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Microsatellite mapping of quantitative trait loci affecting meat quality, stress hormones and production traits in Duroc × Large White F2 pigs

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An F2 cross between Duroc and Large White pigs was carried out in order to detect quantitative trait loci (QTL) for 11 meat quality traits (L, a* and b* Minolta coordinates and water-holding capacity (WHC) of two ham muscles, ultimate pH of two ham and one loin muscles), 13 production traits (birth weight, average daily gain during post-weaning and fattening periods, carcass fat depths at three locations, estimated lean meat content, carcass length and weights of five carcass cuts) and three stress hormone-level traits (cortisol, adrenaline and noradrenaline). Animals from the three generations of the experimental design (including 456 F2 pigs) were genotyped for 91 microsatellite markers covering all the autosomes. A total of 56 QTL were detected: 49 reached the chromosome-wide level (suggestive QTL with a maximal probability of 0.05) and seven were significant at the genome-wide level (with a probability varying from 6×10^{-4} to 3×10^{-3}). Twenty suggestive QTL were identified for ultimate pH, colour measurements and WHC on chromosome (SSC) 5, 6, 7, 8, 9, 11, 13, 14, 15 and 17. For production traits, 33 QTL were detected on all autosomes except SSC6, 8 and 9. Seven of these QTL, located on SSC2, 3, 10, 13, 16 and 17, exceeded the genome-wide significance threshold. Finally, three QTL were identified for levels of stress hormones: a QTL for cortisol level on SSC7 in the cortisol-binding globulin gene region, a QTL for adrenaline level on SSC10 and a QTL for noradrenaline level on SSC13. Among all the detected QTL, seven are described for the first time: a QTL for ultimate pH measurement on SSC5, two QTL affecting birth weight on SSC2 and 10, two QTL for growth rate on SSC15 (during fattening) and 17 (during post-weaning) and two QTL affecting the adrenaline and noradrenaline levels. For each QTL, only one to five of the six F1 sires were found to be heterozygous. It means that all QTL are segregating in at least one of the founder populations used in this study. These results suggest that both meat quality and production traits can be improved in purebred Duroc and Large White pigs through marker-assisted selection. It is of particular interest for meat quality traits, which are difficult to include in classical selection programmes.*

Keywords: pig, QTL, meat quality, production, stress hormones

Implications

The search of molecular markers associated with meat quality traits is of particular interest in pigs as these traits are difficult to assess in live animals and thus, difficult to include in objectives of classical selection programmes.

Introduction

Since the first quantitative trait loci (QTL) mapping study in pigs was published by Andersson *et al.* (1994), more than 5600 QTL affecting almost 550 different traits have been identified in different porcine populations (PigQTLdb; Hu *et al.*, 2007). Although meat quality traits are difficult to assess in live animals and are thus good candidates for marker-assisted selection, only a small part (about 15%) of the QTL identified so far concerns meat quality. Furthermore, most of the QTL were identified in studies using exotic populations of pigs, like Chinese or wild animals. When QTL are detected in such populations, they cannot be directly used in selection programmes and additional studies are required to confirm the existence of these QTL in commercial populations. Nevertheless, genome scans are carried out on an increasing

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number of crosses of commercial populations: Yorkshire × Berkshire (Malek *et al*., 2001a and 2001b), Piétrain × Large White (Nezer *et al*., 2002), Iberian × Landrace (Varona *et al*., 2002), Hampshire × Landrace (Karlskov-Mortensen *et al*., 2005) or Duroc × Piétrain populations (Liu *et al*., 2007; Edwards *et al*., 2008a and 2008b) and even on purebred commercial populations (Evans *et al*., 2003; Vidal *et al*., 2005; Tribout *et al*., 2008). All these studies revealed a large number of QTL, suggesting that different alleles are fixed in distinct commercial populations or that QTL are still segregating in purebred populations after many generations of selection.

