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Linkage and QTL mapping for *Sus scrofa* chromosome 12

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Summary

The SSC12 (*Sus scrofa* chromosome 12) linkage and QTL maps were generated using 11 markers, of which seven to 10 have been used in the three F_2 families based on Wild Boar (W), Meishan (M) and Pietrain (P) crosses. Linkage maps showed identical marker order among the families, but differed in total lengths. They were in agreement with the already published maps, except for the order *SWR1021–SW605*. Most quantitative trait loci (QTLs) affected fat or meat content in carcass, but were also found for some other traits (heart weight, CK_{20} values and teat number). They explained up to 5.4% of F_2 phenotypic variance. Meishan alleles had stimulating effects on fat deposition and decreasing effects on lean content and CK_{20} value. The QTL profiles differed between families, with QTL effects in the vicinity of the *GH1* locus found solely in the M × P family.

Zusammenfassung

Auf der Basis von elf Markern wurden Kopplungs- und QTL-Karten für Chromosom 12 (SSC12) in drei F_2-Familien aus Kreuzungen von Wildschwein (W), Meishan (M) und Pietrain (P) erstellt. Hierbei wurden sieben bis zehn Marker pro F_2-Familie benutzt. Die Kopplungskarten zeigten eine gleichartige Anordnung der Loci für alle Familien, jedoch mit verschiedenen Kartenlängen. Sie stimmen, außer in der Anordnung *SWR1021–SW605*, mit bereits publizierten Karten überein. Quantitative Trait Loci (QTLs) waren hauptsächlich für Merkmale des Fett-oder Fleischanteils im Schlachtkörper festzustellen, daneben aber auch für weitere Merkmale (Herzgewicht, CK_{20}-Wert, Zitzenzahl). Sie erklärten bis zu 5,4% der phänotypischen Varianz in der F_2-Generation. Meishan-Allele waren assoziiert mit einer Steigerung des Fettansatzes sowie einer Reduktion der Anteile wertvoller Teilstücke und der CK_{20}-Werte. Die QTL-Profile unterschieden sich zwischen den Familien und ließen Assoziationen mit dem *GH1*-Locus nur in der Familie M × P erkennen.

Introduction

Published linkage maps of *Sus scrofa* chromosome 12 (SSC12) (http://www.thearkdb.org), based on up to 30 loci, range between 113.1 cM (USDA-MARC.2, Rohrer et al. 1996) and 121.6 cM (NIAI-Japan, Mikawa et al. 1999) in length. Quantitative trait loci (QTLs) have been mapped for reproduction (Cassady et al. 2001), teat number (Hirooka et al. 2001), growth (Paszek et al. 1999; Rohrer 2000), muscling (Paszek et al. 2001), fatness (Korwin-Kossakowska et al. 2001; Malek et al. 2001a) and meat quality (Malek et al. 2001b). Knorr et al. (1997) described strong associations between the candidate gene *GH1* and fat deposition. Preliminary reports on SSC12 QTLs detected in the Hohenheim F_2 families were published by Geldermann et al. (1999) and Yue (1999).

Materials and methods

F_2 families – based on crosses of Meishan (M), European Wild Boar (W) and Pietrain (P) – were used. The family structure, housing, selection of quantitative traits and marker loci as

Table 1. **Markers used for linkage and QTL analysis on SSC12**

Marker locus	Type	Reference	Genotyping
S0083	MS	Ellegren et al. 1993	Hohenheim[1]
S0090	MS	Ellegren et al. 1993	Hohenheim[1]
S0106	MS	Ellegren et al. 1994	Hohenheim[1]
S0143	MS	Wilke et al. 1994	Hohenheim[1]
S0147	MS	Wilke et al. 1994	Hohenheim[1]
SW605	MS	Rohrer et al. 1994	Hohenheim[1]
SW874	MS	Rohrer et al. 1994	Hohenheim[1]
SW957	MS	Rohrer et al. 1994	Hohenheim[1]
SWR1021	MS	Rohrer et al. 1994	Hohenheim[1]
EAD	BG	Hradecky and Linhart 1970	Libechov[2]
GH1-H[3]	RFLP	Larsen and Nielsen 1993	Hohenheim[1]
GH1-A[3]	RFLP	Larsen and Nielsen 1993	Hohenheim[1]

MS, microsatellite; BG, blood group; RFLP, restriction fragment length polymorphism; *EAD*, erythrocyte antigen D; *GH1-H*, growth hormone, *HinPI*-RFLP; *GH1-A*, growth hormone, *ApaI*-RFLP.
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[3]*H* and *A* indicate the restriction enzymes (*HinPI* and *ApaI*) used for genotyping the growth hormone coding locus *GH1*.

well as statistical analysis are described in the initial article of this issue (Geldermann et al. 2003). SSC12 has been genotyped for 11 marker loci (Table 1). Here the locus *GH1* was analysed by using two restriction fragment length polymorphisms. Four of these markers were not tested in the M × P family, three not in W × P and two not in W × M; six markers were genotyped in all three families (Table 2).

