen for a closer examination of the results, and Figure 1 and Figure 2 show the likelihood ratio curves for the traits.

**Drip Loss.** All 5 QTL affecting drip loss detected in this study were significant at the 5% chromosome-wide level but not significant at the 5% genome-wide level. The percentages of phenotypic variance explained by these 5 QTL were low, ranging from 0.74 to 1.46%.

**Meat Color.** In total 20 QTL affecting the Minolta meat color measurement were detected at the 5% chromosome-wide significance level, among which 6 were also significant at the 5% genome-wide level. Most of these QTL explained between 1 and 2% of phenotypic variance. Two QTL associated with the L* value were detected on SSC1 and explained 1.67 and 1.31% of phenotypic variance, respectively. The QTL associated with L* and b* were mapped to the same position on SSC14. Quantitative trait loci associated with all 3 meat color traits were detected on SSC6 at the 5% genome-wide significance level. The QTL associated with a* and b* were mapped to nearby positions, and the QTL associated with the L* value was mapped to the same marker interval as the QTL associated with pHSM and pHLM.

**Credibility Interval**

The 95% credibility intervals of most QTL detected in this study were larger than 20 cM, although 3 QTL were mapped to a region less than 10 cM with 95% reliability. The narrowest region was the 4 cM for the QTL associated with pHSM on SSC15. Although pHSM and pHLM were mapped to the same position on SSC6 and

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**Table 2. Results of QTL analysis of pig meat quality traits in this study**

