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Chronic *Chlamydia* infection in human organoids increases stemness and promotes age-dependent CpG methylation

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Chronic infections of the fallopian tubes with *Chlamydia trachomatis* (*Ctr*) cause scarring and can lead to infertility. Here we use human fallopian tube organoids and genital *Ctr* serovars D, K and E for long-term in vitro analysis. The epithelial monolayer responds with active expulsion of the bacteria into the lumen and with compensatory cellular proliferation— demonstrating a role of epithelial homeostasis in the defense against this pathogen. In addition, *Ctr* infection activates LIF signaling, which we find to be an essential regulator of stemness in the organoids. Infected organoids exhibit a less differentiated phenotype with higher stemness potential, as confirmed by increased organoid forming efficiency. Moreover, *Ctr* increases hypermethylation of DNA, which is an indicator of accelerated molecular aging. Thus, the chronic organoid infection model suggests that *Ctr* has a long-term impact on the epithelium. These heritable changes might be a contributing factor in the development of tubal pathologies, including the initiation of high grade serous ovarian cancer.

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nderstanding the mechanisms of fallopian tube (FT) homeostasis and pathology constitutes an important medical challenge, particularly in light of women's fertility and beyond. Notably, the FT is the likely tissue of origin of highgrade serous ovarian cancer (HGSOC), the deadliest gynecological malignancy¹. Yet, progress in this area has been painstakingly slow, due to the absence of suitable experimental models as well as the lack of diagnostic tools. Among the most common causes of tubal pathology is the Gram negative pathogen *Ctr*, affecting 1.6 million people in 2016 in the USA alone². It frequently leads to chronic infections due to a lack of symptoms and can result in tubal scarring and occlusion, the major cause of infertility and ectopic pregnancy^{3,4}.

As an obligate intracellular pathogen, Ctr has been shown in vitro to subvert host cell metabolism, block apoptosis, and impact genome integrity by causing DNA damage and triggering degradation of p53⁵⁻⁷. Nevertheless, key steps in the development of Ctr-induced tubal inflammation (salpingitis) remain obscure, including the natural progression of infections. In particular, there is a gap in our knowledge concerning the long-term consequences of Ctr infections on epithelial homeostasis. Several early studies reported structural damage to the FT^{8,9}. Previously, we also showed that several paracrine pathways are activated in response to acute *Ctr* infection ex vivo¹⁰, suggesting the existence of broader host defense mechanisms that include both infected and neighboring non-infected cells. Still, it has so far been impossible to analyze the molecular sequels of these initial events during the establishment of chronic Ctr infections in the human model. It is also unclear if protracted microbial colonization of the tube adds to the risk of cellular transformation and ovarian cancer development, since the epidemiological data remain inconsistent^{11,12}.

Establishment of long-term organoid cultures from human primary FT epithelial stem cells¹³ has created an opportunity for a qualitatively new approach to study pathogen–host interactions during *Ctr* infection. Longevity of the organoids, genetic stability, preserved differentiation mechanisms, and high structural similarity of the organoid monolayer to the epithelium in vivo are all essential components of the model, making it an ideal system to investigate the molecular mechanisms of chronic *Ctr* infection. *Ctr* has 15 different serovars, which can be divided into three categories: A–C, which cause ocular disease, D–K, which cause urogenital infections, and L1–L3, which cause invasive lymphoma granuloma venerum (LGV).

Here, we report the establishment of a chronic *Ctr* infection model of FT organoids with genital serovars D, K, and E, which are the major drivers of tubal pathology in vivo. We identify sustained pathogen-driven changes in cellular differentiation of the epithelium that occur over the course of 9 months of infection, showing that *Ctr* not only alters the phenotype of host cells but also leaves a lasting mark in the epigenome.

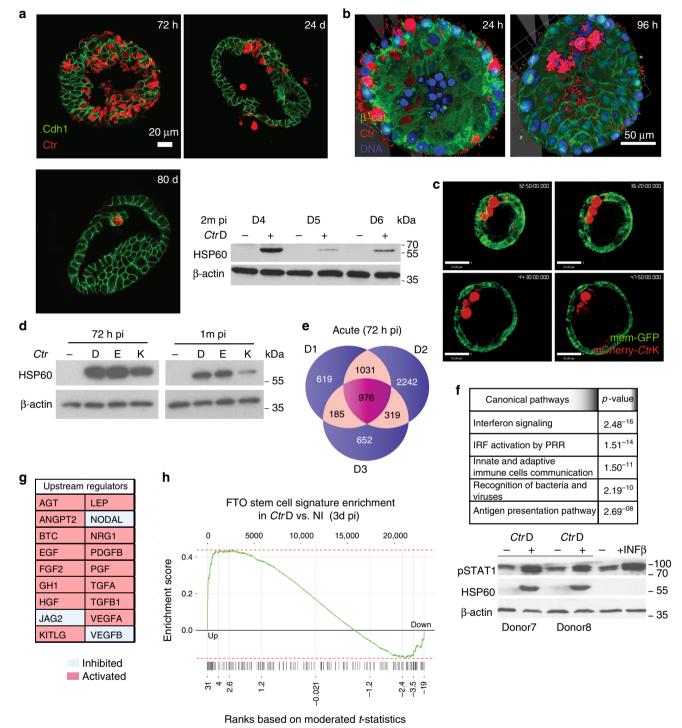
Results

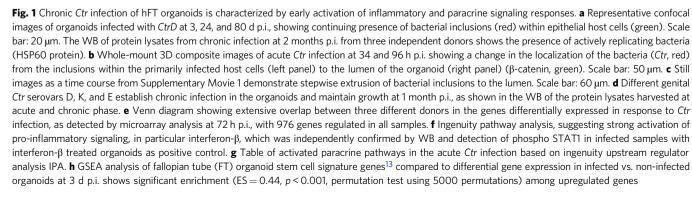
Human FT organoids as a model of chronic *Ctr* infection. We used organoid cultures from human FTs, as described previously¹³, for infection with *Ctr* serovar D (*Ctr*D) and investigated its effect on epithelial homeostasis. In stark contrast to conventional infection models based on transformed cell lines, which allow *Ctr* propagation for only a single life cycle due to lysis of infected cells, the organoids accommodated the bacteria for extended periods of time and continued to expand at a normal rate, despite an ongoing productive infection. Immunofluorescence analyses suggested that ~30% of cells were initially infected. The life cycle duration of ~72 h did not detectably differ from that typically observed for *Ctr* in cell lines, as indicated by

confocal microscopy at 3 d post-infection (p.i.; Fig. 1a). Confocal analysis at later time points revealed that large Chlamydia inclusions were still present in organoids at 1 and even 3 months p.i, although their numbers greatly decreased during that time (Fig. 1a). Actively replicating bacteria were detected in protein lysates at 3 days, 1 month, and 2 months, but at >4 months p.i. no signal was present, as judged by western blot analysis of Ctr HSP60 protein in relation to host cell actin levels in total cell lysates of infected organoids (Supplementary Figure 1a). The presence of chronic infection at 2 months p.i. was further validated in three independent donor cultures (Fig. 1a, WB panel). The infectious potential was determined by infectivity assay at 72 h and 1 month p.i. Successful infection of HeLa cells with retrieved elementary bodies (EBs) (Supplementary Figure 1b) at both time points proved that Ctr is able to complete multiple life cycles within the organoids and stay infectious over time. The titer of retrieved bacteria did gradually decrease, however, indicating the presence of defense mechanisms that contain and eventually eliminate the infection. We observed no large variation in retrieved bacteria between different donors, quantified by number of EBs/cell (Supplementary Figure 1b). Notably, organoid cultures infected with 10 µl of 4×10^8 (CFU ml⁻¹) Ctr EBs always survived, and we have successfully propagated chronically infected organoids for >3 months in 20 of 20 cases, indicating the robustness of this model. Overall, the long-term expandability of infected organoid cultures was maintained for >1 year, indicating that Ctr infection did not impair the stemness potential of the organoids. We wanted to analyze the dynamics of acute Ctr infection in organoids in more detail, including its progression beyond the first 72-96 h. Whole-mount labeling of the infected organoids, which enables a comprehensive 3D view of the epithelial structure, revealed large Ctr inclusions within the monolayer at 24 h p.i. In contrast, at 96 h p.i. the bacteria were predominantly located in the organoid lumen, suggesting the existence of a clearance mechanism (Fig. 1b).

To visualize these events in real time, live-cell imaging was performed from 24 to 72 h p.i. on an organoid line with pCT-Mem-GFP-labeled membranes infected with an mCherry-labeled Ctr strain. This revealed a fast and dynamic process of expulsion of intact Ctr inclusions and/or infected cells from the epithelial layer into the lumen, where they subsequently burst to release infective EBs (Fig. 1c, Supplemental Movie 1). Interestingly, this phenotype was the dominant route of resolution of Ctr-host interaction in the organoids, resulting in an almost complete preservation of epithelial integrity. This is evidence of an intact tissue defense mechanism that limits damage to the host epithelium and enables survival of the organoid. In stark contrast to this, the well-described phenotype of Ctr infection in monolayers results in widespread death of host cells, such that only induction of Ctr persistency by antibiotics can extend the life span of infected cultures beyond 3-4 days. The concurrent robust expulsion of the inclusions and/or infected cells we observed and the maintenance of an intact polarized monolayer with no detectable structural damage also suggest that pathways that respond to changes in cell density, tissue organization and mechano-transduction are involved in maintaining epithelial integrity during the infection. To test whether the observed infection pattern is similar for the other serovars clinically relevant for urogenital infections, we also infected organoids with Ctr K and E strains and confirmed the presence of replicative bacteria at 1 month p.i. by western blotting for hsp60 protein (Fig. 1d). This finding was further validated by immunofluorescence imaging (Supplementary Figure 1c), which revealed no differences in the dynamics of inclusion growth and inclusion shedding between the different strains. Therefore,

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we conclude that chronic organoid infection is likely to reflect the interaction of *Ctr* with the FT epithelium in vivo, regardless of the strain.

Gene expression profile of acute infection in the organoids. To investigate the global host-cell response during the acute phase of the infection, microarray analysis was performed on organoid cultures from three different donors infected with CtrD for 72 h, while technical replicates were kept in long-term culture. Comparative analysis of differentially expressed genes revealed a largely similar response between different donors (Fig. 1e) to Ctr challenge, characterized by strong upregulation of large networks of genes involved in inflammation, pathogen recognition receptors, and communication between innate and adaptive immunity (Fig. 1f). Robust IFN- β signaling was the most prominent hallmark of acute infection, with the majority of known network components upregulated (Supplementary Figure 2a). Western blotting of whole-cell lysates from organoids confirmed that the main mediator of IFN- β signaling, the transcription factor STAT1, was strongly phosphorylated upon Ctr infection (Fig. 1f, lower panel) at levels comparable to that induced by stimulation with exogenous IFN-B. Interestingly, despite the absence of immune cells in our model, our microarray data revealed a strong upregulation of inducible nitric oxide synthase (NO2) (Supplementary Figure 2b) after Ctr infection, which was previously reported to depend on induction by activated T cells^{14,15}, suggesting that the epithelium responds to Ctr infection with a cellautonomous, broad activation of inflammatory pathways. Importantly, in addition to the activation of regulatory networks involved in the innate immune response, we also observed differential regulation of important mediators of paracrine signaling, epithelial differentiation, and homeostasis. Analysis of upstream regulators using the Ingenuity Pathway Analysis IPA software platform identified activated (red) and inhibited (white) networks triggered by potent growth factors, such as EGF, PDGHFB, and TGF- β (Fig. 1g), with a wide range of functions that include control of cell growth, proliferation, and cell survival. As key regulators of epithelial homeostasis, these pathways have proved to be essential for control of epithelial integrity, response to injury, and wound healing in numerous other tissues, thus their activation in response to Ctr illustrates the extent of pathogen-host interaction in the organoids. In addition, we observed a strong upregulation of the leukemia inhibitory factor (LIF) signaling pathway, including LIF itself, as well as its downstream targets, e.g., OCT4, SOCS1, TNF-a, and IGF3BP¹⁶ (Supplementary Figure 3), which suggests changes in both differentiation and inflammation. In confirmation, gene set enrichment analysis (GSEA) (Fig. 1h) comparing the acute infection response to a published set of NOTCH-regulated stemness genes detected in FT organoids¹⁰ revealed a significant enrichment in the group of upregulated genes, suggesting that at 3 days p.i. organoids exhibit an increase in stemness. Taken together, acute Ctr infection of FT organoids triggers a sustained innate inflammatory response coupled with activation of homeostatic mechanisms to repair the injury. These findings are in agreement with the observed phenotypic changes in organoids at early stages of the infection process. Newly infected cultures are characterized by the presence of cellular debris derived from apoptotic cells, as confirmed by the presence of activated caspase-3 during the first 48 h (Supplementary Figure 4a), likely initiated by an early stress response. The absence of caspase-3 activation at 72 h, a time point when intense shedding of inclusions and/or cells occurs, confirms that infected cells do not die by apoptosis. Indeed, confocal images of infected organoids revealed that active caspase-3 signal does not co-localize with inclusion-bearing cells

(Supplementary Figure 4b), thus cell death is likely triggered by a paracrine mechanism in the neighbouring uninfected cells.

Infected organoids regain homeostasis by increased proliferation. In contrast to the acute infection, chronically infected organoids phenotypically resemble controls (Supplementary Figure 4c). Long-term infected cultures also maintain a constant expansion rate over many passages and are passaged at the same time points and ratios as their non-infected sister organoids over the course of many months. We therefore hypothesized that newly infected organoids undergo increased proliferation in order to compensate for the initial cell loss. Analysis of confocal images at 7 d p.i. revealed increased numbers of Ki67+ cells in infected cultures. Positive nuclei were predominantly present in noninfected cells in close proximity to infected cells (Fig. 2a). FACSbased analysis over the course of one month to determine the proportion of EdU-labeled cells in infected vs uninfected organoids from six different donors revealed a significant increase in the proliferation rate, with a peak at 7 d p.i. (Fig. 2b, Supplementary Figure 5a). By 30 d, the proliferation rate in infected organoids had returned to control levels, in congruence with the observed lack of differences in the long-term expansion rate. This suggests that in order to maintain epithelial integrity, noninfected cells transiently increase their expansion rate to replace infected cells that have been extruded from the epithelium. Nevertheless, the observed robust activation of paracrine networks controlling not only cell growth and proliferation but also differentiation and cell fate in general, suggests that Ctr infection has pervasive long-term consequences on the organoid epithelium. We therefore went on to analyze pathways with dual functions that could potentially connect inflammatory responses with those involved in epithelial homeostasis.

LIF signaling regulates organoid formation and differentiation. LIF belongs to the IL-6 family of cytokines and is one of the major regulators of pluripotency during early embryogenesis as well as a crucial determinant of uterine receptivity during implantation in humans. In addition, it has potent antiinflammatory effects, regulating IL-1β, IL-6, IL-7, IL-2Ra, and IFN- γ in a cutaneous inflammation model¹⁷ and limiting the degree of lung injury from E. coli infection¹⁸. Our microarray data revealed that acute Ctr infection consistently triggers LIF upregulation in all three donors. In agreement with this, increased expression of the LIF target gene OCT4 in infected vs noninfected cells was confirmed by qPCR (Fig. 2c, upper panel). Western blot analysis further validated these findings, by revealing increased amounts of LIF protein from as early as 8 h until at least 72 h p.i. (Fig. 2c, lower panel). Considering the functional importance of LIF in preserving stemness in other models, we were interested in whether its induction during acute Ctr infection could contribute to infection-driven changes in homeostasis.

Interestingly, western blot analysis showed that phospho-STAT3, the main downstream effector of LIF, was constitutively active in FT organoids (after 1 d post-seeding), while the passaging procedure induced a transient dephosphorylation that lasted for 8 h, indicating changes in the STAT3 LIF/ STAT3 signaling axis during organoid development, which is reinitiated after every passage (Supplementary Figure 5b). This suggests that the LIF/STAT3 axis may also be involved in the regulation of epithelial homeostasis and differentiation in the FT. Indeed, depletion of LIF transcript via shRNA greatly decreased organoid-forming capacity in epithelial isolates with only few organoids forming (Fig. 2d). Depending on the virus titer, the number of organoids generated dropped to <2% of that observed

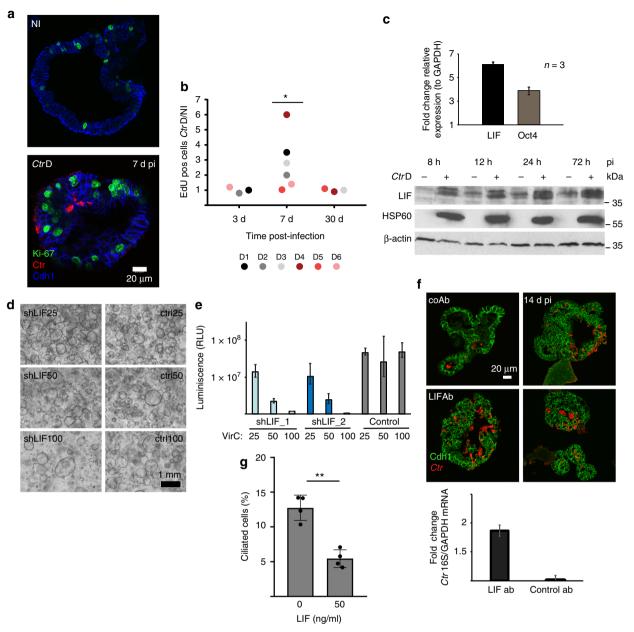


Fig. 2 LIF controls organoid homeostasis and limits replication of Ctr in the epithelium. a Confocal images showing that in infected organoids actively proliferating Ki67+ cells (green) are more frequent in cells neighboring infected cells (Ctr: red, Cdh1: blue) at 7d p.i. Scale bar: 20 μm. b Quantification of the time course experiments from 6 Ctr infections (Donors D1-D6), by number of EdU-positive cells in the infected sample, as detected by FACS normalized to the control. Infected organoids exhibit a transient peak in proliferation at one week p.i., while long-term growth rate, measured at 30 days p.i. remains constant. Significance was determined by paired Student's t-test of EdU measurement data sets in non-infected (NI) and infected (CtrD) conditions. c Upregulation of LIF and its target gene Oct4 in acute Ctr infection was validated by qPCR in three independent donors at 72 h p.i. Data are presented as mean ± sd. Induction of LIF starts from the early phase of Ctr infection, as increased protein levels are already detected at 8 h p.i. by western blot analysis of the first 3 days. d Phase contrast images showing that lentiviral transduction of shRNA against LIF (at 25, 50, or 100 of viral units) greatly reduces the number of generated organoids in a dose-dependent manner. Ctrl: control vector pLKO.5. e The effect on organoid formation upon LIF knockdown by using different concentrations of virus particles (VirC) was quantified by ATP-based viability assay, which detects luminescence signal. Error bars represent technical variation between triplicate wells ± SD. f Inhibition of LIF activation by neutralizing antibody leads to increased bacterial load (Ctr red, Cdh1 green) detected in confocal images at 14 d p.i.; scale bar: 20 µm. The difference was quantified by qPCR at the same time point as the change in abundance of bacterial 16S relative to GAPDH level of the host cells. Data are representative of two independent experiments and presented as mean ± sd of technical replicates. CoAb: control antibody against H. pylori Cag A protein. g Active LIF, at 50 ng/ml promotes a secretory phenotype in the organoids as evidenced by reduction in the number of ciliated cells. Data are representative of two independent experiments. Quantification is performed as number of ciliated cells/nuclei in five independent fields of view (dot plot) (>1000 nuclei/sample) ± sd represents variation between individual images. **p < 0.01 (p = 0.0057) was calculated by paired Student's *t*-test

after transduction with control vector, as quantified by the Cell Titer-Glo® assay, which measures the number of live cells via the ATP content (Fig. 2e). The organoids that did grow still expressed basal levels of LIF protein that were the same between cultures transduced with different amounts of virus particles, suggesting that LIF is essential for organoid growth in vitro (Supplementary Figure 5c). Therefore, we conclude that LIF has a central role during organoid formation, and thus ultimately controls epithelial renewal in the FT. Interestingly, blocking LIF pathway activation with soluble neutralizing antibody at the time of infection increased the chlamydial load in the organoids (Fig. 2f), as visualized by immunofluorescence analysis at 14 d p.i. and confirmed in a separate experiment by qPCR of Ctr 16s (Fig. 2f). While activation of LIF signaling thus limits replication of the pathogen, we were interested in whether it also affects the organoid phenotype. Adding recombinant LIF to non-infected cultures resulted in a reduced percentage of ciliated cells, quantified as the number of cilia per nuclei (Fig. 2g), suggesting that amplification of the LIF signal alone is sufficient to shift the balance of cell types within the epithelium towards a less differentiated, secretory phenotype.

Chronic infection leads to increased stemness in organoids. The robust changes in signaling and in the regulation of cell fate and differentiation factors during the acute phase of the infection suggested that Ctr infection potentially has long-lasting consequences on the epithelium. Quantification of the cell types found in chronically infected cultures by analysis of confocal images of serial sections, revealed that the percentage of ciliated cells significantly decreased by 3 months p.i., as determined by the number of cilia/nuclei compared to non-infected control cultures in chronic infections of organoids from five different donors (Fig. 3a). To test whether this reduction is linked to an increase in the proportion of less differentiated cells, we used FACS to analyze the number of cells expressing stem cell surface markers. Indeed, chronic infection led to an increase in the number of CD24+/EpCam+ cells (Fig. 3b, Supplementary Figure 6a), in four different donors, in agreement with the general shift towards a less differentiated state. Stem cells of both healthy and diseased upper genital tract tissue have previously been defined as CD24⁺/EpCam⁺¹⁹. In addition, in 2 out of 3 donors, infected organoids contained an increased proportion of cells positive for CD133, a surface marker that is associated with an increase in stemness potential²⁰ (Supplementary Figure 6b). Thus, both cell-type composition of the organoids, as well as surface-marker distribution, strongly suggest changes in the homeostasis of chronically infected cultures compared to controls. To test whether there is also a difference in stemness potential, we dissociated organoids to single cells and quantified their organoid forming efficiency. Indeed, cells from chronically infected organoids had a significantly higher organoid forming capacity, as quantified by Cell Titer-Glo 3D viability assay (Fig. 3c). Thus, we conclude that chronic Ctr infection leads to increased stemness of the organoid epithelium. Expansion of the secretory cell phenotype in the FT has been postulated as a cornerstone of transformation during the development of HGSOC¹. In line with our previous observations in FT organoids¹³, lineage tracing in mice has recently confirmed that secretory cells are in fact the precursors of ciliated cells²¹. Therefore, the Ctr-induced expansion of the secretory phenotype due to decreased terminal differentiation may be a potential risk factor for the initiation of sequels that could lead to transformation.

To obtain comprehensive insight into the signaling events that characterize long-term *Ctr* infection in the organoid model, we generated exploratory data sets at multiple time points during chronic infection of organoids from independent donors. As the strongest risk factor for Ctr-driven pathology is known to be the number of episodes of recurrent disease or reinfections, we added groups to examine whether such infections could facilitate longlasting or even heritable changes-which would likely be mediated via epigenetic CpG methylation. To this end, we carried out global gene expression analysis at 72 h and 1 month p. i., and also at 4 months p.i. At this point, cultures were cured and re-infected (chronic infected + reinfected) and compared to the acute infection of organoids from the non-infected arm kept in culture from the start of the experiment (long-term, acute infected) (Fig. 3d). To ensure any residual bacteria were cleared prior to reinfection, all cultures were treated with antibiotics, and the absence of viable bacteria confirmed by infectivity assay (Supplementary Figure 7a). Finally, re-infected organoids were maintained in culture for an additional 4 months and analyzed for changes in DNA methylation in comparison to the methylation profile of non-infected parallel control cultures as well as "baseline" organoid cultures from the same donors, from which genomic DNA had been isolated at passage 0.

The gene expression pattern of organoids infected for 4 months followed by 7 days of antibiotic treatment (chronic infected + cured) compared to control organoids of the same age (long-term non-infected) showed that a number of genes remained dysregulated beyond resolution of infection. We identified 91 significantly regulated genes between cured and never infected samples (log2 fold change < -0.7 or > 0.7, p < 0.01 with an FDR <61%; Supplementary Data 1. Statistics based on moderated t-test adjusting *p*-values for and multiple testing using Benjamini-Hochberg procedure). Interestingly, one of the genes that was consistently upregulated in cultures from all three donors was osteopontin (SPP1) (Fig. 3f). This secreted matricellular protein can mediate migration and cell survival and is involved in the pathogenesis of multiple chronic diseases involving cancer and chronic inflammation²². Also, chronically infected, cured organoids show sustained overexpression of TNFSF14 (LIGHT), a member of the TNF family of ligands. Among the downregulated genes was the homeobox gene HOXA4, a prognostic factor in ovarian cancer that suppresses growth and cell motility²³, as well as HOXA5²⁴, which has been shown to prevent cellular transformation and positively regulates p53 expression. Downregulated genes with major roles in the modulation of the adaptive immunity included ILR17RB receptor, CCR7 or KLRF1.

Interestingly, despite these differences, we did not observe relevant changes in the cellular responses to acute *Ctr* infection between organoids that were previously chronically infected and cured, and control cultures (short or long term) that had not been infected previously. In particular, major immune response effectors like IFN- β 1, TNF, IL-1 β , LIF, STAT1, and NOS1 were strongly upregulated in all acute infection conditions, while chronically infected (1 month) and cured samples did not show such changes (Fig. 3e), suggesting that inflammatory responses subsided. This likely reflects the progressive reduction of bacterial numbers in the organoids over time, as confirmed by qPCR of bacterial 16S rRNA (Supplementary Figure 7b).

