

# Etude de la synthèse des centres fer-soufre à l'apicoplaste et la mitochondrie de Toxoplasma gondii Sarah Pamukcu

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# **THÈSE POUR OBTENIR LE GRADE DE DOCTEUR**

# **DE L'UNIVERSITÉ DE MONTPELLIER**

En Biologie cellulaire et moléculaire

École doctorale Sciences Chimiques et Biologiques pour la Santé (CBS2)

Etude de la synthèse des centres fer-soufre dans l'apicoplaste et la mitochondrie de *Toxoplasma gondii*.

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Sous la direction de Sébastien BESTEIRO

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## Summary:

*Toxoplasma gondii* is a member of the phylum of Apicomplexa that includes many parasites responsible for zoonoses. *T. gondii* is an obligate intracellular parasite with a complex cycle involving various hosts. It harbors two organelles of endosymbiotic origin: the mitochondrion and the apicoplast (originated from secondary endosymbiosis). Both contain metabolic pathways important to the parasites. Among the pathways present in the apicoplast are the FASII fatty acid pathway and the isoprenoid biosynthesis pathway. The proper functioning of these pathways as well as many other cellular functions, such as the mitochondrial respiratory chain, require the use of proteins containing Iron-Sulfur (Fe-S) centers. The biosynthesis pathways for generating Fe-S proteins is largely understudied in Apicomplexa, although some investigations have shown some are essential in the malaria-causing parasite *Plasmodium*.

Within the other branches of the tree of life, different Fe-S biosynthetic pathways have been described: the ISC mitochondrial pathway, the CIA cytoplasmic pathway, the SUF plastidic pathway. As *T. gondii* contains two organelles of endosymbiotic origin (the mitochondrion and the apicoplast), it has these three biosynthetic pathways. During my PhD project, I focused on components of the ISC and SUF pathways and sought to evaluate how they contribute to parasite fitness.

I have discovered that impacting the expression of the SufS cysteine desulfurase leads to a defect in the lytic cycle of *T. gondii*, which is likely linked to a defect in apicoplast-related function. We observed defects in the synthesis of apicoplast-derived fatty acids, which could be linked to a loss of function of the LipA Fe-S protein (which is important for the synthesis of acetyl-CoA, a precursor of the FASII pathway). Impairing the SUF pathway leads to abnormal formation of daughter cells during parasite replication, followed by delayed but irreversible death of the parasites. It thus appears that the SUF pathway is necessary for the survival of *T. gondii*.

On the other hand, impacting the mitochondrial ISC pathway by targeting the IscU scaffold protein, induces stress and metabolic changes (to adapt to the demise of Fe-S-dependent electron transport chain) that did not kill the parasites, but instead allowed its differentiation into an encysted resistance form.

Therefore, our characterization in *T. gondii* of the plastidic and mitochondrial Fe-S cluster synthesis pathways has shown that their function has been conserved during evolution, and that they contribute differently, yet importantly, to the fitness of the parasite. These pathways should then be investigated further to look for new potential therapeutic drug targets.

Key word: Toxoplasma gondii, Iron-Sulfur cluster, apicoplast, metabolism, differentiation.

## <u>Résumé :</u>

*Toxoplasma gondii* est un membre du phylum Apicomplexa qui comprend de nombreux parasites responsables de zoonoses. *T. gondii* est un parasite intracellulaire obligatoire dont le cycle complexe implique différents hôtes. Il abrite deux organelles d'origine endosymbiotique : la mitochondrie et l'apicoplaste (issus d'une endosymbiose secondaire). Tous deux contiennent des voies métaboliques importantes pour les parasites. Parmi les voies essentielles présentes dans l'apicoplaste figurent les voies de biosynthèse des acides gras FASII et des isoprénoïdes. Le bon fonctionnement de ces voies, ainsi que de nombreuses autres dans la cellule, comme la chaîne respiratoire mitochondriale, nécessite l'utilisation de protéines contenant des centres fer-soufre (Fe-S). Les voies de biosynthèse permettant de générer des protéines Fe-S sont largement sous-étudiées chez les Apicomplexes, bien que des recherches aient montré que certaines sont essentielles chez *Plasmodium*.

Dans les autres branches de l'arbre de vie, différentes voies de biosynthèse des clusters Fe-S ont été décrites : la voie mitochondriale ISC, la voie cytoplasmique CIA et la voie plastidique SUF. Comme *T. gondii* contient deux organelles d'origine endosymbiotique, il possède ces trois voies de biosynthèse. Au cours de mon projet de thèse, je me suis concentrée sur les composants des voies ISC et SUF et j'ai cherché à évaluer comment ils contribuent à la survie du parasite.

J'ai mis en évidence qu'interférer avec la fonction de la cystéine désulfurase SufS ou la fonction d'ATPase de SufC, entraîne un défaut dans le cycle lytique de *T. gondii*, probablement lié à un défaut dans des fonctions liées à l'apicoplaste. Nous observons des défauts dans la synthèse des acides gras dérivés de l'apicoplaste, qui pourraient être liés à une perte de fonction de la protéine Fe-S LipA (qui est importante pour la synthèse de l'acétyl-CoA, un précurseur de la voie FASII). L'altération de la voie SUF entraîne une malformation des cellules filles lors de la réplication du parasite, suivie d'une mort retardée, mais irréversible, des parasites. Il semble donc que la voie SUF soit nécessaire à la survie de *T. gondii*. D'autre part, lorsque l'on interfère avec la voie mitochondriale ISC en ciblant la protéine d'échafaudage IscU, cela induit un stress et des changements métaboliques (afin de s'adapter à la disparition de la chaîne de transport d'électrons dépendante de protéines Fe-S) qui ne tuent pas les parasites, mais permettent sa différenciation en une forme de résistance enkystée.

Notre caractérisation, chez *T. gondii*, des voies de synthèse des centres Fe-S plastidiques et mitochondriales a montré que leur fonction semble conservée au cours de l'évolution, et qu'elles contribuent différemment, mais de manière importante, à la survie du parasite. Ces voies devraient être plus étudiées afin de rechercher de nouvelles cibles thérapeutiques potentielles.

Mots-clés : Toxoplasma gondii, centres Fer-Soufre, apicoplaste, métabolisme, différenciation.

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Débute alors un combat psychologique (« non psychologique c'est tout ce qui est à la campagne non ? »). Avec l'aide très précieuse de mes acolytes, il apparait très vite que ce sujet s'apparente à décrypter la machine Enigma pour moi avec pour code possible « les framboises sont perchés sur le tabouret de mon grand-père ».

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Dix petits nègres, Agatha Christie

« Je n'ai plus de patience pour certaines choses. Non pas car je suis devenue arrogante mais tout simplement par ce que je suis arrivée à un point dans ma vie où je ne veux pas perdre plus de temps avec ce qui me blesse ou avec ce qui me déplait. »

Meryl Streep

« Le fait bien réel que les animaux, par la peine qu'ils endurent dans les expériences, contribuent tellement à diminuer la souffrance de l'humanité, indique que nous devrions forger une nouvelle et unique solidarité entre eux et nous. Pour cette seule raison, il incombe à chacun d'entre nous de faire le bien pour toute forme de vie non-humaine. »

Albert Schweitzer Prix Nobel de la paix en 1952.

