



Loss of SDHB Promotes Dysregulated Iron Homeostasis, Oxidative Stress, and Sensitivity to Ascorbate

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1 Loss of SDHB promotes dysregulated iron homeostasis, oxidative
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Abstract

Succinate dehydrogenase is a key enzyme in the tricarboxylic acid cycle and the electron transport chain. All four subunits of succinate dehydrogenase are tumor suppressor genes predisposing to paraganglioma, but only mutations in the SDHB subunit are associated with increased risk of metastasis. Here we generated an *Sdhb* knockout chromaffin cell line and compared it to *Sdhb*-deficient cells. Both cell types exhibited similar SDH loss of function, metabolic adaptation, and succinate accumulation. In contrast, *Sdhb*^{-/-} cells showed hallmarks of mesenchymal transition associated with increased DNA hypermethylation and a stronger pseudo-hypoxic phenotype compared to *Sdhb*^{-/-} cells. Loss of SDHB specifically led to increased oxidative stress associated with dysregulated iron and copper homeostasis in the absence of NRF2 activation. High-dose ascorbate exacerbated the increase in mitochondrial reactive oxygen species, leading to cell death in *Sdhb*^{-/-} cells. These data establish a mechanism linking oxidative stress to iron homeostasis that specifically occurs in SDHB deficient cells and may promote metastasis. They also highlight high-dose ascorbate as a promising therapeutic strategy for SDHB-related cancers.

Statement of significance

Loss of different succinate dehydrogenase subunits can lead to different cell and tumor phenotypes, linking stronger 2-OG-dependent-dioxygenases inhibition, iron overload, and ROS accumulation following SDHB mutation.

Introduction

Succinate dehydrogenase (SDH) is a key enzyme localized in the inner mitochondrial membrane where it participates both in the tricarboxylic acid (TCA) cycle and the electron transport chain (ETC), as complex II. In the TCA cycle, SDH catalyzes the oxidation of succinate into fumarate while in the ETC, it allows the transfer of electrons from succinate to the ubiquinone pool. SDH is constituted of two anchoring subunits (SDHC, SDHD) and two catalytic subunits (SDHA, SDHB) encoded by the four *SDHx* nuclear genes (*SDHA*, *SDHB*, *SDHC* and *SDHD*). SDHA is a flavoprotein to which the substrate succinate binds in order to be oxidized to fumarate, while the resulting electrons are channeled to ubiquinone, through the three Fe-S clusters of SDHB. Since the initial discovery of *SDHD* mutations in 2000(1), all four *SDHx* genes have been demonstrated to act as tumor-suppressor genes (2,3,4). Their mutations predispose to pheochromocytoma and paraganglioma (PPGL), rare neuroendocrine tumors arising from chromaffin cells of the adrenal medulla and from the sympathetic and parasympathetic nervous systems, respectively; as well as gastro-intestinal stromal tumors (GIST) and rare forms of renal cell carcinomas. It is now estimated that mutations in *SDHx* genes stand for almost 50% of inherited cases of PPGL. Interestingly, *SDHB* mutations have been shown to be the highest risk factor of malignancy in patients with PPGL: approximately 50% of PPGL patients carrying *SDHB* mutations will ultimately develop a metastatic form of the disease and a germline mutation in *SDHB* is found in up to 36% of all metastatic PPGL cases (5). In contrast, metastatic forms of the disease are found in only 5% of patients with an *SDHD* gene mutation. Moreover, *SDHB* mutated cancers are more aggressive than non-mutated metastatic ones. The overall survival of patients with metastatic *SDHB*-related PPGL was initially estimated at 42 months after diagnosis of the first metastasis versus 244 months for patients with a metastatic PPGL but without an *SDHB* gene mutation (6). Interestingly, recent studies have revealed that increased follow-up of patients with genetically determined PPGL has significantly improved their survival, demonstrating the beneficial impact of genetic testing in these patients (7,8).

120 In all cases, germline *SDHx* mutations are associated with loss of heterozygosity, which causes the
121 complete loss of SDH function in the tumor (9) and a subsequent accumulation of its substrate,
122 succinate (10). Succinate (as other TCA cycle intermediates such as fumarate and 2-hydroxyglutarate)
123 is considered as an oncometabolite, driving aberrant activation of transcription factors and global
124 epigenetic reprogramming. Indeed, high steady-state levels of these metabolites are known to inhibit
125 2-oxoglutarate (2-OG) dependent dioxygenases, such as the hypoxia-inducible transcription factor
126 (HIF) prolyl-hydroxylases (PHDs) and Ten-eleven translocation (TET) DNA demethylases (11). These
127 enzymes belong to the large family of iron (Fe) and 2-OG-dependent dioxygenases, which activity is
128 based on the use of iron (12), oxygen (13) and ascorbate (14) as main co-factors. Inhibition of PHDs
129 promotes the abnormal stabilization, and thus activity of HIF1 and HIF2, while TET inhibition leads to
130 a lack of DNA demethylation, resulting in pseudo-hypoxic and hypermethylator phenotypes,
131 respectively. These observations were initially revealed in genomic studies performed on large PPGL
132 tumor collections, resulting in a better understanding of the mechanisms of SDH-related
133 tumorigenesis. In these studies, all *SDHx* and *FH* mutated tumors clustered together, showing a
134 transcriptome signature characterized by activation of the hypoxic response pathway (2, 15, 16) and a
135 DNA hypermethylator phenotype (17). Despite this apparent homogeneity, some differences have
136 emerged suggesting that *SDHB*-mutated tumors may display a particularly marked hypermethylator
137 phenotype associated with hallmarks of neuroendocrine-to-mesenchymal transition (NMT), which
138 were not observed in other types of *SDHx*-mutated cases (i.e *SDHA*, *SDHC* and *SDHD* mutated)(18). In
139 order to decipher these mechanisms at the cellular level, we have generated an immortalized mouse
140 chromaffin cell (imCC) line knocked-out for the *Sdhb* gene (17). In these cells, we showed that *Sdhb*-
141 deficiency does promote a marked hypermethylator phenotype mediated by TET1 and/or TET2
142 blockade, which acts in synergy with HIF2 activation to promote NMT and metastatic dissemination
143 (19, 20). *Sdhb*^{-/-} cells also undergo significant metabolic reprogramming becoming critically dependent
144 on aspartate synthesis as a major source of carbon for anabolic purposes, which supports their viability
145 and proliferation, maintained mainly through reductive carboxylation (21).

Despite these important advances in the understanding of the oncogenic consequences of SDHB loss of function, the exact cause of the metastatic phenotype of *SDHB*-related tumors remain mostly unexplained. *SDHA* and *SDHC* mutations are rare in PPGL patients, probably because of low penetrance of the disease in mutation carriers. In contrast, *SDHB* and *SDHD* are the most frequently described mutations in PPGL, with an incidence of 8-10 and 5-7% among all PPGL cases, respectively (22). Genotype-phenotype correlation studies performed in patients with *SDHB* or *SDHD* mutations have undoubtedly demonstrated their different clinical behavior in terms of invasiveness. To address this crucial question in the field, we have generated *Sdhb* knocked-out cell lines in the imCC model. In this new and unique model, we have investigated the different pathways previously identified in SDH-related tumors in order to identify the specificities that may explain their different clinical behavior.

Materials and Methods

Detailed methods are provided in the Supplementary Information section.

Sdhb KO, *Sdhb*-rescue cell generation and cellular analysis

Complete knock-out of *Sdhb* gene was achieved in immortalized mouse Chromaffin Cells (imCC) by transfecting Wild-Type imCC, previously generated by our lab (17), with *in silico* designed targeted gRNA, using the PrecisionX Cas9 SmartNuclease RNA system kit (System Biosciences). *Sdhb*-rescue clones were established by transfecting *Sdhb*^{-/-} imCC with an SDHD-expressing vector (ORIGENE, NM003002). Screening of these clones was performed by SDH activity test, qRT-PCR and direct sequencing of the *Sdhb* gene by Sanger method. Cells used for experiments were maintained in DMEM high glucose Glutamax (Gibco) unless when grown for metabolic or respirometry experiments (see Supplementary Information). Wound scratch assays, proliferation and adhesion tests were performed to assess cellular phenotype. When stated, cells were treated with indicated doses of iron Chloride (Sigma), MitoTEMPO (Sigma), L-Ascorbic acid (Sigma), Talazoparib (MedChemTronica) or N-acetylcysteine (Sigma).

171

172 **RNA-seq and RRBS data analysis**

173 RNA sequencing was performed for 7 samples: 3 *Sdhb*^{-/-}, 2 *Sdhd*^{-/-} and 2 WT imCC. Enriched samples
174 were used to generate sequencing libraries with the Illumina 'TruSeq Stranded mRNA Sample Prep' kit
175 and associated protocol provided by the manufacturer. Libraries were sequenced by IntegraGen (Evry,
176 France) on an Illumina HiSeq 2000 as paired-end 75 bp reads. Reduced Representation Bisulfite
177 Sequencing (RRBS) was also performed by Integragen SA, as previously described (17). **Details of the**
178 **process leading to the evaluation of differential expression and methylation rates are provided in**
179 **the Supplementary Information.** The sequencing data reported in this paper have been deposited to
180 the EGA (European Genome-phenome Archive) database (European Genome-phenome
181 Archive) database (accession number EGAS00001005279).

182

183

184 **Metabolite analysis, high resolution respirometry, enzymatic activities and features of oxidative**
185 **stress assessment**

186 All cell types underwent metabolite extraction using Methanol:H₂O:Chloroform at ratio 1:1:1,
187 following ¹³C-glucose and ¹³C-glutamine labeling. The polar fractions were used for Gas
188 Chromatography – Mass Spectrometry (GC-MS) analysis allowing acquisition of the isotope data. High
189 resolution respirometry was performed by loading Intact or permeabilized cells in an Oxygraph-O2 k
190 (Oroboros instruments) chamber, using Mir05 respiratory media and digitonin for the latter. A pseudo
191 dual-wavelength Varian CARY50 spectrophotometer (Victoria, Australia) was used to assess
192 respiratory chain activities as previously described (23). For the assessment of oxidative stress
193 features, cells treated as stated, were incubated with either CellRox, MitoSox or Bodipy C11 Reagent
194 (Termofisher) and Flow cytometry data were acquired using an LSR FORTRESSA analyzer (BD
195 biosciences).

196

197 **Cellular and tumoral iron and copper analysis**

198 For cellular iron and copper assessment, cells were incubated with the relevant metal-specific probe
199 prior to being analyzed by flow cytometry on a BD Accuri C6 (BD Biosciences). Laser ablation-
200 inductively coupled plasma-mass spectrometry (LA-ICP-MS) was performed on dewaxed and
201 rehydrated formalin-fixed paraffin-embedded tumor sections. **Details of LA-ICP-MS experiments are**
202 **provided in the Supplementary Information.** LA-ICP-MS images were acquired in a fixed dosage mode,
203 with a vertical and horizontal spatial resolution of 20 μm , a detailed list of sample settings is available
204 in Supplementary Table 1. Average ^{56}Fe and ^{63}Cu intensities were calculated from pixels containing a
205 positive elemental tissue marker (^{31}P) ensuring background regions did not influence these
206 calculations.

207

208 **qRT-PCR, Western-blot, immunofluorescence staining and immunohistochemical analyses**

209 For qRT-PCR, total mRNA was extracted from cell pellets using RNeasy plus mini-kit (Qiagen). Reverse
210 transcription was fulfilled using iScriptTM cDNA Synthesis Kit (BIO-RAD) and qRT-PCR was performed on
211 CFX96TM Real-Time System C1000 TouchTM Thermal Cycler (BIO-RAD) using SuperScript SybrGreen
212 (BioRad) to assess the expression of *Sdhb*, *Sdhd*, *Snai1*, *Fn1*, *Epas1*, *MMP9* and *18S*. Western-blot
213 analysis were performed to assess SDHB, SDHA, HIF2 α and TUBULIN expression. RIPA lysis buffer was
214 used for extraction of total protein and concentrations were determined with Bradford colorimetric
215 method. Results were read with a LAS-4000 Mini (Fuji). Actin staining and γH2AX immunofluorescence
216 were performed on cells plated on glass slides, while γH2AX immunohistochemistry was performed on
217 6 μm sections from paraffin-embedded tumors. **Details of primers, primary and secondary antibodies,**
218 **immunostaining, and experimental conditions are provided in the Supplementary Information.**

219

220 **Data analysis**

221 Data are represented as mean (of at least 3 independent experiments) $\pm$ SEM (standard error of the
222 mean). Data were analyzed by one-way or 2-way ANOVA. Statistics tests were carried out using the
223 GraphPad Prism software. All analyses considered a value of $P \leq 0.05$ to be statistically significant. For
224 enrichment analysis, we used an in-house adaptation of the GSEA method to identify gene sets from
225 the MSigDB database overrepresented among up/down-regulated and hyper/hypomethylated genes.

226

227 **Results**

228 ***Loss of SDHB or SDHD leads to similar metabolic dysfunction and respiratory profiles***

229 To investigate the mechanisms underlying the metastatic characteristics of *SDHB* mutated-
230 PPGL but not of *SDHD*-deficient tumors, we knocked-out the *Sdhd* gene using the CRISPR/Cas9
231 procedure in wild-type (WT) imCC (17). We obtained two independent *Sdhd*^{-/-} clones (CIA and CIB)
232 each containing a different homozygous point mutation on exon 3 of *Sdhd*, c.119delC and
233 c.120_121delCA, respectively, both leading to premature stop codons (Fig. 1A). These mutations were
234 predicted to lead to the translation of truncated proteins of 79 and 68 amino acids, respectively,
235 instead of the 159 amino acids of the entire WT SDHD protein. To attest for the absence of off-target
236 effects in *Sdhd*^{-/-} cells, we generated a third cell line, in which SDHD loss was rescued by stably
237 transfecting an *Sdhd*-expressing vector in the *Sdhd*^{-/-} CIA (clone *Sdhd-R*). *Sdhd*-mutated cells showed
238 a decrease in *Sdhd* RNA levels (Supplementary Fig. 1A) when compared with WT and *Sdhd-R* cells,
239 which may be suggestive of nonsense-mediated decay in the mutant clones, and particularly in clone
240 A.

241 SDHD protein expression could not be estimated due to the lack of efficient antibody in mouse.
242 It is worth noting that *Sdhd* mRNA levels were also reduced in *Sdhb*-deficient cells. In contrast, *Sdhb*
243 mRNA levels were absent in *Sdhb*^{-/-} cells, but not significantly reduced in *Sdhd*^{-/-} imCC (Supplementary

Fig. 1B). It has previously been reported that disassembly of the SDH complex in case of *SDHx* mutations leads to the degradation of the SDHB subunit in all *SDHx* mutant cells (24). However, our data show that *Sdhb*^{-/-} clones retain a small but significant level of SDHB protein (Fig. 1B). Similarly, evaluation of SDHB protein by immunohistochemistry in SDH-related PPGL frequently leads to a weak diffuse signal in SDHD deficient tumors, while it is totally negative in SDHB-mutated ones, suggesting that some SDHB remains present in this type of mutants (25). Nevertheless, they exhibited a complete loss of SDH enzymatic activity, similar to that observed in *Sdhb*-deficient cells (Fig. 1C), and in accordance with observations in mutated human PPGL (9,26). Interestingly, it has previously been suggested that succinate accumulation might be less important in SDHD-deficient tumors, which may account for their different metastatic potential (27). Analysis of intracellular succinate levels revealed a substantial accumulation of succinate in *Sdhb*^{-/-} cells that reached that observed in the *Sdhb*^{-/-} imCC model (Fig. 1D). Similarly, levels of the related metabolites, fumarate and 2-oxoglutarate, were strongly reduced in all SDH-deficient cells regardless of the subunit inactivated. *Sdhb*^{-/-} cells showed a profile similar to that of WT imCC (Fig. 1E-F and Supplementary Fig. 1C, D).

Next, we assessed the metabolic and respiratory phenotypes of both types of SDH-deficient cells. ¹³C-glucose tracing experiments revealed that in accordance with previous work (21), cells deficient in SDH-activity undergo a metabolic rewiring in the absence of a fully functional TCA cycle (Fig. 2A). Like *Sdhb*^{-/-} cells, the synthesis of aspartate by *Sdhb*^{-/-} imCC cannot rely on oxidative TCA cycle metabolism (Fig. 2B and C, m+2 isotopomer) and instead increase the aspartate produced through pyruvate carboxylation (PC) (Fig. 2B and C, m+3 isotopomer) for anabolic purposes. Equally, their synthesis of citrate from glucose, a central metabolite for cellular anabolism, was greatly reduced (Fig. 2B). The metabolism of another key nutrient, glutamine was therefore examined. Although both cell lines retain some oxidative metabolism of glutamine to produce succinate, *Sdhb*^{-/-} imCC appear to significantly increase their synthesis of aspartate and citrate using reductive carboxylation (Fig. 2C and D), which is not observed to the same degree in *Sdhb*^{-/-} imCC. We then measured oxygen

consumption of intact and permeabilized imCC (Fig. 2E and F). In both cases, *Sdhb*^{-/-} imCC exhibited no significant change in basal respiration, while *Sdhd*^{-/-} cells showed a decrease, suggesting that a more significant defect in respiration exists in the *Sdhd*^{-/-} cells compared to *Sdhb*^{-/-}. Maximal respiratory capacity (FCCP-mediated uncoupled respiration) was significantly reduced in both SDH-deficient imCC models, in compliance to that previously reported in *Sdhb*^{-/-} cells(28). The relative decrease in respiratory activity observed in *Sdhd*^{-/-} cells compared to those deficient in *Sdhb* was consistent with the increased reliance on reductive carboxylation for the synthesis of aspartate and citrate (Fig. 2C), an effect previously observed in hypoxia (29). Given the decreased oxygen consumption observed in the *Sdhd*-deficient cells compared to those lacking *Sdhb*, we examined whether there was a compensatory increase in pyruvate reduction to lactate to regenerate cytosolic NADH and maintain glycolysis. We indeed saw that while *Sdhb*^{-/-} cells show a small increase in lactate production, this is further increased in *Sdhd*-deficient cells (Fig. 2G). Altogether, these results suggest that massive succinate accumulation and rewired metabolism do not constitute relevant triggers for SDHB-related malignancy, although the extent of mitochondrial respiratory deficit may vary between the two models.

***Sdhb* knockout in mouse chromaffin cells promotes neuroendocrine-to-mesenchymal transition (NMT), unlike *Sdhd* knockout**

We previously reported that *Sdhb*^{-/-} imCC exhibit a mesenchymal-like phenotype with increased adhesion, migration and invasion capacities (19). Morphological observation following phalloidin staining qualitatively revealed that *Sdhd*^{-/-} cells appear to be generally smaller than *Sdhb*^{-/-} cells, and display a less extensive and rather peripheral actin mesh unlike *Sdhb*^{-/-} imCC (Fig. 3A), suggesting that only *Sdhb*^{-/-} cells undergo mesenchymal transformation. Accordingly, markers of NMT activation such as *Snai1*, *Mmp9*, *Fn1* (Fig. 3B) were overexpressed in *Sdhb*^{-/-} imCC but not in *Sdhd*^{-/-} cells. In accordance with the loss of neuroendocrine features, *NCadh* was downregulated in *Sdhb*^{-/-} imCC, while it was actually overexpressed in *Sdhd*^{-/-} cells (Supplementary Fig. 2A). *Sdhd*^{-/-} cells showed

moderate increase in adhesion (Fig. 3C), and no increase in migration, evaluated both in collective (Fig. 3D) and individual migration assays (Supplementary Fig. 2B). *Sdhd*^{-/-} imCC also exhibited a much slower cell growth than *Sdhb*^{-/-} cells (Supplementary Fig. 2C). Hence, despite similar SDH loss-of-function and succinate levels, *Sdhd*-deficient cells do not display the mesenchymal and migratory phenotype of *Sdhb* KO cells, as observed in human paraganglioma(18).

***Sdhb*-deficient cells show greater inhibition of 2OG-dependent dioxygenases**

We have previously established that *SDHB*-mutated PPGL and *Sdhb*^{-/-} imCC display pseudohypoxic and hypermethylator phenotypes, caused by inhibition of PHD and TET enzymes and involved in the mesenchymal-like hallmarks associated with *SDHB* deficiency (17,20). We next performed reduced representation bisulfite sequencing (RRBS) to precisely quantify 5-methylcytosine (5mC) modifications along the genome after enrichment for CpG rich regions in the different cell lines. Compared to WT, both *Sdhb* and *Sdhd* KO cells displayed a DNA hypermethylator phenotype, but this phenotype was less pronounced in *Sdhd*^{-/-} cells (Fig. 3E). In total, *Sdhb*^{-/-} cells displayed 6,847 significantly hypermethylated gene-based features (TSS +/- 500 bp and gene bodies) against only 2,564 for *Sdhd*^{-/-} cells (Fig. 3F and Supplementary Table 2). Hypermethylator phenotypes in *Sdhb*^{-/-} and *Sdhd*^{-/-} cells displayed a significant overlap and correlation (Fig. 3G and H), with 1,084 common hypermethylated features representing 42% and 16% of hypermethylated features in *Sdhd*^{-/-} and *Sdhb*^{-/-} imCC, respectively.

Surprisingly, Western-blot analysis in our cell lines revealed stabilization and massive increase of HIF2 α protein levels in *Sdhb*^{-/-} cells, which was not seen in either *Sdhd*^{-/-}, WT or *Sdhd*-R imCC (Fig. 3I). We thus analyzed the transcriptome of all cell lines using RNA-sequencing. Hierarchical clustering of expression profiles across the 1,000 most variant genes (based on standard deviation) showed that *Sdhd*^{-/-} imCC remain closer to wild-type cells and display less gene expression changes than *Sdhb*^{-/-} cells (Fig. 3J). To investigate more specifically the expression of hypoxia-inducible genes, we analyzed the expression of a previously published list of 52 HIF targets (3), among which 47 were present in the transcriptome of imCCs (Supplementary Table 3). Twenty-four (24) of them were overexpressed in *Sdhb*-

deficient cells compared to WT (mean value >120% of WT), while 17 were overexpressed in *Sdhd*-deficient cells compared to WT (13 overlapping with those high in *Sdhb* KO cells) (Fig. 3K). Comparison of both KO cells showed that 19 of the 28 overexpressed genes showed stronger expression in *Sdhb*^{-/-} cells (Fig. 3L). These data therefore suggested that although HIF2 α was hardly detectable by western blot, *Sdhd*^{-/-} cells did show a mild pseudohypoxic signature. In order to validate this observation, we further analyzed previously-published transcriptome data generated in a collection of 188 human PPGL. In this study, 3 *SDHD*, 1 *SDHA* and 2 *SDHC*-mutated PPGL were evaluated together with 17 *SDHB*-mutated ones (3), which all clustered together using the expression of the 52 HIF-target genes. We have reanalyzed these data, limiting them to the 41 highly expressed ones, and we evaluated their mean expression in *SDHB* versus *SDHD*-mutated tumors. We observed that most genes were overexpressed in *SDHB*-related tumors while the subset of genes over-represented in *SDHD*-mutated tumors corresponded to genes expressed by endothelial cells or associated with angiogenic processes (Supplementary Fig. 3A), therefore reflecting the very high vascular density described in these tumors (15,30). Similar results were obtained on the TCGA cohort of PPGL (Supplementary Fig. 3B)(31).

Altogether, these findings indicate that *Sdhd* inactivation induces less DNA methylation and gene expression changes than *Sdhb* deletion. We next aimed at identifying the causes of the seemingly greater inhibition of 2OG-dependent dioxygenases in *Sdhb*^{-/-} cells.

Iron and copper homeostasis are dysregulated in SDH-deficient cells, and especially in Sdhb KO cells

2OG-dependent dioxygenases are iron-containing enzymes. Because *SDHB* is the iron-sulfur subunit of complex II, we wondered whether its complete loss might lead to disturbances in iron metabolism, which would in turn modulate the activity of 2OG-dependent dioxygenases. We thus used specific fluorescent probes to detect cytosolic and mitochondrial iron in all cell types, as well as assessed iron levels in tumor samples from patients with *SDHB* mutations. We also evaluated mitochondrial copper in all cell types. Indeed, iron and copper are both essential metals with close metabolic interactions that have been known for a long time (32).

We first used the commercial Calcein-AM probe that reveals both Iron(II) and Iron(III) levels, but also other ions such as calcium. This experiment showed a decrease in global labile iron in SDH-deficient cells compared to WT imCC (Fig. 4A). To validate this observation in human PPGL, we performed laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) in 6 pheochromocytomas carrying *NF1* (n=2), *RET* (n=2) or *SDHB* (n=2) mutations, as well as 4 paragangliomas with *SDHB* (n=2) or *SDHD* (n=2) gene mutations. We observed that average ⁵⁶Fe counts were significantly decreased in tumors with *SDHB* mutations compared with tumors with *NF1*, *RET* or *SDHD* mutations (Fig. 4B-F). This decrease was greater in *SDHB*-mutated paragangliomas (Fig. 4D) than in *SDHB*-mutated pheochromocytomas (Fig. 4C). These results obtained in tumors from patients consolidate the hypothesis that loss of the SDHB subunit leads to an altered iron metabolism. Calcein-AM probe being poorly specific, we next examined the subcellular localization of Iron(II) using specific probes of both this ion, and specific cell compartments. Unexpectedly, evaluation of the labile pool of cytosolic Iron(II) revealed a significant increase in *Sdhb*^{-/-} cells only (Fig. 4G). This suggests that the calcein-AM data would actually be imputable to a strong decrease in cytosolic levels of Iron(III) in SDH-deficient cells. In opposition, we observed a significant decrease in the mitochondrial pool of chelatable iron (Iron(II)) in both knockout models, decrease which was especially pronounced in *Sdhb*^{-/-} cells and rescued in *Sdhb-R* imCC (Fig. 4H).

We next evaluated mitochondrial copper levels in all cell types. Concerning the pool of labile mitochondrial Cu(II), no significant changes were observed in the SDH-deficient cells, while mitochondrial Cu(I) was significantly increased in *Sdhb* KO cells only (Supplementary Fig. 4A and B). LA-ICP-MS was also used to quantify the levels of ⁶³Cu in 10 PPGL tumors. This evaluation of global copper was not able to confirm the difference in *SDHB* vs *RET* or *NF1* tumors. However, it suggested that SDHD-deficient PGL had a decrease in copper counts compared with the other genotypes (Supplementary Fig. 4C). Hence, there was a dysregulation in copper and especially in iron pools in cells and tumors depending on their genotypes. In support of these observations, we evaluated the mRNA expression

of several iron and copper transporters as well as of chaperones or different actors of iron/copper homeostasis, which revealed that these pathways were indeed strongly affected in *Sdhb* KO cells (Fig. 4I, J). In particular, these cells showed a differential expression of transporters implicated in the entry of iron and copper in the cell and the mitochondria: high DMT1 (*Slc11a2*) and low Slc25a37 would sustain the increased cytosolic distribution of Iron(II), while low CTR1 (*Slc31a1*) and high Slc25a3, the high mitochondrial Cu(I) levels. Consistently with these observations, human PPGL transcriptome data showed an increase in *DMT1* mRNA levels in SDH tumors as compared with other types of mutated PPGL. SDH tumors also exhibited a slight increase in the expression of other actors involved in iron binding and transport, such as the hypoxia-inducible genes *TF* and *TFRC*. *SLC31A1* was significantly decreased in both SDH and VHL tumors compared to RET or NF1-mutated ones. No differences were detected for *TFR2* nor *SLC25A3* expression (Supplementary Fig. 4D).

***Sdhb*-deficient cells display increased ROS levels without activation of the NRF2 pathway.**

Sdhb-KO cells show increased mitochondrial copper(I) and cytosolic Iron(II) levels, which could cause important oxidative stress in these cell compartments (33). An increase in reactive oxygen species (ROS) might also participate to the sustained inhibition of 2OG-dependent dioxygenases activity (34). Flow cytometry analyses of fluorescent probes revealed that *Sdhb*-deficient cells showed increased ROS both in the cytosol (Fig. 5A) and especially in the mitochondria (Fig. 5B). They also displayed a significant increase in lipid peroxidation levels (Fig. 5C) and in mitochondrial activity (Fig. 5D) but not in overall mitochondrial mass (Fig. 5E). Unexpectedly, none of the *Sdhb*-deficient clones showed any changes in ROS levels as compared to the WT cells.

Because *Sdhb*^{-/-} cells display such a significant increase in ROS, we postulated that they would probably show increased anti-oxidant responses, either through superoxide dismutase (SOD) or through activation of the NRF2 pathway. However, the global superoxide dismutase activity did not differ between the different cell types (Supplementary Fig. 5A). Moreover, RNA-seq analysis showed a

significant downregulation of mitochondrial SOD2, thus demonstrating that *Sdhb*-deficient cells do not detoxify the excess in mitochondrial ROS (Fig. 5F).

We performed gene set enrichment analyses using RNA-seq data of 58 NRF2-target genes (Supplementary Table 4) which showed no activation of the pathway in *Sdhb* nor in *Sdhb* KO cells, compared to WT (Supplementary Fig. 5B). In addition, treating the cells with N-acetyl cysteine (NAC) had no effect on the levels of mitochondrial ROS in any of the cell types studied (Fig. 5G), neither affected their proliferation (Fig. 5H). In order to fully validate this observation in the human context, this list of genes was also tested in the transcriptome data of the human PPGL COMETE collection (Fig. 5I). Mean values of NRF2 targets levels in the groups of sporadic non-mutated tumors (n=49), *RET* (n=19), *NF1* (n=37), *VHL* (n=40), *SDHA*, *C*, *D*- (n=6) and *SDHB*-mutated tumors (n=17) were used to perform unsupervised classification, which confirmed that the NRF2 pathway is not activated in *SDHB*-deficient tumors.

It has previously been reported that *SDHB* loss is associated with increased DNA damage (35), and a sensitivity to inhibitors of poly (ADP-ribose) polymerase (PARP) (35, 36, 37). In addition to the recently demonstrated mechanism associated with oncometabolite-induced inhibition of the lysine demethylase KDM4B, increased ROS levels may participate to such phenotype. We therefore evaluated DNA damage after staining PPGL tumor tissues and imCCs with anti- γ H2AX antibody (Supplementary Fig. 5C and D). Although it was not statistically significant, we observed a slight increase in γ H2AX levels in *SDHB*-deficient tumors, which was not seen in *Sdhb*^{-/-} imCCs. Treating cells with increasing doses of the PARP inhibitor Talazoparib reduced cell survival in all cell types, with an actually higher efficacy in WT and *Sdhb*-R cells (Supplementary Fig. 5E). In this cell model, it seemed that Talazoparib efficiency was not related to *SDH*-deficiency, but was rather related to cell proliferation indexes of the treated cell types.

Modulating Iron(II) and ROS levels affects pseudohypoxia and survival in Sdhb-deficient cells

Altogether, these data suggest that in *Sdhb* KO cells, a combination of succinate accumulation, dysregulation of iron homeostasis and high ROS levels may account for the increased inhibition of TET and PHD hydroxylases. To demonstrate this link, we treated cells with Iron(II) (50 μ M), which had no effect on cytosolic ROS (Supplementary Fig. 6A) but reduced mitochondrial ROS, only in *Sdhb*^{-/-} cells (Fig. 6A). This was associated with a decrease in HIF2 α protein levels in *Sdhb*^{-/-} cells as well (Fig. 6B). Treating cells with increasing doses of ferrous iron revealed a specific sensitivity of *Sdhb*-deficient cells. Indeed, after 48 h of treatment, 0.1 mM doses of Iron(II) led to a 60% decrease in *Sdhb*^{-/-} cells survival while it only moderately affected WT, *Sdhb*-KO or *Sdhb*-R cell types (Fig. 6C). In order to further demonstrate that increased mitochondrial ROS were indeed responsible for the massive HIF2 α stabilization observed in *Sdhb*-deficient cells, we then treated them for 12h with MitoTEMPO, a mitochondrially targeted antioxidant that acts as a specific scavenger of mitochondrial superoxide. MitoTEMPO (MTT) at 2.5 μ M had no effect on cytosolic ROS (Fig. 6D), but significantly decreased mitochondrial ROS in *Sdhb*^{-/-} imCC (Fig. 6E), which was associated with a substantial reduction of HIF2 α levels (Fig. 6F). High doses of MTT are suspected to show a reverse effect, promoting a pro-oxidant response. We therefore treated cells with 2.5 mM of the compound and showed that such high dose increased cytosolic ROS in all cell types and especially in WT and *Sdhb*^{-/-} CIA cells (Fig. 6G), as well as mitochondrial ROS in WT and *Sdhb*^{-/-} cells (Fig. 6H). Strikingly, such treatment promoted a strong pseudohypoxic response in WT, *Sdhb*^{-/-} and *Sdhb*-R cells, thus demonstrating that increasing ROS was sufficient to mediate HIF2 α stabilization. In contrast, this led to the opposite effect in *Sdhb*^{-/-} cells (Fig. 6I) in which HIF2 α protein was almost lost. It actually appeared that high dose MTT was highly toxic for *Sdhb*^{-/-} cells exclusively (Fig. 6J), with perinuclear vacuoles emerging after 12h and leading to the death of all *Sdhb*^{-/-} imCC after 72h. In an attempt to evaluate another pro-oxidant treatment that might be used in a clinical context, we finally tested the vulnerability of imCC to high dose ascorbate. A dose response curve showed that *Sdhb*^{-/-} cells were indeed much more vulnerable to ascorbate with significant increase in cell death appearing from a 1 mM dose onward, a complete lethality being reached at a 2.5 mM ascorbate dose

(Fig. 6K). At the higher dose, 85% of *Sdhb*-deficient cell loss was achieved after 24h, while a similar response was only apparent in *Sdhb* and WT cells after 72h (Fig. 6L). To evaluate the mechanism associated with ascorbate-induced lethality, we measured cytosolic and mitochondrial ROS in cells treated for 48 h with 1 mM ascorbate. At such a dose, there was already a significant lethality of *Sdhb*-KO cells and enough cell material was still available to allow the analyses (Supplementary Fig. 6B). Interestingly, we observed that cytosolic ROS were not modified by ascorbate in any of the cell models (Supplementary Fig. 6C). In contrast, ascorbate led to a massive increase in mitochondrial ROS, specifically in *Sdhb*^{-/-} cells (Fig. 6M). These data suggest that in *Sdhb*-KO cells ascorbate interacts with the increased Iron(II) labile pool to enhance oxidative stress, leading to rapid cell death.

Discussion

It is well-established that a mutation in the *SDHB* gene is a high risk factor for metastatic PPGL (38) and poor prognosis (6), unlike mutations in other *SDHx* genes (*SDHA*, *SDHC* or *SDHD*) that rarely cause metastatic forms of the disease. This question has been unresolved for 20 years. Many studies have been performed in the past years, mainly using cell lines exhibiting a decrease or complete lack in the expression of *Sdhb*. Thereby, previous work from our team has shown that metastatic *SDHB* tumors exhibit a NMT phenotype (18,19), associated with increased DNA methylation in comparison to other *SDHx* mutated tumors (20,39). Further, we have recently demonstrated that this hypermethylated profile is due to TET silencing and that the NMT phenotype observed in *SDHB* mutated tumors is the result of synergistic roles of TET repression and pseudohypoxia, through HIF2 activation (20). Although these data have shed light on some mechanisms undeniably involved in the tumorigenesis of *SDHB* mutated tumors, they do not explain the different clinical outcomes observed in patients carrying mutations in the different *SDHx* genes. In the present study, we were able to characterize and compare two physiologically appropriate cellular models exhibiting a complete

knock-out in *Sdhb* or *Sdhd* genes, which strikingly recapitulate most of the phenotypic characteristics of *SDHB* and *SDHD*-mutated tumors.

Succinate accumulation is probably the major consequence of SDH loss of activity and increased succinate levels in tumor samples are used as a biomarker of SDH-deficiency in PPGL patients (27,40–42). For a long time, it has therefore been considered to be the main trigger of PPGL tumorigenesis. The role of succinate as an oncometabolite was initially demonstrated in 2005, with the demonstration of its inhibiting role on 2OG-dependent PHD enzymes, leading to the subsequent stabilization of HIF α subunits even under normoxia (43,44). Later, it was demonstrated that succinate is also a major epigenetic modifier, inhibiting TET enzymes and promoting a genome wide hypermethylated profile (17,39,45). It has been suggested that a stronger inhibition of 2OG-dependent dioxygenases observed in *SDHB*-mutated tumors versus tumors with mutations in other *SDHx* genes, might be explained by a fuller inactivation of SDH enzyme associated with higher succinate (27). Here, we firmly invalidate this long-held assumption, both *Sdhb*^{-/-} and *Sdhd*^{-/-} imCC models showing the same loss of SDH activity and similar levels of succinate and fumarate (Fig. 1). Indeed, many of the metabolic characteristics investigated were highly similar between the two cell models suggesting that merely measuring overall steady-state succinate and fumarate levels are inadequate for predicting phenotype, and smaller changes in metabolic function may drive downstream. Surprisingly, HIF2 α protein was hardly detectable in *Sdhd*-deficient cells while it was strongly activated in *Sdhb*^{-/-} imCC. This provides further evidence that although aspects of the overall metabolic phenotype were similar between *Sdhb*^{-/-} and *Sdhd*^{-/-} models, as yet unexplored metabolic factors may play a role in the inactivation of the PHD enzymes to stabilize HIF2 α . This was unexpected as previous transcriptome analyses of human tumor samples have classified all *SDHx* mutated tumors together with *VHL*-mutated ones in a “pseudohypoxic” cluster (16,17). However, such classifications were based on global transcriptome and obviously included many other pathways. To our knowledge, only three studies have classified PPGL tumors based on the expression of hypoxia-induced genes. Hensen *et al* compared hypoxia-inducible genes in sporadic head and neck PGL (HNPGL) to HNPGL carrying *PGL2* or *SDHD* gene

mutations (46). This study was not able to identify any differences in the hypoxic signature of these 3 types of tumors. Besides, Flidner *et al* evaluated the expression of HIF target genes in a larger collection of *SDHD* (n=14) and *SDHB* (n=15) related PPGL and also revealed some differences between the two types of tumors, with some genes being less overexpressed in *SDHD*-mutated PGL (47). Based on previously published transcriptome data (3), our present study shows that most HIF-target genes were overexpressed in *SDHB*-related tumors while the subset of targets over-represented in *SDHD*-mutated tumors corresponded to genes expressed by endothelial cells. Hence, although it is most probable that, as previously suggested in other studies (15,48–50), *SDHD* tumors display some induction of pseudo-hypoxia *in vivo*, the combination of our *in vitro* data and human PPGL studies does suggest that this effect is at least much more limited in non-*SDHB* mutated cells and can therefore not be imputable to succinate accumulation only.