Thus, we concluded that while previous chronic *Ctr* infection does not change the immediate response of the fallopian epithelium to a fresh acute challenge, it does cause prolonged changes in the cellular composition of the organoid monolayer and the distribution of stemness markers. Moreover, there is evidence that chronic *Ctr* infection alters the interaction between the epithelium and the microenvironment, due to changes in expression levels of active extracellular proteins (SPP1, SULF1, IGF1) and immunomodulators (CCR7, IL17 RB). This finding could be of great importance for understanding the development

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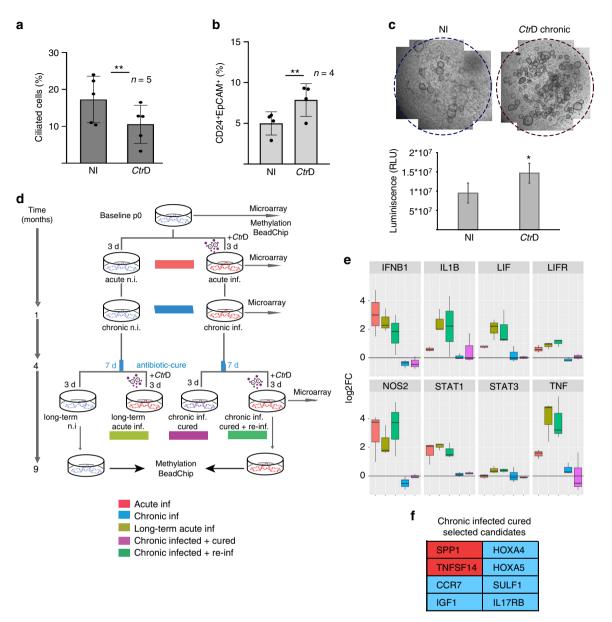


Fig. 3 Chronic Ctr infection leads to fewer ciliated cells, increased stemness markers and downregulation of immunomodulators. a Chronic infection (>3 months) significantly reduces the number of ciliated cells in the organoids. Percentage of ciliated cells was calculated as the number of ciliated cells per nuclei per field of view. Data represent mean ± SD from five independent experiments; dot plot reflects data points from independent infections **p = 0.0059, paired Student's t-test. b Chronically infected organoids show increased numbers of CD24+/EpCam+ cells, as determined by FACS profiling. Data represent mean \pm SD of four independent chronic infections. Data points from independent experiments are represented on dot plot. $\star^* p = 0.0071$ paired Student's t-test. c Chronic Ctr infection causes increase in organoid forming efficiency as visible on phase contrast images of comparative Ctr+/wells of organoids grown from respective single cells suspensions. The effect was quantified by Cell Titer-Glo® assay. *p < 0.05, paired Student's t-test, calculated from measurements of technical replicates. Data are representative of three independent experiments. d Experimental outline of acute/chronic infections, indicating time points at which samples for microarray and methylation analysis were collected. For each infected sample, the non-infected control sample at the same time point served as control. e Differential expression of selected genes across acute (3 d p.i.), chronic (1 m p.i.), and cured (4 m p.i.) infection experiments compared to non-infected control (as determined by microarray analysis) shows a conserved inflammatory response to Ctr, which subsides at later stages of infection and after clearance of the pathogen. Samples are colour-coded as in d, each was compared to the noninfected control culture at the same time point, as shown in d. Box plots show median, quartiles, maximum, and minimum of the log2 fold-changes of three donors. f Selected genes from the table of jointly regulated candidates (Supplementary Data 1) that remained differentially regulated after curing of chronic infection (red: upregulated, blue: downregulated). Genes include regulators of extracellular signaling (SPP1, SULF1), developmental genes (HOX4A and HOX5A), and immunomodulators (CCR7 and IL17 RB)

and clinical sequels of *Ctr*-driven pathology, especially in the context of recurrent episodes of asymptomatic salpingitis.

CpG hypermethylation is increased upon chronic infection. To understand how chronic *Ctr* infection leads to long-lasting

changes in gene expression even after the infection is cured, we examined whether it affects the epigenome of host cells. To identify DNA methylation pattern changes, genomic DNA from organoids cultured for a total of 9 months, which were cured and re-infected at 4 months (Fig. 3d), was analyzed using the Illumina Infinium[®] Methylation EPIC BeadChip, covering >850,000 CpGs of the human genome. We first tried to identify changes across three independent donors between long-term infected and non-infected conditions. Applying a threshold of at least 20% differential methylation and a *p*-value of 0.05, we identified 603 CpGs at a minimal false discovery rate of 76%, of which 179 were located in promoter regions (Supplementary Data 2). For most genes, only a single CpG out of many represented on the array was affected, indicating that there was no strong deterministic effect of long-term infection on DNA methylation compared to control.

As stochastic processes have been implicated in the formation of differentially methylated regions²⁵, we hypothesized that infection might lead to stochastic changes in DNA methylation that may not be detectable in organoid cultures due to the limited number of stem cells that contribute to long-term maintenance. We thus analyzed samples from two different donors to determine differentially methylated CpGs in both infected and non-infected samples, as compared to the baseline DNA methylation profile of the parental organoid cultures. We used data from a control experiment on gastric primary cells to define the magnitude of relevant changes in the absence of replicates (Supplementary Figure 8a, b) and concluded that methylation changes of >20% in any direction most likely represent real biological changes. Using this threshold, ~10-12% of all CpGs on the array were found to be differentially methylated during the course of the experiment. Notably, while changes in DNA methylation were detected in both arms of the experiment, infected samples showed an increased number of hypermethylated CpGs in both donors (Fig. 4a) compared to non-infected samples (χ^2 test, p < 0.001 for both replicates, Supplementary Figure 8c), leading to an increase in the number of hypermethylated genes (Fig. 4b). In order to determine whether there are any common functional denominators or distribution patterns among affected CpGs, data were subjected to Locus overlap analysis (LOLA)²⁶. Identification of the genomic regions where changes in the DNA methylation occurred revealed that differentially methylated CpGs are not randomly distributed. Globally, they are enriched for laminin B1-associated domains (LAD) and depleted for transcriptionally active genomic regions, including transcription start sites (TSS), transcribed segments, and for CpG islands (Fig. 4c). Instead, hypermethylated CpGs in both conditions were enriched for enhancer and promoter flanking sites, as well as regions that, in human embryonic stem cells, are known to bind the polycomb repressive complex 2 (PRC2) members EZH2 and SUZ12-and to show histone modification H3K27me3²⁷. Regulation of DNA methylation by PRC2 and hypomethylation of repetitive genomic regions have both been implicated in the process of molecular ageing across a number of sectional studies²⁸⁻³⁰. To analyze if the detected methylation changes correlate with the gene expression profiles of aged organoid cultures, we have performed microarray analysis of infected and non-infected long-term cultures at 9 months from both donors. At this time point, we could not conclusively confirm a significant correlation, which could be due to the small sample size or the inherent complexity of the regulatory mechanisms that mediate the effect of individual CpGs on gene transcription. Still, we detected distinct changes in the gene expression profile of long-term cultures over time, and upregulation of numerous genes involved in packaging of DNA, chromosome assembly and segregation (K4H20 demethylase network), regulation of replication (MCM4 and MCM10), control of cell cycle (BUB1B, CDKN3) and process of cellular ageing (EZH2, PIF1). All these markers provide a broader context regarding the set of molecular changes at the genomic level that characterize prolonged cultivation of adult stem cells.

Interestingly, the heatmap of candidate genes (Fig. 4d) shows a tendency for higher expression levels in the infected cultures compared to non-infected aged controls, which also supports the conclusion that infection promotes the process of aging.

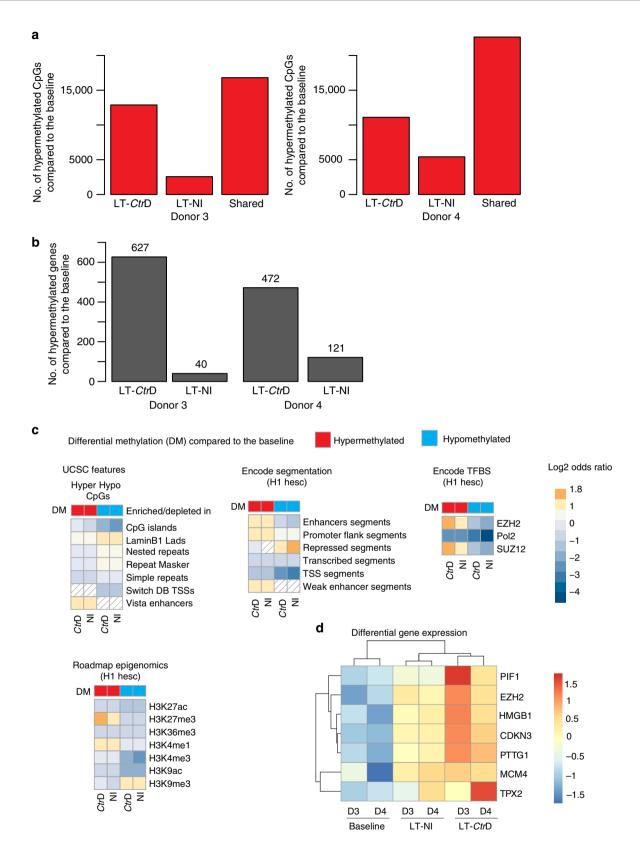
Taken together, our findings demonstrate sustained age-related changes in DNA methylation during a longitudinal study in a controlled experimental model. Thus, organoids appear to undergo an in vitro ageing process that is highly similar to that observed in vivo, further validating the authenticity of this model. Importantly, although there are no apparent qualitative differences in the pattern of CpG changes between experimental arms -indicating that the same underlying process is at workchronic Ctr infection appears to accelerate this process in vitro. Interestingly, while the gene expression data of acute Ctr infection suggests an initial downregulation of the EZH2 transcription factor and corresponding target genes, long-term culture leads to sustained upregulation of EZH2. Overexpression of EZH2 is frequently detected in HGSOC tissue and is a potential therapeutic target³¹. Further studies are needed to determine whether there is a causative relationship between the transcriptional changes in EZH2 and the observed differences in CpG methylation. Altogether, our data provide experimental evidence that chronic Ctr infection causes long-term changes in homeostasis of the host epithelium, gene expression, and the epigenetic landscape, which are maintained beyond the end of the infection.

Discussion

Previous investigations of the effects of Ctr infection on human host cells were performed in 2D models mostly using transformed cell lines. Such models correlate poorly with the structural complexity and cell–cell communication that are key features of the healthy epithelial lining in the genital tract. Importantly, due to the aggressive nature of the Ctr lytic cycle in monolayer culture, it is also impossible to follow the process of infection long-term without induction of persistence. However, it is chronic and asymptomatic Ctr infections that are the main drivers of pathology in the upper genital tract. Thus, there is a great medical need for developing new Ctr infection models in order to understand the molecular basis of disease development.

Analysis of the long-term consequences of both acute and chronic ascending infections in vivo is greatly impeded by the inaccessibility of the FTs to clinical diagnostic tools. Instead, past infections are not usually documented until years later, and based solely on the evidence of positive Ctr serology and structural damage to the tube. Our chronic Ctr infection model now provides unique insights into the nature and cellular mechanisms of Ctr-driven pathogenesis in a human primary FT epithelium that closely resembles the characteristics of the native tissue. We show that chronic infection can be established in organoids with all tested Ctr genital serovars (D, K, E), which underlines the validity of the model for studying the general mechanisms of *Ctr* infection and for investigating the mechanisms that lead to the associated pathology. Our data were generated by thorough long-term analysis of expression data from organoid cultures from 4 different donors, and analysis of methylation changes in organoids from 3 donors, infected with Ctr for 9 months. It thus offers a first insight into the events that characterize the long-term effects of chronic Ctr infection. In addition to data presented here, which originate from 10 donors, we have performed additional chronic infection experiments (>3 months), all of which followed a consistent pattern in terms of course of infection-confirming the robustness of the infection model and the conserved response to Ctr infections, regardless of genetic background.

Our results indicate a profound, yet homeostatic, effect of *Ctr* infection on the regulation of cell fate and differentiation. By



using organoids, it was possible to demonstrate that the epithelium limits the physical damage resulting from infection by efficiently extruding inclusions and infected cells into the lumen. While rupture of the inclusion membrane appears to occur mostly after extrusion from the monolayer, we could not conclusively determine the fate of the infected cells. However, it is clear that Ctr bacteria are able to maintain a prolonged infection in the organoid epithelium, during which shedding into the lumen is followed by fresh cycles of infection and active bacterial replication. The diminishing Ctr titer over time is evidence of a successful defense mechanism of the host epithelium. However, we cannot rule out that it could also reflect limitations of the **Fig. 4** Impact of chronic *CtrD* infection on the methylome. **a** Barplots showing the numbers of CpGs that increase in DNA methylation (hypermethylation; delta beta > 0.2) specifically in long-term (LT; 9 months; compare experimental design in Fig. 3c) infected (*CtrD*) or non-infected (NI) samples compared to baseline, as well as those which are hypermethylated in both arms of the experiment (shared) in donor 3 (left) and donor 4 (right). **b** Barplot displaying the number of genes where hypermethylation, specifically for infected or non-infected samples compared to the baseline, affects at least three CpGs/gene. **c** Heatmaps of enriched and depleted genomic features among differentially methylated CpGs. The color code indicates a significant enrichment (orange) or depletion (blue) based on the log2 odds ratio and a FDR < 5%. No significant enrichment or depletion (FDR > 5%) is displayed by dashed squares. DM differential methylation, H1 hesc H1 human embryonic stem cell line, TFBS transcription factor binding sites. **d** Heatmap representing the differential expression of selected genes comparing baseline, long-term (9 months) non-infected, and infected organoids. The standardized gene expression data (*z*-score) of two patients (D3 and D4) were obtained from single-color microarray analysis

model, e.g., the inevitable loss of infectious EBs into the medium when organoids are broken up for passaging.

Although the acute infection leads to activation of multiple paracrine growth factors (TGF-\$1, EGF, FGF etc.), we identify LIF as a key player in the maintenance of stemness in tubal organoids. This underscores the fundamental role of LIF signaling in the female genital tract, as evidenced by the fact that LIF mutant mice are sterile and have an underdeveloped uterus³². The Ctr-driven amplification of LIF signaling we observed suggests a mechanistic molecular basis for the link between salpingitis and the risk of ectopic pregnancy, which has previously been connected to overexpression of LIF in the FT³³. Due to the dual function of the LIF signaling network in regulating stemness^{34,35} and mediating anti-inflammatory effects, it is possible that the peak in LIF activity is primarily triggered by innate immune mechanisms in order to limit bacterial replication, as evidenced by our pharmacological inhibition of LIFR. Stemnessrelated changes may be a by-product in the course of chronic infection.

The observed gradual decrease in the number of ciliated cells and increase in CD24+Epcam+ and CD133+ cells suggest a sustained shift in the regulation of epithelial renewal during infection. This effect establishes a link towards cell transformation, since expansion of non-ciliated, secretory cells generally precedes HGSOC development¹. It is important to note that the increase in stemness, as measured by the increased organoid forming efficiency, does not imply complete functional competence of the ageing stem cells, as previously demonstrated in other models³⁶. Equally important may be our observation that chronically infected organoids show changes in the expression of the potent immunomodulators IL17 RB, CCR7, and KLRF1, and that this effect persists after the clearance of the bacteria. In context with the detected upregulation of SPP1 and reduction of HOXA4 and HOXA5, this may modify the way the epithelium interacts with the surrounding tissue, including adaptive immune cells. However, determining the precise implications of these findings will require more extended experimental settings, involving immune cells as well as larger numbers of donors to control for individual differences.

Strikingly, our methylation data support a potential role of chronic *Ctr* infection as an epigenetic modulator. The molecular mechanisms that lead to the observed increase in differential CpG hypermethylation of genes known to be regulated by polycomb in mouse and human embryonic stem cells^{27,37} are yet to be determined. Yet, it is conceivable that this process is influenced by the transient spike in proliferation during the early phase of *Ctr* infection and the activation of signaling pathways known to maintain crosstalk with EZH2 polycomb networks³⁸. Studies of hematopoietic stem cells first reported epigenomic changes that enhance self-renewal in the context of ageing²⁹. In this context, it is interesting that we also observed an increase in stemness in chronically infected organoids. It remains to be seen if the shift towards a more de-differentiated phenotype is connected to these

epigenetic changes. Notably, though, the number of cilia in noninfected organoids remained constant over time, in congruence with our previous observations¹³—despite the changes in CpG methylation and molecular ageing that were also observed in the non-infected samples. Therefore, these types of epigenetic changes do not appear to be sufficient to alter organoid composition and imply involvement of additional cellular mechanisms triggered by infection.

Taken together, this study highlights progress in the establishment of a next-generation human epithelial in vitro model, enabling investigation of important aspects of the Ctr-host interaction. Human FT organoids maintain stemness and differentiation programs-both of which are necessary to allow for detection of the long-term effects of infection on the host epithelium. Such programs are not present in standard monolayer cultures, in particular transformed cell lines. Our findings shed tantalizing new light on the effects of *Ctr* on the tubal epithelium that may have a role in the development of tubal pathology. Although Ctr has a relatively high rate of upper genital tract colonization, estimated at ~10% of all infected women, it remains underreported due to the frequent asymptomatic clinical presentation. Given the interference with core developmental mechanisms of epithelial homeostasis, the epigenetic changes and the expression of immune system modifiers we observed, it is clear that future investigation of the long-term consequences of Ctr infection is imperative and will need to take into account the interplay between infected epithelium and its tissue microenvironment. This new approach will thus contribute to a better understanding of the long-term effects of Ctr infections, including its potential to contribute to cell transformation and the etiology of HGSOC.

Methods

Patient material. FT samples were provided by the Department of Gynecology, Charité University Hospital, Campus Virchow Clinic and August-Viktoria Klinikum Berlin, Department of Gynecology and Obstetrics. Scientific usage of the samples for experimental purposes was approved by the Ethics Commission of the Charité, Berlin (EA1/002/07) and informed consent was obtained from all donors. Fragments were sourced from standard surgical procedures for benign gynecological disease. Only anatomically normal FTs were used. Tubes were transported and dissected within 2 to 3 h of removal.

Organoid cultivation. Generation and culture of FT organoids was performed as described in Kessler et al¹³. In brief, epithelial progenitors from human FT tissue samples were isolated by enzymatic digestion with collagenase I (Sigma). The retrieved primary cells were seeded in 2D culture for 5–7 days (ADF medium with 12 mM HEPES, 1% GlutaMAXTM, 10 ng ml⁻¹ human EGF and 9 μM Y-27632) before seeding in MatrigelTM (~30,000 cells/50 μl) for 3D organoid formation. Once the MatrigelTM had set, cultures were overlaid with medium containing a specific growth factor cocktail to preserve stemness and support differentiation (ADF, 25% conditioned mouse Wnt3A-medium as described in Willert et al.³⁹ and 25% conditioned mouse RSPO1 medium⁴⁰, supplemented with 12 mM HEPES, 1% GlutaMAXTM, 2% B27, 1% N2, 10 ng ml⁻¹ human EGF (all from Invitrogen), 100 ng ml⁻¹ human noggin, 100 ng ml⁻¹ human FGF-10 (both from Peprotech), 1 mM nicotinamide, 9 μM ROCK inhibitor (Y-27632, both from Sigma) and 0.5 μM TGF-β RI Kinase Inhibitor IV (SB431542, Calbiochem)). For propagation, organoids were split every 2 to 3 weeks at a ratio of 1:2 to 1:3 using mechanical splitting with a

syringe and needle (26 G gauge). Organoids were kept in a humidified incubator at 5% CO_2 and 37 °C, or 35 °C once infected.

Organoid formation assay. Single cells were prepared from long-term infected organoids (>2 months p.i.) by digestion with collagenase and reseeded at 40,000 cells/25 µl MatrigelTM in triplicate. At 3 weeks post-seeding, cell viability assay was performed on all wells. The Cell Titer-Glo[®] 3D Cell Viability kit (Promega # G9681) was applied to each well according to the manufacturer's protocol and the luminescence measured using a plate reader.

Antibodies. The following antibodies were used in this study: primary-mouse anti-E-Cadherin (1:200 610181, BD Transduction Lab), mouse anti-β-actin (1:200, A5441, Sigma), goat anti-Ctr (OBT0978, AbD Serotec), mouse anti-HSP60 (1:5000, ALX-804-701, Alexis), rabbit anti-Ki67 (9027, Cell Signaling), rabbit anti-pSTAT1 (1:1000, 9167, Cell Signaling), rabbit anti-pSTAT3 (Tyr705) (1:1000 9145, Cell Signaling), cleaved caspase-3 (1:1000, 9664, Cell Signaling), goat anti-LIF (1:500, AF-250-NA, R&D Systems); secondary - sheep anti-mouse-HRP (1:3000, NA931, Amersham), donkey anti-rabbit-HRP (1:3000, NA934, Amersham), donkey antigoat-HRP (1:3000, 800073, Biomol), donkey anti-mouse-Alexa488 (1:300, 715-546-140, Dianova), donkey anti-goat-Cy3 (1:300, 705-165-003, Dianova), donkey antirabbit-Alexa488 (1:300, 711-546-152, Dianova), donkey anti-mouse-Dylight 647 (1:300, 715-605-150, Dianova), CD326 (EpCAM)-FITC antibody (1:50, 130-080-301, Miltenyi), mouse anti-human CD24-BV711 antibody (1:200, 563371, BD Biosciences), mouse anti IgG1-APC (1:100, 130-098-846, Miltenyi), and mouse anti-human CD133/1 (AC133)APC (1:100, 130098829, Miltenyi). As a DNAlabeling agent, Draq5 (5 µM, 62252, Thermo Scientific) was used.

Single cell preparation and fixation. To prepare single cells, organoids were released from Matrigel using cold PBS, pelleted by centrifugation (5 min, $300 \times g$), resuspended in 0.5–1 ml TrypLE and incubated for 15 min at 37 °C. Organoid fragments were then mechanically disrupted by passing 3–4× through a 26 G gauge needle. Next, the cells were taken up in 3 ml Advanced DMEM/F12 and passed through a 40 µm filter. The single cell suspension was pelleted by centrifugation and resuspended in 500 µl 3.7% PFA for 30 min. Cells were then washed by addition of 3 ml PBS/1% BSA and kept at 4 °C for further processing.

Proliferation assay. To determine the number of proliferating cells, the Click-iT-EdU assay (Thermo Fischer, #C10425) was applied. Organoids were treated with 10 μ M EdU for 2 h in culture medium, triturated into single cells and fixed with 3.7% PFA. Labeling of the EdU-positive cells with Alexa488 was done as per manufacturer's instructions. Flow cytometric analysis was performed using a BD FACS CANTOII flow cytometer and the FlowJo vX.0.6 software.

Flow cytometry. Single cells derived from organoids were labelled in 1×PBS/1% BSA using mouse anti-human CD326 (EpCAM)-FITC antibody, mouse antihuman CD24-BV711 antibody and mouse anti-human CD133/1 (AC133)APC. Labeling was performed for 30 min on ice in the dark. Afterwards, cells were washed using 1 ml PBS. Finally, cells were pelleted and resuspended in PBS. The flow cytometric analysis was done using a BD FACS CANTOII flow cytometer and the FlowJo vX.0.6 software.

Quantitative real-time polymerase chain reaction (qRT-PCR). Determination of RNA levels was performed by qRT-PCR using the AB Power SYBR[®] Green RNA-to-CT[™] 1-Step Kit (Applied BiosystemsTM), StepOnePlus[™] Real-Time PCR System (Applied BiosystemsTM), and StepOneTM Software (v2.3, Applied Biosystems).

Å mixture of 10 µl RNA (2–5 ng µl⁻¹), 10 µl SYBR^{*} green mix, 4.3 µl H₂O, 0.2 µl Reverse Transcriptase enzyme mix and 0.5 µl Primer mix (10 µM) was subjected to the following PCR cycler program: 30 min 48 °C; 10 min 95 °C; followed by 40× cycles of 15 s 95 °C/60 s 60 °C.

Each sample was measured in triplicate. The expression levels of all target genes were normalized to expression of the housekeeping gene glyceraldehyde-3-phosphate dehydrogenase (GAPDH). Relative expression levels were determined by calculating $\Delta\Delta C_t$. Fold change was calculated as an average of $\Delta\Delta C_t$ of independent biological replicates ($2-\Delta\Delta C_t$), while s.d. was calculated as $\Delta\Delta C_t + s$ and $\Delta\Delta C_t - s$, where s is the pooled s.d. of the ΔC_t and ΔC_t control values

$(s = \sqrt{\mathrm{sd}(\mathrm{ctt})^2 + \mathrm{sd}(\mathrm{ctc})^2}).$

The following primers were used: *GAPDH*—forward 5'-GGTATCGTGGAAGG ACTCATGAC-3', reverse 5'-ATGCCAGTGAGCTTCCCGTTCAG-3'; *LIF* forward 5'-CAGGAGTTGGGTCCAGATGT-3', reverse 5'-GTCCACAATCTCC CAGAGGA-3'; *Oct4*—forward 5'-GATGTGGTCCGAGTGTGGTTCT-3', reverse 5'-TTGTGCATAGTCGCTGCTTGA-3'; *CtrD* 16S *rRNA*—forward 5'-GGTATCG TGGAAGGACTCATGAC-3', reverse 5'-TCAAATCCAGCGGGTATTAACCG CCT-3'. **Lentiviral manipulation**. Replication-deficient lentiviral particles were produced by transfection of 293T cells with a mixture of the respective lentiviral plasmids and Fugene6 (Promega, #E2691) diluted in Opti-MEM[¬] (Gibco, # 31985088). For a 10 cm dish, 15.6 µl Fugene6 was mixed with 192.4 µl OPTI-MEM and added to 3 µg lentiviral target plasmid, 2.25 µg psPAX2 packaging vector and 0.75 µg pMD.2 G (VSVG) envelope vector diluted in 52 µl OPTI-MEM. After 30 min incubation at RT, the mixture was pipetted dropwise onto the 293T cells. 16 h post transfection the medium was replaced with 10 ml fresh DMEM. 24 h later the medium was aspirated, filtered at 45 µm and mixed with Lenti-XTM Concentrator (Clontech Laboratories, #631231). After concentration, the virus pellet was resuspended in 1 ml ADF (10x concentration) and stocked at −80 °C.

LIF shRNA lentiviral plasmids and the corresponding vector control were obtained from Sigma (pLKO.5, SHC201; pLKO.5-LIFshRNA: TRCN0000308277, 5'-ACCGCATAGTCGTGTACCTTG-3'; pLKO.1-LIFshRNA: TRCN0000058586, TAAGCAGATCATCGCCGTGTT). The pCT-Mem-GFP plasmid was obtained from System Biosciences (#CYTO100-VA-1).

For transduction, early passage 2D primary FTECs at ~70% confluence in a 6-well plate were treated with 1×, 0.5×, or 0.25× concentrated virus diluted in ADF medium supplemented with 12 mM HEPES, 1% GlutaMAX, 10 ng ml⁻¹ human EGF, 9 mM ROCK inhibitor and 5 µg ml⁻¹ polybrene (Sigma, #H9268). The cells were incubated overnight with the virus at 37 °C. When the cells reached ~90% confluence, organoids were prepared and selection with puromycin (0.5 µg ml⁻¹) was started.

RNA and DNA isolation. RNA and DNA were isolated using the Allprep Qiagen Kit.

Microarray RNA isolation, quantification, and quality control. Total RNA was isolated with TRIzol (Life Technologies) according to the supplier's protocol using glycogen as carrier. Quality control and quantification of total RNA was assessed using an Agilent 2100 Bioanalyzer with an RNA Nano 6000 microfluidics kit (Agilent Technologies) and a NanoDrop 1000 UV-Vis spectrophotometer (Kisker).

Microarray expression profiling and data analysis. Microarray experiments were performed as dual-color or single-color hybridizations on either 4 × 44 K human catalogue (Agilent-026652) or 8×60 K human custom (Agilent-048908) microarrays comprising identical features for coding genes. In order to compensate dye-specific effects and to ensure statistically relevant data, color-swap dye-reversal hybridizations were performed⁴¹. RNA labeling was done either with a two-color Quick Amp Labeling Kit (4 × 44 K arrays) or with a Low Input Quick Amp Kit (6 × 60 K arrays) according to the supplier's recommendations (Agilent Technologies). In brief, mRNA was reverse transcribed and amplified using an oligo-dT-T7 promoter primer, and labeled with Cyanine 3-CTP or Cyanine 5-CTP. After precipitation, purification, and quantification, 1 μ g (4 × 44 K arrays) or 300 ng (8 × 60 K arrays) of each labeled cRNA was fragmented and hybridized to whole genome multipack microarrays according to the manufacturer's protocol (Agilent Technologies). Scanning of microarrays was performed with 5 µm resolution and XDR extended range (4 × 44 K arrays) or 3 µm resolution (8 × 60 K arrays) using a G2565CA high-resolution laser microarray scanner (Agilent Technologies). Microarray image data were analyzed and extracted with the Image Analysis/ Feature Extraction software G2567AA v. A.11.5.1.1 (Agilent Technologies) using default settings and the protocol GE2_1100_Jul11. The extracted MAGE-ML files were subsequently analyzed with the Rosetta Resolver, Build 7.2.2 SP1.31 (Rosetta Biosoftware). Ratio profiles comprising single hybridizations were combined in an error-weighted fashion to create ratio experiments. A 1.5-fold change expression cut-off for ratio experiments was applied together with anti-correlation of ratio profiles, rendering the microarray analysis highly significant, robust, and reproducible. Additionally, raw data txt files were analyzed with R packages from the Bioconductor repository. The networks and functional analyses of microarray data were generated via Ingenuity Pathway Analysis (QIAGEN Inc., [https://www qiagenbioinformatics.com/products/ingenuity-pathway-analysis])⁴². The data discussed in this publication have been deposited in NCBI's Gene Expression Omnibus and are accessible through GEO Series accession number GSE107712.

