

Computational and biological approaches for identification of
Hedgehog signaling targets and their application to intestinal
visceral smooth muscle development in the mouse

by

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List of Abbreviations

BS binding site

ChIP Chromatin Immunoprecipitation

DNA Deoxyribonucleic

ICM inner circular muscle

ISM intestinal visceral smooth muscle

OLM outer longitudinal muscle

RNA Ribonucleic acid

TF transcription factor

seq sequencing

SM organ affiliated smooth muscle

Abstract

The Hedgehog (Hh) pathway is an evolutionarily conserved cell-cell signaling pathway that controls organ development and homeostasis in embryos and adults. Hh signaling functions in cell fate choice, patterning, cell survival, proliferation and/or differentiation. Several birth defects are known to result from altered Hh signaling and aberrant Hh signaling is also responsible for several cancers. Despite its central role in development and disease, very little is known about the precise genetic targets of Hh signaling or the genomic enhancers that activate those genes. These target genes and associated Hh-responsive enhancers are themselves responsible for disease initiation and progression. A comprehensive effort to identify these signaling targets and to dissect the context specificity that underlies their expression is therefore a high priority. This work was driven by two Aims: 1) to explore novel computational approaches for the identification of Hh-responsive enhancers; and 2) to understand the contribution of Hh-driven gene expression in the context of a single Hh-responsive cell type, intestinal visceral smooth muscle (ISM).

This work comprised a multi-pronged approach, integrating both computational and biological methods in parallel, to achieve these Aims. First, we explored the degree to which clustered binding sites for the Hh transcription factor, *ci/GLI*, would predict functional enhancers. While this method was somewhat successful in the fly, it could not be applied to the mouse, where Hh enhancers tend not to be homotypically clustered. Therefore, a machine learning strategy was explored with substantial success, resulting in the identification of seven

new enhancers in genes encoding Hh pathway components. Finally, RNA-seq and CHIP-seq data were collected to generate a catalog of smooth muscle genes that are expressed in a specific layer of developing intestinal smooth muscle. Analysis of this data implicated cJUN as a regulatory component in ISM formation and established Hh as an upstream regulator of *cJun* expression in that tissue.

Though this work has focused on Hh signaling, a similar approach could be applied to any transcription factor or signaling pathway to comprehensively analyze the gene regulatory networks governing many normal and disease-related cell states.

Chapter I

Introduction

1.1 Research Overview

1.1.1 Importance of Intestinal Smooth Muscle

The small intestine, consisting of the duodenum, jejunum and ileum is critical to the digestion and absorption of nutrients into the bloodstream. In addition to chemical digestion, begun in the stomach and continued by the intestine, efficient processing and absorption of nutrients also relies on mechanical movement of the food bolus, resulting from the coordinated contraction of the intestinal circular and longitudinal smooth muscle layers. The segmentation contractions of the circular muscle mix partially digested food with enzymes to increase the breakdown into nutrients while the peristaltic contractions of longitudinal muscles direct the movement of material downward through the digestive tract. Despite the critical importance of visceral smooth muscle (ISM) to intestinal function, very little is known about its development or maintenance. For this reason, the ultimate goal of this dissertation was to identify the regulatory programs underlying intestinal smooth muscle development.

Several intestinal diseases result from malformation of, or injury to ISM. Visceral myopathic chronic pseudoobstruction resulting from familial (Anuras et al., 1981; Sipponen et al., 2009) and sporadic cases (Montalvo et al., 2004) have been reported. Infants present with

feeding intolerance and absence of bowel motility, causing the appearance of obstruction, but without evidence of bowel narrowing. Only two susceptibility loci, DNA POLG and ACTG2, are currently known (Vissing et al., 2002; Van Goethem et al., 2003; Giordano et al., 2009; Lehtonen et al., 2012; Holla et al., 2014; Thorson et al., 2014; Wangler et al., 2014). However, cases have been reported indicating that the layers of ISM are differently affected, suggesting involvement of multiple loci that have yet to be discovered (Anuras et al., 1983; Alstead et al., 1988; Smith et al., 1992; Donnell et al., 2008). Muscle contractility can also be disrupted in response to gut inflammation (Ohama et al., 2007b) and irritable bowel syndrome (IBS) (Whorwell et al., 1986; Van der Vliet et al., 1992; Abrams et al., 2012). While roughly 30 million patients in the United States suffer from IBS (Occhipinti and Smith, 2012), almost nothing is known about the genes or signaling pathways that may play a role in this malady. In part, this is because so little is known in general about gene networks that control ISM.

1.1.2 Intestinal Development

The luminal surface of the murine intestine arises from a flat sheet of endoderm. Between E7.25 and E9.5, this endodermal sheet recruits lateral plate mesoderm and wraps into a tube that will eventually give rise to the entire gastrointestinal tract (Zorn and Wells, 2009). The stomach and proximal part of the small intestine arise from foregut endoderm. The rest of the small intestine is considered midgut while the large intestine is derived from the hindgut (Zorn and Wells, 2009). By E9.5, the tube is complete and the interior of the midgut consists of a lumen that is encased by endoderm-derived epithelium and surrounded by mesoderm. Between E9.5 and E14.5, the gut tube expands in length and circumference (Noah et al., 2011). At E14.5, a dramatic restructuring of the epithelium begins, which will result in the emergence of villi,

finger-like protrusions of the apical surface that serve to increase surface area for food absorption. Establishment of the crypts, which harbor stem cell populations that generate replacement cells for the epithelial layer of the villi begins postnatally and is completed by weaning (Spence et al., 2011).

Crosstalk between the interior endoderm-derived epithelial tissue and the underlying mesenchyme is vital for differentiation of intestinal cell types during development. Roles for multiple signaling pathways, including bone morphogenic protein (BMP), Hedgehog (Hh), platelet derived growth factor (PDGF), TGF- β , and Wnt, among others, have been documented (McLin et al., 2009; Spence et al., 2011). Reliance on epithelial:mesenchymal crosstalk is critical to intestinal homeostasis and persists within adult tissue (Kedinger et al., 1998b). The epithelial tissue progenitor and stem cell populations are directed by BMP and Wnt signals (Madison et al., 2005; Kim et al., 2007) while both PDGF and Hh act by paracrine signaling to direct villus formation (Karlsson et al., 2000; Walton et al., 2012). Hh has multiple roles in cell fate specification in the intestinal mesenchyme and is known to signal to at least seven different cell/tissue targets in the stroma underlying the epithelium (Kolterud et al., 2009). In particular, Hh signaling has been clearly demonstrated to be crucial to the development of ISM (Ramalho-Santos et al., 2000; Kolterud et al., 2009).

Within the adult intestine, there are several subtypes of ISM. Close to the luminal surface within the mucosa, are the muscularis mucosa and villus ISM. The muscularis mucosa is a thin muscular layer that lies directly under the epithelium, while the villus ISM consists of thin strands of muscle that travel vertically up the villi from their origin in the muscularis mucosa. Together, these muscles move the villi and epithelium to churn the gut contents. At the outer side

of the intestinal tube is the muscularis externa, comprised of inner circular muscle (ICM) and outer longitudinal muscle (OLM). During development, the ICM forms at E13.5, just prior to the epithelial remodeling of the villi. The OLM forms 48 hours later at E15.5 (Kedinger et al., 1998b; Kolterud et al., 2009; Thomason et al., 2012). ISM strands within the villus cores begin to form at E18, while the final muscle, the muscularis mucosa, develops after birth (Kolterud et al., 2009). All of the ISM populations play roles in gut motility that is required for digestion and absorption of nutrients and all of are known to require Hh signals for development (Ramalho-Santos et al., 2000; Madison et al., 2005; Kolterud et al., 2009; Zacharias et al., 2011). Hh signaling is currently the only known signaling pathway critical to smooth muscle formation.

1.1.3 Hedgehog Signaling

First discovered in the fruit fly (*Drosophila*) (Nusslein-Volhard and Wieschaus, 1980), the Hedgehog (Hh) signaling pathway plays crucial roles in embryonic development in many species, including humans. Predictably, disruption of this pathway is associated with developmental malformations in many tissues; and, since it often regulates cell proliferation, misregulation of the pathway has been shown to cause cancers (Barakat et al., 2010). An important unanswered question is: How does the same Hh signal activate different genes in different cellular contexts? I hypothesized that at least part of this context specificity is accounted for by the distinct regulatory regions that are targeted by Hh signaling.

In *Drosophila*, the hedgehog gene encodes a ligand (hh) that binds to the transmembrane receptor patched (ptc). In the absence of hh ligand, ptc functions to inhibit signaling from its co-receptor, smoothened (smo) and under these conditions, the downstream transcription factor,

cubitus interruptus (*ci*), is phosphorylated and cleaved, generating a repressor protein that goes to the nucleus to suppress target gene activity (Figure 1.1A). However, when the *hh* ligand binds to *ptc*, this inhibition is released and *smo* is then free to interact with the kinesin related protein Costal-2 (*Cos2*). This interaction in turn activates other cytoplasmic components, fused (*fu*) and Suppressor of fused (*SuFu*). As a result of this cascade, *ci* is no longer phosphorylated and therefore, no longer cleaved. The full-length protein then enters the nucleus, where it acts a transcriptional activator (Figure 1.1B). Therefore, the Hh pathway contains a built-in switch: it activates gene expression in the presence of the ligand and actively represses gene transcription in its absence (Barolo and Posakony, 2002; Robbins et al., 2012).

In mammals, Hh signaling originates with the release of one of the three lipid-modified HH ligands, all homologs of the *Drosophila hh* gene (Sonic hedgehog (*Shh*), Indian hedgehog (*Ihh*) and Desert hedgehog (*Dhh*)) (for Review see (Varjosalo and Taipale, 2008)). Release and diffusion of the Hh ligand in the extracellular space is facilitated by the secreted protein Scube and the transmembrane protein Dispatched (Creanga et al., 2012; Jakobs et al., 2014). Once discharged, Hh ligand can interact with several cell membrane proteins. Binding with the transmembrane receptor protein Patched (PTCH1) as well as the cell membrane co-receptors BOC, CDO and GAS1 initiates Hh signaling within target cells, while binding with the membrane-associated Hedgehog-interacting protein (HHIP) can suppress the Hh signal (Figure 1.1CD) (Chuang and McMahon, 1999). Just as in the *Drosophila*, the binding of HH ligand to PTCH results in de-repression of the Smoothened (SMO) transmembrane protein allowing SMO to activate the downstream portion of the pathway.

A major difference in the Hh pathway in higher organisms compared to *Drosophila* is the importance of cilia to signal transduction. Cilia are microtubule-based organelles that are thought to act as cellular sensors (DeRouen and Oro, 2009). Activation of Hh signaling causes SMO to accumulate within cilia (Allen et al., 2011; Izzi et al., 2011) where the GLI transcription factors (mediators of Hh signaling in vertebrates) are processed (Figure 1.1D) (Kim et al., 2009; Beachy et al., 2010). In contrast, in *Drosophila*, cilia do not seem to play a role in signal reception or processing (Goetz and Anderson, 2010).

The vertebrate Hh pathway relies on three transcription factors for signal transduction; all are homologues of *Drosophila* *ci*. GLI1 is not appreciably processed and may function primarily to amplify the Hh signal. In addition to its role as a pathway activator, GLI1 is a known target of Hh signaling (Dai et al., 1999). GLI2 is primarily an activator (Pan et al., 2006), but under some conditions, can act as a repressor. GLI3, typically a repressor, can occasionally act as an activator (Wang et al., 2000). Proteolytic processing, which occurs in the absence of Hh ligand, determines whether the GLI proteins act as repressors or activators. In the presence of the Hh ligand, this processing is inhibited (Kim et al., 2009; Beachy et al., 2010), allowing full-length GLI proteins to traffic to the nucleus and activate gene expression (Dai et al., 1999; Sasaki et al., 1999; Shin et al., 1999; Wen et al., 2010).

1.1.4 Roles for Hedgehog Signaling in Muscle Development

Vertebrates contain three distinct types of muscle: cardiac, skeletal, and smooth (subdivided into vascular smooth muscle and organ affiliated smooth muscle typified by involuntary contractions) with distinct structural and functional roles. All three muscle types

originate from mesoderm tissue. Cardiac muscle arises from the cardiac lateral splanchnic mesoderm (Nathan et al., 2008), skeletal muscle is from the myotome of paraxial mesoderm (Yoon and Wold, 2000), while smooth muscle has multiple origins, including the splanchnic mesoderm (Christ and Ordahl, 1995), neural crest (Le Lievre and Le Douarin, 1975; Etchevers et al., 2001) and local undifferentiated mesenchymal cells (Ruzicka and Schwartz, 1988; Keding et al., 1990; McHugh, 1995). Hh signaling has been connected to the development of each of these different types of muscle, as discussed below.

1.1.4.1 Skeletal Muscle

Hedgehog plays an active role in the development and homeostasis of skeletal muscle, both during developmental specification of tissues and in maintenance of the stem cell population. In the mouse, myogenic regulatory factors *MyoD* and *myogenic factor 5 (Myf5)* control the establishment and maintenance of muscle progenitor cells while *Myogenin (MyoG)* and *Mrf4* facilitate myoblast differentiation (Pownall et al., 2002). Mouse models with deletions of *Myf5* and *MyoD* have demonstrated a redundancy of myogenic function between the two genes (Braun et al., 1992; Rudnicki et al., 1992) and subsequent knockout mouse models have shown that these genes function upstream of *MyoG* and *Mrf4* (Hasty et al., 1993; Kassari-Duchossoy et al., 2004). *MyoD* is activated by the skeletal progenitor factor *Pax-3*, which is regulated by Hh, Wnt, Fgf and BMP signaling (Duprez et al., 1998; Pownall et al., 2002). Downregulation of *Pax-3* by Hh signaling allows the differentiation of *MyoD* and *Myf5* co-expressing cells (Borycki et al., 1998; Hammond et al., 2007). *Shh* null mice exhibit reduced expression of *MyoD* (Borycki et al., 1999) and *Myf5* (Chiang et al., 1996), both of which have been shown to be direct regulatory targets of Hh signaling (Gustafsson, 2002; Borello et al.,

2006; Voronova et al., 2013). MYOD and GLI2 form a protein complex with MEF2C, another direct transcriptional target of Hh signaling (Voronova et al., 2012), promoting myogenic activation through the activation of muscle target genes (Voronova et al., 2013). Unlike for *Myf5*, *MyoD* and *Mef2C*, there is currently no evidence to suggest that *MyoG* or *Mrf4* are direct targets of Hh. However, since *Myf5* and *MyoD* are upstream regulators of *MyoG* and *Mrf4*, which act to drive terminal differentiation of myoblasts, Hh may function primarily in regulating the skeletal muscle progenitor population. Interestingly, *Shh* and *Ihh* seem to have partially redundant and partially distinct temporal roles in skeletal muscle formation, since skeletal muscle develops normally in *Ihh* null mice until after cessation of *Shh* expression, at which point muscle mass is lost (Bren-Mattison et al., 2011).

1.1.4.2 Cardiac Muscle

Mice that lack *Shh* exhibit developmental cardiac abnormalities (Chiang et al., 1996; Tsukui et al., 1999; Washington Smoak et al., 2005). The severity of the cardiac defects is increased in mouse models that remove both *Shh* and *Ihh* or that abrogate Hh signaling entirely by removing *Smo* (Zhang et al., 2001). The expression of the cardiac marker *Nkx2-5* is delayed in these mice, while mice that lack *Ptch1* show an expanded *Nkx2-5* expression (Thomas et al., 2008). Consistent with the phenotype for *Ptch1*, loss of *Sufu*, another negative regulator of the Hh pathway, also produces heart defects (Cooper et al., 2005). In addition to upregulation of *Nkx2-5*, *Shh* induces expression of *Gata-4*, *Mef2C*, *Meox1*, and *BMP-4* during cardiomyogenesis. There are several feed forward relationships among the Hh targeted genes. Activation of *Meox1* increases *Gli2*, *BMP-4*, *Gata-4*, *Mef2C* and *Nkx2-5* expression (Gianakopoulos and Skerjanc,

2005) (Petropoulos et al., 2004) while *Mef2C* and *Gli2* activate each other during cardiomyogenesis (Voronova et al., 2012).

Comparisons between cardiac and skeletal muscle suggest that some components of the regulatory networks are shared between different types of muscle. In addition to their roles in cardiomyogenesis, *Mef2C* and skeletal progenitor factor *Meox1* are both active in skeletal muscle development. Myocardin (*Myocd*), the critical regulator of smooth muscle development (Wang et al., 2003), is also required for cardiomyocyte differentiation (Huang et al., 2009a).

1.1.4.3 Smooth Muscle

Overall, much less is known about smooth muscle formation than either skeletal or cardiac muscle development. However, consistent with other types of muscle development, both vascular and organ affiliated smooth muscle subtypes also require Hh signaling. In developing vertebrates, Hh signaling facilitates vasculogenesis and angiogenesis by targeting vascular growth factors (Byrd and Grabel, 2004) and the lungs of mice that lack *Shh* have decreased vascularization (Pepicelli et al., 1998).

SM subtypes are critical for the function of many organs including respiratory (Tollet et al., 2001; Goyal and Chaudhury, 2008), urogenital (Baker and Gomez, 1998; DiSandro et al., 1998) and gastrointestinal systems. Within bladder, intestine, and ureter, Hh has been shown to function in the ontogeny of SM as well as its homeostasis in the adult (Ramalho-Santos et al., 2000; Caubit et al., 2008; Kolterud et al., 2009; Zacharias et al., 2011). In the intestine, augmenting *Ihh* expression in the epithelium of transgenic mice results in robust expansion of mucosal SM (Madison et al., 2005; Kolterud et al., 2009; Zacharias et al., 2011) while

attenuation of epithelial Hh signaling leads to loss of mucosal SM (Madison et al., 2005; Zacharias et al., 2011). Hh is epithelially secreted and acts upstream of the mesenchymal factors, *Foxf2* and *Myocd*, which are both involved in feedback mechanisms that regulate intestinal smooth muscle development by regulating epithelial Hh, emphasizing the complex nature of epithelial:mesenchymal crosstalk in the intestine (Wang et al., 2003; Ormestad et al., 2006). For example, mice with *Foxf2* conditionally deleted in the smooth muscle population exhibit increased HH (an indirect effect since FOXF2 is mesenchymal while HH is expressed only epithelially), and FOXF2 binds to promoters of the MYOCD and FOXF1 genes (both of which are also HH targets) to modulate signaling (Bolte et al., 2015).

1.2 Dissertation Proposal Objective

The ultimate goal of this dissertation was to identify regulatory programs underlying intestinal smooth muscle development. This work integrated computational and biological methods in parallel to achieve this goal. First, because Hh signaling has a documented role as a regulator of ISM development, computational methods were implemented to globally identify Hh enhancer regions that might drive ISM development (Roberts et al., 1995; De Santa Barbara et al., 2005; Madison et al., 2009; Zacharias et al., 2011; van den Brink and Rubin, 2013; Bolte et al., 2015). The advantage of computational prediction methods is that they are unbiased and allow the simultaneous exploration of all possible enhancers, regardless of spatial or temporal timing of target gene expression. This part was addressed in two different stages; a) I explored ways to identify Hh enhancers in genomic DNA based on the clustering of *ci*/GLI binding sites (presented in Chapter II) and b) I used machine learning to extract sequence information from

GLI bound sequences in ChIP data (Vokes et al., 2007; Vokes et al., 2008; Lee et al., 2010; Peterson et al., 2012) and to predict new Hh enhancers (presented in Chapter III). Finally, I collected biological data to begin to explore the transcriptome of the developing ICM, identifying genes expressed within ISM and thereby allowing prediction of additional regulators of ISM.

Despite the enormous importance of the Hh pathway, little is known about how the Hh signal is transduced into a specific phenotypic response in a given cell type, a key question for elucidating context-specific activation of gene targets. When Hh signals are received by a responsive cell, this results in the binding of *ci*/GLI transcription factors to genomic enhancers of Hh targeted genes. Since so few Hh-regulated enhancers have been identified and functionally validated to respond to Hh signals (Table 1.1), very little is known about what features these enhancers have in common or about how individual enhancers are activated in different contexts. The first aim of my dissertation work was to implement computational approaches to expand the database of known Hh enhancers and to verify them as GLI dependent.

1.3 Identification of Transcription Factor Binding Sites

1.3.1 Enhancer Background

Enhancers are defined as short regions of DNA that contain binding sites for transcription factors that act in an integrated manner to control gene expression in a specific spatiotemporal context (Martinez-Salas et al., 1988). The combinatorial input of all bound transcription factors (reviewed in (Spitz and Furlong, 2012)), both activators and repressors, determines whether the enhancer, as a protein:DNA complex, interacts with promoters to initiate gene transcription. It

has also been shown that enhancers emit transcripts (Kim et al., 2010), which in some cases are required for enhancer function (Melo et al., 2013) and may also serve to perpetuate the openness of the chromatin region. The modular organization of TFBS within enhancers facilitates context dependent initiation of enhancer activity by different combinations of factors. TFs work cooperatively and many have specific interaction partners that result in context specific activation (Lefterova et al., 2008; Bery et al., 2013). For instance, the single zebrafish *wnt8a* enhancer region is activated via two different combinatorial inputs (Narayanan and Lekven, 2012), exemplifying how enhancers can be employed in multiple contexts. Although some enhancer regions are well conserved across species, new enhancers can arise as the result of duplication events (Kikuta et al., 2007), alterations from mobile elements (Sanges et al., 2006; Lowe et al., 2007) and *de novo* generation from accumulated changes in nucleotide sequence (Eichenlaub and Ettwiller, 2011; Domené et al., 2013; Rubinstein and Souza, 2013). Thus enhancers appear to be highly malleable and rapidly evolving (Villar et al., 2015).

In vertebrates, the relationship between enhancers and their gene targets is complex, since genes that are expressed in the same tissue are seldom located in contiguous chromosome regions (Moltó et al., 2009). Initially thought to reside largely in proximal upstream and intronic regions of genes, vertebrate enhancers have been located in every component of the genomic landscape, including exons (Dong et al., 2010; Birnbaum et al., 2012; Khan et al., 2012; Ritter et al., 2012) and intergenic regions such as CpG islands and repeat regions (McBride et al., 2011). Looping mechanisms (reviewed by (Dean, 2011)) facilitate long range interactions that span large genomic distances (Lettice et al., 2003; Gordon et al., 2009a; El-Kasti et al., 2012; Sakabe et al., 2012; Hill and Lettice, 2013)(reviewed by (Harmston and Lenhard, 2013)), which include

upstream and downstream relationships to target genes. Even cross-chromosome interactions have been documented (Spilianakis et al., 2005; Lomvardas et al., 2006).

Individual genes often have several enhancer elements that activate temporal-specific gene expression in different contexts (Gordon et al., 2009a; Hill and Lettice, 2013)(Göttgens et al., 2010). Secondary enhancers can arise from duplication events; these can evolve somewhat divergent functions (Hong et al., 2008), or can provide redundant overlapping expression (Nolte et al., 2013). Others, however, may not be functional in isolation, serving only to augment primary enhancer function (Guerrero et al., 2010). Characterization of the *Pax6* regulatory region by transgenic analysis illuminates how sophisticated enhancer regulation can be; locus expression in the mouse is controlled by several enhancers that facilitate distinct and overlapping gene expression patterns and the locus also contains interdependent enhancer regions that provide protective redundancy (McBride et al., 2011).

1.3.2 Transcription Factor Binding Site Prediction

Over the last decade, largescale genomic studies have provided abundant datasets to start unraveling how enhancers function globally in development and in disease settings (Raney et al., 2011). Computational approaches are well suited for processing and integrating these large datasets in order to identify and predict transcription factor (TF) interactions that result in gene expression within specific cells. Yet despite the increased use of computational methods for these purposes, success rates for predicting enhancer regions remain low. Most problematically, the underlying regulatory logic used by enhancers is still poorly understood.

For some enhancers, multiple copies of a specific transcription factor binding site (TFBS) will be present (Gotea et al., 2010), but the biological function of homotypic clustering is not fully understood. In some instances the presence of multiple copies of the TF is required because multiple proteins are needed to permit activation. For example, the neural crest specific *Sox10* enhancer contains multiple SOX10 binding sites that are required for fully functional enhancer activity (Wahlbuhl et al., 2012). For others, multiple binding sites could serve to maintain the presence of a single TF in the region until it binds to the right site or to preserve enhancer function in the event of mutation.

All enhancers have cofactor relationships (also called heterotypic clustering) that generate combinatorial inputs resulting in cell-specific gene expression (Berman et al., 2004; Morgan et al., 2007; Miller et al., 2012; Wang et al., 2012a). For example, cortical development relies on a cofactor relationship between SOX and POU across multiple enhancers for activation in different cell populations (Bery et al., 2013). Importantly, the organization of TFBS within an enhancer region is modular, and there is evidence that, at least in some cases, the order of binding sites is less important than the presence of these sites (Swanson et al., 2010; Evans et al., 2012; Guo et al., 2012). In contrast, in promoters, the order and distance between binding sites for each factor appears to be more constrained (Hosseinpour et al., 2013). This strict organization of both TF relationships and distances between binding sites makes it easier to mine cell specific cofactor relationships in promoter regions of co-expressed genes compared to the variable proximity relationships between TFBS that occur in most enhancers (Alkema et al., 2004; Gruel et al., 2011; Whitfield et al., 2012). Occasionally, however, it is seen that features found in promoters can be used to find relationships that predict enhancer elements (Nolis et al., 2009).

Another major advantage of promoter mining is that the close proximity to the target gene provides more accurate annotation (Subramanian et al., 2005; Huang et al., 2009b).

Using conservation as a tool for data mining can sometimes be extremely helpful in identifying functional sites, determining whether a TF has multiple TFBS, and establishing the presence of cofactor relationships (Bulyk, 2003). However, some conserved regions exhibit no enhancer activity (Bejerano et al., 2004; Katzman et al., 2007), and deletion of some ultra-conserved regions from genomes can fail to show an obvious phenotype (McLean and Bejerano, 2008). In general, cis-regulatory regions are not stable, and sequence conservation of binding sites is low (Dermitzakis and Clark, 2002). Even among pathways that have strongly conserved functions, rearrangement of TFBS in target enhancers is common (Odom et al., 2007), and this divergent sequence still maintains conserved regulatory function (Göttgens et al., 2010; Taher et al., 2011). Since enhancers are responsible for regulation of conserved functionality as well as diversification, it is not surprising that examples of both positive and negative selection of regulatory regions exist (Smith et al., 2013). Given the apparently rapid evolution of enhancers (perhaps demanded by the fact that these elements are so important to the modulation of gene activity) (Villar et al., 2015), conservation may not work for some types of enhancers. However, enhancer detection methods that allow alteration in the positioning of TFBS, but require a similar distribution of transcription factors, might be more valuable than direct conservation for discovering trends within others.

Statistical learning approaches are valuable in identifying enhancer function since they attempt to learn features that discriminate functional from non-functional regulatory regions with no prior constraint imposed on the system. Machine learning methods are capable of

discriminating sequence characteristics that contribute to TF interaction (Narlikar et al., 2010; Burzynski et al., 2012; Hansen et al., 2012; Lee and Huang, 2012; Ahmad et al., 2014) by deriving an optimal boundary between a training set and a negative set. For example, new regulatory regions have successfully been predicted in human cells by looking for k-mer enrichment against a background set of sequences and using those motifs to predict new regions that contain the same k-mer combinations (Fletez-Brant et al., 2013). One of the challenges in implementing machine learning approaches is that there may not be a good set of known negative regulatory regions for comparison with positive areas, resulting in overfitting. Furthermore, many of these approaches are based exclusively on sequence, but it is possible to integrate multiple datasets in a machine learning approach to extend the information beyond genomic DNA and to incorporate additional regulatory levels that control chromatin access (Yaragatti et al., 2009).

1.3.3 Mining Biological Data Sets for Transcription Factor Binding Sites

Global datasets, including open chromatin regions, chromatin marks associated with enhancers, regions bound by TFs *in vivo* (as determined by DNA protection assays or ChIP-seq), putative DNA motif libraries, and conserved genomic regions provide abundant data to identify genomic regions that are likely to participate functionally in gene regulation. Biologically collected DNA accessible datasets include DNaseI hypersensitivity sites (Neph et al., 2012), FAIRE or Formaldehyde-Assisted Isolation of Regulatory Elements (Song et al., 2011), enhancer transcription (eRNA) (Mousavi et al., 2013), enhancer affiliated markers (CTCF, CBP, and histone modifiers such as P300 and HAT) (Visel et al., 2009) as well as histone marks (H3K4me1, H3K4me2, H3Kac etc) (Jin et al., 2011; Rada-Iglesias et al., 2011) specific enough

to differentiate active and poised enhancers. These features are generally seen in regulatory regions and can be used to restrict the organism's genomic DNA to a subset of putative participating regions when computationally mining for putative TFs or context specific enhancer regions.

However, there are some limitations to using such biological datasets to identify enhancers. ChIP-seq studies are known to generate a high level of false positive peaks. An unknown percentage of the data may be background (e.g., from bulk precipitation) or only indirectly related (such as ChIP-seq peaks that do not contain a binding site for the factor in question) or may contain irrelevant information (such cell contamination or spurious TF binding). And, of course, the fact that a TF binds to DNA region does not confirm its regulatory function (Cusanovich et al., 2014). However, it remains to be seen if some of these apparently non-functional regions, tested in a broader context, might act as secondary enhancers to facilitate primary enhancer activity (Maston et al., 2012). At the same time, due to low affinity TF binding or to poor antibody interactions, some truly functional regions may not be captured. Additionally, if the available data contains a mixed population of cells (i.e., is derived from tissue rather than purified cells), it can be difficult to identify enhancer regions involved in context-specific gene activation.

1.3.4 Prediction of Hedgehog Enhancer Regions

To begin to understand the genomic landscape underlying Hh gene activation, my first approach implemented a computational method to examine the distribution of TFBS for the Hh transcription factor *ci* in the fruit fly genome. Using the *Drosophila* model organism was

advantageous since the small genome facilitates computational strategies and functional testing of the enhancers in transgenic flies is relatively easy and quick. Nevertheless, in total, only seven Hh enhancers had been functionally verified in *Drosophila* prior to our study. Four (regulating *decapentaplegic*, *knot*, *patch*, *wingless*) were known to contain three or more functional ci sites, while the remainder contained two (*stripe*, *hairy*) or one (*orthodenticle*) ci site (Alexandre et al., 1996; Ohlen and Hooper, 1997; Müller and Basler, 2000; Piepenburg et al., 2000; Kwon et al., 2004; Hersh and Carroll, 2005; Blanco et al., 2009). Since the majority of these characterized *Drosophila* Hh enhancers contained clusters of multiple Hh transcription factor binding sites, the work presented in Chapter II tested whether homotypic clustering of Hh transcription factor sites could be used to predict the location of additional enhancers. A sensitive computational algorithm was developed to identify clustered sites and to measure the probability of finding such clusters by chance. Twenty-two predicted clusters were tested in functional assays. Of these, eight, one previously known and seven new, were found to be Hh enhancers; their function was confirmed by an *in vivo* transgenic fly assay and after electroporation of the chicken neural tube. Importantly, all of these Hh enhancers showed direct Hh response since loss of enhancer activity occurred after mutagenesis of the ci binding sites. Since only 32% of the predicted enhancers were functional, we concluded that while clusters of Hh transcription factor binding sites clearly define some active enhancers in the fly genome, homotypic clustering alone is not sufficient to specify a Hh enhancer region and that other features must be involved. Nevertheless, if this rate of prediction were to hold, the data generated in this study could lead to the identification of a very large number of Hh-regulated enhancers.

In the mouse, unlike the fly, most of the previously characterized and functionally validated Hh enhancers contain only one functional GLI site (*FoxA2* (Sasaki et al., 1997), *Gli1*

(Dai et al., 1999), *Nxk2.9* (Santagati et al., 2003), *Myf5* (Gustafsson, 2002), *Cltb*, *Tle1*, *Ncor2*, *Boc*, *Ptch2* (Lee et al., 2010), *Rab34*, *Nkx2.2* (Vokes et al., 2007), *Ptch1* (Agren et al., 2004)). The remaining contain two (*Sox18*, *Ptch1* (Lee et al., 2010), *Has2* (Liu et al., 2013)). Publically available ChIP datasets from mouse models carrying FLAG-tagged GLI proteins (GLI^{FLAG}) also seem to suggest that regions bound by GLI1 or GLI3 proteins contain only one GLI binding site (Vokes et al., 2007; Lee et al., 2010). Indeed, when the cluster finding algorithm that we developed in *Drosophila* was applied to the mouse, using Chromosome 2 as a test, no Hh enhancers were found after testing 40 predicted putative enhancers. Thus, a different approach was needed.

Chapter III describes a strategy for finding mammalian Hh enhancers that takes advantage of four existing GLI ChIP datasets. Though no ChIP-grade antibody for GLI is available, the generation of mouse lines carrying FLAG-tagged alleles of the GLI1 and GLI3 proteins allowed several ChIP analyses to be accomplished in different tissues. I performed a meta-analysis of these datasets in order to capture a library of GLI binding motifs that are representative of possible *in vitro* binding sites (Vokes et al., 2008; Lee et al., 2010; Peterson et al., 2012). Previously, prediction of putative GLI binding motifs relied on *in vitro* binding data which predicted 1,432,161 possible GLI binding sites across the mouse genome (Hallikas et al., 2006). The GLI library based on the *in vivo* meta-analysis, based on GLI motifs enriched in the *in vitro* datasets, suggested substantially fewer, 195,816. Critically, the *in vitro* motifs included predicted binding motifs that did not contain cysteines (C) in the fifth and seventh positions of the binding site; a C in this position is a known requirement for functional GLI binding (Winklmayr et al., 2010). Thus, the putative motifs defined by *in vitro* binding studies likely

contains more false positives than in the *in vivo* generated GLI library, which contains C in the critical positions. To determine whether machine learning could be used to reveal genomic features predictive of Hh enhancers, I applied kmer-SVM to this redefined set of *in vivo* binding sequences culled from the GLI^{FLAG} datasets (Fletez-Brant et al., 2013). Classifiers trained on two of the four GLI^{FLAG} datasets (one done in neural precursor cells and one in the developing limb) were found to be capable of distinguishing members of a positive group from a negative background dataset with high confidence (Vokes et al., 2008; Peterson et al., 2012). Because these datasets were collected from sequences precipitated by two different GLI transcription factors (GLI1 for the neural precursors and GLI3 for the limb), and from different tissues at different time points, we expected that shared targets were most likely to be Hh pathway components, which are active in all contexts. Therefore, both datasets were used to independently predict Hh enhancers across the mouse genome and the resulting predictions were then overlapped and filtered for regions annotated to Hh pathway components. Nine regions annotated to *Boc*, *Dpp6*, *Gli3*, *Hhip*, *Hipk2*, *Ptch1*, *Scube1*, *Shh*, and *Tgfbr2* were tested and seven (78%) were Hh responsive. To confirm direct Hh interaction, putative enhancer regions were co-transfected with modulators that constitutively activate the Hh pathway (Xie et al., 1998); the Hh response was lost after mutation of GLI-binding sites, proving the Hh-dependent nature of enhancer activity and identifying the precise genomic sequence bound by the GLI proteins responsible for driving gene expression within the enhancer. These results suggest that machine learning methods can be successfully applied to identify sequence features that characterize Hh enhancer regions.

1.4 Intestinal Visceral Smooth Muscle Development

In Chapter IV, I concentrated on analysis of developing intestinal smooth muscle, specifically, the inner circular smooth muscle. In this case, I collected new biological data sets (RNA-seq and ChIP-seq) and used these to determine which muscle genes are expressed in ISM and to identify the regions of DNA that regulate expression of these genes. The first of these techniques, RNA-seq, captures a transcriptome profile by utilizing high throughput sequencing to quantitate RNA levels. RNA-seq of the separated epithelial and mesenchyme populations of E14.5 intestine allowed a comparison between a transcriptome profile with no muscle (epithelium) and the muscle enriched mesenchyme during the formation of inner circular muscle (ICM). Using Gene Set Enrichment Analysis (GSEA) and clustering analysis followed by examination of *in situ* data at E14.5, we identified over 100 genes that are expressed in the ICM (Visel et al., 2004; Subramanian et al., 2005; Diez-Roux et al., 2011). The promoters of these genes were then analyzed to determine putative transcription factors involved in the regulation of ISM genes (Gotea and Ovcharenko, 2008). This analysis showed enrichment for cJUN, which was further shown to be expressed exclusively within the ICM. To examine the genomic regions bound by cJUN, ChIP-seq, a method for determining the location of transcription factor binding sites on DNA *in vivo*, was performed. ChIP-seq relies on cross-linking the transcription factor to the DNA in the nucleus, breaking DNA into small pieces, and then using an antibody to capture the segments of DNA bound by transcription factor. These regions are then sequenced to determine the enriched regions. We found that genomic regions bound by cJUN at E14.5 contained characteristics of muscle enhancers, indicating a previously unknown regulatory role for cJUN in ISM. Since previous studies had shown that Hh signaling is also important in the regulation of ISM gene expression in the intestine and that cJUN and GLI have a cofactor relationship in other conditions (Laner-Plamberger et al., 2009), we examined the regulatory

relationship between cJUN and GLI. We found no evidence for co-binding of these factors at cJUN immunoprecipitated regions. However, we established cJUN as a Hh target gene.

Additionally, we established that at least some of the genes that had previously been shown to be regulated by Hh in skeletal muscle are also regulated by Hh in ISM.

1.5 Significance of This Work

The Hedgehog signaling pathway is critical for embryonic organ development and adult tissue homeostasis across animal phyla (McMahon et al., 2003; Jiang and Hui, 2008; Briscoe and Théron, 2013). Additionally, misregulation of this pathway causes a number of developmental malformations as well as adult human diseases, including cancer (Barakat et al., 2010). Thus, there is great interest in determining which genes are regulated by the Hh pathway and which *cis* elements direct this regulation. To answer this question in the context of intestinal inner circular muscle, computation methods to globally predict Hh enhancer regions were implemented in parallel with biological data collection (ChIP-seq, and expression profiling using RNA-seq) to identify Hh target genes and regulatory regions responsible for activating ISM genes. Though this project focused on Hh signaling, this multi-pronged approach could be applied to any transcription factor or signaling pathway to comprehensively analyze the gene regulatory networks governing many normal and disease-related cell states resulting from dysregulation of signaling pathways. This type of knowledge is important in disease settings both acutely (targets may provide effective biomarkers for disease initiation) and chronically (such targets can be used as disease monitors and/or therapeutics). Moreover, the whole genome analysis could have a major impact on the interpretation of Genome Wide Association Studies that identify variations

in DNA regions (often regulatory) linked to disease phenotypes, since many new functional genomic regions are annotated.

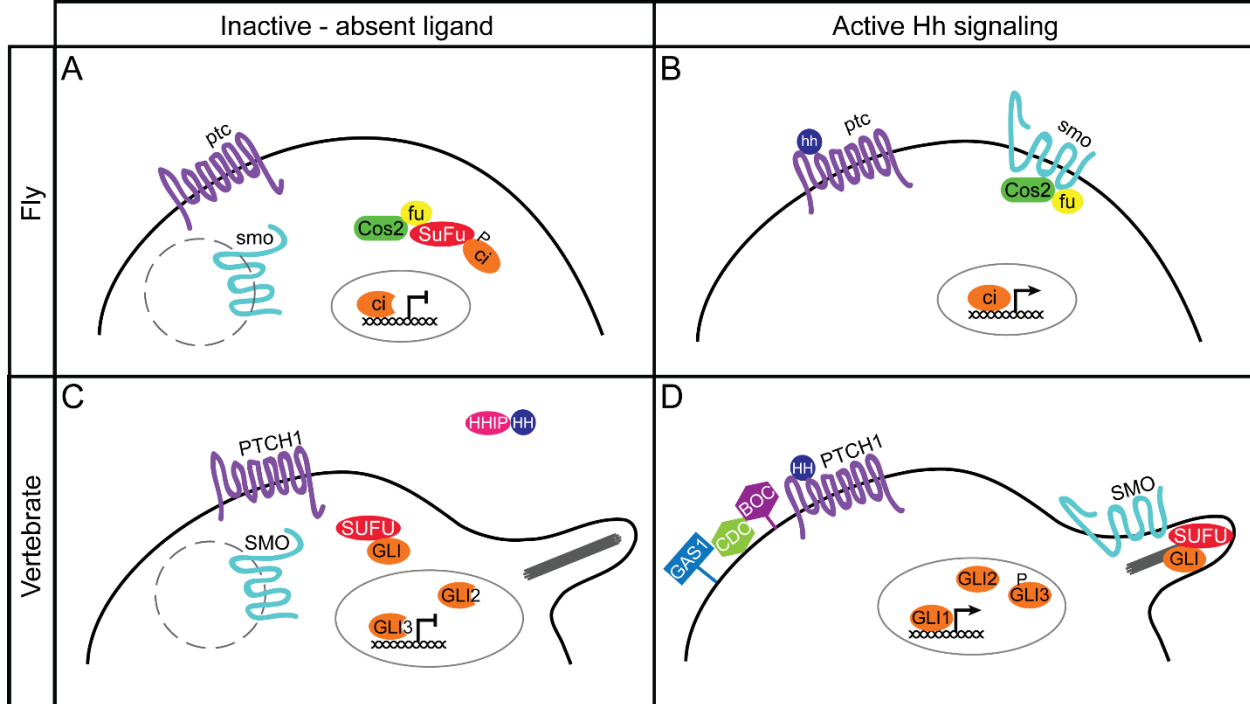


Figure 1.1. Schematic of Hh signaling in Fly and Vertebrate. (A) In the absence of hh ligand, the transmembrane protein ptc inhibits smo, preventing it from engaging the downstream signal transduction pathway. This may involve the sequestration of smo in intracellular vesicles. The Cos2, fu, and SuFu complex phosphorylates ci, which is subsequently cleaved and translocated to the nucleus, where it acts as a repressor. (B) Binding of hh to ptc relieves smo inhibition, allowing it to interact with Cos2 and fu; as a result ci is neither phosphorylated nor cleaved. The full length ci enters the nucleus where it acts as a transcriptional activator. In vertebrates, the Hh signaling pathway relies on cilia. (C) Without HH interaction with PTCH1, either in the absence of HH or when HH is sequestered by HHIP, SMO is inhibited and GLI2 and GLI3 proteins are cleaved into transcriptional repressors. (D) In the presence of HH, several co-receptors (BOC, CDO, GAS1) facilitate binding to PTCH1. SMO then localizes to the cilia where the SUFU GLI complex is trafficked along the microtubules. GLI1 or active forms of GLI2 and GLI3 are not cleaved under these conditions and can enter the nucleus to activate transcription.

Enhancer Gene Target	Organism	Reference
<i>decapentaplegic</i>	<i>Drosophila</i>	Muller et al., 2000
<i>knot</i>	<i>Drosophila</i>	Hersh et al., 2005
<i>hairy</i>	<i>Drosophila</i>	Kwon et al., 2004
<i>orthodenticle</i>	<i>Drosophila</i>	Blanco et al., 2009
<i>patch</i>	<i>Drosophila</i>	Alexandre et al., 1996
<i>stripe</i>	<i>Drosophila</i>	Piepenburg et al., 2000
<i>wingless</i>	<i>Drosophila</i>	Ohlen et al., 1997
<i>Boc</i>	Mouse	Lee et al., 2010
<i>Cltb</i>	Mouse	Lee et al., 2010
<i>FoxA2</i>	Mouse	Sasaki et al., 1997
<i>Gli1</i>	Mouse	Dai et al., 1999
<i>Has2</i>	Mouse	Liu et al., 2013
<i>Myf5</i>	Mouse	Gustafsson et al., 2002
<i>Ncor2</i>	Mouse	Lee et al., 2010
<i>Nkx2.2</i>	Mouse	Vokes et al., 2007
<i>Nkx2.9</i>	Mouse	Santagati et al., 2003
<i>Ptch1</i>	Mouse	Agren et al., 2004; Lee et al., 2010
<i>Ptch2</i>	Mouse	Lee et al., 2010
<i>Rab34</i>	Mouse	Vokes et al., 2007
<i>Sox18</i>	Mouse	Lee et al., 2010
<i>Tle1</i>	Mouse	Lee et al., 2010

Table 1.1. Functionally verified Hh enhancers identified at the time this work was started.

This list includes enhancers from *Drosophila* or mouse for which response to Hh was functionally verified and ci/GLI binding dependence was confirmed by mutagenesis of the TFBS.

Chapter II

Identification and validation of novel Hedgehog-responsive enhancers predicted by computational analysis of ci/GLI binding site density

2.1 Abstract

The Hedgehog (Hh) signaling pathway directs a multitude of cellular responses during embryogenesis and adult tissue homeostasis. Stimulation of the pathway results in activation of Hh target genes by the transcription factor ci/GLI, which binds to specific motifs in genomic enhancers. In *Drosophila*, only a few enhancers (*patched*, *decapentaplegic*, *wingless*, *stripe*, *knot*, *hairy*, *orthodenticle*) have been shown by *in vivo* functional assays to depend on direct ci/GLI regulation. All but one (*orthodenticle*) contain more than one ci/GLI site, prompting us to directly test whether homotypic clustering of ci/GLI binding sites is sufficient to define a Hh-regulated enhancer. We therefore developed a computational algorithm to identify ci/GLI clusters that are enriched over random expectation, within a given region of the genome. Candidate genomic regions containing ci/GLI clusters were functionally tested in chicken neural tube electroporation assays and in transgenic flies. Of the 22 ci/GLI clusters tested, seven novel enhancers (and the previously known *patched* enhancer) were identified as Hh-responsive and ci/GLI-dependent in one or both of these assays, including: *Cuticular protein 100A (Cpr100A)*; *invected (inv)*, which encodes an *engrailed*-related transcription factor expressed at the

Gurdzien K*, Lorberbaum DS*, Udager AM*, Song JY*, Richards N, Parker DS, Johnson LA, Allen BL, Barolo S, Gumucio DL. *Identification and validation of novel Hedgehog-responsive enhancers predicted by computational analysis of Ci/Gli binding site density*. PLOS One.

anterior/posterior wing disc boundary; *roadkill* (*rdx*), the fly homolog of vertebrate *Spop*; the segment polarity gene *gooseberry* (*gsb*); and two previously untested regions of the Hh receptor encoding *patched* (*ptc*) gene. We conclude that homotypic ci/GLI clustering is not sufficient information to ensure Hh-responsiveness; however, it can provide a clue for enhancer recognition within putative Hedgehog target gene loci.

2.2 Introduction

The Hedgehog (Hh) signaling pathway plays multiple roles in embryonic organ development and adult tissue homeostasis across animal phyla (McMahon et al., 2003; Jiang and Hui, 2008; Briscoe and Théron, 2013). Hh signaling directs specific cell fate choices, controls tissue patterning and governs cell proliferation. Several human developmental diseases are caused by altered Hh signaling, including spina bifida, exencephaly (Murdoch and Copp, 2010), holoprosencephaly (Schachter and Krauss, 2008), cleft lip/palate (Lipinski et al., 2010), and a host of malformations in vertebral, anal, cardiac, tracheal, esophageal, renal, and limb tissues (together known as VACTERL Association (Ngan et al., 2013)). Aberrant Hh signaling is also responsible for several cancers, including basal cell carcinoma, medulloblastoma and rhabdomyosarcoma (Teglund and Toftgard, 2010). Recently, cancers of the pancreas, colon, ovary, stomach and lung have also been associated with increased Hh signaling (Barakat et al., 2010; Teglund and Toftgard, 2010), prompting initiation of clinical trials with Hh antagonists for some of these conditions (de Sauvage, 2007; Scales and de Sauvage, 2009; Sekulic et al., 2012; Tang et al., 2012).

The Hh-regulated GLI family transcription factors (including cubitus interruptus (*ci*) in

the fly and GLI1-3 in mammals) are highly conserved across metazoans, as is the sequence of the preferred consensus ci/GLI binding site (Hallikas et al., 2006; Winklmayr et al., 2010).

Despite the functional importance and high conservation of the Hh pathway, surprisingly little is known about its target genes in any organism. These target genes and their associated enhancers, which are responsible for the genomic response to Hh in development and disease, have significant potential therapeutic and diagnostic value.

One method for identifying putative enhancers is chromatin immunoprecipitation (ChIP) (Vokes et al., 2007; Vokes et al., 2008; Lee et al., 2010; Peterson et al., 2012), though such data are subject to the spatiotemporal limitations of the analyzed cells or tissues and can be diluted by a high number of false positive binding sites. While many potential murine Hedgehog-responsive enhancers have been pinpointed in this manner, relatively few have been functionally verified by mutagenesis of transcription factor binding sites (Vokes et al., 2007; Vokes et al., 2008; Lee et al., 2010; Peterson et al., 2012). In *Drosophila*, an alternative approach, DamID which fuses a DNA interacting protein to DNA adenine methyltransferase leading to methylation near binding locations, identified 52 potential ci/GLI target enhancers, though none of these were functionally verified by mutagenesis of ci/GLI sites (Biehs et al., 2010). To date, only seven *Drosophila* enhancers have been shown by mutational analysis to be ci/GLI-dependent (Alexandre et al., 1996; Ohlen and Hooper, 1997; Müller and Basler, 2000; Piepenburg et al., 2000; Hersh and Carroll, 2005; Blanco et al., 2009; Ramos and Barolo, 2013), which limits our understanding of the basic rules that govern their activity and context specificity. Analysis of the known *Drosophila* Hh enhancers reveals that three (regulating *ptc*, *wg*, and *knot*) contain clusters of three or more ci/GLI binding sites, while the remaining enhancers (of the *dpp*, *stripe* and *hairy* genes) contain two sites (Alexandre et al., 1996; Ohlen and Hooper, 1997; Müller and Basler,

2000; Piepenburg et al., 2000; Hersh and Carroll, 2005; Blanco et al., 2009; Ramos and Barolo, 2013). These examples, and findings in other systems (Markstein, 2001; Berman et al., 2002; Rebeiz et al., 2002; Lifanov, 2003; Gotea et al., 2010) suggest that homotypic clustering might be a relevant indicator of Hh enhancer activity in the fly. To test this, we computationally identified regions of the fly genome in which the density of ci/GLI binding sites is enriched relative to chance expectation. We then tested the ability of these regions to: 1) drive Hh-dependent activity in the developing chicken neural tube, and 2) direct tissue-specific gene expression in a *Drosophila* transgenic reporter model. Importantly, the functional significance of the ci/GLI binding motifs was also tested by mutation of these sites within each active enhancer. Of the 17 top clusters, four (23%) drove reporter expression in a known Hh domain and/or in a ci/GLI-dependent fashion in one or both assays. Thus, while some Hh-regulated enhancers indeed contain homotypic clusters of ci/GLI motifs, not all such clusters function as enhancers *in vivo*.

We also asked whether ci/GLI site clustering could be used to predict the location of enhancers in genes that are known or putative targets of Hh signaling. We identified five such ci/GLI site clusters, four of which were subsequently validated as Hh enhancers by functional assays (80%). Thus, altogether, our analysis of clustered ci/GLI sites identified eight Hh enhancers, including seven novel enhancers and one previously identified *ptc* enhancer. These findings double the number of functionally verified Hh enhancers.

2.3 Materials and Methods

2.3.1 Computing Resources

Except where otherwise indicated, all computational steps were performed using custom Perl scripts, which are available for download at <https://github.com/um-gurdziel/GurdzielUdagerLorberbaum2015>. Overlap between coordinates in bed file format were performed using the UCSC Table Browser.

2.3.2 Definition of Putative ci/GLI Binding Sites

A mono-nucleotide distribution matrix for ci binding sites, derived from *in vitro* competitive DNA binding assays with recombinant ci protein and labeled oligonucleotides, was obtained via the Genomatix Software Suite (www.genomatix.de; Genomatix, Germany) (Hallikas et al., 2006). The consensus index vector for such a matrix reflects the degree of nucleotide preference at each position; values range from 0, indicating equal preference for any of the four nucleotides, to 100, indicating strict preference for a single nucleotide (Quandt et al., 1995). The matrix similarity score (MSS) for a given site is calculated as the ratio of its matrix-vector product to that of the consensus site, as described previously (Quandt et al., 1995), and MSS values range from 0 to 1 (where 1 equals an exact match to the consensus site). The first nine of the eleven positions in the ci matrix have consensus index vector values greater than 70, suggesting that they contain a high degree of specific information about potential ci binding. Thus, these matrix positions were used to define a set of 211 9-mers (422 in sense and antisense directions) that pass a minimum level (0.75) of overall matrix similarity (i.e. with a $MSS \geq 0.75$) to the optimal consensus ci site (GACCACCCA) (Table S2.1) (Quandt et al., 1995; Hallikas et al., 2006) and also contain concordant (C and C or G and G) nucleotides in the 4th and 6th position, which are critical for ci binding (Winklmayr et al., 2010).

2.3.3 Identification and Annotation of Predicted ci Binding Sites in Genomic Sequence

Genomic sequence files (chromFa) for *D. melanogaster* (Dm) and *D. pseudoobscura* (Dp) were downloaded from UCSC Genome browser (genome.ucsc.edu) build dm3 (Celniker et al., 2002; Richards et al., 2005; Fujita et al., 2011). The genomic coordinates of predicted ci/GLI binding sites were identified for chr2R, chr2L, chr3R, chr3L, chr4, and chrX (build dm3); and chr2, chr3, chr4 and chrX (build dp3). Each putative ci/GLI binding site was annotated for nearest gene/transcript, distance to nearest gene/transcript, and associated gene/transcript feature transcript using refFlat files obtained from UCSC Genome Bioinformatics. ci/GLI clusters were defined as regions containing at least three and at most ten putative ci/GLI binding sites within a maximum distance of 1000 base pairs (bp) (measured from the outside ends of the flanking sites (Fujita et al., 2011; McQuilton et al., 2012). Predicted sites were also annotated with respect to the nearest CTCF boundary region (Holohan et al., 2007). Cluster regions that contained predicted ci binding sites that mapped to exons or repeat regions were excluded. Repeat regions often have regulatory function (Sawaya et al., 2013; Taher et al., 2015). If clustered regions were identified within repetitive regions and found to be positive we would not know if the activity was dependent on clustering or features of the repetitive sequence.

2.3.4 Background Modeling

To identify regions of the genome that exhibit a higher density of ci/GLI sites than would be expected by chance, we compared the actual distribution of ci/GLI sites to a randomized background model. Three different modes of background modeling were examined. For Model 1

(Random), all bases in the genome were randomized, as was done in a previous analysis of clustered binding sites for Suppressor of Hairless (Rebeiz et al., 2002). For Model 2 (Shuffle 3mer), the genome was parsed into contiguous 3-mers and these were then shuffled to create the background. In Model 3 (Flip GC/AT), each base was randomly flipped between itself and its complementary base pair (e.g., G will randomly become G or C; A will become A or T; C will become C or G; T will become T or A). On the basis of the data shown in Results (Figure S2.1), only the Flip GC/AT model generates background genomes that most closely represent the GC content surrounding ci/GLI sites in the native genome. Since GC rich ci/GLI sites will occur by chance more often in GC rich than AT rich regions, use of a randomization model that homogenizes the AT/GC landscape would artificially reduce the density of expected ci/GLI sites in GC rich areas and increase this density in AT rich regions. Therefore, using the Flip GC/AT strategy, background models were generated separately for the Dm and Dp genomes for comparison to each native genome.

2.3.5 Generation of Artificial Genomic Sequence and Random Genomic Distributions of Binding Sites

On a chromosome-by-chromosome basis, 1000 sets of background genomic sequences were generated using the Flip GC/AT method. However, base flipping resulted in fewer ci/GLI sites in the randomized chromosomes, relative to the native Dm or Dp genome. To correct for this, putative ci/GLI binding sites were identified in each of the 1000 background genomic sequences and the genomic coordinates of each site was recorded. Site motifs, tagged with their location coordinates, were pooled into a master list of possible site positions. This master list was

used to re-create 100 background chromosomes for each chromosome, such that each background chromosome contained the same composition of ci/GLI sites (overall number and motif) as the native Dm or Dp chromosome (see Results).

2.3.6 Assessment of Relative ci/GLI Binding Site Clustering

ci/GLI site clusters were defined as regions containing at least three and at most ten putative ci/GLI sites within a maximum distance of 1000 base pairs (bp; measured from the outside ends of the flanking sites). The genomic coordinates of each cluster were cataloged, and clusters were subsequently filtered for the presence of at least one predicted binding site with a $MSS \geq 0.81$. This was done to decrease the number of clusters comprised entirely of low scoring sites, substantial portions of which are predicted to be non-functional. Clusters that contained exon or repeat elements were excluded. Clusters for which the ci/GLI binding sites themselves accounted for more than 25% of the end-to-end cluster length were also excluded, since the majority of such clusters were composed of repetitive sequence. For each cluster, the number of binding sites expected to be present by chance for that specific genomic region was determined from 100 control reconstructed genomes as described in Results. A clustering coefficient (CC) was defined as the number of ci/GLI sites observed in a given interval of the native genome (at a given location) divided by the average number of ci/GLI sites in the same region of the background genome (at the same location). To enrich for clusters likely to represent enhancers, we selected a CC cutoff of four which captured all of the previously known clustered Hh enhancers. Importantly, the CC score was used as a filter, and not as a ranking tool.

2.3.7 Orthologous Enrichment of ci/GLI Clusters

Clusters were identified and annotated in the Dp genome exactly as described above for Dm. Background modeling for the Dp genome was done by Flip GC/AT; 1000 randomized genomes were generated and corrected as outlined above for number and affinity class to make 100 randomized, corrected Dp genomes for comparison to the native Dp genome. Clusters identified in the Dp genome were selected according to the same criteria as for the Dm genome (cluster size ≤ 1000 ; 3-10 ci/GLI sites; $CC \geq 4$; at least one site with $MSS \geq 0.81$). The coordinates for enriched clusters of ci/GLI binding sites ($CC \geq 4$) were determined for Dm and Dp and compared using the LiftOver tool available from UCSC Genome Bioinformatics (Fujita et al., 2011). All clusters that were present in orthologous positions of the Dm and Dp genomes (i.e., with an overlap of one or more bases, irrespective of sequence identity) were selected for further analysis.

2.3.8 Cloning of Putative Enhancer Regions for Testing

Putative enhancer regions in the Dm genome were visualized in the UCSC Genome Browser, and using the Conservation track (12 Flies, Mosquito, Honeybee, Beetle Multiz Alignments & phastCons Scores), the ends of an individual enhancer element were extended to include contiguous highly conserved sequence (Blanchette et al., 2004). Putative enhancers were amplified from *w¹¹¹⁸* genomic DNA using template-specific PCR primers (Table S2.2). A CACC extension was added to the end of one primer to facilitate directional cloning. PCR fragments were cloned into the pENTR/D-TOPO vector using the standard kit (Invitrogen) and then shuttled into either Ganesh-G2 (Swanson et al., 2008) or HP-desteGFP (Boy et al., 2010) vectors using the Gateway® cloning system (Invitrogen). ci binding site mutations (C4A) were introduced by overlap extension PCR, as previously described (Swanson et al., 2010).

QuikChange mutagenesis (Stratagene) was also used to mutate some ci binding sites. pCIT was generated by replacing eGFP in pCIG (Megason and McMahon, 2002) with TdTOMATO, which was cloned into the location between the third PmlI site and the NotI site in pCIG. *SmoM2*-pCIT was generated by cloning rat *SmoM2* into the XhoI and ClaI sites of pCIT.

2.3.9 *Drosophila* Transgenesis

Transformation was achieved by injection of w^{1118} or *ZH-attP-86Fb* embryos, essentially as described previously (Rubin and Spradling, 1982; Bischof et al., 2007). A current protocol is available at: <http://sitemaker.umich.edu/barolo/injection>. For w^{1118} transgenesis, at least three independent lines were examined; one or more lines were examined for *ZH-attP-86Fb* transgenesis.

2.3.10 *Drosophila* Tissue Analysis

Since Hh is active in a variety of tissue contexts in the embryo (brain, gut, muscle, segmental stripes etc.), we utilized embryos at stages 9-13 to gain an unbiased view of all of these contexts. Additionally, we specifically examined the wing imaginal disc since this is a well-known and well-characterized expression domain for Hh signaling. Of the 22 genes selected for analysis (Table 2.1), 17 are expressed in the embryo or imaginal disc (Tomancak et al., 2002; Tomancak et al., 2007; Hammonds et al., 2013). There are no data on two (CG5475, CG4704) and three others (beat-IV, BDGP, HGTX) are not reported to be expressed in these sites, but these have been incompletely studied. For imaginal disc analysis, 3rd instar wandering larvae were collected from vials, and discs were dissected fresh and fixed in 4% paraformaldehyde. For

embryo analysis, embryos were collected in 6-hour batches at 25°C, dechorionated in 100% bleach, fixed in 4% paraformaldehyde, and devitellinized by shaking in methanol and heptane.

2.3.11 Chicken *in ovo* Electroporations

Chicken neural tube electroporations were performed essentially as described previously (Tenzen et al., 2006). Briefly, 500 ng/μl of reporter vector and 500 ng/μl of either pCIT or *SmoM2*-pCIT was dissolved in PBS with 50 ng/μl of Fast Green and injected into the neural tubes of Hamburger-Hamilton stage 10–12 chicken embryos. Approximately 48 hours following electroporation embryos were recovered and fixed in 4% paraformaldehyde for subsequent immunofluorescent analysis. Fertile eggs were obtained from the Michigan State University Poultry Farm.

2.3.12 Immunofluorescence and Microscopy

Drosophila embryos and imaginal discs were blocked with 10% BSA in phosphate-buffered saline (PBS) with 0.1% Triton X-100. The following primary antibodies were used overnight at 4°C: rabbit anti-GFP IgG antibody (1:200; Life Technologies A11122), mouse anti-Ptc (1:50, DSHB; APA1) and mouse anti-En (1:50, DSHB; 4D9). Samples were then incubated in the following secondary antibodies for 2 hours at room temperatures, Alexa Fluor 488-conjugated goat anti-rabbit IgG antibody (1:2,000; Life Technologies A11008) and/or Alexa Fluor 468-conjugated goat anti-mouse IgG antibody (1:2,000; Life Technologies A11004). Embryos and imaginal discs were mounted on glass slides using ProLong Gold with DAPI and imaged on an Olympus BX-51 upright microscope, Nikon A1 confocal with Ti-E microscope or Olympus FluoView 500 Laser Scanning Confocal Microscope. For direct comparisons, wild type

and mutant constructs were processed in parallel including being imaged on the same day, using the same exposure settings. Immunofluorescent analyses of chicken neural tubes were performed essentially as described previously (Jeong and McMahon, 2005). The antibodies used were as follows: 1:20 Mouse IgG1 anti-NKX6.1 (DSHB; F55A10). DAPI (Life Technologies) was used at a dilution of 1:30,000. All secondary antibodies (Alexa Fluor; Life Technologies) were used at a dilution of 1:500. Primary antibodies were incubated overnight at 4°C, followed by incubation with secondary antibodies for one hour at room temperature. Images were collected with a Leica SP5X confocal microscope.

2.4 Results

2.4.1 Computational Identification of Clustered ci/GLI Sites Across the *Drosophila* Genome

To test if clustering of ci/GLI sites could be used to predicted Hh enhancers, we developed a computational strategy to identify all regions of the genome that contain clusters of 3-10 ci/GLI sites that are enriched above chance expectation. Since the ci/GLI binding sequence is highly GC rich, these sites are more likely to occur by chance in GC rich regions of the genome. Thus, to achieve an unbiased assessment of clustering likelihood, it was important to utilize a background model with a GC landscape similar to that of the native genome. Three different background models were examined (see Materials and Methods for details). The three models were compared by mapping all predicted ci/GLI sites ($MSS \geq 0.75$) and examining the GC content of the genomic sequence surrounding each predicted ci/GLI site (Figure S2.1). Importantly, the randomized (Model 1) and shuffled 3-mer (Model 2) strategies significantly

change (i.e., homogenize) the GC context around ci/GLI sites, while the Flip GC/AT model (Model 3), by its nature, faithfully replicates the GC context of ci/GLI sites in the real genome; thus, this model was selected for use.

An accurate assessment of the relative density of ci/GLI clusters found in the native genome also requires that the background genomes contain a similar composition (number and type) of ci sites as the native genome. After generating background genomes using the Flip GC/AT method, we noticed that the total number of predicted ci/GLI binding sites on each chromosome was consistently reduced compared to the native Dm genome (Figure S2.2A). Left uncorrected, this deficit in total sites would lead to an artificial enrichment of clusters of ci/GLI sites in the Dm genome when compared to the background model. To correct for this discrepancy, we re-built background chromosomes (see detail in Materials and Methods) so that they contained the same number of each type of ci/GLI binding site (based on matrix similarity score) found in the Dm genome (Figure S2.2B). Relative enrichment of ci/GLI clusters in each genomic region was then assessed across the native genome by direct comparison to the 100 rebuilt background chromosomes (Figure S2.2C).

2.4.2 ci/GLI Cluster Analysis in *Drosophila melanogaster* (Dm)

The complete pipeline for identification of enriched clusters of ci/GLI sites and examination of their potential as Hh enhancers is provided in Figure 2.1. Clusters of 3-10 ci/GLI sites (maximum end-to-end distance 1000 bp) were identified in the native Dm and Dp genomes. Background modeling and background correction was performed separately for Dm and Dp. For each putative cluster, a cluster coefficient (CC) was defined as the number of ci/GLI sites in a

given genomic region divided by the average number of ci/GLI sites in the same genomic location in 100 control genomes (schematically illustrated in Figure S2.2C). Only clusters with a CC of greater than or equal to 4 and at least one ci/GLI site with a MSS of 0.81 or greater were chosen for subsequent analysis. These filters (1kb length; $CC \geq 4$; one site \geq MSS of 0.81) were designed to increase the likelihood that functional enhancers would be identified. As an additional stringency filter, we required that ci/GLI site clusters be present in orthologous regions of both Dp and Dm genomes (see Materials and Methods for details). Table S2.4 lists all selected Dm clusters with a CC greater than or equal to 4 (ranked by order of ci/GLI site density and average MSS). When we sorted these results by average MSS (high to low), to strengthen the likelihood that all of the ci/GLI sites located within any putative cluster were capable of binding ci/GLI, a known Hh-regulated enhancer of the *ptc* gene (Alexandre et al., 1996) appeared at the top of the list. In addition to this known enhancer region, we selected the next 16 putative Hh enhancer regions for functional validation (Table 2.1).

2.4.3 Functional Verification of ci/GLI-Driven Enhancers in a Chicken

Neural Tube Assay

We first screened for possible enhancer function of the 16 novel genomic regions (Table 2.1) in the developing chicken neural tube, one of the best-studied sites of Hh signaling (Dessaud et al., 2008). In this assay, Hamburger-Hamilton stage 11 embryos are electroporated with DNA reporter constructs in which the putative enhancer is cloned upstream of a minimal promoter driving EGFP expression (see Materials and Methods). This assay has been previously used to validate enhancers for multiple signaling pathways (Timmer et al., 2001; Uchikawa et al., 2003;

Lei et al., 2006; Lang et al., 2010; Wang et al., 2011; Oosterveen et al., 2012; Peterson et al., 2012; Vadasz et al., 2013). Endogenous Sonic Hedgehog (SHH) produced by the notochord and floorplate drives expression of Hh-dependent enhancers in the ventral half of the neural tube (Dessaud et al., 2008). Additionally, to further increase the sensitivity of our assay, we co-electroporated a constitutively active form of *Smoothened* (*SmoM2*) (Xie et al., 1998), which activates Hh signaling throughout the neural tube. Successful activation of Hh signaling by *SmoM2* is readily detectable as an expansion of the expression domain of the known Hh target gene, NKX6.1 (Oosterveen et al., 2012; Peterson et al., 2012), on the electroporated side of the neural tube. An RFP-expressing plasmid (pCIT) was co-electroporated to confirm the success of the electroporation. For those enhancers that demonstrated apparent Hh activation (expression of the enhancer-containing construct, but not the enhancer-less construct, in the presence of *SmoM2*), *ci*/GLI-dependent activity was further confirmed by mutagenesis of the *ci*/GLI binding sites.

Of the 16 computationally predicted enhancers tested in this way, four drove Hh-enhancer dependent expression in the chicken neural tube assay (Figure 2.2). An intronic sequence of the *invected* (*inv*) gene harbors two of these active regions, each containing a cluster of four *ci*/GLI sites with $MSS \geq 0.81$. Both regions drive expression in the presence of co-electroporated *SmoM2* and mutagenesis of the *ci*/GLI binding sites abrogates this response in both cases (Figure 2.2BC).

Two additional predicted enhancers, located near the genes *Cpr100A* and *Plc21C*, also showed expression in the chicken neural tube assay (Figure 2.2DE). However, mutation of the *ci*/GLI sites abrogated EGFP expression only in the putative *Cpr100A* enhancer (Figure 2.2D),

but not in the *Plc21C* enhancer (Figure 2.2E). Thus, only the former behaved as a direct Hh target; the *Plc21C* enhancer is responsive to Hh pathway activation, but this activity does not depend upon the ci/GLI binding sites. Thus, altogether, in addition to the top scoring, previously validated proximal *ptc* enhancer, three of the 16 novel predicted enhancers were validated by the chicken *in ovo* electroporation assay, for an overall success rate of 4/17 or 23%.

We next tested whether additional information would further improve prediction of Hh enhancers. We searched the list of clusters in Table S2.4 for regions that were annotated to known or suspected Hh target genes and tested five additional regions linked to *roadkill* (*rdx*) (Kent et al., 2006), *retinal homeobox* (*Rx*), *gooseberry* (*gsb*) (Li and Noll, 1993; Von Ohlen et al., 1997) and two additional regions of the *patched* receptor (*ptc*^{-2.8} and *ptc*^{+5.3}). Of these five cluster regions, only *rdx* tested positive in the chicken neural tube assay (Figure 2.2F), reflecting a similar 20% success rate.

To learn more about the sensitivity of the chicken neural tube assay, we also tested 18 clusters with ci/GLI sites of low MSS (0.75-0.8). These may represent clusters of sites of low affinity ci/GLI binding. The regions tested included the known enhancers regulating the *wingless* (*wg*) and *decapentaplegic* (*dpp*) loci (Table S2.5). However, none of these showed activity in the chicken neural tube.

Having identified two closely associated novel regions of the *inv* gene that both act as Hh enhancers in the chicken electroporation assay (Figure 2.2BC), we next utilized this assay to further examine these regions. While both enhancers respond to SmoM2 co-electroporation, only

one (*inv*^{+18.6}), drives EGFP expression in response to endogenous levels of Hh signaling (i.e. in the absence of *SmoM2* co-electroporation) (Figure 2.3).

Notably, though it is not in the top 16 predictions, Table S2.4 lists a third cluster in this region of the *inv* locus, lying between the two active regions tested above. Thus, we also tested a fragment spanning all three of these predicted *inv* ci/GLI clusters, containing a total of 12 ci/GLI binding sites (*inv*^{long}) (Figure 2.4A). This larger construct is activated both by endogenous SHH in the ventral neural tube and by co-electroporation of *SmoM2* (Figure 2.4B). Furthermore, a construct (*inv*^{long}-ciKO) containing mutations in 10 of the 12 ci/GLI binding sites identified computationally (only the two ci/GLI sites with lowest MSS were left intact) fails to activate EGFP expression, even when co-expressed with *SmoM2* (Figure 2.4C), confirming the Hh-dependent activity of this large complex enhancer. Further selective mutagenesis of ci/GLI sites within the larger fragment demonstrates that, in the absence of the *inv*^{+16.8} and *inv*^{+18.6} ci/GLI clusters, the central cluster of ci/GLI binding sites is unable to drive enhancer activity in the chicken neural tube (Construct D, Figure 2.4C).

2.4.4 Functional Verification of ci-Driven Enhancers in Transgenic

Drosophila

To further verify enhancer function in *Drosophila*, we generated transgenic reporter flies in which EGFP was driven by predicted enhancers and examined gene expression in two of the best-studied Hh-responsive contexts: the stage 9-13 embryo (when Hh signaling is active during development of a variety of tissues) and the anterior/posterior boundary of the larval wing imaginal disc (Alexandre et al., 1996; Ohlen and Hooper, 1997; Ramos and Barolo, 2013). The

top computational hit, upstream of the *ptc* gene (Table 2.1, Figure 2.5A) has three consensus ci/GLI binding sites and was previously shown to harbor enhancer activity (Alexandre et al., 1996). This conserved cluster was examined as a minimal fragment, (*ptc*^{-0.6}), which was able to respond to Hh signaling in the wing (Figure 2.5A). When the three consensus ci/GLI binding sites were mutated, enhancer activity was abrogated (Figure 2.5B), confirming that enhancer activity directly depends upon function of the ci/GLI binding motifs. This region was also found to have enhancer activity in a recent unbiased search for imaginal disc enhancers (Jory et al., 2012).

We next examined the other novel 16 top computationally predicted enhancers in *Drosophila* and found that three regions exhibited enhancer activity in the fly assay. Although *inv*^{+16.8} and *inv*^{+18.6} were both active in the chicken neural tube assay when co-electroporated with *SmoM2* (Figure 2.2BC), only *inv*^{+18.6} responded in the wing imaginal disc (Figure 2.5EG). This *inv*^{+18.6} enhancer was also the only enhancer to demonstrate positive activity in the chicken ventral neural tube in the absence of *SmoM2*, in response to endogenous Hh expression (Figure 2.3). When the four predicted ci/GLI binding sites with higher MSS were mutated in *inv*^{+18.6}, this enhancer was no longer able to respond to Hh signaling in the wing imaginal disc (Figure 2.5F), demonstrating its Hh-dependent activity. A larger construct (*inv*^{long}), encompassing the four ci/GLI sites in *inv*^{+16.8}, the four in *inv*^{+18.6}, and the intervening cluster of four predicted sites that was tested in the chicken assay in Figure 2.4A, was also able to drive expression in Hh-responsive cells of the wing imaginal discs of transgenic flies (Figure 2.5C). The *in vivo* activity of this genomic fragment depended on the predicted ci/GLI sites (Figure 2.5D), confirming it as a direct ci/GLI target enhancer.

In addition to confirming direct Hh-responsiveness of the *ptc* and *inv* enhancers, we also examined the other predicted enhancers in Table 2.1 in transgenic fly assays. Both *hth* and *Plc21C* showed enhancer activity in the transgenic fly assay, but neither was Hh-dependent (Figure S2.4). *Hth* exhibited a segmented expression pattern in the fly embryo, which remained unaltered after mutagenesis of the ci/GLI binding sites (Figure S2.3AB). *Plc21C* was expressed in the fly gut and expression persisted after mutation of the ci/GLI binding sites (Figure S2.3CD), consistent with the results in the chicken neural tube assay (Figure 2.2E).

Examination of the five additional ci/GLI clusters selected from known or suspected Hh target genes yielded four potential Hh-responsive enhancers: *rdx*, *ptc*^{-2.8}, *ptc*^{+5.3} and *gsb*. A ci/GLI cluster in the intron of *roadkill* (*rdx*) was active at the A/P boundary of the wing imaginal disc in Hh-responsive cells (Figure 2.5H). Mutating the predicted ci/GLI sites within this cluster abrogated its activity (Figure 2.5I). *Rdx* had previously been shown to be genetically downstream of Hh signaling (Kent et al., 2006), but the enhancer that mediates this response had not been identified. The *Rdx* enhancer identified here also responds to Hh in the chicken neural tube assay (Figure 2.2F).

Within the *ptc* locus, two other ci/GLI binding site clusters are computationally predicted in addition to the previously identified promoter-proximal enhancer that topped the list. The first of these, *ptc*^{-2.8}, is found 2.8 kb upstream of *ptc*, and contains 5 predicted ci/GLI binding sites. When examined in the wing imaginal disc, *ptc*^{-2.8} responds with a stripe of expression largely overlapping Ptc positive cells (Figure 2.5J). Upon mutation of the predicted ci/GLI binding sites in this novel enhancer, its ability to respond to Hh is greatly reduced (Figure 2.5K). A second cluster of ci/GLI sites in the first intron of *ptc* (*ptc*^{+5.3}) is also predicted. This putative enhancer

contains 7 predicted ci/GLI binding sites, one of which matches the optimal consensus site recognized by ci/GLI. In flies containing this transgene, *ptc*-like reporter gene expression is seen in the embryo (Figure 2.5L), but not the wing disc (data not shown). Two stripes of enhancer expression are detected, proximal to cells secreting Hh ligand, marked by *En*, in all segments of the embryonic ectoderm. After mutation of the predicted ci/GLI binding sites contained within this enhancer, the segmentally repeated stripes are lost (Figure 2.5M).

Finally, a region with several clusters of ci/GLI binding sites was identified downstream of the *gooseberry* (*gsb*) coding region. *Gooseberry*, a segment polarity gene, is part of the Hh-Wnt segmentation network, but no direct ci/GLI target enhancer has been identified (Li and Noll, 1993). The only known enhancer of *gsb*, which does not appear to be regulated by ci/GLI, is 5' of the gene (Bouchard et al., 2000). The 3' enhancer identified by our analysis contains five predicted ci/GLI binding sites and is active in segmental stripes in the embryonic ectoderm of transgenic *Drosophila*, posterior to each stripe of Hh-secreting cells at stage 11 (Figure 2.5N). Upon mutation of the ci/GLI binding sites, activity is attenuated, suggesting that the *gsb* enhancer requires direct ci/GLI input in order to respond to Hh signaling in the embryo (Figure 2.5O).

Overall, the fly assay functionally verified six Hh-dependent enhancers out of 22 tested, for a success rate of 27%. The genomic locations of these enhancers, relative to the gene locus, are presented in Figure 2.6. One additional enhancer, *Cpr100A*, was demonstrated to be Hh-dependent in the chicken, but had no activity in the fly assay; thus, it must be considered a potential regulatory element. This result suggested that *Cpr100A* might have been a false-negative in the fly assay, and prompted us to examine it, along with all of the other predicted

enhancers, in a third site of Hh signaling, the adult testis. Although the testis depends on Hh signaling, none of the predicted enhancers were active in this tissue. It is possible, however, that the *Cpr100A* cluster (or any other predicted enhancer that is negative in the chicken and/or fly assays) may be active in another tissue that was not examined (Michel et al., 2012). Altogether, both assays established 7/22 (31.8%) of tested ci/GLI clusters as Hh enhancers, six of which are novel (the potential *Cpr100A* element is not included in this count).

2.5 Discussion

Homotypic clustering of transcription factor binding sites has been observed in multiple settings and has been successfully used to identify potential enhancers (Markstein, 2001; Berman et al., 2002; Lifanov, 2003; Gotea et al., 2010; Suryamohan and Halfon, 2014). Since all but one of the known *Drosophila* Hh-driven enhancers contain two or more ci/GLI sites, we assessed the extent to which clustering of ci/GLI sites can be used to predict the location of Hh-dependent enhancers, a question that has not previously been directly tested. To do this, we utilized a background correction method that preserves local nucleotide topography to allow us to identify genomic regions that appear to have unusually dense ci/GLI binding site representation and tested the extent to which these regions can function as Hh-dependent enhancers.

To establish background genomes for comparison of GLI density, we used a strategy that randomly flips each base to its complementary partner. This approach maintains the GC/AT landscape of the native *Drosophila* chromosomes. Overall, only 43% of the *D. melanogaster* contains G or C bases while the consensus ci/GLI binding site itself is 67% GC rich (Hallikas et al., 2006; Keightley et al., 2009). Distribution of GC content has been strongly correlated with

gene density and other genomic features and the importance of maintaining the original properties of the native sequence when generating a background comparison has been discussed previously (Fitch, 1983). Other background generation methods that preserve dinucleotide frequencies also exist (Fitch, 1983; Coward, 1999). Additional comparisons would be needed to determine which background strategy best strengthens enhancer detection.

The success rate of functional enhancer identification based on the approach used here was 23%, suggesting that clustering of ci/GLI sites alone is not sufficient to effectively predict Hh-regulated enhancers. However, this success rate increased to 80% when examining ci/GLI clusters associated with known or suspected Hh target genes. Together, these data indicate that ci/GLI clustering is not, by itself, an effective means to predict Hh-regulated enhancers. While some Hh enhancers can be identified by virtue of ci/GLI homotypic clustering, not all homotypic clusters function as enhancers. Since one of the previously identified Hh enhancers (in *orthodenticle*) only has one ci/GLI site (Ramos and Barolo, 2013), it is also clear that the presence of clustered ci/GLI sites is not a requirement for functional Hh enhancers. However, in the context of additional information, clustering can be used as one criterion to predict enhancers within a suspected Hh target gene locus. Future studies will be necessary to determine whether the presence of multiple ci/GLI sites are more effective predictors of Hh-regulated enhancers associated with putative Hh target genes, or whether a single ci/GLI site is equally likely to drive Hh-dependent target gene expression. Given that ci/GLI binding site clustering alone is not sufficient to identify Hh-regulated enhancers, this raises the question: what is an effective method to identify Hh-regulated enhancers? One possibility is to pair ci/GLI binding sites with sites for other transcriptional co-activators or co-repressors. *De novo* motif analysis has been

performed previously as part of CHIP-chip analysis of GLI repressor binding in the developing limb (Vokes et al., 2008). More recent studies suggest that GLI proteins cooperate with SOXB1 proteins to drive Hh-regulated gene expression during spinal cord development (Oosterveen et al., 2012; Peterson et al., 2012). However, specific co-factor identification may yield only tissue-specific Hh-regulated enhancers. Thus, other approaches include: 1) examining ci/GLI binding site association with active or repressive chromatin modifications, which has been recently used to investigate Hh-regulated enhancers in the developing neural tube (Nishi et al., 2015), and 2) investigating ci/GLI binding site location near sites of open chromatin using techniques such as DNase I hypersensitivity and FAIRE (Giresi et al., 2007; McKay and Lieb, 2013). It is likely that a combination of these methods will be required to effectively identify a more complete set of Hh-regulated enhancers on a genome wide basis.

One intriguing finding from this work is the identification of multiple discrepancies between the chicken neural tube and transgenic fly assays (Table 2.1). These data emphasize the importance of testing putative enhancers in diverse assay systems to provide several different contexts in which an enhancer can show activity. The chicken neural tube assay is a quick and inexpensive strategy that, in a large-scale study, could improve throughput. It has been successfully used previously to identify Hh-regulated mouse enhancers (Oosterveen et al., 2012; Peterson et al., 2012), and is used here to validate Hh-regulated fly enhancers. However, because some enhancers may require additional species-specific information that is not present in the chicken neural tube, false negative calls are a limitation of this assay. Further, the requirement for context-specific information may also restrict the utility of this assay in the identification of general Hh-regulated enhancers (Vokes et al., 2007). Along these lines, analysis of 18 clusters

containing ci/GLI sites of lower predicted affinity, including the known Hh enhancers in the *wg* and *dpp* loci (Ohlen and Hooper, 1997; Müller and Basler, 2000), showed no activity in the chicken neural tube (Table S2.5). Thus, this assay may only detect Hh enhancers with high affinity ci/GLI binding sites, thereby missing some true positives (Ramos and Barolo, 2013). Nevertheless, the assay can be useful to dissect enhancer activity in the context of a complex developing tissue (Figure 2.4).

The computational study presented here can be compared with a recent analysis of potential ci/GLI-driven enhancers in *Drosophila*, by Biehs et al., who fused ci^{ACT} (activator) and ci^{REP} (repressor) proteins with DNA adenine methyltransferase (Dam) domains to define chromatin regions in stage 10-11 embryos that are occupied by ci/GLI *in vivo* (Biehs et al., 2010). That study listed 1743 sites bound by Dam-ci fusion proteins; of these, 55 sites (3%, listed in Table S2.6) were represented in clusters that were selected by our computational analysis. This limited overlap is likely due to two factors. First, since the computational study was limited to analysis of larger clusters, enhancers that are driven by one or two ci/GLI sites were not selected, by design. Second, because the DamID study was performed in 2-6 hour embryos, ci/GLI binding events were likely limited to chromatin regions that were accessible at that developmental stage. Of the seven previously known Hh/GLI-regulated enhancers, the DamID approach identified ci/GLI binding to two (*ptc* and *wg*), while the computational strategy described here detected three (*ptc*, *wg* and *knot*). The other four previously known enhancers (*stripe*, *hairy*, *dpp* and *orthodenticle*) were not detected computationally because those enhancers have only two ci/GLI sites (our filters selected clusters of 3-10). Of the new enhancers functionally confirmed in our study, none were found to harbor protected regions in the DamID

assay. Biehs et al. used expression assays to identify 147 genes whose expression appeared to correlate with Hh signaling activity. They then asked, of these 147 genes, how many had protected regions within or adjacent to the transcription unit? Protected regions were identified as DamAct or DamRep protection and consisted of a total 2108 protected regions. They identified 52 genomic regions that were DamID-protected and showed expression changes when Hh signaling was modulated. Thus, 35% of the genes that appear to be targets (as assessed by their expression modulation) showed some DamID protection, but only 2.5% of the total DamID protected regions were found to be probable Hh targets (Biehs et al., 2010). Four of these 52 can be found in the list of 55 sites common to the two studies.

An important aspect of the present study is that the direct Hh dependency of all enhancers was verified by *ci*/GLI binding site mutagenesis. While expression assays such as those used by Biehs et al. clearly demonstrate a Hh response, they do not establish whether this response is direct or indirect and do not confirm that the response is mediated through the *ci*/GLI binding sites in the candidate enhancers. Indeed, of the top 17 clusters detected computationally, we found four direct targets and two additional enhancers that showed apparent expression in *ptc*-expressing cells, but this expression persisted after mutation of the *ci*/GLI sites (Figure S2.4) suggesting that other factors might be responsible for this enhancer activity. This raises a cautionary note about assigning potential Hh, or any signaling cascade, responsiveness in the absence of functional verification (Halfon et al., 2011).

Using homotypic *ci*/GLI site clustering as a criterion together with functional analyses, we have doubled the number of previously verified *Drosophila* *ci*/GLI-dependent enhancers, including multiple distinct enhancers that regulate a single Hh-responsive gene (i.e., *ptc*, *inv*, and

gsb). Further testing of other candidate clusters identified in this study might further enlarge the pool of known Hh-responsive enhancers that are active in diverse tissues and organs, providing a robust substrate for the future dissection of the rules that underlie context-specific enhancer function.

2.6 Acknowledgements

The NKX6.1 antibody was obtained from the Developmental Studies Hybridoma Bank developed under the auspices of the NICHD and maintained by The University of Iowa, Department of Biological Sciences, Iowa City, IA. Confocal microscopy was performed in the Microscopy and Image Analysis Laboratory at the University of Michigan. Sequencing of enhancer constructs was performed at the University of Michigan Sequencing Core. The authors would like to thank Dr. Mark Rebeiz for generously sharing scripts and Dr. William J. Zacharias for helpful discussions.

2.7 Authors' contributions

KG, AU and DG conceived and designed the computational methods. Biological experiments were devised by SB, BA, DL and JS. KG, DL, JS, NR, DP, LJ and AU performed the experiments and analyzed the data. The paper was written by KG, DL, JS, AU and senior authors DG, SB, and BA.

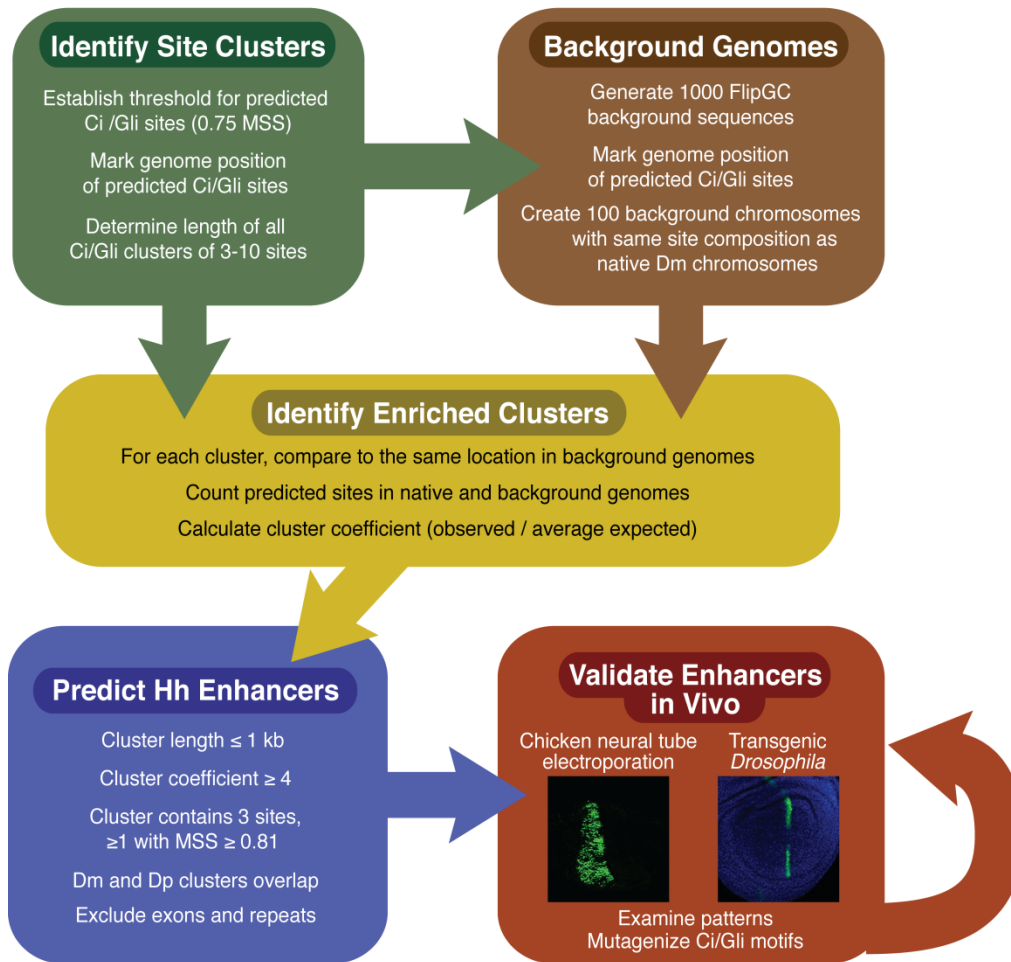


Figure 2.1. Pipeline for detection and validation of Hh-responsive enhancers. ci/GLI cluster identification and background genome generation were performed as outlined in Figure S2.2. The cluster (CC) for a given genomic region was calculated as the total number of sites observed in the Dm or Dp genome (observed) divided by the average number of sites per background genome for that species (expected). Clusters of ci/GLI sites with a (CC) ≥ 4 were further filtered as follows: a) Clusters were required to contain at least one ci/GLI site of ≥ 0.81 MSS; b) Dm Clusters were required to overlap in position (but not sequence) with a cluster in Dp; c) Clusters in exon or repeat regions were excluded. The entire table of selected clusters, sorted by chromosomal location, is provided in Table S2.4. The list of clusters was then ranked by average MSS of the predicted ci/GLI sites and the top 17 were examined functionally (these included 16 novel hits and one known enhancer, *ptc*^{-0.6}). The Hh-responsive enhancer activity of genomic regions containing selected clusters was functionally evaluated by means of a transgenic fly assay as well as by chicken neural tube electroporation. For genomic regions that showed apparent Hh responsiveness, ci/GLI sites were mutated and re-assayed to confirm direct ci/GLI regulation.

Annotated Gene	Genomic coordinates (dm3)	Number of ci/GLI Sites	Average MSS	Hh Responsive in Chicken Neural Tube	Hh Responsive in Transgenic Fly
<i>ptc</i> ^{-0.6}	chr2R:4536264-4536572	3	1.000	+	+
<i>inv</i> ^{+16.8}	chr2R:7378801-7380000	4	0.941	+	-
<i>Sox100B</i>	chr3R:26894840-26896225	3	0.920	-	-
<i>inv</i> ^{+18.6}	chr2R:7380576-7381900	4	0.903	+	+
<i>beat-IV</i>	chr3R:19385801-19387033	5	0.899	-	-
<i>CG6475</i>	chr3R:17227902-17229095	4	0.898	-	-
<i>CG34139</i>	chr3R:16067525-16068300	3	0.893	-	-
<i>Plc21C</i>	chr2L:308225-309200	4	0.892	-	-
<i>CG4704</i>	chr3R:18671231-18671930	3	0.891	-	-
<i>Bi</i>	chrX:4316001-4317440	4	0.886	-	-
<i>HGTX</i>	chr3L:14583895-14584670	4	0.886	-	-
<i>Cpr100A</i>	chr3R:26692110-26692580	3	0.886	+	-
<i>Ets21C</i>	chr2L:550010-551035	4	0.885	-	-
<i>CG12541</i>	chrX:6927600-6928375	5	0.884	-	-
<i>Sp1</i>	chrX:9613671-9614922	4	0.881	-	-
<i>Hth</i>	chr3R:6433650-6434996	5	0.879	-	-
<i>Ko</i>	chr3L:21072420-21073658	3	0.879	-	-
<i>ptc</i> ^{+5.3}	chr2R:4542467-4545417	7	0.875	-	+
<i>ptc</i> ^{-2.8}	chr2R:4531601-4534319	5	0.847	-	+
<i>Rx</i>	chr2R:16820211-16822050	5	0.845	-	-
<i>Rdx</i>	chr3R:9815295-9817061	3	0.838	+	+
<i>Gsb</i>	chr2R:20952400-20953750	7	0.834	-	+

Table 2.1. Assessment of Hh response. The chicken neural tube (CNT) and transgenic fly (TF) assays together identified eight predicted regions as Hh-responsive. Both assays showed positive Hh activity for *inv*^{+18.6} and *rdx* as well as the previously identified *ptc* enhancer region. Five additional regions were positive in only one assay: CNT: *Cpr100A* and *inv*^{+16.8}; TF: *gsb* and two *ptc* additional genomic regions (*ptc*^{+5.3} and *ptc*^{-2.8}). All enhancer regions were verified by mutagenesis to be ci/GLI binding site dependent.

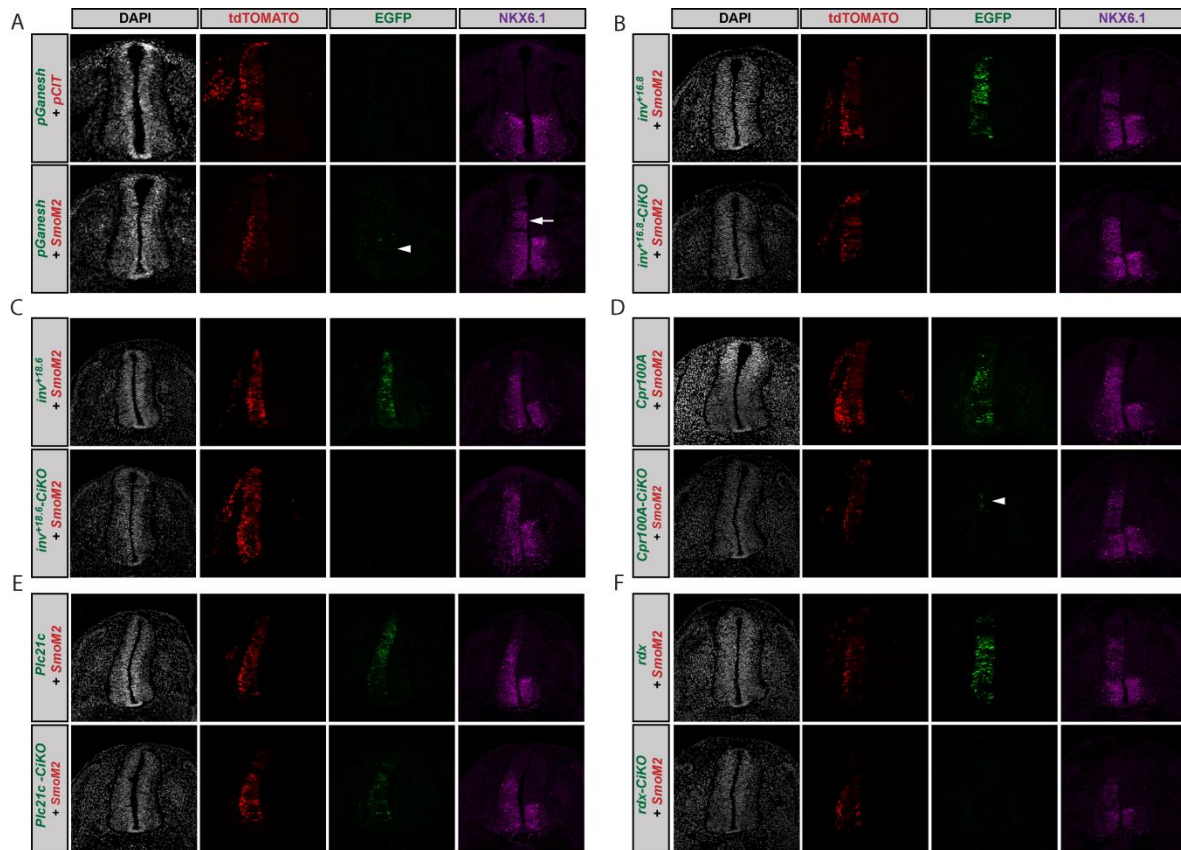


Figure 2.2. Validation of predicted Hh-responsive enhancers in the chicken neural tube.

Transverse sections of Hamburger-Hamilton stage 21-22 chicken embryos are shown. DAPI (grayscale, far left column) depicts nuclei. tdTOMATO (red, middle left column) marks cells electroporated with pCIT or *SmoM2*. GFP (green, middle right column) reports enhancer activation. Anti-NKX6.1 antibody staining (magenta, far right column) denotes Hh-responsive cells. (A) Chicken embryos co-electroporated with an enhancer less pGanesh construct (containing only an Hsp70 minimal promoter) and either pCIT or a constitutively active *SmoM2*. An arrowhead (middle right column; bottom row) depicts a few GFP positive cells in pGanesh electroporated embryos. Note the ectopic NKX6.1 expression (far right column) indicative of overactive Hh signaling in electroporated cells (white arrow). (B-E) Candidate Hh-responsive *inv*^{+16.8} (B top row), *inv*^{+18.6} (C top row), *Cpr100A* (D top row), and *Plc21C* (E top row) constructs all exhibit GFP expression in cells in which Hh is activated by co-electroporation of *SmoM2*. However, chicken embryos co-electroporated with *SmoM2* in combination with a ci/GLI-binding deficient mutant (ciKO) of each candidate (bottom rows) show a complete absence of GFP expression in the case of *inv*^{+16.8}-ciKO (B) and *inv*^{+18.6}-ciKO (C), despite ectopic NKX6.1 expression in both conditions (far right column). *Cpr100A*-ciKO (D) has a greatly diminished expression pattern with only a few GFP positive cells (white arrowhead) remaining (middle right column; bottom row). *Plc21C*-ciKO (E) does not show loss of GFP expression, indicating that it is not a direct Hh target, since its response to Hh signaling is not ci/GLI dependent. *Rdx* (F top row) GFP expression corresponds to Hh expressing cells and shows no expression once ci/GLI sites are mutated (*rdx*-ciKO bottom row).

