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Provisional assignment of the G blood-group locus to chromosome 15 in swine

Gene mapping in swine using natural and induced marker chromosomes

ABSTRACT: Using the lod score test, 85 combinations of 19 biochemical and immunogenetic markers and 7 natural and radiation-induced chromosomal markers were checked with respect to linkage. Highly positive lod scores were obtained for the combination of the G blood-group locus with the rob (15;17) centric-fusion chromosome. Positive lod scores also were obtained for the G blood-group locus and the reciprocal translocation rcp (2p+;15q−) marker chromosome. Thus, it was concluded that the locus for the G blood-group system may be on chromosome 15 of swine. For several combinations of markers it was possible to exclude linkage at certain recombination frequencies.

R. Fries

G. Stranzinger

P. Vögeli

The authors are affiliated with the Institute of Animal Production, Animal Breeding Section, Federal Institute of Technology, Tannenstrasse 1, CH-8092 Zurich, Switzerland. They thank the staff of the Animal Breeding Section for helpful assistance. They also thank Prof. J. Moustgaard and Dr. P. B. Nielsen of the Royal Veterinary and Agricultural University, Copenhagen, for providing the facilities to analyze a part of the blood samples in their department, Dr. D. A. Redmer, and Dr. L. D. Young for their help in translating, and Cheryl Yates for stenographic work. The study was financially supported by the ETH grant no. 5487/41-0735.5.

RELATIVE to the advanced knowledge of the order and chromosomal location of gene loci in man and some laboratory animal species, little is known about gene maps in farm animals. Few gene mapping studies by family analyses and even fewer by somatic cell hybridization techniques have been reported[13].

The present gene map of swine consists of four linkage groups (detected by family analyses) and two syntenic groups (detected by somatic cell hybridization techniques). In 1964, Andresen and Baker[7] found linkage between the C and J blood-group loci. Hruban et al.[16] added the histocompatibility complex (SLA) locus to the C-J linkage group. Andresen[4-6], Andresen and Jensen[8], Juneja et al.[19], and Rasmusen[24] established linkage between the loci for glucosephosphate isomerase (GPI) isozymes, halothane sensitivity (HAL), A-O inhibition (S), H blood groups, postalbumin-2 (PO2) serum proteins, and 6-phosphogluconate dehydrogenase (6PGD) isozymes. Rasmusen[25] found indications that there is linkage between genes at the H blood-group locus and the loci for C and J blood groups. Thus, the loci for SLA, C, J, GPI, HAL, S, H, PO2 and 6PGD may form one large linkage group. Andresen[1] reported linkage between the I blood group and the serum amylase (AM) loci. A further linkage group containing the loci for the K blood group and the hemopexin (Hpx) system was reported by the same author[2]. Imlah[17] found evidence for linkage of the transferrin (Tf) locus with an undefined early lethal factor. In 1980, Gellin et al.[14] and Förster et al.[10] reported synteny between the loci for glucose-6-phosphate dehydrogenase (G6PD), hypoxanthine phosphoribosyltransferase (HPRT) and phosphoglycerate kinase (PGK). Förster et al.[10] assigned this synteny group to the X-chromosome. Gellin et al.[15] indicated that the genes for pyruvate kinase-2 (PK2), mannose-phosphate isomerase (MPI) and nucleoside phosphorylase (NP) were syntenic. According to Echard et al.[9] these genes may be on chromosome 8. Leong et al.[20] found evidence that the gene for soluble superoxide dismutase (SOD1) is on chromosome 9.

The present contribution to the swine gene map was obtained when the linkage relationships of several natural and induced marker chromosomes and immunogenetic and biochemical traits were analyzed by the lod score method.

Materials and Methods

The pigs used in this study were purebred Swiss Landrace or were descendents of a wild boar and Swiss Landrace sows.

Chromosomal preparations were made according to the standard method of Moorhead et al.[21] by pokeweed stimulation of leukocytes. The marker chromosomes are summarized in Table I. The induction of marker chromosomes by sperm irradiation has been described elsewhere[13]. Hybridization of a wild boar (*Sus scrofa scrofa:* $2n = 36$ chromosomes) with domestic pigs (*Sus scrofa domestica;* $2n = 38$ chromosomes) provided hybrids ($2n = 37$ chromosomes) showing a centric fusion between chromosomes 15 and 17. Heteromorphisms of the centromeric heterochromatin were shown by a sequential Q-C-banding technique (see Fries and Stranzinger[11]).