Our data reveal that while *SDHB* expression is completely abolished in *Sdhb*^{-/-} cells, a small fraction of *SDHB* protein remains detectable in *Sdhb*^{-/-} clones, consistently with IHC data on tumors that frequently report a weak diffuse *SDHB* staining in *SDHD*-mutated PPGL (25,51). *SDHB* is the Fe-S subunit of Complex II and contains two highly conserved L(I)YR motifs that are essential for acquisition of Fe-S clusters by recruiting the Fe-S transfer machinery. We postulate that the loss in mitochondrial Fe-S clusters present in the *SDHB* subunit, may be responsible for the significant imbalance in cytosolic and mitochondrial iron distribution, that we observe in *Sdhb*^{-/-} cells. Interestingly, Saxena *et al* reported that 37% of disease-causing missense mutations in *SDHB* were located in either the L(I)YR Fe-S transfer motifs or in the 11 Fe-S cluster-ligating cysteines. Moreover, analyses of reported missense mutations in patients with *SDH*-RCC or GIST revealed that 50% of these patients had *SDHB* mutations in the L(I)YR motif amino acid residues (52). Altogether, these observations point to a central role of Fe-S clusters loss in *SDHB*-related disease, which are further reinforced by our present observations.

This labile iron overload may in turn be responsible for or exacerbate the overproduction of ROS observed in *Sdhb*^{-/-} cells, thereby indirectly activating pseudohypoxia and DNA methylation. Indeed, it has been previously demonstrated in a number of studies that in the context of excessive ROS levels,

these oxidant molecules can act as signals able to trigger the stabilization of HIF α transcription factors in normoxic conditions (53–55; 34). Besides, in the present study we show that the use of MitoTEMPO, a mitochondrially targeted antioxidant at low concentrations led to a significant decrease in mitochondrial ROS, resulting in turn in reduced HIF2 α levels. Conversely, high doses of MTT appear to exert a pro-oxidant action leading to increased cytosolic ROS in all of the cell types, resulting in a strong pseudohypoxic response. Altogether, these results demonstrate the direct link between ROS and HIF2 α stabilization and suggest that the elevated ROS levels observed in *Sdhb*^{-/-} cells are probably responsible for their stronger pseudohypoxic phenotype. The association between SDH-deficiency and ROS production has been controversial, with some studies showing an increase in ROS levels (28,53) and others not (56). Actually, these apparently contradictory data are in total accordance with our observations. Indeed, Selak *et al* first reported the absence of oxidative stress following SDH inactivation, but this was observed in an *SDHD* KD cell model (56). In contrast, Guzy et al. proposed that the mechanism explaining PPGL tumorigenesis following SDH inhibition was an increase in ROS production, acting as messengers able to activate pseudohypoxic responses and probably resulting in oxidative damage to DNA, genomic instability, and tumorigenesis (53). In that study, an *Sdhb*-Knock Down (KD) model was compared to a *Sdha*-KD one, and ROS increase was only observed in *Sdhb* KD cells. At that time, it was suspected that *SDHA* gene mutations were not associated with PPGL, an assumption that we demonstrated to be untrue several years later (3). Based on these observations, their conclusions were that loss of all but the SDHA subunits of SDH would produce such increase in ROS production, explaining SDHB/C/D-mediated tumorigenesis. In view of the actual knowledge on SDH genetics, the combination of these data with our current observations suggests that ROS production is a specific feature of *SDHB*-mutated cells, and may be responsible, not for SDH-related tumorigenesis in general, but for SDHB-related aggressive phenotype.

Our data suggest that the increased oxidative stress observed in *Sdhb*-deficient cells could be the consequence of the dysregulated iron/copper homeostasis. Indeed, redox-active iron strongly interacts with hydrogen peroxide through the Fenton/Haber-Weiss reaction. This usually slow reaction

is catalyzed by labile iron, yielding mainly the highly reactive and toxic hydroxyl radical ($\bullet\text{OH}$) from hydrogen peroxide (H_2O_2) and superoxide ions ($\bullet\text{O}_2^-$): $\text{Iron(III)} + \bullet\text{O}_2^- \rightarrow \text{Iron(II)} + \text{O}_2$; $\text{Iron(II)} + \text{H}_2\text{O}_2 \rightarrow \text{Iron(III)} + \text{OH}^- + \bullet\text{OH}$ (57). Oxidative damage arising from excessive levels of ROS are observed in a variety of pathologies such as neurodegenerative diseases and cancer, and have been linked to malignant transformation, together with an imbalance in iron homeostasis(58). Similar assumptions can be made for copper (59). Our results are also consistent with a recent study demonstrating the role of histone H3-H4 as a copper reductase enzyme that binds Cu(II) and catalyzes its reduction to Cu(I). They showed that active H3-H4 is required for proper utilization of copper for mitochondrial respiration and SOD function. Thereby, the excess of mitochondrial Cu(I) observed here predominantly in *Sdhb*^{-/-} imCC suggests a greater inactivation of H3-H4 and thereby may explain the inhibition of *Sod2* expression and the mitochondrial respiratory deficit observed following *Sdhb*-deficiency (60). In addition, the lack of ROS changes observed in *Sdhb* KO cells might be associated with a residual activity of Complex II in *Sdhb* KO cells. Indeed, while changes in SDH activity coupled to complexes I and III have been shown in a number of different systems to generate ROS, SDH itself has also been suggested to generate ROS when electron flow is compromised (61). It was recently suggested that cells lacking SDHB maintain some form of SDH subunit-containing complex (62), which maintains some level of activity. Although we have no data to validate this hypothesis, one could hypothesize that SDHB-deficient cells can generate ROS due to the retention of an 'SDH-like' complex, while SDHD-deficient cells avoid this through complete loss of SDH.

In this regard, our findings are consistent, although different, with those recently proposed by Liu *et al* (63). Using an *Sdhb* KD cell model, these authors also describe ROS accumulation associated with an increase in the intracellular labile iron pool. Surprisingly, these authors observed an increase in iron pool using the calcein probe while in our model, and in human PPGL, this experiment actually showed a decrease in *Sdhb* KO cells. A possible explanation stands in the fact that the model used in the current study is, as the human PPGL studied, a true genetic KO with no SDHB expression, while the model used by Liu *et al* is a KD in which 30% of SDHB protein expression remains. Hence, these different

models point to similar pathways, but with major differences in the adaptive responses of the cells. Indeed, Liu *et al* propose that the iron overload would be due to increased expression of TF and TFR2, while, as previously mentioned such overexpression was not observed in our model. We did observe a slight increase in TF mRNA levels in SDH tumors as compared with other types of mutated PPGL, but not in TFR2. However, in both cases, levels of expression were actually extremely low in all PPGLs and therefore probably not biologically relevant (Supplementary Fig. 4). Furthermore, these authors showed in the same model, that anti-oxidant responses were increased following *SDHB* KD, notably through the upregulation of the nuclear factor erythroid 2-related factor 2 (NRF2). We did not observe any activation of neither the NRF2 pathway nor superoxide dismutase (SOD) activity in any of our different cell types and these data were further validated by our analysis of the transcriptome of human PPGL. Besides, N-acetyl cysteine (NAC) treatment, an inhibitor of the NRF2 pathway, had no effect on the production of mitochondrial ROS by *Sdhb*^{-/-} cells. Hence, it is quite interesting to notice that although similar pathways seem to be affected in the *Sdhb* KO and KD cells (i.e. iron homeostasis, oxidative stress), it seems that the mechanisms and the adaptive responses involved are not similar.

Collectively, these data demonstrate that cells carrying a complete abolition of *Sdhb* gene are not able to neutralize the oxidative damage caused by the mitochondrial ROS excess, through the up-regulation of any intrinsic anti-oxidant pathway. Since, ROS generation seems to be a critical hallmark of SDHB loss, testing an antioxidant treatment that could be used for clinical purposes on our *Sdhb*^{-/-} model appeared relevant. Ascorbate offers many assets, as it presents few side effects in healthy tissues, even at pharmacological concentrations and is easy to access. However, although at physiological concentration (micromolar), ascorbate acts as an antioxidant, able to decrease ROS levels (64), it has been shown to have pro-oxidant actions when reaching high concentrations (65). In addition to its strong oxidative role, ascorbate also affects iron homeostasis, as it reduces ferric iron (Iron(III)) in a cycle of reactions leading to the fully oxidized form of ascorbate (DHA), ferrous iron (Iron(II)) and eventually resulting in increased intracellular ROS levels (66,67). Therefore, in a context of redox imbalance associated with an elevated pool of labile iron, ascorbate treatment could lead to

unbearably high ROS levels for the cells and thus aggravate an existing oxidative stress burden. Use of ascorbic acid at pharmacologic concentrations was already suggested as a promising therapeutic strategy on various types of tumor cells exhibiting increased ROS levels, increased labile iron and metabolism impairments (58). All the more that, for the past few years many studies have demonstrated the efficacy of ascorbate as an anticancer treatment, killing cancer cells *in vitro* (68,69) and slowing tumor growth *in vivo* (70). In compliance with these reports, our data reveal that high-dose ascorbate treatment led to a higher accumulation of ROS solely in the mitochondria of *Sdhb*^{-/-} imCC, resulting promptly in cell death, thus validating the increased sensitivity of *Sdhb*^{-/-} cells for ascorbate, mediated by ROS overload. Interestingly, Liu *et al* also recently reported that ascorbate treatment increased apoptosis in *SDHB* KD cells *in vitro* and delayed the growth of tumors as well as of hepatic lesions in xenografted mice models *in vivo* (70). Numerous clinical trials are currently evaluating the efficacy of intravenous high-dose pharmacological ascorbate injection for treating different cancer types (67,71). In that context, ascorbate intravenous injections at pharmacological doses appear as a worthy and highly promising therapeutic strategy to treat SDHB-deficient malignancies, which often exhibit a poor answer to current treatments strategies (radiotherapy, chemotherapy, targeted therapy) and could also be tested in combination with other therapies.

Overall, the comprehensive comparison of the first relevant *Sdhb* and *Sdhb* knock-out cellular models, reveals the common and distinctive pathways used by these cells to adapt to these deficiencies, and highlight specific hallmarks associated with *Sdhb* mutations. Lifting the veil on a long-lasting question, we show that *Sdhb*-deficient cells exhibit stronger PHD and TET inhibition than their *Sdhb*-deficient counterparts, explaining their aggressive phenotype and mesenchymal morphology. We demonstrate that *Sdhb*^{-/-} imCC manifest a significantly exacerbated imbalance in copper and iron homeostasis resulting in an increased labile iron pool, associated with significant ROS accumulation. High-dose ascorbate treatment of *Sdhb*^{-/-} imCC offers promising results, as it highly aggravated the oxidative stress burden endured by *Sdhb*-deficient cells, thus rising as a potential original therapeutic approach to treat malignant PPGL.

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Author contributions

J.F., E.L. and D.A.T conceived the study. J.G., A.M., G.G., S.M., C.L.A. designed and performed the experiments, and analyzed the data. S.Mo., K.K., A.P.M., T.J.S., C.L-L., P.B. and A.T. performed the experiments and analyzed the data. J.F., D.A.T., E.L., F.M-G. and R.R. designed the experiments and analyzed the data. J.F. and A-P.G-R. supervised the study. J.F. and J.G. contributed to the management of the project, wrote the manuscript and prepared the figures. E.L. and D.A.T. contributed to the preparation of the manuscript. All the authors discussed the results and reviewed the manuscript.

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Figure legends

Fig. 1 Generation of *Sdhb*-deficient immortalized mouse chromaffin cells. **A**, Electrophoregrams of Sanger sequencing of the exon 3 of *Sdhb* gene showing both homozygous point mutations c.119delC and c.120_121delCA of CIA and CLB respectively compared to a control DNA (WT). **B**, Western-blot showing SDHB protein expression in all cell types. **C**, Spectrophotometrical measurement of SDH activity. Steady-state assessment of TCA cycle organic acids (**D**, succinate, **E**, fumarate and **F**, α -ketoglutarate). Results shown are from at least three independent experiments, presented as mean $\pm$ SEM. In **C-F**, One-way ANOVA was used to assess statistical significance. ns, not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Fig. 2 Metabolic and respiratory profiles of *Sdhb*-deficient imCC and *Sdhb*^{-/-} cells. **A**, Diagram describing the incorporation of carbons from glucose through PDH (blue) or PCX (red) enzymes activity. Abbreviations in metabolic diagram: PDH, pyruvate dehydrogenase; PCX, pyruvate carboxylase; AcCoA, acetyl coenzyme A. **B**, Incorporation of ^{13}C into succinate, aspartate and citrate in stated cell lines. Isotopomers ^{13}C atoms are shown as filled circles, whereas ^{12}C atoms are empty circles. **C**, Incorporation of $^{13}\text{C}_5$ -glutamine into succinate, aspartate and citrate in indicated cell lines and **D**, the associated diagrammatic representation of their oxidative (blue) and reductive (red) metabolism. **E**, Oxygen consumption (respiration) of intact and **F**, permeabilized (CI + CII) cells. ETS refers to electron transfer system capacity and basal respiration to oxygen consumption in non-permeabilised cells. **G**, Lactate production over time. Results shown are from at least three independent experiments, presented as mean $\pm$ SEM. Two-way ANOVA was performed; ns, not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$ relative to WT and \$ $P \leq 0.05$, \$\$\$ $P \leq 0.001$ relative to *Sdhb*^{-/-} imCC.

Fig. 3 *Sdhb*, but not *Sdhb* knockout in mouse chromaffin cells initiates a mesenchymal phenotype associated with stronger 2OG-dependent dioxygenases inhibition. **A**, Actin staining in the indicated cell lines. **B**, qRT-PCR analysis of known epithelial-to-mesenchymal markers (*Snai1*, *Mmp9*, *Fn1*). **C**, Quantification of cell adhesion 1h after plating. **D**, Collective migration assessed after 10h in the stated cell lines, represented as the closure percentage of the wound. **E**, Scatterplot representative of

methylation rates identified by RRBS in *Sdhb*^{-/-} versus WT cells and *Sdhb*^{-/-} versus WT cells, respectively. **F**, number of differentially methylated features in *Sdhb*^{-/-} and *Sdhb*^{-/-} imCC (versus WT) in TSS500 and gene body regions. **G**, Comparison of methylation changes generated by *Sdhb* and *Sdhb* knockout in imCC. **H**, Number and overlap of differentially methylated features in *Sdhb*^{-/-} compared with *Sdhb*^{-/-} imCCs. **I**, Western blot of HIF2 α in total cellular extracts of indicated cell lines. **J**, Heatmap representation of transcriptome-based classification of imCCs according to their genotype resulting in hierarchical clustering. **K**, Number and overlap of overexpressed hypoxia-inducible genes from a selected list of 47 genes in *Sdhb*^{-/-} and *Sdhb*^{-/-} imCCs compared with WT cells. **L**, Relative expression levels of overexpressed hypoxia-inducible genes in *Sdhb*^{-/-} and *Sdhb*^{-/-} imCCs compared with WT. In **A**, **B**, **C**, **D** and **E** data shown are from at least three independent experiments, presented as mean $\pm$ SEM. **K** and **L** data are mean expression levels from RNAseq data generated in 3 *Sdhb*^{-/-}, 2 WT and 2 *Sdhb*^{-/-} clones. One-way ANOVA was used to assess statistical significance; ns, not significant, **P $\leq$ 0.01, ***P $\leq$ 0.001 relative to WT and \$\$\$P $\leq$ 0.001 relative to *Sdhb*^{-/-} imCC.

Fig. 4 SDH-deficient cells exhibit significant alterations in iron homeostasis, notably marked in *Sdhb* KO cells. **A**, Flow cytometry analysis of labile overall iron content in each cell line. **B**, Representative ⁵⁶Fe images generated by LA-ICP-MS in one *NF1*-mutated human pheochromocytoma **C**, one *SDHB*-mutated pheochromocytoma **D**, one *SDHB*-mutated paraganglioma and **E**, one *SDHD*-mutated paraganglioma. Images are displayed using the same threshold to enable a direct visual comparison between tumor sections. Average ⁵⁶Fe counts in 2 *NF1*, 2 *RET*, 4 *SDHB* and 2 *SDHD* tumors are shown in **F**. **G**, Cytosolic Iron(II) content, **H**, mitochondrial Iron(II) content. **I**, Heatmap representation of the expression profiles of several critical actors of iron/copper homeostasis in *Sdhb*^{-/-}, WT and *Sdhb*^{-/-} cells, using mean level values to perform unsupervised classification. **J**, Diagram highlighting the role played by some iron and copper transporters (*DMT1*, *Slc25a37*, *CTR1* and *Slc25a3*) explaining the major alterations induced by *Sdhb* KO in their iron and copper cellular homeostasis. Data shown in **A**, **G** and

H are from three independent experiments, presented as mean $\pm$ SEM. Non-parametric one-way ANOVA was used to assess statistical significance; ns, not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Fig. 5 SDHB-deficient cells display increased ROS levels without activation of the NRF2 pathway.

A, Specific MFI using CellROX probe in all imCC cell types. Similar assays were carried out using **B**, Mitosox **C**, Bodipy C11 probe **D**, TMRM and **E**, Mitotracker probes. **F**, RNA-seq analysis showing the mRNA levels of the different forms of superoxide dismutase (cytoplasmic SOD1, mitochondrial and extracellular SOD3) and catalase. **G**, Specific MFI of MitoSOX probe in all imCC models following N-acetyl-cysteine (NAC) treatment (3 mM) for 48h. **H**, Cell survival percentage of indicated cell lines after treatment with 3 mM of NAC in comparison to vehicle-treated controls for 48h. **I**, Heatmap representation of the expression of 58 NRF2-target genes through the transcriptome data of the COMETE collection of human PPGL. Mean values of NRF2 targets levels in the groups of sporadic non-mutated tumors (n=49), *RET*- (n=19), *NF1*- (n=37), *VHL*- (n=40), *SDHA*, *C*, *D*- (n=6) and *SDHB*-mutated tumors (n=17) were used to perform unsupervised classification. Data shown in **A**, **B**, **C**, **D** and **E** each dot is representative of an independent experiment (n=4), bar plots show means $\pm$ SEM. One-way ANOVA was used to assess statistical significance; ns, not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$ relative to WT and \$ $P \leq 0.05$ relative to *Sdhb*^{-/-} imCC. In **G** and **H** results shown are from at least three independent experiments and presented as means $\pm$ SEM. To assess statistical significance in **F**, **G** and **H**, Two-way ANOVA was used; ns, not significant, * $P \leq 0.05$, *** $P \leq 0.001$.

Fig. 6 Modulation of Iron(II) and ROS levels affects HIF2 α stabilization and survival in Sdhb-deficient

cells. A, Specific MFI of MitoSOX probe in all imCC models following treatment for 48h with either Iron(II) 50 μ M or vehicle. **B**, Western blot of HIF2 α in total cellular extracts of *Sdhb*^{-/-} imCCs not-treated (NT) or treated for 48h with Iron(II) (Fe²⁺). **C**, Dose-response curves showing cell survival of all cell types following 48h of treatment with Iron(II). **D**, Specific MFI of CellROX probe in all imCC models following treatment for 12 hours with MitoTEMPO (MTT) 2.5 μ M in comparison to NT cells. **E**, Same as **D**, using

937 MitoSOX probe. **F**, Western blot of HIF2 α in total cellular extracts NT or treated for 12h with 2.5 μ M
938 MTT. **G**, Same as **D**, after treatment with MTT 2.5 mM. **H**, Same as **G**, using MitoSOX probe. **I**, Same as
939 **F**, after treatment for 12h with 2.5 mM MTT. **J**, Cell morphology following treatment for 12h with MTT
940 2.5 mM. **K**, Same as **C** following Ascorbate treatment. **L**, Time-response curves showing cell survival of
941 all imCC models after treatment with 2.5 mM ascorbate. **M**, Specific MFI of MitoSOX probe in all imCC
942 models following treatment for 48h with either ascorbate 1mM or vehicle. Data for **C**, **K**, and **L** are all
943 relative to vehicle-treated controls and presented as means $\pm$ SEM (n = 3 independent experiments,
944 with 3 technical replicates/experiment). Data from **A**, and **M** are mean of at least three independent
945 experiments and data from **D**, **E**, **G**, and **H** are mean of at least two independent experiments. Data are
946 presented as mean $\pm$ SEM and two-way ANOVA was performed; ns, not significant, *P $\leq$ 0.05,
947 ***P $\leq$ 0.001.
948

Figure 1

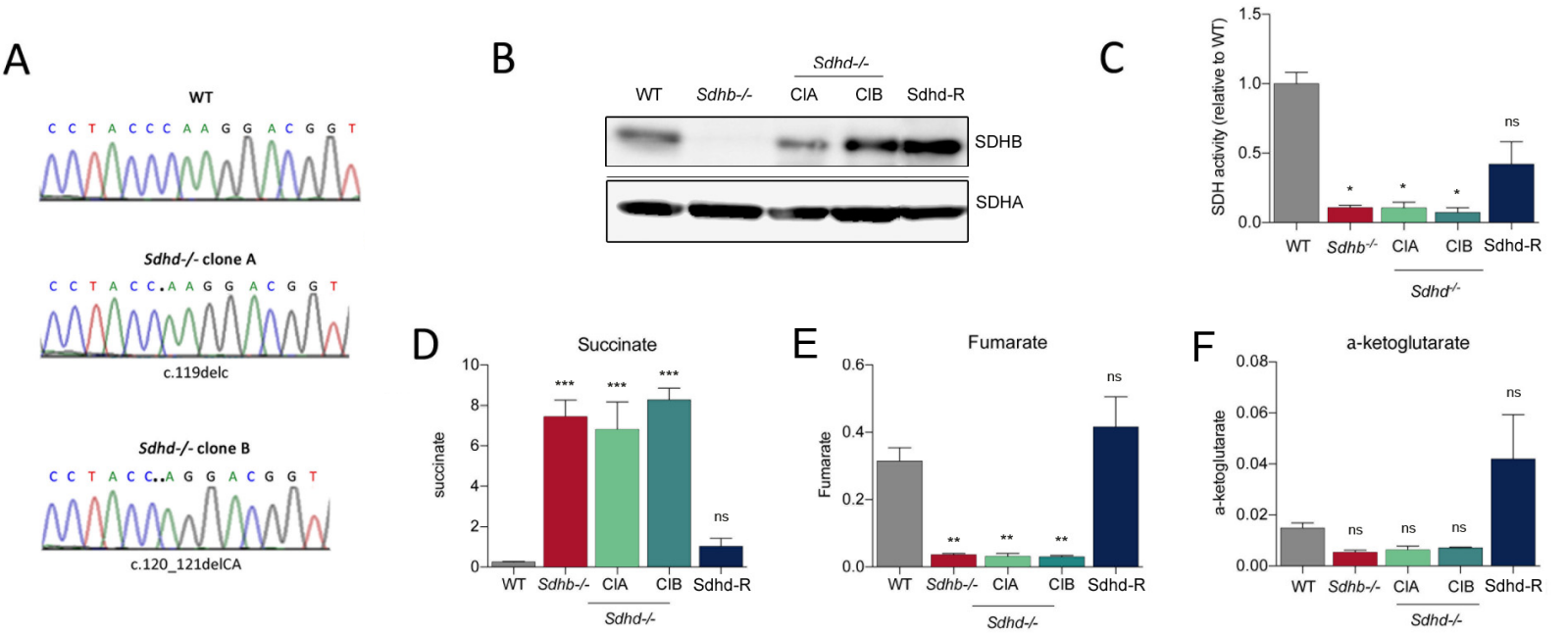


Figure 2

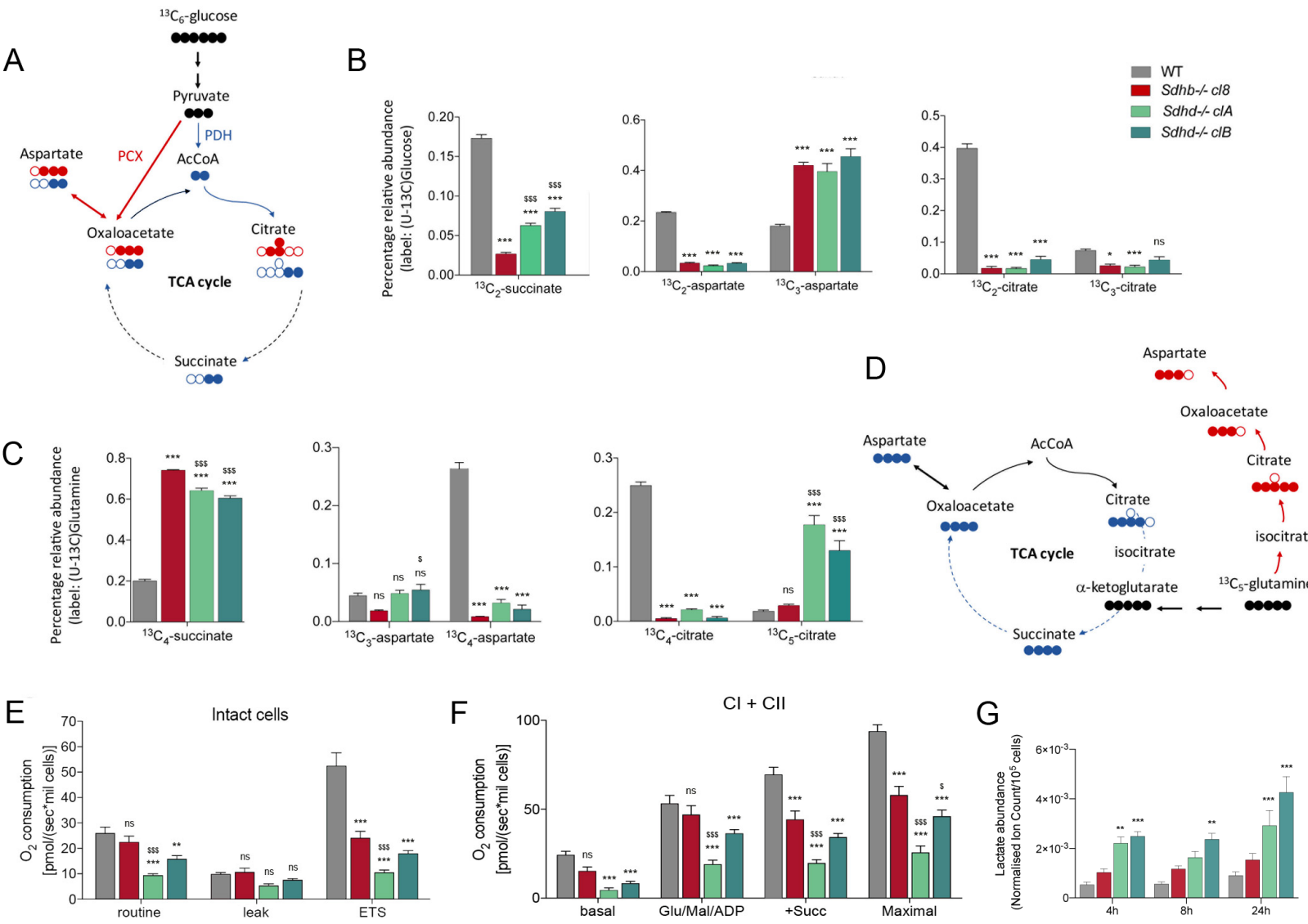


Figure 3

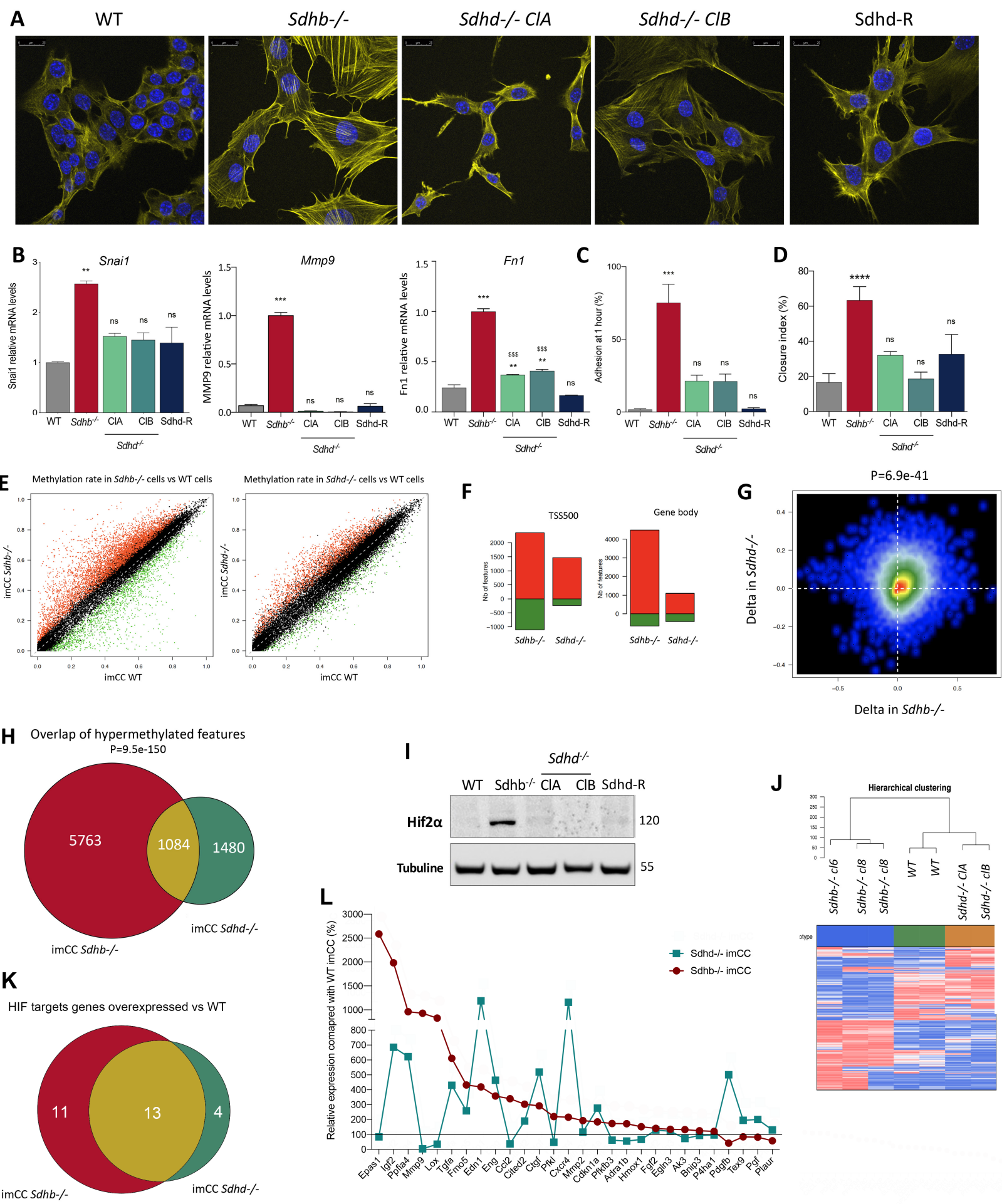


Figure 4

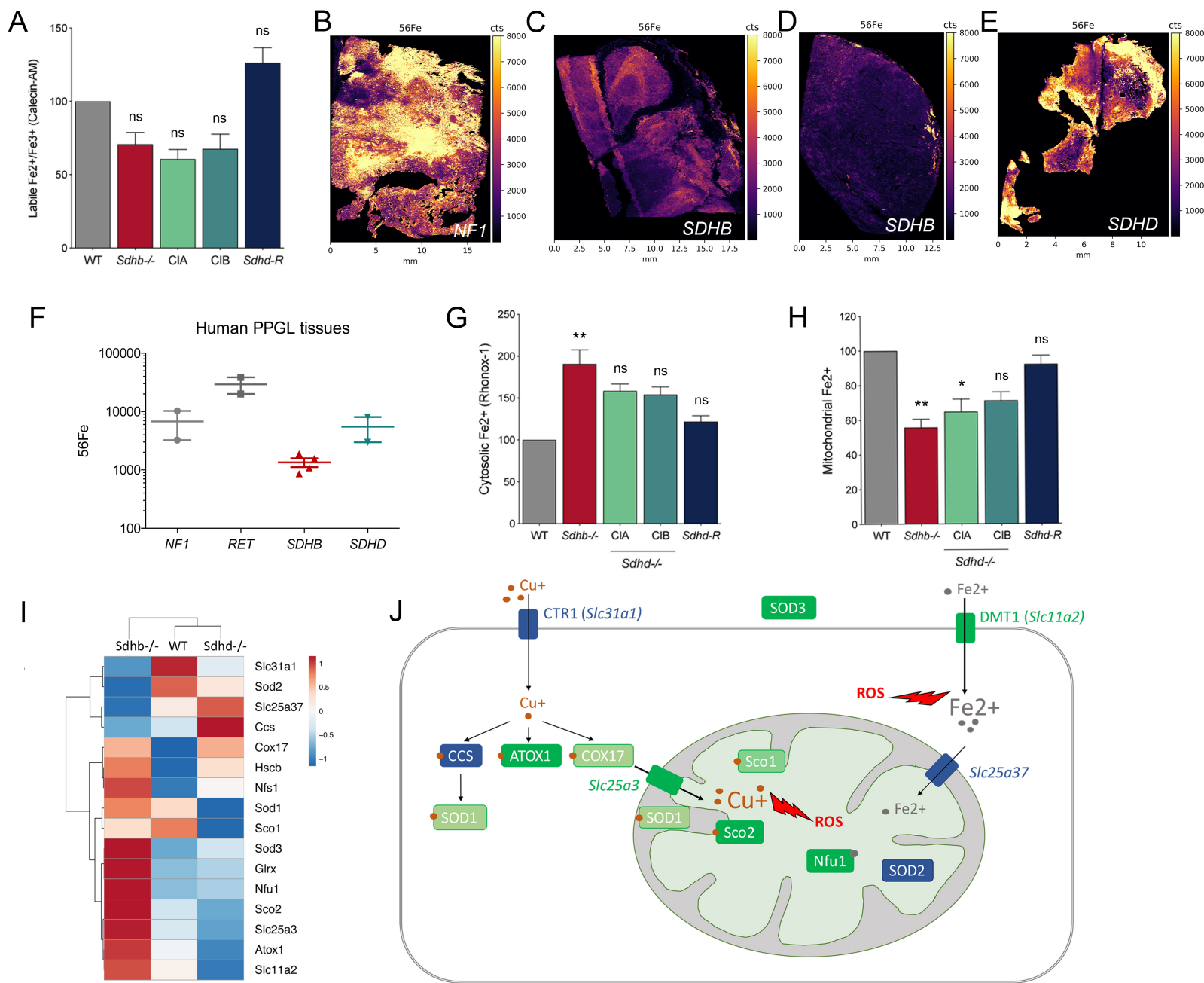


Figure 5

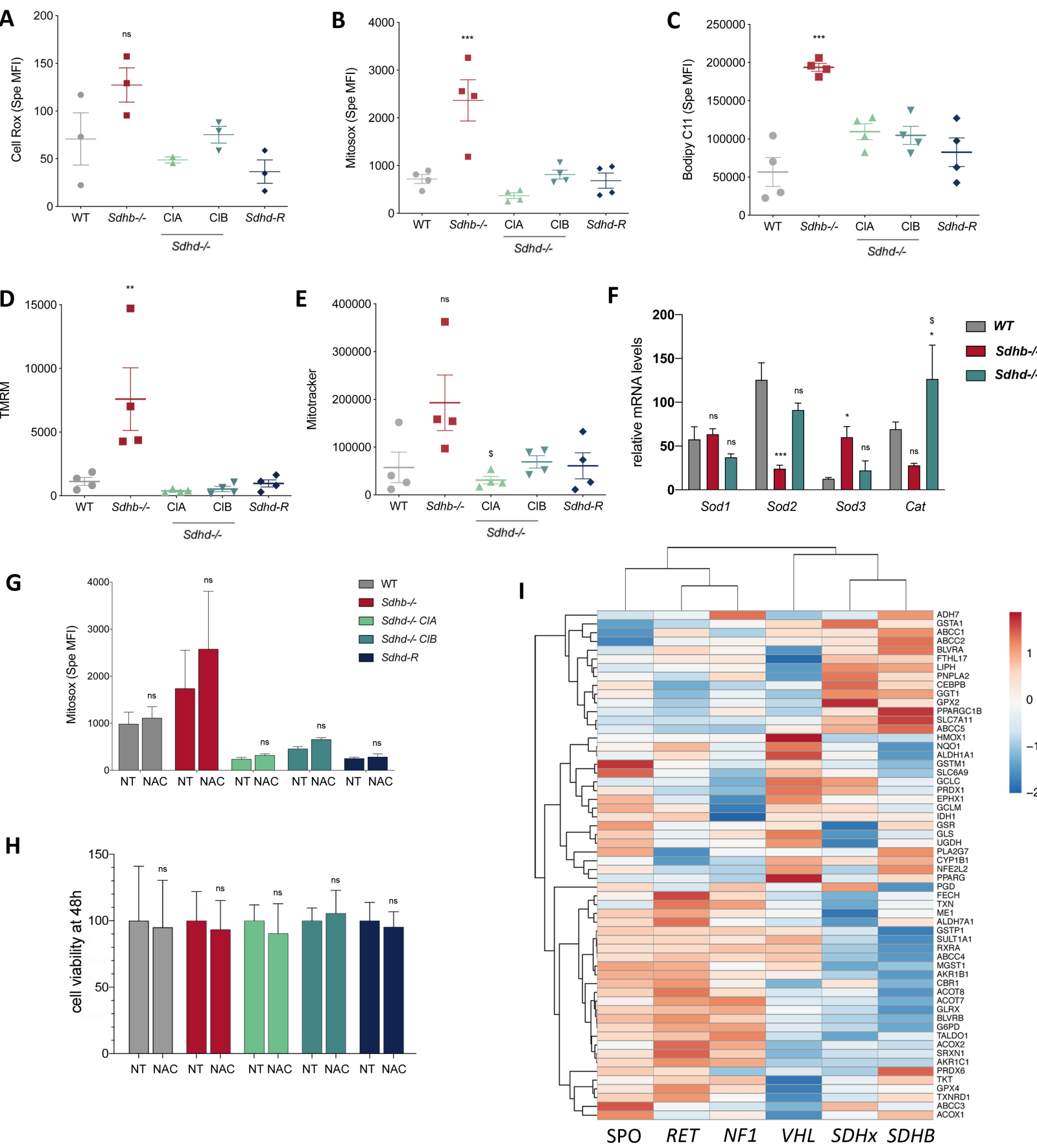
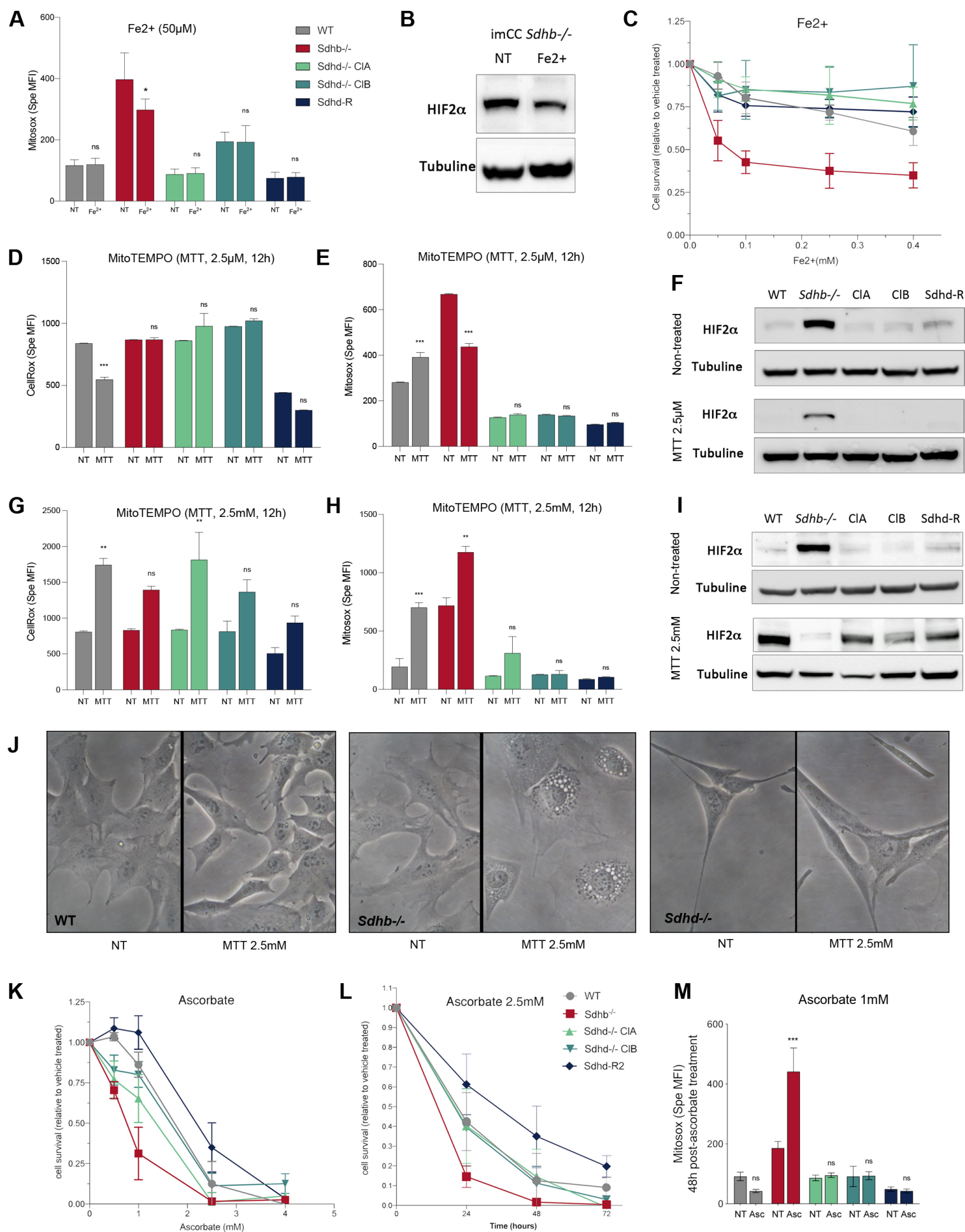


Figure 6



1 Loss of SDHB promotes dysregulated iron homeostasis, oxidative
2 stress and sensitivity to ascorbate.

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33
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Abstract

Succinate dehydrogenase is a key enzyme in the tricarboxylic acid cycle and the electron transport chain. All four subunits of succinate dehydrogenase are tumor suppressor genes predisposing to paraganglioma, but only mutations in the SDHB subunit are associated with increased risk of metastasis. Here we generated an *Sdhb* knockout chromaffin cell line and compared it to *Sdhb*-deficient cells. Both cell types exhibited similar SDH loss of function, metabolic adaptation, and succinate accumulation. In contrast, *Sdhb*^{-/-} cells showed hallmarks of mesenchymal transition associated with increased DNA hypermethylation and a stronger pseudo-hypoxic phenotype compared to *Sdhb*^{-/-} cells. Loss of SDHB specifically led to increased oxidative stress associated with dysregulated iron and copper homeostasis in the absence of NRF2 activation. High-dose ascorbate exacerbated the increase in mitochondrial reactive oxygen species, leading to cell death in *Sdhb*^{-/-} cells. These data establish a mechanism linking oxidative stress to iron homeostasis that specifically occurs in SDHB deficient cells and may promote metastasis. They also highlight high-dose ascorbate as a promising therapeutic strategy for SDHB-related cancers.