« De tous nos actes, seuls ceux que nous accomplissons pour les autres en valent véritablement la peine. »

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# Liste des abréviations

A	Apicoplaste
ABA	Acide abscissique
AID	Système de dégradation inductible par l'auxine
AMA1	Antigène 1 de la membrane apicale
APR	Anneau polaire apical
ATG8	Protéine 8 liée à l'autophagie
ATM	Transporteurs mitochondriaux de type ABC
АТР	Adénosine triphosphate
BSA	Albumine de sérum bovin
С	Cytokinèse
с	Conoïde
cAMP	Cyclic adenosine 3'5'-monophosphat
Cas9	CRISPR associated protein 9
Cdk	Kinase dépendante de la cycline
cGMP	Guanosine monophosphate cyclique
CIA	Assemblage cytosolique de centres fer-soufre
СРА	Cellule présentative d'antigène
CRISPR	Clustered Regularly Interspaced Short Palindromic Repeats
Cys	Cysteine
DAG	Diacylglycerol
DAPI	4',6-diamidino-2-phenylindole
DC	Cellule dendritique
DG	Granule dense
DMAPP	Diphosphate de diméthylallyle
DMEM	Milieu Eagle modifié de Dulbecco
DNA	Acide désoxyribonucléique

ER	Réticulum endoplasmique	
ERAD	Dégradation associée au reticulum endoplasmique	
FACS	Triage cellulaire activé par fluorescence	
FBS	Sérum de veau fetal	
Fe-S	Centres fer-soufre	
FH	Homologue de la frataxine	
FPNs	Ferroportines	
FPP	Farnésyl-pyrophosphate	
FRTs	Ferritines	
FYVE	Domaine Fab, 1YOTB, Vac 1 EEA1	
Fxn	Frataxine	
G	Phase Gap	
GAP	Protéine associée au glideosome	
GBPs	Protéine de liaison au guanylate	
GFP	Protéine de fluorescence verte	
GGPP	Géranylgéranyl-pyrophosphate	
GPI	Glycosylphosphatidyl inositol	
GRAs	Protéines de granules denses	
GTPase	Guanosine triphosphatase	
НА	Hémagglutinine de la grippe humaine	
HFF	Fibroblastes de prépuce humain	
His	Histidine	

IB	Immunoblot	
IFA	Immunofluorescence	
IFN-γ	Interferon gamma	
lg	Immunoglobuline	
IL	Interleukine	

IM	Membranes internes
IMC	Complexe membranaire interne
IP3	Inositol triphosphate
IPP	Isopentényl-pyrophosphate
IPTG	Isopropyl β-D-1-thiogalactopyranoside
IRGs	GTPases liées à l'immunité
IRP1/2	Protéines régulatrices du fer 1 et 2
ISC	Iron-Sulfur Cluster
IscR	Répresseur d'ISC
LipA	Lipoate synthase
Μ	Mitochondrie
m	Micronèmes
MΦ	Macrophage
MACPF	Domaine d'attaque membrane/perforine
MEP/DOXP	Voie indépendante du mévalonate
MIC	Protéine de micronème
MIC	Protéine de micronèmes
MJ	Jonction mobile
MTOC	Centre d'organisation des microtubules
Ν	Noyau
NIF	Fixation du nitrogène
NK	Lymphocytes natural killer
NTA	Acide nitrilotriacétique
O <sub>2</sub>	Oxygène
OM	Membranes externes
PDH	Pyruvate déhydrogénase

PKG	Protéine kinase G	
PLP1	Protéine de type perforine 1	
PM	Membrane plasmique	
PNN	Neutrophiles polynucléaires	
РРС	Compartiment périplastidien	
PV	Vacuole parasitophore	
R	Rhoptries	
RONs	Protéines du col des rhoptries	
ROPs	Protéines du bulbe des rhoptries	
ROS	Réactifs à l'oxygène	
SAGs	Antigènes de surface	
SNP	Protéines du réseau sous pelliculaire	
SOD	Superoxyde dismutase	
SUF	Facteur d'utilisation du soufre	
TCA	Cycle de l'acide tricarboxylique	
Tet-OFF	Syteme tetracycline-off	
Tg	Toxoplasma gondii	
TIC	Translocon des membranes internes de chloroplaste	
TIM	Translocase de la membrane interne	
TLR	Toll like receptor	
TNF-α	Facteur de nécrose tumorale	
ТОС	Translocon des membranes externes de chloroplaste	

- TOM Translocase de la membrane externe
- TP Peptide de transit
- YFP Protéine de fluorescence jaune

# **Introduction**

## Chapitre I : La toxoplasmose dans le monde

### A. Historique et classification

La première description de *T. gondii* fut faite il y a plus d'un siècle, en 1908, à Tunis par Nicolle et Manceaux<sup>1</sup>. Au même moment, une observation similaire est faite au brésil par Splendore<sup>2</sup>. Tout d'abord associé au genre *Leishmania sp*, ce protozoaire parasite est nommé par la suite *Toxoplasma* de par sa forme arquée (du grec *toxo*= arc ; *plasma*= forme). Quant au nom d'espèce, il se rapporte à l'hôte dans lequel le parasite a été observé en Afrique : le gondii (un petit rongeur de la famille des Ctenodactylidae), donnant alors *Toxoplasma gondii*<sup>3</sup>. Ce n'est qu'en 1939 qu'il est identifié comme agent de la toxoplasmose par Wolf, Cowen et Paige<sup>4</sup>.

Dans les années 1970, *T. gondii* est reconnu comme faisant partie de la classe des Coccidies, il est désormais établi qu'il fait partie du phylum des apicomplexes et rejoint alors environ 6000 espèces de protistes parasites. Ce phylum comprend plusieurs classes : Coccidies, Cryptosporidies, Grégarines, et Hématozoaires<sup>5</sup> (**Figure 1**).

La plupart des espèces au sein du phylum des apicomplexes, sont des parasites intracellulaires obligatoires. Cette généralité ne s'applique cependant pas pour la classe des Grégarines. Le réservoir d'hôtes pouvant être infecté par ces différentes classes de parasites est très diversifié puisque l'on retrouve aussi bien des vertébrés et invertébrés qu'ils soient terrestres ou marins. La grande majorité de ces parasites a un cycle de vie complexe faisant intervenir plusieurs hôtes<sup>6</sup>. Mais ils sont différentes en ce qui concerne les modes d'invasions et de transmission ainsi que pour leur tropisme cellulaire.

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Figure 1: Arbre phylogénétique hypothétique des apicomplexes<sup>6</sup>.

### B. Prévalence et génotypes

*T. gondii* est un parasite ubiquitaire qui infecte près d'un tiers de la population mondiale<sup>7,8</sup>. L'identification des génotypes de *T. gondii* a permis de déterminer que les souches prélevées en France ainsi qu'aux Etats-Unis d'Amérique sont des clones issus de trois lignées différentes classées selon leur virulence chez la souris : type I, II et III<sup>9,10</sup>.