<table>
<thead>
<tr>
<th>SSC</th>
<th>Trait</th>
<th>Pos, cM</th>
<th>LR^2</th>
<th>Pc^4</th>
<th>Pg^4</th>
<th>V, %</th>
<th>Nfam^6</th>
<th>95% CI, cM</th>
<th>Span, cM</th>
<th>Dist, cM</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>L*</td>
<td>68.0</td>
<td>9.58</td>
<td>*</td>
<td>ns</td>
<td>1.67</td>
<td>1</td>
<td>56 to 76</td>
<td>20</td>
<td>5.3</td>
</tr>
<tr>
<td>1</td>
<td>L*</td>
<td>112.0</td>
<td>11.26</td>
<td>**</td>
<td>ns</td>
<td>1.31</td>
<td>2</td>
<td>98 to 116</td>
<td>18</td>
<td>1.3</td>
</tr>
<tr>
<td>1</td>
<td>a*</td>
<td>90.0</td>
<td>11.37</td>
<td>*</td>
<td>ns</td>
<td>1.30</td>
<td>1</td>
<td>38 to 100</td>
<td>62</td>
<td>14.6</td>
</tr>
<tr>
<td>1</td>
<td>b*</td>
<td>11.0</td>
<td>14.53</td>
<td>**</td>
<td>*</td>
<td>2.67</td>
<td>3</td>
<td>1 to 24</td>
<td>23</td>
<td>18.4</td>
</tr>
<tr>
<td>2</td>
<td>DRIP</td>
<td>59.0</td>
<td>10.40</td>
<td>*</td>
<td>ns</td>
<td>1.28</td>
<td>1</td>
<td>34 to 112</td>
<td>78</td>
<td>4.7</td>
</tr>
<tr>
<td>3</td>
<td>a*</td>
<td>50.0</td>
<td>7.83</td>
<td>*</td>
<td>ns</td>
<td>1.17</td>
<td>1</td>
<td>36 to 73</td>
<td>37</td>
<td>4.7</td>
</tr>
<tr>
<td>4</td>
<td>pHSM</td>
<td>57.0</td>
<td>9.08</td>
<td>*</td>
<td>ns</td>
<td>0.94</td>
<td>1</td>
<td>32 to 64</td>
<td>32</td>
<td>5.0</td>
</tr>
<tr>
<td>4</td>
<td>DRIP</td>
<td>60.0</td>
<td>9.10</td>
<td>*</td>
<td>ns</td>
<td>1.05</td>
<td>2</td>
<td>45 to 86</td>
<td>41</td>
<td>2.7</td>
</tr>
<tr>
<td>5</td>
<td>b*</td>
<td>104.0</td>
<td>8.87</td>
<td>*</td>
<td>ns</td>
<td>0.84</td>
<td>1</td>
<td>93 to 115</td>
<td>22</td>
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<td>8.32</td>
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<tr>
<td>5</td>
<td>a*</td>
<td>22.0</td>
<td>12.44</td>
<td>*</td>
<td>ns</td>
<td>1.98</td>
<td>3</td>
<td>3 to 42</td>
<td>39</td>
<td>5.0</td>
</tr>
<tr>
<td>5</td>
<td>b*</td>
<td>53.3</td>
<td>8.66</td>
<td>*</td>
<td>ns</td>
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<td>1</td>
<td>6 to 53</td>
<td>47</td>
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<td>6</td>
<td>pHLM</td>
<td>52.9</td>
<td>71.46</td>
<td>***</td>
<td>***</td>
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<td>4</td>
<td>48 to 56</td>
<td>8</td>
<td>0.5</td>
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<tr>
<td>6</td>
<td>pHSM</td>
<td>52.9</td>
<td>62.45</td>
<td>***</td>
<td>***</td>
<td>3.00</td>
<td>5</td>
<td>41 to 56</td>
<td>15</td>
<td>0.5</td>
</tr>
<tr>
<td>6</td>
<td>DRIP</td>
<td>55.0</td>
<td>8.64</td>
<td>*</td>
<td>ns</td>
<td>0.74</td>
<td>2</td>
<td>38 to 100</td>
<td>62</td>
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</tr>
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<td>27.44</td>
<td>***</td>
<td>***</td>
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<td>3</td>
<td>42 to 65</td>
<td>23</td>
<td>0.5</td>
</tr>
<tr>
<td>6</td>
<td>a*</td>
<td>42.0</td>
<td>15.53</td>
<td>**</td>
<td>*</td>
<td>1.41</td>
<td>2</td>
<td>30 to 68</td>
<td>38</td>
<td>10.3</td>
</tr>
<tr>
<td>6</td>
<td>b*</td>
<td>46.0</td>
<td>22.55</td>
<td>***</td>
<td>***</td>
<td>1.35</td>
<td>3</td>
<td>38 to 53</td>
<td>15</td>
<td>1.6</td>
</tr>
<tr>
<td>7</td>
<td>L*</td>
<td>44.0</td>
<td>8.00</td>
<td>*</td>
<td>ns</td>
<td>1.18</td>
<td>2</td>
<td>36 to 62</td>
<td>26</td>
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</tr>
<tr>
<td>8</td>
<td>a*</td>
<td>57.7</td>
<td>14.11</td>
<td>**</td>
<td>*</td>
<td>1.33</td>
<td>2</td>
<td>50 to 72</td>
<td>22</td>
<td>9.0</td>
</tr>
<tr>
<td>9</td>
<td>pHLM</td>
<td>57.0</td>
<td>13.56</td>
<td>**</td>
<td>*</td>
<td>1.41</td>
<td>3</td>
<td>38 to 73</td>
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<tr>
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<td>L*</td>
<td>86.0</td>
<td>8.99</td>
<td>*</td>
<td>ns</td>
<td>1.22</td>
<td>1</td>
<td>68 to 93</td>
<td>25</td>
<td>8.4</td>
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<td>DRIP</td>
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<td>9.39</td>
<td>**</td>
<td>ns</td>
<td>1.46</td>
<td>2</td>
<td>4 to 16</td>
<td>12</td>
<td>0.9</td>
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<tr>
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<td>L*</td>
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<td>9.27</td>
<td>*</td>
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<td>1.02</td>
<td>1</td>
<td>66 to 95</td>
<td>29</td>
<td>2.9</td>
</tr>
<tr>
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<td>a*</td>
<td>89.4</td>
<td>14.21</td>
<td>**</td>
<td>*</td>
<td>1.38</td>
<td>2</td>
<td>81 to 91</td>
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<td>9.03</td>
<td>*</td>
<td>ns</td>
<td>0.82</td>
<td>2</td>
<td>21 to 75</td>
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<td>a*</td>
<td>59.0</td>
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<td>*</td>
<td>ns</td>
<td>0.94</td>
<td>3</td>
<td>28 to 64</td>
<td>36</td>
<td>1.9</td>
</tr>
<tr>
<td>14</td>
<td>b*</td>
<td>51.0</td>
<td>7.27</td>
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<td>ns</td>
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<td>15.69</td>
<td>***</td>
<td>*</td>
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<td>3</td>
<td>53 to 75</td>
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<td>15</td>
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<td>36.71</td>
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<td>***</td>
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<td>60 to 64</td>
<td>4</td>
<td>3.9</td>
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<tr>
<td>15</td>
<td>DRIP</td>
<td>63.0</td>
<td>11.80</td>
<td>**</td>
<td>ns</td>
<td>1.08</td>
<td>2</td>
<td>60 to 82</td>
<td>22</td>
<td>5.2</td>
</tr>
</tbody>
</table>

1^pHLM = ultimate pH in LM; pHSM = ultimate pH in semimembranosus; DRIP = drip loss; L* = lightness; a* = redness; b* = yellowness.
2^Position of peak.
3^−2 × log-likelihood ratio test statistic.
4^Pc: chromosome-wide significance level; Pg: genome-wide significance level; ns: P > 0.05; *P < 0.05; **P < 0.01; ***P < 0.001.
5^V%: the percentage of the total phenotypic variance accounted for by QTL.
6^Number of families segregating at a 0.05 significance level.
7^95% CI: the credibility interval at a 0.05 significance level, lower limit, and upper limit.
8^Span of 95% credibility interval.
9^Distance between flanking markers.
SSC15 separately, their 95% credibility intervals were not completely identical.

