



Mapping Cerebellar Abiotrophy in Australian Kelpies

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Complete List of Authors:	<p>Shearman, Jeremy; University of New South Wales, Biotechnology and Biomolecular Sciences; National Center for Genetic Engineering and Biotechnology, Genome Institute</p> <p>Cook, Roger; University of Melbourne, Faculty of Veterinary Science</p> <p>McCowan, Christina; University of Melbourne, Faculty of Veterinary Science</p> <p>Fletcher, Jessica; The University of Sydney, The Faculty of Veterinary Science</p> <p>Taylor, Rosanne; The University of Sydney, The Faculty of Veterinary Science</p> <p>Wilton, Alan; University of New South Wales, School of Biotechnology and Biomolecular Sciences; University of New South Wales, Clive and Vera Ramaciotti Centre for Gene Function Analysis</p>
Keywords:	cerebellar abiotrophy, mapping, recessive disease, Australian Kelpie, Canine SNP array, homozygosity, genome wide association study, ataxia, dog

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Mapping Cerebellar Abiotrophy in Australian Kelpies

Jeremy R. Shearman ^{*,±}, Roger W. Cook [‡], Christina McCowan [‡], Jessica L. Fletcher [§],
Rosanne M. Taylor [§] and Alan N. Wilton ^{*,†}

* School of Biotechnology and Biomolecular Sciences, University of New South Wales,
Sydney, NSW 2052, Australia

± National Center for Genetic Engineering and Biotechnology, 113 Phaholyothin Rd., Klong
1, Klong Luang, Pathumthani 12120, Thailand

‡ Faculty of Veterinary Science, University of Melbourne, Werribee 3030, Australia

§ The Faculty of Veterinary Science, The University of Sydney, Camperdown, NSW 2006,
Australia

† Clive and Vera Ramaciotti Centre for Gene Function Analysis, University of New South
Wales, Sydney, NSW 2052, Australia

Address for correspondence

Alan Wilton, School of Biotechnology, University of NSW, Sydney NSW 2052, Australia

E-mail: a.wilton@unsw.edu.au

Phone: +61 2 9385 2019

Fax: +61 2 9385 1483

Reprint requests should be directed to the corresponding author

Summary

An autosomal recessive form of cerebellar abiotrophy occurs in Australian Kelpie dogs. Clinical signs range from mild ataxia with intention tremor to severe ataxia with seizures. A whole genome mapping analysis was performed using Affymetrix Canine SNP array v2 on 11 affected and 19 control dogs but there was no significant association with disease. A homozygosity analysis identified a three megabase region likely to contain the disease mutation. The region spans 29.8 to 33 Mb on chromosome 3 for which all affected dogs were homozygous for a common haplotype. Microsatellite markers were developed in the candidate region for linkage analysis that resulted in a LOD score suggestive of linkage. The candidate region contains 29 genes, none of which are known to cause ataxia.

Keywords: cerebellar abiotrophy; mapping; recessive disease; Australian Kelpie; Canine SNP array; homozygosity; genome wide association study; ataxia; dog

Running title: Mapping CA in Kelpies

An autosomal recessive cerebellar abiotrophy (CA) with clinical onset at 5-12 weeks of age has been reported in the Australian Kelpie (Thomas and Robertson 1989). CA is the progressive degeneration of cerebellar elements. Ataxia is the main clinical sign of CA, but ataxia can result from other causes including infections, physical trauma as well as various defects in any one of a long list of seemingly unrelated genes that would all be candidates for the CA gene in kelpies. Online Mendelian Inheritance in Man contains 296 disease entries with a known molecular basis that have ataxia as a symptom (for review see Manto and Marmolino 2009).

The occurrence of CA in numerous distantly related Kelpies suggests that the disease allele is prevalent in the population (Thomas and Robertson 1989; Shearman *et al.* 2008). Clinical signs range from mild, which includes noticeable intention tremor, a barely noticeable dysmetria and a high stepping gait, to severe which includes a pronounced intention tremor, a complete lack of coordination and occasional falling. Cerebellar changes reported in affected dogs between 8 weeks and 5.5 months of age included a loss of Purkinje cells, marked loss of granule cells and a decrease in depth of the granule cell and molecular layers (Thomas and Robertson 1989).