Il existe une certaine disparité géographique concernant ces différentes souches de *T.gondii*<sup>11</sup>. En effet, en Europe le type II est majoritaire avec une prévalence de 69.4% mais l'on retrouve aussi, en plus faible proportion, le type III (**Figure 2**)<sup>8</sup>. Concernant le type I, il est localement très présent autour du bassin méditerranéen<sup>12,13</sup>.

De même, en Amérique du Nord, l'étude d'isolats cliniques révèle que le type II serait lui aussi majoritaire (47,4% de prévalence) suivi par le type I responsable de 19,6% des infections<sup>8</sup>.

Si ces souches-là représentent la majorité de celles retrouvées lors d'infections en Europe ou en Amérique du Nord, il existe une plus grande disparité de souches sur les autres continents<sup>8</sup>. Des études menées en Afrique et Asie démontrent une majorité de cas dus à des souches appartenant à des lignées clonales régionales (comme *Chinese 1* ou *Africa 1* et *3*)<sup>8,12,14,15</sup>.

La prédominance des types I, II et III ne s'applique pas non plus pour l'Amérique du Sud où on observe une diversité génétique très élevée. Ces nouveaux génotypes, découverts plus récemment, sont décrits comme atypiques ou exotiques<sup>16</sup>.

Une forte prévalence est observée dans des zones au climat chaud et humide, mais ce paramètre n'est pas le seul pouvant influencer le taux de personnes infectées. En effet, le régime alimentaire ou les coutumes de certains pays<sup>17</sup>, ainsi que la promiscuité de vie entre humains et animaux, peuvent influencer les infections zoonotiques<sup>18</sup>. Un facteur important dans la dissémination de *T. gondii* concerne sa capacité à infecter un grand nombre d'espèces animales en plus de l'Homme. La toxoplasmose étant une maladie zoonotique, la prévalence du parasite au seins des animaux sauvages et domestiques, doit être prise en compte afin de mieux comprendre les possibles écarts de prévalence entre chaque pays.

Le fait que l'on retrouve des souches très différentes en fonction des zones géographiques étudiées, peut aussi être dut à des flux migratoires d'animaux comme les oiseaux, qui peuvent également être des hôtes intermédiaires de *T. gondii*.

A l'exemple de l'activité migratoire, il faut également noter la présence de nombreuses espèces de félins sauvages en Amazonie comme état un facteur potentiellement responsable de la forte diversité génétique observée en Amérique du Sud. En effet comme nous allons le voir par la suite, les félins sont l'hôte définitif du parasite, et les félins sauvages peuvent couvrir un territoire important. Ils pourraient donc servir d'hôtes à des souches variées issues de territoires géographiques distincts, et donc de contribuer à la grande diversité génétique des souches Sud-Américaines de *T. gondii*<sup>12</sup>.



Figure 2: Distribution géographique des souches de T. gondii dans le monde<sup>8</sup>.

## Chapitre II : Toxoplasma gondii responsable d'une zoonose



*T. gondii* est un parasite ubiquitaire pouvant infecter quelques 350 espèces différentes d'hôtes incluant des mammifères tout comme des oiseaux<sup>19</sup>.

Le parasite a un cycle hétéroxène, qui suit le rythme des relations proie-prédateur.

Le cycle complet se décompose en deux phases : une sexuée chez l'hôte définitif et une asexuée chez un hôte intermédiaire étant un vertébré homéotherme (**Figure 3**).

# 1) La phase sexuée

La partie du cycle comportant la phase de reproduction sexuée de *T. gondii*, se déroule chez l'hôte définitif : les félidés (sauvages comme domestiques)<sup>20</sup>. La majeure partie des infections chez les félidés est due à l'ingestion d'une proie infectée contenant des kystes de *T. gondii*. La paroi de ces formes enkystées est par la suite lysée dans leur système digestif, ce qui libère la forme bradyzoïte. Les nombreux parasites libérés peuvent alors infecter tous types de cellules nuclées<sup>21</sup> dont les cellules épithéliales de l'intestin afin d'entamer leur phase de multiplication nommée schizogonie.

Les schizontes ainsi formés conduisent à la formation de mérozoïtes pouvant alors se différencier en gamètes mâles (microgamètes qui sont flagellés) et femelles (macrogamètes). Les gamètes pourront alors fusionner pour former des zygotes diploïdes. La forme fécondée, mais immature (oocyste non sporulé), est alors entourée par une paroi.

Cette barrière permet à l'oocyste de résister à l'environnement extérieur lors de son élimination avec les fèces du félin (couramment le chat). Un seul chat peut rejeter plus de 100 millions d'oocystes pouvant devenir infectieux<sup>22</sup>. La maturation des oocystes par sporulation survient cinq jours après leur libération dans l'environnement. Les oocystes contiennent alors chacun huit sporozoïtes infectieux

pouvant survivre pendant une longue période allant jusqu'à plus de un an si les conditions sont favorables<sup>23</sup>.

#### 2) La phase asexuée

La phase asexuée du cycle débute lorsqu'un oocyste infectieux est ingéré par un hôte intermédiaire vertébré à sang chaud (oiseau ou mammifère dont l'Homme). Elle peut avoir lieu dans toutes les cellules nucléées de l'organisme.



Figure 4: Cycle lytique de T. gondii<sup>23,24</sup>

Apres ingestion, l'oocyste libère les sporozoïtes pouvant alors devenir des tachyzoïtes (forme virulente du parasite). *T. gondii* étant un parasite intracellulaire obligatoire, le tachyzoïte va pouvoir survivre à court terme dans le milieu extracellulaire, mais pour que la prochaine phase de prolifération puisse avoir lieu il devra envahir une cellule nucléée (**Figure 4**).

Lors du processus d'invasion, le parasite forme une vacuole parasitophore (PV) issue en partie de membrane de la cellule hôte. Au sein de cette

structure protectrice, les formes tachyzoïtes de *T. gondii* vont alors se répliquer par endodyogénie : les cellules filles sont produites au sein de la cellule mère qui disparaît à l'issue de la complétion des cellules néoformées. Chaque parasite permet donc la formation de deux parasites après chaque cycle de réplication. Après plusieurs cycles de multiplication consécutifs, la cellule hôte va être lysée lors de la sortie des tachyzoïtes. Ces tachyzoïtes peuvent alors infecter de nouvelles cellules. La destruction cellulaire et tissulaire engendrée par la multiplication rapide du parasite lors de la phase aiguë est à l'origine des symptômes de la toxoplasmose.

Sous la pression du système immunitaire, lors de la phase chronique de l'infection, de très importants changements surviennent : la forme tachyzoïte se différencie en une forme latente appelée bradyzoïte. La composition de la PV change afin de former une paroi de kyste et de limiter les interactions avec le système immunitaire de l'hôte.

Ces deux formes réplicatives de *T. gondii* se démarquent aussi par quelques changements morphologiques comme l'emplacement plus basal du noyau, une plus grande quantité de micronèmes (organelles sécrétoires) ainsi que la présence de nombreuses granules d'amylopectine chez les bradyzoïtes<sup>24</sup>.

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La caractéristique la plus importante départageant les deux formes, concerne le rythme de multiplication des parasites qui est bien plus lent chez les bradyzoïtes<sup>25</sup>. Lors d'une réactivation, les bradyzoïtes pourront être libérés afin de se différencier en tachyzoïtes.

