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Original research

PARP-1 selectively impairs *KRAS*-driven phenotypic and molecular features in intrahepatic cholangiocarcinoma

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ABSTRACT

Objective Intrahepatic cholangiocarcinoma (iCCA) is the second most common primary liver cancer with limited therapeutic options. *KRAS* mutations are among the most abundant genetic alterations in iCCA associated with poor clinical outcome and treatment response. Recent findings indicate that Poly(ADP-ribose) polymerase1 (PARP-1) is implicated in *KRAS*-driven cancers, but its exact role in cholangiocarcinogenesis remains undefined.

Design *PARP-1* inhibition was performed in patient-derived and established iCCA cells using RNAi, CRISPR/Cas9 and pharmacological inhibition in *KRAS*-mutant, non-mutant cells. In addition, *Parp-1* knockout mice were combined with iCCA induction by hydrodynamic tail vein injection to evaluate an impact on phenotypic and molecular features of *Kras*-driven and *Kras*-wildtype iCCA. Clinical implications were confirmed in authentic human iCCA.

Results PARP-1 was significantly enhanced in *KRAS*-mutant human iCCA. PARP-1-based interventions preferentially impaired cell viability and tumourigenicity in human *KRAS*-mutant cell lines. Consistently, loss of *Parp-1* provoked distinct phenotype in *Kras/Trp53*-induced versus *Akt/Nicd*-induced iCCA and abolished *Kras*-dependent cholangiocarcinogenesis. Transcriptome analyses confirmed preferential impairment of DNA damage response pathways and replicative stress response mediated by CHK1. Consistently, inhibition of CHK1 effectively reversed PARP-1 mediated effects. Finally, *Parp-1* depletion induced molecular switch of *KRAS*-mutant iCCA recapitulating good prognostic human iCCA patients.

Conclusion Our findings identify the novel prognostic and therapeutic role of *PARP-1* in iCCA patients with activation of oncogenic *KRAS* signalling.

INTRODUCTION

Intrahepatic cholangiocarcinoma (iCCA) is the second most common primary liver cancer (PLC) with increasing incidence and rising mortality

WHAT IS ALREADY KNOWN ON THIS TOPIC

⇒ PARP-1 is involved in multiple oncogenic pathways and processes, including DNA repair, genomic stability, chromatin modification, energy metabolism and apoptosis. Evidence suggests an association between *PARP-1* overexpression and *KRAS* mutations in various cancers, such as acute myeloid leukaemia and colorectal cancer. However, there is limited information available on the impact of *PARP-1* expression on therapeutic response in *KRAS*-mutant intrahepatic cholangiocarcinoma (iCCA).

WHAT THIS STUDY ADDS

⇒ Our results demonstrate that *KRAS*-mutant iCCA cells become highly sensitive to PARP-1 depletion and inhibition *in vitro* while *Parp-1* deficient mice show reduced cholangiocarcinogenesis *in vivo*. Mechanistically, PARP-1 effects in *KRAS*-mutant iCCA are mediated through CHK1 activation, and this process can be reversed by chemical inhibition. Inhibiting PARP-1 in *KRAS*-mutant tumours leads to a favourable change in prognostic outcome for human iCCA.

HOW THIS STUDY MIGHT AFFECT RESEARCH, PRACTICE OR POLICY

⇒ These findings reveal a novel prognostic and therapeutic role of PARP-1 in iCCA patients with activated oncogenic *KRAS* signaling and poor prognosis. This knowledge may open new avenues for targeted therapies in this particular subset of iCCA patients.

rates.^{1–3} A profound genetic heterogeneity and diverse spectra of prognostically distinct molecular subgroups render iCCA a prototype for precision oncological approaches.^{4,5} Several druggable alterations in oncogenic signalling pathways (eg, *fibroblast growth factor receptor 2 gene* fusions,

isocitrate dehydrogenase 1 and 2 mutations) have been identified in iCCA. The application of specific inhibitors became a new mainstay of therapy and significantly improved the overall survival of patients. However, despite great progress in molecularly guided therapy, only 30%–40% of the iCCA patients present with the above-mentioned druggable alterations.⁶ Thus, therapeutic options remain severely limited for the majority of patients. Among the most prominent alterations identified in iCCA, *KRAS* mutations historically posed significant challenges for specific targeting.^{2,7} Activating *KRAS* mutations have been observed in around 10%–15% of iCCA patients. Importantly, *KRAS* alterations are characterised by poor response to commonly used chemotherapy and display a reduced overall survival.^{8,9} Besides direct protumourigenic properties and increased proliferative characteristics, activated RAS-signalling results in increased intracellular stress which renders RAS-driven tumours particularly dependent on non-oncogenic mechanisms that promote oxidative stress response, apoptosis, and, particularly, DNA damage response (DDR).^{10,11}

Several lines of evidence suggest that inhibition of the DDR protein PARP-1 might selectively affect the survival of *KRAS*-mutant tumour cells of different entities, including colorectal cancer (CRC) as well as acute myeloid leukaemia (AML).^{12–14} PARP-1 is the most prominent member of the PARP family, involved in several cellular processes such as DDR, genomic stability, chromatin modification, transcription regulation, energy metabolism and programmed cell death. It catalyses poly(ADP-ribosylation) (PARylation) on metabolic, oxidative or genotoxic stress and influences the cellular metabolic status by enhancing NAD⁺ and ATP consumption.^{15,16} Inhibition of PARP-1 is closely linked to the concept of synthetic lethality, as pharmacologically inactivated PARP-1 is trapped onto the DNA, causing stalling of the replication fork and thereby sensitising DDR-deficient cells.¹⁷ Consequently, PARP-1 inhibitors have emerged as a therapeutic option in BRCA1/2-mutant ovarian and breast cancers, as well as in prostate and pancreatic cancer that depend on functional DNA repair mechanisms.^{18,19} Several clinical trials evaluate PARP-1 inhibition in CCA, however, the mechanistic and therapeutic relevance of *PARP-1* and its inhibition in the context of *KRAS*-mutant iCCA is unknown.²⁰ In the presented study, we aimed to dissect phenotypic and molecular characteristics of *PARP-1* in iCCA with a particular focus on *KRAS*-mutant subgroups known to have a high cellular turnover (thus, constitutively activated DNA repair mechanisms).^{10,11}

RESULTS

PARP-1 expression is abundant in *KRAS*-mutant iCCA

Given the relevance of deregulated DNA repair mechanisms in cholangiocarcinogenesis (particularly homologous recombination (HR) and non-homologous end-joining (NHEJ)), we sought to investigate the relationship between *KRAS* mutations and *PARP-1* expression (figure 1A).^{12,13} First, we aimed to investigate a putative association between both molecules in iCCA tissue and analysed the correlation between *PARP-1* and *KRAS* expression in the TCGA patient cohort.^{21,22} The median expression of *PARP-1* and *KRAS* was significantly upregulated in cholangiocarcinoma (CHOL) ($p < 0.01$) (online supplemental figure S1A–C). Further, pairwise correlation analysis showed a positive correlation ($r = 0.6$, $p < 0.0001$) (online supplemental figure S1D,E) between both genes. Interestingly, while *PARP-1* expression was significantly upregulated in both iCCA and HCC, association with *KRAS* could only be confirmed in iCCA. To confirm

these observations, we performed PARP-1 staining using a tissue microarray (TMA) comprising 194 iCCA as well as 54 specimens from normal bile ducts. We confirmed that PARP-1 levels were significantly increased in iCCA versus normal bile duct (online supplemental figure S1F, $p < 0.0001$). In addition, we evaluated the expression of *PARP-1* in an independent iCCA cohort including 151 iCCA, 143 surrounding liver and nine normal bile ducts. Consistently, a significant upregulation of the *PARP-1* on a transcriptome level was observed in iCCA in comparison with the surrounding liver and normal bile ducts (online supplemental figure S1G). In addition, expression of *PARP-1* was positively correlated with genes known to be associated with proliferative capacity (online supplemental figure S1H). Interestingly, expression of *PARP-1* also showed a significant association with overall survival and recurrence-free survival based on *KRAS* status in iCCA (online supplemental figure S1I).

Next, we examined *PARP-1* expression in a variety of different *KRAS*-mutant and *KRAS*-wildtype iCCA cell lines. Consistently, we found a significant overexpression of *PARP-1* in *KRAS*-mutant iCCA cell lines versus non-mutant cell lines (CCC33 vs CCC16 $p = 0.0240$; WITT vs HuCCT1 $p = 0.0142$; WITT vs RBE $p = 0.0034$; HuH28 vs HuCCT1 $p = 0.0113$; HuH28 vs RBE $p = 0.0023$) (figure 1B). Significant increase of *PARP-1* could further be confirmed on protein level (CCC33 vs CCC16 $p = 0.0286$; WITT vs HuCCT1 $p = 0.0105$; WITT vs RBE $p = 0.0122$; HuH28 vs HuCCT1 $p = 0.0162$; HuH28 vs RBE $p = 0.0234$) (figure 1C,D). Together, these investigations support the hypothesis that *PARP-1* is preferentially upregulated on RNA and protein level in *KRAS*-mutant, but not *KRAS*-wildtype iCCA.

KRAS-mutant iCCAs show preferential sensitivity towards *PARP-1* inhibition in vitro

Given the potential association of *KRAS* mutations and *PARP-1* overexpression in iCCA, we next employed selective RNAi knock-down of *PARP-1* in the *KRAS*-mutant and non-mutant iCCA cell lines to further characterise the potential of *PARP-1* as a putative therapeutic target in this subgroup of patients. Successful knock-down of *PARP-1* protein expression was confirmed by Western blotting overall achieving a 66.6%–83.8% reduction compared with control cells (CCC33 78.5%, $p = 0.0091$; CCC16 71.0%, $p = 0.0040$; WITT 66.6%, $p = 0.0358$; HuCCT1 82.4%, $p < 0.0001$; RBE 83.8%, $p = 0.0006$) (figure 1E). Importantly, *PARP-2* protein levels were not affected by the *PARP-1* knock-down. Notably, transfection of the *KRAS*-wildtype iCCA cell line HuH28 was not successful due to the low proliferation rate of this cell line. The impact of *PARP-1* knock-down on proliferation was subsequently demonstrated using CFU and SFU. A significant reduction of colony (CCC16 40.5%, $p = 0.0043$; HuCCT1 38.8%, $p = 0.0243$; RBE 40.4%, $p = 0.0002$) and spheroid (CCC16 40.8%, $p = 0.0041$; HuCCT1 41.5%, $p < 0.0001$; RBE 46.7%, $p < 0.0001$) formation capacity ranging from 35.6% to 45.8% was observed in *KRAS*-mutant versus control cells. In contrast, neither colony nor spheroid formation capacity was affected in *KRAS*-wildtype iCCA cell lines (figure 1F).

Next, we used the FDA-approved *PARP-1* inhibitor olaparib to confirm the association of *PARP-1* and *KRAS* in the context of chemical inhibition. In concordance with the finding from RNAi experiments, *KRAS*-mutant iCCA cell lines showed a significantly reduced viability in response to *PARP-1* inhibition compared with *KRAS*-wildtype cell lines (CCC33 vs CCC16 $p = 0.0068$; WITT vs HuCCT1 $p = 0.0078$; WITT vs RBE $p = 0.0026$; HuH28 vs HuCCT1 $p = 0.0725$; HuH28 vs RBE $p = 0.0114$) (online supplemental figure S2A). Moreover, olaparib caused

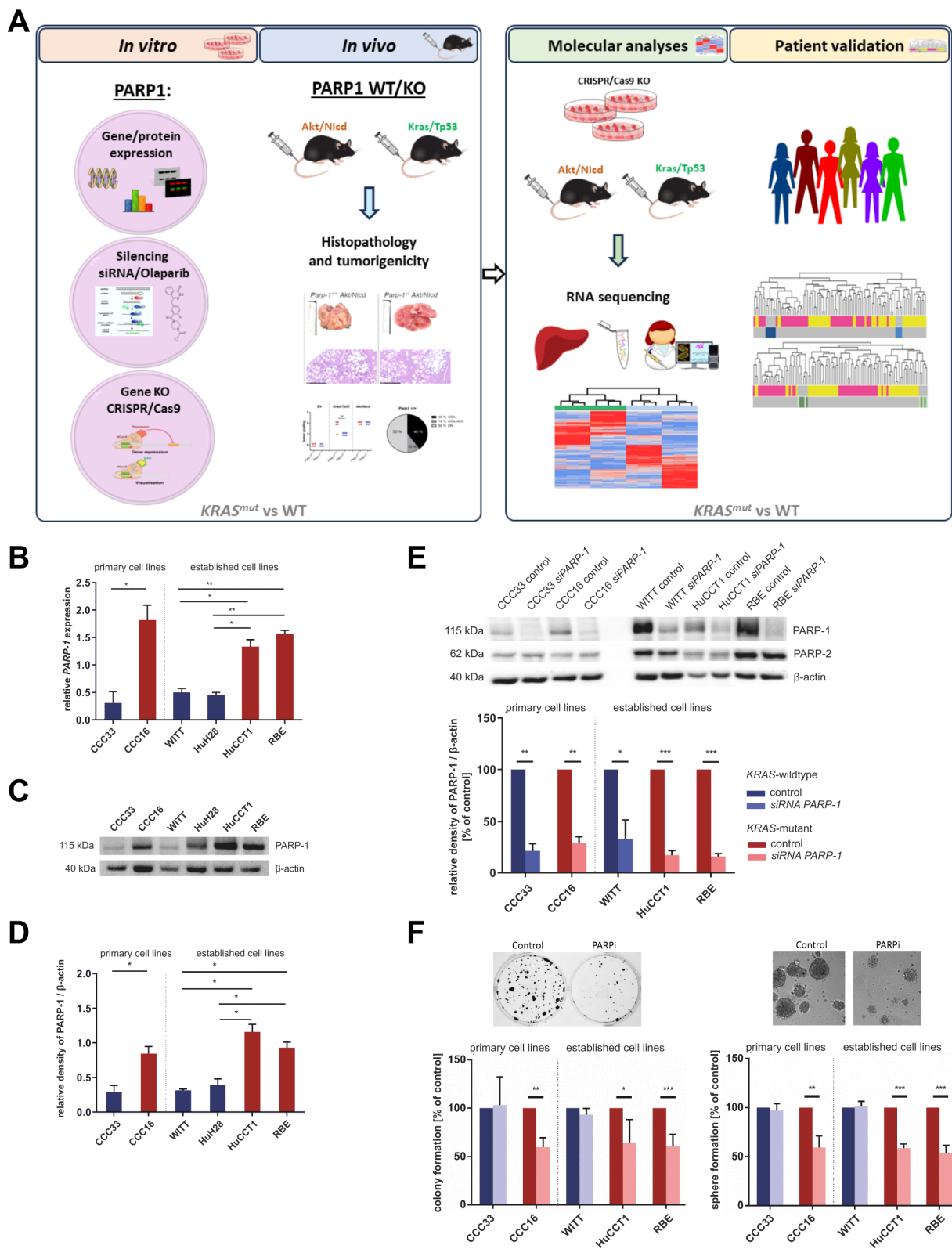


Figure 1 PARP-1 expression in *KRAS*-mutant and *KRAS*-wildtype iCCA and effect of siRNA-mediated knockdown of *PARP-1* on cell viability, colony and sphere formation capacity. (A) Graphical representation of the experimental design. (B) Relative *PARP-1* expression normalised to normal liver tissue in *KRAS*-mutant (CCC16, HuCCT1, RBE; red) and *KRAS*-wildtype iCCA cell lines (CCC33, WITT, Huh28; blue). Mean \pm SD, n=3, *p<0.05, **p<0.01. (C) Representative Western blot and (D) densitometry analysis of basal *PARP-1* protein expression in *KRAS*-mutant and *KRAS*-wildtype iCCA cell lines. Relative density of *PARP-1* expression normalised to β -actin is shown. Mean \pm SD, n=3, *p<0.05. (E) Representative Western blot and densitometric analysis of siRNA-mediated knockdown of *PARP-1* protein expression in *KRAS*-mutant (CCC16, HuCCT1, RBE; red) and *KRAS*-wildtype iCCA cell lines (CCC33, WITT; blue). Relative density of *PARP-1* expression normalised to β -actin is shown. Mean \pm SD, n=3, *p<0.05, **p<0.01, ***p<0.001. (F) Representative images of colony and sphere formation assay as well as % of control after siRNA-mediated *PARP-1* knockdown in *KRAS*-mutant and *KRAS*-wildtype iCCA cell lines. Mean \pm SD, n=3, *p<0.05, **p<0.01, ***p<0.001. iCCA, intrahepatic cholangiocarcinoma.

a selective G1 cell cycle arrest in *KRAS*-mutated primary cells (online supplemental figure S2B).

In addition, PARP-1 inhibition also led to a decrease in the number of CFU and SFU in *KRAS*-mutant iCCA cell lines (CFU: CCC16 50.3%, $p=0.0003$; HuCCT1 51.6%, $p<0.0001$; RBE 49.6%, $p<0.0001$; SFU: CCC16 36.6%, $p<0.0001$; HuCCT1 38.5%, $p=0.0002$; RBE 42.1%, $p<0.0001$). Although olaparib exerted slight effects on colony formation in *KRAS*-wildtype iCCA cell lines CCC33 (27.6%, $p=0.0003$) and WITT (8.4%, $p=0.0171$), the spheroid forming capacity of *KRAS*-wildtype iCCA cell lines remained unaffected in all cell lines on olaparib treatment (online supplemental figure S2C). Notably, reduction in CFU was considerably less pronounced in *KRAS*-wildtype versus *KRAS*-mutant cells, which is presumably due to unspecific toxic effects of olaparib unrelated to PARP-1 inhibition.

To unveil potential synergistic effects between olaparib and cytotoxic compounds used for iCCA therapy, we treated *KRAS*-wildtype and mutated primary cell lines (CCC16 and CCC33) with olaparib in combination with cisplatin and gemcitabine. Combination therapy showed a significantly higher level of synergism for both tested drugs, gemcitabine and cisplatin, in the *KRAS*-mutated cell line (online supplemental figure S2D). To further address whether inhibition of other components of the DDR would induce a similar selective response in *KRAS*-mutated cancers, we tested the efficacy of an additional drug involved in DDR, namely the DNA-PKcs inhibitor KU57788, leading to inhibition of NHEJ. Consistent with a selective effect of PARP-1 inhibition in *KRAS*-mutated iCCA, effect of KU57788 was independent of the mutational status and no significant differences between *KRAS* WT and KO cell lines were observed (online supplemental figure S2E). Taken together, these investigations confirm the preferential antitumourigenic effects of PARP-1-based interventions in *KRAS*-mutant iCCA cell lines and validate the potential utility of combination therapy for the treatment of this subtype of iCCA.

Impact of *PARP-1* depletion on transcriptomic profile, DDR and ROS in *KRAS*-mutant iCCA cell lines

Our functional analyses showed pronounced *KRAS*-dependent differences in iCCA cell lines on PARP-1-based interventions. To further define molecular alterations influenced by PARP-1 inhibition, we generated stable *PARP-1* knockout (*PARP-1* KO) clones of the different iCCA cell lines HuCCT1, RBE, WITT and CCC33 using CRISPR/Cas9 followed by RNA sequencing (online supplemental figure S3A).

First, we explored whole transcriptome differences in *PARP-1* KO in *KRAS*-mutant iCCA cell lines compared with their scrambled control clones using Wald's statistics and revealed a total of 1171 (660 down, 511 up) differentially expressed genes ($p<0.05$; online supplemental table S1). Accordingly, unsupervised hierarchical cluster analyses and principal component analysis plot confirmed that *PARP-1* KO clones of both *KRAS*-mutant iCCA cell lines display distinct molecular profiles (figure 2A).

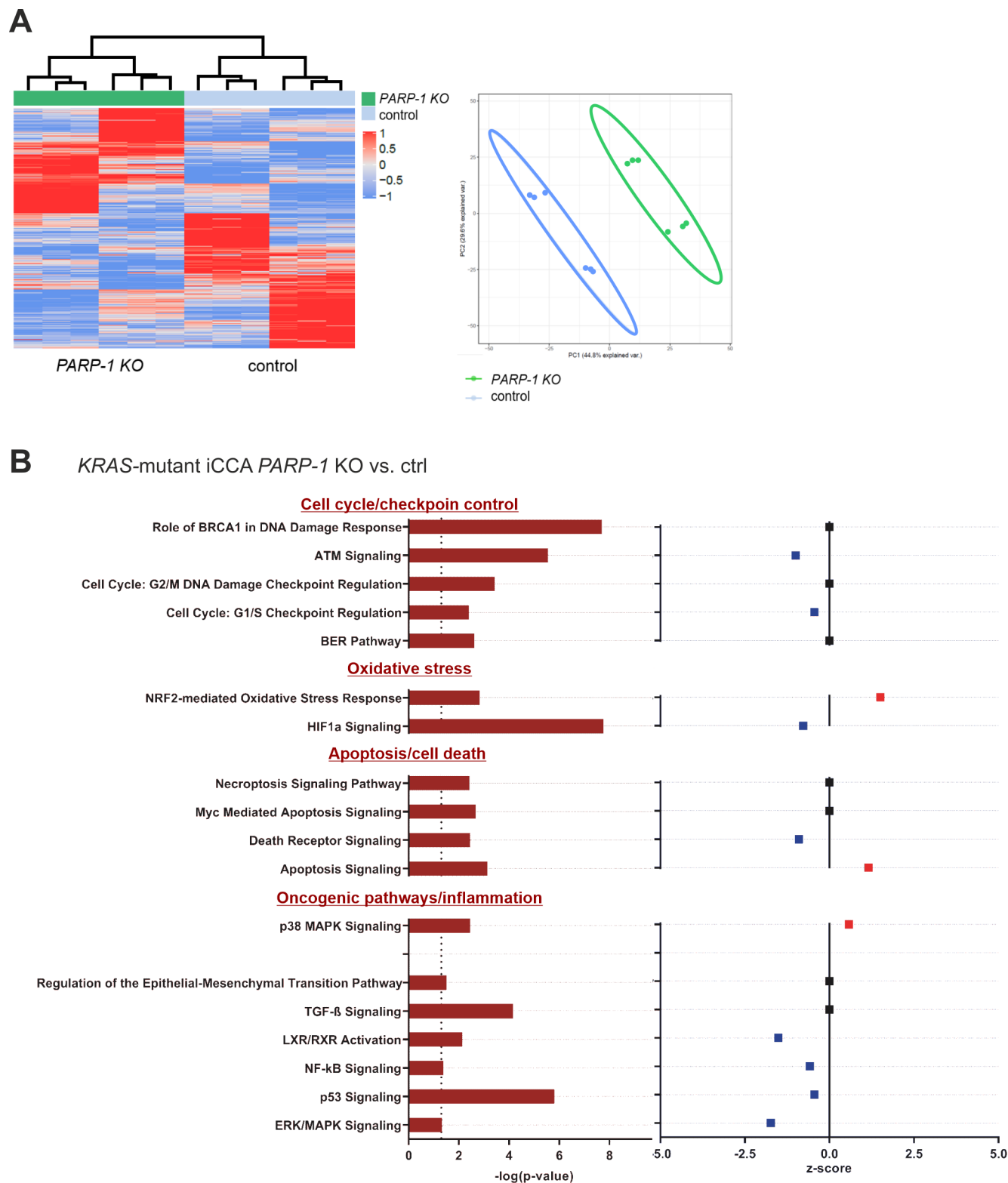
We also evaluated functional signalling pathways related to the differential response to *PARP-1* deficiency and identified that gene sets related to cell cycle control, for example, G1/S checkpoint regulation as well as BRCA1-mediated DNA damage, among others, were significantly dysregulated after *PARP-1* KO (figure 2B). In addition, oxidative stress response (NRF-2 mediated oxidative stress response, HIF1 α signalling) as well as apoptosis-related pathways (death receptor signalling, apoptosis signalling, Necroptosis signalling, and Myc-mediated apoptosis) were affected by selective depletion of *PARP-1* in *KRAS*-mutant

iCCA cells (figure 2B). Further, the cell lines also showed disruption in known oncogenic signalling resembling ERK/MAPK, p53, HIF1 α and NF- κ B signalling after *PARP-1* depletion. Moreover, *PARP-1* KO enhanced adverse processes in *KRAS*-mutant iCCA cell lines (online supplemental figure S4A), known to promote hepatobiliary carcinogenesis. Consistently, gene sets related to DNA repair mechanisms, such as the G2/M DNA damage checkpoint and BER, apoptosis and TGF β signalling were significantly enriched in *KRAS*-mutant *PARP-1* KO cells (online supplemental figure S4B). Overall, transcriptomic analyses indicated a dependency of *KRAS*-mutant iCCA cells on functional DNA repair mechanisms to compensate for increased oxidative stress, apoptotic stimuli and replicative stress induced by a high cellular turnover and proliferative capacity of *KRAS*-mutant iCCA cell lines on *PARP-1* KO, which might confer the distinct effects in *KRAS*-mutant iCCAs.

We further evaluated the impact of irradiation and oxidative stress on *KRAS*-mutant and *KRAS*-wildtype iCCA cell lines on *PARP-1* KO. First, we investigated the impact of irradiation-induced DNA damage in *PARP-1* KO clones by measuring phospho- γ H2AX foci as a marker for DNA double-strand breaks. Irradiation led to a significantly increased number of DNA double-strand breaks in *KRAS*-mutant iCCA cell line RBE only in *PARP-1* KO clones compared with control conditions (online supplemental figure S5A). In contrast, *KRAS*-wildtype iCCA cell line CCC33 showed a significantly increased number of DNA double-strand breaks independent of *PARP-1* KO status. Assessment of ROS level showed that in *KRAS*-mutant iCCA cell line RBE the basal ROS levels were significantly higher in the *PARP-1* KO clones when compared with their respective scrambled control clones. In contrast, the basal status of ROS did not differ in *PARP-1* KO clone of *KRAS*-wildtype iCCA cell line CCC33. Consistently, H₂O₂ administration led to a significant increase in oxidative stress in *KRAS*-mutant iCCA cell lines, whereas levels of oxidative stress in *KRAS*-wildtype iCCA cell line CCC33 remained unaffected (online supplemental figure S5B).

Mechanism of PARP-1 regulation was further explored in authentic iCCA tumours harbouring *KRAS* mutation. *KRAS*-mutated iCCA showed upregulation of genes associated with DNA double-strand break repair mechanisms. In addition, genes associated with HR (eg, *BARD1*, *EXO1*, *RAD54L*, *CHEK1*, *UIMC1*, *RAD51*, *BRCA2*) and both canonical and alternative NHEJ (c-NHEJ; eg, *XRCC4*, *DCLRE1C*; alt-NHEJ; eg, *POLQ*, *LIG1*, *FEN1*, *XRCC1*) were activated (online supplemental figure S5C). We further tested enrichment of gene sets in *KRAS*-mutant tumours to test association with PARP-1 and DNA damage control. Analyses revealed enrichment of BRCA1 and HR in the tumours carrying *KRAS* mutation (online supplemental figure S5D). To substantiate these observations, we performed RPPA analyses of two primary cell lines representing the mutational *KRAS* status and confirmed that proteins involved in HR are significantly increased in *KRAS*-mutated cells (CCC16) (CtIP, RAD50 and RAD51) (online supplemental figure S5E). Thus, these investigations underline that major mechanisms of DNA damage repair, including *PARP-1*, are closely associated with *KRAS* mutation in iCCA.

In addition, we performed single-cell analysis of tumours from 11 iCCA patients. These analyses confirmed differential expression of DDR genes in malignant cells from patients with *KRAS* mutations compared with those cells derived from patients without the mutations. This was not observed in non-malignant cells, suggesting that the phenomenon is tumour cell specific (online supplemental figure S6A-C).



Hepatobiliary carcinogenesis is selectively impaired in *Kras*/*Tp53*-driven tumours with genetic *Parp-1* deficiency

To dissect the relevance of *PARP-1* in *KRAS*-driven and

non-*KRAS*-mutant iCCA development, we employed HDTV-induced hepatobiliary carcinogenesis in genetically modified *Parp-1* proficient and deficient mice. Herein, *Kras* induction

together with *Tp53* knockdown (*Kras/Tp53*) led to preferential occurrence of distinct solid tumours within 10 weeks after injection in *Parp-1* proficient mice (online supplemental figure S7A). Histopathological analyses of an expert hepatopathologist revealed tumours with gland-like structures in accordance with the diagnosis of iCCA, most often well differentiated, in one example also with signs of dedifferentiation with sarcomatoid tumour cells including tumour giant cells (figure 3A, online supplemental figure S8A). No mucin production was observed, that is, the tumours resemble iCCA of small-duct type. In addition, *Parp-1* proficient mice also displayed multiple small-cell dysplastic foci and nodules with development of early hepatocellular carcinoma and focal tumourous vein invasion (online supplemental figure S8B).

In striking contrast, animals with *Parp-1* deficient genotype were characterised by a complete absence of CCA features. Histopathological assessment revealed multiple, diffuse hepatocellular carcinomas as well as dysplastic nodules with focal tumourous vein invasion (figure 3A). Further, moderate macrovesicular steatosis (11%–50%) and disrupted architecture of liver parenchyma was also observed (online supplemental figure S8A,B). These investigations suggest that the *Parp-1* deficiency preferentially inhibits cholangiocarcinogenesis.

Mice with tumours induced by *Kras/Tp53* combination showed significant differences in their average body weight between *Parp-1*^{+/+} and *Parp-1*^{-/-} animals with 27.8 g and 29.7 g, respectively ($p=0.0234$). Further, the average liver weight significantly differed depending on the *Parp-1* status with 2.75 g for *Parp-1*^{+/+} and 6.10 g for *Parp-1*^{-/-} mice ($p<0.0001$), likely due to the presence of tumour nodules (online supplemental figure S7B). Consistently, we observed pronounced differences in liver to body weight (L/B)-ratio and scoring on *Kras/Tp53* injection between *Parp-1*^{+/+} and *Parp-1*^{-/-} experimental groups (L/B-ratio $p<0.0001$, tumour scoring $p=0.003$) (figure 3B–D).

Interestingly, classic biliary marker (Sox9) confirmed cholangiocarcinoma in tumour sections of *Parp-1*^{+/+} mice injected with *Kras/Tp53*, whereas dysplastic nodules in surrounding liver sections of *Parp-1*^{+/+} mice as well as of *Parp-1*^{-/-} mice were expectedly negative for Sox9 expression, confirming the hepatocellular lineage of these cells (figure 3A). Nuclear *Parp-1* expression was detectable in all sections of *Parp-1*^{+/+} mice, whereas no *Parp-1* expression was determined in *Parp-1* deficient liver sections (*Parp-1*^{+/+} tumour vs *Parp-1*^{-/-} dysplastic foci $p<0.0001$; *Parp-1*^{+/+} dysplastic foci vs *Parp-1*^{-/-} dysplastic foci $p<0.0001$) (online supplemental figure S9A). As expected, significantly higher proliferation (Ki67) was detected in tumour tissue of *Parp-1* proficient mice compared with dysplastic nodules (*Parp-1*^{+/+} tumour vs *Parp-1*^{+/+} dysplastic foci $p<0.0001$; *Parp-1*^{+/+} tumour vs *Parp-1*^{-/-} dysplastic foci $p<0.0001$) (online supplemental figure S9A). Further, DNA damage sites represented by γ H2ax positive foci were randomly distributed in both tumour and surrounding liver sections of *Parp-1*^{+/+} mice and significantly more pronounced than in *Parp-1*^{-/-} mice (*Parp-1*^{+/+} tumour vs *Parp-1*^{-/-} dysplastic foci $p<0.0001$; *Parp-1*^{+/+} dysplastic foci vs *Parp-1*^{-/-} dysplastic foci $p=0.009$) (online supplemental figure S9A). Taken together, the histopathological assessment of the *Kras/Tp53*-induced tumours showed differences in tumour entity from the evolution of cholangiocellular carcinoma instead of hepatocellular carcinoma, confirming that iCCA development in *Kras*-mutant cancers is highly dependent on proficient *Parp-1* signalling.

To confirm the relevance of activated *Kras* in a *Parp-1* deficient background, non-*Kras*-driven iCCAs were induced by myrAkt/myc-tagged *Nicd* (combination referred to as *Akt/Nicd*). Average

body and liver weight did not differ significantly dependent on the *Parp-1* genotype in the *Akt/Nicd* model (online supplemental figure S7B). Further, animals injected with *Akt/Nicd* developed tumours and cystic alterations 7 weeks after HDTV with pronounced hepatomegaly as well as steatohepatitis independent of the *Parp-1* genotype (figure 3A, online supplemental figure S8A). An expert pathologist classified the tumours as iCCA with well to moderate differentiation grade (G1–2), severe macrovesicular steatosis (>50%) and disrupted architecture of liver parenchyma due to the occurrence of multiple tumour foci (online supplemental figure S8B). Sporadic or unspecific effects of HDTV were excluded in livers of mice injected with empty vector (EV) control (results not shown). In contrast to *Kras/Tp53*-induced hepatobiliary tumour growth, EV-injected and *Akt/Nicd*-injected animals showed no differences in morphology, histological classification and quantification (L/B-ratio, tumour scoring) of tumours/livers (figure 3B–D, online supplemental figures S8A,B and S9B). Thus, a selective effect of *Parp-1* depletion in *Kras/Tp53*-driven tumours was confirmed.

Impact of *Parp-1* deficiency on the transcriptome of *Kras/Tp53*-induced cholangiocarcinogenesis via HDTV

To further define the molecular features underlying distinct morphological and histopathological differences in the groups, we performed RNA sequencing of HDTV-induced tumours driven by *Kras/Tp53* or *Akt/Nicd*.