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4 CA affected dogs included in this study were examined by local veterinarians and
5 diagnosed with ataxia. Three related affecteds were from a previous study (Thomas and
6 Robertson 1989, Figure S1) and four more were confirmed as CA by histopathology
7 examination (Supplementary information, Figure S2). Severity of CA clinical signs correlated
8 with more noticeable changes to the cerebellum.
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12 A whole genome analysis was undertaken to identify the region containing the
13 causative mutation for CA in the Australian Kelpie. Eleven CA affected Kelpies and 19
14 controls were hybridised to Affymetrix Canine SNP array v2 (Karlsson *et al.* 2007) and
15 28,479 informative SNP calls used for genome wide association analysis (supplementary
16 information) and homozygosity analysis (Figure S3). Genome wide association failed to
17 identify any regions with significant SNP association with CA (Supplementary information,
18 Figure S4, S5). However, a region on chromosome 3 from 29.8 Mb to 33.8 Mb where all 11
19 affected dogs were homozygous for a common haplotype was identified and 10 of the 11
20 were homozygous from 28 Mb to 33.8 Mb (Figure 1, Supplementary information). No other
21 regions of homozygosity greater than 100 kb were shared by all affected dogs. Linkage
22 disequilibrium around the mutation is expected to be greater than 500 kb based on the size of
23 canine haplotype blocks and results from previous mapping experiments (Lindblad-Toh *et al.*
24 2005, Sutter *et al.* 2005, Karlsson *et al.* 2007)
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35 Most Control dogs were heterozygous at 20 SNPs on average of the 52 that define the
36 candidate region (Figure 1). However, six control dogs were homozygous for the same region
37 and three of these were homozygous for the same SNP haplotype as the affected dogs. Three
38 unaffected siblings of a CA case were also homozygous for the SNP haplotype (Figure 1).
39 This sharing of alleles is the reason for the failure of the association study to identify any
40 significant SNPs within the region. The data suggests that the mutation responsible for CA
41 has occurred on a common haplotype and only some copies of the haplotype carry the CA
42 mutation.
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50 Microsatellites were developed in the candidate region to genotype the samples
51 processed on the SNP arrays plus 23 relatives and 56 additional unaffected controls. Six short
52 microsatellites (20-30 dinucleotide repeats, Table S1) showed genetic variation in kelpies
53 (Table S2), but little variation within CA families, consistent with the results for SNPs, (see
54 supplementary information and Figure S6). Five long microsatellites (>30 tetranucleotide
55 repeats) and one minisatellite developed in the region (Table S3) showed a large amount of
56 variation in the Kelpies with between 8 and 18 alleles with size ranges from 60 to 200 bp
57 (Table S4). Variation was also observed among CA affected dogs, with several alleles of
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3 different sizes at each locus that were clustered around one or two main alleles (Table S4).
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5 This suggests that there has been an accumulation of microsatellite mutations on a haplotype
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7 that carries the CA mutation (discussed in supplementary information).
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9 Segregation of the long microsatellite haplotypes in families with CA show
10 inheritance patterns that are consistent with this region containing the CA mutation and not
11 all copies of the SNP haplotype carry the CA mutation (Figure S7), which is consistent with
12 the mutation occurring on a common haplotype. Linkage analysis was performed using
13 SuperLink Online (Silberstein *et al.* 2006; supplementary information) on both sets of
14 microsatellite data independently. The short microsatellites were not informative for linkage
15 (Figures 2, S6). The result for the long microsatellites is suggestive of linkage, with a
16 maximum logarithm of odds (LOD) score of 2.37 (significance threshold: 3). This positive
17 LOD score is supporting evidence that the region on chromosome 3 from 29.8-33 Mb does
18 contain the mutation causing CA in Kelpies.
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26 The 3 Mb region on CFA 3 identified as the location for the CA causing mutation
27 contains 29 genes. None of these genes are known to be associated with CA or ataxia in
28 human or mouse according to OMIM or MGI databases. The wide range in severity of
29 clinical signs for CA suggests that CA could be the result of a regulatory mutation rather than
30 an altered protein sequence. Identifying the causative mutation may require expression
31 analysis of the genes in the region and/or sequencing of the entire candidate region using next
32 generation sequencing.
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39 It is important to note that genome wide association studies can fail to predict the
40 location of a disease gene occurring on a common haplotype. Linkage analysis supported the
41 results of the homozygosity mapping that identified the disease gene location because of the
42 use of long-repeat microsatellite loci with high mutation rates. These high mutation rates
43 resulted in the common haplotype mutating to several new haplotypes over the past few
44 generations allowing for haplotypes identical at the SNP level within families to be
45 distinguished.
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54 Supplemental Data Description

