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Results of a whole-genome quantitative trait locus scan for growth, carcass composition and meat quality in a porcine four-way cross

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Summary

A whole-genome quantitative trait locus (QTL) scan for 31 phenotypes related to growth, carcass composition and meat quality was conducted using 1187 progeny of a commercial four-way cross. Animals were genotyped for 198 microsatellite markers that spanned the entire porcine genome. QTL analysis was conducted to extract information from paternal and maternal meioses separately using a rank-based nonparametric approach for half-sib designs. Nine QTL exceeded genome-wide significance: one QTL affecting growth (average daily gain on SSC1), two QTL influencing carcass composition (fatness on SSC3 and muscle mass on SSC15) and six QTL influencing meat quality (tenderness on SSC4 and SSC14; colour on SSC5, SSC6 and SSCX; and conductivity on SSC16). All but one of these coincided with previously reported QTL. In addition, we present evidence for 78 suggestive QTL with a combined false discovery rate of 40%.

Keywords carcass composition, growth, meat quality, pig, quantitative trait loci.

Introduction

Pig production relies increasingly on crossbreeding systems (e.g. Ollivier 1998). A typical four-way cross would involve specialized grand-parental lines selected in nucleus herds, which are mated in multiplier herds to produce hybrid sow and boar lines, which are in turn mated in commercial herds to produce the commercial product, i.e. finishers. The aim of this strategy is to combine the advantageous features that have been selected in the respective grand-parental lines in a supposedly optimal product, as well as to exploit potential hybrid vigour in both the hybrid parents (e.g. for fertility of the sows) and finishers.

An obvious disadvantage of the approach is the large amount of phenotypic variation in the finishers that inevitably results from the segregation of quantitative trait loci (QTL) for which the hybrid parents are heterozygous. One way to overcome this would be to introgress the most favourable QTL alleles in the respective grand-parental lines to ensure homozygosity of the hybrids at these loci. With this objective in mind, we herein describe the results of a whole-genome scan in a commercial four-way cross. The phenotypes considered in this experiment involved growth, carcass composition and meat-quality traits. We recognize that the introgression of multiple QTL is a tedious process in livestock species. However, the proposed approach could, in the first instance, target the QTL with strongest effects and be accelerated in the future by the synergistic use of marker-assisted selection and germline manipulation (Georges 1991).

In the proposed scheme, heterozygosity at loci contributing to heterosis would have to be maintained. As the utilized four-way cross is not suitable for the mapping of QTL underlying heterosis, we are, in parallel, performing a whole-genome scan in a purpose-built F2 pedigree obtained by intercrossing hybrids of the sow line so as to identify QTL, including heterotic QTL that influence female fertility. The results of this experiment will be described elsewhere.

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Materials and methods

Pedigree description

The pedigree comprised 1187 progeny from a commercial four-way cross. Hybrid sows were obtained by mating two distinct Landrace × Large White composite lines selected for number of piglets born alive, total weaning weight and longevity. Hybrid boars were obtained by mating a Large White and a composite Large White × Piétrain line selected respectively for growth and lean meat. Progeny were reared from May 2000 to April 2001. They were all born on the same farm and were transferred at the age of 2 months to the finishing farm where they were kept until slaughter weight. The number of offspring ranged from 5 to 19 for hybrid sows (mean of 9) and from 169 to 334 for hybrid boars (mean of 237). DNA was extracted from blood or sperm for all hybrid parents and progeny.

The entire pedigree was genotyped by VHL b.v. (Wageningen, the Netherlands) for the *RYR1* R615C mutation associated with increased muscle mass and porcine stress syndrome (Fujii *et al.* 1991), as well as the *PRKAG3* R200Q mutation associated with increased muscle mass (Rendement Napole) and high glycogen content in skeletal muscle (Milan *et al.* 2000). Neither of these two mutations were present in our families. The IGF2-intron3–3072G>A mutation, associated with increased muscle mass when inherited from the father (Van Laere *et al.* 2003), was fixed in the hybrid boars, yet it segregated in the hybrid sows (N. Buys, unpublished observations).

Phenotypic measurements

Progeny were slaughtered at 215 ± 20 days at a target weight of 109 kg (±8). Thirty-one phenotypes, including growth, carcass composition and meat quality measurements were recorded on all progeny (Table S1).

Growth traits Average daily gain (ADG) (kg) was calculated as the live weight gained divided by the numbers of days from birth to slaughter. Average daily carcass lean meat gain (kg) was calculated as the carcass weight multiplied by the carcass lean meat percentage estimated with a CGM device (Capteur Gras/Maigre Sydel, Lorient, France), divided by the number of days from birth to slaughter.

