

# Comparative and physical mapping of 111 previously reported and 105 new porcine microsatellites

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## Summary

Here we report radiation hybrid mapping of 105 new porcine microsatellite markers on the IMpRH<sub>7000</sub> radiation hybrid panel. In addition, we searched flanking sequences of these markers, as well as 673 previously reported RH-mapped microsatellite markers, for orthology to human sequences. Eighty-seven new and 111 previously mapped sequences exhibited orthology to human sequences. Using a stringent sequence alignment, 25 microsatellite-flanking sequences were found to be highly similar to genic sequences, whereas 173 were similar to non-genic sequences in the human genome. Five markers were located near known breakpoints of synteny between human and swine.

**Keywords** microsatellite, pig, porcine, radiation hybrid mapping, swine, synteny.

## Introduction

Over the past several years, there has been an increased focus on the porcine genetic (Rohrer *et al.* 1994, 1996; <http://www.marc.usda.gov/genome/swine/swine.html>) and radiation hybrid (RH) (Hawken *et al.* 1999; Korwin-Kosakowska *et al.* 2002; Krause *et al.* 2002; Rink *et al.* 2002; Robic *et al.* 2003; Fahrenkrug *et al.* 2005; Alexander *et al.* 2006) maps, which will be useful for detection of candidate genes influencing quantitative traits and to assist in assembly of the pig genome sequence.

The pig/human comparative map has grown substantially in recent years due to large-scale expressed sequence tag (EST) projects, physical mapping and comparative sequence analysis (Fahrenkrug *et al.* 2002; Rink *et al.* 2002; Robic *et al.* 2003; Meyers *et al.* 2005). The complete sequence of the human genome can be used to identify regions of orthology, synteny and breakpoints at a high resolution once genomic sequence is available for the pig. Indeed, non-expressed sequences are highly conserved between species, particularly among vertebrates. These sequences, which reside in both genic and inter-genic regions, are sometimes quite extensive in length and may play important roles in gene expression (Sandelin *et al.* 2004; Siepel *et al.* 2005; Wernersson *et al.* 2005; Woolfe

*et al.* 2005). Robic *et al.* (2003) previously identified 623 such conserved sequences in pigs and humans by analysing the flanking sequences of anonymous porcine microsatellite markers. Continued identification of these points of conservation will increase the resolution of comparative maps, important for further identifying large-scale correspondences and rearrangements that have accumulated in the divergent evolution of human and swine genomes (Murphy *et al.* 2005).

Towards this end, we have generated and RH-mapped 105 new porcine microsatellites on the porcine radiation hybrid IMpRH<sub>7000</sub> panel (Yerle *et al.* 1998; Hawken *et al.* 1999). In addition, we have subjected these and previously physically mapped microsatellites (Fahrenkrug *et al.* 2005; Alexander *et al.* 2006) to comparative sequence analysis to identify points of potential pig/human orthology, and to further enhance the comparative map of these two species. Sequences with observed orthology were also mapped onto integrated physical and genetic maps using CARTHAGENE (de Givry *et al.* 2005; <http://www.inra.fr/internet/Departements/MIA/T//CarthaGene/>). In all, 198 new anchored points of pig/human orthology are reported here. Due to the quality of the integrated map and a high stringency for orthology nomination, all but one location are consistent with previously observed and/or predicted orthology. Our results contribute to refinement of the pig/human comparative map, which will assist in assembly and annotation of the pig genome. In addition, because these markers are microsatellites, they will enhance fine mapping efforts aimed at identifying positional candidate genes for economically important traits in pigs.

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## Materials and methods

### Clone isolation, sequencing and primer design

A small insert porcine genomic library was constructed as described previously (Rohrer *et al.* 1994). Briefly MboI-digested genomic DNA was size-fractionated on agarose and the fraction corresponding to 200–800 bp was recovered and ligated into BamHI-digested M13mp18. The resulting library was screened with radiolabelled (CA)<sub>16</sub> and (GT)<sub>16</sub> oligonucleotides. DNA was extracted from positive clones and sequenced on an ABI/PRISM 3100 Genetic Analyzer. Clone sequences were searched for matches with published microsatellite sequences and the presence of artiodactyl repetitive sequences (AREs; Alexander *et al.* 1994). Sequences that matched previously observed microsatellites (MS) or flanked by AREs were discarded. Oligonucleotides were designed using Primer 0.5 (M.J. Daly, S.E. Lincoln and E.S. Lander, unpublished data). Oligonucleotides were purchased from IDT.

### PCR amplification

Oligonucleotide primer pairs designed for each chosen microsatellite locus were amplified using PCR on the IMpRH<sub>7000</sub> panel. To determine optimum PCR conditions and ensure porcine specific amplification, each primer pair was tested with porcine and hamster genomic DNA at 54, 56, 58, 60, 62 and 64 °C annealing temperatures. PCR products were electrophoresed on a 2.5% agarose gel and independently scored by two individuals. Each marker was run in duplicate. Discrepancies between runs or scorers were reanalysed or the PCR repeated until resolved. The size of observed PCR product was recorded and compared to the predicted size from the clone sequence.

### Radiation hybrid mapping

All microsatellite vectors were initially assigned to chromosomes by two-point analysis using the online IMpRH mapping tool with a minimum LOD of 6.0 (<http://www.toulouse.inra.fr/lgc/pig/RH/IMpRH.htm> or <http://rhdev.toulouse.inra.fr/>) and then assigned to individual chromosome input files containing all publicly available vectors. A single map was constructed for each chromosome using TSP/Concorde (Agarwala *et al.* 2000). Markers that did not map near their most significant two-point marker or had very low LOD scores with flanking markers were subjected to re-analysis with CARTHAGENE software (de Givry *et al.* 2005; <http://www.inra.fr/internet/Departements/MIA/T//CarthaGene/>) using the same input file and a LOD threshold of 6.0. Genetic map predictions were derived from the nearest marker on the USMARC linkage map (<http://www.usmarc.usda.gov>) that had also been previously placed on the IMpRH<sub>7000</sub> map.

### Comparative sequence analysis

Mapped microsatellite sequences from this and previous reports (Korwin-Kossakowska *et al.* 2002; Krause *et al.* 2002; Fahrenkrug *et al.* 2005; Alexander *et al.* 2006) were subjected to comparative sequence analysis to identify points of potential pig/human orthology after removing those sequences already identified as having human orthologues by Robic *et al.* (2003). Sequences were compared to known porcine repetitive elements and masked using Censor (Jurka *et al.* 1996). Sequences were then compared to version 10 of the *Sus scrofa* gene index (SSGI; <http://www.tigr.org/tdb/tgi/>) using BLAST (Altschul *et al.* 1990) to identify sequences overlapping with known ESTs. Hits with bit-score >100, expected-value <0.001, and similarity >95% over 60 nucleotides were retained.