GSEA analysis. We derived a stem cell signature using published gene expression data (GSE60919)¹³ from FT organoids upon DBZ treatment. Raw data were normalized using method LOESS and differentially expressed genes determined using R and the BioConductor package LIMMA package⁴³. We selected downregulated genes with FDR < 10% and log2 fold change <-1.5 as putative FT stem cell signature genes. We performed GSEA on those genes pre-ranked by gene expression-based *t*-score between infected and non-infected samples at 3 d p.i., using the fgsea R package⁴⁴ with 5000 permutations.

Live-cell imaging. FT epithelial cells were transduced with a plasmid carrying a GFP-membrane tag (pCT-Mem-GFP plasmid, System Biosciences #CYTO100-VA-1). After selection, GFP mem transduced organoids were infected with mCherry-labeled *Chlamydia* stock according to the standard protocol, seeded into Matrigel in ibidi μ dishes, incubated for 24 h and transferred to an inverted Leica TCS-SP5 confocal microscope equipped with a cell culture incubator. For about

 $50\,h,$ confocal stacks of about 30 frames were generated every 10 min. These stacks were used for 3D reconstruction and videos using Volocity 6.3.

Transformation of Chlamydia with RFP. The protocol was adapted from procedures developed by Wang and colleagues^{45,46}; Agaisse and Derré⁴⁷; Song and colleagues⁴⁸ and Bauler and Hackstadt⁴⁹. In brief, Chlamydia trachomatis K (Ctr K, a kind gift from Lars Köhler) EBs were transformed with p2TK2-SW2 IncDPrommCherry-IncDTerm plasmid DNA. The transformed strain was then selected with increasing concentrations of penicillin G for 7 passages until 100 units ml-1 for further propagation of transformed Ctr K mcherry stock. For the preparation of mCherry Ctr K stocks, chlamydial EBs were propagated in HeLa cells (ATCC® CCL-2) in T150 cm3 cell culture flasks with 25 ml of culture medium. Cells were infected with lysates from earlier passages and incubated at 35 °C in a cell culture incubator under humidified atmosphere with 5% CO2 until time of harvest at 48 h p.i., as described above. The resulting supernatant was collected and centrifuged at 20,000 rcf for 40 min at 4 °C in an SS-34 rotor (Sorval RC 5 C Plus) to pellet chlamydial EBs. The harvested bacteria were resuspended in 5 ml SPG buffer (4 °C). A second centrifugation was performed and the pellet resuspended in 4 ml of SPG buffer (4 °C) and frozen at -80 °C.

Chlamydia infection, cure, and re-infection of FT organoids. For infection with *CtrD* (ATCC[®] VR-885TM), *CtrE* (ATCC[®] VR-3488[¬]) and *CtrK*, 2 wells of organoids were released from MatrigelTM with cold DPBS, pooled and mechanically disrupted by passing them through a 26 gauge needle. The fragmented organoids were divided evenly into 2 tubes for infection and mock control. After centrifugation ($300 \times g$, 5 min) and removal of the supernatant, 10 µl *CtrD* (from a frozen stock with 10⁸ IFU ml⁻¹ as determined by titration on HeLa cells) were added to one tube with the pelleted organoids. The suspension was mixed by pipetting and incubated for 15 min at 35 °C followed by 5 min on ice. The mock control was treated in the same way, but without addition of *CtrD*. Finally, 50 µl MatrigelTM was added to each tube, the organoids seeded and placed in a humidified incubator at 5% CO₂ and 35 °C. Splitting of organoids was done every 3–4 weeks. RNA samples were taken at 72 h p.i. and 1 month p.i.

At around 4 months p.i. the infection was cured by applying a mixture of penicillin (100 U ml⁻¹) and streptomycin (100 μ g ml⁻¹) to the organoid culture for one week. After curing, re-infection was carried out in the same way as the first infection with mechanical splitting, adding of *CtrD* to one half of the organoids and mock treatment of the other half. Control organoids initially infected with *CtrD* were infected or mock-treated again. 72 h post seeding, RNA samples were taken of the now 2× infected (chronic infected + re-infected), chronic infected (chronic cured), acute infected (long-term acute inf), and the never infected organoids (Fig. 3d).

RNA samples for microarray. At the respective time points (3 d p.i., 1 month p.i. and 4 months p.i.) organoids were released from MatrigelTM with ice-cold DPBS and centrifuged ($300 \times g$, 5 min). The cell pellet from one MatrigelTM drop was resuspended in 750 µl TRIzol^{*} reagent (Invitrogen # 15596026) and stored overnight at -80 °C until further isolation.

Infectivity assay. One day before the infectivity assay, HeLa cells were seeded at a density to achieve ~ 70% confluence at the time of infection. Both *Ctr*-infected and non-infected FT organoids were treated as follows: Medium was removed and MatrigelTM dissolved in 1 ml ice-cold RPMI w/o FCS. Organoids were centrifuged for 4 min at 300 × *g*. After removal of the supernatant, cells were resuspended in 1 ml RPMI and homogenized by passing three times through a 26 G gauge needle. After another round of centrifugation and addition of 1 ml ice-cold RPMI, the pellet was transferred to a 50 ml falcon tube with 1 ml sterile glass beads. EBs were released by vigorous vortexing for 5 min. After centrifugation for 4 min at 300 × *g*, the supernatants were transferred to the prepared HeLa cells containing fresh medium. After 24 h (at 35 °C, 5% CO₂) cells were fixed in PFA and subjected to IF staining for detection of inclusions.

Immunofluorescence staining. Organoids were fixed with 3.7% PFA, embedded in paraffin, sectioned and stained for confocal imaging as described previously¹³.

Whole-mount staining. Organoids were released from Matrigel with 1xPBS and pelleted by gravitational flow to maintain 3D structure. After fixing with 3.7% PFA for 1 h at RT, organoids were permeabilized and blocked overnight at 4 °C in 5% donkey serum, 1% FCS, 0.05% Tween-20, 0.5% Triton X-100 and 0.02% sodium azide in 1xPBS. Staining with primary antibodies was performed in blocking buffer (0.0025% Triton X-100) at a dilution of 1:200 for 3 days at 4 °C. Washing (5 × 45 min in 1xPBS with 5% glycerol) was followed by staining with Draq5 and secondary antibody in blocking solution (0.0025% Triton X-100) at a dilution of 1:200 for 2 days at 4 °C. After washing, organoids were transferred onto an ibiTreat μ -slide (ibidi #003031) and *z* stacks performed using confocal microscopy. The 3D structure was reconstructed and visualized using Fiji (Image)].

Western blot. Organoid samples were treated with ice-cold PBS to remove Matrigel, centrifuged ($300 \times g$; 5 min; 4 °C), supernatant was removed and the cell pellet resuspended in 100 µl SDS sample buffer (4% SDS, 32% glycerol, 125 mM Tris pH 6.8, 200 mM β -mercaptoethanol, and bromphenol blue). Samples were boiled for 7 min at 96 °C, then separated via SDS-Page electrophoresis (~90 min at 150 V const) and transferred to a PVDF membrane (2.5 h at 250 mA const. at 4 °C). Membranes were blocked in 5% skim milk/TBS-Tween-20 (0.1%) for 60 min. Primary antibodies were diluted 1:500 or 1:1000 in 5% skim milk/TBS-Tween-20 (0.1%) and incubated with the blocked membranes at 4 °C overnight. After extensive washing in TBS-T for 45 min in total, secondary antibodies anti-mouse-or anti-rabbit-HRP were diluted 1:3000 in 5% skim milk/TBS-Tween-20 (0.1%) and incubated for 1 h at room temperature. ECL detection was performed according to the manufacturer's protocol after washing the membranes with TBS-T for 1 h. Uncropped scan images of all blots are provided in Supplementary Figure 9.

LIF neutralization. For LIF neutralization the general protocol for *CtrD* infection of organoids (as described above) was carried out. Differing from this protocol, the fragmented organoids were resuspended in 90 µl ADF++, which was added with or without *CtrD*, and subsequently mixed with 10 µl of 1:40 pre-diluted antibodies. Neutralization was done using 0.5 µg ml⁻¹ anti-LIF antibody (R&D, AF-250-NA, from goat, 200 µg ml⁻¹) and mock control using 0.5 µg ml⁻¹ goat anti-CagA (Santa Cruz, #sc-6085, 200 µg ml⁻¹). After the specified incubation time for infection, the organoids were seeded in Matrigel and culture medium was added. 14 days p.i. organoids were fixed, embedded and IF labeled for detection of *Chlamydia*.

Methylation array and bioinformatic analysis. For genome-wide DNA methylation analysis, bisulfite conversion of the genomic DNA and hybridization to the Illumina Infinium® MethylationEPIC BeadChip were performed at Life&Brain (Bonn, Germany), according to the manufacturer's protocol. Data analysis was carried out in the R environment⁵⁰. Preprocessing and quality control (QC) were performed following the ChAMP package⁵¹ default filtering steps (probes with a detection *p*-value > 0.01 and with a bead count < 3 were excluded), as well as probes where the sequence overlaps single-nucleotide polymorphisms (SNPs) or that were shown to cross-hybridize according to Zhou et al.⁵² Subset-quantile within array normalization (SWAN) was applied in order to adjust for the type I and type II bias of the methylation array⁵³. Differentially methylated CpGs between infected (CtrD) and non-infected (NI) organoids were determined using limma⁴³ and a moderated paired *t*-test. A false discovery rate (FDR) was computed by adjusting p-values for multiple testing using the Benjamini-Hochberg procedure. For patient-specific DM CpGs upon infection and long-term culture, a cut-off of delta beta > 20% was applied and justified with data from a control experiment (Supplementary Figure 8a,b). Unique DM CpGs compared to the baseline were subjected to a locus overlap analysis (LOLA)²⁶ using the databases ENCODE transcription factor binding sites (TFBSs), ENCODE segmentation³⁷ UCSC features⁵⁴ as well as Roadmap Epigenomics⁵⁵. For the χ^2 test, for each donor the frequency of hypomethylated or unchanged CpGs in each arm was compared with the corresponding number of hypermethylated CpGs. The Methylation BeadChip data generated in this study have been deposited in the National Centre for Biotechnology Information Omnibus (GEO) under the accession code GSE108202.

Reporting summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The microarray and methylation BeadChip data from this manuscript have been deposited in the National Centre for Biotechnology Information Omnibus (GEO) under accession codes GSE107712 and GSE108202. Raw data associated with Figs. 3f and 4 can be found in Supplementary Data 1 and 2, respectively. Other data supporting the findings of this study are available within the paper and its Supplementary Information files, or from the corresponding author upon request. As far as ethical and legal constrains permit, all biological materials are available upon request from the corresponding author.

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Author contributions

M.K. and T.F.M. conceived the project and designed experiments, which were conducted by M.K., K.H., O.T., and A.R.C.; V.B. conducted the live-cell imaging experiment. K.F. and H.B. analyzed methylation Chip data. H.B. and H.-J.M. analyzed microarray data, M.M., J.S. and E.B. selected the patients and provided human FT samples. M.K. and T.F. M. wrote the manuscript, and T.F.M. supervised the project.

Additional information

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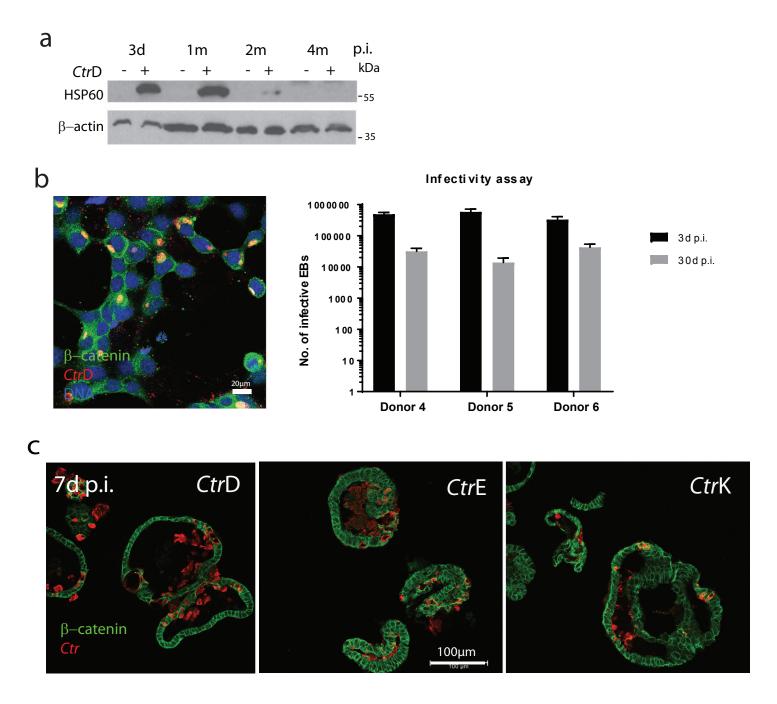
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Supplementary Information

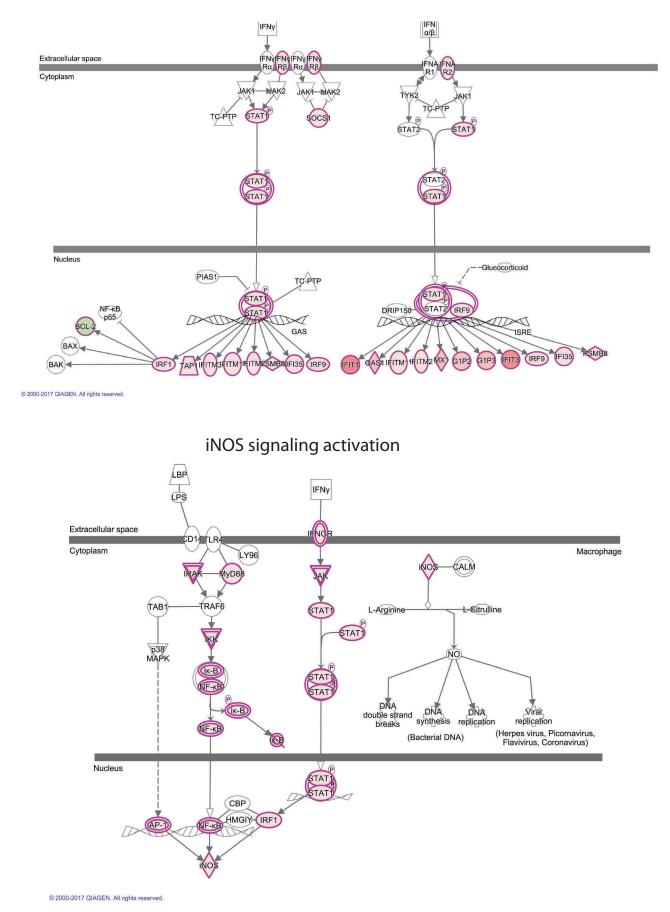
Chronic *Chlamydia* infection in human organoids increases stemness and promotes age-dependent CpG methylation

Kessler M et al



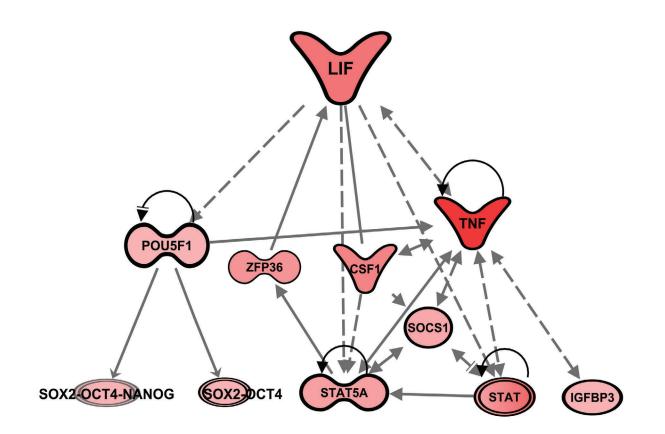
Supplementary Figure 1. Chronic, productive *Ctr* infections in organoids gradually decreases in titer a) Representative blot of HSP60 protein levels from one chronically infected culture at 3 d, 1 month and 4 month p.i. While bacterial load is high at 3 dp.i and remains substantial at 1 month p.i. it decreases to undetectable levels by 4 months p.i. b) Confocal image of HeLa cells containing inclusions filled with *Ctr*, confirming infectious potential of EBs retrieved from infected organoids. The graph represents quantification from 3 independent chronic infections in 3 donors at 3 d and 1 m p.i. ± sd calculated based on inclusion counts from different fields of view. c) Confocal images of representative organoids infected with serovars D, E and K at 7 d p.i. reveals similar infection rates and accumulation of bacteria shed in the organoid lumen.

Interferon signaling activation in acute CtrD infection

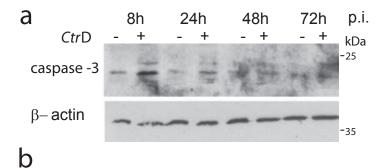


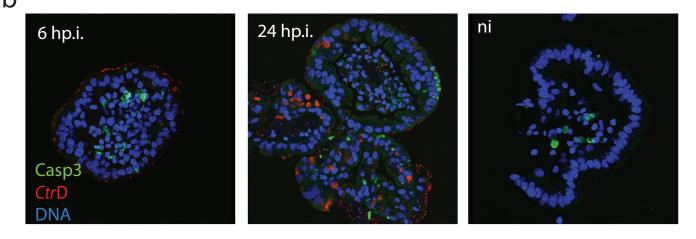
Supplementary Figure 2. Acute *Ctr* infection triggers strong upregulation of interferon response a) Genes in the interferon signaling network that were upregulated (red) during acute *Ctr* infection. b) Genes in the iNOS pathway upregulated during acute *Ctr* infection. Pathways were generated on the IPAtm platform by overlay of canonical networks with microarray data of genes that are regulated in an identical fashion in all 3 donors.

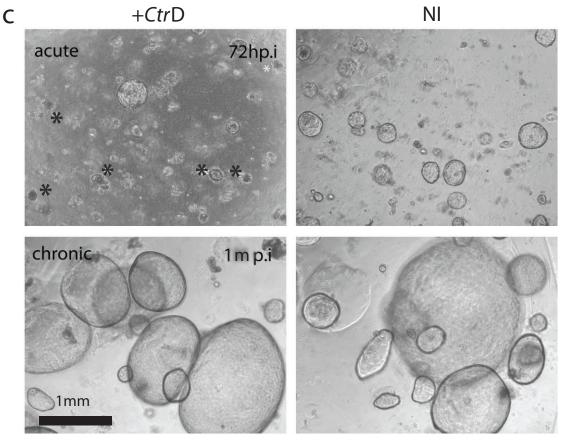
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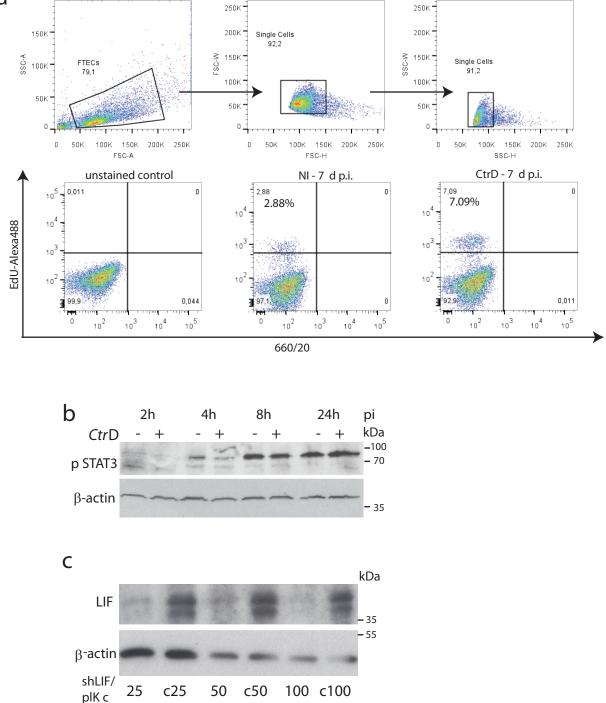
Supplementary Figure 3. Activation of the LIF pathway occurs during acute *Ctr* **infection** Graphical presentation of the strong upregulation of the LIF gene and associated interactors (all in red). The network was generated on the IPAtm platform by pathway analysis of microarray data of all candidate genes which were consistently regulated in 3 different donors.





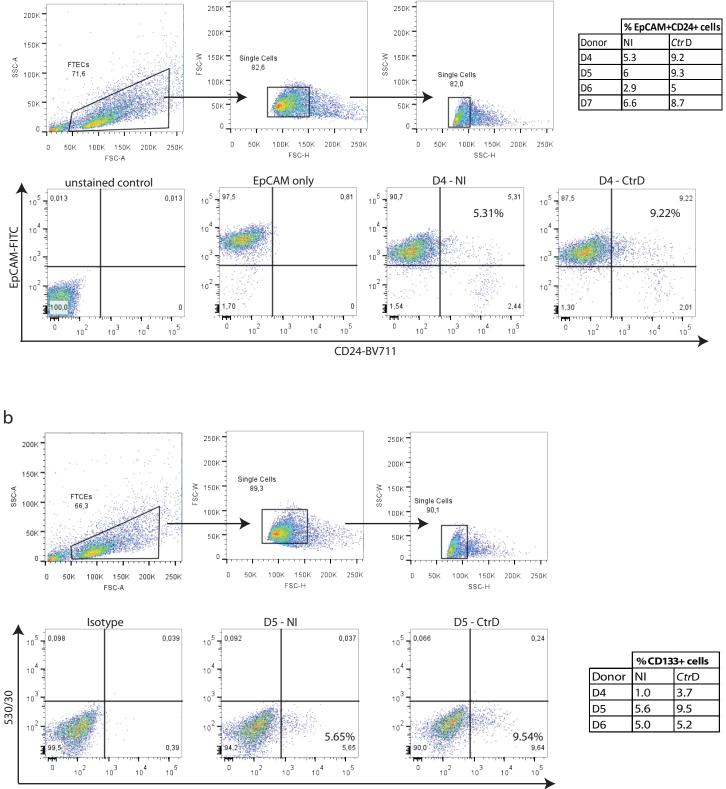


Supplementary Figure 4. Early stress response and apoptosis are compensated during chronic infection a) Western blot for active, cleaved caspase-3 showing a peak in apoptosis in infected organoids at early stages of infection (from 8 -72 h, with decreasing intensity). b) Confocal images of active caspase-3 positive cells at 6 and 24 h p.i. shows an absence of colocalization with inclusion-harboring cells (*Ctr*, red) suggesting a broader stress response and paracrine induction of apoptosis. c) While organoid culture at 72 h p.i. shows clear signs of stress (*) in comparison to control organoids, infected and non–infected cultures at 1 m p.i. have a highly similar phenotype as visible in phase contrast images.



Supplementary Figure 5. LIF signaling is active in organoids independent of presence of *Ctr* a) Gating strategy to count Alexa 488+ (EdU+ proliferative cells) in infected and non-infected organoids over the course of 1 month. b) WB of the time course experiment showing that the pSTAT3 signal transiently disappears after the dissociation of organoids but recovers in both infected and non-infected cultures within a few hours after reseeding c) Depletion of LIF protein by introduction of shLIF is comparable at different virus concentrations, suggesting that a basal level of LIF is required for organoid growth.

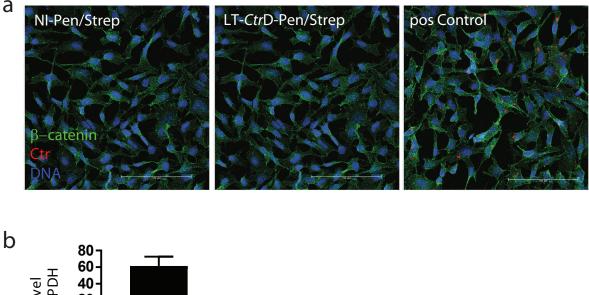
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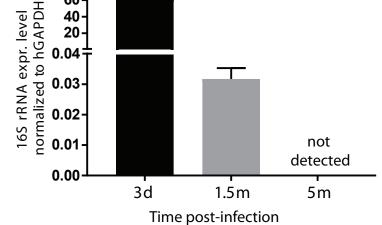




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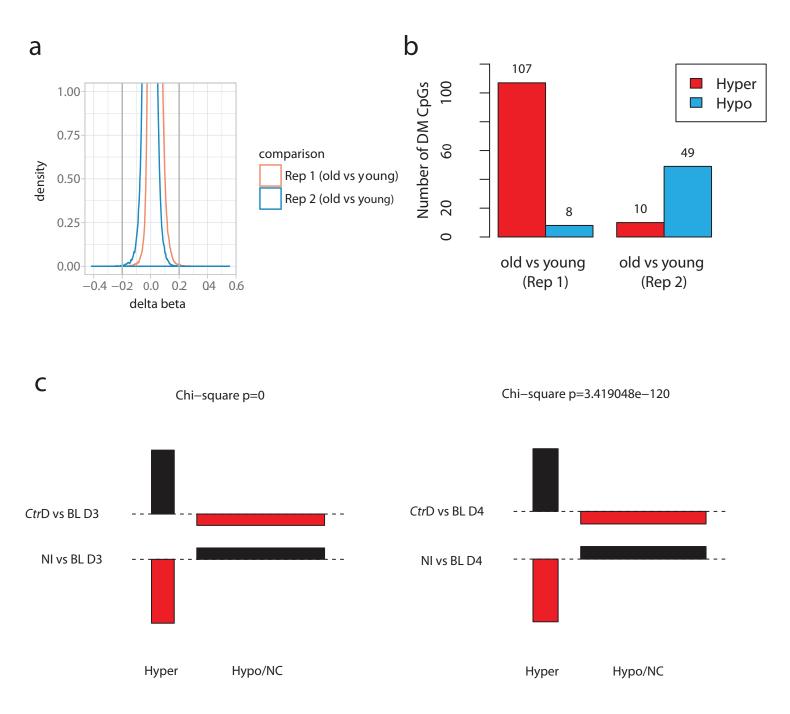
Supplementary Figure 6. Chronically infected organoids show an increase in the CD24 and CD133 positive cell populations. a) Chronically infected organoids show an increase in the number of CD24+/EpCam+ cells. Depicted are representative plots from one of four independent FACS sorting experiments. b) Number of CD133+ cells acquired by FACS analysis of non-infected and infected organoid samples for three independent donors. Two out of three cultures infected with *Ctr*D for 2 months demonstrate a clear increase in the size of the CD133+ population.