Table II gives a summary of the blood-group systems that were studied and the test procedures that were applied, and Table III lists the serum and enzyme systems. Investigation of the polymorphic protein systems was by starch gel electrophoresis.

The statistical examination of the segregation data followed the lod score method of Morton[22]. The significance criteria for acceptance or rejection of linkage were chosen as recommended by Morton[22] for human linkage studies. Lod scores greater than 3 are significant for linkage. Lod scores smaller than −2 are a significant indication that there is no linkage.

Results and Discussion

The lod scores at various recombination frequencies (θ), calculated from 85 pairs of 7 chromosomal and 19 serological and biochemical markers, respectively, are given in Table IV.

The combinations for which it was possible to exclude linkage (lod scores smaller than −2) at certain recombination frequencies are listed in Table VI. Lod scores significant for linkage (greater than 3) could not be found when information on the linkage phase was not involved in the calculations. The lod score of the combination G blood group and the rob (15;17) marker chromosome almost reaches the value of 3 (2.92 for $\theta = 0.20$, Table IV). The segregation of the G blood-group alleles and the rob (15;17) marker was studied mostly in the large family of one boar whose linkage phase was known. The lod scores for this boar were recalculated using the linkage phase information and are summarized in Table V. The lod score at $\theta = 0.20$ is greater than 3 and is therefore significant for linkage.

A lod score of 1.07 at $\theta = 0.20$ was obtained for the combination G blood group and the rcp (2p+;15q−) marker chromosome. The segregation data for this combination were collected from the progeny of one male and two females whose linkage phases were known. The lod scores calculated separately for each animal, incorporating the linkage phase information, are given in Table V. It can be seen that the lod scores for the two females taken together are greater than 3; however, those for the male exclude close linkage.

These results make it possible to provisionally locate the G blood-group locus on chromosome 15. This location mostly was based on the positive lod scores resulting from the combination of the rob (15;17) and rcp (2p+;15q−) chromosomal markers with the G blood-group locus. A lod score significant for linkage was only calculated for the combination rob (15;17) and G blood group. Therefore the G blood-group locus could be located on chromosome 15 or on chromosome 17. The positive lod scores of the combination rcp (2p+;15q−) and the G blood-group locus gave evidence that this locus could be on chromosome 15 rather than 17. Additional evidence was given by the fact that close linkage between another chromosome 17 marker and the G blood-group locus could be excluded (17C+, Table VI).

Since one of the breakpoints in the reciprocal translocation rcp (2p+;15q−) was determined to be in the centromere of chromosome 15 (see Fries and Stranzinger[12]), it was expected that one could find the maximum lod score for this combination at $\theta = 0.20$ (as for the G blood group and the centric-fusion marker rob (15;17)). A maximum lod score at $\theta = 0.20$ for rcp (2p+;15q−) and the G blood group was only calculated when the results from the progeny of the male and female informative parents were taken together (Table V). When the sexes were taken separately, maximum lod scores were calculated at $\theta = 0.05$ for the females and at $\theta = 0.40$ for the male. The most reasonable explanation for this is that the crossing over rate was changed differently in meiosis in the male and female

Table I. Symbols and explanation of chromosomal markers studied

Marker symbol*	Explanation
t (1p+; 16q−)	translocation of a part of chr. 16 to chr. 1 (radiation-induced)
t (5p+; 15q−)	translocation of a part of chr. 15 to chr. 5 (radiation-induced)
rcp (2p+; 15q−)	reciprocal translocation between the chr. 2 and 15 (with the larger fragment deriving from chr. 15; radiation-induced)
inv (9p+; 9q−)	inversion within chr. 9 (radiation-induced)
rob (15; 17)	centromeric (Robertsonian) fusion of the chr. 15 and 17 ("wild-boar-chromosome")
16C+	enlargement of the centromeric region of chr. 16 (natural)
17C+	enlargement of the centromeric region of chr. 17 (natural)

* According to the recommendations of the Paris Conference[23]

Table II. Blood group systems investigated

	System factors	Alleles	Test method†
A	A	AA, A^-	4
D	Da,Db	D^a, D^b	1,3
E	Ea,Eb,Ed,Ee	E^{aegl}, E^{dbg}	1
	Ef,Eg,El	E^{def}, E^{deg}	
F	Fa,Fb	F^a, F^b	1
G	Ga,Gb	G^a, G^b	2,4
H	Ha,Ha*,Hb,Hc	H^a, H^b, H^c, H^-	4
I	Ia,Ib	I^a, I^b	2
J	Ja	J^a, J^-	2
K	Ke	K^{ac}, K^{ace}, K^{ade}	2
	Ka,Kb,Kc,Kd	K^b, K^-	4
L	La	L^{ad}, L^{adk}, L^{bd}	1
	Lb,Ld,Lg,Lk	L^{bg}	3
M	Ma,Mb,Mc	M^a, M^b, M^c, M^-	4
N	Na,Nb	N^a, N^b	2