The microsatellite sequences that did not match sequences in SSGI, along with retrieved SSGI sequences, were compared to the human genome using an iterative process. First, conceptually translated sequences were compared to human proteins (Ensembl human-25.34e) using INPARANOID (Remm *et al.* 2001; O'Brien *et al.* 2005). Unmatched sequences were then compared with Ensembl human cDNA sequences using the WU\_BLASTN program (version 2.0). Hits with bit-score >100, expected-value <0.001 and similarity >70% were considered as matches with human cDNA. Unmatched sequences were compared to human genome sequence using WU\_BLASTN (version 2.0) and hits selected using the same threshold values. A summary of our analyses can be found in Fig. S1.

### Comparative mapping

For comparative mapping, multi-point maps of the resulting linkage groups identified above and the RH vectors from BAC-end sequences (BESs) markers of Meyers *et al.* (2005) were used to construct the comparative physical map using the Build, Annealing and Flips options of CARTHAGENE.

## Results

### Data analyses and RH mapping

In this study, we identified 105 new porcine microsatellites and assigned them to the porcine RH map using the IMpRH<sub>7000</sub> panel. Preliminary sequence analysis of these new marker sequences suggested they were orthologous to human sequences and were prioritized for RH mapping; thus, the success rate of 87 orthologues from 105 new marker sequences should not be considered random. Primer sequences, PCR annealing temperatures, amplicon size, two-point LOD scores and distance to the nearest marker on the genetic linkage map (<http://www.usmarc.usda.gov/genome/swine/swine.html>) are indicated in Table S1. Four markers (UMNp1060, UMNp1612, UMNp1340 and

UMNp1475), could not be placed directly on the genetic linkage map using two-point analysis as there was no significant RH linkage to another marker on the genetic linkage map. The placement of these four markers in Table S1 was based on generating comprehensive maps (<http://rhdev.toulouse.inra.fr>).

Comparative sequence analysis and mapping

In all, 778 microsatellite sequences, including 105 new and 673 previously published (Korwin-Kossakowska *et al.* 2002; Krause *et al.* 2002; Fahrenkrug *et al.* 2005; Alexander *et al.* 2006) sequences, were subjected to comparative sequence analysis. After masking, microsatellite clone sequences were compared to tentative consensus sequences (TCs) in the SSGI (<http://www.tigr.org>, version 11). Thirty matching sequences were retrieved from TIGR, and along with unmatched microsatellites, conceptually translated and compared to the human Ensembl proteins (version 25.34e) using INPARANOID. Of these sequences, eight significantly matched human proteins (Table 1). Sequences that did not match a human protein were then compared to Ensembl human cDNAs using WU-BLASTN, resulting in 17 additional significant matches (Table 2). Sequences still unmatched were compared to human genome sequence (Build 36.1) using WU-BLASTN, which resulted in an additional 173 matches (Table 3). One-hundred and eleven previously mapped markers (Fahrenkrug *et al.* 2005; Alexander *et al.* 2006) and 87 of the 105 new microsatellite markers (Table S1), for a total of 198 markers, exhibited hits to the various databases described above.

We then reanalysed markers that exhibited orthology to human sequences with BES RH vectors (Meyers *et al.* 2005) to generate a pig/human comparative map. The genomic position of the orthologous human sequence (Build 36.1) and the BES linked to these markers by RH mapping (Meyers *et al.* 2005), along with their positions, are indicated in Tables 1–3. No linkage with BES is indicated as NL in these tables.

Our RH mapping results for the autosomes used the physical map of Meyers *et al.* (2005) to determine the corresponding human position for the markers. The majority of markers exhibited LOD scores >6.0 with adjacent markers on the comprehensive map (data not shown). The average two-point LOD score was 11.5 and ranged from 6.0 (our cutoff) to 25.6. The average distance to the nearest anchored marker was about 33 cRays<sub>7000</sub>. We ordered the markers on swine chromosomes based on the RH position with markers on the genetic linkage map (<http://www.usmarc.usda.gov/genome/swine/swine.html>) that had been previously mapped on the IMpRH<sub>7000</sub> map. For SSCX, we used all the public data to align our markers and determine the human position. The majority of our markers mapped to areas of previously established human/porcine

Table 1 Porcine microsatellite markers showing matches to the human sequence using INPARANOID.

Microsatellite	TIGR match	TIGR match bit score	TIGR match E-value	INPARANOID ENSEMBL match	Human gene	BLASTP bit score	BLASTP E-value	RH mapped <sup>1</sup>	HSA chr. match		Closest comp. marker		HSA position		Closest comp. marker		BES interval location	
									start (Mb)	SSC (upper) <sup>2</sup>	start (Mb)	position (Mb)	start (Mb)	distance from human position (Mb) <sup>3</sup>				
UMNp1886	BI399299	276	2.15E-73	ENSP00000369426	PLAA	253	2.00E-68	1	9 (26.89)	1	CL328583	14 (61.78)	CL343339	9 (26.7)	breakpoint			
UMNp1562	CJ009005	198	6.80E-50	ENSP00000307853	MUS81	191	1.00E-49	1	11 (65.38)	2	CL367265	11 (65.38)	CL357942	11 (63.92)				
UMNp1415	BP157085	228	1.67E-84	ENSP00000348674	ZNF674	124	3.00E-29	1	19 (57.21)	6	311884541	19 (57.2)	CL339247	19 (55.05)	0.01			
UMNp1789	TC220489	617	1.11E-175	ENSP00000361052	POMGNT1	1026	0	1	1 (46.43)	6	NL		CL408417	1 (47.53)	1.1			
UMNp1591	TC221147	638	0	ENSP00000335580	C1orf164	249	2.00E-66	1	1 (44.87)	6	NL		CL342704	1 (44.59)	0.28			
UMNp1744	NA	NA	NA	ENSP00000372649	NP_848651.2	131	2.00E-31	1	3 (140.25)	13	CL328348	3 (140.64)	CL389134	3 (141.91)	0.39			
UMNp1417	BI341029	148	2.60E-34	ENSP00000342952	ADCY2	368	1.00E-103	1	5 (7.45)	16	CL362492	5 (8.3)	CL336906	5 (7.49)				
UMNp1580	BI359654	299	1.40E-80	ENSP00000327738	NP_848651.2	307	1.00E-84	1	4 (189.3)	17	CL358823	4 (189.51)	FRG1	4 (191.24)	0.21			

<sup>1</sup>1 = new markers described in this table.  
<sup>2</sup>NL = no linkage to BES (Meyers *et al.* 2005) with a two-point LOD score ≥6.  
<sup>3</sup>Distance (Mb) of the human position from the BES interval location containing our marker. A blank cell means that the human megabase position of our markers falls within the BES interval of Meyers *et al.* (2005).