We identified a total of 7661 differentially expressed genes (4577 downregulated, 3084 upregulated) between liver/tumour tissue samples of *Kras/Tp53 Parp-1*^{+/+} and *Parp-1*^{-/-} animals ($p<0.05$) (figure 4A; online supplemental table S2). Pathways related to cell cycle control, like G1/S checkpoint regulation and G2/M DNA damage checkpoint regulation and ATM signalling were among the prominent molecular changes associated with the phenotype (figure 4B, online supplemental figure S10). Further, the DNA double-strand break repair pathway associated with BRCA1 was predicted to be negatively regulated in *Parp-1* deficient animals versus *Parp-1* proficient animals. These findings suggest that DDR mechanisms are dysregulated in *Kras/Tp53*-injected animals in a *Parp-1*-dependent manner. Further functional networks involved inhibition of oxidative stress pathways (NRF-2-mediated oxidative stress response, HIF1 α signalling), whereas apoptosis-related pathways were activated (death receptor signalling) in *Parp-1* deficient animals. *Kras/Tp53* induced tumours under *Parp-1* KO showed enrichment of LXR/RXR, p53, PTEN and HIPPO signalling. Inhibition of pathways was shown in key oncogenic pathways like TGF β , NF- κ B, Notch and ERK/MAPK signalling (figure 4B). Interestingly, several DNA repair pathways were significantly enriched in *Parp-1*^{+/+} mice injected with *Kras/Tp53*. Besides DNA single-strand break repair mechanisms, also double-strand break repair pathways (NHEJ, HR) were enriched suggesting that *Parp-1* proficiency is important for DDR and repair mechanisms in *Kras*-driven hepatobiliary tumourigenesis (online supplemental figure S11A). Activation of key pathways identified at the transcriptomic level was validated by IHC in *Kras/Tp53 Parp-1*^{-/-} animals (online supplemental figure S10C). These findings are in concordance with our in vitro findings (figure 2, online supplemental figure S4).

To confirm the selective effects of *Kras* in *Parp-1* deficient animals, we analysed transcriptomic profiles of *Parp-1* deficient and proficient mice injected with *Akt/Nicd*. The number of significantly altered genes was considerably less, comprising only 158 (95 down, 63 up) differentially expressed genes ($p<0.05$)

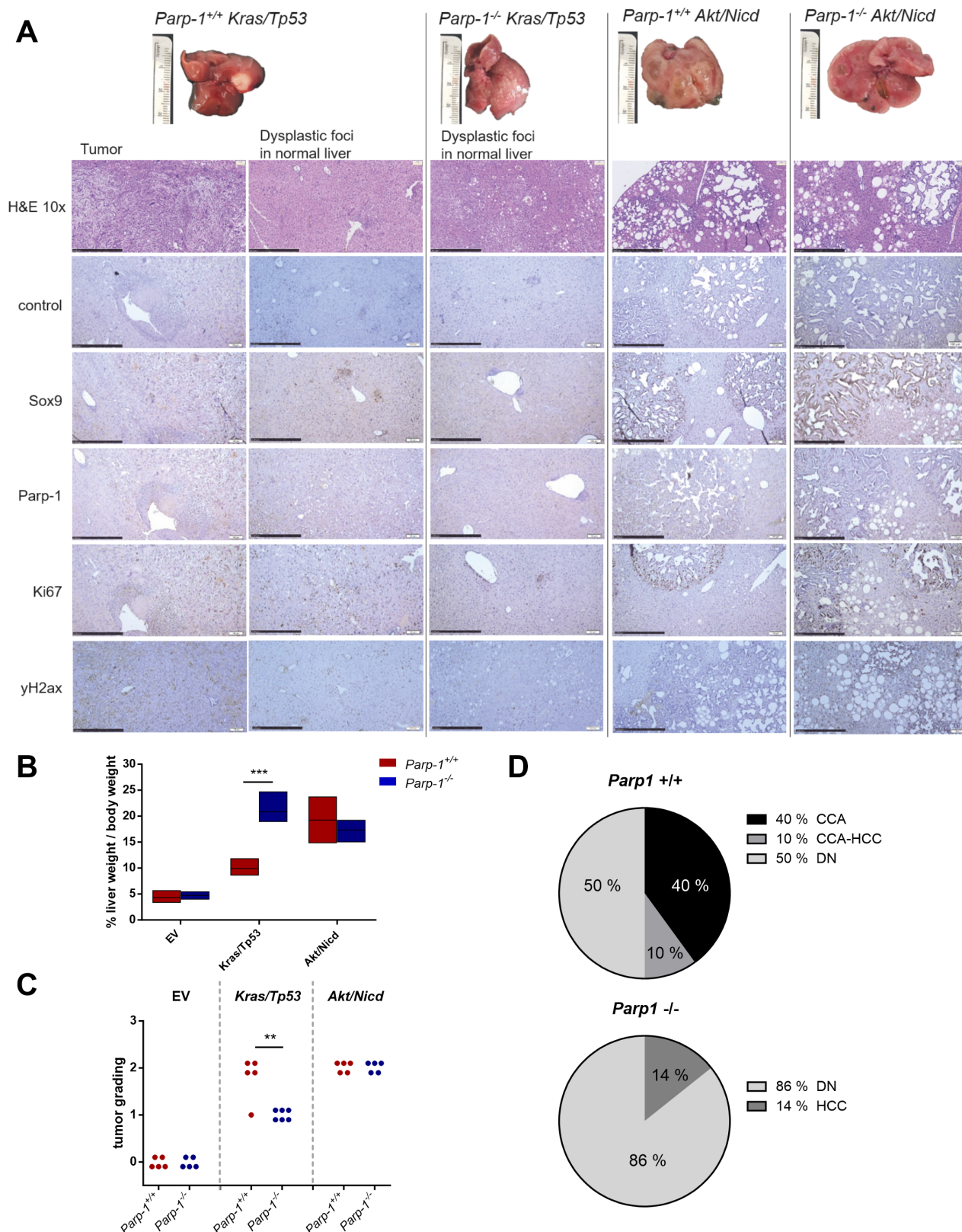


Figure 3 Histology and immunohistochemistry (IHC) of liver sections injected with *Kras/Tp53* via HDTV and *Akt/Nicd* via HDTV and quantification of in vivo tumour growth. (A) Representative images of livers with tumour induction via HDTV (*Kras/Tp53*; *Akt/Nicd*) in *Parp-1^{+/+}* (n=5/6) and *Parp-1^{-/-}* mice (n=6). H&E and IHC staining of selected proteins (Sox9, Parp-1, Ki67 and γ H2ax) of representative paraffin-embedded tumour sections are shown (3.5 μ m). Scale bars indicate 500 μ m (\times 10, H&E) and 1000 μ m (\times 5, IHC). (B) Liver weight/body weight ratio (%) of *Parp-1^{+/+}* mice (blue) and *Parp-1^{-/-}* mice (red) after HDTV of empty vector (EV), *Akt/Nicd* or *Kras/Tp53* plasmid combinations with HSB2. Mean \pm SD, n=5, ***p<0.001. (C) Quantification of tumour growth shown as scores: 0=no tumour, 1=small foci/nodules, 2=distinct solid tumour. EV n=5, *Akt/Nicd* n=5, *Kras/Tp53* n=5/6, **p<0.01. (D) Percentage of different lesions in *Parp-1^{+/+}* and *Parp-1^{-/-}* mice with *Kras/Tp53* plasmid combination. HDTV, hydrodynamic tail vein.

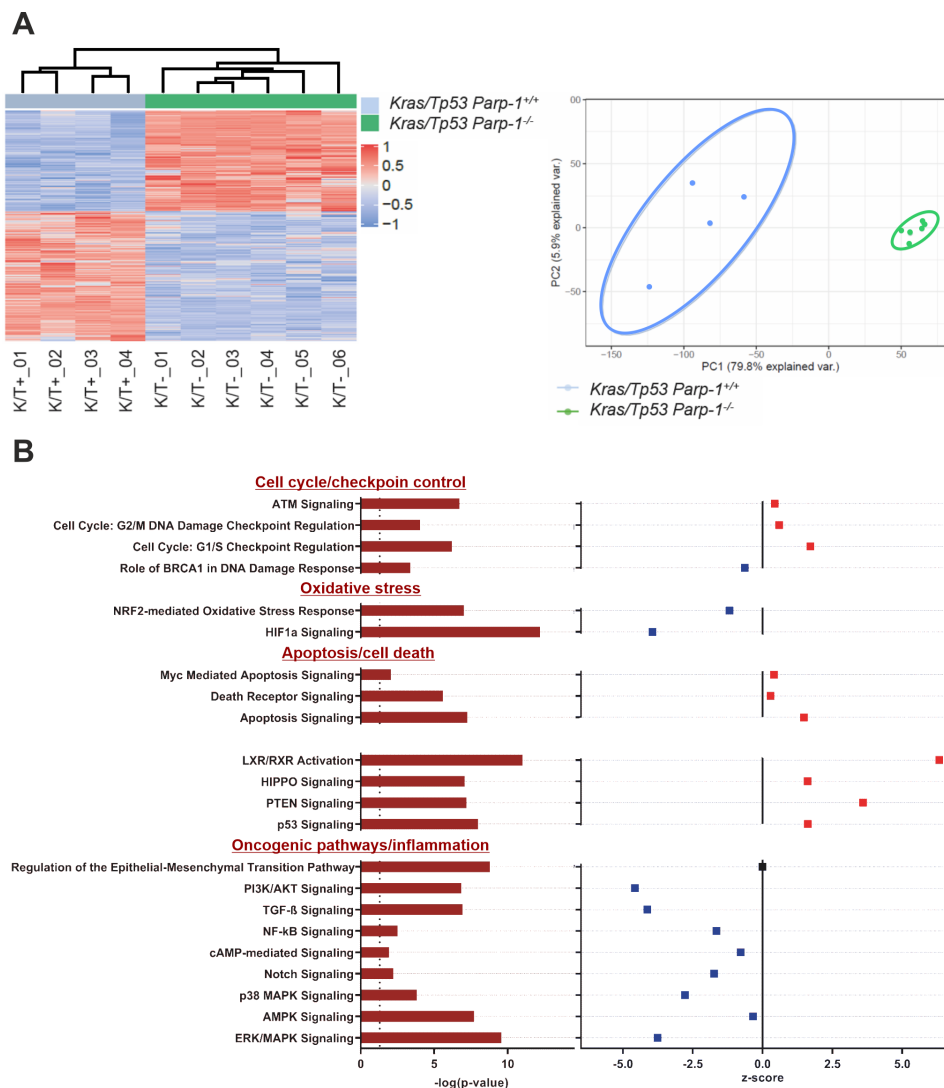


Figure 4 Differential expressed genes after HDTV with *Kras/Tp53* in *Parp-1*^{-/-} versus *Parp-1*^{+/+} mice. (A) Unsupervised cluster and PCA plot of significant genes (p < 0.05) after HDTV with *Kras/Tp53* in *Parp-1*^{-/-} versus *Parp-1*^{+/+} mice. (B) Canonical pathways significantly regulated in tumours induced with *Kras/Tp53* in *Parp-1*^{-/-} versus *Parp-1*^{+/+} mice identified by IPA. Dashed line indicated significance threshold of $-\log(p\text{-value}) > 1.3$. Shown are z-scores of respective canonical pathways (positive z-score=red/activated, negative z-score=blue/inhibited). HDTV, hydrodynamic tail vein; IPA, ingenuity pathway analysis; PCA, principal component analysis.

vs 7661 in *Kras/Tp53* (online supplemental figures S12 and S13; online supplemental tables S2 and S3). These findings are in concordance with the equivalent tumour growth and histopathological features of *Akt/Nicd*-induced cholangiocarcinogenesis independent of the *Parp-1* genotype (figures 3 and 4, online supplemental figure S12). However, several components of DNA repair pathways of DSB repair (NHEJ, HR) showed upregulated expression in *Parp-1* proficient mice injected with *Akt/Nicd* confirming that the role of *Parp-1*, although important for DNA damage control, is independent of cholangiocarcinogenesis in *Akt/Nicd* experimental group.

Mechanisms of *PARP-1* activation in *KRAS*-mutated iCCA

Transcriptome analyses confirmed preferential impairment of cell cycle regulation, DDR pathways and replicative stress response in human iCCA cells, mouse model, as well as patient samples harbouring *KRAS* mutation. To elucidate the molecular mechanisms underlying the selective impairment of these pathways in *KRAS*-mutant iCCA, we first examined the expression of DDR genes in *Kras*-mutant and wild-type animals with

functional *Parp-1*. Genes associated with HR, c-NHEJ and alt-NHEJ were significantly upregulated. In addition, a dominant activation of *Chk1* expression was observed. Interestingly, on *Parp-1* inhibition in *Kras*-mutant animals, the expression of *Chk1* was also downregulated, suggesting an important relevance for *Chk1* kinase in *Kras*-mutated iCCA (figure 5A). We further used GSEA in our different datasets to investigate molecular differences in *KRAS*-mutated and wildtype iCCAs. Commonly enriched set of genes across iCCA models encompassed cell cycle regulation and activation of E2F targets, G2M and spindle checkpoint activation, as well as DNA-damage repair via HR. Importantly, we have consistently observed activation of gene sets associated with *CHK1/CHK2*, key regulators of the cell cycle and cell survival (figure 5B). We further recognised that *CHK1* was highly expressed in iCCA but not normal liver tissue and showed a significant upregulation predominantly in *KRAS*-mutated cancers (figure 5C). Accordingly, public data also show a significant correlation of *CHK1* and *PARP-1* suggesting a regulatory network in *KRAS*-mutated iCCA that might be induced by the high replicative stress in this subgroup of tumours.

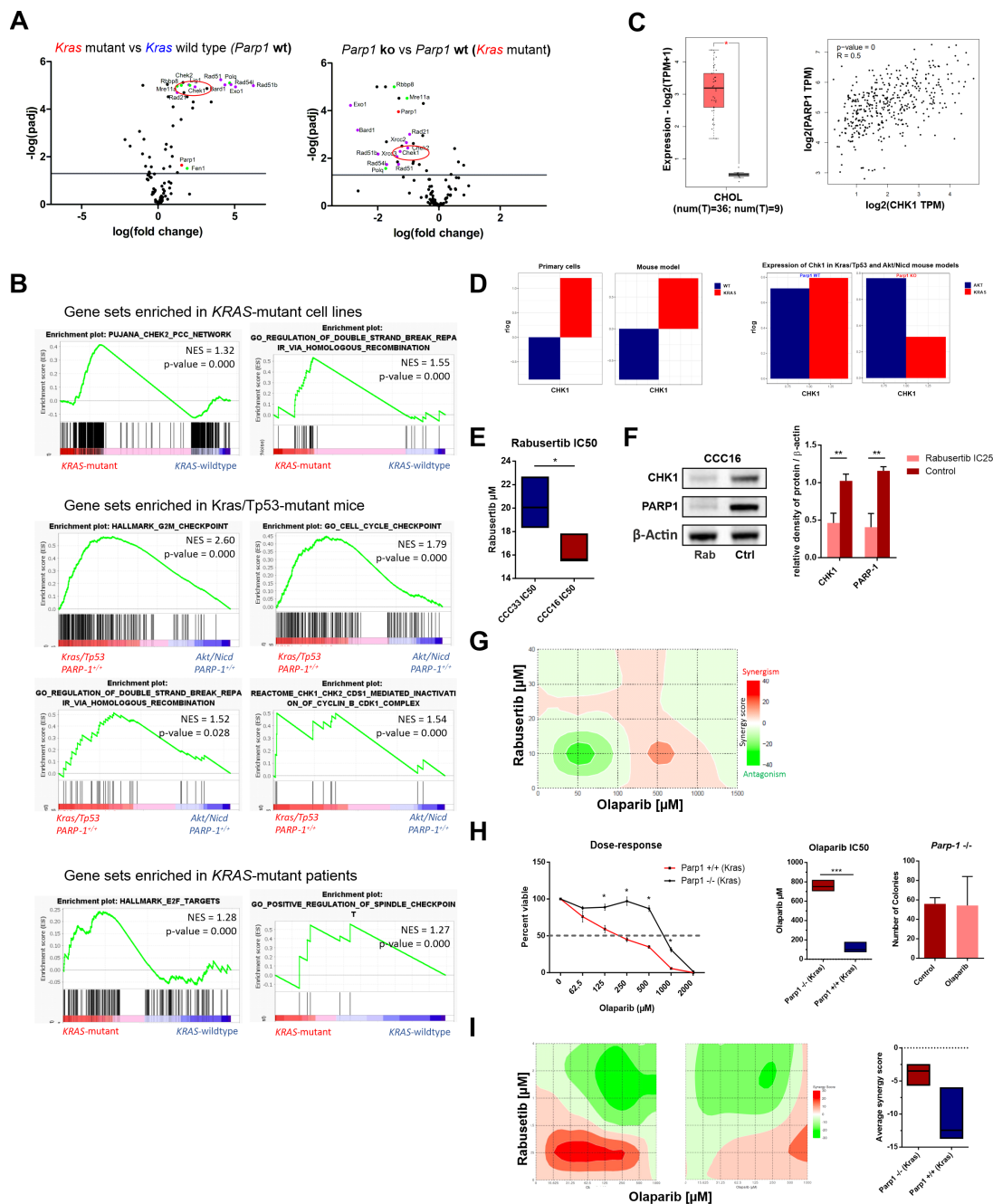


Figure 5 Molecular mechanisms of *PARP-1* regulation in *KRAS*-mutated iCCA. (A) Expression of DNA damage response genes including *Chk1* in *Parp1*^{-/-} and *Parp1*^{+/+} mice after *Kras*/*Trp53* injection. Volcano plots are depicted with the log (fold change) of each gene and the $-\log(p \text{ adjusted})$ was calculated by performing Wald test. Selected genes associated with HR, c-NHEJ and alt-NHEJ are coloured and gene names are displayed. Expression of *Chk1* is depicted with red ellipse (B) Gene set enrichment analysis (GSEA) in *KRAS*-mutated cell lines, *Kras*/*Trp53* *Parp1*^{+/+} mouse model and patient samples. The selection of gene sets was based on statistical significance calculated by nominal $p < 0.05$ and $FDR < 0.25$. NES indicates the degree of overexpression for each group at the peak of the entire gene set. (C) *CHK1* gene expression profiles (TCGA) in cholangiocarcinoma versus normal liver tissue (CHOL) presented in box plots and correlation between *PARP-1* and *CHK1*. Values of $*p < 0.05$ were considered as of significant difference. (D) Upper graphs depict gene expression level of *CHK1* in *KRAS*-mutated cell lines and *Kras*/*Trp53* *Parp1*^{+/+}/wildtype mouse model, Lower graphs show expression of *Chk1* in *Kras*/*Trp53* and *Akt*/*Nicd* mouse model with *Parp1*^{+/+} and *Parp1*^{-/-} genotype. (E) Shown are IC50 concentrations of Rabusertib for *KRAS*-mutated and non-mutated primary iCCA cell lines. Mean \pm SD, $n=3$, $*p < 0.05$. (F) Representative Western blot and densitometric analysis of *CHK1* and *PARP-1* protein expression on treatment with IC25 concentration of Rabusertib in *KRAS*-mutant iCCA cell line. Relative density of *PARP-1* expression normalised to β -actin is shown. Mean \pm SD, $n=3$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. (G) Evaluation of synergistic or antagonistic effects between Rabusertib/Olaparib in primary human cell line. Plots indicate level of synergism between investigated drugs, where red colour represents synergism and green colour antagonism. (H) Dose-response curves of *Kras*-mutant mouse cell lines with and without functional *Parp1* treated with increasing concentrations of olaparib (left) and their respective IC50 values (middle). Right is shown total number of colonies with and without olaparib treatment. Mean \pm SD, $n=3$, $*p < 0.05$. (I) Evaluation of synergistic or antagonistic effects between rabusertib/olaparib in mouse cell lines. Plots indicate level of synergism between investigated drugs, where red colour represents synergism and green colour antagonism. On the right, graph shows average synergy score (ZIP) for both cell lines. iCCA, intrahepatic cholangiocarcinoma; NHEJ, non-homologous end-joining.

Significant upregulation of *CHK1* was further demonstrated in our *KRAS*-mutated cell lines and *Kras/Tp53 Parp-1^{+/+}* mouse model (figure 5D). As already demonstrated for PARP-1 inhibition, *KRAS*-mutated iCCA cells were significantly more sensitive to specific inhibition of CHK1 by the selective CHK1 inhibitor Rabusertib (figure 5E). Inhibition of CHK1 also led to a significant downregulation of PARP-1 while combined treatment with olaparib did not induce synergistic effects (figure 5F,G). Gene expression analysis following CHK1 inhibition showed upregulation of *CDC25C* and downregulation of *RAD51* and *XRCC2*, which could be actors of PARP-1 regulation in *KRAS*-mutated iCCAs. Interestingly, protein–protein interaction confirmed an association of these proteins with PARP-1 (online supplemental figure S14). Lastly, we tested the effect of Olaparib alone and in combination with rabusertib using an ex vivo model of primary cell lines derived from *Parp-1^{-/-} Kras/Tp53* and *Kras^{G12D};Rb^{del};Tp53^{del}*. As expected, cell lines with *Kras* mutation and functional Parp-1 showed significantly higher sensitivity to Parp-1 inhibition while the observed synergistic effects in both cell lines were negative. Colony formation analysis in *Kras/Tp53 Parp-1^{-/-}* after exposure to the IC50 concentration of olaparib unveiled that the number of colonies in the treatment was not significantly different from the control (figure 5H,I). The observed findings confirm that CHK1 has a profound effect on PARP-1 levels in this subtype of highly replicative cancers and contributes to the dependence of *KRAS*-mutated iCCA on functional PARP-1 signalling.

PARP-1 expression as prognostic factor in *KRAS*-mutant iCCA

To evaluate a potential prognostic impact of our molecular profiles, we integrated our identified in vitro and in vivo transcriptomic profiles with different established prognostic subgroups of PLC (poor and good prognosis).⁸ Consistently, *KRAS*-mutant CRISPR/Cas9-mediated *PARP-1* KO clones grouped with good prognosis CCA patients, whereas *KRAS*-mutant control clones recapitulated transcriptomic features of poor prognosis CCA patients (figure 6A). Similarly, integration of in vivo data showed that *Parp-1* deficient mice with *Kras/Tp53* injection clustered with a good prognosis while *Parp-1* proficient mice grouped with poor prognosis (figure 6B). Importantly, mice injected with *Akt/Nicd* revealed no distinct clustering dependent on the *Parp-1* genotype (figure 6B). Overall, these results suggest that *PARP-1* depletion in iCCA with activated *KRAS* mutations leads to a shift from poor to good prognosis.

DISCUSSION

Recently, the PARP family has gained attention in cancer research due to its involvement in various oncogenic pathways and processes (DNA repair, genomic stability, chromatin modification, energy metabolism, apoptosis) mediated by the family members.²³ Elevated *PARP-1* expression was consistently observed in a variety of solid tumours.^{24–28} Further, recent evidence suggests an association between *PARP-1* overexpression and *KRAS* mutations in different tumours, including in AML and CRC models.^{12 13 29} However, until now, only very limited

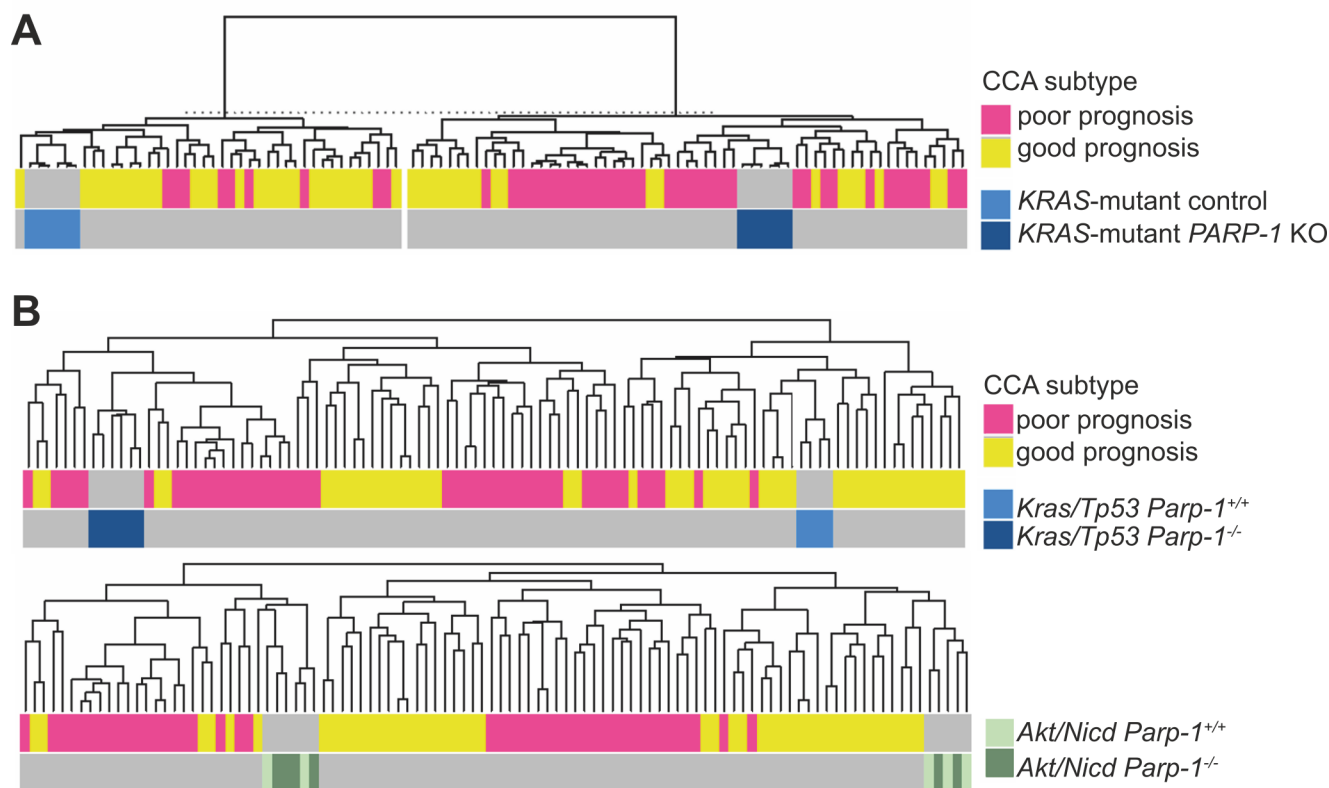


Figure 6 Integration of in vitro and in vivo transcriptomic data with prognostic subgroups of CCA patients. (A) The graph shows the integration of *KRAS*-mutant CRISPR/Cas9 *PARP-1* KO clones (dark blue) and respective control clones (light blue) with a previously published dataset of 45 CCA patients with good (pink) and poor (yellow) prognosis. (B) Upper graph shows the integration of *Parp-1^{-/-}* mice (dark blue) and *Parp-1^{+/+}* mice (light blue) with *Kras/Tp53*-induced carcinogenesis with a previously published dataset of 45 CCA patients with good (pink) and poor (yellow) prognosis. Lower graph shows integration of *Parp-1^{-/-}* mice (dark green) and *Parp-1^{+/+}* mice (light green) with *Akt/Nicd*-induced carcinogenesis with a previously published dataset of 45 CCA patients with good (pink) and poor (yellow) prognosis. CCA, cholangiocarcinoma.

information is available as to the role of *PARP-1* expression in the therapeutic response of *KRAS*-mutant iCCA. Here, we demonstrated an upregulation of *PARP-1* expression in *KRAS*-mutant iCCA tissue and cancer-derived cell lines in comparison to normal intrahepatic bile duct tissue and *KRAS*-wildtype cell lines (figure 1). We were able to show that this patient subgroup has significant association with decreased overall and recurrence-free survival (online supplemental figure S1). In concordance with recent studies, a significantly higher expression, and positive correlation of *KRAS* and *PARP-1* in cholangiocarcinoma (CHOL) tumour samples in comparison to normal tissue samples (online supplemental figure S1).^{9 30 31}

Our data confirm that knockdown of *PARP-1* by RNAi as well as treatment with Olaparib, an effective PARP-1/2 inhibitor, exerted preferential effects in *KRAS*-mutant cell lines compared with *KRAS*-wildtype cell lines (figure 1, online supplemental figure S2). A comprehensive meta-analysis of Ku *et al* recently confirmed reduced proliferation on PARP inhibition in *KRAS*-mutant MCF10a cells (transfected with mutant *KRAS* constructs) compared with *KRAS*-wildtype. The study also implies that *KRAS*-mutant cells are highly dependent on DDR pathways confirming a synthetic lethality in *KRAS*-mutant cancers, which aligns with our hypothesis for *KRAS*-driven iCCA.¹⁴

Molecular analyses of iCCA cell lines on *PARP-1* KO confirmed that the lack of PARP-1 results in dysregulation of several DNA repair pathways (BER, DSB repair) predominantly in *KRAS*-mutant iCCA cell lines (figure 1, online supplemental figure S4).^{12 14 32} This observation supports the hypothesis that *KRAS*-mutant tumours are more dependent on functioning DDR pathways in general and show preferential impairment of the *PARP-1*-associated DNA repair pathway alt-NHEJ.^{13 14} However, stable *PARP-1* depletion lacks the effect of PARP-1-DNA trapping caused by PARP-1 inhibition,³³ which limits therapeutic predictions in this model. Nevertheless, dysregulation of DDR processes on *PARP-1* depletion was explained on the basis of multiple interactions of PARP-1 and PARylation with other DDR factors.^{34 35} PARP-1 activation was associated with enhanced activation of the error-prone alt-NHEJ pathway over c-NHEJ by competing with Ku70 protein on the site of DNA damage.^{36 37}

In addition to changes in DDR pathways, our transcriptomic data indicate an involvement of apoptotic signalling, inflammatory response and oxidative stress (figure 2, online supplemental figure S4). Further analyses are required to clarify the role of these pathways in the context of tumour initiation and progression and the proposed pro-apoptotic and anti-inflammatory effects of *PARP-1* deficiency and PARPi.^{13 32 38} Hähnel *et al* showed that *KRAS*-mutant AML cells are sensitised towards apoptosis on PARP-1 inhibition in combination with the DNA damaging anticancer drug daunorubicin.¹³ Further, *PARP-1* deficiency or PARPi was associated with decreased gene expression of proinflammatory cytokines in previous studies.^{12 39} Other studies hypothesised that *PARP-1* activity might act as a double-edged sword during carcinogenesis, affecting apoptotic and oxidative processes and proinflammatory signalling, dependent on the cellular metabolic status and state of tumorigenesis.^{12 16 23 40 41} Overall, our in vitro experiments exploring diverse modes of PARP-1 inhibition, including RNAi, and CRISPR/Cas9-mediated *PARP-1* KO confirmed that hypersensitivity of *KRAS*-mutant iCCA cell lines is related to altered tumorigenic properties. These findings propose a novel therapeutic strategy for a previously difficult-to-treat subgroup of progressed iCCA patients harbouring *KRAS* mutations. Of note, synergistic effects observed between Olaparib and commonly used chemotherapeutic compounds in *KRAS*-mutant cells indicate that a combination treatment might

be of further therapeutic interest and could be pursued in future investigations (online supplemental figure S2D).

To further determine the role of *PARP-1* in tumour initiation and cancer development, we employed a model of *KRAS*-driven cholangiocarcinogenesis in *Parp-1* deficient animals.^{11 42–44} In consistence with previous reports, *Parp-1* proficient mice display predominant development of solid iCCA (80%) accompanied by dysplastic hepatocellular foci and nodules as well as early hepatocellular carcinoma in the surrounding liver tissue 10 weeks after HDTV with *Kras/Trp53* (figure 3).¹¹ In stark contrast, in *Parp-1*-deficient mice, *Kras*-induced carcinogenesis was characterised by the absence of cholangiocarcinoma and the presence of multiple dysplastic foci and nodules as well as small HCC with tumourous vein invasion. Importantly, transcriptomic analyses of our in vivo data suggest a pronounced inhibition of NOTCH signalling (figure 4, online supplemental figures S8 and S12), a key oncogenic driver of iCCA and predicted factor for transdifferentiation of hepatocytes towards biliary traits, is present in our PARP-1-deficient lesions.^{45 46} Furthermore, Ikenoue *et al* demonstrated that activated *Kras* in combination with active *Pten* results predominantly in HCC, whereas activated *Kras* in combination with homozygous inactive *Pten* leads to iCCA development in vivo.⁴⁷ In line with this, *Parp-1* deficiency in our study confirms activation of *Pten*. Taken together, activation or inactivation of the above-mentioned pathways, although not being exclusively specific to cholangiocarcinogenesis, might explain the absence of iCCA and shift towards HCC development in our *Kras/Trp53*-induced tumour model under *Parp-1* deficiency. Further studies are clearly warranted to define the underlying molecular mechanisms responsible for the phenotypic shift.

Consistent with our in vitro data and previous studies with *Parp-1* deficient mice, our transcriptomic analyses of in vivo data showed enrichment of DNA repair pathways (alt-NHEJ, HR, BER) in all experimental groups of *Parp-1* proficient mice while in *Parp-1*^{-/-} mice DNA repair pathways were not enriched.^{32 48} Decreased gene expression of proinflammatory cytokines was already observed in *Parp-1*^{-/-} mice and on PARPi and might explain the predicted inhibition of proinflammatory pathways (NF-κB, TGFβ) in our data (figure 4, online supplemental figures S10 and S12).^{12 39} Importantly, neither histopathological assessment nor quantification of tumour burden or molecular analyses revealed a dependency on the *Parp-1* genotype in a non-*Kras*-driven iCCA model (*Akt/Nicd*) (figures 3 and 4; online supplemental figures S12 and S13).⁴⁵ The results clearly underscore the selective relevance of oncogenic *Kras* in *Parp-1* deficient background. Taken together, our in vivo studies confirm the association of *Parp-1* expression in *Kras/Trp53*-driven cholangiocarcinogenesis. Reduced cholangiocarcinoma development under *Parp-1* deficiency could be mechanistically explained by dysregulation of apoptotic and inflammatory processes as well as DDR.