Carcass composition Fat thickness at the narrowest part of gluteus medius (SKGFAT) (mm), maximum semimembranosus width (SKGMAX) (mm), minimum carcass width (SKGMIN) (mm) and angle of the semimembranosus (SKGANGL) (°) were measured on the left carcass side using a PG50 apparatus (Eurocontroll Belgium, Vilvoorde, Belgium). Those four physical measurements were combined into an estimate of the carcass lean meat percentage (SKGMEAP) (%) using multiple regression as described (Casteels 1989). The killing-out (KO) yield (%) was calculated as the cold carcass weight divided by the live weight determined just before slaughter. In addition, fat depth covering the longissimus was manually measured at rib 1 (FATRIB1), rib 7 (FATRIB7) and lumbar vertebra 3 (FATLUMB3). The number of ribs (NUMRIB), number of vertebrae (NUMVERT) and carcass length (LENGTH) (cm) were recorded as well.

Meat quality traits The pH was measured 40 min and 24 h postmortem in the longissimus at rib 13 (PH1LOIN and PH2LOIN) and in the semimembranosus (PH1HAM and PH2HAM) using a Knick Portamess 654 pH meter (Knick, Berlin, Germany) equipped with an Ingold Xerolyt electrode (Mettler-Toledo, Greifensee, Switzerland). Temperature (T1LOIN) (°C) was measured 40 min postmortem in the longissimus at a depth of approximately 7 cm, using a Digitap LHM 900 apparatus (Digitap, Bornem, Belgium). Conductivity (μS) was measured 24 h postmortem in the longissimus (PQM2LOIN) and semimembranosus (PQM2HAM) using a Pork Quality Meter (Tecpro GmbH, Aichach, Germany). PH1LOIN, PH2LOIN, MH1HAM, PH2HAM, T1LOIN, PQM2LOIN and PQM2HAM were computed as the average of the corresponding measurements made on the left and right halves of the carcass.

Twenty-four hours postmortem, a piece of longissimus from the right carcass side anterior to the last rib (±7-cm thick) was removed, deboned and sliced (2.5-cm thick, ±150 g). Slices were used for various measurements. Meat colour was assessed using the six-point Japanese colour standards system (JAPCOLOR) (FHK Co., Tokyo, Japan) (Nakai *et al.* 1975) and by determining the CIELAB colour co-ordinates (CIE-a*, CIE-b* and CIE-L*) by means of a HunterLab MiniScan device after a 30-min blooming time (D65 light source, 10° standard observer, 45°/0° geometry, 1 in light surface, white standard; Hunter Associates Laboratory, Inc., Reston, VA, USA). Water holding capacity (WATER) (mg) was assessed using the filter paper method of Kauffman *et al.* (1986), and it represents the uptake of fluid by a filter paper following a standard procedure. Thaw loss (THAWLOSS) (%) was determined as the difference between the initial weight of the sample before frozen storage at −18 °C in a vacuum bag and the weight after overnight thawing at 4 °C, divided by the initial weight. The sample was gently dried with paper towel after thawing. Cooking loss (COOKLOSS) (%) was determined as the difference of the sample weight before and after boiling in a closed plastic bag in water at 70 °C for 40 min followed by cooling in cold tap water for 15 min, divided by the weight before boiling. Shear force (SF) (N), force at first peak (SFP) (N) and total shear work (WORK) (J) of these cooked samples were determined on cylindrical cores (diameter 1.25 cm) taken parallel and sheared (speed 200 mm/min) perpendicular to the longitudinal orientation of muscle fibres using a Lloyd TA 500 Texture Analyser (Analis, Namur, Belgium)

equipped with a triangular Warner–Bratzler shear. Eight measurements were recorded per meat sample (processed with Nexigen3.0/Ondio software; Lloyd Instruments Ltd, Fareham, UK) and were averaged for further analyses.

The raw phenotypes were corrected for sire, dam, sex and year/season when these fixed effects were significant (Table S1). The effects to include in the model were selected by stepwise regression implemented using the SAS software (SAS 9.1.3; SAS Inst., Cary, NC, USA).

Microsatellite genotyping

The entire pedigree was genotyped for 198 microsatellite markers spanning the porcine genome (http://www.animalgenome.org/pigs/maps/marcmap.html). Multiplex polymerase chain reaction and size fractionation were performed using standard procedures and automated capillary sequencers (ABI3100 or ABI3700; Applied Biosystems, Foster City, CA, USA). Alleles were called manually and independently by two experienced scientists using GENOTYPER v3.6 (Applied Biosystems, Foster City, CA, USA). The output of GENOTYPER was loaded in a purpose-built Oracle database (W. Coppieters, unpublished data) that: (i) automatically checks for erroneous identification of internal size standards; (ii) recomputes fragment size based on the local Southern method; (iii) compares the allele calls of the two initial users and allows a 'superuser' to correct discrepancies; (iv) shifts all fragment sizes within a run to maximize between-run fragment size matching for a reference individual (to correct for the use of different sequencers or size standards); (v) allows for manual allele binning based on the distribution of allele sizes across runs; and (vi) performs consistency checks including misinheritances.