**Table 2** Porcine microsatellite markers with significant match to human cDNA sequences.

Microsatellite	TIGR match		INPARANOID ENSEMBL protein match	Human gene	BLAST		RH mapped <sup>1</sup>	HSA chr. match start (Mb)	SSC	Closest comp. marker (upper) <sup>2</sup>	HSA position (Chr:Mb)	Closest comp. marker (lower)	HSA position (Mb)	BES interval location distance from human position (Mb) <sup>3</sup>
	TIGR match bit score	TIGR match E-value			bit score	E-value								
UMNP1309	NA	NA	ENSG00000167306	MYO5B	141	3.7E-35	2	18 (45.6)	1	CL326582	18 (46.49)	CL325701	18 (47.6)	0.89
UMNP644	TC200448	324	ENSG00000140416	TPM1	232	3.8E-94	1	15 (61.12)	1	TC33368	15 (62.15)	CL365788	15 (61.09)	
UMNP1148	NA	NA	ENSG00000197233	ORT12	129	3.70E-32	2	9 (124.32)	1	NL		GSN	9 (121.1)	3.22
UMNP1023	NA	NA	ENSG00000162105	SHANK2	144	3.4E-36	2	11 (70.01)	2	CL356851	11 (3.01)	CL366980	11 (70.73)	
UMNP1321	TC209436	396	ENSG00000173926	MARCH3	188	2.9E-49	2	5 (126.23)	2	CL371501	5 (125.48)	CL349020	5 (126.77)	
UMNP1091	TC206019	193	ENSG00000116132	PRRX1	162	6.6E-96	2	1 (168.90)	4	CL346430	8 (49.35)	CL354584	8 (48.49)	breakpoint
UMNP1505	TC220238	146	ENSG00000183569	SERHL2	582	4.9E-176	3	22 (41.28)	5	CL349377	22 (41.64)	ACO2	22 (40.3)	
UMNP1715	NA	NA	ENSG00000121904	C5MD2	141	4E-35	1	1 (33.75)	6	CL385273	1 (33.19)	CL354717	1 (33.74)	0.01
UMNP1671	NA	NA	ENSG00000168477	TNXB	145	0	1	6 (32.12)	7	345137116	6 (30.63)	311887684	6 (31.75)	0.37
UMNP1597	TC224951	414	ENSG00000169594	BNC1	530	2.8E-165	1	15 (81.72)	7	CL357354	15 (81.7)	CL348748	15 (79.91)	0.02
UMNP1467	BP153836	121	ENSG00000667704	IARS2	177	1.6E-45	1	1 (218.33)	10	CL388648	1 (216.82)	CL409130	1 (218.07)	0.26
UMNP820	CN158278	434	ENSG00000108861	DUSP3	166	9E-74	2	17 (39.2)	12	CL382674	17 (40.19)	CL328454	17 (41.99)	0.99
UMNP1574	NA	NA	ENSG00000144749	LRIG1	136	1.1E-33	1	3 (66.51)	13	CL344509	3 (67.44)	CL364671	3 (68.78)	0.93
UMNP1169	NA	NA	ENSG00000051382	PIK3C1	142	1.6E-35	2	3 (139.86)	13	CL373339	3 (139.05)	CL328348	3 (140.64)	
UMNP1568	B1341033	127	ENST00000358186	BDH1	149	6.38E-35	1	3 (175.5)	13	CL335143	3 (174.43)	CL336852	3 (177.23)	
UMNP947	BQ604235	523	ENSG00000058866	DAGK3	116	1.8E-71	2	3 (187.35)	13	CL343722	3 (186.22)	CL346087	3 (187.53)	
UMNP1017	NA	NA	ENSG00000165046	LETM2	105	5E-23	2	8 (38.36)	15	CL347961	8 (37.52)	U53020	8 (37.74)	0.62

<sup>1</sup>1 = new markers described in Table 1; 2 = Fahrenkrug et al. (2005); 3 = Alexander et al. (2006).

<sup>2</sup>NL = no linkage to BES (Meyers et al. 2005) with a two-point LOD score  $\geq 6$ .

<sup>3</sup>Distance (Mb) of the human position from the BES interval location containing our marker. A blank cell means that the human megabase position of our markers falls within the BES interval of Meyers et al. (2005).

**Table 3** Details of porcine microsatellite markers with orthology to human genomic sequence and their porcine locations.