It is well established that *KRAS*-mutated cancers exhibit enhanced replicative stress and constitutively activated stress response pathways.⁴⁹ Here, CHK1-mediated cell cycle checkpoints maintain genomic integrity and, thus, CHK1 activation might confer key protective mechanisms that protect *KRAS*-driven cancers from this therapeutic liability. Consistently, we could provide evidence that selective induction of PARP-1 in iCCA could be induced by activation of CHK1 in *KRAS*-mutant iCCA (figure 5). We observed a significant upregulation of *CHK1* in *KRAS*-mutated iCCA cell lines and *Kras/Trp53 Parp-1*^{+/+} mice while inhibiting *Parp-1* in *Kras/Trp53 Parp-1*^{-/-} mice resulted in *Chk1* inhibition, as observed in human patients. Furthermore, *KRAS*-mutated iCCA cells were significantly more

sensitive to CHK1 inhibition by Rabusertib, a selective CHK1 inhibitor, than KRAS-wildtype cells or mouse cells deficient in Parp-1 (figure 5). Inhibition of CHK1 significantly influenced components of HR (online supplemental figure S14). Importantly, inhibition of CHK1 also led to a significant reduction of PARP-1 levels in KRAS-mutant. When rabusertib was combined with Olaparib, there was no induction of synergistic effects, further implying a potential regulatory role of CHK1 (figure 5). These investigations are in line with several other recent investigations that established a formal association between CHK1 and PARP-1 in highly replicative cancers that rely on a functional DDR, particularly one mediated by HR.^{50 51} Studies have also described a direct interaction between CHK1 and PARP-1 at the DNA damage site and subsequent promotion of HR.⁵²

Thus, we propose a regulatory axis involving CHK1-mediated PARP-1 activation induced by replicative stress in KRAS-mutant iCCA that maintains cellular survival in this subtype of iCCA.

To validate our findings in authentic human tumours, we integrated our in vitro and in vivo findings with a publicly available dataset of well-characterised CCA patients.⁸ Consistently, transcriptome profiles of the PARP-1-deficient cell lines as well as control cell lines with different established prognostic subgroups of PLC (poor and good prognosis) revealed a shift of KRAS-mutant iCCA cell lines from poor to good prognosis on PARP-1 KO (figure 6). In concordance, Parp-1 deficient samples from mice injected with *Kras/Trp53* clustered with good prognosis iCCA patient samples, whereas Parp-1 proficient samples grouped with poor prognosis. Interestingly, this prognostic shift was not visible in *Akt/Nicd*-induced tumour samples, which clustered randomly together with poor prognostic patients. Hence, the obtained data clearly confirm a clear synthetic vulnerability and provide a rational for therapeutic targeting of PARP-1 in KRAS-mutant iCCA patients.

CONCLUSION

In conclusion, the study presented confirms upregulation of PARP-1 and hypersensitivity towards PARP-1-based intervention preferentially detectable in KRAS-mutant iCCA in vitro and in vivo. Mechanistically, our data revealed that PARP-1 inhibition provoked downregulation of DSB repair pathways and inhibition of oxidative and inflammatory processes.¹³ Thus, our data open novel therapeutic options for this difficult-to-treat iCCA subgroup that warrant further clinical investigations (online supplemental visual abstract).

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Supplementary materials and methods

Cell lines

KRAS-mutant iCCA cell lines, HuCCT1 (*KRAS*^{G12D}) and RBE (*KRAS*^{G12V}) and *KRAS*-wildtype CCA cell lines HuH28 and WITT were obtained from JCRB Cell Bank or kindly provided by Gregory Gores (Mayo Clinic, Rochester, USA). Primary iCCA cell lines (*KRAS*-mutant cell line CCC16 (*KRAS*^{G12D}) and *KRAS*-wildtype cell line CCC33) were established at the University Medical Center, Mainz in accordance with ethical guidelines [1]. Primary mouse Parp1^{-/-} (*Kras*/*Tp53* Parp1^{-/-}) cell line was established at the University Medical Center Mainz upon extraction of the tumors from the HDTV mouse model. *Kras*^{G12D};*Rb*^{del};*Tp53*^{del} cell line was kindly provided by Ursula Ehmer. None of the cell lines harbor a loss of function variant in *BRCA1/2* [1–4]. HuCCT1, RBE, WITT, CCC16, CCC33, *Kras*^{G12D};*Rb*^{del};*Tp53*^{del}, were cultivated in DMEM (Gibco), supplemented with 1 unit/ml penicillin/streptomycin (P/S, Sigma Aldrich), 5% FCS (Pan-Biotech). HuH28 cells were cultivated in RPMI-1640 medium (Sigma Aldrich) (1 unit/ml P/S, 5% FCS) (Pan-Biotech). All cell lines were maintained at 37°C and 5% CO₂, routinely mycoplasma tested and, when possible, either purchased fresh or authenticated by STR testing.

Nucleic acid extraction and RNA sequencing

DNA was extracted by performing peqGOLD Tissue DNA mini kit (VWR International) following the manufacturer's instructions. Total RNA was extracted using peqGOLD total RNA kit (VWR International) according to the manufacturer's instructions. RNA quality and purity was determined by Nanodrop ND-1000 spectrophotometer (NanoDrop Technologies) and the integrity was measured by Agilent 2100 Bioanalyzer (Agilent). RNA sequencing was performed using Illumina Novaseq 6000. DESeq2 pipeline was used for differential expression analysis. Principal Components Analysis (PCA) and unsupervised hierarchical clustering were conducted using ComplexHeatmap [5]. Ingenuity Pathway Analysis (IPA) online tool provided by Qiagen was used to identify the regulation of pathways and networks. The scoring system provided by IPA tool was employed to identify significantly regulated pathways [6]. Gene set enrichment analysis (GSEA) was performed using GSEA software provided by Broad Institute (Broad Institute Inc, Cambridge, USA). Gene sets with nominal $p < 0.05$ and false discovery rate (FDR) < 0.25 were considered enriched in a priori defined sets of genes [7]. Gene expression profiling interactive analysis (GEPIA2) was employed for gene expression and correlation analyses of data sets of cholangiocarcinoma (CHOL) and liver hepatocellular carcinoma (LIHC) from The Cancer Genome Atlas Program (TCGA). Differential analysis was calculated with one-way ANOVA, using disease state (tumor or normal) after $\log_2(\text{TPM}+1)$ transformation [8].

Quantitative real-time polymerase chain reaction

Two-step reverse-transcription quantitative polymerase chain reaction using iScript cDNA Synthesis kit (Bio-Rad Laboratories), SYBR Green Master-Mix (Bio-Rad Laboratories) and CFX Connect (Bio-Rad Laboratories) was performed. Oligonucleotide primers were designed using Primer3 v.0.4.0 (<http://frodo.wi.mit.edu/primer3/>) as described before (*PARP-1* forward 5'-CGAATGCCAGCGTTACAAGC-3', *PARP-1* reverse 5'-AACATGTAGCCTGTACAGGG-3', *PARP-2* forward 5'-TCCCCTGCCAAGAAAACCTCG-3', *PARP-2* reverse 5'-TCAGAGACCCTTTTGCTGGC-3', *GAPDH* forward 5'-CAACGACCACTTTGTCAAGC-3', *GAPDH* reverse 5'-TCTTCCTCTTGCTCTTGC-3', *CHK1* forward 5'-GGCTTGGCAACAGTA-3' *CHK1* reverse 5'-CAGGACCAAACATCA-3', *RAD51* forward 5'-GCAGTGGCTGAGAGGTATGGT-3' *RAD51* reverse 5'-TTCTGTAAAGGGCGGTGGCA-3', *XRCC2* forward 5'-ACCTTCTCATGCCTCTCGACG-3' *RAD51* reverse 5'-TGCTTACCAGTTGCTGCCA-3', *CDC25C* forward 5'-TGGCCAAGGAAAGCTCAGGA-3' *CDC25C* reverse 5'-TTGGCAGCGCACATACCTTG-3') (Eurofins).

Western blotting

Cell lysates were prepared using M-PER tissue extraction buffer (Thermo Fisher) containing complete protease inhibitor cocktail (Gibco). 25 µg of protein lysate were separated by SDS-PAGE and transferred onto nitrocellulose membrane (Sigma Aldrich). Membranes were probed with the indicated antibodies (beta-Actin Clone 2Q1055 (mouse, monoclonal, Santa Cruz #sc-58673); PARP-1 (46D11) (rabbit, monoclonal, Cell signaling #9532), PARP-2 (rabbit, monoclonal, EMD Millipore #MABE18), CHK1 (mouse, monoclonal, Santa Cruz #SC8408)). Quantification of expression levels was performed by densitometric analyses using ImageJ (NIH).

siRNA-mediated knockdown

For transfection, cells were seeded at low confluency (30-50%) in 6-well plates. After 24 h 100 pmol siRNA (non-sense control, two different siRNAs targeting *PARP-1*, Eurofins) was introduced by using transfection reagent Lipofectamine 3000 (Thermo Fisher) following the manufacturer's instructions. Subsequent functional assays were conducted 72 h after transfection.

CRISPR/Cas9-mediated knockout

Cells transfected with Clustered Regularly Interspaced Short Palindromic Repeats/Caspase9 (CRISPR/Cas9) plasmids (pNV-sgRNA-Cas9-2A-GFP; abm; 2 µg) were transferred to 10 cm dishes and after reaching 80-90% confluency sorted into single cells based on the integrated selection marker GFP using BD FACSAria optimally 5-7 days after transfection (Core Facility

Flow Cytometry, Paul-Klein Center for Immune Intervention, University Medical Center Mainz). Successful knockout of single cell clones was verified by Western blot analysis and Sanger Sequencing (StarSEQ GmbH).

Dose response and viability assay

Cell viability was determined using a colorimetric assay (WST-1) following the manufacturer's protocol (Roche). Inhibitor stock solutions were prepared by dissolving in dimethyl sulfoxide (DMSO; Carl Roth), according to the manufacturer's recommendations. Working solutions were prepared by dilution in DMEM (10% FCS, 1% P/S). Into each 96-well, 5×10^3 cells were plated for 24 h before treatment followed by administration and incubation with inhibitors for 72 h. Olaparib (Chemietek) was applied in the range of concentrations from 8-2048 μM alone or in combination with Doxorubin (60 nM) (Sellekchem), while Rabusertib (TargetMol) was applied from 0.25-40 μM alone in combination with Olaparib. Cisplatin was applied in the range from 1.25-80 μM and Gemcitabine from 0.325-20 μM together with Olaparib. KU57788 was applied in the range from 2.5-160 μM . Cell viability was expressed as the absorbance in the treatment group compared to control group as viability percent \pm SD ($n=3$). Median inhibitory concentration (IC₅₀) values were calculated from dose-response curves of three independent experiments by nonlinear regression using Prism software (GraphPad Software). Synergistic effects were determined using SynergyFinder online tool (<http://www.synergyfinderplus.org/#/>)

Colony and sphere formation assay

Cells were treated for 72 h with the cell line specific IC₅₀ of Olaparib, or siRNA-mediated knockdown of *PARP-1*. 1×10^3 cells were plated on 6-well plates for colony formation (CFU) and 1×10^3 cells were plated on 48-well plates for sphere formation (SFU) assay into a semi-solid soft agar (Carl Roth). After 14 days colony and sphere formation capacities were determined and represented as number of colonies/spheres for each treatment group in comparison to the control group in percentage.

Cell cycle analysis

Cells were treated with IC₂₅ concentration of Olaparib for 48 hours, harvested and cell cycle analysis was performed using flow cytometry and propidium iodide staining protocol. A total of 100000 events were recorded and different phases of the cell cycle were determined using FlowJo V10.

Detection of oxidative stress

2',7'-dichlorodihydrofluorescein-diacetate (DCH2FC-DA; Sigma Aldrich) was used to monitor oxidative stress in the iCCA cells. The method is based on the intake of non-fluorescent DCH2FC-DA into the cells by diffusion, where it gets hydrolyzed to 2',7'-dichlorofluorescein (DCFH) and is trapped inside the cells. Upon cellular oxidative stress, DCFH is oxidized by ROS to the highly fluorescent form 2',7'-dichlorofluorescein (DCF), which was detected at a specific excitation/emission spectrum (495 nm / 535 nm) using a microplate spectrofluorometer (TECAN infinite M 200Pro). Oxidation of DCFH was correlated quantitatively to the level of oxidative stress mediated by H₂O₂ (Carl Roth) and other reactive oxygen species.

Induction of DNA damage via irradiation

The iCCA cell lines were seeded on coverslips placed in 3 cm plates (1x10⁵ cells) and cultured in DMEM (10% FBS) for 24 hours. Next, cells were placed into an irradiator (Gammacell 2000) and irradiated with 5 Gy (500 rad = 1:59 sec). After incubation for 1 hour at 37°C, cells were fixed, and immunofluorescence staining was performed. Cells were stained for phosphorylated H2AX (Cell Signaling Technology, 1:500) using standard protocol and visualized and recorded using a Laser Scanning Microscope LSM-710 (Zeiss) with 63 x magnification oil objective.

Experiments involving animals

All procedures were performed in accordance with the National Animal Protection Guidelines following approval by the local authorities. The origin and properties of the mouse strain with *Parp-1* knockout (129/Sv x C56BL/6J genetic background) was previously described [9,10]. Plasmids for HDTV were kindly provided by Matthias S. Matter, Institute of Pathology, University Hospital Basel, Switzerland. HDTV with plasmid solutions of pT3-EF1a-Kras^{G12V}/pT3-EF1a-shRp53-844-866 or pT3-EF1a-myrAkt/pT3-EF1a-Nicd (myc-tagged) in combination with pCMV-HSB2 plasmid (ratio 1:5) was performed as described before [11–13]. Experimental design comprised three experimental groups with 7-8 week old male *Parp-1*^{+/+} and *Parp-1*^{-/-} mice (genotype was determined beforehand). Animals were monitored weekly for signs of liver failure due to tumor growth and significant changes in body weight. Mice injected with *Kras/tp53* were sacrificed after 10 weeks, mice injected with *Akt/Nicd* after 7-8 weeks. Quantification was performed by liver weight / body weight ratio and a scoring system to assess the morphological differences. After sacrifice, the liver was dissected and either fixed in 4% PFA or preserved at -80°C.

Immunohistochemistry and confocal microscopy

Tissue samples were fixed in 4% PFA, embedded in paraffin and cut into 3.5 µm sections. H&E staining was performed by standard techniques using Mayer's Hemalaun (Merck KGaA) and Eosin-y Alcoholic solution (Thermo Fisher). Immunohistochemistry was done by automated immunostaining with DAB staining (Dako) according to the manufacturer's instructions. Visualization was performed by a Zeiss Axioskop microscope with 5x and 10x magnification objectives and analyzed in AxioVision 3.1 software.

Tissue microarray was performed as follows: paraffin-embedded formalin-fixed (FFPE) tissue samples from 197 patients with Cholangiocarcinoma diagnosed with Cholangiocarcinoma at the Institute of Pathology, University Medical Center Mainz, between 2006 and 2020 were collected. These samples were processed following the Tissue Biobank's protocols at the University Medical Center Mainz. Tissue microarrays (TMAs) featuring 2 mm cores were assembled. Immunohistochemistry (IHC) analysis was conducted on FFPE specimens sliced to a thickness of 2-4 µm. A rabbit monoclonal antibody targeting PARP-1 (clone 46D11; Cell Signaling Technology Europe B.V., Leiden, Netherlands) was employed at a 1:600 dilution. The immune reactive score (IRS) system was utilized to assess PARP-1 immunohistochemistry [14], generating scores ranging from 0 to 12, derived from multiplying the proportion of positive cells (scored 0–4) by the staining intensity (scored 0–3). The mean IRS was determined for patients with the same entity.

RPPA

Functional Proteomics RPPA Core facility, supported by MD Anderson Cancer Centre, Houston, Texas. Proteins were extracted from the cell pellets, denatured using 1% SDS + B-Me, serial diluted and arrayed on nitrocellulose-coated slides and the antigen-antibody reaction was determined. The emitted signals were captured by tyramide dye deposition and a DAB colorimetric reaction. The stained slides were scanned on a Huron TissueScope scanner to produce a 16-bit till image and sample densities were quantified by Array-Pro Analyser. Obtained data obtained was further quantitatively analyzed using Supercurve software and presented as expression relative to standard control cells on the array.

STRING

Explore functional connections with the biological implications between targets of interest (i.e., CHK1, PARP1, RAD51, CDC25C, XRCC2) the STRING database (<https://string-db.org/>) (version 12.0) was used. Computational prediction of direct/indirect protein-protein association is based on already reported findings from other databases [15].

Statistical analyses

Statistical analyses were performed using Student's t-test, one-way ANOVA, or Mann-Whitney U test as indicated. $p \leq 0.05$ were considered statistically significant. All results were presented as means \pm standard deviation (SD) from at least three independent experiments.

Supplementary figures

Figure S1: Transcriptomic, correlation and survival analysis of *PARP-1* and *KRAS* expression in TCGA and own dataset.

A) *PARP-1* and B) *KRAS* gene expression profiles (TCGA) in cholangiocarcinoma vs. normal liver tissue (CHOL) and liver hepatocellular carcinoma vs. normal liver tissue (LIHC) presented in box plots. Values of $p < 0.01$ (*) were considered as of significant difference. red=tumor, blue=liver C) Multiple comparisons of *PARP-1* and *KRAS* expression in cholangiocarcinoma vs. normal liver tissue (CHOL) and hepatocellular carcinoma vs. normal liver tissue (LIHC) ($\log_2(\text{TPM}+1)$) D) Pair-wise gene expression correlation analysis of *PARP-1* and *KRAS* expression in cholangiocarcinoma (CHOL) (Pearson correlation coefficient, TCGA CHOL Tumor/TCGA CHOL normal). E) Pair-wise gene expression correlation analysis of *PARP-1* and *KRAS* expression in hepatocellular carcinoma (LIHC) (Pearson correlation coefficient R, TCGA LIHC Tumor/TCGA LIHC normal). F) Immunohistochemical analysis of PARP1 expression in a human cohort of 194 iCCA patients. PARP-1 was evaluated using the mean immunoreactive score (IRS), which ranges from 0 to 12. A score of 0 indicates no staining, whereas a score of 12 signifies the strongest staining possible $p < 0.0001$ (***). G) Expression level of *PARP1* in the Andersen iCCA cohort in comparison with the surrounding liver and normal bile ducts H) Chiang's liver cancer proliferation signature shows a positive correlation with *PARP1* expression. I) Estimated median overall survival and recurrence free survival for iCCA patients with and without *KRAS* mutation obtained from cBioportal. Shown is Kaplan-Meier curve with a total of 412 patients.

Figure S2: Effect of *PARP-1* inhibition via Olaparib treatment on cell viability, colony and sphere formation capacity and synergistic effects with approved iCCA drugs.

A) Shown are dose-response curves of *KRAS*-mutant and *KRAS*-wildtype iCCA cell lines treated with increasing concentrations of Olaparib to determine IC50 value and impact on proliferation. Mean \pm SD, $n=3$, $p < 0.05$ (*), $p < 0.01$ (**). B) Phases of cell cycle after 48 h treatment with IC25 concentration of Olaparib. Shown are normalized values to untreated control cells. Mean \pm SD, $n=3$, $p < 0.01$ (**). C) Colony and sphere formation assay shown as % of control after Olaparib treatment in *KRAS*-mutant and *KRAS*-wildtype iCCA cell lines. Mean \pm SD, $n=3$, $p < 0.05$ (*), $p < 0.001$ (***). D) Synergistic effects of Olaparib/Cisplatin and Olaparib/Gemcitabine in *KRAS*-mutant and *KRAS*-wildtype iCCA cell lines. Plots indicate level of synergism between investigated drugs, where red color represents synergism and green color antagonism. Bars on the right represent quantification of an average synergy score between *KRAS*-mutant and *KRAS*-wildtype iCCA cell lines. Mean \pm SD, $n=3$, $p < 0.001$ (***). E) Shown are IC50 values for primary CCC33 and CCC16 cell lines after treatment with KU-5778 inhibitor. Mean \pm SD, $n=3$.

Figure S3: *PARP-1* protein expression in primary and established iCCA cell lines after CRISPR/Cas9-mediated knockout.

A) Representative Western blot of PARP-1, PARP-2, and β -actin protein levels after *PARP-1* KO in *KRAS*-mutant (HuCC1, RBE; red) and *KRAS*-wildtype iCCA cell lines (CCC33, WITT; blue).

Figure S4: Enriched gene sets in *KRAS*-mutant iCCA cell lines upon *PARP-1* KO.

A) Clinical endpoints and networks significantly regulated in *KRAS*-mutant iCCA cell lines upon *PARP-1* KO vs. control identified by IPA. The dashed line indicates the significance threshold of $-\log(p\text{-value}) > 1.3$. Shown are z-scores of respective canonical pathways (positive z-score = red/activated, negative z-score = blue/inhibited). B) Gene set enrichment analysis (GSEA) in

KRAS-mutant iCCA cell lines upon *PARP-1* KO vs. control clones. The selection of gene sets was based on statistical significance calculated by nominal $p < 0.05$ and $FDR < 0.25$. NES indicates the degree of overexpression for each group at the peak of the entire gene set.

Figure S5: Regulatory mechanism of PARP1 in KRAS mutated human tissue and cell lines

A) Immunofluorescence staining of p- γ H2AX foci by confocal microscopy. Shown is quantification of p- γ H2AX foci in *KRAS*-mutant (RBE; red) and *KRAS*-wildtype iCCA cell lines (CCC33; blue) and their respective *PARP-1* KO clones under control conditions and after irradiation with 5 Gy. Quantification indicating fold change of the number of cells with foci > 5 as % of total cell number. Mean \pm SD, $n=3$, $p < 0.05$ (*), $p < 0.01$ (**). B) Shown are basal and H_2O_2 -induced (25 μ M H_2O_2) changes in redox status using ROS-indicator CM-H2DCF-DA in *KRAS*-mutant (RBE; red) and *KRAS*-wildtype iCCA cell lines (CCC33; blue) and their respective *PARP-1* KO clones. Shown is the mean fluorescence intensity. Mean \pm SD, $n=3$, $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***). C) Analysis of 5 *KRAS* mutated tissue samples and matched non-tumoral liver tissue. Volcano plots are depicted with the $\log(\text{fold change})$ of each gene and the $-\log(p \text{ adjusted})$ was calculated by performing Wald test. Selected genes associated with HR, c-NHEJ, and alt-NHEJ are colored and gene names are displayed. D) Gene set enrichment analysis (GSEA) of *KRAS*-mutant tumor. The selection of gene sets was based on statistical significance calculated by nominal p -value < 0.05 and $FDR < 0.25$. NES indicates the degree of overexpression for each group at the peak of the entire gene set. E) Normalized protein level in primary cell lines with (CCC16) and without (CCC33) *KRAS* mutation detected by Reverse-phase protein array (RPPA). Mean \pm SD, $n=5$, $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

Figure S6: Single cell analysis of DNA damage repair pathways in iCCA patients with or without KRAS mutations tumor cells

Average expression of genes involved in DNA damage repair pathways of A) DNA repair_Hallmarks, B) BER_KEGG and C) NHEJ_KEGG in malignant and non-malignant cells from iCCA patients with or without *KRAS* mutations.

Figure S7: Experimental design of iCCA tumor initiation via HTDV in *Parp-1*^{+/+} and *Parp-1*^{-/-} mice.

A) 7-8-weeks old mice were injected with i) 2000 μ g HSB2-plasmid (empty vector control; EV); ii) 5000 μ g *Kras*^{G12V}-plasmid, 5000 μ g *shRp53*-plasmid and 2000 μ g HSB2-plasmid (*Kras/TP53*); or iii) 2500 μ g *myrAkt*-plasmid, 2500 μ g myc-tagged *Nicd*-plasmid and 1000 μ g HSB2-plasmid (*Akt/Nicd*) and sacrificed at the age of 14-18 weeks. B) List shows information (ID, gender, bodyweight, liver weight on the day of sacrifice) of *Parp-1*^{+/+} and *Parp-1*^{-/-} mice injected with empty vector and plasmid combinations *Kras/TP53* and *Akt/Nicd*. *Mouse was excluded after analysis of transcriptomic data (outlier analysis).

Figure S8: Histopathological classification of *in vivo* tumors.

A) Scheme of histopathological assessment of tumor sections induced by HTDV (*Kras/TP53*; *Akt/Nicd*) in *Parp-1*^{-/-} and *Parp-1*^{+/+} mice. B) Table shows information (grading, number of foci, size, hematogenous spread) of paraffin-embedded tumor sections.

Figure S9: Quantification of immunohistochemistry staining in liver sections after HTDV with *Kras/TP53* and *Akt/Nicd*.

Quantification of selected immunohistochemical markers (Parp-1, Ki67, and γ H2ax) in liver sections of mice injected with A) *Kras/Tp53* and B) *Akt/Nicd*. The number of stained nuclei was determined by ImageJ and adjusted to control staining. Mean \pm SD, n=5, p<0.05 (*), p<0.01 (**), p<0.001 (***).

Figure S10: Expression of the genes and proteins associated with defined pathways after HDTV with *Kras/Tp53* in *Parp-1^{-/-}* and *Parp-1^{+/+}* mice.

Cluster analysis of samples from *Parp-1^{-/-}* and *Parp-1^{+/+}* animals with *Kras/Tp53* mutations. Analysis was performed based on the Broad Institute gene sets regulating cell cycle, Hippo signaling, apoptosis, MAPK, TGF- β using r-log values. A) Heatmaps and cluster analyses of *Kras/Tp53* *Parp-1^{-/-}* vs *Parp-1^{-/-}* empty vector B) Heatmaps and cluster analyses of *Kras/Tp53* *Parp-1^{-/-}* vs of *Kras/Tp53* *Parp-1^{+/+}* C) Immunohistochemistry staining of selected proteins (Cdc25a, Caspase 3, Yap, and Mapk p38) of *Parp-1^{-/-}Kras/Tp53* mouse in normal and tumor tissue. Representative images of normal liver and tumor tissue from animal model are shown. Scale bars indicate 200 μ m (20x magnification).

Figure S11: Enriched gene sets in *Parp-1^{-/-}* mice injected with *Kras/Tp53* vs. *Parp-1^{+/+}* mice.

A) Gene set enrichment analysis (GSEA) of *Parp-1^{-/-}* mice injected with *Kras/Tp53* vs. *Parp-1^{+/+}* mice. Selection of gene sets was based on statistical significance calculated by nominal p<0.05 and FDR<0.25. NES indicates degree of overexpression for each group at the peak of the entire gene set.

Figure S12: Differential expressed genes after HDTV with *Akt/Nicd* in *Parp-1^{-/-}* vs. *Parp-1^{+/+}* mice.

A) Unsupervised cluster and PCA plot of significant genes (p<0.05) after HDTV with *Akt/Nicd* in *Parp-1^{-/-}* vs. *Parp-1^{+/+}* mice. B) Canonical pathways and clinical endpoints and networks significantly regulated in tumors induced with *Akt/Nicd* in *Parp-1^{-/-}* vs. *Parp-1^{+/+}* mice identified by IPA. Dashed line indicated significance threshold of $-\log(p\text{-value} > 1.3)$. Shown are z-scores of respective canonical pathways (positive z-score = red/activated, negative z-score = blue/inhibited).

Figure S13: Enriched gene sets in *Parp-1^{-/-}* mice injected with *Akt/Nicd* vs. *Parp-1^{+/+}* mice.

A) Gene set enrichment analysis (GSEA) of *Parp-1^{-/-}* mice injected with *Akt/Nicd* vs. *Parp-1^{+/+}* mice. Selection of gene sets was based on statistical significance calculated by nominal p<0.05 and FDR<0.25. NES indicates degree of overexpression for each group at the peak of the entire gene set.

Figure S14: Regulatory mechanism of CHK-1 and PARP-1 in KRAS mutated primary human cell lines

A) Relative gene expression of CHK-1, CHK-1-related genes and PARP-1 in KRAS-mutated cell lines CCC16 after treatment with rabusertib. Expression was normalized to untreated CCC16 control cells. Mean \pm SD, n=3, p<0.05 (*), p<0.01 (**), p<0.001 (***). B) STRING functional association network between CHK-1 and its regulators and direct/indirect connection with PARP-1.

Figure S1

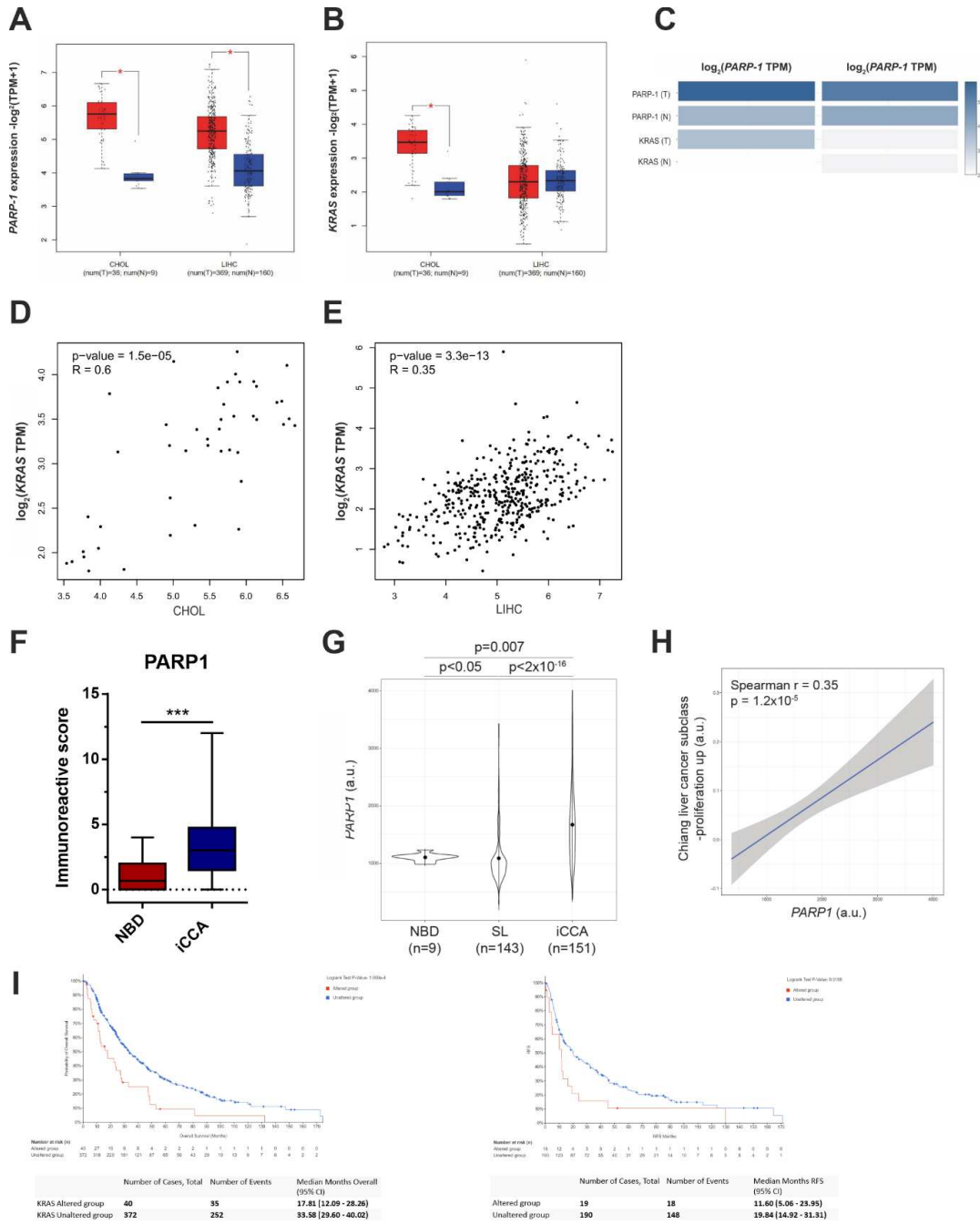
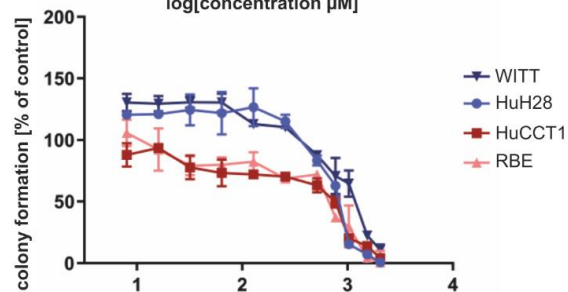
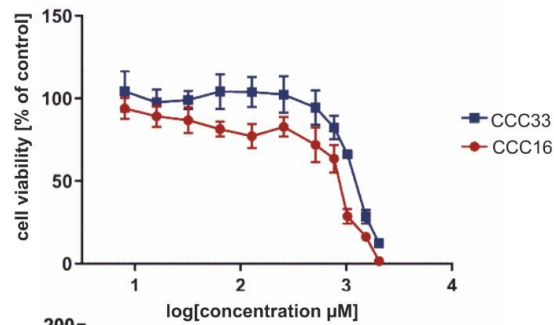
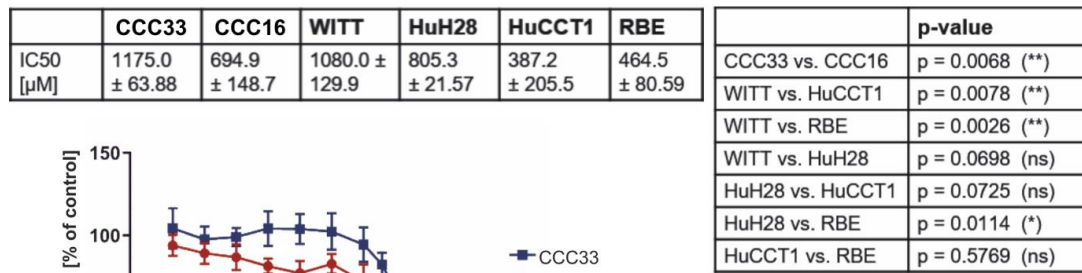
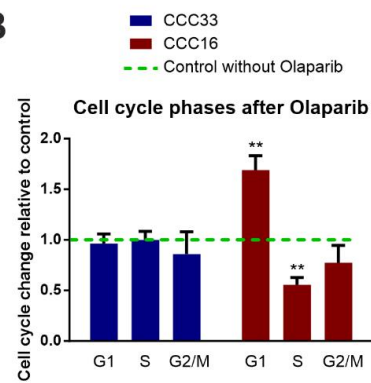