#### B. Voies de transmission

Toxoplasma existe donc sous trois formes infectieuses : les sporozoïtes (issus de l'oocyste), les tachyzoïtes (formes invasives) et les bradyzoïtes (formes quiescentes). De manière générale, la transmission de l'hôte définitif à l'hôte intermédiaire se fait par ingestion d'aliments et d'eau souillés par des oocystes<sup>26</sup>. De même une transmission vers l'hôte définitif passe par la prédation et l'ingestion de la proie contaminée <sup>23</sup>. Une importante voie de transmission du parasite, ne permettant cependant pas la complétion immédiate du cycle, se fait entre hôtes intermédiaires (**Figure 5**).

En effet, le parasite peut être transmis à un nouvel hôte tel que l'Homme par ingestion de viande animale infestée contenant des bradyzoïtes, voire potentiellement par ingestion de lait non pasteurisé contenant des tachyzoïtes. De plus, une transmission verticale peut subvenir entre la mère et le fœtus par passage de la barrière placentaire<sup>27</sup> (**Figure 3**).



Figure 5: Arbre de transmission des oocystes de Toxoplasma gondii<sup>26</sup>

- C. Manifestations cliniques
  - 1) En cas d'immunocompétence chez l'Homme

Lors d'une infection par *T. gondii*, la gravité des symptômes peut varier en fonction de l'état immunitaire du patient ainsi que de la virulence de la souche à l'origine de l'infection. Celle-ci est généralement asymptomatique et sans conséquence. L'infection peut parfois entraîner quelques symptômes bénins pour le patient en bonne condition physique comme des courbatures, maux de tête, fatigue et fièvre<sup>28</sup>.

Après une première phase d'infection, de multiplication et dissémination active du parasite (phase aiguë), le système immunitaire de l'hôte permet en général de contrôler l'infection. Lors d'une seconde phase le parasite va alors persister sous forme enkystée au sein d'organes de son hôte tels que le cerveau ou les muscles (phase chronique).

#### 2) <u>En cas d'immunodéficience chez l'Homme</u>

Une infection par *T. gondii* peut se révéler dangereuse si le patient souffre d'une déficience du système immunitaire telle qu'une préalable infection par le VIH (Virus de l'Immunodéficience Humaine) ou lors d'une immunosuppression dans le contexte d'une transplantation d'organe. La faiblesse du système immunitaire est alors une aubaine pour le parasite pouvant se répliquer de façon non contrôlée, ce qui peut entrainer de graves conséquences : encéphalite, pneumonie, myocardite voire une hépatite pouvant aboutir à la mort du patient.

Une primo infection au cours d'une grossesse peut se propager au fœtus dans approximativement 30% des cas et peut avoir de graves conséquences pour celui-ci<sup>29</sup>. En France, la transmission de l'infection est estimée à 1 cas pour 1000 naissances. En effet, le parasite a la capacité de passer la barrière placentaire et peut donc infecter le fœtus, ce phénomène de transmission est nommé toxoplasmose congénitale. La sévérité de l'infection dépend de plusieurs facteurs : la virulence de la souche parasitaire, le moment de la gestation où intervient l'infection, et donc des facteurs comme la maturité immunitaire du fœtus, ainsi que l'état immunitaire de la mère<sup>30</sup>.

La probabilité d'une infection lors du premier trimestre de grossesse est faible mais peut alors entraîner de graves problèmes de santé au niveau du système nerveux central tels que des hydrocéphalies, une calcification intracrânienne, un ictère et parfois même, aboutir à une fausse couche. Une transmission survenant plus tard au cours de la grossesse a généralement des conséquences moindres sur le fœtus. Des futures réactivations peuvent cependant se déclarer chez des adultes nés avec une toxoplasmose congénitale<sup>31</sup>.

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#### 3) La toxoplasmose animale

*Toxoplasma gondii* est un parasite responsable d'une zoonose, il est donc présent dans diverses espèces animales jouant un rôle essentiel dans la transmission à l'Homme. Ces divers hôtes intermédiaires peuvent être des espèces animales terrestres ou marines, et aussi bien domestiques que d'élevages ou sauvages<sup>26,32</sup>. Les félins, domestiques et sauvages<sup>16,18</sup>, jouent un rôle important dans l'infection des hôtes intermédiaires terrestres ou marins, de par la charge d'oocystes qu'ils libèrent dans l'environnement<sup>33</sup>. Il existe une corrélation directe entre la présence de félidés et la séroprévalence de *T. gondii* chez les hôtes intermédiaires<sup>16</sup>. Pour les animaux domestiques couramment infectés, en particulier les chats, l'infection n'entraîne que peu de symptômes mais, cela fait de ces espèces un réservoir du parasite non négligeable<sup>18,34,35</sup>.

De même, les animaux d'élevage ou de ferme peuvent contracter l'infection en fonction de plusieurs paramètres, comme les conditions d'élevage spécifiques à chaque espèce<sup>34</sup>. En effet, il a été montré que la taille du cheptel ainsi que la présence de rongeurs, impliquant donc des prédateurs tels que les félins, ou l'absence de contrôle sanitaire, engendrent un risque pour le bétail d'être infecté par *T. gondii*<sup>32</sup>. Ceci est largement vérifié si l'on prend l'exemple de porcs issus d'élevages confinés et contrôlés qui ont une prévalence pour *T. gondii* de seulement 1%, contrairement aux porcs élevés en liberté où la prévalence peut atteindre 60%<sup>32</sup>.

Tout comme la toxoplasmose humaine, lorsqu'un animal est infecté il peut ne pas développer de symptômes, notamment chez les petits mammifères tels que les rongeurs<sup>36</sup>. Cependant, il peut également subvenir des avortements dus à une toxoplasmose congénitale<sup>36–38</sup>. Donc, en plus d'un impact sur la santé humaine, la toxoplasmose animale peut également causer des pertes économiques considérables pour les éleveurs<sup>38</sup>. La toxoplasmose du bétail peut avoir un impact important sur la santé humaine puisque des infections peuvent survenir après ingestion de viande contaminée mal cuite ou même de lait non pasteurisé. Même des animaux n'étant pas supposés être homéothermes comme les poissons ou des mollusques peuvent contenir des oocystes<sup>39</sup> et être éventuellement une voie de contamination pour l'Homme.

#### D. Immunité et efficacité de traitements contre *Toxoplasma gondii*

#### 1) Dynamique de l'immunité de l'Homme après infection par T. gondii

L'infection par *T. gondii* induit une réponse immunitaire complexe faisant intervenir à la fois immunité humorale et cellulaire. La réponse immune permet de contrôler aussi bien l'infection aiguë que chronique.

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Lors d'une infection par T. gondii, il y a recrutement de cellules immunitaires (macrophages -MΦ-, neutrophiles polynucléaires -PNNet cellules -DC-) dendritiques site au de l'infection<sup>40</sup>. La détection du parasite les Toll-Like-Receptor entraîne par l'activation des MØ, PNN et DC secrétant des cytokines pros et antiinflammatoires. Le contact entre une cellule présentatrice d'antigène va notamment conduire à la production d'interleukine 12 (IL-12)<sup>41,42</sup>.