Microsatellite	SSC		HSA chr. match bit score	HSA chr. match E-value	RH mapped <sup>1</sup>	HSA chr. match start (Mb)	SSC	Closest comp. marker (upper) <sup>2</sup>	HSA position (Mb)	Closest comp. marker (lower)	HSA position (Mb)	BES interval location distance from human position (Mb) <sup>3</sup>
	SSC TIGR match bit score	SSC TIGR match E-value										
UMNP928	NA	NA	129	3E-29	2	6 (156.13)	1	CL412345	6 (155.82)	CL334958	6 (154.49)	0.31
UMNP1216	NA	NA	103	9.5E-21	2	6 (144.18)	1	BF711055	6 (144.3)	TC20747	6 (144.46)	0.12
UMNP1258	NA	NA	173	1.9E-40	1	6 (112.91)	1	CL413260	6 (112.45)	CL344430	6 (116.14)	
UMNP1285	NA	NA	113	3.7E-35	2	18 (42.18)	1	NL		CL344431	18 (44.08)	1.90
UMNP1606	NA	NA	140	1.5E-32	1	15 (41.4)	1	CL378717	15 (41.74)	CL341406	15 (40.21)	
UMNP1475	NA	NA	419	0	1	15 (37.02)	1	CL348336	15 (36.04)	CL351690	15 (37.45)	
UMNP880	NA	NA	132	2.8E-45	2	15 (96.89)	1	CL332426	15 (96.97)	CL362984	15 (97.58)	0.08
UMNP1681	NA	NA	123	1.9E-34	1	18 (70.49)	1	CL358711	18 (72.34)	CL336443	18 (70.82)	0.23
UMNP1224	NA	NA	169	1.1E-41	2	18 (68.69)	1	CL336443	18 (70.82)	CL339209	18 (68.83)	
UMNP1060	NA	NA	108	1.5E-28	1	15 (67.94)	1	CL360810	15 (67.59)	CL338276	15 (66.47)	0.34
UMNP1166	NA	NA	171	1.2E-40	2	14 (58.42)	1	CL343312	14 (56.92)	CL358331	14 (58.20)	0.22
UMNP784	NA	NA	217	0	2	9 (14.95)	1	CL385499	9 (13.36)	CL379846	9 (12.38)	1.59
UMNP1198	NA	NA	118	1.5E-24	2	9 (19.45)	1	CL334702	9 (19.71)	CL335974	9 (18.57)	
UMNP623	NA	NA	400	0	1	9 (101.22)	1	CL325910	9 (93.7)	CL341592	9 (97.06)	4.16
UMNP948	NA	NA	117	3E-23	2	9 (112.64)	1	CL350990	9 (106.04)	CL351989	9 (107.59)	5.05
UMNP1921	NA	NA	124	2E-27	1	9 (115.49)	1	CL369936	9 (108.75)	CL352780	9 (110.29)	5.2
UMNP1705	NA	NA	209	0	1	9 (119.45)	1	NL		CL339256	9 (114.49)	5.04
UMNP271	NA	NA	307	0	1	9 (125.37)	1	NL		CL371573	9 (120.59)	4.78
UMNP827	NA	NA	225	0	2	11 (57.8)	2	CL413020	11 (59.44)	CL345826	11 (58.00)	0.20
UMNP1435	NA	NA	170	0	1	11 (42.75)	2	CL387830	11 (42.96)	CL328616	11 (41.56)	
UMNP1162	NA	NA	154	6.8E-35	2	11 (35.2)	2	CL410608	11 (37.39)	CL372241	11 (36.01)	0.81
UMNP1595	NA	NA	279	0	1	11 (30.69)	2	CL350043	11 (31.85)	CL354435	11 (30.62)	
UMNP1847	NA	NA	156	9E-45	3	11 (17.55)	2	CL352330	11 (18.63)	CL347458	11 (17.19)	
UMNP1079	NA	NA	115	1.4E-27	2	11 (12.79)	2	CL386986	11 (13.42)	CL364868	11 (12.49)	
UMNP1429	TC203861	560	113	3.1E-73	1	19 (3.42)	2	CL336839	19 (4.37)	CL379799	19 (3.24)	
UMNP716	NA	NA	158	0	2	19 (19.36)	2	CL355918	19 (18.90)	CL378987	19 (19.52)	0.16
UMNP995	NA	NA	103	1.6E-39	1	5 (73.27)	2	CB286244	5 (174.87)	CL327267	5 (73.50)	101.37 (breakpoint)
UMNP1655	NA	NA	102	2.3E-13	1	5 (8.169)	2	CL372277	5 (82.8)	CL366934	5 (84.09)	1.11
UMNP782	NA	NA	188	0	2	5 (88.02)	2	CL351586	5 (87.98)	CL410705	5 (89.38)	
UMNP1056	NA	NA	103	7.2E-22	2	5 (102.38)	2	CL356332	5 (99.59)	CL389974	5 (100.88)	1.50
UMNP1956	NA	NA	102	1.4E-41	3	5 (100.89)	2	CL389974	5 (100.88)	CL345673	5 (102.17)	
UMNP1206	NA	NA	174	7.2E-42	2	5 (103.29)	2	CL345673	5 (102.17)	CL348126	5 (103.38)	
UMNP1096	NA	NA	165	4.3E-55	1	5 (112.69)	2	CL355535	5 (111.51)	CL388357	5 (114.32)	
UMNP1379	NA	NA	177	0	1	5 (130.27)	2	CL363132	5 (132.08)	CL367109	5 (130.74)	0.47
UMNP1116	NA	NA	192	1.1E-53	2	5 (139.04)	2	CL370194	5 (139.17)	CL363935	5 (140.38)	0.13

Table 3 Continued.

