

# Sequence of the Chicken Sex Chromosomes

By

**Daniel Winston Bellott**

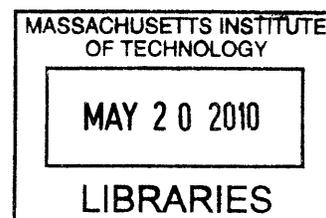
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## **Abstract**

In birds, as in mammals, the chromosome complement determines sex. Male birds are designated ZZ, female ZW. Mammals have the opposite system; males are XY and females XX. Both the avian ZW and mammalian XY pair are believed to have evolved from autosomes, with dramatic changes, both gene loss as well as gene acquisition and amplification occurring on the sex-specific W and Y chromosomes. In contrast, Z and X chromosomes are assumed to have diverged little from their autosomal progenitors.

The Z and W sex chromosomes of the chicken provide a unique opportunity to study the evolution of sex chromosomes in a second lineage with an alternate system of heterogamety. We produced the finished sequence of the chicken Z chromosome and generated female-specific markers necessary to produce a complete sequence of the chicken W chromosome. Already our analysis of the Z chromosome has revealed that the sex chromosomes of birds evolved independently of the sex chromosomes of mammals. Despite this independence, the chicken Z chromosome converged on a suite of features analogous to those of the human X chromosome: low gene density, an enrichment for interspersed repeats, and large multi-copy gene families expressed in the testis. These features arose during the evolution of the Z and X chromosomes as sex chromosomes, overturning the notion that Z and X chromosomes are evolutionarily stable.

Our preliminary efforts on the W chromosome have provided insights into its structure and underscore the ubiquity of gene acquisition and amplification on vertebrate sex chromosomes. As we accumulate genomic data from additional sex chromosomes, explaining the evolutionary forces that result in gene acquisition and amplification will remain a major challenge.

Thesis Supervisor: David C. Page  
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*To my father, for a lifetime of valuable scientific discussions*



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## Chapter 1: Introduction

(Adapted from: “Reconstructing the Evolution of Vertebrate Sex Chromosomes,” a review article submitted to Cold Spring Harbor Symposia on Quantitative Biology)

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## ***Summary***

Sex chromosomes and their evolution have captivated researchers since their discovery. For over 100 years, the dominant model of sex chromosome evolution has held that differentiated sex chromosomes, such as the X and Y chromosomes of mammals or the Z and W chromosomes of birds, evolved from ordinary autosomes, primarily through the degeneration of the sex-specific Y chromosome or W chromosome. At the same time, the sex chromosomes shared between sexes, the X chromosome and Z chromosome, are expected to remain essentially untouched. This model was based on limited cytogenetic and genetic data. Only in the last decade, with the advent of genomics, has the complete sequence of any sex chromosome pair become available. High quality finished sequences of the human and chimpanzee Y chromosomes, as well as the human X chromosome, have revealed sequence features unanticipated by the traditional model of sex chromosome evolution. Large, highly identical, tandem and inverted arrays of testis-expressed genes are major sources of innovation in gene content on sex-specific as well as sex-shared chromosomes. Accounting for the emergence of these ampliconic structures presents a challenge for future studies of sex chromosome evolution.

## ***Introduction***

Since the discovery of sex chromosomes, researchers have sought to explain the evolutionary forces that could produce a pair of chromosomes that differed between the

sexes. During the twentieth century, the fields of classical genetics, evolutionary and population genetics, and cytology converged on a single explanation for the evolution of heteromorphic sex chromosomes: sex chromosomes evolved from autosomes primarily through the degeneration of the sex-specific Y or W chromosome, while the X or Z chromosome faithfully preserved the gene content of the ancestral autosome pair. X and Z chromosomes were museums; Y and W chromosomes were ruins, destined to be lost to the sands of time.

In the last ten years, genomics has revolutionized the study of evolution. Evolution changes the sequence of DNA molecules, and comparing DNA sequences allows us to reconstruct evolutionary events from the past. The availability of DNA sequences from multiple vertebrates has confirmed that the process of sex chromosome evolution envisioned by theorists has played out multiple times in the evolution of vertebrate sex chromosomes. However, complete, high-quality sequences of sex chromosomes have led to discoveries that were unanticipated by existing theory. Sex-specific chromosomes are not doomed to decay, but selection can act to preserve their gene content over long time scales. Amplicons, massive and highly identical arrays of duplicated genes, are sources of innovation in gene content on sex-specific as well as sex-shared chromosomes. These arrays consist of genes expressed exclusively or predominantly in the testis.

The unexpected results of genomic analyses have challenged long-standing assumptions about the evolution of sex chromosomes. It is now clear that sex chromosomes are subject to constant remodeling; they resemble Theseus' ship rather than museums or ruins. The dramatic nature of innovation in gene content on sex

chromosomes presents major theoretical challenges for the field of sex chromosome evolution. What selective forces can generate ampliconic structures? What is the relationship between ampliconic genes and male reproduction? As more sex chromosome sequences become available, including those of multiple mammals as well as the Z and W chromosomes of birds, they will enhance our ability to address these questions.

### ***Theoretical Models of Sex Chromosome Evolution***

The study of sex chromosome evolution shares its origin with that of genetics, in Thomas Hunt Morgan's fly room at Columbia University. In 1913, Alfred Sturtevant produced the first genetic map, consisting of six sex-linked genes (Sturtevant 1913). The following year, his colleague, Calvin Bridges, combined Sturtevant's linear map of sex-linked genes with his own work on non-disjunction of sex chromosomes to demonstrate that Sturtevant's map was that of the X chromosome, and the chromosomes were the material of heredity (Bridges 1914). This suggested that sex chromosomes were not merely a sign, but instead the root cause of sexual dimorphism. The following year, a third member of Morgan's lab, Herman Muller, established the linkage of a gene with the fourth chromosome, the smallest *Drosophila* autosome (Muller 1914). With Muller's publication, all *Drosophila* chromosomes, with the exception of the Y chromosome, had at least one known gene. This fact troubled Muller, who explained it with the first theory of sex chromosome evolution: the X chromosome and the Y chromosome evolved from an ordinary pair of autosomes, but the Y chromosome, unable to recombine in males, had accumulated deleterious mutations, eliminating all of its genes. This simple theory, that

heteromorphic sex chromosomes evolve from autosomes through the decay of the sex-specific chromosome, has been fundamental to the study of sex chromosome evolution for nearly 100 years.

Muller's theory that heteromorphic sex chromosomes were the result of degradation of the sex-specific chromosome was corroborated by the lack of credible Y-linked phenotypes in humans. As was the case in *Drosophila*, the first traits mapped to a human chromosome were mapped to the X chromosome (Morgan 1911a; Morgan 1911b; Wilson 1911). By the middle of the century, X-linked inheritance had been reported for dozens of traits, while only a handful of traits had been mapped to the Y chromosome (Stern 1957; McKusick 1962). In 1957, Curt Stern, another former student of Morgan's and the President of the American Society of Human Genetics, addressed the society's annual meeting (Stern 1957). Stern used his address to systematically debunk every reported case of Y-linkage in humans. Stern noted that no Y-linked trait had been discovered in experimental mammals, but cautioned investigators not to give up the search for Y-linked traits. Two years later it was discovered that the human and mouse Y chromosomes contained the male sex-determining gene (Ford et al. 1959; Jacobs and Strong 1959; Welshons and Russell 1959), but the reputation of the Y chromosome had been irreparably damaged. Apart from sex-determination, geneticists viewed the sex-specific Y chromosome as a "dud" (McKusick 1962).

The idea of the sex-specific chromosome as a degenerate autosome was not only in accord with the genetic data from flies and mammals; it could also account for the diverse sex determining mechanisms of vertebrates. Many vertebrate species have no sex chromosomes; in these species, sex is determined by an environmental cue such as

temperature. Some species have homomorphic sex chromosomes. Homomorphic sex chromosomes are not cytologically distinguishable, but they can be revealed by experiments with artificially sex-reversed animals. Heteromorphic sex chromosomes of the type seen in *Drosophila* predominate in three vertebrate lineages: mammals, birds, and snakes. Susumu Ohno argued that these three states, the absence of sex chromosomes, homomorphic sex chromosomes, and heteromorphic sex chromosomes, represented a continuum that revealed the evolutionary trajectory of the heteromorphic vertebrate sex chromosomes (Ohno 1967). Ohno conjectured that the common ancestor of vertebrates possessed no sex chromosomes, but that in some lineages, a mutation had arisen which caused an ordinary pair of autosomes to behave as homomorphic sex chromosomes, and after this event, the sex-specific chromosome decayed producing heteromorphic sex chromosomes like those of mammals, birds, and snakes.

Ohno also modified Muller's theory to account for differences in recombination between *Drosophila* and vertebrates. Muller's theory relied on the absence of crossing over between homologous chromosomes in *Drosophila* males to automatically isolate any Y chromosome from crossing over, but because recombination occurs in both sexes in vertebrates, the sex-specific chromosomes of vertebrates would not spontaneously begin to degenerate. After the emergence of a new sex-determining gene in a vertebrate, a second event is required to suppress crossing over. Ohno proposed that a pericentric inversion on the sex-specific chromosome that encompassed the region of the sex determining gene could suppress crossing over between sex chromosomes in the heterogametic sex (Ohno 1967). If crossing over occurs within the boundaries of a pericentric inversion, the recombinant chromosomes will be duplicated in part of the

inversion and deficient in the other; if essential genes fall within the boundaries of the inversion, recombinant progeny will die and only those whose sex chromosomes that did not recombine will survive. Once the sex-specific Y chromosome or W chromosome was isolated, it would begin to diverge from the shared X chromosome or Z chromosome by losing its gene content as Muller had predicted.

As the study of population genetics emerged, it became clear that Muller's explanation for the degeneration of the sex-specific chromosome was inadequate. Inspired by his work on chromosomes carrying balanced lethal mutations, Muller initially proposed that a lack of crossing over was sufficient to lead to genetic decay. Each chromosome in a pair carrying balanced lethal mutations exists only in the heterozygous state; recessive mutations on one chromosome are not exposed to selection so long as the other chromosome maintains the ancestral allele. Thus, both chromosomes can accumulate complementary recessive mutations. Muller believed that Y and W chromosomes, held in a heterozygous state by linkage to the sex determining locus, would be sheltered from selection by their partner, while X and Z chromosomes were exposed to selection against recessive mutations in the homogametic sex (Muller 1918). Fisher demonstrated that this explanation could not account for the degeneration of the sex-specific chromosome, because mutation must affect incipient sex chromosomes equally (Fisher 1935). If an X-linked or Z-linked gene suffered a loss of function, the result would be selection against a parallel loss of function in the Y-linked or W-linked counterpart. Fisher showed that for an infinite population, degeneration of the type Muller described could only occur if the mutation rate is much higher on the sex-specific chromosome than in the rest of the genome. In light of this difficulty, it was necessary to

modify Muller's theory to explain why only the sex-specific chromosome was subject to degeneration.

Although Muller's initial explanation for the degeneration of the sex-specific chromosome proved inadequate, population genetic theories designed to explain the benefits of sex and recombination became the source of alternative models which could account for the degeneration of a non-recombining chromosome. Muller proposed that genetic drift could account for the degeneration of non-recombining chromosomes through a mechanism which is now known as "Muller's ratchet" (Muller 1964; Felsenstein 1974). Muller's ratchet is the idea that, in the absence of crossing over, a population cannot generate chromosomes with a smaller mutational load than those that currently exist within the population. If the least-mutated class of chromosomes is lost to drift, it is replaced by one that carries more mutations, and the 'ratchet' has clicked irreversibly towards the decay of the non-recombining chromosome.

Alternative models of degeneration rely on the absolute linkage between all the sites on a non-recombining chromosome. Selection at one site interferes with selection at linked sites, preventing the efficient elimination of deleterious mutations and slowing the spread of beneficial mutations (Felsenstein 1974). Strongly beneficial mutations can sweep through a population, dragging many weakly deleterious mutations along with them (Genetic Hitchhiking) (Maynard Smith and Haigh 1974; Rice 1987); chromosomes with strongly deleterious alleles will be lost from the population before they can spread, increasing the chances that weakly deleterious alleles will become fixed by drift (Background Selection) (Charlesworth et al. 1993; Charlesworth 1994). Both of these models predict reductions in the effective population size of a non-recombining

chromosome, increasing the effects of genetic drift (Charlesworth 1978). Thus, both genetic hitchhiking and background selection should act synergistically with Muller's ratchet to hasten the degeneration of a non-recombining chromosome (Charlesworth 1978; Bachtrog 2008).

Theoretical models of sex chromosome evolution based on population genetics implicitly assumed that the sex-shared X chromosome and Z chromosome were unchanging; Susumu Ohno codified this as an explicit prediction. Ohno predicted that the X chromosome and Z chromosome should preserve the gene content of the ancestral autosome pair from which they evolved (Ohno 1967). As a corollary, the sex chromosomes of species that share a common origin are expected to share the same ancestral gene content. This concept is now most familiar as "Ohno's Law," that genes that are X-linked in one mammal should be X-linked in all others, but Ohno applied his predictions equally to the Z chromosomes of birds and snakes. Ohno and others reasoned that the degeneration of the sex-specific chromosome would result in the evolution of dosage compensation on the sex chromosome shared between the sexes (Ohno 1967; Charlesworth 1978; Jegalian and Page 1998). Once genes were lost from the sex-specific chromosome, the heterogametic sex would only have half the original dose of X-linked genes (Ohno 1967; Charlesworth 1978; Jegalian and Page 1998). A system of dosage compensation would evolve to provide males with the correct expression level for X-linked genes (Ohno 1967; Charlesworth 1978; Jegalian and Page 1998). Ohno argued that autosomal genes could not be added to the X chromosome because they would be expressed at too low a level in males, and X-linked genes could not move to autosomes because they were dependent on the dosage compensation mechanism for proper

expression (Ohno 1967). Thus, while Y chromosomes and W chromosomes were subject to drastic changes in gene content, X chromosomes and Z chromosomes were locked into stably retaining their ancestral genes.

### ***Evolutionary Strata: Reconstructing the Degeneration of Sex-specific Chromosomes***

As DNA sequences from vertebrate sex chromosomes became available, researchers interpreted them in the context of the theories built on Muller's ideas. Pairing and crossing over between the human X and Y chromosomes at meiosis implied that some vestige of the original autosomal homology between them remained (Solari and Tres 1970; Rasmussen and Holm 1978). This suspicion was confirmed by the discovery of pseudoautosomal genes on the mammalian X chromosome and Y chromosome (Cooke et al. 1985; Simmler et al. 1985; Goodfellow et al. 1986). The first sequence map of the Y chromosome showed that even outside the pseudoautosomal region, the human X chromosome and Y chromosome carried homologous genes (Foote et al. 1992; Vollrath et al. 1992). The sequence of these Y-linked genes, when compared to the sequence of their X-linked homologs, revealed a pattern that suggested a pathway for X-Y evolution (Lahn and Page 1999a). Nucleotide divergence between X-linked and Y-linked gene copies was strongly correlated with the position of the X-linked gene copy, such that X-Y pairs formed several groups of increasing divergence from the short arm to the long arm of the X chromosome. Bruce Lahn likened the surviving gene pairs to fossils preserved in layers of stone from different periods in the past, and christened these groups "evolutionary strata." Each stratum contains genes isolated from recombination by the

same event, thus the genes share similar levels of divergence. Lahn postulated at least four inversion events on the Y chromosome to account for his observations, in accordance with Ohno's prediction that inversion events would initiate Y chromosome divergence and that the X chromosome would remain untouched.

Subsequent work on the human X chromosome and the Z chromosome and W chromosome of chickens provided further evidence for the degeneration of the sex-specific chromosome. The finished sequence of the human X chromosome was presented as a foil for the Y chromosome, revealing further details of Y chromosome degeneration (Ross et al. 2005). Ross and colleagues confirmed the existence of the strata identified by Lahn, and identified an additional, more recent stratum. As was the case for the X chromosomes and Y chromosomes of mammals, the first sequence data from the chicken sex chromosomes showed that the Z chromosome and the W chromosome shared genes, suggesting that they too had evolved from a homologous pair of autosomes (Fridolfsson et al. 1998). As more W-linked genes were identified, Handley and colleagues compared them to their Z-linked homologs, and identified strata (Handley et al. 2004). The sex-specific Y chromosome and W chromosome evolved from autosomes along the same pathway of progressive isolation from recombination followed by degeneration.

### ***Conservation, Recombination, and Innovation on the Y chromosome***

The finished sequence of the human Y chromosome, published almost ninety years after Muller's original paper anticipating the degeneration of the non-recombining sex chromosome, represented the first sequence of any sex-specific chromosome

(Skaletsky et al. 2003). The human Y chromosome sequence was assembled from individual BAC (Bacterial Artificial Chromosome) clones from a single man's Y chromosome, allowing a greater degree of completeness in repetitive regions than has been achieved for other human chromosomes (Skaletsky et al. 2003). This effort enabled genomic comparisons that could, for the first time, rigorously test theoretical predictions of the course of sex chromosome evolution. While it was clear that the human X chromosome and Y chromosome had evolved from autosomes, unanticipated findings called into question some of the core assumptions of sex chromosome evolutionary theory. The human Y chromosome appeared to be a mosaic of different sequence classes that had different evolutionary trajectories (Skaletsky et al. 2003). The divergence evident in X-degenerate sequences had defined the evolutionary strata, but subsequent work would show that selection was more effective at preserving the surviving genes from degeneration than had been anticipated. The Y chromosome also gained genes in X-transposed and ampliconic sequences; these sequences demonstrated that Y chromosomes evolved not only by degeneration, but also by growth and elaboration.

Nearly half of the human Y chromosome is composed of X-degenerate sequences that contain genes that have survived the stepwise process of Y degeneration from the ancestral autosome pair that gave rise to the X chromosome and Y chromosome (Skaletsky et al. 2003). The X-degenerate portion of the Y chromosome has unquestionably lost most genes that were present on the ancestral autosome pair; only 16 single-copy genes have survived out of the hundreds which are inferred to have been present on the ancestor of the X and Y chromosomes (Skaletsky et al. 2003). This has led to prominent claims that the Y chromosome is decaying at such a rapid pace that it will

be devoid of genes in 10 million years (Aitken and Graves 2002). However, there is abundant evidence the Y chromosome will not “self-destruct” any time soon. Rozen and colleagues examined variation in these surviving genes across a panel of 105 men representing worldwide Y chromosome diversity (Rozen et al. 2009). They discovered that there is remarkably little variation in X-degenerate protein coding sequences -- on average, two randomly chosen Y chromosomes differ by only a single amino acid change (Rozen et al. 2009). They found that both nucleotide diversity and the proportion of variant sites are higher for silent substitutions than for substitutions which would lead to amino acid changes, implying that natural selection has operated effectively to preserve the coding sequences of the X-degenerate genes during human history (Rozen et al. 2009). Non-recombining sequences can be stable over even longer time scales. Hughes and colleagues systematically compared the human X-degenerate genes to those of the chimpanzee. They found that the human Y has preserved all X-degenerate genes that were present in the common ancestor of humans and chimps (Hughes et al. 2005). Thus, the X degenerate sequences of the human Y chromosome have been stable for at least the past 6 million years.

The sequence of the human Y chromosome showed that not only has the human Y avoided destruction, but it is also undergoing growth and innovation in gene content. The rest of the human Y chromosome is composed of two sequence classes, X-transposed and ampliconic, many of whose genes have been added to the Y chromosome since it began to diverge from the X (Skaletsky et al. 2003). After the divergence of humans and chimpanzees, a transposition event restored a block of two-single copy X-transposed genes to the human Y chromosome (Skaletsky et al. 2003). Ampliconic sequences form

highly identical (>99.9% nucleotide identity) tandem arrays and inverted repeats that could only be resolved by BAC-based finishing strategies. The largest was a nearly perfect palindrome almost three megabases across (Kuroda-Kawaguchi et al. 2001; Skaletsky et al. 2003). The ampliconic portion of the Y chromosome contains nine multi-copy gene families, totaling approximately 60 transcription units (Skaletsky et al. 2003). Two gene families are survivors of Y chromosome decay that have become amplified, while others appear to have moved to the Y chromosome from autosomes (Saxena et al. 1996; Lahn and Page 1999b; Skaletsky et al. 2003). All of these genes are expressed in the testis (Skaletsky et al. 2003), and deletions in these sequences are the most common known genetic cause of spermatogenic failure in humans (Kuroda-Kawaguchi et al. 2001; Repping et al. 2002; Repping et al. 2003). Muller's theory did not predict the existence of this crucial part of the Y chromosome.

Further characterization of mammalian Y chromosomes demonstrated that ampliconic sequences represent a major exception to Muller's theory. The high nucleotide identity between the genes in palindromes on the human Y chromosome could be interpreted as evidence that the ampliconic sequences evolved relatively recently in human evolution, within the last 100,000 years. However, Rozen and colleagues used comparative sequencing in great apes to show that at least six of the eight human Y chromosome palindromes predate the divergence of chimpanzees and humans over six million years ago (Rozen et al. 2003). To explain this result, they hypothesized that the arms of these palindromes must engage in gene conversion, driving the paired arms to evolve in concert. They confirmed this by surveying the diversity of human Y chromosomes to capture instances of gene conversion within the human lineage (Rozen

et al. 2003). Muller and others had assumed that the Y chromosome could not engage in recombination and would inevitably decay, but gene conversion allows for productive recombination between palindrome arms as though they were two alleles on homologous autosomes (Rozen et al. 2003; Skaletsky et al. 2003). This has allowed the ampliconic genes of the Y chromosomes to survive and expand during primate evolution while many single-copy genes have decayed.

Not only are ampliconic regions capable of recombination, this recombination results in the continual remodeling of Y chromosome sequence. Since ampliconic regions are, by definition, highly identical sequences in tandem or inverted repeats, they are prone to rearrangements that lead to variations in copy number as well as inversions. Repping and colleagues surveyed a panel of diverse Y chromosomes and observed extensive structural variation among human Y chromosomes (Repping et al. 2006). Using the phylogenetic tree of human Y chromosomes, they were able to place a lower bound on the rate of rearrangements; most rearrangements occur on the order of  $10^4$  events per father-to-son transmission (Repping et al. 2006). This high rate of rearrangement causes the structure of ampliconic sequences to evolve much more rapidly than X-degenerate sequences. Hughes and colleagues found that while all ampliconic gene families are conserved between humans and chimpanzees, the chimpanzee ampliconic sequences have experienced many more rearrangements than the X-degenerate sequences, producing a completely different structure (Hughes et al. 2010). Unlike the X-degenerate regions of the Y, the ampliconic regions are a source of continual growth and change.

## ***Innovation on the X Chromosome***

Although the finished sequence of the human Y chromosome led to discoveries that challenged the traditional model of the Y chromosome as a rotting autosome by showing growth and change on the Y chromosome, it also reinforced the view of the X chromosome as unchanging. Muller's theory predicts that the decay of genes on Y chromosomes and W chromosomes constrains X chromosomes and Z chromosomes to stably maintain the gene content of the autosomes from which they evolved. In formulating Ohno's Law, Ohno reasoned that an elaborate chromosome-wide mechanism of dosage compensation would also stabilize the gene content of X chromosomes and Z chromosomes, since genes which translocated to or from an X chromosome or Z chromosome would become misregulated (Ohno 1967). As a result, most genomic studies have treated the X chromosome as a control to show the dramatic changes on the Y chromosome, leaving the question of changes in X chromosome gene content unexamined. Only comparisons among X chromosomes or between X chromosomes and the autosomes of other species can test whether the gene content of the X chromosome has changed through the course of X chromosome evolution.

Initial comparisons of X chromosomes and Z chromosomes among species have generally supported Muller and Ohno's predictions of conservation. Comparative mapping experiments have repeatedly shown that the genes of the X chromosome are well conserved among placental mammals (O'Brien et al. 1993; Carver and Stubbs 1997; Chowdhary et al. 1998; Ross et al. 2005). While mammalian X chromosomes have experienced a number of rearrangements, particularly in the rodent lineage, over the course of mammalian evolution they have sustained fewer interchromosomal

translocations than mammalian autosomes (Carver and Stubbs 1997). Outside of mammals, comparative mapping of Z-linked genes in birds by FISH has indicated that the Z chromosome is conserved among avian species (Nanda et al. 2008). Similar results have been reported in comparisons of several snake species (Matsubara et al. 2006). Because comparative mapping experiments are designed to locate the orthologs of the genes from one species on the chromosomes of another, the results of these experiments are biased towards finding conservation rather than novelty.

In line with the predictions of Ohno's law, pseudoautosomal regions have not been as well-conserved as the rest of the X chromosome. Several genes in the mammalian pseudoautosomal region have moved from the PAR to autosomes in mice (Palmer et al. 1995; Carver and Stubbs 1997). Wilcox and colleagues examined the locations of human X-linked genes in marsupials, and monotremes (Wilcox et al. 1996). They discovered that the genes composing the short arm of the human X were present on the autosomes of monotremes and marsupials (Wilcox et al. 1996). This gene traffic to and from the mammalian X chromosome seems like a violation of Ohno's law, but is actually in accord with Ohno's predictions. The region added to the X in eutherian mammals falls into the three most recent strata of the human sex chromosomes; when it translocated to the ancestral eutherian X chromosome, it was added to the pseudoautosomal region, and shared with the Y chromosome. Because pseudoautosomal regions still participate in crossing over, Y-linked gene copies do not decay and the X-linked copies are not subject to dosage compensation. The genes in pseudoautosomal region are free to move between autosomes and the sex chromosomes until they are

locked in by an event that expands the region of suppressed recombination between the sex chromosomes.

Even outside of the pseudoautosomal regions, the gene content of the mammalian X chromosome is not completely stable. Genomic data from human and mouse have allowed researchers to systematically identify gene movement to and from the mammalian X chromosome. Emerson and colleagues found that the mouse and human X chromosomes have both generated and received an excess of genes through retrotransposition (Emerson et al. 2004). By comparing the human and mouse X chromosomes, they found that this process began before humans and mice diverged, and has continued after that divergence in both lineages. Mammalian X chromosomes have also gained genes through the duplication of existing X-linked genes. Warburton and colleagues found that the human X chromosome is enriched for amplicons that contain testis-expressed genes (Warburton et al. 2004). These X chromosome amplicons primarily contain the cancer-testis antigen (CTA) genes. Comparative studies have shown that several CTA gene families expanded in the primate lineage (De Backer et al. 1999; Aradhya et al. 2001; Kouprina et al. 2004). Other CTA gene families, including the MAGE genes, the most abundant gene family on the human X chromosome, have independently expanded in both rodent and primate lineages (Chomez et al. 2001; Chen et al. 2003; Birtle et al. 2005; Ross et al. 2005). Mueller and colleagues found that the mouse X chromosome contained 33 multi-copy gene families, which, like human CTA genes, are expressed in the testis (Mueller et al. 2008). These multi-copy families were arranged in elaborate ampliconic structures covering 19 megabases of the mouse X chromosome (Mueller et al. 2008). Just as ampliconic gene families are a source of

unexpected novel gene content on mammalian Y chromosomes, they are a source of innovation on X chromosomes as well.

Contrary to the expectations of Muller's theory and Ohno's Law, recent research has shown that the gene content of X chromosomes is not static. On the one hand, conservation of gene content is observed throughout the majority of the mammalian X chromosome, where gene loss from the Y and the subsequent evolution of dosage compensation restrict the flow of genes off of and onto the X. On the other hand, pseudoautosomal regions have been sites of gene movement to and from the X chromosome, the most dramatic being the X added region of placental mammals, which accounts for nearly the entire short arm of the human X chromosome. Even outside of pseudoautosomal regions, retrotransposition and gene duplication have reshaped the gene content of mammalian X chromosomes, creating amplicons of testis-expressed genes parallel to those observed on mammalian Y chromosomes. The changes to X chromosomes are as impressive as their conservation.

### ***The Sequence of the Chicken Sex Chromosomes***

For nearly 100 years the evolution of sex chromosomes has been described in the context of Muller's theory that sex chromosomes evolve from autosomes through the degeneration of the sex-specific chromosome. This hypothesis accounts for nearly all the data that were available before the sequences of sex chromosomes were completed. However Muller's theory does not account for the degree to which gene movement and duplication have shaped the evolution of the mammalian sex chromosomes. The

ampliconic sequences of the human Y chromosome are essential for male fertility, and therefore for the continued survival of the Y chromosome, but they were unanticipated in Muller's theory. Amplicons on X chromosomes represent unexpected innovations in gene content on what was presumed to be an unchanging chromosome.

I sought to understand whether the innovation in gene content represented by amplicons was a general feature of sex chromosome evolution, or a result of forces peculiar either to the mammalian clade or male heterogamety. The Z and W sex chromosomes of the chicken provide a unique opportunity to study the evolution of sex chromosomes in a second lineage with an alternate system of heterogamety. However, because the draft sequence of the chicken genome did not include a complete representation of either the W or the Z chromosome (Hillier 2004), the evolutionary relationship between the sex chromosomes of birds and mammals was still unclear (Nanda et al. 1999; Nanda et al. 2002; Grutzner et al. 2004; Rens et al. 2004; Ezaz et al. 2006; Matsubara et al. 2006; Smith and Voss 2007).

In collaboration with colleagues within the lab and at the Washington University Genome Sequencing Center, I produced the finished sequence of the chicken Z chromosome, presented in Chapter 2. The most distinctive feature of the Z chromosome is the Z amplicon massive tandem array of a 30 kb repeat unit containing testis-expressed genes. The complete sequence of the chicken Z chromosome enabled the first truly comprehensive comparisons between avian and mammalian sex chromosomes, which revealed that each evolved independently from different portions of an ancestral genome, from separate pairs of ordinary autosomes. Additionally, we discovered that during the process of sex chromosome evolution, the chicken Z and human X chromosomes

converged on a set of features that distinguish them from autosomes. Furthermore, the Z and X chromosomes both gained ampliconic sequences containing testis-expressed genes.

The chicken W chromosome represents the first female specific chromosome selected for sequencing, and it is expected to provide insights into sex determination in birds as well as female fertility and sex chromosome evolution. A female was selected for the chicken genome project, but only 0.5% of the chicken W chromosome was assembled by the whole genome shotgun sequencing approach. My colleagues and I extended our sequencing collaboration to produce finished sequence of the W chromosome. Chapter 3 presents insights into the structure of the W chromosome resulting from our efforts. We find that the W chromosome has extensive homology with the Z chromosome indicating a large Z-degenerate region. We found no evidence of high-copy number amplicons with repeat units longer than a BAC clone, but did find several high copy amplicons with repeat units shorter than a single BAC, a similar organization to the Z amplicon.

The avian and mammalian sex chromosomes evolved independently from different autosomes in the common ancestor, but possess an analogous set of features. The presence of ampliconic sequences on the chicken Z and W sex chromosomes is a striking example of convergent evolution that raises questions about the origin and evolution of ampliconic sequences. In Chapter 4, I examine the implications of these findings in the context of theories of sex chromosome evolution.

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## **Chapter 2: Convergent Evolution of Chicken Z and Human X Chromosomes by Expansion and Gene Acquisition**

(Adapted from a manuscript submitted to Nature)

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### Author Contributions:

DWB, HS, WW, SR, RKW, and DCP planned the project. DWB and LB performed BAC mapping. DWB performed RT-PCR analysis. TAG and CK were responsible for finished BAC sequencing. DWB and HS performed comparative sequence analyses. TP performed FISH analysis. ERM performed 454 sequencing. DWB and DCP wrote the paper.

## **Summary**

In birds, as in mammals, one pair of chromosomes differs between the sexes. In birds, males are ZZ and females ZW. In mammals, males are XY and females XX. Like the mammalian XY pair, the avian ZW pair is believed to have evolved from autosomes, with most change occurring in the chromosomes found in only one sex – the W and Y chromosomes (Muller 1914; Ohno 1967; Lahn and Page 1999; Skaletsky et al. 2003; Ross et al. 2005). By contrast, the sex chromosomes found in both sexes – the Z and X chromosomes – are assumed to have diverged little from their autosomal progenitors (Ohno 1967). Here we report findings that overturn this assumption for both the chicken Z and human X chromosomes. The chicken Z chromosome, which we sequenced essentially to completion, is less gene-dense than chicken autosomes but contains a massive tandem array containing hundreds of duplicated genes expressed in testes. A comprehensive comparison of the chicken Z chromosome to the finished sequence of the human X chromosome demonstrates that each evolved independently from different portions of the ancestral genome. Despite this independence, the chicken Z and human X chromosomes share features that distinguish them from autosomes: the acquisition and amplification of testis-expressed genes, as well as a low gene density resulting from an expansion of intergenic regions. These features were not present on the autosomes from which the Z and X chromosomes originated but were instead acquired during the evolution of the Z and X as sex chromosomes. We conclude that the avian Z and mammalian X chromosomes followed convergent evolutionary trajectories, despite their evolving with opposite (female vs. male) systems of heterogamety. More broadly, in birds and mammals, sex chromosome evolution involved not only gene loss in sex-

specific chromosomes, but also marked expansion and gene acquisition in sex chromosomes common to males and females.

## ***Introduction***

A century ago, Herman Muller proposed the first theory of sex chromosome evolution -- that the X and Y chromosomes of *Drosophila* evolved from an ordinary pair of autosomes, and that genes on the Y chromosome had gradually deteriorated while their counterparts on the X were preserved (Muller 1914). In the 1960's, Susumu Ohno applied Muller's theory to the sex chromosomes of vertebrates, arguing that while the sex-specific W and Y chromosomes of birds and mammals had degenerated, the content of the Z and X chromosomes remained intact (Ohno 1967). Four decades on, comparisons of the human X and Y chromosomes have underscored the dramatic evolutionary changes on the Y chromosome, (Lahn and Page 1999; Skaletsky et al. 2003; Ross et al. 2005) but the assumption that the X chromosome has been evolutionarily stable has not been examined systematically.

The evolutionary relationship between the mammalian X chromosome and the avian Z chromosome has been the subject of much speculation, but it also remains unresolved. Ohno conjectured that the X chromosomes of mammals were orthologous to the Z chromosomes of birds (Ohno 1967). However, comparative mapping of 30 Z-linked genes indicated that the chicken Z chromosome was orthologous to human chromosomes 5, 8, 9, and 18, not to the human X chromosome (Nanda et al. 1999; Nanda et al. 2002). These findings were supported by the draft sequence of the chicken genome, but only about one third of the sequence of the Z chromosome was present in the assembly,

leaving open the possibility that regions of orthology between the avian Z and mammalian X had yet to be detected (Hillier 2004). The recent discovery that a subset of the five platypus X chromosomes contain orthologs of genes on the chicken Z chromosome renewed speculation that the avian Z and mammalian X share a common origin (Grutzner et al. 2004; Rens et al. 2004; Ezaz et al. 2006; Smith and Voss 2007). To accommodate the results of comparative gene mapping experiments, some have proposed that the chicken Z and human X were derived from different portions of an ancestral proto sex chromosome which broke apart, leaving Z orthologs autosomal in mammals and X orthologs autosomal in birds (Ezaz et al. 2006; Smith and Voss 2007).

## **Results**

To reconstruct and compare the evolutionary trajectories of the avian Z and mammalian X chromosomes, we have produced the finished sequence of the chicken Z chromosome, the first for any Z chromosome (Supplementary Figures 1-3). The resulting sequence spans roughly 80 megabases (Mb), is complete apart from four gaps, and is accurate to about one nucleotide per megabase. The chicken Z chromosome contains ~1000 genes (Supplementary Table 1). This makes the Z chromosome less gene-dense than any chicken autosome, with 11 genes per megabase, which is less than half of the chicken autosomal average of 25 genes per megabase (Table 1) (Hillier 2004).

Conversely, the density of interspersed repeats is 60% higher in the Z chromosome than in chicken autosomes (Supplementary Figure 1, Table 1). Most of these repeats are LINE elements, whose abundance in the Z chromosome is 70% higher than in autosomes (Supplementary Figure 1, Table 1). As a result, the Z chromosome is structurally distinct from the rest of the chicken genome.

**Table 1a: Comparison of structural features of Z and X with autosomes**

	Chicken Z	Chicken autosomes	Human X	Human autosomes
Genes/Mb	12	25	7	12
Interspersed Repeats	15%	9.4%	56%	45%
LINEs	11%	6.4%	32%	21%
Gene Size (kb)	21	27	49	57

**Table 1b: Comparison of structural features of Z-orthologous and X-orthologous autosomal regions with all autosomes**

	Z-orthologous regions of human chromosomes 5, 9, and 18	Human autosomes	X-orthologous regions of chicken chromosomes 1 and 4	Chicken autosomes
Genes/Mb	10	12	23	25
Interspersed Repeats	48%	45%	8.9%	9.4%
LINEs	23%	21%	6.0%	6.4%

Table 1. Comparison of Z chromosome and X chromosome structural features

The Z chromosome's most prominent feature is a previously unrecognized tandem array of testis-expressed genes, extending over 11 megabases at the distal end of the long arm (Fig. 1, Supplementary Figure 4). This array constitutes nearly 15% of the Z chromosome, one-fifth of all chicken segmental duplications, and 1% of the entire chicken genome (Fig. 1A & B) (Hillier 2004). This sequence was initially reported as heterochromatin (Hori et al. 1996), but we find three genes are present in each repeat unit, and a smaller flanking array contains a fourth (Fig. 1C & D, Supplementary Figure 5, Supplementary Table 2). Together, these four gene families total hundreds of copies and comprise almost one third of the protein-coding genes on the Z chromosome (Fig. 1D, Supplementary Table 2). All four gene families are expressed predominantly in the testis (Fig. 1E). We have termed this massive array of testis-expressed genes the Z amplicon.

With the finished sequence of the Z chromosome in hand, we set out to test Ohno's hypothesis that the avian Z and mammalian X chromosomes are orthologous. To reconstruct and visualize evolutionary relationships between chicken and human chromosomes, we systematically plotted the locations of orthologous gene pairs (Supplementary Fig. 6 & 7). We find that none of the ~1000 genes on the chicken Z chromosome has an ortholog on the human X chromosome (Fig. 2A & B, Supplementary Table 1). The Z chromosome is orthologous only to portions of human autosomes 5, 9, and 18 (Fig. 2A). Contrary to initial reports (Nanda et al. 2002), the Z chromosome is not orthologous to human chromosome 8 (Supplementary Fig. 6). In reciprocal fashion, the human X chromosome is orthologous only to portions of chicken autosomes 1 and 4, not to the Z chromosome (Fig. 2B) (Ross et al. 2005). Based on this comprehensive analysis, we conclude that genes that are sex-linked in chickens are autosomal in humans, and vice

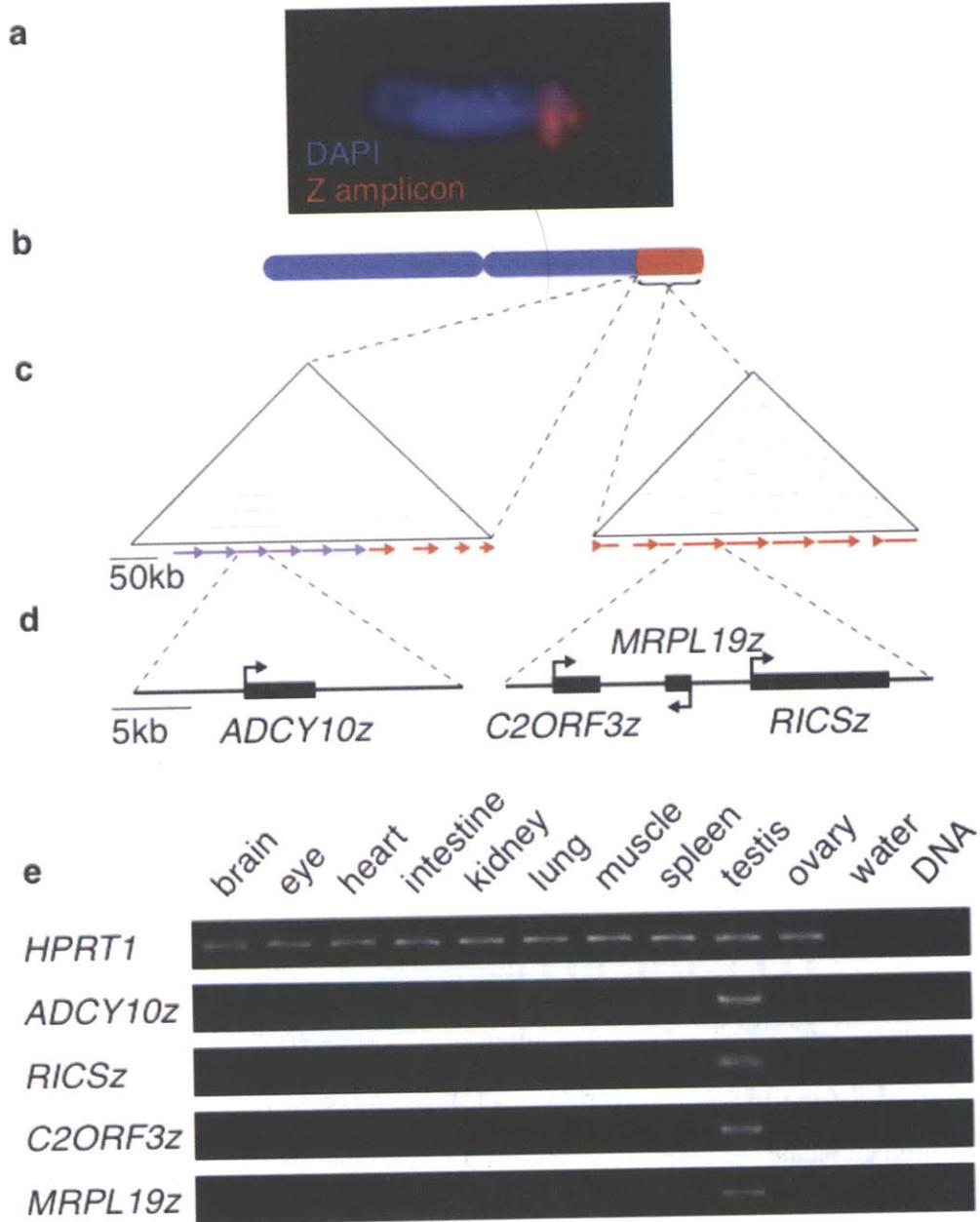
versa, in broad agreement with earlier comparative mapping experiments (Nanda et al. 1999; Nanda et al. 2002).

Although the Z and X chromosomes show no signs of orthology, it is conceivable that they were recruited from different portions of a proto sex chromosome in the common ancestor of birds and mammals (Ezaz et al. 2006). Some investigators have raised this possibility based on comparative gene mapping in the platypus (Ezaz et al. 2006). However, the platypus does not form an outgroup to birds and mammals, and cannot resolve which is the ancestral state: a platypus-like linkage of Z-orthologous genes and X-orthologous genes, or the separation we observe in chicken and human. Others have attempted to resolve this question with comparisons to an outgroup genome that is far from complete (Smith and Voss 2007). Instead, we compared the Z and X chromosomes to the genomes of the four closest out-group species whose genomes are sequenced and assembled. Each species represents a different order of teleost fish, which diverged from land vertebrates over 450 million years ago (Kasahara et al. 2007). After they diverged from birds and mammals, but before they diverged from each other, these fish species experienced a whole genome duplication, complicating the identification of 1:1 orthologs (Kasahara et al. 2007). Nevertheless, we observe that most orthologs of Z and X-linked genes occupy separate portions of each fish genome (Supplementary Fig. 8-11). For example, three-spine stickleback linkage groups 13 and 14 carry the bulk of Z-orthologous genes, while X-orthologous genes mostly reside on stickleback linkage groups 1, 4, 7, and 16 (Fig. 2C). Since we observe that Z-orthologous genes are separated from X-orthologous genes in birds, mammals, and each of these four fish, we conclude that the Z and the X chromosomes have evolved independently from distinct portions of the ancestral vertebrate genome.

## Figure 1: The Z Amplicon

- a. Fluorescence in situ hybridization of Z-amplicon-derived BAC CH261-77N6 (red) to Z chromosome (blue). CH261-77N6 hybridizes to distal Z long arm.
- b. Z amplicon (red) comprises most distal 11 Mb of Z chromosome.
- c. Triangular dot plots each comparing the sequence of a Z-chromosome BAC to itself. Within the plot, each dot represents a perfect match of 50 base pairs. Direct repeats appear as horizontal lines, inverted repeats as vertical lines; scale bar represents 50kb. On left, BAC CH261-73L15 contains small array of six repeats covering 120 kb immediately proximal to Z amplicon. On the right, BAC CH261-137P21, a representative clone from within Z amplicon array. Each 25-30kb repeat unit is ~95% similar to any other, though some units have been disrupted by insertions and deletions.
- d. Genes in repeat units of Z amplicon; scale bar represents 5kb. Each 20kb repeat unit of small array in CH261-73L15 contains one copy of *ADCY10z*. Each 25-30kb repeat unit of Z amplicon contains one copy each of *C2ORF3z*, *MRPL19z*, and *RICSz*.
- e. RT-PCR analysis of Z-amplicon gene expression in adult tissues. *HPRT1* is widely expressed in adult tissues and serves as a positive control for the reverse transcriptase reaction. All Z-amplicon genes are expressed in testis, but not other tissues.

**Figure 1**



Although we rejected the hypothesis that the avian Z and mammalian X chromosomes share a common origin, we discovered that the chicken Z and human X chromosomes share common features. Like the chicken Z chromosome, the human X chromosome has a low gene density; there are only half as many genes per megabase on the X chromosome as on the average human autosome (Fig. 3A, Table 1A) (Ross et al. 2005). Other investigators have observed that low gene density is often associated with increased interspersed repeat content, specifically LINEs (Lander et al. 2001; Ross et al. 2005). We also observe this association on the Z and X chromosomes (Supplementary Fig. 1, Table 1A).

Two scenarios could account for these structural features shared by the chicken Z and human X chromosomes. Either the Z and X chromosomes arose from autosomes pre-adapted for the role of sex chromosomes, or they arose from ordinary autosomes that convergently evolved into specialized sex chromosomes. If the Z and X chromosomes arose from pre-adapted autosomes, then the features shared by the Z and X chromosomes should also be found on the orthologous autosomal regions. We tested this theory by comparing each sex chromosome to the orthologous autosomes in the other species (Fig. 2, Table 1, Supplementary Tables 3 & 4). As a group, the autosomal regions that correspond to the Z and the X chromosomes are typical of their respective genomes (Table 1B). Although these regions show a slight deficit in gene density relative to the average within their respective genomes, the difference is too small to account for the extremely low gene density of the Z and X chromosomes. Because the orthologous autosomes in the other species do not share the structural features common to the Z and X chromosomes, we infer that these convergent features arose during the process of sex chromosome evolution, and not before.

Figure 2: Independent origin of chicken Z and human X chromosomes

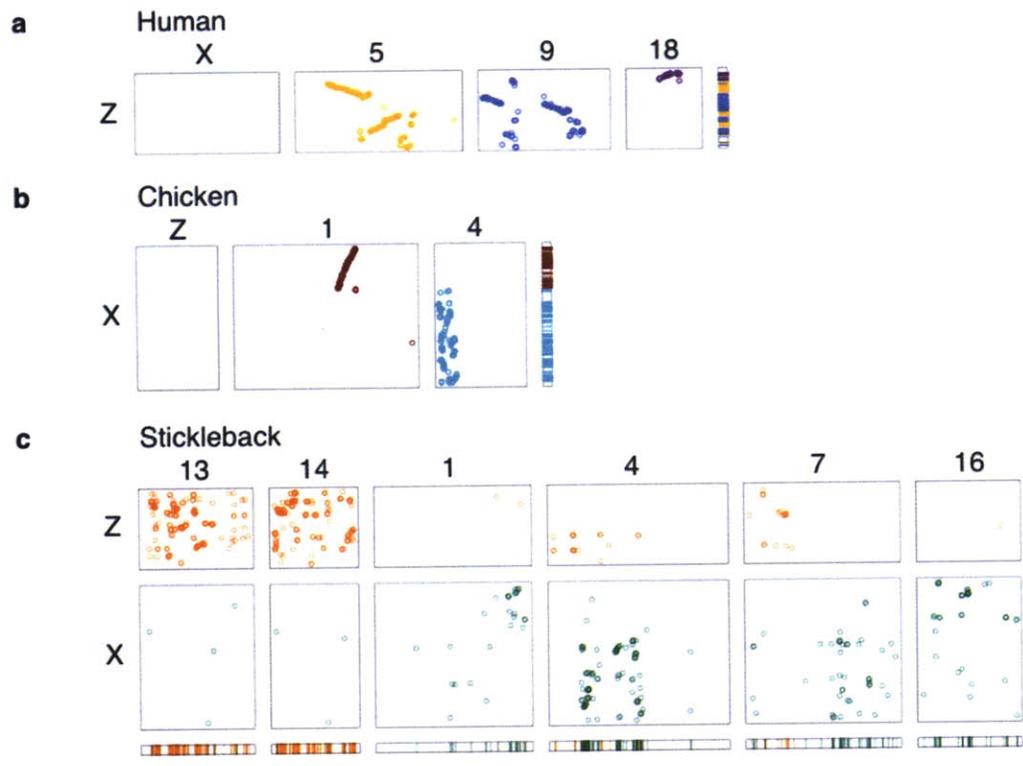
Rectangular dot plots show chromosomal locations of Z-orthologous or X-orthologous genes in other species.

a. Chicken Z chromosome versus selected human chromosomes. Chicken Z chromosome is not orthologous to human X, but is orthologous to portions of human autosomes 5 (yellow), 9 (blue), and 18 (purple). At right: three-color projection of dot plots onto a unified schematic of chicken Z, showing that orthology to human chromosomes 5, 9, and 18 accounts for most of Z chromosome, with exception of Z amplicon on distal long arm.

b. Human X chromosome versus selected chicken chromosomes. Human X chromosome is not orthologous to chicken Z, but is orthologous to portions of chicken autosomes 1 (red) and 4 (cyan). At right: two-color projection of dot plots onto unified schematic of human X, showing that orthology to chicken chromosomes 1 and 4 spans X (colored bar).

c. Chicken Z chromosome (orange) and human X chromosome (green) versus selected stickleback chromosomes. Chicken Z and human X chromosome orthologs occupy separate and distinct locations within stickleback genome. Chicken Z chromosome orthologs are present on stickleback chromosomes 13 and 14, while human X chromosome orthologs are present on stickleback chromosomes 1, 4, 7, and 16.

**Figure 2**



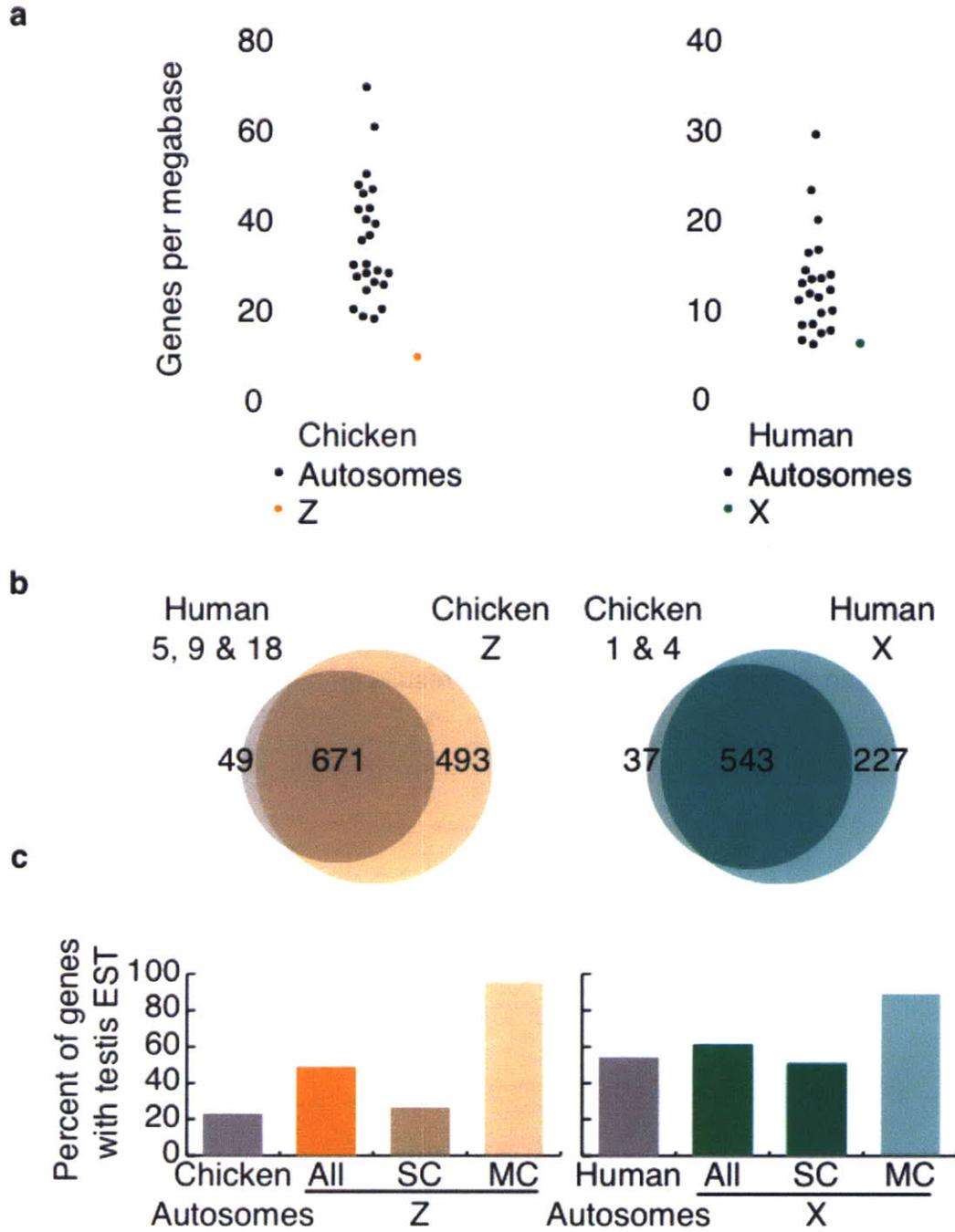
To explain the paucity of genes on the Z and X chromosomes, we looked for evidence that both chromosomes lost genes during sex chromosome evolution. Instead, we observed that both the Z and the X chromosomes gained protein-coding genes. We compared the gene content of the Z and the X chromosomes to the orthologous autosomes from the other species as a surrogate for the ancestral gene content of the Z and X chromosomes (Fig. 2, Fig. 3B, Table 1, Supplementary Tables 3 & 4). We found that only a few dozen genes present on the orthologous autosomes are absent from the Z and X chromosomes (Fig. 3B). In contrast, hundreds of genes present on the Z and X chromosomes are absent from the orthologous autosomes (Fig. 3B). We conclude that both the Z and X chromosomes experienced substantial net gene gain.

The majority of genes gained by the Z and X chromosomes are members of multi-copy families (Fig. 3B, Supplementary Tables 3 & 4). On the chicken Z chromosome, these are the genes of the Z amplicon. The human X chromosome has gained thirteen different cancer-testis antigen gene families (Ross et al. 2005). All of the Z amplicon genes are expressed predominantly in testis (Fig. 1E), as are the cancer-testis antigen genes of the human X chromosome (Scanlan et al. 2004). The addition of these multi-copy gene families has biased the Z and X chromosomes toward testis-expressed genes (Fig. 3C). Both the Z and the X chromosomes have an elevated proportion of genes expressed in testis tissue compared to autosomes as measured by the number of genes with a testis EST in Unigene (Wheeler et al. 2005) datasets (Fig. 3C). However, when multi-copy genes are removed, the remaining conserved single-copy genes show no bias (Fig. 3C). Others have observed a bias towards sex and reproduction related genes on the human X chromosome (Saifi and Chandra 1999). Our comparison suggests that the Z chromosome shares this bias. This bias was not a feature of the autosomes that gave rise to the sex chromosomes of birds and mammals; it arose by gene acquisition and amplification during sex chromosome evolution in each lineage.

Figure 3. Convergent gene gain on the chicken Z and human X chromosomes.

- a. Gene density of Z and X chromosomes compared to autosomes. Both are unusually gene poor, with about half the gene density of a typical autosome.
- b. Venn diagrams comparing gene content of chicken Z and human X chromosomes to orthologous autosomes. Most genes on orthologous autosomes remain on the sex chromosomes; few have been lost. Both chicken Z and human X gained hundreds of genes not present on orthologous autosomes.
- c. Percentage of protein coding genes with testis ESTs in Unigene. Left panel: Compared to chicken autosomes, Z chromosome is enriched for testis-expressed genes. Single-copy Z chromosome genes (SC) show no enrichment for testis ESTs compared to autosomal gene, but nearly all multi-copy (MC) genes are expressed in testis. Right panel: Similar results on human X chromosome.

**Figure 3**



In light of this convergent gene gain, we looked for factors other than gene loss that could account for the low gene density of the Z and X chromosomes. Low gene density could result from Z-linked and X-linked genes that are larger than those on autosomes, resulting in fewer genes in the same amount of sequence. However, we find that genes on both the Z and X chromosomes are smaller, on average, than autosomal genes (Table 1A). The only remaining explanation for the unusually low gene density of the Z and X chromosomes is a massive expansion of non-coding intergenic sequences which spread the genes further apart. We estimate that intergenic regions were expanded by about 40 Mb in the case of the Z chromosome and 80 Mb in the case of the X chromosome – nearly half the present lengths of these chromosomes. No single class of non-coding sequence can account for this change, but the two-fold enrichment for LINES on both the Z and X chromosomes (Table 1A) suggests that the doubling of intergenic sequence may have been driven by recurrent insertion and divergence of transposable elements. In mammalian genomes, high LINE density is associated with reduced rates of crossing over (Wichman et al. 1992), and suppression of crossing over is a key step in the evolution of differentiated sex chromosomes. The Z and X chromosomes, however, exhibit a higher density of LINE elements than autosomal regions with similarly low rates of crossing over (Supplementary Figure 12, Supplementary Note 1).

## ***Discussion***

Our comparison of the finished sequences of the chicken Z and human X chromosomes reveals that each evolved independently from different portions of the ancestral genome, from separate pairs of ordinary autosomes. In each lineage, different portions of the ancestral genome were substantially remodelled to become specialized sex chromosomes. The Z and X chromosomes have converged on a set of structural features that distinguish them from autosomes: a high density of interspersed repeats, and long intergenic distances resulting in low gene density. Furthermore, the Z and X chromosomes have both gained multi-copy gene families that are expressed in testis, biasing the gene content of both chromosomes toward male reproductive functions.

This convergent specialization of Z and X chromosomes for male reproduction is surprising given that the Z chromosome evolved with female heterogamety and the X chromosome evolved in opposite circumstances, with male heterogamety. One might have anticipated that the Z and X chromosome would exhibit opposing rather than convergent biases in gene content. While strong selective pressures drive the evolution of genes related to male reproduction (Wyckoff et al. 2000; Swanson and Vacquier 2002), these selective pressures influence autosomes as well as sex chromosomes. But, unlike autosomes, sex chromosomes are uniquely susceptible to selection for traits that benefit one sex more than the other (Rice 1984). Our results suggest that, in amniotes, selective pressures to preserve or enhance male reproductive functions have trumped the differences between ZW and XY systems to produce the changes in gene content that we observe.

For nearly 100 years, it has been thought that sex chromosome evolution involved dramatic modification of sex-specific chromosomes but only modest change in

chromosomes shared by the sexes (Muller 1914; Ohno 1967). In the past decade, this understanding was reinforced by comprehensive molecular comparisons between the human X and Y chromosomes (Lahn and Page 1999; Skaletsky et al. 2003; Ross et al. 2005), and by more limited comparison of sex chromosome pairs in other plants and animals (Handley et al. 2004; Filatov 2005; Nicolas et al. 2005). Without exception, these X-Y or Z-W comparisons revealed extensive genetic decay in the sex-specific Y or W chromosome, while assuming that Z and X chromosomes faithfully represent their autosomal progenitors. By contrast, the Z to autosome and X to autosome comparisons in this study reveal that the chicken Z chromosome and the human X chromosome have undergone dramatic evolutionary changes that were not anticipated and that previous studies could not detect. In birds and mammals, sex chromosome evolution was not limited to gene loss from sex-specific chromosomes, but extended to expansion and gene acquisition on the chromosomes shared between the sexes.

## ***Methods***

**Mapping and sequencing.** All Z-chromosome BAC and fosmid clones selected for sequencing (Supplementary Table 5) were from six libraries (CH261, TAM31, TAM32, TAM33, J\_AD, and J\_AE) generated from the same female of the inbred line of red jungle fowl (UCD001) as was used for the whole genome shotgun sequence of the chicken (Hillier 2004; Wallis et al. 2004). As a result, the Z chromosome we obtained is that of a single haplotype. We made use of publicly available BAC fingerprint maps and BAC-end sequences as a source of mapping information and markers. Individual BAC fingerprint contigs were ordered and oriented by radiation hybrid mapping using ChickRH6 (Morisson et al. 2002). Unfortunately, no cell line is available from any bird of the UCD001 line, so we used chicken embryonic fibroblasts derived from White

Leghorn (available from Charles River Labs) for FISH experiments to provide independent confirmation of the order and orientation of the sequence (Supplemental Figures 9 – 11).

**Chromosomal FISH.** One- or two-colour FISH to chicken chromosomes was performed as previously described (Saxena et al. 2000).

**Z chromosome sequence similarity.** Analyses of intrachromosomal similarity were performed using BLAT (Kent 2002) to compare all 5-kb sequence segments, in 1-kb steps, to the entire remainder of the Z chromosome sequence. For each segment, we recorded the highest percent identity to a non-overlapping segment.

**Genes and transcription units.** We identified potential transcripts in three ways:

(1) We used human (Ensembl version 52, NCBI 36) (Hubbard et al. 2009) as the informant genome and chicken EST sequences as additional evidence to identify potential transcripts on the repeat-masked chicken Z chromosome, using Twinscan (Korf et al. 2001; Flicek et al. 2003). We compared the output with the Ensembl 52 annotations for chicken and human to identify previously unrecognized genes in our prediction. We considered previously unrecognized chicken genes valid if they were spliced in chicken and conserved to human.

(2) For the novel genes in the Z-amplicon region we relied on BLAST (Altschul et al. 1990) matches to cDNA sequences to identify copies of *ADCY10z*, *C2ORF3z*, *MRPL19z*, and *RICSz* that showed evidence of splicing. We then tested for transcription by RT-PCR across a panel of adult tissues.

(3) We used a combination of methods to locate non-coding transcripts on the chicken Z. We used tRNAscan-SE (Lowe and Eddy 1997) for tRNA predictions. For other non-coding RNAs, we used BLAST to compare our sequence with those of known

chicken non-coding RNAs in GenBank (Benson et al. 2009) and mirBase (Griffiths-Jones et al. 2008)

**Interspersed repeats.** We electronically identified interspersed repeats with RepeatMasker (Smit et al.).

**Triangular dot plots.** We performed dot-plot analysis using custom Perl script (Kuroda-Kawaguchi et al. 2001).

**Expressed Sequence Tags.** We used EST sequences from the BBSRC ChickEST database (Boardman et al. 2002), supplemented by our own 454 EST runs on ovary and testis (SRA# SRP000097).

**Z amplicon size.** To estimate the amount of Z ampliconic sequence missing from our assembly, we compared the average depth of chicken fosmid end sequences on the single copy region of the Z to the depth in the ampliconic region, reasoning that the excess depth in the ampliconic region could be attributed to sequence we could not obtain because the similarity between individual repeat units precluded either cloning or the assembly of BACs. We used BLAT to map 23977 fosmid end sequences to 72.2 Mb of single-copy Z sequence, giving an average of 331 ends per megabase. In the 5.6 Mb of the Z amplicon we found 3787 fosmid end hits, for 666 ends per megabase, roughly a two-fold enrichment. Therefore, we concluded that the Z amplicon comprises roughly 11.4 Mb.

**RT-PCR.** We used chicken total RNA (Zyagen) and the RETROscript Kit (Ambion). We amplified 1 µl of the RT product through 30 cycles of PCR with an annealing temperature of 55°C.

Primers are as follows:

*HPRT1* (116 bp product):

F: GGATTTGAAGTGCCAGACAAA

R: GCTTTGTACTTCTGCTTCCCC

*ADCY10z* (145 bp product):

F: GTTTGTTCAGGTCTCTGTGGGA

R: GTAGAGGTCCTCGAGCAAGGC

*RICSz* (144 bp product):

F: GACAGAGATCAGGGACATGGA

R: AAACAGGAACACCAACTGCAT

*C2ORF3z* (131 bp product):

F: TGTTCAAAATTCCAAGGCAGA

R: AGGTAACGATTCAGCAGCTTG

*MRPL19z* (242 and 60 bp products):

F: CAAGCAGAAGCAGAGAGAGGA

R: TGACCATGGTTGAGGTTTCA

**Orthologous chromosomes.** To identify orthologous chromosomes in inter-species comparisons, we relied on a gene-based approach. We conducted reciprocal BLAT searches using Ensembl 52 peptide sequence databases from *Gallus gallus*, *Homo sapiens*, *Danio rerio*, *Gasterosteus aculeatus*, *Oryzias latipes*, and *Tetraodon*

*nigroviridis*. Considering only the longest peptide sequences for each Ensembl gene, we flagged best reciprocal BLAT hits between two genomes as orthologous genes. We constructed the inter-species dot plots using the chromosomal coordinates extracted from Ensembl (or in the case of the Z chromosome, the coordinates from this study).

Individual dots represent a pair of orthologous genes.

**Gene gain and loss.** We relied on the assignments of chicken and human orthologs in the Ensembl database (Ensembl version 52). However, we manually reviewed genes on chicken chromosomes 1, 4, and Z as well as human chromosomes 5, 9, 18, and X which did not have simple 1:1 orthologs in the Ensembl database to find pairs of orthologous genes that were missing from the database or not properly identified.

To study gene gain and loss on the chicken Z chromosome, we divided genes into several categories on the basis of their location in chickens, humans, and outgroup species:

(A) Z-linked genes with orthologs on human autosomes 5, 9, and 18

(B i) Z-linked genes present only in birds, but not outgroups or human

(B ii) Z-linked genes present in birds and outgroups but not human

(B iii a) Z-linked genes with human orthologs not on autosomes 5, 9, 18 that were not syntenic with neighbors in outgroups or human

(B iii b) Z-linked genes with human orthologs not on autosomes 5, 9, 18 that were syntenic with neighbors in outgroups

(C i) Genes on human autosomes 5, 9, and 18 with orthologs only in mammals, not in outgroups or chicken

(C ii) Genes on human autosomes 5, 9, and 18 with orthologs only in mammals and outgroups, but not chicken

(C iii a) Genes on human autosomes 5, 9, and 18 with chicken orthologs not on the Z chromosome that were not syntenic with neighbors in outgroups or chicken

(C iii b) Genes on human autosomes 5, 9, and 18 with chicken orthologs not on the Z chromosome that were syntenic with neighbors in outgroups

Category (A) was counted as shared, Categories (B i) and (B iii a) were counted as gains to the Z, while Categories (C ii) and (C iii b) were counted as losses from the Z. Category (B ii) and (B iii b) (representing losses from the human autosomes) and categories (C i and C iii a) (representing gains to the human autosomes) were excluded. We carried out an analogous analysis on the human X chromosome and chicken autosomes 1 and 4.

**Biased gene content.** We searched for Unigene (Wheeler et al. 2005) EST clusters from normal chicken and human testis that corresponded with chicken and human genes to identify genes expressed in the testis. We determined the percentage of genes with at least one testis EST for each category (Autosomes, Z or X chromosome total, Z or X chromosome single-copy, Z or X chromosome multi-copy). Multi-copy genes on the Z chromosome include those of the Z amplicon, while multi-copy genes on the X chromosome include those identified as cancer-testis antigen genes in the finished sequence of the X chromosome (Ross et al. 2005).

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## Supplemental Data

### Figures

- Supplementary Figure 1.** Annotated sequence of the chicken Z chromosome.
- Supplementary Figure 2.** Order and orientation of Z chromosome contigs by DNA-FISH
- Supplementary Figure 3.** Location of the Z chromosome centromere
- Supplementary Figure 4.** Z amplicon FISH
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- Supplementary Figure 6.** Dot plots of chicken Z versus all human chromosomes
- Supplementary Figure 7.** Dot plots of human X versus all chicken chromosomes
- Supplementary Figure 8.** Dot plots of chicken Z and human X versus all zebrafish chromosomes
- Supplementary Figure 9.** Dot plots of chicken Z and human X versus all stickleback chromosomes
- Supplementary Figure 10.** Dot plots of chicken Z and human X versus all medaka chromosomes
- Supplementary Figure 11.** Dot plots of chicken Z and human X versus all pufferfish chromosomes
- Supplementary Figure 12.** Recombination, G+C content, and LINE density

Twelve supplementary figures. Figure 1 spans 24 pages. Figures 2-12 are 1 page each. Figure 1 shows the annotated sequence of the chicken Z chromosome. Figure 2 shows the order and orientation of Z chromosome sequence contigs. Figure 3 describes the location of the Z chromosome centromere. Figure 4 demonstrates the specificity of the Z amplicon FISH probe used in main text Figure 1. Figure 5 is a triangular dot plot showing intrachromosomal similarity within the Z amplicon region. Figures 6-11 are between-species dot plots showing the orthology relationships between chromosomes. Figure 12 shows the relationship between recombination, G+C content, and LINE density.

### Tables

- Supplementary Table 1.** Chicken Z chromosome predicted genes and human orthologs
- Supplementary Table 2.** Chicken Z amplicon predicted genes and sequences
- Supplementary Table 3.** Chicken Z gene gain and loss
- Supplementary Table 4.** Human X gene gain and loss
- Supplementary Table 5:** BAC and fosmid clone accession numbers and position in assembly

Five supplementary tables. Table 1, a spreadsheet containing a list of all predicted Z genes along with their human orthologs, spans 20 pages. Table 2, spreadsheet containing a list of predicted Z amplicon genes along with their predicted transcript sequences, spans 9 pages. Table 3, a spreadsheet showing the classification of chicken Z genes into gain and loss categories as described in methods, spans 14 pages. Table 4, a spreadsheet showing the classification of human X genes into gain and loss categories as described in methods, spans 11 pages. Table 5, spreadsheet listing the GenBank accession numbers and positions of BAC and fosmid clones in the chicken Z chromosome sequence assembly, spans 8 pages.

### Note

**Supplementary Note 1:** Additional information for Supplementary Figure 12

One supplementary note. Note 1 occupies a 2 pages.

### **Supplementary Figure 1: Annotated Sequence of the chicken Z chromosome.**

Chart of the Z chromosome sequence showing protein-coding genes, CpG islands, non-coding transcripts, intrachromosomal similarity, G+C content, interspersed repeats, and sequenced clones. All sequence features, BACs, and fosmids are drawn to scale. (a) The positions of all predicted protein-coding genes of the chicken Z chromosome are shown in black. Plus (+) strand above, minus (-) strand below. CpG islands, as predicted by cpgplot, are shown in grey. (b) The positions of non-coding transcripts of the chicken Z chromosome are shown in black. Plus (+) strand above, minus (-) strand below. (c) Intrachromosomal similarity is plotted in windows of 5kb every 1kb, using the percent identity of the best blast hit from a repeat-masked non-overlapping window. All values greater than 90% are shown. (d) G+C content is plotted in sliding windows of 10kb every 5kb. (e) Interspersed repeat content calculated from the RepeatMasker .out file. Repeat content is expressed as percentage of nucleotides in windows of 100kb every 5 kb. DNA transposons are plotted in red, LINE elements are plotted in green, Endogenous Retroviruses (ERV) are plotted in blue. (f) BAC and fosmid clones from the finished sequence of the chicken Z chromosome. 5 physical gaps in the clone map are indicated by gaps in clone coverage. The remaining gaps are spanned by clones (shown in grey) whose sequences were not finished at the time of sequence assembly (June 2009).