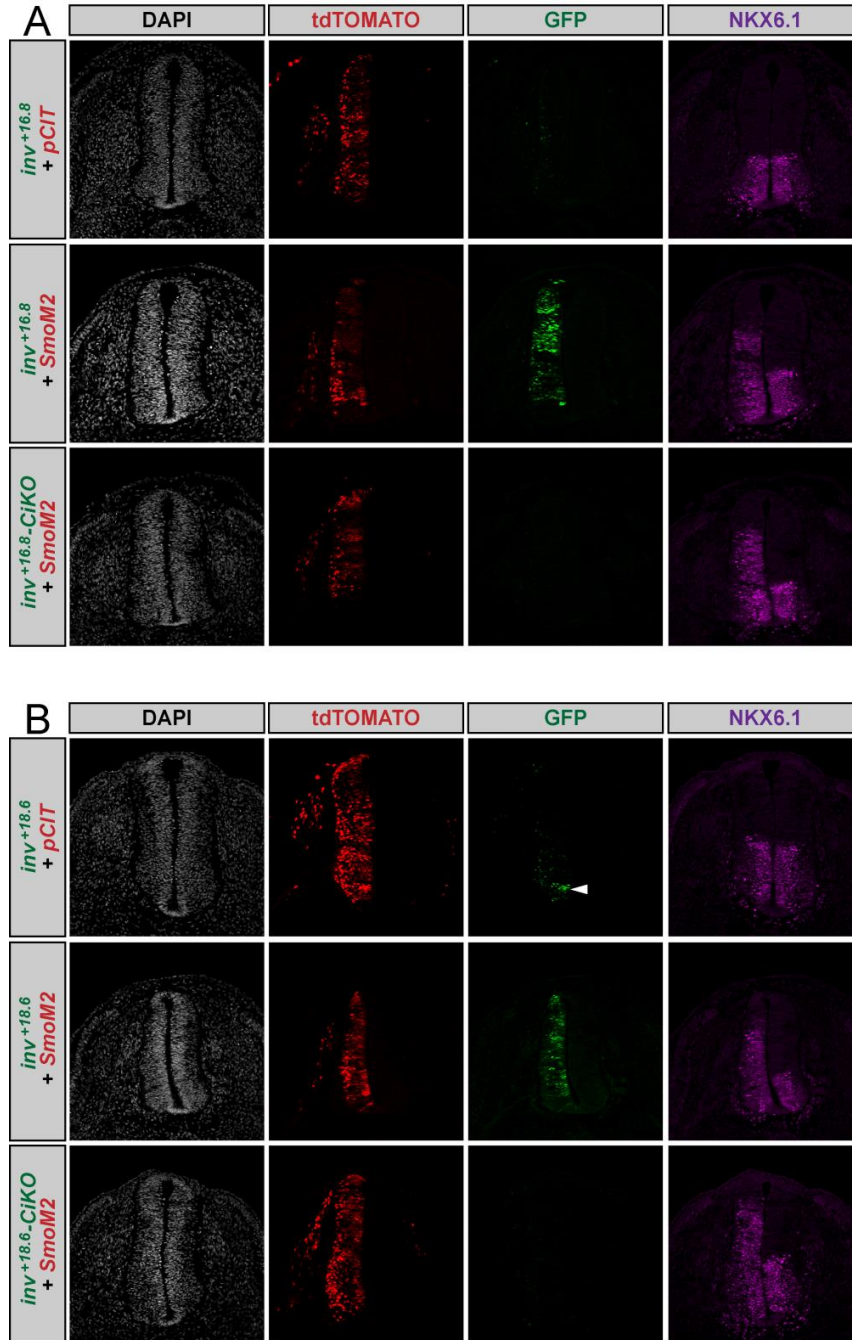


Figure 2.3. Endogenous expression of *inv*^{+16.8} and *inv*^{+18.6} in the chicken neural tube. Transverse sections of Hamburger-Hamilton stage 21-22 chicken embryos are shown. DAPI (grayscale, far left column) depicts nuclei. tdTOMATO (red, middle left column) marks cells electroporated with pCIT. GFP (green, middle right column) reports enhancer activation. Anti-NKX6.1 antibody staining (magenta, far right column) denotes Hh-responsive cells. (A) Chicken embryos electroporated with *inv*^{+16.8} show no GFP expression in the chicken neural tube. (B) Chicken embryos electroporated with *inv*^{+18.6} exhibit GFP expression (white arrowhead).

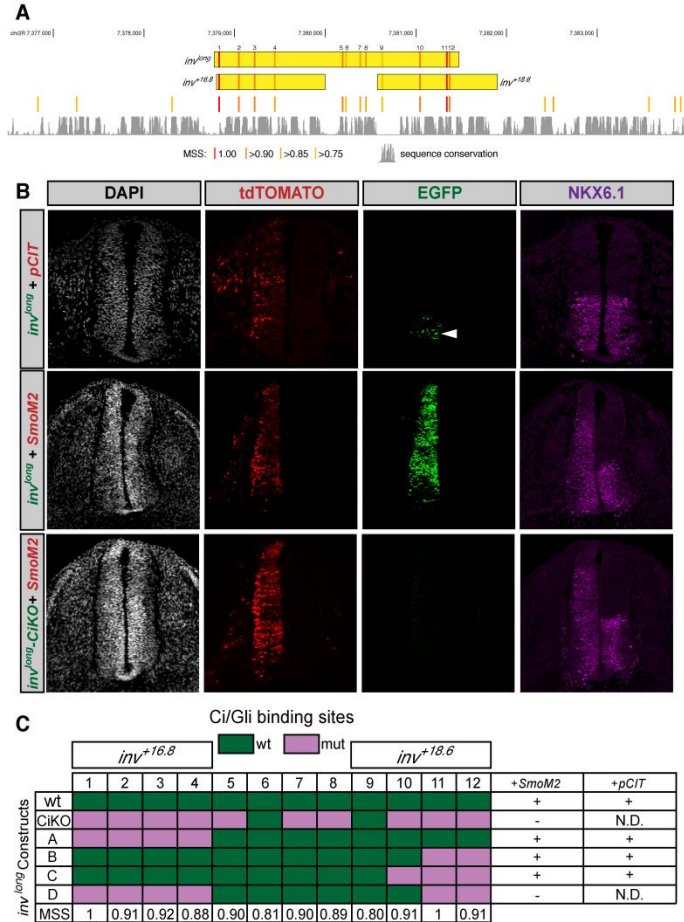


Figure 2.4. Expression of a complex *inv* enhancer in the chicken neural tube and *Drosophila* wing imaginal disc.

(A) Genomic landscape of the *inv* locus depicting the *inv^{long}*, *inv^{+16.8}* and *inv^{+18.6}* constructs. ci/GLI binding sites are shown as red/orange bars; the intensity of red coloration indicates the MSS. Sequence conservation is indicated by the track at bottom of the panel. (B) Transverse sections of Hamburger-Hamilton stage 21-22 chicken embryos are shown as in Figure 2.5. DAPI (gray, far left column) depicts nuclei. tdTOMATO (red, middle left column) marks cells electroporated with pCIT or *SmoM2*. GFP (green, middle right column) reports enhancer activation. Anti-NKX6.1 antibody staining (magenta, far right column) marks Hh-responsive cells. The *inv^{long}* (top row) enhancer demonstrates GFP expression in the ventral neural tube (white arrowhead). The expression of *inv^{long}* is strengthened and broadened with co-electroporation of *SmoM2* (middle row). Mutagenesis of ci/GLI binding sites demonstrates that enhancer activity is ci/GLI dependent (bottom row). (C) Tabulation of activity in the chicken neural tube of *inv^{long}* constructs containing different ci/GLI site compositions. Green boxes indicate wild type ci/GLI sequences; purple boxes indicate mutated ci/GLI sites. Constructs that have functional ci/GLI sites that correspond to *inv^{+18.6}* (Construct A) or *inv^{+16.8}* (Construct B and C) exhibit GFP expression in the neural tube. However, the central ci/GLI binding sites are insufficient to drive enhancer activity alone (construct D).

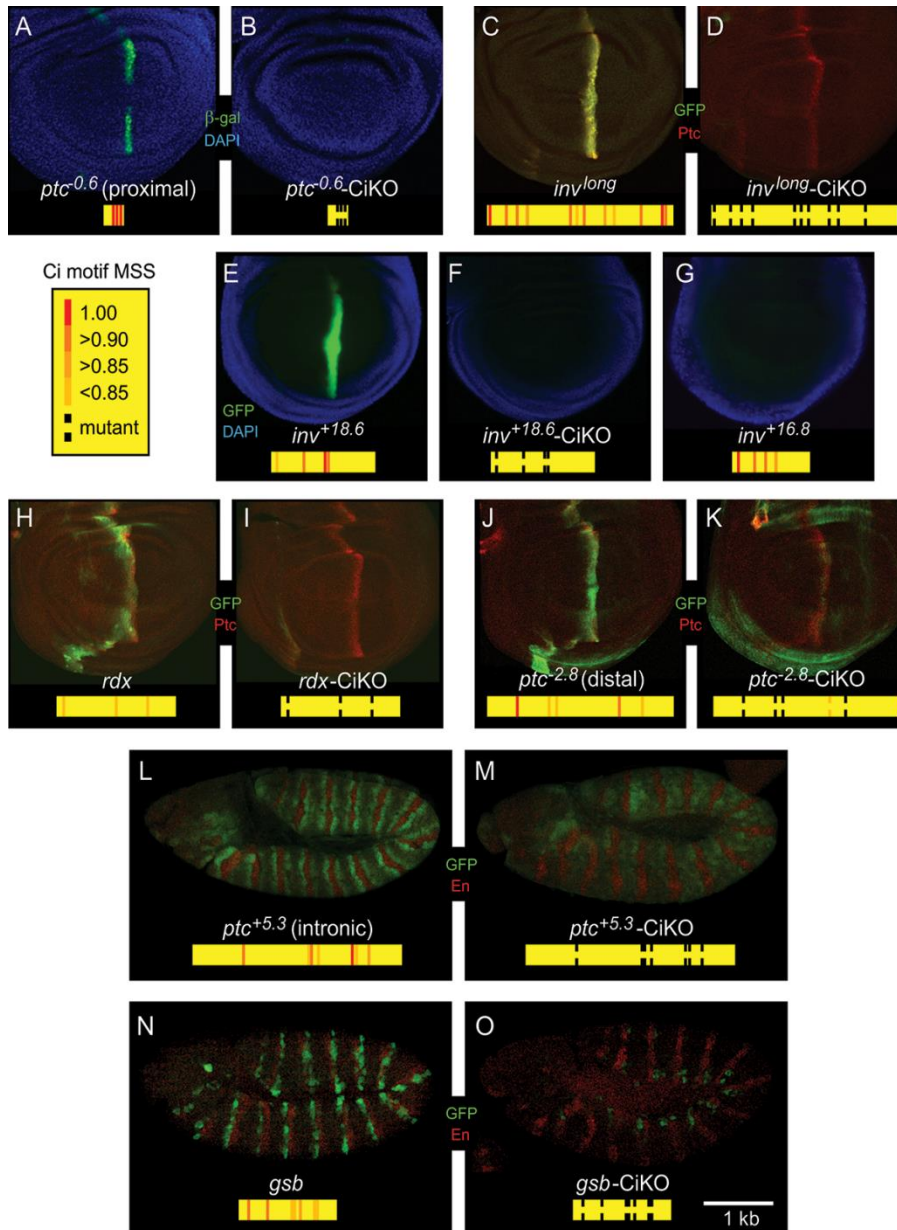


Figure 2.5. Novel enhancers directly respond to Hh signaling in the wing imaginal disc and embryo. (A-K) β -galactosidase or GFP marks the expression of enhancers in the pouch of the wing imaginal disc. A diagram of the fragments tested and location and MSS for all ci/GLI sites is shown for each candidate (yellow rectangles). Each wild type enhancer responds to Hh signaling along the anterior-posterior compartment boundary of the wing disc, with the exception of $inv^{+16.8}$ (G). Active enhancers lose Hh responsiveness in the wing imaginal disc when predicted ci/GLI binding sites are mutated, as shown in the right of each panel. (L-O) GFP marks the expression of the noted enhancers in the embryo. *En* expression (red) marks cells producing Hh ligand. When the predicted ci/GLI binding sites in these enhancers are mutated (M-O), activity in Hh-responsive cells is severely reduced.

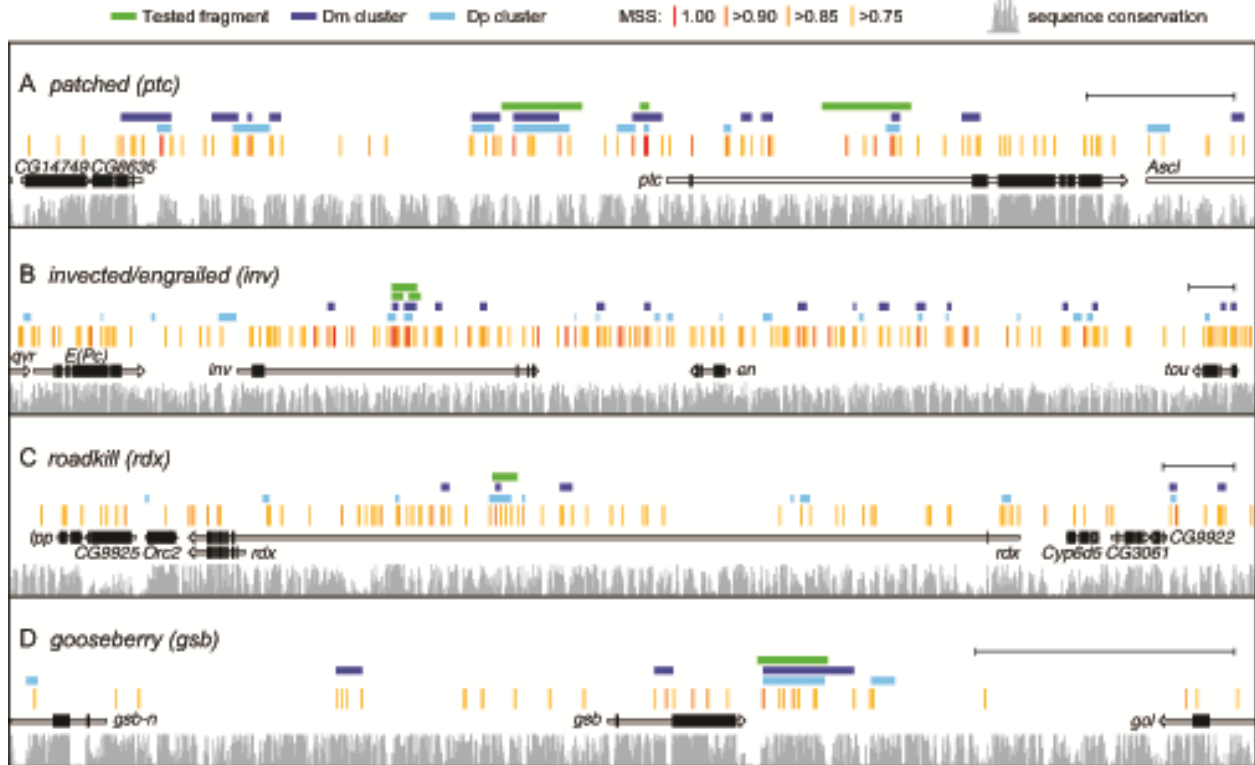


Figure 2.6. Mapping six Hh regulated enhancers in four genetic loci.

(A-D) Genomic landscape of the *ptc*, *inv*, *rdx* and *gsb* loci with fragments tested marked by green bars. All predicted ci/GLI binding sites are highlighted (red/orange tick marks, annotated according to MSS, as noted at top of Figure). The sequence conservation track (gray bars) marks conservation among the 12 sequenced *Drosophila* species, whereas the dark and light blue bars represent clusters of predicted ci/GLI binding sites in Dm and Dp, respectively. Black brackets at right indicate 5Kb.

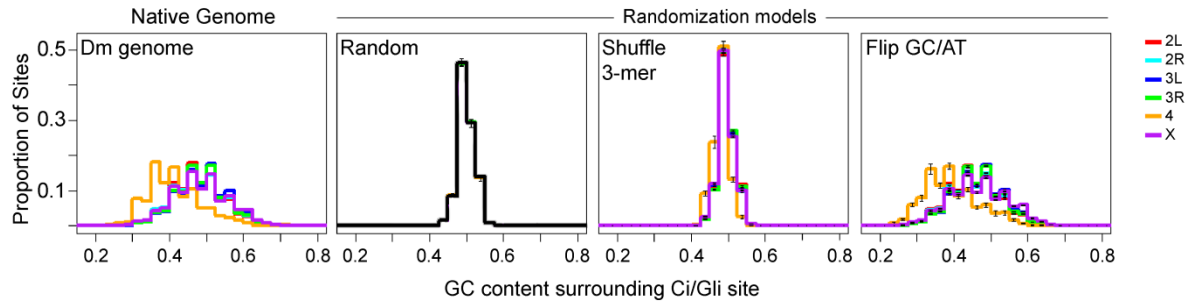


Figure S2.1. Assessment of GC content surrounding ci/GLI sites in the *Drosophila melanogaster* genome.

Forward	Reverse	Matrix Similarity Score (MSS)
GACCACCCA	TGGGTGGTC	1
GACCCCCA	TGGGGGGTC	0.918
GACCTCCA	TGGGAGGTC	0.916
GGCCACCCA	TGGGTGGCC	0.915
GCCACCCA	TGGGTGGGC	0.915
GACCGCCA	TGGGCGGTC	0.914
GTCCACCCA	TGGGTGGAC	0.91
GACCACACA	TGTGTGGTC	0.907
GACCACGCA	TGCGTGGTC	0.899
GACCACTCA	TGAGTGGTC	0.899
GACCACCTA	TAGGTGGTC	0.897
GACCACCAA	TTGGTGGTC	0.897
GACCACCGA	TCGGTGGTC	0.895
GACCACCCC	GGGGTGGTC	0.889
GACCACCCCT	AGGGTGGTC	0.889
GACCACCCG	CGGGTGGTC	0.888
AACCACCCA	TGGGTGGTT	0.882
TACCACCCA	TGGGTGGTA	0.882
CACCACCCA	TGGGTGGTG	0.881
GAACACCCA	TGGGTGTTT	0.879
GAGCACCCA	TGGGTGCTC	0.878
GATCACCCA	TGGGTGATC	0.878
GCCCCCCA	TGGGGGGGC	0.833
GGCCCCCA	TGGGGGGCC	0.833
GGCCTCCA	TGGGAGGCC	0.831
GCCCTCCA	TGGGAGGGC	0.831
GTCCCCCA	TGGGGGGAC	0.829
GGCCGCCA	TGGGCGGCC	0.829
GCCCGCCA	TGGGCGGGC	0.828
GTCCTCCA	TGGGAGGAC	0.826
GACCCACA	TGTGGGGTC	0.825
GTCCGCCA	TGGGCGGAC	0.824
GACCTACA	TGTGAGGTC	0.823
GGCCACACA	TGTGTGGCC	0.822
GCCACACA	TGTGTGGGC	0.822
GACCGACA	TGTGCGGTC	0.82
GTCCACACA	TGTGTGGAC	0.817

Forward	Reverse	Matrix Similarity Score (MSS)
GACCCCGCA	TGCGGGGTC	0.817
GACCCCTCA	TGAGGGGTC	0.817
GACCTCGCA	TGCGAGGTC	0.815
GACCCCTA	TAGGGGGTC	0.815
GACCCCAA	TTGGGGGTC	0.815
GACCTCTCA	TGAGAGGTC	0.815
GGCCACGCA	TGCGTGGCC	0.814
GGCCACTCA	TGAGTGGCC	0.814
GCCACGCA	TGCGTGGGC	0.814
GCCCACTCA	TGAGTGGGC	0.814
GACCCCGA	TCGGGGGTC	0.814
GACCTCCTA	TAGGAGGTC	0.813
GACCTCAA	TTGGAGGTC	0.813
GACCGCGCA	TGCGCGGTC	0.812
GGCCACCTA	TAGGTGGCC	0.812
GGCCACCAA	TTGGTGGCC	0.812
GCCACCTA	TAGGTGGGC	0.812
GCCACCAA	TTGGTGGGC	0.812
GACCGCTCA	TGAGCGGTC	0.812
GACCTCCGA	TCGGAGGTC	0.811
GGCCACCGA	TCGGTGGCC	0.81
GCCACCGA	TCGGTGGGC	0.81
GACCGCCTA	TAGGCGGTC	0.81
GACCGCAA	TTGGCGGTC	0.81
GTCCACGCA	TGCGTGGAC	0.809
GTCCACTCA	TGAGTGGAC	0.809
GACCGCCGA	TCGGCGGTC	0.809
GTCCACCTA	TAGGTGGAC	0.807
GTCCACCAA	TTGGTGGAC	0.807
GACCCCCC	GGGGGGGTC	0.807
GACCCCCCT	AGGGGGGTC	0.807
GACCCCCG	CGGGGGGTC	0.806
GTCCACCGA	TCGGTGGAC	0.805
GACCTCCCC	GGGGAGGTC	0.805
GACCTCCCT	AGGGAGGTC	0.805
GGCCACCCC	GGGGTGGCC	0.804
GGCCACCCT	AGGGTGGCC	0.804

Forward	Reverse	Matrix Similarity Score (MSS)
GCCCACCCC	GGGGTGGGC	0.804
GCCCACCCT	AGGGTGGGC	0.804
GACCACATA	TATGTGGTC	0.804
GACCTCCCG	CGGGAGGTC	0.804
GGCCACCCG	CGGGTGGCC	0.803
GCCCACCCG	CGGGTGGGC	0.803
GACCACAAA	TTTGTGGTC	0.803
GACCACAGA	TCTGTGGTC	0.802
GACCGCCCC	GGGGCGGTC	0.802
GACCGCCCT	AGGGCGGTC	0.802
AACCCCCCA	TGGGGGGTT	0.801
GACCGCCCG	CGGGCGGTC	0.801
TACCCCCCA	TGGGGGGTA	0.8
GTCCACCCC	GGGGTGGAC	0.799
GTCCACCCT	AGGGTGGAC	0.799
CACCCCCCA	TGGGGGGTG	0.799
AACCTCCCA	TGGGAGGTT	0.798
GTCCACCCG	CGGGTGGAC	0.798
GAACCCCCA	TGGGGGGTTC	0.798
TACCTCCCA	TGGGAGGTA	0.798
AGCCACCCA	TGGGTGGCT	0.797
ACCCACCCA	TGGGTGGGT	0.797
CACCTCCCA	TGGGAGGTG	0.797
GATCCCCCA	TGGGGGATC	0.797
TGCCACCCA	TGGGTGGCA	0.797
TCCCACCCA	TGGGTGGGA	0.797
GAACTCCCA	TGGGAGTTC	0.796
AACCGCCCA	TGGGCGGTT	0.796
CGCCACCCA	TGGGTGGCG	0.796
CCCCACCCA	TGGGTGGGG	0.796
GAGCCCCCA	TGGGGGCTC	0.796
TACCGCCCA	TGGGCGGTA	0.796
CACCGCCCA	TGGGCGGTG	0.795
GACCACACC	GGTGTGGTC	0.795
GACCACACG	CGTGTGGTC	0.795
GACCACACT	AGTGTGGTC	0.795
GACCACGAA	TTCGTGGTC	0.795

Forward	Reverse	Matrix Similarity Score (MSS)
GACCACTAA	TTAGTGGTC	0.795
GACCACGTA	TACGTGGTC	0.795
GACCACTTA	TAAGTGGTC	0.795
GATCTCCCA	TGGGAGATC	0.794
GAGCTCCCA	TGGGAGCTC	0.794
GGACACCCA	TGGGTGTCC	0.794
GCACACCCA	TGGGTGTGC	0.794
GACCACGGA	TCCGTGGTC	0.794
GACCACTGA	TCAGTGGTC	0.794
GAACGCCCA	TGGGCGTTC	0.793
GGGCACCCA	TGGGTGCC	0.793
GGTCACCCA	TGGGTGACC	0.793
GCGCACCCA	TGGGTGCGC	0.793
GCTCACCCA	TGGGTGAGC	0.793
GATCGCCCA	TGGGCGATC	0.792
ATCCACCCA	TGGGTGGAT	0.792
TTCCACCCA	TGGGTGGAA	0.792
GAGCGCCCA	TGGGCGCTC	0.791
CTCCACCCA	TGGGTGGAG	0.791
GTACACCCA	TGGGTGTAC	0.79
AACCACACA	TGTGTGGTT	0.789
TACCACACA	TGTGTGGTA	0.789
CACCACACA	TGTGTGGTG	0.788
GTGCACCCA	TGGGTGCAC	0.788
GTTCACCCA	TGGGTGAAC	0.788
GACCACGCC	GGCGTGGTC	0.787
GACCACGCT	AGCGTGGTC	0.787
GACCACTCC	GGAGTGGTC	0.787
GACCACTCT	AGAGTGGTC	0.787
GAACACACA	TGTGTGTTC	0.786
GACCACGCG	CGCGTGGTC	0.786
GACCACTCG	CGAGTGGTC	0.786
GACCACCTG	CAGGTGGTC	0.785
GACCACCAC	GTGGTGGTC	0.785
GACCACCAT	ATGGTGGTC	0.785
GAGCACACA	TGTGTGCTC	0.785
GATCACACA	TGTGTGATC	0.785

Forward	Reverse	Matrix Similarity Score (MSS)	Forward	Reverse	Matrix Similarity Score (MSS)
GACCACCTC	GAGGTGGTC	0.785	GATCACCTA	TAGGTGATC	0.775
GACCACCTT	AAGGTGGTC	0.785	GATCACCAA	TTGGTGATC	0.775
GACCACCGC	GCGGTGGTC	0.784	GAGCACCGA	TCGGTGCTC	0.773
GACCACCGT	ACGGTGGTC	0.784	GATCACCGA	TCGGTGATC	0.773
GACCACCAG	CTGGTGGTC	0.784	AACCACCCC	GGGGTGGTT	0.771
GACCACCGG	CCGGTGGTC	0.783	AACCACCTT	AGGGTGGTT	0.771
AACCACGCA	TGCGTGGTT	0.781	TACCACCCC	GGGGTGGTA	0.771
AACCACCTA	TGAGTGGTT	0.781	TACCACCTT	AGGGTGGTA	0.771
TACCACGCA	TGCGTGGTA	0.781	AACCACCCG	CGGGTGGTT	0.77
TACCACCTA	TGAGTGGTA	0.781	CACCACCCC	GGGGTGGTG	0.77
CACCACGCA	TGCGTGGTG	0.78	CACCACCTT	AGGGTGGTG	0.77
CACCACCTA	TGAGTGGTG	0.78	TACCACCCG	CGGGTGGTA	0.77
AACCACCTA	TAGGTGGTT	0.779	CACCACCCG	CGGGTGGTG	0.769
AACCACCAA	TTGGTGGTT	0.779	GAACACCCC	GGGGTGTTT	0.768
TACCACCTA	TAGGTGGTA	0.779	GAACACCTT	AGGGTGTTT	0.768
TACCACCAA	TTGGTGGTA	0.779	GAACACCCG	CGGGTGTTT	0.767
GAACACGCA	TGCGTGTTT	0.778	GATCACCCC	GGGGTGATC	0.767
CACCACCTA	TAGGTGGTG	0.778	GATCACCTT	AGGGTGATC	0.767
CACCACCAA	TTGGTGGTG	0.778	GAGCACCCG	CGGGTGCTC	0.766
GAACACTCA	TGAGTGTTT	0.778	GATCACCCG	CGGGTGATC	0.766
GATCACGCA	TGCGTGATC	0.777	GAGCACCCC	GGGGTGCTC	0.766
GAGCACGCA	TGCGTGCTC	0.777	GAGCACCTT	AGGGTGCTC	0.766
AACCACCGA	TCGGTGGTT	0.777	AAACACCCA	TGGGTGTTT	0.762
GAGCACTCA	TGAGTGCTC	0.777	TAACACCCA	TGGGTGTTA	0.761
GATCACTCA	TGAGTGATC	0.777	AAGCACCCA	TGGGTGCTT	0.76
TACCACCGA	TCGGTGGTA	0.777	AATCACCCA	TGGGTGATT	0.76
CACCACCGA	TCGGTGGTG	0.776	CAACACCCA	TGGGTGTTG	0.76
GAACACCTA	TAGGTGTTT	0.776	TAGCACCCA	TGGGTGCTA	0.76
GAACACCAA	TTGGTGTTT	0.776	TATCACCCA	TGGGTGATA	0.76
GAACACCGA	TCGGTGTTT	0.775	CAGCACCCA	TGGGTGCTG	0.759
GAGCACCTA	TAGGTGCTC	0.775	CATCACCCA	TGGGTGATG	0.759
GAGCACCAA	TTGGTGCTC	0.775			

Table S2.1. 9-mers with a minimum level (≥ 0.75) ci matrix similarity score.

Annotation	Forward primer	Reverse primer	Genomic coordinates (dm3)
<i>ptc -0.6</i>	CACCGGCGGCCATGCATGCGCA GCCTGCCAC	GTACCGGGTTTCTATTGTTATTC GCATG	chr2R:4536264-4536572
<i>inv +16.8</i>	CACCTGATATCTTAGGTTAGTAGT AT	AATCTAATTTTGCCCTGATATT	chr2R:7378801-7380000
<i>Sox100B</i>	CACCTAAGCTCGGGATATTTGCC	AGCTTAGAGGTCCTGCATAG	chr3R:26894840-26896225
<i>inv +18.6</i>	CACCTATGTTATAAAAATTTGTAAT AT	TTTGTTTATACTGTCTAACAAA	chr2R:7380576-7381900
<i>beat-IV</i>	CACCGTTTTTTTGCATTTACC	AAACTACACGGCTGCCCTG	chr3R:19385801-19387033
<i>CG6475</i>	CACCGACCACACAACAGACGC	TACTTGAGCACCCGATTGG	chr3R:17227902-17229095
<i>CG34139</i>	CACCTTTTCGTTTTATGTTAACG	TTGTTTTTTTCTTTTCGCTGTGCG	chr3R:16067525-16068300
<i>Plc21C</i>	CACCTCGTTATGATGTGCCTTAAA AG	AAAATATTAACGCGAAATAGG	chr2L:308225-309200
<i>CG4704</i>	CACCGTCATATTAGGCTATTTT	CATTTTATTAGCCGAATGC	chr3R:18671231-18671930
<i>bi</i>	CACCGAGAGGGAGCGAGTGAGTA AG	TGAGGCAATCGATAAAAATTAGC	chrX:4316001-4317440
<i>HGTX</i>	CACCTGCAGCCGCTTAATAATTCC	AGTGCCGTGCTTAACCCG	chr3L:14583895-14584670
<i>Cpr100A</i>	CACCATAATGCCAAAAGTCTCTG	TGCTTTTTTGATTTTCCAGTG	chr3R:26692110-26692580
<i>Ets21C</i>	CACCGTTTGTACCCTGTAAAGGG	ACTTAAACGGAGCCACATTTTCT C	chr2L:550010-551035
<i>CG12541</i>	CACCGACAAGAAGCATACCAAA G	ACTATTAGCTACATTTTCTCC	chrX:6927600-6928375
<i>Sp1</i>	CACCTTCGCCGTGTGTATGTATTA GC	TATCAACGGAAATTCATTAC	chrX:9613671-9614922
<i>hth</i>	CACCTAAAGCCGAAAGCCTAAAA TAG	TTTGCTTGTATTTCCGAAC	chr3R:6433650-6434996
<i>ko</i>	CACCAGGAGACAGGTGGTATGGT C	ATTCACAGTGTAATTTACAGC	chr3L:21072420-21073658
<i>ptc +5.3</i>	CACCGGCGGCCGAAGTGCTTAA CAAGTTAAC	GTACCGGGCAGCACACCAATG AGATCG	chr2R:4542467-4545417
<i>ptc -2.8</i>	CACCGGCGGCCTACGTACTCTTA TTACTCCACTC	GTACCGGGGCTATTGCATTTGTC ATTGGC	chr2R:4531601-4534319
<i>Rx</i>	CACCACTCCTTCCCCGACTTAC	GTTTAAACCGAAAAACGTTTAATT TAATCTGG	chr2R:16820211-16822050
<i>Rdx</i>	CACCTTTAGCCAGGTGTGGATTGT G	CCAGCGAAAGCAAACAGAGTAC	chr3R:9815295-9817061
<i>Gsb</i>	CACCGCGAGTCAAACCTATTCCGT G	AAGTGACGGTGAATTC	chr2R:20952400-20953750

Table S2.2. PCR primers used to amplify genomic DNA from the *D. melanogaster* genome (build Dm3).

	2L	2R	3L	3R	4	X
MSS \geq .81	8156	8029	8671	10381	268	8887
MSS \geq .75	30637	30186	33098	38723	1279	33310
Chromosome length (bp)	23,011,544	21,146,708	24,543,557	27,905,053	1,351,857	22,422,827

Table S2.3. Distribution of predicted ci/GLI sites across chromosomes.

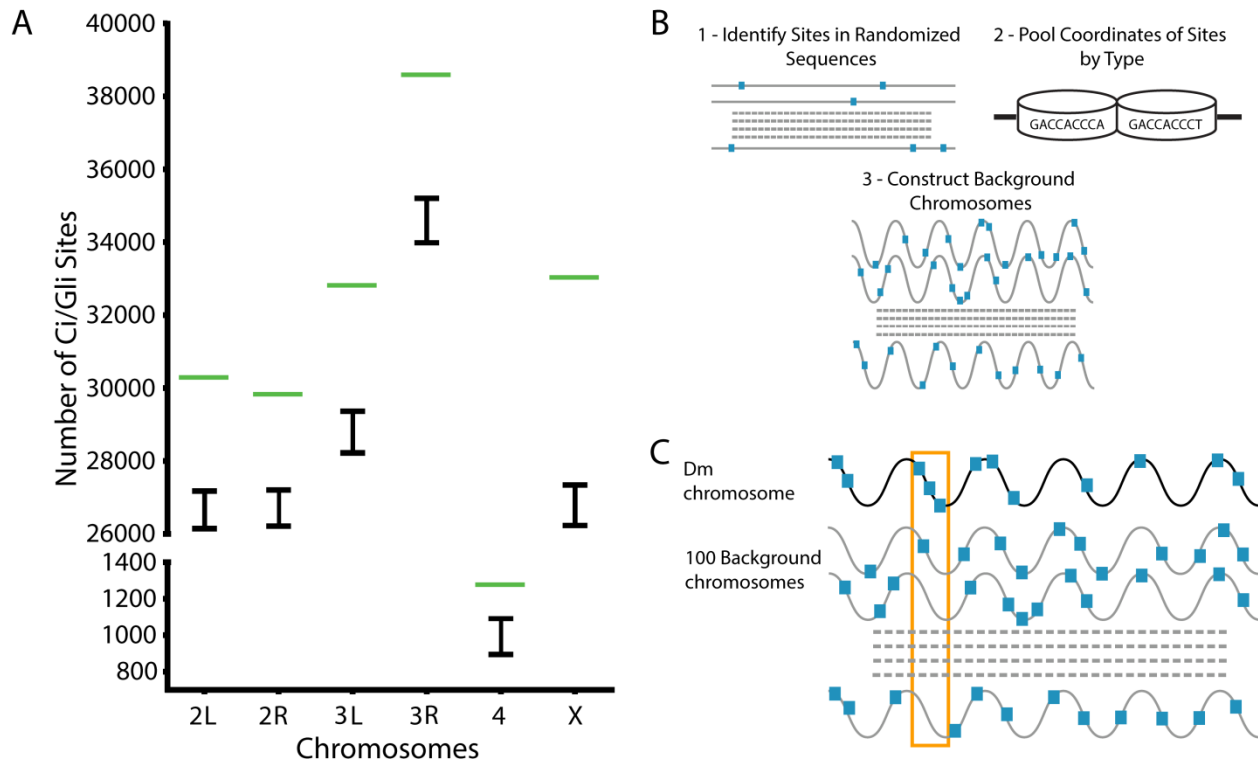


Figure S2.2. Construction of background genomes and determination of cluster enrichment.

(A) The actual number of predicted ci/GLI sites (≥ 0.75 MSS) determined in each Dm chromosome is shown by the green lines. The Flip GC/AT method was used to create 1000 background sequences and the number of predicted ci/GLI sites was tallied for each sequence. Box plots show that randomized chromosomes contain substantially fewer predicted ci/GLI sites. Brackets represent the range in total number of ci/GLI sites across the background sequences for each chromosome. (B) To correct for the depleted number of predicted ci/GLI sites and create background chromosomes that would closely mirror the native Dm genome, the location (coordinates) and type (sequence) of all predicted ci/GLI sites in each of the 1000 background sequences were recorded and pooled. Background genomes were then constructed by randomly selecting coordinates from the pools so that the composition (number and site type) matched that of the corresponding Dm chromosome. (C) Enrichment of clusters of 3-10 ci/GLI sites relative to the background chromosomes was then determined. The example shows analysis of enrichment for clusters of 3 ci/GLI sites (blue boxes). The Dm chromosome (black line) is compared with 100 background chromosomes (grey lines); the diagram shows only three of the 100 background chromosomes. In a moving window, each group of three ci/GLI sites was delineated in the Dm chromosome (one such cluster is outlined in orange) and the average number of ci/GLI sites was determined within that same genomic space in each of the 100 background chromosomes. The cluster outlined by the orange box is considered enriched if the average number of sites in the Dm chromosome is ≥ 4 fold more than the average number of ci/GLI sites per background chromosome.

Chromosome	Cluster Start	Cluster End	Nearest Gene	Cluster Coefficient	Chromosome	Cluster Start	Cluster End	Nearest Gene	Cluster Coefficient
chr2L	224157	224425	kis	8.85	chr2L	2327144	2327509	CG9967	8.639
chr2L	307304	307667	Plc21C	5.54	chr2L	2327300	2327600	CG9967	8.811
chr2L	308379	308837	Plc21C	4.695	chr2L	2464347	2464714	dpp	5.398
chr2L	343561	344047	Plc21C	8.639	chr2L	2485523	2486058	CG15393	5.568
chr2L	469557	470464	MED15	7.102	chr2L	2633436	2633675	CG9962	6.479
chr2L	469557	470477	MED15	7.042	chr2L	2633436	2634110	CG9962	6.452
chr2L	470449	471006	MED15	5.083	chr2L	2676728	2677183	CG31690	7.08
chr2L	550183	550374	Ets21C	8.811	chr2L	2706033	2706864	CG31690	4.062
chr2L	550301	550533	Ets21C	8.811	chr2L	2716048	2716410	CG31690	4.355
chr2L	550301	550896	Ets21C	5.045	chr2L	2716378	2717079	CG31690	6.748
chr2L	589044	589438	Gsc	7.013	chr2L	2748781	2749507	Pgk	8.316
chr2L	589390	589862	Gsc	5.241	chr2L	2749473	2749751	Pgk	6.427
chr2L	675840	676572	ds	5.045	chr2L	2749473	2749866	Pgk	5.489
chr2L	675840	676768	ds	4.181	chr2L	2757532	2758015	snapin	6.645
chr2L	679538	680264	ds	7.576	chr2L	2796200	2797118	Syt1	4.473
chr2L	788590	789216	Pkg21D	4.362	chr2L	2895471	2896008	lilli	5.839
chr2L	895840	896637	Lsp1beta	4.076	chr2L	2895850	2896246	lilli	6.452
chr2L	1076568	1077102	S	4.193	chr2L	3154232	3154808	Mad	5.472
chr2L	1157377	1157954	capt	5.682	chr2L	3409305	3410047	pgant2	5.141
chr2L	1207768	1208263	CG14342	4.425	chr2L	3532301	3532998	CG8853	4.425
chr2L	1208186	1208449	CG14342	5.27	chr2L	3600104	3600390	odd	6.897
chr2L	1349318	1349842	CG5556	4.409	chr2L	3612212	3612502	odd	8.475
chr2L	1417798	1418139	lea	5.27	chr2L	3612268	3612775	odd	6.969
chr2L	1417798	1418404	lea	4.425	chr2L	3664107	3664872	CG34340	6.682
chr2L	1436421	1437406	snRNA:U3:22A	4.537	chr2L	3664480	3665127	CG34340	6.135
chr2L	1455873	1456140	snRNA:U3:22A	6.667	chr2L	3681011	3681491	CG34340	5.997
chr2L	1538844	1539238	Or22b	4.745	chr2L	3681011	3681689	CG34340	5.141
chr2L	1660217	1660479	chinmo	5.083	chr2L	3721146	3721682	Shaw	6.925
chr2L	1660446	1660882	chinmo	4	chr2L	3803866	3804031	l(2)k16918	7.326
chr2L	1722762	1722944	CG18317	12.346	chr2L	3829612	3830403	slp1	5.226
chr2L	1927228	1928142	CG7337	4.062	chr2L	3829710	3830646	slp1	6.404
chr2L	1928046	1928721	CG7337	4.499	chr2L	3830384	3831170	slp1	6.588
chr2L	2076821	2076968	dpr3	10.811	chr2L	3989507	3990200	CG34176	5.61
chr2L	2076821	2077165	dpr3	8.306	chr2L	4162831	4163050	Or24a	10.791
chr2L	2076821	2077373	dpr3	5.401	chr2L	4271949	4272525	Art2	5
chr2L	2131149	2131543	GlyP	5.141	chr2L	4299398	4300399	tutl	4.127
chr2L	2172681	2173528	aop	7.84	chr2L	4300353	4300661	tutl	7.538
chr2L	2173264	2174038	aop	6.701	chr2L	4621866	4622276	BG642163	5.869

chr2L	4705805	4706494	CG34351	7.859	chr2L	7303424	7303790	wg	6.925
chr2L	4706417	4706727	CG34351	6.969	chr2L	7311767	7312687	wg	4.036
chr2L	5094889	5095720	CG5828	4.021	chr2L	7319199	7319903	wg	4.5
chr2L	5098159	5098686	CG4230	4.077	chr2L	7319641	7320043	wg	4.193
chr2L	5120002	5120997	Msp-300	4.454	chr2L	7392657	7393164	CG5160	6.088
chr2L	5301031	5301420	vri	4.802	chr2L	7417064	7417916	chm	7.825
chr2L	5301124	5301596	vri	4.036	chr2L	7417064	7418058	chm	7.538
chr2L	5361619	5362064	nompC	5.764	chr2L	7538294	7539165	Rapgap1	7.013
chr2L	5411889	5412644	H15	6.615	chr2L	7625773	7626160	CG6739	4.695
chr2L	5437299	5438000	CG31647	4.41	chr2L	8089867	8090201	Bsg	15.766
chr2L	5445064	5445591	CG31647	9.592	chr2L	8103360	8103509	Bsg	7.194
chr2L	5445554	5446251	CG31647	4.822	chr2L	8103420	8104130	Bsg	4.745
chr2L	5464393	5464800	mid	7.707	chr2L	8497224	8497950	Dh31	4.532
chr2L	5509164	5509417	CG14020	13.937	chr2L	8511973	8512424	CG13097	10.05
chr2L	5509164	5509869	CG14020	6.502	chr2L	8557017	8557734	Sema-1a	4.963
chr2L	5509164	5510099	CG14020	5.786	chr2L	8639944	8640535	Sema-1a	5.141
chr2L	5617311	5618117	CG14010	4.755	chr2L	8795244	8795688	CG9468	8
chr2L	5656242	5657211	CG31646	4.528	chr2L	8973919	8974766	CG9541	8.316
chr2L	5677620	5678067	CG12511	5.917	chr2L	8974758	8975016	CG9541	9.195
chr2L	5732767	5733434	CG11030	4.499	chr2L	8974939	8975581	CG9541	5.624
chr2L	5733426	5734412	CG11030	5.472	chr2L	9111745	9112729	Or30a	5.54
chr2L	5853722	5854330	CG34381	5.202	chr2L	9168557	9168972	tai	4.963
chr2L	5853809	5854605	CG34381	5.025	chr2L	9445357	9445977	numb	5.61
chr2L	5853809	5854808	CG34381	4.188	chr2L	9509985	9510871	CG33298	4.155
chr2L	5940796	5941704	Sfp26Ad	4.208	chr2L	9510670	9511041	CG33298	6.203
chr2L	6090269	6091255	Kr-h1	4.278	chr2L	9510670	9511480	CG33298	4.38
chr2L	6090571	6091556	Kr-h1	4.464	chr2L	9783289	9783744	IP3K1	5.025
chr2L	6091207	6091658	Kr-h1	6.479	chr2L	9785633	9786483	IP3K1	5.025
chr2L	6091207	6092139	Kr-h1	5.251	chr2L	9894965	9895631	Bka	5.997
chr2L	6150404	6150603	Muc26B	5.997	chr2L	9905220	9905883	CG13124	4.563
chr2L	6150404	6150671	Muc26B	5.4	chr2L	10431448	10431754	TfIIIB	4.454
chr2L	6248734	6249726	Ddr	4.102	chr2L	10562289	10562433	Trim9	6.861
chr2L	6252580	6253012	Ddr	8.639	chr2L	10850047	10850463	porin	6.464
chr2L	6252580	6253354	Ddr	4.438	chr2L	11033089	11034058	Samuel	5.839
chr2L	6539285	6539784	eya	5.045	chr2L	11033137	11034134	Samuel	4.115
chr2L	6539708	6539924	eya	7.205	chr2L	11247749	11247999	ab	6.745
chr2L	6539708	6540049	eya	6.818	chr2L	11289752	11290286	Osi21	5.36
chr2L	6827632	6828030	sens-2	5.839	chr2L	11290100	11290672	Osi21	8.759
chr2L	6832808	6833642	sens-2	4.062	chr2L	11347457	11348317	CG14926	5.54
chr2L	7303281	7303496	wg	5.997	chr2L	11423198	11423454	salm	4.695

chr2L	11436190	11436638	salm	6.452	chr2L	15067078	15067481	vas	5.045
chr2L	11490514	11491226	sala	8.403	chr2L	15104872	15105218	CG15269	13.937
chr2L	11490853	11491330	sala	13.514	chr2L	15105130	15105703	CG15269	15.432
chr2L	11490853	11491535	sala	8.13	chr2L	15105130	15106127	CG15269	9.259
chr2L	11561853	11562485	Mst33A	5.472	chr2L	15106615	15107288	CG15269	6.088
chr2L	11684444	11684719	CG4988	8.85	chr2L	15282712	15282916	CG15263	5.398
chr2L	11755495	11756407	Sfp33A1	4.963	chr2L	15335739	15336710	esg	7.449
chr2L	11761005	11761167	Sfp33A1	10.526	chr2L	15490818	15491648	Tim17b2	4.278
chr2L	11761149	11761414	Sfp33A1	10.292	chr2L	15535363	15536353	CG42448	4.32
chr2L	11761149	11761573	Sfp33A1	7.387	chr2L	15604901	15605503	CG15255	9.195
chr2L	11865562	11865828	Pde1c	8.432	chr2L	15936528	15937235	beat-Ib	5.998
chr2L	11870723	11871367	Pde1c	5.917	chr2L	15937185	15937383	beat-Ib	10.183
chr2L	12105069	12105432	Aats-thr	6.547	chr2L	16007983	16008204	beat-Ic	12.012
chr2L	12159755	12160504	CG31760	4.077	chr2L	16008030	16008398	beat-Ic	13.85
chr2L	12321237	12321677	aret	7.194	chr2L	16523372	16524357	CG5953	8.451
chr2L	12500402	12500911	bun	6.547	chr2L	16540765	16541091	CG31816	7.319
chr2L	12673933	12674380	pdm2	8.523	chr2L	16541032	16542034	CG31816	8.097
chr2L	12674209	12674524	pdm2	7.444	chr2L	16547346	16548248	CG42389	7.795
chr2L	12745734	12746054	MRP	5.141	chr2L	16548122	16548832	CG42389	6.818
chr2L	12849933	12850587	kek1	4.154	chr2L	16548122	16548951	CG42389	5.907
chr2L	12854258	12855018	kek1	5.144	chr2L	16570066	16570842	CG42389	4.036
chr2L	12854798	12855803	kek1	4.362	chr2L	16782148	16782965	Mhc	4.37
chr2L	13078471	13078759	CG5142	7.716	chr2L	17101764	17102010	CG31784	9.009
chr2L	13099315	13100132	CG5142	4.955	chr2L	17209384	17210217	beat-IIIc	4.355
chr2L	13099936	13100679	CG5142	5.192	chr2L	17221217	17221771	beat-IIIc	5.807
chr2L	13426441	13426687	Tehao	11.364	chr2L	17326866	17327077	CG34170	8.639
chr2L	13426441	13426883	Tehao	6.667	chr2L	17346002	17346266	CG31804	9.195
chr2L	13501495	13502045	B4	6.452	chr2L	17355334	17355882	CG31804	4.193
chr2L	14179493	14180268	CG32972	5.083	chr2L	17399685	17400467	CLIP-190	5.27
chr2L	14278893	14279299	wb	7.449	chr2L	17400908	17401354	CLIP-190	4.193
chr2L	14407625	14408505	elB	6.667	chr2L	17433182	17433529	CG5043	5.513
chr2L	14443028	14443926	CG15283	7.338	chr2L	17578043	17578705	Oli	4.545
chr2L	14444204	14444430	CG15283	15.464	chr2L	17584850	17585071	Oli	11.561
chr2L	14444204	14445160	CG15283	4.545	chr2L	17584935	17585209	Oli	15.424
chr2L	14471825	14472643	noc	5.4	chr2L	17584935	17585314	Oli	12.007
chr2L	14745106	14745927	CG42587	8.316	chr2L	17584935	17585409	Oli	9.604
chr2L	14745619	14746060	CG42587	10.811	chr2L	18004718	18005443	CG5693	7.444
chr2L	14773235	14773659	CG4650	4.115	chr2L	18028936	18029643	rdo	4.598
chr2L	14809507	14810378	CG33309	4	chr2L	18737563	18737995	CG15167	5.839
chr2L	14934569	14935180	CG42313	4.092	chr2L	18737823	18738336	CG15167	10.05

chr2L	18814753	18815451	CG17325	4.219	chr2R	3057484	3058321	pk	5.141
chr2L	18973820	18974787	CG10639	4.092	chr2R	3141403	3142377	Gadd45	7.576
chr2L	19015688	19015947	robl37BC	5.445	chr2R	3142362	3142697	Gadd45	11.261
chr2L	19015888	19016804	robl37BC	4.878	chr2R	3344556	3345175	Inos	4.566
chr2L	19020871	19021531	CG15172	5.141	chr2R	3345504	3346174	Inos	4.839
chr2L	19021422	19021718	CG15172	4.963	chr2R	3345853	3346237	Inos	5.059
chr2L	19144519	19145347	brat	6.042	chr2R	3652947	3653720	CG30497	13.937
chr2L	19360312	19361151	dnt	4.193	chr2R	3653712	3653895	CG30497	210.526
chr2L	19514284	19514674	CG10186	6.349	chr2R	3653746	3654118	CG30497	28.777
chr2L	19514284	19514873	CG10186	5.786	chr2R	3653781	3654690	CG30497	4.036
chr2L	19629891	19630237	Lar	4.278	chr2R	3669306	3670079	cn	4.362
chr2L	19824278	19825032	CG13958	4.908	chr2R	3887949	3888104	CG11191	4.646
chr2L	19882749	19883355	sick	5.839	chr2R	3945294	3946197	CG12769	4.695
chr2L	19883248	19883507	sick	6.745	chr2R	4171505	4171947	CG30371	7.707
chr2L	19883248	19883688	sick	4.78	chr2R	4180231	4181023	CG30371	4.38
chr2L	20020671	20021345	CG10659	4.839	chr2R	4188822	4188966	CG30371	17.964
chr2L	20500026	20500384	CG34007	5.917	chr2R	4189031	4189989	CG30371	4.092
chr2L	20500026	20500750	CG34007	5.097	chr2R	4260688	4260855	CG8701	18.018
chr2L	20516462	20517339	CG34007	5.907	chr2R	4260818	4261362	CG8701	7.326
chr2L	20649717	20650264	CG18810	5.398	chr2R	4265757	4265908	CG8701	17.316
chr2L	20845537	20845805	CG31676	8.639	chr2R	4265757	4266177	CG8701	9.47
chr2L	21029388	21030096	CG42238	8.316	chr2R	4265769	4266394	CG8701	5.297
chr2L	21811017	21811841	tsh	4.963	chr2R	4269955	4270182	pdm3	17.316
chr2L	21811017	21811991	tsh	4.5	chr2R	4334990	4335177	Cyp4e1	9.804
chr2L	21958680	21958911	CG2528	6.588	chr2R	4347126	4347551	CG8693	6.897
chr2L	21958669	21959022	CG2528	5.063	chr2R	4463778	4464265	CG42326	8.639
chr2L	21960881	21961186	CG2528	11.583	chr2R	4464050	4464395	CG42326	7.859
chr2L	21960881	21961556	CG2528	6.84	chr2R	4473508	4473691	CG14752	6.237
chr2L	21960881	21961577	CG2528	6.818	chr2R	4475772	4476297	CG14752	5.396
chr2L	21960881	21961713	CG2528	6.05	chr2R	4475772	4476670	CG14752	4.284
chr2R	1661799	1662671	CG11163	4.646	chr2R	4519468	4520108	CG8635	5.226
chr2R	1662663	1663094	CG11163	4.498	chr2R	4531060	4531543	ptc	7.08
chr2R	2014104	2014214	EcR	12.987	chr2R	4532024	4532643	ptc	5.083
chr2R	2566475	2566947	CG9422	6.088	chr2R	4532518	4532669	ptc	142.857
chr2R	2656051	2656477	Epac	6.969	chr2R	4532631	4533543	ptc	4.237
chr2R	2939493	2939787	lbn	12.987	chr2R	4536026	4536527	ptc	5.083
chr2R	2939714	2940347	lbn	6	chr2R	4536453	4537018	ptc	4.208
chr2R	2965576	2965947	CG12831	61.538	chr2R	4544755	4545026	ptc	7.371
chr2R	2997233	2997608	esn	6	chr2R	4599045	4599490	CG14743	4.983
chr2R	3057470	3058313	pk	5.141	chr2R	4619974	4620552	stmA	4.908

chr2R	4620058	4620687	stmA	4.41	chr2R	6657910	6658335	CG33144	4.41
chr2R	4620205	4620845	stmA	4.154	chr2R	6731066	6731903	CG30015	11.662
chr2R	4643981	4644322	CG8740	4.566	chr2R	6741436	6742210	CG30015	4.908
chr2R	4672985	4673404	CG8746	6.173	chr2R	7092641	7093475	shn	6.26
chr2R	4882942	4883426	CG34350	22.727	chr2R	7123813	7124654	CG13217	4.908
chr2R	5084627	5085141	unpg	5.839	chr2R	7136275	7136805	CG34227	6
chr2R	5090819	5091011	CG8027	8.746	chr2R	7162504	7162846	TpnC47D	12.448
chr2R	5091621	5091764	CG8027	5.226	chr2R	7162550	7163139	TpnC47D	8.432
chr2R	5157261	5158001	Pkn	6.645	chr2R	7200893	7201078	nompA	6.068
chr2R	5235163	5235392	CG13739	10.283	chr2R	7262100	7262881	CG13203	4.036
chr2R	5235322	5235475	CG13739	16.598	chr2R	7378828	7379226	inv	7.042
chr2R	5384155	5384985	Wnt2	5.917	chr2R	7379044	7379448	inv	5.495
chr2R	5391184	5392138	brp	4.029	chr2R	7380187	7380454	inv	7.326
chr2R	5397320	5397969	brp	7.496	chr2R	7380383	7380632	inv	5.894
chr2R	5408548	5408869	brp	7.538	chr2R	7380624	7381376	inv	4
chr2R	5445495	5445946	Or45b	5.141	chr2R	7455310	7455887	tou	4.104
chr2R	5488211	5488363	CG1902	48.193	chr2R	7682102	7682696	ths	8.711
chr2R	5488325	5488472	CG1902	23.952	chr2R	7682229	7682570	ths	9.804
chr2R	5491540	5492043	CG1902	7.576	chr2R	7687754	7688607	ths	4.907
chr2R	5774661	5775105	CG12923	10.283	chr2R	7701704	7702389	ths	9.828
chr2R	5788191	5788645	CG1441	5.997	chr2R	7702241	7702627	ths	33.333
chr2R	5788458	5788939	CG1441	5.839	chr2R	7734178	7734370	Sln	210.526
chr2R	5788467	5789280	CG1441	4.854	chr2R	7734302	7734536	Sln	210.526
chr2R	5798378	5798971	CG12140	14.87	chr2R	7734327	7734546	Sln	210.526
chr2R	5869383	5870077	eve	5.333	chr2R	7855414	7855994	CG8979	10.526
chr2R	5906786	5907535	Pka-R2	5.146	chr2R	8011025	8011915	jeb	4.745
chr2R	5989625	5990006	14-3-3zeta	61.538	chr2R	8011707	8012076	jeb	27.027
chr2R	6112204	6112546	Hr46	13.937	chr2R	8153859	8154063	Cam	9.009
chr2R	6112359	6113085	Hr46	10.526	chr2R	8154055	8154361	Cam	8.147
chr2R	6135029	6135681	CG12914	5.78	chr2R	8653016	8653886	CG12374	4.575
chr2R	6136569	6136924	CG12914	21.622	chr2R	8838792	8839271	CG3884	9.823
chr2R	6136569	6137280	CG12914	5.513	chr2R	8838838	8839262	CG3884	10.791
chr2R	6136916	6137462	CG12913	5.396	chr2R	8860704	8861146	Psc	4.049
chr2R	6418353	6418759	lola	8.746	chr2R	8879829	8880583	CG33798	10.05
chr2R	6458687	6459675	psq	6.353	chr2R	8965690	8966054	Drl-2	17.316
chr2R	6461151	6461657	psq	6.748	chr2R	8981205	8981375	Drl-2	21.622
chr2R	6461161	6461507	psq	7.371	chr2R	8985115	8986083	CG13325	10.283
chr2R	6461408	6461657	psq	7.895	chr2R	8985944	8986186	CG13325	400
chr2R	6461408	6462025	psq	6.349	chr2R	8989909	8990177	CG13325	7.712
chr2R	6587668	6588157	stan	6.26	chr2R	9257541	9258057	CG10814	7.905

chr2R	9309045	9309601	CG42321	9.592	chr2R	10998060	10998943	chn	5.4
chr2R	9688042	9688414	Cpr50Cb	4.983	chr2R	11003713	11003984	chn	9.311
chr2R	9688042	9688896	Cpr50Cb	4.237	chr2R	11004180	11005090	chn	6.353
chr2R	9840907	9841682	AGO1	4.545	chr2R	11004904	11005421	chn	8.85
chr2R	9841497	9842022	AGO1	10.05	chr2R	11038670	11039256	CG7544	8.576
chr2R	9955070	9955239	Prosap	19.608	chr2R	11090075	11090569	CG11807	6.757
chr2R	10033422	10034046	Rcd1	4	chr2R	11090432	11091198	CG11807	10.526
chr2R	10157104	10157811	SelD	17.316	chr2R	11093782	11093982	row	9.804
chr2R	10166787	10167355	lh	4.745	chr2R	11100677	11101193	row	5.997
chr2R	10236029	10237011	Shroom	5.202	chr2R	11101185	11102041	row	4.839
chr2R	10342729	10343186	Oaz	5.31	chr2R	11135357	11136230	scb	4.049
chr2R	10540962	10541599	Adgf-E	4.208	chr2R	11138385	11139006	scb	4.839
chr2R	10674327	10674532	kn	28.777	chr2R	11186006	11186788	CG8102	8.711
chr2R	10674327	10674542	kn	14.577	chr2R	11186239	11186828	CG8102	7.326
chr2R	10699557	10700017	CG10200 (knot)	5.059	chr2R	11186315	11187134	CG8102	6.645
chr2R	10699888	10700190	CG10200	4.762	chr2R	11210708	11211466	Arf51F	4.049
chr2R	10742561	10743114	Ciao1	4.695	chr2R	11218534	11218691	Hr51	4.566
chr2R	10756680	10757391	Pcf11	5.396	chr2R	11221366	11221772	Hr51	4.498
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chr2R	10814534	10815122	CG10253	4.91	chr2R	11277182	11277997	SRPK	6.173
chr2R	10854025	10854606	CG12424	7.102	chr2R	11279237	11279402	SRPK	5.495
chr2R	10854101	10854638	CG12424	8.183	chr2R	11279244	11279463	SRPK	4.695
chr2R	10856913	10857173	CG12424	6.479	chr2R	11281951	11282528	SRPK	6.356
chr2R	10856967	10857599	CG12424	6.588	chr2R	11300613	11300919	CG34365	4.155
chr2R	10875846	10876007	pcs	71.429	chr2R	11301690	11301953	CG34365	11.364
chr2R	10875881	10876089	pcs	61.538	chr2R	11301875	11302537	CG34365	6.502
chr2R	10875931	10876305	pcs	10.526	chr2R	11305134	11305956	CG34365	8.639
chr2R	10875931	10876324	pcs	6.84	chr2R	11309355	11309910	CG34365	7.707
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chr2R	10888725	10889522	CG10265	7.326	chr2R	11321080	11321590	CG34365	5.997
chr2R	10911099	10911471	hbs	13.514	chr2R	11336714	11337271	CG34365	5.4
chr2R	10911463	10911962	hbs	6.002	chr2R	11345054	11345780	CG34365	5.682
chr2R	10912720	10913010	hbs	8.811	chr2R	11345651	11345978	CG34365	12.012
chr2R	10922067	10922364	hbs	4.762	chr2R	11377647	11378213	CG12964	4.104
chr2R	10994428	10995433	chn	8.811	chr2R	11377929	11378342	CG12964	4.695
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chr2R	10994748	10995548	chn	10.283	chr2R	11381313	11381965	CG12964	8.811
					chr2R	11409951	11410140	Khc-73	12

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chr2R	11420951	11421424	Khc-73	6.356	chr2R	11844574	11845427	CG8366	7.449
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chr2R	11441808	11442264	CG12963	6.969	chr2R	11853445	11854204	Strn-Mlck	5.61
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chr2R	11484458	11484743	CG42524	18.779	chr2R	11877665	11877930	CG8314	14.388
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chr2R	11493919	11494178	CG42524	10.811	chr2R	11885983	11886882	ATPCL	4.762
chr2R	11503828	11504337	CG42524	5.839	chr2R	11899289	11899697	CG8389	5.78
chr2R	11517843	11518614	CG42524	4.655	chr2R	11906508	11907159	CG8399	6.645
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chr2R	11548317	11549179	fus	4.575	chr2R	11933643	11934629	SP2353	6.969
chr2R	11548638	11548903	fus	6.356	chr2R	11935411	11935606	CG8405	19.108
chr2R	11548890	11549179	fus	7.895	chr2R	11940620	11940973	CG8405	4.63
chr2R	11548890	11549461	fus	5.333	chr2R	11940620	11941229	CG8405	4
chr2R	11563870	11564279	fus	5.31	chr2R	11979617	11980069	Dg	5.917
chr2R	11566797	11567427	Vha14	4.154	chr2R	11980009	11980365	Dg	12
chr2R	11575662	11575911	CG8214	11.364	chr2R	11983948	11984275	Dg	4.839
chr2R	11575842	11576719	CG8214	8.316	chr2R	12020739	12021490	spin	5.27
chr2R	11582841	11583620	CG33461	5.453	chr2R	12026380	12026605	Got1	6.237
chr2R	11590226	11590369	CG30080	11.583	chr2R	12061469	12061801	Ptp52F	4.261
chr2R	11602343	11602564	CG30083	9.804	chr2R	12067735	12068182	Lis-1	27.027
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chr2R	11659638	11659988	Zasp52	4.104	chr2R	12068044	12068917	Lis-1	5.333
chr2R	11716587	11717390	Poxn	9.39	chr2R	12070403	12071055	Lis-1	12.698
chr2R	11716940	11717616	Poxn	11.364	chr2R	12084900	12085115	CG8446	4.839
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chr2R	11728883	11729155	CG8249	4.91	chr2R	12118234	12118590	CG15701	6.452
chr2R	11750736	11751297	Gpo-1	16.598	chr2R	12122228	12122535	CG7786	7.042
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chr2R	11792774	11793189	sli	4.454	chr2R	12148936	12149225	fidipidine	4.261
chr2R	11793119	11793308	sli	5.894	chr2R	12177885	12178354	JhI-26	5.682

chr2R	12191454	12192156	Nox	5.917	chr2R	12498903	12499084	CG5065	6.356
chr2R	12192114	12192650	Nox	9.39	chr2R	12502325	12502745	CG5065	14.87
chr2R	12195766	12196542	Nox	4.802	chr2R	12502350	12502789	CG5065	14.87
chr2R	12196305	12196757	Nox	4.908	chr2R	12507868	12508551	CG5065	4.598
chr2R	12196534	12197162	Nox	5.398	chr2R	12528359	12528634	gprs	6.645
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chr2R	12255922	12256341	CG15711	30.769	chr2R	12580057	12580981	CG30463	4.646
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chr2R	12281340	12281607	CG33960	6.897	chr2R	12619177	12620175	Sfp53D	4.322
chr2R	12281599	12281860	CG33960	9.195	chr2R	12643259	12643744	unc-104	27.027
chr2R	12281852	12282511	CG33960	5.54	chr2R	12643337	12643851	unc-104	30.769
chr2R	12284061	12284394	CG33960	6.237	chr2R	12655982	12656635	unc-104	5.31
chr2R	12332423	12333217	CG4409	4.454	chr2R	12659107	12659386	unc-104	4.323
chr2R	12332538	12333356	CG4409	4.115	chr2R	12666767	12667111	Vkor	7.895
chr2R	12335293	12335640	CG15925	8.31	chr2R	12668783	12669179	resilin	5.025
chr2R	12338151	12338317	CG15925	6	chr2R	12671147	12671617	CG5522	16
chr2R	12351339	12351638	CheB53a	5.31	chr2R	12671587	12672041	CG5522	15.444
chr2R	12358138	12358700	CheB53b	5.146	chr2R	12676473	12676958	CG5522	7.08
chr2R	12358453	12358707	CheB53b	6.356	chr2R	12676636	12677619	CG5522	4.362
chr2R	12381552	12381825	CG4439	28.777	chr2R	12680506	12680857	CG15919	8.639
chr2R	12389087	12389207	Sema-2a	17.964	chr2R	12700969	12701447	CG5550	4
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chr2R	12407530	12407646	Sema-2a	9.524	chr2R	12751749	12752398	Psi	10.283
chr2R	12412235	12412734	Sema-2a	10.05	chr2R	12752295	12752595	Psi	6.745
chr2R	12416993	12417312	Sema-2a	11.364	chr2R	12768607	12769316	CG8910	6
chr2R	12417225	12417557	Sema-2a	8.108	chr2R	12768947	12769539	CG8910	6.897
chr2R	12418572	12419488	Sema-2a	9.592	chr2R	12769308	12769894	CG8910	5.587
chr2R	12422283	12423272	loopin-1	6.088	chr2R	12774256	12774986	CG8910	4.049
chr2R	12454499	12455492	CG4945	4.438	chr2R	12774968	12775251	CG8910	8.108
chr2R	12462190	12463107	CG8317	4.908	chr2R	12775863	12776552	CG8910	4.646
chr2R	12491541	12492061	CG8303	8.811	chr2R	12778070	12778667	CG8910	5.396

chr2R	12778070	12778722	CG8910	5.025	chr2R	13179535	13180223	mbl	6.356
chr2R	12788237	12789106	inaC	4.454	chr2R	13267222	13267629	Sip1	8
chr2R	12802259	12803132	Pkc53E	6.353	chr2R	13267544	13268149	Sip1	4.237
chr2R	12802701	12803177	Pkc53E	10	chr2R	13272752	13273658	Sip1	5.141
chr2R	12803370	12803696	Pkc53E	7.396	chr2R	13288044	13288802	Sip1	4.323
chr2R	12803377	12804009	Pkc53E	6.002	chr2R	13288780	13289540	Sip1	4.566
chr2R	12803399	12804072	Pkc53E	4.655	chr2R	13290583	13291441	Sip1	4.049
chr2R	12847803	12847918	CG9010	9.524	chr2R	13297921	13298403	CG30101	4
chr2R	12854974	12855655	Cbp53E	8.811	chr2R	13298105	13298630	CG30101	6
chr2R	12855516	12855847	Cbp53E	7.371	chr2R	13321315	13321773	EDTP	20.619
chr2R	12858167	12858532	Cbp53E	5.682	chr2R	13352840	13353334	CG14478	8.576
chr2R	12858520	12859371	Cbp53E	4.323	chr2R	13394739	13395102	CG4844	9.39
chr2R	12862997	12863558	Cbp53E	7.194	chr2R	13396570	13396807	CG4844	7.194
chr2R	12863405	12863749	Cbp53E	15.464	chr2R	13396768	13397027	CG4844	8.147
chr2R	12866743	12867068	Cbp53E	4.695	chr2R	13427847	13428336	CG18432	8.639
chr2R	12871345	12871474	Cbp53E	7.538	chr2R	13444225	13444679	Klp54D	5.472
chr2R	12871345	12871652	Cbp53E	6.969	chr2R	13472833	13473051	CG14483	6.897
chr2R	12876736	12877630	Cbp53E	4.545	chr2R	13485394	13486197	lack	8
chr2R	12879141	12879989	Cbp53E	6.757	chr2R	13486148	13486321	lack	22.727
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chr2R	12920927	12921758	RhoGEF2	6.452	chr2R	13509596	13510178	CG10936	4.839
chr2R	12953454	12954335	CG6967	5.682	chr2R	13514476	13514864	CG10936	5.495
chr2R	12963749	12964333	CG30460	7.326	chr2R	13514476	13515363	CG10936	4.036
chr2R	12987166	12987814	GstS1	4.695	chr2R	13520674	13521524	CG10936	5.61
chr2R	12987806	12988578	CG30456	4.802	chr2R	13568765	13569441	Sema-1b	13.937
chr2R	12992760	12993169	CG30456	11.08	chr2R	13582492	13583462	swi2	4
chr2R	13013371	13013957	Amy-d	4.193	chr2R	13604206	13604969	CG10934	10.05
chr2R	13051217	13051370	CG10953	7.371	chr2R	13626923	13627181	CG6401	8.108
chr2R	13072472	13072955	CG10950	10.05	chr2R	13626923	13627711	CG6401	6.203
chr2R	13072947	13073377	CG10950	17.316	chr2R	13646668	13647388	HLH54F	4.104
chr2R	13073362	13073564	CG10950	21.622	chr2R	13656907	13657644	CG18635	4
chr2R	13073369	13074020	CG10950	4.454	chr2R	13680251	13680868	CG5036	5.141
chr2R	13088827	13089178	CG10950	5.297	chr2R	13707725	13708531	grh	5.27
chr2R	13089135	13089485	CG10950	25.478	chr2R	13711493	13711618	grh	9.804
chr2R	13148307	13148548	mbl	8.432	chr2R	13711493	13712315	grh	4.908
chr2R	13163618	13164258	mbl	6.11	chr2R	13714618	13715214	grh	11.662
chr2R	13166630	13167109	mbl	6.608	chr2R	13739187	13739887	olf186-F	5.31
chr2R	13173214	13174144	mbl	4.695	chr2R	13744411	13745217	olf186-F	4.154
chr2R	13174116	13174333	mbl	61.538	chr2R	13774619	13775383	elk	5.839
chr2R	13174123	13174449	mbl	22.727	chr2R	13777941	13778084	elk	12.448

chr2R	13824893	13825436	PpY-55A	5.059	chr2R	14280776	14280886	Idgf5	12.987
chr2R	13828138	13828467	PpY-55A	8.306	chr2R	14282434	14283094	Idgf5	5.682
chr2R	13834690	13835398	PpY-55A	4.284	chr2R	14290388	14290673	GstE4	11.583
chr2R	13843365	13844291	PpY-55A	4.908	chr2R	14299658	14299934	imd	4.104
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chr2R	13857813	13858781	dpr13	4.122	chr2R	14312510	14312722	CG5174	21.583
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chr2R	13859898	13860262	dpr13	11.583	chr2R	14405016	14405199	CG5226	9.259
chr2R	13867079	13867483	dpr13	6.237	chr2R	14405016	14405734	CG5226	6.088
chr2R	13867161	13867889	dpr13	4.261	chr2R	14406048	14406338	CG5226	12.448
chr2R	13870544	13871222	dpr13	4.908	chr2R	14406330	14406908	CG5226	7.707
chr2R	13870585	13871289	dpr13	5.54	chr2R	14423666	14424058	Pepck	8.639
chr2R	13877265	13878137	dpr13	4.854	chr2R	14426693	14427468	Pepck	6.11
chr2R	13907192	13907851	CG5084	4.104	chr2R	14427942	14428238	Rgk2	6.088
chr2R	13924463	13924885	CG5773	7.825	chr2R	14427963	14428365	Rgk2	6.349
chr2R	13924463	13925026	CG5773	5.297	chr2R	14428162	14428609	Rgk2	14.388
chr2R	13944802	13945670	CG10912	5.31	chr2R	14428230	14428658	Rgk2	16
chr2R	13958201	13958361	CG34386	9.259	chr2R	14428357	14428662	Rgk2	27.027
chr2R	13965659	13966038	CG34386	7.194	chr2R	14428601	14428844	Rgk2	13.937
chr2R	14028253	14029036	pAbp	5.869	chr2R	14428650	14428967	Rgk2	9.828
chr2R	14028309	14029041	pAbp	6.068	chr2R	14428650	14429257	Rgk2	4.252
chr2R	14035514	14035706	CG17680	15.464	chr2R	14503648	14504129	CG5327	6.645
chr2R	14041906	14042467	lolal	8.811	chr2R	14557418	14557791	edl	6.349
chr2R	14078946	14079591	CG33958	7.859	chr2R	14560090	14560885	edl	6.11
chr2R	14079468	14080418	CG33958	6.969	chr2R	14571845	14572163	CG15086	7.042
chr2R	14081582	14082117	CG14500	13.072	chr2R	14571971	14572217	CG15086	7.371
chr2R	14082035	14082252	CG14500	61.538	chr2R	14599486	14600458	pncr016:2R	4.695
chr2R	14082082	14082622	CG14500	18.018	chr2R	14610008	14610522	Hs3st-A	7.08
chr2R	14094068	14095069	CG30114	6.547	chr2R	14610323	14610650	Hs3st-A	142.857
chr2R	14111491	14111907	fj	5.297	chr2R	14627581	14627962	Hs3st-A	9.009
chr2R	14165096	14165842	pen-2	4.38	chr2R	14629369	14629836	Hs3st-A	12.987
chr2R	14178483	14178815	sbb	6.757	chr2R	14629760	14630205	Hs3st-A	7.194
chr2R	14185007	14185556	sbb	9.524	chr2R	14653902	14654054	Mctp	27.027
chr2R	14202577	14203233	sbb	4.104	chr2R	14654354	14654955	Mctp	8.811
chr2R	14204726	14205137	sbb	5.587	chr2R	14654376	14655254	Mctp	5.202
chr2R	14208115	14208978	sbb	4.049	chr2R	14656431	14656981	Mctp	7.576
chr2R	14208818	14209188	sbb	9.804	chr2R	14683601	14684243	CG15094	6.452
chr2R	14209631	14210268	sbb	5.146	chr2R	14740539	14741443	Jheh1	4.454
chr2R	14278499	14278974	CG15068	6.356	chr2R	14802430	14803437	sano	4.41
chr2R	14280543	14280784	Idgf5	10.811	chr2R	14802592	14803582	sano	4.646

chr2R	14876769	14877104	abba	14.87	chr2R	16702229	16702475	insec	13.514
chr2R	14978647	14979529	5-HT1A	7.576	chr2R	16778526	16778916	otp	11.662
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chr2R	15094264	15094528	hppy	28.777	chr2R	16809441	16810113	Rx	12.012
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chr2R	15196308	15197315	endoB	6.088	chr2R	16809766	16810185	Rx	39.216
chr2R	15211205	15211546	Rgk1	5.495	chr2R	16835221	16835995	snoRNA:660	6.897
chr2R	15319332	15320192	Fak56D	4.575	chr2R	16843838	16844242	hbn	9.39
chr2R	15348836	15349734	par-1	4.38	chr2R	16843856	16844249	hbn	9.39
chr2R	15456684	15456923	sm	7.042	chr2R	16850198	16851047	hbn	7.576
chr2R	15456871	15457106	sm	10.453	chr2R	16850443	16851167	hbn	9.828
chr2R	15456871	15457203	sm	8.147	chr2R	16851021	16851517	hbn	16
chr2R	15457098	15457623	sm	7.449	chr2R	16851039	16851676	hbn	15.444
chr2R	15515380	15515518	sm	12.987	chr2R	16868353	16868961	CG9313	6.088
chr2R	15563532	15563945	isopeptidase-T-3	7.707	chr2R	16884983	16885515	CG10543	8.065
chr2R	15563709	15564596	isopeptidase-T-3	6.26	chr2R	16913067	16913404	CG9350	8.639
chr2R	15598399	15598522	Obp56e	10.135	chr2R	16990641	16990997	king-tubby	6.745
chr2R	15598399	15599266	Obp56e	6.452	chr2R	17367609	17368319	Sdc	6.356
chr2R	15613598	15614453	snoRNA:185	5.786	chr2R	17394863	17395329	MESK2	10.283
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chr2R	15680992	15681678	Obp56g	5.917	chr2R	17606036	17606670	Tango11	5.61
chr2R	15681187	15682027	Obp56g	5.997	chr2R	17674352	17675063	lox2	6.135
chr2R	15706999	15707450	Obp56h	9.828	chr2R	17674981	17675732	lox2	6.427
chr2R	15743081	15743609	Obp56i	4.077	chr2R	17675702	17675884	lox2	10.453
chr2R	15743458	15743927	Obp56i	5.141	chr2R	17675702	17676229	lox2	6.502
chr2R	16082249	16082501	CG16894	6.356	chr2R	17687946	17688414	CG4386	4.545
chr2R	16082952	16083146	CG16894	4.745	chr2R	17729041	17729163	CG4372	23.077
chr2R	16115878	16116320	CG11044	10.283	chr2R	17734106	17734504	CG4372	7.371
chr2R	16161373	16162286	CG10444	4.077	chr2R	17842591	17842772	CG13494	7.712
chr2R	16207636	16208553	CG8920	4.154	chr2R	17853351	17853844	CG34369	7.194
chr2R	16233903	16234267	CG16741	8.811	chr2R	17893997	17894425	CG34370	9.009
chr2R	16374810	16375635	Obp57c	7.576	chr2R	17894273	17894593	CG34370	11.364
chr2R	16433430	16433632	CG30148	11.08	chr2R	17894405	17895121	CG34370	5.682
chr2R	16433624	16433832	CG30148	10.526	chr2R	17967664	17967998	synj	5.894
chr2R	16433624	16434140	CG30148	7.61	chr2R	17997521	17998455	Vrp1	4.036
chr2R	16478617	16479024	bl	8	chr2R	17999646	17999944	Vrp1	48.193
chr2R	16479016	16479871	bl	7.576	chr2R	18021079	18022021	CG34205	5.31
chr2R	16649188	16649924	CG34202	4.278	chr2R	18125135	18125246	dve	11.583
					chr2R	18153112	18153392	dve	48.193

chr2R	18153153	18153744	dve	8.475	chr2R	19614854	19615107	CG11299	25.478
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chr2R	18178524	18179026	CG5819	17.316	chr2R	19650144	19651022	CG9850	4.092
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chr2R	18260459	18261287	Rtf1	5.141	chr2R	19659936	19660527	CG9850	12.563
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chr2R	18260997	18261502	Rtf1	6.452	chr2R	19660519	19661041	CG9850	4.695
chr2R	18261478	18262039	Rtf1	5.839	chr2R	19698670	19699514	CG5543	6.088
chr2R	18432448	18432907	px	10.526	chr2R	19898675	19899433	Unc-89	4.499
chr2R	18499545	18500177	CG4329	4.41	chr2R	19902967	19903289	CG4324	9.592
chr2R	18499744	18500268	CG4329	6.969	chr2R	20106592	20106738	CG30419	5.31
chr2R	18544757	18545723	CG13510	4.695	chr2R	20161655	20161919	nvy	39.216
chr2R	18570159	18570746	ppa	6.897	chr2R	20161655	20161940	nvy	5.045
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chr2R	18595115	18595517	Obp58d	4.762	chr2R	20184835	20184987	CG3394	10.135
chr2R	18795845	18796244	nahoda	4.695	chr2R	20197767	20198384	betaTub60D	4.91
chr2R	18832101	18833083	CG3831	6.068	chr2R	20272357	20273224	mAcR-60C	6.969
chr2R	18832161	18833087	CG3831	5.682	chr2R	20293002	20293239	SerT	400
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chr2R	19069564	19069732	CG34371	39.216	chr2R	20428425	20429205	CG4622	4.41
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chr2R	19069590	19070449	CG34371	4.092	chr2R	20514402	20514758	CG13594	8.475
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chr2R	19457922	19458495	apt	6.969	chr2R	20874493	20875045	CG3829	5.807
chr2R	19458187	19458531	apt	18.018	chr2R	20952508	20952899	gsb	5.894
chr2R	19458398	19458750	apt	8.639	chr2R	20952819	20953185	gsb	6.452
chr2R	19509447	19509966	CG4019	6.135	chr2R	20952891	20953209	gsb	6.547
chr2R	19519133	19519313	retn	5.587	chr2R	20953201	20953535	gsb	7.371
chr2R	19519174	19519928	retn	4.323	chr2R	20953491	20954256	gsb	4
chr2R	19530473	19531238	retn	4.41	chr2R	20985914	20986866	CG16778	4.153
chr2R	19530562	19531309	retn	4	chr2R	21047715	21048174	CG34038	33.333
chr2R	19559659	19560072	Pde8	19.608	chr3L	123151	123670	Pk61C	4.695
chr2R	19582013	19582267	CG30183	8.746	chr3L	132868	133548	Pk61C	4.91
chr2R	19582148	19582278	CG30183	8.523	chr3L	428959	429081	CG13891	9.524
chr2R	19614486	19614876	CG11299	8.475	chr3L	428959	429206	CG13891	6.969

chr3L	590335	591030	CG17181	5.786	chr3L	4839971	4840334	CG13707	4.762
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chr3L	1218574	1218716	LysP	11.152	chr3L	4955320	4955771	Con	5.226
chr3L	1549358	1549843	Cct1	6.088	chr3L	4992738	4993104	CG32232	7.194
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chr3L	1635809	1635978	n-syb	10.135	chr3L	5101754	5101939	CG34047	5.146
chr3L	1942382	1943128	Mfap1	4.029	chr3L	5156549	5157117	shep	4.955
chr3L	2355306	2355485	CG13801	11.583	chr3L	5500496	5501244	CG34342	5.396
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chr3L	2956438	2956917	CG9965	4.963	chr3L	6011737	6012256	CG32406	5.513
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chr3L	4097082	4097215	CG14995	19.108	chr3L	6690511	6691144	SP1173	4.762
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chr3L	4141753	4142124	Akh	5.587	chr3L	6837019	6837982	vvl	5.059
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chr3L	4240701	4241269	CG14997	4.464	chr3L	6937217	6937378	tow	21.583
chr3L	4305282	4305581	dyl	10.791	chr3L	6937217	6937387	tow	20.619
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chr3L	4417001	4417693	CG11347	4.498	chr3L	7154929	7155391	CG17742	9.695
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chr3L	4839719	4840202	CG13707	5.27	chr3L	7225536	7226217	CG14826	7.042

chr3L	7334727	7335240	lark	4.049	chr3L	10051654	10052045	dpr6	7.895
chr3L	7341592	7341945	qm	6.479	chr3L	10177849	10178654	dpr10	5.917
chr3L	7462032	7462323	Tsp66A	6.11	chr3L	10235128	10235419	Or67c	4.908
chr3L	7481381	7481603	mthl6	5.146	chr3L	10272194	10272927	Or67d	4.038
chr3L	7481587	7482122	mthl6	5.869	chr3L	10272905	10273498	Or67d	4.323
chr3L	7481587	7482175	mthl6	5.682	chr3L	10463258	10463547	CG32063	6.452
chr3L	7506713	7507250	CG7546	4.193	chr3L	10660584	10661588	simj	4.468
chr3L	7592865	7593067	CG33275	12.987	chr3L	10664830	10665710	simj	5.575
chr3L	7600452	7601070	CG33275	4.839	chr3L	10666710	10666936	simj	13.072
chr3L	7784542	7785268	CG32369	7.859	chr3L	10666888	10667081	simj	17.045
chr3L	7807380	7807688	Pdp1	9.524	chr3L	10692837	10693007	NijA	17.316
chr3L	7852808	7853205	Pdp1	12.285	chr3L	10692837	10693737	NijA	6.748
chr3L	7853159	7853859	Pdp1	6.068	chr3L	10804364	10805282	CG12523	4.955
chr3L	7899067	7899483	pbl	7.576	chr3L	10804684	10805110	CG12523	9.524
chr3L	7951595	7952209	exex	4.617	chr3L	10804684	10805282	CG12523	8.639
chr3L	7951793	7952056	exex	7.895	chr3L	10819153	10819707	tna	7.634
chr3L	7951956	7952209	exex	10.791	chr3L	10819153	10819958	tna	6.4
chr3L	7953099	7953586	exex	5.78	chr3L	10949752	10950054	CG34050	4.498
chr3L	8052894	8053443	bip1	4.908	chr3L	10955663	10956218	CG14147	6.11
chr3L	8053050	8053622	bip1	5.333	chr3L	10997695	10998307	klu	4.532
chr3L	8053050	8053845	bip1	4.78	chr3L	11162489	11163213	wls	5.839
chr3L	8204373	8204612	CG8006	4.63	chr3L	11172788	11173004	GlcAT-P	6
chr3L	8489086	8489428	CG6902	9.009	chr3L	11172949	11173529	GlcAT-P	5.513
chr3L	8489086	8489521	CG6902	8.811	chr3L	11359788	11360003	CG6163	7.194
chr3L	8518320	8518937	foi	5.102	chr3L	11359921	11360726	CG6163	6.452
chr3L	8518901	8519618	foi	5.241	chr3L	11506977	11507817	Sgs3	4.278
chr3L	8550155	8550753	rhea	6.969	chr3L	11525874	11526578	Mob2	4.208
chr3L	8635690	8636354	Cpr66D	4.193	chr3L	11708399	11708761	CG14132	6.547
chr3L	8748775	8749219	Fhos	9.009	chr3L	11864451	11864952	CG5906	6.547
chr3L	8819157	8819578	dally	4.695	chr3L	11913663	11913958	CG11588	7.194
chr3L	8819157	8819815	dally	4	chr3L	11913756	11914284	CG11588	7.042
chr3L	9066993	9067647	CG4942	4	chr3L	12117340	12117520	yps	11.494
chr3L	9282659	9282907	Glu-RIB	7.538	chr3L	12283596	12283975	CG4328	4.839
chr3L	9282659	9283201	Glu-RIB	5.472	chr3L	12300350	12300612	CG4328	4.38
chr3L	9497273	9497384	path	7.538	chr3L	12300502	12300954	CG4328	7.194
chr3L	9497347	9497455	path	6.757	chr3L	12300502	12301132	CG4328	5.917
chr3L	9516624	9516931	CG33700	8.639	chr3L	12305290	12305494	CG4328	11.152
chr3L	9684740	9684870	CG6767	21.583	chr3L	12314358	12315199	CG32105	7.08
chr3L	9831200	9831561	Cdk8	4.566	chr3L	12314712	12315559	CG32105	5.54
chr3L	9942787	9943371	CG34356	6.745	chr3L	12315012	12315798	CG32105	4.854

chr3L	12339326	12339581	GRHRII	5.495	chr3L	14618308	14619099	CG9628	5.146
chr3L	12420581	12420861	toe	4	chr3L	14618850	14619657	CG9628	4.695
chr3L	12457913	12458121	eyg	4.646	chr3L	14772091	14772601	bmm	5.396
chr3L	12464845	12465249	CG10616	4.499	chr3L	14814750	14815713	CG17839	8.403
chr3L	12465197	12465851	CG10616	5.764	chr3L	14815520	14815814	CG17839	7.712
chr3L	12682342	12682977	mirr	4.104	chr3L	14847535	14847727	CG17839	9.828
chr3L	12799269	12800223	CG11006	5.357	chr3L	14847535	14848333	CG17839	4.955
chr3L	12821024	12821691	CG10960	7.712	chr3L	14856183	14856701	CG17839	6.098
chr3L	12887600	12888065	CG14118	6.11	chr3L	14856413	14857027	CG17839	5.401
chr3L	12963758	12964425	CG10748	4.63	chr3L	14943391	14943737	BobA	5.682
chr3L	12967834	12968022	CG10749	5.059	chr3L	14969897	14970681	Ocho	7.282
chr3L	13054815	13055253	CG34428	5.931	chr3L	14992693	14993347	Prosbeta2	5.587
chr3L	13117123	13117942	trn	5.31	chr3L	15328258	15328415	Toll-6	10.453
chr3L	13150754	13151412	snky	4.092	chr3L	15368407	15368971	CG33259	7.895
chr3L	13182058	13182870	snky	4.963	chr3L	15458677	15459573	CG7804	4.575
chr3L	13250734	13251100	caps	4.323	chr3L	15459549	15459818	CG7804	7.576
chr3L	13264448	13264649	caps	8.523	chr3L	15480209	15480500	ran-like	6.479
chr3L	13659453	13660087	bru-3	5.869	chr3L	15480209	15480625	ran-like	5.54
chr3L	13659961	13660551	bru-3	4.464	chr3L	15494895	15495370	CG7272	8.993
chr3L	13659961	13660750	bru-3	4.32	chr3L	15497021	15497300	CG7857	6.26
chr3L	13743893	13744019	CG34243	5.587	chr3L	15559340	15559608	CG6498	4.762
chr3L	13820872	13821069	CG8757	11.152	chr3L	15656286	15657242	Eig71Ek	4.655
chr3L	13898946	13899403	Rgl	4.104	chr3L	15671721	15671997	CG7304	5.472
chr3L	13930491	13930668	CG32137	12.448	chr3L	15671985	15672551	CG7304	4.077
chr3L	13930491	13930702	CG32137	10.283	chr3L	15720596	15720887	comm	4.762
chr3L	13930491	13931464	CG32137	6.427	chr3L	15738234	15738481	comm	8.996
chr3L	13930553	13931554	CG32137	5.869	chr3L	15914284	15914862	Pka-C3	4.104
chr3L	13935384	13935775	CG32137	6.479	chr3L	16033745	16033942	th	15.464
chr3L	13941029	13941736	CG32137	10.283	chr3L	16033745	16034326	th	7.194
chr3L	14034586	14035076	Hsc70Cb	9.259	chr3L	16043039	16043629	th	5.764
chr3L	14091870	14092363	Fbp1	6.26	chr3L	16058400	16059034	Mbs	12
chr3L	14094840	14095082	Sox21a	6.11	chr3L	16058400	16059376	Mbs	4.854
chr3L	14095011	14095469	Sox21a	5.587	chr3L	16059026	16059576	Mbs	4.323
chr3L	14119150	14119537	Sox21b	4.104	chr3L	16275329	16276198	CG13049	5.202
chr3L	14216162	14217158	nuf	4.695	chr3L	16289542	16290168	CG4962	4.323
chr3L	14427273	14427944	bbg	5.226	chr3L	16290100	16290612	CG4962	4.983
chr3L	14512813	14513154	CG4613	5.894	chr3L	16328003	16328348	CG13056	4.91
chr3L	14582204	14582618	HGTX	6.969	chr3L	16335782	16336166	CG4998	6.84
chr3L	14583588	14584333	HGTX	4.963	chr3L	16443644	16443847	CG33158	5.61
chr3L	14584275	14584525	HGTX	10.135	chr3L	16504876	16505459	CG42513	7.825

chr3L	16505398	16505711	CG42513	7.013	chr3L	19100342	19100534	CG14082	8.639
chr3L	16505398	16505968	CG42513	5.682	chr3L	19101662	19102638	CG14082	6.645
chr3L	16651878	16652521	Baldspot	5.472	chr3L	19166598	19167178	fz2	4.63
chr3L	16661018	16661248	Galpha73B	5.396	chr3L	19383728	19384039	CG32206	4.049
chr3L	16863689	16864251	Lmpt	4.208	chr3L	19429378	19429494	Chd3	10.453
chr3L	16885804	16886319	Lmpt	6.969	chr3L	19429609	19429901	Chd3	9.195
chr3L	16886283	16886616	Lmpt	4.963	chr3L	19511889	19512682	Cpr76Ba	6.897
chr3L	16892859	16893039	Lmpt	10.453	chr3L	19517561	19517805	Cpr76Bc	5.839
chr3L	16937385	16937810	CG13027	4.63	chr3L	19685192	19685812	verm	4.237
chr3L	16949801	16950337	Nc73EF	5.587	chr3L	19826482	19826739	trc	6.356
chr3L	17122035	17122328	Rbp6	6	chr3L	20245963	20246136	CG13814	12.698
chr3L	17341139	17341588	Mip	6.203	chr3L	20274947	20275570	gogo	7.802
chr3L	17387044	17387201	blot	5.894	chr3L	20275447	20276156	gogo	6.657
chr3L	17453913	17454874	CG7603	4.252	chr3L	20275447	20276226	gogo	6.506
chr3L	17565342	17565597	Eip74EF	4.104	chr3L	20275451	20276382	gogo	4.864
chr3L	17626325	17626470	CG7497	4.695	chr3L	20303559	20304264	polo	5.682
chr3L	17663069	17663922	CG34251	4.91	chr3L	20519639	20519968	CG4858	7.042
chr3L	17663832	17664446	CG34251	6.237	chr3L	20679943	20680222	kni	4.839
chr3L	17663914	17664706	CG34251	5.78	chr3L	20692956	20693766	kni	4.049
chr3L	17697024	17697975	Ccn	4	chr3L	20693687	20694153	kni	10.791
chr3L	17969143	17969696	Eip75B	6.667	chr3L	20783996	20784488	Six4	5.61
chr3L	17969637	17969929	Eip75B	6.645	chr3L	20928008	20928737	fng	4.155
chr3L	17969637	17970167	Eip75B	5.489	chr3L	21041778	21042678	siz	4.735
chr3L	17969637	17970354	Eip75B	4.848	chr3L	21072572	21072709	ko	14.706
chr3L	18002310	18003000	Eip75B	5.141	chr3L	21266774	21266985	AcCoAS	9.804
chr3L	18002916	18003477	Eip75B	13.072	chr3L	21364728	21365283	CG32440	6.479
chr3L	18003457	18004212	Eip75B	4.155	chr3L	21641930	21642622	CG33291	4.278
chr3L	18128023	18128467	Cyp312a1	6.502	chr3L	21762705	21762883	CG7370	7.042
chr3L	18163344	18163639	W	10.799	chr3L	21970523	21970740	CG7470	5.839
chr3L	18163344	18164208	W	5.888	chr3L	22036327	22036793	TyrR	6.353
chr3L	18344382	18344631	rpr	11.152	chr3L	22036327	22037026	TyrR	4.594
chr3L	18418356	18418736	skl	14.388	chr3L	22085977	22086938	msopa	4.545
chr3L	18418356	18419029	skl	8.183	chr3L	22135149	22135557	olf413	5.764
chr3L	18437461	18437704	skl	10.811	chr3L	22326625	22327028	Ten-m	5.333
chr3L	18504760	18504927	AICR2	12.698	chr3L	22446949	22447309	CG11449	5.682
chr3L	18548838	18549485	star1	4.438	chr3L	22449444	22449852	CG11449	4.735
chr3L	18680018	18680759	Cyp12c1	7.102	chr3L	22490509	22490858	CG12377	4.695
chr3L	18748947	18749219	ftz-f1	17.045	chr3L	22536754	22536972	CG11404	7.449
chr3L	18802243	18802522	CG14073	5.083	chr3L	22536677	22537535	CG11404	4.024
chr3L	18819214	18819652	Cat	4	chr3L	22603902	22604308	CG6914	4.598

chr3L	22643943	22644239	CG33771	5.839	chr3R	2745668	2746235	Antp	4.963
chr3L	22703155	22704024	CG11370	4.38	chr3R	2937175	2937693	Alh	4.41
chr3L	22779743	22780274	SPoCk	7.712	chr3R	2938645	2939200	Alh	9.677
chr3L	22782136	22782916	CG14448	6.479	chr3R	2968635	2969037	CG14610	12.012
chr3L	23023493	23024046	nrm	10.135	chr3R	2994981	2995707	sas	12.012
chr3L	23956132	23956827	CG40470	4.036	chr3R	2995600	2996607	sas	4.049
chr3R	165870	166119	CG1103	9.009	chr3R	3005820	3006410	sas	4.537
chr3R	167005	167730	CG1103	4.646	chr3R	3109554	3110428	rn	5.472
chr3R	261728	262406	CG1074	5.472	chr3R	3151053	3151516	CG10029	6.356
chr3R	274370	274850	CG31522	6.349	chr3R	3215484	3216317	Ir84a	4.695
chr3R	277518	278130	CG31522	4.155	chr3R	3331090	3331385	CG1287	10.453
chr3R	277518	278222	CG31522	4	chr3R	3575096	3575785	pyd3	6.757
chr3R	660303	661180	CG14659	4.908	chr3R	3639325	3639830	CG31473	4.104
chr3R	679576	680011	opa	4.695	chr3R	3851992	3852402	CG2747	5.083
chr3R	1101003	1101605	l(3)82Fd	4.695	chr3R	3975341	3975522	grn	9.195
chr3R	1213109	1213856	kkv	4.208	chr3R	3975341	3975786	grn	8
chr3R	1237319	1238266	Or83b	4.208	chr3R	3978441	3978655	grn	6.237
chr3R	1238222	1238675	CG14669	4.362	chr3R	4020770	4021200	CheA84a	5.641
chr3R	1318768	1318914	CG31547	8.31	chr3R	4049815	4050363	CG18249	4.077
chr3R	1319023	1319750	CG31547	4.598	chr3R	4102638	4102804	ato	9.804
chr3R	1367955	1368188	CG2519	23.077	chr3R	4102638	4102927	ato	9.39
chr3R	1473357	1473704	MTA1-like	5.61	chr3R	4338262	4339015	Or85c	4.438
chr3R	1519744	1520464	plx	4.983	chr3R	4403133	4403663	Cenp-C	6
chr3R	1597839	1598445	CG2082	6.757	chr3R	4476135	4477056	Mkk4	4.563
chr3R	1889106	1889512	CG15580	8.646	chr3R	4568470	4569005	CG9801	5.202
chr3R	1908527	1908771	Or83c	6.608	chr3R	4749838	4750820	pyd	5.78
chr3R	1998191	1998459	Osi1	9.677	chr3R	4858119	4859016	neur	4.193
chr3R	1998191	1999037	Osi1	4.799	chr3R	5220388	5220996	Fps85D	11.99
chr3R	2061822	2062640	Osi6	4.355	chr3R	5268610	5269097	ps	4.323
chr3R	2130819	2131261	Osi16	4.261	chr3R	5275729	5276699	CG9362	6.518
chr3R	2146531	2146754	Osi17	6.427	chr3R	5277458	5277826	CG9362	5.472
chr3R	2146742	2146922	Osi17	6.237	chr3R	5277458	5278023	CG9362	5.453
chr3R	2146742	2146976	Osi17	4.854	chr3R	5277458	5278400	CG9362	5.357
chr3R	2239952	2240168	gpp	9.828	chr3R	5307214	5307346	CG16779	12.987
chr3R	2239952	2240374	gpp	5.144	chr3R	5427077	5427227	CG8312	12
chr3R	2245910	2246216	gpp	5.333	chr3R	5427077	5427814	CG8312	6.427
chr3R	2329972	2330257	CG15186	4.38	chr3R	5471944	5472295	Dh	14.706
chr3R	2525381	2526173	pncr002:3R	4.639	chr3R	5473197	5473592	Dh	4.839
chr3R	2565668	2566447	pb	5.931	chr3R	5473408	5473833	Dh	6.11
chr3R	2608915	2609434	Dfd	5.997	chr3R	5569129	5569665	CG34409	5.78