Microsatellite	SSC		HSA chr. match bit score	HSA chr. match E-value	RH mapped <sup>1</sup>	HSA chr. match start (Mb)	SSC	Closest comp. marker (upper) <sup>2</sup>	HSA position (Mb)	Closest comp. marker (lower)	HSA position (Mb)	BES interval location distance from human position (Mb) <sup>3</sup>
	SSC TIGR match score	SSC TIGR match E-value										
UMNP1107	NA	NA	151	6.1E-34	2	5 (141.99)	2	CL363935	5 (140.38)	CL362288	5 (141.72)	0.27
UMNP1290	NA	NA	226	1.9E-56	2	16 (13.05)	3	CL335808	16 (13.44)	CL350034	16 (12.09)	
UMNP1287	NA	NA	131	1E-37	2	16 (9.85)	3	CL360103	16 (10.66)	CL348957	16 (9.28)	
UMNP1867	NA	NA	235	0	1	2 (66.63)	3	CL343356	2 (68.07)	CL413814	2 (66.57)	
UMNP1312	NA	NA	192	0	2	2 (52.52)	3	CL390259	2 (53.10)	CL411423	2 (51.51)	
UMNP1929	NA	NA	139	1.1E-28	1	2 (50.11)	3	CL343825	2 (50.58)	CL347786	2 (49.34)	
UMNP955	NA	NA	154	1E-48	2	2 (40.53)	3	CL343258	2 (40.87)	CL334945	2 (39.90)	
UMNP1340	NA	NA	162	4.1E-51	1	2 (40.33)	3	NL		CL408881	2 (38.31)	2.02
UMNP1142	NA	NA	126	1E-32	2	2 (31.25)	3	NL		CL384063	2 (32.76)	1.45
UMNP953	NA	NA	360	0	2	2 (21.72)	3	CL360107	2 (22.51)	CL388847	2 (21.09)	
UMNP1497	NA	NA	218	0	1	2 (16.69)	3	CL379758	2 (18.11)	CL383219	2 (16.69)	
UMNP1042	NA	NA	128	3.8E-27	2	8 (137.97)	4	CL344191	8 (139.18)	CL341839	8 (137.54)	
UMNP949	NA	NA	127	0	2	8 (124.6)	4	CL408638	8 (125.68)	CL369251	8 (124.49)	
UMNP638	NA	NA	135	4.7E-30	2	8 (119.21)	4	CL411070	8 (119.34)	CL385868	8 (117.99)	
UMNP850	NA	NA	113	7.9E-24	2	8 (56.21)	4	CL411493	8 (55.80)	MOS	8 (57.19)	
UMNP1556	NA	NA	205	0	1	1 (155.09)	4	CL334934	1 (154.8)	CL353117	1 (153.73)	0.29
UMNP793	NA	NA	159	0	2	1 (155.22)	4	AK024570	1 (153.52)	CL353117	1 (153.73)	1.49
UMNP1146	TC229468	0	104	2.3E-40	2	1 (145.7)	4	CL354161	1 (144.60)	CL339576	1 (144.11)	1.1
UMNP1492	NA	NA	181	0	1	1 (102.31)	4	CL378439	1 (103.85)	CL355674	1 (102.26)	0.05
UMNP724	NA	NA	268	0	2	1 (96.22)	4	CL349281	1 (95.05)	CL357011	1 (93.34)	1.17
UMNP751	NA	NA	144	2.3E-75	1	22 (31.53)	5	CL341985	22 (33.36)	CL340318	22 (31.70)	0.17
UMNP1477	NA	NA	106	6.5E-31	1	22 (33.44)	5	CL340318	22 (31.7)	CL341985	22 (33.36)	0.08
UMNP1085	NA	NA	102	1.8E-29	2	12 (51.91)	5	CL385479	12 (53.35)	CB285327	12 (51.93)	0.02
UMNP1043	NA	NA	146	1.3E-32	2	12 (60.49)	5	CL378968	12 (61.82)	CL371933	12 (62.76)	1.33
UMNP1322	TC211647	4E-79	123	6.8E-50	2	12 (6.44)	5	CL363192	12 (9.05)	CL367345	12 (6.68)	0.24
UMNP1960	NA	NA	196	0	1	12 (5.18)	5	NL		CL366005	12 (5.46)	0.28
UMNP1532	NA	NA	204	1.9E-49	3	6 (24.89)	5	CL361781	12 (3.11)	CL366362	12 (0.45)	breakpoint
UMNP1853	NA	NA	120	8E-47	3	16 (52.51)	6	CL349441	16 (52.21)	CL376285	16 (50.81)	0.3
UMNP1476	NA	NA	133	2.1E-29	1	16 (45.47)	6	CL344599	19 (33.32)	311880163	19 (33.82)	breakpoint
UMNP747	NA	NA	109	0	2	19 (52.66)	6	CL387143	19 (52.08)	CL379505	19 (53.36)	
UMNP1612	NA	NA	102	1.1E-37	1	1 (3.28)	6	NL		CL361179	1 (2.9)	0.38
UMNP682	NA	NA	150	3.5E-34	2	1 (18.3)	6	CL343244	1 (17.97)	CL366205	1 (19.94)	
UMNP908	NA	NA	283	0	2	1 (19.15)	6	CL343244	1 (17.97)	CL366205	1 (19.94)	
UMNP977	TC231154	1E-118	189	9.6E-45	2	1 (23.64)	6	CL362878	1 (23.17)	CL350484	1 (24.24)	
UMNP1164	NA	NA	141	4.5E-33	1	18 (7.3)	6	NL		CL369079	18 (5.81)	1.49

Table 3 Continued.

Microsatellite	SSC		HSA chr. match score	HSA chr. match E-value	RH mapped <sup>1</sup>	HSA chr. match start (Mb)	SSC	Closest comp. marker (upper) <sup>2</sup>	HSA position (Mb)	Closest comp. marker (lower)	HSA position (Mb)	BES interval location distance from human position (Mb) <sup>3</sup>
	SSC TIGR match bit score	SSC TIGR match E-value										
UMNP720	NA	NA	177	7.4E-43	2	18 (3.17)	6	CL387184	18 (3.21)	CB286551	18 (0.11)	
UMNP920	NA	NA	114	8.1E-27	2	18 (19.07)	6	CL349170	18 (19.92)	CL345583	18 (21.28)	0.85
UMNP1305	NA	NA	272	4.7E-76	2	18 (18)	6	NL		CL379967	18 (22.65)	4.65
UMNP913	NA	NA	267	5.8E-99	1	18 (28.46)	6	CL361156	18 (29.00)	CL346369	18 (30.24)	0.54
UMNP918	NA	NA	171	4.5E-41	2	18 (37.69)	6	CL346544	18 (38.32)	CL372251	18 (39.63)	0.63
UMNP1498	NA	NA	107	2.5E-23	1	18 (37.0)	6	CL372251	18 (39.63)	CL346544	18 (38.32)	1.32
UMNP1138	NA	NA	139	2E-36	2	6 (13.7)	7	CL352460	6 (13.01)	GMPR	6 (16.34)	
UMNP1217	NA	NA	139	0	2	6 (20.7)	7	CL339993	6 (21.60)	TC29673	6 (19.95)	
UMNP1122	NA	NA	101	2.6E-41	2	6 (23.39)	7	CL339225	6 (22.58)	CL409184	6 (23.74)	
UMNP732	NA	NA	201	1.3E-67	1	6 (39.57)	7	CL387684	6 (38.76)	CL348929	6 (39.67)	
UMNP1707	CJ029398	0	109	4.3E-35	1	6 (43.66)	7	CL358605	6 (43.71)	3T1616568	6 (45.18)	0.05
UMNP1852	NA	NA	277	0	1	6 (44.58)	7	CL358605	6 (43.71)	3T1616568	6 (45.18)	
UMNP859	NA	NA	209	1.1E-73	2	6 (31.73)	7	BAT1	6 (31.61)	3T1887684	6 (31.75)	
UMNP1103	NA	NA	137	1.5E-28	2	15 (71.02)	7	BF198849	15 (70.37)	CL340155	15 (70.94)	0.08
UMNP1332	NA	NA	209	3.5E-59	2	15 (74.24)	7	CL342226	15 (73.98)	CL351692	15 (74.83)	
UMNP1324	NA	NA	215	2.2E-104	2	14 (28.3)	7	CL327316	14 (27.74)	CL388562	14 (26.46)	0.56
UMNP849	NA	NA	122	6.1E-34	2	14 (28.63)	7	CL327316	14 (27.74)	CL388562	14 (26.46)	0.89
UMNP1076	NA	NA	100	8.2E-20	2	14 (73.83)	7	CL352840	14 (72.50)	BG608485	14 (73.25)	0.58
UMNP1230	NA	NA	198	0	2	14 (75.92)	7	CL358370	14 (74.19)	CL359373	14 (75.57)	0.35
UMNP956	NA	NA	179	8.5E-40	2	14 (89.35)	7	CL348388	14 (87.18)	CL364183	14 (88.34)	1.01
UMNP1378	NA	NA	120	2.1E-26	1	14 (98.85)	7	CL411034	14 (97.72)	CL349383	14 (98.88)	
UMNP909	NA	NA	111	8.2E-15	2	4 (5.1)	8	CL354189	4 (5.86)	CL356585	4 (5.03)	
UMNP1058	NA	NA	199	5.8E-48	2	4 (12.85)	8	CL337851	4 (10.67)	CL348674	4 (13.06)	
UMNP1965	NA	NA	101	4.2E-18	1	4 (23.82)	8	CL345704	4 (24.55)	CL387304	4 (23.8)	
UMNP2036	NA	NA	103	1.9E-31	1	4 (28.55)	8	CL356647	4 (27.48)	CL328077	4 (30.55)	
UMNP1273	NA	NA	128	2.8E-37	2	4 (75.44)	8	BG382289	4 (73.57)	CL358575	4 (75.64)	
UMNP832	NA	NA	134	4.6E-29	2	4 (76.19)	8	CL352093	4 (76.43)	CB287184	4 (74.96)	
UMNP1815	NA	NA	281	0	1	4 (137.89)	8	NL		BG894821	4 (142.01)	3.98
UMNP1097	NA	NA	105	3.5E-21	2	11 (93.39)	9	CL388602	11 (93.30)	CL355348	11 (94.46)	
UMNP1137	NA	NA	227	0	2	11 (97.54)	9	CL364540	11 (98.39)	CL411750	11 (99.68)	0.85
UMNP1205	NA	NA	227	0	2	11 (98.64)	9	CL364540	11 (98.39)	CL411750	11 (99.68)	
UMNP1427	NA	NA	109	1.2E-42	1	11 (103.5)	9	CL369211	11 (104.79)	CL342212	11 (103.54)	0.04
UMNP1263	NA	NA	225	0	2	11 (110.23)	9	CL388132	11 (110.66)	CB287025	11 (111.52)	0.43
UMNP764	NA	NA	162	0	2	11 (111.77)	9	CB287025	11 (111.52)	CL355631	11 (111.93)	
UMNP1101	NA	NA	121	0	2	11 (114.15)	9	CL381252	11 (114.70)	CL323535	11 (115.96)	0.55

