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Towards A Unified Model Of Sperm Chromatin Structure

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TOWARDS A UNIFIED MODEL OF SPERM CHROMATIN STRUCTURE

by

GRAHAM D. JOHNSON

DISSERTATION

Submitted to the Graduate School

of Wayne State University,

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Advisor

Date

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LIST OF ABBREVIATIONS

3C	Chromosome Conformation Capture
Ankmy1	Ankyrin Repeat and MYND Domain Containing 1
Boris	Brother of Regulator of Imprinted Sites
Cabyr	Calcium-Binding Tyrosine Phosphorylation-Regulated Protein
ChIP	Chromatin immunoprecipitation
ChIP-seq	Chromatin immunoprecipitation and DNA-sequencing
Cs/Tx	Detergent Demembranated, Sucrose Gradient-Fractionated
CSH	Cross-Species Hybridization
Ctcf	CCCTC Binding Factor
Cyp2c38	Cytochrome P450 2c38
DFF	DNA Fragmentation Factor
DT	Dorsal Tip of the Perinuclear Theca
EGA	Embryonic Genome Activation
ERCC	External RNA Controls Consortium
ES	Equatorial Segment
Esx1	Extra-Embryonic Tissue-Spermatogenesis-Homeobox Gene 1
Evi5l	Ecotropic Viral Integration Site 5-like
Foxa3	Forkhead Box A3
Foxj2	Forkhead Box J2
Gng5	Guanine Nucleotide Binding Protein (G protein), Gamma 5
GRC-RNAs	GAA Repeat-Containing RNAs
HIRA	Histone Cell Cycle Regulator
Hox	Homeobox
IAM	Inner Acrosomal Membrane
ICSI	Intracytoplasmic Sperm Injection
Lamp2	Lysosome-Associated Membrane Glycoprotein 2
LINEs	Long Interspersed Nuclear Elements
lncRNA	Long Non-coding RNA
Malat1	Metastasis Associated Lung Adenocarcinoma Transcript 1
MAR	Matrix Attachment Region
MNase	Micrococcal Nuclease
mRNP	Ribonucleic Protein Particles
MS	Mitochondrial Sheath
Ndufc1	NADH dehydrogenase [ubiquinone] 1 subunit C1
OAM	Outer Acrosomal Membrane
PAS-PT	Post-Acrosomal Sheath of the Perinuclear Theca
Pax6	Paired Box6
PcG	Polycomb Group
PGK	Phosphoglycerate Kinase 1
Pou2f1	POU domain, Class 2, Transcription Factor 1
PP	Principle Piece of the Sperm Tail

PRM	Protamine
PT	Perinuclear Theca
PWM	Position Weight Matrices
Rest	RE1-Silencing Transcription Factor
RNA-seq	RNA Sequencing
ROSI	Round Spermatid Injection
RPKM	Reads Per Kilobase Per Million Mapped Reads
RPM	Reads Per Million Uniquely Aligned Reads
rRNA	Ribosomal RNA
SAL-PT	Sub-Acrosomal Layer of the Perinuclear Theca
SS	Sonicated Spermatozoa
SSP	Short Suspensor
TAD	Topologically Associated Domain
TG	Transgenic
Tlx2	T Cell Leukemia, Homeobox 2
TNP	Transition Protein
TPM	Transcripts Per Million
TTD-PCR	Terminal Transferase-Dependent PCR
VS	Ventral Spur of the Perinuclear Theca
ZGA	Zygotic Genome Activation

CHAPTER ONE

THE SPERM NUCLEUS: CHROMATIN, RNA AND HIGHER ORDER CHROMATIN STRUCTURE

This chapter was adapted from the following publication:

Johnson GD, Lalancette C, Linnemann AK, Leduc F, Boissonneault G and Krawetz SA. (2011). "The sperm nucleus: chromatin, RNA, and the nuclear matrix." *Reproduction* 141(1): 21-36.

I. Summary

Within the sperm nucleus the paternal genome remains functionally inert and protected following protamination. This is marked by a structural morphogenesis that is heralded by a striking reduction in nuclear volume. Despite these changes, both human and mouse spermatozoa maintain low levels of nucleosomes throughout the genome. These regions may be necessary for organizing higher order genomic structure through interactions with a subset of chromatin regulatory proteins which persist following nuclear remodeling. The promoters of this transcriptionally quiescent genome are differentially marked by modified histones that may poise downstream epigenetic effects. This notion is supported by increasing evidence that the embryo inherits these differing levels of chromatin organization. In concert with the suite of RNAs retained in the mature sperm they may synergistically interact to direct early embryonic gene expression. Irrespective, these features reflect the transcriptional history of spermatogenic differentiation.

II. Background

Unlike the vast size of the oocyte the diminutive sperm may have initially seemed unlikely to carry information in excess of its genomic cargo. Indeed, our ability to appreciate the contrary only began to gradually develop over the last two decades. This has been due to several factors, primarily reflecting the distinct nuclear environment of the mature spermatozoon. The sperm genome is repackaged into a near crystalline-state which has proven resistant to dissection. This extensive remodeling both protects the paternal genome and is requisite for the characteristic reduction in nuclear volume which occurs as the head takes on a unique shape [reviewed in, 9]. The assumption that sperm occupy a limited developmental role compared to oocytes has in part

been due to these physical constraints and the appropriate enabling physical, chemical and biological technologies [10].

Despite the near-complete packaging of the sperm genome as protamine-associated DNA, it is increasingly clear that specific regions retain a somatic-like structure [reviewed in, 11, 12-15]. In some cases, modified histones differentially mark these regions in a manner reminiscent of the epigenetic states observed in somatic or stem cells [14, 16]. This feature of sperm chromatin has been suggested to influence the order that genes are repackaged into a nucleosomal bound state and/or expressed following fertilization [reviewed in, 8, 17]. Additionally, sites of histone retention are likely to provide insight into the transcriptional history of spermatogenesis.

RNAs produced during this prior window of transcription are retained in sperm and delivered to the oocyte. The biological role of these transcripts post-fertilization remains a subject of debate. Regardless of their function several of these molecules are currently being developed as biomarkers of male fertility [18-21]. Isolation and characterization of sperm RNAs from fertile and affected men is expected to highlight the importance of the sperm transcriptome to the reproductive health of men [20, 21].

The notion that the male gamete merely delivers paternal DNA to the oocyte is falling by the wayside. This reflects several developments pertaining to the possible retention in sperm of three additional forms of actionable information: chromatin, RNA, and higher order chromatin structure. These potential sources of heritable information will be further expanded upon below.

III. Sperm Chromatin

Spermatogenesis is characterized by ordered histone replacement. As spermatogonia commit to this differentiative pathway they have already begun to incorporate testis-specific histone variants into their chromatin [Figure 1.1; 22, 23, 24]. Synthesis and deposition of these proteins peaks during meiosis [25]. Subsequently, in round spermatids, the majority of histones are first replaced by the transition proteins and next by protamines (PRMs) supported by the

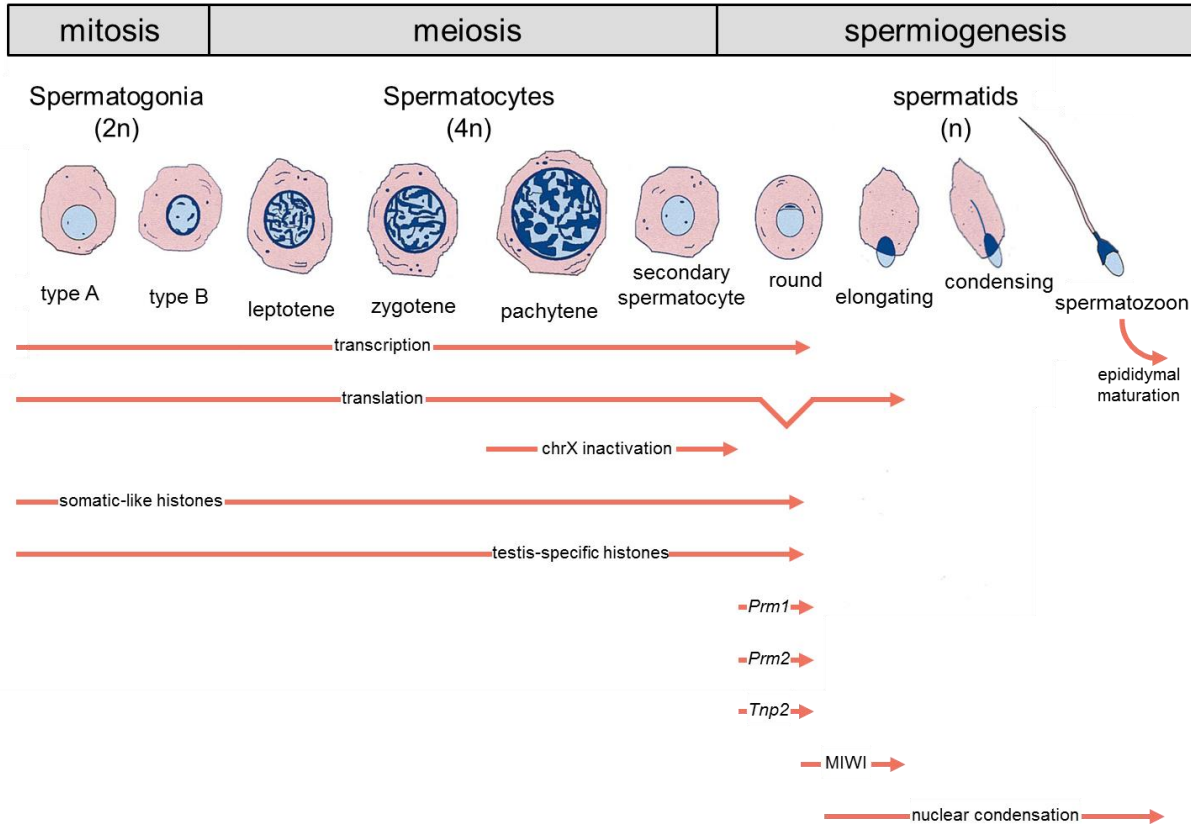


Figure 1.1 Overview of spermatogenesis. Spermatogenesis initiates with clonal expansion of proliferative spermatogonia. Some of these cells develop into type B gonia which commit to meiosis dividing to produce a primary spermatocyte. Throughout this developmental window there is active transcription and translation as well as the deposition of testis-specific histone variants. Following a series of reductive divisions a single spermatocyte results in 4 haploid round spermatids. The protamines and transition proteins are transcribed in the round spermatids but are then then stored as ribonucleic protein particles (mRNPs). Packaged as mRNPs a subset of spermatogenic RNAs evade targeted degrade by the piRNA (MIWI) mediated decay pathway. Following their translation in elongating spermatids, protamine binding condenses the genome while cytoplasmic expulsion further reduces cellular volume. Following condensation the cell is transcriptionally and translationally silent. As the mature gamete leaves the testis and encounters the epididymis it further condenses. Spermatozoa may also engage in signaling pathways through the exchange of vesicles found within the fluid of the male reproductive tract [Figure is adapted from 7].

action of testis-specific histone variants. Some histone variants, as well as canonical histones, are maintained throughout the remaining stages of spermatogenesis [26-34, reviewed in 35, 36, 37].

Chromatin remodeling requires regulated post-translational modifications of histones including acetylation [38-42], ubiquitination [43-45], methylation [46] and phosphorylation [47-49].

Among these modifications, to date, the global hyperacetylation of histones is the best characterized. Incorporation of these marks destabilizes nucleosomes in preparation for their replacement by the transition proteins and, ultimately, by the protamines [50, 51].

Hyperacetylation is essential in mice and men as perturbation is correlated with defective spermatogenesis [52, 53]. This is supported by the observation that species maintaining chromatin in a somatic-like state do not exhibit elevated levels of histone acetylation in sperm [42]. For example, trout spermiogenesis spans several weeks during which spermatids exhibit high steady state levels of hyperacetylation. Extended maintenance of this modification prior to protamination suggests additional factors are needed to complete nuclear remodeling [42, 54]. This view is supported by the observation in *Drosophila* that even precocious hyperacetylation does not prematurely induce the transition to a condensed chromatin state [55].

Even though there are potentially several pathways regulating initiation of chromatin remodeling, inhibition of the ubiquitin proteasome pathway by loss of an ubiquitin ligase can block global histone acetylation, degradation, and protamine deposition, resulting in sterility [45, 56, 57]. In these studies mature spermatozoa were low in number and exhibited altered morphologies, reminiscent of teratazoospermia. Indeed, microarray analysis of sperm RNAs from teratazoospermic patients presents as a severe disruption of the ubiquitination pathway [58].

During murine and human protamination, histones are replaced first by the transition proteins (TNPs); then, they are subsequently displaced by the PRMs [Figure 1.1; 59]. Binding of these small arginine-rich proteins to the negatively charged phosphodiester backbone of the double helix abolishes the electrostatic repulsion between proximal chromatin strands permitting their folding into large globular structures [60]. These structures are further stabilized by inter- and intramolecular disulfide bridges compressing the genome into a semi-crystalline state as the spermatozoon transits through the epididymis [Figure 1.1; 61]. The resulting mature human sperm nucleus is now condensed to $1/13^{\text{th}}$ the size of that of the oocyte [62].

Nuclear remodeling has been proposed to serve three functions [9]. First, the reduced size and shape of the sperm nucleus yields a hydrodynamic structure that is predictive of fertility in bulls and red deer [63-65]. Second, protamination renders the majority of the sperm genome resistant to nuclease activity, irradiation, and shearing forces [8, 66, 67]. Presumably, both features were evolutionarily optimized to protect the paternal genome while traversing the female reproductive tract en route to the oocyte. Third, although a subject of debate, the selective post-meiotic retention of histones provides the zygote a dichotomous chromatin package that could serve to preferentially poise regions for early use [14, 16, 36].

Murine spermatozoa organize about 1-2% of their genome with nucleosomes [16, 68], whereas up to 15% of human sperm DNA is packaged in this manner [37, 69, 70]. Interrogation of isolated nucleosome-associated sequences demonstrated that some of these genomic regions included imprinted regions [71], telomeres [72, 73], retroposon DNA [73], and specific gene loci [8, 73, 74]. Lacking comparable nucleosomal enrichment, the chromatin structure of the centromeric and pericentromeric sequences in mammalian sperm, contains a mixture of nucleosomes and protamines [8]. Specifically, these regions retain modified histones such as H3K9me3 as well as the histone variants CENP-A and H2A.Z [14, 75, 76]. Together these observations led to the hypothesis that the maintenance of nucleosomes at specific sites may prime discreet regions for use shortly after fertilization. Initial support for this premise came from the finding that in human sperm histones bind DNA in a sequence-specific manner around gene regulatory regions [8, 36].

Studies reporting the *in situ* localization of nucleosome-associated genomic regions in the sperm should be met with caution. The compact nuclear environment of the spermatozoa cannot be accurately interrogated by immunofluorescence without prior membrane destabilization and chromatin decondensation. Considering decondensation alters the position of nuclear elements, such treatments may skew interpretations [23]. With this caveat, in human spermatozoa, core histones as well as testes specific histone variants have been observed within the basal portion

of the nucleus proximal to the tail [31, 77]. In contrast, H2B as well as nucleosome associated telomeric regions exhibit a partially overlapping punctuate pattern throughout the nucleus [31, 78]. In the mouse, telomeres are bound by linker H1, which is absent from human sperm, and appear localized to the periphery [37, 73]. As an additional point of comparison the canonical histones found in spermatozoa of the evolutionarily distant marsupial, *Sminthopsis crassicaudata*, are also peripherally located [79]. However, it cannot be excluded that these results primarily reflect nuclear access.

Genome-wide analysis of the chromatin landscape in mature sperm has largely relied on the identification of histone-enriched regions. These approaches were initiated with CGH tiling arrays which established that histone-bound DNA is associated with gene-dense regions and enriched for developmentally regulated promoters as well as CTCF binding sites [12]. The results of this study were quickly complimented by a series of reports which used high-throughput DNA–sequencing technologies to analyze sperm nucleosome-associated DNAs [14]. These sequences exhibited a modest enrichment within the promoters of developmentally important genes including embryonic transcription factors and signaling pathway components, as well as microRNA and imprinted genes clusters.

Independent analysis has demonstrated that internal exons also display significantly greater histone enrichment than flanking intronic sequences [80]. By coupling chromatin immunoprecipitation (ChIP) and DNA-sequencing (ChIP-seq) histone variants and modified histones have been localized to specific sequence elements genome in sperm. Canonical replication-dependent H3.1 and H3.2 were shown to be enriched within promoters bearing the silencing H3K27me3 modification [15]. In contrast nucleosome containing replication-independent H3.3 are correlated with the activate histone modification H3K4me3 within sequences containing an elevated frequency of C-G dinucleotides, known as CpG islands.

These opposing silencing and activating histone modifications, H3K27me3 and H3K4me3, respectively, have also been observed within developmentally regulated promoters [14, 16].The

retention of these epigenetic marks within a transcriptionally silent cell suggested that these genes may be bivalently marked by H3K4me2/3 and H3K27me3. The bivalent promoter is a hallmark of developmentally regulated stem cell genes and has recently been observed in Zebrafish blastomeres [81]. In addition to harboring sites of both active and repressive histone modifications, bivalent promoters are often bound by RNA polymerase and are therefore poised for expression. The coordinated removal of repressive H3K27me3 throughout differentiation permits the initiation of transcription, providing temporal and spatial control of gene expression. Bivalent promoters might reflect the male contribution to early gene expression [82].

Alternatively, it has been suggested that the differential enrichment of histone modifications within specific ontological categories of promoters, and not bivalency, may regulate early embryonic gene expression [16]. In human sperm, H3K4me2 marked promoters of genes associated with spermatogenic and housekeeping processes whereas H3K27me3 was enriched within the promoters of developmentally regulated genes expressed following implantation or in differentiated cells. Further, the degree to which a promoter was occupied by H3K27me3 positively correlated with repression of the corresponding gene during early mouse embryonic development. Together these results argue that the retention of the repressive H3K27me3 modification at specific promoters in human sperm may provide a paternal and possibly transgenerational mark [82].

The two modes of paternally derived epigenetic promoter regulation introduced above, bivalency and differential enrichment of modified histones, are present in sperm of mice and men (Figure 1.2). The use of one mechanism in lieu of the other would be expected to hinge on shared spermatogenic transcriptional requirements and the species specific timing of zygotic and embryonic genome activation (ZGA and EGA, respectively). Whereas promoters of potent developmental regulators in sperm from both species are primarily associated with repressive

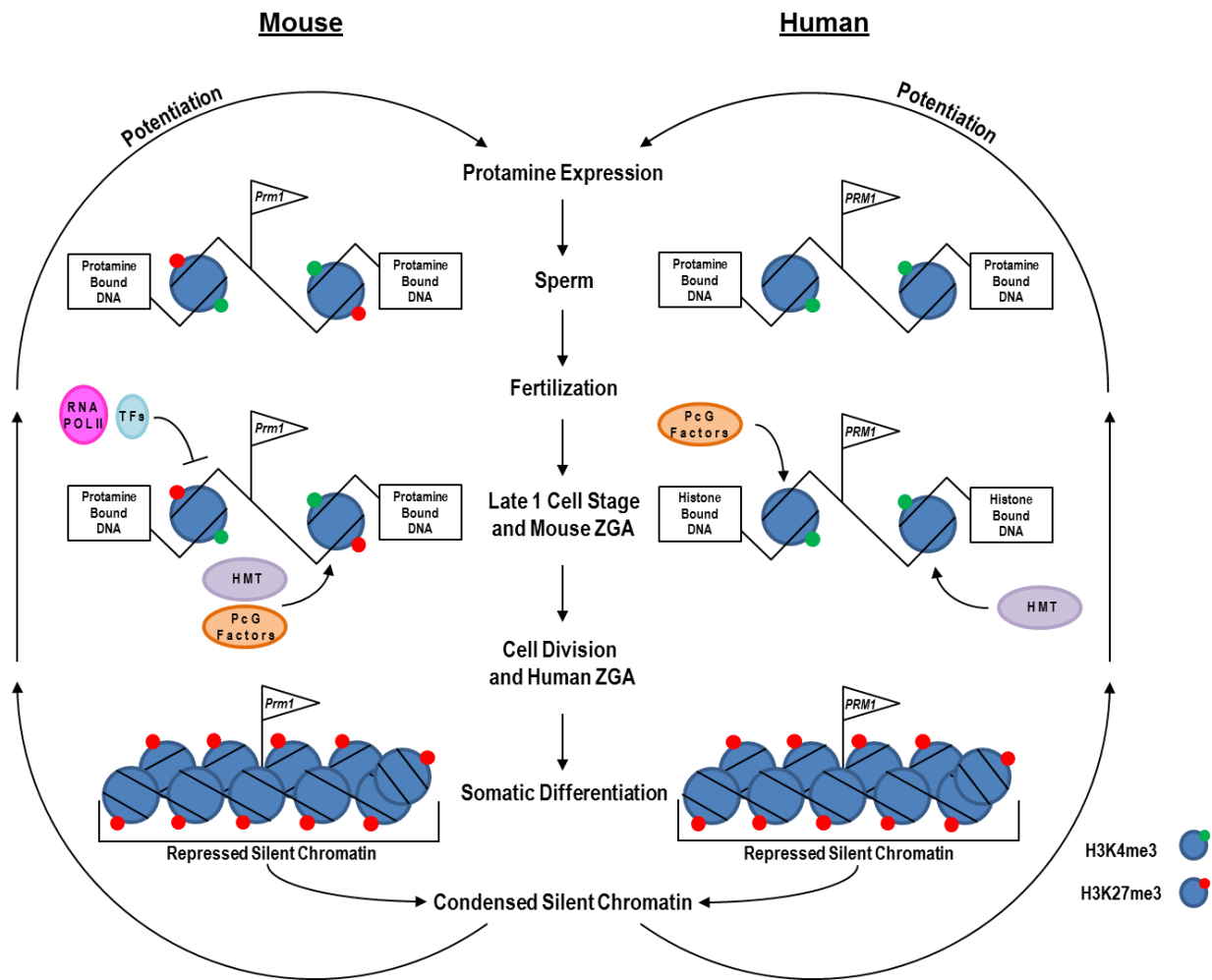


Figure 1.2. The Potential Influence of Zygotic Genome Activation on Paternal Chromatin Structure. In mouse and human sperm the *PRM* genes are bound by nucleosomes residing within a potentiated DNase I-sensitive domain. These regions are differentially marked by modified histones in each species. In mouse the bivalently marked spermatogenic promoters may reflect the early initiation of zygotic expression at the late 1-cell stage. Recruitment of transcriptional machinery (RNA polymerase; RNA POL II, and transcription factors; TFs) is coincident with the activation of silencing pathways (histone methyltransferases, HMTs; and Polycomb factors, PcG). The retention of the silencing H3K27me3 mark in promoters may prevent detrimental expression prior to gene silencing. In comparison, human zygotic genome activation occurs at the 4 or 8 cell stage. This affords the embryo time to silence these genes, which in sperm are marked with the active H3K4me3 modification lacking the repressive mark. In both species the protamine domain remains silenced throughout differentiation by adopting a highly condensed chromatin conformation. During male gametogenesis this region becomes potentiated in spermatocytes prior to its expression in round spermatids.

histone modifications, spermatogenic genes are bivalently marked in murine but not human sperm [16]. The former scenario reflects a shared need for early repression of developmental gene expression. The presence of active modifications in mouse and human spermatogenic promoters likely corresponds to the transcriptional history of these silent cells. In mice these regions are marked by repressive histone modifications to ensure their appropriate regulation following fertilization. Mice initiate zygotic genome activation late in the one cell embryo transcribing rRNA [1, 83, 84], concurrent with DNA replication [85] and an increase in the levels of H3K27me3 within the paternal pronuclei through the activity of Polycomb group (PcG) proteins [86]. Prior to this H3K27me3 cannot be microscopically detected in paternal chromatin of the one cell fertilized oocyte [86-88]. Modified sperm histones are expected to remain reflecting the lack of histone demethylase activity in either the oocyte or zygote [88]. This is likely essential to ensure proper transcriptional regulation from the paternal chromatin during this initial wave of ZGA. Concomitantly, the male pronucleus exhibits a higher level of transcriptional activity [85], an increased concentration of transcription factors [89], and a more transcriptionally permissive chromatin structure compared to the female pronucleus [84, 90].

It is reasonable to assume that the presence of sperm derived H3K27me3 within the bivalent promoters of the paternal spermatogenic genes prevents their transcription enabling polycomb propagation of this repressive mark [16, 91]. This would be expected to block transcription factor recruitment and subsequent expression. Repression of these genes is necessary since expression of *Prm1*, which is bivalently marked in mouse sperm, would likely perturb further development [92]. Indeed, mutant mice lacking the methyltransferase activity responsible for propagating H3K27me3 do not progress past early development [93]. Though undoubtedly this mutation is responsible for a wide range of developmental defects [88, 94], it would be informative to probe these late zygotic mutants for expression of those spermatogenic genes marked by a bivalent promoter in wild type sperm. Comparatively, the delayed EGA of humans [95] should permit PcG mediated repression of orthologous spermatogenic promoters,

thus altering the paternally derived poised chromatin structure. The inability to detect trimethylated paternal H3K27 in G2 tripronuclear zygotes suggests that deposition of this modification occurs sometime after the first cleavage event but before the start of embryonic gene expression at the 4- to 8-cell stage [96].

The number of histone variants and associated secondary modifications found in mammalian sperm has greatly increased in the last two decades [97, reviewed in 98]. Detection of these proteins following fertilization has proven challenging for several reasons. First, the amount of histone-associated chromatin in sperm is limited, ranging from 1 to 15% in mice and men, respectively. Second, epitopes may be inaccessible prior to decondensation which limits detection. Third, deposition of maternal histones, which are virtually indistinguishable from their paternally derived counterparts, directly coincides with sperm chromatin decondensation [87, 99]. This is best exemplified by the replication-independent H3.3. Though, present in mature sperm [15, 37], H3.3 is not microscopically detectable in paternal chromatin until maternally derived histones are deposited at the start of decondensation [87, 100]. The prevalence of this variant in paternal chromatin is conserved and likely essential to remodeling as a mutation of the HIRA chaperone blocks H3.3 incorporation precluding decondensation in *Drosophila* zygotes [101, 102]. This appears to be a well conserved process as deletion of histone cell cycle regulator (HIRA) in murine zygotes blocks rRNA transcription preventing the first cell division [103]

Despite the difficulty in detecting nucleosome-bound DNA delivered by sperm some paternally derived modified histones and histone variants have been observed following fertilization. These include both H4K8ac and H4K12ac [104] as well as the testis specific variants H2AL1 and H2AL2. First detected in the centromeres of spermatids, these variants remain enriched in heterochromatin until displaced from paternal DNA shortly after fertilization [105]. In contrast histone, H3 replication-dependent variants H3.1 and H3.2 [106] are detected following fertilization in decondensed sperm chromatin prior to DNA synthesis, though in much lower abundance than in maternal chromatin [87, 99]. These sperm derived proteins are detected until

the initiation of zygotic S phase, at which point they become indistinguishable from their newly incorporated maternal counterparts [99].

IV. RNA in Sperm

It is now accepted that mature spermatozoa harbor a distinct population of RNAs. The biological role of these transcripts largely remains unknown. Undoubtedly some of the transcripts retained in sperm represent products expressed in various spermatogenic cells. However, the delivery of sperm borne RNAs to the oocyte has been demonstrated suggesting the potential of these transcripts to contribute to early embryonic gene expression [107, 108].

Owing to the observation that mature mammalian sperm are transcriptionally quiescent [10] the presence of mRNAs in these cells was originally thought to represent incomplete expulsion of cytoplasmic elements during nuclear condensation. Indeed, sperm do contain remnants of their developmental expression profile which seemingly serve no purpose in the mature gamete. Further, some of these RNAs are highly abundant in sperm and expected to be detrimental to the embryo [92]. In this regard the protamine transcripts are the most conspicuous. Following their transcription in round spermatids these RNAs are translationally repressed and stored as inactive messenger ribonucleoprotein particles (mRNPs) prior to remodelling [Figure 1.1; 109]. Loss of this repression causes premature protamine translation in these cells. The subsequent developmental arrest is likely due to precocious protamine-dependent nuclear condensation as nuclei from these cells, like those from mature spermatozoa, are resistant to sonication [66, 92]. The affinity of protamines for DNA coupled with the enduring abundance of these transcriptionally repressed transcripts in sperm presents a potentially precarious situation to the zygote. However, failure to detect these transcripts soon after fertilization by Intra-cytoplasmic sperm injection (ICSI) or round spermatid injection (ROSI) despite the persistence of other sperm RNAs [110, 111] suggests the embryo has evolved strategies to efficiently clear some of these RNAs from the cell.

The storage and delayed translation of the PRMs and other transcripts reflect an additional hurdle RNAs must overcome prior to their retention in sperm. A recent study has demonstrated that approximately 60% of the RNAs transcribed in round spermatids succumb to targeted degradation via the piRNA-mediated decay pathway [Figure 1.1; 112, reviewed in 113]. This process, in addition to cytoplasmic expulsion, likely accounts for the absence of intact ribosomal RNAs in total sperm RNA preparations [Figure 1.3; 2, 114]. The storage of transcripts within mRNPs required during the final stages of spermiogenesis, such that they evade degradation, provides a reasonable explanation for the abundance of the PRMs and other RNAs in mature sperm for which there is no obvious role in the embryo. These RNA-protein complexes as well as the ribosomal machinery [115, 116] are likely passively sequestered within the condensing sperm cell and consequently delivered to the oocyte upon fertilization [108]. Regardless of whether these transcripts are actively utilized or simply destroyed the zygote must possess pathways to cope with this consequence of cellular compaction.

An evolutionarily distant precedent for such a mechanism has been observed in *Arabidopsis* [117]. Expressed during male gametogenesis short suspensor (*SSP*) transcripts are translationally repressed and stored in pollen. Following fertilization, repression is relieved and the *SSP* RNAs undergo zygotic translation. Sufficient accumulation of this protein in the seed

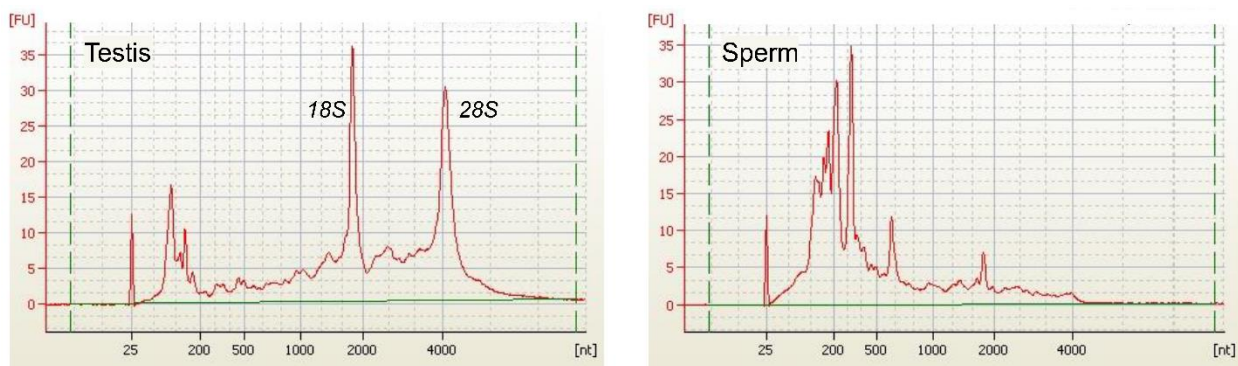


Figure 1.3. Electrophoretic size distribution of RNAs in sperm and testis from human fertile donors. Total RNA from sperm and testes was heat-denatured in the presence of EDTA. RNAs were then resolved on an Agilent Bioanalyzer [Figure is adapted from 2]

activates a MAP kinase signalling cascade, which prompts the first cell division. In this model, embryo patterning is temporally linked to fertilization by a paternally contributed mRNA. Whether such regulation exists in other species is the subject of intense debate. It should be noted that parthenogenetic mice survive to adulthood and produce offspring in the absence of a paternal factor [118, 119]. However, efficient generation of these embryos requires the deletions of both copies of two paternally methylated imprinting-control regions. Further, the possibility that transgenerational effects may present in later generations was not explored.

Early investigations comparing sperm RNAs from pooled and individual fertile ejaculates suggested the existence of a common spermatozoal mRNA fingerprint [120]. Technological advances including the use of microarrays and RNA sequencing (RNA-seq) have since resolved their variability [20]. Several recent studies have provided evidence that sperm RNAs collected from infertile men are altered relative to controls, demonstrating the prognostic value for these transcripts [21, 121]. Beyond the clinic, RNA-seq analysis of fertile sperm has also demonstrated that the mature paternal gamete possesses most if not all of the RNA species observed in other cell types. This includes the 18S:28S rRNAs which were assumed absent from the mature paternal gamete due to the enrichment of short-length transcripts following electrophoretic analysis of total sperm RNAs [Figure 1.3; 2]. However, these RNAs were demonstrated to persist in sperm albeit as cleavage products [2, 114]. In this respect the ribosomal transcripts stand in contrast to a subset of RNAs predicted to be intact in mature sperm and candidates for potential functional roles following fertilization [122]. Though some paternal transcripts may function in the early embryo it seems unlikely that all of the selectively retained RNAs stored by the male gamete should impact development.