Statement of significance

Loss of different succinate dehydrogenase subunits can lead to different cell and tumor phenotypes, linking stronger 2-OG-dependent-dioxygenases inhibition, iron overload, and ROS accumulation following SDHB mutation.

Introduction

Succinate dehydrogenase (SDH) is a key enzyme localized in the inner mitochondrial membrane where it participates both in the tricarboxylic acid (TCA) cycle and the electron transport chain (ETC), as complex II. In the TCA cycle, SDH catalyzes the oxidation of succinate into fumarate while in the ETC, it allows the transfer of electrons from succinate to the ubiquinone pool. SDH is constituted of two anchoring subunits (SDHC, SDHD) and two catalytic subunits (SDHA, SDHB) encoded by the four *SDHx* nuclear genes (*SDHA*, *SDHB*, *SDHC* and *SDHD*). SDHA is a flavoprotein to which the substrate succinate binds in order to be oxidized to fumarate, while the resulting electrons are channeled to ubiquinone, through the three Fe-S clusters of SDHB. Since the initial discovery of *SDHD* mutations in 2000(1), all four *SDHx* genes have been demonstrated to act as tumor-suppressor genes (2,3,4). Their mutations predispose to pheochromocytoma and paraganglioma (PPGL), rare neuroendocrine tumors arising from chromaffin cells of the adrenal medulla and from the sympathetic and parasympathetic nervous systems, respectively; as well as gastro-intestinal stromal tumors (GIST) and rare forms of renal cell carcinomas. It is now estimated that mutations in *SDHx* genes stand for almost 50% of inherited cases of PPGL. Interestingly, *SDHB* mutations have been shown to be the highest risk factor of malignancy in patients with PPGL: approximately 50% of PPGL patients carrying *SDHB* mutations will ultimately develop a metastatic form of the disease and a germline mutation in *SDHB* is found in up to 36% of all metastatic PPGL cases (5). In contrast, metastatic forms of the disease are found in only 5% of patients with an *SDHD* gene mutation. Moreover, *SDHB* mutated cancers are more aggressive than non-mutated metastatic ones. The overall survival of patients with metastatic *SDHB*-related PPGL was initially estimated at 42 months after diagnosis of the first metastasis versus 244 months for patients with a metastatic PPGL but without an *SDHB* gene mutation (6). Interestingly, recent studies have revealed that increased follow-up of patients with genetically determined PPGL has significantly improved their survival, demonstrating the beneficial impact of genetic testing in these patients (7,8).

In all cases, germline *SDHx* mutations are associated with loss of heterozygosity, which causes the complete loss of SDH function in the tumor (9) and a subsequent accumulation of its substrate, succinate (10). Succinate (as other TCA cycle intermediates such as fumarate and 2-hydroxyglutarate) is considered as an oncometabolite, driving aberrant activation of transcription factors and global epigenetic reprogramming. Indeed, high steady-state levels of these metabolites are known to inhibit 2-oxoglutarate (2-OG) dependent dioxygenases, such as the hypoxia-inducible transcription factor (HIF) prolyl-hydroxylases (PHDs) and Ten-eleven translocation (TET) DNA demethylases (11). These enzymes belong to the large family of iron (Fe) and 2-OG-dependent dioxygenases, which activity is based on the use of iron (12), oxygen (13) and ascorbate (14) as main co-factors. Inhibition of PHDs promotes the abnormal stabilization, and thus activity of HIF1 and HIF2, while TET inhibition leads to a lack of DNA demethylation, resulting in pseudo-hypoxic and hypermethylator phenotypes, respectively. These observations were initially revealed in genomic studies performed on large PPGL tumor collections, resulting in a better understanding of the mechanisms of SDH-related tumorigenesis. In these studies, all *SDHx* and *FH* mutated tumors clustered together, showing a transcriptome signature characterized by activation of the hypoxic response pathway (2, 15, 16) and a DNA hypermethylator phenotype (17). Despite this apparent homogeneity, some differences have emerged suggesting that *SDHB*-mutated tumors may display a particularly marked hypermethylator phenotype associated with hallmarks of neuroendocrine-to-mesenchymal transition (NMT), which were not observed in other types of *SDHx*-mutated cases (i.e *SDHA*, *SDHC* and *SDHD* mutated)(18). In order to decipher these mechanisms at the cellular level, we have generated an immortalized mouse chromaffin cell (imCC) line knocked-out for the *Sdhb* gene (17). In these cells, we showed that *Sdhb*-deficiency does promote a marked hypermethylator phenotype mediated by TET1 and/or TET2 blockade, which acts in synergy with HIF2 activation to promote NMT and metastatic dissemination (19, 20). *Sdhb*^{-/-} cells also undergo significant metabolic reprogramming becoming critically dependent on aspartate synthesis as a major source of carbon for anabolic purposes, which supports their viability and proliferation, maintained mainly through reductive carboxylation (21).

Despite these important advances in the understanding of the oncogenic consequences of SDHB loss of function, the exact cause of the metastatic phenotype of *SDHB*-related tumors remain mostly unexplained. *SDHA* and *SDHC* mutations are rare in PPGL patients, probably because of low penetrance of the disease in mutation carriers. In contrast, *SDHB* and *SDHD* are the most frequently described mutations in PPGL, with an incidence of 8-10 and 5-7% among all PPGL cases, respectively (22). Genotype-phenotype correlation studies performed in patients with *SDHB* or *SDHD* mutations have undoubtedly demonstrated their different clinical behavior in terms of invasiveness. To address this crucial question in the field, we have generated *Sdh*d knocked-out cell lines in the imCC model. In this new and unique model, we have investigated the different pathways previously identified in SDH-related tumors in order to identify the specificities that may explain their different clinical behavior.

Materials and Methods

Detailed methods are provided in the Supplementary Information section.

*Sdh*d KO, *Sdh*d-rescue cell generation and cellular analysis

Complete knock-out of *Sdh*d gene was achieved in immortalized mouse Chromaffin Cells (imCC) by transfecting Wild-Type imCC, previously generated by our lab (17), with *in silico* designed targeted gRNA, using the PrecisionX Cas9 SmartNuclease RNA system kit (System Biosciences). *Sdh*d-rescue clones were established by transfecting *Sdh*d^{-/-} imCC with an SDHD-expressing vector (ORIGENE, NM003002). Screening of these clones was performed by SDH activity test, qRT-PCR and direct sequencing of the *Sdh*d gene by Sanger method. Cells used for experiments were maintained in DMEM high glucose Glutamax (Gibco) unless when grown for metabolic or respirometry experiments (see Supplementary Information). Wound scratch assays, proliferation and adhesion tests were performed to assess cellular phenotype. When stated, cells were treated with indicated doses of iron

Chloride (Sigma), MitoTEMPO (Sigma), L-Ascorbic acid (Sigma), Talazoparib (MedChemTronica) or N-acetyl-cysteine (Sigma).

RNA-seq and RRBS data analysis

RNA sequencing was performed for 7 samples: 3 *Sdhb*^{-/-}, 2 *Sdhd*^{-/-} and 2 WT imCC. Enriched samples were used to generate sequencing libraries with the Illumina 'TruSeq Stranded mRNA Sample Prep' kit and associated protocol provided by the manufacturer. Libraries were sequenced by IntegraGen (Evry, France) on an Illumina HiSeq 2000 as paired-end 75 bp reads. Reduced Representation Bisulfite Sequencing (RRBS) was also performed by Integragen SA, as previously described (17). **Details of the process leading to the evaluation of differential expression and methylation rates are provided in the Supplementary Information.** The sequencing data reported in this paper have been deposited to the EGA (European Genome-phenome Archive) database (European Genome-phenome Archive) database (accession number EGAS00001005279).

Metabolite analysis, high resolution respirometry, enzymatic activities and features of oxidative stress assessment

All cell types underwent metabolite extraction using Methanol:H₂O:Chloroform at ratio 1:1:1, following ¹³C-glucose and ¹³C-glutamine labeling. The polar fractions were used for Gas Chromatography – Mass Spectrometry (GC-MS) analysis allowing acquisition of the isotope data. High resolution respirometry was performed by loading Intact or permeabilized cells in an Oxygraph-O2 k (Oroboros instruments) chamber, using Mir05 respiratory media and digitonin for the latter. A pseudo dual-wavelength Varian CARY50 spectrophotometer (Victoria, Australia) was used to assess respiratory chain activities as previously described (23). For the assessment of oxidative stress

features, cells treated as stated, were incubated with either CellRox, MitoSox or Bodipy C11 Reagent (Termofisher) and Flow cytometry data were acquired using an LSR FORTRESSA analyzer (BD biosciences).

Cellular and tumoral iron and copper analysis

For cellular iron and copper assessment, cells were incubated with the relevant metal-specific probe prior to being analyzed by flow cytometry on a BD Accuri C6 (BD Biosciences). Laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) was performed on dewaxed and rehydrated formalin-fixed paraffin-embedded tumor sections. **Details of LA-ICP-MS experiments are provided in the Supplementary Information.** LA-ICP-MS images were acquired in a fixed dosage mode, with a vertical and horizontal spatial resolution of 20 μm , a detailed list of sample settings is available in Supplementary Table 1. Average ^{56}Fe and ^{63}Cu intensities were calculated from pixels containing a positive elemental tissue marker (^{31}P) ensuring background regions did not influence these calculations.

qRT-PCR, Western-blot, immunofluorescence staining and immunohistochemical analyses

For qRT-PCR, total mRNA was extracted from cell pellets using RNeasy plus mini-kit (Qiagen). Reverse transcription was fulfilled using iScriptTM cDNA Synthesis Kit (BIO-RAD) and qRT-PCR was performed on CFX96TM Real-Time System C1000 TouchTM Thermal Cycler (BIO-RAD) using SuperScript SybrGreen (BioRad) to assess the expression of *Sdhb*, *Sdhb*, *Snai1*, *Fn1*, *Epas1*, *MMP9* and *18S*. Western-blot analysis were performed to assess SDHB, SDHA, HIF2 α and TUBULIN expression. RIPA lysis buffer was used for extraction of total protein and concentrations were determined with Bradford colorimetric method. Results were read with a LAS-4000 Mini (Fuji). Actin staining and γH2AX

immunofluorescence were performed on cells plated on glass slides, while γ H2AX immunohistochemistry was performed on 6 μ m sections from paraffin-embedded tumors. **Details of primers, primary and secondary antibodies, immunostaining, and experimental conditions are provided in the Supplementary Information.**

Data analysis

Data are represented as mean (of at least 3 independent experiments) $\pm$ SEM (standard error of the mean). Data were analyzed by one-way or 2-way ANOVA. Statistics tests were carried out using the GraphPad Prism software. All analyses considered a value of $P \leq 0.05$ to be statistically significant. For enrichment analysis, we used an in-house adaptation of the GSEA method to identify gene sets from the MSigDB database overrepresented among up/down-regulated and hyper/hypomethylated genes.

Results

Loss of SDHB or SDHD leads to similar metabolic dysfunction and respiratory profiles

To investigate the mechanisms underlying the metastatic characteristics of *SDHB* mutated-PPGL but not of *SDHD*-deficient tumors, we knocked-out the *Sdhd* gene using the CRISPR/Cas9 procedure in wild-type (WT) imCC (17). We obtained two independent *Sdhd*^{-/-} clones (CIA and CIB) each containing a different homozygous point mutation on exon 3 of *Sdhd*, c.119delC and c.120_121delCA, respectively, both leading to premature stop codons (Fig. 1A). These mutations were predicted to lead to the translation of truncated proteins of 79 and 68 amino acids, respectively, instead of the 159 amino acids of the entire WT SDHD protein. To attest for the absence of off-target effects in *Sdhd*^{-/-} cells, we generated a third cell line, in which SDHD loss was rescued by stably transfecting an *Sdhd*-expressing vector in the *Sdhd*^{-/-} CIA (clone *Sdhd*-R). *Sdhd*-mutated cells

showed a decrease in *Sdhb* RNA levels (Supplementary Fig. 1A) when compared with WT and *Sdhb-R* cells, which may be suggestive of nonsense-mediated decay in the mutant clones, and particularly in clone A.

SDHD protein expression could not be estimated due to the lack of efficient antibody in mouse. It is worth noting that *Sdhb* mRNA levels were also reduced in *Sdhb*-deficient cells. In contrast, *Sdhb* mRNA levels were absent in *Sdhb*^{-/-} cells, but not significantly reduced in *Sdhb*^{-/-} imCC (Supplementary Fig. 1B). It has previously been reported that disassembly of the SDH complex in case of *SDHx* mutations leads to the degradation of the SDHB subunit in all *SDHx* mutant cells (24). However, our data show that *Sdhb*^{-/-} clones retain a small but significant level of SDHB protein (Fig. 1B). Similarly, evaluation of SDHB protein by immunohistochemistry in SDH-related PPGL frequently leads to a weak diffuse signal in SDHD deficient tumors, while it is totally negative in SDHB-mutated ones, suggesting that some SDHB remains present in this type of mutants (25). Nevertheless, they exhibited a complete loss of SDH enzymatic activity, similar to that observed in *Sdhb*-deficient cells (Fig. 1C), and in accordance with observations in mutated human PPGL (9,26). Interestingly, it has previously been suggested that succinate accumulation might be less important in SDHD-deficient tumors, which may account for their different metastatic potential (27). Analysis of intracellular succinate levels revealed a substantial accumulation of succinate in *Sdhb*^{-/-} cells that reached that observed in the *Sdhb*^{-/-} imCC model (Fig. 1D). Similarly, levels of the related metabolites, fumarate and 2-oxoglutarate, were strongly reduced in all SDH-deficient cells regardless of the subunit inactivated. *Sdhb-R* cells showed a profile similar to that of WT imCC (Fig. 1E-F and Supplementary Fig. 1C, D).

Next, we assessed the metabolic and respiratory phenotypes of both types of SDH-deficient cells. ¹³C-glucose tracing experiments revealed that in accordance with previous work (21), cells deficient in SDH-activity undergo a metabolic rewiring in the absence of a fully functional TCA cycle (Fig. 2A). Like *Sdhb*^{-/-} cells, the synthesis of aspartate by *Sdhb*^{-/-} imCC cannot rely on oxidative TCA

cycle metabolism (Fig. 2B and C, m+2 isotopomer) and instead increase the aspartate produced through pyruvate carboxylation (PC) (Fig. 2B and C, m+3 isotopomer) for anabolic purposes. Equally, their synthesis of citrate from glucose, a central metabolite for cellular anabolism, was greatly reduced (Fig. 2B). The metabolism of another key nutrient, glutamine was therefore examined. Although both cell lines retain some oxidative metabolism of glutamine to produce succinate, *Sdhb*^{-/-} imCC appear to significantly increase their synthesis of aspartate and citrate using reductive carboxylation (Fig. 2C and D), which is not observed to the same degree in *Sdhb*^{-/-} imCC. We then measured oxygen consumption of intact and permeabilized imCC (Fig. 2E and F). In both cases, *Sdhb*^{-/-} imCC exhibited no significant change in basal respiration, while *Sdhb*^{-/-} cells showed a decrease, suggesting that a more significant defect in respiration exists in the *Sdhb*^{-/-} cells compared to *Sdhb*^{-/-}. Maximal respiratory capacity (FCCP-mediated uncoupled respiration) was significantly reduced in both SDH-deficient imCC models, in compliance to that previously reported in *Sdhb*^{-/-} cells(28). The relative decrease in respiratory activity observed in *Sdhb*^{-/-} cells compared to those deficient in *Sdhb* was consistent with the increased reliance on reductive carboxylation for the synthesis of aspartate and citrate (Fig. 2C), an effect previously observed in hypoxia (29). Given the decreased oxygen consumption observed in the *Sdhb*-deficient cells compared to those lacking *Sdhb*, we examined whether there was a compensatory increase in pyruvate reduction to lactate to regenerate cytosolic NADH and maintain glycolysis. We indeed saw that while *Sdhb*^{-/-} cells show a small increase in lactate production, this is further increased in *Sdhb*-deficient cells (Fig. 2G).

Altogether, these results suggest that massive succinate accumulation and rewired metabolism do not constitute relevant triggers for SDHB-related malignancy, although the extent of mitochondrial respiratory deficit may vary between the two models.

***Sdhb* knockout in mouse chromaffin cells promotes neuroendocrine-to-mesenchymal transition (NMT), unlike *Sdhb* knockout**

We previously reported that *Sdhb*^{-/-} imCC exhibit a mesenchymal-like phenotype with

increased adhesion, migration and invasion capacities (19). Morphological observation following phalloidin staining qualitatively revealed that *Sdhd*^{-/-} cells appear to be generally smaller than *Sdhb*^{-/-} cells, and display a less extensive and rather peripheral actin mesh unlike *Sdhb*^{-/-} imCC (Fig. 3A), suggesting that only *Sdhb*^{-/-} cells undergo mesenchymal transformation. Accordingly, markers of NMT activation such as *Snai1*, *Mmp9*, *Fn1* (Fig. 3B) were overexpressed in *Sdhb*^{-/-} imCC but not in *Sdhd*^{-/-} cells. In accordance with the loss of neuroendocrine features, *NCadh* was downregulated in *Sdhb*^{-/-} imCC, while it was actually overexpressed in *Sdhd*^{-/-} cells (Supplementary Fig. 2A). *Sdhd*^{-/-} cells showed moderate increase in adhesion (Fig. 3C), and no increase in migration, evaluated both in collective (Fig. 3D) and individual migration assays (Supplementary Fig. 2B). *Sdhd*^{-/-} imCC also exhibited a much slower cell growth than *Sdhb*^{-/-} cells (Supplementary Fig. 2C). Hence, despite similar SDH loss-of-function and succinate levels, *Sdhd*-deficient cells do not display the mesenchymal and migratory phenotype of *Sdhb* KO cells, as observed in human paraganglioma(18).

***Sdhb*-deficient cells show greater inhibition of 2OG-dependent dioxygenases**

We have previously established that *SDHB*-mutated PPGL and *Sdhb*^{-/-} imCC display pseudohypoxic and hypermethylator phenotypes, caused by inhibition of PHD and TET enzymes and involved in the mesenchymal-like hallmarks associated with *SDHB* deficiency (17,20). We next performed reduced representation bisulfite sequencing (RRBS) to precisely quantify 5-methylcytosine (5mC) modifications along the genome after enrichment for CpG rich regions in the different cell lines. Compared to WT, both *Sdhb* and *Sdhd* KO cells displayed a DNA hypermethylator phenotype, but this phenotype was less pronounced in *Sdhd*^{-/-} cells (Fig. 3E). In total, *Sdhb*^{-/-} cells displayed 6,847 significantly hypermethylated gene-based features (TSS +/- 500 bp and gene bodies) against only 2,564 for *Sdhd*^{-/-} cells (Fig. 3F and Supplementary Table 2). Hypermethylator phenotypes in *Sdhb*^{-/-} and *Sdhd*^{-/-} cells displayed a significant overlap and correlation (Fig. 3G and H), with 1,084 common hypermethylated features representing 42% and 16% of hypermethylated features in *Sdhd*^{-/-} and *Sdhb*^{-/-} imCC, respectively.

Surprisingly, Western-blot analysis in our cell lines revealed stabilization and massive increase of

HIF2 α protein levels in *Sdhb*^{-/-} cells, which was not seen in either *Sdhb*^{-/-}, WT or *Sdhb*-R imCC (Fig. 3I). We thus analyzed the transcriptome of all cell lines using RNA-sequencing. Hierarchical clustering of expression profiles across the 1,000 most variant genes (based on standard deviation) showed that *Sdhb*^{-/-} imCC remain closer to wild-type cells and display less gene expression changes than *Sdhb*^{-/-} cells (Fig. 3J). To investigate more specifically the expression of hypoxia-inducible genes, we analyzed the expression of a previously published list of 52 HIF targets (3), among which 47 were present in the transcriptome of imCCs (Supplementary Table 3). Twenty-four (24) of them were overexpressed in *Sdhb*-deficient cells compared to WT (mean value >120% of WT), while 17 were overexpressed in *Sdhb*-deficient cells compared to WT (13 overlapping with those high in *Sdhb* KO cells) (Fig. 3K). Comparison of both KO cells showed that 19 of the 28 overexpressed genes showed stronger expression in *Sdhb*^{-/-} cells (Fig. 3L). These data therefore suggested that although HIF2 α was hardly detectable by western blot, *Sdhb*^{-/-} cells did show a mild pseudohypoxic signature. In order to validate this observation, we further analyzed previously-published transcriptome data generated in a collection of 188 human PPGL. In this study, 3 *SDHD*, 1 *SDHA* and 2 *SDHC*-mutated PPGL were evaluated together with 17 *SDHB*-mutated ones (3), which all clustered together using the expression of the 52 HIF-target genes. We have reanalyzed these data, limiting them to the 41 highly expressed ones, and we evaluated their mean expression in *SDHB* versus *SDHD*-mutated tumors. We observed that most genes were overexpressed in *SDHB*-related tumors while the subset of genes over-represented in *SDHD*-mutated tumors corresponded to genes expressed by endothelial cells or associated with angiogenic processes (Supplementary Fig. 3A), therefore reflecting the very high vascular density described in these tumors (15,30). Similar results were obtained on the TCGA cohort of PPGL (Supplementary Fig. 3B)(31).

Altogether, these findings indicate that *Sdhb* inactivation induces less DNA methylation and gene expression changes than *Sdhb* deletion. We next aimed at identifying the causes of the seemingly greater inhibition of 2OG-dependent dioxygenases in *Sdhb*^{-/-} cells.

Iron and copper homeostasis are dysregulated in SDH-deficient cells, and especially in Sdhb KO cells

2OG-dependent dioxygenases are iron-containing enzymes. Because SDHB is the iron-sulfur subunit of complex II, we wondered whether its complete loss might lead to disturbances in iron metabolism, which would in turn modulate the activity of 2OG-dependent dioxygenases. We thus used specific fluorescent probes to detect cytosolic and mitochondrial iron in all cell types, as well as assessed iron levels in tumor samples from patients with *SDHB* mutations. We also evaluated mitochondrial copper in all cell types. Indeed, iron and copper are both essential metals with close metabolic interactions that have been known for a long time (32).

We first used the commercial Calcein-AM probe that reveals both Iron(II) and Iron(III) levels, but also other ions such as calcium. This experiment showed a decrease in global labile iron in SDH-deficient cells compared to WT imCC (Fig. 4A). To validate this observation in human PPGL, we performed laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) in 6 pheochromocytomas carrying *NF1* (n=2), *RET* (n=2) or *SDHB* (n=2) mutations, as well as 4 paragangliomas with *SDHB* (n=2) or *SDHD* (n=2) gene mutations. We observed that average ⁵⁶Fe counts were significantly decreased in tumors with *SDHB* mutations compared with tumors with *NF1*, *RET* or *SDHD* mutations (Fig. 4B-F). This decrease was greater in *SDHB*-mutated paragangliomas (Fig. 4D) than in *SDHB*-mutated pheochromocytomas (Fig. 4C). These results obtained in tumors from patients consolidate the hypothesis that loss of the SDHB subunit leads to an altered iron metabolism. Calcein-AM probe being poorly specific, we next examined the subcellular localization of Iron(II) using specific probes of both this ion, and specific cell compartments. Unexpectedly, evaluation of the labile pool of cytosolic Iron(II) revealed a significant increase in *Sdhb*^{-/-} cells only (Fig. 4G). This suggests that the calcein-AM data would actually be imputable to a strong decrease in cytosolic levels of Iron(III) in SDH-deficient cells. In opposition, we observed a significant decrease in the mitochondrial pool of chelatable iron (Iron(II)) in both knockout models, decrease which was especially pronounced in *Sdhb*^{-/-} cells and rescued in *Sdhd*^{-R} imCC (Fig. 4H).

We next evaluated mitochondrial copper levels in all cell types. Concerning the pool of labile mitochondrial Cu(II), no significant changes were observed in the SDH-deficient cells, while mitochondrial Cu(I) was significantly increased in *Sdhb* KO cells only (Supplementary Fig. 4A and B). LA-ICP-MS was also used to quantify the levels of ⁶³Cu in 10 PPGL tumors. This evaluation of global copper was not able to confirm the difference in *SDHB* vs *RET* or *NF1* tumors. However, it suggested that SDHD-deficient PGL had a decrease in copper counts compared with the other genotypes (Supplementary Fig. 4C). Hence, there was a dysregulation in copper and especially in iron pools in cells and tumors depending on their genotypes. In support of these observations, we evaluated the mRNA expression of several iron and copper transporters as well as of chaperones or different actors of iron/copper homeostasis, which revealed that these pathways were indeed strongly affected in *Sdhb* KO cells (Fig. 4I, J). In particular, these cells showed a differential expression of transporters implicated in the entry of iron and copper in the cell and the mitochondria: high DMT1 (*Slc11a2*) and low Slc25a37 would sustain the increased cytosolic distribution of Iron(II), while low CTR1 (*Slc31a1*) and high Slc25a3, the high mitochondrial Cu(I) levels. Consistently with these observations, human PPGL transcriptome data showed an increase in *DMT1* mRNA levels in SDH tumors as compared with other types of mutated PPGL. SDH tumors also exhibited a slight increase in the expression of other actors involved in iron binding and transport, such as the hypoxia-inducible genes *TF* and *TFR2*. *SLC31A1* was significantly decreased in both SDH and VHL tumors compared to RET or NF1-mutated ones. No differences were detected for *TFR2* nor *SLC25A3* expression (Supplementary Fig. 4D).

***Sdhb*-deficient cells display increased ROS levels without activation of the NRF2 pathway.**

Sdhb-KO cells show increased mitochondrial copper(I) and cytosolic Iron(II) levels, which could cause important oxidative stress in these cell compartments (33). An increase in reactive oxygen species (ROS) might also participate to the sustained inhibition of 2OG-dependent dioxygenases activity (34). Flow cytometry analyses of fluorescent probes revealed that *Sdhb*-deficient cells showed increased ROS both in the cytosol (Fig. 5A) and especially in the mitochondria

(Fig. 5B). They also displayed a significant increase in lipid peroxidation levels (Fig. 5C) and in mitochondrial activity (Fig. 5D) but not in overall mitochondrial mass (Fig. 5E). Unexpectedly, none of the *Sdhd*-deficient clones showed any changes in ROS levels as compared to the WT cells.

Because *Sdhb*^{-/-} cells display such a significant increase in ROS, we postulated that they would probably show increased anti-oxidant responses, either through superoxide dismutase (SOD) or through activation of the NRF2 pathway. However, the global superoxide dismutase activity did not differ between the different cell types (Supplementary Fig. 5A). Moreover, RNA-seq analysis showed a significant downregulation of mitochondrial SOD2, thus demonstrating that *Sdhb*-deficient cells do not detoxify the excess in mitochondrial ROS (Fig. 5F).

We performed gene set enrichment analyses using RNA-seq data of 58 NRF2-target genes (Supplementary Table 4) which showed no activation of the pathway in *Sdhb* nor in *Sdhd* KO cells, compared to WT (Supplementary Fig. 5B). In addition, treating the cells with N-acetyl cysteine (NAC) had no effect on the levels of mitochondrial ROS in any of the cell types studied (Fig. 5G), neither affected their proliferation (Fig. 5H). In order to fully validate this observation in the human context, this list of genes was also tested in the transcriptome data of the human PPGL COMETE collection (Fig. 5I). Mean values of NRF2 targets levels in the groups of sporadic non-mutated tumors (n=49), *RET* (n=19), *NF1* (n=37), *VHL* (n=40), *SDHA*, *C*, *D*- (n=6) and *SDHB*-mutated tumors (n=17) were used to perform unsupervised classification, which confirmed that the NRF2 pathway is not activated in *SDHB*-deficient tumors.

It has previously been reported that *SDHB* loss is associated with increased DNA damage (35), and a sensitivity to inhibitors of poly (ADP-ribose) polymerase (PARP) (35, 36, 37). In addition to the recently demonstrated mechanism associated with oncometabolite-induced inhibition of the lysine demethylase KDM4B, increased ROS levels may participate to such phenotype. We therefore evaluated DNA damage after staining PPGL tumor tissues and imCCs with anti-γH2AX antibody (Supplementary Fig. 5C and D). Although it was not statistically significant, we observed a slight

increase in γ H2AX levels in SDHB-deficient tumors, which was not seen in *Sdhb*^{-/-} imCCs. Treating cells with increasing doses of the PARP inhibitor Talazoparib reduced cell survival in all cell types, with an actually higher efficacy in WT and *Sdhb*-R cells (Supplementary Fig. 5E). In this cell model, it seemed that Talazoparib efficiency was not related to SDH-deficiency, but was rather related to cell proliferation indexes of the treated cell types.

Modulating Iron(II) and ROS levels affects pseudohypoxia and survival in Sdhb-deficient cells

Altogether, these data suggest that in *Sdhb* KO cells, a combination of succinate accumulation, dysregulation of iron homeostasis and high ROS levels may account for the increased inhibition of TET and PHD hydroxylases. To demonstrate this link, we treated cells with Iron(II) (50 μ M), which had no effect on cytosolic ROS (Supplementary Fig. 6A) but reduced mitochondrial ROS, only in *Sdhb*^{-/-} cells (Fig. 6A). This was associated with a decrease in HIF2 α protein levels in *Sdhb*^{-/-} cells as well (Fig. 6B). Treating cells with increasing doses of ferrous iron revealed a specific sensitivity of *Sdhb*-deficient cells. Indeed, after 48 h of treatment, 0.1 mM doses of Iron(II) led to a 60% decrease in *Sdhb*^{-/-} cells survival while it only moderately affected WT, *Sdhb*-KO or *Sdhb*-R cell types (Fig. 6C).

In order to further demonstrate that increased mitochondrial ROS were indeed responsible for the massive HIF2 α stabilization observed in *Sdhb*-deficient cells, we then treated them for 12h with MitoTEMPO, a mitochondrially targeted antioxidant that acts as a specific scavenger of mitochondrial superoxide. MitoTEMPO (MTT) at 2.5 μ M had no effect on cytosolic ROS (Fig. 6D), but significantly decreased mitochondrial ROS in *Sdhb*^{-/-} imCC (Fig. 6E), which was associated with a substantial reduction of HIF2 α levels (Fig. 6F). High doses of MTT are suspected to show a reverse effect, promoting a pro-oxidant response. We therefore treated cells with 2.5 mM of the compound and showed that such high dose increased cytosolic ROS in all cell types and especially in WT and *Sdhb*^{-/-} CIA cells (Fig. 6G), as well as mitochondrial ROS in WT and *Sdhb*^{-/-} cells (Fig. 6H). Strikingly, such treatment promoted a strong pseudohypoxic response in WT, *Sdhb*^{-/-} and *Sdhb*-R cells, thus

demonstrating that increasing ROS was sufficient to mediate HIF2 α stabilization. In contrast, this led to the opposite effect in *Sdhb*^{-/-} cells (Fig. 6I) in which HIF2 α protein was almost lost. It actually appeared that high dose MTT was highly toxic for *Sdhb*^{-/-} cells exclusively (Fig. 6J), with perinuclear vacuoles emerging after 12h and leading to the death of all *Sdhb*^{-/-} imCC after 72h.

In an attempt to evaluate another pro-oxidant treatment that might be used in a clinical context, we finally tested the vulnerability of imCC to high dose ascorbate. A dose response curve showed that *Sdhb*^{-/-} cells were indeed much more vulnerable to ascorbate with significant increase in cell death appearing from a 1 mM dose onward, a complete lethality being reached at a 2.5 mM ascorbate dose (Fig. 6K). At the higher dose, 85% of *Sdhb*-deficient cell loss was achieved after 24h, while a similar response was only apparent in *Sdhb* and WT cells after 72h (Fig. 6L). To evaluate the mechanism associated with ascorbate-induced lethality, we measured cytosolic and mitochondrial ROS in cells treated for 48 h with 1 mM ascorbate. At such a dose, there was already a significant lethality of *Sdhb*-KO cells and enough cell material was still available to allow the analyses (Supplementary Fig. 6B). Interestingly, we observed that cytosolic ROS were not modified by ascorbate in any of the cell models (Supplementary Fig. 6C). In contrast, ascorbate led to a massive increase in mitochondrial ROS, specifically in *Sdhb*^{-/-} cells (Fig. 6M).

These data suggest that in *Sdhb*-KO cells ascorbate interacts with the increased Iron(II) labile pool to enhance oxidative stress, leading to rapid cell death.

Discussion

It is well-established that a mutation in the *SDHB* gene is a high risk factor for metastatic PPGL (38) and poor prognosis (6), unlike mutations in other *SDHx* genes (*SDHA*, *SDHC* or *SDHD*) that rarely cause metastatic forms of the disease. This question has been unresolved for 20 years. Many studies have been performed in the past years, mainly using cell lines exhibiting a decrease or complete lack in the expression of *Sdhb*. Thereby, previous work from our team has shown that

metastatic *SDHB* tumors exhibit a NMT phenotype (18,19), associated with increased DNA methylation in comparison to other *SDHx* mutated tumors (20,39). Further, we have recently demonstrated that this hypermethylated profile is due to TET silencing and that the NMT phenotype observed in *SDHB* mutated tumors is the result of synergistic roles of TET repression and pseudohypoxia, through HIF2 activation (20). Although these data have shed light on some mechanisms undeniably involved in the tumorigenesis of *SDHB* mutated tumors, they do not explain the different clinical outcomes observed in patients carrying mutations in the different *SDHx* genes. In the present study, we were able to characterize and compare two physiologically appropriate cellular models exhibiting a complete knock-out in *Sdhb* or *Sdhd* genes, which strikingly recapitulate most of the phenotypic characteristics of *SDHB* and *SDHD*-mutated tumors.