Table 3 Continued.

Microsatellite	SSC		SSC	TIGR match bit score	TIGR match E-value	RH mapped <sup>1</sup>	HSA chr.		HSA chr. match E-value	HSA chr.		SSC	Closest comp. marker (upper) <sup>2</sup>		HSA position (Mb)		Closest comp. marker (lower)	HSA position (Mb)		BES interval location distance from human position (Mb) <sup>3</sup>
	SSC TIGR match	SSC TIGR match					match	start		marker	position		marker	position	marker	position				
UMINp1651	NA	NA	NA	135	1E-41	1	11 (119.09)	9	CL338908	11 (117.23)	BG382617	11 (120.03)								
UMINp781	NA	NA	NA	211	0	2	11 (127.66)	9	CL351627	11 (126.16)	CL412931	11 (128.43)								
UMINp1992	NA	NA	NA	103	1.4E-22	3	1 (203.2)	9	CL411937	1 (200.75)	B339312	1 (201.48)		1.72						
UMINp730	NA	NA	NA	142	5.1E-45	2	1 (203.26)	9	BF191000	1 (203.26)	CB286403	1 (204.04)								
UMINp1620	NA	NA	NA	165	2E-38	1	7 (90.07)	9	CL372826	7 (90.13)	CL342284	7 (88.16)								
UMINp808	NA	NA	NA	145	2.9E-33	2	1 (206.21)	9	CL352382	1 (205.00)	BE236076	1 (204.70)		1.21						
UMINp1284	NA	NA	NA	118	8.6E-26	2	1 (206.91)	9	CL352382	1 (205.00)	BE236076	1 (204.70)		1.91						
UMINp814	NA	NA	NA	251	1.6E-66	1	7 (52.76)	9	CL327178	7 (50.61)	CL384967	7 (53.05)								
UMINp1437	NA	NA	NA	265	0	1	1 (216.19)	10	TGFB2	1 (214.91)	CL386296	1 (213.67)		1.28						
UMINp1846	NA	NA	NA	111	3.6E-23	1	10 (32.08)	10	NL		CL377050	10 (32.26)		0.18						
UMINp1422	NA	NA	NA	141	0	1	10 (14.25)	10	CL387543	10 (26.61)	CL346052	10 (14.46)		0.21						
UMINp705	NA	NA	NA	229	0	2	10 (22.24)	10	CL370390	10 (22.35)	CL364296	10 (21.13)								
UMINp1569	NA	NA	NA	286	0	1	10 (21.29)	10	CL364296	10 (21.13)	CL367508	10 (24.19)								
UMINp765	NA	NA	NA	155	7.7E-37	2	13 (32.69)	11	CL389199	13 (32.52)	CL326966	13 (33.10)								
UMINp823	NA	NA	NA	187	1.4E-60	2	13 (36.21)	11	BF185113	13 (35.85)	CL384210	13 (36.95)								
UMINp866	NA	NA	NA	106	3.5E-20	2	13 (43.12)	11	CL344489	13 (43.75)	CL352296	13 (43.02)		0.1						
UMINp1573	NA	NA	NA	206	0	1	13 (78.58)	11	CL355577	13 (79.22)	BF077677	13 (77.42)								
UMINp886	AJ682855	0	453	147	4.8E-37	2	13 (98.34)	11	NL		CL340954	13 (98.20)		0.14						
UMINp1098	NA	NA	NA	164	1.2E-48	1	17 (11.1)	12	CL327427	17 (10.27)	CL324577	17 (12.13)								
UMINp1161	NA	NA	NA	298	3.3E-77	2	17 (2.07)	12	CL349484	17 (1.31)	CL387016	17 (3.32)								
UMINp795	NA	NA	NA	133	4.8E-29	2	17 (39.38)	12	CL328454	17 (41.99)	CL382674	17 (40.19)		0.81						
UMINp1642	NA	NA	NA	159	4.2E-45	1	17 (44.8)	12	CL410240	17 (49.11)	CL358017	17 (46.77)		1.97						
UMINp629	NA	NA	NA	130	0	2	17 (56.8)	12	CL364800	17 (58.92)	CB286227	17 (57.30)		0.5						
UMINp1215	NA	NA	NA	119	2.24E-44	2	3 (132.27)	13	CL387252	3 (132.14)	CL380069	3 (131.25)		0.13						
UMINp868	NA	NA	NA	162	0	2	3 (17.5)	13	CL339773	3 (15.70)	CL366013	3 (17.07)		0.43						
UMINp1180	NA	NA	NA	105	2.9E-30	2	3 (42.72)	13	CL363112	3 (39.37)	CL343272	3 (41.91)		0.81						
UMINp1246	NA	NA	NA	155	2.1E-32	2	3 (45.55)	13	CL363560	3 (44.83)	CL347409	3 (46.47)								
UMINp1130	NA	NA	NA	157	0	2	3 (54.64)	13	NL		CL411965	3 (53.77)		0.87						
UMINp1038	NA	NA	NA	361	0	2	3 (60.17)	13	CL339589	3 (59.18)	CL343955	3 (60.64)								
UMINp1614	NA	NA	NA	111	0	1	3 (73.85)	13	CL325894	3 (72.68)	CL380900	3 (74.02)								
UMINp807	NA	NA	NA	135	6.1E-43	2	3 (141.55)	13	CL328348	3 (140.64)	CL389134	3 (141.91)								
UMINp1909	NA	NA	NA	161	4.9E-56	3	3 (144.78)	13	CL380260	3 (143.35)	CL357558	3 (144.83)								
UMINp873	NA	NA	NA	121	1.6E-33	2	3 (150.58)	13	CL413985	3 (147.28)	CL341583	3 (150.00)		0.58						
UMINp1440	NA	NA	NA	113	3.7E-14	1	3 (147.37)	13	CL343303	3 (148.68)	CL337775	3 (146.2)								
UMINp1524	NA	NA	NA	108	2.4E-17	1	3 (169.01)	13	CL341787	3 (169.74)	CL385817	3 (167.27)								