Family Segregation

For the QTL detected in this study, 21 segregated in only 1 or 2 families, among which 4 were QTL significant at the 5% genome-wide level. The other 10 QTL segregated in more than 2 families, 7 of which were QTL significant at the 5% genome-wide level. Considering the cases where QTL for different traits were detected at common (or nearby) positions, then for every pair of such traits there were families where they both segregated, the exception being the QTL on SSC13 (data not shown). The QTL associated with pHSM, pHLM, L*, and b* on SSC6 segregated simultaneously in 3 families (Figure 3). The QTL associated with pHSM and pHLM on SSC15 also segregated simultaneously in 3 families (Figure 4).

DISCUSSION

In this study, we detected 31 QTL in pigs associated with 6 meat quality traits at the 5% chromosome-wide significance level using a SNP genetic map. In particular, several highly significant QTL associated with pH value were identified in this study.

The QTL affecting pHLM on SSC6 and SSC15 detected in this study are highly significant and (by comparison of microsatellites on the map) close to the regions reported by Malek et al. (2001b) and Yue et al. (2003b), and thereby confirming 2 QTL affecting pH value in the loin on these 2 chromosomes. We also detected a QTL affecting pHLM on SSC9 significant at the 5% genome-wide level, which differs in position from the suggestive QTL affecting pHLM on SSC9 reported by de Koning et al. (2001).

At the same positions as the 2 QTL for pHLM on SSC6 and SSC15, we detected 2 QTL affecting pHSM that were highly significant at the genome-wide level. Kim et al. (2005) also detected QTL affecting pHSM on SSC6 and SSC15, confirming there are genes regulating pHSM on these 2 chromosomes. One QTL affecting pHSM was also detected on SSC4, which was not previously reported.

Many QTL affecting pHLM have been reported previously (de Koning et al., 2001; Malek et al., 2001a; Ovilo et al., 2002; Beeckmann et al., 2003b,c; Cepica et
Figure 2. Quantitative trait loci $-2 \times \log$-likelihood ratio vs. position on SSC15 for drip loss (DRIP), ultimate pH in semimembranosus (pHSM), and ultimate pH in LM (pHLM). The test statistics for different traits at the same position are different, but the shapes of the curves are quite similar.

Figure 3. Quantitative trait loci segregation in different families of L* (lightness), ultimate pH in semimembranosus (pHSM), ultimate pH in LM (pHLM), and b* (yellowness) on SSC6. The arrows indicate QTL affecting these 4 traits on SSC6, which segregated simultaneously in family 4, 8, and 9.
al., 2003; Lee et al., 2003; Yue et al., 2003a,b; Ponsuksilii et al., 2005; van Wijk et al., 2006), with SSC6 and SSC15 being the most frequent 2 chromosomes harboring the QTL affecting pHLM. Only a few QTL affecting pHSM have been reported (Ciobanu et al., 2001; Qu et al., 2002; Kim et al., 2005), and they were located on SSC6, SSC15, and SSC18. In the current study, the QTL affecting pHLM and pHSM were mapped to the same position on SSC6 and SSC15, and their QTL log-likelihood ratio curves were also quite similar on these 2 chromosomes, indicating the same genes on these 2 chromosomes regulate pHLM and pHSM.

Drip loss is an important meat quality trait for the meat processing industry and consumers, and therefore it should be a part of the breeding goal (Borchers et al., 2007). In the current study, the 5 QTL significant at the 5% chromosome-wide level affecting drip loss were mapped to SSC2, SSC4, SSC6, SSC11, and SSC15, respectively. At regions close to the QTL detected in this study, some significant or suggestive QTL were reported by other studies (Bertram et al., 2000; de Koning et al., 2001; Thomsen et al., 2004; Kim et al., 2005; Pires et al., 2005; Rohrer et al., 2005; van Wijk et al., 2006), and these are therefore confirmed by the results of the current study. However, the current study is the first to find significant QTL affecting drip loss on SSC4 and SSC6 compared with the PigQTLdb (http://www.animalgenome.org/QTLdb/pig.html; Hu et al., 2005).