Figure S2

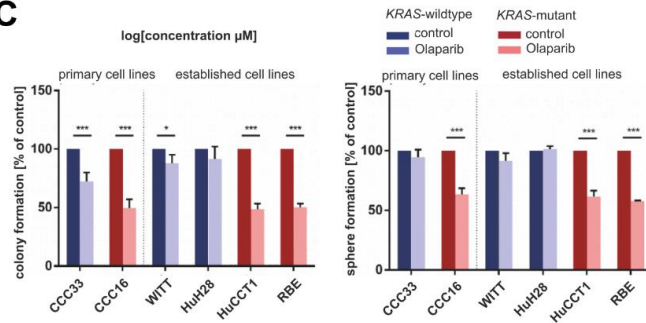
A



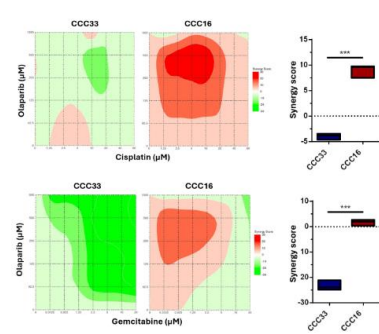
B



C



D



E

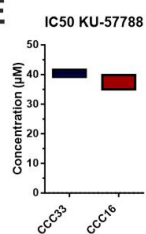


Figure S3

A

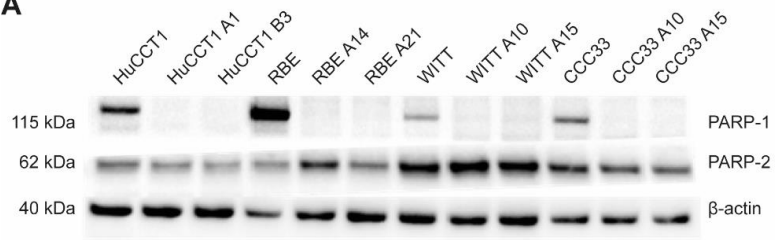
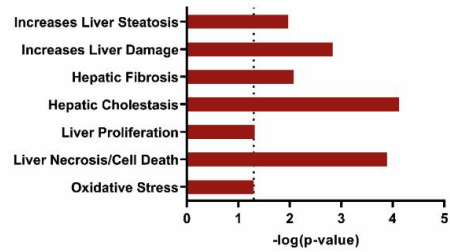


Figure S4

A



B

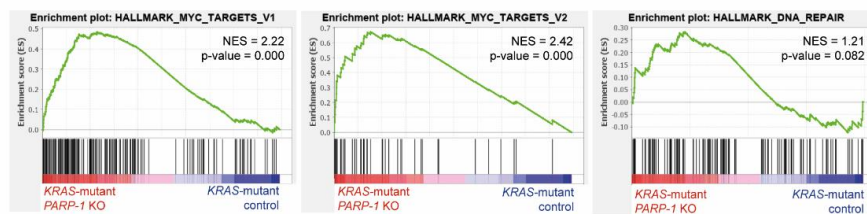
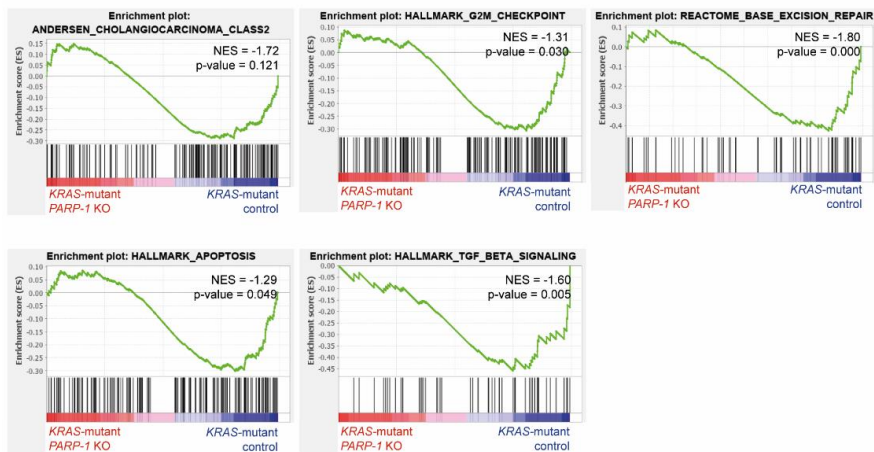
Gene sets enriched in *KRAS*-mutant *PARP-1* KOGene sets enriched in *KRAS*-mutant control

Figure S5

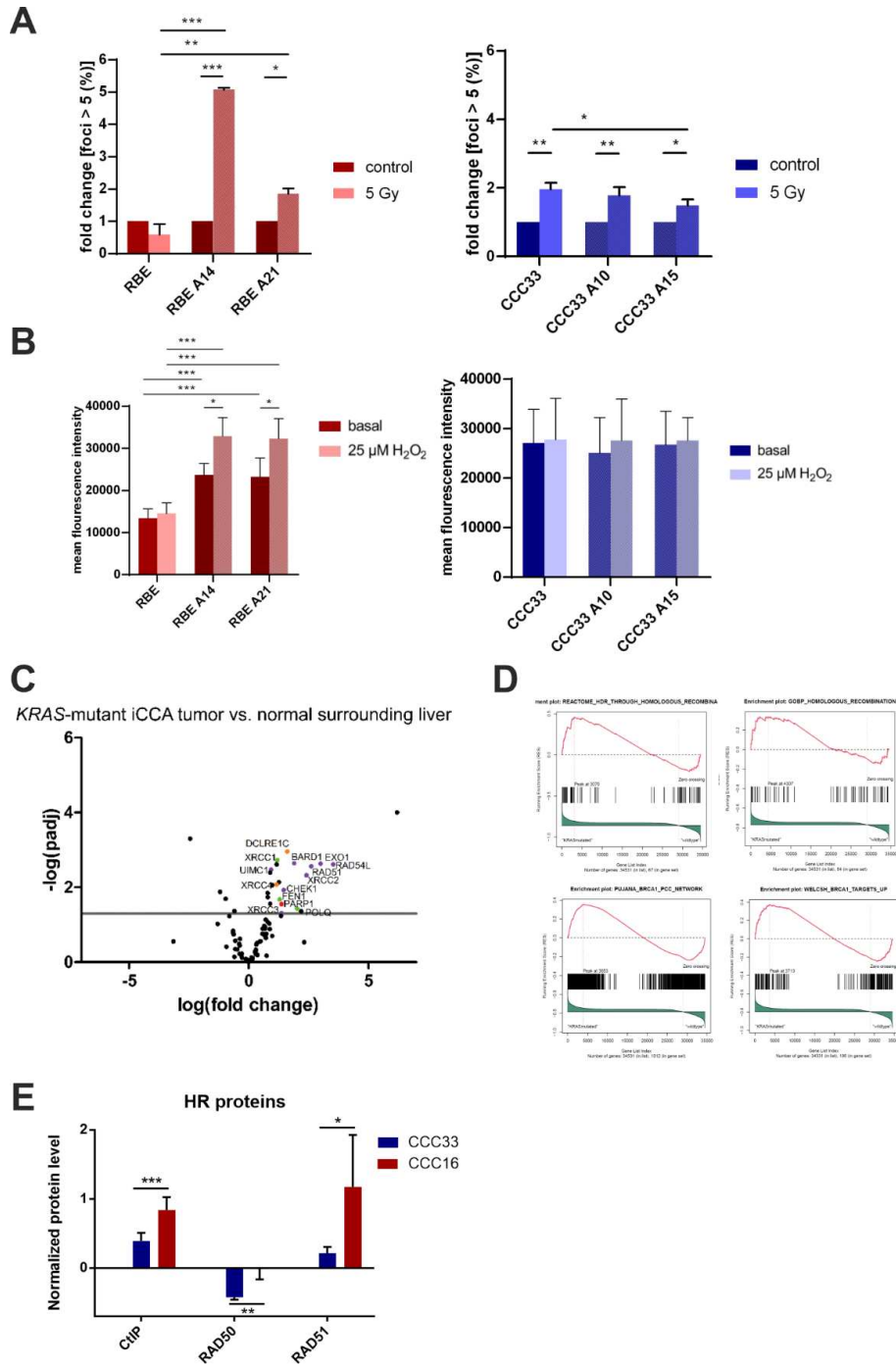


Figure S6

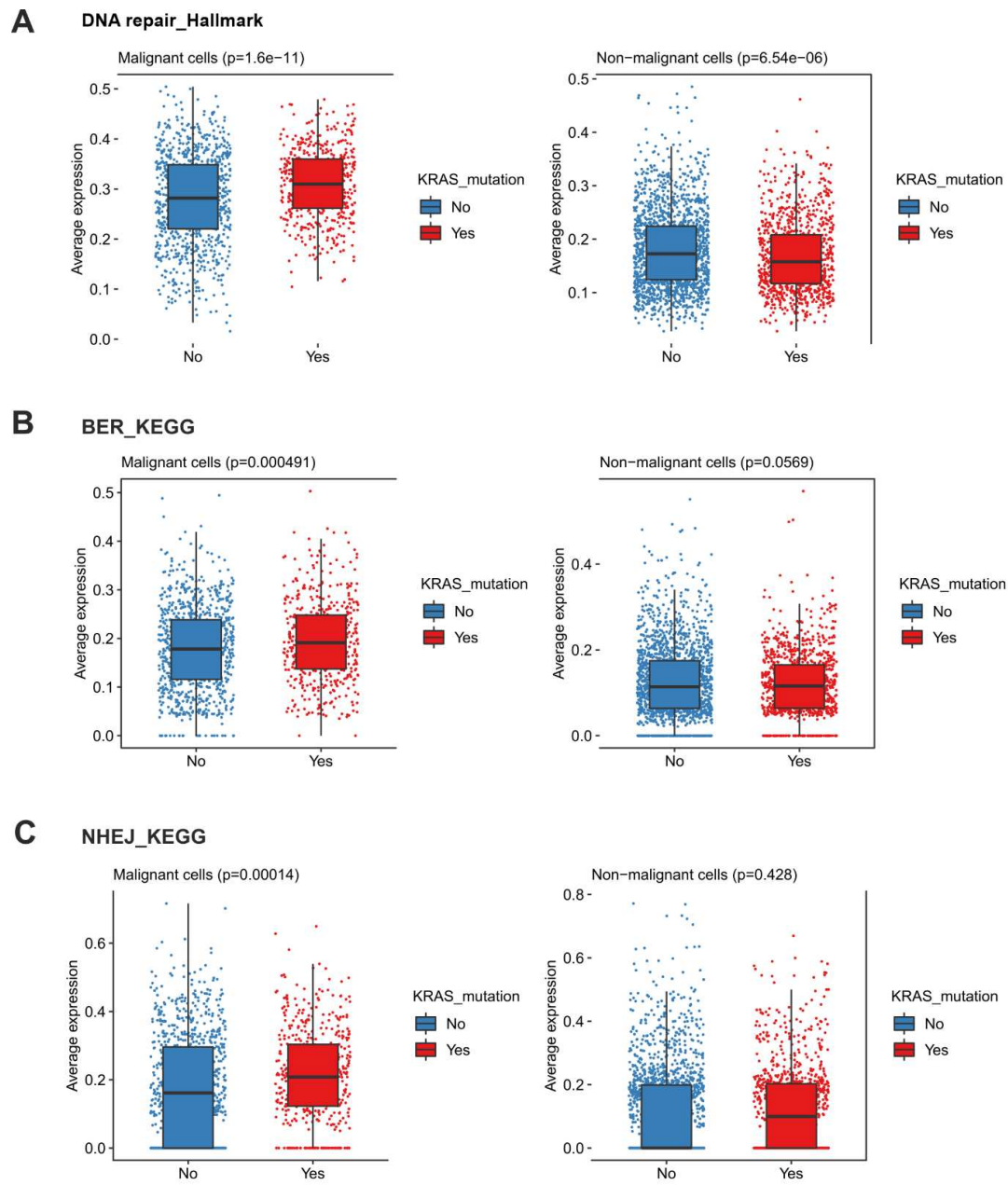
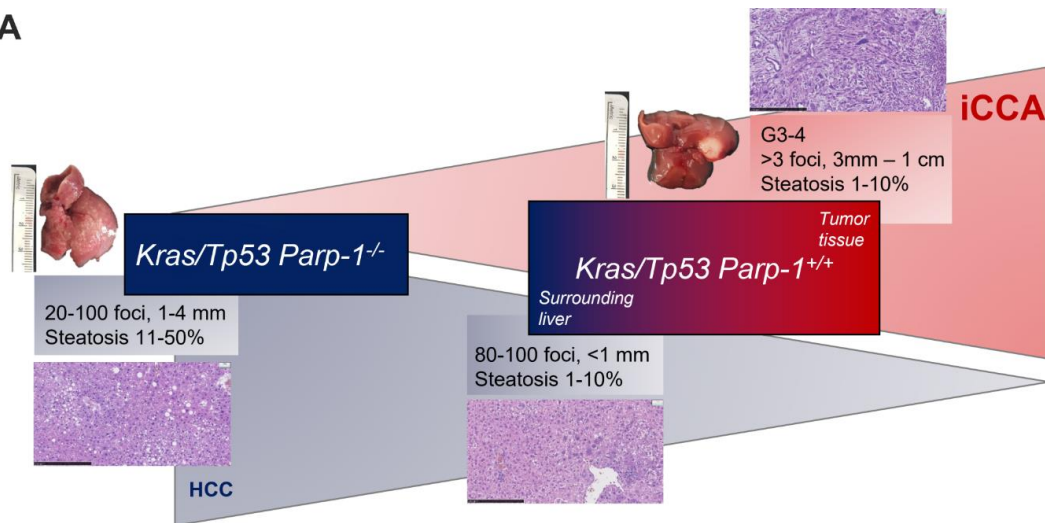


Figure S8

A



B

plasmid	N	genotype	tissue	classification	grading	foci	size	hematogenous spread
Empty vector (HSB2)	5	<i>PARP-1</i> ^{+/+}	normal liver	No tumor	-	-	-	-
	5	<i>PARP-1</i> ^{-/-}	normal liver	No tumor	-	-	-	-
<i>Kras/Tp53</i>	5	<i>PARP-1</i> ^{+/+}	tumor	4x iCCA, 1x iCCA-HCC	G3-4	>3	3 mm – 1 cm	-
			dysplastic foci in normal liver	5x dysplastic foci	n.A.	80-100	<1 mm	V1
	6	<i>PARP-1</i> ^{-/-}	dysplastic foci in normal liver	6x dysplastic foci, 1x HCC	n.A.	20-100	1-4 mm	V1
<i>Akt/Nicd</i>	5	<i>PARP-1</i> ^{+/+}	tumor in normal liver	Multiple iCCA	G1-2	~100	1-4 mm	-
	5	<i>PARP-1</i> ^{-/-}		Multiple iCCA	G1-2	~100	1-4 mm	-

Figure S9

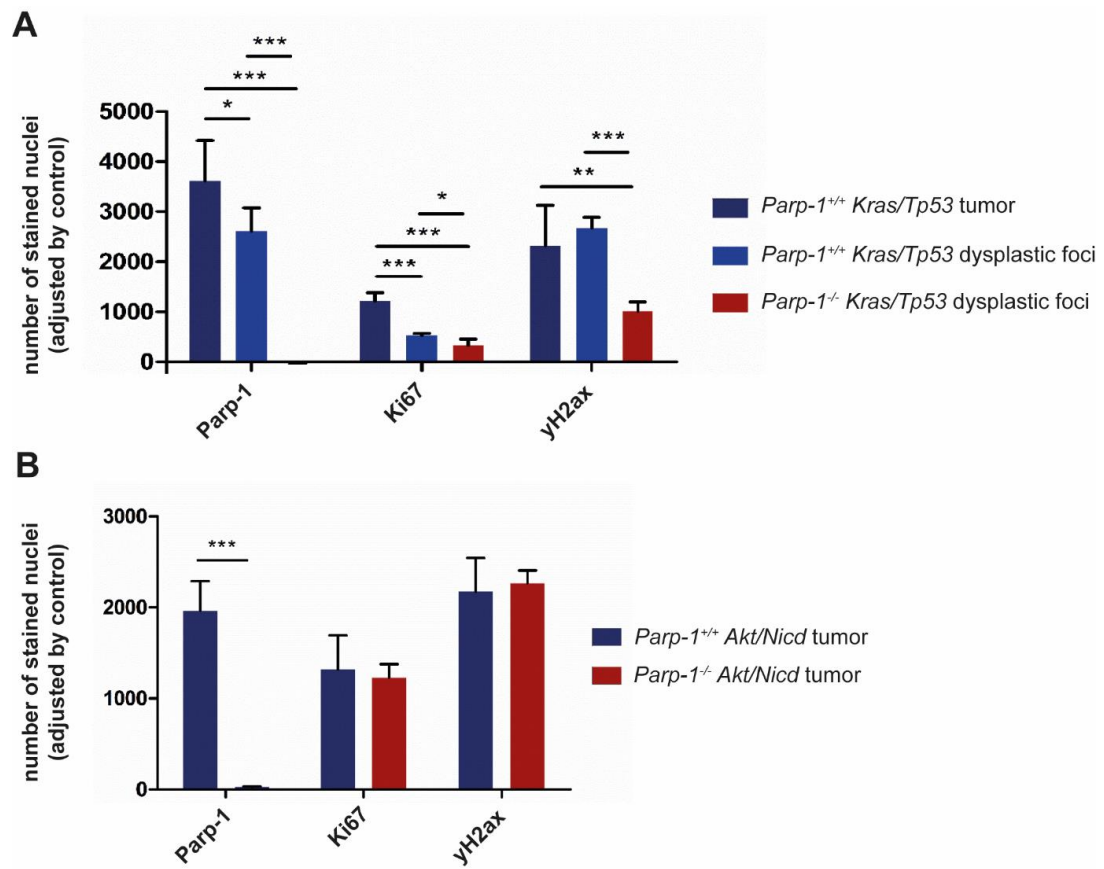


Figure S10

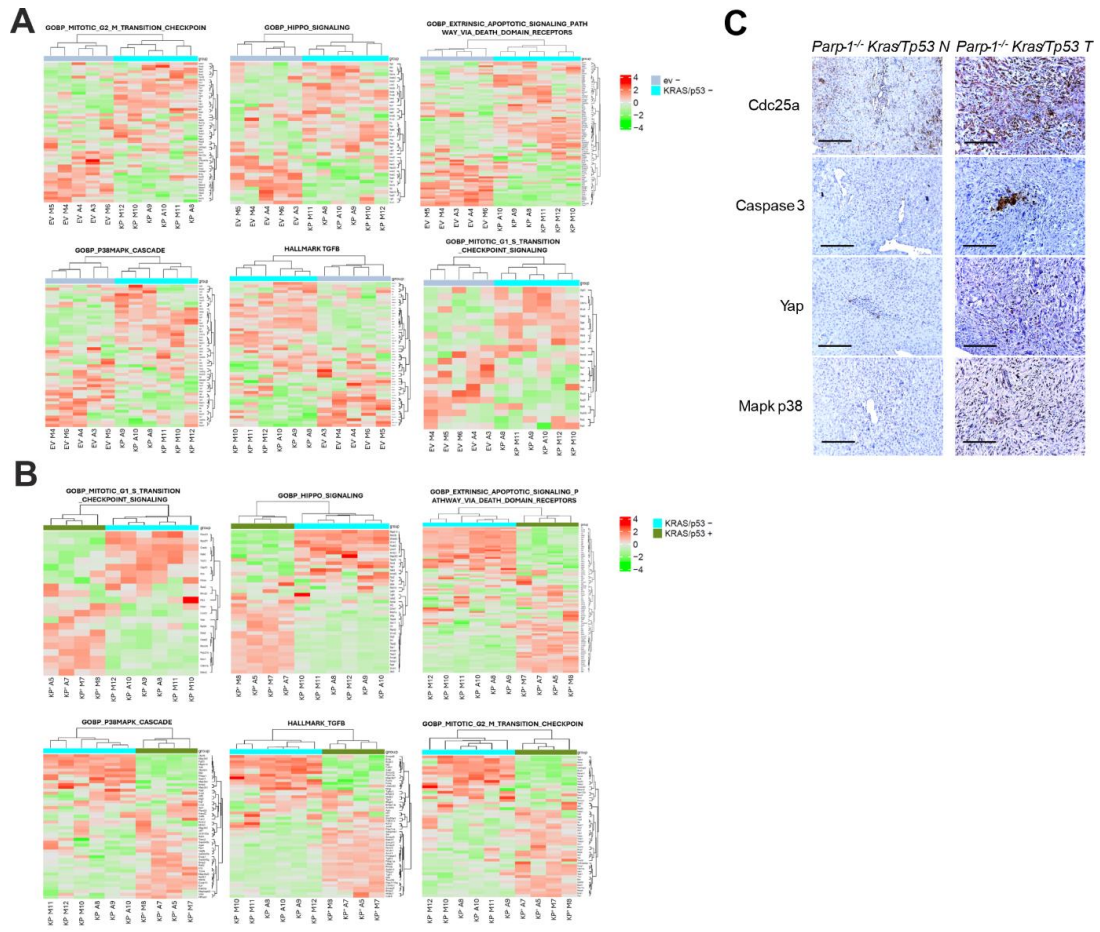


Figure S11

A

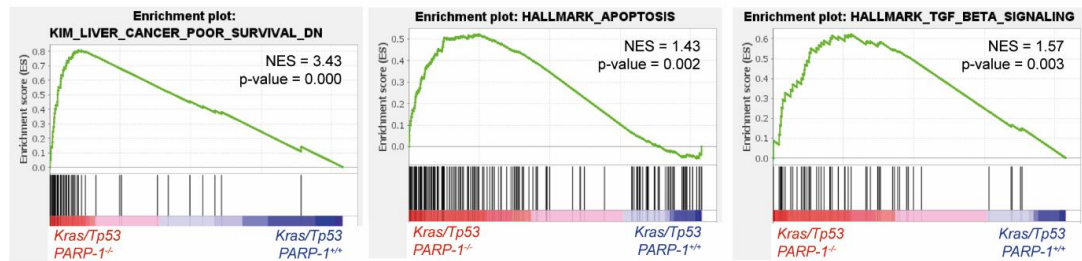
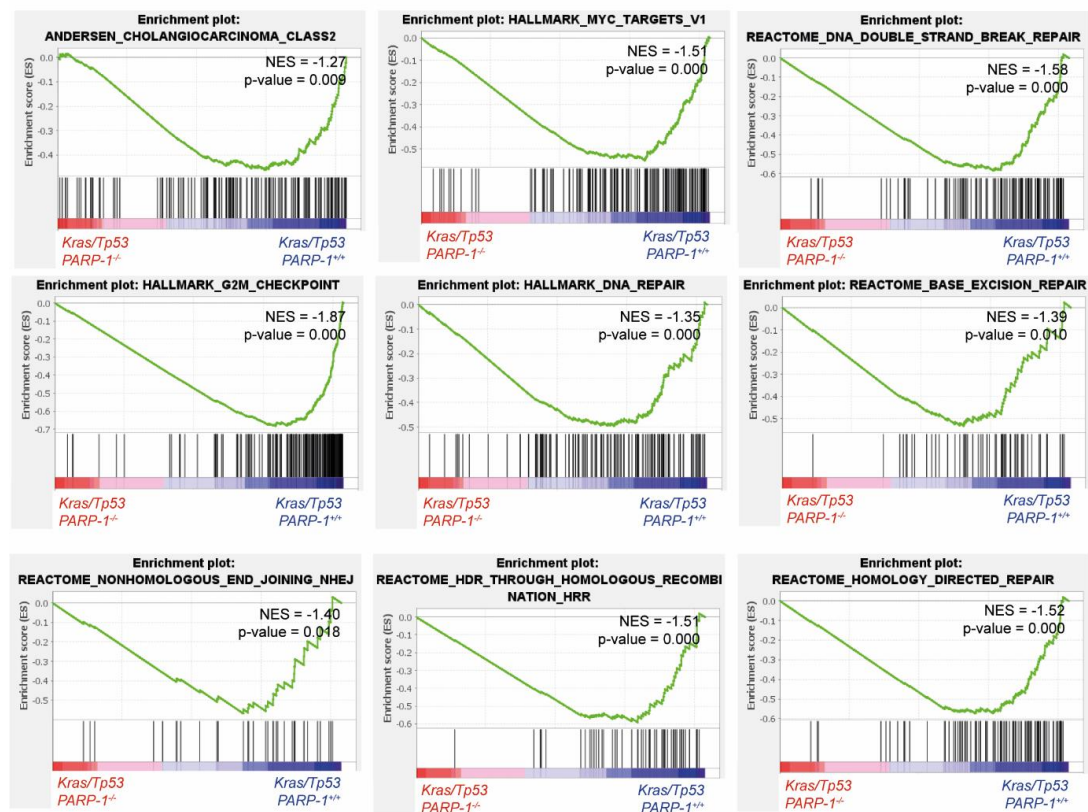
Gene sets enriched in *Kras/Tp53 Parp-1^{-/-}* miceGene sets enriched in *Kras/Tp53 Parp-1^{+/+}* mice

Figure S12

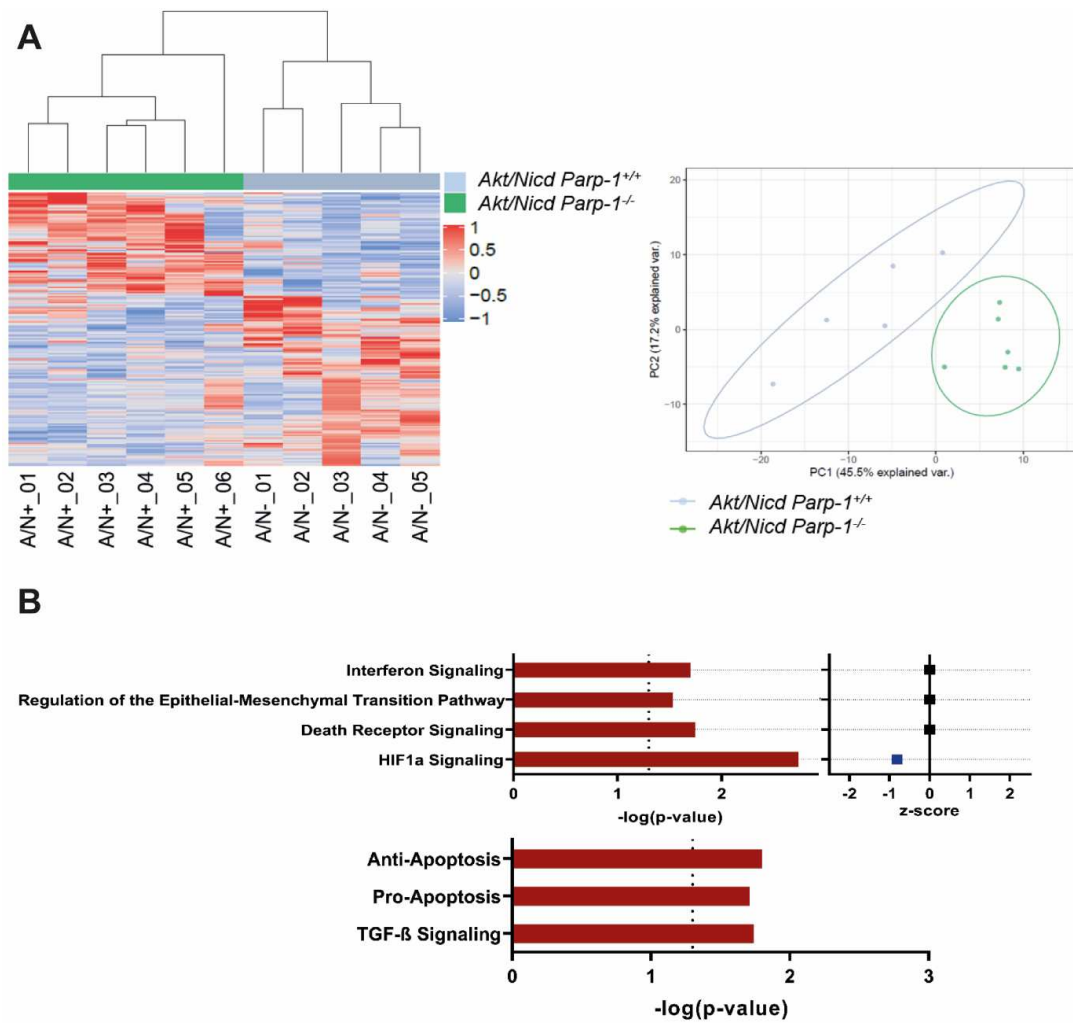


Figure S13

A

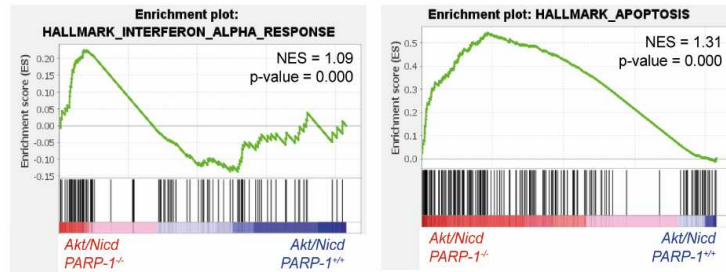
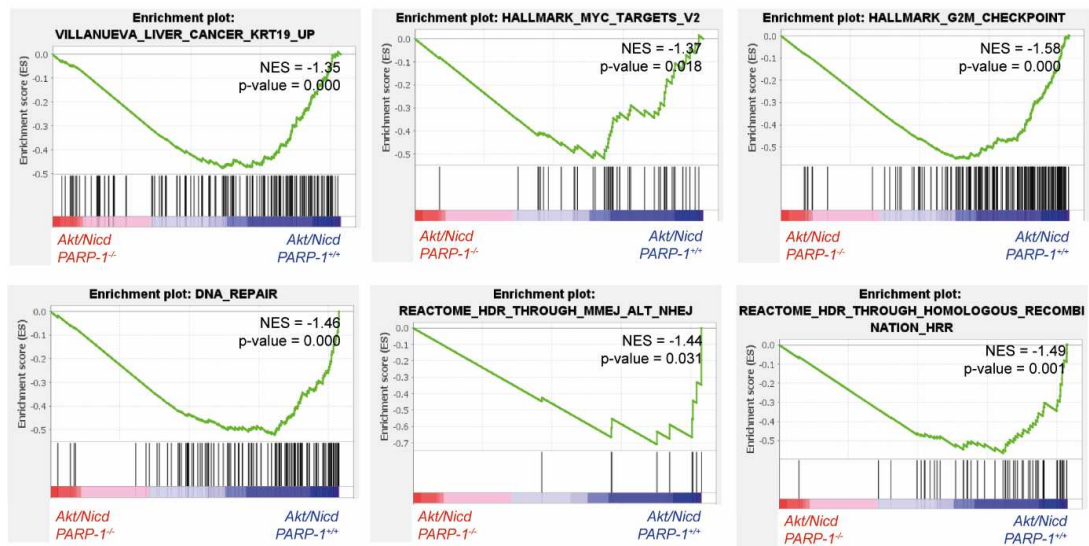
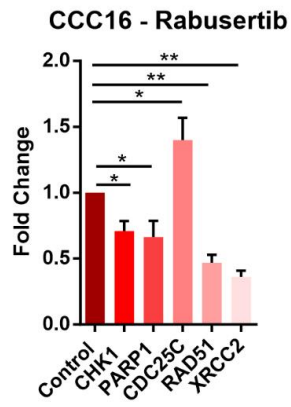
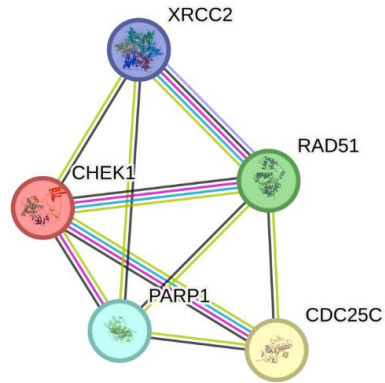
Gene sets enriched in *Akt/Nicd Parp-1^{-/-}* miceGene sets enriched in *Akt/Nicd Parp-1^{+/-}* mice

Figure S14

A



B



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ENSG00000124783	SSR1	0,656780005	0
ENSG00000136159	NUDT15	-0,59266001	0
ENSG00000143799	PARP1	-2,713370085	0
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ENSG00000079337	RAPGEF3	-1,638419986	0,0012
ENSG00000127329	PTPRB	-2,260289907	0,00121
ENSG00000251012	AC083800.1	13,69517994	0,00126
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ENSG00000154229	PRKCA	-1,019919991	0,00129
ENSG00000168502	MTCL1	-0,648829997	0,00129
ENSG00000177025	C19orf18	-3,550209999	0,00131
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ENSG00000275342	PRAG1	-1,850700021	0,00133
ENSG00000165806	CASP7	0,278270006	0,00137
ENSG00000025800	KPNA6	0,207699999	0,00143
ENSG00000144591	GMPPA	0,610610008	0,00143
ENSG00000183317	EPHA10	0,71566999	0,00143
ENSG00000109519	GRPEL1	0,630469978	0,00144
ENSG00000140368	PSTPIP1	-3,2348001	0,00146
ENSG00000227057	WDR46	0,437720001	0,00147
ENSG00000205531	NAP1L4	0,265100002	0,00149
ENSG00000136244	IL6	3,912450075	0,00151
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ENSG00000198758	EPS8L3	2,837759972	0,00152
ENSG00000164117	FBXO8	-0,383410007	0,00153
ENSG00000124383	MPHOSPH10	0,456149995	0,00155
ENSG00000158042	MRPL17	0,481130004	0,00157
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ENSG00000198824	CHAMP1	-0,567990005	0,0016
ENSG00000121741	ZMYM2	-0,526870012	0,00162