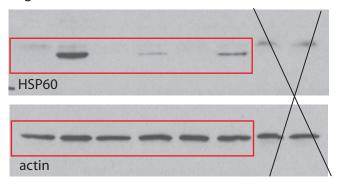
Supplementary Figure 7. Chronically infected organoids show a significantly decreased bacterial load. a) Immunofluorescence labeling of infectivity assay in Hela cells with lysate from long-term infected (LT-CtrD) as well as non-infected (NI) organoids treated for 7 days with Pen/Strep. While the positive control (from 96 hp.i.) contains many inclusions, the absence of inclusions in the NI and P/S -treated chronically infected samples confirms that there were no replicative bacteria left in the culture. b) The relative expression level of bacterial 16S ribosomal RNA was determined by qPCR at different time points of the infected organoid culture and normalized to human GAPDH expression. Data is presented as mean ± sd. At 5 months p.i. the RNA content was below detection level.

а



Supplementary Figure 8. Statistical analysis of methylation data in Fig. 4. a) Density plot (zoomed) of the delta beta distribution from two different donors (Rep 1 and Rep 2) comparing two different types of short-term culture. Grey vertical lines indicate the cut off of |delta beta| > 0.2. b) Barplot showing the number of differentially methylated CpGs that pass the threshold determine in a. c) Association plot of the chi-squared test applied to Fig. 4a showing the Pearson residuals ((observed-expected)/sqrt(expected)) in the height of the boxes and the expected values as width.



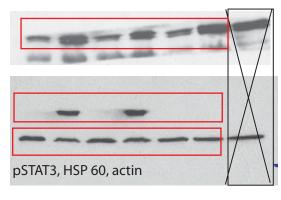


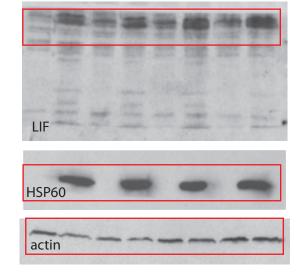
HSP60

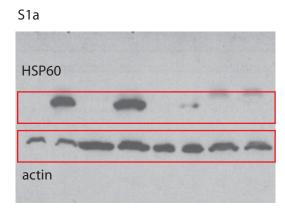
Fig2c

Fig1d

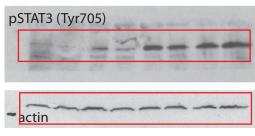
Fig1F

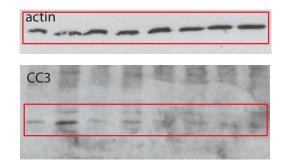




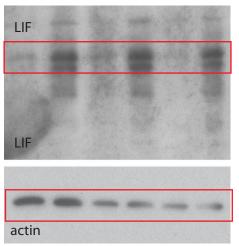


S5b





S5c



Supplementary Figure 9. Uncropped scans of blots presented in the manuscript. Cropped areas are indicated by red boxes.

S4a

Description of Additional Supplementary Files

File Name: Supplementary Data 1

Description: List of 91 genes that were significantly differentially regulated across 3 donors after curing of chronic infection.

File Name: Supplementary Data 2 Description: List of 603 CpGs that were differentially methylated across 3 different donors.

File Name: Supplementary Movie 1

Description: Live cell imaging of infected organoid showing dynamic growth of *Ctr* inclusions within an epithelial monolayer. Notably, inclusions are being expelled into the lumen, after which they burst.

ProbeName A_23_P137484	GeneSymbol	SystematicName	GeneDescription UNE1 type transposase domain containing 1	GencodeV25MappingStatus unique gene, perfect match	GeneSymbol_Gencode L1TD1 PAPPA	protein_coding	1.753881568		t 7.400019239 4.234897419	P.Value 0.00017459 0.004152292	
	JAKMIP2	NM_002581 NM_014790	pappalysin 1 janus kinase and microtubule interacting protein 2	unique gene, perfect match unique gene, perfect match	JAKMIP2	protein_coding protein_coding	1.186540771	4.043196361	5.230338832	0.001339183	0.458489575
A_33_P3293049 A_24_P852756 A_33_P3264910 A_33_P3267375	HLA-DQA2 NKX6-2	NM_002122 NM_020056 NM_177400 NM_000337	major histocompatibility complex, class II, DQ alpha 1 major histocompatibility complex, class II, DQ alpha 2 NK6 homeobox 2 sarcoglycan delta	multiple matching genes unique gene,perfect match unique gene,perfect match unique gene,perfect match	NA HLA-DQA2 NKX6-2 SGCD	NA protein_coding protein_coding protein_coding protein_coding,n	1.124361525 1.043395999		5.997402711 3.819857228 7.899173349 4.485126568	0.006948452 0.000116827	0.586899916 0.393447114
A_33_P3243787	COL28A1	NM_001037763	collagen type XXVIII alpha 1 chain	unique gene, perfect match	COL28A1	onsense_mediat ed_decay	0.977051816	3.789189562	4.160935612	0.004542628	0.557356491
A_24_P66780 A_33_P3477521	FAM83B 8P11-1094H24	NM_001010872	family with sequence similarity 83 member B uncharacterized LOC284080	unique gene,perfect match unique gene,perfect match	FAM83B RP11-1094H24.4	protein_coding lincRNA	0.934928648	3.534132786 4.226817881	4.507344674	0.003003418	0.504914447
A_23_P434398	TXLNB	NM_153235	taxilin beta	unique gene, perfect match	TXLNB	protein_coding	0.934133992	4.603021936	4.299687255	0.003840611	0.521873006
A_24_P237036	TNFSF14	NM_003807	tumor necrosis factor superfamily member 14	unique gene,perfect match	TNFSF14	protein_coding	0.881413048	6.304432327	3.690238071	0.008204209	0.609975047
A_23_P430948	ATP13A4	NM_032279	ATPase 13A4	unique gene,perfect match	ATP13A4	protein_coding,n onsense_mediat ed_decay,proces sed_transcript retained_intron, nonsense media	0.87513634	3.26287191	3.7588693	0.007511008	0.596362749
A_23_P207507	ABCC3	NM_003786	ATP binding cassette subfamily C member 3	unique gene, perfect match	ABCC3	ted_decay,protei n_coding processed_transc	0.85689849	8.520092001	4.576798768	0.002770231	0.499843512
A_23_P25194	HRK	NM_003806	harakiri, BCL2 interacting protein	unique gene,perfect match	HRK	ript,protein_codi ng	0.823776459	8.239627844	4.559184059	0.002827411	0.499843512
A_33_P3353846 A_32_P163739		NM_001010873 NM_020741	translocator protein 2 KIAA1257	unique gene,perfect match unique gene,perfect match	TSPO2 KIAA1257	protein_coding processed_transc ript,protein_codi ng		3.88592795	3.609370628		0.61753414
A_33_P3407350	DBX1	NM_001029865	developing brain homeobox 1	unique gene, perfect match	DBX1 NKD1	protein_coding		3.020204266		0.004776533	
A_23_P429449	INKDI	NM_033119	naked cuticle homolog 1	unique gene,perfect match	NKD1	protein_coding processed_transc	0.809180039	5.0445425	4.8/031/105	0.001985477	0.49030823
A_23_P7313	SPP1	NM_001040058	secreted phosphoprotein 1	unique gene,perfect match	SPP1	ript,protein_codi ng	0.807854449	7.805702845	10.97125629	1.45632E-05	0.373506829
A_33_P3256844	WDR49	ENST00000453925	WD repeat domain 49 [Source:HGNC Symbol;Acc:26587] [ENST00000453925]	unique gene, perfect match	WDR49	protein_coding	0 795274489	3.503853575	4 171002703	0 004487198	0 557356491
						retained_intron,li					
A_24_P691826 A_33_P3284838		ENST00000587298	Unknown Homo sapiens chromosome 10 open reading frame 115 (C10orf115), long non-coding RNA [NR_103721]	unique gene,perfect match unique gene,perfect match	WFDC21P C10orf67	ncRNA nonsense_media ted_decay,protei n_coding	0.79461301	6.01045418	6.125989976	0.007081386	
A_33_P3424187	ARID3C	NM_001017363	AT-rich interaction domain 3C	unique gene, perfect match	ARID3C	protein_coding	0.785358796	3.038758987	3.680482338	0.008308285	0.610977
A_33_P3246418 A_23_P121545	MDFI GPM6A	NM_005586 NM_201591	MyoD family inhibitor glycoprotein M6A	unique gene,perfect match unique gene,perfect match	MDFI GPM6A	protein_coding protein_coding		11.32789197 4.522707783	4.151794025 5.347541658	0.004593617 0.00118281	0.557356491 0.450741399
A_23_P89973 A_33_P3367984	BRSK1 ABCA12	NM_032430 NM_173076	BR serine/threonine kinase 1 ATP binding cassette subfamily A member 12	unique gene,perfect match unique gene,perfect match	BRSK1 ABCA12	protein_coding protein_coding			3.554917799 7.198330236	0.009784222	0.61753414 0.393447114
		NM 001547	interferon induced protein with tetratricopeptide repeats 2		IFIT2	protein_coding		7.513365023			
A_24_P304071 A_33_P3331831		-	PREDICTED: Homo sapiens collagen alpha-1(II) chain-like (LOC101928841), transcript variant X2, mRNA [XM_005275740]	unique gene,perfect match	ADPRHL1	protein_coding		4.186191491			
A 33 P3311083	PHI DB3	ENST00000599242	pleckstrin homology-like domain, family B, member 3 [Source:HGNC Symbol;Acc:30499] [ENST00000599242]	unique gene, perfect match	PHLDB3	protein_coding	0.742035237	3.290824608	3.908290415	0.006212933	0.580408865
A_33_P3240492		NM_032439	phytanoyl-CoA 2-hydroxylase interacting protein like long intergenic non-protein coding RNA 1021 [Source:HGNC	unique gene, perfect match	PHYHIPL	protein_coding		5.273177616		0.00831081	0.610977
A_33_P3821778 A_33_P3396336		ENST00000512067 THC2750096	Symbol;Acc:48995] [ENST00000512067] NA	unique gene,perfect match multiple matching genes	LINC01021 NA	lincRNA NA nonsense_media		4.915276792 3.368495146			
A_33_P3224100		NM_152632	cilia and flagella associated protein 47	unique gene, perfect match	CFAP47	ted_decay,protei n_coding		3.953718094			
A_24_P278747	CCND2	NM_001759	cyclin D2 dynein, axonemal, heavy chain 7 [Source:HGNC	unique gene,perfect match	CCND2	protein_coding	0.703533198	8.844986102	5.198406787	0.0013857	0.458489575
A_32_P351037	DNAH7	ENST00000410072	Symbol;Acc:18661] [ENST00000410072]	unique gene, perfect match	DNAH7	protein_coding	-0.707310739	3.637823717	-5.690997598	0.000830487	0.450741399
						protein_coding,r					
A_23_P142830	ZNF682 PLA2R1	NM_033196 NM_007366	zinc finger protein 682 phospholipase A2 receptor 1	unique gene,perfect match unique gene,perfect match	ZNF682 PLA2R1	etained_intron protein_coding	-0.716709762	5.880969109 5.703151632	-6.172399675		0.441891598
A_24_P365721 A_33_P3302260	SLC6A14 MYRF	NM_007231 NM_013279	solute carrier family 6 member 14 myelin regulatory factor	unique gene,perfect match unique gene,perfect match	SLC6A14 MYRF	protein_coding protein_coding		8.607540933 3.695680134			0.574749161 0.61753414
						protein_coding,p rocessed_transcri					
A_23_P427747	M1AP	NM_138804	meiosis 1 associated protein	unique gene, perfect match	M1AP	pt	-0.726389752	5.517241829	-4.059618712	0.005144449	0.559821553
						retained_intron,					
A_33_P3269109	GUCY1A3	ENST00000512983	guanylate cyclase 1, soluble, alpha 3 [Source:HGNC Symbol;Acc:4685] [ENST00000512983]	unique gene,perfect match	GUCY1A3	protein_coding,n onsense_mediat ed_decay protein_coding,p	-0.727053171	6.852225153	-7.779164404	0.000128424	0.393447114
A 33 P3373960	RD3	NM_183059	retinal degeneration 3	unique gene,perfect match	RD3	rocessed_transcri pt	-0.731483881	4.527801058	-4.46634498	0.003151227	0.514554721
A_23_P138706 A_33_P3352467	ADRA2A	NM_000681 NM_001050	adrenoceptor alpha 2A somatostatin receptor 2	unique gene, perfect match unique gene, perfect match	ADRA2A SSTR2	protein_coding protein_coding		7.422023975 4.522744435			
A_24_P250922	PTGS2	NM_000963	prostaglandin-endoperoxide synthase 2	unique gene,perfect match	PTGS2	protein_coding	-0.75300873	8.443208584	-4.37325968	0.003517622	0.517058911
A_23_P343398 A_33_P3351416		NM_001838	C-C motif chemokine receptor 7 SPARC related modular calcium binding 2	unique gene,perfect match	CCR7 SMOC2	protein_coding protein_coding,n onsense_mediat ed_decay		5.515071853 4.889535161			
A_33_P3590673		NR_045196	small nucleolar RNA host gene 18	unique gene,perfect match	SNHG18	lincRNA		7.973770072	-5.90345578		
A_33_P3303309	LINC01105	NR_026832	long intergenic non-protein coding RNA 1105	unique gene,perfect match	LINC01105	processed_transc ript,TEC processed_transc ript,protein_codi	-0.799848495	3.802075148	-3.69412183	0.008163173	0.609975047
A_33_P3265270 A_33_P3281283		NM_012434 NM_005226	solute carrier family 17 member 5 sphingosine-1-phosphate receptor 3	unique gene,perfect match unique gene,perfect match	SLC17A5 S1PR3	ng protein_coding processed_transc		5.220891388 6.045187706			0.61753414 0.458489575
A_23_P93772	HOXA5	NM_019102	homeobox A5	unique gene,perfect match	HOXA5	ript,protein_codi ng	-0.816628557	5.194612128	-5.284432887	0.00126431	0.458489575
A_33_P3251856 A_33_P3298236		NM_001142552	NA dachsous cadherin-related 2	unique gene,perfect match unique gene,perfect match	AE000662.93 DCHS2	lincRNA protein coding		5.143499494 4.638497083			
A_33_P3314176		NM_017709	family with sequence similarity 46 member C	unique gene,perfect match	FAM46C	protein_coding			-6.14713477		
A_23_P58328	ANXA10	NM_007193	annexin A10	unique gene,perfect match	ANXA10	retained_intron, protein_coding protein_coding,p	-0.87998759	7.079277482	-4.154193075	0.004580175	0.557356491
A_23_P13907	IGF1	NM_000618	insulin like growth factor 1	unique gene, perfect match	IGF1	rocessed_transcri pt	-0.883631549		-6.005642194		
		NM_183240 NM_018242	transmembrane protein 37 solute carrier family 47 member 1	unique gene, perfect match unique gene, perfect match	TMEM37 SLC47A1	protein_coding protein_coding	-0.903893207	7.205389026	-5.804974478	0.000740941	0.450741399
A_23_P69863	PCDHB5	NM_015669	protocadherin beta 5	unique gene,perfect match	PCDHB5	protein_coding protein_coding,p rocessed_transcri		3.746177752			
	FAM3B	NM_058186	family with sequence similarity 3 member B	unique gene,perfect match	FAM3B	pt processed_transc ript,protein_codi		10.11622211			
A_23_P36531 A_33_P3390024 A_33_P3298455		NM_004616 NM_001282314 NR_120386	tetraspanin 8 exocyst complex component 7 long intergenic non-protein coding RNA 1521 potassium voltage-gated channel subfamily E regulatory	unique gene,perfect match unique gene,perfect match unique gene,perfect match	TSPAN8 EXOC7 LINC01521	ng protein_coding lincRNA		5.057861639	-5.04389671 -4.154294363 -3.735972045	0.004579608	0.557356491
A_23_P24948	KCNE3	NM_005472	subunit 3	unique gene, perfect match	KCNE3	protein_coding		10.91636245			
A_24_P366607 A_24_P131580	SERTM1 ALPPL2	NM_203451 NM_031313	serine rich and transmembrane domain containing 1 alkaline phosphatase, placental like 2	unique gene,perfect match unique gene,perfect match	SERTM1 ALPPL2	protein_coding protein_coding processed_transc		5.223940214 15.41707078			
A_32_P158966	KLRF1	NM_016523	killer cell lectin like receptor F1	unique gene,perfect match	KLRF1	ript,nonsense_m ediated_decay,pr otein_coding	-1.032819136	5.34689851	-4.701425318	0.002400478	0.499843512

A_32_P34826 A_23_P47484	B3GALT5-AS1 GLYATL2	NR_026543 NM_145016	B3GALT5 antisense RNA 1 glycine-N-acyltransferase like 2	unique gene, perfect match multiple matching genes	B3GALT5-AS1 NA	antisense NA	-1.077169613 -1.117658881		-6.807559673 -7.338308784	0.000289635 0.00018376	0.400099328 0.393447114
A_23_P152235 A_33_P3392187 A_23_P257231	ZFPM2 IRX3 CCDC85A ETNPPL	NM_002889 NM_018725 NM_002141 NM_012082 NM_024336 NM_001080433 NM_031279	retinoic acid receptor responder 2 interleukin 17 receptor 8 homeobox A4 zinc finger protein, FOG family member 2 iroquois homeobox 3 coiled-coil domain containing 85A ethanolamine-prosphate phospho-lyase	unique gene,perfect match unique gene,perfect match unique gene,perfect match unique gene,perfect match unique gene,perfect match multiple matching genes unique gene,perfect match	RARRES2 IL17RB HOXA4 ZFPM2 IRX3 NA ETNPPL	protein_coding,r etained_intron protein_coding protein_coding protein_coding protein_coding NA protein_coding	-1.150681936 -1.176883106 -1.185886594 -1.209968218	4.362118596 7.218301258 5.921644078 6.225730397 5.257356912 6.765305049	-4.746920007 -4.702114053 -5.757715837 -3.739519952 -3.996986698 -4.310240227	0.000776685 0.007699738 0.00556003 0.003792333	0.499843512 0.499843512 0.450741399 0.599929095 0.574749161 0.521873006
	SMPD3 FUT9	NM_018667 NM 006581	sphingomyelin phosphodiesterase 3 fucosyltransferase 9	unique gene, perfect match unique gene, perfect match	SMPD3 FUT9	protein_coding protein coding	-1.230464633 -1.269212286		-4.542487424 -3.850662026	0.00288282	
		NM_173078	SLIT and NTRK like family member 4	unique gene,perfect match	SLITRK4	protein_coding	-1.287260568			2.18892E-05	
A_33_P3322519 A 23 P55616	VWA5B2 SLC14A1	NM_138345	von Willebrand factor A domain containing 582 solute carrier family 14 member 1 (Kidd blood eroup)	unique gene,perfect match	VWA582 SLC14A1	retained_intron, protein_coding protein_coding,n onsense_mediat ed decay	-1.293599048		-5.034856269	0.00165409	0.462977909
						nonsense_media ted_decay,protei					
A_23_P43164	SULF1	NM_015170	sulfatase 1	unique gene,perfect match	SULF1	n_coding	-1.377724753	5.557053732	-6.032242335	0.000592937	0.441891598
A_23_P365412	MFSD4A	NM_181644	major facilitator superfamily domain containing 4A	unique gene,perfect match	MFSD4A	retained_intron, protein_coding nonsense_media ted decay,protei	-1.411887518	5.523129819	-4.138621773	0.004668198	0.557356491
A_33_P3274501	KLRF1	NM_001291823	killer cell lectin like receptor F1	unique gene,perfect match	KLRF1	n_coding processed_transc ript,protein_codi	-1.539959277	3.802656296	-5.097484746	0.001545003	0.458489575
A_23_P417918 A_23_P427587 A_23_P349463	PENK FGF19 CHP2	NM_006211 NM_005117 NM_022097	proenkephalin fibroblast growth factor 19 calcineurin like EF-hand protein 2	unique gene,perfect match unique gene,perfect match unique gene,perfect match	PENK FGF19 CHP2	ng protein_coding protein_coding	-1.643848653 -1.856610333 -1.913239383		-6.202312976 -7.700718304 -4.366658823	0.00050385 0.00013671 0.003545339	