Succinate accumulation is probably the major consequence of SDH loss of activity and increased succinate levels in tumor samples are used as a biomarker of SDH-deficiency in PPGL patients (27,40–42). For a long time, it has therefore been considered to be the main trigger of PPGL tumorigenesis. The role of succinate as an oncometabolite was initially demonstrated in 2005, with the demonstration of its inhibiting role on 2OG-dependent PHD enzymes, leading to the subsequent stabilization of HIF α subunits even under normoxia (43,44). Later, it was demonstrated that succinate is also a major epigenetic modifier, inhibiting TET enzymes and promoting a genome wide hypermethylated profile (17,39,45). It has been suggested that a stronger inhibition of 2OG-dependent dioxygenases observed in *SDHB*-mutated tumors versus tumors with mutations in other *SDHx* genes, might be explained by a fuller inactivation of SDH enzyme associated with higher succinate (27). Here, we firmly invalidate this long-held assumption, both *Sdhb*^{-/-} and *Sdhd*^{-/-} imCC models showing the same loss of SDH activity and similar levels of succinate and fumarate (Fig. 1). Indeed, many of the metabolic characteristics investigated were highly similar between the two cell models suggesting that merely measuring overall steady-state succinate and fumarate levels are inadequate for predicting phenotype, and smaller changes in metabolic function may drive downstream. Surprisingly, HIF2 α protein was hardly detectable in *Sdhd*-deficient cells while it was

strongly activated in *Sdhb*^{-/-} imCC. This provides further evidence that although aspects of the overall metabolic phenotype were similar between *Sdhb*^{-/-} and *Sdhd*^{-/-} models, as yet unexplored metabolic factors may play a role in the inactivation of the PHD enzymes to stabilize HIF2 α . This was unexpected as previous transcriptome analyses of human tumor samples have classified all *SDHx* mutated tumors together with *VHL*-mutated ones in a “pseudohypoxic” cluster (16,17). However, such classifications were based on global transcriptome and obviously included many other pathways. To our knowledge, only three studies have classified PPGL tumors based on the expression of hypoxia-induced genes. Hensen *et al* compared hypoxia-inducible genes in sporadic head and neck PGL (HNPPGL) to HNPPGL carrying *PGL2* or *SDHD* gene mutations (46). This study was not able to identify any differences in the hypoxic signature of these 3 types of tumors. Besides, Fliedner *et al* evaluated the expression of HIF target genes in a larger collection of *SDHD* (n=14) and *SDHB* (n=15) related PPGL and also revealed some differences between the two types of tumors, with some genes being less overexpressed in *SDHD*-mutated PGL (47). Based on previously published transcriptome data (3), our present study shows that most HIF-target genes were overexpressed in *SDHB*-related tumors while the subset of targets over-represented in *SDHD*-mutated tumors corresponded to genes expressed by endothelial cells. Hence, although it is most probable that, as previously suggested in other studies (15,48–50), *SDHD* tumors display some induction of pseudo-hypoxia *in vivo*, the combination of our *in vitro* data and human PPGL studies does suggest that this effect is at least much more limited in non-*SDHB* mutated cells and can therefore not be imputable to succinate accumulation only.

Our data reveal that while *SDHB* expression is completely abolished in *Sdhb*^{-/-} cells, a small fraction of *SDHB* protein remains detectable in *Sdhd*^{-/-} clones, consistently with IHC data on tumors that frequently report a weak diffuse *SDHB* staining in *SDHD*-mutated PPGL (25,51). *SDHB* is the Fe-S subunit of Complex II and contains two highly conserved L(I)YR motifs that are essential for acquisition of Fe-S clusters by recruiting the Fe-S transfer machinery. We postulate that the loss in mitochondrial Fe-S clusters present in the *SDHB* subunit, may be responsible for the significant

imbalance in cytosolic and mitochondrial iron distribution, that we observe in *Sdhb*^{-/-} cells. Interestingly, Saxena et al reported that 37% of disease-causing missense mutations in SDHB were located in either the L(I)YR Fe-S transfer motifs or in the 11 Fe-S cluster-ligating cysteines. Moreover, analyses of reported missense mutations in patients with SDH-RCC or GIST revealed that 50% of these patients had *SDHB* mutations in the L(I)YR motif amino acid residues (52). Altogether, these observations point to a central role of Fe-S clusters loss in SDHB-related disease, which are further reinforced by our present observations.

This labile iron overload may in turn be responsible for or exacerbate the overproduction of ROS observed in *Sdhb*^{-/-} cells, thereby indirectly activating pseudohypoxia and DNA methylation. Indeed, it has been previously demonstrated in a number of studies that in the context of excessive ROS levels, these oxidant molecules can act as signals able to trigger the stabilization of HIF α transcription factors in normoxic conditions (53–55; 34). Besides, in the present study we show that the use of MitoTEMPO, a mitochondrially targeted antioxidant at low concentrations led to a significant decrease in mitochondrial ROS, resulting in turn in reduced HIF2 α levels. Conversely, high doses of MTT appear to exert a pro-oxidant action leading to increased cytosolic ROS in all of the cell types, resulting in a strong pseudohypoxic response. Altogether, these results demonstrate the direct link between ROS and HIF2 α stabilization and suggest that the elevated ROS levels observed in *Sdhb*^{-/-} cells are probably responsible for their stronger pseudohypoxic phenotype. The association between SDH-deficiency and ROS production has been controversial, with some studies showing an increase in ROS levels (28,53) and others not (56). Actually, these apparently contradictory data are in total accordance with our observations. Indeed, Selak *et al* first reported the absence of oxidative stress following SDH inactivation, but this was observed in an *SDHD* KD cell model (56). In contrast, Guzy et al. proposed that the mechanism explaining PPGL tumorigenesis following SDH inhibition was an increase in ROS production, acting as messengers able to activate pseudohypoxic responses and probably resulting in oxidative damage to DNA, genomic instability, and tumorigenesis (53). In that study, an *Sdhb*-Knock Down (KD) model was compared to a *Sdha*-KD one, and ROS increase was only

observed in *Sdhb* KD cells. At that time, it was suspected that *SDHA* gene mutations were not associated with PPGL, an assumption that we demonstrated to be untrue several years later (3). Based on these observations, their conclusions were that loss of all but the SDHA subunits of SDH would produce such increase in ROS production, explaining SDHB/C/D-mediated tumorigenesis. In view of the actual knowledge on SDH genetics, the combination of these data with our current observations suggests that ROS production is a specific feature of *SDHB*-mutated cells, and may be responsible, not for SDH-related tumorigenesis in general, but for SDHB-related aggressive phenotype.

Our data suggest that the increased oxidative stress observed in *Sdhb*-deficient cells could be the consequence of the dysregulated iron/copper homeostasis. Indeed, redox-active iron strongly interacts with hydrogen peroxide through the Fenton/Haber-Weiss reaction. This usually slow reaction is catalyzed by labile iron, yielding mainly the highly reactive and toxic hydroxyl radical ($\bullet\text{OH}$) from hydrogen peroxide (H_2O_2) and superoxide ions ($\bullet\text{O}_2^-$): $\text{Iron(III)} + \bullet\text{O}_2^- \rightarrow \text{Iron(II)} + \text{O}_2$; $\text{Iron(II)} + \text{H}_2\text{O}_2 \rightarrow \text{Iron(III)} + \text{OH}^- + \bullet\text{OH}$ (57). Oxidative damage arising from excessive levels of ROS are observed in a variety of pathologies such as neurodegenerative diseases and cancer, and have been linked to malignant transformation, together with an imbalance in iron homeostasis(58). Similar assumptions can be made for copper (59). Our results are also consistent with a recent study demonstrating the role of histone H3-H4 as a copper reductase enzyme that binds Cu(II) and catalyzes its reduction to Cu(I). They showed that active H3-H4 is required for proper utilization of copper for mitochondrial respiration and SOD function. Thereby, the excess of mitochondrial Cu(I) observed here predominantly in *Sdhb*^{-/-} imCC suggests a greater inactivation of H3-H4 and thereby may explain the inhibition of *Sod2* expression and the mitochondrial respiratory deficit observed following *Sdhb*-deficiency (60). In addition, the lack of ROS changes observed in *Sdhd* KO cells might be associated with a residual activity of Complex II in *Sdhb* KO cells. Indeed, while changes in SDH activity coupled to complexes I and III have been shown in a number of different systems to generate ROS, SDH itself has also been suggested to generate ROS when electron flow is compromised (61). It

was recently suggested that cells lacking SDHB maintain some form of SDH subunit-containing complex (62), which maintains some level of activity. Although we have no data to validate this hypothesis, one could hypothesize that SDHB-deficient cells can generate ROS due to the retention of an 'SDH-like' complex, while SDHD-deficient cells avoid this through complete loss of SDH.

In this regard, our findings are consistent, although different, with those recently proposed by Liu *et al* (63). Using an *Sdhb* KD cell model, these authors also describe ROS accumulation associated with an increase in the intracellular labile iron pool. Surprisingly, these authors observed an increase in iron pool using the calcein probe while in our model, and in human PPGL, this experiment actually showed a decrease in *Sdhb* KO cells. A possible explanation stands in the fact that the model used in the current study is, as the human PPGL studied, a true genetic KO with no SDHB expression, while the model used by Liu *et al* is a KD in which 30% of SDHB protein expression remains. Hence, these different models point to similar pathways, but with major differences in the adaptive responses of the cells. Indeed, Liu *et al* propose that the iron overload would be due to increased expression of TF and TFR2, while, as previously mentioned such overexpression was not observed in our model. We did observe a slight increase in TF mRNA levels in SDH tumors as compared with other types of mutated PPGL, but not in TFR2. However, in both cases, levels of expression were actually extremely low in all PPGLs and therefore probably not biologically relevant (Supplementary Fig. 4). Furthermore, these authors showed in the same model, that anti-oxidant responses were increased following *SDHB* KD, notably through the upregulation of the nuclear factor erythroid 2-related factor 2 (NRF2). We did not observe any activation of neither the NRF2 pathway nor superoxide dismutase (SOD) activity in any of our different cell types and these data were further validated by our analysis of the transcriptome of human PPGL. Besides, N-acetyl cysteine (NAC) treatment, an inhibitor of the NRF2 pathway, had no effect on the production of mitochondrial ROS by *Sdhb*^{-/-} cells. Hence, it is quite interesting to notice that although similar pathways seem to be affected in the *Sdhb* KO and KD cells (i.e. iron homeostasis, oxidative stress), it seems that the mechanisms and the adaptive responses involved are not similar.

Collectively, these data demonstrate that cells carrying a complete abolition of *Sdhb* gene are not able to neutralize the oxidative damage caused by the mitochondrial ROS excess, through the up-regulation of any intrinsic anti-oxidant pathway. Since, ROS generation seems to be a critical hallmark of SDHB loss, testing an antioxidant treatment that could be used for clinical purposes on our *Sdhb*^{-/-} model appeared relevant. Ascorbate offers many assets, as it presents few side effects in healthy tissues, even at pharmacological concentrations and is easy to access. However, although at physiological concentration (micromolar), ascorbate acts as an antioxidant, able to decrease ROS levels (64), it has been shown to have pro-oxidant actions when reaching high concentrations (65). In addition to its strong oxidative role, ascorbate also affects iron homeostasis, as it reduces ferric iron (Iron(III)) in a cycle of reactions leading to the fully oxidized form of ascorbate (DHA), ferrous iron (Iron(II)) and eventually resulting in increased intracellular ROS levels (66,67). Therefore, in a context of redox imbalance associated with an elevated pool of labile iron, ascorbate treatment could lead to unbearably high ROS levels for the cells and thus aggravate an existing oxidative stress burden. Use of ascorbic acid at pharmacologic concentrations was already suggested as a promising therapeutic strategy on various types of tumor cells exhibiting increased ROS levels, increased labile iron and metabolism impairments (58). All the more that, for the past few years many studies have demonstrated the efficacy of ascorbate as an anticancer treatment, killing cancer cells *in vitro* (68,69) and slowing tumor growth *in vivo* (70). In compliance with these reports, our data reveal that high-dose ascorbate treatment led to a higher accumulation of ROS solely in the mitochondria of *Sdhb*^{-/-} imCC, resulting promptly in cell death, thus validating the increased sensitivity of *Sdhb*^{-/-} cells for ascorbate, mediated by ROS overload. Interestingly, Liu *et al* also recently reported that ascorbate treatment increased apoptosis in *SDHB* KD cells *in vitro* and delayed the growth of tumors as well as of hepatic lesions in xenografted mice models *in vivo* (70). Numerous clinical trials are currently evaluating the efficacy of intravenous high-dose pharmacological ascorbate injection for treating different cancer types (67,71). In that context, ascorbate intravenous injections at pharmacological doses appear as a worthy and highly promising therapeutic strategy to treat SDHB-deficient

malignancies, which often exhibit a poor answer to current treatments strategies (radiotherapy, chemotherapy, targeted therapy) and could also be tested in combination with other therapies.

Overall, the comprehensive comparison of the first relevant *Sdhb* and *Sdhd* knock-out cellular models, reveals the common and distinctive pathways used by these cells to adapt to these deficiencies, and highlight specific hallmarks associated with *Sdhb* mutations. Lifting the veil on a long-lasting question, we show that *Sdhb*-deficient cells exhibit stronger PHD and TET inhibition than their *Sdhd*-deficient counterparts, explaining their aggressive phenotype and mesenchymal morphology. We demonstrate that *Sdhb*^{-/-} imCC manifest a significantly exacerbated imbalance in copper and iron homeostasis resulting in an increased labile iron pool, associated with significant ROS accumulation. High-dose ascorbate treatment of *Sdhb*^{-/-} imCC offers promising results, as it highly aggravated the oxidative stress burden endured by *Sdhb*-deficient cells, thus rising as a potential original therapeutic approach to treat malignant PPGL.

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Author contributions

J.F., E.L. and D.A.T conceived the study. J.G., A.M., G.G., S.M., C.L.A. designed and performed the experiments, and analyzed the data. S.Mo., K.K., A.P.M., T.J.S., C.L-L., P.B. and A.T. performed the experiments and analyzed the data. J.F., D.A.T., E.L., F.M-G. and R.R. designed the experiments and analyzed the data. J.F. and A-P.G-R. supervised the study. J.F. and J.G. contributed to the management of the project, wrote the manuscript and prepared the figures. E.L. and D.A.T.

655 contributed to the preparation of the manuscript. All the authors discussed the results and reviewed
656 the manuscript.

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Figure legends

Fig. 1 Generation of *Sdhd*-deficient immortalized mouse chromaffin cells. **A**, Electrophoregrams of Sanger sequencing of the exon 3 of *Sdhd* gene showing both homozygous point mutations c.119delC and c.120_121delCA of CIA and CLB respectively compared to a control DNA (WT). **B**, Western-blot showing SDHB protein expression in all cell types. **C**, Spectrophotometrical measurement of SDH activity. Steady-state assessment of TCA cycle organic acids (**D**, succinate, **E**, fumarate and **F**, α -ketoglutarate). Results shown are from at least three independent experiments, presented as mean $\pm$ SEM. In **C-F**, One-way ANOVA was used to assess statistical significance. ns, not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Fig. 2 Metabolic and respiratory profiles of *Sdhd*-deficient imCC and *Sdhb*^{-/-} cells. **A**, Diagram describing the incorporation of carbons from glucose through PDH (blue) or PCX (red) enzymes activity. Abbreviations in metabolic diagram: PDH, pyruvate dehydrogenase; PCX, pyruvate carboxylase; AcCoA, acetyl coenzyme A. **B**, Incorporation of ^{13}C into succinate, aspartate and citrate in stated cell lines. Isotopomers ^{13}C atoms are shown as filled circles, whereas ^{12}C atoms are empty circles. **C**, Incorporation of $^{13}\text{C}_5$ -glutamine into succinate, aspartate and citrate in indicated cell lines and **D**, the associated diagrammatic representation of their oxidative (blue) and reductive (red) metabolism. **E**, Oxygen consumption (respiration) of intact and **F**, permeabilized (CI + CII) cells. ETS refers to electron transfer system capacity and basal respiration to oxygen consumption in non-permeabilised cells. **G**, Lactate production over time. Results shown are from at least three independent experiments, presented as mean $\pm$ SEM. Two-way ANOVA was performed; ns, not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$ relative to WT and $\$P \leq 0.05$, \$\$\$ $P \leq 0.001$ relative to *Sdhb*^{-/-} imCC.

Fig. 3 *Sdhb*, but not *Sdhd* knockout in mouse chromaffin cells initiates a mesenchymal phenotype associated with stronger 2OG-dependent dioxygenases inhibition. **A**, Actin staining in the indicated cell lines. **B**, qRT-PCR analysis of known epithelial-to-mesenchymal markers (*Snai1*, *Mmp9*, *Fn1*). **C**, Quantification of cell adhesion 1h after plating. **D**, Collective migration assessed after 10h in the stated cell lines, represented as the closure percentage of the wound. **E**, Scatterplot representative

of methylation rates identified by RRBS in *Sdhb*^{-/-} versus WT cells and *Sdhb*^{-/-} versus WT cells, respectively. **F**, number of differentially methylated features in *Sdhb*^{-/-} and *Sdhb*^{-/-} imCC (versus WT) in TSS500 and gene body regions. **G**, Comparison of methylation changes generated by *Sdhb* and *Sdhb* knockout in imCC. **H**, Number and overlap of differentially methylated features in *Sdhb*^{-/-} compared with *Sdhb*^{-/-} imCCs. **I**, Western blot of HIF2 α in total cellular extracts of indicated cell lines. **J**, Heatmap representation of transcriptome-based classification of imCCs according to their genotype resulting in hierarchical clustering. **K**, Number and overlap of overexpressed hypoxia-inducible genes from a selected list of 47 genes in *Sdhb*^{-/-} and *Sdhb*^{-/-} imCCs compared with WT cells. **L**, Relative expression levels of overexpressed hypoxia-inducible genes in *Sdhb*^{-/-} and *Sdhb*^{-/-} imCCs compared with WT. In **A**, **B**, **C**, **D** and **E** data shown are from at least three independent experiments, presented as mean $\pm$ SEM. **K** and **L** data are mean expression levels from RNAseq data generated in 3 *Sdhb*^{-/-}, 2 WT and 2 *Sdhb*^{-/-} clones. One-way ANOVA was used to assess statistical significance; ns, not significant, **P $\leq$ 0.01, ***P $\leq$ 0.001 relative to WT and \$\$\$P $\leq$ 0.001 relative to *Sdhb*^{-/-} imCC.

Fig. 4 SDH-deficient cells exhibit significant alterations in iron homeostasis, notably marked in *Sdhb* KO cells. **A**, Flow cytometry analysis of labile overall iron content in each cell line. **B**, Representative ⁵⁶Fe images generated by LA-ICP-MS in one *NF1*-mutated human pheochromocytoma **C**, one *SDHB*-mutated pheochromocytoma **D**, one *SDHB*-mutated paraganglioma and **E**, one *SDHD*-mutated paraganglioma. Images are displayed using the same threshold to enable a direct visual comparison between tumor sections. Average ⁵⁶Fe counts in 2 *NF1*, 2 *RET*, 4 *SDHB* and 2 *SDHD* tumors are shown in **F**. **G**, Cytosolic Iron(II) content, **H**, mitochondrial Iron(II) content. **I**, Heatmap representation of the expression profiles of several critical actors of iron/copper homeostasis in *Sdhb*^{-/-}, WT and *Sdhb*^{-/-} cells, using mean level values to perform unsupervised classification. **J**, Diagram highlighting the role played by some iron and copper transporters (*DMT1*, *Slc25a37*, *CTR1* and *Slc25a3*) explaining the major alterations induced by *Sdhb* KO in their iron and copper cellular homeostasis. Data shown in **A**,

G and **H** are from three independent experiments, presented as mean $\pm$ SEM. Non-parametric one-way ANOVA was used to assess statistical significance; ns, not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Fig. 5 SDHB-deficient cells display increased ROS levels without activation of the NRF2 pathway.

A, Specific MFI using CellROX probe in all imCC cell types. Similar assays were carried out using **B**, Mitosox **C**, Bodipy C11 probe **D**, TMRM and **E**, Mitotracker probes. **F**, RNA-seq analysis showing the mRNA levels of the different forms of superoxide dismutase (cytoplasmic SOD1, mitochondrial and extracellular SOD3) and catalase. **G**, Specific MFI of MitoSOX probe in all imCC models following N-acetyl-cysteine (NAC) treatment (3 mM) for 48h. **H**, Cell survival percentage of indicated cell lines after treatment with 3 mM of NAC in comparison to vehicle-treated controls for 48h. **I**, Heatmap representation of the expression of 58 NRF2-target genes through the transcriptome data of the COMETE collection of human PPGL. Mean values of NRF2 targets levels in the groups of sporadic non-mutated tumors (n=49), *RET*- (n=19), *NF1*- (n=37), *VHL*- (n=40), *SDHA*, *C*, *D*- (n=6) and *SDHB*-mutated tumors (n=17) were used to perform unsupervised classification. Data shown in **A**, **B**, **C**, **D** and **E** each dot is representative of an independent experiment (n=4), bar plots show means $\pm$ SEM. One-way ANOVA was used to assess statistical significance; ns, not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$ relative to WT and \$ $P \leq 0.05$ relative to *Sdhb*^{-/-} imCC. In **G** and **H** results shown are from at least three independent experiments and presented as means $\pm$ SEM. To assess statistical significance in **F**, **G** and **H**, Two-way ANOVA was used; ns, not significant, * $P \leq 0.05$, *** $P \leq 0.001$.

Fig. 6 Modulation of Iron(II) and ROS levels affects HIF2 α stabilization and survival in Sdhb-

deficient cells. A, Specific MFI of MitoSOX probe in all imCC models following treatment for 48h with either Iron(II) 50 μ M or vehicle. **B**, Western blot of HIF2 α in total cellular extracts of *Sdhb*^{-/-} imCCs not-treated (NT) or treated for 48h with Iron(II) (Fe²⁺). **C**, Dose-response curves showing cell survival of all cell types following 48h of treatment with Iron(II). **D**, Specific MFI of CellROX probe in all imCC

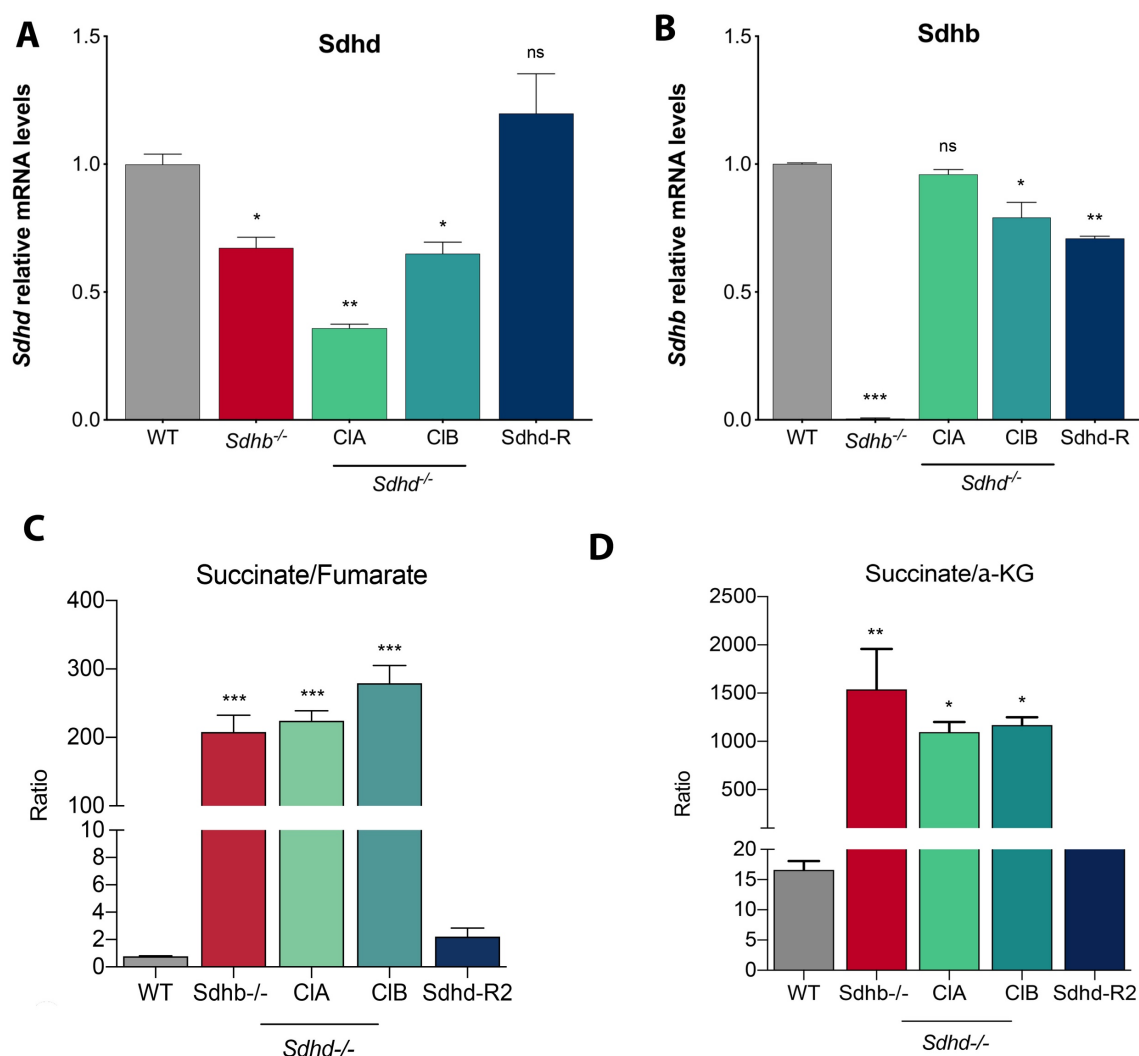
models following treatment for 12 hours with MitoTEMPO (MTT) 2.5 μ M in comparison to NT cells. **E**, Same as **D**, using MitoSOX probe. **F**, Western blot of HIF2 α in total cellular extracts NT or treated for 12h with 2.5 μ M MTT. **G**, Same as **D**, after treatment with MTT 2.5 mM. **H**, Same as **G**, using MitoSOX probe. **I**, Same as **F**, after treatment for 12h with 2.5 mM MTT. **J**, Cell morphology following treatment for 12h with MTT 2.5 mM. **K**, Same as **C** following Ascorbate treatment. **L**, Time-response curves showing cell survival of all imCC models after treatment with 2.5 mM ascorbate. **M**, Specific MFI of MitoSOX probe in all imCC models following treatment for 48h with either ascorbate 1mM or vehicle. Data for **C**, **K**, and **L** are all relative to vehicle-treated controls and presented as means $\pm$ SEM (n = 3 independent experiments, with 3 technical replicates/experiment). Data from **A**, and **M** are mean of at least three independent experiments and data from **D**, **E**, **G**, and **H** are mean of at least two independent experiments. Data are presented as mean $\pm$ SEM and two-way ANOVA was performed; ns, not significant, *P $\leq$ 0.05, ***P $\leq$ 0.001.

Supplementary data

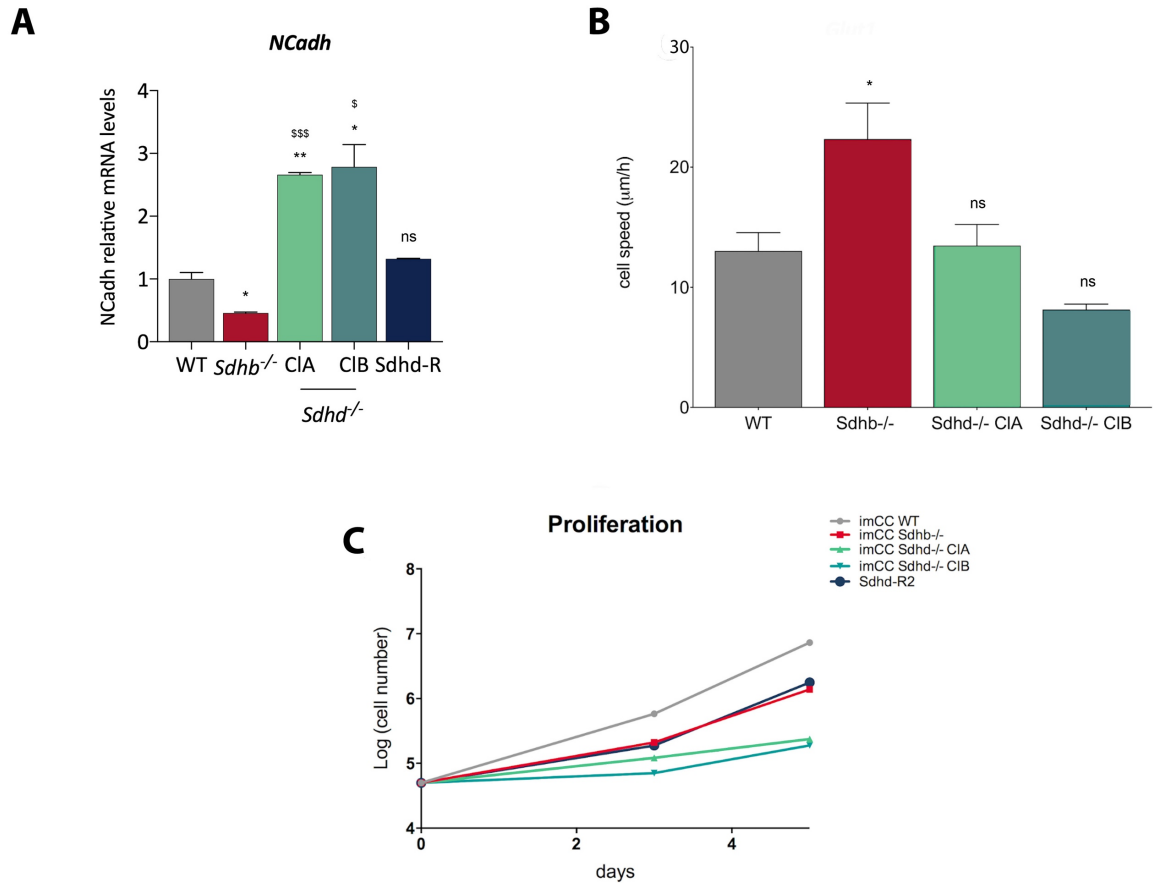
Loss of SDHB, but not SDHD, promotes dysregulated iron homeostasis, oxidative stress and vulnerability to ascorbate.

Judith Goncalves, Sophie Moog, Aurélie Morin, Géraldine Gentric, Sebastian Müller, Alexander P. Morrell, Katarína Kľučková, Theodora J. Stewart⁷, Cynthia L. Andoniadou, Charlotte Lussey-Lepoutre, Paule Bénit, Alpesh Thakker, Lisa Vettore, Jennie Roberts, Raphaël Rodriguez, Fatima Mehta-Grigoriou, Anne-Paule Gimenez-Roqueplo, Eric Letouzé, Daniel A. Tennant and Judith Favier

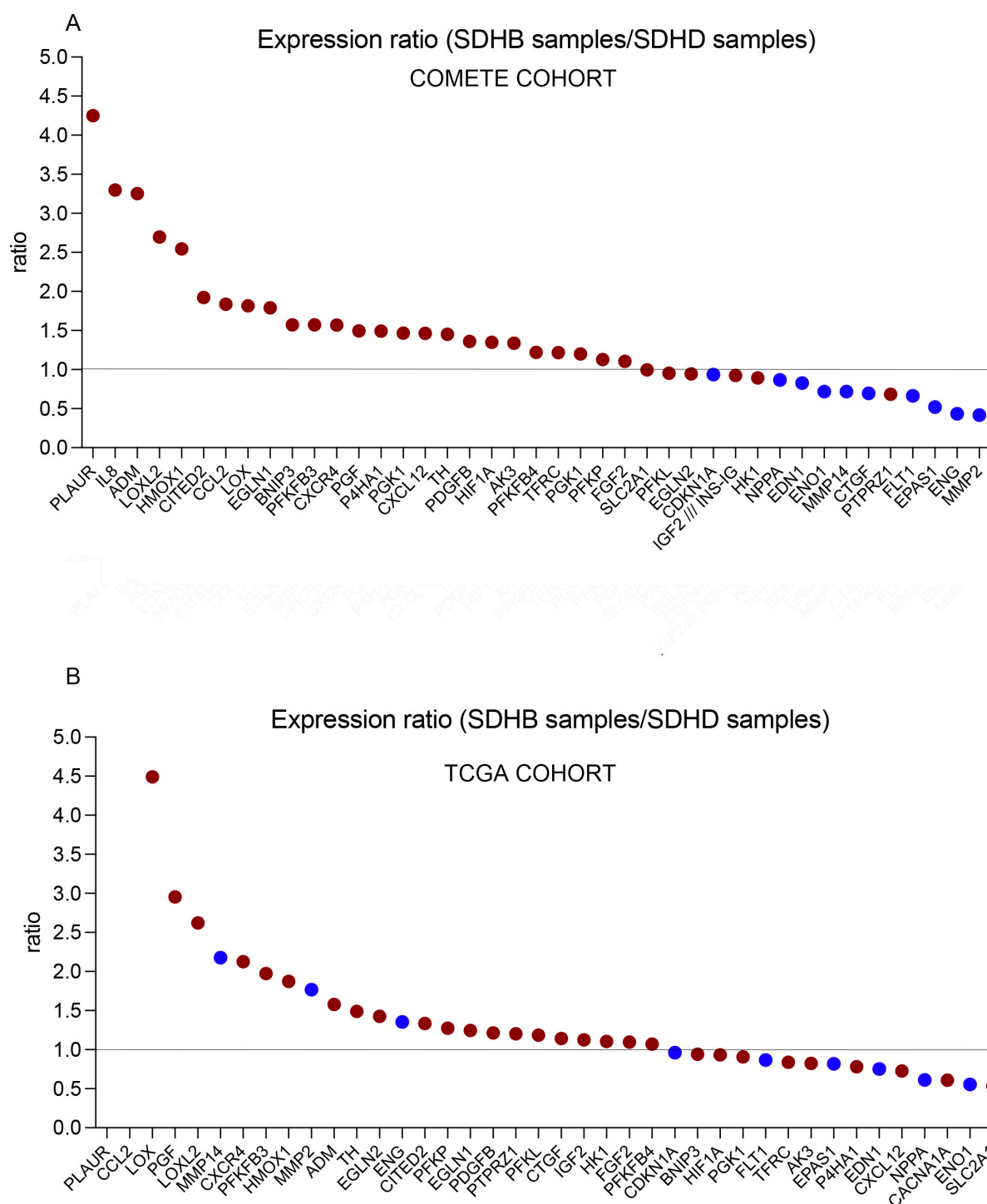
- Supplementary Figure 1
- Supplementary Figure 2
- Supplementary Figure 3
- Supplementary Figure 4
- Supplementary Figure 5
- Supplementary Figure 6
- Supplementary Table 1
- Supplementary Table 2
- Supplementary Table 3
- Supplementary Table 4
- Supplementary Methods



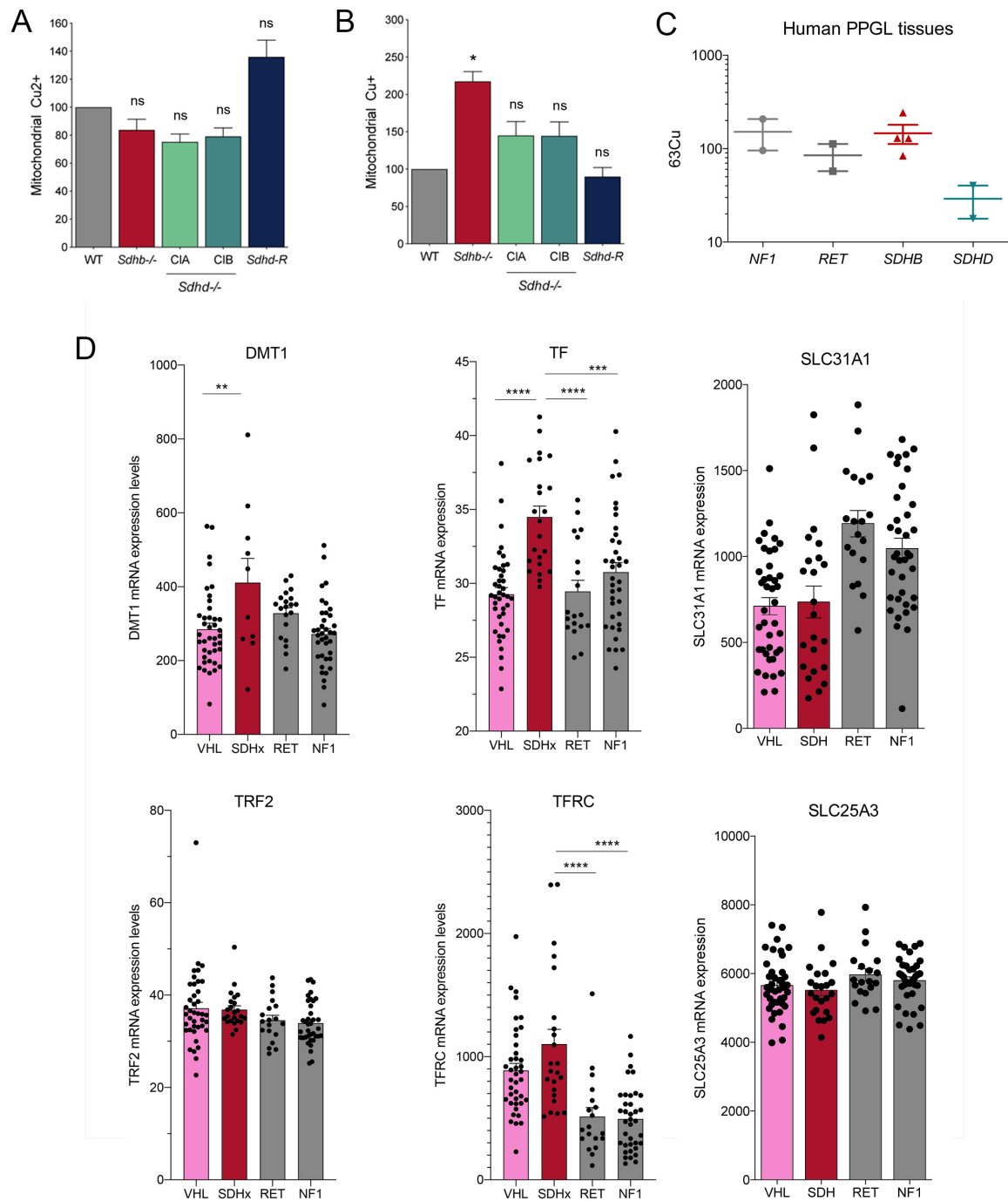
Supplementary Fig. 1 Related to Figure 1. Validation of new *Sdhd* knock-out cell models. **A**, qRT-PCR analysis of *Sdhd* gene in the indicated cell lines. **B**, qRT-PCR analysis of *Sdhb* gene in the indicated cell lines. For **A and B** data shown are from at least six independent experiments, presented as mean $\pm$ SEM. **C**, Succinate to Fumarate ratio and **D**, Succinate to α -ketoglutarate (α -KG) assessed in all the indicated cell lines, using steady-state levels of the former organic acids measured by GS-MS (n=3). Data are shown as mean $\pm$ SEM. Student's test was performed to assess statistical significance; ns, not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.



Supplementary Fig. 2 Related to Figure 3. *Sdhb* KO, but not *Sdhc* KO cells exhibit a mesenchymal metastatic phenotype. **A**, qRT-PCR analysis of *NCadherin* gene in the indicated cell lines. Data shown are from at least three independent experiments, presented as mean $\pm$ SEM. **B**, Individual cell speed was estimated (in $\mu\text{m}/\text{hour}$) by tracking cell nucleus during 12 hours ($n=3$). **C**, Growth curves of all the indicated cell lines were established by counting cells after three, five and seven days. The experiment was performed three times, in duplicates. Data are shown as mean $\pm$ SEM. Student's test was performed to assess statistical significance; ns, not significant, $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$ relative to WT and $\$P \leq 0.05$, $\$\$P \leq 0.001$ relative to *Sdhb*^{-/-} imCC.