Map construction and information content

Marker maps were constructed using CRIMAP v2.4 (Lander & Green 1987). Two 'pedigree' files were generated to extract linkage information from the hybrid boars (PA analysis) and sows (MA analysis) respectively. The PA file included five paternal half-sib families corresponding to the number of hybrid boars. All sibs were considered to be paternal half-sibs (even if actually full-sibs) and to have unrelated mothers. Sows were thus replicated multiple times in these pedigrees, each time with a single offspring. The sows' parents were assumed unknown thus providing no phase and hence no linkage information. The MA file included 127 maternal half-sib pedigrees corresponding to the number of hybrid sows. All maternal half-sibs were assumed to have unrelated fathers. Boars were thus replicated multiple times in these pedigrees, each time with a single offspring. The boars' parents were assumed unknown thus providing no phasing and hence no linkage information. The two files were merged prior to CRIMAP analysis. Mortons test for heterogeneity (Morton 1956) was applied to the two-point LOD scores to detect residual genotyping anomalies. Multipoint marker maps were constructed using the BUILD, FLIP and CHROMPIC options of CRIMAP. The information content (IC) of the maps was measured separately for the male and female meioses as described previously (Coppieters *et al.* 1998).

QTL mapping

Quantitative trait loci mapping was performed using a rank-based nonparametric approach for half-sib designs implemented with the HSQM software (Coppieters *et al.* 1998). The analysis was performed separately to extract information from the paternal (PA analysis) and maternal meioses (MA analysis) respectively, using the pedigree files generated as described above. Because of their distinct origins, hybrid boars and sows can indeed not be assumed to be heterozygous for the same QTL. Moreover, by estimating QTL effects nested within half-sib families one does not make the assumption that alternate QTL alleles are fixed in the respective grand-parental lines.

The statistical significance of a given QTL was determined by comparison of the associated test statistic with the distribution of the largest genome-wide test statistics obtained from the analysis of 10 000 phenotype permutations (Doerge & Churchill 1996). The statistical significance of a QTL was expressed as $\log(1/p)$, where p is the proportion of phenotype permutations for which the QTL test statistic was exceeded anywhere across the genome. QTL were considered significant when $\log(1/p)$ was superior to 1.30 corresponding to a P-value of 0.05. Following Lander & Kruglyak (1995), QTL were considered suggestive if the test statistic exceeded a threshold reached on average once per phenotype permutation. Assuming that 'threshold exceeding events' are Poisson distributed, the proportion of permutations for which the suggestive threshold is not exceeded anywhere in the genome is $e^{-1} = 0.37$. The p value corresponding to the suggestive threshold thus corresponds to the proportion of permutations for which the suggestive threshold is exceeded at least once across the genome which is $1 - 0.37 = 0.63$, and the corresponding $\log(1/p) = 0.2$.

When analysing n distinct traits, the suggestive threshold is expected to be exceeded on average n times under the null hypothesis of no QTL. This expected number of suggestive QTL is independent of the correlation that may exist between traits. To see this, imagine that the n traits are perfectly correlated, thus that one has in fact analysed n times the same trait. One expects the suggestive threshold to be exceeded once somewhere across the genome for that trait; but as the trait has been reanalysed n times, this yields n suggestive QTL with identical position. Now imagine that the n traits are in fact two uncorrelated traits that have each been analysed $n/2$ times. Each trait will yield on average one suggestive QTL replicated $n/2$ times for a total of n suggestive QTL, etc. Obviously if the n traits are uncorrelated, one

expects a different suggestive QTL for each trait for a total of n suggestive QTL. If one finds $m > n$ suggestive QTL with the real data, the expected proportion of true QTL amongst suggestive QTL equals $(m - n)/m$ and the false discovery rate equals n/m. When compiling the number of suggestive QTL, we conservatively considered maximum one QTL per chromosome for a given trait. Indeed, when two suggestive QTL are found on the same chromosome it is often difficult to differentiate whether the two peaks truly reflect the action of distinct or of a single QTL.

Confidence intervals for QTL locations were estimated by bootstrapping (Visscher *et al.* 1996). QTL allele substitution effects were estimated by linear regression as described (Coppieters *et al.* 1998). For the chromosomes with significant QTL in the PA analysis, a chromosome-wide regression analysis was performed separately for each boar family. The allele substitution effect (corresponding to the slope of the regression line) is reported at the most significant within-family position when exceeding the chromosome-wide $\log(1/p)$ value of 1.30 determined by a permutation test.