Both Duroc and Large White breeds are major commercial pig populations. Nevertheless, the two breeds differ to some extent for several meat quality and production traits. In particular, Duroc pigs have a higher intramuscular fat content and are considered to have a better meat quality than Large White pigs. Pig breeds with a higher content of fat like Duroc also produce more cortisol (e.g. see Désautés *et al*., 1997) due to the fact that secretion of cortisol favours the accretion of fat at the expense of proteins (Devenport *et al*., 1989). Other stress hormones (adrenaline and noradrenaline), released by the sympathetic nervous system consecutively to slaughtering stress, can reduce muscle glycogen content and thus *post-mortem* acidification, leading to a degradation of meat quality by producing DFD-type (dark, firm and dry) meat (Fernandez and Tornberg, 1991). The inhibition of stress hormone secretion could thus be associated with an improvement of both some fatness and meat quality traits.

In order to map QTL for meat quality and other associated traits, a three-generation resource population was developed at INRA by mating Large White sows to Duroc boars. The F2 animals were measured for a large number of meat quality traits. Stress hormone levels, which have been found to be related to meat quality in the F2 population (Foury *et al*., 2005), and major production traits were also measured. The F2 Duroc × Large White population has already allowed detecting QTL for intramuscular fat content and fatty acid composition in the *longissimus dorsi* muscle (Sanchez *et al*., 2007). In this study, we investigated the QTL for other meat quality criteria, stress hormone levels and the main growth and carcass traits.

Material and methods

The animals were reared and slaughtered in compliance with national regulations applied in research and commercial slaughtering.

Animals and measurements

An F2 cross between Duroc and Large White pigs was carried out at the INRA GEPA experimental unit (Le Magneraud, Charente-Maritime, France). Eight Duroc boars from a nucleus herd (Selpa, Alliers, France) were mated to 37 Large White sows (F0 generation). Thirty-seven F1 litters were produced, among which 10 sires and 32 dams were randomly selected and mated to produce the next generation. Each F1 dam produced three litters with the same boar and a total of 775 F2 pigs were produced. Male F2 piglets were castrated shortly after birth. Piglets were weaned at 28 days of age and placed in post-weaning collective pens until 10 weeks of age. They were then transferred to a fattening unit and submitted to a performance test until approximately 20 weeks of age. During the fattening period, animals were conducted in contemporary groups (four groups of eight dams, raised for three litters representing 12 contemporary groups in total).

All animals were weighed at birth, at weaning, at the beginning and at the end of the fattening period. Pigs were slaughtered at an average liveweight of 104 kg (from 79 to 125 kg) in a commercial slaughterhouse. Carcass weight and length, as well as carcass fat depths at the shoulder, the last rib and the hip joint were measured shortly after slaughter. Additional fat and lean depths were taken using a Fat-o-Meat'er (SFK Technology A/S, Herlev, Denmark) probe to estimate carcass lean meat content (ELMC). Urine was collected after slaughter from the bladder in 186 F2 pigs in order to measure levels of stress hormones (cortisol, adrenaline and noradrenaline). Details on the measurement of these hormones can be found in Foury *et al*. (2005).

On the day after the slaughter, the whole carcass was weighed and the half-right carcass was divided into five cuts, that is, ham, loin, belly, shoulder and backfat, which were individually weighed. Several meat quality criteria were also recorded on different muscles. Ultimate pH was measured on the *adductor femoris* (pHu-AF), *longissimus dorsi* (pHu-LD) and *gluteus superficialis* (pHu-GS) muscles using a Knick Portaness 910 pH meter (Knick GmbH & Co., Berlin, Germany) with a Mettler Toledo Probe (Mettler-Toledo International Inc., Urdorf, Switzerland) at 4°C. The water-holding capacity (WHC) and colour were also recorded on the *gluteus superficialis* (GS) and *biceps femoris* (BF) muscles. WHC was measured using a piece of filter paper put on the freshly cut surface of the muscle and was defined as the time for the paper to become wet (a higher value is associated with a better WHC). Colour was measured through the three coordinates (L*, a* and b* systems) obtained with a Minolta CR-300 chromameter (Konica Minolta, Tokyo, Japan) using the D65 illuminant option and an 11-mm orifice. Values of L* indicate lightness of the meat (a lower value is associated with a darker meat), while a* and b* represent the degrees of green-redness and blue-yellowness of the meat, respectively.