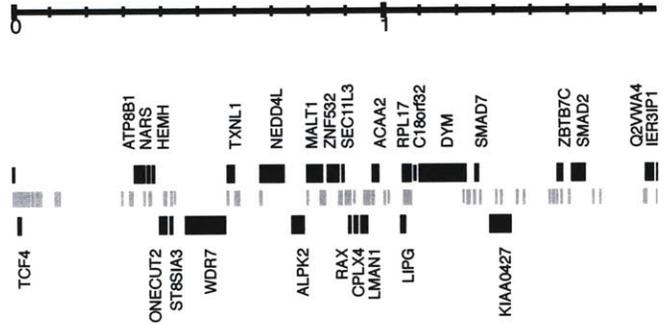
Points of interest along the chicken Z chromosome sequence include:

The Male Hypermethylated Region (MHM), located at 26Mb. This region is especially high in endogenous retroviruses (ERVs) and G+C content. The tandem array of the non-coding MHM transcript is located in this region.

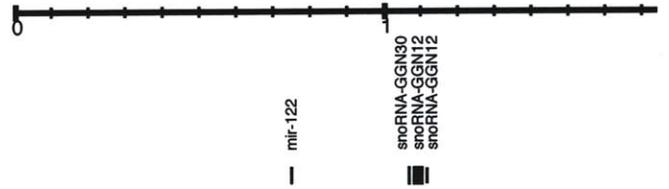
The Z amplicon, located from 73 Mb to the end of the chromosome. This region of high intrachromosomal similarity is low in interspersed repeats and elevated in G+C content. The Z amplicon is interrupted by two single-copy islands at 81 Mb and 83 Mb, which contain protein coding genes with orthologs on human autosomes 5 and 9.

Scale (1Mb)

**a** Coding genes +  
 CpG islands  
 Coding genes -



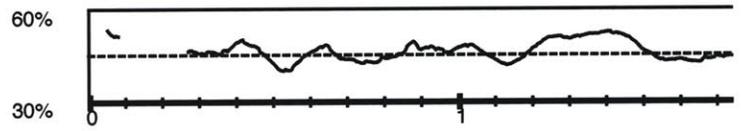
**b** Non-coding transcripts +  
 Non-coding transcripts -



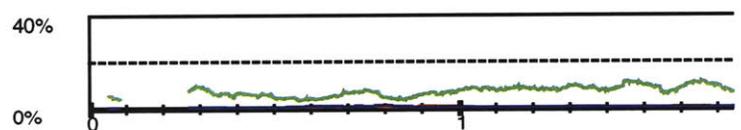
**c** Intrachromosomal similarity (% identity)



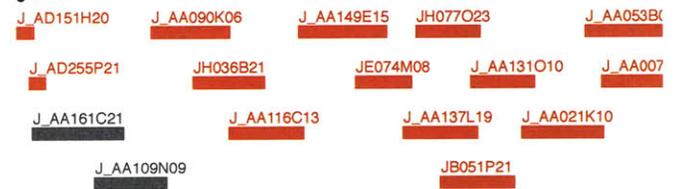
**d** G+C content



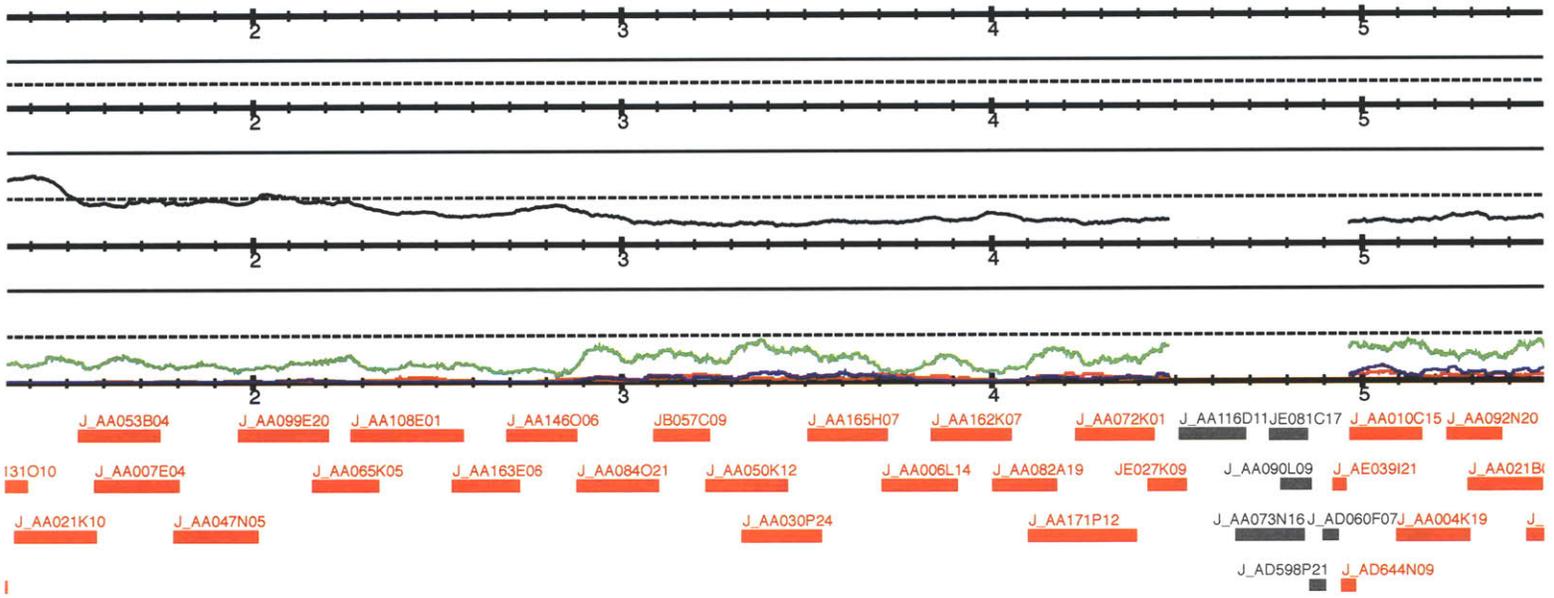
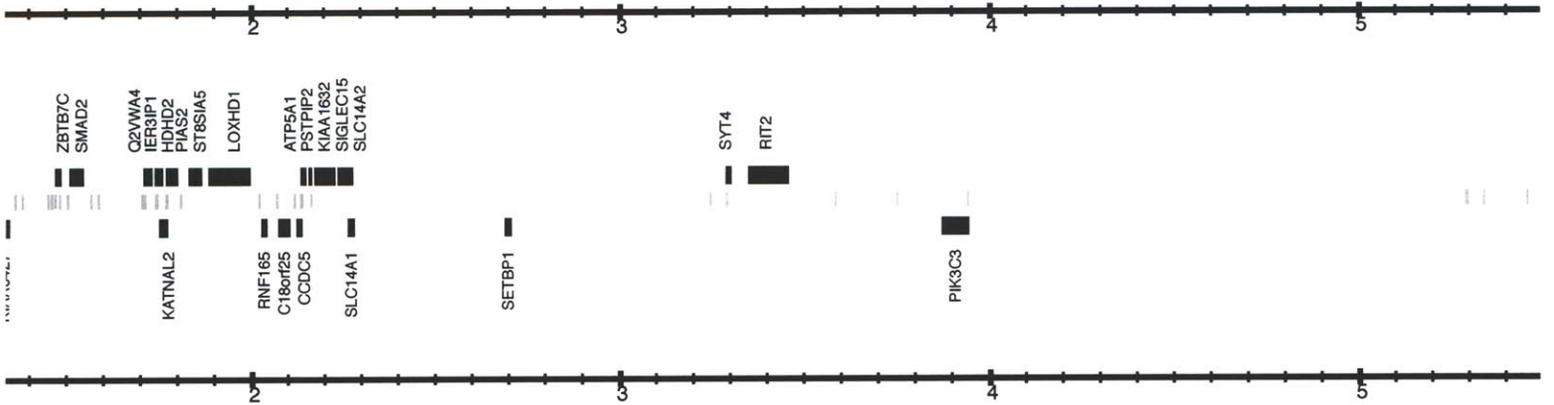
**e** DNA/LINE/ERV densities

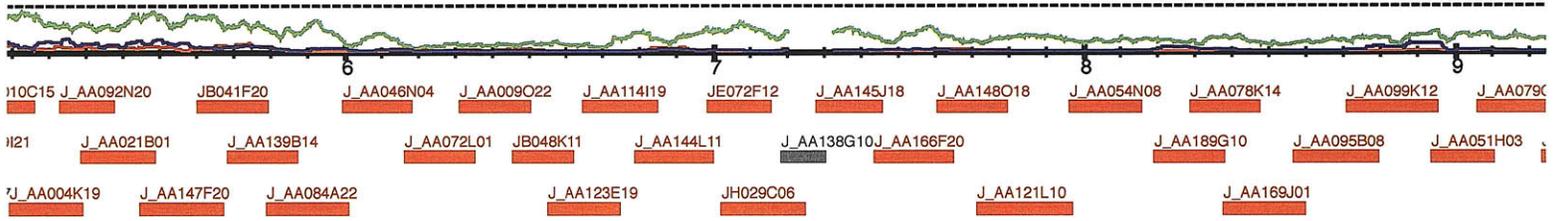
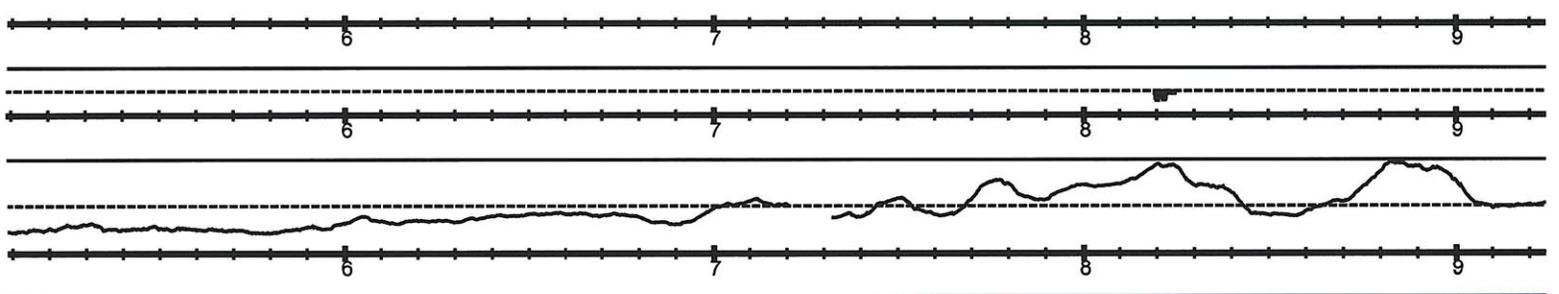
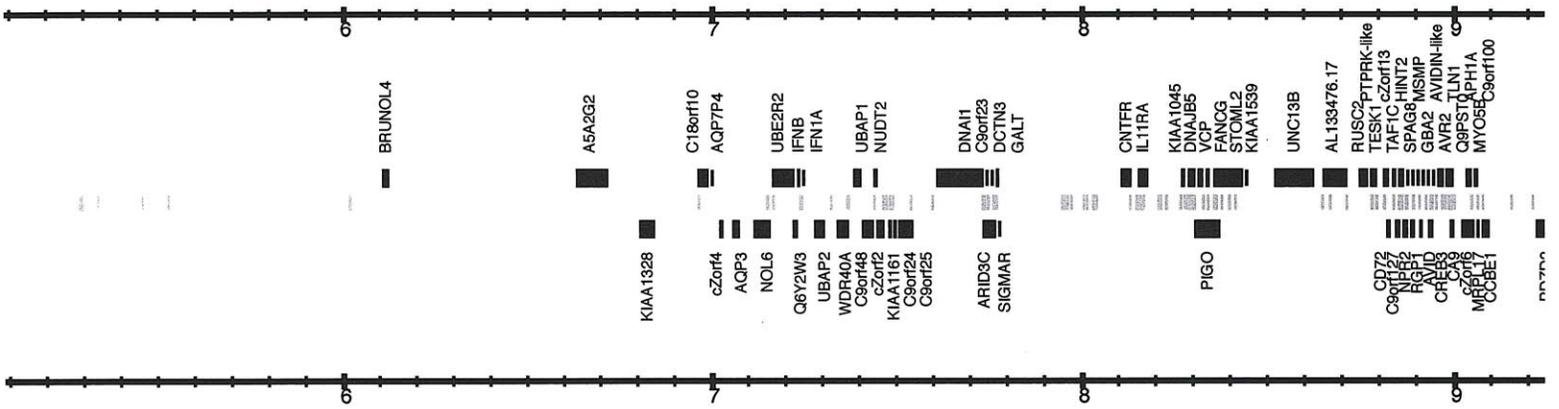


**f** Sequenced BACs and Fosmids

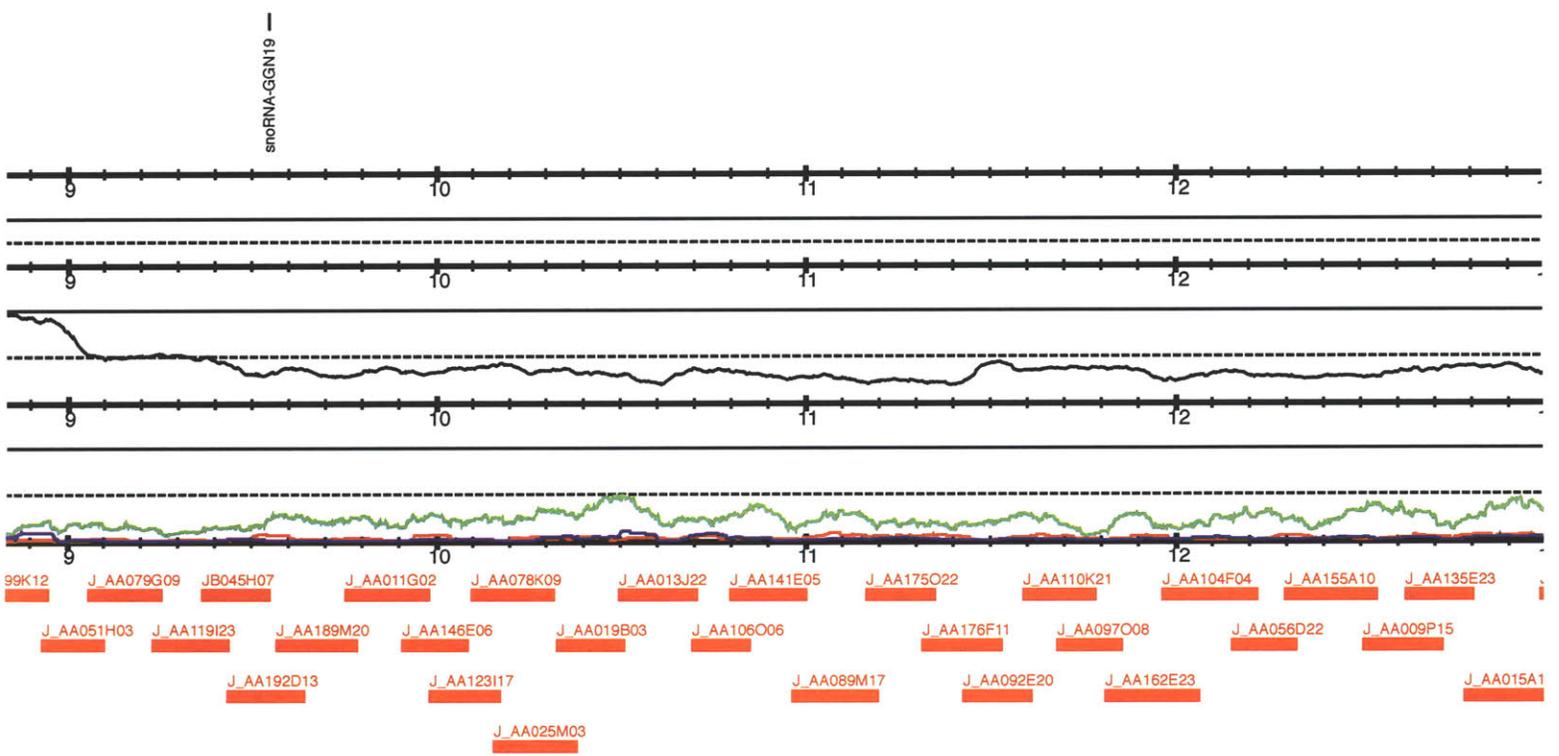
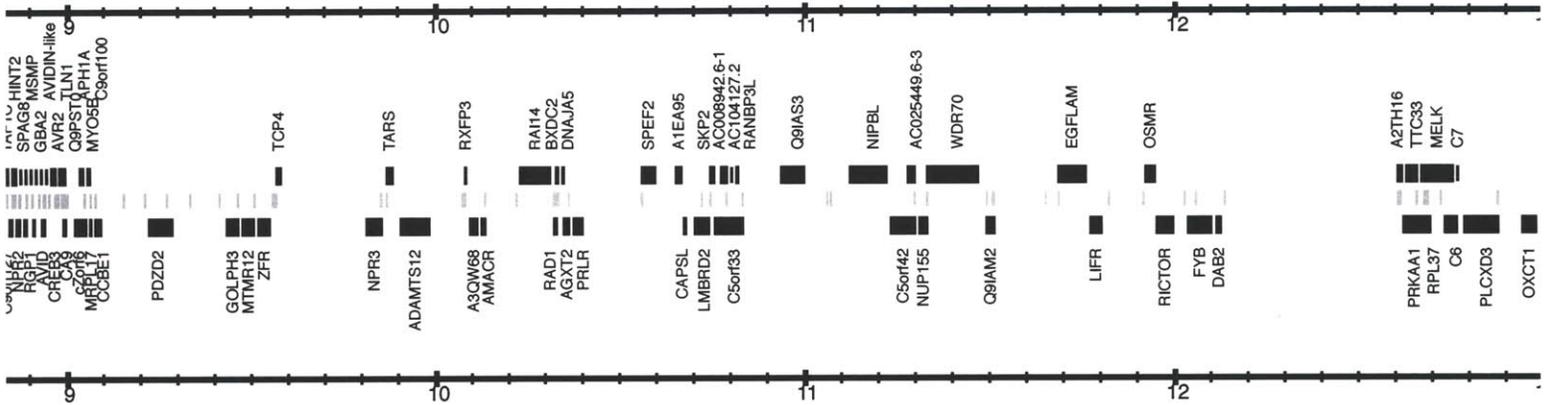


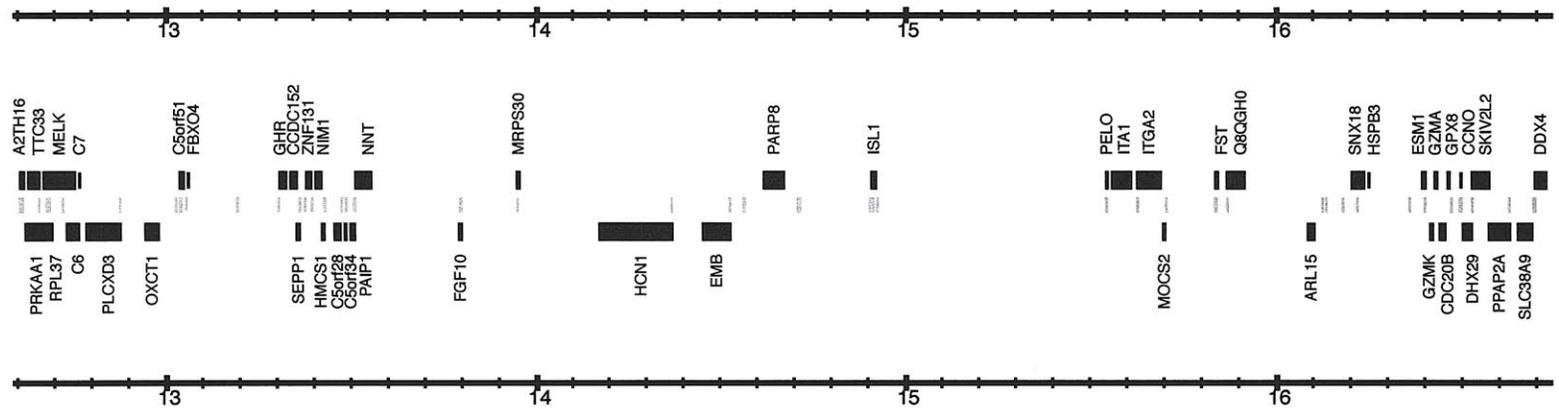
Supplementary Figure 1: Annotated Sequence of the Chicken Z Chromosome



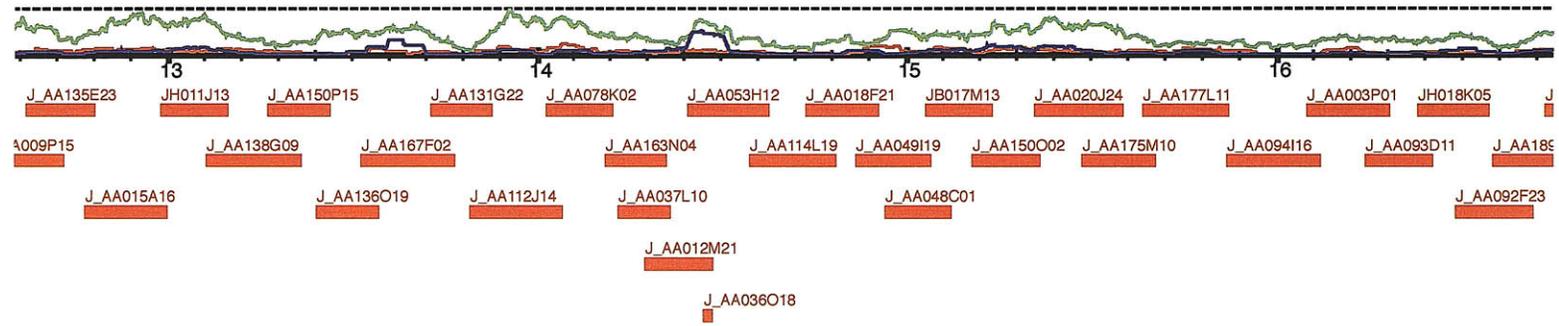
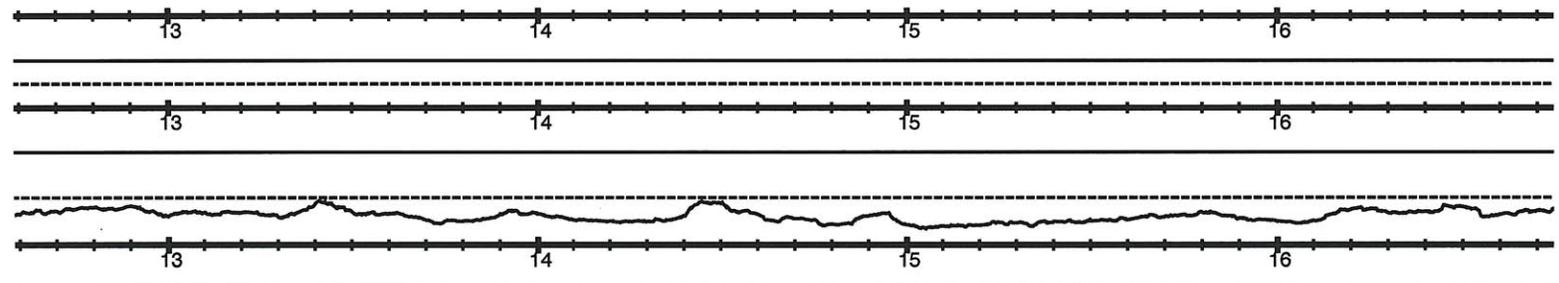


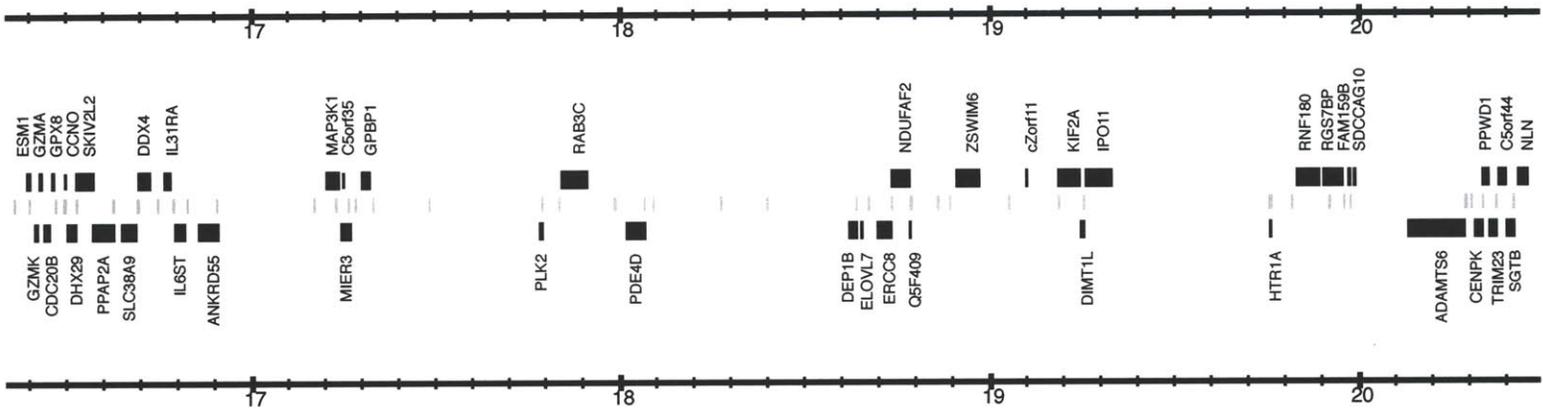
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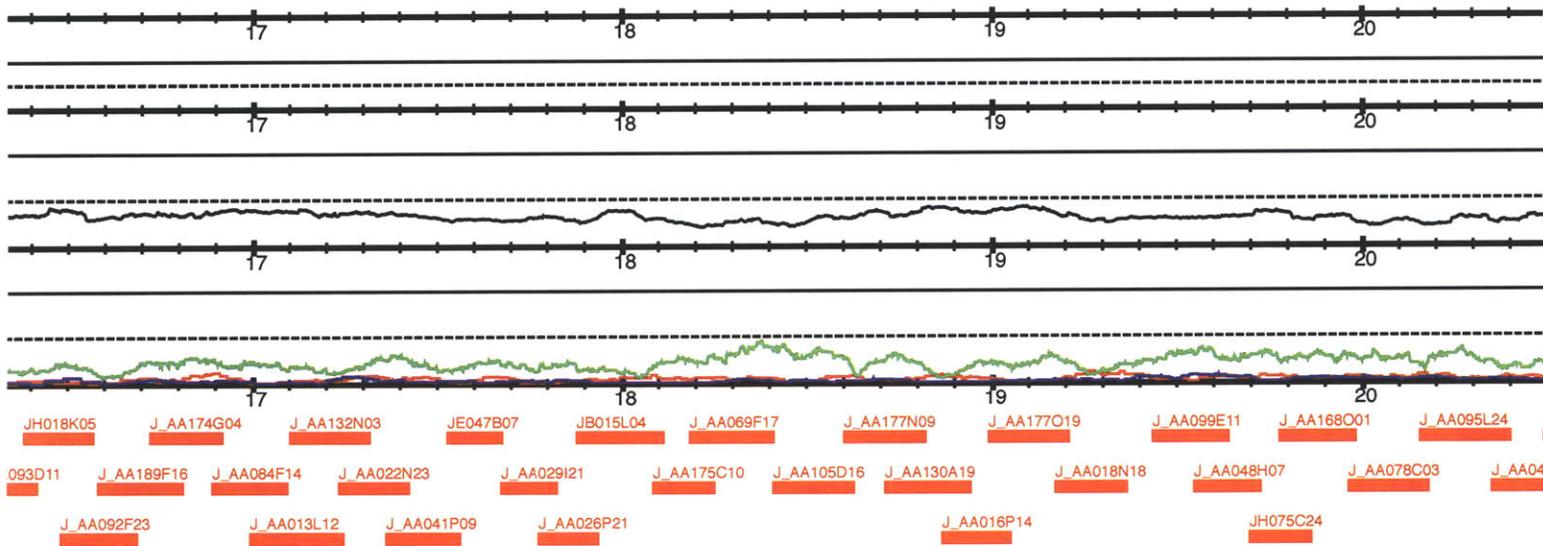
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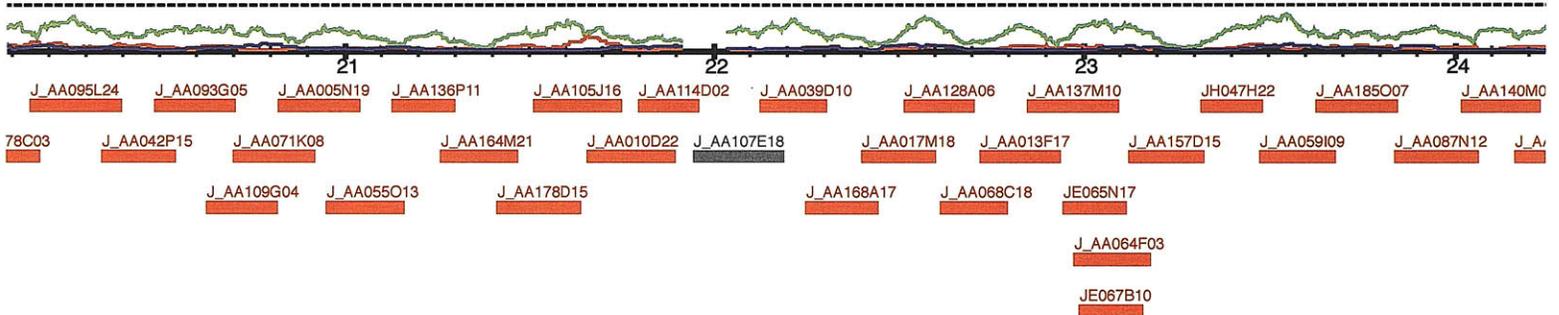
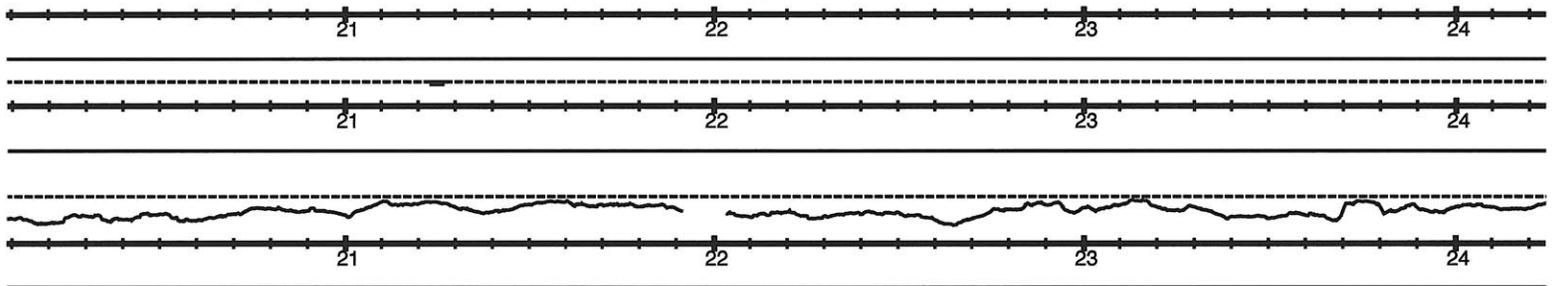
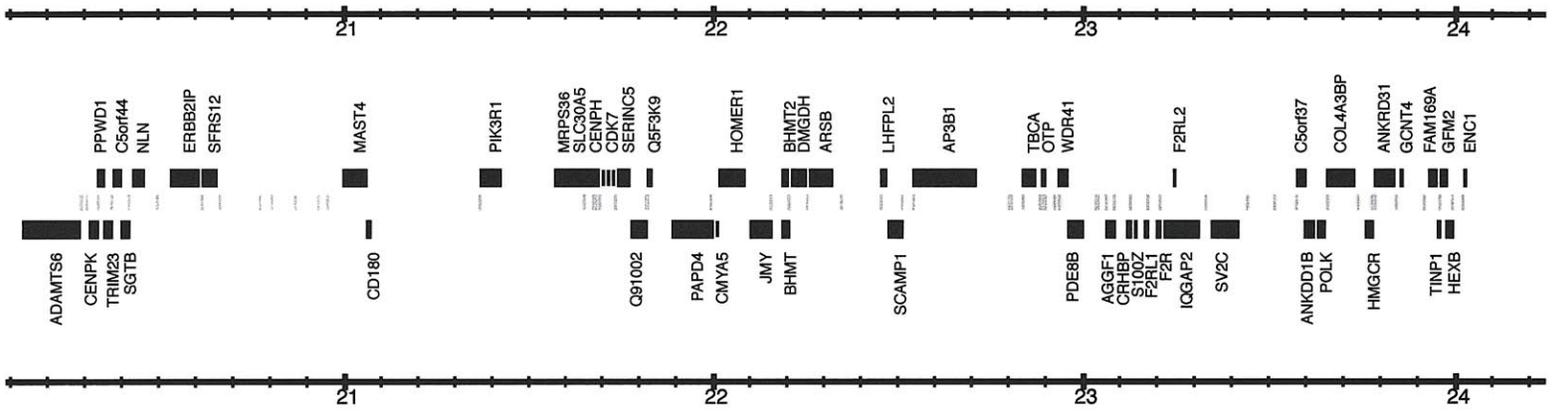


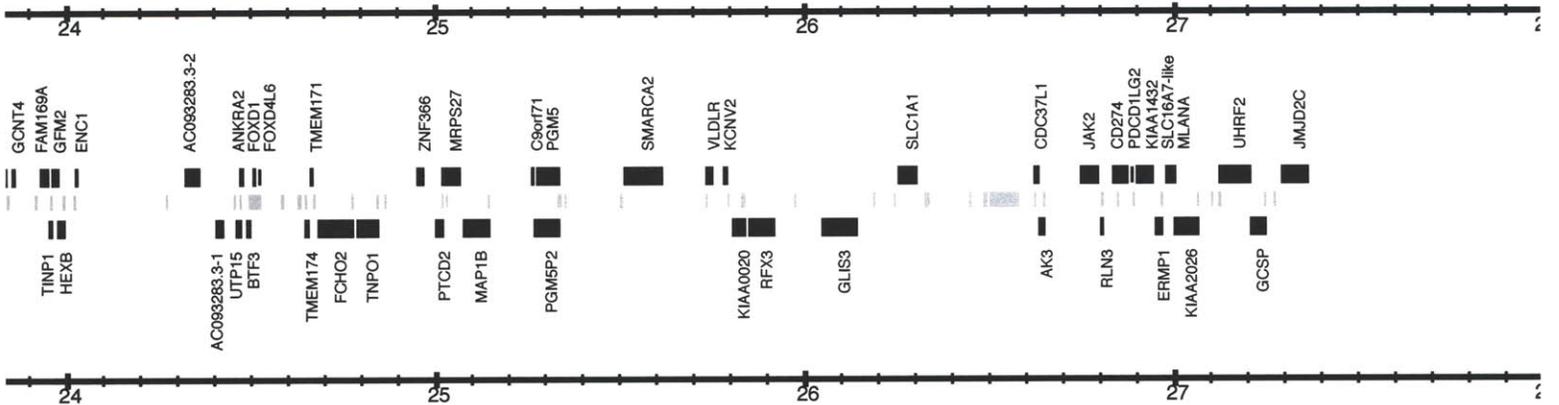


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miR-485

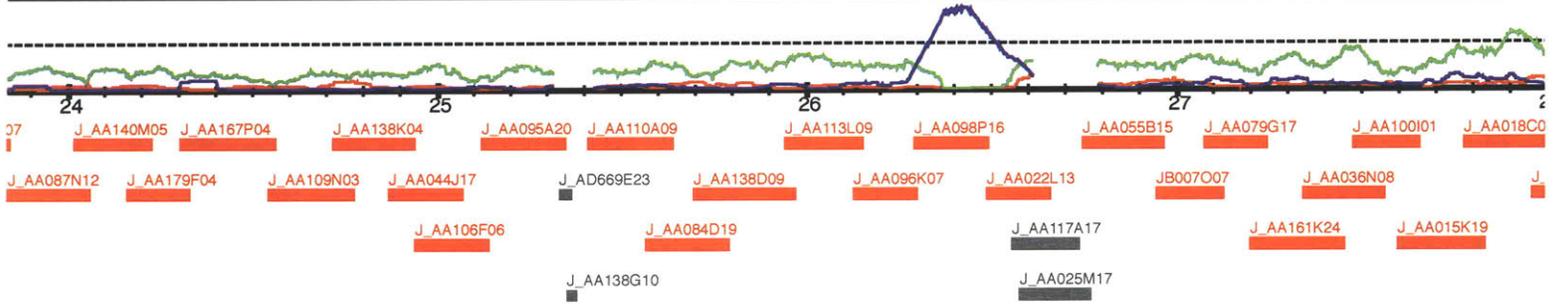
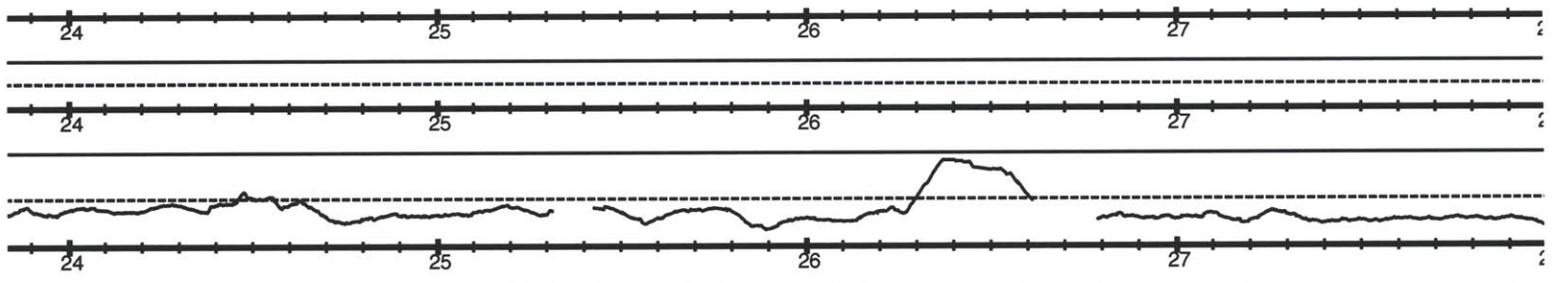
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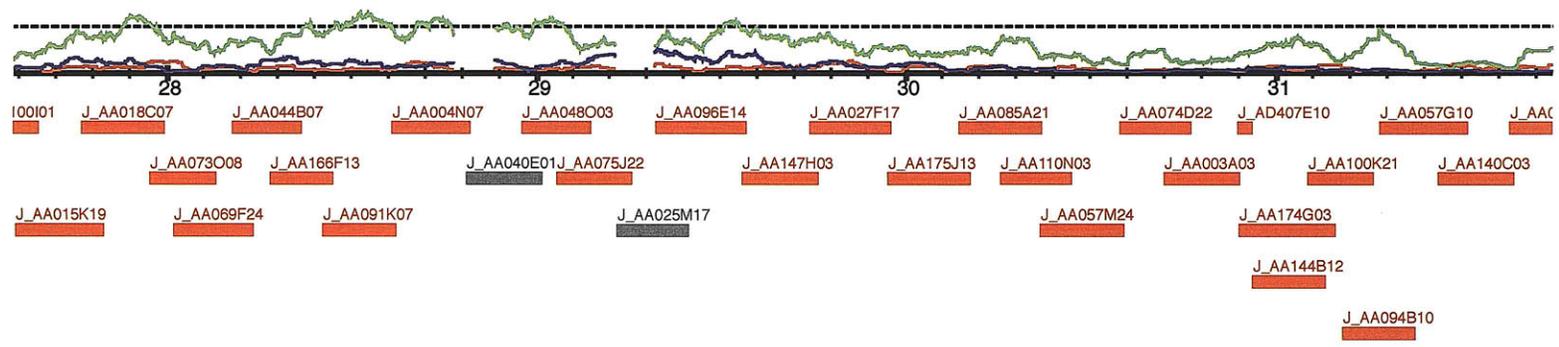
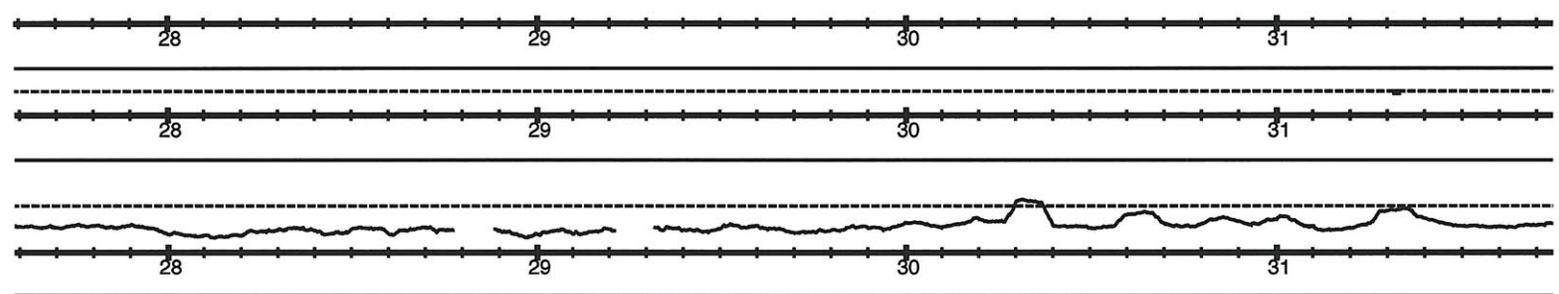
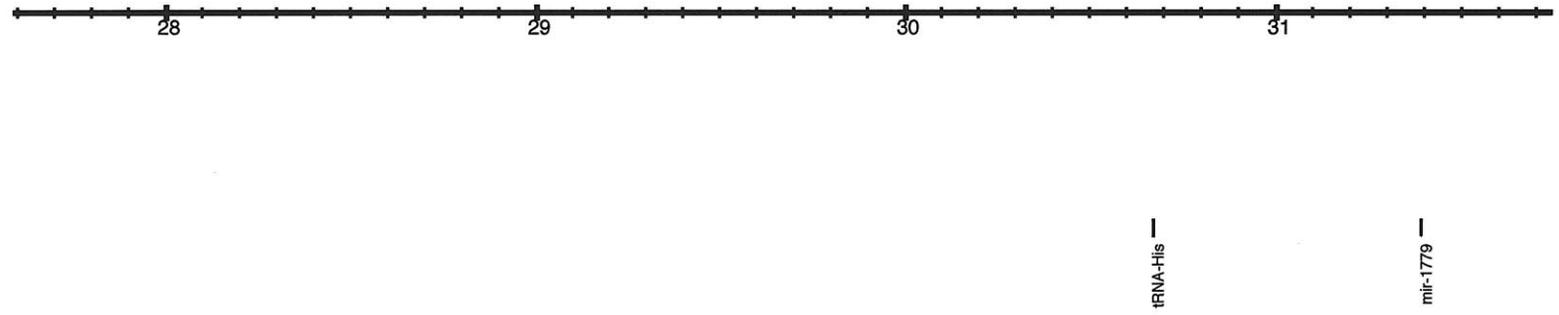
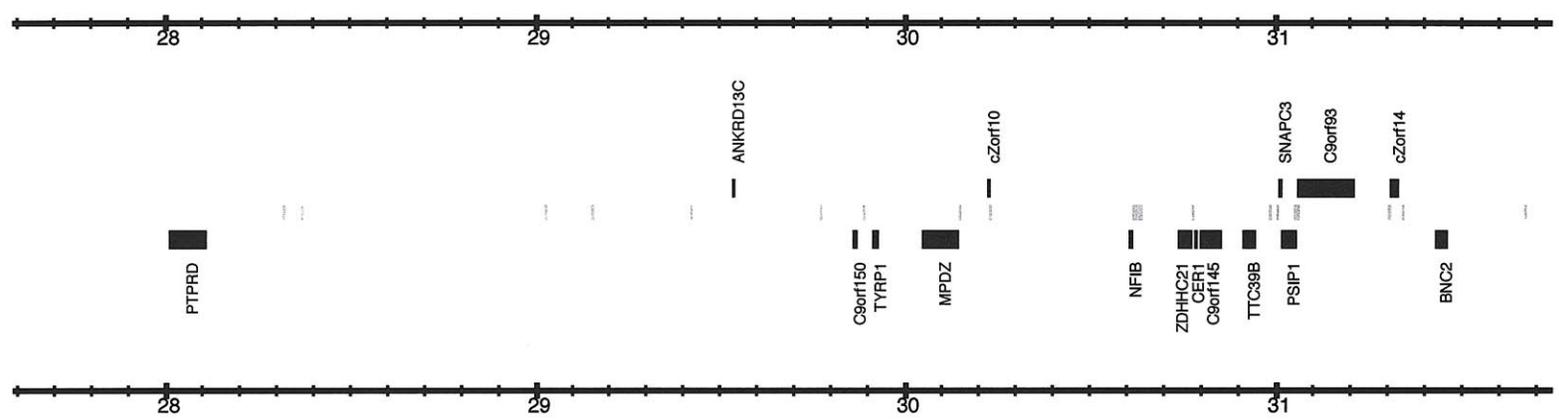


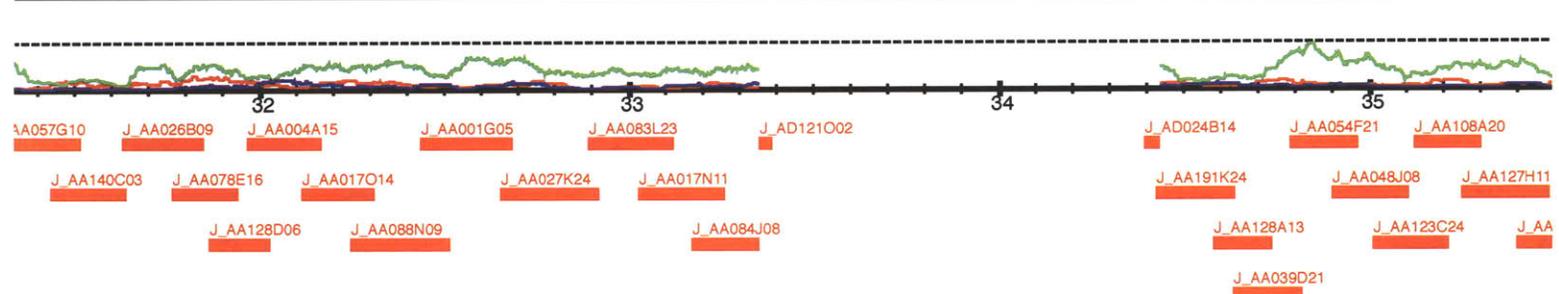
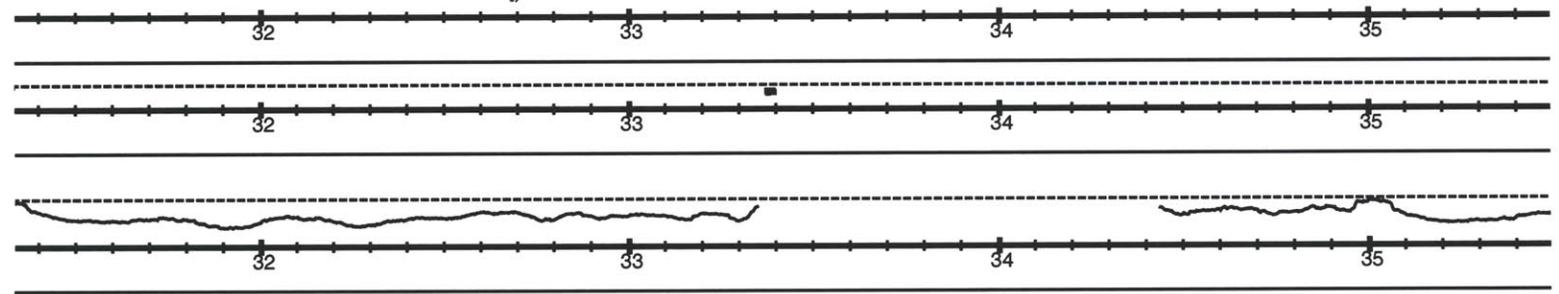
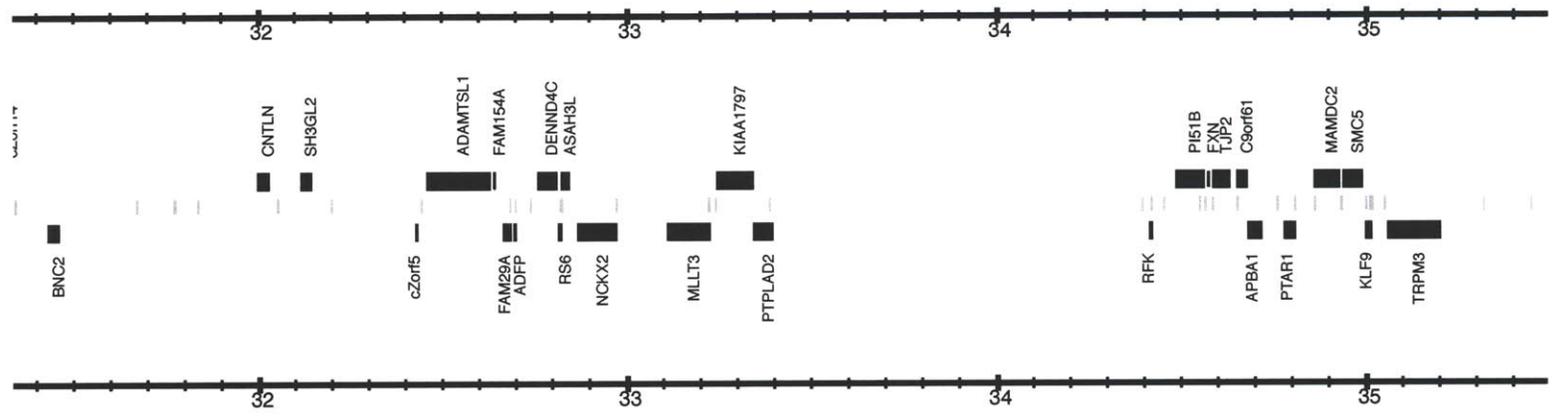




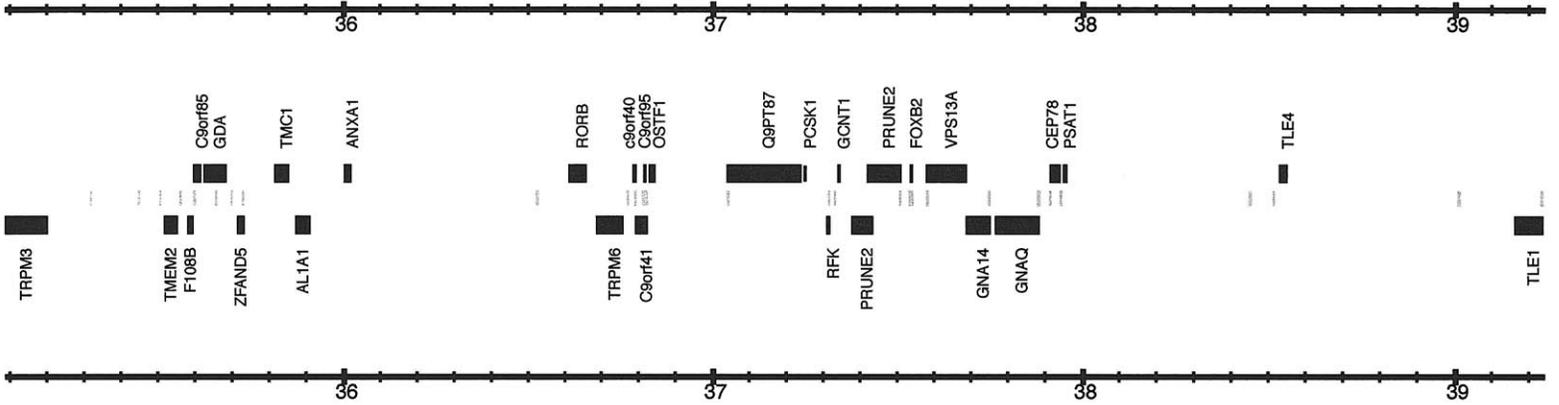
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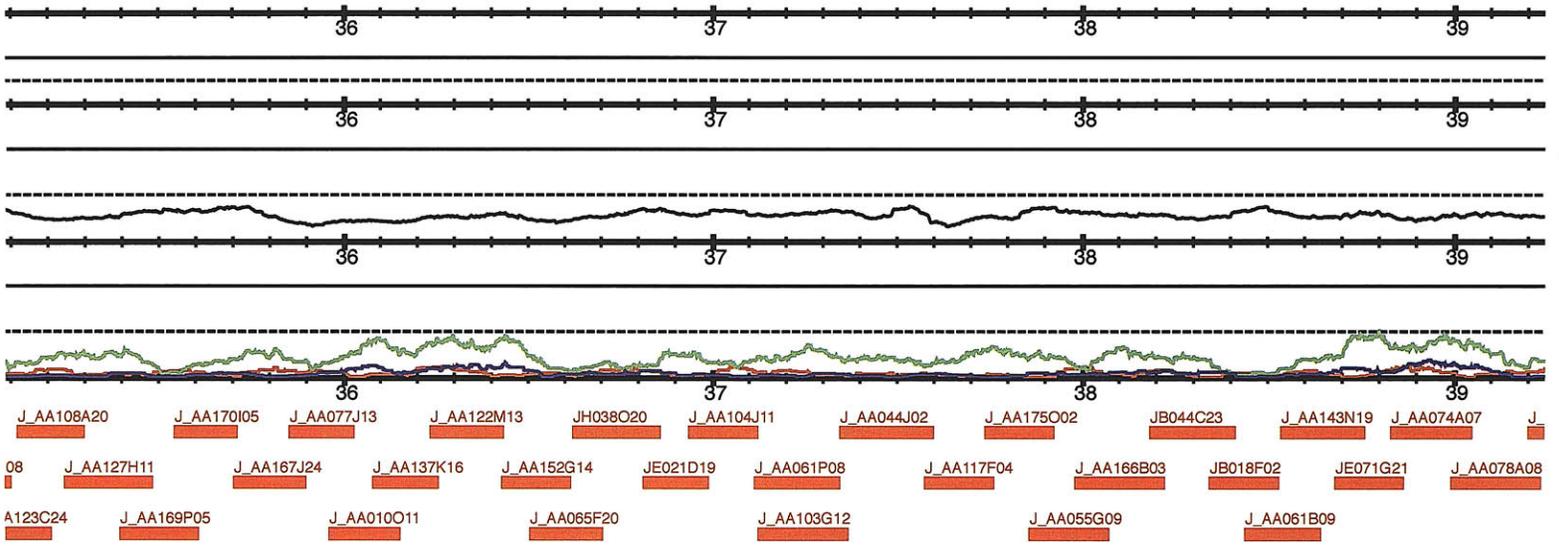


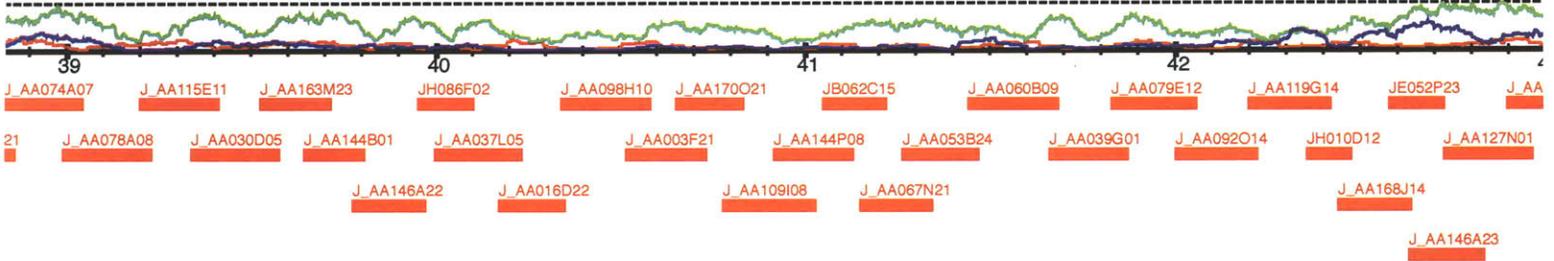
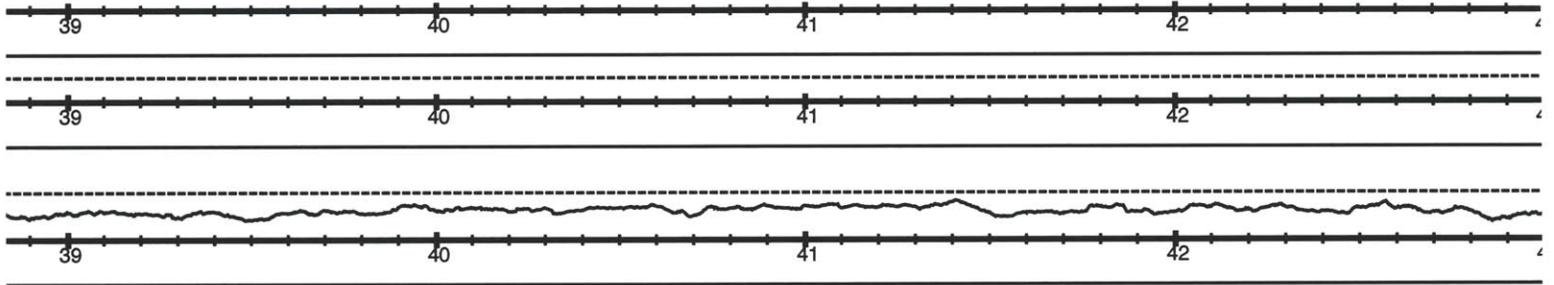
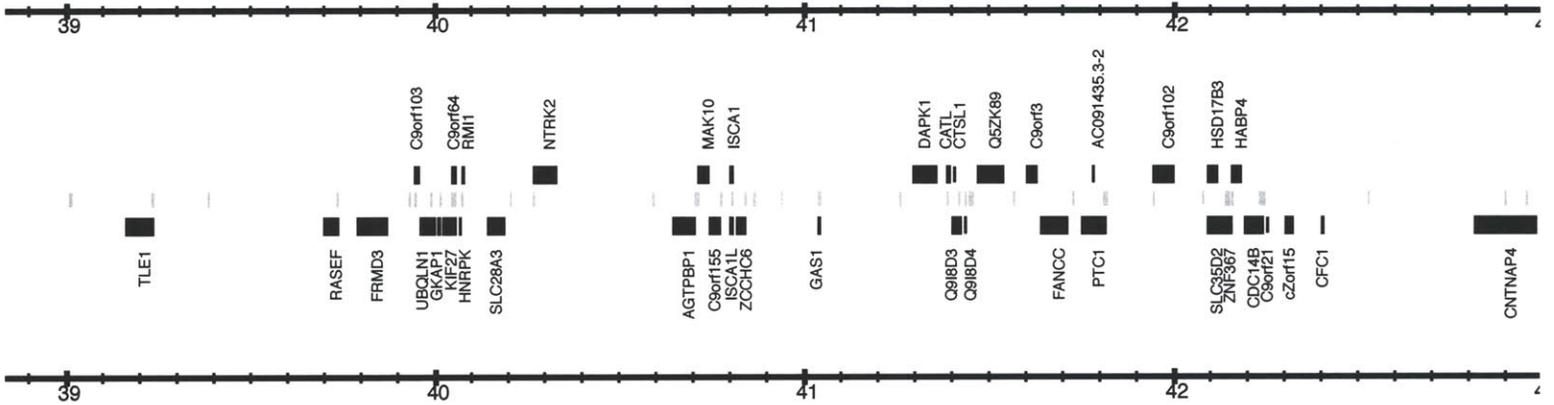


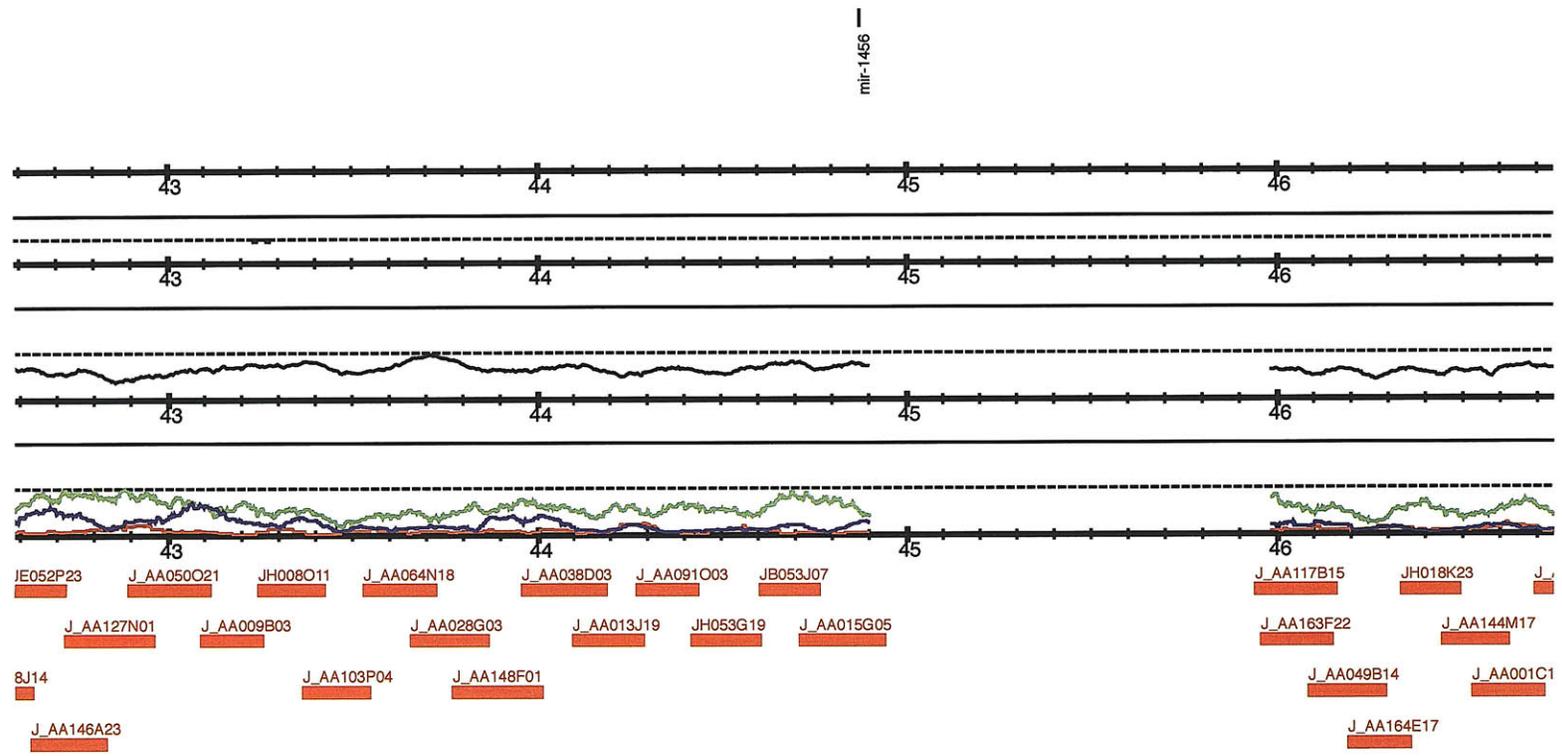
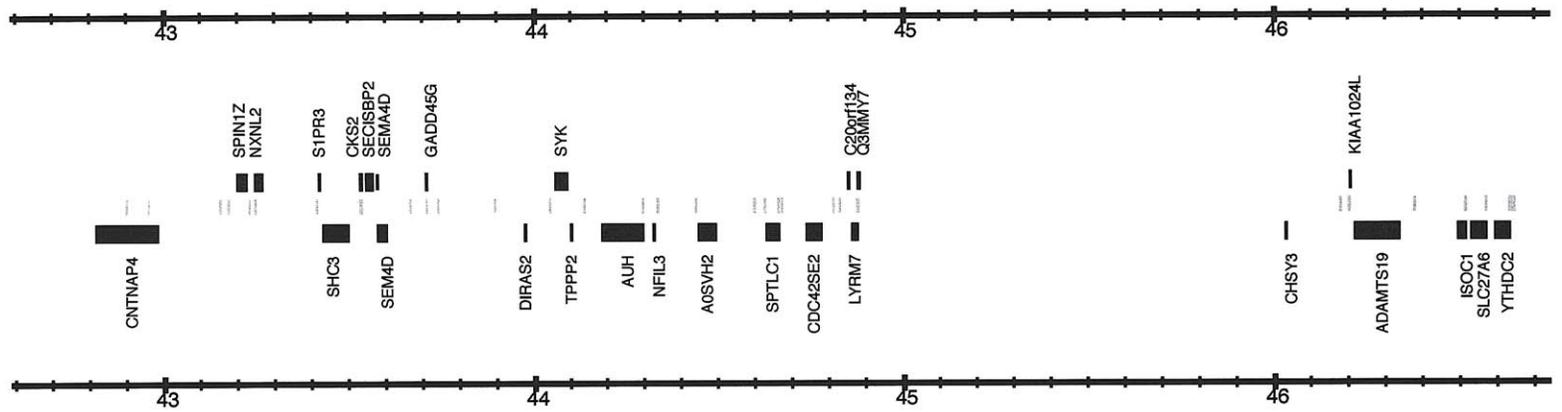
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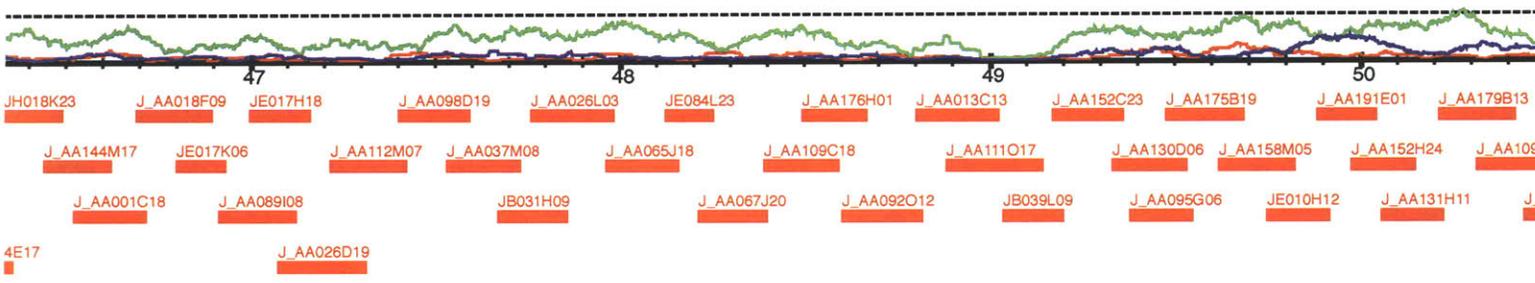
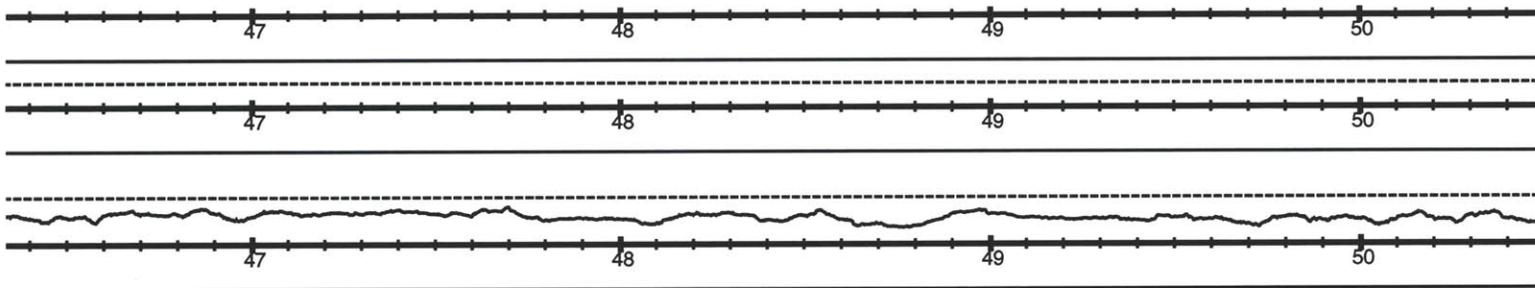
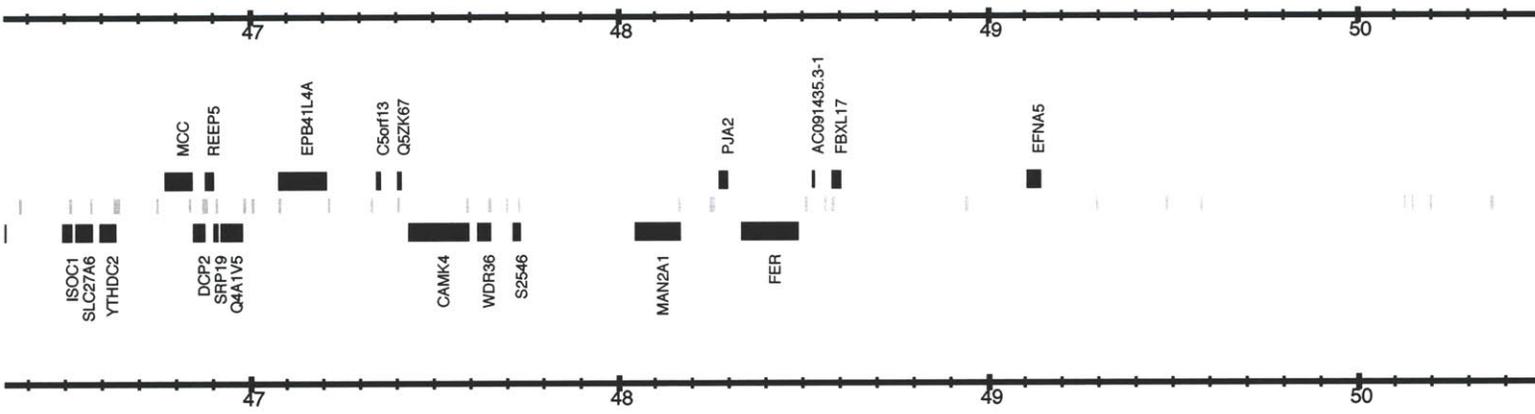


