

**H3K4 methyl marks landscape during *Caenorhabditis elegans* embryogenesis and their implication in lifespan regulation**

A thesis submitted to The University of Manchester for the degree of DOCTOR OF PHILOSOPHY in the Faculty of Biology, Medicine and Health

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## List of Abbreviations

a.a.	Amino acid
ABM	ASH2L binding motif
Ac	Acetylation
AS	Activation segment
ASH-2	Absent small homeotic discs-2
BPTF	Bromodomain and PHD domain transcription factor
BSA	Bovine serum albumin
CFP	CXXC1 finger protein
ChIP	Chromatin immunoprecipitation
CI	Confidence Interval
COMPASS	Complex associated with SET1
CpG	5'-C-phosphate-G-3' (cytosine and guanine separated by a phosphate group)
Cps	COMPASS protein subunit (of yeast)
CTD	C-terminal domain
DAPI	4',6-diamidino-2-phenylindole
DCC	Dosage compensation complex
DIC	Differential interference contrast
DNA	Deoxyribonucleic acid
dNTP	Deoxyribonucleotide triphosphate mix
Down-R	Downregulated
DPY-30	DumPY-30
<i>E. coli</i>	<i>Escherichia coli</i>
EDTA	Ethylenediaminetetraacetic acid
F1	First filial generation
F2	Second filial generation
F3	Third filial generation
F4	Fourth filial generation
F5	Fifth filial generation
gDNA	genomic DNA
GFP	Green fluorescent protein
GH	Glycine-histidine
GO	Gene ontology
H1	Histone 1
H2A	Histone 2A

H2B	Histone 2B
H2O2	Hydrogen peroxide
H3	Histone 3
H3K27	Histone 3 Lysine 27
H3K36	Histone 3 Lysine 36
H3K4	Histone 3 Lysine 4
H3K9	Histone 3 Lysine 9
H4	Histone 4
HAT	Histone acetyltransferase
HCF	Host cell factor
HDAC	Histone
HER-1	Human epidermal growth factor receptor
IF	Immunofluorescence
I-SET	Insertion SET
JMJD	Jumonji domain-containing proteins
KDM	Lysine demethylase
KMT	Lysine methyltransferase
lincRNA	Long intergenic noncoding RNA
LSD	Lysine demethylases
Me1	Mono-methylation
Me2	Di-methylation
Me3	Tri-methylation
MLL	Mixed lineage leukaemia
MYND	Myeloid-Nervy-DEAD1
mRNA	Messenger RNA
P0	Parental generation
PCR	Polymerase chain reactions
PHD	Plant homeodomain
PIC	Preinitiation complex
PRMT	Protein arginine methyltransferase
P-TEFb	Positive transcription elongation factor b
PTM	Post translational modification
qRT-PCR	Quantitative real time polymerase chain reaction
RBBP-5	Retinoblastoma-binding protein 5
RNA	Ribonucleic acid
RNAPII	RNA polymerase II

RPKM	Reads per kilobase permillion reads placed
<i>S. cerevisiae</i>	<i>Saccharomyces cerevisiae</i>
SAGA	Spt-Ada-Gcn5 acetyltransferase
SAM	S-adenosyl-L-methionine-methyl
SDC-2	Sex determination and dosage compensation protein-2
SEM	Standard error of mean
Seq	Sequencing
SET Trithorax	Suppressor of variegation 3-9 (Su(var)3-9), Enhancer of zester (E(z)), and
SPR-5	Suppressor of presenilin defect
SPRY	SPIa and ryanodine receptor
TAF3	Transcription associated factor 3
TBP	TATA-binding protein
TES	Transcription end sites
TF	Transcription factor
TPR	Tetratrico-peptide Repeat
TSS	Transcription start site
TTS	Transcription termination site
Up-R	Upregulated
UTX	Ubiquitously transcribed tetratricopeptide repeat, X chromosome
VPC	Vulval precursor cell
WBM	WDR5 binding motif
WDR-5	WD repeat domain 5
WRAD	WDR5, RbBP5, ASH2L and DPY-30
Xm	Maternal X
XOL-1	XO lethal protein 1
Xp	Paternal X

## Abstract

The University of Manchester

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H3K4 methyl marks landscape during *Caenorhabditis elegans* embryogenesis and their implication in lifespan regulation

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How long organisms may live is not determined by genetic code alone. Recent findings reveal that components of MLL/SET/COMPASS complex, ASH-2, WDR-5 and SET-2, regulate H3K4 methylation levels on genome and limit how long nematode *Caenorhabditis elegans* may live. This suggest that histone modifications could also determine life expectancy. We conducted lifespan assay and transgenerational study to investigate if another core component of the COMPASS complex, RBBP-5, is also a regulator of lifespan. We mapped H3K4me1/me2/me3 attributed to WDR-5 and RBBP-5 and then find any correlation between changes in gene expression and altered methylation levels in *wdr-5(-)* and *rbbp-5(-)*. Our study reveals that in absence of RBBP-5, lifespan is shortened. The H3K4 methylation levels also reduce as the animal aged. Moreover, the *rbbp-5(-)* mutant descendants from wild type ancestors inherit normal lifespan for up to three generations, before gaining back short lifespan. The transgenerational inheritance is specific for lifespan regulation and does not affect brood size (Chapter 3). Mapping of H3K4me1/me2/me3 using *rbbp-5(-)* *C. elegans* embryos reveals severe depletion of all states throughout the genome. In contrast, in absence of WDR-5, we observe global increase in H3K4me1, decrease in H3K4me3 and excessive accumulation of H3K4me2 at chromosome X. Correlation between RNA-seq and ChIP-seq data using *wdr-5(-)* and *rbbp-5(-)* embryos uncover more genes being upregulated than downregulated, despite depletion in H3K4 methylation levels in both mutants. Absence of WDR-5 also causes higher incidence of male, all of which have abnormal tail morphology (Chapter 4). While exploring the landscape of H3K4me1/me2/me3, we developed new technique for the amplification of massive amount of *C. elegans* on solid media (Chapter 5). In conclusion, the work presented in this thesis shows that H3K4 methylation attributed by RBBP prevents lifespan shortening. The work also shows WDR-5 as a key player in promoting the acquisition of H3K4me3 and in preventing excessive accumulation of H3K4me2 at chromosome X.

## Declaration

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# **Chapter 1**

## **General Introduction**

## Chapter 1 : General Introduction

### 1. Inheritance of epigenetic information

Producing the next generation is a major challenge for all species using sexual reproduction. It involves the production of highly specialized and differentiated cells (oocytes and sperms) that must regenerate an entire organism from a one-cell embryo. Fertilization implies reprogramming to produce a totipotent one-cell embryo from which all the other cells of the organism will derive. Crucially, the germ lineage will undergo a fundamentally different program than the somatic lineage. This process ensures continuation of the species. In principle, the next generation does not inherit mild environmental stress that do not change the DNA sequence of the genome in gametes because of the Weissman barrier (Weismann 1892). The Weissman barrier stipulates that information flows from the gametes to the somatic cells and never the other way around. This is especially true for the genetic information; a mutation in somatic cells will not end up in the gametes. However, epigenetic information might behave differently.

Epigenetics is the process by which patterns of gene expression are inherited following mitosis or meiosis. Epigenetics is also highly connected to the environment and provide a degree of plasticity required for animals to adjust and sometimes adapt (Yao et al. 2014; Manikkam et al. 2012; Anway et al. 2005; Dunn & Bale 2011; Lagisz et al. 2014). Klosin and Lehner (2016) proposed the term “epigenetic wounds” as the establishment of epigenetic memory, imparted by environment, in new regions of chromatin that is supposedly be condensed and silenced (heterochromatin). These regions experience temporary inhibition of gene silencing, thus triggering phenotypic adaptation (Klosin & Lehner 2016). It is therefore conceivable that exposure to environmental stresses might change the pattern of gene expression in the gametes. The change could resist embryonic epigenetic reprogramming and hence remains active in progeny for several generations. The epigenetic inheritance then, is either passively lost due to molecule dilution or actively lost by specific eraser complexes (Klosin & Lehner 2016)

*Caenorhabditis elegans* is an excellent system to study epigenetic inheritance and it has the advantage of being devoid of CpG methylation (Chen et al. 2014). Methylation at Histone 3 Lysine 4 (H3K4me) has been identified as an epigenetic mark which could potentially regulate transgenerational inheritance of longevity in *C. elegans* (Greer et al. 2011). The exposure to environmental stresses on the epigenetic landscape could be transmitted for multiple generations and H3K4 methylation might play an important role in this process. The inheritance of H3K4 methylation in human is however unexplored. The general introduction is therefore aimed to introduce the post-translational modifications on chromatin; complexes that write, erase and read H3K4 methylation; association with transcription; inheritance of H3K4 methylation; *C. elegans* as the study model; and *C. elegans*' phenotypes linked with deficiencies in H3K4 methylation.



## 1.1 Chromatin

DNA is not naked in a cell. It is wrapped around nucleosomes. This wrapping allows a 2 m long genome to be packed into few microns of nuclear space. It is also important that mechanisms are in place to allow access to the genome for transcription, replication, and repair to occur. In this section, I will introduce how the nucleosome is important for packaging, how histones are modified to regulate access to DNA, and describe the mechanisms by which the epigenetic state is restored following mitosis.

### 1.1.1 Chromatin packaging

To understand how chromatin modulates nuclear processes, one must understand the organisation of the chromatin. Chromatin is packaged in such a way that DNA wraps around histones to form nucleosomes, nucleosomes align into beads-on-a-string chromatin structure, chromatin condenses into fibers and fibers tightly coil into chromosomes.

The size of the eukaryotic genome is massive. The haploid genome may range from 100 million nucleotides in *C. elegans* (Hodgkin et al. 1995) to three billion nucleotides in human (Venter et al. 2001). If stretched out end to end, the diploid genome can span approximately two meters long (Alberts et al. 2002). It is also negatively charged and constantly producing electrostatic repulsion with adjacent DNA regions. Due to its massive size and charge, it requires a special structuring function to allow it to fit into a 6  $\mu\text{m}$  cell nucleus (Alberts et al. 2002). Packaging is one of the chromatin's many features which allows genetic materials to be compacted and stored into the tiny nucleus. Chromatin comprises DNA and histones. Histones are very important for packaging the genome; they are basic and positively charged proteins overcoming the electrostatic repulsion of DNA (Olins & Olins 1974; Kornberg 1974).

The fundamental unit of chromatin is a nucleosome. A nucleosome core consists of approximately 147 base pairs of DNA double helix wrapped in 1.7 left-handed super-helical turns around a histone octamer (Kornberg 1974). Each histone octamer has two copies of each H2A, H2B, H3 and H4. The octamer is produced when a H3-H4 tetramer combines with two H2A/H2B dimers (Kornberg 1974). Each nucleosome core is held together by a linker histone (H1) and is connected to the next nucleosome by a linker DNA (20 – 80 base pairs). The structure repeats throughout the genome every 160-240 base pairs forming a long strand of nucleosomes, famously described as 'beads-on-a string' (McGhee & Felsenfeld 1980; Olins & Olins 1974; Woodcock 1973). The packaging of chromatin is illustrated in Figure 1.1

Core histone proteins share similar structure in general. Each core histone has a characteristic histone-fold domain (Arents & Moudrianakis 1995) composed of a long central helix that is flanked on each side by a loop and a shorter helix (Ramakrishnan 1994). This resembles an elongated and interlocking structure and is about 7  $\text{\AA}$  in size. In addition to the histone-fold, each core histone also has an N-terminal tail that can vary in amino acid sequence depending on the histone type. The tails appear to have random coils (disordered) and protrude from the nucleosome core.

Interestingly, a striking feature of the N-terminal tail is its amino acid residues, which are subjected to extensive post translational modifications. The post-translational modifications can change the chemical landscape of the nucleosome or orchestrate recruitment of enzyme complexes used for DNA-dependent processes, such as replication, transcription and repair.

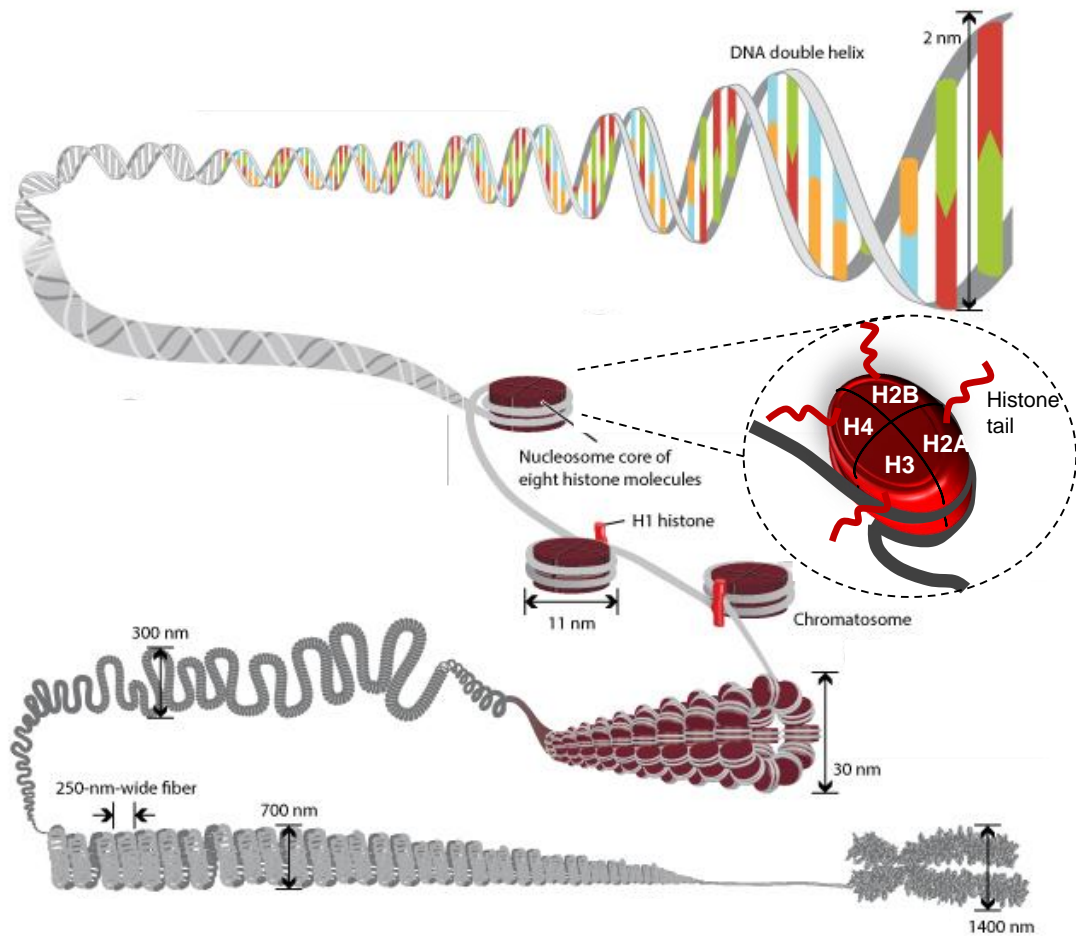
When two tetramers of H3-H4 and H2A-H2B combine to form a histone octamer, a left-handed helical ramp with a pitch of about 28 Å forms along the surface indicative of where the DNA-histones contact is (Ramakrishnan 1994). The histone octamer bears a flat disk shape with a diameter of about 65 Å (Ramakrishnan 1994). The ramp path for the DNA-histones interaction is built along the loops of the core histones (Luger et al. 1997). DNA makes contact with histone proteins primarily through the phosphodiester backbone and not the DNA bases (Luger et al. 1997), thus explaining the sequence-independent nature of nucleosome formation. The order of the DNA-histones contacts is (H2A-H2B)(H3-H4)(H3-H4)(H2A-H2B) (Ramakrishnan 1994; Burlingame et al. 1985).

The beads-on-a string of nucleosomes (10 nm) folds into 30 nm chromatin fibers (Finch & Klug 1976). Since the length of DNA linker can vary, the folding into an intermediate 30 nm chromatin fiber has no uniform structure. Even a variation in 1 base pair can correspond to a 360° rotation and change the entire structure of the fiber (van Holde & Zlatanova 2007). The 30 nm chromatin is further condensed into a higher order chromatin structures. Two models describe the higher order chromatin structures. Based on the “hierarchical helical folding model” the 30 nm fiber is folded into a larger 100 nm fiber and then 200 nm fiber, to form large interphase or mitotic chromatin (Sedat & Manuelidis 1978; Belmont & Bruce 1994; Belmont et al. 1989). On the other hand, the “radial loop model” predicts that the 30 nm fiber is radially looped to form mitotic chromosomes (Paulson & Laemmli 1977; Laemmli et al. 1978; Marsden & Laemmli 1979).

According to the cell cycle chromatin changes its appearance. Chromatin is very condensed at mitosis. Following mitosis and into interphase, most domains of the chromatin de-condense, become transcriptionally accessible and appear as lightly stained regions of the chromatin by Giemsa (G-banding) or C-banding visualization techniques (Goyanes 1980; Dorota et al. 2005). The term for this material is euchromatin. However, there are still some domains surrounding telomeres and centromeres that appear highly condensed and darkly stained by the same visualization techniques (Goyanes 1980; Dorota et al. 2005). This material is called heterochromatin (Eissenberg et al. 2014). Heterochromatin is further categorized into constitutive heterochromatin and facultative heterochromatin. The constitutive heterochromatin is the static, gene-poor, highly dense chromatin that form at pericentromeric and telomere regions (Saksouk et al. 2015). On the other hand, facultative heterochromatin refers to silenced gene regions that may be activated upon cues (Saksouk et al. 2015).

Thus, chromatin packaging involves intricate processes that starts with DNA-histones interactions and end up having an impact on transcription. This impact on transcription is intimately driven by post translational modifications on histone tails. Here, I have described the basic principle of packaging which underlines the importance of the nucleosome to determine accessibility to the

genome. I will next explain how nucleosomes can be used as regulators of DNA templated functions by post-translational modifications of their N terminal tails.



**Figure 1.1 Packaging of chromatin**

A double stranded helical DNA wraps 1.65 times around a histone octamer to form nucleosome. Nucleosome is the fundamental unit of chromatin. The linker histone, H1, binds to the nucleosome and linker DNA to help stabilize the fiber. The 11 nm nucleosome fiber folds into 30 nm fiber that forms loops averaging 300 nm in length. Tight coiling of the fiber produces the chromatid of a chromosome. (Insert) Two H2A-H2B dimers and a H3-H4 tetramer assemble into a histone octamer. Each of the histone subunit has an N-terminal tail protruding from the core. The histone tail may be subjected to various post-translational modifications that could be associated with gene activation (such as H3K4me1/me2/me3 and H3K36me3) or repression (H3K9me3, H3K27me3) (Adapted from Annunziato A.T., 2008).

### 1.1.2 Post translational modification of histones

Post-translational modification (PTM) of histones refers to the covalent addition or removal of a functional group to the tail of histone protein after its synthesis. Most of the modifications on histone tails are reversible. There are specific enzymes that can write or erase these marks. The histone tails are susceptible to modifications such as acetylation, phosphorylation, methylation, ubiquitylation and sumoylation. Figure 1.2 illustrates the structures of these histone post-translational modifications.

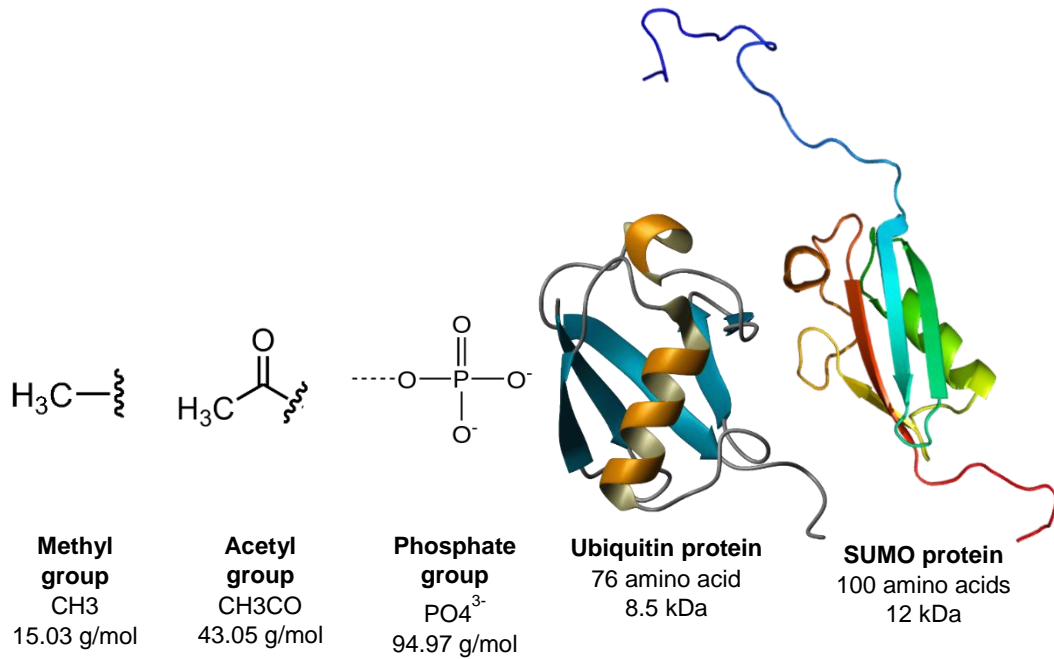
Histone acetylation was the first PTM on histones to be discovered (Phillips 1963). The reactions are catalyzed by histone acetyltransferases (Allis et al. 2007). Acetyl groups are negatively charged (Csordas 1990). Hence, acetylation neutralizes the positive charge on histone surface. It makes the histones become less attractive to the negatively charged DNA, causing the chromatin to loosen up and transcription to gain access to the genome (Hong et al. 1993; Bell & Dutta 2002). Examples of histone acetylation on lysine residues include H3K4ac, H3K9ac, H3K27ac and H3K36ac. ChIP-chip analysis shows that H3K4ac peaks upstream of H3K4me3 at active promoters. It was hypothesised that H3K4ac cooperates with other acetylated histone residues at promoters to increase chromatin accessibility and gene expression (Guillemette et al. 2011). The modification is reversible by the histone deacetylases enzymes. Histone acetylation and deacetylation are both rapid and highly dynamic, making nucleosome accessibility and mobilization also highly dynamic (Barth & Imhof 2010; Waterborg 2002).

Histone phosphorylation has a similar role to acetylation in regulating nucleosome dynamic. Phosphorylation imparts negative charge to its modified residue. The negative charge interrupts the electrostatic interactions between the positively charged histones and negatively charged DNA backbone (Cheung et al. 2000). The histone-DNA contacts are then loosened (Zentner & Henikoff 2013). Phosphorylation occurs at serine and threonine on histone tails such as at the S10, S28, T3 and T11. Phosphorylations of serine and threonine residues on histone tail have been linked to a wide variety of molecular functions and biological contexts, such as DNA repair and development (Paull et al. 2000; Talbert et al. 2012; Kusch et al. 2004; Green & Poccia 1985). For instance, phosphorylation of H3 at S10, S28, T3 and T11 are associated with mitosis and chromatin condensation. H3 phosphorylation opens up the chromatin fibers and allows recruitment of deacetylase, which in turn promotes chromatin condensation (Wilkins et al. 2014; Cheung et al. 2000). Collectively, acetyl and phosphate groups are two chemical moieties which are negatively charged and can weaken the DNA-histone interactions.

Methylation adds a weak positive charge to the already heavily positively charged histone tails. Thus, it does not affect the electrostatic interactions between DNA and histone proteins like acetylation and phosphorylation do. Instead, histone methylation serves as a binding platform for readers that can regulate other modifications (e.g. acetylation, phosphorylation and ubiquitination) (Izzo & Schneider 2010). There are a variety of histone methyltransferase and demethylase enzymes responsible for the addition or removal of methyl marks, making histone methylation reversible too. Various histone methylation marks have been associated with transcription. For instance, H3K9, H3K27, and H4K20 methylation are associated with transcriptional silencing,

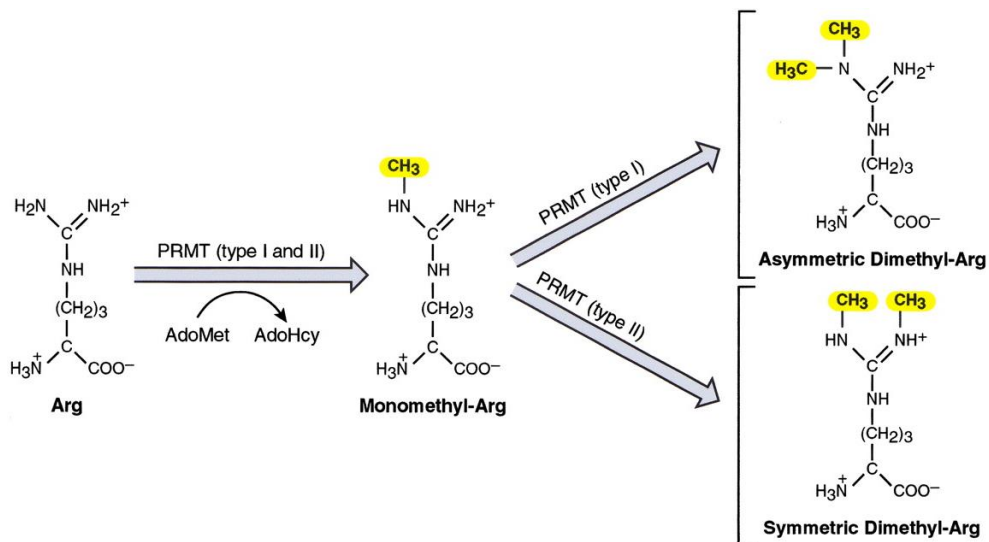
whereas, H3K4 and H3K36 have been implicated in transcriptional activation (Izzo & Schneider 2010; Hublitz et al. 2009). Histone methylation can occur on lysine (K) and arginine (R) (Byvoet et al. 1972; Murray 1964; Fischle et al. 2008). Lysine can be mono-, di- or tri-methylated whereas arginine can be mono- and di-methylated (Murray 1964; Paik & Kim 1967; Gershey et al. 1969; Borun et al. 1972). Dimethylated arginine has asymmetric chemical conformation if catalyzed by Type I protein arginine methyltransferase (PRMT). Otherwise, it acquires a symmetric conformation when catalyzed by Type II PRMT (Figure 1.3) (Zhang & Reinberg 2001). Yeast has tightly coupled symmetric H3R2me2s with K4me3 throughout its active promoters (C.-C. Yuan et al. 2012). On the contrary, asymmetric H3R2me2a peaks more throughout heterochromatin and inactive euchromatin (Kirmizis et al. 2007). H3R2me2a deposition abrogates H3K4 trimethylation (Guccione et al. 2007). In contrast with phosphorylation and acetylation, methylation at histone does not change chromatin charge but serves as platform for the recruitment of readers involve in regulating transcription.

Unlike any other PTMs, ubiquitylation and sumoylation are large histone modifications to a single lysine side chain. Histone modifications by ubiquitylation and sumoylation involve the addition of bigger substrate of a 76 amino acid domain and 100 amino acid domains, respectively (Zentner & Henikoff 2013). In contrast, only small chemical moieties are added during acetylation, phosphorylation and methylation. Both ubiquitylation and sumoylation are known to exert diverse effects on nucleosome dynamics. Ubiquitylation functions to promote or inhibit transcriptional elongation, establish chromatin reassembly and recruit DNA repair proteins (Moyal et al. 2011; Zhou et al. 2008; Lee et al. 2012; Batta et al. 2011; Fleming et al. 2008). For instance, monoubiquitination H2Bub can promote H3K4me2/me3 at actively transcribing genes (Shilatifard 2012). Histone sumoylation is generally associated with transcription repression (Zentner & Henikoff 2013). In conclusion, histone tails are exposed to various post-translational modifications; from smaller chemical moieties such as acetylation, phosphorylation and methylation to larger proteins like ubiquitin and SUMO proteins.



**Figure 1.2 Histone post translational modifications involving small chemical moieties and large proteins**

Chemical structure of methyl, acetyl and phosphate with molar mass shown for each group. Crystal structures of ubiquitin and SUMO proteins and their respective molecular weight.



**Figure 1.3 Chemical structures of histone methylation at arginine**

Arginine can be monomethylated, asymmetric dimethylated or symmetric dimethylated. The methyl groups are highlighted in yellow (Zhang & Reinberg 2001)

## 1.2 Methylation on H3K4

To deposit methyl marks at H3K4, the cell employs a specialized complex conserved from yeast to humans. Essentially, the complex is composed of a core and an enzymatic part. The core complex is obligatory for full enzymatic activity and can be found associated with numerous enzymes with non-redundant functions. I will discuss how methyl marks at H3K4 have been uncovered, how these are deposited, removed, and interpreted by readers.

### 1.2.1 Discovery of H3K4 methylation

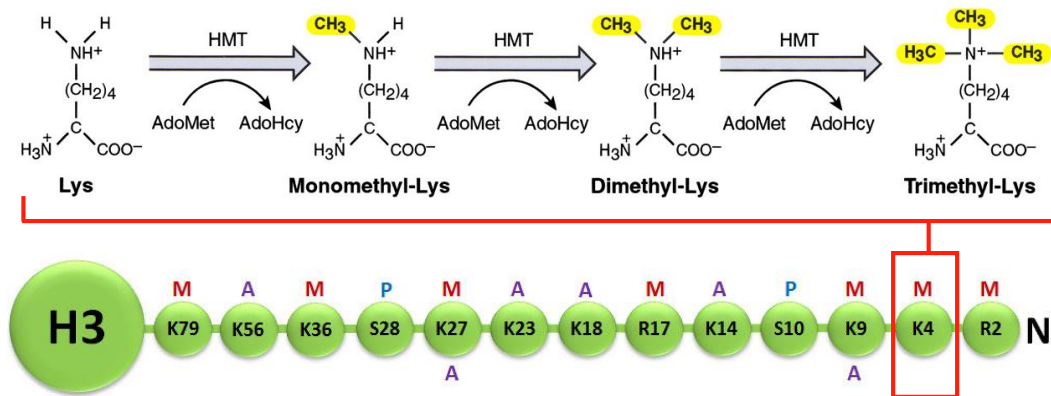
The discovery of histone methylation can be traced back to the work of Sangduk Kim and Woon Ki Paik in 1965. Their successful discovery on methylation of lysine residues on histone tails has open boundless opportunities for the current and future findings on H3K4 methylation. Here, I summarize the discovery of methylation at lysine residue of histone tails and different levels of lysine methylation

The first discovery of  $\epsilon$ -N-methyl-lysine was in the flagellar protein of bacteria *Salmonella typhimurium* approximately sixty years ago (Ambler & Rees 1959). Following the first discovery, histone proteins of calf thymus were also found to be methylated at the  $\epsilon$ -N-lysine residue. Most of the  $\epsilon$ -N-methyl-lysine were found to be on histone 3 and 4 (Murray 1964). The origin of methylation on lysine residue was later found to be as a result of post-translational modification by S-adenosyl-L-methionine-methyl (SAM) instead of incorporation of pre-formed  $\epsilon$ -N-methyl-lysine into histones (Kim & Paik 1965). It was initially thought that this histone methylation might regulate the functions of DNA (Allfrey et al. 1964; Kim & Paik 1965). SAM is the principal biological methyl donor in all living organisms. It can donate its methyl group to a wide range of recipients including nucleic acids, proteins, histones, lipids and secondary metabolites.

It was in 1968 that the three different types (mono-, di- and tri-) of histone methyl-lysine were discovered (Figure 1.4) (Paik & Kim 1967; Hempel et al. 1968) thanks to technological advances in chromatography and amino acid analysis techniques. The amino acids of histone 3 N-terminal tail were completely sequenced and found to be evolutionary conserved across organisms such as bovine, mouse, chicken and yeast (Delange et al. 1972; Ohe & Iwai 1981; von Holt et al. 1989). It was later established that lysines (K4, K9 and K27) of histone 3 are sites of histone post-translational methylation (Wu et al. 1986).

Ever since the discovery of methylation at lysine 4 of histone 3 (H3K4), there has been a growing number of studies on its mechanisms of deposition, removal, recognition and its biological functions. The surge in research interest came about because it has been associated with both active and repressed transcription ((Cheng et al. 2014; Wong et al. 2012)). It serves as a platform that promotes the binding of general transcription factors and histone modifiers such as histone acetyltransferases, deacetyltransferases and demethylases. H3K4 methylation has also been implicated in epigenetic transgenerational inheritance. Detailed description and more recent discoveries on H3K4 methylation will be introduced in the following sections. To summarise, the

uncovering of methylation at H3K4 approximately sixty years ago has led to never-ending investigations on its regulation, association with transcription and its epigenetic inheritance.



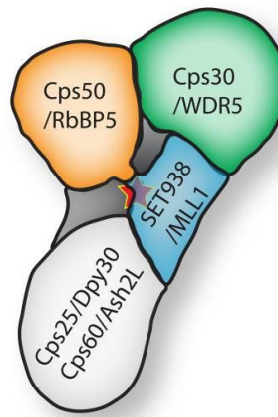
**Figure 1.4 Methylation states of lysine 4 residue in histone 3**

Change in chemical structure illustrating that lysine 4 (K4) can replace each of its hydrogen on  $\epsilon$ -amino group with mono-, di- or tri-methyl group (CH<sub>3</sub>). The letters on H3 tail amino acid residues (lysine (K), arginine (R), and serine (S)) represent different post-translational modifications: methylation (M), acetylation (A) and phosphorylation (P) (Epigenetics 2013; Zhang & Reinberg 2001).

### 1.2.2 The yeast COMPASS complex

About 15 years ago, the COMPASS (Complex associated with SET1) complex was discovered in the yeast *Saccharomyces cerevisiae* (Figure 1.5) (Miller et al. 2001; Roguev et al. 2001). It was the first identified methyltransferase complex for H3K4. Yeast only has one H3K4 methyltransferase complex, which is capable to mono-, di-, and tri-methylate H3K4. The COMPASS complex has two main components: (1) the catalytic H3K4 methyltransferase subunit and (2) the core components of the complex. The catalytic methyltransferase subunit is called the Set1 protein. Set1 is a member of the trithorax gene family and has been implicated in the control of gene transcription. Its gene encodes a large protein of 1080-amino acid, containing a C-terminal SET domain (Nislow et al. 1997). It was later found that the yeast SET domain shares great similarity to its human and *drosophila* homologs. The complex core subunits include: Cps60 (Bre2/Ash2), Cps50 (Swd1/Rbbp5), Cps40 (Spp1), Cps35 (Swd2/Wdr82), Cps30 (Swd3/WDR5), Cps25 (Sdc1/Dpy30) and Cps15. The core protein subunits are essential for full enzyme activity (Shilatifard 2012). The activity of the catalytic H3K4 methyltransferase is greatly influenced by the core components (Meeks & Shilatifard 2017). Without the core complex, the methyltransferases become less active to different degrees depending of the core component lacking. The yeast complex depleted of both Cps60 (Ash2) and Cps25 (Dpy30) has a total loss of H3K4me3 and a great reduction in H3K4me1/me2 (Takahashi et al. 2011). Defective Cps40 (Spp1) reduces the H3K4me3 levels in yeast (Schneider et al. 2005). On the other hand, absence of SET1 leads to complete abolishment of H3K4me1/me2/me3 (Briggs et al. 2001).





**Figure 1.5 Schematic model of yeast Set1/COMPASS**

Schematic model of the yeast core Set1/COMPASS complex showing Set1 (938-1080) methyltransferase in BLUE, Cps50/RbBP5 in ORANGE, and Cps30/WDR5 in GREEN and Cps25/Dpy30-Cps60/Ash2L in WHITE. The red star indicates the binding region between histone peptide and SET1 methyltransferase (Takahashi et al. 2011).

### 1.2.3 The conserved MLL/SET/COMPASS complex

Over the year, more COMPASS-like complexes have been discovered in other organisms such as *C. elegans*, *Drosophila* and *Homo sapiens*. Although most components are conserved, some may be missing. The current section is dedicated to comparing the MLL/SET/COMPASS complexes between human and *C. elegans* and demonstrating that the *C. elegans* complexes are highly conserved.

#### 1.2.3.1 MLL/SET/COMPASS in *Homo sapiens*

The human COMPASS complex is the most diverse. There are at least six family members of H3K4 methyltransferases, which include Set1A (KMT2F), Set1B (KMT2G), MLL1 (KMT2A), MLL2 (KMT2B), MLL3 (KMT2C) and MLL4 (KMT2D) (Eissenberg & Shilatifard 2010; Shilatifard 2008; Malik & Bhaumik 2010). More details on the important domains will be explained in later section when describing the catalytic reaction. Evidences show that human has a wide range of methyltransferases to cater for specific functions or situations. Firstly, human methyltransferase has high enzymatic specificity towards the degree of lysine methylation. For instance, the MLL3 and MLL4 complexes are H3K4 mono-methyltransferases (Hu et al. 2013; Xiao et al. 2003). Secondly, the enzymatic specificity may also be affected by other endogenous members of the complex. It has been shown that purified MLL1 converts H3K4 to H3K4me2 whereas MLL1/COMPASS complex catalyzes H3K4 to H3K4me3 (Dou et al. 2006; Schneider et al. 2005). Thirdly, although SET1A and SET1B are both H3K4 trimethylase (Lee et al. 2007; Gu & Lee 2013), immunostaining study suggests that they have distinct subnuclear localization, suggesting they have different gene targets in vivo (Lee et al. 2007). Abnormal methyltransferases may lead to pathogenesis such as the chromosomal 11 rearrangement at MLL gene that has been

associated with increased risk of acute myeloid leukemia (Muntean & Hess 2012). Hence, human H3K4 methyltransferases are very diverse and have none redundant activities.

The human complexes have all the core components WDR5, ASH2L, RbBP5 and DPY30. Human WD-40 Repeat Protein 5 (WDR5) gene is located on chromosome 9 and is about 24.6kb long. The WDR5 protein is 334 amino acid residues (36 kDa). The full length WDR5 protein has seven WD40 repeats that fold into a seven-blade  $\beta$ -propeller structure which is illustrated in WDR5 crystal structure (Figure 1.6). The WD40 motif is characterized by repeats of 40 amino acids that begins with glycine-histidine (GH) and ends with tryptophan-aspartic acid (WD) (van der Voorn & Ploegh 1992). It is important for the formation of multi-protein complexes (Mylona et al. 2006; Stirnimann et al. 2010). The WD40 repeats in WDR5 protein are located between amino acid 43 and 333. WDR5 can be found in most human tissues in general. Interestingly however, level of WDR5 transcripts are highest in testis (mean reads per kilobase per million reads placed (RPKM):  $24.217 \pm 3.667$ ) compared to the other tissues (mean RPKM: 7.5) ((NCBI) 2017; Fagerberg et al. 2014). How WDR5 influences H3K4 methylation in testis is unknown. However, an in vitro study has shown that WDR5 is a direct target of a sex-determining gene, SRY, which encodes for a transcription factor. WDR5-SRY interaction can further activate expression of the Sox9 gene and repress  $\beta$ -catenin. Sox9 is the master regulator of sex determination, whereas,  $\beta$ -catenin is important for development of ovaries (Xu et al. 2012). Thus, in human, WDR5 is one of the core COMPASS complex complement and is involved in sex determination.

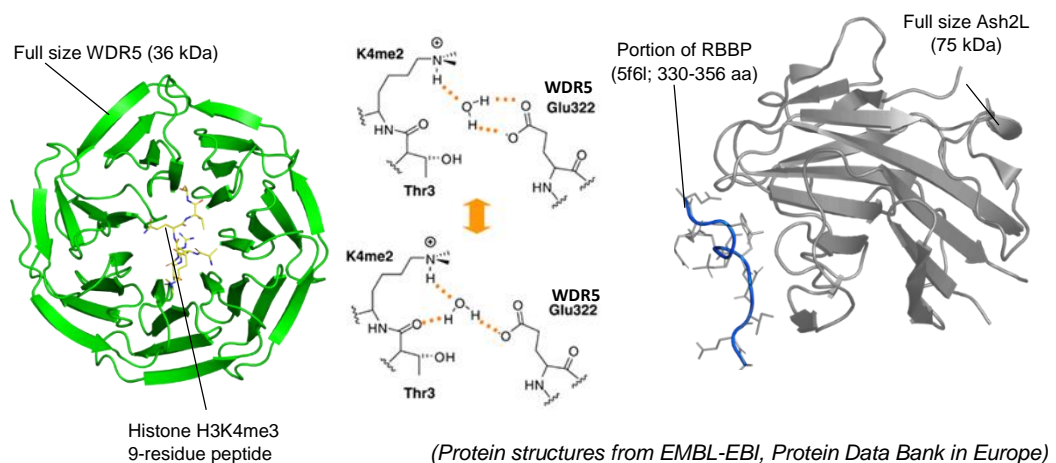
WDR5 recognizes A1, R2 and T3 on histone H3 tail (Couture et al. 2006). H3R2 dips into the central channel of WDR5 hereby exposing the adjacent H3K4me2 to the top face of WDR5 (Schuetz et al. 2006). The N $\epsilon$  atom of H3K4me2 forms a hydrogen bond with a water molecule, which in turn forms another one or two hydrogen bonds with the carboxylate groups of Glu322 of WDR5 (Schuetz et al. 2006). Truncated WDR5 protein missing the Glu322 residue shows no interaction with H3K4me2. On the other hand, H3K4me3 abolishes its interaction with WDR5, whereas H3K4me1 and H3K4me0 hydrophilicity is too high to make interaction with WDR5. H3K4me0/me1 has three and two hydrogen bond donors, respectively, making it greatly hydrophilic (Schuetz et al. 2006). To sum, WDR5 Glu322 places the K4 at a position suitable for the catalytic reaction by H3K4 methyltransferase.

Human Retinoblastoma-binding protein 5 (RbBP5) gene is located on chromosome 1 and is approximately 35.9 kb long. An alternative name for RBBP5 is RBQ3. The gene has 14 exons and encodes for 538 amino acids (60 kDa). RBBP5 protein has six WD40 repeats structure that are located between amino acid 22 and 331. The WD40 repeat sequences allow bindings and interactions between proteins. Thus far, there is no complete protein crystal structure of RBBP5 yet. Only the following portions of the protein crystal structure have been illustrated: RBBP5(369-381)-peptide (Odho et al. 2010); RBBP5(344-355)-peptide (P. Zhang et al. 2015); and RBBP5(330-356)-peptide (Li et al. 2016). The RBBP5 protein can be found in the nuclear of most human tissue, at approximately the same level (Fagerberg et al. 2014).

Absent small homoeotic discs-2-like (ASH2L) gene is located at chromosome 8. The gene, which is approximately 35kb long and has eight exons encodes for ASH2L protein of 75 kDa. ASH2L is

a trithorax protein and has SPRY domain (SP1a and the Ryanodine Receptor), which is a protein interaction module (D’Cruz et al. 2013). DPY-30 gene is located on chromosome 2 and is about 172 kb long. It contains 10 exons and encodes a protein that is about 11 kDa. Several complexes may also have other core components such as CXXC1 Finger Protein 1 (CFP1), WD Repeat Domain 82 (WDR82), Host Cell Factor 1/2 (HCF1/2), Menin and Ubiquitously Transcribed Tetratricopeptide repeat, X chromosome (UTX). CFP1, of the SET1A/1B complex, has a zinc finger domain CXXC that can interact with unmethylated CpG (Carlone et al. 2005). Despite *C. elegans* being deprived of CpG methylation, there is a CFP-1 homolog found at unmethylated CpG (Chen et al. 2014).

The human MLL/SET complexes can be divided into three categories based on their components. Each of these three category retains the conserved WRAD (WDR-5, RbBP-5, ASH2L, and DPY-30) core components. Firstly, the SET1A/SET1B complexes which contain WRAD complex, HCF, CFP1 and WDR82. Secondly, the MLL1/2 complexes containing WRAD complexes, HCF and menin. Lastly, the MLL3/4 complexes which contain WRAD complex, HCF, Pax2 transactivation domain-interacting protein (PTIP), UTX and Lost Plant homeodomains [PHDs] of Trithorax-related [Trr] (LPT) (Table 1.1). The crystal structures of human WDR5, a portion of RBBP5 and ASHL is shown in Figure 1.6. The position of WD40 repeats of WDR5 and RBBP5 are shown in Figure 1.7. Figure 1.8 depicts the levels of WDR5 and RBBP5 transcriptome in human in various tissues. In all, there are at least six human H3K4 methyltransferase complexes and all of them have the conserved WRAD complex as well as a few other components.



**Figure 1.6 Human MLL/SET/COMPASS core components: WDR5, RBBP5 and ASH2L**

Crystal structure models of the core components of the MLL/SET/COMPASS complexes showing WDR5 (green) with histone H3K4me3 9-residue peptide (yellow stick figure), a portion of RBBP5 from amino acid 330 to 356 (blue) and ASH2L (grey). The chemical structure shows that amino acid Glu322 of WDR5 can recognize and form either one or two hydrogen bonds with H3K4me2. Yellow arrow indicates the two types of bonding that WDR5 and Kme2 can have.

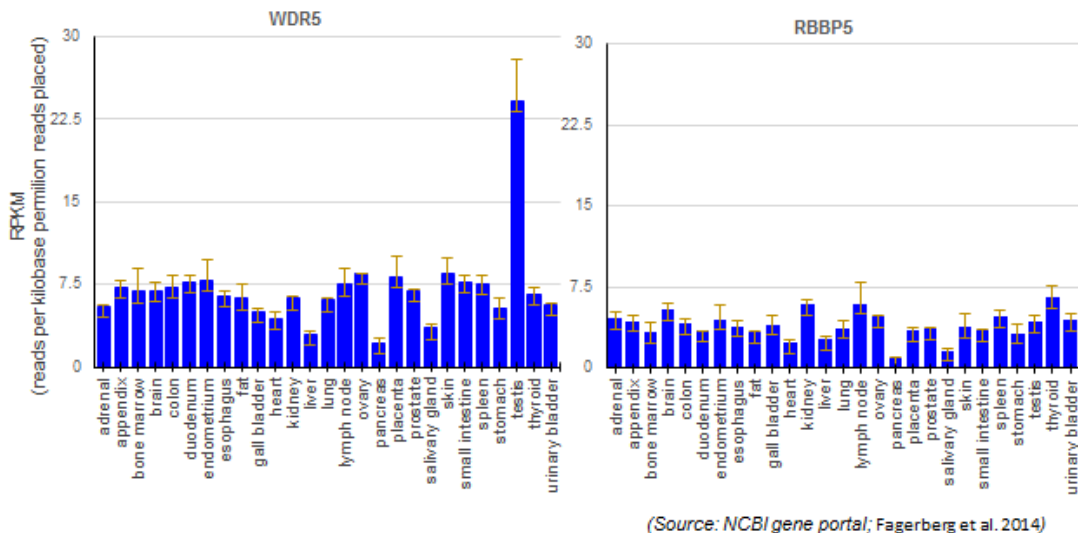
WDR5 (334 aa; 36 kDa)		
Description	a.a. position	Graphical view
WD1	43-82	
WD2	85-126	
WD3	128-168	
WD4	169-208	
WD5	212-253	
WD6	256-296	
WD7	299-333	

RBBP5/RBQ-3 (538 aa; 60 kDa)		
Description	a.a. position	Graphical view
WD1	22-63	
WD2	64-103	
WD3	148-188	
WD4	196-235	
WD5	249-291	
WD6	293-331	

(Data on WD40 position taken from UniProt)

**Figure 1.7 WD40 repeats in human WDR5 and RBBP5 facilitate protein-protein interactions**

Illustrative map showing the positions of seven WD40 repeats in human WDR5 and six WD40 repeats in RBBP5. WD40 repeats is labelled from WD1 to WD7. Amino acid positions indicate the start and end of each WD40 repeats. The dark yellow bars in the graphical view illustrate the position of WD40 repeats in each protein.



(Source: NCBI gene portal; Fagerberg et al. 2014)

**Figure 1.8 WDR5 transcriptome levels is the highest in testis compared to other tissues**

Bar chart showing the transcriptome levels of WDR5 and RBBP5. Y-axis is reads per kilobase per million reads placed. X-axis is the different tissues measured. Bar chart was plotted for mean of RPKM  $\pm$  SEM.

**Table 1.1 The conserved SET/MLL/COMPASS complexes in yeast, human and worm.**

Yeast SET1/ COMPASS	Human SET1/ COMPASS	Human MLL1/2	Human MLL3/4	Worm SET-2	Worm SET-16
Cps60/Bre2	ASH2L	ASH2L	ASH2L	ASH-2	ASH-2
Cps50/Swd1	RBBP5	RBBP5	RBBP5	RBBP-5	RBBP-5
Cpd25/Sdc1	DPY30	DPY30	DPY30	DPY-30	DPY-30
Cps30/Swd3	WDR5	WDR5	WDR5	WDR-5	WDR-5
Cps35/Swd2	WDR82				
Cps40/Spp1	CFP1				
	HCF1/2	HCF1/2	HCF1/2		
		MENIN			
			PTIP		
			UTX		UTX-1
			LPT		
SET1	SET1A/B			SET-2	
		MLL1/2			
			MLL3/4		SET-16

Adapted from (Mohan et al. 2011; Fisher et al. 2010)

### 1.2.3.2 MLL/SET/COMPASS complexes in *C. elegans*

The MLL/SET/COMPASS complexes are highly and structurally conserved even in the *C. elegans*. I will describe the methyltransferases and the core components, with mainly focusing on WDR-5.1 and RBBP-5 to show their similarities with their human counterparts.

*C. elegans* has only two complexes that are involved in H3K4 methylation: The SET-2/COMPASS and SET-16/COMPASS. SET-16/COMPASS was discovered by our lab during a screen for genes that attenuate RAS signaling (Fisher et al. 2010). The catalytic subunits in these complexes are the methyltransferases SET-2 and SET-16. SET-16, which is the orthologue of mammalian MLL3/4, is required for H3K4me3 during embryonic development (Fisher et al. 2010; Wilkins 2016). On the other hand, SET-2, which is the orthologue of yeast SET1, is required for H3K4me2/me3 (Simonet et al. 2007; Wilkins 2016). Interestingly, none of these two complexes are responsible for H3K4me1 deposition (Wilkins 2016). Not long ago, another two new H3K4 methyltransferase SET-17 and SET-30 were discovered. While SET-17 is required for H3K4me1/me2, SET-30 is required for H3K4me1/me2/me3 during larval development (Greer et al. 2014). Perhaps, these are the enzymes that catalyze H3K4me1 methylation. However, SET-17 and SET-30 homology are not similar to any of the SET/MLL family of enzymes. In both of the SET-2/COMPASS and SET-16/COMPASS complexes, the four core components of WDR-5, RBBP-5, ASH-2 and DPY-30 are conserved.

The WDR-5 gene in *C. elegans* is located in chromosome III. WDR-5.1 has 1519 base pairs, produces a transcript of about 1.3 kb long, and encodes a protein which is 376 amino acid long (41 kDa). WDR5 has another protein orthologue, WDR-5.2. However, knockout *wdr-5.2* (ok1444) does not reduce the level of H3K4me2/me3 (Li & Kelly 2011), indicating that it is not required for H3K4 methylation. *C. elegans* WDR-5.1 protein shares 68% protein sequence identity with the human WDR5 (Schuetz et al. 2006). The WD40 repeats in worm WDR5.1 are located between

amino acid 85 and 373 (Figure 1.9) (UniProt ID: Q17963). When the WD40 repeats of worm WDR-5 are aligned with its human homologue (Figure 1.10), great similarities were observed. Importantly, there is a null mutant strain *wdr-5(ok1417)* that carries 695 base pairs deletion targeting its WD40 repeats from WD1 to WD6. Another *C. elegans* knockdown strain, *wdr-5(90743)*, could be an alternative model since depletion in its WDR-5 has also been associated with reduced H3K4 methylation and prolonged lifespan (Greer et al., 2011). The mutant *wdr-5(ok1417)* worm are fertile but has moderate embryo lethality and egg laying defect (Li & Kelly 2011).

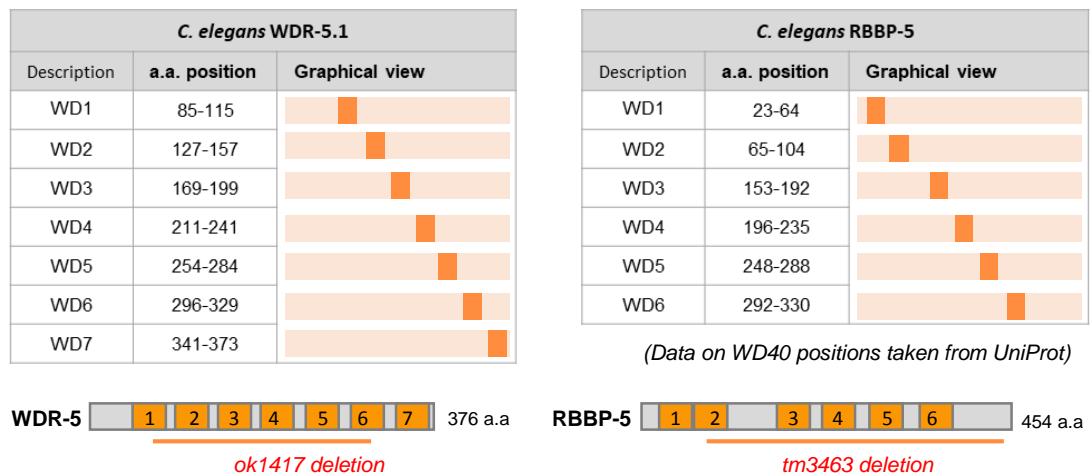
The worm *rbbp-5* gene is located in chromosome II, approximately 1.5 kb long and encodes 454 amino acids. The WD40 repeats which are located between amino acid 23 and 330 (Figure 1.9) (UniProt ID: Q09309), show that the worm RBBP-5 has six WD40 repeats similar to the number of repeats found in human RBBP-5. When aligned based on amino acid sequence and WD positions, great similarities were observed also between worm RBBP-5 and human RBBP5 proteins (Figure 1.11). In addition, *C. elegans* has a mutant strain *rbbp-5(tm3463)* with a deletion of 1005 base pairs out of 1505 base pairs of the *rbbp-5* wild type sequence. The deletion occurs in exon 3 to exon 4, affecting WD2 to WD6. The *rbbp-5(tm3463)* is a null mutant, hence, it does not have a functional RBBP-5. Another *C. elegans* strain with a knockout in *rbbp-5* gene is *rbbp-5(tm3530)*, however, it has been classified as lethal or sterile. The *rbbp-5(-)* mutant worm exhibits Dumpy phenotype, egg laying defect and substantial sterility (24% sterile compared to wild type) (Li & Kelly 2011).

The *ash-2* gene is located on worm chromosome II. It is approximately 2 kb long and encodes a 570 amino acid protein. Similar to human, it also has a SPRY domain. The SPRY domain of *C. elegans* is located between amino acid 272 and 470 (UniProt ID: Q9XXH4). *Dpy-30* gene, which is located in chromosome V, is about 600 bp long and encodes a protein with 123 amino acids. It has been associated with two multiprotein complexes: the MLL/SET/COMPASS complex and the SDC complex. DPY-30 is required in the SDC complex for sex-specific association of dosage compensation (Hsu et al. 1995).

In addition, the SET-16/COMPASS complex in *C. elegans* also contains the ubiquitously transcribed tetratricopeptide repeat, X chromosome protein 1 (UTX-1). The worm UTX-1, which is encoded by the X chromosome, is similar to the human UTX found in MLL3/4 COMPASS complexes (Swigut & Wysocka 2007). Our lab has shown that while SET-16/MLL regulates H3K4 methylation, the UTX-1 regulates H3K27 methylation (Fisher et al. 2010). The UTX-1 protein has tetratricopeptide repeats (Tpr) in the N-terminal half and JmjC domains in the C-terminal half. The Tpr domains are required for H3K27me1 demethylation but are dispensable for the activity on H3K27me2/me3 (Hong et al. 2007). On the other hand, the catalytically active JmjC domain is required for UTX-1 demethylase activity (Hong et al. 2007). UTX-1 is an aging regulator and a demethylase responsible for bulk removal of H3K27me2/me3. RNA interference of UTX-1 in *C. elegans* increases H3K27 methylation and causes lifespan extension (Swigut & Wysocka 2007).

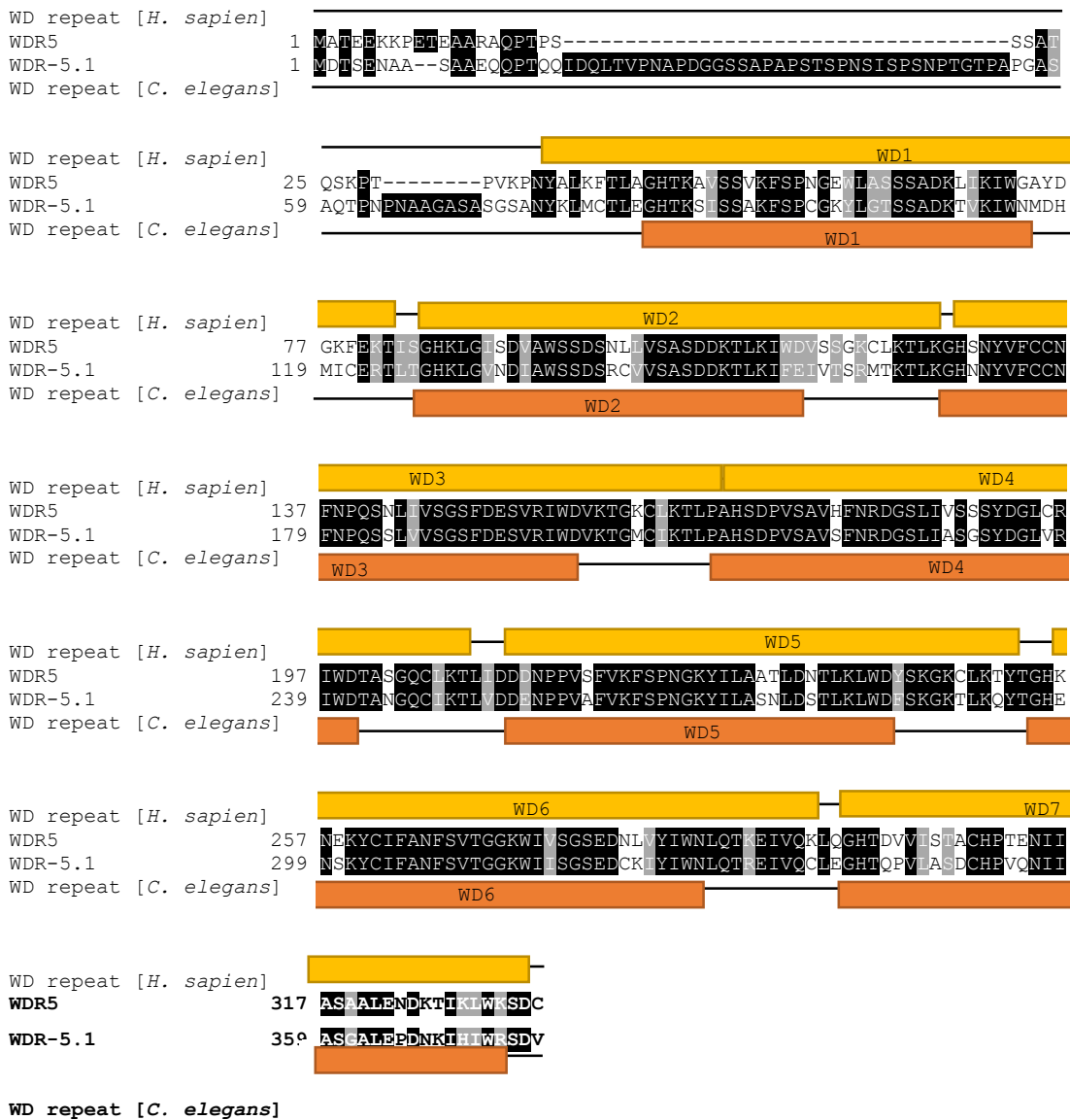
To sum up, the SET1/MLL methyltransferases are highly conserved from yeast to humans. For simplicity, these highly conserved complexes will be referred to as the MLL/SET/COMPASS

complexes. There may be more than one type of catalytic subunit that can associate with the complex. Although human has more diverse H3K4 methylation complexes, the structures and functions of most of the components are highly conserved in other organisms including *C. elegans*.



**Figure 1.9** WD40 repeats in *C. elegans* WDR-5.1 and RBBP-5

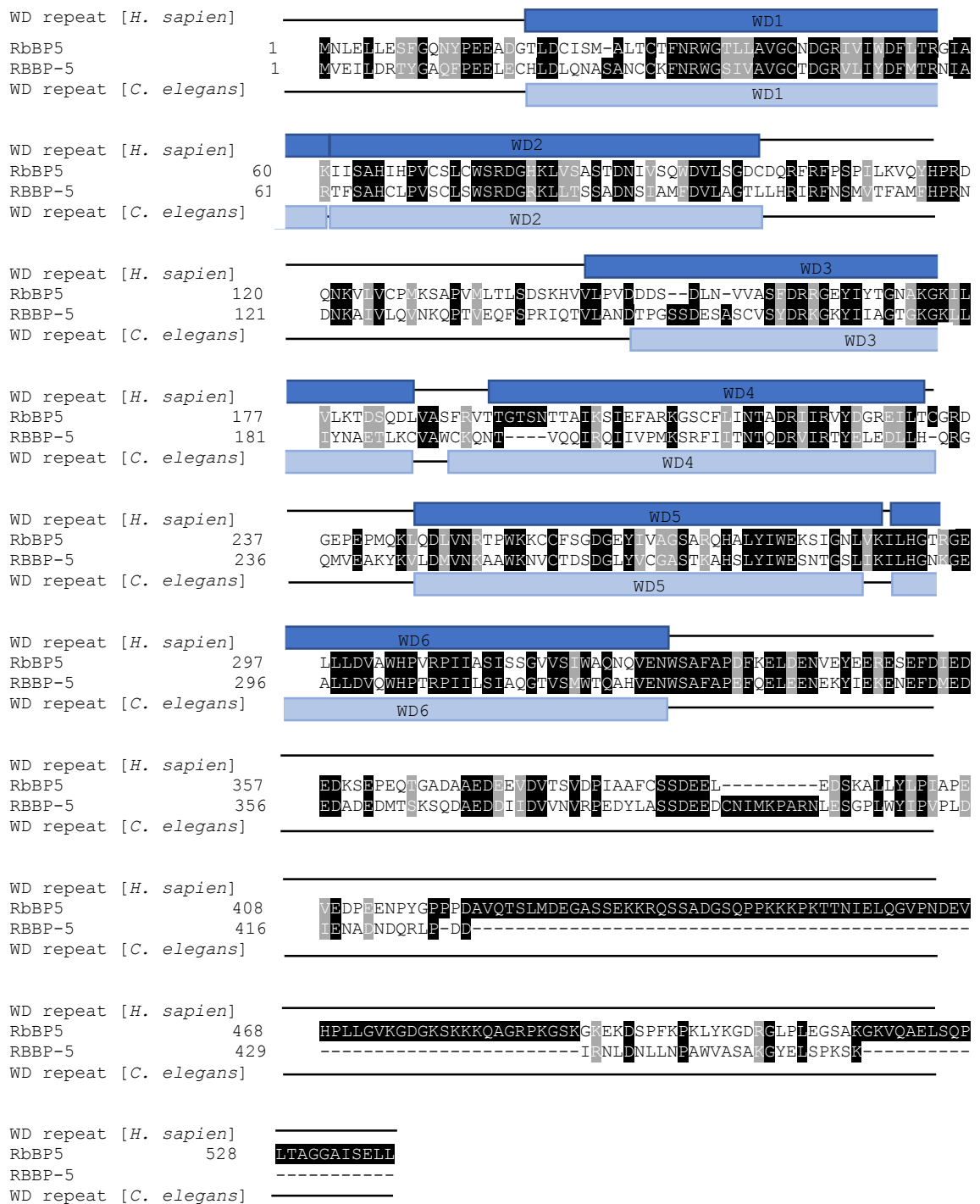
Illustrative map showing the positions of seven WD40 repeats in *C. elegans* WDR-5.1 and six WD40 repeats in RBBP-5. WD40 repeats are labelled from WD1 to WD7. Amino acid positions indicate the start and end of each WD40 repeat. The dark yellow bars in the graphical view illustrate the position of WD40 repeats in each protein.



**Figure 1.10 Conserved WD40 repeats in human WDR5 and worm WDR-5.1**

Comparison between human WDR5 protein sequence alignment (NCBI reference sequence: NP\_438172.1) and *C. elegans* WDR-5.1 protein (WormBase ID WP:CE00901). Amino acids highlighted in black indicate a strong alignment between the two organisms. Grey amino acids indicate less strong alignment between the two. Positions of WD40 repeats are illustrated in yellow box for human and orange box for *C. elegans*, labelled WD1-7.





**Figure 1.11 Conserved WD40 repeats in human RbBP5 and worm RBBP-5**

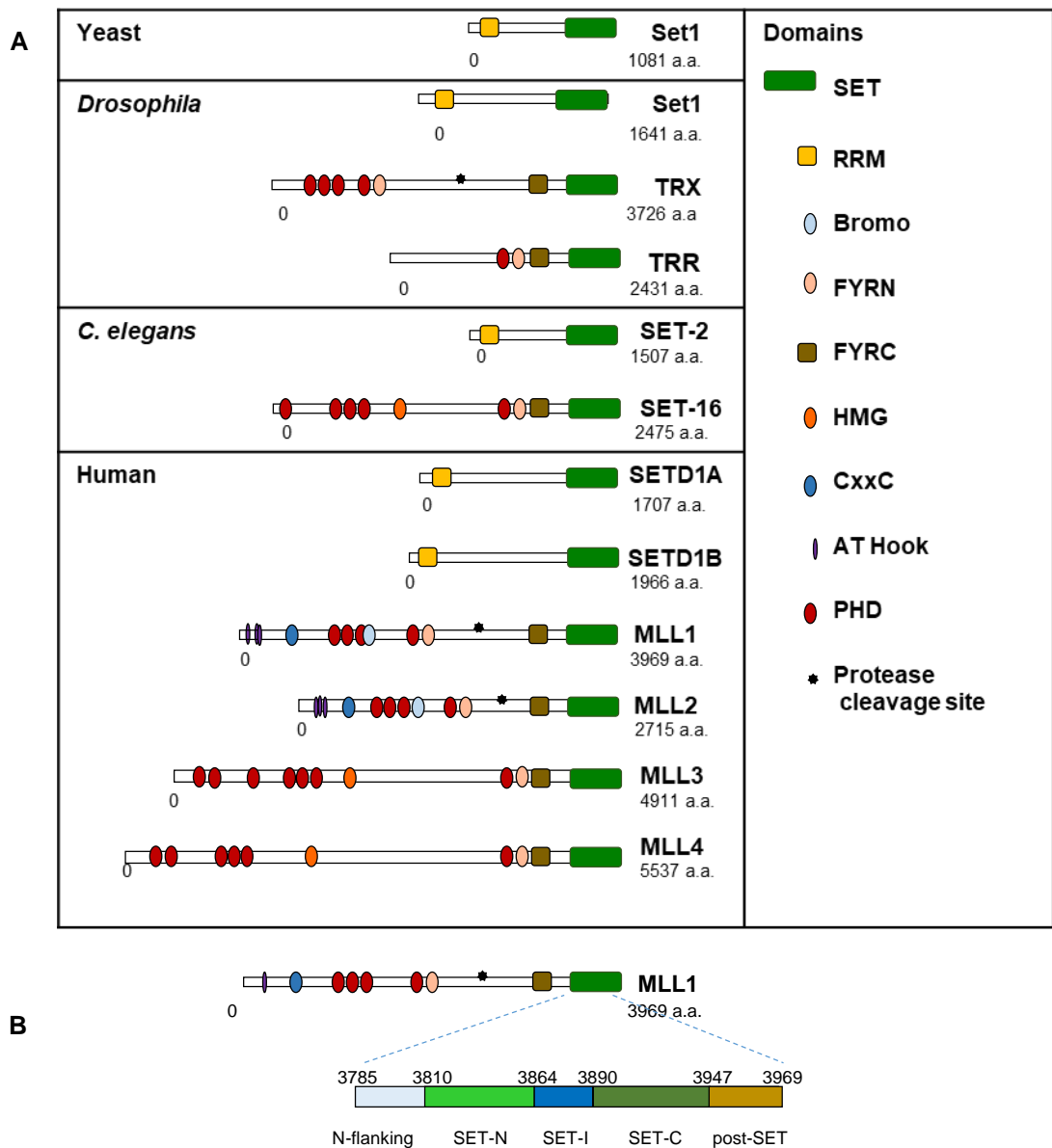
Comparison between human RbBP5 protein sequence alignment (NCBI reference sequence: NP\_005048.2) and *C. elegans* RBBP-5 protein (WormBase ID WP:CE32634). Amino acids highlighted in black indicate strong alignment while grey amino acids indicate less strong alignment between the two species. The positions of the six WD40 repeats (WD1 to WD6) are illustrated as darker blue in human and lighter blue in *C. elegans*.

#### 1.2.4 The structure and function of SET and MLL enzymes

SET-domain-containing methyltransferases are the catalytic subunits of the MLL/SET/COMPASS complex (Mozzetta et al. 2015). It is highly conserved from yeast to human (Figure 1.12A). SET domain is named after the *Drosophila* Suppressor of variegation 3-9 (Su(var)3-9), Enhancer of zester (E(z)), and Trithorax (Trx) proteins. SET is characterized by its approximately 130 amino acid long and it has catalytic activity towards the  $\epsilon$ -amino group of lysine residues (Herz et al. 2013). In this section, I will introduce the structure of the SET domain, its function in catalyzing the methyltransferase activity and other motifs that could be found adjacent to the SET domain.

The catalytic core SET domain is structurally conserved in most lysine methyltransferase (KMT). It is surrounded by adjacent domains such as Pre-SET, N-SET, Myeloid-Nervy-DEAF1 (MYND), Insertion SET (I-SET), Post-SET and C-terminal domain (CTD) (Figure 1.12B) (Schapira 2011). The SET domain adopts a series of folded structure that surrounds a knot-like structure (Upadhyay & Cheng 2011). The I-SET is structurally fixed and static, whereas, the Post-SET is dynamic and highly folded. Together, the I-SET and Post-SET act like a shell around the SET fold and serve as a substrate binding groove for lysine (Schapira 2011). The electropositive histone tail attracts the substrate binding groove, which is electronegative (Schapira 2011). Hence, an electrostatic attraction pulls the KMT to the lysine substrate, causing the lysine side chain to insert into a narrow channel at the junction of SET, Post-SET and I-SET (Xiao et al. 2003; Han et al. 2007; Collins et al. 2008; Huang et al. 2010; Wu et al. 2010). As the narrow channel is hydrophobic, the lysine is shielded from solvent, which is essential for the catalysis to happen (Smith & Denu 2009).

SET methyltransferases catalyze the transfer of methyl group from S-Adenosyl-L-methionine (SAM) to H3K4 residue. The SET domain has two sequence motifs ELx(F/Y)DY and NHS/CxxPN (Dillon et al. 2005; Qian & Zhou 2006; Xiao et al. 2003). In the knot-like structure, these motifs bring S-Adenosyl-L-methionine (SAM)-binding region in close proximity to lysine peptide-binding channel (Upadhyay & Cheng 2011). With the binding of SAM, the initial partially folded Post-SET conformation becomes more stabilized (Schapira 2011). The  $\epsilon$ -nitrogen of the lysine residue on histone tail becomes deprotonated (Smith & Denu 2009). It loses a proton into a solvent. As a result, the deprotonated amino acid group (NH<sub>2</sub>) from lysine attacks the positively charged SAM (Zhang et al. 2003). Following the nucleophilic attack, the lysine is methylated and the SAM by-product, S-adenosyl-homo-cysteine (SAH), is released. The SET-domain methylase is the catalytic subunit of the COMPASS complex. However, without the complex's core components, the enzyme is less active and restricted to monomethylation.



**Figure 1.12 SET domain in H3K4 methyltransferases are highly conserved from yeast to human**

(A) Illustration of SET domain and adjacent motifs in H3K4 methyltransferases in yeast, drosophila, worm and human. SET (green); RNA recognition motif, RRM (yellow); Bromo domain (light blue); FY-rich N-terminal, FYRN (light brown); FY-rich C-terminal, FYRC (dark brown); high mobility group domain, HMG (orange); CxxC (cyan); AT hook (grey disk); PHD fingers (red); and protease cleavage site (\*).

(B) The elements adjacent to the SET domain. N-flanking (light blue); SET-N (green); insertion SET, SET-I (dark blue); SET-C (emerald); and postSET (brown).

### 1.2.5 The structure and function of the core complex

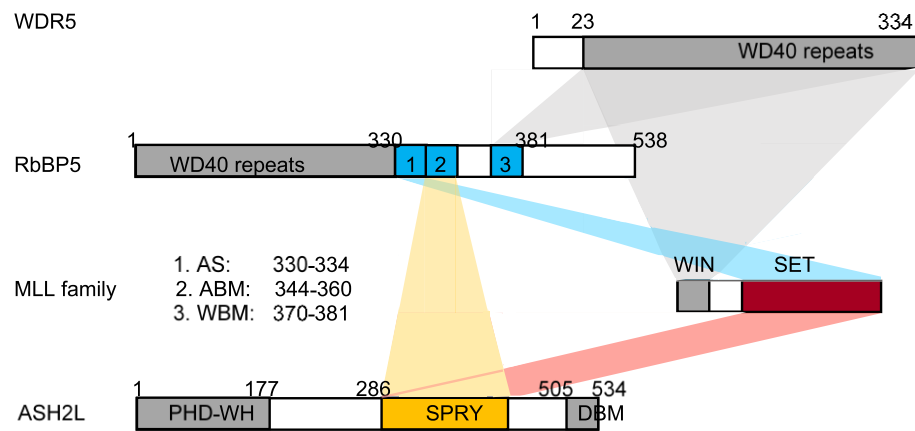
Assembly of the methyltransferase subunit and the WDR5-RBBP5-ASH2L-DPY-30 complex is organized in a specific structural order: MLL1↔WDR5↔RBBP5↔ASH2L↔DPY30 (Dou et al. 2006; Patel et al. 2009; Ernst & Vakoc 2012). The MLL/SET/COMPASS complex activity is highly compromised by the absence of the core components WDR-5, RBBP-5 and ASH-2. For instance, our lab has demonstrated that *rbbp-5(-)* mutant *C. elegans* embryos lack H3K4me1/me2/me3, *ash-2(-)* mutant embryos lack H3K4me2/me3 and *wdr-5(-)* mutant embryos lack H3K4me3 as well as displaying a reduction in H3K4me2 levels (Wang 2015). I will describe the structures of the core components, their roles in the assembly of the complex and their interactions with other proteins or molecules.

WDR5 is known for its seven WD40 repeats. The WD40 repeats on WDR5 interacts with WIN motif located at the carboxy-terminal regions of MLL proteins (Figure 1.13) (Patel et al. 2009). Although human SET1A, SET1B and MLL1-4 each contains WIN motif, they have different binding affinities, which range from 50 to 2800 nM (Dharmarajan et al. 2012). The strongest binding affinity is between MLL3 and WDR5 (Dharmarajan et al. 2012). In addition, the opposite side of the WDR5's  $\beta$ -propeller, which are formed by the folding of the WD40 repeats, can recognize the RBBP5's WDR5 binding motif (WBM) (Figure 1.13) (Odho et al. 2010; Avdic et al. 2011). In human, WDR5 and RBBP5 are required for complex formation and integrity (Meeks & Shilatifard 2017). WDR5 preferentially binds to H3 if the H3 tail is symmetrically dimethylated at H3R2 (Migliori et al. 2012). This explains the tight coupling of H3R2me2s with H3K4me3, which are commonly found at active promoters (C.-C. Yuan et al. 2012). WDR5 has also been shown to physically interact with the product of HOXA locus, the long intergenic noncoding RNA (lincRNA) HOTTIP (Wang et al. 2011). The interaction promotes gene activation at the HOXA locus via MLL-mediated H3K4me3 (Geisler & Paro 2015; Wang et al. 2011).

Other domains found in RBBP5 include WD40 repeats, activation segment (AS) and ASH2L binding motif (ABM) domains (Li et al. 2016). On the other hand, domains of ASH2L proteins are PHD and an SPRY (SPIa and ryanodine receptor) domains (Figure 1.13) (Li et al. 2016). RBBP5's ABM has a cluster of acidic residues of D/E box (Y. Zhang et al. 2015) that recognizes the concave structure of the ASH2L's SPRY domain. ASH2L has a winged-helix domain that can bind to DNA in chromatin (Sarvan et al. 2011; Chen et al. 2011). ASH2L can also bind directly to DPY-30 (Cho et al. 2007). Both ASH2L and CFP1 are required for the implementation of proper levels of H3K4me2/me3 (Meeks & Shilatifard 2017).

Interactions between SET-domain and WDR5-RBBP5-ASH2L structure upregulates H3K4 methylation. For instance, MLL1 is a "slow" H3K4me1 methylase, whereas, the MLL1-WRAD subcomplex (WDR5, RBBP5, ASH2L and DPY-30) is a "fast" H3K4me1/me2 methylase (Shinsky & Cosgrove 2015; Patel et al. 2009). Phosphorylation of RBBP5 stimulates WRAD complex formation and enhance SET1A/B and MLL1-4 H3K4 methyltransferase activity in human (P. Zhang et al. 2015). DPY30 can enhance MLL1 methyltransferase catalytic activity by up to five fold (Southall et al. 2009; Patel et al. 2009).

To sum, SET catalytic activity at H3K4 is regulated by the core components of WDR5, RBBP5, ASH2L and DPY-30 (WRAD). Association with WRAD complex enhances the SET activity. In addition to providing interaction within the MLL/SET/COMPASS complex, WRAD can also interact with other molecules such as H3 protein, DNA and RNA.



**Figure 1.13 Interactions amongst SET-containing enzyme, WDR5, RBBP5 and ASH2L**

WDR5's WD40 repeats (grey) show interactions with RBBP5 and SET enzyme. RBBP5 has WD40 repeats (grey); activation segment; AS (blue, labelled '1'); ASH2L binding motif, ABM (blue, labelled '2'); and a WDR5 binding motif, WBM (blue, labelled '3'). MLL has a SET domain (red) and a WIN motif (grey). ASH2L has PHD fingers (grey) and SPRY domain (yellow). Source (Li et al. 2016).

### 1.2.6 Removal of methylated marks at H3K4

Methylation at H3K4 is mediated through the balance between methyltransferases and demethylases. Demethylases are enzymes that can reverse the methylation at H3K4. Several H3K4 demethylases can be found in human and *C. elegans*.

Within the histone demethylase, there is a catalytic domain and chromatin targeting domains (Zhang et al. 2014). There are two families of demethylase catalytic domains: the amine oxidases family and the Jumonji C-domain-containing dioxygenases family (Greer & Shi 2012). KDM1A (LSD1) and KDM1B (LSD2) are examples of the two earliest discovered flavin-dependent monoamine oxidase family (Shi et al. 2004; Ciccone et al. 2009). Since KDM1A and KDM1B require protonated lysine, they can act only on H3K4me1/me2 but not H3K4me3 (Anand & Marmorstein 2007). In the catalysis, the  $\alpha$ -carbon of the lysine substrate is cleaved, generating imine intermediate. Imine becomes hydrolyzed into carbolamine, which then degrades, releasing formaldehyde and amine (Anand & Marmorstein 2007). Following the catalysis, H3K4me1/me2 is converted to unmodified H3K4 (Shi et al. 2004; Chen et al. 2013; Nowak et al. 2016). The Jumonji dioxygenase histone demethylase family has a wide range of members. There are more than 20 identified members in human, which include KDM2B, KDM5A, KDM5B, KDM5C and KDM5D (Nowak et al. 2016). This family of histone demethylase has a conserved JmjC domain (Nowak et al. 2016). The JmjC domain directs iron to mediate dioxygenase-dependent demethylation reaction (Tsukada et al. 2005).

Histone demethylases often exist within large multi-protein complexes. Domains such as PHD, Tudor and Tetratricopeptide Repeat (TPR), within the complexes help with the complexes binding to histone post-translational modifications (Dimitrova et al. 2015). For instance, the PHD1 domain on the co-repressor and H3K4me2/me3 demethylase, KDM5B, binds to the demethylation product, H3K4me0, to prevent re-methylation of H3K4 (Zhang et al. 2014). Histone demethylases can also have domains that interact with lncRNAs. lncRNAs has been found to bind with WDR5 and KMD1A/CoREST demethyltransferase complex (Wang et al. 2011; Greer & Shi 2012).

In *C. elegans*, there are fewer H3K4 demethylases. *C. elegans* SPR-5 is the homolog of human LSD amine oxidase family. It is the H3K4me1/me2 histone demethylase. Absence of SPR-5 causes progressive impairment in fertility and increases global level of H3K4me2 (Greer et al. 2016; Katz et al. 2009; Nottke et al. 2011). Moreover, loss of SPR-5 leads to transgenerational longevity. The study found that the first five *spr-5(-)* mutant generations had normal lifespan, whereas generation 10 and 20 displayed extended lifespan by 19%-44% (Greer et al. 2016) *rbr-2* is the *C. elegans* homolog of the human JmjC demethylase family (Nishibuchi et al. 2014). It is the H3K4me2/me3 demethylase and is thought to negatively regulate transcription initiation by removing H3K4me3 at Transcription Start Sites (TSS). Absence of RBR-2 result in excess H3K4me3 in *C. elegans* and shortened lifespan (Greer et al. 2010).

To conclude, human and *C. elegans* have H3K4 demethylases, which could be members of either the amine oxidase family or Jumonji family. The demethylases ensure balanced level of H3K4 methylation and allow H3K4 methylation to be reversible.

### 1.2.7 Readers of methylated H3K4

As explained earlier, H3K4 methylation levels does not affect the overall charge of the nucleosome. To impact on transcription, it serves as a binding platform for several chromatin readers. The readers may harbor several domains, such as the PHD fingers, chromodomain, Tudor, and zinc finger (Zf) CW (Yun et al. 2011; Musselman et al. 2012). The readers may have two to four aromatic rings, serving as binding pockets for lysine (Musselman et al. 2012). A smaller or negatively charged pocket prefers H3K4me1/me2 over H3K4me3 binding (Yun et al. 2011). In this section, I will introduce H3K4 methylation readers that have roles in regulating other histone post-translational modifications, chromatin-remodeling mechanisms, and transcription.