Results and discussion

Marker characterization and linkage maps

The 11 loci genotyped in the founder animals revealed 52 different alleles of which 33 occurred solely in one founder group (Table 2a). Eight alleles were identified in all three founder groups. Pietrain and Wild Boar shared more alleles than each does with Meishan consistent with the more distant relationship of the Meishan from the European pigs. Average heterozygosity in the F_1 generations varied between 0.56 in the W × P family and 0.84 in the W × M family, and the numbers of informative meioses were between 451 and 585 per family (Table 2b). Figure 1 illustrates that the information content along SSC12 generally exceeded 0.6, except in the W × P family where the interval *S0143–GH1* had low informativity.

As shown in Fig. 2, gene order in the linkage maps of SSC12 was identical for the three families, but the overall length was up to 48 cM larger in the W × M family compared with the other two families. Maternal maps were significantly longer ($p < 0.001$) than the paternal ones, with ratios between maternal and paternal maps of 1.5 (W × M) to 2.0 (W × P). Average distances between markers were 19.5, 15.9 and 17.6 cM in the M × P, W × P and W × M families, respectively. The markers almost completely covered SSC12, as the most proximal locus *S0143* was located at 7 cM on the USDA-MARC.2 map (http://www.thearkdb.org), and *SW605* and *SWR1021* were the most distal loci on any maps of SSC12. The maps agreed well with published maps (Archibald et al. 1995; Marklund et al. 1996; Mikawa et al. 1999), except for the

Table 2. **Properties of marker alleles**

(a) Alleles in the founder generation

	Alleles in			
	M		P	W
Marker locus	m (1)	f (4)	f (14)	m (1)
S0083	–	–	178, 182, 186, 188, 190, 192	182, 188
S0090	251	251	241[a], 243, 245, 247	241, 243
S0106	–	130, 134	–	138, 140
S0143	162, 164	162, 164	156, 158, 162[b], 164	156, 164
S0147	–	168	160, 162, 168	164, 168
SW605	108, 117	108, 117	113[a], 119, 121, 130	119
SW874	188	188, 198, 203	203[a], 206, 208[a], 210	206
SW957	–	153	–	112, 130
SWR1021	93, 97	85, 93, 97	93, 97, 109, 111, 116	85, 93
EAD	a	a, b	b	b
GH1–H[c]	1, 2	1, 2, 4	1[a], 2, 3, 4	4
GH1–A[c]	2	–	1, 2	2

(b) Number of alleles, heterozygosity and number of informative meioses

	Family								
	M × P			W × P			W × M		
Marker locus	n	h	IM	n	h	IM	n	h	IM
S0083	–	–	–	5	0.93	698	–	–	–
S0090	4	1.00	632	4	0.71	626	3	1.00	732
S0106	–	–	–	–	–	–	4	1.00	730
S0143	4	0.73	464	3	0.57	582	3	0.74	646
S0147	–	–	–	4	0.86	662	2	0.35	328
SW605	5	1.00	702	3	0.39	143	3	1.00	670
SW874	3	1.00	632	4	0.25	229	4	1.00	670
SW957	–	–	–	–	–	–	3	1.00	732
SWR1021	4	0.59	440	6	0.75	640	3	0.87	523
EAD	2	1.00	626	–	–	–	2	0.48	153
GH1–H[c]	4	0.95	666	3	0.29	243	3	1.00	668
GH1–A[c]	2	0.36	252	2	0.29	236	–	–	–
Average	3.5	0.83	552	3.8	0.56	451	3.0	0.84	585

M, Meishan; P, Pietrain; W, Wild Boar; m, male; f, female; n, number of alleles observed in F_1 generation; h, heterozygosity observed in F_1 generation; IM, number of informative meioses; *EAD*, erythrocyte antigen D; –, not tested.

Numbers of founder animals used to generate the F_1 animals are given in parentheses. Sizes of microsatellite alleles are indicated by their lengths in bp. For information content of F_2 generation see Fig. 1.