chr3R	5645486	5645967	CG9458	4.38	chr3R	7927251	7927735	dpr17	13.85
chr3R	5677558	5678105	Teh1	6.173	chr3R	8171724	8172653	CG10038	5.083
chr3R	5682873	5683180	Teh1	7.716	chr3R	8172620	8173194	CG10038	12
chr3R	5682873	5683534	Teh1	4.264	chr3R	8395821	8396186	Octbeta2R	5.894
chr3R	5688552	5688923	Teh1	4.963	chr3R	8557260	8557604	CG5724	6.088
chr3R	5689683	5690190	Teh1	6.417	chr3R	8651703	8651915	CG31345	4.839
chr3R	5707220	5707965	CG34360	4.029	chr3R	8657679	8658038	beat-Va	8
chr3R	6092685	6092852	CG11870	5.78	chr3R	8680509	8681023	CG10126	4.864
chr3R	6093929	6094123	CG11870	6.356	chr3R	8680654	8680843	CG10126	5.682
chr3R	6118388	6118569	CG11870	6.479	chr3R	8680820	8681023	CG10126	12.448
chr3R	6258562	6258727	Cyp12e1	17.316	chr3R	8686732	8687570	CG10126	4.983
chr3R	6391560	6391829	hth	12.853	chr3R	8691020	8691171	CG10126	10.791
chr3R	6416488	6417440	hth	4.036	chr3R	8784044	8784280	granny-smith	4.63
chr3R	6419496	6420159	hth	4.154	chr3R	8928781	8929555	timeout	5.682
chr3R	6433169	6434025	hth	4.029	chr3R	8964169	8964695	timeout	6.757
chr3R	6433779	6434478	hth	4.464	chr3R	8964555	8964831	timeout	8.523
chr3R	6517123	6517663	Skeletor	4.566	chr3R	8998815	8998928	CG8138	46.154
chr3R	6571118	6571523	Takr86C	5.226	chr3R	9033721	9034020	CG8483	8.306
chr3R	6840190	6840769	CG34114	7.538	chr3R	9189968	9190145	poly	8.108
chr3R	6840334	6840501	CG34114	9.804	chr3R	9190074	9190766	poly	4.32
chr3R	6840357	6840769	CG34114	11.152	chr3R	9201976	9202930	CG9813	4.208
chr3R	6845562	6846486	CG34114	4.208	chr3R	9203736	9204027	CG9813	6.897
chr3R	7015706	7015986	CG18577	4.695	chr3R	9335368	9335699	CG12538	4.155
chr3R	7124382	7124765	CG31386	5.682	chr3R	9362646	9363161	CG31337	5.453
chr3R	7124726	7124956	CG31386	4.963	chr3R	9640489	9640644	tal-1A	17.964
chr3R	7196909	7197346	pros	10.135	chr3R	9670696	9671137	CG31495	5.31
chr3R	7214222	7214483	pros	4.91	chr3R	9681387	9681751	CG14362	11.583
chr3R	7214448	7214904	pros	5.624	chr3R	9681457	9681830	CG14362	9.524
chr3R	7316922	7317150	dpr5	4.91	chr3R	9681387	9682123	CG14362	5
chr3R	7393135	7393808	CG6783	4.5	chr3R	9712680	9712937	E5	6.26
chr3R	7417951	7418288	Jupiter	4.908	chr3R	9712787	9713452	E5	4.908
chr3R	7418187	7418850	Jupiter	4.695	chr3R	9742304	9742855	ems	5.146
chr3R	7428790	7428943	Jupiter	7.895	chr3R	9751645	9752592	Art9	4.454
chr3R	7556408	7556918	CG12594	4.104	chr3R	9815059	9815403	rdx	4.323
chr3R	7556905	7557515	CG12594	5.059	chr3R	9922789	9923084	CG9920	12
chr3R	7596614	7596962	l(3)neo38	5.764	chr3R	9997507	9998317	DopR	5.025
chr3R	7678663	7679310	CG6959	5.226	chr3R	10250955	10251272	CG34388	7.538
chr3R	7734433	7735140	CG34307	5.396	chr3R	10250955	10251448	CG34388	5.54
chr3R	7876818	7877107	CG14739	5.059	chr3R	10466922	10467186	CG7886	5.146
chr3R	7927251	7927494	dpr17	20.27	chr3R	10467138	10467327	CG7886	8.31

chr3R	10488088	10488324	Rad17	5.78	chr3R	13902140	13902464	CG14317	6.757
chr3R	10872566	10872894	RpL10Aa	11.99	chr3R	13915032	13915793	sr	5.837
chr3R	10899187	10899615	dpr9	6.042	chr3R	13915760	13916140	sr	9.009
chr3R	10901485	10901716	dpr9	4.438	chr3R	13915760	13916255	sr	8.475
chr3R	10901664	10902372	dpr9	4.839	chr3R	13920475	13920621	sr	11.583
chr3R	11126887	11127353	Tm1	11.152	chr3R	13928588	13929035	sr	4.762
chr3R	11129501	11129610	Tm1	12.448	chr3R	14070738	14071209	14-3-3epsilon	4.499
chr3R	11136288	11137255	Tm2	5.472	chr3R	14071114	14071632	14-3-3epsilon	5.146
chr3R	11297867	11298371	CG14869	6.452	chr3R	14119480	14120332	l(3)05822	5.764
chr3R	11505946	11506743	pxb	6.281	chr3R	14161324	14161942	CG31235	5.31
chr3R	11506717	11506930	pxb	10.453	chr3R	14245139	14245561	fru	11.261
chr3R	11506717	11506968	pxb	8.811	chr3R	14245553	14246197	fru	9.592
chr3R	11654376	11654548	rec	6.356	chr3R	14248598	14248753	fru	9.259
chr3R	11671521	11671839	CG31150	6.757	chr3R	14266986	14267256	fru	7.496
chr3R	11724417	11725138	glob1	4.802	chr3R	14266986	14267838	fru	4.874
chr3R	11765177	11766001	Sap47	4.292	chr3R	14269942	14270781	fru	6.452
chr3R	11821366	11821577	srp	4.438	chr3R	14270754	14270915	fru	8.108
chr3R	11969307	11969478	Sb	5.495	chr3R	14712422	14713265	CG14298	4.115
chr3R	12116724	12117516	gish	5.495	chr3R	14721801	14722128	CG14297	5.146
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chr3R	12216922	12217684	ss	5.059	chr3R	14787777	14788468	CG42613	4
chr3R	12369565	12370418	CG42342	4.839	chr3R	14793874	14794585	CG42613	6.317
chr3R	12370312	12370635	CG42342	7.859	chr3R	14798631	14799000	CG42613	5.764
chr3R	12411217	12412034	Scp2	5.022	chr3R	14942629	14943595	CG6040	4.983
chr3R	12768569	12768775	Abd-B	4.983	chr3R	15071419	15072096	unc79	4.498
chr3R	12787863	12788455	Abd-B	5.045	chr3R	15164129	15164253	Dl	8.108
chr3R	12798431	12799347	CG14909	4.802	chr3R	15313213	15314076	Dys	5.398
chr3R	12836361	12836995	CG8907	4.63	chr3R	15313862	15314130	Dys	9.009
chr3R	12920356	12921242	cher	4.104	chr3R	15324859	15325298	Dys	5.917
chr3R	13192607	13192948	beat-IIa	4.63	chr3R	15495682	15495917	CG7432	7.194
chr3R	13392637	13392937	Hmx	5.61	chr3R	15643170	15643820	bnl	4.104
chr3R	13410168	13410717	CG7587	5.241	chr3R	15662545	15663159	bnl	6.897
chr3R	13727669	13728056	Rim	11.662	chr3R	15696736	15697471	CG4562	4.802
chr3R	13852636	13853077	CG7794	4.745	chr3R	15728209	15728576	CG4538	5.059
chr3R	13857284	13858056	CG7794	4.745	chr3R	16063859	16064154	CG34139	4.104
chr3R	13858042	13858240	CG7794	8.31	chr3R	16066818	16067752	CG34139	6.349
chr3R	13858042	13858366	CG7794	6.349	chr3R	16068036	16069024	CG34139	6.05
chr3R	13885074	13885464	htl	6.281	chr3R	16157495	16158025	Sirt2	4.802
chr3R	13885368	13885611	htl	8.316	chr3R	16224877	16225089	mun	8.523
chr3R	13885368	13885988	htl	5.453	chr3R	16225721	16226191	mun	4.566

chr3R	16491332	16491596	Cpr92F	7.371	chr3R	18576823	18577198	CG7029	7.712
chr3R	16509585	16510376	Oamb	9.333	chr3R	18646858	18647331	CG13840	6.745
chr3R	16575594	16576513	CG42322	4	chr3R	18662696	18663304	CG4704	4.802
chr3R	16576505	16577166	CG42322	16.216	chr3R	18669324	18669812	CG4704	4.955
chr3R	16576505	16577320	CG42322	10.811	chr3R	18671471	18671742	CG4704	4.208
chr3R	16577475	16577731	CG42322	10.453	chr3R	18674304	18675246	CG4704	4.355
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chr3R	16601066	16601460	CG17838	4.762	chr3R	18810681	18811050	Nha2	7.102
chr3R	16623355	16623731	CG17838	5.059	chr3R	18810795	18811043	Nha2	7.712
chr3R	16625779	16626410	CG17838	4.454	chr3R	18811007	18811642	Nha2	4.092
chr3R	16676670	16676847	RpS30	7.194	chr3R	18884197	18885177	sav	4.108
chr3R	16783534	16783995	Atpalpha	5.682	chr3R	19263879	19264407	CG4374	4.566
chr3R	16783724	16784460	Atpalpha	6.281	chr3R	19264362	19264651	CG4374	7.712
chr3R	16865998	16866431	Dhc93AB	4.323	chr3R	19316981	19317556	Ir94h	6.925
chr3R	17114270	17114885	SIFR	7.013	chr3R	19317490	19317764	Ir94h	5.472
chr3R	17166023	17166816	CG16791	4.155	chr3R	19374705	19374956	CG10164	4.566
chr3R	17167092	17167371	CG16791	5.31	chr3R	19386168	19386466	beat-IV	8.85
chr3R	17219899	17220257	CG6475	9.39	chr3R	19406427	19406572	beat-IV	15.464
chr3R	17227902	17228674	CG6475	4.155	chr3R	19406929	19407138	beat-IV	14.388
chr3R	17515932	17516143	CG31176	6.11	chr3R	19411574	19411804	CG10182	6.861
chr3R	17516268	17516623	CG31176	5.807	chr3R	19420818	19421567	CG16723	4.963
chr3R	17516268	17516937	CG31176	5.109	chr3R	19506209	19506541	eIF-3p66	5.025
chr3R	17521863	17522423	CG31176	5.31	chr3R	19542573	19542941	nau	4.63
chr3R	17521969	17522964	CG31176	4.104	chr3R	19692177	19692408	Pli	8.475
chr3R	17622337	17622762	Caki	6.427	chr3R	19692177	19692436	Pli	7.825
chr3R	17622925	17623370	Caki	6.897	chr3R	19692177	19692876	Pli	5.445
chr3R	17622925	17623641	Caki	4.907	chr3R	19827638	19828089	KrT95D	14.205
chr3R	17646250	17646385	Caki	7.712	chr3R	19900658	19900929	4EHP	7.955
chr3R	17761522	17762330	Eip93F	4.029	chr3R	20084274	20084955	jar	5.54
chr3R	17789677	17789958	Eip93F	9.576	chr3R	20306411	20307084	nAcRalpha-96Ab	4.545
chr3R	17789812	17790491	Eip93F	5.821	chr3R	20315040	20315365	nAcRalpha-96Ab	4.104
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chr3R	17842198	17842842	CG6439	5.472	chr3R	20435243	20435531	mld	4.498
chr3R	18169950	18170434	CG5386	4.362	chr3R	20465514	20465646	CG5794	8.746
chr3R	18173135	18173521	CG7077	4.695	chr3R	20488179	20488598	Ppox	4.208
chr3R	18229016	18229193	CG13856	20.27	chr3R	20530072	20530762	slo	7.042
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chr3R	18404128	18404698	CG33110	4					

chr3R	20620671	20621114	Ets96B	9.634	chr3R	23474018	23474314	tau	4.983
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chr3R	20723782	20724644	CG13643	4.636	chr3R	23614347	23614927	CG34353	4.193
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chr3R	21180942	21181629	Fur1	5.54	chr3R	23754794	23755098	CG5508	9.009
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chr3R	21181335	21181629	Fur1	12.853	chr3R	24017535	24017769	CG34354	5.333
chr3R	21181335	21181697	Fur1	10.292	chr3R	24100897	24101008	CG34436	11.152
chr3R	21181335	21181760	Fur1	8.13	chr3R	24192039	24192379	Or98b	7.013
chr3R	21188352	21188646	Fur1	6.925	chr3R	24330924	24331444	Dhc98D	4.438
chr3R	21337084	21337249	CG5111	5.396	chr3R	24362969	24363149	Ppn	7.895
chr3R	21543218	21543658	LpR2	5.764	chr3R	24510479	24510832	CG9990	8.475
chr3R	21593234	21593900	CG17198	4.468	chr3R	24608260	24608415	CG34295	8.108
chr3R	21593778	21593893	CG17198	10.135	chr3R	24743976	24744984	Doa	6.757
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chr3R	21841859	21842512	m2	4.38	chr3R	25030103	25030394	CG14508	10.811
chr3R	22105129	22105441	CG6154	10.791	chr3R	25054148	25054472	CG15817	10.799
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chr3R	22175815	22176001	CG33970	7.538	chr3R	25385815	25386078	Dr	5.495
chr3R	22488463	22488838	beat-VII	4.762	chr3R	25476851	25477000	DopR2	6.356
chr3R	22594220	22594589	CG14247	4.049	chr3R	25476976	25477226	DopR2	5.202
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chr3R	22700735	22701187	Rb97D	4.5	chr3R	25508461	25509106	Gycalpha99B	4.468
chr3R	22701018	22701717	Rb97D	4.036	chr3R	25515317	25515538	Obp99c	6.897
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chr3R	22781437	22782222	CG6330	4.155	chr3R	25525960	25526278	dmrt99B	5.78
chr3R	22794877	22795033	CG5521	16.216	chr3R	25835709	25836647	Nlp	4.292
chr3R	22848651	22849035	CG6277	4.762	chr3R	26085322	26085818	CG18404	4.438
chr3R	23020862	23021206	Ser	7.371	chr3R	26085803	26086001	CG18404	9.804
chr3R	23023485	23023747	Ser	6.452	chr3R	26085803	26086296	CG18404	7.326
chr3R	23024121	23024697	Ser	4.908	chr3R	26085803	26086494	CG18404	5.869
chr3R	23163337	23163694	CG42534	5.587	chr3R	26108882	26109633	hdc	4.208
chr3R	23263704	23264703	side	4.839	chr3R	26109522	26110017	hdc	5.78
chr3R	23312041	23312878	Gr98a	5.472	chr3R	26109522	26110191	hdc	4.193
chr3R	23441585	23442095	CG5612	7.449	chr3R	26183458	26183626	hdc	4.38
chr3R	23441922	23442232	CG5612	6.608	chr3R	26188367	26188684	hdc	5.097

chr3R	26214714	26215533	Fer2LCH	4.049	chrX	699050	699535	CG13358	4.63
chr3R	26262374	26262734	CG15537	5.396	chrX	737955	738428	CG42248	4.91
chr3R	26546831	26547533	CG1340	4.5	chrX	850483	851420	CG3690	4.186
chr3R	26555065	26555263	CG11313	11.583	chrX	851240	851779	CG3690	4.101
chr3R	26555065	26555794	CG11313	5.888	chrX	870800	871012	CG18823	5.333
chr3R	26661279	26661459	CG15544	9.259	chrX	1307325	1308304	futsch	4.854
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chr3R	26683550	26684350	tll	4.284	chrX	1440160	1440622	Mur2B	7.874
chr3R	26691739	26692188	Cpr100A	7.895	chrX	1440160	1440865	Mur2B	6.446
chr3R	26692176	26692520	Cpr100A	12	chrX	1441156	1441517	Mur2B	7.595
chr3R	26749747	26750113	Ptx1	4.208	chrX	1441156	1441768	Mur2B	5.685
chr3R	26782169	26782745	CG15548	5.398	chrX	1532678	1533617	br	4.908
chr3R	26847475	26848082	CG33773	4.104	chrX	1533609	1534076	br	4.049
chr3R	26866687	26867287	CanA1	11.08	chrX	1571335	1571644	CG32809	12.448
chr3R	26895090	26895679	Sox100B	4.498	chrX	1608725	1608877	CG3795	12.987
chr3R	27062927	27063358	CG31005	5.568	chrX	1608725	1609145	CG3795	6.925
chr3R	27087939	27088272	CG18673	7.712	chrX	1621058	1621225	CG3795	9.009
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chr3R	27094788	27095337	CG15555	4.498	chrX	1841463	1841854	CG3600	8.31
chr3R	27094788	27095518	CG15555	4.036	chrX	1927139	1927557	Actn	5.587
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chr3R	27114846	27115037	CG11340	18.587	chrX	1927416	1928168	Actn	4.193
chr3R	27114846	27115598	CG11340	11.561	chrX	2137156	2137659	fs(1)K10	4.264
chr3R	27114846	27115847	CG11340	9.576	chrX	2350394	2350589	boi	7.538
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chr3R	27192639	27193088	gskt	6.237	chrX	2538537	2538727	sgg	9.259
chr3R	27196952	27197404	gskt	6.757	chrX	2538537	2538749	sgg	6.745
chr3R	27436758	27437150	Med	5.682	chrX	2792414	2793123	CG3526	4.695
chr3R	27457913	27458029	pasha	10.135	chrX	2792852	2792987	CG3526	6.757
chr3R	27467495	27467746	kek6	9.195	chrX	2792979	2793123	CG3526	6.608
chr3R	27530248	27530683	CG34046	4.545	chrX	2845399	2845667	rst	5.682
chr3R	27648008	27648312	RhoGAP100F	6.645	chrX	2851042	2851330	rst	5.059
chr3R	27648232	27648499	RhoGAP100F	7.707	chrX	2854369	2854566	rst	4.208
chr3R	27648232	27649091	RhoGAP100F	5.102	chrX	2924312	2925141	kirre	5.226
chr3R	27775745	27776660	heph	5.682	chrX	3176149	3176935	dnc	4.598
chr3R	27802020	27802695	heph	4.63	chrX	3262710	3263206	dm	7.895
chr3R	27802643	27802842	heph	6	chrX	3375036	3375847	CG10804	5.297
chrX	311157	311412	CG32816	8.108	chrX	3441393	3442125	CG32792	4.049
chrX	404694	405164	arg	6.356	chrX	3616273	3616761	tlk	4.575
chrX	502406	503089	CG13366	6	chrX	3698375	3699331	fd3F	5.445

chrX	3719353	3720105	ec	4.874	chrX	5394207	5394371	CG32762	9.804
chrX	3719866	3719984	ec	7.538	chrX	5410399	5410939	CG12730	4.566
chrX	3719976	3720105	ec	10.135	chrX	5539617	5540000	CG42492	4.498
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chrX	3733800	3734008	ec	9.828	chrX	5630409	5631126	CG32758	4.454
chrX	3973166	3973644	CG32790	5.31	chrX	5986995	5987157	Nep1	14.706
chrX	3988556	3989474	CG6379	4.695	chrX	6076385	6076646	CG32750	10
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chrX	4270820	4270990	CG12688	6.757	chrX	6364018	6364304	CG42340	9.259
chrX	4271464	4271719	CG12688	5.78	chrX	6550708	6550822	I(1)G0148	7.895
chrX	4289214	4289722	CG32773	6.645	chrX	6639699	6639937	CG14439	9.009
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chrX	4292753	4292924	CG32773	23.077	chrX	6645361	6645819	CG14439	5.059
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chrX	4316564	4316967	bi	13.937	chrX	6777523	6777958	CG33692	5.141
chrX	4316564	4317147	bi	8.576	chrX	6843460	6844081	CG4575	7.61
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chrX	4537020	4537166	CG3062	5.61	chrX	6896064	6896555	inx7	9.158
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chrX	4743214	4744145	CG12682	4.32	chrX	7044452	7045439	CR32730	4.598
chrX	4744126	4744632	CG12682	7.859	chrX	7045288	7045706	CR32730	12.563
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chrX	4978131	4978353	CG32767	11.152	chrX	7045980	7046834	CR32730	5.575
chrX	5098863	5099530	rg	8.058	chrX	7046259	7046785	CR32730	7.624
chrX	5112012	5112211	rg	4.63	chrX	7046566	7046753	CR32730	11.662
chrX	5112177	5112402	rg	5.61	chrX	7053628	7053864	CR32730	8.147
chrX	5112367	5112555	rg	8.108	chrX	7079903	7080035	CG9650	7.371
chrX	5116018	5116402	rg	5.31	chrX	7085026	7085137	CG9650	16.216
chrX	5236033	5236908	SK	5.059	chrX	7085784	7086000	CG9650	6.417
chrX	5247286	5248227	SK	4.049	chrX	7085946	7086223	CG9650	11.583
chrX	5247364	5248331	SK	4.498	chrX	7088623	7088970	CG9650	5.398
chrX	5267054	5267289	SK	5.869	chrX	7089826	7089950	CG9650	16.216
chrX	5267054	5267896	SK	4.271	chrX	7095907	7096504	CG9650	4.278
chrX	5327068	5327416	CG15784	6	chrX	7171647	7172097	CG1677	6.757
chrX	5327401	5327536	CG15784	9.259	chrX	7254677	7255090	CG1999	4.498

chrX	7279347	7280150	CheA7a	4.908	chrX	8510818	8511123	Caf1-180	4.983
chrX	7309556	7310205	CG34337	5.931	chrX	8546795	8547002	oc	9.259
chrX	7326488	7326735	CG32726	7.449	chrX	8690345	8690999	Lim1	4.537
chrX	7346438	7346712	CG11368	5.587	chrX	9147761	9147923	CG17754	10.453
chrX	7389199	7389687	CG32719	8.316	chrX	9168784	9169201	CG16892	4.155
chrX	7396287	7396430	CG32719	13.514	chrX	9534852	9535748	I(1)G0232	5.025
chrX	7400758	7401576	CG32719	4.501	chrX	9536351	9536666	I(1)G0232	10.283
chrX	7400758	7401692	CG32719	4.086	chrX	9536351	9537227	I(1)G0232	6.502
chrX	7419443	7419878	CG32720	10.135	chrX	9599836	9600677	btd	6.897
chrX	7425629	7426014	CG32720	8.31	chrX	9613824	9614386	Sp1	4.036
chrX	7437421	7437777	CG32720	4.983	chrX	9614371	9614822	Sp1	5.495
chrX	7460473	7460711	CG11369	10.791	chrX	9621433	9621807	Sp1	6.818
chrX	7460473	7460868	CG11369	8.811	chrX	9699819	9700383	CG32698	4.695
chrX	7506368	7507074	ct	8.31	chrX	9759446	9760324	Ser7	4.292
chrX	7506539	7507474	ct	6.969	chrX	9770756	9771412	CG15247	4.438
chrX	7559248	7559662	ct	5.102	chrX	9771299	9771522	CG15247	6.11
chrX	7612152	7612741	CG15478	4.695	chrX	9771404	9771702	CG15247	6
chrX	7613267	7614271	CG15478	4.271	chrX	9771404	9771745	CG15247	5.61
chrX	7613681	7614261	CG15478	6.645	chrX	9855636	9855911	CG1791	6.088
chrX	7614206	7614494	Hira	6.615	chrX	10254526	10255508	I(1)G0289	5.025
chrX	7614206	7614763	Hira	5.686	chrX	10291727	10292031	flw	8
chrX	7614206	7615181	Hira	4.038	chrX	10461749	10462317	CG15296	5.495
chrX	7655614	7656469	Ir7a	4.38	chrX	10506502	10506955	CG9817	4.63
chrX	7656440	7656644	Ir7a	10.135	chrX	10510012	10510280	CG15295	6.26
chrX	7656636	7657132	Ir7a	9.195	chrX	10676100	10676326	Ant2	4.38
chrX	7668886	7669517	CG32718	5.682	chrX	10708160	10708547	Imp	5.587
chrX	7907996	7908130	Tbh	7.371	chrX	10712978	10713427	Imp	5.946
chrX	8129007	8129574	sdt	4.036	chrX	10732085	10732282	sbr	6
chrX	8174077	8174720	nAcRalpha-7E	7.013	chrX	10784434	10784744	Ork1	11.583
chrX	8212775	8213419	nAcRalpha-7E	7.117	chrX	10850959	10851148	Myo10A	6.356
chrX	8212775	8213520	nAcRalpha-7E	6.098	chrX	10851119	10851755	Myo10A	5.398
chrX	8216496	8216804	nAcRalpha-7E	20.27	chrX	11053231	11053416	Dlic	12.987
chrX	8228956	8229167	nAcRalpha-7E	5.146	chrX	11053995	11054812	Dlic	7.042
chrX	8231998	8232257	nAcRalpha-7E	6	chrX	11148599	11149053	CG15198	6.26
chrX	8231998	8232387	nAcRalpha-7E	5.682	chrX	11307286	11307657	Gr10a	6.757
chrX	8279226	8279598	CG1387	4.802	chrX	11343405	11343595	CG11727	5.894
chrX	8369514	8370200	CG33223	5.587	chrX	11343405	11343795	CG11727	4.362
chrX	8375853	8376607	CG33223	4.024	chrX	11421375	11421787	CG32666	9.592
chrX	8503095	8503791	Caf1-180	5.54	chrX	11636134	11636665	inaF-A	4.38
chrX	8509894	8510850	Caf1-180	4.955	chrX	11742444	11742688	CG15740	16.216

chrX	11874048	11874641	cac	4	chrX	14814304	14814454	Flo-2	9.804
chrX	11966741	11967352	CG12721	6	chrX	14818543	14818942	Flo-2	9.195
chrX	11966741	11967366	CG12721	5.472	chrX	14819822	14820139	Flo-2	14.706
chrX	11973362	11973549	CG12721	5.78	chrX	14824106	14824233	Flo-2	9.259
chrX	11981847	11982013	CR32657	4.38	chrX	14824106	14824744	Flo-2	5.839
chrX	12067681	12067895	CG1924	8.31	chrX	14892992	14893713	eag	6.969
chrX	12398458	12399312	CG2556	5.045	chrX	14892992	14893729	eag	6.75
chrX	12469975	12470965	CG11138	5.348	chrX	15219773	15220026	Top1	4.208
chrX	12470856	12471787	CG11138	12.698	chrX	15228168	15229032	HDAC6	4.498
chrX	12535806	12536350	tomosyn	9.524	chrX	15289865	15290159	cngl	15.789
chrX	12536201	12536515	tomosyn	11.152	chrX	15289865	15290317	cngl	10.955
chrX	12538947	12539298	tomosyn	5.78	chrX	15289865	15290335	cngl	10.796
chrX	12680730	12681196	CG32647	12.012	chrX	15419155	15419537	Ac13E	6.745
chrX	13075221	13075333	CG34411	15.464	chrX	15496287	15496937	sog	4.122
chrX	13075211	13075562	CG34411	6.353	chrX	15537132	15537533	CG8117	6.173
chrX	13081685	13082036	CG34411	6.84	chrX	15537501	15538247	CG8117	6.173
chrX	13147890	13148111	mew	6.088	chrX	15545285	15545603	CG8117	9.259
chrX	13172860	13173829	HDAC4	4.154	chrX	16017940	16018051	disco-r	8.523
chrX	13174376	13174683	HDAC4	9.823	chrX	16224236	16224606	CG9919	11.583
chrX	13174624	13175150	HDAC4	12.346	chrX	16224236	16224797	CG9919	10.526
chrX	13174611	13175322	HDAC4	8.759	chrX	16336719	16336920	CG4420	5.495
chrX	13216836	13217068	IP3K2	5.839	chrX	16336719	16337405	CG4420	4.908
chrX	13216836	13217699	IP3K2	5.109	chrX	16662690	16663277	if	8
chrX	13280499	13280940	Yippee	5.587	chrX	17065104	17065830	baz	7.194
chrX	13419065	13419700	CG15753	7.326	chrX	17098306	17098432	CG5070	13.514
chrX	13541445	13541753	NFAT	4.438	chrX	17257031	17257448	B-H1	18.779
chrX	13541648	13542014	NFAT	8.108	chrX	17285901	17286770	B-H1	6.925
chrX	13554716	13554949	NFAT	8.746	chrX	17286069	17286971	B-H1	6.068
chrX	13754142	13754931	CG11071	9.39	chrX	17310658	17310797	CG8611	9.009
chrX	13754406	13755177	CG11071	13.937	chrX	17395644	17396057	CG8557	8.108
chrX	13901702	13902304	Ste12DOR	4.062	chrX	17751152	17751433	CG6762	4.261
chrX	13905574	13906263	Ste12DOR	4	chrX	17889456	17889973	Sh	4.695
chrX	13964053	13964261	Ste:CG33236	6.479	chrX	17921214	17921708	Sh	4.695
chrX	14623820	14624121	NetB	9.009	chrX	18014569	18015181	wupA	5.839
chrX	14758846	14759052	Flo-2	7.371	chrX	18294850	18295166	CG32549	13.85
chrX	14767902	14768311	Flo-2	7.449	chrX	18359402	18359936	CG32547	4
chrX	14768217	14768452	Flo-2	6.547	chrX	18360606	18360815	CG32547	8.108
chrX	14770433	14770621	Flo-2	6.479	chrX	18375717	18376233	CG6361	5.917
chrX	14813513	14814454	Flo-2	4.092	chrX	18431351	18431909	Bx	4.261
chrX	14814116	14814340	Flo-2	6.356	chrX	18431557	18431980	Bx	5.396

chrX	18467562	18467785	Bx	7.042	chrX	20455753	20455893	RunxA	27.027
chrX	18636699	18637191	CG6873	4.598	chrX	20484455	20485306	RunxA	4.963
chrX	18779210	18779915	CG7332	4.566	chrX	20579735	20579983	run	7.371
chrX	19066161	19066500	pncr004:X	7.194	chrX	20579883	20580091	run	10.453
chrX	19105597	19105742	CG14195	10.791	chrX	20579975	20580238	run	9.259
chrX	19105597	19105965	CG14195	6.427	chrX	20585112	20585314	run	4.63
chrX	19482442	19483026	CG14219	4.049	chrX	20601090	20601490	CG1324	6.237
chrX	19656576	19657150	CG12702	4.983	chrX	20601698	20602062	CG1324	6.173
chrX	19657246	19657917	CG12702	4.237	chrX	20613398	20613953	CG15452	5.396
chrX	19710922	19711264	skpC	5.568	chrX	20664649	20665170	shakB	9.174
chrX	19719671	19719926	skpE	6.11	chrX	20665107	20665786	shakB	7.396
chrX	19837078	19838008	CG12655	4.323	chrX	20690628	20691217	CG15450	5.618
chrX	19873652	19874002	Nep3	7.825	chrX	20702805	20703272	CG15450	7.895
chrX	19908406	19908693	D2R	4.208	chrX	20716127	20716427	CG15450	8.31
chrX	19949512	19950051	CG9570	4	chrX	20716127	20716607	CG15450	5.025
chrX	19952231	19952499	CG9570	6.479	chrX	20721449	20722409	CG1314	4.723
chrX	19963547	19964145	CG9570	5.333	chrX	20732323	20732979	CG1314	7.859
chrX	20143096	20143318	inx6	5.226	chrX	21107853	21107985	CG32521	27.027
chrX	20143831	20144581	inx6	7.895	chrX	21227676	21228417	sol	4.065
chrX	20147518	20148336	inx6	4.727	chrX	21303993	21304232	CG42343	5.54
chrX	20429441	20429750	RunxB	5.097	chrX	21350034	21350588	Ir20a	4.261
chrX	20429704	20429964	RunxB	6.588	chrX	21939610	21939833	CG17600	5.146
chrX	20435236	20435939	CG42580	6.203	chrX	22200275	22201278	CG12446	4.386
chrX	20435844	20436118	CG42580	4.983					

Table S2.4. Predicted clusters for the *Drosophila melanogaster* genome (Dm3). Clusters with a cluster coefficient ≥ 4 annotated to the nearest transcription start site.

Annotation	Genomic coordinates (dm3)
<i>dpp</i> +35	chr2L:2464301-2465300
<i>wg</i> -3.7	chr2L:7303415-7303860
<i>wg</i> +4.2	chr2L:7311428-7312755
<i>Sema-1a</i>	chr2L:8639890-8640550
<i>ptc</i> -6.4	chr2R:4530660-4531850
<i>ptc</i> -4.8	chr2R:4532251-4533000
<i>PKA-R2</i>	chr2R:5906490-5907830
<i>kn</i> +11	chr2R:10674125-10674700
<i>kn</i> -13	chr2R:10699301-10700165
<i>Hs3st-A</i> +4.3	chr2R:14609939-14611000
<i>Hs3st-A</i> +21	chr2R:14627251-14628100
<i>dve</i> -6.8	chr2R:18124601-18125550
<i>dve</i> +21	chr2R:18152960-18154300
<i>dve</i> +25	chr2R:18157301-18158200
<i>dally</i>	chr3L:8818181-8820095
<i>PKA-C3</i>	chr3L:15913901-15915270
<i>boi</i>	chrX:2350251-2351550
<i>sgg</i>	chrX:2538250-2539000

S5 Table. Clusters containing ci/GLI sites of low MSS tested in the chicken neural tube assay.

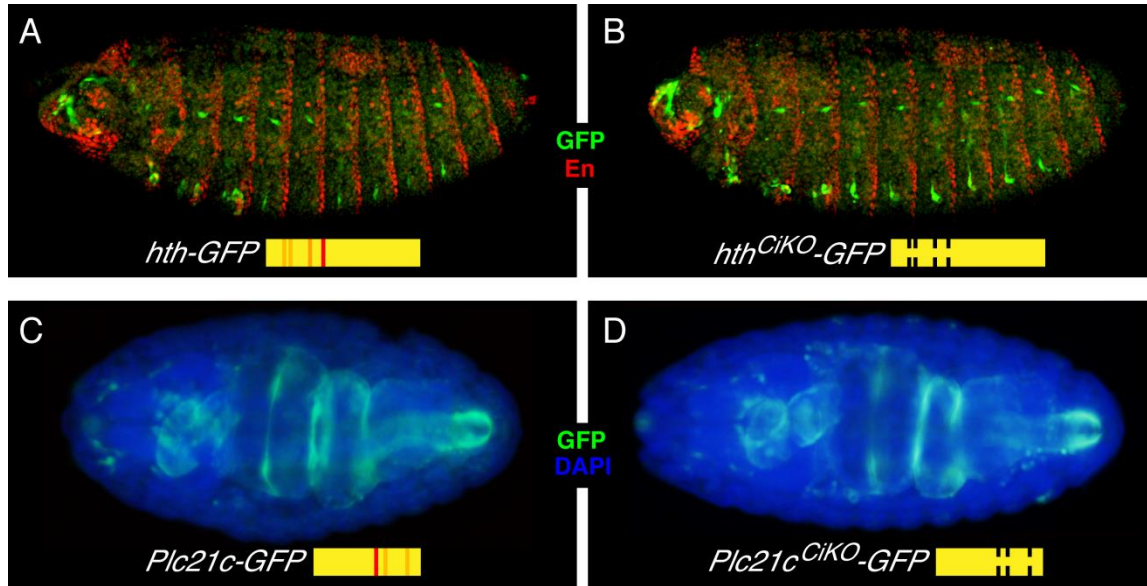


Figure S2.3. Expression of *hth* and *Plc21C* regions in the fly are not ci/GLI-dependent.

Both *hth* and *Plc21C* drive GFP expression in the fly embryo. *Hth* exhibits expression in the brain as well as a punctate segmental pattern parallel but outside of En expression (shown in red) which marks cells that produce and secrete Hh ligand (AB). *Plc21C* expresses throughout the gut (C). Expression for both constructs is not Hh dependent since it persists after mutation of ci/GLI binding sites (BD).

DamID locations from Biehs et al. (Build dm3)						
Chromosome	Start	End	Cluster Start	Cluster End	Symbol	Gene
chr2L	1455284	1456528	1455873	1456140	snRNA:U3:22A	NR_001600
chr2L	1927769	1928140	1927228	1928142	CG7337	NM_001103581
chr2L	7538466	7543325	7538294	7539165	Rapgap1	NM_001103644
chr2L	9111843	9113084	9111745	9112729	Or30a	NM_078796
chr2L	15937296	15944819	15937185	15937383	beat-Ib	NM_078855
chr2L	17431677	17434112	17433182	17433529	CG5043	NM_135994
chr2R	2655624	2656580	2656051	2656477	Epac	NM_001103732
chr2R	6418206	6419765	6418353	6418759	lola*	NM_080027
chr2R	6462021	6462381	6461408	6462025	psq	NM_165790
chr2R	11004693	11007129	11004180	11005090	chn	NM_206119
chr2R	11336766	11337435	11336714	11337271	CG34365	NM_001103852
chr2R	12283866	12284542	12284061	12284394	CG33960	NM_001038863
chr2R	12412600	12412659	12412235	12412734	Sema-2a	NM_166178
chr2R	12414984	12419228	12416993	12417312	Sema-2a	NM_166178
chr2R	12498703	12500537	12498903	12499084	CG5065	NM_137299
chr2R	12658866	12659557	12659107	12659386	unc-104	NM_166192
chr2R	12677166	12679045	12676636	12677619	CG5522	NM_166193
chr2R	13045282	13055248	13051217	13051370	CG10953	NM_137355
chr2R	13073470	13078925	13073362	13073564	CG10950	NM_137356
chr2R	13166767	13167736	13166630	13167109	mbl	NM_176211
chr2R	13391488	13396940	13394739	13395102	CG4844	NM_001032265
chr2R	15209157	15212514	15211205	15211546	Rgk1	NM_137567
chr2R	15681071	15682013	15680992	15681678	Obp56g	NM_137603
chr2R	15742583	15743824	15743081	15743609	Obp56i	NM_166376
chr2R	18226254	18226613	18226458	18226970	CG11206	NM_001103944
chr2R	18259854	18261720	18260459	18261287	Rtf1	NM_137821
chr2R	18431154	18433651	18432448	18432907	px*	NM_001103947
chr2R	20272172	20272571	20272357	20273224	mAcR-60C	NM_079120
chr3L	8052940	8054760	8052894	8053443	bip1	NM_139912
chr3L	11862617	11864769	11864451	11864952	CG5906	NM_140261
chr3L	12458113	12459080	12457913	12458121	eyg	NM_079318
chr3L	13940701	13941699	13941029	13941736	CG32137	NM_168564
chr3L	17339408	17344264	17341139	17341588	Mip	NM_140714
chr3L	20692805	20697982	20692956	20693766	kni*	NM_079463
chr3R	2329935	2332092	2329972	2330257	CG15186	NM_169145
chr3R	3976809	3982873	3978441	3978655	grn	NM_001144554

chr3R	4101609	4106766	4102638	4102804	ato*	NM_169213
chr3R	4401007	4404074	4403133	4403663	Cenp-C	NM_169228
chr3R	5682908	5683267	5682873	5683534	Teh1	NM_141702
chr3R	9669658	9672691	9670696	9671137	CG31495	NM_169559
chr3R	17217597	17220086	17219899	17220257	CG6475	NM_001104389
chr3R	17227813	17229687	17227902	17228674	CG6475	NM_001104389
chr3R	20530764	20536210	20530430	20531229	slo	NM_001170241
chr3R	20549088	20550942	20549943	20550067	tok	NM_170168
chr3R	21180551	21181210	21180942	21181629	Fur1	NM_170654
chrX	3720410	3720469	3719976	3720491	ec	NM_130722
chrX	4249010	4249973	4249936	4250271	norpA	NM_001169190
chrX	4256130	4258561	4256588	4257103	norpA	NM_080330
chrX	4537017	4537076	4537020	4537166	CG3062	NM_131949
chrX	5540520	5540876	5539974	5540628	CG42492	NM_001169205
chrX	6202614	6205080	6202296	6202630	CG3823	NM_132085
chrX	6297612	6298259	6296956	6297618	CG33669	NM_001031872
chrX	7309802	7314072	7309556	7310205	CG34337	NM_001103431
chrX	7400950	7404588	7400758	7401576	CG32719	NM_167128
chrX	15536311	15537530	15537132	15537533	CG8117	NM_132821

Table S2.6. Overlap between clusters predicted in this study and DamID protected sites.

Asterisks indicate four sites that map to one of the 52 probable *ci* target genes identified by Biehs *et al.* (Biehs *et al.*, 2010).

Chapter III

Computational prediction and experimental validation of novel Hedgehog-responsive enhancers linked to genes of the Hedgehog pathway

3.1 Abstract

The Hedgehog (Hh) signaling pathway, acting through three homologous transcription factors (GLI1, GLI2, GLI3) in vertebrates, plays multiple roles in embryonic organ development and adult tissue homeostasis. At the level of the genome, GLI factors bind to specific motifs in enhancers, some of which are hundreds of kilobases removed from the gene promoter. These enhancers integrate the Hh signal in a context-specific manner to control the spatiotemporal pattern of target gene expression. Importantly, a number of genes that encode Hh pathway molecules are themselves targets of Hh signaling, allowing pathway regulation by an intricate balance of feed-back activation and inhibition. However, surprisingly few of the critical enhancer elements that control these pathway target genes have been identified despite the fact that such elements are central determinants of Hh signaling activity. Recently, ChIP studies have been carried out in multiple tissue contexts using mouse models carrying FLAG-tagged GLI proteins (GLI^{FLAG}). Using these datasets, we tested whether a meta-analysis of GLI binding sites, coupled with a machine learning approach, could reveal genomic features that could be used to

empirically identify Hh-regulated enhancers linked to loci of the Hh signaling pathway.

A meta-analysis of four existing GLI^{FLAG} datasets revealed a library of GLI binding motifs that was substantially more restricted than the potential sites predicted by previous *in vitro* binding studies. A machine learning method (kmer-SVM) was then applied to these datasets and enriched k-mers were identified that, when applied to the mouse genome, predicted as many as 37,000 potential Hh enhancers. For functional analysis, we selected nine regions which were annotated to putative Hh pathway molecules and found that seven exhibited GLI-dependent activity, indicating that they are directly regulated by Hh signaling (78% success rate).

The results suggest that Hh enhancer regions share common sequence features. The kmer-SVM machine learning approach identifies those features and can successfully predict functional Hh regulatory regions in genomic DNA surrounding Hh pathway molecules and likely, other Hh targets. Additionally, the library of enriched GLI binding motifs that we have identified may allow improved identification of functional GLI binding sites.

Keywords: Hedgehog signaling; enhancers; machine learning; GLI

3.2 Background

The Hedgehog (Hh) signaling pathway is critical for embryonic organ development and adult tissue homeostasis across animal phyla (McMahon et al., 2003; Jiang and Hui, 2008; Briscoe and Théron, 2013; Petrova and Joyner, 2014). In multiple tissue-specific settings, Hh signaling directs specific cell fate choices, controls tissue patterning and governs cell proliferation. In mammals, Hh signaling originates with any of three ligands (Sonic hedgehog

(*Shh*), Indian hedgehog (*Ihh*) or Desert hedgehog (*Dhh*)) (for Review see (Varjosalo and Taipale, 2008)). Release of the lipid modified HH ligand has been shown to be facilitated by SCUBE in conjunction with the transmembrane protein Dispatched (Burke et al., 1999; Jeong and McMahon, 2002; Creanga et al., 2012; Jakobs et al., 2014). Once discharged, HH ligands interact with the Patched (PTCH1 or PTCH2) receptor protein and with Hh-binding proteins BOC, CDO and GAS1 on target cells to relieve PTCH-dependent inhibition of the Smoothed (SMO) transmembrane protein (Allen et al., 2011; Izzi et al., 2011). HH ligands can also be sequestered by the Hedgehog-interacting protein (HHIP), which dampens signaling (Chuang and McMahon, 1999).

Hh-mediated signal transduction culminates in the nucleus, with the binding of zinc-finger transcription factors (GLI1, GLI2, GLI3) to target gene sequences (Kim et al., 2009; Goetz and Anderson, 2010). However, proteolytic processing determines whether the GLI proteins act as repressors or activators. GLI1, which is not processed, functions exclusively as a transcriptional activator and may act to amplify Hh signals (Dai et al., 1999). GLI2 and GLI3 can be converted to a repressor form in the absence of Hh ligand. In the presence of the Hh ligand, this processing is inhibited, allowing full-length GLI proteins to traffic to the nucleus and activate gene expression (Dai et al., 1999; Sasaki et al., 1999; Shin et al., 1999). Processing of GLI proteins requires passage through the cilia (Kim et al., 2009; Beachy et al., 2010); the kinesin KIF7 helps to properly construct the cilium and is enriched at the cilium tip, along with GLI and SUFU (Suppressor of Fused) (Liem et al., 2009).

The Hh signaling pathway is regulated by both positive and negative feedback. Indeed, a number of Hh pathway components, including *Boc*, *Cdo*, *Gas1*, *Gli1*, *Hhip*, *Ptch1* and *Ptch2* are

thought to be direct transcriptional targets of Hh signaling in multiple tissue contexts (Chuang and McMahon, 1999; Dai et al., 1999; Agren et al., 2004; Rahnama et al., 2004; Tenzen et al., 2006; Aglyamova and Agarwala, 2007; Martinelli and Fan, 2007; Vokes et al., 2007; Vokes et al., 2008; Lee et al., 2010; Peterson et al., 2012; Holtz et al., 2013). Thus, an important aspect of Hh pathway self-regulation is integrated at the level of the enhancers that control response of the pathway target genes to local Hh signaling levels. However, despite the high functional conservation of this pathway, surprisingly little is known about the enhancer elements that control self-regulation in any organism.

One way to identify Hh target enhancers is to perform chromatin immunoprecipitation (ChIP). Genetically modified mouse models carrying inducible FLAG-tagged GLI proteins have allowed analysis of GLI binding sites *in vivo* in several different tissue contexts. Four *in vivo* GLI binding studies, including three ChIP-chip analyses (Vokes et al., 2007; Vokes et al., 2008; Lee et al., 2010) and one ChIP-seq study (Peterson et al., 2012), have been carried out using these models. Interestingly, examination of all four datasets for common GLI binding sites that are annotated to Hh pathway molecules reveals only three such sites (in *Gli1*, *Ptch1*, and *Ptch2* loci (Dai et al., 1999; Agren et al., 2004; Holtz et al., 2013)) that are uniformly detectable. Several other established Hh pathway genes, including *Boc*, *Hhip*, *Gli2*, and *Hipk2*, appear to exhibit different GLI-bound genomic locations, depending on context, suggesting that each of these pathway components is regulated by multiple distinct genomic enhancers that have context-specific features.

Using ChIP studies on diverse tissues, it may be possible to eventually identify all of the multiple enhancers that control each target gene in every context. While a valuable goal, such

analyses are expensive and time consuming. We therefore asked whether analysis of all existing GLI ChIP data could reveal common sequence features that might be used to empirically and globally predict functional enhancers *de novo*. A publicly available machine learning approach, kmer-SVM (Fletez-Brant et al., 2013), was used to predict novel Hh enhancer regions. This tool uses a support vector machine (SVM) to determine sequence features (k-mer frequencies) that identify positive genomic regulatory regions (Lee et al., 2011). SVMs are classifier algorithms that define a boundary between members of two different groups. Kmer-SVM calculates weights for sequence features that determine the effectiveness of that feature to distinguish between positive and negative regulatory regions. Once the features are determined, they can be used to identify novel enhancer regions not present in the original positive set. The strength of this approach is that it relies exclusively on short regions of DNA sequence (length 3-10 bp) which are in the size range of transcription factor binding sites (TFBS). Additionally, the organization of the k-mers within a sequence does not impact the score; this feature is consistent with the variable arrangement of TFBS in enhancers (Spitz and Furlong, 2012; Slattery et al., 2014).

Using the kmer-SVM tool (Fletez-Brant et al., 2013), analysis of the four existing GLI binding datasets identified a set of k-mers that appeared to successfully predict potential GLI-regulated enhancers. Application of this set of k-mers to the mouse genome pinpointed over 37,000 potential enhancers. Several putative enhancers that were annotated to Hh pathway components were then tested for their ability to drive Hh-dependent activity in transfected cells. The functional significance of the GLI binding motifs (GBM) was also tested within each active enhancer by mutation. Of the nine predicted regulatory regions tested, seven (78%) drove reporter expression in a GLI-dependent fashion. These findings substantially increase the number

of functionally verified Hh enhancers found in Hh pathway molecules and validate the use of machine learning on ChIP data as a valuable tool to empirically predict likely Hh-dependent regulatory regions.

3.3 Results and discussion

3.3.1 Analysis of GLI^{FLAG} datasets to identify likely *in vivo* GLI transcription factor binding motifs

A previous *in vitro* analysis of GLI transcription factor binding resulted in the identification of a set of likely binding sites for this factor (Hallikas et al., 2006). However, this spectrum of sites may not accurately represent GLI binding site preferences *in vivo*. To begin to examine this, we performed a meta-analysis of four existing GLI-ChIP datasets. All of these datasets utilize transgenic mice carrying FLAG tagged GLI1 (GLI1^{FLAG}) or GLI3 (GLI3^{FLAG}) in the ROSA26 locus, activated by Cre recombination, in four different tissue contexts: limb bud development (LD) (Vokes et al., 2008), cerebellum development (CD), medulloblastoma (MB) resulting from Hh signaling overexpression (Lee et al., 2010), and neural progenitor cells (NP) (Peterson et al., 2012). An additional study of neural progenitors (Vokes et al., 2007) was excluded from analysis since it contained a low number of significant peaks and mirrors the same experimental conditions as the NP dataset (Peterson et al., 2012). For each of the datasets, the reported percentage of ChIP peak sequences with GLI binding motifs (GBM) was as follows: LD 55%, CD 26%, MB 46%, and NP 91%. However, the definition of GBM was not the same across all datasets: one study allowed only two mismatches from the consensus (Vokes et al.,

2008) and others generated a GLI motif *de novo* based on the sequences of recovered peaks (Lee et al., 2010; Peterson et al., 2012).

To collate the spectrum of GBM observed in all four datasets, we applied a *de novo* motif enrichment analysis to each dataset individually (Heinz et al., 2010). Sequences that contained at least one site that matched the *de novo* motifs were removed from the dataset. The remaining sequences were analyzed for residual motifs that resembled a GBM using DREME (Bailey, 2011) and TOMTOM (Gupta et al., 2007) (see Methods). This resulted in 548 putative GBM (12-mers) (Table S3.1), encompassing the range of GBM that are present in existing ChIP data. This set therefore represents a collection of likely genomic GLI binding sites, although some functional GLI binding sites *in vivo* could be absent from this set and some false positive sites may be included. Each 12-mer was classified as high confidence (HC), medium confidence (MC), or low confidence (LC) if it was found within sequences from all four datasets, two to three datasets, or one dataset, respectively. The sequence logos (Crooks et al., 2004) for each classification, provided in Figure 3.1A, show a nearly absolute representation of CCxC in positions 4-7 for all sites. Indeed, concordant (C and C or G and G) nucleotides at the 5th and 7th position were previously found to be required for GLI binding (Winklmayr et al., 2010). Interestingly, for high confidence sites, there is no variation at 5 of the 12 positions, including the 5th and 7th positions (xGxCCxCxCxxx).

Using the recommended matrix similarity score cutoff of 81% overall matrix similarity to the optimal consensus GLI site as defined by the *in vitro* DNA binding assay (Hallikas et al., 2006) results in 1,432,161 putative GLI TFBS across the mouse genome. This is substantially more than the 191,745 found using the new GLI library defined by the *in vivo* ChIP studies.

However, several of the sites predicted by the *in vitro* binding studies do not contain the concordant (C and C or G and G) nucleotides at the 5th and 7th position. Thus, the newly generated GLI library (Figure 3.1A) may more accurately represent functional GBM.

According to this new library of 548 GBM, 41% of LD, 27% of CD, 32% of MB, and 80% of NP peaks contain putative GLI binding sites. For those sequences that contain a GBM, the vast majority contain only a single site (85.5% LD, 90.7% CD, 88.0% MB, 89.8% NP) (Figure 1B). The overlap of genomic binding regions among datasets is shown in Figure 3.1C; only 26 genomic coordinates are shared among all datasets (Table S3.2). Since pathway components must respond to the Hh signal in all tissues, it might be expected that this common response would be integrated by a single enhancer. However, only three of the 26 shared regions are annotated to known Hh pathway components (*Gli1*, *Ptch1*, *Ptch2*). Indeed, for *Boc* and *Hhip*, distinct genomic GLI binding regions are found in different datasets. This result suggests that some of these genes may have multiple enhancers that work to transduce the Hh signal in different tissue contexts.

Given this apparent complexity in regulatory regions, we next asked whether the existing datasets of ChIP peaks might contain additional sequence information that could be used to predict the location of other Hh-responsive enhancers in the mouse genome. A machine learning approach was employed to test this question.

3.3.2 Assessment of kmer-SVM performance and prediction

3.3.2.1 Kmer-SVM assessment of classification using GLI^{FLAG} datasets

For each GLI^{FLAG} dataset, only sequences with at least one GBM (wGBM, meaning *with GBM*) were used. This was done since a high proportion of the ChIP-chip datasets did not contain a putative GLI binding site as defined in the original papers (LD 55%, CD 26%, MB 46%, and NP 91%) or by our assessment (41% of LD, 27% of CD, 32% of MB, and 80% of NP peaks). Each individual dataset was submitted to kmer-SVM and the ability of each classifier to correctly label a candidate sequence as positive was assessed. Background sequences were randomly selected from the genome, but matched for GC content with the positive set.

Kmer-SVM randomly divides the data as follows: 80% of the sequences are used as a training set and 20% are used as a testing set. The ability of the classifier built with the training set to accurately identify the members of the remaining 20% testing set is then assessed. This is repeated five times, each with a different random division of the data. Receiver operating characteristic (ROC) curves and precision recall curves (PRC) are used to assess the success of the classifier to correctly label regions in the testing set as positive (see Methods).

ROC curves display the cumulative distribution of the true positive rate compared to the false positive rate. This characteristic assesses how well the classifier is able to label the positive sequences from the test set. The area under the curve was 0.898 for LDwGBM (Figure 3.2A), 0.856 for CDwGBM (Figure 3.2B), 0.862 for MBwGBM (Figure 3.2C) and 0.976 for NPwGBM (Figure 3.2D). Thus, the classifier performs best in LD and NP datasets.

PRC displays the predictive value against the true positive rate and represents the accuracy of the labeling. The PRC plots indicated high values for LDwGBM (AUC=0.753) and NPwGBM (AUC=0.880) but low values for CDwGBM (AUC=0.490) (Figure 3.2F) and

MBwGBM (AUC=0.546) (Figure 3.2E-H). The ROC and PRC plots for LDwGBM and NPwGBM datasets suggested that the classifier sequence features used were able to distinguish between positive and negative groups with a low level of false labeling.

3.3.2.2 Predictions

The classifiers for LDwGBM and NPwGBM were then individually run on 600 bp of sequence centered on every GBM in the mouse genome (191,745, as determined using the new GBM from in vivo data, described above). Use of both the LDwGBM and NPwGBM datasets for prediction incorporated data from the GLI1^{FLAG} (predominately activator) and GLI3^{FLAG} (predominantly repressor) transcription factors in two diverse contexts (neuronal precursor and limb development).

The length of 600 bp was selected based on motif enrichment analysis of the LD and NP datasets using MEME-ChIP (Machanick and Bailey, 2011) and Centrimo (Bailey and Machanick, 2012). This analysis showed that, within the ChIP-chip LD dataset, enrichment for the location of GLI motifs (green line) has a broad profile that spans 200 bp to either side of the midpoint (Figure S3.1A). The GLI motif has a narrower profile in the NP data, a feature that is expected for ChIP-seq (Figure S3.1B). The profile for the Sox motif (blue line), an established tissue specific GLI cofactor (Peterson et al., 2012), shows an enrichment peak that is centered around 200 bp on either side of the midpoint (Figure S3.1B) and suggests that cofactors for Hh may reside outside of the immediate vicinity of a GLI binding site. We therefore used 600 bp to capture both common Hh features as well as potential context specific sequence.

For the LDwGBM classifier, scores ranged from -4.33 to 12.00 with 18.4% of the 191,745 analyzed genomic regions scoring as positive (Score > 0). The NPwGBM results ranged from -2.54 to 5.48 with 5.7% positive (Figure 3.3A; Table S3.3). The categorization of a sequence is dependent on the sign of the score and the weight of the value is less important than the ranking. Overall, the correlation between scores for individual genomic regions calculated by the LDwGBM and NPwGBM classifiers is poor (0.68 Pearson) (Figure 3.3B). However, if only sequences with positive scores are considered, the correlation improves (0.85 Pearson). If scores are restricted to values indicating only the high confidence scores (calculated posterior probabilities = 1.0, Figure S3.2), the values are very well correlated (0.96 Pearson). In total, 8627 genomic regions were predicted as Hh enhancers by both classifiers. Of those, 1198 regions (14%) overlapped at least one peak in the four GLI^{FLAG} datasets. Among high confidence scores (LDwGBM: 5951 \geq 1, NPwGM: 547 \geq 1) 528 genomic regions were shared between the two datasets and 187 of these (35%) overlapped with peaks from at least one of the four GLI^{FLAG} datasets. All of the scored regions are listed in Table S3.3.

3.3.2.3 Evaluation of predictions

To assess whether kmer-SVM predictions were likely to represent Hh enhancers, we examined whether the predicted genomic regions overlapped publically available open chromatin and enhancer histone marks in tissues that were likely to be transducing Hh signals. We first examined the DNase I hypersensitive profile collected from mouse mesoderm at E11.5 at genomic regions that were predicted with high confidence as positive ($1 \leq$ score; posterior probability = 1) or negative ($-1 \geq$ score; posterior probability = 0) (Figure S3.2). A significantly higher proportion of overlap was found with the predicted positive regions than with predicted

negative regions (Z -Score = 2.8332; p -value < 0.05) (Table S3.4). We also examined publically available H3K4me1, H3K4me3, and H3K27ac ENCODE data collected from heart and liver at E14.5. Monomethylated H3K4 (H3K4me1) and histone H3 acetyl Lys27 H3K27ac (Creyghton et al., 2010) were used as enhancer markers while trimethylated H3K4 (H3K4me3) was expected to be depleted in enhancer regions (Heintzman et al., 2007). Although Hh signaling is active during early development of both tissues, available *in situ* analysis for GLI1 (GenePaint: EN1215) (Visel et al., 2004; Diez-Roux et al., 2011) shows GLI1 expression in liver but not heart at E14.5 (Figure S3.3). Thus, we expected signals for both H3K4me1 (poised enhancer) and H3K27ac (active enhancer) to be enriched in the predicted positive regions in liver but not heart at this time point. Indeed this was the case: H3K4me1 (Z -Score=2.5511; p -value < 0.01) and H3K27ac (Z -Score=8.076; p -value < 0.01), with no significant difference in H3K4me3 when predicted positive regions were compared to predicted negative regions. As expected, the heart data did not show enrichment for H3K4me1 or H3K27ac. Together, the results (summarized in Table S3.4) are consistent with the conclusion that the kmer-SVM classification correctly identifies Hh enhancer regions.

Next, we evaluated the sequence features, or k-mers, that kmer-SVM identified as primary components of Hh enhancer regions. The weights of k-mers are calculated during the SVM training and reflect the contribution of the k-mer to categorization of a sequence. Weights can be positive or negative and the sum of the weights of iterative k-mers across a sequence comprise the overall score of that sequence. Not surprisingly, alignment of k-mers with high scoring weights shared between both datasets returned a motif that strongly resembles the GBM (Figure 3.3C). Unique high weighted k-mers that occurred in each individual dataset represented

potential context specific features. An E-box motif was identified for the LDwGBM dataset while a Sox motif was returned for NPwGBM (Figure 3.3D). Negative weights that occurred in both datasets include AC and ACC repeats as well as other C rich sequences.

3.3.3 Functional verification of GLI-dependent enhancer activity

Predicted genomic regions were annotated to the two nearest genes using GREAT (McLean et al., 2010). Because our goal was to identify enhancers for Hh pathway components, we selected a subset of predictions that were positive in both the LDwGBM and NPwGBM datasets and that were annotated to members of the GO:0007224 Smoothed signaling pathway gene set. These regions were functionally tested for enhancer activity. The test set consisted of genomic regions annotated to *Boc*, *Gli3*, *Hhip*, *Hipk2*, *Ptch1*, *Scube1*, *Shh*, and *Tgfbr2*. An additional region, annotated to *Dpp6* (near *Shh*) was also tested (Table 3.1).

The nine genomic regions were screened for Hh responsiveness in a cell culture assay that has been previously used to validate Hh enhancers (Zhao et al., 2006; Gerber et al., 2007). In this assay, C2C12 cells are transiently transfected with constructs containing the putative Hh regulatory region cloned upstream of a minimal promoter that drives luciferase expression (see Methods). To induce a Hh response, enhancer reporter constructs were co-transfected with a plasmid that drives constitutive expression of GLI1 in mammalian cells (Vokes et al., 2007). For those candidate enhancers that demonstrated apparent Hh activation, GLI-dependent activity was confirmed by retesting after mutagenesis of the GLI binding sites (GKO). Either complete loss of enhancer activity or attenuation of response in GKO sequence was considered GLI-dependent. An established Hh enhancer region for *Ptch2* was used as a positive control (Holtz et al., 2013).

For the 9 regulatory regions annotated to Hh pathway component genes, 7 exhibited Hh activation that was directly dependent on a GLI binding site (Figure 3.4). The *Ptch2* positive control region showed a complete loss of Hh response after mutation of the GLI site (Figure 3.4) as did the regulatory regions annotated to *Hhip*, *Hipk2*, *Ptch1*, and *Scube1*. Regions annotated to *Boc*, *Dpp6*, and *Tgfbr2* showed a significant decrease in Hh activation upon GLI TFBS mutation, but not a complete loss of response. This suggests that additional regulatory inputs influence the activity of these enhancers. Neither the *Gli3* nor *Shh* region exhibited Hh dependent enhancer activity. However, we cannot rule out the possibility that these regions might be positive if examined in a different cellular context (Vokes et al., 2007).

Two previous *in silico* methods have been described for the identification of Hh-regulated enhancers in vertebrates: Enhancer Element Locator (EEL) and Module Cluster Analysis (MCA). EEL analyzes the estimated energy of a single transcription factor binding event, as well as the possible interaction between adjacent, highly conserved transcription factor binding sites, to detect potential enhancers (Hallikas et al., 2006). In contrast, MCA utilizes Poisson modeling to determine the relative enrichment of binding sites in highly conserved, non-coding sequence and, thereby, identify putative enhancers (Vokes et al., 2007). While both of these methods have had some success (~25%) in detecting putative Hh-regulated enhancers, a disadvantage to these approaches is that the search is limited to regions of high sequence conservation and to regions close to promoters. In contrast, kmer-SVM approach used here employs a genome-wide empirical analysis to locate regions that contain sequence features predictive of Hh enhancer function. The high success rate (78%) of the kmer-SVM predictions far exceed the previous prediction rates for EEL or MCA.

To examine the impact of k-mers that contribute to predictions of the positive regions, weights were plotted across each of the sequences. The *Ptch2* sequence (Figure 3.5A), a known enhancer region (Holtz et al., 2013), contained matching profiles for 8-mers predicted from LDwGBM (red) and NPwGBM (yellow) that are GC rich and similar to the GBM k-mers. However, mutation of the single GLI TFBS (Figure 3.5B, green box) ablates the Hh response, indicating that the presence of this GBM is required to transduce Hh signaling. Mutation of the GBMs annotated by the green boxes for *Hhip*, *Hipk2*, *Ptch1*, and *Scube1* (Figure 3.5EFGH) is also sufficient to abrogate Hh signal transduction. For *Boc*, *Dpp6*, and *Tgfbr2*, which show enhancer activity that remains after ablation of the GBM (Figure 3.5BCJ), there were no sequence characteristics that were indicative of a shared feature responsible for this remaining response to induction by GLI1. The *Boc* profile was the only one that contained a high weighted k-mer (annotated with an asterisk) that was unique to the LDwGBM (red) profile. This k-mer was similar to a Krox motif (TOMTOM p-value < 0.004) (Gupta et al., 2007) and may be enriched in the LDwGBM dataset as a context specific transcription factor, since it has roles in limb development (Levi et al., 1996; Nonchev et al., 1996). In general, most of the tested regions contain distributed high weighted 8-mers in addition to the central GBM and had profiles that contained consistent peaks in both LDwGM and NPwGBM datasets (Figure 3.5).

3.4 Conclusions

Facilitated by a new GBS library generated from a meta-analysis of genomic regions identified in *in vivo* binding studies (Vokes et al., 2007; Vokes et al., 2008; Lee et al., 2010; Peterson et al., 2012), we utilized the kmer-SVM machine learning approach to examine four

existing GLI ChIP databases and to generate classifiers that can empirically predict functional Hh enhancers from genomic DNA. Of nine predicted Hh target regulatory regions tested, seven were functionally verified as GLI-dependent. All of the tested regions were annotated to genes believed to be components of the Hh pathway and important determinants of the Hh response. Given the high success rate of Hh enhancer prediction in this small scale screen (78%), it is quite possible that a large number of the other predicted regions (Score > 0 in Table S3.3) may harbor Hh enhancer activity.

3.5 Methods

3.5.1 Computing resources

Except where otherwise indicated, all computational steps were performed using custom Perl and R scripts.

3.5.2 Publically available datasets

Genomic analysis was conducted on chromosomes 1 to 19, X and Y of mouse build mm9. Mouse ENCODE data (Gerstein et al., 2012) comprising open chromatin DNase I data that was collected at embryonic day 11.5 in the mesoderm and histone (H3K4me1, H3K4me3, and H3K27ac) data collected from embryonic day 14.5 for heart and liver were downloaded from the UCSC genome repository (goldenPath).

3.5.3 Definition of putative GLI binding motifs

The library of putative GLI binding motifs (GBM) was compiled using *de novo* motif analysis (Heinz et al., 2010) on each of the individual GLI^{FLAG} datasets iteratively. Sequences that contained a GBM were removed from the dataset and the remaining sequences were analyzed for enriched motifs using DREME (Bailey, 2011). If TOMTOM (Gupta et al., 2007) returned a GLI motif, the dataset was reanalyzed using Homer. The process continued until no residual GBM remained enriched in the dataset. Confidence in the GBM was classified as high (HC) if it was shared across sequences from all four GLI^{FLAG} datasets, medium (MC) if it was found in two or three datasets, and low (LC) if it only occurred in one.

3.5.4 kmer-SVM parameters and evaluation of classifiers

Training was run on the Beer lab webserver (<http://kmersvm.beerlab.org/>), using a k-mer of length of 8.

Performance of the classifier built by kmer-SVM's training algorithm was assessed using Receiver Operating Characteristic (ROC) and Precision-Recall curves (PRC) generated within the kmer-SVM program. True positive, true negative, false positive and false negative counts were generated by segregating the sets of positive and negative sequences into a training set (80% of the sequences) and a testing set (the remaining 20% of the sequences). Each member (individual sequence) of the testing set that is correctly annotated as positive increases the true positive count while an incorrect prediction of a positive sequence as negative increases the false negative count. ROC curves assess the sensitivity and specificity of the classifier output. A steep curve with a high area under the curve (AUC) indicates a high true positive rate and a low false positive rate. PRC evaluate the accuracy and relevance of the classifier output. A high AUC

indicates that the results have a low false positive rate (high precision) and a low false negative rate. The trained SVM is evaluated by assessing its ability to classify the testing set correctly. The classifier was assessed five times by resetting members in the training set and testing set.

3.5.5 Cloning of putative enhancer regions

Putative enhancers were amplified from C57BL/6 genomic DNA (supplied by Jackson Laboratory) using template-specific PCR primers (Table S3.4). A CACC extension was added to the end of one primer to facilitate directional cloning. PCR fragments were cloned into the pENTR/D-TOPO vector using the standard kit (Invitrogen) and then shuttled into the pGL3-Promoter luciferase vector (Promega) using the Gateway® cloning system (Invitrogen). QuikChange mutagenesis (Stratagene) was used to mutate putative GLI binding sites by replacing the C in the 6th position to a G.

3.5.6 Luciferase assay

C2C12 cells (35,000) were plated per well on 12-well plates (10% fetal bovine serum treated with penicillin, streptomycin and glutamate). After 24 hours, cells were transfected, using lipofectamine, with 400 ng of the construct containing the putative enhancer region plus either a control vector or GLI1 (in equal molecular weight). *Renilla* (Promega pRL-CMV) was also included to normalize transfection efficiency. After an additional 24 hours, cell media was changed to no serum to promote ciliogenesis (Santos and Reiter, 2008). Cell lysate was collected after 48 hours and measured for luciferase activity using the Dual-Luciferase® Reporter Assay System (Promega) on a Perkin Elmer Wallac Victor3 1420 Multilabel Counter. Three experimental replicates were collected for each condition.

3.6 Abbreviations

Hh: Hedgehog

HPC: Hedgehog pathway component

GBM: GLI binding motif

TFBS: transcription factor binding sites

SVM: support vector machine

E14.5: embryonic day 14.5 (mouse)

3.7 Competing interests

The authors have no competing interests to declare.

3.8 Authors' contributions

KG and DG conceived and designed the experiments. KG, GS, and KV performed the experiments. KG, KV, GS, and NR cloned and mutagenized constructs. KG analyzed the data. KG and DG wrote the manuscript. All authors reviewed the final manuscript.

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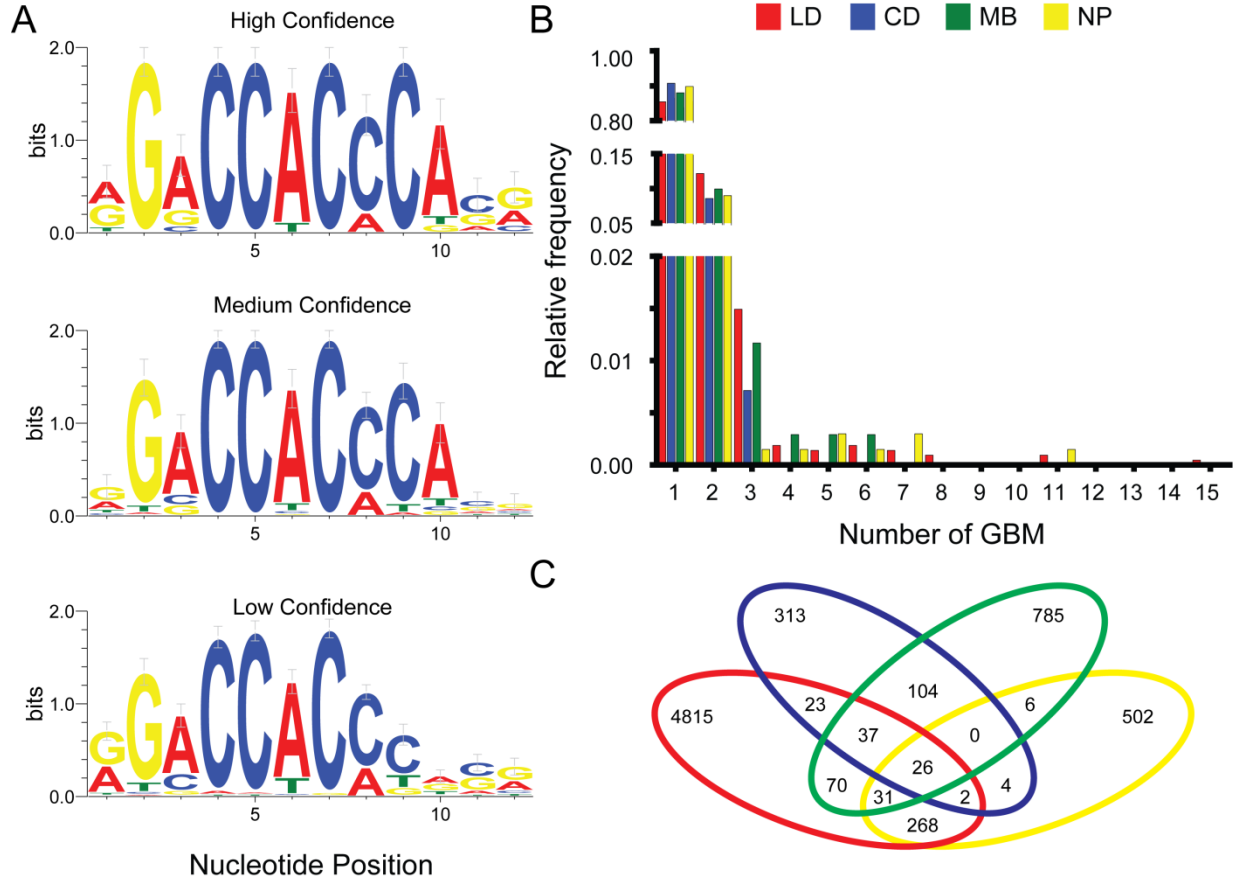


Figure 3.1. Definition of GLI binding motifs (GBM) and characterization of GLI^{FLAG} datasets. (A) Sequence logos (Weblogo) of 12-mer GBM. High confidence (HC), medium confidence (MC), and low confidence (LC) GBM are found in all four (HC), three or two (MC) or one (LC) datasets. Error bars represent twice the small sample correction. (B) Relative frequency of peaks containing one or more GBM in the GLI^{FLAG} ChIP-chip LD (red), CD (blue), MB (green), and GLI^{FLAG} ChIP-seq NP (yellow) datasets. A high proportion of sequences contain only one GBM. (C) Overlap of sequences identified by all four GLI^{FLAG} datasets; only 26 individual peaks are found in all contexts.

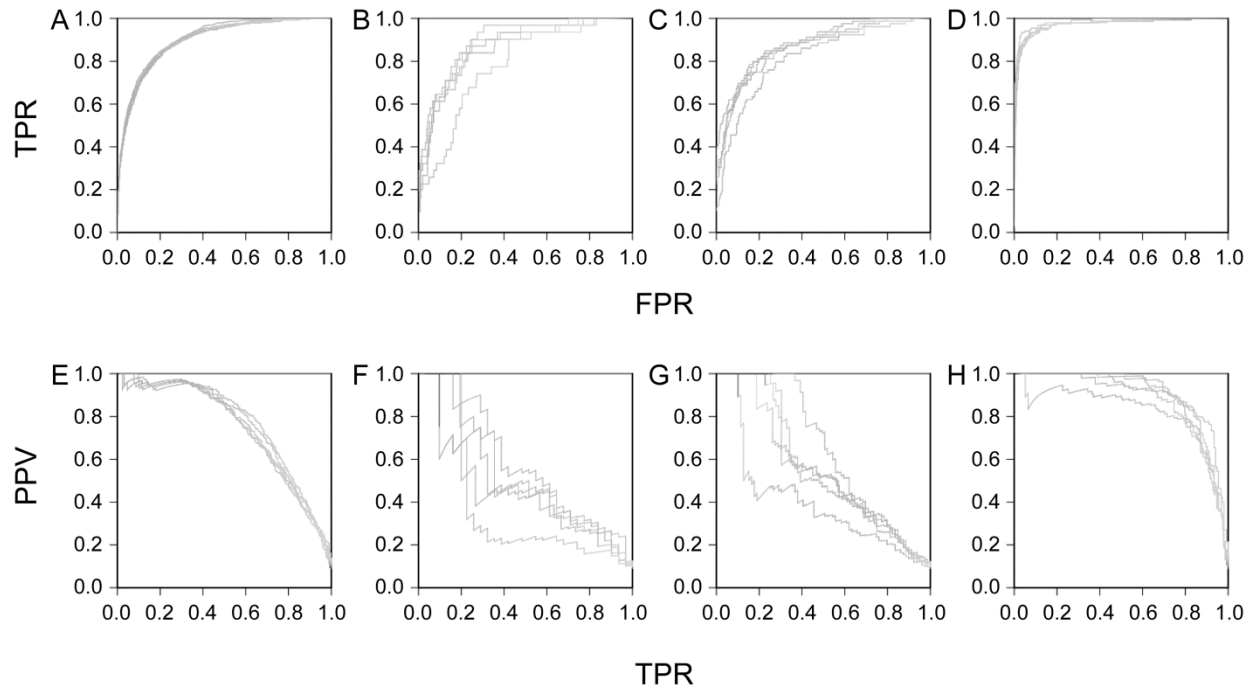


Figure 3.2. Assessment of classification capability of kmer-SVM trained GLI^{FLAG} datasets containing sequences with at least one GBM. For all curves, each dataset is randomly split into 80% for training and 20% for prediction and the prediction is repeated five times (represented by individual lines). Plots assess the likelihood that the specified classifier can successfully predict sequences that have at least one GBM as positive or negative. **(A-D)** ROC plots depicting true positive rates (TPR) and false positive rates (FPR). Area under the curve (AUC) scores as calculated by kmer-SVM are: 0.89 for LDwGBM (A), 0.85 for CDwGBM (B), 0.86 for MBwGBM (C) and 0.97 for NPwGBM (D) datasets. **(E-H)** Precision recall curves depicting the positive predictive value (PPV), calculated as true positive / (true positive + false positive), versus the TPR. AUC of 0.75 for LDwGBM (E) and 0.88 for NPwGBM (H) indicate reasonable confidence in the classification while AUC of 0.49 for CDwGBM (F) and 0.55 for MBwGBM (G) indicate a low probability that the region is correctly labeled when the sequence is classified as positive.

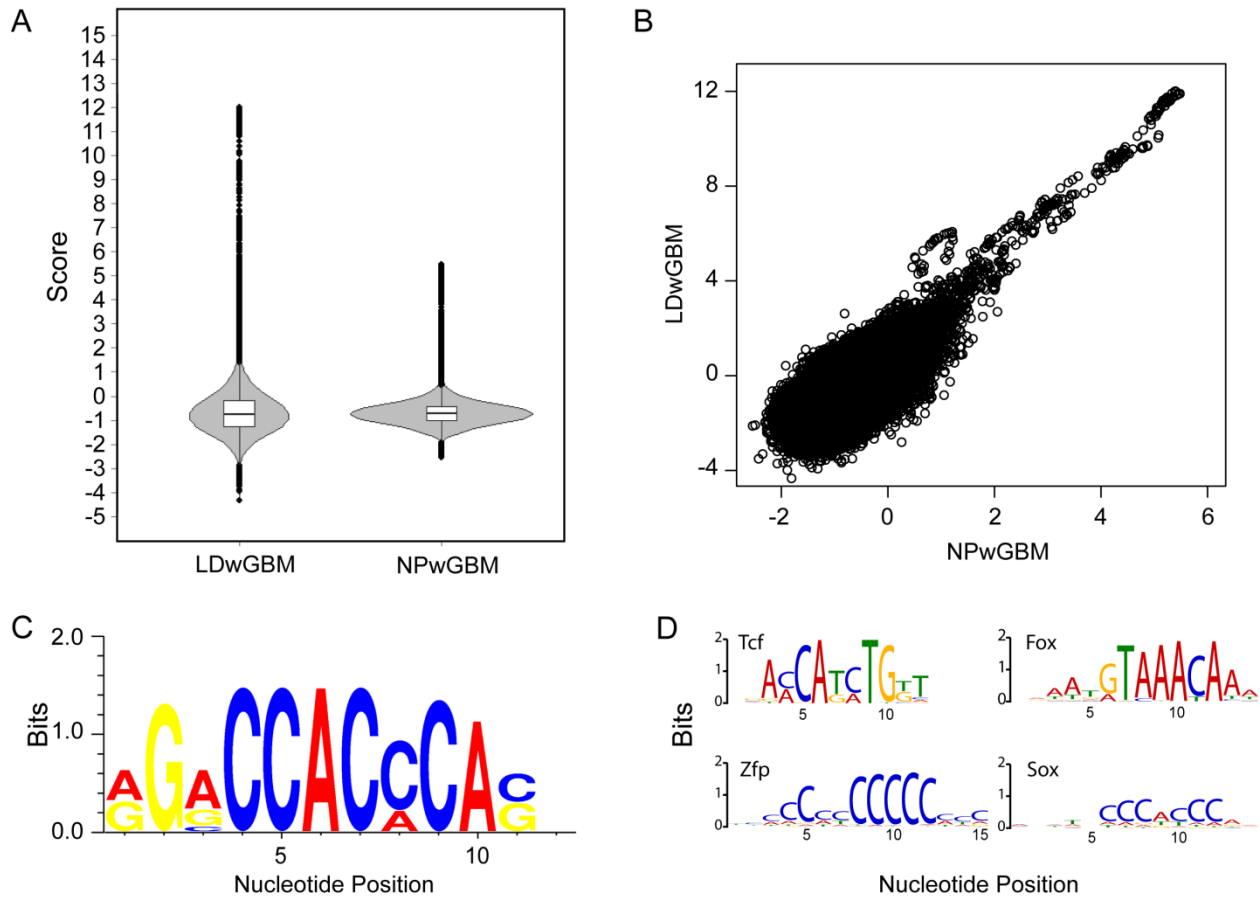


Figure 3.3. Assessment of genomic kmer-SVM predictions using classifiers trained on LDwGBM and NPwGBM datasets. (A) All genomic sequences matching the restricted 548 GBM 12-mers (wGMB) were identified and the 600bp surrounding each GBM were assessed and scored using the kmer-SVM classifier that was trained on each of the two datasets. (B) Correlation plot depicting the relationship between LDwGBM and NPwGBM scores; scores >1 are highly correlated in the two datasets. (C) GLI motif generated from overlapping high weighted k-mers shared between LDwGBM and NPwGBM classifiers. (D) High weighted k-mers (identified by TOMTOM) represented in either LDwGBM (Tcf and Zfp) or NPwGBM (Fox and Sox).

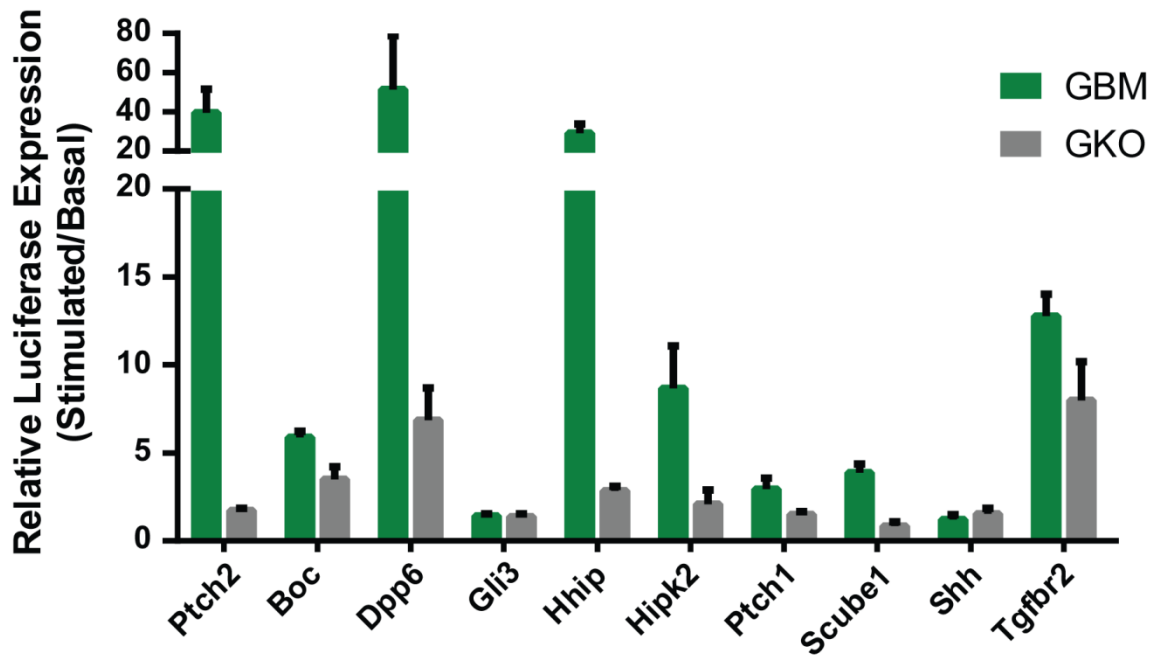


Figure 3.4. Functional verification of GLI-dependent enhancer activity. Putative regulatory regions were cloned upstream of a minimal promoter co-transfected into C2C12 cells, along with a GLI1 expression vector. Relative activity is plotted (stimulated/basal). The Ptch2 region is used as a positive control. Novel regions annotated to the *Boc*, *Dpp6*, *Hhip*, *Hipk2*, *Ptch1*, *Scube1*, and *Tgfbr2* loci exhibit upregulation in response to GLI1 co-transfection (green). Dependence on GLI was assessed by mutating all putative GLI TFBS (GKO) within the sequence and retesting in the assay (gray). Error bars represent the standard deviation of three experimental replicates.

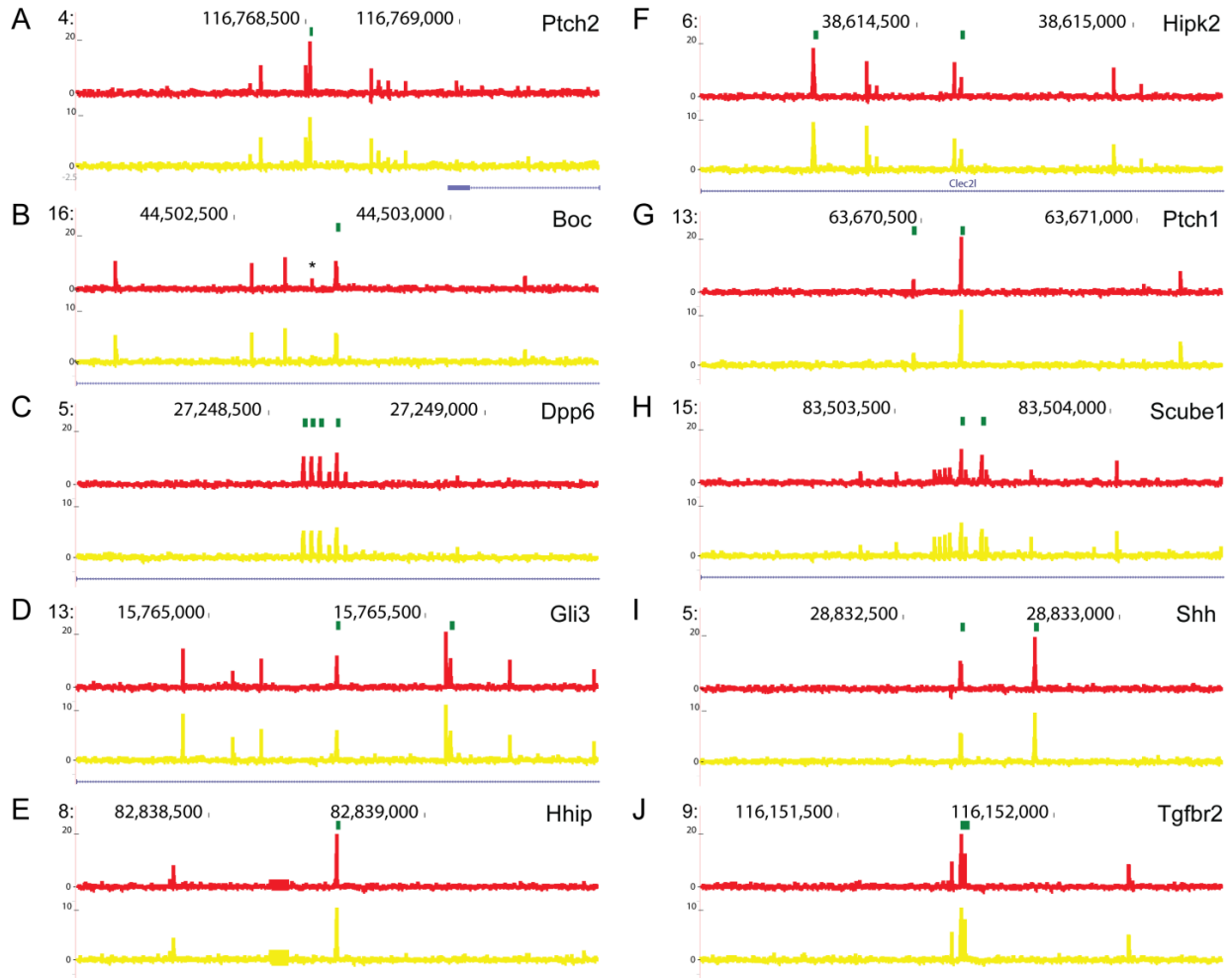


Figure 3.5. K-mer weights plotted across sequences that show enhancer activity. Diagrams were generated in UCSC Genome browser and show coordinate information. Green boxes represent GBM. Weights for LDwGBM and NPwGBM are represented by the red and yellow lines, respectively. Refseq gene annotations are represented in blue. A putative Krox-20 TFBS (*) that has a high weight in the LDwGBM classifier but not the NPwGBM classifier occurs in the sequence annotated to *Boc*. Note that most sequences show weighted k-mers located several hundred bp from the central GBM, suggesting that sequence motifs that predict Hh enhancer activity may be distributed.

Annotated Gene	Genomic Coordinates (mm9)	Hh Responsive	LD	CD	MB	NP
<i>Ptch2</i>	chr4:116,767,757-116,769,455	+	+	+	+	+
<i>Boc</i>	chr16:44,502,136-44,503,346	+	-	+	+	-
<i>Dpp6</i>	chr5:27,248,056-27,249,266	+	+	-	-	-
<i>Gli3</i>	chr13:15,764,694-15,765,904	-	-	-	-	-
<i>Hhip</i>	chr8:82,838,195-82,839,405	+	+	-	-	+
<i>Hipk2</i>	chr6:38,614,001-38,615,211	+	-	-	-	-
<i>Ptch1</i>	chr13:63669992-63671202	+	+	-	+	+
<i>Scube1</i>	chr15:83503053-83504263	+	-	-	-	-
<i>Shh</i>	chr5:28832033-28833243	-	-	-	-	-
<i>Tgfbr2</i>	chr9:116,151,184-116,152,394	+	-	-	-	-

Table 3.1. Assessment of predicted Hh enhancer regions. Seven of the nine regions predicted to be GLI-driven enhancers were indeed determined to be Hh responsive and GLI binding site dependent in a cell culture assay. Overlap of the predicted regions with peaks from the GLI^{FLAG} ChIP datasets (LD, CD, MB, NP) is indicated by the plus sign. *Boc*, *Hipk2*, *Scube1* and *Tgfbr2* were predicted by kmer-SVM and found to be positive, even though those regions do not overlap any of the peaks identified in the LD or NP datasets used to generate the kmer-SVM classifier.