Several H3K4 methylation readers are associated with recruitments of histone acetylations (HATs), histone deacetylations (HDACs) and histone demethylases. Examples of these readers are ING2, ING4, PHF2, PHF8, JMJD2A and JMJD2B. Upon DNA damage during transcription, ING2 binds to H3K4me3 through its PHD domain and recruits Sin3 histone deacetylase complex to silence transcription (Shi et al. 2006). Binding of complexes containing ING4 (or yeast Yng1) to H3K4me2/me3 stimulates acetylation at H3K14 which has been associated with transcription processes (Lalonde et al. 2013; Lalonde et al. 2014; Taverna et al. 2006; Hung et al. 2009). Another example is the PHF2 lysine demethylase, which has a JmjC domain for H3K9me1

demethylation and a PHD domain for H3K4me2/me3 recognition (Wen et al. 2010). PHF8 is a JmjC-containing histone demethylase that recognizes H3K4me3 and removes H3K9me2 repressive marks (Cloos et al. 2008; Horton et al. 2010). Double tudor domains of JMJD2A and JMJD2B demethylases binds to H3K4me3 and H4K20me2. Upon DNA damage, JMJD2 degrades thus exposing H4K20me2 to DNA repair pathway (Mallette et al. 2012). Thus, H3K4 methylation can be associated with readers that function as post-translational modifiers for histone peptides.

Some readers of methylated H3K4 have also been linked to chromatin-modifying and chromatin-remodeling mechanisms such as 'Chromodomain-helicase-DNA-binding protein 1' (CHD1) and 'Bromodomain and PHD domain transcription factor' (BPTF) (Musselman & Kutateladze 2009). The double chromo domain of CHD1 ATP-dependent chromatin remodeling enzyme has a preference for H3K4me2/me3 over H3K4me1 (Flanagan et al. 2005; Pray-Grant et al. 2005; Sims et al. 2005). The CHD1 protein has been implicated in replication-independent histone exchange or assembly (Radman-Livaja et al. 2012). Another domain, PHD of BPTF, is known to bind more strongly to H3K4me3 in presence of H3K9AcK14Ac for nucleosome association (Vermeulen et al. 2010). The BPTF subunit is part of the NURF chromatin remodeling complex (Musselman & Kutateladze 2009). The evidence indicates that H3K4 methylation serves as a platform for a number of chromatin remodelers.

H3K4 methylation readers importantly are directly associated with the general transcriptional machinery. Human TAF3 (Transcription associated factor 3), a subunit of the basal transcription complex TFIID, binds to H3K4me3 through its PHD domain (Lauberth et al. 2013). TFIID then, along with other general transcription factors, forms the PIC complex for transcription initiation. SAGA histone acetyltransferase complex is important in the activation of transcription of RNA polymerase II targets. SAGA is linked to H3K4me2/me3 through a double tudor domain in Sgf29 subunit. The bindings of H3K4 methyl marks to TAF3 and Sgf29 are strengthened in a presence of H3K9AcK14Ac (Vermeulen et al. 2010). Zf-CW domain of AOF1 can recognize H3K4me1/me2 and stimulate the demethylation of these marks (Yang et al. 2010). LSD2/KDM1B/AOF1 associates with H3K36me3-enriched coding regions of transcriptionally active genes. Its demethylase activity coordinates the levels of H3K4me1/me2, H3K9me2 and H3K36me2 (Fang et al. 2010). Thus, some readers of H3K4 methylation are directly associated with transcription processes.

In summary, H3K4 methylation can recruit various readers. Recruitments of these readers are essential for other post-translational modifications on histone proteins, chromatin remodeling and transcription initiation (Table 1.2). One can imagine the wide range of biological consequences that may occur if the levels of H3K4 methylation become aberrant.

**Table 1.2 Readers of H3K4 modifications**

Histone modifications	Recognition module	Protein	Related modifications		Functions	References
			Enhanced by	Inhibited by		
<b>H3</b>	K4me2/me3	Chromo	CHD1			ATP-dependent chromatin remodeling (Flanagan et al. 2005; Sims et al. 2005; Pray-Grant et al. 2005)
	K4me3	PHD	RAG2			Recombination (Ramon-Maiques et al. 2007; Ji et al. 2010)
	K4me3	PHD	ING2			HDAC (Shi et al. 2006)
	K4me3	PHD	BPTF	H3K9Ac H3K14Ac		ATP-dependent chromatin remodeling (Musselman et al. 2012; Vermeulen et al. 2010)
	K4me3	PHD	TAF3	H3K9Ac H3K14Ac	H3R2me2	TFIID transcription Activation (Kungulovski et al. 2016; Vermeulen et al. 2007)
	K4me2/me3	PHD	PHF2			H3K9 demethylation (Wen et al. 2010)
	K4me2/me3	PHD	ING4			HBO1 H3 acetylation (Lalonde et al. 2013; Lalonde et al. 2014; Hung et al. 2009)
	K4me2/me3	PHD	YNG1			NuA3 H3 acetylation (Taverna et al. 2006)
	K4me3	PHD	PHF8	H3K9Ac H3K14Ac		Histone demethylation (Cloos et al. 2008; Horton et al. 2010)
	K4me3	Tudor	JMJD2A			Histone demethylase (Malette et al. 2012)
	K4me3	Tudor	JMJD2C			Histone demethylase (Malette et al. 2012)
	K4me2/me3	Tudor	Sgf29	H3K9Ac H3K14Ac		Histone acetylation (SAGA) (Vermeulen et al. 2010)
	K4me1/me2	zf-CW	AOF1			Histone demethylase (Yang et al. 2010; Fang et al. 2010)
	K4me0	PHD	BHC80			LSD1.com (Yun et al. 2011)
	K4me0	WD40	WDR5/WDR9			HAT (Yun et al. 2011)
	K4me0	Dnmt3L			K4me	DNA methylation (Yun et al. 2011)

Adapted from (Yun et al. 2011)



### 1.3 H3K4 methylation and transcription regulation

In general, methylation at H3K4 has been associated with active transcription. The current section aims to introduce how H3K4 methylation is linked to transcription initiation and elongation, how it is distributed throughout the genome and how it defines bivalent domains.

#### 1.3.1 Initiation of transcription

Initiation of transcription in eukaryotes is a complex process. It involves many multiprotein complexes and requires synergy between the CTD (carboxy terminal domain) and histone codes. Transcription initiation involves RNAPII recruitment, PIC formation, RNAPII CTD phosphorylation and clearance of RNAPII from promoters.

RNA polymerase II (RNAPII) is the protein complex responsible for transcribing the eukaryotic genome into messenger RNA (mRNA) and some noncoding RNA, such as microRNA, eRNA and lncRNA. RNAPII is composed of 12 protein subunits (RNA polymerase II subunit, RPB1-12) (Acker et al. 1997; Edwards et al. 1991). Among the subunits, RPB1 is the largest and contains the CTD (Cramer 2001). The CTD is extended from the catalytic core of the enzymes and is positioned close to the mRNA exit tunnel (Cramer 2001). It has an unusual repetitive sequence of Tyr1-Ser2-Pro3-Thr4-Ser5-Pro6-Ser7 (YSPTSPS) that can undergo extensive post-translational modifications, termed the CTD code (Allison et al. 1985; Corden et al. 1985). Coordination between histone modification and CTD code is essential for the delicate regulation of transcription (Corden 2013; Hsin & Manley 2012). Ser2 and Ser5 of the RNAPII CTD in most species can be phosphorylated at various stages of transcription. In yeast and some mammalian cells, transcription-associated Ser-7 phosphorylation has also been observed.

RNAPII binds to a preinitiation complex (PIC) assembled at the promoters. PIC is a multiprotein complex comprising an unphosphorylated RNAPII, general transcription factors (TFIIA, TFIIB, TFIID, TFIIIE, TFIIF and TFIIH) and a mediator complex (Thomas & Chiang 2006). The selection of promoters is facilitated by TFIID, which is the first step in PIC formation. TFIID is made up of several subunits including TAF1-13 and a TBP (Goodrich & Tjian 2010). Although there are various core promoter elements, the promoters with TATA-box element can be recognized by the TBP subunit of the TFIID complex (Juven-Gershon et al. 2008). Another subunit of the TFIID, TAF3, has a PHD domain that recognizes H3K4me3 (Vermeulen et al. 2007). H3K4me3 is essential for the PHD to bind to native nucleosomes *in vitro* and *in vivo* (Vermeulen et al. 2007). The importance in the H3K4me3-TFIID interaction has been demonstrated in an RNAi experiment against WDR5 (Vermeulen et al. 2007). Depletion in WDR5 leads to reduction in H3K4me3 levels, weakened the TBP/TFIID association with the core promoters and decreased mRNA levels at specific loci (Vermeulen et al. 2007). After binding of TFIID to the promoter, the remaining general transcription factors (TFIIA, TFIIB, TFIIIE, TFIIF and TFIIH) are recruited to form the PIC. The PIC by now is fully formed but will remain poised (Ioshikhes et al. 2006).

Following PIC formation, the TFIIH-kinase (CDK7) is recruited and phosphorylates Ser5 and Ser7 of the RNAPII CTD (Egloff et al. 2007; Kim et al. 2009; Rodriguez et al. 2000). There are also

various kinases that can phosphorylate Ser5. Ser5 phosphorylation marks the transition between transcription initiation and elongation (Ng et al. 2003). The phosphorylated Ser5 (Ser5-P) induces dissociation of mediator complex and stimulates promoter clearance (Rodriguez et al. 2000; Max et al. 2007; Viladevall et al. 2009; Ho & Shuman 1999; Schroeder et al. 2000; Wen & Shatkin 1999).

Clearance of RNAPII from promoters is linked to further chromatin modifications. The phosphorylation at Ser5 results in recruitment of MLL/SET/COMPASS complex at 5' end of active genes by the transcription elongation machinery (Ng et al. 2003). The complex converts H3K4me1 to more active marks, H3K4me2/me3 (Dehé et al. 2005). Deposition of H3K4me3 by the complex creates binding sites for effector proteins, such as the HATs and HDACs, which in turn contribute to gene-specific transcription activation by chromatin remodeling (Ng et al. 2003; Larabee et al. 2005; Li et al. 2007; Kim & Buratowski 2009).

Since transcription has to proceed through chromatinized DNA, the HATs or HDACs chromatin remodelers are necessary to produce open active or close repressive chromatin state, respectively (Santos-Rosa et al. 2002). An example of a HAT complex is the yeast SAGA complex (human STAGA/TFTC). It is a multiprotein complex consists of Tra1, Gcn5, Ada2, Ada3, Spt3, Spt8, Ubp8, Sus1, Sgf11, Sgf73, Spt7, Spt20, Ada1, TAF5, TAF6, TAF9 and TAF12 subunits in yeast (Koutelou et al. 2010). Interestingly, in human, the SAGA complex also has a SGF29 subunit which can bind H3K4me2/me3 (Vermeulen et al. 2010). SAGA is known for its histone acetyltransferase and deubiquitinase activities (Nagy & Tora 2007; Rodríguez-Navarro 2009). ySAGA binds to acetylated H3 (H3K9 and H3K14) and H4 through a bromodomain of its Gcn5 subunit (Li & Shogren-Knaak 2009; Owen et al. 2000). The deubiquitinase activity on H2B sustains RNAPII Ser2, whereas, activity on H2A monoubiquitination promotes histone acetylation and passage of RNAPII (Stock et al. 2007; Wyce et al. 2007; Zhou et al. 2008). The binding potentiates cooperative H3 acetylation which opens up chromatin for the binding of transcription factors and PIC. ySAGA recruits TBP through its Spt3 subunit for PIC formation (Mohibullah & Hahn 2008). To summarize, TAFIID-H3K4me3 interaction strengthen PIC association with promoters; Ser5-P on the CTD promotes the recruitment of the MLL/SET/COMPASS complexes; methylated H3K4 recruits HATs; and acetylation causes chromatin to open up for the next step of transcription.

### **1.3.2 Elongation of transcription**

In order for RNAPII to initiate elongation, it must have promoter clearance and form a transcription bubble. During promoter clearance, RNAPII lost its contact with the PIC and establish a stable connection with the nascent transcript (Luse 2013). RNAPII is modified through insertion of several new elongation-supportive factors. Phosphorylation of RNAPII CTD at Ser2 promotes recruitment of mRNA processing and termination factors (Lee & Greenleaf 1991; Ahn et al. 2004; Bartkowiak et al. 2010). RNAPII CTD Ser2 is catalyzed by CDK9, which interacts with the positive transcription elongation factor b (P-TEFb) (Brès et al. 2008). Hence, Ser2-P on CTD is often used as a marker of transcription elongation. For the formation of the transcription bubble, RNAPII

requires XPB helicase of TFIIH complex since RNAPII cannot drive opening of the DNA template (Tirode et al. 1999; Coin et al. 1999). The newly formed RNA-DNA hybrid is short and unstable. Subsequently, addition of adequate NTPs reduce the chance of transcript abortion (Luse & Jacob 1987; Jiang et al. 1995; Holstege et al. 1997). Bubble collapse marks the end of promoter clearance. Upon quitting the RNA-DNA hybrid state, the future mRNA enters the exit channel (Luse 2013).

It is important to note that once RNAPII encounters a nucleosome during elongation, it must break the nucleosome barrier to gain access to DNA. Breaking the nucleosome barrier can be achieved through nucleosome sliding or exchange of histones. Nucleosome occupancy is generally reduced upstream of the TSS (Transcription Start Site), this area is often referred to as the nucleosome-free region. There is often one nucleosome located exactly at the TSS (Segal & Widom 2009; Kaplan et al. 2009). Interestingly, the nucleosomes marked by H3K4me2/me3 can be recognized by CHD1, which contains double chromo domains (Flanagan et al. 2005; Pray-Grant et al. 2005; Sims et al. 2005). CHD1 co-localizes with RNAPII and interacts with FACT (facilitates chromatin transcription) and RNAPII elongation factor DSIF (DRB (5,6-dichloro-1- $\beta$ -D-ribofuranosylbenzimidazole) sensitivity-inducing factor) (Simic et al. 2003). CHD1 functions to slide the nucleosomes into an ordered array throughout gene bodies (Nodelman & Bowman 2013), whereas FACT mediates the removal and assembly of H2A-H2B dimers. Together, this leads to RNAPII gaining access to DNA.

Another chromatin remodeler, ISW1, also possesses nucleosome-sliding capabilities (Venkatesh & Workman 2015). ISW1 complex can bind to H3K36me3 and H3K4me3 via the PHD fingers of its BPTF subunit and PWWP domain of LOC4, respectively (Ruthenburg et al. 2011). Both H3K36me3 and H3K4 methylation are important marks in gene bodies. Enrichment of H3K36me3 by Set2 methyltransferase marks active exons (Kolasinska-Zwierz et al. 2009; Kizer et al. 2005), whereas introns are enriched for H3K4me1/me2 (Huff et al. 2010). The level of H3K36me3 within alternative exons correlates with their inclusion in spliced transcripts (Kolasinska-Zwierz et al. 2009; Spies et al. 2009). Following the breaking of nucleosome barrier, the methylated nucleosomes are re-incorporated in irregularly spaced manner. ISW1 reinstates properly spaced nucleosome array (Venkatesh & Workman 2015). Histone exchange becomes restricted when H3K36 methylation is enriched at body regions (Venkatesh & Workman 2015). It helps establish the transcription memory that persists through several rounds of transcription.

In conclusion, following transcription initiation, RNAPII is modified to resume transcription elongation. RNAPII has to face several challenges like transcript abortion and nucleosome barriers during the elongation process. Thankfully, H3K4 methylation can recruit readers associated with chromatin remodelers to help overcome the nucleosome barrier.

### **1.3.3 Distribution of histone modifications on active, repressed and poised genes**

Enrichment of specific histone post-translational marks that facilitate transcription processes can be found in enhancer, promoter and gene bodies of active genes. An enhancer is a short DNA

sequence located up to 1 Mbp away upstream or downstream from the TSS. The DNA sequence of an enhancer defines the type of transcription factors recruited. On the other hand, a promoter is not completely defined by the DNA sequence, but by a genomic region where transcription of a particular gene starts. In this section, I will explain the distribution of histone post-translational modifications near enhancer, promoter and gene bodies of active, repressed and poised genes.

H3K4me3 enrichment has been observed in region surrounding the TSS of active promoters in many cells such as the human T cell (Barski et al. 2007), human embryonic stem (ES) cell (Guenther et al. 2007) and human HeLa cells (Heintzman et al. 2007). On the other hand, silent promoters have high levels of H3K27me3 as shown in human T cells (Barski et al. 2007). Hence, H3K4me3 marks active promoters whereas H3K27me3 marks silent promoters.

Enhancer regions are often marked by H3K4me1 as has been shown in human HeLa cells (Heintzman et al. 2007). However, both H3K4me1 and H3K27ac represent putative active enhancers in human embryonic stem cells (hESC) (Rada-Iglesias et al. 2011) and in five different murine cells (Creyghton et al. 2010). The H3K27ac enrichment found in active enhancers distinguish active from poised enhancers (Creyghton et al. 2010).

Enrichment of H3K4me1/me2 can be found downstream of TSS towards the gene body (Kimura 2013; Dunham et al. 2012; Barski et al. 2007; Guenther et al. 2007). Another mark associated with gene bodies of transcriptionally active genes is the H3K36me3. H3K36me3 signals are sharply elevated after the TSSs in active genes in human T cells (Barski et al. 2007). The H3K36me3 is thought to be involved in splicing process (Pradeepa et al. 2012; Luco et al. 2010; Kolasinska-Zwierz et al. 2009).

Promoters that have both H3K4me3 activating marks and H3K27me3 repressive marks are transcriptionally poised. They represent bivalent domains and are chromatin segments that have both activating and repressive epigenetic marks. Genes of self-renewing pluripotent cells often harbor bivalent active H3K4me3 and repressive H3K27me3 marks at promoter regions. Deposition of H3K4me3 is constricted to TSS region while H3K27me3 deposition is relatively broader (Bernstein et al. 2006). The abundance of RNAPII CTD Ser5-P at promoter regions indicate that the bivalent genes are competent in initiating transcription (Brookes et al. 2012). Ser5-P recruits Trithorax MLL/SET/COMPASS complex to trimethylate H3K4 (Ng et al. 2003; Milne et al. 2005). However, since the polycomb repressive complex 2 (PRC2) also deposit H3K27me3 on the same promoters, the transcription become poised, meaning that transcription is blocked but ready to switch into either a fully active or repressive state. The genes are poised until there is cue for differentiation. Upon differentiation, bivalent genes become enriched with transcription factors and lose the H3K27me3 marks (Pan et al. 2007; Zhao et al. 2007). It has been shown in *C. elegans* that the UTX-1 subunit, a member of the SET-16/COMPASS complex, is responsible for the bulk removal of H3K27me3 (Wang et al. 2010). On the other hand, silenced genes will lose H3K4me3 from their promoter regions (Bernstein et al. 2006).

The bivalent genes are capable of initiating transcription but not elongation (Brookes et al. 2012). One factor that inhibits elongation and fortifies gene repression is the co-existence of Polycomb PRC1 and PRC2. PRC1 compacts chromatin (Francis et al. 2004; Grau et al. 2011), which then

stimulates PRC2 to methylate H3K27 (W. Yuan et al. 2012). PRC1-mediated H2AK119Ub1 tracks and restrains RNAPII across the genes, preventing gene expression (Zhou et al. 2008). The coding regions of bivalent genes have no detectable association with the CTD Ser2-P (Brookes et al. 2012) and H3K36me3 (Brookes & Pombo 2009). The initial deposition of H3K27me3 impedes the deposition of H3K36me3 (Schmitges et al. 2011). Nevertheless, RNAPII can escape and produce immature aborted transcripts that are degraded, but importantly there is no production of functional mRNAs.

In summary, there are specific distributions of histone post-translational modifications throughout the genome. Active genes in general are associated with enhancers enriched with H3K4me1 and H3K27ac and promoters with H3K4me3. There are bivalent domains defined by enrichments in both H3K4me3 and H3K27me3. Interestingly, the enrichments and combinations of histone modifications can produce signatures for active, poised or repressed genes.

## **1.4 Epigenetic inheritance**

Epigenetics is the inheritance of patterns of gene expression independent of changes in the DNA sequence. Epigenetic effects can be mediated by mRNAs, noncoding RNAs, proteins (prions), DNA modifications, and histone modifications (Heard & Martienssen 2014). Here, I will describe about heritable traits associated with the transmittance of H3K4 methylation in mitosis and across several generations of progeny (transgenerational).

### **1.4.1 Mitotic inheritance and H3K4 methylation**

Inheritance of H3K4 methylation during mitotic division has been reported in amoeba *Dictyostelium discoideum* and human HeLa cells (Muramoto et al. 2010; Mishra et al. 2009). The cell cycle is comprised of a G1 phase, an S-phase, a G2-phase, and the mitotic phase that further divides into prophase, metaphase, anaphase and telophase. The MLL/SET/COMPASS complex and H3K4 methylation are normally associated with transcriptionally active chromatin in G1 phase. In human HeLa cells, MLL1 dissociates during mitosis and returns only after telophase ended. In contrast, H3K4me3 remains associated with chromatin throughout the cell cycle (Mishra et al. 2009), suggesting that the mark is successfully retained into the daughter cells. H3K4 methylation is associated with active transcription and can persist several hours after the onset of transcription (Santos-Rosa et al. 2002; Ng et al. 2003). To determine if active transcription state is also inherited, Muramoto followed single-gene transcription events through mitotic division in amoeba. Interestingly, absence of Set1, absence of Ash2 or change of H3 Lysine 4 into H3 Alanine 4 eliminate the inheritance of active transcriptional states (Muramoto et al. 2010). Both findings show that H3K4 methylation and active transcription states are inherited during mitotic division. On the other hand, H3K36me3 is not required for inheritance of active transcriptional states during mitosis (Muramoto et al. 2010).

### 1.4.2 Transgenerational inheritance and H3K4 methylation

Parental exposure to environmental factors, such as stress, toxicants, and abnormal nutrition may alter the phenotypes of offspring for up to several generations (Yao et al. 2014; Manikkam et al. 2012; Anway et al. 2005; Dunn & Bale 2011; Lagisz et al. 2014). It has emerged that a variety of non-genetic mechanisms are behind this transgenerational inheritance, including inheritance of DNA methylation, prions, maternal RNAs (mRNAs, lncRNAs, siRNAs), metabolites and histone modifications (Daxinger & Whitelaw 2012). The epigenetic inheritance system allows adaptation response crucial for survival and species continuation.

Among these epigenetic systems, H3K4 methylation and modifiers have been shown to regulate transgenerational inheritance in *C. elegans*. However, the exact mechanism is still unclear. It is believed that even though specific traits can be inherited for several generations, there is no change in the global H3K4 methylation levels, suggesting that subtle changes are sufficient for these specific traits to become inherited (Greer et al. 2011; Kishimoto et al. 2017). In experiments designed to assess epigenetic inheritance, *C. elegans* parents stressed by exposure to stimuli (arsenite, NaCl and caloric restriction) managed to adapt and build resistance. This resistance to stress was passed on to unstressed descendant (F1). No significant changes in the global H3K4me3 levels was observed in both stressed parents and the immediate descendants (Kishimoto et al. 2017). Another piece of evidence showing that the global H3K4me3 levels was not significantly different after several generations was done on transgenerational inheritance of longevity in *C. elegans* (Greer et al. 2011). The descendants are the third genotypically wild-type generation (F3) that inherit extended lifespan from epimutated ancestors (Greer et al. 2011). This transgenerational inheritance is still mostly unexplained, it might be: 1) associated with H3K4me3 level at specific gene loci (Benayoun & Brunet 2012); 2) associated with H3K4me3 within specific tissue; or 3) dependent on only specific methyl marks at H3K4 like H3K4me1/me2, but not H3K4me3. Although the literature on what loci or which H3K4 marks involved is still very sparse, the gametes must serve as the carrier of the transgenerational epigenetic marks.

In mammals, epigenetic marks undergo two large genome-wide erasure events: after fertilization and during the embryonic phase of germline development (Klosin & Lehner 2016; Messerschmidt et al. 2014). Following fertilization between two gametes, massive erasure and reprogramming occurs to facilitate totipotency and generate a whole organism. The epigenetic marks in mature gametes that escape erasure and reprogramming can contribute to the offspring phenotype (Chong et al. 2007; Daxinger & Whitelaw 2012). Interestingly, it has been found that elevated COMPASS-mediated H3K4me3 could correlate with germ cell reprogramming. Its removal by H3K4 demethylase SPR-5/LSD1 along with another remodeler LET-418/Mi2 prevent reprogramming (Käser-Pébernard et al. 2014).

In general, the passage of the epigenetic marks can be through maternal or paternal germline (Daxinger & Whitelaw 2012). For instance, proper levels of H3K4me2/me3 and H3K27me3 in sperm of *Xenopus laevis* can be carried through to the egg upon fertilization to regulate the offspring gene expression during embryogenesis (Teperek et al. 2016). Another evidence corroborating maternally and paternally transgenerational inheritance involves crossing between

H<sub>2</sub>O<sub>2</sub>-stressed male or H<sub>2</sub>O<sub>2</sub>-stressed hermaphrodite *C. elegans* with unstressed mate. Several generations of the unstressed descendant still inherit the increased oxidative resistance trait, regardless if the stressed parent is male or female (Kishimoto et al. 2017). Further investigation is required to determine whether H3K4 methylation can be inherited paternally, maternally, or both in *C. elegans*.

H3K4 methyltransferase or demethylase ensure appropriate reprogramming during gamete maturation and fertilization (Katz et al. 2009). Germline reprogramming facilitates zygote totipotency (Heard & Martienssen 2014). Defective H3K4 methyltransferase or demethylase complexes have been implicated in transgenerational effects on animals. For instance, the SPR-5 demethylase is required for proper resetting of H3K4me<sub>2</sub> across generations. The mutants of SPR-5 display progressive sterility over 20-30 generations, which is resulted from the misregulation of spermatogenesis-expressed genes due to accumulation of H3K4me<sub>2</sub> at those loci (Katz et al. 2009). The study indicates that H3K4me<sub>2</sub> can function as an epigenetic memory and the activity of SPR-5 demethylation reset this memory (Katz et al. 2009). In addition to that, three generations of wild-type *C. elegans*, descendants of worms deficient for subunits of the MLL/SET/COMPASS methyltransferase complex display transgenerational inheritance of longevity by acting in the germline (Greer et al. 2011; Greer et al. 2010). However, only absence in SET-2, ASH-2 and WDR-5 subunit of the MLL/SET/COMPASS was tested in the experiment. It is unknown what effect does depletion of other subunit, like RBBP-5, have on the lifespan. In all, both examples show that manipulation of specific chromatin modifier in one generation can induce lasting effects on offspring traits.

The largest barrier to epigenetic inheritance is the reprogramming of epigenetic patterns between generations. Most of histone marks are erased during this event (Benayoun & Brunet 2012). But many questions remain: how H3K4 methylation marks escape reprogramming, which genetic loci bear the transgenerational marks, and why transgenerational traits can be progressively or abruptly reprogrammed between generations?

## 1.5 *Caenorhabditis elegans*: a model to link epigenetic and ageing

*C. elegans* is a great model for studying epigenetics and ageing rates. Most of the worm's histone modifications and their associated machineries are evolutionary conserved in *C. elegans*. Meanwhile, the ageing studies are facilitated by the short life lifespan of adult worms. In addition, studies on inheritance (epigenetics and genetics) are practical because of its fast developing rate and large brood size. In this section, I will introduce *C. elegans* as the ideal model to study the epigenetics basis of ageing.

### 1.5.1 Introduction to *C. elegans*

*C. elegans* is a small, transparent, non-parasitic soil nematode (roundworm) that feeds mainly on microbes such as bacteria. Many basic physiological processes in higher organisms are conserved in *C. elegans*. In addition, *C. elegans* is an excellent model organism because of its compact genome, ease of maintenance and propagation. The *C. elegans* genome has been completely sequenced, revealing approximately 97-megabase of DNA sequence that encodes about 20,000 genes (*C. elegans* Sequencing Consortium 1998). More than half of the protein products in *C. elegans* are conserved in other organisms including human (*C. elegans* Sequencing Consortium 1998; Kamath et al. 2003). The worm is also amenable to genetic crosses. For instance, genetic recombination can be performed through the mating between male and hermaphrodite worms with different genetic backgrounds. Otherwise, maintenance of descendants with specific genotype can be easily done through the self-fertilizing hermaphrodites. *C. elegans* can be maintained in the laboratory on a nematode growth medium agar plate or in a liquid culture. In laboratory, the *Escherichia coli* OP50 bacteria strain serves as food source for the worm (Brenner 1974). Due to its small size of approximately 1mm in adult, viewing is performed under a microscope. It is also transparent throughout its lifespan, which makes it easy to visualize transgene expressing fluorescent proteins. *C. elegans* is a great model organism for studying ageing. Measuring its lifespan is feasible during a short timeframe because they live for a short period of time (about two to three weeks). Their lifespan is largely invariant making it easy to differentiate short and long-lived worms from those with normal lifespan.

### 1.5.2 From germ lineage in adult gonad to embryo, larva and adulthood

Gametes are the medium for the transmission of epigenetic marks to the next generations. The haploid gamete is generated through mitosis and meiosis. While the gonad's distal ends are filled with germ cells undergoing mitosis, cells in stages of meiosis populate the rest of the gonad (Hubbard 2007). As the germ cells enter leptotene, zygotene, pachytene, diplotene and diakinesis, their duplicated chromosomes go through condensation, synapsis and crossover recombination (Figure 1.14) (Dernburg et al. 1998; Hirsh et al. 1976; MacQueen et al. 2002; Villeneuve 1994). At the end of prophase I, each oocyte have two copies of diploid genome ready for metaphase I (Oegema & Hyman 2006). Haploid sperms are produced during L4 larval stage and stored in the spermatheca (L'Hernault 2006). Fertilization occurs when oocyte squeezes



through spermatheca. Sperm donates its haploid pronucleus and a pair of centrioles (Oegema & Hyman 2006). Meiosis then resumes with metaphase I and finishes with telophase II. Following two rounds of meiotic divisions, two polar bodies are extruded and the two pronuclei (sperm-derived and oocyte-derived) fused (Rose & Kemphues 1998). At this point, the newly formed embryo is in the diploid state.

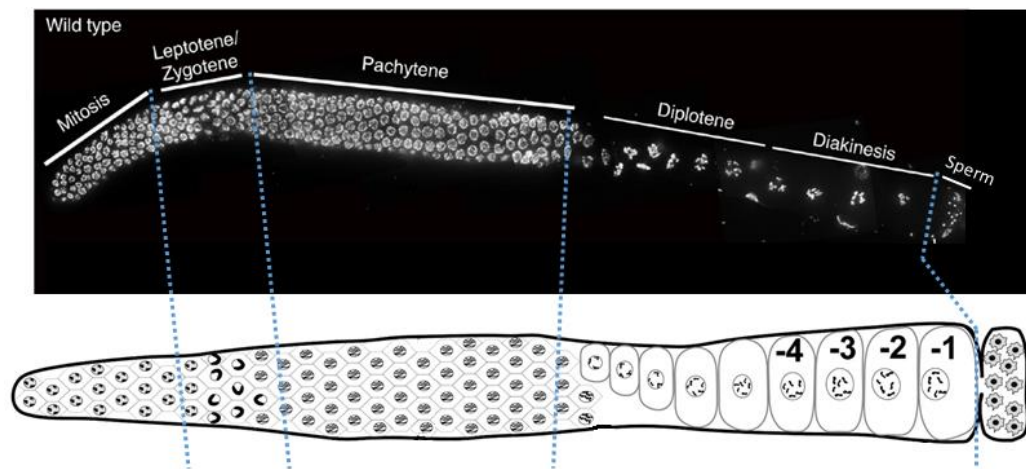
The next step is the proliferation stage of early embryogenesis, which occurs through five asymmetric divisions, where six founder cells AB, MS, E, C, D and P4 are established (Gönczy & Rose 2005). The founder cells are essential in determining the anterior from posterior, distal from ventral and left from right. The final germline blastomere, P4, will divide into Z2 and Z3 (Sulston et al. 1983). Z2-Z3 cells are the germ line precursors which will continuously divide in larva and adulthood (Kimble & Hirsh 1979). Laid embryos will undergo gastrulation to develop three germ layers: ectoderm, mesoderm and endoderm (Bucher & Seydoux 1994). Cells start differentiating to form organs: ectoderm will give rise to hypodermis and neurons; mesoderm turns into pharynx and muscle; and endoderm into germline and intestine (Sulston et al. 1983). Morphogenesis then occurs at “comma/lima bean” stage, where the embryo appears elongated and start to take the form of a worm. Muscle will start to twitch, pharynx will start to pump and embryo is ready to hatch (von Ehrenstein G. & Schierenberg E. 1980; Sulston et al. 1983). The *C. elegans* embryos inherit maternally supplied gene products. The maternal products can last to up to the first 6 to 7 cell cycles and is important for determination of cell lineage and patterning (Laufer et al. 1980; Strome & Wood 1983; Cowan & McIntosh 1985; Edgar et al. 1994; Kemphues et al. 1988). Transcription in early embryo only starts at around 8- to 12-cell stage (Edgar et al. 1994). Following the proliferation and morphogenesis, the embryos are ready to hatch.

Larval development begins with stage L1 and ends with stage L4. Hatched L1 larva can proceed to development when in presence of food (Ambros 2000), but are arrested in the absence of food (Johnson et al. 1984). The worm passes through four larval stages (L1-L4) with the end of each larval stage marked by cuticle molting (Cassada & Russell 1975). If the larva enters an unfavorable environment at the end of L2 stage, it may switch into a facultative dauer stage until the environment becomes favorable. Examples of unfavorable environment includes absence of food, high temperature and presence of a pheromone, which is released by worms in highly dense population (Riddle D. 1988). Dauer larva can live for several months. During the larval stages, the nervous system and the reproduction system continue to develop.

Adult *C. elegans* has a simple, unsegmented, cylindrical body shape that is tapered at the ends. Its outer body wall is covered with a layer of cuticle and is lined with hypodermis, excretory, neuron and muscle systems. The *C. elegans* can be male (XO) or hermaphrodite (XX). The male *C. elegans* has clearer ventral gonad and distinctive tail at lateral end. The tail copulatory apparatus exhibit the following features: a fan equipped with sensory rays, a hook, spicules and post-cloacal (male anus) sensilla (Lints & Hall 2009).

In conclusion, *C. elegans* gametes, which are produced through mitotic and meiotic divisions in adult gonad, give rise to an embryo following fertilization between sperm and oocyte. The worm life cycle then resumes from embryonic stage to larval stage (L1-L4) and to adulthood. The fast

life cycle and easy to manipulate make *C. elegans* a great model for studying the link between epigenetics and ageing.



**Figure 1.14 *C. elegans* hermaphrodite's germ line development inside a gonadal arm.**

DAPI staining (top) and illustration (bottom) showing the different stages of prophase I of first round of meiotic division. The most distal lobe is populated with germ cells in mitosis. Moving towards the arm center, germ cells enter transition zone (leptotene/zygotene) where chromosomes condensed and synapsed. Cells then undergo pachytene, diplotene and diakinesis stages to produce oocyte. Oocyte is fertilized as it squeezed through spermatheca. The first and second rounds of meiotic division resume, releasing two polar bodies. Embryogenesis starts when maternal and paternal pronuclei fused to produce a diploid cell. Figures from (Nadarajan et al. 2016; M.-H. Lee et al. 2007).

## 1.6 Phenotypes associated with altered H3K4 methylation levels in *C. elegans*

Several *C. elegans* phenotypes are affected by the alteration in the levels of H3K4 methylation. In this section, I will introduce the effects of altering H3K4 methyl mark levels on ageing (and lifespan), RAS-signaling, fertility, trans-differentiation and germline defects.

### 1.6.1 Ageing and lifespan regulation

Components of the SET-2/COMPASS complex regulate ageing rates and lifespan. Depletion in the levels of H3K4 methylation resulting from absence in ASH-2, WDR-5 and SET-2, extends the worm lifespan by 20% to 30% (Greer et al. 2010). Interestingly, the longevity effect of *ash-2*, *wdr-5* and *set-2* depletion is transgenerational (Greer et al. 2011). Regulation of lifespan by H3K4 methylation is complicated and not well understood. Initially, it was thought that the reduction in H3K4 methylation causes longevity, whereas increase in H3K4 methylation shortens lifespan. Reason being, when the gene that encodes H3K4 demethylase, *rbp-2*, is mutated, they found that the worm lifespan is shortened (Greer et al. 2010). However, later it was found that *spr-5* mutant from wild type ancestor has normal lifespan in earlier generations (1 to 5) but inherit transgenerational longevity in later generations (10 to 20) (Greer et al. 2016). We also know that depletion of RBBP-5, another core components of the COMPASS complex, also reduced H3K4 methylation (Wang 2015). However, its effect on lifespan regulation has never been reported. Regulations of longevity by ASH-2, SET-2 and WDR-5 require germline and active production of mature eggs (Greer et al. 2010). However, how H3K4 methylation affects lifespan regulation and ageing is still unclear.

### 1.6.2 RAS-signaling

The SET-16/COMPASS complex has been found to constrict the RAS signaling pathway. In *C. elegans*, activation of RAS signaling pathway in several vulval precursor cells (VPCs) is required for cell fate specification during vulval development (Sundaram 2005; Hill & Sternberg 1992; Kimble 1981). In the search for RAS signaling attenuators, Poulin's group investigated the *gap-1* mutant worm, which is known to have a normal vulval development but hypersensitive to increased level of LET-60 RAS signaling (Hajnal et al. 1997). An additional depletion of *set-16*, *rbbp-5*, *wdr-5*, *ash-2* or *utx-1* (all of which are members of the SET-16/COMPASS in worm) increases the number of VPCs adopting vulval fate that causes multiple ventral protrusions (Mvp) (Fisher et al. 2010). Moreover, our lab also found that the SET-16/COMPASS complex cooperates with a histone acetyltransferase, NuA4/TIP60, complex to attenuate RAS signaling (Fisher et al. 2010). The study indicates that the SET-16/COMPASS constricts the RAS signaling pathway to prevent erroneous adoption of the vulval fate.

### 1.6.3 Fertility

Another phenotype associated with H3K4 methylation is fertility. *spr-5* is the H3K4me1/me2 demethylase in worm. When compared to wild type, the *spr-5(-)* mutant has H3K4me2 enrichment. Initially, they are still fertile despite having slight retention of embryos within adult worm and slightly reduced brood size (Katz et al. 2009). However, over generations, H3K4me2 continues to accumulate, brood size steadily declines, germline mortality escalates, and percentage of sterile worms increases (Katz et al. 2009). The germline mortality was due to abnormal oocyte, loss of oocyte and wrongly-placed spermatid in oocyte location in the *spr-5* mutant. Hence, SPR-5 has roles in the epigenetic reprogramming of H3K4me2 mark and failure to reprogram is detrimental to worm fertility.

In addition, *wdr-5* and *rbbp-5* mutants has an increase sterility when grown at 25°C (Li & Kelly 2011). Investigation on the cause of sterility reveals that the gonad of sterile *rbbp-5* mutant at 25°C is populated with endomitotic oocytes (Emo). Emo can be caused by unfertilized eggs that are trapped inside the gonad, undergoing several rounds of DNA replications and has no cytokinesis. The gonad of sterile *wdr-5* mutant at 25°C on the other hand, has high percentage of endomitotic oocytes, low percentage with polyploid nuclei, and detectable masculinization of germline phenotype. Masculinized germline lacks the spermatogenesis to oogenesis transition. Defective sperms in the sterile *wdr-5* and *rbbp-5* contribute to the Emo phenotype (Li & Kelly 2011).

### 1.6.4 Transdifferentiation

Mutation in MLL/SET/COMPASS complex subunit can lower the penetrance of hindgut to neuron cells transdifferentiation (Zuryn et al. 2014). Transdifferentiation from one cell to another allows proper tissue and organ regeneration. In *C. elegans*, there are four KDM6 family members: *jmjd-3.1*, *jmjd-3.2*, *jmjd-3.3* and *utx-1* (Vandamme et al. 2012). The members of the KDM6 subfamily are responsible for the demethylation of H3K27me2/me3. It has been reported that *C. elegans* JMJD-3.1 and MLL/SET/COMPASS complex cooperate for transdifferentiation of post-mitotic hindgut cells into motor neurons. The hindgut cells can disengage from rectal tube and transformed into motor neurons. In lab, null deficiencies of *set-2*, *wdr-5*, *ash-2*, *rbbp-5*, *dpy-30* or *cfp-1* reduced transdifferentiation. The mutant of *set-2* has a mixed population of hindgut cells with fried-egg-shaped nuclear morphology and cells with speckled nuclear morphology. The nuclease inside the hindgut cells of *Jmjd-3.1* mutant on the other hand, are exclusively speckled (Zuryn et al. 2014). Hence, H3K4 methylation is required for natural transdifferentiation to occur properly.

### 1.6.5 Germline defects

The MLL/SET/COMPASS complex help preserve germline pluripotency in *C. elegans*. Loss of H3K4 methylation results in germline transdifferentiation. In particular, SET-2, WDR-5 and ASH-2 are required for proper expression of germline genes and repression of somatic genes in the cells (Robert et al. 2014). Germline deficient for *set-2* and *wdr-5* has misexpression of genes related to somatic cells. The misexpression causes the germline cells to convert into somatic-like cells. For instance, the germline cell lacking H3K4 methylation due to *set-2* loss of function mutation acquires somatic cell fate that resemble neuronal cells, but only at 25°C (Robert et al. 2014).

In addition to that, WDR-5 and RBBP-5 are required for the maintenance of germ line stem cells (GSCs). GSCs, located at the distal end of the gonad, are the proliferative cells that can generate haploid gametes, sperms or oocytes. Absence of SET-2, WDR-5 and RBBP-5 dramatically reduce H3K4me3 in GSCs. Absence of WDR-5 and RBBP-5 causes the *C. elegans* at 25°C to have shorter GSC zones compared to wild type. This suggest that in absence of WDR-5 or RBBP-5, there is an improper maintenance of germline stem cells that reduce the number of nuclei and the length of the pre-meiotic region where GSCs reside (Li & Kelly 2011). In all, alteration in the levels of H3K4 methylation in germline can cause transdifferentiation from germline to somatic cell as well as improper maintenance of germline stem cells.

To summarize, this chapter has provided detailed information on chromatin and H3K4 methylation. I have shown how H3K4 methylation is important for transcription processes and epigenetic inheritance. Alteration in the levels of H3K4 methylation gives a wide range of impact on *C. elegans* phenotype such as ageing, attenuation of RAS signaling, reduced fertility, abnormal transdifferentiation and germline defects. Since the SET-16/MLL and SET-2/COMPASS complexes in *C. elegans* are homologous to the complexes found in human, I will be using *C. elegans* as a model to link epigenetic with ageing.

### 1.7 Aims of the project

The uncovering that H3K4 methylation regulates the rate of ageing was a milestone but its link to transgenerational inheritance of longevity a revelation. Albeit compelling, these studies have left a number of outstanding questions. Are the levels of H3K4 methylation altered during ageing? Is the core component RBBP-5 a regulator of ageing rate? Can short lifespan be transgenerationally inherited? Finally, it has been generally assumed that depleting core components such as WDR-5 or RBBP-5 should mostly affect activation of transcription and that H3K4 methylation will necessarily be down regulated. I will assess these two points using RNA-seq and ChIP-seq. Overall, my project will delineate the function of methyl marks at H3K4 in transgenerational inheritance of the ageing rate and take advantage of the embryo as a system to link alterations in the levels of methyl marks at H3K4 to transcriptional output in *C. elegans*.

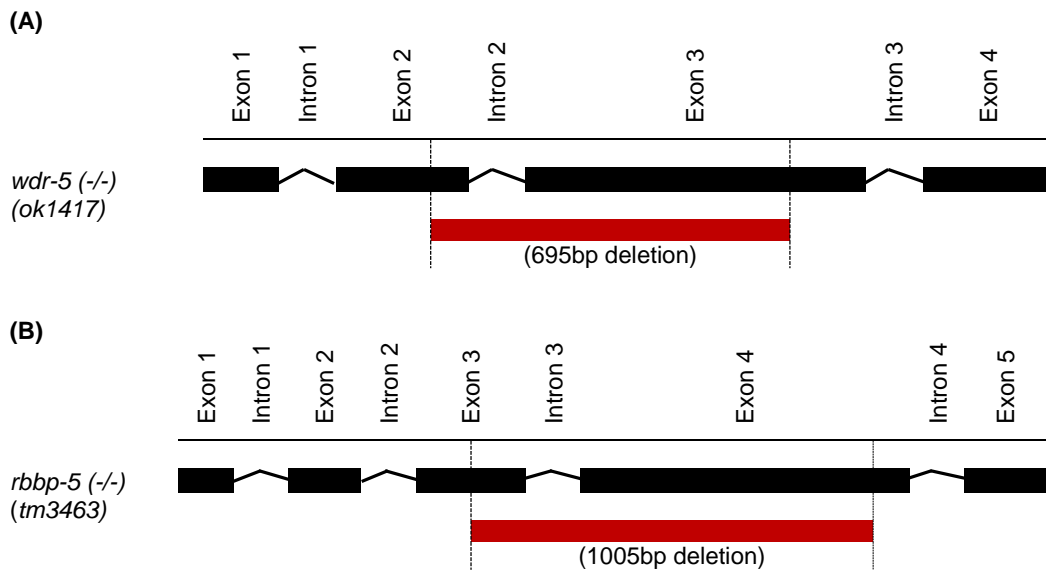
## **Chapter 2**

### **Materials and Methods**

## Chapter 2 : Materials and Methods

### 2.1 Worm strains

*C. elegans* strains were obtained from the Caenorhabditis Genetics Centre (CGC). Worm strains used in this project were: N2 (wild type Bristol), *rbbp-5(tm3463) II*, *wdr-5(ok1417)*. WDR-5 is referred to as WDR-5.1 in WormBase. The deletions in *rbbp-5(tm3463)* and *wdr-5(ok1417)* are shown in Fig. 2.1.



**Figure 2.1 Illustration of the deletion in *C. elegans* mutant strains *rbbp-5(tm3463)* and *wdr-5(ok1417)***

(A) *wdr-5(ok1417)* null deletion of 695 nucleotides, affecting exon 2 and exon 3. (B) *rbbp-5(tm3463)* null deletion of 1005 nucleotides in exon 3 and 4.

### 2.2 General maintenance

The general maintenance described the methodology for worm maintenance, bleaching and synchronisation, genomic DNA extraction, and genotyping by single worm PCR.

#### 2.2.1 Worm maintenance

The strains were maintained as previously described (Brenner 1974). Briefly, strains were maintained on 6 cm plates (Greiner) containing NGM (nematode growth medium) agar (0.05 M NaCl, 0.25% (w/v) bacto-peptone, 1.7 % (w/v) agar, 1 mM CaCl<sub>2</sub>, 12.9 μM cholesterol, 1 mM MgSO<sub>4</sub>, 25 mM KH<sub>2</sub>PO<sub>4</sub> pH6.0), seeded with *E. coli OP50*. Nematode strains were incubated at 20 °C, unless otherwise stated. Five L4 (Larval stage 4) hermaphrodite worms were transferred to fresh NGM plates every 4 to 5 days. For the maintenance of male wild type N2, nine adult wild type males and three L4 wild type hermaphrodites were transferred onto fresh NGM plates.

### **2.2.2 Bleaching and synchronization**

All gravid hermaphrodites from a 6 cm plate were collected into a 15 ml falcon tube. The worms were disintegrated in 1 ml bleaching solution (0.7 M NaOH, 21.4% sodium hypochlorite) to release the eggs. The embryos were rinsed three times with M9 buffer (9 mM Na<sub>2</sub>HPO<sub>4</sub>·12H<sub>2</sub>O, 45 mM KH<sub>2</sub>PO<sub>4</sub>, 85.6 mM NaCl, and 0.1 mM MgSO<sub>4</sub>), transferred onto unseeded NGM plates and allowed to hatch overnight. The synchronized L1 (Larval stage 1) were transferred to NGM plates seeded with OP50.

### **2.2.3 Genomic DNA (gDNA) extraction**

The N2 worms were amplified on a 10 cm OP50 seeded NGM plate and rinsed off into a 15 ml tube with M9 buffer. The pellet was frozen overnight at -80 °C. 1.8 mL of worm lysis buffer (0.1 M Tris-HCl pH 8.5, 0.1 M NaCl, 50 mM EDTA pH 8.0, 1% (w/v) SDS), 80 µl of 20 mg/ml proteinase K and 40 µl of ribonuclease A (boiled to inactivate DNase) was added to a 200ul worm pellet. Worms were mixed by inverting and lysed at 65 °C for 60 minutes. gDNA was extracted with 1 volume of phenol:chloroform. Extraction was repeated by mixing the aqueous layer, first with 1 volume of phenol:chloroform and then with 1 volume of chloroform. 0.1 volume of 3M NaOAc was added to the final aqueous layer and DNA was precipitated with 2.5 volumes ice cold EtOH (100%). The gDNA pellet was washed with ice cold EtOH (70%) and air dried for 10 minutes. The final pellet was re-suspended in ddH<sub>2</sub>O and stored at -80 °C.

### **2.2.4 Genotyping by single worm PCR**

Primers were designed to amplify a region spanning the expected deletion as indicated on WormBase and Fig 2.1. Primers used for single worm PCR are listed in Table 2.1. Briefly, a single worm was transferred using a platinum wire into a 0.2 mL PCR tube containing 3 µl lysis buffer (1x NH<sub>4</sub> reaction buffer (Bioline), 1 mg/mL proteinase K (Sigma)). Worms were frozen at -80 °C for 60 minutes, thawed and frozen for another 30 minutes. Worms were lysed at 65 °C for 90 minutes to release genomic DNA, followed by proteinase K inactivation at 95 °C for 30 minutes. PCR was carried out in a 30 µl volume (0.2 mM dNTP's (Bioline), 1x NH<sub>4</sub> PCR reaction buffer (Bioline), 0.5 µM forward and reverse primers, 1.5 mM MgCl<sub>2</sub> (Bioline), 0.5 µl BioTaq DNA polymerase (Bioline)). Following initial denaturation at 95 °C for 5 minutes, DNA was amplified for 40 cycles. Each cycle consisted of 30 seconds of denaturation at 95 °C, 30 seconds of annealing at 55 °C and 1 minute per kbp of elongation at 72 °C. PCR amplification was completed with a final elongation at 72 °C for 5 minutes. 8 µl of PCR product was analysed on 1% agarose gel (1% (w/v) agarose in 0.5 x TBE (0.04 M Tris, 0.04 M H<sub>3</sub>BO<sub>3</sub>, 0.001 M EDTA, pH 8.0, Sybr Safe) for size. Following confirmation of the correct size product, PCR products were sequenced (GATC Biotech).



**Table 2.1 Primers for genotyping of gDNA and single worm PCR**

Gene	Primer	Extension time (min)	Product size in wild type (bp)	Product size in mutant (bp)
<i>rbbp-5</i>	F: ggggacaagttgtacaaaaagcaggcttcATGGTCGAAATACTCGATCG	2	1753 bp	746 bp
	R: ggggaccactttgtacaagaaagctgggtcTCACTTTGATTTTGGTGAAAAG			
<i>wdr-5</i>	F: ggggacaagttgtacaaaaagcaggcttcATGGATAACCAGCGAAAATGC	1.5	1291 bp	596 bp
	R: ggggaccactttgtacaagaaagctgggtcTTAAACATCCGAGCGCCATATATG			

**Table 2.2 Primers for real time quantitative PCR**

Gene	Forward primer	Reverse primer	RT-qPCR amplicon
<i>act-1</i>	F: GTGATCTTACTGATTACCTC	R: TGTCGGTCAGGAAGTTCGTA	160 bp
<i>gcy-19</i>	F: ACCCGCCGAAGATACTTGA	R: ATTCGTCAGCCCTGCACTT	121 bp
<i>ttr-15</i>	F: GGAGGTTACCCTTTGGGAGA	R: GCCTTCTTCACGTTGCAGTT	162 bp
<i>fbxa-192</i>	F: CCAGGAGAATGCAGAATTGG	R: AGCTCGATGGGCTTCACA	117 bp
<i>ugt-29</i>	F: GGACACATTGACGGAACGA	R: TCCTCATCCAGCGTAACTCC	165 bp
<i>arc-1</i>	F: TTTCATCGAAAGTCGAGTTGTTT	R: GGAGCCATTACTGTGTCCATTT	102 bp
<i>pars-1</i>	F: CTCATCGCGATCTTCCAATC	R: CACGAGTACGAAGGAATGGTGT	90 bp
<i>nxf-2</i>	F: GCATACAGTTGTCTGCTTGTGG	R: TGCACCGTGTGATATTCTGG	148 bp
<i>apc-10</i>	F: ATCGAAGAGTGGACCAACCA	R: CGGAGTGGATTGCCAAAG	70 bp
<i>pqn-74</i>	F: GACAATCGGTCTGCCAAGTC	R: TGCGGAAGTAGCAGCAAAC	66 bp
<i>grl-7</i>	F: CGGTGGACGATTTGATGTG	R: CCCTTTGGTCTCTTGGCAGT	85 bp

## **2.3. Protein analysis by Western Blot**

### **2.3.1 Western Blot**

Samples were prepared by transferring 100 synchronised worms (day 1 adults or day 8 adults) into 50 µl of 1x PBS (140 mM Na Cl, 2.7 mM KCl, 10 mM Na<sub>2</sub>HPO<sub>4</sub> and 1.8 mM KH<sub>2</sub>PO<sub>4</sub>, pH 7.4) and pelleted. 50 µl of 2x Laemmli sample buffer (120 mM Tris-HCl, pH 6.8, 4 % (w/v) sodium dodecyl sulfate, 20 % (w/v) glycerol, 0.02 % (w/v) bromophenol blue, 200 mM DTT) was added and samples were boiled for 10 minutes. Samples underwent sonication for 15 minutes (Diagenode Bioruptor UCD-200, 30 seconds on, 30 seconds off) to ensure complete cell lysis and shearing of DNA. Western blot was carried out using BioRad Mini Trans-Blot® Cell system and standard BioRad protocol. Briefly, 20 µl of samples were loaded and run on a 15% polyacrylamide gel against 5 µl of pre-boiled Colour Pre-stained Protein Standard, Broad Range (11-245kDa) (NEB). Proteins were separated at 120 V for 15 minutes and then at 200 V for 30 minutes. Proteins were then wet transferred to an Amersham Hybond-P membrane (GE Healthcare) at 350 mA for 30 minutes. Membranes were blocked in 10% milk in 1xPBS with 0.2 % tween for blot against H3 antibody. Otherwise, membranes were blocked in 5% BSA in 1xPBS with 0.2% tween for blots against H3K4me1/me2/me3. Primary antibodies were incubated at room temperature for 2 hours. Membrane washing was performed 6x, each time in 1x PBS with 0.2% tween for 10 minutes. Incubation of secondary antibodies was at room temperature for 1 hour. Washing steps were repeated. Detection was performed using the Amersham ECL Plus Western Blotting Detection System (GE Healthcare) by incubating the membrane in ECL for 5 minutes at room temperature and following manufacturer's instruction. The ChemiDoc XRS+ imager system (BioRad) was used to view and capture blot image.

The primary antibodies used in Western Blots analysis were rabbit polyclonal anti-H3 antibody (Abcam, ab1791, 1/1000); mouse monoclonal anti-H3 (tri methyl K4) (Abcam, ab1012, 1/250); rabbit monoclonal anti-H3 (di methyl K4) (Abcam, ab32356, 1/10,000); and rabbit polyclonal H3 (mono methyl K4) (Abcam, ab8895, 1/500).

The secondary antibodies used in Western Blots analysis were Peroxidase-conjugated AffiniPure Goat Anti-Mouse IgG (H+L) (Jackson ImmunoResearch 115-035-003, 1/5000); and Peroxidase-conjugated AffiniPure Goat Anti-Rabbit IgG (H+L) (Jackson ImmunoResearch 111-035-003).

### **2.3.2 Quantification for Western Blots**

Image Processing and Analysis in Java (ImageJ) 1.51j8 software was used to measure the density of Western Blot bands. Western Blot image was saved as 8-bit tiff image. Rectangular selection was made on a horizontal band lane. The selection was analysed to profile the plot peaks. Data analysis was performed using the percentages of peak area after removing background.

## 2.4 Immunofluorescence for embryo

Immunofluorescence by freeze crack was performed on 0.3% poly-lysine treated slides. Slides were treated by application of 75µl of 0.3% poly-lysine, dried 10 minutes at 70°C, quickly rinsed in distilled water and excess liquid is wiped off. The slides were 3 × 14 mm printed wells slides from Fisher Scientific LTD UK. About 30 mothers were placed in a well with a drop of M9 buffer to wash off bacteria. These mothers were transferred into a 7 µl drop of M9 on the poly-lysine treated well by using an eyelash picker. Embryos were released from these mothers by dissecting with a syringe needle. A cover slip (22 mm × 50 mm) was applied at a right angle and placed at -80°C for at least 20 minutes. The cover slip was then promptly removed and the slide with embryos is methanol fixed at -20°C for 10 minutes, washed 5 minutes in PBS, and then followed by two washes in PBS-tween 0.2%. Primary antibody was diluted in PBS-tween 0.2% and incubated overnight at 4 °C in a humid chamber, following with three washes in PBS-tween 0.2%. Secondary antibody was incubated 2 h at 37 °C. Three washes are performed as described above. 5 µl Mowiol was applied to preserve fluorescence.

The primary antibodies used in co-immunofluorescence were mouse monoclonal anti-H3 (tri methyl K4) (Abcam, ab1012, 1/100); rabbit monoclonal anti-H3 (di methyl K4) (Abcam, ab32356, 1/100); mouse anti-H3K4me2 (Millipore CMA303, 1:5,000); and rabbit polyclonal H3 (mono methyl K4) (Abcam, ab8895, 1/100,000).

The secondary antibodies used in co-immunofluorescence were DyLight 594 AffiniPure Goat Anti-Mouse IgG (H+L) (Jackson ImmunoResearch 115-515-146, 1:200); DyLight 488 AffiniPure Goat Anti-Rabbit IgG (H + L) (Jackson ImmunoResearch 111-485-144, 1:200); DyLight 488 Goat Anti-Mouse IgM mu chain (Abcam ab97007, 1:200) and DAPI (Sigma 28718-90-3, 2 ug/ul). Our controls performed without primary antibody show that these secondary antibodies do not produce significant background (data not shown).

## 2.5 Real time quantitative PCR (RT-qPCR)

Embryo pellets were prepared by harvesting synchronised gravid adults, washing the pellet in M9 and bleaching as routine. Total RNA was extracted using TRIzol (Invitrogen) and samples were kept at -80 °C. First strand cDNA synthesis was performed using the SuperScript VILO cDNA Synthesis Kit (Invitrogen), according to the manufacturer's instructions. Quantitative RT-PCR was performed using the FastStart SYBR Green Master (ROX) mix (Roche) on a Biorad C1000 thermal cycler coupled with a CFX96 Real time system. Three biological samples from each strain were prepared and analysed in triplicate by the  $\Delta\Delta\text{CT}$  method (Livak & Schmittgen 2001). act-1 was used as the internal reference for data normalization. Primers used in the RT-qPCR experiments are listed in Table 2.1.

## 2.6 Lifespan assay

### 2.6.1 Lifespan assay using mutant strain

100 synchronised L4 worms were placed onto five OP50 seeded NGM plates. Longevity assay was commenced at day 1 adult stage. Fertile worms were transferred onto fresh seeded NGM plates every 24 hours until they entered post-fertile stage. Lifespan and mortality were recorded every day by checking their movement. Worms were censored and removed from the analysis if they crawled off the plates or became bag of worms. Worms with no movement response to a prodding pick were considered as dead. Using the log-rank function in Online Application for Survival Analysis version 2.0 (OASIS 2), we plot Kaplan Meier survival curves and compare lifespans between different strains. The log-rank test calculation follows the following equations, with  $d_i$  is number of death,  $e_i$  is expected death and  $n_i$  is population size at  $i$ th interval:

$$X^2 = \frac{[\sum_{i:t_i \leq \tau} (d_i - e_i)]^2}{\sum_{i:t_i \leq \tau} (d_i - e_i)} \text{ followed by } Var(d_i - e_i) = \frac{d_i(n_i - d_i)n_{1i}(n_i - n_{1i})}{n_i^2(n_i - 1)}$$

### 2.6.2 Lifespan assay using RNAi by feeding protocol

100 synchronized L1 wild type worms were placed onto five OP50 seeded RNAi plates (0.05 M NaCl, 0.25 % (w/v) bacto-peptone, 1.7 % (w/v) agar, 1 mM CaCl<sub>2</sub>, 12.9 μM cholesterol, 1 mM MgSO<sub>4</sub>, 25 mM KH<sub>2</sub>PO<sub>4</sub> pH6.0, 1 mM isopropyl-b-D-thiogalactopyranoside (IPTG), 25 μg/mL carbenicilin, Nystatin (50,000 units)). The plates were seeded with empty vector (RNAi) (ev(RNAi)) or *wdr-5*(RNAi) HT115 bacteria. Longevity assay was commenced at day 1 adult stage following the general protocol described above.

## 2.7 Transgenerational study

### 2.7.1 Crosses, genotyping and maintenance

To prepare the parental generation (P0) crosses, 10 wild-type adult N2 (Bristol) males were crossed with five L4 *rbbp-5*(tm3463) hermaphrodites referred herein as *rbbp-5*(-) on ten 3 cm plate. Any *rbbp-5*(-) mother with “bag of worms” were immediately removed during the genetic crossing. P0 worms were incubated for two days until they laid sufficient amount of eggs before they were removed. All worm incubation steps in these transgenerational experiments were done at 20 °C, unless otherwise stated. In parallel, wild type and *rbbp-5*(-) control worms were maintained for each generation. Wild type males and wild type hermaphrodites were crossed to generate pure wild type N2 descendants and control for any effect resulting from crossing.

150 of the first filial L4 hermaphrodite progeny (F1) were single cloned on 3 cm plates. The heterozygous *rbbp-5*(+/-) F1 worms were used in the transgenerational lifespan assay. To infer the genotype of F1, six second filial adult progeny (F2) from each of the F1 clone were pooled into a 1.5 mL micro centrifuge tube and genotyped for the *rbbp-5* deletion. Any F1 males and F1 *rbbp-5*(-) from self-fertilizing *rbbp-5*(-) mothers were discarded.

To obtain wild type and mutant progeny from the F1 heterozygous mothers, 48 F2 worms were single cloned onto 6 cm plates. Worms were transferred every day. When they became day 2 adult and laid many eggs, they were genotyped for *rbbp-5* deletion. F2 *rbbp-5(+/-)* clones were discarded from the experiment. Both of the wild type F2 *rbbp-5(+/+)* from F1 *rbbp-5(+/-)* mother and the mutant F2 *rbbp-5(-/-)* from F1 *rbbp-5(+/-)* mother were maintained.

Third, fourth and fifth filial generations (F3, F4 and F5) from the F1 *rbbp-5(+/-)* ancestor, having either the wild type *rbbp-5(+/+)* or the mutant *rbbp-5(-/-)* genotype were collected. For the F3 generation of each condition, the following experimental setup was performed: 100 L4 worms were for maintenance; 100 L4 worms were for transgenerational lifespan assays; 100 L4 worms were for transgenerational Western Blot analysis; and 10 L1 worms were for brood size assays. The worms for brood size assays were incubated at 25 °C. Maintenance worms were left to lay eggs overnight before the mothers were removed. Similar scheme but excluding the brood size assay was used in F4 generation. Similar scheme but excluding the maintenance and brood size assay was used in F5 generation.

### **2.7.2 Transgenerational lifespan assay**

For the transgenerational lifespan assay on F1 generation, 100 wild type, 100 *rbbp-5(-)* and 150 anticipated F1 heterozygous *rbbp-5(+/-)* were used. Pure wild type and mutant controls were placed onto 6 cm NGM plates. The anticipated F1 *rbbp-5(+/-)* worms were single cloned onto 3 cm NGM plates. Worms were transferred every day during their fertile stage. Lifespan assay was started at day 1 adult and data was recorded every day. At this stage, since lifespan was started prior to genotyping, there is a possibility that the anticipated heterozygous F1 population was a mixed between F1 *rbbp-5(+/-)* from the crosses and F1 *rbbp-5(-)* from self-fertilizing mothers. Hence, lifespan needed to be recorded individually for each clone. Following genotyping, worms and data on F1 *rbbp-5(-)* from the self-fertilizing mothers were discarded. Moreover, since worms were initially transferred at L4 stage, any males were also discarded from the study.

For the transgenerational lifespan assays on F3, F4 and F5 generations, 100 wild type, 100 *rbbp-5(-)*, 100 wild type from F1 *rbbp-5(+/-)* ancestor and 100 *rbbp-5(-)* from F1 *rbbp-5(+/-)* were used. Worms from each condition were placed on five 6 cm plates. Lifespan assays were started at day 1 adult. Numbers of worms alive, dead and censored were recorded each day. Crawled off worms and bag of worms were censored and removed from the analysis. Worms with no movement response to a prodding pick were considered dead. Average lifespan was calculated and Kaplan-Meier survival plots (log rank test) were used to compare lifespans between different strains.

### **2.7.3 Transgenerational brood size assay**

Ten F3 larval stage 1 (L1) for each pure wild type, pure *rbbp-5(-)*, wild type from F1 *rbbp-5(+/-)* and *rbbp-5(-)* from F1 *rbbp-5(+/-)* were used in the transgenerational brood size assay. L1 worms were single cloned onto 6 cm plates and maintained at 25 °C. Worms were transferred every day

until they finished laying eggs and then discarded. To determine the brood size assay, the numbers of all F4 progeny were counted when they reached day 1 adult. Mean value and standard error of mean (SEM) were calculated.

#### **2.7.4 Transgenerational Western Blot analysis**

For transgenerational western blot study, precisely 100 wild-type N2; 100 *rbbp-5(tm3463)* control; 100 *rbbp-5(+/+)* worms from heterozygous F1 ancestor; and 100 *rbbp-5(-/-)* from heterozygous F1 ancestor from F3, F4 and F5 generations were used. Adult day 1 worms were picked using an eye lash to omit any bacteria. Worms were transferred into 50  $\mu$ l 1X PBS into which another 50  $\mu$ l of 2X Laemmli sample buffer was added. The protein lysates were kept at -20 °C until used. Western Blots analysis was performed according to the general Western Blot protocol and quantification as described earlier.

### **2.8 Male study**

#### **2.8.1 Male occurrence assay**

Wild type, *rbbp-5(-)* and *wdr-5(-)* strains were used for male occurrence assay. To compensate the different brood size each strain is having, different starting numbers of hermaphrodite mothers were used. Five 6 cm NGM plates were used per condition, with each plate having 10 wild type, 20 *wdr-5(-)* or 30 *rbbp-5(-)* L1 worms. Two experimental sets with different incubation temperatures were used. The first set had the worms incubated at 20 °C, whereas the second set had the worms incubated at 25 °C. The hermaphrodite mothers were transferred onto fresh plates every day and removed once they finished laying eggs. When the progeny reached adulthood, percentages of male from the total number of progeny were counted. Data was represented as mean percentage of male occurrence  $\pm$  SEM.

#### **2.8.2 Male fertility experiment by genetic crossing**

Two sets of genetic crossings were used in this experiment. In the first set, six *wdr-5(-)* males were crossed with two *wdr-5(-)* hermaphrodites. Then, the next progeny was checked for number of males which are expected to be abundant if the genetic crossing is successful. In the second set, six *wdr-5(-)* males were crossed with two wild type hermaphrodites. Then, the number of male progeny was counted and the next progeny was genotyped. Heterozygous progeny for *wdr-5(+/-)* were expected if the genetic cross is successful

#### **2.8.3 Analysis of male tail morphology**

10 wild type, 20 *wdr-5(-)* and 30 *rbbp-5(-)* larval stage 4 (L4) worms were placed on four 6 cm plates. The plates were kept at 25 °C for six days or until the next progeny become adult day 1.

Adult males were mounted on 2% (w/v) agarose pads in 20 mM tetramisole (Sigma). Male tail morphology was observed under differential interference contrast (DIC) microscopy.

## **2.9 RNA-Seq**

### **2.9.1 Embryo preparation for RNA-Seq**

Strains were kept at 20°C. 20 x 10 cm plates of gravid adults were bleached and synchronised L1s were seeded on 2 Corning tissue culture dishes (245 x 245 mm) seeded with 20x OP50. When the synchronised young gravid mothers started to lay eggs, they were bleached to obtain embryos. These embryos were scored to ensure comparative stages between wild type and the mutants. About 10-12% of embryos are at <28-cell stage, 25-30% of embryos are between the 28-cell stage and 100-cell stage, 45-55% are between ~100-cell stage and pre-coma stage (~400 cell), and 5-15% are post-coma stage. Three independent biological replicates were prepared for RNA-seq. Total RNA was extracted using TRIzol (Invitrogen) and samples were frozen at -80°C. First strand cDNA synthesis was performed using the SuperScript VILO cDNA Synthesis Kit (Invitrogen), according to the manufacturer's instructions.

### **2.9.2 Quantification and statistical analysis for RNA-Seq**

Strand-specific RNA-seq libraries were prepared using the Illumina workflow with the TruSeq Stranded mRNA Sample Preparation Kit. 101bp×101bp paired-end reads were generated from each sample. The fastq files generated by HiSeq platform were analysed with FastQC, any low quality reads and contaminated barcodes were trimmed with Trimmomatic (Bolger et al. 2014). All libraries were aligned to ce10 assembly of *C. elegans* genome using Tophat-2.1.0 (Kim et al. 2013) and only matches with the best score were reported for each read. The mapped reads were counted by genes with HTSeq (Anders et al. 2015) against the *C\_elegans* WS220.annotations.gtf. The differentially expressed (DE) genes are identified by comparing the wild type with different mutant with DESeq2 (Love et al. 2014).

## **2.10 ChIP-Seq**

### **2.10.1 Embryo preparation for ChIP-Seq and ChIP-qPCR**

Synchronised population of embryos were prepared from bleached young adult hermaphrodites. These were harvested from 20 Corning tissue culture dishes (245 x 245 mm) seeded with synchronised L1 (larval stage 1) obtained from bleaching large amount of gravid adults. Dishes were pre-seeded with 0.5 ml of 20x OP50 stock left to dry for at least two days before use. To amplify large amount of gravid adults, 20 of these dishes per strain were seeded with synchronised L1s: ~1000 L1s for N2 (wild type), ~2000 L1s for *wdr-5(-)*, and ~3000 L1s for *rbbp-5(-)*. When the F1s reached L4 stages, all worms were harvested and transferred onto 20 new dishes. Otherwise, the worms will run out of food. After reaching adulthood, the worms were

bleached and embryo harvested. To obtain synchronised embryos, an additional step whereby all synchronised L1s were re-seeded onto 20 new dishes was performed. N2 (wild type) were left to grow about 54 h, *wdr-5(-)* and *rbbp-5(-)* 64h. Following bleaching, embryos were collected on routine sucrose gradient, re-suspended in 47 ml of M9 buffer and 2.8 ml of 37% formaldehyde solution (~2% final). Embryos were placed on shaker (50 rpm) at room temperature for 30 minutes. Spun down and pellets collected. Quenched on formaldehyde adding 50 ml 100 mM Tris pH 7.5. Fixed embryos were spun down and washed twice with 50 ml M9. Spun down and added 10 ml FA buffer containing protease inhibitor cocktail. 5 µl of embryos were taken out, fixed with methanol, and stained with DAPI for scoring (store at -20°C). Between 200 and 500 µl of packed embryos can be obtained from this method. The embryo preparations for N2 (wild type), *wdr-5(-)*, and *rbbp-5(-)* used for ChIP-seq were comparable: about 20-40% of embryos are at <28-cell stage, 20-27% of embryos are between the 28-cell stage and the 100-cell stage, 32-52% are >100-cell stage but pre-coma stage (~400 cells), and 0-4% are post-coma stage.

### 2.10.2 Chromatin Immunoprecipitation

ChIP was performed following a detailed protocol from (Ercan et al. 2007) and as previously described (Liu et al. 2011). Briefly, we re-suspended embryo pellets with 1.5 ml FA buffer with protease inhibitor cocktail. The embryos were dounced 40 times on ice using pastel B homogeniser. We aliquoted 250 µl of the embryos in six 1.5 ml eppendorf tubes and then sonicated for 15 minutes, cool every 5 minutes on dry ice for 5 seconds. DNA size (200-600 bp) was verified on 1.5% agarose gel. Then, the sonicated embryos were snapped freeze and kept at -80°C. We used 250 µl for each ChIP experiment. For each ChIP, we topped up to 400 µl with FA buffer containing protease inhibitor cocktail. 25 µl of 20% sarkosyl solution were added (~1.2% final), spun and kept the supernatant. 10% of the ChIP volume was used as input DNA. Magnetic beads (Magna ChIP Protein A+G from Merck Millipore (cat. 16-663)) that has been coupled with antibody were added to supernatant. We washed with 1 ml with FA buffer twice, FA buffer with 1 M NaCl, FA buffer with 500 mM NaCl, TEL buffer and TE buffer. We then eluted twice in 150 µl of ChIP elution buffer at 65°C for 15 minutes and vortexed every 5 minutes. Then we treated with proteinase K for 2 h at 55°C and reversed cross-link at 65°C for 18 h. We purified DNA with Qiaquick PCR Kit from Qiagen and eluted with 50 µl of water. Quantitative PCR was performed using the  $\Delta\Delta$ CT method (Livak and Schmittgen, 2001). For ChIP-PCR against *rgs-6* and *smo-1*, we used anti-H3 (Ab1791), anti-H3K4me3 (Ab1012), and anti-H3K4me2 (Ab32356). For ChIP-seq and ChIP-PCR against untranscribed locus, *act-1* and *ftt-2*, we used anti-H3K4me1 (AM39297), anti-H3K4me2 (AM39141), and anti-H3K4me3 (AM39159). The primers used in the ChIP-qPCR experiment are listed in Table 2.3.



**Table 2.3 Primers for ChIP followed by qPCR**

Gene	Forward primer	Reverse primer
<i>smo-1</i>	F: taccgtaccctcgtgttgct	R: cgttcagagtggtcatggt
<i>rgs-6</i>	F: agtaaacagtggtgaggcaag	R: tcgtcgtagcatcgagtcaag

### 2.10.3 Quantification and statistical analysis for ChIP-Seq

Illumina sequencing libraries were prepared from the ChIP and input DNAs by the standard consecutive enzymatic steps of end-polishing, dA-addition, and adaptor ligation. After a final PCR amplification step, the resulting DNA libraries were quantified and sequenced on Illumina's NextSeq 500 (75 nt reads, single end). Reads were aligned to the *C. elegans* genome (ce6) using the BWA algorithm (default settings) (Li and Durbin, 2009). Duplicate reads were removed and only uniquely mapped reads (mapping quality  $\geq 25$ ) were used for further analysis. Alignments were extended in silico at their 3'-ends to a length of 200 bp, which is the average genomic fragment length in the size-selected library, and assigned to 32-nt bins along the genome. The resulting histograms (genomic "signal maps") were stored in bigWig files. Peak locations were determined using the MACS algorithm (v1.4.2) with a cut off of p-value =  $1e-7$  (Zhang et al. 2008). Signal maps and peak locations were used as input data to Active Motifs proprietary analysis program, which creates Excel tables containing detailed information on sample comparison, peak metrics, peak locations and gene annotations. These tables (Supplementary Table 3, 4, 5) were used for Odds Ratio Statistics analysis.

### 2.10.4 Quantification and statistical analysis for ChIP followed by qPCR

For qPCR analysis primers against regions of interest (Table 2.2) were used to amplify DNA in both ChIPs and inputs. Fold enrichment is calculated as a percentage of input using the following formulae:  $2^X = \text{input dilution factor}$ ; total input Ct value = input Ct - X; sample percentage of input =  $2^{(\text{total input Ct} - \text{sample Ct})} \times 100$ . Values from anti-H3 ChIP are used to normalise. Quantitative PCR (qPCR) reactions were carried out in triplicate on specific genomic regions using SYBR Green Supermix (Bio-Rad). The same calculation was performed using beads only control. Biological duplicates were analysed in triplicates. The data are represented as mean  $\pm$  SEM.

### 2.10.5 Quantification and statistical analysis for odd ratio analysis

We mapped H3K4me1/me2/me3 peaks according to their location (promoters, gene bodies, or downstream of genes) using Supplementary Table 3-5. This mapping produced nine classes of peaks (3 methylation states by 3 genomic locations). We then asked whether these peaks disappear in absence of WDR-5 or RBBP-5, or whether new peaks are produced by the absence of WDR-5 or RBBP-5. We called the former WDR-5 or RBBP-5 dependent peaks and the latter

de novo peaks, since these are not detected in wild type. We used all significantly misregulated genes found by RNA-Seq profiling of *wdr-5(-)* and *rbbp-5(-)* mutants and examined to which peak class they can be associated with. When an association was identified, the misregulated genes of that peak class were categorised as 'Down' or 'Up' regulated genes. Finally, we calculated the number of genes in each 'Down' or 'Up' category and calculated a ratio that is the reference ratio found by dividing the number of genes in 'Down' by the number of genes in 'Up' for the two genetic backgrounds analysed, *wdr-5(-)* and *rbbp-5(-)*. The reference ratio is then compared to the experimental ratio, which is calculated by dividing the number of genes 'Down' and associated with one of the nine classes of peaks by the number of genes 'Up' and associated with the same class of peak. If the experimental ratio is the same as the reference ratio, the correlation between misexpressed genes and the presence of a class of peak is independent of this class of peak. The Odds Ratio are expressed in log2 such as a positive log2(Odds Ratio) indicates a enrichment towards up regulation of gene expression and a negative value a tendency towards down regulation of gene expression. We used the chi-squared test to establish whether differences between the Odds ratios are statistically significant and calculated the 95% Confidence Interval using Odds Ratio statistics. A significant difference between ratios is considered at a p value <0.01 and a 95% C.I. Odds Ratio > 2 fold.

#### **2.10.6 Data and software availability**

The ChIP-seq data have been deposited in the GEO repository under ID code GSE94639 and RNA-seq data have been deposited in the ArrayExpress repository under ID code E-MTAB-5500.

## **Chapter 3**

**RBBP-5 imparts transgenerational memory of normal lifespan regulation in *rbbp-5(-)* mutant descendants of wild type ancestors**

## **Chapter 3 : RBBP-5 imparts transgenerational memory of normal lifespan regulation in *rbbp-5(-)* mutant descendants of wild type ancestors**

### **3.1 Abstract**

Genetics and epigenetics factors are amongst the determinants of ageing process. The absence of WDR-5 or ASH-2, which are subunits of the H3K4 methyltransferase MLL/SET/COMPASS complex, causes longevity in *Caenorhabditis elegans* lifespan. Moreover, the extended lifespan is also transgenerationally inherited in three generations of wild type progeny. Interestingly, there is another core component of the complex, RBBP-5, whose absent causes more detrimental reduction in all H3K4me1/me2/me3 in embryos. Yet, it is unknown whether RBBP regulates lifespan or has transgenerational effects on lifespan regulation. In this study, we undertook the investigation on whether H3K4 methylation attributed by RBBP-5 is required for lifespan regulation and its transgenerational inheritance. We discovered that in absence of RBBP-5, *C. elegans* lifespan is shorten. We also found H3K4 methylation to be reduced as the worm aged. We showed that the complex has a strong reliance on RBBP-5 for maintaining H3K4me1/me2/me3 in young adults. However, as the animal aged, the reliance on RBBP-5 for H3K4me1/me3 lessened. The complex reliance on WDR-5 in both young and old adults, is strong for H3K4me2 but the reliance is minor for H3K4me1/me3. Interestingly, we also uncovered that an ancestor having a wild type copy of RBBP-5 can transmit normal lifespan in three generations of the mutant descendants. The transgenerational inheritance was specific for lifespan regulation and does not affect other *rbbp-5(-)* associated phenotype such as smaller brood size. In conclusion, H3K4 methylation is reduced during ageing and regulation of H3K4 methylation by RBBP-5 is required for normal lifespan.

KEYWORDS: H3K4 methylation, ageing, lifespan assay, transgenerational inheritance, epigenetics

### **3.2 Introduction**

Ageing is a universal phenomenon in the vast majority of living organisms. It is the progressive deterioration of physiological function that accompanies the passage of time over the course of life. How to attain a healthy ageing has been one of the major goals in the bio-gerontology field. However, manipulation of the deterioration processes during ageing remains controversial. Based on the theory of ageing, two crucial allocations of physiological resources during ageing are for the soma maintenance and reproduction (Kirkwood & Holliday 1979). The careful choreography of these two events, described as lifespan regulation, is the determinant of how long an organism lives (Carnes 2011). Lifespan is described as the duration of observed life, short or long, whereas longevity refers to prolonged duration of life (Carnes 2011).