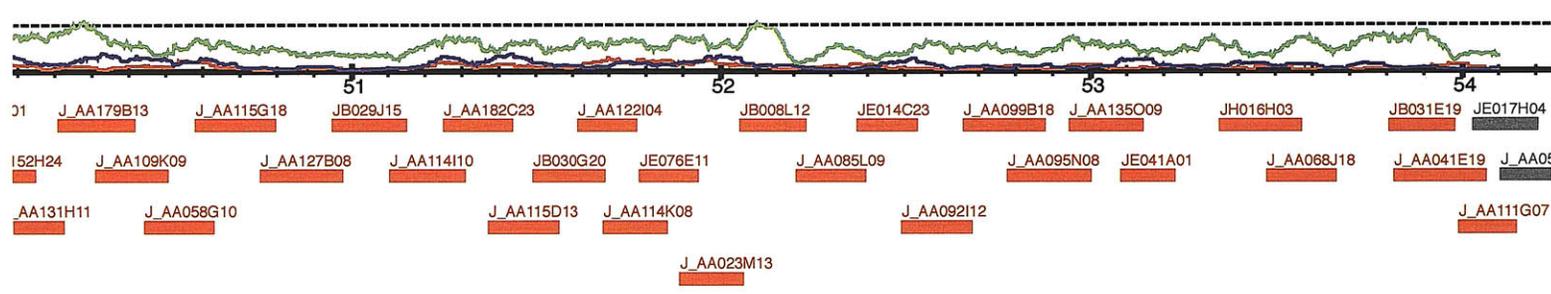
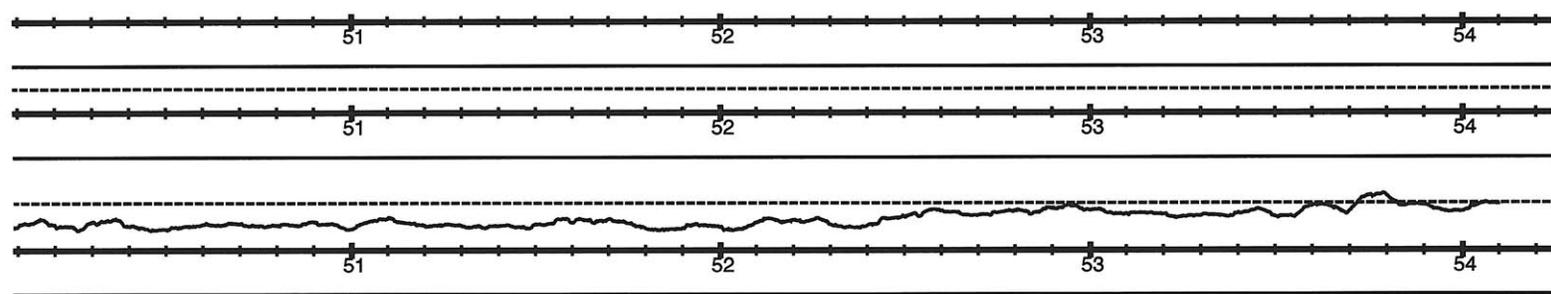
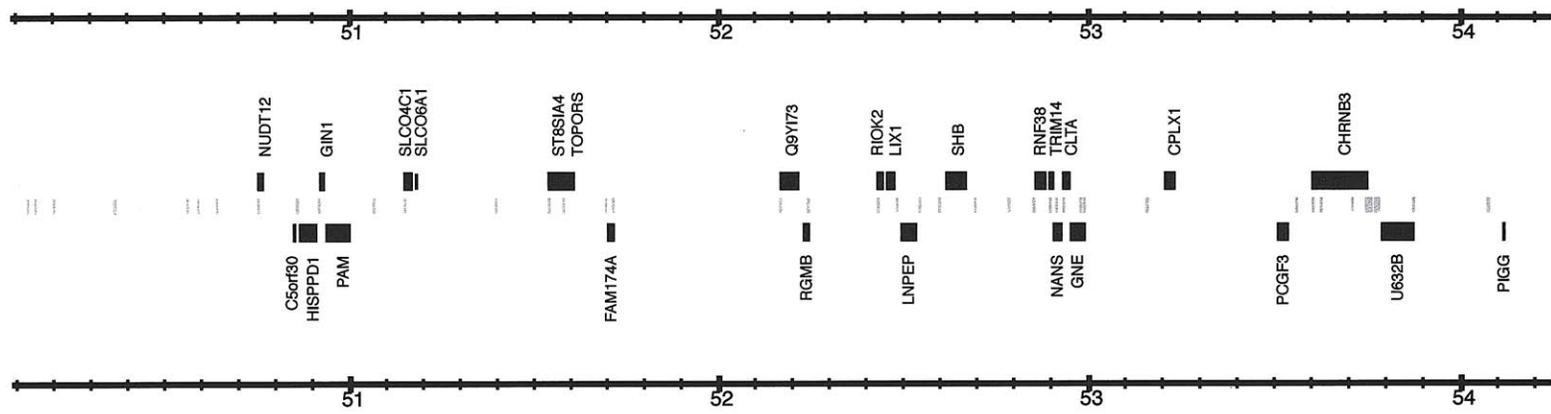
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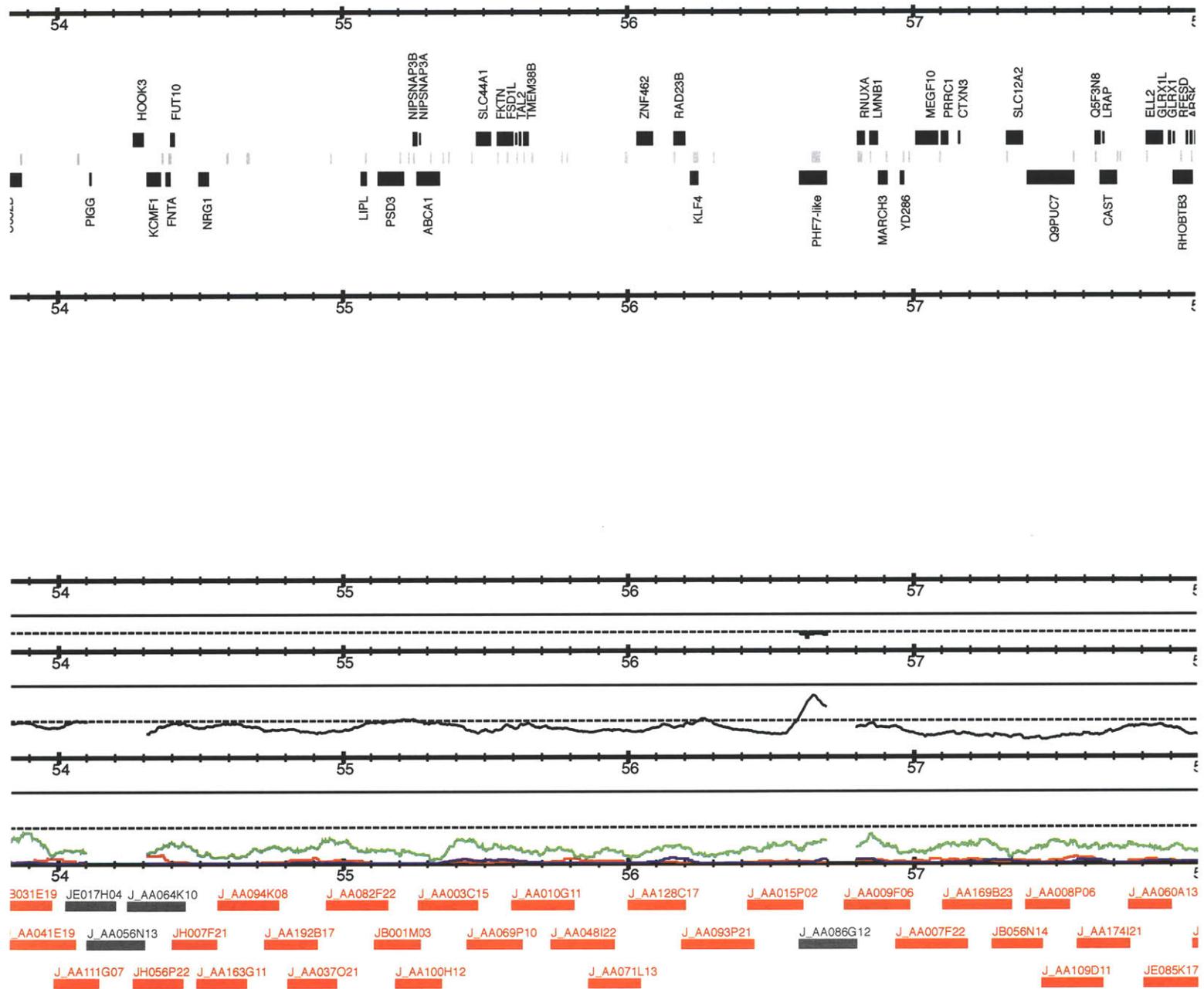


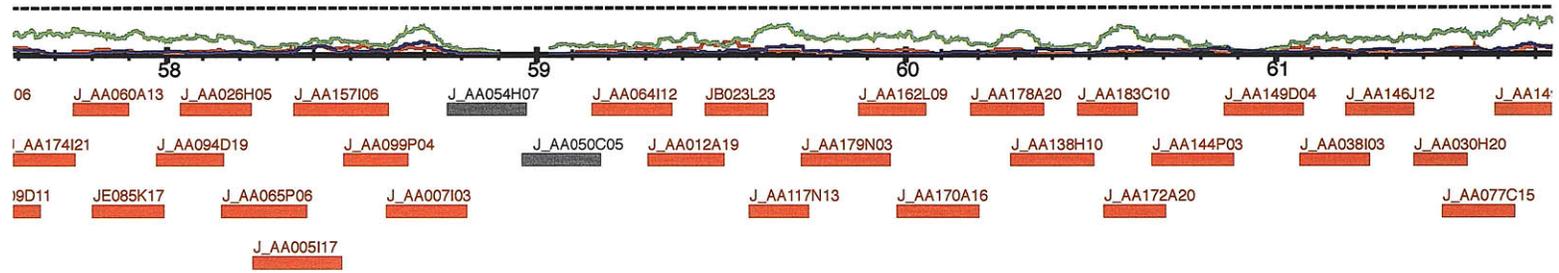
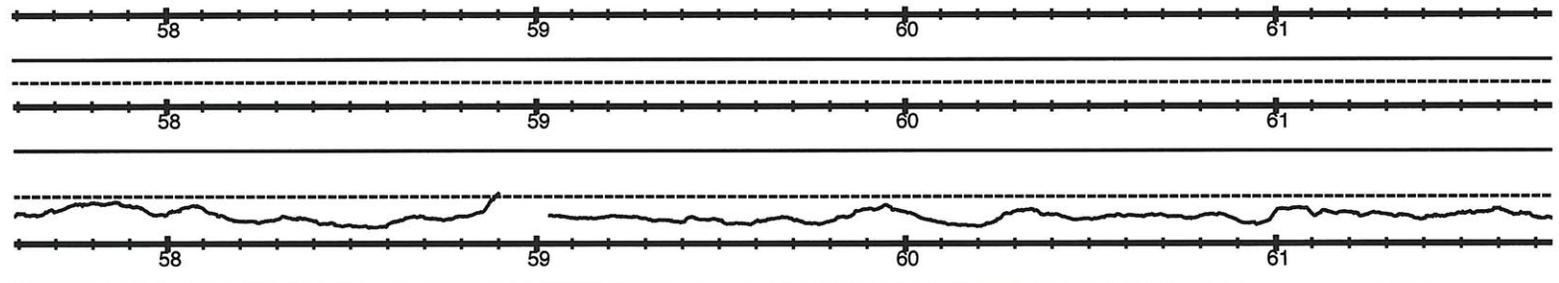
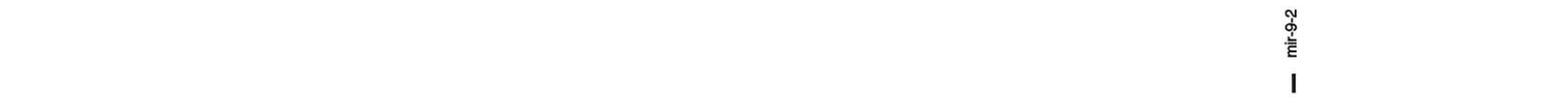
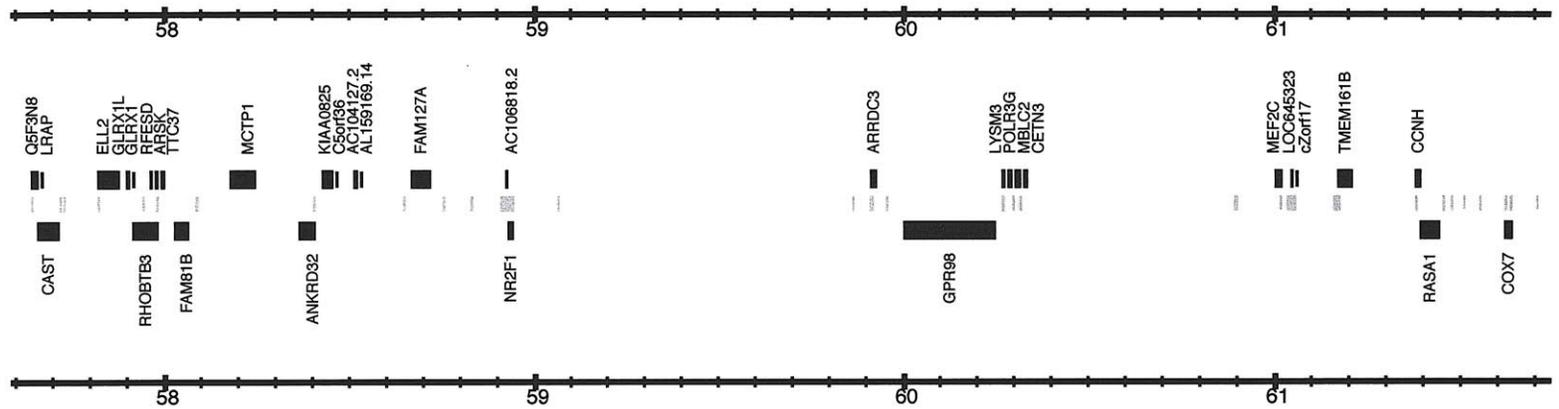


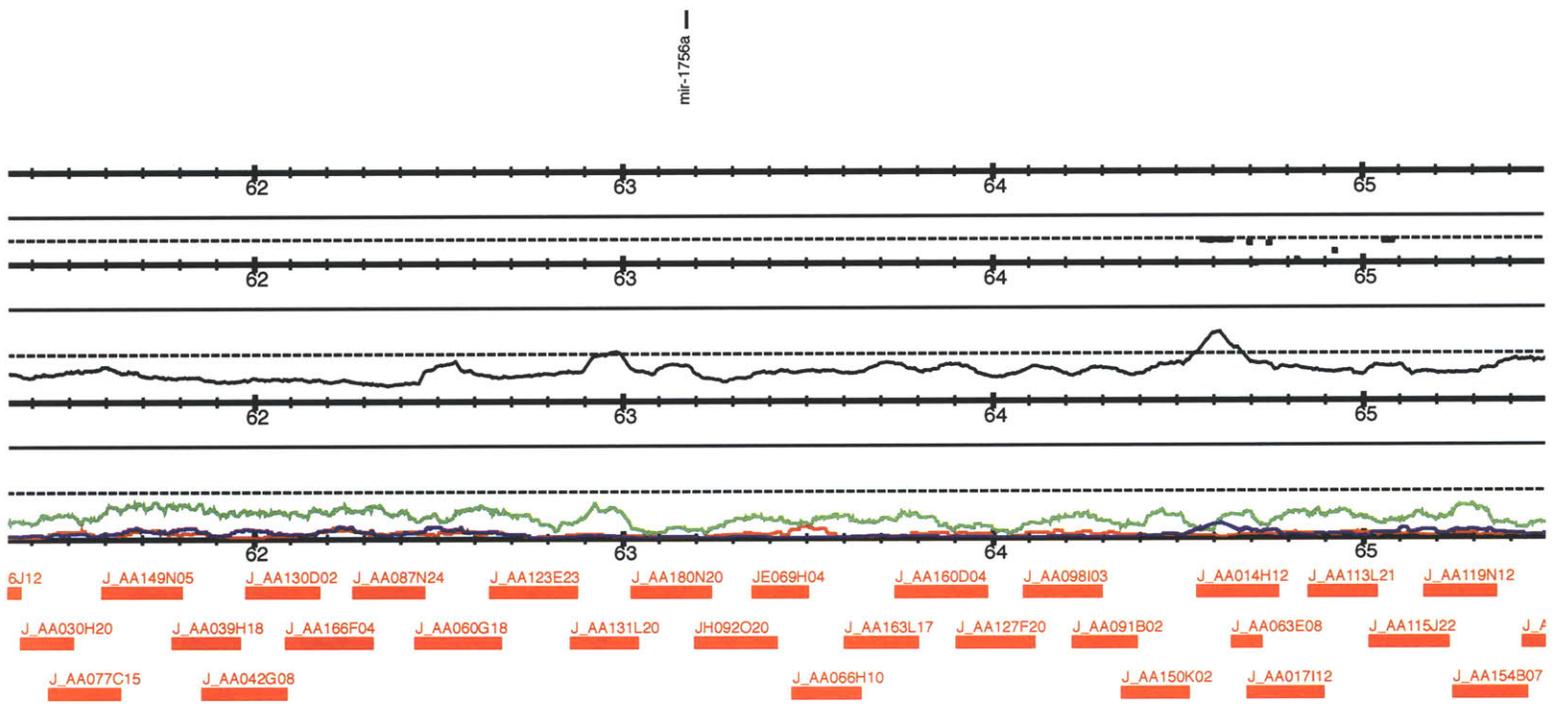
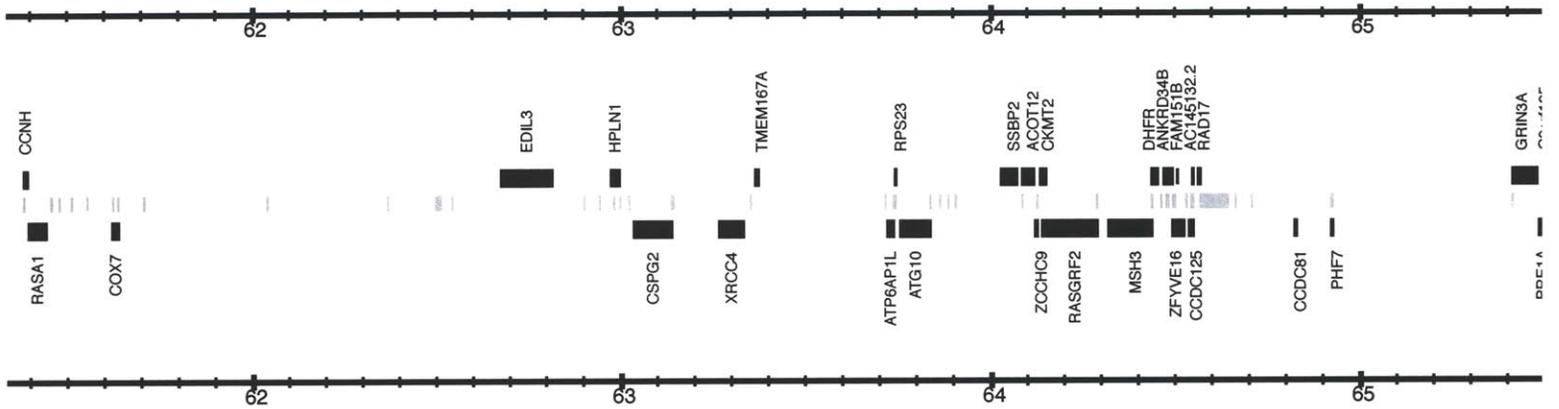


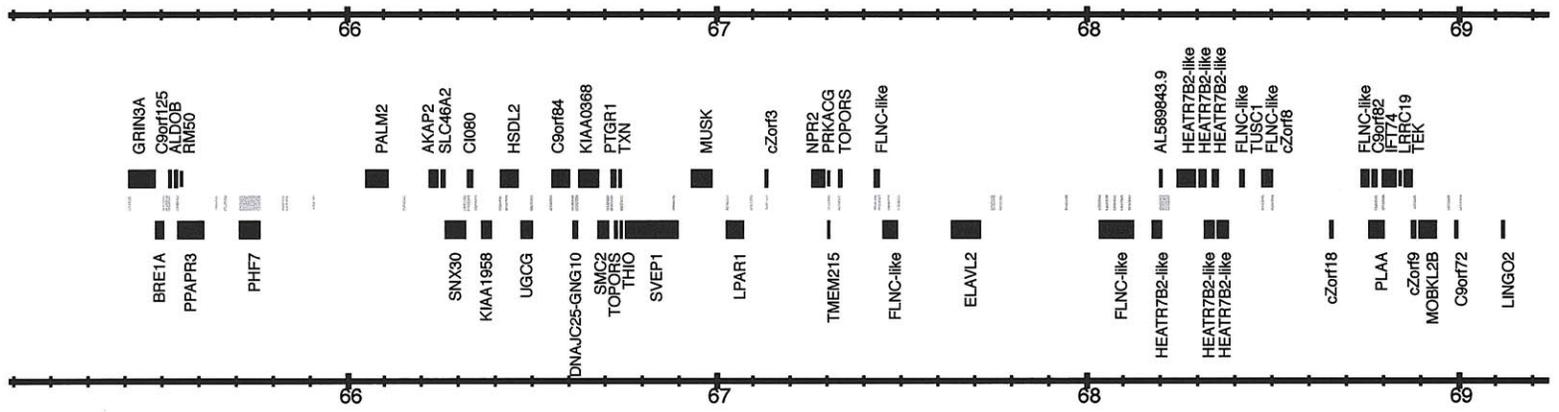




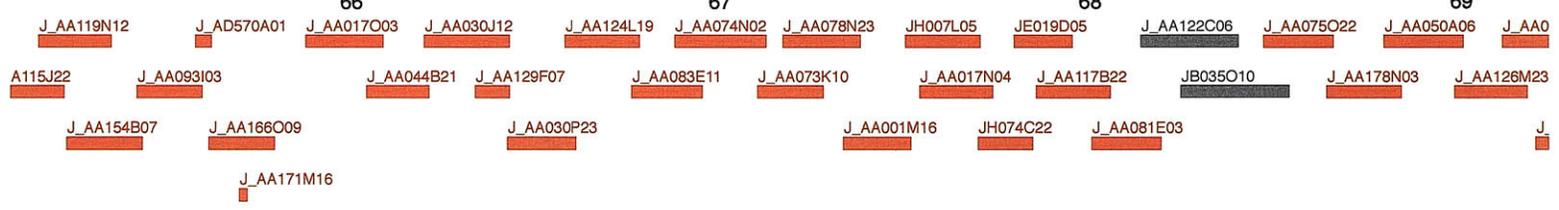
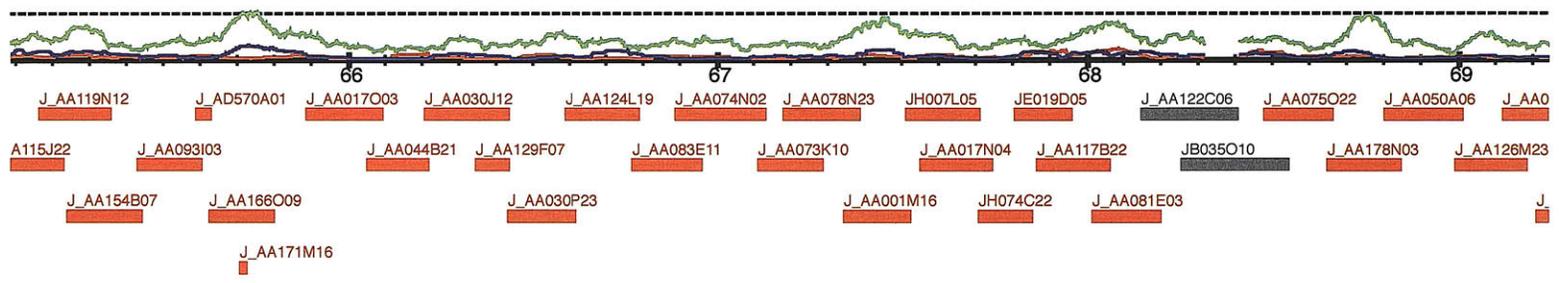
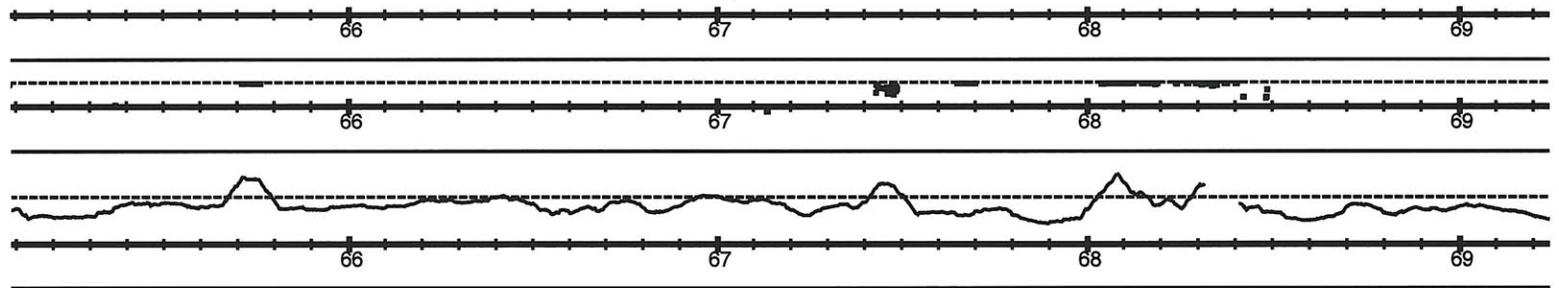


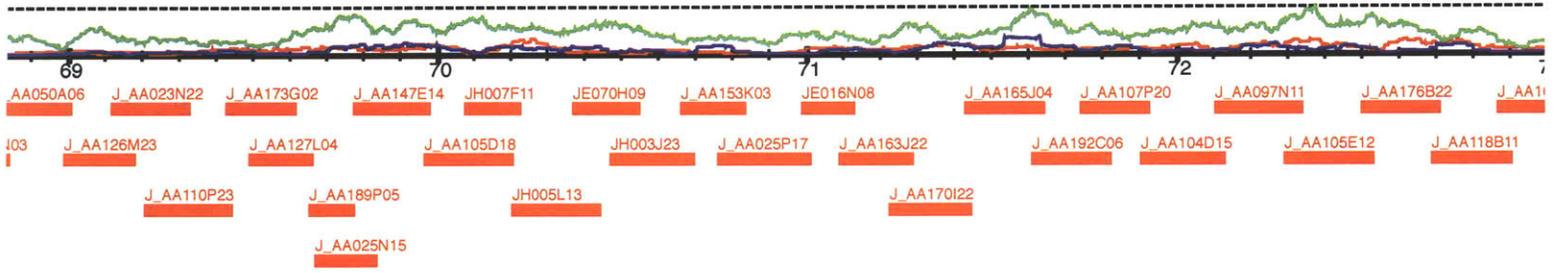
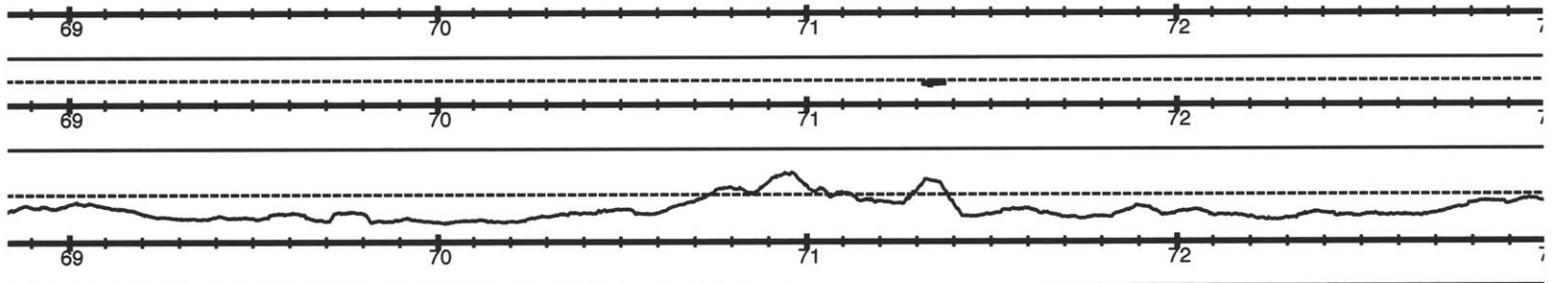
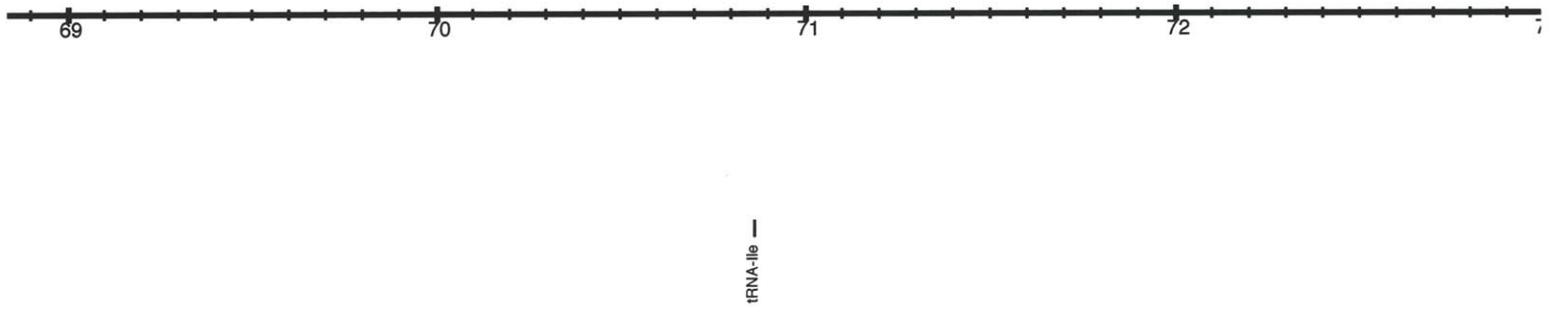
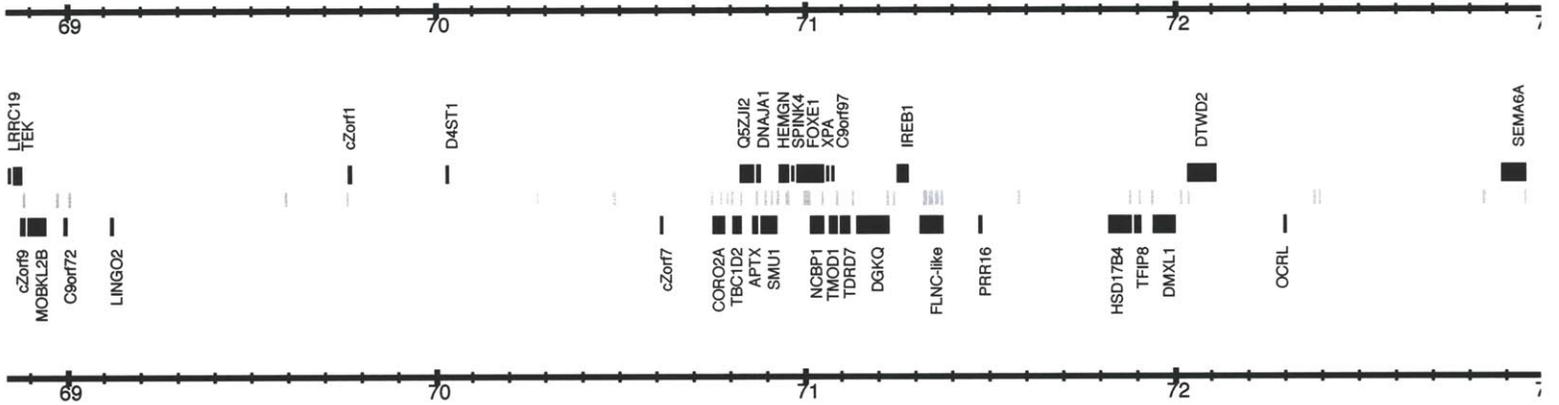


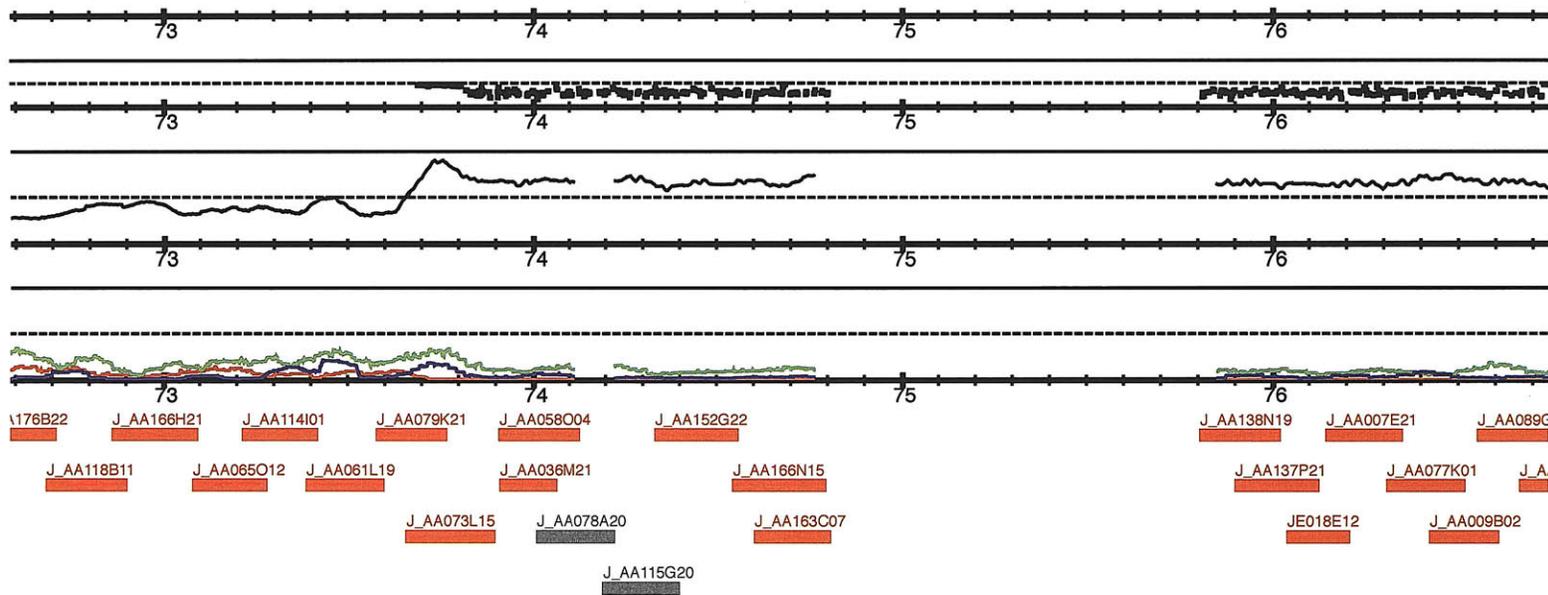
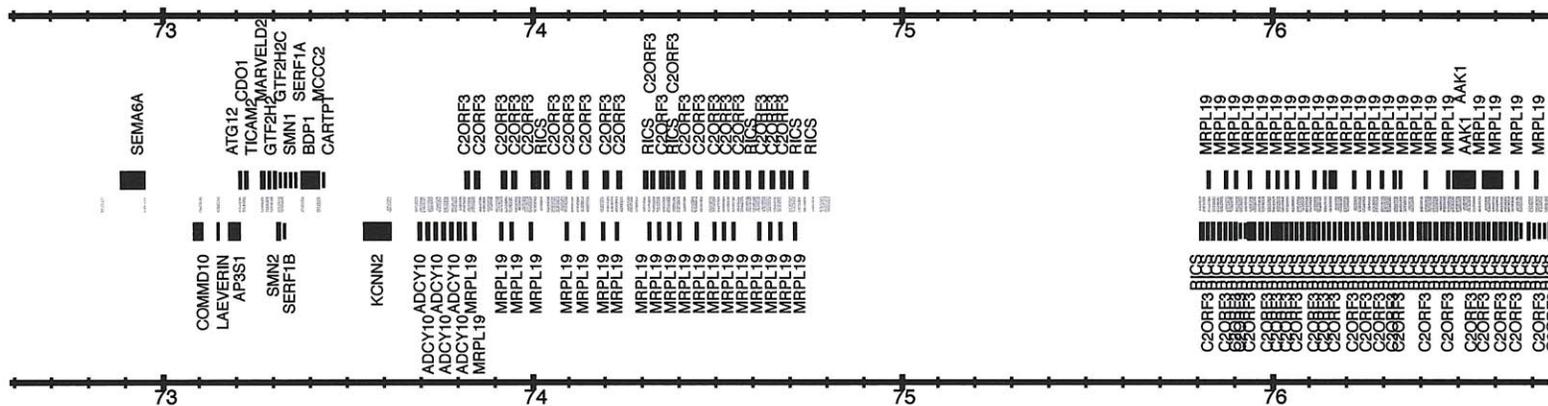


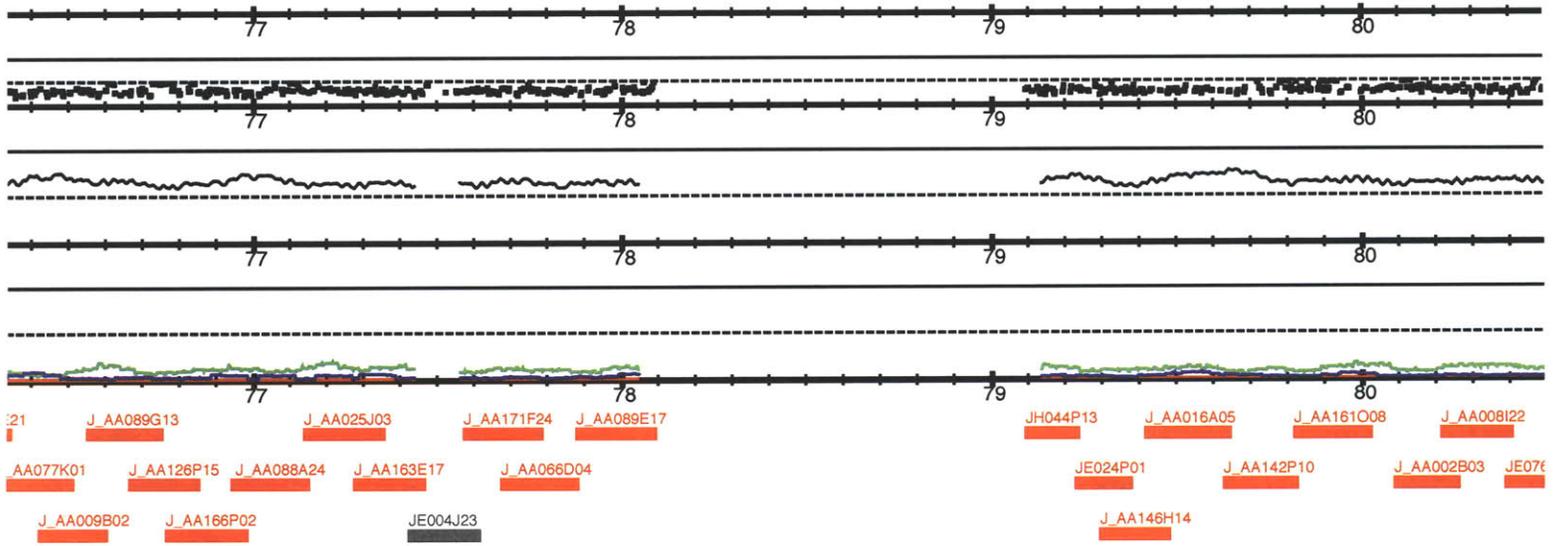
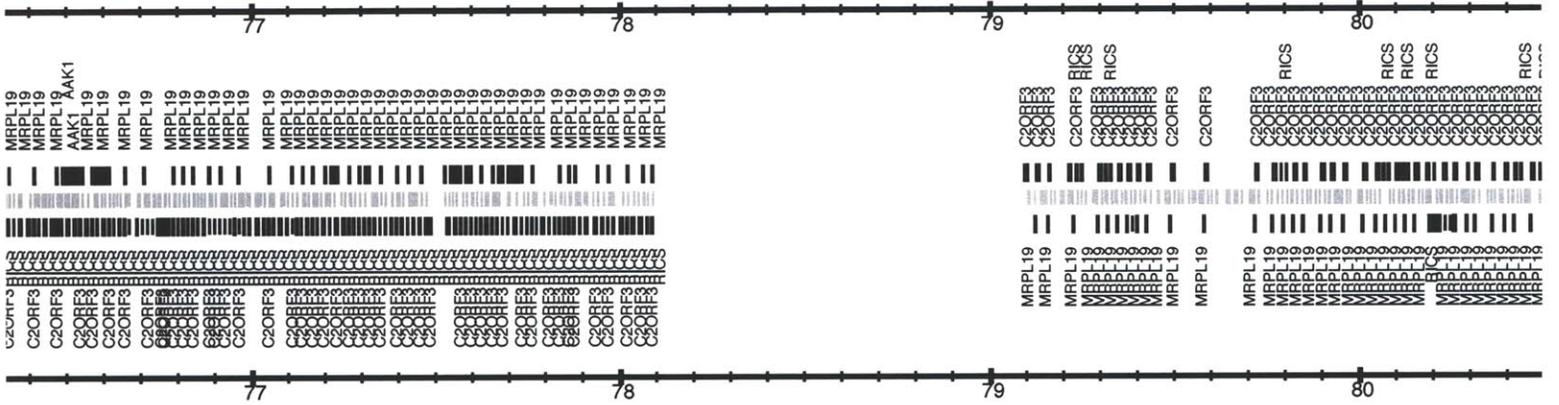


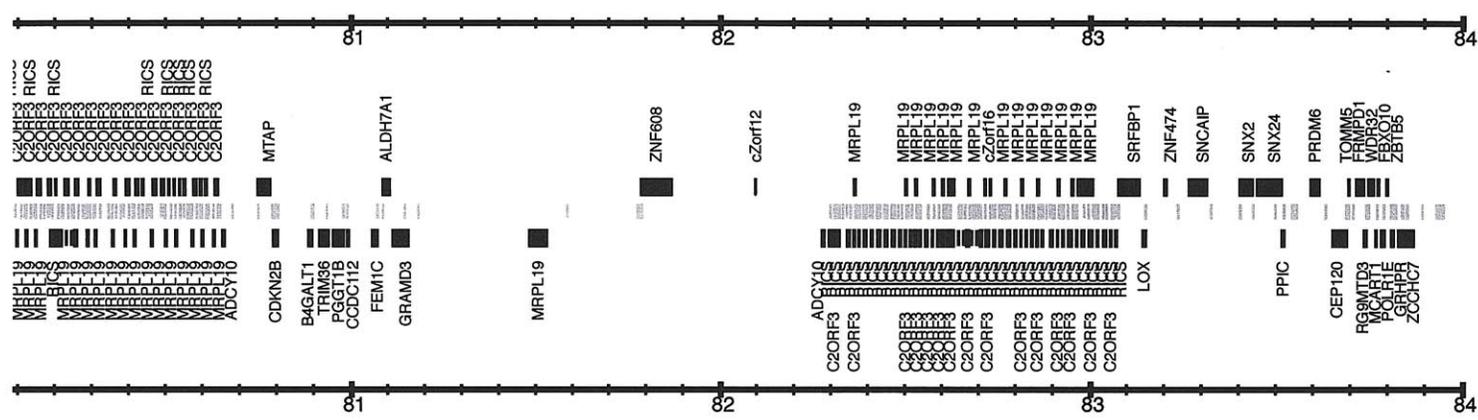
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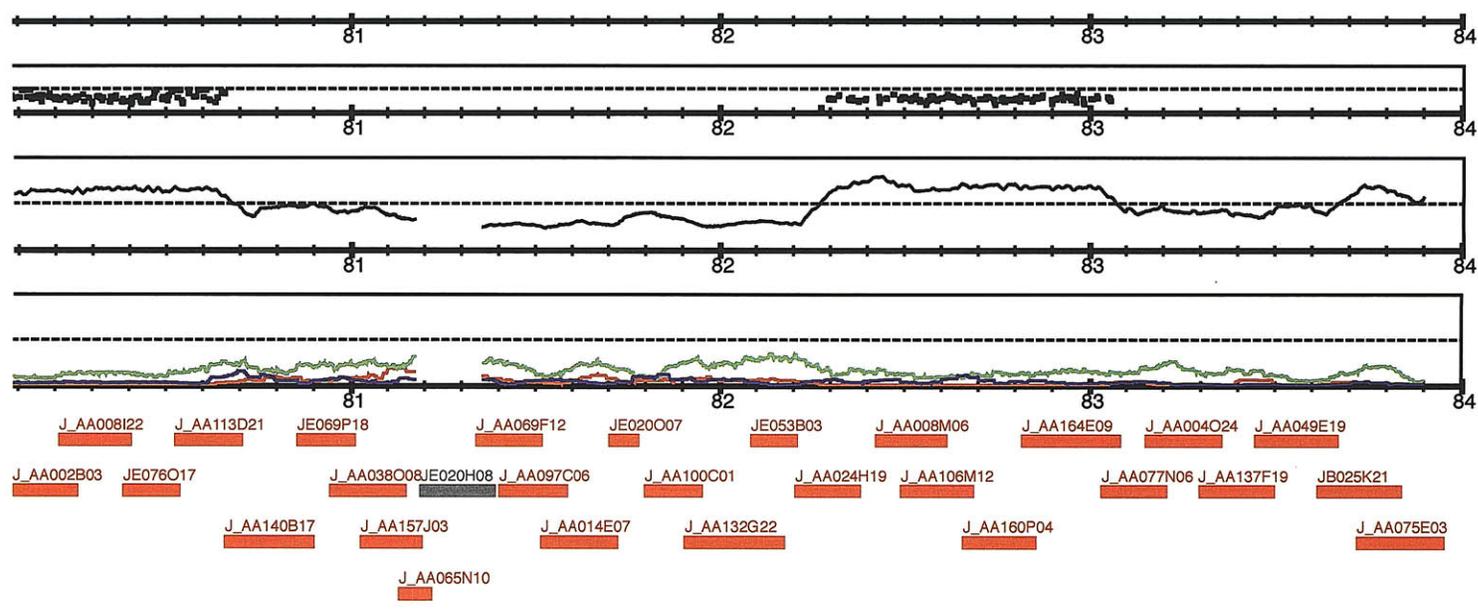


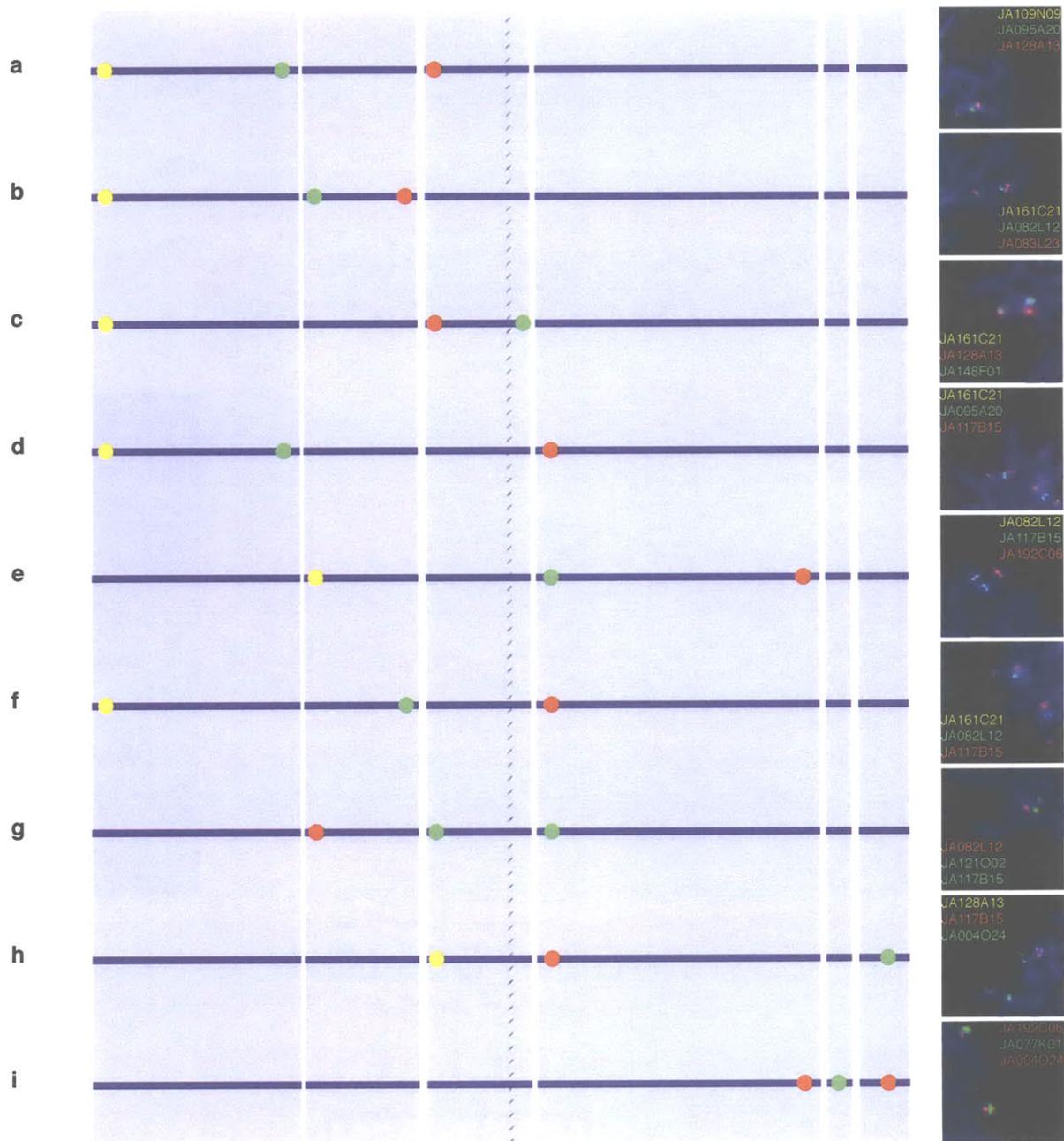






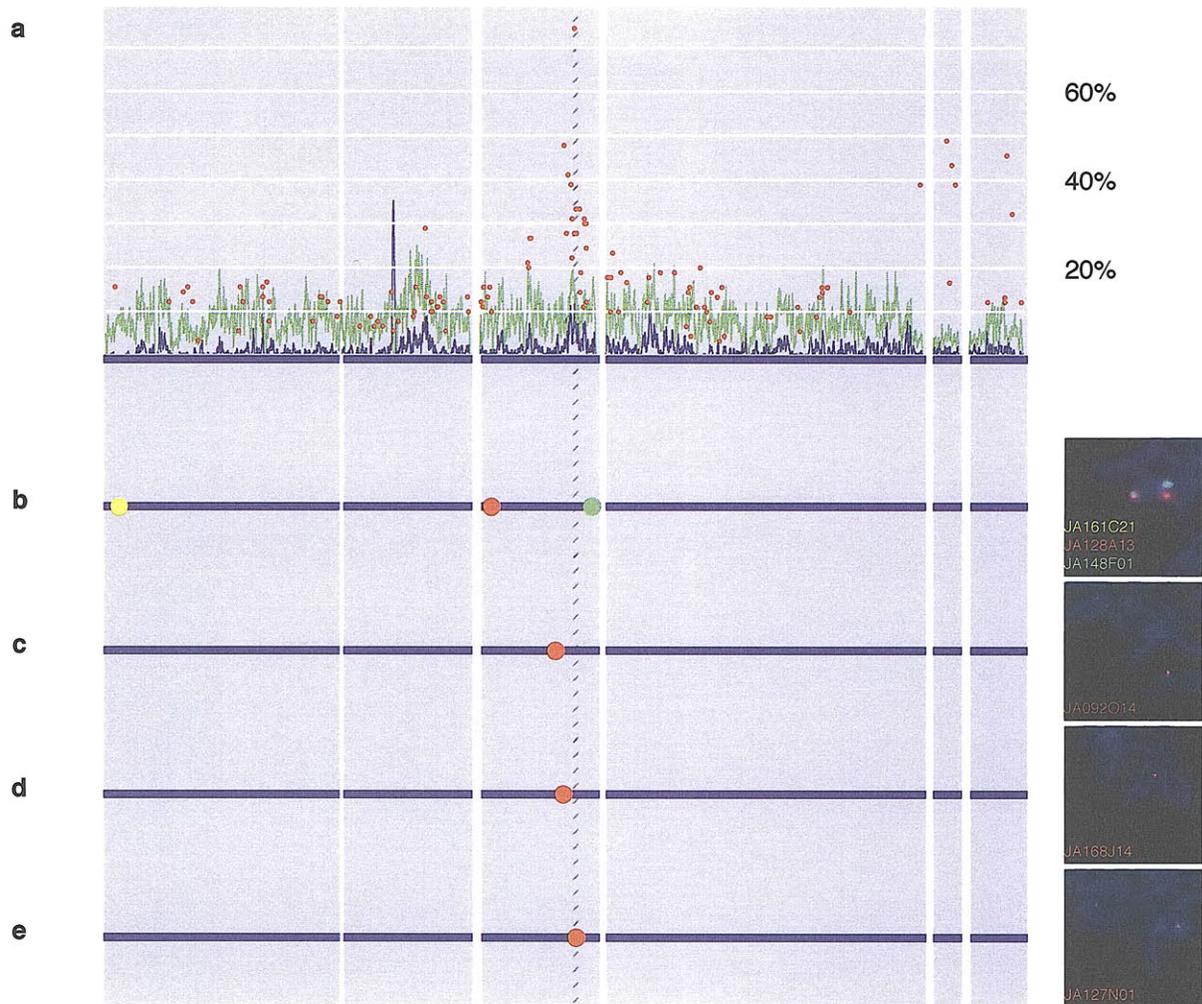
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**Supplementary Figure 2:** Order and orientation of Z chromosome contigs by DNA-FISH.

Schematic diagrams describing the locations of BAC probes (colored circles) within Z chromosome sequence contigs (blue lines). Each schematic is accompanied by a representative FISH image. Centromere position is shown by hashed lines. (a-e) Establish the orientation of the first four contigs and their position relative to the centromere. The first two contigs are on the short arm, the third contains the centromere, and the fourth contig is on the long arm. (f-i) Establish the order of contigs. BAC probe JA077K01 illuminates the Z amplicon, which is flanked by single-copy sequences represented by JA192C06 and JA004O24.



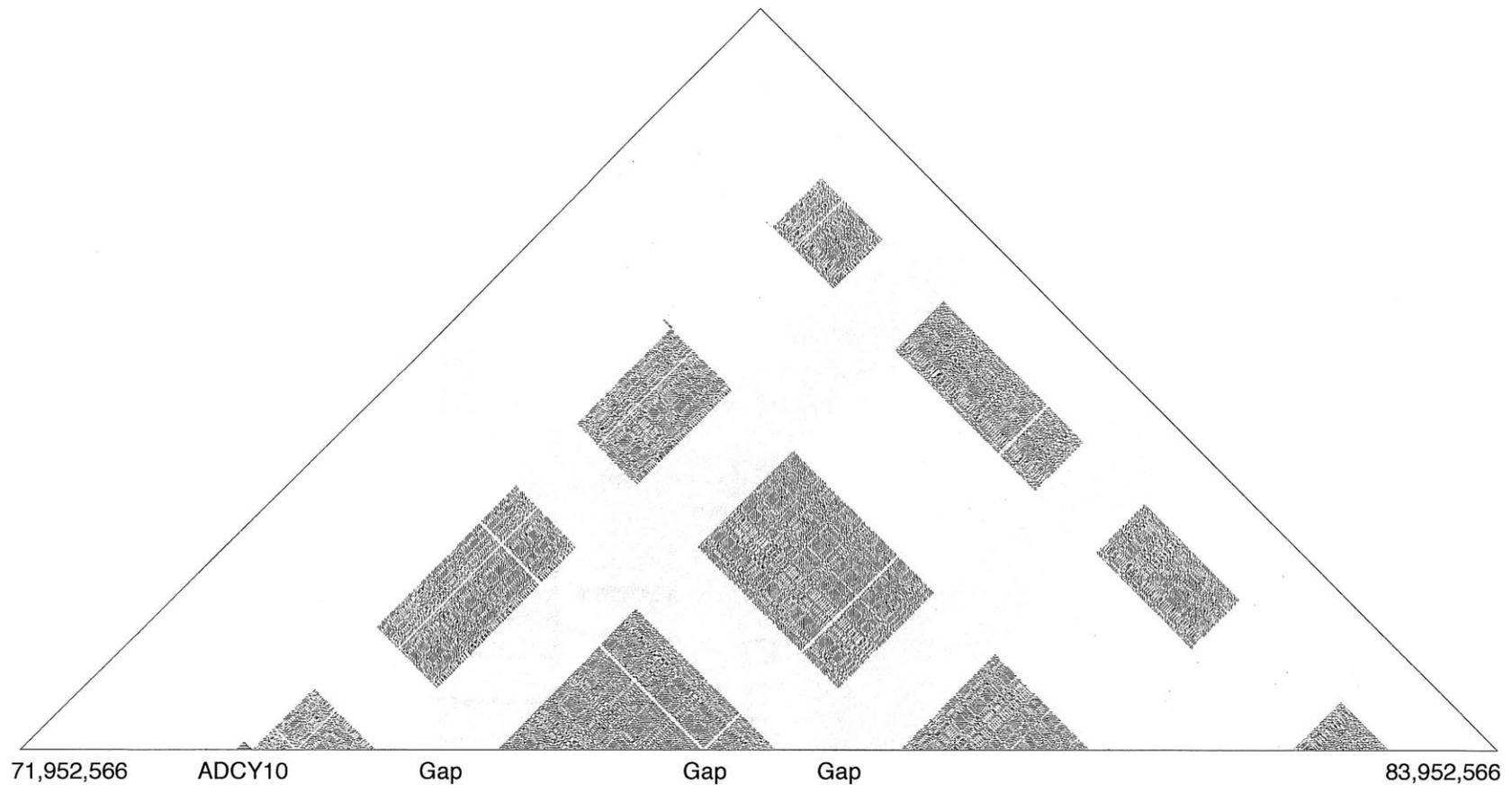
**Supplementary Figure 3:** Location of the Z chromosome centromere.

(a) Graph showing the retention frequency of Z-linked markers on ChickRH6 (red dots), LINE density (green line) and endogenous retrovirus density (blue line). Retention frequency peaks in the third contig on the Z chromosome. This peak coincides with a local peak in LINE and ERV density. (b-e) Schematic diagrams describing the locations of BAC probes (colored circles) within Z chromosome sequence contigs (blue lines). Each schematic is accompanied by a representative FISH image. Centromere position is shown by hashed lines. (b) Establishes the position of the centromere within the third contig. (c-d) Place BACs JA092O14 and JA168J14 on the short arm adjacent to the centromere. (e) Shows JA127N01 at a position indistinguishable from the centromere. A marker (WIBR04610) designed from a BAC end sequence of JA127N01 (GenBank: CC247852.1) is the marker with the highest retention frequency on the RH panel.



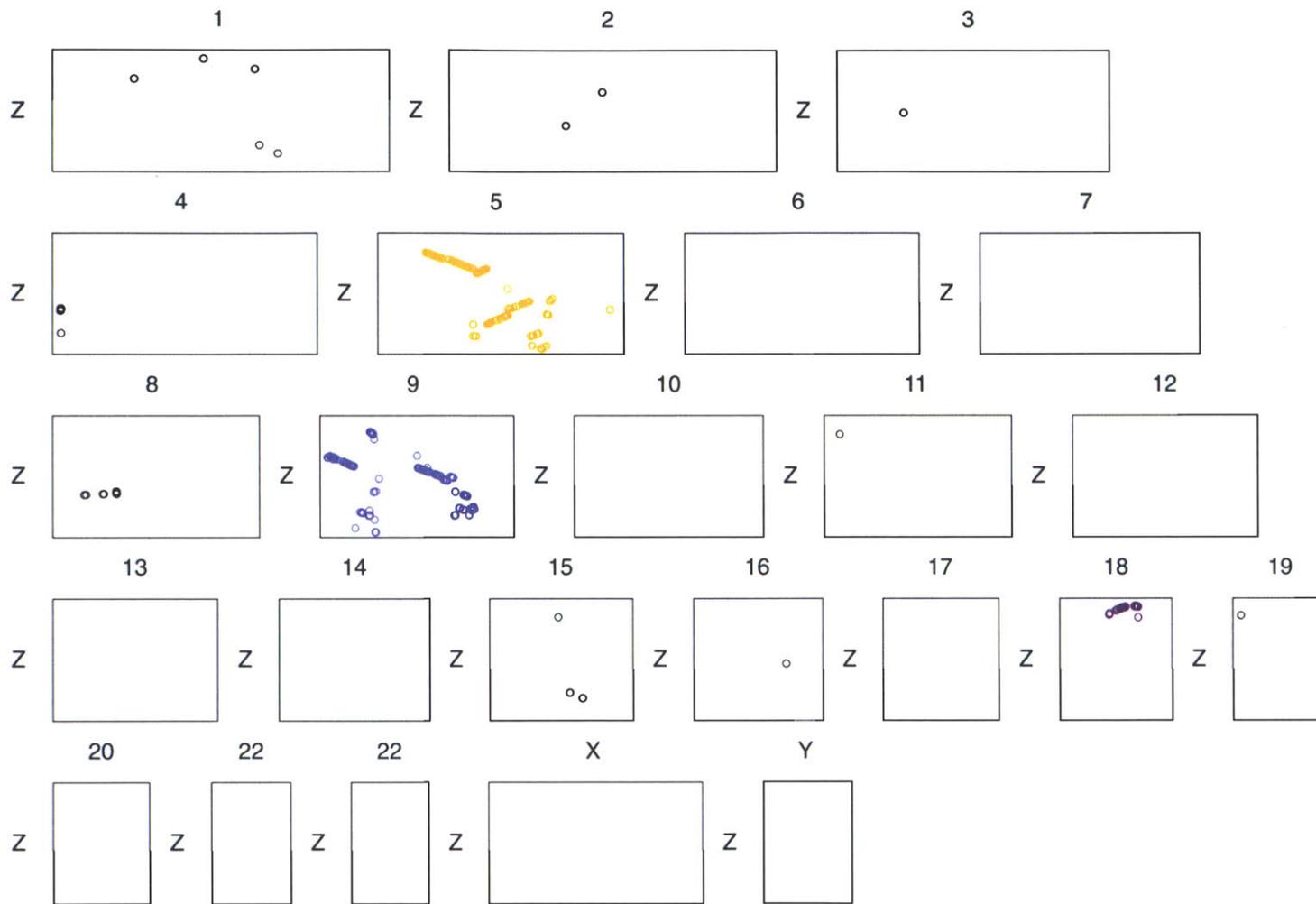
**Supplementary Figure 4: Z amplicon FISH**

Fluorescence in situ hybridization of Z amplicon containing BAC CH261-77N6 (red) to chicken chromosomes (blue). CH261-77N6 hybridizes specifically to distal Z long arm.



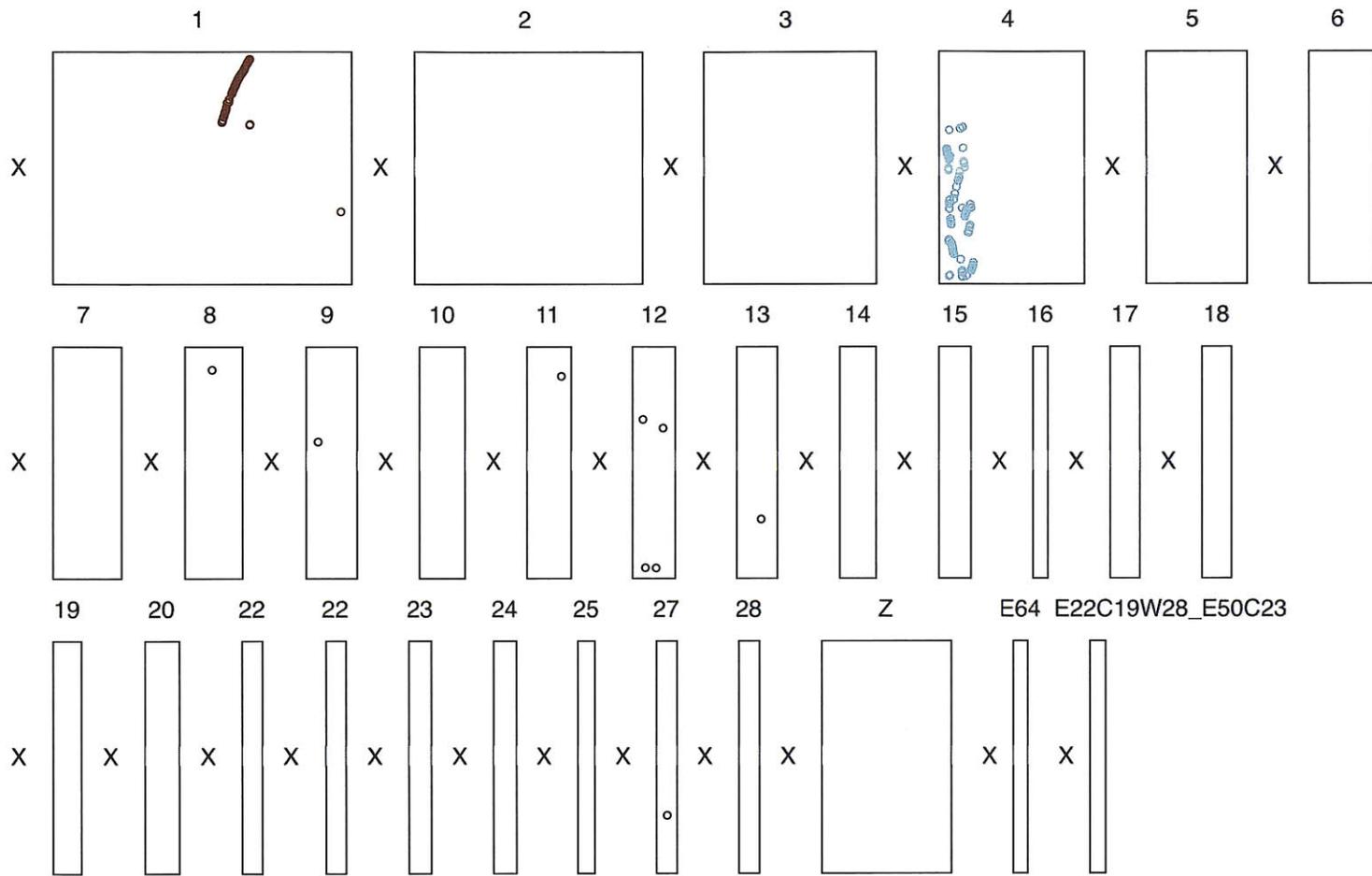
**Supplementary Figure 5:** Triangular dot plot of the Z amplicon region

This dot plot spans the entire Z amplicon region. Each dot represents a perfect match of 100 base pairs. Tandem repeats appear as horizontal lines, inverted repeats as vertical lines. Gaps in the sequence are shaded gray; the sequence contains two physical gaps where further chromosome walking was not possible, represented as 1Mb blocks, and a single gap in clone assembly estimated at 35kb. The orientation of sequences between the two physical gaps has not been determined. The Z amplicon array is interrupted by 2 large single-copy islands containing genes with orthologs on human autosomes 5 and 9. The ADCY10 array is visible as a small tandem array before the main body of the Z amplicon, with copies present at the beginning and end of the first single-copy island.



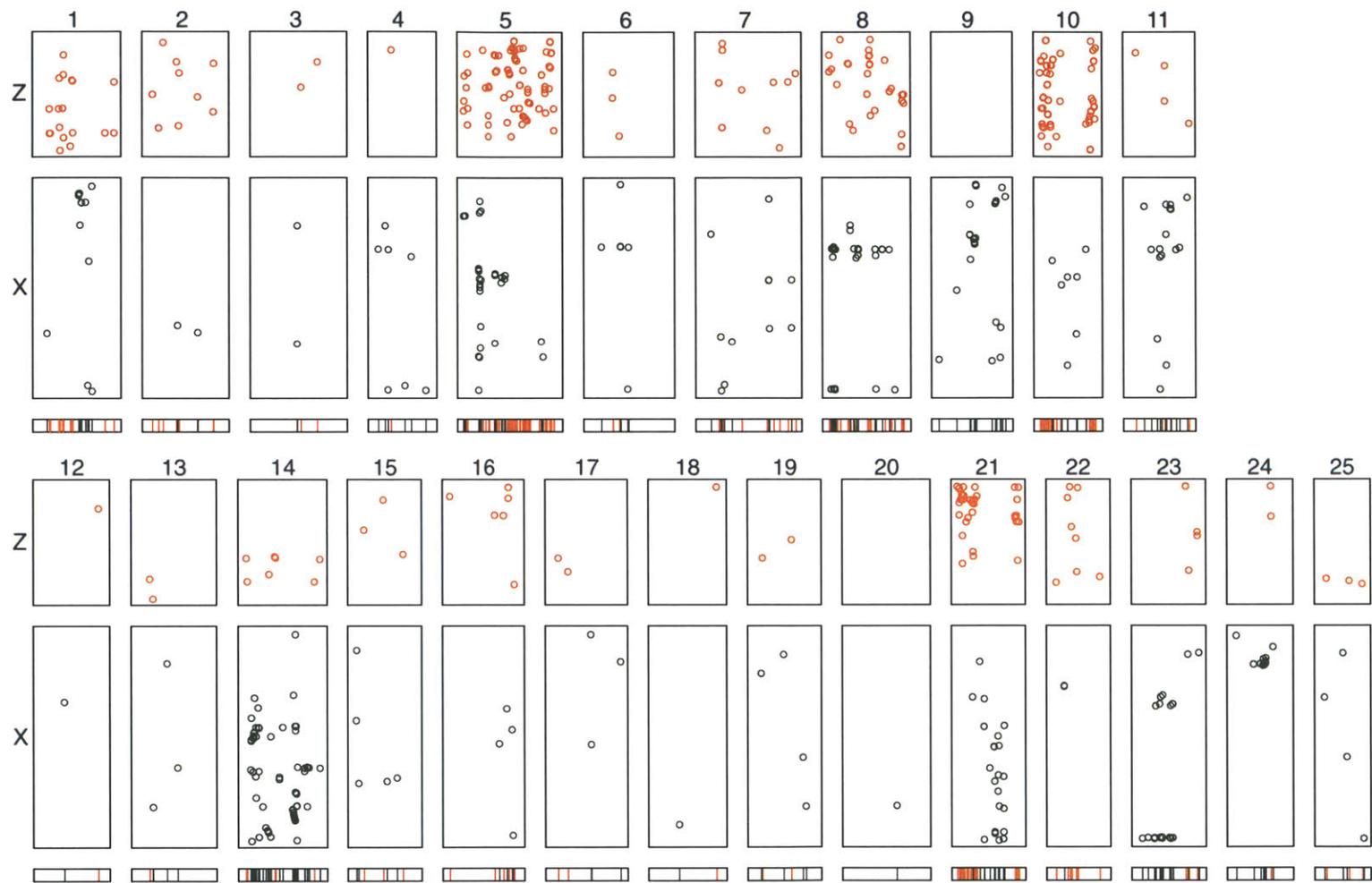
**Supplementary Figure 6:** Dot plots of chicken Z versus all human chromosomes

Square dot plots show the locations of 1:1 orthologs between two species. The chicken Z is orthologous to portions of human autosomes 5 (yellow), 9 (blue), and 18 (purple). Orthology with other chromosomes is limited to a handful of isolated genes.