Gli binding motifs (12mer)	Confidence
AGCCACCCAGG	HC
AGCCACCCACG	HC
AGCCACCCACA	HC
AGACCTCCCAGG	HC
AGACCTCCCACG	HC
AGACCTCCCACA	HC
AGACCACCCTGG	HC
AGACCACCCTCG	HC
AGACCACCCTCA	HC
AGACCACCCGGG	HC
AGACCACCCGCG	HC
AGACCACCCGCA	HC
AGACCACCCATG	HC
AGACCACCCAGG	HC
AGACCACCCAGC	HC
AGACCACCCAGA	HC
AGACCACCCACT	HC
AGACCACCCACG	HC
AGACCACCCACC	HC
AGACCACCCACA	HC
AGACCACCCAAG	HC
AGACCACCCAAC	HC
AGACCACCCAAA	HC
AGACCACACAGG	HC
AGACCACACAGA	HC
AGACCACACACG	HC
AGACCACACACC	HC
AGACCACACACA	HC
AGACCACACAAG	HC
AGGCCACCCAGG	HC
AGGCCACCCAGC	HC
AGGCCACCCAGA	HC
AGGCCACCCACG	HC
AGGCCACCCACC	HC
AGGCCACCCACA	HC
AGGCCACCCAAG	HC
AGGCCACCCAAC	HC
AGGCCACCCAAA	HC
AGGCCACACAGG	HC
AGGCCACACAGA	HC
AGGCCACACACG	HC

Gli binding motifs (12mer)	Confidence
AGGCCACACACG	HC
CGACCACCCACG	HC
GGGCCACCCAGG	HC
GGGCCACCCAGA	HC
GGGCCACCCACG	HC
GGGCCACCCACC	HC
GGGCCACCCACA	HC
GGGCCACCCAAG	HC
GGGCCACACACG	HC
GGCCACCCAGG	HC
GGCCACCCAGA	HC
GGCCACCCACG	HC
GGCCACCCACA	HC
GGACCTCCCAGG	HC
GGACCTCCCACG	HC
GGACCTCCCACA	HC
GGACCACCCTGG	HC
GGACCACCCTGA	HC
GGACCACCCTCG	HC
GGACCACCCTCA	HC
GGACCACCCGGG	HC
GGACCACCCGCG	HC
GGACCACCCGCA	HC
GGACCACCCATG	HC
GGACCACCCATA	HC
GGACCACCCAGG	HC
GGACCACCCAGC	HC
GGACCACCCAGA	HC
GGACCACCCACG	HC
GGACCACCCACC	HC
GGACCACCCACA	HC
GGACCACCCAAG	HC
GGACCACCCAAC	HC
GGACCACCCAAA	HC
GGACCACACAGG	HC
GGACCACACAGA	HC
GGACCACACACG	HC

Gli binding motifs (12mer)	Confidence
GGACCACACACC	HC
GGACCACACACA	HC
GGACCACACAAG	HC
TGACCACCCAGG	HC
TGACCACCCAGA	HC
TGACCACCCACG	HC
TGACCACCCACC	HC
TGACCACCCACA	HC
TGACCACCCAAG	HC
TGGCCACCCACG	HC
TGGCCACCCACA	HC
AGCCCACCCAGA	MC
AGCCCACCCACT	MC
AGCCCACCCACC	MC
AGCCCACCCAAG	MC
AGACCTCCCACC	MC
AGACCTCCCAAG	MC
AGACCCCCCAGG	MC
AGACCACCTAGG	MC
AGACCACCTACG	MC
AGACCACCTACA	MC
AGACCACCTCC	MC
AGACCACCCCGG	MC
AGACCACCCCCG	MC
AGACCACCCATT	MC
AGACCACCCATC	MC
AGACCACCCATA	MC
AGACCACCCAGT	MC
AGACCACCCAAT	MC
AGACCACCAAGG	MC
AGACCACCAACG	MC
AGACCACACATG	MC
AGACCACACAGT	MC
AGACCACACAGC	MC
AGACCACACACT	MC
AGACCACACAAA	MC
ACACCACCCACG	MC

AAACCACCCACG	MC
ATACCACCCAGG	MC
ATACCACCCACG	MC
AGGCCACCCATG	MC
AGGCCACCCACT	MC
CGGCCACCCACG	MC
CGCCCACCCACG	MC
CGACCACCCATG	MC
CGACCACCCAGT	MC
CGACCACCCAGG	MC
CGACCACCCAGC	MC
CGACCACCCAGA	MC
CGACCACCCACT	MC
CGACCACCCACC	MC
CGACCACCCACA	MC
CGACCACCCAAG	MC
CGACCACCCAAA	MC
CGACCACACACG	MC
CGACCACACACA	MC
GAACCACCCAGG	MC
GAACCACCCACG	MC
GTACCACCCAGG	MC
GTACCACCCAGA	MC
GTACCACCCACG	MC
GTACCACCCACC	MC
GTACCACCCACA	MC
GTACCACCCAAG	MC
GGGCTCCACG	MC
GGGCCACCCATG	MC
GGGCCACCCATA	MC
GGGCCACCCAGT	MC
GGGCCACCCAGC	MC
GGGCCACCCACT	MC
GGGCCACCCAAT	MC
GGGCCACCCAAC	MC
GGGCCACCCAAA	MC
GGGCCACACAGG	MC
GGGCCACACACA	MC
GGGCCACCCATG	MC

GGCCACCCAGT	MC
GGCCACCCAGC	MC
GGCCACCCACT	MC
GGCCACCCACC	MC
GGCCACCCAAG	MC
GGCCACCCAAA	MC
GGCCACACACG	MC
GGACCTCCCAGC	MC
GGACCTCCCAGA	MC
GGACCTCCCCT	MC
GGACCTCCCACC	MC
GGACCTCCAAG	MC
GGACCGCCCAGG	MC
GGACCGCCCACG	MC
GGACCCCCAGG	MC
GGACCCCCACG	MC
GGACCCCCACA	MC
GGACCACCTAGG	MC
GGACCACCTAGA	MC
GGACCACCTACT	MC
GGACCACCTACG	MC
GGACCACCTACC	MC
GGACCACCTACA	MC
GGACCACCTAAG	MC
GGACCACCCTTG	MC
GGACCACCCTGC	MC
GGACCACCCTCT	MC
GGACCACCCTCC	MC
GGACCACCCTAG	MC
GGACCACCCGGC	MC
GGACCACCCGGA	MC
GGACCACCCGCT	MC
GGACCACCCGCC	MC
GGACCACCCGAG	MC
GGACCACCCGG	MC
GGACCACCCGA	MC
GGACCACCCCG	MC
GGACCACCCCC	MC
GGACCACCCCA	MC

GGACCACCCAG	MC
GGACCACCCATT	MC
GGACCACCCATC	MC
GGACCACCCAGT	MC
GGACCACCCACT	MC
GGACCACCCAAT	MC
GGACCACCAAGG	MC
GGACCACCAACG	MC
GGACCACACTCG	MC
GGACCACACGCG	MC
GGACCACACATG	MC
GGACCACACATC	MC
GGACCACACATA	MC
GGACCACACAGT	MC
GGACCACACAGC	MC
GGACCACACACT	MC
GGACCACACAAT	MC
GGACCACACAAC	MC
GGACCACACAAA	MC
TGACCTCCCACG	MC
TGACCACCTCG	MC
TGACCACCCATG	MC
TGACCACCCATC	MC
TGACCACCCATA	MC
TGACCACCCAGT	MC
TGACCACCCAGC	MC
TGACCACCCACT	MC
TGACCACCCAAT	MC
TGACCACCCAAC	MC
TGACCACCCAAA	MC
TGACCACACAGG	MC
TGACCACACACG	MC
TGACCACACACC	MC
TGACCACACACA	MC
TGACCACACAAG	MC
TGGCCACCCAGG	MC
TGCCACCCAGG	MC
TGCCACCCACG	MC
AGCCACCCATG	MC

AGCCACCCAGC	MC
AGCCACCCAAA	MC
AGCCACACAGG	MC
AGCCACACACG	MC
AGACCTCCAGA	MC
AGACCACACAAC	MC
AGGCCACACACA	MC
AGACCACCTGA	MC
AGGCCACCTCG	MC
AGGCCACCCAGT	MC
AGGCCACACAGG	MC
GGGCCACCTCG	MC
AGACCACCCGGA	MC
AGACCACACTGG	MC
AGACCACACTCG	MC
AGACCACACGCG	MC
GGACCACACTGG	MC
AGATCACCCACG	LC
AGACTACCCACG	LC
AGACCAGCCACG	LC
AGAACACCCAGG	LC
AGAACACCCACG	LC
ACACCACCCAGG	LC
CGGCCACCCAGG	LC
CGACCACCCATA	LC
CGACCACCCAAC	LC
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GCACCACCCAAG	LC
GAACCACCCACC	LC
GAACCACCCACA	LC
GAACCACCCAAG	LC
GGTCCACCCAGG	LC
GGTCCACCCACG	LC
GGATCACCCAGG	LC

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GGACCTCCCATG	LC
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GGACCTCACACG	LC
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GGAACACCCAAG	LC
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AGCCACACACA	LC
AGACCTCACACG	LC
CGCCACCCACA	LC
TGCCACCCACA	LC
AGGCTCCACG	LC
AGCCACCTGGG	LC
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AGCCACCTGCA	LC

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AGCCACCCTGA	LC
AGCCACCCTCG	LC
AGCCACCCGGG	LC
AGCCACCCGGA	LC
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AGCCACATGGG	LC
AGCCACATGCG	LC
AGCCACACGGG	LC
AGCCACACGGA	LC
AGCCACACGCG	LC
AGCCACACGCA	LC
AGACCTCCTGGG	LC
AGACCTCCTGCG	LC
AGACCTCCCGGG	LC
AGACCTCCCGGA	LC
AGACCTCCCGCG	LC
AGACCTCCCGCA	LC
AGACCACCTTGG	LC
AGACCACCTTGA	LC
AGACCACCTTCG	LC
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AGACCACCTGCG	LC
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GGCCACCGGCG	LC
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GGCCACCCTGA	LC
GGCCACCCTCG	LC
GGCCACCCTCA	LC
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GGCCACCCGGA	LC

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GGCCACATTCG	LC
GGCCACATGGG	LC
GGCCACATGGA	LC
GGCCACATGCG	LC
GGCCACATGCA	LC
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GGCCACAGGGA	LC
GGCCACAGGCG	LC
GGCCACAGGCA	LC
GGCCACACTGG	LC
GGCCACACTGA	LC
GGCCACACTCG	LC
GGCCACACTCA	LC
GGCCACACGGG	LC
GGCCACACGGA	LC
GGCCACACGCG	LC
GGCCACACGCA	LC
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GGACCTCCGGGG	LC
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GGACCTCCCTCG	LC
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GGACCTCACGCG	LC
GGACCTCACGCA	LC
GGACCACCTTGG	LC
GGACCACCTTGA	LC
GGACCACCTTCG	LC
GGACCACCTTCA	LC
GGACCACCTGGG	LC
GGACCACCTGGA	LC
GGACCACCTGCG	LC
GGACCACCTGCA	LC
GGACCACCGTGG	LC
GGACCACCGTGA	LC
GGACCACCGTCG	LC
GGACCACCGTCA	LC
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GGACCACCGGGA	LC
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GGACCACATTGA	LC
GGACCACATTTCG	LC
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GGACCACATGCG	LC
GGACCACATGCA	LC
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GGACCACAGTGA	LC
GGACCACAGTCG	LC
GGACCACAGTCA	LC
GGACCACAGGGG	LC
GGACCACAGGGA	LC
GGACCACAGGCG	LC
GGACCACAGGCA	LC

GGACCACACTGA	LC
GGACCACACTCA	LC
GGACCACACGGG	LC
GGACCACACGGA	LC
GGACCACACGCA	LC
AGCCCACCCAGT	LC
AGCCCACCCAAC	LC
AGACCTCCAGT	LC
AGACCTCCAGC	LC
AGACCTCCACT	LC
AGACCTCCAAA	LC
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AGACCACCCGGC	LC
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AGACCACCCAA	LC
AGACCACCCGG	LC
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AGACCACACATC	LC
AGACCACACATA	LC
AGACCACACAAT	LC
AGACAACCCAGG	LC
AGACAACCCACG	LC
AAACCACCCAGG	LC
AAACCACCCACA	LC
ATGCCACCCACG	LC
ATACCACCCATG	LC
ATACCACCCAGT	LC
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AGGCCACCCCCG	LC
AGGCCACCCATC	LC
AGGCCACCCATA	LC
AGGCCACCCAAT	LC
AGGCCACCCAAC	LC
AGGCCACACAGA	LC

AGGCCACACACC	LC
AGGCCACACAAG	LC
GTGCCACCCACG	LC
GTACCACCCATG	LC
GTACCACCCAGT	LC
GTACCACCCAGC	LC
GTACCACCCACT	LC
GTACCACCCAAT	LC
GTACCACCCAAC	LC
GTACCACCCAAA	LC
GTACCACACAGG	LC
GTACCACACACG	LC
GGGCCACCCATC	LC
GGGCCACACACC	LC
GGGCCACACAAG	LC
GGCCCACCCAAC	LC
GGACCACCTAGC	LC
GGACCACCCTGT	LC
GGACCACCCTAT	LC
GGACCACCCTAC	LC
GGACCACCCTAA	LC
GGACCACCCCTG	LC
GGACCACCCCGT	LC
GGACCACCCCGC	LC
GGACCACCCCT	LC
GGACCACCCAC	LC
GGACCACCCAA	LC
GGACCACACCGG	LC
GGACCACACCCG	LC
GGACCACACATT	LC
GGACAACCCAGG	LC
GGACAACCCACG	LC
TGACCACCCCTGG	LC
TGACCACCCCGG	LC
TGACCACCCCCG	LC
TGACCACCCATT	LC
TGACCACACAGC	LC
TGACCACACAGA	LC
TGACCACACACT	LC

TTACCACCCAGG	LC			TGGCCACCCACC	LC
TTACCACCCACG	LC	TGGCCACCCAGA	LC	TGGCCACCCAAG	LC

Table S3.1. GLI binding motif 12-mers. Library of 12-mers enriched in GLI^{FLAG} datasets. Motifs were considered high confidence (HC) if the 12-mer occurred in all four GLI^{FLAG} datasets, medium confidence (MC) if it occurred in 2 or 3, or low confidence (LC) if it only occurred in one dataset.

Annotated Gene	Genomic location Build mm9
<i>Hdlbp</i>	chr1:95374177-95376523
<i>Slc35f5</i>	chr1:127456701-127457719
<i>Tpd52l1</i>	chr10:31165049-31165879
<i>Gli1</i>	chr10:126775842-126779541
<i>Blmh</i>	chr11:76758416-76760372
<i>Rab34</i>	chr11:78001796-78004008
<i>Mycn</i>	chr12:12944525-12950747
<i>Ptch1</i>	chr13:63663502-63669743
<i>Anks3</i>	chr16:4963972-4964875
<i>Fgf12</i>	chr16:28841169-28841598
<i>Stx5a</i>	chr19:8814998-8816581
<i>Prrg4</i>	chr2:104689887-104690204
<i>Stk35</i>	chr2:129625777-129627521
<i>4933425O20Rik</i>	chr2:130233798-130234557
<i>Ogfr</i>	chr2:180323999-180325004
<i>Zfp704</i>	chr3:9607477-9609137
<i>Ensa</i>	chr3:95428396-95429195
<i>Foxd2</i>	chr4:114493666-114494927
<i>Ptch2</i>	chr4:116767756-116769455
<i>1700041C02Rik</i>	chr4:119087804-119088396
<i>Thrap3</i>	chr4:125878668-125880997
<i>Park7</i>	chr4:150287600-150289290
<i>BC037393</i>	chr5:151467448-151468648
<i>D6Wsu116e</i>	chr6:116157254-116158578
<i>Scap</i>	chr9:110207158-110208277
<i>Eda2r</i>	chrX:94571449-94572464

Table S3.2. Peak coordinates that overlap between all four GLI^{FLAG} datasets. The 26 regions that have shared peaks across all GLI^{FLAG} datasets. Peaks are annotated to nearest genes.

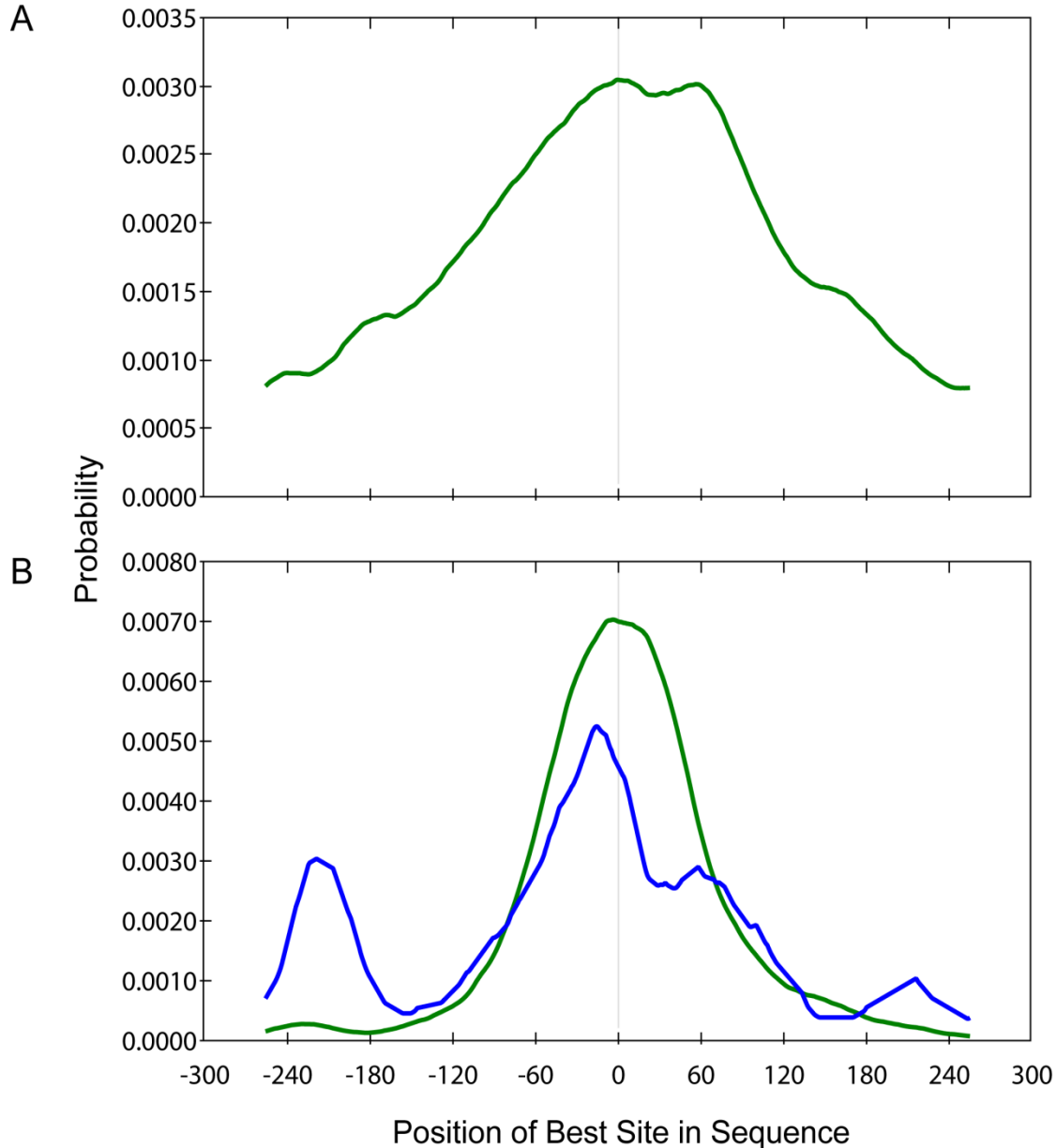


Figure S3.1. Determination of sequence length buffer surrounding the GBM. Plots depicting the positional distribution of the best GLI motif (green) were generated by submitting 300 bp of sequence surrounding the center of each peak to Centrimo. **(A)** LDwGBM shows a broad profile for the best GBM, consistent with ChIP-chip data. **(B)** The profile for the ChIP-seq sequences from NPwGBM is more narrow and suggests that most of the GBM fall within 240 bp around the center of the peak. In neural precursor cells, the motif for the GLI cofactor, Sox, has a profile that contains a central apex plus two additional summits at a distance of 240 bp on either side of the peak. This suggests that context-specific TF binding may occur outside the central peak region.

chromosome	start	end	LDw GBM score	NPw GBM score
chr1	3587497	3588097	0.7	0.3
chr1	3587588	3588188	1.2	0.8
chr1	3587846	3588446	0.4	0.4
chr1	4888793	4889393	0.3	0.2
chr1	5061403	5062003	2.1	0.5
chr1	5723207	5723807	0.7	0.0
chr1	6005639	6006239	0.8	0.6
chr1	6304149	6304749	0.8	0.2
chr1	7026800	7027400	1.0	0.1
chr1	8845727	8846327	0.1	0.2
chr1	8846863	8847463	0.7	0.2
chr1	8903718	8904318	0.7	0.1
chr1	8903766	8904366	0.9	0.1
chr1	9472063	9472663	0.6	0.0
chr1	9547480	9548080	1.3	0.3
chr1	9878331	9878931	0.4	0.1
chr1	10123157	10123757	1.3	0.1
chr1	10159934	10160534	0.4	0.1
chr1	10255539	10256139	1.0	0.0
chr1	10407014	10407614	1.1	0.4
chr1	10476343	10476943	0.3	0.2
chr1	10542821	10543421	1.6	0.2
chr1	10676492	10677092	0.5	0.2
chr1	11556647	11557247	0.6	0.0
chr1	11556678	11557278	0.6	0.2
chr1	11967664	11968264	1.9	0.2
chr1	12059564	12060164	0.3	0.3
chr1	12773280	12773880	0.7	0.1
chr1	12951731	12952331	0.4	0.2
chr1	13504749	13505349	0.2	0.1
chr1	13552845	13553445	2.6	0.7
chr1	13553140	13553740	2.8	0.3
chr1	13963660	13964260	0.5	0.1
chr1	14223396	14223996	0.6	0.1
chr1	15294431	15295031	2.0	0.2
chr1	15417776	15418376	0.9	0.2

chromosome	start	end	LDw GBM score	NPw GBM score
chr1	15965121	15965721	0.7	0.1
chr1	15999414	16000014	1.1	0.2
chr1	16036197	16036797	0.0	0.3
chr1	16126714	16127314	1.4	0.9
chr1	17479394	17479994	0.5	0.0
chr1	17504340	17504940	0.3	0.2
chr1	17731913	17732513	3.0	0.8
chr1	17732042	17732642	3.0	0.6
chr1	19228039	19228639	0.1	0.1
chr1	20839991	20840591	0.8	0.1
chr1	21390250	21390850	0.3	0.1
chr1	21770730	21771330	0.1	0.2
chr1	21808362	21808962	0.3	0.0
chr1	22861086	22861686	1.4	0.2
chr1	23722805	23723405	1.0	0.2
chr1	23722862	23723462	1.2	0.2
chr1	24237238	24237838	0.9	0.0
chr1	24823606	24824206	0.5	0.0
chr1	25077359	25077959	0.2	0.1
chr1	25123198	25123798	1.5	0.2
chr1	25406397	25406997	1.8	0.1
chr1	25406432	25407032	1.8	0.3
chr1	25594072	25594672	1.1	0.1
chr1	26325256	26325856	0.3	0.0
chr1	26864740	26865340	0.3	0.1
chr1	27339458	27340058	1.1	0.2
chr1	27351080	27351680	0.7	0.1
chr1	29105779	29106379	1.3	0.0
chr1	29105799	29106399	1.2	0.0
chr1	29626691	29627291	1.0	0.1
chr1	30035432	30036032	0.4	0.2
chr1	30376569	30377169	0.6	0.2
chr1	31085911	31086511	0.4	0.0
chr1	31088854	31089454	0.0	0.0
chr1	31450635	31451235	0.2	0.0
chr1	31596355	31596955	0.3	0.1

chr1	31742046	31742646	1.1	0.4
chr1	33018590	33019190	0.7	0.1
chr1	33117174	33117774	1.8	0.2
chr1	33518563	33519163	1.5	0.1
chr1	33518617	33519217	1.6	0.1
chr1	33797481	33798081	2.0	0.5
chr1	33797720	33798320	1.2	0.1
chr1	33820583	33821183	0.5	0.6
chr1	34109352	34109952	0.4	0.1
chr1	34593375	34593975	1.4	0.4
chr1	34983602	34984202	1.9	0.4
chr1	34983809	34984409	2.3	0.5
chr1	35984923	35985523	0.0	0.4
chr1	36127397	36127997	2.0	0.4
chr1	36533380	36533980	1.1	0.6
chr1	36576831	36577431	2.6	1.1
chr1	37120191	37120791	0.1	0.2
chr1	37251438	37252038	0.8	0.0
chr1	37310144	37310744	0.8	0.3
chr1	37355221	37355821	0.5	0.1
chr1	37463376	37463976	0.9	0.0
chr1	37463581	37464181	1.1	0.2
chr1	37590466	37591066	1.3	0.3
chr1	37590492	37591092	1.4	0.2
chr1	37590518	37591118	1.5	0.2
chr1	37590544	37591144	1.4	0.3
chr1	37623397	37623997	0.7	0.1
chr1	37928508	37929108	0.0	0.0
chr1	37993942	37994542	1.1	0.4
chr1	37994044	37994644	0.0	0.0
chr1	38316421	38317021	1.2	0.6
chr1	38316480	38317080	1.0	0.6
chr1	38534769	38535369	1.5	0.6
chr1	38721537	38722137	0.4	0.0
chr1	38923902	38924502	0.1	0.5
chr1	38924136	38924736	1.2	0.9
chr1	38924175	38924775	1.5	1.1
chr1	38924292	38924892	1.5	1.2

chr1	38924331	38924931	1.7	1.3
chr1	38924409	38925009	1.9	1.4
chr1	38924448	38925048	1.6	1.2
chr1	39668786	39669386	0.4	0.2
chr1	39705638	39706238	0.5	0.1
chr1	39711932	39712532	0.9	0.1
chr1	39713365	39713965	1.6	0.4
chr1	40067917	40068517	1.6	0.1
chr1	40067981	40068581	1.6	0.2
chr1	40287515	40288115	0.1	0.3
chr1	40287613	40288213	0.6	0.6
chr1	40718882	40719482	0.0	0.4
chr1	40830222	40830822	0.8	0.4
chr1	40935328	40935928	1.1	0.2
chr1	41346635	41347235	0.3	0.2
chr1	41768973	41769573	0.2	0.3
chr1	42164674	42165274	0.8	0.3
chr1	43502070	43502670	1.7	0.1
chr1	44846756	44847356	0.3	0.2
chr1	48043163	48043763	0.8	0.1
chr1	48757381	48757981	1.9	0.7
chr1	48931916	48932516	2.7	0.5
chr1	49335477	49336077	0.2	0.4
chr1	49335721	49336321	1.2	0.6
chr1	49908767	49909367	0.2	0.3
chr1	50956466	50957066	0.1	0.1
chr1	53345598	53346198	0.1	0.3
chr1	53799247	53799847	0.4	0.1
chr1	54047502	54048102	0.5	0.0
chr1	54072278	54072878	1.6	0.3
chr1	54176567	54177167	0.6	0.0
chr1	54288808	54289408	0.7	0.2
chr1	54383175	54383775	1.9	0.5
chr1	54387025	54387625	1.5	0.4
chr1	54387299	54387899	1.6	0.6
chr1	54517139	54517739	1.0	0.3
chr1	54530947	54531547	1.8	0.3
chr1	54567172	54567772	0.7	0.1

chr1	54782868	54783468	0.7	0.6
chr1	54782935	54783535	0.5	0.4
chr1	55016357	55016957	1.0	0.6
chr1	56073425	56074025	1.5	0.8
chr1	56073683	56074283	1.9	1.2
chr1	56205110	56205710	0.4	0.0
chr1	56343351	56343951	0.4	0.3
chr1	56499537	56500137	0.5	0.4
chr1	56661064	56661664	0.4	0.2
chr1	56661089	56661689	0.5	0.2
chr1	57961107	57961707	2.0	0.5
chr1	57961140	57961740	1.9	0.4
chr1	58008076	58008676	2.9	1.5
chr1	58008095	58008695	2.8	1.5
chr1	58107997	58108597	1.3	0.0
chr1	58108152	58108752	1.5	0.2
chr1	58360626	58361226	1.0	0.3
chr1	58431250	58431850	0.9	0.5
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chr1	58656726	58657326	1.1	0.3
chr1	58723003	58723603	0.3	0.1
chr1	59133074	59133674	0.8	0.2
chr1	59432710	59433310	1.2	0.2
chr1	59954114	59954714	1.0	0.1
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chr1	62108284	62108884	1.0	0.1
chr1	62109784	62110384	1.1	0.2
chr1	62114633	62115233	0.5	0.8
chr1	62458899	62459499	1.2	0.6
chr1	62477593	62478193	1.3	0.4
chr1	62683344	62683944	0.8	0.2
chr1	63100532	63101132	1.2	0.4
chr1	63700824	63701424	0.3	0.2
chr1	63700928	63701528	0.3	0.0
chr1	63929166	63929766	0.8	0.2
chr1	64138421	64139021	0.8	0.5
chr1	64384475	64385075	1.3	0.2

chr1	64695128	64695728	0.0	0.3
chr1	64943282	64943882	1.3	0.7
chr1	65251132	65251732	0.2	0.3
chr1	65612857	65613457	2.0	0.9
chr1	65612867	65613467	1.9	0.9
chr1	65842421	65843021	1.1	0.2
chr1	67106933	67107533	0.5	0.1
chr1	67619759	67620359	0.5	0.0
chr1	68029348	68029948	0.8	0.2
chr1	68587471	68588071	0.0	0.2
chr1	69641000	69641600	0.6	0.1
chr1	70114225	70114825	0.5	0.0
chr1	70453531	70454131	0.4	0.3
chr1	70750830	70751430	0.2	0.1
chr1	71887505	71888105	1.0	0.2
chr1	72026765	72027365	0.2	0.0
chr1	72254058	72254658	1.2	0.4
chr1	72751159	72751759	0.9	0.1
chr1	73223612	73224212	1.7	0.2
chr1	73731980	73732580	1.2	0.1
chr1	75359007	75359607	0.7	0.1
chr1	75491418	75492018	0.1	0.1
chr1	75517680	75518280	1.3	0.3
chr1	75525034	75525634	0.4	0.0
chr1	75664087	75664687	0.9	0.6
chr1	76243575	76244175	1.4	0.2
chr1	76546995	76547595	0.1	0.1
chr1	77201537	77202137	0.8	0.5
chr1	77304468	77305068	1.8	0.0
chr1	77798374	77798974	0.9	0.1
chr1	78422306	78422906	0.8	0.1
chr1	79090147	79090747	0.0	0.1
chr1	79932530	79933130	1.4	0.4
chr1	79932820	79933420	0.9	0.4
chr1	80236449	80237049	2.2	0.7
chr1	80264794	80265394	2.4	0.5
chr1	81043211	81043811	0.4	0.1
chr1	81861035	81861635	0.5	0.3

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chr1	82033854	82034454	0.8	0.7
chr1	82258491	82259091	3.4	1.3
chr1	82258781	82259381	4.2	1.2
chr1	82823462	82824062	0.2	0.0
chr1	84036917	84037517	0.7	0.1
chr1	84267874	84268474	0.6	0.0
chr1	84268523	84269123	0.3	0.1
chr1	84321261	84321861	0.5	0.0
chr1	84368458	84369058	0.8	0.3
chr1	84443514	84444114	0.5	0.0
chr1	84579102	84579702	1.2	0.2
chr1	84870201	84870801	0.7	0.1
chr1	87602425	87603025	1.2	0.4
chr1	87813558	87814158	3.1	1.9
chr1	87813802	87814402	2.5	1.8
chr1	87865926	87866526	0.4	0.1
chr1	88038640	88039240	1.8	0.3
chr1	88371531	88372131	0.9	0.3
chr1	89271564	89272164	0.0	0.3
chr1	89532378	89532978	0.3	0.0
chr1	89751849	89752449	0.7	0.0
chr1	90285339	90285939	0.1	0.0
chr1	90616098	90616698	1.1	0.2
chr1	90637623	90638223	0.6	0.3
chr1	90665449	90666049	1.3	0.2
chr1	90665468	90666068	1.3	0.1
chr1	90762002	90762602	0.9	0.3
chr1	90978194	90978794	1.1	0.1
chr1	91090882	91091482	2.0	0.2
chr1	91396066	91396666	1.0	0.3
chr1	91660947	91661547	0.8	0.0
chr1	91711063	91711663	1.4	0.3
chr1	92232131	92232731	1.0	0.6
chr1	92301760	92302360	0.3	0.2
chr1	92301801	92302401	0.4	0.3
chr1	92369536	92370136	0.8	0.0

chr1	92378845	92379445	0.4	0.1
chr1	92379002	92379602	0.2	0.1
chr1	92622432	92623032	1.4	0.4
chr1	92690829	92691429	1.4	0.9
chr1	92952085	92952685	0.1	0.1
chr1	93073516	93074116	0.9	0.6
chr1	93167832	93168432	1.0	0.3
chr1	93180693	93181293	0.2	0.2
chr1	93265187	93265787	0.5	0.2
chr1	93265359	93265959	0.8	0.5
chr1	93563128	93563728	0.3	0.0
chr1	93694993	93695593	0.9	0.1
chr1	93808568	93809168	1.9	0.4
chr1	93808751	93809351	1.7	0.3
chr1	94061751	94062351	0.9	0.3
chr1	94193930	94194530	0.1	0.1
chr1	94507566	94508166	0.8	0.2
chr1	94723808	94724408	0.5	0.2
chr1	94735502	94736102	0.8	0.3
chr1	94811814	94812414	0.1	0.3
chr1	94832832	94833432	0.1	0.3
chr1	94879251	94879851	0.3	0.2
chr1	94879476	94880076	0.8	0.0
chr1	94879488	94880088	0.8	0.0
chr1	94944629	94945229	0.0	0.2
chr1	94989485	94990085	1.7	0.2
chr1	95073408	95074008	1.3	0.5
chr1	95073529	95074129	1.6	0.2
chr1	95073574	95074174	1.5	0.1
chr1	95226272	95226872	0.5	0.0
chr1	95374431	95375031	0.2	0.2
chr1	95374615	95375215	0.0	0.5
chr1	95461016	95461616	1.4	0.5
chr1	95542751	95543351	1.1	0.8
chr1	95595255	95595855	1.3	0.4
chr1	96429589	96430189	0.7	0.5
chr1	96460205	96460805	0.9	0.3
chr1	96554281	96554881	0.4	0.1

chr1	96685689	96686289	0.7	0.1
chr1	97320574	97321174	0.8	0.2
chr1	99947459	99948059	2.1	0.3
chr1	100155930	100156530	0.0	0.2
chr1	100679858	100680458	0.8	0.3
chr1	100680011	100680611	1.2	0.4
chr1	101537290	101537890	0.2	0.2
chr1	102555674	102556274	0.2	0.1
chr1	102616625	102617225	0.9	0.1
chr1	104317551	104318151	1.5	0.1
chr1	107273156	107273756	0.2	0.1
chr1	107451799	107452399	0.6	0.4
chr1	107690411	107691011	0.8	0.4
chr1	107716235	107716835	0.3	0.3
chr1	107766663	107767263	1.8	0.6
chr1	107782299	107782899	0.1	0.2
chr1	108087176	108087776	0.6	0.0
chr1	108268892	108269492	0.7	0.4
chr1	109717474	109718074	0.5	0.2
chr1	110459102	110459702	1.0	0.2
chr1	110955073	110955673	0.4	0.0
chr1	110997170	110997770	0.1	0.1
chr1	112111586	112112186	0.3	0.1
chr1	112971026	112971626	1.7	0.0
chr1	113406467	113407067	0.8	0.6
chr1	113710670	113711270	1.5	0.0
chr1	113998336	113998936	0.1	0.0
chr1	115400418	115401018	0.8	0.1
chr1	116508023	116508623	0.2	0.3
chr1	117078348	117078948	0.5	0.3
chr1	117244322	117244922	0.3	0.3
chr1	118311346	118311946	0.7	0.2
chr1	120544640	120545240	0.1	0.7
chr1	120767868	120768468	0.9	0.0
chr1	120942827	120943427	1.5	0.4
chr1	120943037	120943637	1.6	0.6
chr1	121043940	121044540	0.3	0.3
chr1	121576346	121576946	0.5	0.1

chr1	121965855	121966455	0.4	0.1
chr1	122055225	122055825	0.7	0.2
chr1	122203865	122204465	0.0	0.1
chr1	122771283	122771883	0.8	0.0
chr1	123073168	123073768	0.0	0.7
chr1	123769927	123770527	0.5	0.0
chr1	124021917	124022517	0.1	0.0
chr1	124127903	124128503	1.6	0.3
chr1	124128093	124128693	1.5	0.7
chr1	124352337	124352937	1.0	0.4
chr1	124352519	124353119	0.6	0.2
chr1	125138573	125139173	0.5	0.4
chr1	126130535	126131135	0.9	0.1
chr1	126130629	126131229	0.5	0.1
chr1	126935121	126935721	0.6	0.3
chr1	127456890	127457490	1.1	0.7
chr1	127542776	127543376	1.1	0.2
chr1	127587623	127588223	1.3	0.0
chr1	127611885	127612485	0.8	0.0
chr1	127810549	127811149	0.0	0.4
chr1	129520754	129521354	0.8	0.2
chr1	130146291	130146891	0.2	0.4
chr1	130588519	130589119	1.1	0.0
chr1	130814015	130814615	0.3	0.4
chr1	131264285	131264885	0.1	0.1
chr1	131683795	131684395	2.4	0.7
chr1	131683875	131684475	2.4	0.3
chr1	132491151	132491751	1.2	0.4
chr1	133730886	133731486	0.5	0.2
chr1	133974327	133974927	1.6	0.3
chr1	134070192	134070792	0.9	0.1
chr1	134088495	134089095	0.3	0.4
chr1	134214304	134214904	1.2	0.1
chr1	134935066	134935666	1.2	0.6
chr1	135246492	135247092	0.7	0.2
chr1	135277536	135278136	0.1	0.1
chr1	135328831	135329431	0.4	0.3
chr1	136014721	136015321	0.4	0.1

chr1	136340711	136341311	0.4	0.4
chr1	136547886	136548486	1.4	0.0
chr1	137204467	137205067	0.1	0.1
chr1	137565459	137566059	0.5	0.6
chr1	137776826	137777426	0.5	0.1
chr1	137786132	137786732	0.2	0.1
chr1	137834537	137835137	0.5	0.5
chr1	137991408	137992008	2.0	0.4
chr1	138113880	138114480	0.1	0.2
chr1	138113962	138114562	0.5	0.4
chr1	138114057	138114657	0.1	0.3
chr1	138254303	138254903	0.2	0.1
chr1	139183288	139183888	0.9	0.2
chr1	139789215	139789815	1.6	0.6
chr1	139791383	139791983	1.3	0.0
chr1	140152141	140152741	1.3	0.4
chr1	140313669	140314269	0.5	0.1
chr1	140426693	140427293	0.9	0.1
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chr1	189176968	189177568	2.7	1.2
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chr1	189177216	189177816	2.2	1.0
chr1	189177340	189177940	2.2	0.9
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chr1	189177464	189178064	2.5	1.1
chr1	189177526	189178126	2.4	1.1
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chr1	189177650	189178250	2.6	1.1
chr1	189177712	189178312	2.6	1.1
chr1	189177774	189178374	2.6	1.0
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chr1	189178022	189178622	2.9	1.2
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chr11	52194403	52195003	0.3	0.0
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chr11	53044188	53044788	1.9	0.4

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chr11	53044288	53044888	2.3	0.6
chr11	53044349	53044949	2.8	0.8
chr11	53044392	53044992	2.5	0.6
chr11	53044424	53045024	2.4	0.5
chr11	53044450	53045050	2.4	0.6
chr11	53044490	53045090	2.2	0.5
chr11	53044545	53045145	3.2	0.9
chr11	53044571	53045171	2.9	0.9
chr11	53044605	53045205	2.8	0.8
chr11	53044631	53045231	3.3	1.0
chr11	54579147	54579747	0.5	0.2
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chr11	55136048	55136648	3.0	1.4
chr11	55137105	55137705	0.5	0.1
chr11	55137357	55137957	0.3	0.5
chr11	55755275	55755875	1.2	0.0
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chr11	56955732	56956332	0.0	0.1
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chr11	57600609	57601209	1.6	0.6
chr11	57811695	57812295	0.4	0.4
chr11	57830540	57831140	1.2	0.0
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chr11	58007309	58007909	2.0	1.3
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chr11	58415812	58416412	1.3	0.0
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chr11	58970556	58971156	0.9	0.4

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chr11	59709158	59709758	0.2	0.2
chr11	59725585	59726185	0.5	0.9
chr11	59725731	59726331	1.1	1.2
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chr11	66465625	66466225	0.6	0.1
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chr11	66710564	66711164	1.4	0.4
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chr11	67627323	67627923	2.3	0.2
chr11	67627452	67628052	2.3	0.2
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chr11	69181354	69181954	2.2	0.5
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chr11	69332445	69333045	1.7	0.2
chr11	69332486	69333086	1.6	0.2
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chr11	69332583	69333183	2.0	0.4
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chr11	69651758	69652358	1.6	0.9
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chr11	70032274	70032874	0.6	0.4
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chr11	70609162	70609762	0.6	0.2
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chr11	71685160	71685760	1.5	0.4
chr11	71879192	71879792	1.9	0.1
chr11	71916960	71917560	0.3	0.1
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chr11	76296686	76297286	0.6	0.4
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chr11	79576862	79577462	4.6	2.1
chr11	79576872	79577472	4.7	2.1
chr11	79576882	79577482	4.8	2.1
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chr11	79576902	79577502	4.8	2.1
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chr11	80128313	80128913	0.4	0.0
chr11	80128322	80128922	0.3	0.0
chr11	80241725	80242325	1.2	0.1
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chr11	83261185	83261785	0.6	0.2
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chr11	85115807	85116407	0.0	0.6
chr11	85728010	85728610	0.9	0.2

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chr11	87969933	87970533	1.6	0.8
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chr11	93985699	93986299	0.2	0.2
chr11	94299357	94299957	0.2	0.3
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chr11	94387070	94387670	0.9	0.4
chr11	94455209	94455809	0.4	0.2
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chr11	96302997	96303597	1.2	0.4
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chr11	97420621	97421221	0.1	0.1
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chr11	103556172	103556772	0.0	0.1
chr11	103594408	103595008	0.1	0.1
chr11	103744563	103745163	0.0	0.2
chr11	104112477	104113077	0.2	0.0
chr11	104181604	104182204	1.1	0.4
chr11	104585907	104586507	1.0	0.2
chr11	104586075	104586675	1.9	0.2
chr11	104876082	104876682	1.1	0.6
chr11	104876322	104876922	0.7	0.8

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chr11	105400003	105400603	1.1	0.2
chr11	105991180	105991780	0.7	0.2
chr11	106129287	106129887	1.7	0.7
chr11	106473724	106474324	1.1	0.2
chr11	106473819	106474419	1.2	0.1
chr11	106566303	106566903	0.8	0.1
chr11	106566402	106567002	0.9	0.1
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chr11	110909194	110909794	1.3	0.7
chr11	110953955	110954555	0.4	0.1
chr11	111293838	111294438	0.3	0.4
chr11	111357129	111357729	0.8	0.1
chr11	111603432	111604032	0.7	0.1
chr11	112645909	112646509	1.2	0.4
chr11	112645926	112646526	1.4	0.4
chr11	112750905	112751505	1.6	0.1
chr11	112751114	112751714	2.1	0.3
chr11	112887675	112888275	2.6	0.4
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chr11	113204928	113205528	2.8	1.1
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chr11	113204967	113205567	2.6	1.3

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chr11	113720730	113721330	0.3	0.0
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chr11	115042827	115043427	0.2	0.3
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chr11	117427598	117428198	1.3	0.1
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chr11	118373788	118374388	1.1	0.2
chr11	118373799	118374399	1.0	0.1
chr11	118769286	118769886	0.1	0.0
chr11	118783007	118783607	0.0	0.1
chr11	118939111	118939711	1.0	0.2
chr11	118990085	118990685	1.7	0.7
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chr11	119377301	119377901	0.6	0.2
chr11	119618331	119618931	1.2	0.3
chr11	119618557	119619157	1.5	0.6
chr11	119891333	119891933	0.0	0.2
chr11	119891662	119892262	0.3	0.1
chr11	119931947	119932547	2.5	0.7
chr11	119932233	119932833	2.4	0.9
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chr11	120127048	120127648	0.9	0.7
chr11	120377466	120378066	0.5	0.2
chr11	120377510	120378110	0.3	0.2
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chr11	121418576	121419176	0.6	0.4
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chr11	121570266	121570866	0.4	0.0
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chr12	4178741	4179341	1.6	0.2
chr12	4494741	4495341	0.5	0.1
chr12	5095914	5096514	0.7	0.7
chr12	5102574	5103174	0.6	0.4
chr12	5102662	5103262	0.2	0.6
chr12	5137621	5138221	1.0	0.2
chr12	6006109	6006709	1.0	0.3
chr12	6006188	6006788	1.3	0.5
chr12	6068236	6068836	0.2	0.1
chr12	6075083	6075683	0.6	0.2
chr12	6825538	6826138	0.0	0.1
chr12	7377761	7378361	0.2	0.9
chr12	7505927	7506527	0.5	0.4
chr12	7514039	7514639	0.5	0.0
chr12	7514243	7514843	0.3	0.0
chr12	7544083	7544683	1.1	0.0
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chr12	8601811	8602411	0.8	0.1

chr12	8604332	8604932	0.9	0.3
chr12	8604450	8605050	0.6	0.3
chr12	9036736	9037336	0.7	0.8
chr12	9053345	9053945	1.0	0.2
chr12	10445890	10446490	0.7	0.1
chr12	10698516	10699116	1.6	0.1
chr12	11511376	11511976	0.5	0.2
chr12	12203256	12203856	0.3	0.4
chr12	12203418	12204018	0.5	0.1
chr12	12333460	12334060	1.3	0.3
chr12	12910700	12911300	1.0	0.2
chr12	12910714	12911314	1.2	0.3
chr12	14618698	14619298	0.9	0.3
chr12	15569531	15570131	1.1	0.4
chr12	15756420	15757020	1.7	0.1
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chr12	15951372	15951972	0.2	0.2
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chr12	16739133	16739733	0.1	0.1
chr12	16841491	16842091	1.4	0.4
chr12	17277258	17277858	0.9	0.3
chr12	17277424	17278024	1.3	0.1
chr12	17580452	17581052	0.4	0.1
chr12	17960103	17960703	0.5	0.0
chr12	18480303	18480903	0.3	0.1
chr12	18833161	18833761	0.5	0.4
chr12	20257049	20257649	0.2	0.1
chr12	20532533	20533133	0.2	0.2
chr12	21330919	21331519	0.6	0.1
chr12	21671313	21671913	0.5	0.1
chr12	22041821	22042421	0.5	0.3
chr12	23139036	23139636	0.4	0.3
chr12	23422886	23423486	0.5	0.3
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chr12	24606574	24607174	0.6	0.3

chr12	24892085	24892685	0.4	0.3
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chr12	25471112	25471712	0.3	0.3
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chr12	25642211	25642811	2.3	0.5
chr12	25642217	25642817	2.3	0.5
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chr12	88281306	88281906	0.5	0.1
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chr12	105358022	105358622	6.2	2.6
chr12	105358066	105358666	6.3	2.5
chr12	105358088	105358688	6.3	2.5
chr12	105358132	105358732	6.3	2.4
chr12	105358154	105358754	6.3	2.4
chr12	105358176	105358776	6.1	2.5
chr12	105358242	105358842	5.7	2.5
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chr13	15764999	15765599	1.9	0.4
chr13	15765263	15765863	2.5	1.0
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chr13	16170278	16170878	0.5	0.3
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chr13	20146914	20147514	1.9	0.9
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chr13	28646614	28647214	0.9	1.3
chr13	28646670	28647270	1.2	1.3
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chr13	29097075	29097675	0.7	0.1
chr13	29172897	29173497	1.0	0.1
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chr13	29671695	29672295	0.8	0.4
chr13	30329249	30329849	2.0	1.0
chr13	30329450	30330050	1.2	0.4
chr13	30329511	30330111	1.3	0.3
chr13	30999261	30999861	0.4	0.1
chr13	31058354	31058954	1.0	0.1
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chr13	31119017	31119617	0.2	0.6
chr13	31367668	31368268	0.7	0.0
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chr13	32545735	32546335	0.5	0.3
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chr13	33790276	33790876	2.1	0.9
chr13	33790522	33791122	1.6	0.6
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chr13	49415246	49415846	0.1	0.1
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chr13	52170493	52171093	2.2	0.8
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chr13	58108200	58108800	2.3	0.1
chr13	58108241	58108841	2.3	0.1
chr13	58108282	58108882	2.1	0.0
chr13	58108323	58108923	2.1	0.1
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chr13	63664341	63664941	2.7	2.1
chr13	63667448	63668048	1.4	0.2
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chr13	69362879	69363479	1.6	0.6
chr13	69362908	69363508	2.8	1.2
chr13	69378449	69379049	1.2	0.2
chr13	69479823	69480423	1.2	0.2
chr13	69479836	69480436	1.2	0.2
chr13	69479849	69480449	1.1	0.3
chr13	69490153	69490753	1.1	0.1
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chr13	69632913	69633513	1.8	0.8
chr13	69710370	69710970	3.4	1.2
chr13	69710418	69711018	3.4	1.1
chr13	69710463	69711063	3.7	1.2
chr13	69710511	69711111	3.7	1.1
chr13	69710559	69711159	3.7	1.1
chr13	69836788	69837388	1.4	0.3
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chr13	72319461	72320061	1.4	0.6
chr13	72319501	72320101	1.4	0.6
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chr13	77607226	77607826	1.3	0.1
chr13	77805515	77806115	0.7	0.1
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chr13	86207176	86207776	0.8	0.1
chr13	86215620	86216220	0.3	0.1
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chr13	89694197	89694797	1.0	0.0
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chr13	98758964	98759564	5.3	2.0
chr13	98758984	98759584	5.2	2.1
chr13	98758994	98759594	5.3	2.2
chr13	98759032	98759632	5.5	2.2
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chr13	99343020	99343620	0.8	0.0
chr13	99343424	99344024	1.4	0.6
chr13	99343442	99344042	1.5	0.6
chr13	99921027	99921627	1.4	0.2
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chr13	101203134	101203734	1.0	0.3
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chr13	101203226	101203826	1.0	0.3
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chr13	101269533	101270133	0.1	0.1
chr13	101616486	101617086	0.7	0.1
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chr13	108155870	108156470	0.1	0.1
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chr13	109939587	109940187	0.3	0.1
chr13	110289760	110290360	0.3	0.0
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chr13	112788801	112789401	2.0	0.4
chr13	112893151	112893751	1.8	0.1
chr13	112893369	112893969	2.3	0.5
chr13	112893390	112893990	2.3	0.4
chr13	113128084	113128684	0.2	0.3
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chr13	114124577	114125177	1.2	0.3
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chr13	115421349	115421949	0.1	0.0
chr13	115421377	115421977	0.0	0.0
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chr13	117310091	117310691	1.5	0.8
chr13	117962635	117963235	0.8	0.8
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chr13	117999085	117999685	0.8	0.2
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chr13	117999176	117999776	1.0	0.7
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chr14	9165334	9165934	0.5	0.0
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chr14	11400486	11401086	1.2	0.1
chr14	11400529	11401129	1.3	0.2
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chr14	12888835	12889435	0.2	0.1
chr14	13271373	13271973	0.9	0.1
chr14	13909715	13910315	0.4	0.1
chr14	14176961	14177561	2.0	0.1
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chr14	14738745	14739345	0.8	0.5
chr14	15199243	15199843	0.7	0.1
chr14	15522727	15523327	0.5	0.3
chr14	15522755	15523355	0.4	0.2
chr14	15720649	15721249	0.8	0.1

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chr14	18391203	18391803	0.8	0.2
chr14	18651273	18651873	0.5	0.1
chr14	19953727	19954327	0.2	0.1
chr14	20919764	20920364	1.6	0.0
chr14	20919930	20920530	1.7	0.0
chr14	20964983	20965583	0.7	0.5
chr14	20985859	20986459	0.7	0.4
chr14	21015511	21016111	1.2	0.5
chr14	21518432	21519032	0.6	0.4
chr14	21552737	21553337	0.3	0.1
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chr14	25786216	25786816	0.4	0.0
chr14	25805068	25805668	1.5	0.1
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chr14	25940121	25940721	0.4	0.0
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chr14	26027401	26028001	0.7	0.2
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chr14	26380302	26380902	0.8	0.2
chr14	26437499	26438099	0.6	0.1
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chr14	27440832	27441432	0.7	0.1
chr14	27570118	27570718	0.5	0.0

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chr14	30955801	30956401	0.3	0.2
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chr14	33247821	33248421	0.2	0.0
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chr14	33836733	33837333	1.2	0.9
chr14	33912251	33912851	2.7	0.3
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chr14	55163027	55163627	0.9	0.2
chr14	55386318	55386918	1.9	1.1
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chr14	57788831	57789431	2.2	0.9
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chr14	66614809	66615409	9.6	4.8
chr14	66614825	66615425	9.6	4.8
chr14	66614841	66615441	9.6	4.8
chr14	66614860	66615460	9.7	4.8
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chr14	66614959	66615559	9.7	4.9
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chr14	66615015	66615615	10.0	5.1
chr14	66615031	66615631	10.2	5.1
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chr14	74055666	74056266	2.7	1.1
chr14	74055712	74056312	2.8	1.2
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chr14	75088521	75089121	1.3	0.4

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chr14	75558453	75559053	1.2	0.9
chr14	75558470	75559070	1.3	0.8
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chr14	78665152	78665752	1.2	0.1
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chr14	79086847	79087447	1.6	0.3
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chr14	79819976	79820576	0.4	0.5
chr14	79954568	79955168	0.4	0.3
chr14	80141514	80142114	0.4	0.2
chr14	80311980	80312580	0.0	0.2
chr14	81705322	81705922	0.1	0.4
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chr14	93119308	93119908	1.3	0.8
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chr14	106053561	106054161	0.5	0.2
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chr14	116410768	116411368	0.3	0.2
chr14	116454998	116455598	0.8	0.2
chr14	116541666	116542266	0.1	0.0

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chr14	117028045	117028645	2.2	0.8
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chr14	121255754	121256354	1.0	0.1
chr14	121266996	121267596	0.6	0.0
chr14	122075685	122076285	0.5	0.7
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chr14	122426646	122427246	0.7	0.5
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chr15	3534892	3535492	0.9	0.2
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chr15	4283320	4283920	0.9	0.7
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chr15	8582203	8582803	1.4	0.6
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chr15	10395327	10395927	4.0	1.9
chr15	10395364	10395964	4.0	1.9
chr15	10395401	10396001	4.1	2.0
chr15	10395438	10396038	4.4	2.3
chr15	10395476	10396076	4.6	2.3
chr15	10395513	10396113	4.5	2.3
chr15	10395589	10396189	4.7	2.4
chr15	10395626	10396226	4.4	2.2
chr15	10395663	10396263	4.3	2.1
chr15	10395700	10396300	4.2	2.1
chr15	10395738	10396338	3.7	1.8
chr15	10462928	10463528	3.8	0.7
chr15	10462963	10463563	3.8	0.7
chr15	10462998	10463598	3.7	0.6
chr15	10463033	10463633	3.7	0.7
chr15	10463068	10463668	3.8	0.7
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chr15	16924119	16924719	0.1	0.1
chr15	17130125	17130725	0.6	0.2
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chr15	23015630	23016230	0.7	0.1
chr15	23870791	23871391	0.7	0.1
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chr15	27249413	27250013	0.1	0.2
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chr15	27508449	27509049	1.5	0.3
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chr15	27563049	27563649	0.9	0.5

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chr15	36042283	36042883	1.5	0.4
chr15	36417193	36417793	1.2	0.3
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chr15	37546489	37547089	0.3	0.1
chr15	37764531	37765131	0.5	0.3
chr15	37857266	37857866	0.6	0.2
chr15	37942348	37942948	0.4	0.3
chr15	38116379	38116979	0.8	0.2
chr15	38211882	38212482	1.3	0.6
chr15	38979593	38980193	0.2	0.2
chr15	38979613	38980213	0.2	0.3
chr15	41815333	41815933	1.1	0.2
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chr15	42255247	42255847	0.3	0.1
chr15	42454124	42454724	0.0	0.0
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chr15	46514941	46515541	1.7	0.4
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chr15	51772059	51772659	6.0	2.7
chr15	51772084	51772684	6.1	2.7
chr15	51772109	51772709	6.1	2.7
chr15	51772134	51772734	6.4	2.8
chr15	51772159	51772759	6.6	2.8
chr15	51772284	51772884	6.3	2.6
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chr15	52405302	52405902	0.0	0.2
chr15	53056691	53057291	0.3	0.2
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chr15	54407436	54408036	0.3	0.4
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chr15	59802313	59802913	3.8	1.6

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chr15	79199918	79200518	1.2	0.3
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chr15	83139249	83139849	3.3	1.3
chr15	83139305	83139905	3.4	1.4
chr15	83139356	83139956	3.6	1.5
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chr15	83139480	83140080	3.6	1.4
chr15	83139540	83140140	3.6	1.4
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chr15	83139832	83140432	2.8	0.8
chr15	83139892	83140492	2.4	0.6
chr15	83139952	83140552	2.0	0.3
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chr15	85957824	85958424	2.4	1.4
chr15	85957882	85958482	2.2	1.4
chr15	86426317	86426917	1.2	0.8
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chr15	88805714	88806314	2.7	1.0
chr15	88805756	88806356	2.8	1.0
chr15	88805798	88806398	2.8	1.0
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chr15	88805882	88806482	2.5	0.9
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chr15	88806008	88806608	2.6	0.9
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chr15	88806260	88806860	1.6	0.6
chr15	88806302	88806902	1.6	0.6
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chr15	88985917	88986517	1.2	0.1
chr15	89234263	89234863	1.4	0.4
chr15	89234283	89234883	1.2	0.3
chr15	89234303	89234903	1.3	0.3
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chr15	94234061	94234661	2.2	1.2
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chr15	99733878	99734478	0.2	0.1

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chr15	101769818	101770418	1.9	0.1
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chr16	8198873	8199473	0.6	0.0
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chr16	8708186	8708786	0.3	0.0
chr16	8833487	8834087	0.1	0.1
chr16	9081873	9082473	0.9	0.3
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chr16	9355219	9355819	1.4	0.0
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chr16	9355293	9355893	1.2	0.1
chr16	9384031	9384631	0.4	0.5
chr16	9508651	9509251	1.2	0.1
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chr16	17927729	17928329	1.0	0.1
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chr16	22336886	22337486	0.6	0.5
chr16	23506296	23506896	0.4	0.4
chr16	23589365	23589965	0.0	0.0
chr16	23708572	23709172	0.0	0.0
chr16	23792487	23793087	0.8	0.2
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chr16	30143013	30143613	0.6	0.6
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chr16	30773721	30774321	1.4	0.4
chr16	30773946	30774546	1.2	0.4
chr16	31314282	31314882	0.6	0.2

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chr16	35871606	35872206	0.4	1.0
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chr16	39043417	39044017	0.7	0.6
chr16	39143262	39143862	0.4	0.2
chr16	39143275	39143875	0.4	0.1
chr16	39383097	39383697	0.6	0.2
chr16	40210862	40211462	0.6	0.2
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chr16	43985588	43986188	0.6	0.7
chr16	44285051	44285651	1.5	0.1
chr16	44502441	44503041	0.9	0.1
chr16	44551974	44552574	0.7	0.4
chr16	45716596	45717196	0.3	0.1
chr16	46320290	46320890	0.3	0.0
chr16	46617505	46618105	0.3	0.2
chr16	47046936	47047536	1.0	0.4

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chr16	47668853	47669453	0.7	0.2
chr16	48519846	48520446	0.8	0.3
chr16	48519955	48520555	0.8	0.2
chr16	49300317	49300917	1.6	0.5
chr16	49300426	49301026	1.6	0.5
chr16	51453244	51453844	1.6	0.1
chr16	51764811	51765411	2.6	0.4
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chr16	54442136	54442736	0.4	0.1
chr16	55112504	55113104	1.5	0.3
chr16	55112632	55113232	1.1	0.4
chr16	55253486	55254086	0.8	0.8
chr16	55549058	55549658	1.0	0.2
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chr16	56363629	56364229	0.5	0.0
chr16	56697405	56698005	1.0	0.2
chr16	56697415	56698015	1.0	0.2
chr16	57112982	57113582	1.2	0.3
chr16	57347073	57347673	0.1	0.2
chr16	57419310	57419910	0.5	0.2
chr16	58017749	58018349	0.3	0.2
chr16	58348729	58349329	0.4	0.2
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chr16	58872616	58873216	0.2	0.2
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chr16	77857370	77857970	1.1	0.1
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chr16	84557065	84557665	1.0	0.3
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chr16	84557094	84557694	0.9	0.3
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chr16	90950363	90950963	1.7	0.1
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chr16	92578845	92579445	0.4	0.0
chr16	92605286	92605886	1.2	0.4
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chr16	93309352	93309952	1.5	0.8
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chr16	97576582	97577182	1.7	0.2
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chr17	4442793	4443393	2.5	0.7
chr17	4442812	4443412	2.5	0.7
chr17	4442869	4443469	2.3	0.7
chr17	4442907	4443507	2.1	0.5
chr17	4442926	4443526	2.1	0.5
chr17	4442945	4443545	1.7	0.4
chr17	4442964	4443564	1.7	0.3
chr17	4443021	4443621	2.3	0.7
chr17	4443135	4443735	2.0	0.5
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chr17	4861225	4861825	2.2	0.2
chr17	4861271	4861871	2.2	0.2
chr17	4861293	4861893	2.1	0.1
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chr17	7547048	7547648	3.6	1.5
chr17	7547074	7547674	3.8	1.6
chr17	7547192	7547792	3.9	1.5
chr17	7924638	7925238	0.3	0.0
chr17	7997580	7998180	0.4	0.3
chr17	7997801	7998401	0.7	0.5
chr17	8208967	8209567	1.7	0.3
chr17	8208976	8209576	1.6	0.3
chr17	9034575	9035175	0.2	0.2
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chr17	9752015	9752615	0.1	0.0

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chr17	10763751	10764351	2.8	0.4
chr17	10763802	10764402	2.7	0.3
chr17	10763836	10764436	2.5	0.2
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chr17	12384309	12384909	0.5	0.3
chr17	12401021	12401621	0.5	0.1
chr17	12691729	12692329	0.8	0.0
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chr17	12898156	12898756	1.5	0.4
chr17	12904460	12905060	1.5	0.3
chr17	13061045	13061645	1.3	0.4
chr17	13272138	13272738	3.7	1.6
chr17	13272190	13272790	3.8	1.6
chr17	13272216	13272816	3.6	1.5
chr17	13272334	13272934	4.0	1.5
chr17	13566714	13567314	4.6	2.2
chr17	13566766	13567366	4.3	1.9
chr17	13566818	13567418	4.1	1.7
chr17	13566844	13567444	4.0	1.6
chr17	13566962	13567562	4.5	1.7
chr17	13662177	13662777	0.3	0.5
chr17	13667132	13667732	0.5	0.6
chr17	14100096	14100696	0.9	0.6
chr17	14180646	14181246	1.0	0.6
chr17	14296634	14297234	0.6	0.0
chr17	14405693	14406293	1.8	0.4
chr17	14405714	14406314	1.9	0.4
chr17	14405735	14406335	1.9	0.4
chr17	14405840	14406440	1.9	0.3

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chr17	15841137	15841737	1.5	0.6
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chr17	16355365	16355965	2.1	0.9
chr17	16355383	16355983	2.3	1.0
chr17	16731538	16732138	0.2	0.3
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chr17	17166768	17167368	1.0	0.2
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chr17	17172712	17173312	0.9	0.1
chr17	17172916	17173516	1.7	0.3
chr17	17173074	17173674	1.1	0.1
chr17	17218109	17218709	1.0	0.0
chr17	17221177	17221777	1.3	0.1
chr17	17275307	17275907	1.0	0.0
chr17	17278392	17278992	1.3	0.1
chr17	17394820	17395420	1.1	0.1
chr17	17451728	17452328	0.9	0.2
chr17	18702853	18703453	0.4	0.1
chr17	19093264	19093864	0.5	0.4
chr17	20242100	20242700	0.4	0.4
chr17	21121502	21122102	0.6	0.0
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chr17	21608784	21609384	1.1	0.3
chr17	22566779	22567379	0.2	0.3
chr17	23570405	23571005	0.5	0.0
chr17	23736040	23736640	1.0	0.3
chr17	23960390	23960990	1.0	0.0
chr17	24070721	24071321	0.9	0.4
chr17	24273035	24273635	0.2	0.2
chr17	24582055	24582655	1.2	0.1
chr17	24633241	24633841	2.1	0.5

chr17	24633265	24633865	2.1	0.4
chr17	24633485	24634085	2.1	0.5
chr17	24633510	24634110	2.5	0.6
chr17	24898696	24899296	1.9	0.4
chr17	24898895	24899495	0.9	0.4
chr17	25113173	25113773	2.1	0.2
chr17	25568446	25569046	1.0	0.1
chr17	25580403	25581003	0.3	0.1
chr17	25611107	25611707	1.0	0.5
chr17	25705631	25706231	2.2	0.3
chr17	25707933	25708533	0.9	0.5
chr17	25860260	25860860	1.7	0.3
chr17	25921410	25922010	1.6	0.1
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chr17	42715076	42715676	1.4	0.7
chr17	42715101	42715701	1.4	0.7
chr17	42715126	42715726	1.5	0.7
chr17	42715151	42715751	1.5	0.7
chr17	42715176	42715776	1.5	0.7
chr17	42715201	42715801	1.5	0.7
chr17	42715226	42715826	1.5	0.7
chr17	42715251	42715851	1.4	0.7

chr17	42715276	42715876	1.5	0.7
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chr17	42715351	42715951	1.5	0.7
chr17	42715376	42715976	1.5	0.7
chr17	42715401	42716001	1.5	0.7
chr17	42715426	42716026	1.5	0.7
chr17	42715451	42716051	1.5	0.7
chr17	42715476	42716076	1.5	0.7
chr17	42715501	42716101	1.5	0.7
chr17	42715526	42716126	1.5	0.8
chr17	42715551	42716151	1.6	0.8
chr17	42715576	42716176	1.6	0.8
chr17	42715601	42716201	1.6	0.8
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chr17	42715651	42716251	1.6	0.8
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chr17	42715776	42716376	1.6	0.8
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chr17	42715826	42716426	1.7	0.9
chr17	42715851	42716451	1.7	0.9
chr17	42715876	42716476	1.7	0.9
chr17	42715901	42716501	1.7	0.9
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chr17	42716026	42716626	1.6	0.8
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chr17	43350389	43350989	1.2	0.1
chr17	43507432	43508032	0.1	0.1

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chr17	43953267	43953867	2.0	0.3
chr17	43953305	43953905	1.9	0.3
chr17	43953325	43953925	1.9	0.3
chr17	43953462	43954062	1.6	0.3
chr17	44211934	44212534	0.7	0.1
chr17	44394793	44395393	0.9	0.2
chr17	44394856	44395456	1.1	0.3
chr17	44437696	44438296	0.8	0.4
chr17	44603997	44604597	0.6	0.3
chr17	44965666	44966266	0.3	0.1
chr17	44995781	44996381	1.4	0.3
chr17	45209288	45209888	2.0	0.5
chr17	45399987	45400587	0.4	0.3
chr17	45654098	45654698	1.3	0.6
chr17	45657109	45657709	1.1	0.2
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chr17	46000337	46000937	0.8	0.6
chr17	46003967	46004567	0.9	0.2
chr17	46012284	46012884	1.1	0.0
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chr17	46093419	46094019	1.3	0.1
chr17	46119009	46119609	0.8	0.4
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chr17	46813269	46813869	0.3	0.1
chr17	46936578	46937178	0.9	0.5
chr17	46971282	46971882	0.4	0.1
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chr17	47823229	47823829	0.3	0.0
chr17	48630855	48631455	0.5	0.3
chr17	48751879	48752479	0.5	0.3
chr17	49134505	49135105	0.6	0.4
chr17	49376199	49376799	0.2	0.3

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chr17	49549371	49549971	1.3	0.8
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chr17	49549602	49550202	1.1	1.0
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chr17	50564542	50565142	0.6	0.2
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chr17	51917453	51918053	1.8	0.6
chr17	51917674	51918274	0.9	0.7
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chr17	57039929	57040529	0.8	0.3
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chr17	57202620	57203220	1.9	0.8
chr17	58128515	58129115	1.6	0.2
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chr17	68346117	68346717	0.3	0.4
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chr17	69369443	69370043	1.1	0.2
chr17	69369468	69370068	1.0	0.2
chr17	69369485	69370085	1.0	0.2
chr17	69369538	69370138	1.0	0.2

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chr17	72820710	72821310	0.8	0.2
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chr17	73885302	73885902	1.3	0.2
chr17	74321516	74322116	0.6	0.3
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chr17	74351711	74352311	0.9	0.0
chr17	74357814	74358414	2.1	0.1
chr17	74389983	74390583	0.5	0.0
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chr17	74577714	74578314	1.9	0.3
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chr17	75839875	75840475	0.6	0.1
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chr17	78884332	78884932	0.9	0.1
chr17	78962073	78962673	0.7	0.2
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chr17	83626341	83626941	0.3	0.3
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chr17	85160869	85161469	1.3	0.3
chr17	85962562	85963162	1.0	0.4
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chr17	85982749	85983349	0.4	0.0
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chr17	86303050	86303650	4.0	1.3
chr17	86303072	86303672	3.9	1.3
chr17	86303094	86303694	3.9	1.3
chr17	86303116	86303716	3.7	1.3
chr17	86303138	86303738	3.7	1.4
chr17	86303160	86303760	3.8	1.3
chr17	86303182	86303782	3.6	1.3
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chr17	87212013	87212613	0.0	0.1
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chr17	88133444	88134044	1.9	0.2
chr17	88141323	88141923	0.8	0.1
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chr17	89208403	89209003	1.8	0.0
chr17	90800734	90801334	1.7	0.0
chr17	93357502	93358102	1.4	0.3
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chr18	6636335	6636935	1.2	0.0
chr18	7079103	7079703	1.8	0.1
chr18	7556032	7556632	2.0	0.9
chr18	7556083	7556683	2.3	1.0
chr18	7556134	7556734	2.5	1.1
chr18	7556185	7556785	2.8	1.3
chr18	7556236	7556836	2.9	1.4
chr18	7556287	7556887	2.9	1.4
chr18	7556338	7556938	2.5	1.2
chr18	7556389	7556989	2.4	1.2
chr18	7556440	7557040	2.2	1.2
chr18	8161837	8162437	2.0	1.0
chr18	8162060	8162660	2.7	0.5
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chr18	12653827	12654427	0.7	0.1
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chr18	14291263	14291863	2.1	0.6
chr18	14291327	14291927	2.1	0.6
chr18	14291359	14291959	2.0	0.5
chr18	14291455	14292055	1.7	0.6
chr18	14291487	14292087	1.9	0.6

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chr18	15320933	15321533	1.2	0.2
chr18	15321015	15321615	1.3	0.2
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chr18	31358153	31358753	2.8	0.5
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chr18	36434160	36434760	1.9	0.1
chr18	36434250	36434850	2.1	0.1
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chr18	36447629	36448229	0.5	0.1
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chr18	47027153	47027753	0.1	0.2
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chr18	50388623	50389223	1.0	0.3
chr18	50630452	50631052	1.3	0.1
chr18	51703611	51704211	0.3	0.4
chr18	52289434	52290034	0.2	0.3
chr18	52569375	52569975	1.0	0.2
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chr18	54933806	54934406	0.5	0.1
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chr18	56544329	56544929	1.6	0.2
chr18	56544395	56544995	1.5	0.3
chr18	56548898	56549498	1.7	0.8
chr18	56549152	56549752	2.7	1.2
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chr18	58885967	58886567	0.6	0.4
chr18	58898039	58898639	0.4	0.4
chr18	59120699	59121299	1.3	0.5
chr18	59419439	59420039	1.3	0.2
chr18	59765320	59765920	0.9	0.1
chr18	60117725	60118325	1.2	0.0

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chr18	60458171	60458771	1.5	1.0
chr18	60731188	60731788	1.6	0.5
chr18	60731212	60731812	1.3	0.5
chr18	60864615	60865215	0.4	0.2
chr18	61483170	61483770	0.3	0.5
chr18	61491460	61492060	1.2	0.4
chr18	61491486	61492086	1.3	0.4
chr18	61710599	61711199	0.4	0.2
chr18	61817378	61817978	0.7	0.4
chr18	61820420	61821020	1.5	0.0
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chr18	61954366	61954966	1.5	0.4
chr18	61954442	61955042	1.3	0.2
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chr18	63560248	63560848	0.5	0.2
chr18	64558732	64559332	0.7	0.3
chr18	64829559	64830159	0.5	0.2
chr18	64844496	64845096	0.7	0.1
chr18	65045719	65046319	0.1	0.5
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chr18	65523417	65524017	1.5	0.7
chr18	65523663	65524263	2.0	0.3
chr18	65683738	65684338	1.6	0.1
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chr18	65963661	65964261	1.1	0.0
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chr18	72493113	72493713	0.4	0.2
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chr18	74026830	74027430	1.4	0.5
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chr18	75535128	75535728	0.9	0.3
chr18	75707212	75707812	1.5	0.7
chr18	75707258	75707858	1.6	0.7
chr18	75736134	75736734	0.6	0.3
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chr18	76502304	76502904	0.8	0.5
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chr18	78361963	78362563	0.9	0.8

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chr18	78637513	78638113	1.0	0.0
chr18	78637606	78638206	1.1	0.2
chr18	79180432	79181032	1.2	0.3
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chr18	79828490	79829090	0.7	0.3
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chr18	80499673	80500273	0.3	0.3
chr18	80750488	80751088	0.7	0.4
chr18	80802300	80802900	0.9	0.3
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chr18	82577978	82578578	2.5	0.3
chr18	82577994	82578594	2.4	0.3
chr18	82757388	82757988	0.9	0.3
chr18	83067554	83068154	0.3	0.1
chr18	83630785	83631385	0.4	0.2
chr18	83912329	83912929	0.2	0.5
chr18	83912618	83913218	0.7	0.2
chr18	83964770	83965370	0.1	0.0
chr18	84036044	84036644	2.0	0.2
chr18	84084252	84084852	1.2	0.1
chr18	84933981	84934581	1.3	0.1
chr18	84938270	84938870	0.6	0.2
chr18	84947937	84948537	0.8	0.1
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chr18	86659425	86660025	1.2	0.2
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chr19	3551623	3552223	0.2	0.8
chr19	3840286	3840886	0.3	0.5
chr19	3912405	3913005	1.2	0.3
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chr19	4397426	4398026	0.6	0.0
chr19	4456543	4457143	1.2	0.5
chr19	4688160	4688760	0.6	0.1
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chr19	5134385	5134985	0.3	0.3
chr19	5659295	5659895	0.3	0.0
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chr19	5745767	5746367	0.7	0.2
chr19	5766258	5766858	0.5	0.1
chr19	5943110	5943710	3.1	0.5
chr19	5943120	5943720	3.1	0.5
chr19	5943128	5943728	3.1	0.5
chr19	6261020	6261620	0.8	0.3
chr19	8374973	8375573	0.1	0.1
chr19	8521652	8522252	0.2	0.5
chr19	8640359	8640959	0.9	0.2
chr19	8815455	8816055	0.9	0.2
chr19	8832951	8833551	1.3	0.4
chr19	8833055	8833655	1.3	0.3
chr19	8877091	8877691	0.7	0.0
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chr19	9149900	9150500	0.4	0.0
chr19	9339438	9340038	0.2	0.4
chr19	9746311	9746911	0.2	0.2
chr19	9923156	9923756	0.5	0.2
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chr19	10073575	10074175	1.3	0.2
chr19	10412788	10413388	0.4	0.1
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chr19	10606893	10607493	0.7	0.0
chr19	10864058	10864658	0.3	0.3
chr19	11069521	11070121	0.7	0.3
chr19	11071977	11072577	0.5	0.0
chr19	11328338	11328938	1.1	0.3
chr19	11400623	11401223	0.2	0.3
chr19	11923431	11924031	0.3	0.2
chr19	11951414	11952014	0.5	0.0

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chr19	12306333	12306933	1.0	0.1
chr19	12888784	12889384	2.0	0.8
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chr19	12985733	12986333	1.0	0.3
chr19	13225962	13226562	0.9	0.0
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chr19	15522868	15523468	1.5	0.0
chr19	16128604	16129204	0.2	0.1
chr19	16132433	16133033	1.3	0.5
chr19	16347796	16348396	2.4	0.7
chr19	16347824	16348424	2.6	0.8
chr19	16347852	16348452	2.8	0.7
chr19	16347880	16348480	3.1	0.8
chr19	17849506	17850106	0.2	0.4
chr19	18472251	18472851	2.4	0.4
chr19	18472519	18473119	2.1	0.5
chr19	19015579	19016179	2.0	0.6
chr19	19015603	19016203	2.0	0.6
chr19	19083757	19084357	0.7	0.2
chr19	20072690	20073290	0.9	0.2
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chr19	22937295	22937895	1.0	0.2
chr19	22994179	22994779	0.2	0.4
chr19	23097932	23098532	0.1	0.0
chr19	23690325	23690925	1.5	0.1
chr19	23690403	23691003	1.9	0.3
chr19	24370546	24371146	0.5	0.1
chr19	24463654	24464254	0.6	0.9
chr19	24463759	24464359	0.9	0.7

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chr19	25579617	25580217	0.6	0.0
chr19	25774440	25775040	1.0	0.7
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chr19	27376027	27376627	1.0	0.1
chr19	27541984	27542584	0.9	0.2
chr19	27586568	27587168	0.9	0.7
chr19	28144211	28144811	0.4	0.3
chr19	28982571	28983171	2.4	0.3
chr19	28982636	28983236	2.1	0.3
chr19	29657870	29658470	1.0	0.2
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chr19	32542720	32543320	0.4	0.2
chr19	33230658	33231258	0.5	0.4
chr19	34079233	34079833	0.6	0.2
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chr19	34512887	34513487	1.1	0.3
chr19	34852569	34853169	0.0	0.1
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chr19	36259011	36259611	3.0	1.3
chr19	36259064	36259664	3.0	1.2
chr19	36344219	36344819	1.4	0.4
chr19	36344318	36344918	1.0	0.3
chr19	36350988	36351588	0.2	0.4
chr19	36608778	36609378	0.9	0.2
chr19	36781656	36782256	0.9	0.2
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chr19	38423358	38423958	1.1	0.3
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chr19	43123804	43124404	0.7	0.3
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chr19	48213963	48214563	2.1	0.2

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chr19	49755803	49756403	0.8	0.2
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chr19	49957735	49958335	0.9	0.2
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chr19	57581238	57581838	0.1	0.3
chr19	57859732	57860332	0.0	0.1
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chr2	3290051	3290651	1.5	0.5
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chr2	13609784	13610384	0.8	0.1
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chr2	18946159	18946759	0.7	0.5
chr2	19017452	19018052	1.5	0.1
chr2	20021294	20021894	0.5	0.0
chr2	20156313	20156913	0.5	0.1
chr2	20994376	20994976	1.3	0.1

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chr2	21329330	21329930	1.2	0.2
chr2	21471982	21472582	1.5	0.9
chr2	21472228	21472828	1.9	0.8
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chr2	24150733	24151333	1.4	0.1
chr2	24487501	24488101	1.2	0.2
chr2	24561439	24562039	0.2	0.0
chr2	24561622	24562222	0.8	0.5
chr2	24960496	24961096	0.9	0.2
chr2	24960587	24961187	0.9	0.1
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chr2	25438881	25439481	1.1	0.6
chr2	25438923	25439523	0.6	0.4
chr2	25693856	25694456	4.0	2.0
chr2	25693889	25694489	4.1	2.0
chr2	25693922	25694522	4.1	2.0
chr2	25693955	25694555	4.0	2.0
chr2	25693988	25694588	3.6	2.0
chr2	25694021	25694621	3.8	2.0
chr2	25694054	25694654	3.7	2.0
chr2	25941474	25942074	1.1	0.0
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chr2	26031426	26032026	2.4	0.1
chr2	26031467	26032067	2.3	0.1
chr2	26187836	26188436	0.7	0.3
chr2	26197302	26197902	0.5	0.0
chr2	26271374	26271974	0.2	0.1
chr2	26582014	26582614	0.9	0.1
chr2	26582116	26582716	1.0	0.2
chr2	26916272	26916872	1.5	0.2
chr2	26991730	26992330	0.9	0.2
chr2	27266260	27266860	1.4	0.9
chr2	27266272	27266872	1.5	0.8
chr2	27266340	27266940	1.4	0.6
chr2	27550603	27551203	1.1	0.3

chr2	27919783	27920383	0.7	0.0
chr2	27947043	27947643	1.1	0.1
chr2	27954327	27954927	0.4	0.0
chr2	28042351	28042951	0.5	0.2
chr2	29459481	29460081	1.5	0.4
chr2	29889010	29889610	0.3	0.3
chr2	30423799	30424399	0.2	0.1
chr2	30562956	30563556	0.6	0.7
chr2	30656711	30657311	0.1	0.1
chr2	31032161	31032761	1.0	0.1
chr2	31032256	31032856	1.2	0.3
chr2	31063866	31064466	0.0	0.0
chr2	31699827	31700427	0.9	0.5
chr2	32183219	32183819	1.4	0.5
chr2	32850463	32851063	0.2	0.1
chr2	33033780	33034380	2.0	1.1
chr2	33033918	33034518	2.0	0.8
chr2	33126537	33127137	0.7	0.1
chr2	33437945	33438545	0.3	0.5
chr2	33808231	33808831	0.5	0.1
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chr2	67482437	67483037	1.6	0.7
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chr2	163170860	163171460	0.8	0.2
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chr2	164381862	164382462	1.8	0.8
chr2	164381913	164382513	1.7	0.8
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chr2	164704420	164705020	1.1	0.2
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chr2	171688829	171689429	8.4	3.6
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chr2	171688908	171689508	9.2	4.2
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chr2	180971226	180971826	0.6	0.0
chr2	181008354	181008954	1.8	0.7
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chr2	181171484	181172084	1.6	0.6
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chr3	27915573	27916173	2.8	0.8
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chr3	96155532	96156132	1.2	0.4
chr3	96185863	96186463	1.2	0.4

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chr3	97382505	97383105	1.9	0.5
chr3	97382530	97383130	2.0	0.5
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chr3	97382566	97383166	1.9	0.5
chr3	97382638	97383238	1.9	0.4
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chr3	100900121	100900721	0.8	0.0
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chr3	101119425	101120025	0.2	0.2
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chr3	101471516	101472116	0.3	0.2
chr3	101601582	101602182	0.6	0.0
chr3	101929817	101930417	0.9	0.7
chr3	101993805	101994405	1.8	0.1
chr3	102322262	102322862	1.0	0.3
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chr3	102459899	102460499	2.6	0.5
chr3	102742994	102743594	0.9	0.6
chr3	102937519	102938119	1.2	0.7
chr3	102937553	102938153	1.1	0.6
chr3	102937587	102938187	1.4	0.7

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chr3	104024207	104024807	0.8	0.2
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chr3	104944356	104944956	1.5	0.1
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chr3	113087061	113087661	0.7	0.1
chr3	113119666	113120266	0.8	0.1
chr3	113152271	113152871	0.7	0.1
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chr3	121316102	121316702	0.3	0.3
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chr3	122107816	122108416	2.7	1.5
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chr3	124391124	124391724	0.7	0.2
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chr3	128349493	128350093	0.7	0.5
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chr3	131782718	131783318	1.2	0.2
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chr3	132392767	132393367	1.0	0.3
chr3	132393016	132393616	1.8	0.5
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chr3	135274737	135275337	0.5	0.6
chr3	135517881	135518481	0.1	0.0
chr3	135680985	135681585	1.2	0.5
chr3	135778685	135779285	0.3	0.2
chr3	135834505	135835105	0.1	0.1
chr3	135873077	135873677	0.7	0.1
chr3	135988529	135989129	0.7	0.0
chr3	136029847	136030447	0.2	0.3
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chr3	140839984	140840584	1.7	0.6
chr3	141381104	141381704	1.2	0.0
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chr3	141885706	141886306	1.3	0.0
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chr3	143247512	143248112	0.4	0.1
chr3	143425011	143425611	1.7	0.2
chr3	143529341	143529941	1.0	0.5
chr3	143529429	143530029	0.8	0.4
chr3	144087767	144088367	1.5	0.6
chr3	144088006	144088606	0.5	0.1
chr3	144295269	144295869	1.5	0.3
chr3	144333647	144334247	0.6	0.0
chr3	145172552	145173152	0.7	0.2
chr3	145433383	145433983	0.4	0.5
chr3	145499714	145500314	0.6	0.2
chr3	145580187	145580787	0.5	0.4
chr3	145621161	145621761	0.1	0.1
chr3	145706537	145707137	0.8	0.1
chr3	145895871	145896471	0.0	0.0
chr3	146433532	146434132	0.1	0.4
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chr3	147803200	147803800	0.7	0.1
chr3	148344379	148344979	1.7	0.3
chr3	149070160	149070760	0.1	0.1
chr3	149427248	149427848	1.2	0.3
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chr3	151080554	151081154	0.3	0.1
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chr3	152240816	152241416	0.5	0.8
chr3	152680490	152681090	1.5	0.0
chr3	153083290	153083890	1.1	0.0

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chr3	153375067	153375667	1.8	0.4
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chr3	154035049	154035649	0.4	0.1
chr3	154064338	154064938	1.2	0.3
chr3	154210839	154211439	1.2	0.1
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chr3	155103760	155104360	1.1	0.1
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chr3	157414155	157414755	1.0	0.2
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chr3	158318512	158319112	1.3	0.1
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chr4	4672072	4672672	1.0	0.7
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chr4	13197013	13197613	0.9	0.6
chr4	13643674	13644274	0.9	0.1
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chr4	15192545	15193145	0.4	0.1
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chr4	32747137	32747737	0.8	0.0
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chr4	34244143	34244743	1.3	0.0

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chr4	56150751	56151351	2.4	0.6
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chr4	57784492	57785092	1.8	0.6
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chr4	73872452	73873052	0.4	0.2
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chr4	75846956	75847556	1.1	0.2
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chr4	83764112	83764712	1.0	0.0
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chr4	83764332	83764932	1.9	0.5
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chr4	84704538	84705138	0.5	0.1
chr4	84929883	84930483	1.2	0.8
chr4	84930021	84930621	1.3	0.6
chr4	85339807	85340407	0.1	0.2
chr4	85627155	85627755	1.6	0.4
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chr4	86294091	86294691	1.5	0.3
chr4	86349900	86350500	0.7	0.3
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chr4	123825823	123826423	0.7	0.1
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chr5	3857611	3858211	2.3	0.4
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chr5	19128810	19129410	1.9	1.0
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chr5	27248322	27248922	2.2	1.2
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chr5	123581246	123581846	0.6	0.1
chr5	124177870	124178470	0.3	0.0
chr5	124515282	124515882	1.6	1.0
chr5	124626668	124627268	0.4	0.2
chr5	124642799	124643399	0.2	0.2
chr5	125073140	125073740	0.6	0.1
chr5	125657564	125658164	1.5	0.9

chr5	125659570	125660170	1.2	0.8
chr5	125659577	125660177	1.2	0.8
chr5	125674351	125674951	2.0	0.2
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chr5	126508154	126508754	0.8	0.4
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chr5	127322652	127323252	1.3	0.1
chr5	127322689	127323289	1.4	0.2
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chr5	127852845	127853445	1.8	0.7
chr5	128259319	128259919	0.3	0.1
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chr5	128603751	128604351	1.5	0.2
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chr5	129627146	129627746	1.1	0.3
chr5	129666471	129667071	0.5	0.1
chr5	129675211	129675811	1.2	0.3
chr5	129709714	129710314	0.0	0.2
chr5	129836937	129837537	0.7	0.1
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chr5	130408791	130409391	1.2	0.2
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chr5	134931383	134931983	0.7	0.9
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chr5	146181923	146182523	0.1	0.1
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chr5	148367557	148368157	0.4	0.0
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chr5	148445406	148446006	1.3	0.3
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chr5	148672085	148672685	0.1	0.2
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chr5	149265424	149266024	0.2	0.5
chr5	149401462	149402062	0.9	0.1
chr5	149402722	149403322	0.9	0.2
chr5	149442851	149443451	1.5	0.2
chr5	149443835	149444435	1.5	0.4
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chr5	150040287	150040887	1.8	0.6
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chr6	82993409	82994009	1.3	0.3
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chr6	86638522	86639122	0.7	0.1
chr6	86779373	86779973	0.2	0.0
chr6	87233748	87234348	0.0	0.6

chr6	87294879	87295479	0.6	0.2
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chr6	88430583	88431183	0.9	0.8
chr6	88771451	88772051	1.2	0.2
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chr6	88823166	88823766	1.5	0.0
chr6	90049492	90050092	1.7	0.6
chr6	90049583	90050183	1.3	0.6
chr6	90157817	90158417	2.8	0.5
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chr6	90736938	90737538	0.4	0.0
chr6	91284568	91285168	0.3	0.2
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chr6	92852946	92853546	0.0	0.3
chr6	92890877	92891477	1.2	0.0
chr6	92942427	92943027	0.2	0.4
chr6	93026435	93027035	1.3	0.3
chr6	93109128	93109728	1.0	0.2
chr6	93124539	93125139	0.9	0.1
chr6	93891381	93891981	0.5	0.1
chr6	94000065	94000665	1.7	0.9
chr6	94000125	94000725	1.9	0.9
chr6	94000245	94000845	2.2	0.8
chr6	94113177	94113777	0.7	0.2
chr6	94196906	94197506	0.1	0.1
chr6	94419825	94420425	0.3	0.2
chr6	94567327	94567927	0.4	0.4
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chr6	95993290	95993890	0.6	0.1

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chr6	132262071	132262671	2.5	0.5
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chr6	140146019	140146619	3.0	0.2
chr6	140146063	140146663	2.9	0.2
chr6	140146107	140146707	3.0	0.2
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chr6	140146195	140146795	3.0	0.1

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chr6	142682262	142682862	1.5	0.3
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chr6	144483571	144484171	7.6	3.4
chr6	144483615	144484215	7.6	3.5
chr6	144483631	144484231	7.4	3.3
chr6	144483754	144484354	7.5	3.3
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chr6	145081204	145081804	1.4	0.6
chr6	145081255	145081855	1.3	0.6
chr6	145081306	145081906	1.5	0.6
chr6	145081357	145081957	1.4	0.6
chr6	145081408	145082008	1.7	0.7
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chr7	28883324	28883924	1.6	0.4

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chr7	28933173	28933773	1.5	0.6
chr7	28981690	28982290	1.8	0.6
chr7	28981699	28982299	1.7	0.7
chr7	29349551	29350151	0.6	0.1
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chr7	30132482	30133082	0.6	0.2
chr7	30185249	30185849	0.3	0.1
chr7	30195705	30196305	0.5	0.1
chr7	30196166	30196766	0.2	0.2
chr7	30425221	30425821	0.5	0.0
chr7	31185086	31185686	0.5	0.2
chr7	31311957	31312557	1.4	0.0
chr7	31317933	31318533	0.5	0.5
chr7	31407982	31408582	0.7	0.0
chr7	31408106	31408706	0.6	0.2
chr7	31430422	31431022	2.8	0.5
chr7	31430461	31431061	2.9	0.4
chr7	31989253	31989853	0.4	0.0
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chr7	32887176	32887776	0.3	0.3
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chr7	33620299	33620899	0.7	0.1
chr7	33622877	33623477	0.4	0.4
chr7	33847194	33847794	0.7	0.1
chr7	33849772	33850372	0.4	0.4
chr7	33904109	33904709	1.2	0.3
chr7	34313688	34314288	1.2	0.1
chr7	34678718	34679318	1.2	0.1
chr7	35216048	35216648	6.2	3.1
chr7	35216064	35216664	6.3	3.1
chr7	35216080	35216680	6.5	3.2
chr7	35216096	35216696	6.5	3.2
chr7	35216128	35216728	6.5	3.0
chr7	35623108	35623708	0.3	0.6
chr7	35907948	35908548	1.3	0.1

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chr7	36164531	36165131	1.1	0.3
chr7	36288396	36288996	0.1	0.1
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chr7	37209449	37210049	0.2	0.0
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chr7	38281272	38281872	1.0	0.7
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chr7	74110317	74110917	0.1	0.2
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chr7	78513740	78514340	1.5	0.2
chr7	78513849	78514449	1.5	0.2
chr7	78757256	78757856	1.2	0.4
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chr7	81706151	81706751	4.1	1.3
chr7	81706207	81706807	4.7	1.7
chr7	81706235	81706835	4.6	1.6
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chr7	81706347	81706947	4.4	1.5
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chr7	85876813	85877413	0.5	0.2
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chr7	87026927	87027527	2.5	0.9
chr7	87026937	87027537	2.6	0.8
chr7	87026957	87027557	2.7	0.9
chr7	87026975	87027575	2.5	0.9
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chr7	90307884	90308484	0.5	0.2
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chr7	105645527	105646127	2.6	0.8
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chr7	125459016	125459616	0.7	0.2
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chr7	127556784	127557384	1.7	0.4
chr7	127737271	127737871	1.5	1.2
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chr7	130483095	130483695	4.5	1.6
chr7	130483157	130483757	4.4	1.8
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chr7	130483250	130483850	4.5	1.9
chr7	130483281	130483881	4.6	1.9
chr7	130655615	130656215	0.1	0.2
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chr7	132354855	132355455	0.7	0.5
chr7	132541756	132542356	2.7	0.6

chr7	132541795	132542395	2.6	0.6
chr7	132541831	132542431	2.8	0.6
chr7	132541855	132542455	2.8	0.7
chr7	132541949	132542549	2.9	0.8
chr7	132757949	132758549	0.2	0.0
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chr7	133108832	133109432	0.1	0.2
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chr7	135800679	135801279	0.5	0.1
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chr7	136953608	136954208	0.7	0.0
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chr7	137317793	137318393	0.6	0.3
chr7	137456415	137457015	0.5	0.4
chr7	137578487	137579087	0.5	0.0
chr7	137578720	137579320	0.6	0.0
chr7	137818008	137818608	0.3	0.1
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chr7	138752491	138753091	0.5	0.2
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chr7	138928387	138928987	1.0	0.2
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chr7	139284794	139285394	0.0	0.1
chr7	139560443	139561043	0.6	0.3
chr7	139605350	139605950	0.0	0.2
chr7	139753044	139753644	0.8	0.0
chr7	139912270	139912870	0.1	0.1
chr7	140029938	140030538	0.5	0.0
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chr7	140988958	140989558	1.8	0.1
chr7	141466478	141467078	1.1	0.3
chr7	141807688	141808288	1.3	0.2

chr7	141810732	141811332	1.5	0.3
chr7	141887988	141888588	0.2	0.1
chr7	141899694	141900294	1.7	0.5
chr7	141899792	141900392	1.3	0.6
chr7	142459946	142460546	0.6	0.2
chr7	143401031	143401631	0.9	0.1
chr7	143639372	143639972	0.7	0.2
chr7	143799331	143799931	1.6	0.0
chr7	144241913	144242513	0.9	0.2
chr7	144650461	144651061	0.4	0.2
chr7	146320803	146321403	0.6	0.5
chr7	147301835	147302435	1.1	0.5
chr7	147834646	147835246	0.6	0.1
chr7	147904565	147905165	0.3	0.4
chr7	147904582	147905182	0.3	0.4
chr7	148139260	148139860	0.9	0.1
chr7	148240411	148241011	1.0	0.4
chr7	148240590	148241190	1.2	0.5
chr7	148268556	148269156	0.6	0.0
chr7	148296507	148297107	4.1	1.6
chr7	148296545	148297145	4.0	1.5
chr7	148296564	148297164	3.9	1.5
chr7	148296583	148297183	3.9	1.6
chr7	148296602	148297202	3.9	1.5
chr7	148296621	148297221	3.7	1.4
chr7	148296640	148297240	3.8	1.5
chr7	148296663	148297263	3.8	1.5
chr7	148296686	148297286	3.8	1.6
chr7	148296705	148297305	3.8	1.6
chr7	148296736	148297336	3.7	1.6
chr7	148481871	148482471	0.8	0.0
chr7	148993726	148994326	2.3	0.6
chr7	148993834	148994434	2.4	0.9
chr7	148995835	148996435	2.3	0.6
chr7	148995943	148996543	2.4	0.8
chr7	149056628	149057228	0.5	0.0
chr7	149231610	149232210	0.2	0.1
chr7	149312345	149312945	0.1	0.5

chr7	149557719	149558319	0.1	0.1
chr7	149629061	149629661	0.7	0.4
chr7	149629152	149629752	0.6	0.1
chr7	149629171	149629771	0.8	0.2
chr7	149660502	149661102	1.2	0.2
chr7	149660654	149661254	1.2	0.3
chr7	150197011	150197611	0.7	0.2
chr7	150447928	150448528	1.2	0.0
chr7	150448001	150448601	1.4	0.2
chr7	150665227	150665827	1.0	0.1
chr7	150754119	150754719	0.8	0.0
chr7	150790559	150791159	0.5	0.5
chr7	150826738	150827338	0.5	0.1
chr7	150912613	150913213	0.8	0.2
chr7	151175635	151176235	0.1	0.0
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chr7	151593305	151593905	0.6	0.3
chr7	151593556	151594156	0.6	0.2
chr7	151593563	151594163	0.8	0.2
chr7	151839659	151840259	0.7	0.1
chr7	151967202	151967802	0.9	0.5
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chr7	152196485	152197085	1.0	0.3
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chr8	8210865	8211465	2.6	0.6
chr8	8440815	8441415	0.7	0.2
chr8	8524859	8525459	0.2	0.2
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chr8	8663291	8663891	1.6	0.3
chr8	8663588	8664188	1.2	0.6
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chr8	8930008	8930608	0.2	0.3
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chr8	9388436	9389036	1.2	0.4
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chr8	9824614	9825214	2.1	0.2
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chr8	9960546	9961146	0.4	0.0
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chr8	10264411	10265011	1.1	0.3
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chr8	10467330	10467930	1.5	1.3
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chr8	11914714	11915314	1.0	0.1
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chr8	12698550	12699150	1.7	0.2
chr8	12976724	12977324	0.2	0.3
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chr8	13275915	13276515	1.1	0.1
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chr8	13479552	13480152	0.2	0.2
chr8	13571333	13571933	0.6	0.0
chr8	13757136	13757736	0.9	0.1
chr8	14377192	14377792	1.0	0.2
chr8	14452924	14453524	0.5	0.1
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chr8	15192284	15192884	1.2	0.1
chr8	15192378	15192978	1.2	0.1
chr8	16011472	16012072	0.2	0.1

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chr8	18464767	18465367	1.5	0.1
chr8	18565677	18566277	1.2	0.1
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chr8	19889097	19889697	1.4	0.1
chr8	20016374	20016974	1.2	0.1
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chr8	23851451	23852051	1.3	0.1
chr8	24141881	24142481	0.1	0.1
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chr8	24241797	24242397	0.2	0.1
chr8	24472185	24472785	0.2	0.3
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chr8	26112754	26113354	1.5	0.9
chr8	26112944	26113544	1.3	0.7
chr8	26113210	26113810	0.8	0.5
chr8	26149201	26149801	2.1	0.4
chr8	26149271	26149871	2.4	0.4
chr8	26635362	26635962	1.1	0.0
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chr8	32377786	32378386	0.5	0.4
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chr8	35209817	35210417	1.4	0.2
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chr8	35485354	35485954	0.7	0.1
chr8	36617848	36618448	0.7	0.2
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chr8	36780828	36781428	1.0	0.7
chr8	36993396	36993996	0.6	0.2
chr8	37043913	37044513	0.4	0.2
chr8	37058760	37059360	1.2	0.2
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chr8	45596205	45596805	0.8	0.5
chr8	45596241	45596841	0.8	0.5
chr8	46081756	46082356	1.8	0.8
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chr8	46961340	46961940	2.4	0.2
chr8	46961354	46961954	2.2	0.1
chr8	47947470	47948070	2.5	0.8
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chr8	49706600	49707200	0.4	0.1
chr8	49766960	49767560	1.0	0.2
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chr8	51490730	51491330	1.2	0.3
chr8	53016535	53017135	1.0	0.1
chr8	53207765	53208365	1.2	0.2
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chr8	53676124	53676724	2.2	1.2
chr8	54192347	54192947	0.9	0.0
chr8	54322597	54323197	0.3	0.0
chr8	54697286	54697886	0.5	0.1
chr8	54767754	54768354	0.5	0.1
chr8	54892193	54892793	0.1	0.2
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chr8	58840433	58841033	1.0	0.1
chr8	59461765	59462365	1.9	0.0
chr8	59492843	59493443	0.7	0.2
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chr8	61623439	61624039	0.1	0.2
chr8	62748996	62749596	5.7	2.0
chr8	62749013	62749613	5.8	2.1
chr8	62749030	62749630	5.8	1.9
chr8	62749047	62749647	5.2	1.6
chr8	62749064	62749664	5.1	1.6
chr8	62749081	62749681	5.0	1.7
chr8	62749098	62749698	4.9	1.6
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chr8	63092680	63093280	1.3	0.6
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chr8	63671778	63672378	1.3	0.5
chr8	63671945	63672545	0.9	0.4
chr8	63807179	63807779	1.4	0.1
chr8	63819997	63820597	1.3	0.3
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chr8	65125302	65125902	2.2	1.0
chr8	65125552	65126152	2.2	0.8
chr8	66194858	66195458	0.0	0.0
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chr8	67066875	67067475	0.8	0.2
chr8	67185872	67186472	1.2	0.2
chr8	67623726	67624326	0.2	0.0
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chr8	74293322	74293922	0.9	0.4
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chr8	75000945	75001545	0.9	0.0
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chr8	77375933	77376533	0.9	0.0
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chr8	79548501	79549101	0.9	0.2
chr8	80257583	80258183	0.6	0.4
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chr8	81401152	81401752	2.1	0.3
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chr8	81651122	81651722	0.4	0.1
chr8	81847679	81848279	1.9	0.3
chr8	81847713	81848313	2.0	0.3
chr8	81847755	81848355	1.8	0.3
chr8	81847797	81848397	1.9	0.4
chr8	81847818	81848418	1.9	0.3
chr8	81986733	81987333	2.0	0.4
chr8	82361806	82362406	1.5	0.1
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chr8	83211002	83211602	0.6	0.2
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chr8	86243838	86244438	1.4	0.7
chr8	86243941	86244541	0.8	0.4
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chr8	87179776	87180376	2.5	0.5
chr8	87179793	87180393	2.4	0.3
chr8	87285282	87285882	0.4	0.1
chr8	87361863	87362463	1.2	0.2
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chr8	88076554	88077154	0.5	0.1
chr8	88407829	88408429	0.7	0.1
chr8	88519658	88520258	1.1	0.2
chr8	89833189	89833789	0.7	0.2
chr8	89833378	89833978	0.1	0.0
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chr8	90975664	90976264	2.1	0.1
chr8	91138357	91138957	0.6	0.3
chr8	91138448	91139048	1.2	0.4
chr8	91587950	91588550	0.9	0.1
chr8	91644801	91645401	1.1	0.4
chr8	91693687	91694287	0.4	0.2
chr8	92401412	92402012	1.5	0.5
chr8	92402399	92402999	1.7	0.6
chr8	92758461	92759061	0.1	0.1
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chr8	94884315	94884915	0.2	0.2
chr8	94997357	94997957	1.6	0.1
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chr8	95443397	95443997	0.5	0.0
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chr8	95977529	95978129	0.6	0.5
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chr8	97031118	97031718	0.6	0.0
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chr8	97290034	97290634	1.7	0.8
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chr8	97711137	97711737	1.0	0.1
chr8	98415572	98416172	2.1	0.3
chr8	98415794	98416394	2.0	0.4
chr8	98703957	98704557	0.2	0.0
chr8	98851110	98851710	1.2	0.3
chr8	98851149	98851749	1.0	0.2
chr8	100058842	100059442	1.0	0.2
chr8	101024405	101025005	0.6	0.5
chr8	102201275	102201875	0.0	0.3
chr8	102507130	102507730	1.9	0.2
chr8	103825154	103825754	1.2	0.1
chr8	104444921	104445521	1.8	0.1
chr8	104828044	104828644	0.6	0.1
chr8	106022037	106022637	0.2	0.2
chr8	106308487	106309087	1.3	0.1
chr8	106355422	106356022	0.4	0.0
chr8	106432456	106433056	2.6	0.6
chr8	106432466	106433066	2.7	0.5
chr8	106546761	106547361	1.4	0.0
chr8	107730614	107731214	2.2	0.8

chr8	107730672	107731272	2.3	0.9
chr8	107735856	107736456	1.1	0.1
chr8	107736464	107737064	0.9	0.1
chr8	107832263	107832863	1.4	0.2
chr8	107897802	107898402	0.4	0.3
chr8	108041433	108042033	1.1	0.2
chr8	108041530	108042130	0.5	0.1
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chr8	108379361	108379961	0.6	0.1
chr8	108384619	108385219	0.6	0.2
chr8	108490727	108491327	0.5	0.3
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chr8	108924169	108924769	1.1	0.0
chr8	108924355	108924955	1.3	0.1
chr8	108924551	108925151	1.1	0.1
chr8	108924641	108925241	1.4	0.2
chr8	109089947	109090547	0.6	0.2
chr8	109089967	109090567	0.4	0.1
chr8	109474095	109474695	0.2	0.2
chr8	109829120	109829720	0.4	0.1
chr8	109829223	109829823	1.1	0.4
chr8	110155355	110155955	0.3	0.1
chr8	110504281	110504881	0.8	0.1
chr8	111461184	111461784	1.5	0.9
chr8	112625205	112625805	0.5	0.4
chr8	114159289	114159889	1.0	0.1
chr8	114651130	114651730	0.8	0.7
chr8	114651172	114651772	0.9	0.8
chr8	114927890	114928490	1.1	0.7
chr8	114928124	114928724	1.0	0.4
chr8	115349698	115350298	0.7	0.0
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chr8	116191233	116191833	1.5	0.4
chr8	116355467	116356067	0.3	0.2
chr8	116487009	116487609	0.4	0.7
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chr8	117546146	117546746	2.1	0.8
chr8	117546440	117547040	1.8	0.3

