#### Identification of 15 new bypassable essential genes of fission veast 1

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## 14

#### Abstract 15

Every organism has a different set of genes essential for its viability. This indicates that an 16organism can become tolerant to the loss of an essential gene under certain circumstances during 1718 evolution, via the manifestation of 'masked' alternative mechanisms. In our quest to systematically uncover masked mechanisms in eukaryotic cells, we developed an extragenic 19 suppressor screening method using haploid spores deleted of an essential gene in the fission yeast 20 Schizosaccharomyces pombe. We screened for the 'bypass' suppressors of lethality of 92 2122randomly selected genes that are essential for viability in standard laboratory culture conditions. 23Remarkably, extragenic mutations bypassed the essentiality of as many as 20 genes (22%), 15 of which have not been previously reported. Half of the bypass-suppressible genes were involved in 24mitochondria function; we also identified multiple genes regulating RNA processing. 18 25suppressible genes were conserved in the budding yeast Saccharomyces cerevisiae, but 13 of them 26were non-essential in that species. These trends are consistent with a recent independent 27bypass-of-essentiality (BOE) screening of 142 fission yeast genes conducted with more elaborate 28methodology (Li et al., 2019). Thus, our study reinforces the emerging view that BOE is not a rare 29event and that each organism may be endowed with secondary or backup mechanisms that can 30 31 substitute for primary mechanisms in various biological processes. Furthermore, the robustness of our simple spore-based methodology paves the way for genome-scale BOE screening. 32

#### Introduction 34

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A recent genome-wide study using S. cerevisiae gave an insight into the 'evolvability' of 35 36 essential cellular processes (Liu et al., 2015), which can be also termed 'bypass-of-essentiality' (BOE) (Li et al., 2019). The study surveyed the viability of every essential gene disruptant in S. 37 cerevisiae (1,106 genes), and found that 9% of the gene disruptants proliferate and form colonies 38 spontaneously (i.e. without artificial mutagenesis). Genome analysis showed that most of the 39 proliferating strains had gained an extra chromosome (i.e. aneuploidy), which is typically an 40 outcome of chromosome missegregation. This is a reasonable path to BOE in S. cerevisiae, 41 because its haploid is tolerant to a chromosome gain for 13 of 16 chromosomes (Torres et al., 422007). However, we speculated that there might be many more bypassable essential genes in yeast, 43as some non-bypassable essential gene disruptants might recover their viability by acquiring 44 extragenic mutations, which are rarely introduced without mutagenesis. 45

1 Comprehensive identification of suppressor mutations would help to elucidate secondary or  $\mathbf{2}$ backup mechanisms that can substitute for primary mechanisms. Hitherto 'masked', these alternative mechanisms may act as the dominant pathways in specific cell types and/or diseased 3 4 cells. To this end, we designed a BOE screening using the fission yeast S. pombe, which has a similar number (1,260) of essential genes to S. cerevisiae (Kim et al., 2010). A notable difference  $\mathbf{5}$ from S. cerevisiae is that S. pombe has only 3 chromosomes, and the haploid yeast is inviable 6 when an extra copy of either chromosome I or II (the two larger chromosomes) is inherited (Niwa  $\overline{7}$ and Yanagida, 1985). Thus, BOE via extra chromosome gain is likely an infrequent event in S. 8 9 pombe. In the present study, we carried out BOE screening for randomly selected 92 essential genes in S. pombe, based on UV mutagenesis of spores in which essential genes were deleted. 10

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## 12 Materials and methods

#### 13 Yeast strains and media

A diploid named G29 was used as the host (*h<sup>+</sup> his2 leu1 ura4-D18 ade6-216* / *h<sup>-</sup> leu1 ura4-D18 ade6-210 rpl42.sP56Q*), where *rpl42.sP56Q* allele was used as a counter-selection marker against cycloheximide (Roguev *et al.*, 2007). Conventional genetic experiments followed (Moreno *et al.*, 1991). Yeast was grown on complete YE5S medium (YE supplemented with leucine, uracil, adenine, lysine, and histidine) or the synthetic PMG or EMM medium at 32°C (plate) or 30°C (liquid). Sporulation was induced on the SPA plate or in the EMMG liquid medium (i.e. PMG containing 1 g/L sodium glutamate instead of 3.75 g/L).

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#### 22 Gene disruption

Essential genes were selected based on information found in the Pombase database (Wood et al., 232012). 92 genes on chromosome II were randomly selected. Conventional one-step replacement 24was conducted using ~500-bp homologous sequences (5'UTR and 3'UTR of the gene to be 25deleted) (Krawchuk and Wahls, 1999). A tandem G418-resistance (kanMX) /ura4+ cassette was 2627used as the selection marker (however, *ura4*+ marker was not actually used for selection). For most genes, we directly generated a linear construct (5'UTR-G418-ura4+-3'UTR) by two rounds 28of PCR using two sets of primers (i.e. nested PCR). In some cases, the PCR fragment was cloned 29into a vector using an Infusion kit (Takara), and the linear construct was amplified with T7/T3 30 primer set from the plasmid template. The linear DNA was transformed into the G29 diploid strain 31 32using the standard lithium acetate/PEG-mediated method, and disruption of the target gene was confirmed by colony PCR using KOD-Fx-Neo or KOF-ONE kit (Toyobo). When the endogenous 33 gene and G418-ura4+ cassette had a similar length, we used a longer version of G418-ura4+ 34 cassette to distinguish disrupted and endogenous alleles by length. PCR primers for gene 35 disruptions and their confirmation are listed in Table S1. 36

- 37
- 38 Spore isolation

Exponentially growing heterozygous diploid cells in YE5S (+10  $\mu$ g/ml G418) were harvested and transferred to EMMG medium (1× 10<sup>6</sup> cells/ml). After shaking at 200 rpm and 30°C for ≥36 h, cells were harvested, washed twice with sterile water, and resuspended in 0.5% glusulase solution.

42 The solution was shaken at 80 rpm at room temperature overnight to digest non-sporulated cells.

43 The spores were harvested and further treated with 30% ethanol for 30 min (80 rpm, room

temperature) to further remove diploid cell contamination. The purified spores were resuspended

- 45 in sterile water and stored at 4°C.
- 46

#### 1 Spore quality check

Prior to UV mutagenesis, the viability and purity of spores were determined by plating onto  $\mathbf{2}$ normal YE5S plate and YE5S supplemented with G418 (100 µg/ml) and cycloheximide (100 3 4 µg/ml), respectively. No haploid spores were expected to grow on the G418/cycloheximide plate, since an essential gene had been replaced with G418. However, colonies were always formed  $\mathbf{5}$ 6 typically at  $\sim 1 \times 10^{-6}$  frequencies. Cells in these colonies were diploids, which we interpreted to be derived from diploid spores generated at low frequency during meiosis; diploid spores would also  $\overline{7}$ be resistant to glusulase or ethanol. In cases in which the putative diploid contamination frequency 8 was  $< 5 \times 10^{-5}$ , we moved on to UV mutagenesis and screening. In cases in which the 9 contamination frequency was  $\geq 5 \times 10^{-5}$ , we discarded the sample and repeated the spore isolation 10 process. The reason for differences in the prevalence of putative diploid spores is unknown. 11

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#### 13 BOE screening with UV mutagenesis

 $1 \times 10^7$  spores were plated onto a YE5S plate containing G418 (100 µg/ml) and cycloheximide 14 (100  $\mu$ g/ml), followed by UV irradiation (90 × 100  $\mu$ J/cm<sup>2</sup>: UV Crosslinker, CL-1000, 254 nm, 15100 V, 8 W [UVP/Analytik Jena] or Stratalinker UV crosslinker Model 1800 [Stratagene]). Under 16 these conditions, spore viability was approximately 1%. Cycloheximide allows counter-selection 17against rpl42+ gene; in the presence of cycloheximide, haploids possessing the rpl42.sP56Q allele 18 can grow but not parental heterozygous diploids (Roguev et al., 2007). Plates were incubated at 19 32°C for 7 d. In most cases, we detected colonies. To check if each colony represents BOE or 2021diploid contamination, we replica-plated onto EMM minus adenine and SPA plates. After checking spore formation by iodine treatment on SPA, we selected the Ade- and 22non-spore-forming colonies as candidate BOE haploids; colonies that did not match this criterion 23were likely diploids and disregarded. The candidate colonies were subjected to colony PCR, with 24which the disruption of the target gene was reconfirmed (see Fig. 2B). For  $top3\Delta$ , we performed 25mutagenesis in a rad13A (DNA repair-deficient) background, in order to decrease UV power 26 $(1,500 \text{ }\mu\text{J/cm}^2, 5\% \text{ viability})$  and avoid cytotoxicity. However, since we obtained expected BOE 27results for  $cut7\Delta$  in the presence of rad13+, we did not introduce  $rad13\Delta$  for any other genes. 28

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#### 30 Whole-genome sequencing and sequence analysis

To identify suppressor mutations, bulk segregant analysis was performed. Survivor strains were crossed with a wild-type strain, and spores were plated on G418-containing YE5S plates. After 7 d, ~1,000 colonies were collected and DNA was extracted with Dr. GenTLE (Takara). Genomic DNA (1  $\mu$ g) was sequenced by BGI or Novogene (1 Gb), and the reads were mapped to the reference genome (Schizosaccharomyces\_pombe.ASM294v2.genebank.gb) using CLC Genomics Workbench. Unique and homogenous Indels and SNPs identified for each strain were manually inspected using Integrative Genomics Viewer (IGV).

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#### 39 Results & Discussion

Fig. 1 illustrates the scheme of our BOE screening. A heterozygous diploid in which one copy of an essential gene was replaced with a drug (G418)-resistant marker was sporulated. The spores were plated on G418-containing plates and simultaneously mutagenized by UV irradiation. If a haploid colony is obtained on this plate, it has likely acquired a suppressor mutation(s), indicating that the essentiality of the gene has been bypassed.

We first applied this method to two gene disruptants,  $cut7\Delta$  (kinesin-5) and  $top3\Delta$  (type I topoisomerase), the lethality of which is known to be suppressed by the loss of function of Pkl1

1 (kinesin-14) and Rgh1 (recQ helicase), respectively (Goodwin et al., 1999; Olmsted et al., 2014; Syrovatkina and Tran, 2015). For  $cut7\Delta$ , we obtained a total of 8 haploid colonies in the first  $\mathbf{2}$ experiment and 30 more in a later experiment, in which 5-fold more spores were mutagenized 3 4 (Fig. 2A, B). We analysed 26 colonies by target sequencing of pkl1 and msd1 genes (Msd1 is a positive regulator of Pkl1 (Yukawa et al., 2015)), whole-genome sequencing, and/or genetic  $\mathbf{5}$ 6 linkage test (pkl1 locus is close to the rpl42 locus, at which a mutation was introduced to confer cycloheximide resistance in our strain). The combined results suggested that suppressor mutations  $\overline{7}$ reside in pkl1 for 19 strains and in msd1 for the remaining 7 strains (Fig. 2C, E). Mutagenesis of 8 9 top  $3\Delta$  yielded 3 haploid strains (Fig. 2D), and direct sequencing of the rgh1 gene identified a mutation in all cases (Fig. 2E). Thus, our screening successfully elucidated known BOE 10 relationships. 11

We then expanded the screening to 92 essential genes located on chromosome II. For 20 of these, we obtained  $1\sim17$  haploid colonies, which corresponds to 22% (Fig. 3). This frequency is much higher than that obtained in the previous mutagenesis-free screening in *S. cerevisiae* (Liu et al., 2015).