Row.names	logFC	AveExpr	t		adj.P.Val	в	CHR MAPINFO		e gene		cgi	feat.cgi	UCSC_Islands_Name	SNP_ID	SNP_DISTANCE	
cg20086286 cg16218764 cg20835412		0.43577583 0.34699127 0.35601593	27.88802661 25.30889324 -25.0602735	5.34E-05	0.76464434 0.76464434 0.76464434	1.739205419 1.652898507 1.643362205	x 1.33E+08 15 47043539 19 12460129	F II		IGR IGR IGR	shore opensea opensea	IGR-shore IGR-opensea IGR-opensea	chrX:133305678-133306936	rs139990316;rs569168230;rs116966886 rs111255449;rs549732238;rs567251325;rs192090355	1;25;48 48;34;26;2	
cg20094831 cg15773251	-0.2431605 0.211729749	0.41832476 0.28337085	-23.2902257 22.62581812	7.08E-05 7.81E-05	0.76464434 0.76464434	1.567947517 1.53580219	10 44699412 6 32078602	R II R II	TNXB	IGR TSS1500	shelf opensea	IGR-shelf TSS1500-opensea	chr10:44701884-44702149	rs189051758;rs530108998 rs190189438	15;13	29
cg14804729 cg03151893 cg17110700	0.201394846 -0.22737708 -0.21784673	0.49732904 0.41817364 0.38949792	21.16063023 -20.7589499 -20.6235579	0.00010449	0.76464434 0.76464434 0.76464434	1.456071834 1.431821349 1.423392449	8 22786329 1 33513729 1 1.15E+08	R II	PEBP4	TSS1500 IGR IGR	opensea shelf opensea	TSS1500-opensea IGR-shelf IGR-opensea	chr1:33516594-33516933	rs7449481;rs538045356 rs567271777;rs538106708;rs189518587 rs73473464;rs539506012	2;1 29;2;1 27;26	
cg21051963 cg13614083	-0.20587444 0.23475937	0.58379193 0.65415033	-19.7515532 19.73436609	0.00012364 0.000124	0.76464434 0.76464434	1.365805038 1.364609613	15 36763406 1 6085872	F II F II	KCNAB2	IGR TSS1500	opensea shore	IGR-opensea TSS1500-shore	chr1:6086244-6086494	rs189708343;rs182017911;rs187217980;rs149608124 rs532313666;rs76852674	1;18;20;21 17;28	
cg15625392 cg21647086 cg21218195	-0.27420646 -0.2488086 0.216023022	0.42849469 0.46909532 0.26453503	-19.1046625 -19.0085324 18.56238559	0.00014076	0.76464434 0.76464434 0.76464434	1.319075871 1.311816079 1.276987169	5 28624261 7 34224120 7 98189557	R II		IGR IGR IGR	opensea opensea opensea	IGR-opensea IGR-opensea IGR-opensea		rs190440057 rs142545188;rs77951931 rs568594771	2;1	2
cg03163469 cg20235803	-0.25261524 0.208878575	0.43633504 0.66318007	-18.2860826 18.10857948	0.00016045 0.00016583	0.76464434 0.76464434	1.254439983 1.239542093	1 34150850 2 2.02E+08	F II F II	CSMD2 BZW1	Body TSS1500	opensea shore	Body-opensea TSS1500-shore	chr2:201675989-201677306	rs537528993 rs138257745		0 24
cg02329994 cg27177112 cg07669309	0.255511798 0.356345281 -0.30673398		17.63824033 17.13869458 -16.8107158	0.0001997	0.76464434 0.76464434 0.76464434	1.19842645 1.151986866 1.119833823	7 1.4E+08 18 58221283 16 54691248	F II	TBXAS1	Body IGR IGR	opensea opensea opensea	Body-opensea IGR-opensea IGR-opensea		rs150569322,rs73158676 rs186062109 rs66972758;rs185536251,rs4784409	7;37 9;17;25	0
cg17874353 cg26358634	-0.26545235 -0.31582256	0.48654597 0.64218455	-16.4959627 -16.3140598	0.00022718 0.00023584	0.76464434 0.76464434	1.087659423 1.068449651	2 1.84E+08 5 62365115	F II F II		IGR IGR	opensea opensea	IGR-opensea IGR-opensea		rs139871203;rs536949912 rs543041198;rs544853090;rs558761784	1;35 1;4;50	
cg19972193 cg08752826 cg18730034	0.236991533 0.201198791 -0.24303857	0.3830016 0.6312934 0.40321892	16.27970859 16.13790392 -15.9599516	0.00024463	0.76464434 0.76464434 0.76464434	1.064769913 1.049401011 1.029699429	5 1.8E+08 3 27956103 15 26866630	F II	FLT4 GABRB3	Body IGR Body	shelf opensea opensea	Body-shelf IGR-opensea Body-opensea	chr5:180075688-180076906	rs533092799;rs73812644;rs563676566 rs199499174	37;6;2	50
cg16612867 cg23948537	-0.21116395 -0.20477238	0.39315909 0.32020925	-15.8787423 -15.6600931	0.00025835 0.0002707	0.76464434 0.76464434	1.020551597 0.995419837	6 37210815 15 40606171	F II	TMEM217	Body IGR	opensea opensea	Body-opensea IGR-opensea		rs138787824 rs147589436		1 30
cg01139665 cg04302628 cg16531665	-0.20399449 0.264124088 -0.20798823	0.42095068 0.46259507 0.46969371	-15.3279358 15.0385101 -14.9313976	0.00031025	0.76464434 0.76464434 0.76464434	0.955789977 0.91976217 0.906060675	19 4841356 2 2.41E+08 13 1.12E+08	F II	PLIN3	Body IGR IGR	opensea shelf opensea	Body-opensea IGR-shelf IGR-opensea	chr2:241097404-241097934	rs141379398;rs146269442;rs146941045;rs533892814 rs74128424;rs531080750;rs9555829	1;11;29;35 0;11;41	
cg12480903 cg14334652	0.22211879	0.30009418 0.45633853	14.53888334 -14.5044326	0.0003476	0.76464434 0.76464434	0.854073537	1 1.67E+08 3 1.65E+08	F II	CD247	Body IGR	shore opensea	Body-shore IGR-opensea	chr1:167424088-167425216	rs531506334;rs549823731 rs144248509	2;46	17
cg20251528 cg10889085 cg21581168	-0.20422324 0.248122181 -0.30433095	0.22922587 0.49757461 0.33955664	-14.416944 14.359239 -13.9011375	0.00036244	0.76464434 0.76464434 0.76464434	0.837333677 0.829311276 0.763242476	6 89674094 21 39715656 3 1.8E+08	F II	RNGTT LINC01423	TSS1500 Body IGR	shore opensea opensea	TSS1500-shore Body-opensea IGR-opensea	chr6:89672884-89673579	rs142575461;rs146899019 rs185488926 rs49305610;rs565918019	30;12	0
cg05612984 cg06496489	0.211369508	0.51236992 0.59673929	13.73417825 -13.7048751	0.00042089 0.00042392	0.76464434 0.76464434	0.73806838	4 1.73E+08 15 39110621	R II R II	GALNTL6	Body IGR	opensea opensea	Body-opensea IGR-opensea		rs112531751;rs181185765;rs539872067 rs141236750;rs550634759	29;22;1 13;5	
cg25830548 cg20618433 cg21765032	-0.27099993 0.256722524 -0.21050699	0.50344283 0.59366933 0.67158371	-13.66431 13.26137358 -13.0704632		0.76464434 0.76464434 0.76464434	0.727352878 0.663393435 0.631750812	6 87041914 19 11266919 19 3293547	F II	SPC24 BRUNOL5	IGR TSS1500 3'UTR	opensea shore island	IGR-opensea TSS1500-shore 3'UTR-island	chr19:11266230-11266726 chr19:3293267-3293548	rs568817205,rs532960952,rs551205305 rs572053822,rs313784	0;18;40	
cg19505184 cg04885756	-0.20397429 -0.20736894	0.69368466 0.60882402	-12.7051118 -12.697741	0.0005465 0.00054757	0.76464434 0.76464434	0.568652931 0.567344391	18 66779097 13 51909581	F II R II	Director	IGR IGR	opensea opensea	IGR-opensea IGR-opensea	0.155151075153540	rs549275073 rs555648165		0
cg11507780 cg01996818 cg08922347	-0.24157377 -0.21825356 -0.20902576	0.48131268 0.40334289 0.30806885	-12.5241815 -12.4608934 -12.4602026	0.0005832	0.76464434 0.76464434 0.76464434	0.536112413 0.524520148 0.524393006	6 1.39E+08 X 1.31E+08 11 5409945	R I	MST4 OR51M1	IGR 5'UTR TSS1500	opensea island opensea	IGR-opensea 5'UTR-island TSS1500-opensea	chrX:131156818-131157775	rs149004693;rs527996503;rs187261719 rs200737360;rs574232473;rs536443958;rs150564490	46;12;1	
cg03985452 cg25711246	-0.23010886 -0.20511314	0.34453453 0.62436892	-12.263218 -12.2615925	0.00061525 0.00061552	0.76464434	0.487593039 0.487284782	2 3836042 12 4917426	F II	KCNA6	IGR TSS1500	shore	IGR-shore TSS1500-shore	chr2:3833815-3834318 chr12:4918273-4919657	15200/577500/557452247535304453556/5130084450 rs14461685575507299657s74948631;rs113593166;rs9973392;rs566676513;rs534027419;rs55 rs182554390;rs141063215		
cg27201534 cg11002686 cg01591405	0.266040659 0.244670322 0.208256549		12.13322766 12.06897735 12.04413125	0.00064899	0.76464434 0.76464434 0.76464434	0.462701284 0.450215325 0.445354053	20 42379020 7 55412682 17 18024867	F II	MY015A	IGR IGR Body	opensea island island	IGR-opensea IGR-island Body-island	chr7:55411965-55412772 chr17:18022195-18024868	rs530265982 rs1856889187s201529563	37-38	31
cg07665542 cg06161398	-0.20308227 0.22050275	0.67602707 0.70664141	-11.9296915 11.92500262	0.00067467 0.00067555	0.76464434 0.76464434	0.42272372 0.421788033	16 86215740 9 1.17E+08	F II	WIGISA	IGR IGR	opensea opensea	IGR-opensea IGR-opensea		rs78645930;rs534619492;rs554883626;rs534016771;rs537098664 rs114999856;rs146151304	5;7;12;36;49 9;2	
cg19866637 cg22424764 cg23161350	-0.20839868 0.2170484	0.417551 0.5819861	-11.7391339 11.71604632 11.66971014	0.00071665	0.76464434 0.76464434 0.76464434	0.384149366	1 3057893 10 16830860 4 66655798	R II	PRDM16 RSU1	Body S'UTR	shore opensea	Body-shore S'UTR-opensea	chr1:3059050-3059268	rs522305565,rs551338423,rs77192050 rs12358568 rs17086372;rs575981474,rs191031527	2;14;16	2
cg09811645 cg12349181	0.229990412 -0.20470855 0.215133294	0.40789434 0.2630794 0.41762396	-11.6488716 11.60056376	0.00072619 0.00073054 0.00074075	0.76464434 0.76464434	0.369812478 0.365478971 0.35537921	4 66655798 19 8840675 17 79057046	R II	OR2Z1 BAIAP2	IGR TSS1500 Body	opensea opensea opensea	IGR-opensea TSS1500-opensea Body-opensea		rs540832891;rs559235045;rs117038010;rs147255923	10;8;2 31;10;9;2	
cg10155058 cg19996406	0.20650888 0.20671011	0.77080825 0.6328471	11.36191333 10.98498528 10.95931117	0.00079394 0.00088843	0.76464434 0.76464434	0.304358036 0.219792934	17 37018229 8 8318774	R II F II		IGR IGR	opensea opensea	IGR-opensea IGR-opensea	chr8:144357997-144359075	rs576131835 rs570016507;rs535611968;rs193069989;rs572179613	0;1;5;14	39
cg06070970 cg23328404 cg26843612	0.244599691 0.267583896 -0.24611889	0.33938428 0.52447937 0.28993818	10.75266669	0.00095394 0.00095476	0.76464434 0.76464434 0.76464434	0.213848087 0.165107067 0.164442939	8 1.44E+08 8 19539991 6 16636157	F II F II	GLI4 CSGALNACT1 ATXN1	3'UTR Body 5'UTR	island opensea opensea	3'UTR-island Body-opensea 5'UTR-opensea	Ciro.144359075	rs1921405907rs5445078757rs5641347317rs5331011527rs184539647 rs563896454	0;3;38;43;49	31
cg03224627 cg07078225	-0.24099212 0.200458312	0.47388913 0.41978309	-10.6705906 10.59628119	0.00100158	0.76464434 0.76464434	0.145298275 0.127138193	1 1.78E+08 12 52652377	R I		IGR IGR	opensea island	IGR-opensea IGR-island	chr12:52652018-52652743	rs578065916 rs547361066 rs122006434rs557150580rs147851676		46 8
cg18994840 cg01307684 cg07171710	-0.20837899 -0.23100262 0.217864032	0.47621409 0.50866391 0.39924451	-10.5940118 -10.5035251 10.45401067	0.00103128	0.76464434 0.76464434 0.76464434	0.126580172 0.104164083 0.091759116	10 1.25E+08 4 80886143 3 237960	F II	ANTXR2 CHL1	IGR Body TSS1500	opensea island shore	IGR-opensea Body-island TSS1500-shore	chr4:80885844-80886148 chr3:238391-240140	rs192006434;rs557150580;rs147851676 rs185893895;rs190812100	38;33;2 21;49	
cg08474334 cg15358931	0.209400561 -0.23595451	0.46909025 0.30606437	10.43684178 -10.386213	0.00105334 0.00107049	0.76464434 0.76464434	0.087434589 0.074612126	1 1.57E+08 X 1.15E+08	F II R I	NTRK1	Body IGR	shore island	Body-shore IGR-island	chr1:156814881-156815792 chrX:114546353-114546645	rs548457882		22
cg07100798 cg05885623 cg09312328	0.214064723 0.219915128 0.24111878	0.80443098 0.45108137 0.50275332	10.38010364 10.29625021 10.23904988	0.00110187	0.76464434 0.76464434 0.76464434	0.073057747 0.051567155 0.036738912	14 20851317 17 77247789 6 33038766	F II	TEP1 RBFOX3 HLA-DPA1	Body S'UTR Body	opensea opensea opensea	Body-opensea 5'UTR-opensea Body-opensea		rs201216641;rs142149161 rs143749781;rs116605820;rs117688178;rs538265573 rs230120;rs1138375834;rs148836028;rs192235493;rs575057707;rs67542233;rs143577295	0;44 5;6;24;28 0;1;9;15;20;36;46	
cg11176545 cg08642292	0.201322411 -0.24842868	0.70888791 0.31911092	10.189566 -10.0044427	0.00114063 0.00121214	0.76464434 0.76464434	0.023799381 -0.02554506	18 42792594 15 33873247	R II R II	SLC14A2 RYR3	TSS1500 Body	opensea opensea	TSS1500-opensea Body-opensea		rs538757000 rs147192813;rs553683138	35;2	2
cg14153919 cg04989524 cg10803922	0.203040299 0.205222735 0.228588386	0.61673685 0.34414517 0.66574997	9.984030554 9.977569977 9.853289904	0.001223	0.76464434 0.76464434 0.76464434	-0.03107791 -0.03283296 -0.06695937	15 78631963 X 1.23E+08 11 44719192	R II	CRABP1 LOC101928402	TSS1500 Body IGR	shore island opensea	TSS1500-shore Body-island IGR-opensea	chr15:78632669-78633108 chrX:123093923-123094582	rs563119470		0
cg08876508 cg02885259	-0.21048968 -0.22261988	0.53663421 0.41248609	-9.80770396 -9.78709217	0.00129459 0.00130364	0.76464434 0.76464434	-0.07965302 -0.0854239	17 34068044 3 1.6E+08	R II R II	RASL10B ARL14	Body 1stExon	island opensea	Body-island 1stExon-opensea	chr17:34068043-34068668	rs200365146;rs199649896;rs587644033	37;30;2	-
cg08985499 cg22270262 cg05216340	0.221352549 -0.20729674 -0.22743062	0.39636328 0.72490377 0.32619542	9.476640609 -9.29568858 -9.2269213		0.76464434 0.76464434 0.76464434	-0.17477245 -0.22902618 -0.25008066	10 1.2E+08 14 98153031 4 44427777	R II	LOC100129345 KCTD8	IGR TSS200 Body	opensea opensea opensea	IGR-opensea TSS200-opensea Body-opensea		rs10886150;rs182051485;r;567199464 rs148394160;rs541632711;rs561438649;rs186729962 rs140027518;r16856912;r7691376;rs46871985	7;21;29 50;11;2;1 1;9;31;41	
cg08603868 cg24392939	0.259418674	0.29387226	9.179787148 -9.101141	0.00161104 0.0016574	0.76464434 0.76464434	-0.26465342 -0.28922895	11 1.08E+08 3 97591258	R II	NC100	IGR IGR	opensea opensea	IGR-opensea IGR-opensea		rs548781828;rs567881488 rs142470903	12;2	0
cg03899098 cg23692540 cg26211349	-0.20408131 -0.21755812 0.213740285	0.40721041 0.55422379 0.3707436	-8.87130373 -8.78388616 8.69850887		0.76464434 0.76464434 0.76464434	-0.36295931 -0.39177039 -0.42032923	15 98193650 9 33637473 17 77404555	F II	HRNBP3	IGR IGR 5'UTR	shelf opensea opensea	IGR-shelf IGR-opensea 5'UTR-opensea	chr15:98196021-98196391	n184835054;rs566651132 rs191007824;rs55723277 rs58852646;rs9907346;rs537992591	0;22 1;44 0;6;49	
cg12710648 cg15474337	-0.28553067 -0.21043728	0.34987166 0.46713277	-8.68327347 -8.67851238	0.00193472 0.00193821	0.76464434 0.76464434	-0.42546973 -0.42707892	1 7308091 19 50848247	R II	CAMTA1 NAPSB	Body TSS1500	opensea opensea	Body-opensea TSS1500-opensea		rs140576925;rs144392678 rs73932461;rs533188427;rs545359210;rs73932462	26;2 44;39;2;1	
cg01116873 cg04604383	0.203519983	0.75604646	8.648134539 -8.61225431	0.00198763	0.76464434	-0.43737737 -0.44961091	7 1.21E+08 11 55577412	R II		IGR IGR	opensea opensea	IGR-opensea IGR-opensea		rs566634677;rs538798698;rs559007500 rs80137132 rs87764945;rs587644362;rs587701333	40;24;1	38
cg00774578 cg20367065 cg20657826	-0.21232698 0.207686174 0.218291264	0.63147816 0.52325601 0.50024207	-8.54805366 8.486937916 8.464778464		0.76464434 0.76464434 0.76464434	-0.4716906 -0.4929386 -0.50069856	19 54580929 3 97983253 X 15928372	R II	TARM1 OR5H6	Body 1stExon IGR	opensea opensea opensea	Body-opensea 1stExon-opensea IGR-opensea		rs137937308;rs577340762;rs201340537;rs113835025;rs563136835;rs201236351;rs36040433;rs	1;9;35 1/ 48;46;26;24;17;6;2;1	
cg15977716 cg23569180		0.73775517		0.00222408	0.76464434 0.76464434	-0.5513663	12 1.33E+08 7 37955508	F II	SFRP4	IGR Body	shelf shore	IGR-shelf Body-shore	chr12:132922117-132922443 chr7:37955622-37956555	: rs148867669 rs532952386;rs183186446;rs569781586 rs536156736;rs556111623	4;25;32	1
cg15645815 cg18340923 cg02864688	-0.20080452 0.202613251 0.216879214	0.64184529 0.33504027 0.34639263	-8.27498892 8.255171495 8.230279256		0.76464434 0.76464434 0.76464434	-0.56840112 -0.57560073 -0.5846795	21 37961337 14 93896401 1 11752342	R II	UNC79 MAD2L2	IGR 5'UTR TSS1500	opensea shore island	IGR-opensea 5'UTR-shore TSS1500-island	chr14:93896736-93897466 chr1:11750701-11752651	rs146842606	0;1	1
cg20569128 cg12016495	-0.23236754	0.53055808		0.00232629	0.76464434 0.76464434	-0.59071858 -0.59256796	16 17162569			IGR IGR	island opensea	IGR-island IGR-opensea	chrX:136655909-136657085	rs562780546;rs74012921	0;35	
cg14531496 cg05549773 cg23749034	-0.21380297 0.206720341 0.256049084	0.44517716 0.49684065 0.51216527	-8.20076929 8.189478996 8.187744947		0.76464434 0.76464434 0.76464434	-0.59549391 -0.59964627 -0.60028474	5 1.48E+08 5 1183037 6 35165242			IGR IGR IGR	opensea opensea opensea	IGR-opensea IGR-opensea IGR-opensea		rs77208124 rs5510723347s5693194517s533356658	41;38;27	16
	0.224581999	0.43038214		0.00239439	0.76464434 0.76464434	-0.6084162 -0.61918179	12 5330804 8 1.42E+08			IGR IGR	shore	IGR-opensea IGR-shore	chr8:142427854-142428351	rs564537320;rs533472597;rs7296125 rs188620952;rs55910461	22;14;2 40;32	
cg25274008 cg24916850 cg16867568	0.219683575 -0.22515622 0.270309097	0.63477948	8.125735458 -8.05699081 7.967188485		0.76464434 0.76464434 0.76464434	-0.62324511 -0.64899409 -0.68310481	1 33648648 2 2.17E+08 19 42471655		MREG ATP1A3	TSS1500 TSS1500 Body	shore shore opensea	TSS1500-shore TSS1500-shore Body-opensea	chr1:33646613-33647878 chr2:216877899-216878352	rs547727252;rs182869484 rs371698093;rs577933395	10;2	
cg07122460 cg14196261	-0.22941931 0.20410779	0.48061348 0.41651991	-7.90715781 7.898811685	0.00263805	0.76464434 0.76464434	-0.70621147 -0.70944355		F II	ACOT9	IGR TSS200	opensea island	IGR-opensea TSS200-island	chrX:23761070-23761610	rs147659431,rs183753536 rs542511279rs189338957	1;48	
cg24176731 cg12615982 cg09608709	0.215818964 0.226327192 -0.21889224	0.55304063 0.26275651 0.50737737	7.858783798 7.849044828 -7.84052824		0.76464434 0.76464434 0.76464434	-0.72501139 -0.72881592 -0.73214834	11 73357164 3 1.69E+08 20 34949883	F II	PLEKHB1 TERC DLGAP4	TSS200 TSS1500 5'UTR	opensea shore opensea	TSS200-opensea TSS1500-shore 5'UTR-opensea	chr3:169482338-169483052	rs542511379/rs18938957 rs546654815 rs55940036/rs529627903/rs144487595	34;2 33;2;1	12
cg26345912 cg23594656	-0.22491782 -0.22703987	0.4483791 0.53166829	-7.8036842 -7.78242197	0.00274436 0.00276887	0.76464434 0.76464434	-0.74662327 -0.75501995	5 1.65E+08 7 65796392	R II R II	TPST1	IGR Body	opensea opensea	IGR-opensea Body-opensea		rs10064661;rs561269436;rs531718922;rs549876827;rs571321298;rs532625274	34;30;21;20;19;10	
cg02651643 cg01225622 cg02834433	-0.28527059 -0.2060614 -0.24173168	0.40179846 0.4184802 0.63359261	-7.78036045 -7.76176849 -7.72400071		0.76464434 0.76464434 0.76464434	-0.75583577 -0.76320681 -0.77825601	10 26461882 14 75555285 15 28017186	R II	MYO3A NEK9 OCA2	Body Body Body	opensea opensea shore	Body-opensea Body-opensea Body-shore	chr15:28015346-28015795	rs555962390 rs148482689;rs370650196	40;18	45
cg05725721 cg26189637	-0.22038728 -0.25296213	0.45580846	-7.69765145 -7.69324442	0.00286942 0.00287477	0.76464434 0.76464434	-0.78881571 -0.79058673	3 1.61E+08 19 20214032	F II F II	B3GALNT1 ZNF90	TSS1500 Body	shore opensea	TSS1500-shore Body-opensea	chr3:160822494-160823260	rs554879541;rs567947553;rs537016945;rs1725924;rs62107004;rs188657413	1;15;21;44;45;49	
cg04903930 cg09179637 cg23424136	-0.20956896 0.237248797 0.213770607	0.57731849 0.5639564 0.30979674			0.76464434 0.76464434 0.76464434	-0.79174015 -0.80454244 -0.81848426	4 78352562 6 40492307 7 25765894	R II	LRFN2	IGR 5'UTR IGR	opensea opensea opensea	IGR-opensea 5'UTR-opensea IGR-opensea		rs145520232;rs551636641;rs571432298 rs679821;rs574130059 rs65381606	47;17;2 42;1	0
cg18686270 cg07079560	-0.23160168 -0.22595633	0.66011221 0.6573995	-7.54184604 -7.49655873	0.00306673 0.00312732	0.76464434 0.76464434	-0.85228716 -0.87107259	3 1.46E+08 5 53735028	F II F II	PLSCR1	S'UTR IGR	shelf opensea	5'UTR-shelf IGR-opensea	chr3:146262126-146262505	rs545677412;rs16858468 rs188654175;rs139687029;rs7727143	0;43 1;16;28	
cg01882539 cg27312789 cg10514207	0.201634618 -0.20470696 0.200767273		7.434514549 -7.4298669 7.424363496		0.76464434 0.76464434 0.76464434	-0.89705972 -0.89901815 -0.90133932	17 32481208 11 11809714 13 49384181	F II F II	ACCN1	Body IGR IGR	shelf opensea opensea	Body-shelf IGR-opensea IGR-opensea	chr17:32484007-32484280	rz28592640;rz148777665;rz144806363 rs574849290;rs558205679 rs55333499;rz185069149	27;20;1 6;51 1;43	
cg09496161 cg09023235	-0.20941493 -0.20528135	0.43897947 0.46966197	-7.39023961 -7.36441576	0.0032757 0.0033131	0.76464434 0.76464434	-0.91578354 -0.92677406	19 54155607 18 49922133	F II R II	DCC	IGR Body	shelf opensea	IGR-shelf Body-opensea	chr19:54151076-54152241	rs575844374 rs546401995;rs137929648;rs117572729;rs188671830	29;19;17;13	0
cg25051970 cg17597740 cg25959317	0.201818105 -0.2155002 0.242921299	0.62866083 0.27712826 0.65352028	7.334849151 -7.32309181 7.28172571		0.76464434 0.76464434 0.76464434	-0.93942095 -0.94446898 -0.96231572	10 1.35E+08 4 1.89E+08 2 2.09E+08	R II	SCART1 TRIML1	Body TSS1500 IGR	shelf opensea opensea	Body-shelf TSS1500-opensea IGR-opensea	chr10:135270783-135271061	: r2253522 rs566580703 rs542717212		24 38 11
cg25083484 cg02408697	-0.23178951 0.213791796	0.35514353 0.71131262	-7.27801016 7.255100101	0.00344225 0.00347757	0.76464434 0.76464434	-0.96392532 -0.97387428	5 23384883 10 1416920	R II F I	ADARB2	IGR Body	opensea shore	IGR-opensea Body-shore	chr10:1415976-1416249	rs527672382 rs189357386;rs549665260;rs568882738;rs11250483	1;19;39;42	13
cg23839338 cg19749975 cg00011225	0.202015206 0.229977262 -0.23026018	0.56136748 0.57524935 0.45456707	7.249456856 7.211142012 -7.20522911		0.76464434 0.76464434 0.76464434	-0.97633132 -0.99308048 -0.99567574	14 24834668 1 71547563 2 2.2E+08	F II	NFATC4 ZRANB2 WNT6	TSS1500 TSS1500 Body	shore shore island	TSS1500-shore TSS1500-shore Body-island	chr14:24835810-24836220 chr1:71546486-71546783 chr2:219738081-219738788	rs142887365;rs557642574 rs184816736;rs574415326;rs189240599	18;32 1;9;14	
cg09249159 cg15424233	-0.23191924 -0.20291355	0.43985857 0.61877663	-7.08116243 -7.07646123	0.00376142 0.0037695	0.76464434 0.76464434	-1.05078374 -1.05289669	3 1.79E+08 2 9865477	R II R II		IGR IGR	opensea opensea	IGR-opensea IGR-opensea		rs568380684 rs545032306;rs577601158;rs9789690;rs560113583;rs528665051;rs548801633;rs143229290	35;33;31;30;23;9;1	12
cg12945378 cg18217594 cg08171505	-0.2098917 0.226708658 -0.20671556	0.73425358 0.53808458 0.48251767	-7.05130385 7.005908161 -7.00581673		0.76464434 0.76464434 0.76464434	-1.06423478 -1.08482734 -1.08486899	12 1.18E+08 12 9293085 x 70883292	R II	KSR2 BCYRN1	Body IGR Body	shore opensea opensea	Body-shore IGR-opensea Body-opensea	chr12:118198767-118199287	rs577461650		1
cg08303110 cg09839120	-0.21215111 -0.22982956	0.47102354 0.56573469	-6.97444963 -6.93507468	0.00395032 0.00402307	0.76464434 0.76464434	-1.09919912 -1.11730556	4 68033903 7 1.5E+08	R II F II		IGR IGR	opensea opensea	IGR-opensea IGR-opensea		rs111352377 rs569647745		9 28
cg11761627 cg21396956 cg12490910	-0.20550741 -0.26783899 -0.22602614	0.27509262 0.33049231 0.41409715	-6.93238607 -6.88481979 -6.85418813	0.00411843	0.76464434 0.76464434 0.76464434	-1.11854672 -1.14060752 -1.15491749	5 62283805 18 56340167 7 6712945	F II	MALT1	IGR Body IGR	opensea shore opensea	IGR-opensea Body-shore IGR-opensea	chr18:56338211-56339277	rs148964414;rs550835574;rs113959715 rs148303978	32;23;21	1
cg04328144 cg24000300	0.234489788 0.238826665	0.32097569 0.55151053	6.852772779 6.849993905	0.00418075 0.00418621	0.76464434 0.76464434	-1.15558065 -1.15688321	6 70468286 8 49014558	R II R II	LMBRD1	Body IGR	opensea opensea	Body-opensea IGR-opensea		rs534853428;rs73486006;rs146968588;rs568212006;rs537352504 rs143743819;rs541530138	41;30;24;24;1 18;2	
cg24208650 cg04169075 cg01188753	-0.2017739 -0.21022911	0.52899279 0.3762505	-6.81360105 -6.73212042	0.00425857 0.00442646	0.76464434 0.76464434 0.76464434	-1.17400402 -1.21275903 -1.2143017	3 50515965 15 67215905 20 47897068	R II	CACNA2D2 C20orf199	S'UTR IGR Body	opensea opensea shore	5'UTR-opensea IGR-opensea Body-shore	chr20:47894197-47895199	rs528777980 rs561533516		15 35
cg03468480 cg24366564	-0.23195083 0.2435185	0.54869577 0.43205139	-6.69971524 6.697044299	0.00449557 0.00450133	0.76464434 0.76464434	-1.22833643 -1.22962458	22 37386714 17 2843149	R II R I	RAP1GAP2	IGR Body	opensea opensea	IGR-opensea Body-opensea		rs557751028;rs144045154 rs139091470;rs538011045	47;37 44;29	
cg03100209 cg11050156 cg19858756	0.20476162 -0.20283308 -0.21290004	0.66072005 0.56778945 0.43120255	6.69650096 -6.69363762 -6.6772445	0.0045025 0.00450868	0.76464434 0.76464434 0.76464434	-1.2298867 -1.2312685 -1.23919377	19 49921142 3 1.24E+08 5 1.56E+08	R II	CCDC155 CCDC14 SGCD	3'UTR 5'UTR Body	opensea shore opensea	3'UTR-opensea 5'UTR-shore Body-opensea	chr3:123679785-123680481	rs565287530 rs5478496265rs372873046 rs571004672rs537274047rs145838921;rs150942951	2;1 0:38:39:49	2
cg22328256 cg26969102	-0.26974728 -0.27237019	0.39649322 0.39954371	-6.6717958 -6.63698288	0.00455622 0.00463333	0.76464434 0.76464434	-1.24183333 -1.25876176	6 28757381 19 56954002	F II R II	ZNF667	IGR Body	shelf opensea	IGR-shelf Body-opensea	chr6:28753869-28754138	rs5710046727s5372740477s1458389217s150942951 rs115750861 rs359144747s149168669	0;38;39;49 41;2	27
cg12778228 cg26847392 cg03354203	0.224611478 -0.25095446 0.279180911	0.54794396 0.41130279	6.614799355 -6.60551375 6.586182647	0.00468333 0.00470446	0.76464434 0.76464434 0.76464434	-1.26960664 -1.2741595 -1.2836633	17 16341601 11 55762735 1 30128888	R II	NCRNA00188 OR5F1	TSS1500 TSS1500 IGR	shore opensea opensea	TSS1500-shore TSS1500-opensea IGR-opensea	chr17:16342504-16342897	rs183027316;7s529218163 rs527869828;7s548048721;7s564205068;7s193224152	2;1 1:17:19:33	
cg10791959 cg04318989	-0.21885732 0.226369572	0.40207824 0.65712598	-6.58448446 6.566296067	0.00475277 0.00479507	0.76464434 0.76464434	-1.28449983 -1.29347625	3 1.35E+08 1 2.19E+08	R I R II	EPHB1 LYPLAL1	Body TSS1500	opensea shore island	Body-shore TSS1500-island	chr3:134514085-134515980 chr1:219347109-219347572	rs187690958;rs552191147;rs569218807;rs146324348	40;26;16;13	
cg01999908 cg08514779 cg03545757	0.2011014 0.216565582 0.20884087	0.74017242 0.67212977	6.561076165 6.502519698	0.0048073 0.00494723	0.76464434 0.76464434 0.76464434	-1.29605807 -1.32519509 -1.34284458	7 1.27E+08 13 1.12E+08 16 1366304	R II	PAX4 UBE21	TSS1500 IGR Body	opensea opensea shore	TSS1500-opensea IGR-opensea Body-shore	chr16:1363813-1364496	rs5382555267s327513;rs565689557 rs564339049 rs51003222:rs4638578:rs4017714:rs144204134:rs566948700:rs76747201:rs111956252	1;14;39	17
cg22404419 cg14551114	-0.20417013 -0.21015716	0.55531401 0.51392138	-6.44291392 -6.40345739	0.00509504 0.005196	0.76464434 0.76464434	-1.35518625 -1.37522565	9 79785806 13 52368022	R II F II	DHRS12	IGR Body	opensea opensea	IGR-opensea Body-opensea	10.13030131304430	rs549273205;rs531773966 rs139361426;rs570042307	9;2 0;32	
cg08904591 cg10055165 cg03259333	-0.21369349 -0.24445935 -0.26027978	0.48336631 0.530922 0.58206524		0.00524425 0.00525179 0.00532675	0.76464434 0.76464434 0.76464434	-1.38468034 -1.38615223 -1.4006695	15 96855873 11 1.26E+08 5 1.79E+08	F II	NR2F2-AS1 PATE2 ADAMTS2	Body TSS1500 Body	opensea opensea shore	Body-opensea TSS1500-opensea Body-shore	chr5:178593903-178594656	rs531745232;rs548384719;rs568381155;rs534247714;rs77736520 rs548717091;rs540100153 rs54963497	0;1;5;34;44 1;16	1
cg15636519					0.76464434	-1.40999556	2 1.92E+08		STAT4	3'UTR		3'UTR-opensea		rs3024907		24