Results

The main features of the obtained porcine marker map, which included 189 autosomal and nine X-linked microsatellites, are summarized in Table S2. The number of markers per chromosome averaged 10 (range of 4–15) with a mean marker spacing (mean ± SD) of 12.6 ± 9.6 cM (range of 0–47), 14.3 ± 11.2 cM (range of 0–52.2) and 11.5 ± 10.0 cM (range of 0–45.8) for sex averaged, female and male maps respectively. Marker order was supported by odds superior to 1000 for all but three marker pairs. The most likely order agreed with published marker maps (USDA MARC map 2006; http://www.marc.usda.gov/genome/swine/swine.html) except for three other marker pairs. The sex-averaged autosomal length was 21.64 Morgans (Kosambi), while female and male autosomal maps measured 25.80 and 19.84 Morgans respectively. Despite the overall larger size of the female map as expected, the male recombination rate exceeded the female one for 38.5% (68/174) of marker intervals. Contrary to what is typically observed in human, higher male than female recombination rates were not confined to the ends of chromosome arms. These findings are in general agreement with previous maps (e.g. Marklund *et al.* 1996).

The IC of the marker map for both the PA and MA analyses is shown in Fig. 1. On average, 61% of the potential information was extracted from the paternal chromosomes and 56% from the maternal chromosomes. The IC exceeded 50% for 75% of the genome in the PA analysis, and for 69% of the genome in the MA analysis.

Seven QTL exceeding genome-wide significance were detected in the PA analysis and two in the MA analysis (Fig. 1). One of the padumnal (i.e. transmitted by the father) QTL influenced growth (ADG on SSC1), one fat deposition (SKGFAT on SSC3), one muscularity (SKGMEAP on SSC15) and four meat quality (colour on SSC5 and SSC6, tenderness on SSC14 and conductivity on SSC16). The two madumnal (i.e. transmitted by the mother) QTL affected meat quality (tenderness on SSC4 and colour on SSCX). The most likely marker bracket, confidence interval and allele substitution effects for the significant QTL in the PA (A) and MA (B) analysis are reported in Tables 1 & 2 respectively. Allele substitution effects were estimated separately within each of the five paternal half-sib families using linear regression (Coppieters *et al.* 1998), as the five hybrid boars could not be assumed to be heterozygous for all QTL thus precluding an across-family estimation. Allele substitution effects were not estimated in the MA analysis as the number of offspring per hybrid sow was too small to allow reliable estimates. Despite the fact that some hybrid sows were heterozygous *GA* at the IGF2-intron3-3072 position, no evidence was found in the MA analysis for a QTL affecting carcass composition on SSC2. This was as expected given the known imprinted nature of this QTL (Van Laere *et al.* 2003).

In addition to the seven QTL exceeding genome-wide significance, there were many suggestive QTL scattered throughout the genome (Fig. 1). The suggestive threshold of 0.2 was exceeded 78 times in the PA analysis. In this enumeration, we considered only the highest peak per trait-chromosome combination. Given the fact that we have analysed 31 traits, this is more than twice as much as expected by chance alone, corresponding to an expected proportion of true QTL among suggestive peaks of 60% or a false discovery rate of 40%. The significance and most likely position for the suggestive QTL obtained in the PA analysis are reported in Table 3.

Analysing the output of the MA analysis in a similar way yielded 34 suggestive QTL corresponding to an estimated proportion of true QTL of 9%. These lower figures are likely due to the lower power of the MA analysis as a result of the lower number of offspring per hybrid sow. Because of the associated high false discovery rate, the corresponding suggestive QTL are not reported.

There was no overlap between the significant QTL uncovered in the PA and MA analyses. To further examine whether the analysed traits might be influenced by common QTL in the sow and boar lines, we measured the correlation between the chromosome-wide P-values obtained in the PA and MA analyses. The comparisons were carried out for each trait and at each marker position yielding 5859 observations (189 autosomal markers × 31 traits). Although marginally significant ($P = 0.036$), the correlation was very low (0.027) corresponding to a regression coefficient of 0.016. These results have to be considered with caution as the power of the proposed approach is not known. Nevertheless, they suggest that the analysed traits were influenced by mostly distinct gene sets in the hybrid boar and sow lines.