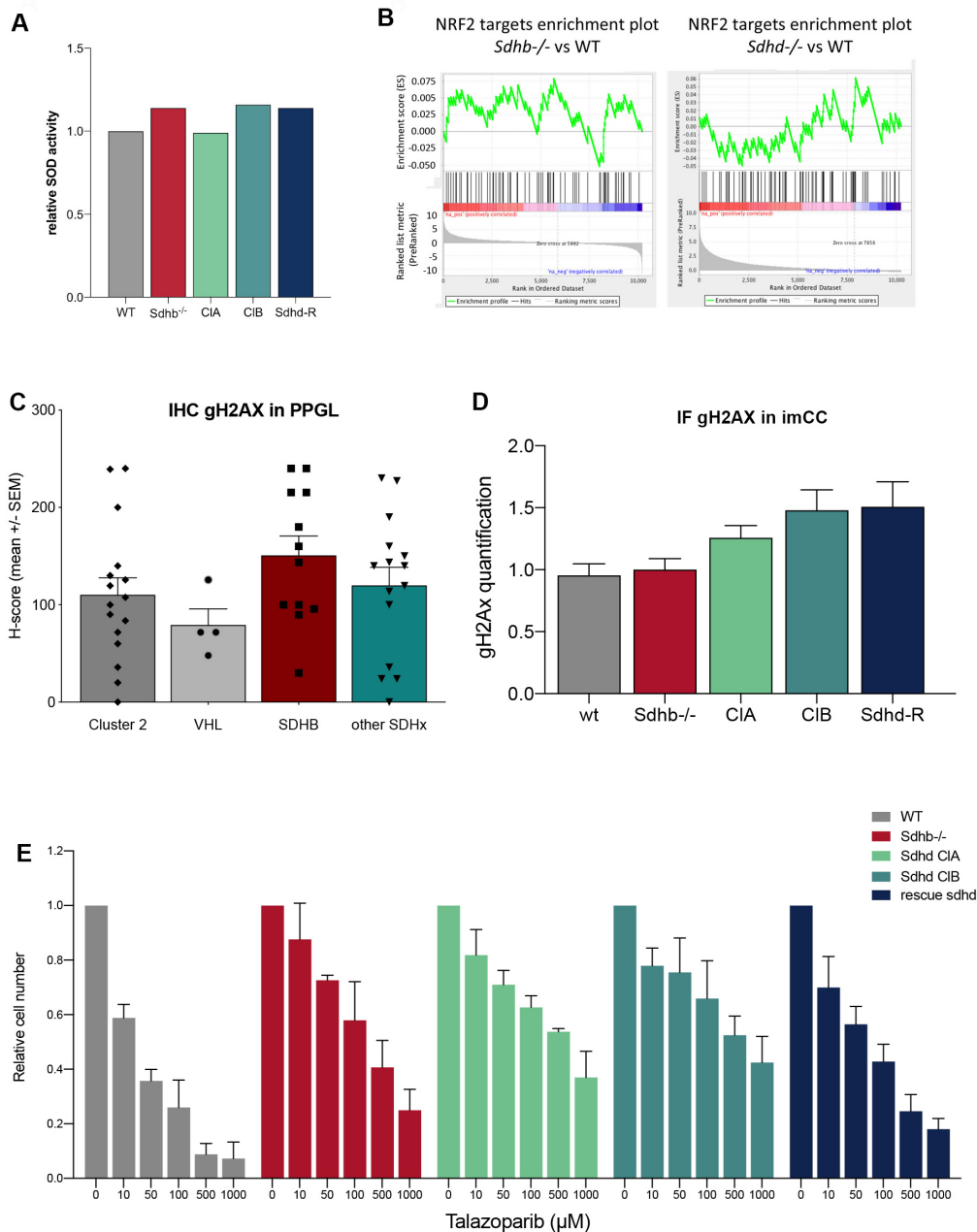


Supplementary Fig. 3 Related to Figure 3. Overexpression of HIF-target genes in *SDHB*-mutated tumors versus *SDHD*-mutated tumors. Ratio between mean expressions of 41 highly expressed HIF-target genes in *SDHB* versus *SDHD*-mutated tumors. Data from A, the CIT COMETE collection and B, the TCGA collection. Both analyses include and compare transcriptomic data from 3 *SDHD* and 17 *SDHB*-mutated tumors. Blue dots indicate genes specifically expressed in endothelial cells.



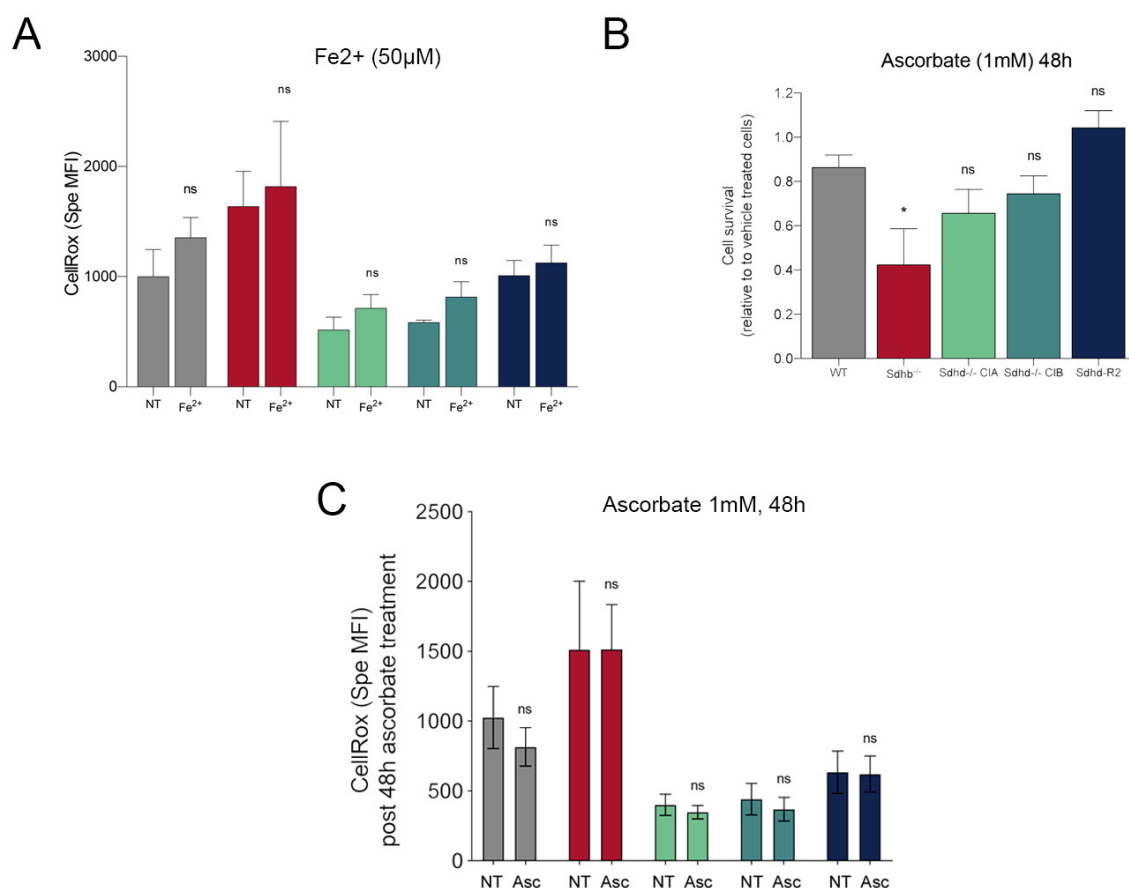
Supplementary Fig. 4 Related to Figure 4. SDH-deficient cells and tumors display alterations in copper homeostasis and *SDHx*-mutated tumors exhibit slight changes in transferrin (TF) mRNA expression levels in comparison to other types of mutated PPGL. A, mitochondrial Cu(II) content using turn-off Cu(II) probe (1) and B, mitochondrial Cu(I) content using turn-on Cu(I) probe (2) C, Average ⁶³Cu counts in 2 NF1, 2 RET, 4 SDHB and 2 SDHD tumors. A and B are from three independent experiments, presented as mean ± SEM. D, Microarray-based expression analysis of several critical

actors of cellular iron homeostasis *DMT1*, *TF*, *TFR2*, *TFRC*, *SLC31A1* and *SLC25A3* in a cohort of human PPGL, including 40 *VHL*-mutated, 19 *RET*-mutated, 37 *NF1*-mutated and 23 *SDHx*-mutated tumors. Expression clusters have been described in Burnichon et al., 2010. Data are presented as means $\pm$ SEM. Non-parametric one-way ANOVA was used to assess statistical significance; ns, not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.



Supplementary Fig. 5 Related to Figure 5. *SDHB*-mutated PGL exhibit significant decrease in ⁵⁶Fe and *Sdhb*-deficient cells do not detoxify the excess in mitochondrial ROS. A, Global superoxide dismutase (SOD) activity measured by spectrophotometry in all the indicated cell lines. **B**, Gene set enrichment analyses using RNA-seq data of 58 NRF2-target genes in *Sdhb* and *Sdhd* KO cells versus WT cells. **C**, H-score (ranging from 0 to 300) representative of the γ H2AX staining intensity in 16 tumors belonging to

cluster 2, 4 VHL, 12 SDHB and 15 other *SDHx* tumors. **D**, Quantification of nucleus foci γ H2AX staining intensity following immunofluorescence in all imCC models. Data are presented as means $\pm$ SEM. **E**, Relative cell number of all imCC models treated for 72 hours with Talazoparib (10 μ M, 50 μ M, 100 μ M, 500 μ M, 1000 μ M) relative to vehicle-treated controls (0 μ M). Data shown are from 3 independent experiments and presented as means $\pm$ SEM.



Supplementary Fig. 6 Related to Figure 6. Iron(II) and ascorbate treatment do not affect cytosolic ROS levels in SDH-deficient cells. A, Specific MFI of CellROX probe in all imCC models following treatment for 48 hours with either Iron(II) 50 μ M or vehicle (PBS 1X). **B**, Same as **A** following ascorbate 1mM treatment. Data from **A** and **B** are mean of at least three independent experiments, presented as mean $\pm$ SEM and two-way ANOVA was performed; ns, not significant, * $P \leq 0.05$, *** $P \leq 0.001$.

Supplementary Table 1 Related to Figure 3 Methods. Experimental parameters and data acquisition parameters used for LA-ICP-MS imaging.

	Tumors	NIST 612 Scans
Teledyne Photon Machines Analyte Excite		
Energy density (J cm ⁻²)	0.5	2.02
Repetition rate (Hz)	125	125
Scan speed (μm s ⁻¹)	500	500
Beam waist diameter (μm)	20 (Circle)	40 (Circle)
Scanning Mode	Fixed Dosage	Fixed Dosage
Scanning Direction	Uni-directional	Uni-directional
Effective Dosage (shots per position)	5	5
He Carrier gas flow rate (L min ⁻¹)	0.5	0.5
Thermo Fisher Scientific iCAP TQ ICP-MS		
RF power (W)	1550	1550
Ar plasma gas flow rate (L min ⁻¹)	14	14
Ar auxiliary gas flow rate (L min ⁻¹)	0.8	0.8
Nebuliser gas flow rate (L min ⁻¹)	1.03	1.03
He gas flow rate (L min ⁻¹)	3.25	3.25
Acquired m/z ratios (amu)	³¹ P, ⁵⁶ Fe, ⁶³ Cu	³¹ P, ⁵⁶ Fe, ⁶³ Cu
Respective dwell times (ms)	2.0, 5.8, 29.6	2.0, 5.8, 29.6
Total scan cycle time (ms)	40	40

Supplementary Table 2 Related to Figure 2. Differentially methylated gene-based features in *Sdhd*-

***/-* versus *Sdhd*-/- imCCs**

See excel file.

Supplementary Table 3 Related to Figure 4. List of 52 HIF-target genes used for transcriptomic analyses

Adm	adrenomedullin
Adra1b	adrenergic receptor, alpha 1b
Ak3	adenylate kinase 3
Bnip3	BCL2/adenovirus E1B interacting protein 3
Cacna1a	calcium channel, voltage-dependent, P/Q type, alpha 1A subunit
Car9	carbonic anhydrase 9
Ccl2	chemokine (C-C motif) ligand 2
Cdkn1a	cyclin-dependent kinase inhibitor 1A (P21)
Cited2	Cbp/p300-interacting transactivator, with Glu/Asp-rich carboxy-terminal domain, 2
Cp	ceruloplasmin
Ctgf	connective tissue growth factor
Cxcl12	chemokine (C-X-C motif) ligand 12
Cxcl8	Interleukin 8
Cxcr4	chemokine (C-X-C motif) receptor 4
Edn1	endothelin 1
Egln1	egl-9 family hypoxia-inducible factor 1
Egln2	egl-9 family hypoxia-inducible factor 2
Egln3	egl-9 family hypoxia-inducible factor 3
Eng	endoglin
Eno1	enolase 1, alpha non-neuron
Epas1	endothelial PAS domain protein 1
Fgf2	fibroblast growth factor 2
Flt1	FMS-like tyrosine kinase 1
Fmo5	flavin containing monooxygenase 5
Hgf	hepatocyte growth factor
Hif1a	hypoxia inducible factor 1, alpha subunit
Hk1	hexokinase 1
Hmox1	heme oxygenase 1
Igf2	insulin-like growth factor 2
Lct	lactase
Lep	leptin
Lox	lysyl oxidase
Loxl2	lysyl oxidase-like 2
Mmp13	matrix metalloproteinase 13
Mmp14	matrix metalloproteinase 14 (membrane-inserted)
Mmp2	matrix metalloproteinase 2
Nppa	natriuretic peptide type A
P4ha1	procollagen-proline, 2-oxoglutarate 4-dioxygenase (proline 4-hydroxylase), alpha 1 polypeptide
Pdgfb	platelet derived growth factor, B polypeptide
Pfkfb3	6-phosphofructo-2-kinase/fructose-2,6-bisphosphatase 3
Pfkfb4	6-phosphofructo-2-kinase/fructose-2,6-bisphosphatase 4
Pfkl	phosphofructokinase, liver, B-type
Pfkp	phosphofructokinase, platelet
Pgf	placental growth factor
Pgk1	phosphoglycerate kinase 1
Plaur	plasminogen activator, urokinase receptor
Ppfia4	protein tyrosine phosphatase, receptor type, f polypeptide (PTPRF), interacting protein (liprin), alpha 4
Ptprz1	protein tyrosine phosphatase, receptor type Z, polypeptide 1
Slc2a1	solute carrier family 2 (facilitated glucose transporter), member 1
Tfrc	transferrin receptor
Th	tyrosine hydroxylase
Trf	transferrin

97 **Supplementary Table 4 Related to Figure 4. List of 58 NRF2-target genes used for transcriptomic**
98 **analyses**

Abcc1	ATP-binding cassette, sub-family C (CFTR/MRP), member 1
Abcc2	ATP-binding cassette, sub-family C (CFTR/MRP), member 2
Abcc3	ATP-binding cassette, sub-family C (CFTR/MRP), member 3
Abcc4	ATP-binding cassette, sub-family C (CFTR/MRP), member 4
Abcc5	ATP-binding cassette, sub-family C (CFTR/MRP), member 5
Acot7	acyl-CoA thioesterase 7
Acot8	acyl-CoA thioesterase 8
Acox1	acyl-Coenzyme A oxidase 1, palmitoyl
Acox2	acyl-Coenzyme A oxidase 2, branched chain
Adh7	alcohol dehydrogenase 7 (class IV), mu or sigma polypeptide
Akr1b1	aldo-keto reductase family 1, member B1 (aldose reductase)
Akr1c1	aldo-keto reductase family 1, member C1
Aldh1a1	aldehyde dehydrogenase family 1, subfamily A1
Aldh7a1	aldehyde dehydrogenase family 7, member A1
Blvra	biliverdin reductase A
Blvrb	biliverdin reductase B (flavin reductase (NADPH))
Cbr1	carbonyl reductase 1
Cebpb	CCAAT/enhancer binding protein (C/EBP), beta
Cyp1b1	cytochrome P450, family 1, subfamily b, polypeptide 1
Ephx1	epoxide hydrolase 1, microsomal
Fech	ferrochelatase
Fthl17	ferritin, heavy polypeptide-like 17
G6pd	glucose-6-phosphate dehydrogenase
Gclc	glutamate-cysteine ligase, catalytic subunit
Gclm	glutamate-cysteine ligase, modifier subunit
Ggt1	gamma-glutamyltransferase 1
Glrx	glutaredoxin
Gls	glutaminase
Gpx2	glutathione peroxidase 2
Gpx4	glutathione peroxidase 4
Gsr	glutathione reductase
Gsta1	glutathione S-transferase, alpha 1 (Ya)
Gstm1	glutathione S-transferase, mu 1
Gstp1	glutathione S-transferase, pi 1
Hmox1	heme oxygenase 1
Idh1	isocitrate dehydrogenase 1 (NADP+), soluble
Liph	lipase, member H
Me1	malic enzyme 1, NADP(+)-dependent, cytosolic
Mgst1	microsomal glutathione S-transferase 1
Nfe2l2	nuclear factor, erythroid derived 2, like 2
Nqo1	NAD(P)H dehydrogenase, quinone 1
Pgd	phosphogluconate dehydrogenase
Pla2g7	phospholipase A2, group VII (platelet-activating factor acetylhydrolase, plasma)
Pnpla2	patatin-like phospholipase domain containing 2
Pparg	peroxisome proliferator activated receptor gamma
Ppargc1b	peroxisome proliferative activated receptor, gamma, coactivator 1 beta
Prdx1	peroxiredoxin 1
Prdx6	peroxiredoxin 6
Rxra	retinoid X receptor alpha
Slc6a9	solute carrier family 6 (neurotransmitter transporter, glycine), member 9
Slc7a11	solute carrier family 7 (cationic amino acid transporter, γ -system), member 11
Srxn1	sulfiredoxin 1 homolog (<i>S. cerevisiae</i>)
Sult1a1	sulfotransferase family 1A, phenol-preferring, member 1
Taldo1	transaldolase 1
Tkt	Transketolase
Txn	thioredoxin
Txnrd1	thioredoxin reductase 1
Ugdh	UDP-glucose dehydrogenase

Supplementary methods

Generation of *Sdhd*^{-/-} Immortalized Mouse Chromaffin Cells by CRISPR-Cas9 method

Targeted gRNA was designed *in silico* by using <http://crispr.genome-engineering.org/> as previously described (3). gRNA was transcribed *in vitro* using the kit PrecisionX Cas9 SmartNuclease RNA system (System Biosciences CAS510A-KIT). Briefly, targeted oligonucleotides were annealed to form double strands, and then cloned into SmartNuclease Linearized T7 gRNA Vector. The resulting recombinant vector was linearized by EcoRI digestion. The generated template was used to produce gRNA by *in vitro* transcription. gRNA was then purified (miRNeasy minikit, Qiagen) and its purity was assessed using the Experion RNA StdSens Analysis Kit (BioRad).

Wild-type immortalized mouse chromaffin cells (WT imCC), previously generated by our lab(4), were transfected with 0.6 µg of gRNA (RNA i-MAX (Life Technologies)) and 2µg of Cas9 (System Biosciences CAS940A-1) and 2µg of YFP plasmids (Lipofectamine 2000 (Life Technologies)). Fluorescent cells were cloned by FACS sorting. Clones were screened by direct sequencing of the targeted sequence of murine *Sdhd* gene. Two consecutive transfections were performed: the first generated three heterozygous clones out of 70, and the second performed on heterozygous clones generated 2 homozygous clones out of 288. Mycoplasma contamination was ruled out using the PCR Mycoplasma Test kit I/C (PromKine, PK-CA91-1048).

Sdhd^{-/-} clones transfection by SDHD expressing plasmid

Sdhd^{-/-} clone A was transfected with 2 µg of SDHD-expressing vector (ORIGENE, NM003002) using Lipofectamine 2000 (Life Technologies). Forty-eight hours later, selection was performed with Geneticin (Sigma, G418, 1200 µg/ml) and selected cells were cloned by FACS sorting. Clones were then screened by SDH activity test and by qRT-PCR in order to assess *Sdhd* expression.

Direct sequencing of *Sdhd* gene

Direct sequencing of the four exons and exon-intron boundaries of the *Sdhd* gene was performed by Sanger method. Specific primers (available upon request) were designed to amplify small amplicons for *Sdhd* gene sequencing. The sequencing reactions were performed using the BigDye Terminator v3.1 kit (Life Technologies), in an ABI Prism3730XL DNA Analyzer (Perkin Elmer Applied Biosystems, Foster City, CA).

Cell culture

imCC were cultured in DMEM high glucose Glutamax (Dulbecco Modified Eagle Medium, Gibco) with 10% FBS (Fetal bovine serum, Gibco) and 1% antibiotics (penicillin/streptomycin, Gibco) unless when grown for metabolic or respirometry experiments, in which case they were supplemented with pyruvate (1 mM) and no antibiotics. Cells were grown at 37°C, in 5% CO₂. When stated, cells were treated with indicated doses of iron Chloride (Sigma, 372870), MitoTEMPO (Sigma, SML0737), L-Ascorbic acid (Sigma, A5960), Talazoparib (MedChemTronica, HY-1606) or 3 mM of N-acetyl-cysteine (Sigma, A9165) for 12 h to 72 h.

¹³C-glucose and ¹³C-glutamine labeling

Cells (3 x 10⁵) were seeded onto five wells of a six-well plate and cultured in standard medium for 24 h, the remaining well was used as a control containing only medium. Cells were washed in PBS and the medium was then replaced by either fresh DMEM (no glucose, no phenol red) with 10 mM ¹³C₆-D-glucose (Sigma) or DMEM (high glucose, no glutamine) supplemented with 2 mM ¹³C₅-L-glutamine (Sigma) for 72 h.

Metabolite extraction

For spent media analysis, 200 µl of cleared media was first extracted. Culture media were then aspirated and cells were washed cold with 0.9% NaCl saline solution before being scraped off the precooled plates into Methanol/water mixture. In all cases, glutaric acid supplied in water was used as internal standard and polar metabolites were extracted using Methanol:H₂O:Chloroform at ratio 1:1:1. Briefly, samples were vortexed vigorously, left to shake with all the solvents for 15 min at 4 °C and then centrifuged at 15 000g for 15 min at 4 °C which led to separation into polar and nonpolar fractions. The polar fractions were transferred to new tubes, evaporated to dryness by SpeedVac concentrator and used for Gas Chromatography – Mass Spectrometry (GC-MS) analysis.

GC-MS analysis

The dried extract was first incubated at 95 °C in open tubes and then solubilized in 40 µl of 2% methoxyamine HCl in pyridine followed by 60 minutes incubation at 60°C and subsequently 60 µl N-tertbutyldimethylsilyl-N-methyltrifluoroacetamide with 1% (w/v) tertbutyldimethyl-chlorosilane derivatisation reagent was added. The suspension was incubated for an hour at 60 °C in a well-sealed tube to prevent evaporation. Finally, the samples were centrifuged at 16000 g for 5 minutes and the clear supernatant was transferred to a chromatography vial with a glass insert (Thermo Fisher Scientific) and proceeded immediately to GC-MS analysis.

For analysis of the derivatised samples an Agilent 7890B Series GC/MSD gas chromatograph with a polydimethylsiloxane GC column coupled, with a mass spectrometer (GC-MS) (Agilent Technologies UK Limited, Stockport, UK) was used. Prior to sample analysis the GC-MS was tuned to a full width at half maximum (FWHM) peak width of 0.60 a.m.u. in the mass range of 50 to 650 mass to charge ratio (m/z) using PFTBA tuning solution. 1 µl of sample was injected into the GC-MS in splitless mode with helium carrier gas at a rate of 1.0 ml min⁻¹. The inlet liner containing glass wool was set to a temperature of 270 °C. Oven temperature was set at 100 °C for 1 minute before ramping to 280 °C at

a rate of 5 °C min⁻¹. Temperature was further ramped to 320 °C at a rate of 10 °C min⁻¹ held at 320 °C for 5 minutes. Compound detection was carried out in full scan mode in the mass range 50 to 650 m/z, with 2-4 scans sec⁻¹, a source temperature of 250 °C, a transfer line temperature of 280 °C and a solvent delay time of 6.5 minutes. The injector needle was cleaned with acetonitrile three times before measurement commencement and three times following every measurement thereafter. The raw GC-MS data was converted to common data format (CDF) using the acquisition software and further processing of the isotope data including isotope correction and mass isotopomer analysis /batch quantification was performed on metabolite detector software. The raw peak area for each analyte of interest was calculated using the metabolite detector software followed by normalizing the response to the internal standard peak area.

High resolution respirometry

For the measurement in intact state, trypsinised cells were resuspended in cell culture media (4.5g/L glucose + 1 mM pyruvate) and loaded in Oxygraph-O2 k (Oroboros instruments) chamber. After closing the chambers and recording routine respiration, oligomycin (2.5 µM) was added to inhibit ATP synthase. Measurements of the non-phosphorylating electron transfer system (ETS) capacity were obtained through stepwise (0.5 µM) titration of the uncoupler, Carbonyl cyanide 4-(trifluoromethoxy)phenylhydrazone (FCCP). Respiration was inhibited by addition of rotenone (0.5 µM) and antimycin A (2.5 µM) at the end of the experiment. For the measurement in permeabilised state, trypsinised and washed cells were resuspended in respiratory media Mir05 (110 mM sucrose, 60 mM K⁺-lactobionate, 0.5 mM EGTA, 3 mM MgCl₂, 20 mM taurine, 10 mM KH₂PO₄, 20 mM HEPES, 1g/L BSA essentially fatty acid free, pH 7.1). After closing the chambers and recording respiration on endogenous substrates, digitonin was added to permeabilise the cells. Substrate combinations were used as indicated in the graphs. The concentrations used were 2 mM malate (M), 10 mM glutamate (G) and 20 mM succinate (SUC). In all experiments on permeabilised cells 3 mM ADP was used and

maximum respiratory capacity was reached by stepwise titration of FCCP. Respiration was inhibited by addition of 0.5 μ M rotenone and antimycin A (2.5 μ M) at the end of the experiment. Values after antimycin A addition were subtracted from all recorded values.

Assessment of enzymatic activities

Respiratory chain activities in subconfluent chromaffin cells were assayed as previously described (5). Malonate-sensitive succinate dehydrogenase (RC complex II; E.C. 1.3.5.1), glycerol 3 phosphate dehydrogenase (EC 1.1.5.3), cyanide-sensitive cytochrome *c* oxidase (RC complex IV; EC 1.9.3.1), malonate-sensitive succinate cytochrome *c* reductase (RC complex II+III; EC 1.3.99.1), and glycerol cytochrome *c* reductase (glycerol 3-phosphate dehydrogenase + RC complex III) were assayed spectrophotometrically at 37°C using a pseudo dual- wavelength Varian CARY50 spectrophotometer (Victoria, Australia) as described previously (6). Protein concentrations were determined by the Bradford method. All chemicals were analytical reagent grade from Sigma Chemical Company.

Quantitative Real-Time PCR

Total RNAs were extracted from cell pellets using RNeasy plus mini-kit (Qiagen) as described by the manufacturer. Reverse transcription was fulfilled using iScript™ cDNA Synthesis Kit (BIO-RAD) during 30 min at 42°C. qRT-PCR was then performed on CFX96™ Real-Time System C1000 Touch™ Thermal Cycler (BIO-RAD) using SuperScript SybrGreen (BioRad). Normalization was performed with 18S amplifications, and comparisons were calculated using the $\Delta\Delta$ Ct method. Primers' sequences were as follows:

18S: F 5'-CGCGGTTCTATTTTGTGGT-3'; R 5'-AACCATAAACGATGCCGAC-3';

Sdhd: F 5'-GGACCAGTGAGAGGGTTGTC-3'; R 5'-AAGCTGAGAGTGCCAAGAGG-3'

Sdhd : F 5'-GCAGCTCCCAGAATCAAAA-3' ; R 5'-CCAGAGTATTGCCTCCGTTG-3'

221 Snai1: F 5'-TGGAAAGGCCTTCTCTAGGC-3'; R 5'-AAAAGCACGGTTGCAGTGG-3'

222 Fn1: F 5'- GAAATCTGCAGCCTGGGTCT-3'; R 5'- ACACCCAGCTTGAAGCCAAT-3'

223 Epas1: F 5'-AGGGCCACAGCAAAGAGAG-3'; R 5'-CATCACGGGATTTCTCCTTC-3'

224 Mmp9: F 5'-CGGCACGCTGGAATGATC-3'; R 5'- TCGAACTTCGACACTGACAAGAA -3

225

226 **Western blot**

227 Total proteins were extracted in RIPA lysis buffer, containing protease and phosphatase inhibitors
228 cocktail (Thermo Fisher, #88669). Protein concentrations were determined with Bradford colorimetric
229 method. Equal quantities of proteins were resolved on NuPAGE® Novex 4–12 % Bis-Tris gradient gel
230 (Invitrogen) and transferred on nitrocellulose membrane. After blocking in PBS-milk solution (5%),
231 membranes were incubated overnight with specific primary antibodies, followed by washing in PBS,
232 0.05% tween-20 and incubation with corresponding HRP-conjugated (anti-rabbit or anti-mouse)
233 secondary antibodies (Bio-FX). The bound antibodies were revealed by chemiluminescence using ECL
234 (Pierce) and the results read with a LAS-4000 Mini (Fuji). The antibodies used were: anti-tubulin
235 (1/2500, Sigma-Aldrich, T9026), anti-HIF2α (1/500, abcam, ab8365), anti-SDHB (1/500, Sigma,
236 HPA002868), anti-SDHA (1/500, abcam, ab14715). The experiment was performed independently
237 three times and representative results are shown.

238

239 **Fluorescent staining**

240 All Fluorescent staining were performed on cells plated on glass slides until 80% confluence. After a
241 wash in PBS 1X, cells were fixed for 10 min in ice-cold 4% paraformaldehyde. For actin staining, a
242 permeabilization step was performed with proper buffer (0.5% triton X-100, 20 mM Tris-HCl (pH=8),
243 50 mM NaCl, 3 mM MgCl₂, 300 mM sucrose) for 10 min at room temperature. Phalloidin-TRITC toxin

(Sigma #P1951) diluted 1/1000 in PBS 1X was incubated for 1h at room temperature and washed before mounting the coverslip in vectashield with Dapi.

For γ H2AX immunofluorescence, after blocking of aspecific sites for 30 min with PBS 1% BSA 0,1% triton, the slides were incubated, overnight at 4°C, anti- γ H2AX (phospho S139) (1/100, Abcam ab81299) diluted in blocking buffer. Primary antibody was washed and the slides were incubated with the secondary antibody, conjugated with Alexa Fluor 488 (1/2000, Invitrogen) for 1 h at room temperature in the dark and then washed with PBS. Finally, the slides were mounted in Vectashield, containing DAPI, for a blue nuclear staining. Image acquisition was performed using a Confocal SP8 Leica microscope and 12 z-stacks of 0.5 μ m were merged. Nucleus foci staining intensity was measured using ImageJ software, and results were shown as the mean +/- SEM staining intensity per cell type normalized to the mean staining of *Sdhb*^{-/-} cells.

Immunohistochemical analyses

Immunohistochemistry was performed on 6 μ m sections from paraffin-embedded tumors with anti- γ H2AX antibody (phospho S139) (1/100, ab26350, Abcam). Antigen retrieval was performed by boiling slides in citrate buffer for 20 min. Revelation was performed using DAB (Dako, Australia). Images were acquired with a Leica DM400B microscope with Leica Application Suite software V.2.8.1 and a Leica DFC420C camera. H-score (ranging from 0 to 300) taking into consideration the staining intensity in conjunction with the percentage of positively stained cells was used as a semi-quantitative measure.

Cell proliferation assay

50.000 cells were plated on 6-well plates. Growth curves were established by counting cells after three, five and seven days. The experiment was performed three times, in duplicates.

Cell migration assay

Wound scratch assays were performed during 10 hours as previously described (7) and analyzed using ImageJ software. The experiment was performed four times.

Cell adhesion assay

After complete detachment from their plates by trypsin EDTA 0.05 % (Gibco), cells were plated in 6-wells plates. Cell adhesion was evaluated by taking pictures 1 h post-seeding. Adherent and non-adherent cells were identified on the basis of their morphology and the percentage of adhesive cells was calculated. The experiment was performed three times.

RNA-seq analysis

RNA sequencing was performed for 7 samples: 3 *Sdhb*^{-/-}, 2 *Sdhd*^{-/-} and 2 wild-type imCC. RNA samples were enriched for polyadenylated RNA from 5 µg of total RNA, and the enriched samples were used to generate sequencing libraries with the Illumina 'TruSeq Stranded mRNA Sample Prep' kit and associated protocol as provided by the manufacturer. Libraries were sequenced by IntegraGen (Evry, France) on an Illumina HiSeq 2000 as paired-end 75 bp reads. Quality of reads was assessed for each sample using FastQC (<http://www.bioinformatics.babraham.ac.uk/projects/fastqc/>). Fastq files were aligned to the reference Human genome hg19/GRCh37 or to the reference Mouse genome mm10 with tophat2 (-p 16 -r 150 -g 2 --library-type fr-firststrand). We removed reads mapping to multiple locations. We used HTSeq to obtain the number of reads associated to each gene in the Gencode vM9 (Mouse) database, restricting to protein-coding genes, antisense and lncRNAs. We used the Bioconductor DESeq package to import raw HTSeq counts for each sample into R statistical software and extract the count matrix. After normalizing for library size, we normalized the count matrix by the coding length of genes to compute FPKM scores (number of fragments per kilobase of exon model and millions of mapped reads). We used the Bioconductor DESeq package to obtain size factors and

dispersion estimates, and perform differential expression analysis. Hierarchical clustering (Euclidean distance, Ward method) was used to classify samples according to their expression profiles across the 1,000 most variant genes (based on standard deviation).

Reduced Representation Bisulfite Sequencing (RRBS) Analyses

RRBS was performed by Integragen SA (Evry, France), as previously described (4). In short, 4 µg of mouse genomic DNA plus CeGX Sequencing Control (3% W/W) were digested with MspI (NEB). After end-repair, A-tailing, and ligation to methylated Illumina adapters, the library fragments of 40–220 bp were gel isolated, subjected to a double bisulfite conversion using the TrueMethyl 24 kit (Cambridge Epigenetix) for each sample according to the manufacturer's instructions, PCR amplified, and sequenced on an Illumina HiSeq2000 sequencer as paired-end 75 bp reads.

We generated approximately 30 million uniquely aligned reads for each sample, which covered ≈ 1.5 million CpG sites. We used BS-Seeker2 (8) to map RRBS data to the Mouse genome mm10 and retrieve the number of methylated and unmethylated cytosines at each covered CpG site. Methylation rates were then integrated across CpG island (CGI)-based and gene-based features. CGI-based features were defined as follows: CpG islands (from UCSC database Mouse mm10), shores (2 kb on each side of the island) and shelves (2 kb on each side of the shores). DNA methylation outside CpG islands was analyzed by grouping CpG sites not located in CGI-based features every 100kb window. Gene-based features were defined based on Ensembl mus musculus GRCm38.78 assembly. We calculated for each gene the methylation rate across the promoter region (TSS $\pm$ 500bp) and the gene body. We compared methylation rates across all CGI-based and gene-based features. *q* values were computed by comparing the number of methylated and unmethylated reads in each condition using a logistic regression and the SLIM method for p-value adjustment, as implemented in the methylKit package (9). We also calculated the methylation rate difference (delta) between each pair of test and reference sample. We considered as differentially methylated every region with a *q*-value <0.05 and a

318 methylation delta >0.05 or <-0.05 in at least 80% of test-reference pairs.

319

320 **Features of Oxidative Stress**

321 Cells were seeded onto six-well plates and grown up to 70% confluency for 2 days. After what they
322 were directly incubated with fluorescent probes for basal conditions. Cells were washed with PBS,
323 trypsinized and resuspended in PBS solution containing 10% FBS for flow cytometric analysis. Flow
324 cytometry data were acquired using an LSR FORTRESSA analyzer (BD biosciences). For ROS
325 quantification upon treatment, cells were treated for 12 or 48 hours with 3 mM of N-acetyl-cysteine
326 (Sigma, A9165), 50 μ M iron chloride (Sigma, 372870), 2.5 μ M or 2.5 mM MitoTEMPO (Sigma, SML0737)
327 or 2.5 mM of L-Ascorbic acid (Sigma, A5960) and then processed, as described above.

328

329 **Cellular and mitochondrial ROS**

330 Cells were incubated with either 5 μ M CellRox Reagent (Thermofisher, #10422) or 5 μ M MitoSox
331 (Thermofisher, #M36008) for 30 min at 37°C in the dark.

332

333 **Lipid Peroxide Product**

334 Cells were incubated with 2 μ M Bodipy C11 Reagent (Termofisher, #D3861) for 30 min at 37°C in the
335 dark.

336

337 **Mitochondrial mass and membrane potential assessment using MitoTracker Probe**

338 Cells were seeded onto six-well plates and grown up to 70% confluency. Mitochondrial content per
339 cell line was estimated using MitoTracker Deep Red FM (Thermofisher #M22426). For assessment of
340 mitochondrial membrane potential, cells were stained with tetramethylrhodamine-methyl-ester

(TMRM, Thermofisher #T668). Cells were stained with 250 nM MitoTracker Deep Red FM or 100 μ M TMRM for 30 min at 37C. Cells were then washed with PBS solution, trypsinized, and resuspended in PBS solution containing 10% FBS for flow cytometric analysis. Flow cytometry data were acquired using an LSR FORTESSA analyzer (BD biosciences).

Cellular levels of iron and copper

Metal-specific probes were synthesized as previously described. For mitochondrial copper and iron probes, cells were incubated at 37°C in the dark with the relevant probe prior to being analyzed by flow cytometry using the following probes and conditions: 1 μ M turn-off Iron(II) probe (10) (1h) for mitochondrial Iron(II) content; 5 μ M Rhonox-1 (turn-on Iron(II)) probe (11) (1h) for cytosolic Iron(II) content ; 1 μ M Calcein-AM probe (Thermofisher, #C1430) (1h) for labile overall iron content ; 10 μ M turn-off Cu(II) probe (1) (1h) for mitochondrial Cu(II) content ; 1 μ M turn-on Cu(I) probe (2) (30min) for mitochondrial Cu(I) content. Cells were trypsinized (TrypLE Express Enzyme, Life Technologies, 12605010) and washed twice with ice cold PBS. Data were recorded on a BD Accuri C6 (BD Biosciences) and processed using Cell Quest (BD Biosciences) and FlowJo (FLOWJO, LLC) software.

Laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS)

For the LA-ICP-MS experiments, an Analyte Excite 193 nm ArF*excimer-based LA system (Teledyne Photon Machines, Bozeman, MT, USA) was used, equipped with the HeEx II two-volume ablation cell. The LA system was coupled to a Thermo Fisher Scientific iCAP TQ ICP-mass spectrometer (Thermo Fisher Scientific, Waltham, MA, USA) via the Aerosol Rapid Introduction System (ARIS). Tuning of the instrument settings was performed using a NIST SRM 612 glass certified reference material (National Institute for Standards and Technology, Gaithersburg, MD, USA), optimizing for low laser-induced elemental fractionation through monitoring of $^{238}\text{U}+ / ^{232}\text{Th}+$ ratios, low oxide formation (<1%) monitoring $^{232}\text{Th}^{16}\text{O}+ / ^{232}\text{Th}+$ ratios, and high sensitivity for $^{59}\text{Co}+$, $^{115}\text{In}+$ and $^{238}\text{U}+$. LA-ICP-MS images

were acquired in a fixed dosage mode, with a vertical and horizontal spatial resolution of 20 μm , a detailed list of sample settings is available in Supplementary Table 1. Formalin-fixed paraffin-embedded tumor tissue sections were dewaxed in xylene immediately prior to imaging, and rehydrated through a descending ethanol series. Two experimental repeats were conducted, each of which consisted of imaging sections from one *NF1* mutant and two *SDHB* mutant tumors (n=6 total tumors interrogated using LA-ICP-MS). Samples were mounted inside a bespoke three slide sample holder of the HelEx II two-volume ablation cell (Teledyne Photon Machines). To correct for instrumental drift, a series of NIST 612 standard ablation scans were performed before and after each tumor image. ICP-MS and positional data were reconstructed using the HDF-based Image Processing software (HDIP, Teledyne Photon Machines Inc., Bozeman, MT, USA). A bespoke pipeline written in Python (version 2.7), was used to generate elemental images from reconstructed data. Negative values, attributed to instrumental noise, were replaced with zeros. All LA-ICP-MS images are displayed using the same threshold to enable a direct visual comparison between tumor sections. Average ^{56}Fe and ^{63}Cu intensities were calculated from pixels containing a positive elemental tissue marker (^{31}P) ensuring background regions did not influence these calculations. Statistical significance between elemental intensities was assessed by Student's t-test.

Statistical analysis

Data are represented as mean (of at least 3 independent experiments) $\pm$ SEM (standard error of the mean). Data were analyzed by one-way or 2-way ANOVA. The results were considered to be significant if $p \leq 0.05$. Statistics tests were carried out using the Graph-Pad software.

Enrichment analysis

We used an in-house adaptation of the GSEA method to identify gene sets from the MSigDB database overrepresented among up/down-regulated and hyper/hypomethylated genes.

391

392 **Data access**

393 The sequencing data reported in this paper have been deposited to the EGA (European Genome-
394 phenome Archive) database (European Genome-phenome Archive) database (accession
395 number EGAS00001005279).

396

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427

Gene-based features showing significantly different methylation in *Sdhb*

chr	start	end	gene name	gene feature
chr1	3670998	3671998	Xkr4	TSS500
chr1	3205901	3670998	Xkr4	body
chr1	3905739	3985715	RP23-333I7.1	body
chr1	4290846	4408741	Rp1	body
chr1	4490931	4496854	Sox17	body
chr1	4808288	4848410	Lypla1	body
chr1	5588966	5606131	Oprk1	body
chr1	5913707	5916898	Npbwr1	body
chr1	6358718	6359718	Fam150a	TSS500
chr1	6487731	6860940	St18	body
chr1	7089420	7173628	Pcmt1	body
chr1	7349406	7397369	Gm26901	body
chr1	7498468	7518149	RP24-181G14.2	body
chr1	9299378	9300378	Sntg1	TSS500
chr1	8361475	9299378	Sntg1	body
chr1	9545908	9547455	Rrs1	body
chr1	9600699	9601699	3110035E14Rik	TSS500
chr1	9601699	9627143	3110035E14Rik	body
chr1	9797607	9798607	Sgk3	TSS500
chr1	9908138	9909138	Mcm2	TSS500
chr1	9909138	9942085	Mcm2	body
chr1	9967432	9968432	Tcf24	TSS500
chr1	10008636	10009636	Ppp1r42	TSS500
chr1	10324720	10719445	Cpa6	body
chr1	10992965	10993965	Prex2	TSS500
chr1	10993965	11303681	Prex2	body
chr1	11413605	11414605	A830018L16Rik	TSS500
chr1	11414605	11975901	A830018L16Rik	body
chr1	12668063	12673090	Gm17644	body
chr1	12992150	12993150	Slco5a1	TSS500
chr1	12866549	12992150	Slco5a1	body
chr1	13126663	13127663	Prdm14	TSS500
chr1	13113457	13126663	Prdm14	body
chr1	13139105	13373583	Ncoa2	body
chr1	13564698	13589410	Tram1	body
chr1	13623330	13660046	Lactb2	body
chr1	13669271	13701723	Xkr9	body
chr1	14309735	14310735	Eya1	TSS500
chr1	14168954	14309735	Eya1	body

chr1	14753437	14776931	Gm9947	body
chr1	14755492	14756492	Msc	TSS500
chr1	14753346	14755492	Msc	body
chr1	15286754	15287754	Kcnb2	TSS500
chr1	15287754	15723750	Kcnb2	body
chr1	15806146	15844052	Terf1	body
chr1	15892222	15893222	Sbspon	TSS500
chr1	16519612	16520612	Stau2	TSS500
chr1	16540790	16618989	Ube2w	body
chr1	16898685	17091631	Gm28376	body
chr1	17097389	17098389	Jph1	TSS500
chr1	17124247	17125247	Gm28783	TSS500
chr1	17144862	17145862	Gdap1	TSS500
chr1	17727146	17728146	Gm16070	TSS500
chr1	17676027	17727146	Gm16070	body
chr1	17727545	17766344	Crispld1	body
chr1	19063300	19104340	Gm15825	body
chr1	19102522	19103522	Tfap2d	TSS500
chr1	19209414	19238576	Tfap2b	body
chr1	20057779	20617564	Pkhd1	body
chr1	20356952	20392300	4930486I03Rik	body
chr1	20890106	20891106	Paqr8	TSS500
chr1	20952126	20990841	Efhc1	body
chr1	21218075	21219075	Tmem14a	TSS500
chr1	21250359	21271093	Gm28836	body
chr1	21961442	21962442	Kcnq5	TSS500
chr1	21960342	21962530	Gm26580	body
chr1	22805224	22806224	Rims1	TSS500
chr1	22286251	22805224	Rims1	body
chr1	23762253	23849158	B3gat2	body
chr1	24178110	24252684	Col9a1	body
chr1	24586972	24587972	Col19a1	TSS500
chr1	24261890	24586972	Col19a1	body
chr1	24963209	24964658	Gm28237	body
chr1	25829207	25830207	Bai3	TSS500
chr1	25067476	25829207	Bai3	body
chr1	32172214	32173214	Khdrbs2	TSS500
chr1	32173214	32658568	Khdrbs2	body
chr1	33852052	33907316	Bend6	body
chr1	34460262	34475733	Ptpn18	body
chr1	34560443	34561443	Prss40	TSS500
chr1	34543968	34560443	Prss40	body
chr1	34579211	34580211	1700101I19Rik	TSS500
chr1	34579157	34580157	Amer3	TSS500

chr1	34580157	34590944	Amer3	body
chr1	34677688	34678688	Arhgef4	TSS500
chr1	36067900	36068900	Hs6st1	TSS500
chr1	36068900	36106446	Hs6st1	body
chr1	36264597	36274179	Neurl3	body
chr1	36368681	36369681	Kansl3	TSS500
chr1	36471120	36472120	Cnnm4	TSS500
chr1	36538929	36539929	ANKRD23	TSS500
chr1	36537507	36546945	Ankrd39	body
chr1	36761298	36762298	Zap70	TSS500
chr1	37027096	37187613	Vwa3b	body
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chr2	33641693	33646354	C130021I20Rik	body
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chr2	35060938	35061938	Hc	TSS500
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chr2	147083316	147084945	Nkx2-4	body
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chr2	147183583	147184583	Nkx2-2os	TSS500
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chrX	36902399	36903399	Nkrf	TSS500
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chrX	37084902	37085902	Rpl39	TSS500
chrX	37091678	37109822	Upf3b	body
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chrX	37190663	37191663	Ndufa1	TSS500
chrX	37213804	37221758	Rhox1	body
chrX	37250419	37258983	Rhox3a	body
chrX	37411567	37412567	Rhox2b	TSS500
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chrX	37459085	37473964	Rhox3c	body
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chrX	37493928	37497623	Rhox2d	body
chrX	37581492	37585496	Rhox3f	body
chrX	37642970	37643970	Rhox2g	TSS500
chrX	37826410	37827410	Rhox6	TSS500
chrX	38104077	38110407	Rhox12	body
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chrX	41794991	41920174	Thoc2	body
chrX	42148817	42149817	Stag2	TSS500
chrX	42149817	42277185	Stag2	body
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chrX	42527866	43428626	Tenm1	body
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chrX	48541625	48594004	Zfp280c	body
chrX	48622913	48623913	Slc25a14	TSS500
chrX	48623913	48662294	Slc25a14	body
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chrX	49797249	49798249	Igsf1	TSS500
chrX	49782536	49797249	Igsf1	body
chrX	50840547	50841547	Stk26	TSS500
chrX	50942210	50943210	Frmd7	TSS500
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chrX	72432681	72656348	Gabra3	body
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chrX	73242630	73243630	Xlr4c	TSS500
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chrX	73484102	73495933	Bgn	body
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chrX	74023098	74024098	Mir5132	TSS500
chrX	74023436	74024436	Mir718	TSS500
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chrX	74296597	74297597	Atp6ap1	TSS500
chrX	74353118	74354118	Lage3	TSS500
chrX	74365718	74372718	Ubl4	body
chrX	74392772	74393772	Fam3a	TSS500
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chrX	75172715	75382115	F8	body
chrX	75513799	75514799	Vbp1	TSS500
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chrX	75550617	75551617	Gm15384	TSS500
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chrX	77510513	77511513	Tbl1x	TSS500
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chrX	79623231	79670935	Mageb16	body
chrX	81070694	81072602	Gm26775	body
chrX	81070198	81071198	Tmem47	TSS500
chrX	81071198	81097872	Tmem47	body
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chrX	82949370	85206141	Dmd	body
chrX	85573522	85574522	Tab3	TSS500
chrX	86250254	86304593	Mageb4	body

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chrX	94541643	94542643	Maged1	TSS500
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chrX	96455859	96574485	Heph	body
chrX	97333840	97376716	Eda2r	body
chrX	99003748	99074728	Stard8	body
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chrX	134717463	134718463	Armxc1	TSS500
chrX	134756095	134757095	Armxc3	TSS500
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chrX	134804145	134808721	Armxc2	body
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chrX	144689407	145122411	Zcchc16	body
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chrX	148858140	148924139	Luzp4	body
chrX	149595070	149636764	Gm10439	body
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chrX	150397773	150458654	Tmem29	body
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chrX	152015795	152016795	Ribc1	TSS500
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chrX	152143768	152144768	Iqsec2	TSS500
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chrX	162159230	162160230	Nhs	TSS500
chrX	161907723	161908723	Gm15202	TSS500
chrX	162643149	162644149	Reps2	TSS500
chrX	162411954	162643149	Reps2	body
chrX	162778919	162828954	Txlng	body
chrX	163760829	163761829	Rnf138rt1	TSS500
chrX	163908517	163909517	Ap1s2	TSS500
chrX	163909517	163933666	Ap1s2	body
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chrX	163976822	164027497	Car5b	body
chrX	164089330	164118860	Tmem27	body
chrX	164139832	164188420	Ace2	body
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chrX	164268871	164269871	Pir	TSS500
chrX	164437494	164459170	Asb11	body
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chrX	166238411	166239411	Gpm6b	TSS500
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chrX	166440074	166441074	Trappc2	TSS500
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chrX	166523007	166585220	Egfl6	body
chrX	166618102	166621042	Gm15226	body
chrX	167028497	167029497	Gm22368	TSS500
chrX	167208815	167209815	Tmsb4x	TSS500
chrX	167346322	167382249	Prps2	body
chrX	167471309	168576731	Frmpd4	body
chrX	168654117	168673398	Msl3	body
chrX	168794599	168795599	Arhgap6	TSS500
chrX	169037674	169106036	Gm15261	body
chrX	169319872	169320872	Hccs	TSS500
chrX	169684699	169685699	Mid1	TSS500
chrX	169685699	170005736	Mid1	body
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chr3	4797058	4798058	1110015O18Rik	TSS500
chr3	7613260	7614260	Il7	TSS500
chr3	8925593	9004223	Tpd52	body
chr3	9427020	9609585	Zfp704	body
chr3	10012048	10013048	Fabp5	TSS500
chr3	10204088	10208076	Fabp4	body

chr3	10244209	10300683	Fabp12	body
chr3	10339953	10350817	Zfand1	body
chr3	10366407	10367407	Chmp4c	TSS500
chr3	13471329	13472329	RP23-333L19.2	TSS500
chr3	13471155	13472155	RP23-333L19.1	TSS500
chr3	13472155	13474596	RP23-333L19.1	body
chr3	13471906	13474096	Gm2464	body
chr3	14641227	14642227	Car13	TSS500
chr3	14863012	14864012	Car3	TSS500
chr3	14885773	14886773	Car2	TSS500
chr3	15153065	15170942	RP24-150C17.1	body
chr3	17790421	17808970	Mir124-2hg	body
chr3	18053674	18054674	Bhlhe22	TSS500
chr3	18054674	18057517	Bhlhe22	body
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chr3	18071950	18242838	Cyp7b1	body
chr3	18341667	18460754	RP23-77D22.1	body
chr3	18468287	18479977	RP24-86E1.1	body
chr3	19693401	19694896	Crh	body
chr3	20034815	20035815	Hps3	TSS500
chr3	20275233	20276233	Cpb1	TSS500
chr3	20366677	20367677	Agtr1b	TSS500
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chr3	26638120	26983212	Spata16	body
chr3	27183465	27284608	Nceh1	body
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chr3	27371851	27378010	Ghsr	body
chr3	28262714	28263714	Tnik	TSS500
chr3	28263714	28675858	Tnik	body
chr3	28698403	28728363	Slc2a2	body
chr3	28702667	28780608	1700112D23Rik	body
chr3	29081523	29082523	Egfem1	TSS500
chr3	29773466	29892677	RP23-212H4.3	body
chr3	29891514	29924191	Mannr	body
chr3	30547508	30548508	Mecom	TSS500
chr3	29951296	30547508	Mecom	body
chr3	30645007	30672431	Lrriq4	body
chr3	30699343	30700343	Lrrc31	TSS500
chr3	30855450	30856450	Gpr160	TSS500
chr3	31038466	31039466	Mir7008	TSS500
chr3	31149420	31150420	Cldn11	TSS500

chr3	31150420	31164324	Cldn11	body
chr3	31309878	31310878	Slc7a14	TSS500
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chr3	32817046	32818046	Usp13	TSS500
chr3	32818046	32938071	Usp13	body
chr3	32949408	33142747	Pex5l	body
chr3	33025277	33088607	4930419G24Rik	body
chr3	33812361	33843810	Ccdc39	body
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chr3	34020579	34069342	Fxr1	body
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chr3	35932545	35933545	Gm15952	TSS500
chr3	36221775	36222775	Qrfpr	TSS500
chr3	37222759	37232118	Il21	body
chr3	37613413	37614413	4930594O21Rik	TSS500
chr3	37639447	37640447	Spry1	TSS500
chr3	38557714	38558714	Gm24462	TSS500
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chr3	38887440	39011985	Fat4	body
chr3	39358628	39359628	Gm9845	TSS500
chr3	40531786	40704774	Intu	body
chr3	40743995	40744995	Hspa4l	TSS500
chr3	40893623	40894623	6430590A07Rik	TSS500
chr3	41066326	41082546	Pgrmc2	body
chr3	45160195	45161195	Gm27989	TSS500
chr3	45377760	45378760	2610316D01Rik	TSS500
chr3	45280437	45377760	2610316D01Rik	body
chr3	45377898	45378898	Pcdh10	TSS500
chr3	46447719	46448719	Pabpc4l	TSS500
chr3	46442197	46447719	Pabpc4l	body
chr3	48608602	48609602	1700018B24Rik	TSS500
chr3	49326180	49367359	RP23-290N20.3	body
chr3	50443114	50444114	Slc7a11	TSS500
chr3	49892526	50443114	Slc7a11	body
chr3	51058910	51074356	Gm29230	body
chr3	51224947	51251644	Ccrn4l	body
chr3	51377524	51378524	RP23-403H2.2	TSS500
chr3	51396238	51397238	Mgarp	TSS500
chr3	51515319	51560379	Setd7	body

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chr3	52134047	52221497	RP24-568B16.4	body
chr3	52268435	52268935	Gm20402	body
chr3	52740216	52776656	RP24-92E18.1	body
chr3	52906756	52927166	RP24-297E7.1	body
chr3	53448588	53462823	Nhlrc3	body
chr3	53656855	53657855	Frem2	TSS500
chr3	53513939	53656855	Frem2	body
chr3	54155557	54156557	Trpc4	TSS500
chr3	54156557	54318470	Trpc4	body
chr3	54631939	54634627	Gm26678	body
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chr3	55054555	55055555	Ccna1	TSS500
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chr3	55182528	55209957	Sohlh2	body
chr3	55243026	55539064	Dclk1	body
chr3	57642904	57651215	Commd2	body
chr3	57666485	57692037	Ankub1	body
chr3	58141707	58163307	1700007F19Rik	body
chr3	59006478	59007478	Med12l	TSS500
chr3	59007478	59318410	Med12l	body
chr3	59343894	59344894	Igsf10	TSS500
chr3	59343771	59344771	RP23-314I1.1	TSS500
chr3	60473330	60629750	Mbnl1	body
chr3	61003286	61004286	RP24-159H19.2	TSS500
chr3	61003295	61008982	P2ry1	body
chr3	61365451	61366451	B430305J03Rik	TSS500
chr3	62340032	62341032	RP23-83N21.1	TSS500
chr3	62337524	62340032	RP23-83N21.1	body
chr3	62337844	62338844	Arhgef26	TSS500
chr3	62338844	62462221	Arhgef26	body
chr3	62529077	62604640	Gpr149	body
chr3	63242037	63386030	Mme	body
chr3	64258961	64286995	Vmn2r3	body
chr3	64388621	64414796	Vmn2r4	body
chr3	64537561	64564798	Vmn2r6	body
chr3	64690660	64844265	Vmn2r7	body
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chr3	65658788	65659788	Mir8120	TSS500
chr3	65665728	65666728	Lekr1	TSS500
chr3	65829116	65871781	RP23-251B16.2	body
chr3	66053558	66296337	Veph1	body
chr3	66220410	66225805	Ptx3	body
chr3	66971727	66981271	Shox2	body

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chr3	67515023	67516023	Rarres1	TSS500
chr3	67478972	67515023	Rarres1	body
chr3	67891720	67892720	lqcj	TSS500
chr3	67892720	68056593	lqcj	body
chr3	67891732	67892732	SCHIP1	TSS500
chr3	67892732	68626466	SCHIP1	body
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chr3	68867917	68869766	Gm17641	body
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chr3	68870086	68872163	1110032F04Rik	body
chr3	69067149	69126613	Kpna4	body
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chr3	69221919	69222919	Arl14	TSS500
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chr3	73047265	73057303	Slitrk3	body
chr3	73066816	73594830	RP23-275B16.1	body
chr3	73329934	73470014	RP24-74B11.1	body
chr3	73351206	73481151	RP24-369K4.1	body
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chr3	79287673	79289848	RP24-253I2.1	body
chr3	79337161	79464129	Gm17359	body
chr3	80055392	80213085	RP23-121N19.3	body
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chr3	82538383	82547584	Npy2r	body
chr3	82926665	83007988	RP24-180K20.1	body
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chr3	83049363	83050363	Fgb	TSS500
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chr3	84155286	84156286	Mnd1	TSS500
chr3	84160439	84304946	Trim2	body
chr3	84479929	84480929	Fhdc1	TSS500
chr3	84582125	84583125	Arfip1	TSS500
chr3	84496426	85887016	RP24-559D1.1	body
chr3	84665692	84666692	Tmem154	TSS500
chr3	85660061	85887018	Fam160a1	body
chr3	86768071	86778153	RP23-438M14.4	body
chr3	86786151	86920352	Dclk2	body
chr3	87250758	87263238	Fcrls	body
chr3	87376887	87402934	Fcrl1	body
chr3	87436273	87500678	Fcrl5	body
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chr3	87736923	87748125	Lrrc71	body
chr3	87747890	87823806	Pear1	body
chr3	87794662	87795662	Ntrk1	TSS500
chr3	87778244	87794662	Ntrk1	body
chr3	87797451	87816101	Insrr	body
chr3	87948166	87949166	Crabp2	TSS500
chr3	87949166	87953376	Crabp2	body
chr3	87970578	87971578	Nes	TSS500
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chr3	88207313	88229959	Gm3764	body
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chr3	89159696	89160696	Hcn3	TSS500
chr3	89182643	89183643	Fam189b	TSS500
chr3	89226588	89227588	Mtx1	TSS500
chr3	89226698	89227698	Mir92b	TSS500
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chr3	89350219	89364753	Dcst1	body

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chr3	89753448	89764132	Chrn2	body
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chr3	89830870	89831870	She	TSS500
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chr3	90253663	90254663	Crtc2	TSS500
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chr3	90385239	90389438	Slc27a3	body
chr3	90465366	90466366	Npr1	TSS500
chr3	90498956	90508998	Chtop	body
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chr3	93015187	93016187	Crc1	TSS500
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chr3	94399719	94404501	Lingo4	body
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chr3	94478331	94479331	Celf3	TSS500
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chr3	94785992	94786992	Cgn	TSS500
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chr3	95527286	95556403	Ctss	body
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chr3	96180651	96181651	Sv2a	TSS500
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chr3	96261682	96262811	Hist2h4	body
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chr3	96601633	96625352	Lix1l	body
chr3	96696884	96706070	Pias3	body
chr3	96708060	96709060	Nudt17	TSS500
chr3	96711490	96727128	Polr3c	body
chr3	96904846	96905846	Gpr89	TSS500
chr3	96918863	96925520	Gja8	body
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chr3	97888207	97889207	Pde4dip	TSS500
chr3	97689824	97888207	Pde4dip	body
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chr3	98618636	98629809	Hsd3b5	body
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chr3	102720231	102734917	Tspan2os	body
chr3	102734029	102735029	Tspan2	TSS500
chr3	102735029	102772292	Tspan2	body
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chr3	103833101	103854618	Bcl2l15	body
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chr3	104767406	104781340	Fam19a3	body
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chr3	104789511	104794459	Rhoc	body
chr3	104961209	104962209	Wnt2b	TSS500
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chr3	105441595	105452455	Kcnd3os	body
chr3	105451830	105452830	Kcnd3	TSS500

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chr3	105996957	106014146	Pifo	body
chr3	106481905	106482905	Dennd2d	TSS500
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chr3	107101067	107102067	Kcna2	TSS500
chr3	107102067	107106879	Kcna2	body
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chr3	107326110	107332789	Rbm15	body
chr3	107517518	107518518	Slc6a17	TSS500
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chr3	107594531	107595531	Alx3	TSS500
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chr3	107926334	107931317	Gstm7	body
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chr3	108211472	108226148	Sypl2	body
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chr3	108853678	108889508	Fndc7	body
chr3	109079969	109080969	Slc25a54	TSS500
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chr3	116488963	116507708	Rtca	body
chr3	116512570	116513570	Dbt	TSS500
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chr3	116968767	116984406	4930455H04Rik	body
chr3	117060517	117077265	1700061I17Rik	body
chr3	117319145	117360376	Lppr4	body
chr3	117322441	117323441	Gm22408	TSS500
chr3	117574727	117575727	Lppr5	TSS500
chr3	117781497	117868436	Snx7	body
chr3	118429824	118430824	Gm26871	TSS500

chr3	118430824	118530022	Gm26871	body
chr3	118434221	118435221	Gm24155	TSS500
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chr5	8072352	8367660	Adam22	body
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chr5	100671359	100678105	Gm15777	body
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chr5	114567516	114568516	Fam222a	TSS500
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chr5	114822960	114823960	Gm20499	TSS500
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chr8	27123832	27128132	Brf2	body
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chr8	27197460	27202047	Got1l1	body
chr8	27225776	27229088	Adrb3	body
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chr8	27413444	27414444	Chrna6	TSS500
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chr8	31088971	31089971	Dusp26	TSS500
chr8	31089971	31097047	Dusp26	body
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chr8	33517238	33585582	Tex15	body
chr8	33653023	33698163	Gsr	body
chr8	33929363	33930363	Rbpms	TSS500
chr8	33782643	33929363	Rbpms	body
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chr8	34049762	34057046	Gm9951	body
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chr8	35826059	35827059	Cldn23	TSS500
chr8	35824709	35826059	Cldn23	body
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chr8	36216064	36249016	Lonrf1	body
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chr8	39006367	39165112	Tusc3	body
chr8	40307958	40386308	Micu3	body
chr8	40634297	40635297	Mtmr7	TSS500
chr8	40551095	40634297	Mtmr7	body

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chr8	40861896	40862896	Slc7a2	TSS500
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chr8	47413629	47415359	Gm10083	body
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chr8	57332618	57340682	5033428I22Rik	body
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chr8	68061786	68062786	Psd3	TSS500
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chr8	68277067	68347694	Sh2d4a	body
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chr8	71405510	71406510	Ankle1	TSS500
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chr8	71536937	71537937	Bst2	TSS500
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chr8	111154421	111258716	Glg1	body
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chr8	111345135	111393324	Fa2h	body
chr8	111449700	111450700	Mir1957b	TSS500
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chr8	121115671	121116671	Foxc2	TSS500
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chr8	123101850	123102850	Rpl13	TSS500
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chr8	125751508	125897817	Pcnxl2	body
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chr12	108334877	108362231	Cyp46a1	body
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chr12	108701806	108702806	Degs2	TSS500
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chr17	23844355	23859776	Prss32	body
chr17	23942172	23945607	Sbp	body
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chr17	23993535	23997600	Prss22	body
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chr17	24203848	24208887	Ntn3	body
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chr17	24649805	24650805	Slc9a3r2	TSS500
chr17	24689455	24690455	Syng3	TSS500
chr17	24685092	24689455	Syng3	body
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chr17	25794571	25796636	Metrn	body
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chr17	25809585	25821244	Fbxl16	body
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chr17	25828367	25829367	Jmjd8	TSS500
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chr17	25951972	25963610	D630044L22Rik	body
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chr17	26095008	26096008	Nme4	TSS500
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chr17	27028509	27029509	Bak1	TSS500
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chr17	28548989	28549989	Clpsl2	TSS500
chr17	28575218	28576218	Lhfpl5	TSS500
chr17	28576218	28583593	Lhfpl5	body
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chr17	28768807	28769807	Mapk13	TSS500
chr17	28859003	28860003	Pnpla1os	TSS500
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chr17	29319377	29329413	Pi16	body
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chr17	30955179	31010708	Umodl1	body
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chr17	34262709	34263709	H2-Ab1	TSS500
chr17	34263709	34269418	H2-Ab1	body
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chr17	34325165	34326165	H2-Eb2	TSS500
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chr17	34878983	34879983	Zbtb12	TSS500
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chr17	34972203	34973203	Hspa1l	TSS500
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chr17	35058535	35059535	Ddah2	TSS500
chr17	35065684	35066684	G6b	TSS500
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chr17	35220334	35221334	Gm16181	TSS500
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chr17	35341742	35342742	H2-Q2	TSS500
chr17	35379792	35380792	Gm11131	TSS500
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chr17	35424350	35425350	H2-Q6	TSS500
chr17	35438655	35439655	H2-Q7	TSS500
chr17	35439655	35443773	H2-Q7	body
chr17	35470589	35474563	H2-Q10	body
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chr17	36989037	36990037	H2-M5	TSS500
chr17	36984061	36989037	H2-M5	body
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chr17	45630204	45658825	Capn11	body
chr17	45733344	45734344	1600014C23Rik	TSS500
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chr17	91092305	91093305	Nrxn1	TSS500
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chr18	4373669	4379480	Gm26865	body
chr18	4375092	4376092	Mtpap	TSS500
chr18	5162880	5165231	Gm26682	body
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chr18	5591360	5592360	Zeb1	TSS500
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chr18	17019551	17137559	1700001G01Rik	body
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chr18	20059054	20060054	Dsc2	TSS500
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chr18	22344383	22345383	Asxl3	TSS500
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chr18	36952148	36953148	Pcdha4	TSS500
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chr18	37662132	37663132	RP23-56B11.7	TSS500
chr18	37668453	37669453	Pcdhga2	TSS500
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chr18	37719869	37720869	Pcdhgb4	TSS500
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chr18	37954579	37955579	Rel2	TSS500
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chr18	43208197	43317481	Stk32a	body
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chr18	43477277	43478277	Gm27325	TSS500
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chr18	44425061	44811682	Mcc	body
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chr18	46212107	46213107	Trim36	TSS500
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chr18	61688435	61692537	Il17b	body
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chr18	61726890	61735917	1500015A07Rik	body
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chr18	64339864	64340864	Onecut2	TSS500
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chr18	65938589	65939589	Rax	TSS500
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chr18	67404767	67448666	Afg3l2	body
chr18	67464349	67465349	Slmo1	TSS500
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chr18	74441436	74771493	Myo5b	body
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chr18	82474646	82475646	Mbp	TSS500
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chr19	6398840	6399840	Rasgrp2	TSS500
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chr19	8160165	8218400	Slc22a29	body

chr19	8335371	8404611	Slc22a30	body
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chr19	16872316	16873330	Foxb2	body
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chr19	23972751	24030519	Fam189a2	body
chr19	24555372	24556372	Pip5k1b	TSS500
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chr19	25506118	25604329	Dmrt1	body
chr19	25610037	25611037	Dmrt3	TSS500
chr19	25671753	25672753	2610016A17Rik	TSS500
chr19	25671134	25671753	2610016A17Rik	body
chr19	25671920	25672920	Dmrt2	TSS500
chr19	25672920	25679010	Dmrt2	body
chr19	26605615	26778321	Smarca2	body
chr19	28834549	28835549	Slc1a1	TSS500
chr19	28835549	28913960	Slc1a1	body
chr19	28967300	28968300	4430402I18Rik	TSS500
chr19	28893042	28967300	4430402I18Rik	body
chr19	29334170	29335170	Rln1	TSS500
chr19	29366890	29367890	Plgrkt	TSS500
chr19	29348599	29366890	Plgrkt	body
chr19	29366955	29367955	Cd274	TSS500

chr19	29411419	29471157	Pdcd1lg2	body
chr19	29486355	29522659	A930007I19Rik	body
chr19	30004290	30006020	Trpd52l3	body
chr19	30030013	30031013	Uhrf2	TSS500
chr19	30174918	30175918	Gldc	TSS500
chr19	30549165	30550165	Dkk1	TSS500
chr19	30545863	30549165	Dkk1	body
chr19	31764533	31765533	Prkg1	TSS500
chr19	30567551	31764533	Prkg1	body
chr19	31868261	31869261	A1cf	TSS500
chr19	32389214	32390214	Sgms1	TSS500
chr19	32388716	32389716	2700046G09Rik	TSS500
chr19	32389716	32391184	2700046G09Rik	body
chr19	33391795	33392795	Rnls	TSS500
chr19	33137747	33391795	Rnls	body
chr19	33409131	33420142	Gm7237	body
chr19	33498037	33517280	Lipo4	body
chr19	33761451	33762451	Lipo1	TSS500
chr19	33517740	33761451	Lipo1	body
chr19	33592213	33593213	Gm27440	TSS500
chr19	33719670	33768642	Lipo2	body
chr19	33786962	33787962	Gm5097	TSS500
chr19	33822408	33823408	Gm5519	TSS500
chr19	34008754	34047903	Lipk	body
chr19	34290159	34291159	Fas	TSS500
chr19	34474635	34475635	Ch25h	TSS500
chr19	34474308	34475308	Gm26902	TSS500
chr19	34475308	34481546	Gm26902	body
chr19	34746789	34747789	Slc16a12	TSS500
chr19	34668403	34746789	Slc16a12	body
chr19	34810894	34878955	Pank1	body
chr19	35835221	35924078	A830019P07Rik	body
chr19	36057007	36058007	Htr7	TSS500
chr19	35958734	36057007	Htr7	body
chr19	36379567	36456192	Pcgf5	body
chr19	36736153	36737153	Ppp1r3c	TSS500
chr19	37173343	37174343	A330032B11Rik	TSS500
chr19	37434310	37435310	Hhex	TSS500
chr19	37435310	37440731	Hhex	body
chr19	37549918	37550918	Exoc6	TSS500
chr19	37550918	37683245	Exoc6	body
chr19	37685081	37686081	Cyp26c1	TSS500
chr19	37697308	37698308	Cyp26a1	TSS500
chr19	37698308	37701528	Cyp26a1	body

chr19	38096579	38097579	Ffar4	TSS500
chr19	38116620	38124821	Rbp4	body
chr19	38132281	38133281	Pde6c	TSS500
chr19	38265282	38308939	Lgi1	body
chr19	38395480	38396480	Slc35g1	TSS500
chr19	38480609	38481609	Plce1	TSS500
chr19	38481609	38785030	Plce1	body
chr19	38931415	38971051	Hells	body
chr19	39007519	39042693	Cyp2c55	body
chr19	39389556	39462575	Cyp2c38	body
chr19	39511362	39568529	Cyp2c39	body
chr19	39608842	39648551	Cyp2c67	body
chr19	39767071	39812314	Cyp2c40	body
chr19	39842660	39886269	Cyp2c69	body
chr19	40037941	40073311	Cyp2c54	body
chr19	40153353	40186833	Cyp2c70	body
chr19	40295049	40401767	Sorbs1	body
chr19	40868886	40874071	E030044B06Rik	body
chr19	40894203	40895203	Mir8092	TSS500
chr19	40894205	40895205	Zfp518a	TSS500
chr19	40928927	40994035	Blnk	body
chr19	41062474	41076613	Opalin	body
chr19	41206274	41207274	Tll2	TSS500
chr19	41384570	41385570	Pik3ap1	TSS500
chr19	41483145	41562246	Lcor	body
chr19	41588151	41589151	Mir8091	TSS500
chr19	41592863	41593863	Al606181	TSS500
chr19	41743165	41744165	Slit1	TSS500
chr19	41766588	41801584	Arhgap19	body
chr19	41982263	42034641	Ubtcd1	body
chr19	42085870	42086870	Morn4	TSS500
chr19	42074939	42085870	Morn4	body
chr19	42163451	42164451	Zfyve27	TSS500
chr19	42164451	42194590	Zfyve27	body
chr19	42201752	42202752	Sfrp5	TSS500
chr19	42283037	42431283	Crtac1	body
chr19	42536850	42562608	Gm16541	body
chr19	42612313	42613313	Loxl4	TSS500
chr19	42752275	42753275	Pyroxd2	TSS500
chr19	43440936	43497212	Cnnm1	body
chr19	43610125	43611125	Gm20467	TSS500
chr19	43611825	43612825	Nkx2-3	TSS500
chr19	43612825	43615892	Nkx2-3	body
chr19	43782692	43840740	Abcc2	body

chr19	44005022	44028747	Cyp2c44	body
chr19	44135376	44136376	Cwf19l1	TSS500
chr19	44145946	44146946	Bloc1s2	TSS500
chr19	44493972	44514273	Wnt8b	body
chr19	44545364	44546364	Sec31b	TSS500
chr19	44516957	44545364	Sec31b	body
chr19	44543722	44552331	Gm20538	body
chr19	44692367	44694775	Gm26644	body
chr19	44755545	44756545	Pax2	TSS500
chr19	44835438	44836438	1700039E22Rik	TSS500
chr19	44988601	44989601	Sema4g	TSS500
chr19	45026906	45046114	Pdzd7	body
chr19	45150180	45151180	Tlx1	TSS500
chr19	45151180	45156943	Tlx1	body
chr19	45158804	45159804	Tlx1os	TSS500
chr19	45232684	45235312	Lbx1	body
chr19	45300454	45310511	Gm29595	body
chr19	45329629	45337823	Gm28578	body
chr19	45742415	45743415	Fgf8	TSS500
chr19	45747734	45749091	Npm3	body
chr19	45750261	45783020	Mgea5	body
chr19	45815561	45816561	Kcnip2	TSS500
chr19	46003978	46006173	Hps6	body
chr19	46131397	46132397	Elovl3	TSS500
chr19	46147826	46148826	Pitx3	TSS500
chr19	46312087	46326656	Psd	body
chr19	46335787	46338538	Gm26792	body
chr19	46341621	46375252	Tmem180	body
chr19	46667165	46672474	Cyp17a1	body
chr19	46762096	46878795	Cnnm2	body
chr19	47014653	47015653	Nt5c2	TSS500
chr19	46886831	47014653	Nt5c2	body
chr19	47014198	47015198	Ina	TSS500
chr19	47015198	47025327	Ina	body
chr19	47033619	47050345	Pcgf6	body
chr19	47157264	47158264	Calhm3	TSS500
chr19	47179320	47259440	Neurl1a	body
chr19	47273089	47274089	Mir6995	TSS500
chr19	47537007	47538007	Obfc1	TSS500
chr19	47866045	47886324	Gsto2	body
chr19	47938212	48035379	Cfap58	body
chr19	48205525	48206525	Sorcs3	TSS500
chr19	48206525	48805505	Sorcs3	body
chr19	50678146	50679146	Sorcs1	TSS500

chr19	50677906	50778662	Gm26629	body
chr19	53076718	53084392	1700054A03Rik	body
chr19	53379214	53390073	Smndc1	body
chr19	53676806	53677806	Rbm20	TSS500
chr19	53677806	53867080	Rbm20	body
chr19	53819354	53824628	Gm16299	body
chr19	53892731	53929861	Pdcd4	body
chr19	54044682	54045682	Adra2a	TSS500
chr19	55181233	55196313	Tectb	body
chr19	55192178	55193178	Mir6715	TSS500
chr19	55198297	55240736	Gucy2g	body
chr19	55252869	55253869	Acsl5	TSS500
chr19	56287637	56320822	Habp2	body
chr19	56320035	56389537	Nrap	body
chr19	56461137	56462137	Plekhs1	TSS500
chr19	56529167	56547722	Dclre1a	body
chr19	56721872	56722872	Adrb1	TSS500
chr19	56722872	56724862	Adrb1	body
chr19	56826709	56870012	Tdrd1	body
chr19	56873749	56874749	Vwa2	TSS500
chr19	56912361	57007728	Afap1l2	body
chr19	57314419	57315419	Ablim1	TSS500
chr19	57323385	57360275	B230217O12Rik	body
chr19	58455409	58456409	Gfra1	TSS500
chr19	58235604	58455409	Gfra1	body
chr19	58860484	58861484	Hspa12a	TSS500
chr19	58795751	58860484	Hspa12a	body
chr19	58943925	58971419	Eno4	body
chr19	59075569	59076569	4930506M07Rik	TSS500
chr19	58973358	59075569	4930506M07Rik	body
chr19	59169556	59170556	Vax1	TSS500
chr19	59166187	59169556	Vax1	body
chr19	59220148	59237370	Kcnk18	body
chr19	59261378	59296012	Slc18a2	body
chr19	59296084	59345280	Pdzd8	body
chr19	59425104	59458135	Emx2os	body
chr19	60144175	60145175	E330013P04Rik	TSS500
chr19	60226197	60227197	Fam204a	TSS500
chr19	60467804	60468804	Prhr	TSS500
chr19	60761116	60790193	Eif3a	body
chr19	60889249	60890249	Grk5	TSS500
chr19	61175809	61176809	Gm7102	TSS500
chr19	61227918	61228918	Csf2ra	TSS500
chr19	61224402	61227918	Csf2ra	body