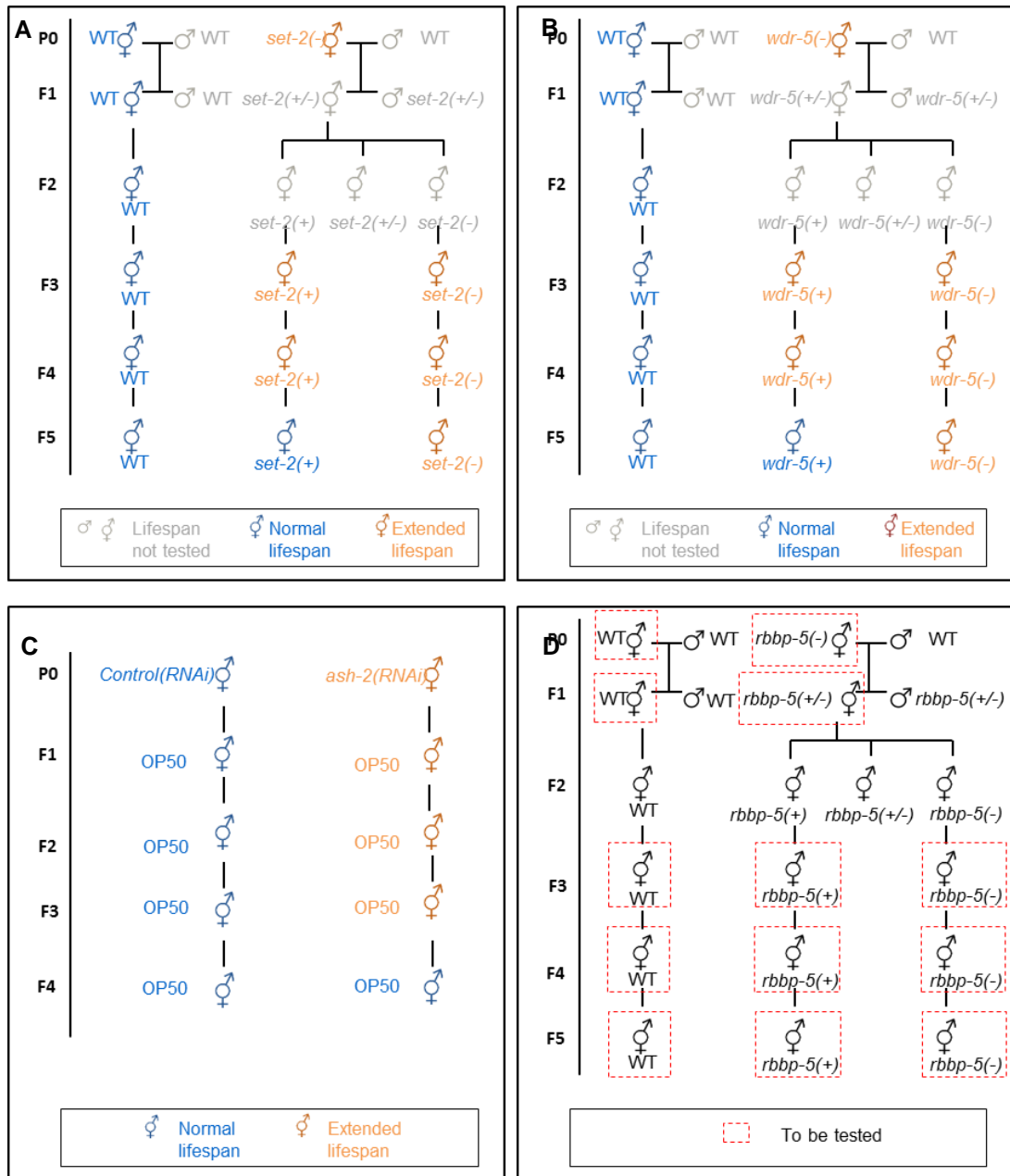
The members of the MLL/SET/COMPASS complex have been implicated in the lifespan regulation of *C. elegans*. The longevity of the soma is determined, in part, by the components of the MLL/SET/COMPASS acting on germline stem cells (Greer et al. 2010). Based on whole-mount immunocytochemistry analysis, germline is highly enriched with ASH-2, SET-2 and H3K4me3 marks (Greer et al. 2010). When SET-2, ASH-2 or WDR-5 is absent, lifespan becomes extended (Greer et al. 2010; Greer et al. 2011). If *set-2*, *ash-2* or *wdr-5* is knocked down in *glp-1* or *pgl-1* sterile worms lacking germline, lifespan is no longer extended (Greer et al. 2010), suggesting the germline requirement for lifespan regulation by MLL/SET/COMPASS complex.

Deposition of H3K4 methylation by the MLL/SET/COMPASS complex has been observed during *C. elegans* embryogenesis and larval development. Whether the level of H3K4 methylation is altered in ageing adults is unknown. Absence of WDR-5 or ASH-2 in embryos has been associated with great reduction in the levels of H3K4me3 and H3K4me2 (Wang et al. 2011). Another core component of the MLL/SET/COMPASS complex is the RBBP-5. Importantly, absence in RBBP-5 causes depletion in all H3K4me1/me2/me3 during embryogenesis (Wang et al. 2011), suggesting a greater reliance on this core component. However, many aspects on the roles of RBBP-5 is still not well understood for instance whether RBBP-5 regulates lifespan or how the depletion of H3K4 methylation in absence of RBBP-5 affects transcription.

Absence in SET-2, WDR-5 and ASH-2, are implicated in inheritance of longevity for several generations (Greer et al. 2011). To prove transgenerational inheritance, the Brunet laboratory used genetic crosses and RNAi approaches. The genetic crossing between wild type males (P0) and mutant hermaphrodites of *wdr-5* or *set-2* re-introduces the wild type allele in the progeny. The Mendelian laws of genetics predicted that the animals should resume a normal lifespan. Instead, the descendants inherit longevity from the mutant ancestor until F4 generation, At F5 generation, the longevity trait was lost, ruling out a spontaneous genetic mutation to explain longevity (Figure 3.1). Using the RNAi approach produced similar results. When wild type hermaphrodite (P0) was treated with *ash-2(RNAi)*, their untreated F1 to F3 wild type descendants were long-lived (Figure 3.1). The inheritance of longevity was lost at the F4 generation. The loss of longevity after a specific number of generations indicates that the inheritance occurs epigenetically rather genetically. This study indicates that deficiency in WDR-5, SET-2 or ASH-2 only in the parental generation (P0) extends the lifespan of descendants for several generations. It is thought that inheritance of longevity is not due to inheritance of global changes in the level of H3K4me3, since global H3K4me3 resumes wild type levels after re-introduction of the *wdr-5* wild type allele. Instead, inheritance might be mediated by heritable changes of H3K4me3 at specific loci. Whether RBBP-5 also has impact on transgenerational lifespan regulation is unknown.

In this study, we aim to gain a more detailed understanding of how ageing and lifespan regulation were modulated by H3K4 methylation. We are interested in investigating whether RBBP-5 has role on lifespan regulation similar to the roles shown by the other components, WDR-5, ASH-2 and SET-2. Interestingly, we found *rbbp-5(-)* mutant to be short-lived. Since involvement of the H3K4 methylation marks over the course of ageing has never been documented before, we determine their levels by Western Blot analysis. In total, we found that there is a reduction in H3K4 methylation that accompanies ageing. We uncovered that RBBP-5 is required to maintain

H3K4me1/me2/me3 in young adult but its reliance to maintain H3K4me1/me3 is reduced in old adults. On the other hand, WDR-5 is required for maintenance of H3K4me2 in young and old adults, as well as for H3K4me1/me3 in old adults, albeit the role is minor. In addition, we found that H3K4 methylation in wild type *rbbp-5* is transgenerationally inherited and normalised lifespan of mutant progenies for up to three generations. The transgenerational inheritance implicated by RBBP-5 is specific for lifespan regulation. Taken together, our work adds to previous finding that components of MLL/SET/COMPASS are involved in lifespan regulation and H3K4 methylation is reduced during ageing.



**Figure 3.1 Schematic illustration of transgenerational inheritance of longevity by components of the MLL/SET/COMPASS complex**

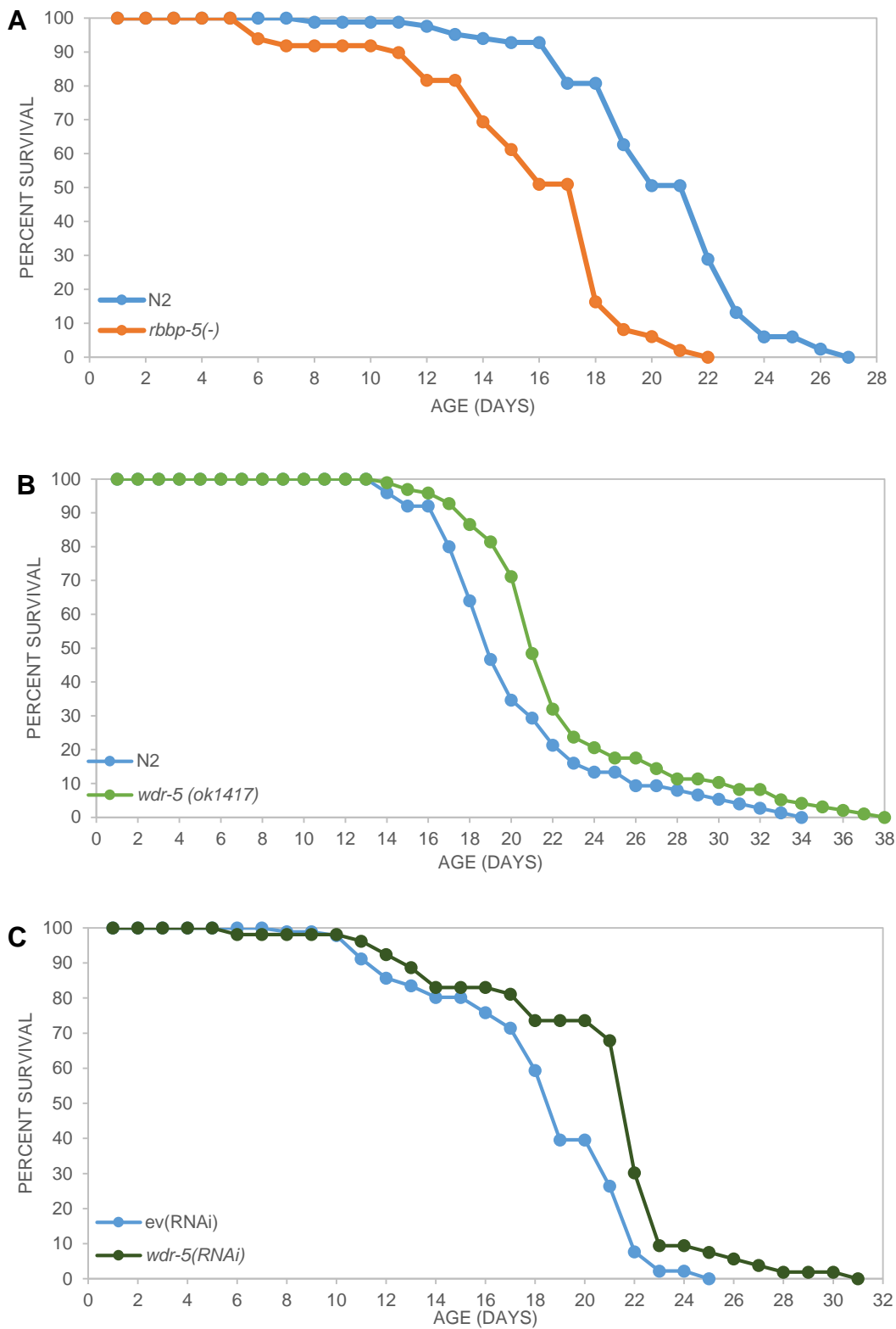
(A-B) Transgenerational inheritance of longevity in wild type progeny (F3 and F4) from crosses between wild type males and *set-2(-)* or *wdr-5(-)* hermaphrodites. (C) Transgenerational inheritance of longevity in normal progeny (F3 and F4) from *ash-2(RNAi)* mother. Normal lifespan (blue); extended lifespan (orange); ancestor generation (P0); First to fifth generations of progeny (F1-F5); wild type (+/+); heterozygous (+/-); and mutant (-/-) lacking *set-2* or *wdr-5*. (D) Schematic illustration of the current study showing the crosses between wild type males (N2) and *rbbp-5(-)* hermaphrodites (P0). The first filial generation F1 which are heterozygous for *rbbp-5* produce wild type, mutant and heterozygous progenies. The generations whose lifespan are to be measured are indicated in red dotted box.

### 3.3 Results

#### 3.3.1 Absence in RBBP-5 shortens *C. elegans* lifespan

The core MLL/SET/COMPASS complex comprises WDR-5, RBBP-5, and ASH-2. It has been reported that absence of WDR-5 or ASH-2 can increase lifespan by preventing H3K4 methylation in germ cells of *C. elegans* (Greer et al. 2010; Greer et al. 2011). Yet the effect of depleting RBBP-5, also a core component, has not been reported. We thus assessed whether lifespan is affected by the absence of RBBP-5. To determine if RBBP-5 is implicated in lifespan regulation, we used a mutant, *rbbp-5(tm3463)*, predicted to be a null allele (referred herein as *rbbp-5(-)*) and conducted lifespan assays comparing with wild type N2. We analysed the data using Kaplan-Meier survival. We found that *rbbp-5(-)* were short-lived compared to the wild type (Figure 3.2A). The median lifespan for wild type N2 was 21 days, whereas, the median lifespan for *rbbp-5(-)* was only 16 days, equivalent to a reduction in median lifespan of 24% ( $P < 0.001$ ) (Table 3.1). To confirm previously published data on WDR-5 and lifespan, we used the same predicted null allele of *wdr-5* and the knockdown by RNAi followed by lifespan assessment. In both cases, we were able to detect the extended lifespan (Figure 3.2B and C) (Greer et al. 2010; Greer et al. 2011). Taken together, the lifespan assays show that even though WDR-5 and RBBP-5 are core components of the same complex, they act differently on lifespan regulation: WDR-5 accelerates ageing whilst RBBP-5 slows ageing rate down.





**Figure 3.2 RBBP-5 and WDR-5 function together to regulate lifespan in *C. elegans***

A) *rbbp-5(tm3463)* mutant worms have short lifespan compared to wild type. B) *wdr-5(ok1417)* mutant worms have extended lifespan compared to wild type. C) Knock down by RNA interference on *wdr-5* extends the lifespan of worms compared to worms treated with empty vector (RNAi). (Replicates, (A) =7, (B) =2, (C) =1)

**Table 3.1 Statistics for lifespan assays on strains deficient for RBBP-5 or WDR-5**

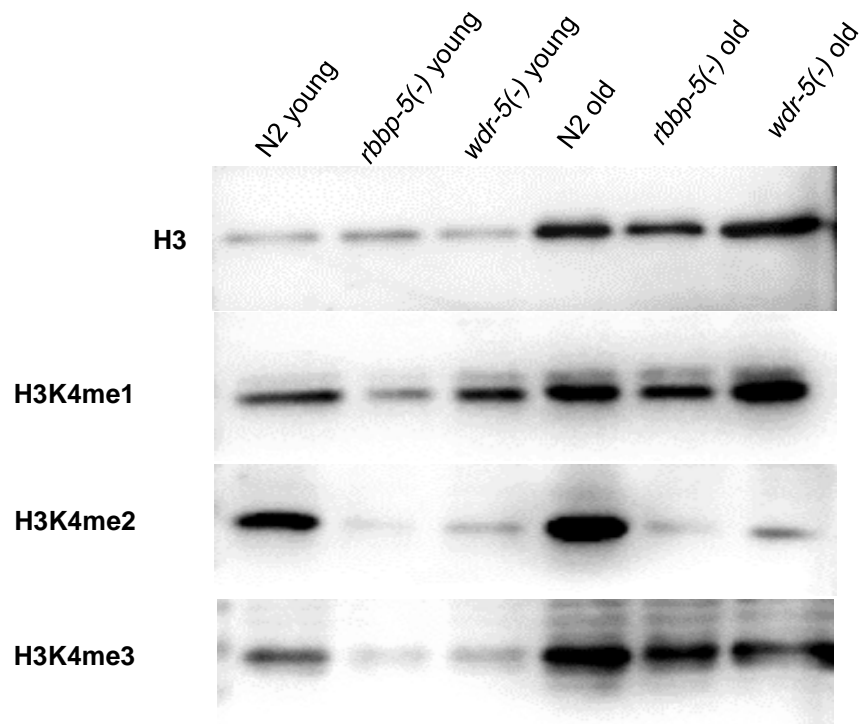
Condition	No of subjects	Days	Standard error	95% CI
Lifespan assay on <i>rbbp-5(-)</i>				
N2	120	21	0.35	20.15 ~ 21.50
<i>rbbp-5(-)</i>	120	16	0.49	15.08 ~ 17.01
Lifespan assay on <i>wdr-5(-)</i>				
N2	97	21	0.49	20.52 ~ 22.46
<i>wdr-5(-)</i>	111	24	0.49	22.67 ~ 24.59
Lifespan assay on <i>wdr-5(RNAi)</i>				
<i>ev(RNAi)</i>	166	19	0.37	18.42 ~ 19.88
<i>wdr-5(RNAi)</i>	102	22	0.56	20.91 ~ 23.09
Condition			P-value	
N2 vs <i>rbbp-5(-)</i>			≤ 0.001	
N2 vs <i>wdr-5(-)</i>			≤ 0.05	
<i>ev (RNAi)</i> vs. <i>wdr-5(RNAi)</i>			≤ 0.001	

Shown is a representative data from seven biological replicates for *rbbp-5(-)*, two for *wdr-5(-)* and one for *wdr-5(RNAi)* replicates.

### 3.3.2 Levels of H3K4 methylation decrease with age

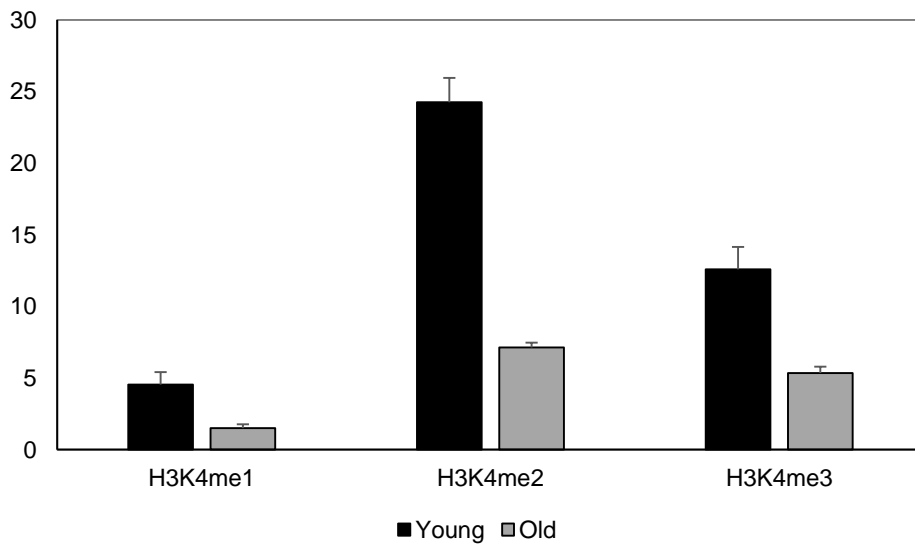
Implication of the MLL/SET/COMPASS complex in lifespan regulation raises the possibility that H3K4 methylation levels could change during ageing. To address this point, we performed Western blot experiments on young (day 1) adults versus old (day 8) adults of the wild type N2 strains (Figure 3.3). To appreciate levels of H3K4 methylation, we expressed their values relative to the global H3 levels in young or old wild type. The Western blot quantification (Figure 3.3) represents the mean  $\pm$  standard error of the mean (SEM) and depicts representative distributions of the quantitative results. An important limitation of this study is we observed an increase in levels of our loading control, H3, during ageing. Due to time constraint, we are unable to provide a different loading control. It would be of interest in future to test if tubulin is a better loading control in ageing study. We observed that the levels of H3K4me1 and H3K4me2 in old wild type adults are three times lower than that found in the young wild type adults. The reduction of H3K4me3 in old wild type adults reached approximately 2.5 times lower compared to the young adults (Figure 3.4). Thus, H3K4me1/me2/me3 levels are reduced during ageing relative to the levels of H3, which are increased during ageing.

To determine whether the H3K4 methylation activity during ageing depends on the RBBP-5 and WDR-5, we used the *rbbp-5(-)* and *wdr-5(-)* mutants and performed Western Blots analysis for H3K4me1/me2/me3 levels as above (Figure 3.3). The western blot quantification compared the levels of H3K4 methylation relative to H3 in the mutants versus the levels of H3K4 methylation relative to H3 in wild type strain. Our data showed that H3K4me1 levels were reduced only in the young adult lacking RBBP-5 (Figure 3.5A). H3K4me2 levels were greatly reduced in either mutant as well as in young or old adults, (Figure 3.5B). H3K4me3 levels were reduced in young adults lacking RBBP-5. But in old adults, the H3K4me3 levels were reduced by the absence of RBBP-5 or WDR-5, though to a lesser extent (Figure 3.5C). Taken together, our data indicate that RBBP-5 is required to maintain H3K4me1/me2/me3 levels in young adults. However, the reliance on RBBP-5 to maintain H3K4me1/me3 is lessening in old adults. On the other hand, WDR-5 is required for H3K4me2 in either young or old. However, its role for maintaining the global levels of H3K4me1/me3 appears minor albeit detectable regardless of the age. Therefore, this analysis revealed that methylation at H3K4 is altered during ageing and suggest that the H3K4 methylation activity in old adults is different than the activity found in young adults.



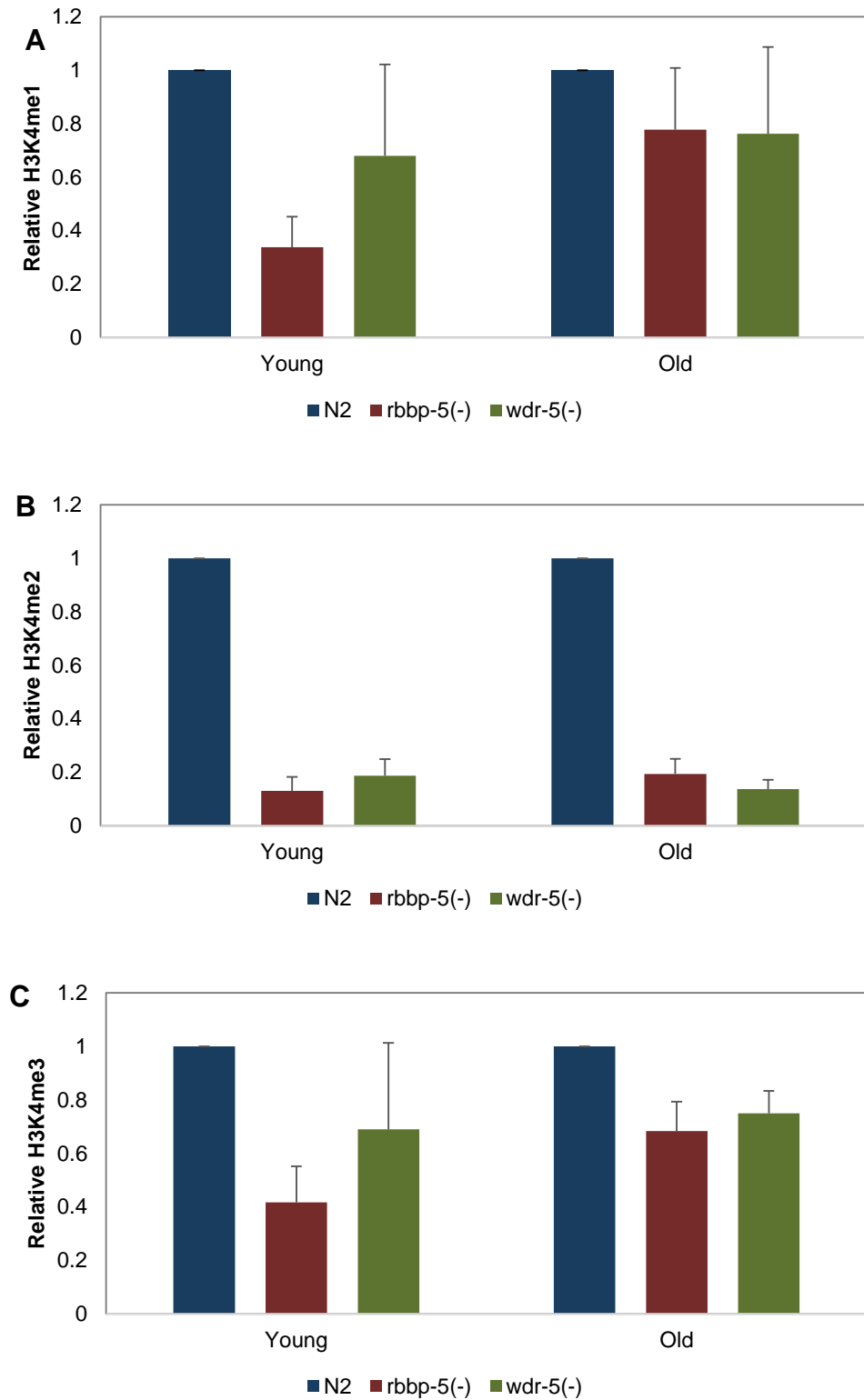
**Figure 3.3 Western blot on young (day 1) and old (day 8) adults extracts**

Representative of four independent western blot experiments for H3K4me1/me2/me3 on young (day 1) and old (day 8) adult extracts (N=5).



**Figure 3.4 Wild type *C. elegans* has reduced H3K4me1/me2/me3 levels during ageing**

Quantification was performed using ImageJ (1.51j8) software on four Western Blot replicates. The plot represents the mean of H3K4me1/me2/me3 levels relative to H3 in young adult (black) wild type and old adult wild type. For each gel, the intensity of the given wild type band was first divided by the intensity of the H3 control of similar age wild type for that treatment. Means and standard error of means (SEM) were then calculated across gels. Data was plotted as mean ± SEM, n=4).



**Figure 3.5 Reliance on RBBP-5 and WDR-5 for H3K4 methylation is different in old and adults.**

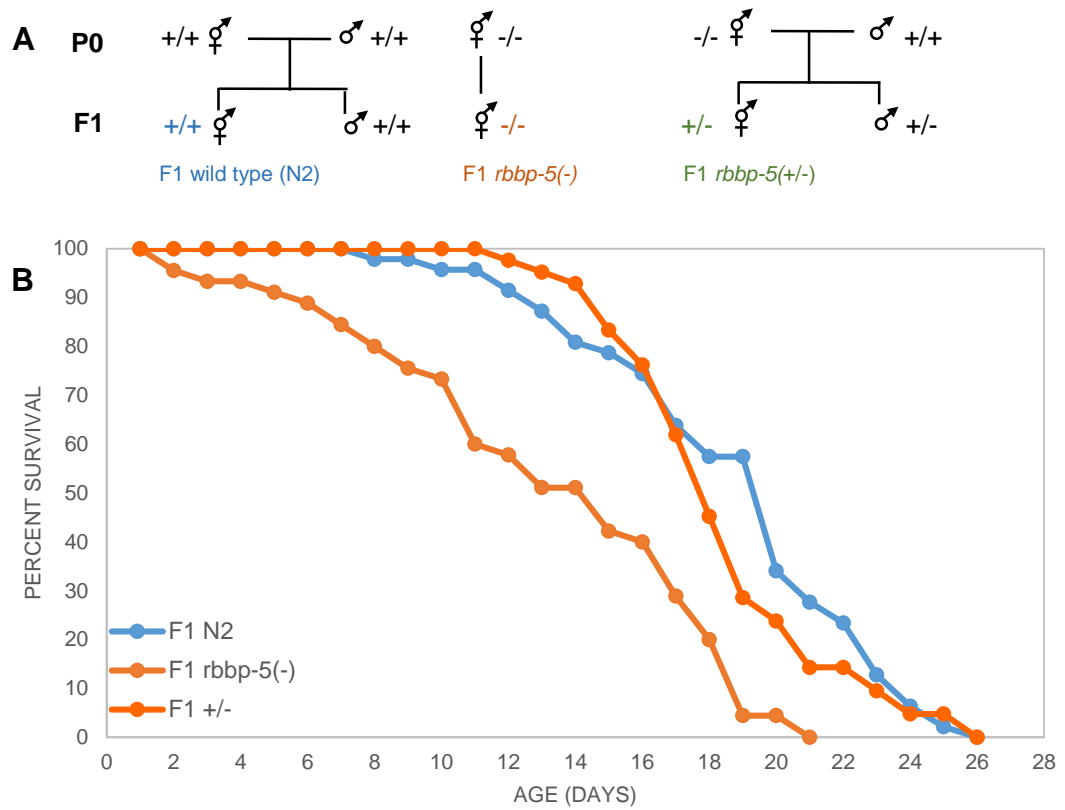
Western blot quantification using ImageJ (1.51j8) software. The plot represents the mean of H3K4me1/me2/me3 levels relative to H3 in young and old adult of mutants rbbp-5(-) and wdr-5(-) when compared to wild type N2. For each gel, the intensity of the given band was first divided by the intensity of the H3 control for that treatment. These normalized values were then divided by the normalized value for the same methylation of the same age of N2 in the same gel. Means and standard error of means (SEM) were then calculated across gels. Data was plotted as mean  $\pm$  SEM (n=4).

### 3.3.3 A copy of functional *rbbp-5* allele rescues lifespan regulation

Transgenerational inheritance of longevity has been observed in the wild type descendants from ancestor lacking WDR-5, ASH-2 or SET-2 (Greer et al. 2011). The long-lived wild type progenies were obtained from self-fertilizing heterozygous, which descended from the cross between the mutant and the wild type strains. It is still unknown whether RBBP-5 is also implicated in the transgenerational inheritance of lifespan. As the starting point of our transgenerational study, we investigated what happen to the lifespan of the heterozygous *rbbp-5(+/-)*.

In this experiment, the wild type and *rbbp-5(-)* strains were used. We crossed the wild type adult males with the *rbbp-5(-)* hermaphrodites and we referred to them as the P0 generation (Figure 3.6A). After an overnight mating and egg-laying, we removed the P0 generation. We then single cloned the next F1 progeny when they reached L4 stage. The genotype of each of the F1 single clones was inferred by pooling six F2 progeny into a tube and performing PCR on them. The genotyping step is crucial to eliminate any self-fertilising progeny from the *rbbp-5(-)* P0 mothers. In parallel to the genotyping step, we started assessing the lifespan of the F1 generation from day 1 adult. We measured the lifespan of the F1 wild type, F1 *rbbp-5(-)* and F1 *rbbp-5(+/-)* strains. We analysed the data using Kaplan Meier survival curve and comparison was made to the wild type.

We found that the median lifespan was 19 days for the wild type and the F1 *rbbp-5(+/-)* strains ( $P > 0.05$ ). The median lifespan was 14 days for *rbbp-5(-)* ( $P \leq 0.001$ ) (Table 3.2). Our data showed that the F1 *rbbp-5(+/-)* has a normal lifespan compared to wild type N2 (Figure 3.6B). Taken together, RBBP-5 deficiency in parental generation does not shorten the lifespan of the next heterozygous descendant. Instead, a single *rbbp-5* wild type allele rescues lifespan regulation, shifting lifespan to normal.



**Figure 3.6 Heterozygous *rbbp-5*(+/-) has a normal lifespan**

(A) Scheme for generating heterozygous F1 *rbbp-5*(+/-). (B) Representative of the Kaplan-Meier survival curves for wild type (blue), *rbbp-5*(-) (orange) and *rbbp-5*(+/-) (dark purple) of F1 generation. The Y axis is the percent survival and the X axis is age in days (N=3).

**Table 3.2 Representative statistics for F1 generation of transgenerational study**

Condition	No of subjects	Days	SE	95% CI
F1 N2	70	19	0.59	17.85 – 20.17
F1 <i>rbbp-5</i> (-)	76	14	0.70	12.45 – 15.19
F1 <i>rbbp-5</i> (+/-)	98	19	0.48	17.69 – 19.56
Condition	P-value			
F1 N2 vs. F1 <i>rbbp-5</i> (-)	≤ 0.001			
F1 N2 vs. F1 <i>rbbp-5</i> (+/-)	Not significant			
F1 <i>rbbp-5</i> (-) vs. F1 <i>rbbp-5</i> (+/-)	≤ 0.001			

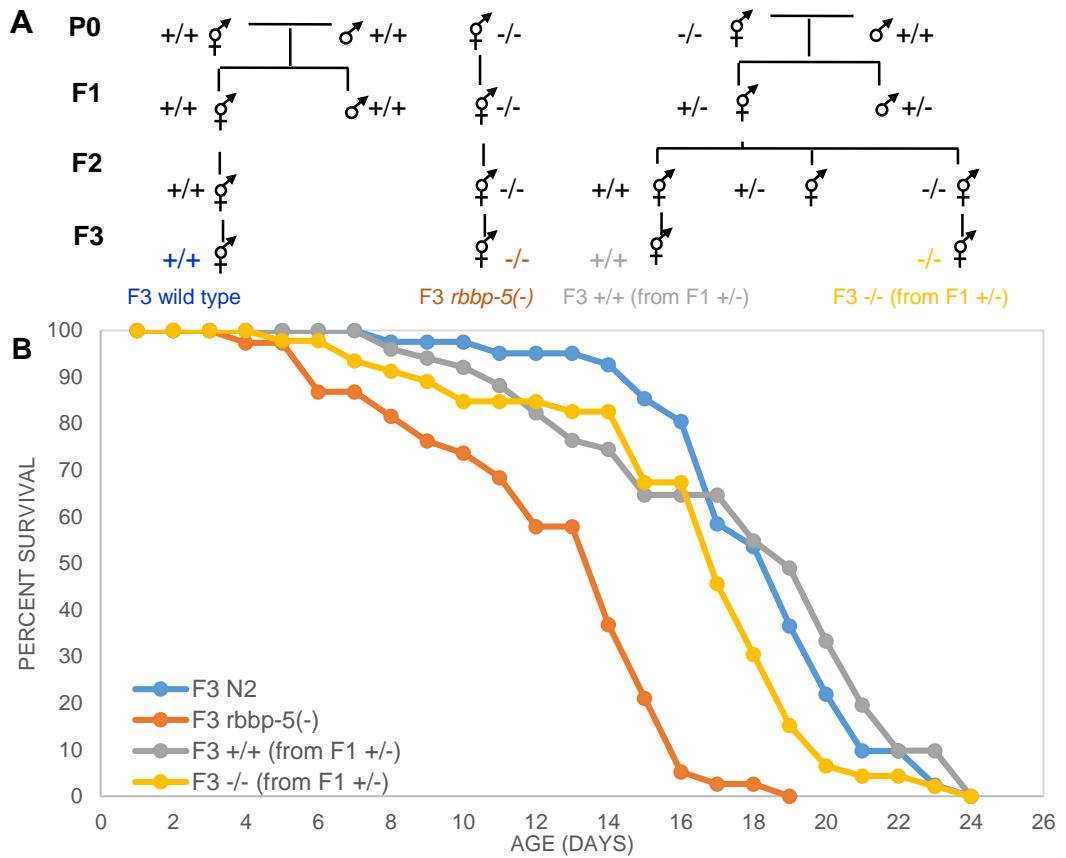
### 3.3.4 Lifespan regulation by RBBP-5 is transgenerationally inherited

Heterozygous *rbbp-5(+/-)* animals have a normal lifespan similar to the wild type. Which negated the investigation of the inheritance of the short lifespan of the *rbbp-5(-)* parents in F3 descendants. But it did not impair the investigation of whether normal lifespan can be resumed in F3 *rbbp-5(-)* mutant descendant from the F1 *rbbp-5(+/-)* mothers. We continued the same mating scheme from the previous experiment (Figure 3.6). The F2 progeny from the F1 *rbbp-5(+/-)* mothers were single cloned, left overnight to lay eggs and then genotyped. Next, we transferred the F3 wild type, F3 *rbbp-5(-)*, F3 +/+ from F1 (+/-) ancestor and F3 -/- from F1 (+/-) ancestor onto fresh plates when they were at L4 stage. We started the lifespan assessment at day 1 adult. The workflow is illustrated in Figure 3.7A.

We envisaged two scenarios if RBBP-5 is implicated in the transgenerational inheritance of lifespan. First, deficiency in RBBP-5 in P0 parent could shorten the lifespan of the F3 +/+ from the F1 +/- ancestor, but this unlikely because one wild allele rescues the short lifespan phenotype. Alternatively, functional RBBP-5 in the heterozygous generation could shift the lifespan of the F3 -/- from F1 +/- ancestor to normal. However, if there is no transgenerational inheritance, the lifespan should be reflective of the genotype. The F3 +/+ from F1 +/- ancestor would have normal lifespan whereas the F3 -/- from F1 +/- would be short-lived.

As expected, the F3 *rbbp-5(-)* was short-lived compared to the wild type (median lifespan = 13 days;  $P \leq 0.001$ ). The median lifespan of wild type was approximately 18 days. The F3 +/+ from F1 +/- ancestor has normal lifespan (median lifespan = 19 days;  $P > 0.05$ ), indicating that deficiency in RBBP-5 in parents does not shorten the lifespan of the wild type descendants. Surprisingly, the F3 -/- from F1 +/- ancestor displayed a normal lifespan (median lifespan = 17 days;  $P > 0.05$ ) (Figure 3.7B and Table 3.3) instead of being genotypically mutant. The data suggest that the wild type allele of *rbbp-5* can impart transgenerational epigenetic memory for lifespan regulation, hence delaying the manifestation of the short lifespan observed in the *rbbp-5(-)* mutant.





**Figure 3.7 Normal lifespan in presence of RBBP-5 is transgenerationally inherited**

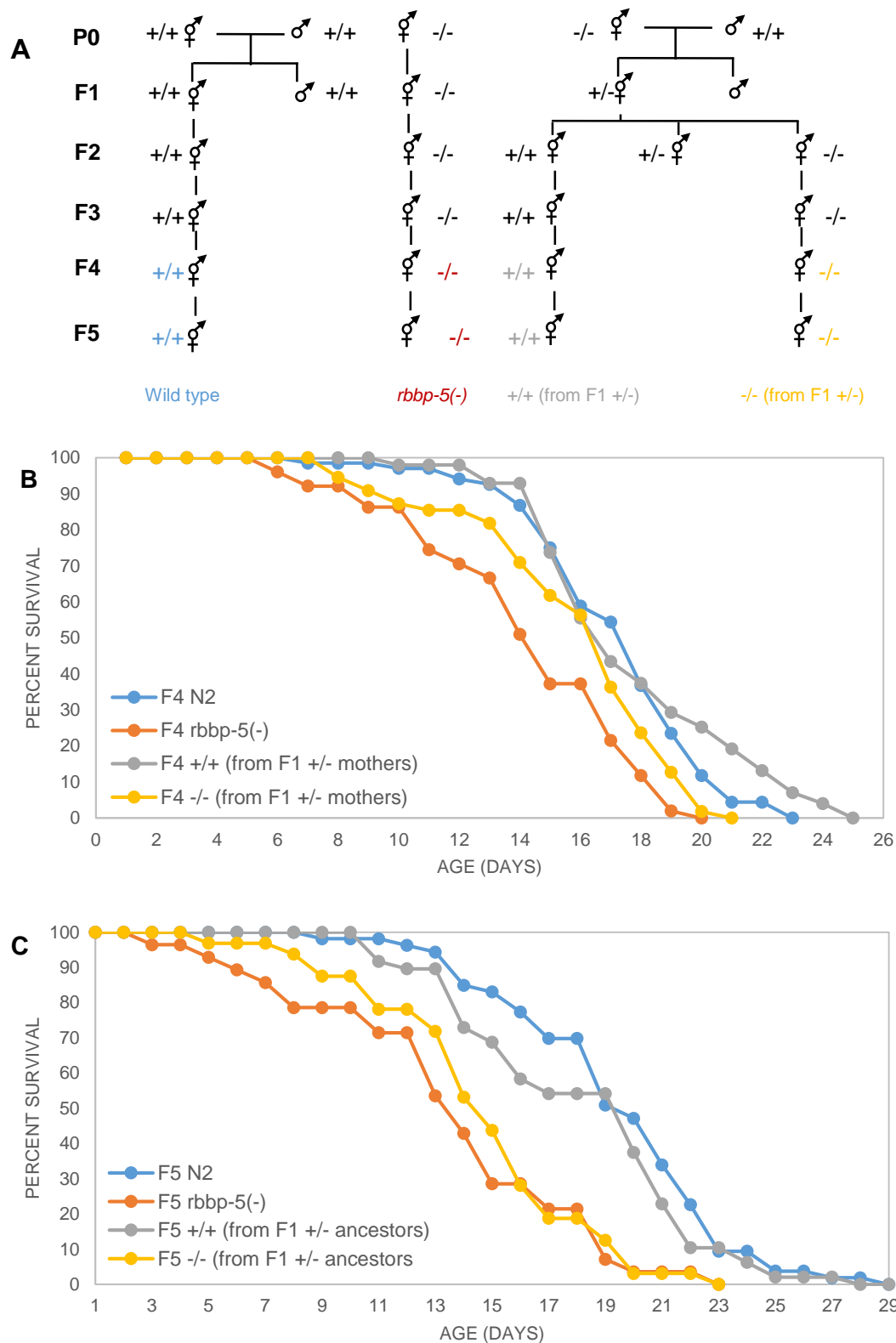
(A) Scheme for generating F3 generation of wild type (+/+) and mutant (-/-) from F1 *rbbp-5*(+/-) ancestor. (B) Representative of Kaplan-Meier survival curves for F3 generation of wild type (blue), *rbbp-5*(-) (orange), +/+ from F1 +/- ancestor (grey) and -/- from F1 +/- ancestor (yellow) (N=3).

**Table 3.3 Representative statistics for F3 generation for the transgenerational lifespan study**

Condition	No of subjects	Days	SE	95% CI
F3 N2	75	18	0.48	17.41 – 19.28
F3 <i>rbbp-5</i> (-)	67	13	0.56	11.59 – 13.77
F3 +/+ (from F1 +/-)	105	19	0.54	17.48 – 19.59
F3 -/- (from F1 +/-)	105	17	0.54	15.65 – 17.76
Condition	P-value			
F3 N2 vs. F3 <i>rbbp-5</i> (-)	≤ 0.001			
F3 N2 vs. F3 +/+ (from F1 +/-)	Not significant			
F3 N2 vs. F3 -/- (from F1 +/-)	Not significant			
F3 <i>rbbp-5</i> (-) vs. F3 +/+ (from F1 +/-)	≤ 0.001			
F3 <i>rbbp-5</i> (-) vs. F3 -/- (from F1 +/-)	≤ 0.001			
F3 +/+ (from F1 +/-) vs. F3 -/- (from F1 +/-)	≤ 0.01			

### 3.3.5 Lifespan regulation is transgenerationally inherited for three generations

The inheritance of longevity from parents having deficiency in WDR-5, ASH-2 or SET-2 can last for up to three generations of the wild type descendants. We have shown that the normal lifespan from the wild type allele of *rbbp-5* +/- parents could be transgenerationally inherited in the *rbbp-5*(-) mutant descendants. Next, we determined for how long the inheritance for normal lifespan imparted by RBBP-5 could last. We performed the previous workflow scheme (Figure 3.8A). We measured the lifespan of F4 wild type, F4 *rbbp-5*(-), F4 +/+ from F1 +/- ancestor and F4 -/- from F1 +/- ancestor. We found that the lifespan of F4 -/- from the F1 +/- ancestor to be intermediate (median lifespan = 16 days). The F4 -/- median lifespan was 6% shorter than wild type ( $P > 0.05$ ; N2 median lifespan = 17 days) but 7% extended from *rbbp-5*(-) ( $P = 0.04$ ; *rbbp-5*(-) median lifespan = 15 days) (Table 3.4). The lifespan of F4 +/+ from F1 +/- ancestor was similar to wild type ( $P > 0.05$ ). Hence, the corrected lifespan regulation from parents with RBBP-5 is partially inherited in the F4 mutant descendants (Figure 3.8B). We performed similar assessment on the F5 generation. Our observation showed that the F5 -/- from F1 +/- ancestor does not inherit normal lifespan anymore. Instead, it has a short lifespan when compared to the F5 wild type ( $P \leq 0.001$ ) (Figure 3.8C and Table 3.5). Thus, the lifespan regulation by wild type RBBP-5 in parents can last for up to three generations of *rbbp-5*(-) mutant descendant.



**Figure 3.8 Genetically mutant descendants from heterozygous *rbbp-5* parents inherit normal lifespan for up to three generations**

(A) Scheme for generating F4 and F5 generations of +/+ from F1 +/- ancestor and -/- from F1 +/- ancestor. (B) Representative of Kaplan-Meier survival curves for F4 generation and (C) F5 generation showing wild type (blue), *rbbp-5*(-) (orange), +/+ from F1 +/- ancestor (grey) and -/- from F1 +/- ancestor (yellow) (N=4).

**Table 3.4 Representative statistics for transgenerational lifespan assay on F4 generation**

Condition	No of subjects	Days	SE	95% CI
F4 N2	100	17	0.34	16.74 ~ 18.09
F4 rbbp-5	100	15	0.48	13.59 ~ 15.46
F4 +/+ (from F1 +/-)	122	18	0.34	17.26 ~ 18.58
F4 -/- (from F1 +/-)	90	16	0.44	15.19 ~ 16.91
Condition	P-value			
F4 N2 vs. F4 rbbp-5	≤ 0.001			
F4 N2 vs. F4 +/+ (from F1 +/-)	Not significant			
F4 N2 vs. F4 -/- (from F1 +/-)	<b>0.0573 (intermediate)</b>			
F4 rbbp-5 vs. F4 +/+ (from F1 +/-)	≤ 0.001			
F4 rbbp-5 vs. F4 -/- (from F1 +/-)	<b>0.0393 (intermediate)</b>			
F4 +/+ (from F1 +/-) vs. F4 -/- (from F1 +/-)	≤ 0.01			

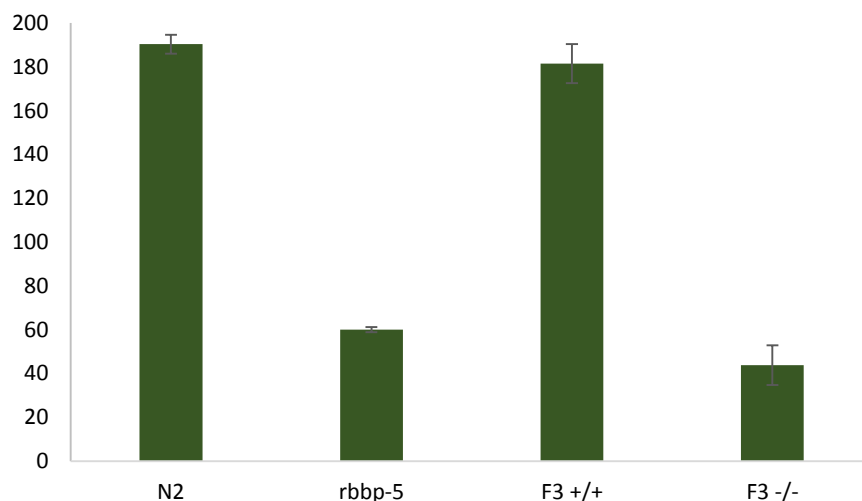
*Bold font indicates that median lifespan for F4 -/- from F1 +/- ancestor is intermediate between the lifespan of wild type and rbbp-5(-).*

**Table 3.5 Representative statistics for transgenerational lifespan assay on F5 generation**

Condition	No of subjects	Days	SE	95% CI
F5 N2	81	19.6	0.53	18.57 – 20.64
F5 rbbp-5(-)	90	14.28	0.75	12.80 – 15.75
F5 +/+ (from F1 +/-)	75	18.54	0.58	17.40 – 19.68
F5 -/- (from F1 +/-)	90	15.28	0.62	14.05 – 16.50
Condition	P-value			
F5 N2 vs. F5 rbbp-5(-)	≤ 0.001			
F5 N2 vs. F5 +/+ (from F1 +/-)	Not significant			
F5 N2 vs. F5 -/- (from F1 +/-)	≤ 0.001			
F5 rbbp-5(-) vs. F5 +/+ (from F1 +/-)	≤ 0.001			
F5 rbbp-5(-) vs. F5 -/- (from F1 +/-)	Not significant			
F5 +/+ (from F1 +/-) vs. F5 -/- (from F1 +/-)	≤ 0.001			

### 3.3.6 Epigenetic memory from RBBP-5 does not affect brood size

The descendants inheriting the normal lifespan are genotypically mutant that lack RBBP-5. Instead of having a short lifespan, they display a normal lifespan for up to three generations. It is unknown if the transgenerational inheritance is specific to lifespan regulation. Hence, we investigated another phenotype linked to deficiency in RBBP-5. Absence of RBBP-5 reduces brood size (Wang et al. 2011). To determine whether the F3 *-/-* from F1 *+/-* ancestor has normal (as for lifespan) or reduced number of progeny, we conducted a brood size assay. We single cloned F3 wild type, F3 *rbbp-5(-)*, F3 *+/+* from F1 *+/-* ancestor and F3 *-/-* from F1 *+/-* ancestor at L4 stage. The worms were incubated at 25 °C and transferred onto a new plate every day. Their progenies were counted and compared to wild type. We found a reduction in brood size of both the F3 *rbbp-5(-)* and F3 *-/-* from F1 *+/-* ancestor when compared to the wild type ( $P \leq 0.01$ ) (Figure 3.9, Table 3.6). The F3 *+/+* from F1 *+/-* ancestor on the other hand has a normal size of progeny. Thus, the presence of RBBP-5 in heterozygous parents can rescue lifespan regulation for up to three generations but does not rescue the reduced brood size phenotype of the F3 *-/-* mutants from the F1 *+/-* ancestors.



**Figure 3.9 Mutant progeny from ancestor having RBBP-5 has smaller brood size and does not inherit normal brood size**

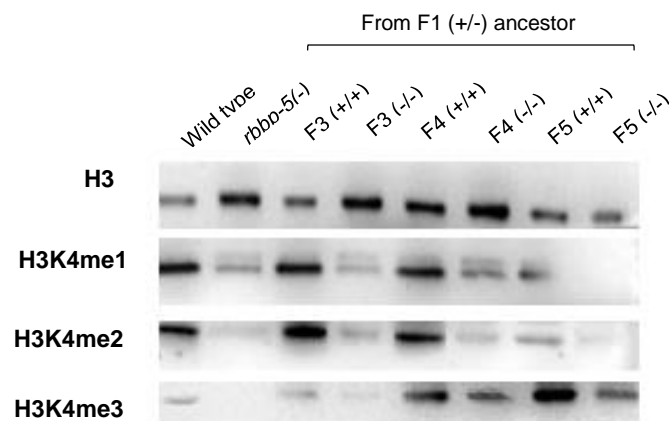
Average number of progeny per worm for wild type, *rbbp-5(-)*, F3 *+/+* from F1 *+/-* ancestor and F3 *-/-* from F1 *+/-* ancestor (n=10, average of 3 biological trials).

**Table 3.6 Parameters and statistics for brood size assay**

Condition	Average brood size	SEM
N2	190	4.32
<i>rbbp-5</i>	60	1.12
F3 +/+	181	8.87
F3 -/-	44	9.05
Condition		P-value
N2 vs. <i>rbbp-5</i>		≤ 0.001
N2 vs. F3 +/+ from F1 +/-		Not significant
N2 vs. F3 -/- from F1 +/-		≤ 0.01
<i>rbbp-5</i> vs. F3 +/+ from F1 +/-		≤ 0.01
<i>rbbp-5</i> vs. F3 -/- from F1 +/-		Not significant

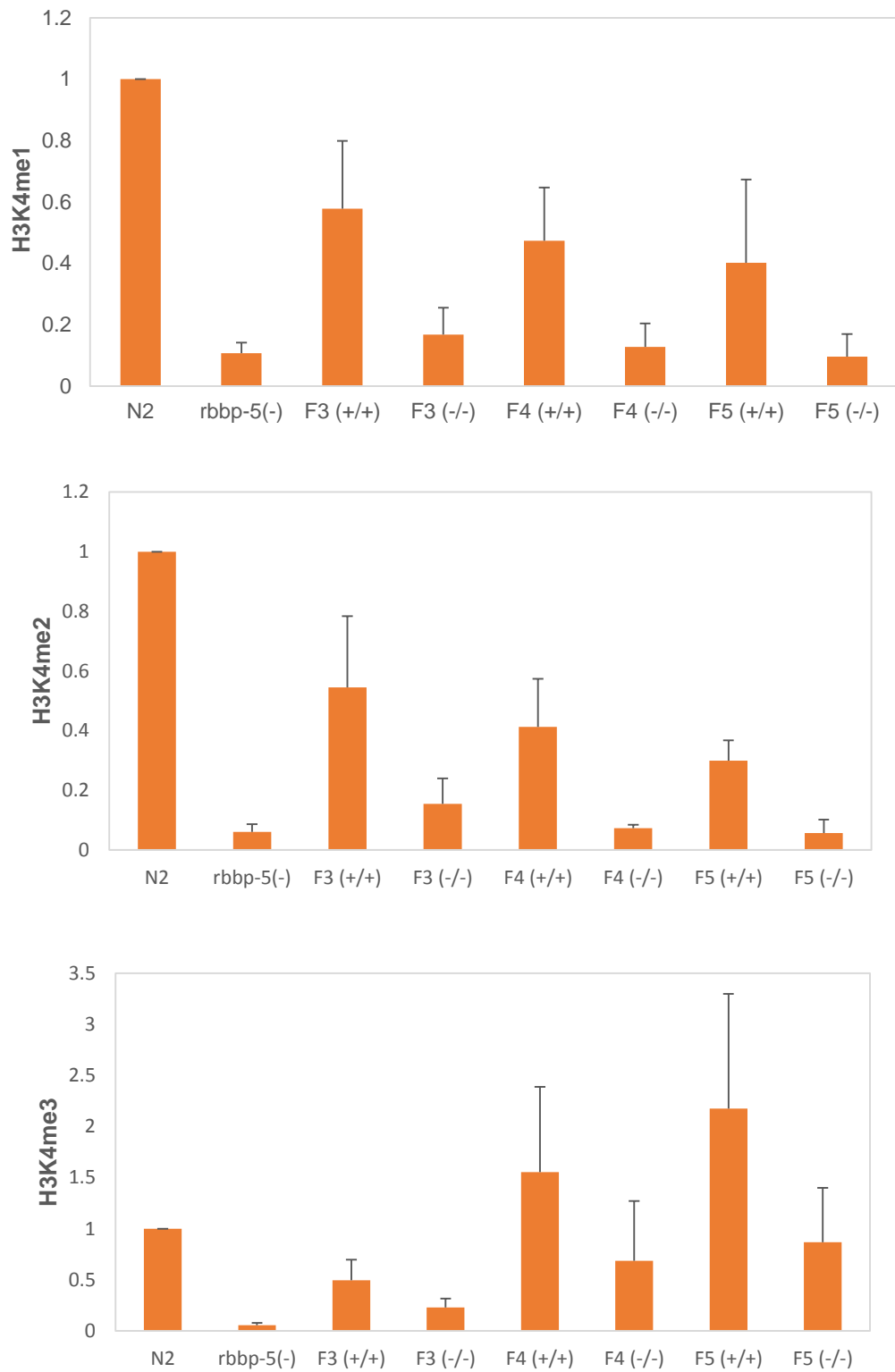
### 3.3.7 Global H3K4 methylation levels were not increased in mutant descendants

Absence in RBBP-5 shortens lifespan. Conversely, lifespan of the F1 *rbbp-5*(+/-) is normal. We reasoned that the shift of lifespan from short to normal might result from RBBP-5-containing complex recapitulating the H3K4 methylation activity at loci important for lifespan regulation. The H3K4 methylation regained during F1 *rbbp-5*(+/-) generation may have been epigenetically inherited in the subsequent generations. We prepared protein lysate of day 1 adult from the following strains: wild type; *rbbp-5*(-); F3 +/+ (from F1 +/-); F3 -/- (from F1 +/-); F4 +/+ (from F1 +/-); F4 -/- (from F1 +/-); F5 +/+ (from F1 +/-); and F5 -/- (from F1 +/-). We assessed the global methylation levels of H3K4me1/me2/me3 by Western Blotting. A representative western blot is shown in Figure 3.10. Western blot quantification for each condition of H3K4 methylation was made relative to H3 levels and compared to wild type. Consistent with our previous finding, *rbbp-5*(-) mutants display a reduction in H3K4me1/me2/me3 levels when compared to wild type. The F3, F4 and F5 mutant descendants from F1 +/- ancestor have reduced H3K4me1/me2/me3 levels compared to the F3, F4 and F5 wild type descendants, respectively (Figure 3.11). A limitation in our sampling is we introduced a wide time interval between control preparations and while waiting from one generation to the next for the descendants of F1(+/-). We observed H3K4 methylation levels in our genetically wild type F5 to be very different from wild type control F5, probably due to variables introduced during the waiting. In future, for every generation of F1(+/-) descendants, the wild type and mutant controls should be collected concurrently and separate Western blot should be performed for each generation, instead of doing it collectively. In sum, the trend indicates that the global levels of H3K4 methylation corresponds to the worm genotype: The H3K4 methylation in F3, F4 and F5 -/- worm descendants from F1 +/- are reduced compared to wild type.



**Figure 3.10 Global level of H3K4 methylation was reduced in *C. elegans* with *rbbp-5*(-) deletion regardless if they descended from mutant or heterozygous ancestor**

Representative Western Blot showing global H3K4me1/me2/me3 levels in F3, F4 and F5 generations compared to wild type (n=3).



**Figure 3.11 Genetically mutant descendants from heterozygous ancestor *rbbp-5(+/-)* have reduced H3K4me1/me2/me3 compared to their respective wild type descendants**

Quantification of western blot analysis on H3K4me1/me2/me3 levels relative to H3, compared to the levels in wild type (n=3).



### 3.4 Discussion

#### 3.4.1 RBBP-5 prevents lifespan shortening

The increasingly appreciated role of MLL/SET/COMPASS complex in regulating lifespan necessitates further understanding at mechanistic level. With the recent data on the absence of ASH-2, WDR-5 or SET-2 causing longevity, we investigate the RBBP-5's role in lifespan regulation. Since absence in RBBP-5 causes greater reduction in H3K4me1/me2/me3 during embryogenesis compared to when WDR-5 or ASH-2 is absence (Wang et al. 2011), we are interested to measure the lifespan of *rbbp-5(-)* mutant worms. Interestingly, our work revealed that in absence of RBBP-5, lifespan is shortened.

Why there is a contrasting effect on lifespan in absence of different MLL/SET/COMPASS core components is unclear. Perhaps, the different levels of the residual H3K4 methylation in absence of different component determine how long an animal lives. Having a slight depletion in H3K4 methylation may cause their lifespan to be extended. The depletion of H3K4 methylation in worms lacking WDR-5, ASH-2 or SET-2 is not fully absolute and does not reduce each state of the H3K4 methylation. Instead, mutant embryos lacking WDR-5 or ASH-2 only have decreased levels of both H3K4me3 and H3K4me2 to various degrees (Wang et al. 2011; Simonet et al. 2007). Similarly, inactivation of *set-2* causes significant reduction in the global level of H3K4me3, but only to a lower degree for the H3K4me2 (Simonet et al. 2007; Wilkins 2016). The reduced residual H3K4 methylation might regulate gene expressions important for longevity.

On the other hand, while partial depletion may extend lifespan, alteration in H3K4 methylation that is too great for the *C. elegans*, can shorten its lifespan. In absence of RBBP-5 for instance, all of the H3K4me1/me2/me3 states are greatly reduced during embryogenesis. The great reduction in H3K4me1/me2/me3 is also observed later during early adulthood as shown by our Western Blot analysis. H3K4 methylation has been associated with active transcription. Greater reduction in H3K4 methylation in the *rbbp-5(-)*, affecting all three methyl marks, may have cause misregulation of genes that can result in acceleration of ageing process.

The hypothesis on prominent alteration in H3K4 methylation shortens *C. elegans* lifespan is also supported by lifespan data on *rbr-2(-)* mutant worms. RBR-2 is the *C. elegans* homolog of the human JmjC H3K4 demethylase (Nishibuchi et al. 2014). Its absence results in a great accumulation of approximately 6.5-fold higher for H3K4me3 and 3.5-fold increase in H3K4me2 in *C. elegans* (Christensen et al. 2007). The enrichment of H3K4me3 in absence of RBR-2 was observed during larval development (L1, L2, L3 and L4) as well as in adult (Christensen et al. 2007). Lifespan analysis on *rbr-2(-)* mutants uncover their short life expectancy (Greer et al. 2010). The determinant of life expectancy could be the levels of H3K4 methylation: partial reduction in H3K4 methylation might cause longevity but prominent reduction or accumulation of H3K4 methylation might shorten the worm lifespan. Further work will be required to confirm the mechanism on how H3K4 methylation can negatively and positively control life expectancy.

### 3.4.2 H3K4 methylation is reduced during ageing process

Histone modification is one of the components of ageing. It mediates the interaction between genome and environment for adaptation and survival. Histone modifications have active roles in ageing if they are functionally associated with ageing phenotypes and if their levels are altered over the course of ageing (Calvanese et al. 2009). Previously, we have shown that reducing the H3K4 methylation through a null mutation in *C. elegans* RBBP-5 can shorten lifespan. We also have successfully confirmed that partially reducing the H3K4 methylation via a null mutation or RNAi treatment on *wdr-5* can extend the worm lifespan. Our work suggests that H3K4 methylation can shorten or extend lifespan possibly by acting on genes that could accelerate or impede ageing process. The next aim of this dissertation is to investigate if H3K4 methylation is altered over the course of ageing. We found that all states, H3K4me1/me2/me3, are reduced during ageing.

A possible explanation on why H3K4 methylation has ageing-associated reduction is that as an animal aged, chromatin function may start to decline. Chromatin is one of the many biological structures that undergo functional decline during ageing (Oberdoerffer & Sinclair 2007). The methylation at H3K4 is a histone modification that gives an additional layer of control over chromatin structure and ultimately over gene expression. It does so by recruiting various readers for chromatin remodelling such as CHD1 and BPTF; readers associated with HATs, HDACs and HDMTs such as ING2, ING4, PHF2, PHF8, JMJD2A and JMJD2B; or readers related to the general transcription factors such as TAF3 and SAGA (Musselman & Kutateladze 2009; Shi et al. 2006; Hung et al. 2009; Wen et al. 2010; Cloos et al. 2008; Mallette et al. 2012). Hence, reduction in H3K4 methylation during ageing may limit the recruitment of readers for H3K4 methylation, which in turn decline chromatin function.

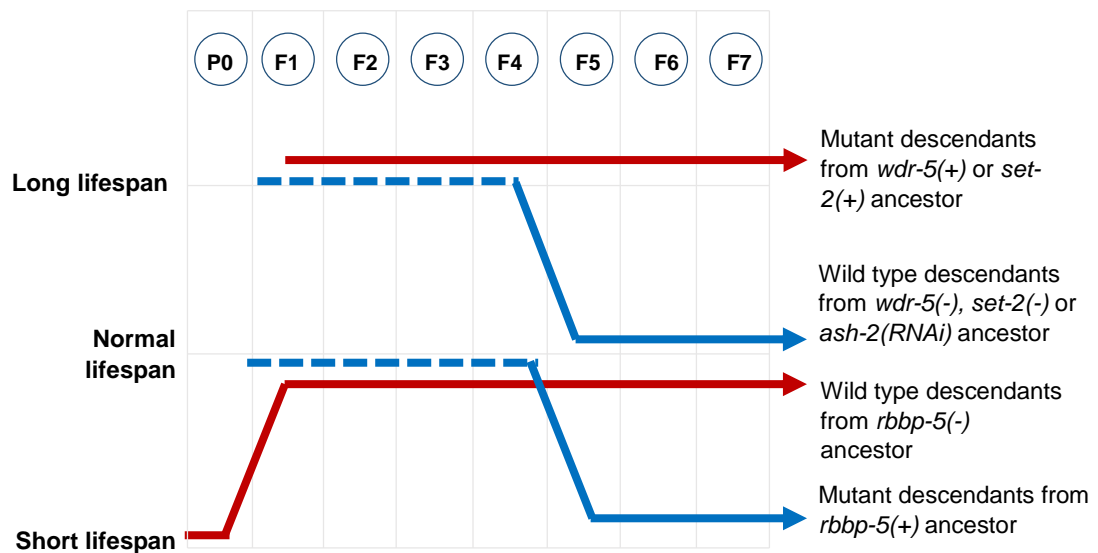
Further supporting our data is that chromatin becomes more heterochromatinised during ageing (Kreiling et al. 2011). In general, chromatin can be either in the form of euchromatin or heterochromatin. Euchromatin is a de-condensed chromatin during interphase and is permissive for transcription. On the other hand, the heterochromatin has a compact structure that hinders transcription activity (Talbert & Henikoff 2006; Berger 2007; Grewal & Jia 2007). It has been documented that ageing mammalian cells exhibit higher levels of heterochromatin-associated proteins, histone macro H2A (mH2A) and heterochromatin protein 1 beta (HP1 $\beta$ ) (Kreiling et al. 2011). In *Drosophila melanogaster*, ageing flies have been shown to exhibit higher repressive marks (H3K9me3) but lower activation marks such as RNA pol II, H3K4me3 and H3K36me3 (Wood et al. 2010). The binding of HP1 protein to H3K9me3 results in gene-silencing activity and the assembly of heterochromatin (Lachner et al. 2001; Bannister et al. 2001; Nakayama et al. 2001; Rice & Allis 2001; Jenuwein 2001). Our data on the global reduction in H3K4me1/me2/me3 during ageing provides a new piece of evidence in *C. elegans*, supporting the claim that activation marks are reduced during ageing in other species. Though, further investigation is required to determine if any heterochromatic mark is reduced in ageing *C. elegans*. The increase in the global heterochromatic marks but decrease in euchromatic marks, such as H3K4 methylation, during ageing may impinge gene expression and important cellular function, resulting in deterioration of physiological function.

### 3.4.3 RBBP-5 imparts transgenerational inheritance on lifespan regulation.

The mechanisms of transgenerational inheritance of a specific phenotype include heritable histone modifications and heritable changes in gene expressions (Greer et al. 2011). Our study, importantly, provides an updated model for the transgenerational inheritance of lifespan regulation by core components of MLL/SET/COMPASS complex. Based on our work and data from Greer et al., (2011), transgenerational inheritance was observed only when there is a reducing degree of life expectancy and never the other way around. For instance, the wild type descendants from ancestor lacking WDR-5, SET-2 or ASH-2 inherit longevity for up to three generations before their lifespans return to normal. In this scenario, there is a reducing degree of life expectancy from long to normal lifespan in the wild type descendants. Similarly, in the mutant descendants from ancestor having wild type RBBP-5, three generations of mutant descendants inherit normal lifespan. Then, the next mutant descendant's lifespan becomes short again. The reducing degree of lifespan expectancy is from normal to short lifespan. Perhaps, the effect on lifespan imparted by components of MLL/SET/COMPASS complex stays longer and is observable only when there is a reducing degree of life expectancy.

On the other hand, in an increasing degree of life expectancy such as from “normal to long” or “short to normal”, transgenerational inheritance for lifespan regulation was not observed. When wild type *wdr-5(+)* or *set-2(+)* ancestors have normal lifespan, the subsequent *wdr-5(-)* or *set-2(-)* descendants immediately have extended lifespan. Similarly, when the mutant *rbbp-5(-)* ancestor has short lifespan, the subsequent wild type descendants immediately have normal lifespan. Life expectancy immediately is in accordance to the genotype. In conclusion, the lifespan regulation imparted by the cores of MLL/SET/COMPASS complex take longer to be erased between generations with reducing degree of life expectancy but were immediately erased between generations with increasing degree of life expectancy.

We tested if inheritance of transgenerational lifespan regulation by RBBP-5 is specific for lifespan regulation. The transgenerational inheritance however, does not affect brood size. It is possible that the *rbbp-5* mutant descendants from wild type mother do not inherit normal brood size-associated gene expressions. They only inherit normal gene expression associated with lifespan regulation. This will be in accordance to previous findings that uncover the transgenerational inheritance of some misregulated longevity genes in wild type descendants from the WDR-5 deficient mothers (Greer et al. 2011). Our data also confirmed that no global changes in H3K4 methylation was inherited from mothers (Greer et al. 2011; Kishimoto et al. 2017). Most, but not all, marks are reprogrammed between generations. Thus, the transgenerational inheritance imparted by the core components of the MLL/SET/COMPASS complex in *C. elegans* has phenotype specificity towards lifespan regulation and not others.



**Figure 3.12 Proposed model for how transgenerational inheritance imparted by components of MLL/SET/COMPASS complex control lifespan regulation**

Transgenerational inheritance for lifespan regulation takes longer to disappear between generations of descendant with reducing degree of life expectancy (“long to normal” or “normal to short”). However, the inheritance immediately disappears in descendants with increasing degree of life expectancy (“normal to long” or “short to normal”). Increasing degree of life expectancy (red line); reducing degree of life expectancy (blue line); transgenerational inheritance of lifespan regulation (blue dashed line); parental generation (P0); filial generation 1-7 (F1-F7).

#### 3.4.4 Summary

In summary, our work demonstrates that RBBP-5 is required to prevent the shortening of *C. elegans* lifespan. Our data also suggests even though the core components are members of the same MLL/SET/COMPASS complex, removal of one of them can have diverse effect on lifespan: either prolonged or shortened. H3K4 methylation level is decreased during ageing, which maintenance requires RBBP-5 and WDR-5. Young adults rely on RBBP-5 for the maintenance of H3K4me1/me2/me3 but the reliance on H3K4me1/me3 reduces in old adults. On the other hand, young and old adults rely on WDR for the maintenance of H3K4me2 but the reliance is minimal for H3K4me1/me3 maintenance. Importantly, we also found that RBBP-5 can impart transgenerational memory on lifespan regulation. Presence of RBBP-5 only in parent causes lifespan to become normal in mutant descendants for up to three generations. The transgenerational inheritance by H3K4 methylation in presence of RBBP5 appears to be specific for lifespan regulation, does not affect brood size and does not increase the global methyl marks at H3K4.

## **Chapter 4**

**WDR-5 prevents excessive accumulation of H3K4  
di-methyl marks on chromosome X**

## Chapter 4 : WDR-5 prevents excessive accumulation of H3K4 di-methyl marks on chromosome X

### 4.1 Abstract

The epigenetic landscape is crucial to establish and maintain patterns of gene expression. Evidence shows that appropriate levels of H3K4 methylation require the core complex comprising WDR-5, ASH-2, and RBBP-5. However, it is unclear whether the core complex contributes to the specific locations of H3K4 methyl marks within the epigenome. To address this, we mapped H3K4me1/me2/me3 using *C. elegans* embryos lacking WDR-5 or RBBP-5. The absence of RBBP-5 reduces the global levels H3K4me1/me2/me3 indistinctive of their locations. In contrast, we found that the absence of WDR-5 increases the levels of H3K4me2 at the chromosomal scale on X, but not of H3K4me3 or me1. Interestingly, RNA-seq and ChIP-seq data show that a significant proportion of genes erroneously enriched for H3K4me2 on chromosome X are up regulated. Taken together, this work revealed that WDR-5 prevents excessive accumulation of H3K4me2 on the chromosome X and dampens X-linked gene expression.

KEYWORDS: Chromatin, H3K4, histone methylation, MLL/SET/COMPASS complex, chromosome X, ChIP-seq, RNA-seq, embryo, *C. elegans*.

### 4.2 Introduction

The epigenetic landscape is important to determine and maintain patterns of gene expression during development. An important contributor of the epigenetic landscape is the methylation state at histone 3 lysine 4 (H3K4) (Piunti & Shilatifard 2016; Ruthenburg et al. 2007). The conserved core complex comprised of WDR5, RBBP5, and ASH2 is key to maintain appropriate levels of H3K4 methylation. However, very little is known about how inactivation of the core complex components affects the precise location and levels of methyl marks at H3K4 within a metazoan epigenome.

Inactivating core complex components can affect functions such as transgenerational inheritance (Greer et al. 2011; Katz et al. 2009; Kerr et al. 2014; Xiao et al. 2011), transdifferentiation (Zuryn et al. 2014), pluripotency (Ang et al. 2011; Käser-Pébernard et al. 2014; Robert et al. 2014), RAS signalling (Fisher et al. 2010), and differentiation of stem cells (Jiang et al. 2011). To understand how H3K4 methylation regulates these important functions will require mapping location and levels as well as the consequences on transcription.

The transfer of methyl groups on H3K4 is performed by the evolutionary conserved SET/COMPASS/MLL complex (Miller et al. 2001; Nagy et al. 2002; Roguev et al. 2001; Shilatifard 2008). The SET/COMPASS/MLL complex consists of specific SET domain-containing enzymes and a structural core complex. Together, they target lysine 4 of histone 3 for mono-, di-, and tri-

methylation (me1, me2, and me3) (Ruthenburg et al. 2007). In *C. elegans*, WDR-5, ASH-2, and RBBP-5 each contributes to varied degrees to maintain the global levels of H3K4me2/me3 (Li & Kelly 2011; Simonet et al. 2007; Chen et al. 2011). However, the role that each component plays in regulating the genomic distribution of H3K4me1/me2/me3 and their levels at precise loci remain unclear. Interestingly, the depletion of H3K4me2 levels in primordial germ cells demonstrated by Schaner et al. (Schaner et al. 2003) has been shown by Xiao et al. to require ASH-2, indicating that ASH-2 can prevent as well as promote deposition of methyl marks at H3K4 (Schaner et al. 2003; Xiao et al. 2011).

H3K4 methylation states have been associated with distinct transcriptional activities. Enrichment in H3K4me3 is found at active transcription start sites (Santos-Rosa et al. 2002). Broad H3K4me3 domains have been shown to regulate transcriptional consistency and expression of tumour suppressor genes (Benayoun et al. 2014; Chen et al. 2015). Enrichment in H3K4me1 is an epigenetic feature of enhancers; its co-occurrence with H3K27 acetylation defines active enhancers (Creyghton et al. 2010; Heintzman et al. 2007). H3K4me1 and H3K27 acetylation are also detected at latent enhancers where they create a stimulus-dependent memory in macrophages, facilitating re-stimulation responses (Ostuni et al. 2013). In addition, enhancer transcription in TLR4-activated macrophages stimulates de novo acquisition of H3K4me1/me2 to produce new enhancer-like regions (Kaikkonen et al. 2013). However, a specific transcriptional state associated with H3K4me2 enrichment remains elusive.

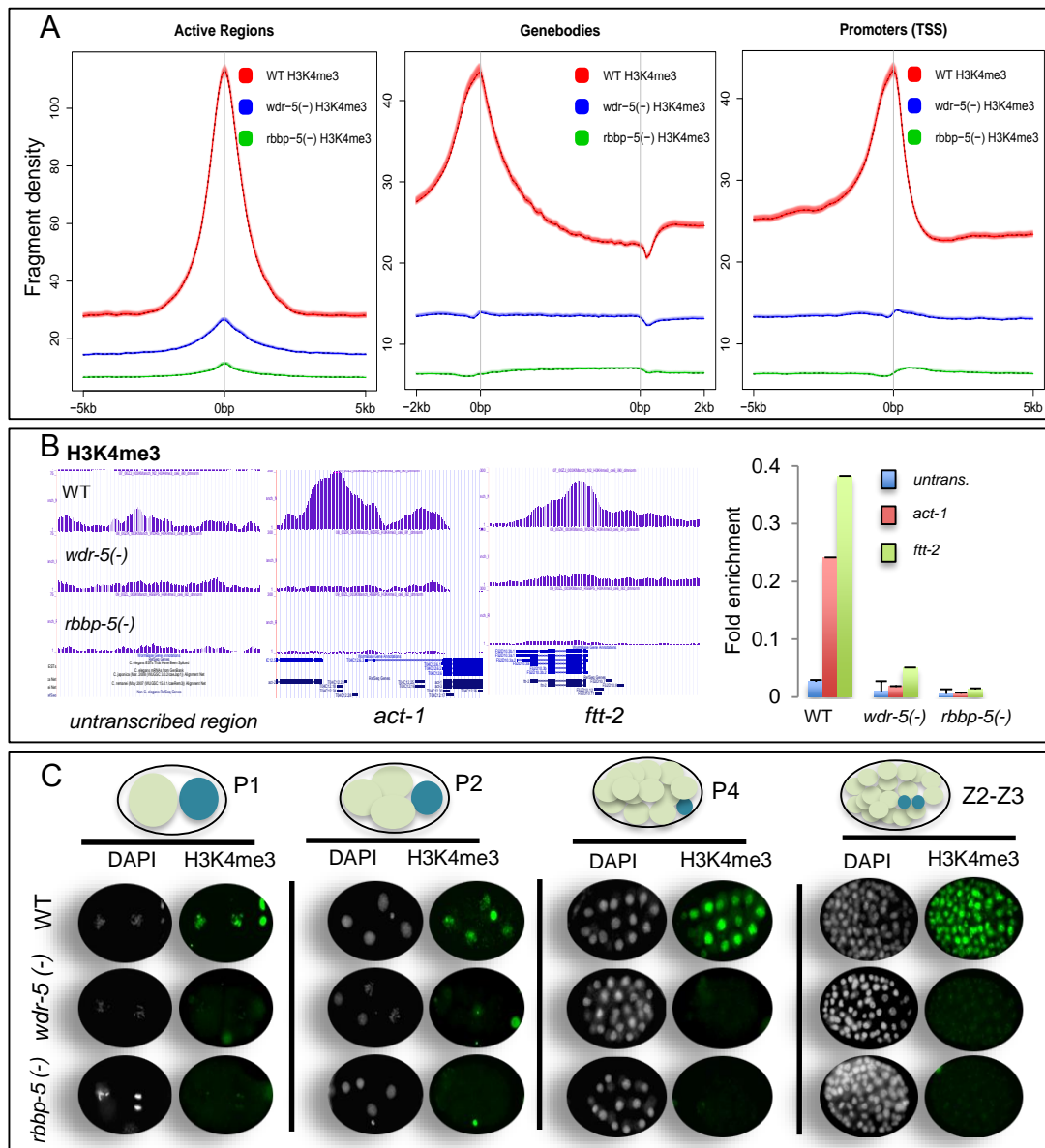
Herein, we used *C. elegans* embryos to determine the contribution of WDR-5 and RBBP-5 towards the precise location and levels of H3K4me1/me2/me3 and address whether their presence correlates with changes in gene expression. Our ChIP-seq data in embryos depleted of WDR-5 revealed excessive acquisition of H3K4me2 at the chromosomal scale on X. This excessive di-methylation at H3K4 is associated with up regulation of gene expression, indicating that dosage compensation is likely affected by de novo H3K4me2. The higher incidence of males observed specifically in the absence of WDR-5 supports this notion. Taken together, this work shows that WDR-5 has a novel activity, which prevents excessive acquisition of H3K4me2 on the chromosome X.

## 4.3 Results

### 4.3.1 H3K4me3 levels are reduced in the absence of either WDR-5 or RBBP-5

To address whether the core complex regulates the genomic distribution of methyl marks at H3K4 as well as their levels, we compared H3K4me1/me2/me3 distribution in the absence of either WDR-5 or RBBP-5 relative to wild type using spiked-in ChIP-seq. I harvested and fixed synchronised embryos mostly of late embryogenesis (Z2-Z3 stage). ActiveMotif performed the ChIP spiked-in by combining *C. elegans* chromatin, antibody of interest (H3K3me1, me2 or me3), *Drosophila melanogaster* chromatin and *Drosophila* specific H2Av antibody into a same tube. Standard immunoprecipitation was performed followed by Next-Generation sequencing. *C. elegans* and *Drosophila* sequence tags were aligned, *Drosophila* tag counts across samples were equalised and the ratios were used to normalise tag counts across *C. elegans* samples. As expected, the absence of either WDR-5 or RBBP-5 caused a strong and general reduction in the levels of H3K4me3. The depletion in H3K4me3 is observed at active regions (enrichment regardless of location and defined by at least one peak), promoters, gene bodies, and downstream of gene bodies (Figure 4.1A and Table 4.1). The effect is stronger in the absence of RBBP-5 than in the absence of WDR-5 (Figure 4.1A). To verify these results, we performed ChIP-qPCR at an untranscribed region, at the house keeping gene *act-1*, and at *ftt-2*, a 14-3-3 gene expressed during embryogenesis. All three loci displayed a reduction in the levels of H3K4me3 in absence of either WDR-5 or RBBP-5 relative to wild type and as indicated by the UCSC genome browser (Figure 4.1B). The levels of H3K4me3 in wild type are higher for the actively transcribed loci than the untranscribed locus (Figure 4.1B). Immunofluorescence staining on *wdr-5(-)* and *rbbp-5(-)* mutant embryos confirmed that H3K4me3 levels are depleted relative to wild type (Figure 4.1C). Taken together, these data show that WDR-5 and RBBP-5 are crucial to ensure robust levels of H3K4me3 in embryos.





**Figure 4.1 Genomic distribution and relative abundance of H3K4me3 in the absence of WDR-5 or RBBP-5**

(A) Spiked-in ChIP-seq shows that WDR-5 and RBBP-5 are important to maintain high levels of H3K4me3. At active regions, the maximal values (peak of fragment density) are averaged and set to 0bp with  $\pm 5$  kb of flanking values (see methods; Chip-seq). Genebodies values are averaged along the relative position of genes. Transcription Start Sites (TSS) and Transcription End Sites (TES) are set respectively at 0 bp with  $\pm 2$ kb of flanking values. Promoters values are averaged along their relative position to genes determined by Transcription Start Sites (TSS) set at 0bp with  $\pm 5$ kb of flanking values. (B) UCSC genome browser screen shots from ChIP-seq data at three loci and ChIP-qPCR for these loci. The ChIP-qPCR data show that H3K4me3 levels are significantly depleted in the absence of WDR-5 or RBBP-5. Data were presented as fold enrichment calculated by normalising the values of percent input relative to H3. Percent input was calculated by  $100 \times 2^{-(Ct \text{ total input} - Ct \text{ sample})}$ . Data are represented as mean  $\pm$  SEM. (C) Immunostaining on embryos lacking WDR-5 or RBBP-5 showing their global contributions towards H3K4me3 during embryonic development. P1, P2, P4, and Z2-Z4 stages of embryogenesis are depicted on top. Dark green cells represent the germlastomere or their descendants. The DAPI staining is shown in grey tone and H3K4me3 in green.