Name Name<			0.55521425	-6.3337964	0.00538054	0.76464434	-1.4109729	15 32954373 R	II SCG5	Body	opensea	Body-opensea		rs180896699;rs529718089	2;1	
Alt </td <td>cg06266516</td> <td>-0.26889318</td> <td>0.38612641</td> <td>-6.28948936</td> <td>0.00550227</td> <td>0.76464434</td> <td>-1.43395653</td> <td></td> <td></td> <td>IGR</td> <td>opensea</td> <td>IGR-opensea</td> <td></td> <td>rs140649679;rs185125452;rs145814385;rs137929049</td> <td></td> <td>29</td>	cg06266516	-0.26889318	0.38612641	-6.28948936	0.00550227	0.76464434	-1.43395653			IGR	opensea	IGR-opensea		rs140649679;rs185125452;rs145814385;rs137929049		29
NNN <td>cg18316031</td> <td>0.237012953</td> <td>0.50268557</td> <td>6.260392142</td> <td>0.00558413</td> <td>0.76464434</td> <td>-1.44915594</td> <td></td> <td>II DYNCIII</td> <td>IGR</td> <td>opensea</td> <td>IGR-opensea</td> <td>chr7-27135342-27136736</td> <td>rs78503251;rs542132807;rs144907806;rs530976001</td> <td>0;5;27;31</td> <td></td>	cg18316031	0.237012953	0.50268557	6.260392142	0.00558413	0.76464434	-1.44915594		II DYNCIII	IGR	opensea	IGR-opensea	chr7-27135342-27136736	rs78503251;rs542132807;rs144907806;rs530976001	0;5;27;31	
Name Name<	cg16620039 cg26312935	-0.21842999 0.206493409	0.47931446 0.48949059	-6.2408711 6.195070319	0.00563991 0.00577362	0.76464434 0.76464434	-1.45940036 -1.48358624	14 1.02E+08 R 15 59279406 F	II II RNF111		opensea	IGR-opensea TSS1500-shore		rs117159770;rs370598031;rs182489377 rs529901828;rs62002482	10;2;1 19;35	
def	cg05672337	-0.20406916	0.42716491	-6.19054788	0.00578704	0.76464434	-1.48598588	12 86580421 F			opensea opensea	S'UTR-opensea		rs570043794	1;40	
Name <td>cg05334656</td> <td>0.230778238</td> <td>0.62739696</td> <td>6.162738464</td> <td>0.00587044</td> <td>0.76464434</td> <td>-1.50078738</td> <td>4 4866047 R</td> <td>11</td> <td>IGR</td> <td></td> <td>IGR-shore</td> <td>chr4:4866438-4866813</td> <td>rs186128404</td> <td></td> <td>20</td>	cg05334656	0.230778238	0.62739696	6.162738464	0.00587044	0.76464434	-1.50078738	4 4866047 R	11	IGR		IGR-shore	chr4:4866438-4866813	rs186128404		20
def aMM	cg20995564 cg15743533	-0.29824085 0.216659021	0.49851915 0.52401727	-6.13056671 6.108274461	0.00596884 0.00603826	0.76464434 0.76464434	-1.5180092 -1.53000478	2 1.45E+08 R 20 815345 F	II ZEB2	Body TSS1500	opensea	Body-opensea TSS1500-shore	chr20:814120-814755	rs549658388;rs139922284	48;11	
NetN	cg10950266	-0.23563261	0.24846149	-6.08847496	0.00610077	0.76464434	-1.54070204 >	1.01E+08 F		TSS200		TSS200-island	chrX:100673191-100673673			
Name <t< td=""><td>cg25361961</td><td>0.228875351</td><td>0.48163396</td><td>6.065882403</td><td>0.00617312</td><td>0.76464434</td><td>-1.55295806</td><td>19 58070048 F</td><td>11</td><td>IGR</td><td></td><td>IGR-shore</td><td>chr19:58070553-58071273</td><td>rs10221464</td><td></td><td>16</td></t<>	cg25361961	0.228875351	0.48163396	6.065882403	0.00617312	0.76464434	-1.55295806	19 58070048 F	11	IGR		IGR-shore	chr19:58070553-58071273	rs10221464		16
111	cg06787637	-0.20682356	0.62966079	-6.02889394	0.00629394 0.00635771	0.76464434	-1.57313868	8 86347111 F 1 3144113 F	II I PRDM16	IGR		IGR-shelf		rs11985029		5
NameNam	cg10105501	-0.20458819	0.52871546	-5.94928094	0.00656437	0.76464434	-1.61706514	1 42836436 F	11	IGR	opensea	IGR-opensea				
NNN <th< td=""><td>cg12545533</td><td>0.200320975</td><td>0.65428925</td><td>5.907603107</td><td>0.00671184</td><td>0.76464434</td><td>-1.64033114</td><td>1 1.14E+08 R</td><td>II PTPN22</td><td>Body</td><td>opensea</td><td>Body-opensea</td><td></td><td></td><td>26;31;38;39;48</td><td>20</td></th<>	cg12545533	0.200320975	0.65428925	5.907603107	0.00671184	0.76464434	-1.64033114	1 1.14E+08 R	II PTPN22	Body	opensea	Body-opensea			26;31;38;39;48	20
	cg24559073	-0.20461211	0.40930942 0.68459014	-5.87258364 -5.8646166	0.00683902	0.76464434	-1.66002558 >	47342471 F		TSS200 IGR	island	TSS200-island		rs138226527		2
	cg22549339	-0.21371388	0.34311369	-5.82906286	0.00700137	0.76464434	-1.68468778	15 27891472 F		IGR	opensea opensea	IGR-opensea		rs141584988;rs188257383	10;48	
<th< td=""><td>cg20630344</td><td>0.215846151</td><td>0.39350856</td><td>5.780458193</td><td>0.00718852</td><td>0.76464434</td><td>-1.71247799</td><td>16 80604078 F</td><td>II LINC01227</td><td>Body</td><td>opensea</td><td>Body-opensea</td><td>chr1:63782394-63790471</td><td></td><td>6;38</td><td></td></th<>	cg20630344	0.215846151	0.39350856	5.780458193	0.00718852	0.76464434	-1.71247799	16 80604078 F	II LINC01227	Body	opensea	Body-opensea	chr1:63782394-63790471		6;38	
Image No. 1 No. 1 No. 1 <t< td=""><td>cg20495964</td><td>0.208326359</td><td>0.37950815</td><td>5.724891855</td><td>0.00741034</td><td>0.76464434</td><td>-1.74457172</td><td>6 36744880 F</td><td></td><td>Body</td><td>opensea opensea</td><td>Body-opensea</td><td></td><td>rs186890</td><td>33;41</td><td></td></t<>	cg20495964	0.208326359	0.37950815	5.724891855	0.00741034	0.76464434	-1.74457172	6 36744880 F		Body	opensea opensea	Body-opensea		rs186890	33;41	
Name Name Nam Name	cg12788111 cg18395637	-0.21558514	0.32310698	5.687394133 -5.68245407	0.00758562	0.76464434	-1.76931759	4 1.13E+08 F	II RNF111 II	IGR	opensea	IGR-opensea	chr15:59279741-59280720	rs529901828;rs62002482 rs190457554	32;48	12
	cg00576773	0.204788738	0.50634111	5.66167251	0.00767338	0.76464434	-1.78151039	15 89909904 R		TSS1500		TSS1500-shore	chr15:89910521-89912177	rs560153254		2
	cg21456399	0.228107917	0.63561721	5.6335584	0.00779416	0.76464434	-1.79808421	2 2.3E+08 F	II DNER	Body		Body-opensea			17;18;38;39	20
Image Math 	cg04109543	0.262706781	0.61974662	5.625547454	0.00782902	0.76464434	-1.80282351	6 10422874 F	11	IGR	shore shore	IGR-shore		rs529375746;rs551015906		25
No. No. No. No. No. No. No. No. No. No. <	cg24786671	-0.2109805	0.43899635	-5.58550838	0.00800623	0.76464434	-1.82662234	21 31722001 R		TSS1500		TSS1500-opensea		rs78545747	38;11;7	
Name Name Name Name	cg17259303	0.232210241	0.48817256	5.555450769	0.00814262	0.76464434	-1.84461125	3 1.57E+08 R		IGR		IGR-opensea		rs530570534	14;12;2	2
	cg12347792	0.206434098	0.52254596	5.472289343	0.00853564	0.76464434	-1.89493801	4 1.86E+08 F		TSS1500		TSS1500-shore	chr4:186392574-186393184	rs28429774		49
Same al	cg21498923	0.20203871	0.41722138	5.469838875	0.00854759	0.76464434	-1.89643347	20 2187540 R	II LOC388780	TSS200	island	TSS200-island		rs556981361;rs148299112	47;27	
Matrix Mat	cg07820966	0.200907943	0.48518552	5.450551382	0.00864232	0.76464434	-1.9082293	4 1.86E+08 R	II II WNT3A	IGR	opensea	IGR-opensea		rs555561029;rs572260369;rs534860733;rs75748238;rs73873171		44
Name Name Name Name N	cg06445384 cg09675542	0.244576156 0.21548971	0.60898635 0.54178282	5.43104538 5.412317842	0.00873949	0.76464434	-1.9202044 -1.93174495	6 1.59E+08 F 7 19548878 R		IGR IGR	opensea	IGR-opensea IGR-opensea		rs4721778;rs116670532;rs540808487;rs561660382	38;37;8;1	
	cg11845620	-0.20058567	0.56977967	-5.39194415	0.00893847	0.76464434	-1.9443484	17 37197733 F		IGR	opensea opensea	IGR-opensea		rs117807470		1 5
Name	cg10236447	-0.24687395	0.40363771	-5.38633021	0.00896751	0.76464434	-1.94783017 >	53077495 F			opensea	TSS1500-opensea	chr19:56125349-56128167			
	cg16247474	0.225793136	0.71516313	5.38265361	0.00898659	0.76464434	-1.95011249	5 1.74E+08 R	II LINC01411		opensea	Body-opensea	chr11:82400585-82400858	rs139415988;rs149628702		23
Name Nam	cg19439713 cg23552876	0.205009123	0.31381429	5.345531592	0.00918217	0.76464434	-1.97324972	17 26697752 R	II II SARM1		shore	TSS1500-shore	chr17:26698359-26699557	rs16964236	10;11;16;40	
Success State Success State Success State Success S	cg12806613	0.213013738	0.23800882	5.31792638	0.00933111	0.76464434	-1.99056572	1 63540205 F			opensea	IGR-opensea			1.11.42	14
	cg24759795	-0.26055389	0.5503056	-5.28935584	0.0094885	0.76464434	-2.00858708	8 1.14E+08 R	II CSMD3	Body	shore	Body-shore		rs114251401;rs1478675;rs187400358;rs551518133	51;18;8;3	
	cg10595547	0.257800558	0.33859158	5.27261188	0.0095823	0.76464434	-2.01919609	10 1.19E+08 F	1	IGR	shore	IGR-shore	chr10:119311204-119312104	rs71475030;rs371459821		2
with with with with with with with with	cg21482921	0.226252998	0.40745822	5.251172735	0.00970413	0.76464434	-2.03283147	10 5084043 F		IGR	opensea	IGR-opensea		rs552389111;rs144104296;rs114115777;rs184467508;rs568378496	0;1;28;35;46	
with with with with with with with with	cg18861197	-0.2214465	0.52924505	-5.23014502	0.00982553	0.76464434	-2.0462616	8 27209336 R	II PTK2B	5'UTR	opensea	5'UTR-opensea			0,1,0	43
Math	cg04490079 cg16203262	0.295873804 0.271322115	0.61188059 0.4670498	5.149664995 5.139279076	0.01030829 0.01037275	0.76464434 0.76464434	-2.09818428 -2.10494561	3 98216207 R 13 78495961 F	II OR5K2 II EDNRB	TSS1500 5'UTR	opensea shelf	TSS1500-opensea 5'UTR-shelf	chr13:78492425-78493382	rs191372428;rs573187805 rs147843823;rs533251846		
Name	cg06477065	-0.21440166	0.69755451	-5.13355004	0.01040853	0.76464434	-2.10868126	11 46406856 R	II CHRM4	1stExon	shore	1stExon-shore		rs200378895;rs2229163	49;1	2
witz witz<	cg04017943	-0.24133938	0.34745605	-5.10278158	0.01060338	0.76464434	-2.12881704	2 53437876 F	II BCAS3 II	IGR	opensea	IGR-opensea		rs532294671	44:19	
state <td>cg13516479</td> <td>0.208810791</td> <td>0.5453429</td> <td>5.07786752</td> <td>0.01076454</td> <td>0.76464434</td> <td>-2.14521223</td> <td>6 1.22E+08 F</td> <td>II MARCH4</td> <td>IGR</td> <td></td> <td>IGR-opensea</td> <td></td> <td>rs149391054</td> <td></td> <td>17</td>	cg13516479	0.208810791	0.5453429	5.07786752	0.01076454	0.76464434	-2.14521223	6 1.22E+08 F	II MARCH4	IGR		IGR-opensea		rs149391054		17
Norm Norm Norm Norm N	cg00407329	0.209192682	0.53201249	5.07311086	0.01079566	0.76464434	-2.14835172	6 1.01E+08 R		Body	shore	Body-shore		rs558514962;rs5772563;rs113398528;rs574407600;rs543065823	41;12;10;7;2	
	cg05833905	-0.21669216	0.38169653	-5.04179079	0.01100343	0.76464434	-2.16909814	6 1.24E+08 R	II TRDN	Body	opensea	Body-opensea	chr5:162932454-162932946	** 79015109***192156050***570101567***70177409	12-21-26-46	
Norm Norm Norm Norm N	cg24536007	0.221514624	0.59669988	5.023201264	0.01112914	0.76464434	-2.18147333	17 32309520 F		Body		Body-opensea		rs550156246;rs570015025		11
Norm Norm <th< td=""><td>cg10125277</td><td>0.260572624</td><td>0.62988622</td><td>4.964199491</td><td>0.01154035</td><td>0.76757652</td><td>-2.22105727</td><td>11 1.18E+08 R</td><td></td><td>Body</td><td>opensea</td><td>Body-opensea</td><td></td><td>rs549952198</td><td></td><td>32 15</td></th<>	cg10125277	0.260572624	0.62988622	4.964199491	0.01154035	0.76757652	-2.22105727	11 1.18E+08 R		Body	opensea	Body-opensea		rs549952198		32 15
B B	cg03425812	-0.26624504	0.58735298	-4.93881353	0.01172317	0.76802395	-2.23823289	15 45005363 R	II II B2M	Body		Body-shore	chr15:45003460-45004345	rs576358838;rs114697986	21;2	
	cg03230989	-0.25959774	0.36196258 0.44211062	-4.9257549 -4.9247786	0.01181864 0.01182581	0.76802395	-2.24710217 -2.24776619	9 26066126 F		TSS1500		TSS1500-opensea		rs549615519;rs569456109	46;2	
	cg07189394	-0.21379242	0.44192695	-4.91806483	0.01187531	0.76802395	-2.25233604	3 1.32E+08 F		IGR		IGR-opensea		rs77034109;rs545710267;rs560643538	18;24;41	
BARDER BARDER BARDER BARDER BARDER BARDER BARDER BARDER BARDER BARDER BARDER BARDER BARDER BARDER BARDER BARDER	cg24018963	-0.2094569	0.34418282	-4.89782736	0.01202612	0.76802395	-2.26614833	15 83226022 F	II CPEB1	Body		Body-opensea		rs548832200	48;1	15
NUMB NUMB NUMB NUMB N	cg23008023	-0.20771572	0.74090856	-4.85632451	0.01234302	0.76802395	-2.29465049	10 1.25E+08 R	11	IGR	opensea	IGR-opensea	chr6:34111735-34113944	rs190540013;rs551970092;rs138074324;rs180695528	48;43;32;1	15
	cg21803548	-0.20124681	0.4328035	-4.84042626	0.0124672	0.76806503	-2.3056317	3 1.44E+08 R	11	IGR	opensea	IGR-opensea		rs58537913		26
Norm Norm Norm Norm N	cg04786038	0.206477557	0.32669607	4.838419962	0.01248298	0.76806503	-2.30701998	18 2147655 F	11	IGR	opensea	IGR-opensea			47;26;16	1
Barbon Barbon Barbon Barbon </td <td>cg08869206</td> <td>-0.23796598</td> <td>0.55563303</td> <td>-4.82123473</td> <td>0.01261921</td> <td>0.76806503</td> <td>-2.31893445</td> <td>7 57521583 R</td> <td></td> <td>Body</td> <td>opensea</td> <td>Body-opensea</td> <td></td> <td>rs11972967;rs117553144;rs184915495;rs35357268 rs189965512;rs9411251</td> <td>33;25;13;2 20:27</td> <td></td>	cg08869206	-0.23796598	0.55563303	-4.82123473	0.01261921	0.76806503	-2.31893445	7 57521583 R		Body	opensea	Body-opensea		rs11972967;rs117553144;rs184915495;rs35357268 rs189965512;rs9411251	33;25;13;2 20:27	
bit bit<	cg10277551 cg19744045	0.235196104 -0.20856726	0.46261275 0.34504745	4.808429101 -4.80464615	0.01272194 0.01275248	0.76806503 0.76806503	-2.32783935 -2.33047437	6 99871388 F 4 22457802 R	II ADGRA3	5'UTR Body	shore opensea	5'UTR-shore Body-opensea				17
char char <td>cg06606091</td> <td>0.201249784</td> <td>0.50620744</td> <td>4.792208608</td> <td>0.01285358</td> <td>0.76806503</td> <td>-2.33915188</td> <td>16 3082291 F</td> <td>II LOC100128770</td> <td>TSS200</td> <td>shelf</td> <td>TSS200-shelf</td> <td>chr11:66059287-66059935 chr16:3078141-3078553</td> <td>rs552611889;rs2717713;rs2717712</td> <td>4;36;48</td> <td></td>	cg06606091	0.201249784	0.50620744	4.792208608	0.01285358	0.76806503	-2.33915188	16 3082291 F	II LOC100128770	TSS200	shelf	TSS200-shelf	chr11:66059287-66059935 chr16:3078141-3078553	rs552611889;rs2717713;rs2717712	4;36;48	
BADDE BADDE BADDE	cg26112621 cg03788849	-0.20708602 0.24897775	0.48691423 0.36287702	-4.78472302 4.752527762	0.01291491 0.01318293	0.76806503 0.76806503	-2.34438495 -2.36698228	6 1.61E+08 F 10587190 F	II II MID1	IGR 5'UTR	opensea	IGR-opensea 5'UTR-shore		rs139127244;rs560243394;rs368059805		
charge	cg23452259 cg06877840	0.201026615 -0.22939844	0.61979376 0.57739617	4.745384776 -4.74494927	0.01324334 0.01324703	0.76806503 0.76806503	-2.37201571 -2.37232283	2 2.2E+08 R 10 95362344 F	II CDK5R2 II RBP4	TSS1500 TSS1500	shore shore	TSS1500-shore TSS1500-shore	chr2:219824151-219825864	rs553956647		3 35
bit bit<	cg07205796	-0.20094464	0.37852209	-4.74080352	0.01328227	0.76806503	-2.37524778	16 1187722 F		IGR	opensea	IGR-opensea			9;11;14;36;47	45
visible <	cg03735233 cg05832246	0.219928734 -0.25928617	0.69906867 0.50055443	4.73013207 -4.7285949	0.01337351 0.01338671	0.76807709 0.76825146	-2.38278807 -2.38387554	16 68318873 R 11 1.12E+08 F	II SLC7A6	Body TSS1500	opensea	Body-opensea TSS1500-shore	chr11:111741953-111742292	rs527550469;rs140164262	15;27	
circle circle circle circle <td>cg25662013 cg01940576</td> <td>0.251900302 0.214355696</td> <td>0.43761187 0.70252681</td> <td>4.726595298 4.721465183</td> <td>0.01340392 0.01344819</td> <td>0.76853595 0.76903666</td> <td>-2.38529067 -2.38892389</td> <td>2 1.79E+08 R 14 36946996 F</td> <td>II II SFTA3</td> <td>IGR Body</td> <td>opensea opensea</td> <td>IGR-opensea Body-opensea</td> <td></td> <td>rs564396134;rs181853991;rs550203734 rs561831615</td> <td>29;2;1</td> <td>10</td>	cg25662013 cg01940576	0.251900302 0.214355696	0.43761187 0.70252681	4.726595298 4.721465183	0.01340392 0.01344819	0.76853595 0.76903666	-2.38529067 -2.38892389	2 1.79E+08 R 14 36946996 F	II II SFTA3	IGR Body	opensea opensea	IGR-opensea Body-opensea		rs564396134;rs181853991;rs550203734 rs561831615	29;2;1	10
Bind Bind Constraint Constraint <thc< td=""><td>cg02146412</td><td>-0.24502264</td><td>0.51403354</td><td>-4.7046321</td><td>0.01359475</td><td>0.77029122</td><td>-2.40087174</td><td>11 83501743 R</td><td>II DLG2</td><td>Body</td><td>opensea</td><td>Body-opensea</td><td></td><td>rs537572890</td><td></td><td>29</td></thc<>	cg02146412	-0.24502264	0.51403354	-4.7046321	0.01359475	0.77029122	-2.40087174	11 83501743 R	II DLG2	Body	opensea	Body-opensea		rs537572890		29
number number<	cg07462756	0.214558438	0.28441206	4.703239211	0.01360697	0.77029523	-2.4018622	4 4859985 R		TSS1500	island	TSS1500-island	chr4:4859632-4860191	rs139913705;rs528852346	51;49	
statistic statistic <t< td=""><td>cg19870626</td><td>0.251850607</td><td>0.62791019</td><td>4.670321315</td><td>0.01389976</td><td>0.77088228</td><td>-2.42535087</td><td>1 1.76E+08 F</td><td>1</td><td>IGR</td><td>opensea</td><td>IGR-opensea</td><td></td><td>rs112615490</td><td></td><td>1</td></t<>	cg19870626	0.251850607	0.62791019	4.670321315	0.01389976	0.77088228	-2.42535087	1 1.76E+08 F	1	IGR	opensea	IGR-opensea		rs112615490		1
cp cp< cp<< cp<< cp<< <	cg19231141	0.2070927	0.68647567	4.624997104	0.01431599	0.77088228	-2.45794842	5 1.7E+08 F	I KCNMB1	5'UTR	opensea	S'UTR-opensea	chr10:119311204-119312104	rs542650098		0
ch:0 0	cg00761644	-0.25097029	0.57508507	-4.61891198	0.01437307	0.77088228	-2.46234765	7 1.39E+08 R		Body	shore	Body-shore		rs143494441		35
cp cp< cp< cp< cp<	cg16678267 cg08013396	-0.21923085 0.247894586	0.30675877 0.58205056	-4.61838395 4.598570329	0.01437803 0.01456593	0.77088228 0.7722674	-2.46272964 -2.4770929	8 31896371 F 10 1.34E+08 F	II NRG1-IT1 II	Body IGR	opensea shelf	Body-opensea IGR-shelf		rs550425484;rs567132630;rs368427001 rs540039405;rs74161713;rs576650144	6;9;18	
cp214948 cp238078 cp338078 cp388078	cg00600521	-0.22712794	0.69905259	-4.58992042	0.01464893	0.77239126	-2.48338143	7 1.22E+08 R		TSS1500	shore	TSS1500-shore	chr7:121783946-121784663	rs549827662	12.0	8 47
opp: opp: <th< td=""><td>cg23447131</td><td>0.228801726</td><td>0.33442378</td><td>4.571371202</td><td>0.01482893</td><td>0.77239126</td><td>-2.49690392 -2.51860292</td><td>2 70312835 F 14 1.02E+08 R</td><td></td><td>Body</td><td>shore</td><td>Body-shore</td><td>chr2:70313200-70315490</td><td>rs527812602;rs541390747;rs11884681;rs533020241</td><td>22;29;45;49</td><td></td></th<>	cg23447131	0.228801726	0.33442378	4.571371202	0.01482893	0.77239126	-2.49690392 -2.51860292	2 70312835 F 14 1.02E+08 R		Body	shore	Body-shore	chr2:70313200-70315490	rs527812602;rs541390747;rs11884681;rs533020241	22;29;45;49	
cp:239867 cp:239867 <t< td=""><td>cg09179973 cg27241753</td><td>0.256660315 -0.21631349</td><td>0.3065644 0.54461651</td><td>4.539452483 -4.5154617</td><td>0.01514523 0.01538856</td><td>0.77305885 0.77438217</td><td>-2.52029187 -2.5379704</td><td>11 33843608 F 8 53205926 F</td><td></td><td>IGR 5'UTR</td><td>opensea</td><td>IGR-opensea 5'UTR-opensea</td><td></td><td>rs12276001</td><td></td><td>1</td></t<>	cg09179973 cg27241753	0.256660315 -0.21631349	0.3065644 0.54461651	4.539452483 -4.5154617	0.01514523 0.01538856	0.77305885 0.77438217	-2.52029187 -2.5379704	11 33843608 F 8 53205926 F		IGR 5'UTR	opensea	IGR-opensea 5'UTR-opensea		rs12276001		1
cp001947 cp0.14646 6.4449784 4.6915280 0.516188 0.7952174 2.5449787 7.8497897 7.8497897 8 0 0.97186 0.971868 0.9718768 0.9718768 0.97187688 0.9718768 0.97187688 0.97187688	cg23949067 cg00209050	-0.20379916	0.79283987	-4.50335916	0.01551317	0.77438217	-2.54692123	20 16801919 R		IGR	opensea	IGR-opensea				
ability c </td <td>cg20013963</td> <td>0.207142646</td> <td>0.61449784</td> <td>4.493192506</td> <td>0.01561883</td> <td>0.77492141</td> <td>-2.55445727</td> <td>7 34978959 R</td> <td></td> <td>Body</td> <td>opensea</td> <td>Body-opensea</td> <td></td> <td></td> <td></td> <td></td>	cg20013963	0.207142646	0.61449784	4.493192506	0.01561883	0.77492141	-2.55445727	7 34978959 R		Body	opensea	Body-opensea				
aligned	cg01233015 cg14997132	-0.28879803 0.291443568	0.48523001 0.43057201	-4.48696174 4.475632137	0.01568404 0.01580348	0.77498654 0.77521251	-2.5590835 -2.56751049	7 1.53E+08 R 5 82771274 R	II II VCAN	IGR 5'UTR	shore	IGR-shore 5'UTR-shore			-,	
cp0525464 0.5245417 0.5549333 4.4731270 0.010702 0.775686 -2.5886564 20.502118 0.8 0.00110 0.00110 0.575686 -2.5886564 20.502118 0.8 0.00110 0.00110 0.775686 -2.5886564 20.502118 0.8 0.00110 0.011111 0.011111 0.0111	cg18935575 cg00637744	-0.21625845 -0.2087027	0.47310361 0.39632561	-4.4616169 -4.45351325	0.01595281 0.01603997	0.7754526	-2.57796183 -2.58401837	7 1.14E+08 F 2 59239404 R		IGR Body	opensea opensea	IGR-opensea Body-opensea		rs11687358;rs113060170;rs549098507	38;30;20	
cg055230 2.5292/44 0.5292/44 <td< td=""><td>cg00626846</td><td>0.221546147</td><td>0.53493353</td><td>4.447316276</td><td>0.01610702</td><td>0.7756896</td><td>-2.58865661</td><td>20 58028119 R</td><td></td><td>IGR</td><td>opensea</td><td>IGR-opensea</td><td></td><td></td><td></td><td></td></td<>	cg00626846	0.221546147	0.53493353	4.447316276	0.01610702	0.7756896	-2.58865661	20 58028119 R		IGR	opensea	IGR-opensea				
q213978/9 0.2040598/3 0.53909316 4.434838 0.015332 0.7583497 2.6635618 1 2.6636618 1 SUB0 1078-b0ce hrlp210805879-2108656 hrlp212805879-2108656 hrlp212805879-21086568 hrlp212805879-21086568 hrlp212805879-210865879 hrlp2128058799-210865879 hrlp21280587999 hrlp212805879999 hrlp2128058799999999999999999999999999778049999999778049999999999	cg08592304 cg00495320	-0.23924644 0.215961342	0.28577128 0.4661852	-4.43015478 4.428681769	0.01629456 0.01631078	0.77617979 0.77617979	-2.60153185 -2.60263904	15 35060564 R 8 73454968 F	II LOC101928174 II KCNB2	Body 5'UTR	opensea opensea	Body-opensea 5'UTR-opensea		rs187576245;rs112428392 rs560702797		0
22139362 0.21120231 0.5982534 4.3757012 0.0169071 0.7771592 2.45426779 3 1.514-08 H 05571 0 body commes Body-commes millit/02388 002483554 0.0257917 0.6512731 4.36756242 0.0169799 0.77740107 2.4571280 3 1.8581454 F 0.104 TS200 0.0121738-0547 (millitra).2586518-358746 millitra).2586518-358746	cg21397540	0.243735115	0.57363923	4.383367398	0.01681994	0.77709472	-2.6368618	1 2.48E+08 R		IGR	opensea	IGR-opensea		rs10925000;rs533876990;rs12043526		40
	cg21930362	-0.21120233	0.59682514	-4.37574712	0.01690751	0.77715927	-2.64264779	3 1.51E+08 R	II IGSF10	Body	opensea	Body-opensea		rs181702818		48