A total of 27 traits described in Table 1 were analysed: 11 meat quality traits, 13 production traits and three stress hormone concentrations. The number of F2 animals with both phenotype and genotype data ranged from 174 to 456 depending on the trait.

Molecular analyses

The six F1 boar families with the largest number of offspring (from 71 to 101) were selected for molecular analyses. F1 sires were genotyped for 157 microsatellite markers, among which a set of 91 informative markers covering the porcine autosomes was selected. From three (for SSC15 and 18) to nine markers (for SSC7) were typed per chromosome.

Table 1 *Number of records, means and s.d. for traits measured*

Traits	Abbreviations	*n*	Mean	s.d.
Production traits				
Birth weight (kg)	BW	456	1.545	0.313
Average daily gain during the post-weaning period (kg/J)	ADG-pw	454	0.539	0.101
Average daily gain during the fattening period (kg/J)	ADG-f	454	0.880	0.107
Carcass fat depths (mm)				
At the shoulder	CFD-shoulder	453	15.1	4.3
At the last rib	CFD-rib	454	17.9	3.9
At the hip joint	CFD-hip	454	32.3	5.3
Estimated lean meat content (%)	ELMC	454	59.2	3.3
Carcass length (mm)	Length	454	972	27
Cut weights (kg)				
Backfat	Backfat wt	453	3.04	0.63
Shoulder	Shoulder wt	453	6.14	0.48
Ham	Ham wt	453	10.67	0.73
Loin	Loin wt	452	11.69	0.93
Belly	Belly wt	451	5.11	0.59
Meat quality traits				
In *biceps femoris* muscle				
L*	L*-BF	454	51.22	4.46
a*	a*-BF	454	8.79	3.49
b*	b*-BF	454	6.03	3.08
Water-holding capacity (10 s)	WHC-BF	454	5.3	6.6
In *gluteus superficialis* muscle				
L*	L*-GS	454	48.76	3.86
a*	a*-GS	454	8.41	3.07
b*	b*-GS	454	5.05	2.77
Water-holding capacity (10 s)	WHC-GS	454	41	54
Ultimate pH	pHu-GS	454	5.71	0.21
Ultimate pH of *adductor femoris*	pHu-AF	454	6.00	0.26
Ultimate pH of *longissimus dorsi*	pHu-LD	454	5.79	0.19
Stress hormone levels (ng/mg creatinine)				
Cortisol	Cortisol	186	56.7	48.8
Adrenaline	Adrenaline	174	20.8	16.1
Noradrenaline	Noradrenaline	174	30.1	17.4

The telomeric parts of some chromosomes (SSC4, 5, 6, 12 and 15) were not covered by genotype markers. The average distance between adjacent markers was 24.6 cM on the sex-averaged map (see Sanchez *et al*. (2007) for the genetic map). One to six F1 boars were heterozygous (4.4 in average) for the 91 microsatellite markers. Thirty-one F0 animals, 27 F1 animals (six boars and 21 sows) and 456 F2 pigs were genotyped for this set of markers using DNA extracted from blood samples at the Labogena laboratory (Jouy-en-Josas, France).

Statistical analyses

Before QTL mapping analyses, traits were adjusted for environmental effects using the GLM procedure of SAS Institute (1999). All traits were corrected for the fixed effects of sex and contemporary group (fattening batch). Carcass traits were additionally adjusted for carcass weight, whereas meat quality traits and stress hormone levels were corrected for the date of measurement nested within a fattening batch.

Interval mapping analyses were performed on adjusted data using the QTLMAP software (Le Roy *et al*., 1998). A combined half-sib–full-sib model assuming that the population is a mixture of half- and full-sib families was used. For each cM along a chromosome, the hypothesis of one QTL (H1) linked to the set of markers considered was compared to the hypothesis of no QTL (H0) at the same location. Under H1, a QTL with a gene substitution effect for each sire and for each dam was fitted to the data. Likelihoods were then maximized under each hypothesis and the test statistic was computed as the ratio of likelihoods (LR). At the location with the highest LR, average substitution effects were estimated within each sire and dam family. Additional details on likelihood and gene substitution effect computations are given in Le Roy *et al*. (1998). Approximate confidence intervals of QTL position were determined by the 'drop-off' method (Lander and Kruglyak, 1995).