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chr8	119122972	119123572	0.9	0.7
chr8	119123067	119123667	1.1	0.7
chr8	119814852	119815452	0.9	0.6
chr8	119925785	119926385	0.6	0.0
chr8	120309560	120310160	1.0	0.4
chr8	120513612	120514212	0.6	0.2
chr8	120891550	120892150	1.3	0.3
chr8	121655168	121655768	1.7	0.2
chr8	121655404	121656004	1.5	0.3
chr8	121877193	121877793	0.4	0.2
chr8	121886692	121887292	0.5	0.1
chr8	122023390	122023990	0.8	0.2
chr8	122377778	122378378	0.2	0.7
chr8	122382545	122383145	1.1	0.0
chr8	122493190	122493790	1.0	0.1
chr8	122687593	122688193	0.2	0.2
chr8	122854855	122855455	2.0	0.5
chr8	122855032	122855632	1.9	0.8
chr8	122949036	122949636	0.2	0.1
chr8	123008639	123009239	2.0	0.5
chr8	123093618	123094218	0.4	0.2
chr8	123264123	123264723	1.5	1.0
chr8	123270211	123270811	1.4	0.6
chr8	123270305	123270905	1.6	0.7
chr8	123375181	123375781	1.4	0.1
chr8	123384534	123385134	0.8	0.2
chr8	123398699	123399299	1.3	0.4
chr8	123398756	123399356	1.8	0.5
chr8	123422849	123423449	1.4	0.3
chr8	123436283	123436883	1.6	0.1
chr8	123436323	123436923	1.3	0.1
chr8	123527365	123527965	1.3	0.2
chr8	123527425	123528025	1.3	0.2

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chr8	123567097	123567697	1.6	0.5
chr8	123567116	123567716	1.5	0.5
chr8	123567135	123567735	1.5	0.4
chr8	123567178	123567778	1.8	0.4
chr8	123651319	123651919	0.2	0.3
chr8	123746618	123747218	1.2	0.5
chr8	123804028	123804628	1.6	0.5
chr8	124539916	124540516	0.5	0.0
chr8	124598497	124599097	1.4	0.2
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chr8	124716923	124717523	0.8	0.2
chr8	124783785	124784385	1.6	0.1
chr8	124856011	124856611	1.6	0.8
chr8	124856060	124856660	2.1	0.9
chr8	124856105	124856705	2.1	0.9
chr8	124856330	124856930	1.6	0.7
chr8	125061088	125061688	1.6	1.1
chr8	125061310	125061910	1.8	0.6
chr8	125140039	125140639	0.7	0.1
chr8	125224537	125225137	0.8	0.3
chr8	125709238	125709838	2.1	0.3
chr8	125957342	125957942	0.7	0.0
chr8	126415356	126415956	1.2	0.4
chr8	126802497	126803097	0.1	0.0
chr8	126819861	126820461	0.7	0.5
chr8	126820105	126820705	0.2	0.2
chr8	126854421	126855021	1.6	0.2
chr8	126854459	126855059	1.6	0.2
chr8	127325885	127326485	4.5	1.7
chr8	127325927	127326527	4.7	1.9
chr8	127325969	127326569	4.8	1.8
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chr8	127326053	127326653	4.9	1.7
chr8	127358644	127359244	0.2	0.0
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chr8	127963832	127964432	0.9	0.4
chr8	127963934	127964534	0.6	0.4

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chr8	128550545	128551145	0.9	0.1
chr8	129080307	129080907	0.6	0.8
chr8	129080321	129080921	0.5	0.8
chr8	129135087	129135687	0.6	0.1
chr8	129457656	129458256	0.2	0.0
chr8	129562062	129562662	0.1	0.3
chr8	130241704	130242304	0.2	0.0
chr8	130503312	130503912	1.9	0.8
chr8	130503433	130504033	2.4	0.8
chr8	130709522	130710122	0.1	0.1
chr8	130812059	130812659	1.4	0.2
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chr8	131584648	131585248	0.7	0.1
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chr9	4258122	4258722	0.6	0.1
chr9	6426537	6427137	0.5	0.3
chr9	7150289	7150889	0.7	0.2
chr9	7221952	7222552	0.5	0.3
chr9	8704726	8705326	0.4	0.4
chr9	8704861	8705461	0.7	0.3
chr9	9100484	9101084	0.5	0.0
chr9	9166111	9166711	2.4	0.5
chr9	9191718	9192318	0.3	0.2
chr9	9421590	9422190	1.5	0.0
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chr9	13271501	13272101	0.5	0.2
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chr9	13379805	13380405	0.8	0.5
chr9	14417333	14417933	0.8	0.3
chr9	14444368	14444968	0.5	0.0
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chr9	14544142	14544742	0.0	0.0

chr9	14544213	14544813	0.1	0.2
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chr9	16118583	16119183	1.7	0.5
chr9	18056205	18056805	0.4	0.1
chr9	18526262	18526862	0.6	0.7
chr9	18763337	18763937	0.7	0.7
chr9	19796348	19796948	1.9	0.2
chr9	21420021	21420621	1.7	0.3
chr9	21634296	21634896	0.6	0.1
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chr9	21651182	21651782	1.7	0.6
chr9	21766202	21766802	1.1	0.0
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chr9	22467988	22468588	0.0	0.2
chr9	22834004	22834604	1.2	0.3
chr9	23345731	23346331	0.9	0.4
chr9	23570871	23571471	0.5	0.3
chr9	23571054	23571654	0.6	0.4
chr9	23625116	23625716	1.9	0.0
chr9	25253445	25254045	1.2	0.0
chr9	25253700	25254300	1.2	0.0
chr9	25987110	25987710	1.7	0.6
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chr9	45480110	45480710	3.3	1.5
chr9	45480152	45480752	3.0	1.2
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chr9	45480345	45480945	3.0	0.9
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chr9	46953461	46954061	0.2	0.2
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chr9	50640641	50641241	7.2	3.1
chr9	50640689	50641289	7.1	3.0
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chr9	50640857	50641457	7.0	2.9
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chr9	50640905	50641505	7.2	3.0
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chr9	50641001	50641601	7.5	3.2
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chr9	50641073	50641673	7.2	3.1
chr9	50641121	50641721	7.0	3.0
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chr9	50641169	50641769	6.7	2.8
chr9	50641193	50641793	6.8	2.9
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chr9	55210200	55210800	0.5	0.7
chr9	55777612	55778212	3.1	1.1
chr9	55777880	55778480	1.8	0.9
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chr9	59116164	59116764	0.9	0.4
chr9	59235205	59235805	1.4	0.4
chr9	59739667	59740267	1.4	0.8
chr9	59787859	59788459	1.6	0.3
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chr9	60641753	60642353	1.3	0.4
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chr9	60984017	60984617	1.1	0.9
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chr9	62335434	62336034	2.0	0.5
chr9	62335471	62336071	2.0	0.4
chr9	62335480	62336080	1.9	0.4
chr9	62335525	62336125	1.9	0.4
chr9	62335566	62336166	1.9	0.4
chr9	62335615	62336215	1.7	0.3
chr9	62335651	62336251	1.3	0.3
chr9	62438712	62439312	1.0	0.0
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chr9	62911783	62912383	1.0	0.5
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chr9	63150519	63151119	1.2	0.8
chr9	63150565	63151165	1.3	0.9
chr9	63211301	63211901	0.2	0.1
chr9	63560483	63561083	0.9	0.2
chr9	63560547	63561147	0.7	0.2
chr9	63560643	63561243	0.8	0.1

chr9	63582632	63583232	1.7	0.7
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chr9	65117675	65118275	0.7	0.2
chr9	65394459	65395059	0.2	0.3
chr9	65478723	65479323	0.4	0.1
chr9	66829100	66829700	0.1	0.2
chr9	66886925	66887525	0.4	0.1
chr9	66918876	66919476	0.9	0.0
chr9	66946614	66947214	0.6	0.0
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chr9	67166768	67167368	0.4	0.0
chr9	67209739	67210339	0.1	0.6
chr9	67306686	67307286	0.5	0.2
chr9	67369841	67370441	0.4	0.2
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chr9	67845171	67845771	0.6	0.2
chr9	68846966	68847566	0.7	0.4
chr9	69554973	69555573	1.4	0.0
chr9	69555111	69555711	0.3	0.1
chr9	69611616	69612216	1.2	0.2
chr9	70224194	70224794	0.7	0.8
chr9	70224203	70224803	0.7	0.9
chr9	70224293	70224893	1.3	0.6
chr9	70665088	70665688	0.4	0.5
chr9	70698803	70699403	0.2	0.4
chr9	71118079	71118679	1.3	0.3
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chr9	72611990	72612590	0.6	0.0

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chr9	74336612	74337212	0.7	0.2
chr9	75684789	75685389	0.8	0.7
chr9	75684799	75685399	0.8	0.6
chr9	75684819	75685419	1.0	0.7
chr9	76488643	76489243	1.0	0.3
chr9	77470537	77471137	0.1	0.0
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chr9	78688949	78689549	0.6	0.3
chr9	78813596	78814196	1.6	0.2
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chrX	103417558	103418158	0.5	0.1
chrX	103980577	103981177	2.4	0.0
chrX	103980846	103981446	2.0	0.3
chrX	104508166	104508766	2.7	1.0
chrX	105045932	105046532	0.1	0.1
chrX	105605730	105606330	1.9	0.2
chrX	106538065	106538665	0.4	0.3
chrX	107470367	107470967	1.2	0.2
chrX	107470436	107471036	1.3	0.4
chrX	107515410	107516010	1.2	0.7
chrX	107684568	107685168	1.5	0.8
chrX	107684818	107685418	1.5	0.2
chrX	109025139	109025739	0.3	0.1
chrX	109519437	109520037	1.0	0.5
chrX	110556029	110556629	1.6	0.6

chrX	112715125	112715725	0.4	0.4
chrX	112769264	112769864	0.1	0.3
chrX	113178324	113178924	1.1	0.4
chrX	113235014	113235614	1.7	0.2
chrX	113235104	113235704	1.9	0.2
chrX	113657251	113657851	0.1	0.0
chrX	113733249	113733849	1.4	0.1
chrX	114407155	114407755	1.9	0.1
chrX	114549089	114549689	0.7	0.1
chrX	114549190	114549790	1.0	0.1
chrX	114712096	114712696	0.7	0.6
chrX	115752005	115752605	0.1	0.2
chrX	115797910	115798510	1.0	0.4
chrX	115797989	115798589	1.1	0.3
chrX	117485369	117485969	0.5	0.1
chrX	117611945	117612545	0.2	0.0
chrX	118838623	118839223	0.4	0.3
chrX	119521144	119521744	0.4	0.8
chrX	119521245	119521845	0.3	0.7
chrX	121404169	121404769	0.7	0.4
chrX	122058060	122058660	0.7	0.4
chrX	122830774	122831374	1.2	0.1
chrX	122999039	122999639	0.4	0.2
chrX	124186820	124187420	0.7	0.3
chrX	124622891	124623491	1.8	0.2
chrX	125947393	125947993	1.2	0.7
chrX	127000540	127001140	1.2	0.0
chrX	127172924	127173524	0.9	0.3
chrX	127703399	127703999	0.6	0.4
chrX	129379897	129380497	0.5	0.1
chrX	129427233	129427833	0.3	0.2
chrX	129627676	129628276	0.7	0.0
chrX	130017058	130017658	0.5	0.5
chrX	131202379	131202979	0.9	0.4
chrX	131293320	131293920	0.1	0.1
chrX	132619204	132619804	0.9	0.3
chrX	132619391	132619991	1.4	0.5
chrX	132792437	132793037	0.8	0.3

chrX	132902002	132902602	0.4	0.1
chrX	132936149	132936749	0.4	0.1
chrX	133250817	133251417	1.3	0.5
chrX	133250970	133251570	1.4	0.6
chrX	133531367	133531967	0.2	0.1
chrX	133572588	133573188	2.4	0.8
chrX	133698727	133699327	0.3	0.1
chrX	134120898	134121498	1.3	0.3
chrX	134251649	134252249	1.0	0.1
chrX	135219553	135220153	0.2	0.2
chrX	135888928	135889528	0.2	0.0
chrX	136442945	136443545	1.6	0.1
chrX	136442971	136443571	1.9	0.1
chrX	136873226	136873826	0.9	0.7
chrX	136873366	136873966	0.8	0.6
chrX	137388746	137389346	0.4	0.0
chrX	137491259	137491859	0.6	0.2
chrX	137673919	137674519	0.4	0.0
chrX	137897967	137898567	3.7	1.2
chrX	137898236	137898836	2.6	1.0
chrX	138199435	138200035	0.5	0.3
chrX	138411515	138412115	1.7	0.5
chrX	138443280	138443880	1.1	0.5
chrX	139928123	139928723	0.1	0.1
chrX	140004105	140004705	0.6	0.0
chrX	140191708	140192308	1.4	0.8
chrX	140191754	140192354	1.4	0.7
chrX	142209172	142209772	0.1	0.2
chrX	143212241	143212841	0.8	0.3
chrX	143212504	143213104	0.8	0.3
chrX	144080578	144081178	0.0	0.2
chrX	144120978	144121578	1.3	0.4
chrX	144571373	144571973	0.8	0.0
chrX	144890742	144891342	0.8	0.0
chrX	145063857	145064457	0.8	0.0
chrX	145674152	145674752	0.8	0.0
chrX	145843186	145843786	0.8	0.1
chrX	145956632	145957232	0.8	0.0

chrX	145990147	145990747	0.7	0.1
chrX	147102679	147103279	1.5	0.5
chrX	147240025	147240625	1.2	0.2
chrX	147733228	147733828	0.4	0.1
chrX	148726016	148726616	2.0	0.7
chrX	152087385	152087985	1.4	0.3
chrX	152194045	152194645	0.3	0.2
chrX	153109221	153109821	0.0	0.1
chrX	153928051	153928651	1.7	1.1
chrX	153928221	153928821	1.5	0.8
chrX	153939813	153940413	1.5	0.1
chrX	154018749	154019349	0.5	0.3
chrX	154095817	154096417	1.8	0.3
chrX	154095881	154096481	1.5	0.1
chrX	154242950	154243550	0.3	0.0
chrX	156554318	156554918	0.1	0.1
chrX	157693189	157693789	0.6	0.1
chrX	158047878	158048478	0.7	0.0
chrX	158156223	158156823	0.4	0.1
chrX	158156275	158156875	0.6	0.3
chrX	158366447	158367047	1.3	0.3
chrX	158472601	158473201	0.7	0.2

chrX	158678799	158679399	1.2	0.4
chrX	159024164	159024764	0.3	0.1
chrX	159394422	159395022	0.9	0.4
chrX	159475703	159476303	0.6	0.0
chrX	161433803	161434403	1.1	0.1
chrX	162214490	162215090	1.9	0.3
chrX	162214515	162215115	1.9	0.2
chrX	162862448	162863048	0.8	0.3
chrX	163129181	163129781	1.2	0.2
chrX	163129329	163129929	1.5	0.3
chrX	163500366	163500966	0.4	0.0
chrX	163598635	163599235	0.1	0.0
chrX	163973351	163973951	0.3	0.0
chrX	166116121	166116721	0.4	0.9
chrX	166517629	166518229	2.1	0.5
chrX	166517848	166518448	2.2	0.7
chrX	166640384	166640984	2.1	0.5
chrX	166640603	166641203	2.2	0.7
chrY	789610	790210	0.7	0.0
chrY	1041707	1042307	2.0	0.1
chrY	2877772	2878372	0.7	0.3

Table S3.3 GLI^{FLAG} dataset kmer-SVM scores. kmer-SVM scores for LDwGBM and NPwGBM datasets.

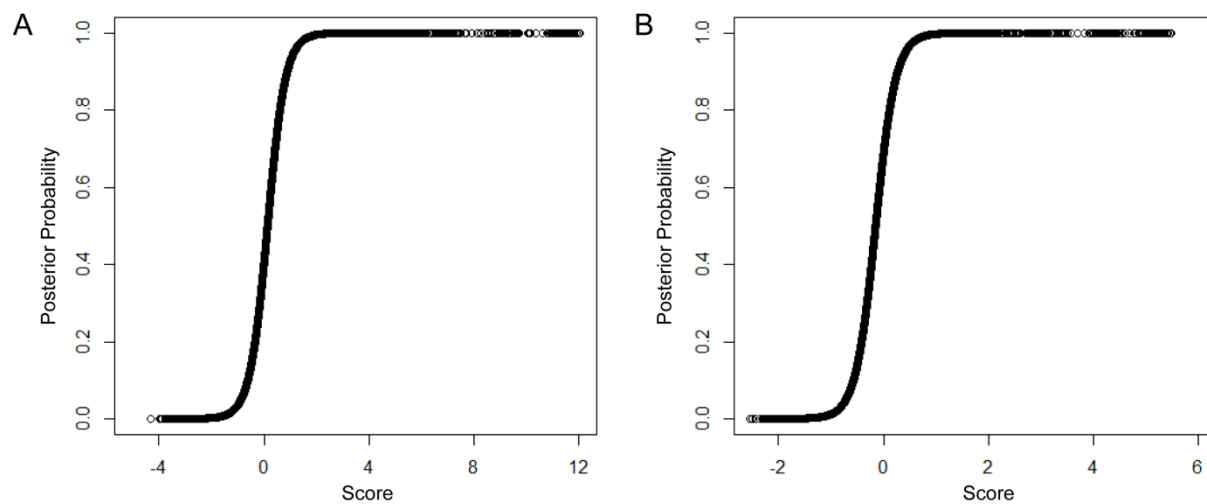


Figure S3.2. Posterior probability of kmer-SVM scores. Plots depicting the posterior probabilities assigned to scores for both (A) LDwGBM and (B) NPwGBM datasets. The graphs indicate that scores above 1 have a high confidence of being Hh regulatory regions.

Open Chromatin Markers	Positive (kmer-SVM score ≥ 1 ; posterior probability = 1)		Negative (kmer-SVM score ≤ -1 ; posterior probability = 0)		Z-Test	two-tailed p-value
	Number that overlap with markers	Number with no overlap	Number that overlap with markers	Number with no overlap		
DNase I Mesoderm E11.5	112	416	5970	30023	2.8332	p < 0.05
H3K4me1 Heart	37	491	5011	30982		
H3K4me3 Heart	7	521	541	35452		
H3K27ac Heart	8	520	1064	34929		
H3K4me1 Liver	75	453	3864	32129	2.5511	p < 0.01
H3K4me3 Liver	9	519	494	35499		
H3K27ac Liver	43	485	905	35088	8.076	p < 0.0

Table S3.4. Overlap of predicted high confidence positive and negative regions with embryonic open chromatin. Tabulation of the number of genomic regions predicted by both LDwGBM and NPwGBM that are classified with high confidence as Hh enhancer regions or as nonregulatory regions that overlap with mesoderm DNase I (E 11.5) or enhancer markers (E14.5).



Figure S3.3. Expression of GLI1 within E14.5 mouse embryo. *In situ* hybridization of GLI1 (image from genepaint.org, EN1215) showing active Hh signaling at E14.5 in liver but not heart.

Annotated Hedgehog Pathway Gene	Forward Primer	Reverse Primer
<i>Boc</i>	GGTAGAGAGGATGCAGGGC	GGTAGAGAGGATGCAGGGC
<i>Dpp6</i>	CTCATTTCAAGATGAGGCTAG	GACCAGAGAGCCATTCAATCG
<i>Gli3</i>	TAATGCTGATGAATTCTCCG	TAATGCTGATGAATTCTCCG
<i>Hhip</i>	GCAAGACCTTCCTCCCAGTC	CAGCCTGCCTCTCTTACTTTC
<i>Hipk2</i>	GTACTTCTCACGCTTCTACC	TGAATGGAGGTAGGGCACC
<i>Ptch1</i>	GTATGGCATCGCTCTATAGACG	TGTCATCCTAGCACTTGGAC
<i>Scube1</i>	AGGCTCTAAGCACAGCCTTG	CTGGCCTGAGGCTAATGGAT
<i>Shh</i>	CATCACAGGCAGAAAGCTCA	CTCAGCTTCTCCTGCACCAT
<i>Tgfbr2</i>	GGCAATGCTTTGACATGAGAC	ACATACGTGTCCTAGCCAGG
<i>Hhat</i>	CAGCTGTGAGAGGAACCAC	CTGTGTATGGCTGCTGGGC

Table S3.5. PCR primers for amplification of mouse genomic regions. Mouse genomic coordinates (mm9) for primer sequence used to amplify candidate regions. **Format: xls**

Chapter IV

Transcriptome of the inner circular smooth muscle of the developing mouse intestine: evidence for regulation of visceral smooth muscle genes by the Hedgehog target gene, *cJun*

4.1 Abstract

Two layers of visceral smooth muscle comprise the intestinal muscularis externa: the inner circular muscle (ICM) and outer longitudinal muscle (OLM). Coordinated contraction of these layers facilitates digestion. During development, the ICM forms two days earlier than the OLM. Exploiting this developmental timing difference, we performed transcriptome analysis of intestinal mesenchyme tissue at E14.5, when the ICM, but not the OLM is present, to investigate the transcriptional program of the ICM.

We identified 3967 genes enriched in E14.5 intestinal mesenchyme. The gene expression profiles were clustered and annotated to known muscle genes identifying a muscle-enriched subcluster. Using publically available *in situ* data, 127 were verified as expressed in ICM. Examination of the promoter and regulatory regions for these co-expressed genes revealed enrichment for cJUN transcription factor binding sites and cJUN protein was also enriched in ICM. cJUN ChIP-seq was then performed at E14.5, revealing that cJUN regulatory regions contain characteristics of muscle enhancers. Additional analysis established that cJUN is a target of Hedgehog signaling.

Gurdziel K, Vogt KR, Walton KD, Scheider GK, Gumucio DL. *Transcriptome of the inner circular smooth muscle of the developing intestine: evidence for regulation of visceral smooth muscle genes by Hedgehog target gene, cJun*. Developmental Dynamics.

This work provides the first transcriptional catalog for the developing ICM and suggests that cJUN is an important regulator of gene expression in the ICM.

4.2 Introduction

Smooth muscle (SM) is a critical component for the function of many organs, including respiratory (Tollet et al., 2001; Goyal and Chaudhury, 2008), urogenital (Baker and Gomez, 1998; DiSandro et al., 1998) and gastrointestinal tissues. The adult intestine contains several populations of visceral smooth muscle (ISM), located in different regions of the tube. A thin muscularis mucosa lies just beneath the epithelium, while the muscularis externa (ME) forms the outside of the tube, surrounding the mucosa and submucosa. The bi-layered ME contains an inner circular (ICM) and outer longitudinal muscle (OLM), with enteric nerves nestled between these layers (Gabella, 1985; Thomason et al., 2012).

The smooth muscle populations of the ME are of particular clinical interest because of their critical role in gut motility (Bitar, 2003). Alterations to muscle contractility are seen in irritable bowel syndrome (Whorwell et al., 1986; Van der Vliet et al., 1992; Abrams et al., 2012) and during gut inflammation (Ohama et al., 2007a). Some forms of chronic intestinal pseudoobstruction are also rooted in ISM pathology (visceral myopathy) (Antonucci et al., 2008). Both familial (Anuras et al., 1981; Sipponen et al., 2009) and sporadic cases (Montalvo et al., 2004) of visceral myopathy have been reported and a few susceptibility loci have been identified, including DNA POLG (Ch. 21) (Vissing et al., 2002; Van Goethem et al., 2003; Giordano et al., 2009) and ACTG2 (Ch. 2) (Lehtonen et al., 2012; Holla et al., 2014; Thorson et al., 2014; Wangler et al., 2014). Interestingly, the various ISM layers can be differently affected.

Pathological changes specific to the muscularis mucosae (Alstead et al., 1988) or to the OLM (Anuras et al., 1983) have been reported and loss of alpha-smooth muscle actin expression has been noted specifically in the ICM (Smith et al., 1992; Donnell et al., 2008).

In addition to their distinct patterns of pathology, the layers of ISM develop in different time windows. The ICM is the first layer to appear; it is well developed by embryonic day 14 (E14). The OLM becomes clearly organized by E16 (Kedinger et al., 1990; Thomason et al., 2012). Development of villus smooth muscle occurs at approximately E18, while the sub-epithelial muscularis mucosa matures after birth (Kolterud et al., 2009; Zacharias et al., 2011).

Despite their critical importance to gut homeostasis, little is known about the molecular characteristics or gene regulatory programs of any of the ISM layers. In this study, we report the first transcriptome profile for the embryonic ISM. The early development of the ICM allowed us the opportunity to restrict the analysis to that layer. Using clustering analysis of RNA-seq data in combination with publically available *in situ* expression data for the E14.5 mouse (Visel et al., 2004; Diez-Roux et al., 2011), we identified a subcluster of over 100 genes with confirmed expression in the ICM and analyzed the promoters of co-clustered genes to identify transcription factors that might be involved in the regulation of these ISM genes. Among these enriched transcription factors was cJUN; antibody staining of intestinal sections confirmed that cJUN protein is strongly expressed in ICM. Further ChIP-seq studies identified 2741 potential cJUN regulatory regions that are also expressed in ICM. Our data suggest a previously undocumented role for cJUN in the regulation of the ICM transcriptional program.

We also further explored the regulatory relationship between cJUN and Hedgehog (Hh) signaling with respect to ICM gene regulation. Hh has been previously shown to be important in activating gene expression in smooth muscle of several tissues, including the bladder (Shiroyanagi et al., 2007; Liu et al., 2010; Tasian et al., 2010), intestine (Sukegawa et al., 2000; Kolterud et al., 2009; Zacharias et al., 2011; Huang et al., 2013) and ureter (Yu et al., 2002; Caubit et al., 2008). Here, we document that cJUN is a Hh target and identify an enhancer that mediates Hh-dependent cJUN induction.

4.3 Results and Discussion

4.3.1 Identification of intestinal visceral smooth muscle genes

We began this analysis by identifying genes that are enriched in the mesenchymal layer of the E14.5 intestine. To do this, we separated epithelial and mesenchymal tissue populations from WT mouse intestines at E14.5 and collected RNA from each layer for high-throughput sequencing (see Methods). The two transcriptomes were compared to identify genes that were differentially expressed between the intestinal mesenchyme (which contains muscle) and the intestinal epithelial tissue (which is devoid of muscle) ($n = 3$). This analysis identified 3967 (adjusted p -value ≤ 0.05) genes that were at least 2 fold enriched in the mesenchyme tissue (Supplemental Table 1).

To begin to identify potential smooth muscle genes within this enriched set, we used Gene Set Enrichment Analysis (GSEA) (Subramanian et al., 2005). Although its Molecular Signatures Database contained no sets of enriched muscle genes derived from SM tissue, we reasoned that due to its contractile nature, some smooth muscle genes might overlap with genes

identified in vascular, cardiac and skeletal muscle. Indeed, overlap between gene expression and regulatory programs in muscle subtypes has been observed (Li et al., 1996). Comparing those muscle gene sets to our 3967 mesenchymally enriched genes identified 253 putative ISM genes (enriched muscle gene sets, $p\text{-value} \leq 0.05$, are listed in Table 1). Using publically available *in situ* images (Visel et al., 2004; Diez-Roux et al., 2011), we next examined the expression pattern of each of these 253 genes in E14.5 mouse intestine. This analysis confirmed 33 genes that exhibited clear expression in the area of the ICM (Figure 4.1A).

To further expand this ISM dataset, we hierarchically clustered genes upregulated in the mesenchyme compared to epithelial tissue (Eisen et al., 1998). Since many of the 33 identified genes were structural genes that are associated with contractility, we expected that they might be expressed at similar levels within the mesenchyme and that other, similarly expressed genes might also cluster with these genes. Indeed, Figure 4.1B shows that when the expression profiles of 9490 mesenchymally expressed genes are clustered, all 33 genes with verified expression in the ICM domain (annotated with black tick marks) cluster together. Other genes within this same subcluster, with an average expression value >500 were then examined for localized expression within the ICM (Visel et al., 2004; Diez-Roux et al., 2011). This comparison identified an additional 94 genes that are expressed in the ICM (Figure 4.1C).

Among the genes that are express in the ICM, several (e.g., *Actc1*, *Lmod1*, *Myom1*, *Tnnt2*) were associated with other muscle types (Gunning et al., 1984; Vinkemeier et al., 1993; Townsend et al., 1994; Zhang et al., 1996). Others are apparently unique to smooth muscle (e.g., *Cav1*, *Cnn1*, *Myl9*, *Smtn*, *Tagln*) (Lees-Miller et al., 1987; Kumar et al., 1989; Strasser et al., 1993; van der Loop et al., 1996; Austin et al., 2012). Several expected muscle regulatory factors

(e.g., *Mef2C*, *Myocd*, and *SRF*) are present in the expression profile and are expressed in the ICM according to the *in situ* analysis (Miano, 2003; Wang et al., 2003; Creemers et al., 2006). Additionally, several components or known targets of the Hh signaling pathway (e.g., *Boc*, *Gli1*, *Gli3*, *Hhip*, *Mef2C*, *Myocd*) several of which are known to be enriched in ISM (Kolterud et al., 2009), are present in the list.

These 127 genes are clearly not a comprehensive catalog of ICM gene expression. The analysis is based on one developmental time period (E14.5) and the study was purposefully initiated using genes that are mesenchymally enriched at this time and expressed at medium to high levels. For example, *Arid5b*, a regulator of smooth muscle differentiation (Watanabe et al., 2002), is not differentially expressed between epithelial and mesenchyme tissue (Teillet et al., 1998) and the SM-associated genes, *Il1b* and *Mitf* are both expressed in the mesenchyme but at low levels (Chen et al., 2006; Chi et al., 2007). We also excluded genes that are not expressed in the ICM at E14.5. For example, *Pbx1*, a transcription factor associated with myogenic programs (Berkes et al., 2004), is mesenchymally enriched in our dataset but is not present in the ICM at this time point (Genepaint ID: ES1284).

4.3.2 Identification of transcriptional regulators of intestinal visceral smooth muscle genes

To begin to identify transcription factors that might be responsible for coordinating smooth muscle gene expression, we next analyzed the promoter regions of the subcluster containing the 127 muscle genes with verified ICM expression using DiRE (Gotea and Ovcharenko, 2008). The top ten transcription factors enriched in these gene promoters included

several known to be involved in regulatory programs in skeletal muscle or in vascular smooth muscle, including RP58, NF1, TAL1, NOTCH1, PAX4, cJUN, HOXA9, and MEIS1 (Figure 4.2A) (Kami et al., 1995; Tao et al., 1998; Knoepfler et al., 1999; Daury et al., 2001; Ema et al., 2003; Di Padova et al., 2007; Yokoyama et al., 2009; Kossler et al., 2011; Raines et al., 2013; Mourikis and Tajbakhsh, 2014; Summers et al., 2015). To narrow this putative regulator list to those potentially relevant to ICM regulation, we again turned to the *in situ* patterns. Of the top 10 enriched transcription factors, cJUN is unique in that it is expressed robustly in the inner circular muscle region at E14.5 (Figure 4.2K). Thus, we further examined the role of cJUN in intestinal ISM expression.

To confirm cJUN expression in ICM, we examined whether this protein co-localizes with the smooth muscle marker, alpha smooth muscle actin (α SMA) and with GLI1, a target of Hedgehog signaling that is required for intestinal smooth muscle development and maintenance (Ramalho-Santos et al., 2000; Sukegawa et al., 2000; Madison et al., 2005; Kolterud et al., 2009; Zacharias et al., 2011). Intestines from *Gli1*^{eGFP/+} mice were immunostained with anti-cJUN, anti- α SMA and anti-eGFP (*Gli1*) at key time points during ISM development (E12.5, E14.5, E16.5 and E18.5). At E12.5, prior to formation of the ICM, α SMA staining marks subepithelial mesenchymal cells. Neither GLI1 nor cJUN localize with cells staining positive for α SMA at this stage (Figure 4.3A-D). However, GLI1 and cJUN co-localize in a different subset of mesenchymal cells of unknown type (Figure 4.3RT). By E14.5, when the ICM is clearly formed, cJUN co-localizes entirely with α SMA (Figure 4.3GH). GLI1 (EGFP) expression is most robust in the inner boundary of the ICM (Figure 4.3F), as shown previously (Kolterud et al., 2009). At E16.5 cJUN and α SMA mark both the ICM and the newly established outer longitudinal muscle

(OLM) layer (Figure 4.3KL). GLI1 remains most strongly expressed in the ICM (Figure 4.3J). At E18.5, α SMA marks the cells in the inner circular, outer longitudinal and villus core muscle (Figure 4.3W). Neither GLI1 nor cJUN are expressed in the villus core muscle prior to birth; however, both are still expressed within the ICM (Figure 4.3NP). In addition, these two markers stain a population of vascular smooth muscle cells in the submucosal vascular plexus (Figure 4.3VX).

4.3.3 Identification of cJUN binding locations in E14.5 intestines

Taken together, these data suggest that cJUN may be a regulator of intestinal ISM genes; it is enriched in the promoters of mesenchymally enriched genes and it exclusively marks the ICM region at E14.5. To investigate this further, we used ChIP-seq to identify cJUN binding sites. Intestines from E14.5 C57BL/6J fetuses were harvested and grown in culture under conditions identical to the collection of the epithelial and mesenchyme profiles except that the tissue separation was not done. ChIP was performed on whole intestines with cJUN antibody and the resulting libraries were sequenced. In total, 21.1 million cJUN immunoprecipitated and 23.5 million input 50-bp short reads were generated. Using a p-value threshold of < 0.05 , 2741 sequence peaks were identified by comparing read enrichment from cJUN immunoprecipitated DNA to input control.

The sequence peaks (Supplemental Table 2) were annotated to the nearest gene by measuring the distance between the coordinates of the center of the peak and the transcriptional start sites (TSS) of neighboring genes. Location of the peak was then categorized as 5' distal, within 2Kbp of the promoter, within the gene, 3' proximal, 3' distal, or within a gene desert

(>100 Kbp from the TSS or TES). All peaks that mapped within genes were intronic. Since the majority of peaks were found in gene deserts outside of the immediate vicinity of a gene (Figure 4.4A), we examined the conservation of these regions (Figure 4.4B). This analysis demonstrated that conservation was highest in the central peak regions, suggesting that these regions are functionally important (Figure 4.4B).

Enhancers are expected to lie in open chromatin in the tissues in which they are expressed, a feature which makes them typically DNase I sensitive (Malin et al., 2013). Indeed, 37% of cJUN peaks overlap with DNase I hypersensitivity sites identified in the axial somatic and lateral plate mesoderm of headless and limbless E11.5 mice (expected to include tissue that will give rise to ICM one day later). We also examined the overlap between the set of cJUN peaks and publically available data for genomic regions containing enhancer histone marks. Approximately 40% of cJUN peaks overlap with genomic regions that contain at least one enhancer affiliated histone mark annotated in whole small intestines of adult mice. Additionally, we noticed that the number of cJUN peaks with a H3K27me3 mark, thought to represent a poised enhancer (Rada-Iglesias et al., 2011) was relatively high (27%). Interestingly, the ENCODE data reveals that adult small intestine has a significantly larger proportion of poised enhancers than does the adult cerebellum (Z-Score 8.03; p-value <0.01) (Figure 4.4C). The basis for this tissue specificity in poised enhancers is unknown.

Motif analysis of the cJUN peaks revealed enrichment of several muscle-associated transcription factors (Figure 4.4D). Of particular interest here is the enrichment for SRF, which, with its co-factor, Myocd, is a master regulator of smooth muscle gene expression (Wang et al., 2003; Wang et al., 2004). Enrichment of SRF sites with cJUN sites further supports the idea that

these regulatory regions are active in ISM. Other enriched factors of the SOX, FOXO, HOX, TEAD and EGR families were also noted. Members of all of these families have been implicated in the regulation of cardiac muscle, skeletal muscle or vascular smooth muscle (Wang et al., 2001; Schmidt et al., 2003; Wada et al., 2003; Lee et al., 2004; Liu et al., 2005; Meeson et al., 2007; Papanicolaou et al., 2008; Qiu et al., 2011; Benhaddou et al., 2012; Fan et al., 2013; Wang et al., 2013; Liu et al., 2014; Sanchez et al., 2014), though none have been previously characterized in visceral smooth muscle.

To functionally verify enhancer activity, four cJUN peaks were screened for responsiveness in a muscle cell culture assay. The putative regulatory regions were cloned upstream of a minimal promoter that drives luciferase expression and transiently transfected into C2C12 cells along with either a plasmid encoding full length cJUN or a dominant negative version of cJUN (see Methods). For the four regulatory regions tested, all were up-regulated when co-expressed with cJUN. In all cases, co-transfection with the dominant negative cJUN construct diminished luciferase expression (Figure 4.5A).

4.3.4 Relationship between Hh signaling and cJUN transcription in intestinal ISM development

Previous studies suggested the possibility that cJUN and GLI1 might act together to co-regulate genes, since the two factors bind together at the human cJUN promoter (Laner-Plamberger et al., 2009; Amable et al., 2014). The Hh signaling pathway is an established regulator of the development of both the ME and the villus smooth muscle populations (Sukegawa et al., 2000; Yu et al., 2002; Shiroyanagi et al., 2007; Caubit et al., 2008; Kolterud et

al., 2009; Liu et al., 2010; Tasian et al., 2010; Zacharias et al., 2011; Huang et al., 2013) and our studies here suggest that cJUN is a regulator of ME genes as well. However, we found no enrichment for predicted GLI TFBS within the cJUN peaks; only 54 predicted GLI TFBS were found within the 2741 cJUN peaks. Though it remains quite possible that these two regulatory factors bind separate enhancers for the same genes, it appears that the co-binding paradigm seen in the human cJUN promoter is not a prevalent regulatory pattern for ISM.

To further probe a possible regulatory relationship between cJUN and GLI in the control of ICM gene expression, we treated E14.5 intestines with the Hh inhibitor, cyclopamine, (Chen et al., 2002) and examined the response of the verified ICM genes ($n = 3$) (Figure 4.1AB). Of the 127 ICM genes, 33% were downregulated at least 2 fold by cyclopamine, confirming a substantial effect of Hh signaling on the maintenance of ICM gene expression. As expected, Hh pathway components were also robustly downregulated by cyclopamine treatment (fold change (FC): *Gli1*, -138.14; *Ptch2*, -51.27; *Hhip*, -29.86; *Ptch1*, -9.64; *Gli2*, -4.17) as were other intestinal Hh target genes (FC: *Foxl1*, -31.56; *Foxf2*, -7.41; *Foxf1*, -3.84; *Grem1*, -3.56; *Myocd*, -2.13) (Supplemental Table 3). Additionally, other downregulated genes suggest similar roles for Hh in ISM to those previously seen in skeletal muscle (Duprez et al., 1998; Borycki et al., 1999; Pownall et al., 2002; Singh et al., 2012). Several downregulated genes were modulators of Wnt signaling, affiliated with proliferation of muscle precursors or involved in promotion of differentiation into muscle cells (Table 2).

Surprisingly, however, *cJun* itself was not strongly downregulated by cyclopamine treatment (*cJun* FC: -1.21), despite the fact that *cJun* is a Hh target in other settings (Kudo et al., 2012). To further investigate this finding, we used qPCR in C2C12 myoblast cells to test whether

endogenous *cJun* responds to upregulated Hh signaling induced by SAG treatment over an 8-hour period. These studies revealed that *cJun* transcription is upregulated by increased Hh signaling with similar kinetics to PTCH1 upregulation (Figure 4.5B), consistent with the idea that *cJun* is a transcriptional target of Hh signaling in C2C12 cells. Additionally, we separated E14.5 intestinal mesenchyme from epithelium and cultured the isolated mesenchyme in the presence or absence of the Hh agonist, SAG. Under these conditions, cJUN was again upregulated (FC: 2.30) at a comparable level to PTCH1 (FC: 2.01) (Figure 4.5C). Together, these data suggest that *cJun* is likely to be a direct Hh target in muscle cells, but that additional signals may maintain *cJun* levels (or the transcript may be very stable) in the context of the cyclopamine-treated whole intestine. In accord with the idea that acute reduction in Hh signaling by cyclopamine does not alter cJUN levels, only 7% of the genes associated with cJUN peaks (363/2741) were down-regulated by cyclopamine treatment.

Because *cJun* appears to be a direct target of Hh signaling in intestinal ISM, we looked for a Hh-responsive enhancer region that could be responsible for directing *cJun* transcription. In a previous study, we used kmer-SVM (Fletez-Brant et al., 2013), a machine learning method, to globally identify Hh regulatory regions. That analysis identified a putative Hh enhancer upstream of *cJun*. This genomic region was cloned into a luciferase reporter plasmid and co-transfected with a plasmid that drives constitutive expression of GLI1 in C2C12 cells (Vokes et al., 2007). As shown in Figure 4.5D, this *cJun* enhancer is indeed activated by GLI1; this activation depends on the GLI1 binding site since expression of luciferase is attenuated when the enhancer GLI binding site is mutated (GKO, Figure 4.5D). These data establish a mechanism by which Hh signaling can activate cJUN in the ICM.

4.4 Conclusions

Using transcriptome profiling paired with *in situ* datasets, we have identified a catalog of 127 ISM genes with confirmed expression in the E14.5 inner circular muscle. Subsequent promoter analysis of co-clustered genes implicated cJUN as a regulatory component in intestinal ISM formation. Using ChIP-seq on intestinal tissue, we identified 2741 potential cJUN binding locations and found enrichment of other muscle TFBS within these regions, indicating that they are likely enhancers for visceral muscle genes. Previously, cJUN has been linked to proliferation of skeletal muscle and vascular smooth muscle (Kami et al., 1995) (Daury et al., 2001) (Yasumoto et al., 2001; Chiba et al., 2014); this study further enlarges this regulatory landscape to include ISM.

Since Hh is an important regulator of ISM gene expression, we further explored the possible regulatory relationships between cJUN and GLI in the regulation of ISM genes. Our data show that co-binding of the two transcription factors at the same enhancer is rare. However, *cJun* is likely a direct target of Hh signaling in the ICM (Figure 4.5BC) and we have identified an enhancer element in the *cJun* gene that could control this regulation. Thus, in addition to its direct effect on ISM gene transcription, Hh signaling could further influence ISM gene expression through induction of *cJun*, which we establish as a regulator of ISM gene expression.

4.5 Experimental Procedures

4.5.1 Intestine collection

Intestines were collected from C57BL/6J mouse fetuses at E14.5. Fetal stages were determined by date of coitus and confirmed by Theiler staging. Isolated intestines were grown on transwell membranes with BGJb media supplemented with ascorbic acid (5mg/mL) and Penicillin-Streptomycin-Glutamine (50mg/mL). Conditions were no treatment epithelial, no treatment mesenchyme and whole intestines treated with cyclopamine (5 μ M) as well as mesenchyme treated with or without SAG (1 μ m) (Walton et al., 2012). After 24 hours of culture, the entire intestine from below the common bile duct to above the cecum was collected.

4.5.2 Epithelial-Mesenchymal Separation

Each intestine was treated for at least one hour with BD Biosciences Cell Recovery Solution on ice to facilitate the mechanical separation into two distinct epithelial and mesenchyme tissue populations as previously described (Li et al., 2009).

4.5.3 Immunohistochemistry

Intestines collected from Gli1^{eGFP/+} mice at E12.5, E14.5, E16.5 and E18.5 were fixed overnight in 4% paraformaldehyde and then embedded in 7% agarose. Vibratome sections of 50 μ m were permeabilized in 0.5% TritonX-100 for 25 minutes at room temperature and then blocked with 20% goat serum, 0.1% Tween20 for 30 minutes. Sections were sequentially stained with rabbit anti-cJUN (1:400; Santa Cruz sc-44) overnight at 4° followed by anti-rabbit secondary antibody for 45 minutes at room temperature (1:1000; Life Technologies A-21244) and then anti-GFP-488 (1:500; Life Technologies A-21311), anti- α SMA-CY3 (1:1000; Sigma C6198), and DAPI overnight at 4°. Stained sections were mounted on slides with Prolong gold and imaged on a Nikon A1 confocal microscope.

4.5.4 RNA collection and mRNA-seq

Total RNA was collected for each sample using the Life Technologies mirVana™ miRNA Isolation Kit following the standard protocol. mRNA-seq on three biological replicates for each condition was performed by the University of Michigan DNA Sequencing Core following Illumina guidelines.

4.5.5 ChIP assay

ChIP was performed following a previously described protocol (Vokes et al., 2007). Prior to experimental collection, antibodies (16 uL of 0.05 ug/uL into 100uL) were coupled to magnetic beads (Dynabeads Protein G) at 4° C for 24 hours. Between six and eight pups harvested from the same litter were pooled for each ChIP experiment. Intestines were snap-frozen in liquid nitrogen and ground with a mortar and pestle to dissociate the tissue into single cells. DNA and protein were cross-linked with 1% formaldehyde for 10 minutes and then treated with 0.125 M glycine to halt the reaction. DNA was sonicated to an average fragment size of 500 bp. DNA fragments were incubated with cJUN (Polyclonal Rabbit; Santa Cruz sc-44 or sc-1694) or IgG (Polyclonal Rabbit; Santa Cruz sc-2027) bound beads overnight at 4°C. cJUN bound DNA was eluted from the beads overnight at 70° C and purified with phenol-chloroform DNA extraction after RNase and DNase treatment. Both cJUN immunoprecipitated and input DNA were submitted to the University of Michigan DNA Sequencing Core for sequencing.

4.5.6 Sequencing and data analysis

RNA and DNA were sequenced on an Illumina HiSeq machine generating 50 cycle single reads. Reads containing up to 1 mismatch were mapped to the mouse reference genome (Build mm9) using TopHat for RNA (Trapnell et al., 2009) and Bowtie for DNA (Langmead et al., 2009). Three replicates were collected for each of the three conditions (isolated epithelium, isolated mesenchyme, and cyclopamine treated whole intestine). Experiments were barcoded and run on three lanes with paired epithelial and mesenchyme samples within the same lane. Reads for each sample ranged from 29 million to 33 million. Differential expression of RNA samples was determined using DESeq (estimateSizeFactors and estimateDispersions functions) (Anders and Huber, 2010). ChIP peaks were identified using MACS (version 1.4) (Zhang et al., 2008). Raw and processed data files were deposited in GEO under accession number GSE74993.

4.5.7 qPCR

cDNA was reverse transcribed from 400 µg of RNA using the iScript kit. Three samples per condition were tested in triplicate with the following primer sets: (*18sRNA*: GTAACCCGTTGAACCCATT, CCATCCAATCGGTAGTAGCG; *Rp113a*: GACCTCCTCCTTTCCCAGGC, GCCTCGGCCATCCAATACC; *Ptch1*: GGCTACTGGCCGGAAAGC, GAATGTAACAACCCAGTTTAAATAAGAGTCT; *cJun*: GTGTGGGACGACGATCAAAAG, TGACCACTAACAGGGAAGGAC). After adjusting for primer efficiency (E) expression values for *cJun* (E: 107.1%) and *Ptch1* (E: 90.4%) were normalized to *18sRNA* (E: 98.4%) and *Rp113a* (E: 90.4%).

4.5.8 Computing resources

Except where otherwise indicated, all computational steps were performed using custom Perl and R scripts.

4.5.9 Publically available datasets

Mouse ENCODE data (Bernstein et al., 2012) comprising: 1) open chromatin DNase I treated samples from E11.5 mesoderm (axial somatic and lateral plate mesoderm of headless and limbless bodies) and 2) histone (H3K4me1, H3K4me3, H3K27me3 and H3K27ac) marks from adult (8 week) mouse small intestine and cerebellum were downloaded from the UCSC genome repository (goldenPath). The refFlat file containing annotation information for mouse build mm9 was also downloaded from UCSC.

4.5.10 Cluster analysis

Hierarchical clustering analysis of transcript expression data was performed within Cluster 3.0 using uncentered correlation with average linkage (Eisen et al., 1998). Java Treeview was used to visualize the clustered data (Saldanha, 2004).

4.5.11 Conservation analysis

A total of 1250 bp of sequence from both sides of the center of each peak was uploaded to the UCSC genome browser. The PhastCons score (phastCons30way) for each nucleotide position was downloaded from the UCSC table browser. Scores were averaged across all peak positions and binned in 25 bp increments.

4.5.12 Motif analysis

To identify enriched motifs, 100 bp of sequence from the center of each peak was submitted to DREME (Bailey, 2011). Discovered motifs were annotated using the JASPAR vertebrate database in Tomtom (Gupta et al., 2007).

4.5.13 Gene Set Enrichment Analysis

A gene list comprising the upregulated mesenchyme genes was run using the GseaPreranked tool (1000 permutations) (Subramanian et al., 2005).

4.5.14 Cloning of putative enhancer regions

Putative enhancers were amplified from C57BL/6 genomic DNA (supplied by Jackson Laboratory) using template-specific PCR primers (*Gpr125*: GAGTGGAGTGGAAGGGGTTT, CTTTCTGCCACTCCTTCTGC; *Lmo4*: GGAGAAGTACAACAGACCCTTCA, ACAATCACAGCGAAGAAGCA; *Mef2C*: CCTAGCCAAAGTCATTGTGGA, GGCATCATCCTGAGTGAGGT; *Rnf182*: CCAGATTCAGTAGAGCACCCA, TACCTACATGCGAAGGCAAG; *cJun*: CTTAAGTGTTGAGGGCAGGCAG, CATGAGAAAATGCAGGGGATCT). A CACC extension was added to the end of one primer to facilitate directional cloning. PCR fragments were cloned into the pENTR/D-TOPO vector using the standard kit (Invitrogen) and then shuttled into the pGL3-Promoter luciferase vector (Promega) using the Gateway cloning system (Invitrogen). QuikChange mutagenesis (Stratagene) was used to mutate putative GLI binding sites in the *cJun* regulatory region by replacing the C in the 6th position to a G (GAAAAGACAAGAGACCAGCCATCCCAGCCTTTGAT, ATCAAAGGCTGGGATGGCTGGTCTCTTGTCTTTTC;

GAACTCCATGGGACCAGCCAGAAGAGGCTGATG,
CATCAGCCTCTTCTGGCTGGTCCCATGGAGTTC).

4.5.15 Luciferase assay

C2C12 cells (35,000 per well) were plated on 12-well plates and grown with DMEM media supplemented with 10% fetal bovine serum, 1x penicillin, streptomycin and glutamate. After 24 hours, cells were lipofectamine transfected with 400 ng of the construct containing the putative enhancer region plus either a control vector, GLI1 (pCIG) (Vokes et al., 2007), cJUN (pMIEG3-c-Jun; Addgene 40348) or dominant negative cJUN (pMIEG3-JunDN; Addgene 40350) (in equal molecular weight). *Renilla* (Promega pRL-CMV) was also included to normalize transfection efficiency. After an additional 24 hours, cells were changed to serum-free media to promote ciliogenesis required for Hh signaling (Santos and Reiter, 2008). Cell lysates were collected after 48 hours and measured for luciferase activity using the Dual-Luciferase Reporter Assay System (Promega) on a Perkin Elmer Wallac Victor3 1420 Multilabel Counter. Three experimental replicates were collected for each condition.

4.6 Acknowledgements

The authors would like to thank Dr. Will Zacharias for helpful comments and Dr. Steve Vokes and Dr. Lihong Shi for generously providing advice on ChIP-seq.

4.7 Authors' contributions

KG and DG conceived and designed the experiments. KG, KV and GS performed the experiments. KW performed imaging. KG and DG wrote the manuscript.

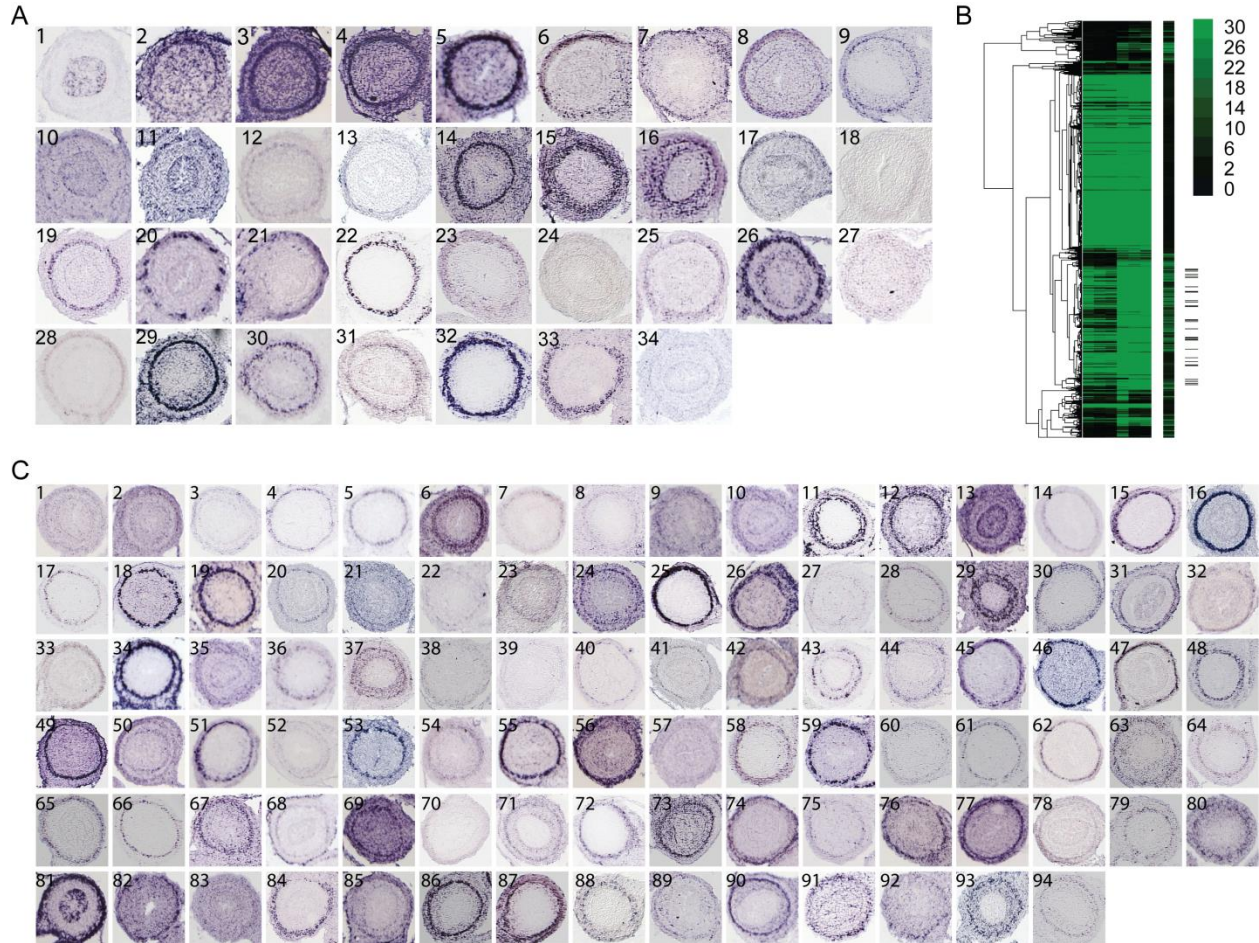


Figure 4.1. Identification of intestinal visceral smooth muscle genes. (A) RNA *in situ* localization images of (A1) epithelial marker Cdx1 [EH4673] and (A2-34) GSEA identified prospective intestinal smooth muscle genes with ICM localization at E14.5. Intestinal cross sections are from Genepaint.org (Set ID in brackets). Panels are (2) ACTC1 [DC37], (3) ACTA2 [EH2333], (4) ACTG2 [ES688], (5) ADCY5 [MH851], (6) ATP1A2 [EN427], (7) BOC [EB1453], (8) CACNA1H [ES1420], (9) CALD1 [EG423], (10) CCL2 [EH401], (11) CNP1 [EH672], (12) DDR2 [EH3223], (13) DES [EH1766], (14) FLNA [EN2546], (15) FN1 [EN386], (16) FOXF2 [MH3070], (17) FXYD2 [EH804], (18) GLI3 [MH1026], (19) LMOD1 [EH4061], (20) MAPT [EH1455], (21) MEF2C [MH765], (22) MYL9 [EB2526], (23) NCAM1 [ES2731], (24) PLAU [MH1483], (25) PLCB4 [EH4161], (26) RBP1 [EH1743], (27) SALL2 [EH4737], (28) SLC8A1 [MH1892], (29) SMTN [EH1228], (30) SORBS1 [EH2043], (31) SVIL [EN1436], (32) TAGLN [EB415], (33) TGFBR2 [EB1113] and (34) TNNT2 [EH505] (B) Hierarchically clustered expression data, three replicates of epithelial and mesenchyme read counts, for genes upregulated in mesenchyme. Fold change is depicted in the additional column. The location of the confirmed smooth muscle genes (A2-34) are denoted on the right with black tick marks. (C) RNA *in situ* analysis of 94 other genes within the subcluster of confirmed GSEA enriched genes showing ICM localization. (1) ABI2 [EH4750], (2) ACOT7 [EH3555], (3) ADAM19 [EB509],

(4) ADAMTS8 [EB1785], (5) ADCY5 [MH851], (6) AKAP2 [EH3708], (7) AKAP6 [EH3709], (8) AKAP12 [EB1789], (9) AKT3 [EH2186], (10) ATP2B4 [EG2318], (11) CAV1 [EG91], (12) CASQ1 [EN103], (13) CBX6 [EH1869], (14) CCKAR [EH3710], (15) CHRM2 [EH2853], (16) CNN1 [EH1511], (17) CRISPLD2 [ES1352], (18) CRMP1 [ES1162], (19) CTTNBP2 [EH1103], (20) EFS [EH2735], (21) CUEDC1 [EH1301], (22) DDR2 [EH3223], (23) DUSP10 [MH1605], (24) CSPR1 [HD13], (25) ENC1 [MH749], (26) FNBP1 [ES598], (27) FBXO32 [ES255], (28) FOXP2 [EG742], (29) EMILIN3 [EB1359], (30) FOXF1 [MH3518], (31) GDNF [EH574], (32) GAB2 [EN1340], (33) FREM2 [EN2329], (34) FZD3 [MH732], (35) GAS1 [MH360], (36) GEM [EH1664], (37) GNAQ [EN2590], (38) GPR20 [EH2873], (39) GLI1 [EN1215], (40) HAND1 [MH519], (41) GREM2 [EH1239], (42) GREM1 [EB63], (43) HOXB5 [EH612], (44) HHIP [EB1363], (45) HOXA5 [EN692], (46) HOXD3 [EN1290], (47) HOXB4 [MH3073], (48) ID4 [EN2437], (49) ITIH5 [EH3960], (50) ITGA9 [EH3560], (51) ITGA5 [EH3234], (52) KCNIP1 [EH1584], (53) LEBREL1 [EH4020], (54) IGFBP2 [ES388], (55) LRG1 [MH431], (56) MYADM [EG746], (57) MTAP1B [ES1557], (58) MRVI1 [ES819], (59) LTBP1 [EH4243], (60) MAPK8IP1 [EH3404], (61) NEXN [ES414], (62) MYOCD [EN2445], (63) NCAM1 [ES2731], (64) MYOM1 [DC35], (65) NCALD [EG960], (66) NELL2 [EG1866], (67) NRBP2 [EH2160], (68) PSD [EB1667], (69) NPNT [MH2326], (70) PCDH7 [EB2060], (71) NKD1 [EB1514], (72) PKRG1 [EB1942], (73) PTN [EH3730], (74) PTMS [EG1747], (75) RGMA [EH2791], (76) RSPO3 [EN1484], (77) RARB [EH1089], (78) PYGL [MH3193], (79) SOX12 [MH3020], (80) SMOC2 [EH2269], (81) TGFB2 [EB1113], (82) SLC24A3 [MH3376], (83) SLC22A17 [MH2066], (84) SOX4 [MH3053], (85) TGFB1I1 [EG2803], (86) TGFB3 [EH2000], (87) TSPAN9 [EH2385], (88) THBS4 [MH1698], (89) THBS2 [ES844], (90) TMEM47 [EH2893], (91) TSHZ1 [EB2573], (92) TULP4 [MY240], (93) ZYX [EG1608], (94) WWTR1 [EH904]

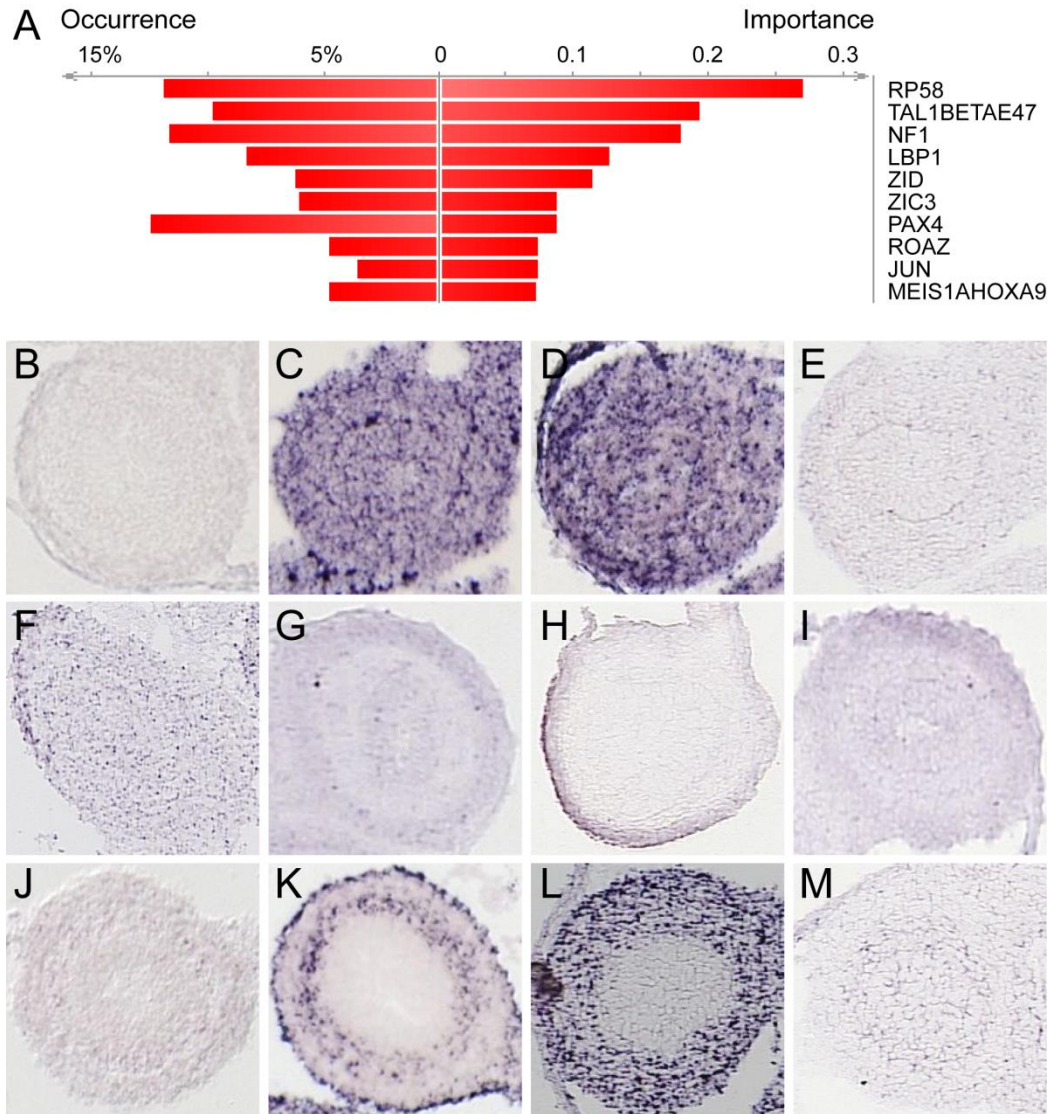


Figure 4.2. cJUN is enriched in the promoters of upregulated mesenchyme genes and is expressed in intestinal ICM at E14.5. (A) The top ten promoter enriched transcription factors include known muscle regulators RP58, NF1, ZIC3 and the MEIS1/HOXA9 complex. *In situ* images from Genepaint.org (Set ID in brackets) of E14.5 intestinal cross sections for (B) RP58 (ZFP238) [MH813], (C) TAL1 [EH2794], (D) E47 (TCF3) [MH770], (E) NF1 [ES1724], (F) LBP1 (UBP1) [EN293], (G) ZID (ZBTB6) [MH3098], (H) ZIC3 [EB2075], (I) PAX4 [MH3124], (J) ROAZ (ZFP423) [MH1157], (K) JUN [MH524], (L) MEIS1 [EG1701], and (M) HOXA9 [EB2525].

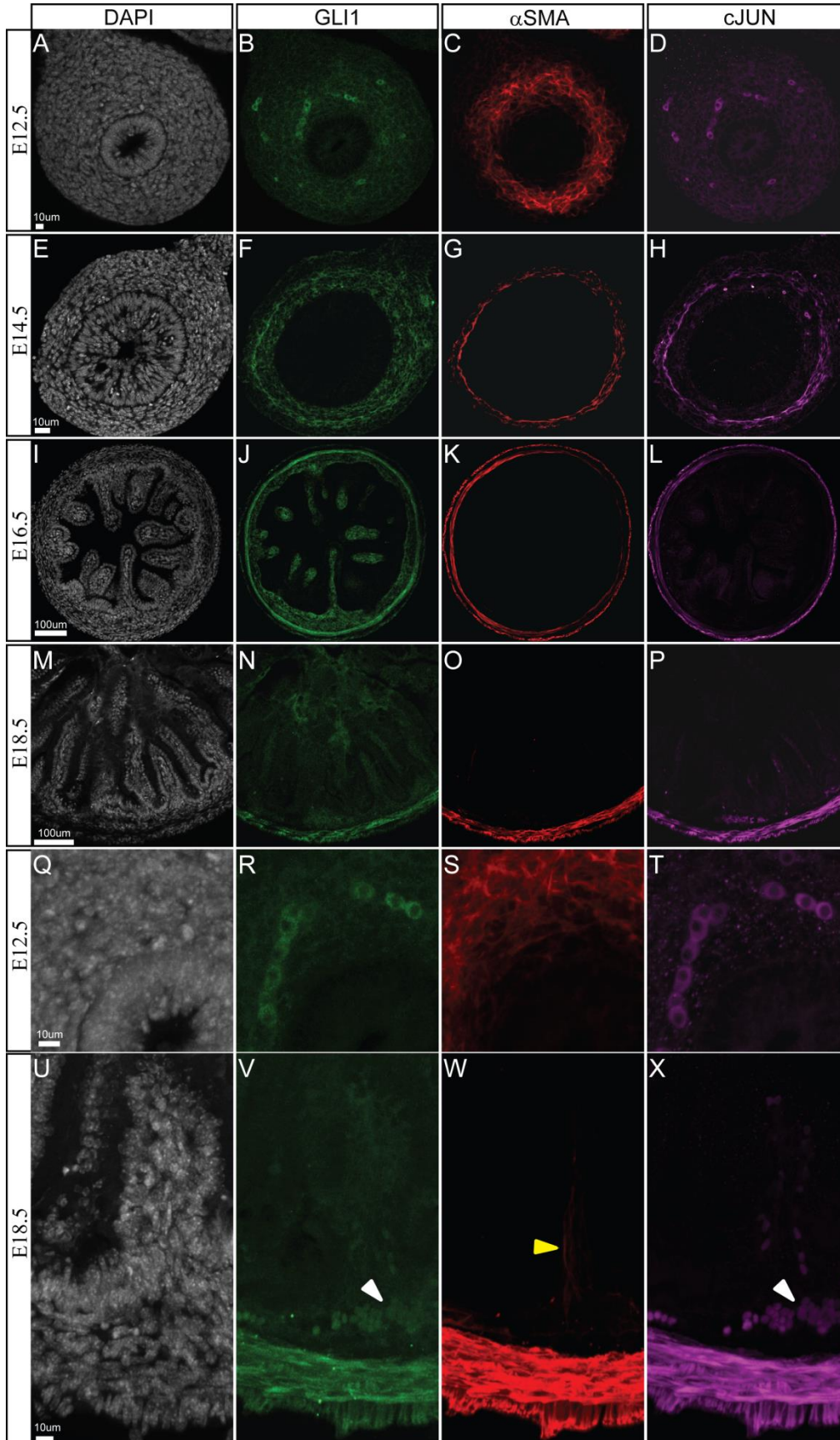


Figure 4.3. GLI1 and cJUN co-localize with visceral smooth muscle during intestinal development. Intestines collected from *Gli1^{eGFP/+}* mice were cross sectioned and stained for DAPI (gray), eGFP (green), the smooth muscle marker α SMA (red) and cJUN (purple) at E12.5 (**A-D; Q-T**), E14.5 (**E-H**), E16.5 (**I-L**) and E18.5 (**M-P; U-X**). cJUN co-localizes with α SMA in the ICM and OLM within the GLI1 expression domain. GLI1 is also expressed in the mesenchymal cluster cells (Figure 3J) where an essential role for Hh signaling has been demonstrated for villus development (Walton et al., 2012). At E18.5 GLI1 and cJUN stain an additional cell population (VX white arrowheads) to the ISM. However, neither GLI1 or cJUN co-localizes with villus smooth muscle (W yellow arrowhead).

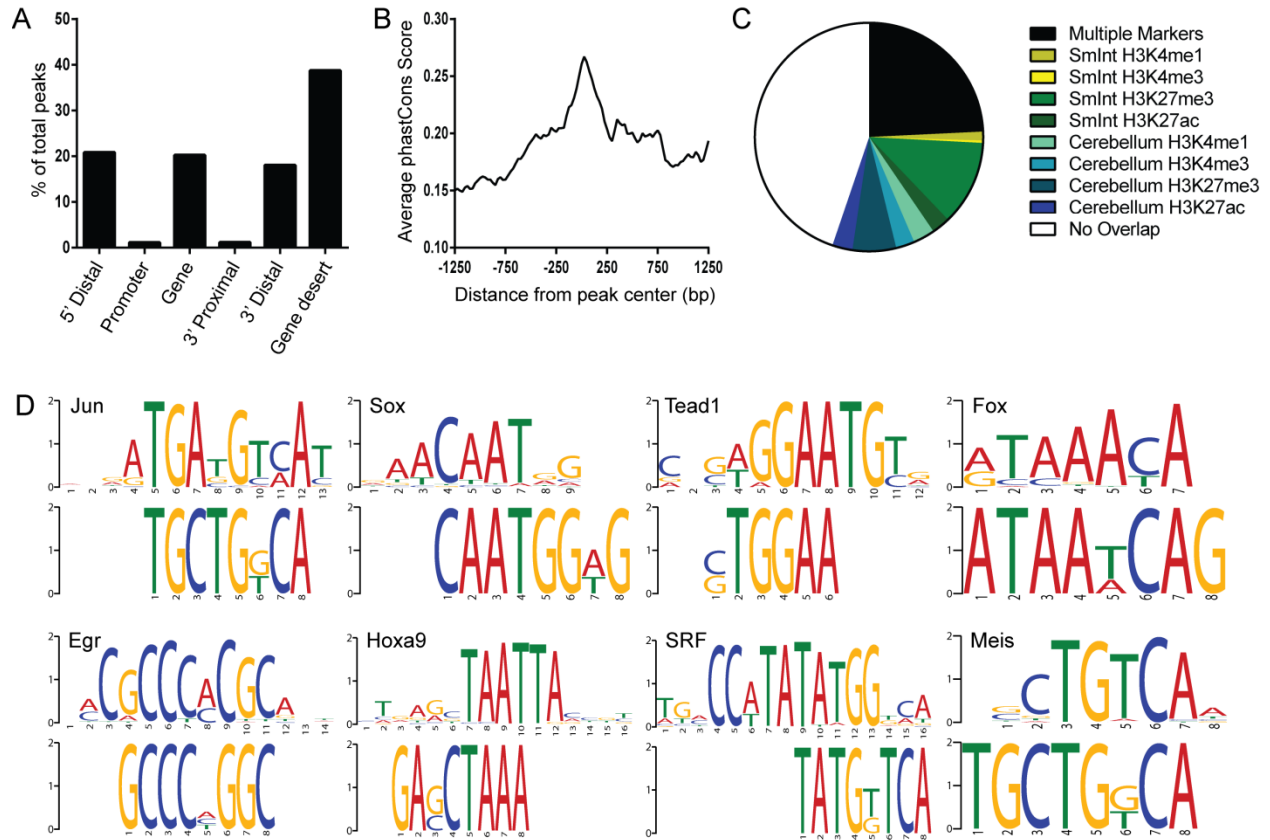


Figure 4.4. Characterization of genomic regions bound by cJUN in E14.5 intestine. (A)

Distribution of peaks relative to the nearest transcription start site (TSS) or transcription end site (TES) of the closest gene. Location of the peak is categorized as within a gene if it is between the TSS and TES, gene desert if it is greater than 100 Kbp from the gene, 5' distal if it is between 100 Kbp and 2 Kbp upstream of the TSS, promoter if it is ≤ 2 Kbp upstream of the TSS, 3' proximal if it is ≤ 2 Kbp downstream of the TES or 3' distal if it is between 2 Kbp and 100 Kbp from the TES. **(B)** Average vertebrate phastCons score for each nucleotide position mapped from the center of the peak. **(C)** Percentage of peaks that overlap with ENCODE enhancer histone markers. Regions categorized as multiple markers overlapped with more than one histone marker or overlapped within both tissues. **(D)** Motif enrichment analysis of the central 100 bps of the peaks identified several transcriptional factors involved in muscle development.

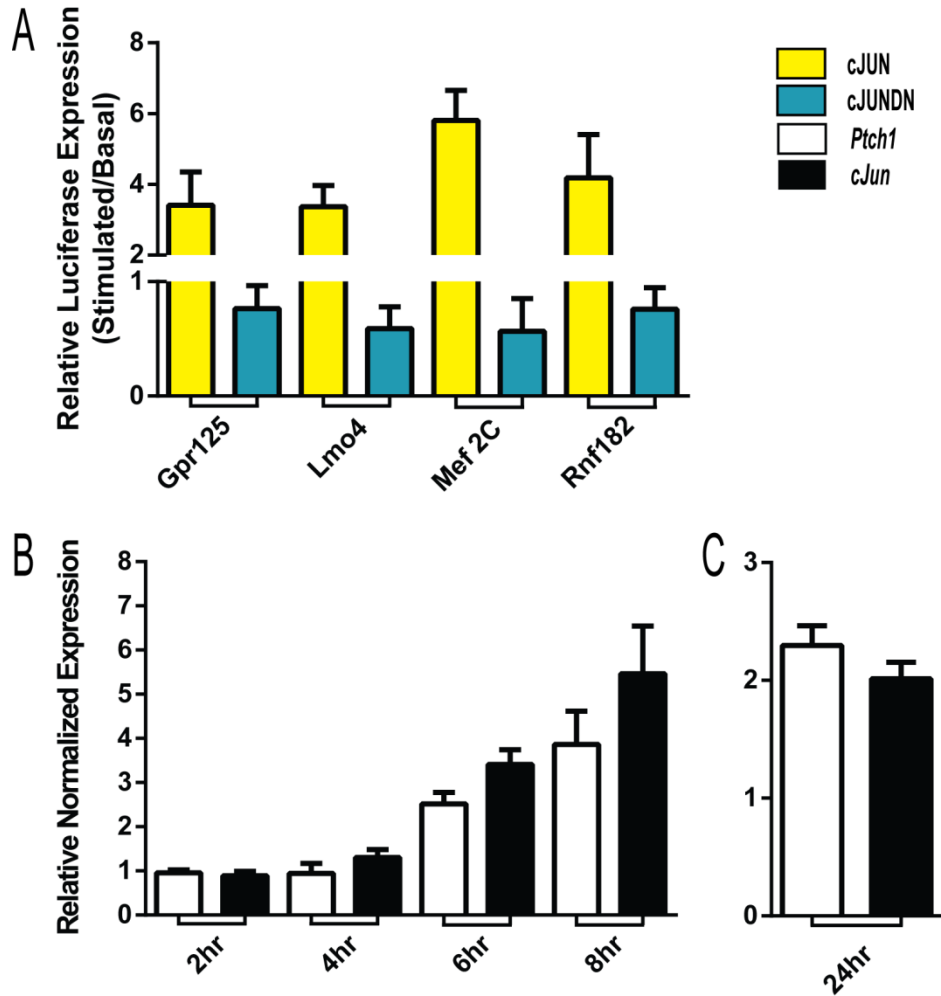


Figure 4.5. Response of ISM enhancers to *cJun* and response of *cJun* to Hh signaling.

(A) Putative regulatory regions from cJUN ChIP peaks, cloned upstream of a minimal luciferase promoter, were transfected into C2C12 cells with cJUN (yellow) or dominant negative cJUN (blue). Relative activity is plotted (stimulated/basal). cJUN responsive enhancer activity was confirmed for regions annotated to *Gpr125*, *Lmo4*, *Mef2C* and *Rnf182*. (B) Relative transcript levels measured by qPCR. (C) Fold change of *Ptch1* (white) and *cJun* (black) comparing untreated and SAG treated C2C12 cells at two-hour intervals after stimulation. (D) Fold change of *Ptch1* and *cJun* 24 hours after SAG treatment of E14.5 isolated mesenchyme tissue. Error bars represent the standard deviation of three experimental replicates.

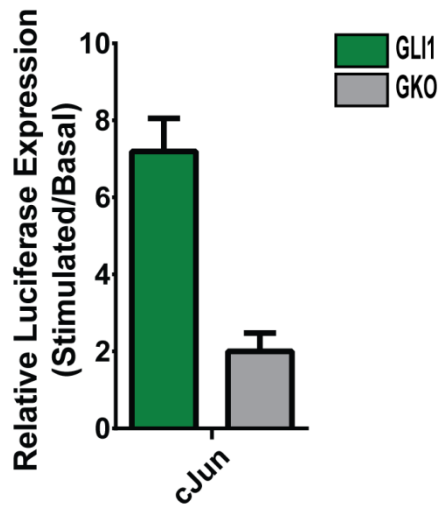


Figure 4.6. Functional verification of GLI-dependent enhancer upstream of *cJun*.

(A) A putative Hh regulatory region upstream of *cJun* cloned upstream of a minimal luciferase promoter then co-transfected into C2C12 cells with a GLI1 expression vector exhibits characteristic Hh responsiveness (green). Specificity of the response is confirmed to be GLI dependent by mutagenesis of the GLI TFBS (GKO) (gray). Error bars represent the standard deviation of three experimental replicates.

Gene Set	Genes Found	Set Size	Enrichment Score
KEGG_VASCULAR_SMOOTH_MUSCLE_CONTRACTION	37	115	0.378421
KEGG_CARDIAC_MUSCLE_CONTRACTION	25	81	0.374815
REACTOME_MUSCLE_CONTRACTION	18	48	0.321722
KAYO_CALORIE_RESTRICTION_MUSCLE_DN	15	89	0.297956
KAYO_AGING_MUSCLE_UP	59	206	0.249085
ROME_INSULIN_TARGETS_IN_MUSCLE_DN	34	246	0.204829
KAYO_CALORIE_RESTRICTION_MUSCLE_UP	30	95	0.201314
MUSCLE_DEVELOPMENT	35	93	0.149875

Table 4.1. GSEA muscle gene sets enriched in E14.5 intestinal mesenchyme tissue.

Gene	Fold Change	Affiliation	Reference
<i>Dkk1</i>	-84.45	Wnt modulator	He et al. 2013
<i>Edar</i>	-21.86	Wnt modulator	Wells et al. 2010
<i>Sall1</i>	-17.75	Wnt modulator	Kiefer et al. 2010
<i>Mmp9</i>	-16.22	Muscle Stem Cell	Zimowska et al. 2008
<i>Epha8</i>	-10.70	Muscle Stem Cell	Star et al. 2011
<i>Il1b</i>	-12.82	Muscle Stem Cell	Luo et al. 2003; Chen et al. 2006
<i>Klhl14</i>	-32.90	Muscle Differentiation	Abou-Elhamd et al. 2009
<i>Mir24-1</i>	-8.34	Muscle Differentiation	Sun et al. 2008

Table 4.2. Muscle affiliated genes downregulated by attenuation of Hh signaling.

Gene	Epi	Mes	FC	pval	Gene	Epi	Mes	FC	pval
Grik2	11.8	259.6	22.0	7.7E-32	Slc14a1	2.5	18.2	7.4	7.9E-03
Cacnb2	14.5	189.4	13.0	5.5E-20	Kcnj15	2.4	42.3	17.4	2.3E-05
Itgax	9.5	139.9	14.7	1.4E-04	Pcp4	11.7	274.7	23.4	7.4E-10
Apod	0.8	7.6	9.8	2.8E-02	Kcnj10	3.8	89.0	23.4	2.4E-04
Ncam1	125.5	5006.5	39.9	6.9E-13	Glis1	3.2	37.3	11.7	2.4E-02
Ppfa2	2.9	103.7	35.2	1.5E-19	Fermt2	292.7	5320.9	18.2	4.3E-51
Abca4	5.7	64.9	11.5	1.2E-09	Ccl11	26.8	1060.4	39.6	1.1E-35
Fkbp14	143.2	894.4	6.2	8.7E-26	Hpcal4	9.6	273.9	28.6	6.1E-25
Sarm1	10.4	166.7	16.0	2.1E-12	Pcdhac2	20.1	185.3	9.2	1.5E-20
Cd34	69.2	2018.4	29.2	1.3E-80	Aldh1a2	76.9	2060.9	26.8	2.5E-34
Pcdhb13	4.7	70.1	15.0	5.6E-10	Ticam2	3.9	17.5	4.5	7.1E-03
Rgs9	40.2	904.7	22.5	5.4E-55	Ddah2	426.2	2509.5	5.9	2.1E-15
Spock1	12.3	153.4	12.5	2.8E-11	Myom1	133.2	1247.3	9.4	3.0E-38
Cd84	6.0	48.7	8.1	1.5E-07	Gprc5b	90.7	1385.0	15.3	2.4E-40
Pmepa1	283.5	2869.9	10.1	2.3E-45	Cetn4	2.8	12.7	4.6	1.9E-02
Pxylp1	288.6	1237.1	4.3	8.4E-20	Il7r	2.0	16.8	8.4	2.5E-03
Icam2	10.7	503.4	47.0	5.5E-62	Cyth3	491.1	2135.7	4.3	4.3E-22
St8sia1	33.8	1149.9	34.1	8.5E-12	Cyp26b1	18.4	324.5	17.6	6.3E-11
Nfic	280.5	3270.4	11.7	2.7E-04	Hhat1	2.5	23.9	9.7	8.8E-04
Hoxb7	52.8	253.0	4.8	1.2E-12	C530044C16Rik	2.4	38.3	15.7	2.3E-05
Map6d1	5.9	55.0	9.3	1.3E-02	Lrat	9.3	161.4	17.3	1.4E-13
Rsad2	4.2	40.2	9.6	1.9E-08	Myo16	2.2	42.7	19.4	2.2E-04
Hsd11b2	5.8	64.8	11.1	1.8E-04	Fnbp1	328.2	1906.9	5.8	7.0E-27
Emilin3	125.8	3571.5	28.4	5.2E-88	Cux2	133.6	827.1	6.2	2.3E-05
Gm21949	82.6	1183.4	14.3	4.2E-22	Gpr88	1.7	24.3	14.4	5.6E-04
Gna14	35.1	554.3	15.8	1.5E-39	Otor	0.3	9.2	34.3	6.0E-04
Nodal	0.2	16.1	67.1	4.3E-04	D430019H16Rik	78.8	1252.4	15.9	1.2E-24
Tnni3	5.7	27.9	4.9	8.1E-03	Fam179a	0.7	9.1	12.7	2.1E-02
Cysltr1	10.9	124.9	11.4	1.2E-14	Tnfrsf26	1.7	21.6	12.6	4.8E-03
Cpxm2	3.9	28.9	7.5	6.0E-04	Rasgrp3	26.7	903.5	33.9	3.4E-71
Gstt1	15.5	72.3	4.7	3.7E-05	Chat	2.0	43.6	21.5	8.5E-09
Ptgs2os2	0.2	9.2	38.6	6.9E-04	Arhgap20	3.2	116.7	36.3	2.8E-21
Fabp7	24.4	400.2	16.4	2.2E-09	Pla2g4a	145.9	1795.4	12.3	1.2E-22
Cldn11	6.2	138.1	22.3	7.4E-07	Sprn	0.8	23.5	29.1	2.8E-07
Lrrc4	7.9	162.6	20.5	1.0E-02	Csrp1	780.3	5049.9	6.5	1.2E-28
Tlr12	17.3	345.3	19.9	4.8E-24	Pesk2os2	2.4	48.7	20.1	1.8E-06
Efcc1	2.7	35.7	13.1	6.8E-06	Nmur2	0.2	38.3	160.0	4.4E-09
Apbb1	198.0	1130.4	5.7	4.0E-28	Cacnb4	15.0	77.9	5.2	4.9E-07
Il33	32.1	748.6	23.3	5.0E-56	Nid2	254.2	3554.4	14.0	3.3E-60
Ifitm7	0.7	21.3	29.2	2.9E-05	Fyb	9.0	119.2	13.2	5.5E-15

Pitpnc1	255.7	2289.7	9.0	5.7E-14
Gm20748	13.9	325.2	23.4	7.4E-08
Col22a1	9.3	237.8	25.5	1.5E-15
Clvs1	199.7	865.5	4.3	1.5E-16
Celf3	270.5	2108.6	7.8	2.7E-09
Sapcd1	10.1	61.0	6.0	4.0E-06
Ero1lb	24.3	104.3	4.3	3.3E-06
Gm5868	6.0	57.8	9.7	1.3E-07
Gfra1	134.7	2867.4	21.3	2.9E-62
3110007F17Rik	1.0	23.1	22.9	2.1E-05
Ushbp1	20.5	527.8	25.7	7.0E-28
Stmn4	14.9	240.4	16.1	3.2E-12
C920009B18Rik	0.3	8.2	30.4	1.8E-02
Bai3	5.1	141.6	27.7	5.4E-24
Ssc5d	66.1	1855.8	28.1	2.0E-21
F13a1	6.0	65.4	11.0	2.0E-06
Kenmb1	9.4	190.7	20.4	1.3E-12
1810041L15Rik	18.6	217.7	11.7	3.8E-20
Fndc4	211.3	973.2	4.6	5.0E-20
Ank2	520.0	2251.0	4.3	3.6E-14
Gdap11l	25.0	220.4	8.8	6.8E-21
Abca8a	1.7	34.9	20.5	1.6E-06
Mapk8ip2	40.3	407.0	10.1	8.3E-20
Apcdd1	28.6	123.6	4.3	1.9E-07
Lrig1	751.8	5849.8	7.8	2.2E-41
9930012K11Rik	21.5	91.6	4.3	2.5E-06
Pik3cg	15.3	432.4	28.2	5.3E-38
Sec14l1	536.4	4127.2	7.7	2.5E-21
Dock3	17.4	73.1	4.2	1.4E-04
Drp2	24.7	119.2	4.8	5.3E-07
Rbms3	129.4	2405.2	18.6	1.6E-23
Tll1	10.9	252.1	23.2	3.8E-28
Cadm3	18.9	499.6	26.5	4.4E-35
Pcdh20	6.4	155.7	24.5	9.7E-24
Dusp10	41.4	536.1	13.0	2.3E-35
Hapln3	1.7	42.3	24.5	3.3E-07
B3gat1	0.7	33.4	46.5	5.5E-08
Flnc	241.9	4762.9	19.7	1.2E-19
B3galt1	4.9	146.5	30.1	2.1E-23
Rfx2	66.4	303.8	4.6	2.0E-10
Slc2a12	3.9	42.9	11.1	4.6E-06
Rcsd1	136.2	1908.6	14.0	1.1E-56
Hand1	31.7	667.2	21.1	1.7E-51
2810468N07Rik	26.1	130.6	5.0	6.5E-08
Lrp1b	4.4	22.2	5.1	2.1E-02
H1fx	110.4	555.7	5.0	7.8E-13
Slc18a2	77.0	453.3	5.9	5.4E-19
Atp2b4	306.0	4112.2	13.4	4.6E-13
Fmo1	6.8	130.5	19.3	9.2E-16
Tmem158	46.3	769.6	16.6	4.2E-17
Fabp4	57.5	1610.7	28.0	3.3E-10
Sox10	60.8	1119.1	18.4	1.4E-32
Clec4a2	5.5	52.2	9.5	3.1E-07
Serpini1	50.8	818.0	16.1	2.2E-37
Apol7c	49.2	732.3	14.9	5.8E-06
Pcdha6-g	729.4	5876.7	8.1	1.6E-12
Rem1	11.2	275.4	24.6	5.2E-19
Gm10591	2.9	34.8	12.0	1.3E-05
Vipr2	16.7	126.1	7.5	2.8E-10
Snhg18	52.4	657.1	12.6	8.3E-38
Fry	77.2	608.1	7.9	1.6E-03
Rora	59.7	362.1	6.1	5.9E-05
Fhl3	124.3	523.3	4.2	9.1E-05
Dclk3	4.5	32.9	7.4	4.5E-04
Ppp2r2c	1.8	46.2	26.3	1.9E-11
Igf1	43.0	1361.9	31.7	5.7E-14
Actl6b	2.7	58.4	21.4	4.4E-11
Snai2	40.7	1538.4	37.8	4.1E-84
2700070H01Rik	0.3	8.1	32.5	2.4E-02
Cacna1b	34.9	444.1	12.7	7.5E-07
Asc1l	59.7	1053.2	17.6	6.5E-34
Tlr1	3.0	36.0	12.1	1.7E-07
Dmpk	246.9	2559.7	10.4	4.8E-34
2610307P16Rik	4.4	79.3	18.1	9.2E-07
Slc12a4	284.2	1606.1	5.7	3.5E-26
Arhgap30	11.4	153.1	13.5	2.8E-10
Esrrb	2.0	61.5	30.5	2.4E-05
Rbfox1	4.4	95.2	21.9	2.1E-14
Dmp1	29.1	208.5	7.2	7.3E-10
Pcdha11	19.3	172.5	9.0	5.2E-19
Zmat4	2.2	25.1	11.3	9.2E-04
Serpinf1	146.7	1535.8	10.5	5.1E-07

Prph	132.7	1606.8	12.1	8.5E-30
Arl5c	2.0	32.2	16.0	8.1E-06
Kirrel	158.1	2757.5	17.4	7.6E-10
Adams7	97.5	2509.6	25.7	1.1E-47
Map7d1	544.2	3843.9	7.1	3.3E-38
Stmn2	65.4	1205.3	18.4	5.2E-32
Hdgfrp3	53.4	1490.0	27.9	1.5E-78
Sh3gl3	30.4	466.9	15.3	4.3E-36
Clec4a1	6.2	60.3	9.8	4.7E-08
Prex2	74.9	1140.8	15.2	2.2E-25
Tacr2	1.0	36.9	37.7	5.9E-07
Gnb4	44.7	1007.3	22.5	8.5E-62
Sostdc1	1.5	39.7	26.0	2.4E-07
Fam65c	5.2	133.7	25.8	1.0E-20
Lrrn4	26.4	250.5	9.5	2.4E-03
Eln	130.1	3077.9	23.7	1.0E-59
Antxr2	360.1	1643.9	4.6	1.4E-22
Klf14	7.8	71.0	9.1	6.2E-08
Fibin	50.4	1313.1	26.0	1.6E-43
Olfml3	132.5	3459.9	26.1	4.1E-84
AW549542	18.6	141.9	7.6	1.1E-10
Fit4	19.1	810.4	42.3	8.5E-21
Dcx	19.8	412.1	20.8	6.5E-25
Tmem130	9.0	74.6	8.2	9.4E-09
2810442N19Rik	0.5	11.2	23.4	1.5E-02
Mapkbp1	173.5	1009.4	5.8	4.1E-12
Lyz2	98.0	598.2	6.1	9.6E-26
Pcdhgc3	943.2	8857.7	9.4	1.5E-10
C2cd4a	10.2	56.2	5.5	3.6E-04
Rnf122	131.9	1027.2	7.8	3.9E-31
Ptpn5	3.2	67.0	20.9	1.1E-11
Tnfsf13	9.7	47.1	4.8	2.0E-04
Amotl2	261.4	1320.3	5.1	1.6E-20
6530402F18Rik	3.5	61.4	17.7	3.6E-08
Evi2a	6.2	81.7	13.1	7.0E-10
Ntf3	6.9	176.0	25.4	1.1E-23
Scn7a	3.3	55.6	17.0	7.9E-08
2610203C22Rik	2.5	25.3	10.1	4.1E-04
Pcnx12	1.6	50.6	32.3	7.1E-03
Sh2b2	28.7	170.2	5.9	1.1E-10
Pcdhal	18.3	168.9	9.2	4.8E-19
Trib2	49.7	1001.3	20.1	1.1E-57
Calcr1	98.0	2465.7	25.2	2.1E-17
Mtss11	400.9	3299.2	8.2	4.6E-08
Tnnt2	5.8	69.0	12.0	9.6E-07
9530026P05Rik	1.9	23.8	12.3	6.4E-03
49215111I17Rik	0.5	27.2	56.8	9.3E-06
Lyst	238.4	1020.0	4.3	5.2E-04
Srpx	6.2	186.1	29.9	3.7E-31
Nkain4	27.3	417.1	15.3	2.1E-32
Gm3893	0.2	21.8	91.0	1.6E-03
Laptm5	58.1	836.1	14.4	1.8E-08
D030025P21Rik	0.7	11.0	14.7	2.7E-02
Slc7a10	10.9	46.2	4.2	2.9E-03
Gdf5	1.7	15.9	9.3	1.1E-02
B230216N24Rik	1.5	34.8	23.2	3.2E-05
Ier51	70.3	380.4	5.4	1.5E-15
Il2rb	0.5	11.9	25.0	5.9E-03
Acr	0.5	12.5	25.5	1.1E-02
Ndrg4	35.4	393.4	11.1	3.6E-30
Chrdl2	0.5	8.1	16.5	1.3E-02
Mtc11	80.0	1782.6	22.3	3.5E-14
Pbx3	113.3	1043.5	9.2	4.5E-38
Sema4f	5.0	78.4	15.8	2.0E-13
Hlx	35.2	983.0	27.9	1.4E-47
Cabyr	4.5	31.7	7.0	4.7E-02
Synpr	3.0	77.3	25.9	6.7E-15
Lpl	92.3	530.4	5.7	1.1E-21
Elk3	159.5	2093.2	13.1	4.2E-21
Gprasp1	744.4	3578.5	4.8	1.3E-26
Rbpjl	0.7	31.0	41.9	2.4E-02
Tek	9.4	248.8	26.4	7.2E-30
Fam19a2	13.6	265.7	19.5	2.4E-34
Pcdhb9	3.8	104.9	27.9	8.4E-19
Clip4	22.9	249.5	10.9	1.3E-20
Thbd	207.8	5759.9	27.7	3.6E-91
Usp13	12.6	92.4	7.3	7.3E-09
Cnr1	30.4	306.6	10.1	2.7E-26
Zcchc12	30.8	414.4	13.5	7.1E-36
Gad1	1.0	12.4	12.2	3.3E-02
Klhdc8b	219.1	1685.9	7.7	1.2E-37
Wnt5a	125.6	2875.6	22.9	7.0E-21