-/- or *Sdhb* -/- as compared with wt imCC.

methylation in wt imCC	methylation in <i>Sdhb</i> -/- imCC	methylation delta in <i>Sdhb</i> -/- imCC
0.509265832	0.41424196	-0.095023872
0.39638233	0.530415891	0.134033561
0.40961911	0.320359281	-0.089259829
0.218380282	0.363013699	0.144633417
0.583560345	0.526897214	-0.05666313
0.707889499	0.801075269	0.09318577
0.407329809	0.657243816	0.249914007
0.566013015	0.713764813	0.147751798
0.326561176	0.109324759	-0.217236417
0.473768075	0.583745195	0.10997712
0.579848971	0.63592233	0.05607336
0.409922295	0.474226804	0.064304509
0.292764511	0.485185185	0.192420674
0.657544937	0.534883721	-0.122661216
0.530751278	0.625542535	0.094791257
0.170365707	0.080952381	-0.089413326
0.66875	0.717213115	0.048463115
0.70540356	0.607352941	-0.098050619
0.134341314	0.014218009	-0.120123305
0.575786695	0.762295082	0.186508387
0.446760102	0.577586207	0.130826105
0.634047295	0.523229734	-0.110817561
0.306053637	0.397297297	0.09124366
0.569049789	0.715419693	0.146369904
0.255688272	0.166666667	-0.089021605
0.516469351	0.580495868	0.064026517
0.391919789	0.335311573	-0.056608216
0.499216473	0.678710395	0.179493921
0.669521806	0.946428571	0.276906766
0.272258369	0.057416268	-0.214842101
0.569099994	0.681835419	0.112735425
0.504216142	0.630071599	0.125855457
0.581201036	0.612238622	0.031037587
0.502926942	0.610811505	0.107884562
0.502081981	0.695839311	0.19375733
0.420413574	0.344943068	-0.075470507
0.438813108	0.624472574	0.185659466
0.42038311	0.041420118	-0.378962991
0.44209707	0.66892464	0.226827571

0.630264279	0.419225634	-0.211038645
0.599938753	0.362648221	-0.237290531
0.70019664	0.537037037	-0.163159603
0.602270337	0.638012618	0.035742281
0.506962257	0.61229611	0.105333854
0.298555171	0.415670651	0.11711548
0.552113307	0.678449259	0.126335951
0.307774652	0.056285178	-0.251489474
0.224568949	0.390625	0.166056051
0.617243497	0.684752105	0.067508608
0.492500497	0.483785572	-0.008714925
0.74618882	0.86993007	0.123741249
0.297379516	0.537313433	0.239933917
0.324949464	0.676595745	0.35164628
0.339020848	0.530726257	0.191705409
0.329403356	0.536908078	0.207504722
0.292481188	0.475609756	0.183128568
0.200568018	0.322632424	0.122064406
0.504703053	0.611560466	0.106857412
0.52505878	0.613497891	0.088439111
0.007936508	0.253731343	0.245794835
0.124885461	0.111714156	-0.013171304
0.719938792	0.827586207	0.107647415
0.052392344	0.136268344	0.083875999
0.520719219	0.666666667	0.145947448
0.58666332	0.344805195	-0.241858125
0.542399674	0.182628571	-0.359771103
0.153183145	0.257952974	0.104769829
0.47140249	0.611140265	0.139737775
0.452313045	0.447352999	-0.004960046
0.515020703	0.586797842	0.071777139
0.354656863	0.491048593	0.136391731
0.51842478	0.616034625	0.097609845
0.497654809	0.567099567	0.069444758
0.5669051	0.497761194	-0.069143906
0.45272056	0.546742982	0.094022422
0.542345052	0.359375	-0.182970052
0.435639853	0.595078834	0.159438981
0.719585323	0.742494715	0.022909391
0.569585662	0.680917623	0.11133196
0.585381914	0.6875	0.102118086
0.518416664	0.603773585	0.085356921
0.428698233	0.682953914	0.254255682
0.428698233	0.682953914	0.254255682

0.701226796	0.669811321	-0.031415475
0.492215753	0.391554702	-0.100661051
0.110099191	0.018925057	-0.091174134
0.448338472	0.579158317	0.130819845
0.5073074	0.639766484	0.132459084
0.126095898	0.057534247	-0.068561651
0.029273504	0.104826546	0.075553042
0.222314719	0.489655172	0.267340453
0.624681859	0.637784725	0.013102866
0.473047551	0.652054795	0.179007244
0.548541204	0.702006336	0.153465132
0.553616292	0.66894198	0.115325687
0.569411453	0.651870119	0.082458666
0.673036149	0.612125163	-0.060910986
0.247774881	0.048016701	-0.199758179
0.607523367	0.723087339	0.115563972
0.362359315	0.270491803	-0.091867511
0.151651946	0.233811172	0.082159225
0.737092992	0.678883072	-0.05820992
0.304906899	0.548507463	0.243600564
0.472112871	0.596875	0.124762129
0.547443532	0.688045912	0.14060238
0.475107233	0.648648649	0.173541416
0.10487583	0.044534413	-0.060341417
0.561931084	0.636911281	0.074980197
0.517468944	0.766233766	0.248764822
0.413173794	0.610441767	0.197267973
0.135298892	0.183098592	0.0477997
0.26290658	0.099260824	-0.163645756
0.669681031	0.749559859	0.079878828
0.368121432	0.469041278	0.100919847
0.194656303	0.520938023	0.32628172
0.670307283	0.795152232	0.124844949
0.22872935	0.536398467	0.307669117
0.675231172	0.822695035	0.147463863
0.743311501	0.732072151	-0.01123935
0.453123476	0.603361345	0.150237868
0.248875798	0.340375587	0.091499788
0.458368245	0.4140625	-0.044305745
0.206090192	0.404709748	0.198619557
0.437485811	0.529210796	0.091724985
0.378521491	0.458037825	0.079516334
0.527754057	0.511635476	-0.016118581
0.544477829	0.489696312	-0.054781517

0.29083026	0.055288462	-0.235541798
0.468804217	0.563354267	0.094550049
0.041165097	0.113721805	0.072556707
0.387002453	0.269085412	-0.117917041
0.786483552	0.827027027	0.040543475
0.194638086	0.330522766	0.135884679
0.531619805	0.629172714	0.097552909
0.364873875	0.462822014	0.097948139
0.516226435	0.5852194	0.068992965
0.376596192	0.452309985	0.075713793
0.585587495	0.659407666	0.07382017
0.327474919	0.430618581	0.103143662
0.195509978	0.341232227	0.14572225
0.536700125	0.63562753	0.098927405
0.198791237	0.041666667	-0.15712457
0.606591217	0.673097535	0.066506317
0.381403519	0.471137988	0.089734469
0.411333591	0.524958403	0.113624812
0.416181454	0.532487091	0.116305638
0.002768499	0.056338028	0.053569529
0.593987837	0.495896835	-0.098091002
0.547083522	0.689217134	0.142133613
0.616097233	0.671247357	0.055150125
0.47932129	0.59	0.11067871
0.025963194	0.117647059	0.091683865
0.728851886	0.003030303	-0.725821583
0.525344348	0.422817331	-0.102527017
0.21494578	0.325396825	0.110451045
0.44669397	0.553892216	0.107198245
0.084235879	0.018463811	-0.065772068
0.391062995	0.64644714	0.255384145
0.475229266	0.134715026	-0.34051424
0.692679964	0.75	0.057320036
0.397594975	0.215976331	-0.181618644
0.52824088	0.594303875	0.066062995
0.178103224	0.282041729	0.103938505
0.542431484	0.621179815	0.078748332
0.545188037	0.644513827	0.09932579
0.582741521	0.567088608	-0.015652913
0.693429016	0.743066884	0.049637868
0.674025656	0.786102063	0.112076407
0.272786495	0.18786924	-0.084917255
0.228597061	0.129807692	-0.098789369
0.724404002	0.488549618	-0.235854383

0.325467128	0.491651206	0.166184078
0.30737567	0.457436857	0.150061187
0.563616238	0.760797342	0.197181104
0.528370915	0.676732385	0.14836147
0.62473056	0.686838124	0.062107564
0.570929779	0.48255814	-0.088371639
0.020113442	0.110344828	0.090231385
0.736436837	0.710804824	-0.025632013
0.730935844	0.709536082	-0.021399761
0.187149244	0.05416843	-0.132980814
0.715510827	0.823459716	0.107948889
0.509057971	0.640564827	0.131506856
0.363675805	0.551348999	0.187673194
0.072531072	0.091127098	0.018596026
0.732945344	0.845454545	0.112509201
0.591168263	0.664348632	0.07318037
0.603397683	0.586538462	-0.016859222
0.64718602	0.712418301	0.065232281
0.427694481	0.755319149	0.327624668
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0.439820297	0.717948718	0.278128421
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0.37758692	0.58135861	0.20377169
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0.253565898	0.386904762	0.133338864
0.552510058	0.677649528	0.125139469
0.265339922	0.337828247	0.072488325
0.465525078	0.575025176	0.109500099
0.470078744	0.461919505	-0.008159239
0.788361345	0.672413793	-0.115947551
0.633627181	0.736038486	0.102411305
0.770342719	0.670250896	-0.100091823
0.14174908	0.065121413	-0.076627667
0.782508518	0.72183908	-0.060669438
0.568643189	0.655496225	0.086853037
0.420113256	0.573129962	0.153016706
0.396655312	0.547580519	0.150925207
0.286808778	0.417525773	0.130716995

0.354670159	0.490500261	0.135830103
0.715846209	0.823639775	0.107793566
0.068277486	0.042180402	-0.026097084
0.186617401	0.119946985	-0.066670416
0.610672367	0.714860335	0.104187968
0.581867291	0.703649635	0.121782344
0.205341522	0.347587719	0.142246197
0.176312948	0.383630048	0.2073171
0.550556282	0.65451664	0.103960358
0.54185712	0.692307692	0.150450573
0.632064447	0.733118971	0.101054524
0.26488727	0.19972067	-0.065166599
0.562855912	0.692656929	0.129801016
0.611467596	0.732290831	0.120823235
0.745837548	0.745794393	-4.32e-05
0.62621664	0.703761148	0.077544508
0.32426682	0.497326203	0.173059383
0.325851314	0.314165128	-0.011686186
0.694728386	0.77064551	0.075917124
0.291852894	0.4552498	0.163396906
0.644254092	0.70051609	0.056261998
0.257902959	0.543847242	0.285944283
0.699650286	0.756529273	0.056878988
0.016503911	0.069439895	0.052935984
0.528912629	0.611437312	0.082524683
0.154032249	0.291459782	0.137427532
0.66916281	0.727740492	0.058577683
0.531678818	0.727052303	0.195373486
0.342300147	0.430833333	0.088533186
0.582099167	0.667947733	0.085848566
0.361478076	0.458085452	0.096607375
0.435000518	0.526888816	0.091888298
0.636777465	0.717607973	0.080830509
0.647200701	0.59030837	-0.056892331
0.232785231	0.259666414	0.026881183
0.51697889	0.562588235	0.045609345
0.168780775	0.23225241	0.063471635
0.202599841	0.131714496	-0.070885345
0.809891366	0.626923077	-0.18296829
0.662838496	0.802405498	0.139567002
0.038184874	0.100153139	0.061968266
0.576220568	0.687220733	0.111000164
0.655169836	0.690322581	0.035152744
0.380276326	0.438296112	0.058019786

q-value of methylation difference in Sdhb -/- imCC	methylation in Sdhb -/- imCC	methylation delta in Sdhb -/- imCC
7.61e-10	0.683904632	0.1746388
1.02e-34	0.451618034	0.055235704
0.000120323	0.399159396	-0.010459715
0.000362561	0.145098039	-0.073282242
6.13e-09	0.684014846	0.100454501
0.000409511	0.753329118	0.045439619
1.93e-11	0.440131579	0.03280177
5.02e-16	0.620254346	0.054241332
6.29e-29	0.209420598	-0.117140579
2.56e-26	0.509119161	0.035351085
0.003242297	0.616399844	0.036550873
0.026718201	0.181114329	-0.228807966
1.76e-07	0.342926753	0.050162242
1.12e-16	0.771132559	0.113587623
1.42e-49	0.559763895	0.029012617
8.27e-14	0.141576937	-0.02878877
0.175328411	0.825126263	0.156376263
4.81e-05	0.667517007	-0.037886553
3.43e-31	0.168076661	0.033735347
2.31e-21	0.71654061	0.140753915
0.025587136	0.475566806	0.028806704
7.99e-25	0.779242507	0.145195212
0.00378684	0.436872977	0.13081934
3.04e-75	0.611301153	0.042251364
1.91e-13	0.282020562	0.026332291
1.05e-07	0.47248256	-0.043986791
0.001642819	0.566766859	0.17484707
5.58e-98	0.545477637	0.046261164
1.89e-13	0.831119598	0.161597792
6.23e-58	0.511792774	0.239534406
3.09e-38	0.623119701	0.054019707
3.6e-09	0.498102824	-0.006113318
0.002530606	0.692719389	0.111518353
5.14e-57	0.496027753	-0.00689919
1.02e-16	0.509153972	0.007071991
4.82e-06	0.378890377	-0.041523198
5.13e-14	0.459240976	0.020427867
1.58e-24	0.663549618	0.243166509
2.81e-31	0.430668414	-0.011428655

4.52e-43	0.722271361	0.092007082
7.69e-37	0.653068349	0.053129596
6.45e-10	0.86068182	0.160485181
0.001168828	0.701261684	0.098991346
9.98e-33	0.527362276	0.02040002
2.22e-08	0.320183511	0.02162834
4.27e-08	0.574559151	0.022445843
7.58e-39	0.404661922	0.096887269
7.24e-26	0.208197544	-0.016371404
2.67e-07	0.618395889	0.001152391
0.298795292	0.765692311	0.273191813
4.21e-17	0.793528837	0.047340016
1.98e-09	0.61887626	0.321496745
2.18e-17	0.285206718	-0.039742746
6.94e-11	0.292275906	-0.046744942
1.57e-33	0.252016857	-0.077386499
3.18e-37	0.540140469	0.247659281
5.4e-08	0.26420502	0.063637003
2.39e-34	0.589833934	0.08513088
2.23e-29	0.517653476	-0.007405304
2.85e-09	0.028089888	0.02015338
0.070030046	0.229165086	0.104279625
1.37e-14	0.794862069	0.074923277
1.23e-06	0.048695781	-0.003696564
0.008157915	0.510058024	-0.010661195
3.1e-56	0.674086127	0.087422808
0	0.684888982	0.142489308
2.21e-15	0.196241409	0.043058264
3.59e-143	0.527576992	0.056174501
0.277385974	0.553600098	0.101287053
7.88e-10	0.502742185	-0.012278518
1.28e-06	0.370784335	0.016127473
4.63e-49	0.561253045	0.042828265
0.045895156	0.616002215	0.118347406
8.77e-06	0.62722518	0.06032008
2.55e-63	0.489288705	0.036568145
2.07e-31	0.571928649	0.029583597
7.7e-66	0.476139615	0.040499763
0.024666642	0.818031849	0.098446525
4.23e-09	0.597598894	0.028013231
0.031986384	0.588697534	0.00331562
0.011140856	0.602013423	0.083596759
2.48e-74	0.415994516	-0.012703716
2.48e-74	0.415994516	-0.012703716

0.247665535	0.850336276	0.14910948
7.57e-05	0.53666736	0.044451607
2.36e-31	0.102049658	-0.008049532
1.03e-42	0.589159221	0.140820749
1.72e-30	0.490904744	-0.016402656
0.006919158	0.025744465	-0.100351432
1.02e-21	0.096104358	0.066830854
9.58e-16	0.360627178	0.138312459
0.188307256	0.732003144	0.107321284
9.39e-09	0.496229757	0.023182206
1.53e-135	0.569417292	0.020876088
2.41e-06	0.536257707	-0.017358586
1.56e-21	0.56529677	-0.004114683
9.46e-05	0.69688867	0.023852521
2.25e-48	0.602084274	0.354309393
9.14e-25	0.57338205	-0.034141318
4.58e-09	0.486531121	0.124171806
7.5e-17	0.112570589	-0.039081357
0.016002347	0.773554247	0.036461256
2.5e-10	0.332318234	0.027411335
0.000223133	0.528827644	0.056714773
0	0.567482699	0.020039167
6.27e-23	0.575062344	0.099955111
0.001560767	0.273177509	0.168301679
4.03e-07	0.53431264	-0.027618444
6.73e-07	0.516949153	-0.000519792
4.63e-05	0.624849687	0.211675893
0.000537667	0.434161342	0.298862451
3.39e-26	0.48143072	0.21852414
1.16e-30	0.656609963	-0.013071068
8.35e-18	0.30159182	-0.066529612
2.23e-77	0.172633982	-0.022022321
4.44e-38	0.711216111	0.040908829
1.19e-19	0.385057	0.156327649
1.73e-06	0.762581623	0.087350451
0.153955396	0.797942833	0.054631332
1.67e-26	0.477550485	0.024427008
1.08e-08	0.288780047	0.039904249
0.111889921	0.248930818	-0.209437427
4.14e-47	0.32769232	0.121602128
7.94e-14	0.430662929	-0.006822882
4.07e-07	0.45695641	0.078434919
0.032767696	0.614975164	0.087221107
8.88e-05	0.444014168	-0.100463661

1.1e-29	0.330516458	0.039686199
9.28e-16	0.463229619	-0.005574598
6.53e-15	0.032789564	-0.008375533
7.13e-21	0.512405094	0.125402641
0.017818993	0.701186128	-0.085297423
1.23e-08	0.242040701	0.047402615
1.34e-08	0.609533736	0.077913931
2.07e-21	0.401652135	0.03677826
3.94e-12	0.56737235	0.051145915
7.04e-10	0.393628762	0.01703257
1.15e-05	0.636838978	0.051251483
4.83e-25	0.364997636	0.037522716
1.99e-05	0.283086811	0.087576833
1.19e-05	0.558666775	0.02196665
1.48e-29	0.587847454	0.389056217
3.76e-13	0.646080037	0.039488819
5.99e-10	0.409894696	0.028491178
1.58e-19	0.4525609	0.041227309
1.04e-36	0.478720192	0.062538738
7.13e-10	0.021908333	0.019139834
6.01e-06	0.586047673	-0.007940164
9.59e-42	0.5680553	0.020971778
0.005933573	0.649392251	0.033295018
1.22e-22	0.517263766	0.037942476
1.14e-07	0.072725095	0.046761901
1.26e-164	0.785936551	0.057084665
6.35e-27	0.562032317	0.03668797
0.000140527	0.162985972	-0.051959808
0.000729392	0.443556423	-0.003137547
1.3e-21	0.187749373	0.103513494
2.46e-43	0.354529235	-0.03653376
7.34e-35	0.569662555	0.094433288
0.020472105	0.707995926	0.015315961
2.15e-09	0.492044275	0.0944493
3.74e-22	0.580137042	0.051896162
8.94e-27	0.204839723	0.026736499
3.31e-06	0.48326798	-0.059163504
9.81e-15	0.52900526	-0.016182777
0.170290721	0.66864285	0.085901329
1.59e-07	0.765430983	0.072001967
2.4e-08	0.714851431	0.040825775
4.79e-16	0.294310716	0.021524221
5.3e-30	0.179081879	-0.049515182
1.58e-05	0.547625858	-0.176778144

5.12e-14	0.275731544	-0.049735584
3.5e-20	0.28271414	-0.02466153
2.87e-41	0.534181824	-0.029434414
7.82e-144	0.550629419	0.022258505
0.006253012	0.701081637	0.076351077
0.022285404	0.419977511	-0.150952268
1.74e-07	0.082268314	0.062154872
0.001410551	0.820252288	0.083815451
0.00539262	0.813613523	0.082677679
5.4e-58	0.039263192	-0.147886052
2.52e-08	0.55937314	-0.156137687
4.04e-06	0.561114228	0.052056257
3.52e-55	0.389495125	0.02581932
0.349850336	0.188163212	0.11563214
0.000385077	0.733299458	0.000354114
4.12e-08	0.668228513	0.077060251
0.190368276	0.745311248	0.141913565
0.030209821	0.411849165	-0.235336855
3.99e-14	0.584513007	0.156818526
0.001989144	0.733272234	0.159739804
7.41e-11	0.265188191	-0.249029021
0.312104963	0.63085568	-0.098724204
0.078015439	0.477407403	0.122923638
2.62e-50	0.523322631	0.017434555
5.33e-05	0.666362986	0.06018707
8.5e-37	0.484246012	0.017993672
7.86e-06	0.552606381	0.045799639
0.153858356	0.79673913	0.12647588
1.88e-10	0.677473814	-0.02462992
0.018897169	0.754467114	-0.094811913
6.92e-61	0.09221359	-0.02296517
0.045890894	0.291287547	0.051305538
0.045890894	0.291287547	0.051305538
0.023957017	0.176960784	0.071405229
0.398955205	0.5359847	0.137003108
4.03e-30	0.422998334	0.110074133
3.56e-06	0.40010171	-0.002447545
3.62e-15	0.517799025	-0.002238106
2.58e-07	0.519487773	0.149848517
9.36e-45	0.41383325	0.102437488
1.89e-67	0.599096997	0.045829965
0.108601796	0.351137968	0.28013153
5.6e-10	0.605892469	0.056577819
5.11e-06	0.757018653	0.029336458

0.011998448	0.665450106	0.026988568
0.10208494	0.249509691	-0.195129139
1.2e-21	0.511141249	0.03607554
0.008096404	0.682671695	0.054348577
4.67e-05	0.622250653	0.003422112
5.78e-25	0.587952562	0.048039003
0.004475562	0.554195102	0.073629425
2.49e-60	0.296683754	-0.038497542
3.08e-24	0.200385627	0.050020885
3.19e-10	0.536555886	0.116952637
3.28e-06	0.258638747	0.045041194
2.65e-58	0.434857457	0.137506679
1.02e-11	0.248654239	0.006653578
4.49e-15	0.140203656	-0.012231722
0.138365694	0.386192581	0.122627418
5.72e-15	0.465440718	0.081834389
3.97e-07	0.681705823	0.012757662
0.000531141	0.398642847	0.25489681
7.61e-14	0.101541755	0.028374492
1.06e-09	0.439712779	0.131531798
3.51e-34	0.714680633	0.029944051
1.2e-49	0.749919419	0.064594798
5.42e-06	0.469742947	-0.11497358
0.000309541	0.268136558	-0.046265065
7.5e-38	0.62769394	0.069128258
3.75e-72	0.75676859	0.008699562
1.16e-28	0.330116144	-0.064673955
7.54e-64	0.418445547	0.029551576
6.96e-16	0.639339023	0.007592092
0.012338702	0.136926524	0.073542992
0.002824998	0.380691183	-0.020706333
7.9e-46	0.354210753	0.014444622
4.6e-27	0.370606127	-0.009766729
6.71e-10	0.413826616	0.000933958
5.51e-05	0.627159226	0.136398565
0.038721564	0.796376812	0.142540494
4.73e-11	0.683883476	-0.003630537
0.00324276	0.435707402	-0.105906158
0.02970449	0.437554094	0.143126809
2.17e-09	0.657817613	0.020411279
6.66e-36	0.063335686	-0.023070145
0.043705874	0.659456522	0.011476724
0.090555026	0.368649009	0.138227906
2.35e-15	0.752407299	0.050375214

0.070798999	0.342818487	-0.057511236
8.62e-13	0.230568787	0.006320085
1,00E-16	0.423824215	0.065447848
2.8e-08	0.232641771	-0.060174643
2.8e-08	0.232641771	-0.060174643
3.49e-14	0.184230545	-0.102630383
2.62e-21	0.029756726	-0.022074398
1.75e-21	0.029595644	-0.023704484
1.52e-12	0.505339326	0.180339326
5.3e-14	0.394811836	-0.010048814
7.16e-21	0.617876286	0.067650445
6.59e-35	0.186180712	-0.115001019
5.24e-98	0.534122585	0.010633392
2.16e-06	0.683052242	0.044880675
7.54e-25	0.33708891	-0.006809023
7.82e-09	0.481845127	0.002394299
6.61e-09	0.426853495	0.074911696
4.67e-08	0.415481626	0.079690849
0.199422825	0.404937109	0.068840212
0.002709743	0.556954157	0.008601682
0.033217369	0.466599701	-0.08024645
1.37e-16	0.529119426	0.121191425
0.227523732	0.783621166	0.128926899
5.64e-12	0.66039676	0.163554569
9.63e-12	0.048687716	-0.005171731
1.51e-15	0.567224201	-0.010977335
2.51e-14	0.576047975	0.014686364
6.99e-26	0.52883522	0.069333544
1.63e-12	0.257107889	-0.179193887
4.26e-63	0.176564231	0.117141782
0.001026943	0.606906339	-0.056745442
0.002308773	0.632291667	0.140582896
1.85e-23	0.605180578	0.095564094
1.44e-13	0.489243863	0.040169704
2.89e-05	0.32926423	-0.17905476
8.08e-09	0.621109498	0.013010829
1.01e-16	0.204195323	0.065247628
3.7e-52	0.594252174	0.052645565
1.44e-47	0.154261963	0.048072932
7.67e-07	0.552479807	0.053360452
0.00048186	0.640292669	0.063157217
1.57e-23	0.439044614	0.170311247
5.14e-27	0.718461846	0.085294068
0.025249371	0.192955264	0.098830278

6.93e-14	0.577801362	-0.024011489
6.93e-14	0.577801362	-0.024011489
4.55e-14	0.578989379	-0.025384614
2.35e-08	0.550169707	-0.005364203
2.35e-08	0.550169707	-0.005364203
2.14e-08	0.550169707	-0.005364203
1.06e-08	0.54728647	-0.007848318
1.68e-08	0.520658762	-0.022733888
1.33e-08	0.354391075	-0.024928436
9.83e-21	0.466332754	0.034477304
2.19e-09	0.340541579	-0.04894777
6.01e-05	0.578152964	-0.040190186
1.27e-24	0.579017872	-0.002934335
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9.94e-33	0.682090162	0.055590367
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3.94e-37	0.278991471	-0.143664684
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1.89e-43	0.576960795	0.033540351
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7.62e-10	0.672865567	0.021479206
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4.89e-53	0.03585744	0.000454091
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4.35e-93	0.558482324	-0.023178192
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5.77e-08	0.353741755	0.101340471
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1.99e-09	0.477275239	0.0270624
7.87e-08	0.464479538	0.074512433
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7.81e-18	0.534722312	0.021917418
3.88e-07	0.466289179	0.081984801
4.11e-08	0.732261237	0.115378424
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3.7e-07	0.32798994	-0.165301417
1.1e-43	0.817038775	0.076368163
8.74e-13	0.598347436	0.055908559
1.08e-23	0.670951301	0.053924201
8.56e-134	0.389540143	0.019139577
1.55e-09	0.882109944	0.125195965
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2.11e-07	0.443482822	0.047626966
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1.34e-06	0.305400198	0.057863583
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6.88e-05	0.723032794	0.041471233
3.45e-30	0.605158673	0.040166522
3.11e-23	0.41295729	-0.181136117

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4.24e-13	0.561769322	0.124707484
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6.15e-06	0.568289378	0.230454129
1.65e-08	0.671452827	0.060215908
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2.8e-05	0.587824228	0.042539566
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1.57e-11	0.599088575	0.019078576
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3.51e-33	0.854745669	0.02994344
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3.95e-05	0.396789192	0.108683167
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4.62e-16	0.640735261	0.074437896
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2.24e-11	0.563529657	0.354510938
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4.98e-55	0.744681914	0.164516783
2.27e-30	0.679414261	0.068493061
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8.42e-10	0.464661828	0.064251957
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8.08e-36	0.205260638	0.134051729
9.37e-15	0.040074471	0.023432352
1.37e-80	0.642690028	0.09940903
7.49e-05	0.403817669	-0.121381201
1.02e-09	0.118866236	0.027519347
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1.07e-23	0.489207053	0.1555675
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3.1e-34	0.742469789	0.104132677
4.5e-34	0.858966966	0.10448319
5.27e-40	0.175727883	-0.00106788
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8.16e-31	0.561287958	0.004197982
1.88e-09	0.670520776	0.024052311
5.18e-14	0.172003875	0.053421103
1.99e-40	0.634862145	-0.020829865
6.28e-11	0.730229897	-0.024714524
2.32e-06	0.496016727	0.135838352
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3.04e-22	0.454168005	0.095321702
0.000418408	0.811329282	0.100626975
5.77e-72	0.319492204	0.105091642

3.76e-54	0.226525491	0.076862911
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1.9e-113	0.44716653	0.148151261
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8.76e-45	0.513497384	0.057250824
1.81e-07	0.775427158	0.133371084
4.44e-07	0.651582382	0.296347725
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1.59e-29	0.406717241	0.008934348
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1.5e-11	0.612743443	0.075468777
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7.96e-63	0.36945316	0.071841854

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1.48e-24	0.637799686	0.049980468
2.65e-32	0.438831188	0.025007019
5.98e-16	0.526566714	0.014006037
3.02e-12	0.780854197	0.061480703
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2.57e-85	0.175182582	0.015093395
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4.95e-36	0.332092377	-0.036932808
1.57e-22	0.620849906	0.027390397
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2.41e-25	0.650393036	0.029942045
8.99e-07	0.383612414	-0.085939664
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2.4e-32	0.626437182	0.005124861
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7.14e-14	0.915136272	0.344493402
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2.06e-05	0.185002118	-0.16684569
6.82e-52	0.242817812	-0.06576951
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4.45e-06	0.577989905	0.018966877
1.71e-12	0.645198646	-0.010492996

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1.32e-32	0.548126105	0.001258941
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3.9e-12	0.740084847	0.014830119
2.39e-05	0.750847509	0.133440103
2.62e-05	0.766241597	0.097995265
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1.42e-05	0.48382566	0.076102293
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2.18e-15	0.764377406	0.049217958
2.4e-19	0.620817555	-0.015158278
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3.13e-47	0.472378788	0.084993751
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3.34e-13	0.412717991	0.085979235
4.31e-12	0.400929808	0.085069556
2.76e-57	0.590149355	-0.003064772
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1.19e-07	0.084679204	-0.047887982
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1.8e-70	0.365273086	0.156463291
4.75e-106	0.490924202	0.073242798
1.07e-26	0.414389396	-0.027957606
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5.94e-08	0.029761905	0.029761905

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1.02e-139	0.341200328	0.085572041
6.52e-27	0.609495221	0.001201882
2.3e-23	0.727301337	0.066866406
2.69e-35	0.517146937	0.061477679
6.08e-56	0.734779311	0.179856375
1.5e-104	0.638976138	0.119723146
1.27e-15	0.393972144	0.059884905
4.14e-19	0.734909428	0.111149208
2.14e-24	0.533234462	0.066719269
2.58e-14	0.47690043	0.119184999
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1.21e-12	0.456383644	0.141685632
6.53e-05	0.753641999	0.238293391
4.13e-20	0.54248998	0.090132634
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2.59e-12	0.441866575	0.005955962
1.14e-60	0.138531386	0.039416341
2.81e-30	0.098713235	0.029438669
8.29e-06	0.220772691	0.120860434
2.11e-08	0.71548878	0.019250354
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2.97e-109	0.259366885	0.035163786
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1.54e-20	0.55492345	0.218798341
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5.21e-83	0.235454073	-0.019057602
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9.26e-05	0.438836318	0.098025195
4.26e-21	0.515519631	0.06441072
0.093325617	0.268445256	0.0982747
3.87e-05	0.702586207	0.049741632
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5.64e-11	0.545518005	0.076510209
4.22e-16	0.460751147	-0.095514257

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7.64e-63	0.284401193	0.124070847
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2.48e-41	0.403593409	0.034040839
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9.29e-05	0.81322208	0.039018176
6.07e-13	0.672728016	0.03700858
1.4e-31	0.441631961	0.049067278
8.9e-51	0.269378173	0.108466535
4.4e-21	0.410416343	0.107036392
5.62e-10	0.136883957	0.021848278
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6.47e-72	0.140917672	-0.008691014
4.5e-89	0.260944223	0.02430133
6.19e-09	0.609031058	-0.008561834
7.85e-83	0.585849993	0.017128652
3.46e-220	0.059310582	-0.035722359
1.51e-10	0.554806062	0.100529448
2.43e-100	0.73872629	0.18478016
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4.03e-26	0.808341364	0.185157199
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8.98e-86	0.018000757	0.009527995
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2.96e-37	0.132063683	0.031520633
4.18e-26	0.775461563	0.26994441
4.42e-51	0.573679831	0.057305887
7.57e-11	0.104505179	0.092242666
3.41e-47	0.093900966	0.021267875
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1.87e-26	0.478215142	0.010062782
1.33e-24	0.335753044	0.045588436
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1.53e-20	0.568159957	0.052969481
1.22e-07	0.124354309	-0.029613581
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2.96e-43	0.625912232	0.014319739
7.89e-23	0.767287982	-0.024593417
5.29e-12	0.023745732	-0.00790049
8.45e-21	0.272565212	0.039944198
1.13e-26	0.508758186	0.006349957
9.7e-13	0.062120314	-0.024455622
5.19e-142	0.49535088	0.010311878
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1.86e-46	0.341594375	0.053362251
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1.07e-48	0.254807259	0.034261602
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2.47e-13	0.644562167	0.045068352
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1.07e-20	0.548954247	-0.014064838
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2.33e-165	0.4788739	0.054859872
3.58e-33	0.658445369	-0.010628557
2.62e-16	0.482686575	0.057203982
3.15e-32	0.323286724	-0.081113303
7.9e-69	0.385902661	0.112016356
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2.91e-13	0.653741032	0.043164565
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9.97e-17	0.248410977	0.059923902
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2.77e-23	0.770855991	0.122452073

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5.69e-88	0.718673378	0.241269977
1.48e-05	0.553683964	0.034383787
1.67e-92	0.550920622	-0.023178842
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0.224973726	0.200926423	0.106006136
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3.37e-36	0.436438624	0.038535185
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1.21e-117	0.374491365	0.100259922
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2.34e-17	0.75434291	0.188904302
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2.89e-65	0.56920663	0.067300696
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5.16e-40	0.053371779	-0.03064602
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6.8e-05	0.396832043	-0.104578943
7.49e-29	0.706339737	0.114752118
6.99e-26	0.694458647	0.009059226

3.36e-11	0.630883963	0.103585272
1.59e-18	0.611071721	0.11990194
1.59e-18	0.611071721	0.11990194
3.3e-55	0.597308416	0.002586551
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4.11e-35	0.284644827	-0.113742972
2.59e-150	0.384113428	0.043624641
3.84e-26	0.440090293	0.02529038
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5.92e-06	0.731608158	0.13751077
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9.01e-10	0.531309977	0.009948969
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1.41e-52	0.668323347	0.020851347
3.13e-208	0.61858548	0.070870268
4.44e-53	0.675373518	0.250529634
1.93e-54	0.562131673	0.213303102
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1.37e-06	0.817301369	0.102400153
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8.03e-06	0.204981597	0.103405209
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0.146845	0.502289636	0.343448717
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8.3e-61	0.348569746	0.075036823
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1.33e-29	0.476631773	0.026157636
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2.18e-73	0.405822691	0.014512583
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0.262403281	0.345140212	0.213219666
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2.01e-35	0.422010855	-0.014508934
2.84e-19	0.485136161	0.074636634
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6.38e-26	0.556492435	0.015367829
3.09e-05	0.848424527	0.152514684

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7.68e-38	0.510233118	-0.001603619
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1.67e-19	0.689930687	0.03599389
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1.08e-12	0.401846206	-0.202494767
0.000232361	0.018181818	-0.103874186
2.16e-14	0.453740648	-0.059721732
5.04e-29	0.338977674	0.044521522
0.015275821	0.208959685	-0.123011275
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3.87e-10	0.646356722	0.109815522
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4.33e-14	0.411788495	-0.057059468
2.93e-14	0.557813268	-0.109124322
7.61e-05	0.46833524	0.2075759
1.89e-38	0.099861627	0.014206471
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1.59e-07	0.451391654	0.104864069
3.57e-61	0.287877924	-0.002994458
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2.74e-33	0.549613551	0.021891919
6.98e-124	0.474882729	0.125494186
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1.51e-61	0.222283145	0.072161165
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5.65e-97	0.476714365	0.193192028
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6.79e-18	0.526117121	0.076787917
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9.42e-88	0.31870062	0.062620183
6.73e-67	0.332434541	0.157771477
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5.98e-37	0.238429041	0.098973791
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4.11e-56	0.695228504	0.018578939
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2.55e-45	0.467859273	-0.085904868
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1.77e-156	0.221107582	0.033632559
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1.35e-11	0.731004635	0.017696568
4.47e-12	0.639845093	0.073720832
9.77e-17	0.045008951	0.032276345
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6.13e-45	0.609850046	0.007859568
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1.89e-17	0.21619054	-0.214875164