The 20 suppressible genes possess divergent known biological functions. 10 genes (50%) 16were related to mitochondrial function (Fig. 4A). This may be partly explained by the fact that, in 17the regular medium containing >2% glucose, cell proliferation does not depend much on 18 mitochondrial respiration (Takeda et al., 2015). 6 genes were associated with RNA processing and 19 ribosome functions; the basis of these trends are unclear. Overall, 90% of the genes had clear 2021orthologues in S. cerevisiae and H. sapiens, indicating that BOE is not limited to unconserved genes (Fig. 4B, C). However, the orthologues of 70% genes were reported to be non-essential in S. 22cerevisiae (Fig. 4D). An obvious next step would be to identify suppressor mutations of each 23survivor to understand how an essential mechanism can be bypassed. 24

In the course of this project, a conceptually identical study was published (Li et al., 2019). In 2526this study using S. pombe haploid, BOE was screened by 3 methods: chemical mutagenesis 27(termed C-BOE), transposon-based mutagenesis (T-BOE), and gene library overexpression (OP-BOE). While C-BOE is the most similar approach to ours, the methodology employed is 28different. Li et al (2019) did not use spores; instead, the essential gene disruptant was kept viable 29by the transformation of a plasmid that contains the deleted gene: if a colony that had lost the 30 plasmid was recovered, it was interpreted to indicate BOE. Li et al. (2019) obtained survivors for 31 3227% of the genes in one or more BOE assays, which is a similar frequency to ours.

Coincidentally, in the two studies, 29 common essential genes were screened. Upon comparison, 21 genes were not bypassable in both studies, whereas 5 genes were common BOE hits. 2 and 1 hits were uniquely found in their and our studies, respectively (Fig. 3). Thus, the comparison indicates that both screens had a good agreement in bypassability, but also suggests that a single screen cannot identify all possible BOE.

Li et al (2019) further identified suppressor genes responsible for BOE. For example, they 38 found that the mutation/overexpression of 6 components of the 19S proteasome compensates for 39 mitochondrial dysfunction, suggesting a link between proteasome alteration and mtDNA 40 dispensability. To test if our screen identified the same set of extragenic suppressor genes as Li et 41 al., we determined the whole-genome sequences of 3 BOE strains for mrpl8 (mitochondrial 42ribosome protein), which was a C-BOE hit in Li et al (2019). Interestingly, we identified 43mutations in *atp1* (F1-F0 ATP synthase alpha subunit (Falson *et al.*, 1991)) and *rpt3* (19S proteasome 44 base subcomplex ATPase subunit (Kitagawa et al., 2014)), which are very similar to what were found 45in Li et al. (2019) (atp3; F1-F0 ATP synthase gamma subunit: mts4; 19S proteasome regulatory subunit 46

1 (Wilkinson *et al.*, 1997)). In addition, our screen uniquely identified *hul5* (HECT-type ubiquitin-protein 2 ligase E3 (Fang *et al.*, 2011)), which might function upstream of the proteasome. *pir2* (RNA silencing 3 factor (Sugiyama *et al.*, 2016)) was another common hit, and Li et al. (2019) reported a single gene 4 mutation in *dis3* (exosome 3'-5' exoribonuclease subunit (Murakami *et al.*, 2007). However, we could 5 not find *dis3* mutations in any of the 3 BOE strains we obtained, indicating that other genes had 6 acquired suppressive mutations.

7 In summary, we have established an alternative sensitive—and perhaps less 8 labour-intensive—methodology for mutagenesis-based BOE screening in fission yeast, and 9 expanded the list of genes whose essentiality is bypassable. Our methodology allows for a 10 straightforward scale-up of the screen, from which we expect to reveal masked cellular 11 mechanisms.

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#### 23 Author contributions

G.G. conceived the project. G.G., S.S. H.O. and K.E.S. designed the research. A.T. and G.G. performed experiments. A.T., K.E.S. and G.G. analysed the data. S.S. and K.E.S. contributed resources. G.G. wrote the paper. S.S., H.O. and K.E.S. reviewed and edited the paper.

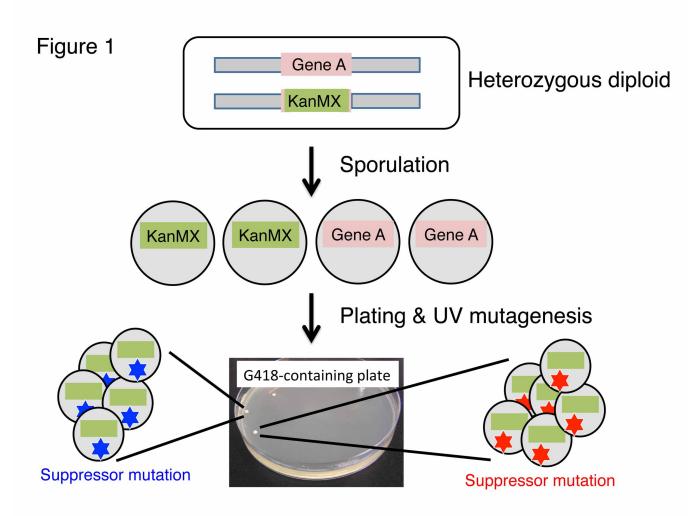
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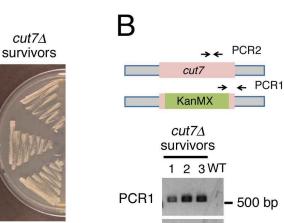


#### Figure 1. Flowchart of BOE screening using haploid spores of fission yeast

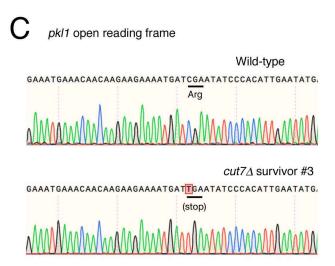
A copy of an essential gene (named 'A' in this figure) is replaced by the G418-resistant cassette (KanMX) in the diploid strain. This heterozygous diploid is viable since another copy of gene A remains intact. The diploid is sporulated in the nitrogen-limited medium. Spores with or without gene A are obtained at 1:1 ratio. The spores are spread onto G418-containing plate and then immediately irradiated with UV for mutagenesis. Only a spore with a suppressor mutation can grow and form a colony on the medium. The lack of gene A is confirmed by colony PCR.

500 bp

# Figure 2



PCR2



D

A

top3∆ survivors E



Essential gene	Suppressor gene	#	Identified mutations
cut7	<b>pkl1</b> (kinesin-14)	16	Indel, nonsense/missense mutation (e.g. T780I/Y781F)
(kinesin-5)	<b>msd1</b> (kinesin-14 regulator)	7	Indel, nonsense/missense mutations (e.g. L110P)
top3 (topo-III)	<b>rqh1</b> (recQ helicase)	3	Nonsense/missense mutation (e.g. G564E)

#### Figure 2. Successful identification of known BOE

(A) Three viable strains after UV mutagenesis of  $cut7\Delta$  strain. In total, we obtained 38 BOE strains after UV mutagenesis of 6 x 10<sup>7</sup>  $cut7\Delta$  spores. (B) PCR to verify the lack of cut7 gene for 3 haploid strains that formed colonies. (C) Sequencing result to show the appearance of a premature stop codon in *pkl1* gene in a  $cut7\Delta$  BOE strain. (D) 3 viable strains after UV mutagenesis of  $top3\Delta$  spores. (E) Summary of extragenic suppressor mutations of  $cut7\Delta$  and  $top3\Delta$ .