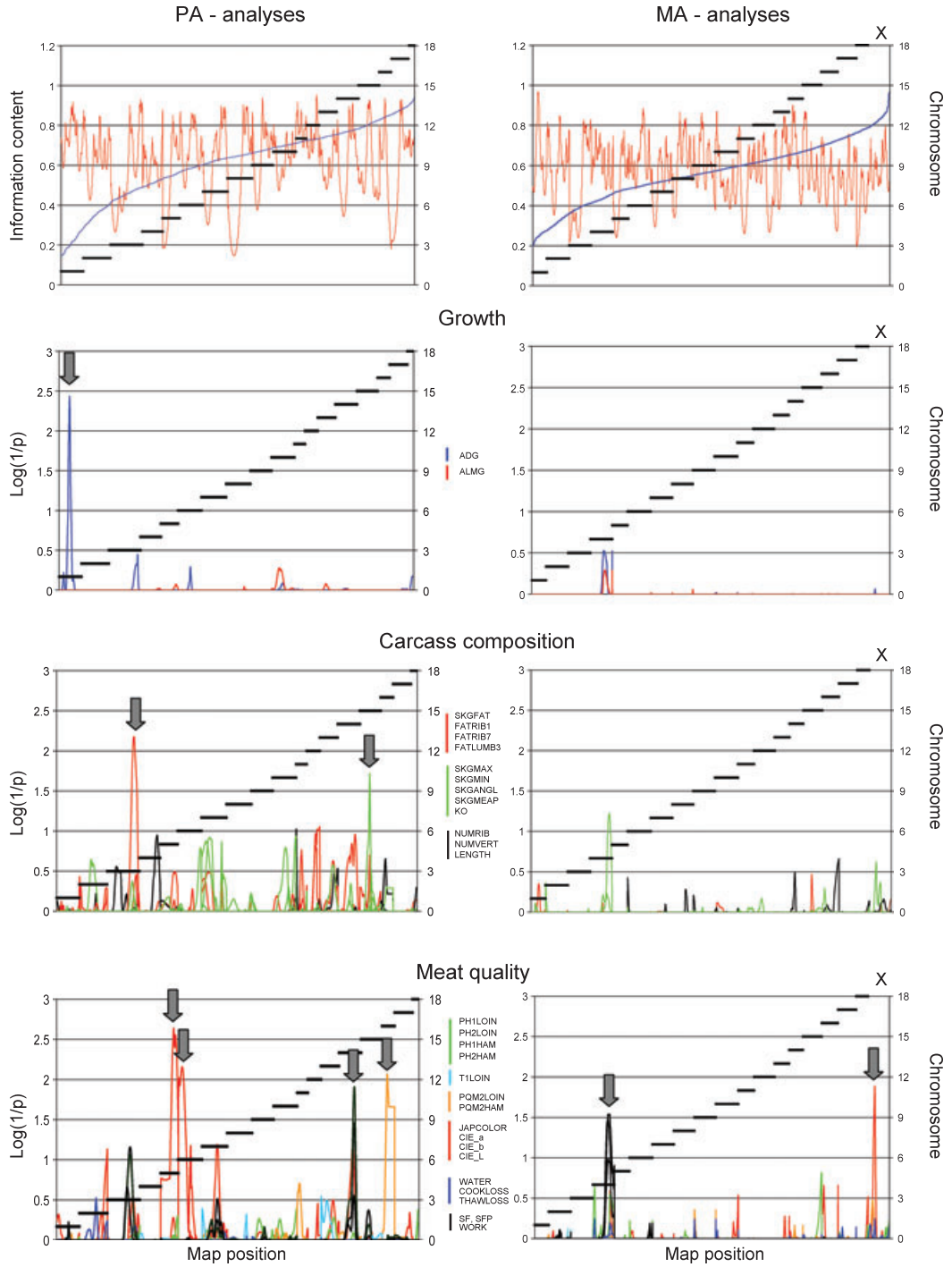

Figure 1 Genome-wide information content and location scores (log(1/*p*)) for growth, carcass composition and meat quality traits in the PA (left) and MA (right) analysis. The red line shows the information content along the porcine marker map (black horizontal bars correspond to individual chromosomes); the blue line shows map positions sorted by increasing (left to right) information content. The location scores along the marker map are shown for all traits grouped as indicated (1. growth: average daily gain and average daily carcass lean meat gain; 2. carcass composition: fat deposition, muscle mass and length; 3. meat quality: pH, temperature, conductivity, colour, water loss and tenderness). Quantitative trait loci exceeding genome-wide significance are marked by the arrows.

Discussion

In this study, one QTL influencing growth (ADG on SSC1), two QTL influencing carcass composition (SKGFAT on SSC3 and SKGMEAP on SSC15) and six QTL influencing meat quality (tenderness on SSC4 and SSC14; colour on SSC5, SSC6 and SSCX; and conductivity on SSC16) were identified. We feel quite confident that most if not all these nine

Table 1 Genome-wide significant quantitative trait loci (QTL): PA analysis.