Significance thresholds were empirically determined at the chromosome (suggestive) level, by performing simulations under H0, using the assumption of a polygenic infinitesimal model (Le Roy *et al*., 1998). A total of 5000 simulations were achieved for each chromosome $\times$ trait combination, and an

approximate Bonferroni correction as described by Bidanel *et al*. (2001) was applied to obtain genome-wide (significant) levels. A genome-wide probability of 0.05 corresponded then to a chromosome-wide probability of 0.0027. When a suggestive or significant QTL was detected, values of effects estimated for each sire were tested using a Student's *t*-test. When the probability (*P*) associated with the test statistics was lower than 5%, we considered that the value of the effect was different of zero and thus, that the sire was heterozygous for the QTL. Otherwise ($P > 5\%$), the sire was considered as homozygous.

Results

The number of records, means and standard deviations of the traits studied are listed in Table 1.

The analyses led to the detection of 56 QTL. Seven QTL exceeded the genome-wide significance threshold. The 49 others only reached the suggestive threshold. All autosomes contained at least one QTL. One (SSC3 and 8) to nine (SSC17) QTL were detected per chromosome. In all, 24 of the 27 traits investigated were affected by one or several (up to seven) QTL. The only three traits with no QTL detected were carcass fat depth at the hip joint, belly weight and a* value of the *gluteus superficialis* muscle. Twenty QTL affected meat quality traits, 33 affected production traits and three QTL were identified for levels of stress hormones. For all QTL detected, one to five of the six F1 sires were found to be heterozygous, suggesting that QTL alleles were not fixed in Duroc and Large White founders.

QTL for meat quality traits

A total of 20 QTL affecting meat quality traits were detected on 11 chromosomes (4, 5, 6, 7, 8, 9, 11, 13, 14, 15 and 17). For each of these chromosomes, one to four traits related to meat quality were found significant at the chromosome-wide significance threshold (Table 2). We have identified four suggestive regions for pH measurements, nine suggestive regions for meat colour traits and two suggestive regions for WHC.

For pH measurements, the most important effects (~0.4 ph s.d. (phenotypic standard deviation)) were found for pHu-LD on SSC6. For this QTL, two F1 boar families were found to be heterozygous. Significant, but less important, effects (about 0.2 ph s.d.) were observed for pHu-AF on the same chromosome, but at a slightly different position. Other suggestive effects were found for ultimate pH measurements on SSC5, 9 and 15.

A total of 13 suggestive QTL were detected for traits related to meat colour in nine chromosomal regions. In four of these regions located on SSC4, 6, 7 and 17, QTL effects were close to 0.5 ph s.d. for at least one F1 sire. On SSC6, two distinct QTL were detected, the first one affecting a*-BF at 62 cM and the second one affecting L*-BF (Figure 1a). Meat colour

Table 2 *QTL detected for meat quality traits*

SSC	Traits[a]	LR	Position and confidence interval (cM)	Markers at maximum location or flanking markers	Heterozygous sires with a < 0		Heterozygous sires with a > 0	
					Nh[b]	a[c]	Nh[b]	a[c]
4	b*-GS	50.2^{+}	30 (30–42)	SW2547	1	−0.44	1	0.26
5	pHu-LD	50.8^{+}	57 (52–62)	SW1482-SW2425	1	−0.20	–	–
5	a*-BF	51.2^{+}	133 (130–133)	SW378	–	–	2	0.33
6	a*-BF	58.9^{++}	62 (53–67)	S0087	2	−0.24	–	–
6	pHu-AF	54.8^{+}	109 (99–113)	S0228-S0121	1	−0.24	2	0.22
6	pHu-LD	52.7^{+}	132 (120–140)	S0121-SW2419	–	–	2	0.38
6	L*-BF	55.7^{+}	134 (126–141)	S0121-SW2419	2	−0.27	2	0.43
7	L*-BF	53.9^{+}	0 (0–8)	S0383-S0025	1	−0.46	1	0.20
7	a*-BF	64.4^{++}	98 (92–107)	S0102-SW352	1	−0.17	1	0.52
8	b*-GS	55.9^{+}	27 (22–32)	SW905-SWR1101	2	−0.20	–	–
9	pHu-AF	52^{+}	3 (1–14)	SW983-SW911	1	−0.28	–	–
11	a*-BF	52.7^{+}	23 (12–34)	SW1632-S0382	1	−0.37	1	0.17
11	WHC-BF	51.6^{+}	27 (15–34)	SW1632-S0382	–	–	3	0.19
13	L*-GS	52^{+}	78 (61–85)	SW225-SW38	1	−0.26	1	0.26
14	WHC-GS	61.8^{++}	108 (101–108)	SW2515	2	−0.62	1	0.29
15	pHu-LD	47.1^{+}	36 (27–43)	SW1111-S0088	2	−0.16	2	0.32
15	b*-BF	49.7^{+}	79 (70–79)	SW936	2	−0.19	3	0.32
17	a*-BF	59^{++}	25 (23–29)	SW24-SW2441	1	−0.22	3	0.24
17	b*-BF	60.3^{++}	27 (23–31)	SW24-SW2441	–	–	2	0.25
17	L*-BF	50.4^{+}	37 (33–43)	SW24-SW2441	1	−0.25	1	0.44