mrps17         micchondrial ribosomal protein subunit Mrp21         F           mrp18         micchondrial ribosomal protein subunit Mrp21         F           ew17         Frp12 complex subunit         F           micchondrial lipoic acid synthetase Lp5         1           ew18         micchondrial lipoic acid synthetase Lp5         1           micchondrial lipoic acid synthetase Lp5         1           micchondrial lipoic acid synthetase Lp5         1           micchondrial lipoic acid synthetase Lp5         0           mg21         GF binding protein Mitting AlPsace complex Lem3 family subunit         0           mg21         Gelg transport complex subunit         0           mg22         Gelg transport complex subunit         0           mg23         Gelg transport complex subunit         0           mg24         Gelg transport complex subunit         0           mg25         Gelg transport complex subunit         0           mg34         Transport complex subunit         0           mg35         Transport complex subunit         0           mg36         Toka Amplex and NNA subunit         0           mg36         Toka Amplex and NNA subunit         0           mg37         Toka Amplex and NNA subunit         0	Li et al (2019) BOE result	Li et al (2019) C-BOE mutation	S. cerevisiae (S288C) essentiality
mito:         mito:         4           evr/1         Pri1's complex subunit         4           pri2         NUR8 complex subunit.         4           mito:         NUR8 complex subunit.         1           simino:         1         1           simino:         1         1           simino:         1         1           simino:         1         1         1           simino:         1         1         1         1           simino:         1	C-BOE, OP-BOE	atp3, mts4	non-essential
cv/r/         Prp15 complex subunit         4           pip2         NURS complex subunit, it/C2R4 type zinc finger protein         31           isfn5         mitochondrial ispoir acid synthetase Lp5         11           isfn5         mitochondrial space complex class         0           mug89         phospholipid-translocating AIPase complex Lem3 family subunit         0           more         15P indring protein Brins         0           more         15P indring protein Brins         0           more         15P indring protein Brins         0           more         15P indring protein informations         0           more         15P indring protein informations         0           more         15P indring three subunit	C-BOE, OP-BOE	atp3, mts4	non-essential
pip2         NURS complex subunit, 7C2H2 type zinc finger protein         3           lip5         mitochondrial appragine-fINA ligase         0           nug89         phospholipId-transfaccing, APPase complex Lem3 family subunit         0           lot1         algoreterity-id/phosphate detta-homerase         0           org         Gig transport complex subunit         0           cog 2         Gig transport complex subunit         0           org         Ord         annel subunit         0           ord         origin recognition complex subunit         0           ord         origin recognition complex subunit         0           ord         Ord         origin recognition complex subunit         0           ord         Div Amoted TNA auxiliary tactor small subunit, U2AF-59         0           pip2         U2 small nuclear FNA auxiliary tactor small subunit, U2AF-59         0           pip3         Div Amoted TNA auxiliary tactor small subunit, U2AF-59         0           pip4         GINS complex subunit         0           rm1         nucle	C-BOE, OP-BOE	atp3, mts4	non-essential
IbpS         mitochondrial sporta         1           slintS         mitochondrial sporta         0           mug89         phospholipid-translocating ATPses complex Lem3 family subunit         0           ibit         lisopentary-dphosphate deta-somerase         0           ibit         lisopentary-dphosphate-deta-somerase         0           ibit         lisopentary-dphosphate-deta-somerase         0           ibit         lisopentary-dphosphate-deta-somerase         0 </td <td>non-bypassable</td> <td></td> <td>non-essential</td>	non-bypassable		non-essential
alints         mitochondrial asparagine-fRNA ligase         0           mug89         Dispesholigid-Tanslocating ATPses complex Lon3 family subunit         0           idi1         Signettray-Lightophia delta-iomerase         0           ipi1         doube-stara-agenetic complex Lon3 family subunit         0           opi2         doube-stara-agenetic complex Lon3 family subunit         0           opi2         doube-stara-agenetic complex subunit         0           opi2         doube-stara-agenetic complex subunit         0           opi3         doube-stara-agenetic complex subunit         0           opi3         doube-stara-agenetic complex subunit         0           opi3         origin recognition complex subunit         0           opi3         origin recognition complex subunit         0           opi3         DivA recorder RNA auxillary factor small subunit. U2AF-39         0           opi3         DivA recorder RNA auxillary factor small subunit. U2AF-39         0           opi3         DivA recorder RNA auxillary factor small subunit. U2AF-39         0           opi3         DivA recorder RNA auxillary factor small subunit. DivA recorder RNA auxillary factor small subunit.         0           opi3         DivA recorder RNA auxillary factor small subunit.         0           opi3	C-BOE	dis3	(unconserved)
mug89         phospholipid-transico.ang APPase complex Len3 family subunit         0           idi1         sopentery-dphosphate deta-somerase         0           ipr7         fig protessome regulatory subunit         0           ouble-strand-specific ribonuclease         0           ouble-strand-specific ribonuclease         0           ouble-strand-specific ribonuclease         0           ord         0         0         0	C-BOE	atd1	non-essential
bms1         GTP binding protein Bms1         0           id1         isopentery-diposphate defta-somenase         0           pac1         double-strand-specific inboruclease         0           cog2         Golg transport complex subunit         0           erg1         sequence monocogenese         0           fd2         barned/thoracine protein Knade         0           erg3         barned/thoracine SMC subunit         0           erg3         barned/thoracine SMC subunit         0           erg4         barned/thoracine SMC subunit         0           pp64         DNA dericetel RNA polymerase I complex subunit         0           pp72         U2 smait nuclear RNA autility factor small subunit         0           mp12         Gills complex subunit         0           pp64         DNA dericetel RNA polymerase I complex subunit         0           mp14         RNA polymerase I complex subunit         0           mm14         RNA polymerase I complex subunit         0           rm14         RNA polymerase I compl	C-BOE, OP-BOE	atp3, mts4	non-essential
Idi1     isopertery/-ciphosphate defla-somerase     0       pp71     Idi2 protessome regulatory subunit     0       cog2     Goig transport complex subunit     0       cog2     Goig transport complex subunit     0       cog3     Coig transport complex subunit     0       cog4     Goig transport complex subunit     0       cog5     congram complex subunit     0       cog5     Congram complex subunit     0       cog6     Condensin complex SUC subunit Stord     0       cog7     Condensin complex SUC subunit Stord     0       cog7     Condensin complex SUC subunit Stord     0       cog7     Condensin complex subunit     0       cog7     Condensin complex subunit     0       pp91     INAse Pard FNAse MFP subunit     0       rm11     FNA polymerase of general transcription initiation factor subunit     0       rm11     FNA polymerase of general transcription initiation factor subunit     0       rm11     FNA polymerase of general transcription initiation factor subunit     0       rm11     FNA polymerase of general transcription initiation factor subunit     0       rm11     FNA polymerase of general transcription initiation factor subunit     0       rm11     FNA polymerase of general transcription initiatio factor subunit     0	C-BOE, OP-BOE	itr2	non-essential essential
mpr7         195 professorie regulatory subunit         0           mpr7         195 professorie regulatory subunit         0           cog2         Golg transport complex subunit         0           reg1         siguatere monocoxygenase         0           erg3         franseydiphosphatefarnesydiphosphatefarnesyliransferase         0           ord5         ordjin recognition complex subunit         0           ord5         ordjin recognition complex subunit         0           ord5         ordjin recognition complex subunit         0           ord6         ordjin recognition complex subunit         0           ord6         ONA-directed TAN DAY Complex subunit         0           mp84         DNA-directed TAN DAY Daynomrase I complex subunit         0           mp12         Kineschore component         0           rm11         RNA polymerase I general transcription initiation factor subunit         0           rm11         RNA polymerase I general transcription initiation factor subunit         0           rm11         RNA polymerase I general transcription initiation factor subunit         0           rm11         RNA polymerase I general transcription initiation factor subunit         0           rm11         RNA polymerase I general transcription subunit S23         0	non-bypassable		essential
part         double-strand-specific ribonuclease         0           cog2         Golg transport complex subunit         0           reg3         transsylidphosphatefarmesylidphosphatefarmesylitransferase         0           reg3         transsylidphosphatefarmesylidphosphatefarmesylitransferase         0           reg3         transsylidphosphatefarmesylitransferase         0           reg3         transsylidphosphatefarmesylitransferase         0           reg3         transsylidphosphatefarmesylitransferase         0           reg3         transsylitransferase         0           reg3         transsylitransferase         0           reg3         transferase         0           reg4         transferase         0           reg4         transferase         0           reg3         transferase         0           reg4	non-bypassable non-bypassable		essential
cog2         Golg transport complex subunit         0           tor2         serine Threonine protein Kinase         0           erg9         transvidphosphate farmesyldphosphatefarmesyltransferase         0           orG5         ordigin recognition complex subunit         0           cui3         condination complex subunit         0           pp14         DNA opinemase defla subunit         0           mit12         RAIA polymerase defla subunit         0           mit12         RAIA polymerase defla subunit         0           pp14         DNA doffwarease defla subunit         0           setter         TMAS polymerase defla subunit         0           setter         TMAS polymerase defla subunit         0           setter         TMAS transformed subunit         15           setter         TMAS transformed subunit         16	non-bypassable	+	essential
erg1         scualere monocoxygenase         0           tor2         scinnAthreonine protein kinase         0           erg9         farnesydighosphate farnesydighosphatefarnesytiransferase         0           orc5         origin recognition complex subunit         0           ord5         origin recognition complex subunit         0           ord6         condensin complex SWC subunit         0           ord6         condensin complex SWC subunit         0           ord6         DNA directed RNA polymerase I complex subunit         0           ord6         DNA orderect RNA polymerase I complex subunit         0           mita12         Kinetochore component         0           mita2         Kinetochore component         0           sed5         SNARE         0           sed4         SNARE         0           rm33         mitochondriai ribosomal protein subunit S23         10           rm34         Tibosomal protein subunit S23         10           rm35         SNARE         5           sp86C2F12.01         Set         5           sp86C2F12.01         Set         5           sp86C3F12.01         Set         5           sp86C3F12.01         Set <t< td=""><td>non-bypassable</td><td></td><td>essential</td></t<>	non-bypassable		essential
toi2         serine.Witenonine protein         0           reg9         Innesvidiphosphatefarnesvidiphosphatefarnesvitransferase         0           orc5         ordigin recognition complex SUC suburit         0           out3         condensin complex SUC suburit         0           out3         condensin complex SUC suburit         0           out3         condensin complex SUC suburit         0           pp4         DNA objernesse delta suburit         0           pp4         DNA objernesse delta suburit         0           mis12         Kinacchore component         0           signit         DNA Parimerse regeneral transcription initiation factor suburit         0           mis12         SINARE         10           signit         Dox HIACA snoRNP assembly protein         0           mischondrial ribosomal protein suburit S23         10         0           rms4         Tibosomal protein suburit L33         10         0           rms1         ribosomal protein suburit L33         5         5           sPBC212:10         mitochondrial ribosomal protein suburit L35         5           sPBC24:11:0         Sibosocaltad protein suburit L35         5           sPBC24:12:0         Sibosocaltad protein suburit L35         5 </td <td>non-bypassable</td> <td></td> <td>essential</td>	non-bypassable		essential
erg9         famesydiphosphate famesydiphosphatefamesytransferase         0           orc5         origin recognition complex subunit         0           orc5         ordigin recognition complex subunit         0           orc6         condensin complex SWC subunit Smc4         0           pp24         U2 small nuclear RNA auxiliary factor small subunit, U2AF-59         0           pp45         DNA-directed RNA polymerase I complex subunit         0           occ0         GiNS complex subunit         0           pp42         CiNS complex subunit         0           mis12         Kinetochore component         0           seds         SiAARE         0	non-bypassable		essential
Ist 31         encyl reductase         0           ord5         ord6/in recognition complex SMCs subunit Smc4         0           pr02         U2 small nuclear RNA auxiling xators small subunit, U2AF-59         0           pr04         DNA-directed RNA polymerase II complex subunit         0           pop3         RNase P and RNase MP subunit         0           pop3         RNase P and RNase MP subunit         0           pop3         RNase IP and RNase MP subunit         0           mis12         Kinetochree component         0           sed5         SNARE         0           sed5         SNARE         0           sed5         SNARE         0           pip2         Pip64//CA sonONP assembly protein         0           mucleoporin         17         17           eec22         SNARE         16           pip2         Pip64/// Piosone biogeneis protein subunit S23         16           rm1         riboore biogeneis protein subunit S3         5           reg824         48         Rosemal protein subunit S3         5           reg827         40         Rosemal protein subunit S3         5           reg827         48         Rosemal protein subunit S3         5 <td>non-bypassable</td> <td></td> <td>essential</td>	non-bypassable		essential
condensin complex SMC subunit Smc4         0           prp2         U2 small nuclear NNA auxiliar factor small subunit, U2AF-59         0           cob27         DNA polymerase defla subunit         0           cob27         DNA polymerase defla subunit         0           pppB         RNase P and RNase MRP subunit         0           mis12         Kinetochor component         0           psg2         GINS complex subunit         0           set5         SNARE         0           set7         TMo2 translocase complex subunit         0           runp44         nucleoporth         117           sec22         SNARE         16           psp2         SNARE         16           psp2         SNARE         17           sec22         SNARE         16           psp2         SNARE         16           psp2         SNARE         16           psp2         SNARE         16           psp2         SNARE         16 <tr< td=""><td>non-bypassable</td><td></td><td>essential</td></tr<>	non-bypassable		essential