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 |
 | 5 0.01723641
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 | -2.66412622 | 2 2.37E+08 R
 | н
 | IGR |
 |
 | GR-opensea | | rs529891862;rs187393350;rs192287729
 | 42;41;30 |

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| 10852 0.227269799
64946 0.26052389
32772 0.2664134
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 | | 4 72903914 F
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20 1612808 F
 | II NPFFR
II
II SIRPG-
 | IGR | R op
 | pensea Bo
pensea IG
 | Body-opensea
GR-opensea
ISS1500-opensea | | rs188528011
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rs14375401;rs1535883;rs183513542
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18 21417764 F
 | II HEATR
 | R2 Boo | idy sh
 | hore Bo
 | Sody-shore
Body-opensea | chr7:821689-822634 | rs14375040175155588375183513542
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 | II LAMA:
II
II NRXN3
 | IGR | R sh
 | hore IG
 | GR-shore
GR-shore
Body-opensea | chr10:132583720-132584164 | rs569567690;rs146218562
rs191472210;rs74065956;rs549181868
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49;48;2 |
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 | 3 0.01802825
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 | -2.7142668 2 | 12 1.03E+08 F
22 24912201 F
 | II PAH
II UPB1
 | Boo | idy op
 | pensea Bo
 | xonBnd-opensea
Body-opensea | | rs187133779;rs191142120;rs140175796;rs200366386
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19;31;46;47 |
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 | 4 0.60652732

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 | 7 0.01813162
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8 98572582 F
 | II CFAP2
 | IGR | R op
 | pensea IG
 | Body-opensea
GR-opensea | | rs12999064;rs59301232
rs554126070;rs115542777
 | 17;13
29;32 |
| 04474 0.209342089
70191 -0.203095
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 | 0.77890514 0.77890514
 | -2.72080346 X
-2.72537462 1 | 1.3E+08 F
 | II FLI300
 | 358 TSS
IGR |
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 | SS1500-shore
GR-opensea | chrX:130192131-130192735 | rs534196352;rs74793897
 | 34;17 |
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5 27110547 F
 | II DPP10
 |)-AS3 TSS
IGR | S1500 op
 | pensea TS
 | SS1500-opensea
GR-opensea | | rs185033505
rs181966226rs535157011
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 | 4 0.37354972

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99400 0.26179811
 | 4 0.51967355

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 | II ZNF88
II HOXA3
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 | Body-opensea
S'UTR-shore | chr7:27154999-27155426 | rs116612685
rs569887316
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15 50411535 F
 | II AUTS2
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ISS200-opensea | | rs542338290;rs145453170
rs533592730
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 | 0.54305502

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 | II TM4SF
II PROKF
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SS1500-shore | chr2:68870351-68871055 |
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9 0.01906792
 |
 | | 11 65802195 R
6 84567967 F
 | II CYB5R
 | IGR
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S1500 sh
 |
 | GR-opensea
SS1500-shore | chr6:84569263-84569619 | rs373871707;rs549282848
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-2.79675049 |
 | II
II LDB2
 | IGR
Boo | R sh
 | hore IG
 | GR-shore | chr11:2890388-2891337 | rs149925594;rs550041173;rs182299256
 | 34;9;1 |
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 | 0.54894839

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 | 2 0.01958965
 | 0.77973473
 | -2.80722699 1 | 16 1214867 R
 | I CACNA
 | A1H Boo | idy sh
 | helf Bo
 | Body-opensea
Body-shelf | chr16:1217128-1217336 | rs545001665;rs564923919;rs527401151
 | 36;29;1 |
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63498 0.2020571
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 | 0.77973473 0.77973473
 | | 5 5166415 F
10 50588096 F
 | II ADAM
II DRGX
 | ITS16 Boo
Boo |
 |
 | Body-opensea
Body-opensea | | rs34627029;rs551430566
rs147934589;rs536450334
 | 0;3
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13176 0.221851004
 |

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 | -2.81831779
-2.82790742 1 | 6 68606787 R
12 4497426 F
 |
 | IGR
IGR |
 |
 | GR-opensea
GR-opensea | | rs558552483
rs115661923
 | |
| 24362 0.20435670
37581 -0.2294413
 | 0.4393252

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5 7374151 F
 | II SPCS3
 | | S1500 sh
 | hore TS
 | SS1500-shore
GR-opensea | chr4:177240935-177241832 | rs540036294:rs555130873
 | 15:28 |
| 05103 -0.28190820
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 | 0.78007271
 | -2.83476659 1 | 11 1.1E+08 R
 |
 | IGR | R op
 | pensea IG
 | GR-opensea | | rs539499504;rs557749236;rs566822399
 | 46;36;18 |
| 4541 -0.2940450
8646 0.21618122
 | 2 0.5262504

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3 1.67E+08 R
 | II
II SERPIN
 | IGR
NI1 5'U |
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 | GR-opensea
S'UTR-opensea | | rs550445450;rs571874890;rs16870587
rs193036369;rs185298005
 | 14;29;32
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 | 6 0.02026393
3 0.02032014
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 | -2.84518375
-2.84829246 1 | 3 51861073 F
 | II IQCF3
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 | LstExon-opensea
Body-opensea | | rs546221559
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| 9646 0.21206278
 | 0.48793542

 | 4.102234027
 | 7 0.02046658
 | 0.78043338
 | -2.85635324 1 | 17 47297268 F
 | I ABI3
 | Boo | idy isla
 | land Bo
 | Body-island | chr17:47296969-47297314 | rs573287028;rs199635084;rs616338
 | 2;26;29 |
| 8001 0.22541916:
0428 0.2251458:
 | 0.57428013

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 | 4 0.02053478
 | 0.78043338
 | -2.86008858 1 | 8 97399716 F
16 3243304 R
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 | IGR
IGR |
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GR-island | chr16:3243303-3243583 | rs569081179;rs531597015
rs575170324;rs144106111;rs547294631
 | 0;34
43;39;34 |
| 6637 -0.2033531
3682 0.20709586
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 | -2.86682104 1
-2.86863162 | 13 26380861 F
1 1.58E+08 F
 | II ATP8A
II CD1C
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 | Body-opensea
ISS1500-opensea | | rs553176162;rs557886007
rs190508207
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| 2280 0.21118674
 | 15 0.52576822

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 | 0.78095369
 | -2.87523936 | 3 1.13E+08 F
 | II CFAP4
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 | land TS
 | SS1500-island | chr3:113160299-113160641 | rs183606005;rs568588213;rs535542797
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 | II TET1
II MSX1
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 | hore TS
 | Body-opensea
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rs537228783
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| 4294 0.2588729
7735 -0.2147123
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 | 8 0.02150624
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3 28070292 F
 | II HOXAS
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IGR |
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rs560607552;rs17020851;rs145663859
 | 0;9;21 |
| 9412 0.204902009
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 | 0.29300322

 | 4.027784085
 | 5 0.02159392
 | 0.78302419
 | | 18 44776850 F
7 18868877 F
 | II HDACS
 | IGR | R sh
 | hore IG
 | GR-shore
Body-opensea | chr18:44777632-44778084 | rs77243045
rs115552810;rs138291818
 | 28;30 |
| 2217 -0.2051584
 | 6 0.34157985

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 | 9 0.02170637
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 | 3266 Boo | dy op
 | pensea Bo
 | Body-opensea | | rs564694781;rs576927628
 | 50;1 |
| 6935 0.266940523
6934 0.20516359
 | 9 0.39193155

 | 4.014598064
 | 4 0.0218016
 | 0.78337569
 | -2.92737046 X | 7 1.4E+08 R
40035961 F
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 | ody-opensea
UTR-island | chrX:40034239-40036007 | rs140597201;rs577466422
 | 51;1 |
| 6282 -0.2305557
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7 35560296 F
 | II STATH
 | I TSS
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GR-opensea | | rs141720087
rs557437971
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| 2952 -0.2317340
 | 0.55565385

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 | -2.94142137 1 | 13 38020806 R
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 | pensea IG
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| 8655 -0.20026993
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3 8407419 R
 | II COL15
 | 1-AS1 Boo | idy op
 | pensea Bo
 | Body-opensea
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 | 35;39 |
| 121 0.2595787
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 | 2 0.52087201

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 | II TSSC4
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 | hore TS
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Body-opensea | chr11:2421040-2422474 | rs556954315
rs537514224;rs554763142;rs574530836;rs147474497
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 | 2 0.02237158
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 | II FEZ1
 | TSS | \$1500 sh
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| 924 0.222863742
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 | 0.6397008

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 | 5 0.02239507
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 | | 8 42127640 F
 | II GRAP2
II IKBKB
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SS1500-shore | chr8:42128689-42129141 | rs370366466
rs17875739;rs193007451;rs7825781
 | 3;14;16 |
| 0271 0.21029801
 | 0.54023971

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 | 8 0.02246007
 | 0.78337569
 | | 12 99549103 R
8 90913629 R
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II OSGIN
 | LB TSS | S1500 op
S1500 sh
 | pensea TS
 | SS1500-opensea
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rs570502869
 | 39;34 |
| 9991 0.24442312
9226 -0.23311434
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 | 8 0.02282322
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10 26599430 R
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 | | idy op
 | pensea Bo
 | Body-opensea | | rs522569074,rs188941686,rs77373343,rs550788567
rs532107921
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| 0050 -0.2064115
 | 8 0.57154075

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 | 8 0.02333692
 | 0.78457276
 | -3.00401189 | 8 41255897 R
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 | pensea IG
 | GR-opensea
GR-opensea | | rs187076722;rs192329240
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| 0432 -0.2641252
0551 0.32219825
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-3.01982435 | 2 52022999 F
2 25051151 F
 | II ADCY3
 | IGR
B Boo |
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 | GR-opensea
Body-opensea | | rs374034298
 | |
| 1972 0.216317964
 | 64 0.5899675

 | 3.900489469
 | 9 0.02370689
 | 0.78521751
 | -3.02174746 | 8 1.43E+08 R
6 1.18E+08 R
 | I
II ROS1
 | IGR
Boo | R sh
 | hore IG
 | GR-shore
Body-opensea | chr8:143202654-143202868 | rs148630342;rs10096519;rs10095704;rs555443159;rs574384209;rs538493344
 | 44;43;39;33;23;12 |
| 2711 0.207762402
 | 0.63274947

 | 3.886594999
 | 9 0.02395282
 | 0.78558449
 | -3.03338857 1 | 15 44964622 R
 | II PATL2
 | Boo | dy op
 | pensea Bo
 | Body-opensea | | rs374952072;rs553403732
 | 44;39 |
| 0244 -0.2066527
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 | -3.87265484
 | 4 0.02420275
 | 0.78632817
 | -3.04510078 1 | 8 59476467 R
15 31763329 F
 | II SDCBP
 | > 5'U
IGR | R op
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rs549195859
 | 39;12 |
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IGR |
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GR-island | chrX:106749879-106750862 |
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| 1189 0.2270721
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 | 45;46 |
| 4957 0.203192131
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 | 2 0.52761333

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 | 4 0.02442547
 |
 | -3.05366537 1
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 | II CA10
II HOXAS
 | 5 TSS | \$1500 isla
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rs183291358;rs566898073;rs535764423;rs555627142;rs575463907
 | 14;15
7;19;33;36;44 |
| 0408 0.20227174
9134 -0.2085038
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 | -3.05619624 2
-3.05668949 | 20 21378211 F
2 2.1E+08 F
 | I NKK2~
 | 4 TSS
IGR |
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 | SS200-island
GR-opensea | chr20:21376358-21378245 | rs527557171
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| 9556 0.25265121
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 | 15 0.56600645

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 | | UTR op
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 | UTR-opensea
GR-opensea | | rs555517622
rs114233552
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| 7915 0.24318991
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 | UTR-opensea | | rs200160059;rs573777098
 | 0;37 |
| 1824 0.229068941
5283 -0.26520141
 | 8 0.43152798

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2 75865060 F
 | II HHLA2
II
 | 2 Exc
IGR |
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GR-opensea | | rs578129688
rs191330338;rs151015908;rs555710288;rs574298020
 | 0;1;25;51 |
| 0574 -0.2625209
5215 0.22326459
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 | 7 0.02526871
4 0.02542819
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-3.100873 1 | 14 1.02E+08 F
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 |
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IGR |
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GR-opensea | | rs11622062;rs144976013
rs2193
 | 4;11 |
| 3032 -0.2811526
 | 8 0.41142874

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 | 7 0.02549364
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 | IGR | R op
 | pensea IG
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 | 24;22;2 |
| 1218 -0.2116003
2985 0.24092349
 | 0.67104442

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 | 9 0.02601902
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20 61498871 F
 | II ZKSCAI
II
 | N1 TSS
IGR |
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 | SS1500-shore
GR-opensea | chr7:99613104-99613797 | rs575427038;rs546119032
 | 1;20 |
| 8483 0.239432694
8896 -0.28586051
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 | 0.78718522 0.78718522
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15 45005365 R
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 | IGR
Boo |
 |
 | GR-opensea
Body-shore | cbr15-45003460-45004345 | rs575898253
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| 1652 -0.20899244
6984 -0.20957654
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7 27198374 F
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rs189813246.rs578060226.rs568423281
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5987 0.20194704
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-3.15725133 X | 7 6713037 F
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II PIN4
 | IGR
Boo | dy op
 | pensea Bo
 | GR-opensea
Body-opensea | | rs532098609
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| 0994 -0.2498539
5913 -0.2438201
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 | 5 0.02704189
3 0.02720304
 | 0.78811565 0.78811565
 | | 19 8642571 R
6 66819090 F
 | II MYO1
 | F TSS
IGR |
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 | 'SS1500-opensea
GR-opensea | | rs148681216;rs7252938
rs562211785
 | 22;21 |
| 1075 0.204324559
 | 9 0.54412574

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 | 4 0.02724361
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II PEKM
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rs11168408rs563225742
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Boo | S1500 sh
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 | 45;14
44;29;27;7 |
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 | pensea Bo
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rs79171793
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 | hore Bo
 | Body-shore | chr11:31820060-31821416 | rs571551224
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| 1661 0.23381812
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 | | 21 42219853 F
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 | | S1500 sh
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| 6865 -0.23378162
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 | IGR
IGR | S1500 sh
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hore IG
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GR-shore | chr8:38644473-38645760
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chr2:219906107-219906328 |
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-3.2335006
-3.24034335 1
-3.2417959 1
-3.24205069 2 | 2 2.2E+08 F
5 1.81E+08 R
17 6502578 R
19 12266489 R
20 61609595 R
 | II
II KIAA0
I ZNF62
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helf IG
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pensea Bo
hore S ¹
helf IG
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Body-opensea
GR-shelf
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| 5865 -0.23378162 5712 -0.3318859 5542 0.209064062 5224 0.20853582 2578 0.24934799 1489 0.221902076 9447 -0.21172402
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5 1.81E+08 R
17 6502578 R
19 12266489 R
20 61609595 R
3 1.7E+08 R
17 10561350 F
 | II
II KIAA0
I ZNF62
II
II PHC3
II MYH3
 | IGR
1GR
753 Boo
15 S'U
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TSS
TSS | S1500 sh R sh R sh idy op UTR sh S1500 sh S1500 sh S1500 op
 | hore TS
helf IG
pensea Bo
hore S ¹
helf IG
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chr3:169898946-169899626 | n6981210
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n7880742
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| 5865 -0.2337816 5712 -0.3318859 9542 0.20906406 5224 0.20853582 2578 0.24934799 1489 0.22190207 9447 -0.2117240 3682 -0.2010522
 | 9 0.3446788 62 0.51066127 94 0.51570973 51 0.41720103 94 0.5056121 95 0.5135538 98 0.39925704 91 0.513329159 925 0.46349102