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ENSG00000185737	NRG3	4,749879837	0,0017
ENSG00000185338	SOCS1	2,120729923	0,0017
ENSG00000102466	FGF14	-2,248409986	0,00173
ENSG00000198804	MT-CO1	-0,38714999	0,00175
ENSG00000147854	UHRF2	-0,369870007	0,00176
ENSG00000143870	PDIA6	0,501380026	0,00176
ENSG00000005102	MEOX1	-2,556090117	0,00177
ENSG00000129009	ISLR	-3,665999889	0,00178
ENSG00000103429	BFAR	0,272689998	0,00182
ENSG00000198898	CAPZA2	-0,304179996	0,00183
ENSG00000115761	NOL10	0,406040013	0,00184
ENSG00000088448	ANKRD10	-0,96837002	0,00184
ENSG00000143546	S100A8	5,300630093	0,00187
ENSG00000151224	MAT1A	2,960289955	0,00188
ENSG00000005156	LIG3	0,347640008	0,00194
ENSG00000136104	RNASEH2B	-0,567260027	0,00194
ENSG00000148337	CIZ1	-0,571879983	0,00199
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ENSG00000114767	RRP9	0,56825	0,002
ENSG00000104093	DMXL2	-0,451299995	0,00201
ENSG00000170454	KRT75	-3,356869936	0,00205
ENSG00000185437	SH3BGR	-1,853839993	0,00206
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ENSG00000152520	PAN3	-0,351139992	0,0021
ENSG00000079112	CDH17	-3,294209957	0,00214
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ENSG00000116209	TMEM59	-0,290989995	0,00221
ENSG00000102962	CCL22	2,351289988	0,00222
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ENSG00000112624	BICRAL	-0,496230006	0,00229
ENSG00000077942	FBLN1	-0,691460013	0,00229
ENSG00000137440	FGFBP1	-3,711220026	0,00232
ENSG00000128591	FLNC	-0,829789996	0,00233
ENSG00000126787	DLGAP5	-0,840510011	0,00233
ENSG00000221164	SNORA11F	1,44303	0,00233
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ENSG00000130988	RGN	-5,189360142	0,00234
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ENSG00000006607	FARP2	0,500919998	0,00237

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ENSG00000132507	EIF5A	0,395900011	0,00242
ENSG00000283740	TAF11L11	-4,224150181	0,00243
ENSG00000163218	PGLYRP4	6,371250153	0,00244
ENSG00000105643	ARRDC2	-0,640999973	0,00246
ENSG00000160179	ABCG1	1,418149948	0,00246
ENSG00000197110	IFNL3	3,094189882	0,00248
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ENSG00000120699	EXOSC8	-0,556940019	0,00286
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ENSG00000172159	FRMD3	-1,293630004	0,00287
ENSG00000134326	CMPK2	1,372230053	0,00287
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ENSG00000121075	TBX4	-3,119149923	0,00305
ENSG00000162885	B3GALNT2	0,319330007	0,00306
ENSG00000185585	OLFML2A	-2,61390996	0,00307
ENSG00000139832	RAB20	-1,271989942	0,00316
ENSG00000105968	H2AFV	-0,388579994	0,0032
ENSG00000136861	CDK5RAP2	-0,37560001	0,00322
ENSG00000147155	EBP	-1,416290045	0,00323
ENSG00000184908	CLCNKB	-3,653919935	0,00323
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ENSG00000047457	CP	-0,91069001	0,00329
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ENSG00000132394	EEFSEC	-0,330190003	0,00334
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ENSG00000107959	PITRM1	0,452800006	0,00397
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ENSG00000007062	PROM1	3,363820076	0,00397
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ENSG00000154914	USP43	0,38567999	0,00421
ENSG00000100767	PAPLN	-1,723520041	0,00423
ENSG00000132792	CTNBL1	0,397280008	0,00423
ENSG00000065243	PKN2	-0,263790011	0,00425
ENSG00000122042	UBL3	-0,349869996	0,00427
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ENSG00000073331	ALPK1	-0,370689988	0,00432
ENSG00000197694	SPTAN1	-0,553849995	0,00433
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ENSG00000072952	MRVI1	-1,529060006	0,00439
ENSG00000127663	KDM4B	-0,406150013	0,00444
ENSG00000146021	KLHL3	-1,08209002	0,00446
ENSG00000163312	HELQ	-0,349350005	0,0045
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ENSG00000125089	SH3TC1	-1,07494998	0,00455
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ENSG00000170579	DLGAP1	2,600509882	0,00494
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ENSG00000050393	MCUR1	0,382669985	0,00508
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ENSG00000139618	BRCA2	-0,54569	0,00523
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ENSG00000135372	NAT10	0,507950008	0,00538
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ENSG00000117450	PRDX1	0,867810011	0,00551
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ENSG00000113240	CLK4	-0,465079993	0,00634
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ENSG00000204308	RNF5	0,778970003	0,00651
ENSG00000117152	RGS4	-1,513560057	0,00653
ENSG00000116459	ATP5PB	0,142539993	0,00661
ENSG00000198585	NUDT16	0,280149996	0,00662
ENSG00000167522	ANKRD11	-0,643450022	0,00663
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ENSG00000126953	TIMM8A	0,580829978	0,00684
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ENSG00000277925	RF00024	-2,706419945	0,00694
ENSG00000182957	SPATA13	-1,06329	0,00694
ENSG00000154620	TMSB4Y	-5,442599773	0,00697
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ENSG00000204315	FKBPL	0,627260029	0,00706
ENSG00000104848	KCNA7	-1,962059975	0,00706
ENSG00000102606	ARHGEF7	-0,674780011	0,0072
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ENSG00000185201	IFITM2	-0,360929996	0,00725
ENSG00000158669	GPAT4	-0,318450004	0,00728
ENSG00000169245	CXCL10	2,277440071	0,00735
ENSG00000072832	CRMP1	-0,723749995	0,00738
ENSG00000173258	ZNF483	-2,082910061	0,00749
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ENSG00000242485	MRPL20	0,223299995	0,00756
ENSG00000101413	RPRD1B	0,227750003	0,00759
ENSG00000135763	URB2	0,62480998	0,00766
ENSG00000167977	KCTD5	0,595529974	0,00772
ENSG00000006652	IFRD1	-0,839519978	0,00774
ENSG00000204227	RING1	0,153200001	0,00779
ENSG00000109323	MANBA	-0,622229993	0,00783
ENSG00000272674	PCDHB16	-1,142889977	0,00784
ENSG00000168925	CTRB1	-3,103179932	0,00787
ENSG00000145743	FBXL17	-0,816829979	0,0079
ENSG00000115539	PDCL3	0,58039999	0,00792
ENSG00000189266	PNRC2	0,439529985	0,00794
ENSG00000126803	HSPA2	-1,404829979	0,00801
ENSG00000119669	IRF2BPL	-0,547439992	0,00803
ENSG00000140937	CDH11	2,61135006	0,00803
ENSG00000131969	ABHD12B	-0,907289982	0,00804
ENSG00000173141	MRPL57	-0,556800008	0,00804
ENSG00000204304	PBX2	0,746529996	0,00808
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ENSG00000078369	GNB1	-0,166480005	0,00812
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ENSG00000196378	ZNF34	-0,566619992	0,00888
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ENSG00000124217	MOCS3	0,324889988	0,00899
ENSG00000083544	TDRD3	-0,514230013	0,00902
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ENSG00000144677	CTDSPL	-0,91516	0,00925
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ENSG00000099797	TECR	-0,471929997	0,00935
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ENSG00000126368	NR1D1	-1,321859956	0,00945
ENSG00000145912	NHP2	0,796570003	0,00948
ENSG00000101298	SNPH	1,09434998	0,00961
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ENSG00000188282	RUFY4	-2,827159882	0,00969
ENSG00000112619	PRPH2	-3,664289951	0,00971
ENSG00000137817	PARP6	-0,470149994	0,00973
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ENSG00000109572	CLCN3	-0,348340005	0,00982
ENSG00000160818	GPATCH4	0,376720011	0,00982
ENSG00000204899	MZT1	-0,211730003	0,01
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ENSG00000115993	TRAK2	-0,294719994	0,01038
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ENSG00000040633	PHF23	0,297600001	0,0104
ENSG00000119314	PTBP3	-0,605300009	0,01045
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ENSG00000204560	DHX16	0,404390007	0,01063
ENSG00000196177	ACADSB	0,943939984	0,01063
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ENSG00000203697	CAPN8	-1,797039986	0,01068
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ENSG00000162981	FAM84A	4,363729954	0,01072
ENSG00000136153	LMO7	-1,613170028	0,01076
ENSG00000169248	CXCL11	2,689680099	0,01077
ENSG00000163492	CCDC141	2,323199987	0,0108
ENSG00000253958	CLDN23	-1,893769979	0,01082
ENSG00000171747	LGALS4	2,484100103	0,01083
ENSG00000175874	CREG2	-1,534950018	0,01089
ENSG00000126218	F10	-1,828959942	0,01099
ENSG00000130706	ADRM1	0,444480002	0,01099
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ENSG00000042781	USH2A	1,225200057	0,01105
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ENSG00000168792	ABHD15	-0,534690022	0,03756
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ENSG00000142082	SIRT3	0,183170006	0,0419
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ENSG00000129055	ANAPC13	0,312299997	0,04191
ENSG00000159792	PSKH1	-0,43829	0,04195
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ENSG00000159714	ZDHHC1	-0,805840015	0,04686
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ENSMUSG00000022442	Ttll1	-1,343539953	0,00001
ENSMUSG00000027660	Skil	-1,310600042	0,00001
ENSMUSG00000021428	Riok1	-1,038519979	0,00001
ENSMUSG00000017376	Nlk	-0,948939979	0,00001
ENSMUSG00000024603	Dctn4	-0,824109972	0,00001
ENSMUSG00000022558	Mroh1	-0,802850008	0,00001
ENSMUSG00000038302	Afg1l	0,754310012	0,00001
ENSMUSG00000031671	Setd6	0,881049991	0,00001
ENSMUSG00000033720	Sfxn5	0,99138999	0,00001

ENSMUSG00000026781	Acbd5	1,467839956	0,00001
ENSMUSG00000010663	Fads1	1,841330051	0,00001
ENSMUSG00000028150	Rorc	2,138659954	0,00001
ENSMUSG00000047797	Gjb1	2,392110109	0,00001
ENSMUSG00000057346	Apol9a	2,554749966	0,00001
ENSMUSG00000020159	Gabrp	-5,964240074	0,00002
ENSMUSG00000035352	Ccl12	-4,207300186	0,00002
ENSMUSG00000031595	Pdgfrl	-3,418149948	0,00002
ENSMUSG00000038256	Bcl9	-1,849020004	0,00002
ENSMUSG00000022475	Hdac7	-1,296499968	0,00002
ENSMUSG00000027680	Fxr1	-0,72487998	0,00002
ENSMUSG00000029518	Rab35	-0,691429973	0,00002
ENSMUSG00000031399	Fam3a	0,614859998	0,00002
ENSMUSG00000025825	Iscu	1,264520049	0,00002
ENSMUSG00000028756	Pink1	1,353449941	0,00002
ENSMUSG00000021868	Ppif	1,412719965	0,00002
ENSMUSG00000023921	Mut	1,672600031	0,00002
ENSMUSG00000004633	Chn2	1,73100996	0,00002
ENSMUSG00000074639	Rdh16f2	2,857180119	0,00002
ENSMUSG00000053030	Spink2	-8,696669579	0,00002
ENSMUSG00000021047	Nova1	-7,937759876	0,00002
ENSMUSG00000028487	Bnc2	-7,530789852	0,00002
ENSMUSG00000034551	Hdx	-4,222469807	0,00002
ENSMUSG00000040594	Ranbp17	-3,922990084	0,00002
ENSMUSG00000038732	Mboat1	-3,204969883	0,00002
ENSMUSG00000047330	Kcne4	-2,86439991	0,00002
ENSMUSG00000027955	Fam198b	-2,640969992	0,00002
ENSMUSG00000057098	Ebf1	-2,584429979	0,00002
ENSMUSG00000028111	Ctsk	-2,439429998	0,00002
ENSMUSG00000065226	Gm25791	-2,349129915	0,00002
ENSMUSG00000047712	Ust	-2,340830088	0,00002
ENSMUSG00000051335	Gfod1	-2,338279963	0,00002
ENSMUSG00000049130	C5ar1	-2,254839897	0,00002
ENSMUSG00000024660	Incenp	-1,747650027	0,00002
ENSMUSG00000092730	Snora24	-1,631389976	0,00002
ENSMUSG00000096472	Cdkn2d	-1,553239942	0,00002
ENSMUSG00000011158	Brf1	-0,827970028	0,00002
ENSMUSG00000003808	Farsa	-0,779190004	0,00002
ENSMUSG00000040006	Ginm1	0,927150011	0,00002
ENSMUSG00000031245	Hmgn5	1,004299998	0,00002
ENSMUSG00000037706	Cd81	1,033290029	0,00002
ENSMUSG00000008348	Ubc	1,185760021	0,00002
ENSMUSG00000042903	Foxo4	1,190969944	0,00002
ENSMUSG00000062908	Acadm	1,385239959	0,00002
ENSMUSG00000029173	Sepsecs	1,502519965	0,00002
ENSMUSG00000035936	Aldh5a1	1,594470024	0,00002
ENSMUSG00000022742	Cpox	1,625609994	0,00002

ENSMUSG00000028479	Gne	1,713150024	0,00002
ENSMUSG00000034177	Rnf43	1,728180051	0,00002
ENSMUSG00000049115	Agtr1a	2,04479003	0,00002
ENSMUSG00000039628	Hs3st6	2,128350019	0,00002
ENSMUSG00000031883	Car7	2,345849991	0,00002
ENSMUSG00000051652	Lrrc3	2,37293005	0,00002
ENSMUSG00000058656	Samd12	-5,88888979	0,00002
ENSMUSG00000022686	B3gnt5	-3,362499952	0,00002
ENSMUSG00000059974	Ntm	-3,105890036	0,00002
ENSMUSG00000049775	Tmsb4x	-2,686049938	0,00002
ENSMUSG00000022199	Slc22a17	-2,461009979	0,00002
ENSMUSG00000025001	Hells	-2,415940046	0,00002
ENSMUSG00000001228	Uhrf1	-2,374000072	0,00002
ENSMUSG00000024664	Fads3	-2,097860098	0,00002
ENSMUSG00000003992	Ssbp2	-1,987759948	0,00002
ENSMUSG00000026972	Arrdc1	-1,846480012	0,00002
ENSMUSG00000094910	D430019H16Rik	-1,691570044	0,00002
ENSMUSG00000030499	Kctd15	-1,677780032	0,00002
ENSMUSG00000026496	Parp1	-1,322630048	0,00002
ENSMUSG00000030471	Zdhhc13	-1,316020012	0,00002
ENSMUSG00000033166	Dis3	-1,202550054	0,00002
ENSMUSG00000071652	Ints5	-0,843509972	0,00002
ENSMUSG00000054405	Dnajc8	-0,746010005	0,00002
ENSMUSG00000007815	Rhoa	-0,642159998	0,00002
ENSMUSG00000028164	Manba	-0,608959973	0,00002
ENSMUSG00000001445	Mrpl10	0,539279997	0,00002
ENSMUSG00000040746	Rnf167	0,576489985	0,00002
ENSMUSG00000028550	Atg4c	0,803839982	0,00002
ENSMUSG00000031402	Mpp1	0,988439977	0,00002
ENSMUSG00000027180	Fbxo3	0,997380018	0,00002
ENSMUSG00000013997	Nit1	1,295330048	0,00002
ENSMUSG00000028085	Gatb	1,30606997	0,00002
ENSMUSG00000049858	Suox	1,454409957	0,00002
ENSMUSG00000053460	Ggcx	1,606789947	0,00002
ENSMUSG00000020644	Id2	1,676399946	0,00002
ENSMUSG00000053886	Sh2d4a	1,813500047	0,00002
ENSMUSG00000004035	Gstm7	2,096260071	0,00002
ENSMUSG00000030237	Slco1a4	2,455319881	0,00002
ENSMUSG00000039323	Igfbp2	2,877360106	0,00002
ENSMUSG00000030364	Clec2h	3,999279976	0,00002
ENSMUSG00000072244	Trim6	-2,530440092	0,00002
ENSMUSG00000042784	Muc1	-2,48390007	0,00002
ENSMUSG00000032717	Mdfi	-2,41753006	0,00002
ENSMUSG00000036390	Gadd45a	-2,038460016	0,00002
ENSMUSG00000031728	Zfp821	-1,595309973	0,00002
ENSMUSG00000040747	Cd53	-1,573510051	0,00002
ENSMUSG00000071337	Tia1	-1,55151999	0,00002

ENSMUSG00000029106	Add1	-1,013139963	0,00002
ENSMUSG00000001175	Calm1	-0,762049973	0,00002
ENSMUSG00000031447	Lamp1	0,605440021	0,00002
ENSMUSG00000032583	Mon1a	0,77601999	0,00002
ENSMUSG00000033126	Ybey	1,005800009	0,00002
ENSMUSG00000073609	D2hgdh	1,130820036	0,00002
ENSMUSG00000024247	Pkdcc	1,418830037	0,00002
ENSMUSG00000020733	Slc9a3r1	1,429829955	0,00002
ENSMUSG00000030739	Myh14	1,606050014	0,00002
ENSMUSG00000029136	Rbks	1,837129951	0,00002
ENSMUSG00000049152	Ugt3a2	2,319380045	0,00002
ENSMUSG00000031844	Hsd17b2	2,325649977	0,00002
ENSMUSG00000031877	Ces2g	2,380810022	0,00002
ENSMUSG00000026787	Gad2	-9,668499947	0,00002
ENSMUSG00000029576	Radil	-5,730750084	0,00002
ENSMUSG00000041193	Pla2g5	-5,033360004	0,00002
ENSMUSG00000060093	Hist1h4a	-4,421000004	0,00002
ENSMUSG00000033491	Prss35	-3,510519981	0,00002
ENSMUSG00000022099	Dmtn	-2,590039968	0,00002
ENSMUSG00000034906	Ncaph	-1,915660024	0,00002
ENSMUSG00000000489	Pdgfb	-1,811550021	0,00002
ENSMUSG00000028873	Cdca8	-1,807389975	0,00002
ENSMUSG00000047434	Xxylt1	-1,769889951	0,00002
ENSMUSG00000039081	Zfp503	-1,768919945	0,00002
ENSMUSG00000057406	Nsd2	-1,432629943	0,00002
ENSMUSG00000020184	Mdm2	-1,173879981	0,00002
ENSMUSG00000046441	Cmtr2	-1,055529952	0,00002
ENSMUSG00000020211	Sf3a2	-0,969860017	0,00002
ENSMUSG00000038497	Tmco3	-0,908460021	0,00002
ENSMUSG00000027433	Xrn2	-0,873260021	0,00002
ENSMUSG00000032590	Apeh	0,738460004	0,00002
ENSMUSG00000004798	Ulk2	0,934589982	0,00002
ENSMUSG00000041957	Pkp2	1,04350996	0,00002
ENSMUSG00000073838	Tufm	1,063509941	0,00002
ENSMUSG00000035759	Bbs10	1,103440046	0,00002
ENSMUSG00000024818	Slc25a45	1,128260016	0,00002
ENSMUSG00000032064	Dixdc1	1,233150005	0,00002
ENSMUSG00000066442	Mthfs	1,275329947	0,00002
ENSMUSG00000030275	Etnk1	1,319169998	0,00002
ENSMUSG00000028527	Ak4	1,321539998	0,00002
ENSMUSG00000040820	Hlcs	1,532799959	0,00002
ENSMUSG00000032092	Mpzi2	1,567620039	0,00002
ENSMUSG00000021794	Glud1	1,671120048	0,00002
ENSMUSG00000022847	Thpo	1,790400028	0,00002
ENSMUSG00000045636	Mtus1	1,799649954	0,00002
ENSMUSG00000030670	Cyp2r1	1,889610052	0,00002
ENSMUSG00000024899	Papss2	2,081520081	0,00002

ENSMUSG00000031443	F7	2,131649971	0,00002
ENSMUSG00000023963	Cyp39a1	2,306809902	0,00002
ENSMUSG00000027227	Sord	2,350090027	0,00002
ENSMUSG00000000049	ApoH	2,558559895	0,00002
ENSMUSG00000062410	Hsd3b3	2,65060997	0,00002
ENSMUSG00000026295	Spp2	2,661870003	0,00002
ENSMUSG00000028051	Hcn3	2,81836009	0,00002
ENSMUSG00000056679	Gpr173	-5,655529976	0,00002
ENSMUSG00000028463	Car9	-3,716660023	0,00002
ENSMUSG00000057092	Fxyd3	-3,505929947	0,00002
ENSMUSG0000001020	S100a4	-3,254159927	0,00002
ENSMUSG00000069920	B3gnt9	-3,078000069	0,00002
ENSMUSG00000024855	Pacs1	-2,479020119	0,00002
ENSMUSG00000045328	Cenpe	-2,473170042	0,00002
ENSMUSG00000022661	Cd200	-2,196160078	0,00002
ENSMUSG00000025140	Pycr1	-2,152050018	0,00002
ENSMUSG00000040389	Wdr47	-1,963379979	0,00002
ENSMUSG00000036718	Micall2	-1,819390059	0,00002
ENSMUSG00000015143	Actn1	-1,797309995	0,00002
ENSMUSG00000073987	Ggh	-1,791560054	0,00002
ENSMUSG00000050379	Sept6	-1,560670018	0,00002
ENSMUSG00000032939	Nup93	-1,058159947	0,00002
ENSMUSG00000040652	Oaz2	-0,929939985	0,00002
ENSMUSG00000038544	Inip	-0,900439978	0,00002
ENSMUSG00000029267	Mtf2	-0,84641999	0,00002
ENSMUSG00000000776	Polr3d	-0,738179982	0,00002
ENSMUSG00000021116	Eif2s1	-0,737190008	0,00002
ENSMUSG00000033285	Wdr3	-0,608340025	0,00002
ENSMUSG00000027575	Arfgap1	-0,578170002	0,00002
ENSMUSG00000061244	Exoc5	-0,49368	0,00002
ENSMUSG0000003099	Ppp5c	0,495759994	0,00002
ENSMUSG00000047694	Yipf6	0,759019971	0,00002
ENSMUSG00000036552	Ermard	0,881280005	0,00002
ENSMUSG00000001482	Def8	0,888750017	0,00002
ENSMUSG00000025453	Nnt	1,173900008	0,00002
ENSMUSG00000033684	Qsox1	1,217880011	0,00002
ENSMUSG00000016319	Slc25a5	1,274600029	0,00002
ENSMUSG00000022885	St6gal1	1,361580014	0,00002
ENSMUSG00000039062	Anpep	1,369400024	0,00002
ENSMUSG00000022214	Dcaf11	1,539530039	0,00002
ENSMUSG00000050323	Ndufaf6	1,668230057	0,00002
ENSMUSG00000036880	Acaa2	1,847460032	0,00002
ENSMUSG00000035112	Wnk4	2,001379967	0,00002
ENSMUSG00000032204	Aqp9	2,068429947	0,00002
ENSMUSG00000017453	Pipox	2,352570057	0,00002
ENSMUSG00000041794	Myrip	4,219649792	0,00002
ENSMUSG00000034164	Emid1	-3,680809975	0,00003

ENSMUSG00000013415	Igf2bp1	-10,69085979	0,00003
ENSMUSG000000096140	Ankrd66	-7,353079796	0,00003
ENSMUSG00000026387	Sctr	-5,070859909	0,00003
ENSMUSG000000053475	Tnfaip6	-4,323770046	0,00003
ENSMUSG00000016458	Wt1	-4,102220058	0,00003
ENSMUSG000000070526	Peg12	-3,706099987	0,00003
ENSMUSG00000022494	Shisa9	-3,652220011	0,00003
ENSMUSG000000042116	Vwa1	-2,763220072	0,00003
ENSMUSG000000027469	Tpx2	-2,450099945	0,00003
ENSMUSG00000027555	Car13	-2,329169989	0,00003
ENSMUSG00000019539	Rcn3	-2,1057899	0,00003
ENSMUSG000000042099	Kank3	-1,234459996	0,00003
ENSMUSG000000025666	Tmem47	-1,216519952	0,00003
ENSMUSG000000034889	Cactin	-0,954479992	0,00003
ENSMUSG000000004677	Myo9b	-0,886150002	0,00003
ENSMUSG000000024515	Smad4	-0,815930009	0,00003
ENSMUSG000000028790	Khdrbs1	-0,746959984	0,00003
ENSMUSG000000029017	Pmpcb	1,048149943	0,00003
ENSMUSG000000066441	Rdh11	1,396860003	0,00003
ENSMUSG000000040964	Arhgef10l	1,47428	0,00003
ENSMUSG000000055027	Smyd1	1,621549964	0,00003
ENSMUSG000000048368	Omd	1,701769948	0,00003
ENSMUSG000000071711	Mpst	1,830189943	0,00003
ENSMUSG000000037710	Cisd1	2,029769897	0,00003
ENSMUSG000000002032	Tmem25	2,343369961	0,00003
ENSMUSG000000054385	Ceacam2	2,573970079	0,00003
ENSMUSG000000032773	Chrm1	3,687289953	0,00003
ENSMUSG000000040420	Cdh18	3,948060036	0,00003
ENSMUSG000000034648	Lrrn1	-5,317550182	0,00003
ENSMUSG000000030428	Ttyh1	-2,932590008	0,00003
ENSMUSG000000079560	Hoxa3	-2,641940117	0,00003
ENSMUSG000000052105	Mtcl1	-2,43166995	0,00003
ENSMUSG000000037217	Syn1	-2,343440056	0,00003
ENSMUSG000000001120	Pcbp3	-2,222490072	0,00003
ENSMUSG000000039199	Zdhhc1	-1,745110035	0,00003
ENSMUSG000000020573	Pik3cg	-1,62480998	0,00003
ENSMUSG000000039108	Lsm14b	-0,851849973	0,00003
ENSMUSG000000019087	Atp6ap1	-0,812269986	0,00003
ENSMUSG000000036693	Nop14	-0,683189988	0,00003
ENSMUSG000000026192	Atic	-0,681299984	0,00003
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ENSMUSG000000020130	Tbc1d15	0,967419982	0,00003
ENSMUSG000000028673	Fuca1	1,18208003	0,00003
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ENSMUSG000000038521	C1s1	1,931210041	0,00003
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ENSMUSG00000049670	Morn4	-3,239279985	0,00003
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ENSMUSG00000024349	Tmem173	-1,436290026	0,00003
ENSMUSG00000032712	Resf1	-1,331050038	0,00003
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ENSMUSG00000019920	Lims1	-0,887489974	0,00003
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ENSMUSG00000046707	Csnk2a2	-0,704289973	0,00003
ENSMUSG00000031754	Nudt21	-0,642780006	0,00003
ENSMUSG00000022503	Nubp1	0,632619977	0,00003
ENSMUSG00000029571	Tmem106b	0,852689981	0,00003
ENSMUSG00000026307	Scly	1,37124002	0,00003
ENSMUSG00000037542	Aldh8a1	2,389290094	0,00003
ENSMUSG00000025396	Hsd17b6	2,788150072	0,00003
ENSMUSG00000036027	1810046K07Rik	4,2355299	0,00003
ENSMUSG00000045027	Prss22	-8,418669701	0,00003
ENSMUSG00000029838	Ptn	-5,023310184	0,00003
ENSMUSG00000041078	Grid1	-3,784729958	0,00003
ENSMUSG00000017897	Eya2	-3,220669985	0,00003
ENSMUSG00000037995	Igsf9	-2,970989943	0,00003
ENSMUSG00000080316	Spaca6	-2,145669937	0,00003
ENSMUSG00000020901	Pik3r5	-1,806710005	0,00003
ENSMUSG00000022610	Mapk12	-1,548560023	0,00003
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ENSMUSG00000029710	Ephb4	-0,861180007	0,00003
ENSMUSG00000002803	Btbd6	0,586380005	0,00003
ENSMUSG00000056216	Cebpg	0,846350014	0,00003
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ENSMUSG00000038745	Nlrp6	2,517240047	0,00003
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ENSMUSG00000040220	Gas8	-1,571529984	0,00003

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ENSMUSG00000090523	Gypc	-0,818379998	0,00003
ENSMUSG00000020432	Tcn2	0,47093001	0,00003
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ENSMUSG00000020919	Stat5b	1,167600036	0,00003
ENSMUSG00000022763	Aifm3	1,888100028	0,00003
ENSMUSG00000034258	Flvcr2	1,989269972	0,00003
ENSMUSG00000023828	Slc22a3	2,047230005	0,00003
ENSMUSG00000000154	Slc22a18	2,385529995	0,00003
ENSMUSG00000027559	Car3	2,76970005	0,00003
ENSMUSG00000033207	Mamdc2	-2,050800085	0,00004
ENSMUSG00000020334	Slc22a4	-2,029690027	0,00004
ENSMUSG00000002732	Fkbp7	-1,770069957	0,00004
ENSMUSG00000031872	Bean1	-4,729320049	0,00004
ENSMUSG00000028841	Cnksr1	-4,023910046	0,00004
ENSMUSG00000028587	Orc1	-2,825500011	0,00004
ENSMUSG00000042842	Serpinb6b	-1,792000055	0,00004
ENSMUSG00000045679	Pqlc3	-1,727370024	0,00004
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ENSMUSG00000037235	Mxd4	0,654030025	0,00009
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ENSMUSG000000024826	Dpf2	-0,655439973	0,00018
ENSMUSG000000025130	P4hb	0,909370005	0,00018
ENSMUSG000000045160	Bola3	1,34465003	0,00018
ENSMUSG000000089678	Agxt2	2,051179886	0,00018
ENSMUSG000000031109	Enox2	0,729080021	0,00019
ENSMUSG000000020251	Glt8d2	-3,358330011	0,00019
ENSMUSG000000027331	Knstrn	-1,718979955	0,00019
ENSMUSG000000073599	Ecscr	-1,65297997	0,00019
ENSMUSG000000033233	Trim45	-1,627030015	0,00019

ENSMUSG00000024423	Impact	-0,929539979	0,00019
ENSMUSG00000020755	Sap30bp	-0,560720026	0,00019
ENSMUSG00000021779	Thrb	1,788579941	0,00019
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ENSMUSG00000002459	Rgs20	-6,512420177	0,00019
ENSMUSG00000032323	Cyp11a1	-4,720510006	0,00019
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ENSMUSG00000015889	Lta4h	-0,507439971	0,00019
ENSMUSG00000041733	Coq5	0,626980007	0,00019
ENSMUSG00000007777	0610009B22Rik	0,99752003	0,00019
ENSMUSG00000021930	Spryd7	1,103160024	0,00019
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ENSMUSG00000041012	Cmtm8	1,940189958	0,0002
ENSMUSG00000041895	Wipi1	-1,000650048	0,0002
ENSMUSG00000022704	Qtrt2	-0,855790019	0,0002
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ENSMUSG00000052906	Ubxn8	0,606220007	0,0002
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ENSMUSG00000040356	Skiv2l	0,520030022	0,00021
ENSMUSG00000032812	Arap1	0,819480002	0,00021
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ENSMUSG00000037509	Arhgef4	-1,913869977	0,00025
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ENSMUSG00000047146	Tet1	-3,569109917	0,00027
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ENSMUSG00000035181	Heatr5a	-1,484509945	0,00028
ENSMUSG00000032178	Ilf3	-0,984089971	0,00028
ENSMUSG00000026854	Usp20	-0,768819988	0,00028
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ENSMUSG00000017868	Sgk2	2,093470097	0,0003
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ENSMUSG00000036885	Arhgef26	1,572610021	0,0003
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ENSMUSG00000027861	Casq2	-3,854360104	0,0003
ENSMUSG00000054203	Ifi205	-1,966510057	0,0003
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ENSMUSG00000027939	Nup210l	-5,237080097	0,00035
ENSMUSG00000041347	Bdkrb1	-4,467380047	0,00035
ENSMUSG00000097789	Gm2115	-3,775540113	0,00035
ENSMUSG00000025935	Tram1	0,915639997	0,00035
ENSMUSG00000020364	Zfp354a	1,007609963	0,00035
ENSMUSG00000026621	Marc1	2,151370049	0,00035
ENSMUSG00000034126	Pomt2	0,557150006	0,00035
ENSMUSG00000033931	Rbm34	-0,463079989	0,00035
ENSMUSG00000037872	Ackr1	1,938050032	0,00035
ENSMUSG00000070287	Slc35g2	-2,031199932	0,00036
ENSMUSG00000005566	Trim28	-0,750320017	0,00036
ENSMUSG00000034867	Ankrd27	0,746200025	0,00036
ENSMUSG00000020882	Cacnb1	-1,826480031	0,00036
ENSMUSG00000027618	Nfs1	0,700699985	0,00036
ENSMUSG00000009646	Pla2g12b	2,099159956	0,00036
ENSMUSG00000021929	Kpna3	-0,386720002	0,00036
ENSMUSG00000014905	Dnajb9	1,03094995	0,00036
ENSMUSG00000079652	Fam71f2	-3,522540092	0,00036
ENSMUSG00000029389	Ddx55	-0,577820003	0,00037
ENSMUSG00000022351	Sqle	1,053449988	0,00037
ENSMUSG00000030494	Rhpn2	1,489159942	0,00037
ENSMUSG00000046031	Calhm6	2,210469961	0,00037