pp2         U2 small nuclear NNA auxiliary factor small subunit. U2A-F:99         0           cd227         DNA optoymerase delta subunit         0           pp68         RNase P and RNAse MAR Psubunit         0           pm87         GINS complex subunit         0           pm87         GINS complex subunit         0           pm87         GINS complex subunit         0           rm11         RNA polymerase 1 general transcription initiation factor subunit         0           sed5         SNARE         0	non-bypassable		essential
rpb4         DNA-diverse ella subunit         0           cdc27         DNA polymerase ella subunit         0           pp68         RNase P and RNase MPP subunit         0           mis12         Kinetochor component         0           pg12         GINS complex subunit         0           sed5         SNARE         0           shq1         box HACA anRNP assembly protein         0           nup44         nucleoporin         0           reg2         SNARE         0           ph53         Dox HACA anRNP assembly protein         0           rmido-tondrial ribosomal protein subunit 23         10           rrst         ribosome biogenesis protein subunit 23         5           sp8C212.10.11         fibsosomal protein subunit 13         5           sp8C241.21.20         ribosomal protein subunit 13         3           sp8C21.41.11C         Schizosaccharomyces specific protein         3           sp8C21.41.11C         Schizosaccharomyces specific protein         3	non-bypassable		essential
cit27         DNA polymerase delta subunit         0           pp68         RNase P and RNase MRP subunit         0           mi12         Kinetochore component         0           ps62         GINS complex subunit         0           rm11         RNA polymerase I general transcription initiation factor subunit         0           sed5         SNARE         0           strate         0         0           rm14         RNA polymerase I general transcription initiation factor subunit         0           rm14         RNAcO and RNP assembly protein         0           rm24         nucleoporin         0           rsec22         SNARE         16           pp12         phoaducin family protein         17           rsec23         101         17           rsr1         ribosome biogenesis protein         8           ps61         14         16           ps7         mitochondrial protein subunit S3         5           rsr16         5         5           SPBC1A110         4         16           imaso         Issochondrial protein subunit S3         5           rsr11         ribochondrial translation elongetion factor EF-Tu         1	non-bypassable		non-essential
pop8         RNase P and RNase MRP subunit         0           mi612         GINS complex subunit         0           rm11         RNA polymersel general transcription initiation factor subunit         0           sed5         SNARE         0           sed5         SNARE         0           imito         0         0           tim50         TIM24 translocase complex subunit         0           nup44         nucleoparin         17           sec22         SNARE         18           pip2         phosducin family protein         17           sec22         SNARE         18           rms3         mitochondrial ribosomal protein subunit S23         10           rms4         Hosonad protein subunit L35         5           sp210         Ads ribosomal protein subunit L35         5           sp212.10.1000         mitochondrial protein subunit L35         5           sp210.101         Schizosocharmyces specific protein         3           sp210.102.00         mitochondrial ribosomal protein subunit Ym6         3           sp210.102.00         mitochondrial ribosomal protein subunit Ym6         3           sp210.102.00         mitochondrial ribosomal protein subunit Ym6         3	non-bypassable		non-essential
misi2         Knetochore component         0           pel2         GINS complex subunit         0           rm11         RNA polymerase 1 general transcription initiation factor subunit         0           sed5         SNARE         0           sht1         box HACA anoRNP assembly protein         0           rmy44         nucleoporin         0           sec22         SNARE         16           pl2         phoaducin family protein         17           resc23         SNARE         16           pg31         CDP-diacylgreord-glycerol-3-phosphatis-phosphatidyltransferase         7           SPBC24212.10         mitochondrial protein subunit S23         5           rep31601         40         5           SPBC2426.630         mitochondrial protein subunit S3         5           seffici.41.11         Schizosscharbaromyces specific protein         4           lam3         Lsm24 complex subunit         0         1           seffici.41.11         Schizosscharbaromyces specific protein         3           stf01         mitochondrial translation indicator BF30         0           rtrii         mitochondrial translation indicator BF30         0           rtriid3         trassocontraining T-complex teta sub	non-bypassable		non-essential
pel2         GINS complex subunit         0           rm11         RNA polymersel general transcription initiation factor subunit         0           shq1         box HACA ancRNP assembly protein         0           inition         TIM23 translocase complex subunit         0           nup44         nucleoporin         17           sec22         SNARE         16           php2         phosducin family protein         17           sec22         SNARE         16           php2         phosducin family protein         17           sec22         SNARE         16           pp12         phosducin family protein         15           rem23         mitochondrial robosmal protein subunit 25         5           SPEC24.10.06         mitochondrial protein -SINA         4           sm3         Lsm24 complex subunit         3           SPEC4A.105         Schizosaccharomyces specific protein         3           SPEC4A.105         Schizosaccharops factor vIC30         0	non-bypassable		essential
mn11         RNA polymerase 1 general transcription initiation factor subunit         0           sed5         SNARE         0           itim50         TM23 transcase complex subunit         0           nup44         nucleoporin         0           sec22         SNARE         17           sec22         SNARE         17           sec23         SNARE         17           sec32         SNARE         16           pip2         phosducin family protein         15           rms1         mitochondrial ribosomal protein subunit S23         10           rms1         Mitochondrial robusomal protein subunit L35         5           SPBC271:20         Mitochondrial protein subunit L35         5           SPBC271:20         Mitochondrial protein subunit L35         5           SPBC271:20         Mitochondrial protein subunit L35         5           SPBC201:00:80         mitochondrial robusomation subunit TM6         3           tim1         mitochondrial robusomation subunit L7         0           translation inlibor complex subunit T20         0         0           reg1         mRNA guarylytransferase         0         0           rp14         Gbr2071P exchange factor, WD repeat protein         0 <td>non-bypassable</td> <td></td> <td>essential</td>	non-bypassable		essential
sed5         SNAFE         0           shq1         Dox H1/ACA snoFNP assembly protein         0           nup44         nucleoporin         17           sec22         SNAFE         16           pp12         Drosducin family protein         15           rsm23         mitochondrial ribosomal protein subunit S23         10           rrs1         ribosoma logenesis protein subunit L35         5           rspE30212.01         Mitochondrial protein subunit Va6         5           SPBC242.01         mitochondrial protein subunit Vm16         3           SPBC210.08c         mitochondrial translaton elongation factor EF-Tu         1           cct8         chaperonin-contaling Tras0         0         0           mito2         mitochondrial ribosomal protein subunit T20         0         0           tras0         ribosome biogenesis protein         0         0           grap10         mitochondrial ribosomal protein subunit L3         0         0 <t< td=""><td>non-bypassable</td><td></td><td>essential</td></t<>	non-bypassable		essential
shq1         box HACA snoPNP assembly protein         0           tims0         TM23 translocase complex subunit         0           nup44         nucleoporin         17           sec22         SNARE         16           pip2         phoseducin family protein         16           rem33         mitochondrial ribosomal protein subunit S23         10           rsm1         dibosomal protein subunit L35         5           ps1601         405 ribosomal protein subunit L35         5           ps1601         100 contain station elongation factor EF-ru         4           tims3         tsm24 containing T-complex theta subunit         0           cct8         chaperonin-containing T-complex theta subunit         0           cct91         mRIxA guarylyttransferase         0           mp170         mitochondrial robosomal protein subunit L7         0           translation initions factor eIF3g         0         0           sp141         GDP/GTP exchange factor. WD repeat protein         0           ops14 <t< td=""><td>non-bypassable</td><td></td><td>essential</td></t<>	non-bypassable		essential
Ittm20         TMA21 translocase complex subunit         0           nup44         nup1experime         0           resc22         SNARE         16           plp2         phosetucin family protein         16           rsm33         mitochondrial ribosomal protein subunit S23         10           rsm43         mitochondrial ribosomal protein S10         8           pgs160         02P-disciptylexerol-stycerol-3-phosphate3-phosph	non-bypassable		essential
nup44         nucleoporin         17           sec22         SNARE         16           pip2         phosducin family protein         15           rinza3         mitochondrial ribasomal protein subunit S23         10           rrs1         mitochondrial ribasomal protein subunit S23         10           rs2         mitochondrial ribasomal protein subunit L35         5           SPBC27E120         mitochondrial ribosomal protein subunit L35         5           SPBC24120.03         mitochondrial proline-rRNA ligase         5           sef2         U3 snoRNP-associated protein         4           Ism3         Lsm2-8 complex subunit         3           SPBC2010.08         mitochondrial ribosomal protein subunit Ym6         3           trin         mitochondrial ribosomal protein subunit L7         1           cc81         rtRAPP complex subunit Trs20         0           tris20         TrAPP complex subunit Trs20         0           tris35         translation initiation factor eIF3g         0           spPC1810.03         GDPG17F exchange factor. WD repeat protein         0           npp17 <mitochondrial (mpp)="" complex="" petidase="" processing="" subunit<="" td="">         0         0           npp16         diabsome biogenessis protein         0         <td< td=""><td>non-bypassable</td><td></td><td>essential</td></td<></mitochondrial>	non-bypassable		essential
sec22         SNARE         [16]           plp2         phosducin family protein         [15]           rmm23         mitochondrial ribosomal protein subunit S23         [16]           rms1         ribosome biogenesis protein         [8]           pgs1         CDP-diacylgiycerol-glycerol-3-phosphat63-phosphat1dyltransferase         7           SPBC2F12.10         mitochondrial protein S16         5           sef2         U3 sonNP-associated protein         [4]           lsm3         Lsm24 complex subunit         3           SPBC1A.116         Schizosaccharomyces specific protein         3           SPBC100.08c         mitochondrial translation elongation factor EF-Tu         1           cct8         chaperonin-containing T-complex theta subunit         0           rtr32         mitochondrial recombinase Mbr1         0           rts20         TRAPP complex subunit Trs20         0           ttr35         translation initiation factor eIF3g         0           SPBC141.10;         Cmitochondrial probabilide cylt/ly/ltransferase         0           soft 4         GDPG1P exchange factor, WD repeat protein         0           nops         ribosome biogenesis protein         0           apt10         anaphase-promoling complex substrate recognition subun	non-bypassable		essential
pip2         phosducin family protein         15           rsm23         100         15           rsm1         ribosome biogenesis protein         8           pgs1         CDP-diacylglycerol-glycerol-3-phosphata3-phosphatidyltransferase         7           SPBC221C30         mitochondrial robosomal protein subunit L35         5           gs1601         405 ribosomal protein S16         5           gs16224205         mitochondrial proline-tRNA tigase         5           esf2         U3 sonRIV-associated protein         3           SPBC201C056         mitochondrial robosomal protein subunit Ym16         3           tsm3         tsm36         mitochondrial robosomal protein subunit Ym16         3           tsm3         tsm36         chaperonin-containing T-complex theta subunit         0           ceg1         mitochondrial robosomal protein subunit L7         0         0           ttr35         tranatoin initiation lactor elF3g         0         0           SPBC1410.17c         mitochondrial recombinase Mir1         0         0           clc1         clatinin light chain         0         0           npp8         ribosome biogenesis protein         0         0           npp8         ribosome biogenesis protein nod <t< td=""><td>N.D.</td><td></td><td>essential</td></t<>	N.D.		essential
rem23         mitochondrial ribosomal protein subunit S23         10           rrs1         ribosome biogenesis protein         8           pgs10         CDP-diacyt/glycerol-3/protein subunit L35         5           SPBC2F12.10         mitochondrial ribosomal protein subunit L35         5           sps101         405 ribosomal protein S16         5           SPBC2A205.03         mitochondrial proline-tRNA ligase         5           est2         U3 anoRHV-associated protein         44           Ism3         Lsm2-8 complex subunit         3           SPBC2A115         Schizosaccharomyces specific protein         3           SPBC2D10.08c         mitochondrial ribosomal protein subunit Yml6         3           stuft         mitochondrial ribosomal protein subunit Yml6         3           cell         chaperonin-containing T-complex heta subunit L7         1           trus20         TRAPP complex subunit Ts20         0           translation instation factor eIF3g         0         0           clathrin light chain         0         0         0           app14         GDP/GTP exchange factor, WD repeat protein         0         0           app14         GDP/GTP exchange factor, WD repeat protein         0         0           app14	N.D.		non-essential
rint         rint         8           rgs1         CDP-diacylglycerol-glycerol-3-phosphata3-phosphatidyltransferase         7           SPBC2F12.10         mitochondrial ribosomal protein subunit L35         5           rgs1601         405 ribosomal protein S16         5           SPBC24C6.05         mitochondrial proline-TRNA ligase         5           esf2         U3 snoRNP-associated protein         4           Ism3         Lsm24 complex subunit         3           SPBC24C0.06         mitochondrial ribosomal protein subunit Yml6         3           cta1         mitochondrial ribosomal protein subunit Yml6         3           cta1         mitochondrial ribosomal protein subunit L7         0           cts2         trasperonin-containing T-complex subunit L7         0           ttrs20         TRAPP complex subunit Trs20         0           ttrs20         TRAPP complex subunit Trs20         0           sp5141810.17.07         0         0           sp5141810.17.07         0         0           sp5141810.17.07         0         0           sp5141810.17.07         0         0           sp514110.16.00         0         0           sp5141         0         0         0	N.D.		essential
pgs1         CDP-diacyt/giverol-givecrol-3-phosphate3-phosphatidytransferase         7           SPBC2F12.10         405 ribosomal protein subunit L35         5           SPG28712.10         405 ribosomal protein subunit L35         5           SPG2820.03         mitochondrial proline-tRNA tigase         5           est2         U3 anoRNP-associated protein         4           Ism3         Lsm2-8 complex subunit         3           SPBC1A4.11         Schizosoca-charomyces specific protein         3           SPBC1A5.11         Schizosoca-charomyces specific protein         0           registrice         Mitochondrial translation insubunit Vm66         3           strint         mitochondrial translation insubunit L7         0           trix20         TRAPP complex subunit Trs20         0           strint         GD         0         0           spinol         0         0         0           spinol         0         0         0         0           spinol         GDP/GTP excharge fac	N.D.		non-essential
