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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 $IMpRH_{7000}$ 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-Kossakowska *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 $IMpRH_{7000}$ 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 $(CA)_{16}$ and $(GT)_{16}$ 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 $IMpRH_{7000}$ 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 $IMpRH_{7000}$ 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 $IMpRH_{7000}$ 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 $cRays_{7000}$. 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 $IMpRH_{7000}$ 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 protein match	Human gene	BLASTP bit score	BLASTP *E*-value	RH mapped[1]	HSA chr. match start (Mb)	SSC	Closest comp. marker (upper)[2]	HSA position (Mb)	Closest comp. marker (lower)	HSA chr. match start (Mb)	BES interval location distance from human position (Mb)[3]
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	*CL361265*	11 (65.38)	*CL357942*	11 (63.92)	
UMNp1415	BP157085	228	1.67E-84	ENSP00000348674	*ZNF614*	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

[1]1 = new markers described in this table.
[2]NL = no linkage to BES (Meyers *et al.* 2005) with a two-point LOD score ≥6.
[3]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	TIGR match bit score	TIGR match *E*-value	INPARANOID ENSEMBL protein match	Human gene	BLAST bit score	BLAST *E*-value	RH mapped[1]	HSA chr. match start (Mb)	SSC	Closest comp. marker (upper)[2]	HSA position (Chr:Mb)	Closest comp. marker (lower)	HSA position (Mb)	BES interval location distance from human position (Mb)[3]
UMNp1309	NA	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	0	ENSG00000140416	*TPM1*	232	3.8E-94	1	15 (61.12)	1	*TC33368*	15 (62.15)	*CL365788*	15 (61.09)	
UMNp1148	NA	NA	NA	ENSG00000197233	*OR1J2*	129	3.70E-32	2	9 (124.32)	1	NL		*GSN*	9 (121.1)	3.22
UMNp1023	NA	NA	NA	ENSG00000162105	*SHANK2*	144	3.4E-36	2	11 (70.01)	2	*CL356851*	11 (3.01)	*CL366980*	11 (70.73)	
UMNp1321	TC209436	396	1E-109	ENSG00000173926	*MARCH3*	188	2.9E-49	2	5 (126.23)	2	*CL371501*	5 (125.48)	*CL349020*	5 (126.77)	
UMNp1091	TC206019	193	0	ENSG00000116132	*PRRX1*	162	6.6E-96	2	1 (168.90)	4	*CL346430*	8 (49.35)	*CL354584*	8 (48.49)	breakpoint
UMNp1505	TC220238	146	4.19E-78	ENSG00000183569	*SERHL2*	582	4.9E-176	3	22 (41.28)	5	*CL349377*	22 (41.64)	*ACO2*	22 (40.3)	
UMNp1715	NA	NA	NA	ENSG00000121904	*CSMD2*	141	4E-35	1	1 (33.75)	6	*CL385273*	1 (33.19)	*CL354717*	1 (33.74)	0.01
UMNp1671	NA	NA	NA	ENSG00000168477	*TNXB*	145	0	1	6 (32.12)	7	*345137116*	6 (30.63)	*311887684*	6 (31.75)	0.37
UMNp1597	TC224951	414	0	ENSG00000169594	*BNC1*	530	2.8E-165	1	15 (81.72)	7	*CL357354*	15 (81.7)	*CL348748*	15 (79.91)	0.02
UMNp1467	BP153836	121	1.73E-62	ENSG00000067704	*IARS2*	177	1.6E-45	1	1 (218.33)	10	*CL388648*	1 (216.82)	*CL409130*	1 (218.07)	0.26
UMNp820	CN158278	434	1E-21	ENSG00000108861	*DUSP3*	166	9E-74	2	17 (39.2)	12	*CL382674*	17 (40.19)	*CL328454*	17 (41.99)	0.99
UMNp1574	NA	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	NA	ENSG00000051382	*PIK3C1*	142	1.6E-35	2	3 (139.86)	13	*CL373339*	3 (139.05)	*CL328348*	3 (140.64)	
UMNp1568	BI341033	127	1.8112E-28	ENST00000358186	*BDH1*	149	6.38E-35	1	3 (175.5)	13	*CL335143*	3 (174.43)	*CL336852*	3 (177.23)	
UMNp947	BQ604235	523	1E-148	ENSG00000058866	*DAGK3*	116	1.8E-71	2	3 (187.35)	13	*CL343722*	3 (186.22)	*CL346087*	3 (187.53)	
UMNp1017	NA	NA	NA	ENSG00000165046	*LETM2*	105	5E-23	2	8 (38.36)	15	*CL347961*	8 (37.52)	*U53020*	8 (37.74)	0.62

[1]1 = new markers described in Table 1; 2 = Fahrenkrug *et al.* (2005); 3 = Alexander *et al.* (2006).