QTL = quantitative trait loci; LR = likelihood ratio; +, ++ = 5% and 1% chromosome-wide significance levels, respectively.
[a]See Table 1.
[b]Number of heterozygous F1 sires.
[c]Average allele substitution effect of heterozygous F1 sires: Large White–Duroc alleles in phenotypic standard deviation.

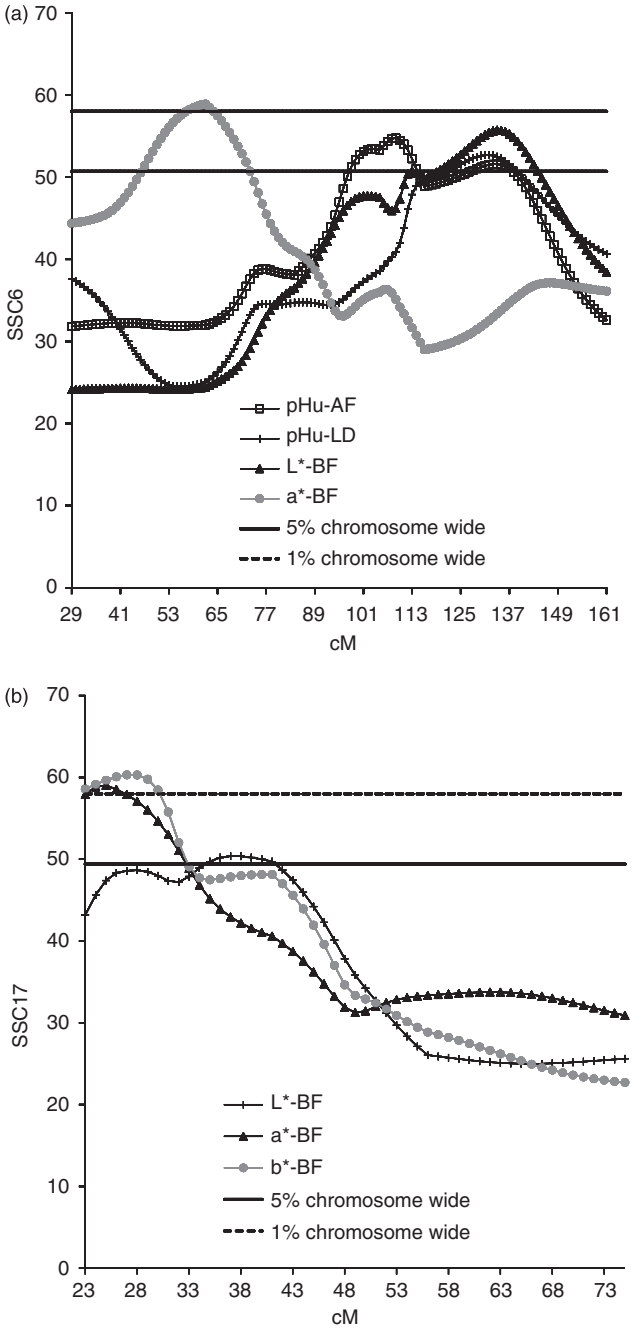

Figure 1 Likelihood ratio profile for meat quality traits on chromosomes 6 (a) and 17 (b).