SPBC2F12.10         mitochondrial ribosomal protein subunit L35         5           rps1601         40S ribosomal protein S16         5           SBPC2AC6.03         mitochondrial proline-rRNA ligase         5           est2         U3 snoRNP-associated protein         4           Ism3         Lsm2-8 complex subunit Ym16         3           SPBC2D10.06         mitochondrial rbsomal protein subunit Ym16         3           SPBC2D10.06         mitochondrial rbsomal protein subunit Ym16         3           CdB         chaperonin-containing T-complex theta subunit         0           cdg1         mRNA guanylyltransferase         0           mv11         mitochondrial recombinase Mnr1         0           SpBC18H10.17c         mitochondrial recombinase Mnr1         0           cd1         clathrin light chain         0           sp014         GDP/GTP Exohange factor, WD repeat protein         0           ncc3         chaperonin-containing T-complex gamma subunit         0           atrial         mitochondrial phosphatidate cytidylytransferase         0           sof1         U3 snoRNP-associated protein         0           app5         attrin-like protein Arp4         0         0           gp11         GDP/GTP exohange factor, WD repeat prote	N.D.		essential
rps1601         405 ribosomal protein 516         5           SPBC24C6.03         mitochondrial proline-tRNA ligase         5           est2         U3 snoRNP-associated protein         4           Ism3         Lsm2-8 complex subunit         3           SPBC1A4.115         Schizosocharomyces specific protein         3           SPBC1A5.115         Schizosocharomyces specific protein         3           SPBC1A4.115         Schizosocharomyces specific protein         3           SPBC1A4.115         Schizosocharomyces specific protein         3           SPBC1A4.115         Chizosocharomyces specific protein         0           ceg1         mRNA guanylyltransferase         0         0           mtochondrial rbosomal protein subunit L7         0         0         0           translation initation factor eIF3g         0         0         0           spost14         GDP/GTP exchange factor, WD repeat protein         0         0           nop8         ribosome biogenesis protein         0         0         0           ct31         chaprenoni-containing T-complex gamma subunit         0         0         0           gso14         GDP/GTP exchange factor.WD repeat protein ap4         0         0         0         0         0 </td <td>N.D.</td> <td></td> <td>essential</td>	N.D.		essential
SPBC24C6.03         mitochondrial proline-tRNA ligase         5           esf2         U3 sonGNP-associated protein         4           Ism3         Lsm2-8 complex subunit         3           SPBC210.08         mitochondrial ribosomal protein subunit Ymi6         3           SPBC210.086         mitochondrial ribosomal protein subunit Ymi6         3           tuf1         mitochondrial ribosomal protein subunit Ymi6         3           ceg1         mRINA guanylyltransferase         0           mpi7         mitochondrial ribosomal protein subunit L7         0           trasslation initiation lactor eIF3g         556(18)(17.07         0           SPBC18H10.17         0         0         0           sp14         GDPG1P exchange factor, WD repeat protein         0           app14         GDPG1P exchange factor, WD repeat protein         0           sp11         GINS complex subunit         0           sp	N.D.		non-essential
esf2         U3 snoRNP-associated protein         4           Ism3         SPBC1A4.11c         Schizosaccharomyces specific protein         3           SPBC2D10.08c         mitochondrial ribosomal protein subunit Yml6         3           Suff         mitochondrial translation elongation factor EF-Tu         1           cct8         chaperonin-containing T-complex theta subunit         0           reg1         mRINA gaurylyttransferase         0           mrp77         mitochondrial ribosomal protein subunit L7         0           trasslation initiation factor eIF3g         0         0           SPBC18H10.17c         mitochondrial recorebinase Mnr1         0           cla1         clathrin light chain         0           sp014         GDP/GTP exchange factor, WD repeat protein         0           app10         anaphase-promoting complex substrate recognition subunit         0           app11         anaphase-promoting complex substrate recognition subunit         0           cct3         chaperonin-containing T-complex gamma subunit         0           qct1         U3 snoRNP-associated protein         0           qct1         GINS complex subunit         0           qct1         GINS complex subunit         0           qct1         GINS c	N.D.		non-essential
Ism3         Lsm2-8 complex subunit         3           SPBC1A4.11c         Schizosaccharomyces specific protein         3           SPBC2D10.08c         mitochondrial ribosomal protein subunit Ym16         3           tuff         mitochondrial ranslation elongation factor EF-Tu         1           ccl8         chaperonin-containing T-complex theta subunit         0           mPI7         mitochondrial robosomal protein subunit L7         0           trs20         TRAPP complex subunit Trs20         0           tl35         translation initiation factor eIF3g         0           SPBC18H10.17c         mitochondrial recombinase Mnr1         0           cl1         clathrin light chain         0           sp014         dDP/GTP exchange factor, WD repeat protein         0           nop8         ribosome biogenesis protein         0           apo10         anaphase-promoting complex substrate recognition subunit         0           tar41         mitochondrial processing peptidase (MPP) complex bata subunit         0           apt5         actin-like protein Arp4         0           sof1         U3 snoRNP-associated protein         0           qcr1         mitochondrial processing peptidase (MPP) complex bata subunit         0           upt8         c	N.D.		non-essential
SPBC1A4.11c         Schizosaccharomyces specific protein         3           SPBC2D10.08c         mitochondrial ribosomal protein subunit Yml6         3           utif         mitochondrial ranslation elongation factor EF-Tu         1           cct8         chaperonin-containing T-complex theta subunit         0           reg1         mRINA guarylyttransferase         0           mp77         mitochondrial ribosomal protein subunit L7         0           translation initiation factor elF3g         0         0           sp514         Clathrin light chain         0           oct1         clathrin light chain         0           opp14         GDP/GTP exchange factor. WD repeat protein         0           opp14         GDP/GTP exchange factor.WD repeat protein         0           opp14         GDP/GTP exchange factor.WD repeat protein         0           opp14         GDS exchange factor.WD repeat protein         0           opp14         GTas fara	N.D. N.D.		essential essential
SPBC2D10.08c         mitochondrial translation elongation factor EF-Tu         1           cct8         chaperonin-containing T-complex theta subunit         0           cct91         mRNA guanylyttransferase         0           mrp17         mitochondrial ribosomal protein subunit L7         0           trs20         TRAPP complex subunit Trs20         0           trs31         translation initiation factor elF3g         0           SPBC18H10.17c         mitochondrial recombinase Mhr1         0           clc1         clathrin light chain         0           spo14         GDP/GTP exchange factor, WD repeat protein         0           nop8         ribosome biogenesis protein         0           apc10         anaphase-pormoting complex substrate recognition subunit         0           apd1         U3 sonRNP-associated protein         0           cd1         haperonin-containing T-complex subunit         0           qcr1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           utp18         CGI-48 family         0           ismd         CEI-48 family         0           utp18         pister chromatid separation inhibitor         0           cd14         Sinx component         0	N.D.		(unconserved)
tuff         mitochondrial translation elongation factor EF-Tu         1           cct8         chaperonin-containing T-complex theta subunit         0           mp17         mitochondrial ribosomal protein subunit L7         0           ftrs20         TFAPP Complex subunit Trs20         0           trs35         translation initiation factor elF3g         0           SPBC18H10.17c         mitochondrial recombinase Mhr1         0           clc1         clatinin light chain         0           sp14         GDP/GTP exchange factor, WD repeat protein         0           opp14         GDP/GTP exchange factor, WD repeat protein         0           apc10         anaphase-promoting complex substrate recognition subunit         0           apc11         U3 snoRINP-associated protein         0           cd1         U3 snoRINP-associated protein         0           cd1         Us noRINP-associated protein         0           qc11         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           qc11         mitochondrial processing peptidase (MPP) complex alpha subunit         0           cls1         sertine palmitotytransferase complex subunit         0           cls1         sertine palmitotytransferase complex subunit         0	N.D.		essential
cct8         chaperonin-containing T-complex theta subunit         0           mRNA guanylytransferase         0           mrtp7         mitochondrial ribosomal protein subunit L7         0           trs20         TFAAPP complex subunit Trs20         0           trs35         translation initiation factor eIF3g         0           SPBC18H10.17c         mitochondrial recombinase Mhr1         0           clc1         clathrin light chain         0           spo14         GDP/GTP exchange factor, WD repeat protein         0           nop8         ribosome biogenesis protein         0           apc10         anaphase-promoting complex substrate recognition subunit         0           aps1         disosone hordenesis protein         0           cct3         chaperonin-containing T-complex gamma subunit         0           apl5         actn-like protein Arp4         0           qcr1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           up18         CGI-48 family         0           ibid         cEI-48 family         0           cct1         escurin, sister chromatif separation inhibitor         0           sad1         spindle pole body SUN domain protein         0           cct1	N.D.		non-essential
ceg1         mRNA guanylyttransferase         0           mrp17         mitochondrial ribosomal protein subunit L7         0           trs20         TRAPP complex subunit Trs20         0           trs35         translation initiation factor elF3g         0           SPBC1BH10.17c (mitochondrial recombinase Mhr1         0         0           clc1         clathrin light chain         0           sp014         GDP/GTP exchange factor, WD repeat protein         0           app10         anaphase-promoting complex substrate recognition subunit         0           app10         anaphase-promoting complex gamma subunit         0           ccl3         chaperonin-contraining 7-complex gamma subunit         0           dpf1         GINS complex subunit         0           qer1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           up18         CGI-84 family         0         0           iblt3         cCl-18 tortholog         0         0           ms2         mitochondrial processing peptidase (MPP) complex alpha subunit         0         0           cut18         CGI-48 family         0         0         0           mas2         mitochondrial procesin in protein inbibitor         0         0	N.D.		essential
mp17         mitochondrial ribosomal protein subunit L7         0           trs20         TRAPP complex subunit Trs20         0           tif35         translation initiation factor elF3g         0           SPBC18H10.17c         mitochondrial recombinase Mhr1         0           cla1hri light chain         0           nop8         ribosome biogenesis protein         0           nop8         ribosome biogenesis protein         0           apc10         anaphase-promoting complex substrate recognition subunit         0           tarm41         mitochondrial phosphatidate cytidylytransferase         0           cd1         Ja snoRNP-associated protein         0           cd2         chaperonin-containing T-complex gamma subunit         0           actn-like protein Arp4         0         0           ger1         Dischondrial processing peptidase (MPP) complex beta subunit Mas1         0           up18         CGI-48 family         0         0           mitochondrial processing peptidase (MPP) complex alpha subunit         0         0           mas2         mitochondrial processing peptidase (MPP) complex alpha subunit         0           cd1-48 family         0         0         0           mas2         mitochondrial processing peptidase (	N.D.	+	essential
trs20         TRAPP complex subunit Trs20         0           tit35         translation initiation factor eIF3g         0           SPBC18H10.17c mitochondrial recombinase Mhr1         0           clc1         clathrin light chain         0           spo14         GDP/GTP exchange factor, WD repeat protein         0           apoto         anaphase-promoting complex substrate recognition subunit         0           tam41         mitochondrial phosphatidate cytidylyttransferase         0           cxt3         chaperonin-containing T-complex gamma subunit         0           alp51         ginsphase-promoting complex subunit         0           qcr1         mitochondrial phosphatidate cytidylyttransferase         0           cxt3         chaperonin-containing T-complex gamma subunit         0           qcr1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           isfm4         CENP-K ortholog         0           sim4         CENP-K ortholog MD domain protein         0           cxt1         chaperonin-containing T-complex alpha subunit         0           cxt2         securin, sister chromatid separation inhibitor         0           sad1         spindle pole body SUM domain protein         0           cxt2         secu	N.D.	+	non-essential
tit35         translation initiation factor eIF3g         0           SPBC18H10.17c         mitochondrial recombinase Mhr1         0           clc1         clathrin light chain         0           nop8         ribosome biogenesis protein         0           apc10         anaphase-promoting complex substrate recognition subunit         0           titam41         mitochondrial phosphatidate cytidylytransferase         0           cc13         chaperonin-containing T-complex gamma subunit         0           alp5         actin-like protein Arp4         0           qpr1         GlINS complex subunit         0           qcr1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           utp18         CGI-481 family         0           securin, sister chromatid separation inhibitor         0         0           cut2         securin, sister chromatid separation inhibitor         0           cut3         cha	N.D.	+	essential
clc1       clathrin light chain       0         sp014       GDP/GTP exchange factor, WD repeat protein       0         np03       ribosome biogenesis protein       0         apc10       anaphase-promoting complex substrate recognition subunit       0         tam41       mitochondrial phosphatidate cytidylyltransferase       0         oct3       chaperonin-containing T-complex gamma subunit       0         alp5       actin-like protein Arp4       0         qcr1       mitochondrial prosphaticate cytidylyltransferase       0         ops11       GINS complex subunit       0         qcr1       mitochondrial processing peptidase (MPP) complex beta subunit Mas1       0         ops14       CENP-K ortholog       0         sim4       CENP-K ortholog       0         cut2       securin, sister chromatid separation inhibitor       0         cut2       securin, sister chromatid separation inhibitor       0         cut3       bioliquitin-like protein modifier for cullin       0         cdt14       SIN component       0         rad60       DNA repair protein, SUMO-related       0         up3       GTPase activating protein       0         slin17       human KIN ortholog       0	N.D.		essential