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Supplementary Data includes seven figures and four tables with discussion of histopathology results, microsatellite genotyping, linkage results, and genome wide association study (GWAS) results.

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Figure Legends:

Figure 1: SNP calls for 11 CA affected Kelpies, 19 control Kelpies and 3 unaffected siblings to a CA case for SNPs from the candidate region between 27.6 and 35.7 Mb on chromosome 3. Samples are across the figure divided into affecteds, controls and unaffected siblings. SNPs (named according to genomic position) are down the figure with names on the left. For allele calls, 0 (shaded green) and 2 (shaded blue) represent homozygotes at alternate alleles and 1 (shaded red) represents heterozygotes.

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4 **Figure 2: LOD scores from Multipoint linkage analysis of long microsatellites and short**
5 **microsatellites for the candidate region on chromosome 3.**
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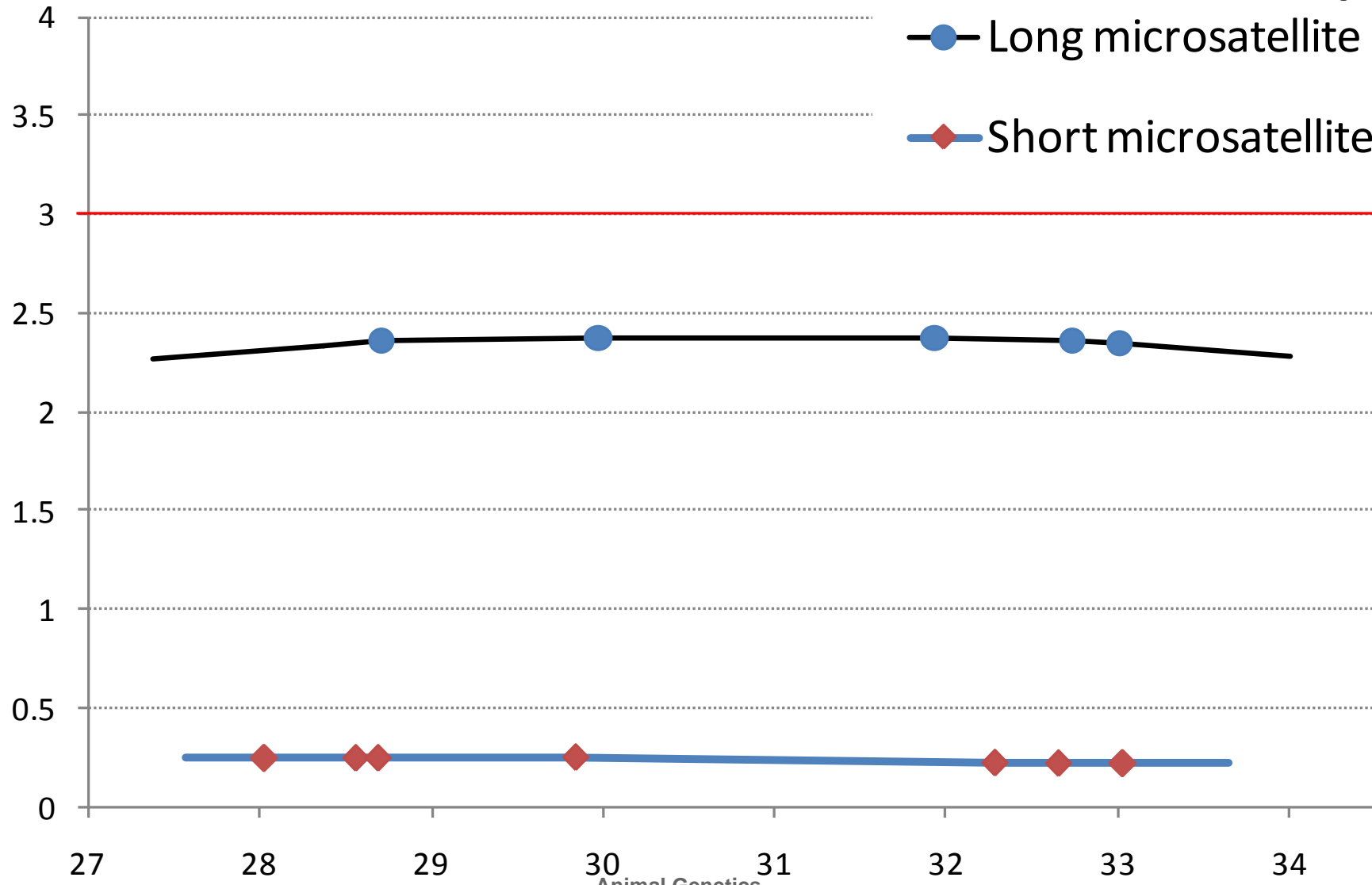
7 Significance threshold is indicated by the red line at 3. X-axis shows chromosomal location
8 in megabases.
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For Peer Review