Cckar	31.2	699.3	22.4	4.2E-50
Cap2	7.6	294.2	38.5	8.4E-39
H2-Ab1	9.3	50.4	5.4	4.4E-05
Cdyl2	72.3	292.8	4.0	3.0E-04
Rab13	76.5	317.9	4.2	8.7E-05
Doc2b	139.6	789.0	5.7	7.0E-19
Kif1a	491.1	2027.8	4.1	7.1E-10
Cd1d2	4.0	49.0	12.3	1.2E-08
Gpr137c	7.9	86.7	11.0	5.5E-10
Cyfp2	208.5	1297.4	6.2	4.5E-13
Scx	10.8	51.9	4.8	5.5E-06
Wisp1	169.5	3154.9	18.6	6.5E-13
Slc35f1	42.8	329.7	7.7	2.1E-20
Arap3	97.2	2420.2	24.9	5.4E-36
Tagln3	28.0	466.4	16.6	2.8E-40
C1ql1	18.0	424.3	23.6	8.1E-38
Fam219aos	10.9	95.6	8.8	1.3E-09
Jam2	5.7	128.6	22.6	1.1E-18
Dkk1	0.8	28.0	37.2	4.6E-05
Ptp4a3	875.2	3636.8	4.2	4.6E-21
Rgs4	16.0	356.9	22.4	3.7E-45
Synpo	87.3	2130.7	24.4	7.1E-07
4732416N19Rik	7.5	82.5	11.0	6.9E-06
Serping1	29.5	917.5	31.1	6.9E-68
Ssbp2	92.4	1040.8	11.3	9.6E-44
Sdk1	114.3	3145.6	27.5	2.9E-12
Akap5	22.7	236.3	10.4	2.7E-18
Lrrn3	29.1	499.7	17.2	4.6E-46
Vgll3	3.1	25.3	8.2	5.3E-05
Gm12429	0.5	24.1	47.5	2.2E-02
Agap2	36.3	825.5	22.7	8.3E-15
5730409E04Rik	29.8	301.1	10.1	3.1E-25
Rhoh	2.2	28.3	12.6	1.3E-04
Chma3	27.8	672.1	24.2	1.1E-58
Dok7	1.5	15.2	10.1	4.2E-03
Ccdc65	0.7	10.8	15.1	1.5E-02
Nos3	20.9	449.9	21.5	1.7E-39
Irf2bpl	408.2	1782.7	4.4	9.4E-12
Pik3r5	6.5	74.1	11.4	1.0E-08
Oasl2	17.7	104.5	5.9	3.0E-09
Apba2	10.4	229.4	22.1	5.6E-29
Lats2	179.4	949.6	5.3	2.9E-22
Emcn	12.6	535.7	42.4	1.0E-14
Usp44	1.8	14.9	8.4	5.0E-03
AW011738	6.9	105.8	15.3	5.3E-13
Slc8a3	13.6	149.2	11.0	2.3E-13
A630019J02Rik	1.0	12.7	13.2	5.9E-03
Gfra4	3.2	68.7	21.6	8.6E-10
Fhl1	72.1	426.7	5.9	3.9E-21
Ccl21b	2.9	34.0	11.7	2.5E-05
Phox2b	96.8	2111.3	21.8	2.6E-70
Nxn	440.7	1866.5	4.2	2.4E-21
Atp1a4	1.0	13.1	13.5	2.7E-02
Shisa3	8.2	575.4	70.6	9.0E-75
C5ar2	1.1	9.6	9.1	4.0E-02
Arhgef6	12.4	194.9	15.8	3.1E-22
Angpt2	72.5	329.6	4.5	8.3E-06
Cpa2	22.2	397.1	17.9	2.1E-02
I830077J02Rik	1.0	23.7	23.4	3.3E-04
Nrros	40.9	682.2	16.7	2.1E-43
Insc	7.5	131.3	17.6	7.2E-18
Itga1	35.1	885.7	25.2	9.8E-46
1700018A04Rik	1.8	54.2	30.5	4.5E-08
AW551984	56.1	557.9	9.9	2.2E-17
Arhgef15	15.5	377.6	24.4	1.4E-36
Crispld2	57.9	1888.8	32.6	2.2E-82
Rai2	18.3	604.6	33.1	1.5E-31
Myo1f	16.2	136.9	8.4	2.0E-13
Stxbp1	164.1	1712.3	10.4	1.8E-16
Kcnq4	3.7	135.7	37.0	5.2E-19
Cyrr1	2.2	128.2	58.4	2.3E-05
Lepre1	287.6	1541.5	5.4	1.8E-17
Cnn1	60.4	1643.3	27.2	5.4E-34
Rbpm2	52.1	292.1	5.6	1.1E-09
Slit2	183.2	1644.6	9.0	2.1E-11
Cdk5r2	12.9	92.0	7.1	2.8E-05
Ptpdc1	49.8	555.4	11.1	6.1E-32
Epha8	10.4	108.9	10.5	6.9E-08
Mmp10	0.3	14.6	54.4	5.4E-04
Sema4c	501.4	2130.9	4.3	1.4E-20
Sema7a	11.0	186.5	16.9	6.4E-24
Oaz2	396.9	1989.3	5.0	9.1E-26

Tmem108	45.4	248.5	5.5	5.1E-06	5830444B04Rik	1.0	15.0	15.2	1.7E-02
Shisa4	19.6	262.6	13.4	7.8E-25	Zmat1	12.0	81.0	6.8	4.4E-09
Soga3	9.9	358.1	36.1	3.7E-28	St18	34.8	217.3	6.3	6.2E-06
Klhl1	2.5	28.5	11.5	7.5E-07	Fxyd2	14.6	135.7	9.3	2.5E-08
Sv2b	4.7	106.7	22.8	2.3E-17	Adams3	16.8	360.0	21.5	8.9E-09
Draxin	1.7	33.1	19.5	5.3E-07	Dagla	179.4	935.4	5.2	3.0E-03
Nkd1	50.5	1145.6	22.7	8.2E-59	Vcam1	6.6	152.3	23.1	3.1E-15
Kcnma1	18.1	506.1	28.0	1.5E-26	Pthlh	2.2	13.7	6.2	4.0E-02
Scn1b	2.9	25.9	8.9	6.1E-04	Ptger2	3.1	71.0	22.6	1.0E-10
Msc	1.0	30.4	31.4	3.6E-06	Sorcs2	191.6	2185.1	11.4	3.1E-28
Krt17	9.0	50.3	5.6	4.9E-05	Ermap	1.5	10.8	7.4	3.1E-02
Gjd2	4.7	149.4	31.9	2.6E-28	Irx3	0.8	14.7	18.6	4.7E-03
Syt17	14.6	171.8	11.7	3.9E-19	Rftn2	43.3	1054.3	24.3	3.6E-63
Cryab	10.0	94.8	9.5	1.7E-10	Fcgr4	1.0	22.9	22.9	7.8E-06
Cthrc1	17.2	370.2	21.5	1.3E-37	A430090L17Rik	2.2	61.4	28.2	2.5E-03
Neur11a	44.2	605.3	13.7	1.7E-15	Dram1	25.5	124.9	4.9	4.2E-08
Agtr1b	0.7	9.1	12.5	1.9E-02	6330403A02Rik	5.8	184.8	31.9	2.2E-07
Frmf6	144.0	648.9	4.5	1.6E-16	Gper1	10.2	181.3	17.8	6.3E-19
Elavl2	21.5	214.7	10.0	1.5E-24	Med12l	101.4	564.8	5.6	3.6E-18
Tcf4	1251.3	6513.0	5.2	1.5E-29	Gm684	1.7	14.6	8.4	1.0E-02
Arrdc3	198.2	2747.3	13.9	3.6E-61	E130310I04Rik	23.4	517.9	22.1	3.1E-17
Nell2	30.7	805.5	26.2	9.5E-26	Cox4i2	2.2	56.5	25.1	4.0E-10
Cacna1d	41.1	1114.7	27.1	9.1E-10	Batf	2.5	33.9	13.5	2.0E-05
Nme5	1.0	8.5	8.4	4.0E-02	Ildr2	26.9	302.7	11.2	3.4E-09
Slc44a5	3.9	75.3	19.4	7.4E-13	Kank4	25.5	950.3	37.3	5.4E-16
Lsamp	2.2	43.8	20.1	9.7E-08	Cartpt	6.6	152.4	23.1	2.9E-21
Clec2l	2.0	29.1	14.3	1.9E-06	Ina	31.9	508.2	15.9	1.5E-32
Sh3rf3	4.7	74.5	15.7	7.6E-06	Nfix	60.7	1898.7	31.3	3.1E-05
Exoc3l	37.4	442.8	11.8	1.1E-20	A330074K22Rik	7.9	201.1	25.5	2.8E-02
Il18rap	3.0	18.9	6.2	1.7E-02	Adcy3	85.6	676.7	7.9	1.4E-27
Aff3	47.8	1765.9	37.0	1.8E-12	Zap70	1.3	12.0	9.4	3.3E-02
Spats2l	180.8	1131.6	6.3	3.3E-29	Chd5	96.4	516.9	5.4	1.8E-11
Tmem178	3.2	59.5	18.8	1.4E-10	Bank1	0.3	36.2	134.3	1.5E-08
Tmem132d	2.6	14.1	5.4	2.0E-02	Ryr3	25.8	260.1	10.1	6.8E-09
Arrb1	701.4	3160.8	4.5	2.4E-06	Col14a1	105.7	4431.5	41.9	1.6E-26
Frem1	159.7	4348.4	27.2	2.6E-16	Lrrc4b	23.6	462.0	19.5	4.8E-26
Zcchc18	17.7	348.0	19.7	3.0E-38	Adam33	0.8	38.0	49.4	4.3E-07
Chrna4	2.0	62.9	32.0	1.4E-12	Hoxc4	17.2	755.1	43.8	1.1E-16
Card11	3.2	26.7	8.2	4.9E-04	Ntrk3	18.3	770.3	42.0	1.2E-40
Id4	36.5	637.3	17.5	3.4E-45	Jph2	53.7	1410.6	26.3	1.4E-72
Icos	1.0	11.7	12.0	2.2E-02	A530058N18Rik	1.0	12.2	12.6	2.1E-03

Clstn2	13.2	59.1	4.5	5.1E-04
Edar	5.4	189.0	34.9	7.0E-17
Bmp3	121.4	3662.3	30.2	1.1E-85
Ppp1r18	149.5	1784.1	11.9	7.1E-48
Hoxa2	34.7	459.0	13.2	4.4E-30
Mapk8ip1	230.0	1253.6	5.4	1.1E-25
Etv1	66.6	1624.6	24.4	2.7E-30
Ptprs	1969.6	12588.7	6.4	2.1E-35
Slc8a2	37.4	896.7	24.0	2.2E-24
Pitpnm3	24.5	651.1	26.6	1.7E-10
Alas2	4.5	52.5	11.6	1.2E-03
Dusp15	0.2	7.1	29.6	3.1E-02
S100a4	6.9	31.4	4.5	4.8E-03
Fnd3c2	0.5	46.7	91.7	3.1E-10
Kcnd3	55.8	2180.5	39.1	2.0E-12
Efemp2	194.6	1621.4	8.3	1.3E-38
Pkd2	569.9	3580.7	6.3	1.6E-34
Ltbp2	6.4	136.1	21.3	7.0E-13
Csmd2	5.3	90.8	17.0	1.0E-04
Gpr45	0.5	8.0	15.7	2.5E-02
Abca6	0.7	21.8	29.1	1.7E-05
Arhgef40	337.8	4616.3	13.7	5.2E-62
Efhb	0.7	16.7	22.4	9.2E-04
Id3	130.8	1618.4	12.4	5.3E-32
Slc2a4	43.6	1114.7	25.6	2.0E-63
Unc79	14.9	182.3	12.3	7.7E-11
Trp53inp2	280.0	2065.9	7.4	1.2E-28
Nbl1	256.6	1596.0	6.2	2.9E-29
Cpz	3.3	61.8	18.9	1.4E-09
Pnma3	2.5	34.1	13.8	4.1E-05
N28178	3.5	49.7	14.4	3.2E-03
Bgn	81.7	1932.3	23.6	2.0E-13
Dnm3os	182.8	3986.0	21.8	1.0E-75
Slc6a13	1.2	9.5	7.8	1.9E-02
Pcdhga8	786.1	6075.7	7.7	3.8E-11
Gpc4	128.9	554.9	4.3	3.4E-15
Siglec1	2.8	39.1	14.1	1.6E-02
Hear1	15.8	85.0	5.4	4.1E-05
Tnf	4.0	33.0	8.3	3.1E-04
Apol7e	5.5	27.4	5.0	9.3E-03
Zfp580	91.0	489.9	5.4	1.5E-04
Matn4	6.1	164.0	26.9	1.2E-14
Gria2	14.7	244.8	16.6	2.7E-26
Il17rd	192.9	1030.8	5.3	4.5E-07
Chrm1	18.2	89.4	4.9	2.0E-02
Gpr114	9.1	92.0	10.1	7.3E-04
Fermt3	27.2	187.3	6.9	2.5E-08
Il1r1	39.7	546.1	13.7	3.5E-34
B3gnt8	5.8	132.0	22.7	1.7E-17
Thsd7a	59.3	320.9	5.4	2.7E-10
Actg2	289.1	6985.2	24.2	3.8E-63
Celf4	46.2	390.5	8.4	1.1E-23
Fmpd4	0.5	21.0	42.9	9.8E-07
Plekhg1	137.5	1284.2	9.3	7.6E-08
Prss35	4.7	59.4	12.8	2.8E-07
Plekha2	33.0	132.9	4.0	1.2E-06
Foxd2os	26.0	120.6	4.6	1.4E-03
Hoxb9	10.3	63.2	6.1	9.8E-06
Armex2	367.5	3045.3	8.3	4.8E-42
Ffar3	2.2	18.7	8.3	2.7E-03
Eva1a	57.4	349.8	6.1	1.8E-13
Vstm2b	0.3	15.5	62.0	4.1E-04
Tmem121	12.5	172.9	13.8	1.0E-18
Hoxb6	56.8	639.9	11.3	5.5E-22
Necab1	1.5	44.1	29.0	7.7E-10
Abca1	97.0	1694.1	17.5	1.5E-14
Lag3	3.8	50.0	13.0	6.3E-07
6330403K07Rik	79.8	1323.7	16.6	6.2E-59
Ptms	1199.3	7092.9	5.9	1.5E-31
Pcdha10	18.6	177.1	9.5	1.4E-19
Unc13a	54.7	304.5	5.6	1.3E-13
Adam5	0.2	5.6	23.5	2.5E-02
Hhip1l	7.6	32.2	4.2	1.8E-02
Snap25	23.2	259.6	11.2	3.1E-24
1700023L04Rik	0.8	9.1	11.7	1.5E-02
Pdgfrl	7.7	67.7	8.8	2.5E-08
S1pr2	170.3	1067.8	6.3	5.3E-22
Zfp941	5.9	52.4	9.0	5.7E-08
Gjc2	2.8	35.2	12.7	1.2E-06
Caenalc	37.5	903.6	24.1	4.9E-07
Lhx6	1.5	16.4	11.0	1.2E-02
Mir1903	1.9	16.1	8.3	2.0E-03

Cbln1	2.4	17.7	7.3	4.0E-03
Kenab1	5.0	87.3	17.5	4.5E-11
Pcbp3	117.2	1088.2	9.3	5.2E-37
Acsf6	16.6	94.8	5.7	2.0E-07
Zfp449	86.4	383.6	4.4	6.0E-14
Myh11	617.3	17746.4	28.7	3.6E-53
Pcdhgb2	751.2	6059.9	8.1	5.7E-12
Cd93	127.2	4897.8	38.5	2.6E-17
Ttc12	15.5	77.2	5.0	9.8E-06
Dnase1l3	16.2	224.0	13.8	1.2E-09
Pik3r6	5.2	148.8	28.4	1.1E-21
Ikzf4	36.4	209.2	5.8	2.3E-02
Abcg1	52.3	304.7	5.8	6.5E-06
Snai1	15.6	517.0	33.2	6.9E-06
Ccdc69	3.2	15.6	4.8	2.2E-02
Tnfrsf12Tnfrsf13	17.9	152.5	8.5	4.2E-08
Bai2	16.5	544.1	32.9	3.8E-51
Thbs4	89.5	2771.5	31.0	3.1E-28
Dnah2	16.3	89.4	5.5	2.9E-04
Fgf10	5.0	203.4	40.5	1.4E-31
Dnaic1	1.5	42.4	28.5	1.2E-06
Tmem151b	38.6	640.8	16.6	4.8E-10
Pknox2	28.3	1066.1	37.7	1.6E-54
Bmp1	645.6	5654.3	8.8	6.6E-46
Alk	4.2	129.7	31.0	7.9E-14
Galnt14	3.6	16.9	4.7	4.1E-02
Maneal	6.4	115.3	18.0	6.6E-17
9930111J21Rik2	0.7	11.6	15.8	3.5E-03
Dsc3	5.6	30.9	5.5	7.6E-03
Olfir78	0.2	10.6	44.3	5.3E-03
Wnt5b	20.8	181.9	8.8	2.4E-17
Hpse2	30.7	770.6	25.1	8.0E-11
Fam196b	0.3	11.7	43.6	1.3E-03
Bmper	13.5	311.7	23.1	1.1E-18
Cacna1i	0.7	20.1	28.1	6.4E-04
2900011O08Rik	1.5	37.4	25.6	1.5E-09
Ulk2	384.9	1603.9	4.2	2.0E-20
Bcl6b	81.0	1305.1	16.1	3.6E-54
Nr2f1	13.1	296.9	22.6	2.4E-32
Trmp1	14.8	88.4	6.0	3.1E-07
Cyp2d9	0.2	11.4	47.8	1.4E-02
Pmp22	47.5	756.3	15.9	4.0E-50
Cdh12	0.7	36.9	51.4	1.4E-06
Prrx2	1.5	18.3	12.3	4.4E-04
Ebf3	21.4	218.8	10.2	6.5E-23
Adcyap1	1.9	34.2	17.5	1.7E-07
Gm15319	2.7	81.1	29.9	3.1E-03
Pcdh15	4.7	77.8	16.5	1.9E-08
Irs4	11.5	177.2	15.3	6.0E-06
A730056A06Rik	4.9	101.0	20.7	6.4E-18
Col4a1	1204.3	31774.2	26.4	5.8E-72
Prima1	1.7	35.9	20.6	1.9E-06
Tagln	194.5	3967.4	20.4	4.8E-24
Sema3a	26.5	772.5	29.1	5.4E-33
Maml2	25.9	409.5	15.8	2.1E-08
Bnc1	19.1	161.6	8.4	1.6E-05
Gprin1	52.0	238.1	4.6	2.4E-11
D630003M21Rik	14.1	349.2	24.8	5.2E-30
Fap	16.8	719.0	42.9	2.8E-13
Fgf11	38.6	212.1	5.5	7.6E-04
Gm5535	0.2	8.1	34.0	4.0E-02
Elfn1	2.2	16.0	7.2	1.6E-02
Sneg	13.0	161.3	12.4	3.8E-13
9930111J21Rik1	1.7	19.1	11.3	2.1E-03
GpnmB	106.8	537.6	5.0	4.3E-03
Gm16702	2.5	41.8	16.7	8.4E-07
Csmd1	2.6	26.1	10.1	5.1E-03
Csf1r	128.0	1484.6	11.6	1.3E-46
Cdh2	90.6	1940.4	21.4	7.1E-61
ApoE	620.2	3527.2	5.7	1.1E-06
Fstl4	13.5	291.3	21.6	6.8E-08
Wnk3	62.6	352.4	5.6	5.9E-08
Col4a5	137.4	1916.3	13.9	2.5E-55
Ifitm3	112.4	1903.8	16.9	4.4E-17
Kcnh8	8.1	33.0	4.1	5.1E-03
Fndc9	4.1	71.6	17.3	1.2E-03
Sgcd	3.6	89.2	24.8	5.5E-12
A4galt	8.8	123.0	14.0	8.4E-15
Hs3st5	3.2	69.6	21.5	2.1E-11
Fbln2	146.7	1024.7	7.0	1.2E-09
Iqgap2	630.2	3898.0	6.2	3.1E-17
C430049B03Rik	23.1	380.2	16.5	1.0E-17

Tnc	37.0	703.4	19.0	2.4E-45	Mmp17	19.8	298.6	15.1	1.1E-27
Ptchd2	13.4	83.2	6.2	2.1E-02	Pcdhb20	12.8	219.6	17.2	3.6E-27
Ltbp1	114.3	2029.3	17.8	5.1E-38	Asb4	23.2	949.3	41.0	4.7E-49
Pcdh19	5.5	255.2	46.5	3.3E-15	Gfra2	11.5	247.5	21.4	1.0E-30
Smoc2	439.3	4381.1	10.0	1.9E-49	Dlg2	37.1	774.6	20.9	1.4E-25
Aoc3	19.3	577.6	29.9	2.6E-13	Snn	322.6	2420.2	7.5	1.4E-37
Colq	0.7	31.1	43.4	1.4E-07	Lppr2	108.8	471.0	4.3	8.9E-11
Kcnn3	43.2	1016.2	23.5	6.7E-06	Sh3bgr	17.1	139.1	8.1	3.1E-09
Kcnb1	27.3	749.5	27.5	1.6E-08	Atp2b2	6.0	130.4	21.9	3.1E-13
Lgi1	1.2	11.1	9.1	7.5E-03	Slmo1	4.2	55.1	13.1	1.1E-07
Cerk	266.8	1386.2	5.2	8.6E-24	Sh3bp5	137.1	1299.3	9.5	1.5E-29
P2rx1	3.2	50.3	15.9	4.0E-04	Ccdc141	42.9	536.2	12.5	3.4E-23
Fzd4	148.8	721.3	4.8	1.2E-08	Gdnf	21.9	745.2	34.1	3.0E-21
Gpr179	3.6	23.0	6.5	8.4E-03	Bmp7	244.7	1049.6	4.3	1.3E-17
Zcchc16	1.9	14.4	7.4	3.1E-03	Flrt1	7.6	113.8	15.0	2.0E-02
Megf10	13.0	167.5	12.8	5.7E-18	Aspdh	0.8	10.3	13.5	2.3E-02
Nrgn	3.0	38.6	12.9	2.7E-05	Fbxo32	72.9	517.2	7.1	3.8E-22
Camsap2	478.2	2040.2	4.3	1.8E-20	Tgfb2	51.3	814.8	15.9	8.0E-30
Ppap2b	107.3	2114.5	19.7	2.4E-67	Gm11549	1.5	15.1	10.0	7.6E-03
Cpxm1	70.8	1129.8	16.0	8.0E-46	Fhl4	2.0	14.2	7.2	1.9E-02
Olfrl372-ps1	6.0	37.2	6.2	2.1E-03	Plcl1	24.2	456.6	18.9	2.5E-34
Gpr141	3.5	28.4	8.1	2.1E-03	Kcnh3	4.9	28.9	5.9	7.4E-03
Susd5	0.3	11.1	41.1	2.1E-03	Rasd2	51.3	232.8	4.5	2.3E-02
Myt11	4.2	98.8	23.4	2.3E-17	Mapk11	26.4	380.7	14.4	1.9E-29
Gimap4	14.8	434.0	29.3	1.3E-31	Emilin2	6.8	64.3	9.4	1.5E-07
Pnpla3	6.3	29.0	4.6	9.6E-04	Xylt1	21.8	137.0	6.3	5.9E-03
Fam57b	9.0	149.3	16.6	3.6E-06	Pygl	56.3	433.6	7.7	1.6E-26
Ifi27	18.6	328.6	17.6	4.7E-33	Cd38	106.3	655.9	6.2	2.7E-25
Pcdhb6	1.7	45.0	26.4	4.1E-10	Lrp12	252.6	1049.7	4.2	2.4E-18
A230057D06Rik	2.4	41.7	17.1	3.2E-06	Unc5c	95.4	2290.3	24.0	2.3E-32
Lifr	27.8	727.5	26.1	1.0E-22	Cspg5	13.1	125.7	9.6	2.9E-12
Plp1	91.1	365.3	4.0	2.5E-12	Btdb11	19.5	248.5	12.7	5.9E-05
Hoxc8	36.1	481.0	13.3	1.4E-03	Rab8b	275.1	1328.6	4.8	1.2E-23
9030612E09Rik	0.7	11.0	15.1	9.9E-03	Creg2	2.0	21.0	10.7	1.0E-04
Fam124a	23.7	148.6	6.3	2.2E-11	Nlgn3	20.6	349.9	17.0	4.2E-08
Ggta1	105.1	1421.2	13.5	2.1E-49	Il1rap	83.2	355.1	4.3	5.7E-14
Cplx1	7.3	35.4	4.9	5.0E-04	Myh3	5.3	75.3	14.3	4.2E-04
Loxl4	3.2	51.5	16.0	1.6E-06	Ap1s2	68.2	599.7	8.8	1.0E-30
Arhgap15	0.5	6.4	13.2	1.5E-02	Cd300lb	2.0	14.2	6.9	2.2E-02
Scnn1b	1.7	9.2	5.3	2.7E-02	Ggt5	32.7	1078.5	33.0	2.1E-31
St3gal5	65.4	343.3	5.3	9.4E-18	Foxl1	26.0	860.4	33.1	6.2E-23

Slc1a6	2.3	23.8	10.4	5.7E-04
Atp8b4	1.2	15.5	12.9	4.3E-03
Fmo2	1.7	16.5	9.8	7.4E-03
Ltc4s	11.1	72.6	6.6	7.5E-03
Tlr8	0.8	5.0	6.5	2.5E-02
Glyat13	0.5	18.8	36.1	6.8E-05
Zeb2	137.6	4076.6	29.6	2.3E-51
Cntln	107.5	933.4	8.7	5.4E-21
Usp35	101.4	413.6	4.1	2.2E-08
Smad5	1084.6	4728.8	4.4	1.8E-12
Abcg3	6.7	69.8	10.4	8.9E-09
Evc	232.8	1439.9	6.2	4.0E-28
Serpinh1	5013.8	23480.5	4.7	7.8E-14
Heg1	164.2	2110.1	12.8	2.7E-03
Chl1	24.2	539.9	22.3	2.1E-50
Reep5	260.8	1807.7	6.9	1.8E-35
Tnn	33.1	907.7	27.5	1.6E-55
Fzd3	253.5	1209.2	4.8	2.9E-07
Gm15663	13.3	55.7	4.2	1.2E-06
Dio3	3.0	38.8	13.0	1.0E-05
Pamr1	104.0	1337.9	12.9	1.4E-49
Rassf8	30.5	347.3	11.4	8.8E-18
Tbkbp1	65.7	1103.2	16.8	1.8E-28
Ankrd45	1.4	30.2	20.9	3.9E-07
Serpina6	9.4	197.2	21.0	4.2E-03
Grid1	1.7	9.4	5.6	3.8E-02
Pltp	143.1	1290.1	9.0	4.4E-24
Il21r	1.0	10.0	9.8	7.6E-03
4931403E22Rik	1.7	17.8	10.4	2.2E-02
Caskin1	63.3	542.3	8.6	7.2E-13
Nkx3-2	4.8	118.4	24.5	8.9E-12
Gm1987	1.2	24.2	20.2	7.5E-05
Gmfg	4.0	21.8	5.5	3.3E-03
Ephb1	27.7	696.1	25.1	1.6E-55
Kcnt2	36.6	186.9	5.1	2.0E-11
Plxn3	2.7	61.9	22.6	4.8E-09
Gbp9	11.7	155.2	13.2	2.8E-16
Hic1	254.8	5450.6	21.4	5.5E-25
Sall2	416.9	1971.0	4.7	3.5E-10
AI504432	9.2	228.5	24.8	7.1E-29
Mfrp	6.6	171.4	25.8	5.4E-21
Timp1	40.5	179.8	4.4	6.3E-09
Mmd2	1.8	33.3	18.9	8.7E-07
Dusp8	138.5	560.9	4.1	4.9E-05
Hck	6.9	95.9	14.0	1.1E-05
Pdlim2	7.3	54.3	7.4	1.3E-06
Ddr2	133.9	3916.8	29.3	6.2E-57
Rufy4	3.3	21.1	6.4	6.1E-03
Gpr50	9.1	146.1	16.1	5.8E-14
B230217C12Rik	4.7	87.3	18.7	8.2E-14
AF357359	6.9	53.4	7.7	1.2E-05
Eno2	93.8	401.6	4.3	7.7E-08
Madcam1	4.5	111.3	25.0	3.4E-21
Zfp9	52.2	691.9	13.3	1.8E-39
Hba-a1	386.5	3153.0	8.2	4.5E-28
Wwtr1	609.0	3702.2	6.1	1.7E-33
Sparc	731.3	15324.7	21.0	9.4E-68
LOC100505025	0.7	29.8	41.5	3.3E-07
Eya1	10.5	335.3	31.8	4.5E-18
Gpr176	1.3	17.9	13.9	4.8E-03
Dok5	0.5	12.5	26.1	2.3E-04
42067	11.8	54.7	4.6	1.9E-03
Postn	166.4	4176.8	25.1	1.6E-26
Serpinb9	26.1	346.1	13.2	5.6E-28
Smoc1	153.8	2276.3	14.8	1.2E-57
Chsy3	2.7	85.4	31.1	1.5E-15
Tubb6	198.9	1775.5	8.9	3.0E-20
Gm15217	0.5	29.6	58.2	2.1E-03
Dcde2a	1.2	25.4	21.0	4.7E-02
Ntm	7.6	60.6	8.0	2.8E-06
Gabbr3	32.2	147.6	4.6	9.4E-11
Nrg3	1.0	42.0	42.0	1.8E-08
Pik3cd	30.6	375.1	12.2	1.0E-27
Pcdhb4	4.0	56.0	14.1	2.2E-09
Caeng8	0.8	33.5	43.1	6.9E-06
Tril	68.6	1926.5	28.1	1.7E-17
Apln	29.6	700.1	23.6	2.2E-49
Numbl	118.4	950.3	8.0	5.7E-27
Duxbl3	36.3	217.6	6.0	2.0E-13
Stab2	3.3	26.5	8.1	3.1E-02
Smardc3	72.2	543.2	7.5	6.9E-20
8430408G22Rik	25.6	226.2	8.8	7.0E-18

Gpr22	19.3	445.1	23.1	2.9E-40	Actc1	2.2	75.5	34.3	3.5E-18
Arpp21	0.7	14.2	19.0	1.6E-03	Rims3	3.3	53.4	16.3	3.1E-09
Zkscan2	27.8	179.0	6.4	1.2E-11	Dzip11	59.4	578.4	9.7	1.9E-28
Vim	1285.1	14949.3	11.6	4.6E-29	Ccdc177	2.5	17.7	7.2	1.4E-03
Abcc9	334.5	8870.1	26.5	3.5E-22	Saa1	0.2	7.6	32.0	4.3E-02
Zfp286	103.5	533.7	5.2	4.9E-17	Dnah7b	9.3	54.8	5.9	1.5E-05
Col5a1	1017.3	18936.5	18.6	1.7E-78	Gbp10	4.0	26.2	6.6	6.6E-04
Nlrp3	1.3	17.4	13.7	2.8E-03	Acap1	21.8	342.8	15.7	7.2E-29
Sparcl1	351.8	7229.6	20.6	8.3E-32	3425401B19Rik	0.3	21.5	79.7	1.9E-02
Igtp	25.8	177.9	6.9	5.3E-08	Nrxn3	3.1	127.0	40.5	2.2E-04
Adarb2	2.5	11.5	4.7	1.7E-02	Mboat2	153.3	669.1	4.4	1.2E-17
Eltld1	8.2	282.0	34.2	3.0E-38	Coro2b	37.1	848.3	22.8	2.5E-14
Fendrr	63.0	2843.3	45.1	2.2E-03	4930578C19Rik	0.3	17.6	70.2	1.1E-04
Gja5	4.4	99.0	22.6	1.6E-05	Dusp2	20.4	246.4	12.1	1.1E-22
Pcdhgc4	739.9	6058.5	8.2	1.7E-11	Tenn2	9.8	184.5	18.9	4.2E-08
Ccl3	3.3	43.2	13.1	5.7E-07	Mdga2	1.0	24.1	24.1	1.5E-04
Kena2	1.3	46.7	36.9	3.3E-11	Pcdhb2	1.7	23.4	13.8	9.8E-05
Pacsin1	12.1	50.1	4.1	5.7E-04	Tbxa2r	13.9	303.8	21.9	6.9E-25
Hnmt	0.5	17.5	35.0	6.8E-06	Kcnmb2	5.2	67.4	12.9	4.7E-08
Col2a1	3.0	88.0	29.2	4.6E-11	Lsp1	211.9	4151.0	19.6	1.9E-26
Rasip1	102.2	1197.8	11.7	6.1E-43	Gng3	47.3	222.4	4.7	3.2E-12
Trpa1	7.2	70.5	9.7	2.9E-06	Map2	83.5	607.0	7.3	1.3E-28
Timp2	295.3	3393.5	11.5	5.9E-47	D430041D05Rik	1.3	10.2	8.1	1.5E-02
Syt1	25.0	658.3	26.3	1.1E-28	A830082K12Rik	1.4	43.1	29.8	1.3E-08
Pgbd5	16.6	254.8	15.3	1.0E-27	Wnt11	2.7	34.7	12.8	7.2E-05
Prtn3	2.2	10.7	4.8	4.0E-02	Fndc1	17.9	580.9	32.5	3.5E-07
Adam11	47.6	233.3	4.9	9.3E-06	Dync1i1	1.2	8.3	6.6	3.4E-02
Pcdha12	19.3	180.3	9.3	5.8E-20	42251	6.9	206.6	30.0	4.6E-15
Meis1	267.5	3016.7	11.3	2.2E-51	Fam171b	16.7	495.8	29.6	2.3E-23
Cd33	9.3	136.3	14.6	5.6E-15	Entpd1	21.6	451.3	20.9	1.9E-40
Epor	13.2	165.4	12.6	2.5E-15	C2cd4d	0.5	11.7	24.0	7.6E-03
Sv2c	4.4	66.6	15.0	8.7E-09	Gpr63	9.2	37.8	4.1	1.1E-02
Obscn	27.9	115.4	4.1	1.1E-05	Lppr5	1.5	96.6	63.6	6.3E-23
Fndc5	3.4	54.5	16.0	3.1E-08	Aard	2.2	26.7	11.9	2.8E-05
Cd244	0.8	8.7	11.4	4.8E-02	Zfp354c	246.8	2097.6	8.5	4.0E-41
Iigp1	7.3	181.8	25.0	2.5E-12	Zfp287	32.1	333.7	10.4	1.1E-21
Trim62	56.3	458.8	8.1	2.1E-10	Gsg11	6.3	150.5	23.9	1.9E-18
Olfml1	11.7	193.3	16.6	9.2E-27	Golga7b	4.2	30.3	7.2	6.1E-06
Klhl8	35.3	230.3	6.5	2.6E-16	Tmem119	114.7	2573.9	22.4	3.1E-54
Mx2	6.0	26.2	4.4	1.5E-02	Tmem8b	82.6	568.4	6.9	1.9E-12
Dclk1	16.6	351.4	21.2	1.6E-39	4930429F24Rik	1.2	18.3	15.0	2.8E-04

Bdh2	10.7	84.0	7.9	1.6E-09
Mettl24	2.5	46.6	18.7	3.8E-07
A930011O12Rik	11.8	392.5	33.2	3.3E-10
Filip11	188.8	1735.1	9.2	2.0E-42
Pcdhb14	6.3	94.1	14.9	1.2E-13
Gm5415	0.5	15.3	32.0	3.8E-03
Pou2f2	7.8	81.8	10.5	1.2E-06
Ccl21c	2.9	35.1	12.0	1.1E-05
Ccdc136	78.0	827.1	10.6	7.5E-36
Cxcr6	3.3	29.5	9.0	1.4E-03
Lynx1	2.8	31.7	11.3	2.6E-05
Gm13629	0.7	9.8	13.1	3.2E-02
Slc45a1	2.9	51.8	17.7	1.7E-09
Akap2	237.9	3685.1	15.5	8.6E-36
Adamts19	12.7	307.2	24.1	3.7E-35
Trpc6	3.2	54.3	16.8	1.0E-10
Has2os	1.7	39.3	23.0	4.4E-07
Soga1	434.9	6150.4	14.1	5.3E-03
Csf3r	2.8	27.9	10.1	8.0E-05
Slc2a3	58.3	757.7	13.0	3.4E-21
Glis3	9.9	125.7	12.8	3.2E-02
Leprel2	127.6	2096.2	16.4	1.0E-34
Nkain2	9.4	54.9	5.8	9.4E-07
Notch3	518.8	3165.8	6.1	1.9E-03
Msr1	12.9	181.9	14.1	7.3E-04
Sepr1	399.3	2030.2	5.1	1.4E-10
Cuedc1	122.7	1345.0	11.0	3.1E-44
Gpr137b-ps	67.2	288.8	4.3	4.0E-11
Pla2r1	2.7	43.3	16.3	2.0E-06
Sox2ot	4.7	52.8	11.3	6.4E-08
Mybph	4.2	56.5	13.5	2.7E-02
Rasgrp2	10.4	251.8	24.2	3.2E-28
Crispld1	6.7	89.1	13.3	2.9E-13
Gpihbp1	21.3	374.7	17.6	3.4E-28
Rtn2	58.4	409.3	7.0	7.7E-23
Ctnnd2	21.6	239.5	11.1	2.6E-20
Gpm6b	81.1	1346.9	16.6	3.1E-56
Mir6992	2.3	18.4	8.0	2.2E-02
Ccdc184	6.0	29.5	4.9	2.3E-04
6030408B16Rik	13.3	265.1	20.0	4.0E-25
Sdk2	13.5	439.6	32.6	1.8E-05
Pcdhga12	744.0	6055.1	8.1	4.7E-12
Agtr2	10.1	87.5	8.7	1.3E-06
Xkr4	8.7	52.3	6.0	2.6E-02
Tcp11l2	56.7	644.8	11.4	1.0E-35
Stmn3	22.3	349.1	15.7	7.5E-21
Fgf5	2.4	19.0	7.8	5.2E-03
Angptl1	91.7	2737.5	29.9	5.6E-19
Gm13889	16.6	441.4	26.6	2.9E-19
Klhl14	1.8	29.7	17.0	1.1E-04
Pgm5	140.5	4184.6	29.8	3.9E-92
Gm2115	3.0	49.8	16.6	2.1E-08
Tceal3	9.0	78.2	8.7	1.7E-11
Adamts5	4.2	91.3	21.8	4.2E-14
Ccdc60	3.9	39.2	9.9	1.2E-05
Fgf13	21.8	481.9	22.1	2.6E-36
Isl2	4.5	139.3	31.1	2.1E-14
Pxdn	1108.1	14285.4	12.9	1.5E-44
Hcls1	33.4	252.8	7.6	2.4E-05
Klhl4	8.9	372.0	41.8	1.0E-32
Grik3	18.5	498.4	26.9	1.1E-10
Trim30d	2.5	29.7	12.0	3.1E-05
Ror1	14.3	567.1	39.6	4.1E-11
Spock3	19.4	318.1	16.4	1.8E-20
Mos	0.7	9.0	12.4	1.3E-02
Amer3	2.2	69.1	30.9	6.6E-11
Sv2a	52.9	482.8	9.1	2.6E-26
Pcdhb8	4.4	52.2	11.7	3.5E-08
Mansc4	5.8	28.8	5.0	1.9E-04
Sat2	33.8	145.4	4.3	5.8E-07
Igfbp7	51.0	1154.0	22.6	6.2E-12
Scn9a	5.9	129.0	21.7	1.5E-22
Adam12	55.7	1038.1	18.7	1.4E-18
Xkr7	1.5	32.8	21.8	7.3E-07
Cybrd1	148.7	964.0	6.5	3.4E-09
Atp2b3	2.7	35.8	13.0	1.5E-06
Lhfp13	0.3	4.1	16.4	2.2E-02
Fam150b	4.5	34.6	7.7	1.2E-05
Slitrk5	20.6	526.7	25.5	1.4E-15
Nsg2	38.2	695.4	18.2	2.7E-50
Cbr3	3.8	30.1	7.9	6.2E-05
Sema3g	23.7	343.4	14.5	1.1E-22

Cdh4	26.8	118.7	4.4	1.5E-06
Hey2	6.9	141.1	20.4	1.9E-21
Lgals1	353.7	5797.2	16.4	1.5E-07
Wnt4	33.2	333.9	10.0	6.8E-19
Cd40	9.3	168.9	18.2	6.7E-20
Cx3cr1	22.0	277.5	12.6	1.9E-26
Frzb	3.7	49.7	13.3	3.7E-07
Csf1	41.8	1070.0	25.6	1.3E-59
Mog	1.2	13.3	10.8	4.1E-02
Csmd3	4.7	104.3	22.1	1.5E-04
Mapk10	11.6	380.0	32.6	5.4E-50
9230102K24Rik	4.4	48.9	11.1	3.5E-06
Al607873	10.0	113.3	11.3	1.9E-12
Ap3b2	10.2	184.4	18.0	2.6E-27
Pde7b	8.9	161.9	18.2	6.2E-20
Duxbl1	21.2	129.0	6.1	3.9E-10
Ypel3	160.4	909.7	5.7	1.8E-23
Fam114a1	92.6	805.8	8.7	3.5E-35
Ppp1r9b	693.4	4028.7	5.8	1.3E-30
Fat4	131.1	8267.5	63.1	7.8E-09
Tlr9	3.1	46.4	15.2	2.3E-04
Thsd1	32.2	241.7	7.5	1.4E-16
Col6a4	511.9	16206.4	31.7	1.2E-22
Disc1	3.6	46.4	12.9	4.1E-02
42250	47.6	1035.0	21.8	1.3E-38
Pcdha5	20.3	176.7	8.7	1.0E-18
Pcdhga3	758.0	6103.7	8.1	2.9E-12
6330409D20Rik	1.2	34.9	29.2	3.5E-04
Plod1	205.4	2410.2	11.7	3.2E-46
Slc2a10	23.2	300.9	13.0	1.9E-23
Dnah7a	3.5	16.3	4.7	4.9E-02
F2r13	12.8	402.2	31.4	4.0E-41
Hand2	96.7	1789.7	18.5	8.2E-67
Plac1	1.5	14.4	9.6	6.7E-04
Iqck	20.6	160.7	7.8	1.9E-14
Ccdc158	8.0	64.8	8.1	3.0E-06
Arl4d	39.3	173.1	4.4	4.2E-11
Dock2	9.9	123.0	12.4	6.6E-14
Tcf15	1.7	38.2	22.0	2.4E-08
Gjd3	1.5	24.0	16.1	1.4E-03
S1pr3	118.2	3028.4	25.6	2.0E-32
Dpp6	4.5	69.7	15.5	1.1E-12
Mamdc2	6.1	145.8	24.1	1.3E-22
Lrrc4c	9.8	245.7	25.1	1.9E-32
Ano1	169.8	1648.7	9.7	3.2E-19
Copg2	1490.4	6724.2	4.5	2.0E-24
Btnl9	9.6	295.1	30.7	6.8E-39
Prickle1	195.5	1280.1	6.5	2.0E-17
Colgalt2	7.8	127.4	16.3	1.3E-18
Fcgrt	192.4	1068.8	5.6	3.9E-25
Npy1r	1.6	19.4	12.2	1.7E-05
Tnfrsf2	34.1	283.2	8.3	7.4E-04
Adarb1	39.6	173.4	4.4	1.7E-06
Nipal4	5.4	59.4	11.0	2.5E-10
Pdlim4	28.4	361.3	12.7	4.7E-31
Peli2	215.4	1141.1	5.3	4.5E-08
Rftn1	9.3	122.5	13.2	2.2E-15
Upp1	15.1	114.5	7.6	6.4E-10
Tgfbli1	128.7	3898.0	30.3	1.9E-55
Oprl1	5.7	93.0	16.3	4.7E-14
Kcne4	23.2	377.1	16.3	4.3E-31
Itga11	61.8	1797.7	29.1	4.6E-44
Zfp300	10.2	83.1	8.1	1.1E-09
Coro1a	44.1	482.9	11.0	1.0E-08
Tgtp1	2.9	23.1	7.9	3.9E-03
Fam26e	0.5	28.2	56.4	3.9E-08
Rasl11b	141.3	973.7	6.9	2.0E-30
Srrm4os	0.7	44.8	60.0	3.5E-02
Klrb1c	1.9	53.8	27.9	1.2E-07
Adamts8	56.0	1318.7	23.5	8.3E-65
Cav2	13.4	298.5	22.3	4.9E-41
Fgf12	1.6	8.5	5.5	2.2E-02
Rab40b	9.9	61.8	6.3	1.9E-07
Syp	77.1	524.5	6.8	5.7E-24
Sema5b	15.2	236.0	15.5	1.6E-12
Adcy1	146.6	615.7	4.2	1.4E-04
Btk	5.5	43.3	7.8	1.8E-05
Rarb	36.2	470.5	13.0	1.2E-35
Gm11747	11.2	244.0	21.9	4.8E-10
Hivep2	245.3	1113.7	4.5	7.7E-04
Col9a2	59.4	1208.1	20.3	1.5E-11
Lrp1	5628.1	23258.5	4.1	1.1E-02

Ccdc106	43.0	277.5	6.5	1.5E-16	Hoxa3	95.5	1101.7	11.5	1.2E-07
4933407L21Rik	0.2	10.8	45.1	3.9E-03	Egflam	66.2	2140.9	32.3	9.8E-79
Gm14005	1.8	24.2	13.8	2.7E-03	Aplnr	31.3	675.5	21.6	9.5E-06
Agt	4.3	60.7	14.2	4.8E-09	Col25a1	42.8	293.4	6.9	3.9E-12
Ephb3	226.8	1398.5	6.2	5.0E-15	5430435G22Rik	5.9	40.2	6.8	7.3E-06
Pcdhgb6	770.1	6271.2	8.1	2.8E-12	Olfml2b	29.1	522.6	17.9	5.3E-21
Colec10	63.1	2468.5	39.1	3.2E-79	Vamp5	9.0	84.9	9.4	9.8E-10
Foxp2	85.3	1529.2	17.9	5.1E-63	Mrc1	30.3	168.3	5.6	5.0E-14
Sphk1	6.1	113.7	18.6	2.9E-13	Hmx2	2.3	44.9	19.7	8.7E-11
Lrrc36	0.5	9.4	18.4	2.2E-02	Nwd2	6.3	109.7	17.3	5.6E-09
Amdhd1	4.8	42.2	8.7	6.4E-05	Odf3l1	0.5	31.5	65.9	3.4E-07
Col9a3	8.4	48.8	5.8	1.3E-04	Foxf2	100.6	3759.7	37.4	1.4E-58
She	14.5	540.5	37.3	1.2E-56	Fcgr1	6.2	76.5	12.4	2.7E-10
Smad9	19.3	948.8	49.1	4.5E-37	Dgki	1.0	47.3	48.0	4.5E-09
Enpp2	24.8	599.0	24.2	3.2E-18	A330076H08Rik	4.0	34.7	8.7	4.3E-04
Parvg	6.0	73.0	12.1	1.1E-09	Pcsk6	79.1	593.0	7.5	3.8E-26
Mfng	52.6	623.0	11.8	1.1E-36	Pcdhb5	6.9	96.0	13.9	3.4E-14
Arhgef3	98.5	709.0	7.2	9.5E-29	Cdk17	291.3	1602.9	5.5	4.3E-28
Ablim3	4.4	140.8	31.8	4.8E-22	Gng2	98.3	2019.9	20.5	2.4E-73
9630013A20Rik	1.5	18.3	12.3	4.5E-03	Csn3	1.7	48.9	28.2	9.5E-09
Pcdhac1	18.1	168.8	9.3	1.8E-19	Hspa12b	33.8	654.5	19.4	3.5E-46
Sox18	21.4	826.5	38.6	3.2E-40	She4	25.8	213.8	8.3	6.6E-19
Cxcl14	2.5	82.5	33.1	4.1E-08	Trim67	10.2	266.5	26.0	1.2E-08
Bach2os	5.1	53.6	10.5	1.4E-02	Cdk5r1	49.5	233.1	4.7	1.3E-12
Nap1l3	13.9	74.8	5.4	6.6E-10	Rarres1	1.8	23.3	13.2	8.6E-05
Tead2	717.1	4549.7	6.3	2.3E-36	Pcdhgc5	732.6	5969.9	8.1	1.9E-11
Zfp128	64.4	287.4	4.5	1.6E-11	Chst3	40.3	922.6	22.9	3.9E-15
Uchl1os	4.2	49.4	11.7	4.3E-08	Pik3ip1	43.0	297.8	6.9	2.0E-19
Stard8	53.6	241.1	4.5	9.5E-11	Fam184b	20.6	324.8	15.8	4.4E-32
Pcdha6	18.1	167.1	9.3	2.2E-19	Dlc1	174.2	3923.2	22.5	2.3E-13
Fcrls	6.7	113.6	17.0	4.2E-19	Gypc	39.8	859.5	21.6	1.3E-53
Podx12	79.8	1530.7	19.2	2.3E-30	Msrb3	64.0	1448.9	22.6	1.5E-69
Lonrf2	40.4	264.1	6.5	2.0E-07	Rspo1	12.6	167.2	13.2	9.5E-19
Sorcs1	12.4	332.5	26.9	1.1E-27	Aph1c	26.3	144.3	5.5	2.0E-07
Tdo2	0.8	29.5	37.9	1.2E-05	St6galnac4	59.8	533.1	8.9	1.0E-25
Ddo	0.2	13.5	56.4	2.4E-03	Nmnat2	5.9	103.9	17.6	8.5E-12
Rgs2	71.9	513.0	7.1	1.7E-10	Rnf150	45.6	684.4	15.0	1.9E-21
Lama4	224.8	6436.4	28.6	7.1E-72	Hspb6	120.0	677.9	5.7	1.6E-11
Ecm2	6.0	69.8	11.7	1.7E-08	Brsk2	15.5	363.0	23.4	1.4E-23
Dennd5a	1009.4	4857.7	4.8	7.9E-27	Kcnn2	3.0	25.5	8.6	2.2E-04
Ccdc109b	2.7	12.1	4.5	3.6E-02	Trpm5	17.1	362.4	21.2	6.3E-18

Kctd17	52.9	1093.9	20.7	5.9E-56	Smtn	355.4	2814.0	7.9	1.2E-37
Prelp	6.6	228.1	34.4	1.7E-08	Fxyd6	59.0	897.4	15.2	2.9E-51
Thsd7b	0.2	28.6	119.5	4.6E-09	Mfhas1	90.6	619.6	6.8	3.1E-08
Dzip1	75.4	940.5	12.5	1.4E-44	Metrn	212.1	1196.2	5.6	7.4E-26
Pcdhb17	23.6	341.5	14.5	8.0E-33	Mcam	437.2	4106.1	9.4	2.1E-27
Nexn	36.0	644.9	17.9	6.8E-15	Syt6	3.6	90.3	24.9	4.0E-16
Angptl2	104.5	2110.7	20.2	1.5E-50	Adcy4	16.3	281.9	17.3	1.6E-25
Thr7	10.2	132.5	13.0	8.0E-17	Sox5	36.5	619.9	17.0	1.5E-10
Col5a2	614.6	11490.2	18.7	2.8E-24	Zfp30	67.4	273.0	4.0	3.0E-12
Itpr1	581.6	2768.5	4.8	4.1E-13	Stk33	0.2	6.0	25.0	1.5E-02
Serp2	8.2	55.4	6.7	3.2E-07	Cav1	45.8	1241.0	27.1	1.0E-76
Trps1	104.2	1732.6	16.6	2.1E-14	DQ267102	0.7	9.4	12.9	3.8E-02
Kcng2	5.1	27.1	5.3	7.3E-03	AB124611	4.6	34.8	7.6	5.7E-03
D730005E14Rik	1.0	10.8	11.3	2.0E-02	Bcl2a1d	2.5	14.8	5.9	3.0E-03
Hvcn1	94.8	605.9	6.4	1.0E-22	Tmtc1	57.6	1372.0	23.8	7.2E-15
Rab39b	29.5	152.4	5.2	2.6E-10	Ptprv	3.9	21.5	5.5	2.8E-02
Mmp2	561.4	15966.8	28.4	2.0E-98	Efs	82.9	1738.0	21.0	5.8E-28
Pecam1	91.4	2216.1	24.2	2.5E-48	Pnma2	12.8	71.3	5.5	5.8E-08
Pcdhgb5	748.0	6050.9	8.1	6.7E-12	Svop	5.2	94.8	18.2	8.6E-18
Arhgap24	21.4	450.1	21.0	1.6E-27	Oprk1	7.2	42.1	5.8	4.0E-02
Gpr153	52.0	1401.5	27.0	4.9E-69	Adamts12	2.4	102.8	42.0	2.6E-16
Ccdc36	9.3	52.6	5.6	7.1E-05	Fabp5	172.6	754.5	4.4	3.6E-10
Amot1	767.8	4869.6	6.3	1.7E-05	Gpr37	0.7	31.1	41.6	4.8E-08
Npr3	58.2	1227.7	21.1	6.5E-12	Leprel1	17.9	486.1	27.1	5.4E-35
2810405F15Rik	0.5	38.7	80.9	1.8E-04	Prrt1	1.0	13.5	13.9	1.5E-02
Scn1a	3.5	56.2	16.2	2.0E-07	Rasa3	143.4	1257.1	8.8	4.6E-37
Cdh13	11.7	144.3	12.3	8.3E-15	Prr33	14.3	518.6	36.4	1.5E-04
Pdpn	44.4	876.0	19.7	6.0E-54	Dlk1	1010.1	14775.1	14.6	2.2E-26
Chst7	6.2	70.9	11.5	1.2E-08	Ntrk1	1.5	16.0	10.9	6.5E-03
Ppp1r14c	5.8	32.7	5.7	2.0E-03	Inpp5d	19.0	276.9	14.5	1.3E-23
Cnksr2	5.9	86.2	14.6	5.1E-05	Pkia	86.5	506.9	5.9	5.6E-14
Ogfr1	41.9	281.5	6.7	4.1E-19	Lbp	6.7	29.7	4.4	4.0E-02
Boc	59.7	1143.0	19.1	1.4E-22	Art3	1.7	17.5	10.4	1.8E-03
Mmrn1	5.1	133.8	26.2	9.3E-17	Mkx	20.2	98.7	4.9	3.4E-06
Dpysl3	367.3	8740.2	23.8	4.4E-74	Ets1	349.3	4805.4	13.8	2.5E-27
Cdo1	11.5	82.6	7.2	4.4E-09	Serpnb8	3.8	32.3	8.6	6.1E-05
Hectd2	27.1	224.7	8.3	4.9E-16	Klhl32	6.2	57.2	9.3	6.9E-08
Htra1	15.5	91.5	5.9	1.2E-07	Cxx1b	159.2	1050.3	6.6	1.8E-26
Il1b	4.1	75.1	18.1	1.9E-09	Scn2b	53.0	222.7	4.2	1.1E-05
Ccdc80	93.8	1646.5	17.5	1.3E-53	Kcnq5	11.1	135.9	12.3	1.8E-16
Clec1a	2.4	150.3	61.6	2.6E-31	Azin2	21.1	213.5	10.1	4.0E-20

Slc10a4	21.2	464.7	21.9	1.4E-42	Zfp41	230.3	1045.5	4.5	2.7E-13
Pdlim3	51.4	1275.8	24.8	2.2E-29	Nhs12	57.3	766.8	13.4	1.2E-03
Magel2	13.0	130.9	10.0	2.9E-12	Kcnc1	6.0	99.8	16.6	3.6E-04
Nfkbie	25.6	104.4	4.1	5.7E-07	Kcna5	15.3	419.5	27.4	3.3E-45
Irf5	20.1	233.4	11.6	8.4E-18	Shank3	66.3	1355.7	20.5	4.7E-03
Ltb	1.5	42.0	28.7	4.9E-07	Slco2b1	6.7	123.9	18.4	7.3E-17
Resp18	3.6	33.3	9.4	6.3E-06	Afap1	365.9	1547.7	4.2	3.0E-03
B3gnt5	26.6	388.9	14.6	4.1E-38	Htr3b	0.5	24.8	51.7	4.9E-08
Hdac7	307.8	1936.2	6.3	2.3E-08	Cadm1	282.7	2562.8	9.1	1.3E-34
Ms4a6d	15.3	146.3	9.6	2.2E-07	Amy2a2	5.7	51.3	9.0	4.5E-02
Fut8	166.3	682.6	4.1	6.7E-17	Unc5a	19.1	118.3	6.2	4.3E-09
Hip1	698.1	4627.7	6.6	1.0E-08	Wnt7b	1.8	17.0	9.4	3.9E-02
Tnnt3	0.2	16.7	69.8	2.6E-04	Sorcs3	2.8	34.4	12.4	2.0E-05
Mir24-1	2.1	20.5	9.9	1.6E-02	Tekt2	28.6	118.4	4.1	7.2E-06
Kcnk13	2.5	20.2	8.2	1.7E-03	Pabpc4l	18.0	338.4	18.8	4.6E-39
Ptrf	449.2	4495.6	10.0	7.0E-53	Emr1	17.9	173.6	9.7	1.6E-21
Nos1	3.0	51.0	17.1	3.0E-03	Vash1	196.4	4387.5	22.3	6.1E-20
Csrnp3	8.4	218.1	26.0	2.2E-20	Hmcn1	16.6	487.8	29.4	4.2E-06
Ms4a7	7.2	98.7	13.8	4.7E-15	Ctxn1	183.9	1352.9	7.4	1.8E-31
Gm5084	1.4	21.2	14.6	1.3E-03	Gpsm1	307.4	1401.3	4.6	3.3E-19
5330439B14Rik	4.3	228.8	52.8	1.9E-05	Icam5	1.0	9.1	9.5	2.9E-02
Anks1b	1.2	21.0	17.2	1.3E-03	Nkx2-3	78.3	2230.0	28.5	5.9E-67
Pcdh18	100.6	3251.7	32.3	5.0E-86	Disp2	55.6	321.1	5.8	8.8E-06
Paqr7	60.1	468.0	7.8	1.7E-14	H2-Aa	1.3	26.0	20.8	5.8E-04
Dact3	102.1	2003.8	19.6	1.7E-24	Dusp1	52.3	398.8	7.6	2.3E-22
Ramp3	20.1	174.3	8.7	6.2E-15	Epha4	208.1	1418.5	6.8	1.6E-30
Dlgap2	4.3	36.4	8.5	4.6E-05	Zc2hc1c	21.3	115.8	5.4	4.4E-08
Gabrb2	19.9	171.3	8.6	3.2E-15	Kcnd3os	0.5	18.5	38.7	6.8E-04
Gm527	30.9	177.7	5.8	6.1E-12	Ppef2	12.3	65.0	5.3	3.2E-03
Pln	0.7	35.9	49.3	1.4E-02	Pcdh9	8.7	315.9	36.2	7.5E-43
Ikbip	206.9	902.5	4.4	3.0E-19	Fosl1	20.7	84.6	4.1	1.7E-04
Arhgap23	103.9	1409.6	13.6	5.4E-10	Alox12	2.3	21.1	9.2	3.2E-03
Gm21119	9.2	171.6	18.6	4.0E-04	Slc22a17	208.6	2055.7	9.9	4.2E-43
Fam110b	154.8	842.8	5.4	2.1E-22	Kit	422.1	2275.9	5.4	7.2E-16
Aatk	23.4	803.4	34.4	1.2E-58	Sacs	3.7	89.9	24.4	2.4E-03
Npr2	35.7	955.5	26.7	4.2E-61	Ehd2	177.9	2440.3	13.7	1.4E-56
Fbll1	1.7	30.6	17.5	1.9E-06	Rims1	4.2	145.2	34.5	3.6E-24
1700001K19Rik	2.3	22.9	10.1	4.1E-03	Mef2c	24.4	597.7	24.5	6.4E-55
Cd248	87.8	2233.8	25.4	9.6E-15	Slc10a6	0.3	14.0	52.0	1.8E-03
Stx11	2.2	31.8	14.3	2.2E-07	Slc25a45	6.9	103.4	14.9	2.4E-13
Gulp1	63.7	322.4	5.1	2.0E-17	Prr18	10.3	66.0	6.4	3.7E-04

Ctsf	129.7	659.7	5.1	4.6E-13
Ncf1	42.3	379.2	9.0	2.3E-10
Pou6f1	73.1	874.2	12.0	5.0E-17
Il23a	2.0	18.0	8.8	4.4E-03
Tshz1	764.1	3153.4	4.1	6.0E-12
Kndc1	1.0	20.9	21.0	3.4E-04
Pirt	17.0	427.3	25.1	5.1E-36
Nrp2	889.9	4250.4	4.8	3.3E-17
Akap12	255.7	6878.0	26.9	7.4E-92
Gsn	328.5	2772.9	8.4	3.0E-11
Prrx1	1.2	17.6	14.1	4.3E-04
Akap6	29.3	1067.9	36.5	9.3E-15
Igfbp6	8.1	58.5	7.2	3.3E-06
Pcsk2	4.6	54.3	11.8	6.4E-09
Chrm2	21.1	654.7	31.0	3.6E-23
1810011H11Rik	5.2	48.9	9.4	1.7E-04
Mapt	71.7	816.5	11.4	9.5E-27
Parp12	73.8	311.1	4.2	1.4E-12
Gnaz	19.8	81.4	4.1	2.2E-05
Col4a2	683.7	18005.9	26.3	2.2E-94
Myzap	13.0	279.6	21.5	7.3E-32
Robo1	137.6	3635.1	26.4	3.4E-49
Fam49a	45.4	831.3	18.3	2.3E-52
Synpo2	179.6	7255.8	40.4	6.8E-23
Jam3	74.1	1201.0	16.2	2.4E-55
Serpina3g	3.8	34.2	9.1	1.5E-04
Nkain3	1.4	42.5	29.6	3.8E-09
Satb1	183.4	1143.8	6.2	9.2E-23
Rgs12	97.2	1366.8	14.1	4.2E-31
Lrrc49	97.5	436.8	4.5	1.9E-16
Lix1l	126.8	2557.3	20.2	1.3E-71
Scarf1	21.8	315.5	14.5	1.5E-29
Nr2f2	312.6	2283.7	7.3	6.5E-08
Nckap1l	42.6	321.7	7.5	6.5E-20
Brinp1	49.9	352.1	7.1	7.3E-22
Prnd	51.3	1777.4	34.6	5.9E-87
Zfp61	104.5	444.7	4.3	3.4E-15
F730043M19Rik	9.7	72.5	7.4	1.3E-06
4930503L19Rik	196.8	862.5	4.4	7.6E-15
D930028M14Rik	5.2	21.0	4.0	2.6E-02
Ttyh1	24.8	302.1	12.2	4.5E-27
Ltbp3	173.1	2680.5	15.5	5.8E-21
Spon1	58.1	720.3	12.4	1.1E-14
Atp1b2	18.5	651.0	35.2	1.2E-06
4933428G20Rik	6.7	59.5	8.9	6.5E-06
Fst	33.9	387.7	11.4	4.1E-06
Mgat5b	7.0	205.3	29.2	2.5E-08
Snph	16.9	321.8	19.0	4.0E-13
Syt4	11.1	361.6	32.4	1.6E-47
Casz1	194.2	1051.3	5.4	2.8E-03
Zfp462	566.1	2381.7	4.2	3.7E-02
Lamc3	2.8	34.0	12.1	5.2E-05
Aif1l	99.3	412.3	4.2	2.8E-14
Slc38a5	7.0	67.7	9.7	1.5E-05
Tmem35	7.6	135.4	17.7	8.4E-23
Zfp366	1.2	56.4	46.7	1.7E-10
Susd2	25.9	167.4	6.5	5.1E-12
Fam180a	2.8	23.5	8.4	5.5E-04
Kcnip2	3.5	30.7	8.8	5.7E-04
Palmd	0.5	19.5	39.0	5.0E-06
Bdnf	6.7	122.9	18.2	1.9E-20
Shank1	27.1	582.8	21.5	3.8E-02
Nlrp1a	1.3	15.6	12.2	9.6E-03
Clqc	49.5	554.5	11.2	4.3E-11
Vwf	8.1	127.4	15.7	2.5E-05
Tmem169	4.6	102.5	22.1	1.6E-21
Cacng1	0.5	8.5	16.6	1.2E-02
Cass4	4.3	46.7	10.8	6.2E-05
Mir351	1.2	12.3	10.1	3.4E-02
Fstl5	13.8	337.3	24.5	1.6E-25
Cacna2d3	1.7	47.5	27.6	1.4E-08
Bmp6	15.3	79.0	5.2	2.5E-07
Lingo2	1.3	14.5	11.5	2.9E-03
2810032G03Rik	0.5	23.2	48.4	3.8E-08
Kif5c	61.8	1685.6	27.3	3.8E-33
Mid2	65.2	480.9	7.4	1.1E-21
Tmeff2	18.9	531.9	28.1	5.8E-44
Nuak1	18.8	146.4	7.8	5.9E-10
Zim1	245.8	1078.6	4.4	3.4E-08
Spi1	14.1	205.0	14.6	2.5E-11
Cdkn1c	877.0	6155.6	7.0	1.4E-20
Epha3	21.7	228.9	10.6	5.3E-06

Timd4	4.0	50.0	12.6	2.7E-03
Mmp14	1358.8	6879.0	5.1	3.2E-29
Triqk	27.7	113.1	4.1	2.4E-08
Ppfia4	36.2	243.0	6.7	9.9E-11
Gm5577	10.7	126.2	11.8	5.3E-12
Fam167b	2.9	67.4	23.5	1.9E-08
B630019K06Rik	31.5	146.5	4.7	4.8E-09
Scube1	31.9	786.1	24.7	7.7E-41
Dkk3	42.6	992.5	23.3	1.9E-42
4930467E23Rik	6.7	98.0	14.6	4.3E-05
Sfrp2	46.2	871.8	18.9	6.9E-16
Chodl	14.8	345.8	23.3	4.2E-22
Hoxa6	2.2	93.1	42.0	3.1E-08
Ccr1	6.0	54.4	9.1	6.5E-09
Pcdh17	34.9	1088.6	31.2	4.4E-14
Basp1	167.8	2045.8	12.2	7.1E-47
Gbp3	6.5	71.7	11.1	2.2E-06
Gpc2	241.6	1030.6	4.3	4.1E-18
Ust	7.5	277.0	37.0	7.5E-38
Rbp1	375.3	1747.9	4.7	7.7E-07
Syt9	41.6	182.0	4.4	2.1E-11
Ccl2	5.7	114.9	20.2	3.9E-16
Foxc2	1.2	11.4	9.5	3.6E-02
Prtg	26.6	155.4	5.9	6.6E-04
Pde1a	20.8	717.9	34.4	9.4E-69
Gm14057	7.8	54.5	7.0	6.3E-04
Vstm4	23.2	980.9	42.2	2.8E-22
Cd52	7.3	56.7	7.8	2.0E-07
Mmp16	91.9	455.5	5.0	1.0E-10
Csf2rb2	4.2	53.3	12.7	3.5E-06
Pam	377.2	4299.3	11.4	1.5E-13
Gm16793	1.4	24.8	17.1	1.1E-04
Tmem200b	5.0	106.6	21.5	1.0E-17
Stab1	131.6	1314.2	10.0	5.7E-40
Steap4	1.8	27.6	15.6	4.8E-06
Syne3	5.1	21.9	4.3	9.0E-03
1700071M16Rik	8.2	119.8	14.6	5.0E-11
Tmem136	66.1	387.2	5.9	5.1E-16
2010111I01Rik	565.2	2498.1	4.4	1.1E-21
Casq2	1.3	21.8	17.3	1.2E-03
Kcna3	1.0	67.3	70.3	7.6E-05
Phyhipl	16.5	182.7	11.1	3.4E-20
Calhm2	12.7	178.0	14.0	1.8E-20
Tspan2	52.5	1061.7	20.2	7.5E-59
Irs1	63.7	1740.7	27.3	2.7E-04
Osr1	51.4	753.8	14.7	1.9E-43
Scn5a	18.3	155.1	8.5	1.1E-07
1500017E21Rik	9.4	99.2	10.5	1.7E-10
Syndig1	7.1	72.5	10.3	1.4E-10
Bend5	48.2	357.0	7.4	1.4E-19
Fbxo41	11.2	79.1	7.1	5.9E-05
Lhfp14	8.8	196.5	22.2	1.5E-32
Lrrtm2	4.4	174.8	39.5	1.3E-19
Esm1	34.6	981.3	28.4	3.0E-27
Slc8a1	96.8	1083.0	11.2	5.2E-29
Pcdhga5	759.1	6033.3	7.9	1.5E-11
Slc13a5	0.5	23.4	46.0	1.2E-05
Elavl3	34.1	799.1	23.4	2.8E-57
Edn3	45.1	572.7	12.7	1.5E-27
Rtn1	38.6	813.8	21.1	8.5E-58
Cxcl5	0.7	35.1	48.1	2.2E-07
Mira	14.1	126.8	9.0	2.7E-07
Nrbp2	202.0	851.5	4.2	7.9E-08
Slc1a2	1.5	26.2	17.0	2.5E-05
Itgal	23.8	198.5	8.3	1.4E-14
Hs3st3b1	43.5	833.2	19.2	2.8E-14
Kank2	529.1	2361.2	4.5	5.7E-12
Syde1	268.7	1604.0	6.0	1.8E-17
Slc24a4	4.4	102.6	23.2	2.8E-13
Fam124b	2.5	44.1	17.8	6.4E-10
Rgma	55.6	1759.8	31.6	1.1E-06
Kcnj8	109.8	2141.8	19.5	6.4E-67
Sliitrk1	2.9	89.1	30.7	6.0E-17
Cxcr4	112.7	2192.3	19.5	4.2E-67
C1qtnf1	69.0	1528.3	22.2	1.9E-07
Rasal3	9.5	66.6	7.0	4.3E-06
Fam155a	6.9	118.0	17.0	3.7E-18
Ptprb	63.0	642.3	10.2	1.8E-10
Hcn4	13.3	109.5	8.2	1.5E-05
Tlr6	0.5	20.8	43.6	1.3E-05
Rnf165	14.4	300.3	20.9	1.7E-04
B3galt5	21.4	195.4	9.1	4.2E-04

Dcn	195.4	4604.2	23.6	5.0E-33	Tcerg11	0.3	8.4	33.5	1.8E-02
Fbxl13	2.8	31.9	11.4	2.2E-04	Sptssb	14.4	99.2	6.9	9.3E-13
Kcnk3	78.4	2605.8	33.2	8.7E-32	Adamts18	3.0	82.4	27.8	8.3E-13
Slit3	54.8	1794.4	32.7	1.2E-12	A430105I19Rik	20.1	312.6	15.5	2.1E-28
Abcg4	13.6	225.3	16.5	2.7E-16	Cadps	71.6	519.1	7.2	2.2E-26
Tgtp2	5.4	44.4	8.2	8.2E-05	Hoxa4	46.8	842.1	18.0	1.2E-21
Il1rap11	0.5	27.1	56.7	1.3E-06	Reln	10.1	91.0	9.0	2.9E-02
Sipa1	360.7	1984.4	5.5	2.5E-25	Il10ra	8.0	108.7	13.6	2.2E-11
Ifi47	6.5	70.7	10.9	3.0E-08	Igln5	20.6	601.3	29.2	4.3E-46
Runx2	7.7	164.2	21.4	4.5E-07	F630028O10Rik	3.5	40.3	11.5	3.7E-05
Rgs6	2.0	18.6	9.1	1.0E-02	Mest	758.1	14656.6	19.3	3.4E-80
Ncam2	12.2	119.8	9.8	4.0E-08	Gm12709	2.3	42.3	18.7	2.0E-07
Adcy2	21.0	522.4	24.9	1.4E-44	Scn2a1	13.3	127.8	9.6	1.1E-12
Inhbb	8.5	182.2	21.4	1.8E-22	Hivep3	10.4	198.3	19.1	3.6E-02
Gpr85	12.8	121.3	9.5	4.0E-14	Gng8	7.3	183.8	25.0	1.7E-16
Cmya5	2.9	76.6	26.4	9.5E-15	Slc26a4	0.3	11.0	43.9	2.3E-03
Abtb2	35.7	309.2	8.6	1.8E-23	Amy2b	1.3	12.6	9.9	4.0E-02
Sgip1	19.2	466.5	24.3	1.5E-46	Ccdc3	55.7	223.7	4.0	6.4E-12
Gpr173	18.8	273.2	14.5	1.1E-11	Cldn10	0.3	23.1	92.1	1.7E-02
Nap112	20.9	159.6	7.6	3.5E-11	Efna5	99.7	1868.1	18.7	5.8E-09
Gm16617	10.7	155.4	14.6	2.8E-05	Caeng7	39.5	1056.5	26.7	4.5E-62
Il16	15.9	239.4	15.0	2.6E-23	C5ar1	10.7	106.1	9.9	5.9E-12
Myo5a	366.1	1703.4	4.7	6.7E-18	Syn2	8.9	62.3	7.0	1.1E-08
Rhbd13	10.4	107.7	10.3	7.0E-15	Mxsl0s	2.0	11.2	5.6	4.7E-03
Ccdc88a	164.6	1619.4	9.8	1.3E-44	9630001P10Rik	1.6	12.1	7.7	8.3E-03
St8sia2	24.2	802.8	33.1	1.1E-13	Scg3	49.6	263.5	5.3	9.0E-10
Otx2	1.0	27.9	29.1	8.9E-05	Chrd11	4.5	250.4	55.6	1.5E-44
Hpgd	61.3	345.8	5.6	5.7E-20	Ifitm1	69.2	1947.7	28.2	1.4E-75
Fam102b	292.0	2081.1	7.1	1.1E-28	Cxcl10	11.4	103.8	9.1	1.6E-09
Aldh1a3	16.6	462.8	27.9	2.3E-30	Nckap51	298.0	1654.5	5.6	7.4E-04
Cldn1	10.4	58.0	5.6	3.4E-06	Nfatc1	44.4	325.0	7.3	3.6E-03
Slc18a3	7.0	256.9	36.5	2.3E-35	Begain	58.4	441.0	7.5	4.5E-05
Fhod3	22.7	444.0	19.6	5.6E-40	Mchr1	0.8	8.1	10.6	8.1E-03
Six4	12.6	99.7	7.9	3.8E-09	A330009N23Rik	6.2	58.6	9.4	1.6E-06
Slc6a17	23.6	106.6	4.5	7.6E-07	Gabrg2	2.0	42.5	21.1	6.5E-07
Ica11	2.0	29.8	15.2	1.9E-05	Gpm6a	15.3	84.0	5.5	1.9E-04
Gm2002	75.1	437.8	5.8	3.2E-20	4930570G19Rik	0.3	17.3	64.1	1.4E-04
Cntn2	3.2	50.2	15.7	4.1E-08	Pnck	16.1	218.1	13.5	2.2E-22
Abca9	4.0	48.8	12.2	1.5E-08	Ank1	6.6	35.8	5.4	3.1E-03
Fbxl7	59.3	982.6	16.6	1.2E-23	Chn1	74.3	540.6	7.3	2.9E-26
Jph4	55.1	517.1	9.4	1.1E-05	Klhl29	28.8	666.3	23.2	2.1E-19

Ncoa7	99.2	440.4	4.4	3.5E-15
Pde1b	24.4	327.7	13.4	1.6E-28
Esam	28.8	915.4	31.8	1.6E-68
Spns2	19.8	197.0	9.9	5.0E-07
Pth1r	73.8	680.5	9.2	1.1E-29
Mmrn2	30.0	1050.7	35.1	5.8E-69
AF251705	3.0	40.7	13.5	2.4E-06
Pdzd4	114.6	912.7	8.0	1.2E-30
Lingo1	7.6	119.3	15.6	3.5E-09
Ache	29.2	311.1	10.7	3.9E-18
Sgk1	35.0	524.7	15.0	1.6E-37
L1cam	105.3	1346.1	12.8	8.3E-27
Slc24a3	40.6	1325.3	32.7	2.2E-72
Lalba	0.3	7.4	27.4	4.3E-02
Adam22	48.8	407.1	8.3	6.1E-20
Lilrb4	9.3	86.8	9.3	4.8E-09
A730046J19Rik	1.2	12.1	9.9	1.1E-02
Ret	119.5	1524.0	12.8	5.2E-30
Cplx2	236.5	1240.6	5.2	4.3E-23
Gal3st3	5.5	80.5	14.6	6.5E-08
Sult5a1	3.7	51.9	14.1	2.1E-08
Unc13c	0.5	11.2	22.0	2.6E-03
Bcl2a1b	1.5	19.8	13.0	7.9E-05
Vip	10.1	246.1	24.4	1.7E-36
Cep85l	11.4	232.6	20.3	4.8E-15
Trim16	143.8	603.2	4.2	2.1E-14
Tceal6	6.0	34.0	5.7	2.4E-04
Gm11837	0.8	20.6	27.1	3.3E-06
Pcdhb7	10.3	128.6	12.5	4.8E-16
Gm10125	0.3	19.7	78.4	4.0E-03
Clec5a	2.7	48.3	17.7	9.0E-08
Cadm2	2.9	32.3	11.1	8.6E-05
Dpysl2	294.4	2060.4	7.0	3.0E-02
Lrrtm4	4.6	79.3	17.1	1.5E-06
Map1b	719.3	7417.2	10.3	2.9E-04
Mir214	6.6	101.6	15.4	1.9E-07
Trim47	19.0	223.9	11.8	5.6E-19
Sphkap	34.1	270.4	7.9	2.9E-16
Cybb	26.7	341.7	12.8	2.3E-28
Gpr65	2.5	14.4	5.7	8.2E-04
Cbln3	8.3	53.5	6.4	1.2E-04
Car5b	2.5	28.0	11.4	4.7E-04
Slc2a6	6.9	27.7	4.0	3.0E-02
Brdt	11.5	118.3	10.3	9.2E-13
St3gal2	149.6	1374.9	9.2	5.1E-29
E130307A14Rik	38.2	169.0	4.4	9.8E-09
Nap115	12.5	195.1	15.6	1.8E-13
Mxd4	180.3	739.3	4.1	1.5E-16
Tie1	54.9	1909.7	34.8	5.6E-39
Zc3h12b	14.3	84.9	5.9	2.3E-02
Des	67.8	1189.2	17.5	4.0E-50
Optc	1.5	41.3	27.8	1.6E-10
Adams2	24.3	812.9	33.5	6.1E-16
Siglec5	0.3	12.0	44.7	7.1E-03
Celf6	5.2	63.2	12.1	7.4E-13
Tspan18	209.0	2978.0	14.2	2.8E-10
Irgm2	44.2	491.5	11.1	1.4E-30
Bdkrb2	6.7	114.4	17.2	1.4E-13
Cntnap4	4.1	115.0	27.8	4.2E-18
Slamf8	0.8	8.8	11.4	4.5E-02
Frmpl1	6.3	139.0	22.2	1.1E-18
Tspyl3	50.0	249.0	5.0	3.9E-12
Lum	294.0	7421.9	25.2	2.0E-37
Cdon	496.0	2918.7	5.9	2.6E-09
Gm10677	17.0	120.3	7.1	1.3E-08
Islr2	14.4	373.7	26.0	1.8E-46
Cd74	14.9	242.1	16.2	7.8E-17
Best1	0.5	10.5	21.9	3.8E-03
Rgs10	13.8	367.7	26.7	1.2E-34
Cend1	3.4	51.4	15.0	4.4E-12
Fam184a	16.1	162.9	10.1	2.6E-16
AA414768	11.1	51.6	4.6	1.6E-05
Hoxb8	36.9	843.0	22.8	1.1E-08
Rasgrp1	2.3	25.7	11.3	4.3E-04
Lrrtm1	11.7	129.9	11.1	6.5E-08
Gm13304	2.9	34.8	12.0	1.3E-05
Klrb1b	4.7	26.4	5.6	4.0E-03
Tub	58.4	1206.2	20.7	9.5E-61
Fam81a	2.5	22.5	9.1	1.4E-03
Pcdhb15	3.7	78.0	21.1	4.7E-03
Tg	1.4	29.3	20.2	2.0E-03
Tubb2a	518.8	2678.7	5.2	1.2E-29

Shd	19.1	286.5	15.0	1.9E-22
Stom	256.0	2300.7	9.0	1.6E-28
Ebf2	2.5	34.9	13.9	5.8E-05
Nefl	15.9	189.2	11.9	7.2E-25
Cd86	3.5	38.1	10.9	6.6E-06
Spon2	26.4	361.6	13.7	1.3E-32
Nnat	175.5	2643.5	15.1	2.5E-39
Dpp10	3.6	58.3	16.2	1.0E-12
Hes5	1.0	7.7	7.8	2.2E-02
Nkd2	9.2	156.0	16.9	2.8E-18
Brinp3	0.2	19.5	81.5	1.3E-05
Cd180	5.0	72.2	14.4	4.5E-12
Limch1	18.8	324.5	17.2	2.7E-23
Ifi2712a	1.2	20.2	16.4	3.4E-05
Il2rg	9.5	117.3	12.3	1.8E-13
Asphd2	15.6	289.8	18.5	1.3E-31
Asic4	10.0	229.1	22.8	9.0E-30
Stac	6.6	72.5	11.0	4.4E-11
Cacna1h	254.2	5272.1	20.7	1.4E-12
Acss1	126.9	683.0	5.4	6.7E-21
Htr2b	4.2	69.1	16.4	9.2E-10
Pdel10a	2.9	110.7	38.0	4.1E-20
Hbb-bt	150.6	1214.7	8.1	3.0E-15
Tacr1	7.3	284.0	39.1	1.4E-20
Tmem252	18.0	485.3	26.9	3.6E-46
Spry4	190.8	1534.1	8.0	3.3E-02
Gramd1a	352.2	3321.9	9.4	3.1E-45
Mafb	25.3	287.4	11.4	4.9E-23
Prokr2	0.3	3.6	13.4	4.7E-02
Ttc28	475.0	3433.0	7.2	1.4E-02
B230312C02Rik	0.8	8.8	10.8	1.7E-02
Rspo2	4.8	190.7	39.9	4.6E-40
Dzank1	17.2	70.2	4.1	2.4E-05
Fam131b	7.0	123.1	17.6	1.3E-18
6720468P15Rik	3.4	46.4	13.9	3.9E-07
Cdh11	352.5	8101.9	23.0	1.4E-24
Flt1	16.7	728.2	43.6	5.9E-27
Mamstr	12.8	116.1	9.0	4.4E-04
Cers1	44.1	305.1	6.9	2.3E-07
Fn1	2205.4	21584.8	9.8	3.1E-09
Cnih2	23.4	237.5	10.1	3.0E-19
Grpr	1.7	39.1	23.4	3.0E-03
Ncan	7.7	198.7	25.8	3.6E-08
Pak3	15.6	146.2	9.3	3.8E-17
Hoxc6	30.7	724.8	23.6	1.6E-07
Klf12	99.8	577.3	5.8	4.6E-04
Lrp3	206.6	943.3	4.6	8.0E-11
Adra1b	1.4	51.2	35.4	3.6E-05
Msantd3	139.1	563.3	4.1	9.0E-16
Dbn1	523.8	4665.3	8.9	5.0E-29
Ankrd50	346.0	2046.5	5.9	8.7E-10
Cpe	374.3	3709.6	9.9	7.6E-18
Col1a1	1413.6	39723.6	28.1	5.3E-23
Nrcam	9.5	138.4	14.6	1.4E-19
Grem2	15.3	830.0	54.1	5.4E-75
Rit2	1.0	14.5	14.8	8.1E-04
Tnr	1.5	109.9	74.4	4.8E-05
Shc3	0.8	8.5	11.0	4.6E-02
Grik1	3.7	50.6	13.8	6.7E-04
Phactr2	181.5	946.5	5.2	1.9E-06
Sdpr	65.4	2073.1	31.7	1.5E-37
Galnt18	28.8	434.9	15.1	1.2E-27
Kcnb2	11.2	134.2	11.9	3.1E-04
Fndc3c1	17.8	514.4	28.9	9.7E-50
Npy2r	2.7	108.5	40.7	4.9E-15
Nab2	101.1	884.9	8.8	6.1E-33
My19	278.4	6816.0	24.5	1.5E-28
Sobp	14.8	349.4	23.7	1.6E-05
Tmem63c	0.7	44.9	61.6	4.6E-10
Sptbn4	6.5	50.4	7.8	1.1E-06
Gm1564	2.3	37.4	16.6	1.2E-05
Jakmip3	1.5	20.0	13.4	2.4E-03
Adamts11	11.2	193.3	17.2	1.9E-13
Runx1	44.5	294.0	6.6	1.2E-03
Gsg1	0.8	11.2	14.5	1.0E-02
Peg13	161.4	939.9	5.8	8.0E-14
Zfp382	14.0	126.3	9.0	4.8E-12
Rhoj	66.1	1137.3	17.2	2.1E-55
Pdgfrb	449.6	8848.6	19.7	8.2E-12
Kcnj12	7.9	159.8	20.2	1.0E-22
Aldh3b1	4.2	24.5	5.8	2.4E-03
Mrc2	151.5	3422.6	22.6	4.3E-64

Coch	1.8	19.2	10.7	3.7E-02
F2r	152.3	2786.3	18.3	2.7E-69
Camk2a	12.3	83.0	6.8	1.4E-07
Slfn5	3.0	34.3	11.5	4.5E-03
Samd14	179.2	1892.1	10.6	1.7E-45
Olfm2	15.3	130.3	8.5	8.5E-12
Pcdha7-g	730.1	5878.4	8.1	1.8E-12
Sardh	23.5	522.4	22.2	1.5E-46
B3gnt9	81.6	484.4	5.9	2.1E-19
Gngt2	5.4	92.2	17.0	7.2E-06
Marveld1	280.2	1354.2	4.8	1.8E-21
Nxf2	1.7	16.0	9.5	4.2E-03
Tgfbr3	317.7	2570.5	8.1	3.0E-08
Gm14207	12.5	95.8	7.7	3.9E-09
A2m	0.5	10.2	20.0	2.5E-02
Fam105a	31.8	236.5	7.4	9.6E-17
Aldh1a7	60.0	374.3	6.2	2.2E-11
Tgfbi	350.2	6230.9	17.8	3.9E-68
42066	6.1	29.4	4.8	1.4E-02
Acvrl1	41.7	1088.0	26.1	3.2E-30
Pygo1	11.6	278.5	24.1	2.6E-16
Tgfb1	110.6	1158.8	10.5	2.8E-11
Mir1668	9.2	85.5	9.3	1.1E-06
Rgs16	14.6	215.5	14.7	1.9E-26
Slc6a11	9.5	100.6	10.6	2.6E-08
Fzd1	240.7	2767.0	11.5	5.7E-52
Zcchc24	156.3	3300.5	21.1	4.4E-44
Myo1b	516.8	3794.2	7.3	1.1E-40
Pianp	8.4	50.4	6.0	1.1E-04
Pde8a	45.3	193.6	4.3	8.9E-09
Prrg3	120.1	1051.1	8.8	3.5E-17
Chrb4	13.8	527.4	38.3	7.8E-28
Itih3	2.0	39.5	19.9	2.3E-06
Alcam	160.5	873.8	5.4	1.3E-16
Pcdhb19	12.0	225.9	18.7	3.3E-27
Col6a6	1.3	62.2	49.5	5.6E-06
Ltbp4	416.4	8293.3	19.9	1.7E-28
Raly1	2.2	38.1	17.1	1.5E-07
Nyap2	0.2	31.1	130.1	4.4E-05
4930511M06Rik	0.5	32.8	68.4	1.0E-03
C1qb	66.0	716.1	10.8	2.2E-08
Cdh6	5.9	122.1	20.8	3.0E-09
Adcyap1r1	75.5	1603.6	21.2	1.7E-20
Emp3	77.8	823.4	10.6	2.7E-30
Prkcq	12.4	194.3	15.7	1.7E-19
Stk32c	1.5	46.9	32.0	5.7E-10
Wscd1	21.0	129.4	6.2	2.7E-10
Hoxd9	1.0	13.1	13.4	7.9E-03
Chrd	24.3	413.4	17.0	6.0E-33
Rspo3	26.9	915.3	34.0	3.2E-62
Pcdhgb1	775.2	6001.9	7.7	1.9E-11
Fam227a	26.8	120.5	4.5	4.8E-06
Nhs	42.5	196.0	4.6	4.5E-05
Amy2a3	5.7	51.6	9.1	4.6E-02
Mpdz	265.4	2168.1	8.2	3.4E-40
Grk5	115.5	477.9	4.1	5.5E-15
Sh3pxd2a	1740.5	8690.3	5.0	1.5E-04
Zfpm2	6.6	215.5	32.8	2.3E-28
Eml1	78.5	1913.6	24.4	2.9E-31
Adamts12	23.5	530.4	22.6	9.9E-15
Cd200r1	2.2	29.1	13.1	9.8E-06
Ptx3	5.5	27.4	5.0	2.4E-03
Fgfr1	276.7	4058.0	14.7	2.2E-61
Ptpn7	7.1	54.9	7.7	1.9E-06
Pkd1	854.1	8472.3	9.9	8.5E-04
Prickle2	67.4	1798.6	26.7	2.9E-18
Fcer1g	31.6	344.1	10.9	3.1E-13
Arhgap6	98.3	597.7	6.1	1.8E-21
Map1a	94.4	1420.4	15.1	1.7E-07
Pdzr4	7.1	159.4	22.4	2.5E-25
Syng3	5.7	87.5	15.4	4.1E-16
Tac2	4.6	42.5	9.3	1.1E-04
Daam2	99.2	2057.7	20.7	1.6E-20
Bai1	4.2	50.7	12.2	4.3E-07
Prune2	42.5	201.1	4.7	1.7E-03
Qpct	10.6	72.1	6.8	4.3E-10
Cpa1	43.4	605.9	14.0	4.4E-02
Maf	122.6	1161.1	9.5	5.9E-40
Hoga1	8.1	40.5	5.0	1.5E-03
Gm16336	0.7	24.2	33.1	8.5E-06
Prkar2b	71.4	938.5	13.1	2.4E-36
Pcdhgb7	754.3	6160.1	8.2	1.5E-11

Tbx2	85.5	1564.8	18.3	2.1E-54
Hba-a2	380.8	3101.3	8.1	7.5E-28
Sox17	5.7	154.2	27.0	1.3E-25
Atp1a3	6.8	210.6	31.1	1.7E-22
Spred3	100.3	613.4	6.1	1.5E-03
Pcdha4	19.0	176.0	9.2	1.7E-19
Tmem178b	1.0	24.9	26.0	1.6E-04
Mpeg1	93.6	1346.6	14.4	4.7E-52
Dclk2	49.5	940.7	19.0	1.1E-21
Cnn2	676.1	3271.5	4.8	3.2E-27
2610305D13Rik	7.2	32.9	4.6	1.8E-04
Glipr2	234.7	1221.7	5.2	1.0E-25
Cd36	24.2	192.0	7.9	1.0E-05
Negr1	12.5	318.5	25.5	4.3E-29
Adora2a	15.8	230.4	14.6	8.9E-24
2900041M22Rik	0.5	9.8	19.2	4.3E-03
Ncf2	33.6	141.9	4.2	1.3E-06
Mapre3	128.2	610.5	4.8	8.4E-15
Bmp4	69.2	1579.8	22.8	3.2E-66
Myo1g	8.1	33.2	4.1	1.2E-03
Zyx	747.7	3300.5	4.4	5.6E-05
Mir143hg	21.3	806.0	37.9	5.6E-04
Mmd	286.0	1171.5	4.1	2.0E-17
Tnfrsf25	6.4	28.8	4.5	2.2E-02
Dlx1	25.8	432.6	16.8	1.3E-40
Lrrc32	34.3	1433.0	41.8	2.2E-12
Bcl2a1a	1.0	8.7	8.9	2.3E-02
Nfia	136.5	3065.2	22.5	1.8E-03
Gem	66.7	1028.6	15.4	1.3E-51
Armc2	1.3	13.5	10.6	1.5E-02
Rab31	315.5	1580.4	5.0	4.6E-24
Purg	83.0	378.9	4.6	2.7E-14
Hba-x	10.9	123.7	11.4	1.7E-07
Ebf1	15.5	280.4	18.1	1.9E-26
Lphn3	45.3	959.4	21.2	1.1E-09
Opcml	16.6	225.5	13.6	1.9E-13
Serpine2	244.1	2481.6	10.2	1.2E-50
Rassf2	67.6	819.0	12.1	2.5E-40
Trim9	5.7	48.6	8.5	2.5E-05
Fam19a1	3.5	165.8	48.0	1.5E-25
Vtn	2.8	20.9	7.5	3.5E-02
Gm2a	90.3	655.8	7.3	2.6E-27
Itga8	85.7	1938.1	22.6	4.5E-72
A430078G23Rik	1.7	37.5	21.6	8.2E-06
Nin	280.2	2322.9	8.3	2.5E-29
Iqsec3	1.3	49.0	38.9	1.9E-11
Magi2	11.0	137.2	12.5	3.5E-16
Clea5	9.7	353.1	36.2	6.7E-39
Tm6sf1	12.5	399.9	32.0	1.1E-49
Rimklb	22.5	360.7	16.0	9.0E-35
Fmn13	564.2	2719.6	4.8	5.7E-25
Col6a1	1347.0	38396.4	28.5	4.3E-101
Zfp521	90.0	941.4	10.5	5.8E-22
Gpr162	30.2	449.9	14.9	3.7E-17
Ren1	0.7	9.2	12.6	4.0E-02
Mirg	72.9	490.4	6.7	3.0E-07
Amigo2	48.5	376.1	7.8	3.1E-19
Ifi205	0.5	6.7	13.8	3.9E-02
Filip1	7.6	238.0	31.3	7.7E-37
Plekho2	77.7	590.2	7.6	2.1E-26
Ms4a4d	0.5	18.9	37.7	1.7E-04
Pdgfra	330.4	10076.2	30.5	1.0E-46
Frm4a	177.1	2971.0	16.8	4.4E-29
C230035I16Rik	9.5	66.2	7.0	3.1E-06
Pcdha4-g	730.3	5885.6	8.1	1.8E-12
Capn6	89.1	1672.8	18.8	1.4E-28
Adm	7.5	104.6	14.0	4.8E-13
9330158H04Rik	0.5	25.9	54.1	7.5E-08
Zfp488	1.7	78.4	46.2	4.4E-04
Enox1	12.8	293.8	22.9	1.1E-33
Nfam1	11.0	156.0	14.2	2.9E-16
Wt1os	1.3	7.3	5.7	2.9E-02
Col13a1	44.6	969.0	21.7	2.6E-06
Col6a5	5.7	106.6	18.8	2.4E-12
Radil	4.8	32.9	6.8	5.6E-04
Setbp1	237.3	2114.7	8.9	2.0E-06
Serpine1	4.0	30.8	7.6	2.1E-03
Kcnk10	1.0	6.6	6.5	2.3E-02
Anxa6	882.7	10869.0	12.3	7.7E-09
Nanos3	5.3	23.8	4.5	3.5E-02
Rian	1875.0	7685.8	4.1	2.5E-22
Pcdhb18	12.9	188.5	14.6	3.1E-10

Dgkb	6.2	142.3	22.9	3.7E-23	Adap2	4.8	39.9	8.3	3.9E-05
Vstm2l	2.0	21.4	10.6	1.6E-04	Itga9	80.7	2541.8	31.5	2.2E-36
Klhl6	17.9	281.3	15.7	3.3E-26	Slc26a7	7.3	65.2	8.9	2.1E-04
Bmp5	21.8	538.9	24.7	1.1E-46	Glp2r	9.2	251.1	27.4	7.4E-17
Tmem145	3.9	108.1	27.5	2.9E-06	Sbspon	14.0	234.6	16.8	5.7E-26
Calb1	0.3	20.8	83.1	5.7E-07	Ctla2a	7.9	124.4	15.8	6.1E-17
Pdzn3	280.8	2076.7	7.4	1.5E-37	Fam131a	42.9	275.7	6.4	3.8E-16
Lyl1	7.8	61.5	7.9	5.5E-07	Nptx2	16.3	279.6	17.2	2.4E-21
Nrsn1	3.4	60.1	17.6	6.7E-13	Slc4a3	227.8	1122.1	4.9	4.7E-20
Sp110	1.2	10.7	8.7	2.0E-02	Gbp8	3.2	39.5	12.5	2.3E-05
Nxph4	6.2	112.7	18.1	3.0E-15	Ncf4	5.6	37.4	6.7	2.6E-04
5430427O19Rik	1.2	9.2	7.6	2.2E-02	Fbln5	50.7	327.8	6.5	1.4E-17
Ptch2	24.8	743.6	30.0	1.3E-09	Unc45b	2.5	74.0	30.1	1.3E-06
Podn	14.9	62.1	4.2	1.3E-02	Anks6	22.4	178.1	8.0	2.8E-14
Cped1	106.1	3140.2	29.6	2.7E-35	Epyc	0.7	12.7	16.9	1.0E-02
Ngfr	66.7	953.9	14.3	1.1E-34	Fli1	28.0	528.0	18.8	1.3E-43
Cald1	338.1	9118.2	27.0	1.3E-86	Camk1g	20.9	319.9	15.3	3.4E-27
Arhgef25	231.9	3017.5	13.0	7.0E-27	Fsd1	34.5	320.8	9.3	3.7E-22
Slc11a1	12.1	121.4	10.1	1.8E-14	Tnfsf12	17.3	278.7	16.1	5.7E-27
Ppp1r3c	11.2	145.2	13.0	1.1E-19	Olfir1033	1.9	31.4	16.3	3.7E-06
Haglr	19.4	268.4	13.8	1.6E-25	Gm13305	64.7	400.4	6.2	6.2E-21
Trpc3	9.8	80.2	8.2	4.0E-07	Hoxa5	80.2	1861.6	23.2	3.7E-74
Ifi203	2.3	16.8	7.4	4.4E-03	Fam65b	6.6	65.8	9.9	2.8E-08
Xlr	0.5	9.2	17.7	1.6E-02	Notch4	58.9	1762.0	29.9	2.1E-28
C3ar1	17.0	186.6	11.0	6.8E-23	Hsd11b1	0.2	6.1	25.4	4.3E-02
Skida1	61.4	395.3	6.4	9.1E-19	Tmcc2	52.8	904.4	17.1	3.4E-50
Csdc2	19.0	289.2	15.2	2.0E-08	Kcnk2	35.9	823.9	23.0	7.2E-15
Pros1	148.2	1180.3	8.0	6.4E-24	Cdh19	7.1	104.7	14.7	1.5E-14
Pde4b	29.7	723.6	24.4	7.5E-41	Prmt8	0.5	9.5	18.7	1.5E-02
Nfasc	70.4	889.7	12.6	2.2E-14	Klf2	5.5	70.1	12.7	2.1E-06
Ahnak	1046.1	10815.6	10.3	2.2E-02	Cdkn2c	19.1	184.7	9.7	5.9E-10
A730036I17Rik	1.2	18.4	15.0	3.6E-03	Nov	4.4	21.9	4.9	1.4E-02
Tyrobp	22.9	270.4	11.8	1.3E-05	Adams17	54.9	454.3	8.3	6.3E-09
Creb3l1	414.9	1703.3	4.1	1.3E-02	Igfbp3	327.4	6115.3	18.7	2.7E-75
Dpysl5	82.4	909.8	11.0	1.3E-18	Carns1	18.0	86.9	4.8	3.1E-04
Tmem204	27.2	470.2	17.3	2.8E-38	Cntn3	7.9	310.2	39.2	3.0E-46
A730017C20Rik	4.6	109.5	23.7	2.2E-21	Cd109	18.4	558.9	30.4	7.6E-23
Arsj	4.2	72.7	17.4	6.2E-09	Pcdhb11	4.7	61.3	13.0	1.5E-09
Tex15	20.4	214.3	10.5	1.1E-17	Fbn2	327.0	9433.5	28.8	1.7E-18
Dnm3	23.1	311.7	13.5	3.0E-16	Cyp7b1	8.8	252.4	28.6	1.3E-35
Arhgap33	92.2	728.6	7.9	1.8E-05	Stat4	2.2	23.4	10.9	8.4E-06