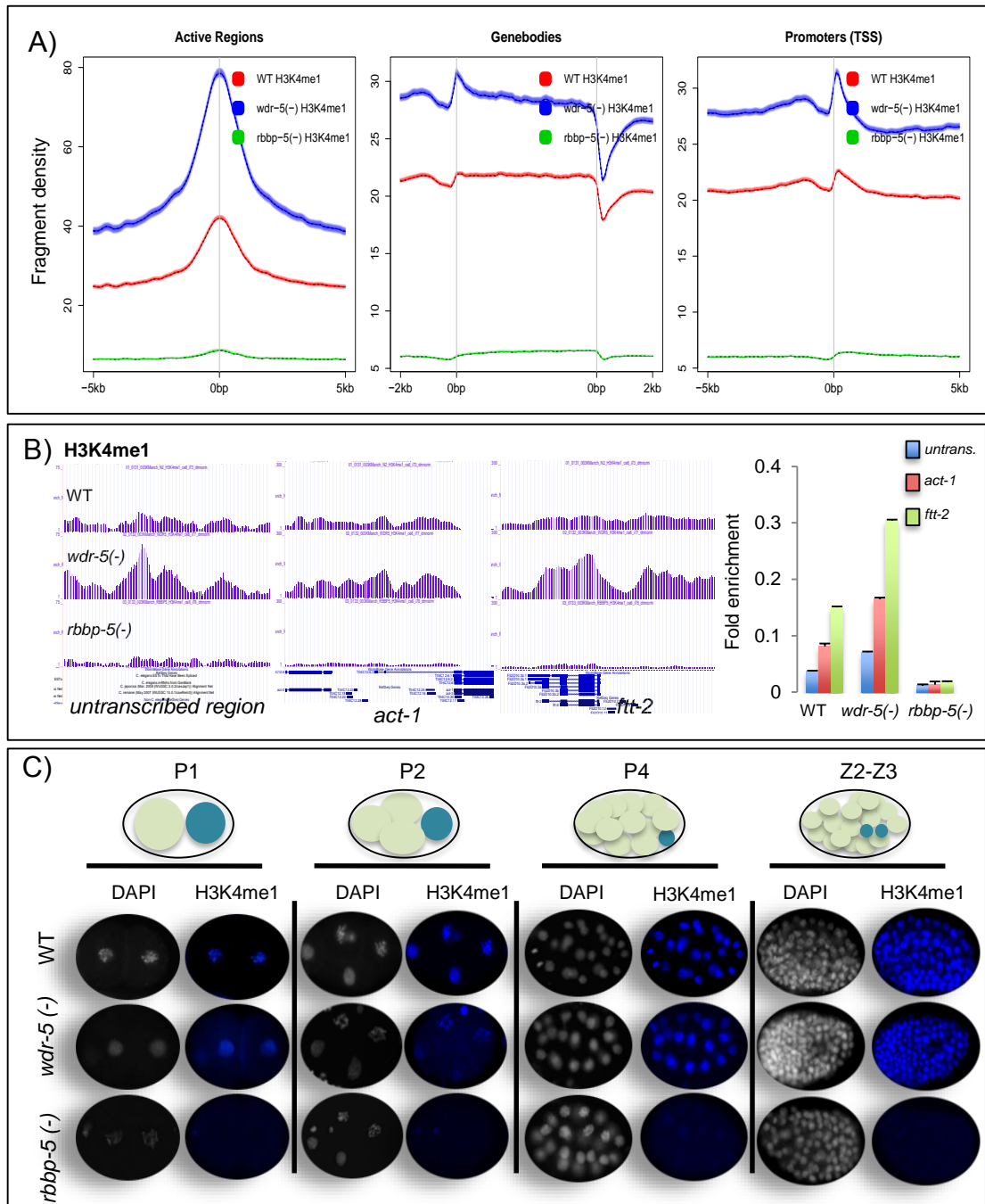
**Table 4.1 H3K4me3 peaks in active regions**

N2	<i>wdr-5(-)</i>	<i>rbbp-5(-)</i>	Peaks	
YES	x	x	2,314	
x	YES	x	429	
YES	YES	x	621	
x	x	YES	157	
YES	x	YES	67	
x	YES	YES	205	
YES	YES	YES	312	
3,314	1,567	741	4,105	<b>TOTAL PEAKS</b>

YES indicates in which background(s) the peaks were counted from.

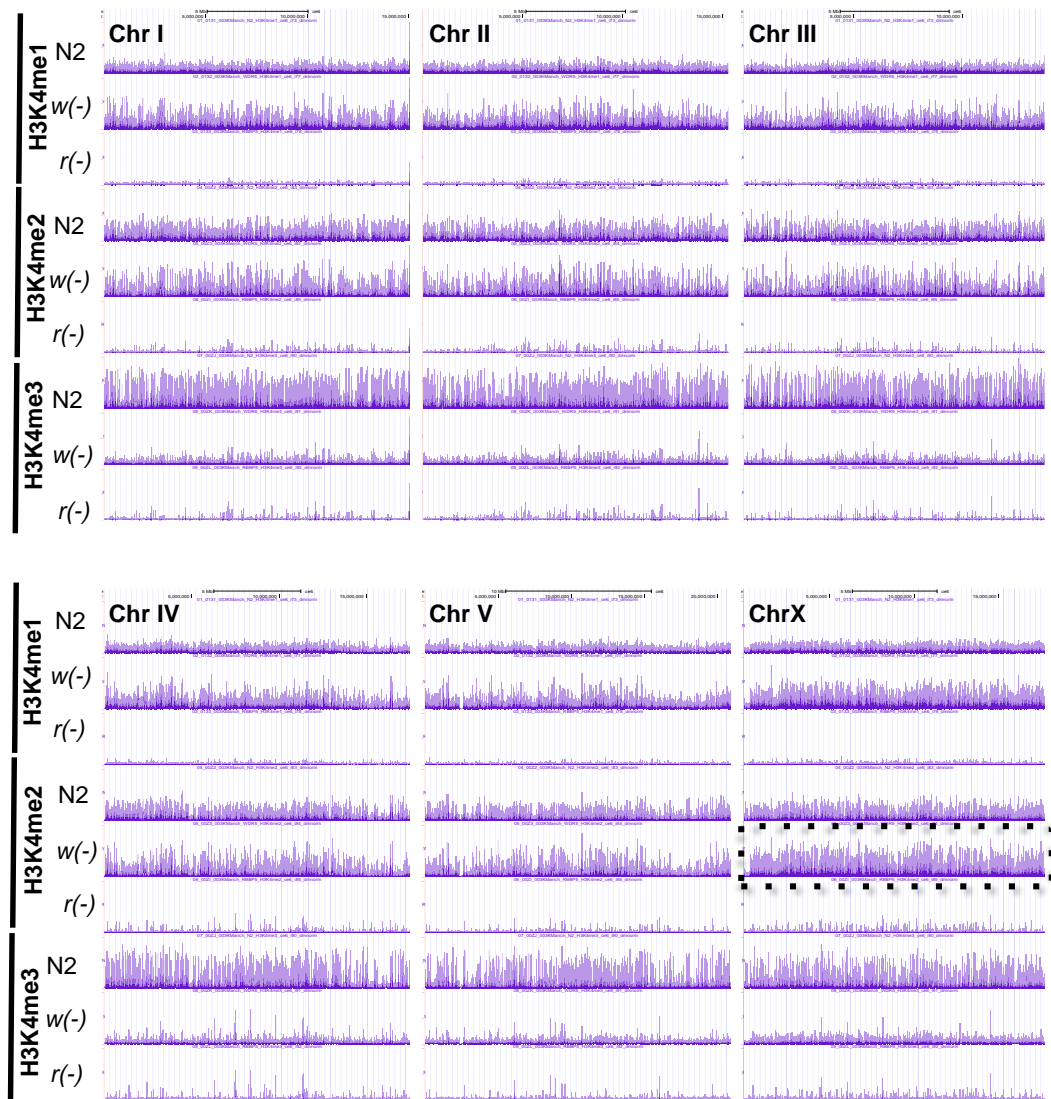
#### 4.3.2 Global levels of H3K4me1 increase in the absence of WDR-5

We found that WDR-5 and RBBP-5 regulate H3K4me1 differentially. *Wdr-5(-)* mutants display a global increase in H3K4me1 levels (Figure 4.2A). The overall number of active regions is increased by 183.5%, with 1,445 unique to the *wdr-5(-)* mutant (Table 4.2). Accordingly, the averaged levels of H3K4me1 at active regions increase by 1.8 folds relative to wild type. The increase is evident at promoters, gene bodies, and downstream of gene bodies (Figure 4.2A). Moreover, the total number of reads after normalisation, regardless of enrichment or not, is increased in the *wdr-5(-)* mutant (140.2%). These effects can be visualised at a whole genome scale using the UCSC genome browser (Figure 4.3). ChIP-qPCR at the same three loci as for H3K4me3 showed significant increase (~2 fold) in the H3K4me1 levels (Figure 4.2B). Immunofluorescence against H3K4me1 during embryogenesis did not detect the increase in the H3K4me1 levels found by ChIP-seq and ChIP-qPCR. We concluded that our immunofluorescence staining lacks in sensitivity to detect small increase in the global levels of H3K4me1. On the other hand, the *rbbp-5(-)* mutant display general reduction in the levels of H3K4me1 relative to wild type as detected by ChIP-seq, ChIP-qPCR, and immunofluorescence (Figure 4.2A-C). Thus, RBBP-5 is crucial to maintain the bulk of embryonic H3K4me1 and WDR-5 is essential to prevent excessive and global accumulation of H3K4me1.



**Figure 4.2 The global levels of H3K4me1 increase in the absence of WDR-5.**

(A) Spiked-in ChIP-seq shows that WDR-5 prevents excessive mono-methylation at H3K4. The levels of H3K4me1 are strikingly reduced in absence of RBBP-5. For detailed explanation see legend Figure 1. (B) UCSC genome browser screen shots from ChIP-seq data at three loci and ChIP-qPCR for these loci. The data show that H3K4me1 levels are increased significantly in the absence of WDR-5 but depleted by a lack of RBBP-5. Data were presented as fold enrichment calculated by normalising the values of percent input relative to H3. Percent input was calculated by  $100 \times 2^{\Delta Ct}$  (Ct total input – Ct sample). Data are represented as mean  $\pm$  SEM. (C) Immunostaining on embryos lacking WDR-5 or RBBP-5 showing their global contributions towards H3K4me1 during embryonic development. Embryos lacking WDR-5 appear not affected, but embryos lacking RBBP-5 are depleted in H3K4me1. DAPI staining is shown in grey tone and H3K4me1 in blue.



**Figure 4.3 Whole genome displayed by chromosomes as indicated**

The levels of H3K4me1/me2/me3 in three different backgrounds are represented by purple bars. The dotted box indicates the X chromosome levels of H3K4me2 in the absence of WDR-5. These were taken as screenshots from GeneBrowser.

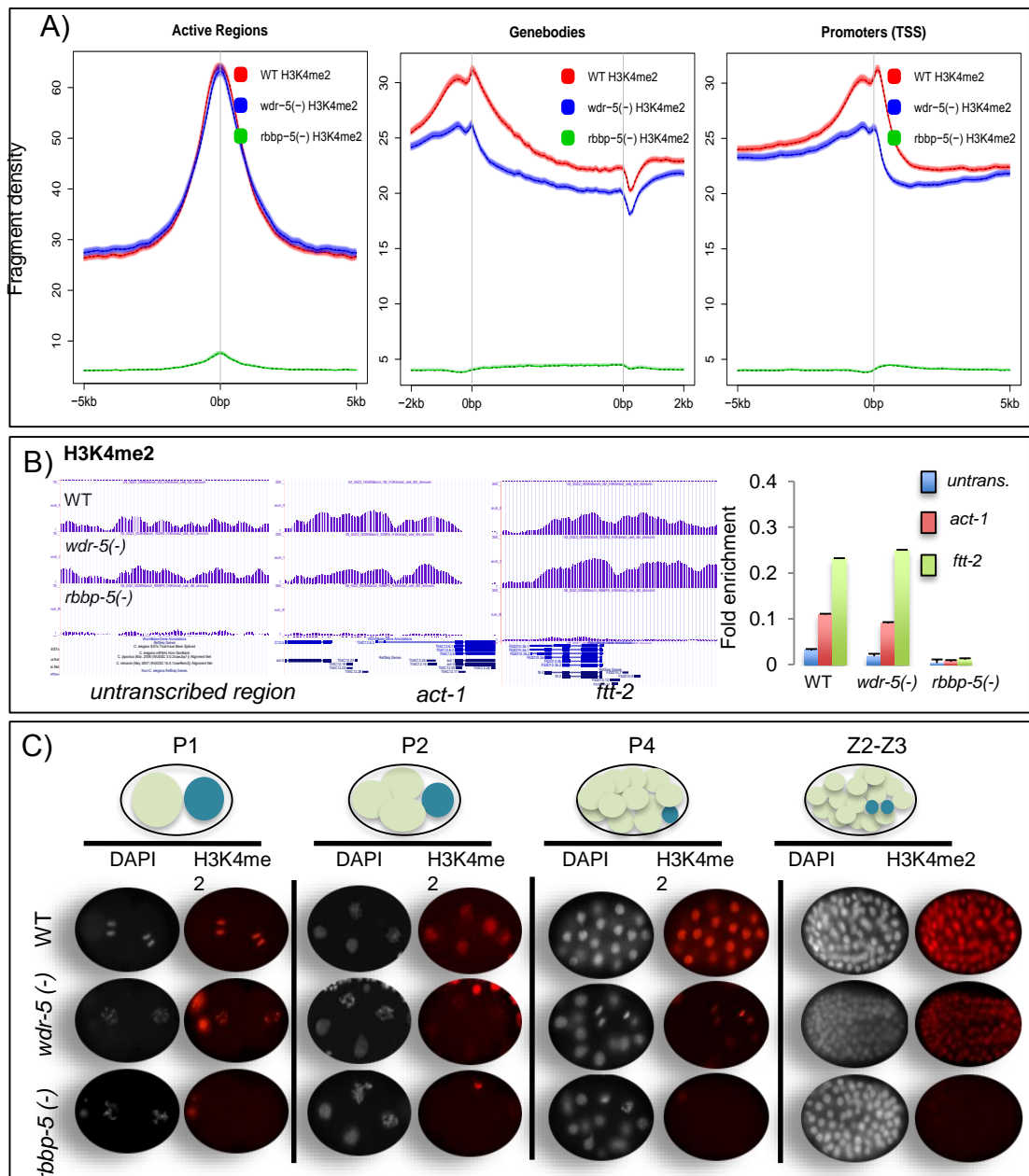
**Table 4.2 H3K4me1 at active regions**

N2	<i>wdr-5(-)</i>	<i>rbbp-5(-)</i>	Peaks	
YES	x	x	222	
x	YES	x	1,445	
YES	YES	x	1,244	
x	x	YES	193	
YES	x	YES	9	
x	YES	YES	92	
YES	YES	YES	89	
1,564	2,870	383	3,294	<b>TOTAL PEAKS</b>

YES indicates in which background(s) the active regions were counted from.

### 4.3.3 WDR-5 has a dual function toward H3K4me2

When analysing the levels of H3K4me2 in the absence of WDR-5 or RBBP-5, we uncovered a complex function for WDR-5. In the *wdr-5(-)* mutant, we found that the H3K4me2 levels at active regions are comparable to wild type. However, we found that the total number of active regions in *wdr-5(-)* mutants is reduced to 85% compared to wild type, suggesting that an increase in the levels of H3K4me2 occurs at some loci to produce comparable levels found in active regions between the *wdr-5(-)* mutant and wild type (Figure 4.4, Table 4.3). Moreover, if we focus the analysis at genic regions, we found that the levels of H3K4me2 are reduced compared to wild type (Figure 4.4A). Since active regions are found at both genic and intergenic regions, we can deduce that intergenic regions are displaying higher levels of H3K4me2 than genic regions in the absence of WDR-5. Importantly, these ChIP-seq data show that the effect that the absence of WDR-5 has on H3K4me2 enrichment is complex and depends on the genomic location implicated. ChIP-qPCR results at the previously described three loci for H3K4me2 show no significant effect in the absence of WDR-5 and match the ChIP-seq data displayed in the UCSC genome browser tool (Figure 4.4B). Immunofluorescence experiments show that the *wdr-5(-)* late embryos display reduced levels of H3K4me2 (Figure 4.4C). But, this reduction is more penetrant at earlier stages of embryogenesis (Figure 4.4C). The absence of RBBP-5 reduces the levels of H3K4me2 as detected by all three methods used herein (ChIP-seq, ChIP-qPCR, and immunofluorescence) (Figure 4.4A-C). In aggregate, these data have underpinned a dual role for WDR-5 in the acquisition of H3K4me2, indicating that it can promote as well as prevent the acquisition of H3K4me2 depending on the genomic location implicated.



**Figure 4.4 The levels of H3K4me2 are altered differentially in the absence of WDR-5.**

(A) Spiked-in ChIP-seq shows that the absence of WDR-5 alters di-methylation at H3K4 according to the genomic location. Active regions are not affected but genic regions show a decrease. The levels of H3K4me2 are strikingly reduced in absence of RBBP-5. For detailed explanation see legend Figure 1. (B) UCSC genome browser screen shots from ChIP-seq data at three loci and ChIP-qPCR for these loci. The data show that H3K4me2 levels are mostly unaffected in the absence of WDR-5. The H3K4me2 levels are depleted in the absence of RBBP-5. Data were presented as fold enrichment calculated by normalising the values of percent input relative to H3. Percent input was calculated by  $100 \times 2^{(Ct \text{ total input} - Ct \text{ sample})}$ . Data are represented as mean  $\pm$  SEM. (C) Immunostaining on embryos lacking WDR-5 or RBBP-5 showing their global contributions towards H3K4me2 during embryonic development. Embryos lacking WDR-5 or RBBP-5 are depleted in H3K4me2. In the case of *wdr-5(-)*, the effect is most apparent during early embryogenesis. DAPI staining is shown in grey tone and H3K4me2 in red.

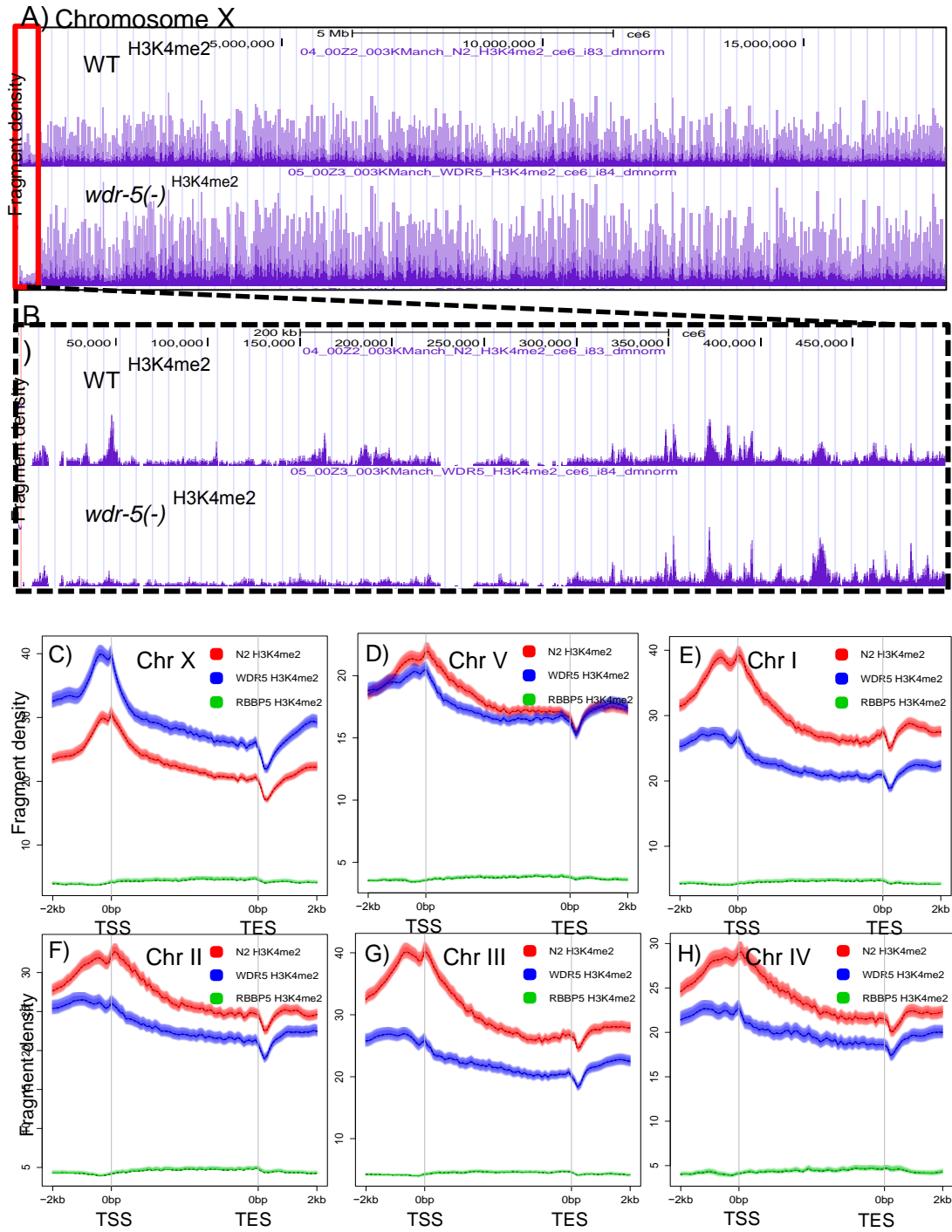
**Table 4.3 H3K4me2 peaks in active regions**

N2	<i>wdr-5(-)</i>	<i>rbbp-5(-)</i>	Peaks	
YES	x	x	1,521	
x	YES	x	986	
YES	YES	x	1,431	
x	x	YES	300	
YES	x	YES	103	
x	YES	YES	136	
YES	YES	YES	384	
3,439	2,937	923	4,861	<b>TOTAL PEAKS</b>

YES indicates in which background(s) the peaks were counted from.

#### 4.3.4 H3K4me2 levels increase on the chromosome X in the absence of WDR-5

The complex function that WDR-5 has on the acquisition of H3K4me2 motivated us to analyse more closely its distribution. We examined whether autosomes and the X chromosome could be differentially affected by the loss of WDR-5 or RBBP-5. We found an increase in the levels of H3K4me2 in the *wdr-5(-)* mutants spread out on almost the whole of the chromosome X relative to wild type (Figure 4.5A). An exception to this is on the extreme left region of chromosome X. A band of ~300 kb appears to be protected against excessive accumulation of H3K4me2 (Figure 4.5A and B). Interestingly, this band is enriched in H3K9me2/me3 in wild type embryos (Gerstein et al. 2010), suggesting that enrichment in H3K9me2/me3 blocks the excessive accumulation of H3K4me2. At a gene-by-gene level, we found that ~45% of the genes on the X chromosome (1,145 out of 2,487 genes) display H3K4me2 peak values higher than wild type in the absence of WDR-5. This is an effect specific to chromosome X, since the levels of H3K4me2 on chromosomes I, II, III, and IV are reduced when compared with wild type (Figure 4.5E-H). Little or no effect is found on chromosome V (Figure 4.5H). We did not detect a chromosome X effect for H3K4me1 or H3K4me3 in either *wdr-5(-)* or *rbbp-5(-)* backgrounds (data not shown and Figure 4.3). Taken together, these data show that WDR-5 acts at a chromosomal scale to dampen down the levels of H3K4me2 on the X.



**Figure 4.5 The levels of H3K4me2 are increased on the chromosome X.**

(A) The whole chromosome X is depicted from a UCSC genome browser screen shot with the levels of H3K4me2 in wild type (WT) and *wdr-5(-)* represented by purple bars along the chromosome (B) The left side of the chromosome X is protected from excessive di-methylation at H3K4. The dotted box indicates the first ~500 kb of the chromosome X. There is a decrease or no effect on the levels of H3K4me2 between wild type (WT) and *wdr-5(-)* for roughly the first ~300 kb. (C-H) WDR-5 prevents excessive accumulation of H3K4me2 on the chromosome X. Wild type, *wdr-5(-)*, and *rbbp-5(-)* backgrounds were analysed for the genomic distribution and abundance of H3K4me2 for each chromosome, as indicated. Transcription Start Sites (TSS) and Transcription End Sites (TES) are set respectively at 0 bp with  $\pm 2$ kb of flanking values. There is no effect on chromosome V and a reduction at genic regions on chromosomes I, II, III, and IV. All chromosomes are depleted in H3K4me2 in the absence of RBBP-5.

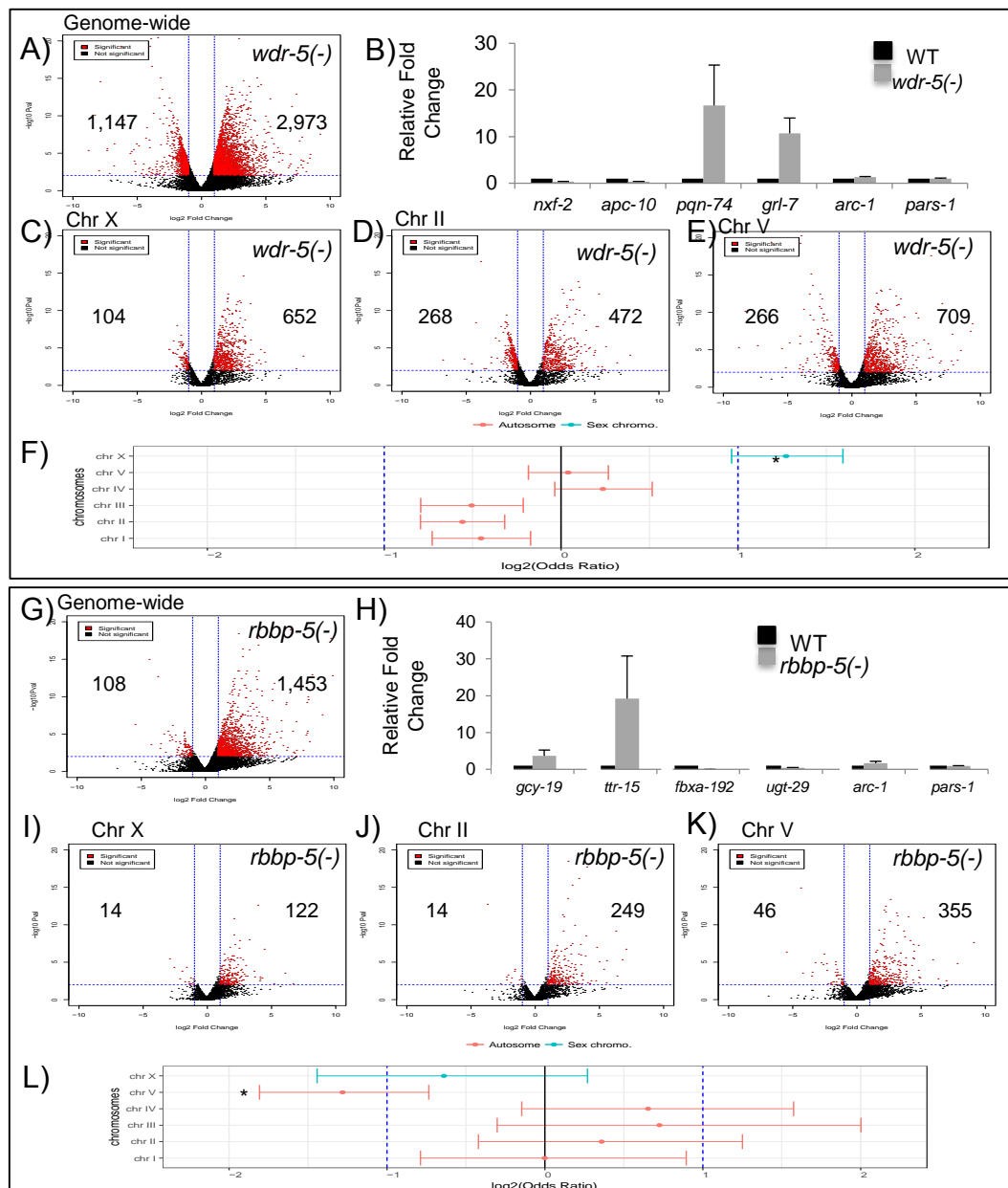


### 4.3.5 Differential expression is linked to specific chromosomes

Ablation of different members of the core complex has profoundly different effects on the levels of H3K4 methylation. To determine whether these different alterations in H3K4 methylation affect the respective transcriptomes differentially, we used RNA-seq. We found 4,120 differentially expressed genes between wild type and *wdr-5(-)* (Figure 4.6A ( $p < 0.01$  and fold change  $> 2$ )). For different cut offs see Table 4.4. Consistent with our RNA-seq, qRT-PCR showed similar trends to RNA-seq. In *wdr-5(-)* mutant, we detected an increase in expression for *pqn-74* and *grl-7*; a decrease in expression for *nfx-2* and *apc-10*; and no significant effect for *arc-1* and *pars-1* (Figure 4.6B). In *rbbp-5(-)* mutants, we found 1,561 differentially expressed genes compare with wild type (Figure 4.6G). QRT-PCR results are consistent with our RNA-seq data. We found an increase in expression for *gcy-19* and *ttr-15*; a decrease for *fbxa-192* and *ugt-29*; and no significant effect on *arc-1* and *pars-1* (Figure 4.6H). Since WDR-5 and RBBP-5 sit in the same MLL/SET/COMPASS complex, we would like to determine whether they have shared and/or specific targets. We compared the set of misregulated genes in absence of WDR-5 with the misregulated genes in absence of RBBP-5 from the RNA-Seq data. Out of the 4,120 genes targeted by WDR-5 and out of 1,561 RBBP-5 gene targets, 1,148 targets are shared between both WDR-5 and RBBP-5 (Table 4.5). Hence, since WDR-5 and RBBP-5 are components of the core complex, accordingly they share many of their targets.

We next assessed the number of genes up or down regulated in each mutant. We found more genes up regulated (2,973) in *wdr-5(-)* embryos than down regulated (1,147) (Figure 4.6A). The bias towards up regulation of gene expression is even more pronounced in absence of RBBP-5: 1,453 genes are up regulated compared to only 108 down regulated (Figure 4.6G). Thus, the absence of WDR-5 produces the most altered transcriptome with over 4,000 genes misregulated.

To examine whether differential expression is influenced by chromosomal location, we used Odds Ratios statistics. The Odds Ratios is calculated from the frequency of down regulated versus up regulated genes found at each chromosome relative to the genome wide frequency. In the *wdr-5(-)* mutant, we found that gene located on the chromosome X will tend to be up regulated far more frequently than the frequency observed across the genome (Figure 4.6C and F). The genes at the chromosome I to V are found at roughly the same frequency as the frequency found at the whole genome level (Figure 4.6D-F). Moreover, there is no overlap between the confidence intervals of autosomes and the chromosome X, indicating that this is a distinctive feature unique to chromosome X. We analysed similarly the *rbbp-5(-)* mutant. We found that genes located on the chromosome V tend to be down regulated more frequently than observed across the genome, indeed nearly half of the down regulated genes are found on chromosome V (Figure 4.6K and L). However, albeit statistically significant, the confidence interval overlaps with both chromosomes I and X and is as such not as distinctive as the chromosome X effect found in absence of WDR-5 (Figure 4.6F). Thus, our analysis shows that RBBP-5 and WDR-5 regulate gene expression preferentially on chromosome V and X, respectively. RBBP-5 tends to stimulate expression of genes on chromosome V and WDR-5 to dampen expression on the chromosome X.



**Table 4.4 Number of genes misregulated according to stringency levels.**

Up-R and Down-R indicates the number of genes up regulated and down regulated excluding the genes we considered silenced (Sil.) and desilenced (Desil.). These genes with less than 10 normalised counts are considered not expressed and this is used to form the silenced and desilenced categories.

Mutant	Stringency level		Up-R	Down-R	Sil.	Desil.	Total
	p-val	fold change					
<i>wdr-5(-)</i>	<0.01	≥2	2714	1103	44	259	4120
	<0.01	≥1.5	3024	1659	44	259	4986
	<0.05	≥2	3373	1259	62	434	5128
	<0.05	≥1.5	3963	2882	62	434	7341
<i>rbbp-5(-)</i>	<0.01	≥2	1263	105	3	190	1561
	<0.01	≥1.5	1460	127	3	190	1780
	<0.05	≥2	1945	170	6	383	2504
	<0.05	≥1.5	2499	371	6	383	3259

**Table 4.5 WDR-5 and RBBP-5 have both shared and specific gene targets**

	WDR-5	RBBP-5
Total number of genes	4120	1561
Specific targets	2972	413
Shared	1148	

#### 4.3.6 H3K4me2 de novo peaks on the chromosome X are associated with up regulation of gene expression

To address whether the altered levels of H3K4 methylation in *wdr-5(-)* and *rbbp-5(-)* mutants correlate with changes in gene expression, we analysed our RNA-seq and ChIP-seq data using Odds Ratio statistics (see Methods). For each mutant, we calculated the frequency of down regulated versus up regulated genes found at 18 specific genomic features relative to the genome wide frequency. These 18 genomic features are comprised of de novo H3K4me1/me2/me3, loss of H3K4me1/me2/me3 peaks found at three possible genomic locations (upstream of gene bodies, in gene bodies, and downstream of gene bodies).

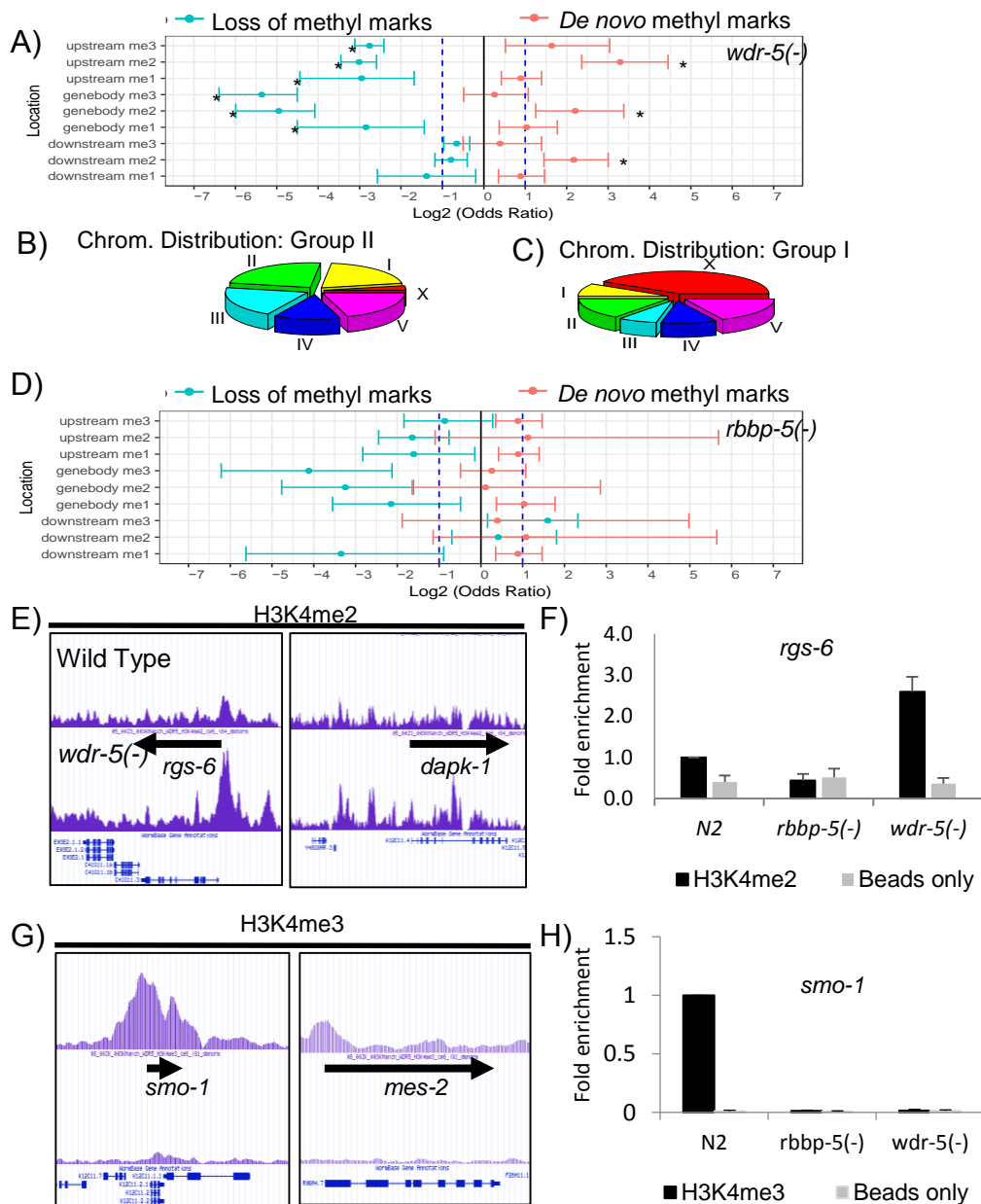
The analysis shows that WDR-5 regulated genes segregate into two groups. In group I, a population of genes that tends to be up regulated is linked to de novo H3K4me2, but not to de novo H3K4me1 or me3 (Figure 4.7A; in red). This de novo H3K4me2 associated with up regulation of gene expression is independent of the genomic locations because it is found upstream of gene bodies, in gene bodies, as well as downstream of gene bodies (Figure 4.7A; in red). In group II, a population of genes down regulated is linked to the loss of H3K4me1, me2, or

me3 peaks (Figure 4.7A; in blue). However, this loss of H3K4me1/me2/me3 associated with down regulation of gene expression is found upstream of gene bodies and in gene bodies (Figure 4.7A; in blue). This indicates that the genomic location at which these H3K4me1/me2/me3 peaks are lost is determinant because no association is found downstream of gene bodies (Figure 4.7A; in blue).

For both group I and II, we analysed whether the associated genes display enrichment at a particular chromosome. In group II, which shows an association with down regulation of gene expression and loss of H3K4me1/me2/me3, we found that the chromosome X is under represented (Figure 4.7B). In contrast, in group I, which shows an association with up regulation of gene expression and de novo H3K4me2, the X chromosome is over represented. The *rbbp-5(-)* mutant did not display enrichment in regards to de novo H3K4 methylation (Figure 4.7D; in red). The loss of H3K4 methyl marks bare no significance because the number of genes down regulated per genomic features is too low (Figure 4.7D; in blue). Thus, there no correlation between changes in gene expression and alterations in the levels of H3K4 methylation could be established in the absence of RBBP-5.

Two examples of de novo H3K4me2 are shown using the UCSC genome browser at *rgs-6* (regulator of G protein signalling) and *dapk-1* (death associated protein kinase) loci (Figure 4.7E). These genes display an increase in levels of mRNA expression [3.9 and 2.1 fold, respectively (Supplementary Table 1)]. ChIP-qPCR against H3K4me2 at the *rgs-6* locus confirmed an increase in H3K4me2 levels (Figure 4.7F). Two examples in loss of H3K4me3 peaks are shown using the UCSC genome browser at *smo-1* and *mes-2* loci (Figure 4.7G). These genes display a concurrent reduction in their expression [2.6 and 2.1 fold, respectively (Supplementary Table 1)]. ChIP-qPCR against H3K4me3 at the *smo-1* locus confirmed the decrease in H3K4me3 levels (Figure 4.7H).

Taken together, these experiments show that WDR-5 regulated levels of H3K4 methylation impact on activation of gene expression in two ways. The loss of H3K4me1/me2/me3 peaks associates with down regulation of gene expression and the acquisition of H3K4me2 de novo peaks associates with up regulation in of gene expression. Interestingly, most H3K4me2 de novo peaks associated with up regulated transcription are found on the chromosome X and most H3K4me1/me2/me3 lost peaks associated with down regulated transcription are on autosomes.



**Figure 4.7 Correlation between the H3K4 methylation states at specific genomic features and gene expression.**

(A) The presence of de novo H3K4me2 peaks and the loss of H3K4me peaks (produced in the absence of WDR-5) are associated with up and down regulated genes, respectively. Odds ratio statistics was used to analyse whether the presence of de novo H3K4 methylation (red) and the loss of H3K4me peaks (blue) are associated with an effect on gene expression. Each peak was assigned a position: upstream of gene body, gene body, or downstream of gene body as indicated on the Y axis. The statistical significance is set at  $p$ -value  $< 0.001$  and  $\pm 1 \log_2$  (Odds Ratio) as indicated by asterisks and dotted lines, respectively. Whiskers indicate the 95% CI (confidence interval). A positive Odds ratio indicates a bias towards up regulation of gene expression and a negative ratio towards down regulation of gene expression. (B) Genes on the chromosome X are underrepresented compared to genes on the autosomes. The 401 genes associated with down regulation of gene expression, as indicated by a negative  $\log_2$  (Odds Ratio), were assigned to their respective chromosomes. (C) Genes on the chromosome X are over represented compared to genes on the autosomes. The 399 genes associated with up regulation of gene expression, as indicated by a positive  $\log_2$ (Odds Ratio), were assigned to their respective chromosomes. (D) There is no correlation between de novo or loss of H3K4 methyl marks and gene expression. Odds ratio statistics was used as in panel A. The confidence interval in absence of RBBP-5 is larger due to fewer misregulated genes than in the absence of WDR-5. (E) Screen shots from the UCSC genome browser showing an increase in the levels of H3K4me2 at two genes (*rgs-6* and *dapk-1*). (F) ChIP-qPCR experiments showing a decrease in the levels of H3K4me2 in the *rbbp-5(-)* mutant but an increase in the *wdr-5(-)* mutant. ChIP-qPCR was performed from

three independent biological samples in triplicates. Fold enrichment was calculated by normalising the values of percent input relative to H3. Percent input was calculated by  $100 \times 2^{(Ct \text{ total input} - Ct \text{ sample})}$ . Data are represented as mean  $\pm$ SEM. Beads only is the omission of antibody and represent an estimate of the background ChIP. (G) Screen shots from the UCSC genome browser showing a decrease in the H3K4me3 levels at two genes (*smo-1* and *mes-2*). (H) ChIP-qPCR experiments showing a decrease in the levels of H3K4me3 in either the *rbbp-5(-)* or the *wdr-5(-)* background. ChIP-qPCR was performed as in panel F.

#### **4.3.7 Genes up regulated and associated with de novo H3K4me2 are enriched for neuron functions**

Our association study between altered levels of H3K4 methylation and regulation of gene expression has identified 800 differentially expressed genes forming two groups: group I (399 genes) and group II (401 genes). To determine whether there is any specific functions associated with these two groups, we performed Gene Ontology analysis on each set of genes. The group I genes, of which 41% of these are located on the chromosome X (Figure 4.7C), are involved in processes such as signal transduction, synaptic transmission, and behaviour (Supplementary Table 2). The gene products tend to be found at the plasma membrane and the cilium, a structure found in sensory neurones. The group II genes, mostly found on autosomes (Figure 4.7B), are enriched for processes such as reproduction, embryonic development, chromosomal organisation, and DNA replication as well as associated with the spliceosome and proteins containing the F box motif involved in protein degradation (Supplementary Table 2). The exceptionally strong enrichment for F-box containing proteins suggests a link with proteostasis. In aggregate, Gene Ontology analysis of the *wdr-5(-)* mutant reveals that group I is a neuro-enriched group of up regulated genes coinciding with de novo H3K4me2 peaks. Group II is a development-enriched group of down regulated genes associated with the loss of H3K4me peaks.

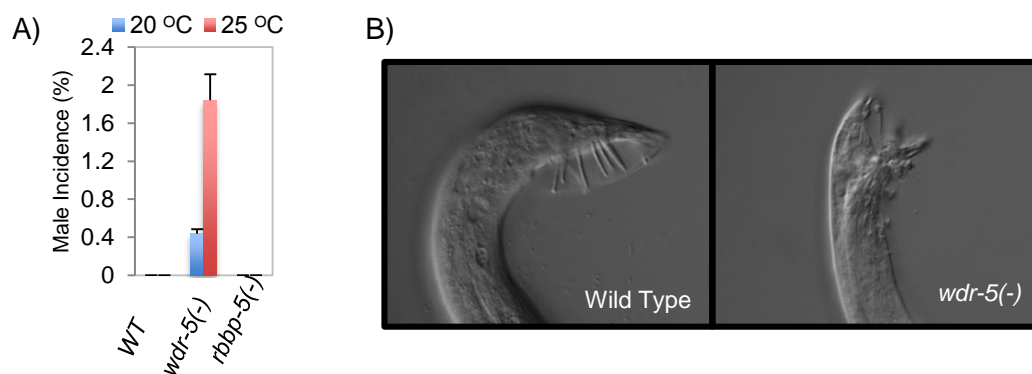
#### **4.3.8 The absence of WDR-5 increases male incidence**

Chromosome-wide up regulation of gene expression on the X chromosome is an indicator of a dosage compensation problem. Dosage compensation is the mechanism by which gene expression on sex chromosomes is balanced between genders. In *C. elegans*, dosage compensation and sex determination are triggered by the same signal, the ratio of X chromosomes to sets of autosomes. Thus, dosage compensation and sex determination are two interwoven processes. This is reflected in the Dosage Compensation Complex composition, which involves components that regulate both dosage compensation and sex determination, such as XOL-1, SDC-2, and HER-1.

We first examined whether the genes up regulated on chromosome X in the absence of WDR-5 are genes regulated by the dosage compensation complex (DCC). From an analysis based on a study from Kramer et al. (Kramer et al. 2015), we identified 241 DCC regulated genes (J. Semple, personal communication). 66 of those (~28%) are up regulated in the absence of WDR-5. This result shows an overlap between WDR-5- and DCC-regulated genes. It also suggests that a large

number of up regulated genes on chromosome X (>500 genes) appears dosage compensated yet not under the regulation of the DCC.

We next asked whether sex-enriched genes identified by transcription profiling (Thoemke et al. 2005) and located on the X chromosome are also up regulated genes in the absence of WDR-5. We found that ~30% of genes (11/37) differentially expressed between male and hermaphrodite larvae are up regulated in the *wdr-5(-)* mutants. This result prompted us to directly assess whether sex determination is affected in the absence of WDR-5. To this end, we scored large populations of nematodes for males. For the *wdr-5(-)* mutant, the incidence of males is of 0.44% (n=4034; Figure 4.8A). We did not observe any males in either wild type (n=3670; pval=0.00014) or *rbbp-5(-)* mutants (n=2474; pval=0.0021). We also examined the incidence of males at 25°C and found a 4-fold increase, reaching an average of 1.8% (n=2591) for the *wdr-5(-)* background. No males were found in wild type (n=2227; p=6.8e-10) or *rbbp-5(-)* backgrounds (n=2117; p=1.8e-9) (Figure 4.8A). DIC microscopy shows that the *wdr-5(-)* males display defects in the fan and ray structures (Figure 4.8B). The absence of males in the *rbbp-5(-)* mutants suggests that the higher than normal incidence of males in the *wdr-5(-)* mutants is not caused by a generic defect in chromosomal segregation. Taken together, the up regulation of gene expression on the chromosome X and the increase in incidence of males indicate that WDR-5 contributes positively to dosage compensation and appropriate sex determination.



**Figure 4.8 Incidence of males is increased in the absence of WDR-5.**

(A) Large populations were analysed for the presence of males. At 20°C, 3670 wild type, 4037 *wdr-5(-)*, and 2473 *rbbp-5(-)* animals were counted and 18 males were found in the *wdr-5(-)* background as indicated. At 25°C, 2227 wild type, 2591 *wdr-5(-)*, and 2117 *rbbp-5(-)* were counted and 46 males were found in the *wdr-5(-)* background as indicated. Data are represented as mean percentage of male occurrence  $\pm$  SEM. The experiments were independently repeated at least three times. (B) DIC image showing the tails of wild type and *wdr-5(-)* males. The tails of *wdr-5(-)* mutants display notable abnormalities in the fan and rays.

## 4.4 DISCUSSION

Modifications on histones are highly repeated on each chromosome. Their enrichment and under-enrichment create peaks, troughs, and plains defining what is often referred to as the epigenetic landscape. The role of WDR-5 and RBBP-5 in the genome distribution and abundance of methyl marks at H3K4 and hence their contributions towards the epigenetic landscape had yet to be explored in metazoans. Herein, we used spiked-in ChIP-seq and RNA-seq technologies in *C. elegans* embryos and revealed unsuspected functions unique to WDR-5 such as preventing excessive methylation at H3K4.

### 4.4.1 WDR-5 prevents deposition of mono-methyl marks at H3K4

This work has revealed that WDR-5 can prevent global and excessive accumulation of H3K4me1. This result suggests that a core complex comprised of RBBP-5 and ASH-2 is sufficient to stimulate the deposition of methyl marks at H3K4. In support for an active core complex minus WDR-5 is a recent structural study, which has identified a 'minimized human RBBP5/ASH2L heterodimer'. This RBBP5/ASH2L heterodimer is sufficient to activate most enzymes known to associate with the complete core complex (Li et al. 2016). Thus, one possibility to explain the global and excessive mono-methylation at H3K4 is a lack of regulation towards a core complex lacking WDR-5.

There is also the possibility that WDR-5 could antagonise the deposition of H3K4me1. Indeed, a number of studies have shown that WDR5 inhibits MLL3, an H3K4 monomethyl transferase (Herz et al. 2012; Hu et al. 2013; Shinsky & Cosgrove 2015). A possible MLL3/4 homologue in *C. elegans* is SET-16 (Fisher et al. 2010; Smith et al. 2011). Thus, the global increase in H3K4me1 levels could come from the erroneous activation of SET-16, or another H3K4 monomethyl transferase yet to be identified, due to a lack of WDR-5. However, we cannot rule out other possibilities such as impaired recruitment of H3K4 demethylases, increased enhancer transcription (Kaikkonen et al. 2013; Ostuni et al. 2013), and incapacity to transform H3K4me1 into H3K4me3.

### 4.4.2 WDR-5 prevents deposition of di-methyl marks at H3K4; an early defect in spermatogenesis?

Excess H3K4me2 is different from H3K4me1 because it mostly targets the chromosome X. The chromosome X differs from autosomes in many aspects (Strome et al. 2014). It is poor in essential genes (Kamath et al. 2003), transcriptionally inactive in germlines (Kelly et al. 2002), dosage compensated (Meyer 2010), and paternally imprinted via meiotic sex chromosome inactivation (Arico et al. 2011). In the gametes, the paternal X (Xp) is transcriptionally inactivated and depleted in the levels of H3K4me2, in contrast the maternal X (Xm) is enriched in H3K4me2 and transcriptionally active. This differential pattern in H3K4me2 levels of gametes is maintained in the early embryo, but at around 24-cell stage this distinction between Xp and Xm is lost. Thus, the embryo inherits two X chromosomes with strikingly different transcriptional and epigenetic



histories (Strome et al. 2014). Our CHIP-seq data show an increase in the levels of H3K4me2 mostly directed on the chromosome X, in the absence of WDR-5. It is possible that this defect occurs early, perhaps during spermatogenesis. This would imply that the accumulation of H3K4me2 on chromosome X could persist until late embryogenesis. There is a precedent for histone methylation mitotic heritability. H3K27me3 in sperms can resist several rounds of replication cycles in *C. elegans* embryos (Gaydos et al. 2014), perhaps H3K4me2 also has this ability.

#### **4.4.3 WDR-5 prevents deposition of di-methyl marks at H3K4; a dosage compensation defect?**

Excessive accumulation of H3K4me2 could as well be a consequence of aberrant transcription caused by a defect in the dosage compensation complex. It has previously been shown that a component of the core SET/COMPASS/MLL complex, DPY-30, is also part of the dosage compensation complex (Pferdehirt et al. 2011). Dosage compensation is a mechanism to ensure that both sexes express similar levels of transcription of genes located on chromosome X. In *C. elegans* hermaphrodites, both X chromosomes are transcriptionally dampened by 50% to express genes at the same levels as in males, which have only one chromosome X. WDR-5 does not physically interact with the dosage compensation complex, however, its absence may disrupt the stoichiometry of the other subunits (ASH-2 and DPY-30) part of both the dosage compensation and the core SET/COMPASS/MLL complexes. This would lead to an increase in gene expression on the chromosome X.

#### **4.4.4 WDR-5 contributes to dosage compensation and sex determination**

The dosage compensation and sex determination pathways share key components such as XOL-1, SDC-2, and HER-1, of which two, *xol-1* and *sdc-2*, are down regulated by ~2 fold in the absence of WDR-5 (Strome et al. 2014). We also show that the absence of WDR-5 increases the incidence of males (Figure 4.8) and up regulates gene expression on chromosome X, indicating that WDR-5's function could be at the intersection of these two pathways. However, the complete elimination of the dosage compensation complex is lethal in hermaphrodites (Dawes et al. 1999) and a partial defect produces the dumpy phenotype. These phenotypes are not observed in *wdr-5(-)* animals. In fact, the *wdr-5(-)* mutants live longer and is generally healthy (Greer et al. 2010). Nevertheless, the increase in the incidence of males and the up regulation of >650 genes on chromosome X are highly significant. In addition, in line with the higher than normal incidence of males, *wdr-5(-)* hermaphrodites raised at 25°C have been reported to display a masculinisation of the germline phenotype (Li & Kelly 2011). Taken together, these data provide strong evidence that WDR-5 contributes positively towards appropriate dosage compensation and sex determination.

In conclusion, our data show that WDR-5 is a key player in promoting the acquisition of H3K4me3 and of H3K4me2 at genic regions. Unexpectedly, WDR-5 also prevents excessive accumulation of H3K4me2 at a chromosomal-scale on X. This de novo acquisition of H3K4me2 is associated with increased gene expression. Interestingly, the H3K4 methylation mark that associates the strongest with regulation of gene expression is H3K4me2, since both H3K4me2 depletion and its de novo occurrence are consistent with a role in active transcription. A limitation in our study is we have not looked into any possible correlation between our ChIP-seq/RNA-seq data and known ageing genes. It will be an interesting field of investigation for future researchers.

## **Chapter 5**

### **Design and implementation for harvesting *C. elegans* embryos from large-scale solid culture media**

## Chapter 5 : Design and implementation for harvesting *C. elegans* embryos from large-scale solid culture media

### 5.1 Abstract

*C. elegans* can be propagated either in liquid media in flask or on solid in plates at small scale. However, only liquid media techniques have been developed for large-scale propagation of *C. elegans*. Maintaining the technique for culturing worms can minimise any variations from the usual method of worm maintenance that may influence the biological process, development or gene expression of the worms. I have designed and implemented a new protocol for harvesting large volume of *C. elegans* embryos from solid culture. In this chapter, I present the required material, workflow for growing worms on solid medium, and series of experimentations for harvesting large amount of synchronised *C. elegans* embryos with a majority of population at >100-cell stage. Using this newly developed method, a large volume of worm embryos (0.5 ml to 1.0 ml) were reliably harvested suitable for use in all of the ChIP-Seq and ChIP-qPCR analyses as described previously in Chapter 4.

KEYWORDS: Large-scale, *C. elegans*, amplification, synchronised, solid culture, Nematode Growth Medium (NGM), chromatin immunoprecipitation.

### 5.2 Introduction

Model organisms have prominent roles in understanding basic, molecular and cellular biology as well as to making advances in these fields. The non-parasitic nematode, *C. elegans*, has been identified as a model organism for pursuing various fields for instance in developmental, molecular and neuro biology. Many disease pathways and cellular as well as molecular complexity are conserved between *C. elegans* and higher organisms like *Homo sapiens*. Since *C. elegans* is a very small organism, it is convenient to culture them in lab. In general, there are two techniques for culturing worms in laboratory: Liquid culture and solid medium.

I have constantly been using *C. elegans* embryos as my study model. I have analysed H3K4 methylation levels, using Western Blot, in mutants lacking core components of the MLL/SET/COMPASS complex, which is responsible for regulating H3K4 methylation levels. The wild type N2 (Bristol) and the mutants used in the study were *rbbp-5(-)* (*tm3463*) and *wdr-5(-)* (*ok1417*). We have also used the same mutants to measure lifespan and evaluate gene expressions by means of RNA-Seq method and quantitative real time PCR. The *C. elegans* served as the perfect model organism since its MLL/SET/COMPASS complexes are highly conserved to the complexes found in human and other organisms. All of my experiments were done on solid Nematode Growth Medium (NGM) at small-scale worm amplification. The amplification was usually done on 30 mm or 55 mm NGM plates seeded with *E. coli* OP50.

I next aimed to embark on a study dedicated to mapping the landscape of H3K4 methylation attributed to RBBP-5 and WDR-5 of the MLL/SET/COMPASS complexes. To do so, I would pull down all DNA fragments interacting with H3K4me1/me2/me3 in wild type, *rbbp-5(-)*, and *wdr-5(-)*

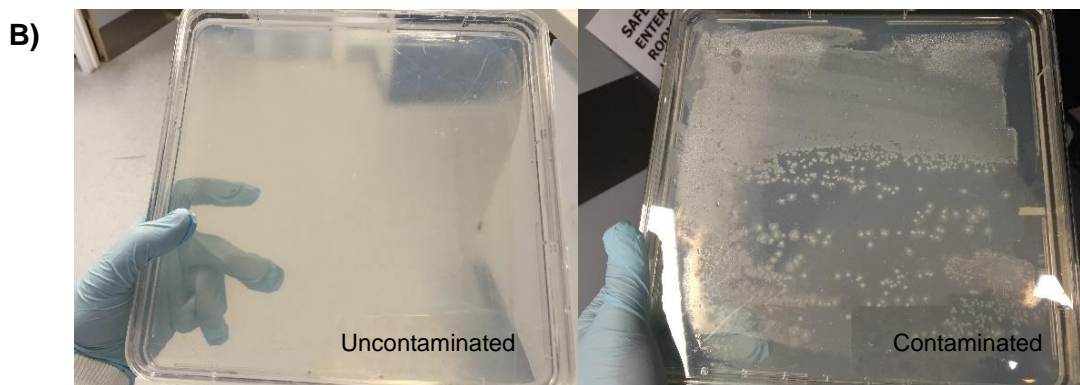
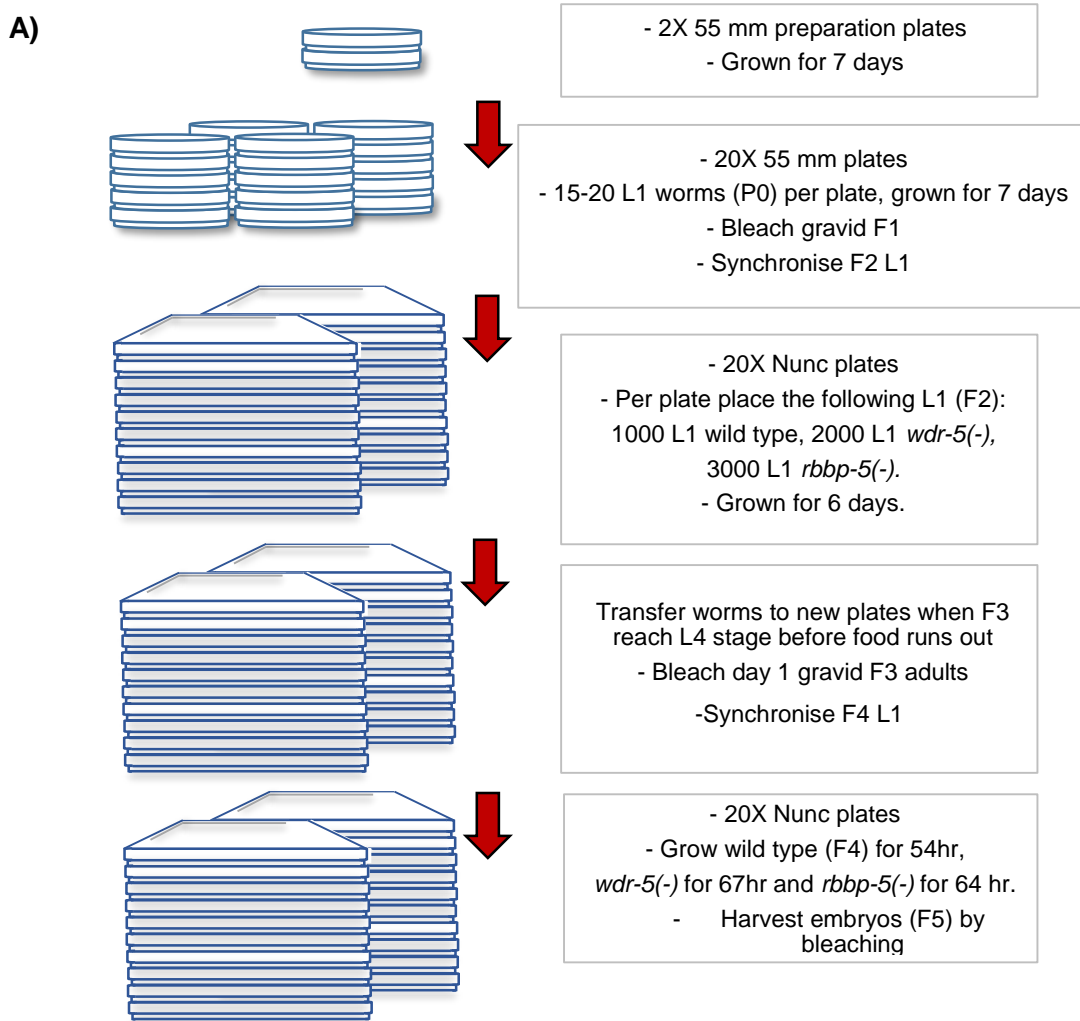
background by using chromatin immunoprecipitation (ChIP) technique. Then, I would analyse and map the DNA fragment by using next generation sequencing (ChIP-Seq). However, it is important to note that a large scale *C. elegans* culture is required for ChIP sample preparation for *C. elegans*. Thus far, protocols for growing large-scale *C. elegans* have been developed only for liquid culture. The protocol for large-scale amplification in liquid culture is considerably straightforward. Worms are basically grown in large swirling flasks containing 500 ml of liquid media (S-Medium, 1X PSN antibiotics, 1X nystatin antifungal), seeded with concentrated *E. coli* OP50 or other strains such as HB101 as the food source and grown at 20 °C in an incubator shaking at 100 rpm (Lewis & Fleming 1995; Ercan et al. 2007). However, growing worms in liquid culture may introduce different oxygenation and environmental stresses to the worms, as worms grown in liquid culture tend to thinner and more elongated (Lewis & Fleming 1995; Rahmani et al. 2015).

Hence, I designed and implemented a new protocol for growing large-scale *C. elegans* on solid medium.

## 5.3 Results

### 5.3.1 Preparation of Nunc dishes

Large-scale *C. elegans* amplification is commonly performed in large flasks. In my study, the worm amplification was performed on solid media using 55 mm petri dishes and 245 mm x 245 mm x 25 mm Nunc dishes. The preparation of Nunc dishes comprises of three important steps: the sterilisation, media preparation and seeding with concentrated *Escherichia coli* OP50. Plate contamination can be reduced by cleaning the dishes with a multi-purpose disinfectant (Virkon), drying and ultra violet cross-linking at 265 nm with energy dose of 0.400 J/cm<sup>2</sup> (Fisher Scientific UV Crosslinker FB-UVXL-1000). Short wave UV light at approximately 254 nm has been shown to have strong sterilisation effect and can effectively kill microorganisms by disrupting their nucleic acids (Soloshenko et al. 2000; Kubyshkina et al. 2011). To each dish, 200 ml of nematode growth medium (NGM) (0.05 M NaCl, 0.25 % (w/v) bacto-peptone, 1.7 % (w/v) agar, 1 mM CaCl<sub>2</sub>, 12.9 µM cholesterol, 1 mM MgSO<sub>4</sub>, 25 mM KH<sub>2</sub>PO<sub>4</sub> PH6.0) was poured in a sterile flow hood and set to dry. Finally, 0.5 ml of 20X OP50 were pipetted to each plate and spread using a cell spreader. Each strain amplification requires three batches of plate preparation, with each batch having at least 20 dishes. My study involves the use of P0 to F5 worm generations. The first batch of at least 20 dishes were for the amplification of F2 worms, second batch for F3 and third batch for F4 generation as shown in the schematic workflow in Figure 5.1. Hence, in total, NGM were prepared on at least 60 Nunc dishes for each strain amplification for chromatin immunoprecipitation study.



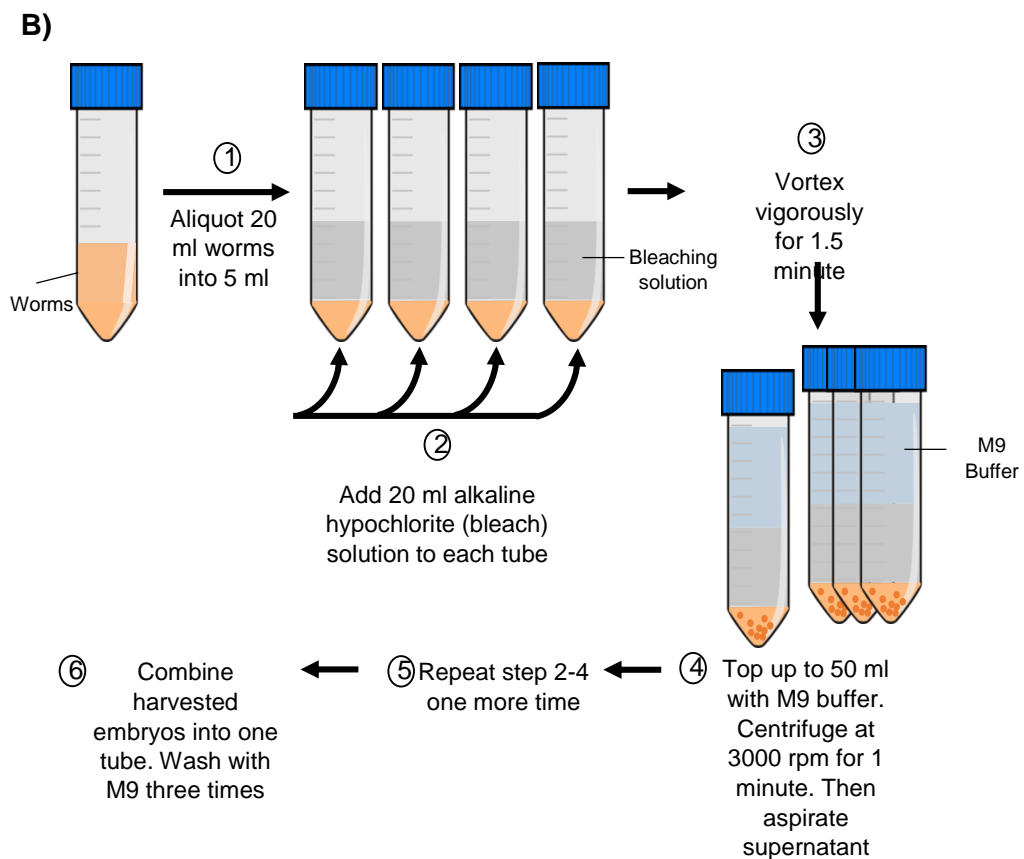
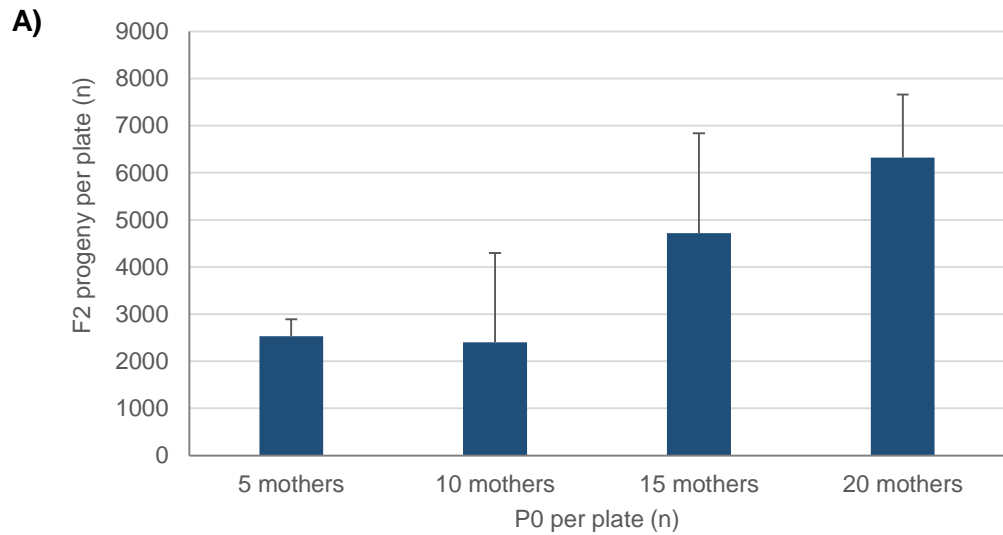
**Figure 5.1 Schematic workflow for preparation of plates and dishes for the large-scale amplification of *C. elegans* on solid nematode growth media**

(A) Worms were grown on Nematode Growth Media (NGM) in 55 mm petri plates and 245 mm x 245 mm Nunc dishes. Each of the Nunc plate were seeded with 0.5 ml of 20X concentrated OP50. (B) Representative image of clean (uncontaminated) plate used in the worm propagation and contaminated plate, which were discarded.

### 5.3.2 Amplification of *C. elegans* grown on solid culture media

In the early series of experiments, I determined the amplification technique for harvesting massive amount of *C. elegans* from solid Nematode Growth Media (NGM). I established worm amplification factor from P0 to F2 generation, sets of 5, 10, 15 and 20 L1 (P0) wild type were grown on 6 cm plates for 7 days. Their gravid L1 (F1) progenies were bleached and then synchronised L1 of F2 generation were counted. I discovered that approximately 5000 F2 generation can be harvested from 15 to 20 P0 mothers grown on solid media (Figure 5.2A). Accordingly, I developed a large-scale worm amplification technique as illustrated in Figure 5.1. The strains used in this experiment were wild type N2, *rbbp-5(-) (tm34643)* mutants and *wdr-5(-) (ok1417)* mutants. Approximately 15-20 L1 (P0) of each strain, harvested from preparation plates, were placed on each of twenty 6 cm and grew for 7 days until F1 worms reached day 1 adult stage. Then the F1 gravid mothers were bleached to harvest F2 embryos. The *wdr-5(-)* and *rbbp-5(-)* mutants have smaller brood size compared to the wild type (Wang et al. 2011). According to the amplification factor (Figure 5.2A) and the brood size of the mutants, I could obtained approximately 100,000 wild type, 50,000 *wdr-5(-)* and 25,000 *rbbp-5(-)* in total. Next, on twenty Nunc plates, I transferred L1 (F2) larvae and cultured for 6 days (1000 for wild type, 2000 for *wdr-5(-)* and 3000 for *rbbp-5(-)* per plate due to their different brood size) (Wang et al. 2011). To avoid running out of food, I transferred F3 at L4 stage to fresh Nunc plates, bleached them the day after, and harvested embryos (F4). Synchronised L1 of F4 generation were placed on new 20 Nunc plates before they were bleached at day 1 adult to harvest their embryos (F5). Approximately 0.5 ml to 1 ml embryos can be obtained by this method.

I also assessed bleaching and embryo synchronisation techniques. Large scale culture produces approximately 15 to 20 mL total worm pellet, hence, it requires alteration in the bleaching technique. I divided equally the worm pellet into 5 mL in each of a 50 mL falcon tube (Figure 5.2B). The tube was added with 20 mL of alkaline hypochlorite (bleach) solution, vortexed for 1.5 minutes, topped up with M9 buffer to 50 mL, centrifuged at 3000 rpm for 1 minute, and supernatant was removed by aspiration. The bleaching to aspiration steps were repeated one more time and then eggs were collected and washed three times with M9 buffer. Approximately 0.5 to 1 mL of F5 embryo pellet were obtained. I encountered that the bleached embryos tended to clump together if synchronised in liquid growth media (M9) on a rocker at 20°C, even if the embryos were diluted. Synchronisation is highly effective if embryos were diluted in 2 ml M9 buffer, spread on two unseeded Nunc plates, and left overnight at 20°C to hatch.



**Figure 5.2 Propagation of *C. elegans* on solid culture containing NGM**

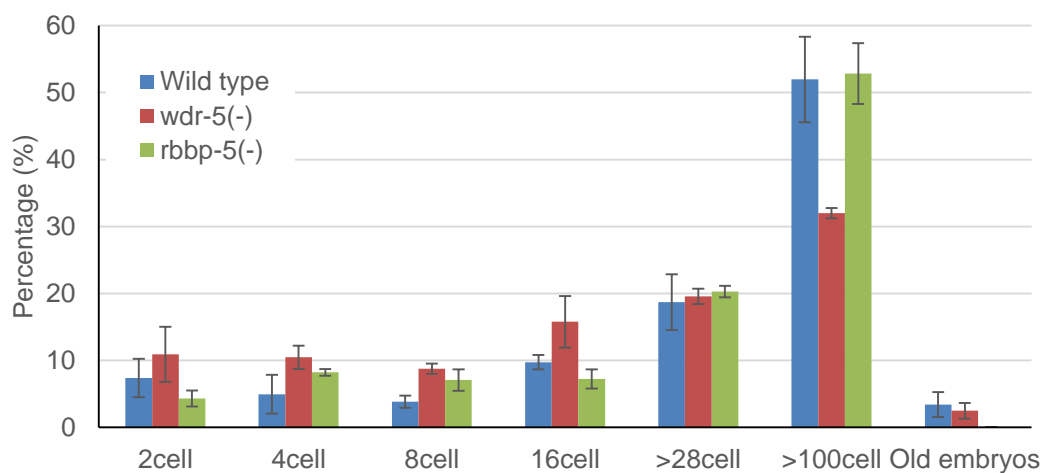
(A) Amplification factor of P0 wild type hermaphrodites to F2 progeny. (B) Modified bleaching technique for harvesting embryos from large volume of worms.

### 5.3.3 Harvesting synchronised embryos

The next experiment aimed to evaluate the synchronised embryos that I have harvested. I first defined conditions for the *C. elegans* embryos for my chromatin immunoprecipitation analysis. Proliferation stage of early embryogenesis produces several developmental stages such as P0 (1 cell), P1 (2 to 3 total cells in an embryo), P2 (4 to 7 cells), P3 (8 to 15 cells), P4 (16 to 100



cells) and Z2-Z3 (more than 100). The aim of the amplification step is to harvest a synchronised population of >100-cell stage embryos from day 1 gravid hermaphrodites for chromatin immunoprecipitation (ChIP) analysis. The reasons for the selection were the cells as well as embryos were the most abundant, and importantly, the embryos have their own embryonic transcription at this stage (Edgar et al. 1994). To obtain a majority population of >100-cell stage embryos, I harvested embryos from synchronised F4 mothers in my worm amplification (Figure 5.1). The F4 synchronised L1 were placed on newly prepared Nunc dishes and then grown for 54 hours for wild-type, 67 hours for *wdr-5(-)* and 64 hours for *rbbp-5(-)*. I bleached the day 1 gravid hermaphrodites (F4). Following fixation in formaldehyde and quenching of cross-linking with Tris-HCl 100 mM, 5 µl of embryo extract was fixed in 100% methanol for storage at -20°C until further DAPI staining. Embryos were then scored according to the following categories 2-cell, 4-cell, 8-cell, >16-cell, >28-cell, >100 cell embryos and old embryos, which comprised of comma-stage embryos. I found that all of the wild-type, *wdr-5(-)* and *rbbp-5(-)* repeats that were used in my chromatin immunoprecipitation have a majority population of >100-cell stage embryos. Taken together, massive amount of >100-cell stage embryos can be harvested from large-scale amplification of *C. elegans* solid culture media.



**Figure 5.3 Synchronisation of *C. elegans* embryos for harvesting a majority of >100-cell stage embryo population.**

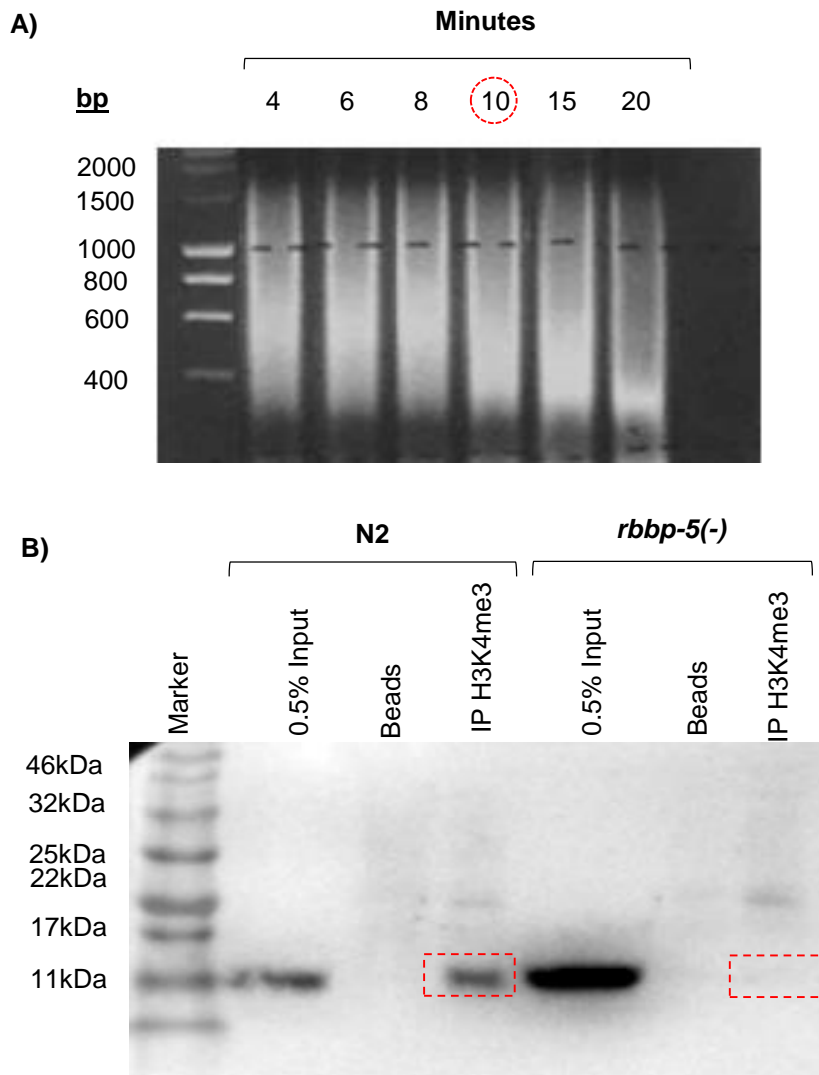
Comparison of the embryo scoring of wild type (BLUE), *wdr-5(-)* (RED), and *rbbp-5(-)* (GREEN).

#### 5.3.4 Verification of chromatin immunoprecipitation technique for H3K4me3 by Western Blot

Chromatin immunoprecipitation (ChIP) is a powerful tool to study DNA-protein interactions. It allows a delicate detection and mapping of histone modifications throughout the genome. ChIP requires small chromatin fragments between 300 and 600 base pairs. Hence, my first aim for immunoprecipitation technique was to evaluate the sonication time suitable for the large-scale *C. elegans* embryos. Approximately 500 µl of packed embryos were topped up to 1.5 ml with FA buffer

(with protease inhibitor cocktail) and dounced on ice for 40 strokes with a pastel B glass homogeniser. The mixture was then aliquoted to 250 µl in 1.5 ml micro-centrifuge tube and sonicated using Bioruptor UCD-200 (Diagenode). Sonication was performed under the cycle of 30 second ON and 30 second OFF for a total of 4, 6, 8, 10, 15 or 20 minutes. The levels of fragmentation were then observed using 1.5% gel electrophoresis. I found that the desired fragments of 300-600 base pairs were obtained when samples sonicated for a total of 15 minutes (5 seconds rest in dried ice-ethanol bath after every 2.5 minutes of sonication). Shorter sonication time (4, 6, 8 or 10 minutes) produced inadequate fragmentation whereas longer period (20 minutes) caused excessive fragmentation.

Next, I performed chromatin immunoprecipitation and verified my pull down technique using Western Blot. I performed ChIP for H3K4me3 on wild type and *rbbp-5(-)* embryos and verify the result using Western Blot against H3. For each strain, I prepared 0.5% input, beads only control and immunoprecipitated samples. I used strains which levels of H3K4 methylation has been tested before. Based on immunofluorescent staining, in absence of RBBP-5, *C. elegans* embryo lacks H3K4me3 when compared to the wild type (Wang et al. 2011). Hence, I expected to observe a Western Blot band for H3 in the wild type but not in the *rbbp-5(-)* as there would be no H3K4me3 being pulled down in the mutant. As illustrated in Figure 5.4B, H3 band is detected in the wild type but not in the *rbbp-5(-)*, supporting the immunofluorescence results that there was no H3K4me3 in the mutant. H3 is presence in both of the wild type and *rbbp-5(-)* 0.5% input controls, which were original samples that were not immunoprecipitated for H3K4me3. Beads mixed with lysate without antibody did not have the H3 band, as expected, suggesting that there is no detectable cross reaction in the background. To sum, my new model for the large-scale amplification of *C. elegans* yield high quality synchronised embryos suitable for chromatin immunoprecipitation. My chromatin immunoprecipitation reproduces and verifies the previous immunofluorescence data on mutant *rbbp-5(-)* embryos lacking H3K4me3.



**Figure 5.4 Chromatin immunoprecipitation for H3K4me3 using embryo sample harvested from the newly designed large-scale worm amplification on solid media**

(A) Sonication at different time length of 4, 6, 8, 10, 15 and 20 minutes. (B) Verification of chromatin immunoprecipitation for the pulling down of H3K4me3 in wild type and *rbbp-5(-)* mutant, followed by Western blot for H3. The red dotted boxes illustrate the absence of H3K4me3 pull down from *rbbp-5(-)* mutant sample.

## 5.4 Discussion

The two general methods for growing *C. elegans* are liquid and solid culture. For a large-scale amplification, only liquid culture method has been described in detail before. Worms are basically amplified in large swirling flasks containing S-Medium seeded with concentrated *E. coli* OP50 as the food source (Lewis & Fleming 1995). The method is easy to manage since the concentrated *E. coli* can be added as needed throughout the amplification to prevent worm starvation. However, differences in oxygenation and environmental variables between solid and liquid culture have been shown to influence many biological aspects such as the worm phenotype, growth and development. For instance, worms harvested from liquid culture tend to be longer, thinner and

more prone to retain eggs (Lewis & Fleming 1995; Rahmani et al. 2015). In view of this, I designed and developed a method for growing large quantities of *C. elegans* on solid medium with the aim to maintain my method of culturing *C. elegans* throughout the study.

#### **5.4.1 Ease of containing contamination**

My large-scale *C. elegans* amplification on solid medium involved the use of stacks of 245 x 245 mm Nunc dishes. At least 60 dishes were used per strain in total. Although plenty of works were needed, especially in preparing the solid medium dishes, I have populations of worm that were contained in sets of isolated dish setting. In other words, my *C. elegans* amplification method has an advantage of containing further spread of unwanted contamination. The dishes do get contaminated by fungus or bacteria at times. The sources of contamination may come from the surrounding or also from the bacteria inside the worm's gut (Johnstone 2002). Since worms were grown on dishes, contamination can be curbed easily by discarding the sample from contaminated dishes. Decontamination could also be performed during the bleaching of gravid mothers to harvest embryos. More dishes could be prepared as a precaution for contamination. Growing a large-scale worm in liquid culture for chromatin immunoprecipitation study is done generally by transferring embryos to a flask containing 500 ml liquid media (S medium, 1X Penicillin-Streptomycin-Neomycin antibiotics (PSN) and antifungal nystatin) that is swirled at 100 rpm at 20 °C (Ercan et al. 2007). Extra precautions are needed because the liquid culture can get contaminated even in presence of antibiotics and antifungal. Moreover, the contamination will affect the whole population. Hence repeating the whole amplification would be more preferable as some contamination may make worms sick or have influences on the biological processes.

#### **5.4.2 Produced synchronised population of harvest**

It is sometimes essential to synchronise *C. elegans* to the same embryo, larval or adult stage in experiments. Mainly synchronisation is required for the reproducibility of the data. In this report, I established a protocol for harvesting large-scale *C. elegans* embryos with a majority of population are at >100-cell stage. The embryos were harvested from young hermaphrodites grown at specific times. The wild type worms were grown for exactly 54 hours from L1, *rbbp-5(-)* for 64 hours and *wdr-5(-)* for 67 hours. In my study, I managed to obtain embryos with approximately 52% of wild type, 53% of *rbbp-5(-)* and 32% of *wdr-5(-)* to be in the >100-cell stage. I have adjusted the time for harvesting *wdr-5(-)* from 67 hours to 64 hours but I saw no difference in the percentage of the scored embryos. Despite *wdr-5(-)* having the smallest percentage amongst all, the massive number of cells within the embryos make up the majority of similar stage of cell population. A wild-type *C. elegans* embryo can produce a total of 671 cells (Sulston et al. 1983). The >100-cell stage embryo I are interested to harvest has approximately between ~101 and ~550 cells. Embryos with >550-cells present are bean and comma stage embryos, which I referred to as the old embryos (Richards et al. 2013). The 671 cells will eventually decline to 558 cells due to cell death after the onset of movement at hatching (Sulston et al. 1983). The large

number of cells (101-550 cells) within each of the >100-cell embryos make up the majority source of my extracted chromatin in my study.