ENSMUSG00000022387	Brd1	-0,857550025	0,00037
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ENSMUSG00000029056	Pank4	-0,588670015	0,00037
ENSMUSG00000025903	Lypla1	1,188339949	0,00037
ENSMUSG00000074272	Ceacam1	2,279910088	0,00037
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ENSMUSG00000021687	Scamp1	0,694360018	0,00037
ENSMUSG00000041058	Wwp1	0,999989986	0,00037
ENSMUSG00000051065	Mb21d2	1,217190027	0,00037
ENSMUSG00000021187	Tc2n	2,000129938	0,00037
ENSMUSG00000020620	Abca8b	2,187669992	0,00037
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ENSMUSG00000026239	Pde6d	-0,871630013	0,00038
ENSMUSG00000027048	Abcb11	2,285279989	0,00038
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ENSMUSG00000040502	March9	-1,833330035	0,00038
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ENSMUSG00000057068	Fam47e	2,37541008	0,00038
ENSMUSG00000047344	Lancl3	-6,373250008	0,00038
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ENSMUSG00000044149	Nkrf	-0,611509979	0,0004
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ENSMUSG00000040818	Dennd6a	0,655229986	0,0004
ENSMUSG00000020651	Slc26a4	2,950429916	0,0004
ENSMUSG00000042250	Pglyrp4	-3,615020037	0,00041
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ENSMUSG00000024735	Prpf19	0,493699998	0,00041
ENSMUSG00000055963	Triqk	-3,354769945	0,00042
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ENSMUSG00000026843	Fubp3	-0,719649971	0,00044
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ENSMUSG00000001632	Brpf1	-1,035079956	0,00044
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ENSMUSG00000026202	Tuba4a	1,470370054	0,00044
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ENSMUSG00000071855	Ccdc112	-2,078399897	0,00045
ENSMUSG00000002871	Tpra1	0,572629988	0,00045
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ENSMUSG00000040963	Asgr2	2,121870041	0,00045
ENSMUSG00000005681	Apoa2	2,324660063	0,00045
ENSMUSG00000049800	Sertad2	-0,885240018	0,00045
ENSMUSG00000061718	Ppp1r1b	2,469820023	0,00045
ENSMUSG00000056531	Ccdc18	-1,998499999	0,00045
ENSMUSG00000079057	Cyp4v3	1,704939961	0,00045
ENSMUSG00000033278	Ptprm	-1,437780023	0,00046
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ENSMUSG00000051220	Ercc6l	-1,589100003	0,00046
ENSMUSG00000030701	Plekhh1	1,370159984	0,00046
ENSMUSG00000028949	Smarcd3	-1,76098001	0,00046
ENSMUSG00000054115	Skp2	-1,391700029	0,00046
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ENSMUSG00000037904	Ankrd9	-1,75285995	0,00048
ENSMUSG00000059323	Tonsl	-1,184999943	0,00048
ENSMUSG00000032782	Cntrob	-0,91170001	0,00048
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ENSMUSG00000027811	4930579G24Rik	-1,582299948	0,00049
ENSMUSG00000059791	Nrm	-1,120830059	0,00049
ENSMUSG00000038150	Ormdl3	0,746999979	0,00049
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ENSMUSG00000017639	Rab11fip4	1,873250008	0,00049
ENSMUSG00000066798	Zbtb6	-0,584230006	0,00049
ENSMUSG00000037787	Apopt1	1,016450047	0,00049
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ENSMUSG00000009575	Cbx5	-0,895070016	0,00049
ENSMUSG00000022889	Mrpl39	0,51779002	0,00049
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ENSMUSG00000031951	Tmem231	-2,789720058	0,00049
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ENSMUSG00000018572	Phf23	-1,069059968	0,0005
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ENSMUSG00000034601	2700049A03Rik	-1,17031002	0,0005
ENSMUSG00000027540	Ptpn1	-0,734120011	0,0005
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ENSMUSG00000028607	Cpt2	1,235520005	0,00052
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ENSMUSG00000030762	Aqp8	1,993139982	0,00052
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ENSMUSG00000046598	Bdh1	2,08585	0,00053
ENSMUSG00000071226	Cecr2	2,251790047	0,00053
ENSMUSG00000031189	Aff2	-7,75770998	0,00053
ENSMUSG00000041552	Ptchd1	-6,022510052	0,00053
ENSMUSG00000032968	Inha	-4,39343977	0,00053
ENSMUSG00000021270	Hsp90aa1	-1,224949956	0,00053
ENSMUSG00000037013	Ss18	-0,636520028	0,00053

ENSMUSG00000028914	Casp9	0,727869987	0,00053
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ENSMUSG00000038298	Pdzk1	2,148139954	0,00054
ENSMUSG00000033039	Micall1	-1,746979952	0,00054
ENSMUSG00000058440	Nrf1	-0,60115999	0,00054
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ENSMUSG00000045136	Tubb2b	-2,275779963	0,00054
ENSMUSG00000032815	Fanca	-1,884430051	0,00055
ENSMUSG00000022771	Ppil2	0,361380011	0,00055
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ENSMUSG00000033809	Alg3	0,768710017	0,00055
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ENSMUSG00000025145	Lrrc45	-0,736769974	0,00055
ENSMUSG00000030990	Pgap2	0,64477998	0,00055
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ENSMUSG00000035109	Shc4	-2,850029945	0,00055
ENSMUSG00000020740	Gga3	-1,070459962	0,00055
ENSMUSG00000027963	Extl2	-0,422619998	0,00055
ENSMUSG00000038793	Lefty1	-2,090600014	0,00055
ENSMUSG00000020973	Dnaaf2	-1,149260044	0,00055
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ENSMUSG00000028862	Map3k6	-2,229720116	0,00056
ENSMUSG00000049504	Proser1	-1,06348002	0,00056
ENSMUSG00000029596	Sdsl	2,034919977	0,00056
ENSMUSG00000036106	Prr5	-0,886160016	0,00056
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ENSMUSG00000063253	Scoc	-0,826730013	0,00056
ENSMUSG00000029610	Aimp2	-0,739239991	0,00056
ENSMUSG00000015189	Casd1	0,530040026	0,00056
ENSMUSG00000026207	Spep	-1,692000031	0,00056
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ENSMUSG00000028156	Eif4e	-0,450309992	0,00057
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ENSMUSG00000047866	Lonp2	1,297140002	0,00057
ENSMUSG00000002475	Abhd3	1,802440047	0,00057
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ENSMUSG00000028933	Xrcc2	-1,061910033	0,00058
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ENSMUSG00000094103	1700047117Rik2	-3,128489971	0,0006
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ENSMUSG00000069743	Zfp820	-0,971099973	0,0006
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ENSMUSG00000022149	C9	2,109339952	0,0006
ENSMUSG00000003282	Plag1	-6,187590122	0,00061
ENSMUSG00000044250	Pced1b	-1,24732995	0,00061
ENSMUSG00000029338	Antxr2	-0,90030998	0,00061
ENSMUSG00000029684	Wasl	0,573939979	0,00061
ENSMUSG00000071369	Map3k5	0,85345	0,00061
ENSMUSG00000038253	Hoxa5	-1,913419962	0,00061
ENSMUSG00000028163	Nfkb1	-0,706260026	0,00061
ENSMUSG00000038055	Dexi	0,993560016	0,00061
ENSMUSG00000033735	Spr	1,511719942	0,00061
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ENSMUSG00000032965	Ift57	-1,742789984	0,00062

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ENSMUSG00000026922	Agpat2	1,260040045	0,00062
ENSMUSG00000035283	Adrb1	1,453189969	0,00062
ENSMUSG00000042918	Mamstr	-2,605859995	0,00062
ENSMUSG00000045382	Cxcr4	-1,493239999	0,00062
ENSMUSG00000074825	Itpripl1	-0,719659984	0,00062
ENSMUSG00000028713	Cyp4b1	1,974939942	0,00062
ENSMUSG00000040543	Pitpnm3	-3,512639999	0,00062
ENSMUSG00000025347	Mettl7b	2,110090017	0,00062
ENSMUSG00000051906	Cd209f	4,908070087	0,00062
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ENSMUSG00000022096	Hr	-2,354310036	0,00063
ENSMUSG00000032737	Inppl1	-0,895340025	0,00063
ENSMUSG00000028454	Pigo	0,695900023	0,00063
ENSMUSG00000028412	Slc44a1	0,800660014	0,00063
ENSMUSG00000030225	Dera	0,926180005	0,00063
ENSMUSG00000024799	Tm7sf2	1,66711998	0,00063
ENSMUSG00000027210	Meis2	-1,239439964	0,00063
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ENSMUSG00000062054	Iah1	1,587960005	0,00063
ENSMUSG00000058022	Adtrp	1,981209993	0,00063
ENSMUSG00000024827	Gldc	2,151410103	0,00063
ENSMUSG00000027333	Smox	-1,202290058	0,00063
ENSMUSG00000021765	Fst	1,702900052	0,00063
ENSMUSG00000070348	Ccnd1	-2,183880091	0,00064
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ENSMUSG00000050605	Zfp61	-1,556869984	0,00065
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ENSMUSG00000038462	Uqcrfs1	1,16700995	0,00066
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ENSMUSG00000043943	Naalad2	-1,355909944	0,00066
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ENSMUSG00000092680	Snord55	-2,1426301	0,00069
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ENSMUSG00000034311	Kif4	-1,634230018	0,00074
ENSMUSG00000022255	Mtdh	-1,154399991	0,00074
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ENSMUSG00000028247	Coq3	0,979489982	0,00079
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ENSMUSG00000037669	Ldah	0,662349999	0,00079
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ENSMUSG00000005371	Fbxo11	-0,699060023	0,0008
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ENSMUSG00000032602	Slc25a20	0,956200004	0,00081
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ENSMUSG00000027349	Fam98b	-0,502629995	0,00082
ENSMUSG00000058454	Dhcr7	1,389590025	0,00082
ENSMUSG00000031637	Lrp2bp	1,693490028	0,00082
ENSMUSG00000029082	Bst1	-2,021859884	0,00082
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ENSMUSG00000094651	Gal3st2	-4,745880127	0,00083
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ENSMUSG00000038213	Tapbp1	1,069599986	0,00084
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ENSMUSG00000028923	Necap2	-1,117040038	0,00084
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ENSMUSG00000024858	Grk2	-0,529240012	0,00085
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ENSMUSG00000020638	Cmpk2	1,626449943	0,00086
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ENSMUSG00000026715	Serpinc1	1,951570034	0,00087
ENSMUSG00000040883	Tmem205	1,993530035	0,00087
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ENSMUSG00000027160	Ccdc34	-1,419319987	0,00104
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ENSMUSG00000020024	Cep83	-0,668900013	0,00104
ENSMUSG00000000881	Dlg3	-0,862770021	0,00104
ENSMUSG00000044707	Ccnjl	-2,666970015	0,00104
ENSMUSG00000050777	Tmem37	1,730999947	0,00104
ENSMUSG00000026417	Pigr	2,033200026	0,00104

ENSMUSG00000010064	Slc38a3	2,082030058	0,00104
ENSMUSG00000039395	Mreg	1,817409992	0,00105
ENSMUSG00000028773	Fabp3	-3,84187007	0,00105
ENSMUSG00000035818	Plekhs1	-1,946840048	0,00105
ENSMUSG00000033721	Vav3	-0,918889999	0,00105
ENSMUSG00000029521	Chek2	-1,02252996	0,00105
ENSMUSG00000045658	Pid1	1,679080009	0,00105
ENSMUSG00000037548	H2-DMb2	-1,62282002	0,00106
ENSMUSG00000039981	Zc3h12d	1,973399997	0,00106
ENSMUSG00000031825	Crispld2	-2,882200003	0,00106
ENSMUSG00000056004	9330182L06Rik	-2,161509991	0,00106
ENSMUSG00000027983	Cyp2u1	2,219630003	0,00106
ENSMUSG00000021809	Nudt13	0,989989996	0,00107
ENSMUSG00000053338	Tarm1	-6,636660099	0,00107
ENSMUSG00000018476	Kdm6b	-1,562819958	0,00107
ENSMUSG00000042613	Pbxip1	-0,783460021	0,00107
ENSMUSG00000041488	Stx3	-0,545180023	0,00107
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ENSMUSG00000035329	Fbxo33	-0,814670026	0,00109
ENSMUSG00000014074	Rnf168	0,48041001	0,00109
ENSMUSG00000025494	Sigirr	1,173979998	0,00109
ENSMUSG00000026896	Ifih1	1,451910019	0,00109
ENSMUSG00000036216	Leap2	2,280499935	0,00109
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ENSMUSG00000032776	Mctp2	1,215610027	0,0011
ENSMUSG00000060459	Kng2	1,78125	0,0011
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ENSMUSG00000022292	Rrm2b	-1,235499978	0,0011
ENSMUSG00000028453	Fancg	-0,891099989	0,00111
ENSMUSG00000024835	Coro1b	-0,547060013	0,00111
ENSMUSG00000021130	Galnt16	-5,808169842	0,00111
ENSMUSG00000058254	Tspan7	-1,078099966	0,00111
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ENSMUSG00000053289	Ddx10	-0,441139996	0,00111
ENSMUSG00000039782	Cpeb2	1,086969972	0,00111

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ENSMUSG00000036529	Sbf1	-0,79223001	0,00111
ENSMUSG00000030689	Ino80e	-0,743690014	0,00111
ENSMUSG00000036879	Phkb	0,849020004	0,00111
ENSMUSG00000028636	Ppcs	1,415120006	0,00111
ENSMUSG00000020149	Rab1a	0,386059999	0,00112
ENSMUSG00000025393	Atp5b	0,480269998	0,00112
ENSMUSG00000052033	Pfdn4	-1,430080056	0,00112
ENSMUSG00000036057	Ptpn23	-1,218009949	0,00112
ENSMUSG00000021938	Pspc1	-0,797140002	0,00112
ENSMUSG00000046516	Cox17	-1,08991003	0,00112
ENSMUSG00000001911	Nfix	1,015750051	0,00112
ENSMUSG00000063232	Serpina11	2,087310076	0,00112
ENSMUSG00000038859	Baiap211	-0,967490017	0,00113
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ENSMUSG00000025270	Alas2	1,671259999	0,00113
ENSMUSG00000049755	Zfp672	0,592980027	0,00113
ENSMUSG00000022792	Yars2	0,750349998	0,00114
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ENSMUSG00000023259	Slc26a6	1,041610003	0,00114
ENSMUSG00000039238	Zfp750	1,742840052	0,00114
ENSMUSG00000079144	A130010J15Rik	0,884519994	0,00114
ENSMUSG00000029275	Gfi1	-3,128629923	0,00115
ENSMUSG00000028078	Dclk2	-1,920590043	0,00116
ENSMUSG00000053581	Zfand2a	-0,926869988	0,00116
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ENSMUSG00000047143	Dmrta2	-4,003109932	0,00116
ENSMUSG00000073176	Zfp449	-1,698889971	0,00116
ENSMUSG00000050212	Eva1b	-1,638389945	0,00116
ENSMUSG00000079491	H2-T10	1,247419953	0,00116
ENSMUSG00000071856	Mcc	1,500699997	0,00116
ENSMUSG00000001517	Foxm1	-1,977980018	0,00117
ENSMUSG00000022009	Nufip1	-0,658779979	0,00117
ENSMUSG00000028944	Prkag2	0,736570001	0,00118
ENSMUSG00000018707	Dync1h1	-0,820829988	0,00118
ENSMUSG00000036052	Dnajb5	-0,65267998	0,00118
ENSMUSG00000027406	Idh3b	0,621770024	0,00118
ENSMUSG00000020493	Prr11	-2,526859999	0,00118
ENSMUSG00000033965	Slc16a2	1,55448997	0,00118
ENSMUSG00000020593	Lpin1	1,74822998	0,00119
ENSMUSG00000027115	Kif18a	-1,581179976	0,00119
ENSMUSG00000021495	Fam193b	-0,813059986	0,00119

ENSMUSG00000031099	Smarca1	-3,652770042	0,0012
ENSMUSG00000038646	Ramac	0,624989986	0,0012
ENSMUSG00000006395	Hyi	1,49714005	0,0012
ENSMUSG000000045319	Proser2	1,237380028	0,0012
ENSMUSG000000032554	Trf	1,835690022	0,0012
ENSMUSG000000001095	Slc13a2	2,321860075	0,00121
ENSMUSG000000044164	Rnf182	-6,428929806	0,00121
ENSMUSG000000017561	Crlf3	-0,45262	0,00121
ENSMUSG000000024897	Apba1	-2,016599894	0,00121
ENSMUSG000000040359	Ufl1	1,146669984	0,00121
ENSMUSG000000043924	Ncmap	-2,023180008	0,00122
ENSMUSG000000036916	Zfp280c	-0,764840007	0,00122
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ENSMUSG000000026832	Cytip	-1,264600039	0,00123
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ENSMUSG000000044254	Pcsk9	1,530019999	0,00123
ENSMUSG000000066643	Wdr35	-1,168830037	0,00124
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ENSMUSG000000005686	Ampd3	-1,344830036	0,00124
ENSMUSG000000031889	D230025D16Rik	0,916580021	0,00124
ENSMUSG000000067144	Slc22a7	2,333669901	0,00124
ENSMUSG000000031779	Ccl22	-3,156919956	0,00125
ENSMUSG000000024381	Bin1	-1,076439977	0,00125
ENSMUSG000000018326	Ywhab	-0,27895999	0,00125
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ENSMUSG000000035227	Spcs2	0,950269997	0,00125
ENSMUSG000000018669	Cdk5rap3	0,99673003	0,00125
ENSMUSG000000020447	Npc1l1	2,18295002	0,00125
ENSMUSG000000036833	Pnpla7	1,698559999	0,00125
ENSMUSG000000030123	Plxnd1	-0,701009989	0,00126
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ENSMUSG00000027875	Hmgcs2	1,748999953	0,0013
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ENSMUSG00000052056	Zfp217	-1,109570026	0,00131
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ENSMUSG00000019992	Mtfr2	-2,048229933	0,00137
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ENSMUSG00000029575	Mmab	1,388380051	0,00138
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ENSMUSG00000033577	Myo6	0,770110011	0,00139
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ENSMUSG00000020029	Nudt4	0,669510007	0,00142
ENSMUSG00000063063	Ctnna2	-3,262059927	0,00143
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ENSMUSG00000059890	Ube4a	0,642539978	0,00143
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ENSMUSG00000021103	Mnat1	-0,832409978	0,0015
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ENSMUSG00000024558	Mapk4	-1,758170009	0,00156
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ENSMUSG00000036078	Sigmar1	0,945190012	0,00162
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ENSMUSG00000002718	Cse1l	-0,411139995	0,00162
ENSMUSG00000000948	Gm38393	1,708889961	0,00163
ENSMUSG00000008450	Nutf2	-0,736679971	0,00163
ENSMUSG00000011257	Pabpc4	-0,313080013	0,00164
ENSMUSG00000025289	Prdx4	1,311529994	0,00164
ENSMUSG00000018068	Ints2	-1,647250056	0,00165
ENSMUSG00000019796	Lrp11	-1,160069942	0,00165
ENSMUSG00000003360	Ddx23	-0,355399996	0,00166
ENSMUSG00000037474	Dtl	-1,610399961	0,00166
ENSMUSG00000028800	Hdac1	-0,608560026	0,00166
ENSMUSG00000047033	Pcdhb15	-4,861780167	0,00167
ENSMUSG00000030342	Cd9	-1,271119952	0,00167
ENSMUSG00000019945	Cabcoco1	1,752359986	0,00167
ENSMUSG00000031788	Kifc3	1,113759995	0,00168
ENSMUSG00000018965	Ywhah	-0,732930005	0,00168
ENSMUSG00000026672	Optn	1,022269964	0,00168
ENSMUSG00000064602	Snora41	-2,217880011	0,00168
ENSMUSG00000009863	Sdhd	1,284459949	0,00168
ENSMUSG00000027397	Slc20a1	-1,019680023	0,00169

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ENSMUSG00000034820	Cpsf7	-0,715680003	0,00169
ENSMUSG00000031023	Akip1	1,072720051	0,00169
ENSMUSG00000022941	Ripply3	1,342829943	0,00169
ENSMUSG00000030470	Csrp3	1,711320043	0,00169
ENSMUSG00000057572	Zbtb8os	1,185009956	0,00169
ENSMUSG00000017718	Afmid	1,850469947	0,00169
ENSMUSG00000026009	Icos	1,988759995	0,0017
ENSMUSG00000070576	Mn1	1,580139995	0,0017
ENSMUSG00000048905	4930539E08Rik	2,649549961	0,0017
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ENSMUSG00000092558	Med20	-0,318199992	0,00171
ENSMUSG00000030706	Mrpl48	0,918500006	0,00171
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ENSMUSG00000019878	Hsf2	0,580060005	0,00172
ENSMUSG00000044469	Tnfaip8l1	1,127020001	0,00172
ENSMUSG00000068923	Syt11	-1,202139974	0,00172
ENSMUSG00000035392	Dennd1a	0,88726002	0,00172
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ENSMUSG00000043782	Bicdl2	-2,924129963	0,00173
ENSMUSG00000038903	Ccdc68	-1,663599968	0,00173
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ENSMUSG00000018830	Myh11	-1,548169971	0,00174
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ENSMUSG00000072568	Fam84b	1,394909978	0,00174
ENSMUSG0000003420	Fcgrt	1,442999959	0,00174
ENSMUSG00000050445	Cyp8b1	2,096669912	0,00174
ENSMUSG00000014873	Surf2	-0,512250006	0,00174
ENSMUSG00000056204	Pgpep1	0,662109971	0,00175
ENSMUSG00000038604	Ripor1	-1,107540011	0,00175
ENSMUSG00000054892	Txk	-3,242880106	0,00176
ENSMUSG00000003623	Crot	1,536339998	0,00176
ENSMUSG00000049502	Dtx3l	1,521309972	0,00176
ENSMUSG00000044042	Fmn1	1,299239993	0,00176
ENSMUSG00000067818	Myl9	-1,63191998	0,00177
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ENSMUSG00000074677	Sirpb1c	-1,63864994	0,00178
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ENSMUSG00000052221	Ppp1r36	-3,285459995	0,00179
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ENSMUSG00000011884	Gltpl	-0,939419985	0,00181
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ENSMUSG00000027931	Npr1	1,134490013	0,00184
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ENSMUSG00000052712	BC004004	0,981599987	0,00185
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ENSMUSG00000041870	Ankrd13a	-0,695850015	0,00188
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ENSMUSG00000016541	Atxn10	-0,769919991	0,00189
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ENSMUSG00000017802	Retreg3	0,477609992	0,0019
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ENSMUSG00000038233	Fam198a	2,308000088	0,0019
ENSMUSG00000005373	Mlxipl	1,963850021	0,0019
ENSMUSG00000024176	Sox8	-3,548190117	0,00191
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ENSMUSG00000028127	Abcd3	1,256500006	0,00191
ENSMUSG00000035041	Creb3l3	1,743839979	0,00192
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ENSMUSG00000023868	Pde10a	-2,16257	0,00194
ENSMUSG00000022899	Slc15a2	2,160020113	0,00194
ENSMUSG00000023861	Mpc1	1,450819969	0,00195
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ENSMUSG00000035403	Crb2	-4,098589897	0,00196
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ENSMUSG00000064254	Ethe1	1,40655005	0,00198
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ENSMUSG00000049643	2310022A10Rik	-0,63944	0,00202
ENSMUSG00000040548	Tex2	1,335430026	0,00202
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ENSMUSG00000011752	Pgam1	-1,147269964	0,00204
ENSMUSG00000059923	Grb2	-0,294640005	0,00204
ENSMUSG00000021792	Fam213a	0,957560003	0,00204
ENSMUSG00000004655	Aqp1	1,086979985	0,00205
ENSMUSG00000067235	H2-Q10	1,870650053	0,00205
ENSMUSG00000029512	Ulk1	1,070700049	0,00205
ENSMUSG00000028521	Slc35d1	1,279270053	0,00206
ENSMUSG00000021902	Phf7	0,639389992	0,00206
ENSMUSG00000044231	Nhlrc1	0,887889981	0,00207
ENSMUSG00000051674	Dcun1d4	0,890030026	0,00208
ENSMUSG00000024778	Fas	1,482879996	0,00209
ENSMUSG00000059060	Rad51b	-1,988800049	0,0021
ENSMUSG00000023905	Tnfrsf12a	-1,178709984	0,0021
ENSMUSG00000022883	Robo1	1,413879991	0,0021
ENSMUSG00000008734	Gprc5b	-1,784929991	0,0021
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ENSMUSG00000009079	Ewsr1	-0,522549987	0,00212
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ENSMUSG00000038980	Rbbp8nl	-3,890280008	0,00219
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ENSMUSG00000031104	Rab33a	-3,915669918	0,0022
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ENSMUSG00000064563	Snora7a	-1,869619966	0,00224
ENSMUSG00000022476	Polr3h	-0,728519976	0,00224
ENSMUSG00000044328	Trp53i13	-1,457460046	0,00225
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ENSMUSG00000053470	Kdm3a	-1,129469991	0,00226
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ENSMUSG00000029053	Prkcz	1,129799962	0,00226
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ENSMUSG00000032177	Pde4a	-1,336910009	0,0023
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ENSMUSG00000022555	Dgat1	-0,47183001	0,00233
ENSMUSG00000003235	Eif2b5	0,466540009	0,00233
ENSMUSG000000030945	Acsm2	1,811169982	0,00233
ENSMUSG00000006390	Elovl1	0,44047001	0,00233
ENSMUSG00000031232	Magt1	0,714919984	0,00233
ENSMUSG00000017390	Aldoc	0,886089981	0,00233
ENSMUSG00000040028	Elavl1	-0,754329979	0,00234
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ENSMUSG00000043998	Mgat2	0,49267	0,00247
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ENSMUSG00000029458	Brap	0,748130023	0,00249
ENSMUSG00000054582	Pabpc1l	-2,722609997	0,00249
ENSMUSG00000030347	D6Wsu163e	0,593900025	0,00251
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ENSMUSG00000026834	Acvr1c	-5,597819805	0,00251
ENSMUSG00000004341	Gpx6	2,334959984	0,00251
ENSMUSG00000089929	Bcl2a1b	-2,100699902	0,00252

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ENSMUSG00000053111	Fank1	-3,383899927	0,00253
ENSMUSG00000031865	Dctn1	-0,783219993	0,00253
ENSMUSG00000002825	Qtrt1	-0,928960025	0,00254
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ENSMUSG00000028953	Abcf2	-0,454430014	0,00255
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ENSMUSG00000000223	Drp2	-3,1338799	0,00256
ENSMUSG00000031916	Cog8	0,488090008	0,00256
ENSMUSG00000039474	Wfs1	-1,185220003	0,00257
ENSMUSG00000026883	Dab2ip	-0,878709972	0,00257
ENSMUSG00000027428	Rbbp9	0,510299981	0,00257
ENSMUSG00000035139	Secisbp2	0,461100012	0,00258
ENSMUSG00000059900	Tmem40	-3,727839947	0,00259
ENSMUSG00000033014	Trim33	-0,923479974	0,00259
ENSMUSG00000021597	Slf1	-0,759949982	0,00259
ENSMUSG00000001847	Rac1	-0,650030017	0,00259
ENSMUSG00000078676	Casc3	-0,531449974	0,00259
ENSMUSG00000002799	Jag2	-2,335380077	0,0026
ENSMUSG00000042182	Bend6	-2,988369942	0,0026
ENSMUSG000000064267	Hvcn1	-1,083019972	0,0026
ENSMUSG00000041459	Tardbp	-0,550530016	0,0026
ENSMUSG00000027305	Ndufaf1	0,930329978	0,0026
ENSMUSG00000020988	L2hgdh	1,053910017	0,00261
ENSMUSG00000062960	Kdr	1,211269975	0,00261
ENSMUSG00000033276	Stk36	-1,891450047	0,00261
ENSMUSG00000021177	Tdp1	-0,780809999	0,00261
ENSMUSG00000026213	Stk11ip	-0,680899978	0,00261
ENSMUSG00000001334	Fndc5	-1,870419979	0,00262
ENSMUSG00000015354	Pcolce2	-1,748870015	0,00262
ENSMUSG00000030110	Ret	-8,514399529	0,00263
ENSMUSG00000030327	Necap1	0,547800004	0,00264
ENSMUSG00000068876	Cgn	1,612149954	0,00264
ENSMUSG00000041417	Pik3r1	0,50395	0,00265
ENSMUSG00000035969	Rusc2	-1,109050035	0,00266
ENSMUSG00000000568	Hnrnpd	-0,654150009	0,00266
ENSMUSG00000032382	Snx1	-0,62984997	0,00266
ENSMUSG00000030278	Cidec	1,930410028	0,00266
ENSMUSG00000029708	Gcc1	0,471740007	0,00266
ENSMUSG00000002332	Dhrs1	0,939939976	0,00266
ENSMUSG00000029599	Ddx54	-0,509090006	0,00267
ENSMUSG00000029254	Stap1	2,173079967	0,00267

ENSMUSG00000009470	Tnpo1	-0,738049984	0,00268
ENSMUSG00000022035	Ccdc25	0,617709994	0,00268
ENSMUSG00000023942	Slc29a1	0,829249978	0,00269
ENSMUSG00000047281	Sfn	-1,56558001	0,0027
ENSMUSG00000049928	Glp2r	3,065720081	0,0027
ENSMUSG00000028597	Gpx7	-1,450500011	0,0027
ENSMUSG00000032419	Tbx18	-9,841810226	0,00271
ENSMUSG00000026480	Ncf2	-1,220729947	0,00272
ENSMUSG00000002014	Ssr4	0,891340017	0,00272
ENSMUSG00000045659	Plekha7	1,322399974	0,00272
ENSMUSG00000038009	Dnajc22	1,448580027	0,00272
ENSMUSG00000025958	Creb1	-0,649269998	0,00272
ENSMUSG00000048429	Timm29	0,382470012	0,00273
ENSMUSG00000048728	Zfp454	1,777999997	0,00273
ENSMUSG00000058173	Smco4	1,349449992	0,00273
ENSMUSG00000054764	Mtnr1a	2,304440022	0,00273
ENSMUSG00000045273	Cenph	-2,022190094	0,00274
ENSMUSG00000051246	Msantd1	-1,90407002	0,00274
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ENSMUSG00000066705	Fxyd6	-2,192169905	0,00274
ENSMUSG00000020801	Med31	-1,25988996	0,00274
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ENSMUSG00000033610	Pank1	1,559559941	0,00274
ENSMUSG00000063354	Slc39a4	1,593000054	0,00274
ENSMUSG00000025993	Slc40a1	1,207129955	0,00275
ENSMUSG00000037034	Pax1	-5,169690132	0,00276
ENSMUSG00000019806	Aig1	-1,060969949	0,00276
ENSMUSG00000092920	Mirt2	2,093139887	0,00276
ENSMUSG00000032407	U2surp	-0,529999971	0,00276
ENSMUSG00000026589	Sec16b	1,794870019	0,00276
ENSMUSG00000031626	Sorbs2	1,321730018	0,00277
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ENSMUSG00000031622	Sin3b	-1,343240023	0,00277
ENSMUSG00000038615	Nfe2l1	-0,499370009	0,00277
ENSMUSG00000028789	Azin2	-1,741639972	0,00278
ENSMUSG00000038618	Rassf7	0,961070001	0,00278
ENSMUSG00000019831	Wasf1	-1,162539959	0,00279
ENSMUSG00000039005	Tlr4	-0,931360006	0,00279
ENSMUSG00000028693	Nasp	-0,833530009	0,00279
ENSMUSG00000040653	Ppp1r14c	-10,13564014	0,0028
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ENSMUSG00000034486	Gbx2	-7,135749817	0,0028
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ENSMUSG00000028618	Tmem59	0,580879986	0,0028
ENSMUSG00000079494	Nat8f5	2,812510014	0,00281
ENSMUSG00000021287	Xrcc3	-1,368950009	0,00282
ENSMUSG00000005442	Cic	-0,95431	0,00282