[2]NL = no linkage to BES (Meyers *et al.* 2005) with a two-point LOD score ≥6.

[3]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 TIGR match	SSC TIGR match bit score	SSC TIGR match *E*-value	HSA chr. match bit score	HSA chr. match *E*-value	RH mapped[1]	HSA chr. match start (Mb)	SSC	Closest comp. marker (upper)[2]	HSA position (Mb)	Closest comp. marker (lower)	HSA position (Mb)	BES interval location distance from human position (Mb)[3]
UMNp928	NA	NA	NA	129	3E-29	2	6 (156.13)	1	*CL412345*	6 (155.82)	*CL334958*	6 (154.49)	0.31
UMNp1216	NA	NA	NA	103	9.5E-21	2	6 (144.18)	1	*BF711055*	6 (144.3)	*TC20747*	6 (144.46)	0.12
UMNp1258	NA	NA	NA	173	1.9E-40	1	6 (112.91)	1	*CL413260*	6 (112.45)	*CL344430*	6 (116.14)	
UMNp1285	NA	NA	NA	113	3.7E-35	2	18 (42.18)	1	NL		*CL344131*	18 (44.08)	1.90
UMNp1606	NA	NA	NA	140	1.5E-32	1	15 (41.4)	1	*CL378717*	15 (41.74)	*CL341406*	15 (40.21)	
UMNp1475	NA	NA	NA	419	0	1	15 (37.02)	1	*CL348336*	15 (36.04)	*CL351690*	15 (37.45)	
UMNp880	NA	NA	NA	132	2.8E-45	2	15 (96.89)	1	*CL332426*	15 (96.97)	*CL362984*	15 (97.58)	0.08
UMNp1681	NA	NA	NA	123	1.9E-34	1	18 (70.49)	1	*CL358711*	18 (72.34)	*CL336443*	18 (70.82)	0.23
UMNp1224	NA	NA	NA	169	1.1E-41	2	18 (68.69)	1	*CL336443*	18 (70.82)	*CL339209*	18 (68.83)	
UMNp1060	NA	NA	NA	108	1.5E-28	1	15 (67.94)	1	*CL360810*	15 (67.59)	*CL338276*	15 (66.47)	0.34
UMNp1166	NA	NA	NA	171	1.2E-40	2	14 (58.42)	1	*CL343312*	14 (56.92)	*CL358331*	14 (58.20)	0.22
UMNp784	NA	NA	NA	217	0	2	9 (14.95)	1	*CL385499*	9 (13.36)	*CL379846*	9 (12.38)	1.59
UMNp1198	NA	NA	NA	118	1.5E-24	2	9 (19.45)	1	*CL334702*	9 (19.71)	*CL335974*	9 (18.57)	
UMNp623	NA	NA	NA	400	0	1	9 (101.22)	1	*CL325910*	9 (93.7)	*CL341592*	9 (97.06)	4.16
UMNp948	NA	NA	NA	117	3E-23	2	9 (112.64)	1	*CL350990*	9 (106.04)	*CL351989*	9 (107.59)	5.05
UMNp1921	NA	NA	NA	124	2E-27	1	9 (115.49)	1	*CL369936*	9 (108.75)	*CL352780*	9 (110.29)	5.2
UMNp1705	NA	NA	NA	209	0	1	9 (119.45)	1	NL		*CL339256*	9 (114.49)	5.04
UMNp271	NA	NA	NA	307	0	1	9 (125.37)	1	NL		*CL371573*	9 (120.59)	4.78
UMNp827	NA	NA	NA	225	0	2	11 (57.8)	2	*CL413020*	11 (59.44)	*CL345826*	11 (58.00)	0.20
UMNp1435	NA	NA	NA	170	0	1	11 (42.75)	2	*CL387830*	11 (42.96)	*CL328616*	11 (41.56)	
UMNp1162	NA	NA	NA	154	6.8E-35	2	11 (35.2)	2	*CL410608*	11 (37.39)	*CL372241*	11 (36.01)	0.81