[a]Alleles occurring in the W × P family, but not in the M × P family.

[b]Alleles occurring in the M × P family, but not in the W × P family.

[c]*H* and *A* indicate the restriction enzymes (*HinPI* and *ApaI*) used for genotyping the growth hormone coding locus *GH1*.

order *SWR1021–SW605* in our three families which agreed with the USDA-MARC.1 map (Rohrer et al. 1994), but contradicts the USDA-MARC.2 map (Rohrer et al. 1996). The blood group system erythrocyte antigen D (*EAD*) was assigned to SSC12 by Cepica et al. (1996).

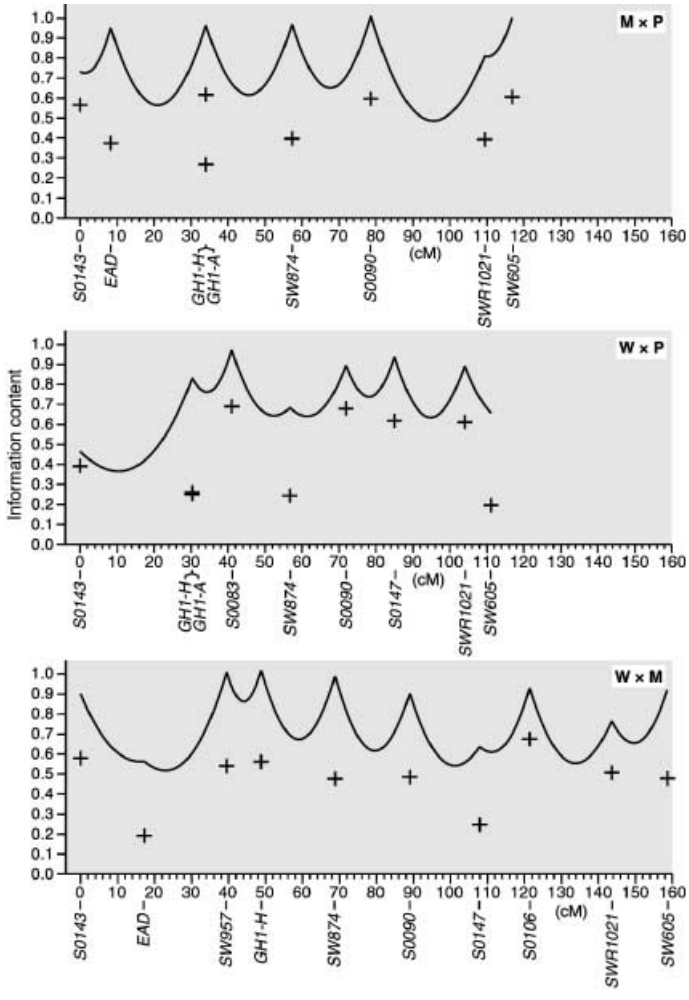

Fig. 1. Information content for SSC12. For individual marker loci, the polymorphism information content (PIC) values are shown as crosses. The cumulative information content across the chromosome is indicated by the solid line. Distances between loci are given in sex-averaged cM. *GH1-H* and *GH1-A* indicate different RFLPs used for genotyping the locus *GH1*

Map positions and effects of QTLs

Most QTLs found on SSC12 affected mainly fat or meat content traits (Table 3). Other QTLs were mapped for CK_{20} value, weight of heart and number of teats. In general, QTL effects on SSC12 were relatively minor, explaining up to 5.4% of the F_2 phenotypic variance. Meishan QTL alleles were associated with increased fat deposition, decreased lean content and decreased CK_{20} value. Large dominance effects were often observed, and in the M × P family they were often larger than the additive effects.

The QTL profiles (Fig. 3) differed between the families. QTLs for weight of heart and ham were only found in the W × P family (Table 3) and similar to the positions of the QTLs for back-fat and colour score of meat mapped by Malek et al. (2001a,b) in a Berkshire × Yorkshire F_2 generation in the interval *S0147–SW2180*. Hirooka et al.