Page 7 of 8	Affecteds										Controls										unaffected sibling											
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chr3.27587058	0	0	1	0	0	0	2	2	1	0	1	0	1	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	1	1		
chr3.27587343	2	2	1	2	2	2	0	0	1	2	1	2	2	1	2	2	1	1	2	2	1	1	2	2	2	2	2	2	1	1		
chr3.27861785	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	1	0	0	1	1	1	1	0	2	2	0	1	1		
chr3.27972664	1	1	1	2	2	2	0	0	1	2	1	2	1	1	2	1	0	0	2	0	1	1	1	1	0	0	0	2	1	1		
chr3.27996340	0	0	1	1	0	0	2	2	1	0	1	0	1	0	1	2	2	0	2	2	1	1	1	1	1	0	1	0	1	1		
chr3.28291082	2	2	1	2	2	2	2	2	2	2	2	1	2	2	2	2	0	2	2	2	2	1	2	2	1	0	1	2	2	2		
chr3.28354775	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	1	0	2	2	1	1	2	1	1	2	2	2	2	2		
chr3.28945514	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	2	2	2	1	2	0	1	2	2	1	2	2	2		
chr3.29002208	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	2	2	2	1	2	2	2	2	2	2	2	2	2		
chr3.29459535	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0		
chr3.29465502	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	1	2	2	0	0	0		
chr3.29700176	2	2	1	2	2	2	2	2	2	2	2	1	2	0	1	1	0	2	0	0	1	1	0	1	2	0	0	2	2	2		
chr3.29723351	0	0	1	0	0	0	0	0	0	0	1	0	2	1	0	1	1	0	0	2	0	1	0	1	1	2	1	0	0	0		
chr3.29763908	2	2	1	2	2	2	2	2	2	2	1	2	1	1	2	1	1	1	2	0	1	2	2	2	2	2	2	2	2	2		
chr3.29768263	0	0	1	0	0	0	0	0	0	0	1	0	2	1	0	1	1	1	0	2	1	1	0	1	1	2	1	0	0	0		
chr3.29780756	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0		
chr3.29869180	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2		
chr3.29903841	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	2	1	0	0	0		
chr3.29949728	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	1	2	0	2	2	2	2	1	1	2	2	2	2		
chr3.30002398	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	2	0	1	0	0	0	0	0	0	0		
chr3.30002474	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	2	0	1	0	0	0	0	0	0	0		
chr3.30059175	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	2	1	1	2	0	0	2	2	0	0	0		
chr3.30143129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	2	0	0	2	2	0	0		
chr3.30241896	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	1	1	0	1	2	2	1	2	2	2		
chr3.30326469	2	2	2	2	2	2	2	2	2	2	1	2	1	1	2	1	2	1	1	0	2	0	1	1	0	1	1	2	1	2	2	
chr3.30364362	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	1	2	0	1	2	0	2	2	2	1	2	2		
chr3.30416931	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	1	0	2	1	1	0	1	0	0		
chr3.30545981	2	2	2	2	2	2	2	2	2	2	1	2	2	1	2	1	1	1	2	0	1	2	0	1	1	2	1	2	2	2		
chr3.30597963	2	2	2	2	2	2	2	2	2	2	1	2	1	1	2	1	1	1	1	2	0	1	1	0	1	1	2	1	2	2	2	