UMNp1595	NA	NA	NA	279	0	1	11 (30.69)	2	*CL350043*	11 (31.85)	*CL354435*	11 (30.62)	
UMNp1847	NA	NA	NA	156	9E-45	3	11 (17.55)	2	*CL352330*	11 (18.63)	*CL347458*	11 (17.19)	
UMNp1019	NA	NA	NA	115	1.4E-27	2	11 (12.79)	2	*CL386986*	11 (13.42)	*CL364868*	11 (12.49)	
UMNp1429	TC203861	560	0	113	3.1E-73	1	19 (3.42)	2	*CL336839*	19 (4.37)	*CL379799*	19 (3.24)	
UMNp716	NA	NA	NA	158	0	2	19 (19.36)	2	*CL355918*	19 (18.90)	*CL378987*	19 (19.52)	0.16
UMNp995	NA	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	NA	102	2.3E-13	1	5 (81.69)	2	*CL372277*	5 (82.8)	*CL366934*	5 (84.09)	1.11
UMNp782	NA	NA	NA	188	0	2	5 (88.02)	2	*CL351586*	5 (87.98)	*CL410705*	5 (89.38)	
UMNp1056	NA	NA	NA	103	7.2E-22	2	5 (102.38)	2	*CL356332*	5 (99.59)	*CL389974*	5 (100.88)	1.50
UMNp1956	NA	NA	NA	102	1.4E-41	3	5 (100.89)	2	*CL389974*	5 (100.88)	*CL345673*	5 (102.17)	
UMNp1206	NA	NA	NA	174	7.2E-42	2	5 (103.29)	2	*CL345673*	5 (102.17)	*CL348126*	5 (103.38)	
UMNp1096	NA	NA	NA	165	4.3E-55	1	5 (112.69)	2	*CL355535*	5 (111.51)	*CL388357*	5 (114.32)	
UMNp1379	NA	NA	NA	177	0	1	5 (130.27)	2	*CL363132*	5 (132.08)	*CL361109*	5 (130.74)	0.47
UMNp1116	NA	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 TIGR match	SSC TIGR match bit score	SSC TIGR match *E*-value	HSA chr. match bit score	HSA chr. match *E*-value	RH mapped[1]	HSA chr. match start (Mb)	SSC	Closest comp. marker (upper)[2]	HSA position (Mb)	Closest comp. marker (lower)	HSA position (Mb)	BES interval location distance from human position (Mb)[3]
UMNp1107	NA	NA	NA	151	6.1E-34	2	5 (141.99)	2	*CL363935*	5 (140.38)	*CL362288*	5 (141.72)	0.27
UMNp1290	NA	NA	NA	226	1.9E-56	2	16 (13.05)	3	*CL335808*	16 (13.44)	*CL350034*	16 (12.09)	
UMNp1287	NA	NA	NA	131	1E-37	2	16 (9.85)	3	*CL360103*	16 (10.66)	*CL348957*	16 (9.28)	
UMNp1867	NA	NA	NA	235	0	1	2 (66.63)	3	*CL343356*	2 (68.07)	*CL413814*	2 (66.57)	
UMNp1312	NA	NA	NA	192	0	2	2 (52.52)	3	*CL390259*	2 (53.10)	*CL411423*	2 (51.51)	
UMNp1929	NA	NA	NA	139	1.1E-28	1	2 (50.11)	3	*CL343825*	2 (50.58)	*CL347786*	2 (49.34)	
UMNp955	NA	NA	NA	154	1E-48	2	2 (40.53)	3	*CL343258*	2 (40.87)	*CL334945*	2 (39.90)	
UMNp1340	NA	NA	NA	162	4.1E-51	1	2 (40.33)	3	NL		*CL408881*	2 (38.31)	2.02
UMNp1142	NA	NA	NA	126	1E-32	2	2 (31.25)	3	NL		*CL384063*	2 (32.76)	1.45