#### **5.4.3 Large-scale solid culture for *C. elegans* is largely flexible**

The protocol described in this chapter illustrate a basic framework for obtaining reproducible synchronised stage of embryos. By making some alterations, this protocol can be adapted for harvesting worms under a variety of conditions. For instance, it can be used for harvesting different *C. elegans* mutant strains, different developmental stages in *C. elegans*, other worm species, or for use with different bacterium as source of food. However, the amplification factor for other worm strains must be determined prior to growing worms using this method to be careful not to cause starvation. It is important to frequently check the plates and transfer worms to new plates before food runs out. It is always a good idea to have well prepared dishes ready. Starvation in *C. elegans* has been shown to cause various effects. Starvation can induce adult reproductive diapause (Angelo & Van Gilst 2009), promote developmental arrest and cause multigenerational increase in the lifespan of progeny (Rechavi et al. 2014). Moreover, if there is no concern to harvest specific stage of embryos, the eggs can be harvested by bleaching gravid F3 adults (Figure 5.1A). The step for growing F4 worms for specific hours is unnecessary in this case. Hence, with the method developed in this chapter, it is now possible to grow large-scale *C. elegans* on solid medium.

I believe that large-scale amplification of *C. elegans* on solid medium could contribute to consistency, especially when other experiments performed in the study were also performed on solid media. It would not only provide comparable oxidation levels but would also offer almost equivalent environmental variables, thus reducing any possible alteration in biological process between the experiments.

## **Chapter 6**

### **General discussion**

## Chapter 6 : General Discussion

Our study was conducted with the main purposes to investigate if RBBP-5 is a regulator of ageing rate; where on genome H3K4 methylation levels are depleted in absence of WDR-5 or RBBP-5; and whether depleting core components WDR-5 and RBBP-5 decreases H3K4 methylation and thus will affect activation of transcription. In the process of answering these questions, I have developed a procedure for amplifying large amount of *C. elegans* on solid NGM media and harvesting large amount of embryos from it (Chapter 5). As a summary, our study found that H3K4 methylation by RBBP-5 regulate lifespan and has transgenerational effects. We also found that removal of RBBP-5 depletes H3K4 methylations levels throughout the genome, whereas removal of WDR-5 depletes H3K4me<sub>3</sub>, increases H3K4 methylation and causes excessive accumulation of H3K4me<sub>2</sub> at chromosome X. The loss of WDR-5 and RBBP-5 causes more upregulation of genes than downregulation. The study uncovers several new and novel findings which I will discuss in this chapter.

### 6.1 RBBP-5 prevents short-lifespan and its regulation on lifespan is transgenerationally inherited

Components of the MLL/SET/COMPASS complex are regulators of lifespan in *Caenorhabditis elegans*. Depleting ASH-2, WDR-5 or SET-2 causes lifespan extension. On the other hand, deficiency in the H3K4-demethylase RBR-2, shortens lifespan (Greer et al. 2010). My work supports another core components of MLL/SET/COMPASS complex, RBBP-5, is also a regulator of lifespan. However, we found that lifespan is shortened in RBBP-5 absence. Could the lifespan extension in worms lacking ASH-2, WDR-5 or SET-2; or shortening of lifespan in absence of RBBP-5 or RBR-2 correlated to the lack or de novo H3K4 methylations at specific loci. For instance, our ChIP-seq analysis has uncovered that there is de novo H3K4me<sub>2</sub> marks on chromosome X and loss of H3K4me<sub>3</sub> marks in autosomes. It is possible that these alterations may influence gene expressions involved in lifespan regulations. However further study is required to find the correlation between alterations in the levels of H3K4 methylations and change in lifespan regulation in the absence of core components of the MLL/SET/COMPASS complex.

The findings from our study and Greer et al., (2011) have importantly illustrate that components within the same MLL/COMPASS/COMPLEX can impart transgenerational inheritance on lifespan regulation of *C. elegans*. Epigenetic inheritance, however, is not foreign in animal kingdom. Fruit fly, *Drosophila melanogaster*, for instance, with a high-sugar maternal diet produced two generations of obese off-springs (Buescher et al., 2013). Fly embryos exposed to gamma irradiation enhances lifespan and resistance to heat shock and starvation for two generations (Shameer et al., 2015). In rodents, utero exposure to maternal obesity increases offspring's risks of developing metabolic syndrome, type 2 diabetes and cardiovascular disease (Dunn et al., 2011). Exposure to insecticide dichlorodiphenyltrichloroethane (DDT) in pregnant rodents increase the risk of developing tumours and disorders of prostate, kidney and ovary in the next

offspring (Skinner et al., 2013). Epigenetic inheritance has also been observed in human. For an example, two generations of offspring of women exposed to great Netherlands famine in 1944 had 1.8-folds increase risk in developing health problems (Painter et al., 2008). The epigenetic inheritance observed in fly, rodents and human mostly are intergenerational. It implies that stressor is directly exposed to parents (P0), germ cells or fetus in utero (F1) and developing germ cells of F1 (F2). On the other hand, our study illustrates transgenerational effect, where transmission occurs till F3 generation even though this generation had no direct exposure to the stressor. In future study, *C. elegans* might be amongst the best candidate models for discovering the underlying molecular mechanisms in transgenerational epigenetic inheritance.

Levels of H3K4 methylation in ancestors may influence the lifespan of the subsequent generations. I have shown that in the presence of RBBP-5 in wild type parents, the next three generations of mutant *rbbp-5(-)* progeny inherit normal lifespan. This implies that some ancestral H3K4 methylation marks were not completely erased across generations. After three generations, the inheritance of normal lifespan in *rbbp-5(-)* descendants from wild type ancestor was lost. Passive removal by molecule dilution or actively by specific eraser complexes could result in the loss (Klosin & Lehner 2016). The plasticity and reversible nature of the H3K4 methyl marks supports the transgenerational inheritance of lifespan regulation. If the lifespan longevity fate is written in the genes, it will not change after three generation of descendants.

We proposed a model (Figure 3.12) that illustrates the occurrence of transgenerational inheritance only if there is a reducing degree of life expectancy and never the other way around. An example of reducing degree of life expectancy is when descendant gain long or normal lifespan from ancestors, before losing it and returned to having normal or short lifespan, respectively. Wild type *C. elegans* is supposed to have normal lifespan. Instead, the wild type descendants from mutant *wdr-5(-)*, *set-2(-)* or *ash-2(RNAi)* ancestors inherit longevity that would last for up to three generations (Greer et al. 2011). Similarly, the *rbbp-5(-)* mutant descendants from ancestor having sufficient RBBP-5 (*rbbp-5(+/-)*), instead of being short-lived they acquire normal lifespan that would also last for up to three generations. However, if there is an increasing degree of life expectancy, the altered levels of H3K4 methylation for lifespan regulation is quickly lost across generations (Figure 3.12). We observed that wild type descendants of *rbbp-5(-)* ancestors do not inherit short lifespan, instead they quickly acquire normal lifespan. Similarly, *wdr-5(-)* and *set-2(-)* mutant descendants from wild type ancestors do not inherit normal lifespan but they immediately acquire longevity, which correspond to their genotype.

Previously, Greer et al. (2011) uncovers that there is no global decrease in H3K4me3 in wild type *C. elegans* that inherit longevity from parents with WDR-5, SET-2 or ASH-2 deficiency. Our Western blot data supports the findings and shows that there is no global increase in mutant progenies that inherit normal lifespan from the heterozygous *rbbp-5(+/-)* parents. This suggest that the reduction of H3K4 methylation occurs at specific loci instead of globally. Our ChIP-seq data uncover the alteration patterns in embryos lacking WDR-5 or RBBP-5. In absence of WDR-5, H3K4me3 is reduced; H3K4me1 is increased; and H3K4me2 is increased at chromosome X but decreased at genic and promotor regions. We also found that there is an extreme decline in the overall levels of H3K4me1/me2/me3 throughout the genome of *rbbp-5(-)* embryos. Future



works may be required to analyse which of these loci are involved in lifespan regulation and in its transgenerational inheritance.

In conclusion, my data shows that RBBP-5 is another component of the MLL/SET/COMPASS complex that is a regulator of lifespan in *C. elegans*. Depletion of H3K4 methylation due to absence in RBBP-5 is linked to lifespan limitation. This H3K4 methylation that is attributed to RBBP-5 can be transgenerationally inherited. It rescues the lifespan regulation in *rbbp-5(-)* mutant progeny, causing them to have normal instead of short lifespan for up to three generations. The transgenerational inheritance of lifespan probably involves heritable changes of H3K4 methylation at specific loci.

## **6.2 The landscape of H3K4 methylation attributed by WDR-5 and RBBP-5 during embryogenesis**

WDR-5 and RBBP-5 are core components of the MLL/SET/COMPASS complex. They regulate the complex for the deposition of H3K4 methylation. Previous immunofluorescent and Western blot analyses have documented great reduction in global H3K4 methylation in *wdr-5(-)* and *rbbp-5(-)* mutant embryos (Fisher et al. 2010; Wang et al. 2011; Simonet et al. 2007). However, prior to my study, it was not known where exactly on the genome the H3K4 methylation was reduced in absence of either WDR-5 or RBBP-5. Hence, our ChiP-Seq analysis provides data on the deposition of H3K4 methylation attributed to WDR-5 and RBBP-5 during *C. elegans* embryogenesis.

This work has revealed that RBBP-5 contributes to the deposition of H3K4me1/me2/me3 throughout the whole genome during *C. elegans* embryogenesis. In the absence of RBBP-5 during embryogenesis, H3K4me1/me2/me3 were almost entirely depleted throughout the genome. This suggests that RBBP-5 absence can highly compromise the MLL/SET/COMPASS complex activity. Human RBBP5 has been shown to have domains that allow bindings and interactions with MLL proteins, ASH2L and WDR5 (Li et al. 2016). For instance, its activation segment (AS) interacts with SET domain; ASH2L binding motif (ABM) with ASH2L's SPRY domain; and WDR5 binding motif with WDR5's WD40 repeats (Li et al. 2016). Without RBBP-5, the MLL/SET/COMPASS complex formation may severely be impaired, reducing the complex activity.

Our ChiP-Seq analysis also uncovers the distinctive regulatory roles that WDR-5 has in the deposition of methyl marks at H3K4 during embryogenesis. We have observed that WDR-5 prevents excessive accumulation of H3K4me1 at a global level (Figure 4.2); while boosts the deposition of H3K4me3 (Figure 4.1). On the other hand, H3K4me2 attributed to WDR-5 is more complex because it implicates specific genomic and chromosomal regions. WDR-5 contributes to the deposition of H3K4me2 at gene bodies and promoters while possibly limiting H3K4me2 at intergenic regions. Interestingly, WDR-5 also prevents excessive accumulation of H3K4me2 on the entire chromosome X.

Why loss of RBBP-5 globally and severely disrupts every methylation levels but loss of WDR-5 has regional and chromosomal effects on specific methyl states? A potential explanation is WDR-5 might be dispensable while RBBP-5 is not. WDR5 can directly interact with MLL/SET domain and stabilises its interaction with the RBBP5/ASH2L heterodimer (Dou et al. 2006). The activation allows methyl transfer following H3 substrate binding (Li et al. 2016). However, without WDR-5, human RBBP5-ASH2L heterodimer could still sufficiently interact, stabilise and activate MLL family histone methyltransferases (Li et al. 2016). This notion supports the hypothesis that WDR5 in *C. elegans* is also dispensable for the COMPASS complex activity. On the other hand, RBBP-5 might not be dispensable because of its many motifs that are important for the interactions with WDR5, ASH-2, and MLL family. Reducing RBBP-5 can potentially compromise the complex stability and activity.

Two known catalytic subunits for *C. elegans* MLL/SET/COMPASS complex are SET-2 and SET-16 (Simonet et al. 2007; Fisher et al. 2010). SET-2 and SET-16 are the orthologue of human SET1 and MLL3/4, respectively. During *C. elegans* embryogenesis, SET-2 is required for H3K4me2/me3 while SET-16 for H3K4me3 (Wilkins 2016). It is possible that the removal of WDR-5 from the complex could sufficiently activate SET-2 and SET-16, but in non-optimal manner, and disrupt their activities to varying degrees. In support of this, loss of interaction with WDR5 in human cells has been shown to affect SET/MLL family to varying degrees, The loss severely reduce MLL1 and SETd1A activities, but not MLL2/4 and SETd1B (Alicia-Velázquez et al. 2016). Erroneous or non-optimal activation of the complexes, in absence of WDR-5, may severely reduce the deposition of H3K4me3. We have also seen excessive accumulation of H3K4me2 at chromosome X and possibly intergenic regions. However, a gap in our study is that we cannot rule out whether accumulation in those regions is resulted from more H3K4me2 being deposited or H3K4me2 is halted from being transformed into H3K4me3.

### **6.3 Roles of WDR-5 and RBBP-5 in influencing transcription and worm phenotypes**

One of the aim of this study was to find a possible link between alterations in the levels of H3K4 methylation and transcriptional output. In general, H3K4 methylation has been associated with active gene expression. For instance, there are many readers of H3K4 methylation, such as TAF3 (of TFIID), Sgf29 (SAGA complex), ING4 and PHF8, that are linked to active gene expression (Lauberth et al. 2013; Vermeulen et al. 2010; Taverna et al. 2006; Cloos et al. 2008; Horton et al. 2010). Previous study investigates the role of SET-2 in *C. elegans* germline found that loss of H3K4 methylation in germlines due to removal of SET-2 or WDR-5 could also result in more genes being upregulated (87% and 73%, respectively) than downregulated (Robert et al. 2014). However, only limited H3K4 methylation readers have been associated with repression of genes up until now. As an example, binding of ING2 to H3K4me3 leads to recruitment Sin3 histone deacetylase that promote gene repression during DNA damage (Shi et al. 2006).

Our data reveals that absence in RBBP-5 causes more upregulation of genes (1,453) than downregulation (108). Similarly, loss of WDR-5 also upregulates more genes (2,973) than downregulates (1,147). Our findings add further support to previous research that H3K4

methylation could be associated with both activation and repression of gene expression. We have selected several loci with down- or up-regulation of gene expressions from our RNA-seq data and verified their misregulated expressions using qPCR. The chosen upregulated genes in absence of WDR-5 are *pqn-74* and *grl-7* and downregulated genes are *nxf-2* and *apc-10*. Loss of NXF-2 or APC-10 in *C. elegans* has been linked with reduced embryonic viability, while PQN-74 is important for eggshell synthesis as well as early embryonic development, and GRL-7 is involved in intercellular signalling in intestine, hypodermis and seam cells (Piano et al., 2000; Tan et al., 2000; Johnston et al., 2006). Loss of NXF-2 and APC-10 might be amongst the many factors of why *wdr-5(-)* mutants have 4% increase in embryonic lethality and almost 2-fold reduction in brood size (Wang et al., 2011). Whereas, the chosen upregulated genes in absence of RBBP-5 are *gcy-19* and *ttr-15* and downregulated genes are *fbxa-192* and *ugt-29*. All of the misregulated genes are located on autosomes. GCY-19 is predicted to involve in chemosensory signal transduction (Birnby et al., 2000), FBXA-192 in protein-protein interaction (Kipreos et al., 2000), UGT-29 in detoxification of detrimental compounds to host (Wong et al., 2014), and TTR-15 to be enriched in germline precursor cell, hypodermis and intestine (Reinke et al., 2017).

X inactivation is the transcriptional silencing of one of the X chromosome per diploid nucleus, as observed in mammalian females (XX). It is one of the mechanisms of dosage compensation for equalisation of X-linked gene products between females and males (O'Neill et al. 2003). (O'Neill et al. 2003). On the other hand, dosage compensation in *C. elegans* hermaphrodites (XX) is through the reduction of transcript levels by half in both of the X chromosomes (Meyer & Casson 1986). 'Open' and transcriptionally active chromosomes have been generally associated with histones hyper-acetylation, hyper-H3K4me and hypo-H3K9me (O'Neill et al. 2003). Interestingly, there is an evidence that shows upon X inactivation, mammalian female exhibits reduced histone acetylation, reduced H3K4me2 and increased H3K9me2 on chromosome X. This distinctive 'close' chromatin patterns observed in the mammalian females may subsequently facilitate transcriptional silencing for dosage compensation. Our data supports the view. Excessive accumulation of H3K4me2 on chromosome X was observed in embryos from self-fertilising *wdr-5(-)* hermaphrodites. Surprisingly, we uncover that the lack of WDR-5 is also associated with higher incidence of males. Together, our data suggests that sex determination and dosage compensation may occur as early as during embryogenesis and the processes may be facilitated by the levels of H3K4me2 at chromosome X.

In addition, an alternative explanation for an increase in male incidence in *wdr-5(-)* mutant could be due to elevation of nondisjunction during meiosis. In normal condition, wild type males are maintained at low frequency in populations of self-fertilising hermaphrodites. It was proposed that males are spontaneously maintained through nondisjunction of sex chromosomes during meiosis in hermaphrodites (Chasnov & Chow, 2002). Nondisjunction is a phenomenon where chromosome failed to separate, hence producing male *C. elegans* (XO) and females (XX) (Hodgkin et al., 1979). However, there are mutants such as 'high incidence of males' (*him*) with increased X-chromosome nondisjunction and decreased male fertility (Hodgkin et al., 1979). Coincidentally, *wdr-5(-)* mutants also have high incidence of males and decreased fertility. It will be interesting to further compare *wdr-5(-)* mutant with meiotic mutants like *him*.

Karyotyping could be done in future to determine if the high incidence of males observed in *wdr-5(-)* are true 'males' with XO. Reason being, the sterile *wdr-5(-)* hermaphrodites at 25°C has been linked with detectable masculinisation of germline phenotype (Li & Kelly, 2011). Masculinisation of germline alters sexual fate. Instead of developing as a hermaphrodite, the worm develops as a male (Graham & Kimble, 1993). For instance, *mog-1* worm is a masculinised hermaphrodite (XX), produces sperm continuously, does not switch to oocyte production and possesses female tail because *mog-1* does not masculinise hermaphrodite soma (Graham & Kimble, 1993). Masculinisation may also affect the soma like masculinised tails. In a different worm species, *C. briggsae* *Cb-tra-2(nm1)* and *Cb-tra-2(ed23ts)* are XX but with incomplete masculinisation, abnormal male tails lacking sensory rays, and lack of male mating behaviour (Kelleher et al., 2008). Abnormal tail sensory rays and lack of male mating behaviour were also observed in the high incidence of spontaneous males in *wdr-5(-)*. To investigate if the *wdr-5(-)* 'males' are XX or XO will delineate whether its occurrence is due to masculinisation or X-chromosome nondisjunction.

In conclusion, we show that WDR-5 contributes to acquisition of H3K4me3 and genic H3K4me2 but prevents excessive H3K4me2 accumulation at chromosome X. Crucially, we found that WDR-5 dampens expressions on chromosome X. It, however, stimulate expressions on autosomal chromosomes by preventing the loss of H3K4me1/me2/me3 peaks.

#### **6.4 Future perspectives**

The study on epigenetic transmission is important since growing number of studies found that many chronic diseases in human are contributed by both genetic and epigenetic mechanisms (Kaelin & McKnight 2013; Jones & Baylin 2007). Since my work is on transgenerational inheritance of H3K4 methylation for lifespan regulation, it is hoped that future works on it will help us better understand the pattern of epigenetic transmission across generations. A new area for investigation could be where on the genome the H3K4 methylation for lifespan regulation is transgenerationally inherited. For instance, our ChIP-Seq data reveals that *rbbp-5(-)* mutants severely lack H3K4me1/me2/me3 throughout the genome. To find the specific loci associated with transgenerational inheritance for lifespan, one could investigate any newly acquired H3K4 methylation peaks in *rbbp-5(-)* mutant descendants from wild type ancestors. Alternative investigation is on which genes with altered expression could be inherited for lifespan regulation of subsequent generation. For instance, a microarray study to compare gene expression between F4 and F5 generations. Strains to be used could be *rbbp-5(-)* mutant descendants from wild type ancestors and *rbbp-5(-)* ancestors, as well as wild type descendants from wild type ancestors. F4 generation of *rbbp-5(-)* mutants from wild type ancestors would still inherit the normal lifespan, whereas the F5 would already lost it.

Another suggestion for future work is a closer investigation into how the MLL/SET/COMPASS complex may contribute to dosage compensation. A subunit of MLL/SET/COMPASS complex, DPY-30, is shared with the dosage compensation complex (DCC). DPY-30 facilitates DCC to target X chromosomes for transcriptional regulation (Pferdehirt et al. 2011). Removal of DPY-30

compromises the binding of DCC to chromatin (Petty et al. 2011) but disruption of DCC (by the removal of SDC-2 subunit) does not affect H3K4 methylation levels (Pferdehirt et al. 2011). Interestingly, we have shown that absence of WDR-5 leads to increase incidence of males, all with defective tail morphology. Since the dosage compensation and sex determination pathways share key components, H3K4 methylation in some way may be involved with the process of dosage compensation.

## 6.5 Conclusion

To conclude, the major findings of our study demonstrate:

1. H3K4 methylation by RBBP-5 is a regulator of lifespan, depleting its levels shorten the lifespan of *C. elegans*. The regulation of lifespan by H3K4 methylation attributed to RBBP-5 is transgenerationally inherited.
2. Removal of RBBP-5 depletes H3K4 methylations levels throughout the genome, whereas removal of WDR-5 depletes global H3K4me3, increases global H3K4me1 and causes excessive accumulation of H3K4me2 throughout chromosome X.
3. The loss of WDR-5 and RBBP-5 causes more upregulation of genes than downregulation. WDR-5 deficient *C. elegans* has higher incidence of males, possibly associated with defective dosage compensation and excessive accumulation of H3K4me2 at chromosome X.

## Chapter 7 : Appendix

**Supplementary Table 1. Raw data from the RNA-Seq data using wild type and *wdr-5(-)* embryos**

The base mean value comparison between wild type (N2) and *wdr-5(-)* embryos. Log2 fold change lower than 1 (negative) indicates that the gene is downregulated in *wdr-5(-)* compared to wild type. Log2 fold change greater than 1 (positive) indicates the gene in *wdr-5(-)* is more upregulated than in wild type. Only raw data with P-value < 0.01 was shown. Padj is adjusted P-value.

gene WB name	baseMean N2	baseMean WDR-5	log2 Fold Change	pval	padj	gene WB name	baseMean N2	baseMean WDR-5	log2 Fold Change	pval	padj	gene WB name	baseMean N2	baseMean WDR-5	log2 Fold Change	pval	padj
WBGene00010212	20059	239	-6.39	1.21E-51	2.18E-47	WBGene00006418	261	1110	2.09	3.61E-11	7.54E-09	WBGene00044411	74	430	2.54	1.46E-09	1.53E-07
WBGene00001730	8	523	6.04	1.09E-31	9.77E-28	WBGene00014955	785	61	-3.68	3.88E-11	7.93E-09	WBGene00022675	658	2587	1.98	1.55E-09	1.62E-07
WBGene00011654	14	601	5.41	2.70E-31	1.62E-27	WBGene00077697	556	2238	2.01	3.89E-11	7.93E-09	WBGene00012704	318	1380	2.12	1.66E-09	1.72E-07
WBGene00011594	166	2078	3.65	9.88E-30	4.44E-26	WBGene00007891	62	459	2.9	4.15E-11	8.35E-09	WBGene00007919	137	655	2.25	1.81E-09	1.87E-07
WBGene00006474	45320	3707	-3.61	2.44E-24	8.75E-21	WBGene00015227	98	613	2.65	4.18E-11	8.35E-09	WBGene00019111	113	595	2.4	1.87E-09	1.91E-07
WBGene00017496	394	2	-7.71	7.11E-24	2.13E-20	WBGene00017727	366	1513	2.05	4.74E-11	9.36E-09	WBGene00013083	553	2031	1.88	1.88E-09	1.91E-07
WBGene00007131	44	708	4	2.34E-23	6.00E-20	WBGene00000723	50	353	2.81	4.90E-11	9.58E-09	WBGene00017297	19	210	3.43	1.88E-09	1.91E-07
WBGene00021226	2392	185	-3.69	5.83E-23	1.31E-19	WBGene00008453	262	1174	2.17	4.98E-11	9.58E-09	WBGene00044414	1001	183	-2.45	1.92E-09	1.94E-07
WBGene00014954	223	0	-11.12	2.48E-22	4.94E-19	WBGene00010714	892	3233	1.86	5.01E-11	9.58E-09	WBGene00020757	12986	2351	-2.47	1.96E-09	1.97E-07
WBGene00044608	10242	885	-3.53	2.85E-22	5.12E-19	WBGene00009109	125	694	2.47	5.21E-11	9.85E-09	WBGene00019914	149	673	2.17	2.03E-09	2.03E-07
WBGene00013030	6138	606	-3.34	3.56E-21	5.82E-18	WBGene00020051	719	3109	2.11	5.70E-11	1.07E-08	WBGene00008300	26	249	3.24	2.09E-09	2.08E-07
WBGene00018920	1380	93	-3.89	5.04E-21	7.02E-18	WBGene00018639	461	1975	2.1	5.81E-11	1.08E-08	WBGene00013119	83	461	2.47	2.13E-09	2.10E-07
WBGene00015236	421	3268	2.96	5.08E-21	7.02E-18	WBGene00020329	21	256	3.63	6.03E-11	1.11E-08	WBGene00019967	137	635	2.22	2.26E-09	2.22E-07
WBGene00010295	314	4	-6.22	4.56E-20	5.85E-17	WBGene00014300	266	1324	2.32	6.32E-11	1.15E-08	WBGene00022295	107	521	2.29	2.29E-09	2.23E-07
WBGene00012564	1164	74	-3.97	5.30E-20	6.34E-17	WBGene00016957	294	1164	1.99	6.58E-11	1.18E-08	WBGene00006759	4115	13351	1.7	2.29E-09	2.23E-07
WBGene00008187	25	482	4.27	1.12E-18	1.25E-15	WBGene00022335	2659	587	-2.18	6.73E-11	1.20E-08	WBGene00020125	470	1731	1.88	2.46E-09	2.38E-07
WBGene00013079	3	207	6.21	2.31E-18	2.44E-15	WBGene00018910	805	3	-8.26	6.89E-11	1.21E-08	WBGene00010166	26	1088	5.37	2.48E-09	2.38E-07
WBGene00044213	186	0	-10.86	3.26E-18	3.25E-15	WBGene00044461	100	607	2.6	7.71E-11	1.34E-08	WBGene00007152	2016	6134	1.61	2.55E-09	2.43E-07
WBGene00019142	1022	73	-3.81	2.34E-17	2.21E-14	WBGene00018298	16	229	3.85	7.78E-11	1.34E-08	WBGene00008711	3915	12062	1.62	2.55E-09	2.43E-07
WBGene00009608	15	305	4.36	7.22E-16	6.25E-13	WBGene00003055	553	2040	1.88	8.03E-11	1.37E-08	WBGene00004003	14	170	3.64	2.57E-09	2.43E-07
WBGene00018912	1442	165	-3.13	7.31E-16	6.25E-13	WBGene00019988	1036	3556	1.78	8.23E-11	1.39E-08	WBGene00000645	208	1374	2.72	2.71E-09	2.54E-07
WBGene00001622	52	517	3.31	2.24E-15	1.83E-12	WBGene00021325	974	3501	1.85	9.17E-11	1.54E-08	WBGene00007401	121	618	2.36	2.71E-09	2.54E-07
WBGene00022754	293	1	-7.82	2.67E-15	2.08E-12	WBGene00022744	204	942	2.2	9.54E-11	1.57E-08	WBGene00045416	0	69	9.43	3.09E-09	2.88E-07
WBGene00001692	21	528	4.68	6.15E-15	4.60E-12	WBGene00018731	64	421	2.71	9.55E-11	1.57E-08	WBGene00011439	343	1286	1.9	3.17E-09	2.92E-07
WBGene00019154	6326	24911	1.98	1.01E-14	7.12E-12	WBGene00007177	8	264	5.03	1.05E-10	1.72E-08	WBGene00010204	292	1794	2.62	3.18E-09	2.92E-07
WBGene00011548	11	240	4.43	1.03E-14	7.12E-12	WBGene00044144	67	443	2.73	1.23E-10	1.97E-08	WBGene00009158	5756	17181	1.58	3.28E-09	3.00E-07
WBGene00001775	29	394	3.75	1.26E-14	8.40E-12	WBGene00014077	73	473	2.7	1.23E-10	1.97E-08	WBGene00016886	5749	1513	-1.93	3.29E-09	3.00E-07
WBGene00045062	482	2577	2.42	1.37E-14	8.79E-12	WBGene00010258	849	2895	1.77	1.24E-10	1.97E-08	WBGene00019001	3313	9770	1.56	3.42E-09	3.11E-07
WBGene00021566	1105	137	-3.01	2.42E-14	1.50E-11	WBGene00001451	44	355	3.02	1.25E-10	1.97E-08	WBGene00000244	444	1630	1.88	3.55E-09	3.21E-07
WBGene00003590	264	1369	2.38	3.29E-14	1.97E-11	WBGene00009326	147	734	2.32	1.26E-10	1.97E-08	WBGene00015216	488	2288	2.23	3.71E-09	3.33E-07
WBGene00012912	24	347	3.85	6.61E-14	3.78E-11	WBGene00009595	145	721	2.31	1.40E-10	2.17E-08	WBGene00009593	98	522	2.41	3.76E-09	3.36E-07
WBGene00013489	72	571	2.99	6.73E-14	3.78E-11	WBGene00009917	218	994	2.19	1.49E-10	2.28E-08	WBGene00016880	6504	1828	-1.83	3.78E-09	3.36E-07
WBGene00016845	1	131	7.42	1.06E-13	5.76E-11	WBGene00009433	559	2783	2.32	1.53E-10	2.31E-08	WBGene00018669	343	19	-4.2	4.01E-09	3.55E-07
WBGene00009968	359	1748	2.28	1.10E-13	5.79E-11	WBGene00012565	5650	1300	-2.12	1.53E-10	2.31E-08	WBGene00017781	183	724	1.98	4.14E-09	3.65E-07
WBGene00009723	222	1147	2.37	1.21E-13	6.23E-11	WBGene00015704	630	2327	1.89	1.55E-10	2.32E-08	WBGene00015815	6940	1955	-1.83	4.29E-09	3.76E-07

WBGene00010041	169	968	2.52	1.38E-13	6.90E-11	WBGene00012640	655	103	-2.66	1.67E-10	2.48E-08	WBGene00015522	39	305	2.98	4.38E-09	3.82E-07
WBGene00017807	31	371	3.59	1.48E-13	7.17E-11	WBGene00015731	3760	836	-2.17	1.83E-10	2.69E-08	WBGene00000136	187	1002	2.42	4.58E-09	3.97E-07
WBGene00019592	52	479	3.21	1.87E-13	8.85E-11	WBGene00017717	410	2205	2.43	2.06E-10	3.01E-08	WBGene00008495	78	787	3.33	4.90E-09	4.24E-07
WBGene00010285	1215	4725	1.96	2.34E-13	1.08E-10	WBGene00018915	478	52	-3.2	2.24E-10	3.25E-08	WBGene00011331	1495	4639	1.63	5.25E-09	4.49E-07
WBGene00008016	4253	783	-2.44	3.60E-13	1.59E-10	WBGene00009541	336	1336	1.99	2.50E-10	3.60E-08	WBGene00006632	76	414	2.44	5.25E-09	4.49E-07
WBGene00001864	1082	114	-3.24	3.63E-13	1.59E-10	WBGene00001476	397	2426	2.61	2.55E-10	3.64E-08	WBGene00011433	349	1298	1.9	5.63E-09	4.80E-07
WBGene00044395	141	864	2.62	4.75E-13	2.03E-10	WBGene00010644	15	196	3.75	2.78E-10	3.94E-08	WBGene00001052	41	319	2.95	5.77E-09	4.87E-07
WBGene00004397	4	163	5.37	5.18E-13	2.17E-10	WBGene00020567	92	498	2.44	2.86E-10	4.01E-08	WBGene00004793	373	1346	1.85	5.77E-09	4.87E-07
WBGene00003485	776	3335	2.1	5.90E-13	2.41E-10	WBGene00016768	158	783	2.31	2.92E-10	4.06E-08	WBGene00003741	189	969	2.36	6.02E-09	5.06E-07
WBGene00007440	27	296	3.48	6.11E-13	2.44E-10	WBGene00007149	24	279	3.54	2.95E-10	4.07E-08	WBGene00021928	258	1062	2.04	6.20E-09	5.18E-07
WBGene00009958	1483	5675	1.94	7.93E-13	3.10E-10	WBGene00006772	2372	7735	1.71	3.02E-10	4.14E-08	WBGene00015632	731	2417	1.73	6.30E-09	5.24E-07
WBGene00013882	533	2366	2.15	8.33E-13	3.18E-10	WBGene00001091	277	1347	2.28	3.19E-10	4.34E-08	WBGene00017270	10	149	3.87	6.32E-09	5.24E-07
WBGene00008076	445	2073	2.22	9.07E-13	3.39E-10	WBGene00006064	312	1422	2.19	3.24E-10	4.38E-08	WBGene00009957	226	1039	2.2	6.52E-09	5.34E-07
WBGene00016095	22	310	3.85	1.42E-12	5.21E-10	WBGene00013449	130	2	-6.01	3.39E-10	4.54E-08	WBGene00022689	2366	716	-1.72	6.54E-09	5.34E-07
WBGene00009297	7181	1491	-2.27	1.60E-12	5.74E-10	WBGene00001386	452	1677	1.89	3.50E-10	4.66E-08	WBGene00014164	939	2945	1.65	6.54E-09	5.34E-07
WBGene00004831	741	3138	2.08	2.08E-12	7.32E-10	WBGene00016505	31	549	4.13	3.62E-10	4.77E-08	WBGene00016335	217	900	2.05	6.69E-09	5.43E-07
WBGene00000902	1294	5442	2.07	2.45E-12	8.46E-10	WBGene00016578	9729	2751	-1.82	3.64E-10	4.77E-08	WBGene00019828	102	492	2.27	6.74E-09	5.46E-07
WBGene00009626	29	301	3.36	3.34E-12	1.13E-09	WBGene00009579	199	882	2.15	4.09E-10	5.33E-08	WBGene00011656	23	690	4.92	7.13E-09	5.75E-07
WBGene00017101	1895	265	-2.84	3.61E-12	1.20E-09	WBGene00001447	8	148	4.23	4.15E-10	5.36E-08	WBGene00013819	888	2823	1.67	7.18E-09	5.76E-07
WBGene00000169	54	471	3.12	3.76E-12	1.23E-09	WBGene00016292	3885	12214	1.65	4.65E-10	5.96E-08	WBGene00004058	291	1089	1.9	8.00E-09	6.38E-07
WBGene00020192	234	2273	3.28	4.26E-12	1.37E-09	WBGene00015270	2007	423	-2.25	5.07E-10	6.45E-08	WBGene00001242	1033	3278	1.67	8.08E-09	6.41E-07
WBGene00010348	51	426	3.06	4.80E-12	1.51E-09	WBGene00017489	68	398	2.55	5.64E-10	7.13E-08	WBGene00019998	152	920	2.6	8.10E-09	6.41E-07
WBGene00007343	346	2752	2.99	4.90E-12	1.52E-09	WBGene00011197	3	119	5.21	5.81E-10	7.30E-08	WBGene00000233	185	1067	2.53	8.24E-09	6.49E-07
WBGene00018470	166	868	2.38	5.43E-12	1.65E-09	WBGene00019314	44	368	3.05	5.99E-10	7.48E-08	WBGene00008229	68	636	3.23	8.52E-09	6.68E-07
WBGene00011185	484	2012	2.06	5.66E-12	1.69E-09	WBGene00004719	3007	9371	1.64	6.47E-10	8.02E-08	WBGene00044463	153	847	2.47	8.57E-09	6.69E-07
WBGene00000556	1	104	7.08	6.41E-12	1.86E-09	WBGene00000784	46	371	3.02	7.16E-10	8.81E-08	WBGene00003178	86	534	2.64	8.63E-09	6.71E-07
WBGene00018031	83	604	2.87	6.42E-12	1.86E-09	WBGene00007153	137	890	2.7	7.22E-10	8.82E-08	WBGene00020086	80	493	2.62	8.69E-09	6.73E-07
WBGene00007325	382	1563	2.03	7.14E-12	2.04E-09	WBGene00002178	1495	5073	1.76	7.36E-10	8.90E-08	WBGene00017374	1121	3191	1.51	8.77E-09	6.76E-07
WBGene00015225	19	252	3.7	8.18E-12	2.26E-09	WBGene00009110	25	229	3.22	7.38E-10	8.90E-08	WBGene00017942	1700	469	-1.86	9.47E-09	7.27E-07
WBGene00000048	82	704	3.11	8.19E-12	2.26E-09	WBGene00021587	1	89	7.41	7.47E-10	8.95E-08	WBGene00013081	2556	7821	1.61	9.84E-09	7.53E-07
WBGene00011705	452	1954	2.11	8.60E-12	2.34E-09	WBGene00021059	887	2891	1.7	7.72E-10	9.18E-08	WBGene00000490	885	2875	1.7	1.01E-08	7.73E-07
WBGene00021389	250	3138	3.65	9.31E-12	2.50E-09	WBGene00045509	1398	324	-2.11	7.79E-10	9.21E-08	WBGene00012256	17077	48541	1.51	1.02E-08	7.75E-07
WBGene00017772	335	1395	2.06	9.77E-12	2.58E-09	WBGene00020483	38	317	3.06	8.43E-10	9.90E-08	WBGene00007191	775	2422	1.64	1.06E-08	8.03E-07
WBGene00009619	16	234	3.84	1.02E-11	2.65E-09	WBGene00013592	338	1334	1.98	9.17E-10	1.07E-07	WBGene00018985	607	1925	1.67	1.08E-08	8.13E-07
WBGene00000722	43	493	3.52	1.15E-11	2.95E-09	WBGene00006693	306	1275	2.06	9.50E-10	1.10E-07	WBGene00018414	50	379	2.92	1.09E-08	8.13E-07
WBGene00001403	603	2465	2.03	1.24E-11	3.14E-09	WBGene00044774	405	1534	1.92	9.85E-10	1.13E-07	WBGene00012916	10006	2878	-1.8	1.13E-08	8.45E-07
WBGene00021253	20	248	3.64	1.29E-11	3.22E-09	WBGene00010907	166	734	2.14	1.00E-09	1.15E-07	WBGene00018791	133	608	2.19	1.15E-08	8.57E-07
WBGene00010873	273	1247	2.19	1.32E-11	3.24E-09	WBGene00012851	13576	3683	-1.88	1.03E-09	1.17E-07	WBGene00044202	731	146	-2.33	1.16E-08	8.57E-07
WBGene00008292	467	1874	2.01	1.46E-11	3.56E-09	WBGene00005468	292	38	-2.94	1.04E-09	1.17E-07	WBGene00009515	66	384	2.55	1.17E-08	8.59E-07
WBGene00011866	216	1061	2.29	1.49E-11	3.57E-09	WBGene00010128	123	644	2.39	1.05E-09	1.17E-07	WBGene00011287	64	394	2.61	1.23E-08	9.02E-07
WBGene00045210	66	440	2.75	1.56E-11	3.69E-09	WBGene00003835	3615	815	-2.15	1.10E-09	1.23E-07	WBGene00016717	2068	434	-2.25	1.32E-08	9.61E-07
WBGene00044734	3021	541	-2.48	1.67E-11	3.91E-09	WBGene00020807	20	218	3.47	1.15E-09	1.27E-07	WBGene00001479	1711	7992	2.22	1.34E-08	9.71E-07
WBGene00022623	577	2148	1.9	1.74E-11	4.00E-09	WBGene00006662	249	1110	2.16	1.21E-09	1.34E-07	WBGene00016119	3	104	5.29	1.36E-08	9.84E-07
WBGene00001373	59	426	2.86	1.80E-11	4.09E-09	WBGene00017792	56	390	2.79	1.22E-09	1.34E-07	WBGene00016776	3	98	5.17	1.38E-08	9.93E-07
WBGene00019263	219	999	2.19	1.93E-11	4.34E-09	WBGene00013711	357	1419	1.99	1.25E-09	1.36E-07	WBGene00010811	428	1485	1.8	1.40E-08	1.00E-06
WBGene00011561	396	3562	3.17	2.05E-11	4.54E-09	WBGene00020581	4216	13519	1.68	1.26E-09	1.37E-07	WBGene00010652	170	702	2.05	1.43E-08	1.03E-06
WBGene00002259	401	1592	1.99	2.27E-11	4.96E-09	WBGene00003057	404	3109	2.95	1.30E-09	1.40E-07	WBGene00020143	443	1715	1.95	1.45E-08	1.04E-06
WBGene00010350	750	2940	1.97	2.55E-11	5.52E-09	WBGene00017515	490	1834	1.9	1.33E-09	1.42E-07	WBGene00018726	99	694	2.81	1.56E-08	1.11E-06
WBGene00044131	1608	315	-2.35	2.59E-11	5.54E-09	WBGene00020651	123	592	2.26	1.35E-09	1.43E-07	WBGene00020330	1518	4701	1.63	1.58E-08	1.11E-06
WBGene00013450	42	369	3.12	2.63E-11	5.56E-09	WBGene00010252	974	3131	1.68	1.39E-09	1.47E-07	WBGene00007254	224	797	1.83	1.61E-08	1.13E-06

WBGene00010293	1271	305	-2.06	1.61E-08	1.13E-06	WBGene00004119	0	71	7.86	7.35E-08	3.86E-06	WBGene00001187	9408	23799	1.34	2.26E-07	9.47E-06
WBGene00013306	824	168	-2.29	1.62E-08	1.13E-06	WBGene00019037	11418	2706	-2.08	7.42E-08	3.89E-06	WBGene00001505	460	1684	1.87	2.27E-07	9.49E-06
WBGene00004364	1708	6888	2.01	1.65E-08	1.15E-06	WBGene00004878	30	213	2.8	7.51E-08	3.90E-06	WBGene00018216	1110	3044	1.45	2.29E-07	9.54E-06
WBGene00194692	17	186	3.44	1.66E-08	1.15E-06	WBGene00017429	3094	8255	1.42	7.52E-08	3.90E-06	WBGene00044921	214	718	1.74	2.29E-07	9.54E-06
WBGene00044564	476	1545	1.7	1.69E-08	1.17E-06	WBGene00044107	338	1127	1.74	7.52E-08	3.90E-06	WBGene00017506	97	699	2.85	2.32E-07	9.64E-06
WBGene00020029	670	2180	1.7	1.72E-08	1.18E-06	WBGene00013860	2441	6697	1.46	7.65E-08	3.96E-06	WBGene00043994	557	1632	1.55	2.32E-07	9.64E-06
WBGene00017449	150	716	2.26	1.75E-08	1.20E-06	WBGene00022101	1642	461	-1.83	7.93E-08	4.09E-06	WBGene00044283	431	1319	1.61	2.40E-07	9.94E-06
WBGene00021527	38	268	2.83	1.76E-08	1.20E-06	WBGene00009547	198	835	2.08	8.01E-08	4.12E-06	WBGene00014235	153	561	1.87	2.41E-07	9.95E-06
WBGene00044484	148	1011	2.77	1.88E-08	1.28E-06	WBGene00007083	706	118	-2.58	8.08E-08	4.15E-06	WBGene00001664	55	311	2.5	2.43E-07	1.00E-05
WBGene00010170	8	270	5.06	1.89E-08	1.28E-06	WBGene00043147	158	8	-4.28	8.13E-08	4.16E-06	WBGene00010977	10	125	3.68	2.44E-07	1.00E-05
WBGene00002041	242	963	1.99	1.93E-08	1.30E-06	WBGene00009144	379	1483	1.97	8.44E-08	4.31E-06	WBGene00011559	6291	1980	-1.67	2.53E-07	1.04E-05
WBGene00022055	2357	506	-2.22	1.94E-08	1.30E-06	WBGene00020083	1472	4244	1.53	8.55E-08	4.35E-06	WBGene00016973	160	615	1.94	2.56E-07	1.05E-05
WBGene00012259	23	214	3.23	1.94E-08	1.30E-06	WBGene00009916	28	228	3	8.73E-08	4.42E-06	WBGene00009475	563	1720	1.61	2.63E-07	1.07E-05
WBGene00001795	495	2246	2.18	1.97E-08	1.31E-06	WBGene00044502	111	496	2.16	8.77E-08	4.42E-06	WBGene00009430	8	130	4.02	2.66E-07	1.08E-05
WBGene00003565	77	426	2.48	1.99E-08	1.32E-06	WBGene00021719	7786	2447	-1.67	8.78E-08	4.42E-06	WBGene00006861	1261	3470	1.46	2.72E-07	1.11E-05
WBGene00018099	1322	216	-2.62	2.03E-08	1.34E-06	WBGene00018517	656	1994	1.6	8.78E-08	4.42E-06	WBGene00019346	1080	3201	1.57	2.74E-07	1.11E-05
WBGene00015619	632	2047	1.7	2.04E-08	1.35E-06	WBGene00016044	158	667	2.08	8.90E-08	4.47E-06	WBGene00009299	3345	1015	-1.72	2.76E-07	1.12E-05
WBGene00013960	415	1477	1.83	2.13E-08	1.40E-06	WBGene00002057	1032	3841	1.9	9.00E-08	4.50E-06	WBGene00010225	15	163	3.4	2.77E-07	1.12E-05
WBGene00010111	2556	7463	1.55	2.16E-08	1.41E-06	WBGene00011049	10718	3272	-1.71	9.02E-08	4.50E-06	WBGene0001593	25	178	2.83	2.80E-07	1.13E-05
WBGene00016945	29	227	2.96	2.19E-08	1.42E-06	WBGene00009408	654	1950	1.58	9.07E-08	4.51E-06	WBGene00005715	11	137	3.59	2.81E-07	1.13E-05
WBGene00021089	89	460	2.37	2.19E-08	1.42E-06	WBGene00008478	2	86	5.5	9.25E-08	4.59E-06	WBGene00006747	1237	4985	2.01	2.85E-07	1.14E-05
WBGene00010660	268	1234	2.2	2.24E-08	1.45E-06	WBGene00001594	523	1637	1.65	9.29E-08	4.60E-06	WBGene00008161	3	84	4.95	2.85E-07	1.14E-05
WBGene00019155	32	248	2.94	2.32E-08	1.50E-06	WBGene00012648	858	3778	2.14	9.42E-08	4.65E-06	WBGene00018436	13809	4774	-1.53	2.88E-07	1.15E-05
WBGene00011054	1487	386	-1.95	2.40E-08	1.55E-06	WBGene00011454	276	1363	2.31	9.81E-08	4.83E-06	WBGene00007999	5049	13051	1.37	2.90E-07	1.16E-05
WBGene00019355	38	265	2.79	2.42E-08	1.55E-06	WBGene00019243	3659	1259	-1.54	1.02E-07	4.99E-06	WBGene00016033	2377	8472	1.83	2.92E-07	1.16E-05
WBGene00015504	3053	827	-1.88	2.42E-08	1.55E-06	WBGene00009500	734	2283	1.64	1.09E-07	5.32E-06	WBGene00010442	1423	3943	1.47	3.15E-07	1.25E-05
WBGene00022155	407	1327	1.71	2.47E-08	1.57E-06	WBGene00010274	88	440	2.33	1.09E-07	5.32E-06	WBGene00020903	112	453	2.02	3.15E-07	1.25E-05
WBGene00018416	26925	8393	-1.68	2.55E-08	1.62E-06	WBGene00008900	114	495	2.12	1.10E-07	5.37E-06	WBGene00009558	1465	3900	1.41	3.17E-07	1.25E-05
WBGene00011971	5002	13909	1.48	2.56E-08	1.62E-06	WBGene00021950	2242	6291	1.49	1.12E-07	5.44E-06	WBGene00044078	23	282	3.58	3.17E-07	1.25E-05
WBGene00011392	1579	4641	1.56	2.59E-08	1.63E-06	WBGene00001387	1834	7869	2.1	1.12E-07	5.44E-06	WBGene00013852	4554	11948	1.39	3.19E-07	1.25E-05
WBGene00012429	247	1453	2.56	2.74E-08	1.72E-06	WBGene00019484	204	730	1.84	1.13E-07	5.45E-06	WBGene00016018	765	2183	1.51	3.26E-07	1.28E-05
WBGene00003850	130	771	2.56	2.76E-08	1.73E-06	WBGene00006691	35	238	2.78	1.14E-07	5.51E-06	WBGene00016343	180	648	1.84	3.34E-07	1.31E-05
WBGene00020194	7911	21479	1.44	2.80E-08	1.75E-06	WBGene00008776	2497	7389	1.57	1.15E-07	5.51E-06	WBGene00021054	2572	835	-1.62	3.37E-07	1.32E-05
WBGene00013941	0	62	9.28	2.84E-08	1.76E-06	WBGene00017580	125	524	2.07	1.18E-07	5.64E-06	WBGene00018675	603	1720	1.51	3.38E-07	1.32E-05
WBGene00012255	15475	41434	1.42	2.86E-08	1.77E-06	WBGene00008865	5686	14565	1.36	1.18E-07	5.64E-06	WBGene00017838	199	989	2.31	3.48E-07	1.35E-05
WBGene00022562	746	2482	1.73	2.89E-08	1.78E-06	WBGene00001619	89	406	2.19	1.18E-07	5.64E-06	WBGene00009100	85	511	2.59	3.49E-07	1.36E-05
WBGene00010597	148	608	2.04	3.09E-08	1.90E-06	WBGene00016219	72	508	2.82	1.19E-07	5.67E-06	WBGene00019420	4554	1440	-1.66	3.51E-07	1.36E-05
WBGene00022391	139	773	2.48	3.17E-08	1.95E-06	WBGene00010059	6499	17173	1.4	1.20E-07	5.68E-06	WBGene00044150	292	996	1.77	3.60E-07	1.39E-05
WBGene00012247	2089	579	-1.85	3.23E-08	1.98E-06	WBGene00001819	1574	4422	1.49	1.21E-07	5.72E-06	WBGene00012099	277	995	1.85	3.65E-07	1.41E-05
WBGene00012857	292	1068	1.87	3.27E-08	1.99E-06	WBGene00018349	10732	29848	1.48	1.21E-07	5.72E-06	WBGene00002173	1943	5294	1.45	3.67E-07	1.41E-05
WBGene00006774	736	2288	1.64	3.47E-08	2.11E-06	WBGene00012844	8738	2649	-1.72	1.22E-07	5.72E-06	WBGene00019328	101	441	2.13	3.78E-07	1.45E-05
WBGene00007754	208	1211	2.54	3.51E-08	2.12E-06	WBGene00017156	619	1837	1.57	1.28E-07	6.02E-06	WBGene00020654	192	715	1.89	3.79E-07	1.45E-05
WBGene00019866	699	2344	1.74	3.52E-08	2.12E-06	WBGene00011222	311	1078	1.79	1.29E-07	6.02E-06	WBGene00016450	39	418	3.41	3.85E-07	1.47E-05
WBGene00020114	2355	6883	1.55	3.66E-08	2.20E-06	WBGene00044612	360	1224	1.77	1.30E-07	6.07E-06	WBGene00000953	1285	3576	1.48	3.85E-07	1.47E-05
WBGene00000241	764	2343	1.62	3.68E-08	2.21E-06	WBGene00008977	967	2816	1.54	1.32E-07	6.15E-06	WBGene00012165	462	1396	1.59	3.94E-07	1.50E-05
WBGene00000481	65	351	2.43	3.70E-08	2.21E-06	WBGene00001119	650	1897	1.54	1.35E-07	6.29E-06	WBGene00017013	1811	4688	1.37	4.07E-07	1.55E-05
WBGene00009730	1044	3139	1.59	3.78E-08	2.25E-06	WBGene00009658	8065	2822	-1.51	1.40E-07	6.49E-06	WBGene00044553	843	2414	1.52	4.14E-07	1.57E-05
WBGene00012130	796	2719	1.77	3.82E-08	2.27E-06	WBGene00011315	130	570	2.14	1.45E-07	6.70E-06	WBGene00006055	96	525	2.45	4.25E-07	1.61E-05
WBGene00012118	169	761	2.17	3.85E-08	2.28E-06	WBGene00010209	129	8	-4	1.46E-07	6.72E-06	WBGene00019727	2219	5701	1.36	4.26E-07	1.61E-05
WBGene00022747	39	260	2.74	3.94E-08	2.32E-06	WBGene00004219	15602	41060	1.4	1.47E-07	6.77E-06	WBGene00019405	13	138	3.44	4.37E-07	1.64E-05



WBGene00001669	1138	3256	1.52	3.95E-08	2.32E-06	WBGene00009830	1345	4267	1.67	1.49E-07	6.82E-06	WBGene00014814	2622	894	-1.55	4.46E-07	1.68E-05
WBGene00000402	555	1760	1.67	4.12E-08	2.41E-06	WBGene00004890	2152	5646	1.39	1.51E-07	6.89E-06	WBGene00001544	634	1792	1.5	4.51E-07	1.69E-05
WBGene00009843	324	1136	1.81	4.14E-08	2.42E-06	WBGene00016133	6601	17036	1.37	1.59E-07	7.24E-06	WBGene00013508	49662	16301	-1.61	4.54E-07	1.70E-05
WBGene00006761	1181	3351	1.51	4.19E-08	2.44E-06	WBGene00013610	1738	411	-2.08	1.59E-07	7.25E-06	WBGene00019853	26	193	2.91	4.59E-07	1.71E-05
WBGene00004222	5	111	4.38	4.33E-08	2.51E-06	WBGene00008906	7	112	4.05	1.63E-07	7.38E-06	WBGene00006744	32	289	3.19	4.60E-07	1.71E-05
WBGene00007375	784	2232	1.51	4.37E-08	2.52E-06	WBGene00016237	2073	6056	1.55	1.64E-07	7.40E-06	WBGene00021212	40	267	2.73	4.61E-07	1.72E-05
WBGene00022012	35	292	3.06	4.37E-08	2.52E-06	WBGene00006475	46	279	2.61	1.66E-07	7.48E-06	WBGene00006809	420	1296	1.63	4.63E-07	1.72E-05
WBGene00010344	51	309	2.6	4.45E-08	2.55E-06	WBGene00001136	110	476	2.11	1.67E-07	7.51E-06	WBGene00007097	8	417	5.65	4.64E-07	1.72E-05
WBGene00013024	10948	3525	-1.63	4.46E-08	2.55E-06	WBGene00008515	428	1911	2.16	1.68E-07	7.55E-06	WBGene00007695	262	902	1.79	4.65E-07	1.72E-05
WBGene00001592	102	583	2.51	4.50E-08	2.57E-06	WBGene00006914	4022	15565	1.95	1.70E-07	7.60E-06	WBGene00017437	1173	3434	1.55	4.76E-07	1.75E-05
WBGene00003572	68	419	2.63	4.53E-08	2.57E-06	WBGene00009226	58	588	3.35	1.71E-07	7.65E-06	WBGene00003762	477	1572	1.72	4.77E-07	1.75E-05
WBGene00011678	69	355	2.35	4.62E-08	2.62E-06	WBGene00012841	5475	1739	-1.65	1.72E-07	7.68E-06	WBGene00011520	373	1124	1.59	4.78E-07	1.75E-05
WBGene00013328	725	2137	1.56	4.74E-08	2.68E-06	WBGene00001133	67	428	2.68	1.73E-07	7.68E-06	WBGene00002977	4239	10706	1.34	4.79E-07	1.76E-05
WBGene00015294	211	915	2.11	4.85E-08	2.73E-06	WBGene00004507	780	2458	1.66	1.73E-07	7.68E-06	WBGene00003426	78	1	-6.74	4.86E-07	1.78E-05
WBGene00045253	38	263	2.8	5.11E-08	2.87E-06	WBGene00015376	98	444	2.18	1.74E-07	7.69E-06	WBGene00017555	270	43	-2.66	4.98E-07	1.82E-05
WBGene00013054	1132	185	-2.61	5.16E-08	2.89E-06	WBGene00020260	70	389	2.47	1.75E-07	7.74E-06	WBGene00044743	626	1928	1.62	5.02E-07	1.83E-05
WBGene00006960	185	776	2.06	5.36E-08	2.98E-06	WBGene00000007	16	221	3.76	1.78E-07	7.83E-06	WBGene00002048	4270	11427	1.42	5.10E-07	1.85E-05
WBGene00018590	64	349	2.44	5.36E-08	2.98E-06	WBGene00021008	426	1364	1.68	1.80E-07	7.89E-06	WBGene00019414	4542	1536	-1.56	5.27E-07	1.91E-05
WBGene00004233	2060	5710	1.47	5.51E-08	3.06E-06	WBGene00019166	924	2733	1.56	1.81E-07	7.91E-06	WBGene00008176	22	179	2.99	5.37E-07	1.94E-05
WBGene00021164	39	254	2.72	5.62E-08	3.11E-06	WBGene00018236	3886	1314	-1.56	1.82E-07	7.96E-06	WBGene00018730	63	398	2.67	5.40E-07	1.95E-05
WBGene00022322	1537	394	-1.96	5.78E-08	3.19E-06	WBGene00009060	237	937	1.98	1.84E-07	8.02E-06	WBGene00002018	4280	940	-2.19	5.47E-07	1.97E-05
WBGene00017513	1035	2904	1.49	5.85E-08	3.22E-06	WBGene00010227	4869	1095	-2.15	1.84E-07	8.02E-06	WBGene00017945	439	1312	1.58	5.55E-07	2.00E-05
WBGene00016455	7605	2575	-1.56	6.17E-08	3.38E-06	WBGene00016328	209	715	1.77	1.87E-07	8.10E-06	WBGene00013290	197	6	-4.99	5.56E-07	2.00E-05
WBGene00019908	164	686	2.06	6.23E-08	3.40E-06	WBGene00008167	703	2150	1.61	1.89E-07	8.16E-06	WBGene00018442	3001	957	-1.65	5.57E-07	2.00E-05
WBGene00019682	208	1084	2.38	6.50E-08	3.54E-06	WBGene00016448	287	1060	1.89	1.92E-07	8.28E-06	WBGene00004401	201	1010	2.33	5.62E-07	2.01E-05
WBGene00001044	696	147	-2.24	6.55E-08	3.56E-06	WBGene00011782	0	62	7.67	1.96E-07	8.46E-06	WBGene00011727	36	215	2.58	5.68E-07	2.03E-05
WBGene00001816	4003	1273	-1.65	6.83E-08	3.69E-06	WBGene00050935	447	104	-2.11	1.98E-07	8.51E-06	WBGene00006831	3543	10194	1.52	5.70E-07	2.03E-05
WBGene00009791	548	2356	2.1	6.87E-08	3.71E-06	WBGene00006309	729	2121	1.54	2.00E-07	8.58E-06	WBGene00012668	147	557	1.93	5.72E-07	2.03E-05
WBGene00008698	10	149	3.91	6.92E-08	3.72E-06	WBGene00020340	582	2061	1.82	2.05E-07	8.75E-06	WBGene00077585	332	71	-2.23	5.86E-07	2.08E-05
WBGene00000746	40	276	2.79	7.02E-08	3.77E-06	WBGene00000401	4831	12230	1.34	2.08E-07	8.88E-06	WBGene00050904	6	101	4.04	5.88E-07	2.08E-05
WBGene00011508	8527	25770	1.6	7.12E-08	3.80E-06	WBGene00020897	444	1614	1.86	2.09E-07	8.89E-06	WBGene00000006	508	1930	1.93	5.90E-07	2.09E-05
WBGene00003707	219	785	1.84	7.14E-08	3.80E-06	WBGene00017666	374	1151	1.62	2.16E-07	9.16E-06	WBGene00002974	658	1966	1.58	6.04E-07	2.13E-05
WBGene00018971	146	598	2.03	7.15E-08	3.80E-06	WBGene00013230	5896	1900	-1.63	2.16E-07	9.16E-06	WBGene00009721	3306	1074	-1.62	6.09E-07	2.14E-05
WBGene00019754	77	640	3.06	7.18E-08	3.81E-06	WBGene00021704	519	87	-2.58	2.18E-07	9.19E-06	WBGene00018992	518	1543	1.57	6.17E-07	2.17E-05
WBGene00013842	14	154	3.42	7.28E-08	3.84E-06	WBGene00018217	1662	4324	1.38	2.18E-07	9.20E-06	WBGene00044169	191	1011	2.4	6.20E-07	2.18E-05
WBGene00003175	2289	6788	1.57	7.29E-08	3.84E-06	WBGene00005655	1434	3771	1.39	2.21E-07	9.31E-06	WBGene00008542	1093	2981	1.45	6.31E-07	2.21E-05
WBGene00015035	183	624	1.77	6.33E-07	2.21E-05	WBGene00016217	160	848	2.41	1.30E-06	3.89E-05	WBGene00000727	189	756	2	2.17E-06	5.67E-05
WBGene00007675	2986	1048	-1.51	6.33E-07	2.21E-05	WBGene00001519	1194	2992	1.33	1.30E-06	3.89E-05	WBGene00003983	16457	5809	-1.5	2.17E-06	5.67E-05
WBGene00000673	98	358	1.87	6.36E-07	2.21E-05	WBGene00007502	27	184	2.75	1.30E-06	3.89E-05	WBGene00008784	27419	9620	-1.51	2.21E-06	5.77E-05
WBGene00016453	46842	17315	-1.44	6.41E-07	2.23E-05	WBGene00018133	738	2064	1.48	1.31E-06	3.90E-05	WBGene00022296	12900	4950	-1.38	2.23E-06	5.82E-05
WBGene00017343	5199	1857	-1.49	6.44E-07	2.23E-05	WBGene00007071	8	152	4.29	1.32E-06	3.91E-05	WBGene00004998	1585	4662	1.56	2.26E-06	5.87E-05
WBGene00017344	3614	1136	-1.67	6.52E-07	2.26E-05	WBGene00020390	1061	2890	1.45	1.32E-06	3.92E-05	WBGene00012289	1285	4369	1.77	2.26E-06	5.88E-05
WBGene00002142	495	1469	1.57	6.64E-07	2.29E-05	WBGene00002128	2290	7019	1.62	1.32E-06	3.92E-05	WBGene00016485	4647	1585	-1.55	2.28E-06	5.91E-05
WBGene00011928	65	524	3.01	6.71E-07	2.31E-05	WBGene00016190	104	775	2.9	1.35E-06	3.99E-05	WBGene00020385	14	147	3.43	2.28E-06	5.91E-05
WBGene00015478	1422	3752	1.4	6.71E-07	2.31E-05	WBGene00008199	173	603	1.8	1.40E-06	4.13E-05	WBGene00017337	748	155	-2.27	2.29E-06	5.92E-05
WBGene00016221	37	214	2.54	6.72E-07	2.31E-05	WBGene00007525	13	145	3.46	1.40E-06	4.13E-05	WBGene00004780	33	197	2.59	2.29E-06	5.92E-05
WBGene00000173	5	98	4.21	6.73E-07	2.31E-05	WBGene00021519	261	916	1.81	1.41E-06	4.16E-05	WBGene00018073	5407	19558	1.85	2.30E-06	5.94E-05
WBGene00015112	56089	18578	-1.59	6.75E-07	2.31E-05	WBGene00016106	4571	10998	1.27	1.42E-06	4.17E-05	WBGene00011676	460	1154	1.33	2.32E-06	5.98E-05
WBGene00022848	269	907	1.76	6.82E-07	2.33E-05	WBGene00003597	2981	7231	1.28	1.42E-06	4.17E-05	WBGene00008093	1717	4240	1.3	2.33E-06	5.99E-05
WBGene00044500	1271	3705	1.54	6.83E-07	2.33E-05	WBGene00001059	336	1613	2.26	1.42E-06	4.17E-05	WBGene00004316	349	1843	2.4	2.37E-06	6.08E-05

WBGene00009157	302	988	1.71	6.85E-07	2.33E-05	WBGene00019840	9	113	3.57	1.44E-06	4.21E-05	WBGene00015936	19	159	3.11	2.39E-06	6.15E-05
WBGene00008168	1941	5077	1.39	6.87E-07	2.33E-05	WBGene00018282	756	2838	1.91	1.44E-06	4.21E-05	WBGene00011515	3	83	4.76	2.41E-06	6.18E-05
WBGene00000522	59	308	2.38	6.90E-07	2.34E-05	WBGene00017227	43	207	2.27	1.45E-06	4.21E-05	WBGene00007949	463	1326	1.52	2.42E-06	6.18E-05
WBGene00019485	11	120	3.48	6.98E-07	2.36E-05	WBGene00017306	38	230	2.61	1.45E-06	4.21E-05	WBGene00021224	1145	7	-7.29	2.43E-06	6.22E-05
WBGene00009304	10212	26227	1.36	7.09E-07	2.39E-05	WBGene00012532	1667	4196	1.33	1.45E-06	4.22E-05	WBGene00175034	8	98	3.7	2.44E-06	6.22E-05
WBGene00013019	8426	2487	-1.76	7.09E-07	2.39E-05	WBGene00000633	135	620	2.2	1.46E-06	4.23E-05	WBGene00000441	519	1540	1.57	2.44E-06	6.22E-05
WBGene00017288	3171	1169	-1.44	7.11E-07	2.39E-05	WBGene00016468	166	591	1.83	1.46E-06	4.23E-05	WBGene00000679	186	658	1.82	2.46E-06	6.26E-05
WBGene00021863	15915	5630	-1.5	7.20E-07	2.42E-05	WBGene00015202	21	220	3.4	1.47E-06	4.26E-05	WBGene00007174	1442	5061	1.81	2.47E-06	6.26E-05
WBGene00018538	8	113	3.88	7.30E-07	2.45E-05	WBGene00022396	5340	15102	1.5	1.48E-06	4.27E-05	WBGene00016100	5	89	4.06	2.47E-06	6.27E-05
WBGene00017157	129	528	2.04	7.38E-07	2.47E-05	WBGene00012421	976	2424	1.31	1.49E-06	4.30E-05	WBGene00018690	1746	667	-1.39	2.49E-06	6.31E-05
WBGene00009901	26	189	2.84	7.40E-07	2.47E-05	WBGene00004816	38266	14074	-1.44	1.51E-06	4.35E-05	WBGene00010440	135	520	1.94	2.53E-06	6.41E-05
WBGene00015947	122	404	1.73	7.42E-07	2.47E-05	WBGene00007804	1	62	5.98	1.52E-06	4.36E-05	WBGene00010275	115	807	2.81	2.54E-06	6.42E-05
WBGene00044701	69	682	3.31	7.57E-07	2.51E-05	WBGene00006600	167	601	1.85	1.52E-06	4.38E-05	WBGene00000692	512	2195	2.1	2.55E-06	6.42E-05
WBGene00020317	157	779	2.31	7.57E-07	2.51E-05	WBGene00010248	1259	382	-1.72	1.53E-06	4.38E-05	WBGene00015921	57	284	2.31	2.60E-06	6.54E-05
WBGene00000042	32	256	3.01	7.59E-07	2.52E-05	WBGene00016346	1508	503	-1.58	1.55E-06	4.44E-05	WBGene00008462	232	758	1.71	2.63E-06	6.62E-05
WBGene00010101	5913	1402	-2.08	7.65E-07	2.53E-05	WBGene00019703	22830	7976	-1.52	1.55E-06	4.44E-05	WBGene00009842	129	594	2.21	2.68E-06	6.72E-05
WBGene00016303	8010	2655	-1.59	7.68E-07	2.53E-05	WBGene00013962	10631	25846	1.28	1.56E-06	4.44E-05	WBGene00022419	652	1692	1.38	2.68E-06	6.72E-05
WBGene00018515	363	1220	1.75	7.77E-07	2.56E-05	WBGene00004925	225	734	1.71	1.57E-06	4.46E-05	WBGene00000720	9	111	3.66	2.68E-06	6.72E-05
WBGene00018486	30	235	2.96	7.79E-07	2.56E-05	WBGene00008570	125	786	2.66	1.57E-06	4.46E-05	WBGene00016415	5194	12417	1.26	2.71E-06	6.79E-05
WBGene00010970	20	173	3.15	7.80E-07	2.56E-05	WBGene00010712	12	131	3.44	1.58E-06	4.50E-05	WBGene00001984	679	1882	1.47	2.72E-06	6.80E-05
WBGene00018576	158	603	1.93	7.83E-07	2.56E-05	WBGene00044049	1706	4450	1.38	1.59E-06	4.50E-05	WBGene00000403	12164	27260	1.16	2.72E-06	6.80E-05
WBGene00006200	221	25	-3.12	7.83E-07	2.56E-05	WBGene00013762	11	131	3.52	1.60E-06	4.52E-05	WBGene00015620	2707	6670	1.3	2.74E-06	6.84E-05
WBGene00003977	72914	25359	-1.52	7.88E-07	2.57E-05	WBGene00020605	144	494	1.78	1.60E-06	4.52E-05	WBGene00020191	27	184	2.75	2.76E-06	6.87E-05
WBGene00020266	6	101	3.96	8.30E-07	2.70E-05	WBGene00018885	109	536	2.3	1.61E-06	4.53E-05	WBGene00011317	13	145	3.43	2.79E-06	6.93E-05
WBGene00001691	77	1302	4.09	8.31E-07	2.70E-05	WBGene00002054	7132	19371	1.44	1.62E-06	4.55E-05	WBGene00016447	91	2	-5.22	2.86E-06	7.10E-05
WBGene00010158	73670	25854	-1.51	8.63E-07	2.80E-05	WBGene00001452	260	809	1.64	1.62E-06	4.55E-05	WBGene00014188	34	621	4.2	2.87E-06	7.12E-05
WBGene00015061	11791	29980	1.35	8.71E-07	2.83E-05	WBGene00008270	339	996	1.55	1.62E-06	4.55E-05	WBGene00044404	286	933	1.71	2.88E-06	7.13E-05
WBGene00016314	101	457	2.17	8.90E-07	2.88E-05	WBGene00194682	546	34	-3.99	1.64E-06	4.59E-05	WBGene00016005	585	1660	1.5	2.89E-06	7.13E-05
WBGene00003736	996	5168	2.37	8.90E-07	2.88E-05	WBGene00008582	349	1929	2.47	1.65E-06	4.61E-05	WBGene00000370	1033	2770	1.42	2.92E-06	7.21E-05
WBGene00012201	429	1305	1.6	8.98E-07	2.90E-05	WBGene00045024	5	91	4.34	1.66E-06	4.63E-05	WBGene00019128	358	1154	1.69	2.94E-06	7.25E-05
WBGene00007746	587	2794	2.25	9.03E-07	2.91E-05	WBGene00010066	3812	1150	-1.73	1.66E-06	4.63E-05	WBGene00019536	702	1791	1.35	2.97E-06	7.30E-05
WBGene00009340	3965	10429	1.4	9.14E-07	2.94E-05	WBGene00009826	160	562	1.81	1.66E-06	4.63E-05	WBGene00017798	366	1053	1.52	3.02E-06	7.43E-05
WBGene00021213	1957	4826	1.3	9.27E-07	2.97E-05	WBGene00019204	371	1076	1.54	1.67E-06	4.64E-05	WBGene00017351	72	328	2.19	3.04E-06	7.46E-05
WBGene00011653	19	509	4.78	9.28E-07	2.97E-05	WBGene00016425	7	233	4.99	1.68E-06	4.66E-05	WBGene00007769	1124	320	-1.81	3.07E-06	7.53E-05
WBGene00018823	315	963	1.61	9.51E-07	3.04E-05	WBGene00022645	65	448	2.78	1.68E-06	4.66E-05	WBGene00017620	3737	1207	-1.63	3.09E-06	7.57E-05
WBGene00013518	1963	4828	1.3	9.52E-07	3.04E-05	WBGene00138717	6505	2230	-1.54	1.69E-06	4.67E-05	WBGene00020331	205	699	1.77	3.12E-06	7.63E-05
WBGene00002039	13357	32816	1.3	9.56E-07	3.04E-05	WBGene00010214	80	303	1.91	1.69E-06	4.67E-05	WBGene00011836	560	1962	1.81	3.13E-06	7.64E-05
WBGene00006217	479	1356	1.5	9.64E-07	3.06E-05	WBGene00009090	11	124	3.45	1.70E-06	4.69E-05	WBGene00000225	5777	13350	1.21	3.18E-06	7.74E-05
WBGene00019285	2404	9361	1.96	9.74E-07	3.09E-05	WBGene00077592	77	424	2.45	1.71E-06	4.71E-05	WBGene00138721	5	98	4.26	3.21E-06	7.81E-05
WBGene00008654	153	1016	2.73	9.75E-07	3.09E-05	WBGene00009393	12	148	3.67	1.72E-06	4.72E-05	WBGene00008782	14925	5345	-1.48	3.22E-06	7.82E-05
WBGene00017912	5720	2035	-1.49	9.78E-07	3.09E-05	WBGene00011684	129	518	2.01	1.72E-06	4.73E-05	WBGene00020438	4495	1434	-1.65	3.23E-06	7.84E-05
WBGene00006985	2073	5682	1.45	9.84E-07	3.11E-05	WBGene00006526	125	472	1.92	1.73E-06	4.75E-05	WBGene00000085	49	250	2.36	3.25E-06	7.88E-05
WBGene00021520	5	99	4.27	9.86E-07	3.11E-05	WBGene00000172	830	3083	1.89	1.74E-06	4.75E-05	WBGene00011090	221	711	1.69	3.25E-06	7.88E-05
WBGene00012300	3337	761	-2.13	9.89E-07	3.11E-05	WBGene00006767	1113	3099	1.48	1.74E-06	4.75E-05	WBGene00011182	2356	7045	1.58	3.29E-06	7.94E-05
WBGene00000719	14	142	3.33	1.01E-06	3.17E-05	WBGene00013415	733	1930	1.4	1.76E-06	4.80E-05	WBGene00004223	172	576	1.74	3.30E-06	7.96E-05
WBGene00119203	128	498	1.96	1.04E-06	3.26E-05	WBGene00002053	15186	36112	1.25	1.76E-06	4.81E-05	WBGene00008123	8	107	3.74	3.31E-06	7.98E-05
WBGene00015843	801	153	-2.39	1.04E-06	3.26E-05	WBGene00008987	2347	5632	1.26	1.78E-06	4.84E-05	WBGene00016337	4087	1550	-1.4	3.38E-06	8.13E-05
WBGene00014094	173	977	2.5	1.06E-06	3.31E-05	WBGene00020579	369	2352	2.67	1.78E-06	4.84E-05	WBGene00022010	644	2715	2.08	3.40E-06	8.17E-05
WBGene00010294	169	6	-4.82	1.09E-06	3.39E-05	WBGene00010385	346	1272	1.88	1.79E-06	4.86E-05	WBGene00019156	43	297	2.8	3.45E-06	8.27E-05
WBGene00019230	38	242	2.66	1.10E-06	3.41E-05	WBGene00011335	428	1694	1.98	1.80E-06	4.88E-05	WBGene00012904	8388	3008	-1.48	3.45E-06	8.28E-05

WBGene00018879	27	224	3.03	1.10E-06	3.43E-05	WBGene00004808	27934	6832	-2.03	1.82E-06	4.93E-05	WBGene00019765	65	303	2.23	3.46E-06	8.28E-05
WBGene00008352	35	215	2.62	1.11E-06	3.43E-05	WBGene00022283	6670	16817	1.33	1.84E-06	4.97E-05	WBGene00007420	266	816	1.62	3.49E-06	8.34E-05
WBGene00018706	198	771	1.96	1.11E-06	3.44E-05	WBGene00044021	39	232	2.58	1.84E-06	4.97E-05	WBGene00007339	514	1870	1.86	3.52E-06	8.39E-05
WBGene00001159	2069	5314	1.36	1.12E-06	3.45E-05	WBGene00020543	6217	2321	-1.42	1.89E-06	5.09E-05	WBGene00010202	29	318	3.47	3.52E-06	8.39E-05
WBGene00015762	2	61	5.07	1.12E-06	3.45E-05	WBGene00001621	240	848	1.82	1.93E-06	5.20E-05	WBGene00016705	1665	621	-1.42	3.52E-06	8.39E-05
WBGene00006453	335	1206	1.85	1.12E-06	3.45E-05	WBGene00022824	251	785	1.65	1.97E-06	5.30E-05	WBGene00013699	18962	7462	-1.35	3.53E-06	8.41E-05
WBGene00010109	126	831	2.72	1.15E-06	3.54E-05	WBGene00018438	28655	10535	-1.44	1.98E-06	5.32E-05	WBGene00012041	4532	1770	-1.36	3.56E-06	8.46E-05
WBGene00012163	47	253	2.42	1.15E-06	3.55E-05	WBGene00011075	555	1588	1.52	2.01E-06	5.38E-05	WBGene00013895	415	1250	1.59	3.59E-06	8.52E-05
WBGene00016210	2909	7176	1.3	1.16E-06	3.56E-05	WBGene00044737	171	587	1.78	2.02E-06	5.39E-05	WBGene00001413	5475	2006	-1.45	3.62E-06	8.58E-05
WBGene00004363	4997	12131	1.28	1.16E-06	3.56E-05	WBGene00003892	901	2446	1.44	2.02E-06	5.39E-05	WBGene00000535	90	757	3.07	3.63E-06	8.60E-05
WBGene00017193	679	3096	2.19	1.18E-06	3.61E-05	WBGene00003808	34	234	2.8	2.03E-06	5.40E-05	WBGene00004347	222	662	1.58	3.67E-06	8.67E-05
WBGene00044156	20	209	3.42	1.18E-06	3.61E-05	WBGene00016059	1680	4385	1.38	2.06E-06	5.48E-05	WBGene00000059	120	423	1.82	3.70E-06	8.74E-05
WBGene00002052	719	2991	2.06	1.19E-06	3.63E-05	WBGene00189995	3030	7482	1.3	2.06E-06	5.48E-05	WBGene00004281	955	2493	1.38	3.75E-06	8.82E-05
WBGene00021870	1954	5616	1.52	1.20E-06	3.64E-05	WBGene00003672	64	710	3.46	2.08E-06	5.52E-05	WBGene00017842	1046	3395	1.7	3.75E-06	8.82E-05
WBGene00011077	61	409	2.73	1.21E-06	3.67E-05	WBGene00020766	77	336	2.12	2.10E-06	5.56E-05	WBGene00011762	723	2155	1.58	3.75E-06	8.82E-05
WBGene00003969	696	1923	1.47	1.23E-06	3.72E-05	WBGene00086562	1578	547	-1.53	2.11E-06	5.60E-05	WBGene00021985	8956	3341	-1.42	3.80E-06	8.93E-05
WBGene00019797	3094	1042	-1.57	1.23E-06	3.72E-05	WBGene00011078	62	305	2.3	2.12E-06	5.60E-05	WBGene00005559	5	92	4.29	3.82E-06	8.95E-05
WBGene00019550	50	499	3.31	1.26E-06	3.81E-05	WBGene00006655	1032	2650	1.36	2.15E-06	5.67E-05	WBGene00019370	89	375	2.07	3.82E-06	8.95E-05
WBGene00019313	15167	5465	-1.47	1.27E-06	3.82E-05	WBGene00000510	726	1862	1.36	2.15E-06	5.67E-05	WBGene00000144	2087	491	-2.09	3.83E-06	8.95E-05
WBGene00014144	6830	2414	-1.5	1.27E-06	3.82E-05	WBGene00020571	1586	4537	1.52	2.16E-06	5.67E-05	WBGene00003093	107	399	1.9	3.86E-06	9.01E-05
WBGene00003563	69	317	2.2	1.28E-06	3.86E-05	WBGene00014021	1040	2733	1.39	2.16E-06	5.67E-05	WBGene00017568	725	2105	1.54	3.90E-06	9.08E-05
WBGene00021304	169	799	2.24	1.29E-06	3.86E-05	WBGene00006690	369	1115	1.59	2.17E-06	5.67E-05	WBGene00011314	569	1526	1.42	3.90E-06	9.08E-05
WBGene00004856	140	515	1.88	3.90E-06	9.08E-05	WBGene00010974	962	2418	1.33	5.97E-06	0.000125	WBGene00008278	20	143	2.88	8.54E-06	0.0001626
WBGene00008512	675	2808	2.06	3.94E-06	9.13E-05	WBGene00012593	14	219	3.98	5.98E-06	0.0001252	WBGene00004275	13	129	3.36	8.73E-06	0.000166
WBGene00004910	2977	8477	1.51	3.94E-06	9.13E-05	WBGene00020196	781	2326	1.57	6.00E-06	0.0001253	WBGene00021458	22254	7856	-1.5	8.74E-06	0.0001661
WBGene00019034	1975	739	-1.42	3.94E-06	9.13E-05	WBGene00009546	9228	3442	-1.42	6.03E-06	0.0001259	WBGene00018444	4792	1864	-1.36	8.96E-06	0.0001699
WBGene00000368	3601	8476	1.24	3.95E-06	9.13E-05	WBGene00013319	6174	1807	-1.77	6.05E-06	0.0001261	WBGene00018283	242	733	1.6	8.99E-06	0.0001703
WBGene00002393	2123	5309	1.32	3.95E-06	9.13E-05	WBGene00010099	1046	320	-1.71	6.06E-06	0.0001261	WBGene00004921	244	1936	2.99	9.01E-06	0.0001706
WBGene00011794	1866	4683	1.33	3.97E-06	9.16E-05	WBGene00011432	23639	9554	-1.31	6.07E-06	0.0001261	WBGene00017295	77	332	2.11	9.02E-06	0.0001706
WBGene00043985	41	236	2.52	3.97E-06	9.16E-05	WBGene00018479	43	208	2.26	6.09E-06	0.0001264	WBGene00010722	137	506	1.89	9.05E-06	0.0001709
WBGene00003527	41	339	3.05	3.98E-06	9.17E-05	WBGene00019870	86	339	1.99	6.11E-06	0.0001266	WBGene00007353	485	1300	1.42	9.13E-06	0.0001722
WBGene00008993	116	444	1.93	4.07E-06	9.37E-05	WBGene00003143	4971	11414	1.2	6.14E-06	0.0001271	WBGene00007453	3	89	4.92	9.14E-06	0.0001722
WBGene00010104	2412	865	-1.48	4.08E-06	9.38E-05	WBGene00000631	63	525	3.05	6.14E-06	0.0001271	WBGene00000089	403	1153	1.52	9.15E-06	0.0001722
WBGene00009537	5225	1735	-1.59	4.14E-06	9.51E-05	WBGene00000082	1829	4651	1.35	6.17E-06	0.0001276	WBGene00004246	784	271	-1.53	9.16E-06	0.0001724
WBGene00001569	17151	6269	-1.45	4.18E-06	9.58E-05	WBGene00011587	750	1952	1.38	6.25E-06	0.000129	WBGene00008277	431	2352	2.45	9.22E-06	0.000173
WBGene00019108	721	1847	1.36	4.19E-06	9.60E-05	WBGene00019174	94	402	2.09	6.28E-06	0.0001295	WBGene00010899	2159	4964	1.2	9.22E-06	0.000173
WBGene00006637	1452	3661	1.33	4.20E-06	9.60E-05	WBGene00010185	496	12	-5.4	6.29E-06	0.0001295	WBGene00016307	14692	6219	-1.24	9.23E-06	0.000173
WBGene00016626	587	1530	1.38	4.20E-06	9.60E-05	WBGene00050875	90	474	2.4	6.30E-06	0.0001297	WBGene00021134	10	106	3.45	9.24E-06	0.0001731
WBGene00016308	4365	1797	-1.28	4.22E-06	9.61E-05	WBGene00006476	14083	31077	1.14	6.37E-06	0.0001308	WBGene00019448	329	966	1.55	9.36E-06	0.0001751
WBGene00020231	92	368	2	4.22E-06	9.61E-05	WBGene00006752	1622	9178	2.5	6.39E-06	0.0001312	WBGene00017721	726	2867	1.98	9.42E-06	0.000176
WBGene00021439	177	811	2.2	4.25E-06	9.66E-05	WBGene00016506	133	420	1.66	6.42E-06	0.0001316	WBGene00044206	1	55	6.16	9.49E-06	0.0001773
WBGene00012554	6386	18949	1.57	4.28E-06	9.72E-05	WBGene00007615	3902	1506	-1.37	6.44E-06	0.0001319	WBGene00010519	19673	6901	-1.51	9.54E-06	0.000178
WBGene00001184	3244	7765	1.26	4.29E-06	9.73E-05	WBGene00013715	79	657	3.06	6.45E-06	0.0001319	WBGene00001457	52	252	2.28	9.61E-06	0.0001791
WBGene00018729	39	210	2.43	4.31E-06	9.75E-05	WBGene00010972	559	1890	1.76	6.46E-06	0.0001319	WBGene00007182	5036	1998	-1.33	9.63E-06	0.0001792
WBGene00006670	111	466	2.07	4.31E-06	9.75E-05	WBGene00012921	21	265	3.63	6.52E-06	0.0001331	WBGene00018772	298	835	1.49	9.63E-06	0.0001792
WBGene00005003	214	677	1.66	4.32E-06	9.75E-05	WBGene00011393	6591	15326	1.22	6.56E-06	0.0001338	WBGene00017327	622	1667	1.42	9.64E-06	0.0001792
WBGene00009862	3069	1179	-1.38	4.32E-06	9.75E-05	WBGene00022661	32	211	2.72	6.57E-06	0.0001339	WBGene00010451	3010	1202	-1.32	9.71E-06	0.0001802
WBGene00016108	108	403	1.9	4.34E-06	9.79E-05	WBGene00017467	151	526	1.8	6.63E-06	0.0001349	WBGene00008874	7	90	3.61	9.81E-06	0.0001818
WBGene00019239	3731	1539	-1.28	4.39E-06	9.88E-05	WBGene00012701	7173	2771	-1.37	6.64E-06	0.0001349	WBGene00003775	11	118	3.46	9.86E-06	0.0001826
WBGene00017320	82	320	1.97	4.41E-06	9.91E-05	WBGene00015645	442	1202	1.44	6.65E-06	0.000135	WBGene00018274	575	1360	1.24	9.90E-06	0.0001831