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cg01970812	0.213827171		3 369631577	0.03585269	0.80011972	-3.49033195	10	1.11E+08 E		RNU6-53P	Body	opensea	Body-opensea	0112.177024301-177023052	rs182514883		1
cg25124045	-0.20647512	0.59546389	-3.36933511	0.03586139	0.80011972	-3.49060761		52749655 F		11100-331	IGR	opensea	IGR-opensea		rs529868118:rs78334675:rs187617960	20:27:46	•
cg24075412	0.213427275	0.6598358	3.362822049	0.03605315	0.80011972	-3.49666765	17	77479966 R	1	HRNBP3	TSS1500	opensea	TSS1500-opensea				
cg05760182	0.209987606	0.67404064	3.356495027	0.03624065	0.80053425	-3.50256193	6	39078002 R		SAYSD1	5'UTR	opensea	5'UTR-opensea		rs566374917		35
cg22164577	-0.22499918	0.5183824	-3.3552789	0.03627682	0.80076787	-3.50369571		1.71E+08 F		UBR3	Body	shore	Body-shore	chr2:170683860-170684629	rs180704430		38
cg21501097	-0.20556863	0.25000293	-3.34990487	0.03643722	0.80082951	-3.50870905	12	1.33E+08 R			IGR	opensea	IGR-opensea		rs28460341;rs192374624;rs536028040	17;16;3	
cg24406162	-0.22300747		-3.34525365	0.03657674	0.80102284	-3.51305231		24017943 F		RPL11		shore	TSS1500-shore	chr1:24018355-24018567			
cg13753868	0.216647602			0.03670134	0.80102284	-3.51691709	19	2865997 F	п	ZNF556		opensea	TSS1500-opensea		rs143368970;rs550934709	25;34	
cg26154201		0.53925036	3.33204484	0.03697657	0.80135238	-3.52540791	20	238217 F		DEFB132	TSS200	opensea	TSS200-opensea		rs530991007;rs550888095;rs62189854	0;3;19	
cg17753390 cg13069322	-0.24456467 0.280827438	0.62472755 0.62028934	-3.33167739 3.326000249	0.03698777 0.03716133	0.80136763 0.80183329	-3.52575207 -3.53107259	5	1.7E+08 R 22047028 R		KCNIP1	5'UTR IGR	opensea	5'UTR-opensea		rs540996629;rs551495166 rs141315331:rs1174968:rs547318600	50;1	
cg13069322 cg22282089		0.62028934		0.03716133	0.80183329	-3.53107259		22047028 R 30686841 F			IGR	opensea shelf	IGR-opensea IGR-shelf	chr13:30688864-30689335	rs377526591;rs618752;rs565508780	43;9;1 9:24:49	
cg05005604	-0.24345576	0.55102472	-3.32080685	0.03732097	0.80183329	-3.53594488		92810338 F		SLC24A4	Body	opensea	Body-opensea	CIII 13-50088804-500855555	1557/320391,15018/32,1590308780	3,24,43	
cg11220654		0.39621919		0.03741529	0.80103329	-3 53881381		59279345 R		RNF111		shore	TSS1500-shore	chr15:59279741-59280720	rs72745097:rs73414877	32-22	
cg03975781			3.317521202		0.8019428	-3.53902989	11	1 2E+08 E		101111	IGR	opensea	IGR-opensea	011333273741-33200720	rs538872354;rs557354111;rs575907975	39;45;46	
cg27497857		0.58215904	-3.31667555	0.03744857	0.80197357	-3.53982422	7	1.29E+08 F			IGR	opensea	IGR-opensea				
cg13634918	0.226037581	0.57872537	3.315829583	0.03747476	0.80197357	-3.54061897	16	28984918 R		SPNS1	TSS1500	shore	TSS1500-shore	chr16:28985881-28986661	rs534948062		41
cg26892192	0.2730041	0.48286421	3.305316639	0.03780217	0.80215634	-3.55050633	7	25712342 R			IGR	opensea	IGR-opensea		rs564161345;rs190526049;rs146512706	23;12;1	
cg23376861	0.204242678	0.39657105	3.300339932	0.03795838	0.80265868	-3.55519389	18	43678713 F		ATP5A1	5'UTR	shore	5'UTR-shore	chr18:43677956-43678352			
cg15311873	-0.23669332	0.39364212	-3.29411823	0.03815479	0.80324868	-3.56106042	5	1.66E+08 F			IGR	opensea	IGR-opensea				
cg20426806		0.56263288		0.03820242	0.80348226	-3.56247875		32606102 R	п	FRY-AS1		shore	TSS1500-shore	chr13:32605320-32605903	rs424118;rs147785987;rs433551	35;27;17	
cg07378312	-0.23085979	0.44133187	-3.28939632	0.03830468	0.80388036	-3.56551747	2	2E+08 F			IGR	opensea	IGR-opensea		rs191272188		9
cg11148469	-0.20782323	0.45488107	-3.28760528	0.03836172	0.80402199	-3.5672091	5	1.4E+08 F		PCDHA5		shore	TSS1500-shore	chr5:140202573-140203610	rs6885319		16
cg14028400 cg06185593	0.20581618 0.333918304		3.283424366 3.270632592	0.03849529 0.03890751	0.80419764	-3.57116024 -3.58326871		28793656 R 55348912 F			IGR	opensea	IGR-opensea IGR-opensea		rs576670650;rs541551798;rs564467400 rs114233552;rs149078899	47;23;2 0:50	
cg05185593 cg07899997		0.3372857	-3.26506689	0.03908855	0.80444183 0.80507989	-3.58326871		55348912 F 85671892 R			IGR IGR	opensea shore	IGR-opensea	chr12:85673878-85674700	rs74343919	0;50	12
cg19472218	-0.22886705	0.30028337	-3.25123183	0.03954307	0.80526532	-3.60168986		90420449 R		EFCAB11	5'UTR	shore	5'UTR-shore	chr14:90422142-90422593	1574543919		12
cg03228974	0.259828084		3.248921922	0.03954307	0.80526532	-3.6038877		30067855 F		EPGABII	IGR	shore	IGR-shore	chr6:30068492-30068794	rs1264695		37
cg04026169	0 20400084		3 245695998	0.03972676	0.80535056	-3 60695873		85422265 F	ï		IGR	shore	IGR-shore	chr4-85422929-85423190	rs10005941;rs537150735;rs192835192	5;15;18	
cg17586988	-0.20344003	0.54566464	-3.24135932	0.03987138	0.80572074	-3.61109015	18	5892245 F	i.	TMEM200C	TSS200	shore	TSS200-shore	chr18:5890292-5891682		-11	
cg24199558	-0.21166498	0.27566541	-3.23962418	0.03992942	0.80586257	-3.61274413	10	1.22E+08 R			IGR	opensea	IGR-opensea		rs544637640		5
cg04507598	0.207249088	0.59400112	3.239591046	0.03993053	0.80586257	-3.61277572	12	45990453 R			IGR	opensea	IGR-opensea		rs140620534;rs545612979;rs10880824	36;20;13	
cg13315744	0.219031935	0.53351648	3.237979056	0.03998455	0.80586257	-3.61431281	2	1287787 F		SNTG2	Body	shore	Body-shore	chr2:1286393-1286642	rs544820175;rs188647699	9;34	
cg12102690	-0.20671956	0.42752344	-3.23396166	0.04011957	0.80586257	-3.61814559	х	29503497 F		IL1RAPL1	Body	opensea	Body-opensea				
cg13796843		0.41506914	-3.22604777	0.04038719	0.80586257	-3.62570439		76303634 F		NRG4	5'UTR	opensea	5'UTR-opensea		rs541257185		31
cg13784283	0.225644375	0.64222157		0.04044029	0.80586257	-3.62719839		33163627 R		RXRB	Body	shelf	Body-shelf	chr6:33159991-33160263	rs547479013;rs559052660	29;2	
cg22496559	-0.20721704	0.49057144	-3.22292618	0.04049335	0.80586257	-3.62868904	3	1.96E+08 F		TM4SF19	TSS200	opensea	TSS200-opensea		rs563644689;rs531066377	1;9	
cg07889765	-0.25011675	0.44915979	-3.21930943	0.04061677	0.805909	-3.63214937		96123159 F	п	NOC3L	TSS1500	shore	TSS1500-shore	chr10:96122540-96122904	rs138366586		20
cg01233718	-0.25336712	0.65971736	-3.21836791	0.04064898	0.80591913	-3.63305055		24599115 F		SYNDIG1	Body	opensea	Body-opensea	chr19:39737689-39739288	443402343		20
cg02672759 cg19724485	0.20059884	0.42259034 0.4343795	-3.215875441 -3.21405316	0.04073439	0.80598808 0.80610548	-3.63543703 -3.63718253		39739058 R 55999683 F		OR5T2	IGR 1stExon	island opensea	IGR-island 1stExon-opensea	chr19:39737689-39739288	rs117436747 rs141189792;rs567353421;rs535373491;rs143289732;rs557241694	1:9:17:38:41	39
		0.4343795															
			2 20916006	0.04100012	0.00636033	2 64292061	10				Deaths		Derly energy				
cg18735473	-0.22965031	0.42407387	-3.20816096 -2.19707612	0.04100013	0.80635023	-3.64283061		35015946 R		BRUNOL4	Body	opensea	Body-opensea Rody-opensea		rs541184485;rs151317773	17;2	
cg24254317	-0.21465547	0.36687306	-3.19707612	0.04138571	0.80699061	-3.65347332	7	35015946 R 1.58E+08 F		BRUNOL4 PTPRN2	Body	opensea	Body-opensea	ch-9-90112514-90112817	rs541184485;rs151317773	17,2	
cg24254317 cg08719486	-0.21465547 0.247706774	0.36687306 0.4327996	-3.19707612 3.196836607	0.04138571 0.04139409	0.80699061 0.80701683		7 9	35015946 R		BRUNOL4 PTPRN2 DAPK1	Body TSS1500	opensea shore	Body-opensea TSS1500-shore	chr9:90112514-90113817	rs5411844857s151317773 rs1897751677s557342418	17;2 43;27	
cg24254317	-0.21465547	0.36687306	-3.19707612 3.196836607 -3.17088667	0.04138571	0.80699061	-3.65347332 -3.65370353	7 9	35015946 R 1.58E+08 F 90112101 R		BRUNOL4 PTPRN2	Body TSS1500	opensea	Body-opensea	chr9:90112514-90113817	rs541184485;rs151317773	17,2	
cg24254317 cg08719486 cg04846432	-0.21465547 0.247706774 -0.23174168	0.36687306 0.4327996 0.39565858	-3.19707612 3.196836607 -3.17088667	0.04138571 0.04139409 0.04231443	0.80699061 0.80701683 0.80765045	-3.65347332 -3.65370353 -3.67870704	7 9 3 1	35015946 R 1.58E+08 F 90112101 R 1.87E+08 R		BRUNOL4 PTPRN2 DAPK1	Body TSS1500 3'UTR	opensea shore opensea	Body-opensea TSS1500-shore 3'UTR-opensea	chr9:90112514-90113817	rs541184485xrs151317773 rs189775167xrs57342418 rs532003765xr5191487026	17;2 43;27 15;1	
cg24254317 cg08719486 cg04846432 cg00121963	-0.21465547 0.247706774 -0.23174168 0.296819208	0.36687306 0.4327996 0.39565858 0.58655414	-3.19707612 3.196836607 -3.17088667 3.170198497	0.04138571 0.04139409 0.04231443 0.04233918	0.80699061 0.80701683 0.80765045 0.80765045	-3.65347332 -3.65370353 -3.67870704 -3.67937178	7 9 3 1 20	35015946 R 1.58E+08 F 90112101 R 1.87E+08 R 2.1E+08 F		BRUNOL4 PTPRN2 DAPK1	Body TSS1500 3'UTR IGR	opensea shore opensea opensea	Body-opensea TSS1500-shore 3'UTR-opensea IGR-opensea	chr9:90112514-90113817	n:541184485;n:151317773 n:189775167;n:557342418 n:533203765;n:191487036 n:155579375;n:5984805;n:555431789;n:181098427	17;2 43;27 15;1 1;45;46;51	
cg24254317 cg08719486 cg04846432 cg00121963 cg20575254	-0.21465547 0.247706774 -0.23174168 0.296819208 -0.23535806 -0.20828527	0.36687306 0.4327996 0.39565858 0.58655414 0.52669915	-3.19707612 3.196836607 -3.17088667 3.170198497 -3.16737073 -3.16710034	0.04138571 0.04139409 0.04231443 0.04233918 0.04244104	0.80699061 0.80701683 0.80765045 0.80765045 0.80765045	-3.65347332 -3.65370353 -3.67870704 -3.67937178 -3.68210417	7 9 3 1 20 16	35015946 R 1.58E+08 F 90112101 R 1.87E+08 R 2.1E+08 F 54777948 F		BRUNOL4 PTPRN2 DAPK1 MASP1	Body TSS1500 3'UTR IGR IGR Body	opensea shore opensea opensea opensea	Body-opensea TSS1500-shore 3'UTR-opensea IGR-opensea IGR-opensea	chr9:90112514-90113817 chr4:74486044-74486258	n:541184485,rs15117773 n:1897751617,rs57342418 n:150779737,rs13704405,rs5541789,rs181098427 n:15079737,rs13704405,rs5541789,rs181098427	17;2 43;27 15;1 1;45;46;51 0;6;24;25	6
cg24254317 cg08719486 cg04846432 cg00121963 cg20575254 cg19709862 cg15779586 cg24746838	-0.21465547 0.247706774 -0.23174168 0.296819208 -0.23535806 -0.20828527 0.202531676 -0.20115209	0.36687306 0.4327996 0.39565858 0.58655414 0.52669915 0.65954471 0.52033166 0.74852509	-3.19707612 3.196836607 -3.17088667 3.170198497 -3.16737073 -3.16710034 3.166870493 -3.16351552	0.04138571 0.04139409 0.04231443 0.04233918 0.04244104 0.0424508 0.0424591 0.04258041	0.80699061 0.80701683 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045	-3.65347332 -3.65370353 -3.67870704 -3.67937178 -3.68210417 -3.68236552 -3.68258769 -3.68583171	7 9 3 1 20 16 4 7	35015946 R 1.58E+08 F 90112101 R 1.87E+08 R 2.1E+08 F 54777948 F 47239315 R 74486675 F 64452895 F		BRUNOL4 PTPRN2 DAPK1 MASP1 ITFG1 RASSF6 ZNF117	Body TSS1500 3'UTR IGR IGR Body TSS1500 TSS1500	opensea shore opensea opensea opensea shore opensea	Body-opensea TSS1500-shore 3'UTR-opensea IGR-opensea IGR-opensea Body-opensea TSS1500-shore TSS1500-opensea	chr4:74486044-74486258	n54118448,n151317773 n189775167,n557342418 n531507765,1174,075555421789,n151098427 n5007897,n531704859,n525527057,n6224897 n507885540 n557885540 n55788540	17:2 43:27 15:1 1:45:46:51 0:6:24:25 32:31 0: 0:1:9:10:11:34:35:36	6
cg24254317 cg08719486 cg04846432 cg00121963 cg20575254 cg1970982 cg15779586 cg24746838 cg16747564	-0.21465547 0.247706774 -0.23174168 0.296819208 -0.23535806 -0.20828527 0.202531676 -0.20115209 0.213031707	0.36687306 0.4327996 0.39565858 0.58655414 0.52669915 0.65954471 0.52033166 0.74852509 0.35623601	-3.19707612 3.196836607 -3.17088667 3.170198497 -3.16737073 -3.16710034 3.166870493 -3.16351552 3.156590235	0.04138571 0.04139409 0.04231443 0.04233918 0.04244104 0.0424508 0.0424591 0.04258041 0.04283216	0.80699061 0.80701683 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.80786542 0.80786542	-3.65347332 -3.65370353 -3.67870704 -3.67937178 -3.68210417 -3.68236552 -3.68258769 -3.68583171 -3.69253443	7 9 3 1 20 16 4 7 13	35015946 R 1.58E+08 F 90112101 R 1.87E+08 R 2.1E+08 F 47239315 R 74486675 F 64452895 F 1.13E+08 F		BRUNOL4 PTPRN2 DAPK1 MASP1 ITFG1 RASSF6	Body TSS1500 3'UTR IGR IGR Body TSS1500 TSS1500 TSS1500	opensea shore opensea opensea opensea shore opensea shore	Body-opensea TSS1500-shore 3'UTR-opensea IGR-opensea IGR-opensea Body-opensea TSS1500-shore TSS1500-opensea TSS1500-shore		n541184485,n151317773 n1897756107,n557342418 n1505795737,n5170644057,n555417897,n181098427 n0204691,n57378885,n5555267057,n024692 n5472724724,n11345449 n557885540 n200800773,n112355189,n55402965,n189142639,n71554295,n738653707,n19981905,n20	17:2 43:27 15:1 1:45:46:51 0:6:24:25 32:31 0: 0:1:9:10:11:34:35:36 0:38	6
cg24254317 cg08719486 cg04846432 cg00121963 cg20575254 cg19709862 cg15779586 cg24746838 cg16747564 cg16588114	-0.21465547 0.247706774 -0.23174168 0.296819208 -0.23535806 -0.20828527 0.202531676 -0.20115209 0.213031707 -0.21955447	0.36687306 0.4327996 0.39565858 0.58655414 0.52669915 0.65954471 0.52033166 0.74852509 0.35623601 0.54130119	-3.19707612 3.196836607 -3.17088667 3.170198497 -3.16737073 -3.16710034 3.166870493 -3.1655552 3.156590235 -3.15546084	0.04138571 0.04139409 0.04231443 0.04233918 0.04244104 0.0424508 0.0424508 0.04258041 0.04258041 0.04283216 0.04287339	0.80699061 0.80701683 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.80795045 0.80791217	-3.65347332 -3.65370353 -3.67870704 -3.67937178 -3.68210417 -3.68236552 -3.68258769 -3.68583171 -3.69253443 -3.69362836	7 9 3 1 20 16 4 7 13 2	35015946 R 1.58E+08 F 90112101 R 1.87E+08 R 2.1E+08 F 47239315 R 74486675 F 64452895 F 1.13E+08 F 78578138 F		BRUNOL4 PTPRN2 DAPK1 MASP1 ITFG1 RASSF6 ZNF117 SOX1	Body TSS1500 3'UTR IGR Body TSS1500 TSS1500 TSS1500 IGR	opensea opensea opensea opensea opensea shore opensea shore opensea	Body-opensea TSS1500-shore 3'UTR-opensea IGR-opensea Body-opensea TSS1500-shore TSS1500-shore IGR-opensea	chr4:74486044-74486258	n54118448,n151317773 n189775167,n557342418 n531507765,1174,075555421789,n151098427 n5007897,n531704859,n55527057,n6224897 n507885540 n557885540 n55788540	17:2 43:27 15:1 1:45:46:51 0:6:24:25 32:31 0: 0:1:9:10:11:34:35:36	6
cg24254317 cg08719486 cg04846432 cg00121963 cg20575254 cg19709862 cg15779586 cg24746838 cg16747564 cg16747564 cg23870749	-0.21465547 0.247706774 -0.23174168 0.296819208 -0.296819208 -0.20828527 0.202531676 0.2015209 0.213031707 -0.21955447 0.217199064	0.36687306 0.4327996 0.39565858 0.58655414 0.52669915 0.65954471 0.52033166 0.74852509 0.35623601 0.54130119 0.41321747	-3.19707612 3.196836607 -3.17088667 3.170198497 -3.16737073 -3.16710034 3.166870493 3.165870493 3.155552 3.155550235 -3.155546084 3.146914244	0.04138571 0.04139409 0.04231443 0.04233918 0.04244104 0.0424508 0.0424509 0.04258041 0.04258041 0.04287339 0.04287339	0.80699061 0.80701683 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.80786542 0.80791217 0.80791217 0.80804348	-3.65347332 -3.65370353 -3.67870704 -3.67937178 -3.68210417 -3.68236552 -3.68258769 -3.68258769 -3.68583171 -3.68253443 -3.69352843 -3.70191409	7 9 3 1 20 16 4 7 13 2 1	35015946 R 1.58E+08 F 90112101 R 1.87E+08 R 2.1E+08 F 54777948 F 47239315 R 74486675 F 64452895 F 1.13E+08 F 78578138 F 2.27E+08 R		BRUNOL4 PTPRN2 DAPK1 MASP1 ITFG1 RASSF6 ZNF117 SOX1 PSEN2	Body TSS1500 3'UTR IGR Body TSS1500 TSS1500 TSS1500 IGR Body	opensea opensea opensea opensea opensea shore opensea shore opensea opensea opensea	Body-opensea TSS1500-shore 3'UTR-opensea IGR-opensea Body-opensea TSS1500-shore TSS1500-shore IGR-opensea Body-opensea	chr4:74486044-74486258 chr13:112720564-112723582	n541184485,n151317773 n1897756107,n557342418 n1505795737,n5170644057,n555417897,n181098427 n0204691,n57378885,n5555267057,n024692 n5472724724,n11345449 n557885540 n200800773,n112355189,n55402965,n189142639,n71554295,n738653707,n19981905,n20	17:2 43:27 15:1 1:45:46:51 0:6:24:25 32:31 0: 0:1:9:10:11:34:35:36 0:38	6
cg24254317 cg08719486 cg04846432 cg00121963 cg20575254 cg19709862 cg15779586 cg24746838 cg16747564 cg16588114 cg23870749 cg18863922	-0.21465547 0.247706774 -0.23174168 0.296819208 -0.23535806 -0.20828527 0.202531676 -0.20115209 0.210301707 -0.21955447 -0.219199064 -0.204363	0.36687306 0.4327996 0.39565858 0.58655414 0.52669915 0.55954471 0.52033166 0.74852509 0.35623601 0.54130119 0.41321747 0.50653713	-3.19707612 3.196836607 -3.17088667 3.170188497 -3.16737073 -3.16710034 3.166870493 -3.16351552 3.166590235 -3.15546084 -3.145914244 -3.14160499	0.04138571 0.04139409 0.04231443 0.04233918 0.0424308 0.0424404 0.0424508 0.0424509 0.04258041 0.04283216 0.04287339 0.04318695 0.04338316	0.80699061 0.80701683 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.80791217 0.80791217 0.80791217 0.80804348 0.80826853	-3.65347332 -3.65370353 -3.67870704 -3.67937178 -3.68210417 -3.68236552 -3.68258769 -3.68583171 -3.69253443 -3.69362836 -3.70191409 -3.70706798	7 9 3 1 20 16 4 7 13 2 1 1	35015946 R 1.58E+08 F 90112101 R 1.87E+08 R 2.1E+08 F 54777948 F 47239315 R 74486675 F 64452895 F 1.13E+08 F 78578138 F 2.27E+08 R 1.57E+08 R		BRUNOL4 PTPRN2 DAPK1 MASP1 ITFG1 RASSF6 ZNF117 SOX1 PSEN2 C1orf92	Body TSS1500 3'UTR IGR Body TSS1500 TSS1500 TSS1500 IGR Body TSS1500	opensea shore opensea opensea opensea shore opensea shore opensea shore	Body-opensea TSS1500-shore 3'UTR-opensea IGR-opensea Body-opensea TSS1500-shore TSS1500-shore IGR-opensea Body-opensea Body-opensea	chr4:74486044-74486258 chr13:112720564-112723582 chr11:156890243-156890806	n54118486,7115131773 n189775167,755734248 n159775167,75573444035,555178937181098427 n159775167,75517084057,75524178937181098427 n59727744,7111395429 n5972744,7111395429 n5972782056,7551139427 n5667282056,7551134271	17:2 43:27 15:1 1:45:46:51 0:6:24:25 32:31 0: 0:1:9:10:11:34:35:36 0:38	6
cg24254317 cg08719486 cg04846432 cg00121963 cg20575254 cg19709862 cg25779586 cg24746838 cg16747564 cg26588114 cg23870749 cg18863922 cg23979631	-0.21465547 0.247706774 0.23174168 0.296819208 -0.23535806 -0.20828527 0.202351676 0.2013509 0.213031707 -0.21955447 0.217199064 0.204363 0.237153533	0.36687306 0.4327996 0.39565858 0.58655414 0.52669915 0.65954471 0.52033166 0.74852509 0.35623601 0.54130119 0.41321747 0.50653713 0.50633713	-3.19707612 3.196836607 -3.17088667 3.170188497 -3.16737073 -3.16710034 3.166870493 -3.16351552 3.156590235 -3.15546084 3.146914244 -3.14160499 3.14096897	0.04138571 0.04139409 0.04231443 0.0423918 0.04244104 0.0424508 0.0424508 0.0424591 0.04285216 0.04287339 0.04318695 0.04338316 0.04340673	0.80699061 0.80701683 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.8078542 0.8078542 0.80791217 0.80791217 0.80791217 0.80804348 0.80804348	-3.65347332 -3.65370353 -3.67870704 -3.67870704 -3.68230552 -3.68258769 -3.68258769 -3.69362836 -3.70191409 -3.70706798 -3.70706573	7 9 3 1 20 16 4 7 13 2 1 1 7	35015946 R 1.58±408 F 90112101 R 1.87±408 R 2.1±408 F 54777948 F 74486675 F 6445295 F 74486675 F 1.13±408 F 78578138 F 2.27±408 R 1.57±408 R 2.7142427 F		BRUNOL4 PTPRN2 DAPK1 MASP1 ITFG1 RASSF6 ZNF117 SOX1 PSEN2	Body TSS1500 3'UTR IGR Body TSS1500 TSS1500 IGR Body TSS1500 TSS1500 TSS1500 TSS1500	opensea shore opensea opensea opensea shore opensea shore opensea shore shore shore shore	Body-opensea TSS1500-shore 3'UTR-opensea IGR-opensea Body-opensea TSS1500-shore TSS1500-shore TSS1500-shore IGR-opensea Body-opensea TSS1500-shore	chr4:74486044-74486258 chr13:112720564-112723582	n541184485,n151317773 n189775167,7557342418 n531301795,n1145,0025,0554171897,181098427 n6024691,n137383883,n55554075,n6024692 n557885340 n55788540 n5578540 n557885400 n55785400 n55785400 n55785400 n55785400 n557854000000000	17,2 43,27 15,1 145,46,51 0,6,24,25 32,31 0,1-3:10,11,34,35,36 0,38 7,51	6
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cg24254317 cg08719486 cg04846432 cg00121963 cg20575254 cg19709862 cg25779586 cg24746838 cg16747564 cg26588114 cg23870749 cg18863922 cg23979631	-0.21465547 0.247706774 0.23174168 0.296819208 -0.23535806 -0.20828527 0.202351676 0.2013509 0.213031707 -0.21955447 0.217199064 0.204363 0.237153533	0.36687306 0.4327996 0.39565858 0.58655414 0.52669915 0.65954471 0.52033166 0.74852509 0.35623601 0.54130119 0.41321747 0.50653713 0.50633713	-3.19707612 3.196836607 -3.17088667 3.170188497 -3.16737073 -3.16710034 3.166870493 -3.16351552 3.156590235 -3.15546084 3.146914244 -3.14160499 3.14096897	0.04138571 0.04139409 0.04231443 0.0423918 0.04244104 0.0424508 0.0424508 0.0424591 0.04285216 0.04287339 0.04318695 0.04338316 0.04340673	0.80699061 0.80701683 0.80765045 0.80765045 0.80765045 0.80765045 0.80765045 0.8078542 0.8078542 0.80791217 0.80791217 0.80791217 0.80804348 0.80804348	-3.65347332 -3.65370353 -3.67870704 -3.67870704 -3.68230552 -3.68258769 -3.68258769 -3.69362836 -3.70191409 -3.70706798 -3.70706573	7 9 3 1 20 16 4 7 13 2 1 1 7 3 16	35015946 R 1.58±408 F 90112101 R 1.87±408 R 2.1±408 F 54777948 F 74486675 F 6445295 F 74486675 F 1.13±408 F 78578138 F 2.27±408 R 1.57±408 R 2.7142427 F		BRUNOL4 PTPRN2 DAPK1 MASP1 ITFG1 RASSF6 ZNF117 SOX1 PSEN2 C1orf92	Body TSS1500 3'UTR IGR Body TSS1500 TSS1500 IGR Body TSS1500 TSS1500 TSS1500 TSS1500	opensea shore opensea opensea opensea shore opensea shore opensea shore shore shore shore	Body-opensea TSS1500-shore 3'UTR-opensea IGR-opensea Body-opensea TSS1500-shore TSS1500-shore TSS1500-shore IGR-opensea Body-opensea TSS1500-shore	chr4:74486044-74486258 chr13:112720564-112723582 chr11:156890243-156890806	n541184485,n151317773 n189775167,7557342418 n531301795,n1145,0025,0554171897,181098427 n6024691,n137383883,n55554075,n6024692 n557885340 n55788540 n5578540 n557885400 n55785400 n55785400 n55785400 n55785400 n557854000000000	17,2 43,27 15,1 145,46,51 0,6,24,25 32,31 0,1-3:10,11,34,35,36 0,38 7,51	6
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For	all st	atistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.
n/a	Cor	firmed
		The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
	\square	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
		The statistical test(s) used AND whether they are one- or two-sided Only common tests should be described solely by name; describe more complex techniques in the Methods section.
	\square	A description of all covariates tested
	\square	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
		A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
	\boxtimes	For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i>) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted Give <i>P</i> values as exact values whenever suitable.
\boxtimes		For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
\boxtimes		For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
\boxtimes		Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated
		Our web collection on <u>statistics for biologists</u> contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection Provide a description of all commercial, open source and custom code used to collect the data in this study, specifying the version used OR state that no software was used.

Data analysis

fgsea R package (Sergushichev, A. An algorithm for fast preranked gene set enrichment analysis using cumulative statistic calculation. bioRxiv doi: 10.1101/060012(2016).)

ChAMP package (Morris, T.J., et al. ChAMP: 450k Chip Analysis Methylation Pipeline. Bioinformatics 30, 428-430 (2014).) limma (Ritchie, M.E., et al. limma powers differential expression analyses for RNA-sequencing and microarray studies. Nucleic Acids Res. 43, e47 (2015)) The networks and functional analyses of microarray data (igure 1 f, g, and S2 a, b and S3) were generated through the use of IPA

(QIAGEN Inc., https://www.qiagenbioinformatics.com/products/ingenuity-pathway-analysis; Causal analysis approaches in Ingenuity Pathway Analysis. Bioinformatics. 2014 Feb 15;30(4):523-30.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The microarray and methylation BeadChip data from this manuscript have been deposited in the National Centre for Biotechnology Information Omnibus (GEO)

under accession codes GSE107712 and GSE108202.

Raw data associated with Fig. 3f and Fig 4 can be found in Supplementary Tables 1 and 2, respectively.

Quantitative data supporting the findings of this study are available within the paper and its supplementary information files. All other data supporting these findings are available from the corresponding author upon reasonable request.

Field-specific reporting

 Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

 If sciences
 Behavioural & social sciences

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For a reference copy of the document with all sections, see <u>nature.com/documents/nr-reporting-summary-flat.pdf</u>

Life sciences study design

All studies must dis	close on these points even when the disclosure is negative.
Sample size	No statistical methods were used to predetermine sample size
Data exclusions	No data were excluded from the experiments
Replication	All attempts at replication were successful. All graphs represent data with at least two biological replicates, all images represent findings reproduced at least twice in the laboratory
Randomization	No specific procedures were carried out for randomization
Blinding	The investigator was blinded for image and quantitative analysis

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

MRI-based neuroimaging

Materials & experimental systems

Methods

 \boxtimes

 \boxtimes

n/a Involved in the study

ChIP-seq

n/a	Involved in the study							
	Antibodies							
	Eukaryotic cell lines							
\boxtimes	Palaeontology							
\boxtimes	Animals and other organisms							
	Human research participants							
\boxtimes	Clinical data							

Antibodies

Antibodies used	mouse anti-E-Cadherin (1:200 610181, BD Transduction Lab), mouse anti-β-actin (1:200, A5441, Sigma), goat anti-Ctr (OBT0978, AbD Serotec), mouse anti-HSP60 (1:5000, ALX-804-701, Alexis), rabbit anti-Ki67 (9027, Cell Signaling), rabbit anti-pSTAT1 (1:1000, 9167, Cell Signaling), rabbit anti-pSTAT3 (Tyr705) (1:1000 9145, Cell Signaling), cleaved caspase-3 (1:1000, 9664, Cell Signaling), goat anti-LIF (1:500, AF-250-NA, R&D Systems), sheep anti-mouse-HRP (1:3000, NA931, Amersham), donkey anti-rabbit-HRP (1:3000, NA934, Amersham), donkey anti-goat-HRP (1:3000, 800073, Biomol), donkey anti-mouse-Alexa 488 (1:300, 715-546-140, Dianova), donkey anti-goat-Cy3 (1:300, 715-605-150, Dianova), donkey anti-rabbit-Alexa 488 (1:300, 715-605-150, Dianova), donkey anti-mouse-Dylight 647 (1:300, 715-605-150, Dianova), CD326 (EpCAM)-FITC (1:50, 130-080-301, Miltenyi), mouse anti-human CD24-BV711 (1:200, 563371, BD Biosciences), mouse anti IgG1-APC (1:100, 130-098-846, Miltenyi) and mouse anti-human CD133/1 (AC133)-APC (1:100, 130-098-829, Miltenyi).
Validation	Validation was performed by the manufacturers; positive and negative controls were used in the lab for validation of each antibody

Eukaryotic cell lines

Policy information about <u>cell lines</u>

Cell line source(s)

HeLa cells, ATCC® CCL-2

Authentication	HeLa cells were ordered as an authenticated cell line from ATCC	
Mycoplasma contamination	All cell lines tested negative for mycoplasma contamination.	
Commonly misidentified lines (See <u>ICLAC</u> register)	We used HeLa cells for Chlamydia stock expansion and infectivity assay as they are the standard cell line used for confirming infection with Chlamydia trachomatis.	

Human research participants

Policy information about stud	ies involving human research participants					
Population characteristics	Tissue was donated by female patients aged 40 to 75					
Recruitment	2014-2018					
Ethics oversight	Ethics comimssion Charite Medical University Berlin					
Note that full information on the approval of the study protocol must also be provided in the manuscript						

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Flow Cytometry

Plots

Confirm that:

The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).

The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).

 \square All plots are contour plots with outliers or pseudocolor plots.

A numerical value for number of cells or percentage (with statistics) is provided.

Methodology

Sample preparation	CtrD infected as well as non-infected fallopian tube organoids were split at indicated time points into single cells by enzymatic (TrypLE, 15 min, 37°C) and mechanical (needle, 26G) treatment. Single cell suspensions were filtered (0.45 μ m), fixed in 3.7% PFA (30 min, RT) and washed with 1%BSA/PBS. Fixed cells were stained in 1%BSA/PBS with either CD24-BV711 and EpCAM-FITC or CD133-APC (30 min on ice). After staining, cells were washed with PBS and analysed using a flow cytometer. For assessing the number of proliferating cells a Click-iT-EdU assay (C10425, Thermo Fisher) was performed. For this organoids were incubated for 2 h with 10 μ M EdU, followed by single cell preparation and fixation. Permeabilization and labeling of EdU positive cells with Alexa488 azide was performed according to the manufacturer's protocol.
Instrument	BD FACS CANTOII flow cytometer (BD Biosciences)
Software	BD FACSDiva Software and FlowJo (FlowJo LLC)
Cell population abundance	Only flow cytometric analysis but no sorting was performed.
Gating strategy	From the initial cell population, which was gated in FSC-A/SSC-A by eliminating debris, singlets were discriminated using forward scatter (FSC-H/FSC-W) and side scatter (SSC-H/SSC-W) plots. Boundaries between positive and negative populations were defined using unstained or isotype controls. Representative gating strategies for each analysis are depicted in Supplementary Figures 5a and 6.

X Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.