UMNp953	NA	NA	NA	360	0	2	2 (21.72)	3	*CL360107*	2 (22.51)	*CL388847*	2 (21.09)	
UMNp1497	NA	NA	NA	218	0	1	2 (16.69)	3	*CL379758*	2 (18.11)	*CL383219*	2 (16.69)	
UMNp1042	NA	NA	NA	128	3.8E-27	2	8 (137.97)	4	*CL344191*	8 (139.18)	*CL341839*	8 (137.54)	
UMNp949	NA	NA	NA	127	0	2	8 (124.6)	4	*CL408638*	8 (125.68)	*CL369251*	8 (124.49)	
UMNp638	NA	NA	NA	135	4.7E-30	2	8 (119.21)	4	*CL411070*	8 (119.34)	*CL385868*	8 (117.99)	
UMNp850	NA	NA	NA	113	7.9E-24	2	8 (56.21)	4	*CL411493*	8 (55.80)	*MOS*	8 (57.19)	
UMNp1556	NA	NA	NA	205	0	1	1 (155.09)	4	*CL334934*	1 (154.8)	*CL353117*	1 (153.73)	0.29
UMNp793	NA	NA	NA	159	0	2	1 (155.22)	4	*AK024570*	1 (153.52)	*CL353117*	1 (153.73)	1.49
UMNp1146	TC229468	712	0	104	2.3E-40	2	1 (145.7)	4	*CL354161*	1 (144.60)	*CL339576*	1 (144.11)	1.1
UMNp1492	NA	NA	NA	181	0	1	1 (102.31)	4	*CL378439*	1 (103.85)	*CL355614*	1 (102.26)	0.05
UMNp724	NA	NA	NA	268	0	2	1 (96.22)	4	*CL349281*	1 (95.05)	*CL357011*	1 (93.34)	1.17
UMNp751	NA	NA	NA	144	2.3E-75	1	22 (31.53)	5	*CL341985*	22 (33.36)	*CL340318*	22 (31.70)	0.17
UMNp1477	NA	NA	NA	106	6.5E-31	1	22 (33.44)	5	*CL340318*	22 (31.7)	*CL341985*	22 (33.36)	0.08
UMNp1085	NA	NA	NA	102	1.8E-29	2	12 (51.91)	5	*CL385479*	12 (53.35)	*CB285327*	12 (51.93)	0.02
UMNp1043	NA	NA	NA	146	1.3E-32	2	12 (60.49)	5	*CL378968*	12 (61.82)	*CL371933*	12 (62.76)	1.33
UMNp1322	TC211647	295	4E-79	123	6.8E-50	2	12 (6.44)	5	*CL363192*	12 (9.05)	*CL367345*	12 (6.68)	0.24
UMNp1960	NA	NA	NA	196	0	1	12 (5.18)	5	NL		*CL366005*	12 (5.46)	0.28
UMNp1532	NA	NA	NA	204	1.9E-49	3	6 (24.89)	5	*CL361781*	12 (3.11)	*CL366362*	12 (0.45)	breakpoint
UMNp1853	NA	NA	NA	120	8E-47	3	16 (52.51)	6	*CL349441*	16 (52.21)	*CL376285*	16 (50.81)	0.3
UMNp1476	NA	NA	NA	133	2.1E-29	1	16 (45.47)	6	*CL344599*	19 (33.32)	*311880163*	19 (33.82)	breakpoint
UMNp747	NA	NA	NA	109	0	2	19 (52.66)	6	*CL387143*	19 (52.08)	*CL379505*	19 (53.36)	
UMNp1612	NA	NA	NA	102	1.1E-37	1	1 (3.28)	6	NL		*CL361179*	1 (2.9)	0.38
UMNp682	NA	NA	NA	150	3.5E-34	2	1 (18.3)	6	*CL343244*	1 (17.97)	*CL366205*	1 (19.94)	
UMNp908	NA	NA	NA	283	0	2	1 (19.15)	6	*CL343244*	1 (17.97)	*CL366205*	1 (19.94)	
UMNp977	TC231154	426	1E-118	189	9.6E-45	2	1 (23.64)	6	*CL362878*	1 (23.17)	*CL350484*	1 (24.24)	
UMNp1164	NA	NA	NA	141	4.5E-33	1	18 (7.3)	6	NL		*CL369079*	18 (5.81)	1.49

Table 3 Continued.