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ENSMUSG00000028292	Rars2	0,506799996	0,00282
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ENSMUSG00000030780	BC017158	1,047170043	0,00283
ENSMUSG00000041144	Dnah7b	-3,42711997	0,00284
ENSMUSG00000029127	Zbtb49	-0,964049995	0,00284
ENSMUSG00000031505	Naxd	0,811689973	0,00285
ENSMUSG00000040877	Wdr25	0,656840026	0,00286
ENSMUSG00000046985	Tapt1	0,628350019	0,00286
ENSMUSG00000029147	Ppm1g	-0,499240011	0,00287
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ENSMUSG00000072704	Smim10l1	0,921249986	0,00288
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ENSMUSG00000030144	Clec4d	-2,641669989	0,0029
ENSMUSG00000071042	Rasgrp3	-1,040799975	0,0029
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ENSMUSG00000092416	Zfp141	0,534240007	0,00291
ENSMUSG00000036966	Spryd3	-0,573920012	0,00291
ENSMUSG00000078798	Sult2a1	3,83513999	0,00291
ENSMUSG00000077734	Snord83b	-2,931139946	0,00292
ENSMUSG00000000869	Il4	-1,976709962	0,00292
ENSMUSG00000031155	Pim2	-0,988099992	0,00292
ENSMUSG00000022223	Sdr39u1	0,477050006	0,00292
ENSMUSG00000026304	Rab17	1,643820047	0,00292
ENSMUSG00000092035	Peg10	-1,711699963	0,00294
ENSMUSG00000024258	Polr2d	-1,303529978	0,00294
ENSMUSG00000074259	Gramd2	-3,764489889	0,00295
ENSMUSG00000060550	H2-Q7	1,439939976	0,00295
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ENSMUSG00000078570	1110065P20Rik	1,006469965	0,00296
ENSMUSG00000052296	Ppp6r1	0,644819975	0,00296
ENSMUSG00000037353	Letmd1	0,404029995	0,00297
ENSMUSG00000025151	Maged1	-0,390709996	0,00297
ENSMUSG00000051910	Sox6	1,648200035	0,00298
ENSMUSG00000015133	Lrrk1	-0,897790015	0,00298
ENSMUSG00000030621	Me3	-2,838089943	0,00299
ENSMUSG00000027245	Hypk	-1,408980012	0,00299
ENSMUSG00000022696	Sidt1	2,300829887	0,00299
ENSMUSG00000044338	Aplnr	-2,88973999	0,003
ENSMUSG00000028337	Coro2a	-1,465790033	0,003
ENSMUSG00000038357	Camp	-5,22533989	0,00301
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ENSMUSG00000008575	Nfib	0,929650009	0,00302
ENSMUSG00000028289	Epha7	-1,414520025	0,00302
ENSMUSG00000048782	Insc	1,828609943	0,00302
ENSMUSG000000031145	Prickle3	-1,053869963	0,00303
ENSMUSG00000024905	Tesmin	1,378340006	0,00303
ENSMUSG00000038354	Ankrd35	-3,216779947	0,00303
ENSMUSG00000034607	Pof1b	-2,814280033	0,00304
ENSMUSG00000068922	Msto1	-0,670840025	0,00304
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ENSMUSG00000049625	Tifab	-1,055840015	0,00305
ENSMUSG00000030074	Gxylt2	-3,203949928	0,00305
ENSMUSG00000037025	Foxa2	1,149420023	0,00306
ENSMUSG00000030972	Acsn5	2,030080008	0,00306
ENSMUSG00000035824	Tk2	0,627099991	0,00306
ENSMUSG00000023345	Poc1a	-0,794610023	0,00306
ENSMUSG00000024943	Smc5	-0,678550005	0,00306
ENSMUSG00000037553	Zdhhc18	0,412369996	0,00306
ENSMUSG00000021400	Wrnip1	0,548420012	0,00306
ENSMUSG00000031198	Fundc2	-1,015580058	0,00307
ENSMUSG00000005823	Gpr108	-0,420870006	0,00307
ENSMUSG00000069049	Eif2s3y	0,62331003	0,00307
ENSMUSG00000042207	Kdm5b	-0,915120006	0,00308
ENSMUSG00000047879	Usp14	-0,459340006	0,00308
ENSMUSG00000002748	Baz1b	-0,646740019	0,00308
ENSMUSG00000040943	Tet2	-1,689249992	0,00308
ENSMUSG00000025785	Exosc7	0,875540018	0,00309
ENSMUSG00000043415	Otud1	-0,649800003	0,0031
ENSMUSG00000046269	Usp27x	-1,308840036	0,0031
ENSMUSG00000038375	Trp53inp2	0,634259999	0,0031
ENSMUSG00000030200	Bcl2l14	1,75838995	0,00311
ENSMUSG00000020873	Slc35b1	0,751339972	0,00311
ENSMUSG00000020692	Nle1	-0,713549972	0,00312
ENSMUSG00000028919	Arhgef19	0,763029993	0,00312
ENSMUSG00000027489	Necab3	-3,132509947	0,00312
ENSMUSG00000021010	Npas3	-3,359440088	0,00313
ENSMUSG00000004054	Map3k11	0,220300004	0,00313
ENSMUSG00000025790	Slco3a1	-1,037999988	0,00313
ENSMUSG00000005534	Insr	1,021379948	0,00313
ENSMUSG00000022949	Clic6	-3,68640995	0,00314
ENSMUSG00000013787	Ehmt2	-0,444840014	0,00314
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ENSMUSG00000000690	Hoxb6	-3,192100048	0,00314
ENSMUSG00000049295	Zfp219	-0,592149973	0,00315
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ENSMUSG00000068742	Cry2	0,779280007	0,00319
ENSMUSG00000022829	Stxbp5l	4,295199871	0,00319
ENSMUSG00000041891	Lman1	0,968230009	0,00319
ENSMUSG00000050930	Map10	-1,327559948	0,0032
ENSMUSG00000049001	Ndnf	-7,498209953	0,00321
ENSMUSG00000057880	Abat	1,930330038	0,00321
ENSMUSG00000002372	Ranbp3	-0,523419976	0,00322
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ENSMUSG00000014767	Tbp	-0,45273	0,00323
ENSMUSG00000020594	Pum2	-0,625739992	0,00324
ENSMUSG00000003452	Bicd1	-2,147259951	0,00324
ENSMUSG00000042787	Exog	-0,943099976	0,00325
ENSMUSG00000024747	Aldh1a7	1,597409964	0,00326
ENSMUSG00000087141	Plcxd2	1,613250017	0,00326
ENSMUSG00000026816	Gtf3c5	-0,656050026	0,00326
ENSMUSG00000029063	Nadk	0,568560004	0,00327
ENSMUSG00000026269	Rnpepl1	0,514159977	0,00328
ENSMUSG00000027316	Gfra4	-3,026410103	0,00329
ENSMUSG00000026687	Aldh9a1	1,279270053	0,00329
ENSMUSG00000028718	Stil	-2,14267993	0,0033
ENSMUSG00000020994	Pnn	-1,030140042	0,00331
ENSMUSG00000026791	Slc2a8	0,562349975	0,00332
ENSMUSG00000079508	Apoo	0,966960013	0,00332
ENSMUSG00000073234	Gm8773	-4,695940018	0,00333
ENSMUSG00000040536	Necab1	2,017659903	0,00333
ENSMUSG00000022758	P2rx6	-2,170969963	0,00334
ENSMUSG00000025791	Pgm1	0,623510003	0,00334
ENSMUSG00000022184	Fbxo4	0,659420013	0,00334
ENSMUSG00000057967	Fgf18	-5,281690121	0,00334
ENSMUSG00000039629	Strip2	-2,185230017	0,00334
ENSMUSG00000001964	Emd	-0,604770005	0,00334
ENSMUSG00000074030	Exoc8	-0,379970014	0,00334
ENSMUSG00000026723	Trdmt1	0,791220009	0,00334
ENSMUSG00000041143	Tmco4	0,845619977	0,00334
ENSMUSG00000022236	Ropn1l	1,756330013	0,00334
ENSMUSG00000023951	Vegfa	-1,115630031	0,00335
ENSMUSG00000039206	Daglb	0,804069996	0,00335
ENSMUSG00000063480	Snu13	-0,865199983	0,00335
ENSMUSG00000045555	Mettl24	-3,802580118	0,00336
ENSMUSG00000031833	Mast3	-1,195490003	0,00337
ENSMUSG00000037149	Ddx1	0,286680013	0,00337
ENSMUSG00000073481	Marc2	1,601819992	0,00337
ENSMUSG00000001103	Sebox	2,209719896	0,00337
ENSMUSG00000073409	H2-Q6	1,373749971	0,00338
ENSMUSG00000041617	Ccdc74a	-2,206680059	0,00338
ENSMUSG00000069495	Epc2	-0,687070012	0,00339

ENSMUSG00000018459	Slc13a3	1,509729981	0,00339
ENSMUSG00000028341	Nr4a3	-2,745369911	0,0034
ENSMUSG00000022353	Mtss1	0,796010017	0,0034
ENSMUSG00000021464	Ror2	-5,659969807	0,00341
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ENSMUSG00000025759	Mfsd8	0,594389975	0,00341
ENSMUSG00000029524	Sirt4	0,640990019	0,00342
ENSMUSG00000052915	Msl1	-0,366820008	0,00342
ENSMUSG00000002204	Napsa	-1,815840006	0,00343
ENSMUSG00000028962	Slc4a2	-0,703320026	0,00343
ENSMUSG00000053119	Chmp3	0,369120002	0,00343
ENSMUSG00000079427	Mthfsl	0,980449975	0,00345
ENSMUSG00000008461	Fut1	2,063250065	0,00347
ENSMUSG00000035773	Kiss1r	-1,271620035	0,00347
ENSMUSG00000012819	Cdh23	-2,704590082	0,00348
ENSMUSG00000030159	Clec1b	1,690009952	0,00348
ENSMUSG00000029208	Guf1	0,318610013	0,00349
ENSMUSG00000038128	Camk4	-1,735409975	0,0035
ENSMUSG00000027634	Ndr3	-0,609440029	0,00352
ENSMUSG00000027765	P2ry1	0,934520006	0,00353
ENSMUSG00000050052	Tdrp	1,236879945	0,00353
ENSMUSG00000038696	Mapkap1	0,43520999	0,00354
ENSMUSG0000002763	Pex6	1,034070015	0,00354
ENSMUSG00000017499	Cdc6	-1,75443995	0,00355
ENSMUSG00000029110	Rnf4	-0,326020002	0,00356
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ENSMUSG00000000811	Txnrd3	-0,787129998	0,00357
ENSMUSG00000039018	Mtg1	0,883040011	0,00357
ENSMUSG00000023829	Slc22a1	1,803079963	0,00357
ENSMUSG00000045751	Mms22l	-0,959169984	0,00358
ENSMUSG00000036504	Phpt1	-1,515439987	0,0036
ENSMUSG00000027599	Armc1	0,386059999	0,0036
ENSMUSG00000058761	Rnf169	0,711880028	0,0036
ENSMUSG00000061132	Blnk	1,257730007	0,0036
ENSMUSG00000029587	Zfp12	-0,690100014	0,0036
ENSMUSG00000045064	Zc2hc1c	0,769320011	0,0036
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ENSMUSG00000024045	Akap8	-0,612399995	0,00362
ENSMUSG00000026116	Tmem131	-0,92031002	0,00363
ENSMUSG00000028273	Pdlim5	-0,831019998	0,00364
ENSMUSG00000027086	Fastkd1	0,673810005	0,00364
ENSMUSG00000032604	Qars	-0,356770009	0,00365
ENSMUSG00000044788	Fads6	1,717290044	0,00366
ENSMUSG00000069255	Dusp22	0,939400017	0,00367
ENSMUSG00000040432	Ltb4r2	1,771039963	0,00367

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ENSMUSG00000036432	Siah2	0,693170011	0,00369
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ENSMUSG00000035062	Zc4h2	-1,180230021	0,0037
ENSMUSG00000020844	Nxn	-1,018260002	0,0037
ENSMUSG00000035273	Hpse	-0,865260005	0,0037
ENSMUSG00000074676	Foxs1	-1,779189944	0,00371
ENSMUSG00000069844	Sco1	0,517939985	0,00371
ENSMUSG00000029060	Mib2	0,327650011	0,00371
ENSMUSG00000025350	Rdh5	1,266589999	0,00371
ENSMUSG00000055538	Zcchc24	0,769739985	0,00372
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ENSMUSG00000027901	Dennd2d	1,132629991	0,00373
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ENSMUSG00000036687	Tmem184a	1,297719955	0,00377
ENSMUSG00000059436	Max	-0,756079972	0,00377
ENSMUSG00000060152	Pop5	1,320520043	0,00377
ENSMUSG00000044244	Il20rb	-1,514449954	0,00378
ENSMUSG00000027620	Rbm39	-0,38440001	0,00378
ENSMUSG00000057858	Fam204a	-0,776650012	0,00379
ENSMUSG00000030966	Trim21	0,934499979	0,00379
ENSMUSG00000040170	Fmo2	2,008719921	0,00379
ENSMUSG00000030483	Cyp2b10	2,446010113	0,00379
ENSMUSG00000022325	Pop1	-0,812259972	0,0038
ENSMUSG00000024526	Cidea	-2,271100044	0,0038
ENSMUSG00000044807	Zfp354c	-1,897469997	0,00382
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ENSMUSG00000025982	Sf3b1	-0,553489983	0,00382
ENSMUSG00000073792	Alg6	0,53648001	0,00382
ENSMUSG00000048330	Ric3	-1,549579978	0,00383
ENSMUSG00000071662	Polr2g	-1,249969959	0,00384
ENSMUSG00000058186	Zfp980	3,711980104	0,00384
ENSMUSG00000030127	Cops7a	0,319460005	0,00385
ENSMUSG00000074570	Cass4	-2,693660021	0,00386
ENSMUSG00000028393	Alad	1,584540009	0,00386
ENSMUSG00000026568	Mpc2	1,886849999	0,00386
ENSMUSG00000076617	Ighm	1,591609955	0,00387
ENSMUSG00000030431	Tmem238	1,736170053	0,00387
ENSMUSG00000038214	Bend3	-0,574750006	0,00389
ENSMUSG00000062593	Gm49339	-0,869759977	0,0039
ENSMUSG00000048347	Pcdhb18	-3,416610003	0,00391

ENSMUSG00000026617	Bpnt1	0,631410003	0,00391
ENSMUSG00000038084	Opa1	0,703589976	0,00391
ENSMUSG00000057074	Ces1g	1,757869959	0,00391
ENSMUSG00000031481	Tpte	2,358959913	0,00391
ENSMUSG00000096546	Smlr1	1,950369954	0,00392
ENSMUSG00000020435	Osbp2	-2,260740042	0,00393
ENSMUSG00000030824	Nucb1	0,497460008	0,00393
ENSMUSG00000035270	Impg2	1,698799968	0,00393
ENSMUSG00000041660	Bbox1	1,799119949	0,00394
ENSMUSG00000062949	Atp11c	1,34363997	0,00395
ENSMUSG00000015776	Med22	-0,557389975	0,00395
ENSMUSG00000020884	Asgr1	1,804370046	0,00396
ENSMUSG00000030528	Blm	-1,00909996	0,00396
ENSMUSG00000050122	Vwa3b	1,689579964	0,00397
ENSMUSG00000025260	Hsd17b10	1,207149982	0,00397
ENSMUSG00000062937	Mtap	-0,461080015	0,00397
ENSMUSG00000038403	Hfe2	1,675559998	0,00397
ENSMUSG00000039117	Taf4	-0,441689998	0,00398
ENSMUSG00000068747	Sort1	1,247949958	0,00398
ENSMUSG00000022365	Derl1	0,656470001	0,00398
ENSMUSG00000063704	Mapk15	1,404539943	0,00398
ENSMUSG00000078651	Aoc2	-1,52252996	0,00399
ENSMUSG00000028161	Ppp3ca	-0,839850008	0,004
ENSMUSG00000035561	Aldh1b1	1,764660001	0,004
ENSMUSG00000029032	Arhgef16	1,112040043	0,00401
ENSMUSG00000034724	Cnot6l	0,66049999	0,00401
ENSMUSG00000022849	Hspbap1	0,711629987	0,00402
ENSMUSG00000053774	Ubxn7	-0,546530008	0,00403
ENSMUSG00000048058	Ldlrad3	0,888080001	0,00403
ENSMUSG00000021388	Aspn	-4,283400059	0,00404
ENSMUSG00000068686	Cd59b	1,269279957	0,00404
ENSMUSG00000060560	Ces4a	2,714139938	0,00405
ENSMUSG00000038943	Prc1	-1,620489955	0,00405
ENSMUSG00000023367	Tmem176a	1,358260036	0,00406
ENSMUSG00000032068	Plet1	-1,42335999	0,00407
ENSMUSG00000032123	Dpagt1	0,563530028	0,00409
ENSMUSG00000037049	Smpd1	0,630599976	0,00409
ENSMUSG00000026944	Abca2	1,136669993	0,00409
ENSMUSG00000049422	Chchd10	1,71528995	0,0041
ENSMUSG00000036676	Tmtc3	-1,202859998	0,00411
ENSMUSG00000034997	Htr2a	-7,91091013	0,00412
ENSMUSG00000038024	Dennd4c	1,162299991	0,00413
ENSMUSG00000028576	Ift74	-0,884679973	0,00414
ENSMUSG00000033065	Pfkm	-0,601429999	0,00414
ENSMUSG00000025732	Mcrip2	1,50988996	0,00415
ENSMUSG00000028629	Exo5	-0,754559994	0,00417
ENSMUSG00000014601	Strip1	-0,617739975	0,00418

ENSMUSG00000078765	U2af1l4	0,407440007	0,00418
ENSMUSG00000033948	Zswim5	1,185559988	0,00418
ENSMUSG00000096370	Gm21992	-3,002599955	0,00419
ENSMUSG00000050017	Pitpnb	0,345459998	0,00419
ENSMUSG00000022372	Sla	-1,194460034	0,00419
ENSMUSG00000049092	Gpr137c	-2,884180069	0,0042
ENSMUSG00000031723	Txn14b	0,943639994	0,0042
ENSMUSG00000035486	Plk5	1,599519968	0,0042
ENSMUSG00000001105	lft20	0,795210004	0,00422
ENSMUSG00000031604	Msmo1	1,060230017	0,00422
ENSMUSG00000064741	Snord14a	-3,703380108	0,00423
ENSMUSG00000070371	Prss36	0,852289975	0,00424
ENSMUSG00000006235	Epor	1,273200035	0,00424
ENSMUSG00000027107	Chrna1	-12,24732018	0,00424
ENSMUSG00000060860	Ube2s	-1,207700014	0,00425
ENSMUSG00000046718	Bst2	1,703850031	0,00425
ENSMUSG00000038721	Hoxb7	-3,138390064	0,00425
ENSMUSG00000050321	Neto1	3,139209986	0,00427
ENSMUSG00000022092	Ppp3cc	-1,01225996	0,00427
ENSMUSG00000031441	Atp11a	-1,501189947	0,00428
ENSMUSG00000021127	Zfp36l1	1,093999982	0,00428
ENSMUSG00000022032	Scara5	-1,789610028	0,00429
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ENSMUSG00000025781	Atp5c1	0,703199983	0,0043
ENSMUSG00000016619	Nup50	-0,459060013	0,00431
ENSMUSG00000032579	Hemk1	1,041749954	0,00432
ENSMUSG0000003070	Efna2	-2,371629953	0,00432
ENSMUSG00000066861	Oas1g	1,516639948	0,00432
ENSMUSG00000060188	Cxcl17	1,97160995	0,00433
ENSMUSG00000020366	Mapk9	0,620079994	0,00434
ENSMUSG00000033730	Egr3	-5,824920177	0,00435
ENSMUSG00000031592	Pcm1	-1,001610041	0,00435
ENSMUSG00000029152	Ociad1	0,389530003	0,00435
ENSMUSG00000014177	Tvp23b	0,590160012	0,00435
ENSMUSG00000018387	Shroom1	1,102699995	0,00435
ENSMUSG00000057147	Dph6	-0,999719977	0,00435
ENSMUSG00000028845	Tekt2	-2,526560068	0,00436
ENSMUSG00000022587	Ly6e	1,217309952	0,00436
ENSMUSG00000039783	Kmo	1,641690016	0,00437
ENSMUSG00000000934	Top1mt	0,591400027	0,00437
ENSMUSG00000046679	C87436	0,394829988	0,00438
ENSMUSG00000036611	Eepd1	1,114109993	0,00438
ENSMUSG00000003934	Efnb3	-3,958529949	0,00439
ENSMUSG00000037316	Bag4	0,521539986	0,00439
ENSMUSG00000013663	Pten	0,60532999	0,0044
ENSMUSG00000025525	Apool	0,873870015	0,0044
ENSMUSG00000020954	Strn3	-0,449070007	0,0044

ENSMUSG00000063450	Syne2	-1,275650024	0,00441
ENSMUSG00000025532	Crcp	0,527249992	0,00441
ENSMUSG00000061859	Patj	1,15328002	0,00441
ENSMUSG00000025983	Ccdc150	-4,418550014	0,00441
ENSMUSG00000027935	Rab13	-0,879320025	0,00442
ENSMUSG00000048707	Tprn	-1,128280044	0,00443
ENSMUSG00000048109	Rbm15	-0,657509983	0,00443
ENSMUSG00000066191	Anks6	-1,481480002	0,00445
ENSMUSG00000010914	Pdhx	0,665279984	0,00445
ENSMUSG00000075229	Ccdc58	1,096480012	0,00445
ENSMUSG00000049728	Zfp668	-0,787090003	0,00446
ENSMUSG00000035864	Syt1	1,454419971	0,00447
ENSMUSG00000040498	Igsf23	1,773900032	0,00447
ENSMUSG00000027487	Cdk5rap1	0,79539001	0,00447
ENSMUSG00000065265	Gm23455	-1,281509995	0,00448
ENSMUSG00000024600	Slc27a6	-2,764800072	0,00449
ENSMUSG00000018849	Wwc1	0,884679973	0,00449
ENSMUSG00000031480	Thsd1	-0,675320029	0,0045
ENSMUSG00000070811	Sult2a2	3,184580088	0,0045
ENSMUSG00000024350	Dnajc18	-0,511900008	0,0045
ENSMUSG00000033356	Pus7l	-0,842570007	0,00451
ENSMUSG00000032109	Nlrx1	0,548879981	0,00451
ENSMUSG00000010609	Psen2	1,576290011	0,00451
ENSMUSG00000048307	Ankrd46	0,708790004	0,00452
ENSMUSG00000019302	Atp6v0a1	0,642560005	0,00452
ENSMUSG00000038074	Fkbp14	-0,709510028	0,00453
ENSMUSG00000084497	Gm22107	-1,940709949	0,00453
ENSMUSG00000017009	Sdc4	0,815559983	0,00453
ENSMUSG00000004056	Akt2	0,461199999	0,00454
ENSMUSG00000054604	Cggbp1	0,245529994	0,00455
ENSMUSG00000074749	Kiz	0,548189998	0,00455
ENSMUSG00000015214	Mtmr1	0,879939973	0,00455
ENSMUSG00000003273	Car11	-2,110029936	0,00456
ENSMUSG00000025496	Drd4	-4,94382	0,00457
ENSMUSG00000052942	Glis3	-1,761849999	0,00457
ENSMUSG00000091803	Cox16	0,883840024	0,00458
ENSMUSG00000028796	Phc2	-1,026859999	0,00458
ENSMUSG00000001542	Eil2	0,68434	0,00458
ENSMUSG00000094724	Rnaset2b	1,616700053	0,00459
ENSMUSG00000047875	Gpr157	0,988900006	0,0046
ENSMUSG00000030987	Stim1	1,530719995	0,0046
ENSMUSG00000038533	Cbfa2t2	-0,696449995	0,00461
ENSMUSG00000044708	Kcnj10	1,781200051	0,00461
ENSMUSG00000028261	Ndufaf4	0,823930025	0,00461
ENSMUSG00000029195	Klb	1,825270057	0,00462
ENSMUSG00000052087	Rgs14	-1,44133997	0,00463
ENSMUSG00000058258	Idi1	1,409150004	0,00463

ENSMUSG00000047649	Cd3eap	-0,680570006	0,00465
ENSMUSG00000032417	Rwdd2a	-1,471840024	0,00466
ENSMUSG00000015342	Xk	1,173930049	0,00467
ENSMUSG00000029062	Cdk11b	-0,431989998	0,00467
ENSMUSG00000061100	Retnla	-6,428100109	0,00468
ENSMUSG00000042436	Mfap4	-1,823609948	0,00471
ENSMUSG00000037730	Mynn	-0,664290011	0,00471
ENSMUSG00000026463	Atp2b4	-1,200970054	0,00472
ENSMUSG00000044390	Tigd3	-2,292949915	0,00472
ENSMUSG00000074582	Arfgef2	0,944660008	0,00472
ENSMUSG00000022982	Sod1	1,513260007	0,00473
ENSMUSG00000025856	Pdgfa	-1,241870046	0,00473
ENSMUSG00000022108	Itm2b	0,774999976	0,00473
ENSMUSG00000021263	Degs2	-1,563830018	0,00474
ENSMUSG00000022978	Mis18a	-1,067819953	0,00474
ENSMUSG00000026283	Ing5	-0,546570003	0,00475
ENSMUSG00000043419	Rnf227	-1,37785995	0,00476
ENSMUSG00000029472	Anapc5	-0,451139987	0,00476
ENSMUSG00000010358	Ifi35	1,037510037	0,00476
ENSMUSG00000028832	Stmn1	-1,456689954	0,00478
ENSMUSG00000036040	Adamtsl2	-1,301800013	0,00478
ENSMUSG00000031971	Ccsap	-1,576990008	0,00479
ENSMUSG00000033634	Nat8f2	1,666509986	0,0048
ENSMUSG00000017299	Dnttip1	-0,432300001	0,00481
ENSMUSG00000035696	Rnf38	-1,02718997	0,00483
ENSMUSG00000067825	Pex26	0,621150017	0,00483
ENSMUSG00000064302	Clasp1	-0,981440008	0,00483
ENSMUSG00000022811	Zfp148	0,580879986	0,00484
ENSMUSG00000014355	Anapc1	-0,856249988	0,00485
ENSMUSG00000030232	Aebp2	-0,516839981	0,00485
ENSMUSG00000026784	Pdss1	-0,621159971	0,00486
ENSMUSG00000026601	Axdnd1	-5,381720066	0,00488
ENSMUSG00000021038	Vipas39	-0,617730021	0,00489
ENSMUSG00000030317	Timp4	-4,596600056	0,00489
ENSMUSG00000004270	Lpcat3	0,889810026	0,00489
ENSMUSG00000026971	Itgb6	-2,682509899	0,00491
ENSMUSG00000015568	Lpl	1,718140006	0,00491
ENSMUSG00000060477	Irak2	0,562579989	0,00492
ENSMUSG00000003299	Mrpl4	0,699469984	0,00492
ENSMUSG00000020010	Vnn3	1,79629004	0,00493
ENSMUSG00000025188	Hps1	-0,49109	0,00494
ENSMUSG00000031246	Sh3bgrl	0,564689994	0,00494
ENSMUSG00000034674	Tdg	-0,834940016	0,00495
ENSMUSG00000028964	Park7	0,930180013	0,00495
ENSMUSG00000052572	Dlg2	-3,245460033	0,00496
ENSMUSG00000027804	Ppid	-0,631190002	0,00496
ENSMUSG00000022781	Pak2	-0,56607002	0,00497

ENSMUSG00000073889	Il11ra1	1,186130047	0,00497
ENSMUSG00000038425	Poli	-0,820630014	0,00499
ENSMUSG00000068394	Cep152	-1,133149981	0,005
ENSMUSG00000022462	Slc38a2	-0,844139993	0,005
ENSMUSG00000035914	Cd276	-0,755959988	0,005
ENSMUSG00000032065	Tex12	1,877140045	0,00501
ENSMUSG00000072662	Mansc4	1,891649961	0,00501
ENSMUSG00000089943	Ugt1a5	2,579849958	0,00501
ENSMUSG00000022178	Ajuba	-0,788869977	0,00501
ENSMUSG00000038777	Sema6c	-1,341619968	0,00502
ENSMUSG00000036959	Bcor1	-0,860050023	0,00502
ENSMUSG00000070462	Tlnrd1	-0,679350019	0,00503
ENSMUSG00000037999	Arap2	0,845809996	0,00503
ENSMUSG00000025916	Ppp1r42	2,095860004	0,00504
ENSMUSG00000028825	Rhd	-3,106529951	0,00504
ENSMUSG00000041607	Mbp	-1,435160041	0,00504
ENSMUSG00000042121	Ssh1	-0,74713999	0,00504
ENSMUSG00000032582	Rbm6	-0,469709992	0,00504
ENSMUSG00000022443	Myh9	-1,366440058	0,00506
ENSMUSG00000046096	Mosmo	-0,581449986	0,00507
ENSMUSG00000004661	Arid3b	-0,890299976	0,00509
ENSMUSG00000043418	Lrit2	2,061130047	0,00509
ENSMUSG00000028687	Mutyh	-1,355260015	0,0051
ENSMUSG00000021193	Pitrm1	-0,819480002	0,0051
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ENSMUSG00000028048	Gba	-0,638830006	0,00512
ENSMUSG00000069300	Hist1h2bj	-2,266619921	0,00513
ENSMUSG00000061898	Rbak	-0,711470008	0,00513
ENSMUSG00000018841	Rad51d	0,633979976	0,00513
ENSMUSG00000047904	Sstr2	1,971439958	0,00513
ENSMUSG00000074182	Znhit6	-0,551400006	0,00515
ENSMUSG00000045103	Dmd	1,101719975	0,00515
ENSMUSG00000016763	Scube1	-1,949470043	0,00517
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ENSMUSG00000033629	Hacd3	0,759019971	0,0052
ENSMUSG00000009563	Tor2a	0,637969971	0,00521
ENSMUSG00000040412	5330417C22Rik	1,916710019	0,00521
ENSMUSG00000068762	Gstm6	1,495679975	0,00522
ENSMUSG00000035021	Baz1a	-0,876739979	0,00523
ENSMUSG00000036622	Atp13a2	0,42513001	0,00524
ENSMUSG00000040061	Plcb2	-0,924589992	0,00524
ENSMUSG00000020694	Tlk2	-0,404339999	0,00525
ENSMUSG00000032841	Prr5l	1,43441999	0,00526
ENSMUSG00000055148	Klf2	-1,543470025	0,00527
ENSMUSG00000024269	Tpgs2	-0,882380009	0,00527
ENSMUSG00000026399	Cd55	1,173149943	0,00527
ENSMUSG00000022142	Nup155	-0,738319993	0,00528

ENSMUSG0000005882	Uqcc1	0,520699978	0,00528
ENSMUSG00000037434	Slc30a1	0,961709976	0,00529
ENSMUSG00000019732	Calr3	1,14233005	0,00529
ENSMUSG00000037636	Slc25a43	-1,883129954	0,0053
ENSMUSG00000026238	Ptma	-0,698949993	0,00533
ENSMUSG00000040204	Pclaf	-1,531000018	0,00533
ENSMUSG00000022526	Zfp251	-1,07348001	0,00534
ENSMUSG00000076435	Acsf2	1,278419971	0,00534
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ENSMUSG00000028865	Cd164l2	-3,368330002	0,00537
ENSMUSG00000055652	Klhl25	0,658479989	0,00537
ENSMUSG00000039304	Tnfsf10	1,517259955	0,0054
ENSMUSG00000029279	Brdt	0,821799994	0,0054
ENSMUSG00000052681	Rap1b	-0,730260015	0,00544
ENSMUSG00000029810	Tmem176b	1,334280014	0,00545
ENSMUSG00000044629	Cnrip1	-1,231189966	0,00546
ENSMUSG00000026096	Osgepl1	0,802869976	0,00546
ENSMUSG00000075224	Lrrc55	-3,181999922	0,00548
ENSMUSG00000069272	Hist1h2ae	-1,644379973	0,00548
ENSMUSG00000000308	Ckmt1	-3,02147007	0,00549
ENSMUSG00000037833	Sh2d4b	-3,158400059	0,00551
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ENSMUSG00000018909	Arrb1	-1,114850044	0,00553
ENSMUSG00000031483	Erlin2	-0,668229997	0,00554
ENSMUSG00000033054	Npat	-0,86372	0,00555
ENSMUSG00000073471	Rsph3a	0,589039981	0,00555
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ENSMUSG00000028792	Ak2	0,928979993	0,00559
ENSMUSG00000040034	Nup43	-0,723330021	0,0056
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ENSMUSG00000005470	Asf1b	-1,709010005	0,00561
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ENSMUSG00000048581	E130311K13Rik	0,914200008	0,00562
ENSMUSG00000031295	Phka2	0,711310029	0,00562
ENSMUSG00000034353	Ramp1	-1,519019961	0,00563
ENSMUSG00000034832	Tet3	-0,870540023	0,00563
ENSMUSG00000028255	Clca1	-6,648900032	0,00564
ENSMUSG00000046792	Zfp787	0,645860016	0,00564
ENSMUSG00000052684	Jun	-1,07122004	0,00564
ENSMUSG00000056174	Col8a2	-2,797909975	0,00565
ENSMUSG00000031681	Smad1	-0,469819993	0,00567
ENSMUSG00000019779	Frk	-0,86996001	0,00567
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ENSMUSG00000040242	Fgfr1op2	0,315809995	0,00569
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ENSMUSG00000052821	Cysltr1	-1,391049981	0,00572
ENSMUSG00000024431	Nr3c1	0,976549983	0,00572
ENSMUSG00000020216	Jsrp1	-5,377359867	0,00573
ENSMUSG00000089694	Nat8f7	3,462949991	0,00573
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ENSMUSG00000041426	Hibch	1,181609988	0,00574
ENSMUSG00000033295	Ptprf	1,084139943	0,00575
ENSMUSG00000047710	Champ1	-0,554019988	0,00575
ENSMUSG00000002233	Rhoc	-1,248180032	0,00577
ENSMUSG00000041506	Rrp9	-0,888329983	0,00577
ENSMUSG00000024132	Eci1	1,05625999	0,00577
ENSMUSG00000066637	Ttc32	1,376139998	0,00577
ENSMUSG00000091648	C2cd4d	1,910599947	0,00578
ENSMUSG00000075502	Kbtbd6	-2,506819963	0,0058
ENSMUSG00000041444	Arhgap32	-0,994109988	0,0058
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ENSMUSG00000091896	Ube2d2a	-0,500699997	0,00587
ENSMUSG00000030306	Tmtc1	-1,577859998	0,00587
ENSMUSG00000021235	Coq6	0,516099989	0,00588
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ENSMUSG00000058799	Nap1l1	-0,766229987	0,0059
ENSMUSG00000028626	Col9a2	-3,757329941	0,00591
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ENSMUSG00000029163	Emilin1	-0,72744	0,00594
ENSMUSG00000023806	Rsph3b	0,820659995	0,00594
ENSMUSG00000064901	Snora21	-3,952950001	0,00595
ENSMUSG00000027288	Zfp106	-0,637350023	0,00595
ENSMUSG00000029863	Casp2	-0,905889988	0,00596
ENSMUSG00000005312	Ubqln1	0,404309988	0,00596
ENSMUSG00000043155	Hpdl	-2,198940039	0,00597
ENSMUSG00000027015	Cybrd1	-2,629070044	0,00597
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ENSMUSG00000026994	Galnt3	-1,487499952	0,00599
ENSMUSG00000037197	Rbm17	-0,65061003	0,00599
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ENSMUSG00000074476	Spc24	1,145359993	0,006
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ENSMUSG00000079685	Ubp1	-3,878249884	0,00628
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ENSMUSG00000055994	Nod2	-1,462520003	0,00631
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ENSMUSG00000028461	Ccdc107	1,455819964	0,00662
ENSMUSG00000030685	Kctd13	-0,677760005	0,00666
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ENSMUSG00000031133	Arhgef6	-0,820159972	0,01246

ENSMUSG00000032840	2410131K14Rik	-0,455179989	0,01246
ENSMUSG00000032046	Abhd12	-0,347030014	0,01246
ENSMUSG00000032766	Gng11	-1,473219991	0,01248
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ENSMUSG00000037649	H2-DMa	-1,213660002	0,01249
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ENSMUSG00000042793	Lgr6	-10,63265991	0,01256
ENSMUSG00000027222	Pex16	1,251999974	0,01256
ENSMUSG00000079598	Clec2l	-3,271529913	0,01259
ENSMUSG00000039683	Sdk1	-1,668280005	0,01259
ENSMUSG00000026725	Tnn	-6,836299896	0,0126
ENSMUSG00000053113	Socs3	-1,49416995	0,01261
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ENSMUSG00000000275	Trim25	0,678979993	0,01265
ENSMUSG00000055681	Cope	0,717390001	0,01267
ENSMUSG00000026102	Inpp1	0,871930003	0,01267
ENSMUSG00000063929	Cyp4a32	1,591179967	0,01268
ENSMUSG00000040936	Ulk4	-1,814800024	0,01268
ENSMUSG00000015202	Cnksr3	-0,93787998	0,01269
ENSMUSG00000030083	Abtb1	0,568589985	0,01271
ENSMUSG00000006777	Krt23	1,351140022	0,01272
ENSMUSG00000005410	Mcm5	-0,976329982	0,01273
ENSMUSG00000001435	Col18a1	0,783550024	0,01278
ENSMUSG00000026014	Raph1	1,188150048	0,01278
ENSMUSG00000040703	Cyp2s1	-2,194950104	0,01278
ENSMUSG00000061759	Armt1	0,396479994	0,01279
ENSMUSG00000060716	Plekhh1	-2,556139946	0,0128
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ENSMUSG00000026117	Zap70	1,657259941	0,01284
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ENSMUSG00000020623	Map2k6	-1,24635005	0,01288
ENSMUSG00000017421	Zfp207	-0,231749997	0,01289
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ENSMUSG00000069237	Fam8a1	0,48179999	0,0129
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ENSMUSG00000026167	Wnt10a	-4,525129795	0,01291
ENSMUSG00000038578	Susd1	0,722069979	0,01292
ENSMUSG00000021285	Ppp1r13b	0,573899984	0,01293
ENSMUSG00000039842	Mcph1	-0,719900012	0,01294
ENSMUSG00000054723	Vmac	0,785969973	0,01294