Ramp1	13.8	163.5	11.8	2.1E-18	Ackr3	32.6	1120.9	34.3	4.2E-73
Lrrn2	13.0	244.6	18.9	1.6E-27	Tmem132c	2.7	42.5	15.6	9.3E-05
Samd5	30.7	574.2	18.7	2.0E-13	Khdrbs2	2.0	35.0	17.2	2.1E-07
Lincenc1	2.0	14.9	7.4	5.4E-03	Apc2	71.3	1644.2	23.1	4.3E-10
Ren2	0.7	8.7	12.0	4.9E-02	Slfn5os	0.5	11.0	22.9	2.8E-02
Ctsk	21.3	333.9	15.7	4.6E-14	Hoxa7	7.1	84.1	11.8	1.9E-10
Plau	52.8	1115.6	21.1	2.6E-58	Fam43a	73.2	1031.5	14.1	3.4E-46
Tlr4	7.3	109.5	15.1	1.4E-14	Nnmt	2.0	15.8	7.9	2.9E-02
Ptgir	16.3	400.9	24.6	7.2E-17	Gm7457	1.0	36.9	38.6	3.3E-05
Edaradd	1.2	26.6	21.3	6.5E-06	Syt5	9.8	68.4	7.0	3.8E-09
Mxra8	123.9	2338.8	18.9	3.1E-66	Kcnip1	19.7	448.8	22.8	1.1E-25
Eva1b	100.8	537.9	5.3	6.2E-18	Pcdhga2	780.7	6111.3	7.8	1.7E-11
Smyd1	1.5	20.7	13.6	5.2E-03	P2ry14	1.7	94.0	54.1	4.1E-19
Fgfr2	1238.5	5474.3	4.4	1.8E-23	Olfm1	146.6	1017.8	6.9	2.4E-28
Qk	347.5	3312.1	9.5	3.6E-47	Dlx5	5.5	77.5	14.1	3.4E-10
Fosb	6.0	26.4	4.4	2.4E-02	Tnfaip811	35.3	263.2	7.5	2.1E-20
Chst2	59.0	1238.5	21.0	1.4E-27	Cdh10	9.3	159.2	17.0	3.4E-12
C130030K03Rik	1.0	24.9	25.0	2.3E-05	Pcdha8	18.3	165.3	9.0	6.6E-19
Bean1	5.1	95.4	18.6	7.1E-16	Ano2	0.7	6.1	8.3	4.0E-02
Cdh5	108.7	3754.1	34.5	1.6E-77	Adam23	7.0	159.3	22.9	4.7E-18
Cdk14	206.4	924.4	4.5	5.2E-20	Hoxd8	17.3	263.2	15.2	2.2E-27
Tmem59l	2.9	35.1	11.9	9.2E-07	Ptgs1	35.2	526.4	14.9	6.9E-16
Cdh22	4.0	56.2	14.1	2.0E-02	Map6	9.9	313.6	31.6	3.2E-22
Col18a1	354.7	4336.9	12.2	4.2E-15	Casq1	26.1	544.3	20.9	1.7E-46
A830082N09Rik	22.9	149.1	6.5	1.9E-07	Col8a1	3.4	28.6	8.3	3.6E-04
Grk4	12.4	60.1	4.9	3.4E-04	Ecel1	5.4	51.2	9.5	2.5E-04
H2-Eb1	5.5	23.2	4.2	2.5E-02	Efemp1	13.9	86.0	6.2	1.4E-09
Chst15	120.4	3808.5	31.6	6.1E-41	Astn2	5.6	177.4	31.6	7.7E-29
Slc4a10	19.0	427.4	22.5	2.8E-06	Lgi2	80.9	886.9	11.0	3.6E-37
Ifi44	0.8	9.4	12.2	1.7E-02	Ccl7	0.7	15.5	21.6	1.3E-03
Npas4	1.7	54.3	32.0	2.9E-10	Lrrk2	28.5	268.8	9.4	4.1E-19
Mfap4	221.0	6618.7	30.0	2.7E-80	Igfbp5	4576.7	21820.8	4.8	1.9E-06
Thbs1	232.8	1993.3	8.6	7.5E-18	Bves	16.0	198.9	12.5	2.0E-18
Gpr4	17.5	154.9	8.8	1.4E-05	Fez1	16.8	215.4	12.8	1.2E-10
Ly6h	22.9	289.2	12.6	3.9E-21	Six5	309.2	1630.1	5.3	4.9E-12
Myct1	3.4	223.2	64.8	8.1E-41	Mturn	37.5	641.1	17.1	1.1E-48
Tmem173	102.5	454.4	4.4	5.3E-14	Copz2	19.4	338.2	17.4	4.0E-11
Nsg1	53.9	778.2	14.5	4.9E-49	Tspan9	412.3	4711.8	11.4	3.6E-54
Adamdec1	424.5	12337.6	29.1	4.7E-16	At1l	28.8	137.2	4.8	5.6E-10
H2-DMb2	0.5	7.9	16.5	4.7E-02	Ntng1	6.6	128.4	19.5	3.5E-20
Nrxn2	11.6	254.0	21.8	5.9E-31	Smarca1	145.7	1096.5	7.5	3.9E-19

Tppp	13.6	138.8	10.2	3.9E-16
Fos	22.9	128.2	5.6	1.4E-08
Gm6377	2.0	19.6	9.6	7.6E-03
Chn1os3	15.2	87.6	5.8	2.5E-06
Fcgr3	23.2	220.5	9.5	3.3E-11
Snap91	14.8	364.6	24.6	2.5E-43
Apela	2.5	72.8	28.9	5.4E-13
Scarf2	77.3	1633.3	21.1	3.1E-60
Ramp2	47.9	926.7	19.3	1.8E-50
Akt3	135.3	1672.8	12.4	3.8E-29
Sema3d	19.9	215.8	10.9	9.4E-11
Pcdhb21	5.6	87.0	15.4	3.8E-11
Cmklr1	19.6	455.9	23.3	2.2E-05
Igfbp4	2618.5	14229.2	5.4	3.7E-31
Zfyve28	5.7	75.7	13.3	9.5E-09
Dixdc1	33.1	560.9	16.9	2.3E-43
Sema6c	57.6	803.5	13.9	4.7E-29
Ccm2l	3.7	119.1	32.3	5.2E-18
Fcgr2b	3.7	17.7	4.7	7.2E-03
Mn1	35.1	975.3	27.8	1.2E-03
Ptprm	38.6	1321.5	34.2	1.9E-42
Tcf21	111.0	2685.9	24.2	3.7E-66
Slc5a7	9.0	292.2	32.5	7.1E-43
Adamts6	28.8	575.6	20.0	4.5E-29
Ptgs2	13.2	198.5	15.1	1.8E-21
Col8a2	19.1	317.7	16.7	1.7E-22
Fkbp7	28.9	347.0	12.0	1.5E-19
Sfmbt2	21.3	248.5	11.7	2.4E-09
Cd300a	17.3	145.9	8.4	2.2E-10
Myl1	1.5	44.7	30.0	9.2E-10
Grem1	31.1	1406.1	45.2	4.0E-84
Pcdhga1	762.1	5987.6	7.9	2.0E-12
Elmod1	1.7	14.2	8.5	1.3E-02
Dach1	80.9	710.0	8.8	1.6E-21
Ccr5	1.2	20.8	17.0	4.2E-05
Slc7a2	150.3	661.2	4.4	3.2E-03
Zfp423	21.0	527.5	25.1	2.1E-05
Fat3	16.4	423.9	25.9	8.8E-04
Gbp2	10.9	111.3	10.2	1.1E-05
Phox2a	30.6	443.1	14.5	4.5E-23
Aldh1a1	229.4	3551.2	15.5	3.5E-10
Pcdhb16	10.1	194.6	19.3	2.5E-09
Dner	7.2	126.3	17.5	6.2E-18
Scimp	0.5	12.7	26.6	1.3E-02
Nrep	658.2	8582.4	13.0	1.2E-66
Sntg2	18.2	447.6	24.5	4.9E-34
Chst1	29.1	796.3	27.4	2.9E-16
Dock4	158.5	887.8	5.6	1.4E-12
Slitrk3	2.0	85.1	42.6	1.5E-17
Cyth4	16.2	152.0	9.4	1.7E-15
Sod3	1.0	8.8	8.8	3.3E-02
Sez6	1.5	36.8	25.3	5.5E-07
Syngap1	274.5	1652.1	6.0	8.2E-04
Gm21541	2.9	34.8	12.0	1.3E-05
Pnoc	2.8	41.9	15.1	2.5E-06
Kcnj2	102.3	1058.3	10.3	2.8E-21
Tmem196	0.5	23.6	47.1	1.4E-03
Notum	3.1	13.8	4.5	5.0E-02
Bach2	54.9	1015.9	18.5	1.1E-05
Celsr3	73.9	883.7	12.0	3.6E-10
Lmtk3	268.1	1090.3	4.1	7.8E-05
Rnf112	11.5	110.4	9.6	9.2E-12
Ism1	4.2	101.2	24.3	9.5E-11
Rab12	282.4	1420.0	5.0	1.7E-25
Cygb	49.4	1117.9	22.6	4.6E-61
Upk1b	17.8	71.6	4.0	7.7E-05
Scube3	23.5	204.3	8.7	1.3E-07
Rhov	6.4	26.6	4.1	3.3E-02
Sema3e	8.9	142.5	16.1	4.9E-10
Gja4	10.1	424.7	42.0	4.5E-47
Lrrc19	2.7	15.0	5.5	2.7E-02
E130114P18Rik	1.9	66.8	34.4	9.3E-14
Fam26f	2.3	19.5	8.5	2.3E-03
Dbh	0.5	7.8	15.9	1.2E-02
Nrk	68.5	612.3	8.9	2.8E-10
4833422C13Rik	6.6	122.3	18.5	1.2E-06
Wdr86	14.6	263.8	18.1	6.9E-30
Gucy1b3	142.3	3960.1	27.8	5.4E-64
Antxr1	110.4	2550.1	23.1	1.2E-51
Fam162b	2.9	67.1	23.4	2.3E-10
Dusp27	1.2	25.4	20.7	6.7E-09
Aebp1	123.3	1728.4	14.0	4.4E-52

Pcdhga9	740.9	6051.7	8.2	2.9E-11
C1ql3	16.1	82.7	5.1	1.2E-06
Rgs7bp	11.5	221.7	19.3	3.4E-24
Trpc1	27.9	233.5	8.4	1.1E-18
Rriad1	7.2	36.1	5.0	8.2E-04
Plvap	28.8	587.0	20.4	1.4E-12
2610316D01Rik	1.2	25.9	21.1	8.3E-06
Zfx4	85.8	2648.6	30.9	1.4E-06
Cebpd	51.7	291.2	5.6	2.5E-16
A1593442	0.3	4.4	17.4	3.8E-02
Ppp1r14a	41.9	391.9	9.3	8.1E-10
Hbb-b1	218.0	1625.1	7.5	1.1E-13
Sall1	43.8	1267.9	29.0	5.1E-09
N4bp2l1	26.8	130.1	4.8	5.5E-07
Ehd3	23.5	455.0	19.4	1.3E-37
Glb1l2	5.8	31.1	5.4	1.2E-03
Meis2	136.1	2929.6	21.5	5.1E-74
Cpa4	0.7	25.8	35.9	3.4E-05
Lax1	2.2	18.5	8.3	1.9E-02
Maged1	2991.6	16121.2	5.4	3.8E-33
B3galnt1	21.2	420.0	19.8	1.5E-43
A830018L16Rik	4.2	110.2	26.2	1.7E-18
6030419C18Rik	18.3	276.6	15.1	2.0E-25
Ednrb	305.4	8780.2	28.8	1.9E-43
Lmo2	25.9	662.5	25.6	3.4E-36
Kenh4	0.8	33.8	43.4	7.7E-07
Kcnip3	11.6	204.2	17.6	7.0E-26
Adora1	59.7	371.5	6.2	1.6E-03
Apba1	15.5	286.8	18.5	2.8E-22
Cdkl1	1.7	16.3	9.4	4.1E-03
Clec4n	8.3	129.1	15.6	2.6E-15
Themis2	4.5	79.6	17.7	1.9E-10
Ch25h	4.6	56.4	12.3	1.5E-06
Ly9	1.2	21.0	16.9	1.2E-04
Cd4	2.3	15.4	6.8	1.3E-02
Ppp1r16b	17.9	501.8	28.1	1.2E-20
Jakmip2	5.8	110.6	19.2	2.0E-12
A630075F10Rik	1.0	30.6	31.5	3.0E-02
Trem2	7.1	52.5	7.4	1.2E-07
Tmem179	2.2	48.0	21.3	1.9E-12
Add2	24.4	462.1	18.9	2.3E-26
Tcp1l1l1	79.3	361.0	4.6	2.7E-02
Kcnc2	4.2	86.9	20.6	6.2E-13
Fgd1	278.9	1233.4	4.4	7.4E-10
Gja1	684.9	3047.5	4.4	2.6E-24
Gm10638	8.4	70.8	8.4	2.4E-07
Hoxb4	85.1	1112.5	13.1	1.1E-43
Arc	11.1	112.3	10.1	6.0E-05
Myocd	37.0	1734.2	46.9	9.8E-09
Dact1	106.0	1975.7	18.6	1.0E-64
Cyp2j9	6.9	75.3	10.9	2.9E-09
Tmem47	95.5	1293.0	13.5	1.6E-53
Thbs3	99.2	1118.2	11.3	1.3E-10
Foxs1	2.9	13.9	4.9	1.8E-02
Ajap1	12.4	191.2	15.5	8.6E-20
Col4a6	32.2	508.3	15.8	9.8E-35
Sspn	14.2	320.8	22.5	1.2E-37
Grid2	0.8	19.3	25.4	2.5E-04
Slfn2	12.3	87.3	7.1	6.5E-09
Pdlim7	262.1	2645.2	10.1	2.0E-48
Csf2rb	13.3	172.2	12.9	1.9E-06
Msx1	2.5	16.4	6.6	2.8E-04
Hhex	11.7	68.2	5.8	1.6E-07
Bnc2	41.1	1445.5	35.1	1.8E-05
Lox1l	36.6	553.1	15.1	1.4E-39
Casp12	5.0	155.6	31.2	9.1E-25
Ankfn1	0.2	8.2	34.3	2.9E-02
Gm11627	2.2	37.9	17.3	1.1E-08
Adcy7	56.1	352.6	6.3	2.4E-15
Cxx1c	32.6	405.5	12.5	3.4E-30
Sstr2	2.5	19.6	7.8	7.8E-03
Gsap	4.8	72.8	15.3	1.3E-09
Nlgn1	4.6	91.7	19.9	1.5E-15
Pcyt1b	30.5	140.6	4.6	1.3E-10
Slc16a2	37.5	625.0	16.7	1.4E-10
Acta2	674.1	15717.6	23.3	1.0E-32
Col5a3	12.5	176.8	14.1	2.6E-17
Vegfc	41.9	217.5	5.2	7.5E-11
Bhlhe22	3.1	46.2	15.0	8.4E-08
Ptn	188.6	2899.8	15.4	3.2E-11
Parp3	33.3	213.2	6.4	6.2E-04
P2rx7	7.6	80.8	10.6	4.6E-11

Arhgap36	0.5	23.6	43.8	7.3E-06	Masp1	0.5	33.2	69.3	3.7E-08
Proca1	3.0	30.4	10.1	1.4E-02	Tmem132b	16.1	140.4	8.7	8.8E-04
Grrp1	5.9	112.3	18.9	8.6E-09	Zfp641	17.0	74.6	4.4	3.5E-04
Nell1	4.7	86.6	18.3	5.7E-14	Chst10	11.2	84.7	7.5	8.2E-12
Lox	32.7	800.2	24.4	1.1E-55	Lhfp	57.4	1196.6	20.9	2.2E-54
Psd2	9.6	46.5	4.8	5.2E-04	Stx1b	11.4	240.1	21.0	2.2E-24
Wscd2	6.6	242.4	36.9	5.9E-17	Sncaip	27.7	618.4	22.3	4.8E-54
Trpv2	10.4	127.9	12.4	9.8E-16	Pdp1	138.9	940.0	6.8	5.2E-30
Wasf3	9.1	258.0	28.3	5.4E-14	Gp49a	3.0	33.7	11.0	6.5E-07
Palm2	10.9	447.1	41.0	5.4E-07	Adamts1	207.3	1629.8	7.9	2.0E-31
Gm16897	4.4	111.7	25.2	3.3E-12	Ccdc151	3.8	21.1	5.5	6.2E-03
Nrg1	13.4	479.1	35.7	7.3E-46	Slc38a4	508.1	3441.8	6.8	9.1E-24
Atcay	11.1	184.7	16.6	2.0E-24	Cfh	2.2	43.7	19.8	5.9E-10
Plxnc1	15.1	302.6	20.1	1.7E-30	Siglech	0.3	7.1	28.5	4.7E-02
Evi2b	4.0	46.7	11.8	1.3E-02	Ctxn3	0.7	12.8	17.2	3.3E-03
Plag1	214.6	1174.7	5.5	7.3E-06	Grm7	2.4	30.8	12.7	8.2E-05
Mgp	29.3	548.9	18.7	3.8E-15	Dock10	26.5	601.7	22.7	2.4E-21
Cntfr	48.9	1437.5	29.4	2.2E-23	Cabp1	11.1	53.9	4.9	4.2E-04
Cacna2d1	257.7	2289.4	8.9	1.8E-44	Fbln7	6.9	85.6	12.4	9.2E-11
Sh3kbp1	124.3	1903.8	15.3	3.9E-57	Calcr	4.7	20.7	4.4	4.1E-02
Pcdha2	20.1	169.7	8.4	1.4E-18	Trpc4	5.2	99.3	19.0	1.8E-18
Phldb1	387.6	1956.8	5.0	4.3E-23	3830408C21Rik	16.6	84.6	5.1	1.5E-05
Ccr12	3.3	31.6	9.6	3.2E-05	Slc9a3r2	116.2	1186.0	10.2	4.7E-41
Adamts10	513.1	2802.2	5.5	2.9E-28	Kcnmb4	8.6	117.0	13.6	5.2E-14
Sgcb	74.5	581.5	7.8	4.4E-29	Sp7	2.0	57.1	28.9	8.4E-09
Tlr3	20.6	158.1	7.7	3.0E-13	Twist1	16.5	266.5	16.2	2.4E-25
Wnt2b	22.8	177.9	7.8	2.0E-04	Lmo1	1.8	15.7	8.8	1.8E-02
Aif1	6.6	94.7	14.3	5.3E-04	Col28a1	1.5	47.6	31.6	3.0E-04
Clec4a4	0.5	10.6	21.7	1.0E-02	Stox1	2.5	12.3	4.9	4.3E-02
Pcdhga7	809.8	6111.5	7.5	2.3E-11	Pappa	43.9	1516.7	34.6	8.5E-08
Fmod	3.9	50.9	13.2	8.8E-04	Sh2d3c	110.8	1091.6	9.8	5.2E-37
Gli1	121.1	3807.6	31.4	3.2E-86	Cpne2	20.0	142.4	7.1	2.2E-11
Kif26b	140.7	3042.6	21.6	2.6E-05	Tenc1	229.4	3165.3	13.8	1.2E-14
Kctd15	335.5	1358.4	4.0	1.4E-18	BC028528	8.4	96.4	11.5	3.4E-09
9330182L06Rik	21.1	152.7	7.2	6.0E-12	Camk4	42.5	202.3	4.8	2.5E-06
Itpr12	598.1	2997.5	5.0	2.2E-19	Tnxb	80.3	2103.9	26.2	3.8E-05
Rgs1	1.0	10.4	10.6	2.6E-02	Ccdc88b	21.0	150.2	7.2	1.8E-08
Gli3	173.1	2371.3	13.7	1.1E-10	2610203C20Rik	91.7	2369.4	25.8	2.0E-08
Angpt1	34.9	455.2	13.1	7.2E-16	Ranbp31	38.1	343.6	9.0	1.5E-18
Islr	154.1	4515.1	29.3	7.3E-90	Sez6l	34.2	700.3	20.5	5.0E-07
Nwd1	3.7	57.9	15.5	5.9E-04	Cxcl12	120.8	2520.3	20.9	1.5E-19

Pcdhga4	753.2	6049.8	8.0	3.9E-12
C77370	6.3	56.7	9.0	7.6E-07
Acot7	158.0	750.2	4.7	3.0E-12
Lrrc15	1.0	32.2	33.2	4.9E-05
Cdc42ep3	43.8	502.2	11.5	3.7E-34
Ak5	4.5	26.7	6.0	1.1E-03
Rbfox3	6.1	53.8	8.9	7.4E-07
Axl	771.2	4042.4	5.2	6.0E-29
Ndufa4l2	31.6	205.0	6.5	6.5E-12
Cmtm5	1.2	19.4	16.2	1.4E-04
C1qtnf2	0.5	11.9	23.3	1.7E-04
Slc13a4	2.2	12.4	5.5	2.3E-02
Arsi	7.6	150.4	19.8	6.5E-21
Tmem229a	2.8	135.0	48.5	4.3E-28
Vcan	1309.3	13133.2	10.0	3.3E-15
Ptpro	10.0	119.7	11.9	2.3E-10
Ndst3	2.5	100.8	40.0	4.0E-16
Pcdhb12	4.4	47.3	10.7	6.6E-06
Sfxn4	26.3	106.6	4.1	3.0E-05
D930007P13Rik	1.0	18.3	18.6	1.5E-03
Samsn1	4.2	69.7	16.5	7.3E-11
Gli2	52.5	2065.1	39.3	6.0E-06
Mab21l1	26.4	496.6	18.8	1.2E-44
S1pr1	30.0	689.5	23.0	9.1E-56
Fn3k	6.3	46.1	7.3	6.7E-05
Th	1.7	13.1	7.7	1.3E-02
Plek	12.0	117.2	9.8	5.6E-18
Cacna1e	5.1	205.9	40.0	9.8E-09
Shisa9	1.0	25.7	26.9	6.6E-07
Ankrd6	64.5	286.7	4.4	7.8E-12
Adcy5	44.0	1154.5	26.2	5.3E-29
Cel	8.1	96.8	11.9	3.6E-02
Fut10	55.1	722.5	13.1	1.2E-40
Ms4a6b	12.1	157.0	13.0	1.1E-17
Unc93b1	83.8	379.7	4.5	4.7E-06
Fxyd7	6.0	154.2	25.9	3.8E-21
Ly86	7.3	80.0	11.0	8.3E-10
Cpne4	1.0	16.5	16.8	4.7E-03
Casp1	4.8	34.3	7.2	1.9E-04
9430020K01Rik	99.6	1948.2	19.6	1.2E-43
Dll4	115.5	1413.8	12.2	4.7E-48
Fxyd5	9.6	120.6	12.5	1.2E-05
Tmem132e	7.1	196.6	27.6	2.0E-26
Apbb1ip	4.8	41.8	8.7	1.0E-05
Elovl4	22.0	248.3	11.3	3.9E-25
Gnao1	129.2	1432.7	11.1	9.4E-07
Epha5	2.9	50.3	17.4	1.9E-09
Scrt1	7.0	110.0	15.7	7.8E-07
Ctgf	44.8	288.8	6.4	2.5E-18
Kctd1	48.6	229.0	4.7	1.5E-09
Adamts20	9.3	179.3	19.3	2.0E-11
Klhl38	6.9	118.9	17.4	2.0E-18
Rassf5	18.7	95.0	5.1	8.7E-06
Emilin1	465.6	11914.1	25.6	1.2E-93
Gm266	19.9	286.3	14.4	1.6E-29
Rab37	15.0	108.8	7.3	7.5E-05
Ogn	10.8	209.0	19.4	7.6E-31
Gm11149	6.6	237.9	36.3	2.0E-05
Syt2	3.6	48.4	13.3	8.8E-07
Arhgap28	337.5	2107.0	6.2	9.2E-16
Rbm24	8.0	305.2	38.0	4.7E-37
Gria1	2.0	38.5	19.2	4.9E-07
Ptpre	19.9	313.5	15.8	7.8E-07
Bicc1	75.7	975.8	12.9	1.6E-21
Zfp532	299.7	1837.4	6.1	6.1E-12
Nog	8.6	338.7	39.5	4.2E-33
Nptxr	41.6	384.6	9.2	1.2E-06
Ggt7	20.5	165.6	8.1	1.2E-13
Ndn	181.3	1546.2	8.5	1.4E-42
Clea1	9.0	127.6	14.1	1.7E-13
Lrrc18	1.4	13.3	9.3	1.3E-03
3010001F23Rik	3.5	21.9	6.2	2.9E-03
Svil	1415.2	6574.6	4.6	7.7E-23
Scara3	32.9	423.3	12.9	3.2E-33
Htr2a	0.5	8.3	17.4	2.2E-02
Erich2	0.7	14.8	19.9	1.4E-03
Gria4	14.7	439.9	30.0	6.8E-49
Cacng4	12.7	337.0	26.6	7.2E-24
Emp1	426.9	2989.2	7.0	8.3E-37
E030013I19Rik	4.3	74.3	17.3	5.5E-12
C1qtnf5	6.6	171.2	25.7	6.0E-21
Tmem154	3.9	72.3	18.4	5.4E-11

Pcdhga6	754.1	6052.5	8.0	2.7E-12
Uchl1	117.8	1287.3	10.9	1.8E-21
Cd28	5.3	60.6	11.4	1.2E-07
4930432J09Rik	1.0	14.9	14.9	5.7E-03
Luzp2	3.3	28.2	8.5	1.5E-04
Prdm8	1.2	33.7	27.3	3.2E-03
Car2	40.8	450.6	11.0	4.4E-12
Erg	12.9	492.1	38.2	7.2E-52
Adrb3	1.2	59.0	48.1	6.2E-12
Epas1	30.6	468.2	15.3	5.4E-08
Layn	7.6	47.2	6.2	3.6E-04
Pbx1	502.4	3959.9	7.9	1.8E-17
Meox2	0.5	7.6	15.8	1.3E-02
Rab3c	28.5	260.9	9.1	8.2E-22
Ptpn13	170.8	1109.4	6.5	8.2E-19
Eif4e3	71.3	510.5	7.2	6.0E-23
Hfm1	5.2	45.6	8.8	3.5E-06
Pcdh8	4.9	21.2	4.4	1.6E-02
Ras112	5.2	24.9	4.8	1.1E-02
Lgi3	3.5	68.0	19.6	1.7E-12
Ccr7	0.8	11.0	14.5	9.1E-03
Dscam	1.6	38.9	24.8	2.6E-08
Il11ra2	74.6	434.0	5.8	3.8E-20
Fam171a2	71.8	1367.8	19.0	9.1E-60
Slitrk2	4.9	200.7	41.0	4.6E-29
Col6a3	816.6	22225.2	27.2	1.4E-09
Gm10584	3.3	111.2	33.9	1.3E-16
Pcdhga10	756.3	6075.6	8.0	1.0E-11
Tmem26	25.3	395.6	15.7	2.0E-18
Nlrx1	44.3	222.6	5.0	4.0E-06
Slco5a1	12.6	140.8	11.2	1.3E-13
Gpr123	0.3	5.0	20.1	4.3E-02
Agtr1a	2.5	94.5	38.0	4.1E-07
Grm8	1.7	82.1	47.5	5.6E-17
Parvb	25.5	738.8	28.9	1.3E-10
Gpx7	27.6	327.1	11.9	1.0E-27
Plxnd1	216.7	6108.4	28.2	2.3E-63
Mfap2	202.7	4496.3	22.2	1.5E-61
B930003M22Rik	2.7	30.0	11.2	1.2E-04
Myl4	3.5	26.1	7.4	1.0E-03
Ednra	89.8	2350.6	26.2	5.6E-62
Slc12a5	30.2	274.8	9.1	4.9E-07
Grap	8.1	191.6	23.6	7.0E-26
Cers4	183.9	832.4	4.5	2.9E-18
Tm4sf1	12.6	231.5	18.4	2.1E-25
Mir6244	1.2	17.5	14.1	2.4E-02
Pcsk2os1	0.3	5.4	20.1	4.0E-02
Arhgap31	73.2	1864.3	25.5	1.7E-08
St8sia5	1.2	19.7	16.3	7.7E-04
Stard13	349.8	1523.4	4.4	4.7E-17
Fam198a	7.9	131.7	16.7	4.3E-09
Adam19	131.8	3600.4	27.3	4.9E-28
St8sia6	2.3	17.7	7.7	2.2E-02
Scn3a	43.7	347.2	7.9	2.6E-22
Has2	37.6	1003.0	26.7	5.4E-61
Vps37d	41.4	260.0	6.3	6.2E-16
Efnb3	99.3	1166.6	11.8	1.5E-38
Lbh	499.5	2332.4	4.7	1.3E-22
B230119M05Rik	0.5	16.9	35.3	7.9E-04
Srrm4	24.6	549.8	22.3	8.3E-06
Kctd8	1.6	11.0	6.9	2.1E-02
Nos2	12.5	263.7	21.2	3.2E-27
Adamts15	68.4	1176.2	17.2	8.8E-16
Cpt1c	179.9	1092.6	6.1	8.9E-18
LOC102634401	0.7	7.9	11.0	1.5E-02
Gfod1	20.8	356.5	17.1	4.5E-29
Gm13298	3.5	57.1	16.5	3.4E-05
Sertm1	1.3	27.5	21.4	1.8E-05
Lix1	8.2	176.0	21.4	2.7E-30
Kdelr3	78.2	756.3	9.7	2.7E-33
Prnp	186.5	1594.9	8.6	5.7E-40
Mpped1	0.5	6.2	11.5	3.7E-02
Itm2a	323.3	5764.2	17.8	1.5E-33
LOC102633315	7.1	113.2	15.9	2.6E-04
Sertad4	98.7	1149.9	11.6	2.8E-17
Crb2	32.0	290.5	9.1	9.9E-04
A330033J07Rik	1.5	63.7	41.6	2.0E-10
Zfp811	21.9	271.5	12.4	1.1E-24
Fam20a	2.3	32.4	14.1	3.6E-05
Pcdha7	18.8	168.6	9.0	4.7E-19
Sdc3	218.1	4612.0	21.2	5.2E-20
Thbs2	99.5	4224.5	42.4	1.3E-104

Dio2	1.7	20.4	11.7	1.9E-04
Syt11	239.6	2084.7	8.7	1.0E-36
Rab3b	3.5	46.5	13.2	5.6E-09
Tceal1	36.7	270.0	7.4	2.1E-11
Dmc1	6.0	61.2	10.2	4.3E-07
Apobec3	11.9	139.8	11.7	2.9E-15
Arhgap25	6.4	171.4	26.7	1.5E-25
Kcna6	9.1	341.8	37.6	1.7E-15
Gdf10	22.9	472.6	20.6	8.4E-27
Tifab	10.2	175.2	17.3	6.0E-18
A930012L18Rik	2.5	86.4	34.5	3.8E-03
Batf3	14.5	129.6	8.9	4.0E-11
Dlx1as	15.7	230.6	14.7	5.2E-26
Col23a1	369.3	10733.3	29.1	9.8E-31
Adamts4	24.0	564.7	23.5	4.4E-29
Gm16596	11.4	186.2	16.4	3.6E-20
2210416O15Rik	2.0	37.5	18.8	2.5E-06
Dse	48.7	919.6	18.9	1.9E-55
Plagl1	2037.1	13048.7	6.4	1.2E-27
Aox3	0.2	7.6	32.0	4.4E-02
Dnajc6	6.3	145.7	23.0	2.3E-25
Nlrp5-ps	18.0	137.6	7.7	1.9E-03
Itgb2	3.8	69.4	18.4	1.5E-05
Ifi204	5.3	36.5	6.9	2.2E-05
Tro	114.3	2783.0	24.4	3.1E-31
Foxf1	212.9	7047.1	33.1	1.7E-97
Kcnab2	31.2	251.0	8.0	1.1E-17
Tal1	6.5	85.6	13.1	1.1E-13
Traf5	43.1	389.0	9.0	3.9E-25
Cyp46a1	4.7	62.1	13.1	1.3E-04
Pcdhgb4	761.3	6005.4	7.9	7.3E-12
Eng	109.3	2311.6	21.2	2.4E-12
Penk	39.8	534.8	13.5	1.9E-27
Cntn4	0.5	7.5	15.3	3.7E-02
Cpeb1	2.2	16.5	7.5	7.1E-03
Nrxn1	10.6	118.6	11.1	3.9E-14
Rgmb	320.3	2231.8	7.0	3.0E-19
Reck	89.7	1482.5	16.5	2.1E-41
Gria3	74.5	449.3	6.0	1.0E-17
Gdf6	5.5	146.8	26.9	7.3E-19
Miat	215.5	3756.2	17.4	2.3E-13
Lgr6	1.9	120.5	62.2	8.1E-20
Tmem215	2.2	40.7	18.3	2.2E-08
Hbb-y	58.4	705.2	12.1	1.4E-12
Lrrc7	5.4	198.7	36.5	2.5E-05
Tppp3	17.2	153.3	8.9	2.6E-14
Tslp	1.5	49.6	33.8	2.6E-10
Hgf	48.0	391.3	8.1	1.0E-20
Lzts1	1.8	20.7	11.8	2.2E-04
Dsel	152.8	624.7	4.1	4.1E-17
Lphn1	1801.4	7238.8	4.0	4.9E-03
Fbn1	234.1	7820.7	33.4	1.0E-95
Mrgprf	0.2	60.9	254.7	1.6E-14
Gpbar1	4.6	153.3	33.1	1.5E-05
Tnfrsf11b	78.0	361.4	4.6	2.3E-15
Kcng1	17.1	654.3	38.2	3.7E-09
Ttbk1	6.2	151.9	24.6	3.1E-10
Pcdh10	15.5	271.9	17.6	2.1E-30
Gas1	239.8	6135.4	25.6	2.7E-88
Ttc9b	1.2	36.9	30.1	2.6E-10
Exoc3l4	12.5	158.1	12.6	3.2E-15
Tns1	156.5	4251.5	27.2	4.0E-05
Kcng3	1.2	71.4	58.2	2.6E-05
C030023E24Rik	0.3	12.8	47.5	2.7E-03
Prrt2	61.5	685.3	11.2	4.1E-05
Ngf	2.4	77.3	31.7	9.6E-13
Dlx3	2.3	19.1	8.2	4.3E-03
Clmp	63.8	1890.5	29.6	6.8E-82
9430041J12Rik	0.7	20.0	26.7	4.3E-04
Lrfn5	1.5	38.0	24.7	1.4E-10
Ntsr1	7.8	262.2	33.7	1.8E-23
Pf4	4.0	34.8	8.8	1.4E-06
Gm19461	5.2	87.2	16.8	1.3E-02
Fkbp10	347.8	2911.1	8.4	4.9E-42
Brinp2	2.1	57.0	27.5	1.4E-10
Pcdha9	20.8	180.8	8.7	3.3E-19
Loxl2	332.0	5700.5	17.2	6.7E-30
Chrna5	6.3	91.5	14.4	3.6E-16
Nrsn2	2.4	26.5	10.8	1.3E-05
Hmx3	5.2	95.0	18.3	7.6E-17
Il12rb1	2.8	15.1	5.4	2.1E-02
Atp10a	12.1	166.1	13.7	1.2E-17

Pcolce	81.8	1310.5	16.0	3.2E-31
Wt1	25.5	189.7	7.5	9.1E-14
Inpp4b	17.3	276.4	16.0	1.5E-25
Fam189a1	12.6	101.1	8.0	8.6E-04
Dpysl4	31.8	635.6	20.0	3.3E-49
Gpc6	521.3	3839.8	7.4	3.7E-08
Npr1	17.3	250.7	14.5	8.8E-24
Npnt	309.4	3663.5	11.8	1.3E-57
Pld4	18.7	231.6	12.4	2.2E-22
Kctd12b	19.5	686.6	35.3	1.8E-63
Rapgef3	44.6	323.9	7.3	6.1E-18
Ptch1	804.8	8255.6	10.3	7.3E-04
Zcchc5	6.6	78.7	11.9	1.9E-09
Cd48	3.3	40.4	12.4	3.5E-07
Egr3	5.8	98.6	17.1	3.3E-13
Cemip	9.2	52.0	5.7	1.4E-09
Ccr2	3.5	24.7	7.0	1.4E-03
Sh2d1b1	0.5	8.5	17.4	2.5E-02
Hoxc5	23.6	666.5	28.3	5.5E-35
Srgn	2.0	44.2	21.7	8.2E-09
Wdr54	12.5	74.2	6.0	1.3E-05
Efna2	112.3	656.0	5.8	3.7E-20
Ankrd63	1.7	87.3	50.8	2.0E-13
Psd3	237.5	1119.5	4.7	2.8E-09
Tmem255b	0.5	27.6	55.1	2.4E-06
Chst5	3.5	34.2	9.8	1.2E-05
Sctr	1.5	72.0	49.3	3.5E-06
Parp8	30.3	460.4	15.2	7.8E-35
Gata2	2.4	61.7	25.3	2.9E-10
Wnt9a	13.2	182.9	13.8	3.7E-19
Hspa12a	80.1	455.3	5.7	5.4E-18
Crmp1	113.5	1913.2	16.9	2.5E-61
Gfap	1.2	20.5	16.6	3.8E-04
Tunar	5.5	35.6	6.5	1.4E-03
Adamts9	54.6	1420.2	26.0	5.0E-58
Nav1	1139.5	6552.6	5.8	2.8E-02
42248	16.1	148.9	9.3	5.2E-14
Cd59a	16.2	92.9	5.7	1.8E-08
Gap43	59.8	703.2	11.8	2.6E-46
Gpr156	3.7	49.5	13.4	8.4E-07
2610028E06Rik	1.2	54.8	45.3	4.1E-11
Abca5	77.5	565.2	7.3	3.4E-26
Pld5	0.7	8.6	12.0	1.9E-02
Nrp1	276.9	4224.7	15.3	1.5E-52
Sla	8.3	74.8	9.1	1.8E-09
LOC102636514	26.4	432.2	16.4	9.0E-37
Gm9767	4.2	68.0	16.2	1.6E-10
Itgb8	7.7	130.0	16.9	1.1E-16
Tmem100	30.9	881.3	28.5	5.6E-60
Frem2	629.6	2754.3	4.4	6.3E-04
Ccna1	0.5	6.9	13.6	1.5E-02
Hecw2	5.6	242.2	43.1	3.6E-22
Atp2a3	444.6	2783.3	6.3	6.3E-16
Kdr	66.7	2396.2	35.9	3.1E-81
Lppr1	4.2	38.5	9.1	2.5E-07
Tnfrsf11	0.7	9.5	13.0	2.2E-02
Slc9a9	7.4	62.4	8.4	3.5E-09
Gpc1	605.7	4629.3	7.6	5.8E-40
Tmem74	1.8	32.6	18.6	3.0E-08
Sdc2	324.0	1643.5	5.1	3.7E-27
1700026D08Rik	0.5	10.4	21.3	3.2E-02
Rin3	269.3	1179.3	4.4	5.5E-03
Sema3f	214.7	1883.0	8.8	9.9E-38
St8sia4	25.7	604.8	23.5	3.1E-53
Mical1	192.3	927.5	4.8	3.8E-21
Gpr17	43.1	940.1	21.8	4.1E-45
Il1rl2	14.8	336.3	22.7	9.7E-33
Aspn	13.2	497.9	37.7	9.0E-17
Plxdc2	91.7	935.6	10.2	5.3E-37
Mex3b	84.9	1305.6	15.4	9.0E-53
Mir3074-1	3.6	30.5	8.5	7.5E-03
Pcdh7	55.9	1172.8	21.0	3.8E-43
Galnt16	18.8	276.1	14.7	9.8E-17
Dnah8	3.3	24.2	7.4	1.7E-03
Il1r2	0.7	21.8	29.2	1.0E-05
Apol7b	7.3	41.8	5.7	5.8E-04
Dock9	974.5	6699.8	6.9	2.6E-38
Plcb4	87.8	478.9	5.5	1.1E-09
Robo2	75.5	1650.1	21.8	7.7E-44
Aoah	4.0	45.7	11.6	4.3E-07
Jph3	15.5	180.4	11.7	7.5E-21
Piezo2	50.0	1594.7	31.9	1.5E-18

Ipw	0.7	26.7	36.0	3.3E-05
Man2a2	1302.9	5680.0	4.4	4.8E-16
Lst1	1.7	18.3	10.6	8.6E-04
Mr1	12.1	371.5	30.6	9.5E-41
Igsf10	143.0	3444.7	24.1	2.4E-27
Tlx2	17.2	348.3	20.2	1.3E-38
Wdfy4	7.1	105.7	15.0	1.4E-07
Mcc	73.2	1502.4	20.5	4.4E-06
Klhl34	2.0	24.3	12.1	7.6E-03
Hecw1	2.5	106.5	43.0	1.6E-20
Mt3	1.1	8.7	8.2	1.6E-02
Kctd12	477.1	3208.5	6.7	5.9E-36
B430306N03Rik	1.6	17.0	10.8	1.9E-03
Dkk2	31.0	717.9	23.1	4.8E-40
Zfp583	24.4	121.8	5.0	2.3E-08
Dlgap1	9.8	119.6	12.2	2.1E-15
Maged2	721.5	5459.1	7.6	3.3E-14
Col6a2	1310.4	36168.8	27.6	6.7E-76
Cd1d1	25.6	302.0	11.8	8.3E-29
Col16a1	118.0	2171.6	18.4	4.0E-09
Myh1	0.3	9.2	36.8	9.4E-03
Clec7a	16.9	158.8	9.4	2.1E-10
Slc46a3	12.2	56.7	4.6	1.3E-04
Mtap7d3	3.9	22.7	5.9	1.1E-02
Palld	682.5	2814.3	4.1	1.0E-19
Havcr2	4.2	28.3	6.7	5.1E-03
Magee1	70.2	905.1	12.9	2.7E-42
Pcdhgal1	747.7	6082.7	8.1	9.1E-12
Col12a1	178.6	3827.4	21.4	3.0E-28
Cd97	348.0	3858.7	11.1	5.2E-53
Dtx1	20.7	322.8	15.6	1.8E-29
Myt1	92.2	593.0	6.4	3.9E-18
Cadm4	99.2	482.4	4.9	7.1E-15
Sec24d	406.0	4409.6	10.9	5.1E-51
Amph	8.3	124.9	15.1	1.6E-17
Stc1	61.1	775.3	12.7	5.8E-20
P2ry13	4.0	46.6	11.7	2.7E-05
Gpr116	158.6	1636.7	10.3	1.5E-42
Peg10	225.2	8530.4	37.9	1.3E-16
Mmp9	93.1	1645.5	17.7	2.3E-13
Plxna2	393.1	2441.1	6.2	5.7E-06
Kcnd2	5.1	81.5	16.0	1.0E-14
Msn	223.9	4020.7	18.0	1.5E-71
Fbxl16	57.2	427.7	7.5	1.8E-22
3110035E14Rik	0.3	26.6	98.9	8.5E-03
Mir6935	6.6	35.0	5.3	7.7E-03
Ccbe1	7.3	217.6	29.9	8.3E-33
Dtx4	961.5	5010.8	5.2	2.3E-27
Dnaja4	48.4	237.4	4.9	2.2E-11
Creb5	5.0	131.5	26.3	3.4E-05
Mir199a-2	1.2	24.4	20.2	1.7E-04
Mc5r	0.2	16.8	70.3	2.6E-04
Lamb1	2327.3	14847.5	6.4	2.9E-38
Izkf1	10.6	109.3	10.3	4.0E-11
Dpfl	36.1	254.5	7.0	1.7E-15
Medag	4.2	35.4	8.3	2.2E-06
Tmem44	73.8	388.3	5.3	4.9E-16
Cobl	139.2	1400.5	10.1	8.2E-07
Stac2	1.8	16.5	9.2	2.2E-02
Rbm46	18.7	490.4	26.2	3.9E-19
Egln3	386.7	1640.7	4.2	9.8E-20
Lrrc75b	4.4	81.5	18.5	2.7E-17
Ccl21a	1.2	24.4	20.4	6.5E-05
Tshz2	444.7	4610.0	10.4	7.5E-08
Scg5	45.1	229.2	5.1	4.0E-10
Chst14	114.4	778.0	6.8	6.3E-14
Hbb-b2	150.3	1218.5	8.1	1.9E-15
Art4	3.4	63.2	18.5	3.7E-11
Otogl	4.5	27.4	6.1	2.9E-02
Artn	10.2	147.7	14.5	1.3E-06
Gpr27	7.0	57.9	8.3	4.3E-07
Samd4	89.4	1104.0	12.4	7.9E-14
Sgtb	30.8	235.3	7.6	3.8E-17
Enho	7.6	198.9	26.3	1.4E-29
Vat1l	17.6	397.9	22.7	6.3E-43
Mir1906-1	44.0	255.0	5.8	1.7E-02
Itga7	11.5	95.5	8.3	2.8E-08
Slc7a14	12.0	354.6	29.6	8.8E-18
Col24a1	26.5	977.2	36.9	9.6E-70
9330159F19Rik	13.1	279.3	21.3	1.6E-33
Cdh18	1.3	11.3	9.0	1.1E-02
Igflr	574.8	5472.3	9.5	5.1E-03

Snx32	37.6	178.2	4.7	2.5E-09
Adrb1	2.0	24.7	12.3	3.1E-04
Syt16	1.8	20.9	11.8	1.8E-04
Duxbl2	36.3	217.6	6.0	2.0E-13
Pyroxd2	14.2	87.8	6.2	1.4E-06
Pnliprp1	55.5	671.6	12.1	3.9E-02
Slc16a7	12.0	68.8	5.8	2.5E-06
Ptafr	3.0	36.0	11.9	1.8E-06
Cxx1a	155.2	924.7	6.0	3.2E-24
Gpr68	1.4	20.5	14.1	1.5E-03
Itga5	622.1	5579.9	9.0	2.6E-46
Vstm2a	5.2	58.7	11.2	2.9E-09
Ldlrad4	15.1	407.5	27.1	6.4E-37
Gas7	76.7	1444.5	18.8	1.0E-30
Vwa5b1	0.7	13.0	17.6	1.2E-02
Lrfn2	2.7	68.8	25.3	2.1E-11
Cxcl1	0.2	9.6	40.2	8.5E-03
Snx20	8.2	53.5	6.5	6.4E-06
Popdc2	11.7	278.3	23.7	2.9E-34
Gm11541	1.7	47.1	28.1	6.3E-07
Cacng5	0.3	9.4	37.5	1.4E-02
Ly6e	365.2	1521.7	4.2	2.1E-15
Armcx4	509.3	3869.3	7.6	9.7E-25
Sox8	17.2	334.8	19.4	7.4E-29
Vav1	6.7	95.7	14.2	6.7E-12
Slc16a9	1.5	77.1	50.4	3.1E-15
Evi2a-evi2b	4.7	62.7	13.3	4.9E-03
Zdhhc14	36.7	242.5	6.6	1.5E-13
Speg	157.3	1508.2	9.6	5.5E-08
Panx2	4.3	38.1	8.8	1.9E-04
Mmp25	2.2	90.0	40.8	2.6E-14
Elavl4	75.8	1407.7	18.6	3.0E-58
Zc3h12c	72.5	589.7	8.1	8.2E-17
Cacna1g	160.4	3892.2	24.3	2.3E-13
Ahrr	20.3	86.5	4.3	4.2E-03
Frrs11	3.2	33.6	10.4	2.4E-05
Crtac1	8.8	189.0	21.5	1.4E-22
Zfp467	331.9	1648.1	5.0	2.7E-02
Itih5	53.0	1677.1	31.7	5.8E-54
Gm12295	0.5	15.9	32.4	2.4E-04
Clvs2	3.9	58.7	14.9	3.0E-13
Tmprss5	2.4	44.8	18.4	5.6E-07
Plxna4	30.2	799.2	26.4	1.3E-08
Mmp11	90.2	981.5	10.9	1.3E-40
2510009E07Rik	129.0	1979.8	15.4	1.5E-58
Rgs5	38.7	1528.4	39.5	9.5E-31
Spp1	54.3	368.1	6.8	2.2E-02
Hhip	55.2	1968.1	35.7	3.3E-14
Ccl6	3.9	20.4	5.3	2.1E-03
Rasl10b	12.5	170.6	13.7	9.9E-24
Cntn1	3.5	104.1	29.7	1.1E-20
Arhgdib	16.7	179.2	10.7	9.6E-21
Slit1	14.9	106.0	7.1	5.5E-09
Ptprz1	14.3	453.8	31.8	9.4E-49
Ackr1	2.2	53.3	23.8	7.4E-09
Srgap3	199.6	1136.0	5.7	9.5E-04
Zeb2os	3.5	108.5	31.0	1.7E-19
Dock6	694.6	4147.0	6.0	3.4E-04
Man1c1	36.4	475.6	13.1	8.2E-27
Hdac9	6.5	123.7	18.9	4.4E-11
Fes	24.2	262.9	10.9	9.5E-12
Stxbp6	76.0	345.7	4.5	1.1E-13
Gpr133	1.7	47.0	27.1	3.4E-08
Fgd5	23.9	746.1	31.3	5.5E-59
Col9a1	3.6	155.3	42.9	2.3E-13
Pi15	10.0	166.5	16.7	6.8E-10
Lrm4cl	10.3	59.7	5.8	8.8E-06
Cyp2d22	24.1	549.1	22.8	1.4E-41
Rtn4rl2	9.9	143.6	14.6	1.6E-02
Ptges	10.0	223.5	22.3	2.1E-24
Inpp4a	191.7	818.6	4.3	7.1E-04
Foxo6	14.7	115.4	7.8	2.3E-07
Gm20597	0.5	8.9	18.5	1.3E-02
Tbxas1	2.5	19.5	7.7	4.5E-03
Fam13c	18.5	376.2	20.3	1.5E-37
Schip1	84.3	1193.3	14.2	2.3E-21
Tshz3	55.3	1618.0	29.2	2.7E-09
Was	4.7	45.3	9.6	2.6E-05
Mndal	0.5	9.6	19.2	9.3E-04
Robo4	28.1	1083.4	38.5	2.3E-71
Myh10	1814.1	8005.5	4.4	2.8E-16
Ptchd1	1.5	57.3	38.5	1.4E-16

Nrip3	7.8	34.5	4.4	5.7E-03	Pou3f1	0.8	32.4	42.7	7.5E-07
Kcnt1	5.3	52.5	9.9	1.9E-04	Asap3	86.2	386.1	4.5	7.8E-13
Tram111	27.8	248.7	8.9	3.4E-22	Mill2	1.7	26.2	15.1	1.3E-04
2700069I18Rik	1.0	13.8	13.4	5.1E-03	Tet1	164.0	1341.6	8.2	2.9E-05
Fam212a	24.4	397.1	16.2	3.9E-35	Nptx1	17.0	328.1	19.3	9.2E-07
Slc24a1	0.2	12.7	53.2	8.4E-03	Otof	5.7	296.0	51.7	3.7E-04
Limd2	312.5	1550.0	5.0	1.1E-24	Sez6l2	68.1	499.1	7.3	1.7E-10
Col3a1	3826.6	82206.0	21.5	6.2E-18	Nacad	34.1	430.9	12.6	1.5E-11
Prdm6	7.8	104.3	13.4	1.6E-15	Ntng2	2.5	31.7	12.6	4.3E-04
Gpr126	18.6	295.6	15.9	4.1E-30	Itgb3	20.9	760.1	36.3	2.0E-64
Ccdc13	2.0	27.3	13.8	5.8E-04	St6galnac3	56.9	775.4	13.6	3.1E-42
Lrrc55	11.4	366.4	32.1	1.2E-35	Lcat	4.8	33.9	7.1	9.4E-04
Mgll	82.8	2904.4	35.1	1.5E-93	Gpr20	47.7	844.4	17.7	1.2E-49
Slc6a12	5.9	54.1	9.2	1.5E-05	Kcnmb4os1	3.0	40.9	13.8	2.5E-08
C1qtnf6	77.3	1108.4	14.3	2.8E-48	Figl2	73.2	366.8	5.0	3.8E-02
Il17b	1.0	14.6	15.3	6.9E-04	Igsf6	22.2	134.5	6.1	2.8E-08
Gdf1	46.6	309.4	6.6	3.0E-07	Dlg4	177.9	1515.8	8.5	2.8E-07
Tgfb3	50.6	1317.4	26.0	8.6E-49	Astn1	11.3	347.7	30.7	3.9E-45
Htra3	78.2	2849.2	36.4	5.3E-91	Avpr1a	1.9	71.0	36.9	4.0E-06
Epha10	1.7	33.9	19.8	4.5E-06	Sgce	44.9	750.8	16.7	8.1E-29
Lama2	20.4	869.1	42.6	1.1E-14	Cldn5	26.6	700.4	26.3	1.2E-42
Plcb2	5.7	165.2	29.1	5.4E-14	Hey1	23.4	692.8	29.5	6.8E-61
Rgag1	2.5	82.9	33.3	1.1E-14	Slc15a3	27.8	170.2	6.1	1.1E-10
Ms4a6c	8.7	101.2	11.6	6.7E-14	Dpt	0.8	17.7	22.9	9.5E-05
Prkd1	25.9	509.6	19.7	2.0E-41	Igfbp2	126.4	1372.6	10.9	1.6E-20
Alox5ap	3.5	23.7	6.7	2.4E-03	Scrn1	10.6	71.3	6.7	1.3E-10
Flna	5517.8	40785.7	7.4	4.2E-43	Kcnv1	1.5	26.0	17.7	3.9E-07
Rrad	5.2	45.1	8.6	9.4E-07	Col1a2	1250.3	29205.8	23.4	1.7E-30
Eml5	482.0	2247.0	4.7	8.8E-23	Palm	384.1	1768.7	4.6	2.0E-21
Lpar4	16.9	482.3	28.5	8.0E-50	Sorbs1	169.9	1443.1	8.5	7.6E-29
Ptgis	39.9	574.1	14.4	3.9E-37	Zfp804a	16.4	406.2	24.8	2.1E-27
Srpx2	10.5	630.0	60.0	1.4E-15	Cd53	12.1	147.8	12.2	2.3E-07
Tmem200a	43.3	854.3	19.7	7.9E-54	4632428N05Rik	176.1	734.0	4.2	6.8E-17
Slco3a1	41.7	410.0	9.8	8.3E-27	Gprin2	0.7	14.9	20.1	4.6E-03
Eef1a2	2.9	87.7	29.9	6.9E-18	Gm12250	3.7	26.7	7.3	1.4E-03
Smarca2	428.5	2825.8	6.6	1.8E-35	Pilrb1	0.2	11.6	48.5	5.7E-03
Rarres2	70.3	419.5	6.0	1.2E-05	Gucy1a3	111.6	4068.3	36.4	5.8E-99
Fscn1	782.2	4722.7	6.0	5.6E-20	BC024386	0.2	9.3	38.7	1.7E-02
Itpkb	341.1	2006.9	5.9	2.0E-05	Fam78b	11.8	309.1	26.3	2.8E-14
C1qtnf7	4.9	81.8	16.8	3.1E-14	Abi3bp	15.2	487.8	32.0	7.6E-18
Tspan11	17.0	545.4	32.1	4.2E-42	Gabra2	0.5	17.8	36.4	3.8E-04

Ctnnbp2	100.8	787.5	7.8	1.0E-26
Pard6g	173.5	920.4	5.3	3.5E-22
Pnmal1	15.6	102.6	6.6	8.3E-10
Gbp5	1.8	17.1	9.6	8.6E-03
Bik	7.7	54.6	7.1	9.1E-07
Pde5a	1089.8	4684.5	4.3	2.8E-22
Iffo1	41.3	587.3	14.2	6.3E-36
Dusp26	16.1	321.8	20.0	3.6E-23
S100b	3.3	82.9	25.0	1.1E-13
Kalrn	121.2	1440.0	11.9	2.9E-12
Ecsr	20.5	345.1	16.8	3.1E-34
Flrt2	58.6	794.9	13.6	8.0E-17
Afap1l2	85.2	1837.6	21.6	5.6E-68
Dnaaf3	23.5	112.3	4.8	3.1E-06
Prkcdbp	42.8	686.8	16.0	4.3E-22
Crip2	51.8	855.1	16.5	2.2E-49
Dysf	16.7	556.3	33.3	2.9E-50
Sash3	8.3	59.2	7.2	2.0E-07
Pcdhb3	5.9	61.1	10.3	1.7E-08
Pea15a	487.7	2129.9	4.4	2.1E-23
Gm4980	8.1	87.8	10.8	1.3E-04
Slc6a15	29.3	284.1	9.7	6.1E-25
Ntn1	63.4	2815.6	44.4	4.2E-63
Atxn1	100.3	411.9	4.1	6.3E-03
Caly	2.0	20.7	10.2	7.8E-04
Hoxd3	117.4	1087.6	9.3	4.4E-36
Lmod1	18.6	579.4	31.2	1.6E-58
Celf5	21.9	193.4	8.8	1.6E-07
Nod2	2.8	27.0	9.5	7.5E-04
Car11	30.2	198.0	6.5	1.3E-11
Slc1a3	97.6	410.2	4.2	4.6E-11
Nol4	7.5	93.1	12.4	1.1E-12
Phactr1	10.8	279.2	25.9	1.0E-29
Nova2	31.2	695.8	22.3	2.8E-02
Pcdhb22	19.0	227.7	12.0	9.8E-23
5330434G04Rik	0.3	39.4	146.5	1.0E-02
Sox2	6.9	145.1	21.1	9.1E-16
Hk3	11.4	100.0	8.8	3.1E-03
Foxd3	13.2	191.1	14.5	4.8E-20
Mab21l2	257.5	7267.2	28.2	6.4E-94
Mdgal	11.4	150.7	13.3	5.7E-14
Ntn3	35.4	1157.5	32.7	1.5E-28
Ctla2b	2.7	50.4	19.0	8.1E-11
Cecr6	4.8	37.7	7.9	9.9E-06
Hlf	9.8	189.0	19.3	1.7E-13
Gal	4.0	45.1	11.2	8.6E-05
Fstl1	507.8	10566.3	20.8	2.1E-67
Rerg	61.0	673.3	11.0	1.3E-15
Ptger3	4.4	32.5	7.3	2.7E-04
3110099E03Rik	2.6	13.9	5.4	9.1E-03
Gm8221	22.6	383.4	17.0	1.6E-04
Gpr97	4.3	40.6	9.5	6.6E-05
Itga4	25.7	257.0	10.0	1.2E-19
P2ry12	2.2	45.6	20.5	1.3E-09
Pcp4l1	16.8	493.0	29.4	1.1E-45
Sned1	22.0	327.9	14.9	4.5E-04
Sox4	814.1	3972.4	4.9	6.2E-17
Gm10190	2.8	15.7	5.6	4.5E-02
Ryr2	31.3	367.5	11.7	1.8E-06
Sema6b	46.5	237.9	5.1	1.1E-11
Asb10	1.0	12.6	13.2	5.1E-03
B130024G19Rik	6.9	107.9	15.7	3.0E-12
Myo18b	1.2	33.7	27.9	1.1E-07
Prkg1	35.8	1127.4	31.5	2.2E-73
Apold1	11.6	243.8	21.0	2.5E-21
H2-DMb1	2.5	14.0	5.6	1.7E-02
Runx1t1	48.8	859.7	17.6	1.4E-17
Psd	211.4	2929.0	13.9	1.1E-37
Hoxb5	87.8	1926.0	21.9	4.3E-34
Tsku	82.7	952.3	11.5	5.5E-22
Nox4	41.8	170.5	4.1	9.6E-10
Cd83	12.0	125.9	10.5	2.2E-16
Edil3	16.3	598.0	36.7	9.1E-18
Igsf3	385.2	2750.4	7.1	1.5E-05
Gpsm3	21.6	306.2	14.2	5.7E-11
Nalcn	11.7	267.0	22.8	2.0E-23
Nrg2	1.7	72.4	41.5	4.5E-15
Kcnj3	2.1	10.6	5.2	4.4E-02
Cntnap5a	0.7	17.2	23.5	2.5E-04
Itgam	15.7	132.2	8.4	1.3E-12
Gm15612	31.8	678.2	21.3	4.9E-38
Sfrp1	265.7	12761.9	48.0	1.6E-121

Cep170	437.9	3470.7	7.9	1.4E-35
Colec12	97.8	1858.2	19.0	2.6E-68
Gbp4	5.7	58.9	10.3	6.7E-05
A630001G21Rik	4.5	24.8	5.4	5.4E-03
Nxph3	2.3	19.4	8.5	3.5E-04
Efna3	27.5	192.4	7.0	1.1E-14
Trim30a	5.5	71.9	13.0	6.5E-11
Tmem151a	10.6	113.4	10.7	4.0E-05
Fmn2	16.6	220.7	13.3	7.9E-14
Ube2q1l	1.0	13.7	13.7	7.7E-03
Cd302	40.4	211.8	5.2	1.2E-11
Ankrd34a	3.7	77.9	21.0	1.6E-10
Glt8d2	11.1	136.6	12.3	2.9E-07
Hrct1	1.0	10.8	10.8	2.4E-02
Cnrip1	27.1	421.6	15.6	2.3E-36
Gabra3	3.7	89.6	24.0	5.1E-16
Gm5607	5.7	109.2	19.3	9.0E-13
H2-Oa	0.5	10.0	19.7	1.9E-02
Cilp	3.7	193.6	53.0	1.7E-04
Abcd2	6.6	107.8	16.2	2.4E-18
Lcp2	11.6	179.9	15.6	6.4E-12
Ccdc30	8.5	35.4	4.2	3.6E-03
Il11ra1	118.0	688.9	5.8	1.0E-12
Pla2g7	77.0	936.2	12.2	3.6E-04
Ppp2r2b	9.8	132.1	13.5	3.3E-15
Hspb7	9.0	119.1	13.3	1.2E-20
Ypel4	7.9	126.8	16.0	1.4E-07
Lrrc25	5.6	52.9	9.5	5.5E-07
Fam19a5	16.3	264.6	16.3	1.6E-30
F930015N05Rik	2.7	77.4	28.8	4.4E-10
Syn1	23.1	215.1	9.3	4.9E-08
Phactr3	5.3	108.5	20.6	4.7E-18
Procr	35.9	1152.2	32.1	1.5E-16
Adamts14	5.2	137.0	26.6	1.5E-14
Pcdhb10	2.2	38.2	17.4	3.1E-08
Mylk	592.5	17998.1	30.4	1.7E-101
Tmem255a	29.0	1116.8	38.5	1.4E-29
Lppr4	0.7	12.8	17.8	6.8E-04
Apol10b	1.5	23.6	15.6	1.2E-04
Klh130	1.2	9.5	7.8	2.8E-02
Cdh20	2.0	43.9	21.8	2.9E-09
Cspg4	144.9	3683.6	25.4	3.9E-03
Wbscr17	3.7	71.0	19.1	2.5E-11
Slitrk6	180.5	3225.4	17.9	9.0E-70
Plekho1	87.2	1335.2	15.3	3.1E-22
Lair1	5.2	56.5	10.9	9.2E-08
C920021L13Rik	13.7	112.1	8.2	2.5E-09
Garnl3	69.9	361.3	5.2	1.4E-14
Cpne5	8.8	345.1	39.1	8.0E-19
Bhlhe41	17.8	72.4	4.1	2.5E-04
Tecta	5.7	63.8	11.2	3.1E-08
4933409K07Rik	6.3	68.9	10.9	3.7E-03
Tubb3	140.6	2033.6	14.5	4.0E-62
AI662270	2.5	38.8	15.6	9.2E-07
Syne1	141.9	1839.4	13.0	3.4E-16
Hs3st3a1	6.4	162.8	25.3	8.7E-13
Lrrc17	32.7	1038.1	31.8	6.6E-39
Lrrn1	11.5	338.2	29.5	6.0E-43
Dnah1	17.5	267.9	15.3	6.5E-18
4930426D05Rik	1.5	13.1	8.6	3.4E-02
Kif26a	59.4	1510.6	25.4	7.1E-12
Twist2	5.9	111.1	18.9	2.4E-15
Zfp575	5.3	110.4	20.8	3.4E-10
2010015L04Rik	4.2	58.1	13.7	5.3E-07
Dio3os	1.2	23.3	19.0	2.3E-04
Rnf182	2.3	64.8	28.7	3.7E-11
Gnb3	0.2	13.0	54.5	6.5E-04
Ocstamp	2.8	81.0	29.2	2.1E-03
Gm9899	5.4	142.0	26.2	1.4E-21
C1qa	40.0	565.9	14.2	3.5E-08
Nfatc4	246.0	2894.6	11.8	1.3E-21
Lrrtm3	10.9	260.5	24.0	8.1E-28
Ube2l6	66.7	336.3	5.0	3.1E-15
Plce1	142.3	689.2	4.8	1.8E-15
Tlr13	4.2	53.3	12.6	8.1E-10
Dgkh	44.4	249.6	5.6	3.9E-02
C4b	4.7	44.5	9.5	2.1E-03
4930512B01Rik	18.9	79.8	4.2	1.5E-05
P4ha2	173.5	1049.2	6.0	2.0E-06
Tspyl4	54.7	796.7	14.6	2.2E-47
Dmrt3	0.3	9.0	36.0	5.0E-03
Mras	37.0	320.0	8.7	1.4E-22

Tspan5	144.8	763.3	5.3	2.1E-20
Rdx	294.9	4423.5	15.0	2.3E-43
Mctpl	3.6	24.0	6.7	8.9E-04
2810433D01Rik	0.3	11.7	43.6	2.5E-03
9530077C05Rik	15.9	88.5	5.6	2.8E-06
Anxa5	662.1	3114.3	4.7	6.4E-06
Pdzd2	266.0	1269.7	4.8	2.6E-02
Lrmp	1.5	36.2	24.0	3.9E-07
Dlx2	21.0	371.4	17.6	2.0E-12
Erp27	0.2	11.9	49.9	1.2E-03
Aplp1	266.4	1224.2	4.6	3.9E-22
Rab39	5.0	22.8	4.6	3.1E-03
Ptplad2	10.5	64.9	6.2	4.4E-07
Cyp1b1	13.9	316.5	22.7	2.5E-37
Pald1	429.5	2024.7	4.7	3.3E-23
Snx33	134.3	795.4	5.9	4.8E-06
Diras1	4.0	48.1	12.1	4.3E-07
Mrvi1	59.2	1556.7	26.3	1.8E-64
Asphd1	2.0	16.5	8.1	3.4E-02
Ptpn	48.0	435.9	9.1	2.3E-25
Gab2	266.3	1775.7	6.7	2.5E-09
B3galt2	1.0	47.8	49.9	1.3E-02
Tmem45a	18.4	550.6	29.9	1.6E-15
Ctnna2	31.2	669.7	21.5	1.7E-24
Scel	2.6	14.4	5.5	9.6E-03
Ctss	48.1	505.3	10.5	1.5E-05
Meox1	7.5	127.3	17.1	1.2E-15
Oaf	443.2	2529.4	5.7	5.6E-30
Ppp1r1a	5.0	85.9	17.1	2.8E-13
Ldb2	59.0	1377.0	23.3	3.5E-67
Tnni1	1.0	8.9	9.2	1.2E-02
Tnfaip6	1.2	13.8	11.5	2.9E-03
Sox7	27.7	1395.9	50.4	1.8E-15
Rab38	9.6	52.2	5.4	2.8E-05
Tpbg	95.8	620.2	6.5	1.4E-24
Pcdhgb8	734.7	5944.1	8.1	1.2E-11
Gbgt1	16.9	378.2	22.3	4.3E-12
Nav3	4.4	125.0	28.2	9.3E-11
Ldhb	78.3	721.6	9.2	2.2E-37
Aff2	5.6	114.8	20.4	2.1E-05
Rnf144a	185.4	2148.7	11.6	1.3E-37
Srrm3	6.6	106.3	16.0	4.9E-15
Naalad2	7.3	64.7	8.9	2.5E-08
Cntnap3	14.5	322.5	22.2	3.2E-20
Slc37a2	18.4	149.2	8.1	3.4E-11
Cacnb1	38.8	569.0	14.7	2.3E-36
Fam214b	68.5	332.9	4.9	2.0E-12
Fxyd1	7.1	144.0	20.3	2.2E-05
Mmp13	3.7	69.7	18.9	3.9E-10
Rorb	1.4	10.4	7.2	4.5E-02
Sstr4	1.0	48.6	49.6	6.2E-11
Gm4951	0.7	11.9	16.1	9.5E-03
Fgl2	21.8	222.5	10.2	4.0E-09
Pak7	1.5	41.3	27.2	1.1E-09
Sema5a	336.9	5750.7	17.1	3.8E-08
Trhde	1.2	11.7	9.6	1.1E-02
Ankrd34b	0.5	5.2	10.3	3.4E-02
Bag3	147.6	1436.2	9.7	1.3E-15
Fam210b	129.3	531.4	4.1	5.3E-15
Arl11	4.0	39.4	9.9	2.9E-06
St6galnac5	3.0	24.2	8.1	5.5E-04
Fam101a	2.8	60.4	21.8	1.1E-08
5830432E09Rik	2.3	33.6	14.4	9.5E-03
Col15a1	62.8	2286.7	36.4	2.6E-87
Insrr	2.4	33.4	13.8	1.3E-03
Gbp6	9.4	81.8	8.7	2.0E-07
Mamld1	21.1	110.0	5.2	4.8E-04
Kcnq2	3.6	145.3	39.9	4.5E-08
Gpr137b	36.6	197.8	5.4	3.6E-12
Nid1	392.3	9114.9	23.2	5.5E-85
Fam181b	4.8	61.3	12.8	1.1E-10
Galnt9	1.0	10.8	10.9	4.8E-03
St6gal1	170.0	1053.8	6.2	2.4E-17
Pappa2	0.2	19.4	81.2	8.2E-05
Plscr4	25.5	350.5	13.7	7.5E-30
3830403N18Rik	2.6	19.6	7.7	9.6E-04
Lrrc8c	16.6	389.6	23.5	2.0E-12
Htr3a	3.5	61.1	17.6	4.7E-07
Dpep2	1.2	18.4	14.9	6.6E-04
Fgf1	5.5	47.6	8.6	3.1E-03
Ppm1e	19.5	228.9	11.7	3.8E-23
Timp3	395.7	4973.1	12.6	1.0E-22

Rac2	21.3	243.8	11.5	2.6E-22
Clip3	143.5	3817.2	26.6	6.1E-08
Fzd2	275.5	2990.5	10.9	5.8E-21
Pcdh12	13.4	600.7	44.9	1.4E-65
Chrna7	2.0	29.0	14.7	3.0E-07
Amy2a4	5.7	51.3	9.0	4.5E-02
Svopl	1.3	19.7	14.9	4.8E-02
Pcsk1n	16.0	222.3	13.9	7.2E-26
Cxcr5	4.8	22.9	4.8	1.3E-02
Ahi1	104.8	694.4	6.6	8.3E-25
Gpx8	143.5	846.5	5.9	4.9E-15
Thy1	2.3	36.4	16.1	1.2E-05
Clec14a	5.2	199.3	38.4	1.0E-34
Creb3l2	161.5	1736.3	10.8	2.2E-04
Mir7025	0.7	36.4	49.9	3.7E-05
Tmod2	153.4	982.1	6.4	2.0E-09
Kcp	59.9	1154.7	19.3	1.8E-11
Tcte1	5.0	120.5	24.2	1.2E-11
Mmp19	122.3	591.4	4.8	1.2E-09
Hoxb2	101.2	930.6	9.2	2.2E-35
Synn	20.5	279.1	13.6	1.0E-24
Kirrel3	13.1	179.6	13.7	7.5E-04
Plekhh2	506.8	3744.9	7.4	2.5E-25
Fam163a	21.2	429.5	20.3	9.4E-17
Pde2a	107.6	1428.7	13.3	7.9E-51
Ckap4	562.4	3125.0	5.6	1.7E-29
4930474M22Rik	2.5	29.5	11.8	9.5E-05
Rcn3	234.6	4357.9	18.6	1.8E-14
Kcng4	1.7	40.3	23.6	6.4E-05
Gpr161	50.3	346.9	6.9	6.7E-05
4930447K03Rik	1.5	10.2	6.8	1.8E-02
Megf6	54.6	668.4	12.2	9.7E-16
Npas3	21.9	168.8	7.7	1.1E-05
Reep2	27.7	228.0	8.2	7.9E-18
Rab11fip5	161.8	768.5	4.8	4.9E-14
Vwa1	28.0	525.8	18.8	5.0E-44
C1s1	4.5	49.5	11.0	1.0E-08
Pcdha3	20.8	167.9	8.1	7.1E-18
Tmem200c	3.1	14.0	4.5	2.6E-02
Atp1a2	30.4	647.7	21.3	1.9E-36
Cxcl9	2.5	17.6	7.1	2.0E-02
Heyl	55.3	1390.2	25.1	2.1E-13
Syt15	2.0	12.7	6.4	3.5E-02
Vmn1r90	1.5	23.0	15.3	2.2E-02
Gm13446	4.0	57.7	14.5	2.0E-08
Zeb1	105.3	2554.1	24.2	2.6E-44
AU021063	2.7	20.4	7.5	1.4E-03
Grap2	0.5	9.9	20.2	3.3E-02
Gdap1	17.0	148.9	8.8	5.0E-17
Gpr124	282.0	6864.4	24.3	1.6E-36
Ago4	26.1	222.5	8.5	4.6E-17
Dchs1	335.0	11679.5	34.9	1.7E-05
Larp6	5.7	57.8	10.1	3.1E-09
Cytip	3.2	41.4	12.7	2.0E-05
Rin1	9.9	53.1	5.3	2.4E-05
Gpr183	3.3	95.6	29.1	6.7E-03
Gjc3	2.0	87.7	43.7	2.7E-15
Clec9a	0.7	26.2	36.5	1.8E-06
Ncald	55.7	784.7	14.1	1.5E-41
Gprasp2	77.6	1069.3	13.8	7.3E-50
Adamts13	2.4	129.0	52.8	1.8E-14
Ypel1	61.7	257.1	4.2	1.3E-11
Camta1	155.4	724.6	4.7	5.0E-20
Tnfaip8l2	6.5	67.9	10.4	7.8E-09
Ndst4	1.8	96.9	54.0	2.2E-19
Ssu2	0.5	15.0	30.5	1.6E-04
Pgf	29.3	637.4	21.8	1.6E-49
Sulf1	98.7	1752.9	17.8	4.5E-17
Dennd2a	197.5	2139.5	10.8	2.8E-37
Vasn	370.4	1961.4	5.3	4.3E-06
Gjc1	309.9	1718.3	5.5	2.8E-27
Rab9b	1.2	13.8	11.6	5.2E-04
Scube2	1.5	31.4	21.1	7.1E-07
Cnp	190.6	791.8	4.2	6.4E-18
Kif5a	50.2	1086.4	21.6	8.7E-43
1700025G04Rik	686.7	3235.1	4.7	2.2E-11
Stra6	22.5	414.4	18.4	1.2E-14
Prn	58.0	1818.0	31.4	3.4E-84
Asb2	22.9	598.7	26.2	1.8E-55
Svep1	21.3	1057.2	49.6	8.2E-09
Krt14	13.0	61.1	4.7	8.9E-05
Lepr	1.3	38.8	30.6	6.2E-08

Prex1	232.6	1302.2	5.6	1.5E-16	Lims2	6.6	150.0	22.6	4.2E-19
Hoxb3	126.8	1846.3	14.6	9.5E-55	Crb1	1.3	14.3	10.9	1.1E-02
Hmgn3	54.3	257.0	4.7	5.6E-06	Tpm2	166.2	3484.3	21.0	5.6E-08
Zfp536	8.8	311.0	35.5	4.9E-07	Hapln1	11.6	78.2	6.8	5.3E-13
Pnmal2	77.6	1481.3	19.1	1.6E-59	Zbtb46	17.8	255.0	14.4	5.3E-13
Enc1	690.1	3096.1	4.5	3.2E-19	Gimap6	26.1	651.0	25.0	2.1E-31
Scn3b	15.0	200.0	13.4	2.1E-20	Col11a1	25.3	950.9	37.6	1.2E-28
Selp1g	4.5	28.7	6.4	2.4E-04	Mir1906-2	43.5	253.3	5.8	1.9E-02
Osmr	8.4	213.1	25.3	4.4E-13	Lmo3	4.0	156.4	39.3	1.1E-23
Car3	2.5	44.9	17.8	6.1E-13	Hbb-bs	218.0	1622.6	7.4	1.2E-13

Table S4.1. Genes expressed in E14.5 intestinal epithelial and mesenchyme tissues by mRNA-Seq. Average read counts for genes 2 fold (FC) upregulated in mesenchyme (Mes) when compared to epithelial (Epi) (p-value ≤ 0.05).

Chr	Peak Start	Peak End	Enrichment	LOG P
chr2	10618201	10618402	45.25	163.92
chr13	43791436	43791578	29.97	89.6
chr1	79734413	79734535	29.48	88.49
chr12	3061656	3061799	29.48	93.81
chr17	86824432	86824599	29.48	98.38
chr2	108779130	108779253	29.48	88.16
chr2	150938008	150938138	29.48	98.1
chr3	30640809	30641026	29.48	85.75
chr6	65157495	65157619	29.48	100.23
chr6	86524473	86524616	29.48	82.01
chrX	129100326	129100511	29.48	82.36
chrX	161662873	161662960	29.48	94.27
chr15	33416594	33416686	29.13	101.46
chr7	50575370	50575471	28.42	80.25
chr1	107959856	107959927	28.14	118.51
chr10	8915193	8915293	28.14	110.36
chr2	70619999	70620078	27.79	132.32
chr8	92745420	92745598	27.55	96.99
chr16	66384262	66384407	27.2	89.6
chr10	82514973	82515075	25.79	69.37
chr10	109801734	109801826	25.79	81.6
chr10	117040466	117040562	25.79	69.37
chr11	37571637	37571760	25.79	76.12
chr13	54058547	54058755	25.79	87.77
chr13	59206342	59206498	25.79	67.49
chr14	80450008	80450169	25.79	55.93
chr14	92830897	92831010	25.79	79.24
chr14	110259259	110259422	25.79	87.96
chr14	120757226	120757442	25.79	107.75
chr16	85239133	85239234	25.79	69.37
chr17	9684635	9684816	25.79	72.54
chr17	54210943	54211064	25.79	76.72
chr18	19446697	19446880	25.79	72.11
chr18	32921985	32922073	25.79	81.6
chr19	21294497	21294631	25.79	96.73
chr19	33361154	33361382	25.79	73.24
chr19	45168315	45168415	25.79	69.37
chr2	78201905	78202120	25.79	119.37

chr2	117256751	117256840	25.79	81.6
chr2	144170647	144170757	25.79	80.23
chr3	143585765	143585892	25.79	74.95
chr4	9421198	9421300	25.79	69.37
chr4	12247073	12247286	25.79	86.64
chr4	13854435	13854671	25.79	71.76
chr4	23066032	23066162	25.79	74.1
chr4	60991172	60991253	25.79	94.27
chr4	112600137	112600259	25.79	76.42
chr4	130779237	130779363	25.79	75.24
chr4	143601042	143601189	25.79	69.63
chr5	29205165	29205296	25.79	73.82
chr5	47548981	47549159	25.79	95.28
chr5	125071963	125072062	25.79	69.37
chr6	11698665	11698820	25.79	90.2
chr6	72756976	72757095	25.79	77.33
chr6	83729069	83729174	25.79	81.6
chr7	97840989	97841088	25.79	69.37
chr7	101458950	101459052	25.79	69.37
chr7	145456762	145456858	25.79	69.37
chr8	15680782	15680926	25.79	70.38
chr8	86383139	86383323	25.79	128.87
chr8	103984972	103985066	25.79	69.37
chr8	116126816	116126969	25.79	79.28
chr8	121371046	121371170	25.79	75.82
chr9	24706523	24706614	25.79	81.6
chrX	18087719	18087832	25.79	79.24
chrX	48789864	48789966	25.79	69.37
chrX	55918512	55918606	25.79	69.37
chrX	89101814	89101951	25.79	72.19
chrX	115524203	115524318	25.79	78.59
chrX	138269822	138269960	25.79	71.92
chrX	161195340	161195456	25.79	78.27
chr3	148461827	148461980	25.12	67.23
chr7	23770561	23770712	24.79	67.23
chr1	39148413	39148486	24.62	105.25
chr1	149928854	149929061	24.62	65.42
chr14	112248657	112248757	24.62	67.86
chr17	5864718	5864820	24.62	67.86
chr17	52613440	52613536	24.62	67.86

chr3	111494363	111494467	24.62	79.89
chr4	56448273	56448458	24.62	69.84
chr5	86981683	86981886	24.62	66.18
chr4	60094570	60094802	24.35	77.28
chr2	89114849	89114997	24.3	78.21
chr7	138638183	138638331	24.3	89.6
chr15	71420336	71420532	24.13	76.91
chr7	24477695	24477788	23.99	106.52
chr5	37353868	37354012	23.64	67.23
chr7	39350780	39351005	23.45	89.85
chr9	94727301	94727458	23.45	74.42
chr7	16007756	16007858	23.23	65.97
chr6	13721083	13721177	23.15	65.85
chr1	109957786	109957972	22.9	76.91
chr1	7985417	7985599	22.41	66.77
chr9	12025331	12025422	22.41	76.42
chr6	139775888	139775979	22.39	76.38
chrX	120870194	120870296	22.39	64.77
chr3	78576013	78576171	22.23	66.77
chr1	16729772	16729904	22.11	85.27
chr1	19678020	19678209	22.11	70.83
chr1	26529999	26530142	22.11	59.7
chr1	30760454	30760591	22.11	61.07
chr1	48796796	48796996	22.11	68.59
chr1	61555000	61555146	22.11	69.88
chr1	68520230	68520369	22.11	60.6
chr1	72173461	72173617	22.11	56.93
chr1	74290175	74290288	22.11	79.24
chr1	77479332	77479561	22.11	83.19
chr1	101083462	101083626	22.11	76.49
chr1	108745760	108745982	22.11	74.4
chr1	113528090	113528212	22.11	64.8
chr1	115700573	115700696	22.11	64.54
chr1	117512575	117512714	22.11	60.6
chr1	140730198	140730310	22.11	67.58
chr1	143929422	143929553	22.11	73.82
chr1	153309187	153309311	22.11	75.82
chr1	162569025	162569212	22.11	71.25
chr1	168400843	168401035	22.11	80.72
chr10	11513344	11513480	22.11	72.45

chr10	22138577	22138794	22.11	75.38
chr10	29940689	29940867	22.11	73.21
chr10	31204002	31204110	22.11	68.76
chr10	50083146	50083291	22.11	59.25
chr10	50263519	50263631	22.11	67.58
chr10	65404254	65404467	22.11	66.11
chr10	81437305	81437490	22.11	61.4
chr10	86144316	86144465	22.11	58.39
chr10	103978398	103978557	22.11	66.8
chr10	105408944	105409057	22.11	67.29
chr10	107443109	107443277	22.11	64.83
chr10	113012795	113013001	22.11	77.65
chr10	114301325	114301453	22.11	63.25
chr10	129407760	129407919	22.11	77.73
chr11	3634914	3635060	22.11	59.03
chr11	8225330	8225500	22.11	64.41
chr11	10571080	10571282	22.11	68.2
chr11	15186262	15186381	22.11	65.61
chr11	21809122	21809277	22.11	57.13
chr11	56027367	56027503	22.11	72.45
chr11	64386701	64386878	22.11	73.43
chr11	88775526	88775663	22.11	61.07
chr12	39616570	39616685	22.11	66.72
chr12	43639414	43639561	22.11	58.82
chr12	45160728	45160877	22.11	69.14
chr12	97999814	97999948	22.11	61.78
chr12	99104883	99105033	22.11	58.17
chr12	116924062	116924294	22.11	92.99
chr12	120989216	120989419	22.11	68
chr13	3111500	3111668	22.11	75.52
chr13	8470841	8471003	22.11	66.13
chr13	10700702	10700909	22.11	67.24
chr13	11337067	11337179	22.11	67.58
chr13	15362521	15362682	22.11	55.93
chr13	15980177	15980291	22.11	67
chr13	19086689	19086833	22.11	59.47
chr13	26144856	26144993	22.11	61.07
chr13	29562088	29562235	22.11	58.82
chr13	29978099	29978204	22.11	69.37
chr13	50175661	50175816	22.11	57.13

chr13	54926768	54926892	22.11	64.28
chr13	64684131	64684285	22.11	79.02
chr13	65098018	65098242	22.11	74.01
chr13	82628192	82628313	22.11	65.07
chr13	82711737	82711919	22.11	83.08
chr13	83581054	83581183	22.11	63
chr13	87282880	87283053	22.11	74.35
chr13	108149357	108149495	22.11	60.84
chr14	19029066	19029185	22.11	65.61
chr14	23552870	23553022	22.11	79.54
chr14	36637007	36637155	22.11	104.28
chr14	41599790	41599929	22.11	60.6
chr14	44254546	44254732	22.11	71.46
chr14	53205389	53205605	22.11	96.7
chr14	79066140	79066282	22.11	70.88
chr14	91817101	91817264	22.11	65.91
chr14	91988959	91989117	22.11	67.03
chr14	103155232	103155452	22.11	64.85
chr14	107363262	107363368	22.11	69.37
chr14	119201826	119201950	22.11	75.82
chr14	123582509	123582642	22.11	62.02
chr14	124828091	124828304	22.11	86.64
chr15	4674128	4674261	22.11	62.02
chr15	7877134	7877320	22.11	71.46
chr15	15849282	15849450	22.11	64.83
chr15	22954851	22954980	22.11	74.38
chr15	31873811	31873959	22.11	58.6
chr15	33345959	33346126	22.11	75.76
chr15	39698543	39698711	22.11	86.62
chr15	44078743	44078957	22.11	86.41
chr15	49086270	49086405	22.11	72.72
chr15	53703311	53703437	22.11	63.76
chr15	69401882	69402082	22.11	58.65
chr15	71097086	71097206	22.11	65.34
chr15	84578654	84578883	22.11	63.29
chr15	90285658	90285777	22.11	65.61
chr15	97881679	97881809	22.11	62.75
chr16	3386116	3386303	22.11	92.89
chr16	12343469	12343642	22.11	74.35
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chr7	67037232	67037501	7.28	53.71
chr6	47609169	47609633	7.27	91.15
chr1	147581414	147581489	7.26	68.45
chr13	53365268	53365364	7.24	150.28

chr6	47706684	47707365	7.24	83.23
chr12	74719547	74719631	7.22	53.95
chr6	29697880	29698655	7.22	367.93
chr6	47617124	47617661	7.22	105.44
chr6	47703466	47704009	7.2	87.23
chr3	159494853	159494921	7.18	71.42
chr1	159529595	159529707	7.16	88.28
chr10	52248389	52248971	7.15	84.1
chr9	90197137	90197235	7.15	94.86
chr6	47635840	47636720	7.09	165.2
chr1	19166310	19166423	7.07	54.71
chr15	6266895	6266972	7.04	71.07
chr5	63370483	63370712	7.04	53.55
chr3	148715715	148715944	7.01	62.13
chr7	67028222	67028782	6.99	77.33
chr12	75904868	75905022	6.97	51.4
chr14	8703417	8704140	6.97	103.75
chrX	166443466	166443758	6.92	134.24
chr14	13370175	13370266	6.86	60.59
chr1	63676438	63676712	6.84	86.24
chr10	94055178	94055272	6.84	100.93
chr13	74667006	74667177	6.84	55.76
chr14	105114985	105115293	6.84	57.4
chr1	149524793	149524861	6.83	70.49
chr18	43073568	43073665	6.82	107.5
chr2	57481806	57482159	6.79	189.63
chr16	49584479	49584596	6.78	52.06
chr6	47631527	47632280	6.76	144.26
chr7	67045117	67045261	6.75	51.29
chr6	47601605	47602084	6.74	64.55
chr14	69780402	69780503	6.73	54.4
chr14	69780049	69780155	6.71	132.31
chr2	98503828	98504259	6.71	844.69
chr7	67034848	67035506	6.7	103.02
chr7	67012022	67012449	6.68	89.84
chr8	57981044	57981332	6.66	61.64
chr8	103670007	103670093	6.66	50.01
chr10	52249630	52249885	6.64	51.19
chr5	110503495	110503581	6.64	130.36
chr11	18231979	18232288	6.62	73.87

chrX	131577633	131577934	6.62	61.75
chr17	68090701	68090875	6.61	89.6
chr9	115259944	115260045	6.61	141.81
chr19	53118296	53118363	6.6	56.06
chr1	143223048	143223120	6.59	80.83
chr6	47726867	47727195	6.59	62.64
chr8	19759407	19760421	6.5	155.17
chr6	47634520	47634959	6.46	86.96
chr12	16754622	16754720	6.45	121.8
chr6	47612004	47612333	6.45	80.71
chr7	67024633	67025282	6.44	65.56
chr1	78570908	78571223	6.43	71.96
chr3	128639637	128639732	6.42	75.56
chr8	20036846	20037256	6.4	60.02
chr6	47630215	47630651	6.39	65.78
chr6	103264591	103264774	6.38	122.31
chr1	102635460	102635564	6.37	75.71
chr6	47694075	47694668	6.35	91.93
chr1	195054005	195054153	6.34	103.22
chr4	31281334	31281416	6.31	143.69
chr10	79222514	79222581	6.29	55.39
chr6	47627992	47628757	6.28	113.23
chr9	121840342	121840638	6.28	53.46
chr13	74666399	74666512	6.26	119.89
chr10	37540255	37540341	6.24	119.94
chr3	23742074	23742176	6.24	54.02
chr13	77578163	77578318	6.21	390.24
chr15	86025419	86025750	6.21	72.24
chr16	5403565	5403628	6.21	53.38
chr16	93686947	93687010	6.21	53.38
chr9	95326320	95326451	6.21	153
chr11	88943134	88943364	6.19	128.64
chr6	47635025	47635629	6.19	82.92
chr8	19908630	19909040	6.19	56.43
chr2	98505030	98505379	6.18	771.06
chr7	67009366	67010147	6.18	110.93
chr16	18533224	18533412	6.17	54.24
chrX	122653116	122653573	6.17	62.15
chr6	47617729	47618117	6.15	59.95
chr11	110283562	110283649	6.12	90.59

chr9	3027377	3038415	6.12	3189.25
chrX	92159702	92159983	6.12	54.19
chr6	47715105	47716510	6.1	183.44
chr8	36197953	36198052	6.08	104.04
chr12	94815426	94815664	6.06	85.57
chr19	50385106	50385189	6.06	106.86
chr9	3000000	3019519	6.06	291.66
chr1	135492186	135492664	6.05	110.2
chr13	116983103	116983198	6.04	130.66
chr3	120925931	120925992	6.01	59.52
chr10	121200273	121200343	5.98	93.49
chr8	19926127	19927227	5.96	490.21
chr6	47699092	47699832	5.95	105.25
chr8	54520443	54520503	5.91	58.75
chr7	97590474	97590543	5.89	98.95
chr2	110133772	110133860	5.88	120.94
chr7	67020447	67020892	5.87	94.62
chr16	5709256	5709348	5.83	105.06
chr19	61275596	61275823	5.83	51.6
chr6	47608487	47608998	5.78	76.16
chr7	67027126	67027396	5.78	58.15
chr7	117203057	117203131	5.78	54.33
chr6	47704037	47704526	5.77	62
chr5	46827004	46827079	5.74	113.87
chr6	47688387	47688720	5.74	52.65
chr14	91310973	91311062	5.71	121.6
chr15	64272335	64272393	5.71	57.16
chr7	67004241	67004883	5.7	65.05
chr6	47633753	47634232	5.69	66.97
chr13	113368372	113368530	5.67	59.44
chr4	93511096	93511194	5.66	58.17
chr6	47689898	47690279	5.64	54.96
chr4	29547479	29547549	5.63	50.34
chr1	44258101	44258187	5.62	51.23
chr14	119686162	119686236	5.62	120.47
chr8	56198977	56199637	5.62	106.84
chr8	71998730	71999012	5.61	143.95
chr10	7232165	7232404	5.59	62.71
chr6	47622869	47623654	5.59	119.76
chrX	166427209	166427527	5.59	79.59

chr17	93445774	93445844	5.58	87.39
chr4	118219804	118221346	5.58	1241.44
chr16	30829613	30829716	5.57	64.24
chr6	47708267	47709019	5.57	140.02
chr18	3005174	3005552	5.54	74.18
chr6	47610692	47611414	5.54	89.33
chr6	47627523	47627982	5.54	98.22
chr6	47700302	47701484	5.51	148.56
chr6	103599040	103599289	5.5	474.75
chr1	64463470	64463542	5.49	68.23
chr10	7232499	7235308	5.49	1433.76
chr6	47618721	47619101	5.49	66.87
chr8	19924002	19926114	5.45	609.47
chr8	57997900	57998210	5.45	54.08
chr9	3019522	3027346	5.44	3100
chr18	68851719	68851968	5.41	79.89
chr6	47629458	47630207	5.41	69.49
chr6	47702050	47702534	5.41	71.18
chr1	183673115	183673899	5.39	106.4
chr6	47633164	47633730	5.37	76.71
chr10	7231149	7231722	5.36	272.18
chr17	53291811	53291955	5.35	50.08
chr7	66930199	66930491	5.33	56.49
chr12	75905129	75905494	5.31	117.39
chrX	106468144	106468224	5.28	56.25
chr2	109211944	109212012	5.26	63.34
chr12	34758613	34758683	5.23	81.78
chr2	143210313	143210378	5.23	53.7
chr6	47603579	47604112	5.23	81.87
chr5	80929912	80929991	5.22	110.32
chr6	47625554	47626312	5.2	111.91
chr6	47609898	47610583	5.18	63.72
chr7	67029542	67029777	5.17	58.97
chr9	24346455	24346605	5.17	87.2
chr6	47605382	47606315	5.16	161.39
chr6	47689039	47689596	5.16	75.51
chr16	57391230	57391792	5.15	107.71
chrX	166527166	166527506	5.15	506.51
chr6	56183651	56183743	5.12	85.78
chr10	7236727	7237128	5.1	176.53

chr6	47696239	47697173	5.07	98.27
chr6	47698225	47698968	5.04	72.72
chr10	7231816	7232083	5.03	136.01
chr17	3379790	3379866	5.03	65.65
chr10	7229298	7230583	5.02	592.5
chr6	47622100	47622842	5.01	82.02
chr1	111472754	111472818	5	59.49
chr10	102131266	102131337	5	101.4
chr5	106605800	106605878	4.99	103.17
chrX	39993112	39993182	4.92	52.3
chr1	135491289	135492174	4.91	80.44
chr16	34743083	34743171	4.9	51.56
chr2	92008268	92008344	4.88	79.81
chr3	59724068	59724132	4.88	72.65
chr10	7236089	7236668	4.83	304.03
chr11	57116135	57116203	4.78	73.35
chr12	3109866	3110124	4.78	922.22
chr1	71125913	71125989	4.77	87.13
chr2	20821474	20821836	4.75	90.82
chr6	47713805	47714278	4.73	89.36
chr16	93598171	93598238	4.71	64.07
chr2	19430946	19431023	4.7	86.31
chr6	47693231	47694054	4.69	95.34
chr15	63458454	63458512	4.66	54.72
chr10	114174434	114174503	4.61	83.92
chr8	15519757	15520122	4.61	73.16
chr2	98502384	98503147	4.58	2821.78
chr6	47623866	47624974	4.56	90.72
chr8	73956987	73957069	4.52	54.53
chr2	98506392	98507492	4.51	3100
chr6	3150763	3151669	4.48	141.76
chr6	47615376	47615963	4.47	53.51
chr5	147072568	147072899	4.37	54.42
chr9	47766423	47766492	4.37	72.74
chr12	104131172	104131234	4.36	70.47
chr6	47687049	47688336	4.36	82.35
chr8	40240697	40241218	4.34	57.65
chr14	123850840	123850906	4.33	64.48
chr10	29690764	29690845	4.32	66.87
chr6	47702567	47703443	4.32	107.22

chr7	93955096	93955157	4.29	50.59
chr19	23431914	23431989	4.27	59.69
chr9	35112795	35113178	4.27	1638.31
chr10	57690558	57691224	4.26	82.91
chr3	100120375	100120452	4.26	67.91
chr10	57685673	57686316	4.15	61.67
chr6	47606796	47607994	4.14	82.9
chr8	56203858	56205488	4.14	101.08
chr6	4874136	4874199	4.06	53.64
chr15	74916669	74917478	4.04	252
chr1	78570272	78570692	4.01	57.96
chr6	50997469	50997534	4	58.71

chr4	25399420	25399489	3.97	64.56
chr6	47615997	47616708	3.96	51.68
chr10	51864279	51864343	3.94	62.96
chr8	56201204	56201912	3.93	60.87
chr9	123782210	123782296	3.83	59.55
chr6	47694705	47695522	3.77	74.36
chr8	56205500	56209057	3.75	266.86
chr8	56201933	56202418	3.49	64.56
chr16	86821030	86821490	3.42	75.22
chr17	39979941	39985862	3.04	748.7
chr1	24618373	24623102	2.4	68.9

Table S4.2. Prospective cJUN target genes identified from cJUN ChIP-seq peaks.
Statistically enriched cJUN peak regions. Enrichment (Fold Enrichment) LOG P (-10*LOG10(pvalue)).