was also influenced by two QTL regions on SSC7, with significant effects on L*-BF and on a*-BF. For L*-BF, the Duroc allele was associated with a lighter meat. Finally, a region of SSC17 had significant effects on the three Minolta coordinates of the *biceps femoris* muscle, with very similar most likely positions (Figure 1b). Additional suggestive QTL affecting meat colour traits were detected in our population on SSC5, 8, 11, 13 and 15, but their effects were lower than those of the above-mentioned QTL.

Finally, two QTL acting on WHC were identified on chromosomes 11 and 14, with, in both cases, three boars identified as heterozygous. Large White alleles were systematically associated with a better WHC for the SSC11 QTL, but had favourable effects for only one of the three heterozygous F1 boars in the case of the SSC14 QTL.

QTL for production traits

A total of 33 QTL were detected for production traits. They were located on all autosomes except SSC6, 8 and 9. Seven of them, located on SSC2, 3, 10, 13, 16 and 17 exceeded the genome-wide significance threshold (Table 3).

The QTL located in the p-terminal region of SSC2, that is, in the *IGF2* gene region, had genome-wide significant effects on ELMC and suggestive effects on backfat weight. The SSC3 QTL had significant effects on post-weaning growth. Two other QTL, located on SSC10 and 13, had genome-wide significant effects on shoulder fat depth. The SSC13 QTL had particularly large effects on the trait (−0.8 ph s.d.). Furthermore, on SSC17, genome-wide significant effects were detected for shoulder weight and carcass length and chromosome-wide significant effects were detected for several other traits. Finally, a genome-wide significant QTL was detected for body weight at birth on SSC16 (17 cM).

For all the heterozygous sires, the effects of the Duroc alleles were favourable for the SSC2 QTL, but unfavourable for the SSC13 and SSC16 QTL. For the three other QTL (SSC3, 10 and 17), the sense of the effect varied depending on the sire.

Additional QTL were suggested for birth weight on SSC2, 10 and 12; for growth rate on SSC1, 2, 15 and 17 and for body composition traits on almost all autosomes except SSC3, 6, 8, 9 and 10.

QTL for stress hormone levels

Three QTL with significant effects on stress hormone levels were detected on SSC7, 10 and 13. The SSC7 QTL affected the cortisol level. Four F1 sires were found to be heterozygous, with positive effects of Duroc alleles in two families and negative effects in the remaining two sires. The two other QTL were located on SSC10 and 13 and affected the noradrenaline and adrenaline levels, respectively. For these QTL, three and two F1 boars, respectively, were heterozygous. Duroc alleles were associated with a lower level of noradrenaline for the SSC10 QTL, but led to higher adrenaline levels for the SSC13 QTL (Table 4).

Discussion

The low number of heterozygous F1 Duroc × Large White sires might explain the relatively low number of genome-wide significant QTL in this study. For 44 out of the 56 identified QTL, only one to three F1 boars were found to be heterozygous.

Owing to the great number of QTL detection studies in pigs for production traits and to a lesser extent for meat quality traits (237 papers are referenced in the PigQTLdb from 1994 to 2009; Hu *et al.*, 2007), most of the effects we found confirmed QTL, which had previously been described