Microsatellite	SSC TIGR match	SSC TIGR match bit score	SSC TIGR match *E*-value	HSA chr. match bit score	HSA chr. match *E*-value	RH mapped[1]	HSA chr. match start (Mb)	SSC	Closest comp. marker (upper)[2]	HSA position (Mb)	Closest comp. marker (lower)	HSA position (Mb)	BES interval location distance from human position (Mb)[3]
UMNp720	NA	NA	NA	177	7.4E-43	2	18 (3.17)	6	*CL387184*	18 (3.21)	*CB286551*	18 (0.11)	
UMNp920	NA	NA	NA	114	8.1E-27	2	18 (19.07)	6	*CL349170*	18 (19.92)	*CL345583*	18 (21.28)	0.85
UMNp1305	NA	NA	NA	272	4.7E-76	2	18 (18)	6	NL		*CL379967*	18 (22.65)	4.65
UMNp913	NA	NA	NA	267	5.8E-99	1	18 (28.46)	6	*CL361156*	18 (29.00)	*CL346369*	18 (30.24)	0.54
UMNp918	NA	NA	NA	171	4.5E-41	2	18 (37.69)	6	*CL346544*	18 (38.32)	*CL372251*	18 (39.63)	0.63
UMNp1498	NA	NA	NA	107	2.5E-23	1	18 (37.0)	6	*CL372251*	18 (39.63)	*CL346544*	18 (38.32)	1.32
UMNp1138	NA	NA	NA	139	2E-36	2	6 (13.7)	7	*CL352460*	6 (13.01)	*GMPR*	6 (16.34)	
UMNp1217	NA	NA	NA	139	0	2	6 (20.7)	7	*CL339993*	6 (21.60)	*TC29673*	6 (19.95)	
UMNp1122	NA	NA	NA	101	2.6E-41	2	6 (23.39)	7	*CL339225*	6 (22.58)	*CL409184*	6 (23.74)	
UMNp732	NA	NA	NA	201	1.3E-67	1	6 (39.57)	7	*CL387684*	6 (38.76)	*CL348929*	6 (39.67)	
UMNp1707	CJ029398	558	0	109	4.3E-35	1	6 (43.66)	7	*CL358605*	6 (43.71)	*311616568*	6 (45.18)	0.05
UMNp1852	NA	NA	NA	277	0	1	6 (44.58)	7	*CL358605*	6 (43.71)	*311616568*	6 (45.18)	
UMNp859	NA	NA	NA	209	1.1E-73	2	6 (31.73)	7	*BAT1*	6 (31.61)	*311887684*	6 (31.75)	
UMNp1103	NA	NA	NA	137	1.5E-28	2	15 (71.02)	7	*BF198849*	15 (70.37)	*CL340155*	15 (70.94)	0.08
UMNp1332	NA	NA	NA	209	3.5E-59	2	15 (74.24)	7	*CL342226*	15 (73.98)	*CL351692*	15 (74.83)	
UMNp1324	NA	NA	NA	215	2.2E-104	2	14 (28.3)	7	*CL327316*	14 (27.74)	*CL388562*	14 (26.46)	0.56
UMNp849	NA	NA	NA	122	6.1E-34	2	14 (28.63)	7	*CL327316*	14 (27.74)	*CL388562*	14 (26.46)	0.89
UMNp1076	NA	NA	NA	100	8.2E-20	2	14 (73.83)	7	*CL352840*	14 (72.50)	*BG608485*	14 (73.25)	0.58
UMNp1230	NA	NA	NA	198	0	2	14 (75.92)	7	*CL358310*	14 (74.19)	*CL359373*	14 (75.57)	0.35
UMNp956	NA	NA	NA	179	8.5E-40	2	14 (89.35)	7	*CL348388*	14 (87.18)	*CL364183*	14 (88.34)	1.01
UMNp1378	NA	NA	NA	120	2.1E-26	1	14 (98.85)	7	*CL411034*	14 (97.72)	*CL349383*	14 (98.88)	
UMNp909	NA	NA	NA	111	8.2E-15	2	4 (5.1)	8	*CL354189*	4 (5.86)	*CL356585*	4 (5.03)	
UMNp1058	NA	NA	NA	199	5.8E-48	2	4 (12.85)	8	*CL337851*	4 (10.67)	*CL348674*	4 (13.06)	
UMNp1965	NA	NA	NA	101	4.2E-18	1	4 (23.82)	8	*CL345704*	4 (24.55)	*CL387304*	4 (23.8)	
UMNp2036	NA	NA	NA	103	1.9E-31	1	4 (28.55)	8	*CL356647*	4 (27.48)	*CL328077*	4 (30.55)	
UMNp1273	NA	NA	NA	128	2.8E-37	2	4 (75.44)	8	*BG382289*	4 (73.57)	*CL358575*	4 (75.64)	
UMNp832	NA	NA	NA	134	4.6E-29	2	4 (76.19)	8	*CL352093*	4 (76.43)	*CB287184*	4 (74.96)	
UMNp1815	NA	NA	NA	281	0	1	4 (137.89)	8	NL		*BG894821*	4 (142.01)	3.98
UMNp1097	NA	NA	NA	105	3.5E-21	2	11 (93.39)	9	*CL388602*	11 (93.30)	*CL355348*	11 (94.46)	
UMNp1137	NA	NA	NA	227	0	2	11 (97.54)	9	*CL364540*	11 (98.39)	*CL411750*	11 (99.68)	0.85
UMNp1205	NA	NA	NA	227	0	2	11 (98.64)	9	*CL364540*	11 (98.39)	*CL411750*	11 (99.68)	
UMNp1427	NA	NA	NA	109	1.2E-42	1	11 (103.5)	9	*CL369211*	11 (104.79)	*CL342212*	11 (103.54)	0.04
UMNp1263	NA	NA	NA	225	0	2	11 (110.23)	9	*CL388132*	11 (110.66)	*CB287025*	11 (111.52)	0.43
UMNp764	NA	NA	NA	162	0	2	11 (111.77)	9	*CB287025*	11 (111.52)	*CL355631*	11 (111.93)	
UMNp1101	NA	NA	NA	121	0	2	11 (114.15)	9	*CL381252*	11 (114.70)	*CL323535*	11 (115.96)	0.55

Table 3 Continued.