V. Higher Order Chromatin Structure in the Male Gamete

As discussed above, appreciation of the mature spermatozoon as more than a vehicle for the delivery of inert DNA has evolved with the acceptance that distinct regions of the paternal genome remain nucleosome-bound [8, 12, 14, 74]. Complementing this development was the

discovery that sperm also delivers a suite of RNAs to the oocyte [123]. Both have contributed to the expanding genetic influence of the male gamete post-fertilization. Our understanding of how these elements coalesce to potentially influence embryonic development would not be complete without consideration of the higher order chromatin structure.

Genomic regulation requires the ordered positioning of approximately 2 meters of DNA within the limited confines of the nucleus. Over the last decade, several foundational studies have demonstrated the ability of the genome to act as its own structural platform through which to accomplish this task [6, 124, 125]. This feat is achieved primarily through the formation of chromatin loops which simultaneously permit interactions between distant genomic regions while necessarily folding and therefore reducing the physical volume of the genome. Identification of these looping events initiated within single loci with the development of the chromosome conformation capture (3C) technique [124]. Briefly, these looping interactions are identified by chemically cross-linking chromatin, digestion with an endonuclease and subsequent intra-molecular ligation of free DNA ends. If two loci are proximally positioned within the nucleus, despite being separated by a large linear distance within the genome, following ligation they will form a chimeric DNA. The interaction frequency of the two hypothetical loci is inferred from the prevalence of their corresponding chimeric DNAs. For a sufficiently small region or number of regions PCR or microarray analysis can adequately interrogate these products [126, 127]. To infer genome wide higher order chromatin structure DNA-sequencing is required [125]. After further refinement this approach has recently been used to map approximately 10,000 looping events throughout the human genome [6].

The first global analysis of higher order chromatin structure broadly segregated the genome into two categories: type A and type B [125]. These designations, or compartments, are generally analogous to the more biologically descriptive terms euchromatin and heterochromatin, respectively. Genomic regions classified as “compartment A” exhibited an enrichment in coding regions, transcription, and relaxed chromatin structures. In contrast, for a given genomic interval

the interaction frequency of loci within “compartment B” is elevated relative to “compartment A”, indicative of a more densely packed closed chromatin state.

With continual improvements in DNA sequencing throughput the resolution of the 3C techniques has increased. Consequently, the binary compartment classification has given way to the more nuanced division of chromatin into units termed topologically associated domains [TADs; 5]. These structures can in turn be further subdivided into sub-domains or sub-compartments [128, 129]. Classification of these sub-domains reflects the general dichotomy of the A/B compartments though the increased resolution permits consideration of additional variables such as replication timing [130] and the degree of association with structural nuclear landmarks such as the nucleolus and nuclear lamina [6].

The influence of Ctf binding on domain stratification can be appreciated when interrogating higher order chromatin structure at the level of the TAD [5]. The binding of this factor promotes DNA loop formation which is central to domain topology [6]. This is evidenced by the enrichment of occupied Ctf sites demarcating the boundaries of TADs [5]. Partitioned in this manner the frequency of intra- relative to inter-domain interactions between two loci is elevated. Looping events across boundaries and between chromosomes do occur, but infrequently [6, 131].

Intra-domain looping interactions commonly include those observed between active promoters and their cognate enhancers [132]. This is best exemplified by expression of the α -globin locus which is mediated in a developmental specific context by a DNA looping event resulting in the physical interaction of its promoter region and upstream *cis* regulatory elements [+33 - 48 kb; 126, 127, 133]. Though cell type specific loops are observed and result in changes in gene expression [134], TADs are generally conserved across species and between cell types [5]. Disruption of this domain structure by altering a Ctf binding site results in perturbed gene expression [135]. Though higher order chromatin structure has been shown to be relatively invariant, the genome wide 3C approach has only been undertaken within a limited number of cell types and has yet to be convincingly applied to the germline.

Studies of higher order chromatin structure in sperm have been based on the supposition that a skeletal network of proteins underlies the spatial and therefore functional organization of the haploid genome [136]. This is exemplified by the prevalence of framing the results of these studies within the context of the Donut Loop Model [137] of sperm chromatin organization. Operating on the tenant that the structure and function of the genome requires its binding to a proteinaceous network termed the nuclear matrix this model predicts DNA loops in sperm are packaged into toroidal structures that are anchored to the matrix by nucleosome-bound DNAs [138]. This model has been invaluable in promoting the need to understand macromolecular nuclear organization in the male gamete and its potential impacts on fertility and embryonic function. However, it has two limitations.

The first of these limitations is universality [139]. After decades of study in many cell types the nuclear matrix remains poorly defined and is observable only under harsh extraction conditions [140]. Paradoxically these treatments require the removal of the majority of chromatin proteins which must provide structural contributions *in vivo*.

The second limitation of this Donut Loop Model is summarized within its name and is specific to the male gamete. The term 'Donut' refers to the toroidal structures thought to be the primary packaging unit of the protamine-bound genome. While toroids containing DNA readily form in solution they have yet to be observed in native or partially decondensed sperm chromatin. In contrast, several studies have reported the packing of sperm DNA within large globular fibers [141, 142]. A potential precursor to this genomic structure has also been observed in prior spermatogenic cell types in humans and rodents [60, 143].

Drawing from the results generated by 3C studies in somatic cells, these globular units may reflect the protamine packaging of single topological domain units. Though not yet attempted in post-meiotic testicular cell types (an exception is provided below), in a haploid cell line, 3C analysis has demonstrated that a reduced genome still conforms to the organizing principles first observed in the diploid nucleus [6]. This would suggest that in testis the chromatin of post-meiotic

cells is organized into TADs. A novel model of sperm chromatin structure can be synthesized from this principle.

During spermatogenic nuclear remodeling it is expected that the timing and degree of TNP/PRM deposition will resemble other chromatin regulatory events and exhibit greater inter-domain than intra-domain variance. As nuclear remodeling progresses sub-domain structures are expected to be lost due to the eviction of chromatin proteins. However, some structural factors, such as Ctf and topoisomerase II, are predicted to be retained throughout spermatid maturation or removed relatively later during remodeling. The presence of these factors is predicted to maintain larger stable domain structures within the bounds of which protamine binding disrupts smaller sub-compartments compacting the genome. Sites of factor retention may be maintained in nucleosomal conformation in mature sperm.

Though 3C techniques likely have limited applications in spermatozoa due to the high degree of nuclear condensation a recent study has reported the use of this approach in a singleton experiment in mouse [144]. These results undoubtedly require independent validation and the accompaniment of well documented controls. However, the reported results strongly support a globular model of sperm chromatin. This model is also readily testable by applying the 3C approach genome wide in round and elongating spermatids. Loci exhibiting close spatial proximity prior to and during nuclear remodeling would be predicted to maintain this relationship in mature sperm. These interactions could subsequently be verified by DNA-FISH.

VI. Overview

The appreciation that sperm functionally package several layers of developmentally important information has become apparent. In human sperm, the genomic landscape, though dominated by protamines, is enriched in histones at both promoters and exons. Understanding how this locus is regulated is complicated by difficulties in obtaining testicular tissue. Chapter two summarizes the characterization of a transgenic mouse model of the human protamine gene cluster. This technology permits the simultaneous interrogation of the human and mouse protamine loci in a

single experiment. In both species protamine transcription occurs at a similar developmental time point after which the transcripts are packaged as mRNPs as they await translation (Figure 1.1).

Chapter three discusses the likely consequence of mRNP RNA storage mechanism with respect to the physical positioning of transcripts within the mature sperm cell. This analysis demonstrated that sperm RNAs exhibit a preferential peripheral localization and were depleted from the nucleus. Also discussed is the possibility of extracellular vesicle mediated exchange of RNAs between sperm and its environment. A notable observation within this chapter is the dramatic peripheral enrichment of Malat1 in mouse sperm. This would suggest that during nuclear remodeling chromatin associations with this prototypical nuclear noncoding RNA are strongly reduced. However Malat1 is still present within the interior of the mature sperm cell. Therefore this RNA may contribute domain demarcation as outlined by the globular model of sperm chromatin architecture.

The results of a genome wide nucleosome mapping study in wild type and transgenic mouse sperm are discussed in chapter four. The region of chromosome 19 harboring the transgenic protamine gene cluster, characterized in chapter two, was found to be packaged in a nuclease insensitive conformation in mature murine sperm. These results were used to inform potential past chromatin events including the expected transcriptional suppression of the human transgenes. Further analysis identified the presence of nuclease footprints throughout the genome corresponding to known chromatin regulators such as Ctcf and members of the homeobox domain family of transcription factors. Sites of Ctcf retention in mature mouse sperm were correlated with past studies of the protamine locus and available 3C and *cis* regulatory datasets to suggest a novel means of regulating the robust expression of the endogenous protamine gene cluster. Analysis of the Ctcf sites identified in mature sperm was used to inform the novel model of sperm chromatin compaction discussed above as well suggest potential roles for these sequences in the embryo. Lastly, chapter five summarizes these results and suggests several experimental avenues expected to compliment the results reported herein.

CHAPTER TWO

INTERROGATING THE TRANSGENIC GENOME: DEVELOPMENT OF AN INTERSPECIES TILING ARRAY

This chapter was adapted from the following publication:

Johnson GD, Platts AE, Lalancette C, Goodrich R, Heng HH and Krawetz SA. (2011).
"Interrogating the transgenic genome: development of an interspecies tiling array." *Systems
Biology in Reproductive Medicine* 57(1-2): 54-62.

I. Summary

A single copy of the human protamine domain was randomly inserted into the mouse genome within an intron of *Cyp2c38*. The development of an interspecies tiling array was pursued to enable direct comparison of the orthologous protamine domains in a single experiment. Probe design was adapted to generate species specific high resolution probe sets that would tolerate repetitive elements. Results from competitive hybridizations demonstrate that interspecies tiling arrays are a valuable tool for parallel analysis of highly similar DNA sequences. This approach provides a rapid and reliable means of interrogating samples prior to deep sequencing analysis. These arrays should readily compliment most DNA isolation techniques such as ChIP, nuclease sensitivity and chromosome conformation capture assays.

II. Introduction

Spermiogenesis, the differentiation of a haploid spermatid into a mature spermatozoon, is characterized by dramatic morphological changes including a marked reduction in nuclear volume [145]. In mammals, this remodeling of the sperm nucleus results from the compaction of the genome through the replacement of histones by sperm specific proteins [reviewed in 9, 11]. The histone-protamine transition initiates with the global acetylation of histones facilitating deposition of the TNPs and sperm specific histone variants [35, 50, 51, 55, 146]. In elongating spermatids the transition proteins and the majority of histones that remain are replaced by protamines, resulting in the condensed paternal genome [147]. Despite the persistence of nucleosome bound regions sperm are transcriptionally quiescent [10].

Protamines are the most abundant nuclear proteins in the sperm of many species [148, 149]. In mammals, the genes encoding these proteins are found in a multigenic cluster containing *PRM1*, *PRM2*, and *TNP2* on chromosomes 16p13.2 and 16qA1 in human and mouse, respectively [150-152]. The coding regions are well conserved between mice and men [153, 154]. Following meiosis, the genes are transcribed in round spermatids and subsequently translated by the elongating spermatids [155, 156]. Expression of these genes is essential as perturbation compromises fertility or results in sterility [157-165]. In several species, this gene cluster contains a fourth open reading frame, *PRM3* [166, 167]. In mouse, this gene is believed to encode a small cytoplasmic acidic protein transcribed in early round spermatids. Mice lacking *Prm3* are fertile despite deficiencies in sperm motility [168].

The human protamine locus, encompassing many of the *cis* elements necessary for expression, is approximately 40 kb in length. Introduction of this entire sequence into the mouse genome retains native temporal and tissue expression independent of the site of insertion [169, 170]. The humanized mouse produces no phenotypic abnormalities. Within the extended locus lies a ~28 kb DNase I sensitive domain containing *PRM1*, *PRM2*, and *TNP2*. In both human and mouse this linear gene array is flanked by boundary elements, which have been shown to be essential for expression [170, 171]. Mutations in the 3' boundary element have been correlated with decreased protamine expression in two infertile men [172]. A similar decrease in locus expression was observed in transgenic mice harboring a single copy of the human protamine gene cluster lacking this 3' region [169].

Expression of the protamine domain is preceded by potentiation of the locus in pachytene spermatocytes from a closed repressed conformation to an open accessible state that is then permissible to the trans-factor binding necessary to initiate expression [7, 173]. Once potentiated the open chromatin conformation persists throughout spermiogenesis, which may reflect specific nucleosome retention [8, 170, 173].

Though the total amount of histone remaining in mature spermatozoa varies between species, those regions that remain bound by nucleosomes are not random [8, 36, 72]. Promoter regions of genes essential to embryonic development are particularly enriched [12, 14, 74]. Nucleosome retention within these regions in sperm may influence or direct the initial expression of the paternal genome during early embryonic development [36].

Three techniques have been instrumental in furthering our understanding of the relationship between primary sequence, epigenetic modification and the resultant chromatin structure. PCR assays, now commonplace, are useful for determining the representation of a specific sequence within a pool of DNA. The specificity, sensitivity, and relative speed of this approach routinely permits the selective enrichment of singular DNA sequences up to 3 kb in length [174]. However, this assay is an inefficient means of enriching all individual DNA sequences comprising a large genomic tract. DNA microarrays and next generation sequencing are currently the most reliable methods of efficiently achieving the coverage needed to capture entire genic domains, individual chromosomes, or even entire genomes. Though current sequencing technologies are capable of achieving greater resolution and higher coverage than DNA microarrays the associated cost is currently prohibitive for many laboratories. Microarray strategies are cost efficient, when restricting coverage to defined regions of interest, but this technology is not without limitations. Commercial array platforms commonly omit repetitive regions from analysis due to the inability to accurately distinguish between highly related sequences. Similarly, this logic would suggest that representation of orthologous sequences from more than one species on a single array should be avoided.

Prior to undertaking comparative studies of locus control in the transgenic system an efficient complimentary method of analysis was required. Accordingly, an orthologous mouse domain interspecies tiling array was developed to enable one to simultaneously query the many repetitive regions of the human transgenic protamine locus [167]. The maskless method of array design outlined in this study should be readily adaptable to the interrogation of most non-unique

sequences. Importantly, interspecies tiling array technology fundamentally differs from cross-species hybridization (CSH) [175]. An adaptation of traditional array technology, CSH utilizes a reference genome differing from that of the target DNA to determine the extent of sequence conservation between species [176, 177]. This technique has also been performed when a species of interest lacks a representative commercially available platform [178]. Though useful in these instances CSH is unable to quantitatively ascertain the relative ratios of homologous targets within samples [179]. The proof-of-principle demonstrated in this communication establishes the interspecies tiling array as a novel genomic tool capable of rapid parallel analysis of orthologous sequences within many transgenic models.

III. Materials and Methods

Transgenic Animals

All live animal protocols were approved by Wayne State University Animal Investigation Committee A02-04-08. Transgenic animals were generated by pronuclear microinjection as described previously [169]. Restriction endonuclease digestion of cosmid hp3.1 with Sall and EagI released an approximately 40 kb fragment of DNA containing the complete human protamine domain. Following microinjection of purified DNA into fertilized C57BL/6 eggs, newborn pups harboring the transgene were detected by PCR [180]. Technical replicates of triplicate reactions were repeated three times. Offspring from a transgenic founder and wild type mates were bred to homozygosity. Homozygous animals were used for all subsequent experiments.

Transgene copy number was established by real time PCR of serially diluted tail clip DNA. Primers sets specifically targeting a ~350 bp region within either the human or mouse protamine domain were utilized in separate reactions (Table 2.1). The relative template values from all reactions were determined using the KLab PCR algorithm [181]. A single copy insertion was considered to be represented by a 1:1 ratio of transgenic and endogenous templates values.

Table 2.1. Primers used for determination of copy number.

PRIMER NAME	FORWARD (5' – 3')	REVERSE (5' – 3')	AMPLICON SIZE (bp)
COPY NUMBER PRIMERS			
Mm Ch16 10.8MB PRM1	CTCCAAGGCAACTCTTAAT CAGAGCCGGAGCAGATATTAC	TTAAAGATAATGCGGGATGTAT ATTTATTGACAGGCGGCATTGTT	373 359
TERMINAL TRANSFERASE DEPENDENT PCR PRIMERS			
Biotinylated Extension Primer	TTCAATCTAGAATCCCACGTT		
Nested 1	AAATGCGAGGACGGTACAC	AGTAATAATAAGCAAACCTGG	96
Nested 2	TACACGGCGACCCAAG	ACCTGGAAAAGACCCACACG	67

FISH Analysis

Transgenic mouse lymphocytes were isolated from spleen and cultured in supplemented RPMI. Slides of colcemid treated cells were prepared by conventional means of hypotonic swelling and fixation. The inserted human locus was detected by labeled cosmid clone hp3.1 as described previously [182-184]. One hundred fields were evaluated using a fluorescent microscope. Images were captured using a CCD camera and analyzed with RS Image software (Photometrics, Surrey, BC).

Site of Insertion

The site of insertion was fine mapped using terminal transferase-dependent PCR [TTD-PCR; 185, 186]. A distal end of the transgene and neighboring endogenous sequence was linearly amplified using a biotinylated primer and the Clontech Advantage HD Taq Polymerase system (*PRIMER SEQs*; Clontech, Mountain View, CA). The resultant blunt end reaction products were enriched by streptavidin capture followed by the addition of a riboguanosine tail (Promega, Madison, WI) by terminal deoxynucleotidyl transferase (Invitrogen, Carlsbad, CA). Ligation of a known linker sequence by T4 DNA ligase (Roche; Madison, WI) added additional priming sites to ribo-tailed DNA. Reaction products from nested primers were sequenced (Table 2.1).

Probe Design

A multistep design approach was implemented to generate high resolution species specific probe sets targeting functional domains, independent of repetitive elements [187].

Targeted domains in mouse included: Protamine (chromosome 16: 10,782,515 – 10,802,516), Acrosin (chromosome 15: 89398500-89405500), Hox A (chromosome 6; 52080000 – 52220001), Hox B (chromosome 11; 96090000-96220001), Hox C (chromosome 15; 102720000-102920001), Hox D (chromosome 2; 74460000, 74600001), *Phosphoglycerate kinase 1* (chromosome 20; 102385000-102410001), *Phosphoglycerate kinase 2* (chromosome 17; 39668500-39673501). Probes targeting sequence within an extended human protamine domain were also designed (chromosome 16: 11,312,500 – 11,452,413).

Genomes of interest were indexed utilizing a sliding 14 bp window with a 1 bp step. The number of iterations of each 14 bp subsequence throughout the entire genome was recorded. Regions of interest were divided into potential probes using a 55 bp sliding window with a 1 bp overlap. Each potential probe sequence was aligned to the genome(s) of interest and all nonspecific sequences were rejected. Remaining probes were ranked based on sequence complexity, adherence to an optimized T_m, and absence of GC rich subregions or sequences prone to intramolecular hybridization. A total of 43,020 oligonucleotide probe sequences were synthesized by Agilent utilizing their 4 × 44 K custom CGH array platform (Agilent Technologies, Inc., Santa Clara, CA). The final suite of probe sequences corresponding to the mouse and human loci are available in Appendices A and B.

CGH Array Profiling

Genomic DNA was isolated from HeLa cells, wild type and transgenic tailclips by phenol-chloroform extraction and subsequent by ethanol precipitation [188]. Isolated samples were fragmented, labeled, and hybridized according to the manufacturer's instructions (User Manual version 3.1; Agilent Technologies, Inc., Santa Clara, CA). Hybridizations and array scanning were performed by the Toxicology Core Facility at Wayne State University School of Medicine.

IV. Results and Discussion

Transgene Insertion and Localization

A 40 kb segment of human cosmid hp3.1 containing the protamine gene cluster was released by digestion with Sall and EagI. This sequence containing the entire genic domain flanked up- and downstream by boundary elements was inserted into the mouse genome by DNA microinjection into fertilized oocytes [169]. As shown in Figure 2.1, *in situ* hybridization of a transgene-specific fluorescent probe localized the insertion site to region 3' of mouse chromosome 19. The presence of four foci within the stained metaphase chromosomes affirms a single insertion event. This was confirmed by establishing the ratio of the human and mouse gene copy number [181] utilizing

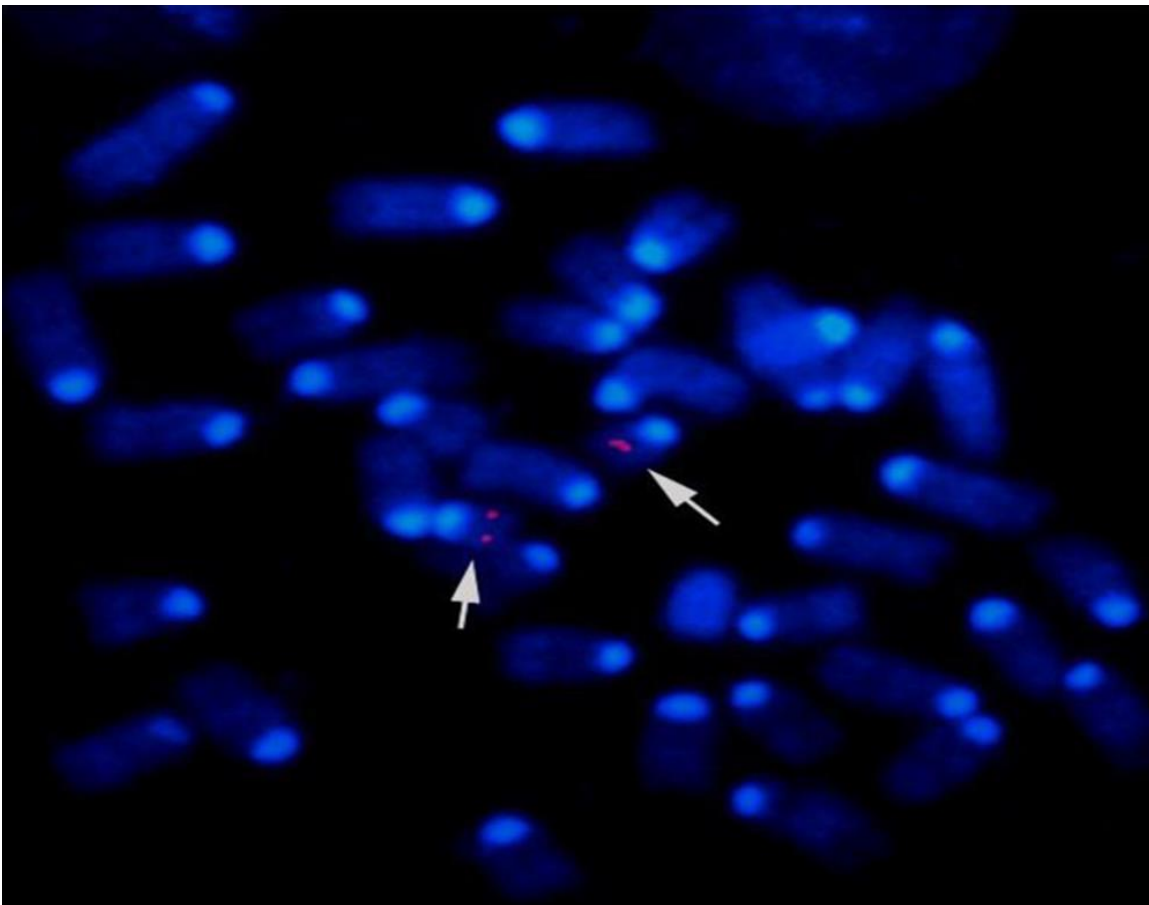


Figure 2.1. Detection of the site of insertion by fluorescent *in situ* hybridization. Metaphase chromosomes were isolated from homozygous transgenic mouse lymphocytes and fixed onto slides. The site of insertion was detected using a fluorescently labeled cosmid clone hp3.1 (red and arrows). Individual chromosomes were identified by DAPI banding. FISH signals from 100 fields were observed under fluorescence. The hybridization signal was localized to mouse chromosome 19, region C3.

Table 2.2. Genomic coordinates of the regions of interest represented on the tiling array.

REGION OF INTEREST	GENOMIC COORDINATES USED: BUILD 36.1	GENOMIC COORDINATES: BUILD 37.1
Acrosin	Chr 15: 89,395,836 – 89,402,836	Chr15: 89,398,500 – 89,405,500
α - Globin	Chr11: 32,158,235 – 32,218,234	Chr11: 32,158,235 – 32,218,234
Cytochrom P450 2c38	Chr19: 39,442,867 – 39,516,386	Chr19: 39,464,046 – 39,537,565
HoxA Cluster	Chr6: 5,2080,000 - 52,220,001	Chr6: 52,100,416 – 52,240,417
HoxB Cluster	Chr11: 9,606,000 – 96,220,001	Chr11: 96,105,224 – 96,265,225
HoxC Cluster	Chr15: 102,720,000 – 102,920,001	Chr15: 102,722,397 – 102,922,398
HoxD Cluster	Chr2: 74,460,000 – 7,460,001	Chr2: 74,497,218 – 74,637,219
Phosphoglycerate Kinase 1	ChrX: 102,385,000 – 102,410,001	ChrX: 103,382,463 – 103,399,038
Phosphoglycerate Kinase 2	Chr17: 39,668,500 – 39,673,501	Chr17: 40,341,974 – 40,346,975
Protamine Domain (Human)	Chr16: 11,159,950 – 11,270,000	Chr16: 11,312,500 - 11,452,413
Protamine Domain (Mouse)	Chr16: 10,696,000 – 10,716,001	Chr16: 10,782,515 – 10,802,516

species-specific primers shown in Table 2.1. Gene equivalency coupled with the results from the FISH analysis confirmed that the transgenic construct inserted as a single copy.

Terminal transferase-dependent PCR (TTD-PCR) was subsequently utilized to establish the genomic coordinates of the site of insertion [185, 186]. Sequencing of the TTD-PCR reaction products evidenced the faithful incorporation of the complete human protamine locus within the seventh intron of cytochrome P450 2c38 (*Cyp2c38*), as shown in Figure 2.2. *Cyp2c38* is expressed throughout mouse, but not in testes [189]. The absence of phenotypic abnormalities suggests that expression of the cytochrome gene was not perturbed and/or that the translated product from the inserted locus is functionally redundant in mice.

Interspecies Tiling Array

The development of an interspecies tiling array was pursued to simultaneously interrogate the orthologous protamine domains in the transgenic mouse model. Of particular interest were the boundary elements flanking the human protamine locus (Figure 2.2). Both elements lie within repetitive regions, which are often excluded from commercial arrays. To address this constraint a maskless array synthesis strategy was adopted [187]. As shown below, this strategy generated

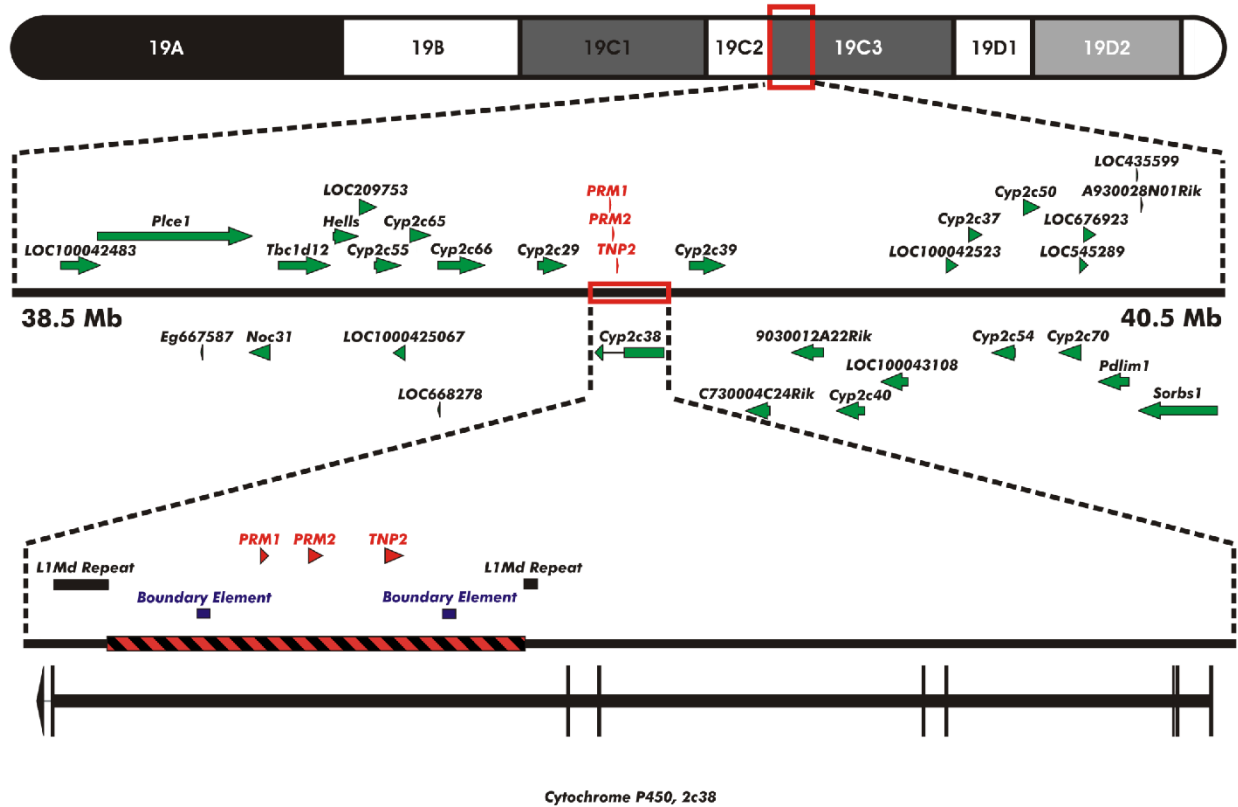
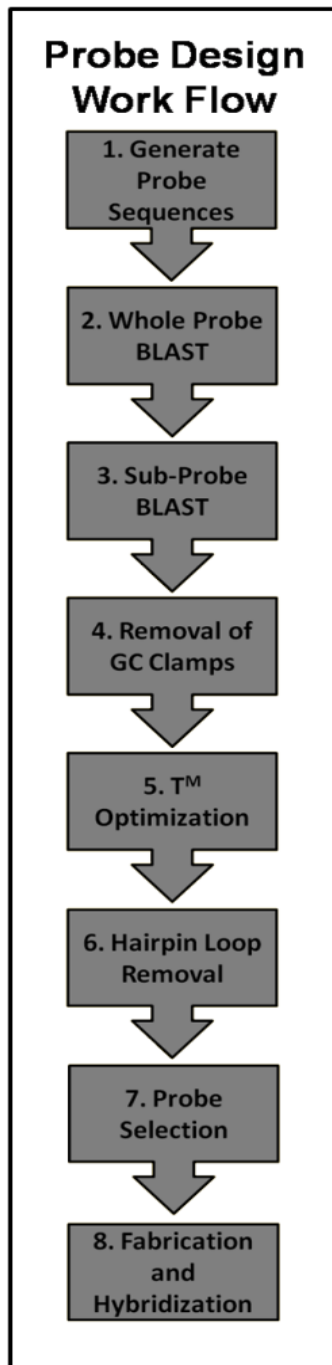


Figure 2.2. Genomic location of insertion site. The cosmid DNA fragment encompassing the human protamine domain (chromosome 16; 11,349,856 - 11,390,141; red hatched box), including the *PRM1*, *PRM2*, and *TNP2* genes flanked by boundary elements, was determined by terminal transferase-dependent PCR to have inserted within cytological band C3 of mouse chromosome 19. Integration occurred within an L1Md T repeat element of the seventh intron of the cytochrome P450c38 gene.

high resolution probe sets of sufficient specificity to discreetly capture sequences from functional domains independent of repetitive elements or sequence conservation. By utilizing this approach the largest gap within either of the protamine domains was 48 bp.

The efficiency of the tiling array is enhanced by the ability to achieve simultaneous high resolution coverage of multiple regions of interest (Table 2.2). Other loci were chosen for representation on the array based on their role in spermatogenesis or embryo development. These included the *Hox A*, *B*, *C*, and *D* clusters, acrosin, phosphoglycerate kinase 1 and 2 (*PGK1* and 2), α -*globin*. The *Hox* genes, which encode a family of potent developmental regulators, have recently been shown in human and mouse spermatozoa to retain a significant level of histones

[12, 14, 190, 191]. Transcribed during the meiotic phase of spermatogenesis acrosin is also nucleosome enriched in mature sperm [192]. *Pgk1* is somatically expressed. Its transcription is terminated by X-inactivation at the start meiosis at which point *Pgk2* is expressed from



chromosome 17 [193]. In contrast to the closed chromatin conformations of acrosin, *PGK1/2* at the termination of spermatogenesis, the *PRM1*, *PRM2*, *TNP2*, are found in a potentiated DNase I-sensitive open chromatin conformation [173, 194, 195]. These established differences in histone retention, chromatin structure, and in the timing of potentiation provide a representative sampling of spermatogenesis.