Table 3 Continued.

Microsatellite	SSC		SSC		RH mapped <sup>1</sup>	HSA chr. match		SSC	Closest comp. marker (upper) <sup>2</sup>		HSA position (Mb)		Closest comp. marker (lower)	HSA position (Mb)		BES interval location from human position (Mb) <sup>3</sup>
	TIGR match bit score	TIGR match E-value	HSA chr. match score	HSA chr. match E-value		HSA chr. match start (Mb)	HSA chr. match end (Mb)		Closest comp. marker (lower)	HSA position (Mb)	HSA position (Mb)	HSA position (Mb)				
UMNP1083	NA	NA	174	4.6E-62	1	21 (25.98)	13	CL366886	21 (25.18)	CL327163	21 (27.56)					
UMNP855	NA	NA	158	1.4E-41	2	21 (33.36)	13	CL372354	21 (32.38)	CL377885	21 (33.82)					
UMNP901	NA	NA	168	0	2	8 (23.88)	14	CL369234	8 (22.55)	CL347310	8 (24.14)					
UMNP944	NA	NA	167	1.1E-39	2	10 (99.27)	14	CL344905	10 (98.44)	CL358216	10 (99.35)					
UMNP1293	NA	NA	109	1.3E-20	2	10 (105.4)	14	CL380099	10 (105.33)	CL341859	10 (106.26)					
UMNP1413	NA	NA	139	2.5E-30	1	10 (112.37)	14	CL388345	10 (112.3)	CL382692	10 (113.23)					
UMNP1447	NA	NA	217	0	1	10 (120.02)	14	311779136	10 (118.71)	CL386363	10 (119.9)					
UMNP1123	NA	NA	118	7.50E-46	1	2 (149.59)	15	CL347145	2 (148.74)	CL362058	2 (150.24)					
UMNP1249	NA	NA	213	0	2	2 (116.91)	15	CL334146	2 (116.40)	CL327343	2 (117.91)					
UMNP1499	NA	NA	119	1.4E-24	1	8 (32.5)	15	BG834615	8 (32.48)	CL355234	8 (31.74)					
UMNP1843	NA	NA	145	0	1	8 (31.45)	15	NL		CL355234	8 (31.74)					
UMNP1513	NA	NA	173	7.2E-40	1	2 (153.98)	15	CL386994	2 (154.9)	CL338491	2 (156.27)					
UMNP1914	NA	NA	140	0	1	2 (165.13)	15	CL357234	2 (166.29)	CL361827	2 (164.82)					
UMNP1546	NA	NA	113	1.8E-23	1	2 (189.99)	15	CL378789	2 (191.87)	CL367576	2 (190.45)					
UMNP684	NA	NA	123	1.3E-34	2	5 (19.99)	16	CL372377	5 (19.58)	CL373351	5 (21.21)					
UMNP1717	NA	NA	265	0	1	5 (29.21)	16	CL369981	5 (28.41)	CL383973	5 (30.07)					
UMNP755	NA	NA	119	3.3E-25	2	5 (31.85)	16	NL		CL440214	5 (31.49)					
UMNP1163	NA	NA	172	5.3E-21	2	5 (4.11)	16	CL344958	5 (4.52)	311771575	5 (3.97)					
UMNP648	NA	NA	103	1.1E-40	1	5 (173.88)	16	CL347112	5 (173.51)	CL381019	5 (173.71)					
UMNP1576	NA	NA	114	2.3E-48	2	5 (168.41)	16	CL378582	5 (169.41)	CL355081	5 (168.21)					
UMNP1425	NA	NA	102	1.5E-38	1	20 (9.98)	17	CL352905	20 (10.6)	CL372614	20 (9.11)					
UMNP952	NA	NA	130	6.3E-36	1	20 (17.62)	17	ZNF133	20 (18.22)	BFS1	20 (17.42)					
UMNP910	NA	NA	144	2.7E-41	1	20 (19.82)	17	CL410017	20 (18.78)	CL363318	20 (20.37)					
UMNP993	NA	NA	135	2.5E-33	2	20 (21.74)	17	CL349746	20 (20.64)	CL339322	20 (22.37)					
UMNP1028	NA	NA	121	2E-34	2	20 (29.75)	17	CL334168	20 (1.17)	CL411518	20 (30.94)					
UMNP1822	NA	NA	176	5.1E-29	2	7 (120.07)	18	CL361069	7 (120.49)	CL355453	7 (119.28)					
UMNP969	NA	NA	135	1.90E-113	1	X (17.44)	X	TC36002	X (19.09)	AR030H07	X (19.32)					
UMNP1677	NA	NA	226	3.20E-35	1	X (40.06)	X	CH242-230H13	X (39.98)	TC41385	X (40.06)					
UMNP1618	NA	NA	212	6.10E-76	1	X (92.87)	X	AB050318	X (91.69)	CH242-78P6	X (90.16)					
UMNP1657	TC230092	6E-87	127	2.60E-126	1	X (99.92)	X	Pigl-582H10	X (100.74)	KIAA0443	X (101.71)					
UMNP1432	NA	NA	161	2.40E-49	1	X (107.01)	X	TC35554	X (105.93)	AR066G03	X (106.76)					
UMNP891	NA	NA	130	1.30E-51	1	X (109.53)	X	B1343796	X (109.26)	TC45532	X (107.69)					
	NA	NA	130	7.10E-65	1	X (110.10)	X	TC45532	X (107.69)	B1343796	X (109.26)					

<sup>1</sup>1 = new markers described in Table 1; 2 = Fahrenkrug et al. (2005); 3 = Alexander et al. (2006).