WBGene00016953	100	520	2.38	4.41E-06	9.91E-05	WBGene00195143	1	55	5.92	6.66E-06	0.0001351	WBGene00016309	13489	5463	-1.3	1.01E-05	0.0001864
WBGene00009088	3613	1175	-1.62	4.42E-06	9.91E-05	WBGene00007206	376	1277	1.76	6.68E-06	0.0001352	WBGene00044382	18	170	3.27	1.01E-05	0.0001864
WBGene00010918	1613	3817	1.24	4.42E-06	9.91E-05	WBGene00002024	727	2735	1.91	6.75E-06	0.0001366	WBGene00009609	1	50	6.36	1.02E-05	0.0001888
WBGene00000397	9066	23352	1.36	4.47E-06	1.00E-04	WBGene00007314	42	226	2.42	6.79E-06	0.0001372	WBGene00004220	3533	9144	1.37	1.03E-05	0.0001893
WBGene00010642	1289	3442	1.42	4.48E-06	0.00010017	WBGene00012096	1671	622	-1.43	6.85E-06	0.0001381	WBGene00009811	930	2199	1.24	1.03E-05	0.0001896
WBGene00016160	36	210	2.56	4.49E-06	0.00010017	WBGene00004285	24	162	2.78	6.85E-06	0.0001381	WBGene00011427	1367	4148	1.6	1.03E-05	0.0001896
WBGene00017549	2874	753	-1.93	4.50E-06	0.00010021	WBGene00020367	1168	2765	1.24	6.96E-06	0.0001403	WBGene000001171	950	2699	1.51	1.03E-05	0.0001896
WBGene00013273	546	1409	1.37	4.55E-06	0.00010123	WBGene00020222	32	289	3.18	7.01E-06	0.000141	WBGene00009850	684	1815	1.41	1.03E-05	0.0001896
WBGene00000211	8451	3316	-1.35	4.59E-06	0.00010195	WBGene00009356	45	282	2.64	7.03E-06	0.0001413	WBGene00002017	7915	2073	-1.93	1.04E-05	0.0001898
WBGene00011911	56	0	-7.3	4.61E-06	0.00010227	WBGene00017014	230	666	1.53	7.10E-06	0.0001425	WBGene00004830	6548	15985	1.29	1.04E-05	0.0001904
WBGene00004127	1496	4611	1.62	4.62E-06	0.00010227	WBGene00004854	7296	16749	1.2	7.16E-06	0.0001436	WBGene00003860	195	740	1.92	1.04E-05	0.0001904
WBGene00016533	147	506	1.78	4.62E-06	0.00010227	WBGene00022696	827	2093	1.34	7.22E-06	0.0001445	WBGene00012716	5370	2046	-1.39	1.04E-05	0.0001905
WBGene00019518	234	955	2.03	4.64E-06	0.00010255	WBGene00016266	195	682	1.81	7.22E-06	0.0001445	WBGene00014261	568	1967	1.79	1.05E-05	0.0001918
WBGene00020665	16859	6283	-1.42	4.66E-06	0.00010308	WBGene00014035	24	152	2.68	7.27E-06	0.0001453	WBGene00013425	4655	1828	-1.35	1.05E-05	0.000192
WBGene00007802	121	408	1.75	4.68E-06	0.00010332	WBGene00008194	1101	5018	2.19	7.29E-06	0.0001455	WBGene00013433	2538	840	-1.59	1.05E-05	0.0001922
WBGene00002986	3144	1151	-1.45	4.69E-06	0.00010332	WBGene00013086	14074	4865	-1.53	7.31E-06	0.0001457	WBGene00012066	2722	1058	-1.36	1.06E-05	0.0001925
WBGene00008727	212	1022	2.27	4.69E-06	0.00010332	WBGene00009388	5	90	4.12	7.37E-06	0.0001468	WBGene00000768	3157	8029	1.35	1.06E-05	0.0001927
WBGene00016817	293	851	1.54	4.73E-06	0.00010403	WBGene00019522	2230	943	-1.24	7.38E-06	0.0001469	WBGene00011556	21	128	2.62	1.07E-05	0.0001946
WBGene00008829	725	236	-1.62	4.74E-06	0.00010403	WBGene00010365	10307	3289	-1.65	7.43E-06	0.0001476	WBGene00010904	521	1606	1.62	1.07E-05	0.000195
WBGene00003956	1087	3702	1.77	4.77E-06	0.00010467	WBGene00008558	130	478	1.88	7.44E-06	0.0001476	WBGene00000730	36	203	2.49	1.09E-05	0.0001976
WBGene00017252	5003	1797	-1.48	4.78E-06	0.00010467	WBGene00023486	2	109	5.67	7.48E-06	0.0001483	WBGene00010019	74	314	2.09	1.10E-05	0.0001982
WBGene00005485	43	0	-8.74	4.80E-06	0.00010505	WBGene00013539	125	438	1.81	7.51E-06	0.0001488	WBGene00009797	840	2155	1.36	1.10E-05	0.0001982
WBGene00008547	4182	9781	1.23	4.81E-06	0.00010519	WBGene00020075	340	1063	1.65	7.53E-06	0.0001489	WBGene00000069	137	512	1.9	1.10E-05	0.0001983
WBGene00018174	200	1092	2.45	4.82E-06	0.00010529	WBGene00019579	25	189	2.9	7.56E-06	0.0001492	WBGene00004238	1086	2594	1.26	1.10E-05	0.0001987
WBGene00007883	632	2535	2	4.83E-06	0.00010539	WBGene00016310	53	239	2.16	7.56E-06	0.0001492	WBGene00001559	6123	13979	1.19	1.11E-05	0.0001993
WBGene00009142	257	793	1.63	4.84E-06	0.00010541	WBGene00019417	2496	960	-1.38	7.57E-06	0.0001492	WBGene00000043	18	146	3.01	1.11E-05	0.0001997
WBGene00018266	278	1010	1.86	4.85E-06	0.00010541	WBGene00012254	686	2152	1.65	7.76E-06	0.0001529	WBGene00077495	390	105	-1.89	1.11E-05	0.0002002
WBGene00020484	274	801	1.55	4.92E-06	0.00010679	WBGene00018668	1545	585	-1.4	7.78E-06	0.0001529	WBGene00008144	395	1393	1.82	1.12E-05	0.0002007
WBGene00013458	5776	13473	1.22	4.92E-06	0.00010683	WBGene00009876	15	127	3.12	7.79E-06	0.0001529	WBGene00020450	549	179	-1.61	1.12E-05	0.0002016
WBGene00008375	167	738	2.15	5.07E-06	0.00010985	WBGene00007342	4910	1898	-1.37	7.79E-06	0.0001529	WBGene00017236	63	279	2.15	1.12E-05	0.0002017
WBGene00001104	37703	13830	-1.45	5.13E-06	0.00011099	WBGene00008996	19	137	2.82	7.80E-06	0.0001529	WBGene00195190	2352	836	-1.49	1.12E-05	0.0002017
WBGene00015913	698	2058	1.56	5.18E-06	0.00011204	WBGene00017365	4549	1369	-1.73	7.81E-06	0.0001529	WBGene00015002	100	371	1.89	1.13E-05	0.0002031
WBGene00018874	37	320	3.12	5.23E-06	0.00011283	WBGene00019752	27	184	2.76	7.83E-06	0.0001532	WBGene00021113	125	3	-5.5	1.14E-05	0.0002044
WBGene00011020	35	227	2.72	5.24E-06	0.00011311	WBGene00010742	13312	30580	1.2	7.88E-06	0.000154	WBGene00007170	8258	18777	1.19	1.15E-05	0.0002057
WBGene00044197	6133	2402	-1.35	5.32E-06	0.00011444	WBGene00007552	2189	5581	1.35	7.90E-06	0.0001542	WBGene00007938	614	1882	1.62	1.15E-05	0.0002057
WBGene00044387	530	1704	1.69	5.32E-06	0.00011444	WBGene00009932	482	1447	1.59	7.98E-06	0.0001555	WBGene00008731	738	1848	1.33	1.15E-05	0.0002057
WBGene00020490	1285	3318	1.37	5.33E-06	0.00011444	WBGene00006875	3161	7129	1.17	7.98E-06	0.0001555	WBGene00016234	275	869	1.66	1.16E-05	0.0002072
WBGene00012387	321	934	1.54	5.36E-06	0.00011485	WBGene00013566	946	203	-2.22	8.00E-06	0.0001556	WBGene00012560	2023	608	-1.73	1.17E-05	0.0002074
WBGene00021966	9692	2978	-1.7	5.36E-06	0.00011485	WBGene00006682	102	428	2.07	8.00E-06	0.0001556	WBGene00044314	3209	1270	-1.34	1.17E-05	0.0002074
WBGene00012811	185	613	1.73	5.37E-06	0.00011485	WBGene00021876	3086	8069	1.39	8.02E-06	0.0001558	WBGene00011028	786	1810	1.2	1.17E-05	0.0002075
WBGene00009130	1	87	6.08	5.37E-06	0.00011485	WBGene00020451	1029	260	-1.98	8.03E-06	0.0001559	WBGene00000037	3323	7471	1.17	1.17E-05	0.0002076
WBGene00017253	10897	4343	-1.33	5.40E-06	0.00011527	WBGene00018369	1907	5092	1.42	8.06E-06	0.0001563	WBGene00017904	9997	24194	1.28	1.17E-05	0.0002079
WBGene00004221	911	2430	1.41	5.42E-06	0.00011554	WBGene00006845	350	957	1.45	8.15E-06	0.0001577	WBGene00020849	68	285	2.06	1.17E-05	0.0002079
WBGene00016273	606	2061	1.77	5.42E-06	0.00011554	WBGene00001805	3	68	4.67	8.23E-06	0.0001588	WBGene00009607	0	46	6.94	1.18E-05	0.0002081
WBGene00011723	447	1554	1.8	5.44E-06	0.00011576	WBGene00011959	2361	881	-1.42	8.24E-06	0.0001588	WBGene00017653	486	1390	1.52	1.18E-05	0.0002082
WBGene00000518	906	2323	1.36	5.50E-06	0.00011682	WBGene00006783	259	811	1.65	8.25E-06	0.0001588	WBGene00020256	505	1307	1.37	1.18E-05	0.0002086
WBGene00001074	49	250	2.35	5.53E-06	0.00011752	WBGene00043981	1361	4087	1.59	8.26E-06	0.0001588	WBGene00021723	1400	489	-1.52	1.18E-05	0.0002086
WBGene00007368	647	1796	1.47	5.61E-06	0.00011903	WBGene00195051	21	141	2.74	8.26E-06	0.0001588	WBGene00045362	971	281	-1.79	1.18E-05	0.0002086
WBGene00013899	1305	3476	1.41	5.65E-06	0.00011971	WBGene00010808	44573	17362	-1.36	8.26E-06	0.0001588	WBGene00022319	1709	551	-1.63	1.19E-05	0.000209
WBGene00020590	1011	2485	1.3	5.71E-06	0.00012074	WBGene00044074	68	312	2.19	8.26E-06	0.0001588	WBGene00002011	5410	15707	1.54	1.19E-05	0.0002094

WBGene00010575	105	367	1.8	5.73E-06	0.00012106	WBGene00022389	1196	4042	1.76	8.31E-06	0.0001595	WBGene00015935	3	82	4.85	1.19E-05	0.0002099
WBGene00021586	196	822	2.07	5.73E-06	0.00012106	WBGene00015753	379	2065	2.45	8.36E-06	0.0001603	WBGene00015129	3033	875	-1.79	1.20E-05	0.0002111
WBGene00044630	2070	5121	1.31	5.75E-06	0.00012129	WBGene00011428	53	255	2.26	8.40E-06	0.0001608	WBGene00018272	152	533	1.81	1.22E-05	0.0002134
WBGene00013794	5534	1935	-1.52	5.83E-06	0.00012285	WBGene00010755	3431	7430	1.11	8.40E-06	0.0001608	WBGene00020606	37	178	2.27	1.24E-05	0.0002165
WBGene00001690	563	3180	2.5	5.86E-06	0.00012318	WBGene00018247	1105	354	-1.64	8.43E-06	0.0001609	WBGene00020929	130	417	1.69	1.24E-05	0.0002172
WBGene00017424	26	196	2.94	5.90E-06	0.00012392	WBGene00017969	407	2118	2.38	8.43E-06	0.0001609	WBGene00009410	2036	815	-1.32	1.25E-05	0.0002183
WBGene00019649	39	269	2.8	5.92E-06	0.00012421	WBGene00007739	14	107	2.97	8.51E-06	0.0001622	WBGene00019999	3	67	4.58	1.25E-05	0.0002187
WBGene00044227	70	360	2.37	5.95E-06	0.00012477	WBGene00010592	98	453	2.21	8.54E-06	0.0001626	WBGene00004992	714	1722	1.27	1.26E-05	0.0002197
WBGene00017755	91049	37701	-1.27	1.26E-05	0.0002199	WBGene00012034	8	112	3.8	1.77E-05	0.000284	WBGene00009349	183	684	1.9	2.43E-05	0.0003631
WBGene00019415	11176	4161	-1.43	1.27E-05	0.00022213	WBGene00004821	15314	4995	-1.62	1.77E-05	0.000284	WBGene00008296	321	1257	1.97	2.43E-05	0.0003631
WBGene00008285	152	494	1.7	1.28E-05	0.00022308	WBGene00000224	19829	43811	1.14	1.78E-05	0.0002852	WBGene00018340	375	1009	1.43	2.43E-05	0.0003631
WBGene00020662	27	174	2.71	1.29E-05	0.00022359	WBGene00013825	9	104	3.54	1.78E-05	0.0002865	WBGene00019411	120	557	2.21	2.45E-05	0.0003658
WBGene00001557	19	188	3.31	1.29E-05	0.00022472	WBGene00017254	4182	1728	-1.27	1.79E-05	0.0002867	WBGene00013835	239	697	1.54	2.46E-05	0.0003665
WBGene00006832	300	1537	2.36	1.29E-05	0.00022475	WBGene00021977	544	1322	1.28	1.80E-05	0.0002886	WBGene00007447	5883	2783	-1.08	2.47E-05	0.0003676
WBGene00017251	4884	1908	-1.36	1.30E-05	0.00022621	WBGene00022497	849	4949	2.54	1.83E-05	0.0002928	WBGene00008066	5413	2114	-1.36	2.50E-05	0.0003719
WBGene00003746	204	1365	2.74	1.32E-05	0.00022871	WBGene00016773	2	57	5.06	1.84E-05	0.0002939	WBGene00022252	140	421	1.59	2.50E-05	0.0003719
WBGene00006583	487	2269	2.22	1.32E-05	0.00022871	WBGene00008988	32	174	2.45	1.85E-05	0.0002955	WBGene00003075	452	2019	2.16	2.51E-05	0.000373
WBGene00004814	45236	18763	-1.27	1.32E-05	0.00022897	WBGene00018951	693	2162	1.64	1.86E-05	0.0002974	WBGene00014171	699	1816	1.38	2.52E-05	0.0003738
WBGene00021071	140	591	2.08	1.33E-05	0.00022932	WBGene00009819	210	625	1.57	1.87E-05	0.0002977	WBGene00021299	7997	2977	-1.43	2.52E-05	0.0003738
WBGene00002174	4221	9520	1.17	1.33E-05	0.00022955	WBGene00016722	1768	4816	1.45	1.87E-05	0.0002977	WBGene00077457	509	97	-2.39	2.53E-05	0.000375
WBGene00005005	0	36	8.51	1.33E-05	0.00022955	WBGene00009543	157	472	1.58	1.89E-05	0.0003011	WBGene00009724	398	934	1.23	2.53E-05	0.000375
WBGene00007480	148	483	1.71	1.33E-05	0.00022955	WBGene00008500	230	723	1.65	1.89E-05	0.0003012	WBGene00007981	512	1372	1.42	2.54E-05	0.0003757
WBGene00007779	5262	11102	1.08	1.33E-05	0.00022955	WBGene00008263	1386	3309	1.26	1.90E-05	0.0003021	WBGene00020158	1304	3023	1.21	2.55E-05	0.0003764
WBGene00022610	299	876	1.55	1.34E-05	0.00022955	WBGene00016165	1028	2513	1.29	1.90E-05	0.0003026	WBGene00077664	1558	653	-1.25	2.57E-05	0.0003801
WBGene00017857	28	190	2.77	1.34E-05	0.00023012	WBGene00022557	13199	5447	-1.28	1.91E-05	0.0003034	WBGene00009895	35	186	2.41	2.59E-05	0.0003822
WBGene00006067	598	1497	1.32	1.34E-05	0.00023029	WBGene00000702	134	576	2.11	1.92E-05	0.0003042	WBGene00006641	888	2046	1.2	2.60E-05	0.0003839
WBGene00009885	713	2144	1.59	1.35E-05	0.00023154	WBGene00020788	1437	4518	1.65	1.92E-05	0.0003047	WBGene00000242	718	1828	1.35	2.61E-05	0.000384
WBGene00010539	4385	9459	1.11	1.37E-05	0.00023387	WBGene00022179	425	1113	1.39	1.94E-05	0.0003071	WBGene00021635	423	1114	1.4	2.61E-05	0.000384
WBGene00005643	3262	1408	-1.21	1.37E-05	0.00023442	WBGene00077663	2484	937	-1.41	1.94E-05	0.0003071	WBGene00013666	120	410	1.78	2.62E-05	0.0003854
WBGene00015566	537	1388	1.37	1.37E-05	0.00023489	WBGene00011809	14289	5528	-1.37	1.94E-05	0.0003071	WBGene00008089	482	2090	2.12	2.63E-05	0.0003866
WBGene00012134	653	1763	1.43	1.38E-05	0.00023637	WBGene00008342	7	95	3.68	1.96E-05	0.0003101	WBGene00017063	17	129	2.93	2.64E-05	0.0003876
WBGene00006902	58558	22301	-1.39	1.39E-05	0.00023637	WBGene00006865	62	331	2.43	1.97E-05	0.0003104	WBGene00009061	14	114	3.02	2.65E-05	0.000389
WBGene00016633	417	1057	1.34	1.39E-05	0.00023727	WBGene00019203	544	1367	1.33	2.00E-05	0.0003151	WBGene00022488	17970	6752	-1.41	2.67E-05	0.000391
WBGene00019922	19998	8065	-1.31	1.39E-05	0.00023733	WBGene00018746	9646	3706	-1.38	2.01E-05	0.0003157	WBGene00016585	248	848	1.78	2.67E-05	0.000391
WBGene00001110	2190	850	-1.37	1.40E-05	0.00023754	WBGene00008498	183	555	1.6	2.01E-05	0.0003158	WBGene00016596	89	2832	5	2.69E-05	0.0003929
WBGene00013456	469	1791	1.93	1.41E-05	0.00023898	WBGene00021984	692	2461	1.83	2.01E-05	0.0003163	WBGene00016289	4094	11241	1.46	2.71E-05	0.0003956
WBGene00017262	183	1508	3.04	1.41E-05	0.00024002	WBGene00016586	7355	3031	-1.28	2.01E-05	0.0003163	WBGene00022767	159	498	1.64	2.71E-05	0.0003956
WBGene00020478	1331	3303	1.31	1.42E-05	0.00024055	WBGene00002224	313	979	1.64	2.02E-05	0.0003167	WBGene00017779	86	307	1.84	2.73E-05	0.0003979
WBGene00022797	170	608	1.84	1.42E-05	0.00024117	WBGene00010704	9872	4672	-1.08	2.02E-05	0.0003167	WBGene00007593	4050	8902	1.14	2.74E-05	0.0003994
WBGene00000785	19	334	4.11	1.44E-05	0.0002437	WBGene00010098	3471	1294	-1.42	2.03E-05	0.0003172	WBGene00013875	6112	2426	-1.33	2.74E-05	0.0003998
WBGene00011805	30696	11192	-1.46	1.45E-05	0.00024551	WBGene00002015	7110	2009	-1.82	2.03E-05	0.0003173	WBGene00003886	668	1638	1.29	2.75E-05	0.0004001
WBGene00009796	877	2567	1.55	1.46E-05	0.00024658	WBGene00018446	13933	5759	-1.27	2.03E-05	0.0003173	WBGene00007146	584	1453	1.32	2.76E-05	0.0004001
WBGene00011436	2727	6719	1.3	1.47E-05	0.00024762	WBGene00019480	187	529	1.5	2.04E-05	0.0003187	WBGene00044058	529	2021	1.93	2.76E-05	0.0004001
WBGene00009617	689	1609	1.22	1.47E-05	0.00024801	WBGene00000553	1954	5939	1.6	2.04E-05	0.0003189	WBGene00001852	137	433	1.66	2.76E-05	0.0004001
WBGene00017911	3115	1308	-1.25	1.47E-05	0.00024821	WBGene00011131	766	254	-1.59	2.05E-05	0.0003193	WBGene00006646	3268	7000	1.1	2.76E-05	0.0004001
WBGene00017362	40	191	2.27	1.48E-05	0.00024882	WBGene00017229	10	114	3.52	2.05E-05	0.0003198	WBGene000021158	31	168	2.42	2.77E-05	0.0004001
WBGene00019640	106	430	2.02	1.48E-05	0.00024882	WBGene00000491	946	2389	1.34	2.07E-05	0.0003223	WBGene00014746	621	197	-1.65	2.77E-05	0.0004014
WBGene00009432	63	367	2.54	1.48E-05	0.00024891	WBGene00019035	8192	2902	-1.5	2.09E-05	0.0003244	WBGene00004993	80	295	1.89	2.78E-05	0.0004028
WBGene00000438	530	1409	1.41	1.49E-05	0.00024957	WBGene00016749	16878	36392	1.11	2.10E-05	0.0003258	WBGene00002991	3492	7619	1.13	2.79E-05	0.0004034
WBGene00011906	5734	13204	1.2	1.49E-05	0.00025003	WBGene00006811	1038	4146	2	2.11E-05	0.0003269	WBGene00006532	225	705	1.65	2.81E-05	0.0004065

WBGene00000054	229	660	1.52	1.50E-05	0.00025125	WBGene00016107	69	283	2.03	2.12E-05	0.0003287	WBGene00011591	349	91	-1.93	2.82E-05	0.0004066
WBGene00001966	1831	528	-1.79	1.50E-05	0.00025135	WBGene00007211	5035	2170	-1.21	2.12E-05	0.0003294	WBGene00017961	142	405	1.51	2.83E-05	0.0004083
WBGene00013155	2494	1047	-1.25	1.50E-05	0.00025135	WBGene00010138	71	300	2.09	2.14E-05	0.0003317	WBGene00006822	183	536	1.55	2.83E-05	0.0004086
WBGene00020100	525	1431	1.45	1.51E-05	0.00025168	WBGene00001548	270	845	1.64	2.15E-05	0.0003334	WBGene00000232	651	1770	1.44	2.84E-05	0.0004094
WBGene00017570	10	104	3.41	1.51E-05	0.00025177	WBGene00001366	3567	7707	1.11	2.16E-05	0.0003339	WBGene00015984	10	98	3.23	2.85E-05	0.0004105
WBGene00021542	11855	4781	-1.31	1.53E-05	0.00025534	WBGene00001129	386	991	1.36	2.16E-05	0.0003342	WBGene00012810	56	254	2.18	2.85E-05	0.0004105
WBGene00019593	54	464	3.09	1.54E-05	0.00025666	WBGene00023355	496	139	-1.84	2.17E-05	0.0003343	WBGene00009306	12650	26337	1.06	2.86E-05	0.0004105
WBGene00015607	5704	2450	-1.22	1.55E-05	0.00025768	WBGene00016354	12569	28925	1.2	2.17E-05	0.0003347	WBGene00012364	9	107	3.58	2.87E-05	0.0004118
WBGene00010632	186	558	1.59	1.56E-05	0.00025975	WBGene00011791	6009	2504	-1.26	2.18E-05	0.0003359	WBGene00020360	3473	7787	1.16	2.87E-05	0.0004118
WBGene00009312	31	234	2.89	1.57E-05	0.00026021	WBGene00001699	65	359	2.46	2.20E-05	0.0003385	WBGene00021877	1739	612	-1.51	2.88E-05	0.0004125
WBGene00015662	177	32	-2.47	1.57E-05	0.00026078	WBGene00007890	3	69	4.51	2.20E-05	0.0003386	WBGene00019227	1922	4498	1.23	2.89E-05	0.0004141
WBGene00010172	29	183	2.66	1.57E-05	0.00026078	WBGene00011784	41	207	2.33	2.21E-05	0.0003389	WBGene00008254	204	1078	2.4	2.90E-05	0.0004153
WBGene00000747	615	1812	1.56	1.58E-05	0.00026163	WBGene00001814	1581	3585	1.18	2.24E-05	0.0003437	WBGene00013759	1714	601	-1.51	2.92E-05	0.0004171
WBGene00000750	115	603	2.39	1.58E-05	0.00026231	WBGene00007247	26	152	2.54	2.24E-05	0.0003443	WBGene00003768	406	1566	1.95	2.92E-05	0.0004171
WBGene00022664	161	579	1.85	1.59E-05	0.00026297	WBGene00017402	21273	5657	-1.91	2.27E-05	0.0003448	WBGene00018377	32	146	2.2	2.92E-05	0.0004176
WBGene00021180	2420	939	-1.37	1.59E-05	0.00026344	WBGene00001616	78	671	3.1	2.27E-05	0.000348	WBGene00006372	1280	3014	1.24	2.93E-05	0.0004177
WBGene00008932	623	1497	1.27	1.60E-05	0.0002635	WBGene00003400	7431	15749	1.08	2.28E-05	0.0003482	WBGene00002089	56	309	2.47	2.93E-05	0.0004178
WBGene00014210	139	627	2.17	1.61E-05	0.00026586	WBGene00015622	217	889	2.03	2.28E-05	0.0003485	WBGene00006712	421	1131	1.43	2.94E-05	0.0004185
WBGene00045409	2116	5916	1.48	1.62E-05	0.00026732	WBGene00015741	693	1669	1.27	2.29E-05	0.0003499	WBGene00010200	53	250	2.24	2.94E-05	0.0004185
WBGene00003980	1672	4718	1.5	1.63E-05	0.00026861	WBGene00013477	4334	9532	1.14	2.29E-05	0.0003499	WBGene00001705	490	2008	2.04	2.97E-05	0.0004227
WBGene00044452	58	279	2.26	1.64E-05	0.00026934	WBGene00044692	16204	6646	-1.29	2.29E-05	0.0003499	WBGene00004999	234	1293	2.46	2.98E-05	0.0004237
WBGene00000084	70	300	2.09	1.64E-05	0.00027002	WBGene00018367	6649	14673	1.14	2.31E-05	0.0003515	WBGene00011423	1401	3294	1.23	2.98E-05	0.0004238
WBGene00015748	1949	4419	1.18	1.65E-05	0.00027041	WBGene00020073	44716	19354	-1.21	2.32E-05	0.0003539	WBGene00022669	14788	4831	-1.61	3.02E-05	0.000428
WBGene00006468	1778	4575	1.36	1.65E-05	0.00027108	WBGene00017448	3299	7464	1.18	2.33E-05	0.0003551	WBGene00015706	27	158	2.56	3.02E-05	0.0004289
WBGene00011923	38	203	2.4	1.65E-05	0.00027108	WBGene00017041	78	291	1.91	2.36E-05	0.0003582	WBGene00044132	216	793	1.88	3.03E-05	0.0004292
WBGene00013652	5455	2315	-1.24	1.67E-05	0.00027283	WBGene00012433	570	3338	2.55	2.36E-05	0.0003585	WBGene00007261	5055	10826	1.1	3.04E-05	0.0004302
WBGene00007717	64	383	2.58	1.67E-05	0.00027387	WBGene00016753	179	38	-2.22	2.37E-05	0.0003591	WBGene00014132	9	124	3.73	3.04E-05	0.0004307
WBGene00019040	4033	1718	-1.23	1.68E-05	0.00027495	WBGene00044043	34	440	3.67	2.37E-05	0.0003596	WBGene00010646	189	710	1.91	3.05E-05	0.0004311
WBGene00016507	1145	2435	1.09	1.71E-05	0.00027858	WBGene00007396	485	1373	1.5	2.37E-05	0.0003596	WBGene00013028	11	111	3.28	3.06E-05	0.0004321
WBGene00000667	25	235	3.25	1.72E-05	0.00028035	WBGene00044253	739	232	-1.67	2.38E-05	0.0003596	WBGene00021774	8402	3500	-1.26	3.07E-05	0.0004331
WBGene00015320	314	58	-2.45	1.72E-05	0.00028035	WBGene00003578	1687	3859	1.19	2.38E-05	0.0003596	WBGene00004155	17528	45365	1.37	3.08E-05	0.0004337
WBGene00014067	1028	5398	2.39	1.72E-05	0.00028035	WBGene00005153	775	2091	1.43	2.38E-05	0.0003596	WBGene00015869	3	63	4.38	3.08E-05	0.0004345
WBGene00015910	125	782	2.65	1.73E-05	0.00028073	WBGene00010345	2266	6292	1.47	2.38E-05	0.0003596	WBGene00045382	635	152	-2.06	3.09E-05	0.0004351
WBGene00019829	2	61	4.65	1.74E-05	0.0002823	WBGene00004790	1436	3339	1.22	2.39E-05	0.0003605	WBGene00016677	51	374	2.87	3.09E-05	0.0004351
WBGene00006464	44	398	3.19	1.74E-05	0.0002823	WBGene00019458	2889	970	-1.57	2.40E-05	0.0003611	WBGene00016246	74	296	1.99	3.10E-05	0.0004351
WBGene00017576	6771	15237	1.17	1.74E-05	0.00028242	WBGene00012135	20	160	3.02	2.40E-05	0.0003611	WBGene00013080	337	1447	2.1	3.10E-05	0.0004354
WBGene00007229	1028	3403	1.73	1.74E-05	0.00028242	WBGene00012592	272	792	1.54	2.40E-05	0.0003611	WBGene00003091	127	479	1.91	3.12E-05	0.0004384
WBGene00019700	15705	6663	-1.24	1.74E-05	0.00028242	WBGene00006531	199	1100	2.46	2.40E-05	0.0003611	WBGene00015914	1542	571	-1.43	3.14E-05	0.0004398
WBGene00013651	16657	6761	-1.3	1.75E-05	0.00028243	WBGene00014307	3342	11554	1.79	2.41E-05	0.0003611	WBGene00017900	5154	16123	1.65	3.16E-05	0.0004427
WBGene00015055	585	1407	1.27	1.75E-05	0.00028276	WBGene00013746	604	2154	1.84	2.41E-05	0.0003611	WBGene00013410	3467	1431	-1.28	3.18E-05	0.0004448
WBGene00008207	4944	1424	-1.8	1.75E-05	0.00028303	WBGene00009229	196	702	1.84	2.41E-05	0.0003613	WBGene00003890	169	914	2.43	3.22E-05	0.0004498
WBGene00021157	16	235	3.83	1.75E-05	0.00028303	WBGene00044792	243	730	1.59	2.41E-05	0.0003618	WBGene00003567	10571	25314	1.26	3.23E-05	0.0004519
WBGene00020168	3872	1433	-1.43	1.76E-05	0.00028353	WBGene00001588	38	208	2.44	2.43E-05	0.0003631	WBGene00021160	26	156	2.58	3.24E-05	0.0004519
WBGene00013254	9594	2956	-1.7	1.76E-05	0.00028399	WBGene00000951	68	305	2.17	2.43E-05	0.0003631	WBGene00044617	29	167	2.54	3.24E-05	0.0004521
WBGene00010568	20075	7972	-1.33	3.25E-05	0.00045323	WBGene00010901	284	1311	2.21	4.16E-05	0.0005439	WBGene00044694	6587	3038	-1.12	5.28E-05	0.0006492
WBGene00014101	177	568	1.68	3.27E-05	0.0004553	WBGene00022847	196	607	1.63	4.17E-05	0.0005441	WBGene00017060	451	1139	1.34	5.28E-05	0.0006497
WBGene00011756	2585	5737	1.15	3.27E-05	0.0004553	WBGene00009288	4529	10373	1.2	4.17E-05	0.0005441	WBGene00016561	9981	4722	-1.08	5.30E-05	0.0006515
WBGene00003232	133	722	2.44	3.29E-05	0.00045707	WBGene00020862	4	70	4.28	4.17E-05	0.0005441	WBGene00019343	2055	775	-1.41	5.33E-05	0.0006546
WBGene00007757	2	67	4.93	3.29E-05	0.00045707	WBGene00014064	2475	697	-1.83	4.18E-05	0.0005451	WBGene00008571	6680	14789	1.15	5.35E-05	0.0006555
WBGene00014789	887	338	-1.39	3.30E-05	0.00045782	WBGene00016274	7	93	3.65	4.18E-05	0.0005451	WBGene00016294	6483	2848	-1.19	5.35E-05	0.0006555

WBGene00010050	304	927	1.61	3.30E-05	0.00045782	WBGene00010944	743	2902	1.97	4.20E-05	0.0005465	WBGene00000544	666	231	-1.53	5.38E-05	0.000659
WBGene00013816	3900	1439	-1.44	3.30E-05	0.00045782	WBGene00045269	807	1964	1.28	4.20E-05	0.0005466	WBGene00010796	3168	11448	1.85	5.38E-05	0.000659
WBGene00003773	1794	5139	1.52	3.31E-05	0.00045858	WBGene00022611	1044	4617	2.14	4.25E-05	0.0005523	WBGene00013849	3213	6650	1.05	5.39E-05	0.0006595
WBGene00010219	6752	2706	-1.32	3.33E-05	0.00046074	WBGene00004823	4360	1311	-1.73	4.25E-05	0.0005525	WBGene00011908	7845	3253	-1.27	5.39E-05	0.0006595
WBGene00008723	4459	2024	-1.14	3.34E-05	0.00046202	WBGene00013534	42	290	2.78	4.26E-05	0.0005531	WBGene00015300	295	1505	2.35	5.40E-05	0.0006595
WBGene00015859	443	1192	1.43	3.37E-05	0.00046555	WBGene00000759	102	442	2.11	4.29E-05	0.0005563	WBGene00008401	3235	6849	1.08	5.43E-05	0.0006631
WBGene00012178	45	250	2.46	3.37E-05	0.00046587	WBGene00010039	4794	10229	1.09	4.35E-05	0.0005639	WBGene00016023	1804	704	-1.36	5.43E-05	0.0006631
WBGene00011877	78	272	1.81	3.38E-05	0.00046641	WBGene00017076	31	166	2.43	4.37E-05	0.0005654	WBGene00004813	96125	38919	-1.3	5.44E-05	0.0006639
WBGene00017296	1439	3205	1.16	3.38E-05	0.00046657	WBGene00001053	97	342	1.82	4.37E-05	0.0005656	WBGene00007916	685	2922	2.09	5.46E-05	0.0006659
WBGene00007660	8	91	3.58	3.38E-05	0.00046659	WBGene00002976	296	800	1.43	4.37E-05	0.0005656	WBGene000050943	88	319	1.86	5.49E-05	0.0006692
WBGene00008241	582	191	-1.61	3.39E-05	0.00046745	WBGene00012481	6781	2592	-1.39	4.38E-05	0.0005662	WBGene00009476	110	361	1.71	5.55E-05	0.0006756
WBGene00011659	1	52	5.64	3.42E-05	0.00047071	WBGene00013637	54	241	2.16	4.39E-05	0.0005662	WBGene00022558	1179	334	-1.82	5.58E-05	0.0006788
WBGene00016951	321	804	1.32	3.42E-05	0.00047071	WBGene00014516	1529	534	-1.52	4.39E-05	0.0005662	WBGene00023415	129	444	1.79	5.59E-05	0.0006798
WBGene00044245	17	226	3.73	3.42E-05	0.00047071	WBGene00013124	2765	5993	1.12	4.41E-05	0.0005683	WBGene00020294	457	2308	2.34	5.60E-05	0.0006807
WBGene00020254	46	200	2.11	3.43E-05	0.00047085	WBGene00012654	1859	751	-1.31	4.41E-05	0.0005683	WBGene00008802	4434	1864	-1.25	5.62E-05	0.0006819
WBGene00021416	636	1483	1.22	3.44E-05	0.00047179	WBGene00022574	6	101	3.96	4.41E-05	0.0005683	WBGene00018109	10385	3663	-1.5	5.65E-05	0.0006851
WBGene00013896	232	747	1.69	3.44E-05	0.00047213	WBGene00012127	156	476	1.6	4.42E-05	0.0005683	WBGene00013278	5568	2146	-1.38	5.69E-05	0.00069
WBGene00021219	1746	495	-1.82	3.45E-05	0.00047213	WBGene00007140	80	255	1.67	4.43E-05	0.0005699	WBGene00001964	1346	359	-1.91	5.70E-05	0.0006905
WBGene00007868	59	503	3.09	3.46E-05	0.0004741	WBGene00014074	811	2062	1.35	4.44E-05	0.0005703	WBGene00009798	108	339	1.65	5.70E-05	0.0006905
WBGene00012063	3146	1294	-1.28	3.47E-05	0.00047528	WBGene00016332	1366	2916	1.09	4.46E-05	0.0005724	WBGene00006462	1617	3571	1.14	5.72E-05	0.0006914
WBGene00015830	2482	904	-1.46	3.48E-05	0.0004755	WBGene00013137	4738	1929	-1.3	4.48E-05	0.0005743	WBGene00018472	1906	4126	1.11	5.72E-05	0.0006916
WBGene00007932	391	1340	1.78	3.49E-05	0.00047609	WBGene00007850	3958	1589	-1.32	4.48E-05	0.000575	WBGene00003168	59	242	2.03	5.72E-05	0.0006916
WBGene00007629	98	336	1.78	3.49E-05	0.00047639	WBGene00002242	12	98	3.06	4.49E-05	0.0005754	WBGene00022829	40	196	2.29	5.78E-05	0.0006977
WBGene00020863	93	340	1.87	3.49E-05	0.00047639	WBGene00008239	595	1522	1.36	4.50E-05	0.0005757	WBGene00007959	1427	5228	1.87	5.79E-05	0.0006981
WBGene00044758	411	93	-2.15	3.50E-05	0.00047686	WBGene00020345	668	230	-1.54	4.51E-05	0.0005767	WBGene00020586	28	210	2.88	5.79E-05	0.0006981
WBGene00014163	3936	1365	-1.53	3.51E-05	0.00047835	WBGene00022277	11856	4717	-1.33	4.56E-05	0.000583	WBGene00021931	58	454	2.97	5.81E-05	0.0007005
WBGene00044644	28	734	4.7	3.51E-05	0.00047835	WBGene00017794	81	506	2.65	4.57E-05	0.0005845	WBGene00007857	19	240	3.64	5.86E-05	0.0007055
WBGene00011772	16	125	2.94	3.54E-05	0.00048163	WBGene00003097	490	2268	2.21	4.58E-05	0.0005848	WBGene00008611	2441	918	-1.41	5.87E-05	0.0007055
WBGene00008568	142	413	1.55	3.56E-05	0.00048401	WBGene00012038	3287	1107	-1.57	4.58E-05	0.0005849	WBGene00019047	23	140	2.61	5.87E-05	0.0007055
WBGene00015803	3491	11890	1.77	3.57E-05	0.00048523	WBGene00008256	19	130	2.8	4.59E-05	0.0005849	WBGene00010355	19	190	3.34	5.88E-05	0.0007071
WBGene00010503	724	1746	1.27	3.58E-05	0.00048544	WBGene00010134	3481	8074	1.21	4.61E-05	0.000587	WBGene00018245	3055	1185	-1.37	5.89E-05	0.0007078
WBGene00017267	9	112	3.6	3.60E-05	0.00048765	WBGene00017976	577	1395	1.27	4.61E-05	0.000587	WBGene00016544	26	153	2.56	5.91E-05	0.000709
WBGene00005138	94	13	-2.87	3.62E-05	0.00049037	WBGene00012199	805	2516	1.64	4.64E-05	0.0005899	WBGene00005611	4	67	3.99	5.92E-05	0.0007101
WBGene00009270	5441	2237	-1.28	3.63E-05	0.00049081	WBGene00008080	17707	7045	-1.33	4.65E-05	0.0005906	WBGene00023163	674	258	-1.39	5.95E-05	0.0007135
WBGene00017914	269	1044	1.96	3.64E-05	0.00049226	WBGene00020175	1254	488	-1.36	4.66E-05	0.0005925	WBGene00011229	12548	5056	-1.31	5.96E-05	0.0007137
WBGene000195077	2202	810	-1.44	3.66E-05	0.00049417	WBGene00007154	32	170	2.4	4.67E-05	0.0005929	WBGene00007817	13	116	3.15	5.97E-05	0.0007147
WBGene00019896	9	93	3.38	3.67E-05	0.00049515	WBGene00001433	1602	617	-1.38	4.69E-05	0.0005949	WBGene00009257	31	279	3.17	5.99E-05	0.000716
WBGene00003165	459	1441	1.65	3.67E-05	0.00049528	WBGene00020883	800	256	-1.64	4.74E-05	0.0006002	WBGene00023492	8	73	3.26	6.03E-05	0.000721
WBGene00009995	87	585	2.76	3.68E-05	0.00049599	WBGene00019791	29197	13007	-1.17	4.74E-05	0.0006002	WBGene00009415	1937	795	-1.29	6.04E-05	0.0007215
WBGene00019408	2361	5729	1.28	3.69E-05	0.00049674	WBGene00022287	319	1644	2.37	4.74E-05	0.0006005	WBGene00008736	24	140	2.54	6.05E-05	0.0007216
WBGene00006436	15352	32778	1.09	3.74E-05	0.00050326	WBGene00077441	4813	1814	-1.41	4.76E-05	0.0006018	WBGene00017947	246	629	1.36	6.07E-05	0.0007239
WBGene00003515	22205	44753	1.01	3.75E-05	0.00050389	WBGene00017713	9056	3644	-1.31	4.78E-05	0.0006048	WBGene00014182	30	670	4.48	6.11E-05	0.000728
WBGene00001674	547	1338	1.29	3.75E-05	0.00050389	WBGene00020503	26	178	2.79	4.80E-05	0.000606	WBGene00021543	321	1130	1.82	6.14E-05	0.0007308
WBGene00007951	183	572	1.65	3.76E-05	0.00050506	WBGene00010105	3811	1335	-1.51	4.81E-05	0.0006068	WBGene00007887	6732	3154	-1.09	6.14E-05	0.0007308
WBGene00013877	12463	5836	-1.09	3.77E-05	0.00050622	WBGene00021541	16050	6545	-1.29	4.86E-05	0.0006129	WBGene00010716	70	315	2.17	6.16E-05	0.0007332
WBGene00005936	60	280	2.23	3.78E-05	0.00050647	WBGene00018899	359	1214	1.76	4.87E-05	0.0006143	WBGene00003106	349	864	1.31	6.19E-05	0.0007354
WBGene00000075	3984	1656	-1.27	3.78E-05	0.00050647	WBGene00044623	4404	18680	2.08	4.88E-05	0.0006145	WBGene00015523	2801	5789	1.05	6.19E-05	0.0007359
WBGene000194956	370	98	-1.92	3.79E-05	0.00050832	WBGene00009311	252	1101	2.13	4.89E-05	0.0006156	WBGene00008560	66	354	2.42	6.21E-05	0.000737
WBGene00021343	788	2061	1.39	3.80E-05	0.0005086	WBGene00045366	12739	5870	-1.12	4.91E-05	0.0006174	WBGene00000853	2232	10527	2.24	6.22E-05	0.0007377
WBGene00014059	7582	3197	-1.25	3.81E-05	0.00050991	WBGene00006980	235	867	1.89	4.91E-05	0.0006174	WBGene00010509	166	646	1.96	6.22E-05	0.0007379

WBGene00010870	8209	17663	1.11	3.82E-05	0.00050997	WBGene00000484	1033	2329	1.17	4.94E-05	0.0006208	WBGene00016628	91	368	2.01	6.25E-05	0.0007409
WBGene00022503	506	1245	1.3	3.82E-05	0.00051034	WBGene00018510	2001	4467	1.16	4.94E-05	0.0006208	WBGene00003917	14413	5536	-1.38	6.27E-05	0.0007426
WBGene00013891	361	2714	2.91	3.86E-05	0.00051486	WBGene00019825	5712	1875	-1.61	4.95E-05	0.0006209	WBGene00013445	3648	1457	-1.32	6.29E-05	0.0007439
WBGene00045498	9284	3705	-1.33	3.90E-05	0.00052072	WBGene00008634	3	93	4.76	4.96E-05	0.0006222	WBGene00016619	735	1809	1.3	6.29E-05	0.0007441
WBGene00009800	3739	8299	1.15	3.91E-05	0.0005208	WBGene00020337	453	112	-2.02	5.00E-05	0.0006253	WBGene00019815	4629	1827	-1.34	6.30E-05	0.0007447
WBGene00012446	529	1220	1.21	3.92E-05	0.00052218	WBGene00014946	2799	1132	-1.31	5.00E-05	0.0006253	WBGene00006812	4527	10466	1.24	6.31E-05	0.0007451
WBGene00013408	5655	2159	-1.39	3.92E-05	0.00052225	WBGene00011600	3276	1245	-1.4	5.00E-05	0.0006253	WBGene00002274	74	358	2.26	6.32E-05	0.0007454
WBGene00011330	3323	8158	1.3	3.98E-05	0.00052875	WBGene00014053	34	143	2.08	5.00E-05	0.0006255	WBGene00022304	531	188	-1.49	6.36E-05	0.0007505
WBGene00018581	189	818	2.12	3.98E-05	0.00052875	WBGene00007863	1184	515	-1.2	5.01E-05	0.000626	WBGene00000866	5735	1999	-1.52	6.38E-05	0.0007521
WBGene00016247	2	60	5.04	4.00E-05	0.00053128	WBGene00001624	49	318	2.69	5.01E-05	0.000626	WBGene00045481	202	645	1.67	6.38E-05	0.0007521
WBGene00009271	199	664	1.73	4.01E-05	0.00053234	WBGene00008607	2752	6641	1.27	5.03E-05	0.0006276	WBGene00000527	3714	8080	1.12	6.43E-05	0.0007568
WBGene00011655	0	35	8.46	4.02E-05	0.00053234	WBGene00010587	1168	2800	1.26	5.04E-05	0.0006276	WBGene00000286	241	1037	2.11	6.43E-05	0.0007569
WBGene00017129	278	896	1.69	4.03E-05	0.00053367	WBGene00015587	6882	2816	-1.29	5.04E-05	0.0006276	WBGene00016625	1722	3737	1.12	6.44E-05	0.0007574
WBGene00010540	2106	4580	1.12	4.03E-05	0.0005338	WBGene00018679	3155	1271	-1.31	5.05E-05	0.0006284	WBGene00004370	5625	12960	1.2	6.48E-05	0.0007617
WBGene00017632	1010	222	-2.18	4.04E-05	0.0005338	WBGene00044260	550	1769	1.69	5.06E-05	0.0006295	WBGene00019520	5310	14191	1.42	6.50E-05	0.0007627
WBGene00007799	2845	9244	1.7	4.05E-05	0.0005352	WBGene00044445	57	449	2.97	5.09E-05	0.0006322	WBGene00020369	2040	4284	1.07	6.50E-05	0.0007627
WBGene00000485	1770	4308	1.28	4.05E-05	0.0005352	WBGene00000602	13	138	3.41	5.09E-05	0.0006328	WBGene00022265	18661	7267	-1.36	6.50E-05	0.0007627
WBGene00000088	47	206	2.14	4.06E-05	0.00053543	WBGene00000039	32443	67274	1.05	5.10E-05	0.000633	WBGene00009108	132	446	1.76	6.51E-05	0.0007631
WBGene00012655	958	251	-1.93	4.06E-05	0.00053571	WBGene00020321	956	2120	1.15	5.13E-05	0.0006361	WBGene00018060	210	829	1.98	6.53E-05	0.000765
WBGene00022559	7401	2921	-1.34	4.07E-05	0.00053677	WBGene00017390	66	209	1.67	5.13E-05	0.0006361	WBGene00045497	30	239	2.97	6.55E-05	0.000766
WBGene00012276	15747	4867	-1.69	4.09E-05	0.00053798	WBGene00012162	102	357	1.8	5.14E-05	0.0006361	WBGene00000266	8512	18645	1.13	6.55E-05	0.000766
WBGene00000009	35	164	2.22	4.09E-05	0.00053798	WBGene00021322	1098	3722	1.76	5.14E-05	0.0006361	WBGene00019497	216	624	1.53	6.55E-05	0.000766
WBGene00013698	18491	7897	-1.23	4.09E-05	0.00053798	WBGene00011326	1021	2505	1.29	5.15E-05	0.0006373	WBGene00194710	285	738	1.37	6.59E-05	0.0007692
WBGene00022472	7	82	3.5	4.10E-05	0.00053847	WBGene00001612	282	1461	2.37	5.18E-05	0.00064	WBGene00044291	127	417	1.72	6.61E-05	0.0007715
WBGene00010047	12100	26099	1.11	4.11E-05	0.00053949	WBGene00020362	6995	3036	-1.2	5.19E-05	0.0006411	WBGene00011104	2108	7622	1.85	6.62E-05	0.0007718
WBGene00018219	363	928	1.35	4.12E-05	0.00054078	WBGene00007116	3466	7441	1.1	5.19E-05	0.0006411	WBGene00001121	1157	2699	1.22	6.63E-05	0.0007726
WBGene00022386	243	742	1.61	4.13E-05	0.00054119	WBGene00009625	141	863	2.61	5.20E-05	0.0006419	WBGene00011999	244	985	2.01	6.64E-05	0.0007733
WBGene00018293	255	953	1.9	4.14E-05	0.00054267	WBGene00021978	328	739	1.17	5.21E-05	0.0006419	WBGene00021442	3672	1484	-1.31	6.64E-05	0.0007733
WBGene00015638	16771	7343	-1.19	4.15E-05	0.00054393	WBGene00007734	42	453	3.42	5.24E-05	0.0006451	WBGene00008521	458	1186	1.37	6.65E-05	0.0007733
WBGene00006445	928	2665	1.52	4.16E-05	0.00054394	WBGene00020336	336	75	-2.16	5.26E-05	0.0006472	WBGene00003179	24	202	3.1	6.65E-05	0.0007733
WBGene00013881	2546	1034	-1.3	6.67E-05	0.00077447	WBGene00017207	3090	1298	-1.25	8.44E-05	0.0009291	WBGene00009328	973	3334	1.78	0.0001035	0.0010827
WBGene00018641	294	1066	1.86	6.67E-05	0.00077447	WBGene00015264	21	132	2.67	8.51E-05	0.0009357	WBGene00001468	191	652	1.77	0.0001038	0.0010843
WBGene00008830	1540	641	-1.26	6.69E-05	0.00077688	WBGene00012016	464	1389	1.58	8.53E-05	0.0009371	WBGene00018021	7691	3346	-1.2	0.000104	0.0010862
WBGene00017909	396	992	1.33	6.71E-05	0.00077866	WBGene00018741	31	161	2.37	8.53E-05	0.0009371	WBGene00018256	7922	16399	1.05	0.0001044	0.0010897
WBGene00001454	87	639	2.88	6.76E-05	0.00078346	WBGene00009337	9863	20253	1.04	8.55E-05	0.0009384	WBGene00003705	113	360	1.68	0.0001045	0.0010899
WBGene00018424	25647	7835	-1.71	6.76E-05	0.00078346	WBGene00016841	5522	11290	1.03	8.56E-05	0.0009392	WBGene00002038	4331	13054	1.59	0.0001047	0.0010916
WBGene00010683	171	1154	2.75	6.80E-05	0.00078724	WBGene00001965	400	110	-1.86	8.64E-05	0.0009479	WBGene00017671	232	1192	2.36	0.0001048	0.0010917
WBGene00189954	2924	1144	-1.35	6.81E-05	0.00078727	WBGene00011879	118	369	1.65	8.65E-05	0.0009479	WBGene00001054	196	1287	2.72	0.0001055	0.0010985
WBGene00015900	17	107	2.66	6.82E-05	0.00078792	WBGene00015605	0	102	7.79	8.66E-05	0.0009484	WBGene00008963	198	1013	2.36	0.0001064	0.0011071
WBGene00022665	1956	8122	2.05	6.83E-05	0.00078923	WBGene00022300	8231	3659	-1.17	8.70E-05	0.0009524	WBGene00013854	111	10	-3.42	0.0001066	0.0011087
WBGene00000497	3555	11815	1.73	6.84E-05	0.00078923	WBGene00008503	5143	2231	-1.2	8.71E-05	0.0009525	WBGene00008929	1600	3538	1.14	0.0001066	0.0011087
WBGene00022518	12214	29949	1.29	6.85E-05	0.00079071	WBGene00008673	159	936	2.56	8.72E-05	0.0009536	WBGene00017757	34129	14412	-1.24	0.0001068	0.0011092
WBGene00009095	41	188	2.2	6.89E-05	0.00079399	WBGene00022465	346	852	1.3	8.74E-05	0.0009552	WBGene00010399	0	38	7.97	0.0001069	0.0011092
WBGene00009008	836	1879	1.17	6.92E-05	0.00079687	WBGene00000285	206	849	2.04	8.76E-05	0.0009561	WBGene00018214	445	1779	2	0.0001069	0.0011092
WBGene00016695	3503	1066	-1.72	7.01E-05	0.00080719	WBGene00001189	787	3023	1.94	8.76E-05	0.0009562	WBGene00004818	28751	11184	-1.36	0.0001069	0.0011092
WBGene00003174	38	170	2.17	7.01E-05	0.00080719	WBGene00015610	39340	17491	-1.17	8.77E-05	0.0009563	WBGene00012019	2652	5741	1.11	0.0001072	0.0011116
WBGene00001372	9181	3494	-1.39	7.04E-05	0.00080961	WBGene00011453	129	411	1.68	8.78E-05	0.0009563	WBGene00009539	6428	2166	-1.57	0.0001076	0.0011145
WBGene00004086	11060	4723	-1.23	7.04E-05	0.00080961	WBGene00000388	11638	4925	-1.24	8.78E-05	0.0009563	WBGene00021711	905	345	-1.39	0.0001078	0.0011154
WBGene00002012	281	875	1.64	7.07E-05	0.00081152	WBGene00045457	1	40	4.96	8.80E-05	0.000958	WBGene00011217	73	433	2.57	0.0001079	0.0011154
WBGene00009152	33	174	2.4	7.07E-05	0.00081152	WBGene00000907	384	1047	1.45	8.81E-05	0.0009581	WBGene00016662	0	38	7.96	0.0001079	0.0011154



WBGene00001812	5257	2416	-1.12	7.08E-05	0.00081162	WBGene00001681	263	1063	2.01	8.85E-05	0.0009616	WBGene00012522	12738	5857	-1.12	0.0001079	0.0011154
WBGene00001968	384	105	-1.88	7.08E-05	0.00081178	WBGene00020045	24	125	2.39	8.85E-05	0.0009616	WBGene00020884	233	1622	2.8	0.0001082	0.0011171
WBGene00008065	23	140	2.6	7.11E-05	0.00081429	WBGene00009789	126	360	1.52	8.85E-05	0.0009616	WBGene00013574	1133	3696	1.71	0.0001082	0.0011171
WBGene00016659	85	1226	3.84	7.11E-05	0.00081429	WBGene00020858	1649	538	-1.62	8.87E-05	0.0009623	WBGene00007070	7322	3383	-1.11	0.0001084	0.0011183
WBGene00000601	34	221	2.7	7.13E-05	0.00081537	WBGene00020753	3	68	4.38	8.87E-05	0.0009625	WBGene00011589	16773	7485	-1.16	0.0001085	0.0011187
WBGene00001555	145	418	1.53	7.20E-05	0.00082255	WBGene00019482	377	967	1.36	8.89E-05	0.0009641	WBGene00008926	297	913	1.62	0.0001089	0.0011225
WBGene00004234	396	1672	2.08	7.21E-05	0.00082255	WBGene00012346	511	2122	2.05	8.91E-05	0.000965	WBGene00016371	10	89	3.18	0.0001097	0.0011304
WBGene00017692	521	1212	1.22	7.22E-05	0.00082255	WBGene00011886	6659	2576	-1.37	8.95E-05	0.0009683	WBGene00019272	17745	36197	1.03	0.0001098	0.0011304
WBGene00014858	622	235	-1.4	7.22E-05	0.00082255	WBGene00007687	838	3803	2.18	8.95E-05	0.0009683	WBGene00002087	5	64	3.63	0.0001105	0.0011366
WBGene00015017	22084	10353	-1.09	7.23E-05	0.00082255	WBGene00019934	84	378	2.17	8.95E-05	0.0009683	WBGene00019418	9211	3958	-1.22	0.0001108	0.001139
WBGene00003166	870	3383	1.96	7.23E-05	0.00082255	WBGene00010756	1488	3788	1.35	9.00E-05	0.0009723	WBGene00008997	257	796	1.63	0.0001111	0.0011412
WBGene00006591	360	927	1.37	7.23E-05	0.00082255	WBGene00044047	3037	1272	-1.26	9.01E-05	0.0009737	WBGene00011407	291	674	1.21	0.0001111	0.0011412
WBGene00010521	10	94	3.17	7.24E-05	0.00082255	WBGene00011689	1029	342	-1.59	9.04E-05	0.0009757	WBGene00021353	2532	6818	1.43	0.0001112	0.0011416
WBGene00007155	290	764	1.4	7.24E-05	0.00082255	WBGene00006547	15936	6669	-1.26	9.13E-05	0.000985	WBGene00016769	264	1421	2.43	0.0001115	0.0011435
WBGene00021730	3809	1129	-1.75	7.24E-05	0.00082255	WBGene00021320	1027	3226	1.65	9.15E-05	0.0009871	WBGene00010192	1683	5448	1.69	0.0001115	0.0011435
WBGene00010135	656	1601	1.29	7.25E-05	0.00082255	WBGene00020457	1740	665	-1.39	9.16E-05	0.0009872	WBGene00008425	32	256	3.02	0.0001117	0.0011451
WBGene00010195	5312	1958	-1.44	7.25E-05	0.00082255	WBGene00018387	779	264	-1.56	9.17E-05	0.0009872	WBGene00001000	32021	64137	1	0.0001121	0.0011477
WBGene00017481	27962	11480	-1.28	7.25E-05	0.00082255	WBGene00001695	142	636	2.16	9.22E-05	0.0009925	WBGene00019360	71	275	1.95	0.0001129	0.0011556
WBGene00019923	11399	5306	-1.1	7.25E-05	0.00082255	WBGene00003998	7178	3185	-1.17	9.23E-05	0.0009925	WBGene00015137	703	1590	1.18	0.0001133	0.0011591
WBGene00019956	16522	7844	-1.07	7.29E-05	0.00082666	WBGene00017232	4	66	3.99	9.24E-05	0.0009932	WBGene00000050	101	353	1.81	0.0001135	0.00116
WBGene00017052	132	964	2.87	7.32E-05	0.00082919	WBGene00020786	130	506	1.96	9.26E-05	0.0009947	WBGene00020458	1037	414	-1.32	0.0001139	0.0011635
WBGene00017135	19081	7765	-1.3	7.34E-05	0.00083037	WBGene00020188	4779	11217	1.23	9.28E-05	0.0009968	WBGene00012958	2144	989	-1.12	0.0001141	0.0011652
WBGene00004033	696	2818	2.02	7.36E-05	0.00083215	WBGene00021362	1334	2800	1.07	9.37E-05	0.0010053	WBGene00008777	851	3414	2	0.0001151	0.001174
WBGene00044138	231	635	1.46	7.39E-05	0.00083513	WBGene00044798	6259	2601	-1.27	9.41E-05	0.0010091	WBGene00022026	1189	2712	1.19	0.0001151	0.001174
WBGene00008311	2560	5764	1.17	7.40E-05	0.00083602	WBGene00194915	461	1092	1.24	9.41E-05	0.0010091	WBGene00007374	99	390	1.98	0.0001156	0.0011784
WBGene00003601	43119	17797	-1.28	7.41E-05	0.0008369	WBGene00010238	12	97	2.99	9.49E-05	0.0010165	WBGene00008033	1697	3469	1.03	0.0001164	0.001186
WBGene00009091	15	244	4.03	7.44E-05	0.00083953	WBGene00022271	136	540	1.99	9.64E-05	0.0010317	WBGene00044662	189	788	2.06	0.0001179	0.0012002
WBGene00022877	10	111	3.45	7.45E-05	0.00083983	WBGene00013898	7346	15359	1.06	9.65E-05	0.0010329	WBGene00008343	4757	1701	-1.48	0.0001194	0.0012156
WBGene00011704	4608	1449	-1.67	7.48E-05	0.00084324	WBGene00000841	79	292	1.88	9.66E-05	0.0010329	WBGene00019868	493	2028	2.04	0.0001198	0.0012188
WBGene00013797	3289	1111	-1.57	7.49E-05	0.00084381	WBGene00020261	38730	15871	-1.29	9.67E-05	0.0010329	WBGene00012540	2055	9189	2.16	0.0001205	0.0012246
WBGene00016424	3	58	4.52	7.50E-05	0.00084464	WBGene00004169	3757	11870	1.66	9.67E-05	0.0010333	WBGene00010100	2902	1250	-1.22	0.0001215	0.0012348
WBGene00018678	4745	1981	-1.26	7.53E-05	0.00084711	WBGene00018221	296	822	1.47	9.68E-05	0.0010335	WBGene00020577	158	750	2.25	0.0001217	0.0012354
WBGene00017405	5207	2170	-1.26	7.55E-05	0.00084823	WBGene00021655	2954	1257	-1.23	9.69E-05	0.0010336	WBGene00006779	12819	33000	1.36	0.0001222	0.0012403
WBGene00022360	4780	2139	-1.16	7.57E-05	0.00085029	WBGene00003748	78	548	2.82	9.71E-05	0.0010346	WBGene00015291	7083	2309	-1.62	0.0001224	0.0012412
WBGene00003495	10873	29332	1.43	7.61E-05	0.00085483	WBGene00044248	132	414	1.65	9.71E-05	0.0010346	WBGene00020582	225	1225	2.44	0.0001224	0.0012412
WBGene00019798	2269	912	-1.31	7.64E-05	0.00085719	WBGene00016542	771	2913	1.92	9.76E-05	0.0010391	WBGene00018923	7553	3217	-1.23	0.0001226	0.0012417
WBGene00016513	89	302	1.76	7.69E-05	0.00086179	WBGene00013292	55	386	2.82	9.77E-05	0.0010393	WBGene00009155	1406	2868	1.03	0.0001226	0.0012417
WBGene00021834	8074	16653	1.04	7.78E-05	0.00087152	WBGene00021861	2405	1046	-1.2	9.78E-05	0.0010405	WBGene00003474	16	106	2.75	0.0001227	0.0012417
WBGene00019591	8461	3933	-1.11	7.78E-05	0.00087159	WBGene00019780	1753	4858	1.47	9.82E-05	0.0010435	WBGene00009722	829	1954	1.24	0.0001229	0.0012429
WBGene00013383	15606	6658	-1.23	7.83E-05	0.00087685	WBGene00044760	169	473	1.49	9.83E-05	0.0010444	WBGene00044695	1362	582	-1.23	0.000123	0.0012429
WBGene00006614	211	606	1.52	7.87E-05	0.0008807	WBGene00021528	1334	4716	1.82	9.87E-05	0.0010482	WBGene00007061	906	3396	1.91	0.000123	0.0012429
WBGene00007755	41	330	3.02	7.93E-05	0.00088595	WBGene00010522	228	1136	2.31	9.89E-05	0.0010493	WBGene00012802	6159	2752	-1.16	0.0001231	0.0012434
WBGene00003519	232	807	1.8	7.96E-05	0.00088951	WBGene00017447	9768	20356	1.06	9.90E-05	0.0010494	WBGene00018242	7180	3664	-0.97	0.0001234	0.0012454
WBGene00020572	467	1092	1.23	8.00E-05	0.00089342	WBGene00001518	144	1128	2.97	9.91E-05	0.0010494	WBGene00021963	2002	4821	1.27	0.0001237	0.001248
WBGene00000789	2263	4862	1.1	8.01E-05	0.00089364	WBGene00010205	543	1208	1.15	9.91E-05	0.0010494	WBGene00006672	2478	7222	1.54	0.0001239	0.0012488
WBGene00010793	1397	3651	1.39	8.03E-05	0.00089492	WBGene00009293	555	1381	1.32	9.92E-05	0.0010498	WBGene00002056	663	3549	2.42	0.0001239	0.0012488
WBGene00005642	731	1957	1.42	8.04E-05	0.00089567	WBGene00015052	21	150	2.82	9.92E-05	0.0010498	WBGene00011381	110	327	1.58	0.0001243	0.0012512
WBGene00020855	1311	3540	1.43	8.05E-05	0.0008961	WBGene00010049	386	1907	2.31	9.98E-05	0.0010556	WBGene00019413	5427	2577	-1.07	0.0001249	0.0012565
WBGene00018418	17666	36114	1.03	8.06E-05	0.00089692	WBGene00019704	12181	5208	-1.23	0.00010572	0.0010572	WBGene00002177	315	1141	1.86	0.0001249	0.0012565
WBGene00011284	1	42	6.33	8.07E-05	0.00089719	WBGene00015536	37	161	2.12	0.0001003	0.0010593	WBGene00020692	490	1194	1.28	0.000126	0.0012663

WBGene00018350	7450	15249	1.03	8.07E-05	0.00089719	WBGene00012439	104	425	2.03	0.0001004	0.0010593	WBGene00008612	3779	1821	-1.05	0.0001264	0.0012699
WBGene00018500	10	87	3.1	8.10E-05	0.00090004	WBGene00006915	1557	6441	2.05	0.0001004	0.0010593	WBGene00019864	8785	4243	-1.05	0.0001266	0.0012712
WBGene00018828	12193	4778	-1.35	8.11E-05	0.00090004	WBGene00015272	100	15	-2.7	0.0001012	0.0010672	WBGene00017751	1190	456	-1.38	0.0001267	0.0012716
WBGene00016254	248	831	1.75	8.18E-05	0.00090751	WBGene00010106	3219	1432	-1.17	0.0001013	0.0010676	WBGene00011819	4158	1711	-1.28	0.0001271	0.0012746
WBGene00004211	169	456	1.43	8.20E-05	0.00090982	WBGene00015306	2	56	4.53	0.0001019	0.0010727	WBGene00016189	13445	6145	-1.13	0.0001271	0.0012746
WBGene00017848	2332	813	-1.52	8.23E-05	0.00091191	WBGene00010171	7	248	5.11	0.0001019	0.0010727	WBGene00021333	1146	2649	1.21	0.0001276	0.0012786
WBGene00003173	104	725	2.8	8.28E-05	0.00091721	WBGene00021298	1071	438	-1.29	0.000102	0.0010727	WBGene00003516	40032	81234	1.02	0.0001279	0.0012805
WBGene00017708	1879	557	-1.75	8.29E-05	0.00091732	WBGene00000950	775	1714	1.15	0.0001021	0.0010733	WBGene00044649	30	169	2.48	0.0001282	0.0012824
WBGene00013902	565	1752	1.63	8.30E-05	0.00091789	WBGene00045050	41	294	2.84	0.0001022	0.0010733	WBGene00019921	8909	3926	-1.18	0.0001282	0.0012824
WBGene00001553	386	935	1.28	8.32E-05	0.00091973	WBGene00015087	195	516	1.4	0.0001024	0.0010753	WBGene00007903	866	2228	1.36	0.0001296	0.0012955
WBGene00008301	1	52	5.18	8.33E-05	0.00092036	WBGene00008844	7291	2397	-1.6	0.0001026	0.0010768	WBGene00015718	1	41	6.06	0.0001297	0.0012958
WBGene00045277	254	776	1.61	8.34E-05	0.00092036	WBGene00003090	578	3163	2.45	0.0001028	0.0010769	WBGene00019436	39	155	2	0.0001299	0.0012973
WBGene00010672	2	46	4.88	8.34E-05	0.00092036	WBGene00077772	3526	1559	-1.18	0.0001028	0.0010769	WBGene00008365	37	170	2.19	0.0001302	0.0012991
WBGene00020735	2949	6411	1.12	8.37E-05	0.00092251	WBGene00007638	35	189	2.45	0.0001028	0.0010769	WBGene00017507	1370	652	-1.07	0.0001308	0.0013042
WBGene00008384	7154	2345	-1.61	8.37E-05	0.00092251	WBGene00008508	54	1	-5.19	0.000103	0.0010786	WBGene00015293	171	849	2.31	0.0001311	0.0013068
WBGene00018039	22	216	3.27	8.43E-05	0.00092852	WBGene00013799	8423	2432	-1.79	0.0001034	0.0010814	WBGene00000878	671	193	-1.8	0.0001319	0.0013146
WBGene00003943	1074	2387	1.15	0.00013226	0.00131698	WBGene00012124	4587	9169	1	0.0001633	0.0015522	WBGene00007908	102	312	1.62	0.0002007	0.0018247
WBGene00003804	26165	11335	-1.21	0.00013378	0.00133145	WBGene00013846	2348	4751	1.02	0.0001641	0.0015591	WBGene00011672	32	152	2.23	0.0002012	0.0018287
WBGene00014308	2464	5654	1.2	0.0001342	0.00133482	WBGene00044143	46	197	2.11	0.0001643	0.0015598	WBGene00010689	5679	1947	-1.54	0.0002018	0.0018328
WBGene00001055	618	1435	1.21	0.00013438	0.00133596	WBGene00016766	62	215	1.78	0.0001655	0.0015706	WBGene00020765	12354	6035	-1.03	0.0002021	0.0018346
WBGene00009834	31340	10922	-1.52	0.00013565	0.00134782	WBGene00006634	61	754	3.63	0.0001659	0.001573	WBGene00022240	137	659	2.27	0.0002025	0.0018371
WBGene00011310	1480	3023	1.03	0.00013574	0.00134791	WBGene00022262	7223	2803	-1.37	0.0001662	0.0015754	WBGene00014194	0	31	8.27	0.0002028	0.0018394
WBGene00010505	48	437	3.18	0.00013675	0.00135722	WBGene00008877	5016	2216	-1.18	0.0001665	0.0015777	WBGene00020887	95	590	2.63	0.0002034	0.0018432
WBGene00007006	38	221	2.56	0.00013699	0.00135887	WBGene00005898	82	246	1.58	0.0001671	0.0015825	WBGene00020471	110	335	1.61	0.0002035	0.0018432
WBGene00021557	20816	7166	-1.54	0.00013734	0.00136156	WBGene00003375	10219	20993	1.04	0.000168	0.0015903	WBGene00044705	87	343	1.99	0.0002037	0.0018441
WBGene00022312	1318	601	-1.13	0.00013805	0.00136786	WBGene00043992	547	1240	1.18	0.0001692	0.0016004	WBGene00021773	8763	4119	-1.09	0.0002047	0.0018517
WBGene00012098	1321	565	-1.23	0.00013832	0.00136978	WBGene00011984	60	235	1.96	0.0001693	0.0016011	WBGene00003759	105	427	2.02	0.0002047	0.0018517
WBGene00021493	1503	3185	1.08	0.00013881	0.00137386	WBGene00021938	11637	4800	-1.28	0.0001694	0.0016012	WBGene00013077	74	764	3.37	0.0002048	0.0018517
WBGene00020569	10	137	3.75	0.00013896	0.00137424	WBGene00022720	38	274	2.83	0.0001697	0.0016024	WBGene00011763	11042	32442	1.55	0.0002049	0.0018519
WBGene00001863	3259	11565	1.83	0.00013906	0.00137424	WBGene00021147	167	745	2.16	0.0001698	0.0016025	WBGene00001517	76	341	2.17	0.0002052	0.0018528
WBGene00009943	18	112	2.63	0.00013915	0.00137424	WBGene00002210	3655	9281	1.34	0.0001709	0.0016116	WBGene00015107	254	709	1.48	0.0002053	0.0018528
WBGene00004017	1517	5825	1.94	0.00013915	0.00137424	WBGene00011613	665	250	-1.41	0.0001709	0.0016116	WBGene00017640	2849	5694	1	0.0002059	0.0018572
WBGene00007079	497	174	-1.52	0.00013945	0.00137639	WBGene00004100	250	833	1.73	0.0001715	0.0016155	WBGene00009846	1468	599	-1.29	0.0002059	0.0018572
WBGene00043054	58	264	2.19	0.00013999	0.00138098	WBGene00020487	148	429	1.53	0.0001715	0.0016155	WBGene00021081	2	47	4.25	0.0002066	0.0018626
WBGene00009438	417	1722	2.04	0.00014049	0.00138457	WBGene00000799	15175	6943	-1.13	0.0001717	0.001616	WBGene00021709	5363	2666	-1.01	0.0002074	0.0018688
WBGene00008579	565	1237	1.13	0.00014051	0.00138457	WBGene00019788	12528	5333	-1.23	0.0001717	0.001616	WBGene00001764	5350	921	-2.54	0.0002079	0.0018714
WBGene00020201	15	120	3	0.00014059	0.00138466	WBGene00018392	4600	9495	1.05	0.0001724	0.0016215	WBGene00010832	14	94	2.76	0.0002079	0.0018714
WBGene00009019	5248	2471	-1.09	0.00014076	0.00138558	WBGene00019690	2843	1279	-1.15	0.0001732	0.0016282	WBGene00016101	1606	3292	1.04	0.0002083	0.0018739
WBGene00044556	286	771	1.43	0.000141	0.00138715	WBGene00021036	6953	16760	1.27	0.0001734	0.0016295	WBGene00022591	5964	11793	0.98	0.0002087	0.0018766
WBGene00195253	41	173	2.09	0.00014124	0.00138876	WBGene00008594	38	156	2.03	0.0001738	0.001632	WBGene00017039	17	108	2.66	0.0002091	0.0018789
WBGene00000647	662	226	-1.55	0.00014254	0.00140063	WBGene00012670	333	1433	2.11	0.0001744	0.0016367	WBGene00022067	10567	5084	-1.06	0.0002094	0.0018796
WBGene00016891	1467	619	-1.24	0.00014261	0.00140063	WBGene00006830	2336	4941	1.08	0.0001746	0.0016375	WBGene00009291	713	1544	1.12	0.0002094	0.0018796
WBGene00018522	2793	7443	1.41	0.00014336	0.00140727	WBGene00017463	1683	4110	1.29	0.0001748	0.0016385	WBGene00004819	29156	11900	-1.29	0.0002095	0.0018796
WBGene00015132	6946	3029	-1.2	0.00014415	0.00141399	WBGene00007244	3601	1438	-1.32	0.0001753	0.0016425	WBGene00020205	52155	24503	-1.09	0.000211	0.0018922
WBGene00022063	1427	683	-1.06	0.0001442	0.00141399	WBGene00018042	877	2022	1.2	0.0001756	0.0016451	WBGene00008260	2191	6429	1.55	0.0002113	0.0018938
WBGene00020394	1949	535	-1.87	0.00014431	0.00141426	WBGene00019768	4683	1918	-1.29	0.0001758	0.001646	WBGene00019759	3869	8118	1.07	0.0002117	0.0018972
WBGene00013250	1227	536	-1.2	0.0001449	0.00141871	WBGene00013561	9151	4096	-1.16	0.000176	0.0016469	WBGene00014761	40	182	2.17	0.0002122	0.0019003
WBGene00001368	5405	10889	1.01	0.00014492	0.00141871	WBGene00001394	1100	2219	1.01	0.0001762	0.0016481	WBGene00022074	27165	12231	-1.15	0.0002127	0.0019034
WBGene00017835	1729	6332	1.87	0.00014543	0.00142295	WBGene00017426	1090	2252	1.05	0.0001773	0.001657	WBGene00001990	289	1188	2.04	0.0002141	0.0019151
WBGene00017892	1465	5243	1.84	0.00014575	0.00142526	WBGene00019428	154	1024	2.73	0.0001774	0.001657	WBGene00011551	61	257	2.09	0.0002144	0.0019168