spo14         GDP/GTP exchange factor, WD repeat protein         0           nop8         ribosome biogenesis protein         0           apc10         anaphase-promoting complex substrate recognition subunit         0           tam41         mitochondrial phosphatidate cytidylytransferase         0           cct3         chaperonin-containing T-complex gamma subunit         0           alp5         actin-like protein Arp4         0           giN5         actin-like protein Arp4         0           qcr1         mitochondrial processing petidase (MPP) complex beta subunit Mas1         0           dcr14         Stinke complex subunit         0           dcr14         Serine palmitoyltransferase complex subunit         0           mitochondrial processing petidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           cut2         securin, sister chromatid separation inhibitor         0           cut3         spindle pole body SUN domain protein         0           cut4         Sli component         0           dcdt14         Sli component         0           dcdt14         Sli complex subunit Protein, SUMO-related         0           ucp3         GTPase activating protein	N.D.		non-essential
nop8         Inbosome biogenesis protein         0           apc10         anaphase-promoting complex substrate recognition subunit         0           tam41         mitochondrial phosphatidate cytidylytransferase         0           cct3         snoFNV-associated protein         0           cct3         cchaperonin-containing T-complex gamma subunit         0           alp6         actin-like protein Arp4         0           opf1         GINS complex subunit         0           qcr1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           up18         CGI-48 family         0           sim4         CENP-K ortholog         0           mas2         mitochondrial processing peptidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           cut2         securin, sister chromatid separation inhibitor         0           cdt1         chaperonin-containing T-complex alpha subunit         0           ned8         ubiquitin-like protein modifier for cullin         0           cdt1         DNA binding factor         0           rad60         DNA repair protein, SUMO-related         0           ucp3         GTPase activating protein	N.D.		non-essential
apc10         anaphase-promoting complex substrate recognition subunit         0           tarn41         mitcchondrial phosphatidate cylidylytransferase         0           osof1         U3 snoRNP-associated protein         0           cct3         chaperonin-containing T-complex gamma subunit         0           alp5         actin-like protein Arp4         0           ops11         GINS complex subunit         0           qcr1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           lp15         Serine palmitoyltransferase complex subunit         0           sim4         CENP-K ortholog         0           mas2         mitochondrial processing peptidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           cut3         spindle pole body SUN domain protein         0           cut4         spindle pote body SUN domain protein         0           cut5         securin, sister chromatid separation inhibitor         0           cut4         SIN component         0         0           tbf1         DNA binding factor         0         0           rad60         DNA repair protein, SUMO-related         0         0           sp	N.D.		essential
tam41         mitochondrial phosphatidate cylidylytransferase         0           sof1         U3 snoRNP-associated protein         0           cct3         chaperonin-containing T-complex gamma subunit         0           alp5         actin-like protein Arp4         0           gINS complex subunit         0         0           qcr1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           dup18         CGI-48 family         0           lcb1         serine palmitoyltransferase complex subunit         0           mitochondrial processing peptidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           cut2         securin, sister chromatid separation inhibitor         0           cut3         spindle pole body SUN domain protein         0           cut1         chaperonin-containing T-complex alpha subunit         0           cd14         SIN component         0         0           tbf1         DNA binding factor         0         0           rad60         DNA repair protein, SUMO-related         0         0           ucp3         GTPase activating protein         0         0           pintot cohesin complex alpha subuni	N.D.		essential
soft         U3 snoRNP-associated protein         0           cct3         chaperonin-containing T-complex gamma subunit         0           alp5         actin-like protein Arp4         0           opf1         GINS complex subunit         0           qcr1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           utp18         CGI-48 family         0           sim4         CENP-K ortholog         0           sim4         CENP-K ortholog         0           ortas2         mitochondrial processing peptidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           cut2         securin, sister chromatid separation inhibitor         0           cd1         chaperonin-containing T-complex alpha subunit         0           ned8         ubiquitin-like protein modifier for cullin         0           cd14         SIN component         0           tbf1         DNA binding factor         0           glad         GTPase activating protein         0           glin1         RCC1 family Ran GDP/GTP exchange factor         0           glin1         RCC1 family Ran GDP/GTP exchange factor         0           splicite procep	N.D.		non-essential
cct3         chaperonin-containing T-complex gamma subunit         0           alp5         actn-like protein Arp4         0           qcr1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           up18         CGI-84 family         0           lcb1         serine palmitoyltransferase complex subunit         0           serine palmitoyltransferase complex subunit         0           mitochondrial processing peptidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           cut2         securin, sister chromatid separation inhibitor         0           cut2         securin, on sister chromating T-complex alpha subunit         0           cut2         securin, sister chromating T-complex alpha subunit         0           cut2         securin, sister chromating T-complex alpha subunit         0           cut2         securin, sister chromating T-complex alpha subunit         0           dct4         SIN component         0         0	N.D.		essential
alp5       actin-like protein Arp4       0         psf1       GINS complex subunit       0         qcr1       mitochondrial processing peptidase (MPP) complex beta subunit Mas1       0         lcb1       serine palmitoyltransferase complex subunit       0         sim4       CENP-K ortholog       0         mitochondrial processing peptidase (MPP) complex alpha subunit       0         cut2       securin, sister chromatid separation inhibitor       0         cut2       securin, sister chromatid separation inhibitor       0         cut2       securin, sister chromatid separation inhibitor       0         cut1       chaperonin-containing T-complex alpha subunit       0         cd14       SIN component       0         tb11       DNA binding factor       0         rad60       DNA repair protein, SUMO-related       0         ucp3       GTPase activating protein       0         pim1       RCC1 family Ran GDP/GTP exchange factor       0         splicing factor       0       0         wrs1       pim1       motic cohesin complex subunit       0         gramat       mitochondrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs       0         motic       ordigin recognition complex subunit       0 <td>N.D.</td> <td></td> <td>essential</td>	N.D.		essential
psf1         GINS complex subunit         0           qcr1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           lcb1         serine palmitoyltransferase complex subunit         0           sim4         CENP-K ortholog         0           mitochondrial processing peptidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           cut3         spindle pole body SUM domain protein         0           cd1         chaperonin-containing T-complex alpha subunit         0           ncd3         SIN component         0           duiptif altor         0         0           rad60         DNA repair protein, SUMO-related         0           up3 GTPase activating protein         0         0           slin1 7         human KIN ortholog         0           psm1         mitotic cohesin complex ATPase subunit Smc1         0	N.D.		essential
qcr1         mitochondrial processing peptidase (MPP) complex beta subunit Mas1         0           utp18         CGI-48 family         0           lcb1         serine palmicloytransferase complex subunit         0           serine palmicloytransferase complex subunit         0           mitochondrial processing peptidase (MPP) complex alpha subunit         0           mas2         mitochondrial processing peptidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           cxt1         chaperonin-containing T-complex alpha subunit         0           ned8         ubiquitin-like protein modifier for cullin         0           cdc14         SIN component         0           tbf1         DNA binding factor         0           rad60         DNA repair protein, SUMO-related         0           ucp3         GTPase activating protein         0           splicing factor         0         0           splicing factor         0         0           splicing factor         0         0           orc1         origin recognition complex AtPase subunit Psm1/Smc1         0           orc1         origin recognition complex AtPase subunit mitiation repressor         0           ms	N.D.		essential
up18         CGI-48 family         0           lcb1         serine palmikoyltransferase complex subunit         0           sim4         CENP-K ortholog         0           mas2         mitochondrial processing peptidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           sad1         spindle pole body SUN domain protein         0           cut2         securin, sister chromatid separation inhibitor         0           cad1         chaperonin-containing T-complex alpha subunit         0           cdc14         SIN component         0           cdc14         SIN component         0           tbf1         DNA binding factor         0           rad60         DNA repair protein, SUMO-related         0           ucp3         GTPase activating protein         0           pim1         RCC1 family Ran GDP/GTP exchange factor         0           skin17         human KIN ortholog         0           psn1         mitolic cohesin complex alphase subunit Psm1/Smc1         0           orc1         origin recognition complex subunit         0           ms10         mitol-abck protein         0           ms11         TATA-binding protein-associ	N.D.		essential
Icb1         serine palminoytransferase complex subunit         0           sim4         CENP-K ortholog         0           mas2         mitochondrial processing peptidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           sad1         spindle pole body SUM domain protein         0           cct1         chaperonin-containing T-complex alpha subunit         0           oct1         chaperonin-containing T-complex alpha subunit         0           oct1         chaperonin-containing T-complex alpha subunit         0           odditation         0         0           dct14         SIN component         0           ucp3         GTPase activating protein         0           pim1         RCC1 family Ran GDP/GTP exchange factor         0           sli7         splicing factor         0           ski17         human KIN ortholog         0           psm1         mitotic cohesin complex ATPase subunit Psm1/Smc1         0           orc1         origin recognition complex subunit         0           mtot         motorial neashock protein         0           smtot         motorial neatshock protein         0           smtot condrial neator complex	N.D.		essential
sim4         CENP-K ortholog         0           mas2         mitochondrial processing peptidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           sad1         spindle pole body SUN domain protein         0           cct1         chaperonin-containing T-complex alpha subunit         0           ned8         ubiquith-like protein modifier for cullin         0           cdc14         SIN component         0           tbf1         DNA binding factor         0           rad60         DNA repair protein, SUMO-related         0           ucp3         GTPase activating protein         0           pim1         RCC1 family Ran GDP/GTP exchange factor         0           splicing factor         0         0           splicing factor         0         0           orc1         orligin recognition complex AtPase subunit Psm1/Smc1         0           orc1         origin recognition complex subunit         0           splicing protein-associated transcription initiation repressor         0           mst1         TATA-binding protein-associated transcription initiation repressor         0           splici         mst2Aboldrait heatshabok protein         0	N.D. N.D.		essential essential
mas2         mitochondrial processing peptidase (MPP) complex alpha subunit         0           cut2         securin, sister chromatid separation inhibitor         0           sad1         spindle pole body SUM domain protein         0           cct1         chaperonin-containing T-complex alpha subunit         0           ned8         ubiquitin-like protein modifier for cullin         0           cdc14         SIN component         0           tbf1         DNA binding factor         0           rad60         DNA repair protein, SUMO-related         0           ucp3         GTPase activating protein         0           pim1         RCC1 family Ran GDP/GTP exchange factor         0           skin17         human KIN ortholog         0           psrint         mitotic cohesin complex subunit         0           ordi or figin recognition complex subunit         0         0           mrs1         mitochondrial heatshock protein         0           mrs1         mitochondrial heatshock protein         0           spindle protein-associated transcription initiation repressor         0           shift         Sin SnRNP core protein         0           spindle gamma-tubulin         0         0           spindle gamma-tubulin	N.D.		non-essential
cut2         securin, sister chromatid separation inhibitor         0           sad1         spindle pole body SUN domain protein         0           cct1         chaperonin-containing T-complex alpha subunit         0           ned8         ubiquitin-like protein modifier for cullin         0           dct14         SIN component         0           tbf1         DNA binding factor         0           rad60         DNA repair protein, SUMO-related         0           ucp3         GTPase activating protein         0           pim1         RCC1 family Ran GDP/GTP exchange factor         0           splicing factor         0         0           kin17         human KIN ortholog         0           psm1         mitotic cohesin complex ATPase subunit Psm1/Smc1         0           orf or recognition complex AtPase subunit Psm1/Smc1         0           sPBC2G5.05         transketolase         0           mtot         ort         1         0           splichting protein-associated transcription initiation repressor         0           smf1         TaTA-binding protein-associated transcription initiation repressor         0           smf1         Sm snRNP core protein         0         0           splic1	N.D.		essential
sad1         spindle pole body SUN domain protein         0           cct1         chaperonin-containing T-complex alpha subunit         0           ned8         ubiquith-like protein modifier for cullin         0           cdt4         SIN component         0           dbf1         DNA binding factor         0           rad60         DNA repair protein, SUMO-related         0           ucp3         GTPase activating protein         0           pim1         RCC1 family Ran GDP/GTP exchange factor         0           slu7         splicing factor         0           skin17         human KIN ortholog         0           psm1         mitotic cohesin complex xIPase subunit Psm1/Smc1         0           orc1         origin recognition complex subunit         0           splicing recognition complex subunit         0         0           mst1         TATA-binding protein-associated transcription initiation repressor         0           msr11         Sm snRNP core protein         0           spic1         INCENP ortolog         0           gdycine decarboxylase complex subunit H         0           gcv3         glycine decarboxylase complex subunit H         0           gpot4         RNase P and RNase MRP subunit H	N.D.	1	essential