<sup>2</sup>NL = no linkage to BES (Meyers et al. 2005) with a two-point LOD score ≥6.

<sup>3</sup>Distance (Mb) of the human position from the BES interval location containing our marker. A blank cell means that the human position falls within the BES interval.

synteny (<http://www.toulouse.inra.fr/lgc/pig/compare/compare.htm>; Meyers *et al.* 2005) (data not shown).

Markers *UMNp993* (HSA20/SSC17), *UMNp995* (HSA5/SSC5), *UMNp1091* (HSA8/SSC4), *UMNp1476* (HSA16/SSC19), *UMNp1477* (HSA22/SSC5) and *UMNp1886* (HSA14/SSC1) mapped close to known human/pig breakpoints. There were five additional markers for which comparative sequence analysis suggested orthology to segments of the human genome that were inconsistent with known conserved synteny and physical mapping data. The best BLAST result for *UMNp730* (SSC9; Table 3) (*E*-value 2.1E-46, bit score 162) indicated a match on HSA5; however, there was a secondary match on HSA1 (*E*-value 5.1E-45, bit score 142) which is consistent with known synteny and our RH mapping results. *UMNp1532* (Table 3) mapped to SSC5 and was linked to BES *CL361781* and *CL366362* which were shown to have synteny with HSA12 by Meyers *et al.* (2005). However, our BLAST results predict orthology with a sequence on HSA6. Two other matches for *UMNp1532*, with much lower *E*-values (*c.* 5.1E-37 and 4.1E-36), mapped to HSA16.

The distance where the BES that flanked these markers differed from the predicted human location are shown in Tables 1–3, whereas blanks in these tables indicate that the marker was within the interval defined by the BES. All but nine BES mapped within 2 Mb of the human location corresponding to the marker sequence, excluding markers near known breakpoints, as described above.

## Discussion

Based on our physical mapping and comparative sequence analysis using sequences flanking microsatellites, we have added 198 new anchor points of orthology to the pig/human comparative map. These microsatellites will serve as an important resource for physical mapping by RH analysis, genetic mapping in reference populations, and comparison to the human and other genomes. The alignment of sequences flanking microsatellites with the human genome and their inferred comparative map positions adds detailed resolution to the current porcine physical map. Using a targeted approach, additional RH markers should easily define breakpoint and rearranged regions in the porcine genome.

In the vast majority of cases, our comparative mapping results are consistent with previously reported human/porcine synteny correspondences (Tables 1–3). We identified six markers that were near predicted human/swine comparative breakpoints. The predicted interval of the BES flanking *UMNp993* is at 29.77 Mb on HSA20. Although this region of SSC17 is syntenic with HSA20, there is a rearrangement in the pig genome between the BES markers, thus *UMNp993* at 29.75 Mb further defines this rearrangement. *UMNp995*, located at 73.27 Mb, mapped to a 101.37-Mb region of HSA5, indicating rearranged synteny

relative to this chromosome on SSC2. *UMNp1477* mapped to a location on HSA22 at 33.44 Mb near a previously predicted breakpoint between HSA2 and HSA22 (HSA2:HSA22/SSC5). *UMNp1091* (corresponding to *PRRX1*, Table 2) was predicted to be orthologous to a region on HSA1 at 168.90 but RH mapping placed it on SSC4 in a segment with known synteny to HSA8. This is consistent with the HSA1:HSA8 breakpoint known to occur in this area and further refines this breakpoint. *UMNp1886* (SSC1), at 26.89 Mb on HSA9, was placed at a predicted break point corresponding to HSA9 and HSA14. Likewise the rearrangement (HSA16:19/SSC6) near *UMNp1476*, located at 45.47 Mb on HSA16, was consistent with previous reports.

*UMNp730* (SSC9) had two hits of similar values on HSA1 and HSA5 at 203.26 and 162.96 Mb respectively. The weaker BLAST hit places this marker on HSA1 which is consistent with known synteny. This might be explained by segmental duplication in the human genome where the original sequence on HSA1 mutated faster than the duplication on HSA5. *UMNp1532* (SSC5; Table 3) had three hits above a match bit score of 100: one on HSA6 (*E*-value 1.90E-49, bit score 204 at 24.82 Mb) and two on HSA16 (5.1E-37, bit score 107 and 1E-36, bit score 104 at 18.09 and 16.39 Mb respectively). Although there is a striking conservation in sequence, none of these predicted points of orthology are consistent with pig physical mapping data; *UMNp1532* was linked to *CL363720* with a two-point LOD of 11.75 using the IMPRH server (<http://rhdev.toulouse.inra.fr>), which placed it near the centromere on SSC5 (INRA maps; <http://rhdev.toulouse.inra.fr/Do=C&carte=8>).

Excluding those markers near known breakpoints, nine BES intervals encompassing these markers mapped to more than 4 Mb from the human location. Three markers exhibited linkage to only one BES with a two-point LOD score >6. Linkage to another flanking BES may have resulted in marker being placed closer than 2 Mb to the human position. Six of these markers were all in the interval 101–125 Mb on HSA9, corresponding to SSC1 (Tables 2 and 3), and were located 3.22–5.05 Mb outside the BES. The positions of the markers were inferred from the flanking BES markers from Meyers *et al.* (2005) which used Build 33 of the human genome draft sequence (April 2003 release) to establish the human position. In contrast, our comparative sequence analysis used Build 36.1. After reanalysis of those BES against Build 36.1, all six of the markers mapped to within 2 Mb of the corresponding human sequence locations. Excluding markers at known breakpoints, and *UMNp1532*, there were only two markers (*UMNp1305* and *UMNp1815*) that were more than 2 Mb from the BES interval predicted by Meyers *et al.* (2005). These discrepancies could be due to the use of two different human builds, or the Mb values associated with the closest BES are based on comprehensive map order and there is often little statistical support for one local order over another. Thus

these markers may be distal or proximal to the BES markers indicated in Tables 1–3.

The assignment of 198 microsatellite marker positions that are comparatively anchored can be used as genetic markers for QTL experiments, aid in characterizing the evolution of the swine genome, and will assist in the assembly of the swine genomic sequence.

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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.1365-2052.2007.01651.x>

**Figure S1** Iterative sequence analysis for establishing pig to human orthology.

**Table S1** Porcine microsatellite information.

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