As summarized in Figure 2.3, array design was a multistep process beginning with the initial indexing of the mouse genome and the extended human protamine domain. Using a 14 bp sliding window with a 1 bp step the number of iterations of all 14 bp subsequences was determined. Each genic domain was divided into potential probe sequences using a 55 bp sliding window with a 1 bp step. All potential probe sequences were then aligned to the genomes of interest. Probe sequences were rejected if they aligned outside of the region of interest from which they were derived. The remaining candidate probes were subsequently assigned a quality score reflecting overall sequence complexity and the influence of base distribution on hybridization thermodynamics. The quality score of a probe was penalized for each multiple occurrence of a 14 bp subsequence within the murine genome or human protamine domain. Probes were also

Figure 2.3. Procedural flowchart of maskless probe design.

penalized for the presence of subregions containing sequences that are problematic to synthesize or prone to GC clamping. In order to

prevent the formation of intra-molecular bonds, probes exceeding a set palindromic sequence threshold were penalized. Lastly, probes with a salt-adjusted melting temperatures deviating from a set isothermic range were penalized [188]. Probes specific to each domain were then selected on the basis of this score and their location with respect to neighboring probes. In some cases the lack of sequence complexity resulted in minimal representation of that segment by high quality probes. A lower quality probe was then used if its absence would otherwise result in a gap of coverage exceeding the maximum allowable length (99 bp). The assignment of a quality score to all probes allowed for *a priori* predictions of probe performance prior to sample hybridization. Such information was useful in instances of large signal discrepancies between neighboring probes. Utilizing this method of array design 43,020 oligonucleotide probe sequences were generated and synthesized on the Agilent 4 × 44 K custom array platform. This approach can be readily adapted to any genome.

As shown in Figure 2.4, competitive hybridization of wild type mouse and human genomic DNA samples to the interspecies tiling array demonstrated the efficacy of the species specific probe design. Essentially the entire signal throughout the mouse protamine probe set corresponds to the hybridization of mouse DNA (Figure 2.4A). As expected, this is mirrored by the probe set targeting the extended human domain hybridized to human DNA (Figure 2.4B). Probe specificity due to hybridization of the transgenic DNA is clearly observed (Figure 2.4C). Upon competitive hybridization of the transgenic DNA containing the human locus to the 110,050 bp region of human DNA that encompasses the domain. The signals from the 2,282 probes representing the inserted domain are essentially exclusive to the human segment. As expected, probes corresponding to regions flanking the inserted sequence display levels of hybridization which are below background as these sequences are essentially equally matched between the samples. This clearly demonstrates the specificity of the probes and the utility of this probe design strategy.

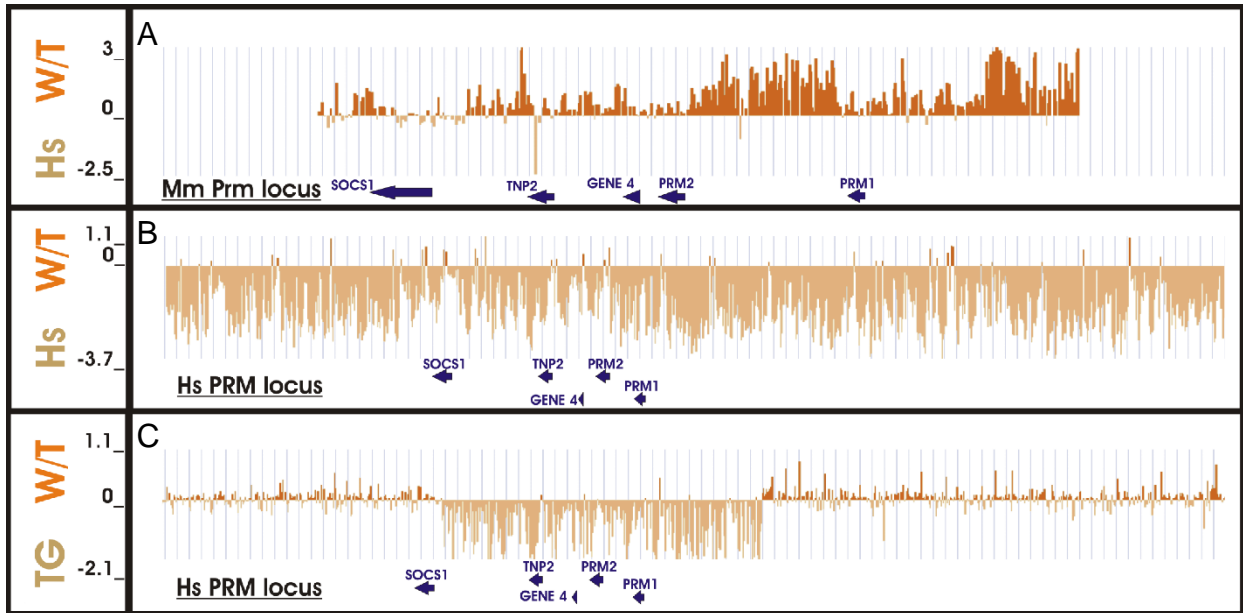


Figure 2.4. Interspecies comparative CGH array analysis of human, wild type, and transgenic mouse genomic DNA. Competitive hybridization of wild type mouse and human genomic DNA to probes targeting the mouse protamine domain (A; chromosome 16: 10,782,515 – 10,802,516; GRCh37) and the extended human protamine domain (B; chromosome 16: 11,312,500 – 11,452,413; GRCh37). Both sets of probes exhibit species specificity. Competitive hybridization of wild type and homozygous transgenic mouse genomic DNA to probes targeting the extended human protamine domain (C) confirms insertion of the complete transgenic locus. Elevated transgenic signal is directly representative of the inserted human DNA sequence (chromosome 16: 11,349,856 - 11,390,141; GRCh37); signal ratio corresponding to the regions flanking the protamine domain is ~1:1. Y axis is Log2.

Development of an interspecies tiling array provides an ideal tool to compliment the transgenic mouse model of the human protamine locus. The design strategy outlined in this study generated probe sets capable of simultaneously querying the orthologous domains in a single experiment independent of repetitive elements. With proof of principle now established this approach could move forward to begin dissecting the mechanisms that regulate the selective expression of the protamine locus.

CHAPTER THREE

CHROMATIN AND EXTRACELLULAR VESICLE ASSOCIATED SPERM RNAs

This chapter was adapted from the following publication:

Johnson GD, Mackie P, Jodar M, Moskovtsev S and Krawetz SA (2015). "Chromatin and extracellular vesicle associated sperm RNAs." *Nucleic Acids Research* 43(14): 6847-6859.

I. Summary

A diverse pool of RNAs remain encapsulated within the transcriptionally silent spermatozoon despite the dramatic reduction in cellular and nuclear volume following cytoplasm/nucleoplasm expulsion. The impact of this pronounced restructuring on the distribution of transcripts inside the sperm essentially remains unknown. To define their compartmentalization, total long RNA was extracted from sonicated spermatozoa (SS) and detergent demembranated, sucrose gradient-fractionated (Cs/Tx) sperm heads. Sperm RNAs predominately localized towards the periphery. The corresponding distribution of transcripts and thus localization and complexity were then inferred by RNA-seq. Interestingly, the number of annotated RNAs in the CsTx sperm heads exhibiting reduced peripheral enrichment was restricted. However this included Cabyr, the calcium-binding tyrosine phosphorylation-regulated protein encoded transcript. It is present in murine zygotes prior to the maternal to the zygotic transition yet absent in oocytes, consistent with the delivery of internally positioned sperm-borne RNAs to the embryo. In comparison, transcripts enriched in sonicated sperm contributed to the mitochondria and exosomes along with several nuclear transcripts including the metastasis associated lung adenocarcinoma transcript 1 (*Malat1*) and several small nucleolar RNAs. This supports the view that non-coding RNAs are also removed from the condensing nucleus as part of the nucleoprotein exchange.

II. Introduction

Following spermatogenesis the mature male gamete remains in a transcriptionally and translationally quiescent state yet harbors a unique population of RNAs [4, 122, 123, 196]. Many

of these transcripts possess a clearly defined role during spermatogenesis providing a rich source for the discovery of male fertility biomarkers [197]. Still other sperm RNAs await functional assignment. Notably, these sequences in sperm may not require translation to be of functional importance within the cell or following fertilization [107, 198]. Regardless of their coding potential attributing function to sperm RNAs has been complicated by a poor understanding of basic principles governing these transcripts including their cellular localization. Some RNAs likely remain bound to protein chaperones as ribonucleoprotein particles that are observed following their transcription in round spermatids [109, 199]. Yet, others, may complex with the paternal chromatin [200, 201]. Nevertheless, assigning functional roles to all sperm transcripts necessitates understanding their cellular localization.

Various studies have used FISH to establish the presence of specific RNAs within the context of the spermatozoon [202, 203]. However, localizing an internally positioned target within the mature sperm head is challenging due to the extreme compaction of this structure. The stability of proteins relative to RNAs offers greater flexibility in their immunological localization as chemical agents can be employed to increase penetrance and thereby the chance of detection [204]. However, microscopy is not conducive to identifying the major sites of sperm RNA compartmentalization in a high-throughput manner.

As illustrated in Figure 3.1, the extra-nuclear and intra-nuclear compartments provide at least two sites within the limited volume of the sperm head that should be capable of harboring RNA. PCR analysis of others has shown that specific transcripts are lost when sperm nuclei were demembrated [205]. This is consistent with previous detergent based sperm purification methods which are expected to compromise membranes, impacting RNA-seq profiles [206].

Fractionation of nuclei and subsequent isolation and analysis by RNA-seq is a routine procedure in somatic cells [207] but has yet to be attempted in sperm. To discern the global

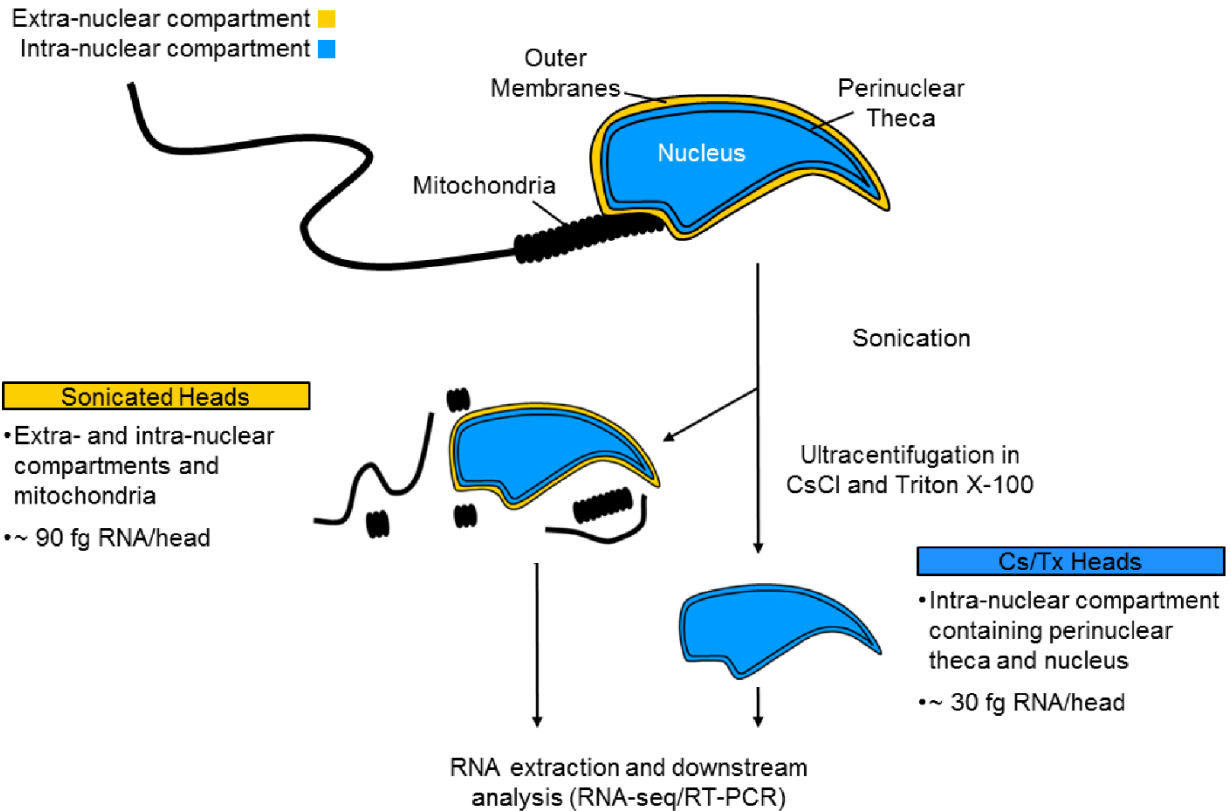


Figure 3.1. Potential sites of RNA localization in sperm. RNAs extracted from sonicated sperm can localize to three generalized compartments: (1) Mitochondria; (2; yellow) extra-nuclear compartment that includes the plasma membrane, the acrosome and associated membranes; (3; blue) the intra-nuclear compartment which includes the nucleus, the nuclear envelope, and the perinuclear theca. Fractionation and demembranation produces a population of sperm heads that remain associated with the perinuclear theca but lack the extra-nuclear compartment as well as the mitochondrial sheath and tail. RNA-seq analyses of transcripts extracted from SS or Cs/TX heads were used to identify compartment specific patterns of RNA enrichment.

pattern of transcript compartmentalization in mouse spermatozoa, total RNA was extracted from sonicated sperm (SS) and detergent demembranated gradient fractionated (Cs/TX) sperm heads. RNA quantification demonstrated that the majority of RNA in sperm is associated with the peripheral membranes which are lost following treatment with detergent. To identify sperm transcripts that exhibited preferential enrichment in either the intra- or extra-nuclear compartment (Figure 3.1) RNAs extracted from SS and Cs/TX sperm heads were subjected to RNA-seq analysis. The Cs/TX heads exhibited suppressed coverage of annotated RNAs supporting their general depletion from the nucleus and perinuclear theca and localization within the outer sperm

membranes. As expected transcripts enriched in these samples by RNA-seq displayed a reduced peripheral enrichment when evaluated by RT-PCR and included RNAs associated with the cytoskeleton and spermatogenesis. In comparison RNA-seq analysis highlighted a set of preferentially extra-nuclear localized RNAs, many of which are associated with extracellular vesicles. This association was supported by a cross-species comparison of the mouse and human homologs enriched in the sperm extra-nuclear compartment and exosomes recovered from semen. These results contribute to the growing evidence for the presence of exosomes on the surfaces of the male gamete [208-214]. Additional classes of RNAs also appeared to be associated with the outer sperm membranes including nuclear-encoded mitochondrial transcripts and some nuclear RNAs. The preferential peripheral localization suggests that chromatin remodeling during spermiogenesis is not limited to nucleoproteins as described in the following.

III. Materials and Methods

Sonicated and Cs/Tx Sperm Head Preparation and RNA Extraction

Sperm fractions were prepared and RNAs extracted essentially as described [Figure 3.1; 140, 215, 216]. In brief, mature spermatozoa from transgenic line HP3.1 [217] were isolated from cauda epididymides and vas deferens harvested from individual four month old transgenic mice on ice into 50 mM Tris-HCl, pH 7.4, buffer. The cells were washed twice following filtration through an 80 micron mesh, resuspended in 0.5 mL 50 mM Tris-HCl, pH 7.4, buffer and subjected to sonication with a TekMar TM-50 sonic disruptor (TekMar, Cincinnati, OH) at 70% maximum output for two minutes on ice to separate heads from tails and to lyse potential cellular contaminants. The sonicated sperm suspension was washed twice and $1 - 5 \times 10^7$ sperm per sample were diluted to a volume of 7.5 mL in 1 M sucrose buffered with 50 mM Tris-HCl, pH 7.4, containing 5 mM MgCl₂. A triple-step gradient was prepared by overlaying diluted samples onto cushions consisting of 2 M sucrose buffered with 50 mM Tris-HCl, pH 7.4, containing 5 mM MgCl₂ and 0.45 g/mL CsCl buffered with 25 mM Tris-HCl, pH 7.4, buffer containing 0.5% Triton X-100. Sperm heads were recovered by ultracentrifugation at 75,600 x rcf for 45 minutes at 4° C and

subsequently washed twice with 25 mM Tris-HCl, pH 7.4, buffer containing 0.5% Triton X-100. Following resuspension in 0.5 mL RLT buffer (Qiagen) supplemented with 1.5% β -mercaptoethanol (Amresco), 0.2 mm stainless steel beads were added to the samples and the Cs/TX sperm heads mechanically lysed with a Disruptor Genie (Scientific Industries, Inc., Bohemia, NY). After the addition of an equal volume of Qiazol (Qiagen) nucleic acids were recovered using the RNeasy system (Qiagen). Following sonication and washing sonicated sperm RNAs were equivalently extracted. Total RNAs were DNased (Turbo DNase, Ambion) and subsequently subjected to RT-PCR with intron-spanning primers to Prm2 [Table 3.1; 217].

Table 3.1. Primer sets used for RT-PCR validation of GFold RNA-seq predictions

PRIMER NAME	FORWARD (5' - 3')	REVERSE (5' - 3')	ANNEALING TEMPERATURE °C	cDNA AMPLICON (bp)
ERCC-00148	GTCCTTGCTCGATGTTGACC	CGCTCCATAAATTCAACTACGG	56	151
Novel RNA*	ATTGGGAAGTCAGTATAGGA	AGTATTTCTCGTTCGGCCTG	56	159
Ankmy1	GTCCCGTAGCCTTCTCGTTG	CCTACCATGGGCAGTTTTACCG	56	115
Evi5l	CGACTGATGCAGGAGTACCG	CAGGACGATGCATACATGGAC	56	164
Tnp2	CCGTGCACTCTCGACACTCAC	ACATCCTGGAGTGCGTCACTTGT	61	176
Prm2	GCACCATGGTTCGCTACCG	GTGGCCTCACATGATGTTGCT	56	420
Prdx1	ATTGCTTTCAGTGATAGAGCC	CTTCATCAGCCTTTAAGACTCC	56	202
Rps4x	GCGGGATTCTTTTGTGCCT	GTCGCTTGTGTTTCATCGT	56	93
rRNA	GCCTCACGATCCTTCTGACCTT	TGGGTGAACAATCCAACGCTT	65	177
Snora81	TAGATGTTAAGGACTGACGA	ATTGCACCGAATCTTATGACA	56	92
Lamp2	TTGTTGCACATATAAGAACTTCC	CATGTATTTGGCTAATGGCTC	56	93
Ndufc1	AACTTAACCATGCAAAACGTG	TCCTTCCTCTGGATTACCC	61	132
Cox6c	AGAAACTATTCTTAGCCACACA	CAAGAAAGAAGGCGTATGCAG	56	205
Gng5	AGAATGCTCAACATGACC	TAGATGTTAAGGACTGACGA	56	226
Malat1	ATCGATTAAAGTAAATGGGCTA	TTACATGCAGGAACATTGACA	56	100

Isolation of RNA from Human Sperm and Seminal Vesicles

Normozoospermic semen (WHO 2010) was collected from healthy donors with proven fertility by masturbation after 2-5 days of sexual abstinence. Following analysis excess semen was stored at -80 °C. Samples were thawed at room temperature for 20 min and exosomes were isolated from the seminal fluid by differential centrifugation at 4 °C as follows: 3,000 rcf for 10 min to pellet sperm fraction which was stored at -80 °C, followed by 12,000 rcf for 45 min to pellet cellular debris and larger vesicles. The supernatant was centrifuged at 110,000 rcf (Beckman Coulter Optimax MLA-13 rotor) for 70 min. The resulting exosomal pellet was washed with 1 ml PBS (Dulbecco's Phosphate Buffered saline), pelleted again at 110,000 rcf for 70 min and stored at -80 °C until RNA extraction. The sperm pellet was thawed and processed through a 50%

PureSperm (Nidacon) cushion prior to RNA extraction. Exosomal and sperm RNA-seq libraries were prepared as outlined below.

Transmission Electron Microscopy

Aliquots of SS and Cs/TX sperm were subjected to transmission electron microscopy at the Microscopy Imaging Laboratory (University of Toronto, ON) using standard protocols. Briefly, cells were pelleted by centrifugation, fixed in a 4% paraformaldehyde with 1% glutaraldehyde buffered with 0.1 M sodium phosphate monobasic buffer (NaH_2PO_4), pH 7.2, at 4°C and subsequently post-fixed with 1% osmium tetroxide buffered with 0.1 M sodium phosphate dibasic buffer (NaH_2PO_4), pH 7.2, for 1 hour. Dehydration of the cells was achieved with a series of increasing concentrations of ethanol to allow for infiltration of the Epon embedding resin. The resin was sectioned on an ultramicrotome (Leica) and transferred to a copper TEM grid. Reynolds lead citrate and 5% uranyl acetate was used for contrast staining and micrographs were taken on a Hitachi H 7000 at 75 Kv (25uA beam current) using an AMT XR-60 digital camera.

Sequencing Library Preparation and Analysis

Stock synthetic spike-in External RNA Controls Consortium ERCC (ERCC) RNAs (Invitrogen) were diluted 1:10,000 and pooled with 5 nanograms of total sperm RNAs prior to reverse transcription and amplification using the Seq-plex system [Sigma; 218]. Pre-amplified cDNA libraries were subjected to sequencing library construction (DNA Ultra-Low, NEB) followed by 50 cycles of paired-end sequencing on the Illumina Hi-Seq 2500 platform. Sequencing reads were aligned simultaneously to the mouse genome assembly Mm10 in addition to the ERCC FASTA sequences with Tophat2 [version 2.0.12; 219] using the following parameters: tophat2 -r 30 --mate-std-dev 50 --no-coverage-search -G genes.gtf. Novel transcript structures were assembled using Cufflinks [version 2.1.1; 220] after removal of PCR-duplicates with Picard tools (<http://picard.sourceforge.net>). Assembled transcripts exceeding twice the average fragment length (135 bp) were combined with UCSC gene annotations (Mm10).

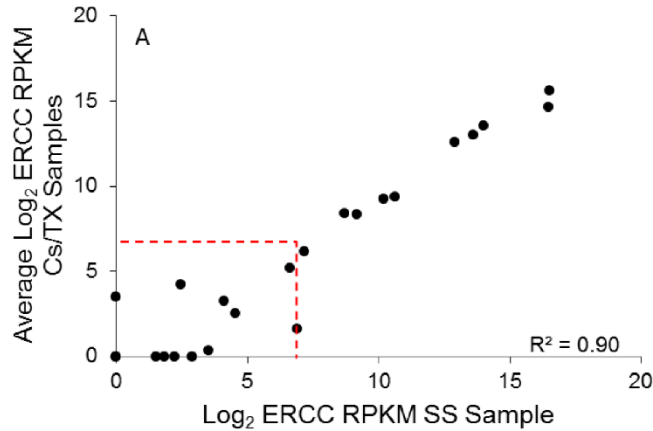


Figure 3.2. Determining the RPKM cutoff. To determine a lower limit of detection synthetic ERCC RNAs were added in equal amounts to all samples prior to cDNA synthesis. Coverage of ERCCs present in all samples was calculated using uniquely aligned sequencing reads and the log₂ (RPKM + 1) values for the nuclei 1 and whole sperm samples plotted. ERCC coverage was highly correlated across all samples ($r^2 > 0.90$; Figure E1). This linear relationship was strongest among the most abundant ERCCs demonstrating that inter-sample comparisons of RNAs exceeding 116 RPKM were reliable (dashed red line). Differentially enriched transcripts failing to exceed this cutoff were not reported.

Preliminary analysis of aligned sequencing reads was carried out with the Samtools [version 0.1.19; 221] and Bedtools [version v2.19.1-2; 222] suites. Ranked predicted fold change and RPKM values for enrichment analyzes were calculated using uniquely aligned reads and the GFold package [223]. A lower limit of detection was determined by analysis of ERCC coverage. Log normalized ERCC RPKM values were correlated across samples ($r^2 > 0.90$; Figure 3.2) demonstrating that inter-sample comparisons of RNAs exceeding 116 reads per kilobase per million mapped reads (RPKM) were reliable. To derive enrichment predictions the Cs/TX samples were independently compared to the SS sample and the intersection of transcripts with an absolute GFold value greater than zero and a RPKM value exceeding the ERCC cutoff were considered for RT-PCR validation. Differential enrichment analysis of the human ejaculate exosomes and human sperm RNA-seq samples as well as mouse embryo and oocyte analyzes were performed with both with the HT-Seq and DEseq2 software packages [1, 224, 225] as well as GFold [226].

Plots and browser graphics were generated using the ggplot2 R package and the UCSC genome browser, respectively. Ontological analyzes were performed using GOrilla and associations presented as FDR corrected q-values [227]. A hypergeometric probability function in R was used to assess the likelihood of overlap observed between sperm datasets and nuclear encoded mitochondrial transcripts taken from the Mitocarta database [228] and human ejaculate RNA-seq datasets.

Genomic coordinates of repeat elements were retrieved from the Repeat Master track of the UCSC genome browser and analyzed with Bedtools. To determine the relative coverage of repeat families unmapped and multiply-mapped reads were aligned to the rodent RepBase v19.0 repeat sequences [229]. Following alignment the number of uniquely aligned sequencing reads corresponding to each repeat family was summed and those values combined with those obtained from the initial unique alignments from the same sample. Estimates of subfamily abundance of sperm LINEs were determined by equivalently subsampling and aligning FASTQ files to canonical sequences for each of the actively transcribed mouse LINE elements retrieved from RepBase [230]. Only uniquely aligned sequencing reads were considered.

RT-PCR Validation

Samples (n = 6) used for RT-PCR validation of the RNA-seq results were isolated as above with minor changes. Sonicated and washed sperm from a single mouse were counted on a hemocytometer and split into two equal aliquots. Subsequently sperm were either subjected to ultracentrifugation through a triple-step gradient or left on ice prior to nucleic acid extraction. SS and Cs/TX pellets were divided into two aliquots and used for separate RNA and DNA extractions. Prior to RNA extraction sperm samples were lysed with RLT buffer supplemented with 1.5% β -mercaptoethanol and Qiazol as above and following disruption with 0.2 mm stainless steel beads stored at -80°C . Sperm pellets were digested with proteinase-K in the presence of β -mercaptoethanol and DNAs recovered by phenol-chloroform extraction with phase-lock tubes (5Prime) followed by ethanol precipitation with linear acrylamide. DNAs were quantified with

Picogreen (Invitrogen) and used to equilibrate the stored RNA extractions with respect to sperm concentration per volume of lysate. For each individual animal equal volumes of the SS and Cs/TX lysate were passed through the RNeasy column such that RNA was recovered from equivalent number of match sonicated and demembrated sperm heads. Subsequently, eluted RNAs were DNased as above prior to quantification with Ribogreen (Invitrogen). First-strand cDNA was synthesized using equal volumes of total RNA with the addition of 1 μ l of diluted ERCC, (1:1,000), 40 units of RNase Block (Agilent), 100 ng of random primers (Invitrogen) and the Superscript III kit (Invitrogen). Diluted SS and Cs/TX cDNA products were analyzed in parallel triplicate reactions by real-time PCR using Hot-Star Taq Polymerase system (Qiagen) and 0.5 mM of each forward and reverse oligonucleotide primer (Supplementary Dataset 1) for 50 cycles. Delta-Ct values are calculated as follows: $\Delta Ct = Ct_{Cs/TX} - Ct_{SS}$.

IV. Results and Discussion

Isolation of Compartmentalized RNAs

The highly condensed mature spermatozoon possesses distinct structural features and organelles which may harbor site-specific populations of RNAs. To elucidate whether patterns of RNA retention vary between the peripheral structures contained in the extra-nuclear compartment of the gamete and those found within the intra-nuclear compartment, sperm samples were briefly sonicated and aliquots subjected to gradient fractionation in the presence of detergent. Electron microscopy confirmed the separation of sperm heads and tails following sonication as well as the absence of contaminating cell types (Figure 3.3). Despite the absence of an intact acrosome the SS retained the inner acrosomal membrane (IAM) as well as portions of the outer acrosomal membrane [OAM; 231]. Ultracentrifugation of the SS heads through a sucrose cesium chloride step gradient and detergent demembration produced sperm heads free of tail and mitochondrial sheath remnants. In addition, the Cs/TX heads lacked all peripheral membranes while retaining the perinuclear theca. This network of cytosolic and nuclear proteins attaches the inner acrosomal

membrane to the nuclear envelope and is resistant to extraction with both ionic and non-ionic detergents such as Triton X-100 used in this study [231, 232].

Isolation of RNAs from SS and Cs/TX heads demonstrated that the long RNA fraction (> 200 nt) in sperm is primarily peripherally localized (Figure 3.4). Accounting for the RNA recovered from Cs/TX sperm heads, 61.45% of the 87 femtograms of RNA retained in each spermatozoon must be found within the membranes removed during isolation of the nucleus and perinuclear theca (Figure 3.1 and 3.3). This supports prior work demonstrating that treatment with detergents alters the transcript profile of the sperm cell [206]. Resolution of whether the RNAs recovered

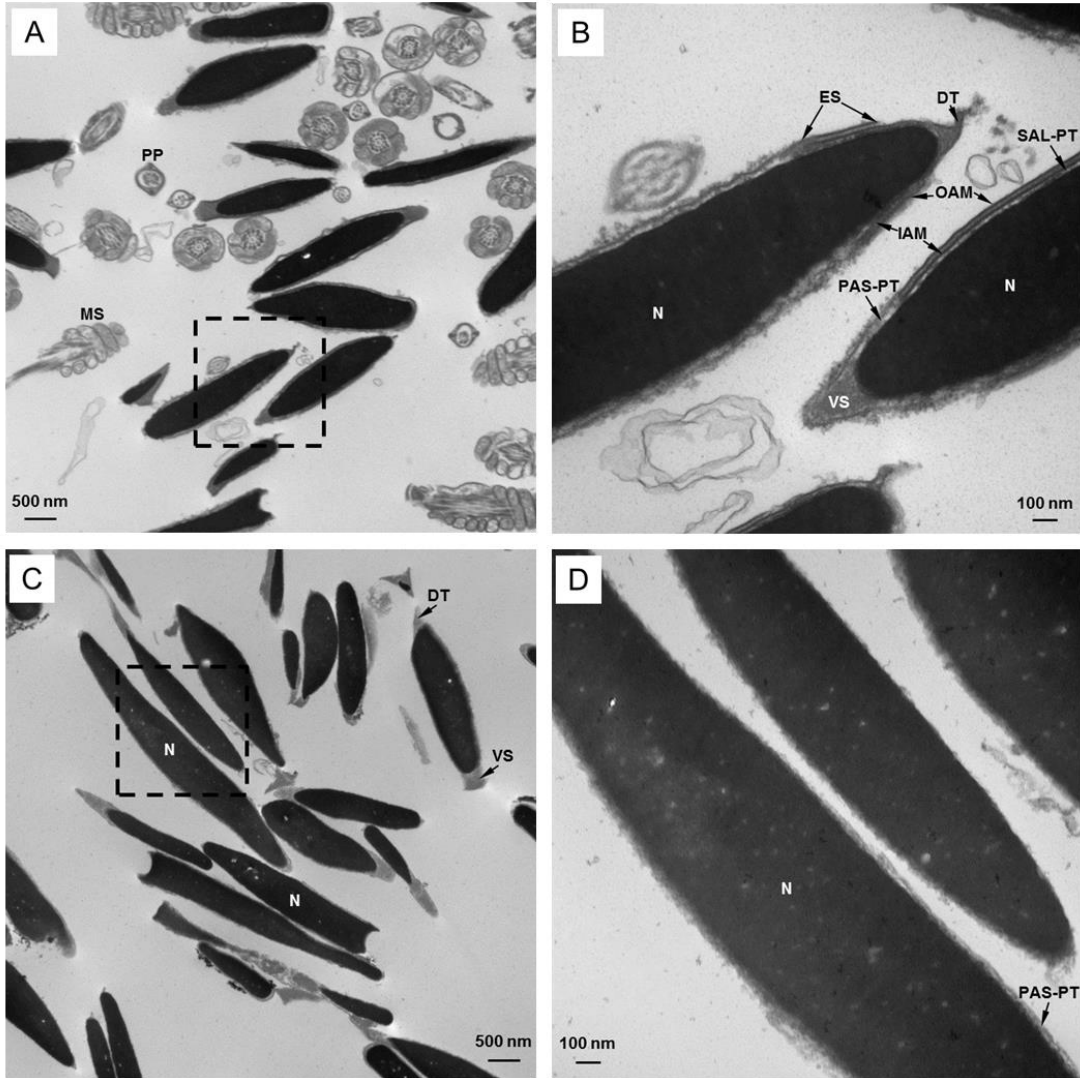


Figure 3.3. Cs/TX fractionated sperm heads lack peripheral membranes. (A and B) Sonication separates the tail from the sperm head while preserving the outer membrane structures. Fragments of the sperm tail (PP) and mitochondrial sheath (MS) are observed following sonication whereas potential somatic contaminants are not. (C and D) Fractionation through a sucrose-cesium chloride gradient in the presence of Triton X-100 enriches a population of sperm heads free from tail and mitochondrial remnants. The Cs/TX sperm nucleus remains surrounded by the perinuclear theca (PT) as evidenced by the dorsal tip (DT) and ventral spur (VS) structures but lacks the peripheral membranes observed in the sonicated sample. Dashed boxes in A and C (Magnification x 12,000; scale bar = 500 nm) are presented at higher magnification in B and D (Magnification x 50,000; scale bar = 100 nm). Equatorial segment (ES); inner acrosomal membrane (IAM); mitochondrial sheath (MS); nucleus (N); outer acrosomal membrane (OAM); perinuclear theca (PT) postacrosomal sheath of the PT (PAS-PT), principle piece (PP) of the sperm tail; subacrosomal layer of the PT (SAL-PT).