cct1         chaperonin-containing T-complex alpha subunit         0           ned8         ubiquitin-like protein modifier for cullin         0           cdc14         SIN component         0           tbf1         DNA binding factor         0           rad60         DNA repair protein, SUMO-related         0           ucp3         GTPase activating protein         0           pim1         RCC1 family Ran GDP/GTP exchange factor         0           skl7         splicing factor         0           skl7         splicing factor         0           skl7         human KIN ortholog         0           psm1         mitotic cohesin complex ATPase subunit Psm1/Smc1         0           ord1         ordjin recognition complex subunit         0           SPBC265.05         transketolase         0           mrs1         mitochondrial hastshock protein         0           smf1         SmRNP core protein         0           sp224         Kinetochore component         0           pic1         INCENP ortholog         0           gdman         gg/gg/gg/gg/gg/gg/gg/gg/gg/gg/gg/gg/gg/	N.D.	1	essential
ned8         ubiquitin-like protein modifier for cullin         0           cdc14         SIN component         0           tbf1         DNA binding factor         0           rad60         DNA repair protein, SUMO-related         0           ucp3         GTPase activating protein         0           pim1         RCC1 family Ran GDP/GTP exchange factor         0           splicing factor         0         0           kin17         human KIN ortholog         0           psm1         nitotic cohesin complex ATPase subunit Psm1/Smc1         0           orc1         origin recognition complex subunit         0           SPBC2G5.05         transketolase         0           mtott condrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs         0           mtot1         TATA-binding protein-associated transcription initiation repressor         0           spl24         Kinetochore component         0           pic1         INCENP ortholog         0           gtb1         gamma-tubulin         0           opo4         RNase P and RNase KMP subunit         0           rio2         protein kinase, RIO family         0           opt4         RNase P and RNase MP subunit         0	N.D.		essential
cdc14         SIN component         0           tbf1         DNA binding factor         0           rad60         DNA repair protein, SUMO-related         0           ucp3         GTPase activating protein         0           pim1         RCC1 family Ran GDP/GTP exchange factor         0           splicing factor         0         0           kin17         human KIN ortholog         0           psm1         mitotic cohesin complex ATPase subunit Psm1/Smc1         0           orc1         origin recognition complex subunit         0           orc1         origin recognition complex subunit         0           sm17         Tansketolase         0           mitochondrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs         0           mot1         TATA-binding protein-associated transcription initiation repressor         0           smf1         Sm snRNP core protein         0           hsp78         mitochondrial heatshock protein         0           spc24         Kinetochore component         0           glvcine decarboxylase complex subunit H         0         0           gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0	N.D.		non-essential
bf1         DNA binding factor         0           rad60         DNA repair protein, SUMO-related         0           ucp3         GTPase activating protein         0           pim1         RCC1 family Ran GDP/GTP exchange factor         0           sli7         splicing factor         0           kin17         human KIN ortholog         0           psm1         mitotic cohesin complex ATPase subunit Psm1/Smc1         0           orc1         origin recognition complex AtPase subunit         0           SPBC2G5.05         transketolase         0           mitochondrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs         0           omt1         TATA-binding protein-associated transcription initiation repressor         0           smf1         Sm snRNP core protein         0           sp24         Kinetochore component         0           pic1         INCENP ortholog         0           gtb1         garma-tubulin         0           gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           vpt1         GTPase         0           ortigin recognition complex subunit         0           ortigin recognition compl	N.D.	1	(unconserved)
rad60       DNA repair protein, SUMC-related       0         ucp3       GTPase activating protein       0         pim1       RCC1 family Ran GD/GTP exchange factor       0         slu7       splicing factor       0         kin17       human KIN ortholog       0         psm1       mktot: cohesin complex ATPase subunit Psm1/Smc1       0         orc1       origin recognition complex subunit       0         SPBC2G5.05       transketolase       0         mtotto: cohesin complex ATPase subunit family Ran GD/Game       0         mtotto: nordiral and cytoplasmic arginine-tRNA ligase Rrs1/Mrs       0         mtotto: nordiral heatshock protein       0         spf24       Kinetochore component       0         pic1       INCENP ortholog       0         gtv:rd       gamma-tubulin       0         opo4       RNase P and RNase Complex subunit H       0         ro2       protein kinase, RIO family       0         ypt1       GTPase       0         ortigh recognition complex subunit       0       0         ypt2       UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe       0	N.D.		essential
ucp3         GTPase activating protein         0           pim1         RCC1 family Ran GDP/GTP exchange factor         0           slu7         splicing factor         0           kin17         human KIN ortholog         0           psm1         mitotic cohesin complex ATPase subunit Psm1/Smc1         0           orc1         origin recognition complex subunit         0           SPBC2G5.05         transketolase         0           mrs1         mitochondrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs         0           mrs1         Sm snRNP core protein         0           hsp78         mitochondrial heatshock protein         0           sp24         Kinetochore component         0           gev3         glycine decarboxylase complex subunit H         0           gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           orc6         origin recognition complex subunit         0           origin recognition complex subunit         0         0	N.D.		non-essential
pim1         RCC1 family Ran GDP/GTP exchange factor         0           slu7         splicing factor         0           kin17         human KIN ortholog         0           psm1         mitotic cohesin complex ATPase subunit Psm1/Smc1         0           ordig in recognition complex AtPase subunit Psm1/Smc1         0           ordig in recognition complex subunit         0           SPBC2G5.05         transketolase         0           mtit chondrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs         0           mtit TATA-binding protein-associated transcription initiation repressor         0           smf1         Tat A-binding protein-associated transcription initiation repressor         0           sp224         Kinetochore component         0           pic1         INCENP ortholog         0           gtvia         garma-tubulin         0           pcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           ypt1         GTPase         0           ort6         origin recognition complex subunit         0           orc6         origin recogniticon complex subunit         0	N.D.		non-essential
kin17         human KIN ortholog         0           psm1         mitotic cohesin complex ATPase subunit Psm1/Smc1         0           orcin         origin recognition complex subunit         0           SPBC265.05         transketolase         0           mrs1         mitochondrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs         0           mrs1         mitochondrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs         0           mot1         TATA-binding protein-associated transcription initiation repressor         0           smf1         Sm snRNP core protein         0           hsp78         mitochondrial heatshock protein         0           sp224         Kinetochore component         0           gev3         glycine decarboxylase complex subunit H         0           gp04         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           ypt1         GTPase         0           orcign recognition complex subunit         0           g	N.D.		essential
kin17         human KIN ortholog         0           psm1         mitotic cohesin complex ATPase subunit Psm1/Smc1         0           orc1         origin recognition complex subunit         0           SPBC265.05         transketolase         0           mrs1         mitochondrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs         0           mrs1         mitochondrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs         0           mot1         TATA-binding protein-associated transcription initiation repressor         0           smf1         Sm snRNP core protein         0           hsp78         mitochondrial heatshock protein         0           sp224         Kinetochore component         0           gb1         garma-tubulin         0           gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           ypt1         GTPase         0           orc6         origin recognition complex subunit         0           orc6         origin recognition complex subunit         0           orc6         origin recognition complex subunit         0           orc6         orig	N.D.		essential
orc1         origin recognition complex subunit         0           SPBC2G5.05         transketolase         0           mrs1         mitochondrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs         0           mot1         TATA-binding protein-associated transcription initiation repressor         0           ms11         Sm snRNP core protein         0           hsp78         mitochondrial heatshock protein         0           spc24         Kinetochore component         0           pic1         INCENP ortholog         0           gb/b1         gamma-tubulin         0           gcv3         glycine decarboxylase complex subunit H         0           rio2         protein kinase, RIO family         0           ypt1         GTPase         0           orc6         origin recognition complex subunit         0           gt2         UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe         0	N.D.		essential
SPBC2G5.05         transketolase         0           mrs1         mitochondrial and cytoplasmic arginine-tRNA ligase Rrs1/Mrs         0           mot1         TATA-binding protein-associated transcription initiation repressor         0           smf1         Sm snRNP core protein         0           hsp78         mitochondrial heatshock protein         0           spc24         Kinetochore component         0           gb1         INICENP ortholog         0           gb23         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           orc6         origin recognition complex subunit         0           orc6         origin recognition complex subunit         0           gt2         UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe         0	N.D.		essential
mrs1         mitochondrial and cytoplasmic arginine-IRNA ligase Rrs1/Mrs         0           mot1         TATA-binding protein-associated transcription initiation repressor         0           smf1         Sm snRNP core protein         0           hsp78         mitochondrial heatshock protein         0           spc24         Kinetochore component         0           pic1         INCENP ortholog         0           gtb1         gamma-tubulin         0           gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           ypt1         GTPase         0           orc6         origin recognition complex subunit         0           gt2         UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe         0	N.D.		essential
mot1         TATA-binding protein-associated transcription initiation repressor         0           sm11         Sm snRNP core protein         0           hsp78         mitochondrial heatshock protein         0           spc24         Kinetochore component         0           pic1         INCENP ortholog         0           gbt1         gamma-tubulin         0           gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           orc6         origin recognition complex subunit         0           orc6         origin recognition complex subunit         0           gt/UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe         0	N.D.		non-essential
smf1         Sm snRNP core protein         0           hsp78         mitochondrial heatshock protein         0           spc24         Kinetochore component         0           pic1         INCENP ortholog         0           gbtj         garma-tubulin         0           gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           ypt1         GTPase         0           orc66         origin recognition complex subunit         0           gt2         UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe         0	N.D.	I	essential
hsp78         mitochondrial heatshock protein         0           spc24         Kinetochore component         0           pic1         INCENP ortholog         0           gtb1         gamma-tubulin         0           gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           ypt1         GTPase         0           orc6         origin recognition complex subunit         0           gt2         UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe         0	N.D.		essential
spc24         Kinetochore component         0           pic1         INCENP ortholog         0           gbb1         gamma-tubulin         0           gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           ypt1         GTPase         0           orc6         origin recognition complex subunit         0           gt2U         UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe         0	N.D.		essential
pic1         INCENP ortholog         0           gtb1         gamma-tubulin         0           gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           ypt1         GTPase         0           orc6         orgin recognition complex subunit         0           gpt2         UDP-N-acetylglucosaminedolichyl-phosphate N-acetylglucosaminephosphotransfe         0	N.D.		non-essential
gtb1         gamma-tubulin         0           gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           ypt1         GTPase         0           orc6         origin recognition complex subunit         0           gt2         UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe         0	N.D.		essential
gcv3         glycine decarboxylase complex subunit H         0           pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           ypt1         GTPase         0           orc6         origin recognition complex subunit         0           gpt2         UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe         0	N.D.		non-essential
pop4         RNase P and RNase MRP subunit         0           rio2         protein kinase, RIO family         0           ypt1         GTPase         0           orc6         origin recognition complex subunit         0           gpt2         UDP-N-acetylglucosaminedolichyl-phosphate N-acetylglucosaminephosphotransfe         0	N.D.		essential
rio2 protein kinase, RIO family 0 ypt1 GTPase 0 orc6 origin recognition complex subunit 0 gpt2 UDP-N-acety/glucosaminedolichyl-phosphate N-acety/glucosaminephosphotransfe 0	N.D.		non-essential
ypt1 GTPase 0 orc6 origin recognition complex subunit 0 gpt2 UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe 0	N.D.		essential
orc6 origin recognition complex subunit 0 gpt2 UDP-N-acetylglucosamine-dolichyl-phosphate N-acetylglucosaminephosphotransfe 0	N.D.		essential
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	N.D.		essential
LITER A TRADECIDION TACTOR LETTER COMPLEX SUBJURIT TATE TIKE	N.D. N.D.		essential essential
taf73 transcription factor TFIID complex subunit Taf5-like 0 brf1 transcription factor TFIIIB complex subunit 0	N.D.	1	essential