Across-family analysis					Within-family analysis				
SSC	Trait	Marker interval	CI[1]	Log(1/*p*)[2]	Fam[3]	Pos[4]	Log(1/*p*)[5]	ASE[6]	References[7]
Growth traits									
1	ADG (kg)	*S0331–SW1301*	60–129	2.43	1	62	3.52	0.024	Casas-Carrillo *et al.* (1997), Paszek *et al.* (1998) and Rohrer (2000)
					4	81	1.77	0.014	Kim *et al.* (2000), Bidanel *et al.* (2001) and Beeckmann *et al.* (2003a)
Carcass composition									
3	SKGFAT (mm)	*SW102–SW349*	116–175	2.17	2	157	3.15	2.17	Su *et al.* (2002b) and Beeckmann *et al.* (2003b)
15	SKGMEAP (%)	*KS911–SW1119*	0–114	1.72	2	55	2.62	0.869	Kuryl *et al.* (2003)
					3	55	2.52	0.964	
Meat quality traits									
5	CIE-b*	*ACR–SW310*	0–91	2.64	3	58	1.99	0.368	Malek *et al.* (2001b) and Rohrer *et al.* (2005)
					4	80	1.61	0.248	
					5	70	1.88	0.382	
6	CIE-a*	*S0035–SW824*	0–92	2.15	1	19	1.48	0.39	Geldermann *et al.* (2003) and Nii *et al.* (2005)
					2	75	1.47	0.32	
					4	37	4.30	0.49	
					5	1	1.41	0.33	
14	SF (N)	*SW1631–SW1557*	0–109	1.30	4	78	2.85	2.375	Malek *et al.* (2001b)
	SFP (N)	*SW1631–SW2515*	0–120	1.91	5	100	1.37	1.925	
					4	79	3.22	2.43	
					5	99	1.39	1.94	
16	PQM2HAM (μS)	*S0111–S0026*	0–81	2.06	1	65	2.85	1.762	Pierzchala *et al.* (2003)
					3	34	1.97	0.693	
					4	25	1.79	0.590	

[1]Confidence interval obtained by bootstrapping (cM).
[2]Genome-wide log(1/*p*) – rank-based method.
[3]Half-sib family.
[4]Position at highest chromosome-wide log(1/*p*) value (cM).
[5]Chromosome-wide log(1/*p*) – linear regression.
[6]Allele substitution effect.
[7]Papers reporting QTL with similar effects at comparable positions (non-exhaustive list).

Table 2 Genome-wide significant quantitative trait loci (QTL): MA analysis.

SSC	Trait	Marker interval	CI[1]	log(1/*p*)[2]	References[3]
Meat quality traits					
X	CIE-b*	*SW980–SW2470*	17–61	1.89	–
4	SFP (N)	*SW839–SW856*	73–159	1.54	Rohrer *et al.* (2005)
	Work (J)	*SW839–SW856*	73–159	1.54	

[1]Confidence interval obtained by bootstrapping (cM).
[2]Genome-wide log(1/*p*) – rank-based method.
[3]Papers reporting QTL with similar effects at comparable positions (non-exhaustive list).

QTL are true, as: (i) the utilized threshold for significance was very stringent and (ii) very similar QTL (in terms of affected trait and location) have been reported by others for eight of the nine QTL (Tables 1 & 2). Their effect is large enough that at least some of them should be amenable to fine mapping if not to positional identification of the causal quantitative trait nucleotides (QTN). The feasibility of QTN identification in livestock populations has recently been demonstrated in at least four cases (e.g. Grisart *et al.* 2002, 2004; Van Laere *et al.* 2003; Cohen-Zinder *et al.* 2005; Clop *et al.* 2006). These early successes should, however, be downtoned to some extent by the recent demonstration in *Saccharomyces cerevisiae* of the sometimes extremely complex molecular architecture of QTL (Steinmetz *et al.* 2002; Deutschbauer & Davis 2005). Identifying the QTN or at least haplotypes in strong linkage disequilibrium should allow for marker assisted selection, including the selection for the most favourable QTL alleles in the grand-parental lines so as to increase homozygosity of the hybrid parents at the corresponding loci.

In addition to these nine significant QTL, we present evidence in this work for an estimated approximately 47 true QTL amongst the 78 peaks exceeding the suggestive threshold. The genuine nature of many of these QTL is

Table 3 Genome-wide suggestive quantitative trait loci (QTL): PA analysis.