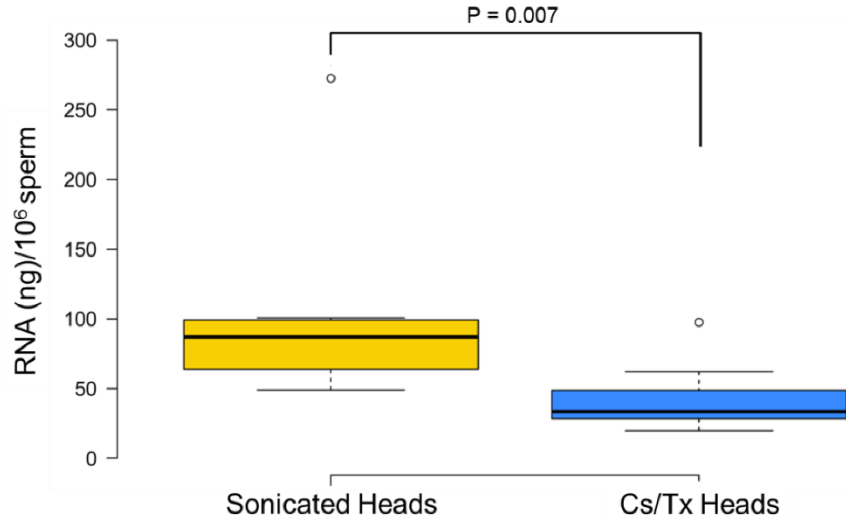


Figure 3.4. The majority of the RNA retained in sperm is localized to the sperm periphery. RNAs were quantified after recovery from equal numbers of sperm heads from the same animal ($n = 9$) following sonication and Cs/TX fractionation. The SS cells contained significantly more RNA than matched Cs/TX heads ($P = 0.007$, two-tailed paired T-test). After accounting for the presence of the intra-nuclear compartment within each SS sperm cell approximately 53.47 fg of RNA is associated within the peripheral structures of the extra-nuclear compartment. Center lines show the medians (87.03 and 33.56 fg of RNA per sperm head, SS and Cs/TX, respectively); box limits indicate the 25th and 75th percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, outliers are represented by dots and represent matched SS and Cs/TX samples from the same animal.

from the Cs/TX heads reside within the nucleus and/or the perinuclear theca remains a technical challenge. To better understand patterns of transcript localization throughout the male gamete RNA from the SS and Cs/TX sperm heads was subjected to RNA-seq analysis.

Library Characteristics

Mitochondrial encoded transcripts

The efficacy of the sample fractionation established by microscopy was confirmed by the reduced sequencing coverage of the mitochondrial genome in the Cs/TX sperm heads (Figure 3.5A). In contrast, the SS heads exhibited a ten-fold enrichment in coverage of mitochondrial RNAs corresponding to greater than 7% of all uniquely aligning reads. This value is within the

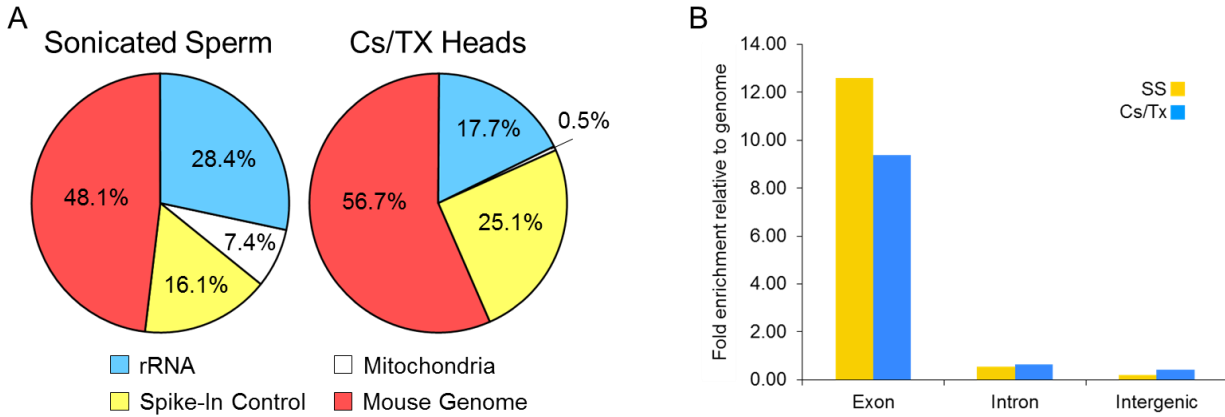


Figure 3.5. Sequencing coverage and enrichment in annotated regions vary between the SS and Cs/TX sperm heads. (A) RNAs extracted from SS or Cs/TX samples were subjected to RNA-seq. Following alignment the percentage of uniquely aligned sequencing reads attributed to specific classes of sequences was determined. The largest contribution of alignments in both the Cs/TX and SS RNA-seq libraries corresponded to the nuclear genome in a treatment dependent manner. Coverage of the rRNAs and the ERCC control RNAs in libraries also varied by preparation. The reduced sequencing coverage of the mitochondrial genome in the Cs/TX sperm heads confirmed the efficacy of the sample fractionation. (B) SS cells exhibited a greater enrichment of uniquely aligned sequencing reads in coding regions relative to that observed for the Cs/TX samples. Fold enrichment values for uniquely aligned sequencing reads within exons, introns and intragenic regions are presented for SS and Cs/TX RNA-seq libraries. Enrichment was determined by dividing the percentage of genomic bases in an element class by the percentage of unique sequencing reads aligned to that class.

range (3.5 - 36%) observed in other mouse sperm RNA-seq datasets [4, 196, 233] indicative of significant differences in sample and library preparation [206].

Ribosomal RNAs

In addition to a greater proportion of mitochondrial transcripts, the SS heads possessed greater amounts of ribosomal RNAs (rRNAs, Figure 3.5A). Together these transcripts and their associated pseudogenes constituted 28% and 17% of all unique sequencing reads in the SS and Cs/TX libraries, respectively, even though unlike other cell types, sperm rRNAs are fragmented [2, 114]. It is not obvious why the ribosomal transcripts persist at elevated levels in both sperm fractions. Within the SS samples the elevated levels of rRNA reflect the additional contribution of membrane-associated ribosomal transcripts in addition to those retained following isolation of the Cs/TX sperm head structures (Figures 3.1 and 3.3). The abundance of the rRNAs in SS relative

to demembrated Cs/TX samples may reflect entrapment of cytoplasmic constituents during condensation and concurrent membrane restructuring and/or be acquired from or maintained in external structures such as membrane-bound extracellular vesicles. These structures have been observed *in vivo* in physical association with spermatozoa [208, 211, 213, 214]. Unlike cytoplasmic droplets which are osmotically sensitive structures formed by maturing spermatids as they expel their cytoplasm and often lost during routine sperm processing [234], sperm-bound exosomes fuse with the gamete [212]. Further support that the elevated levels of ribosomal transcripts in the SS cells relative to that observed in the Cs/TX heads may result from the packaging of these sequences in extracellular vesicles is the recent observation that this class of RNA is the most abundant observed in exosomes retrieved from human semen [210].

Greater than 17% of the uniquely aligned reads in the Cs/TX RNA-seq libraries corresponded to the ribosomal transcripts. Considering that rRNAs are not commonly observed in somatic nuclear RNA [207] and in the absence of evidence for their translocation into the nucleus these transcripts are presumed to be intimately associated with but likely outside of the highly condensed nucleus. In this manner these transcripts might persist within partially assembled ribosomes as has been observed in cytoplasmic droplets [114]. The abundance of the rRNAs and their associated proteins would suggest that they are not completely expelled during the final stages of spermiogenesis. This may lead to the sequestration of the translational machinery within the perinuclear theca as has been observed in proteomic analysis of detergent-treated sperm nuclei [235]. As these proteins are not known to contribute to this cytoskeletal nucleus-acrosomal interface they may be passively retained along with bound rRNAs through prior association. Whether this mechanism resolves other RNA associations within the sperm nucleus, as has been previously suggested [205], remains unclear.

ERCC control RNAs

To determine a lower limit of detection synthetic ERCC (External RNA Controls Consortium) RNAs were added in equal amounts to all samples prior to cDNA synthesis.

Coverage of the control transcripts was highly correlated across all samples ($r^2 > 0.90$; Figure 3.2) while their absolute levels varied between fractionation methods. Of all uniquely aligning sequencing reads approximately, 25% Cs/TX and 16% SS sperm head reads corresponded to the ERCC transcripts in the corresponding RNA-seq libraries. The increased representation of these synthetic sequences in the Cs/TX sequencing libraries was likely a consequence of the reduced availability of biological and or accessible RNA templates following the loss of the outer sperm membranes. Supporting this observation the Cs/TX heads exhibited a 10% increase in the percentage of reads aligned to the nuclear genome and a concomitant decrease in coverage of annotated regions relative to the SS heads (Figure 3.5B). This is reminiscent of the observation that the use of detergents to remove somatic cell contaminants from human sperm negatively impacts transcript levels compared to samples purified by other means [206]. Representation of intronic sequences were equivalently suppressed in all libraries (Figure 3.5B) reflecting the cessation of nascent RNA production prior to nuclear condensation.

Identification of Putative SS and Cs/TX Enriched Transcripts

Mature spermatozoa possess a unique morphology and a comparatively small quantity of RNA. These limitations required that sonicated sperm containing nuclei surrounded by perinuclear theca be compared to the demembrated Cs/TX heads rather than independently sampling compartments as can be accomplished for somatic cells [207]. By mass approximately 38.55% of the RNA within a sonicated sperm cell can be attributed to the structures contained within a Cs/TX head (perinuclear theca, and nucleus; Figure 3.1 and 3.3). Therefore transcripts enriched within the more external regions of the spermatozoon will be diluted by RNAs present within the mitochondrial sheath, the perinuclear theca, and nucleus, reducing their representation when resolved by RNA-seq. Consequently, the sampling methods employed herein are expected to under- and over-report putative externally (SS) and internally (Cs/TX) localized transcripts, respectively. In addition, the limited data suggested an alternative to standard differential expression analysis pipelines was necessary to identify patterns of RNA localization within the

mature spermatozoon. Accordingly, GFold was used to rank transcripts by the posterior distribution of their normalized expression values and candidate transcripts putatively enriched within either the SS or Cs/TX heads were selected for downstream RT-PCR analysis.

The GFOLD analysis identified a total of 308 transcripts that were preferentially enriched in the Cs/TX RNA-seq libraries. Together this set of RNAs included 184 annotated and 116 novel transcripts as well as all ERCC control transcripts exceeding the minimum threshold of detection. Ontological analysis of the annotated RNAs enriched in these samples identified terms related to spermatogenesis ($q < 1.0 \times 10^{-6}$). Within this set of RNAs, the *Prm1* transcript, as well as *Erich2* and *Fam71e2* (formerly *4933404M02Rik* and *4930401F20Rik*, respectively), were previously identified within the mouse sperm nucleus by RT-PCR though their preferential localization within the gamete could not be inferred from that study [205].

As expected fewer transcripts were predicted to be enriched in the SS RNA-seq libraries relative to the Cs/TX heads ($n = 152$). This set of putatively enriched sonicated sperm RNAs included many nuclear-encoded mitochondrial protein mRNAs ($n = 20$; $P < 1.9 \times 10^{-20}$; Figure 3.6A). These RNAs comprised 17% of the transcripts enriched in the SS RNA-seq libraries and only 2% of the Cs/TX enriched RNAs [$n = 4$; 228]. This association was supported by ontological analysis of the predicted SS RNAs which revealed terms related to the mitochondrial membrane ($q < 5.9 \times 10^{-05}$). Together this likely represents the evolutionarily conserved shuttling of cytosolic ribosomes bound with nuclear-encoded mitochondrial mRNAs to the surface of the mitochondria prior to condensation [236-238]. These transcripts are expected to be lost along with the mitochondrial sheath and proximal structures during fractionation of the Cs/TX heads.

Additional ontological categories were also significantly associated with the RNAs enriched in the SS sample. These included terms related to exosomes ($q < 1.05 \times 10^{-9}$). The enrichment of exosomal-associated RNAs in the SS RNA-seq libraries supports prior observations that the outer sperm membranes are associated with extracellular vesicles. This set of transcripts includes guanine nucleotide binding protein (G protein), gamma 5 (Gng5; Figure

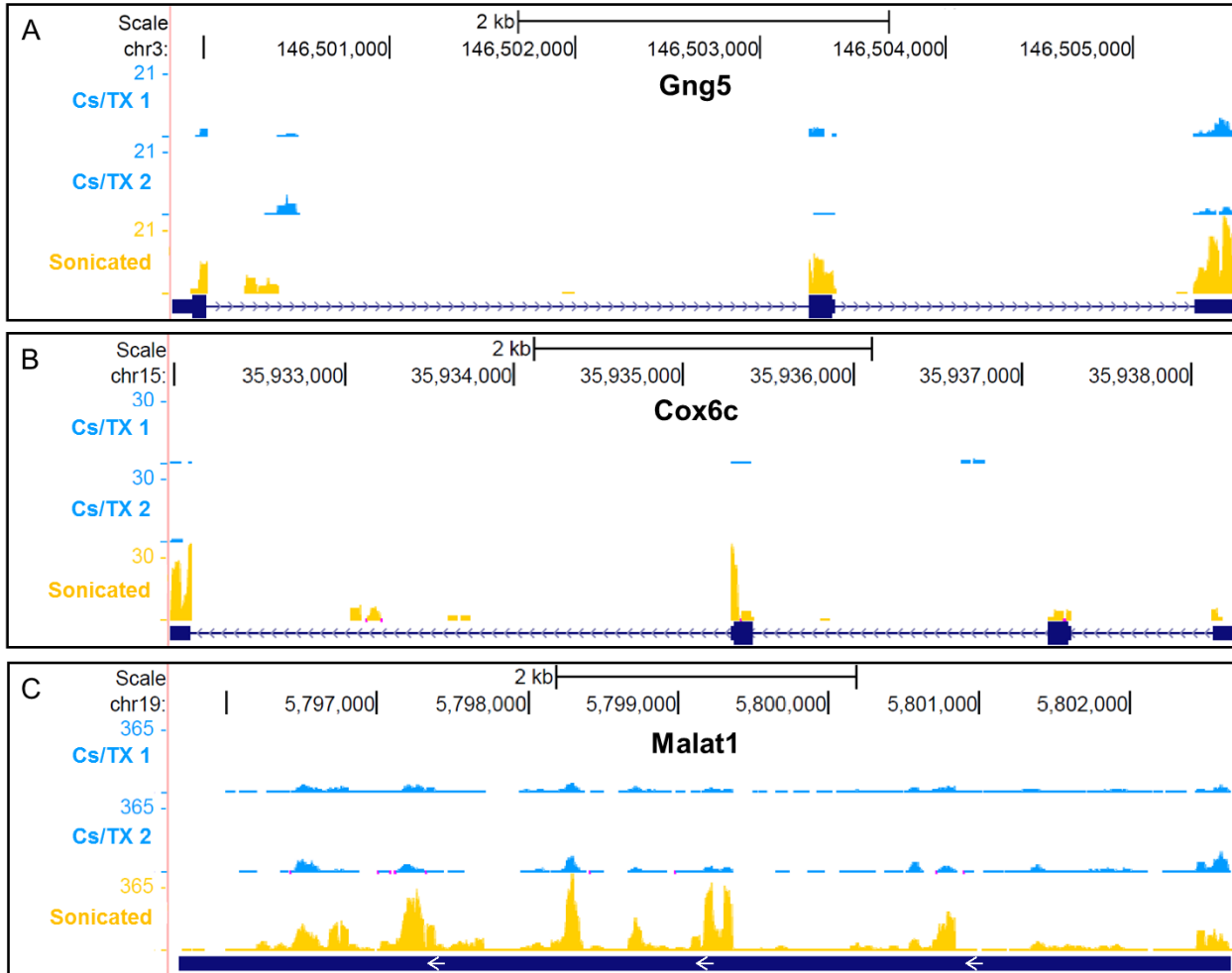


Figure 3.6. RNAs representative of specific cellular functions and organelles are enriched within the peripheral sperm membranes. Coverage of uniquely aligned sequencing reads are presented for three transcripts on the UCSC genome browser. Reads per million uniquely aligned reads (RPM) are presented on the Y-axis for each sample with the maximum value corresponding to that observed in the SS sample for each RNA panel. The direction of transcription is depicted by arrows. (A) *Cox6c* is nuclear-encoded mitochondrial transcript. (B) The *Gng5* RNA and corresponding membrane-associated G protein product are enriched in exosomes from several tissues and species. (C) *Malat1* is a conserved long non-coding RNA that is enriched at active loci and within paraspeckles where it recruits splicing factors.

3.6B) for which both the RNA and protein products have been observed in exosomes recovered from multiple tissues in human and mouse [239-241]. Interestingly, of the 42 SS enriched transcripts associated with the exosome ontological category, only three were present above background in both Cs/TX samples. This set of SS RNAs exhibited a median fold increase of 5.9

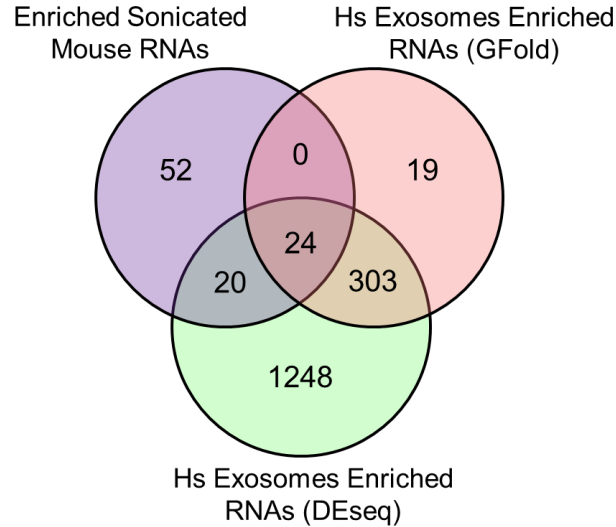


Figure 3.7. Mouse homologs predicted to be enriched in sonicated sperm cells are differently enriched in exosomes recovered from human semen. RNAs were extracted from exosomes and sperm cells collected from human semen and subjected to differential expression analysis with DEseq and GFold. Subsequent analyzes were restricted to mouse and human homologs taken from the Biomart Database (<http://www.biomart.org/>). The majority (95%) of transcripts predicted by GFold to be enriched in the exosome RNA-seq libraries were also found to be significantly enriched in these datasets by DEseq. A hypergeometric probability test was used to compare the overlap of differentially enriched exosome homologs to those predicted to be enriched in the sonicated sperm RNA-seq sample, $P < 6.4 \times 10^{-19}$, hypergeometric probability test.

(range = 2.6 – 192.9) relative to the Cs/TX samples demonstrating that these transcripts are externally localized relative to the perinuclear theca and nucleus and therefore may be delivered to the gamete by exosomes and incorporated during epididymal maturation or within the vas deferens. Further, greater than 45% of all mouse homologs enriched in the SS RNA-seq library were also differentially expressed in human ejaculate exosomes relative to sperm collected from the same semen samples ($P < 6.4 \times 10^{-19}$, hypergeometric probability test; Figure 3.7). By comparison only 8% of the RNAs predicted to be enriched in the Cs/TX libraries were significantly enriched in the human exosome dataset ($p > 0.8$). The depletion of these transcripts following exposure to Triton-X100 reflects the loss of external sperm membranes that serve as sites of exosome attachment and likely harbor RNAs some of which may possess an origin other than sperm [209].



Figure 3.8. Human exosome homologs enriched in the sonicated sperm are present at elevated level compared to their counterparts identified in detergent treated sperm. Sonicated and detergent treated sperm RNA-seq datasets were analyzed by GFold. The \log_2 normalized RPKM values of human exosome homologs predicted to be enriched in sonicated sperm ($n = 544$) and in detergent treated mouse sperm [$n = 500; 4$] are presented as density plots. Exosome homologs were present at greater levels than their counterparts identified in detergent treated mouse sperm ($P < 2.2 \times 10^{-16}$, Mann–Whitney U-test). White circles show the medians; black box limits indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles; polygons represent density estimates of data and extend to extreme values.

To test the proposed link between the detection of exosomal RNAs and the presence of external sperm membranes GFold was used to identify transcripts predicted to be differentially enriched in either the SS sample or in a previously published mouse sperm RNA-seq dataset prepared following detergent incubation [4]. Differentially expressed human ejaculate exosome homologs were present in the set of SS enriched RNAs at levels significantly exceeding that expected by chance ($P < 1.2 \times 10^{-26}$, hypergeometric probability test). This relationship was not observed in the detergent treated sperm ($P = 0.99$). Similarly the human exosome homologs enriched in the SS sample were present at elevated levels ($P < 2.2 \times 10^{-16}$, Mann–Whitney U-test; Figure 3.8) and exhibited a stronger ontological enrichment in exosome associated terms than their counterparts enriched in the detergent treated sample ($q < 3.83 \times 10^{-49}$ and $q < 3.84 \times 10^{-16}$, respectively). Analogous to the Cs/TX sperm head fractionation used in the current study,

detergent treatment [4] would have been expected to produce a sperm nucleus surrounded by the perinuclear theca at the expense of external membranes. Since these external structures harbor the majority of spermatozoal RNA in addition to serving as the site of exosome attachment their loss would be expected.

Several of the SS transcripts included well known somatic nuclear RNAs such as Small Nucleolar RNAs, H/ACA Box (*Snora23*, *Snora52*, *Snora81*), Small Cajal Body-Specific RNA 13 (*Scarna13*), and the long non-coding RNA (lncRNA) *Malat1* (Figure 3.6C). The persistence of an elevated level of *Malat1* in all sperm samples and its extra-nuclear enrichment can be ascribed to the presence of a triple helix structure at its 3' end which stabilizes the transcript [242]. Association of this archetypal nuclear RNA with more external regions of the spermatozoon suggests *Malat1*, *Snora* RNAs, *Scarna13* and potentially other ncRNAs are expelled along with the nucleoplasm. Bereft of a nucleus or Cajal bodies these transcripts appear as if they may not be essential to the mature male gamete or the next generation [205]. However, the retention of a minor pool of nuclear-associated *Malat1* transcripts (Figure 3.6C) may result from the direct interaction of these lncRNAs with regions of the sperm genome which remain in a "poised" chromatin configuration [12-14, 243].

A series of oligonucleotide primers were designed to validate patterns of preferential transcript compartmentalization in sperm by RT-PCR. RNAs from individual mice ($n = 6$) were extracted from equal numbers of SS or Cs/TX sperm heads and reverse transcribed with random primers. The addition of ERCC RNAs to the first-strand synthesis reaction served as a loading and synthesis control (Figure 3.9A). Although the fold-changes estimated from the RNA-seq datasets and delta-Ct values were well correlated ($r^2 = 0.86$; Figure 3.9 B) all queried transcripts were found to be enriched in the sonicated sperm samples suggesting that globally, RNAs are peripherally localized in the mature male gamete (Figure 3.3). This included the first and third most enriched protein-coding transcripts in the Cs/TX libraries, Ankyrin repeat and MYND domain

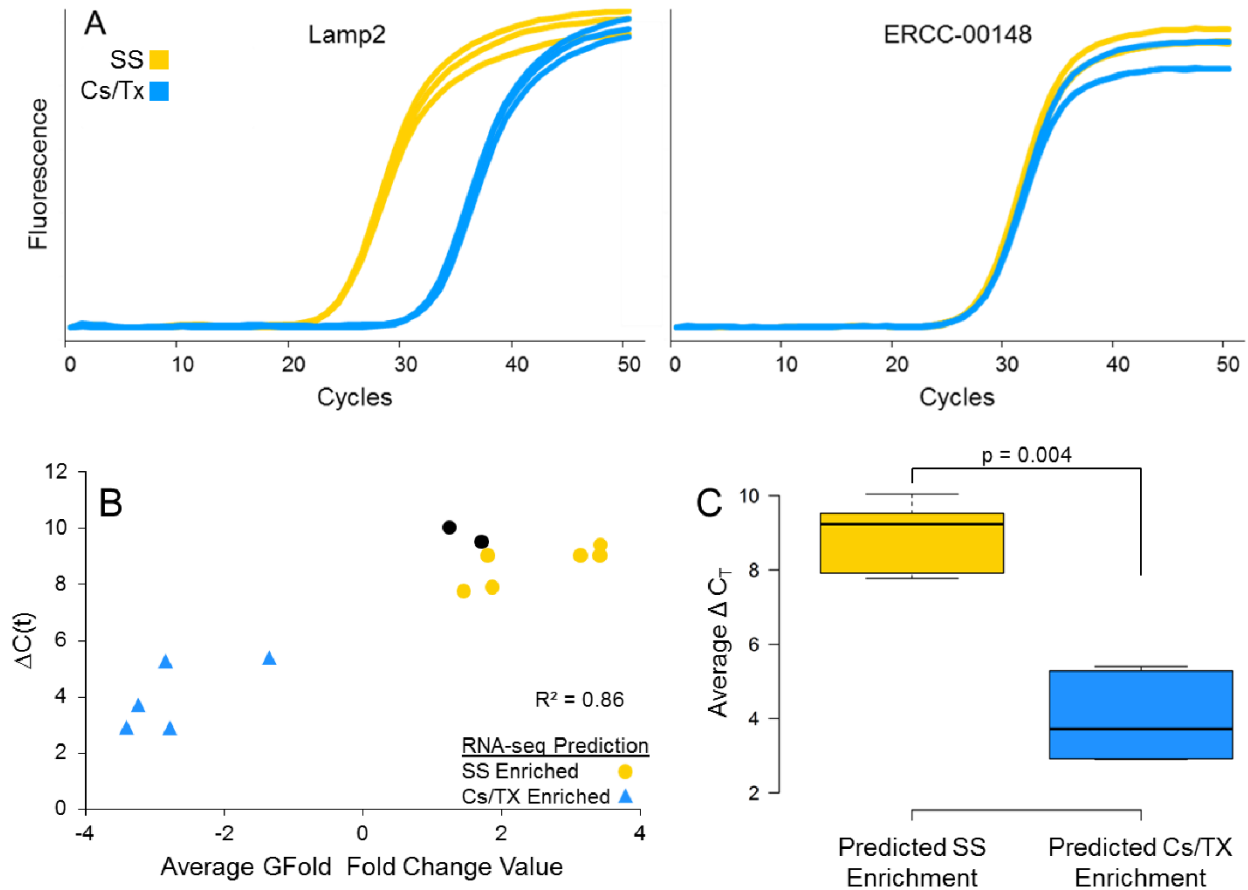


Figure 3.9. RT-PCR validation of peripheral sperm RNA enrichment. (A) To validate patterns of transcript enrichment predicted by RNA-seq RNAs from individual mice ($n = 6$) were extracted from equal numbers of sonicated or Cs/TX sperm heads and subjected to RT-PCR analysis. The transcript encoding lysosome-associated membrane glycoprotein 2 (*Lamp2*) is enriched in sonicated sperm indicating the preferential localization of this RNA within the outer sperm membranes. ERCC spike-in RNAs served as a loading control and exhibited no preferential enrichment. (B) Estimated RNA-seq fold-changes and delta-Ct values were well correlated ($r^2 = 0.86$). Transcripts exceeding the RPKM cutoff (> 116 RPKM; Figure 3.2) are presented in red while *Lamp2* and NADH dehydrogenase [ubiquinone] 1 subunit C1 (*Ndudc1*) are presented in black (~ 85 RPKM in SS). (C) Transcripts predicted by RNA-seq to be enriched in the SS samples ($n = 6$) exhibited significantly greater delta-Ct values ($p = 0.004$, Mann-Whitney U-test) than transcripts predicted to be enriched in the Cs/TX heads ($n = 5$). Center lines show the median delta-Ct values of the SS- and Cs/TX-predictions from RNA-seq (9.23 and 3.72, respectively); box limits indicate the 25th and 75th percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, outliers are represented by dots.

Table 3.2. Sperm RNAs are enriched in the extra-nuclear compartment

Transcript	$\Delta C(t)$	SEM	Extra-nuclear enrichment*	GFold prediction
ERCC-00148	0.12	0.07	1.08	N/A
Novel RNA†	2.90	0.26	7.45	Intra-nuclear
Ankmy1	2.92	0.43	7.57	
Evi5l	3.72	0.39	13.19	
Tnp2	5.28	0.59	38.90	
Prm2	5.40	0.40	42.11	
Prdx1	7.77	0.68	218.02	Extra-nuclear
Rps4x	7.91	0.56	239.69	
rRNA	8.92	0.51	485.32	
Lamp2	9.03	0.55	524.37	
Ndufc1	9.04	0.55	527.92	
Cox6c	9.42	0.61	683.44	
Gng5	9.52	0.62	735.03	
Malat1	10.04	0.52	1,049.15	
Snora81	> 9.04	N/A	‡	

Paired comparisons, n = 6; standard error of the mean (SEM); $\Delta C(t) = (Ct_{Cs/TX}) - (Ct_{SS})$

* $2^{\Delta C(t)}$

†Novel RNA = TCONS_00003257; Supplementary Dataset 2

‡Absence of Cs/TX amplification in some matched samples

containing 1 (Ankmy1) and ecotropic viral integration site 5-like (Evi5l). However, the RNAs predicted by GFold to be enriched in the Cs/TX heads exhibited significantly reduced delta-Ct values compared to those observed for the set of transcripts predicted to be enriched in the sonicated sperm ($P < 0.004$, Mann–Whitney U-test; Figure 3.9C). These results suggest that while the majority of RNA within the mature spermatozoon can be localized to the periphery of the cell the strength of this association varies between transcripts as some are expected to be varyingly retained within the intra-nuclear compartment. On one hand, the relative depletion of Malat1 and Snora81 RNAs (Table 3.2) from the Cs/TX samples predicts that in the male gamete these transcripts are unlikely to contribute to nuclear organization in a manner reminiscent of that observed in somatic cells. On the other hand, some Malat1 remains within the Cs/TX heads and may be sufficient to contribute to the packaging of the limited number of histone-associated

Table 3.3. Cs/TX RNA-seq libraries contain more transcribed repeats sequences

Repeat	Cs/TX	SS	Fold Change
LINE			
L1	5.14%	1.898%	2.71
L2	0.277%	0.183%	1.52
DNA			
hAT-Tip100	0.028%	0.016%	2.38
LTR			
LTR	0.006%	0.002%	2.36
Gypsy	0.006%	0.003%	2.1
ERVK	1.353%	0.841%	1.61
Satellite	0.32%	0.053%	6.05
Low complexity	1.594%	0.448%	3.56
Simple repeat	2.823%	0.915%	3.09

% percent of uniquely mapped reads

promoters present in sperm chromatin [13, 243]. Alternatively, other RNAs such as the repetitive RNAs may participate in packaging the paternal genome.

Repetitive RNAs in Mouse Sperm

Retained repetitive RNAs are of particular interest as they may contribute to nuclear structure as has been observed in somatic cells or may participate in genome confrontation and consolidation observed in plants and animals whereby parental genome compatibility is ensured [197, 244]. To better understand the role and abundance of these RNAs, the coverage of all individual repetitive elements was determined initially using uniquely aligned sequencing reads (Table 3.3). The Cs/TX libraries were enriched in repeat sequences such as satellite, simple, and low complexity repeats (Table 3.3). The presence of satellite RNAs may reflect opportunistic transcription as heterochromatic structures relax prior to protamine deposition. A series of complementary sequences were consistently enriched in the Cs/TX sperm head RNA-seq libraries relative to sonicated sperm (Table 3.3). The representation of these sequences

Table 3.4. Simple and low complexity repeat RNAs are present at significant levels relative to the genomic background in the SS and Cs/TX RNA-seq libraries

Cs/TX heads			SS cells		
Repeats	# above threshold	p-value	Repeats	# above threshold	p-value
(GAAA)n	110	4.80E-71	(TTTTG)n	83	5.31E-18
(TTTC)n	86	7.65E-47	(T)n	100	6.69E-18
(GGAA)n	44	8.88E-22	(A)n	86	2.89E-12
(TTC)n	37	2.72E-21	(TTTG)n	78	1.98E-08
(TTCC)n	42	7.26E-20	(CAAA)n	76	4.72E-08
(GAA)n	34	1.18E-18	(TTTTTG)n	31	3.24E-07
(T)n	36	1.65E-02	(GAAA)n	41	5.41E-07
(A)n	29	2.03E-01	(CAAAA)n	52	1.34E-05
(TC)n	25	9.96E-01	(CAA)n	29	2.47E-04
(CA)n	28	1.00E+00	(TTTC)n	30	3.28E-03
			(CA)n	75	1.0
			(TG)n	61	1.0

Restricting coverage of simple and low complexity repeats to uniquely aligned reads these sequences were ranked by the number of instances exceeding the ERCC threshold ($n = 1301$ and 852 , SS and Cs/TX, respectively) and the probability of observing these sequence over the genomic background was calculated for the top 10% of repeat types using a hypergeometric probability test.

within the Cs/TX samples was well above their genomic background resolving as a pattern of poly-purine or -pyrimidine RNA enrichment in these samples (Table 3.4). Interestingly, GAA repeat-containing RNAs (GRC-RNAs) have been observed previously in the several somatic cell types wherein they contributed to chromatin structure by directly binding nuclear matrix proteins [245]. These chromatin-associated RNAs (CARs) form discrete DNase insensitive foci that are lost following RNase treatment. Assigning a similar nuclear function and even localization to the simple repeat sperm RNAs is an intriguing possibility, their lack of sequence complexity precludes RT-PCR validation and precise mapping.