Table 3 *QTL detected for production traits*

SSC	Traits[a]	LR	Position and confidence interval (cM)	Markers at maximum location or flanking markers	Heterozygous sires with a < 0		Heterozygous sires with a > 0	
					Nh[b]	a[c]	Nh[b]	a[c]
1	Shoulder wt	53.9^{+}	21 (9–33)	SW552-S0008	4	−0.34	1	0.17
1	ADG-pw	51.4^{+}	128 (120–135)	SW1828-SW1301	1	−0.15	1	0.17
2	BW	57.8^{+}	2 (2–8)	SWC9-SW2623	–	–	1	0.16
2	ELMC	66*	3 (2–7)	SWC9-SW2623	2	−0.52	–	–
2	Backfat wt	51.6^{+}	7 (2–16)	SWC9-SW2623	–	–	2	0.46
2	ADG-f	52.2^{+}	61 (53–69)	SW240-S0226	1	−0.82	1	0.40
3	ADG-pw	61.7*	97 (96–101)	S0372-S0397	2	−0.25	1	0.16
4	CFD-rib	57.1^{+}	37 (30–48)	SW2547-SW839	1	−0.27	2	0.27
5	Length	59.7^{++}	39 (39–49)	SW1482	1	−0.26	–	–
5	CFD-rib	52.3^{+}	73 (63–85)	SW2425-SW1987	2	−0.23	–	–
7	Length	54.3^{+}	108 (98–119)	SW352	2	−0.50	3	0.27
7	Shoulder wt	58.7^{+}	136 (124–143)	SW632-S0101	–	–	1	0.01
10	CFD-shoulder	63.6*	37 (26–47)	SWR136-SW2491	1	−0.50	2	0.27
10	BW	50.6^{+}	78 (71–84)	S0070-SW951	2	−0.27	1	0.27
11	Ham wt	52.7^{+}	34 (27–40)	SW1632-S0382	1	−0.20	3	0.29
12	BW	49.3^{+}	40 (40–48)	SW1307	2	−0.23	1	0.13
12	Length	59.2^{++}	105 (99–105)	SW2180	1	−0.46	–	–
13	ELMC	49.8^{+}	18 (14–56)	SWR1941-S0222	–	–	2	0.28
13	Ham wt	52.7^{+}	24 (14–31)	SWR1941-S0222	–	–	1	0.18
13	Length	52.5^{+}	90 (52–102)	SW225-SW38	1	−0.39	2	0.44
13	CFD-shoulder	65.7*	102 (92–102)	SW38	3	−0.81	–	–
14	Loin wt	57.5^{+}	94 (90–99)	SW55-SW2515	–	–	2	0.29
15	ELMC	46.1^{+}	40 (27–50)	SW1111-S0088	2	−0.26	3	0.17
15	ADG-f	52.8^{++}	50 (46–59)	SW1111-S0088	–	–	3	0.21
16	BW	65.5*	17 (13–21)	SW2411	–	–	1	0.20
16	Backfat wt	63.9^{++}	41 (36–51)	SW2411-S0026	1	−0.30	3	0.20
17	Length	62.7*	29 (24–43)	SW24-SW2441	1	−0.41	2	0.43
17	CFD-shoulder	50.3^{+}	31 (27–33)	SW24-SW2441	2	−0.66	–	–
17	Shoulder wt	59.6*	32 (31–34)	SW24-SW2441	2	−0.20	1	0.26
17	Backfat wt	52.3^{+}	68 (52–75)	SW1920-S0359	1	−0.22	–	–
17	ADG-pw	53.6^{+}	75 (71–75)	S0359	–	–	3	0.25
18	CFD-shoulder	48.5^{+}	13 (2–18	SW2540-SW1984	1	−0.40	2	0.29
18	Ham wt	50.6^{+}	20 (9–26)	SW2540-SW1984	3	−0.25	2	0.29

QTL = quantitative trait loci; LR = likelihood ratio; * = 5% genome-wide significance levels respectively; +, ++ = 5% and 1% chromosome-wide significance levels, respectively.
[a]See Table 1.
[b]Number of heterozygous F1 sires.
[c]Average allele substitution effect of heterozygous F1 sires: Large White–Duroc alleles in phenotypic standard deviation.

in other populations. However, we have located QTL, which has not been previously reported in the literature. The QTL located on SSC5, acting on ultimate pH of *longissimus dorsi*, had never been previously described. In addition, four new QTL were identified in our population for production traits: two with effects on birth weight and two with effects on growth rates. The first QTL acting on birth weight was located in the *IGF2* region of SSC2. The effects of the *IGF2-intron3–G3072A* mutation were reported on carcass leanness and backfat thickness in several studies (e.g. Jeon *et al.*, 1999; Nezer *et al.*, 1999) and also on prolificacy in sows (Buys *et al.*, 2006), but no significant effects were previously described on birth weight. However, another QTL close to the *IGF2* region and acting on birth weight has been previously suspected in a Pietrain × Large White cross (Sanchez *et al.*, 2006). We also identified a second QTL for birth weight on SSC10, the Large White allele being responsible for an increase or a decrease of birth weight depending on the family. For QTL acting on growth rates, the first one detected on SSC17 had an effect on the post-weaning growth rate, whereas the second one, detected on SSC15, had an effect on the fattening growth rate. Although these five QTL had moderate effects, from 0.16 to 0.26 ph s.d., depending on the sire–trait combination considered, they could be useful to improve meat quality and growth traits in commercial populations.