WBGene00013180	2031	3964	0.97	0.00014653	0.00143211	WBGene00002126	209	1041	2.32	0.000178	0.0016617	WBGene00011382	130	593	2.19	0.0002158	0.0019282
WBGene00017752	2534	1005	-1.33	0.00014716	0.0014375	WBGene00017009	44	294	2.73	0.0001783	0.001664	WBGene00018462	1121	2380	1.09	0.0002159	0.0019282
WBGene00011833	12232	24865	1.02	0.00014737	0.0014388	WBGene00018567	95	303	1.67	0.0001793	0.0016724	WBGene00010881	27	135	2.3	0.0002161	0.0019298
WBGene00044188	3137	1368	-1.2	0.00014825	0.00144657	WBGene00014252	175	1127	2.68	0.0001806	0.0016834	WBGene00016734	568	1416	1.32	0.0002179	0.0019441
WBGene00017933	858	372	-1.21	0.00014835	0.00144675	WBGene00014124	22069	10593	-1.06	0.0001814	0.0016902	WBGene00007253	200	498	1.31	0.000218	0.0019449
WBGene00007405	2610	5708	1.13	0.00014925	0.0014544	WBGene00019975	205	516	1.33	0.0001828	0.0017022	WBGene00018732	52	360	2.79	0.0002185	0.0019476
WBGene00000836	54145	23572	-1.2	0.00014929	0.0014544	WBGene00010318	517	1182	1.19	0.000183	0.0017031	WBGene00017305	6	129	4.37	0.0002187	0.0019491
WBGene00008964	2768	11121	2.01	0.00014942	0.00145486	WBGene00008746	245	885	1.85	0.0001831	0.0017035	WBGene00019753	19	120	2.69	0.0002189	0.0019491
WBGene00014148	1716	4844	1.5	0.00014994	0.0014549	WBGene00001954	118	370	1.65	0.0001834	0.0017057	WBGene00011339	1338	3020	1.17	0.000219	0.0019491
WBGene00017386	186	24	-2.98	0.00015001	0.0014549	WBGene00022346	189	498	1.4	0.0001837	0.0017069	WBGene00015402	141	403	1.52	0.0002198	0.0019561
WBGene00009818	7189	14750	1.04	0.00015043	0.00146206	WBGene00015842	1175	305	-1.94	0.0001846	0.0017143	WBGene00000220	30222	59119	0.97	0.0002205	0.0019605
WBGene00020542	4229	1977	-1.1	0.00015049	0.00146206	WBGene00002243	4350	9043	1.06	0.000185	0.0017171	WBGene00017249	5555	2571	-1.11	0.0002211	0.0019652
WBGene00000942	26832	57402	1.1	0.00015064	0.00146272	WBGene00013665	221	559	1.34	0.0001854	0.00172	WBGene00004746	59310	29789	-0.99	0.0002224	0.0019761
WBGene00011388	9322	4475	-1.06	0.00015124	0.00146778	WBGene00022789	1877	7235	1.95	0.0001856	0.0017205	WBGene00004267	1012	4663	2.2	0.0002227	0.0019776
WBGene00018468	1548	6752	2.12	0.000152	0.00147435	WBGene00005652	78	453	2.55	0.0001857	0.0017205	WBGene00020042	40	177	2.13	0.0002231	0.0019804
WBGene00019723	1890	694	-1.44	0.00015242	0.0014763	WBGene00008366	894	1932	1.11	0.0001857	0.0017205	WBGene00020650	26	179	2.76	0.0002235	0.0019826
WBGene00010269	1632	3438	1.08	0.00015242	0.0014763	WBGene00011238	412	996	1.27	0.0001862	0.0017239	WBGene00013558	16518	7365	-1.17	0.0002237	0.0019838
WBGene00014143	3518	1257	-1.48	0.00015245	0.0014763	WBGene00018688	11991	5830	-1.04	0.0001866	0.0017268	WBGene00018376	40	421	3.39	0.0002239	0.0019847
WBGene00013588	6	66	3.55	0.00015267	0.00147771	WBGene00004944	409	1770	2.11	0.0001869	0.0017293	WBGene00021656	626	283	-1.15	0.0002246	0.0019898
WBGene00016550	1773	780	-1.18	0.00015354	0.00148468	WBGene00012581	3208	1395	-1.2	0.0001872	0.0017308	WBGene00020674	32	150	2.24	0.0002253	0.0019944
WBGene00194674	44	179	2.03	0.0001536	0.00148468	WBGene00012111	1791	737	-1.28	0.0001875	0.0017321	WBGene00020962	3205	1500	-1.1	0.0002254	0.0019944
WBGene00012325	17	113	2.74	0.00015367	0.00148468	WBGene00005059	650	228	-1.51	0.0001875	0.0017321	WBGene00005649	15	103	2.74	0.0002258	0.001996
WBGene00009873	1	37	4.69	0.00015373	0.00148468	WBGene00006749	952	4617	2.28	0.0001877	0.0017325	WBGene00022612	3245	7812	1.27	0.0002258	0.001996
WBGene00001957	287	697	1.28	0.00015405	0.00148659	WBGene00009355	855	3995	2.22	0.0001881	0.0017357	WBGene00012478	3813	9661	1.34	0.0002264	0.0020005
WBGene00014918	390	125	-1.64	0.00015409	0.00148659	WBGene00044437	583	1326	1.19	0.0001889	0.0017423	WBGene00013611	148	14	-3.43	0.000227	0.0020046
WBGene00013500	9517	3855	-1.3	0.00015418	0.00148672	WBGene00019772	22	190	3.14	0.0001893	0.0017447	WBGene00015261	1084	393	-1.46	0.0002273	0.0020059
WBGene00044693	4626	1875	-1.3	0.00015448	0.00148789	WBGene00008450	2200	4543	1.05	0.0001896	0.001746	WBGene00012253	288	1564	2.44	0.0002273	0.0020059
WBGene00007925	5455	11222	1.04	0.00015449	0.00148789	WBGene00010872	16337	7833	-1.06	0.0001896	0.001746	WBGene00010191	391	1806	2.21	0.0002275	0.0020065
WBGene00019042	6034	2703	-1.16	0.00015455	0.00148789	WBGene00019364	365	839	1.2	0.0001902	0.0017507	WBGene00000778	6315	12884	1.03	0.000228	0.0020101
WBGene00017473	1444	446	-1.7	0.00015482	0.0014897	WBGene00003417	3193	1327	-1.27	0.0001913	0.0017592	WBGene00014044	524	149	-1.81	0.0002283	0.0020112
WBGene00018002	15	129	3.14	0.00015493	0.00148992	WBGene00044905	1255	562	-1.16	0.0001914	0.0017595	WBGene00006559	1117	426	-1.39	0.0002284	0.0020112
WBGene00009601	11	83	2.93	0.00015582	0.00149762	WBGene00003934	21274	42125	0.99	0.0001917	0.0017611	WBGene00009070	8774	4216	-1.06	0.0002291	0.0020162
WBGene00019233	962	199	-2.27	0.0001559	0.00149763	WBGene00021293	18243	6179	-1.56	0.0001918	0.0017611	WBGene00017018	1149	4645	2.01	0.0002296	0.0020197
WBGene00017562	746	1671	1.16	0.00015614	0.00149917	WBGene00003859	41	234	2.52	0.0001919	0.0017616	WBGene00000047	574	2944	2.36	0.0002306	0.0020281
WBGene00016930	1478	453	-1.71	0.00015658	0.00150257	WBGene00001240	3184	6177	0.96	0.0001925	0.0017666	WBGene00004213	12633	24851	0.98	0.0002313	0.0020327
WBGene00011960	26	138	2.38	0.0001574	0.00150966	WBGene00007694	10189	4739	-1.1	0.0001936	0.0017756	WBGene00015050	5	64	3.59	0.0002325	0.0020424
WBGene00006669	160	464	1.53	0.00015753	0.00151009	WBGene00008732	1604	4838	1.59	0.0001942	0.0017797	WBGene00020077	21	127	2.58	0.0002329	0.0020452
WBGene00021484	349	113	-1.62	0.0001581	0.00151447	WBGene00003739	51	209	2.04	0.0001945	0.0017814	WBGene00013650	10241	4671	-1.13	0.0002333	0.0020477
WBGene00015885	704	210	-1.74	0.00015816	0.00151447	WBGene00001103	9117	3643	-1.32	0.000195	0.0017856	WBGene00003641	18	115	2.63	0.0002339	0.002052
WBGene00007520	3823	12260	1.68	0.00015882	0.00151957	WBGene00013779	2909	1201	-1.28	0.0001962	0.0017951	WBGene00020676	1067	3112	1.54	0.0002346	0.002057
WBGene00011452	7	77	3.55	0.00015886	0.00151957	WBGene00000287	114	351	1.62	0.0001967	0.0017974	WBGene00004173	101	457	2.19	0.0002349	0.0020577
WBGene00018271	5888	12413	1.08	0.00015985	0.00152826	WBGene00044733	3938	1791	-1.14	0.0001967	0.0017974	WBGene00005256	356	106	-1.75	0.0002349	0.0020577
WBGene00010774	351	866	1.3	0.0001602	0.0015308	WBGene00017964	157	471	1.58	0.0001967	0.0017974	WBGene00015103	69	381	2.47	0.0002356	0.0020626
WBGene00018275	2839	5964	1.07	0.00016054	0.00153322	WBGene00013150	15317	5439	-1.49	0.0001969	0.0017983	WBGene00003033	146	600	2.04	0.0002361	0.0020654
WBGene00010142	16326	6411	-1.35	0.00016094	0.00153619	WBGene00008600	209	486	1.22	0.0001974	0.0018019	WBGene00016759	176	694	1.98	0.0002362	0.0020654
WBGene00020712	7	89	3.7	0.00016127	0.00153848	WBGene00002123	4878	12461	1.35	0.0001977	0.0018036	WBGene00044976	3552	1707	-1.06	0.0002369	0.0020708
WBGene00017577	43	189	2.13	0.00016177	0.00154245	WBGene00006556	1732	723	-1.26	0.0001978	0.0018039	WBGene00016135	2896	5904	1.03	0.0002371	0.002072
WBGene00001985	2233	745	-1.58	0.0001621	0.00154478	WBGene00007960	204	43	-2.24	0.0001985	0.0018096	WBGene00021721	3023	1315	-1.2	0.0002376	0.0020748
WBGene00010690	1635	665	-1.3	0.00016248	0.00154764	WBGene00009145	6439	2606	-1.3	0.0001994	0.0018161	WBGene00004988	203	691	1.77	0.0002379	0.0020765
WBGene00016486	662	248	-1.42	0.00016287	0.00155053	WBGene00007495	72	454	2.66	0.0001997	0.0018185	WBGene00010457	902	2006	1.15	0.0002381	0.0020776

WBGene00004969	1379	2795	1.02	0.00016299	0.00155056	WBGene00015148	1228	2574	1.07	0.0002005	0.0018247	WBGene00000176	135	438	1.7	0.0002383	0.0020778
WBGene00013796	7167	2504	-1.52	0.00016305	0.00155056	WBGene00006636	179	498	1.48	0.0002006	0.0018247	WBGene00011475	28471	13398	-1.09	0.0002398	0.0020897
WBGene00003876	148	755	2.35	0.00024004	0.00209119	WBGene00020715	122	4	-5.1	0.0002849	0.0023827	WBGene00006777	1715	6720	1.97	0.0003375	0.0027141
WBGene00019424	264	676	1.35	0.00024282	0.00211386	WBGene00007953	752	1578	1.07	0.0002852	0.0023836	WBGene00007664	147	586	2	0.0003378	0.0027141
WBGene00009350	41	190	2.2	0.00024288	0.00211386	WBGene00017865	191	533	1.48	0.0002853	0.0023836	WBGene00007220	156	443	1.5	0.0003378	0.0027141
WBGene00011981	2791	1094	-1.35	0.00024339	0.00211735	WBGene00011193	3739	1515	-1.3	0.0002856	0.0023852	WBGene00019300	80	434	2.44	0.0003392	0.0027237
WBGene00044551	1	39	5.03	0.00024356	0.00211776	WBGene00008783	1139	2374	1.06	0.0002864	0.0023904	WBGene00010554	55	204	1.89	0.0003396	0.0027261
WBGene00004779	127	480	1.91	0.0002441	0.00212144	WBGene00015735	475	1762	1.89	0.0002865	0.0023904	WBGene00022154	348	1152	1.73	0.0003401	0.0027283
WBGene00007494	71	229	1.69	0.00024432	0.0021223	WBGene00003625	5142	12199	1.25	0.000287	0.0023938	WBGene00016903	2462	4831	0.97	0.0003406	0.0027315
WBGene00018738	2389	4839	1.02	0.00024455	0.00212306	WBGene00022644	130	2155	4.06	0.0002882	0.0024026	WBGene00011479	197	497	1.33	0.0003409	0.0027319
WBGene00004859	4879	9601	0.98	0.00024464	0.00212306	WBGene00019476	10	80	2.99	0.0002889	0.0024068	WBGene00000053	60	246	2.04	0.000341	0.0027319
WBGene00009032	461	1859	2.01	0.00024481	0.00212345	WBGene00050903	7097	3103	-1.19	0.0002896	0.0024117	WBGene00017280	18485	8410	-1.14	0.0003413	0.0027325
WBGene00015332	22	116	2.42	0.00024529	0.0021266	WBGene00003133	38956	19312	-1.01	0.0002901	0.0024152	WBGene00015423	72	247	1.78	0.0003413	0.0027325
WBGene00008644	78	249	1.68	0.00024549	0.0021266	WBGene00001076	#####	593975	0.94	0.0002904	0.0024166	WBGene00013845	88	460	2.38	0.0003427	0.0027422
WBGene00015271	992	289	-1.78	0.00024552	0.0021266	WBGene00019148	4052	16243	2	0.0002917	0.0024256	WBGene00017408	2979	1293	-1.2	0.0003437	0.0027493
WBGene00018628	50	286	2.5	0.0002457	0.0021271	WBGene00012220	6185	2479	-1.32	0.000292	0.0024274	WBGene00016329	1294	4267	1.72	0.0003439	0.0027494
WBGene00018358	6457	3227	-1	0.00024607	0.00212809	WBGene00010349	420	1453	1.79	0.0002928	0.0024327	WBGene00011404	907	1984	1.13	0.0003441	0.0027494
WBGene00019687	6468	3294	-0.97	0.00024609	0.00212809	WBGene00021814	115	342	1.58	0.0002932	0.0024349	WBGene00010374	2910	5916	1.02	0.0003449	0.0027549
WBGene00000492	969	2149	1.15	0.00024627	0.00212809	WBGene00013043	37	161	2.14	0.0002933	0.0024349	WBGene00016806	265	1204	2.19	0.0003457	0.0027603
WBGene00012416	4	55	3.65	0.00024629	0.00212809	WBGene00019072	1392	596	-1.22	0.0002942	0.0024413	WBGene00011949	76	526	2.79	0.0003459	0.0027605
WBGene00008718	1233	2540	1.04	0.00024751	0.00213767	WBGene00010320	18	119	2.69	0.0002945	0.0024428	WBGene00017663	318	1662	2.39	0.0003478	0.0027734
WBGene00007044	4573	9037	0.98	0.00024778	0.00213894	WBGene00020541	4302	2065	-1.06	0.0002969	0.0024613	WBGene00007285	324	1022	1.65	0.0003479	0.0027734
WBGene00018965	6568	12751	0.96	0.00024874	0.00214617	WBGene00043050	98	328	1.75	0.0002973	0.002463	WBGene00010989	1813	830	-1.13	0.000348	0.0027734
WBGene00045146	20	118	2.57	0.00024893	0.00214678	WBGene00016860	147	454	1.63	0.0002974	0.002463	WBGene00018598	6776	2407	-1.49	0.0003481	0.0027734
WBGene00001751	176	460	1.38	0.00024937	0.00214957	WBGene00013241	20901	9317	-1.17	0.0002978	0.0024651	WBGene00000493	2563	5320	1.05	0.0003489	0.0027786
WBGene00016132	105	670	2.68	0.00024962	0.00214998	WBGene00001973	10905	4774	-1.19	0.0002983	0.0024686	WBGene00044764	7	71	3.39	0.0003495	0.0027816
WBGene00003450	207	9	-4.45	0.00024966	0.00214998	WBGene00022643	114	565	2.3	0.0002985	0.0024686	WBGene00012217	20	105	2.41	0.000351	0.0027922
WBGene00001608	183	669	1.87	0.00024984	0.00215054	WBGene00012669	114	357	1.64	0.0002986	0.0024688	WBGene00017208	9791	4742	-1.05	0.0003535	0.0028101
WBGene00009904	60	639	3.41	0.00025343	0.00218036	WBGene00008047	133	545	2.03	0.0003003	0.0024816	WBGene00016460	1250	506	-1.31	0.0003535	0.0028101
WBGene00020825	1283	2812	1.13	0.00025422	0.00218608	WBGene00000476	3136	6127	0.97	0.0003007	0.002483	WBGene00021583	337	1627	2.27	0.0003539	0.0028119
WBGene00007197	221	563	1.35	0.00025459	0.00218825	WBGene00001494	1083	2238	1.05	0.0003008	0.002483	WBGene00022564	1361	588	-1.21	0.0003541	0.0028123
WBGene00006788	15184	34012	1.16	0.00025509	0.00219146	WBGene00020657	78	320	2.04	0.0003009	0.002483	WBGene00044605	2658	5369	1.01	0.0003553	0.0028201
WBGene00019983	22162	10449	-1.08	0.00025596	0.00219791	WBGene00003981	168	518	1.62	0.0003014	0.0024853	WBGene00019935	1038	3269	1.65	0.0003558	0.0028232
WBGene00008915	3521	1583	-1.15	0.00025613	0.00219834	WBGene00006363	2461	8815	1.84	0.0003015	0.0024853	WBGene00011878	65	305	2.24	0.0003567	0.0028229
WBGene00018429	41	170	2.05	0.00025632	0.00219845	WBGene00001182	3979	9380	1.24	0.0003024	0.0024916	WBGene00011755	4300	8373	0.96	0.0003569	0.0028229
WBGene00018560	80	256	1.68	0.00025648	0.00219845	WBGene00017454	200	53	-1.93	0.0003031	0.002496	WBGene00019041	3576	1731	-1.05	0.0003573	0.0028315
WBGene00004346	227	1259	2.47	0.00025651	0.00219845	WBGene00006792	256	1207	2.24	0.0003032	0.002496	WBGene00009237	52	207	1.99	0.0003576	0.0028325
WBGene00003685	1375	2761	1.01	0.00025664	0.0021985	WBGene00018636	5848	2548	-1.2	0.0003038	0.0024997	WBGene00008432	155	433	1.48	0.0003599	0.0028492
WBGene00018824	2090	4067	0.96	0.00025733	0.00220333	WBGene00005241	508	207	-1.29	0.000304	0.0025005	WBGene00000239	507	1147	1.18	0.0003602	0.0028503
WBGene00020315	9388	4257	-1.14	0.00025914	0.0022178	WBGene00008438	1192	2582	1.12	0.0003044	0.0025015	WBGene00007904	31807	16022	-0.99	0.0003606	0.0028506
WBGene00010235	0	58	6.98	0.00025959	0.00222045	WBGene00008226	899	1966	1.13	0.0003044	0.0025015	WBGene00006598	14	103	2.87	0.0003607	0.0028506
WBGene00000666	10	87	3.18	0.0002597	0.00222045	WBGene00004320	68181	24924	-1.45	0.0003045	0.0025015	WBGene00013672	1691	4152	1.3	0.0003609	0.0028506
WBGene00007950	209	564	1.44	0.00025998	0.00222178	WBGene00007541	0	34	7.8	0.0003052	0.0025058	WBGene00021815	6225	3185	-0.97	0.000361	0.0028506
WBGene00001627	1370	2976	1.12	0.00026028	0.0022233	WBGene00018405	2462	7794	1.66	0.0003057	0.0025083	WBGene00010493	5067	2137	-1.25	0.0003611	0.0028506
WBGene00019979	146	902	2.63	0.000261	0.00222843	WBGene00020808	18738	53417	1.51	0.0003074	0.0025216	WBGene00045302	1441	648	-1.15	0.0003612	0.0028506
WBGene00018573	23	273	3.55	0.00026121	0.0022291	WBGene00018483	10770	4906	-1.13	0.0003089	0.0025329	WBGene00002252	149	1207	3.02	0.0003613	0.0028506
WBGene00003640	651	1816	1.48	0.00026133	0.0022291	WBGene00009030	403	928	1.2	0.0003112	0.00255	WBGene00044779	27	141	2.37	0.0003617	0.0028521
WBGene00019737	176	657	1.9	0.00026175	0.00223166	WBGene00016429	689	1469	1.09	0.0003119	0.0025551	WBGene00018736	19	150	2.96	0.000362	0.0028535
WBGene00021165	5256	1779	-1.56	0.00026206	0.00223244	WBGene00006549	458	148	-1.62	0.0003124	0.0025575	WBGene00010449	566	1255	1.15	0.0003622	0.0028535
WBGene00016152	244	619	1.34	0.00026209	0.00223244	WBGene00022227	1176	494	-1.25	0.0003127	0.002558	WBGene00008726	181	427	1.24	0.0003631	0.0028589

WBGene00008146	116	807	2.8	0.00026298	0.00223894	WBGene00017957	277	737	1.41	0.0003127	0.002558	WBGene00018654	338	801	1.25	0.0003632	0.0028589
WBGene00006508	14306	28404	0.99	0.00026403	0.00224685	WBGene00009697	14918	7560	-0.98	0.0003131	0.0025589	WBGene00016566	10382	5224	-0.99	0.000364	0.0028635
WBGene00018445	1489	629	-1.24	0.00026465	0.00224919	WBGene00012018	2337	9673	2.05	0.0003131	0.0025589	WBGene00015595	1066	402	-1.41	0.0003643	0.0028635
WBGene00009318	723	2196	1.6	0.00026465	0.00224919	WBGene00004950	1120	2760	1.3	0.0003135	0.0025607	WBGene00022297	18805	8562	-1.14	0.0003644	0.0028635
WBGene00020134	4160	8063	0.95	0.00026468	0.00224919	WBGene00021939	736	2303	1.65	0.0003138	0.0025627	WBGene00012496	14712	7152	-1.04	0.0003645	0.0028635
WBGene00022047	131	522	1.99	0.00026544	0.00225458	WBGene00001248	3323	6495	0.97	0.0003143	0.0025637	WBGene00019958	177	659	1.89	0.0003646	0.0028635
WBGene00022278	17078	8163	-1.06	0.00026593	0.00225763	WBGene00019918	24230	11400	-1.09	0.0003144	0.0025637	WBGene00004212	2301	7508	1.71	0.0003686	0.0028938
WBGene00044493	2176	1046	-1.06	0.000267	0.00226569	WBGene00008142	21	118	2.5	0.0003144	0.0025637	WBGene00007483	13	88	2.8	0.0003695	0.0028995
WBGene00004924	554	3415	2.62	0.00026776	0.00227101	WBGene00006947	6087	24932	2.03	0.0003145	0.0025637	WBGene00014003	14	88	2.65	0.0003697	0.0029001
WBGene00021914	7035	3238	-1.12	0.0002683	0.00227453	WBGene000195255	30	140	2.22	0.0003149	0.0025655	WBGene00001461	123	556	2.18	0.0003706	0.0029059
WBGene00008220	34	136	2	0.0002685	0.00227514	WBGene00008215	1142	5924	2.38	0.0003155	0.0025677	WBGene00005004	43	169	1.96	0.0003711	0.0029083
WBGene00016865	857	1737	1.02	0.00027006	0.00228729	WBGene00014820	1063	468	-1.18	0.0003155	0.0025677	WBGene00015265	902	333	-1.44	0.0003731	0.0029224
WBGene00008314	906	3187	1.82	0.00027029	0.00228799	WBGene00000447	339	1143	1.75	0.0003159	0.00257	WBGene00019261	484	1532	1.66	0.0003732	0.0029224
WBGene00003167	172	472	1.46	0.0002704	0.00228799	WBGene00019226	33	185	2.5	0.000317	0.0025777	WBGene00019604	13114	4736	-1.47	0.0003748	0.0029334
WBGene00009218	4894	12986	1.41	0.00027084	0.00229068	WBGene00023318	250	86	-1.54	0.0003171	0.0025778	WBGene00012527	7026	3120	-1.17	0.0003752	0.0029354
WBGene00003751	100	662	2.73	0.00027105	0.00229139	WBGene00012368	890	379	-1.23	0.0003185	0.0025877	WBGene00138711	178	524	1.56	0.0003759	0.0029394
WBGene00015136	2027	797	-1.35	0.00027195	0.00229789	WBGene00001711	201	767	1.93	0.0003189	0.0025899	WBGene00043990	264	87	-1.6	0.0003774	0.0029501
WBGene00018754	1981	971	-1.03	0.00027329	0.00230643	WBGene00009804	979	1949	0.99	0.0003204	0.0026012	WBGene00077775	19	229	3.57	0.0003777	0.0029513
WBGene00007075	1263	560	-1.17	0.0002733	0.00230643	WBGene00010838	2090	4326	1.05	0.0003218	0.0026098	WBGene00004264	5934	20194	1.77	0.0003782	0.0029527
WBGene00009647	1448	2936	1.02	0.00027338	0.00230643	WBGene00012234	10118	5155	-0.97	0.0003219	0.0026098	WBGene00002149	38	158	2.06	0.0003782	0.0029527
WBGene00022302	813	278	-1.55	0.00027347	0.00230643	WBGene00005392	179	38	-2.23	0.0003219	0.0026098	WBGene00010161	7724	3861	-1	0.0003797	0.0029618
WBGene00044618	271	661	1.29	0.00027461	0.00231432	WBGene00013841	9	157	4.11	0.0003225	0.0026122	WBGene00003995	105	325	1.62	0.0003798	0.0029618
WBGene00015057	3084	1486	-1.05	0.00027467	0.00231432	WBGene00003861	426	1171	1.46	0.0003225	0.0026122	WBGene00002037	18706	36173	0.95	0.0003799	0.0029618
WBGene00012951	13225	6207	-1.09	0.00027578	0.00232263	WBGene00021529	1193	2476	1.05	0.0003234	0.002618	WBGene00001997	3225	1429	-1.17	0.000382	0.0029771
WBGene00044350	255	671	1.4	0.00027904	0.00234898	WBGene00006582	5052	9992	0.98	0.0003251	0.0026298	WBGene00022228	46	199	2.1	0.0003826	0.0029807
WBGene00019149	30	140	2.24	0.00027948	0.00235052	WBGene00044696	76	504	2.72	0.0003251	0.0026298	WBGene00010594	318	1576	2.31	0.000383	0.0029817
WBGene00012395	16368	7441	-1.14	0.00027949	0.00235052	WBGene00009820	5760	2580	-1.16	0.0003265	0.0026395	WBGene00045300	4194	1727	-1.28	0.0003831	0.0029817
WBGene00011073	180	829	2.2	0.00027973	0.00235143	WBGene00011522	661	2556	1.95	0.0003272	0.0026439	WBGene00000913	54517	26487	-1.04	0.0003836	0.0029847
WBGene00022415	4995	18224	1.87	0.00028015	0.00235366	WBGene00006962	4164	1813	-1.2	0.0003281	0.0026499	WBGene00015135	1564	3403	1.12	0.0003838	0.0029847
WBGene00001445	23	121	2.41	0.00028025	0.00235366	WBGene00007431	88	287	1.7	0.0003314	0.0026759	WBGene00007102	2357	969	-1.28	0.0003845	0.002989
WBGene00020009	1110	4093	1.88	0.00028053	0.00235491	WBGene00007914	9240	4767	-0.95	0.0003334	0.0026909	WBGene00021211	2361	973	-1.28	0.0003853	0.0029937
WBGene00020560	659	3504	2.41	0.00028181	0.0023645	WBGene00020561	180	841	2.22	0.0003347	0.0027002	WBGene00008440	26194	9345	-1.49	0.0003864	0.0030009
WBGene00009700	237	802	1.76	0.000282	0.00236503	WBGene00020729	1720	548	-1.65	0.000335	0.0027006	WBGene00020666	431	150	-1.52	0.0003871	0.0030005
WBGene00000524	325	1501	2.21	0.00028216	0.00236525	WBGene00012391	626	1422	1.18	0.0003351	0.0027006	WBGene00009562	91	282	1.63	0.0003886	0.0030152
WBGene00020414	151	24	-2.67	0.00028306	0.0023717	WBGene00008227	292	661	1.18	0.0003355	0.0027026	WBGene00011586	13	85	2.74	0.0003892	0.0030187
WBGene00020838	5503	10353	0.91	0.00028341	0.00237352	WBGene00009049	10250	4631	-1.15	0.0003362	0.0027074	WBGene00022164	868	2525	1.54	0.0003895	0.0030187
WBGene00016397	1168	2651	1.18	0.0002839	0.00237652	WBGene00003885	1637	3361	1.04	0.0003373	0.002714	WBGene00018423	4216	1787	-1.24	0.0003896	0.0030187
WBGene00013897	1139	2640	1.21	0.00028454	0.00238076	WBGene00011313	13	125	3.27	0.0003374	0.002714	WBGene00019183	26	121	2.23	0.0003897	0.0030187
WBGene00000772	8189	3803	-1.11	0.00038993	0.00301928	WBGene00009586	721	1587	1.14	0.0004555	0.0034006	WBGene00011345	9894	18242	0.88	0.0005247	0.0037827
WBGene00021112	7694	3875	-0.99	0.00039022	0.0030202	WBGene00019188	7564	16322	1.11	0.0004583	0.0034168	WBGene00019944	2793	6463	1.21	0.0005252	0.0037846
WBGene00016751	4032	8261	1.03	0.00039066	0.00302235	WBGene00003029	800	1667	1.06	0.0004583	0.0034168	WBGene00000975	2237	795	-1.49	0.0005263	0.0037896
WBGene00012257	17198	47756	1.47	0.00039238	0.00303433	WBGene00013264	265	906	1.77	0.0004584	0.0034168	WBGene00006676	18	104	2.52	0.0005263	0.0037896
WBGene00044372	3789	1399	-1.44	0.00039348	0.00304151	WBGene00012950	8838	4023	-1.14	0.0004584	0.0034168	WBGene00000428	24	120	2.34	0.0005281	0.0038007
WBGene00011283	26103	50321	0.95	0.00039444	0.00304609	WBGene00000284	534	1239	1.22	0.0004587	0.0034178	WBGene00001188	1647	3532	1.1	0.0005283	0.003801
WBGene00001490	2195	7397	1.75	0.00039456	0.00304609	WBGene00018427	3265	1086	-1.59	0.0004608	0.0034322	WBGene00002006	952	422	-1.17	0.0005289	0.0038034
WBGene00012271	1486	3010	1.02	0.00039458	0.00304609	WBGene00019598	3554	1678	-1.08	0.0004629	0.0034463	WBGene00013170	2676	1335	-1	0.0005293	0.0038005
WBGene00009063	1245	459	-1.44	0.00039546	0.00305159	WBGene00010795	769	1505	0.97	0.0004638	0.0034516	WBGene00022455	22834	10011	-1.19	0.0005305	0.0038123
WBGene00008157	3819	1672	-1.19	0.00039624	0.0030563	WBGene00006675	106	301	1.5	0.0004647	0.0034564	WBGene00005129	9	79	3.18	0.0005313	0.0038161
WBGene00000797	2772	1242	-1.16	0.00039692	0.00306018	WBGene00017673	84	10	-3.05	0.0004649	0.0034564	WBGene00004748	18	103	2.48	0.0005319	0.003819
WBGene00013103	1770	3851	1.12	0.00039765	0.00306407	WBGene00005248	20	110	2.48	0.0004668	0.0034677	WBGene00007565	60	233	1.96	0.0005326	0.0038228

WBGene00011374	150	1088	2.86	0.00039776	0.00306407	WBGene00020308	47	165	1.81	0.0004668	0.0034677	WBGene00008572	1208	3226	1.42	0.0005331	0.0038241
WBGene00013970	300	863	1.52	0.00039806	0.00306505	WBGene00009799	1047	3313	1.66	0.0004701	0.0034912	WBGene00022803	6977	3075	-1.18	0.0005333	0.0038241
WBGene00021873	11	75	2.76	0.00039901	0.00307107	WBGene00017738	15582	6155	-1.34	0.0004709	0.0034955	WBGene00009621	361	1183	1.71	0.0005337	0.0038261
WBGene00021174	546	221	-1.3	0.00040055	0.00308103	WBGene00195155	1689	727	-1.22	0.0004711	0.0034958	WBGene00003646	1634	3051	0.9	0.0005359	0.0038397
WBGene00006454	12	80	2.78	0.00040112	0.00308103	WBGene00004005	25	124	2.32	0.0004719	0.0035	WBGene000045237	2277	965	-1.24	0.0005364	0.0038422
WBGene00001117	2076	4122	0.99	0.00040115	0.00308103	WBGene00015795	261	616	1.24	0.0004728	0.0035042	WBGene000044724	578	7751	3.74	0.0005387	0.0038571
WBGene00000886	14383	5729	-1.33	0.00040117	0.00308103	WBGene00019198	3080	5821	0.92	0.0004728	0.0035042	WBGene00000215	950	3215	1.76	0.0005394	0.0038603
WBGene00016046	2226	4425	0.99	0.00040127	0.00308103	WBGene00014181	1859	3609	0.96	0.000475	0.0035191	WBGene00007414	819	3320	2.02	0.000542	0.0038776
WBGene00016396	655	2099	1.68	0.00040134	0.00308103	WBGene00021053	5314	2784	-0.93	0.0004754	0.0035205	WBGene000077670	166	28	-2.57	0.0005436	0.0038874
WBGene00003542	24	121	2.35	0.00040329	0.00309438	WBGene00021480	460	1124	1.29	0.0004768	0.003529	WBGene00019603	13	89	2.77	0.0005461	0.003904
WBGene00016085	76	233	1.61	0.00040342	0.00309438	WBGene00018175	3554	7181	1.01	0.0004775	0.0035328	WBGene00020349	697	223	-1.64	0.0005473	0.0039099
WBGene00003469	61	1	-6.76	0.00040382	0.00309521	WBGene00010240	3960	1888	-1.07	0.0004777	0.0035332	WBGene00011267	4254	2084	-1.03	0.0005474	0.0039099
WBGene00016847	12	91	2.92	0.00040387	0.00309521	WBGene00003667	12	87	2.9	0.0004793	0.0035436	WBGene00006668	844	3699	2.13	0.0005503	0.0039293
WBGene00003715	249	617	1.31	0.00040505	0.00310293	WBGene00016933	10	84	3.13	0.0004803	0.0035485	WBGene00009133	2860	8967	1.65	0.000551	0.0039322
WBGene00019887	260	1223	2.23	0.0004053	0.00310352	WBGene00001618	133	378	1.51	0.0004804	0.0035485	WBGene00013327	948	405	-1.23	0.0005513	0.0039329
WBGene00006839	36522	68485	0.91	0.00040586	0.00310646	WBGene00008755	2391	1107	-1.11	0.0004807	0.0035496	WBGene00009865	175	441	1.34	0.0005517	0.0039342
WBGene00011725	2	47	4.63	0.00040759	0.00311841	WBGene00010316	45	195	2.11	0.000481	0.0035498	WBGene00017970	2991	10372	1.79	0.0005577	0.0039758
WBGene00019347	2232	5945	1.41	0.00040828	0.00312234	WBGene00019859	237	1098	2.21	0.0004821	0.003557	WBGene00006778	4293	8169	0.93	0.0005579	0.0039758
WBGene00017704	502	163	-1.62	0.00040874	0.00312454	WBGene00020781	67270	32992	-1.03	0.0004836	0.0035664	WBGene00016293	14	92	2.71	0.0005609	0.003995
WBGene00014006	5	70	3.7	0.00040895	0.00312476	WBGene00016763	131	817	2.64	0.0004861	0.0035831	WBGene00002136	3955	1853	-1.09	0.0005611	0.003995
WBGene00001185	147	381	1.38	0.00040957	0.00312822	WBGene00008785	285	688	1.27	0.000487	0.0035883	WBGene000044807	65	235	1.85	0.0005634	0.0040098
WBGene00077765	953	309	-1.63	0.00041035	0.00313283	WBGene00012664	135	421	1.64	0.0004887	0.0035995	WBGene00000623	122	357	1.55	0.0005637	0.0040105
WBGene00003986	1941	8993	2.21	0.00041109	0.00313717	WBGene00012698	1146	449	-1.35	0.0004892	0.003602	WBGene00019025	46	173	1.91	0.0005646	0.004015
WBGene00017759	17476	7600	-1.2	0.00041284	0.00314825	WBGene00194769	18	110	2.6	0.0004895	0.0036026	WBGene00003714	73	270	1.89	0.0005655	0.0040201
WBGene00011041	61	246	2	0.0004129	0.00314825	WBGene00019237	20906	39408	0.91	0.0004907	0.0036095	WBGene00007551	24	123	2.36	0.0005658	0.0040205
WBGene00015409	1406	527	-1.42	0.00041466	0.00316036	WBGene00010330	7107	1572	1.13	0.0004924	0.0036208	WBGene00009950	607	184	-1.72	0.0005662	0.0040208
WBGene00022790	730	1685	1.21	0.00041611	0.00317008	WBGene00018871	38	323	3.09	0.0004933	0.0036258	WBGene00004912	387	2073	2.42	0.0005663	0.0040208
WBGene00020517	19354	8557	-1.18	0.00041699	0.00317543	WBGene00012457	265	638	1.27	0.0004949	0.0036361	WBGene00019789	1181	498	-1.25	0.0005667	0.0040209
WBGene00009059	3079	6192	1.01	0.00041766	0.00317915	WBGene00004510	15698	8429	-0.9	0.0004966	0.003647	WBGene00018964	7005	3516	-0.99	0.0005667	0.0040209
WBGene00003936	12055	29661	1.3	0.00041809	0.00318106	WBGene00004750	18949	8169	-1.21	0.0004971	0.0036484	WBGene00001774	44	345	2.97	0.0005692	0.0040365
WBGene00000274	16651	7999	-1.06	0.00041931	0.00318898	WBGene00013181	65	442	2.76	0.0004972	0.0036484	WBGene00004179	1590	3235	1.03	0.0005696	0.0040382
WBGene00022399	2963	1322	-1.16	0.00041948	0.00318898	WBGene00006978	4131	8327	1.01	0.0004974	0.0036486	WBGene00194657	257	646	1.33	0.0005715	0.004048
WBGene00014821	524	1743	1.73	0.00041967	0.00318909	WBGene00021446	172	469	1.45	0.0004996	0.0036628	WBGene00001204	1737	3342	0.94	0.0005716	0.004048
WBGene00003248	1057	2232	1.08	0.00042016	0.00319143	WBGene00020854	911	4290	2.23	0.0005006	0.0036683	WBGene00008559	322	1349	2.07	0.0005717	0.004048
WBGene00015287	96	317	1.73	0.00042045	0.00319228	WBGene00020544	12361	6103	-1.02	0.0005007	0.0036683	WBGene00002067	3227	10027	1.64	0.0005721	0.0040494
WBGene00022359	2089	984	-1.09	0.00042081	0.00319366	WBGene00020358	118	354	1.58	0.000501	0.0036692	WBGene00018407	2294	4525	0.98	0.0005734	0.0040567
WBGene00019048	163	421	1.37	0.00042102	0.00319389	WBGene00009958	4796	9228	0.94	0.0005019	0.0036738	WBGene00002234	652	1396	1.1	0.0005737	0.0040567
WBGene00044394	274	1621	2.56	0.00042198	0.00319987	WBGene00019039	5634	2285	-1.3	0.0005021	0.003674	WBGene00011038	143389	51359	-1.48	0.000574	0.0040567
WBGene00000503	366812	165148	-1.15	0.00042274	0.00320423	WBGene00013349	5141	1816	-1.5	0.0005038	0.0036838	WBGene00019849	26	131	2.34	0.000574	0.0040567
WBGene00013501	9545	3878	-1.3	0.00042539	0.00322301	WBGene00001137	37615	92449	1.3	0.0005041	0.0036838	WBGene00010149	12387	4271	-1.54	0.0005754	0.0040647
WBGene00011683	2	45	4.51	0.0004261	0.00322703	WBGene00004259	61200	29059	-1.07	0.0005042	0.0036838	WBGene00019925	1758	682	-1.37	0.0005763	0.0040695
WBGene00008172	2668	1003	-1.41	0.00042677	0.00323072	WBGene00012132	552	1510	1.45	0.0005044	0.0036838	WBGene00194921	116	372	1.68	0.0005769	0.004072
WBGene00018458	3099	1472	-1.07	0.00042716	0.00323213	WBGene00008643	194	487	1.33	0.0005046	0.0036838	WBGene00022626	213	565	1.41	0.0005775	0.0040747
WBGene00009280	1190	422	-1.5	0.00042732	0.00323213	WBGene00010968	136	758	2.48	0.0005047	0.0036838	WBGene00016196	13	97	2.87	0.000579	0.0040835
WBGene00012945	58	227	1.97	0.00042773	0.0032339	WBGene00012131	409	959	1.23	0.0005049	0.0036841	WBGene00017990	47165	23887	-0.98	0.00058	0.0040888
WBGene00022107	7371	3435	-1.1	0.00042984	0.00324845	WBGene00000867	11088	5082	-1.13	0.0005052	0.0036847	WBGene00018849	81233	39577	-1.04	0.0005802	0.0040888
WBGene00001156	60	228	1.93	0.00043113	0.00325683	WBGene00009896	4	53	3.56	0.0005056	0.0036891	WBGene00003617	711	1421	1	0.0005816	0.0040974
WBGene00020081	18941	8512	-1.15	0.00043183	0.00326081	WBGene00009848	577	1186	1.04	0.0005065	0.0036915	WBGene00001462	309	820	1.41	0.000582	0.0040974
WBGene00009689	4638	2242	-1.05	0.00043228	0.00326282	WBGene00016242	417	2080	2.32	0.000507	0.0036931	WBGene000022191	409	1063	1.38	0.0005821	0.0040974
WBGene00007709	####	83065	-1.44	0.00043277	0.00326514	WBGene00043989	466	199	-1.23	0.0005083	0.003701	WBGene00000770	700	251	-1.48	0.0005827	0.0041003

WBGene00020426	820	2967	1.86	0.00043725	0.00329756	WBGene00000936	465	1038	1.16	0.00051	0.0037125	WBGene00016948	2022	887	-1.19	0.0005833	0.0041027
WBGene00018571	101	279	1.47	0.00043778	0.00330019	WBGene00003161	45300	20000	-1.18	0.0005109	0.0037165	WBGene00077787	396	139	-1.51	0.0005845	0.0041098
WBGene00017923	4092	7757	0.92	0.00043908	0.00330857	WBGene00044259	609	1228	-2.32	0.000511	0.0037165	WBGene00014041	719	232	-1.63	0.0005861	0.0041178
WBGene00012185	25	283	3.48	0.0004396	0.00331107	WBGene00014009	74	726	3.3	0.0005121	0.0037227	WBGene00020599	296	702	1.25	0.0005861	0.0041178
WBGene00019672	739	321	-1.2	0.00044018	0.00331407	WBGene00022500	7516	27506	1.87	0.0005127	0.0037256	WBGene00020485	23	115	2.31	0.0005865	0.0041187
WBGene00001988	163	478	1.55	0.00044094	0.00331838	WBGene00019839	6351	24101	1.92	0.0005133	0.0037284	WBGene00000546	9766	4517	-1.11	0.0005892	0.0041362
WBGene00019014	515	1136	1.14	0.00044216	0.00332621	WBGene00007595	217	556	1.35	0.0005138	0.0037307	WBGene00021846	5234	2529	-1.05	0.0005901	0.0041409
WBGene00008117	23602	10916	-1.11	0.00044301	0.00333117	WBGene00001607	29917	12407	-1.27	0.0005142	0.0037318	WBGene00044412	1429	637	-1.17	0.0005909	0.0041449
WBGene00043067	32	129	2.03	0.00044401	0.00333735	WBGene00010002	13420	6093	-1.14	0.0005155	0.0037404	WBGene00017328	28694	13480	-1.09	0.0005911	0.0041449
WBGene00007800	2105	6781	1.69	0.00044436	0.00333856	WBGene00000732	9	74	3.06	0.0005164	0.0037434	WBGene00012225	1599	4934	1.63	0.0005927	0.0041539
WBGene00004124	40	318	2.98	0.00044606	0.00334992	WBGene00012490	2874	956	-1.59	0.0005166	0.0037434	WBGene00020179	270	66	-2.04	0.0005943	0.0041638
WBGene00013173	535	3565	2.74	0.00044645	0.00335148	WBGene00018228	3	54	4.09	0.0005166	0.0037434	WBGene00002058	1700	4487	1.4	0.0005949	0.0041667
WBGene00011757	232	1018	2.13	0.00044689	0.00335306	WBGene00008258	2856	5705	1	0.0005171	0.0037434	WBGene00021570	60	5	-3.52	0.000597	0.0041793
WBGene00006533	45	346	2.93	0.00044704	0.00335306	WBGene00001981	14320	6647	-1.11	0.0005173	0.0037434	WBGene00014848	264	927	1.81	0.0005974	0.0041807
WBGene00009616	17	123	2.88	0.00044777	0.00335716	WBGene00022202	428	2070	2.27	0.0005174	0.0037434	WBGene00020646	26	132	2.37	0.0005981	0.0041838
WBGene00020624	1111	527	-1.08	0.00044831	0.0033598	WBGene00016080	8472	4323	-0.97	0.0005175	0.0037434	WBGene00008372	163	454	1.48	0.0005985	0.0041847
WBGene00020157	74	286	1.96	0.00045015	0.00337149	WBGene00008448	87	274	1.66	0.0005177	0.0037434	WBGene00009177	21983	11022	-1	0.0005989	0.0041862
WBGene00044670	1183	554	-1.09	0.00045025	0.00337149	WBGene00045301	3642	1563	-1.22	0.0005178	0.0037434	WBGene00020475	12401	5396	-1.2	0.0006	0.0041921
WBGene00016522	50	208	2.07	0.00045054	0.00337226	WBGene00021716	1622	792	-1.03	0.0005189	0.0037489	WBGene00006407	3806	14294	1.91	0.0006007	0.0041952
WBGene00020022	1726	3820	1.15	0.0004518	0.00337974	WBGene00016134	788	2611	1.73	0.000519	0.0037489	WBGene00018837	2101	4282	1.03	0.0006009	0.0041952
WBGene00020012	4372	11063	1.34	0.00045191	0.00337974	WBGene00013129	11851	5903	-1.01	0.0005202	0.0037563	WBGene00020847	42	368	3.14	0.0006022	0.0042027
WBGene00044636	216	521	1.27	0.00045294	0.00338602	WBGene00016835	696	195	-1.84	0.0005209	0.0037592	WBGene00021579	103	11	-3.17	0.0006026	0.0042034
WBGene00011835	18500	8958	-1.05	0.00045358	0.00338938	WBGene00004811	0	36	6.88	0.0005216	0.0037631	WBGene00003549	4	71	4.09	0.0006031	0.0042034
WBGene00019306	107	502	2.23	0.0004541	0.00339186	WBGene00006705	1268	2780	1.13	0.0005238	0.0037772	WBGene00001543	203	503	1.31	0.0006031	0.0042034
WBGene00044898	450	1812	2.01	0.00060323	0.00420345	WBGene00019473	1260	483	-1.38	0.0006871	0.0046336	WBGene00003587	56698	21957	-1.37	0.0008044	0.0052548
WBGene00019058	4	53	3.87	0.00060493	0.00421247	WBGene00012175	658	1626	1.3	0.0006877	0.0046353	WBGene00003999	66	272	2.05	0.0008005	0.0052564
WBGene00000998	13526	28199	1.06	0.000605	0.00421247	WBGene00044440	4870	2267	-1.1	0.0006904	0.0046485	WBGene00001190	219	558	1.35	0.0008053	0.0052569
WBGene00002132	3322	6383	0.94	0.00060604	0.00421812	WBGene00005724	82	269	1.71	0.0006904	0.0046485	WBGene00001522	9773	4949	-0.98	0.0008059	0.0052585
WBGene00013397	27	122	2.19	0.00060715	0.00422417	WBGene00021831	8806	4543	-0.95	0.0006904	0.0046485	WBGene00010605	809	3700	2.19	0.0008129	0.0053023
WBGene00021412	618	285	-1.12	0.00060771	0.00422647	WBGene00017027	3539	1785	-0.99	0.0006909	0.0046505	WBGene00022196	1334	2667	1	0.0008139	0.0053072
WBGene00021411	19745	10086	-0.97	0.00060874	0.00423194	WBGene00007928	43	167	1.97	0.0006921	0.0046567	WBGene00014136	39	228	2.55	0.0008142	0.0053073
WBGene00000952	88	288	1.72	0.00060908	0.00423272	WBGene00044686	89	634	2.83	0.0006928	0.0046593	WBGene00011726	802	1893	1.24	0.0008164	0.0053196
WBGene00008851	10591	21517	1.02	0.00061174	0.00424951	WBGene00022000	439	143	-1.62	0.0006951	0.0046723	WBGene00010502	16011	8840	-0.86	0.000817	0.0053212
WBGene00013421	43	179	2.07	0.00061308	0.00425716	WBGene00014807	1853	755	-1.3	0.0006952	0.0046723	WBGene00016520	49387	24600	-1.01	0.0008182	0.0053275
WBGene00018744	86	397	2.2	0.00061349	0.00425838	WBGene00019576	1894	840	-1.17	0.0006962	0.0046772	WBGene00012005	3294	7100	1.11	0.0008185	0.0053275
WBGene00017980	4718	9061	0.94	0.00061515	0.00426725	WBGene00009490	17	100	2.59	0.0006977	0.0046852	WBGene00004205	7531	3634	-1.05	0.0008193	0.0053309
WBGene00021326	412	2572	2.64	0.00061524	0.00426725	WBGene00003889	89	347	1.97	0.0006985	0.0046891	WBGene00077763	5	56	3.5	0.0008206	0.0053371
WBGene00020850	90	277	1.62	0.00061583	0.00426967	WBGene00020301	13288	25000	0.91	0.0007009	0.0047036	WBGene00003681	11163	20111	0.85	0.0008213	0.0053396
WBGene00003220	10397	4860	-1.1	0.00061768	0.00428089	WBGene00022413	792	2267	1.52	0.0007018	0.0047074	WBGene00008309	210	759	1.86	0.0008222	0.0053422
WBGene00011925	4175	1805	-1.21	0.00061835	0.00428386	WBGene00018841	667	1357	1.03	0.0007024	0.0047101	WBGene00003371	15429	38674	1.33	0.0008228	0.0053455
WBGene00017065	2706	5279	0.96	0.00061866	0.00428434	WBGene00000072	754	1595	1.08	0.0007049	0.0047251	WBGene00001644	341	729	1.1	0.0008245	0.0053548
WBGene00000822	2054	7871	1.94	0.00062064	0.00429488	WBGene00010845	41589	20805	-1	0.0007052	0.0047255	WBGene00017979	2267	5493	1.28	0.0008248	0.0053548
WBGene00008580	3812	1507	-1.34	0.00062066	0.00429488	WBGene00011760	8973	17859	0.99	0.0007067	0.0047334	WBGene00001754	113	383	1.76	0.0008263	0.0053626
WBGene00010120	4706	2339	-1.01	0.00062815	0.00434502	WBGene00000511	1178	480	-1.29	0.0007078	0.0047393	WBGene00010520	19	158	3.07	0.0008272	0.0053664
WBGene00008407	38	146	1.94	0.00062963	0.00435364	WBGene00004380	3470	1582	-1.13	0.0007106	0.0047552	WBGene00007856	1318	2803	1.09	0.0008284	0.0053723
WBGene00004907	19	108	2.52	0.00063048	0.00435779	WBGene00012125	861	1777	1.05	0.0007107	0.0047552	WBGene00007725	236	1032	2.13	0.0008305	0.0053839
WBGene00012112	3179	1559	-1.03	0.00063117	0.00436044	WBGene00017204	48	180	1.91	0.0007127	0.0047665	WBGene00022395	327	118	-1.47	0.000831	0.0053852
WBGene00005648	27685	13183	-1.07	0.00063135	0.00436044	WBGene00014874	786	363	-1.12	0.0007176	0.0047975	WBGene00012767	13202	6571	-1.01	0.0008315	0.0053866
WBGene00022627	128	394	1.62	0.00063181	0.00436194	WBGene00018036	73	454	2.64	0.0007197	0.0048099	WBGene00006743	4677	8715	0.9	0.0008334	0.0053971
WBGene00015479	4326	2144	-1.01	0.00063452	0.00437896	WBGene00009052	9846	4860	-1.02	0.0007209	0.0048159	WBGene00007961	3440	1287	-1.42	0.0008347	0.0054033

WBGene00016163	1111	469	-1.24	0.00063502	0.00438018	WBGene00016114	345	1343	1.96	0.0007236	0.0048321	WBGene00006609	481	1039	1.11	0.0008416	0.0054459
WBGene00009861	7565	3574	-1.08	0.00063518	0.00438018	WBGene00011154	1681	3318	0.98	0.0007241	0.0048333	WBGene00022737	1237	566	-1.13	0.0008419	0.0054464
WBGene00001041	31552	13992	-1.17	0.00063559	0.00438134	WBGene00016172	1205	2511	1.06	0.0007245	0.0048333	WBGene00018653	28	132	2.23	0.0008433	0.0054532
WBGene00013256	21127	10065	-1.07	0.00063679	0.00438791	WBGene00002176	2217	5311	1.26	0.0007246	0.0048333	WBGene00003413	6397	3035	-1.08	0.0008449	0.0054617
WBGene00021502	8243	4088	-1.01	0.00063799	0.00439446	WBGene00010264	2998	1518	-0.98	0.0007251	0.0048351	WBGene00045486	3494	1506	-1.21	0.0008455	0.0054635
WBGene00017625	206	552	1.43	0.00063861	0.00439709	WBGene00003919	11006	5606	-0.97	0.0007259	0.0048386	WBGene00004048	21154	39671	0.91	0.0008462	0.0054666
WBGene00007336	81	547	2.75	0.00064128	0.00441374	WBGene00077751	134	35	-1.92	0.0007262	0.0048387	WBGene00004820	56141	22739	-1.3	0.0008477	0.0054739
WBGene00017127	88	258	1.55	0.00064257	0.00442093	WBGene00022311	725	279	-1.38	0.0007281	0.0048495	WBGene00016559	193	515	1.41	0.0008502	0.0054879
WBGene00001680	7085	13565	0.94	0.00064301	0.00442228	WBGene00015131	148	651	2.13	0.0007294	0.0048569	WBGene00011584	1	39	4.76	0.0008512	0.0054924
WBGene00006311	7484	3003	-0.32	0.00064346	0.00442371	WBGene00017140	18380	7496	-1.29	0.0007306	0.0048627	WBGene00019718	325	793	1.29	0.0008585	0.0055376
WBGene00013959	2734	5219	0.93	0.00064466	0.00443024	WBGene00004810	3	45	3.83	0.0007314	0.0048662	WBGene00009131	7893	3785	-1.06	0.0008628	0.0055633
WBGene00019757	9770	4016	-1.28	0.00064526	0.00443265	WBGene00019717	191	627	1.71	0.0007335	0.0048787	WBGene00001824	119204	232203	0.96	0.0008644	0.0055717
WBGene00005018	#####	510313	1.1	0.00064609	0.00443666	WBGene00015934	5197	10055	0.95	0.0007349	0.0048849	WBGene00012240	12492	6677	-0.9	0.0008652	0.0055745
WBGene00003134	22588	10736	-1.07	0.00064667	0.00443899	WBGene00044803	146	873	2.58	0.000735	0.0048849	WBGene00020563	4342	2045	-1.09	0.0008657	0.0055762
WBGene00002214	9777	4844	-1.01	0.00064705	0.00443985	WBGene00016567	6636	2990	-1.15	0.0007359	0.0048869	WBGene00006723	12557	5429	-1.21	0.0008668	0.0055812
WBGene00045248	32	284	3.17	0.00064776	0.00444306	WBGene00018466	43	166	1.93	0.0007359	0.0048869	WBGene00044019	162	1168	2.85	0.0008679	0.0055854
WBGene00013583	7751	3031	-1.35	0.00064914	0.00445081	WBGene00006784	2753	5898	1.1	0.0007384	0.0049021	WBGene00000062	21	105	2.32	0.0008681	0.0055854
WBGene00011951	217	433	1	0.00064966	0.00445229	WBGene00007225	#####	134737	-1.08	0.0007389	0.0049035	WBGene00004328	329	1171	1.83	0.0008707	0.0056
WBGene00001456	77	347	2.17	0.00065036	0.00445424	WBGene00010329	580	1439	1.31	0.0007396	0.0049066	WBGene00045058	11279	5792	-0.96	0.0008732	0.0056139
WBGene00019769	1736	867	-1	0.00065038	0.00445424	WBGene00007072	1549	709	-1.13	0.0007403	0.0049089	WBGene00002141	697	1986	1.51	0.0008737	0.0056157
WBGene00020743	455	1622	1.83	0.00065102	0.00445689	WBGene00017067	31	172	2.48	0.0007405	0.0049089	WBGene00003756	96	440	2.2	0.0008751	0.0056224
WBGene00011913	40	158	2	0.00065258	0.00446586	WBGene00007691	529	1935	1.87	0.000742	0.0049166	WBGene00021264	557	234	-1.25	0.0008759	0.0056256
WBGene00012529	37	315	3.07	0.0006531	0.00446774	WBGene00018737	2422	10531	2.12	0.0007423	0.0049166	WBGene00013234	7640	3803	-1.01	0.0008768	0.0056292
WBGene00019817	3430	1704	-1.01	0.00065335	0.00446774	WBGene00010159	14652	6775	-1.11	0.0007439	0.0049253	WBGene00007500	42062	21731	-0.95	0.0008774	0.0056311
WBGene00001161	31155	15060	-1.05	0.00065522	0.00447885	WBGene00020588	#####	43661	-1.21	0.0007441	0.0049253	WBGene00010334	124	326	1.4	0.0008777	0.0056311
WBGene00012888	20482	9729	-1.07	0.00065624	0.00448277	WBGene00009806	132	1125	3.09	0.0007484	0.0049517	WBGene00020270	61	477	2.98	0.0008788	0.0056345
WBGene00007073	86	246	1.51	0.0006563	0.00448277	WBGene00011786	175	1121	2.68	0.0007488	0.0049528	WBGene00001537	2243	1112	-1.01	0.0008789	0.0056345
WBGene00013542	1537	4949	1.69	0.00065726	0.00448398	WBGene00021702	615	1603	1.38	0.0007522	0.0049736	WBGene00008471	0	28	7.54	0.0008798	0.0056382
WBGene00015100	43	175	2.03	0.00065735	0.00448398	WBGene00021898	1573	827	-0.93	0.0007534	0.0049791	WBGene00019225	2	45	4.32	0.0008809	0.0056434
WBGene00006954	191	2304	3.59	0.00065744	0.00448398	WBGene00011289	62	303	2.29	0.0007603	0.0050233	WBGene00000908	1761	5318	1.59	0.0008824	0.0056474
WBGene00001719	1771	4275	1.27	0.00065747	0.00448398	WBGene00001400	1188	2430	1.03	0.000765	0.0050512	WBGene00008930	9485	4306	-1.14	0.0008824	0.0056474
WBGene00000523	1726	3470	1.01	0.00065793	0.00448408	WBGene00001872	728	314	-1.21	0.0007651	0.0050512	WBGene00194952	3	57	4.06	0.0008825	0.0056474
WBGene00022447	2519	1267	-0.99	0.00065798	0.00448408	WBGene00022246	7	57	2.99	0.0007685	0.0050719	WBGene00012189	2	53	4.91	0.0008839	0.0056549
WBGene00045299	4077	1790	-1.19	0.00066007	0.00449657	WBGene00017389	57	199	1.8	0.0007711	0.0050871	WBGene00010351	4815	2285	-1.07	0.0008845	0.0056564
WBGene00006939	3869	2041	-0.92	0.00066122	0.00450232	WBGene00020341	327	731	1.16	0.0007773	0.005126	WBGene00007957	59	207	1.82	0.0008859	0.0056637
WBGene00006452	7407	13748	0.89	0.00066141	0.00450232	WBGene00001046	2352	1076	-1.13	0.000778	0.0051288	WBGene00000454	22	112	2.32	0.0008918	0.005699
WBGene00007811	19504	9905	-0.98	0.00066184	0.00450354	WBGene00022160	4250	11816	1.48	0.0007788	0.0051307	WBGene00021948	1145	2341	1.03	0.0008933	0.0057069
WBGene00000955	75	364	2.29	0.00066283	0.00450851	WBGene00018900	28456	14732	-0.95	0.0007789	0.0051307	WBGene00009236	1	36	4.81	0.0008949	0.0057147
WBGene00020126	4	118	5.01	0.00066466	0.0045193	WBGene00020722	37	121	1.71	0.0007828	0.0051547	WBGene00013212	2207	1088	-1.02	0.0008959	0.005719
WBGene00008956	852	1957	1.2	0.00066492	0.00451931	WBGene00015768	53	282	2.41	0.0007845	0.0051639	WBGene00010117	2109	7026	1.74	0.0008995	0.0057393
WBGene00013862	6653	3172	-1.07	0.00066654	0.00452866	WBGene00008116	66	322	2.3	0.0007849	0.0051643	WBGene00017556	434	153	-1.5	0.0008998	0.0057393
WBGene00021580	34	297	3.13	0.00066778	0.00453536	WBGene00015580	3873	7442	0.94	0.0007851	0.0051643	WBGene00017950	1025	2547	1.31	0.0009	0.0057393
WBGene00007424	119	409	1.78	0.00067127	0.00455582	WBGene00017949	7895	3554	-1.15	0.0007862	0.0051697	WBGene00018173	325	744	1.2	0.0009007	0.0057418
WBGene00021663	104	14	-2.91	0.00067202	0.00455582	WBGene00019002	12068	5613	-1.1	0.0007868	0.0051716	WBGene00002021	151	391	1.37	0.0009013	0.0057433
WBGene00005036	31	148	2.26	0.00067206	0.00455582	WBGene00021867	1152	486	-1.25	0.0007877	0.0051759	WBGene00020043	2	40	4.38	0.0009019	0.0057456
WBGene00017358	13321	5513	-1.27	0.00067207	0.00455582	WBGene00021713	165	35	-2.25	0.0007888	0.0051794	WBGene00016988	184	448	1.29	0.000903	0.0057503
WBGene00020247	106	309	1.54	0.00067222	0.00455582	WBGene00043988	773	380	-1.02	0.0007888	0.0051794	WBGene00009212	82558	39993	-1.05	0.0009035	0.0057512
WBGene00021060	498	1085	1.12	0.00067232	0.00455582	WBGene00008583	1126	545	-1.05	0.000791	0.0051919	WBGene00015334	144	747	2.38	0.0009074	0.0057739
WBGene00022504	1631	6108	1.9	0.00067334	0.00456087	WBGene00021927	816	1697	1.06	0.0007919	0.0051957	WBGene00000460	22294	10406	-1.1	0.0009078	0.0057745
WBGene00010834	1570	7132	2.18	0.00067357	0.00456087	WBGene00002246	2218	957	-1.21	0.0007938	0.0052061	WBGene00011572	720	2513	1.8	0.0009102	0.0057879



WBGene00019146	32	144	2.16	0.00067396	0.00456178	WBGene00012109	4996	2379	-1.07	0.0007951	0.0052131	WBGene00013612	50	3	-3.99	0.0009127	0.0058016
WBGene00015628	70	229	1.7	0.00067992	0.0046004	WBGene00003630	3626	6771	0.9	0.0007966	0.0052207	WBGene00022560	1646	753	-1.13	0.0009132	0.0058029
WBGene00008526	1254	489	-1.36	0.00068081	0.00460467	WBGene00009434	7	64	3.29	0.0007972	0.0052224	WBGene00017814	8502	15907	0.9	0.0009157	0.0058168
WBGene00001258	36118	17255	-1.07	0.00068197	0.00461081	WBGene00003966	677	2189	1.69	0.0007974	0.0052224	WBGene00000038	249	623	1.32	0.0009167	0.005821
WBGene00013916	146	408	1.48	0.00068319	0.00461732	WBGene00020280	1578	3018	0.94	0.0007995	0.0052342	WBGene00017398	235	526	1.16	0.000918	0.0058274
WBGene00016976	25	175	2.83	0.00068348	0.00461751	WBGene00001784	80	1206	2.52	0.0008001	0.0052345	WBGene00019277	1091	2184	1	0.00092	0.005838
WBGene00009086	1167	532	-1.13	0.00068393	0.00461881	WBGene00010643	210	240	1.58	0.0008002	0.0052345	WBGene00013233	10385	5245	-0.99	0.0009207	0.0058404
WBGene00021463	23456	12557	-0.9	0.00068476	0.00462273	WBGene00013409	2774	1387	-1	0.0008015	0.0052413	WBGene00021124	388	1129	1.54	0.0009225	0.0058496
WBGene00020893	155	588	1.92	0.00068609	0.00462995	WBGene00000035	1173	2970	1.34	0.0008029	0.0052484	WBGene00044663	91	407	2.17	0.0009229	0.0058501
WBGene00020250	398	1809	2.18	0.00068696	0.00463358	WBGene00008589	42	438	3.37	0.0008042	0.0052548	WBGene00015870	0	34	6.8	0.0009236	0.0058522
WBGene00004229	2554	4926	0.95	0.00092429	0.0058547	WBGene00007762	5711	2473	-1.21	0.001019	0.0062645	WBGene00010081	1849	617	-1.58	0.0011946	0.0071335
WBGene00006748	81	869	3.43	0.00092556	0.00586065	WBGene00044294	15485	35557	1.2	0.0010195	0.0062658	WBGene00012266	3	48	4.15	0.0011949	0.0071335
WBGene00019177	65	324	2.33	0.0009259	0.00586079	WBGene00021075	29	151	2.37	0.0010207	0.0062708	WBGene00012763	341	1853	2.44	0.0011958	0.0071366
WBGene00008302	0	24	7.91	0.00092701	0.00586575	WBGene00008838	6611	3017	-1.13	0.0010223	0.0062782	WBGene00012728	32	343	3.44	0.0011975	0.0071443
WBGene00013455	534	1397	1.39	0.00092881	0.0058717	WBGene00004990	848	3514	2.05	0.0010245	0.00629	WBGene00012160	527	214	-1.3	0.0012075	0.0072018
WBGene00021799	162	768	2.25	0.000929	0.0058717	WBGene00007416	161	4037	1.44	0.0010256	0.0062942	WBGene00011576	6025	3109	-0.93	0.0012087	0.0072047
WBGene00016014	9528	5014	-0.93	0.0009291	0.0058717	WBGene00018498	113	282	1.32	0.0010261	0.0062957	WBGene00005690	41	175	2.09	0.0012091	0.0072047
WBGene00006666	3528	11098	1.65	0.00092926	0.0058717	WBGene00016918	10368	19015	0.87	0.0010277	0.0063033	WBGene00022845	329	803	1.29	0.0012092	0.0072047
WBGene00022577	942	3067	1.7	0.00093258	0.00588768	WBGene00020672	4963	2808	-0.82	0.0010283	0.0063046	WBGene00017036	184	570	1.63	0.0012121	0.0072196
WBGene00013018	9137	4575	-1	0.00093266	0.00588768	WBGene00012792	736	294	-1.32	0.0010307	0.0063172	WBGene00020537	15026	6587	-1.19	0.0012127	0.0072205
WBGene00007493	12978	6325	-1.04	0.00093277	0.00588768	WBGene00018646	127	478	1.92	0.0010376	0.0063561	WBGene00015179	16	90	2.52	0.0012132	0.0072212
WBGene00000977	3	44	3.7	0.00093443	0.00589604	WBGene00019924	5313	2668	-0.99	0.0010378	0.0063561	WBGene00013848	64	207	1.7	0.0012153	0.0072315
WBGene00003745	105	479	2.2	0.0009366	0.00590765	WBGene00021354	216	477	1.15	0.0010413	0.0063735	WBGene00015471	229	579	1.34	0.0012159	0.0072326
WBGene00003525	146	735	2.33	0.00093878	0.00591937	WBGene00022320	1536	657	-1.22	0.0010413	0.0063735	WBGene00021516	7713	3580	-1.11	0.0012169	0.007236
WBGene00000068	4466	9294	1.06	0.00094056	0.00592852	WBGene00015160	7964	4088	-0.96	0.001042	0.0063754	WBGene00022561	2192	1063	-1.04	0.0012192	0.0072474
WBGene00018299	459	975	1.09	0.00094105	0.00592951	WBGene00021850	2277	4331	0.93	0.0010427	0.0063775	WBGene00012032	2537	10413	2.04	0.0012205	0.0072525
WBGene00009696	16012	8585	-0.9	0.00094163	0.00592962	WBGene00003497	13403	26286	0.97	0.0010459	0.0063949	WBGene00007751	385	1902	2.3	0.0012218	0.0072568
WBGene00006622	6	63	3.31	0.00094173	0.00592962	WBGene00001172	2177	6470	1.57	0.0010473	0.0064	WBGene00010110	1282	3947	1.62	0.001222	0.0072568
WBGene00004815	28744	11467	-1.33	0.00094245	0.00593107	WBGene00016912	13	80	2.63	0.0010474	0.0064	WBGene00019367	16	96	2.56	0.0012232	0.0072616
WBGene00021361	2669	5576	1.06	0.00094262	0.00593107	WBGene00018651	19	104	2.49	0.0010533	0.0064336	WBGene00020322	5383	2528	-1.09	0.00123	0.0072996
WBGene00021884	669	273	-1.29	0.00094434	0.0059389	WBGene00022834	393	884	1.17	0.0010612	0.0064797	WBGene00007650	15009	7957	-0.92	0.001231	0.0073031
WBGene00022734	33600	16113	-1.06	0.00094453	0.0059389	WBGene00003431	114	14	-3.03	0.0010623	0.0064841	WBGene00021518	39	191	2.28	0.0012346	0.007322
WBGene00077536	15	104	2.77	0.0009452	0.00594109	WBGene00010864	10	71	2.79	0.0010645	0.0064954	WBGene00013738	5134	2484	-1.05	0.0012351	0.0073225
WBGene00010361	1395	695	-1	0.00094583	0.00594292	WBGene00004135	495	1602	1.7	0.0010649	0.0064956	WBGene00017250	83	263	1.66	0.0012372	0.0073318
WBGene00007041	314	2093	2.74	0.00094867	0.00595872	WBGene00011422	1426	2907	1.03	0.0010665	0.0065032	WBGene00020365	1106	2116	0.94	0.0012375	0.0073318
WBGene00077683	6	52	3.23	0.00094932	0.00596006	WBGene00009606	4975	2391	-1.06	0.0010675	0.0065064	WBGene00000399	84	202	1.27	0.001239	0.0073386
WBGene00003602	8756	20694	1.24	0.00094955	0.00596006	WBGene00016958	651	1502	1.21	0.0010677	0.0065064	WBGene00018488	3694	6891	0.9	0.0012401	0.0073405
WBGene00020375	28940	14285	-1.02	0.00095009	0.00596138	WBGene00009492	27	101	1.9	0.0010691	0.0065126	WBGene00044059	11	84	2.96	0.0012402	0.0073405
WBGene00018976	4707	8588	0.87	0.00095065	0.00596283	WBGene00021103	6891	3302	-1.06	0.0010719	0.0065276	WBGene00006557	3512	1471	-1.26	0.0012409	0.0073426
WBGene00010332	1933	903	-1.1	0.00095262	0.00597308	WBGene00013946	2270	1148	-0.98	0.0010755	0.0065471	WBGene00014183	74	1116	3.91	0.0012435	0.0073552
WBGene00044680	3	53	4.01	0.00095318	0.00597308	WBGene00011380	1105	2256	1.03	0.0010763	0.0065499	WBGene00006819	2274	8724	1.94	0.0012487	0.0073832
WBGene00004740	181	451	1.32	0.00095347	0.00597308	WBGene00018252	1905	996	-0.94	0.001077	0.0065517	WBGene00014117	49854	18648	-1.42	0.001249	0.0073832
WBGene00019578	780	346	-1.18	0.00095362	0.00597308	WBGene00007128	5318	2507	-1.08	0.0010784	0.0065579	WBGene00008795	13	78	2.58	0.0012506	0.0073901
WBGene00015650	3595	10010	1.48	0.00095599	0.00598584	WBGene00013436	7392	3488	-1.08	0.0010818	0.0065764	WBGene00044702	389	138	-1.5	0.0012523	0.0073973
WBGene00006375	6775	3084	-1.14	0.00095721	0.00599078	WBGene00014826	130	758	2.55	0.0010863	0.0066015	WBGene00003652	5399	8960	0.73	0.0012526	0.0073973
WBGene00008577	77	248	1.68	0.00095745	0.00599078	WBGene000194904	716	1278	0.84	0.001088	0.0066095	WBGene00016094	6	59	3.31	0.0012544	0.0074054
WBGene00009444	15848	7500	-1.08	0.00095855	0.00599561	WBGene00017478	578	2241	1.96	0.0010959	0.0066554	WBGene00020811	27	132	2.29	0.0012557	0.0074079
WBGene00003397	37338	20055	-0.9	0.00095891	0.00599578	WBGene00020374	7928	3465	-1.19	0.001097	0.00666	WBGene00077669	232	539	1.21	0.0012561	0.0074079
WBGene00017120	1145	2228	0.96	0.0009597	0.00599863	WBGene00016798	339	127	-1.42	0.0010977	0.0066618	WBGene00011076	71	506	2.84	0.0012567	0.0074079
WBGene00004230	376	2428	2.69	0.00096194	0.00600968	WBGene00000539	66	197	1.57	0.0010985	0.0066623	WBGene00008246	59	173	1.57	0.0012567	0.0074079

WBGene00003369	16074	46205	1.52	0.00096214	0.00600968	WBGene00016744	1326	2623	0.98	0.0010988	0.0066623	WBGene00015608	1234	2570	1.06	0.0012569	0.0074079
WBGene00016632	11365	5708	-0.99	0.00096346	0.00601421	WBGene00008043	11	77	2.85	0.0010989	0.0066623	WBGene00007474	1294	2481	0.94	0.001258	0.0074107
WBGene00020771	2014	765	-1.4	0.00096353	0.00601421	WBGene00015957	40	189	2.24	0.0010993	0.0066628	WBGene00007212	748	252	-1.57	0.0012582	0.0074107
WBGene00015527	182	439	1.27	0.00096585	0.00602659	WBGene00003062	28676	14317	-1	0.0011009	0.0066701	WBGene00004824	8594	4376	-0.97	0.0012605	0.0074219
WBGene00007076	772	354	-1.13	0.00096643	0.00602767	WBGene00014008	387	784	1.02	0.0011015	0.006671	WBGene00194917	356	737	1.05	0.0012635	0.0074369
WBGene000021445	66	212	1.69	0.0009667	0.00602767	WBGene00017226	19	96	2.31	0.0011018	0.006671	WBGene00012672	4149	1651	-1.33	0.0012661	0.0074499
WBGene00020677	381	1006	1.4	0.00096751	0.0060291	WBGene00044788	1	36	4.64	0.0011033	0.0066777	WBGene00045404	33	125	1.9	0.0012684	0.0074611
WBGene00014140	470	1020	1.12	0.00096763	0.0060291	WBGene00020069	137	708	2.37	0.0011039	0.0066794	WBGene00011856	1192	4117	1.79	0.0012697	0.0074649
WBGene00010150	765	2904	1.92	0.00096793	0.0060291	WBGene00022519	2287	5133	1.17	0.0011064	0.0066921	WBGene00015545	1871	6583	1.81	0.0012699	0.0074649
WBGene00009774	61	221	1.87	0.00096837	0.00602972	WBGene00008499	91	522	2.52	0.0011082	0.0067009	WBGene00007302	523	1105	1.08	0.0012717	0.0074706
WBGene00004773	6751	13583	1.01	0.00096975	0.00603545	WBGene00015822	332	1383	2.06	0.0011103	0.0067114	WBGene00015116	1099	1845	0.75	0.001272	0.0074706
WBGene00010492	16363	6795	-1.27	0.00097024	0.00603545	WBGene00000796	25437	12908	-0.98	0.0011117	0.0067174	WBGene00019779	434	1488	1.78	0.0012721	0.0074706
WBGene00020279	94	443	2.23	0.00097029	0.00603545	WBGene00044455	11	79	2.83	0.0011152	0.006736	WBGene00018366	5243	2057	-1.35	0.0012733	0.0074733
WBGene00010549	3437	1690	-1.02	0.00097198	0.00604386	WBGene00008477	184	1072	2.54	0.0011175	0.0067477	WBGene00011882	46	172	1.89	0.0012734	0.0074733
WBGene00014040	2016	1041	-0.95	0.00097423	0.00605423	WBGene00020023	21	137	2.71	0.0011199	0.0067599	WBGene00008728	717	334	-1.1	0.0012743	0.0074758
WBGene00003402	141	533	1.92	0.00097433	0.00605423	WBGene00019858	261	1061	2.02	0.0011225	0.0067733	WBGene00000979	1625	2927	0.85	0.0012747	0.0074776
WBGene00009495	76	251	1.72	0.00097707	0.00606919	WBGene00044191	47	181	1.94	0.001123	0.0067743	WBGene00015390	179	473	1.4	0.0012764	0.0074832
WBGene00013474	65	4	-4.06	0.00097882	0.00607665	WBGene00014871	452	197	-1.2	0.0011278	0.0068008	WBGene00012272	157	426	1.44	0.0012839	0.0075247
WBGene00014242	506	200	-1.34	0.00097913	0.00607665	WBGene00011952	252	1388	2.46	0.001129	0.0068056	WBGene00020506	17	134	2.98	0.0012853	0.0075308
WBGene00044661	459	161	-1.51	0.00097929	0.00607665	WBGene00016699	50	185	1.9	0.0011349	0.0068389	WBGene00011571	330	1979	2.58	0.0012866	0.0075361
WBGene00010703	2735	5133	0.91	0.00098298	0.00609745	WBGene00018337	2526	1054	-1.26	0.0011373	0.0068513	WBGene00013042	1443	3495	1.28	0.001288	0.0075415
WBGene00017616	11	78	2.76	0.00098349	0.0060985	WBGene00003664	66	395	2.58	0.0011408	0.0068703	WBGene00011517	882	1636	0.89	0.001291	0.0075565
WBGene00015797	323	117	-1.46	0.00098416	0.00610051	WBGene00007743	597	1206	1.01	0.001142	0.0068753	WBGene00044221	28	120	2.1	0.0012925	0.0075615
WBGene00015647	10156	25717	1.34	0.00098449	0.00610051	WBGene00000637	7	92	3.8	0.0011502	0.00692	WBGene00022608	9	69	2.95	0.0012927	0.0075615
WBGene00020404	3496	1573	-1.15	0.00098566	0.00610562	WBGene00021040	439	180	-1.29	0.0011502	0.00692	WBGene00050912	379	748	0.98	0.0012978	0.0075892
WBGene00010453	377	814	1.11	0.00098698	0.00610979	WBGene00021244	332	804	1.28	0.001152	0.006928	WBGene00007221	8410	4525	-0.89	0.0013033	0.0076186
WBGene00007290	941	414	-1.18	0.00098701	0.00610979	WBGene00008509	140	497	1.83	0.0011547	0.0069419	WBGene00008040	253	670	1.4	0.0013041	0.0076196
WBGene00012251	24	114	2.24	0.00098764	0.00611162	WBGene00006394	5669	2661	-1.09	0.0011626	0.0069872	WBGene00011768	8474	18300	1.11	0.0013043	0.0076196
WBGene00000501	62	247	1.99	0.00098978	0.00612273	WBGene00010921	2854	1435	-0.99	0.0011632	0.0069884	WBGene00011139	6493	3387	-0.94	0.0013052	0.0076223
WBGene00003716	848	1642	0.95	0.00099263	0.00613824	WBGene00004243	6182	2993	-1.05	0.0011643	0.0069927	WBGene00018346	81	236	1.55	0.001308	0.0076365
WBGene00008868	518	1543	1.57	0.00099591	0.00615642	WBGene00004702	27927	12424	-1.17	0.0011653	0.0069964	WBGene00020449	125	294	1.24	0.0013118	0.0076559
WBGene00021247	2691	5228	0.96	0.00099696	0.00616077	WBGene00010255	421	121	-1.8	0.0011668	0.0070031	WBGene00013037	88	289	1.72	0.0013125	0.0076562
WBGene00012042	34	135	1.99	0.00099868	0.00616926	WBGene00045406	985	419	-1.23	0.0011686	0.0070113	WBGene00004256	531	2570	2.27	0.0013129	0.0076562
WBGene00013833	47	348	2.9	0.00099926	0.00617076	WBGene00021025	2781	5227	0.91	0.0011727	0.0070314	WBGene00016993	2806	1478	-0.92	0.0013131	0.0076562
WBGene00010173	9	91	3.38	0.00100002	0.00617334	WBGene00010760	16	100	2.63	0.001173	0.0070314	WBGene00008548	2615	1389	-0.91	0.0013163	0.0076695
WBGene00020689	376	767	1.03	0.00100065	0.00617508	WBGene00018437	12577	6424	-0.97	0.0011731	0.0070314	WBGene00019812	119	329	1.47	0.0013165	0.0076695
WBGene00012776	500	1052	1.07	0.00100487	0.00619898	WBGene00009173	2445	1211	-1.01	0.0011762	0.0070475	WBGene00007248	407	115	-1.83	0.0013167	0.0076695
WBGene00012989	631	1924	1.61	0.00100619	0.00620502	WBGene00017420	446	2380	2.42	0.0011784	0.0070588	WBGene00003893	62107	113084	0.86	0.0013203	0.0076879
WBGene00019683	1112	508	-1.13	0.00100728	0.00620921	WBGene00019463	226	476	1.07	0.0011793	0.0070615	WBGene00017124	100	563	2.49	0.0013216	0.0076934
WBGene00001552	41	210	2.35	0.00100772	0.00620921	WBGene00021056	9773	4244	-1.2	0.001181	0.0070697	WBGene00009292	5944	17785	1.58	0.0013232	0.0077003
WBGene00021917	1518	3047	1.01	0.00100791	0.00620921	WBGene00015949	248	816	1.72	0.0011818	0.007072	WBGene00021042	7	56	3.09	0.001324	0.0077024
WBGene00007084	209	524	1.33	0.00101046	0.0062228	WBGene00006387	7821	3553	-1.14	0.0011862	0.0070961	WBGene00011741	23320	8861	-1.4	0.0013247	0.0077038
WBGene00000563	26	124	2.27	0.00101035	0.00623825	WBGene00002072	8675	4559	-0.93	0.0011873	0.0070982	WBGene00022827	444	1445	1.7	0.0013264	0.0077112
WBGene00019899	152	389	1.36	0.00101401	0.00623825	WBGene00016892	20822	7974	-1.38	0.0011874	0.0070982	WBGene00012405	5013	1988	-1.33	0.0013273	0.0077141
WBGene00001116	1668	6546	1.97	0.00101401	0.00623825	WBGene00000883	76098	37462	-1.02	0.0011903	0.0071113	WBGene00018716	214	521	1.28	0.0013284	0.0077177
WBGene00019400	18180	9516	-0.93	0.0010182	0.00626185	WBGene00009831	1068	2235	1.07	0.0011917	0.0071191	WBGene00003955	157861	73373	-1.11	0.0013311	0.007731
WBGene00000151	11612	5923	-0.97	0.00133243	0.00773616	WBGene00017001	30	177	2.58	0.0014886	0.0084094	WBGene00009503	389	1438	1.89	0.0016529	0.0090914
WBGene00002978	30097	69898	1.22	0.00133517	0.0077496	WBGene00002076	60296	32350	-0.9	0.0014922	0.0084257	WBGene00017441	648	1380	1.09	0.0016534	0.0090914
WBGene00020738	75430	32397	-1.22	0.00133638	0.00775413	WBGene00016058	89	8	-3.45	0.0014925	0.0084257	WBGene00012322	66	208	1.64	0.0016582	0.0091148
WBGene00015455	13	120	3.17	0.00133906	0.00776714	WBGene00003686	525	1036	0.98	0.0014962	0.0084442	WBGene00003002	83666	47572	-0.81	0.0016596	0.0091201