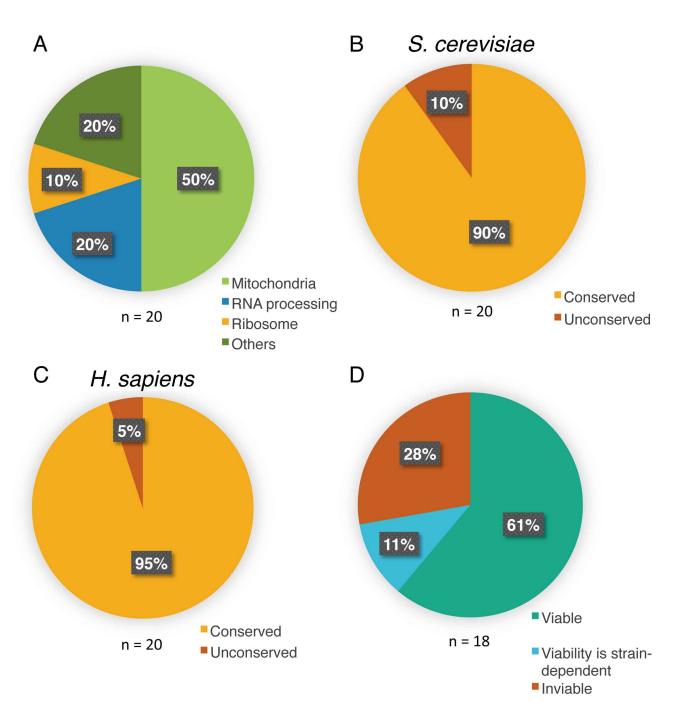


C-BOE: Chemical mutagenesis T-BOE: Transposon-based mutagenesis OP-BOE: Gene library expression

#### Figure 3. Summary of BOE screening

The gene product was listed based on the information found in Pombase. Information on other BOE screens (Li et al. 2019) and *S. cerevisiae* orthologues (*Saccharomyces* Genome Database (SGD)) are also listed. Bold letters indicate bypassable essential genes identified in our study and/or Li et al. (2019).

## Figure 4



#### Figure 4. Features of bypassable essential genes

(A) Classification of the function of 20 bypassable essential genes identified in this study. (B, C) Conservation of the identified genes in *S. cerevisiae* (B) or *H. sapiens* (C). (D) Essentiality of the *S. cerevisiae* orthologues (based on *Saccharomyces Genome Database (SGD)*).