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5.42e-50	0.392011646	0.05641944
4.46e-26	0.752249108	0.03773078
2.58e-43	0.627692625	0.033879163
2.09e-64	0.194621315	-0.05496514
1.16e-155	0.706006235	0.310750134
1.12e-177	0.624129568	0.063901925
0.075106121	0.608776818	0.117142326
1.53e-05	0.634517324	0.050846471
7.31e-10	0.243188365	-0.015823325
2.72e-14	0.188934636	-0.020746288
0.16947055	0.695563021	-0.128527655
3.1e-28	0.608946609	0.30342757
3.1e-28	0.608946609	0.30342757
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5.78e-13	0.547811489	0.014126515
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2.41e-21	0.576259581	0.126941705
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1.41e-55	0.631884784	0.133298506
4.46e-22	0.445512507	0.155539288
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4.69e-24	0.059410301	-0.042853333
6.11e-07	0.694684575	0.041914162
0.000685814	0.687027447	0.065645816
0.289927888	0.030029838	-0.060241447
1.47e-39	0.520059854	0.019753739
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1.15e-87	0.76131471	0.240243718
1.15e-87	0.76131471	0.240243718
6.28e-41	0.657064394	0.11222895
8.43e-22	0.661287244	0.006192045
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1.69e-16	0.610039224	0.189372189
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3.63e-16	0.614466459	0.032146085
7.15e-07	0.534090909	0.090929068
5.18e-24	0.28501157	0.147887229
7.18e-46	0.657289971	0.167138527
5.26e-55	0.650565642	0.164801425
2.28e-58	0.162680802	0.01321037
3.52e-05	0.814404762	0.068533975
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2.9e-07	0.550616039	-0.063252669
3.47e-17	0.46107852	0.076968694
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7.41e-11	0.099929188	0.014877295
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4.85e-27	0.558201265	0.018532327
6.04e-32	0.558215697	-0.017008737
1.2e-13	0.49520941	0.139742855
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9.47e-13	0.051943752	-0.118652402
7.35e-09	0.340754703	0.102990468
5.01e-22	0.545494099	0.036877071
1.93e-25	0.375215469	0.108161477
1.56e-77	0.744316694	0.174808362
4.48e-83	0.253889355	0.012340301
7.23e-23	0.049285793	0.007974712
4.04e-07	0.611006301	0.040684629
6.58e-14	0.721173867	0.02439018
1.91e-09	0.572928555	0.097140813
3.58e-05	0.305623148	0.024419775
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3.19e-14	0.336206937	0.012697518
1.51e-29	0.454896987	0.099260699
8.63e-23	0.055600465	0.009925039
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4.81e-05	0.317218439	0.081916324
2.35e-06	0.64717323	0.030507578
3.02e-06	0.406363043	0.121295028
1.12e-16	0.723061067	0.005486249
2.9e-53	0.418754458	0.106062871
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2.3e-43	0.566940174	0.233224066
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1.64e-53	0.745514425	0.160621022
1.82e-27	0.407178752	0.032730574
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1.42e-192	0.509247289	0.084121736
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1.17e-12	0.395486547	0.095281485
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1.18e-13	0.503803855	0.06044214
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2.71e-91	0.521838761	0.041663588
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1.31e-200	0.127306278	0.067840446
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5.57e-06	0.676364146	0.130035517
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7.68e-29	0.725310156	0.293010867
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5.26e-09	0.340144557	0.079784841
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4.36e-20	0.651302418	0.005818611
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4.48e-19	0.204202203	0.026189684

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1.19e-288	0.118487674	5.3e-05
1.04e-64	0.339343915	0.009850715
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2.5e-08	0.832018319	0.072128158
7.33e-101	0.596757717	0.015593381
6.83e-22	0.396951195	-0.095370584
6.59e-74	0.624080206	0.092421252
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1.46e-16	0.360753284	0.148266604
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4.02e-45	0.550290694	0.013808689
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3.46e-101	0.478377049	0.004057582
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1.07e-146	0.327408806	0.031237029
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3.46e-43	0.554649755	0.09099774
1.55e-42	0.554780774	0.092128549
1.34e-54	0.041119269	0.015161428
1.7e-172	0.413662567	0.005876832
9.94e-33	0.176849372	0.043825777
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1.95e-25	0.619835667	0.032439544
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1.59e-15	0.297747056	0.077523731
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4.51e-18	0.492397441	0.128752698
7.89e-88	0.606251092	0.230306593

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2.74e-31	0.308291908	0.031885069
7.78e-10	0.597245255	0.077674388
4.56e-10	0.657756804	0.236054206
3.56e-68	0.524818674	0.045767924
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8.87e-15	0.486353616	0.110033592
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1.2e-13	0.61896911	0.047607248
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1.02e-44	0.567836171	0.050639971
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3.92e-27	0.292586445	0.03658774
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2.47e-47	0.291502451	0.166431993
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7.62e-31	0.441625156	0.065095539
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1.01e-44	0.66127941	0.035968499
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1.28e-230	0.210874754	0.125480598
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4.33e-140	0.576696103	0.068316273
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3.95e-16	0.128315745	0.002321003
6.09e-06	0.500792115	0.000168784
2.49e-36	0.20334961	0.091870251
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1.95e-08	0.64541538	0.074830268
3.97e-14	0.642165932	-0.013547279
1.97e-55	0.627220554	0.021612726
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1.13e-118	0.46004651	0.133346883
6.62e-161	0.612940078	0.029478111
5.25e-09	0.776022274	0.002734452
1.16e-108	0.693434112	0.093869567
5.12e-83	0.628156334	0.039994738
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2.52e-144	0.745733401	0.091154402
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3.56e-05	0.454538984	0.005037195
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6.71e-10	0.588521918	0.040784462
4.9e-16	0.199749595	0.088055972
3.5e-10	0.609302773	0.078065451
1.08e-67	0.088531385	0.042193036
1.67e-209	0.389056139	0.05673951
1.67e-07	0.606428138	0.003654983
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4.61e-20	0.311203167	-0.071017689
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8.06e-186	0.522888767	0.041904077
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5.05e-36	0.796568116	0.046508758
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0.036532547	0.383944538	-0.038454338
0.030628913	0.648771005	0.136660378
8.36e-05	0.672044695	0.05632557
5.68e-13	0.627481079	-0.016364405
2.26e-09	0.594821024	0.10006868
0.06175539	0.780336642	0.200313086
1.7e-06	0.666823726	0.129602289
1.74e-13	0.718235671	-0.062223305
5.4e-48	0.640796944	0.053256448
3.43e-82	0.444034114	0.284680455
8.36e-41	0.593890507	-0.018481863
3.68e-07	0.259684631	-0.015649149
6.5e-07	0.449235993	0.102023884
7.82e-34	0.034933508	-0.024654436
1.8e-46	0.26273391	0.014460726
0.00265899	0.748623853	0.087708826
0.000112506	0.710923103	-0.051717775
1.49e-20	0.591017286	0.028309767

0.039764752	0.54764162	-0.113064225
3.8e-14	0.799284142	0.088004129
0.000283096	0.860612579	0.027872794
2.64e-106	0.820127542	0.239842183
2.84e-25	0.78093041	0.160468258
0.190699358	0.589465207	0.272836607
0.003449447	0.698628503	0.009568856
3.2e-248	0.346905784	0.023060151
3.17e-23	0.515118243	0.010169487
5.23e-10	0.661627245	0.039237575
0.011561639	0.368049955	-0.125635478
0	0.519213841	0.089888073
1.27e-17	0.516860317	0.044651838
0.043999687	0.758385897	0.210801697
1.28e-35	0.694701717	0.137233599
9.63e-07	0.748351157	0.248181193
8.86e-09	0.527367855	0.012291065
5.03e-41	0.619736124	0.083137717
3.02e-45	0.64173943	0.18783459
1.3e-10	0.468978324	-0.122450911
3.89e-21	0.055939026	-0.006096144
2.65e-09	0.231073446	-0.024986128
7.84e-07	0.054038282	-0.008906862
4.63e-05	0.382267868	-0.176543271
3.09e-09	0.443209877	-0.122176857
6.14e-13	0.276095461	-2.57e-05
4.13e-15	0.755735713	0.048534759
1.05e-10	0.18071609	-0.014664154
9.83e-19	0.122001528	0.0918564
4.29e-26	0.782491817	0.041643994
1.92e-11	0.748066306	0.041000124
0.00506372	0.53117321	0.172484088
4.48e-57	0.672486762	0.132312884
7.51e-90	0.531434246	-0.002057243
3.62e-38	0.42749488	0.088100768
1.74e-29	0.269836761	0.120055297
0.189183533	0.176800967	0.099397523
0.00029408	0.756068796	0.153436427
1.36e-05	0.233515085	-0.06371875
8.38e-20	0.651199514	0.037810875
1.03e-15	0.832498337	0.078617526
2.27e-29	0.763342354	-0.013483026
3.46e-17	0.836381075	0.053999605
0.068471494	0.567212914	0.176775653

4.11e-05	0.704803519	0.233013015
7.15e-22	0.265632853	0.082133896
3.57e-41	0.219800891	-0.059313504
1.16e-29	0.533316339	-0.016165281
3.85e-15	0.586882998	0.047899208
3.87e-15	0.303090659	-0.002623626
1.18e-39	0.54710857	-0.000530905
1.08e-07	0.491635145	-0.118500107
6.24e-07	0.244401274	-0.042034744
2.09e-45	0.416486316	0.111735621
7.99e-16	0.705679323	-0.030555589
2.49e-06	0.246639541	0.138944659
7.54e-13	0	0
1.61e-20	0.235695651	0.059001828
4.55e-11	0.059782609	0.02132107
0.00058614	0	-0.054617676
3.45e-39	0.23821593	-0.007052398
9.7e-18	0.671689723	0.147026412
0.037056522	0.591296296	0.182149543
0.320589746	0.818181818	0.079561129
5.38e-07	0.435718367	0.062331449
6.74e-15	0.305687155	-0.078520984
3,00E-38	0.063034188	-0.012555639
0.000545281	0.739334189	0.01240813
3.53e-155	0.137440609	0.071033049
2.24e-30	0.564735033	-0.022874528
5.01e-119	0.507507639	0.021130197
7.09e-13	0.701237531	0.220504882
0.001989975	0.42486125	0.146882184
0.002181659	0.71354648	0.01812006
1.2e-09	0.120815416	-0.088733172
0.00268721	0.535025059	0.074958987
1.34e-22	0.729177073	0.038010191
1.34e-15	0.393994352	0.132634807
7.1e-12	0.172045252	-0.102509942
1.35e-72	0.095916447	-0.000863138
2.01e-08	0.634670928	-0.011532446
1.13e-66	0.614882993	-0.069736863
2.5e-16	0.739103528	-0.001270334
1.05e-05	0.635301118	0.014890842
7.57e-12	0.165834933	-0.074983768
2.71e-05	0.590024186	-0.020057391
1.31e-09	0.455604874	-0.009855811
4.3e-28	0.386217501	0.173958817

2.55e-06	0.313269888	0.064710154
0.007290995	0.639285714	0.004778252
6.17e-05	0.280417444	-0.01608933
0.01729503	0.178859116	-0.045312367
5.79e-16	0.265683098	-0.059246494
9.4e-93	0.419753791	0.125218672
9.74e-102	0.437987761	0.149242385
1.38e-18	0.366797792	0.018729876
0.020391504	0.28462529	0.081731422
0.0397014	0.145914978	-0.206544039
2.44e-06	0.020414181	-0.049872432
1.17e-67	0.29543702	0.09477043
2.46e-14	0.50221564	-0.04553969
1.71e-06	0.0978936	0.032645398
1.39e-34	0.205921053	0.046615995
5.91e-12	0.601231955	0.035451661
5.24e-69	0.20883841	-0.015022957
0.081495497	0.617256578	0.056489781
1.42e-10	0.301139077	-0.023264334
5.38e-06	0.867722136	0.16402357
0.249651302	0.122802958	-0.111693597
0.153575142	0.65990136	0.208590499
0.000414463	0.541735365	-0.046906849
9.59e-56	0.807556833	0.141139181
3.71e-07	0.692458522	0.061221749
1.75e-18	0.58311285	0.090718286
1.98e-09	0.637563195	0.004679949
0.002424178	0.69859469	0.067138717
2.35e-06	0.546284893	0.113993227
0.005164623	0.41280013	0.023126217
6.18e-06	0.646825681	0.05284237
2.52e-49	0.449788874	0.069475888
1.2e-07	0.459164487	0.093601573
4.9e-15	0.657365466	0.048520775
6.74e-22	0.41138784	0.154056831
5.6e-20	0.143979852	-0.022223852
1.44e-07	0.178655319	-0.139966625
3.46e-08	0.746049454	0.040272174
2.79e-13	0.290586759	-0.092131018
0.056161777	0.709635417	-0.170380863
0.009903184	0.462016908	-0.050871152
0.23522221	0.099478175	0.079729611
4.86e-05	0.453893718	-0.145686452
1.81e-50	0.240146332	0.071957143

3.39e-189	0.5803742	-0.036696094
2.48e-23	0.42900192	0.109281116
2.23e-66	0.41001477	0.114806665
2.46e-25	0.16843033	0.037092758
0.197038055	0.214368503	-0.095339991
1.1e-28	0.622340711	0.133557107
2.63e-79	0.507364925	0.030892427
3.33e-18	0.591071708	0.063908644
0.09055231	0.525636077	0.100249172
7.45e-37	0.440568733	-0.011764215
0.212473746	0.325157974	-0.075923091
2.44e-35	0.517395968	-0.04096234
4.61e-17	0.390838943	-0.02488733
0.00039162	0.355203821	0.148516988
1.01e-133	0.44609087	-0.027690191
1.72e-14	0.654101051	0.036495351
1.05e-08	0.771224553	0.032118011
2.33e-20	0.088313811	-0.050871669
5.39e-54	0.665162922	-0.002644592
7.88e-15	0.382449628	0.165357591
0.000309586	0.721591202	-0.002673363
0.19478606	0.233650402	0.183336926
9.98e-48	0.436343304	-0.022932889
1.72e-13	0.331405965	-0.068200518
3.06e-08	0.526032984	0.158441795
7.82e-21	0.45380221	0.174800225
9.44e-267	0.637949341	0.021434401
0.044825867	0.534586076	0.102008277
4.95e-158	0.623332336	0.015842722
2.35e-49	0.618650393	0.081711383
5,00E-08	0.648810451	0.256266122
1.78e-23	0.316437084	-0.005701445
5.92e-07	0.255980861	-0.095459495
4.6e-23	0.316437084	-0.004316506
3.52e-13	0.763185407	0.251502083
2.27e-229	0.536561469	0.02250245
4.34e-46	0.451713085	0.134653307
2.21e-64	0.527926429	0.004724229
4.09e-50	0.792488385	0.215446956
1.32e-61	0.317424505	-0.023212948
1.9e-16	0.434216391	0.02588966
1.57e-07	0.146155065	-0.048088717
0.014882632	0.245794724	-0.131480636
1.57e-07	0.146155065	-0.048088717

1.07e-26	0.632418995	0.057186004
5,00E-80	0.510276588	0.128283161
2.79e-17	0.926456095	0.214924585
6.48e-131	0.094118821	-0.093564859
1.02e-15	0.748463768	0.195059531
0.00111795	0.585141941	0.075250784
2.75e-11	0.752147376	0.131134196
4.53e-28	0.298789382	0.106698761
1.93e-134	0.491991981	0.022261813
4.44e-15	0.655450389	0.054129304
5.73e-05	0.100178734	-0.149180587
0.004125527	0.042399621	-0.089632769
0.000550305	0.463186813	-0.068012927
7.68e-222	0.002417795	-0.037595135
2.86e-31	0.604788874	0.033863184
9.98e-25	0.544823232	0.117217773
4.94e-12	0.542311662	0.20403495
3.2e-06	0.839349254	-0.015991027
1.57e-40	0.524572154	-0.006587203
6.4e-08	0.358555714	0.011632638
8.51e-14	0.573792139	0.023712612
5.07e-32	0.508906883	0.027240834
2.02e-21	0.525101071	0.075310126
4.97e-08	0.893272543	0.131349952
1.02e-05	0.154651163	0.04062893
1.2e-67	0.782981891	0.185434908
1.2e-67	0.782981891	0.185434908
0.054773181	0.575493612	0.167323352
3.37e-22	0.438372093	0.099750238
2.98e-19	0.752296085	0.053880258
6.53e-23	0.306723958	-0.009120943
1.37e-05	0.429068448	0.095617877
9.41e-26	0.61924721	0.203254785
2.56e-05	0.518524636	-0.001753952
8.27e-42	0.137198113	-0.088307277
3.78e-305	0.384837652	0.185564531
1.61e-22	0.497049671	0.090656977
9.8e-85	0.422892559	0.048282963
2.59e-66	0.544675155	-0.025134615
6.86e-81	0.261481609	-0.136340447
6.58e-16	0.474030268	0.038384136
3.95e-09	0.700624969	-0.007832862
1.99e-68	0.440586622	0.14840683
4.49e-17	0.616751962	0.079671267

1.65e-08	0.347659696	0.145719743
2.52e-26	0.62900379	0.029902314
0.008437907	0.767297585	0.089625701
6.72e-13	0.63591825	0.044425087
0.032495445	0.384025336	0.236405879
1.12e-24	0.316883929	0.093450606
9.38e-92	0.62190064	0.009891881
0.000311978	0.433650212	0.053379228
0.000593678	0.595728063	0.111444214
1.25e-12	0.633150762	-0.012449728
2.63e-11	0.5962552	0.044869293
0.000740332	0.466953337	-0.101728774
0.277595859	0.321804967	-0.171245337
3.4e-05	0.690863254	0.110930453
0.109526826	0.266369955	-0.16581628
1.55e-41	0.347010335	-0.065938683
9.19e-50	0.681392194	-0.009664997
0.000167184	0.792036167	0.070041235
3.81e-16	0.431452475	-0.048632339
6.27e-13	0.428764322	-0.037286834
4.5e-13	0.621789683	0.005797023
0.002334358	0.528103065	0.106710282
4.3e-20	0.474342158	0.233230652
9.24e-33	0.559794041	0.207304076
0.064406938	0.27363876	-0.124790733
0.093116267	0.938575269	0.126819738
0.001170943	0.715467747	0.118876838
4.09e-58	0.39159776	0.054507813
0.005296485	0.787005534	0.02802026
4.65e-20	0.277154928	-0.044586699
8.2e-13	0.243905536	0.078983067
0.015321345	0.692266336	0.338400903
3.64e-14	0.542234973	0.082430906
9.06e-19	0.369050141	-0.007817628
1.16e-20	0.500018228	0.137844192
5.78e-68	0.51394845	0.00319711
0.036257408	0.647432908	0.088173649
2.96e-08	0.177139678	-0.00807949
2.27e-07	0.278104994	0.007801602
5.6e-43	0.568093093	0.052376905
0.035144637	0.815387374	0.229700579
0.094308143	0.687720255	0.127428799
0.00267327	0.605316993	0.187081703
2.2e-18	0.677412794	0.0026038

3.47e-06	0.706287808	0.037665914
3.77e-05	0.231080836	0.171812323
8.97e-24	0.046465802	-0.085128672
7.44e-102	0.384890227	0.038978768
1.15e-39	0.465265725	0.166484064
3.2e-16	0.761217943	0.096532125
9.85e-28	0.529668269	0.084486343
7.3e-11	0.469308036	0.165814977
3.09e-172	0.109126147	0.00869069
2.79e-06	0.456415431	0.138033854
2.21e-07	0.52834499	0.168547818
0.000445545	0.728035744	0.08447523
9.13e-16	0.568443327	0.092963312
1.82e-32	0.412548182	0.062669118
1.24e-05	0.62285402	-0.12166006
5.94e-17	0.45447826	0.125561887
6.52e-63	0.11816784	-0.037303344
8.98e-11	0.404925174	0.119728404
0.029398972	0.475498655	0.216589356
4.73e-06	0.164567197	0.017418299
1.83e-14	0.417427999	0.068660026
3.81e-17	0.340340699	0.003346826
0.011386336	0.479030408	-0.169595707
0.000201717	0.185217773	-0.011059437
1.25e-30	0.275170257	0.117303724
1.23e-12	0.578183453	-0.011907763
3.99e-06	0.311502118	-0.041112891
3.25e-43	0.318984244	0.064246877
7.99e-08	0.755613941	0.060561361
3.03e-57	0.6460261	0.034013161
2.7e-14	0.5377609	0.284195002
4.89e-92	0.546393165	-0.006116893
3.59e-06	0.523728866	0.258388944
1.47e-08	0.647834866	0.182309788
0.323480738	0.357676643	-0.1124021
0.003857798	0.77120743	-0.017153914
8.3e-128	0.690608483	0.056981302
1.68e-05	0.744956603	-0.025386115
4.36e-06	0.029371635	-0.112377445
4.81e-08	0.791562771	0.009054252
4.59e-49	0.606076088	0.0374329
1.91e-64	0.654037112	0.233923856
6.53e-229	0.449291576	0.052636264
2.36e-37	0.649882094	0.363073315

1.49e-67	0.603342918	0.248672759
1.18e-06	0.638305847	-0.077540362
0.000396744	0.162772278	0.094494791
6.63e-09	0.295397271	0.10877987
6.73e-136	0.605699659	-0.004972709
5.87e-06	0.607002801	0.02513551
2.05e-45	0.191275607	-0.014065916
2.4e-139	0.375717118	0.19940417
5.7e-11	0.608156268	0.057599986
1.69e-07	0.708552086	0.166694967
1,00E-19	0.637376978	0.00531253
0.00023551	0.438628901	0.173741631
9.1e-48	0.535490812	-0.0273651
7.36e-131	0.578623687	-0.032843909
0.390430028	0.865777146	0.119939598
3.91e-10	0.598203186	-0.028013454
1.17e-26	0.344098905	0.019832085
0.080499108	0.447081076	0.121229762
2.53e-12	0.667579799	-0.027148588
3.08e-56	0.354022488	0.062169594
8.56e-14	0.656437481	0.012183389
1.41e-62	0.453044111	0.195141152
1.02e-19	0.675033808	-0.024616478
9.23e-33	0.041511723	0.025007812
1.33e-75	0.546285012	0.017372383
1.4e-30	0.339140271	0.185108022
7.84e-21	0.682510523	0.013347713
6.47e-65	0.5801718	0.048492982
1.02e-08	0.268357091	-0.073943057
3.26e-28	0.647023055	0.064923889
9.24e-27	0.4369553	0.075477224
6.09e-31	0.531512473	0.096511955
0.000114233	0.638908882	0.002131417
0.000238676	0.651833017	0.004632316
0.007312532	0.102527223	-0.130258008
4.18e-06	0.379817885	-0.137161005
3.2e-05	0.173645366	0.004864591
9.25e-09	0.17076221	-0.031837631
1.85e-07	0.823990683	0.014099317
4.11e-12	0.776587714	0.113749218
2.14e-31	0.019317112	-0.018867762
2.38e-08	0.680848604	0.104628035
0.013197415	0.503245144	-0.151924692
3.23e-26	0.36162982	-0.018646506

**q-value of methylation
difference in Sdhd -/- imCC**

1.59e-47
1.17e-14
0.305609256
0.00267426
1.93e-40
0.053721157
0.081738
0.001597197
1.99e-16
2.29e-05
0.030770864
1.61e-14
0.062322137
2.17e-23
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Figure 1

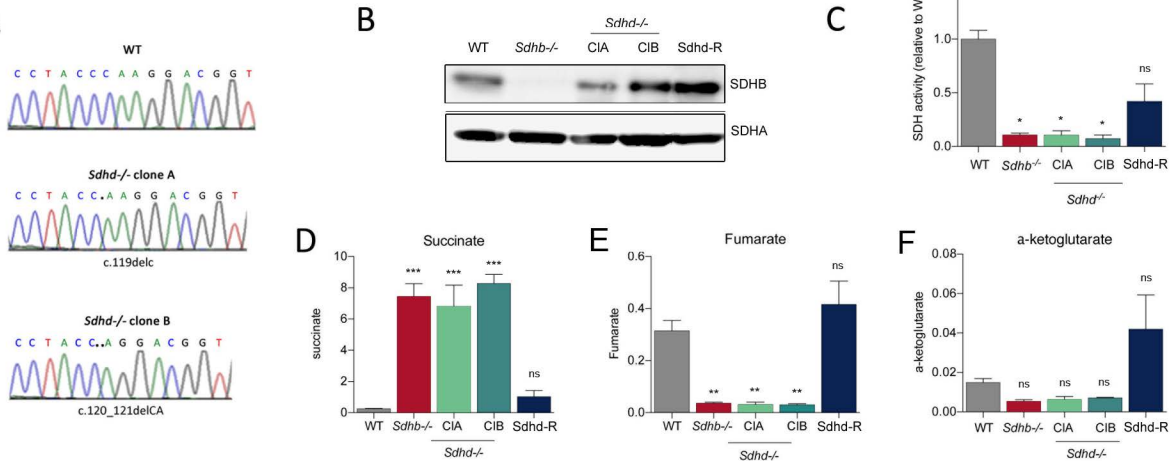


Figure 2

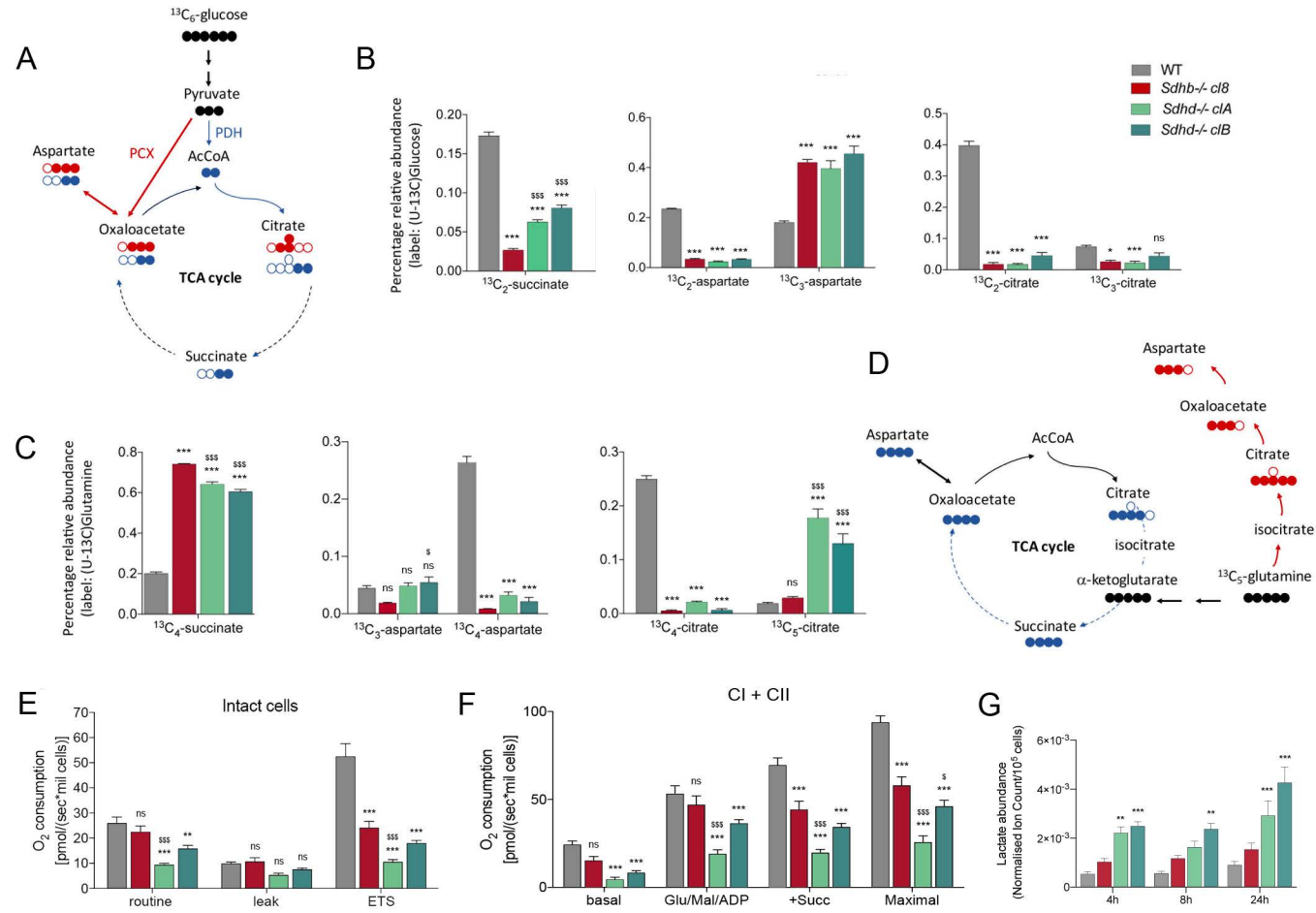


Figure 3

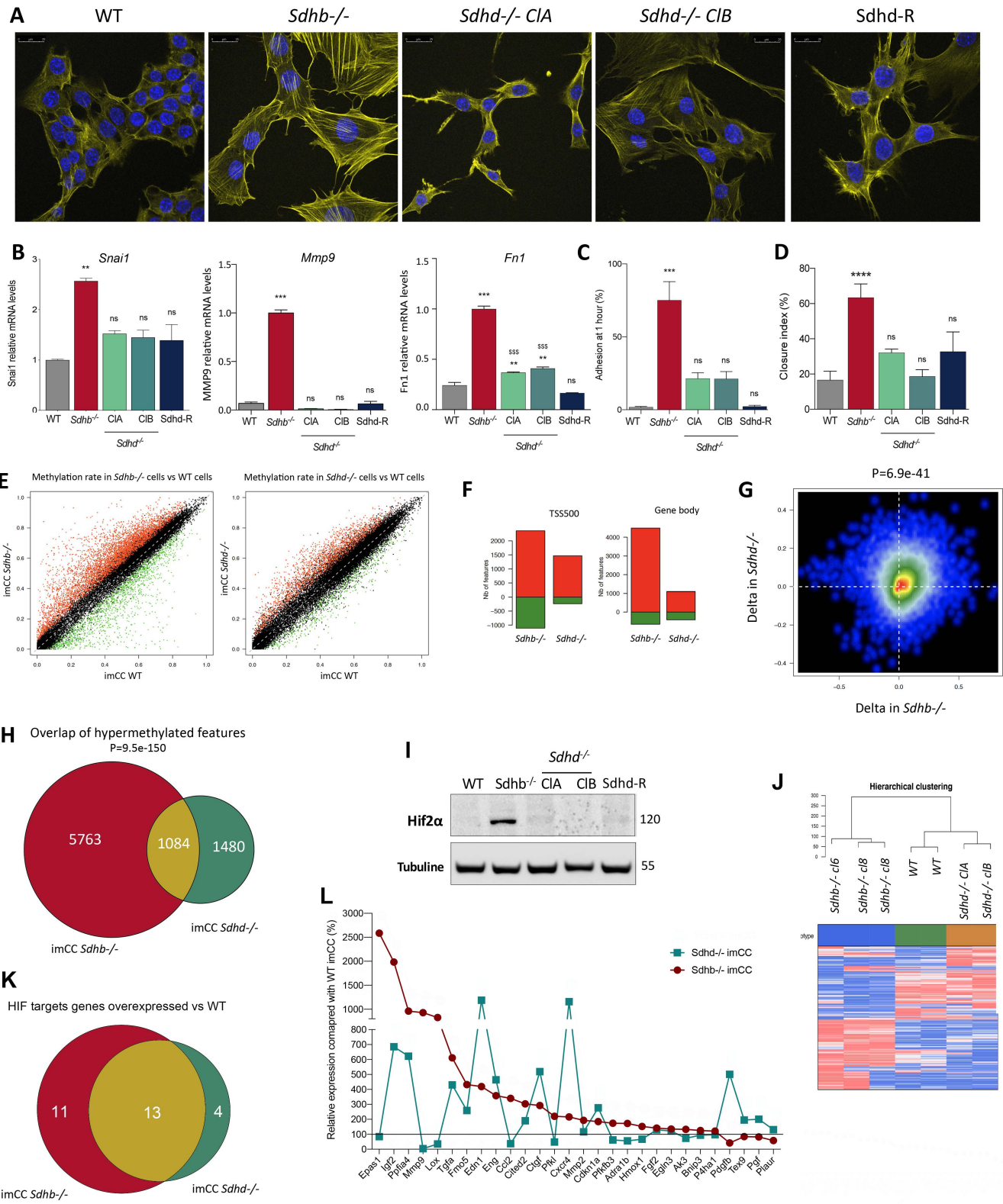


Figure 4

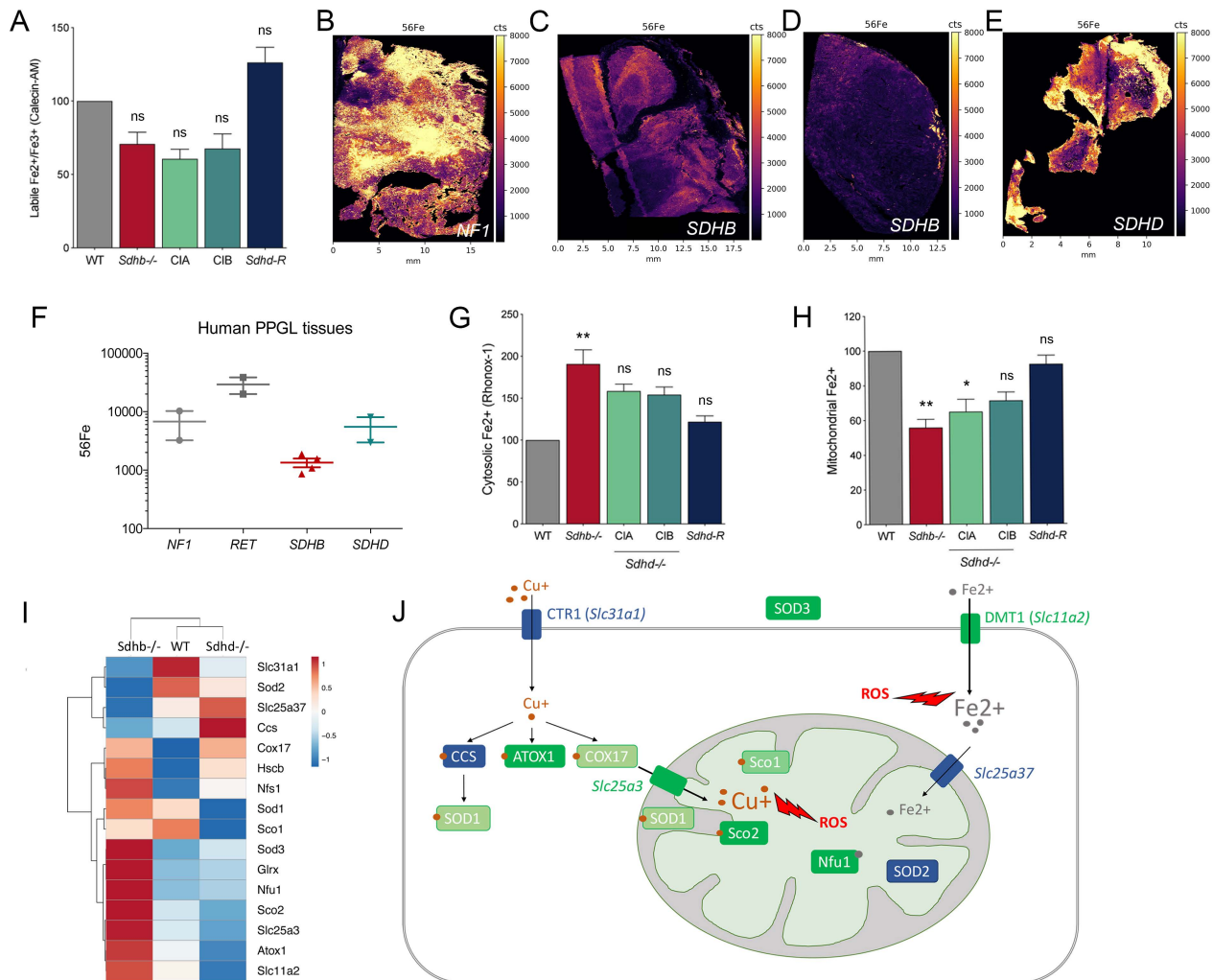


Figure 5

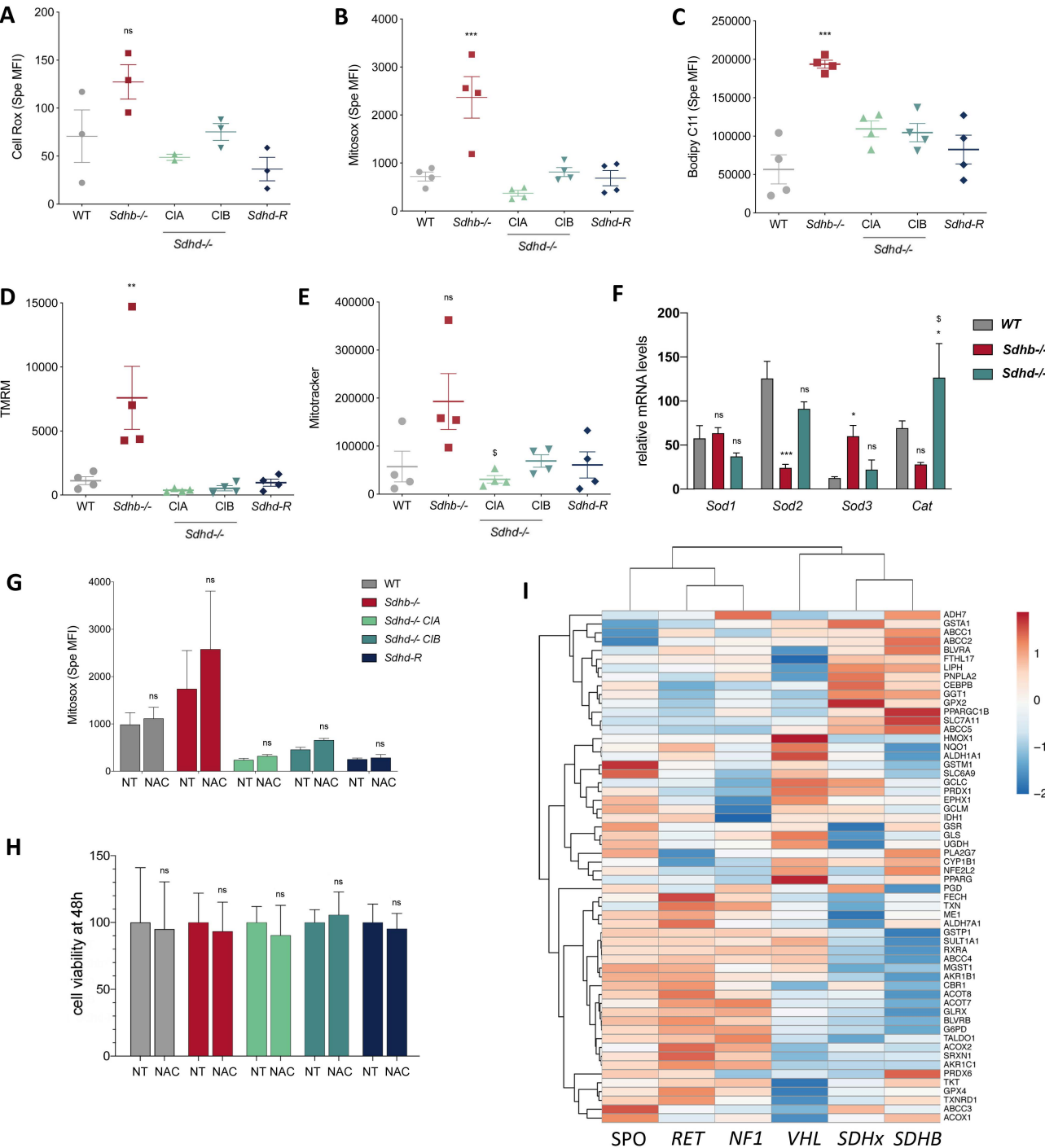


Figure 6