La sécrétion d'IL-12 entraîne la production d'Interféron gamma (IFN-γ) par les lymphocytes NK <sup>40</sup>.

L'IFN-γ est un facteur important dans le contrôle de l'infection par *T. gondii,* qui permet de limiter la multiplication du parasite. Son action passe par

Figure 6: Réponse immunitaire de l'hôte à une infection par T. gondii<sup>40</sup>

l'activation des macrophages mais aussi de cellules non-hématopoïétiques (Figure 6).

L'IFN- $\gamma$  va engendrer plusieurs réponses qui vont ralentir la croissance des parasites ou entraîner leur élimination. Un mécanisme général, présent à la fois dans les macrophages mais aussi dans les cellules non-hématopoïétiques, inclut la stimulation de la production des protéines de liaison au guanylate (GBPs) ainsi que de GTPases liées à l'immunité (IRGs). Ces protéines vont alors dégrader la PV<sup>37</sup>. Dans les macrophages, des mécanismes additionnels de contrôle incluent l'induction d'un stress oxydatif ou la carence en nutriments<sup>42</sup>. Par la même occasion, l'action du TNF- $\alpha$  (tumor necrosis factor) sur les macrophages infectés permet une clairance des parasites par fusion de lysosomes avec la PV<sup>37</sup>. Ces processus permettent d'éliminer une grande partie des formes tachyzoïtes, mais l'initiation de la réponse immunitaire adaptative déclenche aussi la conversion en bradyzoïtes.

Après contrôle de l'infection aiguë, une mémoire immunitaire se met en place avec la production d'immunoglobulines IgG, IgA, IgE, IgM par les plasmocytes, ce qui permet d'agir rapidement lors d'une possible réinfection. En effet, plusieurs mécanismes pourront alors agir tels que l'opsonisation des

parasites, l'inhibition de l'attachement ou de l'invasion des parasites. De même, une réponse par les lymphocytes T CD4+ et CD8+ est essentielle pour empêcher la réactivation de kystes<sup>37</sup>.

Chez la femme enceinte, la réponse immunitaire diffère lors de la gestation, la production d'IL-12 et de TNF- $\alpha$  semble diminuer, alors que celle de l'IL-10 (cytokine anti-inflammatoire) augmente. Ces conditions pourraient rendre la femme enceinte plus vulnérable à l'infection<sup>29</sup>. De plus, le système immunitaire du fœtus n'est pas complètement fonctionnel, avec notamment une faible quantité de cellules immunitaires lors des premières semaines de développement, là encore offrant une grande vulnérabilité à l'infection par le parasite<sup>29,43</sup>. Le bon déroulement de la gestation dépend aussi de l'équilibre dans la réponse immunitaire de la mère. En effet une réponse immunitaire trop importante de la part de la mère amène à un excès en IFN- $\gamma$  et une augmentation de l'activité des lymphocytes NK qui entraîne une inflammation et une apoptose des tissus pouvant aboutir à une fausse couche<sup>29</sup>.

#### 2) <u>Les stratégies de lutte existantes</u>

Il existe des gestes simples pour éviter une contamination par *T. gondii*. La prophylaxie consiste en plusieurs niveaux de mesures : le contrôle de la prévalence de la maladie chez l'animal (faisant baisser la transmission) ; éviter la consommation de viande peu cuite ; une plus grande attention à l'hygiène lors de la préparation de fruits et légumes ; un suivi sérologique des femmes enceintes au cours de la grossesse<sup>29</sup>.

Parmi les stratégies envisagées pour lutter contre la toxoplasmose, on retrouve notamment des vaccins générés à partir de souches atténuées, des vaccins à ADN ou à antigènes protéiques (ceux-ci

éventuellement pouvant être vectorisés par des vésicules comme des exosomes)<sup>41</sup>. La stratégie la plus efficace envisagée est de générer à un vaccin pouvant impacter au minimum deux des trois formes infectieuses de T. *gondii*<sup>44,45</sup>. Pour cela des études portent sur divers antigènes caractéristiques des formes infectieuses (Figure 7). Un seul vaccin commercial (le Toxovax<sup>®</sup>), obtenu à partir d'une souche atténuée existe pour les ovins mais



Figure 7: Récapitulatif des antigènes impliqués dans un, deux ou trois stades (tachyzoïte, bradyzoïte et sporozoïte) de T. gondii.<sup>43</sup>

aucun vaccin contre la toxoplasmose humaine n'a encore été développé. En effet, le développement d'un vaccin entièrement efficace contre le parasite doit pouvoir répondre à plusieurs contraintes<sup>41,44,46</sup>: immunisation de l'hôte contre toutes les souches génétiquement différentes de *T.gondii*; induire une forte protection contre toutes les formes du parasite; choix d'un adjuvant pouvant être à l'origine d'effets secondaires. Toutes ces contraintes font qu'il n'existe toujours pas de vaccin pouvant prévenir l'Homme de la toxoplasmose.

Concernant les traitements médicamenteux, il existe plusieurs familles de molécules fonctionnelles dans les modèles murins qui n'ont pas toutes été transposées aux infections humaines à *T. gondii*. De nombreuses cibles des traitements médicamenteux font partie de voies métaboliques essentielles (**Figure 8**). En effet, le traitement le plus couramment utilisé est une combinaison de deux agents bloquants la synthèse de l'acide folique d'origine parasitaire (la pyriméthamine et la sulfadiazine). Ce traitement est utilisé pour traiter les infections aiguës<sup>47</sup>. Or, même s'il y a peu de phénomène de résistance chez *T. gondii*, il faut noter que des souches comportant une mutation au niveau du gène de la dihydropteroate synthase (*DHPS*) ont acquis une résistance à la sulfadiazine<sup>47</sup>.

Various secretory	Drug	Target
	Pyrimethamine	Folic acid synthesis, dihydrofolate reductase (C)
Mitochondrion (Mi)	Sulfonamide	Folic acid synthesis, dihydropteroate synthetase (C)
Apicoplast (Ap)	Trimethoprim	Folic acid synthesis, dihydrofolate reductase (C)
	Azithromycin	Protein translation, 23S rRNA (AP)
	Clindamycin	Protein translation, 23S rRNA (AP)
Nucleus	Spiramycin	Protein translation, 23S rRNA (AP)
	Clarithromycin	Protein translation, 23S rRNA (AP)
Endoplasmic /	Atovaquone	Mitochondrial electron transport, cytochrome bc1 complex (Mi)
	Dapsone	Folic acid synthesis, dihydropteroate synthetase (C)
Cytoplasm (C)		

#### Figure 8: Voies parasitaires ciblées par les médicaments anti T. gondii en usage clinique<sup>48</sup>

De plus, du fait de leur toxicité, certaines molécules actives contre des voies essentielles du métabolisme de *T. gondii* ont vu leur utilisation entièrement arrêtée telles que les dérivés de fluoroquinolones inhibant la synthèse de l'ADN en ciblant la topoisomérase IV<sup>49,50</sup>.