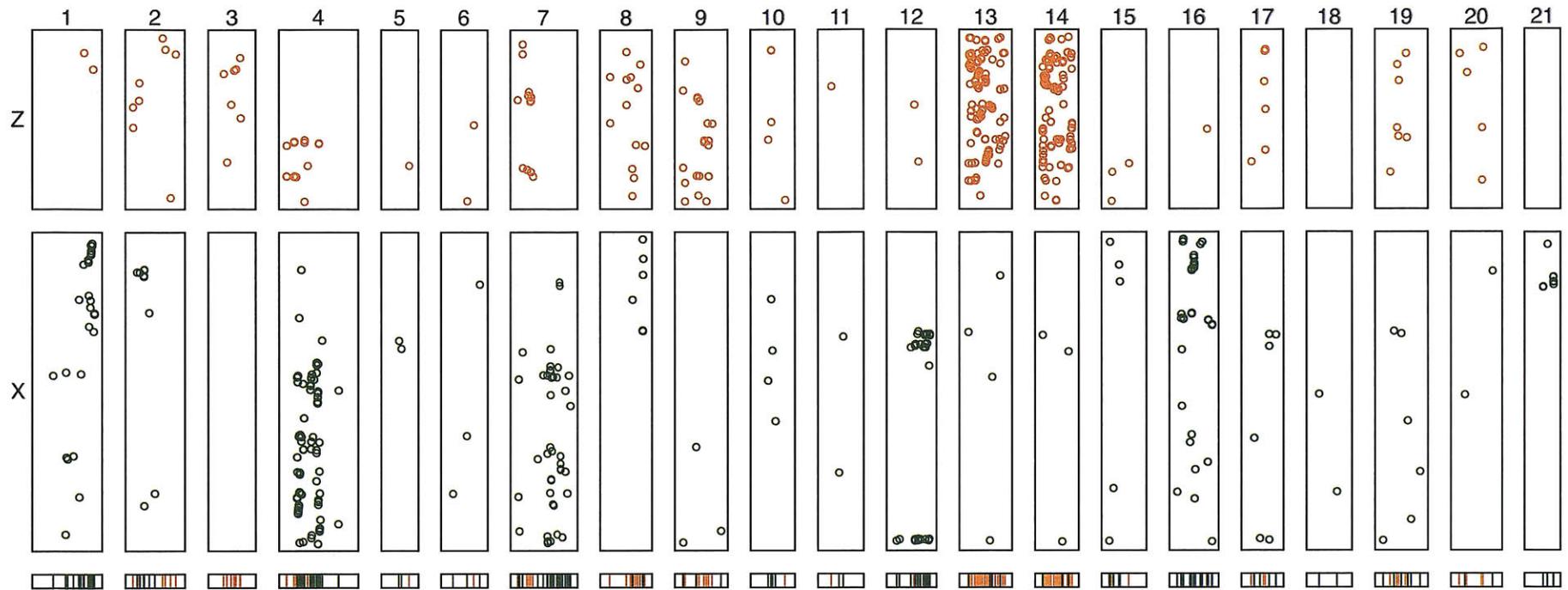
**Supplementary Figure 7: Dot plots of human X versus all chicken chromosomes**

Square dot plots show the locations of 1:1 orthologs between two species. The human X is orthologous to portions of chicken autosomes 1 (red) and 4 (cyan). Orthology with other chromosomes is limited to a handful of isolated genes.



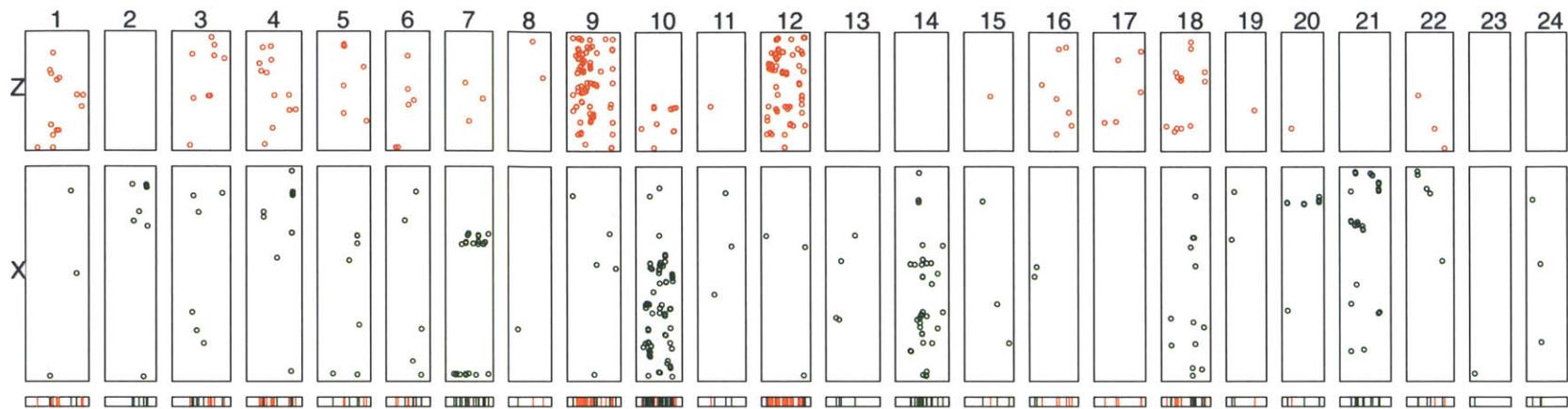
**Supplementary Figure 8:** Dot plots of chicken Z and human X versus all zebrafish chromosomes

Square dot plots show the locations of 1:1 orthologs between two species. These locations are projected onto bars to show the relative contribution of chicken Z and human X orthologs. Orthologs of genes on the chicken Z (orange) are concentrated on zebrafish chromosomes 5, 10, and 21. Orthologs of genes on the human X (green) are concentrated on zebrafish chromosomes 9 and 14. Other chromosomes contain scattered Z and X orthologs.



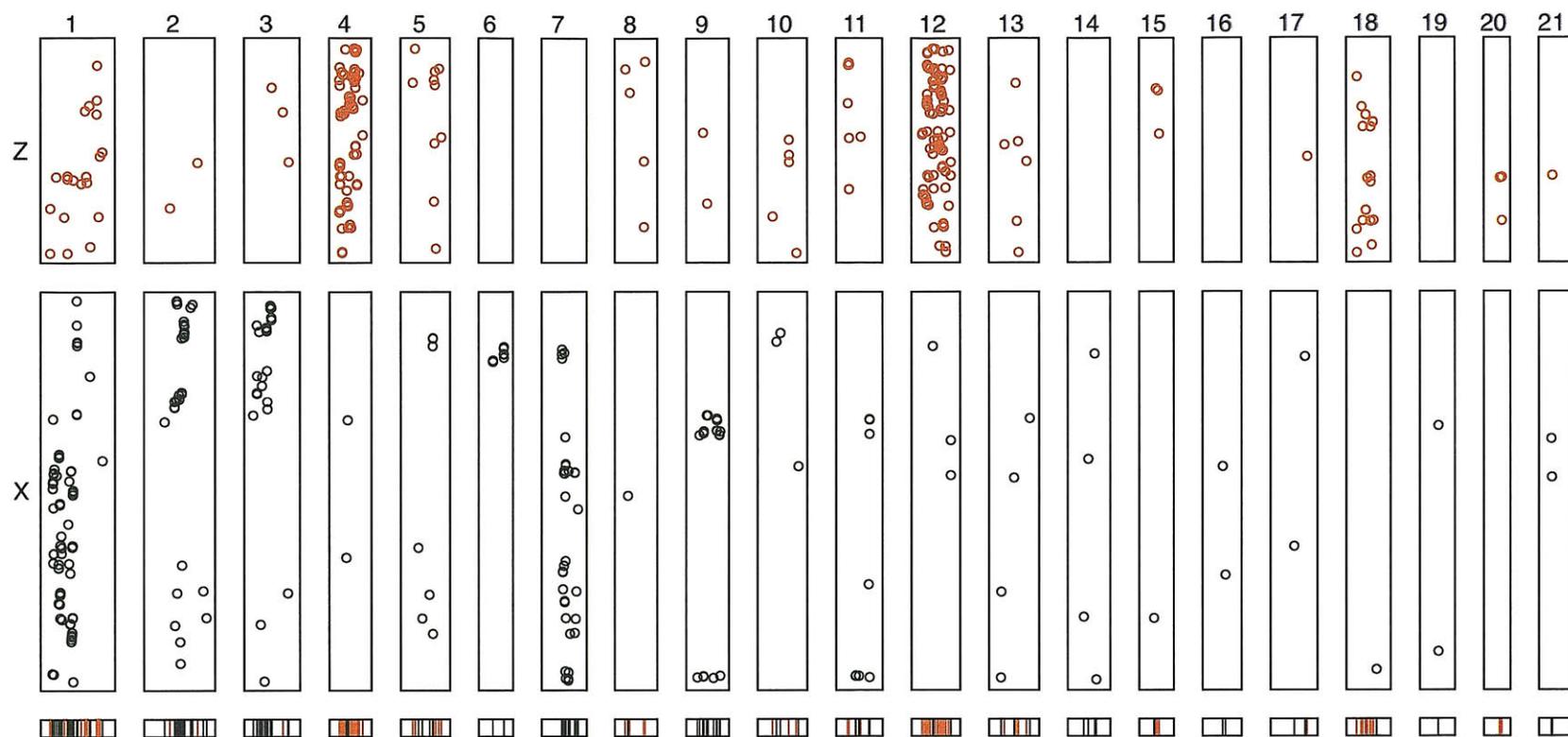
**Supplementary Figure 9: Dot plots of chicken Z and human X versus all stickleback chromosomes**

Square dot plots show the locations of 1:1 orthologs between two species. These locations are projected onto bars to show the relative contribution of chicken Z and human X orthologs. Orthologs of genes on the chicken Z (orange) are concentrated on stickleback chromosomes 13 and 14. Orthologs of genes on the human X (green) are concentrated on stickleback chromosomes 1, 4, 7, and 16. Other chromosomes contain scattered Z and X orthologs.



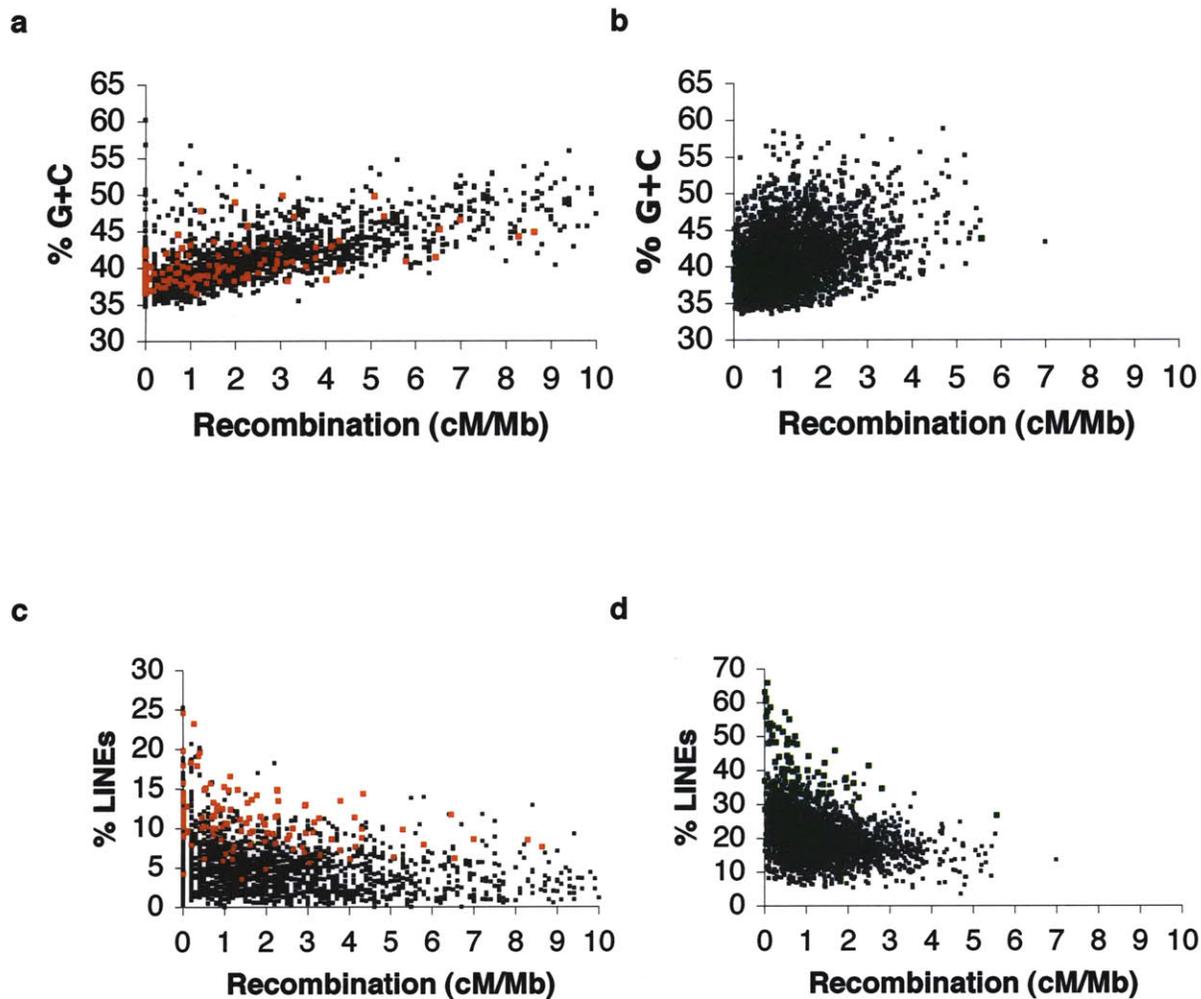
**Supplementary Figure 10:** Dot plots of chicken Z and human X versus all medaka chromosomes

Square dot plots show the locations of 1:1 orthologs between two species. These locations are projected onto bars to show the relative contribution of chicken Z and human X orthologs. Orthologs of genes on the chicken Z (orange) are concentrated on medaka chromosomes 9 and 12. Orthologs of genes on the human X (green) are concentrated on medaka chromosomes 10, 14, and 21. Other chromosomes contain scattered Z and X orthologs.



**Supplementary Figure 11: Dot plots of chicken Z and human X versus all pufferfish chromosomes**

Square dot plots show the locations of 1:1 orthologs between two species. These locations are projected onto bars to show the relative contribution of chicken Z and human X orthologs. Orthologs of genes on the chicken Z (orange) are concentrated on pufferfish chromosomes 4 and 12. Orthologs of genes on the human X (green) are concentrated on pufferfish chromosomes 1, 2, 3, and 7. Other chromosomes contain scattered Z and X orthologs.



**Supplementary Figure 12: Recombination, G+C content, and LINE density**

Each point represents an interval of sequence bounded by adjacent markers on the chicken or human genetic map. G+C content is positively correlated with recombination rate in both the chicken (a) and human (b) genomes. The G+C content of intervals on the Z chromosome (orange) and X chromosome (green) are similar to the G+C content of autosomal intervals (grey) with the same recombination rate.

LINE density is inversely correlated with recombination rate in both chicken (c) and human (d) genomes. Intervals on the Z chromosome (orange) and X chromosome (green) are enriched in LINES compared to autosomes (grey). For additional information, see Supplementary Note 1.

Supplementary Table 1: Chicken Z chromosome predicted genes and human orthologs

ID	NAME	Unigene	Ensembl-Chicken	Chicken Chr	Chicken Beg	Chicken End	Strand	Ensembl-Human	Human Chr	Human Beg	Orthology Group
1	TCF4			Z	13014	17394		1 ENSG00000196628	18	51040560	A
2	ATP8B1	Gga#S6825579	ENSGALG00000003253	Z	330300	353647		0 ENSG000000081923	18	53464656	A
3	NARS	Gga#S22197061	ENSGALG00000003087	Z	354861	365087		0 ENSG00000134440	18	53418894	A
4	HEMH	Gga#S19183308	ENSGALG00000003066	Z	368798	379356		0 ENSG000000066926	18	53366535	A
5	ONECUT2			Z	397502	412327		1 ENSG00000119547	18	53253915	A
6	ST8SIA3	Gga#S19789285	ENSGALG00000003049	Z	423931	427969		1 ENSG00000177511	18	53170719	A
7	WDR7	Gga#S35713644	ENSGALG00000003019	Z	467783	571672		1 ENSG000000091157	18	52469614	A
8	TXNL1	Gga#S33768431	ENSGALG00000002948	Z	581344	595586		0 ENSG000000091164	18	52421053	A
9	NEDD4L	Gga#S21385972	ENSGALG00000002917	Z	669845	729868		0 ENSG000000049759	18	53862778	A
10	ALPK2	Gga#S21385973	ENSGALG00000002898	Z	756230	783843		1 ENSG00000198796	18	54299459	A
11	MALT1	Gga#S35713641	ENSGALG00000002872	Z	796591	834296		0 ENSG00000172175	18	54489598	A
12	ZNF532	Gga#S21044103	ENSGALG00000002852	Z	852028	878250		0 ENSG000000074657	18	54681041	A
13	SEC11L3	Gga#S18605452	ENSGALG00000002839	Z	887557	892444		0 ENSG00000166562	18	54958105	A
14	RAX	Gga#S19183220	ENSGALG000000013431	Z	909472	910876		1 ENSG00000134438	18	55085247	A
15	CPLX4		ENSGALG00000002817	Z	916265	928729		1 ENSG00000166569	18	55113634	A
16	LMAN1	Gga#S23830855	ENSGALG00000002805	Z	933892	955923		1 ENSG000000074695	18	55148088	A
17	ACAA2	Gga#S22197721	ENSGALG00000002777	Z	973832	985606		0 ENSG00000167315	18	45563873	A
18	LIPG	Gga#S21385980	ENSGALG00000002712	Z	1050384	1057572		1 ENSG00000101670	18	45342425	A
19	OR13J1			Z	1055458	1073157		ENSG00000168828	9	35859260	
20	RPL17	Gga#S33765682	ENSGALG00000002696	Z	1066621	1072642		0 ENSG00000215472	18	45269794	A
21	C18orf32		ENSGALG000000018565	Z	1071736	1071865		0 ENSG00000177576	18	45262027	A
22	DYM	Gga#S22197716	ENSGALG00000002677	Z	1082467	1221575		0 ENSG00000141627	18	44824170	A
23	SMAD7	Gga#S21388974	ENSGALG000000018639	Z	1251091	1255784		0 ENSG00000101665	18	44700222	A
24	KIAA0427	Gga#S35713638	ENSGALG000000023718	Z	1291621	1343370		1 ENSG00000134030	18	44319425	A
25	ZBTB7C	Gga#S21390332	ENSGALG000000014696	Z	1473518	1482905		0 ENSG00000184828	18	43807746	A
26	SMAD2	Gga#S19551184	ENSGALG000000014697	Z	1512559	1543682		0 ENSG00000175387	18	43613464	A
27	Q2VWA4	Gga#S35713637	ENSGALG00000001867	Z	1712534	1729287		0 ENSG00000215474	18	43011492	A
28	IER3IP1	Gga#S33769616		Z	1742146	1743588		0 ENSG00000134049	18	42935413	A
29	HDHD2	Gga#S21393316	ENSGALG00000001865	Z	1747422	1752346		0 ENSG00000167220	18	42887780	A
30	KATNAL2	Gga#S21393317	ENSGALG00000001851	Z	1754244	1770631		1 ENSG00000167216	18	42780785	A
31	PIAS2	Gga#S22196587	ENSGALG00000001843	Z	1773475	1798385		0 ENSG000000078043	18	42646058	A
32	ST8SIA5	Gga#S19871246	ENSGALG00000001808	Z	1835018	1863877		0 ENSG00000101638	18	42513079	A
33	LOXHD1		ENSGALG00000001787	Z	1888711	1995369		0 ENSG00000167210	18	42310933	A
34	RNF165	Gga#S21393320	ENSGALG00000001766	Z	2031598	2040710		1 ENSG00000141622	18	42168185	A
35	C18orf25	Gga#S21393321	ENSGALG00000001763	Z	2077902	2102792		1 ENSG00000152242	18	42007986	A
36	CCDC5	Gga#S33763497	ENSGALG00000001761	Z	2127364	2136065		1 ENSG00000152240	18	41938323	A
37	ATP5A1	Gga#S33769889	ENSGALG00000014644	Z	2139446	2147186		0 ENSG00000152234	18	41918108	A
38	PSTPIP2	Gga#S35713634	ENSGALG00000001745	Z	2148849	2162986		0 ENSG00000152229	18	41817500	A
39	KIAA1632	Gga#S21393323	ENSGALG00000001732	Z	2164879	2211990		0 ENSG00000152223	18	41681573	A
40	SIGLEC15		ENSGALG000000021416	Z	2217016	2219837		0 ENSG00000197046	18	41659543	A
41	SLC14A2			Z	2239719	2274692		0 ENSG00000132874	18	41448780	A
42	SLC14A1	Gga#S35713632	ENSGALG00000001705	Z	2267294	2277893		1 ENSG00000141469	18	41558147	A
43	SETBP1	Gga#S35713631	ENSGALG00000001677	Z	2693022	2703754		1 ENSG00000152217	18	40514861	A
44	SYT4	Gga#S21397150	ENSGALG00000008893	Z	3292215	3299863		0 ENSG00000132872	18	39101857	A
45	RIT2	Gga#S35713630	ENSGALG00000017593	Z	3353261	3455732		0 ENSG00000152214	18	38577191	A
46	PIK3C3	Gga#S19182635	ENSGALG00000008887	Z	3875564	3942528		1 ENSG000000078142	18	37789197	A
47	BRUNOL4		ENSGALG000000018499	Z	6110732	6122308		0 ENSG00000101489	18	33077828	A
48	ASA2G2	Gga#S35713627	ENSGALG00000002413	Z	6636818	6716710		0 ENSG00000101489	18	33077828	A
49	KIAA1328	Gga#S23831017	ENSGALG00000002419	Z	6809182	6843536		1 ENSG00000150477	18	32663078	A
50	C18orf10	Gga#S21385929	ENSGALG00000002429	Z	6966627	6988931		0 ENSG00000134779	18	32630033	A
51	AQP7P4		ENSGALG000000018534	Z	6992391	6995442		0 ENSG00000176115	9	66961803	A
52	cZorf4	Gga#S21385927	ENSGALG000000017527	Z	7025006	7028689		1 ENSGALG000000017527			B2
53	AQP3	Gga#S21385926	ENSGALG00000002452	Z	7060177	7072863		1 ENSG00000165272	9	33431161	A
54	NOL6	Gga#S18605824	ENSGALG000000014168	Z	7118021	7155958		1 ENSG00000165271	9	33451354	A
55	UBE2R2	Gga#S22196269	ENSGALG00000001668	Z	7167734	7220058		0 ENSG00000107341	9	33807182	A
56	Q6Y2W3	Gga#S35713672	ENSGALG000000013809	Z	7223381	7230115		1 ENSG00000137073	9	33911691	A
57	IFNB	Gga#S22520332	ENSGALG00000005759	Z	7235572	7236234		0 ENSGALG00000005759			B1
58	IFN1A		ENSGALG000000013245	Z	7241179	7241760		0 ENSGALG000000013245			B1

59 UBAP2		ENSGALG00000013809	Z	7282021	7302577	1 ENSG000000137073	9	33911691 A
60 WDR40A	Gga#S23830976	ENSGALG00000005800	Z	7342184	7367710	1 ENSG000000198876	9	34076386 A
61 UBAP1	Gga#S21389972	ENSGALG000000021378	Z	7387534	7401743	0 ENSG000000165006	9	34169011 A
62 C9orf48	Gga#S6731917	ENSGALG00000005806	Z	7410737	7435569	1 ENSG000000186638	9	34242379 A
63 NUDT2	Gga#S18606387	ENSGALG00000005810	Z	7442541	7445953	0 ENSG000000164978	9	34319504 A
64 cZorf2	Gga#S21389979	ENSGALG00000005813	Z	7450248	7464354	1 ENSGALG00000005813		B2
65 KIAA1161	Gga#S21389978	ENSGALG00000005814	Z	7481951	7483921	1 ENSG000000164976	9	34358907 A
66 C9orf24	Gga#S21274402	ENSGALG00000005818	Z	7491114	7495150	1 ENSG000000164972	9	34369017 A
67 C9orf25	Gga#S35713622	ENSGALG00000005821	Z	7504745	7542257	0 ENSG000000164970	9	34388182 A
68 DNAI1	Gga#S35713620	ENSGALG00000005831	Z	7612638	7732417	0 ENSG000000122735	9	34448811 A
69 ARID3C	Gga#S21389976	ENSGALG00000005839	Z	7737308	7765961	1 ENSG000000205143	9	34611455 A
70 C9orf23		ENSGALG00000005833	Z	7737442	7737853	0 ENSG000000164967	9	34600493 A
71 DCTN3		ENSGALG00000021365	Z	7741849	7748828	0 ENSG000000137100	9	34603549 A
72 SIGMAR	Gga#S22197487		Z	7769786	7771276	1 ENSG000000147955	9	34624719 A
73 GALT	Gga#S33762530		Z	7771931	7774233	0 ENSG000000213930	9	34636635 A
74 CNTFR	Gga#S19183023	ENSGALG00000007275	Z	8109916	8130764	0 ENSG000000122756	9	34541432 A
75 IL11RA	Gga#S22414595	ENSGALG00000005848	Z	8155875	8176128	0 ENSG000000137070	9	34643932 A
76 KIAA1045	Gga#S21389965	ENSGALG00000001900	Z	8272396	8275121	0 ENSG000000122733	9	34948192 A
77 DNABJ5	Gga#S21389964	ENSGALG00000001918	Z	8290987	8303144	0 ENSG000000137094	9	34979742 A
78 PIGO	Gga#S35713616	ENSGALG00000002023	Z	8307850	8370054	1 ENSG000000165282	9	35078685 A
79 VCP		ENSGALG00000001986	Z	8307852	8324030	0 ENSG000000165280	9	35046904 A
80 FANCG		ENSGALG00000002009	Z	8338237	8341273	0 ENSG000000221829	9	35063837 A
81 STOML2		ENSGALG00000002064	Z	8359674	8430745	0 ENSG000000165283	9	35089891 A
82 KIAA1539		ENSGALG00000002069	Z	8365469	8396354	0 ENSG00000005238	9	35094109 A
83 UNC13B		ENSGALG00000002165	Z	8522690	8621277	0 ENSG000000198722	9	35151989 A
84 AL133476.17	Gga#S21389937	ENSGALG00000002326	Z	8652284	8710304	0 ENSG000000179766	9	35396765 A
85 RUSC2	Gga#S35713614	ENSGALG00000002371	Z	8750054	8765789	0 ENSG000000198853	9	35480124 A
86 PTPRK-like	Gga#S21389959	ENSGALG000000021355	Z	8769950	8790528	0 ENSGALG000000021355		B1
87 TESK1	Gga#S21512829		Z	8814651	8822244	0 ENSG000000107140	9	35595281 A
88 CD72	Gga#S19183050	ENSGALG00000005194	Z	8823764	8826769	1 ENSG000000137101	9	35599530 A
89 cZorf13	Gga#S19629597		Z	8839177	8841670	0		B1
90 C9orf127	Gga#S19634228	ENSGALG00000002386	Z	8847140	8852615	1 ENSG000000137103	9	35804448 A
91 TAF1C			Z	8854602	8863256	0		B1
92 HINT2			Z	8857351	8859999	0 ENSG000000137133	9	35802957 A
93 SPAG8			Z	8862363	8862449	0 ENSG000000137098	9	35797782 A
94 NPR2	Gga#S6749376	ENSGALG00000023627	Z	8864356	8873409	1 ENSG000000159899	9	35782151 A
95 MSMP			Z	8880560	8881890	0 ENSG000000215183	9	35742990 A
96 RGP1	Gga#S23830910	ENSGALG00000002394	Z	8883531	8892025	1 ENSG000000107185	9	35739340 A
97 GBA2	Gga#S6717936	ENSGALG00000002412	Z	8892641	8901913	0 ENSG00000070610	9	35726864 A
98 AVIDIN-like	Gga#S21389933	ENSGALG000000021848	Z	8903176	8903946	0 ENSGALG000000021848		B1
99 AVID		ENSGALG000000023622	Z	8911953	8912993	1 ENSGALG000000023622		B1
100 AVR2	Gga#S7088877	ENSGALG00000002446	Z	8915587	8920538	0 ENSGALG00000002446		B1
101 also similar to	Gga#S14752369	ENSGALG000000023622	Z	8931274	8932328			B1
102 also similar to	AVIDIN	ENSGALG000000023622	Z	8931274				B1
103 CREB3	Gga#S21389956	ENSGALG00000002523	Z	8935185	8941063	1 ENSG000000107175	9	35722317 A
104 TLN1	Gga#S19183604	ENSGALG00000002548	Z	8942836	8969650	0 ENSG000000137076	9	35687336 A
105 Q9PST0	Gga#S7089362	ENSGALG00000002563	Z	8973864	8982209	0 ENSG000000198467	9	35671990 A
106 APH1A	Gga#S33769572	ENSGALG00000002578	Z	8988105	8991723	0 ENSG000000117362	1	148502512 B3a
107 CA9	Gga#S35713605	ENSGALG000000021340	Z	8993052	8997637	1 ENSG000000107159	9	35663853 A
108 cZorf6	Gga#S21389954	ENSGALG000000021338	Z	9024424	9051879	1 ENSGALG000000021338		B1
109 MYO5B			Z	9037011	9044454	0 ENSG000000167306	18	45603099 A
110 C9orf100	Gga#S21389931	ENSGALG00000002599	Z	9052340	9062390	0 ENSG000000137135	9	35649341 A
111 MRPL17	Gga#S33765425	ENSGALG00000002605	Z	9064611	9065251	1 ENSG000000158042	11	6659456 B3a
112 CCBE1		ENSGALG00000002613	Z	9070159	9091921	1 ENSG000000183287	18	55252129 A
113 PDZD2	Gga#S21389952	ENSGALG00000002854	Z	9223760	9284959	1 ENSG000000133401	5	31834788 A
114 GOLPH3	Gga#S21389951	ENSGALG000000003151	Z	9434929	9463508	1 ENSG000000113384	5	32160581 A
115 MTMR12	Gga#S21389950	ENSGALG000000003168	Z	9476201	9505530	1 ENSG000000150712	5	32262868 A
116 ZFR	Gga#S21389949	ENSGALG000000003235	Z	9520947	9549545	1 ENSG000000056097	5	32390214 A
117 TCP4	Gga#S22197116	ENSGALG000000003248	Z	9569665	9579538	0 ENSG000000113387	5	32621434 A
118 NPR3	Gga#S6905136	ENSGALG00000017405	Z	9814902	9853936	1 ENSG000000113389	5	32747422 A

119 TARS	Gga#S22197714	ENSGALG00000003288	Z	9869024	9883210	0 ENSG00000113407	5	33476655 A
120 ADAMTS12	Gga#S35713600	ENSGALG00000003295	Z	9907419	9983087	1 ENSG00000151388	5	33563043 A
121 RXFP3	Gga#S21389928	ENSGALG000000017411	Z	10081770	10083110	0 ENSG00000182631	5	33972246 A
122 A3QW68	Gga#S37260020	ENSGALG000000003310	Z	10095465	10112682	1 ENSG00000164175	5	33980481 A
123 AMACR	Gga#S22197466	ENSGALG000000003326	Z	10114770	10135049	1 ENSG000000082196	5	34023069 A
124 RAI14	Gga#S21389942	ENSGALG000000003353	Z	10231367	10311412	0 ENSG000000039560	5	34692275 A
125 RAD1	Gga#S33763646	ENSGALG000000003365	Z	10324779	10330087	1 ENSG00000113456	5	34938268 A
126 BXDC2	Gga#S33765254	ENSGALG000000003373	Z	10330247	10333640	0 ENSG00000113460	5	34951577 A
127 DNAJA5	Gga#S21389939	ENSGALG000000003387	Z	10334847	10348909	0 ENSG00000168724	5	34965455 A
128 AGXT2	Gga#S21389926	ENSGALG000000003432	Z	10351118	10362824	1 ENSG00000113492	5	35033965 A
129 PRLR	Gga#S19551205	ENSGALG000000003446	Z	10377880	10399479	1 ENSG00000113494	5	35084621 A
130 SPEF2	Gga#S18606629	ENSGALG000000003459	Z	10561297	10595393	0 ENSG00000152582	5	35653746 A
131 A1EA95	Gga#S36019312	ENSGALG00000013372	Z	10653651	10666612	0 ENSG00000168685	5	35892748 A
132 CAPSL	Gga#S33760266	ENSGALG000000013376	Z	10675092	10679076	1 ENSG00000152611	5	35940157 A
133 LMBRD2	Gga#S23830864	ENSGALG000000013377	Z	10704936	10740976	1 ENSG00000164187	5	36139171 A
134 SKP2	Gga#S22197852	ENSGALG000000003547	Z	10746116	10755093	0 ENSG00000145604	5	36187946 A
135 C5orf33	Gga#S35713597	ENSGALG000000003558	Z	10759830	10832868	1 ENSG00000152620	5	36228451 A
136 AC008942.6-1			Z	10775905	10789431	0 ENSG00000219830	5	36263356 A
137 AC104127.2			Z	10789482	10789366	0 ENSG00000218494	5	93515468 B1
138 RANBP3L		ENSGALG000000021304	Z	10801765	10820148	0 ENSG00000164188	5	36284862 A
139 Q9IAS3	Gga#S21389921	ENSGALG000000003582	Z	10938885	10999058	0 ENSG00000079215	5	36642446 A
140 NIPBL	Gga#S21389920	ENSGALG000000003605	Z	11124762	11220600	0 ENSG00000164190	5	36912649 A
141 C5orf42	Gga#S35713596	ENSGALG000000003629	Z	11234645	11298031	1 ENSG00000197603	5	37142087 A
142 AC025449.6-3		ENSGALG000000003631	Z	11280703	11297128	0 ENSG00000215147	5	37241214 A
143 NUP155	Gga#S21389916	ENSGALG000000003688	Z	11300366	11331197	1 ENSG00000113569	5	37327698 A
144 WDR70	Gga#S22196679	ENSGALG000000003708	Z	11332836	11468048	0 ENSG000000082068	5	37415169 A
145 Q9IAM2	Gga#S7087632	ENSGALG000000003716	Z	11493411	11512674	1 ENSG00000168621	5	37848536 A
146 EGFLAM	Gga#S21389913	ENSGALG000000003726	Z	11687383	11759688	0 ENSG00000164318	5	38294290 A
147 LIFR	Gga#S19183650	ENSGALG000000003733	Z	11774693	11801832	1 ENSG00000113594	5	38510823 A
148 OSMR	Gga#S21389912	ENSGALG000000003747	Z	11923198	11947381	0 ENSG00000145623	5	38881893 A
149 RICTOR	Gga#S35713594	ENSGALG000000003775	Z	11953811	11996704	1 ENSG00000164327	5	38973779 A
150 FYB	Gga#S22196342	ENSGALG000000003792	Z	12039412	12100134	1 ENSG000000082074	5	39141115 A
151 DAB2	Gga#S35713592	ENSGALG000000003803	Z	12115936	12125706	1 ENSG00000153071	5	39407537 A
152 A2TH16	Gga#S36661938	ENSGALG00000014824	Z	12607398	12616434	0 ENSG00000171522	5	40715789 A
153 PRKAA1	Gga#S29944157	ENSGALG00000014832	Z	12622605	12679307	1 ENSG00000132356	5	40795238 A
154 TTC33		ENSGALG00000014826	Z	12622607	12657710	0 ENSG00000113638	5	40747439 A
155 MELK		ENSGALG00000016438	Z	12668035	12754479	0 ENSG00000165304	9	36562873 A
156 RPL37	Gga#S29401688	ENSGALG00000014833	Z	12684859	12687274	1 ENSG00000145592	5	40867187 A
157 C7	Gga#S21390271	ENSGALG00000014835	Z	12703690	12722765	0 ENSG00000112936	5	40945356 A
158 C6		ENSGALG00000014840	Z	12734366	12765066	1 ENSG000000039537	5	41178093 A
159 PLCXD3	Gga#S33767385	ENSGALG00000014845	Z	12787286	12877282	1 ENSG00000182836	5	41342805 A
160 OXCT1	Gga#S22980535	ENSGALG00000014846	Z	12946701	12981067	1 ENSG000000083720	5	41765925 A
161 C5orf51	Gga#S21390267	ENSGALG00000014849	Z	13040107	13048827	0 ENSG00000205765	5	41940227 A
162 FBXO4		ENSGALG00000014851	Z	13043626	13049228	0 ENSG00000151876	5	41961113 A
163 GHR	Gga#S20191471	ENSGALG00000014855	Z	13309802	13324824	0 ENSG00000112964	5	42459783 A
164 CCDC152		ENSGALG00000023503	Z	13339262	13353835	0 ENSG00000198865	5	42792687 A
165 SEPP1	Gga#S26468079	ENSGALG00000014857	Z	13355763	13361809	1 ENSG00000211446	5	42836579 A
166 ZNF131		ENSGALG00000014859	Z	13381238	13392714	0 ENSG00000172262	5	43157399 A
167 NIM1	Gga#S19788932	ENSGALG00000014861	Z	13381239	13420388	0 ENSG00000177453	5	43228084 A
168 HMCS1	Gga#S19184021	ENSGALG00000014862	Z	13423735	13428723	1 ENSG00000112972	5	43325250 A
169 C5orf28	Gga#S21390262	ENSGALG00000014863	Z	13457746	13471854	1 ENSG00000151881	5	43480112 A
170 C5orf34	Gga#S21390261	ENSGALG00000014865	Z	13476867	13487725	1 ENSG00000172244	5	43522567 A
171 PAIP1	Gga#S35713588	ENSGALG00000014867	Z	13491966	13510448	1 ENSG00000172239	5	43562129 A
172 NNT	Gga#S35713586	ENSGALG00000014869	Z	13514136	13554968	0 ENSG00000112992	5	43638582 A
173 FGF10	Gga#S19183813	ENSGALG00000014872	Z	13794014	13798918	1 ENSG00000070193	5	44340831 A
174 MRPS30	Gga#S19182977	ENSGALG00000014874	Z	13950132	13955320	0 ENSG00000112996	5	44844784 A
175 HCN1		ENSGALG00000014875	Z	14175748	14370192	1 ENSG00000164588	5	45295125 A
176 EMB	Gga#S19183635	ENSGALG00000014877	Z	14455744	14527304	1 ENSG00000170571	5	49730236 A
177 PARP8	Gga#S21390257	ENSGALG00000014880	Z	14620858	14672681	0 ENSG00000151883	5	49998570 A
178 ISL1	Gga#S19184025	ENSGALG00000014884	Z	14911245	14921769	0 ENSG00000016082	5	50714715 A

179 PELO	Gga#S22197054	ENSGALG00000022377	Z	15545840	15548128	0 ENSG000000152684	5	52119531 A
180 ITA1	Gga#S19183074	ENSGALG00000014891	Z	15561360	15610882	0 ENSG000000213949	5	52119893 A
181 ITGA2		ENSGALG00000014903	Z	15629071	15690951	0 ENSG000000164171	5	52320913 A
182 MOCS2	Gga#S35713583	ENSGALG00000014906	Z	15699045	15702608	1 ENSG000000164172	5	52427266 A
183 FST	Gga#S19183202	ENSGALG00000014908	Z	15839352	15844782	0 ENSG000000134363	5	52812174 A
184 Q8QGHO	Gga#S22196913	ENSGALG00000014909	Z	15870578	15915856	0 ENSG000000164258	5	52892242 A
185 ARL15	Gga#S35713577	ENSGALG00000014911	Z	16087162	16103232	1 ENSG000000185305	5	53216371 A
186 SNX18	Gga#S35713580	ENSGALG00000014914	Z	16205099	16236941	0 ENSG000000178996	5	53849350 A
187 HSPB3		ENSGALG00000014912	Z	16205290	16205539	0 ENSG000000169271	5	53787202 A
188 ESM1			Z	16394708	16401071	0 ENSG000000164283	5	54309915 A
189 GZMK	Gga#S21387347	ENSGALG00000013546	Z	16416503	16421730	1 ENSG000000113088	5	54355864 A
190 GZMA	Gga#S16073703	ENSGALG00000013548	Z	16428650	16432527	0 ENSG000000145649	5	54434230 A
191 CDC20B	Gga#S21387346	ENSGALG00000023476	Z	16441685	16454042	1 ENSG000000164287	5	54444580 A
192 GPX8	Gga#S29405208	ENSGALG00000013553	Z	16462732	16465296	0 ENSG000000164294	5	54491744 A
193 CCNO			Z	16497435	16497436	0 ENSG000000152669	5	54562740 A
194 DHX29	Gga#S21390331	ENSGALG00000014700	Z	16504263	16525288	1 ENSG000000067248	5	54587831 A
195 SKIV2L2	Gga#S22198004	ENSGALG00000014709	Z	16528159	16572487	0 ENSG000000039123	5	54639594 A
196 PPAP2A	Gga#S19551293	ENSGALG00000014711	Z	16572872	16627708	1 ENSG000000067113	5	54756442 A
197 SLC38A9	Gga#S21390328	ENSGALG00000014712	Z	16651237	16687783	1 ENSG000000177058	5	54957430 A
198 DDX4	Gga#S19183831	ENSGALG00000014713	Z	16696396	16725120	0 ENSG000000152670	5	55069627 A
199 IL31RA	Gga#S21390327	ENSGALG00000014714	Z	16766573	16780434	0 ENSG000000164509	5	55182964 A
200 IL6ST	Gga#S19183968	ENSGALG00000014716	Z	16794968	16819363	1 ENSG000000134352	5	55266680 A
201 ANKRD55		ENSGALG00000014717	Z	16859047	16909279	1 ENSG000000164512	5	55431264 A
202 MAP3K1	Gga#S21390322	ENSGALG00000014718	Z	17206212	17237622	0 ENSG000000095015	5	56146657 A
203 C5orf35		ENSGALG00000014719	Z	17231696	17237616	0 ENSG000000155542	5	56240857 A
204 MIER3	Gga#S21390320	ENSGALG00000014721	Z	17246424	17269405	1 ENSG000000155545	5	56251186 A
205 GPBP1	Gga#S21390318	ENSGALG00000014724	Z	17302941	17321708	0 ENSG000000062194	5	56505701 A
206 PLK2	Gga#S21390316	ENSGALG00000014725	Z	17786738	17792050	1 ENSG000000145632	5	57785571 A
207 RAB3C	Gga#S35713572	ENSGALG00000014726	Z	17845969	17912113	0 ENSG000000152932	5	57914696 A
208 PDE4D	Gga#S35713571	ENSGALG00000014727	Z	18020720	18068366	1 ENSG000000113448	5	58300629 A
209 DEP1B	Gga#S22197535	ENSGALG00000014729	Z	18623218	18641333	1 ENSG000000035499	5	59928506 A
210 ELOVL7		ENSGALG00000014730	Z	18644828	18655891	1 ENSG000000164181	5	60083376 A
211 ERCC8	Gga#S21390313	ENSGALG00000014732	Z	18699479	18733810	1 ENSG000000049167	5	60205415 A
212 NDUFAF2	Gga#S35713570	ENSGALG00000014733	Z	18737368	18783477	0 ENSG000000164182	5	60276791 A
213 Q5F409	Gga#S23831133	ENSGALG00000023443	Z	18785922	18786146	1 ENSG000000188725	5	60489297 A
214 ZSWIM6	Gga#S21388339	ENSGALG00000014735	Z	18912440	18971457	0 ENSG000000130449	5	60852928 A
215 cZorf11		ENSGALG00000020570	Z	19100605	19100858	0 X10	5	A
216 KIF2A	Gga#S22197361	ENSGALG00000014737	Z	19187940	19243256	0 ENSG000000068796	5	61637746 A
217 DIMT1L	Gga#S19721885	ENSGALG00000020569	Z	19248664	19255397	1 ENSG000000086189	5	61720108 A
218 IPO11	Gga#S35713569	ENSGALG00000014740	Z	19262666	19329722	0 ENSG000000086200	5	61744351 A
219 HTR1A		ENSGALG00000014742	Z	19760841	19762082	1 ENSG000000178394	5	63292034 A
220 RNF180		ENSGALG00000014743	Z	19834120	19891919	0 ENSG000000164197	5	63497427 A
221 RGS7BP	Gga#S35713560	ENSGALG00000014744	Z	19834664	19955713	0 ENSG000000186479	5	63838208 A
222 FAM159B		ENSGALG00000014745	Z	19973950	19976074	0 ENSG000000153006	5	64049736 A
223 SDCCAG10	Gga#S21390307	ENSGALG00000014747	Z	19978630	19987968	0 ENSG000000153015	5	64100511 A
224 ADAMTS6	Gga#S21390306	ENSGALG00000014751	Z	20135955	20286225	1 ENSG000000049192	5	64480322 A
225 CENPK	Gga#S18605356	ENSGALG00000014753	Z	20316278	20334806	1 ENSG000000123219	5	64849349 A
226 PPWD1	Gga#S21390303	ENSGALG00000014756	Z	20337264	20351383	0 ENSG000000113593	5	64894873 A
227 TRIM23	Gga#S21390302	ENSGALG00000014765	Z	20355383	20373025	1 ENSG000000113595	5	64921268 A
228 C5orf44	Gga#S22196445	ENSGALG00000014767	Z	20380292	203997639	0 ENSG000000113597	5	64956628 A
229 SGTB	Gga#S22196798	ENSGALG00000014768	Z	20402293	20420231	1 ENSG000000197860	5	64997520 A
230 NLN	Gga#S21390299	ENSGALG00000014769	Z	20433278	20458832	0 ENSG000000123213	5	65053834 A
231 ERBB2IP	Gga#S21390277	ENSGALG00000014773	Z	20535250	20607717	0 ENSG000000112851	5	65258158 A
232 SFRS12	Gga#S21390298	ENSGALG00000014775	Z	20618630	20656342	0 ENSG000000153914	5	65475841 A
233 MAST4	Gga#S35713559	ENSGALG00000014784	Z	21001540	21060798	0 ENSG000000069020	5	65927932 A
234 CD180	Gga#S35713558	ENSGALG00000023411	Z	21064239	21071674	1 ENSG000000134061	5	66513872 A
235 PIK3R1	Gga#S21390295	ENSGALG00000014786	Z	21372177	21422773	0 ENSG000000145675	5	67558218 A
236 MRPS36		ENSGALG00000014789	Z	21573150	21689819	0 ENSG000000134056	5	68549329 A
237 SLC30A5	Gga#S22197557	ENSGALG00000014787	Z	21652603	21672629	0 ENSG000000145740	5	68425638 A
238 CENPH	Gga#S19183693	ENSGALG00000014788	Z	21677685	21683126	0 ENSG000000153044	5	68521131 A

239 CDK7	Gga#S18613538	ENSGALG00000014790	Z	21683992	21714386	0 ENSG00000134058	5	68566471 A
240 SERINC5	Gga#S21390291	ENSGALG00000014798	Z	21742485	21773158	0 ENSG00000164300	5	79466607 A
241 Q91002	Gga#S21390290	ENSGALG00000014804	Z	21782331	21820439	1 ENSG00000113296	5	79366859 A
242 Q5F3K9	Gga#S23830918	ENSGALG00000014807	Z	21825182	21833664	0 ENSG00000177034	5	79313964 A
243 PAPP4		ENSGALG00000014810	Z	21893340	21998820	1 ENSG00000164329	5	78944152 A
244 CMYA5		ENSGALG00000014809	Z	21893340	21998820	1 ENSG00000164309	5	78,985,659 A
245 HOMER1	Gga#S21390284	ENSGALG00000014813	Z	22019772	22084974	0 ENSG00000152413	5	78704215 A
246 JMY	Gga#S35713554	ENSGALG00000014819	Z	22103814	22157572	1 ENSG00000152409	5	78568095 A
247 BHMT	Gga#S21393334	ENSGALG00000004518	Z	22189559	22205238	1 ENSG00000145692	5	78443360 A
248 BHMT2		ENSGALG00000004518	Z	22189657	22202301	0 ENSG00000132840	5	78401339 A
249 DMGDH	Gga#S35713553	ENSGALG00000004491	Z	22205667	22250674	0 ENSG00000132837	5	78329186 A
250 ARSB	Gga#S35713552	ENSGALG00000004438	Z	22255809	22321578	0 ENSG00000113273	5	78108795 A
251 LHFPL2	Gga#S21393336	ENSGALG00000004437	Z	22456798	22468723	0 ENSG00000145685	5	77816796 A
252 SCAMP1	Gga#S21393337	ENSGALG00000004425	Z	22476737	22512615	1 ENSG00000085365	5	77692163 A
253 AP3B1	Gga#S35713564	ENSGALG00000004390	Z	22543480	22710351	0 ENSG00000132842	5	77333909 A
254 TBCA	Gga#S33762210	ENSGALG00000004353	Z	22840066	22871586	0 ENSG00000171530	5	77022751 A
255 OTP	Gga#S21537018	ENSGALG00000017547	Z	22892634	22898393	0 ENSG00000171540	5	76960294 A
256 WDR41	Gga#S29405206	ENSGALG00000004350	Z	22937594	22958072	0 ENSG00000164253	5	76763826 A
257 PDE8B		ENSGALG00000004339	Z	22963774	22999799	1 ENSG00000113231	5	76542462 A
258 AGGF1	Gga#S21393341	ENSGALG00000004311	Z	23065947	23085838	1 ENSG00000164252	5	76361988 A
259 CRHBP	Gga#S21390233	ENSGALG00000014994	Z	23121208	23129094	1 ENSG00000145708	5	76284436 A
260 S100Z		ENSGALG00000014989	Z	23142189	23143721	1 ENSG00000171643	5	76181582 A
261 F2RL1	Gga#S23831254	ENSGALG00000014984	Z	23168989	23175642	1 ENSG00000164251	5	76150610 A
262 F2R	Gga#S21390235	ENSGALG00000014983	Z	23201330	23208612	1 ENSG00000181104	5	76047542 A
263 IQGAP2	Gga#S33768853	ENSGALG00000014978	Z	23215777	23311601	1 ENSG00000145703	5	75734905 A
264 F2RL2		ENSGALG00000023379	Z	23247284	23248160	0 ENSG00000164220	5	75947064 A
265 SV2C	Gga#S21390230	ENSGALG00000014967	Z	23348601	23417166	1 ENSG00000122012	5	75415060 A
266 C5orf37	Gga#S21390237	ENSGALG00000014960	Z	23577811	23597483	0 ENSG00000152359	5	75005705 A
267 ANKDD1B	Gga#S21390231	ENSGALG00000014958	Z	23598899	23620675	1 ENSG00000189045	5	74948395 A
268 POLK	Gga#S19183294	ENSGALG00000014956	Z	23626041	23649779	1 ENSG00000122008	5	74843337 A
269 COL4A3BP	Gga#S21390238	ENSGALG00000014952	Z	23658812	23729233	0 ENSG00000113163	5	74702684 A
270 HMGCR	Gga#S17668715	ENSGALG00000014948	Z	23762420	23778919	1 ENSG00000113161	5	74668855 A
271 ANKRD31	Gga#S21390239	ENSGALG00000014945	Z	23786543	23836231	0 ENSG00000145700	5	74478817 A
272 GCNT4	Gga#S21390240	ENSGALG00000014944	Z	23856387	23859301	0 ENSG00000176928	5	74356927 A
273 FAM169A	Gga#S21390232	ENSGALG00000014943	Z	23932608	23949835	0 ENSG00000198780	5	74109155 A
274 TINP1	Gga#S33766211	ENSGALG00000014942	Z	23956233	23959862	1 ENSG00000164346	5	74098859 A
275 GFM2	Gga#S21390242	ENSGALG00000014939	Z	23960621	23977800	0 ENSG00000164347	5	74052790 A
276 HEXB	Gga#S21390243	ENSGALG00000014933	Z	23978873	23994208	1 ENSG00000049860	5	74016767 A
277 ENC1	Gga#S21390244	ENSGALG00000014930	Z	24027213	24028982	0 ENSG00000171617	5	73958991 A
278 AC093283.3-2		ENSGALG00000014923	Z	24323707	24358768	0 ENSG00000038102	5	73215339 A
279 AC093283.3-1	Gga#S35713548	ENSGALG00000023365	Z	24406557	24422883	1 ENSG00000214944	5	72957739 A
280 UTP15	Gga#S23830846	ENSGALG00000013510	Z	24461874	24470980	1 ENSG00000164338	5	72897336 A
281 ANKRA2	Gga#S22196475	ENSGALG00000013511	Z	24471977	24477533	0 ENSG00000164331	5	72883919 A
282 BTF3	Gga#S6899977	ENSGALG00000013512	Z	24490421	24496689	1 ENSG00000145741	5	72830006 A
283 FOXD1	Gga#S19182964	ENSGALG00000012644	Z	24508180	24510389	0 ENSG00000183900	5	72,778,548 A
284 FOXD4L6			Z	24508606	24508911	0 ENSG00000204793	9	68489300 A
285 TMEM174	Gga#S20465368	ENSGALG00000015021	Z	24648961	24655176	1 ENSG00000164325	5	72504804 A
286 TMEM171		ENSGALG00000015020	Z	24663703	24666679	0 ENSG00000157111	5	72452158 A
287 FCHO2	Gga#S35713545	ENSGALG00000015019	Z	24684518	24775699	1 ENSG00000157107	5	72287655 A
288 TNPO1	Gga#S21390221	ENSGALG00000015014	Z	24790135	24844203	1 ENSG00000083312	5	72148171 A
289 ZNF366		ENSGALG00000015008	Z	24953864	24967029	0 ENSG00000178175	5	71774990 A
290 PTCO2	Gga#S6944166	ENSGALG00000023361	Z	25003818	25020249	1 ENSG00000049883	5	71651956 A
291 MRPS27	Gga#S21390224	ENSGALG00000015002	Z	25021547	25066621	0 ENSG00000113048	5	71551112 A
292 MAP1B	Gga#S35713543	ENSGALG00000014999	Z	25078838	25145954	1 ENSG00000131711	5	71438874 A
293 C9orf71	Gga#S6919983	ENSGALG00000023357	Z	25264050	25265568	0 ENSG00000181778	9	70341320 A
294 PGM5P2	Gga#S21390226	ENSGALG00000014995	Z	25271323	25336593	1 ENSG00000204794	9	68131062 A
295 PGM5		ENSGALG00000014995	Z	25271325	25336593	0 ENSG00000154330	9	70161635 A
296 SMARCA2	Gga#S19183135	ENSGALG00000010164	Z	25515676	25614585	0 ENSG00000080503	9	2005342 A
297 VLDLR	Gga#S19183879	ENSGALG00000010166	Z	25736496	25750571	0 ENSG00000147852	9	2611793 A
298 KCNVD		ENSGALG00000010173	Z	25784889	25790421	0 ENSG00000168263	9	2707526 A

299 KIAA0020	Gga#S22197843	ENSGALG00000010178	Z	25808662	25839016	1 ENSG00000080608	9	2794152 A
300 RFX3	Gga#S35713539	ENSGALG00000010179	Z	25851663	25918160	1 ENSG00000080298	9	3214649 A
301 GLIS3	Gga#S35713538	ENSGALG00000010180	Z	26050553	26140746	1 ENSG000000107249	9	3814128 A
302 SLC1A1	Gga#S21390037	ENSGALG00000010187	Z	26256592	26302309	0 ENSG000000106688	9	4480444 A
303 CDC37L1	Gga#S21386590	ENSGALG00000014448	Z	26623580	26632316	0 ENSG000000106993	9	4669559 A
304 AK3	Gga#S29404829	ENSGALG00000014447	Z	26636085	26648087	1 ENSG000000147853	9	4701158 A
305 JAK2	Gga#S18388718	ENSGALG00000015027	Z	26749540	26793291	0 ENSG000000096968	9	4975245 A
306 RLN3	Gga#S6946419	ENSGALG00000015028	Z	26804237	26806467	1 ENSG000000171136	19	13998501 B3a
307 CD274	Gga#S21390212	ENSGALG00000015031	Z	26836539	26873661	0 ENSG000000120217	9	5440559 A
308 PDCD1LG2		ENSGALG00000015032	Z	26870422	26874376	0 ENSG000000197646	9	5500579 A
309 KIAA1432	Gga#S33764522	ENSGALG00000015036	Z	26891551	26941704	0 ENSG000000107036	9	5619120 A
310 ERMP1	Gga#S21386366	ENSGALG00000000438	Z	26952283	26967236	1 ENSG000000099219	9	5774571 A
311 SLC16A7-like		ENSGALG00000015045	Z	26981246	26988445	0 ENSGALG00000015045		B2
312 MLANA	Gga#S6876186	ENSGALG00000019756	Z	26994424	26998541	0 ENSG000000120215	9	5880908 A
313 KIAA2026	Gga#S21390209	ENSGALG00000015050	Z	27003498	27065271	1 ENSG000000183354	9	5909008 A
314 UHRF1	Gga#S18608049	ENSGALG00000015052	Z	27124767	27205681	0 ENSG000000147854	9	6403151 A
315 GCSP	Gga#S19183413	ENSGALG00000015053	Z	27209583	27246907	1 ENSG000000178445	9	6522469 A
316 JMJD2C	Gga#S35713531	ENSGALG00000020557	Z	27293694	27361393	0 ENSG000000107077	9	6747654 A
317 PTPRD	Gga#S35713530	ENSGALG00000015058	Z	28013444	28107930	1 ENSG000000153707	9	8304246 A
318 ANKRD13C	Gga#S21395048	ENSGALG00000011311	Z	29538166	29538513	0 ENSGALG00000011311	1	70500138 B1
319 C9orf150	Gga#S14755341	ENSGALG00000023301	Z	29864578	29869219	1 ENSG000000153714	9	12765012 A
320 TYRP1	Gga#S19551224	ENSGALG00000015205	Z	29917192	29927109	1 ENSG000000107165	9	12683435 A
321 MPDZ	Gga#S35713525	ENSGALG000000005846	Z	30051725	30143174	1 ENSG000000107186	9	13095703 A
322 cZorf10		ENSGALG00000023299	Z	30228735	30229724	0 ENSGALG00000023299		B1
323 NFIB	Gga#S19183156	ENSGALG000000005441	Z	30609950	30614151	1 ENSG000000147862	9	14071847 A
324 ZDHC21	Gga#S23830955	ENSGALG00000005437	Z	30742134	30772589	1 ENSG000000175893	9	14607036 A
325 CER1	Gga#S19184037	ENSGALG000000005434	Z	30786099	30787106	1 ENSG000000147869	9	14709731 A
326 C9orf145	Gga#S21390032	ENSGALG000000005426	Z	30796598	30852623	1 ENSG000000164946	9	14727150 A
327 TTC39B	Gga#S21390033	ENSGALG000000005416	Z	30915607	30943071	1 ENSG000000155158	9	15161561 A
328 SNAPC3			Z	31011579	31014713	0 ENSG000000164975	9	15412732 A
329 PSIP1	Gga#S22197548	ENSGALG00000015105	Z	31019104	31053210	1 ENSG000000164985	9	15454067 A
330 C9orf93	Gga#S35713522	ENSGALG00000015103	Z	31061876	31208610	0 ENSG000000164989	9	15543005 A
331 cZorf14	Gga#S19630187		Z	31311449	31327765	0		B1
332 BNC2	Gga#S35713520	ENSGALG00000015101	Z	31433118	31458332	1 ENSG000000173068	9	16399501 A
333 CNTLN	Gga#S35713518	ENSGALG00000015097	Z	32001002	32027913	0 ENSG000000044459	9	17124980 A
334 SH3GL2	Gga#S19183608	ENSGALG00000015096	Z	32118463	32143265	0 ENSG000000107295	9	17569194 A
335 cZorf5	Gga#S6903113	ENSGALG00000020553	Z	32430230	32430963	1 ENSGALG00000020553		B1
336 ADAMTSL1	Gga#S21390189	ENSGALG00000015095	Z	32460253	32628168	0 ENSG000000178031	9	18464098 A
337 FAM154A			Z	32642078	32641812	0 ENSG000000155875	9	18917890 A
338 FAM29A	Gga#S22197326	ENSGALG00000015091	Z	32667625	32684489	1 ENSG000000147874	9	19043142 A
339 ADFP	Gga#S23831043	ENSGALG00000015090	Z	32686008	32696172	1 ENSG000000147872	9	19105760 A
340 DENND4C	Gga#S21390196	ENSGALG00000015083	Z	32761406	32810410	0 ENSG000000137145	9	19280749 A
341 RS6	Gga#S7028314	ENSGALG00000015082	Z	32818539	32822774	1 ENSG000000137154	9	19366254 A
342 ASAH3L	Gga#S21390197	ENSGALG00000015081	Z	32826134	32843629	0 ENSG000000177076	9	19398925 A
343 NCKX2	Gga#S20791224	ENSGALG00000015080	Z	32870923	32971723	1 ENSG000000155886	9	19505978 A
344 MLLT3	Gga#S21390199	ENSGALG00000015078	Z	33112528	33223467	1 ENSG000000171843	9	20334968 A
345 KIAA1797	Gga#S21390200	ENSGALG00000015071	Z	33246023	33341239	0 ENSG000000188352	9	20648308 A
346 PTPAD2	Gga#S18607689	ENSGALG00000015063	Z	33346086	33393917	1 ENSG000000188921	9	20996365 A
347 RFK	Gga#S22197975	ENSGALG000000000004	Z	34416803	34420467	1 ENSG000000135002	9	78190253 B1
348 PI51B	Gga#S22196761	ENSGALG00000015107	Z	34489103	34560962	0 ENSG000000107242	9	70510436 A
349 FXN		ENSGALG00000015108	Z	34554237	34560950	0 ENSG000000165060	9	70840164 A
350 TJP2	Gga#S19183902	ENSGALG00000015109	Z	34574005	34630090	0 ENSG000000119139	9	70956382 A
351 C9orf61	Gga#S21390185	ENSGALG00000015110	Z	34653275	34677000	0 ENSG000000135063	9	71134061 A
352 APBA1	Gga#S21390184	ENSGALG00000015111	Z	34683359	34715772	1 ENSG000000107282	9	71235022 A
353 PTAR1	Gga#S21390174	ENSGALG00000015113	Z	34781304	34806863	1 ENSG000000188647	9	71522874 A
354 MAMDC2	Gga#S35713516	ENSGALG00000015115	Z	34862273	34926493	0 ENSG000000165072	9	71848340 A
355 SMC5	Gga#S23831005	ENSGALG00000015118	Z	34934161	34988662	0 ENSG000000198887	9	72063698 A
356 KLF9			Z	35001426	35013592	1 ENSG000000119138	9	72189333 A
357 TRPM3	Gga#S21390181	ENSGALG00000015126	Z	35060901	35198923	1 ENSG000000083067	9	72339769 A
358 TMEM2	Gga#S35713512	ENSGALG00000015138	Z	35519468	35550588	1 ENSG000000135048	9	73371332 A

359 F108B	Gga#S22196704	ENSGALG00000015139	Z	35583298	35593002	1	ENSG00000107362	9	73667188 A
360 C9orf85		ENSGALG00000023262	Z	35599234	35613709	0	ENSG00000155621	9	73716243 A
361 GDA			Z	35599235	35682102	0	ENSG00000119125	9	73716243 A
362 ZFAND5	Gga#S22196967	ENSGALG00000015144	Z	35717496	35731043	1	ENSG00000107372	9	74156161 A
363 TMC1	Gga#S22186796	ENSGALG00000015145	Z	35818485	35851294	0	ENSG00000165091	9	74211091 A
364 AL1A1	Gga#S19182900	ENSGALG00000015147	Z	35874482	35908355	1	ENSG00000165092	9	74705408 A
365 ANXA1	Gga#S18607676	ENSGALG00000015148	Z	36006206	36019978	0	ENSG00000135046	9	74956601 A
366 RORB	Gga#S19183095	ENSGALG00000015150	Z	36614497	36656084	0	ENSG00000198963	9	76302072 A
367 TRPM6		ENSGALG00000015154	Z	36689226	36755868	1	ENSG00000119121	9	76527231 A
368 c9orf40		ENSGALG00000021845	Z	36787940	36791894	0	ENSG00000135045	9	76752786 A
369 C9orf41	Gga#S21390171	ENSGALG00000015155	Z	36794883	36822197	1	ENSG00000156017	9	76785754 A
370 C9orf95		ENSGALG00000015156	Z	36817607	36818725	0	ENSG00000106733	9	76858809 A
371 OSTF1	Gga#S29405459	ENSGALG00000017447	Z	36831169	36843039	0	ENSG00000134996	9	76893275 A
372 Q9PT87	Gga#S33765204	ENSGALG00000015164	Z	37043370	37237756	0	ENSG00000099139	9	77695406 A
373 PCSK1		ENSGALG00000014681	Z	37144735	37180528	0	ENSG00000175426	5	95751875 A
374 RFK	Gga#S21390168	ENSGALG00000015165	Z	37312591	37315967	1	ENSG00000135002	9	78190253 A
375 GCNT1	Gga#S21390167	ENSGALG00000015166	Z	37342732	37343733	0	ENSG00000187210	9	78263888 A
376 PRUNE2	Gga#S35713508	ENSGALG00000015167	Z	37379702	37432067	1	ENSG00000106772	9	78416112 A
377 PRUNE2		ENSGALG00000015168	Z	37422325	37508633	0	ENSG00000156035	9	78593130 A
378 FOXB2			Z	37538384	37539406	0	ENSG00000204612	9	78824391 A
379 VPS13A	Gga#S6829468	ENSGALG00000015170	Z	37582363	37684842	0	ENSG00000197969	9	78982181 A
380 GNA14		ENSGALG00000015176	Z	37689899	37749380	1	ENSG00000156049	9	79228369 A
381 GNAQ	Gga#S23830824	ENSGALG00000015177	Z	37768121	37881851	1	ENSG00000156052	9	79525020 A
382 CEP78	Gga#S21390160	ENSGALG00000015179	Z	37916677	37938341	0	ENSG00000148019	9	80040811 A
383 PSAT1	Gga#S18605917	ENSGALG00000015180	Z	37943444	37957095	0	ENSG00000135069	9	80101879 A
384 TLE4	Gga#S19183342	ENSGALG00000015184	Z	38533080	38548233	0	ENSG00000106829	9	81376508 A
385 TLE1	Gga#S35713505	ENSGALG00000012575	Z	39164058	39234185	1	ENSG00000196781	9	83388423 A
386 RASEF	Gga#S6830557	ENSGALG00000012576	Z	39701409	39736451	1	ENSG00000165105	9	84787144 A
387 FRMD3	Gga#S18605543	ENSGALG00000012577	Z	39791861	39869490	1	ENSG00000172159	9	85047725 A
388 C9orf103	Gga#S21389904	ENSGALG00000012583	Z	39947251	39956171	0	ENSG00000148057	9	85427786 A
389 UBQLN1	Gga#S21389903	ENSGALG00000012585	Z	39963291	39999131	1	ENSG00000135018	9	85464699 A
390 GKAP1	Gga#S21389902	ENSGALG00000012586	Z	40001299	40010876	1	ENSG00000165113	9	85544156 A
391 KIF27	Gga#S35713502	ENSGALG00000012588	Z	40021651	40056063	1	ENSG00000165115	9	85641433 A
392 C9orf64		ENSGALG00000012589	Z	40048670	40055922	0	ENSG00000165118	9	85743049 A
393 HNRPK	Gga#S21389899	ENSGALG00000012591	Z	40058585	40069653	1	ENSG00000165119	9	85772912 A
394 RMI1	Gga#S22196311	ENSGALG00000012592	Z	40076870	40078753	0	ENSG00000178966	9	85785517 A
395 SLC28A3	Gga#S21389898	ENSGALG00000012593	Z	40146170	40188037	1	ENSG00000197506	9	86082933 A
396 NTRK2	Gga#S19183883	ENSGALG00000012594	Z	40269999	40330023	0	ENSG00000148053	9	86473286 A
397 AGTPBP1	Gga#S35713499	ENSGALG00000012595	Z	40647979	40704068	1	ENSG00000135049	9	87351275 A
398 MAK10	Gga#S22196305	ENSGALG00000012598	Z	40716200	40741261	0	ENSG00000135040	9	87745877 A
399 C9orf155	Gga#S21389896	ENSGALG00000012601	Z	40747156	40772724	1	ENSG00000135052	9	87830876 A
400 ISCA1L	Gga#S35713503	ENSGALG00000012606	Z	40802890	40807468	1	ENSG00000217416	5	62106958 A
401 ISCA1		ENSGALG00000012606	Z	40802892	40807459	0	ENSG00000135070	9	88069287 A
402 ZCCHC6	Gga#S35713498	ENSGALG00000012607	Z	40811435	40841061	1	ENSG00000083223	9	88092468 A
403 GAS1		ENSGALG00000017658	Z	41041582	41042705	1	ENSG00000180447	9	88749098 A
404 DAPK1	Gga#S23831250	ENSGALG00000012608	Z	41297175	41357508	0	ENSG00000196730	9	89302616 A
405 CATL	Gga#S21389890	ENSGALG00000012610	Z	41388689	41393773	0	ENSG00000136943	9	98834760 A
406 CTSL1		ENSGALG00000012610	Z	41389800	41393770	0	ENSG00000135047	9	89530254 A
407 Q9IBD3	Gga#S21389889	ENSGALG00000012612	Z	41403269	41423061	1	ENSG00000130957	9	96360826 A
408 Q9IBD4	Gga#S33769360	ENSGALG00000012613	Z	41427925	41437326	1	ENSG00000165140	9	96405244 A
409 Q5ZK89	Gga#S22197142	ENSGALG00000012615	Z	41471576	41537908	0	ENSG00000148120	9	96528804 A
410 C9orf3		ENSGALG00000012615	Z	41604281	41627643	0	ENSG00000148120	9	96528804 A
411 FANCC	Gga#S22317532	ENSGALG00000012618	Z	41642520	41710813	1	ENSG00000158169	9	96901158 A
412 PTC1	Gga#S19182955	ENSGALG00000012620	Z	41753566	41814880	1	ENSG00000185920	9	97245083 A
413 AC091435.3-2			Z	41783208	41783339	0	ENSG00000205783	5	38856410 A
414 C9orf102	Gga#S21389885	ENSGALG00000012621	Z	41947296	41999318	0	ENSG00000182150	9	97677721 A
415 SLC35D2	Gga#S21389880	ENSGALG00000012630	Z	42094735	42142637	1	ENSG00000130958	9	98122834 A
416 HSD17B3			Z	42094758	42117488	0	ENSG00000130948	9	98037410 A
417 ZNF367		ENSGALG00000012629	Z	42146087	42150372	1	ENSG00000165244	9	98190057 A
418 HABP4	Gga#S19183826	ENSGALG00000012628	Z	42159867	42180876	0	ENSG00000130956	9	98252235 A