ENSMUSG00000073968	Trim68	0,934409976	0,01296
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ENSMUSG00000045045	Lrfn4	-1,640239954	0,01304
ENSMUSG00000030666	Calcb	-5,443329811	0,01306
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ENSMUSG00000056812	St8sia3	-1,833899975	0,01324
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ENSMUSG00000032932	Hspa13	0,657989979	0,0133
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ENSMUSG00000042293	Gm5617	1,467350006	0,01351
ENSMUSG00000017950	Hnf4a	1,533149958	0,01352
ENSMUSG00000025154	Arhgap19	-0,69066	0,01354
ENSMUSG00000018900	Slc22a5	0,615149975	0,01354
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ENSMUSG00000021061	Sptb	-1,386620045	0,01356
ENSMUSG00000070939	Tgfbrap1	0,872160017	0,01357
ENSMUSG00000030806	Stx1b	1,48281002	0,01359
ENSMUSG00000009108	Gnat2	1,064090014	0,0136
ENSMUSG00000040016	Ptger3	-2,937880039	0,01361
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ENSMUSG00000009630	Ppp2cb	-0,696770012	0,01361

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ENSMUSG00000020718	Polg2	0,816179991	0,01368
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ENSMUSG00000062981	Mrpl42	0,628970027	0,01374
ENSMUSG00000022671	Mzt2	1,044759989	0,01374
ENSMUSG00000026614	Slc30a10	1,636950016	0,01375
ENSMUSG00000034403	Pja1	0,280900002	0,01376
ENSMUSG00000021497	Txndc15	0,806710005	0,01376
ENSMUSG00000028820	Sfpq	-0,503130019	0,01377
ENSMUSG00000042340	Ctf1	0,999000013	0,01377
ENSMUSG00000025240	Sacm1l	0,666170001	0,01378
ENSMUSG00000019470	Xab2	-0,406300008	0,0138
ENSMUSG00000042404	Dennd4b	-0,480769992	0,01381
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ENSMUSG00000038518	Jarid2	-0,66227001	0,01393
ENSMUSG00000030854	Ptpn5	-5,02008009	0,01396
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ENSMUSG00000027868	Tbx15	-6,346650124	0,01403
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ENSMUSG00000044702	Palb2	-1,055619955	0,01406
ENSMUSG00000029076	Sdf4	0,501909971	0,01407
ENSMUSG00000028782	Adgrb2	-3,800839901	0,0141
ENSMUSG00000030131	Mug2	1,664139986	0,01411
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ENSMUSG00000015542	Nat9	0,976549983	0,01413
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ENSMUSG00000027439	Gzf1	0,502340019	0,01427
ENSMUSG00000037685	Atp8a1	-0,588379979	0,01431
ENSMUSG00000006423	C330007P06Rik	0,423940003	0,01431
ENSMUSG00000028890	Mtf1	0,57960999	0,01432
ENSMUSG00000006169	Clint1	0,570259988	0,01433
ENSMUSG00000026303	Mlph	-1,180430055	0,01434
ENSMUSG00000020315	Sptbn1	-1,07238996	0,01437
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ENSMUSG00000027997	Casp6	-0,684920013	0,01442
ENSMUSG00000038451	Spsb2	0,842850029	0,01442
ENSMUSG00000035245	Eogt	-0,544700027	0,01444
ENSMUSG00000041750	Cd1d2	1,621979952	0,01444
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ENSMUSG00000039518	Cdsn	-2,941509962	0,01447
ENSMUSG00000027667	Zfp639	-0,542180002	0,01451
ENSMUSG00000067199	Frat1	1,105859995	0,01451
ENSMUSG00000066512	Klk1b5	3,178770065	0,01451
ENSMUSG00000030188	Magohb	-1,327579975	0,01456
ENSMUSG00000018846	Pank3	0,583620012	0,01456
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ENSMUSG00000071014	Ndufb6	0,998430014	0,01465
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ENSMUSG00000092300	Cdk3-ps	-2,430779934	0,01474
ENSMUSG00000033831	Fgb	1,422799945	0,01478
ENSMUSG00000054003	Tdrd9	-6,23927021	0,0148
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ENSMUSG00000021356	Irf4	-1,697129965	0,01481
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ENSMUSG00000022109	Med4	-0,487029999	0,01488
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ENSMUSG00000033880	Lgals3bp	0,88282001	0,01495
ENSMUSG00000037364	Srrt	-0,367879987	0,01496
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ENSMUSG00000015647	Lama5	-1,429859996	0,01502
ENSMUSG00000053368	Rxfp2	-4,845990181	0,01502
ENSMUSG00000027244	Atg13	0,700209975	0,01504
ENSMUSG00000017550	Atad5	-1,515210032	0,01505
ENSMUSG00000037406	Htra4	2,467890024	0,01505
ENSMUSG00000014599	Csf1	-0,671150029	0,01507
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ENSMUSG00000029016	Clcn6	-0,77779001	0,01511
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ENSMUSG00000026864	Hspa5	0,737829983	0,01512
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ENSMUSG00000022263	Trio	-1,161569953	0,01522
ENSMUSG00000053178	Mterf1b	-1,041980028	0,01524
ENSMUSG00000053647	Gper1	-3,749969959	0,01527
ENSMUSG00000032436	Cmtm7	-1,16068995	0,01528
ENSMUSG00000020077	Srgn	-1,156890035	0,01528
ENSMUSG00000017176	Nt5c3b	-0,816590011	0,01528
ENSMUSG00000059406	Tmprss9	-2,678060055	0,01531
ENSMUSG00000039533	Mmd2	1,801159978	0,01535
ENSMUSG00000006517	Mvd	0,889209986	0,0154
ENSMUSG00000022799	Arhgap31	-1,015840054	0,01543
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ENSMUSG00000046691	Chtf8	-0,366380006	0,01545
ENSMUSG00000077222	Gm22270	-1,027369976	0,01547
ENSMUSG00000070730	Rmdn3	0,708389997	0,01551
ENSMUSG00000017692	Rhbdl3	-1,734850049	0,01556
ENSMUSG00000031398	Plxna3	-1,343039989	0,01561
ENSMUSG00000059839	Zfp874b	0,545679986	0,01562
ENSMUSG00000030638	Sh3gl3	-7,922550201	0,01564
ENSMUSG00000034110	Kctd7	0,708410025	0,01565
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ENSMUSG00000007122	Casq1	-2,55298996	0,01568
ENSMUSG00000004994	Ccdc130	-0,637910008	0,01569
ENSMUSG00000050195	Scd4	-3,433700085	0,0157
ENSMUSG00000029461	Fam168a	0,833949983	0,01573
ENSMUSG00000041264	Uspl1	-0,412510008	0,01573
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ENSMUSG00000039990	Edrf1	0,514530003	0,01597
ENSMUSG00000054021	Sirt5	0,942120016	0,01597
ENSMUSG00000075410	Prcd	-1,990560055	0,01598
ENSMUSG00000023349	Clec4n	-1,165949941	0,01598
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ENSMUSG00000062585	Cnr2	0,886110008	0,01599
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ENSMUSG00000037894	H2afz	-0,731949985	0,01603
ENSMUSG00000030895	Hpx	1,608860016	0,01606
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ENSMUSG00000033860	Fgg	1,474449992	0,01615
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ENSMUSG00000012123	Crybg2	1,785030007	0,01618
ENSMUSG00000037824	Tspan14	-0,579580009	0,01619
ENSMUSG00000090264	Eif4ebp3	1,697100043	0,01619
ENSMUSG00000078763	Slfn1	-1,383370042	0,0162
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ENSMUSG00000049103	Ccr2	-1,328959942	0,01638
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ENSMUSG00000019194	Scn1b	1,00285995	0,01645
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ENSMUSG00000060212	Pcnx2	-2,506680012	0,0165
ENSMUSG00000030465	Psd3	1,080430031	0,01656
ENSMUSG00000043535	Setx	-0,581629992	0,01657
ENSMUSG00000057234	Mettl15	0,716530025	0,01657
ENSMUSG00000051184	Zfp524	1,001719952	0,01657
ENSMUSG00000032171	Pin1	-0,469980001	0,01659
ENSMUSG00000018415	Gid4	0,358960003	0,0166
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ENSMUSG00000048154	Kmt2d	-0,97766	0,01665
ENSMUSG00000063015	Ccni	-0,435380012	0,01665
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ENSMUSG00000039670	Oxid1	1,229210019	0,01666
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ENSMUSG00000015149	Sirt2	0,383789986	0,01674
ENSMUSG00000017428	Psm11	0,37597999	0,01675
ENSMUSG00000021374	Nup153	-0,627979994	0,01679
ENSMUSG00000022602	Arc	-2,204900026	0,01681
ENSMUSG00000038155	Gstp2	1,92437005	0,01681
ENSMUSG00000040843	Tipr1	-0,489549994	0,01685
ENSMUSG00000010175	Prox1	1,455189943	0,01691
ENSMUSG00000045665	Mfsd5	-0,704940021	0,01692
ENSMUSG00000056050	Mia3	1,027670026	0,01693
ENSMUSG00000018417	Myo1b	0,555410028	0,017
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ENSMUSG00000004707	Ly9	1,266639948	0,01722
ENSMUSG00000005150	Wdr83	0,792970002	0,01726
ENSMUSG00000040525	Cblc	1,114300013	0,01729
ENSMUSG00000029097	Trmt44	-0,595210016	0,01732
ENSMUSG00000061947	Serpina10	1,495110035	0,01732
ENSMUSG00000029245	Epha5	-9,898659706	0,01734
ENSMUSG00000052516	Robo2	-1,217929959	0,01736
ENSMUSG00000053091	Lins1	-0,494219989	0,01737
ENSMUSG00000036138	Acaa1a	1,025930047	0,01737
ENSMUSG00000024052	Lpin2	0,894739985	0,01739
ENSMUSG00000029804	Herc3	-0,938920021	0,01741
ENSMUSG00000022533	Atp13a3	0,65911001	0,01741
ENSMUSG00000029436	Mmp17	-1,461670041	0,01742
ENSMUSG00000021553	Slc28a3	-3,340759993	0,01744
ENSMUSG00000003228	Grk5	-0,992709994	0,01745
ENSMUSG00000035295	Wdr38	-1,916479945	0,01747
ENSMUSG00000038884	A230050P20Rik	1,266080022	0,0175
ENSMUSG00000022322	Shcbp1	-1,375030041	0,01753
ENSMUSG00000031532	Saraf	0,550149977	0,01756

ENSMUSG00000054702	Ap1s3	-1,286190033	0,01759
ENSMUSG00000031667	Aktip	-0,525020003	0,01761
ENSMUSG00000059183	Mtfmt	-0,308380008	0,01761
ENSMUSG00000040658	Dnph1	1,181959987	0,01762
ENSMUSG00000055401	Fbxo6	0,530939996	0,01763
ENSMUSG00000020474	Polm	-1,028560042	0,01764
ENSMUSG00000028980	H6pd	1,180729985	0,01765
ENSMUSG00000022217	Emc9	1,003509998	0,01769
ENSMUSG00000036873	2410004B18Rik	-0,870280027	0,01769
ENSMUSG00000006586	Runx1t1	-2,385879993	0,01775
ENSMUSG00000031197	Vbp1	-0,561380029	0,01777
ENSMUSG00000006241	Ccdc159	0,650279999	0,01783
ENSMUSG00000040940	Arhgef1	-0,298909992	0,01784
ENSMUSG00000028132	Tmem56	1,520679951	0,01785
ENSMUSG00000010517	Faf1	0,497480005	0,01786
ENSMUSG00000028976	Slc2a5	1,505319953	0,01786
ENSMUSG00000038122	Tbc1d32	0,775409997	0,01789
ENSMUSG00000007570	Fance	-0,559859991	0,0179
ENSMUSG00000020131	Pcsk4	1,132969975	0,01791
ENSMUSG00000039183	Nubp2	0,478249997	0,01793
ENSMUSG00000031712	Il15	1,087200046	0,01793
ENSMUSG00000047260	Emc6	0,864849985	0,018
ENSMUSG00000053914	Kdm4d	-3,65395999	0,01802
ENSMUSG00000037896	Rcor1	-0,728380024	0,01805
ENSMUSG00000046410	Kcnk6	-0,836880028	0,01807
ENSMUSG00000070565	Rasal2	-0,735819995	0,01811
ENSMUSG00000038390	Gpr162	-1,191740036	0,01817
ENSMUSG00000003531	Dgcr6	0,983749986	0,01818
ENSMUSG00000029821	Gsdme	0,924359977	0,01819
ENSMUSG00000023336	Wfdc1	1,067280054	0,01823
ENSMUSG00000040297	Suco	-0,706110001	0,01827
ENSMUSG00000027710	Acad9	0,358110011	0,01828
ENSMUSG00000008167	Fbxw9	0,976979971	0,01829
ENSMUSG00000035765	Dym	0,35078001	0,01832
ENSMUSG00000025867	Cplx2	-0,903490007	0,01834
ENSMUSG00000003949	Hlf	1,516010046	0,01836
ENSMUSG00000031351	Zfp185	-2,123080015	0,01837
ENSMUSG00000022313	Utp23	-0,526329994	0,01837
ENSMUSG00000001827	Folr1	-2,342210054	0,01843
ENSMUSG00000022194	Pabpn1	-0,703530014	0,01845
ENSMUSG00000030545	Pex11a	0,994069993	0,01846
ENSMUSG00000030019	Fbxl14	-0,442790002	0,01849
ENSMUSG00000016494	Cd34	-0,984130025	0,0185
ENSMUSG00000044576	Garem2	-5,925849915	0,01853
ENSMUSG00000019718	L3hypdh	0,685469985	0,01856
ENSMUSG00000037979	Ccdc92	-1,828310013	0,01858
ENSMUSG00000030867	Plk1	-1,201979995	0,0186

ENSMUSG00000044201	Cdc25c	-1,713469982	0,01863
ENSMUSG00000029875	Ccdc184	-3,811180115	0,01864
ENSMUSG00000065041	Gm24044	-1,442219973	0,01865
ENSMUSG00000031985	Gnpat	0,319359988	0,01866
ENSMUSG00000021838	Samd4	-0,722609997	0,0187
ENSMUSG00000040329	Il7	-1,642689943	0,01871
ENSMUSG00000012126	Ubxn11	-1,381379962	0,01872
ENSMUSG00000042015	Wdr41	0,298090011	0,01877
ENSMUSG00000091055	Siglec15	-9,67031002	0,01878
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ENSMUSG00000025780	Itih5	1,538079977	0,01878
ENSMUSG00000054400	Cklf	-1,245100021	0,0188
ENSMUSG00000028212	Ccne2	-1,138090014	0,0188
ENSMUSG00000006538	Ihh	1,252570033	0,01881
ENSMUSG00000026616	Cr2	1,744390011	0,01882
ENSMUSG00000074088	Snrnp40	-0,576300025	0,01883
ENSMUSG00000061024	Rrs1	-0,687600017	0,01885
ENSMUSG00000059995	Atxn7l3	-0,653410017	0,01887
ENSMUSG00000032279	Idh3a	-0,587119997	0,01893
ENSMUSG00000034066	Farp2	0,948450029	0,01893
ENSMUSG00000018076	Med13l	-1,121389985	0,01897
ENSMUSG00000070305	Mpzl3	0,723540008	0,01897
ENSMUSG00000023909	Paqr4	-0,94788003	0,01898
ENSMUSG00000019842	Traf3ip2	-1,141170025	0,01898
ENSMUSG00000041028	Ghitm	0,53549999	0,01902
ENSMUSG00000029198	Grpel1	0,895780027	0,01905
ENSMUSG00000000127	Fer	-0,736079991	0,01909
ENSMUSG00000026361	Cdc73	-0,439539999	0,01909
ENSMUSG00000092260	Zfp963	0,725989997	0,01911
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ENSMUSG00000025092	Hspa12a	1,151200056	0,01911
ENSMUSG00000039068	Zzz3	-0,603460014	0,01912
ENSMUSG00000023460	Rab12	-0,505620003	0,01915
ENSMUSG00000021835	Bmp4	0,922150016	0,01915
ENSMUSG00000045467	Ttll13	1,336449981	0,01917
ENSMUSG00000028278	Rragd	-1,203619957	0,01918
ENSMUSG00000000538	Tom1l2	-0,427769989	0,01921
ENSMUSG00000056258	Kcnq3	-5,311729908	0,01922
ENSMUSG00000038244	Mical2	-1,534430027	0,01925
ENSMUSG00000010025	Aldh3a2	0,840650022	0,01925
ENSMUSG00000059991	Nptx2	-5,436130047	0,01927
ENSMUSG00000007946	Phox2a	-7,981649876	0,01936
ENSMUSG00000058076	Sdhc	0,820609987	0,01942
ENSMUSG00000054690	Emcn	-1,090800047	0,01945
ENSMUSG00000001229	Dpp9	0,702620029	0,01947
ENSMUSG00000000958	Slc7a7	0,75357002	0,01947
ENSMUSG00000025968	Ndufs1	0,565609992	0,0195

ENSMUSG00000061079	Zfp143	-0,407079995	0,01951
ENSMUSG00000048827	Pkd1l3	-1,314020038	0,01952
ENSMUSG00000030247	Kcnj8	1,072679996	0,01953
ENSMUSG00000035798	Zdhhc17	-0,714280009	0,01956
ENSMUSG00000028466	Creb3	0,468809992	0,01956
ENSMUSG00000024325	Ring1	0,49188	0,01956
ENSMUSG00000041268	Dmxl2	0,706659973	0,01963
ENSMUSG00000052794	1700030K09Rik	-0,756760001	0,01966
ENSMUSG00000026927	Entr1	-0,442799985	0,01968
ENSMUSG00000063810	Alms1	-1,447440028	0,0197
ENSMUSG00000039620	Trmt9b	1,155809999	0,01974
ENSMUSG00000063698	Sfxn4	-1,558429956	0,01975
ENSMUSG00000018750	Zbtb4	-0,620369971	0,01977
ENSMUSG00000024339	Tap2	1,064010024	0,01977
ENSMUSG00000010205	Raver1	-0,672710001	0,01978
ENSMUSG00000027463	Slc52a3	-1,341060042	0,0198
ENSMUSG00000029452	Tmem116	-1,815969944	0,01981
ENSMUSG00000029209	Gnpda2	-1,180349946	0,01982
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ENSMUSG00000060038	Dhps	-0,797720015	0,01984
ENSMUSG00000000094	Tbx4	-4,209070206	0,01986
ENSMUSG00000020866	Cacna1g	-2,373559952	0,01986
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ENSMUSG00000032038	St3gal4	0,640600026	0,01993
ENSMUSG00000019789	Hey2	-1,889000058	0,01994
ENSMUSG00000040188	Scamp2	-0,432130009	0,01995
ENSMUSG00000026270	Capn10	0,632770002	0,02
ENSMUSG00000071550	Cfap44	2,411720037	0,02003
ENSMUSG00000034842	Art3	1,088099957	0,02006
ENSMUSG00000005362	Crbn	0,402060002	0,02007
ENSMUSG00000031927	1700012B09Rik	-11,9945097	0,02013
ENSMUSG00000040586	Ofd1	-0,61036998	0,02014
ENSMUSG00000007837	Prrg2	0,745299995	0,0202
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ENSMUSG00000021240	Abcd4	-0,646380007	0,02027
ENSMUSG00000063049	Ing2	-0,856679976	0,02031
ENSMUSG00000047613	A430005L14Rik	1,011719942	0,02032
ENSMUSG00000026749	Nek6	0,615980029	0,02033
ENSMUSG00000080486	Snord100	-1,950440049	0,02035
ENSMUSG00000020048	Hsp90b1	0,621630013	0,02035
ENSMUSG00000034855	Cxcl10	1,340049982	0,02036
ENSMUSG00000088929	Gm24299	-1,720729947	0,02038
ENSMUSG00000053641	Dennd4a	0,913810015	0,02039
ENSMUSG00000033342	Plppr5	2,42366004	0,02039
ENSMUSG00000004789	Dlst	0,288569987	0,02043

ENSMUSG00000033208	S100b	-2,815969944	0,02044
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ENSMUSG00000026197	Zfand2b	0,934930027	0,02045
ENSMUSG00000002908	Kcnn1	0,750500023	0,02048
ENSMUSG00000030720	Cln3	-0,454129994	0,02049
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ENSMUSG00000064390	Rnu73b	-2,511420012	0,02055
ENSMUSG00000056487	Mettl7a2	2,734479904	0,02056
ENSMUSG00000031095	Cul4b	-0,334850013	0,02057
ENSMUSG00000073598	1700066B19Rik	-2,04144001	0,02059
ENSMUSG00000035356	Nfkbiz	-0,818880022	0,02062
ENSMUSG00000044881	Coa4	0,667150021	0,02062
ENSMUSG00000028567	Txndc12	0,679889977	0,02062
ENSMUSG00000027326	Kn11	-1,769330025	0,02069
ENSMUSG00000046994	Mars2	-0,813009977	0,02074
ENSMUSG00000092212	Slc22a13b-ps	-1,564599991	0,02081
ENSMUSG00000034488	Edil3	-9,623259544	0,02086
ENSMUSG00000026227	2810459M11Rik	1,376440048	0,02089
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ENSMUSG00000022012	Enox1	-6,198979855	0,02094
ENSMUSG00000025812	Pard3	0,624890029	0,02094
ENSMUSG00000020840	Blmh	0,717480004	0,02095
ENSMUSG00000010307	Tmem86a	0,949509978	0,02106
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ENSMUSG00000041308	Sntb2	-1,190569997	0,02109
ENSMUSG00000029201	Ugdh	0,723240018	0,02111
ENSMUSG00000022296	Baalc	-6,859049797	0,02113
ENSMUSG00000029265	Dr1	-0,263509989	0,02113
ENSMUSG00000070390	Nlrp1b	-1,461689949	0,02114
ENSMUSG00000027171	Prrg4	-2,448029995	0,02118
ENSMUSG00000031521	Aga	0,607949972	0,02121
ENSMUSG00000015093	Clic3	1,841259956	0,02123
ENSMUSG00000061535	C1qtnf7	-1,47755003	0,02128
ENSMUSG00000026773	Pfkfb3	-1,223180056	0,0213
ENSMUSG00000071516	Hist1h2ai	-2,64861989	0,02135
ENSMUSG00000021720	Rnf180	-1,687039971	0,02135
ENSMUSG00000029814	Igf2bp3	-2,783159971	0,02136
ENSMUSG00000068114	Ccdc134	-0,612119973	0,02139
ENSMUSG00000040464	Gtpbp10	0,261810005	0,02141
ENSMUSG00000048967	Yjefn3	-1,393409967	0,02143
ENSMUSG00000050132	Sarm1	-1,563500047	0,02148
ENSMUSG00000032333	Stoml1	-0,775659978	0,02148
ENSMUSG00000041809	Efhc1	-1,561740041	0,0215
ENSMUSG00000033386	Frrs1	-0,443729997	0,0215
ENSMUSG00000051439	Cd14	-1,322299957	0,02151
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ENSMUSG00000059811	Atl2	0,720109999	0,02154
ENSMUSG00000045962	Wnk1	-0,661090016	0,02155
ENSMUSG00000029426	Scarb2	0,677380025	0,02155
ENSMUSG00000055150	Zfp78	1,079560041	0,02156
ENSMUSG00000033111	3830406C13Rik	0,516390026	0,02157
ENSMUSG00000032194	Kank2	0,556020021	0,02168
ENSMUSG00000024074	Crim1	-0,445439994	0,02169
ENSMUSG00000020787	P2rx1	-2,178859949	0,0217
ENSMUSG00000071715	Ncf4	-0,885429978	0,0217
ENSMUSG00000025877	Hk3	0,659099996	0,02173
ENSMUSG00000030930	Chst15	-0,602869987	0,02174
ENSMUSG00000056091	St3gal5	0,914929986	0,02174
ENSMUSG00000017548	Suz12	-0,436549991	0,02175
ENSMUSG00000032667	Pon2	0,506150007	0,02175
ENSMUSG00000028236	Sdr16c5	3,656820059	0,02176
ENSMUSG00000027475	Kif3b	-0,524290025	0,02179
ENSMUSG00000062929	Cfl2	-0,401620001	0,02183
ENSMUSG00000039747	Orai2	-0,935140014	0,02187
ENSMUSG00000020549	Elac2	0,363620013	0,02189
ENSMUSG00000028975	Pex14	0,46746999	0,02201
ENSMUSG00000002812	Flii	-0,641520023	0,02203
ENSMUSG00000039285	Azi2	0,333279997	0,02204
ENSMUSG00000079235	Ccdc13	-3,367150068	0,02205
ENSMUSG00000034327	Kctd9	-0,469949991	0,02205
ENSMUSG00000058709	Egln2	0,781729996	0,02205
ENSMUSG00000023087	Noct	-1,421569943	0,02206
ENSMUSG00000006269	Atp6v1b1	-2,675349951	0,02207
ENSMUSG00000020361	Hspa4	-0,298040003	0,02207
ENSMUSG00000028238	Atp6v0d2	1,133069992	0,02207
ENSMUSG00000024487	Yipf5	0,376960009	0,02212
ENSMUSG00000010760	Phlda2	1,199470043	0,02214
ENSMUSG00000029490	Mfsd7a	0,827759981	0,02214
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ENSMUSG00000052212	Cd177	-2,519099951	0,02224
ENSMUSG00000061143	Maml3	-0,965610027	0,02228
ENSMUSG00000096225	Lhx8	-11,79518986	0,0223
ENSMUSG00000051586	Mical3	-0,655369997	0,02236
ENSMUSG00000059409	Ppp2r5d	-0,395480007	0,02236
ENSMUSG00000032215	Rsl24d1	-0,706160009	0,02237
ENSMUSG00000029370	Rassf6	0,733640015	0,02244
ENSMUSG00000016552	Foxred2	-1,383290052	0,02246
ENSMUSG00000055745	Rtl6	-1,510319948	0,02249
ENSMUSG00000077575	Gm24888	-1,524309993	0,02251

ENSMUSG00000036197	Gxylt1	-0,469940007	0,02251
ENSMUSG00000032549	Rab6b	-1,058009982	0,02254
ENSMUSG00000013766	Ly6g6e	1,844370008	0,02254
ENSMUSG00000041548	Hspb8	0,800109982	0,02256
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ENSMUSG00000026799	Med27	-0,380650014	0,0228
ENSMUSG00000029408	Abcb9	-0,738820016	0,02284
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ENSMUSG00000039741	Bahcc1	-1,20559001	0,0229
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ENSMUSG00000014776	Nol3	-0,983889997	0,02307
ENSMUSG00000032735	Ablim3	0,922599971	0,02315
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ENSMUSG00000040560	Wdr7	0,589820027	0,02318
ENSMUSG00000038705	Gmeb2	-0,526449978	0,02323
ENSMUSG00000063052	Lrrc40	-0,376419991	0,02323
ENSMUSG00000031847	1700030J22Rik	-1,387689948	0,02325
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ENSMUSG00000005204	Senp3	-0,511799991	0,02331
ENSMUSG00000048478	Spata33	-1,716539979	0,02336
ENSMUSG00000062761	Zfp512	-0,510800004	0,02336
ENSMUSG00000026576	Atp1b1	1,358150005	0,02336
ENSMUSG00000032238	Rora	1,097219944	0,02338
ENSMUSG00000020894	Vamp2	-0,655589998	0,02344
ENSMUSG00000028037	Ifi44	1,321609974	0,02346
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ENSMUSG00000032459	Mrps22	0,497110009	0,02363

ENSMUSG00000070639	Lrrc8b	-2,9582901	0,02364
ENSMUSG00000023143	Nagpa	0,433970004	0,02367
ENSMUSG00000022010	Tsc22d1	-0,827520013	0,0237
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ENSMUSG00000041845	Rhod	0,790740013	0,024
ENSMUSG00000095687	Rnaset2a	1,189450026	0,02406
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ENSMUSG00000028882	Ppp1r8	-0,484930009	0,02415
ENSMUSG00000038916	Soga3	-2,036420107	0,02416
ENSMUSG00000023033	Scn8a	1,268479943	0,02416
ENSMUSG00000051671	Coa6	1,057260036	0,02417
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ENSMUSG00000038331	Satb2	-1,393460035	0,02422
ENSMUSG00000015837	Sqstm1	0,430860013	0,02422
ENSMUSG00000040675	Mthfd1l	-1,06219995	0,02423
ENSMUSG00000038742	Angptl6	1,065639973	0,02423
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ENSMUSG00000029433	Diablo	0,423070014	0,02424
ENSMUSG00000064125	Prr36	-0,692770004	0,02425
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ENSMUSG00000042185	Nfrkb	-0,561489999	0,02429
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ENSMUSG00000023826	Prkn	2,293989897	0,02461
ENSMUSG00000070644	Etnk2	1,385589957	0,02462
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ENSMUSG00000064115	Cadm2	-6,819900036	0,02471
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ENSMUSG00000028001	Fga	1,371739984	0,02474
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ENSMUSG00000037440	Vnn1	1,451820016	0,0248

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ENSMUSG00000006398	Cdc20	-1,147089958	0,03204
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ENSMUSG00000039230	Tbcd	0,393099993	0,03207

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ENSMUSG00000039568	Ubald1	-0,384359986	0,03261
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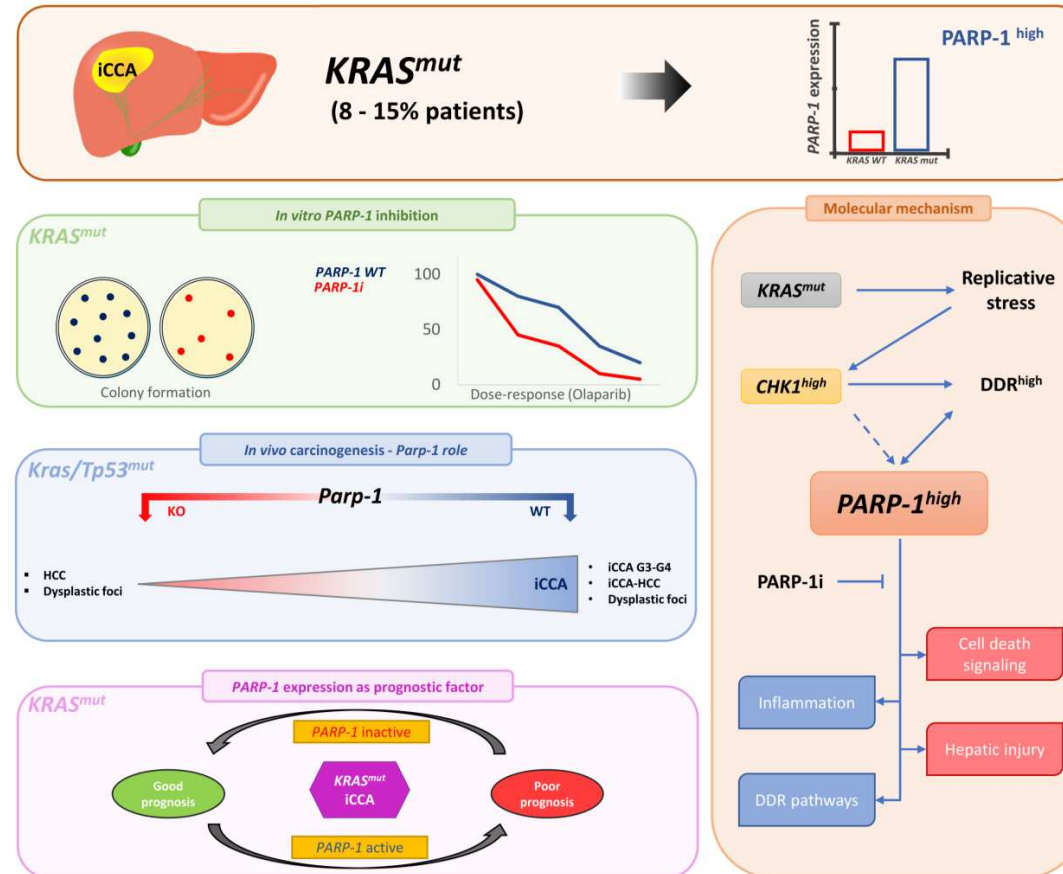
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ENSMUSG00000035551	Igfbpl1	-1,674640059	0,03977
ENSMUSG00000043747	1520401A03Rik	3,304209948	0,04004
ENSMUSG00000014813	Stc1	-1,568179965	0,04015
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ENSMUSG00000087651	1500009L16Rik	-1,60837996	0,04219
ENSMUSG00000042826	Fgf11	-1,298159957	0,04249
ENSMUSG00000026546	Cfap45	-1,190840006	0,0425
ENSMUSG00000032648	Pygm	0,904380023	0,04269
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ENSMUSG00000040483	Xaf1	0,847299993	0,04319
ENSMUSG00000030921	Trim30a	0,732079983	0,04328
ENSMUSG00000037860	Aim2	0,781340003	0,04404
ENSMUSG00000035692	Isg15	1,196869969	0,04425
ENSMUSG00000068263	Efcc1	1,154999971	0,04428
ENSMUSG00000000365	Rnf17	3,551650047	0,04433
ENSMUSG00000027313	Chac1	-0,864589989	0,04473
ENSMUSG00000037161	Mgarp	-2,920559883	0,04508

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ENSMUSG00000058186	Zfp980	2,01673007	0,04558
ENSMUSG00000042265	Trem1	-2,164520025	0,04573
ENSMUSG00000005980	Dnase1	1,24131	0,04628
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ENSMUSG00000028369	Svep1	1,303660035	0,04716
ENSMUSG00000026558	Uck2	-0,684050024	0,04742
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ENSMUSG00000019055	Plod1	-0,217710003	0,04746
ENSMUSG00000038530	Rgs4	-1,207759976	0,04749
ENSMUSG00000020067	Mypn	-2,714240074	0,04796
ENSMUSG00000048126	Col6a3	0,930830002	0,04865
ENSMUSG00000023078	Cxcl13	-1,021080017	0,04869
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ENSMUSG00000026418	Tnni1	-2,220999956	0,04935
ENSMUSG00000046020	Pofut1	0,265929997	0,04954
ENSMUSG00000020335	Zfp354b	0,576969981	0,04958
ENSMUSG00000019848	Popdc3	-3,180439949	0,04972
ENSMUSG00000029272	Sult1e1	2,389489889	0,04979

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