A contrario, les dérivés de macrolides tels que l'azithromycine ont une longue demi-vie et sont adaptables à une formulation orale, ce qui permet le traitement d'infections aiguës<sup>48</sup>. Leur mécanisme d'action consiste à bloquer la synthèse protéique au sein de l'apicoplaste de *T. gondii* (une organelle endosymbiotique dont je détaillerai la fonction plus tard). Dans le contexte de la toxoplasmose congénitale, un traitement lui aussi à base d'antibiotiques de la famille des macrolides (comme la spiramycine) est préconisé. Ce traitement permet de réduire la probabilité de transmission au fœtus mais elle ne permet pas de soigner les fœtus déjà infectés.

Une autre organelle d'origine endosymbiotique importante d'un point de vue métabolique, la mitochondrie, est aussi la cible de molécules, comme les dérivés de l'hydroxynaphtoquinone tels que l'Atovaquone, inhibant la chaîne respiratoire<sup>50</sup>.

Malgré tout, un certain nombre de contraintes sont associées aux traitements existants : ils nécessitent une prise de relativement longue durée et, de façon importante, ne sont pas actifs contre la forme enkystée du parasite. La forme chronique de la toxoplasmose est donc incurable. La recherche de nouvelles cibles thérapeutiques potentielles et de nouvelles molécules candidates est donc plus que jamais d'actualité.

## Chapitre III : Ultrastructure du tachyzoïte

*T. gondii* est un organisme eucaryote, sa forme tachyzoïte comporte donc des organelles universelles aux eucaryotes, tels que le noyau (N), le réticulum endoplasmique (ER), l'appareil de Golgi (G) et la mitochondrie (M)<sup>51</sup>. Le parasite contient aussi différentes organelles spécifiques (certaines impliquées dans les processus d'attachement et d'invasion de la cellule hôte, dont l'origine et les fonctions seront décrites dans les prochains chapitres) : l'apicoplaste (A), les micronèmes (m), les rhoptries (R), les granules denses (DG) et un cytosquelette structuré de façon unique (**Figure 9**).



Figure 9: Ultrastructure d'un tachyzoïte de T. gondii<sup>52</sup>.

Microscopie électronique d'une section de tachyzoïte contenant les organelles conventionnelles (N : noyau, G : appareil de golgi, PM : membrane plasmique, M : mitochondrie) et spécifiques (C : conoïde, m : micronèmes, R : rhoptries, A : apicoplaste, PV : vacuole parasitophore, DG : granules denses).

En effet, étant un membre du phylum des apicomplexes, il est caractérisé par un complexe apical (**Figure 10**) qui est un assemblage d'organelles nécessaires à l'attachement du parasite et à l'invasion de la cellule hôte pour s'établir au sein d'une PV.

# A. Complexe apical et cytosquelette

Le cytosquelette de *T. gondii* est composé d'éléments de base tels que l'actine, la myosine et la tubuline retrouvés aussi chez les autres modèles eucaryotes. Néanmoins,

l'organisation du cytosquelette contient des spécificités propres à T. gondii.

### 1) <u>Le conoïde</u>

Le conoïde est un complexe apical d'environ 380 nm de diamètre, composé de deux anneaux préconoïdaux et de protofilaments d' $\alpha$  et  $\beta$  tubuline organisés en spirale<sup>52</sup> (**Figure 10**). Au sein de cette structure, on retrouve deux populations de microtubules : des microtubules intra-conoïdaux en fuseau et d'autres structuraux organisés en spirale et formant un cône. La (les) fonction(s) de cette organelle ne sont pas complètement élucidée(s), mais elle(s) semble(nt) être nécessaire(s) à l'invasion de la cellule hôte par le parasite<sup>53,54</sup>.

Le conoïde une structure dynamique polarisée, pouvant s'extruder et se rétracter, ce qui pourrai avoir un rôle mécanique lors de la sécrétion de protéines.
A la base du conoïde, se trouve l'anneau polaire apical (APR)<sup>55</sup> qui sert de centre d'organisation des microtubules (MTOC) et d'où sont originaires 22 microtubules sous-pelliculaires organisés en spirale et couvrant environ deux tiers de la longueur du parasite<sup>56</sup>. Ces microtubules sont nécessaires à la forme et au maintien de la structure et la polarité du parasite<sup>57,58</sup>.



Figure 10: Représentation du complexe apical d'un tachyzoïte de T. gondii<sup>60</sup>.

## 2) <u>La pellicule</u>

La pellicule couvre la surface du tachyzoïte et, est composée de deux couches (**Figure 11**). On trouve la membrane plasmique (PM), ainsi qu'un réseau sous-jacent nommé: complexe membranaire interne (IMC)<sup>59</sup> qui est constitué de sacs membranaires aplatis appelés alvéoles. Enfin, l'IMC et son réseau protéique associé appelé réseau sous pelliculaire (SNP)<sup>25,60</sup>, sont liés avec le réseau de microtubules sous-pelliculaires du coté cytoplasmique. La principale fonction de la pellicule consiste à maintenir la forme, la polarité et la structure du tachyzoïte.

L'IMC est discontinu, notamment afin de permettre les échanges avec le milieu extérieur, et il comporte une ouverture au niveau du pôle apical au-dessus du conoïde. De même, il n'est pas fermé au niveau de l'extrémité postérieure du parasite, nommée complexe basal. L'IMC est une composante importante de la structure du parasite puisqu'elle lui confère de la stabilité par association avec le réseau de microtubules sous-pelliculaires de l'APR<sup>59</sup>. De plus, il soutient le glideosome qui est la machinerie d'actine/myosine permettant la motilité par glissement de *T. gondii*<sup>61–63</sup>.



Figure 11: Cytosquelette et mécanisme de glissement d'un tachyzoïte<sup>59,64</sup> (A) Structure du cytosquelette de T. gondii ; (B) Composition du glideosome et mécanisme d'invasion par glissement.

# 3) Les organelles sécrétrices

Le complexe apical abrite deux types d'organelles sécrétées séquentiellement et impliquées dans les processus d'attachement et d'invasion de la cellule hôte.

# a) Les micronèmes

Les micronèmes sont des structures en forme de grain de riz d'une taille approximative de 250x50nm<sup>65</sup> et localisées au pôle apical du parasite (**Figure 10**). Elles contiennent des protéines, nommées MICs, qui sont impliquées dans l'attachement à la cellule hôte, qui est la première étape du processus d'invasion de celle-ci<sup>65</sup>. En effet, lorsqu'un tachyzoïte est extracellulaire, les MICs, qui sont des protéines transmembranaires, sont alors transférées à la membrane plasmique de *T. gondii* où elles peuvent alors interagir avec les protéines de surface de l'hôte<sup>66</sup>. De même par leur partie cytoplasmique elles interagissent avec la machinerie de glissement utilisant le moteur d'actine/myosine<sup>61,67</sup>.

#### b) Les rhoptries

Les rhoptries, sont au nombre de ~12 pour un tachyzoïte et ont une longueur de 2 à 3  $\mu$ m<sup>65</sup>. Elles ont deux parties morphologiquement distinctes : le col et le bulbe, qui contiennent aussi deux types distincts de protéines<sup>68</sup>. Dans un premier temps, les protéines RONs (contenues dans le col) sont libérées et permettent la formation d'une structure appelée la jonction mobile, qui se trouve à l'interface du point d'invasion du parasite avec la cellule hôte<sup>69</sup>. La jonction mobile est une structure dynamique se déplaçant de l'extrémité apicale du parasite vers l'extrémité basale assurant ainsi

l'ancrage du parasite et donc l'invasion de la cellule hôte<sup>68,69</sup>.