419 CDC14B	Gga#S21389881	ENSGALG00000012627	Z	42195236	42240926	1 ENSG000000081377	9	98298390 A
420 C9orf21	Gga#S6775438	ENSGALG00000012624	Z	42243556	42246985	1 ENSG000000158122	9	98443355 A
421 cZorf15			Z	42305380	42322181	1		B1
422 CFC1	Gga#S19183819	ENSGALG00000012623	Z	42403097	42405144	1 ENSG000000152093	2	130995137 B3a
423 CNTNAP4		ENSGALG00000023179	Z	42818176	42983228	1 ENSG000000152910	16	74868677 B3a
424 SPIN1Z	Gga#S19183727	ENSGALG00000014916	Z	43201334	43224018	0 ENSG000000106723	9	90193117 A
425 NXNL2	Gga#S33769109		Z	43248626	43266323	0 ENSG000000130045	9	90339840 A
426 S1PR3	Gga#S21386037	ENSGALG00000010683	Z	43421238	43422380	0 ENSG000000213694	9	90796182 A
427 SHC3		ENSGALG00000010688	Z	43432797	43498804	1 ENSG000000148082	9	90817891 A
428 KKS2	Gga#S18608052	ENSGALG00000010693	Z	43532603	43535166	0 ENSG000000123975	9	91115933 A
429 SECISBP2	Gga#S21386039	ENSGALG00000010694	Z	43537413	43564658	0 ENSG000000187742	9	91123232 A
430 SEMA4D		ENSGALG00000024457	Z	43567245	43569813	0 ENSG000000188091	9	91165526 A
431 SEM4D	Gga#S21386038	ENSGALG00000010697	Z	43580685	43601904	1 ENSG000000187764	9	91181972 A
432 GADD45G	Gga#S18611515		Z	43710713	43711467	0 ENSG000000130222	9	91409748 A
433 DIRAS2	Gga#S18609684	ENSGALG00000005323	Z	43976707	43977306	1 ENSG000000165023	9	92411934 A
434 SYK	Gga#S22196794	ENSGALG00000015216	Z	44060329	44089767	0 ENSG000000165025	9	92603891 A
435 TPPP2	Gga#S19647441	ENSGALG00000015213	Z	44101613	44102506	1 ENSG000000179636	14	20568249 B3a
436 AUH	Gga#S7028435	ENSGALG00000015210	Z	44188416	44297278	1 ENSG000000148090	9	93015926 A
437 NFIL3	Gga#S19183702	ENSGALG00000015209	Z	44326831	44328192	1 ENSG000000165030	9	93211148 A
438 AOSVH2	Gga#S35717825	ENSGALG00000015208	Z	44449304	44494056	1 ENSG000000169071	9	93365194 A
439 SPTLC1	Gga#S21387391	ENSGALG00000013493	Z	44632198	44664438	1 ENSG000000090054	9	93833248 A
440 CDC42SE2	Gga#S35713485	ENSGALG00000017686	Z	44740727	44778793	1 ENSG000000158985	5	130627601 A
441 C20orf134	Gga#S21389274	ENSGALG00000006803	Z	44853870	44854835	0 ENSGALG00000006803	20	31717965 B3b
442 LYRM7	Gga#S18611572	ENSGALG00000023163	Z	44863938	44877389	1 ENSG000000186687	5	130534535 A
443 Q3MMY7	Gga#S14761353	ENSGALG00000000428	Z	44879562	44883365	0 ENSG000000169567	5	130522776 A
444 CHSY3	Gga#S21394256	ENSGALG00000023161	Z	46033372	46034937	1 ENSG000000198108	5	129268422 A
445 KIAA1024L			Z	46206067	46206175	0 ENSG000000186367	5	129124054 A
446 ADAMTS19	Gga#S21394254	ENSGALG00000000151	Z	46219209	46336504	1 ENSG000000145808	5	128824002 A
447 ISOC1	Gga#S21394253	ENSGALG00000000161	Z	46496019	46515083	1 ENSG000000066583	5	128458341 A
448 SLC27A6	Gga#S35713478	ENSGALG00000000184	Z	46531183	46570046	1 ENSG000000113396	5	128329109 A
449 YTHDC2	Gga#S21394252	ENSGALG00000000189	Z	46595992	46633350	1 ENSG000000047188	5	112877309 A
450 MCC	Gga#S21394251	ENSGALG00000000208	Z	46773519	46840728	0 ENSG000000171444	5	112385695 A
451 DCP2	Gga#S19182649	ENSGALG00000000215	Z	46849891	46874546	1 ENSG000000172795	5	112340332 A
452 REEP5	Gga#S35713477	ENSGALG00000023157	Z	46882270	46899022	0 ENSG000000129625	5	112239980 A
453 SRP19	Gga#S18610453	ENSGALG00000000218	Z	46904962	46910712	1 ENSG000000153037	5	112224892 A
454 Q4A1V5	Gga#S35713475	ENSGALG00000000220	Z	46921661	46977190	1 ENSG000000134982	5	112101483 A
455 EPB41L4A	Gga#S21394246	ENSGALG00000000234	Z	47082160	47205840	0 ENSG000000129595	5	111507433 A
456 C5orf13	Gga#S19183969	ENSGALG00000000236	Z	47347968	47352552	0 ENSG000000134986	5	111092408 A
457 Q5ZK67	Gga#S22197120	ENSGALG00000000241	Z	47404649	47408803	0 ENSG000000164211	5	110861921 A
458 CAMK4	Gga#S227877489	ENSGALG00000000244	Z	47434514	47592002	1 ENSG000000152495	5	110587981 A
459 WDR36	Gga#S22196327	ENSGALG00000000247	Z	47621806	47651128	1 ENSG000000134987	5	110455769 A
460 S2546	Gga#S22196516	ENSGALG00000000253	Z	47718398	47731645	1 ENSG000000164209	5	110102653 A
461 MAN2A1	Gga#S35713473	ENSGALG00000000255	Z	48049550	48166070	1 ENSG000000112893	5	109053055 A
462 PJA2	Gga#S21394242	ENSGALG00000000264	Z	48276387	48294204	0 ENSG000000198961	5	108698309 A
463 FER	Gga#S21394241	ENSGALG00000000273	Z	48337851	48485346	1 ENSG000000151422	5	108111422 A
464 AC091435.3-1			Z	48529426	48529361	0 ENSG000000205785	5	38848753 A
465 FBXL17	Gga#S21394239	ENSGALG00000000276	Z	48581814	48600195	0 ENSG000000145743	5	107223348 A
466 EFNA5		ENSGALG00000000280	Z	49109111	49139735	0 ENSG000000184349	5	106744250 A
467 NUDT12	Gga#S35713470	ENSGALG000000015268	Z	50754756	50765384	0 ENSG000000112874	5	102912456 A
468 C5orf30	Gga#S35713469	ENSGALG00000015265	Z	50851570	50852193	1 ENSG000000181751	5	102622341 A
469 HISPPD1	Gga#S21390144	ENSGALG00000015264	Z	50867449	50909809	1 ENSG000000145725	5	102483867 A
470 GIN1	Gga#S21390145	ENSGALG00000015257	Z	50922945	50931198	0 ENSG000000145723	5	102449603 A
471 PAM	Gga#S21390146	ENSGALG00000015256	Z	50939370	50999788	1 ENSG000000145730	5	102229422 A
472 SLC04C1	Gga#S35713467	ENSGALG00000015251	Z	51151799	51168829	0 ENSG000000173930	5	101597589 A
473 SLC06A1		ENSGALG00000015251	Z	51171330	51171453	0 ENSG000000205359	5	101735553 A
474 ST8SIA4	Gga#S19183384	ENSGALG00000015245	Z	51541004	51594479	0 ENSG000000113532	5	100170803 A
475 TOPORS		ENSGALG00000020523	Z	51602367	51603296	0 ENSG000000197579	9	32530545 B1
476 FAM174A	Gga#S33768526	ENSGALG00000015243	Z	51703750	51716926	1 ENSG000000174132	5	99898943 A
477 Q9YI73	Gga#S19182973	ENSGALG00000014642	Z	52171039	52216302	0 ENSG000000153922	5	98218819 A
478 RGM8	Gga#S21390142	ENSGALG00000015284	Z	52232820	52244515	1 ENSG000000174136	5	98132900 A

479	RIOK2	Gga#S22980533	ENSGALG00000015288	Z	52433158	52444712	0	ENSG00000058729	5	96524397	A
480	LIX1	Gga#S19183438	ENSGALG00000015290	Z	52447600	52475883	0	ENSG00000145721	5	96453331	A
481	LNPEP	Gga#S21390140	ENSGALG00000015301	Z	52497506	52534127	1	ENSG00000113441	5	96296854	A
482	SHB	Gga#S21390139	ENSGALG00000015302	Z	52619106	52669729	0	ENSG00000107338	9	37578417	A
483	RNF38	Gga#S21390138	ENSGALG00000015311	Z	52860161	52884300	0	ENSG00000137075	9	36326401	A
484	TRIM14	Gga#S22196601	ENSGALG00000015315	Z	52898712	52905831	0	ENSG00000106785	9	99871395	A
485	NANS	Gga#S22197931	ENSGALG00000015320	Z	52909475	52927789	1	ENSG00000095380	9	99858842	A
486	CLTA	Gga#S7022146	ENSGALG00000015326	Z	52935223	52949670	0	ENSG00000122705	9	36180892	A
487	GNE	Gga#S23831006	ENSGALG00000015331	Z	52955730	52990871	1	ENSG00000159921	9	36204430	A
488	CPLX1	Gga#S7081596	ENSGALG00000015332	Z	53209391	53231697	0	ENSG00000168993	4	768,746	B3a
489	PCGF3	Gga#S21390132	ENSGALG00000015333	Z	53512279	53536311	1	ENSG00000185619	4	689573	B3a
490	CHRN3	Gga#S19183201	ENSGALG00000015384	Z	53604801	53749371	0	ENSG00000147432	8	42,671,719	B3a
491	U632B	Gga#S19722641	ENSGALG00000015337	Z	53790867	53873651	1	ENSG00000186854	2	84902285	B3a
492	PIGG	Gga#S21390129	ENSGALG00000015349	Z	54117240	54117422	1	ENSG00000174227	4	483010	B3a
493	HOOK3	Gga#S35713463	ENSGALG00000015390	Z	54269799	54300335	0	ENSG00000168172	8	42871190	B3a
494	KCMF1	Gga#S35713462	ENSGALG00000015391	Z	54317186	54360166	1	ENSG00000176407	2	85051727	B3a
495	FNTA	Gga#S21390120	ENSGALG00000015397	Z	54384193	54393539	1	ENSG00000168522	8	43030599	B3a
496	FUT10	Gga#S10817583	ENSGALG00000015399	Z	54400778	54409177	0	ENSG00000172728	8	33347884	B3a
497	NRG1	Gga#S19183235	ENSGALG00000015422	Z	54499792	54528995	1	ENSG00000157168	8	31617043	B3a
498	LIP1	Gga#S20923106	ENSGALG00000015425	Z	55070219	55084620	1	ENSG00000175445	8	19840870	B3a
499	PSD3	Gga#S35713460	ENSGALG00000015428	Z	55130416	55215236	1	ENSG00000156011	8	18429093	B3a
500	NIPSNAP3B	Gga#S21390118	ENSGALG00000015430	Z	55254072	55262461	0	ENSG00000165028	9	106566272	A
501	NIPSNAP3A		ENSGALG00000015430	Z	55255595	55262458	0	ENSG00000136783	9	106549786	A
502	ABCA1	Gga#S19183258	ENSGALG00000015433	Z	55267049	55343041	1	ENSG00000165029	9	106583104	A
503	SLC44A1	Gga#S35713459	ENSGALG00000015439	Z	55476287	55521394	0	ENSG00000070214	9	107046724	A
504	FKTN	Gga#S21390115	ENSGALG00000015443	Z	55549504	55600065	0	ENSG00000106692	9	107360232	A
505	FSD1L		ENSGALG00000015442	Z	55553358	55575629	0	ENSG00000106701	9	107250146	A
506	TAL2	Gga#S21390114	ENSGALG00000023114	Z	55613173	55626428	0	ENSG00000186051	9	107464559	A
507	TMEM38B	Gga#S18956107	ENSGALG00000015447	Z	55641266	55653978	0	ENSG00000095209	9	107496646	A
508	ZNF462	Gga#S21390106	ENSGALG00000015451	Z	56038738	56088721	0	ENSG00000148143	9	108665199	A
509	RAD23B	Gga#S21390105	ENSGALG00000015540	Z	56167663	56201918	0	ENSG00000119318	9	109085365	A
510	KLF4	Gga#S35712320		Z	56225597	56246903	1	ENSG00000136826	9	109286954	A
511	PHF7-like	Gga#S14762358	ENSGALG00000005023	Z	56607183	56697147	1	ENSGALG00000005023			B1
512	RNUXA	Gga#S22197733	ENSGALG00000014691	Z	56809755	56830010	0	ENSG00000164902	5	125964532	A
513	LMNB1	Gga#S19183064	ENSGALG00000014692	Z	56853516	56876328	0	ENSG00000113368	5	126140732	A
514	3-Mar	Gga#S21430556	ENSGALG00000014693	Z	56884148	56909636	1	ENSG00000173926	5	126233454	A
515	YD286	Gga#S16114692	ENSGALG00000023109	Z	56959897	56967452	1	ENSG00000164241	5	126415368	A
516	MEGF10	Gga#S21390351	ENSGALG00000014699	Z	57014806	57086602	0	ENSG00000145794	5	126654514	A
517	PRRC1	Gga#S23830889	ENSGALG00000014703	Z	57104223	57122684	0	ENSG00000164244	5	126881238	A
518	CTXN3	Gga#S21512692	ENSGALG00000023106	Z	57164117	57164296	0	ENSG00000205279	5	127012635	A
519	SLC12A2	Gga#S35713455	ENSGALG00000014690	Z	57332497	57384360	0	ENSG00000064651	5	127447382	A
520	Q9PUC7	Gga#S21390359	ENSGALG00000014686	Z	57405152	57564801	1	ENSG00000138829	5	127621500	A
521	Q5F3N8	Gga#S35713454	ENSGALG00000014684	Z	57644105	57657051	0	ENSG00000164307	5	96122270	A
522	LRAP			Z	57644515	57652105	0	ENSG00000164308	5	96237960	A
523	CAST	Gga#S21390361	ENSGALG00000014682	Z	57661110	57713801	1	ENSG00000153113	5	96023533	A
524	ELL2	Gga#S21390363	ENSGALG00000014678	Z	57823409	57876479	0	ENSG00000118985	5	95246560	A
525	GLRX1L	Gga#S24577812	ENSGALG00000014676	Z	57901244	57904236	0	ENSG00000173221	5	95175431	A
526	GLRX1		ENSGALG00000014676	Z	57901369	57904233	0	ENSG00000118990	5	161110059	A
527	RHOBTB3	Gga#S22197143	ENSGALG00000014675	Z	57917986	57981871	1	ENSG00000164292	5	95092606	A
528	RFESD		ENSGALG00000014673	Z	57965175	57965424	0	ENSG00000175449	5	95008239	A
529	ARSK		ENSGALG00000014672	Z	57971485	57981127	0	ENSG00000164291	5	94916581	A
530	TTC37	Gga#S21390368	ENSGALG00000014670	Z	57983325	57999067	0	ENSG00000198677	5	94825355	A
531	FAM81B	Gga#S21390356	ENSGALG00000014669	Z	58030722	58063731	1	ENSG00000153347	5	94752804	A
532	MCTP1	Gga#S21390369	ENSGALG00000014668	Z	58181266	58244548	0	ENSG00000175471	5	94068957	A
533	ANKRD32	Gga#S21390371	ENSGALG00000014667	Z	58367976	58406091	1	ENSG00000133302	5	93979808	A
534	KIAA0825	Gga#S35713452	ENSGALG00000014664	Z	58430591	58453393	0	ENSG00000175483	5	93774435	A
535	C5orf36			Z	58452718	58453390	0	ENSG00000185261	5	93880683	A
536	AC104127.2			Z	58516419	58520380	0	ENSG00000218494	5	93515468	A
537	AL159169.14			Z	58516420	58516551	0	ENSG00000215261	9	14545513	A
538	FAM127A	Gga#S22197097	ENSGALG00000014661	Z	58671520	58718184	0	ENSG00000113391	5	92979531	A

539	AC106818.2			Z	58926024	58926257	0	ENSG00000205434	5	92961819	A
540	NR2F1	Gga#S21512816	ENSGALG0000007000	Z	58932511	58940805	1	ENSG00000175745	5	92944799	A
541	ARRDC3	Gga#S21390377	ENSGALG00000014658	Z	59915827	59926569	0	ENSG00000113369	5	90700299	A
542	GPR98	Gga#S18609689	ENSGALG00000014657	Z	60005948	60247627	1	ENSG00000164199	5	89890373	A
543	LYSM3	Gga#S22197253	ENSGALG00000014651	Z	60271243	60273884	0	ENSG00000176018	5	89847200	A
544	POLR3G		ENSGALG00000014650	Z	60279514	60293048	0	ENSG00000113356	5	89806437	A
545	MBLC2	Gga#S23830745	ENSGALG00000014649	Z	60299932	60316205	0	ENSG00000176055	5	89789778	A
546	CETN3	Gga#S33762838	ENSGALG00000014648	Z	60319272	60335348	0	ENSG00000153140	5	89725287	A
547	MEF2C	Gga#S35713449	ENSGALG00000014645	Z	61006062	61019285	0	ENSG00000081189	5	88051922	A
548	LOC645323	mir	ENSGALG00000023094	Z	61048183	61048693	0	ENSG00000207570	5	87096020	A
549	cZorf17	Gga#S19789066		Z	61052944	61053228	0				B1
550	TMEM161B	Gga#S21385865	ENSGALG00000010896	Z	61174226	61208259	0	ENSG00000164180	5	87526779	A
551	CCNH	Gga#S21390080	ENSGALG00000015641	Z	61382749	61391507	0	ENSG00000134480	5	86725844	A
552	RASA1	Gga#S21390081	ENSGALG00000017706	Z	61395572	61442268	1	ENSG00000145715	5	86599838	A
553	COX7	Gga#S18613577	ENSGALG00000015631	Z	61621765	61637322	1	ENSG00000127184	5	85949540	A
554	EDIL3	Gga#S21390082	ENSGALG00000015630	Z	62677037	62816062	0	ENSG00000164176	5	83273882	A
555	HPLN1	Gga#S19183795	ENSGALG00000015627	Z	62975431	62997318	0	ENSG00000145681	5	82972502	A
556	CSPG2	Gga#S19551199	ENSGALG00000015624	Z	63036969	63139071	1	ENSG00000038427	5	82803339	A
557	XRCC4	Gga#S6764692	ENSGALG00000015620	Z	63268416	63333306	1	ENSG00000152422	5	82409073	A
558	TMEM167A			Z	63365737	63374214	0	ENSG00000174695	5	82387742	A
559	ATP6AP1L	Gga#S21390084	ENSGALG00000015618	Z	63722635	63738228	1	ENSG00000205464	5	81611037	A
560	RPS23	Gga#S16163113	ENSGALG00000015617	Z	63743719	63745460	0	ENSG00000186468	5	81604899	A
561	ATG10	Gga#S21390086	ENSGALG00000020531	Z	63757721	63837549	1	ENSG00000152348	5	81303630	A
562	SSBP2	Gga#S35713446	ENSGALG00000023089	Z	64030122	64071422	0	ENSG00000145687	5	80751428	A
563	ACOT12	Gga#S21390076	ENSGALG00000015616	Z	64086779	64117534	0	ENSG00000172497	5	80661580	A
564	ZCCHC9	Gga#S21390088	ENSGALG00000015603	Z	64121893	64127081	1	ENSG00000131732	5	80633178	A
565	RASGRF2	Gga#S21390089	ENSGALG00000015598	Z	64135616	64289517	1	ENSG00000113319	5	80292314	A
566	CKMT2		ENSGALG00000015602	Z	64135618	64150353	0	ENSG00000131730	5	80564895	A
567	MSH3	Gga#S35713445	ENSGALG00000015589	Z	64320644	64437435	1	ENSG00000113318	5	79986050	A
568	DHFR	Gga#S22980532	ENSGALG00000015579	Z	64437558	64452725	0		5	79,957,801	A
569	ANKRD34B	Gga#S21390093	ENSGALG00000015578	Z	64470560	64492615	0	ENSG00000189127	5	79888331	A
570	FAM151B		ENSGALG00000015577	Z	64477711	64485937	0	ENSG00000152380	5	79819556	A
571	ZFYVE16	Gga#S21390094	ENSGALG00000015576	Z	64493658	64524680	1	ENSG00000039319	5	79739594	A
572	CCDC125	Gga#S21390096	ENSGALG00000015572	Z	64531130	64549224	1	ENSG00000183323	5	68612278	A
573	AC145132.2		ENSGALG00000020534	Z	64547685	64549215	0	ENSG00000185057	5	68683311	A
574	RAD17	Gga#S22196976	ENSGALG00000015571	Z	64549420	64568810	0	ENSG00000152942	5	68700880	A
575	CCDC81			Z	64824086	64828545	1				B1
576	PHF7		ENSGALG00000015672	Z	64923606	64926924	1	ENSG00000010318	3	52419567	B3b
577	GRIN3A	Gga#S35713440	ENSGALG00000015551	Z	65413247	65479999	0	ENSG00000198785	9	103371456	A
578	BRE1A	Gga#S22197676	ENSGALG00000015548	Z	65486375	65502637	1	ENSG00000155827	9	103335954	A
579	C9orf125	Gga#S21390100	ENSGALG00000015545	Z	65522004	65523026	0	ENSG00000165152	9	103275274	A
580	ALDOB	Gga#S41350201	ENSGALG00000015544	Z	65536495	65540131	0	ENSG00000136872	9	103222681	A
581	RM50	Gga#S6830031	ENSGALG00000015543	Z	65542199	65542834	0	ENSG00000136897	9	103192070	A
582	PPAPR3	Gga#S18956435	ENSGALG00000015542	Z	65545830	65610841	1	ENSG00000148123	9	102830852	A
583	PHF7		ENSGALG00000015643	Z	65712165	65762403	1	ENSG00000010318	3	52419567	B3b
584	PALM2		ENSGALG00000015655	Z	66054047	66108810	0	ENSG00000157654	9	111442893	A
585	AKAP2	Gga#S21390070	ENSGALG00000015656	Z	66225483	66243499	0	ENSG00000157654	9	111442893	A
586	SLC46A2	Gga#S6753774		Z	66256609	66262040	0	ENSG00000119457	9	114681022	A
587	SNX30	Gga#S21390069	ENSGALG00000015660	Z	66268598	66317605	1	ENSG00000148158	9	114552955	A
588	CI080	Gga#S29405727	ENSGALG00000020528	Z	66328245	66337488	0	ENSG00000148153	9	114488618	A
589	KIAA1958	Gga#S21390049	ENSGALG00000023083	Z	66366436	66387030	1	ENSG00000165185	9	114289069	A
590	HSDL2	Gga#S19183993	ENSGALG00000015663	Z	66417411	66459965	0	ENSG00000119471	9	114182038	A
591	UGCG	Gga#S21390064	ENSGALG00000015682	Z	66473592	66498454	1	ENSG00000148154	9	113698867	A
592	C9orf84			Z	66556906	66598827	0	ENSG00000165181	9	113488274	A
593	DNAJC25-GNC	Gga#S35713436	ENSGALG00000015684	Z	66615726	66622928	1	ENSG00000059769	9	113433453	A
594	KIAA0368	Gga#S21390063	ENSGALG00000015689	Z	66631560	66679804	0	ENSG00000136813	9	113162793	A
595	SMC2	Gga#S19183884	ENSGALG00000015691	Z	66683471	66706274	1	ENSG00000136824	9	105896362	A
596	PTGR1	Gga#S22196537	ENSGALG00000015702	Z	66718539	66726189	0	ENSG00000106853	9	113365074	A
597	TOPORS	Gga#S35713434	ENSGALG00000020523	Z	66728419	66729981	0	ENSG00000197579	9	32530545	B1
598	THIO	Gga#S6936840	ENSGALG00000015704	Z	66738618	66743670	1	ENSG00000168454	18	9875723	A

599 TXN		ENSGALG00000015704	Z	66738620	66741096	0 ENSG00000136810	9	112046121 A
600 SVEP1	Gga#S21390061	ENSGALG00000015721	Z	66755902	66895213	1 ENSG00000165124	9	112167352 A
601 MUSK	Gga#S19183224	ENSGALG00000015728	Z	66936215	66986427	0 ENSG00000030304	9	112470960 A
602 LPAR1	Gga#S18605826	ENSGALG00000015729	Z	67030757	67072021	1 ENSG00000198121	9	112675365 A
603 cZorf3	Gga#S20464696	ENSGALG00000015743	Z	67135866	67137490	0 ENSGALG00000015743		B1
604 NPR2		ENSGALG00000015753	Z	67262210	67291298	0 ENSG00000159899	9	35782151 B1
605 PRKACG			Z	67295456	67295163	0 ENSG00000165059	9	70817241 A
606 TMEM215	Gga#S19721868	ENSGALG00000015754	Z	67304854	67305573	1 ENSG00000188133	9	32773497 A
607 TOPORS	Gga#S21390057	ENSGALG00000020523	Z	67334749	67337868	0 ENSG00000197579	9	32530545 A
608 FLNC-like		ENSGALG00000014707	Z	67431089	67439731	0		B1
609 FLNC-like		ENSGALG00000014707	Z	67454863	67488277	1		B1
610 ELAVL2	Gga#S35713431	ENSGALG00000015799	Z	67640308	67712613	1 ENSG00000107105	9	23680102 A
611 FLNC-like		ENSGALG00000014707	Z	68038980	68126270	1		B1
612 HEATR7B2-like	Gga#S21401175	ENSGALG00000022510	Z	68181694	68201693	1		B1
613 ALS89843.9			Z	68201881	68201801	0 ENSG00000204328	9	98531217 A
614 HEATR7B2-like		ENSGALG00000016539	Z	68248604	68291789	0		B1
615 HEATR7B2-like		ENSGALG00000017045	Z	68306886	68320418	0		B1
616 HEATR7B2-like	Gga#S35717399		Z	68320942	68341622	1		B1
617 HEATR7B2-like	Gga#S35717392	ENSGALG00000016539	Z	68342923	68352811	0		B1
618 HEATR7B2-like	Gga#S21389337	ENSGALG00000016305	Z	68353493	68379853	1		B1
619 FLNC-like		ENSGALG00000023076	Z	68416411	68422570	0		B1
620 TUSC1		ENSGALG00000017510	Z	68475264	68475489	0 ENSG00000198680	9	25667681 A
621 FLNC-like	Gga#S21390024	ENSGALG00000023076	Z	68481344	68484851	0		B1
622 cZorf8	Gga#S35713430	ENSGALG00000021457	Z	68493506	68499255	0 ENSGALG00000021457		B1
623 cZorf18			Z	68658939	68661707	1		B1
624 FLNC-like			Z	68742706	68758689	0		B1
625 PLAA	Gga#S21390021	ENSGALG00000001782	Z	68763380	68799347	1 ENSG00000137055	9	26894518 A
626 C9orf82		ENSGALG00000001765	Z	68763388	68779646	0 ENSG00000120159	9	26830685 A
627 IFT74	Gga#S18606345	ENSGALG00000001801	Z	68799954	68831136	0 ENSG00000096872	9	26946410 A
628 LRRC19			Z	68805841	68817308	0 ENSG00000184434	9	26983590 A
629 TEK	Gga#S21390018	ENSGALG00000001840	Z	68839484	68874924	0 ENSG00000120156	9	27099286 A
630 cZorf9	Gga#S21274270	ENSGALG00000023074	Z	68877876	68884134	1 ENSGALG00000023074		B1
631 MOBKL2B		ENSGALG00000001856	Z	68893975	68939791	1 ENSG00000120162	9	27319129 A
632 C9orf72	Gga#S21390016	ENSGALG00000001864	Z	68994661	68997217	1 ENSG00000147894	9	27536544 A
633 LINGO2	Gga#S21390013	ENSGALG00000001869	Z	69120285	69122106	1 ENSG00000174482	9	27938076 A
634 cZorf1	Gga#S21390015	ENSGALG00000001871	Z	69766395	69769246	0 ENSGALG00000001871		B1
635 D4ST1			Z	70031990	70032313	0	15	38550505 B1
636 cZorf7		ENSGALG00000021452	Z	70612481	70613287	1 ENSGALG00000021452		B1
637 CORO2A	Gga#S21390011	ENSGALG00000001933	Z	70755261	70781411	1 ENSG00000106789	9	99926299 A
638 TBC1D2	Gga#S21390010	ENSGALG00000001944	Z	70808452	70826156	1 ENSG00000095383	9	100001132 A
639 Q5ZJ12	Gga#S22196885	ENSGALG00000001947	Z	70828726	70859950	0 ENSG00000070061	9	110669622 A
640 APTX	Gga#S18344609	ENSGALG00000001954	Z	70862437	70870850	1 ENSG00000137074	9	32962609 A
641 DNAJA1	Gga#S22197006	ENSGALG00000023066	Z	70871418	70877979	0 ENSG00000086061	9	33015242 A
642 SMU1	Gga#S22197901	ENSGALG00000002014	Z	70885347	70922855	1 ENSG00000122692	9	33031850 A
643 HEMGN	Gga#S19788841	ENSGALG00000023061	Z	70934253	70954695	0 ENSG00000136929	9	99728894 A
644 SPINK4		ENSGALG00000021842	Z	70934511	70936260	0 ENSG00000122711	9	33208363 A
645 FOXE1			Z	70956493	71048754	0 ENSG00000178919	9	99655358 A
646 XPA	Gga#S19183988	ENSGALG00000023059	Z	71008924	71014845	0 ENSG00000136936	9	99477013 A
647 NCBP1	Gga#S22197049	ENSGALG00000002087	Z	71018547	71048827	1 ENSG00000136937	9	99435526 A
648 C9orf97	Gga#S21390004	ENSGALG00000002110	Z	71049017	71063060	0 ENSG00000136925	9	99402183 A
649 TMOD1	Gga#S19183024	ENSGALG00000002125	Z	71069570	71085199	1 ENSG00000136842	9	99303742 A
650 TDRD7	Gga#S21387586	ENSGALG00000012350	Z	71090535	71119044	1 ENSG00000196116	9	99214123 A
651 DGKQ	Gga#S21390003	ENSGALG00000002142	Z	71144055	71225245	1 ENSG00000145214	4	942676 B3a
652 IREB1	Gga#S26668021	ENSGALG00000002162	Z	71253152	71277041	0 ENSG00000122729	9	32374618 A
653 FLNC-like	Gga#S21390000	ENSGALG00000021429	Z	71314359	71371431	1		B1
654 PRR16	Gga#S35713418	ENSGALG00000002183	Z	71473437	71475638	1 ENSG00000184838	5	119827918 A
655 HSD17B4	Gga#S19182971	ENSGALG00000002187	Z	71824883	71880000	1 ENSG00000133835	5	118816122 A
656 TFP8	Gga#S22196431	ENSGALG00000002196	Z	71895405	71906620	1 ENSG00000145779	5	118752897 A
657 DMXL1	Gga#S21389998	ENSGALG00000002227	Z	71945413	71998841	1 ENSG00000172869	5	118434983 A
658 DTWD2	Gga#S22197840	ENSGALG00000002250	Z	72038121	72109569	0 ENSG00000169570	5	118203135 A

659 OCRL	Gga#S35713417		Z	72298698	72299198	1		B1
660 SEMA6A	Gga#S21389996	ENSGALG00000002294	Z	72889583	72950475	0	ENSG00000092421	5 115807150 A
661 COMMD10	Gga#S29404121	ENSGALG00000002308	Z	73086836	73106860	1	ENSG00000145781	5 115448622 A
662 LAEVERIN		ENSGALG00000002318	Z	73150779	73151183	1	ENSG00000172901	5 115326170 A
663 AP3S1	Gga#S22196845	ENSGALG00000002341	Z	73181806	73208280	1	ENSG00000177879	5 115205518 A
664 ATG12	Gga#S33762255	ENSGALG00000002345	Z	73209804	73211461	0	ENSG00000145782	5 115193714 A
665 CDO1	Gga#S21389992	ENSGALG00000002358	Z	73220241	73229322	0	ENSG00000129596	5 115168333 A
666 TICAM2	Gga#S22197559	ENSGALG00000002140	Z	73269208	73275108	0	ENSG00000134970	5 114942238 A
667 MARVELD2	Gga#S21389990	ENSGALG00000002361	Z	73283097	73289428	0	ENSG00000152939	5 68746699 A
668 GTF2H2		ENSGALG00000002399	Z	73294960	73305497	0	ENSG00000145736	5 70366717 A
669 GTF2H2C	Gga#S33765061	ENSGALG00000002399	Z	73294961	73305509	0	ENSG00000183474	5 68891830 A
670 SMN2	Gga#S33763759	ENSGALG00000002430	Z	73311950	73316153	1	ENSG00000205571	5 69381106 A
671 SMN1		ENSGALG00000002430	Z	73312795	73316141	0	ENSG00000172062	5 70256524 A
672 SERF1B	Gga#S35713414	ENSGALG000000021397	Z	73317286	73321027	1	ENSG00000205572	5 69356852 A
673 SERF1A		ENSGALG000000021397	Z	73317300	73317999	0	ENSG00000172058	5 70232270 A
674 BDP1	Gga#S35713413	ENSGALG00000002439	Z	73323283	73342300	0	ENSG00000145734	5 70787198 A
675 MCCC2	Gga#S21389988	ENSGALG00000002529	Z	73378467	73421983	0	ENSG00000131844	5 70918910 A
676 CARTPT			Z	73421628	73421980	0	ENSG00000164326	5 71050750 A
677 KCNN2	Gga#S19184068	ENSGALG00000002539	Z	73547389	73616384	1	ENSG00000080709	5 113725565 A
678 ADCY10	Gga#S21389984	ENSGALG00000002611	Z	73695051	73699038	1	ENSG00000143199	1 166045507 B1
679 ADCY10	Gga#S21389984	ENSGALG00000002611	Z	73716606	73720592	1	ENSG00000143199	1 166045507 B1
680 ADCY10	Gga#S21389984	ENSGALG00000002611	Z	73737915	73741901	1	ENSG00000143199	1 166045507 B1
681 ADCY10	Gga#S21389984	ENSGALG00000002611	Z	73759212	73763199	1	ENSG00000143199	1 166045507 B1
682 ADCY10	Gga#S21389984	ENSGALG00000002611	Z	73780533	73784520	1	ENSG00000143199	1 166045507 B1
683 ADCY10	Gga#S21389984	ENSGALG00000002611	Z	73801592	73805579	1	ENSG00000143199	1 166045507 B1
684 MRPL19			Z	73816665	73819302	1	ENSG00000115364	2 75,727,417 B1
685 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	73821257	73828763	0	ENSG00000005436	2 75,742,802 B1
686 MRPL19			Z	73842730	73845373	1	ENSG00000115364	2 75,727,417 B1
687 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	73847331	73856135	0	ENSG00000005436	2 75,742,802 B1
688 MRPL19			Z	73916344	73918987	1	ENSG00000115364	2 75,727,417 B1
689 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	73920762	73929355	0	ENSG00000005436	2 75,742,802 B1
690 MRPL19			Z	73943959	73946576	1	ENSG00000115364	2 75,727,417 B1
691 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	73948530	73956197	0	ENSG00000005436	2 75,742,802 B1
692 MRPL19			Z	73996179	73998828	1	ENSG00000115364	2 75,727,417 B1
693 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74000771	74006894	0	ENSG00000005436	2 75,742,802 B1
694 RICS	Gga#S35715088	ENSGALG00000022113	Z	74011028	74016962	11	ENSG00000134909	11 128,343,052 B1
695 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74036789	74043220	0	ENSG00000005436	2 75,742,802 B1
696 MRPL19			Z	74092772	74095409	1	ENSG00000115364	2 75,727,417 B1
697 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74097369	74105909	0	ENSG00000005436	2 75,742,802 B1
698 MRPL19			Z	74138718	74141368	1	ENSG00000115364	2 75,727,417 B1
699 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74143304	74151417	0	ENSG00000005436	2 75,742,802 B1
700 MRPL19			Z	74193678	74196341	1	ENSG00000115364	2 75,727,417 B1
701 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74198298	74206607	0	ENSG00000005436	2 75,742,802 B1
702 MRPL19			Z	74230880	74233522	1	ENSG00000115364	2 75,727,417 B1
703 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74235458	74242632	0	ENSG00000005436	2 75,742,802 B1
704 RICS	Gga#S35715088	ENSGALG00000022113	Z	74307171	74313473	0	ENSG00000134909	11 128,343,052 B1
705 MRPL19			Z	74319344	74321086	1	ENSG00000115364	2 75,727,417 B1
706 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74323027	74331151	0	ENSG00000005436	2 75,742,802 B1
707 MRPL19			Z	74345722	74348344	1	ENSG00000115364	2 75,727,417 B1
708 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74350287	74358843	0	ENSG00000005436	2 75,742,802 B1
709 RICS	Gga#S35715088	ENSGALG00000022113	Z	74362537	74368706	0	ENSG00000134909	11 128,343,052 B1
710 MRPL19			Z	74373072	74374828	1	ENSG00000115364	2 75,727,417 B1
711 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74376783	74385691	0	ENSG00000005436	2 75,742,802 B1
712 MRPL19			Z	74400072	74402733	1	ENSG00000115364	2 75,727,417 B1
713 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74404606	74413986	0	ENSG00000005436	2 75,742,802 B1
714 MRPL19			Z	74446793	74449456	1	ENSG00000115364	2 75,727,417 B1
715 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74451393	74459459	0	ENSG00000005436	2 75,742,802 B1
716 MRPL19			Z	74495534	74497360	1	ENSG00000115364	2 75,727,417 B1
717 C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74499314	74506368	0	ENSG00000005436	2 75,742,802 B1
718 MRPL19			Z	74520495	74523147	1	ENSG00000115364	2 75,727,417 B1

719	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74525108	74531755	0	ENSG00000005436	2	75,742,802	B1
720	MRPL19			Z	74546714	74549357	1	ENSG00000115364	2	75,727,417	B1
721	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74551319	74559403	0	ENSG00000005436	2	75,742,802	B1
722	RICS	Gga#S35715088	ENSGALG00000022113	Z	74585095	74591181	0	ENSG00000134909	11	128,343,052	B1
723	MRPL19			Z	74615699	74618352	1	ENSG00000115364	2	75,727,417	B1
724	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74620308	74627801	0	ENSG00000005436	2	75,742,802	B1
725	MRPL19			Z	74645744	74648371	1	ENSG00000115364	2	75,727,417	B1
726	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74650306	74656290	0	ENSG00000005436	2	75,742,802	B1
727	MRPL19			Z	74673047	74675672	1	ENSG00000115364	2	75,727,417	B1
728	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	74677614	74684867	0	ENSG00000005436	2	75,742,802	B1
729	RICS	Gga#S35715088	ENSGALG00000022113	Z	74699924	74705841	0	ENSG00000134909	11	128,343,052	B1
730	MRPL19			Z	74712063	74714708	1	ENSG00000115364	2	75,727,417	B1
731	RICS	Gga#S35715088	ENSGALG00000022113	Z	74740504	74746391	0	ENSG00000134909	11	128,343,052	B1
732	RICS	Gga#S35715088	ENSGALG00000022113	Z	75808552	75814748	1	ENSG00000134909	11	128,343,052	B1
733	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	75819948	75826723	1	ENSG00000005436	2	75,742,802	B1
734	MRPL19			Z	75828678	75831341	0	ENSG00000115364	2	75,727,417	B1
735	RICS	Gga#S35715088	ENSGALG00000022113	Z	75837523	75843435	1	ENSG00000134909	11	128,343,052	B1
736	RICS	Gga#S35715088	ENSGALG00000022113	Z	75855812	75862066	1	ENSG00000134909	11	128,343,052	B1
737	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	75865799	75873948	1	ENSG00000005436	2	75,742,802	B1
738	MRPL19			Z	75875884	75878543	0	ENSG00000115364	2	75,727,417	B1
739	RICS	Gga#S35715088	ENSGALG00000022113	Z	75883329	75889673	1	ENSG00000134909	11	128,343,052	B1
740	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	75893368	75901132	1	ENSG00000005436	2	75,742,802	B1
741	MRPL19			Z	75902997	75905641	0	ENSG00000115364	2	75,727,417	B1
742	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	75908035	75901132	1	ENSG00000005436	2	75,742,802	B1
743	RICS	Gga#S35715088	ENSGALG00000022113	Z	75910277	75916240	1	ENSG00000134909	11	128,343,052	B1
744	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	75930663	75937116	1	ENSG00000005436	2	75,742,802	B1
745	MRPL19			Z	75939057	75941715	0	ENSG00000115364	2	75,727,417	B1
746	RICS	Gga#S35715088	ENSGALG00000022113	Z	75947234	75953082	1	ENSG00000134909	11	128,343,052	B1
747	RICS	Gga#S35715088	ENSGALG00000022113	Z	75967446	75973757	1	ENSG00000134909	11	128,343,052	B1
748	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	75977518	75986718	1	ENSG00000005436	2	75,742,802	B1
749	MRPL19			Z	75988312	75990923	0	ENSG00000115364	2	75,727,417	B1
750	RICS	Gga#S35715088	ENSGALG00000022113	Z	75995300	76001670	1	ENSG00000134909	11	128,343,052	B1
751	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76005095	76011391	1	ENSG00000005436	2	75,742,802	B1
752	MRPL19			Z	76013322	76015959	0	ENSG00000115364	2	75,727,417	B1
753	RICS	Gga#S35715088	ENSGALG00000022113	Z	76020375	76026796	1	ENSG00000134909	11	128,343,052	B1
754	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76029333	76036983	1	ENSG00000005436	2	75,742,802	B1
755	MRPL19			Z	76038926	76041587	0	ENSG00000115364	2	75,727,417	B1
756	RICS	Gga#S35715088	ENSGALG00000022113	Z	76048046	76053938	1	ENSG00000134909	11	128,343,052	B1
757	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76057685	76065029	1	ENSG00000005436	2	75,742,802	B1
758	MRPL19			Z	76067785	76070422	0	ENSG00000115364	2	75,727,417	B1
759	RICS	Gga#S35715088	ENSGALG00000022113	Z	76076327	76082418	1	ENSG00000134909	11	128,343,052	B1
760	RICS	Gga#S35715088	ENSGALG00000022113	Z	76095003	76101326	1	ENSG00000134909	11	128,343,052	B1
761	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76104953	76111541	1	ENSG00000005436	2	75,742,802	B1
762	MRPL19			Z	76113502	76116129	0	ENSG00000115364	2	75,727,417	B1
763	RICS	Gga#S35715088	ENSGALG00000022113	Z	76119420	76125630	1	ENSG00000134909	11	128,343,052	B1
764	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76130222	76138965	1	ENSG00000005436	2	75,742,802	B1
765	MRPL19			Z	76140887	76143367	0	ENSG00000115364	2	75,727,417	B1
766	RICS	Gga#S35715088	ENSGALG00000022113	Z	76148157	76154223	1	ENSG00000134909	11	128,343,052	B1
767	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76158097	76168896	1	ENSG00000005436	2	75,742,802	B1
768	MRPL19			Z	76170855	76143367	0	ENSG00000115364	2	75,727,417	B1
769	RICS	Gga#S35715088	ENSGALG00000022113	Z	76178127	76184188	1	ENSG00000134909	11	128,343,052	B1
770	RICS	Gga#S35715088	ENSGALG00000022113	Z	76197324	76202880	1	ENSG00000134909	11	128,343,052	B1
771	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76209795	76218338	1	ENSG00000005436	2	75,742,802	B1
772	MRPL19			Z	76220277	76222928	0	ENSG00000115364	2	75,727,417	B1
773	RICS	Gga#S35715088	ENSGALG00000022113	Z	76227549	76233892	1	ENSG00000134909	11	128,343,052	B1
774	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76248684	76257542	1	ENSG00000005436	2	75,742,802	B1
775	MRPL19			Z	76259441	76262075	0	ENSG00000115364	2	75,727,417	B1
776	RICS	Gga#S35715088	ENSGALG00000022113	Z	76266737	76272472	1	ENSG00000134909	11	128,343,052	B1
777	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76282995	76292595	1	ENSG00000005436	2	75,742,802	B1
778	MRPL19			Z	76294363	76297039	0	ENSG00000115364	2	75,727,417	B1

779	RICS	Gga#S35715088	ENSGALG00000022113	Z	76301840	76307588	1	ENSG00000134909	11	128,343,052	B1
780	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76317626	76326372	1	ENSG00000005436	2	75,742,802	B1
781	MRPL19			Z	76328316	76330956	0	ENSG00000115364	2	75,727,417	B1
782	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76335284	76342783	1	ENSG00000005436	2	75,742,802	B1
783	MRPL19			Z	76344722	76346002	0	ENSG00000115364	2	75,727,417	B1
784	RICS	Gga#S35715088	ENSGALG00000022113	Z	76350596	76356887	1	ENSG00000134909	11	128,343,052	B1
785	RICS	Gga#S35715088	ENSGALG00000022113	Z	76371588	76377106	1	ENSG00000134909	11	128,343,052	B1
786	RICS	Gga#S35715088	ENSGALG00000022113	Z	76393405	76399648	1	ENSG00000134909	11	128,343,052	B1
787	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76402967	76409733	1	ENSG00000005436	2	75,742,802	B1
788	MRPL19			Z	76411669	76414309	0	ENSG00000115364	2	75,727,417	B1
789	RICS	Gga#S35715088	ENSGALG00000022113	Z	76418987	76424641	1	ENSG00000134909	11	128,343,052	B1
790	RICS	Gga#S35715088	ENSGALG00000022113	Z	76437110	76443425	1	ENSG00000134909	11	128,343,052	B1
791	RICS	Gga#S35715088	ENSGALG00000022113	Z	76454769	76460708	1	ENSG00000134909	11	128,343,052	B1
792	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76463960	76470532	1	ENSG00000005436	2	75,742,802	B1
793	MRPL19			Z	76472494	76475153	0	ENSG00000115364	2	75,727,417	B1
794	AAK1	Gga#S19647549		Z	76475021	76523237	0	ENSG00000115977	2	69,542,036	B1
795	RICS	Gga#S35715088	ENSGALG00000022113	Z	76479951	76486007	1	ENSG00000134909	11	128,343,052	B1
796	RICS	Gga#S35715088	ENSGALG00000022113	Z	76499056	76505164	1	ENSG00000134909	11	128,343,052	B1
797	RICS	Gga#S35715088	ENSGALG00000022113	Z	76517221	76523240	1	ENSG00000134909	11	128,343,052	B1
798	AAK1			Z	76525150	76530275	0	ENSG00000115977	2	69,542,036	B1
799	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76530629	76534097	1	ENSG00000005436	2	75,742,802	B1
800	MRPL19			Z	76540273	76542936	0	ENSG00000115364	2	75,727,417	B1
801	RICS	Gga#S35715088	ENSGALG00000022113	Z	76550003	76555686	1	ENSG00000134909	11	128,343,052	B1
802	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76558978	76566980	1	ENSG00000005436	2	75,742,802	B1
803	MRPL19			Z	76568933	76616720	0	ENSG00000115364	2	75,727,417	B1
804	RICS	Gga#S35715088	ENSGALG00000022113	Z	76576393	76582642	1	ENSG00000134909	11	128,343,052	B1
805	RICS	Gga#S35715088	ENSGALG00000022113	Z	76595970	76601845	1	ENSG00000134909	11	128,343,052	B1
806	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76605344	76613236	1	ENSG00000005436	2	75,742,802	B1
807	RICS	Gga#S35715088	ENSGALG00000022113	Z	76620657	76626522	1	ENSG00000134909	11	128,343,052	B1
808	RICS	Gga#S35715088	ENSGALG00000022113	Z	76637455	76643071	1	ENSG00000134909	11	128,343,052	B1
809	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76646821	76654723	1	ENSG00000005436	2	75,742,802	B1
810	MRPL19			Z	76656699	76659331	0	ENSG00000115364	2	75,727,417	B1
811	RICS	Gga#S35715088	ENSGALG00000022113	Z	76662632	76668613	1	ENSG00000134909	11	128,343,052	B1
812	RICS	Gga#S35715088	ENSGALG00000022113	Z	76688494	76690346	1	ENSG00000134909	11	128,343,052	B1
813	RICS	Gga#S35715088	ENSGALG00000022113	Z	76690556	76694658	1	ENSG00000134909	11	128,343,052	B1
814	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76698368	76705249	1	ENSG00000005436	2	75,742,802	B1
815	MRPL19			Z	76708133	76710793	0	ENSG00000115364	2	75,727,417	B1
816	RICS	Gga#S35715088	ENSGALG00000022113	Z	76715417	76721713	1	ENSG00000134909	11	128,343,052	B1
817	RICS	Gga#S35715088	ENSGALG00000022113	Z	76738989	76745055	1	ENSG00000134909	11	128,343,052	B1
818	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76748529	76752232	1	ENSG00000005436	2	75,742,802	B1
819	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76754084	76761976	1	ENSG00000005436	2	75,742,802	B1
820	RICS	Gga#S35715088	ENSGALG00000022113	Z	76769210	76775276	1	ENSG00000134909	11	128,343,052	B1
821	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76778761	76786425	1	ENSG00000005436	2	75,742,802	B1
822	MRPL19			Z	76788363	76791011	0	ENSG00000115364	2	75,727,417	B1
823	RICS	Gga#S35715088	ENSGALG00000022113	Z	76795656	76801515	1	ENSG00000134909	11	128,343,052	B1
824	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76805390	76812408	1	ENSG00000005436	2	75,742,802	B1
825	MRPL19			Z	76814389	76817030	0	ENSG00000115364	2	75,727,417	B1
826	RICS	Gga#S35715088	ENSGALG00000022113	Z	76821676	76827669	1	ENSG00000134909	11	128,343,052	B1
827	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76831835	76839372	1	ENSG00000005436	2	75,742,802	B1
828	MRPL19			Z	76841328	76843978	0	ENSG00000115364	2	75,727,417	B1
829	RICS	Gga#S35715088	ENSGALG00000022113	Z	76848612	76854456	1	ENSG00000134909	11	128,343,052	B1
830	RICS	Gga#S35715088	ENSGALG00000022113	Z	76865841	76872153	1	ENSG00000134909	11	128,343,052	B1
831	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76875112	76876066	1	ENSG00000005436	2	75,742,802	B1
832	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76875997	76882848	1	ENSG00000005436	2	75,742,802	B1
833	MRPL19			Z	76884790	76887433	0	ENSG00000115364	2	75,727,417	B1
834	RICS	Gga#S35715088	ENSGALG00000022113	Z	76894596	76900910	1	ENSG00000134909	11	128,343,052	B1
835	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76904316	76913509	1	ENSG00000005436	2	75,742,802	B1
836	MRPL19			Z	76915444	76918090	0	ENSG00000115364	2	75,727,417	B1
837	RICS	Gga#S35715088	ENSGALG00000022113	Z	76923614	76929675	1	ENSG00000134909	11	128,343,052	B1
838	RICS	Gga#S35715088	ENSGALG00000022113	Z	76946827	76952655	1	ENSG00000134909	11	128,343,052	B1

839	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	76956974	76958904	1	ENSG00000005436	2	75,742,802	B1
840	MRPL19			Z	76964253	76966895	0	ENSG00000115364	2	75,727,417	B1
841	RICS	Gga#S35715088	ENSGALG00000022113	Z	76972941	76978915	1	ENSG00000134909	11	128,343,052	B1
842	RICS	Gga#S35715088	ENSGALG00000022113	Z	76989720	76995631	1	ENSG00000134909	11	128,343,052	B1
843	RICS	Gga#S35715088	ENSGALG00000022113	Z	77012894	77018983	1	ENSG00000134909	11	128,343,052	B1
844	RICS	Gga#S35715088	ENSGALG00000022113	Z	77027992	77034078	1	ENSG00000134909	11	128,343,052	B1
845	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77037573	77045046	1	ENSG00000005436	2	75,742,802	B1
846	MRPL19			Z	77047930	77050586	0	ENSG00000115364	2	75,727,417	B1
847	RICS	Gga#S35715088	ENSGALG00000022113	Z	77055363	77061355	1	ENSG00000134909	11	128,343,052	B1
848	RICS	Gga#S35715088	ENSGALG00000022113	Z	77074876	77080989	1	ENSG00000134909	11	128,343,052	B1
849	RICS	Gga#S35715088	ENSGALG00000022113	Z	77091364	77097486	1	ENSG00000134909	11	128,343,052	B1
850	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77101213	77104010	1	ENSG00000005436	2	75,742,802	B1
851	MRPL19			Z	77109959	77112606	0	ENSG00000115364	2	75,727,417	B1
852	RICS	Gga#S35715088	ENSGALG00000022113	Z	77115873	77121786	1	ENSG00000134909	11	128,343,052	B1
853	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77128846	77136156	1	ENSG00000005436	2	75,742,802	B1
854	MRPL19			Z	77139062	77141408	0	ENSG00000115364	2	75,727,417	B1
855	RICS	Gga#S35715088	ENSGALG00000022113	Z	77147816	77153699	1	ENSG00000134909	11	128,343,052	B1
856	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77156724	77164737	1	ENSG00000005436	2	75,742,802	B1
857	MRPL19			Z	77166672	77169335	0	ENSG00000115364	2	75,727,417	B1
858	RICS	Gga#S35715088	ENSGALG00000022113	Z	77173273	77179386	1	ENSG00000134909	11	128,343,052	B1
859	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77191103	77198242	1	ENSG00000005436	2	75,742,802	B1
860	MRPL19			Z	77200243	77202881	0	ENSG00000115364	2	75,727,417	B1
861	RICS	Gga#S35715088	ENSGALG00000022113	Z	77207496	77213450	1	ENSG00000134909	11	128,343,052	B1
862	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77228014	77234169	1	ENSG00000005436	2	75,742,802	B1
863	MRPL19			Z	77236103	77202881	0	ENSG00000115364	2	75,727,417	B1
864	RICS	Gga#S35715088	ENSGALG00000022113	Z	77246556	77252743	1	ENSG00000134909	11	128,343,052	B1
865	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77255963	77263717	1	ENSG00000005436	2	75,742,802	B1
866	MRPL19			Z	77265679	77268062	0	ENSG00000115364	2	75,727,417	B1
867	RICS	Gga#S35715088	ENSGALG00000022113	Z	77272807	77279018	1	ENSG00000134909	11	128,343,052	B1
868	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77283130	77291123	1	ENSG00000005436	2	75,742,802	B1
869	MRPL19			Z	77292948	77295592	0	ENSG00000115364	2	75,727,417	B1
870	RICS	Gga#S35715088	ENSGALG00000022113	Z	77301653	77307644	1	ENSG00000134909	11	128,343,052	B1
871	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77311401	77319296	1	ENSG00000005436	2	75,742,802	B1
872	MRPL19			Z	77321244	77295592	0	ENSG00000115364	2	75,727,417	B1
873	RICS	Gga#S35715088	ENSGALG00000022113	Z	77329409	77335400	1	ENSG00000134909	11	128,343,052	B1
874	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77342390	77349481	1	ENSG00000005436	2	75,742,802	B1
875	MRPL19			Z	77351248	77353893	0	ENSG00000115364	2	75,727,417	B1
876	RICS	Gga#S35715088	ENSGALG00000022113	Z	77358526	77364734	1	ENSG00000134909	11	128,343,052	B1
877	RICS	Gga#S35715088	ENSGALG00000022113	Z	77375185	77381254	1	ENSG00000134909	11	128,343,052	B1
878	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77384227	77393043	1	ENSG00000005436	2	75,742,802	B1
879	MRPL19			Z	77394946	77397622	0	ENSG00000115364	2	75,727,417	B1
880	RICS	Gga#S35715088	ENSGALG00000022113	Z	77404122	77410517	1	ENSG00000134909	11	128,343,052	B1
881	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77417151	77424962	1	ENSG00000005436	2	75,742,802	B1
882	MRPL19			Z	77426901	77429556	0	ENSG00000115364	2	75,727,417	B1
883	RICS	Gga#S35715088	ENSGALG00000022113	Z	77435330	77441215	1	ENSG00000134909	11	128,343,052	B1
884	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77451090	77459048	1	ENSG00000005436	2	75,742,802	B1
885	MRPL19			Z	77460833	77463470	0	ENSG00000115364	2	75,727,417	B1
886	RICS	Gga#S35715088	ENSGALG00000022113	Z	77468059	77474174	1	ENSG00000134909	11	128,343,052	B1
887	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77477224	77483110	1	ENSG00000005436	2	75,742,802	B1
888	MRPL19			Z	77524483	77527147	0	ENSG00000115364	2	75,727,417	B1
889	RICS	Gga#S35715088	ENSGALG00000022113	Z	77531085	77537529	1	ENSG00000134909	11	128,343,052	B1
890	RICS	Gga#S35715088	ENSGALG00000022113	Z	77549205	77555496	1	ENSG00000134909	11	128,343,052	B1
891	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77559806	77566851	1	ENSG00000005436	2	75,742,802	B1
892	MRPL19			Z	77568813	77527147	0	ENSG00000115364	2	75,727,417	B1
893	RICS	Gga#S35715088	ENSGALG00000022113	Z	77576854	77583352	1	ENSG00000134909	11	128,343,052	B1
894	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77588089	77595726	1	ENSG00000005436	2	75,742,802	B1
895	MRPL19			Z	77597661	77527147	0	ENSG00000115364	2	75,727,417	B1
896	RICS	Gga#S35715088	ENSGALG00000022113	Z	77604240	77610560	1	ENSG00000134909	11	128,343,052	B1
897	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77614844	77621577	1	ENSG00000005436	2	75,742,802	B1
898	MRPL19			Z	77623539	77626207	0	ENSG00000115364	2	75,727,417	B1

899	RICS	Gga#S35715088	ENSGALG00000022113	Z	77634580	77640580	1	ENSG00000134909	11	128,343,052	B1
900	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77644269	77652499	1	ENSG00000005436	2	75,742,802	B1
901	MRPL19			Z	77654438	77657075	0	ENSG00000115364	2	75,727,417	B1
902	RICS	Gga#S35715088	ENSGALG00000022113	Z	77661856	77667822	1	ENSG00000134909	11	128,343,052	B1
903	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77674448	77681379	1	ENSG00000005436	2	75,742,802	B1
904	MRPL19			Z	77683318	77657075	0	ENSG00000115364	2	75,727,417	B1
905	RICS	Gga#S35715088	ENSGALG00000022113	Z	77690385	77696432	1	ENSG00000134909	11	128,343,052	B1
906	RICS	Gga#S35715088	ENSGALG00000022113	Z	77712524	77718571	1	ENSG00000134909	11	128,343,052	B1
907	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77723014	77733642	1	ENSG00000005436	2	75,742,802	B1
908	MRPL19			Z	77735581	77657075	0	ENSG00000115364	2	75,727,417	B1
909	RICS	Gga#S35715088	ENSGALG00000022113	Z	77742722	77748828	1	ENSG00000134909	11	128,343,052	B1
910	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77751704	77760288	1	ENSG00000005436	2	75,742,802	B1
911	MRPL19			Z	77762245	77764890	0	ENSG00000115364	2	75,727,417	B1
912	RICS	Gga#S35715088	ENSGALG00000022113	Z	77769275	77775308	1	ENSG00000134909	11	128,343,052	B1
913	RICS	Gga#S35715088	ENSGALG00000022113	Z	77788766	77794925	1	ENSG00000134909	11	128,343,052	B1
914	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77801311	77809860	1	ENSG00000005436	2	75,742,802	B1
915	RICS	Gga#S35715088	ENSGALG00000022113	Z	77819216	77824941	1	ENSG00000134909	11	128,343,052	B1
916	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77828357	77835958	1	ENSG00000005436	2	75,742,802	B1
917	MRPL19			Z	77837938	77840596	0	ENSG00000115364	2	75,727,417	B1
918	RICS	Gga#S35715088	ENSGALG00000022113	Z	77845223	77850933	1	ENSG00000134909	11	128,343,052	B1
919	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77854354	77861378	1	ENSG00000005436	2	75,742,802	B1
920	MRPL19			Z	77863311	77865970	0	ENSG00000115364	2	75,727,417	B1
921	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77871705	77877961	1	ENSG00000005436	2	75,742,802	B1
922	MRPL19			Z	77879718	77882367	0	ENSG00000115364	2	75,727,417	B1
923	RICS	Gga#S35715088	ENSGALG00000022113	Z	77886821	77893217	1	ENSG00000134909	11	128,343,052	B1
924	RICS	Gga#S35715088	ENSGALG00000022113	Z	77906751	77912635	1	ENSG00000134909	11	128,343,052	B1
925	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77931822	77937966	1	ENSG00000005436	2	75,742,802	B1
926	MRPL19			Z	77939908	77942255	0	ENSG00000115364	2	75,727,417	B1
927	RICS	Gga#S35715088	ENSGALG00000022113	Z	77948403	77954607	1	ENSG00000134909	11	128,343,052	B1
928	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	77959120	77967967	1	ENSG00000005436	2	75,742,802	B1
929	MRPL19			Z	77969927	77972568	0	ENSG00000115364	2	75,727,417	B1
930	RICS	Gga#S35715088	ENSGALG00000022113	Z	77978021	77984035	1	ENSG00000134909	11	128,343,052	B1
931	RICS	Gga#S35715088	ENSGALG00000022113	Z	78001389	78007512	1	ENSG00000134909	11	128,343,052	B1
932	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	78011567	78018821	1	ENSG00000005436	2	75,742,802	B1
933	MRPL19			Z	78020759	78023418	0	ENSG00000115364	2	75,727,417	B1
934	RICS	Gga#S35715088	ENSGALG00000022113	Z	78032122	78038717	1	ENSG00000134909	11	128,343,052	B1
935	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	78053085	78060205	1	ENSG00000005436	2	75,742,802	B1
936	MRPL19			Z	78062143	78064806	0	ENSG00000115364	2	75,727,417	B1
937	RICS	Gga#S35715088	ENSGALG00000022113	Z	78069460	78075522	1	ENSG00000134909	11	128,343,052	B1
938	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	78078486	78085990	1	ENSG00000005436	2	75,742,802	B1
939	MRPL19			Z	78087928	78090591	0	ENSG00000115364	2	75,727,417	B1
940	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79094872	79103080	0	ENSG00000005436	2	75,742,802	B1
941	MRPL19			Z	79122574	79125199	1	ENSG00000115364	2	75,727,417	B1
942	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79127137	79134421	0	ENSG00000005436	2	75,742,802	B1
943	MRPL19			Z	79157414	79158752	1	ENSG00000115364	2	75,727,417	B1
944	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79160692	79164508	0	ENSG00000005436	2	75,742,802	B1
945	RICS	Gga#S35715088	ENSGALG00000022113	Z	79214876	79220743	0	ENSG00000134909	11	128,343,052	B1
946	MRPL19			Z	79225773	79228430	1	ENSG00000115364	2	75,727,417	B1
947	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79229819	79237855	0	ENSG00000005436	2	75,742,802	B1
948	RICS	Gga#S35715088	ENSGALG00000022113	Z	79242072	79247963	0	ENSG00000134909	11	128,343,052	B1
949	MRPL19			Z	79291811	79294456	1	ENSG00000115364	2	75,727,417	B1
950	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79296227	79303204	0	ENSG00000005436	2	75,742,802	B1
951	RICS	Gga#S35715088	ENSGALG00000022113	Z	79307481	79313382	0	ENSG00000134909	11	128,343,052	B1
952	MRPL19			Z	79318997	79321642	1	ENSG00000115364	2	75,727,417	B1
953	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79323580	79329987	0	ENSG00000005436	2	75,742,802	B1
954	MRPL19			Z	79344982	79347645	1	ENSG00000115364	2	75,727,417	B1
955	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79349607	79356857	0	ENSG00000005436	2	75,742,802	B1
956	MRPL19			Z	79371223	79373036	1	ENSG00000115364	2	75,727,417	B1
957	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79374630	79382756	0	ENSG00000005436	2	75,742,802	B1
958	MRPL19			Z	79379360	79373036	1	ENSG00000115364	2	75,727,417	B1

959	MRPL19			Z	79396195	79398851	1	ENSG00000115364	2	75,727,417	B1
960	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79400636	79408017	0	ENSG00000005436	2	75,742,802	B1
961	MRPL19			Z	79423729	79426370	1	ENSG00000115364	2	75,727,417	B1
962	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79428201	79436538	0	ENSG00000005436	2	75,742,802	B1
963	MRPL19			Z	79488067	79490742	1	ENSG00000115364	2	75,727,417	B1
964	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79492698	79500625	0	ENSG00000005436	2	75,742,802	B1
965	MRPL19			Z	79579755	79582422	1	ENSG00000115364	2	75,727,417	B1
966	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79584382	79591214	0	ENSG00000005436	2	75,742,802	B1
967	MRPL19			Z	79716628	79719253	1	ENSG00000115364	2	75,727,417	B1
968	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79721216	79727501	0	ENSG00000005436	2	75,742,802	B1
969	MRPL19			Z	79764061	79766505	1	ENSG00000115364	2	75,727,417	B1
970	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79768291	79775644	0	ENSG00000005436	2	75,742,802	B1
971	RICS	Gga#S35715088	ENSGALG00000022113	Z	79783843	79789756	0	ENSG00000134909	11	128,343,052	B1
972	MRPL19			Z	79793019	79795658	1	ENSG00000115364	2	75,727,417	B1
973	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79797594	79804403	0	ENSG00000005436	2	75,742,802	B1
974	MRPL19			Z	79820024	79822643	1	ENSG00000115364	2	75,727,417	B1
975	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79824605	79831446	0	ENSG00000005436	2	75,742,802	B1
976	MRPL19			Z	79846526	79849167	1	ENSG00000115364	2	75,727,417	B1
977	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79851105	79857767	0	ENSG00000005436	2	75,742,802	B1
978	MRPL19			Z	79893555	79896215	1	ENSG00000115364	2	75,727,417	B1
979	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79898151	79906623	0	ENSG00000005436	2	75,742,802	B1
980	MRPL19			Z	79920823	79923473	1	ENSG00000115364	2	75,727,417	B1
981	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79925429	79932965	0	ENSG00000005436	2	75,742,802	B1
982	MRPL19			Z	79954660	79957301	1	ENSG00000115364	2	75,727,417	B1
983	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	79959168	79966638	0	ENSG00000005436	2	75,742,802	B1
984	MRPL19			Z	80007115	80009777	1	ENSG00000115364	2	75,727,417	B1
985	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80011718	80020048	0	ENSG00000005436	2	75,742,802	B1
986	MRPL19			Z	80044298	80044677	1	ENSG00000115364	2	75,727,417	B1
987	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80046628	80053327	0	ENSG00000005436	2	75,742,802	B1
988	RICS	Gga#S35715088	ENSGALG00000022113	Z	80058082	80063980	11	ENSG00000134909	11	128,343,052	B1
989	MRPL19			Z	80069254	80070575	1	ENSG00000115364	2	75,727,417	B1
990	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80072529	80081302	0	ENSG00000005436	2	75,742,802	B1
991	MRPL19			Z	80095929	80097261	1	ENSG00000115364	2	75,727,417	B1
992	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80099199	80106963	0	ENSG00000005436	2	75,742,802	B1
993	RICS	Gga#S35715088	ENSGALG00000022113	Z	80110372	80116506	0	ENSG00000134909	11	128,343,052	B1
994	MRPL19			Z	80121140	80123777	1	ENSG00000115364	2	75,727,417	B1
995	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80125713	80133628	0	ENSG00000005436	2	75,742,802	B1
996	MRPL19			Z	80147228	80148969	1	ENSG00000115364	2	75,727,417	B1
997	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80150929	80159802	0	ENSG00000005436	2	75,742,802	B1
998	RICS	Gga#S35715088	ENSGALG00000022113	Z	80181531	80187603	0	ENSG00000134909	11	128,343,052	B1
999	MRPL19			Z	80192367	80195005	1	ENSG00000115364	2	75,727,417	B1
1000	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80196947	80202696	0	ENSG00000005436	2	75,742,802	B1
1001	RICS	Gga#S35715088	ENSGALG00000022113	Z	80217077	80187603	11	ENSG00000134909	11	128,343,052	B1
1002	MRPL19			Z	80222235	80224876	1	ENSG00000115364	2	75,727,417	B1
1003	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80226813	80234948	0	ENSG00000005436	2	75,742,802	B1
1004	MRPL19			Z	80250734	80253397	1	ENSG00000115364	2	75,727,417	B1
1005	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80255338	80262457	0	ENSG00000005436	2	75,742,802	B1
1006	MRPL19			Z	80287270	80289918	1	ENSG00000115364	2	75,727,417	B1
1007	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80291820	80294282	0	ENSG00000005436	2	75,742,802	B1
1008	MRPL19			Z	80309330	80311975	1	ENSG00000115364	2	75,727,417	B1
1009	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80313915	80322286	0	ENSG00000005436	2	75,742,802	B1
1010	MRPL19			Z	80355939	80358577	1	ENSG00000115364	2	75,727,417	B1
1011	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80360543	80364341	0	ENSG00000005436	2	75,742,802	B1
1012	MRPL19			Z	80390411	80391705	1	ENSG00000115364	2	75,727,417	B1
1013	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80393145	80400634	0	ENSG00000005436	2	75,742,802	B1
1014	MRPL19			Z	80415063	80417715	1	ENSG00000115364	2	75,727,417	B1
1015	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80419655	80425685	0	ENSG00000005436	2	75,742,802	B1
1016	RICS	Gga#S35715088	ENSGALG00000022113	Z	80430628	80436730	0	ENSG00000134909	11	128,343,052	B1
1017	MRPL19			Z	80462133	80464456	1	ENSG00000115364	2	75,727,417	B1
1018	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80466388	80473630	0	ENSG00000005436	2	75,742,802	B1