SSC	Trait	Marker interval	Position[1]	Log(1/*p*)	References[2]
Growth traits					
3	ADG	*S0167–SW314*	156.4	0.44	Casas-Carrillo *et al.* (1997), Bidanel *et al.* (2001), De Koning *et al.* (2001b) and Beeckmann *et al.* (2003b)
6	ADG	*SW1473*	70.4	0.29	Rohrer (2000), Bidanel *et al.* (2001), De Koning *et al.* (2001b), Su *et al.* (2002a) and Sato *et al.* (2003)
10	ALMG	*SW1894–SW2195*	45.1	0.28	Wada *et al.* (2000) and De Koning *et al.* (2001b)
Carcass composition					
2	SKGFAT	*S0036*	149.9	0.23	Knott *et al.* (1998), De Koning *et al.* (1999, 2000), Nezer *et al.* (1999), Milan *et al.* (2002) and Varona *et al.* (2002)
2	SKGANGL	*SW1201–SW1026*	62.1	0.65	–
2	FATRIB1	*SWR2516–KVLQT1*	5.1	0.35	Knott *et al.* (1998) and De Koning *et al.* (1999, 2000)
2	FATRIB7	*SWR2516–KVLQT1*	0	0.43	Nezer *et al.* (1999), Milan *et al.* (2002) and Varona *et al.* (2002)
2	NUMVERT	*S0370–SWR2157*	89.4	0.22	–
3	SKGANGL	*SW102–SW2047*	126.2	0.37	–
3	FATRIB1	*S0358–S0167*	154.6	0.46	Knott *et al.* (1998) and Beeckmann *et al.* (2003b)
3	LENGTH	*SW1443*	99	0.21	Beeckmann *et al.* (2003b)
3	NUMVERT	*SW2021–SW72*	45.2	0.55	–
4	NUMVERT	*SW58–SW856*	103.7	0.95	–
5	FATRIB7	*S0005–SW152*	76.9	0.49	Knott *et al.* (1998), Malek *et al.* (2001a), Milan *et al.* (2002), Lee *et al.* (2003), Rohrer *et al.* (2005) and Van Wijk *et al.* (2006)
6	SKGFAT	*S0228–SW824*	85.2	0.28	De Koning *et al.* (2001b), Ovilo *et al.* (2002), Varona *et al.* (2002) and Yue *et al.* (2003a)
6	SKGANGL	*SW322–SW607*	133.2	0.79	–
7	SKGFAT	*SWR773–SW581*	108.1	0.43	Rohrer & Keele (1998), Rohrer (2000), Wada *et al.* (2000), Bidanel *et al.* (2001), Malek *et al.* (2001a), Varona *et al.* (2002) and Yue *et al.* (2003b)
7	SKGMEAP	*SWR773–SW581*	108.1	0.87	Milan *et al.* (2002)
7	SKGMIN	*SW1873–SW1369*	22.2	0.87	–
7	SKGANGL	*SW1873–SW1369*	38.6	0.92	–
7	FATRIB1	*SW1873–SW1369*	12.2	0.41	Rohrer & Keele (1998), Rohrer (2000), Wada *et al.* (2000) and Bidanel *et al.* (2001)
7	FATRIB7	*SW1873–SW1369*	34.4	0.49	Malek *et al.* (2001a), Varona *et al.* (2002) and Yue *et al.* (2003b)
8	SKGMEAP	*S0178*	132.2	0.22	–
9	SKGANGL	*SW983*	0	0.21	–
10	SKGFAT	*SW951–SWR67*	114.8	0.21	Rohrer & Keele (1998) and Rohrer *et al.* (2005)
10	SKGANGL	*SW2067*	131.7	0.94	–
10	KO	*SW920*	92.3	0.29	–
11	SKGFAT	*S0009–SW1377*	32.8	0.76	Dragos-Wendrich *et al.* (2003a)
11	SKGMEAP	*SW66*	60.8	0.25	–
11	NUMRIB	*S0385*	0	1.02	–
12	SKGFAT	*SW605*	74.2	1.05	Malek *et al.* (2001a) and Yue *et al.* (2003c)
12	FATLUMB	*SW1307–SW874*	51.3	0.82	Malek *et al.* (2001a) and Yue *et al.* (2003c)
13	SKGFAT	*SW1495–SW398*	73.6	0.63	Yu *et al.* (1995), Malek *et al.* (2001a) and Nezer *et al.* (2002)
13	SKGMEAP	*SW1495–SW398*	72.8	0.58	Van Wijk *et al.* (2006)
13	NUMVERT	*S0289*	99.8	0.53	–
14	SKGFAT	*SW886–SW761*	94.7	0.96	Rohrer & Keele (1998), Malek *et al.* (2001a), Varona *et al.* (2002) and Dragos-Wendrich *et al.* (2003b)
14	SKGANGL	*SW210–SW2504*	67.8	0.34	–
15	SKGFAT	*SW1111–SW1989*	53.5	0.69	Knott *et al.* (1998) and Kuryl *et al.* (2003)
15	SKGANGL	*SW2131–SW1263*	62.7	0.48	–
15	FATRIB1	*SW1119*	113.9	0.24	Knott *et al.* (1998) and Kuryl *et al.* (2003)
15	FATRIB7	*KS911–SW2072*	2.5	0.30	Knott *et al.* (1998) and Kuryl *et al.* (2003)
16	SKGMAX	*SW977–S0026*	33.5	0.30	–
16	NUMRIB	*S0298–SW81*	27.8	0.65	–
18	NUMRIB	*SWR414*	29.9	0.29	–

Table 3 Continued.