Reminiscent of the results obtained for annotated and novel RNAs long interspersed nuclear elements (LINEs) exhibited greater RNA-seq coverage in the Cs/TX samples relative to sonicated sperm yet RT-PCR suggested that they were approximately eighty times more enriched in the SS samples (data not shown). Alignment to the LINE-1 (L1) repeat class on average

contributed to more than 5% of all unique reads in the Cs/TX samples. Realignment to all canonical repeat sequences showed that approximately 25% of all uniquely aligned reads corresponded to the L1 family in the Cs/TX samples (Table 3.2). This was nearly twice the amount observed for the next most abundant family. To determine which of the L1 repeats was most actively transcribed during the final stages of spermatogenesis the RNA-seq libraries were realigned to canonical sequences for each active subfamily [230]. In all samples the most abundant L1 transcripts corresponded to subfamily III of the L1MdTf lineage. The potential paternal contribution of L1 RNAs to the zygote, thought to perhaps spur autoregulated embryonic transcription of such elements, has been discussed [197, 246]. LINE transcripts have also recently been shown to directly contribute to somatic chromatin structure in an RNase sensitive manner [247]. However, this association is not observed in the condensed somatic heterochromatin. Perhaps during the later stages of spermatogenesis the LINE transcripts are depleted either passively or actively from the sperm nucleus contributing to sperm chromatin condensation as is observed following RNase treatment in interphase cells [247, 248]. In the present study this would resolve as and be consistent with their observed extra-nuclear enrichment.

Identification of Sperm-borne RNAs Post-fertilization

The delivery of RNAs by human sperm to an oocyte has been shown [110, 123]. To ascertain whether mouse spermatozoa may potentially fulfill a similar function murine oocyte and pronuclei embryos sampled prior to zygotic genome activation were subjected to differential expression analysis [1]. A total of 88 differentially enriched embryonic transcripts were identified which exhibited no coverage in the oocyte but were detected in all three sperm RNA-seq datasets in the current study. A previous mouse sperm RNA-seq study proposed that the *Wnt4* and *Foxg1* transcripts may be delivered by sperm to the oocyte [249]. These RNAs were not detected in the embryonic datasets nor were they consistently present in published sperm RNA-seq datasets. Though the majority of the differentially enriched mouse embryo RNAs identified above were

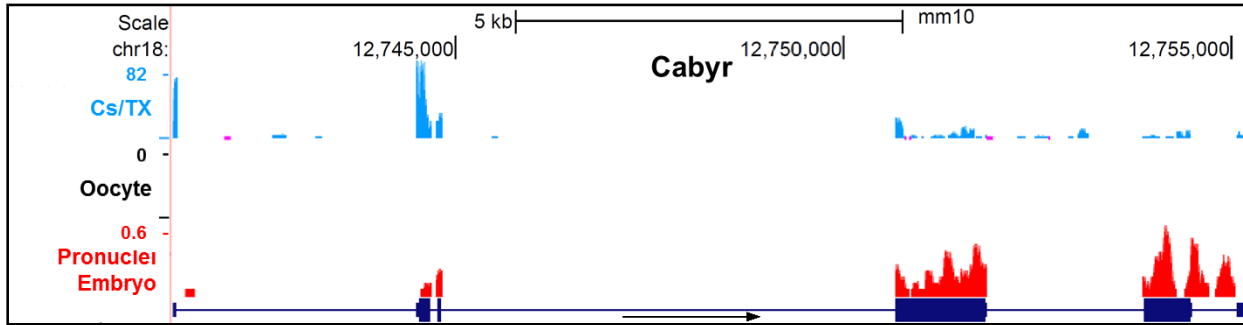


Figure 3.10 Detection of male germline specific RNAs in fertilized oocytes prior to zygotic genome activation. Cabyr is observed in sperm (blue) absent from oocytes and present in pronuclei embryos [black and red respectively; 1] following natural mating. Coverage for each sample is presented as reads per million uniquely aligned reads (RPM) on the Y-axis. The direction of transcription is depicted under the gene model.

present at low levels in sperm (median RPKM ~1.4) the transcript encoding the Calcium-binding tyrosine phosphorylation-regulated protein (Cabyr; Figure 3.10) was consistently detected at elevated levels in both SS and Cs/TX samples and was observed in all available mouse sperm RNA-seq datasets [4, 196, 233]. Interestingly, this transcript was enriched in the Cs/Tx heads by RNA-seq suggesting that it may exhibit a reduced peripheral enrichment similar to that observed for the set of predicted Cs/TX RNAs evaluated by RT-PCR (Figure 3.9 and Table 3.I). Despite being present at diminished levels relative to the outer membranes, these transcripts likely persist within either the perinuclear theca or the nucleus and would therefore be expected to reach the oocyte cytoplasm following fertilization [250]. It is unclear whether this transcript if delivered to the oocyte would be of functional importance considering the established role of its protein product in modulating intracellular calcium levels during capacitation [251]. Irrespective, in human males, it is considered of diagnostic value for idiopathic male factor infertility [252]. Nevertheless, detection of a testis-specific RNAs encoding a protein restricted to the post-meiotic male germline in naturally fertilized embryos prior to zygotic genome activation strongly suggests that sperm RNA persists throughout the normal lifecycle of the paternal gamete and is delivered to the oocyte.

The Distribution of RNAs within the Spermatozoon

The mature spermatozoon is host to a cadre of RNAs that are not evenly distributed throughout the limited volume of the sperm head. By mass approximately 66% of the RNAs greater than approximately 200 nucleotides in length were enriched within the limited volume of the extra-nuclear compartment (plasma membrane, the acrosome and associated membranes as well as the sperm tail and mitochondrial sheath) of the sperm cell. Approximately one-third of the RNAs observed in sperm are expected to be within the nucleus/perinuclear theca. As determined by RT-PCR the strength of their preferential compartmentalization varied in accord with the RNA-seq results. Together these results provide a list of candidate extra- and intra-nuclear associated transcripts which serve as the foundation for future studies delineating the RNAs within the mature sperm. Intriguingly, the set of RNAs exhibiting the strongest external localization included many transcripts linked to exosomes and transcripts commonly localized to specific organelles in somatic cells including the nucleus and mitochondria. Whether these transcripts are passively retained within the external sperm membranes following expulsion of the cytoplasm or are packaged within extracellular vesicles to serve a later function will be resolved when the contents of sperm-bound exosomes are more fully described. The peripheral enrichment of non-coding RNAs such as Malat1 and the LINE transcripts which are known to modulate somatic cell chromatin structure suggests that nuclear remodeling in the sperm is not limited to nucleoprotein exchange. The fraction of these RNAs that remain associated with the intra-nuclear compartment may be restricted to the few poised histone-bound accessible regions that persist following protamination. Representative of the population of transcripts which exhibit the least peripheral enrichment is testis-specific RNA Cabyr. This RNA is likely delivered by sperm to the embryo and is a diagnostic element indicative of idiopathic male infertility [252].

CHAPTER FOUR
NUCLEASE FOOTPRINTS IN SPERM PREDICT PAST AND FUTURE CHROMATIN
REGULATORY EVENTS

I. Summary

Nuclear remodeling is a developmental hallmark of spermatogenesis. This is achieved by genome wide replacement of the histones with protamines condensing the cell. Following this process nucleosome-bound chromatin does persist but to a limited extent. This suggests that these regions may be of past or future functional significance. To determine potential roles for somatic-like chromatin in mature sperm, nucleosome-associated DNAs were isolated from sperm of wild type and transgenic mice harboring a single copy insert of the human protamine cluster. Suppression of the transgenic model was correlated with chromatin structure in mature sperm. A nuclease footprinting approach suggested the chromatin environment harboring the transgenes was likely responsible for their reduced expression. This approach also highlighted potential regulatory mechanism for driving the robust expression of the endogenous protamines. Genome wide footprints were associated with genomic elements and chromatin features such as promoters, enhancers and sites marked by active histone modifications in testis. Motifs predicted to be occupied in sperm were also associated with promoters of genes expressed in the zygote and 2-cell embryo. Ctf footprints were significantly enriched with the boundaries of TADs and sites bound by this factor in testis and ESCs. This suggested that these sites are marked in sperm thereby permitting rapid reconstitution of global chromatin organization following fertilization. Interestingly, Ctf footprints are absent in human or bull sperm which exhibit comparatively slower preimplantation embryonic development.

II. Introduction

Spermatogenesis is characterized by a series of morphological changes resulting in a motile, haploid and highly condensed cell. This is achieved in part through the compaction and restructuring of the nuclear architecture. This process initiates prior to meiosis with the

incorporation of histone modifications and testis-specific histone variants. The haploid expression and progressive deposition of transition proteins and protamines within the chromatin fiber displaces the majority of histones from the double helix [204]. The degree to which the histones are replaced varies between species though in mouse it is estimated that between 1 - 5% of the sperm genome remains in a histone bound state. Once bound the protamines silence and condense the genome through the formation of inter- and intramolecular disulfide bridges. Through the later stages of spermiogenesis and until fertilization the paternal gamete possesses a unique genomic packaging scheme unlike that of any other cell type in the body.

Studies of spermatogenic nuclear remodeling following meiosis have largely focused on the mechanics of single loci and their fate following protamine condensation [7, 74]. Understanding the transcriptional regulation underlying the expression of the protamine gene cluster has been a logical target of investigation considering the requisite role of these proteins during spermatogenesis [162]. In both mice and men this locus is found within a DNase-I sensitive conformation in round spermatids which persists into the mature gamete [170, 253]. Prior studies of the human PRM gene cluster correlated perturbed transcription with the loss of a Ctcf (CCCTC-binding factor) binding site situated upstream of the *TNP2* gene [169]. Ctcf is a ubiquitous insulator protein which acts in concert with its binding partner Cohesin forming chromatin loops [6]. The corresponding orthologous region is bound by Ctcf in mouse round spermatids [254] and mutations within this region are correlated with infertility in men [172]. This suggests the intriguing possibility that a DNA looping event is required to achieve the robust expression levels of the locus encoding the protein products necessary for producing a static genome. It is assumed that the higher order chromatin structure of the haploid genome will be dictated by Ctcf in a manner conforming to that observed in somatic cells while in a nucleosome-bound conformation [5]. Other chromatin binding proteins undoubtedly contribute to regulating the paternal genome prior to condensation however they largely remain unknown or poorly characterized.

Nuclease mapping in conjunction with high-throughput DNA sequencing is a powerful tool for rapidly and efficiently surveying chromatin landscapes [255]. These approaches can be used to infer chromatin structure in a probabilistic manner based on the relative accessibility of a DNA sequence to nuclease cleavage [256]. In sperm, DNAs released following nuclease digestion are thought to be primarily histone-associated, as evidenced by the discreet banding pattern they produce following electrophoretic resolution [72]. Adapting genome wide nuclease mapping approaches for the study of sperm chromatin has highlighted the potential roles nucleosome-bound DNAs may play in the mature gamete and following fertilization [12, 14-16]. Despite these advances, a generalized model of how sperm chromatin is ordered during and after nuclear condensation remains elusive.

To understand the cell type specific chromatin packaging strategy employed within the mature male gamete mouse sperm cells were digested with nuclease and released nucleosome-associated DNAs subjected to high throughput DNA sequencing. The susceptibility of the spermatozoon to enzymatic dissection was compared in sperm from wild type mice and a homozygous transgenic mouse model harboring a single copy insert of the human protamine cluster. The presence of this 40 kb sequence was stable over many generations and did not alter spermatogenesis or impact fertility [217]. Transcriptomic and proteomic analysis demonstrated that the absence of an observable phenotype in these animals reflected decreased transcriptional activity of the human locus as compared to the endogenous mouse locus. To determine the potential cause of this suppression a nuclease footprinting approach in sperm was undertaken. Regions predicted to be bound by a regulatory factor in mature sperm were correlated with genomic landmarks and available higher order chromatin structure datasets. This analysis suggested potential roles for the sperm bound sites in either regulating past spermatogenic events or early embryonic genomic function. A series of candidate enhancer-bound regulatory proteins were identified by this approach that are expected to contribute to a Ctfc mediated DNA looping

interaction, potentially contributing to the robust expression of the orthologous protamine gene clusters. A focused analysis of Ctf binding throughout the sperm genome informed a novel model of how nuclear condensation may proceed and suggested potential functions for this sperm bound factor in the mouse gamete and embryo. However, an interspecies comparison of nuclease footprints failed to identify the presence of Ctf binding in either human or bull sperm strongly suggesting its role(s) are likely species specific.

Materials and Methods

Sperm chromatin digestion and sequencing library construction

All procedures were carried out in accordance with the current Wayne State University Animal Investigation Committee protocol (A 12-01-13). Wild type C57BL/6 mice were purchased from Charles River Laboratories, Inc, Wilmington, MA. Homozygous transgenic mice from transgenic line HP3.1 were bred as described [Chapter Two; 217]. Mature spermatozoa were isolated from cauda epididymides and vas deferens harvested from individual 6 month old mice on ice into PBS. Following filtration through an 80 micron mesh the cells were washed twice and resuspended in 1 mL of a PBS solution containing 0.5% Triton X-100. The cells were incubated for 10 minutes on ice with occasional mixing. Subsequently, ice cold PBS was added to 10 mL and the cells were washed twice prior to counting with a hemocytometer. Tritonized sperm suspensions were adjusted to 5×10^6 cells/mL in 5 mM CaCl_2 , 10 mM dithiothreitol, buffered with 50 mM Tris-HCl, pH 7.9. The suspension was placed 37 °C for 30 min. Subsequently, the sample was diluted with prewarmed reaction buffer to a final concentration of 2.5×10^6 cells/mL in 5 mM CaCl_2 , 10 mM dithiothreitol, 10 gel units/mL MNase (New England BioLabs), buffered with 50 mM Tris-HCl, pH 7.9. The sample was digested and the reactions were stopped with the addition of 0.5 M EDTA pH 8.0 to a final concentration of 20 mM. The cell suspension was then rotated at 4°C for 30 minutes prior to centrifugation at 20,000 rcf for 10 minutes. Sperm digested with DFF were similarly collected and permeabilized. Following washing sperm were resuspended to $5 \times$

10⁶ cells/mL in 1x NEB1 [10 mM Bis-Tris-Propane-HCl; 10 mM MgCl₂; 1 mM dithiothreitol; pH 7.0] (New England BioLabs), supplemented with 10 mM dithiothreitol. Following incubation at 37 °C for 30 min the sperm suspension was diluted to 2.5 x 10⁶ cells/mL with prewarmed 1x NEB1 and 10 units Tobacco Etch Virus (TEV) protease and 20 of µl DFF enzyme added. DFF enzyme was graciously provided by Dr. Nick Gilbert.

Human sperm nucleosome libraries were prepared as above with the following adjustments. Following liquefaction sperm were washed twice and frozen as dry pellets in liquid nitrogen. Sperm were thawed on ice and washed twice with PBS prior to permeabilization with Triton X-100 as above.

Enzymatically released soluble DNAs were recovered from the supernatant to a fresh screw cap tube and digested overnight with proteinase K at 55°C in the presence of 1% β-mercaptoethanol. The remaining sperm pellets were washed once with PBS and similarly digested by proteinase K alongside tail clips from the sacrificed mice. Subsequently the DNAs were recovered by phenol–chloroform extraction, precipitated with ethanol and quantified with Picogreen (Invitrogen). Genomic DNA from wild type and transgenic tail clips were digested with MNase and purified as above. Mononucleosome DNA fragments were resolved by gel electrophoresis and extracted from separate agarose plugs with the Qiagen MinElute Gel Extraction kit. Digested control genomic DNAs were gel size selected (~150 bp) and similarly purified. Recovered DNAs were quantified as above and used to construct multiplexed DNA sequencing libraries with the NEBNext ChIP-Seq kit (New England BioLabs). All libraries were subjected to 50 cycles of paired-end sequencing on the Illumina HiSeq 2500 or MiSeq platforms.

Testis RNA isolation and sequencing library construction

Total RNAs were separately isolated from the decapsulated testes of four transgenic adult mice. Following homogenization in 0.5 ml RLT buffer (Qiagen) supplemented with 1.5% β-mercaptoethanol (Amresco), with a PRO Scientific 200 homogenizer (PROScientific Inc., Oxford,

CT) RNAs were extracted as described [Chapter 3; 108, 218]. Following DNase treatment (Turbo DNase, Ambion) the size and quality of the purified RNAs were assayed using the 2100 bioanalyzer with a RNA Pico chip (Agilent Technologies, Palo Alto, CA, USA). Prepared mouse and commercially available human total testes RNAs [Ambion; 122] were used to construct individual RNA-seq libraries according to established protocols and sequenced as above (Chapter 3).

Analysis of sequencing libraries

DNA sequencing libraries were aligned to the mouse genome assembly Mm10 with Bowtie [version 2.0.2; 257]. Transgenic samples were additionally aligned to a custom version of the Mm10 build containing the inserted human protamine domain at nucleotide position chr19:39397384-39397385 [217]. After removing PCR duplicates analysis of aligned sequencing libraries was restricted to properly paired reads with a quality score ≥ 10 . Published single-end datasets used in the current study were restricted to a similar criterion ignoring the paired requirement. Processing of alignment files, including midpoint and 5' calculations, genomic intersections, and Jaccard statistics were carried out with the Samtools [version 0.1.19; 221] and Bedtools [version v2.19.1–2; 222] suites. Mappability tracks were constructed using the GemTools suite [258]. ChIP-seq peaks were identified from spermatid datasets [254] with the MACS2 software suite using default settings [259]. Heatmaps and figures were generated using the ggplot2 and the deepTools packages [260, 261]. Hi-C interaction maps were retrieved from the Hi-C browser [<http://promoter.bx.psu.edu/hi-c/>; 5, 6].

Promoter regions were considered to span 5 kb upstream and 0.25 kb downstream from TSS, with respect to strand orientation. Testis promoter regions corresponded to genes exhibiting non-zero coverage in all testis RNA-seq samples. Pronuclei embryo promoters corresponded to the subset of genes identified as differentially expressed in pre-ZGA embryos and oocytes [Chapter 3; 1].

Nuclease footprinting analysis

Sequencing read midpoint coordinates and position weight matrices (PWM) scores and binding site positions were prepared for nuclease footprinting analysis with in-house scripts prior to implementation of the CENTIPEDE algorithm in R [256]. For each factor PWM scores [262] were calculated for all genomic sequences conforming to a known motif. Sites with a mappability score $\geq 99\%$ were ranked according to their PWM score and the top quintile used for the primary footprinting analysis. The average conservation score (60way.phastCons60wayPlacental) and 5-base percent GC dinucleotide frequency immediately up- and downstream with the exclusion of the query was calculated for each motif. A generalized linear model was used to evaluate the prognostic value of the three scored variables (PWM, GC%, and phastCons) and those factors exhibiting a PWM z-score ≥ 5 were used for further analysis. Within this set of factors motifs exhibiting a posterior probability ≥ 0.95 were considered bound. The extended analysis of the 5 Mb search regions was performed as described with the following changes. All sites identified within the search regions meeting the following criterion were included in the footprint analysis regardless of their PWM rank: mappability scores $\geq 90\%$, PWM ≥ 14 . A reduced stringency analysis of potential Ctf sites was also undertaken in which all motifs with a PWM ≥ 13 were evaluated. The 5' genomic start site of sequencing reads was used for single-end sequencing CENTIPEDE analysis. Footprints were lifted over to Mm 9 genome build for comparisons with ENCODE datasets [3, 263].

III. Results and Discussion

Nuclease sensitivity in wild type and transgenic mouse spermatozoa

Nucleosome-associated DNAs were released from wild type and transgenic mouse sperm with either micrococcal nuclease (MNase) or DNA fragmentation factor [DFF; 264, 265, 266]. Use of the latter nuclease provided a novel complimentary approach to probe sperm chromatin structure while also serving as a control against potential MNase cleavage bias [267, 268].

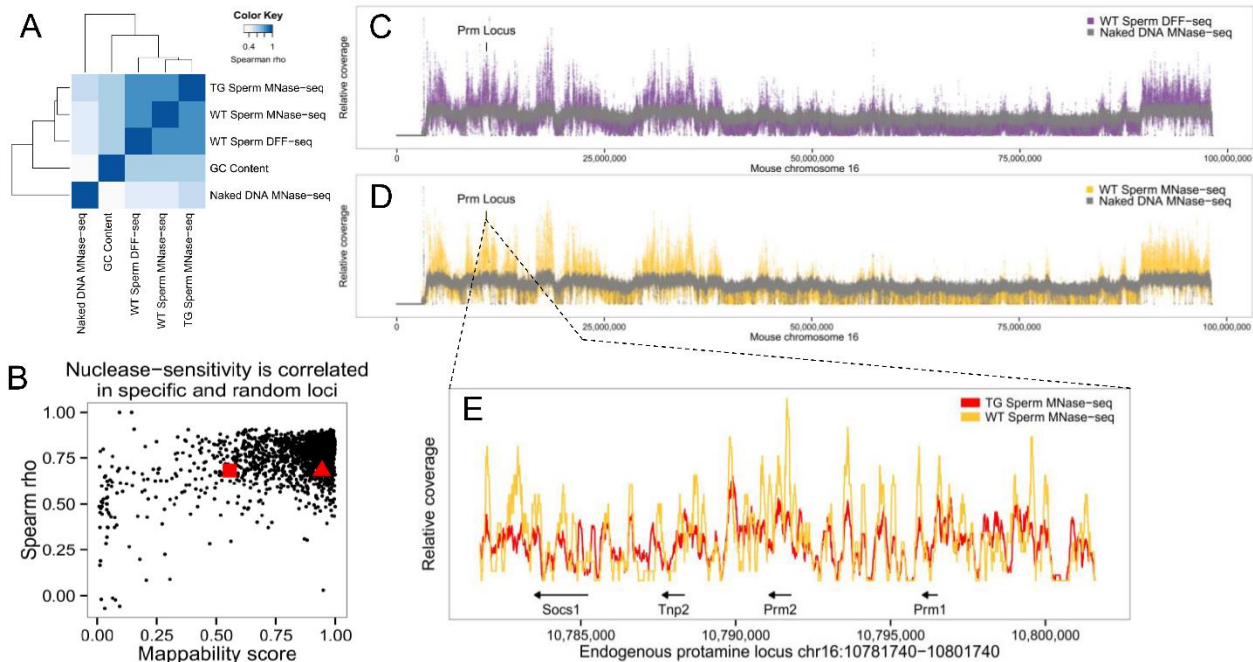


Figure 4.1. Mouse sperm chromatin nuclease-sensitivity is correlated across samples and not impacted by choice of nuclease or genotype. (A) Hierarchical clustering of pairwise spearman rho correlation coefficients for genome-wide nuclease-sensitivity data from in situ digested sperm chromatin binned into 500 base pair windows demonstrated consistent nucleosome coverage regardless of nuclease choice or genotype, relative to naked DNA controls. GC content represents the average percentage of GC dinucleotides in the window (B) Sperm MNase-seq coverage of the endogenous mouse protamine locus (red triangle), the sequences flanking the transgene insertion site (red square), and randomly selected loci were well correlated (y axis) and only marginally influenced by (x axis) mappability. The midpoints of paired-end sequencing fragments were binned into 50 base pair windows along 20 kb regions and correlation coefficient calculated using a 5 window running average. (C + D) Sperm chromatin exhibits similar patterns of nuclease-sensitivity regardless of digestion with MNase of DFF (purple and orange, respectively), relative to naked DNAs (gray). Coverage of chromosome 16 is presented as normalized paired-end sequencing midpoint counts in 500 base pair windows using a 10 window running average. (E) Sperm MNase-seq midpoint coverage of the endogenous mouse protamine locus in wild type and transgenic sperm presented as 150 bp running averages.

Genome-wide nuclease sensitivity was well correlated amongst sperm samples and distinct from that observed following either enzymatic or mechanical fragmentation of purified mouse DNAs ($\rho \sim 0.89 - 0.91$; Figure 4.1A). Nucleosome retention varied across sperm chromosomes highlighting the presence of broad regions of heightened nuclease sensitivity that could not be explained by GC content (Figure 4.1A). This global survey localized the mouse protamine domain within a region of elevated nucleosomal coverage relative to controls (Figure 4.1C, D). Previously this locus had

been shown to lie within a DNase I-sensitive structure established during meiosis and persisting throughout the round spermatid stage [7, 253]. The chromatin conformation of this discrete region of chromosome 16, assumed prior to nuclear condensation, may reflect the generalized nuclease sensitivity of a larger domain which persists within the mature male gamete.

Transgenic sperm did not exhibit altered nuclease sensitivity genome wide despite the integration of an additional protamine locus. To assess the impact of this inserted sequence at a higher resolution, MNase-seq coverage of specific regions of the mouse genome were correlated using a running average. Applying this approach to 20 kb regions centered on the endogenous mouse protamine locus, on the site of the integration [chr19:39,397,384-39,397,385; 217], or on two thousand randomly selected regions of equal size demonstrated that chromatin packaging within these regions was ($\rho \sim 0.68$) similar across all samples (Figure 4.1B). Together, this suggested that the introduction of a gene cluster encoding additional DNA-binding proteins did not perturb the chromatin structure at the global or local level.

The absence of altered chromatin structure in the transgenic sperm indicated that expression of the human protamines may be perturbed. Testis RNA and sperm protein levels were analyzed to determine if the lack of an observable phenotype in the transgenic mice was due to transcriptional regulation or alternatively impaired incorporation of the transgenic protein during chromatin condensation. RNA-seq analysis of total transgenic testis RNAs from four animals demonstrated that the transgenes were consistently transcribed across all samples and present at elevated levels (Figure 4.2A). Despite their abundance within the testis transcriptome the transgenic RNAs exhibited reduced expression relative to their orthologs transcribed from the mouse protamine domain. The transgenic *PRMs* and *TNP2* were also reduced in comparison to their analogs in human testis (Figure 4.2B). This reduction was more apparent in the case of the *PRMs* which were decreased by 70 - 77% relative to that observed in man. The average ratio of the transgenic protamines (TG *PRM1*/TG *PRM2* ~ 1.02) also differed from that observed in human

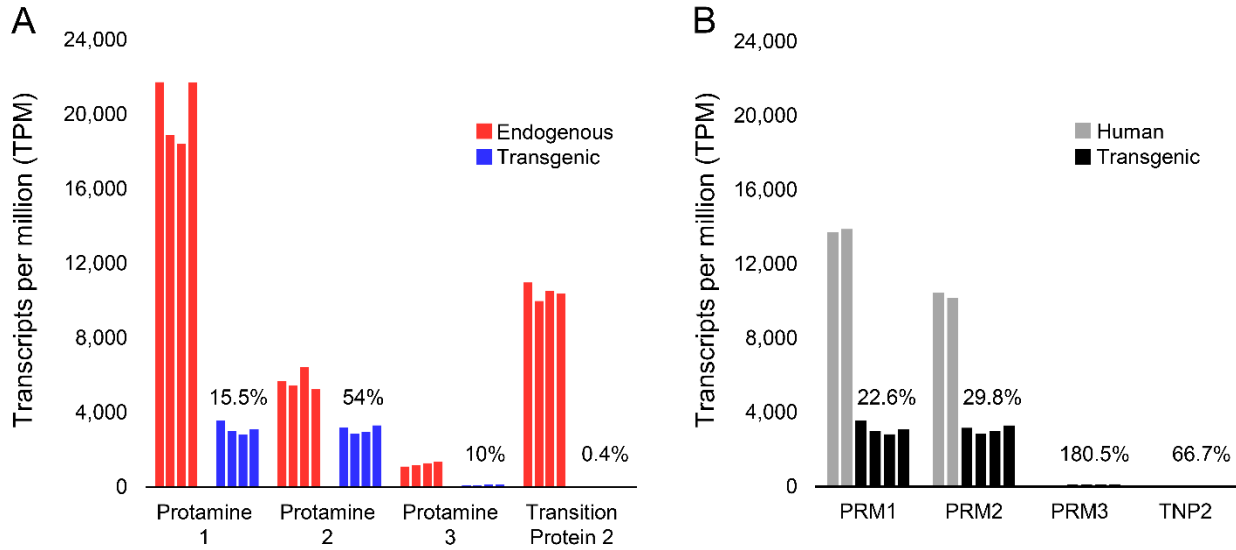


Figure 4.2. Expression of the human transgenes in mouse testis was suppressed. (A + B) RNA-seq analysis of transgenic mouse (n = 4, A) and human (n = 2, B) total testes RNAs demonstrated that transcription of the integrated human protamine genes was reduced relative to the observed from both the endogenous loci. Expression values are presented as transcripts per million (TPM). TPM ratios for each comparison are presented above the transgenes.

testis (Hs *PRM1*/Hs *PRM2* ~1.34) and that of the endogenous mouse protamines (Mm *Prm1*/Mm *Prm2* ~3.57). The failure of the transgenes to recapitulate expression levels of either the endogenous human or mouse gene clusters was further evidenced by an increase in transgenic PRM3 which was nearly double that observed in human testis. Prior mouse models in which the human protamine gene cluster integrated as a multi-copy insertion also exhibited reduced levels of expression relative to the endogenous protamines [170]. However, transgene expression was restricted to the testis in all lines bearing the 40 kb human gene cluster [169, 217]. This supports a model in which full expression of the locus cannot be promoted solely from regulatory elements within the inserted sequence despite their ability to block ectopic activation.

The RNA-seq results suggested that the absence of an observed chromatin phenotype in the transgenic animals was due to suppression of the transgenic RNAs. This was confirmed by proteomic analysis of acid extracted transgenic sperm chromatin proteins (Jodar, M., et al; manuscript in preparation). Transgenic protein incorporation within the sperm genome was

reduced relative to that observed for the endogenous proteins. The ratio of transgenic to endogenous protamine complimented the trends observed by testis RNA-seq. This suggested that the relative amount of protamine protein utilized by the gamete directly corresponded to testis RNA levels. It remains unclear whether the absolute protamine load within the transgenic spermatozoon differed from that of wild type. Regardless, these results suggested that the similarity in nuclease sensitivity observed in wild type and transgenic mouse sperm was likely due to the suppression of transcription of the inserted human sequence in the transgenic mouse preventing excessive incorporation of protamine proteins during spermiogenic nuclear remodeling.

Chromatin structure of the human and transgenic protamine locus

Global and local patterns of nuclease sensitivity in transgenic and human sperm were compared to elucidate a potential cause for the suspected suppression of the transgenic protamine locus. Mononucleosome DNAs were released by MNase from human sperm collected from a single donor and subjected to high-throughput sequencing. Analysis of these nucleosome-associated DNAs at the level of the chromosome revealed broad regions of variable nuclease sensitivity reminiscent of trends observed in mouse sperm (Figure 4.3A). Similar to its syntenic region in mouse (Figure 4.1C, D), the human protamine gene cluster, which has been shown to form a DNase-I sensitive structure in mature sperm [170], lies within an extended region of elevated nuclease sensitivity relative to sheared control DNAs. In contrast to the endogenous protamine loci, the transgenic sequence exhibited elevated nuclease sensitivity relative to controls but was flanked by regions of extensive nuclease insensitivity (Figure 4.3B, C). In all sequencing libraries this region of mouse chromosome 19 exhibited a general reduction in mapped reads due to the presence of repetitive sequences which impede the alignment of short fragments. However, nucleosome coverage was consistently reduced in this region relative to controls and independent

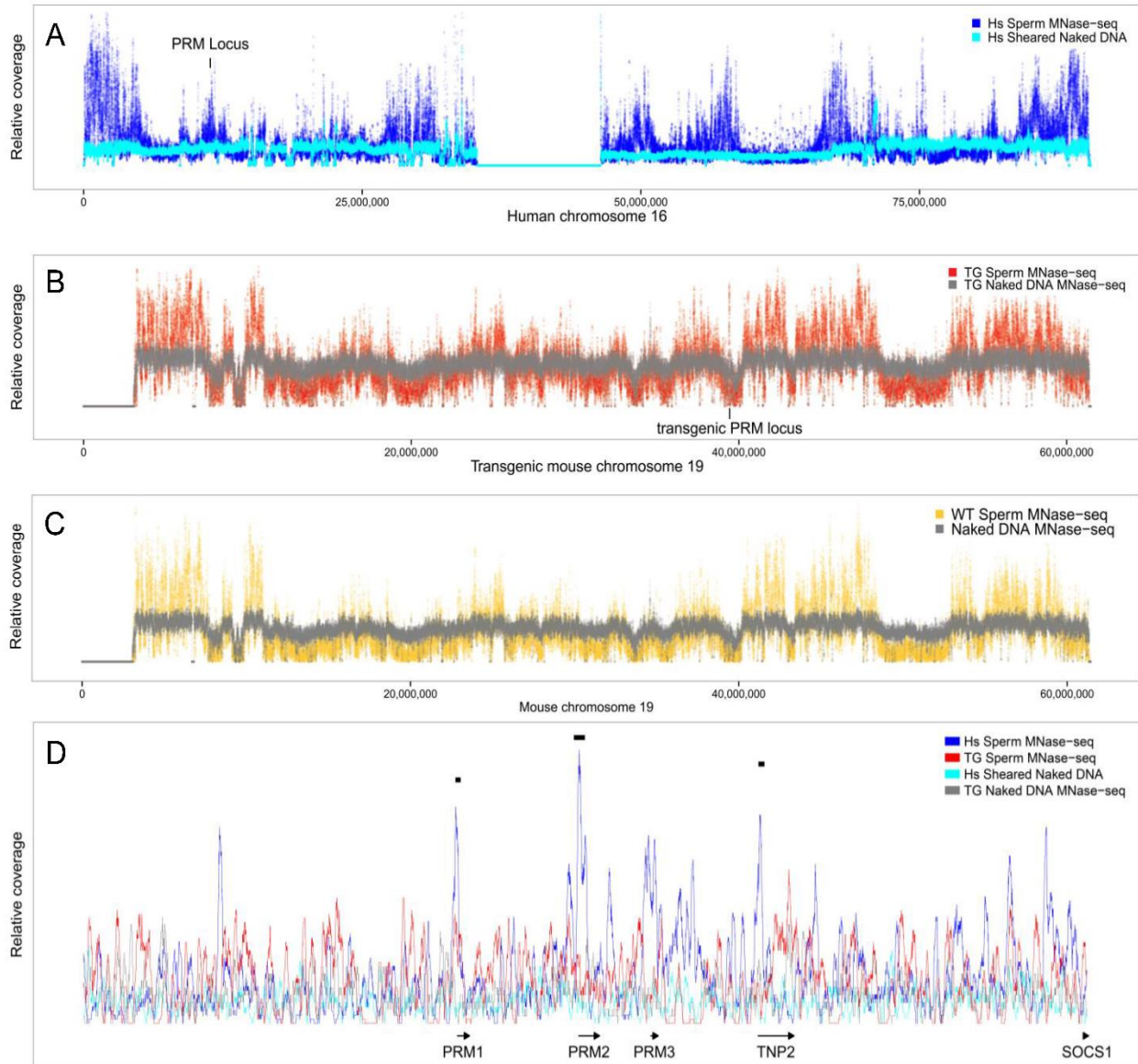


Figure 4.3. The human protamine sequences in sperm are packaged within nuclease-sensitive chromatin. The human protamine sequences in sperm are packaged within nuclease-sensitive chromatin. (A + B) The human protamine locus exhibits elevated nuclease sensitivity in mouse and man but is associated with regional variations in MNase-seq coverage. Normalized paired-end sequencing coverage of human and transgenic sperm MNase-seq libraries are presented relative to sheared or digested controls, respectively. The endogenous human protamine locus resides within a large region of elevated nuclease sensitivity (A). In contrast while the transgenic domain (B) is locally enriched in MNase-seq coverage it resides within a nuclease insensitive region of mouse chromosome 19. (C) The presence of the transgenes did not impact the chromatin structure of the neighboring sequences as this region is also nuclease insensitive in wild type mouse sperm. (D) The PRM locus in human and transgenic mouse sperm exhibits varied levels of nuclease sensitivity. Coverage of the locus is plotted with respect to locus orientation in the transgenic animals and presented as 150 bp running averages. Black boxes denote probe positions previously used to identify nucleosome-associated sequences in human sperm [8].

of genotype. This suggested that these sequences are packaged in a nuclease resistant conformation in mouse sperm (Figure 4.1B, Figure 4.3C).