Microsatellite	SSC TIGR match	SSC TIGR match bit score	SSC TIGR match *E*-value	HSA chr. match bit score	HSA chr. match *E*-value	RH mapped[1]	HSA chr. match start (Mb)	SSC	Closest comp. marker (upper)[2]	HSA position (Mb)	Closest comp. marker (lower)	HSA position (Mb)	BES interval location distance from human position (Mb)[3]
UMNp1651	NA	NA	NA	135	1E-41	1	11 (119.09)	9	*CL338908*	11 (117.23)	*BG382617*	11 (120.03)	
UMNp781	NA	NA	NA	211	0	2	11 (127.66)	9	*CL351627*	11 (126.16)	*CL412931*	11 (128.43)	
UMNp1992	NA	NA	NA	103	1.4E-22	3	1 (203.2)	9	*CL411937*	1 (200.75)	*BI339312*	1 (201.48)	1.72
UMNp730	NA	NA	NA	142	5.1E-45	2	1 (203.26)	9	*BF191000*	1 (203.26)	*CB286403*	1 (204.04)	
UMNp1620	NA	NA	NA	165	2E-38	1	7 (90.07)	9	*CL372826*	7 (90.13)	*CL342284*	7 (88.16)	
UMNp808	NA	NA	NA	145	2.9E-33	2	1 (206.21)	9	*CL352382*	1 (205.00)	*BE236076*	1 (204.70)	1.21
UMNp1284	NA	NA	NA	118	8.6E-26	2	1 (206.91)	9	*CL352382*	1 (205.00)	*BE236076*	1 (204.70)	1.91
UMNp814	NA	NA	NA	251	1.6E-66	1	7 (52.76)	9	*CL327178*	7 (50.61)	*CL384967*	7 (53.05)	
UMNp1437	NA	NA	NA	265	0	1	1 (216.19)	10	*TGFB2*	1 (214.91)	*CL386296*	1 (213.67)	1.28
UMNp1846	NA	NA	NA	111	3.6E-23	1	10 (32.08)	10	NL		*CL371050*	10 (32.26)	0.18
UMNp1422	NA	NA	NA	141	0	1	10 (14.25)	10	*CL387543*	10 (26.61)	*CL346052*	10 (14.46)	0.21
UMNp705	NA	NA	NA	229	0	2	10 (22.24)	10	*CL370390*	10 (22.35)	*CL364296*	10 (21.13)	
UMNp1569	NA	NA	NA	286	0	1	10 (21.29)	10	*CL364296*	10 (21.13)	*CL367508*	10 (24.19)	
UMNp765	NA	NA	NA	155	7.7E-37	2	13 (32.69)	11	*CL389199*	13 (32.52)	*CL326966*	13 (33.10)	
UMNp823	NA	NA	NA	187	1.4E-60	2	13 (36.21)	11	*BI185113*	13 (35.85)	*CL384210*	13 (36.95)	
UMNp866	NA	NA	NA	106	3.5E-20	2	13 (43.12)	11	*CL344489*	13 (43.75)	*CL352296*	13 (43.02)	0.1
UMNp1573	NA	NA	NA	206	0	1	13 (78.58)	11	*CL355577*	13 (79.22)	*BF077677*	13 (77.42)	
UMNp886	AJ682855	453	0	147	4.8E-37	2	13 (98.34)	11	NL		*CL340954*	13 (98.20)	0.14
UMNp1098	NA	NA	NA	164	1.2E-48	1	17 (11.1)	12	*CL327427*	17 (10.27)	*CL324577*	17 (12.13)	
UMNp1161	NA	NA	NA	298	3.3E-77	2	17 (2.07)	12	*CL349484*	17 (1.31)	*CL387016*	17 (3.32)	
UMNp795	NA	NA	NA	133	4.8E-29	2	17 (39.38)	12	*CL328454*	17 (41.99)	*CL382674*	17 (40.19)	0.81
UMNp1642	NA	NA	NA	159	4.2E-45	1	17 (44.8)	12	*CL410240*	17 (49.11)	*CL358017*	17 (46.77)	1.97
UMNp629	NA	NA	NA	130	0	2	17 (56.8)	12	*CL364800*	17 (58.92)	*CB286227*	17 (57.30)	0.5