SSC	Trait	Marker interval	Position[1]	Log(1/*p*)	References[2]
Meat quality traits					
1	CIE-a*	*SW64–SW2130*	9.1	0.32	De Koning *et al.* (2001a) and Rohrer *et al.* (2005)
1	WORK	*SWR337–SW970*	68.9	0.22	–
2	CIE-b*	*S0036*	149.9	1.13	Malek *et al.* (2001b), Rohrer *et al.* (2005) and Van Wijk *et al.* (2006)
2	CIE-L*	*SW1879–SWR345*	117.1	0.34	
2	WATER	*S0036*	149.9	0.23	
2	COOKLOSS	*S0370–SWR2157*	89.4	0.52	
3	CIE-L*	*SW102–SW2047*	133.8	0.54	–
3	SF	*SW102–SW2047*	118.5	1.15	–
3	SFP	*SW102–SW2047*	117.6	1.05	–
3	WORK	*SW1443–SW902*	100.1	0.66	–
5	PH2LOIN	*SW152*	88.7	0.30	Malek *et al.* (2001b)
5	CIE-a*	*SW2425–S0005*	63.5	0.28	Malek *et al.* (2001b) and Rohrer *et al.* (2005)
7	T1LOIN	*SW1873*	0	0.39	–
7	JAPCOLOR	*SW1369–SW1856*	49.4	0.25	De Koning *et al.* (2001a), Malek *et al.* (2001b) and Ovilo *et al.* (2002)
7	CIE-b*	*SW175–SW632*	78.6	1.19	
7	CIE-L*	*SW1369–SW1856*	49.4	0.21	
7	SF	*SW175–SW632*	79.4	0.25	–
7	SFP	*SW1369–SW1856*	46.7	0.25	–
7	WORK	*SW175–SW632*	79.4	0.51	–
8	T1LOIN	*S0017*	101	0.32	–
9	PH1HAM	*SW911*	38.1	0.26	De Koning *et al.* (2001a)
10	PH1LOIN	*SW2067*	131.7	0.39	–
11	PQM2LOIN	*S0391–SW1632*	13.6	0.70	–
12	CIE-a*	*SW168–S0090*	57.4	0.45	Malek *et al.* (2001b)
13	PH1LOIN	*SW1495–SW398*	73.6	0.28	Rohrer *et al.* (2005) and Van Wijk *et al.* (2006)
13	T1LOIN	*S0282*	0	0.54	–
13	CIE-a*	*SW168–S0090*	67	0.50	De Koning *et al.* (2001a)
14	CIE-b*	*SW210–SW2504*	71.4	1.17	De Koning *et al.* (2001a) and Rohrer *et al.* (2005)
14	WORK	*SW210–SW2504*	78.7	0.55	
15	SF	*SW2072–S0004*	38.8	0.37	Rohrer *et al.* (2005)
17	CIE-b*	*S0359–S0332*	80.6	0.34	Malek *et al.* (2001b) and Rohrer *et al.* (2005)
18	PH2LOIN	*SWR414*	29.9	0.22	De Koning *et al.* (2001a) and Dragos-Wendrich *et al.* (2003c)
18	PH2HAM	*SWR414*	29.9	0.37	Van Wijk *et al.* (2006)

[1]Position at maximal log(1/*p*) value (cM).

[2]Papers reporting QTL with similar effects at comparable positions (non-exhaustive list).

further supported by the fact that very similar effects at comparable positions have been reported by others (Table 3). These large numbers of suggestive QTL, combined with evidence that the analysed traits are mainly controlled by distinct set of genes in the paternal and maternal lines, supports the true polygenic nature of the analysed traits with – as expected from classical quantitative genetic theory (e.g. Hayes & Goddard 2001; Orr 2005) – few QTL with large 'detectable' effects and many more QTL with moderate-to-small effects. Identifying or even fine mapping the QTN underlying these moderate-sized effects is likely to be much more challenging. Therefore, approaches that aim to take advantage of the extensive linkage disequilibrium that has been observed in most domestic species (Farnir *et al.* 2000; Sutter *et al.* 2004; Harmegnies *et al.* 2006) and the availability of large numbers of SNP markers for most livestock species combined with cost-effective, high-throughput genotyping technology (Murray 2005; Hachmann & Lebl 2006; Ireland *et al.* 2006) to capture at least part of the corresponding polygenic variation in so-called 'genomic selection' strategies (Meuwissen *et al.* 2000) without necessarily understanding the molecular details of the underlying biology, may today be a pragmatic compromise.

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Supplementary Material

The following supplementary material is available for this article online from http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2052.2006.01523.x:

Table S1 Description of the analysed traits.

Table S2 Porcine marker map.

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