* Factor for distinguishing between H^a/H^{a-} and H^a/H^- genotypes

† 1: direct agglutination test, 2: antiglobulin (Coombs) test, 3: dextran test, 4: hemolytic test

Table III. Serum protein and enzyme systems investigated

System*	Types	Alleles
Hpx (hemopexin)+	0,1,2,3	Hpx^0, Hpx^1 Hpx^2, Hpx^3
Tf (transferrin)+	A,B,C	Tf^A, Tf^B, Tf^C
ADA (adenosine deaminase)++	A,B,O	Ada^A, Ada^B, Ada^0
AM (serum-amylase)++	1,2,2F	Am^1, Am^2, Am^{2F}
6PGD (6-phosphogluconate dehydrogenase)++	A,B	Pgd^A, Pgd^B
PGM (phosphoglucomutase)++	A,B	Pgm^A, Pgm^B
GPI (glucose-phosphate isomerase)++	A,B	Phi^A, Phi^B

* Serum protein system−+; enzyme system−++

by the reciprocal translocation.

The lod scores for the combination t (5p+;15q−) and G blood group do not add much information regarding the location of the G blood-group locus, because they were calculated from only three informative descendents (Table IV).

According to Andresen[3] close linkage between the G blood-group locus and the other known porcine gene loci can be excluded. In spite of this Jørgensen[18] reported a linkage disequilibrium between the HAL and the G blood-group locus. The HAL locus had been shown to be closely linked to the H blood-group locus and other loci of the large linkage group SLA-C-J-GPI-HAL-S-H-PO2-6PGD. The lod scores from the combination of the loci of this linkage group and markers of chromosome 15 were especially interesting. A positive lod score for the H blood group could only be calculated for the rob (15;17) marker (based on only three informative descendants). On the other hand a lod score of 0.83 at θ = 0.40 was found for the GPI locus and the rob (15;17) marker (100 informative descendants). The analyses of linkage of the 6GPD locus with t (5p+;15q−), rcp (2p+;15q−) and rob (15;17) provided positive lod scores at higher recombination frequencies. Positive lod scores at higher recombination frequencies have been obtained for J and rcp (2p+;15q−) and rob (15;17). However, these are very weak indications that the linkage group SLA-C-J-GPI-HAL-S-H-PO2-6PGD is located on chromosome 15, especially when considering there was a lod score of 0.80 calculated for the combination of the GPI locus and the 16C+ marker. The linkage group would be located far from the centromere of chromosome 15.

Table IV. Lod scores for chromosomal and immunogenetic and biochemical markers, respectively, at various recombination frequencies