Gene	Cyc	FC	pval	Up in Mes
Baz2b	1402.8	0.465	5.97E-07	
Tmem204	233.7	0.497	1.66E-04	+
Chpf	1197.6	0.468	3.11E-06	+
Nckap5l	547.6	0.331	3.62E-02	+
Pi4ka	981.2	0.475	6.68E-07	
Tro	1261.8	0.453	2.99E-03	+
Masp2	324.1	0.351	1.83E-04	
Adams7	767.0	0.306	2.43E-09	+
Arhgef11	856.0	0.496	5.78E-05	
Brsk1	374.1	0.422	2.97E-07	+
Scube3	71.7	0.351	8.97E-03	+
Ypel4	34.6	0.273	1.15E-02	+
Gm11541	0.3	0.007	3.62E-09	+
Daam2	576.2	0.280	2.85E-05	+
Whrn	187.2	0.247	7.90E-06	
Ppp1r13l	143.6	0.484	2.62E-03	
Adcy5	500.5	0.434	1.57E-03	+
Ttll4	567.1	0.476	2.13E-04	
Fam189b	428.9	0.500	3.21E-02	
Zfyve28	20.8	0.275	1.82E-03	+
Zscan18	162.9	0.478	9.36E-05	+
Snx32	83.3	0.467	2.00E-03	+
Lrrc16b	179.7	0.327	2.40E-10	+
Apol7b	12.1	0.291	1.04E-02	+
Ankrd34a	25.5	0.328	1.05E-02	+
Vegfa	1280.0	0.308	3.71E-09	
Gpr17	298.3	0.317	1.44E-08	+
Ccdc141	257.6	0.480	3.54E-03	+
Ikzf1	52.2	0.477	2.79E-02	+
Pknox2	308.4	0.289	1.28E-09	+
Unc13a	133.0	0.437	3.02E-04	+
Safb2	754.1	0.482	3.64E-08	
Kcp	317.3	0.275	2.52E-03	+
Mettl17	227.4	0.453	2.81E-07	
1700029J07Rik	46.8	0.478	9.16E-03	
Prickle1	602.3	0.471	8.06E-04	+
Itgal	426.6	0.482	3.19E-04	+
Ccdc114	50.5	0.435	8.32E-03	+

Sec31b	8.6	0.233	9.56E-03	
Lrrc55	22.3	0.061	1.87E-26	+
Bank1	10.6	0.293	3.63E-02	+
Lgr6	15.2	0.126	9.79E-09	+
Ii20rb	39.2	0.441	3.84E-02	
Dnaaf3	47.3	0.421	9.75E-03	+
Acsf6	41.2	0.434	6.85E-03	+
Dnah1	103.7	0.387	1.67E-03	+
I830077J02Rik	3.2	0.135	1.19E-02	+
Piezo1	1229.7	0.366	4.26E-05	
Adam15	624.0	0.475	3.09E-06	
Csflr	472.7	0.318	2.97E-13	+
Gm6377	3.3	0.170	2.99E-02	+
Dyrk1b	337.7	0.439	3.39E-03	+
Clec5a	13.4	0.278	4.10E-03	+
Gngt2	31.9	0.346	4.02E-02	+
Emc1	683.2	0.419	3.33E-04	
Gm14137	10.4	0.184	1.50E-02	
Kcnd3	225.9	0.104	2.48E-06	+
Slc22a15	164.2	0.480	1.01E-03	+
Piezo2	414.6	0.260	2.34E-04	+
4930467E23Rik	19.0	0.193	1.34E-02	+
Mroh8	50.7	0.488	1.93E-04	
Evi5l	154.4	0.498	6.02E-04	+
Iffo1	228.3	0.389	1.56E-06	+
Tmem120b	87.7	0.444	2.04E-04	
Peg10	2872.8	0.337	9.70E-03	+
Cd74	46.5	0.192	5.33E-08	+
Smad7	258.8	0.369	1.21E-02	+
Eml1	617.8	0.323	1.26E-06	+
Timp1	83.9	0.467	2.08E-03	+
Akna	310.0	0.397	8.76E-03	
Scimp	0.9	0.072	3.07E-02	+
Mink1	657.5	0.370	6.25E-10	
Dysf	192.1	0.345	1.55E-07	+
Syne1	845.2	0.460	1.45E-02	+
Fgfr1	1346.2	0.332	4.87E-13	+
Vamp1	82.2	0.309	1.35E-05	
Prdm10	137.2	0.452	1.92E-02	
Cass4	4.1	0.087	5.42E-05	+

Parp8	210.4	0.457	5.83E-05	+
Srgap2	878.3	0.461	1.15E-02	+
Adams6	210.6	0.366	3.36E-05	+
Dock9	1973.0	0.294	2.15E-17	+
Ptpn23	1036.1	0.377	2.83E-02	
Adams14	14.5	0.106	1.02E-08	+
Kcng1	16.0	0.024	1.66E-09	+
Kcnq4	30.1	0.222	8.99E-06	+
Lama5	1684.0	0.194	1.29E-12	
Frmpd1	58.1	0.418	3.83E-03	+
Kif13b	333.4	0.370	4.34E-04	
Gpr116	705.4	0.431	3.08E-07	+
Flnc	2084.9	0.438	1.16E-02	+
Fam65a	648.0	0.400	3.52E-02	+
Vcan	4562.1	0.347	2.65E-04	+
Uggt2	355.9	0.361	3.68E-09	+
Hpse2	240.3	0.312	9.95E-03	+
Ccdc142	166.2	0.431	4.89E-06	
Ccdc88b	63.1	0.420	6.10E-03	+
Trio	1728.2	0.407	1.68E-04	
Ppp1r12b	129.5	0.435	4.88E-04	+
Slc9a5	113.2	0.142	3.66E-16	+
Plekhg4	7.9	0.145	1.36E-04	
Sipa112	804.3	0.498	8.37E-03	+
Cped1	1270.5	0.405	8.24E-05	+
Trrap	2415.1	0.384	1.49E-02	
Adams3	103.3	0.287	1.53E-02	+
Klhl14	0.9	0.030	2.00E-05	+
Fndc1	59.5	0.102	4.19E-04	+
Rbm24	103.8	0.340	5.48E-06	+
Gtf2ird1	1221.7	0.492	9.36E-07	
Pik3r6	51.4	0.345	1.33E-04	+
Sap25	49.0	0.285	1.25E-04	
Mkl1	601.0	0.396	1.92E-03	
Itgam	63.8	0.482	3.87E-03	+
Ubp1	1890.3	0.498	3.39E-06	
Cacna1d	273.4	0.245	6.39E-03	+
Gria2	109.0	0.445	1.82E-04	+
Pth1r	336.0	0.494	3.15E-05	+
Ndufa4l2	81.6	0.398	4.49E-04	+

Ajap1	46.0	0.241	9.22E-08	+
Zkscan16	68.7	0.357	1.83E-02	+
Myof	411.2	0.449	2.23E-07	
Pnmal2	633.7	0.428	3.62E-07	+
Adat3	82.9	0.417	1.42E-04	
Cyp4f17	60.5	0.400	1.05E-02	+
Gsg11	33.4	0.222	1.63E-06	+
Prrt2	155.7	0.227	1.19E-02	+
Col6a6	12.1	0.195	3.39E-02	+
Rai2	245.7	0.406	7.34E-04	+
Gas7	532.4	0.369	4.34E-05	+
Phf21a	999.8	0.433	7.43E-03	+
Cbfa2t3	119.1	0.350	1.51E-03	
Trpc2	91.7	0.428	6.22E-04	
Ebf4	327.6	0.315	3.77E-05	+
Cd33	45.9	0.337	4.76E-04	+
Atg16l2	149.2	0.370	5.82E-06	
Wdfy1	189.0	0.319	4.99E-10	
Ptprc	111.6	0.356	2.58E-02	+
Ifitm1	768.9	0.395	2.85E-09	+
Ncam1	1562.1	0.312	1.66E-02	+
Lrrc32	347.2	0.242	4.58E-03	+
Ltbp4	2755.4	0.332	1.88E-05	+
Stxbp1	696.7	0.407	1.75E-03	+
Pdlim7	1044.6	0.395	1.05E-10	+
Smarcc2	2133.9	0.434	3.39E-09	
Pnpla6	523.2	0.367	8.90E-11	
Upf1	1321.3	0.495	1.16E-06	
Il1r1	250.7	0.459	1.55E-04	+
Sema4c	1043.4	0.490	3.45E-06	+
Acrbp	44.3	0.325	1.47E-03	
Gm1564	11.3	0.302	3.88E-02	+
Arhgef1	1050.6	0.462	2.71E-08	
Prickle2	854.2	0.475	4.22E-02	+
Ccdc62	39.3	0.445	9.28E-03	
Cntfr	654.9	0.456	2.13E-02	+
Cyp1a1	21.6	0.044	6.47E-14	
Ptger4	63.6	0.395	5.72E-04	+
Atat1	294.6	0.451	1.76E-04	+
Vwa5b2	109.3	0.465	4.58E-02	

Gm13889	108.4	0.245	6.02E-06	+
Runx2	25.7	0.156	1.21E-03	+
Lgals3	229.4	0.391	2.73E-02	+
Gpr114	7.3	0.080	2.38E-04	+
Parp4	196.4	0.357	3.32E-02	
Hk1	840.1	0.445	1.27E-07	+
Smoc1	780.0	0.343	2.50E-12	+
Eng	431.4	0.187	4.97E-05	+
Smtn	974.9	0.346	1.61E-11	+
Upp1	47.0	0.410	2.98E-03	+
Igfbp7	120.0	0.104	8.90E-08	+
Adcy3	295.3	0.436	4.57E-06	+
Klrb1c	16.4	0.306	3.67E-02	+
Ubr4	2550.6	0.299	6.43E-03	
Megf8	1560.7	0.472	9.17E-03	+
Kif26b	648.6	0.213	3.24E-02	+
Mthfr	1047.2	0.491	3.96E-05	
T2	3.0	0.170	4.15E-02	
Stra6	113.5	0.274	3.25E-04	+
Igsf10	862.2	0.250	4.33E-07	+
2410089E03Rik	557.9	0.464	2.16E-02	+
Eme2	143.8	0.479	1.34E-03	
C2cd4a	19.4	0.344	2.69E-02	+
Col4a5	717.4	0.374	8.76E-11	+
Begain	148.1	0.336	3.35E-02	+
Cmip	1448.7	0.419	1.05E-03	
Tubgcp6	820.4	0.481	3.06E-04	
Clk2	522.7	0.458	4.24E-07	
Rhpn1	35.1	0.431	8.03E-03	+
Hectd2	110.8	0.493	5.55E-03	+
Cyp2d22	119.8	0.218	1.95E-13	+
Stard13	689.7	0.453	5.28E-06	+
Emcn	213.9	0.399	1.47E-02	+
Osbpl3	343.1	0.392	1.62E-08	+
Wdr90	351.1	0.416	1.33E-07	
Taok2	1207.0	0.491	1.10E-05	
Ntf3	68.0	0.386	2.12E-04	+
Rerg	159.7	0.237	2.68E-07	+
Efemp2	632.4	0.390	3.93E-10	+
Sipa1	637.0	0.321	1.96E-12	+

Igln5	272.2	0.453	2.14E-04	+
Znf512b	1393.3	0.335	2.14E-12	+
Adams20	47.3	0.264	9.08E-04	+
Rgs9	290.8	0.321	1.55E-10	+
Pias3	465.0	0.409	2.37E-07	+
2010015L04Rik	11.6	0.200	9.02E-04	+
Fam129c	22.6	0.415	9.60E-03	
Mgl1	1398.6	0.482	3.05E-07	+
Sec1411	1388.8	0.336	3.38E-07	+
Rhbdf2	325.3	0.429	5.20E-06	
Sirt4	110.3	0.351	1.01E-06	
Tcirg1	382.7	0.281	3.88E-12	
Col6a5	8.5	0.080	6.83E-10	+
Sugp2	434.9	0.413	2.52E-07	
Nfatc4	1197.9	0.414	6.78E-04	+
Pla2g4c	16.7	0.328	4.98E-03	
Tsku	470.3	0.494	6.83E-03	+
Tifab	72.6	0.414	3.13E-03	+
Sbfl	1024.5	0.421	2.72E-08	
Trim66	37.6	0.060	1.99E-03	
Pcdha4-g	2841.0	0.483	2.12E-02	+
Dbn1	2278.1	0.488	3.76E-05	+
Ubr2	1546.8	0.434	3.03E-07	
Usp35	158.3	0.383	1.28E-04	+
Slc25a22	311.9	0.483	2.16E-04	
Gm2897	35.7	0.472	4.75E-02	
Rapgef3	111.3	0.344	6.04E-07	+
Adams13	42.4	0.328	9.78E-03	+
Camta2	433.2	0.309	2.51E-04	
Kcnipl	30.4	0.068	9.55E-21	+
Kirrel3	39.2	0.218	3.11E-02	+
Dlc1	1550.4	0.395	2.93E-02	+
Tgfbr3l	20.2	0.335	2.04E-02	
Dclk2	280.0	0.298	3.25E-05	+
Prr22	18.1	0.453	2.25E-02	
Frem1	1807.7	0.416	3.03E-02	+
Arhgef2	1527.0	0.343	1.62E-12	
Prrc2a	6514.0	0.416	2.91E-02	
Macf1	4201.9	0.472	1.58E-02	+
Slc44a2	910.2	0.437	3.04E-07	+

Fbxl13	6.6	0.208	9.93E-03	+
Hdac7	723.2	0.374	3.71E-03	+
Trim47	77.8	0.347	3.26E-05	+
Cyb5r2	14.3	0.199	1.10E-04	
Arap3	624.5	0.258	1.32E-08	+
Ano1	285.7	0.173	1.59E-12	+
Col6a3	4256.9	0.192	1.23E-03	+
Fam193a	936.5	0.461	4.43E-03	
Pde2a	613.7	0.430	3.67E-08	+
Tle2	102.3	0.234	8.49E-12	+
Cpt1c	289.9	0.265	1.06E-10	+
Ecm1	94.4	0.467	2.56E-03	+
Kcnma1	224.5	0.444	5.20E-03	+
Slc12a4	429.4	0.267	2.21E-16	+
Irx3	2.4	0.163	4.94E-02	+
Itgal	51.2	0.258	2.51E-07	+
Gbp4	14.2	0.241	1.03E-02	+
Myo7a	251.8	0.442	8.04E-06	
Eif4g3	2227.4	0.384	1.19E-10	
Arrb2	337.2	0.465	1.32E-06	
Sorbs3	568.1	0.439	4.26E-03	+
Nfam1	66.8	0.428	5.38E-03	+
4930426D05Rik	1.1	0.086	2.49E-02	
Ampd3	47.9	0.457	1.30E-02	+
Nxf1	1673.6	0.335	1.87E-14	
Chrd	110.1	0.266	4.85E-10	+
Syngap1	334.8	0.203	2.97E-03	+
Cacnb1	263.3	0.463	1.33E-04	+
42251	50.2	0.243	1.11E-04	+
Tead2	2172.7	0.478	7.24E-08	+
Paqr7	172.2	0.368	1.19E-04	+
Trim3	390.0	0.473	5.42E-06	+
Ncf1	132.5	0.349	7.83E-04	+
Lepre1	609.0	0.395	6.20E-07	+
Otx2	4.5	0.161	1.45E-02	+
Tsc2	1117.5	0.441	2.82E-06	
Hgf	67.5	0.173	1.08E-15	+
Pitpnm2	522.3	0.441	3.84E-02	
Exoc3l4	63.8	0.403	2.63E-03	+
Egflam	827.7	0.387	1.62E-09	+

Tgfb1l1	1482.2	0.380	1.43E-06	+
Celf3	834.9	0.396	6.27E-03	+
Kctd17	422.5	0.386	2.67E-08	+
2010111I01Rik	1190.4	0.477	1.18E-06	+
Col12a1	1350.9	0.353	4.52E-05	+
Vsig10l	87.2	0.453	4.29E-02	
Snape4	379.8	0.450	6.79E-06	
Flna	17960.0	0.440	4.77E-09	+
Kmt2b	1313.9	0.390	1.42E-02	
Ppp1r3f	133.2	0.266	9.42E-09	+
Cd302	84.8	0.401	7.93E-05	+
Ebf1	114.6	0.409	4.02E-04	+
Aff3	480.0	0.272	6.55E-03	+
Lmtk3	217.7	0.200	3.32E-06	+
Sema6d	908.5	0.497	3.86E-02	+
Mapk7	848.7	0.495	9.18E-04	
Adam8	24.4	0.260	1.70E-04	
Polr2a	3198.0	0.278	3.12E-02	
Pcsk6	224.8	0.379	6.89E-08	+
Slit2	775.4	0.472	2.37E-02	+
Aebp1	597.1	0.345	6.17E-11	+
Apela	34.1	0.469	4.15E-02	+
Inpp4b	87.8	0.318	2.73E-06	+
Agap2	251.8	0.305	2.11E-03	+
Ede4	948.0	0.483	1.80E-06	
Pcdha6-g	2840.2	0.483	2.12E-02	+
Pcdha7-g	2845.3	0.484	2.17E-02	+
Fst	71.0	0.183	5.43E-04	+
Aatk	193.2	0.241	7.09E-14	+
Adcy7	91.2	0.259	2.74E-09	+
Angpt2	87.0	0.264	7.12E-05	+
Agtr2	34.2	0.391	2.78E-02	+
Speg	517.6	0.343	1.21E-02	+
Bcat1	199.0	0.271	1.68E-12	+
Bmp4	407.6	0.258	2.85E-17	+
Bmp5	228.9	0.425	7.13E-06	+
Cd28	20.1	0.331	8.11E-03	+
Ovgp1	15.7	0.200	2.03E-06	
Cit	168.4	0.444	1.74E-02	
Clk4	1094.6	0.401	1.92E-06	

Col11a1	299.0	0.314	1.52E-05	+
Col13a1	192.1	0.198	4.99E-03	+
Col5a2	5402.2	0.470	1.63E-03	+
Col7a1	15.5	0.239	8.95E-05	
Col9a2	462.6	0.383	8.48E-03	+
Col1a1	10200.4	0.257	1.51E-05	+
Col1a2	9259.1	0.317	1.30E-06	+
Csf1	351.6	0.329	4.69E-10	+
Csf2rb2	17.6	0.330	4.11E-02	+
Csn3	17.4	0.356	2.62E-02	+
Ctsk	151.6	0.454	8.25E-03	+
Cybb	159.7	0.467	1.45E-04	+
Gadd45a	151.9	0.220	4.96E-04	
Dlg4	530.2	0.350	1.45E-02	+
Dll1	456.0	0.262	1.03E-08	+
Dnase113	7.7	0.034	1.98E-13	+
Ednrb	3785.3	0.431	3.91E-05	+
Eln	1481.8	0.481	6.38E-06	+
Enc1	1160.5	0.375	5.77E-09	+
Enpep	1196.0	0.224	5.94E-14	
Epha4	700.4	0.494	2.04E-05	+
Epha8	10.2	0.093	8.39E-08	+
Eps15l1	729.8	0.485	1.29E-06	
F2rl3	110.8	0.275	3.69E-09	+
Fap	188.6	0.262	1.38E-03	+
Fbn1	3421.3	0.437	2.19E-08	+
Foxl1	27.3	0.032	2.15E-22	+
Fit4	258.0	0.318	1.84E-03	+
Gapdhs	25.1	0.355	4.28E-03	
Slc6a9	557.4	0.220	9.06E-19	
Gna14	270.0	0.487	5.93E-05	+
Grik5	998.9	0.433	3.86E-04	+
Mr1	145.3	0.391	1.27E-05	+
Has2	256.1	0.255	3.30E-15	+
Hcls1	103.9	0.411	3.16E-02	+
Map4k1	61.2	0.422	1.62E-04	
Hspg2	4157.3	0.241	2.25E-02	
Igfbp2	660.1	0.481	1.03E-03	+
Igfbp6	26.7	0.457	4.71E-02	+
Il10ra	48.1	0.443	2.92E-02	+

Il1b	5.8	0.078	3.50E-08	+
Lrig1	2799.9	0.479	5.80E-07	+
Itga2	222.5	0.445	7.00E-04	
Itga7	22.2	0.232	5.46E-05	+
Itih3	6.4	0.161	1.00E-03	+
Lama1	332.4	0.394	1.37E-03	+
Lama2	397.3	0.457	4.39E-02	+
Lamb1	5494.1	0.370	4.23E-13	+
Lamb2	1185.2	0.406	1.20E-09	
Lcat	8.7	0.256	1.61E-02	+
Lrp1	4222.5	0.182	1.79E-03	+
Lrp5	1508.4	0.485	1.32E-03	
Ltbp3	1173.3	0.438	4.51E-03	+
Ltc4s	9.2	0.126	3.74E-03	+
Tm4sf1	87.6	0.378	4.48E-05	+
Mfap2	1884.5	0.419	3.66E-08	+
Mcpt1	0.9	0.050	8.38E-03	
Mdm4	729.9	0.460	6.93E-04	
Cxcl9	1.9	0.107	9.89E-03	+
Mmp13	14.6	0.209	8.71E-05	+
Mmp14	3179.8	0.462	2.45E-08	+
Mmp2	4578.9	0.287	2.07E-19	+
Mpp1	685.8	0.483	1.34E-05	
Mrc2	1137.8	0.332	4.19E-11	+
Msi1	174.9	0.427	7.65E-03	
Nbl1	617.6	0.387	1.05E-09	+
Ncoa3	953.9	0.355	3.62E-04	
Nid2	1655.5	0.466	5.68E-07	+
Nkx2-3	947.1	0.425	7.44E-08	+
Nog	148.6	0.439	4.23E-04	+
Nos3	198.7	0.442	7.98E-05	+
Notch3	949.1	0.300	4.45E-02	+
Npc1	714.2	0.376	2.82E-05	
Npr1	102.8	0.410	1.33E-04	+
Ntn1	1383.0	0.491	3.76E-04	+
Cldn11	25.6	0.185	2.45E-03	+
Pcolce	627.8	0.479	2.14E-04	+
Pde8a	92.0	0.475	2.42E-03	+
Pde9a	502.6	0.473	1.38E-04	+
Pdgfrb	2075.2	0.235	5.14E-04	+

Peg3	5454.7	0.477	1.44E-02	
Pim1	180.2	0.434	5.65E-05	
Prkd1	153.3	0.301	2.71E-10	+
Prkcq	44.7	0.230	7.50E-08	+
Plau	415.7	0.373	2.34E-09	+
Plxna1	1933.8	0.443	1.98E-02	
Plxna2	746.3	0.306	3.13E-03	+
Plxna3	567.8	0.382	2.89E-05	+
Ppox	327.6	0.420	9.70E-08	
Ptch1	854.7	0.104	9.82E-04	+
Ptch2	14.5	0.020	1.09E-11	+
Ptger2	25.3	0.356	1.06E-02	+
Ptgir	161.9	0.404	1.67E-02	+
Ptgis	281.1	0.490	1.47E-04	+
Ptgs1	258.9	0.492	1.52E-02	+
Ptprm	527.3	0.399	3.65E-05	+
Ptpn	210.0	0.482	1.69E-04	+
Rem1	81.6	0.296	1.78E-04	+
Rfng	412.7	0.491	4.57E-03	
Rfx1	350.0	0.386	9.43E-08	
Rfx2	97.7	0.322	2.50E-06	+
Slc50a1	357.6	0.483	3.30E-04	
Rgl2	739.6	0.424	2.91E-08	
S100b	33.7	0.407	8.77E-03	+
Atxn2	801.8	0.308	2.83E-03	
Scn7a	19.8	0.356	3.60E-02	+
Sh3bp1	215.2	0.272	4.57E-13	+
Slc2a4	504.0	0.452	1.47E-06	+
Slc4a3	365.6	0.326	7.08E-11	+
Stc1	284.8	0.367	2.55E-04	+
Tbx2	751.8	0.480	2.55E-05	+
Tbxa2r	147.9	0.487	1.30E-02	+
Tcea2	82.4	0.315	5.05E-07	+
Phf1	219.6	0.288	2.38E-12	+
Tert	110.3	0.381	6.33E-04	
Tgfb3	514.9	0.391	3.25E-06	+
Tgm2	1305.6	0.333	1.01E-14	+
Tg	4.7	0.162	3.93E-02	+
Thbd	1395.1	0.242	1.63E-22	+
Thy1	9.5	0.260	1.63E-02	+

Tiam1	615.8	0.497	6.99E-03	
Tll1	103.2	0.409	5.53E-04	+
Tnfaip2	67.2	0.237	2.24E-02	+
Ulk1	981.0	0.455	6.13E-03	+
Vegfc	105.3	0.484	3.99E-03	+
Wnt4	111.1	0.333	5.02E-06	+
Wnt5a	1398.7	0.486	2.18E-02	+
Pcgf2	629.3	0.432	8.42E-05	
Abcg1	72.6	0.238	2.96E-04	+
Chrb1	66.9	0.421	1.05E-03	
Acvr11	427.5	0.393	2.89E-04	+
Adam19	1613.5	0.448	6.92E-03	+
Adm	47.5	0.454	1.27E-02	+
Ahrr	24.1	0.279	1.10E-02	+
Anxa5	1539.3	0.494	2.07E-02	+
Aoc3	125.4	0.217	4.26E-04	+
Nr2f2	893.4	0.391	1.46E-02	+
Atp10a	47.3	0.285	3.21E-06	+
Bdkrb2	25.2	0.221	1.20E-05	+
C4b	7.4	0.165	9.93E-03	+
Cacna1g	960.7	0.247	7.62E-04	+
Car11	76.4	0.386	4.14E-04	+
Car2	123.1	0.273	9.78E-05	+
Casp1	14.2	0.414	4.28E-02	+
Cckar	229.5	0.328	1.86E-10	+
Cdc7	624.7	0.401	1.75E-05	
Cdh10	67.5	0.424	8.99E-03	+
Cdh11	3810.7	0.470	2.58E-03	+
Cdh4	48.1	0.405	2.43E-03	+
Ch25h	8.2	0.145	1.01E-04	+
Clcn2	265.4	0.427	1.03E-06	
Cln3	197.9	0.453	2.81E-06	
Col11a2	52.0	0.488	5.89E-04	
Col15a1	754.2	0.330	8.79E-13	+
Col18a1	1805.2	0.416	3.30E-03	+
Col3a1	33354.4	0.406	2.17E-03	+
Col4a1	7181.6	0.226	4.49E-20	+
Col4a2	3763.4	0.209	7.95E-28	+
Col6a1	7260.8	0.189	1.93E-32	+
Cpt1b	28.5	0.315	1.65E-04	

Csf2ra	267.2	0.488	9.80E-03	
Clip2	1275.1	0.409	9.12E-09	+
Cyp2d9	0.6	0.050	3.57E-02	+
Cyp46a1	15.5	0.250	3.59E-02	+
Dkk1	0.3	0.012	1.17E-05	+
Dlk1	6954.3	0.471	2.79E-03	+
Dmc1	21.0	0.343	1.10E-02	+
Dnm1	878.2	0.451	1.89E-02	
Edar	8.6	0.046	4.02E-14	+
Efnb1	961.3	0.350	1.88E-12	+
Efs	864.8	0.498	1.32E-02	+
Rhbdf1	630.1	0.478	2.85E-06	
Pou6f1	424.2	0.485	2.09E-02	+
Ephb3	660.3	0.472	1.77E-03	+
Epor	43.0	0.260	4.74E-06	+
Fbln1	2687.0	0.496	9.87E-07	+
Fbn2	2658.1	0.282	3.29E-04	+
Fbrs	633.4	0.392	1.58E-02	
Fes	118.3	0.450	7.36E-03	+
Ii4i1	42.9	0.397	2.48E-03	+
Fkbp10	1215.4	0.418	2.96E-09	+
Foxf2	506.3	0.135	6.81E-23	+
Flt1	231.8	0.318	2.15E-04	+
Fmo1	45.6	0.350	4.48E-04	+
Fn1	4775.7	0.221	8.50E-05	+
Fosl1	35.1	0.415	2.13E-02	+
Ggta1	663.6	0.467	3.68E-06	+
Gli1	27.6	0.007	1.18E-136	+
Gng8	51.9	0.282	3.99E-04	+
Pdpm	358.7	0.409	4.08E-08	+
H2-DMA	43.4	0.431	5.16E-03	
Herc2	1829.4	0.436	3.85E-03	
Foxf1	1835.4	0.260	1.45E-19	+
Hoxa3	419.4	0.381	4.78E-02	+
Hoxa7	35.8	0.426	8.08E-03	+
Hoxb4	431.8	0.388	7.66E-08	+
Hoxb8	255.5	0.303	2.66E-02	+
Hoxc6	189.2	0.261	1.88E-02	+
Hsd17b1	0.9	0.059	8.39E-03	

Igfbp5	9447.2	0.433	1.70E-02	+
Ii18bp	21.0	0.214	3.28E-02	
Inpp5d	110.8	0.400	3.35E-04	+
Inpp11	1485.8	0.394	2.18E-10	
Irs4	35.4	0.200	5.65E-03	+
Itga5	2263.9	0.406	6.49E-10	+
Itpr1	1147.8	0.415	5.71E-05	+
Jup	1950.4	0.433	1.15E-07	
Kcnk2	302.5	0.367	8.01E-03	+
Kcnk3	940.4	0.361	1.67E-04	+
Kifc2	131.6	0.300	8.92E-04	+
Lama4	1881.0	0.292	4.31E-14	+
Lamc1	5614.3	0.388	8.46E-08	+
Lcp2	68.0	0.378	3.46E-03	+
Lipe	185.9	0.442	1.15E-03	+
Myom1	406.3	0.326	4.68E-12	+
Ncoa1	760.0	0.469	1.97E-03	
Nid1	2909.0	0.319	6.85E-15	+
Nnmt	1.8	0.112	2.39E-02	
Nos2	95.1	0.361	6.10E-05	+
Notch4	681.4	0.387	1.20E-03	+
Pnoc	14.2	0.339	3.25E-02	+
Ntn3	321.6	0.278	6.19E-06	+
P4ha1	1131.2	0.431	1.68E-03	+
P4ha2	271.4	0.259	2.32E-04	+
Furin	1172.5	0.496	1.85E-03	
Per1	342.2	0.424	3.45E-02	
Per2	198.0	0.439	7.28E-05	
Prkcg	10.4	0.292	1.71E-02	
Plaur	129.8	0.329	1.63E-06	
Plod1	808.1	0.335	3.12E-12	+
Pltp	111.5	0.086	1.07E-28	+
Ppard	448.5	0.448	4.10E-02	
Ppef2	17.0	0.261	1.58E-02	+
Mapk11	182.7	0.480	8.98E-04	+
Procr	51.9	0.045	3.65E-14	+
Lgmn	1140.1	0.431	1.43E-03	
Ptgs2	80.5	0.406	1.63E-04	+
Ptpr	91.5	0.406	3.48E-04	+
Ptprs	4778.7	0.380	7.35E-11	+

Rasgrp2	53.5	0.213	4.44E-10	+
S100a4	9.5	0.301	2.12E-02	+
Ccl11	94.1	0.089	8.70E-20	+
Ccl2	42.2	0.367	6.79E-04	+
Serpinf1	397.4	0.259	2.24E-03	+
Sema3f	451.6	0.240	4.12E-18	+
Spi1	71.4	0.348	2.70E-03	+
Slc7a5	1663.7	0.423	5.36E-05	
Slit3	486.7	0.271	4.23E-03	+
C4a	7.8	0.297	3.57E-02	
Ncor2	1745.4	0.271	4.62E-02	
Snai1	72.8	0.141	7.91E-03	+
Sox5	214.7	0.346	1.57E-02	+
Tead3	734.6	0.475	3.27E-06	+
Tgfb1	276.6	0.239	3.95E-05	+
Tgfb3	863.3	0.336	4.14E-03	+
Thbs1	868.6	0.436	5.97E-04	+
Thbs2	1276.0	0.302	1.26E-16	+
Thbs4	937.9	0.338	2.71E-05	+
Tia1	1986.3	0.481	2.68E-07	+
Tie1	911.4	0.477	6.66E-04	+
Tln1	3111.9	0.348	8.42E-13	+
Fmn13	1082.2	0.398	6.19E-10	+
Zim1	360.7	0.334	9.42E-05	+
Aplnr	175.6	0.260	3.75E-02	+
C1ql1	124.4	0.293	1.66E-08	+
Gdf15	77.1	0.495	8.84E-04	
Ggt5	385.3	0.357	1.46E-04	+
Grem1	395.7	0.281	2.21E-15	+
Esyt1	780.4	0.416	6.86E-10	+
Nt5e	105.5	0.318	2.01E-06	+
Spry2	695.6	0.478	1.19E-04	+
Tekt2	35.8	0.302	1.29E-04	+
Angptl2	1039.0	0.492	2.06E-04	+
Cd97	891.2	0.231	3.82E-23	+
Cln6	222.8	0.442	1.34E-05	
Cln7	518.8	0.379	1.12E-09	
Mapkbp1	452.0	0.448	2.49E-03	+
Map3k3	755.1	0.483	4.28E-06	
Creb3l1	407.8	0.239	1.02E-02	+

Plod3	963.6	0.420	6.48E-10	
Spag1	47.8	0.254	5.83E-08	
Abca1	790.1	0.466	3.74E-02	+
Anxa6	3958.6	0.364	7.02E-03	+
Eno2	158.3	0.394	7.68E-04	+
Stom	963.8	0.419	3.66E-06	+
Flt3l	11.4	0.343	2.97E-02	
Gfpt2	81.3	0.498	9.56E-03	+
Gpr162	173.3	0.385	2.50E-03	+
Leprel2	785.8	0.375	9.49E-07	+
Hoxc4	288.7	0.382	2.77E-02	+
Kcnh2	795.7	0.497	6.10E-04	+
Ksr1	249.0	0.463	2.43E-03	
Loxl3	346.0	0.472	3.40E-06	+
Ltbp2	38.2	0.281	8.32E-04	+
Matn4	30.0	0.183	5.62E-06	+
Mc5r	3.3	0.194	4.50E-02	+
Mmp9	101.7	0.062	5.29E-13	+
Ngf	20.9	0.271	7.58E-04	+
Pam	1977.4	0.460	5.94E-03	+
Sema4b	425.9	0.465	2.57E-05	
Sema5b	67.2	0.285	7.30E-04	+
Sema6b	108.2	0.455	5.68E-04	+
Thbs3	307.2	0.275	1.83E-04	+
Itgb1bp2	3.6	0.154	1.56E-02	
Pla2g7	196.1	0.209	1.61E-02	+
Dok3	27.9	0.362	2.41E-03	
Pald1	849.4	0.420	1.57E-08	+
Magel2	62.4	0.477	1.74E-02	+
Abcc5	971.6	0.456	2.38E-07	
Plk3	52.1	0.321	2.03E-06	
Jag1	421.6	0.419	1.48E-05	+
Abca7	468.7	0.337	8.04E-12	
Bag3	535.5	0.373	5.49E-04	+
Ndr2	477.2	0.426	5.69E-06	+
Zfp385a	305.8	0.433	3.40E-02	
Mapk12	106.6	0.454	2.26E-03	+
Dpf1	79.2	0.311	6.20E-07	+
Heyl	299.7	0.216	2.40E-04	+
Adamts8	467.2	0.354	4.59E-11	+

Apln	267.8	0.383	4.68E-07	+
Usp21	562.1	0.460	6.26E-07	
Mapk8ip3	1135.1	0.342	4.54E-12	
Ddx25	69.9	0.437	3.76E-03	+
Col5a1	5032.5	0.266	3.17E-20	+
Slit1	48.7	0.459	1.37E-02	+
Sufu	899.0	0.486	1.03E-02	+
Dkk3	462.5	0.466	7.83E-05	+
Capn15	292.3	0.403	3.47E-05	
Syt3	25.1	0.194	1.21E-06	+
Clasrp	236.9	0.243	1.56E-11	
Atp2a3	1158.0	0.416	1.46E-04	+
Dmp1	60.5	0.290	2.42E-05	+
Cntnap1	67.2	0.239	3.12E-02	
Nptx2	99.4	0.356	7.29E-05	+
Srrm1	2152.5	0.452	1.71E-04	
Chst3	310.3	0.336	4.01E-03	+
Vamp5	33.9	0.399	3.15E-03	+
Col5a3	52.3	0.296	1.59E-05	+
Krt14	24.7	0.404	1.60E-02	+
Stag3	56.1	0.359	2.61E-05	
Akap8l	397.1	0.414	3.71E-09	
Cd244	0.5	0.061	4.41E-02	
Scn1a	16.3	0.290	1.18E-02	+
Rassf5	40.7	0.428	2.48E-02	+
Calcr1	1051.7	0.427	7.37E-03	+
Prpf40b	443.2	0.390	1.10E-09	
Arc	17.2	0.153	7.55E-04	+
Plxnc1	91.6	0.303	1.75E-07	+
Hs3st3b1	198.6	0.238	6.94E-05	+
Sh2b2	81.3	0.478	6.29E-03	+
Wisp1	564.3	0.179	6.37E-06	+
Cpxm2	8.1	0.279	1.86E-02	+
Tmem131	2168.2	0.451	1.06E-02	
Avpr2	0.3	0.024	4.88E-02	
Cacng4	160.4	0.476	9.41E-03	+
Gabbr1	841.4	0.444	8.89E-07	+
Irgm2	234.2	0.477	1.02E-04	+
Ramp2	347.6	0.375	7.04E-08	+
Grk4	23.8	0.396	3.91E-02	+

Trpc3	34.5	0.431	4.26E-02	+
Grasp	179.9	0.486	5.60E-05	
Htra1	39.7	0.434	4.90E-03	+
Cxcl14	27.7	0.336	3.96E-02	+
Plxnb3	16.1	0.260	4.58E-03	+
Tmem45a	259.2	0.471	3.06E-02	+
Wsb1	3704.0	0.475	8.92E-08	+
Ddx39b	3671.4	0.494	1.04E-07	
Cpxm1	516.9	0.458	1.74E-06	+
Cdh13	62.5	0.434	4.10E-03	+
Runx3	9.5	0.210	2.28E-03	
Ggcx	288.2	0.343	3.46E-08	+
Git2	731.0	0.478	5.43E-06	
Copz2	118.5	0.350	3.50E-03	+
Tdo2	2.5	0.083	9.73E-04	+
Clef1	67.5	0.423	2.60E-02	
Supt20	420.0	0.404	8.60E-09	
Clec4n	52.8	0.409	2.00E-03	+
Mtor	975.8	0.475	3.07E-05	
Fgf21	3.5	0.189	4.15E-02	
Slc37a2	71.1	0.476	2.44E-02	+
Hhip	66.1	0.034	2.16E-13	+
Ank	685.0	0.407	7.88E-09	
Ehd3	203.3	0.447	1.30E-04	+
Cramp11	817.2	0.471	3.41E-02	
Nrip3	9.8	0.283	1.81E-02	+
Abcc9	2733.5	0.308	2.69E-04	+
Cxcl10	50.2	0.483	4.42E-02	+
Plcg1	1360.7	0.331	1.12E-14	+
Evc	486.0	0.338	1.61E-11	+
Itgax	8.3	0.059	6.91E-05	+
Kcne4	101.6	0.270	4.47E-10	+
Neur1a	281.9	0.466	2.29E-02	+
Pappa	109.6	0.072	3.70E-05	+
Sall1	71.2	0.056	2.90E-07	+
Rab37	25.2	0.232	2.51E-03	+
Mmp19	294.1	0.497	1.02E-02	+
Cacna1h	838.2	0.159	6.91E-06	+
Adamdec1	5736.4	0.465	1.81E-02	+
Rps6kb2	150.9	0.311	3.93E-11	

Med12	910.3	0.307	1.36E-13	
Huwe1	6213.6	0.481	6.49E-03	
Slc22a17	834.3	0.406	1.17E-08	+
Agri	4870.8	0.480	5.30E-06	
Doc2g	34.3	0.353	8.68E-05	
Fxyd7	66.4	0.431	3.90E-03	+
Parvg	32.3	0.442	1.78E-02	+
Herpud1	905.2	0.485	5.10E-07	
Ptges	104.7	0.469	5.74E-03	+
Fndc4	459.0	0.472	3.56E-06	+
Ddr2	1563.2	0.399	3.01E-06	+
Nisch	7609.3	0.479	3.46E-04	
Svep1	309.3	0.293	4.43E-02	+
Pmepa1	776.1	0.270	8.80E-17	+
Slc9a3r2	547.5	0.462	7.27E-07	+
Pkmyt1	408.5	0.479	9.28E-04	
Jam3	598.4	0.498	3.08E-06	+
Tmem132e	93.2	0.474	4.89E-03	+
Isyna1	1266.6	0.434	4.13E-09	
Tnfrsf22	58.6	0.248	6.64E-03	
Lime1	306.1	0.364	4.80E-09	
Wdr54	31.6	0.426	3.86E-02	+
Gdpc3	17.1	0.260	1.56E-03	
Fbln7	42.1	0.492	3.60E-02	+
Mxra8	1065.4	0.456	2.92E-07	+
Ipo4	846.0	0.444	3.17E-08	
Bves	70.0	0.352	5.53E-05	+
Tnfrsf23	28.1	0.120	1.80E-05	+
Stx1b	60.9	0.254	3.43E-07	+
Sharpin	313.5	0.493	2.08E-05	
Pcp4l1	126.7	0.257	1.08E-11	+
Exoc2	744.0	0.364	4.14E-12	+
Abi3	77.4	0.380	1.47E-03	+
Pnir	1850.0	0.455	9.68E-09	
Col27a1	1004.8	0.266	2.69E-05	+
Aspn	231.6	0.465	1.93E-02	+
Dnase1l2	21.1	0.304	1.62E-03	
Kcng4	6.1	0.151	1.06E-02	+
Plbd1	26.1	0.320	1.77E-03	
Smardc3	211.1	0.389	3.54E-06	+

Cap2	115.2	0.391	1.85E-05	+
Plxdc2	425.1	0.454	4.52E-06	+
Plxdn1	2192.7	0.359	1.90E-08	+
Tmem100	192.8	0.219	1.04E-17	+
Ppm1m	304.7	0.429	8.68E-08	+
Murc	26.2	0.310	2.80E-02	
Rcn3	1755.7	0.403	4.10E-03	+
Sdccag3	778.3	0.483	2.19E-06	
Col6a4	614.7	0.038	5.06E-21	+
Cthrc1	163.6	0.442	2.11E-05	+
Srpx2	129.6	0.206	1.42E-04	+
Cdan1	479.1	0.435	7.90E-07	
Sec31a	2343.7	0.451	1.20E-07	
Kmt2e	2449.1	0.442	3.33E-03	+
Sat2	67.8	0.466	7.90E-03	+
Dennd6b	124.5	0.345	6.36E-09	
Clic3	7.9	0.237	2.00E-02	
Sec24d	1272.9	0.289	3.18E-16	+
Col22a1	39.8	0.167	5.78E-07	+
Zmynd8	1617.4	0.410	7.74E-07	
Nkd1	435.4	0.380	3.46E-08	+
Chp2	2.9	0.098	1.51E-02	
Mier2	414.1	0.448	3.57E-06	
Ddo	0.6	0.042	8.47E-03	+
Sik3	828.8	0.480	1.25E-02	
Spef1	194.6	0.489	1.93E-04	
4933413G19Rik	31.2	0.458	4.23E-02	
Col24a1	334.5	0.342	2.02E-10	+
Izumo4	47.5	0.477	7.91E-03	
Rarres2	202.6	0.483	3.61E-02	+
Syde1	540.0	0.337	2.02E-07	+
Gramd1a	751.2	0.226	1.25E-22	+
Amdhd1	8.7	0.207	2.23E-03	+
Caskin1	161.9	0.299	4.54E-05	+
Osgin1	31.3	0.353	8.91E-05	
Zswim8	1694.4	0.354	5.64E-12	
Arhgef25	974.5	0.323	1.39E-07	+
Cda	44.4	0.463	9.52E-03	
Nkd2	45.2	0.290	1.12E-05	+
Fryl	880.3	0.443	1.20E-02	

Vps9d1	296.9	0.405	4.29E-07	+
Shmt2	1953.2	0.426	5.08E-09	
Rbm33	1279.9	0.463	3.11E-02	
Dzip1l	204.0	0.353	1.34E-07	+
Col16a1	833.3	0.384	1.76E-02	+
Anks3	437.8	0.473	6.06E-07	
Hspa12b	280.7	0.429	2.56E-06	+
Angptl1	1313.1	0.480	1.25E-02	+
Neil1	76.5	0.483	1.17E-03	
Fam101a	6.4	0.107	7.93E-06	+
Pear1	442.3	0.302	2.04E-04	
Bmper	113.6	0.364	7.99E-04	+
Col20a1	9.6	0.227	6.44E-03	
Rasip1	561.6	0.469	9.28E-06	+
1700094D03Rik	88.8	0.426	1.16E-03	
Btbd11	60.3	0.243	2.52E-02	+
Slc25a27	170.5	0.457	1.03E-03	+
Rftn2	495.9	0.470	1.79E-06	+
Syvn1	598.2	0.439	1.26E-03	
Ampd2	1032.8	0.326	4.59E-14	
Robo4	332.2	0.307	6.39E-12	+
Crtc2	398.8	0.386	7.45E-08	
Mau2	1353.5	0.488	1.83E-05	
Glb1l	293.2	0.444	4.66E-06	+
Ocstamp	3.9	0.049	4.69E-03	+
Atp13a2	924.5	0.452	1.17E-07	+
Lmbr1l	169.9	0.469	6.50E-05	
Hspb9	4.0	0.175	2.31E-02	
Ep400	2119.6	0.461	4.62E-02	
Fam227a	44.6	0.370	2.26E-03	+
Bcor	1202.7	0.493	2.04E-02	
Abcc3	71.6	0.498	3.53E-02	+
Gper1	48.2	0.266	4.68E-06	+
2310014L17Rik	12.7	0.135	7.82E-05	
Ppp1r12c	972.9	0.336	3.58E-07	+
Rgs7bp	90.2	0.407	6.40E-04	+
Fam162b	14.2	0.211	1.91E-04	+
Ptprb	299.2	0.466	4.38E-02	+
Chst15	1696.4	0.445	6.97E-04	+
Nup210l	15.5	0.274	1.28E-04	

Adamts12	17.3	0.169	2.05E-06	+	
Batf3	19.1	0.147	3.03E-09	+	
Htra3	1233.9	0.433	9.32E-08	+	
Clip4	86.9	0.348	4.56E-06	+	
Usp54	544.9	0.474	2.35E-03	+	
Sfi1	266.0	0.494	4.66E-05		
Dync1h1	5270.8	0.388	2.82E-05		
Igsf6	50.4	0.375	2.47E-03	+	
Tmprss5	15.9	0.356	4.10E-02	+	
Dtx3	1351.7	0.278	8.51E-06	+	
Sorcs2	916.8	0.420	5.38E-05	+	
Id4	259.8	0.408	1.78E-07	+	
Ift122	368.6	0.500	2.49E-05		
Tex15	99.5	0.464	3.70E-03	+	
Fstl3	31.1	0.428	1.11E-02	+	
Cnnm1	14.8	0.186	4.66E-06		
Bicc1	436.6	0.447	1.20E-03	+	
Srrt	1673.4	0.439	3.04E-10		
Gigyf1	733.7	0.232	1.21E-20		
Dpp7	253.5	0.463	7.56E-05		
Otof	19.0	0.064	7.26E-03	+	
Wasf1	389.5	0.408	1.48E-03	+	
Plvap	96.8	0.165	7.02E-06	+	
Dmpk	1093.5	0.427	3.79E-06	+	
Rnf123	409.6	0.465	9.92E-07		
Tnfrsf25	6.3	0.219	2.54E-02	+	
	42255	1461.1	0.471	2.60E-04	+
B3galt5	10.3	0.053	7.64E-06	+	
Loxl2	2832.8	0.497	2.43E-03	+	
Rab34	630.8	0.384	3.65E-11	+	
Slc4a10	45.7	0.107	3.21E-04	+	
Pcdhgb1	2880.3	0.480	2.47E-02	+	
Pcdhgb2	2907.9	0.480	2.34E-02	+	
Pcdhgb4	2904.8	0.484	2.48E-02	+	
Pcdhgb5	2903.4	0.480	2.41E-02	+	
Pcdhgb6	3030.8	0.483	2.38E-02	+	
Pcdhgb7	2971.2	0.482	2.92E-02	+	
Pcdhgb8	2856.3	0.481	2.67E-02	+	
Pcdhgc3	4061.6	0.459	3.76E-02	+	
Pcdhgc4	2882.8	0.476	2.64E-02	+	

Pcdhgc5	2842.8	0.476	2.66E-02	+
Pcdhga1	2896.2	0.484	2.03E-02	+
Pcdhga2	2942.0	0.481	2.59E-02	+
Pcdhga3	2949.4	0.483	2.29E-02	+
Pcdhga4	2914.1	0.482	2.29E-02	+
Pcdhga5	2906.6	0.482	2.67E-02	+
Pcdhga6	2929.5	0.484	2.27E-02	+
Pcdhga7	2995.2	0.490	2.88E-02	+
Pcdhga8	2893.2	0.476	2.51E-02	+
Pcdhga9	2890.5	0.478	2.93E-02	+
Pcdhga10	2932.0	0.483	2.66E-02	+
Pcdhga11	2935.5	0.483	2.73E-02	+
Pcdhga12	2922.9	0.483	2.49E-02	+
Adam33	8.4	0.221	1.77E-02	+
Fxyd2	8.0	0.059	5.81E-11	+
Fgd6	397.3	0.307	2.10E-02	+
Loxl4	12.3	0.240	8.72E-03	+
Cox4i2	21.9	0.387	1.95E-02	+
Trim8	692.6	0.495	7.68E-03	
Col4a6	158.5	0.312	2.21E-08	+
Slc24a3	465.3	0.351	3.73E-10	+
Antxr1	1144.0	0.449	2.52E-05	+
Gpr124	3078.0	0.448	9.14E-04	+
Gpr98	16.0	0.347	3.23E-02	
Mta1	1266.1	0.473	2.30E-06	
Necab2	33.2	0.430	1.32E-02	+
Bag6	2526.9	0.458	8.09E-08	
Cttnbp2	175.4	0.223	1.16E-15	+
Adcy4	81.8	0.290	5.99E-07	+
Celsr3	357.8	0.405	2.58E-02	+
Gjc3	29.4	0.335	4.16E-03	+
Synpo2	3349.5	0.462	3.90E-02	+
Ppap2b	999.8	0.473	1.06E-06	+
Emid1	410.4	0.468	9.94E-07	
Caskin2	671.8	0.387	1.52E-05	
Zcchc14	2251.0	0.478	4.74E-02	
Slc2a10	102.7	0.341	7.47E-06	+
Sp7	9.6	0.169	4.08E-04	+
Baiap2	189.8	0.362	1.88E-08	
Cacng7	343.9	0.325	1.05E-10	+

Il1rl2	101.7	0.302	1.92E-07	+
Znrf1	1035.3	0.473	1.35E-04	+
Slc8b1	159.5	0.310	2.10E-09	+
Atp13a1	915.2	0.443	1.11E-07	
Mapre3	213.1	0.349	1.73E-07	+
Erg	222.9	0.453	5.40E-05	+
Slc6a12	0.6	0.011	1.72E-10	+
Ier3	108.7	0.434	6.32E-04	+
Antxr2	794.0	0.483	9.40E-07	+
Ssbp4	456.7	0.499	1.11E-04	
Olfml3	1521.5	0.440	8.14E-09	+
Chpf2	685.0	0.482	2.41E-05	+
Krba1	665.0	0.489	2.69E-02	
Unc45a	612.9	0.484	5.29E-07	
Farp1	1052.4	0.490	7.10E-05	
Kdelr3	286.3	0.379	2.86E-08	+
Sgsm3	272.0	0.325	1.10E-12	
Gpsm3	76.7	0.251	3.16E-04	+
Actn1	3032.0	0.418	2.21E-10	
Havcr2	5.0	0.178	1.02E-02	+
Slc26a6	120.4	0.485	1.99E-04	
Mical1	388.0	0.418	3.04E-08	+
Arhgap4	50.1	0.458	8.13E-03	
Prpf8	4724.5	0.491	1.62E-06	
Abcg4	106.8	0.474	3.27E-02	+
Gbgt1	108.7	0.287	3.15E-03	+
Cytip	9.6	0.231	8.97E-03	+
Vasn	677.2	0.345	3.97E-03	+
Otoa	2.1	0.128	3.31E-02	
Prdm15	374.8	0.451	1.91E-06	
Tmem63a	387.6	0.434	1.53E-06	
Camk1g	108.6	0.340	2.06E-06	+
Nrbp2	367.6	0.432	2.02E-03	+
Dus3l	562.0	0.465	2.06E-08	
Lims2	50.3	0.335	2.41E-04	+
Pcnxl3	1434.6	0.459	8.73E-03	
Eml3	500.1	0.354	7.54E-11	
Rad9b	70.7	0.418	7.15E-04	
Tmem150a	191.0	0.439	1.53E-05	
Tnrc6a	2027.9	0.483	4.45E-04	

Sez6l2	233.3	0.467	1.82E-02	+
Map7d1	1604.3	0.417	7.98E-10	+
Lgi2	262.9	0.296	8.68E-12	+
Crtac1	72.2	0.382	4.03E-04	+
Mgat5	207.8	0.292	8.21E-03	
Gtpbp6	286.9	0.454	3.31E-07	
Angptl6	285.8	0.318	4.05E-09	
Pla2g4b	113.7	0.475	5.02E-04	
Fam193b	739.5	0.486	9.79E-04	
Pxk	319.5	0.383	1.78E-09	
Cerk	637.1	0.460	8.28E-07	+
P2rx3	57.5	0.412	1.16E-03	
Ccm2l	51.5	0.432	1.71E-02	+
Mypop	119.3	0.346	1.99E-03	+
Igflr1	41.8	0.303	5.61E-06	
Prr14	577.4	0.495	1.35E-05	
C1qtnf5	30.3	0.177	6.35E-09	+
Gdf10	133.7	0.283	1.65E-06	+
Pitpnc1	925.8	0.404	2.06E-03	+
Ranbp10	816.8	0.496	1.18E-03	
Xylt2	591.2	0.448	4.65E-07	+
Tpcn1	758.2	0.317	2.35E-04	
Cc2d1a	358.9	0.421	9.98E-09	
Hip1	1623.8	0.351	1.97E-03	+
Col6a2	5761.6	0.159	1.57E-29	+
Arhgap9	29.4	0.319	1.47E-04	+
Chd3	5860.9	0.287	1.13E-12	+
Plekhh3	361.3	0.458	7.21E-06	
Atf7	114.6	0.431	2.22E-04	
Zdhhc14	94.8	0.391	1.59E-04	+
Fam13b	796.7	0.466	9.13E-08	
Apbb3	231.2	0.356	5.48E-09	
Afap1l2	766.8	0.417	1.01E-08	+
Tesk2	212.2	0.432	2.07E-06	+
Tmem119	1187.6	0.461	3.20E-06	+
Lrch4	466.2	0.434	9.61E-07	
Cnot3	803.9	0.464	4.36E-06	
Ccdc106	123.4	0.445	8.02E-05	+
B3gnt8	55.5	0.420	9.41E-03	+
Wdr62	165.3	0.472	1.48E-04	

Tpcn2	148.4	0.490	4.53E-04	
Mfrp	30.6	0.178	7.09E-09	+
Rbm5	1791.6	0.435	6.86E-10	
Slco4a1	30.9	0.064	4.38E-31	+
Slc1a3	144.3	0.352	3.03E-06	+
Slc8a2	447.7	0.499	3.01E-02	+
Plcd3	55.6	0.469	1.58E-02	
Nmur2	11.0	0.287	2.56E-02	+
Sec16a	1684.7	0.483	2.27E-02	
Mmrn2	435.9	0.415	6.05E-07	+
Svil	3244.5	0.493	1.08E-05	+
BC037034	305.1	0.391	2.38E-08	
Cpne5	106.5	0.309	1.09E-03	+
Csrnp1	115.4	0.490	1.29E-02	+
Col23a1	3801.8	0.354	6.04E-05	+
Gpr156	19.4	0.391	4.15E-02	+
Gpsm1	674.4	0.481	2.43E-05	+
Nphp4	73.2	0.341	5.45E-05	+
Ankrd23	69.0	0.323	1.19E-05	
Cpne2	70.3	0.494	7.86E-03	+
Tenc1	917.7	0.290	1.99E-04	+
Adcy2	120.2	0.230	7.53E-14	+
Phldb1	837.4	0.428	3.10E-07	+
Aldh1l2	531.4	0.280	7.50E-16	
Strip1	1047.1	0.490	1.86E-07	
Mill2	8.0	0.304	4.14E-02	+
Acap1	94.2	0.275	3.20E-09	+
Scarf2	572.0	0.350	6.23E-10	+
Cpne7	13.0	0.169	1.50E-05	+
Adam1b	11.1	0.271	1.22E-02	
Adam1a	57.5	0.228	1.60E-07	+
Zdhhc8	862.0	0.461	1.55E-02	
Slc24a4	15.1	0.147	8.16E-07	+
Mark4	331.9	0.413	5.50E-07	
2210018M11Rik	565.4	0.496	1.29E-04	
Plcg2	71.9	0.466	2.40E-04	
Slc36a4	195.2	0.471	2.01E-02	+
Gpc2	509.5	0.494	1.52E-05	+
Ccdc134	131.5	0.414	8.06E-06	+
Cfap69	31.4	0.372	5.48E-03	

Adamts18	22.2	0.269	6.75E-04	+
Dennd2a	1022.4	0.478	4.65E-05	+
Cobl	387.2	0.276	4.50E-03	+
Dcaf15	536.5	0.479	1.59E-06	
Boc	529.1	0.463	1.03E-02	+
Polrmt	406.8	0.433	2.36E-08	
Hlf	74.4	0.394	1.70E-02	+
Unk	672.2	0.465	7.58E-06	
Lhfp12	535.6	0.350	1.25E-07	+
Ldlrad4	158.6	0.389	3.52E-05	+
Pogz	1426.2	0.474	4.78E-04	
Gcn1l1	1694.2	0.477	5.84E-06	
Fgd5	371.3	0.498	1.39E-04	+
Leng8	1327.8	0.252	4.17E-09	
Gramd1b	59.2	0.260	2.54E-09	
Gbp9	69.6	0.448	5.05E-03	+
Dock4	382.1	0.430	7.00E-04	+
Adamts4	242.2	0.429	1.55E-03	+
Kank4	163.0	0.171	1.18E-05	+
Slc6a11	2.4	0.024	1.96E-14	+
Man2a2	2304.0	0.406	1.11E-06	+
Nlgn3	95.7	0.274	9.82E-03	+
Ankrd13b	597.4	0.471	4.00E-06	
Mtcl1	420.7	0.236	1.28E-04	+
Sap130	827.0	0.487	3.21E-02	
4930503L19Rik	349.1	0.405	1.23E-06	+
Pank4	499.8	0.353	1.16E-12	
Ssc5d	735.7	0.396	6.78E-03	+
Gpr97	11.3	0.278	1.51E-02	+
Gga3	476.1	0.430	2.42E-04	
Bai2	268.3	0.493	6.21E-04	+
Chd6	2064.5	0.450	1.35E-03	+
Leprel1	141.9	0.292	4.93E-08	+
Bmp3	518.0	0.141	1.02E-34	+
Arsj	7.9	0.108	1.96E-06	+
Ube2o	715.2	0.476	6.88E-06	
Zfp641	31.0	0.415	4.41E-02	+
Npr2	402.0	0.421	3.69E-07	+
Slc41a1	591.6	0.490	5.12E-05	+
Phf12	1189.0	0.446	2.34E-03	

Impg2	38.5	0.361	1.31E-03	
Gpbar1	7.1	0.046	8.57E-05	+
Slc38a2	6147.4	0.458	6.03E-08	
Dnaic1	7.1	0.167	3.36E-03	+
Zdhhc1	159.9	0.319	1.17E-07	+
Atxn7l2	297.9	0.359	2.10E-08	
Kif27	39.1	0.460	2.51E-02	+
Dock10	240.8	0.400	9.47E-04	+
Chdh	41.7	0.362	7.28E-04	+
2700081O15Rik	2824.0	0.484	3.87E-06	+
Apol7c	50.8	0.069	6.46E-06	+
Gsap	30.6	0.420	3.48E-02	+
Sliirk6	1578.4	0.489	8.80E-07	+
Hcar1	37.6	0.443	4.94E-02	+
Zfp384	955.5	0.466	1.21E-04	
Adamts2	318.6	0.392	1.13E-02	+
Tnfrsf26	4.0	0.184	4.43E-02	+
Gpr4	39.1	0.252	5.54E-03	+
Glp2r	37.1	0.148	6.20E-08	+
A230050P20Rik	167.2	0.281	9.40E-10	
Snhg11	98.7	0.311	1.74E-03	
Hoxc5	259.7	0.390	1.60E-04	+
Leprel4	746.3	0.498	4.11E-04	+
Bptf	2663.7	0.476	1.19E-02	
Itga11	209.2	0.116	7.65E-22	+
Fbx17	387.6	0.395	5.29E-04	+
Dock6	791.8	0.191	7.94E-04	+
Fstl4	50.9	0.175	1.25E-03	+
Fndc9	11.2	0.157	2.94E-02	+
Adrbk2	748.6	0.459	8.12E-03	+
Casc1	3.6	0.166	1.08E-02	
Ankrd16	230.6	0.438	1.93E-06	
Itgb8	49.8	0.383	1.04E-03	+
Zfp653	169.8	0.431	2.12E-06	
Ust	131.1	0.473	5.23E-04	+
Micall1	1231.7	0.497	4.12E-02	+
Slx4	499.9	0.500	1.06E-04	
Arhgef15	168.8	0.447	4.06E-04	+
Plcb2	56.5	0.342	1.01E-02	+
Mkx	39.5	0.400	6.64E-03	+

Plekhh2	980.6	0.262	1.12E-12	+
Ryr3	95.1	0.366	1.48E-02	+
D630003M21Rik	45.6	0.131	1.61E-15	+
Fhod1	267.6	0.253	2.09E-14	
4933408B17Rik	21.8	0.199	8.71E-06	
Trpa1	17.0	0.241	1.50E-03	+
Prex1	528.5	0.406	1.91E-05	+
Exoc3l	165.7	0.374	3.31E-05	+
Mettl24	14.6	0.312	2.07E-02	+
Sh2d4b	2.1	0.134	4.15E-02	
Med12l	236.5	0.419	1.14E-05	+
Sdk1	1099.1	0.349	1.89E-02	+
Tmem150b	135.5	0.381	8.79E-06	+
Mapk15	6.4	0.237	1.10E-02	
Lrrtm2	67.9	0.388	9.19E-03	+
Setd1a	1304.9	0.370	3.54E-04	
Trim62	158.0	0.344	1.38E-03	+
Amigo2	98.4	0.262	1.13E-09	+
Arrb1	1341.8	0.425	9.43E-03	+
Hapln3	8.5	0.201	2.12E-03	+
Sorbs1	605.1	0.419	4.49E-06	+
Gpr153	633.3	0.452	2.00E-06	+
Nrg1	110.7	0.231	1.85E-11	+
Rcsd1	937.7	0.491	8.73E-07	+
Gjd3	2.5	0.105	5.66E-03	+
Uvrag	783.7	0.452	1.55E-07	
Oaf	990.4	0.392	1.52E-10	+
Tigd5	125.9	0.452	1.90E-02	+
Lrrtm3	63.9	0.245	2.99E-08	+
Clca5	68.2	0.193	1.12E-12	+
Dpy19l3	378.2	0.443	3.82E-03	+
Zfp592	1128.4	0.467	3.89E-02	
Plscr4	172.2	0.492	4.36E-04	+
Slc26a11	134.9	0.477	1.07E-03	
Pced1a	319.0	0.428	1.46E-06	
Rasal3	22.8	0.342	6.91E-03	+
Vstm4	222.3	0.227	4.00E-06	+
Hs3st3a1	56.2	0.345	4.27E-03	+
Dcun1d4	923.3	0.425	2.39E-08	+
Prkd2	342.1	0.374	5.64E-03	+

Pld4	113.5	0.490	1.04E-03	+
Gbf1	1163.1	0.475	3.70E-06	
Aoc2	51.1	0.346	1.32E-02	
Slc25a29	55.6	0.491	3.79E-02	+
Pxdn	6052.4	0.424	9.43E-07	+
Ushbp1	211.1	0.400	2.22E-04	+
Gpr141	6.6	0.231	2.46E-02	+
Fam167b	26.9	0.398	2.42E-02	+
Ntrk3	306.0	0.397	2.70E-04	+
Zfp692	249.9	0.353	1.53E-10	
Atxn2l	1615.2	0.335	7.94E-07	
Helz2	407.5	0.447	1.74E-02	
Fsd1	115.0	0.359	6.96E-07	+
Fat4	1508.3	0.182	9.86E-03	+
Proser3	206.5	0.448	1.03E-02	
Klhl6	103.3	0.367	1.16E-05	+
Gbp6	32.3	0.395	2.42E-02	+
Rnf31	284.6	0.485	1.34E-04	
Atg2a	500.6	0.343	6.64E-06	
1700025G04Rik	1592.3	0.492	3.16E-03	+
Cuedc1	506.0	0.376	3.81E-10	+
Ranbp3l	9.3	0.027	1.38E-35	+
Tbkbp1	445.6	0.404	2.23E-04	+
Tmem63b	730.7	0.481	1.12E-06	
Szt2	688.0	0.315	3.73E-04	
Arhgef40	1532.4	0.332	2.29E-14	+
Tanc1	1009.6	0.440	1.01E-04	
Klhl17	327.3	0.447	8.63E-06	
Ablim3	53.3	0.379	3.59E-04	+
Tmtc1	267.8	0.195	1.55E-05	+
Dgkq	361.0	0.460	1.02E-05	
Zfp335	549.7	0.382	7.76E-09	
Jade2	206.4	0.384	1.24E-02	
Ece1	2183.8	0.487	2.36E-06	+
Dot1l	988.1	0.439	1.06E-06	
Cdh24	254.0	0.438	1.09E-05	+
Ccdc84	86.1	0.318	1.57E-08	
Tlr12	21.1	0.061	4.12E-22	+
Mycbp2	2430.4	0.489	2.23E-03	
Gpr137	213.0	0.452	5.04E-05	+

Lmo3	57.4	0.367	2.43E-04	+
Acap3	460.0	0.438	2.04E-06	
Gtf3c1	1836.2	0.440	4.51E-08	
Plexd1	228.5	0.461	1.22E-06	
Egfr	587.4	0.435	2.58E-04	+
Ccnl2	1575.6	0.462	2.00E-08	
Dnm3os	1104.1	0.277	5.13E-17	+
Has2os	11.1	0.283	1.38E-02	+
Snhg1	282.6	0.399	5.85E-09	
Pvt1	73.6	0.492	2.65E-03	
Neat1	498.5	0.368	9.62E-04	
Pisd-ps1	526.1	0.388	2.38E-04	
Pisd-ps3	526.7	0.389	2.37E-04	
ChkbCpt1b	339.0	0.413	7.22E-09	
3830408C21Rik	36.6	0.433	2.94E-02	+
2610203C20Rik	614.9	0.260	1.75E-02	+
C2300351I16Rik	24.0	0.362	8.87E-03	+
A230057D06Rik	13.9	0.333	3.99E-02	+
Rab10os	85.8	0.488	2.61E-03	
4933439C10Rik	121.5	0.466	2.31E-04	
4732416N19Rik	16.3	0.198	1.53E-03	+
Peg3os	889.8	0.491	7.91E-03	+
Gm5577	41.5	0.329	9.29E-04	+
Clk1	4273.8	0.464	1.73E-05	
Ppp4r1l-ps	140.1	0.404	5.67E-05	+
D930048N14Rik	103.9	0.468	3.70E-03	
Gm5607	44.7	0.409	2.62E-02	+
Mirg	157.9	0.322	2.16E-03	+
AI450353	25.3	0.250	3.49E-02	
4930404I05Rik	5.2	0.193	3.33E-02	
Ftx	236.4	0.414	7.83E-07	
4930528A17Rik	23.8	0.413	2.22E-02	
9230102K24Rik	19.3	0.395	4.43E-02	+
F930015N05Rik	25.5	0.329	9.65E-03	+
Snord88c	0.9	0.074	4.29E-02	
Snord37	1.4	0.098	1.72E-02	
Snora17	0.9	0.059	5.21E-03	
Gm14005	0.5	0.022	2.24E-04	+
1700018A04Rik	3.6	0.066	3.58E-06	+
6530402F18Rik	13.1	0.213	1.01E-03	+

Gm11149	46.4	0.195	4.11E-02	+
Ppp1r3fos	18.6	0.418	4.42E-02	
Mir24-1	2.5	0.119	2.35E-02	+
Mir214	30.1	0.296	1.64E-02	+
Mir199a-2	6.2	0.254	4.13E-02	+
Mir671	16.8	0.360	4.29E-02	+
Mir761	0.6	0.108	4.44E-02	
Mir702	4.5	0.221	1.26E-02	
Gm4532	19.6	0.348	3.20E-03	
2810410L24Rik	88.6	0.388	1.01E-04	+
Mir22hg	48.2	0.492	1.56E-02	
F630028O10Rik	13.7	0.339	4.79E-02	+
Foxd2os	21.4	0.177	2.28E-04	+
Zfp57	549.3	0.427	8.93E-08	+
Gm20605	531.9	0.414	1.79E-07	
Bmp1	1719.2	0.304	2.31E-16	+
Prr33	67.8	0.131	2.50E-02	+
BC065397	43.0	0.451	1.44E-02	
Npff	16.5	0.295	2.96E-02	
AI504432	93.3	0.408	8.75E-05	+
Gm8221	27.4	0.072	3.40E-04	+
Miat	1474.4	0.393	1.56E-02	+
6030408B16Rik	19.1	0.072	5.46E-21	+
Gm5084	1.5	0.073	1.61E-03	+
Chkb	332.6	0.435	9.74E-08	
Mir3064	89.8	0.404	1.72E-04	+
Mir3074-1	4.1	0.133	9.95E-03	+
Adams10	582.6	0.208	6.29E-25	+
1600020E01Rik	101.0	0.430	3.97E-05	
4930579G18Rik	78.1	0.340	2.71E-03	
4931403G20Rik	3.7	0.085	2.80E-02	
E230016M11Rik	45.4	0.250	2.75E-04	
Gm19434	5.2	0.194	2.78E-02	
Gm19897	39.2	0.281	9.56E-07	
Gm16796	3.4	0.380	4.09E-02	
Gm10785	21.0	0.295	4.39E-02	
Gm9899	70.0	0.493	8.07E-03	+
C920021L13Rik	38.4	0.342	1.38E-03	+
Pesk2os2	5.7	0.116	2.26E-04	+
E130102H24Rik	34.8	0.474	1.32E-02	

A930011O12Rik	80.1	0.204	2.07E-03	+
Kcnd3os	2.5	0.134	2.19E-02	+
2700038G22Rik	36.9	0.378	3.25E-03	
Slc2a4rg-ps	100.8	0.315	2.97E-05	
2900076A07Rik	53.9	0.481	1.62E-02	
Gm20748	78.0	0.240	1.11E-02	+
1700071M16Rik	22.6	0.188	1.41E-05	+
Fendrr	259.8	0.091	4.49E-02	+
2210416O15Rik	9.0	0.240	6.41E-03	+
Klc2	408.6	0.477	1.62E-06	
AW549542	63.8	0.450	9.95E-03	+
E130310I04Rik	167.9	0.324	2.91E-04	+
Gm16617	39.1	0.252	2.56E-02	+
Gm16596	55.0	0.296	4.27E-06	+
A430090L17Rik	7.8	0.127	4.42E-02	+
B130024G19Rik	24.1	0.223	3.51E-05	+
Gm15612	318.6	0.470	7.62E-05	+
Gm11747	79.7	0.327	2.06E-02	+
Frs3os	10.8	0.259	8.78E-03	
9530052E02Rik	13.8	0.282	5.94E-03	
4732471J01Rik	24.6	0.373	1.80E-02	
Milr1	17.0	0.336	2.60E-02	+

Ager	31.7	0.242	6.11E-06	+
Phc1	982.1	0.454	4.36E-06	
Sema6c	324.7	0.404	7.64E-05	+
Pitpnm1	252.1	0.493	1.51E-04	
A330033J07Rik	5.5	0.087	2.35E-06	+
Cd22	5.7	0.282	4.27E-02	
Plekhg5	343.8	0.429	4.05E-06	+
Xntrpc	314.3	0.498	1.31E-04	
Mir6418	50.0	0.338	3.70E-07	
Mir6935	9.4	0.269	3.85E-02	+
Mir6991	1.8	0.109	6.92E-03	
Mir6992	2.3	0.128	2.58E-02	+
Mir7077	0.3	0.054	2.80E-02	
Mir8093	3.2	0.178	4.75E-03	
Mir8094	215.3	0.405	1.79E-08	
Mir1668	15.1	0.177	6.31E-05	+
Tmem67	181.4	0.498	2.04E-04	+
Map4k2	312.1	0.262	3.72E-15	+
Ndst3	42.4	0.420	1.82E-02	+
Trim46	121.0	0.257	1.09E-04	
Mb21d1	78.1	0.398	2.91E-04	+

Table S4.3. Genes downregulated by loss of Hh signaling. Average read counts for genes in whole intestine downregulated 2 fold (FC) by cyclopamine (Cyc) treatment (p -value ≤ 0.05)

Chapter V

Conclusions

In multiple tissue-specific settings, Hh signaling directs specific cell fate choices, controls tissue patterning and governs cell proliferation. While it is well established that Hh signaling is critical to the formation of several cell types in the developing intestine as well as influencing at least seven cell types in the adult intestine, almost nothing is known about *how* it does so. The critical questions are: What specific genes are activated? Which genomic enhancers activate those genes? How is context (cell-type) specificity of response established? This work has made several advances towards understanding characteristics of Hh enhancers as well as expanding on the role of Hh signaling in one context, the developing intestinal inner circular muscle (ICM), a component of the ISM. Computational methods, described in Chapter II and III, have made advances towards understanding characteristics of Hh enhancers. Results presented in Chapter II reveal that although some *Drosophila* Hh enhancer regions contain homotypic clustering of *ci*/GLI sites, homotypic clustering alone is insufficient information to predict Hh enhancers. Chapter III validates machine learning as a prediction method that has a high success rate for the identification of mammalian Hh enhancers and also establishes a new *in vitro* GLI library containing higher confidence binding sites for this factor. Finally, biological data presented in Chapter IV demonstrate a previously unknown role for the Hh target gene *cJun* in

development of the ICM. Additionally, the work in Chapter IV suggests that Hh signaling may play similar roles in SM and skeletal muscle. Together, these results make important advances to understanding methods for identifying Hh signaling targets and suggest additional areas that require further study.

5.1 Computational Prediction

5.1.1 Effectiveness of Using Highly Conserved Sequence and Clustering for Hh Enhancer Prediction

Prior to the computational prediction methods presented in Chapters II and III, two computational tools had been developed to globally predict Hh enhancer regions: Enhancer Element Locator (EEL) and Module Cluster Analysis (MCA) (Hallikas et al., 2006; Vokes et al., 2007). EEL relies on the presence of clusters of TFBS within orthologous sequences from two species to predict active enhancer regions. Using human to mouse conservation and the presence of at least two predicted GLI TFBS, the authors identified only 42 elements as putative Hh enhancers in the mouse genome. Two of these 42 were previously known Hh enhancers for *Gli1* and *Ptch1* (Dai et al., 1999; Agren et al., 2004; Ikram et al., 2004), but none of the other 40 have ever been tested for Hh-responsiveness in functional assays. Therefore, the rate of false positive selection using this method is not clear. However, the false negative rate is very high. The set of 42 missed the other known Hh enhancer at the time *FoxA2* (Sasaki et al., 1997) and does not contain any of twelve additional Hh enhancer regions (Table 1.1) or regulatory regions confirmed as GLI dependent within this dissertation (*Boc*, *cJun*, *Dpp6*, *Hhip*, *Hipk2*, *Ptch1*, *Scube1*, *Tgfbr2*).

MCA predicts Hh enhancer regions by searching for enrichment of GLI TFBS against a background Markov model within highly conserved (across mouse, rat, human, dog and zebrafish) sequences. Using qPCR of GLI^{FLAG} ChIP peaks from SHH treated embryoid bodies, the authors confirmed that 11/28 predicted regions, six previously identified, were bound by GLI1. The total number of MCA predicted enhancers was not reported. While almost 50% of predicted regions appear to be bound, none of these were actually tested for Hh responsiveness or for loss of responsiveness upon mutation of the GLI binding sites.

Both of these methods rely on the presence of more than one GLI TFBS and on the presence of highly conserved surrounding sequence. These approaches are most similar to the homotypic ci/GLI clustering method outlined in Chapter II, which searches for enrichment of ci/GLI binding sites against background chromosomes containing the same GC/AT landscape and have the same number and type of ci/GLI binding sites as the native genome. This method which identified 8/22 enhancers, one previously known, includes a conservation component, although it is far less restrictive than the ones used in EEL and MCA, only requiring a minimal overlap between enriched clusters in *D. melanogaster* and *D. pseudoobscura*. Comparing the success rate for MCA (22%, excluding previously known enhancers), to the method in Chapter II (33%), suggests that conservation might not be an important factor for predicting Hh enhancer regions. The low yields for these results also suggest that while some Hh enhancers may contain multiple ci/GLI sites, not all clusters function as enhancers. Indeed, the machine learning method implemented in Chapter III, using only sequence information from GLI^{FLAG} ChIP peaks, predicts Hh enhancers with a much higher accuracy 77% (Fletez-Brant et al., 2013).

The strength of these types of machine learning approaches is that no prior knowledge of enhancer characteristics is required for prediction. The kmer-SVM method implemented in Chapter III has no prior constraints regarding clustering of TFBS, conservation, or other parameters. However, it does rely on high quality biological data to use for training and such data might not be readily available in all cases. In fact, evaluation of the five publically available GLI^{FLAG} datasets (Vokes et al., 2007; Vokes et al., 2008; Lee et al., 2010; Peterson et al., 2012) resulted in only two (Vokes et al., 2008; Peterson et al., 2012) that were useful for prediction (Figure 3.2). One data set contained too few data points for training (Vokes et al., 2007) while the other two datasets (Lee et al., 2010) contained too much variability across its sequences for the classifier to effectively distinguish true from false positives within the training set (Figure 3.2FG).

The approach in Chapter III was designed to remove context specific characteristics by overlapping predictions generated in two different contexts and focusing on Hh pathway components, which should hypothetically be shared across any tissue with Hh activity. The results suggest that when Hh regulates its own pathway components in different tissues, multiple Hh enhancers may exist for regulation in each tissue context. The identification of additional Hh enhancers for *Hhip* and *Ptch1* is consistent with the analysis of the GLI1^{FLAG} and GLI3^{FLAG} datasets, which collect multiple peaks for *Boc*, *Hhip*, *Gli2*, *Hhipk2*, and *Ptch1*. It remains unclear whether these enhancers are active in different contexts or if they function together as secondary enhancers in an enhancer complex to drive gene expression. It would be interesting to link these enhancers to reporters and test their tissue and temporal specificity in transgenic mice. Evidence currently suggests that *Boc*, *Hhip*, *Gli2*, and *Hipk2* (Figure 3.4), as well as the *Drosophila ptc*

enhancers (Table 2.1), have different enhancer regions that are active in different contexts. This is in line with work in other enhancer settings that suggests that the totality of the gene expression domain for a given gene might be determined by a large number of individual enhancers that are expressed in different spatial and temporal contexts (Goto et al., 1989). On the other hand, *Ptch1* appears to have multiple enhancers that are active at the same place and time (Vokes et al., 2007; Vokes et al., 2008; Lee et al., 2010; Peterson et al., 2012). The origin of these enhancers has not been studied. It is possible that they arose from duplication, or they may have independently evolved similar expression patterns, though the driving force for the latter is difficult to imagine.

5.1.2 Context Specific Predictions

The machine learning approach implemented in Chapter III might also work for predicting context specific features. In fact, the analysis of the neural progenitor dataset detected a SOX motif, likely representing the binding site for the neural specific GLI1 cofactor *Sox2* (Peterson et al., 2012). In addition, a TFBS for KROX-20, a putative limb factor was also detected in the GLI3^{FLAG} limb data. However, the successful use of machine learning to detect context specific features relies on the availability of high quality biological data.

5.1.3 Control of Regulatory Regions

The temporal and spatial specific activation of genes results from a complex regulatory circuitry, involving transcription factors as well as higher order regulatory elements (histone modifications) within chromatin that are modified to affect access to DNA (Calo and Wysocka, 2013). In order for transcription to initiate (RNA polymerase binding to a promoter) the DNA

needs to be open and the transcription factors that complex into the enhancer need to be present. The ENCODE project is helping to strengthen predictions of putative enhancer regions (on a tissue specific level) by assaying multiple types of chromatin modifications across multiple cell types on a global scale. In particular, DNase I sensitive regions, P300 binding and histone marker combinations such as H3K4me1 and H3K4ac have been shown to correlate with enhancer activity and can be used to both uncover new enhancers as well as indicate the contexts in which a known enhancer is active (Heintzman et al., 2009; Rada-Iglesias et al., 2012). The approaches used in this dissertation focused on only on sequence features of transcription factor binding sites. Thus, while these genomic features predict the possibility of gene expression, it is likely that each Hh enhancer will only be active in a subset of contexts because of chromatin access (Figure 5.1). Newer machine learning methods have now been successfully implemented that incorporate chromatin accessibility with sequence information (Tsai et al., 2015). However, these methods require robust biological datasets that pair markers of open chromatin with GLI binding information. These currently do not exist.

5.1.4 Null Model Selection

Intrinsic properties of the native sequence are critical to genomic function but still poorly understood (Parker et al., 2009). For this reason, determining what to use as a background for sequence comparisons still remains an unresolved issue in enhancer prediction although the importance of maintaining the original properties of the native sequence when generating a background comparison has been discussed previously (Fitch, 1983). Distribution of GC content has been strongly correlated with gene density and regulatory features (Lander et al., 2001; Wang et al., 2012b). Therefore, when establishing background genomes for comparison of

ci/GLI density, in Chapter II, we used a strategy that randomly flips each base to its complimentary partner. This approach maintains the GC/AT landscape of the native *Drosophila* chromosomes. This is particularly important because of the disparity between the average GC content of the *D. melanogaster* genome (43%) and the GC rich ci/GLI binding site (67%) (Hallikas et al., 2006; Keightley et al., 2009). However, generation of background sequence in this way ignores the relationship between sequential nucleotide sequences, such as those captured in dinucleotide frequencies. One way to incorporate intrinsic properties of the native sequence is to select background regions from the native genome. kmer-SVM randomly selects sequences with matching GC content from the native genome to compare the positive sequences against. The disadvantage to this approach is that it may include functional enhancers within the background sequence, which may train the classifier to miss some components of functional enhancers.

5.1.5 Evaluation of Prediction Methods

One of the issues in enhancer prediction is inconsistency in the methods used to verify predictions. While the gold standard is to test enhancer activity and to show that enhancer activity relies on transcription factor binding, this is very seldom done. For example, Biehs et al. used a DAM methylase protection assay to define Hh enhancers for *Drosophila*. They identified 52 supposed target genes that had protected regions and that were modulated when Hh signaling was increased or decreased, but none of these were actually functionally tested in enhancer assays (Biehs et al., 2010). A more appropriate and meaningful validation focuses on actually testing the proportion of true positives within a predicted positive set and this was the level of assessment that we performed in Chapter II and Chapter III. Of critical importance, we also

verified positives as directly dependent on GLI binding. This is particularly important for evaluating Hh signaling, since it is an upstream regulator of many other transcription factors. Without the mutagenesis of GLI TFBS, it would be impossible to distinguish if enhancer activity in response to Hh signaling is direct or indirect. An additional strength would be to include predicted negatives in evaluations. Since only a small proportion of the hundreds of predictions can be biologically validated, including predicted negatives would help determine effectiveness of the method. If the prediction method correctly identifies 50% of putative positives but only 10% of the putative negatives are true negatives, it should not be considered successful. Of course, testing can be done on several levels. One approach is the use of transfected cell lines. However, while these generally reveal the potential for regulation, they do not always correctly reflect context specificity *in vivo*. A major challenge for functional testing is establishment of an assay system that can actually detect specific spatiotemporal activity. Perhaps the best assessment tool is the transgenic animal (e.g., transgenic *Drosophila* or mice), but these models require a significant amount of time and expense to generate and evaluate, especially in the case of mice. In addition, if the objective is to functionally test enhancers that were found by computational means and the spatiotemporal expression pattern is unknown (as was the case for our study in Chapter II), the requirement to analyze a large number of tissues and time points to find the specific site of expression can greatly complicate the analysis.

5.1.6 Annotation of Enhancers to Target Genes

A critical component to understanding gene regulation is linking enhancer regions to their target genes. Computationally, this still remains a large challenge since enhancers can target genes from great distances. Currently, most enhancer regions are annotated to the nearest

neighboring genes; this is the annotation method we employed in Chapters II and III. Additionally, in Chapter II the other genes within the CCCTC-binding factor (CTCF) boundaries were also reported, since it is expected that enhancers would most likely target genes within the same boundaries (Chen et al., 2012). Without proper annotation, initial assessment of predictions using GO or GSEA may be misleading. Annotation is also of critical importance to understanding the underlying biology of the system. As high throughput chromatin interaction techniques including ChIA-PET, 3C, 5C, and Hi-C continue to advance and become more prominent, data that links enhancers to target genes will become increasingly available.

5.2 Biological Conclusions and Future Directions

5.2.1 Regulators of ISM

Chapters II and III of this thesis start with computational strategies to predict features of biological systems that can be further tested in order to understand biological function. In Chapter IV, the analysis was run in the other direction: biological data was generated and then analyzed computationally to uncover how one of the visceral smooth muscle layers of the intestine, the ICM, is formed. Although ISM is of critical importance to the function of the intestine, surprisingly little is known about what genes are transcribed in this tissue or what molecular pathways control its development. One signaling pathway that had previously been linked to the development and homeostasis of ISM is Hedgehog. Acting downstream of Hh signaling, BMP is known to regulate smooth muscle progenitor populations (Kedinger et al., 1998a; Torihashii et al., 2009), while MYOCD, a master regulator of smooth muscle, is likely involved in maintenance of ISM in the adult (Zacharias et al., 2011).

Although these anecdotal studies have pinpointed some aspects of ISM transcriptional control, I reasoned that a more comprehensive analysis of gene expression in ISM might reveal important upstream regulators of ISM development. Therefore, I performed transcriptome profiling during early muscle development to identify genes that are enriched in intestinal mesenchyme tissue. Using gene set enrichment and clustering analysis followed by examination of *in situ* data at E14.5, I identified over 100 genes that are expressed in the ICM. The promoters of these genes were then analyzed to identify transcription factors that might be involved in the regulation of ISM genes. This analysis identified *cJun* as a regulator of ISM, expanding its previously suggested role as a regulator of both vascular and skeletal muscle cell homeostasis (Kami et al., 1995; Daury et al., 2001; Yasumoto et al., 2001; Chiba et al., 2014).

Since Hh signaling had been shown to be a regulator of *cJun* in some contexts (Laner-Plamberger et al., 2009; Amable et al., 2014), we confirmed that the same is true in muscle (Figure 4.5C). To identify a possible Hh enhancer, we examined the results presented in Chapter III and identified a predicted Hh-controlled regulatory region 60 kb upstream of *cJun*. This genomic region was found to drive gene activation in response to Hh and GLI-dependent activity was confirmed by retesting after mutagenesis of the GLI binding site (GKO). Attenuated response of the GKO sequence confirmed GLI-dependent activity (Figure 5.6).

This is the first study to recognize a potential role for *cJun* in the regulation of ISM. Analysis of the regions bound by cJUN in our ChIP-seq analysis revealed that many of these regions are also bound by factors known to be important for muscle development, including SRF and MYOCD. This finding implicates *cJun* as a participant in a transcriptional cascade that directs smooth muscle identity. Previous studies of cJUN primarily emphasize its role in the

stimulation of gene expression in adult tissues that is mediated by cellular stressors, such as inflammation or UV light. In this context, it works as a heterodimer with cFOS, which, like cJUN, is a cellular oncogene. It has also been established that in some cases, cells require cJUN for progression through the cell cycle and *cJun* null cells are arrested in G1 (Wisdom et al., 1999). In fact, previous analyses had demonstrated that *cJun* is required for proliferation of vascular smooth muscle (Yasumoto et al., 2001). We speculate that this proliferation function could be important in the context of the developing ISM as well. It will be important to functionally test the degree to which *cJun* actually participates in smooth muscle proliferation and differentiation by conditionally removing this factor from ISM. This could be accomplished with a conditional deletion of *cJun* using the Twist2-Cre line that expresses Cre recombinase throughout the mesenchymal compartment at E14.5 (Šošić et al., 2003).

The fact that *cJun* appears to be a Hh target, coupled with the potential role of cJUN as an important regulator of ISM genes suggests that Hh might function as a master regulator in this tissue. To examine other muscle regulatory factors downstream of Hh signaling, I next examined the transcriptome of the ICM after downregulating the Hh pathway using cyclopamine. In addition to the previously known Hh target *Myocd* (fold change with adj. p-values < 0.05 (FC): -2.13), several genes implicated in stem cell regulation or shown to regulate differentiation in other muscle types were also downregulated (Table 4.2). These data suggest dual roles for Hh in proliferation of smooth muscle precursors and promotion of differentiation into ISM. This is similar to skeletal muscle where Hh regulates both *MyoD* and *Myf5* (Borycki et al., 1999) (Chiang et al., 1996) (Gustafsson, 2002; Borello et al., 2006; Voronova et al., 2013), to control the establishment and maintenance of muscle progenitor cells (Pownall et al., 2002), as well as

Pax-3, to initiate differentiation (Borycki et al., 1998; Duprez et al., 1998; Pownall et al., 2002; Hammond et al., 2007). Additionally in skeletal muscle, Wnt acts downstream of Hh to coordinate the progenitor cell population (Braun and Gautel, 2011; Singh et al., 2012). The downregulation of several modulators of Wnt signaling by cyclopamine in our analysis (FC: *Dkk1*, -84.45; *Edar*, -21.86; *Sall1*, -17.75) suggests that a similar phenomenon might also occur in SM (He et al., 2013) (Kiefer et al., 2010; Wells et al., 2010). This would be of interest to directly test, by carrying out a ChIP-seq for Hh targets in the ISM. Though no ChIP grade GLI antibody is available, a mouse line has been described that carries a FLAG-tagged version of GLI1. This line has been used successfully in several other studies, as described in Chapter III. Use of the Twist2-Cre driver to activate GLI1^{FLAG} at E14.5, in combination with the cyclopamine data already obtained, would provide an excellent approach to the elucidation of the Hh transcriptome in ISM. Hh signaling is likely to be very important in ISM, since overexpression of Hh has been shown to greatly amplify the SM population in the intestinal mesenchyme (Zacharias et al., 2011).

Surprisingly, *cJun* (fold change with adj. p-values > 0.05 (FCNS): -1.21) was not downregulated in this dataset. Since we showed that *cJun* was a direct target of Hh in muscle (Figure 4.5B) and had seen upregulation of *cJun* (Figure 4.5C) when intestinal mesenchyme (without epithelial tissue) was treated with the Hh agonist, SAG, it is likely that either the transcript is very stable or that additional signals maintain *cJun* levels in the context of the cyclopamine-treated whole intestine. One obvious possibility is *Mef2C*, which has been shown to modulate *cJun* through promoter interaction (Han et al., 1992; Han and Prywes, 1995) and was also not downregulated (FCNS: -1.03) in this dataset. The ERK pathway, which stimulates

critical muscle factors, including *Caldesmon* and *IL-1 β* (Hedges et al., 2000a; Hedges et al., 2000b) in airway smooth muscle, has been shown to act upstream of *Mef2C* to upregulate *cJun* (Fanger et al., 1997). However, imaging of *cJun* and *Mef2C* at this time point indicates that *Mef2C* expression occurs outside the ICM (Figure 5.2). Interestingly, muscle fibers stained with *Mef2C* appear to run in the longitudinal direction and overlap with the *Gli2* expression domain where the OLM will develop (Figure 5.2) (Kolterud et al., 2009). Since MEF2C and GLI2 have been previously shown to both regulate each other's expression and to form a cofactor complex in both cardiac and skeletal muscle (Voronova et al., 2012; Voronova et al., 2013), it would be interesting to test whether a similar phenomenon is occurring in the OLM of developing intestine.

5.2.2 Regulation and Timing of Hh Components (Coordination of Gene Targets)

Hh signaling was previously known to target muscle transcription factors *FoxF1*, *Mef2C* and *Myocd* with the data presented in Chapter IV expanding this list to include *cJun*. The next challenge is to determine how the downstream targets of Hh are coordinated. Many of the Hh muscle targets regulate each other; feedback and feedforward regulation is likely. A protein interaction between cJUN and MYOCD has been described in vascular smooth muscle that indicates that over expression of *cJun* represses *Myocd* function (Gordon et al., 2009b). Additionally, FOXF2 interacts with promoters of *Myocd* and *FoxF1* to modulate SRF signaling (Bolte et al., 2015). Determining the organization of these feedback loops would require functional experiments in genetic mouse models, coupled with gene expression analyses.

However, given recent successes in the use of embryonic stem cells to generate specific tissues *in vitro*, it is also interesting to imagine the development of an *in vitro* assay system for smooth muscle development and differentiation. Given the current paucity of good cell lines for the study of smooth muscle biology, this would provide a much needed and valuable tool.

Another important consideration regarding Hh signaling in the context of the intact tissue is the possibility that a morphogen gradient of Hh is important in smooth muscle specification. Experiments done over a decade ago by Sukegawa et al. suggested that a high concentration of Hh ligand is actually inhibitory to smooth muscle development. These authors concluded that this requirement for lower concentrations of Hh ligand accounts for the fact that the muscularis externa develops so far away from the epithelium, the source of the ligand. In fact, they made intestinal sandwich cultures in which the epithelium was placed on the outside of the intestinal tube and found that this shifted the location of smooth muscle development (Sukegawa et al., 2000). Though later experiments showed that this may be an over-simplification (i.e., overexpression of Hh in the epithelium causes ectopic muscle to develop in mesenchyme directly adjacent to the epithelium) (Zacharias et al., 2011), it is nevertheless true that Hh does act as a morphogen in several settings (Vokes et al., 2007; Vokes et al., 2008; Peterson et al., 2012) and it is interesting to consider how this could play out at the level of the enhancers. It is likely that these complex questions about spatial patterning might be best tackled by developing simple systems such as the *in vitro* models discussed above, in which both Hh concentration and tissue patterning could be engineered.

5.3 Outcomes

In conclusion, the results of this dissertation emphasize the importance of integrating computational methods with biological data. By using both in parallel, advances have been made in understanding characteristics of Hh enhancers and critical findings, determining gene targets as well as regulatory regions, within the context of inner circular muscle development were uncovered. These findings further implicate Hh signaling as a master regulator of intestinal smooth muscle development and identify a new role for *cJun* within this cascade. Together these results may lead to a greater understanding of disorders of the intestine.

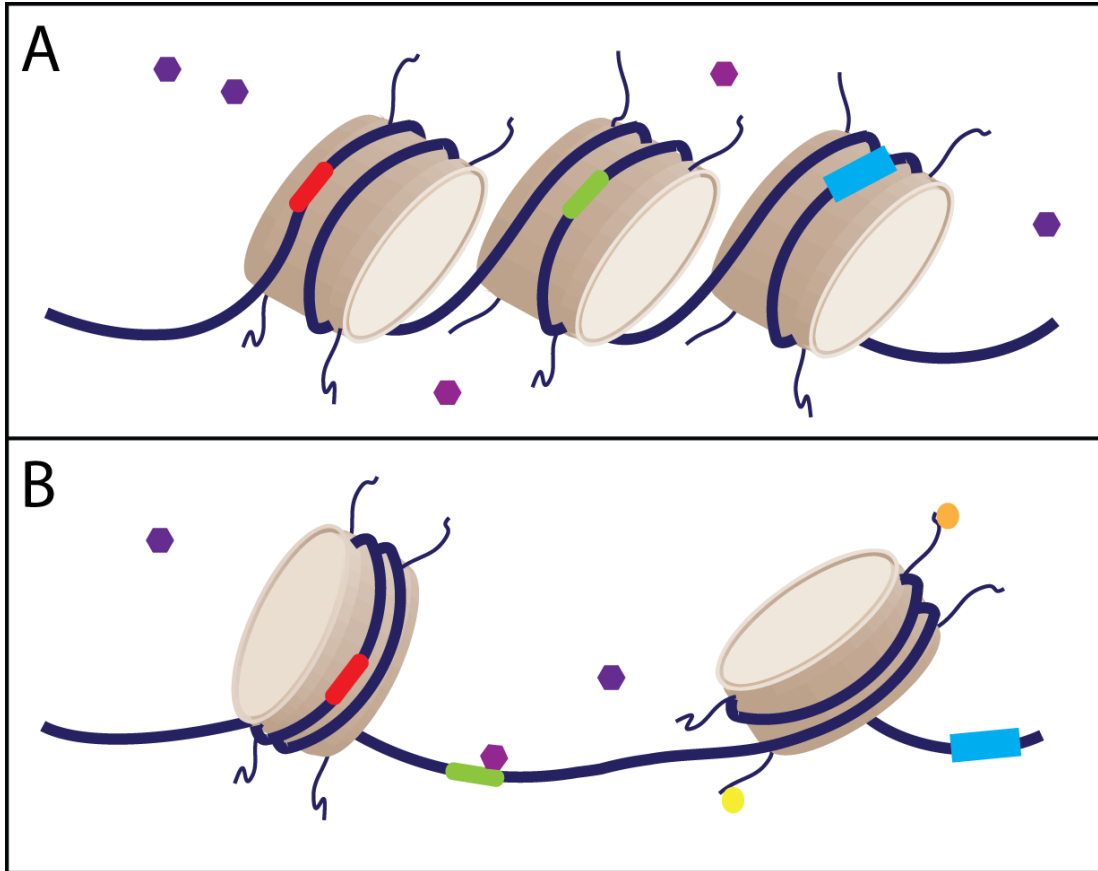


Figure 5.1. Effect of chromatin accessibility on enhancer function. (A) Nucleosomes limiting access of regulatory regions (red and green) and gene (blue) to transcriptional machinery. (B) Histone modifications (yellow circles) exposing an enhancer (green) region to transcription factors (purple).

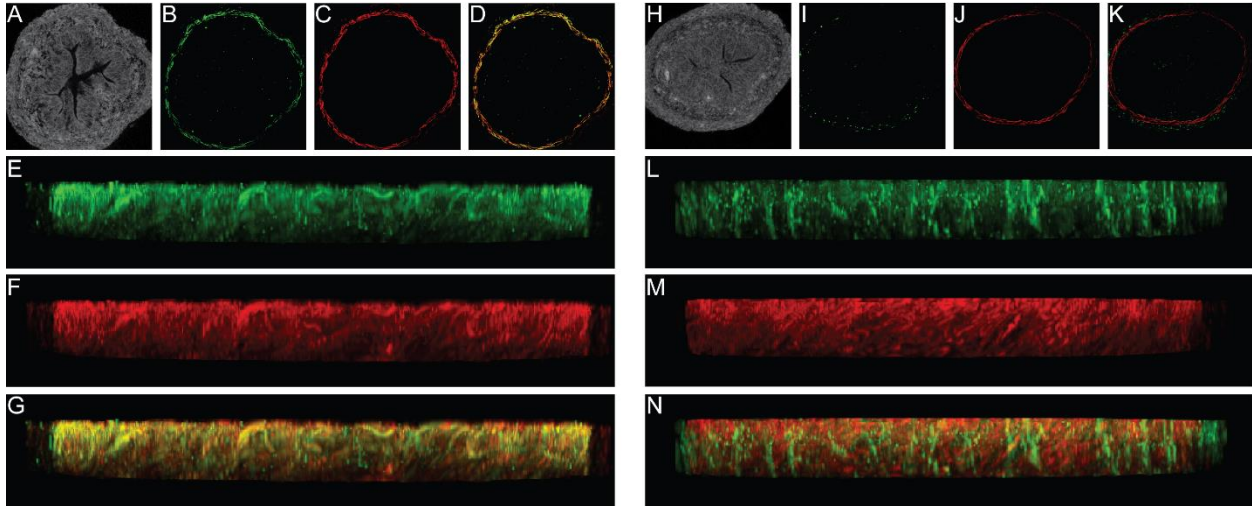


Figure 5.2. cJUN and MEF2C localize to different populations in E14.5 intestines. Intestines collected from BL6 mice were cross sectioned and stained for DAPI (grey) (**AH**), the smooth muscle marker α SMA (red) (**CFGJMN**), cJUN (green) (**BEG**) or MEF2C (green) (**ILN**). Images for cross sectioned intestines (**ABCDHIJK**) and the side profile of the intestine (**EFGLMN**) are shown. At E14.5, α SMA exclusively stains the ICM. cJUN co-localizes with α SMA (**DG**). MEF2C staining occurs outside of the ICM in the region where the OLM will develop (**KN**).

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