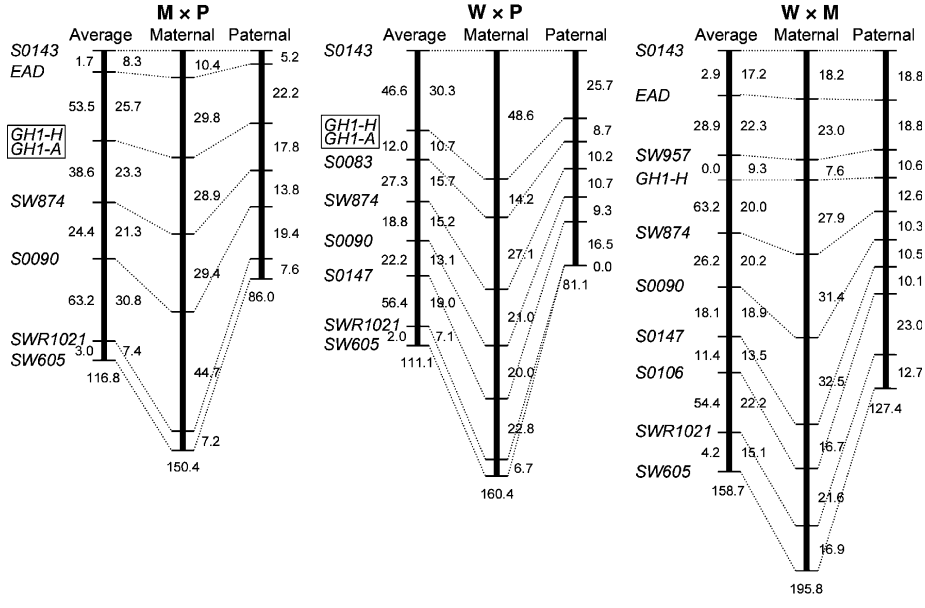

Fig. 2. Genetic linkage maps of SSC12. For each family the sex-averaged (left), maternal (middle) and paternal (right) maps are shown with the estimated Kosambi map distances (cM) between loci (numbers at right-hand side of the maps). To the left-hand side of the sex-averaged maps the statistical supports for the pair-wise order of markers are given. The total lengths of the maps are shown at the bottom of each bar. *GH1-H* and *GH1-A* indicate different RFLPs used for genotyping the locus *GH1*

Table 3. **Significant QTL effects on SSC12**

Trait	*F* ratio	Position (cM)	a ± SE	d ± SE	VF_2 (%)
(a) M × P family					
Lean cuts (%)	7.7*	26.3	−0.76 ± 0.29	1.28 ± 0.47	4.8
Fat cuts (%)	7.0*	47.0	0.63 ± 0.25	−1.04 ± 0.41	4.3
Back-fat depth on M.l.d. at 13th/14th rib (mm)	6.9*	34.0	0.68 ± 0.39	−1.83 ± 0.58	4.3
Loin fat depth (mm)	6.4*	42.0	1.34 ± 0.52	−2.01 ± 0.85	3.9
CK_{20}-value (log_{10} U/ml)	5.8*	69.3	−0.09 ± 0.03	−0.09 ± 0.05	3.5
Fat area on M.l.d. at 13th/14th rib (cm^2)	5.5*	34.0	0.77 ± 0.35	−1.24 ± 0.52	3.3
(b) W × P family					
Weight of heart (g)	6.0*	111.1	−9.62 ± 3.28	7.92 ± 5.35	3.8
Ham weight (kg)	5.7*	111.1	−0.39 ± 0.13	0.22 ± 0.21	3.6
(c) W × M family					
Lean cuts (%)	9.2**	1.0	1.03 ± 0.26	−0.61 ± 0.38	5.4
Number of teats	6.7*	41.5	−0.17 ± 0.05	0.05 ± 0.07	3.8
Fat depth at approximately 10th rib (mm)	5.8*	0.0	−1.58 ± 0.47	−0.30 ± 0.67	3.2

Significant at *p < 0.05 chromosome-wide threshold and **p < 0.05 genome-wide threshold.
QTL, quantitative trait locus; SSC12, *Sus scrofa* chromosome 12; a, additive effect (positive/negative signs indicate the superior/inferior trait values inherited from the paternal resource group); d, dominance effect (positive for higher values of heterozygous individuals than the mean of homozygotes; negative for lower values); VF_2 (%), percentage of F_2 phenotypic variance explained by the QTL; M.l.d., Musculus longissimus dorsi.