MNase-seq coverage was compared within the human and transgenic protamine gene clusters to determine whether local chromatin structure in mature sperm could inform prior transgene suppression. Within the endogenous human locus an increase in MNase sensitivity was observed within the transcription start sites and gene bodies of the protamines and TNP2. Demonstrating the efficacy of the genome wide nucleosome mapping approach these peaks of nuclease sensitivity directly correspond to regions previously identified as nucleosome bound in human sperm [8]. The sequence corresponding to *PRM3* which had not been previously assayed also exhibited nuclease sensitivity relative to controls. In contrast no distinct MNase sensitive peaks were identified within the transgenic locus. The discordant MNase-seq coverage of the human protamine gene cluster in transgenic mouse and human sperm demonstrated that the inserted sequence did not recapitulate endogenous histone placement. Of potential importance, the transgenic gene cluster was also flanked by nuclease insensitive chromatin. This differed substantially from observations of the endogenous human or mouse loci and may suggest a potential role for the surrounding chromatin in contributing to locus suppression.

The altered nucleosome coverage observed within the transgenic human protamine locus strongly suggests that histone retention in sperm is not sequence-dependent but driven by other factors. Recent reports have characterized the impact of higher order chromatin structures on regulating genomic function [269]. Three-dimensional genomic organization is functionally stratified into large sub-chromosomal compartments correlated with either active or silent chromatin [270]. Further partitioning of these compartments identifies regional preferences in chromatin interactions which form the basis of TADs [5]. At this level of genomic organization interactions between discrete loci occur with increased frequency within domains relative to across domain boundaries [6]. This is best characterized by intra-domain DNA looping events,

such as those observed between promoters and their cognate enhancers [132]. Conserved across species and between cell types, TADs are established through the binding of insulator proteins such as Ctf. Perturbation of Ctf binding sites within TAD boundaries alters domain structure and looping interactions consequently impacting gene expression [135]. Accordingly, we sought to identify structural landmarks that may influence chromatin packaging in mature sperm (Figure 4.4). The protamine loci of both species lie within domains that are approximately 0.5 Mb in length and largely invariant in all examined cell types (Figure 4.5). Within a 5 Mb region centered on the mouse protamine gene cluster, 100 enhancers are predicted to be active in testis of which 18 are found within the sub-domain housing the protamine genes. Analysis of ChIP-seq data collected from haploid round spermatids identified a similar distribution of Ctf peaks within the 5 Mb search region and 0.43 Mb sub-domain ($n = 17$ and 102 , respectively; Figure 4.4A). Several of these peaks are located immediately upstream of *Tnp2* and are found to be overlapping a nuclear matrix attachment site previously identified in mouse round spermatids and mature human sperm [194, 253]. These regions are thought to contribute to nuclear structure and function by promoting genomic attachment to the nuclear matrix, a poorly defined proteinaceous scaffold proposed to contribute to nuclear organization [204]. In mouse testis the *Ppm1*, *Tnp2*, *Ppm2* transcripts are the 2nd, 5th, and 6th most abundant RefSeq RNAs, respectively (Figure 4.4A). This magnitude of expression from a single gene cluster is likely achieved through the binding of Ctf to the *Socs1-Tnp2* proximal matrix attachment region (MAR) thereby promoting a DNA looping event in which the protamine promoters are brought into contact with one or more of the neighboring testis enhancer elements. Mutations within this MAR are correlated with infertility in men while the absence of this sequence in prior transgenic models of the human protamine locus subjects the transgenes to position effects [169, 172]. This is in accordance with results following experimental manipulation of Ctf binding sites [135]. Perturbation of this proposed Ctf mediated looping event may account for the suppression and altered chromatin structure of the transgenic protamine genes.

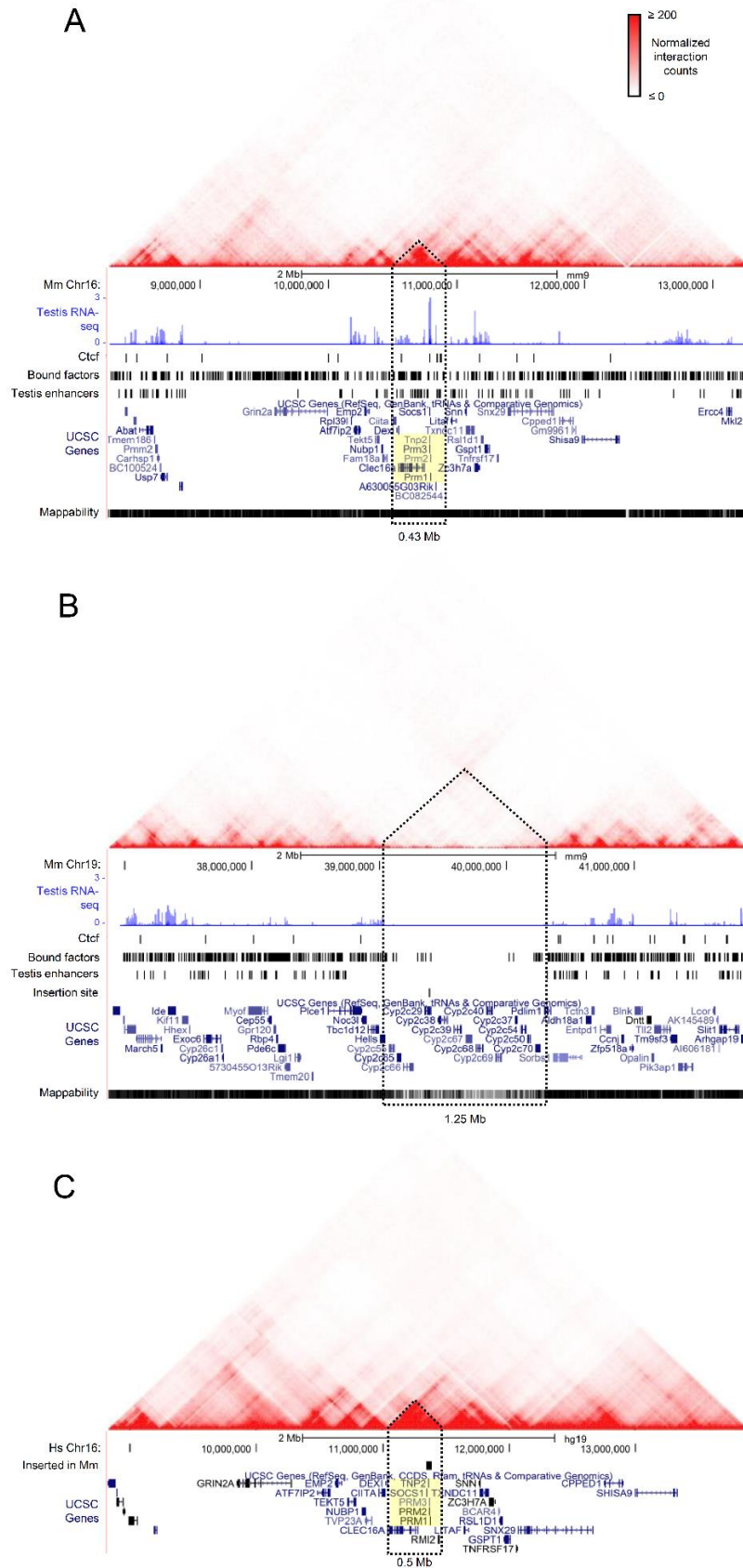


Figure 4.4. The chromatin domains harboring the abundantly expressed endogenous protamine locus and the suppressed transgenes exhibit different regulatory features. The relative positioning of cis regulatory elements and testis RNA-seq coverage along 5 Mb regions centered on the mouse protamine locus (A) or the transgene insertion site (B) are presented within the context of intra-chromosomal contact data from Hi-C analyses of CH-12 cells [5]. Mean coverage of uniquely aligned sequencing reads from total transgenic testes RNAs ($n = 4$) aligned to the wild type mouse genome are presented as \log_{10} normalized values. Nuclease footprints corresponding to Ctf and other factors bound in mature mouse sperm are displayed as separate tracks. Predicted testis single nucleotide enhancer peaks were provided by the mouse ENCODE project [3]. (C) The ~40 kb human protamine sequence inserted in mouse corresponds to less than 10% of the contour length contained within the chromatin interaction domain housing these genes in their native state. Human Hi-C interaction data is from GM12878 cells [6]. The locations of the endogenous protamine domains are highlighted in yellow. The site of transgene insertion within mouse chromosomes 19 is marked on a separate track. Peaks of Hi-C interaction frequencies containing the loci of interest are demarcated by dashed lines and are considered chromatin sub-domains.

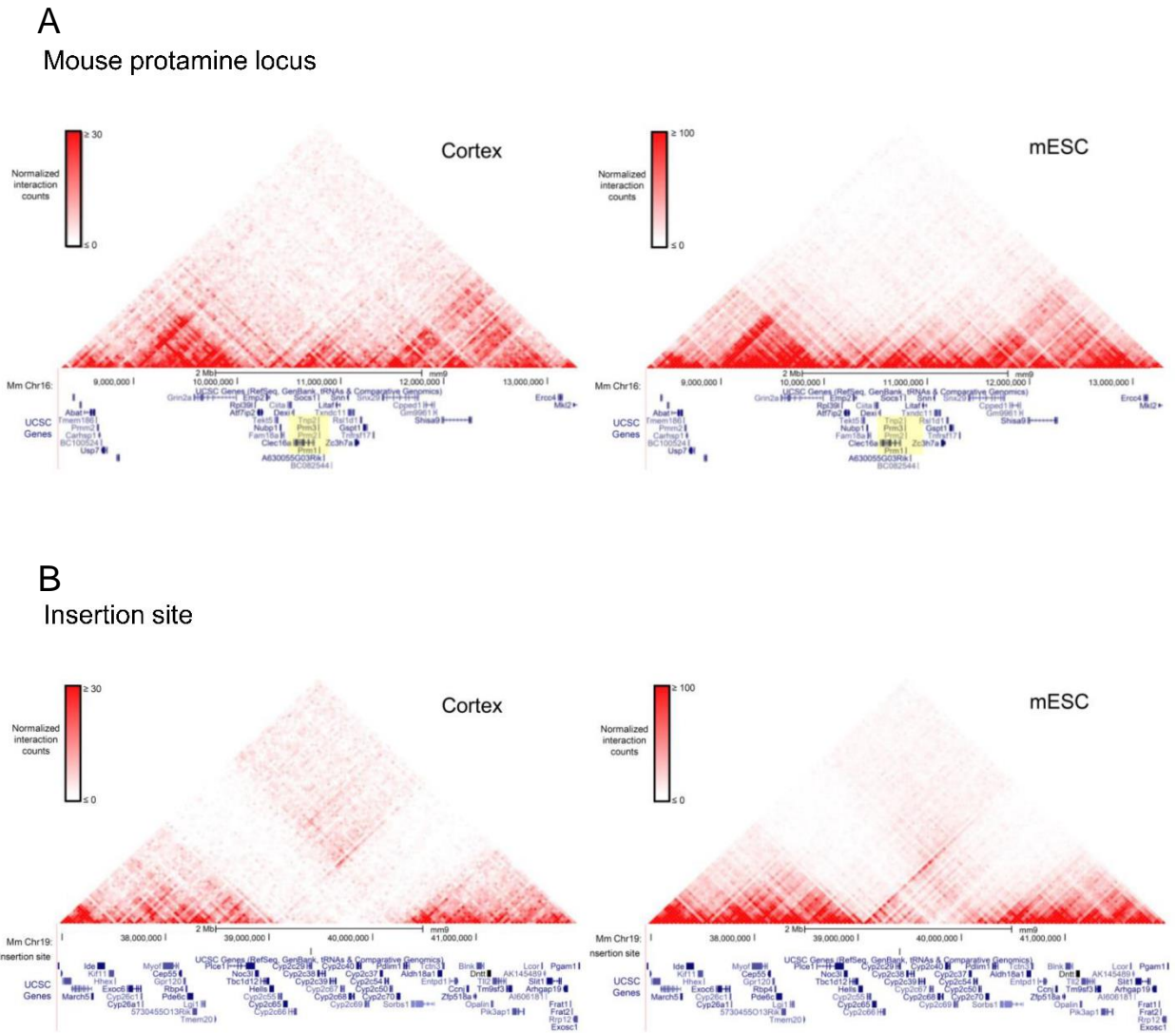
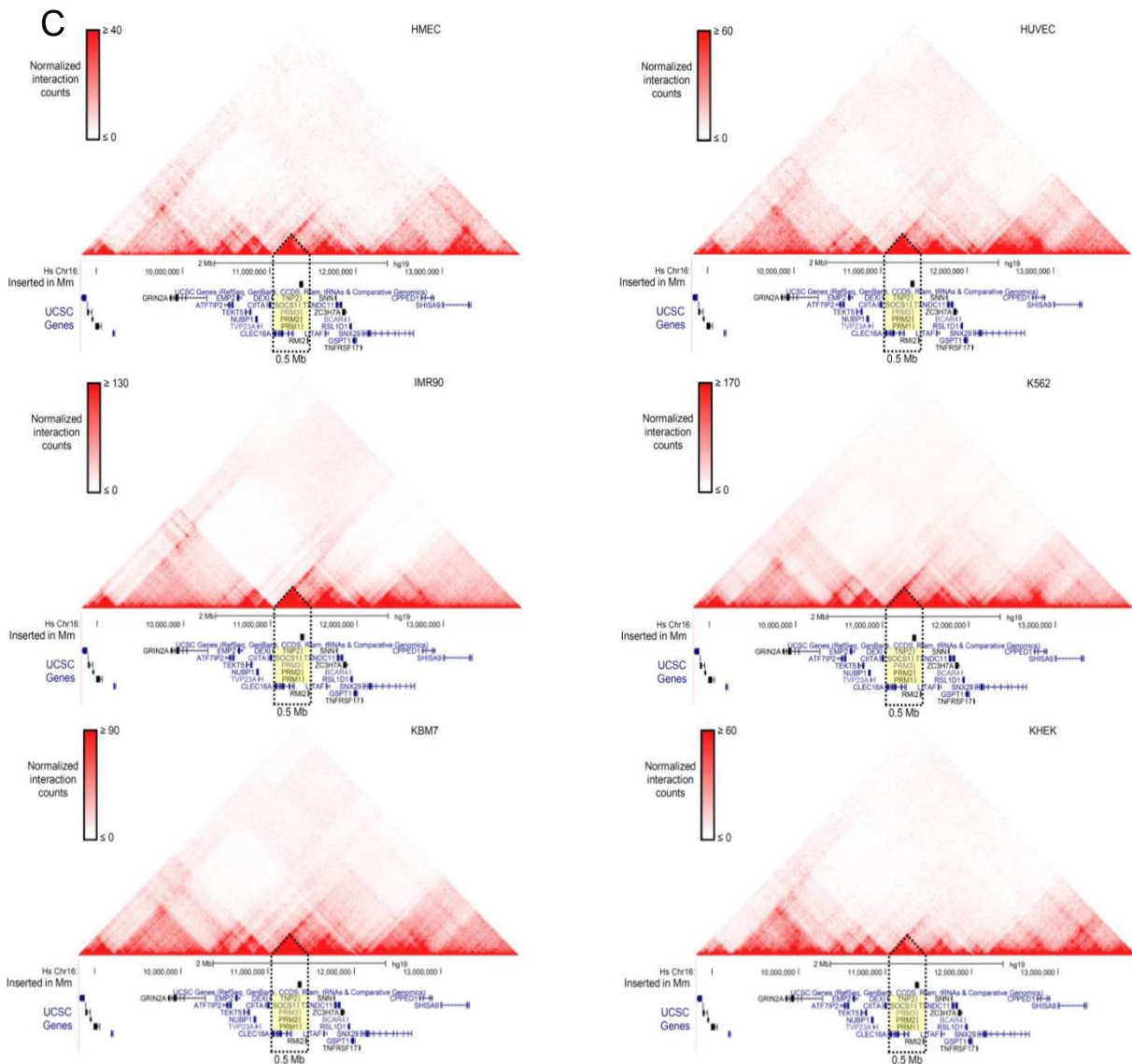


Figure 4.5. Chromatin interaction data from available cell types. Mouse Hi-C cortex (left) and ESCs (right) data corresponding to either the 5 Mb search region centered on the endogenous mouse protamine locus (A) or the insertions site (B). Data generated in cortex and ESCs are at lower resolution than CH-12 cells (Figure 4.4). (C) Alternative Hi-C data for the 5 Mb region centered on the human protamine locus. Six additional datasets are available and all are of the same resolution as the primary figure. The location of the protamine domain is highlighted in yellow and bracketed by dotted lines demarcating its positions within the higher order chromatin interaction domains.



The presence of the *SOCS1*-*MAR*-*TNP2* Ctf site within the inserted sequence argues that the expected enhancer(s) is/are positioned outside of the syntenic endogenous protamine locus. Though relevant candidate enhancers await identification in human testis, removed from its native chromatin environment the transgenic locus would be reliant on local elements. In contrast to the chromatin domains harboring the endogenous human and mouse gene clusters, the inserted sequence integrated into a comparatively large, repeat dense region exhibiting relatively few DNA looping events and no predicted testis enhancers (Figure 4.4B). While long

range intra- or inter-chromosomal contacts between the transgenic promoters and distant enhancers cannot be excluded, such events occur infrequently [5, 6]. To test if transgenic locus suppression reflects enhancer element accessibility and not the failure of Ctfc to bind the inserted sequence, Ctfc occupancy genome wide was inferred from transgenic sperm MNase-seq data using CENTIPEDE [256]. The conserved *Socs1*-MAR-*Tnp2* present in the integrated human sequence was predicted to be bound by Ctfc in mature transgenic sperm. Similarly the orthologous site found in the endogenous domain was also predicted to be occupied in both transgenic and wild type mouse sperm. ChIP-seq analysis in wild type round spermatids demonstrated that this region is bound by Ctfc. This binding event occurs during the window of *Prm* expression consistent with the proposed role of this factor in driving transcription of the locus. The inserted human *SOCS1*-MAR-*TNP2* is presumed to be similarly bound prior to nuclear condensation in the absence of transgenic ChIP-seq data. However, this binding activity likely cannot coordinate the promoter-enhancer interaction(s) expected to drive the 1.9 - 234.0 fold increase in endogenous gene expression relative to the transgenes (Figure 4.2A) due to the integrated sequence residing within a chromatin domain depleted of testis regulatory elements (Figure 4.4B). Yet surprisingly this sequence is still expressed. The regions flanking the insertion site are predicted to exhibit limited transgene interaction and therefore likely undergo nuclear condensation as evidenced by their relative nuclease-resistance. In contrast transcription of the interested locus ensures its packaging within a localized nuclease-sensitive conformation (Figure 4.3B). The endogenous human and mouse protamine promoters are predicted to interact with regulatory elements within their domain through Ctfc binding. This may temper protamine deposition within adjoining sequences which resolve as the broader nucleosome-associated regions surrounding the endogenous protamine loci in mature human and mouse sperm (Figure 4.1C, D; Figure 4.3A).

Mouse spermatozoa harbor bound chromatin factors

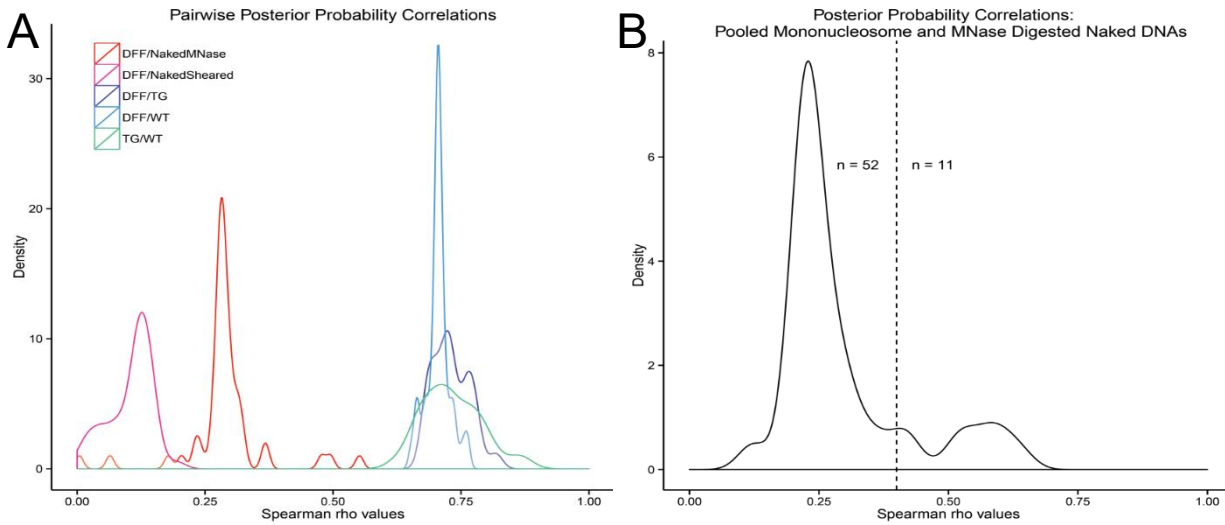


Figure 4.6. CENTIPEDE binding predictions were correlated across all sperm samples. (A) Density plots of pairwise posterior probability correlations for all individual samples for each factor in the union of factors exhibiting a PWM Z-score ≥ 5 in sperm. The posterior probability of all sites were tested. (B) Sperm nucleosome data was pooled and reanalyzed with CENTIPEDE. As in A, correlations were performed with posterior probabilities derived from pooled sperm nucleosome data ($n = 3$) and digested naked DNAs.

Sperm MNase-seq data was used to infer the binding status of Ctcf at the endogenous and transgenic *Socs1*-MAR-*Tnp2* site as well as genome wide. It is known that nuclease sensitive sperm DNAs are enriched in Ctcf motifs [12] and prior MNase-seq analysis of sperm chromatin has identified this protein and its corresponding nuclease footprint in mouse spermatozoa [13]. However, this study did not extensively report whether additional chromatin proteins remain bound in sperm. To determine whether the mouse spermatozoal chromatin landscape contains factors of potential regulatory importance in addition to Ctcf, sites corresponding to known PWMs [271, 272] were identified throughout the genome and their occupancy status inferred from the sperm nuclease-seq datasets with CENTIPEDE. Analysis of the transgenic sample was restricted to wild type alignments due to the lack of a discernable chromatin phenotype (Figure 4.1). Regardless of genotype (TG vs WT) or nuclease selection (MNase vs DFF) posterior probabilities of binding were well correlated for all factors in which the motif PWM score, was predictive of the

Figure 4.7 Nuclease footprinting establishes the presence of bound regulatory factors in mouse sperm chromatin. Pooled nuclease-seq (MNase and DFF) data sets and PWM scores were used to infer the occupancy status of regulatory factor binding sites in mouse sperm. The potential prognostic value of additional variables to factor binding predictions was assessed with a generalized linear model. PWM Z-scores were compared to those corresponding to either GC content (%GC \pm 200 motif, A) or conservation within the motif (phastCons, B). Alternative variable Z-scores are plotted against PWM Z-score for each of the fifty-two motifs for which PWM was predictive of binding (Z-scores $>$ 5). (C) Heat map demonstrating the similarity (Jaccard index) of genomic coordinates for factors predicted to be bound in sperm. Homeobox factors (right hand cluster, dashed box) bind a highly similar motif and consequently cluster together. Factors in this cluster are labelled in green in panels A and B. Asterisks denote motifs identified in other species with no known mouse homolog.

CENTIPEDE footprint (Z-score \geq 5; Figure 4.6). The sperm datasets were pooled and reanalyzed identifying 46 chromatin factors corresponding to 52 motifs that were predicted be bound in mature sperm (Figure 4.7). In addition to the PWM score the influence of GC content (\pm 200 bp motif) and local sequence conservation on occupancy predictions was estimated using a generalized linear model. The CENTIPEDE Ctf model was a clear outlier exhibiting elevated conservation and PWM Z-scores and was only modestly influenced by the sequence context neighboring the factor motifs (Figure 4.7A, B).

The majority of the CENTIPEDE footprint models suggested that occupied motifs were positioned within nucleosome-bound chromatin (n=38). However, many exhibited trends indicative of over-digestion (Figure 4.8A). This suggested that factor-binding site interactions can be compromised during chromatin preparations since mouse sperm MNase digestions were not driven to mononucleosomes (Figure 4.8B). Factor disassociation presumably occurs during protamine disulfide reduction, which is necessary to interrogate the interior of the sperm nucleus. MNase cleavage of sterically accessible vacated binding sites would be expected to occur with greater frequency within A-T dinucleotide sequence context [273, 274]. Supporting this tenet, the frequency of cleavage was reduced within the four motifs not enriched in A-T dinucleotides and their immediate flanking regions. Further, sperm chromatin fixation halts progressive MNase exonuclease activity within the sequences surrounding the A-T dinucleotide containing motifs

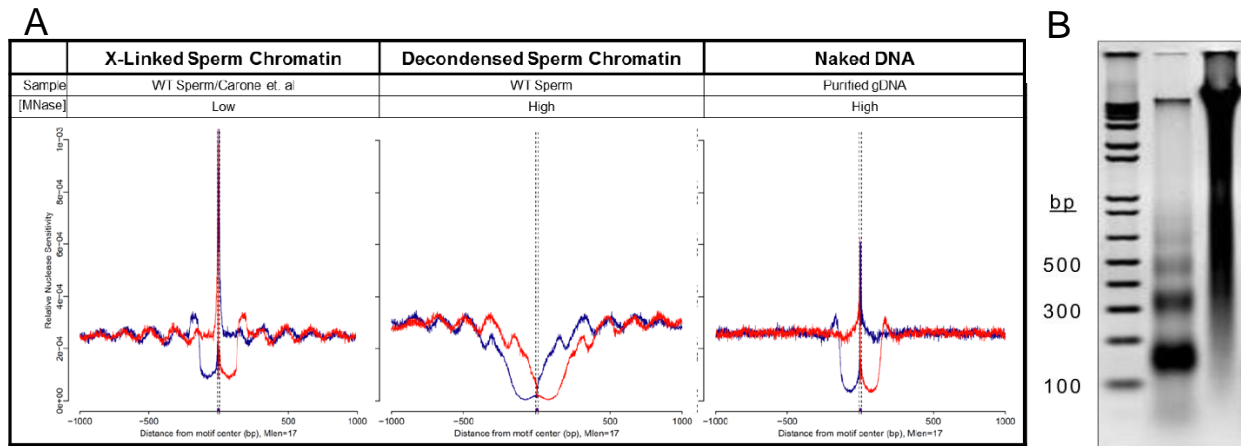


Figure 4.8. Preferential digestion of A-T rich motifs. (A) Motifs containing A-T dinucleotides produced patterns characteristic of over digestion. Fixation and lower nuclease concentrations reduce this effect which is also seen prominently in digest naked DNAs. (B) Despite suppressed coverage of A-T dinucleotide containing motifs samples were not over-digested as evidence by the nucleosome banding pattern.

[Figure 4.8A; 13]. However, treating with a crosslinking reagent strongly alters the distribution of nucleosome coverage relative to the native chromatin preparations used in this study ($p < 0.1$).

Hierarchical clustering of bound motifs according to their genomic distributions (Jaccard similarity index) identified a subset of overlapping binding sites utilized by the homeobox domain protein family ($n=27$; Figure 5C, dashed box; Figure 4.9). The proteins in this cluster possess largely invariant PWMs (Figure 4.10) but exhibit a broad range of RNA levels in testis (Appendix C). This would suggest that the majority of the homeobox motifs are likely utilized by relatively few family members. Within this subset of proposed sperm chromatin factors Pax6 (Paired box 6) and Esx1 (Extra-embryonic tissue-spermatogenesis-homeobox gene 1) have been previously observed in testis. However, Pax6 was not detected in mature sperm and its relative RNA level in testis is 3% that of Esx1 [275]. In contrast, *Esx1* exhibited the 2nd highest RNA levels of all homeobox family members predicted to be present in sperm. Esx1 protein has been localized to late spermiogenic cell types including the mature gamete [276]. Though proposed to serve as a

marker of spermatozoa containing the X chromosome, this trend was not observed in the nuclease-seq data for either the individual or a merged set of homeobox bound motifs.

Prioritizing motifs with a corresponding testis expressed factor and a nuclease footprint indicative of flanking nucleosome periodicity identified 17 sperm chromatin bound factors (non-homeobox: 5 factors, 7 motifs; homeobox: 13; Appendix C). The two motifs corresponding to the homeobox domain protein Pou2f1 (POU domain, class 2, transcription factor 1) were partitioned into separate groups after hierarchical clustering (Figure 4.9). A prior study identified this factor in mature mouse sperm and correlated its motif with nuclease sensitive DNAs [277]. Similarly, in addition to Ctf, Pax6, Esx1, and Pou2f1, two members of the winged helix transcription factor family are expected to be bound in sperm and have previously been identified in the male germline. Similar to Pax6, both Foxj2 (Forkhead box J2) and Foxa3 (Forkhead box A3) are expressed in round spermatids and in other testicular cell types, but have yet to be identified in the mature gamete suggesting that if bound in sperm the factors are not abundant [278-280]. The remaining factors corresponding to the reported nuclease footprints await confirmation in mouse sperm.