Combinations of markers		Recombination frequency (θ)					N*	N†
		0.05	0.10	0.20	0.30	0.40		
t (1p+;16q−)	A	−0.35	0.09	0.33	0.28	0.11	9	1
	D	−10.56	−6.44	−2.77	−1.07	−0.25	32	1
	E	−9.01	−5.23	−2.00	−0.63	−0.11	34	2
	G	−12.44	−7.25	−3.18	−1.19	−0.27	40	2
	H	−6.58	−3.69	−1.29	−0.37	−0.05	29	2
	I	−7.68	−4.67	−2.00	−0.77	−0.18	24	1
	M	−0.33	−0.11	−0.03	0.04	0.02	9	1
	N	0.26	0.21	0.13	0.06	0.02	2	1
	Hpx	−0.96	−0.03	0.56	0.57	0.28	16	1
	ADA	−6.00	−3.14	−0.80	0.04	0.14	30	1
	GPI	−6.14	−3.50	−1.30	−0.42	−0.08	26	2
t (5p+;15q−)	D	−3.55	−2.00	−0.84	−0.31	0.07	12	2
	E	−3.86	−1.85	−0.31	−0.13	0.10	25	3
	G	−0.72	−0.44	−0.19	−0.08	−0.02	3	1
	H	−3.35	−2.00	−0.84	−0.31	−0.07	13	2
	I	−1.81	−0.84	−0.12	0.06	0.04	14	2
	K	−2.98	−1.48	−0.33	0.01	0.04	19	2
	L	−5.51	−3.33	−1.42	−0.54	−0.12	19	2
	M	−3.81	−2.23	−0.90	−0.33	−0.07	16	2
	N	−2.16	−1.33	−0.58	−0.23	−0.53	7	1
	GPI	−2.16	−1.33	−0.58	−0.23	−0.53	7	1
	6PGD	−1.35	−0.61	−0.06	0.07	0.41	10	1
rcp (2p+;15q−)	D	−2.63	−1.56	−0.64	−0.24	−0.05	10	1
	E	−7.86	−4.64	−1.87	−0.67	−0.15	29	3
	G	−0.14	0.69	1.07	0.86	0.36	21	3
	H	−3.26	−1.73	−0.53	−0.11	−0.01	18	2
	J	−2.42	−0.96	0.10	0.33	0.19	21	2
	K	−8.84	−5.30	−2.20	−0.81	−0.18	30	3
	L	−7.21	−4.44	−1.94	−0.76	−0.18	21	2
	M	−0.00	0.58	0.77	0.55	0.19	10	1
	N	−2.88	−1.77	−0.78	−0.30	−0.07	9	2
	Hpx	−3.61	−2.22	−0.97	−0.38	−0.09	10	1
	PGM	−4.33	−2.66	−1.16	−0.45	−0.11	14	2
	6PGD	−1.54	−0.59	0.06	0.17	0.07	15	2
inv (9p−;9q+)	A	−0.35	0.09	0.33	0.28	0.11	9	1
	E	−0.35	0.09	0.33	0.28	0.11	9	1
	G	−2.89	−1.77	−0.78	−0.30	−0.07	9	1
	H	0.54	0.47	0.32	0.17	0.05	3	1
	N	0.26	0.21	0.13	0.06	0.02	2	1
	M	−0.33	−0.11	0.03	0.04	0.01	9	1
	GPI	0.54	0.47	0.32	0.17	0.05	3	1

* Number of informative progeny † Number of informative parents

Therefore it would be practically impossible to significantly prove its location on chromosome 15 by the markers studied here and by the method of family analyses. Experiments for investigating the chromsomal localization of the 6PGD and GPI loci by somatic cell hybridization techniques are in progress.

Inconsistent information resulted from the lod scores of the combinations I—17C+ and I—rob (15;17). For I—rob (15;17), linkage can be excluded for a recombination frequency of $\theta = 0.20$ while for I—17C+ a positive lod

Table V. Lod scores calculated when linkage phase was known

Combinations of markers		Sex	Recombination frequency (θ) 0.05	0.10	0.20	0.30	0.40	N*
rob (15;17)	G	♂	0.48	2.39	3.36	2.97	1.82	43
rcp (2p+;15q−)	G	♂	−2.61	−1.52	−0.57	−0.16	0.01	9
		♀	1.95	1.79	1.42	1.03	0.55	7
		♀	1.40	1.28	1.02	0.73	0.40	5
		Total ♀	3.35	3.07	2.44	1.76	0.95	12
		Total ♂/♀	0.74	1.55	1.87	1.60	0.96	21

* Number of informative progeny

Table IV. Cont'd.