(2001) mapped a QTL for the number of teats between *S0090* and *S0106*. A QTL for the number of teats was observed also in the W × M family. Its position was more proximal in the interval *SW957–GH1*, than with further peaks along the chromosome. In the M × P

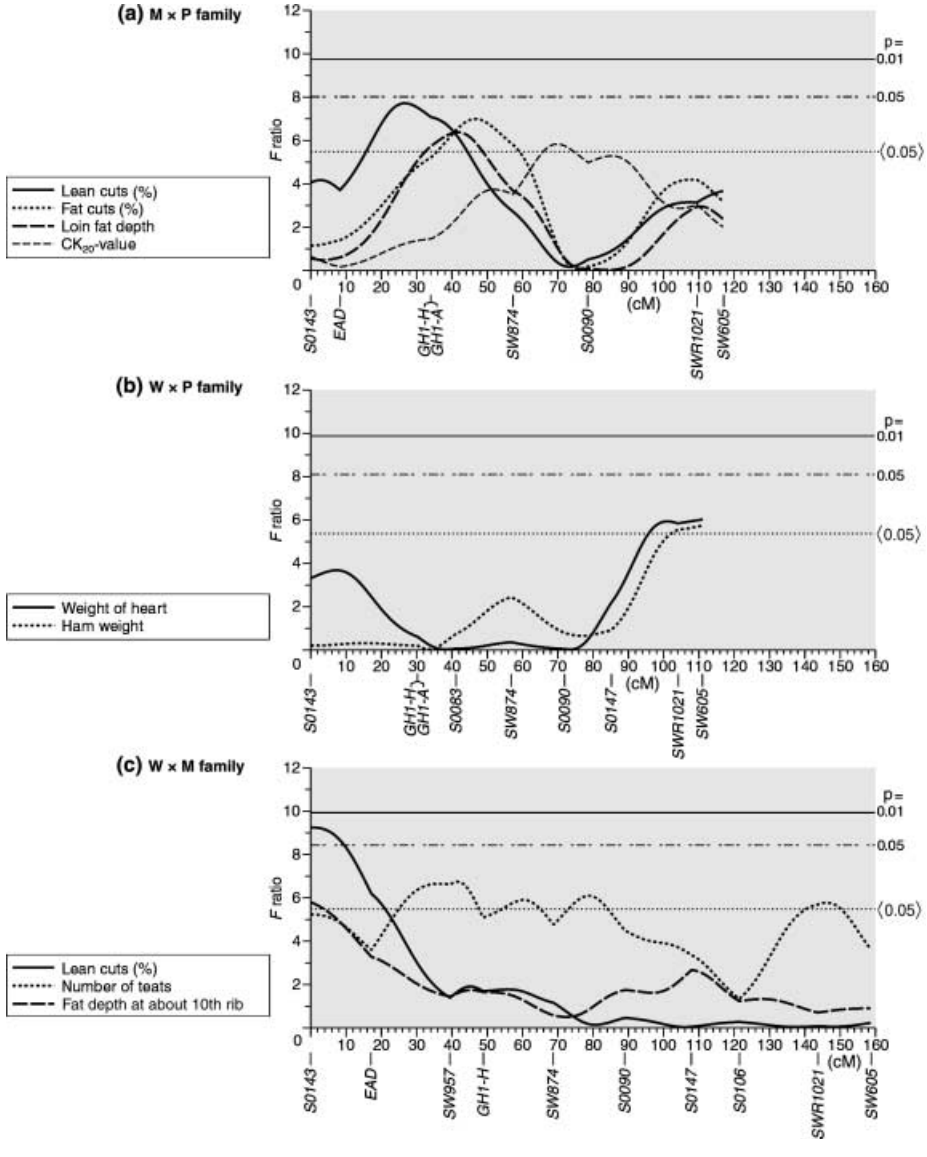

Fig. 3. Profiles of *F* ratio values on SSC12 for traits from different trait complexes and with the highest levels of significance (compare Table 3). p = 0.01 and p = 0.05 indicate the genome-wide thresholds, ⟨p = 0.05⟩ indicates the chromosome-wide threshold. *GH1-H* and *GH1-A* indicate different RFLPs used for genotyping the locus *GH1*

family, QTLs for fat and meat contents were mapped between 25 and 50 cM, near the growth hormone locus (*GH1*). Highly significant associations between growth hormone genotypes and fat deposition have previously been reported by Knorr et al. (1997). Likewise Paszek et al. (2001) mapped QTLs for loin muscle area and intramuscular fat in the vicinity of the *GH1* locus, and Korwin-Kossakowska et al. (2001) described a QTL for abdominal fat in carcass near the *GH1* locus. However in our study, no influence of the

GH1 locus was found in the W × P and W × M families. The family-specific effects point to QTL alleles, which are most different between Meishan and Pietrain, but minor differences in allele effects between the other founder groups were below the threshold of detection.

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