UMNp1215	NA	NA	NA	119	2.24E-44	2	3 (132.27)	13	*CL387252*	3 (132.14)	*CL380069*	3 (131.25)	0.13
UMNp868	NA	NA	NA	162	0	2	3 (17.5)	13	*CL339773*	3 (15.70)	*CL366013*	3 (17.07)	0.43
UMNp1180	NA	NA	NA	105	2.9E-30	2	3 (42.72)	13	*CL363112*	3 (39.37)	*CL343272*	3 (41.91)	0.81
UMNp1246	NA	NA	NA	155	2.1E-32	2	3 (45.55)	13	*CL363560*	3 (44.83)	*CL347409*	3 (46.47)	
UMNp1130	NA	NA	NA	157	0	2	3 (54.64)	13	NL		*CL411965*	3 (53.77)	0.87
UMNp1038	NA	NA	NA	361	0	2	3 (60.17)	13	*CL339589*	3 (59.18)	*CL343955*	3 (60.64)	
UMNp1614	NA	NA	NA	111	0	1	3 (73.85)	13	*CL325894*	3 (72.68)	*CL380900*	3 (74.02)	
UMNp807	NA	NA	NA	135	6.1E-43	2	3 (141.55)	13	*CL328348*	3 (140.64)	*CL389134*	3 (141.91)	
UMNp1909	NA	NA	NA	161	4.9E-56	3	3 (144.78)	13	*CL380260*	3 (143.35)	*CL357558*	3 (144.83)	
UMNp873	NA	NA	NA	121	1.6E-33	2	3 (150.58)	13	*CL413985*	3 (147.28)	*CL341583*	3 (150.00)	0.58
UMNp1440	NA	NA	NA	113	3.7E-14	1	3 (147.37)	13	*CL343303*	3 (148.68)	*CL337775*	3 (146.2)	
UMNp1524	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 TIGR match	SSC TIGR match bit score	SSC TIGR match *E*-value	HSA chr. match bit score	HSA chr. match *E*-value	RH mapped[1]	HSA chr. match start (Mb)	SSC	Closest comp. marker (upper)[2]	HSA position (Mb)	Closest comp. marker (lower)	HSA position (Mb)	BES interval location distance from human position (Mb)[3]
UMNp1083	NA	NA	NA	174	4.6E-62	1	21 (25.98)	13	*CL336886*	21 (25.18)	*CL327163*	21 (27.56)	
UMNp855	NA	NA	NA	158	1.4E-41	2	21 (33.36)	13	*CL372354*	21 (32.38)	*CL377885*	21 (33.82)	
UMNp901	NA	NA	NA	168	0	2	8 (23.88)	14	*CL369234*	8 (22.55)	*CL341310*	8 (24.14)	
UMNp944	NA	NA	NA	167	1.1E-39	2	10 (99.27)	14	*CL344905*	10 (98.44)	*CL358216*	10 (99.35)	
UMNp1293	NA	NA	NA	109	1.3E-20	2	10 (105.4)	14	*CL380099*	10 (105.33)	*CL341859*	10 (106.26)	
UMNp1413	NA	NA	NA	139	2.5E-30	1	10 (112.37)	14	*CL388345*	10 (112.3)	*CL382692*	10 (113.23)	
UMNp1447	NA	NA	NA	217	0	1	10 (120.02)	14	*311779136*	10 (118.71)	*CL386363*	10 (119.9)	0.12
UMNp1123	NA	NA	NA	118	7.50E-46	1	2 (149.59)	15	*CL341745*	2 (148.74)	*CL362058*	2 (150.24)	
UMNp1249	NA	NA	NA	213	0	2	2 (116.91)	15	*CL334146*	2 (116.40)	*CL327343*	2 (117.91)	
UMNp1499	NA	NA	NA	119	1.4E-24	1	8 (32.5)	15	*BG834615*	8 (32.48)	*CL355234*	8 (31.74)	0.02
UMNp1843	NA	NA	NA	145	0	1	8 (31.45)	15	NL		*CL355234*	8 (31.74)	0.29