Sperm chromatin bound factors are enriched within regulatory regions

To establish candidate prior and future functions of the chromatin factors predicted by the sperm nuclease footprints, occupied motifs were compared to known regulatory regions and promoters. Analysis of ENCODE testis ChIP-seq datasets highlighted associations between nuclease footprints and active chromatin features [3]. Predicted regions of Ctf, Foxj2 and Rest (RE1-silencing transcription factor) binding in sperm were significantly associated with peaks of active histone modifications including H3K4me3 and H3K27ac ($P < 1.3 \times 10^{-13} - 6.2 \times 10^{-286}$, Fisher exact test). Rest, Foxj2, and Pou2f1 sites in sperm also were significantly enriched within promoters of genes expressed in the male germline ($P < 8.2 \times 10^{-6} - 1.9 \times 10^{-79}$, Fisher exact test),

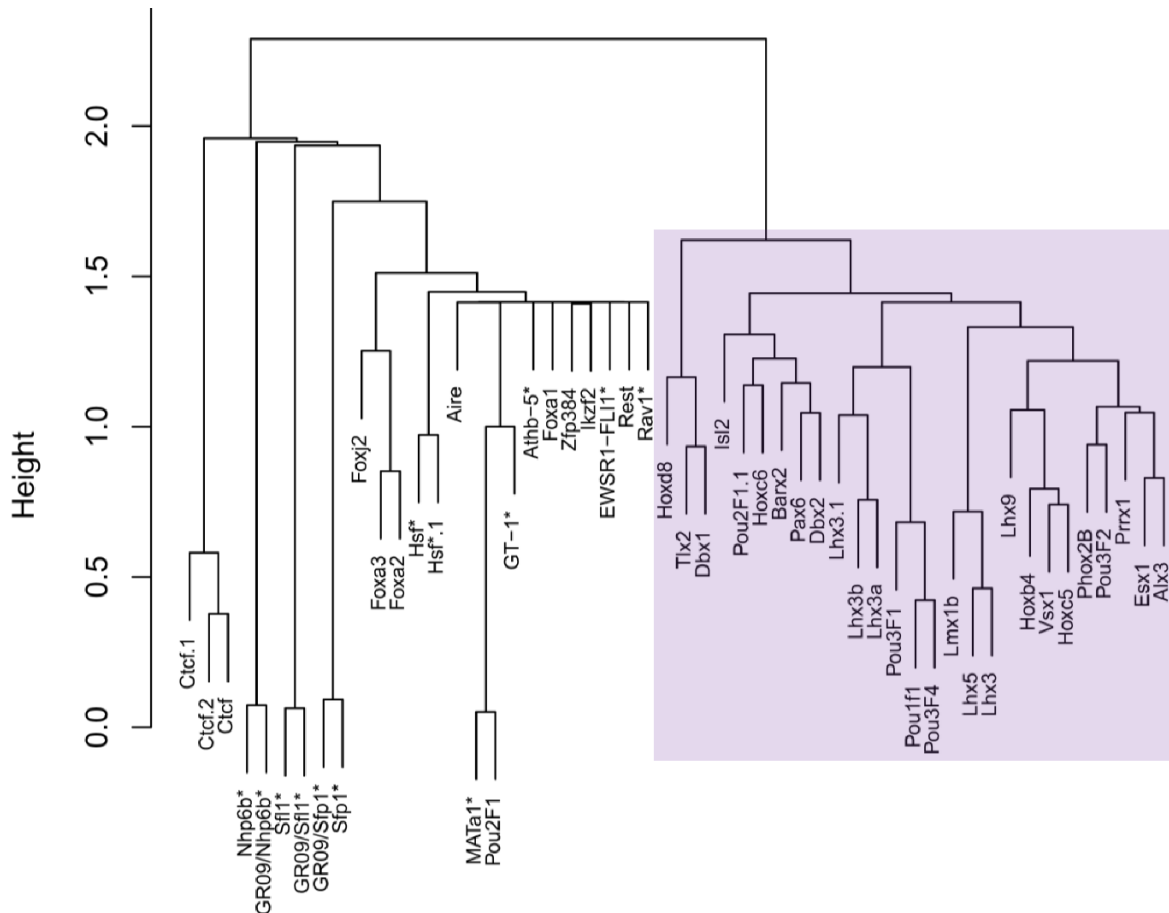
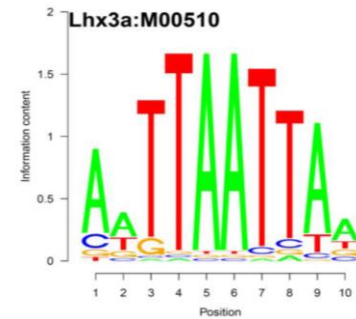
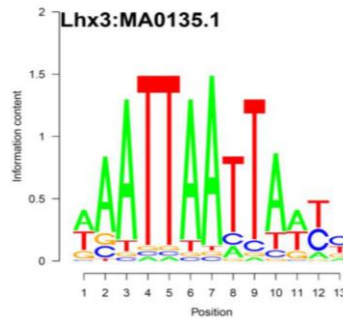
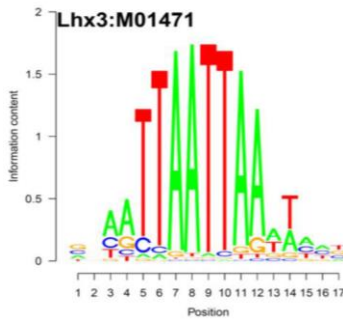
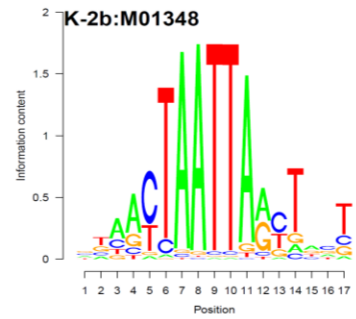
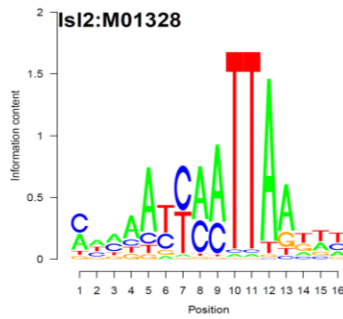
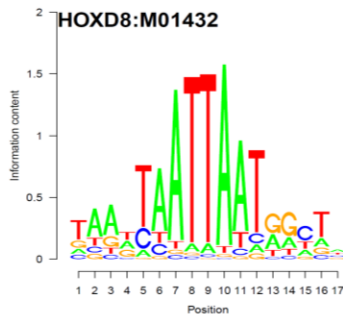
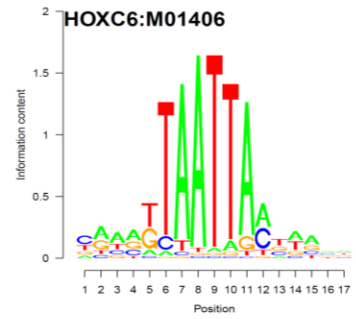
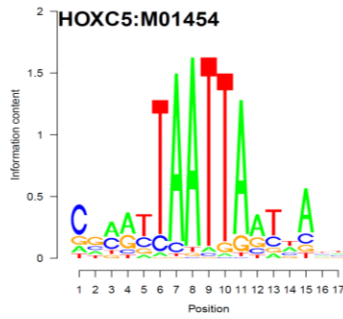
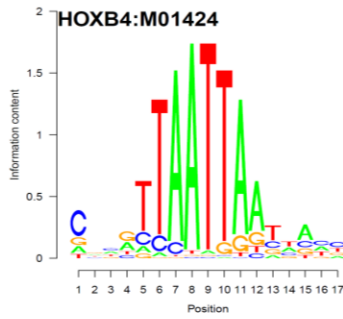
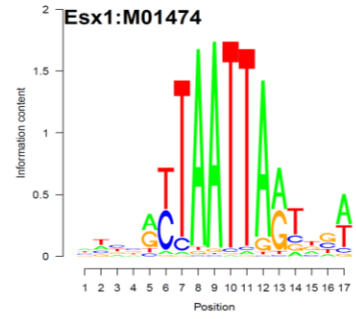
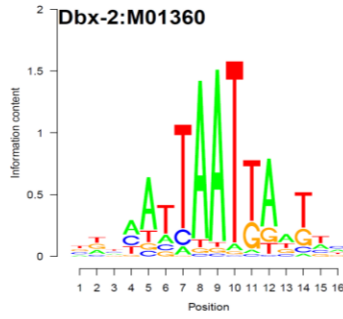
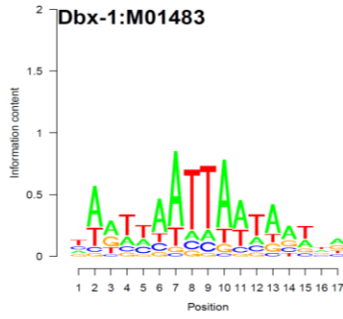
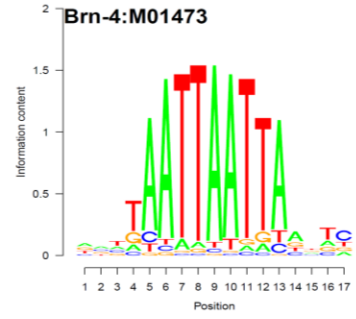
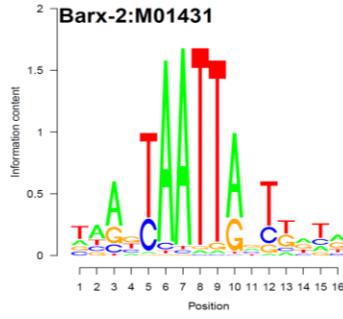
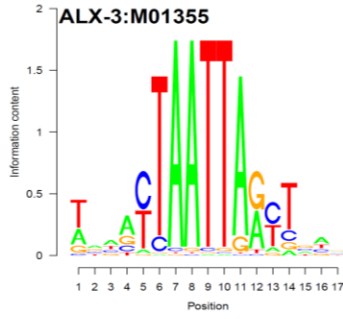


Figure 4.9. Hierarchical clustering identifies binding at identical homeobox motifs. Two groups are identified by hierarchical clustering on genomic distributions of bound factor sites (Jaccard index). The homeobox factors (purple) share a common motif resulting in overlapping predictions of binding. Asterisks denote motifs identified in other species with no known mouse homolog.

complementing their above enrichment within regions bearing active histone modifications in testis. Together motifs bound by Foxj2 and Pou2f1 were found within 4,386 testis promoters suggesting that these transcription factors are important regulators of spermatogenic transcription. A similar analysis of all RefSeq gene promoters demonstrated that only Rest exhibited a significant enrichment within this broad set of regions ($P < 2.5 \times 10^{-171}$, Fisher exact test). Cctf sperm footprints were not enriched in the above promoter sets but were significantly associated with predicted testis enhancers reflecting the role of this factor in regulating chromatin interactions ($P < 3.6 \times 10^{-224}$, Fisher exact test). Bound motifs corresponding to Foxj2 and Rest



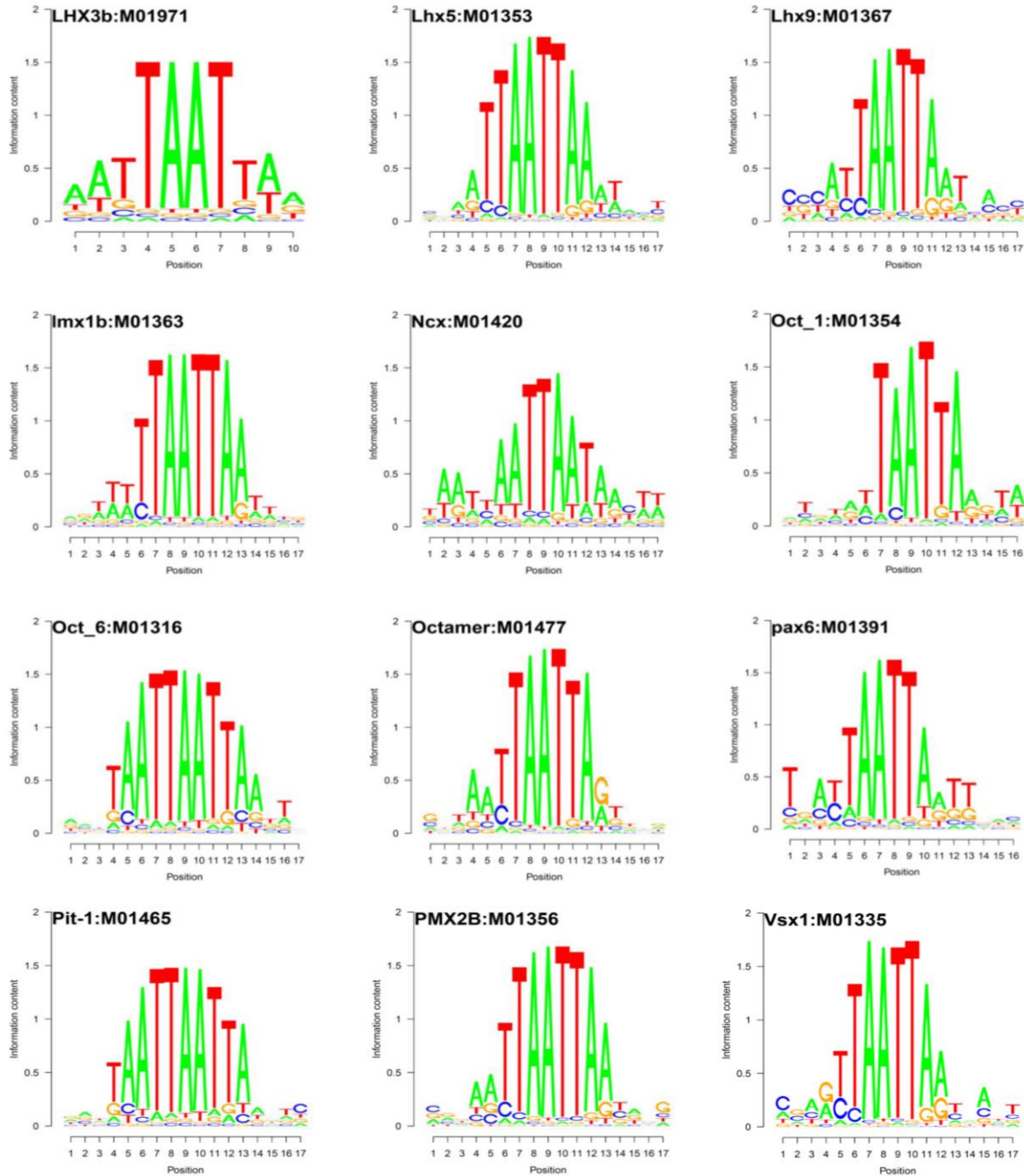


Figure 4.10. Homeobox motifs. Motifs corresponding to the factors in the second cluster (dashed box, Figure 4.7; purple box, Figure 4.9).

were also significantly associated with testis enhancers though to a lesser degree ($P < 2.7 \times 10^{-3}$ and $P < 0.014$, Fisher exact test, respectively). Together these results demonstrate the potential for past regulatory action by the factors retained in mature mouse sperm.

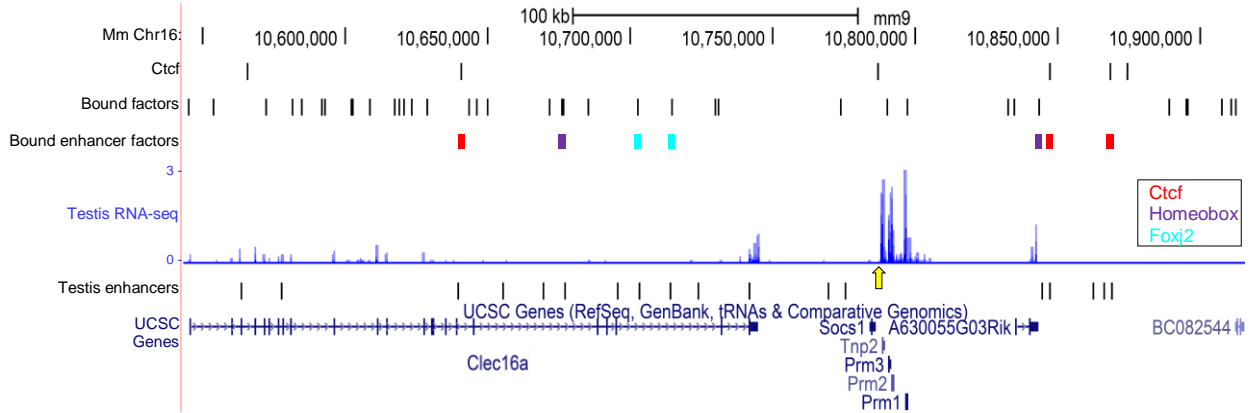


Figure 4.11. Footprint analysis of endogenous protamine locus. Footprint analysis of endogenous protamine locus. To identify potential regulators of prior endogenous protamine transcription the CENTIPEDE footprint analysis was relaxed to test the occupancy status of additional motifs found within the 5 Mb region centered on the mouse protamine locus. Footprints (2 kb CENTIPEDE window; see Methods) overlapping testes enhancers are colored according to their name. Average log₁₀ normalized total testis RNA-seq coverage is depicted in blue. Yellow arrow designates the Ctf site bound upstream of Tnp2. Predicted testis single nucleotide enhancer peaks were provided by the mouse ENCODE project [26]. Additional footprints identified in sperm that do not intersect a testis enhancer are presented in a separate track (motif length, ~20 bp).

The distribution of sperm nuclease footprints across the 5 Mb search regions centered on the endogenous or transgenic protamine loci was determined to evaluate the potential contribution of these factors to expression of either gene cluster. A similar number of footprints were observed within both extend regions of chromosome 19 (transgenic *PRM*) and chromosome 16 (endogenous *Prm*; $n = 650$ and 598 , respectively). The number of footprints within the domains harboring the transgenes or the endogenous *Prms* was also similar ($n = 50$ and 43 , respectively; dashed boxes). However, the relative density of footprints was greater proximal to the endogenous genes. This domain is approximately 1/3 the length of the domain containing the integrated sequence. Ctf exhibited a limited presence in this larger domain which contained only seven spermatid ChIP-seq peaks and zero sperm footprints corresponding to this factor. In contrast the shorter domain was relatively enriched in Ctf, containing 17 ChIP-seq peaks and 3 footprints. A single site identified in sperm overlapped a predicted testis enhancer element. To

Table 4.1. Regulatory Factors in Sperm Overlapping Testis Enhancers

Factor	Footprint Coordinates	Testis Enhancer Peak*
Ctcf	chr16: 10,639,310 – 10,641,331	chr16: 10,639,400
Homeobox	chr16: 10,675,153 – 10,677,169	chr16: 10,676,700
Foxj2	chr16: 10,701,314 – 10,703,331	chr16: 10,703,100
Foxj2	chr16: 10,713,448 – 10,715,465	chr16: 10,713,800
Homeobox	chr16: 10,842,275 – 10,844,301	chr16: 10,844,000
Ctcf	chr16: 10,845,809 – 10,847,828	chr16: 10,846,800
Ctcf	chr16: 10,867,176 – 10,869,197	chr16: 10,868,600

*(Shen, Yue et al. 2012)

identify additional regulatory factor enhancer interactions, which may contribute to the regulation of the protamine loci, the initial stringent sperm footprint analysis was repeated relaxing parameters for sites identified in either 5 Mb search region. Recapitulating the prior results both 5 Mb regions and domains contained a similar number of footprints. This expanded analysis identified six nuclease footprints overlapping testis enhancer elements. This included Ctcf and Foxj2 as well as the homeobox motif (Table 4.1). Additional occupied sites were localized within the protamine gene cluster (Figure 4.11). Factors bound to testis enhancers in sperm are expected to have inherited this association from prior cell types as was observed for Ctcf in round spermatids and the mature gamete. Therefore these regulatory proteins are strong candidates for driving expression of the protamine gene cluster through their involvement with the proposed DNA looping interaction mediated by Ctcf binding to the *Socs1*-MAR-*Tnp2*.

Sperm chromatin bound factors are enriched near sites of embryonic transcription

The group of homeobox domain motifs identified by hierarchical clustering did not exhibit a significant association with testis promoters or regulatory regions. Rather this group of related factors, including Hoxd8 (Homeobox D8), Tlx2 (T cell leukemia, homeobox 2), and Lhx5 (LIM homeobox protein 5), were significantly enriched upstream of ribosomal RNA sequences ($n = 62 - 128$, $P < 2.7 \times 10^{-3} - 5.5 \times 10^{-8}$). Foxa3 and Foxj2 sperm footprints also exhibited a significant

association with these regions ($n = 139$, $P < 6.4 \times 10^{-6}$; $n = 167$, $P < 2.5 \times 10^{-4}$, Fisher exact test, respectively). Zygotic ribosomal RNA transcription has recently been shown to be required for the first cell division [103]. This process is dependent on the deposition of H3.3 within the paternal pronucleus by the Hira histone chaperone. Sperm chromatin retention of transcription factors within a nucleosome associated conformation upstream of the rRNA sequences may contribute to this process by serving as sites of nucleation for further histone incorporation [204]. Sperm derived nucleosomes may also contribute to the establishment of embryonic chromatin in other regions of the genome. Perturbation of spermatogenic polyADP-ribose metabolism was shown to alter histone positioning within the gamete and was correlated with altered expression the olfactory receptor genes in the 2-cell embryos sired by treated males [281]. Promoters of these genes were significantly enriched in homeobox domain nuclease footprints identified in sperm (merged homeobox sites, $n = 354$, $P < 1.7 \times 10^{-38}$; Fisher exact test). In total the merged set of bound homeobox domain motifs overlapped 31% of all olfactory receptor gene promoters (354/1130). The alternative Pou2f1 motif was also significantly enriched within these regions ($n = 151$, $P < 3.5 \times 10^{-96}$; Fisher exact test). These factors may serve a similar function as those proposed to prime the rRNA genes for early transcription.

Intriguingly, a set of Ctcf nuclease footprints was also enriched within the promoters of genes differentially expressed in pronuclei mouse embryos relative to oocytes ($n = 106$, $P < 2.8 \times 10^{-284}$, respectively; Fisher exact test). The binding of Ctcf to these regions in round or elongating spermatids is predicted to preserve their nucleosomal chromatin conformation thereby imparting a preferentially accessible structure necessary for early utilization by the embryo (Figure 4.12).

Characterization of Ctcf in mouse sperm

Nucleosome coverage across the endogenous and transgenic loci suggested a potential role for Ctcf in coordinating expression of these sequences. This is expected to occur through the

Ctcf Footprints in
pre-ZGA promoters

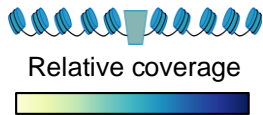
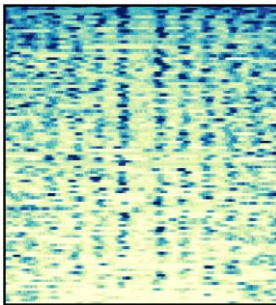


Figure 4.12. In mouse sperm Ctcf sites flanked by nucleosomes are enriched within the promoters of genes expressed in the zygote. Pooled sperm nucleosome coverage is shown \pm 1 kb of the Ctcf motifs occupied in sperm that overlap promoters of differentially expressed genes in pre-ZGA embryos relative to oocytes [n = 106; 1]. Elevated nucleosome sequencing coverage is in blue.

binding of Ctcf to the *Socs1*-MAR-*Tnp2* thereby promoting intra-domain chromatin interactions between the locus and *cis* regulatory elements. It seems reasonable to expect that mechanisms of regulating expression in haploid cells possessing nucleosome-bound genomes parallel those of their diploid somatic counterparts. However, it remains unclear what role Ctcf serves within the static sperm nucleus, though any proposed functions must necessarily bookend sperm maturation and fertilization due to chromatin condensation. In somatic cells the binding of Ctcf, in addition to establishing chromatin domains, locally results in well positioned arrays of polynucleosomes [282, 283]. Approximately 95 - 99% of histone have undergone replacement by protamines following spermatogenic nuclear remodeling in mouse, yet nuclease digestion of mouse sperm chromatin reveals a similar relationship between Ctcf and nucleosome periodicity in the histone-depleted gamete (Figure 4.13). Recapitulating observations from somatic cells this nucleosome periodicity extends for approximately 1.5 kb in sperm. In contrast, aggregate nucleosome coverage is indistinguishable from control DNAs in the absence of a binding event. These nucleosome arrays contained both canonical and replication-independent histones proteins (Figure 4.14). Ctcf

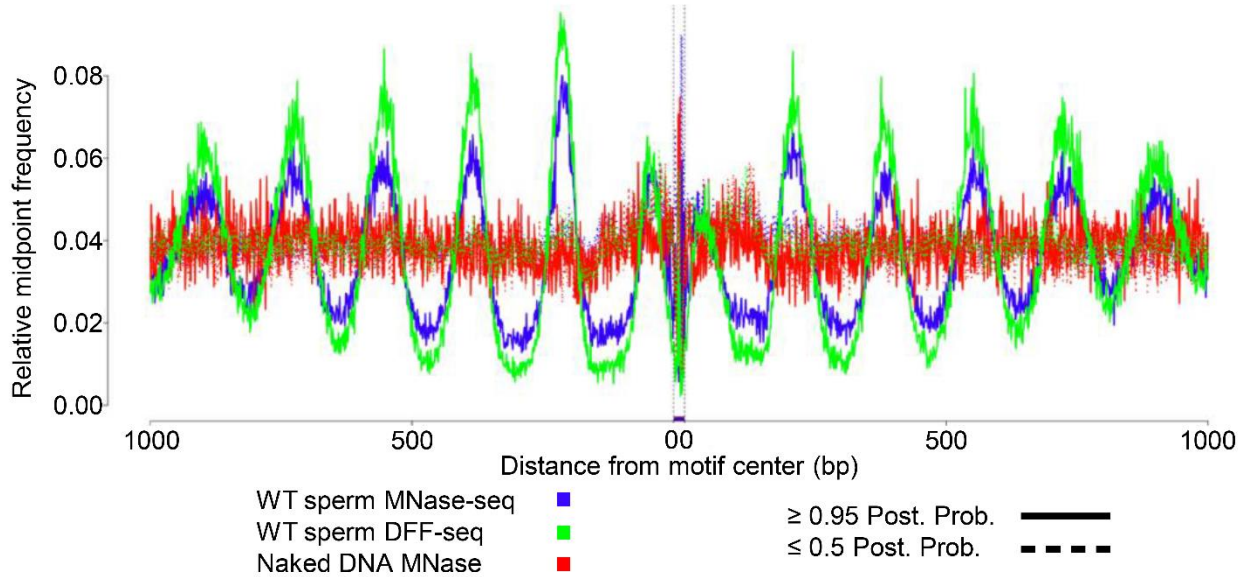


Figure 4.13. Bound Ctf motifs are associated with well positioned nucleosomes. Ctf footprints from WT sperm digested with either MNase or DFF (blue and green, respectively) are revealed by plotting sequencing fragment midpoints aligned within the regions flanking bound motifs (solid line, posterior probability ≥ 0.95). Sequencing coverage proximal to bound sites is correlated with periodic increases in midpoint frequency approximately every 160 bp reflecting an increase in protected nucleosome-bound DNA relative to digested linker regions. In contrast, unoccupied motifs in mouse sperm (dashed line, posterior probability ≤ 0.5) and naked control DNAs (red) do not exhibit variable levels of nuclease susceptibility.

footprints were also observed in modified H3K27me3 sperm datasets but not H3K4me3 [15]. This likely reflects the varied distributions (broad and diffuse vs narrow and dense, respectively) of the opposing histone modifications [3].

Ctf footprints identified within nucleosome bound sperm chromatin were substantiated by ChIP-seq analysis of this factor in round spermatids [$P \sim 0$, Fisher exact test; Figure 4.15A; 254]. The majority of footprints identified in the initial CENTIPEDE analysis (86%, $n = 5009/5797$) corresponded to Ctf ChIP-seq peaks in the earlier cell type (Figure 4.15E). Relaxing the minimum PWM score used to identify Ctf binding sites in sperm returned 2,170 additional footprints of which approximately 76.5% overlapped a ChIP-seq peak ($n = 6109/7967$). Occupied Ctf motifs in sperm which lacked a corresponding ChIP-seq peak reflect sites which failed to

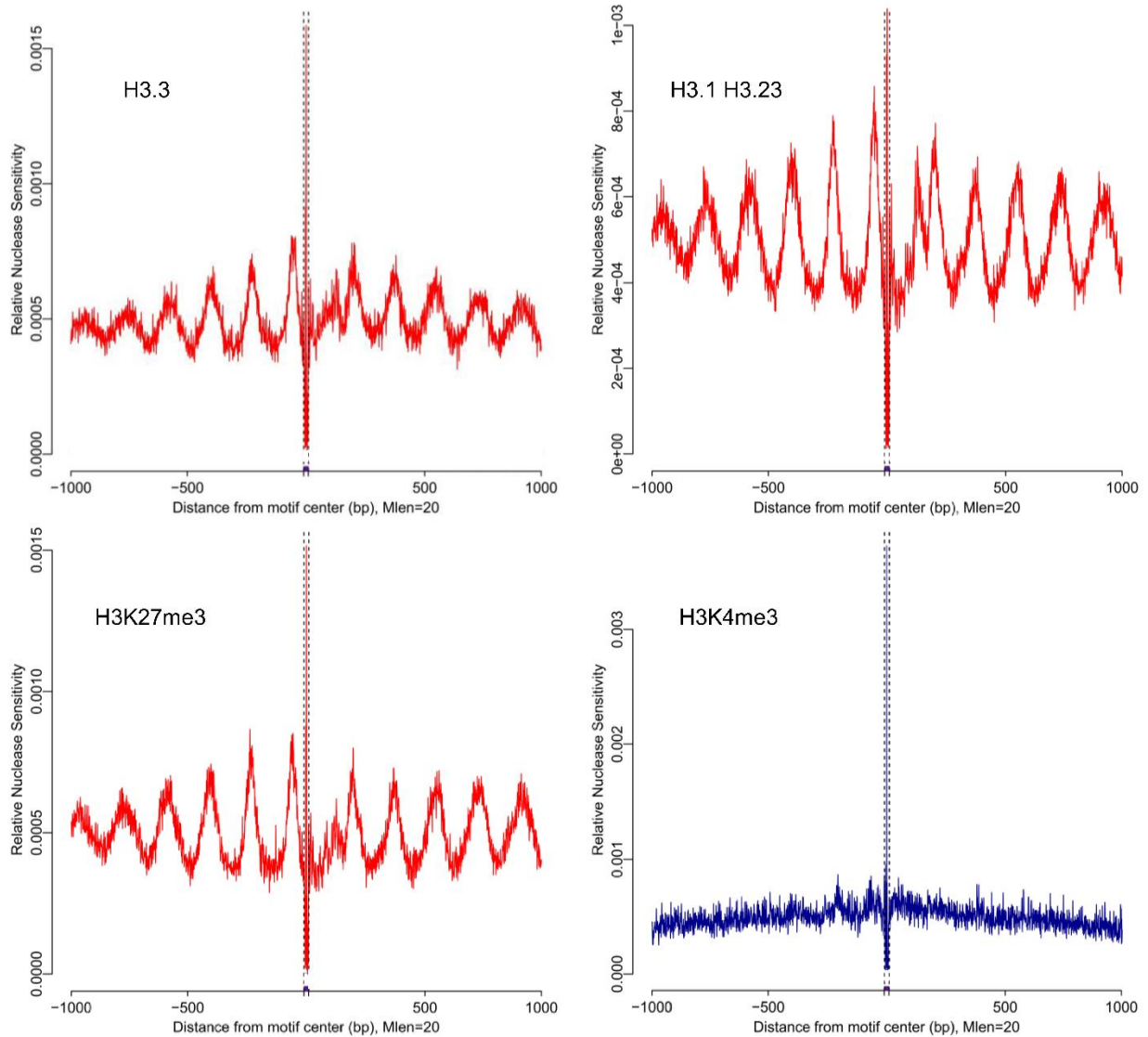


Figure 4.14. The sperm Ctf footprint is observed in modified and variant histone sequencing data. Ctf footprints were identified in MNase ChIP-seq datasets from mature mouse sperm with CENTIPEDE (Erkek, Hisano et al. 2013). The use of single-end sequencing data required plotting the 5' ends of sequencing reads.

reach significance in spermatids and not the presence of exclusive binding within the gamete (Figure 4.15C). A minor subset of sperm Ctf footprints (~13.5%, Figure 4.15E) coincide with regions bound by both Ctf and the highly related protein Boris (Brother of Regulator of Imprinted Sites; Figure 4.15B). This includes the *Socs1*-MAR-*Tnp2*. Contrary to recent reports [254], Ctf

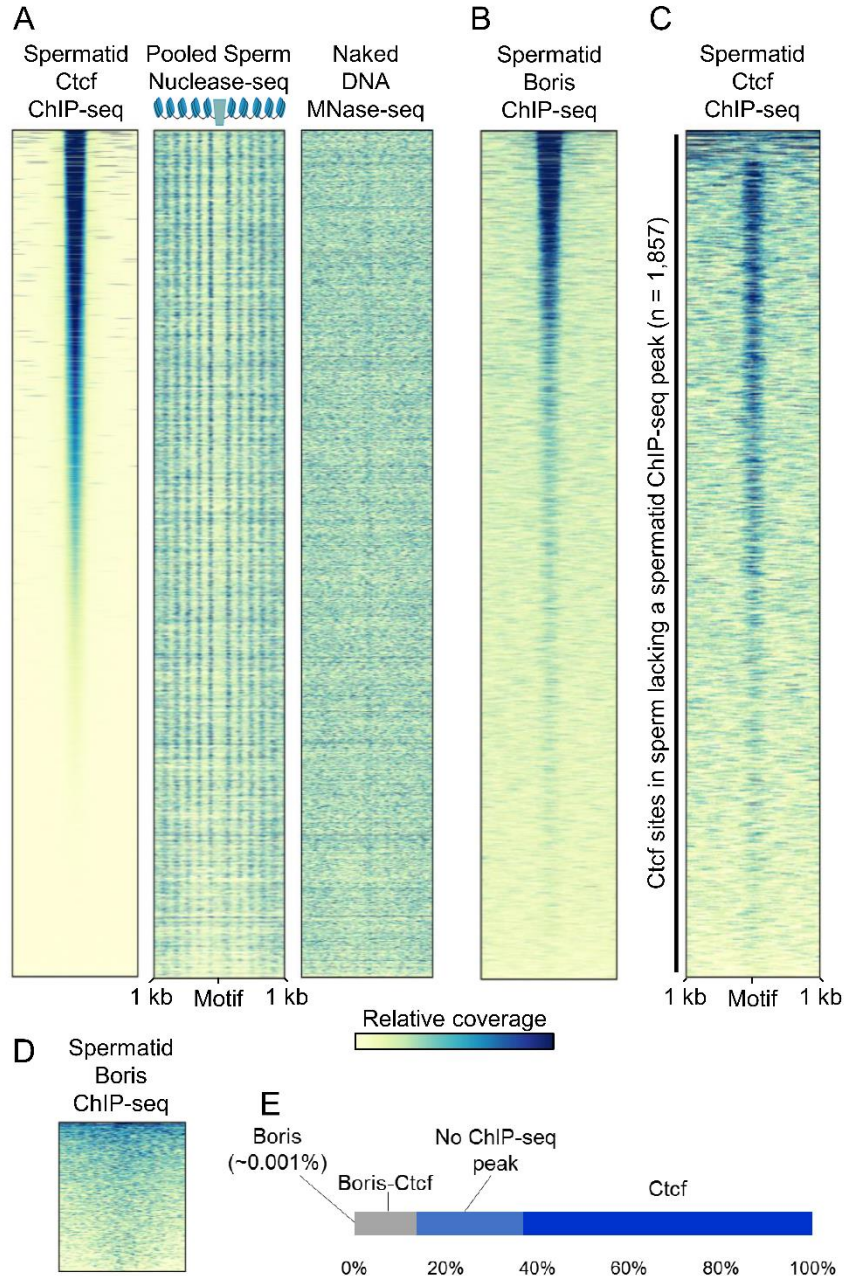


Figure 4.15. Sperm Ctf footprints are retained from round spermatids. Heatmaps of relative ChIP-seq, sperm nucleosome, and control sequencing coverage in 2 kb windows centered on the complete set of 7,967 Ctf sites predicted to be bound in mature mouse sperm (Methods). ChIP-seq against Ctf and Boris in round spermatids are presented in A and B, respectively. Sites are presented in descending order according ChIP-seq signals. (C) Ctf ChIP-seq coverage of occupied Ctf motifs in sperm which do not intersect a significant peak in round spermatids. (D) Sperm nucleosome coverage of Boris ChIP-seq sites lacking a Ctf co-peak. (E) The majority of the Ctf sites predicted to be bound in sperm ($n = 7,967$) are occupied solely by Ctf in round spermatids ($n = 5,034$, 63.2%). A subset of sperm Ctf sites correspond to co-occupied Boris-Ctf peaks in rounds ($n = 1,075$, 13.5%) or lack a corresponding ChIP-seq peak in the prior cell type ($n = 1,857$, 23.3%). In the latter case this was due to peaks below the significance threshold (C).