La jonction mobile permet aussi l'établissement d'un filtre sélectif déterminant la composition moléculaire de la PV, qui se forme simultanément lors de l'invasion à partir de la membrane plasmique de la cellule hôte<sup>70</sup>. La PV fournit au parasite un environnement contrôlé et protecteur pour sa division, empêchant notamment sa dégradation par les lysosomes de l'hôte<sup>68</sup>.

Les protéines du bulbe des rhoptries (ROPs) sont sécrétées rapidement après les RONs. Elles vont être libérées dans le cytoplasme cellulaire et s'associer à la membrane de la PV, ou au-delà comme dans le noyau de la cellule hôte. Les ROPs jouent un rôle important dans le contrôle de la réponse immunitaire en modulant des voies de signalisation particulières<sup>71</sup>.

#### c) Les granules denses

Les granules denses sont un autre compartiment de sécrétion qui ne sont pas spécifiques du complexe apical mais sont distribuées dans tout le cytosol. Ces vésicules sphériques de 300nm de diamètre contiennent des protéines appelées GRAs qui sont sécrétées en dernier, après complétion du processus d'invasion. Ces protéines participent à l'établissement à long terme du parasite dans la cellule, notamment pour l'acquisition de nutriments et la modulation de la réponse immune de l'hôte<sup>72-75</sup>.

#### B. Apicoplaste et mitochondrie : une origine endosymbiotique

*T. gondii* contient plusieurs organelles d'origine endosymbiotique. Le processus d'endosymbiose (incorporation et rétention d'un organisme pour rétablir une relation symbiotique) a eu des conséquences importantes dans l'évolution des eucaryotes. Par exemple, il y a environ 1.3 milliard d'années, une endosymbiose primaire a eu lieux : une cyanobactérie photosynthétique fut phagocytée et retenue par un organisme eucaryote hétérotrophe. Ceci a permis l'émergence de trois grandes lignées : les glaucophytes ; les algues et plantes vertes et enfin les algues rouges<sup>5,76</sup>. Ces lignées ont pu par la suite subir de nouvelles endosymbioses nommées endosymbioses secondaires.

Les apicomplexes font partie, avec les ciliés et dinoflagellés, du groupe des Alvéolés, lui-même appartenant au supergroupe des chromoalvéolés. Ce supergroupe semble être issus d'un ancêtre commun acquis par endosymbiose secondaire une algue rouge<sup>77,78</sup>.

Bien que possédant originellement leur propre génome, les organelles endosymbiotiques ont transféré une large partie de leurs gènes vers le génome nucléaire de l'hôte au fur et à mesure de l'établissement de la relation de symbiose.

#### 1) La mitochondrie

La mitochondrie est une organelle acquise par endosymbiose primaire. Elle n'est pas spécifique aux apicomplexes et contient un génome propre réduit. Contrairement à plusieurs autres eucaryotes, chez *T. gondii*, il n'y a pas une population de mitochondries dynamiques qui se déplacent, se divisent et fusionnent continuellement, mais une seule mitochondrie en réseau<sup>79</sup>. Les mitochondries eucaryotes permettent, entre autres fonctions, de fournir l'énergie nécessaire aux cellules par production d'adénosine triphosphate (ATP) au cours du cycle de l'acide tricarboxylique (TCA)<sup>80</sup>. De façon similaire, *T. gondii* possède un cycle TCA conventionnel capable de générer de l'énergie au sein de sa mitochondrie<sup>81,82</sup>. La chaîne respiratoire mitochondriale de *T. gondii* a quelques particularités : une absence de complexe I et des sous-unités additionnelles pour les complexes II, III, IV et V<sup>83–85</sup>. La mitochondrie est aussi impliquée dans d'autres voies métaboliques tels que la voie de biosynthèse de l'hème qui sera décrite dans les prochains chapitres.

#### 2) <u>L'apicoplaste</u>

L'apicoplaste est une organelle spécifique aux apicomplexes. Elle est située en position apicale par rapport au noyau et est entourée de quatre membranes<sup>86</sup>. Cette particularité de l'apicoplaste n'est autre que le témoin de son origine complexe, car issu d'une endosymbiose secondaire<sup>87,88</sup> (**Figure 12**). En effet, les deux membranes les plus internes de l'apicoplaste correspondent à la structure en double membrane des cyanobactéries car le premier événement d'endosymbiose fut l'incorporation d'une

cyanobactérie, donnant naissance à une algue rouge. Ceci est étayé par leur composition qui est analogue aux membranes internes (IM) et externes (OM) des chloroplastes<sup>78</sup>. Le sous-compartiment entre ces deux membranes et les membranes périphériques est nommé compartiment périplastidien (PPC). Concernant les membranes périphériques, elles proviennent de l'endosymbiose secondaire de l'algue rouge par un ancêtre des apicomplexes. La membrane périphérique la plus interne venant de l'algue rouge et étant appelée membrane périplastidique (PPM). La membrane externe (OM) est probablement



Figure 12: Schéma de l'endosymbiose secondaire à l'origine de l'apicoplaste présent dans le phylum des Apicomplexes<sup>81</sup>.

analogue à l'endomembrane de l'hôte qui a phagocyté l'algue rouge<sup>78,88,89</sup>.

Malgré une origine végétale, ce plaste a perdu sa capacité photosynthétique suite à l'évolution de l'ancêtre des apicomplexes vers un mode de vie parasitaire. Cependant cette organelle reste impliquée dans de nombreuses voies métaboliques importantes (décrites dans les prochains chapitres). De plus, tout comme la mitochondrie, elle comporte un génome extra-chromosomique (~35Kb)<sup>87</sup>. Ce génome code essentiellement pour une machinerie d'origine cyanobactérienne permettant l'expression et la stabilité du reste du génome<sup>90</sup>. L'apicoplaste a été perdu dans certains apicomplexes (*Cryptosporidium* et grégarines par exemple), mais est essentiel pour la viabilité de plusieurs stades de développement chez les apicomplexes où il persiste.

#### 3) Maturation et export de protéines vers les organelles endosymbiotiques

Les protéines fonctionnant au sein de la mitochondrie ou de l'apicoplaste peuvent donc être codées soit directement par l'organelle, soit plus couramment par le noyau de la cellule. Ces dernières, issues du génome nucléaire, nécessitent donc des modifications et un adressage post-traductionnel afin d'être associées à leur organelle respective et être fonctionnelles. Le mécanisme de transport de ces protéines vers les organelles endosymbiotiques est globalement semblable à celui observé chez les autres organismes eucaryotes (vers les mitochondries ou les chloroplastes par exemple)<sup>91</sup>.