UMNp1513	NA	NA	NA	173	7.2E-40	1	2 (153.98)	15	*CL386994*	2 (154.9)	*CL338491*	2 (156.27)	0.92
UMNp1914	NA	NA	NA	140	0	1	2 (165.13)	15	*CL357234*	2 (166.29)	*CL361827*	2 (164.82)	
UMNp1546	NA	NA	NA	113	1.8E-23	1	2 (189.99)	15	*CL378789*	2 (191.87)	*CL367576*	2 (190.45)	0.46
UMNp684	NA	NA	NA	123	1.3E-34	2	5 (19.99)	16	*CL372377*	5 (19.58)	*CL373351*	5 (21.21)	
UMNp1717	NA	NA	NA	265	0	1	5 (29.21)	16	*CL369981*	5 (28.41)	*CL383973*	5 (30.07)	
UMNp763	NA	NA	NA	119	3.3E-25	2	5 (31.85)	16	NL		*CL440214*	5 (31.49)	0.36
UMNp755	NA	NA	NA	102	5.3E-21	2	5 (4.11)	16	*CL344958*	5 (4.52)	*311771575*	5 (3.97)	
UMNp1163	NA	NA	NA	172	1.1E-40	1	5 (173.88)	16	*CL347112*	5 (173.51)	*CL381019*	5 (173.71)	0.17
UMNp648	NA	NA	NA	103	2.3E-48	2	5 (168.41)	16	*CL378582*	5 (169.41)	*CL355081*	5 (168.21)	
UMNp1576	NA	NA	NA	114	1.5E-38	1	20 (9.98)	17	*CL352905*	20 (10.6)	*CL372614*	20 (9.11)	
UMNp1425	NA	NA	NA	102	6.3E-36	1	20 (17.62)	17	*ZNF133*	20 (18.22)	*BFSP1*	20 (17.42)	
UMNp952	NA	NA	NA	130	2.7E-41	1	20 (19.82)	17	*CL410017*	20 (18.78)	*CL363318*	20 (20.37)	
UMNp910	NA	NA	NA	144	2.5E-33	2	20 (21.74)	17	*CL349746*	20 (20.64)	*CL339322*	20 (22.37)	
UMNp993	NA	NA	NA	131	2E-34	2	20 (29.75)	17	*CL334168*	20 (1.17)	*CL411518*	20 (30.94)	1.19 (breakpoint)
UMNp1028	NA	NA	NA	125	5.1E-29	2	7 (120.07)	18	*CL361069*	7 (120.49)	*CL355453*	7 (119.28)	
UMNp1822	NA	NA	NA	176	1.90E-113	1	X (17.44)	X	*TC36002*	X (19.09)	*AR030H07*	X (19.32)	1.65
UMNp969	NA	NA	NA	135	3.20E-35	1	X (40.06)	X	*CH242–230H13*	X (39.98)	*TC41385*	X (40.06)	
UMNp1677	NA	NA	NA	226	6.10E-76	1	X (92.87)	X	*AB050318*	X (91.69)	*CH242–78P6*	X (90.16)	1.18
UMNp1618	NA	NA	NA	212	2.60E-126	1	X (99.92)	X	*Pigl-582H10*	X (100.74)	*KIAA0443*	X (101.71)	0.82
UMNp1657	TC230092	321	6E-87	127	2.40E-49	1	X (107.01)	X	*TC35554*	X (105.93)	*AR066G03*	X (106.76)	0.25
UMNp1432	NA	NA	NA	161	1.30E-51	1	X (109.53)	X	*BI343796*	X (109.26)	*TC45532*	X (107.69)	0.27
UMNp891	NA	NA	NA	130	7.10E-65	1	X (110.10)	X	*TC45532*	X (107.69)	*BI343796*	X (109.26)	0.84

[1]1 = new markers described in Table 1; 2 = Fahrenkrug *et al.* (2005); 3 = Alexander *et al.* (2006).

[2]NL = no linkage to BES (Meyers *et al.* 2005) with a two-point LOD score ≥6.

[3]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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