chr3.30606257	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	2	1	0	0	1	0	0		
chr3.30648725	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	0	0		
chr3.30684680	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0		
chr3.30684786	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	2	0	1	0	0	0	0	0	0		
chr3.30695678	2	2	2	2	2	2	2	2	2	2	1	2	1	1	2	1	1	1	1	2	0	2	1	2	1	1	2	2	2	2		
chr3.30769780	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
chr3.310774041	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
chr3.30782110	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	2	1	1	2	0	1	2	2	0	0	
chr3.30899994	2	2	2	2	2	2	2	2	2	2	1	2	2	1	2	1	1	1	1	2	0	2	2	2	2	1	2	2	2	2	2	
chr3.30942338	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0	1	1	2	0	0	1	2	0	0	
chr3.30943402	2	2	2	2	2	2	2	2	2	2	1	2	1	1	2	1	2	1	1	2	2	2	1	2	2	1	2	2	2	2	2	
chr3.30949459	2	2	2	2	2	2	2	2	2	2	1	2	1	1	2	1	2	1	1	2	2	2	1	2	1	1	2	2	2	2	2	
chr3.30986655	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0		
chr3.31010174	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	1	2	2	0	1	2	2	2	
chr3.31059268	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	0	0	0	
chr3.31108824	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	1	2	0	2	1	0	0	2	2	2	2	
chr3.31163217	2	2	2	2	2	2	2	2	2	2	1	2	1	1	2	2	1	2	2	2	2	1	1	1	1	2	1	2	2	2	2	
chr3.31766592	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
chr3.31823224	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
chr3.32049502	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	1	1	2	2	1	2	2	2	
chr3.32288273	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	1	2	1	1	2	2	1	2	2	2	
chr3.32292529	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	2	1	0	0	0	
chr3.32310426	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	1	2	2	2	2	2	1	2	1	0	1	2	2	2	
chr3.32610115	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	2	1	1	0	0	0	0	0	0	0	
chr3.32913190	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	0	1	2	1	0	0	0	
chr3.33008129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	
chr3.33061677	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	1	2	2	1	2	1	1	1	1	1	1	2	0	1	2	2	2
chr3.33202953	2	2	2	2	2	2	2	2	2	2	1	2	2	1	2	1	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	
chr3.33836297	1	1	2	1	1	2	0	0	1	2	1	2	1	2	2	1	1	2	2	0	0	1	1	0	1	2	0	0	2	1	1	
chr3.33856364	1	1	0	1	1	0	2	2	1	0	1	0	1	0	0	0	1	1	0	0	2	1	1	2	1	1	2	2	0	1	1	
chr3.34131884	1	1	2	1	1	2	0																									

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—●— Long microsatellite
—◆— Short microsatellite



Animal Genetics
Chromosomal location (Mb)