1019	RICS	Gga#S35715088	ENSGALG00000022113	Z	80488687	80494770	0	ENSG00000134909	11	128,343,052	B1
1020	MRPL19			Z	80499584	80502204	1	ENSG00000115364	2	75,727,417	B1
1021	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80504140	80509478	0	ENSG00000005436	2	75,742,802	B1
1022	RICS	Gga#S35715088	ENSGALG00000022113	Z	80518080	80523993	0	ENSG00000134909	11	128,343,052	B1
1023	MRPL19			Z	80527256	80529895	1	ENSG00000115364	2	75,727,417	B1
1024	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80531831	80538641	0	ENSG00000005436	2	75,742,802	B1
1025	RICS	Gga#S35715088	ENSGALG00000022113	Z	80543073	80549344	0	ENSG00000134909	11	128,343,052	B1
1026	MRPL19			Z	80571877	80574513	1	ENSG00000115364	2	75,727,417	B1
1027	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80576449	80583376	0	ENSG00000005436	2	75,742,802	B1
1028	RICS	Gga#S35715088	ENSGALG00000022113	Z	80587643	80593777	0	ENSG00000134909	11	128,343,052	B1
1029	MRPL19			Z	80598411	80601048	1	ENSG00000115364	2	75,727,417	B1
1030	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80602984	80610899	0	ENSG00000005436	2	75,742,802	B1
1031	MRPL19			Z	80630068	80632660	1	ENSG00000115364	2	75,727,417	B1
1032	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	80634594	80641647	0	ENSG00000005436	2	75,742,802	B1
1033	ADCY10	Gga#S21389984	ENSGALG00000002611	Z	80655525	80659514	1	ENSG00000143199	1	166045507	B1
1034	MTAP	Gga#S22196260	ENSGALG00000008174	Z	80750848	80782536	0	ENSG00000099810	9	21792635	A
1035	CDKN2B	Gga#S10831372		Z	80792252	80803814	1	ENSG00000147883	9	21992909	A
1036	B4GALT1		ENSGALG00000002022	Z	80888067	80896654	1	ENSG00000086062	9	33100642	A
1037	TRIM36	Gga#S21386046	ENSGALG00000008188	Z	80917175	80940431	1	ENSG00000152503	5	114488377	A
1038	PGGT1B	Gga#S35713406	ENSGALG00000008197	Z	80947277	80981169	1	ENSG00000164219	5	114575476	A
1039	CCDC112	Gga#S35713405	ENSGALG00000023042	Z	80983091	80991575	1	ENSG00000164221	5	114630784	A
1040	FEM1C	Gga#S6958921	ENSGALG00000008204	Z	81059386	81072595	1	ENSG00000145780	5	114884507	A
1041	ALDH7A1	Gga#S21386045	ENSGALG00000008229	Z	81087897	81105581	0	ENSG00000164904	5	125905432	A
1042	GRAMD3	Gga#S21386044	ENSGALG00000008237	Z	81115165	81155670	1	ENSG00000155324	5	125787000	A
1043	MRPL19			Z	81483987	81529593	1	ENSG00000115364	2	75,727,417	B1
1044	ZNF608	Gga#S21386047	ENSGALG00000005016	Z	81788132	81869506	0	ENSG00000168916	5	123994027	A
1045	cZorf12		ENSGALG00000023041	Z	82097080	82097386	0	X12	5	123037225	A
1046	ADCY10	Gga#S21389984	ENSGALG00000002611	Z	82277743	82282321	1	ENSG00000143199	1	166045507	B1
1047	RICS	Gga#S35715088	ENSGALG00000022113	Z	82290979	82297030	1	ENSG00000134909	11	128,343,052	B1
1048	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82300500	82306461	1	ENSG00000005436	2	75,742,802	B1
1049	RICS	Gga#S35715088	ENSGALG00000022113	Z	82317212	82323390	1	ENSG00000134909	11	128,343,052	B1
1050	RICS	Gga#S35715088	ENSGALG00000022113	Z	82345496	82351232	1	ENSG00000134909	11	128,343,052	B1
1051	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82355806	82362651	1	ENSG00000005436	2	75,742,802	B1
1052	MRPL19			Z	82364437	82367091	0	ENSG00000115364	2	75,727,417	B1
1053	RICS	Gga#S35715088	ENSGALG00000022113	Z	82371546	82377628	1	ENSG00000134909	11	128,343,052	B1
1054	RICS	Gga#S35715088	ENSGALG00000022113	Z	82390060	82396252	1	ENSG00000134909	11	128,343,052	B1
1055	RICS	Gga#S35715088	ENSGALG00000022113	Z	82407064	82412904	1	ENSG00000134909	11	128,343,052	B1
1056	RICS	Gga#S35715088	ENSGALG00000022113	Z	82427257	82433507	1	ENSG00000134909	11	128,343,052	B1
1057	RICS	Gga#S35715088	ENSGALG00000022113	Z	82446643	82452687	1	ENSG00000134909	11	128,343,052	B1
1058	RICS	Gga#S35715088	ENSGALG00000022113	Z	82466261	82472251	1	ENSG00000134909	11	128,343,052	B1
1059	RICS	Gga#S35715088	ENSGALG00000022113	Z	82483782	82489950	1	ENSG00000134909	11	128,343,052	B1
1060	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82493698	82501440	1	ENSG00000005436	2	75,742,802	B1
1061	MRPL19			Z	82503377	82506029	0	ENSG00000115364	2	75,727,417	B1
1062	RICS	Gga#S35715088	ENSGALG00000022113	Z	82511511	82517513	1	ENSG00000134909	11	128,343,052	B1
1063	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82520810	82527664	1	ENSG00000005436	2	75,742,802	B1
1064	MRPL19			Z	82529606	82532243	0	ENSG00000115364	2	75,727,417	B1
1065	RICS	Gga#S35715088	ENSGALG00000022113	Z	82536790	82542823	1	ENSG00000134909	11	128,343,052	B1
1066	RICS	Gga#S35715088	ENSGALG00000022113	Z	82554915	82561152	1	ENSG00000134909	11	128,343,052	B1
1067	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82568636	82575654	1	ENSG00000005436	2	75,742,802	B1
1068	MRPL19			Z	82577618	82580254	0	ENSG00000115364	2	75,727,417	B1
1069	RICS	Gga#S35715088	ENSGALG00000022113	Z	82585000	82591165	1	ENSG00000134909	11	128,343,052	B1
1070	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82594594	82600743	1	ENSG00000005436	2	75,742,802	B1
1071	MRPL19			Z	82602689	82605307	0	ENSG00000115364	2	75,727,417	B1
1072	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82607594	82632412	1	ENSG00000005436	2	75,742,802	B1
1073	RICS	Gga#S35715088	ENSGALG00000022113	Z	82609915	82615956	1	ENSG00000134909	11	128,343,052	B1
1074	MRPL19			Z	82634348	82605307	0	ENSG00000115364	2	75,727,417	B1
1075	RICS	Gga#S35715088	ENSGALG00000022113	Z	82640517	82646376	1	ENSG00000134909	11	128,343,052	B1
1076	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82653492	82668195	1	ENSG00000005436	2	75,742,802	B1
1077	RICS	Gga#S35715088	ENSGALG00000022113	Z	82655818	82661700	1	ENSG00000134909	11	128,343,052	B1
1078	MRPL19			Z	82673865	82676511	0	ENSG00000115364	2	75,727,417	B1

1079	RICS	Gga#S35715088	ENSGALG00000022113	Z	82681268	82687143	1	ENSG00000134909	11	128,343,052	B1
1080	RICS	Gga#S35715088	ENSGALG00000022113	Z	82699714	82705551	1	ENSG00000134909	11	128,343,052	B1
1081	cZorf16			Z	82717437	82718977	0				B1
1082	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82719815	82727522	1	ENSG00000005436	2	75,742,802	B1
1083	MRPL19			Z	82729461	82732124	0	ENSG00000115364	2	75,727,417	B1
1084	RICS	Gga#S35715088	ENSGALG00000022113	Z	82738576	82744462	1	ENSG00000134909	11	128,343,052	B1
1085	RICS	Gga#S35715088	ENSGALG00000022113	Z	82757948	82763956	1	ENSG00000134909	11	128,343,052	B1
1086	MRPL19			Z	82771853	82774525	0	ENSG00000115364	2	75,727,417	B1
1087	RICS	Gga#S35715088	ENSGALG00000022113	Z	82779212	82784867	1	ENSG00000134909	11	128,343,052	B1
1088	RICS	Gga#S35715088	ENSGALG00000022113	Z	82795822	82801510	1	ENSG00000134909	11	128,343,052	B1
1089	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82805487	82814997	1	ENSG00000005436	2	75,742,802	B1
1090	MRPL19			Z	82816932	82819478	0	ENSG00000115364	2	75,727,417	B1
1091	RICS	Gga#S35715088	ENSGALG00000022113	Z	82824290	82830214	1	ENSG00000134909	11	128,343,052	B1
1092	RICS	Gga#S35715088	ENSGALG00000022113	Z	82841200	82846837	1	ENSG00000134909	11	128,343,052	B1
1093	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82851575	82858159	1	ENSG00000005436	2	75,742,802	B1
1094	MRPL19			Z	82860120	82862765	0	ENSG00000115364	2	75,727,417	B1
1095	RICS	Gga#S35715088	ENSGALG00000022113	Z	82868289	82874267	1	ENSG00000134909	11	128,343,052	B1
1096	RICS	Gga#S35715088	ENSGALG00000022113	Z	82894762	82900630	1	ENSG00000134909	11	128,343,052	B1
1097	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82907839	82914126	1	ENSG00000005436	2	75,742,802	B1
1098	MRPL19			Z	82916089	82918730	0	ENSG00000115364	2	75,727,417	B1
1099	RICS	Gga#S35715088	ENSGALG00000022113	Z	82923367	82929456	1	ENSG00000134909	11	128,343,052	B1
1100	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82943759	82951285	1	ENSG00000005436	2	75,742,802	B1
1101	MRPL19			Z	82953224	82955873	0	ENSG00000115364	2	75,727,417	B1
1102	RICS	Gga#S35715088	ENSGALG00000022113	Z	82960479	82966342	1	ENSG00000134909	11	128,343,052	B1
1103	RICS	Gga#S35715088	ENSGALG00000022113	Z	82979734	82985570	1	ENSG00000134909	11	128,343,052	B1
1104	C2ORF3	Gga#S21398230	ENSGALG00000016732	Z	82999486	83007035	1	ENSG00000005436	2	75,742,802	B1
1105	MRPL19			Z	83008961	82955873	0	ENSG00000115364	2	75,727,417	B1
1106	RICS	Gga#S35715088	ENSGALG00000022113	Z	83016646	83022863	1	ENSG00000134909	11	128,343,052	B1
1107	RICS	Gga#S35715088	ENSGALG00000022113	Z	83038416	83044395	1	ENSG00000134909	11	128,343,052	B1
1108	C2ORF3	Gga#S21388675	ENSGALG00000023046	Z	83047878	83056366	1	ENSG00000005436	2	75,742,802	B1
1109	RICS	Gga#S35715088	ENSGALG00000022113	Z	83066638	83072596	1	ENSG00000134909	11	128,343,052	B1
1110	SRFBP1	Gga#S21386066	ENSGALG00000005316	Z	83078659	83134104	0	ENSG00000151304	5	121325555	A
1111	LOX	Gga#S19183798	ENSGALG00000005317	Z	83144006	83151247	1	ENSG00000113083	5	121429918	A
1112	ZNF474		ENSGALG00000023040	Z	83202672	83206163	0	ENSG00000164185	5	121493114	A
1113	SNCAIP	Gga#S21386066	ENSGALG00000005330	Z	83268214	83314714	0	ENSG00000064692	5	121675719	A
1114	SNX2	Gga#S23831130	ENSGALG00000005337	Z	83404634	83437117	0	ENSG00000205302	5	122138649	A
1115	SNX24	Gga#S7080224	ENSGALG00000018874	Z	83440114	83515384	0	ENSG00000064652	5	122209170	A
1116	PPIC	Gga#S35713403	ENSGALG00000005346	Z	83517560	83522680	1	ENSG00000168938	5	122386979	A
1117	PRDM6		ENSGALG00000005351	Z	83595205	83617242	0	ENSG00000061455	5	122452715	A
1118	CEP120	Gga#S21386060	ENSGALG00000005368	Z	83654557	83690322	1	ENSG00000168944	5	122708478	A
1119	TOMM5	Gga#S19627866	ENSGALG00000005372	Z	83696982	83697349	0	ENSG00000175768	9	37578410	A
1120	FRMPD1		ENSGALG00000023036	Z	83717485	83736450	0	ENSG00000070601	9	37641052	A
1121	RG9MTD3	Gga#S35713402		Z	83738618	83743905	1	ENSG00000165275	9	37743802	A
1122	WDR32	Gga#S6960614	ENSGALG00000017558	Z	83744490	83763129	0	ENSG00000122741	9	37790790	A
1123	MCART1	Gga#S6786262		Z	83769220	83770092	1	ENSG00000122696	9	37869400	A
1124	FBXO10			Z	83775680	83775785	0	ENSG00000147912	9	37500899	A
1125	POLR1E	Gga#S33767871	ENSGALG00000005395	Z	83778718	83791988	1	ENSG00000137054	9	37475945	A
1126	ZBTB5	Gga#S21386049	ENSGALG00000005354	Z	83798960	83800981	0	ENSG00000168795	9	37428111	A
1127	GRHPR	Gga#S18609824	ENSGALG00000005423	Z	83811176	83816244	1	ENSG00000137106	9	37412663	A
1128	ZCCHC7	Gga#S21386055	ENSGALG00000005433	Z	83829957	83870405	1	ENSG00000147905	9	37110469	A
1129	PDE6B		ENSGALG00000015373	J_AA056N13	117342	96671		ENSG00000133256	4	609,373	B3a
1130	ATP5I		ENSGALG00000015372	J_AA056N13	89443	91311		ENSG00000169020	4	656,228	B3a
1131	MFS07		ENSGALG00000020538	J_AA068J18	126844	141407		ENSG00000169026	4	665,614	B3a
1132	GAK		ENSGALG00000015352	J_AA056N13	35747	403		ENSG00000178950	4	833,066	B3a
1133	TMEM175		ENSGALG00000015368	J_AA056N13	74842	88517		ENSG00000127419	4	916,260	B3a
1134	SLC26A1		ENSGALG00000015380	J_AA056N13	172734	176096		ENSG00000145217	4	962,865	B3a
1135	IDUA		ENSGALG00000015376	J_AA056N13	187087	140010		ENSG00000127415	4	970,785	B3a
1136	HEATR7B2			Z	68289325	68291682	1	ENSG00000171495	5	41033880	A
1137	PART1			J_AA105D16				ENSG00000152931	5	59819516	A
1138	ERCC8		XM_414249	Z	18699479	18733810	1	ENSG00000215032	5	60205418	A

1139 TAF9		J_AA063E08				ENSG00000085231	5	68696327 A
1140 OCLN		JE085K17	116822	117988		ENSG00000197822	5	68823875 A
1141 AC140134.2-1		J_AA114I01	91029	91410		ENSG00000179978	5	69424621 A
1142 BIRC1		J_AA114I01	91029	91410		ENSG00000081770	5	70300066 A
1143 AC026698.6		J_AA163L10				ENSG00000205462	5	81714520 A
1144 TMEM232		JB031H09	73194	198894		ENSG00000186952	5	109931539 A
1145 C5orf48		J_AA009F06	75724	75849		ENSG00000196900	5	125995305 A
1146 THAP1	ENSGALG00000015385	J_AA064K10				ENSG00000131931	8	42,810,975 B3a
1147 RNF170	ENSGALG00000015386	J_AA064K10				ENSG00000120925	8	42,825,091 B3a
1148 CBWD1	ENSGALG00000010147	JB056D03	144422	163054		ENSG00000147996	9	111039 A
1149 DOCK8	ENSGALG00000010156	JB056D03	117942	54192		ENSG00000107099	9	263048 A
1150 KANK1	ENSGALG00000010158	J_AA082L12	180184	2107		ENSG00000107104	9	460291 A
1151 DMRT1	ENSGALG00000010160	J_AA086C16				ENSG00000137090	9	831690 A
1152 DMRT3	ENSGALG00000010161	J_AA086C16				ENSG00000064218	9	966964 A
1153 C9orf68		J_AA025M17				ENSG00000106686	9	4578827 A
1154 RCL1	ENSGALG00000015024	J_AA025M17				ENSG00000120158	9	4782937 A
1155 IFNB1		Z		IFN array Gap		ENSG00000171855	9	21067104 A
1156 IFNW1		J_AD0121O02	12852	12391		ENSG00000177047	9	21130213 A
1157 IFNE		J_AD0121O02	12891	12349		ENSG00000184995	9	21471067 A
1158 DMRTA1		J_AA086C16	76478	76648		ENSG00000176399	9	22436840 A
1159 C9orf11		J_AA050A06	77870	154222		ENSG00000120160	9	27274667 A
1160 PAX5	ENSGALG00000016431	J_AE0093B11	35762	25576		ENSG00000196092	9	36828539 A
1161 ZNF72		J_AA128H23	73499	74188		ENSG00000197550	9	69137176 A
1162 ZNF169		JE016N08				ENSG00000175787	9	96061399 A
1163 SUSD1	ENSGALG00000015677	J_AA135B11	138453	117326		ENSG00000106868	9	113842886 A
1164 ROD1	ENSGALG00000015669	J_AA129F07	119735	68103		ENSG00000119314	9	114020536 A
1165 GRP		J_AA149E15	138568	139186		ENSG00000134443	18	55038380 A

Supplementary Table 2: Chicken Z amplicon predicted genes and coordinates

ID	NAME	Chicken Chr	Chicken Beg	Chicken End	Chicken Stranc
678	ADCY10	Z	73695051	73699038	1
679	ADCY10	Z	73716606	73720592	1
680	ADCY10	Z	73737915	73741901	1
681	ADCY10	Z	73759212	73763199	1
682	ADCY10	Z	73780533	73784520	1
683	ADCY10	Z	73801592	73805579	1
1033	ADCY10	Z	80655525	80659514	1
1046	ADCY10	Z	82277743	82282321	1
685	C2ORF3	Z	73821257	73828763	0
687	C2ORF3	Z	73847331	73856135	0
689	C2ORF3	Z	73920762	73929355	0
691	C2ORF3	Z	73948530	73956197	0
693	C2ORF3	Z	74000771	74006894	0
695	C2ORF3	Z	74036789	74043220	0
697	C2ORF3	Z	74097369	74105909	0
699	C2ORF3	Z	74143304	74151417	0
701	C2ORF3	Z	74198298	74206607	0
703	C2ORF3	Z	74235458	74242632	0
706	C2ORF3	Z	74323027	74331151	0
708	C2ORF3	Z	74350287	74358843	0
711	C2ORF3	Z	74376783	74385691	0
713	C2ORF3	Z	74404606	74413986	0
715	C2ORF3	Z	74451393	74459459	0
717	C2ORF3	Z	74499314	74506368	0
719	C2ORF3	Z	74525108	74531755	0
721	C2ORF3	Z	74551319	74559403	0
724	C2ORF3	Z	74620308	74627801	0
726	C2ORF3	Z	74650306	74656290	0
728	C2ORF3	Z	74677614	74684867	0
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Supplementary Table 3: Chicken Z gene gain and loss

Gene Name	Chicken Chr	Chicken Pos	Chicken ENS ID	Human Chr	Human Pos	Human ENS ID	Category	Notes
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NARS	Z	354861	ENSGALG00000003087	18		53418894	ENSG00000134440	A
HEMH	Z	368798	ENSGALG00000003066	18		53366535	ENSG00000066926	A
ONECUT2	Z	397502		18		53253915	ENSG00000119547	A
ST8SIA3	Z	423931	ENSGALG00000003049	18		53170719	ENSG00000177511	A
WDR7	Z	467783	ENSGALG00000003019	18		52469614	ENSG00000091157	A
TXNL1	Z	581344	ENSGALG00000002948	18		52421053	ENSG00000091164	A
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ALPK2	Z	756230	ENSGALG00000002898	18		54299459	ENSG00000198796	A
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CD72	Z	8823764	ENSGALG000000005194	9		35599530	ENSG00000137101	A
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ARSB	Z	22255809	ENSGALG00000004438	5	78108795	ENSG00000113273	A
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AL159169.14	Z	58516420		9	14545513	ENSG00000215261	A
FAM127A	Z	58671520	ENSGALG000000014661	5	92979531	ENSG00000113391	A
AC106818.2	Z	58926024		5	92961819	ENSG00000205434	A
NR2F1	Z	58932511	ENSGALG000000007000	5	92944799	ENSG00000175745	A
ARRDC3	Z	59915827	ENSGALG000000014658	5	90700299	ENSG00000113369	A
GPR98	Z	60005948	ENSGALG000000014657	5	89890373	ENSG00000164199	A
LYSM3	Z	60271243	ENSGALG000000014651	5	89847200	ENSG00000176018	A
POLR3G	Z	60279514	ENSGALG000000014650	5	89806437	ENSG00000113356	A
MBLC2	Z	60299932	ENSGALG000000014649	5	89789778	ENSG00000176055	A
CETN3	Z	60319272	ENSGALG000000014648	5	89725287	ENSG00000153140	A
MEF2C	Z	61006062	ENSGALG000000014645	5	88051922	ENSG00000081189	A
LOC645323	Z	61048183	ENSGALG000000023094	5	87096020	ENSG00000207570	A
TMEM161B	Z	61174226	ENSGALG000000010896	5	87526779	ENSG00000164180	A
CCNH	Z	61382749	ENSGALG000000015641	5	86725844	ENSG00000134480	A
RASA1	Z	61395572	ENSGALG000000017706	5	86599838	ENSG00000145715	A
COX7	Z	61621765	ENSGALG000000015631	5	85949540	ENSG00000127184	A
EDIL3	Z	62677037	ENSGALG000000015630	5	83273882	ENSG00000164176	A
HPLN1	Z	62975431	ENSGALG000000015627	5	82972502	ENSG00000145681	A
CSPG2	Z	63036969	ENSGALG000000015624	5	82803339	ENSG00000038427	A

XRCC4	Z	63268416	ENSGALG00000015620	5	82409073	ENSG00000152422	A
TMEM167A	Z	63365737		5	82387742	ENSG00000174695	A
ATP6A1L	Z	63722635	ENSGALG00000015618	5	81611037	ENSG00000205464	A
RPS23	Z	63743719	ENSGALG00000015617	5	81604899	ENSG00000186468	A
ATG10	Z	63757721	ENSGALG00000020531	5	81303630	ENSG00000152348	A
SSBP2	Z	64030122	ENSGALG00000023089	5	80751428	ENSG00000145687	A
ACOT12	Z	64086779	ENSGALG00000015616	5	80661580	ENSG00000172497	A
ZCCHC9	Z	64121893	ENSGALG00000015603	5	80633178	ENSG00000131732	A
RASGRF2	Z	64135616	ENSGALG00000015598	5	80292314	ENSG00000113319	A
CKMT2	Z	64135618	ENSGALG00000015602	5	80564895	ENSG00000131730	A
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DHFR	Z	64437558	ENSGALG00000015579	5	79,957,801		A
ANKRD34B	Z	64470560	ENSGALG00000015578	5	79888331	ENSG00000189127	A
FAM151B	Z	64477711	ENSGALG00000015577	5	79819556	ENSG00000152380	A
ZFYVE16	Z	64493658	ENSGALG00000015576	5	79739594	ENSG00000039319	A
CCDC125	Z	64531130	ENSGALG00000015572	5	68612278	ENSG00000183323	A
AC145132.2	Z	64547685	ENSGALG00000020534	5	68683311	ENSG00000185057	A
RAD17	Z	64549420	ENSGALG00000015571	5	68700880	ENSG00000152942	A
GRIN3A	Z	65413247	ENSGALG00000015551	9	103371456	ENSG00000198785	A
BRE1A	Z	65486375	ENSGALG00000015548	9	103335954	ENSG00000155827	A
C9orf125	Z	65522004	ENSGALG00000015545	9	103275274	ENSG00000165152	A
ALDOB	Z	65536495	ENSGALG00000015544	9	103222681	ENSG00000136872	A
RM50	Z	65542199	ENSGALG00000015543	9	103192070	ENSG00000136897	A
PPAPR3	Z	65545830	ENSGALG00000015542	9	102830852	ENSG00000148123	A
PALM2	Z	66054047	ENSGALG00000015655	9	111442893	ENSG00000157654	A
AKAP2	Z	66225483	ENSGALG00000015656	9	111442893	ENSG00000157654	A
SLC46A2	Z	66256609		9	114681022	ENSG00000119457	A
SNX30	Z	66268598	ENSGALG00000015660	9	114552955	ENSG00000148158	A
CI080	Z	66328245	ENSGALG00000020528	9	114488618	ENSG00000148153	A
KIAA1958	Z	66366436	ENSGALG00000023083	9	114289069	ENSG00000165185	A
HSDL2	Z	66417411	ENSGALG00000015663	9	114182038	ENSG00000119471	A
UGCG	Z	66473592	ENSGALG00000015682	9	113698867	ENSG00000148154	A
C9orf84	Z	66556906		9	113488274	ENSG00000165181	A
DNAJC25-GNC	Z	66615726	ENSGALG00000015684	9	113433453	ENSG00000059769	A
KIAA0368	Z	66631560	ENSGALG00000015689	9	113162793	ENSG00000136813	A
SMC2	Z	66683471	ENSGALG00000015691	9	105896362	ENSG00000136824	A
PTGR1	Z	66718539	ENSGALG00000015702	9	113365074	ENSG00000106853	A
THIO	Z	66738618	ENSGALG00000015704	18	9875723	ENSG00000168454	A
TXN	Z	66738620	ENSGALG00000015704	9	112046121	ENSG00000136810	A
SVEP1	Z	66755902	ENSGALG00000015721	9	112167352	ENSG00000165124	A
MUSK	Z	66936215	ENSGALG00000015728	9	112470960	ENSG00000030304	A
LPAR1	Z	67030757	ENSGALG00000015729	9	112675365	ENSG00000198121	A
PRKACG	Z	67295456		9	70817241	ENSG00000165059	A
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TOPORS	Z	67334749	ENSGALG00000020523	9	32530545	ENSG00000197579	A
ELAVL2	Z	67640308	ENSGALG00000015799	9	23680102	ENSG00000107105	A
AL589843.9	Z	68201881		9	98531217	ENSG00000204328	A
TUSC1	Z	68475264	ENSGALG00000017510	9	25667681	ENSG00000198680	A
PLAA	Z	68763380	ENSGALG000000001782	9	26894518	ENSG00000137055	A
C9orf82	Z	68763388	ENSGALG00000001765	9	26830685	ENSG00000120159	A
IFT74	Z	68799954	ENSGALG000000001801	9	26946410	ENSG00000096872	A
LRRC19	Z	68805841		9	26983590	ENSG00000184434	A
TEK	Z	68839484	ENSGALG00000001840	9	27099286	ENSG00000120156	A
MOBK12B	Z	68893975	ENSGALG00000001856	9	27319129	ENSG00000120162	A
C9orf72	Z	68994661	ENSGALG000000001864	9	27536544	ENSG00000147894	A
LINGO2	Z	69120285	ENSGALG000000001869	9	27938076	ENSG00000174482	A
CORO2A	Z	70755261	ENSGALG000000001933	9	99926299	ENSG00000106789	A
TBC1D2	Z	70808452	ENSGALG000000001944	9	100001132	ENSG00000095383	A
Q5ZJ12	Z	70828726	ENSGALG000000001947	9	110669622	ENSG00000070061	A
APTX	Z	70862437	ENSGALG000000001954	9	32962609	ENSG00000137074	A
DNAJA1	Z	70871418	ENSGALG000000023066	9	33015242	ENSG00000086061	A
SMU1	Z	70885347	ENSGALG000000002014	9	33031850	ENSG00000122692	A
HEMGN	Z	70934253	ENSGALG000000023061	9	99728894	ENSG00000136929	A
SPINK4	Z	70934511	ENSGALG000000021842	9	33208363	ENSG00000122711	A
FOXE1	Z	70956493		9	99655358	ENSG00000178919	A
XPA	Z	71008924	ENSGALG000000023059	9	99477013	ENSG00000136936	A
NCBP1	Z	71018547	ENSGALG000000002087	9	99435526	ENSG00000136937	A
C9orf97	Z	71049017	ENSGALG000000002110	9	99402183	ENSG00000136925	A
TMOD1	Z	71069570	ENSGALG000000002125	9	99303742	ENSG00000136842	A
TDSD7	Z	71090535	ENSGALG000000012350	9	99214123	ENSG00000196116	A
IREB1	Z	71253152	ENSGALG000000002162	9	32374618	ENSG00000122729	A
PRR16	Z	71473437	ENSGALG000000002183	5	119827918	ENSG00000184838	A
HSD17B4	Z	71824883	ENSGALG000000002187	5	118816122	ENSG00000133835	A
TFIP8	Z	71895405	ENSGALG000000002196	5	118752897	ENSG00000145779	A
DMXL1	Z	71945413	ENSGALG000000002227	5	118434983	ENSG00000172869	A
DTWD2	Z	72038121	ENSGALG000000002250	5	118203135	ENSG00000169570	A
SEMA6A	Z	72889583	ENSGALG000000002294	5	115807150	ENSG00000092421	A
COMMD10	Z	73086836	ENSGALG000000002308	5	115448622	ENSG00000145781	A
LAEVERIN	Z	73150779	ENSGALG000000002318	5	115326170	ENSG00000172901	A
AP3S1	Z	73181806	ENSGALG000000002341	5	115205518	ENSG00000177879	A
ATG12	Z	73209804	ENSGALG000000002345	5	115193714	ENSG00000145782	A
CDO1	Z	73220241	ENSGALG000000002358	5	115168333	ENSG00000129596	A
TICAM2	Z	73269208	ENSGALG000000021410	5	114942238	ENSG00000134970	A
MARVELD2	Z	73283097	ENSGALG000000002361	5	68746699	ENSG00000152939	A
GTF2H2	Z	73294960	ENSGALG000000002399	5	70366717	ENSG00000145736	A
GTF2H2C	Z	73294961	ENSGALG000000002399	5	68891830	ENSG00000183474	A
SMN2	Z	73311950	ENSGALG000000002430	5	69381106	ENSG00000205571	A
SMN1	Z	73312795	ENSGALG000000002430	5	70256524	ENSG00000172062	A
SERFB	Z	73317286	ENSGALG000000021397	5	69356852	ENSG00000205572	A
SERF1A	Z	73317300	ENSGALG000000021397	5	70232270	ENSG00000172058	A
BDP1	Z	73323283	ENSGALG000000002439	5	70787198	ENSG00000145734	A
MCCC2	Z	73378467	ENSGALG000000002529	5	70918910	ENSG00000131844	A
CARTPT	Z	73421628		5	71050750	ENSG00000164326	A
KCNM2	Z	73547389	ENSGALG000000002539	5	113725565	ENSG00000080709	A
MTAP	Z	80750848	ENSGALG000000008174	9	21792635	ENSG00000099810	A
CDKN2B	Z	80792252		9	21992909	ENSG00000147883	A
B4GALT1	Z	80888067	ENSGALG000000002022	9	33100642	ENSG00000086062	A
TRIM36	Z	80917175	ENSGALG000000008188	5	114488377	ENSG00000152503	A
PGT1B	Z	80947277	ENSGALG000000008197	5	114575476	ENSG00000164219	A
CCDC112	Z	80983091	ENSGALG000000023042	5	114630784	ENSG00000164221	A
FEM1C	Z	81059386	ENSGALG000000008204	5	114884507	ENSG00000145780	A
ALDH7A1	Z	81087897	ENSGALG000000008229	5	125905432	ENSG00000164904	A
GRAMD3	Z	81115165	ENSGALG000000008237	5	125787000	ENSG00000155324	A

ZNF608	Z	81788132	ENSGALG00000005016	5	123994027	ENSG00000168916	A	
cZorf12	Z	82097080	ENSGALG00000023041	5	123037225	X12	A	
SRFBP1	Z	83078659	ENSGALG00000005316	5	121325555	ENSG00000151304	A	
LOX	Z	83144006	ENSGALG00000005317	5	121429918	ENSG00000113083	A	
ZNF474	Z	83202672	ENSGALG00000023040	5	121493114	ENSG00000164185	A	
SNCAIP	Z	83268214	ENSGALG00000005330	5	121675719	ENSG00000064692	A	
SNX2	Z	83404634	ENSGALG00000005337	5	122138649	ENSG00000205302	A	
SNX24	Z	83440114	ENSGALG00000018874	5	122209170	ENSG00000064652	A	
PPIC	Z	83517560	ENSGALG00000005346	5	122386979	ENSG00000168938	A	
PRDM6	Z	83595205	ENSGALG00000005351	5	122452715	ENSG00000061455	A	
CEP120	Z	83654557	ENSGALG00000005368	5	122708478	ENSG00000168944	A	
TOMM5	Z	83696982	ENSGALG00000005372	9	37578410	ENSG00000175768	A	
FRMPD1	Z	83717485	ENSGALG00000023036	9	37641052	ENSG00000070601	A	
RG9MTD3	Z	83738618		9	37743802	ENSG00000165275	A	
WDR32	Z	83744490	ENSGALG00000017558	9	37790790	ENSG00000122741	A	
MCART1	Z	83769220		9	37869400	ENSG00000122696	A	
FBXO10	Z	83775680		9	37500899	ENSG00000147912	A	
POLR1E	Z	83778718	ENSGALG00000005395	9	37475945	ENSG00000137054	A	
ZBTB5	Z	83798960	ENSGALG00000005354	9	37428111	ENSG00000168795	A	
GRHPR	Z	83811176	ENSGALG00000005423	9	37412663	ENSG00000137106	A	
ZCCHC7	Z	83829957	ENSGALG00000005433	9	37110469	ENSG00000147905	A	
CBWD1	Z		ENSGALG00000010147	9	111039	ENSG00000147996	A	
DOCK8	Z		ENSGALG00000010156	9	263048	ENSG00000107099	A	
KANK1	Z		ENSGALG00000010158	9	460291	ENSG00000107104	A	
DMRT1	Z		ENSGALG00000010160	9	831690	ENSG00000137090	A	
DMRT3	Z		ENSGALG00000010161	9	966964	ENSG00000064218	A	
RCL1	Z		ENSGALG00000015024	9	4782937	ENSG00000120158	A	
ROD1	Z		ENSGALG00000015669	9	114020536	ENSG00000119314	A	
SUSD1	Z		ENSGALG00000015677	9	113842886	ENSG00000106868	A	
PAX5	Z		ENSGALG00000016431	9	36828539	ENSG00000196092	A	
C9orf68	Z		NM_001031282	9	4578827	ENSG00000106686	A	
AC104113.3	Z		XM_414249	5	60205418	ENSG00000215032	A	
AC012622.6	Z			5	109931539	ENSG00000186952	A	
AC026698.6	Z			5	81714520	ENSG00000205462	A	
AC109486.2-2	Z			5	59819516	ENSG00000152931	A	
AC140134.2-1	Z			5	69424621	ENSG00000179978	A	
BIRC1	Z			5	70300066	ENSG00000081770	A	
C5orf48	Z			5	125995305	ENSG00000196900	A	
C9orf11	Z			9	27274667	ENSG00000120160	A	
DMRTA1	Z			9	22436840	ENSG00000176399	A	
GRP	Z			18	55038380	ENSG00000134443	A	
HEATR7B2	Z			5	41033880	ENSG00000171495	A	
IFNB1	Z			9	21067104	ENSG00000171855	A	
IFNE	Z			9	21471067	ENSG00000184995	A	
IFNW1	Z			9	21130213	ENSG00000177047	A	
OCLN	Z			5	68823875	ENSG00000197822	A	
TAF9	Z			5	68696327	ENSG00000085231	A	
ZNF169	Z			9	96061399	ENSG00000175787	A	
ZNF72	Z			9	69137176	ENSG00000197550	A	
IFNB	Z	7235572	ENSGALG00000005759				B1	Birds Only?
IFNB1A	Z	7241179	ENSGALG00000013245				B1	Birds Only?
PTPRK-like	Z	8769950	ENSGALG00000021355				B1	Birds Only?
cZorf13	Z	8839177					B1	Birds Only?
TAF1C	Z	8854602					B1	Chicken Only?
AVIDIN-like	Z	8903176	ENSGALG00000021848				B1	Birds Only?
AVID	Z	8911953	ENSGALG00000023622				B1	Birds Only?
AVR2	Z	8915587	ENSGALG00000002446				B1	Chicken Only?
also similar to	Z	8931274	ENSGALG00000023622				B1	Birds Only?
also similar to	Z	8931274	ENSGALG00000023622				B1	Birds Only?
cZorf6	Z	9024424	ENSGALG000000021338				B1	Birds Only?
AC104127.2	Z	10789482		5	93515468	ENSG00000218494	B1	
ANKRD13C	Z	29538166	ENSGALG00000011311	1	70500138		B1	Duplicated -- True orth on GGA8
cZorf10	Z	30228735	ENSGALG00000023299				B1	Chicken Only?
cZorf14	Z	31311449					B1	Chicken Only?
cZorf5	Z	32430230	ENSGALG00000020553				B1	Chicken Only?
RFK	Z	34416803	ENSGALG00000000004	9	78190253	ENSG00000135002	B1	
cZorf15	Z	42305380					B1	Chicken Only?
TOPORS	Z	51602367	ENSGALG00000020523	9	32530545	ENSG00000197579	B1	
PHF7-like	Z	56607183	ENSGALG00000005023				B1	Chicken Only?
cZorf17	Z	61052944					B1	No annotated gene -- but possible
CCDC81	Z	64824086					B1	Chicken Only?
TOPORS	Z	66728419	ENSGALG00000020523	9	32530545	ENSG00000197579	B1	
cZorf3	Z	67135866	ENSGALG00000015743				B1	Birds Only?
NPR2	Z	67262210	ENSGALG00000015753	9	35782151	ENSG00000159899	B1	Duplicated -- True orth on GGAZ
FLNC-like	Z	67431089	ENSGALG00000014707				B1	Novel Gene?
FLNC-like	Z	67454863	ENSGALG00000014707				B1	Novel Gene?
FLNC-like	Z	68038980	ENSGALG00000014707				B1	Novel Gene?
HEATR7B2-like	Z	68181694	ENSGALG00000022510				B1	Novel Gene?
HEATR7B2-like	Z	68248604	ENSGALG00000016539				B1	Novel Gene?
HEATR7B2-like	Z	68306886	ENSGALG00000017045				B1	Novel Gene?
HEATR7B2-like	Z	68320942					B1	Novel Gene?
HEATR7B2-like	Z	68342923	ENSGALG00000016539				B1	Novel Gene?
HEATR7B2-like	Z	68353493	ENSGALG00000016305				B1	Novel Gene?
FLNC-like	Z	68416411	ENSGALG00000023076				B1	Novel Gene?
FLNC-like	Z	68481344	ENSGALG00000023076				B1	Novel Gene?
cZorf8	Z	68493506	ENSGALG00000021457				B1	Chicken Only?
cZorf18	Z	68658939					B1	No annotated gene -- but possible
FLNC-like	Z	68742706					B1	Chicken Only?
cZorf9	Z	68877876	ENSGALG00000023074				B1	Chicken Only?
cZorf1	Z	69766395	ENSGALG00000001871				B1	Chicken Only?
D4ST1	Z	70031990		15	38550505		B1	Duplicated -- True orth on GGA5
cZorf7	Z	70612481	ENSGALG00000021452				B1	Diapsids Only?
FLNC-like	Z	71314359	ENSGALG00000021429				B1	Novel Gene?
OCLN	Z	72298698					B1	Duplicated -- True orth on GGA4
ADCY10	Z	73695051	ENSGALG00000002611	1	166045507	ENSG00000143199	B1	Z amplicon gene
ADCY10	Z	73716606	ENSGALG00000002611	1	166045507	ENSG00000143199	B1	Z amplicon gene
ADCY10	Z	73737915	ENSGALG00000002611	1	166045507	ENSG00000143199	B1	Z amplicon gene
ADCY10	Z	73759212	ENSGALG00000002611	1	166045507	ENSG00000143199	B1	Z amplicon gene
ADCY10	Z	73780533	ENSGALG00000002611	1	166045507	ENSG00000143199	B1	Z amplicon gene
ADCY10	Z	73801592	ENSGALG00000002611	1	166045507	ENSG00000143199	B1	Z amplicon gene
MRPL19	Z	73816665		2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	73821257	ENSGALG00000016732	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	73842730		2	75,727,417	ENSG00000115364	B1	Z amplicon gene







MRPL19	Z	80147228	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80150929	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
R1CS	Z	80181531	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
MRPL19	Z	80192367	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80196947	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
R1CS	Z	80217077	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
MRPL19	Z	80222235	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80226813	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	80250734	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80255338	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	80287270	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80291820	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	80309330	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80313915	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	80355939	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80360543	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	80390411	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80393145	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	80415063	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80419655	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
R1CS	Z	80430628	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
MRPL19	Z	80462133	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80466388	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
R1CS	Z	80488687	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
MRPL19	Z	80499584	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80504140	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
R1CS	Z	80518080	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
MRPL19	Z	80527256	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80531831	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
R1CS	Z	80543073	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
MRPL19	Z	80571877	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80576449	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
R1CS	Z	80587643	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
MRPL19	Z	80598411	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80602984	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	80630068	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	80634594	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
ADCY10	Z	80655525	1	166045507	ENSG00000143199	B1	Z amplicon gene
MRPL19	Z	81483987	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
ADCY10	Z	82277743	1	166045507	ENSG00000143199	B1	Z amplicon gene
R1CS	Z	82290979	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82300500	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
R1CS	Z	82317212	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82345496	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82355806	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	82364437	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82371546	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82390060	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82407064	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82427257	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82446643	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82466261	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82483782	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82493698	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	82503377	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82511511	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82520810	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	82529606	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82536790	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82554915	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82568636	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	82577618	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82585000	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82594594	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	82602689	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
C2ORF3	Z	82607594	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
R1CS	Z	82609915	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
MRPL19	Z	82634348	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82640517	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82653492	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
R1CS	Z	82655818	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
MRPL19	Z	82673865	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82681268	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82699714	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
cZorf16	Z	82717437	2			B1	Chicken Only?
C2ORF3	Z	82719815	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	82729461	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82738576	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82757948	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
MRPL19	Z	82771853	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82779212	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82795822	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82805487	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	82816932	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82824290	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82841200	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82851575	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	82860120	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82868289	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82894762	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82907839	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	82916089	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82923367	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82943759	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	82953224	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	82960479	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	82979734	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	82999486	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
MRPL19	Z	83008961	2	75,727,417	ENSG00000115364	B1	Z amplicon gene
R1CS	Z	83016646	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
R1CS	Z	83038416	11	128,343,052	ENSG00000134909	B1	Z amplicon gene
C2ORF3	Z	83047878	2	75,742,802	ENSG00000005436	B1	Z amplicon gene
R1CS	Z	83066638	11	128,343,052	ENSG00000134909	B1	Z amplicon gene

cZorf4	Z	7025006	ENSGALG00000017527			B2	Lost in Mammals; Present in Birds and Fish	
cZorf2	Z	7450248	ENSGALG00000005813			B2	Lost in Mammals; Present in Birds and Fish	
SLC16A7-like	Z	26981246	ENSGALG00000015045			B2	Lost in Mammals; Present in Birds and Fish	
APH1A	Z	8988105	ENSGALG00000002578	1	148502512	ENSG00000117362	B3a	not ancestrally linked
MRPL17	Z	9064611	ENSGALG00000002605	11	6659456	ENSG00000158042	B3a	not ancestrally linked
RLN3	Z	26804237	ENSGALG00000015028	19	13998501	ENSG00000171136	B3a	transposed on in chicken
CFC1	Z	42403097	ENSGALG00000012623	2	130995137	ENSG00000152093	B3a	not ancestrally linked
CNTNAP4	Z	42818176	ENSGALG00000023179	16	74868677	ENSG00000152910	B3a	transposed on in birds
TPPP2	Z	44101613	ENSGALG00000015213	14	20568249	ENSG00000179636	B3a	transposed on in chicken
CPLX1	Z	53209391	ENSGALG00000015332	4	768,746	ENSG00000168993	B3a	minor syntenic block
PCGF3	Z	53512279	ENSGALG00000015333	4	689573	ENSG00000185619	B3a	minor syntenic block
CHRN3	Z	53604801	ENSGALG00000015384	8	42,671,719	ENSG00000147432	B3a	minor syntenic block
U632B	Z	53790867	ENSGALG00000015337	2	84902285	ENSG00000186854	B3a	not ancestrally linked
PIGG	Z	54117240	ENSGALG00000015349	4	483010	ENSG00000174227	B3a	minor syntenic block
HOOK3	Z	54269799	ENSGALG00000015390	8	42871190	ENSG00000168172	B3a	minor syntenic block
KCMF1	Z	54317186	ENSGALG00000015391	2	85051727	ENSG00000176407	B3a	not ancestrally linked
FNTA	Z	54384193	ENSGALG00000015397	8	43030599	ENSG00000168522	B3a	minor syntenic block
FUT10	Z	54400078	ENSGALG00000015399	8	33347884	ENSG00000172728	B3a	minor syntenic block
NRG1	Z	54499792	ENSGALG00000015422	8	31617043	ENSG00000157168	B3a	minor syntenic block
LIP1	Z	55070219	ENSGALG00000015425	8	19840870	ENSG00000175445	B3a	minor syntenic block
PSD3	Z	55130416	ENSGALG00000015428	8	18429093	ENSG00000156011	B3a	minor syntenic block
DGKQ	Z	71144055	ENSGALG00000002142	4	942676	ENSG00000145214	B3a	minor syntenic block
GAK	Z		ENSGALG00000015352	4	833,066	ENSG00000178950	B3a	minor syntenic block
TMEM175	Z		ENSGALG00000015368	4	916,260	ENSG00000127419	B3a	minor syntenic block
ATP5I	Z		ENSGALG00000015372	4	656,228	ENSG00000169020	B3a	minor syntenic block
PDEF6B	Z		ENSGALG00000015373	4	609,373	ENSG00000133256	B3a	minor syntenic block
IDUA	Z		ENSGALG00000015376	4	970,785	ENSG00000127415	B3a	minor syntenic block
SLC26A1	Z		ENSGALG00000015380	4	962,865	ENSG00000145217	B3a	minor syntenic block
THAP1	Z		ENSGALG00000015385	8	42,810,975	ENSG00000131931	B3a	minor syntenic block
RNF170	Z		ENSGALG00000015386	8	42,825,091	ENSG00000120925	B3a	minor syntenic block
MFS07	Z		ENSGALG00000020538	4	665,614	ENSG00000169026	B3a	minor syntenic block
C20orf134	Z	44853870	ENSGALG00000006803	20	31717965	ENSG00000182584	B3b	Mammals not in ancestral configuration
PHF7	Z	64923606	ENSGALG00000015672	3	52419567	ENSG0000010318	B3b	Mammals not in ancestral configuration
CBWD5	Z	65712165	ENSGALG00000015643	3	52419567	ENSG0000010318	B3b	Mammals not in ancestral configuration
CBWD3	Z		ENSGALG00000010147	9	69671824	ENSG00000172785	C1	duplicated in mammals
CBWD6	Z		ENSGALG00000010147	9	70046662	ENSG00000196873	C1	duplicated in mammals
CBWD7	Z		ENSGALG00000010147	9	68494376	ENSG00000204790	C1	duplicated in mammals
RAP1B	Z		ENSGALG00000010147	5	42661911	ENSG00000215126	C1	duplicated in mammals
ZNF782	Z			9	75501666	ENSG00000176276	C1	insertion in human intron of sv2c
AL353795.13-2				9	98619094	ENSG00000196597	C1	mammals only
AC008869.5				5	35137398	ENSG00000215198	C1	Human Chimp Gorilla Macaque only
AC008875.9				5	37849694	ENSG00000212720	C1	Human Chimp Gorilla only
AC020901.8				5	43050282	ENSG00000177738	C1	Human Chimp Gorilla only
AL353732.14				5	80514754	ENSG00000214858	C1	Human Chimp Gorilla only
AL365171.8				5	21444270	ENSG00000171889	C1	Human Chimp Gorilla only
AL365190.16				9	43077952	ENSG00000215068	C1	Human Chimp Gorilla Orang only
AL365202.19-1				5	83464846	ENSG00000214935	C1	Human Chimp Gorilla Orang only
AC025178.8-1				9	3442305	ENSG00000203286	C1	Human Chimp Macaque only
AL158825.12				9	32184855	ENSG00000183359	C1	Human Chimp Orang only
C9orf107				9	76709393	ENSG00000204638	C1	Human Chimp Orang only
AC009271.7				18	104321715	ENSG00000204250	C1	Human Chimp Orang only
AC138409.1-1				5	51821842	ENSG00000206129	C1	Human Chimp Orang only
AC025181.8-2				5	34210910	ENSG00000215159	C1	Human Macaque only
AC008847.7-1				5	32245527	ENSG00000215163	C1	Human only
CR769776.8-1				5	64465552	ENSG00000215023	C1	Human only
C5orf23				9	68669831	ENSG00000204788	C1	Human only
AC139792.2				5	32824702	ENSG00000181495	C1	Mammal only
AC138409.1-2				5	34214831	ENSG00000215158	C1	Mammal only
CARD6				5	34225895	ENSG00000215156	C1	Mammal only
C5orf39				5	40877043	ENSG00000132357	C1	Mammal only
CCL28				5	43075258	ENSG00000177721	C1	Mammal only
GAPT				5	43417357	ENSG00000151882	C1	Mammal only
AC094086.2				5	57825203	ENSG00000175857	C1	Mammal only
AC114982.2-1				5	61018466	ENSG00000178722	C1	Mammal only
AC092373.2-2				5	61865238	ENSG00000198679	C1	Mammal only
CCNB1				5	65527873	ENSG00000205619	C1	Mammal only
AC139495.2				5	68498669	ENSG00000134057	C1	Mammal only
AC131392.2				5	68964790	ENSG00000214997	C1	Mammal only
AC139277.2				5	69230352	ENSG00000197848	C1	Mammal only
AC146944.1-2				5	69252309	ENSG00000212653	C1	Mammal only
AC139272.3				5	69842535	ENSG00000205565	C1	Mammal only
AC139834.2				5	70106234	ENSG00000197284	C1	Mammal only
AC145138.2-1				5	70127358	ENSG00000205561	C1	Mammal only
AC093251.2-2				5	70471472	ENSG00000205550	C1	Mammal only
ZBED3				5	75734628	ENSG00000205518	C1	Mammal only
AC026410.5-4				5	76408288	ENSG00000132846	C1	Mammal only
SPZ1				5	79631253	ENSG00000184188	C1	Mammal only
SPATA9				5	79651599	ENSG00000164299	C1	Mammal only
TSLP				5	95014545	ENSG00000145757	C1	Mammal only
FAM170A				5	110435081	ENSG00000145777	C1	Mammal only
INSL6				9	118993153	ENSG00000164334	C1	Mammal only
RLN2				9	5153793	ENSG00000120210	C1	Mammal only
RLN1				9	5289868	ENSG00000107014	C1	Mammal only
IL33				9	5324969	ENSG00000107018	C1	Mammal only
C9orf123				9	6231678	ENSG00000137033	C1	Mammal only
C9orf146				9	7786490	ENSG00000137038	C1	Mammal only
C9orf92				9	13917970	ENSG00000205636	C1	Mammal only
IFNA21				9	16193933	ENSG00000205549	C1	Mammal only
IFNA4				9	21155636	ENSG00000137080	C1	Mammal only
IFNA14				9	21176693	ENSG00000147877	C1	Mammal only
IFNA7				9	21191234	ENSG00000186809	C1	Mammal only
IFNA10				9	21191468	ENSG00000214042	C1	Mammal only
IFNA16				9	21196180	ENSG00000186803	C1	Mammal only
IFNA17				9	21206372	ENSG00000147885	C1	Mammal only
IFNA5				9	21217242	ENSG00000214040	C1	Mammal only
IFNA6				9	21294325	ENSG00000147873	C1	Mammal only
IFNA13				9	21339834	ENSG00000120235	C1	Mammal only
IFNA2				9	21357423	ENSG00000120247	C1	Mammal only
IFNA8				9	21374253	ENSG00000188379	C1	Mammal only
IFNA1				9	21399146	ENSG00000120242	C1	Mammal only
CDKN2A				9	21430440	ENSG00000197919	C1	Mammal only
C9orf134				9	21957751	ENSG00000147889	C1	Mammal only
				9	24533227	ENSG00000205442	C1	Mammal only

AL356791.9			9	26056673	ENSG00000196478	C1	Mammal only
AL139008.10-1			9	33607801	ENSG00000205274	C1	Mammal only
AL139008.10-2			9	33619138	ENSG00000183938	C1	Mammal only
AL139008.10-3			9	33628035	ENSG00000178161	C1	Mammal only
ENHO			9	34511042	ENSG00000168913	C1	Mammal only
CCL27			9	34651894	ENSG00000213927	C1	Mammal only
AL162231.20-1			9	34655027	ENSG00000187186	C1	Mammal only
AL162231.20-2			9	34713229	ENSG00000205108	C1	Mammal only
AL162231.20-3			9	34716490	ENSG00000215204	C1	Mammal only
AL162231.20-4			9	34820265	ENSG00000159797	C1	Mammal only
C9orf144			9	34820901	ENSG00000215202	C1	Mammal only
C9orf131			9	35014143	ENSG00000174038	C1	Mammal only
SIT1			9	35639300	ENSG00000137078	C1	Mammal only
CCDC107			9	35648301	ENSG00000159884	C1	Mammal only
C9orf128			9	35808427	ENSG00000204930	C1	Mammal only
HRCT1			9	35896189	ENSG00000196196	C1	Mammal only
OR252			9	35947105	ENSG00000122718	C1	Mammal only
BX255923.13			9	68542665	ENSG00000196400	C1	Mammal only
AL512605.13-2			9	69473030	ENSG00000204778	C1	Mammal only
C9orf57			9	73856119	ENSG00000204669	C1	Mammal only
C9orf40			9	76752371	ENSG00000135045	C1	Mammal only
AL158154.28-2			9	83718172	ENSG00000204562	C1	Mammal only
AL158154.28-1			9	83718273	ENSG00000214931	C1	Mammal only
AL158154.28-3			9	83733218	ENSG00000189357	C1	Mammal only
AL355985.18-2			9	83793507	ENSG00000214929	C1	Mammal only
FAM75B			9	83865480	ENSG00000204561	C1	Mammal only
C9orf153			9	88025001	ENSG00000187753	C1	Mammal only
AL160279.21-1			9	89563922	ENSG00000214888	C1	Mammal only
CTSL3			9	89577650	ENSG00000188029	C1	Mammal only
C9orf79			9	89687592	ENSG00000177992	C1	Mammal only
C9orf47			9	90795598	ENSG00000186354	C1	Mammal only
ANKRD19			9	94611301	ENSG00000218940	C1	Mammal only
ZNF484			9	94648173	ENSG00000127081	C1	Mammal only
FAM120AOS			9	95248604	ENSG00000188938	C1	Mammal only
C9orf130			9	97672387	ENSG00000214847	C1	Mammal only
AL159167.23-1			9	97772706	ENSG00000218011	C1	Mammal only
ZNF510			9	98557968	ENSG00000081386	C1	Mammal only
ZNF782			9	98619094	ENSG00000196597	C1	Mammal only
CYLC2			9	104791360	ENSG00000155833	C1	Mammal only
C9orf152			9	112001662	ENSG00000188959	C1	Mammal only
INSL4			9	5221443	ENSG00000120211	C1	Primate only
C9orf170			9	88953379	ENSG00000204446	C1	Primate only
C9orf118			9	96458174	ENSG00000204343	C1	Primate only
AL354861.11			9	97561303	ENSG00000175611	C1	Primate only
TTC23L			5	34875026	ENSG00000205838	C2	Lost in birds?
UGT3A1			5	35988967	ENSG00000145626	C2	Lost in birds?
UGT3A2			5	36070881	ENSG00000168671	C2	Lost in birds?
C9			5	39320763	ENSG00000113600	C2	Lost in birds?
AC008898.6			5	64022207	ENSG00000145642	C2	Lost in Synapsids?
C9orf46			9	5347973	ENSG00000107020	C2	missing from chicken
DDX58			9	32445300	ENSG00000107201	C2	missing from chicken
CCDC11			18	46007564	ENSG00000172361	C2	missing from chicken
MBD1			18	46049215	ENSG00000141644	C2	missing from chicken
CXXC1			18	46062713	ENSG00000154832	C2	missing from chicken
C18orf24			18	46155390	ENSG00000154839	C2	missing from chicken
MAPK4			18	46340482	ENSG00000141639	C2	missing from chicken
MRO			18	46578572	ENSG00000134042	C2	missing from chicken
ME2	Un_random	27351040	ENSGALG00000022329	46659433	ENSG00000082212	C2	missing from chicken
ELAC1			18	46748385	ENSG00000141642	C2	missing from chicken
SMAD4			18	46810611	ENSG00000141646	C2	missing from chicken
MEX3C			18	46954918	ENSG00000176624	C2	missing from chicken
DCC			18	48121156	ENSG00000187323	C2	missing from chicken
MBD2	28?		18	49934573	ENSG00000134046	C2	missing from chicken
POLI			18	50049847	ENSG00000101751	C2	missing from chicken
STARD6			18	50104962	ENSG00000174448	C2	missing from chicken
C18orf54			18	50139169	ENSG00000166845	C2	missing from chicken
C18orf26			18	50409388	ENSG00000178690	C2	missing from chicken
RAB27B			18	50646706	ENSG00000041353	C2	missing from chicken
CCDC68			18	50719792	ENSG00000166510	C2	missing from chicken
OMD			18	94216359	ENSG00000127083	C2	missing from chicken
C9orf156	12		9	99706593	ENSG00000136932	C2	Missing from synapsids
GPR150			9	94981538	ENSG00000178015	C2	moved in chicken
FAM133B	2	22635559	ENSGALG00000009475	60706670	ENSG00000183055	C3a	synteny not conserved
AC145146.2-1			5	68825796	ENSG00000205575	C3a	synteny not conserved
PMCHL2	1	57419753	ENSGALG00000012757	70707368	ENSG00000169040	C3a	synteny not conserved
AC113404.3	1	37085902	ENSGALG00000009927	75501666	ENSG00000176276	C3a	synteny not conserved
AC020937.6	2	106529413	ENSGALG00000015093	78331972	ENSG00000214890	C3a	synteny not conserved
NBPF22P			5	85614018	ENSG00000205449	C3a	synteny not conserved
AC092278.3-1			5	99425834	ENSG00000214802	C3a	synteny not conserved
AC010228.8-1	3	64410057	ENSGALG00000014873	108414912	ENSG00000176857	C3a	synteny not conserved
ZRSR1	1	125314815	ENSGALG00000016552	112255212	ENSG00000212643	C3a	synteny not conserved
TSSK1B			5	112796150	ENSG00000212122	C3a	synteny not conserved
RPS17P2			5	116079834	ENSG00000197575	C3a	synteny not conserved
AC008629.7-1			5	118337159	ENSG00000197744	C3a	synteny not conserved
FTMT			5	121215549	ENSG00000181867	C3a	synteny not conserved
CSNK1G3			5	122875692	ENSG00000151292	C3a	synteny not conserved
PPAPDC2	8	4324081	ENSGALG00000003029	4652298	ENSG00000205808	C3a	synteny not conserved
IGHEP2			9	5103549	ENSG00000215285	C3a	synteny not conserved
RANBP6	1	149330116	ENSGALG00000016887	6001043	ENSG00000137040	C3a	synteny not conserved
TPDS2L3	20	9516727	ENSGALG00000004683	6318375	ENSG00000170777	C3a	synteny not conserved
RPS26P3			9	9080876	ENSG00000212829	C3a	synteny not conserved
RRAGA	4		9	19039372	ENSG00000155876	C3a	synteny not conserved
KLHL9	4	3190314	ENSGALG00000005982	21319670	ENSG00000198642	C3a	synteny not conserved
FAM166B			9	35551946	ENSG00000215187	C3a	synteny not conserved
EXOSC3	6	5481076	ENSGALG00000002426	37770308	ENSG00000107371	C3a	synteny not conserved
ANKRD20A4	1	26091172	ENSGALG000000009104	68671801	ENSG00000172014	C3a	synteny not conserved
CCDC29	1	26091172	ENSGALG000000009104	68715488	ENSG00000221917	C3a	synteny not conserved
AL445665.20	3	50541007	ENSGALG000000012412	68940083	ENSG00000182021	C3a	synteny not conserved
FOXD4L5			9	69465527	ENSG00000204779	C3a	synteny not conserved
FOXD4L4			9	69666443	ENSG00000184659	C3a	synteny not conserved
FOXD4L3			9	70107603	ENSG00000187559	C3a	synteny not conserved
FAM122A	4	4086089	ENSGALG000000006127	70584833	ENSG00000187866	C3a	synteny not conserved
C9orf135			9	71625551	ENSG00000204711	C3a	synteny not conserved

CHCHD9	19	4868198	ENSGALG0000002495	9	81196014	ENSG00000186940	C3a	synteny not conserved
CCRK				9	89771183	ENSG00000156345	C3a	synteny not conserved
AL136097.10				9	93979281	ENSG00000214877	C3a	synteny not conserved
FAM22F				9	96120299	ENSG00000130950	C3a	synteny not conserved
FAM22G				9	98721960	ENSG00000188152	C3a	synteny not conserved
HIATL2				9	98751014	ENSG00000196312	C3a	synteny not conserved
ZNF322B				9	98999356	ENSG00000188801	C3a	synteny not conserved
ANP32B	10			9	99785310	ENSG00000136938	C3a	synteny not conserved
ZNF189				9	103200976	ENSG00000136870	C3a	synteny not conserved
PPP3R2				9	103393718	ENSG00000188386	C3a	synteny not conserved
OR13F1				9	106306365	ENSG00000186881	C3a	synteny not conserved
OR13C4				9	106328355	ENSG00000148136	C3a	synteny not conserved
OR13C3				9	106337872	ENSG00000204246	C3a	synteny not conserved
OR13C8				9	106371270	ENSG00000186943	C3a	synteny not conserved
OR13C5				9	106400559	ENSG00000204245	C3a	synteny not conserved
OR13C2				9	106406773	ENSG00000179074	C3a	synteny not conserved
OR13C9				9	106419350	ENSG00000136839	C3a	synteny not conserved
OR13D1				9	106496524	ENSG00000179055	C3a	synteny not conserved
AL359846.11-2				9	106524437	ENSG00000188712	C3a	synteny not conserved
ACTL7B	10			9	110656692	ENSG00000148156	C3a	synteny not conserved
ACTL7A	10			9	110664367	ENSG00000187003	C3a	synteny not conserved
TXNDC8				9	112105622	ENSG00000204193	C3a	synteny not conserved
OR2K2				9	113129584	ENSG00000171133	C3a	synteny not conserved
ZNF483				9	113327260	ENSG00000173258	C3a	synteny not conserved
ACTBL2	5	19700610		5	56813161	ENSG00000169067	C3a	synteny not conserved
KIAA1529	17	7502569	ENSGALG0000003320	9	99040600	ENSG00000197816	C3b	synteny conserved in outgroups
KIAA1529	Un_random	36135993	ENSGALG00000022225	9	99040600	ENSG00000197816	C3b	synteny conserved in outgroups
FOXE1	8	22697482	ENSGALG00000023293	9	99655358	ENSG00000178919	C3b	synteny conserved in outgroups
C9orf29	27	1512096	ENSGALG00000000239	9	113404932	ENSG00000204173	C3b	synteny conserved in outgroups
FHOD3	2	85359668	ENSGALG00000013124	18	32131700	ENSG00000134775	C3b	synteny conserved in outgroups
HIATL1	28			9	96176654	ENSG00000148110	C3b	synteny conserved in outgroups
IFNK	Un_random	24396419	ENSGALG00000015062	9	27514302	ENSG00000147896	C3b	synteny conserved in outgroups
NDUFB6	14	14154940	ENSGALG00000002033	9	32543523	ENSG00000165264	C3b	synteny conserved in outgroups
TAF1L	4	2201431	ENSGALG00000005464	9	32620097	ENSG00000122728	C3b	synteny conserved in outgroups
BAG1	2	87931265	ENSGALG00000013157	9	33244163	ENSG00000107262	C3b	synteny conserved in outgroups
CHMP5	2	87941041	ENSGALG00000013160	9	33255000	ENSG00000086065	C3b	synteny conserved in outgroups
NFX1	2	56511374	ENSGALG00000012482	9	33280510	ENSG00000086102	C3b	synteny conserved in outgroups
ANKRD18B	1	26091172	ENSGALG00000009104	9	33514392	ENSG00000159712	C3b	synteny conserved in outgroups
CCL19	Un_random	17081160	ENSGALG00000005851	9	34679564	ENSG00000172724	C3b	synteny conserved in outgroups
CCL21	Un_random	17081160	ENSGALG00000005851	9	34699002	ENSG00000137077	C3b	synteny conserved in outgroups
RECK	2	57122003	ENSGALG00000012626	9	36026906	ENSG00000122707	C3b	synteny conserved in outgroups
GLIPR2	2	92069763	ENSGALG00000013578	9	36126032	ENSG00000122694	C3b	synteny conserved in outgroups
CCIN	5			9	36159391	ENSG00000185972	C3b	synteny conserved in outgroups
AL356489.14-	1	81183459	ENSGALG00000014750	9	33639098	ENSG00000215206	C3b	synteny conserved in outgroups
PRSS3	1	81258371	ENSGALG00000010231	9	33740515	ENSG00000010438	C3b	synteny conserved in outgroups
AC011139.8	17	7532190	ENSGALG00000003197	18	35168834	ENSG00000175886	C3b	synteny conserved in outgroups

Supplementary Table 4: Human X gene gain and loss

Gene Name	Chicken Chr	Chicken Pos	Chicken ENS ID	Human Chr	Human Pos	Human ENS ID	Category	Note
PLP1	4	1977392	ENSGALG000000000112	X		102918410	ENSG00000123560	A
KLF8	1	159947131	ENSGALG000000000373	X		56275632	ENSG00000102349	A
Q5J1N8_CHIC	4	1705649	ENSGALG0000000003860	X		106956116	ENSG00000080561	A
PIN4	4	1662322	ENSGALG0000000003878	X		71318251	ENSG00000102309	A
ERCC6L	4	1655797	ENSGALG0000000003881	X		71341232	ENSG00000186871	A
OCRL	4	1636260	ENSGALG0000000003920	X		128501933	ENSG00000122126	A
XPNPEP2	4	1629935	ENSGALG0000000003949	X		128700627	ENSG00000122121	A
NP_00102628	4	1622918	ENSGALG0000000003951	X		128741641	ENSG00000122122	A
ZDHC9	4	1610436	ENSGALG0000000003962	X		128766596	ENSG00000188706	A
BCORL1	4	1581961	ENSGALG0000000003976	X		128944350	ENSG00000085185	A
NP_00100749	4	1565973	ENSGALG0000000004003	X		129091018	ENSG00000156709	A
RBMX2	4	1553805	ENSGALG0000000004025	X		129363624	ENSG00000134597	A
NP_00101290	4	1545933	ENSGALG0000000004063	X		129301699	ENSG00000102078	A
GPR119	4	1543986	ENSGALG0000000004069	X		129346095	ENSG00000147262	A
ENOX2	4	1518548	ENSGALG0000000004079	X		129585031	ENSG00000165675	A
CHM1B_CHIC	4	1509856	ENSGALG0000000004086	X		79414226	ENSG00000215104	A
NP_989437.1	4	1492764	ENSGALG0000000004093	X		79156911	ENSG00000122145	A
NP_00101258	4	1454028	ENSGALG0000000004107	X		78502541	ENSG00000078596	A
NP_00100846	4	1439057	ENSGALG0000000004111	X		78313125	ENSG00000147138	A
LPAR4	4	1389744	ENSGALG0000000004121	X		77896957	ENSG00000147145	A
CYSLTR1	4	1330046	ENSGALG0000000004128	X		77414787	ENSG00000173198	A
	4	1269659	ENSGALG0000000004187	X		77271902	ENSG00000187325	A
KIF4A_CHICK	4	1250810	ENSGALG0000000004195	X		69426620	ENSG00000090889	A
PDZ11_CHICK	4	1247336	ENSGALG0000000004198	X		69422936	ENSG00000120509	A
A4L917_CHIC	4	1222323	ENSGALG0000000004251	X		69404880	ENSG00000120500	A
P2RY4	4	1204244	ENSGALG0000000004346	X		69394745	ENSG00000186912	A
	4	1199256	ENSGALG0000000004367	X		69177117	ENSG00000147160	A
	4	1199256	ENSGALG0000000004367	X		69314061	ENSG00000184210	A
	4	1199256	ENSGALG0000000004367	X		69371271	ENSG00000204195	A
XR_026669.1	4	1115502	ENSGALG0000000004481	X		68752636	ENSG00000158813	A
EFNB1_CHICK	4	998906	ENSGALG0000000004537	X		67965556	ENSG00000090776	A
STARDB	4	554692	ENSGALG0000000004575	X		67784229	ENSG00000130052	A
YIPF6	4	511954	ENSGALG0000000004584	X		67635611	ENSG00000181704	A
OPHN1	4	465929	ENSGALG0000000004589	X		67179440	ENSG00000079482	A
NP_00103517	4	416134	ENSGALG0000000004596	X		66680599	ENSG00000169083	A
EDA2R	4	347826	ENSGALG0000000004599	X		65732204	ENSG00000131080	A
HEPH	4	269455	ENSGALG0000000004638	X		65299388	ENSG00000089472	A
VSIG4	4	241320	ENSGALG0000000004677	X		65158307	ENSG00000155659	A
NP_00102628	4	113861	ENSGALG0000000004709	X		64804283	ENSG00000147065	A
Q5ZIQO_CHIC	4	68298	ENSGALG0000000004713	X		64649188	ENSG00000001497	A
ZC3H12B	4	54275	ENSGALG0000000004715	X		64625431	ENSG00000102053	A
KIAA1166	4	35524	ENSGALG0000000004716	X		64052987	ENSG00000126970	A
NP_00102628	4	1799818	ENSGALG0000000004730	X		154158720	ENSG00000155962	A
NP_00100658	4	1832440	ENSGALG0000000004742	X		50670475	ENSG00000130385	A
XR_026872.1	4	1836705	ENSGALG0000000004801	X		71715389	ENSG00000067177	A
HDAC8	4	1853106	ENSGALG0000000004825	X		71466091	ENSG00000147099	A
RBM41	4	1868007	ENSGALG0000000004832	X		106194306	ENSG00000089682	A
	4	1871417	ENSGALG0000000004856	X		106253367	ENSG00000198088	A
Cxorf41	4	1880366	ENSGALG0000000004870	X		106336518	ENSG00000080572	A
FRMPD3	4	1926696	ENSGALG0000000004876	X		106652336	ENSG00000147234	A
PRPS1	4	1948779	ENSGALG0000000004908	X		106758403	ENSG00000147224	A
RAB9B	4	1969782	ENSGALG0000000004918	X		102963914	ENSG00000123570	A
GLRA4	4	1990373	ENSGALG0000000004936	X		102848808	ENSG00000188828	A
GLA	4	1999445	ENSGALG0000000004948	X		100539435	ENSG00000102393	A
BTK_CHICK	4	2009589	ENSGALG0000000004958	X		100491091	ENSG00000106711	A
TIMM8A	4	2020681	ENSGALG0000000004963	X		100487308	ENSG00000126953	A
DRP2	4	2037248	ENSGALG0000000005031	X		100361414	ENSG00000102385	A
CENPL_CHICK	4	2061546	ENSGALG0000000005038	X		100239827	ENSG00000102384	A
TMEM35	4	2079246	ENSGALG0000000005041	X		100220519	ENSG00000126950	A
Cxorf34	4	2083767	ENSGALG0000000005049	X		100150992	ENSG00000188917	A
DKC1_CHICK	4	2098487	ENSGALG0000000005054	X		153637340	ENSG00000130826	A
NP_00100791	4	2107568	ENSGALG0000000005071	X		153660162	ENSG00000130830	A
Q804X3_CHIC	4	2126164	ENSGALG0000000005077	X		153717257	ENSG00000185010	A
	4	2151835	ENSGALG0000000005381	X		153908258	ENSG00000165775	A
BRCC3	4	2169589	ENSGALG0000000005383	X		153952889	ENSG00000185515	A
Q52KF0_CHIC	4	2183183	ENSGALG0000000005425	X		70669658	ENSG00000147162	A
	4	2201431	ENSGALG0000000005464	X		70502839	ENSG00000147133	A
ITGB1BP2	4	2243816	ENSGALG0000000005493	X		70438353	ENSG00000147166	A
NP_00102670	4	2255310	ENSGALG0000000005507	X		70420165	ENSG00000147140	A
ZMYM3	4	2280063	ENSGALG0000000005533	X		70376199	ENSG00000147130	A
NP_989702.1	4	2304599	ENSGALG0000000005541	X		70351769	ENSG00000169562	A
NLGN3	4	2307335	ENSGALG0000000005553	X		70281436	ENSG00000196338	A
MED12	4	2338077	ENSGALG0000000005624	X		70255131	ENSG00000184634	A
NP_989858.1	4	2374517	ENSGALG0000000005638	X		70243979	ENSG00000147168	A
FOXO4	4	2393791	ENSGALG0000000005658	X		70232751	ENSG00000184481	A
NP_00102670	4	2403867	ENSGALG0000000005659	X		70192907	ENSG00000147164	A
SLC7A3	4	2415110	ENSGALG0000000005727	X		70062163	ENSG00000165349	A
TEX11	4	2430982	ENSGALG0000000005775	X		69665515	ENSG00000120498	A
DLG3	4	2460956	ENSGALG0000000005817	X		69581449	ENSG00000082458	A
GDPD2	4	2516841	ENSGALG0000000005842	X		69559716	ENSG00000130055	A
HTR2C	4	2779925	ENSGALG0000000005853	X		113724807	ENSG00000147246	A
LRCH2	4	2854385	ENSGALG0000000005882	X		114251441	ENSG00000130224	A
NP_00100643	4	2968317	ENSGALG0000000005930	X		114701740	ENSG00000102024	A
AGTR2	4	3001900	ENSGALG0000000005936	X		115215986	ENSG00000180772	A
SLC6A14	4	3035074	ENSGALG0000000005957	X		115481818	ENSG00000087916	A
NP_00102628	4	3190314	ENSGALG0000000005982	X		116915804	ENSG00000003096	A
WDR44	4	3284702	ENSGALG0000000005997	X		117364070	ENSG00000131725	A
XR_027238.1	4	3325083	ENSGALG0000000006017	X		117513900	ENSG00000147251	A
IL13RA1	4	3387161	ENSGALG0000000006032	X		117745587	ENSG00000131724	A
NP_00102628	4	3420382	ENSGALG0000000006049	X		130984926	ENSG00000134602	A
NP_00101259	4	3465682	ENSGALG0000000006061	X		131164734	ENSG00000123728	A
NP_00101259	4	3493228	ENSGALG0000000006066	X		131339862	ENSG00000076770	A
H6ST2_CHICK	4	3590877	ENSGALG0000000006071	X		131587719	ENSG00000171004	A
GPC4	4	3771522	ENSGALG0000000006080	X		132262730	ENSG00000076716	A
GPC3	4	3845309	ENSGALG0000000006087	X		132497448	ENSG00000147257	A
PHF6	4	3994211	ENSGALG0000000006094	X		133335008	ENSG00000156531	A
HPRT_CHICK	4	4031786	ENSGALG0000000006098	X		133421923	ENSG00000165704	A
FAM122B	4	4075584	ENSGALG0000000006108	X		133731262	ENSG00000156504	A
F122A_CHICK	4	4086089	ENSGALG0000000006127	X		133768890	ENSG00000156500	A
MOSPD1	4	4105920	ENSGALG0000000006132	X		133849323	ENSG00000101928	A
DDX26B	4	4140961	ENSGALG0000000006157	X		134482250	ENSG00000165359	A