Several QTL affecting meat L* value (de Koning et al., 2001; Pérez-Enciso et al., 2002; Sato et al., 2003; Thomsen et al., 2004; Edwards et al., 2008) have been reported, but only a few of them were significant at a 5% chromosome-wide level. In the current study 8 QTL were found affecting meat L* value at the 5% chromosome-wide level, 2 of which were mapped to SSC1. The QTL affecting meat L* value on SSC6 is significant at the 1% genome-wide level, and that QTL has not been reported previously.

Previously, few QTL affecting a* values have been reported. Here we detected 8 QTL associated with a* values at the 5% chromosome-wide level. The QTL on SSC8 was mapped close to regions reported by Ovilo et al. (2002) and Beeckmann et al. (2003a). One genome-wide significant QTL also affecting the a* value was detected in the current study but at a different position from those reported by Yue et al. (2003b) and Edwards et al. (2008) on SSC6. The QTL affecting the a* value on SSC13 was mapped to the region close to the suggestive QTL position found by de Koning et al. (2001), indicating that some genes in the region may regulate the a* value. Only a few suggestive QTL affecting the b* value (de Koning et al., 2001; Edwards et al., 2008) have been detected previously. All 4 QTL detected in the current study were new; the QTL on SSC1 and SSC6 were significant at the 5 and 0.1% genome-wide level, respectively.

Meat quality traits are correlated genetically to each other (Le Bihan-Duval et al., 2003; Suzuki et al., 2005) to some extent. In our study, pHSM, pHLM, L*, and b* have similarly shaped log-likelihood ratio curves on SSC6. For the detected QTL positions, the estimated QTL effects for these traits were correlated with absolute values of estimated Pearson correlations greater than 0.88, indicating that the same gene on SSC6 regulates these traits simultaneously. Similarly, on SSC15, drip loss, pHLM, and pHSM have similarly shaped

Figure 4. Quantitative trait loci segregation in different families of drip loss (DRIP), ultimate pH in semimembranosus (pHSM), and ultimate pH in LM (pHLM) on SSC15. The arrows indicate QTL affecting pHLM and pHSM on SSC15 that segregated simultaneously in family 2, 4, and 5. The QTL affecting DRIP segregated in family 6 and 9.
log-likelihood ratio curves, and the correlation of the estimated QTL effects is 0.60 between drip loss and pHLM, −0.63 between drip loss and pHSM, and 0.79 between pHLM and pHSM. The QTL associated with L* and b* were mapped to the same position on SSC14, and the correlation between their estimated QTL effects is 0.85.

The results from the segregation analysis are consistent with the above interpretation. The QTL affecting L*, pHLM, pHSM, and b* on SSC6 segregated simultaneously in family 4, 8, and 9; and the QTL affecting pHLM and pHSM on SSC15 segregated simultaneously in family 2, 4, and 5. However, the QTL affecting drip loss on SSC15 segregated in family 6 and 9. Credibility intervals for the positions of QTL significant at the 5% genome-wide level were generally narrower than for those only significant at the 5 or 1% chromosome-wide level, and these QTL also seemed to segregate in more families. However, some QTL significant at the 5% chromosome-wide level segregated in 3 families, but their credibility intervals were wider. The width of a credibility interval of QTL for an outbred population depends on not only the QTL effect and whether there is 1 gene or several nearby genes affecting the trait, but also on the number of families segregating, the marker intensity in the region, and possibly also on segregation bias for the QTL. The likelihood profile curve is an integration of these factors.

In conclusion, numerous QTL associated with meat quality traits were revealed in this study. The results are very important because they give us more insights into traits that are not easily measured for breeding animals. Many QTL associated with meat quality traits with favorable and unfavorable alleles exist in the Duroc population, and favorable alleles can be used for pig breeding and may improve quality (and possibly profit) of pork products. Future research on MAS for meat quality traits would use a SNP chip to genotype a large number of densely spaced markers. The detected QTL may then be refined using such a chip and using maternal information and linkage disequilibrium (Meuwissen and Goddard, 2000; Lund et al., 2003), and then possibly be used in a selection scheme. However, the new paradigm for MAS is genomic selection (Meuwissen et al., 2001), where not just QTL with large effects (exceeding a certain stringent significance threshold) are used but also all QTL with minor effects (not exceeding any significance threshold). It seems likely that a future MAS scheme would be a genomic selection scheme.

**LITERATURE CITED**


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Supplementary Material

Supplementary material can be found at:
http://jas.fass.org/content/suppl/2010/08/13/jas.2009-2590.DC1.html

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