Combinations of markers		Recombination frequency (θ) 0.05	0.10	0.20	0.30	0.40	N*	N†
rob (15;17)	A	−13.57	−7.88	−2.99	−0.95	−0.16	102	3
	E	−34.60	−19.90	−8.33	−2.90	−0.56	117	3
	G	−0.33	1.79	2.92	2.61	1.50	48	2
	H	0.54	0.47	0.32	0.17	0.05	3	1
	I	−11.45	−6.82	−2.78	−0.99	−0.21	38	1
	J	−6.65	−3.48	−0.88	0.05	0.19	56	1
	K	−0.72	−0.44	−0.19	−0.08	−0.02	3	1
	L	−28.71	−16.81	−6.47	−2.02	−0.26	101	2
	M	−0.72	−0.44	−0.19	−0.08	−0.02	3	1
	N	−0.93	−0.46	−0.12	−0.02	−0.00	4	1
	Hpx	−12.68	−7.11	−2.42	−0.55	0.33	53	2
	Tf	0.02	0.62	0.86	0.67	0.27	16	1
	AM	−17.94	−10.82	−4.52	−1.67	−0.37	56	1
	GPI	−19.78	−10.17	−2.33	0.46	0.83	100	2
	6PGD	−20.98	−11.93	−4.25	−1.07	0.02	82	3
16C+	D	−0.19	0.02	0.12	0.09	0.03	5	1
	E	−2.81	−1.54	−0.52	−0.14	−0.02	17	4
	F	−0.19	0.02	0.12	0.09	0.03	5	1
	G	−5.15	−2.72	−0.87	−0.24	−0.04	21	3
	H	−1.18	−0.67	−0.25	−0.09	−0.02	8	3
	J	0.54	0.47	0.32	0.17	0.05	3	1
	K	−0.72	−0.44	−0.19	−0.08	−0.02	3	1
	L	−1.44	−0.89	−0.39	−0.15	−0.04	6	2
	M	−2.11	−1.13	−0.37	−0.11	−0.02	10	2
	N	−1.18	−0.55	−0.17	−0.07	−0.02	9	1
	Hpx	−1.44	−0.89	−0.39	−0.15	−0.04	6	2
	PGM	−2.16	−1.33	−0.58	−0.23	−0.05	6	1
	ADA	−2.88	−1.77	−0.78	−0.30	−0.07	9	2
	GPI	−0.90	0.28	0.80	0.58	0.18	18	2
	6PGD	−0.72	−0.44	−0.19	−0.08	−0.02	3	1
17C+	D	−2.16	−1.33	−0.58	−0.23	−0.05	7	1
	E	0.37	0.53	0.52	0.36	0.13	7	1
	F	−0.84	−0.08	0.47	0.45	0.19	17	2
	G	−3.09	−1.79	−0.70	−0.25	−0.05	13	2
	H	−0.19	0.25	0.48	0.40	0.17	17	2
	I	1.09	0.98	0.72	0.44	0.14	5	1
	K	−3.35	−2.00	−0.84	−0.31	−0.07	13	2
	L	−3.61	−2.22	−0.97	−0.38	−0.09	10	1
	M	−0.72	−0.44	−0.19	−0.08	−0.02	3	1
	N	−3.55	−2.00	−0.84	−0.31	−0.07	12	2
	Hpx	−0.63	−0.17	0.13	0.15	0.06	8	1
	AM	−0.63	−0.17	0.13	0.15	0.06	8	1
	GPI	−1.44	−0.89	−0.39	−0.15	−0.04	5	1
	6PGD	−2.16	−1.33	−0.58	−0.23	−0.05	6	1

Table VI. Combinations for which linkage can be excluded to certain recombination frequencies

Recombination frequency (θ)	Combinations of markers	
$\theta < 0.30$	rob (15;17)	E
	rob (15;17)	L
$\theta < 0.20$	t (1p+;16q−)	D
	t (1p+;16q−)	E
	t (1p+;16q−)	G
	t (1p+;16q−)	I
	rcp (2p+;15q−)	K
	rob (15;17)	A
	rob (15;17)	I
	rob (15;17)	Hpx
	rob (15;17)	AM
	rob (15;17)	GPI
	rob (15;17)	6PGD
$\theta < 0.10$	t (1p+;16q−)	H
	t (1p+;16q−)	ADA
	t (1p+;16q−)	GPI
	t (1p+;16q−)	D
	t (1p+;16q−)	H
	t (1p+;16q−)	L
	t (1p+;16q−)	M
	rcp (2p+;5q−)	E
	rcp (2p+;5q−)	L
	rcp (2p+;5q−)	Hpx
	rcp (2p+;5q−)	PGM
	rcp (2p+;5q−)	J
	16C+	G
	17C+	K
	17C+	J
	17C+	N
$\theta < 0.05$	t (5p+;15q−)	E
	t (5p+;15q−)	K
	t (5p+;15q−)	N
	t (5p+;15q−)	GPI
	rcp (2p+;15q−)	D
	rcp (2p+;15q−)	H
	rcp (2p+;15q−)	J
	rcp (2p+;15q−)	N
	rcp (2p+;15q−)	Hpx
	inv (9p−;9q+)	G
	16C+	E
	16C+	M
	16C+	PGM
	16C+	ADA
	17C+	D
	17C+	G
	17C+	6PGD

score of 1.09 was calculated at $\theta = 0.05$. These scores, as well as those of other combinations, will become interesting only when further knowledge is available about the chromosomal location of the loci studied.

In the absence of other information about the location of these gene loci, all results are provisional. The linkage exclusions and the evidence for linkage require confirmation in other porcine breeds and by other laboratories to become definitive.

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