TMEM32	4	4186140	ENSGALG00000006162	X	134871897	ENSG00000169446	A
SLC9A6	4	4189431	ENSGALG00000006180	X	134895252	ENSG00000198689	A
FHL1	4	4237102	ENSGALG00000006190	X	135057346	ENSG00000022267	A
MAP7D3	4	4246166	ENSGALG00000006256	X	135123047	ENSG00000129680	A
GPR112	4	4315284	ENSGALG00000006393	X	135210788	ENSG00000156920	A
NP_989737.1	4	4332640	ENSGALG00000006406	X	135397791	ENSG00000102239	A
QSZKD3_CHIC	4	4343017	ENSGALG00000006410	X	135407337	ENSG00000102241	A
VGLL1	4	4360259	ENSGALG00000006412	X	135441977	ENSG00000102243	A
CD40L_CHICK	4	4377227	ENSGALG00000006415	X	135558002	ENSG00000102245	A
ARHG6_CHIC	4	4386284	ENSGALG00000006439	X	135575372	ENSG00000129675	A
QSZKQ9_CHIC	4	4422127	ENSGALG00000006457	X	135783288	ENSG00000147274	A
ZIC3	4	4561401	ENSGALG00000006497	X	136476012	ENSG00000156925	A
NP_00100174	4	4765422	ENSGALG00000006508	X	137541401	ENSG00000129682	A
FA9_CHICK	4	5025917	ENSGALG00000006513	X	138440561	ENSG00000101981	A
SRPK3	1	14823226	ENSGALG00000006544	X	152699656	ENSG00000184343	A
MCF2	4	5044846	ENSGALG00000006562	X	138491596	ENSG00000101977	A
ATP11C	4	5096694	ENSGALG00000006623	X	138636171	ENSG00000101974	A
ARL13A	4	5151228	ENSGALG00000006636	X	100111356	ENSG00000174225	A
	4	5160873	ENSGALG00000006637	X	100055090	ENSG00000182489	A
NOX1	4	5166311	ENSGALG00000006707	X	99984969	ENSG00000007952	A
NP_00100643	4	5171532	ENSGALG00000006760	X	99962004	ENSG00000101811	A
XR_026989.1	4	5183290	ENSGALG00000006786	X	99816144	ENSG00000102362	A
SRPX2	4	5190431	ENSGALG00000006796	X	99785819	ENSG00000102359	A
TS PAN6	4	5197934	ENSGALG00000006808	X	99770451	ENSG00000000003	A
NP_996868.1	4	5206031	ENSGALG00000006821	X	99726446	ENSG00000000005	A
Q9YGR0_CHIC	4	5230869	ENSGALG00000006822	X	99433300	ENSG00000165194	A
DIAPH2	4	5830990	ENSGALG00000006839	X	95826365	ENSG00000147202	A
	4	2428435	ENSGALG00000006843	X	106924107	ENSG00000170935	A
Q9YQG6_CHIC	4	6991590	ENSGALG00000006851	X	90920960	ENSG00000102290	A
KLHL4	4	8139648	ENSGALG00000006877	X	86659425	ENSG00000102271	A
NP_990126.1	4	8338908	ENSGALG00000006886	X	85290118	ENSG00000126733	A
NP_00102629	4	8622348	ENSGALG00000006906	X	85002841	ENSG00000188419	A
POF1B	4	8727041	ENSGALG00000006919	X	84419058	ENSG00000124429	A
O42424_CHIC	4	8732862	ENSGALG00000006929	X	84385653	ENSG00000147180	A
APOOL_CHICK	4	8784189	ENSGALG00000006978	X	84145559	ENSG00000155008	A
NP_00102629	4	8996663	ENSGALG00000007041	X	83459541	ENSG00000165259	A
RPS6KA6	4	9057466	ENSGALG00000007097	X	83205640	ENSG00000072133	A
NP_00101259	4	9416983	ENSGALG00000007128	X	80344278	ENSG00000131171	A
BRWD3	4	9493699	ENSGALG00000007151	X	79818351	ENSG00000165288	A
FAM46D	4	9561524	ENSGALG00000007157	X	79562602	ENSG00000174016	A
	4	9586935	ENSGALG00000007160	X	130019897	ENSG00000147256	A
CLCN5	4	9635234	ENSGALG00000007234	X	49573965	ENSG00000171365	A
SLITRK4	4	9985572	ENSGALG00000007242	X	142543610	ENSG00000179542	A
CH03_CHICK	4	10594559	ENSGALG00000007243	X	139412818	ENSG00000134595	A
GABRA3	4	10844309	ENSGALG00000007269	X	151086290	ENSG00000011677	A
CNGA2	4	11001806	ENSGALG00000007282	X	150653874	ENSG00000183862	A
PRRG3	4	11020781	ENSGALG00000007290	X	150614607	ENSG00000130032	A
RIPPLY1	4	11029609	ENSGALG00000007309	X	106029951	ENSG00000147223	A
CLDN2	4	11034232	ENSGALG00000007311	X	106050290	ENSG00000165376	A
TM1H_CHICK	4	11092947	ENSGALG00000007443	X	154372967	ENSG00000185973	A
A0FK59_CHIC	4	11125304	ENSGALG00000007448	X	154650645	ENSG00000168939	A
QSZL74_CHIC	4	11274074	ENSGALG00000007476	X	154764207	ENSG00000124333	A
ZNF185	4	11312405	ENSGALG00000007488	X	151833653	ENSG00000147394	A
NSDHL	4	11367738	ENSGALG00000007493	X	151750167	ENSG00000147383	A
	4	11378406	ENSGALG00000007510	X	151746529	ENSG00000147400	A
GL05	4	11435361	ENSGALG00000007542	X	48509178	ENSG00000171433	A
	4	11560652	ENSGALG00000007574	X	55760897	ENSG00000083750	A
NP_00101271	4	11716305	ENSGALG00000007590	X	63404687	ENSG00000102043	A
ASB12	4	11747271	ENSGALG00000007594	X	63360801	ENSG00000198881	A
FAM123B	4	11758741	ENSGALG00000007599	X	63321722	ENSG00000184675	A
ARHGEF9	4	11866519	ENSGALG00000007608	X	62771572	ENSG00000131089	A
HMD2_CHICK	4	12178111	ENSGALG00000007656	X	72583813	ENSG00000131264	A
NP_00102629	4	12213205	ENSGALG00000007660	X	72699769	ENSG00000204116	A
SLC16A2	4	12405103	ENSGALG00000007748	X	73557810	ENSG00000147100	A
NP_990159.1	4	12438000	ENSGALG00000007750	X	73726678	ENSG00000131263	A
KIAA2022	4	12469998	ENSGALG00000007755	X	73869409	ENSG00000050030	A
ABC7	4	12608591	ENSGALG00000007788	X	74189834	ENSG00000131269	A
UPP_CHICK	4	12653329	ENSGALG00000007793	X	74410650	ENSG00000094841	A
ZDHHC15	4	12680612	ENSGALG00000007800	X	74508786	ENSG00000102383	A
NP_00103811	4	12887028	ENSGALG00000007806	X	76596299	ENSG00000196468	A
	4	12905188	ENSGALG00000007843	X	76647015	ENSG00000085224	A
IAG2_CHICK	4	12984311	ENSGALG00000007861	X	76968520	ENSG00000102158	A
	4	13000791	ENSGALG00000007863	X	77041627	ENSG00000131174	A
	4	13002692	ENSGALG00000007902	X	77052850	ENSG00000165240	A
PGK_CHICK	4	13036123	ENSGALG00000007936	X	77246425	ENSG00000102144	A
AMOT	4	13076510	ENSGALG00000007952	X	111904387	ENSG00000126016	A
TRPCS	4	13176785	ENSGALG00000007972	X	110904198	ENSG00000072315	A
HAKAI_CHICK	1	15799779	ENSGALG00000007975	X	22200986	ENSG00000175809	A
Cxorf45	4	13250373	ENSGALG00000007976	X	110811069	ENSG00000101901	A
NP_989666.1	4	13329698	ENSGALG00000007993	X	110423663	ENSG00000077279	A
CAPN6	4	13432038	ENSGALG00000008006	X	110374987	ENSG00000077274	A
PAK3	4	13491746	ENSGALG00000008058	X	110226244	ENSG00000077264	A
CRDL1_CHICK	4	13612341	ENSGALG00000008072	X	109803740	ENSG00000101938	A
AMMECR1	4	13722017	ENSGALG00000008074	X	109324071	ENSG00000101935	A
NP_00101290	4	13801069	ENSGALG00000008076	X	109132979	ENSG00000157600	A
ACSL4	4	13863906	ENSGALG00000008088	X	108771222	ENSG00000068366	A
NP_00100643	4	13910739	ENSGALG00000008092	X	108665666	ENSG00000101888	A
IRS4	4	13980728	ENSGALG00000008107	X	107862368	ENSG00000133124	A
COL4A5	4	14007548	ENSGALG00000008141	X	107569810	ENSG00000188153	A
COL4A6	4	14169851	ENSGALG00000008266	X	107285494	ENSG00000197565	A
ATG4A	4	14161690	ENSGALG00000008282	X	107221590	ENSG00000101844	A
PSMD10	4	14225330	ENSGALG00000008287	X	107214093	ENSG00000101843	A
	1	13884450	ENSGALG00000008288	X	100764776	ENSG00000102401	A
	1	13884450	ENSGALG00000008288	X	101740752	ENSG00000125962	A
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	1	13884450	ENSGALG00000008288	X	101853760	ENSG00000158301	A
	1	13884450	ENSGALG00000008288	X	100796923	ENSG00000184867	A
	1	13884450	ENSGALG00000008288	X	101862310	ENSG00000198908	A
	1	13884450	ENSGALG00000008288	X	101792950	ENSG00000198932	A
	1	13884450	ENSGALG00000008288	X	100756772	ENSG00000198960	A
	1	13884450	ENSGALG00000008288	X	100739145	ENSG00000204072	A
NP_00100174	4	14232583	ENSGALG00000008290	X	107174856	ENSG00000101842	A
RAB39B	4	14310386	ENSGALG00000008384	X	154140721	ENSG00000155961	A

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VBP1	4	14315921	ENSGALG00000008389	X	154097744	ENSG00000155959	A
GAB3	4	14367598	ENSGALG00000008408	X	153556725	ENSG00000160219	A
SMARCA1	4	14429611	ENSGALG00000008431	X	128408159	ENSG00000102038	A
TEN1_CHICK	4	15412731	ENSGALG00000008442	X	123339504	ENSG00000009694	A
SH2D1A	4	15655550	ENSGALG00000008447	X	123307831	ENSG00000183918	A
STAG2	4	15699100	ENSGALG00000008482	X	122921743	ENSG00000101972	A
NP_989919.1	4	15779875	ENSGALG00000008491	X	122821729	ENSG00000101966	A
THOC2	4	15807785	ENSGALG00000008507	X	122562094	ENSG00000125676	A
NP_990546.1	4	15868385	ENSGALG00000008512	X	122145687	ENSG00000125675	A
C1GALT1C1	4	16510949	ENSGALG00000008513	X	119643564	ENSG00000171155	A
Q5Z142_CHIC	4	16513180	ENSGALG00000008517	X	119622049	ENSG00000101898	A
CUL4B	4	16523380	ENSGALG00000008559	X	119542476	ENSG00000158290	A
LAMP2_CHICK	4	16551769	ENSGALG00000008572	X	119446367	ENSG00000005893	A
NP_00103811	4	16570195	ENSGALG00000008593	X	119379995	ENSG00000101892	A
FAM70A	4	16578979	ENSGALG00000008604	X	119276534	ENSG00000125355	A
A0MPA7_CHIC	4	16607080	ENSGALG00000008611	X	119268635	ENSG00000177485	A
NDUFA1	4	16624390	ENSGALG00000008613	X	118889762	ENSG00000125356	A
Q5ZH0V0_CHIC	4	16625245	ENSGALG00000008618	X	118852017	ENSG00000125351	A
NP_00102629	4	16638499	ENSGALG00000008633	X	118633715	ENSG00000125354	A
NP_00101290	4	16664299	ENSGALG00000008645	X	118606328	ENSG00000186416	A
NP_990196.1	4	16676640	ENSGALG00000008648	X	118592527	ENSG00000077721	A
Cxor56	4	16684530	ENSGALG00000008652	X	118556140	ENSG00000186100	A
SLC25A5	4	16692570	ENSGALG00000008675	X	118486436	ENSG00000005022	A
SLC25A43	4	16697566	ENSGALG00000008682	X	118397679	ENSG00000077713	A
LONRF3	4	16827120	ENSGALG00000008860	X	117992629	ENSG00000175556	A
XR_027143.1	4	16867025	ENSGALG00000008872	X	103297957	ENSG00000123575	A
IL1RAPL2	4	17149659	ENSGALG00000008888	X	103697652	ENSG00000189108	A
NP_00102629	4	17338667	ENSGALG00000008970	X	104953192	ENSG00000123572	A
Cxor57	4	17441484	ENSGALG00000008990	X	105741858	ENSG00000147231	A
RNF128	4	17475942	ENSGALG00000009000	X	105823724	ENSG00000133135	A
TBC1D8B	4	17517668	ENSGALG00000009040	X	105932566	ENSG00000133138	A
NP_00102629	4	17648229	ENSGALG00000009065	X	150315696	ENSG00000160131	A
HMMGB3	4	17789155	ENSGALG00000009071	X	149902421	ENSG00000029993	A
CD99L2	4	17825428	ENSGALG00000009075	X	149685470	ENSG00000102181	A
MTMR1	4	17846604	ENSGALG00000009085	X	149612527	ENSG00000006360	A
MTM1	4	17882694	ENSGALG00000009096	X	149487727	ENSG00000171100	A
XR_027150.1	4	17938835	ENSGALG00000009098	X	149282209	ENSG00000013619	A
	4	18191899	ENSGALG00000009128	X	148848949	ENSG00000197021	A
TMEM185A	4	18191899	ENSGALG00000009128	X	148430463	ENSG00000197620	A
	4	18195850	ENSGALG00000009139	X	148486016	ENSG00000155984	A
	4	18220571	ENSGALG00000009154	X	148368206	ENSG00000010404	A
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	4	18343130	ENSGALG00000009168	X	147389831	ENSG00000155966	A
Q5ZHM3_CHIC	4	18824681	ENSGALG00000009177	X	146801173	ENSG00000102081	A
SLITRK2	4	19235977	ENSGALG00000009192	X	144707381	ENSG00000185985	A
NP_00102665	1	30281578	ENSGALG00000009497	X	152821179	ENSG00000126895	A
	4	46313892	ENSGALG00000010885	X	73322489	ENSG00000204113	A
NP_00100624	1	62071951	ENSGALG00000012974	X	154903161	ENSG00000182484	A
TBL1X	1	129009396	ENSGALG00000013366	X	9391352	ENSG00000101849	A
	1	24029741	ENSGALG00000014012	X	47541297	ENSG00000188459	A
NP_00101283	1	95221218	ENSGALG00000015459	X	152336975	ENSG00000189420	A
	4	84627578	ENSGALG00000015609	X	154342270	ENSG00000185978	A
	4	84627578	ENSGALG00000015609	X	153766511	ENSG00000198082	A
	4	84627578	ENSGALG00000015609	X	154263622	ENSG00000198307	A
Cxor36	1	114371799	ENSGALG00000016215	X	44892563	ENSG00000147113	A
	1	114402920	ENSGALG00000016217	X	44617415	ENSG00000147050	A
FUNDC1	1	114588674	ENSGALG00000016219	X	44267847	ENSG00000006950	A
EFHC2_CHICK	1	114628575	ENSGALG00000016221	X	43892072	ENSG00000183690	A
NDP	1	114771903	ENSGALG00000016222	X	43692970	ENSG00000124479	A
Q5MOR0_CHIC	1	114806172	ENSGALG00000016223	X	43510804	ENSG00000006953	A
NP_00102597	1	114866376	ENSGALG00000016224	X	43400353	ENSG00000189221	A
CASK	1	115430266	ENSGALG00000016226	X	41263408	ENSG00000147044	A
Q6KE1_CHIC	1	115480420	ENSGALG00000016227	X	41433170	ENSG00000171659	A
NYX	1	115582715	ENSGALG00000016228	X	41191631	ENSG00000188937	A
NP_00102597	1	115609204	ENSGALG00000016231	X	41077595	ENSG00000215301	A
	1	115667615	ENSGALG00000016236	X	40829832	ENSG00000124486	A
MED14	1	115816329	ENSGALG00000016238	X	40392502	ENSG00000180182	A
NP_00102597	1	115861428	ENSGALG00000016241	X	40325160	ENSG00000182220	A
	1	115950951	ENSGALG00000016245	X	39794012	ENSG00000183337	A
NP_998740.1	1	116300801	ENSGALG00000016249	X	38545651	ENSG00000165175	A
TSPAN7	1	116329009	ENSGALG00000016251	X	38305553	ENSG00000156298	A
OTC_CHICK	1	116461327	ENSGALG00000016254	X	38096680	ENSG00000036473	A
RPRR	1	116488949	ENSGALG00000016255	X	38013368	ENSG00000156313	A
SRPX	1	116581253	ENSGALG00000016256	X	37893539	ENSG00000101955	A
SYTL5	1	116609189	ENSGALG00000016258	X	37750779	ENSG00000147041	A
DYNLT3	1	116702731	ENSGALG00000016259	X	37580954	ENSG00000165169	A
CYBB	1	116720415	ENSGALG00000016261	X	37524239	ENSG00000165168	A
NP_00102999	1	116756003	ENSGALG00000016262	X	37430052	ENSG000000047597	A
LANCL3	1	116780945	ENSGALG00000016265	X	37315741	ENSG00000147036	A
PRRG1	1	116850031	ENSGALG00000016266	X	37093467	ENSG00000130962	A
Cxor22	1	116920646	ENSGALG00000016268	X	35847779	ENSG00000165164	A
TMEM47	1	117473225	ENSGALG00000016272	X	34555104	ENSG00000147027	A
DMD_CHICK	1	118069256	ENSGALG00000016281	X	31042729	ENSG00000198947	A
MAP3K7IP3	1	119178962	ENSGALG00000016284	X	30755480	ENSG00000157625	A
	1	119230770	ENSGALG00000016285	X	30581397	ENSG00000198814	A
Cxor21	1	119288623	ENSGALG00000016286	X	30486862	ENSG00000120280	A
NP_989924.1	1	119395075	ENSGALG00000016287	X	30232507	ENSG00000169297	A
IL1RAPL1	1	119540327	ENSGALG00000016288	X	28515437	ENSG00000169306	A
Q59J86_CHIC	1	121296470	ENSGALG00000016312	X	24621957	ENSG00000101868	A
PCYT1B	1	121514569	ENSGALG00000016318	X	24486125	ENSG00000102230	A
NP_00100625	1	121541235	ENSGALG00000016323	X	24393475	ENSG000000067992	A
Q7LZ62_CHIC	1	121641933	ENSGALG00000016327	X	24077783	ENSG000000005889	A
IF2G_CHICK	1	121677562	ENSGALG00000016340	X	23982986	ENSG00000130741	A
KLH15_CHICK	1	121703650	ENSGALG00000016345	X	23915884	ENSG00000174010	A
APOO	1	121733603	ENSGALG00000016347	X	23761402	ENSG00000184831	A
SAT1_CHICK	1	121771899	ENSGALG00000016348	X	23711211	ENSG00000130066	A
NP_00101284	1	121778541	ENSGALG00000016351	X	23631698	ENSG00000123130	A
PRDX4	1	121803585	ENSGALG00000016357	X	23592300	ENSG00000123131	A
PTCHD1	1	121889476	ENSGALG00000016358	X	23262906	ENSG00000165186	A
PHEX	1	122345891	ENSGALG00000016375	X	21960842	ENSG00000102174	A
NP_00102597	1	122454861	ENSGALG00000016379	X	21868754	ENSG00000102172	A
MBTPS2	1	122526313	ENSGALG00000016382	X	21767670	ENSG00000012174	A
KLHL34	1	122629229	ENSGALG00000016388	X	21582729	ENSG00000185915	A

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CNKS2R	1	122634436	ENSGALG0000016391	X	21302481	ENSG00000149970	A
RP56KA3	1	123229204	ENSGALG0000016406	X	20077951	ENSG00000177189	A
MAP7D2	1	123339559	ENSGALG0000016415	X	19935150	ENSG00000184368	A
CXorf23	1	123401479	ENSGALG0000016418	X	19841403	ENSG00000173681	A
NP_00102597	1	123425184	ENSGALG0000016420	X	19462046	ENSG00000147010	A
XR_027145.1	1	123679971	ENSGALG0000016426	X	19288095	ENSG00000180815	A
NP_00101256	1	123735114	ENSGALG0000016430	X	19271972	ENSG00000131828	A
GPR64	1	123842168	ENSGALG0000016511	X	18917348	ENSG00000173698	A
PHKA2	1	123866428	ENSGALG0000016518	X	18820802	ENSG00000044446	A
PPEF1	1	123907060	ENSGALG0000016522	X	18618967	ENSG00000086717	A
XR_026808.1	1	123954222	ENSGALG0000016523	X	18567733	ENSG00000102104	A
CDKL5	1	123970718	ENSGALG0000016529	X	18353646	ENSG00000008086	A
SCML2	1	124117128	ENSGALG0000016537	X	18167355	ENSG00000102098	A
RAI2	1	124198127	ENSGALG0000016538	X	17728092	ENSG00000131831	A
CXorf20	1	124369929	ENSGALG0000016541	X	18090974	ENSG00000177324	A
NHS	1	124403905	ENSGALG0000016543	X	17303802	ENSG00000188158	A
NP_00102597	1	124723087	ENSGALG0000016545	X	16874735	ENSG00000169891	A
RBBP7_CHICK	1	124845745	ENSGALG0000016546	X	16772385	ENSG00000102054	A
	1	124857795	ENSGALG0000016547	X	16714526	ENSG00000086712	A
SYAP1	1	124882770	ENSGALG0000016548	X	16647676	ENSG00000169895	A
PYRG2_CHICK	1	124901293	ENSGALG0000016549	X	16516047	ENSG00000047230	A
NP_989738.1	1	125139798	ENSGALG0000016550	X	16051345	ENSG00000126010	A
NP_00100626	1	125276190	ENSGALG0000016551	X	15753850	ENSG00000182287	A
	1	125314815	ENSGALG0000016552	X	15718495	ENSG00000169249	A
TMEM27	1	125336876	ENSGALG0000016553	X	15555372	ENSG00000147003	A
ACE2	1	125364331	ENSGALG0000016554	X	15489077	ENSG00000130234	A
BMX	1	125389430	ENSGALG0000016557	X	15392290	ENSG00000102010	A
NP_989899.1	1	125472478	ENSGALG0000016558	X	15273640	ENSG00000165197	A
NP_00102597	1	125514501	ENSGALG0000016559	X	15247503	ENSG00000165195	A
ASB11	1	125527662	ENSGALG0000016562	X	15209759	ENSG00000165192	A
NP_00100626	1	125552594	ENSGALG0000016563	X	15172030	ENSG00000102048	A
MOSPD2	1	125737284	ENSGALG0000016568	X	14801484	ENSG00000130150	A
FANCB	1	125770710	ENSGALG0000016569	X	14771450	ENSG00000181544	A
GLRA2	1	125818242	ENSGALG0000016571	X	14457565	ENSG00000101958	A
GEMIN8	1	126207687	ENSGALG0000016574	X	13934766	ENSG00000046647	A
NP_00101256	1	126252299	ENSGALG0000016575	X	13698983	ENSG00000046653	A
OFD1	1	126359777	ENSGALG0000016576	X	13662785	ENSG00000046651	A
NP_00100626	1	126388987	ENSGALG0000016578	X	13640282	ENSG00000196459	A
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	1	126408830	ENSGALG0000016581	X	13581146	ENSG00000176896	A
EGFL6	1	126433335	ENSGALG0000016584	X	13497645	ENSG00000198759	A
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NP_00100626	1	126836633	ENSGALG0000016592	X	12719414	ENSG00000101911	A
FRMPD4	1	126932572	ENSGALG0000016594	X	12066506	ENSG00000169933	A
MSL3L1	1	127455688	ENSGALG0000016598	X	11686199	ENSG00000005302	A
ARHGAP6	1	127872311	ENSGALG0000016602	X	11065584	ENSG00000047648	A
NP_989460.1	1	128243953	ENSGALG0000016603	X	10373596	ENSG00000101871	A
CLCN4	1	128567209	ENSGALG0000016607	X	10084985	ENSG00000073464	A
WWC3	1	128607877	ENSGALG0000016611	X	9943795	ENSG00000047644	A
SHROOM2	1	128802319	ENSGALG0000016614	X	9714496	ENSG00000146950	A
GPR143	1	128971289	ENSGALG0000016615	X	9653454	ENSG00000101850	A
KALM_CHICK	1	129616326	ENSGALG0000016616	X	8456915	ENSG000000011201	A
PNPLA4	1	130120480	ENSGALG0000016618	X	7826804	ENSG00000006757	A
STS	1	130349862	ENSGALG0000016622	X	7147472	ENSG00000101846	A
HDHD1A	1	130453764	ENSGALG0000016623	X	6976961	ENSG00000130021	A
	1	130855539	ENSGALG0000016628	X	5818085	ENSG00000146938	A
	1	132169227	ENSGALG0000016629	X	3532415	ENSG00000183943	A
MXRA5	1	132390251	ENSGALG0000016635	X	3236606	ENSG00000101825	A
NP_989703.1	1	132548048	ENSGALG0000016636	X	2832011	ENSG00000006756	A
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GYG2	1	132614111	ENSGALG0000016655	X	2756859	ENSG00000056998	A
XG	1	132633051	ENSGALG0000016656	X	2680115	ENSG00000124343	A
DHRX	1	132779441	ENSGALG0000016681	X	2147557	ENSG00000169084	A
HIOM_CHICK	1	133127530	ENSGALG0000016685	X	1694024	ENSG00000196433	A
CXorf3	1	133142878	ENSGALG0000016686	X	1670486	ENSG00000197976	A
P2RY8_CHICK	1	133187192	ENSGALG0000016687	X	1541468	ENSG00000182162	A
ASMTL	1	133224452	ENSGALG0000016689	X	1482032	ENSG00000169093	A
NM_204231.2	1	133256379	ENSGALG0000016691	X	1465144	ENSG00000169100	A
	1	133397371	ENSGALG0000016696	X	1274885	ENSG00000205755	A
Q00G66_CHIC	1	133843672	ENSGALG0000016698	X	505079	ENSG00000185960	A
PPP2R3B	1	134064583	ENSGALG0000016702	X	214970	ENSG00000167393	A
	1	134174603	ENSGALG0000016717	X	160025	ENSG00000178605	A
Q5ZIV4_CHIC	1	134186576	ENSGALG0000016721	X	132989	ENSG00000182378	A
RGM_CHICK	1	134230907	ENSGALG0000016724	X	46822719	ENSG00000130988	A
PHF16	1	134253123	ENSGALG0000016727	X	46656680	ENSG00000102221	A
XRP2_CHICK	1	134314101	ENSGALG0000016728	X	46581319	ENSG00000102218	A
SLC9A7	1	134378528	ENSGALG0000016734	X	46351081	ENSG00000065923	A
	1	141538564	ENSGALG0000016823	X	132178363	ENSG00000183434	A
FOXP3	1	78726042	ENSGALG0000019005	X	48994354	ENSG00000049768	A
	1	133309331	ENSGALG0000019147	X	1415509	ENSG00000185291	A
	1	133309331	ENSGALG0000019147	X	1347693	ENSG00000198223	A
SMPX	1	122571767	ENSGALG0000019157	X	21634012	ENSG00000091482	A
	1	117148698	ENSGALG0000019164	X	36238869	ENSG00000205081	A
CXorf30	1	117047650	ENSGALG0000019165	X	36156656	ENSG00000205082	A
	1	71995193	ENSGALG0000019262	X	148481974	ENSG00000171129	A
	1	70500859	ENSGALG0000019266	X	148664132	ENSG00000171116	A
PGRC1_CHICK	4	16741598	ENSGALG0000020260	X	118254279	ENSG00000101856	A
AKAP14	4	16620499	ENSGALG0000020261	X	118913828	ENSG00000186471	A
NP_00100643	4	16614499	ENSGALG0000020262	X	118943052	ENSG00000101882	A
GBRG4_CHICK	4	10924256	ENSGALG0000020292	X	150872253	ENSG00000102287	A
NP_00104154	4	2822772	ENSGALG0000020316	X	114144794	ENSG00000123496	A
ACRC	4	2174236	ENSGALG0000020322	X	70714986	ENSG00000147174	A
FAM155B	4	836001	ENSGALG0000020329	X	68641803	ENSG00000130054	A
IGBP1	4	1192386	ENSGALG0000020330	X	69270043	ENSG00000089289	A
Q5ZLE4_CHIC	4	1418423	ENSGALG0000020331	X	78087485	ENSG00000078589	A
PKFBF1	1	3392564	ENSGALG0000022191	X	54976315	ENSG00000158571	A
	1	62299079	ENSGALG0000022555	X	152606586	ENSG00000130821	A
KCNE1L	4	13903372	ENSGALG0000023613	X	108753585	ENSG00000176076	A
	4	2164580	ENSGALG0000023937	X	153943098	ENSG00000214827	A
	4	1606880	ENSGALG0000024039	X	128866195	ENSG00000156697	A
RAB33A	4	1556095	ENSGALG0000024049	X	129133454	ENSG00000134594	A

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CD99	1	132659666	ENSGALG00000024488	X	2619228	ENSG00000002586	A	
PIR	1	125400230	Part of FGF	X	15312847	ENSG000000087842	A	deeply conserved
TIMP1	1	55164198	Real	X	47326634	ENSG00000102265	A	deeply conserved
Cxor59	1	116994255	Real	X	35967054	ENSG00000176034	A	deeply conserved
ARX	1	43732581		X	24932213	ENSG00000004848	A	
SYN1	1	55118079		X	47316244	ENSG00000008056	A	not in ensalg
PRICKLE3	1	31438896		X	48918847	ENSG00000012211	A	not in ensalg
WAS	1	24025413		X	48427141	ENSG00000015285	A	deeply conserved
SLC38A5	1	32782142		X	48201866	ENSG00000017483	A	not in ensalg
SCML1	1	124185588		X	17665509	ENSG00000047634	A	not in ensalg
ZNF275	1	62048453		X	152252807	ENSG00000063587	A	not in ensalg
PDZD4	1	31069384		X	152720817	ENSG00000067840	A	not in ensalg
ATP2B3	1	45300295		X	152436328	ENSG00000067842	A	not in ensalg
ATP6AP1	1	24172382		X	153310172	ENSG00000071553	A	not in ensalg
FAM50A	1	116527414		X	153325698	ENSG00000071859	A	not in ensalg
FAM3A	1	25015605		X	153387696	ENSG00000071889	A	not in ensalg
SMC1A	1	72580822		X	53417795	ENSG00000072501	A	not in ensalg
ARAF	1	59005904		X	47305522	ENSG00000078061	A	not in ensalg
ARHGAP4	1	35426007		X	152826015	ENSG00000089820	A	not in ensalg
H2BFM	1	50048754		X	103154925	ENSG00000101812	A	not in ensalg
GUCY2F	1	198484671		X	108502791	ENSG00000101890	A	not in ensalg
TLR8	1	126824445		X	12834679	ENSG00000101916	A	not in ensalg
SUV39H1	1	7869719		X	48440075	ENSG00000101945	A	not in ensalg
ABCD1	1	16352134		X	152643517	ENSG00000101986	A	not in ensalg
CACNA1F	1	63646141		X	48948467	ENSG00000102001	A	not in ensalg
ELF4	1	170036155		X	129026539	ENSG00000102034	A	not in ensalg
KCND1	1	75800037		X	48703583	ENSG00000102057	A	not in ensalg
UBE2NL	1	46733229		X	142794839	ENSG00000102069	A	not in ensalg
PIM2	1	20467990		X	48655407	ENSG00000102096	A	not in ensalg
GATA1	1	4350543		X	48529906	ENSG00000102145	A	not in ensalg
GPR50	4	17750652		X	150095717	ENSG00000102195	A	not in ensalg
PCTK1	1	47707862		X	46962576	ENSG00000102225	A	not in ensalg
USP11	1	34794327		X	46977258	ENSG00000102226	A	not in ensalg
FGD1	1	61109506		X	54488614	ENSG00000102302	A	not in ensalg
TAF7L	4	2027949		X	100409898	ENSG00000102387	A	not in ensalg
NUDT10	1	46724098		X	51091823	ENSG00000122824	A	not in ensalg
H2BFWT	1	50048754		X	103152376	ENSG00000123569	A	not in ensalg
ESX1	1	86492969		X	103381376	ENSG00000123576	A	not in ensalg
IQSEC2	1	62219955		X	53278784	ENSG00000124313	A	not in ensalg
JARID1C	1	62386925		X	53237381	ENSG00000126012	A	not in ensalg
ELK1	1	47678162		X	47379864	ENSG00000126767	A	not in ensalg
PNCK	1	6806182		X	152588379	ENSG00000130822	A	not in ensalg
PLXNA3	1	2532874		X	153339817	ENSG00000130827	A	not in ensalg
DUSP9	1	45171605		X	152561182	ENSG00000130829	A	not in ensalg
UBA1	4	53135110		X	46935204	ENSG00000130985	A	not in ensalg
MORC4	1	110097971		X	106070620	ENSG00000133131	A	not in ensalg
CCNB3	1	176875780		X	49856156	ENSG00000147082	A	not in ensalg
ZNF182	1	62048219		X	47719195	ENSG00000147118	A	not in ensalg
ZNF41	1	62048306		X	47191352	ENSG00000147124	A	not in ensalg
RAB41	4	1235106		X	69418793	ENSG00000147127	A	not in ensalg
GABRQ	1	135548828		X	151557293	ENSG00000147402	A	not in ensalg
SHROOM4	1	146009938		X	50351387	ENSG00000158352	A	not in ensalg
FAAH2	4	1790858		X	57329864	ENSG00000165591	A	not in ensalg
FRMD7	4	3452335		X	131038702	ENSG00000165694	A	not in ensalg
PASD1	4	17567796		X	150482663	ENSG00000166049	A	not in ensalg
Cxor48	1	21498494		X	134118129	ENSG00000169551	A	not in ensalg
GPR82	1	115468554		X	41468378	ENSG00000171657	A	not in ensalg
HCFC1	1	56719909		X	152866204	ENSG00000172534	A	not in ensalg
PHF8	1	58765222		X	53979834	ENSG00000172943	A	not in ensalg
ZNF449	1	62048498		X	134306387	ENSG00000173275	A	not in ensalg
EIF1AX	1	123269626	ENSGALG00000016410	X	20056095	ENSG00000173674	A	
ZNF674	1	62048231		X	46243490	ENSG00000175176	A	not in ensalg
SAGE1	4	4174201		X	134803451	ENSG00000181433	A	not in ensalg
LHFPL1	1	175252837		X	111760535	ENSG00000182508	A	not in ensalg
MTCP1	4	2160784		X	153943091	ENSG00000182712	A	not in ensalg
FAM9A	1	625013		X	8718836	ENSG00000183304	A	not in ensalg
FAM120C	1	165381420		X	54111482	ENSG00000184083	A	not in ensalg
GPR173	1	28482924		X	53095231	ENSG00000184194	A	not in ensalg
SATL1	1	121772972		X	84222096	ENSG00000184788	A	not in ensalg
BCAP31	1	15746672		X	152619146	ENSG00000185825	A	not in ensalg
NAP1L3	1	39,818,228		X	92812585	ENSG00000186310	A	not in ensalg
ZNF75D	1	62048636		X	134247386	ENSG00000186376	A	not in ensalg
NAP1L2	1	39819092		X	72348860	ENSG00000186462	A	not in ensalg
ERAS	4	3474775		X	48572227	ENSG00000187682	A	not in ensalg
AL158055.12	1	104487104		X	51166507	ENSG00000187690	A	not in ensalg
ANKRD58	4	51203648		X	118776604	ENSG00000187808	A	not in ensalg
WDR42B	1	33175939		X	27907570	ENSG00000189186	A	not in ensalg
NUDT11	1	46724098		X	51249603	ENSG00000196368	A	not in ensalg
WNK3	1	62596564		X	54239580	ENSG00000196632	A	not in ensalg
POU3F4	1	96217787		X	82649941	ENSG00000196767	A	not in ensalg
ZNF81	1	62048219		X	47581245	ENSG00000197779	A	not in ensalg
RPS4X	4	1862926		X	71409178	ENSG00000198034	A	not in ensalg
PLXNB3	4	82767944		X	152682845	ENSG00000198753	A	not in ensalg
L1CAM	1	30496406		X	152780163	ENSG00000198910	A	not in ensalg
RPL39	4	16633302		X	118804497	ENSG00000198918	A	not in ensalg
GD1I	1	944310		X	153318705	ENSG00000203879	A	not in ensalg
NHSL2	1	124407543		X	71270224	ENSG00000204131	A	not in ensalg
RP5-1091N2.E	4	2377946		X	70240562	ENSG00000204165	A	not in ensalg
DGKK	1	170623134		X	50128637	ENSG00000204466	A	not in ensalg
ALS13007.5	1	99015294		X	73723307	ENSG00000212631	A	not in ensalg
INGX	1	143467605		X	70628694	ENSG00000212633	A	not in ensalg
ZBED1	1	132787319		X	2414455	ENSG00000214717	A	not in ensalg
AC004835.2	1	133149514		X	118270637	ENSG00000214992	A	not in ensalg
AC004386.1	1	99015291		X	73334464	ENSG00000215107	A	not in ensalg
ZNF630	1	62048219		X	47802547	ENSG00000221994	A	not in ensalg
PDHA1	1	123735114	ENSGALG00000016430	X	19283385	ENSG00000163114	A	
RPL36A	4	2006692	ENSGALG00000004952	X	113730376	ENSG00000165502	A	
Q5ZKQ9_CHIK	4	4422127	ENSGALG00000006457	X	114330261	ENSG00000170748	A	
PGK_CHICK	4	13036123	ENSGALG00000007936	X	77265348	ENSG00000170950	A	
XK	4	5160873	ENSGALG00000006637	X	37472073	ENSG00000172967	A	
NP_00101255	4	2231941	ENSGALG00000005475	X	70489192	ENSG00000177105	A	
CETN2	4	11378406	ENSGALG00000007510	X	151748963	ENSG00000177143	A	
CSTF2	4	5171532	ENSGALG00000006760	X	99963894	ENSG00000177613	A	

TAF7	4	2026182	ENSGALG0000004999	X	100425228	ENSG00000178913	A	
XIAP	4	15779875	ENSGALG00000008491	X	122868524	ENSG00000180152	A	
IF2G_CHICK	1	121677562	ENSGALG00000016340	X	23999592	ENSG00000180574	A	
	4	1269659	ENSGALG00000004187	X	77271902	ENSG00000187866	A	
NKAP	4	16614499	ENSGALG00000020262	X	118943390	ENSG00000189134	A	
GK	1	119230770	ENSGALG00000016285	X	30648889	ENSG00000196475	A	
KLHL13	4	3190314	ENSGALG00000005982	X	116928087	ENSG00000198642	A	
CHM	4	8622348	ENSGALG00000006906	X	85098025	ENSG00000203668	A	
ZRSR2	1	125314815	ENSGALG00000016552	X	15743719	ENSG00000212643	A	
NUP62CL	4	1871417	ENSGALG00000004856	X	106284125	ENSG00000213024	A	
RBMX	4	4422127	ENSGALG00000006457	X	114330261	ENSG00000213516	A	
RL39_CHICK	4	16633035	ENSGALG00000008620	X	118808002	ENSG00000214289	A	
UTP14A	4	1606880	ENSGALG00000024039	X	128881052	ENSG00000214320	A	
HTATSF1	4	4343017	ENSGALG00000006410	X	135412600	ENSG00000215074	A	
GTPBP6	1	134174603	ENSGALG00000016717	X	168295	ENSG00000215634	A	
ATP7A	4	13002692	ENSGALG00000007902	X	77155029	ENSG00000215761	A	
IAG2_CHICK	4	12984311	ENSGALG00000007861	X	77017750	ENSG00000215762	A	
ATP7A	4	13002692	ENSGALG00000007902	X	77155029	ENSG00000215763	A	
ATRX	4	12905188	ENSGALG00000007843	X	76826743	ENSG00000215766	A	
HSF3_CHICK	4	251929	ENSGALG00000004644	X	65403953	ENSG000000089472	A	misidentified by ensembl
HM14A_CHICK	4	9458044	ENSGALG00000007131	X	80263772	ENSG00000198157	A	misidentified by ensembl
	4	13000791	ENSGALG00000007863	X	77047537	ENSG00000131174	A	misidentified by ensembl
	4	1269659	ENSGALG00000004187	X	77281835	ENSG00000187325	A	misidentified by ensembl
	4	2006692	ENSGALG00000004952	X	100553941	ENSG00000126945	A	misidentified by ensembl
FUND2C	4	2151835	ENSGALG00000005381	X	153938384	ENSG00000165775	A	misidentified by ensembl
TMSB4X	1	126,774,748		X	12903150	ENSG00000205542	A	misidentified by ensembl
NP_00100846	4	16846725	ENSGALG00000008867	X	103,292,352		A	misidentified by ensembl
MTCP1	4	2164580	ENSGALG00000023937	X	153646932	ENSG00000100721	A	misidentified by ensembl
TRMT12	4	5178432	ENSGALG00000006773	X	79580677	ENSG00000183665	A	misidentified by ensembl
NP_00100846	4	16846725	ENSGALG00000008867	X	103,292,352	ENSG00000170619	A	misidentified by ensembl
BX649443.16				X	2245371	ENSG00000205681	B1	chimp/orang/maqaque
VXC3A				X	6461660	ENSG00000169059	B1	chimp/gorilla/orang/maqaque
VXC				X	7770303	ENSG00000182583	B1	chimp/gorilla/orang/maqaque
VXC2				X	8097985	ENSG00000177504	B1	chimp/gorilla/orang/maqaque
VXC3B				X	8392871	ENSG00000205642	B1	chimp/gorilla/orang/maqaque
FAM9B				X	8953036	ENSG00000177138	B1	chimp/gorilla/orang/maqaque
FAM9C				X	12963658	ENSG00000187268	B1	chimp/orang/maqaque
S100G				X	16578202	ENSG00000169906	B1	mammals only?
FTHL17				X	30999279	ENSG00000132446	B1	Retrogene
FTH1				X	37236164	ENSG00000219186	B1	Retrogene
Cxorf27				X	37735014	ENSG00000187516	B1	mammals only?
Z93403.1				X	42029377	ENSG00000212635	B1	chimp only?
AC136488.3				X	44893599	ENSG00000212634	B1	mammals only?
Cxorf31				X	46631800	ENSG00000204904	B1	mammals only?
Cxorf24				X	47227914	ENSG00000196741	B1	mammals only?
Cxorf25				X	47467857	ENSG00000187893	B1	mammals only?
SSX6				X	47852032	ENSG00000171483	B1	mammals only?
SSX5				X	47930600	ENSG00000165583	B1	mammals only?
SSX1				X	47957054	ENSG00000126752	B1	mammals only?
SSX10				X	48021100	ENSG00000185319	B1	mammals only?
SSX9				X	48039829	ENSG00000204648	B1	mammals only?
SSX3				X	48090807	ENSG00000165584	B1	mammals only?
SSX4				X	48127912	ENSG00000204645	B1	mammals only?
SSX4B				X	48146468	ENSG00000198946	B1	mammals only?
AF196972.1				X	48272500	ENSG00000204620	B1	mammals only?
PCSK1N				X	48574451	ENSG00000102109	B1	mammals only?
PPP1R3F				X	49013261	ENSG00000049769	B1	mammals only?
GAGE13				X	49047069	ENSG00000215269	B1	mammals only?
GAGE10				X	49047092	ENSG00000215276	B1	mammals only?
GAGE12J				X	49047131	ENSG00000215275	B1	mammals only?
GAGE2E				X	49084527	ENSG00000222023	B1	mammals only?
GAGE2C				X	49084570	ENSG00000205775	B1	mammals only?
GAGE2D				X	49094060	ENSG00000215274	B1	mammals only?
GAGE2B				X	49122652	ENSG00000215253	B1	mammals only?
GAGE12D				X	49183724	ENSG00000198716	B1	mammals only?
GAGE12E				X	49202836	ENSG00000216649	B1	mammals only?
GAGE12F				X	49202856	ENSG00000217977	B1	mammals only?
GAGE12G				X	49212424	ENSG00000068990	B1	mammals only?
GAGE12H				X	49231496	ENSG00000215266	B1	mammals only?
GAGE1				X	49241043	ENSG00000205777	B1	mammals only?
GAGE2A				X	49241043	ENSG00000189064	B1	mammals only?
PAGE1				X	49339010	ENSG00000068985	B1	mammals only?
PAGE4				X	49480601	ENSG00000101951	B1	mammals only?
RP11-114H20.1				X	51810705	ENSG00000182776	B1	mammals only?
RP11-363G10.2				X	51959703	ENSG00000179028	B1	mammals only?
XAGE2				X	52128793	ENSG00000155622	B1	mammals only?
XAGE1				X	52255543	ENSG00000204382	B1	mammals only?
XAGE1B				X	52271944	ENSG00000204379	B1	mammals only?
XAGE2B				X	52397079	ENSG00000185751	B1	mammals only?
XAGE1C				X	52528494	ENSG00000183461	B1	mammals only?
XAGE1D				X	52544884	ENSG00000204376	B1	mammals only?
XAGE1E				X	52557778	ENSG00000204375	B1	mammals only?
SSX7				X	52689836	ENSG00000204368	B1	mammals only?
SSX2				X	52742671	ENSG00000187754	B1	mammals only?
SSX2B				X	52797033	ENSG00000157950	B1	mammals only?
SPANXN5				X	52841911	ENSG00000204363	B1	mammals only?
XAGE5				X	52857953	ENSG00000171405	B1	mammals only?
XAGE3				X	52908285	ENSG00000171402	B1	mammals only?
FAM156B				X	52943081	ENSG00000179304	B1	mammals only?
FAM156A				X	52993187	ENSG00000182646	B1	mammals only?
PAGE2B				X	55118221	ENSG00000187761	B1	mammals only?
PAGE2				X	55132210	ENSG00000221833	B1	mammals only?
PAGE5				X	55263515	ENSG00000158639	B1	mammals only?
PAGE3				X	55301573	ENSG00000204279	B1	mammals only?
AL159987.19				X	55697879	ENSG00000169164	B1	mammals only?
AL354865.9				X	56772443	ENSG00000204272	B1	mammals only?
Cxorf62				X	68316125	ENSG00000215162	B1	chimp/orang/maqaque
AL590763.2				X	70596245	ENSG00000215120	B1	chimp only?
AL590763.2				X	70628887	ENSG00000215116	B1	chimp only?
Cxorf49				X	70850946	ENSG00000215115	B1	mammals only?
BX276092.9				X	70900227	ENSG00000215113	B1	mammals only?
DMRTC1				X	71913697	ENSG00000184911	B1	mammals only?
DMRTC1B				X	72008584	ENSG00000159123	B1	mammals only?

AL353999.2	X	72074728	ENSG00000204119	B1	mammals only?
CPXCR1	X	87888882	ENSG00000147183	B1	mammals only?
AL136362.10	X	91241192	ENSG00000204089	B1	human only?
ARMCX4	X	100627118	ENSG00000196440	B1	mammals only?
TCEAL2	X	101267316	ENSG00000184905	B1	mammals only?
TCEAL6	X	101281589	ENSG00000204071	B1	mammals only?
BEX5	X	101295340	ENSG00000184515	B1	mammals only?
	X	101356936	ENSG00000215046	B1	
	X	101601896	ENSG00000215029	B1	
BEX1	X	102204244	ENSG00000133169	B1	mammals only?
BEX4	X	102356708	ENSG00000102409	B1	mammals only?
TCEAL8	X	102394582	ENSG00000180964	B1	mammals only?
TCEAL5	X	102415275	ENSG00000204065	B1	mammals only?
BEX2	X	102450938	ENSG00000133134	B1	mammals only?
TCEAL7	X	102471813	ENSG00000182916	B1	mammals only?
WBP5	X	102498036	ENSG00000185222	B1	mammals only?
NGFRAP1	X	102517910	ENSG00000166681	B1	mammals only?
TCEAL4	X	102718054	ENSG00000133142	B1	mammals only?
TCEAL3	X	102749035	ENSG00000196507	B1	mammals only?
TCEAL1	X	102770304	ENSG00000172465	B1	mammals only?
TMEM31	X	102852493	ENSG00000179363	B1	mammals only?
TEX13A	X	104350269	ENSG00000133149	B1	mammals only?
TEX13B	X	107110750	ENSG00000170925	B1	mammals only?
AL359079.15	X	109305763	ENSG00000212738	B1	gorilla only?
AC005191.1	X	111011781	ENSG00000204025	B1	mammals only?
Cxorf55	X	114331227	ENSG00000175718	B1	chimp/orang
LUZP4	X	114430548	ENSG00000102021	B1	mammals only?
Cxorf61	X	115506878	ENSG00000204019	B1	mammals only?
KIAA1210	X	118096627	ENSG00000175553	B1	mammals only?
RHOXF2B	X	119090257	ENSG00000203989	B1	mammals only?
RHOXF1	X	119127053	ENSG00000101883	B1	mammals only?
RHOXF2	X	119176495	ENSG00000131721	B1	mammals only?
RP1-321E8.3	X	119890485	ENSG00000203983	B1	mammals only?
RP6-166C19.11	X	119895375	ENSG00000213505	B1	mammals only?
RP6-166C19.10	X	119900236	ENSG00000203981	B1	mammals only?
RP6-166C19.9	X	119905096	ENSG00000213503	B1	mammals only?
RP6-166C19.6	X	119909957	ENSG00000213499	B1	mammals only?
RP6-166C19.8	X	119909957	ENSG00000213504	B1	mammals only?
RP6-166C19.7	X	119914817	ENSG00000203979	B1	mammals only?
RP6-166C19.5	X	119924561	ENSG00000203978	B1	mammals only?
RP6-166C19.4	X	119929421	ENSG00000203977	B1	mammals only?
RP6-166C19.3	X	119934281	ENSG00000203976	B1	mammals only?
RP6-166C19.2	X	119939141	ENSG00000197443	B1	mammals only?
RP6-166C19.1	X	119944007	ENSG00000203975	B1	mammals only?
Cxorf64	X	125781432	ENSG00000183631	B1	mammals only?
AL022162.1	X	128502018	ENSG00000214977	B1	mammals only?
APLN	X	128607007	ENSG00000171388	B1	mammals only?
AC004409.1	X	133198743	ENSG00000203952	B1	mammals only?
PLAC1	X	133527539	ENSG00000170965	B1	mammals only?
FAM127C	X	133982209	ENSG00000212747	B1	mammals only?
FAM127B	X	133983721	ENSG00000203950	B1	mammals only?
FAM127A	X	133993999	ENSG00000134590	B1	mammals only?
AL590325.10	X	134083233	ENSG00000203949	B1	chimp/orang
RP11-274K13.2	X	134883732	ENSG00000203945	B1	mammals only?
Cxorf19	X	138271925	ENSG00000173954	B1	mammals only?
RP11-35F15.2	X	138865550	ENSG00000203933	B1	mammals only?
RP11-177G6.2	X	139619590	ENSG00000203930	B1	mammals only?
CDR1	X	139692236	ENSG00000184258	B1	mammals only?
SPANXB2	X	139912422	ENSG00000198820	B1	mammals only?
SPANXB1	X	139924427	ENSG00000203929	B1	mammals only?
LDOC1	X	140097596	ENSG00000182195	B1	mammals only?
SPANXC	X	140163265	ENSG00000198573	B1	mammals only?
SPANXA2	X	140499475	ENSG00000198021	B1	mammals only?
SPANXA1	X	140505291	ENSG00000203926	B1	mammals only?
SPANXD	X	140613237	ENSG00000196406	B1	mammals only?
SPANXN4	X	141941370	ENSG00000189326	B1	mammals only?
SPANXN3	X	142424231	ENSG00000189252	B1	mammals only?
SPANXN2	X	142622721	ENSG00000203924	B1	mammals only?
SPANXN1	X	144136799	ENSG00000203923	B1	mammals only?
Cxorf1	X	144716888	ENSG00000221870	B1	orang only?
Z97180.1	X	145508397	ENSG00000185351	B1	chimp only?
FMR1NB	X	146870541	ENSG00000176988	B1	mammals only?
FATE1	X	150635164	ENSG00000147378	B1	mammals only?
MAGEA5	X	151033182	ENSG00000183686	B1	mammals only?
CSAG2	X	151627400	ENSG00000184324	B1	mammals only?
CSAG4	X	151646636	ENSG00000214915	B1	mammals only?
CSAG1	X	151653884	ENSG00000198930	B1	mammals only?
AF002997.4	X	151678543	ENSG00000197463	B1	orang/maquaque
U52112.2	X	152799321	ENSG00000196987	B1	mammals only?
EMD	X	153260917	ENSG00000102119	B1	mammals only?
LAGE3	X	153358435	ENSG00000196976	B1	mammals only?
Cxorf52	X	153452673	ENSG00000197371	B1	chimp/orang/lemur
CTAG1A	X	153466601	ENSG00000183678	B1	mammals only?
AF277315.6	X	153480579	ENSG00000203873	B1	human only?
CTAG1B	X	153499059	ENSG00000184033	B1	mammals only?
Cxorf52B	X	153514068	ENSG00000212744	B1	chimp/orang/lemur
CTAG2	X	153533446	ENSG00000126890	B1	mammals only?
RP11-115M6.5	X	153704817	ENSG00000203870	B1	mammals only?
AKAP4	X	49842146	ENSG00000147081	B2	deeply conserved
AL034485.16	X	103103880	ENSG00000158427	B2	deeply conserved
AMELX	X	11221454	ENSG00000125363	B2	deeply conserved
APEX2	X	55043505	ENSG00000169188	B2	deeply conserved
ARD1A	X	152848561	ENSG00000102030	B2	deeply conserved
CCDC120	X	48803460	ENSG00000147144	B2	deeply conserved
CCDC22	X	48978885	ENSG00000101997	B2	deeply conserved
CFP	X	47368557	ENSG00000126759	B2	deeply conserved
Cxorf26	X	75309173	ENSG00000102390	B2	deeply conserved
Cxorf38	X	40373229	ENSG00000185753	B2	deeply conserved
Cxorf50	X	72079451	ENSG00000212630	B2	deeply conserved
Cxorf58	X	23836044	ENSG00000165182	B2	deeply conserved
DNASE1L1	X	153282773	ENSG00000013563	B2	deeply conserved
EBP	X	48265177	ENSG00000147155	B2	deeply conserved
FAM47A	X	34057794	ENSG00000185448	B2	deeply conserved

FAM47B	X	34870852	ENSG00000189132	B2	deeply conserved
FAM47C	X	36936391	ENSG00000198173	B2	deeply conserved
FAM58A	X	152506579	ENSG00000147382	B2	deeply conserved
FOXR2	X	55666558	ENSG00000189299	B2	deeply conserved
FTSJ1	X	48219493	ENSG00000068438	B2	deeply conserved
G6PD	X	153412800	ENSG00000160211	B2	deeply conserved
GPXOW	X	48857278	ENSG00000068394	B2	deeply conserved
GPR101	X	135939973	ENSG00000165370	B2	deeply conserved
GRIPAP1	X	48715078	ENSG00000068400	B2	deeply conserved
GS1-484O17.2	X	30545410	ENSG00000178556	B2	deeply conserved
IKBKG	X	153423672	ENSG00000073009	B2	deeply conserved
IRAK1	X	152929154	ENSG00000184216	B2	deeply conserved
ITIH5L	X	54792341	ENSG00000102313	B2	deeply conserved
MAGEA1	X	152134716	ENSG00000198681	B2	deeply conserved
MAGEA10	X	151053566	ENSG00000124260	B2	deeply conserved
MAGEA11	X	148575479	ENSG00000185247	B2	deeply conserved
MAGEA12	X	151649952	ENSG00000197172	B2	deeply conserved
MAGEA2	X	151669043	ENSG00000184750	B2	deeply conserved
MAGEA2B	X	151633746	ENSG00000183305	B2	deeply conserved
MAGEA3	X	151685309	ENSG00000213401	B2	deeply conserved
MAGEA4	X	150831652	ENSG00000147381	B2	deeply conserved
MAGEA6	X	151617901	ENSG00000221867	B2	deeply conserved
MAGEA8	X	148770653	ENSG00000156009	B2	deeply conserved
MAGEA9	X	148671395	ENSG00000166008	B2	deeply conserved
MAGEA9B	X	148471105	ENSG00000123584	B2	deeply conserved
MAGEB1	X	30171769	ENSG00000214107	B2	deeply conserved
MAGEB10	X	27736028	ENSG00000177689	B2	deeply conserved
MAGEB16	X	35726380	ENSG00000189023	B2	deeply conserved
MAGEB17	X	16095525	ENSG00000182798	B2	deeply conserved
MAGEB18	X	26066381	ENSG00000176774	B2	deeply conserved
MAGEB2	X	30143601	ENSG00000099399	B2	deeply conserved
MAGEB3	X	30158474	ENSG00000198798	B2	deeply conserved
MAGEB4	X	30170090	ENSG00000120289	B2	deeply conserved
MAGEB5	X	26145340	ENSG00000188408	B2	deeply conserved
MAGEB6	X	26120478	ENSG00000176746	B2	deeply conserved
MAGEC1	X	140819346	ENSG00000155495	B2	deeply conserved
MAGEC2	X	141117797	ENSG00000046774	B2	deeply conserved
MAGEC3	X	140753768	ENSG00000165509	B2	deeply conserved
MAGED1	X	51562895	ENSG00000179222	B2	deeply conserved
MAGED2	X	54850757	ENSG00000102316	B2	deeply conserved
MAGED4	X	51944659	ENSG00000154545	B2	deeply conserved
MAGED4B	X	51821663	ENSG00000187243	B2	deeply conserved
MAGEE1	X	75564521	ENSG00000198934	B2	deeply conserved
MAGEE2	X	74919548	ENSG00000186675	B2	deeply conserved
MAGEH1	X	55495263	ENSG00000187601	B2	deeply conserved
MAGIX	X	48906005	ENSG00000017621	B2	deeply conserved
MCART6	X	103230555	ENSG00000176274	B2	deeply conserved
MECP2	X	152940218	ENSG00000169057	B2	deeply conserved
NAP1L6	X	72262601	ENSG00000204118	B2	deeply conserved
NDUFB11	X	46886559	ENSG00000147123	B2	deeply conserved
NSBP1	X	80255856	ENSG00000198157	B2	deeply conserved
NXF2	X	101356936	ENSG00000185554	B2	deeply conserved
NXF2B	X	101501972	ENSG00000185945	B2	deeply conserved
NXF3	X	102217408	ENSG00000147206	B2	deeply conserved
NXF4	X	101691549	ENSG00000196970	B2	deeply conserved
NXF5	X	100973741	ENSG00000126952	B2	deeply conserved
PLP2	X	48915217	ENSG00000102007	B2	deeply conserved
PNMA3	X	151975530	ENSG00000183837	B2	deeply conserved
PNMA5	X	151908025	ENSG00000198883	B2	deeply conserved
PNMA6A	X	151991521	ENSG00000198013	B2	deeply conserved
PNMA6B	X	151994652	ENSG00000203902	B2	deeply conserved
PORCN	X	48252307	ENSG00000102312	B2	deeply conserved
PYY3	X	49807454	ENSG00000204474	B2	deeply conserved
RBM3	X	48317780	ENSG00000102317	B2	deeply conserved
RENBP	X	152853910	ENSG00000102032	B2	deeply conserved
RGAG1	X	109548941	ENSG00000181110	B2	deeply conserved
RIBC1	X	53466575	ENSG00000158423	B2	deeply conserved
RP13-36C9.1	X	134756363	ENSG00000203947	B2	deeply conserved
RP13-36C9.2	X	134693880	ENSG00000203948	B2	deeply conserved
RP13-36C9.3	X	134711154	ENSG00000213444	B2	deeply conserved
RP13-36C9.6	X	134773630	ENSG00000213441	B2	deeply conserved
RP13-36C9.7	X	134790881	ENSG00000203946	B2	deeply conserved
RPL10	X	153278689	ENSG00000147403	B2	deeply conserved
RP526L1	X	71180984	ENSG00000196933	B2	deeply conserved
SLC10A3	X	153368842	ENSG00000126903	B2	deeply conserved
SPACA5	X	47748678	ENSG00000171489	B2	deeply conserved
SPACA5B	X	47875014	ENSG00000171478	B2	deeply conserved
SPIN2A	X	57177688	ENSG00000147059	B2	deeply conserved
SPIN2B	X	57162840	ENSG00000186787	B2	deeply conserved
SPIN3	X	57033990	ENSG00000204271	B2	deeply conserved
SPIN4	X	62483832	ENSG00000186767	B2	deeply conserved
SSR4	X	152712165	ENSG00000180879	B2	deeply conserved
TAZ	X	153293071	ENSG00000102125	B2	deeply conserved
TBC1D25	X	48283019	ENSG00000068354	B2	deeply conserved
TEX28	X	153152124	ENSG00000185254	B2	deeply conserved
TEX28P1	X	153115008	ENSG00000182242	B2	deeply conserved
TEX28P2	X	153077878	ENSG00000102080	B2	deeply conserved
TIMM17B	X	48635676	ENSG00000126768	B2	deeply conserved
TMEM187	X	152891185	ENSG00000177854	B2	deeply conserved
TMSL8	X	101655266	ENSG00000158164	B2	deeply conserved
TSPYL2	X	53128274	ENSG00000184205	B2	deeply conserved
TSR2	X	54483578	ENSG00000158526	B2	deeply conserved
UBL4A	X	153365254	ENSG00000102178	B2	deeply conserved
UCL5IP	X	152363372	ENSG00000183479	B2	deeply conserved
UCL5IP	X	152366318	ENSG00000213397	B2	deeply conserved
UXT	X	47396140	ENSG00000126756	B2	deeply conserved
WDR13	X	48332467	ENSG00000101940	B2	deeply conserved
WDR40B	X	125511050	ENSG00000198889	B2	deeply conserved
WDR40C	X	125126195	ENSG00000198354	B2	deeply conserved
WDR45	X	48819036	ENSG00000196998	B2	deeply conserved
XX-FW88277B6.1	X	134674851	ENSG00000187267	B2	deeply conserved
Z82254.1	X	103245459	ENSG00000166707	B2	deeply conserved
ZCCHC12	X	117841774	ENSG00000174460	B2	deeply conserved

ZCCHC16				X	111584383	ENSG00000187823	B2	deeply conserved
ZCCHC5				X	77798222	ENSG00000179300	B2	deeply conserved
RP3-36411.1	8	17291550		X	109476356	ENSG00000133136	B3a	AMMECR1 Exon
Q5ZM59_CHIC	24	5523892	ENSGALG00000007323	X	73011598	ENSG00000182707	B3a	breakdown in synteny at xist
TRO	E64_random	538727		X	54963969	ENSG00000067445	B3a	duplication in mammals from chr 10?
HSD17B10	Un_random	17700410	ENSGALG00000018747	X	53474931	ENSG00000072506	B3a	Gap on GGA 1
NP_00102644	8	14024470	ENSGALG00000005571	X	11039342	ENSG00000004961	B3a	mammals not in ancestral configuration
ZNF280C	10	8647480	ENSGALG00000014375	X	129164372	ENSG00000056277	B3a	mammals not in ancestral configuration
IDH3G	10	4725876		X	152704416	ENSG00000067829	B3a	mammals not in ancestral configuration
OTUD5	25	1795521		X	48664432	ENSG00000068308	B3a	mammals not in ancestral configuration
HUWE1	10	8917961		X	53575782	ENSG00000086758	B3a	mammals not in ancestral configuration
HDAC6	2	29442230		X	48545051	ENSG00000094631	B3a	mammals not in ancestral configuration
	18	3338797	ENSGALG00000001545	X	102078856	ENSG00000102128	B3a	mammals not in ancestral configuration
SERPINA7	5	48043692		X	105163853	ENSG00000123561	B3a	mammals not in ancestral configuration
NP_00103225	10	21826523	ENSGALG00000008146	X	102817080	ENSG00000123562	B3a	mammals not in ancestral configuration
IL9R	14	7381016	ENSGALG00000006394	X	154880440	ENSG00000124334	B3a	mammals not in ancestral configuration
NP_989827.1	13	13659657	ENSGALG00000005955	X	100532633	ENSG00000126945	B3a	mammals not in ancestral configuration
USP26	7	24065178		X	131986325	ENSG00000134588	B3a	mammals not in ancestral configuration
ZNF157	2	461370		X	47114943	ENSG00000147117	B3a	mammals not in ancestral configuration
ZNF673	16	394296		X	46191673	ENSG00000147121	B3a	mammals not in ancestral configuration
IGSF1	2	54566872	ENSGALG00000023010	X	130235161	ENSG00000147255	B3a	mammals not in ancestral configuration
	28	2510984	ENSGALG00000009709	X	105298954	ENSG00000157502	B3a	mammals not in ancestral configuration
TSC22D3	9	25234233		X	106843107	ENSG00000157514	B3a	mammals not in ancestral configuration
F133_CHICK	2	22635559	ENSGALG00000009475	X	92815861	ENSG00000179083	B3a	Mammals not in ancestral orientation
AL034369.1	6	30334299		X	107513285	ENSG00000189372	B3a	Mammals not in ancestral orientation
BX890604.9	5	52,075,173		X	3834245	ENSG00000205662	B3a	Mammals not in ancestral orientation
BX890604.9	5	52,075,173		X	3792439	ENSG00000205663	B3a	Mammals not in ancestral orientation
RP11-706O15	5	52,075,173		X	3745569	ENSG00000205664	B3a	Mammals not in ancestral orientation
	11	19967982	ENSGALG00000005855	X	15666313	ENSG00000169239	B3a	Mammals not in ancestral orientation
CA5BL	11	19970458		X	15602976	ENSG00000186312	B3a	Mammals not in ancestral orientation
	18	3338797	ENSGALG00000001545	X	102641334	ENSG00000172476	B3a	Mammals not in ancestral orientation
NP_00102587	18	9012406	ENSGALG00000004434	X	55186260	ENSG00000182518	B3a	Mammals not in ancestral orientation
ZMAT1	22	2569623		X	101023918	ENSG00000166432	B3a	Mammals not in ancestral orientation
NP_00101285	22	825699	ENSGALG00000000275	X	104536840	ENSG00000181819	B3a	Mammals not in ancestral orientation
	23	5802475	ENSGALG000000024047	X	106402468	ENSG00000204053	B3a	Mammals not in ancestral orientation
	E64	7485	ENSGALG00000005375	X	152336975	ENSG00000189420	B3a	Mammals not in ancestral orientation
				X	83002826	ENSG00000183035	B3a	mammals only
OTU6B_CHIC	2	129518738	ENSGALG00000015920	X	69199066	ENSG00000189401	B3a	Retrogene -- not ancestral
SLC17A5	3	84286082	ENSGALG00000015928	X	22928008	ENSG00000184735	B3a	Retrogene -- not ancestral
NP_00102638	5	51008399	ENSGALG00000017388	X	21784026	ENSG00000198767	B3a	Retrogene -- not ancestral
DHE3_CHICK	6	3646956	ENSGALG00000002020	X	12000913	ENSG00000182890	B3a	Retrogene -- not ancestral
PGAM1_CHIC	6	23773144	ENSGALG00000007606	X	77111027	ENSG00000186076	B3a	Retrogene -- not ancestral
NP_00102641	6	31488972	ENSGALG00000009336	X	129456814	ENSG00000221930	B3a	Retrogene -- not ancestral
	14	9057526	ENSGALG00000007133	X	134383634	ENSG00000178947	B3a	Retrogene -- not ancestral
	14	4611000	ENSGALG000000004773	X	49531315	ENSG00000180991	B3a	Retrogene -- not ancestral
	14	9057526	ENSGALG00000007133	X	133952634	ENSG00000184785	B3a	Retrogene -- not ancestral
	14	4611000	ENSGALG000000004773	X	55529687	ENSG00000185295	B3a	Retrogene -- not ancestral
Q5ZLF1_CHIC	14	107939	ENSGALG00000002910	X	15103267	ENSG00000189369	B3a	Retrogene -- not ancestral
	14	9057526	ENSGALG00000007133	X	134060093	ENSG00000196972	B3a	Retrogene -- not ancestral
CXCR3	15	10187390		X	70752492	ENSG00000186810	B3a	Retrogene -- not ancestral
	15	11113456	ENSGALG00000007765	X	44588194	ENSG00000189037	B3a	Retrogene -- not ancestral
PABPC5	23	5732127	ENSGALG00000003800	X	90576250	ENSG00000174740	B3a	Retrogene -- not ancestral
PABPC1L2B	23	5738660		X	72140077	ENSG00000184388	B3a	Retrogene -- not ancestral
PABPC1L2A	23	5738660		X	72213840	ENSG00000186288	B3a	Retrogene -- not ancestral
NP_00102606	23	1420617	ENSGALG00000000734	X	96025668	ENSG00000204086	B3a	Retrogene -- not ancestral
F8A3	Un_random	11824563		X	154339769	ENSG00000185990	B3a	Retrogene -- not ancestral
F8A1	Un_random	11824561		X	153767829	ENSG00000197932	B3a	Retrogene -- not ancestral
F8A2	Un_random	11824562		X	154264943	ENSG00000198444	B3a	Retrogene -- not ancestral
	Z	46561985	ENSGALG00000000264	X	68297422	ENSG00000181191	B3a	Retrogene -- not ancestral
	Z	39452993	ENSGALG00000012585	X	56606797	ENSG00000188021	B3a	Retrogene -- not ancestral
ACTRT1	21			X	127012622	ENSG00000123165	B3a	Retrogene -- not ancestral
ATX3_CHICK	5	47024941	ENSGALG00000010766	X	13246276	ENSG00000123594	B3a	Retrogene -- not ancestral
NP_00100439	27	2689834	ENSGALG00000000538	X	118888466	ENSG00000125352	B3a	Retrogene -- not ancestral
TGIF2LX	2	103923416		X	89063537	ENSG00000153779	B3a	Retrogene -- not ancestral
SLC35A2	8	12657184		X	48645403	ENSG00000102100	B3a	unmapped in chicken
PQBP1	13	848807		X	48640139	ENSG00000102103	B3a	unmapped in chicken
CITED1	3	55892256		X	71438222	ENSG00000125931	B3a	unmapped in chicken
CHST7	9	11755104		X	46318136	ENSG00000147119	B3a	unmapped in chicken
TKTL1	12	7182008		X	153177345	ENSG00000007350	B3b	Chr 12 Block
TFE3	12	16045909		X	48772613	ENSG00000068323	B3b	Chr 12 Block
SYP	12	13780555		X	48931201	ENSG00000102003	B3b	Chr 12 Block
PRAF2	12	15756716		X	48815762	ENSG00000102050	B3b	Chr 12 Block
OPN1LW	12	20164767		X	153062939	ENSG00000102076	B3b	Chr 12 Block
GNL3L	12	735677		X	54570464	ENSG00000130119	B3b	Chr 12 Block
OPN1MW	12	20164767		X	153101348	ENSG00000147380	B3b	Chr 12 Block
OR13H1	5	117659		X	130505729	ENSG00000171054	B3b	Moved in Chicken
ALAS2	12	2766841		X	55052213	ENSG00000158578	B3b	Chr 12 Block
OPN1MW2	12	20164767		X	153138479	ENSG00000166160	B3b	Chr 12 Block
BGN	12	3613647		X	152413605	ENSG00000182492	B3b	Chr 12 Block
RBM10	12	2963602		X	46889575	ENSG00000182872	B3b	Chr 12 Block
ZCCHC13	12	5261203		X	73440750	ENSG00000187969	B3b	Chr 12 Block
FLNA	12	9144416		X	153230091	ENSG00000196924	B3b	Chr 12 Block
	12	10959085	ENSGALG00000006277	X	57949867	ENSG00000198205	B3b	Chr 12 Block
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	1	127527509	ENSGALG000000018518	X			C1	birds only
	1	132167869	ENSGALG000000022781	X			C1	birds only
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	4	2409863	ENSGALG000000020319	X			C1	birds only
	4	4538633	ENSGALG000000006495	X			C1	birds only
	4	11761534	ENSGALG000000007600	X			C1	birds only
	4	1192554	ENSGALG000000024093	X			C1	chicken only
	1	95269982	ENSGALG000000022860	X	32637833		C1	chicken only
	1	95273120	ENSGALG000000019210	X			C1	chicken only
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	4	9359368	ENSGALG00000007110	2	102745490		C2	deeply conserved
	4	11695058	ENSGALG00000020283	4	42094906		C2	deeply conserved
	4	12237058	ENSGALG00000007683	4	53951932		C2	deeply conserved
	4	12046226	ENSGALG00000007646	4	54848360		C2	deeply conserved
	4	11440627	ENSGALG00000007546	4	56463267		C2	deeply conserved
	4	2380807	ENSGALG00000005648	6	109591432		C2	deeply conserved
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	4	2422924	ENSGALG00000005747	11	86197048		C2	deeply conserved
	4	158517	ENSGALG00000004692	11	109832851		C2	deeply conserved
	4	1181747	ENSGALG00000004401	12	1625428		C2	deeply conserved
	4	12328044	ENSGALG00000007710	13	26745215		C2	deeply conserved
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	4	11292291	ENSGALG00000007482	13	77218652		C2	deeply conserved
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	1	116963398	ENSGALG000000016269				C2	deeply conserved
	1	117011946	ENSGALG00000022793				C2	deeply conserved
	1	121615619	ENSGALG000000016326				C2	deeply conserved
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	4	1813693	ENSGALG00000003841	2	234011601		C3a	synteny not conserved
	4	306601	ENSGALG000000004619	4	156354686		C3a	synteny not conserved
GBRB4_CHIC	4	10736799	ENSGALG00000007255	4	46858023		C3a	synteny not conserved
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C8orf48	4	11648254	ENSGALG00000007580	8	13468870	ENSG00000164743	C3a	synteny not conserved
	1	115653671	ENSGALG000000016232	8	145985959	ENSG00000161016	C3a	moved in human
INPPL1	4	1211412	ENSGALG00000004336	11	71613473	ENSG00000165458	C3a	moved in human
KCTD12	4	11480977	ENSGALG00000009628	13	76352313	ENSG00000178695	C3a	break in synteny
	4	11536786	ENSGALG00000007570	13	72547843		C3a	synteny not conserved
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AIPL1	4	2032806	ENSGALG00000005014	17	6267784	ENSG00000129221	C3a	moved in human
	4	11383181	ENSGALG00000020288	18	570526		C3a	break in synteny

4	16723439	ENSGALG00000008687		19	19484230	ENSG00000178093	C3a	synteny not conserved
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Supplementary Table 5: BAC and fosmid clones: GenBank accession numbers and positions in chicken Z sequence assembly

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JH077O23	AC188996.2	1079671	1248247
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J_AA053B04	AC188606.2	1535960	1750598
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J_AA084O21	AC188445.6	2883586	3098533
JB057C09	AC190409.2	3090903	3237028
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JE016N08	AC187119.3	GAP	GAP
JE085K17	AC192759.2	GAP	GAP
J_AA056N13	AC189115.3	GAP	GAP
J_AA063E08	AC193214.3	GAP	GAP
J_AA068J18	AC192588.2	GAP	GAP
J_AA082L12	AC192785.3	GAP	GAP
J_AA086C16	AC189113.2	GAP	GAP
J_AA114I01	AC188817.3	GAP	GAP
J_AA128H23	AC174384.2	GAP	GAP
J_AA129F07	AC186354.3	GAP	GAP
J_AA135B11	AC192387.4	GAP	GAP
J_AA149E15	AC191339.3	GAP	GAP
J_AD0121O02	AC234262.3	GAP	GAP
J_AE0093B11	AC234463.2	GAP	GAP
J_AA064K10	AC186840.1	GAP	GAP
J_AA025M17	AC190246.4	GAP	GAP

## **Supplementary Note 1:** Additional information for Supplementary Figure 12

The analyses of Supplementary Figure 12 are based on the human and chicken sex-averaged recombination rates as reported in Kong et al. 2002 *Nature Genetics* 31:241-247 and Elferink et al. 2010 *BMC Genetics* 2010 11:11, with recombination rates for the Z and X corrected to 2/3 of the reported homogametic rate.