WBGene00007242	3231	6269	0.96	0.00134046	0.00777278	WBGene00013763	145	523	1.85	0.0014997	0.0084611	WBGene00020489	397	1149	1.53	0.0016613	0.0091265
WBGene00020844	50	192	1.95	0.00134176	0.00777776	WBGene00195183	1928	980	-0.98	0.0015006	0.0084634	WBGene00011955	757	3082	2.02	0.0016647	0.0091421
WBGene00020911	30521	16305	-0.9	0.00134224	0.00777805	WBGene00010012	2738	6675	1.29	0.0015014	0.0084653	WBGene00021043	17667	41451	1.23	0.0016656	0.0091443
WBGene00022688	14	93	2.72	0.00134349	0.00778277	WBGene00012021	20976	11281	-0.89	0.0015019	0.0084654	WBGene00002189	4970	15125	1.61	0.0016674	0.0091506
WBGene00006753	12109	24360	1.01	0.00134475	0.00778643	WBGene00017858	78	357	2.19	0.0015031	0.0084697	WBGene00000939	40773	21942	-0.89	0.0016677	0.0091506
WBGene00001390	77	223	1.53	0.00134498	0.00778643	WBGene00013865	190	708	1.9	0.0015043	0.0084739	WBGene00009007	24890	11982	-1.05	0.0016695	0.0091575
WBGene00018670	82	4	-4.52	0.00135032	0.00781481	WBGene00012107	410	2708	2.72	0.0015049	0.0084744	WBGene00007753	3129	1797	-0.8	0.0016737	0.0091768
WBGene00011693	14	91	2.7	0.00135253	0.00782411	WBGene00015105	5258	2741	-0.94	0.0015067	0.0084819	WBGene00010535	46	3	-3.76	0.001674	0.0091768
WBGene00020098	3709	1377	-1.43	0.0013528	0.00782411	WBGene00017628	7	60	3.08	0.0015077	0.0084848	WBGene00001070	12	167	3.78	0.0016759	0.0091843
WBGene00016000	22	113	2.38	0.00135476	0.00783088	WBGene00012680	85	316	1.9	0.0015081	0.0084849	WBGene00018406	269	103	-1.38	0.001678	0.0091928
WBGene00001650	4331	8365	0.95	0.00135484	0.00783088	WBGene00013280	9033	3687	-1.29	0.0015126	0.0085074	WBGene00006742	9534	17344	0.86	0.0016793	0.0091974
WBGene00000057	42	137	1.7	0.00135644	0.00783758	WBGene00000526	2906	5758	0.99	0.0015158	0.0085227	WBGene00021167	576	1181	1.04	0.0016827	0.0092133
WBGene00004721	15451	8156	-0.92	0.00135747	0.00784102	WBGene00015310	7643	4152	-0.88	0.0015173	0.0085263	WBGene00009969	51	182	1.83	0.0016837	0.0092158
WBGene00021396	3388	6239	0.88	0.00135928	0.00784895	WBGene00008557	99	590	2.58	0.0015174	0.0085263	WBGene00003848	38	129	1.76	0.0016874	0.0092333
WBGene00016979	4026	7507	0.9	0.00136117	0.00785612	WBGene00016218	141	843	2.58	0.0015184	0.0085293	WBGene00018728	72	236	1.72	0.00169	0.0092448
WBGene00021791	119	28	-2.08	0.00136182	0.00785612	WBGene00000779	14424	30148	1.06	0.0015189	0.0085293	WBGene00008496	2636	8875	1.75	0.0016954	0.0092711
WBGene00010898	3189	5870	0.88	0.00136183	0.00785612	WBGene00017269	8227	3994	-1.04	0.0015198	0.0085311	WBGene00019241	15456	8150	-0.92	0.0016968	0.0092763
WBGene00009183	282	652	1.21	0.00136305	0.00786061	WBGene00013721	16317	5067	-1.69	0.0015201	0.0085311	WBGene00004903	2386	1380	-0.79	0.0017041	0.0093134
WBGene00018348	18	84	2.24	0.00136482	0.00786827	WBGene00009874	22	136	2.63	0.001523	0.0085442	WBGene00012045	5	57	3.4	0.0017152	0.0093711
WBGene00018717	3531	1798	-0.97	0.00136548	0.00786957	WBGene00007195	24546	11149	-1.14	0.0015253	0.0085546	WBGene00018415	161	389	1.27	0.0017165	0.0093732
WBGene00007388	663	1251	0.92	0.00136781	0.00787807	WBGene00003690	1614	3082	0.93	0.0015262	0.0085571	WBGene00009813	5229	9265	0.83	0.0017169	0.0093732
WBGene00044007	19	180	3.27	0.00136783	0.00787807	WBGene00022843	15	101	2.71	0.0015279	0.0085619	WBGene00018727	1075	2119	0.98	0.0017172	0.0093732
WBGene00008511	2771	5401	0.96	0.0013702	0.00788922	WBGene00000660	51	163	1.67	0.001528	0.0085619	WBGene00011736	3202	8260	1.37	0.0017207	0.0093894
WBGene00006663	852	2434	1.51	0.00137356	0.00790599	WBGene00009875	3	43	3.79	0.0015307	0.0085742	WBGene00001613	231	658	1.51	0.0017224	0.009396
WBGene00019020	85	234	1.47	0.0013741	0.00790658	WBGene00006412	4303	8100	0.91	0.0015344	0.0085921	WBGene00001571	4554	2300	-0.99	0.0017237	0.0094003
WBGene00006374	2769	1006	-1.46	0.00137488	0.00790853	WBGene00019538	387	1086	1.49	0.0015393	0.0086168	WBGene00000405	58741	30970	-0.92	0.0017251	0.0094051
WBGene00003991	1912	3428	0.84	0.00137896	0.00792944	WBGene00020545	319	132	-1.28	0.0015424	0.0086315	WBGene00003843	735	1858	1.34	0.0017269	0.0094118
WBGene00003841	29	136	2.21	0.00137965	0.00793089	WBGene00021913	57604	30419	-0.92	0.0015437	0.0086361	WBGene00022420	16515	7981	-1.05	0.0017281	0.009414
WBGene00023414	106	455	2.1	0.00138661	0.00796833	WBGene00019311	20776	12043	-0.79	0.0015442	0.0086366	WBGene00019738	38	340	3.14	0.0017283	0.009414
WBGene00013160	25194	13214	-0.93	0.00138967	0.0079815	WBGene00194892	5934	3178	-0.9	0.001547	0.0086492	WBGene00011732	864	2876	1.74	0.0017324	0.0094306
WBGene00004225	2175	5524	1.34	0.00138979	0.0079815	WBGene00012110	2095	960	-1.13	0.0015478	0.0086509	WBGene00013481	240	618	1.37	0.0017324	0.0094306
WBGene00003155	66876	32616	-1.04	0.00139346	0.00800002	WBGene00007203	150	344	1.2	0.0015518	0.0086704	WBGene00008385	7804	4249	-0.88	0.001733	0.0094311
WBGene00016799	3288	1196	-1.46	0.00139572	0.00801047	WBGene00006592	4610	8341	0.86	0.0015522	0.0086704	WBGene00012328	28	122	2.12	0.0017343	0.0094352
WBGene00016939	3152	1612	-0.97	0.00139689	0.00801461	WBGene00021342	384	143	-1.43	0.0015542	0.0086785	WBGene00021875	67	214	1.68	0.0017404	0.0094644
WBGene00000288	63	469	2.89	0.00140388	0.00805041	WBGene00010695	3874	7125	0.88	0.0015546	0.0086785	WBGene00020107	49022	24988	-0.97	0.0017411	0.0094644
WBGene00020688	7101	3701	-0.94	0.00140403	0.00805041	WBGene00013949	347	741	1.1	0.0015562	0.0086834	WBGene00012304	12	138	3.54	0.0017413	0.0094644
WBGene00000520	12492	6483	-0.95	0.00140592	0.00805868	WBGene00012947	10	98	3.31	0.0015565	0.0086834	WBGene00014091	62	255	2.04	0.0017466	0.0094903
WBGene00018302	14943	6766	-1.14	0.00140718	0.00806333	WBGene00011338	31213	17252	-0.86	0.0015612	0.008707	WBGene00007344	54	458	3.09	0.0017504	0.0095082
WBGene00019321	19	107	2.53	0.0014094	0.00807348	WBGene00012270	15	92	2.6	0.0015644	0.0087224	WBGene00009182	374	147	-1.35	0.0017516	0.009512
WBGene00013322	713	1408	0.98	0.00141349	0.00809432	WBGene00018907	48	155	1.7	0.0015672	0.008735	WBGene00008476	1955	1056	-0.89	0.001755	0.0095276
WBGene00001538	1498	2992	1	0.00141553	0.00810155	WBGene00021945	13198	6743	-0.97	0.0015681	0.0087356	WBGene00006584	17754	31260	0.82	0.001759	0.0095464
WBGene00003724	627	1221	0.96	0.00141565	0.00810155	WBGene00000086	5014	9365	0.9	0.0015686	0.0087356	WBGene00013312	3235	6174	0.93	0.0017656	0.0095765
WBGene00014173	26	424	4.04	0.00141755	0.00810985	WBGene00003891	833	3117	1.9	0.0015687	0.0087356	WBGene00014205	3399	1588	-1.1	0.0017656	0.0095765
WBGene00007329	34417	18406	-0.9	0.00141945	0.00811602	WBGene00020195	1502	5555	1.89	0.0015699	0.008739	WBGene00019412	9127	4835	-0.92	0.0017683	0.009588
WBGene00020155	7	119	4.19	0.00141992	0.00811602	WBGene00010180	175	58	-1.58	0.0015707	0.008739	WBGene00006068	142	782	2.46	0.0017701	0.0095949
WBGene00004265	312	1504	2.27	0.00141999	0.00811602	WBGene00010102	3051	1458	-1.07	0.0015712	0.008739	WBGene00019814	11382	5182	-1.14	0.0017759	0.0096233
WBGene00004150	580	1484	1.36	0.00142277	0.00812933	WBGene00016022	3988	13094	1.72	0.0015713	0.008739	WBGene00005024	2195	1062	-1.05	0.0017776	0.0096299
WBGene00017538	12016	5155	-1.22	0.00142493	0.00813906	WBGene00000175	4204	10497	1.32	0.0015762	0.0087637	WBGene00003744	46	308	2.74	0.0017811	0.0096461
WBGene00007609	9086	4097	-1.15	0.00142796	0.00815382	WBGene00000960	50	587	3.55	0.0015811	0.0087875	WBGene00017212	2539	1195	-1.09	0.001788	0.0096806
WBGene00017901	211	833	1.98	0.00142992	0.0081615	WBGene00009315	112	510	2.19	0.0015815	0.0087875	WBGene00016840	144	340	1.25	0.0017895	0.0096855

WBGene00010877	20140	10655	-0.92	0.00143022	0.0081615	WBGene00006527	10536	21156	1.01	0.001582	0.0087878	WBGene00018137	18936	9808	-0.95	0.0017917	0.0096945
WBGene00021886	4710	2501	-0.91	0.00143093	0.00816298	WBGene00018412	38	113	1.57	0.0015836	0.0087939	WBGene00018551	238	64	-1.88	0.0017951	0.0097103
WBGene00000036	3227	6266	0.96	0.00143213	0.00816722	WBGene00019957	1363	4999	1.87	0.0015876	0.0088127	WBGene00019320	1744	3101	0.83	0.0017968	0.0097162
WBGene00020648	2461	4610	0.91	0.0014326	0.00816734	WBGene00007736	36471	20013	-0.87	0.001588	0.0088127	WBGene00010753	14	141	3.37	0.0017979	0.0097192
WBGene00010983	2660	1264	-1.07	0.00143324	0.00816774	WBGene00044468	1	31	5.35	0.001589	0.0088154	WBGene00010723	310	1502	2.28	0.001799	0.0097222
WBGene00015394	18	202	3.49	0.00143358	0.00816774	WBGene00015307	2796	1291	-1.11	0.0015909	0.0088234	WBGene00003158	50495	25524	-0.98	0.0018013	0.0097319
WBGene00018027	102	435	2.1	0.00143989	0.00820106	WBGene00000773	21372	11396	-0.91	0.0015935	0.0088351	WBGene00044431	12002	5569	-1.11	0.0018022	0.0097337
WBGene00014125	101	293	1.54	0.00144147	0.00820747	WBGene00018103	10033	5309	-0.92	0.0015983	0.0088588	WBGene00003104	2422	6922	1.52	0.0018112	0.0097795
WBGene00006950	625	3549	2.51	0.0014487	0.00824602	WBGene00019082	6970	3493	-1	0.0016008	0.0088702	WBGene00013434	16033	7416	-1.11	0.0018136	0.0097893
WBGene00021626	3897	2033	-0.94	0.00145297	0.0082677	WBGene00010079	467	908	0.96	0.001602	0.0088737	WBGene00011898	8403	3809	-1.14	0.0018163	0.0097999
WBGene00021279	5233	9560	0.87	0.00145563	0.00828021	WBGene00012666	6330	2932	-1.11	0.0016066	0.008894	WBGene00000718	20	283	3.85	0.0018166	0.0097999
WBGene00016635	260	624	1.26	0.00145628	0.00828129	WBGene00015238	10772	5420	-0.99	0.001607	0.008894	WBGene00018861	2164	4123	0.93	0.0018189	0.0098091
WBGene00003771	1392	5168	1.89	0.00145802	0.00828614	WBGene00015751	203	465	1.19	0.0016073	0.008894	WBGene00014241	29	101	1.81	0.0018202	0.0098131
WBGene00019268	3216	6198	0.95	0.00145805	0.00828614	WBGene00014666	249	1771	2.83	0.0016076	0.008894	WBGene00018074	172	624	1.86	0.0018261	0.0098423
WBGene00008545	158	426	1.43	0.00145898	0.00828732	WBGene00011892	26933	11235	-1.26	0.0016091	0.0088997	WBGene00000558	103	605	2.55	0.0018277	0.0098478
WBGene00016684	44	176	1.99	0.00145918	0.00828732	WBGene00004795	3606	1725	-1.06	0.0016116	0.0089109	WBGene00022048	17100	29398	0.78	0.0018299	0.0098527
WBGene00009079	24	97	1.98	0.00145969	0.00828755	WBGene00004802	893	430	-1.05	0.0016178	0.0089404	WBGene00019236	339	2302	2.76	0.00183	0.0098527
WBGene00015548	7161	13124	0.87	0.00146083	0.00829143	WBGene00010060	29	256	3.14	0.001618	0.0089404	WBGene00007797	3745	1474	-1.34	0.0018302	0.0098527
WBGene00044501	51	155	1.59	0.00146136	0.00829198	WBGene00009921	7787	4033	-0.95	0.0016202	0.0089497	WBGene000000135	52	173	1.73	0.0018333	0.0098644
WBGene00004338	16990	8437	-1.01	0.00146463	0.00830565	WBGene00004326	13377	6632	-1.01	0.0016316	0.0090094	WBGene00013167	2594	1288	-1.01	0.0018407	0.0099032
WBGene00007801	2161	4255	0.98	0.00146472	0.00830565	WBGene00015954	355	1072	1.59	0.001632	0.0090094	WBGene00008642	7228	3772	-0.94	0.0018426	0.0099105
WBGene00020813	72	226	1.66	0.00146536	0.00830664	WBGene00012307	219	756	1.79	0.0016332	0.0090136	WBGene00018237	5742	15053	1.39	0.0018439	0.0099142
WBGene00012315	9212	4485	-1.04	0.0014676	0.00831672	WBGene00007978	13251	6737	-0.98	0.0016361	0.0090267	WBGene00009015	1474	668	-1.14	0.0018452	0.0099184
WBGene00019232	3367	597	-2.5	0.00146998	0.00832755	WBGene00020527	672	290	-1.21	0.0016391	0.0090406	WBGene00017726	8	64	2.98	0.0018461	0.00992
WBGene00018514	72	357	2.3	0.00147123	0.00833202	WBGene00000191	5	50	3.22	0.0016408	0.0090473	WBGene00021311	17124	8817	-0.96	0.0018466	0.0099202
WBGene00004161	31887	16083	-0.99	0.00147463	0.00834864	WBGene00018040	514	1164	1.18	0.0016418	0.0090496	WBGene00000238	2003	3832	0.94	0.0018548	0.0099613
WBGene00002268	4227	17392	2.04	0.00147754	0.00836246	WBGene00015857	34	300	3.14	0.0016425	0.0090507	WBGene00044212	26	110	2.08	0.0018559	0.0099624
WBGene00008760	42710	77931	0.87	0.00147937	0.00837022	WBGene00023460	511	1051	1.04	0.0016431	0.0090515	WBGene00019881	7730	3811	-1.02	0.0018565	0.0099624
WBGene00021526	232	523	1.17	0.00148068	0.00837496	WBGene00004242	5269	2543	-1.05	0.001646	0.0090604	WBGene00013856	348	893	1.36	0.0018572	0.0099624
WBGene00011180	151	543	1.85	0.00148595	0.00840214	WBGene00015789	4810	2582	-0.9	0.0016462	0.0090604	WBGene00016984	118	321	1.44	0.0018573	0.0099624
WBGene00022269	8114	4153	-0.97	0.00148722	0.00840444	WBGene00021392	18069	8277	-1.13	0.0016463	0.0090604	WBGene00015327	10907	4607	-1.24	0.0018597	0.0099724
WBGene00014178	224	1198	2.42	0.00148729	0.00840444	WBGene00021981	778	1544	0.99	0.0016474	0.0090639	WBGene00007171	3809	1660	-1.2	0.0018614	0.0099783
WBGene00008049	39	152	1.97	0.00186219	0.00997983	WBGene00019803	704	1456	1.05	0.0019409	0.0103032	WBGene00001436	17100	8164	-1.07	0.0020136	0.0105889
WBGene00009660	2262	4823	1.09	0.00186473	0.00999047	WBGene00000240	3432	6256	0.87	0.0019424	0.010306	WBGene00001437	2704	1298	-1.06	0.0020182	0.0106099
WBGene00009653	37356	63505	0.77	0.0018675	0.01000232	WBGene00006856	27002	12899	-1.07	0.0019428	0.010306	WBGene00195043	245	515	1.07	0.002019	0.0106103
WBGene00017530	503	1099	1.13	0.00186855	0.0100041	WBGene00045405	140	42	-1.73	0.0019431	0.010306	WBGene00018303	23	234	3.34	0.0020194	0.0106103
WBGene00010548	9	66	2.92	0.00186895	0.0100041	WBGene00001311	1215	452	-1.43	0.0019503	0.0103411	WBGene00009624	20	94	2.24	0.0020215	0.0106182
WBGene00012306	11597	36395	1.65	0.00187284	0.01002195	WBGene00009024	21	168	3	0.001952	0.0103468	WBGene00021929	22775	10653	-1.1	0.0020239	0.0106277
WBGene00006558	918	399	-1.2	0.00187741	0.01004123	WBGene00008290	0	26	7.43	0.0019541	0.0103531	WBGene00009787	15	76	2.38	0.002025	0.0106305
WBGene00002179	9672	19905	1.04	0.00187756	0.01004123	WBGene00019368	318	614	0.95	0.0019543	0.0103531	WBGene00019655	76	318	2.06	0.0020256	0.0106305
WBGene00044182	7	62	3.08	0.00188	0.01005127	WBGene00003877	2783	9201	1.73	0.0019583	0.010371	WBGene00019294	3069	5866	0.93	0.0020366	0.0106849
WBGene00007268	20	105	2.42	0.00188132	0.01005534	WBGene00044079	11190	20443	0.87	0.0019608	0.0103813	WBGene00020290	5234	2563	-1.03	0.0020413	0.0107034
WBGene00009261	731	3416	2.23	0.00188314	0.01005728	WBGene00001591	212	586	1.47	0.0019676	0.010409	WBGene00016779	1974	826	-1.26	0.0020413	0.0107034
WBGene00016431	14	138	3.26	0.00188314	0.01005728	WBGene00008418	13138	6537	-1.01	0.0019677	0.010409	WBGene00011231	20425	9645	-1.08	0.0020426	0.0107072
WBGene00016570	22	179	3.04	0.00188336	0.01005728	WBGene00045305	280	981	1.81	0.0019678	0.010409	WBGene00015716	190	707	1.9	0.0020461	0.0107213
WBGene00009716	31	244	2.98	0.00189024	0.01009104	WBGene00015539	1121	2184	0.96	0.0019741	0.0104365	WBGene00011462	11	71	2.75	0.0020465	0.0107213
WBGene00001586	44	154	1.82	0.00189466	0.01010929	WBGene00019495	138	354	1.36	0.0019741	0.0104365	WBGene00022736	286	675	1.24	0.0020529	0.0107518
WBGene00019627	12734	6929	-0.88	0.00189479	0.01010929	WBGene00011524	6781	17353	1.36	0.0019751	0.0104385	WBGene00044466	1605	669	-1.26	0.002056	0.0107587
WBGene00009528	158	808	2.35	0.00189636	0.01011468	WBGene00010785	####	125347	-0.98	0.001977	0.0104426	WBGene00010661	273	748	1.45	0.002056	0.0107587
WBGene00010146	24	238	3.29	0.00189994	0.01012947	WBGene00003003	3010	14965	2.31	0.001977	0.0104426	WBGene00008786	13	234	4.14	0.002056	0.0107587

WBGene00010887	144	314	1.13	0.00190026	0.01012947	WBGene00011765	158	363	1.2	0.0019828	0.0104699	WBGene00015480	4862	9338	0.94	0.0020625	0.0107894
WBGene00008437	386	890	1.2	0.00190129	0.01013195	WBGene00007509	3542	1903	-0.9	0.0019843	0.0104748	WBGene00021194	346	133	-1.38	0.0020725	0.0108385
WBGene00010743	124	338	1.45	0.00190275	0.0101367	WBGene00015180	4417	1719	-1.36	0.0019864	0.0104828	WBGene00004302	186140	82494	-1.17	0.0020758	0.0108527
WBGene00008749	10889	5786	-0.91	0.00190763	0.01015969	WBGene00016016	3	46	3.77	0.001989	0.0104936	WBGene00019948	155	752	2.28	0.0020892	0.0109194
WBGene00011694	680	1202	0.82	0.00191327	0.01018669	WBGene00013224	10805	5519	-0.97	0.0019905	0.0104985	WBGene00011212	20	198	3.29	0.0020914	0.0109279
WBGene00004036	2819	6669	1.24	0.00191607	0.01019859	WBGene00009966	22702	11121	-1.03	0.0019935	0.0105113	WBGene00023245	5026	2692	-0.9	0.0020931	0.0109336
WBGene00022692	469	179	-1.39	0.00191755	0.01020346	WBGene00007935	766	2891	1.92	0.0019945	0.0105126	WBGene00194814	16	112	2.81	0.002098	0.0109521
WBGene00022112	28764	13624	-1.08	0.00192376	0.01023347	WBGene00022038	182	855	2.23	0.001995	0.0105126	WBGene00019636	389	1063	1.45	0.0020981	0.0109521
WBGene00008307	65	188	1.52	0.00192997	0.01026069	WBGene00011445	145	391	1.43	0.0020009	0.010541	WBGene00017149	26	416	3.98	0.0020985	0.0109521
WBGene00006864	35	136	1.94	0.00193002	0.01026069	WBGene00010916	9	62	2.83	0.0020023	0.0105449	WBGene00021443	14097	7435	-0.92	0.002101	0.0109621
WBGene00017841	280	1846	2.72	0.00193436	0.01028073	WBGene00018311	162	405	1.32	0.0020031	0.0105463	WBGene00019284	889	1680	0.92	0.0021018	0.0109631
WBGene00012100	3036	6685	1.14	0.0019384	0.0102971	WBGene00017313	26815	13817	-0.96	0.0020048	0.0105517	WBGene00009099	18	89	2.29	0.0021048	0.0109756
WBGene00009888	5537	14911	1.43	0.00193859	0.0102971	WBGene00013040	7866	4245	-0.89	0.0020053	0.0105517	WBGene00011698	1072	497	-1.11	0.0021092	0.0109953
WBGene00006787	43242	87873	1.02	0.0019399	0.01030104	WBGene00019734	202	485	1.27	0.0020096	0.0105714	WBGene00002240	6098	3151	-0.95	0.0021101	0.0109969

**Supplementary Table 2-A. Gene ontology analysis for the genes in embryo sample lacking WDR-5**

Gene function classification for upregulated genes that are associated with de novo H3K4me2 and downregulated genes that are associated with depleted H3K4me1/me2/me3, during *wdr-5(-)* embryogenesis.

399 up regulated genes and associated with de novo H3K4me2

Function	Pathway	FDR
Process	single organism signaling	0.00139
Process	cell communication	0.00184
Process	signal transduction	0.00799
Process	regulation of membrane potential	0.0196
Process	detection of abiotic stimulus	0.0256
Process	behavior	0.034
Process	synaptic transmission	0.0399
Component	plasma membrane	0.00000571
Component	neuron part	0.00249
Component	nonmotile primary cilium	0.0184
Component	contractile fiber part	0.0221
Component	extracellular matrix	0.0278
Component	dystrophin-associated glycoprotein complex	0.0376
Component	sarcoplasmic reticulum	0.0376
INTERPRO	Zona pellucida domain	0.0391

399 down regulated genes and associated with WDR-5 depleted methylation

Function	Pathway	FDR
Process	reproduction	0.004
Process	embryo development	0.004
Process	chromo. organization involved in meiosis	0.004
Process	DNA metabolic process	0.009
Process	DNA replication	0.013
Process	positive regulation of cell cycle	0.049
Component	chromosome	0.002
Component	nuclear part	0.006
KEGG pathway	RNA transport	0.005
KEGG pathway	Spliceosome	0.012
PFAM	F-box associated	3.81E-45

### Supplementary Table 3. ChIP-seq raw data on average peak value for H3K4me1

Average peak value for H3K4me1 in wild type, *wdr-5(ok1417)* and *rbbp-5(tm3463)*. Details on peak position is not shown

Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5
WBGene00022279	73	99	11	WBGene00017116	60	78	12	WBGene00018370	55	77	11	WBGene00020701	91	181	16	WBGene00021724	68	93	14
WBGene00022275	70	113	13	WBGene00001983	60	78	12	WBGene00018371	92	230	14	WBGene00015155	74	105	10	WBGene00015854	47	82	32
WBGene00021678	66	89	15	WBGene00017119	64	133	17	WBGene00018366	92	230	14	WBGene00021061	51	81	14	WBGene00195072	47	82	32
WBGene00000812	59	81	12	WBGene00017120	64	133	17	WBGene00015418	72	167	14	WBGene00015648	51	81	14	WBGene00021721	94	118	19
WBGene00021681	56	102	16	WBGene00017121	64	133	17	WBGene00022505	52	85	9	WBGene00016029	45	111	16	WBGene00000647	94	118	19
WBGene00004274	56	102	16	WBGene00004432	64	133	17	WBGene00015337	63	80	12	WBGene00018363	64	134	12	WBGene00021715	94	118	19
WBGene00004418	55	86	18	WBGene00021202	64	133	17	WBGene00015336	63	80	12	WBGene00004212	64	134	12	WBGene00021714	94	118	19
WBGene00018774	55	86	18	WBGene00021201	76	123	17	WBGene00015747	79	134	17	WBGene00018365	64	134	12	WBGene00044378	86	166	50
WBGene00018773	61	110	11	WBGene00021204	88	113	16	WBGene00000439	79	134	17	WBGene00015173	54	105	10	WBGene00021118	86	166	50
WBGene00000622	77	179	13	WBGene00194835	83	113	14	WBGene00017696	79	134	17	WBGene00019329	78	130	21	WBGene00021117	86	166	50
WBGene00004962	77	179	13	WBGene00021205	83	113	14	WBGene00017694	42	72	52	WBGene00019327	78	130	21	WBGene00000648	86	166	50
WBGene00003229	92	248	14	WBGene00021206	83	113	14	WBGene00017693	42	72	52	WBGene00019331	78	130	21	WBGene00021116	54	79	11
WBGene00018772	92	248	14	WBGene00021200	77	112	11	WBGene00017698	42	72	52	WBGene00019332	67	108	10	WBGene00003367	50	101	21
WBGene00004225	47	95	13	WBGene00020006	64	82	13	WBGene00001443	55	105	45	WBGene00001392	67	108	10	WBGene00014848	63	144	14
WBGene00018958	70	127	15	WBGene00003694	64	82	13	WBGene00019801	46	106	11	WBGene00019326	67	108	10	WBGene00077658	36	58	28
WBGene00021671	80	192	13	WBGene00015330	68	143	12	WBGene00003253	62	113	12	WBGene00021170	91	176	28	WBGene00010910	78	109	13
WBGene00021672	68	163	13	WBGene00015327	72	115	14	WBGene00019800	77	120	13	WBGene00020758	91	176	28	WBGene00219205	58	135	16
WBGene00021675	41	84	11	WBGene00015329	72	115	14	WBGene00019301	77	120	13	WBGene00020759	91	176	28	WBGene00010990	58	135	16
WBGene00016904	78	206	11	WBGene00015328	67	113	11	WBGene00019304	42	104	8	WBGene00020760	91	176	28	WBGene00010991	58	135	16
WBGene00016902	74	117	15	WBGene00014997	84	127	11	WBGene00219329	62	104	13	WBGene00044681	91	176	28	WBGene00010992	98	152	11
WBGene00016906	69	97	25	WBGene00043147	70	87	13	WBGene00018833	71	143	19	WBGene00020762	65	101	16	WBGene00004215	78	139	13
WBGene00002077	69	97	25	WBGene00016053	70	87	13	WBGene00006975	91	223	32	WBGene00020763	65	101	16	WBGene00009356	91	183	35
WBGene00020089	75	141	27	WBGene00021157	38	58	37	WBGene00018834	91	223	32	WBGene00020448	58	90	12	WBGene00000472	91	183	35
WBGene00004143	75	141	27	WBGene00006745	80	130	11	WBGene00018835	91	223	32	WBGene00019912	58	90	12	WBGene00000658	91	183	35
WBGene00006385	75	141	27	WBGene00001411	101	180	15	WBGene00010475	82	151	13	WBGene00019913	67	112	15	WBGene00009352	91	183	35
WBGene00020090	65	124	13	WBGene00001093	101	180	15	WBGene00014033	47	54	32	WBGene00019915	67	112	15	WBGene00009354	70	127	13
WBGene00021733	65	124	13	WBGene00020465	50	66	12	WBGene00011146	73	144	13	WBGene00015268	66	137	14	WBGene00009729	70	127	13
WBGene00021734	43	78	13	WBGene00001439	57	115	13	WBGene00010307	52	88	18	WBGene00006697	77	77	22	WBGene00006788	66	134	12
WBGene00015570	52	81	11	WBGene00004804	68	128	16	WBGene00010308	52	88	18	WBGene00004277	72	64	19	WBGene00004478	71	84	10
WBGene00006593	103	206	20	WBGene00020585	68	128	16	WBGene00010309	52	88	18	WBGene00022357	72	64	19	WBGene00003076	71	84	10
WBGene00021026	73	145	16	WBGene00000247	69	134	10	WBGene00006977	81	121	10	WBGene00003917	72	64	19	WBGene00009575	71	84	10
WBGene00021027	73	145	16	WBGene00044500	69	134	10	WBGene00004269	81	121	10	WBGene00022104	36	38	28	WBGene00009576	71	84	10
WBGene00021025	66	183	15	WBGene00016955	81	158	16	WBGene00010310	77	119	11	WBGene00022103	55	108	14	WBGene00044917	71	84	10
WBGene00235388	66	183	15	WBGene00016667	90	130	12	WBGene00010311	73	117	11	WBGene00003978	61	117	34	WBGene00044916	71	84	10
WBGene00022037	92	149	17	WBGene00016664	51	98	15	WBGene00003518	65	78	11	WBGene00022487	55	130	12	WBGene00000851	76	127	10
WBGene00022038	92	149	17	WBGene00003636	61	121	15	WBGene00011298	65	78	11	WBGene00022486	49	139	11	WBGene00006853	79	134	15
WBGene00022033	90	201	19	WBGene00016291	74	129	13	WBGene00011299	71	102	15	WBGene00001236	67	116	27	WBGene00008164	107	168	16
WBGene00022043	90	201	19	WBGene00015541	67	106	10	WBGene00011300	76	126	18	WBGene00022336	67	116	27	WBGene00008165	107	168	16
WBGene00022042	90	201	19	WBGene00019257	62	111	8	WBGene00000549	76	126	18	WBGene00022348	67	116	27	WBGene00011994	72	121	14
WBGene00007009	38	78	15	WBGene00019255	74	129	16	WBGene00003001	93	170	15	WBGene00022349	71	147	14	WBGene00011995	63	114	13
WBGene00004332	73	96	14	WBGene00019296	74	129	16	WBGene00044406	93	170	15	WBGene00022334	71	147	14	WBGene00011999	46	99	11
WBGene00004028	87	73	14	WBGene00019295	75	141	20	WBGene00008513	93	170	15	WBGene00021245	49	114	44	WBGene00011996	46	99	11
WBGene00044434	101	50	13	WBGene00002129	75	141	20	WBGene00008514	89	138	19	WBGene00021247	49	114	44	WBGene00012201	52	130	29
WBGene00022518	60	149	12	WBGene00004494	76	152	23	WBGene00001609	89	138	19	WBGene00004128	154	322	17	WBGene00004699	52	130	29
WBGene00022388	37	118	8	WBGene00019297	92	180	48	WBGene00013979	62	78	31	WBGene00001063	30	50	42	WBGene00004698	52	130	29
WBGene00022389	85	244	17	WBGene000006780	98	197	16	WBGene00013980	85	132	26	WBGene00021697	84	120	22	WBGene00012202	52	130	29
WBGene00022386	85	244	17	WBGene00019205	63	120	11	WBGene00000863	85	132	26	WBGene00021705	117	164	17	WBGene00000196	56	114	10

WBGene00003238	111	243	18	WBGene00023486	76	155	12	WBGene00013982	92	152	17	WBGene00016527	47	86	12	WBGene00012203	56	114	10
WBGene00018787	86	181	15	WBGene00000535	76	155	12	WBGene00001720	92	152	17	WBGene00016520	47	86	12	WBGene00002227	56	114	10
WBGene00018788	61	118	11	WBGene00002245	94	214	14	WBGene00000425	77	118	14	WBGene00021863	71	103	9	WBGene00006660	51	89	38
WBGene00016932	63	97	13	WBGene00006974	63	68	23	WBGene00013850	61	124	14	WBGene00021864	71	103	9	WBGene00007142	51	89	38
WBGene00021334	87	259	13	WBGene00019751	64	99	18	WBGene00013847	61	124	14	WBGene00206486	71	103	9	WBGene00007149	51	89	38
WBGene00001745	87	259	13	WBGene00001853	54	126	44	WBGene00013849	61	124	14	WBGene00021020	92	173	11	WBGene00007013	78	124	25
WBGene00022837	97	210	15	WBGene00005738	54	126	44	WBGene00004391	90	124	13	WBGene00021019	92	173	11	WBGene000077453	78	124	25
WBGene00021685	76	105	16	WBGene00022251	77	96	13	WBGene00011963	90	124	13	WBGene00021018	92	173	11	WBGene00013387	78	124	25
WBGene00003400	63	110	17	WBGene00003237	77	96	13	WBGene00011962	77	115	14	WBGene00017099	64	96	18	WBGene00010055	84	165	25
WBGene00045052	87	158	15	WBGene00022233	77	96	13	WBGene00011964	63	106	15	WBGene00004884	64	96	18	WBGene00010054	84	165	25
WBGene00045053	87	158	15	WBGene00194832	65	95	10	WBGene00000934	63	91	12	WBGene00021849	84	148	14	WBGene00010053	86	161	12
WBGene00004888	87	158	15	WBGene00004881	65	95	10	WBGene00011365	62	75	9	WBGene00000464	84	137	16	WBGene00001031	86	161	12
WBGene00019673	87	158	15	WBGene00044350	64	83	12	WBGene00001263	62	98	11	WBGene00022191	49	81	9	WBGene00195146	69	181	11
WBGene00018159	59	104	26	WBGene00016610	69	80	43	WBGene00010573	53	105	13	WBGene00019212	46	102	8	WBGene00010057	78	158	23
WBGene00004969	71	116	22	WBGene00006621	69	80	43	WBGene00006576	63	83	13	WBGene00022171	72	44	11	WBGene00010051	86	134	34
WBGene00001773	95	140	15	WBGene00016611	94	123	14	WBGene00008001	63	83	13	WBGene00022185	72	44	11	WBGene00219434	86	134	34
WBGene00005077	33	51	32	WBGene00016612	94	123	14	WBGene00008000	63	83	13	WBGene00022170	72	44	11	WBGene00010050	86	134	34
WBGene00003111	55	106	12	WBGene00018167	62	102	28	WBGene00001689	63	83	13	WBGene00022169	72	44	11	WBGene00010049	86	134	34
WBGene00044348	93	172	13	WBGene00018166	62	102	28	WBGene00206422	66	107	12	WBGene00018990	39	90	10	WBGene00008546	69	136	14
WBGene00006702	68	185	31	WBGene00018165	62	102	28	WBGene00206421	66	107	12	WBGene00020597	81	177	12	WBGene00003791	69	136	14
WBGene00003080	68	185	31	WBGene00018164	62	102	28	WBGene00012061	66	107	12	WBGene00020599	81	177	12	WBGene00008549	70	156	28
WBGene00022153	68	185	31	WBGene00017481	62	102	28	WBGene00012062	66	107	12	WBGene00019994	83	196	11	WBGene00008136	65	129	16
WBGene00022152	63	95	13	WBGene00017480	62	102	28	WBGene00001284	59	111	19	WBGene00019997	55	100	14	WBGene00008137	65	129	16
WBGene00006771	70	133	16	WBGene00001090	55	106	13	WBGene00010035	59	111	19	WBGene00194747	55	100	14	WBGene00008138	61	104	16
WBGene00022148	64	180	14	WBGene00015278	93	123	13	WBGene00010037	59	111	19	WBGene00019157	55	100	14	WBGene00008139	61	104	16
WBGene00022160	64	180	14	WBGene00015280	65	119	19	WBGene00010039	70	107	15	WBGene00021917	52	87	11	WBGene00002184	59	76	12
WBGene00022161	64	180	14	WBGene00001858	65	119	19	WBGene00010040	67	97	15	WBGene00021915	46	98	11	WBGene00008741	43	86	12
WBGene00044746	86	178	20	WBGene00015935	68	103	9	WBGene00010038	59	75	17	WBGene00006725	69	105	17	WBGene00001679	66	135	16
WBGene00016907	86	178	20	WBGene00015934	68	103	9	WBGene00004980	59	75	17	WBGene00019168	69	105	17	WBGene00009691	89	177	19
WBGene00004441	86	178	20	WBGene00006608	47	99	12	WBGene00014222	63	51	14	WBGene00021808	83	162	14	WBGene00009692	89	177	19
WBGene00001196	82	146	18	WBGene00022727	96	214	14	WBGene00014223	63	51	14	WBGene00021803	83	162	14	WBGene00001016	91	168	13
WBGene00001309	66	94	14	WBGene00016085	66	144	14	WBGene00014219	63	51	14	WBGene00021924	46	95	14	WBGene00219294	91	168	13
WBGene00003750	53	73	13	WBGene00015553	58	109	13	WBGene00014221	63	133	13	WBGene00008347	65	99	26	WBGene00009657	106	212	14
WBGene00006461	53	73	13	WBGene00015552	58	109	13	WBGene00014225	63	133	13	WBGene00008348	65	99	26	WBGene00009663	106	212	14
WBGene00004743	94	238	26	WBGene00015551	56	86	15	WBGene00194691	63	133	13	WBGene00007923	91	154	12	WBGene00005013	59	109	12
WBGene00022139	94	238	26	WBGene00021542	78	119	14	WBGene00006755	65	123	14	WBGene00007924	91	154	12	WBGene00009662	59	109	12
WBGene00021764	72	61	17	WBGene00000942	62	126	11	WBGene00014226	67	113	14	WBGene00007928	91	154	12	WBGene00009659	59	109	12
WBGene00021346	71	101	12	WBGene00022619	57	109	11	WBGene00008169	67	113	14	WBGene00010813	75	109	12	WBGene00009660	34	61	26
WBGene00021347	71	101	12	WBGene00022620	51	91	11	WBGene00008170	67	113	14	WBGene00008288	75	109	12	WBGene00009658	34	61	26
WBGene00021348	71	101	12	WBGene00016405	55	66	16	WBGene00008171	67	113	14	WBGene00000248	61	142	19	WBGene00003789	70	121	24
WBGene00021349	71	101	12	WBGene00016400	55	57	12	WBGene00001831	60	133	13	WBGene00044166	61	142	19	WBGene00000659	83	150	17
WBGene00235158	56	88	19	WBGene00000687	55	57	12	WBGene00001955	60	133	13	WBGene00008180	72	115	9	WBGene00010785	64	99	25
WBGene00021009	82	138	12	WBGene00000441	63	61	12	WBGene00001570	55	119	13	WBGene00004213	59	148	14	WBGene00014155	102	152	22
WBGene00000020	65	183	14	WBGene00206380	63	61	12	WBGene00007405	65	141	18	WBGene00004765	103	243	15	WBGene00014156	133	196	25
WBGene000000408	87	169	19	WBGene00004822	63	61	12	WBGene00007403	108	231	27	WBGene00007859	70	171	13	WBGene00014152	133	196	25
WBGene00021469	87	169	19	WBGene00017052	76	132	17	WBGene00007400	108	231	27	WBGene00007860	65	184	13	WBGene00014153	92	137	14
WBGene00021470	81	131	35	WBGene00001241	76	132	17	WBGene00006579	108	231	27	WBGene00008121	62	134	9	WBGene00014154	92	137	14
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WBGene00018107	68	119	16	WBGene00009974	77	142	16	WBGene00009043	43	104	11	WBGene00015358	65	117	30	WBGene00011067	65	132	25
WBGene00018109	71	128	18	WBGene00009975	98	177	17	WBGene00009044	43	104	11	WBGene00006454	70	157	14	WBGene00011069	44	99	10
WBGene00018108	74	133	18	WBGene00009977	72	95	11	WBGene00010878	50	77	11	WBGene00006408	70	157	14	WBGene00015755	76	137	15
WBGene00018104	76	120	17	WBGene00010088	66	88	15	WBGene00010879	50	77	11	WBGene00001434	86	177	14	WBGene00015752	76	146	18
WBGene00018103	76	120	17	WBGene00004767	66	88	15	WBGene00001523	50	77	11	WBGene00018532	75	171	12	WBGene00017045	59	57	15
WBGene00018102	73	92	12	WBGene00010089	66	88	15	WBGene00011755	60	139	13	WBGene00018026	75	171	12	WBGene00086546	59	57	15
WBGene00015609	73	131	26	WBGene00010259	60	129	14	WBGene00011759	76	100	13	WBGene00018027	81	165	11	WBGene00016803	59	57	15
WBGene00044417	73	131	26	WBGene00010260	62	115	29	WBGene00011760	76	100	13	WBGene00001335	38	99	9	WBGene00006818	87	143	10
WBGene00015613	73	131	26	WBGene00000097	62	115	29	WBGene00012175	76	100	13	WBGene00018025	38	99	9	WBGene00206533	87	143	10
WBGene00015610	73	131	26	WBGene00003916	59	119	15	WBGene00004155	44	68	32	WBGene00018024	70	180	16	WBGene00016239	87	143	10
WBGene00015607	73	131	26	WBGene00007085	62	125	16	WBGene00012177	44	68	32	WBGene00001441	54	156	14	WBGene00016238	50	92	11
WBGene00020362	58	107	13	WBGene00010510	60	95	15	WBGene00012178	44	68	32	WBGene00019359	54	156	14	WBGene00004342	50	92	11

WBGene00020363	58	107	13	WBGene00013024	67	88	16	WBGene00010045	64	91	15	WBGene00000441	34	94	10	WBGene00015350	50	92	11
WBGene00020361	68	116	12	WBGene00013025	67	88	16	WBGene00009202	64	91	15	WBGene00002987	65	145	12	WBGene00015352	75	144	13
WBGene00017207	62	76	11	WBGene00013026	67	88	16	WBGene00011924	57	92	15	WBGene00018569	56	133	11	WBGene00003952	75	144	13
WBGene00219315	62	76	11	WBGene00006775	80	125	12	WBGene00011925	57	92	15	WBGene00018570	53	133	12	WBGene00015347	75	144	13
WBGene00004149	62	106	15	WBGene00003922	96	198	14	WBGene00011926	57	92	15	WBGene00018571	58	132	10	WBGene00015346	75	144	13
WBGene00020537	62	106	15	WBGene00007616	96	198	14	WBGene00011927	57	92	15	WBGene00006321	53	166	14	WBGene00017322	67	128	8
WBGene00020533	62	106	15	WBGene00007617	96	198	14	WBGene00006875	43	104	9	WBGene00020670	61	131	30	WBGene00003243	77	143	12
WBGene00020073	64	82	11	WBGene00009079	96	198	14	WBGene00008432	47	77	15	WBGene00020667	61	131	30	WBGene00017358	75	158	15
WBGene00016548	67	122	13	WBGene00001170	96	198	14	WBGene00004259	49	67	24	WBGene00003007	47	113	14	WBGene00022579	89	63	13
WBGene00016553	67	122	13	WBGene00009081	96	198	14	WBGene00008427	40	59	26	WBGene00015822	75	150	29	WBGene00022581	89	63	13
WBGene00016547	67	122	13	WBGene00235335	120	262	18	WBGene00008431	40	59	26	WBGene00015823	102	187	44	WBGene00044801	89	63	13
WBGene00016546	67	122	13	WBGene00010976	120	262	18	WBGene00007917	59	107	8	WBGene00015824	102	187	44	WBGene00044802	89	63	13
WBGene00016549	42	95	11	WBGene000077577	120	262	18	WBGene00007918	59	107	8	WBGene00019828	66	151	13	WBGene00006840	80	132	15
WBGene00016545	42	95	11	WBGene00010979	120	262	18	WBGene00000432	59	107	8	WBGene00019830	66	151	13	WBGene00019881	80	132	15
WBGene00016544	56	122	8	WBGene00004337	52	96	10	WBGene00010681	127	199	16	WBGene00019827	66	151	13	WBGene00007008	80	132	15
WBGene00016342	56	95	13	WBGene00004060	52	96	10	WBGene00000220	100	157	13	WBGene00019826	43	99	13	WBGene00019882	76	111	12
WBGene00016334	56	95	13	WBGene00008143	71	74	39	WBGene00010683	100	157	13	WBGene00044021	43	99	13	WBGene00019878	76	111	12
WBGene00021985	56	95	13	WBGene00000915	71	74	39	WBGene00001505	72	114	10	WBGene00017308	73	153	13	WBGene00019877	76	111	12
WBGene00019593	48	88	10	WBGene00044180	71	74	39	WBGene00000240	72	137	13	WBGene00017309	73	153	13	WBGene00019883	76	111	12
WBGene00235164	48	88	10	WBGene00008144	77	86	30	WBGene00010682	72	137	13	WBGene00022745	68	155	14	WBGene00022697	93	150	11
WBGene00019590	48	88	10	WBGene00006836	83	98	21	WBGene00002295	72	137	13	WBGene00022746	68	155	14	WBGene00022704	93	150	11
WBGene00006882	70	151	15	WBGene00008145	83	98	21	WBGene00004790	74	162	26	WBGene00006410	78	171	16	WBGene00023405	76	121	14
WBGene00004129	70	151	15	WBGene00006795	58	101	13	WBGene00008563	74	162	26	WBGene00003412	62	96	14	WBGene00000414	53	88	14
WBGene00005559	86	122	16	WBGene00013048	58	101	13	WBGene00008557	74	162	26	WBGene00006921	77	122	20	WBGene00022862	41	76	17
WBGene00001546	86	122	16	WBGene00013049	58	101	13	WBGene00008559	59	104	11	WBGene00017628	77	122	20	WBGene00004460	59	96	12
WBGene00017712	68	112	16	WBGene00008183	86	184	14	WBGene00008560	59	104	11	WBGene00001994	92	213	24	WBGene00016249	59	96	12
WBGene00018021	68	112	16	WBGene00012293	88	189	20	WBGene00011580	115	251	22	WBGene00020922	92	213	24	WBGene00018369	55	77	11
WBGene00018022	68	112	16	WBGene00004336	75	151	16	WBGene00002251	115	251	22	WBGene00005716	56	128	20	WBGene00001451	60	125	9
WBGene00020231	41	108	13	WBGene00013883	54	86	24	WBGene00000378	62	115	12	WBGene00006393	56	128	20	WBGene00003411	45	97	8
WBGene00044367	41	108	13	WBGene00013886	35	44	26	WBGene00011883	62	115	12	WBGene00005717	56	128	20	WBGene00003909	71	170	14
WBGene00017912	66	84	12	WBGene00050943	35	44	26	WBGene00011884	62	115	12	WBGene00016867	97	178	16	WBGene00009720	103	229	17
WBGene00017911	66	84	12	WBGene00013887	35	44	26	WBGene00011885	62	115	12	WBGene00016866	97	178	16	WBGene00004353	103	229	17
WBGene00017249	66	84	12	WBGene00044272	35	44	26	WBGene00009717	67	127	12	WBGene00003179	97	178	16	WBGene00004354	103	229	17
WBGene00017250	60	79	15	WBGene00010379	35	44	26	WBGene00009504	70	153	18	WBGene00000510	70	121	12	WBGene00008973	53	146	18
WBGene00017251	53	73	17	WBGene00013889	35	44	26	WBGene00011980	67	105	16	WBGene00003907	70	121	12	WBGene00008974	62	133	23
WBGene00017252	68	96	17	WBGene00004308	57	152	9	WBGene00011976	67	105	16	WBGene00016868	70	121	12	WBGene00008975	71	119	27
WBGene00017253	68	96	17	WBGene00007719	57	152	9	WBGene00004446	67	105	16	WBGene00004106	62	130	13	NoWBGene_ID67	71	119	27
WBGene00017254	68	96	17	WBGene00007718	57	152	9	WBGene00011977	112	206	25	WBGene00017472	58	121	12	WBGene00008978	52	110	11
WBGene00019691	68	93	9	WBGene00007720	64	144	12	WBGene00011978	86	155	19	WBGene00017471	58	121	12	WBGene00008606	74	116	12
WBGene00003678	94	126	19	WBGene00001021	70	135	14	WBGene00011979	106	179	19	WBGene00017474	55	83	12	WBGene00008605	74	116	12
WBGene00019513	80	141	17	WBGene00006808	70	135	14	WBGene00001950	106	179	19	WBGene00219368	62	95	11	WBGene00007526	67	170	14
WBGene00019512	80	141	17	WBGene00005278	28	33	27	WBGene00007421	106	179	19	WBGene00017475	62	95	11	WBGene00011679	60	124	28
WBGene00019511	69	131	24	WBGene00006110	28	33	27	WBGene00012002	62	95	9	WBGene00020120	62	95	11	WBGene00000618	60	124	28
WBGene00016576	69	131	24	WBGene00013568	61	50	12	WBGene00012005	61	96	10	WBGene00219369	69	106	9	WBGene00011680	60	124	28
WBGene00016575	69	131	24	WBGene00000883	61	50	12	WBGene00007633	55	93	9	WBGene00020121	69	106	9	WBGene00011681	89	139	13
WBGene00016574	69	131	24	WBGene00013569	55	67	19	WBGene00006367	50	106	13	WBGene00003084	52	113	12	WBGene00011683	89	139	13
WBGene00016573	69	131	24	WBGene00000879	55	67	19	WBGene00006659	60	102	11	WBGene00017476	48	63	42	WBGene00010356	47	104	13
WBGene00044370	69	131	24	WBGene00013573	55	67	19	WBGene00002299	64	103	11	WBGene00017794	48	63	42	WBGene00009552	49	93	20
WBGene00016578	69	131	24	WBGene00004037	49	83	25	WBGene00000170	90	207	27	WBGene00023460	53	142	16	WBGene00009789	60	149	9
WBGene00005543	110	240	16	WBGene00045402	49	83	25	WBGene00007224	90	207	27	WBGene00000959	57	126	14	WBGene00002203	95	240	16
WBGene00015200	110	240	16	WBGene00011948	47	97	40	WBGene00007225	76	144	18	WBGene00004356	65	158	21	WBGene00004777	51	84	38
WBGene00002997	92	174	18	WBGene00004153	47	97	40	WBGene00007226	76	144	18	WBGene00005008	80	187	29	WBGene00003681	68	154	14
WBGene00021293	74	107	19	WBGene00005428	81	113	14	WBGene00007227	61	80	8	WBGene00015561	95	215	36	WBGene00012441	68	154	14
WBGene00021294	74	107	19	WBGene00005429	81	113	14	WBGene00006510	54	104	14	WBGene00003963	95	215	36	WBGene00012442	51	76	12
WBGene00195073	80	157	17	WBGene00007372	81	113	14	WBGene00007229	73	139	26	WBGene00003628	81	161	10	WBGene00012443	47	83	11
WBGene00017181	80	157	17	WBGene00008997	35	91	17	WBGene00000289	73	132	17	WBGene00015560	103	248	14	WBGene00012444	87	198	18
WBGene00017182	80	157	17	WBGene00008995	35	91	17	WBGene000008403	70	130	12	WBGene00206364	103	248	14	WBGene00007877	59	125	13
WBGene00005575	64	103	13	WBGene00008996	76	147	51	WBGene00008402	68	114	12	WBGene00001821	103	248	14	WBGene00007878	57	132	13
WBGene00044375	64	103	13	WBGene00000057	76	147	51	WBGene00004286	66	98	11	WBGene00000133	62	155	12	WBGene00006462	57	132	13
WBGene00018201	67	167	13	WBGene00009978	55	88	13	WBGene00006520	66	98	11	WBGene00015494	62	155	12	WBGene00009560	91	179	9
WBGene00018198	69	157	10	WBGene00006122	35	59	45	WBGene00001134	66	98	11	WBGene00020496	61	99	18	WBGene00004123	91	179	9

WBGene00021729	46	89	11	WBGene00006121	35	59	45	WBGene00006433	97	178	10	WBGene00004148	82	146	21	WBGene00017900	42	104	9
WBGene00021730	46	89	11	WBGene00003692	35	59	45	WBGene00009627	97	178	10	WBGene00016706	41	87	12	WBGene00017923	61	113	13
WBGene00021727	46	89	11	WBGene00003674	35	59	45	WBGene00003196	97	178	10	WBGene00016705	55	112	13	WBGene00004205	67	113	19
WBGene00021726	68	93	14	WBGene00011688	60	79	13	WBGene00011849	90	125	12	WBGene00016704	69	136	13	WBGene00000685	67	113	19
WBGene00021725	68	93	14	WBGene00011689	60	79	13	WBGene00001368	72	119	11	WBGene00044567	80	113	12	WBGene00017924	67	113	19
WBGene00017925	67	113	19	WBGene00017920	65	121	13	WBGene00017919	63	129	7	WBGene00044482	63	115	10	WBGene00019543	65	92	21
WBGene00013677	65	92	21																



### Supplementary Table 4. ChIP-seq raw data on average peak value for H3K4me2

Average peak value for H3K4me2 in wild type, *wdr-5(ok1417)* and *rbbp-5(tm3463)*. Details on peak position is not shown

Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5
WBGene00022277	75	38	6	WBGene00219239	75	66	20	WBGene00002202	129	71	11	WBGene00004822	126	58	14	WBGene00004997	79	55	7
WBGene00022276	117	28	12	WBGene00019412	67	50	13	WBGene00185075	132	119	18	WBGene00006251	126	58	14	WBGene00002260	79	55	7
WBGene00022278	110	26	9	WBGene00019420	67	50	13	WBGene00007271	132	119	18	WBGene00017052	150	246	13	WBGene00011932	79	55	7
WBGene00022279	82	52	6	WBGene00019421	67	50	13	WBGene00007269	135	167	24	WBGene00001241	150	246	13	WBGene00007360	72	91	7
WBGene00022275	98	69	9	WBGene00022556	127	118	37	WBGene00004392	135	167	24	WBGene00015531	60	127	9	WBGene00007364	72	91	7
WBGene00044345	121	39	9	WBGene00194714	127	118	37	WBGene00007273	135	167	24	WBGene00015530	60	127	9	WBGene00007363	72	91	7
WBGene00021677	121	39	9	WBGene00022558	127	118	37	WBGene00007270	135	167	24	WBGene00001713	109	42	12	WBGene00007365	72	91	7
WBGene00000812	117	151	8	WBGene00022559	127	118	37	WBGene00007631	69	29	10	WBGene00004477	109	42	12	WBGene00011192	107	60	8
WBGene00021676	82	34	6	WBGene00022560	127	118	37	WBGene00007630	69	29	10	WBGene00018349	76	79	11	NoWBGene_ID32	107	60	8
WBGene00189949	82	34	6	WBGene00022557	127	118	37	WBGene00006448	69	29	10	WBGene00018350	43	115	9	WBGene00011194	107	60	8
WBGene00021681	123	56	11	WBGene00022561	127	118	37	WBGene00007627	96	34	10	WBGene00020444	133	171	6	WBGene00011195	107	60	8
WBGene00004274	164	77	16	WBGene00022555	127	118	37	WBGene00007626	96	34	10	WBGene00020447	106	163	7	WBGene00010259	59	121	11
WBGene00004418	164	77	16	WBGene00022562	127	118	37	WBGene00007625	96	34	10	WBGene00016739	78	155	8	WBGene00010260	151	98	49
WBGene00018774	164	77	16	WBGene00022563	149	147	8	WBGene00007624	96	34	10	WBGene00001187	43	85	8	WBGene00000097	151	98	49
WBGene00018773	164	77	16	WBGene00022564	149	147	8	WBGene00003073	68	29	6	WBGene00015217	71	143	7	WBGene00001311	151	98	49
WBGene00000622	164	77	16	WBGene00022554	149	147	8	WBGene00011278	82	48	6	WBGene00017416	71	143	7	WBGene00011625	88	23	5
WBGene00004962	137	196	9	WBGene00022553	149	147	8	WBGene000206525	82	48	6	WBGene00018902	91	49	13	WBGene00010249	88	23	5
WBGene00003229	137	196	9	WBGene00005844	149	147	8	WBGene00001034	129	93	18	WBGene00018901	91	49	13	WBGene00045405	55	43	27
WBGene00018772	137	196	9	WBGene00003734	48	58	25	WBGene00006959	129	93	18	WBGene00018904	91	49	13	WBGene00045406	55	43	27
WBGene00018958	101	95	8	WBGene00019037	48	58	25	WBGene00011279	117	75	19	WBGene00018900	103	135	78	WBGene00008392	55	43	27
WBGene00018957	109	68	8	WBGene00019038	48	58	25	WBGene00011280	71	31	8	WBGene00001935	114	221	143	WBGene00001864	55	43	27
WBGene00018955	109	68	8	WBGene00019036	59	56	17	WBGene00011281	71	31	8	WBGene00001936	114	221	143	WBGene00003916	69	132	7
WBGene00000227	103	43	7	WBGene00019035	70	54	9	WBGene00011282	71	31	8	WBGene00001934	114	221	143	WBGene00007085	82	141	8
WBGene00021671	84	134	11	WBGene00019034	84	72	13	WBGene00003401	101	172	8	WBGene00001933	114	221	143	WBGene00007082	53	92	6
WBGene00021672	88	123	10	WBGene00019039	84	72	13	WBGene00023423	100	161	9	WBGene00018899	114	221	143	WBGene00013873	89	23	5
WBGene00016904	83	167	6	WBGene00019040	97	90	17	WBGene00011604	22	30	25	WBGene00001624	85	72	9	WBGene00006613	89	23	5
WBGene00016903	89	34	7	WBGene00019041	97	90	17	WBGene00011605	233	262	78	WBGene00019900	85	72	9	WBGene00013877	84	60	7
WBGene00016905	89	34	7	WBGene00019042	97	90	17	WBGene00011198	233	262	78	WBGene00019899	85	72	9	WBGene00013878	78	97	9
WBGene00016902	86	76	9	WBGene00019043	97	90	17	WBGene00006331	233	262	78	WBGene00004039	85	68	10	WBGene00010510	46	126	25
WBGene00016906	136	81	18	WBGene00019044	97	90	17	WBGene00011200	173	152	46	WBGene00019898	84	64	10	WBGene00013024	122	107	14
WBGene00002077	136	81	18	WBGene00018439	103	87	39	WBGene00003157	113	42	13	WBGene00019901	84	64	10	WBGene00013025	103	71	11
WBGene00002079	152	38	10	WBGene00018443	103	87	39	WBGene00011201	113	42	13	WBGene00019902	51	100	6	WBGene00013026	83	35	8
WBGene00021660	152	38	10	WBGene00018438	96	80	27	WBGene00011202	113	42	13	WBGene00003914	92	99	27	WBGene00000877	83	35	8
WBGene00020089	160	121	33	WBGene00018444	96	80	27	WBGene00011206	112	69	9	WBGene00018636	92	99	27	WBGene00013027	83	35	8
WBGene00004143	160	121	33	WBGene00018445	96	92	24	WBGene00011205	112	69	9	WBGene00000996	92	99	27	WBGene00006775	85	118	9
WBGene00006385	160	121	33	WBGene00018437	104	112	33	WBGene00001352	118	73	18	WBGene00018637	108	78	18	WBGene00007614	115	68	10
WBGene00020090	137	158	7	WBGene00018436	104	112	33	WBGene00010428	124	77	27	WBGene00018638	108	78	18	WBGene00003834	115	68	10
WBGene00021733	137	158	7	WBGene00018435	104	112	33	WBGene00006478	124	77	27	WBGene00018635	108	78	18	WBGene00007619	115	68	10
WBGene00015570	39	81	10	WBGene00018433	112	105	10	WBGene00044911	124	77	27	WBGene00002074	124	57	9	WBGene00003835	115	68	10
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WBGene00003106	88	112	8	WBGene00019994	83	167	7	WBGene00016955	66	123	11	WBGene00007609	63	47	4	WBGene00011229	79	92	53
WBGene00020836	144	126	8	WBGene00019997	196	169	7	WBGene00019263	62	38	5	WBGene00007606	63	47	4	WBGene00009069	79	92	53
WBGene00020834	144	126	8	WBGene00194747	196	169	7	WBGene00019264	62	38	5	WBGene00007607	63	47	4	WBGene00044638	79	92	53
WBGene00020835	144	126	8	WBGene00019157	196	169	7	WBGene00016664	120	192	13	WBGene00007608	63	47	4	WBGene00009067	65	85	36
WBGene00015646	62	87	9	WBGene00019158	77	38	7	WBGene00003636	120	192	13	WBGene00219330	113	45	10	WBGene00009068	65	85	36
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WBGene00021097	121	38	11	WBGene00021917	78	119	7	WBGene00015540	66	41	8	WBGene00004738	113	45	10	WBGene00002051	34	61	30
WBGene00021093	110	65	9	WBGene00021915	78	119	7	WBGene00015538	66	41	8	WBGene00013902	47	97	38	WBGene00004745	97	109	8
WBGene00021098	110	65	9	WBGene00019170	144	68	17	WBGene00015541	71	105	8	WBGene00013907	47	97	38	WBGene00006674	37	93	31
WBGene00021101	110	65	9	WBGene00006725	144	68	17	WBGene00019257	45	81	5	WBGene00013896	29	68	6	WBGene00007523	109	171	9
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WBGene00003599	71	101	6	WBGene00003175	43	76	9	WBGene00019295	124	132	16	WBGene00013900	67	129	8	WBGene00206382	52	108	12
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WBGene00206416	71	101	6	WBGene00020103	110	36	13	WBGene00004494	106	108	16	WBGene00011589	91	34	4	WBGene00018187	161	233	8
WBGene00206417	71	101	6	WBGene00020102	110	36	13	WBGene00019297	183	263	83	WBGene00011283	80	175	13	WBGene00003555	74	102	19
WBGene00020207	110	127	26	WBGene00021800	102	30	29	WBGene00006780	183	263	83	WBGene00011284	61	134	8	WBGene00019422	40	60	30
WBGene00020205	102	105	17	WBGene00050917	102	30	29	WBGene00019205	72	110	6	WBGene00011285	62	140	9	WBGene00020795	40	60	30
WBGene00020204	102	105	17	WBGene00021801	102	30	29	WBGene00023486	146	239	9	WBGene00011286	62	140	9	WBGene00020794	57	84	5
WBGene00020181	126	30	9	WBGene00021808	153	163	13	WBGene00000535	146	239	9	WBGene00003738	63	146	10	WBGene00020793	85	122	14
WBGene00020172	126	30	9	WBGene00021803	153	163	13	WBGene00002245	131	209	9	WBGene00011802	104	94	10	WBGene00003933	58	94	14
WBGene00020171	125	187	7	WBGene00021815	150	29	8	WBGene00006974	110	48	14	WBGene00194787	104	94	10	WBGene00003883	50	70	47
WBGene00017874	75	89	4	WBGene00021813	150	29	8	WBGene00019751	82	92	12	WBGene00219337	104	94	10	WBGene00019519	55	65	78
WBGene00017873	75	89	4	WBGene00021812	150	29	8	WBGene00015701	82	31	10	WBGene00004151	104	94	10	WBGene00019518	35	61	56
WBGene00021578	136	200	23	WBGene00021811	138	175	8	WBGene00015703	82	31	10	WBGene00001233	104	94	10	WBGene00000401	53	91	16
WBGene00021576	131	182	24	WBGene00021816	173	50	18	WBGene00015702	82	31	10	WBGene00011307	104	94	10	WBGene000045272	38	60	35
WBGene00000106	131	182	24	WBGene00021810	173	50	18	WBGene00006809	82	31	10	WBGene00005113	85	44	9	WBGene00019102	78	105	30
WBGene00019927	90	115	7	WBGene00001559	39	84	8	WBGene00001853	121	177	116	WBGene00011306	85	44	9	WBGene00015547	124	172	30
WBGene00019926	94	104	10	WBGene00008347	94	136	47	WBGene00005738	121	177	116	WBGene00011309	85	44	9	WBGene00015546	87	147	38
WBGene00019925	94	104	10	WBGene00008348	123	109	31	WBGene00022250	114	67	31	WBGene00003031	78	38	9	WBGene00015545	58	68	36



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WBGene00019923	98	93	12	WBGene00010303	152	81	14	WBGene00003082	108	65	30	WBGene00004793	71	31	9	WBGene00018373	111	176	8
WBGene00045302	98	93	12	WBGene00010304	152	81	14	WBGene00004783	101	62	28	WBGene00008851	44	78	6	WBGene00018374	111	176	8
WBGene00019928	108	111	26	WBGene00003795	149	55	12	WBGene00022251	87	90	19	WBGene00138724	44	78	6	WBGene00017726	66	111	11
WBGene00019922	108	111	26	WBGene00010305	145	29	10	WBGene00003237	87	90	19	WBGene00001109	44	78	6	NoWBGene_ID21	66	111	11
WBGene00019929	109	122	16	WBGene00010302	145	29	10	WBGene00022233	72	117	9	WBGene00001389	44	78	6	WBGene00017729	66	111	11
WBGene00019930	110	133	6	WBGene00010306	30	31	18	WBGene00004881	101	31	9	WBGene00001388	62	134	7	WBGene00017725	99	125	6
WBGene00019921	110	133	6	WBGene00010450	30	31	18	WBGene00022253	101	31	9	WBGene00008848	53	99	24	WBGene00001837	56	100	7
WBGene00019920	127	132	8	WBGene00010449	30	31	18	WBGene00000256	101	31	9	WBGene00045418	59	129	7	WBGene00015672	143	198	11
WBGene00019919	121	102	10	WBGene00007920	119	15	7	WBGene00022240	101	31	9	WBGene00008849	59	129	7	WBGene00015676	143	198	11
WBGene00019918	98	73	10	WBGene00007921	130	28	9	WBGene00022255	73	122	7	WBGene00008850	90	185	9	WBGene00020144	52	133	9
WBGene00019917	77	69	15	WBGene00007927	141	41	10	WBGene00022248	70	115	7	WBGene00001475	90	185	9	WBGene00020146	53	114	7
WBGene00016303	56	65	20	WBGene00007922	143	85	9	WBGene00022231	32	34	27	WBGene00007152	99	76	8	WBGene00020142	95	135	8
WBGene00016302	148	172	10	WBGene00007923	145	128	7	WBGene00044350	56	109	6	WBGene00002250	99	76	8	WBGene00000294	109	158	9
WBGene00016309	161	200	10	WBGene00007924	145	128	7	WBGene00015311	87	38	20	WBGene00007907	76	143	8	WBGene00006067	109	158	9
WBGene00235351	161	200	10	WBGene00007928	145	128	7	WBGene00015308	87	38	20	WBGene00007909	76	143	8	WBGene00020633	92	135	9
WBGene00016306	161	200	10	WBGene00010814	103	48	19	WBGene00015307	87	38	20	WBGene00003143	44	103	9	WBGene00020630	92	135	9
WBGene00016300	125	129	12	WBGene00004428	103	48	19	WBGene00016610	107	135	69	WBGene00007150	52	119	11	WBGene00018204	99	178	20
WBGene00016307	88	58	14	WBGene00010809	103	48	19	WBGene00006621	107	135	69	WBGene00001137	78	216	11	WBGene00016253	97	151	94
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WBGene00016308	135	104	7	WBGene00010812	97	29	11	WBGene00016612	136	210	6	WBGene00007152	78	216	11	WBGene00016251	97	151	94
WBGene00016298	135	104	7	WBGene00010811	97	29	11	WBGene00018160	113	121	8	WBGene00007154	140	197	9	WBGene00018712	68	70	18
WBGene00044419	107	91	7	WBGene00010813	124	149	8	WBGene00018161	89	32	9	NoWBGene_ID33	140	197	9	WBGene00018710	144	220	10
WBGene00016297	78	78	7	WBGene00008288	110	153	8	WBGene00001029	89	32	9	WBGene00011647	109	137	9	WBGene00018713	50	128	11
WBGene00016296	78	78	7	WBGene00000248	96	156	8	WBGene00002274	89	32	9	WBGene00001874	81	45	8	WBGene00019347	72	99	7
WBGene00016295	130	97	9	WBGene00044166	96	156	8	WBGene00018167	117	126	35	WBGene00009337	51	117	7	WBGene00004121	76	122	9
WBGene00018456	130	97	9	WBGene00008180	92	201	8	WBGene00018166	117	126	35	WBGene00007747	75	156	7	WBGene00018033	51	92	8
WBGene00018455	130	97	9	WBGene00004213	65	99	8	WBGene00018165	117	126	35	WBGene00008218	81	27	8	WBGene00015583	78	93	10
WBGene00018457	96	70	7	WBGene00004765	176	240	9	WBGene00018164	117	126	35	WBGene00008219	81	27	8	WBGene00015586	80	129	14
WBGene00018458	96	70	7	WBGene00007859	144	199	10	WBGene00017481	117	126	35	WBGene00003719	78	114	9	WBGene00015587	80	129	14
WBGene00018452	96	70	7	WBGene00007860	111	158	10	WBGene00017480	90	113	22	WBGene00008221	78	114	9	WBGene00015588	93	104	12
WBGene00018459	96	70	7	WBGene00006822	100	62	7	WBGene00001090	52	85	9	WBGene00008222	78	114	9	WBGene00015589	105	78	9
WBGene00018461	96	70	7	WBGene00008118	94	45	8	WBGene00015278	68	118	8	WBGene00006072	78	114	9	WBGene00019576	67	75	6
WBGene00018460	96	70	7	WBGene00008117	94	45	8	WBGene00015280	91	182	36	WBGene00006016	76	132	10	WBGene00019577	67	75	6
WBGene00018448	81	39	15	WBGene00008120	94	45	8	WBGene00001858	91	182	36	WBGene00010867	76	132	10	WBGene00019578	113	132	24
WBGene00019700	81	39	15	WBGene00008119	97	41	8	WBGene00003030	73	47	5	WBGene00010868	106	181	21	WBGene00020725	97	121	19
WBGene00019699	81	39	15	WBGene00008121	71	97	11	WBGene00019259	128	98	8	WBGene00009979	106	181	21	WBGene00020726	120	153	13
WBGene00019702	150	115	15	WBGene00012084	94	146	8	WBGene00015928	105	50	12	WBGene00003222	118	31	7	WBGene00007011	120	153	13
WBGene00019703	150	115	15	WBGene00008885	164	162	34	WBGene00006917	105	50	12	WBGene00009136	82	48	9	WBGene00015121	86	94	9
WBGene00019705	150	115	15	WBGene00003962	164	162	34	WBGene00015929	105	50	12	WBGene00009135	82	48	9	WBGene00015119	86	94	9
WBGene00006195	131	103	15	WBGene00007573	164	162	34	WBGene00015935	75	138	8	WBGene00009137	82	48	9	WBGene00002207	84	140	9
WBGene00019704	112	90	14	WBGene00007574	122	101	23	WBGene00015934	75	138	8	WBGene00001496	75	19	4	WBGene00020365	49	85	7
WBGene00019311	82	88	20	WBGene00006474	122	101	23	WBGene00020234	91	52	19	WBGene00009138	75	19	4	WBGene00020366	100	113	16
WBGene00019313	82	88	20	WBGene00007576	122	101	23	WBGene00020235	91	52	19	WBGene00009139	75	19	4	WBGene00020812	151	140	25
WBGene00020475	109	26	9	WBGene00007581	82	59	10	WBGene00004458	108	35	12	WBGene00011692	75	19	4	WBGene00004270	99	148	9
WBGene00021103	109	26	9	WBGene00007577	89	44	10	WBGene00020683	108	35	12	WBGene00011696	77	57	8	WBGene00020813	99	148	9
WBGene00006387	153	126	9	WBGene00007579	92	28	11	WBGene00020682	99	33	10	WBGene00001808	77	57	8	WBGene00000993	115	202	15
WBGene00021104	153	126	9	WBGene00007578	79	28	11	WBGene00020687	90	30	8	WBGene00000233	77	57	8	WBGene00020811	115	202	15
WBGene00004076	112	109	9	WBGene00009372	130	119	9	WBGene00195051	90	30	8	WBGene00001726	74	36	11	WBGene00020817	115	202	15
WBGene00018734	63	74	7	WBGene00009377	130	119	9	WBGene00020681	90	30	8	WBGene00008224	76	28	11	WBGene00219274	59	72	21
WBGene00018572	175	249	23	WBGene00009373	130	119	9	WBGene00022727	120	214	9	WBGene00008225	76	28	11	WBGene00021500	41	45	21
WBGene00021970	78	72	9	WBGene00009374	130	119	9	WBGene00016085	59	117	8	WBGene00000250	76	28	11	WBGene00016350	121	127	10
WBGene00021966	60	58	18	WBGene00000070	67	87	7	WBGene00016083	79	66	8	WBGene00009993	88	31	8	WBGene00016346	100	88	8
WBGene00021965	42	44	26	WBGene00003476	115	174	10	WBGene00016082	79	66	8	WBGene00009992	88	31	8	WBGene00016345	78	49	6
WBGene00021973	147	80	8	WBGene00011974	115	174	10	WBGene00015553	113	125	8	WBGene00009994	88	31	8	WBGene00004220	83	127	9
WBGene00000112	147	80	8	WBGene00006591	115	174	10	WBGene00015552	147	184	7	WBGene00009996	88	31	8	WBGene000044770	66	157	10

WBGene00018974	169	93	16	WBGene00001086	138	166	21	WBGene00015551	121	183	6	WBGene00044200	119	152	23	WBGene00016900	95	115	7
WBGene00006924	191	105	24	WBGene00000137	138	166	21	WBGene00015555	77	28	9	WBGene00010425	96	161	20	WBGene00016899	95	115	7
WBGene00018816	154	29	10	WBGene00011260	108	118	27	WBGene00015549	77	28	9	WBGene00010279	93	139	14	WBGene00017339	118	173	8
WBGene00018815	154	29	10	WBGene00007970	108	118	27	WBGene00000585	77	28	9	WBGene00010280	113	107	10	WBGene00017340	118	173	8
WBGene00021786	154	29	10	WBGene00007963	108	118	27	WBGene00002228	77	28	9	WBGene00010282	92	30	7	WBGene00017342	90	128	12
WBGene00021785	154	29	10	WBGene00000264	92	54	11	WBGene00006572	72	108	6	WBGene00006442	92	30	7	WBGene00006886	90	128	12
WBGene00021784	154	29	10	WBGene00007969	147	160	20	WBGene00003695	72	108	6	WBGene00010283	92	30	7	WBGene00017376	36	51	20
WBGene00021789	90	24	8	WBGene00004414	202	266	29	WBGene00021542	118	124	16	WBGene00011326	88	149	5	WBGene00017379	36	51	20
WBGene00021781	90	24	8	WBGene00006575	202	266	29	WBGene00021543	112	81	27	WBGene00011328	88	149	5	WBGene00017378	36	51	20
WBGene00021790	90	24	8	WBGene00003930	149	180	12	WBGene00021544	112	81	27	WBGene00011327	88	149	5	WBGene00000792	78	111	13
WBGene00019209	157	153	10	WBGene00014204	149	180	12	WBGene00004473	112	81	27	WBGene00008986	85	126	9	WBGene00003891	78	131	8
WBGene00019207	157	153	10	WBGene00014203	149	180	12	WBGene00000942	76	102	17	WBGene00009973	132	162	12	WBGene00017375	118	112	20
WBGene00021776	81	84	33	WBGene00007980	106	93	8	WBGene00022619	40	122	7	WBGene00009974	132	162	12	WBGene00016489	118	112	20
WBGene00021774	81	84	33	WBGene00007982	107	151	8	WBGene00022620	60	78	7	WBGene00009975	157	226	11	WBGene00044683	118	112	20
WBGene00021773	81	84	33	WBGene00007983	140	176	16	WBGene00022618	79	33	7	WBGene00009976	152	209	13	WBGene00016490	76	90	5
WBGene00019416	81	84	33	WBGene00006537	172	142	23	WBGene00016403	92	36	8	WBGene00009977	152	209	13	WBGene00003369	72	83	7
WBGene00044697	75	74	29	WBGene00011367	172	142	23	WBGene00000888	92	36	8	WBGene00010088	132	116	8	WBGene00022647	72	83	7
WBGene00019415	68	63	24	WBGene00011368	172	142	23	WBGene00016404	92	36	8	WBGene00004767	132	116	8	WBGene00022648	72	83	7
WBGene00045486	68	63	24	WBGene00002038	47	90	7	WBGene00016405	94	38	9	WBGene00010089	124	123	8	WBGene00006602	86	94	8
WBGene00019417	73	63	21	WBGene00004322	71	25	8	WBGene00016400	91	53	6	WBGene00003812	115	129	7	WBGene00020085	169	267	9
WBGene00019414	78	63	17	WBGene00001943	71	25	8	WBGene00000687	91	53	6	WBGene00011929	61	51	11	WBGene00206419	169	267	9
WBGene00019418	80	68	29	WBGene00001944	71	25	8	WBGene00004411	126	58	14	WBGene00002259	61	51	11	WBGene00020086	169	267	9
WBGene00019413	80	68	29	WBGene00006811	129	71	11	WBGene00206380	126	58	14	WBGene00011930	61	51	11	WBGene00017939	127	179	7
WBGene00015868	112	150	57	WBGene00019211	119	195	6												

### Supplementary Table 5. ChIP-seq raw data on average peak value for H3K4me3

Average peak value for H3K4me3 in wild type, *wdr-5(ok1417)* and *rbbp-5(tm3463)*. Details on peak position is not shown

Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5	Gene ID	N2	WDR5	RBBP5
WBGene00022277	139	21	8	WBGene00016307	141	29	16	WBGene00016527	227	52	15	WBGene00050916	215	21	15	WBGene00002985	192	21	14
WBGene00022276	189	22	12	WBGene00016299	134	35	14	WBGene00016520	227	52	15	WBGene00018898	215	21	15	WBGene00009329	265	41	24
WBGene00022278	155	19	12	WBGene00016308	127	40	12	WBGene00016528	227	52	15	WBGene00021286	243	86	66	WBGene00009336	265	41	24
WBGene00022279	160	21	12	WBGene00016298	127	40	12	WBGene00021863	98	36	11	WBGene00004419	243	86	66	WBGene00009330	265	41	24
WBGene00022275	235	17	10	WBGene00044419	127	40	12	WBGene00021864	98	36	11	WBGene00021282	243	86	66	WBGene00009335	265	41	24
WBGene00044345	235	17	10	WBGene00016295	148	31	9	WBGene00021857	260	21	15	WBGene00021285	243	82	15	WBGene00001303	265	41	24
WBGene00021677	235	17	10	WBGene00018456	148	31	9	WBGene00021865	258	20	12	WBGene00021281	243	82	15	WBGene00009331	265	41	24
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WBGene00020207	185	37	32	WBGene00022055	270	23	11	WBGene00017907	123	65	10	WBGene00009059	126	58	9	WBGene00020770	116	39	11
WBGene00020205	161	31	22	WBGene00022053	270	23	11	WBGene00017906	61	64	13	WBGene00001178	126	58	9	WBGene00018187	180	79	13
WBGene00020204	161	31	22	WBGene00022057	287	23	11	WBGene00006970	93	62	24	WBGene00007952	213	20	12	WBGene00003555	41	35	31
WBGene00020181	256	20	10	WBGene00022052	287	23	11	WBGene00000009	93	62	24	WBGene00007953	213	20	12	WBGene00019422	27	40	41
WBGene00020172	256	20	10	WBGene00021245	63	84	62	WBGene00018547	66	58	11	WBGene00009108	213	20	12	WBGene00020795	27	40	41
WBGene00020171	61	51	11	WBGene00021247	63	84	62	WBGene00020930	134	78	14	WBGene00006460	151	25	8	WBGene00003883	49	53	85
WBGene00021578	286	73	23	WBGene00021248	327	30	17	WBGene00018066	283	25	21	WBGene00195256	151	25	8	WBGene00019519	49	53	85
WBGene00021576	275	65	28	WBGene00002025	327	30	17	WBGene00018065	283	25	21	WBGene00006934	165	19	10	WBGene00019518	35	56	65
WBGene00000106	275	65	28	WBGene00021442	224	21	14	WBGene00018064	289	25	20	WBGene00011890	165	19	10	WBGene00045272	41	67	58
WBGene00020304	105	37	16	WBGene00021441	224	21	14	WBGene00003955	295	24	18	WBGene00011892	165	19	10	WBGene00019102	152	65	43
WBGene00019927	105	37	16	WBGene00004249	210	21	12	WBGene00006951	295	24	18	WBGene00003065	165	19	10	WBGene00015547	149	48	27
WBGene00019926	117	38	18	WBGene00021443	210	21	12	WBGene00020981	84	24	13	WBGene00011893	165	19	10	WBGene00018373	65	47	6
WBGene00019925	117	38	18	WBGene00004163	70	37	31	WBGene00020982	84	24	13	WBGene00011898	121	18	12	WBGene00018374	65	47	6
WBGene00019924	129	39	19	WBGene00021446	233	28	12	WBGene000006173	69	20	16	WBGene00011897	121	18	12	WBGene00017725	140	35	12
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WBGene00016302	162	46	16	WBGene00021702	192	39	12	WBGene00018086	269	32	35	WBGene00008372	173	21	12	WBGene00015586	105	27	13
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WBGene00016306	175	58	19	WBGene00021697	184	60	33	WBGene00020978	215	21	15	WBGene00206498	192	21	14	WBGene00019578	68	47	29
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WBGene00006602	90	33	8	WBGene00017342	161	28	7	WBGene00021500	56	46	42	WBGene00004270	260	38	8	WBGene00020726	175	38	13
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WBGene00020086	161	119	10	WBGene00017375	235	38	27	WBGene00016345	139	21	13	WBGene00020811	117	67	26	WBGene00015119	92	35	12
WBGene00017939	104	63	10	WBGene00016489	235	38	27	WBGene00004770	37	50	14	WBGene00020817	117	67	26	WBGene00002207	107	40	14
WBGene00015868	138	68	54	WBGene00044683	235	38	27	WBGene00017339	92	56	13	WBGene00219274	44	40	27	WBGene00020366	225	47	27
WBGene00019211	85	51	13	WBGene00016490	137	26	9	WBGene00017340	92	56	13	WBGene00020810	44	40	27	WBGene00020812	225	47	27
WBGene00007069	114	24	15	WBGene00007068	114	24	15												

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