Very few programmes were conducted to detect QTL for stress hormone levels. Cortisol levels were measured in the

Table 4 *QTL detected for stress hormone traits at the 5% chromosome-wide significant level*

SSC	Trait[a]	LR	Position and confidence interval (cM)	Markers at maximum location or flanking markers	Heterozygous sires with a < 0		Heterozygous sires with a > 0	
					Nh[b]	a[c]	Nh[b]	a[c]
7	Cortisol	46.2^{+}	139 (131–146)	SW632–S0101	2	−0.39	2	0.41
10	Noradrenaline	38.1^{+}	62 (55–71)	S0070	–	–	3	0.40
13	Adrenaline	37.3^{+}	14 (14–20)	SWR1941	2	−0.30	–	–

QTL = quantitative trait loci; LR = likelihood ratio.
[a]See Table 1.
[b]Number of heterozygous F1 sires.
[c]Average allele substitution effect of heterozygous F1 sires: Large White–Duroc alleles in phenotypic standard deviation.

French experimental F2 Meishan × Large White population and a QTL for cortisol level was detected at 139 cM on SSC7 by Désautés *et al.* (2002). Later, Ousova *et al.* (2004) found a QTL for the plasma concentration of cortisol-binding globulin (CBG) and showed that the *CBG* gene, located in this chromosomal region, was a strong candidate locus for this QTL. QTL for noradrenaline and adrenaline levels were, to our knowledge, searched for the first time in our study, and therefore, no QTL were previously detected for these traits.

In the region of the *CBG* gene, where a QTL was identified for the cortisol level, we did not find any significant effect on production or meat quality traits. In the French F2 Meishan × Large White population, significant effects of the CBG region were identified for both cortisol level and leanness traits (Désautés *et al.*, 2002; Ousova *et al.*, 2004). These results have not been confirmed in the F2 Duroc × Large White population. No pleiotropic effects of QTL for levels of catecholamines (noradrenaline and adrenaline) were found for meat quality traits, although some relationships may exist between these two kinds of traits. However, QTL acting on catecholamines also acted on some fatness or leanness traits. Nevertheless, the results we have obtained in the Duroc × Large White population should be considered with caution as less than 200 F2 animals were measured for stress hormone levels.

The fact that only one to five of the six F1 sires were heterozygous for each identified QTL means that all QTL are segregating in at least one of the founder populations we used in this study. In particular, the QTL identified in the p-terminal end of chromosome 2 could be the *IGF2* mutation (Van Laere *et al.*, 2003; Markljung *et al.*, 2009), although the animals were not tested for this mutation. The non-mutated allele, which has undesirable effects on carcass composition, would thus be present at a non-negligible frequency in the Large White population. In the same way, when opposite effects were found for different boars, as was the case for most of the QTL, it means that both favourable and unfavourable alleles are segregating in each of the Large White and Duroc parental populations. These results, therefore, suggest that not only meat quality traits but also stress hormone levels and production traits could be improved by the use of molecular markers in purebred Duroc and Large White pigs. It is of particular interest for meat quality traits, which are difficult to include in classical selection programmes.

Conclusion

Numerous QTL were detected in the F2 Duroc × Large White population. The use of the Duroc and Large White populations led to the identification of QTL, which are segregating in commercial populations, and thus that could be directly included in breeding schemes. In order to select efficiently favourable alleles, the use of markers very close to the causal mutation is necessary. High-density single-nucleotide polymorphism markers could be very useful to refine the location of some QTL. It could be particularly interesting for meat quality traits, which are often difficult to assess in live animals.

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