Recombination data for the human genome is available from the UCSC genome browser as an average over one megabase intervals on the 2006 assembly of the human genome, which includes the finished sequence of the human X chromosome. Recombination data for the chicken genome is available in approximately half-megabase intervals. For the Z chromosome, we mapped the locations of markers from Elferink et al. onto our assembly using BLAT.

For each interval, we tabulated the corresponding G+C content and LINE density. We then segmented the data by recombination rate, using 1 cM/Mb bins. For both G+C content and LINE density, we performed a Mann-Whitney U test on each bin, comparing the location of data for the Z chromosome to the chicken autosomes. We repeated this analysis with the data from humans, comparing the location of data from the X chromosome with the human autosomes.

Consistent with the predictions of a model of biased gene conversion towards GC, we observed no statistically significant difference in G+C content between intervals on the Z and X chromosomes and intervals on autosomes with similar rates of crossing over.

Models of transposable element distribution based on ectopic exchange or NAHR-mediated deletion predict that LINEs will be more abundant in regions where crossing over is rare. We observe this trend in both the chicken and human genomes. However, the LINE density of Z and X chromosomes is significantly different from autosomal regions with similar rates of crossing over. Additional mechanisms of LINE element accumulation are necessary to account for the enrichment we observe.

On the Z chromosome, we observed statistically significant ( $P < 0.05$ ) differences in LINE density between intervals on the Z chromosome and intervals on chicken autosomes with a similar rates of crossing over, in bins up to 7 cM/Mb, beyond which significance tests are impossible due to the low number of Z intervals.

On the X chromosome, we observed statistically significant ( $P < 0.05$ ) differences in LINE density between intervals on the X chromosome and intervals on human autosomes with a similar rates of crossing over, in bins up to 3 cM/Mb, beyond which significance tests are impossible due to the low number of X intervals.



## **Chapter 3: STS marker design yields inferences about the structure of the chicken W chromosome**

Daniel Winston Bellott

Author Contributions:

DWB performed the analyses and wrote the chapter

## ***Summary***

The chicken W chromosome is the first female-specific chromosome targeted for sequencing, and it is expected to provide insights into sex determination in birds as well as female fertility and sex chromosome evolution. To capture the sequence of this chromosome, a female was selected for the chicken genome project. However, the shotgun sequencing approach employed by the project produced only 0.5% of the sequence of the W chromosome. This was partly due to low coverage of the sex chromosomes but also due to the inability of whole genome shotgun approach to cope with the ampliconic structures prevalent on other sex specific chromosomes. As a prelude to sequencing the chicken W chromosome by an iterative mapping and sequencing approach, I have generated 184 new female-specific STS markers. In addition to using approaches that required no prior knowledge of the sequence and structure of the W chromosome, I also used approaches designed to detect some of the unique features of sex-specific chromosomes. My results shed light on the structure of the W chromosome sequence, suggesting that it maintains extensive homology with its partner, the Z chromosome, and contains ampliconic sequences with short repeat units which may be refractory to even an iterative mapping and sequencing approach.

## ***Introduction***

In birds, as in mammals, the chromosome complement determines sex. Female mammals are XX and males are XY, but, in birds, the situation is reversed. Male birds are ZZ, and female birds are ZW, although it is unknown whether sex determination is

controlled by Z chromosome dosage or the presence or absence of the W chromosome (Ellegren 2009; Kuroiwa 2009). Sequencing the W chromosome will shed light on the process of sex determination in birds, just as key insights into the genetic mechanisms of sex determination came from the study of mammalian Y chromosomes (Ford et al. 1959; Jacobs and Strong 1959; Welshons and Russell 1959; Berta et al. 1990; Gubbay et al. 1990; Lovell-Badge and Robertson 1990; Sinclair et al. 1990; Koopman et al. 1991). In addition, the sequence of the human Y chromosome has led to a greater understanding of male germ cell development and male infertility (Blanco et al. 2000; Kamp et al. 2000; Kuroda-Kawaguchi et al. 2001; Repping et al. 2002; Repping et al. 2003; Machev et al. 2004; de Llanos et al. 2005; Ferlin et al. 2005; Hucklenbroich et al. 2005). As the mirror image of the male-specific Y chromosome, the sequence of the female-specific W chromosome promises to provide unparalleled insights into female fertility. Because the sex chromosomes of birds evolved independently from those of mammals (Nanda et al. 1999; Nanda et al. 2002; Matsubara et al. 2006), the sequence of the W chromosome will also serve as an important outgroup for studies of mammalian Y chromosome evolution.

Sequencing a single chromosome would seem to be a trivial task. Widespread adoption of the whole genome shotgun (WGS) sequencing strategy has led to a dramatic increase in the availability of genomic data. Over a hundred animals have been selected to have their genomes sequenced (NHGRI 2010), and there are proposals to increase that number to ten thousand in the near future (Haussler et al. 2009). However, only two sex-specific chromosomes have been completed from any species – the human Y chromosome and the chimpanzee Y chromosome (Skaletsky et al. 2003; Hughes et al. 2010). Furthermore, no female-specific W chromosome has been sequenced from any

species. Sequencing efforts for sex specific Y and W chromosomes lag behind those for whole genomes for two reasons. First, it is now standard practice for whole genome shotgun sequencing projects to target the homogametic sex in order to ensure adequate coverage of the X or Z chromosome. Second, sex-specific Y and W chromosomes differ from the rest of the genome in ways that preclude whole genome shotgun sequencing strategies.

Unlike autosomes, sex-specific Y and W chromosomes are, by definition, only present in one copy in the heterogametic sex. Whole genome shotgun sequencing projects are designed to provide sufficient coverage of autosomes to enable their assembly. Sequencing the heterogametic sex would provide only half as much coverage to the sex chromosomes, resulting in an increased number of gaps. Sequencing the heterogametic sex at twice the optimal coverage for autosomes would provide the correct level of coverage for the sex chromosomes, but this strategy is rarely employed. Sequencing the heterogametic sex at double the depth would double the costs of a project and only obtain the sequence of one additional chromosome compared to sequencing the homogametic sex at normal coverage. But even if cost were no object, it is likely that a whole genome shotgun strategy would fail to produce a complete assembly of a sex-specific Y or W chromosome.

Previous attempts to use a whole genome shotgun sequencing strategy to sequence sex-specific chromosomes have not been successful. The *Drosophila melanogaster* genome was sequenced using a whole genome shotgun strategy on DNA from a mixed-sex (XX and XY individuals) sample (Adams et al. 2000). While the autosomes and X chromosome were assembled using this strategy, the Y chromosome

could not be assembled (Adams et al. 2000). Similarly, the chicken genome was sequenced using a heterogametic (ZW) female, in hopes that the assembly would capture both the Z chromosome and the W chromosome (McPherson et al. 2002). Nearly 10% of the genome could not be assigned to any chromosome (Hillier 2004). About 30% of the Z chromosome was assembled, but the female-specific W chromosome fared even worse; less than 0.5% of the chicken W chromosome was assembled from whole genome shotgun data (Hillier 2004).

The human and chimpanzee Y chromosome sequences demonstrated that sex-specific chromosomes are enriched for sequences that cannot be assembled by a whole genome shotgun strategy. About 5% of the human genome consists of large (greater than 1kb), highly identical (greater than 90% nucleotide identity) duplications called segmental duplications, or amplicons (Bailey et al. 2002). Each copy of an ampliconic sequence is so similar to the others that individual shotgun reads do not contain enough information to be uniquely assigned to one repeat unit or the other. Instead, the reads from multiple repeat units “collapse” into a non-redundant sequence when shotgun reads are assembled, making whole genome shotgun methods ineffective. Amplicons make up 45% of the human Y chromosome and 56% of the chimp Y chromosome (Skaletsky et al. 2003; Hughes et al. 2010). The amplicons on the human and chimpanzee Y chromosomes are some of the longest (greater than 100 kb) and most identical (greater than 99.9% nucleotide identity) in the entire genome (Skaletsky et al. 2003; Hughes et al. 2010). Whole genome shotgun strategies are not likely to be able to produce reliable assemblies of sex-specific chromosomes rich in amplicons.

A specialized sequencing approach, called iterative mapping and sequencing, is needed to address the unique challenges presented by sex-specific chromosomes (Kuroda-Kawaguchi et al. 2001; Tilford et al. 2001; Skaletsky et al. 2003). Individual BAC or fosmid clones are subjected to shotgun sequencing to generate contiguous sequence from within a single amplicon repeat unit. The large-insert size of BACs (~150kb) and fosmids (~40kb) results in sequences that are long enough to contain the necessary information to distinguish between distinct amplicon copies. Only rare, subtle differences (such as single nucleotide substitutions or dinucleotide repeat length alterations), called sequence family variants, or SFVs, exist between non-allelic copies of ampliconic sequences. SFVs emerge during the sequencing process as discrepancies between BACs that had been expected to overlap. BACs containing newly discovered SFVs are assigned to a different repeat unit of an amplicon. Potential neighbors are screened for the newly discovered SFVs to identify truly overlapping clones, which are sequenced. This process is iterated until all BACs have no discrepancies in overlapping regions and all BACs can be fitted onto a BAC-based physical map on the basis of the SFVs that defines the BAC tiling path.

Successful sequencing of a sex-specific chromosome by an iterative mapping and sequencing strategy requires a suite of specialized resources. First of all, the strategy is dependent upon the existence of several large-insert libraries produced from a single heterogametic individual, providing deep coverage of the sex-specific chromosome. Deep (>10-fold) coverage from multiple libraries, ideally generated by different restriction enzymes or by shearing, reduces the likelihood of gaps in the final assembly due to poor coverage or cloning bias. The use of libraries from a single individual avoids the

possibility of confounding allelic differences between individuals with SFVs that distinguish between ampliconic repeat units. Secondly, a physical mapping resource, such as a radiation hybrid map or a deletion map, is necessary to orient contiguous sequences within the assembly. While assemblies of autosomes, X chromosomes, and Z chromosomes can all be anchored by a genetic map, the sex-specific portion of a Y or W chromosome does not engage in crossing over with a partner, and no genetic map can be constructed outside of the pseudoautosomal region. Thirdly, in order to select clones, it is necessary to establish a dense collection of known sequences (STSs) from the sex specific chromosome that can be used to establish a physical map and select clones.

The chicken W chromosome presented a unique challenge. Many key resources were in place to mount an iterative mapping and sequencing effort, but there was no source of female-specific STSs. When the draft sequence of the chicken genome was published in 2005, the whole genome shotgun assembly contained only 0.5% of the W chromosome (Hillier 2004). Much more sequence had been erroneously assigned to the W chromosome on the basis of “W-specific repeats” which turned out to be genome typical interspersed repeats instead (Hillier 2004; Granevitze et al. 2007). Although the shotgun assembly of the W chromosome was poor, large-insert library resources were plentiful. There are four BAC libraries from the individual hen whose genome was sequenced, giving a combined 13-fold coverage of the W chromosome (Lee et al. 2003). Both a BAC-fingerprint based physical map and a radiation hybrid map of the chicken genome were available (Morisson et al. 2002; Ren et al. 2003; Wallis et al. 2004).

Unfortunately, every genomic resource constructed during the process of chicken genome sequencing was female. The easiest way to generate STSs for a sex-specific

chromosome is to use a subtraction-based approach. Sequences from the heterogametic sex are compared to sequences from the homogametic sex; sequences shared between the sexes are eliminated, and sequences specific to the heterogametic sex are used to design sex-specific STS. There were no ZZ male resources available as a basis for subtraction. The major challenge of the chicken W chromosome sequencing project lay in the design of female-specific STSs that could be used to identify W chromosome BACs.

While there were few resources available for subtraction, there was reason to believe that the W chromosome was similar in structure to mammalian Y chromosomes. The human Y chromosome possesses six different heterochromatic satellite repeat families in large, homogeneous tandem arrays (Skaletsky et al. 2003). Similarly, the “W-specific” repeats form three families of heterochromatic satellite repeats that reside in distinct domains on the W chromosome (Table 1) (Tone et al. 1982; Tone et al. 1984; Kodama et al. 1987; Saitoh et al. 1991; Itoh and Mizuno 2002). The W chromosome retains traces of its autosomal origins in homologs of Z-linked genes (Table 2) (Ellegren 1996; Fridolfsson et al. 1998; Hori et al. 2000; Mizuno et al. 2000; Itoh et al. 2001; Handley et al. 2004; Hillier 2004; Yamada et al. 2004; Nam and Ellegren 2008), in analogy to the X-degenerate genes of the human and chimpanzee Y chromosomes (Skaletsky et al. 2003; Hughes et al. 2005). The chicken W chromosome also possesses ampliconic sequences; the *HINTw* gene resides in tandem array (Hori et al. 2000), reminiscent of the human *TSPY* array (Skaletsky et al. 2003) and the mouse *Rbmy* array (Alföldi 2008).

I set out to identify female-specific sequences to serve as STS markers in advance of future W chromosome sequencing efforts. I used the few sequence features of the W

chromosome that were known to design a small number of STS markers, but then were forced to resort to other approaches. To address the lack of ZZ male resources, I adopted two approaches that were not based on subtraction. First, I applied known properties of mammalian Y chromosomes to search for W linked sequences in the data generated by the chicken genome project. Second, I sought to directly sequence the W chromosome by generating a library from DNA enriched for W chromosomes. Ultimately, new sequencing technologies emerged which made it feasible to generate whole genome shotgun sequences from a ZZ male. I used this male sequence as a basis for subtraction of male-female common sequences from the female whole genome shotgun sequence of the chicken.

Table 1: Chicken Satellite Repeat Families Adapted from Schmid et al. 2005

Family	Repeat Unit	Estimated Total
XhoI	0.7 kb	21 Mb
XhoI	1.1 kb	
EcoRI	1.2 kb	11 Mb
SspI	0.5 kb	6 Mb
Other	N/A	6 Mb
Total		44 Mb

Table 2: Chicken Z-W Gene Pairs

Reference	Gene Name
Ellegren, 1996	<i>CHD1</i>
Fridolfsson et al., 1998	<i>ATP5A1</i>
Hori et al., 2000	<i>HINT</i>
Itoh et al., 2001	<i>SPIN</i>
Mizuno et al. 2002	<i>SMAD2</i>
Handley, et al., 2003	<i>UBAP2</i>
Yamada, et al., 2004	<i>VCP</i>
Hillier, et al., 2004	<i>NIPBL, UBE2R2</i>
Nam and Ellegren, 2008	<i>HNRNPK, KCMF, MIER3, ZFR, ZNF532</i>

Table 3: Results of STS Testing

Method	STS		Success Rate	Use Unassigned Contigs?
	Tested	Specific		
Z-degenerate Genes	158	43	27 %	Y
Flow-sorted 454	77	15	19 %	Y
Solexa Subtraction	1225	94	7.67 %	Y
Deep WGS Coverage	67	5	7.5 %	Y
Flow-sorted Sanger	113	3	3 %	N
Ovary-specific ESTs	344	8	2.3 %	Y
Satellite Repeat Families	387	9	2.3 %	N
Deep BAC Coverage	1409	7	0.50 %	N
Total	3780	184	4.87%	

## **Results**

### **Satellite Repeat Families**

Three families of heterochromatic satellite repeats occupy large blocks of the W chromosome (Table 1) (Tone et al. 1982; Saitoh et al. 1991; Itoh and Mizuno 2002). These sequences were initially believed to be W-specific (Tone et al. 1982); as a result, some WGS contigs were erroneously assigned to the W chromosome because they contained these repeats (Hillier 2004; Granevitze et al. 2007). Although these repeats are present in other regions of the genome, they are still enriched on the W chromosome (Schmid et al. 2005).

The short repeat units of these satellite families are likely to make these regions of the chromosome impossible to sequence by any conventional means. Restriction enzyme cut sites will either be present in every short repeat unit, or only rarely in the entire array, causing gaps in library coverage. Thus, large-insert BAC and Fosmid clones are unlikely to contain these families. Even if these families are fully represented in large-insert clone libraries, the repeat units are short enough to cause the assemblies of individual clones to collapse.

Nevertheless, these arrays are important structural landmarks on the W chromosome. Each repeat family resides in a distinct domain along the W chromosome (Saitoh and Mizuno 1992; Solovei et al. 1998), and each family is likely to constitute a continuous tandem array. I wished to be able to obtain at least the edges of these arrays. To identify BAC clones spanning the edges of the arrays, I looked for BAC clones with one end sequence matching these repeats, and another end matching unique sequence in

the WGS assembly. I designed STS from the unique BAC end sequences and tested them for female-specificity by PCR (Table 3). This method was one of the least effective at generating STS markers. Of the 387 STS markers I designed, only 9 were female-specific. This would be expected if the satellite repeat families are dispersed in small arrays across most of the genome but are concentrated into only a few large, continuous arrays on the W chromosome.

### **Z-degenerate Genes**

Both avian and mammalian sex chromosomes show traces of evolution from autosomes (Fridolfsson et al. 1998; Lahn and Page 1999a; Skaletsky et al. 2003; Handley et al. 2004; Hughes et al. 2005; Nam and Ellegren 2008). A class of “X-degenerate” genes have survived the processes of Y chromosome degeneration and persist on the male specific regions of mammalian Y chromosomes as differentiated homologs of their X counterparts: 16 such genes on the human Y chromosome, and 12 on the chimpanzee Y chromosome (Skaletsky et al. 2003; Hughes et al. 2005). Similarly, the Z and W chromosomes of chickens are known to share 14 differentiated pairs of homologous genes (Table 2) (Ellegren 1996; Fridolfsson et al. 1998; Hori et al. 2000; Mizuno et al. 2000; Itoh et al. 2001; Handley et al. 2004; Hillier 2004; Yamada et al. 2004; Nam and Ellegren 2008).

I used the predicted coding sequences of genes from the chicken Z chromosome to search through unassigned WGS contigs for “Z-degenerate” genes that might be present on the W chromosome. I designed STS from suspected Z-degenerate contigs, and

tested them for female-specificity by PCR (Table 3). Out of 158 STS markers, 43 were female-specific, making this the single most effective method and the second most productive.

### **Ampliconic Sequences**

In addition to single-copy X-degenerate genes, mammalian Y chromosomes possess abundant ampliconic sequences (Conway et al. 1994; Skaletsky et al. 2003; Alföldi 2008; Hughes et al. 2010). Due to the presence of these amplicons, the gene content of Y chromosome is functionally coherent (Lahn and Page 1997). The human and chimpanzee Y chromosomes each possess a large set of multi-copy gene families expressed specifically in the testis (Lahn and Page 1997; Skaletsky et al. 2003; Hughes et al. 2010). The chicken W chromosome also possesses at least one ampliconic gene. The *HINTw* gene resides in a 5.6 kb repeat unit which is tandemly repeated about 40 times (Hori et al. 2000). *HINTw* is represented in the WGS assembly in collapsed contigs (Hillier 2004).

I reasoned that I might identify additional ampliconic sequences by searching chicken genome project data for sequences with much deeper coverage than autosomes. I examined both the depth of BAC clone coverage as well as the depth of shotgun sequencing reads.

The amplicons of mammalian Y chromosomes appear to be specialized to preserve or enhance male reproductive function (Lahn and Page 1997; Kuroda-Kawaguchi et al. 2001; Skaletsky et al. 2003; Alföldi 2008; Hughes et al. 2010).

Theorists have long predicted that genes advantageous to males should accumulate on the male-specific Y chromosome (Fisher 1931; Rice 1984), and this prediction applies equally to the accumulation of genes advantageous to females on W chromosomes. I reasoned that the gene content of the chicken W chromosome may mirror that of mammalian Y chromosomes and be specialized for genes expressed in the ovary. Therefore, I also looked for ampliconic sequences on the basis of ovary-specific expression.

#### Deep BAC Coverage

The chicken genome project produced a physical map of the chicken genome based on contiguous paths of BAC clone coverage (Ren et al. 2003; Wallis et al. 2004). Individual BAC clones were subjected to complete restriction enzyme digestion, and automated software was used to detect bands in the resulting “fingerprint” of each clone giving an estimate of clone size. BACs are assembled into contigs on the basis of matches between the bands of their fingerprints (Soderlund et al. 2000).

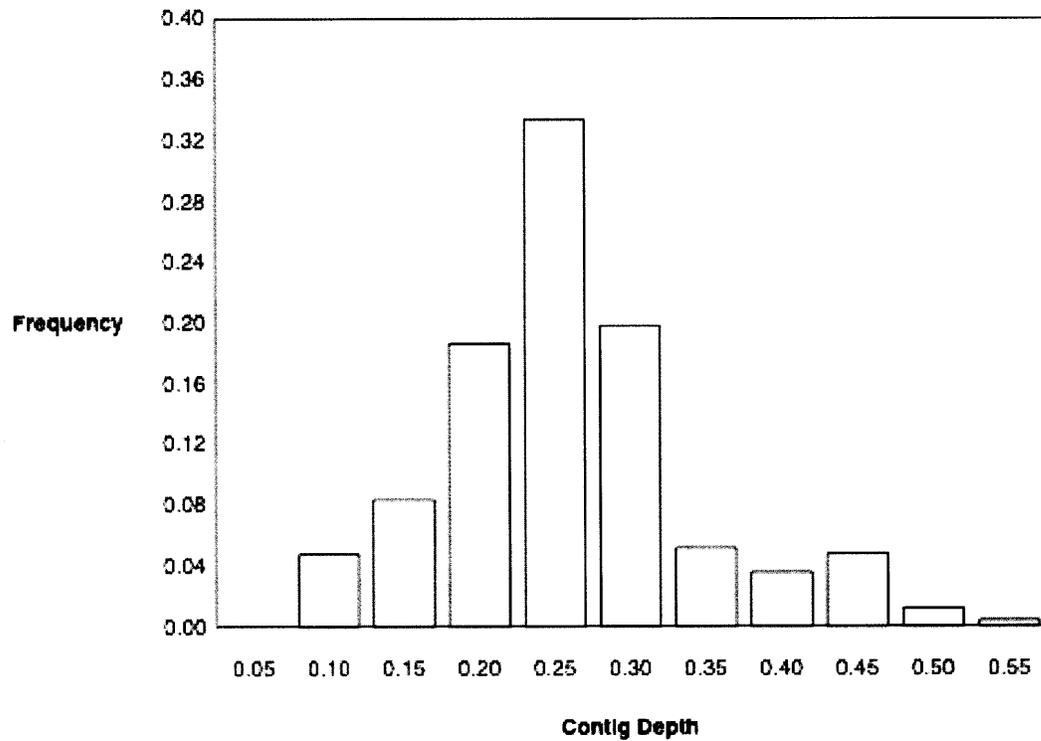
Depending on repeat unit length, ampliconic sequences may or may not be identified as deep fingerprint contigs. BAC clones that contain multiple short ampliconic repeat units will often generate simple fingerprints with only a few bands. Simple fingerprints do not give sufficient information to unambiguously identify overlapping clones, and thus these clones are excluded from contigs.

If an ampliconic repeat unit spans a greater distance than a single BAC, the BACs within the amplicon will generate complex fingerprints. Ampliconic BACs with complex

fingerprints can be assembled into a contig, but fingerprints typically will not provide enough information to distinguish BACs from different repeat units of the same amplicon. The resulting contig will be the length of a single repeat unit, but its depth will vary with the copy number of the ampliconic sequence.

I calculated the average depth of each fingerprint contig and selected the deepest contigs for further analysis (Figure 1). These contigs are greater than two standard deviations away from the average depth of all fingerprint contigs. I designed STS from the BAC end sequences of clones within these contigs and tested them for female-specificity by PCR (Table 3). This method was the least effective; out of 1409 STS markers, only 7 were female-specific (Table 3). If I had truly identified female-specific amplicons, the end sequences of several BACs in the same contig should have produced female-specific STS markers. Instead, the few STS markers I identified are likely the result of errors in BAC end sequence databases or fingerprint databases.

**Figure 1**



**Figure 1: BAC Fingerprint Contig Depth**

Frequency plot showing the relative abundance of BAC fingerprint contigs by coverage depth (arbitrary units). Depth was calculated by dividing the number of BACs in each contig by contig length as estimated by FPC (arbitrary units). Contigs with coverage depth greater than 0.40 were selected for further analysis.

## Deep Whole Genome Shotgun Coverage

The chicken genome was assembled by a WGS strategy, with an average read depth of 6.6X (Hillier 2004). Ampliconic sequences, like those of the Z amplicon, or the *HINTw* gene, collapsed in the shotgun assembly to form unusually deep contigs. I obtained a list of WGS contigs in the chicken genome assembly with read depth greater than 30x (Shiaw-Pyng Yang, pers. comm.). I designed STS from contigs that were not assigned to any chromosome, and tested them for female-specificity by PCR (Table 3). From 67 STS markers I identified 5 that were female-specific. These contigs are deeper than 30X in reads, and the single-copy W contig should receive 3.3X coverage of WGS reads, these ampliconic sequences are present in more than 9 copies. These contigs vary in size from 0.7 kb to 12.7 kb, indicating that this method has identified short, high-copy number amplicons similar to the *HINTw* array.

## Ovary-specific ESTs

To identify genes specifically expressed in the ovary, I aligned EST data to unassigned WGS contigs to identify contigs with multiple hits to ovary ESTs and no hits to ESTs from other tissues. I generated 557,764 ESTs from the adult ovary. Additionally, I generated 355,635 ESTs from adult chicken testes and used the 339,314 existing ESTs from a broad array of somatic tissues in both sexes (Boardman et al. 2002) to identify contigs with transcription in other tissues. I identified unassigned contigs with greater

than six hits to ESTs from adult ovary but no hits to ESTs from other tissues as potential W-linked contigs. I designed STS for these contigs and tested them by male vs. female PCR (Table 3). This method was one of the least effective, tied for next to last with selecting BAC ends on the basis of satellite repeat families. Of 387 STS markers, only 9 were female-specific.

### **Directly Sequencing Flow-sorted W Chromosomes**

In addition to identifying W-linked sequences based on the characteristics of other sex specific chromosomes, I also directly sequenced the W chromosome from flow-sorted material. The invention of flow-sorters in the 1970s made it possible to sort individual chromosomes on the basis of size (Gray et al. 1975; Gray et al. 1979). This technology enabled the resolution of the chicken karyotype by FISH when Masabanda and colleagues produced “chromosome paints” by amplifying flow-sorted chromosomes, including the W chromosome (Masabanda et al. 2004).

Darren Griffin of the University of Kent provided us with approximately 1000 flow-sorted W chromosomes. Because flow-sorting causes DNA breakage and produces very little material (1000 W chromosomes constitute only 60 pg of DNA), it is technically challenging to create large-insert libraries from flow-sorted material. Instead, I amplified, sheared, and cloned the flow-sorted chromosomes to produce a small insert library. In collaboration with the Washington University Genome Sequencing Center, I sequenced 14,000 clones from this library by Sanger sequencing, assembled the sequences into contigs, and searched for sequences which either matched unassigned

contigs, or those which had no match to any sequence in GenBank (Table 4). I designed STS from these sequences, and tested them for female-specificity by PCR (Table 3).

W-specific sequences were not well represented among the flow-sorted sequences. Of 113 STS markers I tested, only 3 were female-specific. This could be the result of contamination or biases in either amplification or library construction. Massively parallel pyrosequencing (454 sequencing) of flow-sorted chromosomes was successfully used to assess the completeness of the chimpanzee Y chromosome (Hughes et al. 2010). This procedure does not require a cloning step and produces reads with an average length in the 100-300 base-pair range, long enough to be suitable for marker design (Margulies et al. 2005).

I decided to apply this procedure to the W chromosome. I obtained 200,000 chromosomes in a second sort from Barbara Trask of the Fred Hutchinson Research Institute. The Washington University Genome Sequencing Center produced 641,863 reads by pyrosequencing. I mapped these reads back to the chicken WGS assembly; about 75% of the reads mapped to the chicken genome (Table 5). Unfortunately, 99% of the reads mapping to the chicken genome matched autosomes or the Z chromosome (Table 5). Those that did match the autosomes showed a tendency towards piling up over a few short sequences. For instance, 58% of the reads matched 5 short (less than 1 kb) sequences on chicken chromosomes 4 and 8. While pile-ups of 454 reads had been observed previously in the chimpanzee Y chromosome project, they were not as severe. Nevertheless, I was able to identify unassigned contigs with hits to flow-sorted material (Table 5). I designed STS from these contigs and tested them by male vs. female PCR

(Table 3). This method was the second most effective; 15 of the 77 contigs I tested produced female-specific STS markers.

**Table 4: Results of W Chromosome Flow-sort and Sanger Sequencing**

Initial Reads		14,000
Total Contigs		776
Removed from consideration		
	Environmental Contaminants	261
	Chicken Interspersed Repeats	290
	Chicken Autosomes and Z	100
	Chicken W	12
	Total	663
Candidate Sequences		
	Chicken Unassigned	12
	No hit in GenBank	101
	Total	113

**Table 5: Results of W Chromosome Flow-sort and 454 Sequencing**

Initial Reads		641,863
Removed from consideration		
	No hit to chicken genome	75,388
	Chicken Autosomes and Z	560,604
	Chicken W	488
	Total	636,480
Candidate Sequences		
	Chicken Unassigned	5,383

## **Solexa Subtraction**

Finally, I generated genomic resources from a male to serve as the basis for subtraction. New sequencing technologies made it feasible to rapidly and inexpensively generate whole genome shotgun data from a single individual. While the short read lengths employed by these new technologies require much greater depth to produce a WGS assembly (Li et al. 2009), a low coverage run provides enough information for electronic subtraction experiments.

In collaboration with Nancy Chen and Andrew Clark of Cornell University, I sequenced a male white leghorn chicken to 0.09X coverage in 36 base-pair Illumina/Solexa reads. This corresponds to approximately one read per kilobase of sequence. I mapped these short reads to the female WGS assembly to identify contigs with low coverage in male reads. To find an appropriate coverage cut-off, I fragmented finished BAC sequences into virtual contigs with the same size distribution as unassigned contigs and plotted the number of mapped reads as a function of contig length (Figure 2 & 3). I used Z-linked BACs as a negative control, representing sequences common to both males and females (Figure 2). W-linked BACs served as a positive control for female-specific sequences (Figure 3). I determined that contigs with coverage less than the cut-off were potential W-linked sequences (Figure 4). I selected unassigned contigs that met these criteria and designed STS to test by PCR (Figure 4, Table 3).

#### Figure 2: Male Solexa Data Mapped to Simulated Male-Female Common Contigs

Each blue circle represents a simulated contig plotted to show the number of hits from male chicken Illumina/Solexa reads as a function of contig size. The dashed line indicates the cut-off used to select real unassigned contigs for further analysis. Simulated contigs generated from the Z chromosome show that in sequences common to both males and females, the number of hits to contigs increase linearly as a function of contig size.

#### Figure 3: Male Solexa Data Mapped to Simulated Female-Specific Contigs

Each red circle represents a simulated contig plotted to show the number of hits from male chicken Illumina/Solexa reads as a function of contig size. The dashed line indicates the cut-off used to select real unassigned contigs for further analysis. Simulated contigs generated from W chromosome BACs in GenBank show that female-specific sequences have few, if any, hits in the male genome.

#### Figure 4: Male Solexa Subtraction to Identify W-Linked contigs

Each circle represents a genuine unassigned contig plotted to show the number of hits from male chicken Illumina/Solexa reads as a function of contig size. The cut-off for selecting candidate W chromosome contigs is shown as dashed line.

The cut-off is:  $\text{Contig length} > (\text{Hits} + 9) / 0.09$

Unassigned contigs from the female whole genome shotgun sequence appear like a mixture of the distributions plotted in Figures 2 & 3. Large contigs with few hits (those under the dashed line) were selected for STS marker design and testing. Contigs verified to be female-specific are plotted in black.

Figure 2

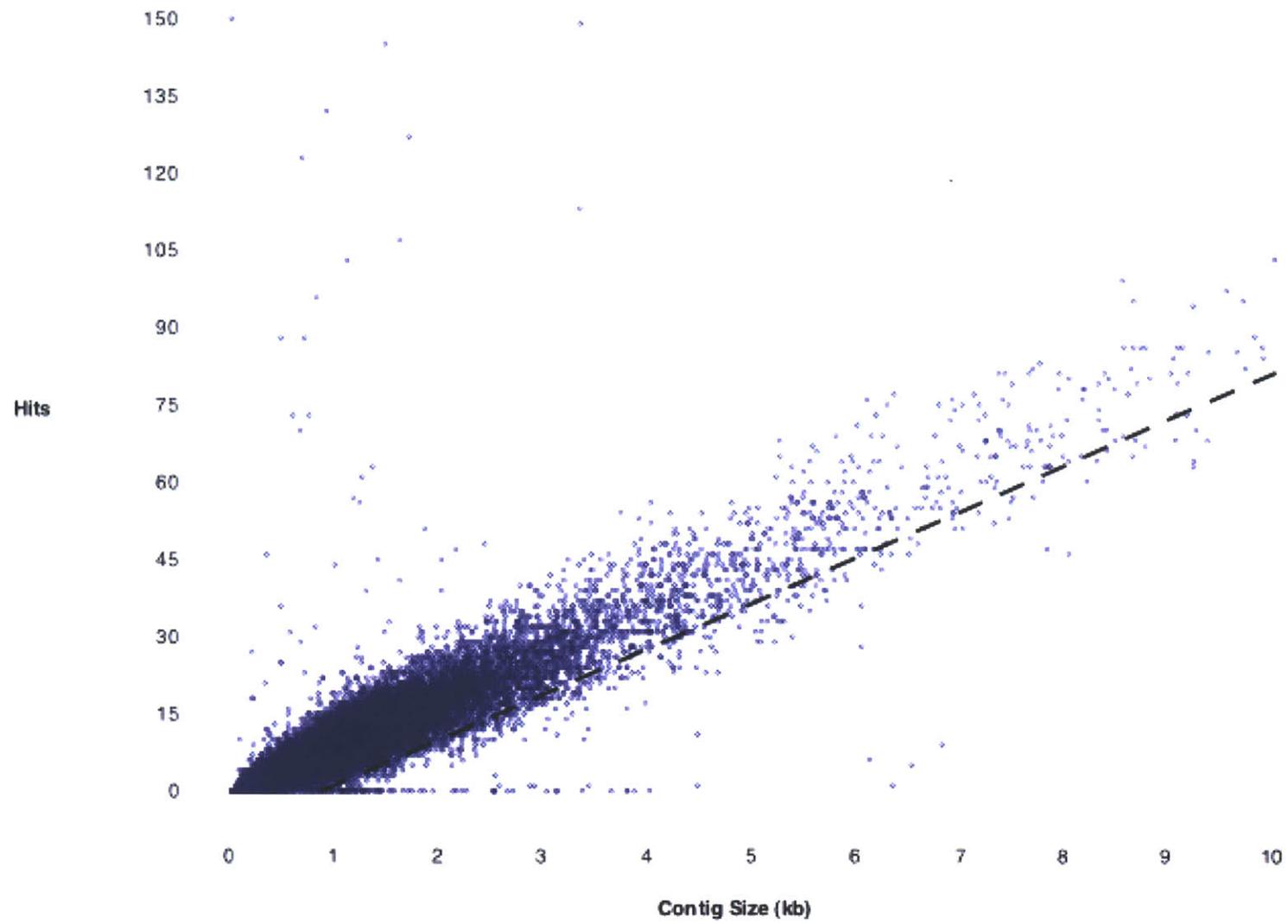


Figure 3

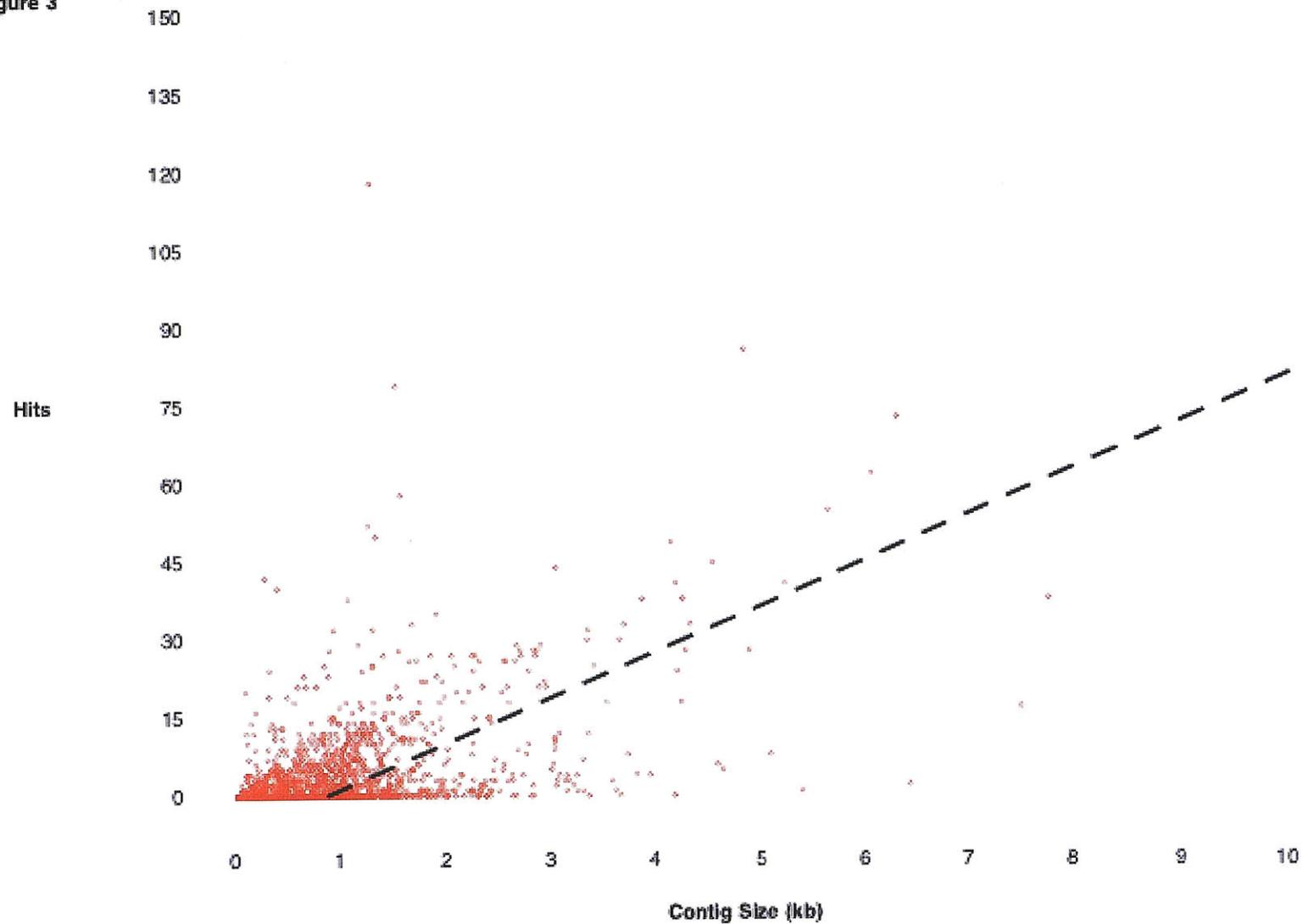
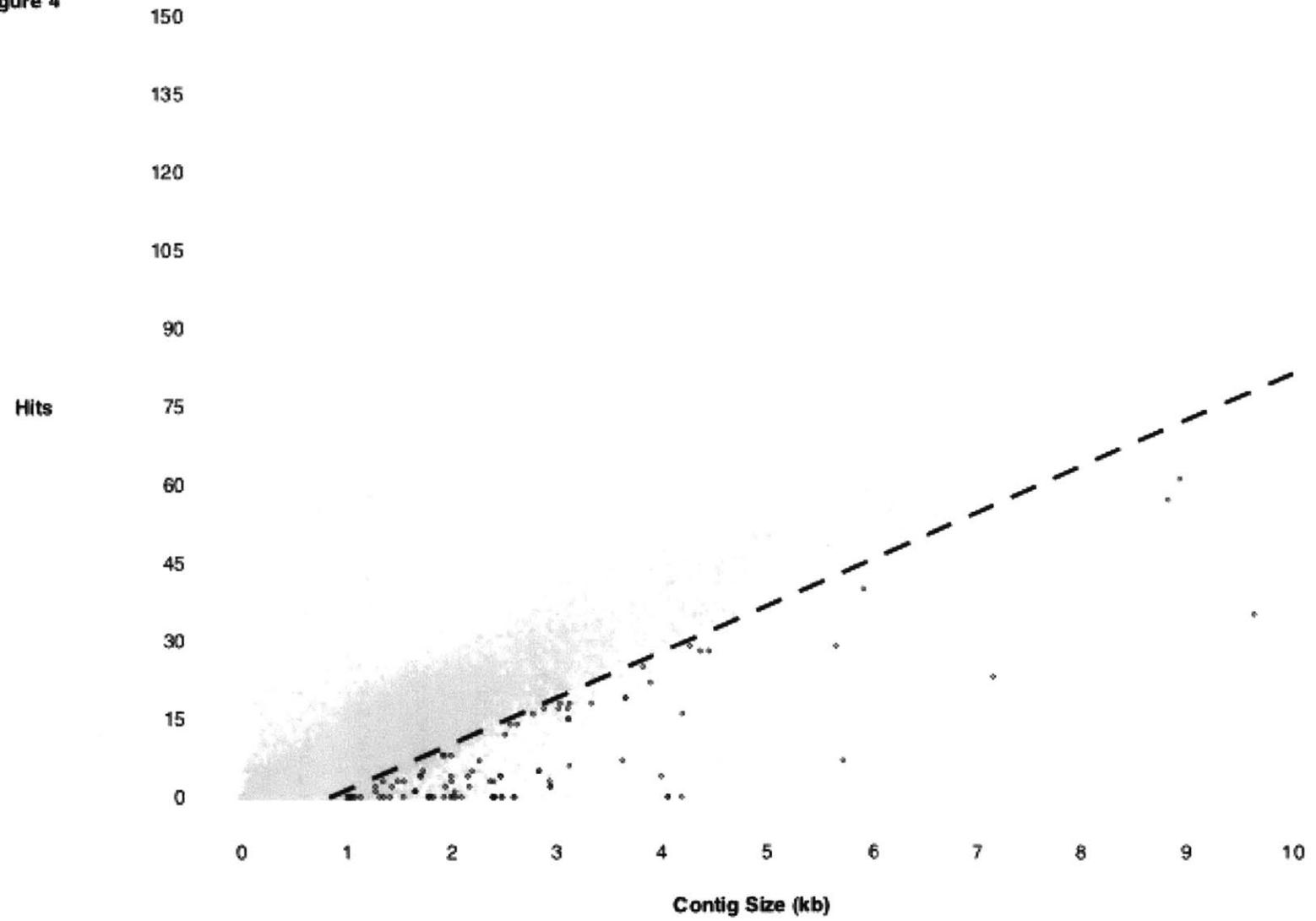


Figure 4



## ***Discussion***

In total, I produced 184 new female-specific STS markers that will be essential for further progress towards the complete sequence of the W chromosome. Each marker serves as a beachhead from which iterative mapping and sequencing efforts can expand. I tested a total of 3708 STS markers to find these 184 female-specific STS markers, giving a success rate of 4.87% (Table 3). This low overall success rate, as well as the variation in the success rate between STS marker design methods, may provide information about the structure of the W chromosome.

Half of the STS marker design methods used here appear to perform more poorly than choosing WGS contigs at random from the whole genome. The W chromosome represents about 3% of a diploid female genome (Schmid et al. 2005). But in most cases, STS markers were not designed from sequences selected from the genome as a whole, but only from WGS sequences not assigned to any chromosome (Table 3). These unassigned sequences constitute only about 10% of the genome (Hillier 2004). If we consider that W chromosome sequences are mostly unassigned, then as many as 30% of unassigned sequences should be from the W. Under these circumstances, the marker design process appears to be even more inefficient.

The low overall success rate may be partly explained by the prevalence of repeated sequences on the W chromosome. The satellite repeat families of the W chromosome will be poorly represented in the WGS assembly for two reasons: first,

cloning biases may reduce their representation among shotgun sequencing libraries; second, PCAP, the assembly algorithm used for the WGS sequence of chicken, ignores reads with greater than 60x coverage during the assembly process (Huang et al. 2003). Assuming that these repeats account for about 70% of the W chromosome sequence (Schmid et al. 2005), and that most unassigned sequences are nearly unique, then the remaining W chromosome sequences should constitute about 1% of the diploid female genome, or, at most, 10% of unassigned sequences.

Other factors complicate the process of designing specific STS markers from the remaining W chromosome sequences in unassigned contigs. Unassigned sequences are enriched for genome-typical interspersed repeats that complicate WGS assembly. Interspersed repeats make up 38.7% of unassigned sequences compared to 9.4% for the genome as a whole. The W chromosome also shares some homology with the Z chromosome, which is evident from my success at designing STS markers from contigs containing Z-degenerate genes. If the Z and W chromosomes diverged in a stepwise fashion like the mammalian X and Y chromosomes (Lahn and Page 1999a; Handley et al. 2004; Ross et al. 2005; Nam and Ellegren 2008), more recently diverged sequences may not produce specific STS markers. Recent transpositions from elsewhere in the genome will also reduce the amount of truly female-specific sequence. The human Y chromosome has gained several genes from other chromosomes through transposition events (Page et al. 1984; Saxena et al. 1996; Mumm et al. 1997; Schwartz et al. 1998; Lahn and Page 1999b). The *KCNA1w* gene on the W chromosome appears to be the result of a recent transposition from chicken chromosome 1 (unpublished observations).

Taking all these factors into account, I suggest that less than 5% of unassigned sequences may be capable of generating a female-specific marker.

Several of the STS marker design methods performed well in spite of these inherent difficulties. Half of the STS marker design methods exceeded a 5% success rate, indicating that they enriched for W-specific sequences (Table 3). The most successful method, searching for Z-degenerate genes, entailed 5-fold enrichment for W chromosome sequences. Interestingly, next two most successful methods should give a relatively unbiased representation of the W chromosome, while the search for unusually deep WGS contigs should enrich for ampliconic sequences.

Of all the methods for identifying female-specific sequences, subtraction was the most powerful. Searching for Z-degenerate gene sequences had the highest success rate, but quickly exhausted all contigs with identifiable homology to the Z chromosome. The Solexa subtraction approach produced 94 STS markers, twice as many markers as were produced by searching for Z-degenerate genes. And, unlike searching for Z-degenerate genes, Solexa subtraction required no prior knowledge of the Z chromosome sequence. The STS markers generated by subtraction are also likely to be more random, since they are not confined to areas of homology with the Z chromosome. Low read depth in the male Solexa data restricts my ability to identify female-specific contigs smaller than 1000 base pairs. Additional coverage from the male genome could be used to increase my ability to identify shorter contigs.

Directly sequencing the W chromosome from flow-sorted material was much less productive than I had anticipated. Like the subtraction method, the flow-sort requires no prior knowledge about the sequence of the W chromosome and presumably produces a

more random distribution of STS markers. However, both the purity of the sort and the proportion of the W chromosome that is female-specific limit the success of this method. The small amount of DNA produced by flow-sorting makes amplification necessary, and amplification can introduce additional biases. Designing markers from unassigned contigs on the basis of hits to 454 reads from flow-sorted W chromosomes had a 19% success rate, but this comes at the cost of rejecting 99% of all reads. Flow-sorting will only be effective for other sex-specific chromosomes if they can be sorted in greater abundance and higher purity.

STS marker design methods that rely on known features of sex-specific chromosomes yield not only STS markers, but also information about the structure and evolution of the W chromosome. The Z-degenerate sequences of the W chromosome may be much more extensive than corresponding X-degenerate sequences on the human and chimpanzee Y chromosomes. The ampliconic sequences identified on the W chromosome have shorter repeat units than those of mammalian Y chromosomes. Contrary to expectations, the genes in W chromosome amplicons are probably not predominantly expressed in the adult ovary.

The most successful STS marker design strategy was to identify contigs with homology to Z-linked genes; 27% percent of these STS markers confirmed as female-specific. This method detected homology to 26 different Z-linked genes. If all of these genes are intact, the Z-degenerate genes of the W chromosome will be nearly equal to the number of all gene families on the human Y chromosome (Skaletsky et al. 2003). A variety of processes cause the loss of ancestral genes from the sex-specific chromosome over time (Bachtrog 2008). The ZW sex determination system is conserved across all

birds (Nanda et al. 2008), which diverged around 120 million years ago (van Tuinen and Hedges 2001), while the XY system is found only in marsupials and eutherians, diverged 180 million years ago (Kumar and Hedges 1998; Woodburne et al. 2003). The high number of Z-degenerate genes could be viewed as consistent with the younger age of the avian sex chromosomes. However, comparisons between the degeneration of the chicken W chromosome and mammalian Y chromosomes are complicated by the stepwise divergence implied by the existence evolutionary strata (Bachtrog 2008). Different portions of the mammalian sex chromosomes began diverging at different times in the past (Lahn and Page 1999a; Ross et al. 2005), and the strata of the chicken Z and W chromosomes have not been fully characterized.

Searching for deep coverage in whole genome data reveals information about the ampliconic sequences of the W chromosome. High-copy, long repeat unit amplicons similar to those of the mouse Y chromosome should appear as unusually deep BAC contigs (Alföldi 2008). The 7 female-specific STS markers out of the 1409 designed by this method are likely to be the result of a handful of BAC clones erroneously identified with fingerprints from these contigs. If these contigs were truly female-specific, I would have obtained hundreds of female-specific STS markers. The low success rate of designing W-specific STS markers in these deep BAC contigs suggests that the chicken W chromosome does not have female-specific amplicons that resemble those of the mouse Y chromosome. I was not able to investigate the prevalence of low-copy number, long repeat unit amplicons, like the human AZFc region. Palindromes on the sex chromosomes will have BAC coverage equivalent to the single-copy sequences on autosomes in a BAC library derived from a diploid heterogametic individual.

High-copy number, short repeat unit amplicons are also indistinguishable by BAC coverage. The BAC contigs that contain the Z amplicon have 0.2X coverage, which places them in the middle of the depth distribution for BAC fingerprint contigs (Figure 1). Interrogating deep WGS contigs had a success rate of 7.5%, a modest enrichment for female-specific STS markers comparable to that obtained by Solexa subtraction (Table 3). The short amplicons we identified among deep WGS contigs are likely similar to the known structure of the *HINTw* with short repeat units with tens of copies (Hori et al. 2000). Together, the 5 contigs I identified represent about 21 kb of non-redundant sequence. The depth of these contigs indicates that each is present in more than 9 copies, which means these amplicons comprise about 190 kb of the W chromosome sequence. Together, these newly-identified amplicons make up 1% of the euchromatic portion of the W chromosome, effectively doubling the amount of known ampliconic sequence. Because of their short repeat units, an iterative mapping and sequencing approach may be unable to resolve this type of amplicon.

Ampliconic sequences in the human genome are predominantly expressed in the adult testes; I found only 8 W-specific sequences with expression restricted to the adult ovary. There are two possible explanations. The first is that these sequences are ampliconic and present in multiple copies in the genome, but have collapsed in the WGS assembly. The second possibility is that chicken W amplicons are not expressed in the adult ovary, but in other tissues or developmental stages that have an impact on female fertility. Chickens invest large amounts of energy into their eggs after ovulation. Both the magnum, where the albumen is added to the egg, and the shell gland may be tissues where W ampliconic genes are expressed. Unlike the adult testis, the adult ovary does not

contain mitotically dividing germ cells. In both birds and mammals, only the embryonic ovary contains proliferating germ cells. Thus, the embryonic ovary may have an expression profile with greater parallels to the adult testis. Further characterization of these tissue types will be necessary to resolve these questions.

While subtraction is a powerful approach to developing STS markers, alternative approaches relying on the known properties of sex-specific chromosomes yield useful information regarding the structure of the W chromosome. In addition to extensive heterochromatic arrays, the W chromosome has a large Z-degenerate region and multiple ampliconic sequences. The W chromosome shares extensive homology with the Z chromosome, with a Z-degenerate region spanning twice as many genes as the X-degenerate region of the human Y chromosome. The W chromosome is not likely to contain long repeat unit, high-copy amplicons of the type seen on the mouse Y, but long repeat unit, low-copy amplicons, similar to the type that exist on the human and chimpanzee Y chromosomes, are not excluded. The short repeat units of known W chromosome amplicons are likely to create difficulties, even for an iterative mapping and sequencing approach.

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## **Methods**

**STS Marker Design.** I designed all STS markers using Primer-3 (Rozen and Skaletsky 2000) on repeat-masked sequences (Smit et al. 1996-2004).

**Male versus Female PCR.** I performed PCR in duplicate on DNA from 2 males and 2 females of the sequenced UCD001 Red Jungle Fowl strain (Maintained by Mary E. Delany of University of California, Davis). I amplified 0.1 $\mu$ g of genomic DNA through 40 cycles of PCR with an annealing temperature of 55°C.

**Satellite Repeat Families.** I aligned BAC end sequences to the XhoI, EcoRI, and SspI repeat units using BLAST (Altschul et al. 1990).

**Z-degenerate Genes.** I aligned predicted cDNA sequences from the Z chromosome to unassigned WGS contigs using BLAT (Kent 2002).

**Deep BAC coverage.** I identified BAC fingerprint contigs with deep coverage using the databases generated by FPC (Soderlund et al. 2000).

**ESTs.** I generated 454 ESTs (SRA# SRP000097) as previously described (Torres et al. 2008). I extracted total RNA extracted with Trizol (Ambion) from adult ovary and adult testis of white leghorn chickens (Charles River Labs). I also used EST sequences from the BBSRC ChickEST database (Boardman et al. 2002). I compared ESTs to the chicken genome using BLAT.

**Flow-sorted Chromosomes.** For Sanger sequencing, I amplified 1000 W chromosomes using the GenomiPhi kit (GE Healthcare). Flow-sorted, amplified material was subjected to shearing by nebulization to an average size of 400 base pairs. Size fractionated DNA was blunted and cloned into the pSMART HC-amp vector using the CloneSmart Kit (Lucigen).

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## **Chapter 4: Conclusions and Future Directions**

(Adapted from: “Reconstructing the Evolution of Vertebrate Sex Chromosomes,” a review article submitted to Cold Spring Harbor Symposia on Quantitative Biology)

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## ***Conclusions***

In the past ten years, genomic data from vertebrate sex chromosomes have allowed reconstructions of the process of sex chromosome evolution, and these reconstructions have revealed surprising exceptions to Muller's theory. The sequences of the human and chimpanzee Y chromosomes have led to a new understanding that Y chromosomes are continually renovated rather than condemned to decay. Likewise, reciprocal comparisons of the finished sequences of the chicken Z and human X chromosomes to the orthologous autosomal regions in the other species have revealed substantial innovations in gene content, as well as an enormous expansion of intergenic regions, on what had been assumed to be unchanging chromosomes. Our preliminary analyses of the W chromosome revealed new ampliconic sequences, demonstrating that ampliconic sequences are a general feature of vertebrate sex chromosomes. In the same way that the development of population genetics reshaped the description of Y degeneration under Muller's theory, it is necessary to amend Muller's hypothesis in light of genomic data to account for the emergence of ampliconic sequences.

A greater understanding of the forces that generate amplicons will result from a more complete description of their function. One possibility is that the high copy number of ampliconic genes reflects selection for increased expression. Ampliconic genes might be duplicated to facilitate high levels of transcription, as has been proposed for ribosomal RNAs, transfer RNAs, and histone genes (Finnegan et al. 1978; Kedes 1979; Long and Dawid 1980). The high frequency of transcription of mouse X ampliconic genes despite the general post-meiotic silencing of single-copy genes on the X chromosome would be

consistent with this hypothesis. Alternatively, repetitive DNA structures may provide a chromatin environment that is permissive for gene expression in germ cells. This would be consistent with the widespread expression of ampliconic genes in the testis. The low number of W chromosome contigs identified by searching for adult ovary specific transcription may indicate that this expression is optimized not just for germ cells, but for germline stem cells. As an alternative to hypotheses based on gene expression, amplicons may play a role in preserving functional gene copies in regions where crossing over with a homologous chromosome rarely, if ever, occurs. The amplicons on the Y chromosome of primates engage in gene conversion, providing a mechanism to preserve the function of genes in the face of chromosome-wide degradation. Ideally, a unified theory would explain why amplicons are more prevalent on sex chromosomes than in the rest of the genome, but it is entirely possible, though aesthetically unfortunate, that amplicons are present on different sex chromosomes for different reasons.

While escape from post meiotic silencing on sex chromosomes could serve as a compelling explanation for the location of amplicons in mammals, it does not explain the presence of the Z amplicon in the chicken. Unlike XY male mammals, ZW female birds do not appear to silence unpaired chromosomes during meiosis (Solari 1977). During the diplotene stage of female meiosis, the Z chromosome and W chromosome of chickens are highly transcriptionally active, forming lamp-brush chromosomes (Hutchison 1987). If ampliconic sequences exist in birds, they will require an alternative explanation.

An alternative to the avoidance of meiotic silencing is that sex-linked amplicons are the result of sexually antagonistic selection. Sexually antagonistic genes are those that produce a phenotype which benefits one sex more than the other. These traits are more

likely to become fixed on sex chromosomes than on autosomes because the sex chromosomes are not evenly exposed to selection in both sexes (Rice 1984). Male benefit genes should accumulate on Y chromosomes, and female benefit genes should accumulate on W chromosomes. The case for X chromosomes and Z chromosomes is more complex. Dominant traits that benefit the homogametic sex should accumulate because they are exposed to selection twice as often in the homogametic sex. Recessive traits that benefit the heterogametic sex should accumulate because they are always exposed to stronger selection in the heterogametic sex than in the homogametic sex, where they can be masked by other alleles. Eventually sexually antagonistic genes are expected to evolve sex-limited expression to avoid costs to the sex where they are not beneficial (Rice 1984). As a result, one would expect to find that sex chromosomes would become enriched for genes expressed only in one sex.

Sexually antagonistic selection is an attractive explanation for the enrichment of amplicons on the sex chromosomes, but there are incongruities with the existing data. There do not appear to be any female-benefit amplicons on X chromosomes, where they might be expected to arise because the X chromosome is exposed to more frequent selection in females than in males. All known ampliconic sequences on X chromosomes are expressed in the testis. The presence of testis-expressed amplicons on X chromosomes is striking because gene duplication was classically imagined as a dominant gain of function mutation (Muller 1932), but the theory of sexually antagonistic selection predicts that only recessive male-benefit alleles should accumulate on X chromosomes. If sexually antagonistic selection is responsible for the generation of testis-expressed amplicons, then gene duplication on the X chromosome may be preceded

by the evolution of male-limited expression, so that duplications are only subjected to selection in males.

Amplicons could also be involved in intragenomic conflict through segregation distortion in the germline. Autosomal segregation distortion due to the t-haplotype of chromosome 17 in mice is well known (Silver 1993). On the sex chromosomes, a segregation-distorting locus could function as a sex ratio distorter. Since most organisms are constrained to a 1:1 sex ratio, any sex ratio distorter that meets with success immediately increases the selective advantage for a second distorter to restore the sex ratio to equilibrium (Fisher 1930; Nur 1974). This could lead to an evolutionary arms race between sex chromosomes. There are indications that the mouse X chromosome and Y chromosome are involved in segregation distortion; deletions on the long arm of the mouse Y chromosome lead to an excess of female offspring, suggesting that the multi-copy genes on the mouse Y chromosome may suppress X chromosome segregation distortion (Conway et al. 1994).

While the segregation distortion model may be applicable to the situation in mammals, it is not as applicable to birds. If amplicons are primarily generated as a result of intragenomic conflict between the sex chromosomes, birds and snakes would be expected to accumulate genes that are expressed during female meiosis to influence the partition of the Z and W chromosomes between the oocyte and the first polar body (Rutkowska and Badyaev 2008). However, the genes of the Z amplicon are expressed in the testis, not the ovary. If the Z amplicon is involved in segregation distortion in males, it can only be because of competition between Z chromosomes.

Muller's theory must be amended to explain the convergent intergenic bloat and high density of LINEs on the human X chromosome and the chicken Z chromosome. Mary Lyon had proposed that the abundance of LINE elements on the X chromosome were part of the mechanism of X inactivation. She hypothesized that LINEs acted as way-stations for the spreading of heterochromatin from the X inactivation center (Lyon 2000; Ross et al. 2005). This theory would not explain the high density of LINEs on the chicken Z chromosome, which is not subject to inactivation in males (Schmid et al. 1989; McQueen et al. 2001; Kuroiwa et al. 2002). It is possible that the recurrent insertion of retro-elements could facilitate the evolution of the regulatory sequences required for dosage compensation, but the existence and extent of dosage compensation in birds is a contested issue (Ellegren et al. 2007; Itoh et al. 2007; Melamed and Arnold 2007; Mank and Ellegren 2008).

An alternative hypothesis revolves around the correlation between LINE element density and regions of low recombination (Montgomery et al. 1987; Dolgin and Charlesworth 2008). If LINE element distribution is primarily controlled by the removal of LINEs by gene conversion, then regions of reduced crossing over, like the sex chromosomes, should have elevated levels of LINE density. However, the density of LINEs on the human X chromosome and the chicken Z chromosome is far in excess of what would be expected based on the correlation between LINE density and local rates of crossing over on autosomes. Alternatives to explanations of LINE density based on dosage compensation or crossover rate are also possible. It may be that the sex chromosomes are favored for LINE element insertion on the basis of a unique chromatin

state, or that increases in transposable element insertions contribute to the suppression of crossing over between incipient sex chromosome pairs.

### ***Future Directions***

Additional insights into the forces that shape the evolution of amplicons can only come with additional high quality finished sequencing efforts. Ampliconic sequences could not have been described without the BAC-based, “clone-by-clone” methods used to determine the sequence of the human sex chromosomes. Shotgun sequencing technologies collapse highly identical repeats into single contigs, obscuring rather than revealing their structure and organization. This deficiency of shotgun methods only worsens with shorter read lengths. Only BAC-based sequencing provides the positional information needed to disentangle long repeats. While these BAC-based sequencing technologies are slower and more expensive than their whole genome shotgun counterparts, they have resulted in insights that would have been impossible to obtain in any other way, and which were unanticipated by a century of theory.

We can look forward to the availability of additional sex chromosome sequences that will enable us to extend our analyses of sex chromosomes. Sequencing efforts for several mammalian Y chromosomes are underway. These will permit comparisons of Y chromosomes over a range of evolutionary time scales: from the divergence of human populations through primate evolution, to the very base of the mammalian tree. The finished sequence of the chicken W chromosome will enable the first intra-specific comparisons between the Z and W chromosomes and will reveal whether the course of W

evolution has been parallel to that of the degeneration and elaboration of the human Y chromosome. A full description of ampliconic sequences on the W chromosome is also likely to be revealing. There are at least two multi-copy gene families on the W chromosome, but they are ubiquitously expressed and their genomic structure is unknown. W amplicons, if they exist, may display a functional coherence akin to that of the human Y, revealing genes that are essential for female fertility.

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