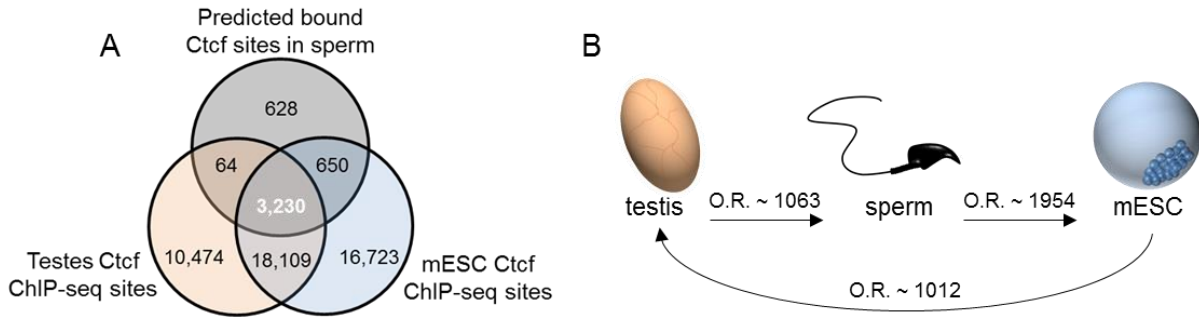


Figure 4.16. The continuity of Ctcf occupancy in testis, sperm, and ESCs. The majority of Ctcf sites predicted to be bound in sperm are observed in mouse ENCODE testis and mESC ChIP-seq datasets (A). Odds ratios (O.R.) from Fisher exact tests are presented between cell types comparisons [B; 3].

and not Boris appears associated with nucleosomes in mature mouse sperm (Figure 4.15D). Localized to pre-meiotic spermatogenic cells [284], this factor is likely depleted in the latter spermatogenic cell types as fewer ChIP-seq peaks corresponding to this factor were identified in spermatids relative to Ctcf ($n = 5,393$ and $42,493$, respectively). Ctcf also exhibited greater testis transcript levels in comparison to Boris (24.2 and 16.4 TPM, respectively). Regardless, eviction of Boris and the majority of Ctcf proteins from elongating/condensing spermatid chromatin is likely coincident with the histone-protamine transition. Complementing the observed conservation of Ctcf sites in spermatids and the mature gamete, regions bound by this factor in sperm also exhibited a significant intersection with ENCODE testis and ESC Ctcf ChIP-seq peaks ($p < 0.0001$, odds ratio ~ 1063 , Fisher exact test; Figure 4.16). These results suggest the continuity of global chromatin organization as mediated by Ctcf through the murine male germline and potentially into the next generation.

The most prevalent model of sperm chromatin organization, the Donut-Loop Model, predicts that, in the gamete, DNA loops anchored to the nuclear matrix within nucleosome enriched regions condense following deposition of the protamines into toroidal structures [136, 138, 204]. In this study the *Socs1*-MAR-*Tnp2* was observed to be bound by Ctcf/Boris in round spermatids and retained in the mature cell. However, Ctcf footprints in mature mouse sperm are

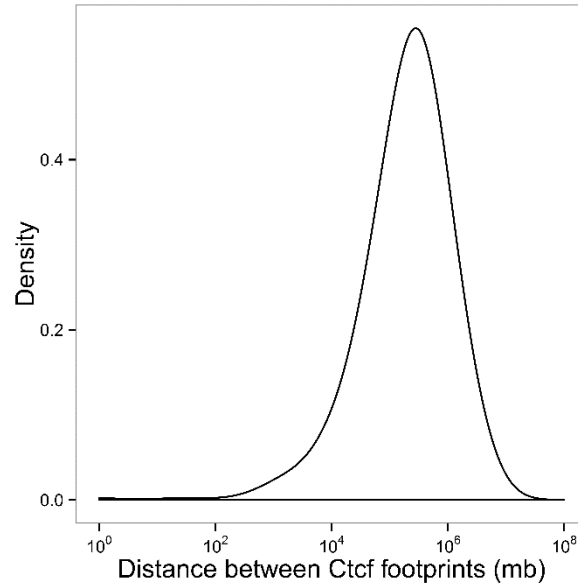


Figure 4.17. Distances between Ctf footprints in sperm. The distribution of intra-chromosomal lengths between occupied Ctf footprints in sperm is presented. Sites are separated by a median distance of 0.23 Mb on average.

log-normally distributed along the chromosomes, exhibiting a median distance between sites of approximately 230.5 kb (S.D. ~ 1 Mb; Figure 4.17). This exceeds the expected uniform DNA loop length observed following sperm nuclear matrix extractions (~ 25 - 50 kb) [140, 194]. Considering the nuclear matrix is a structure observed under harsh extraction conditions, an alternative model of sperm chromatin architecture can be considered that incorporates testis and sperm datasets [12-15] as well as insights from the last decade of chromatin conformation studies [6, 124, 132]. Ctf footprints identified in the mature gamete are significantly enriched within Ctf ChIP-seq peaks from testis and embryonic stem cells, although, sites occupied by this factor in sperm are relatively few in number (Figure 4.16). This reflects the eviction of the majority of chromatin proteins during the histone-protamine transition and the absence of active chromatin regulation in the mature gamete. Occupied Ctf motifs in mouse sperm (posterior probability > 0.95) are significantly enriched within the boundaries of ESC TADs ($P < 4.3 \times 10^{-232}$, Fisher exact test; $P < 1.0 \times 10^{-4}$, Empirical p-value) to a greater degree than unbound sites (posterior probability > 0.5;

$P < 1.8 \times 10^{-20}$, Fisher exact test; $P < 4.5 \times 10^{-2}$, Empirical p-value). Preferential retention in sperm of Ctf proteins demarcating higher order chromatin structures suggests the paternal gamete packages DNA in a manner conducive to the inheritance of global genomic organization by future cell types. This could be achieved during nuclear remodeling, by maintaining large stable chromatin domains at the expense of disrupting the smaller domains they envelope [6, 128, 129]. As spermatogenic nuclear remodeling initiates it likely resembles other chromatin regulatory events [6, 130] in that the timing and degree of remodeling vary within and between genomic compartments and TADs. However, as this process perpetuates Ctf binding sites are progressively vacated thereby disrupting the distinct regulatory environment of individual TAD sub-compartments and imparting a degree of uniformity upon the chromatin landscape (ie protamination). This model would suggest that during sperm chromatin remodeling stratified nuclear organization is lost within smaller sub-compartments while larger domain structures persist. Ctf sites detected in mature mouse sperm preferentially delineate these larger stable domains permitting the usage following fertilization. In other species which do not retain Ctf in mature sperm these sites likely exhibit delayed eviction as suggested by the enrichment of Ctf binding sites within nuclease accessible chromatin released from human sperm. The above model does not require the nuclear matrix. Similar to the somatic chromatin fiber the haploid genome bound by Ctf and other factors likely serves as its own structural platform. This self-organization is progressively lost as the TNPs and PRMs bind the intervening regions between retained Ctf proteins.

Ctf is absent from man and bull

Ctf motifs predicted to be bound in murine spermatozoa (posterior probability > 0.95) exhibited a greater degree of conservation than sites lacking a nuclease footprint (posterior probability > 0.5; $P < 2.2 \times 10^{-16}$, Mann–Whitney U-test; Figure 4.18A). This suggested that the retention of this chromatin insulator in sperm may be a conserved facet of paternal gametes. Prior

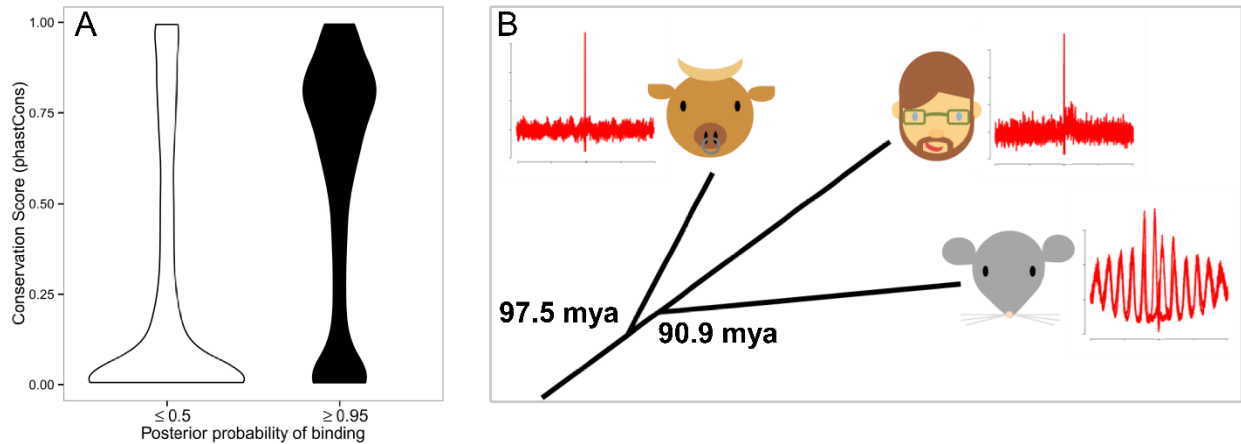


Figure 4.18. Ctcf footprints in mouse sperm are highly conserved but unoccupied in the mature male gamete of other species. (A) Ctcf motifs predicted by CENTIPEDE to be bound in mouse sperm (posterior probability ≥ 0.95 , black) exhibit greater conservation (phastCons) than unbound sites (posterior probability ≤ 0.5 , white). (B) The Ctcf footprint is not observed in either human or bull sperm.

studies have correlated CTCF binding sites with nucleosome-associated DNAs in human sperm [12] and transcripts encoding this factor are abundant in human testis. Subjecting human and bull [285] sperm mononucleosome MNase-seq libraries to the CENTIPEDE footprinting approach demonstrated that Ctcf is not bound in mature sperm of either species (Figure 4.18B). The availability of previously published human sperm datasets demonstrated that this finding was sample-independent and unlikely to be a consequence of single-end sequencing [16, 285]. Further, exhaustive analysis of available PWMs indicated that well phased polynucleosomal arrays are not associated with known motifs in the human sperm sample. These differences in sperm genome architecture may reflect species specific patterns of embryo development. In mouse pre-implantation milestones such as EGA [95, 286, 287] and compaction [288-290] occur earlier than that observed in human or bovine embryos [291]. In contrast, the retention of regulatory factors within murine spermatozoa may contribute to the accelerated developmental timing of the mouse embryo. Nuclease footprinting in mouse spermatozoa demonstrated that proteins, including members of the homeobox family and Ctcf, are likely situated within histone-bound chromatin and enriched within genomic regions that undergo transcription in the zygote or

2-cell embryo [1, 103, 281]. Zygotic transcription from the paternal pronucleus exceeds that from the maternal supporting a potential role for these sperm borne regulatory factors in genome activation [292]. Whether this might be achieved by recruitment of remodeling and/or transcriptional machinery remains unclear. Ctfc footprints identified in mouse sperm are enriched within the promoters of differentially expressed pronuclear genes and preferentially localized to boundaries of mouse ESCs TADs. Maintenance of these interactions following spermatogenic nuclear condensation in mouse likely primes the paternal genome for rapid initiation of regulatory events, potentially including early embryonic transcription and establishment of higher order chromatin structures. This feature of mouse reproductive biology appears distinct from that of human or bovine and may be an adaptation to the accelerated preimplantation development of this species.

CHAPTER FIVE

CONCLUSIONS AND FUTURE DIRECTIONS

I. Sperm RNAs

The essential function of the spermatozoon is the delivery of the paternal genome to the oocyte. The developing sperm cell produces additional layers of information to accomplish this task. As discussed in the previous chapters, these potential sources of information include RNAs, specific chromatin states and associated proteins, as well as the global chromatin architecture. It is likely that many other molecular cues await discovery within the male gamete. However, following fertilization the three forms of information highlighted here are known to reach the oocyte cytoplasm. In each case, factors from without the sperm cell are required to interact with these potentially functional byproducts of spermatogenesis. It seems likely that the embryo possesses mechanisms other than degradative pathways with which to process the additional cargo delivered by the sperm cell.

To identify the potential function of RNAs retained in mature sperm, these transcripts were localized within the mature gamete. In this analysis, the sperm cell was broadly considered to be comprised of two compartments: the intra-nuclear compartment, containing the nucleus encapsulated within the perinuclear theca, and the extra-nuclear compartment, including the plasma membrane, the acrosome and associated membranes (Figure 3.1). RNA was extracted from sonicated sperm and detergent demembranated gradient fractionated sonicated sperm heads to determine if RNAs in the paternal gamete exhibit preferential retention in either compartment total. The efficacy of the fractionation procedure was demonstrated by electron microscopy. Though sonication reliably separated sperm heads and tails, the peripheral membranes of the cells in this treatment remained intact. In contrast, the sonicated mouse sperm heads lacked peripheral membranes but retained readily identifiable perinuclear structures following ultracentrifugation and demembranation (Figure 3.3). A clear preferential peripheral

retention of sperm RNA was observed following total RNA quantification. Approximately 61% of the estimated 87 femtograms of RNA in each spermatozoon was localized to these extra-nuclear compartment, despite the reduced volume of these structures relative to the remainder of the gamete (Figure 3.4).

To determine if the intra- and extra-nuclear compartments possessed different populations of transcripts total, RNAs were subjected to RNA-seq. Ontological analysis demonstrated RNAs retained within the sperm interior were solely associated with spermatogenesis. These transcripts included both *Prm1* and *Prm2*, which are packaged as mRNPs following their transcription in round spermatids. RNAs transcribed alongside the protamines are likely similarly bound by protein chaperones such that they evade the recently identified piRNA mediated decay pathway in elongating spermatids. These RNAs consequently exhibit delayed translation. Due to this delay, these RNAs are likely associated with the translational machinery as the cell begins to condense resulting in their passive sequestration within the perinuclear theca. This structure surrounds the nucleus and is enriched in ribosomal proteins. Having escaped degradation in this manner, the final transcriptional products of the developing sperm cell are embed within the intra-nuclear compartment. This series of molecular events likely explains the efficacy of sperm RNA-seq analysis in diagnosing idiopathic infertility [21, 108]. RNA homologs identified in the mouse intra-nuclear sperm compartment were significantly enriched within a subset predictive of fertility status in humans. Although the intra-nuclear sperm compartment contained RNAs which exhibited a significant association with spermatogenesis the interior of the sperm cell was not enriched in any annotated RNAs.

Supporting the significantly greater RNA mass in the extra-nuclear compartment, RT-PCR analysis demonstrated at minimum a nearly three-fold preferential peripheral enrichment for all evaluated RNAs. This included transcripts associated with extra-cellular vesicles. The sperm cell encounters tissue-specific vesicle-containing fluids as it moves through the testis, epididymis and

vas deferens. It remains unclear whether the enrichment transcript associated with vesicles signals their production by the developing gamete or only their delivery to the mature cell. Though the latter has been extensively observed, the former possibility suggests the spermatozoon may possess the ability to engage in a form of vesicular inter-cellular signaling.

The extra-nuclear compartment was also enriched in well-known somatic nuclear RNAs. These included several small nucleolar and Cajal Body-Specific transcripts, as well as *Malat1*. This suggested that, during nuclear remodeling, these RNAs are removed from the nucleus. Although *Malat1* exhibits an approximately ten-fold peripheral enrichment, it is still relatively abundant within the intra-nuclear compartment. This may suggest that this chromatin-associated RNA remains associated within those select regions of the sperm genome which harbor histone and are therefore preserved within a nucleosome-bound conformation.

The analysis of sperm RNA retention in the intra- and extra-nuclear compartments also provided the first evidence of the delivery of a sperm RNA to the oocyte following natural mating (Figure 3.10). This transcript, *Cabyr*, is a testis-specific RNA which encodes a protein that is restricted to the post-meiotic cell types. It was also found to be differentially enriched pronuclei mouse embryo relative to oocytes. It is likely that *Cabyr* transcripts, similar to the *Prm* RNAs, are bound within mRNPs and become sequestered within the sperm perinuclear theca following condensation. Embedded within the interior of the sperm cell, this RNA contacts the oocyte cytoplasm following fertilization. However, final outcome of *Cabyr* transcripts, and likely many other RNAs, once inside the embryo remains unclear.

II. Local and Global Sperm Chromatin Structure

An existing transgenic model system of the human protamine locus was characterized in chapters two and four. FISH analysis of transgenic mouse lymphocytes localized the insertion event within chromosome 19 (Figure 2.1). Fine-mapping demonstrated that the complete 40 kb

segment of human cosmid hp3.1 had integrated as a single copy within the seventh intron of *Cyp2c38* splitting an L1Md-T repeat (Figure 2.2). The transgenic sequence produced no observable phenotype and was stably passed through the germline for several generations.

Due to their required and robust expression the protamines are ideal candidates for the study of transcriptional regulation in the haploid genome. Furthermore, several studies have described the local chromatin features of this sequence in human sperm, providing a comparator for results generated by the model. In human spermatozoa, this locus has been shown to be packaged within a DNase-I sensitive conformation and to retain nucleosomes within TSSs. Previously identified patterns of chromatin packaging in the mature gamete histone-associated DNAs were released from transgenic mouse sperm with MNase to determine if the integrated locus recapitulated. Analysis of a human sperm MNase-seq library supported the prior observation that the promoter regions of genes in the human protamine locus are associated with nucleosomes (Figure 4.3). This pattern was not observed within the integrated locus suggesting that retention of nucleosome in mature sperm is not determined by sequence alone.

Comparison of transgenic and wild type sperm MNase-seq libraries established the chromatin packaging was equivalent regardless of genotype including within the region containing the endogenous protamine gene cluster. In all mouse sperm samples, this locus exhibited heightened nuclease sensitivity. In contrast to the results from the endogenous human protamine locus, defined peaks of nucleosome coverage were not associated with the TSSs of the mouse protamine gene cluster (Figure 4.1 and 4.3). This likely reflects the differential levels of histone retention in mice and men (~1% and ~15%, respectively).

The lack of a discernable phenotype following integration of an additional protamine locus in mouse was correlated with suppressed transcriptional regulation of the transgenes. However, irrespective of genotype or species the protamine sequences exhibited localized nuclease-

sensitivity in sperm. This likely reflected the active transcription of all loci prior to condensation. In both human and mouse, the regions flanking the endogenous gene clusters exhibited elevated nucleosome coverage whereas the sequences neighboring the transgenes did not. Analysis of predicted testis enhancer datasets and 3C interaction maps suggested that the chromatin context flanking the transgenes differed from that harboring the endogenous mouse protamine locus and presumably the human as well. Enhancer elements were observed proximal to the mouse protamine gene cluster whereas the inserted sequence was positioned within a repeat dense region lacking *cis* regulatory elements. Several observations suggested that transgene suppression was linked to the regulatory potential of its host chromatin domain and not due to the absence of elements within the inserted sequence. This included the lack of ectopic transgene expression and the predicted binding of Ctfc upstream of the locus in sperm (Figure 4.11). This factor was likely bound while the locus was transcribed in round spermatids, as was observed within the orthologous region of the endogenous gene cluster. Perturbation of this binding site in humans results in infertility while its absence in a prior transgenic model produced position effects. Together this suggested that Ctfc binding may mediate a DNA looping event between the protamine promoter regions and a proximal enhancer element in mice and men. Positioned outside of its native chromatin environment the integrated sequence cannot achieve this regulation resulting in suppression despite being actively transcribed.

A nuclease footprint strategy was used to predict the presence of Ctfc within the transgenic and mouse protamine loci in paternal gamete. In mouse sperm, application of this approach genome wide identified additional Ctfc footprints as well as those associated with other regulatory factors. Occupied sperm motifs were flanked by well positioned nucleosome arrays extending for approximately 1 - 1.5 kb. In mouse sperm, several of these sites were localized to the chromatin domain containing the endogenous protamine gene cluster, where they were predicted to be bound to testis enhancer regions in transcriptional active round spermatids. These factors are

candidates for participation in an anticipated DNA looping event mediated by Ctcf and responsible for driving the robust expression of the protamines.

Nuclease footprints were significantly enriched within genomic elements and chromatin features in testis. This included expressed promoters and enhancers as well as regions marked by active histone modifications. Members of the homeobox domain family predicted to be bound in mouse sperm were significantly associated with expressed sequences in zygote and the 2-cell embryo. This included approximately 30% of all olfactory receptor gene promoters as well as the upstream regions of the rRNA sequences. Occupied Ctcf sites in the paternal mouse gamete were also significantly enriched with the promoter regions of a subset of genes differentially expressed in pronuclei embryos relative to oocytes (Figure 4.12).

Ctcf footprints in mature mouse sperm were strongly associated with ChIP-seq peaks identified in mouse testis and ESCs. Analysis of Ctcf binding in round spermatids demonstrated that approximately 15% of these sites are likely retained in the mature gamete and may be of functional consequence during nuclear remodeling and following fertilization. In contrast, a similar footprinting approach failed to identify Ctcf in either human or bull sperm. The observed differences in sperm chromatin packaging within these species likely reflects the accelerated preimplantation development of mouse embryos. This may require that regulatory factors such as Ctcf remain bound in murine spermatozoa to assist in decondensing and activating the paternal genome.

III. Conclusions

Mouse sperm preferentially retain a host of RNAs within the peripheral regions of the cell. It is likely that some of these transcripts passively persist following cytoplasmic expulsion yet others may be packaged within extracellular vesicles. Though the presence of these structures along the surface of the spermatozoon has long been known, identification of exosomal-

associated RNAs within the extra-nuclear compartment of the paternal gamete may suggest sperm are also a source of vesicles. The binding and shedding of exosomes containing RNA as spermatozoa pass through the various fluids of the male reproductive tract may be an as yet poorly described form of intercellular signaling. There seems no reason why this form of communication must end following ejaculation and perhaps sperm vesicular crosstalk exists within the vaginal tract.

The interior of the sperm cell, specifically the perinuclear theca, is thought to be enriched in spermatogenic transcripts. It seems likely that these RNAs become sequestered within partially disassembled ribosomes as the cell condenses. Sperm may also possess mechanisms of actively storing transcripts, perhaps within mRNPs. These RNAs provide the oocyte, the researcher and, likely soon, the clinician potential information regarding the transcriptional history of the developing sperm cell.

Following fertilization, the sperm nucleus also imparts information to the oocyte in excess of the genome. In this respect, the lingering abundance of Malat1 within the intra-nuclear compartment of the mouse sperm cell and the regulatory factors identified by nuclease footprinting may maintain discreet regions of the sperm genome in a preferentially accessible chromatin conformation such that they can be utilized rapidly by the mouse embryo. In this species, this may include the Ctfc mediated inheritance of higher order chromatin organization. However, the absence of this factor in human and bull sperm does not preclude its potential role in regulating spermatogenic nuclear remodeling as is expected for mouse. As the haploid genome condenses the minority of Ctfc sites demarcating large stable chromatin domains restrict protamination to the intervening sequences producing the globular protamine-DNA condensates reliably observed in mature mammalian sperm. These sites are expected to exhibit delayed eviction in bull and human elongating spermatids. In contrast, retention of Ctfc in mature murine

spermatozoa assists in restructuring the paternal genome following fertilization such that it can contribute to accelerated preimplantation embryonic development.

APPENDIX A: Human Protamine Locus Tiling Array Probes

PROBE SEQUENCE	PROBE LENGTH	PROBE START
GGAACAAGTTAGGAGGAAAGCTTTCTAAACATGAAATTCTGCCAGAGCACTTGCC	55	1
GAACAAGTTAGGAGGAAAGCTTTCTAAACATGAAATTCTGCCAGAGCACTTGCCA	55	2
AGTTAGGAGGAAAGCTTTCTAAACATGAAATTCTGCCAGAGCACTTGCCACCGAA	55	7
GTTAGGAGGAAAGCTTTCTAAACATGAAATTCTGCCAGAGCACTTGCCACCGAAT	55	8
GAGGAAAGCTTTCTAAACATGAAATTCTGCCAGAGCACTTGCCACCGAATG	51	13
AGGAAAGCTTTCTAAACATGAAATTCTGCCAGAGCACTTGCCACCGAATGGGTTT	55	14
AGCTTTCTAAACATGAAATTCTGCCAGAGCACTTGCCACCGAATGGGTTTCT	52	19
GCTTTCTAAACATGAAATTCTGCCAGAGCACTTGCCACCGAATGGGTTTCT	51	20
ACCGAATGGGTTTCTCCCTACTGGTGATAAGTGGTATTGCAACTCAGCTCTATTA	55	56
CGAATGGGTTTCTCCCTACTGGTGATAAGTGGTATTGCAACTCAGCTCTATTAGA	55	58
GAATGGGTTTCTCCCTACTGGTGATAAGTGGTATTGCAACTCAGCTCTATTAGAC	55	59
GGTTTCTCCCTACTGGTGATAAGTGGTATTGCAACTCAGCTCTATTAGACAAAAG	55	64
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ACAACCCGTCACCAGAAAACAAGGGCACAGAATGGAGCAAAGGAACAAAAT	51	138258
AACAAAATGGGGCCATGAGAACTTCACCCCTGTCTACCCAGGAGTTCTGC	51	138301
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GGCTGTTTTAACCTGGTCCCTACCCATATCTTTAATTAGGATCCACGTGCT	52	139862
GCTGTTTTAACCTGGTCCCTACCCATATCTTTAATTAGGATCCACGTGCTG	52	139863

APPENDIX B: Mouse Protamine Locus Tiling Array Probes

PROBE SEQUENCE	PROBE LENGTH	PROBE START
CAGTGCCACAGGGCCAACCAGAAGCCAGGTGAAGGGCAACTGTTTTAAAG	51	50
AGTACAAGCCAGGCAACGGTGAGGCCTCACCCCAAGAGCTTTTCTTTGCCT	51	124
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AGCAGCCACTTCCTCTGAACGTGATCATTAAAGCATTAGGAAAGCCACTAGAA	52	500
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ACTTCCTCTGAACGTGATCATTAAAGCATTAGGAAAGCCACTAGAAGCATGTCCCA	55	507
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GATGAAAAAGGAGTGGAGATCTGAAGACCACTTTGACATCAAAATGGAGATGCA	55	19943

APPENDIX C: Factors identified by CENTIPEDE

MOTIF ID	MOUSE GENE SYMBOL	SPEARMAN RHO (POOLED SPERM VS CONTROL)	NUCLEOSOME PERIODICITY	HOMEBOX MOTIF	AVERAGE TESTIS TPM
M01432	Hoxd8	0.21	TRUE	TRUE	25.43
M01200	Ctcf	-0.03	TRUE	FALSE	24.21
M01259	Ctcf	-0.03	TRUE	FALSE	24.21
MA0139.1	Ctcf	-0.10	TRUE	FALSE	24.21
M01474	Esx1	0.23	TRUE	TRUE	21.04
MA0138.2	Rest	0.12	TRUE	FALSE	18.34
M00138	Pou2F1	0.26	TRUE	FALSE	13.00
M01354	Pou2F1	0.21	TRUE	TRUE	13.00
M00422	Foxj2	0.29	TRUE	FALSE	4.62
M01348	Prrx1	0.25	TRUE	TRUE	4.52
M01406	Hoxc6	0.21	TRUE	TRUE	1.77
M01367	Lhx9	0.22	TRUE	TRUE	1.57
M01328	Isl2	0.24	TRUE	TRUE	1.08
M01420	Tlx2	0.22	TRUE	TRUE	1.01
M01391	Pax6	0.24	TRUE	TRUE	0.72
M01316	Pou3F1	0.23	TRUE	TRUE	0.64
M01454	Hoxc5	0.23	TRUE	TRUE	0.61
M01477	Pou3F2	0.23	TRUE	TRUE	0.48
M01353	Lhx5	0.23	TRUE	TRUE	0.40
M01355	Alx3	0.24	TRUE	TRUE	0.10
M01431	Barx2	0.22	TRUE	TRUE	0.10
M01356	Phox2B	0.23	TRUE	TRUE	0.10
M00510	Lhx3A	0.22	TRUE	TRUE	0.08
M01471	Lhx3	0.23	TRUE	TRUE	0.08
M01971	Lhx3B	0.24	TRUE	TRUE	0.08
MA0135.1	Lhx3	0.22	TRUE	TRUE	0.08
M01360	Dbx2	0.22	TRUE	TRUE	0.08
M01424	Hoxb4	0.23	TRUE	TRUE	0.03
M00724	Foxa3	0.37	TRUE	FALSE	0.03
M01335	Vsx1	0.23	TRUE	TRUE	0.03
M00791	Foxa2	0.32	TRUE	FALSE	0.00
M01363	Lmx1B	0.23	TRUE	TRUE	0.00
M01465	Pou1F1	0.22	TRUE	TRUE	0.00
M01473	Pou3F4	0.21	TRUE	TRUE	0.00
M01483	Dbx1	0.26	TRUE	TRUE	0.00

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ABSTRACT**TOWARDS A UNIFIED MODEL OF SPERM CHROMATIN STRUCTURE**

by

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Sperm possess several layers of information that are delivered to the oocyte alongside the paternal DNA. Examples of potential sperm borne molecular cues of probable use to the embryo include RNAs and local and global chromatin structure. To identify candidate sperm RNAs that likely reach the oocyte cytoplasm following fertilization patterns of transcript compartmentalization in the mature gamete were identified. Though all sperm RNAs exhibited a preferential peripheral enrichment, a subset of RNAs were identified in which this trend was reduced. These RNAs are thought to be embedded with perinuclear theca and are correlated with late spermatogenic transcription. Malat1, a well-known nuclear non-coding RNAs, was relatively abundant within the intra-nuclear compartment of the gamete although enriched within the sperm extra-nuclear compartment. If these transcript are localized to the condensed sperm nucleus Maltat1 may contribute to the retention of somatic-like chromatin structures following nuclear remodeling. Histone-bound regions which persist in mature sperm are of interest as they may be informative of past spermatogenic and future embryonic genomic regulation. Genome wide nucleosome mapping in mature mouse sperm was complimented with a nuclease foot printing approach to identify sites of factor retention throughout the paternal gamete. Applying this analysis to a transgenic mouse model harboring the human protamine locus, highlighted the potential regulatory impact of the chromatin environment at the local and domain level.

Consideration of these results within the context of the endogenous mouse protamine locus identified a candidate transcriptional regulatory mechanism. Factors predicted to be bound in mature sperm were correlated with genomic elements utilized in the testis and the very early embryo. This included Ctf, which was significantly enriched within the boundary regions of topologically associated domains and the promoter regions of genes expressed in the zygote. These patterns were not observed in human or bull sperm. It is suggested that delivery of the paternal genome in association with regulatory factors may reflect the accelerated preimplantation development of the murine embryo. Sites of Ctf retention in mature sperm were considered within a novel model of spermatogenic nuclear remodeling.

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