#### a) Adressage à la mitochondrie

Une majorité des protéines de T. gondii devant être dirigées vers la mitochondrie contiennent une préséquence, clivable, en position N-terminale. Cette pré-séquence permet aux protéines néosynthétisées d'être acheminées, à l'état déplié, vers les membranes de l'organelle<sup>92,93</sup>. Les préséquences N-terminales ont comme caractéristique de former des hélices amphiphiles chargées positivement et sont en général clivées lors de l'importation de la protéine dans les mitochondries. La mitochondrie est une organelle possédant deux membranes qui doivent pouvoir être traversées pour l'adressage de protéines du matrice de l'organelle par exemple. Ceci est possible grâce à des complexes protéiques nommés translocons<sup>94,95</sup>. Chaque membrane a un translocon qui lui est spécifique : le TOM pour la membrane externe, et le TIM qui permet la traversée de la membrane interne de l'organelle<sup>96,97</sup>. La séquence d'adressage est reconnue par le translocon sur la membrane externe de la mitochondrie. La translocation de la protéine peut être partielle en présence d'un ou plusieurs motif(s) hydrophobe(s), ce qui va alors permettre son ancrage à la membrane. Si la translocation au travers du TOM est complète, alors la protéine va se retrouver dans l'espace intermembranaire. Selon la séquence d'adressage de la protéine, cette dernière pourra alors être dirigée vers le TIM, d'où elle pourra de nouveau être importée partiellement ou totalement. Lorsque la protéine est ancrée dans une des membranes ou libérée dans la matrice de l'organelle, la séquence d'adressage en N-terminal

va pouvoir être clivée par une peptidase. Cela aboutit à un changement conformationnel par la prise en charge par des protéines chaperonnes, menant à la maturation de la protéine cible, qui devient alors fonctionnelle<sup>93</sup>. A noter que certaines autres protéines mitochondriales sont synthétisées sans pré-séquence clivable et contiennent des signaux de ciblage au sein de la protéine mature.

#### b) Adressage à l'apicoplaste

L'adressage des protéines à l'apicoplaste nécessite généralement comme pour les mitochondries la présence d'une extension protéique N-terminale (même s'il peut aussi y avoir des séquences d'adressage internes). Cette séquence est constituée de deux parties<sup>98</sup>: les 20 à 30 acides aminés N-terminaux fonctionnent comme une séquence signal classique pour l'entrée dans le réticulum endoplasmique et la voie de sécrétion. Le clivage de la séquence signal expose ensuite un peptide de transit de longueur variable (50 à 200 acides aminés) qui est nécessaire pour diriger les protéines vers l'apicoplaste<sup>89,99,100</sup>. Plusieurs voies de trafic ont été proposées pour les protéines membranaires des apicoplastes chez les apicomplexes<sup>100</sup>.

Il y a plusieurs hypothèses pour le passage de la voie de sécrétion à l'apicoplaste. La première consiste à un trafic classique du ER à l'apicoplaste avec une étape intermédiaire à l'appareil de Golgi<sup>101</sup>. Une seconde possibilité serait un transport facilité par un flux protéique direct grâce à la contiguïté entre la membrane de l'ER et l'apicoplaste. Enfin, le transport pourrait être vésiculaire directement de l'ER vers l'apicoplaste<sup>102,103</sup>. Il est possible ces trois voies de transport co-existent<sup>104</sup>.

Comme pour la mitochondrie, ou pour d'autres plastes, le passage des membranes pour un adressage interne nécessite des translocons, mais la problématique ici est que l'apicoplaste comporte jusqu'à quatre membranes à traverser (**Figure 13**).

Les mécanismes permettant de traverser ces quatre barrières sont différents à cause de l'origine respective de chaque membrane<sup>78,88</sup>. La protéine, acheminée à la membrane externe de l'organelle, peut, par la suite, être potentiellement prise en charge par le translocon DER1 de la machinerie SELMA (symbiont-specific ERAD-like machinery) de *T. gondii*. C'est une machinerie de type ERAD (dégradation associée au réticulum endoplasmique) spécifique au symbiote permettant, avec le concours d'autres composants, la traversée de la seconde membrane de l'apicoplaste<sup>105,106</sup>. Après avoir traversé la membrane périplastidienne, l'importation des protéines s'effectue par des complexes protéiques homologues aux translocons classiques des membranes externes (TOC) et internes (TIC) des chloroplastes<sup>96,107–109</sup>. Une fois la matrice de l'apicoplaste atteint, le peptide de transit est clivé, ce qui permet une maturation de la protéine pour la rendre fonctionnelle<sup>110</sup>.



*Figure 13: Modèle d'importation des protéines d'apicoplastes via un possible système de sécrétion et la machinerie ERAD (adapté de <sup>111</sup>)* 

*SP: peptide signal ; TP: peptide de transit ; SP+TP: séquence d'adressage ; DER1: protéine 1 de dégradation dans le ER; TOC: translocon de la membrane externe; TIC: translocon de la membrane interne.* 

# Chapitre IV : cycle lytique du tachyzoïte

## A. Invasion de la cellule hôte

Les tachyzoïtes extracellulaires ne se répliquent pas et comme vu précédemment, ils ne peuvent survivre qu'un temps limité dans le milieu extracellulaire. La forme extracellulaire de *T. gondii* a donc besoin d'envahir une cellule hôte nucléé afin de pouvoir se répliquer.

Comme évoqué précédemment, l'invasion d'une cellule hôte fait intervenir de nombreuses interactions moléculaires entre celle-ci et le parasite. L'invasion est dépendante de la motilité du parasite grâce à la machinerie du glideosome (déplacement par glissement dépendant du moteur d'actine/myosine) (**figure 11**). L'attachement et l'ancrage du parasite à la surface de la cellule hôte dépend d'une séquence d'interactions moléculaires entre le parasite et l'hôte. Tout d'abord il y a fixation du parasite à surface de la cellule hôte par interaction entre les antigènes de surface (SAGs) avec les protéoglycanes de l'hôte. Des protéines MICs participent ensuite à l'ancrage du parasite à la surface de la cellule hôte et à sa propulsion à l'intérieur de celle-ci. Ce premier contact est suivi de la libération d'autres protéines MICs et RONs afin de stabiliser l'ancrage et de former la jonction mobile nécessaire à l'invasion<sup>64</sup>. A l'issue du processus d'invasion, le parasite se retrouve inclus dans une PV<sup>70</sup>.

#### B. Réplication intracellulaire

Une fois la cellule hôte envahie, les tachyzoïtes intracellulaires peuvent alors se répliquer par un mode de division spécifique nommé endodyogénie. Ce processus permet l'assemblage de deux cellules filles au sein même de la cellule mère<sup>112</sup>. Ce mécanisme est coordonné et les parasites au sein d'une même PV sont synchronisés.

*T. gondii* est un organisme haploïde dont le mode de division est constitué de trois phases<sup>112</sup>. Les phases Gap 1 (G1), de synthèse (S) sont suivies de la phase M qui englobe la mitose (ou la ségrégation du matériel génétique) et la cytokinèse (ou le partage des composants cytoplasmiques dans la progéniture). Un cycle de division d'un tachyzoïte mère en deux tachyzoïtes filles dure entre 6 ou 8 heures (**Figure 14**) selon la souche parasitaire<sup>113,114</sup>. De plus, il semble y avoir une corrélation entre la durée du cycle et la virulence de la souche (le type I étant le plus virulent à la durée de réplication la plus courte)<sup>114</sup>.



#### 1) La phase de croissance et réplication du génome

Pendant la division cellulaire, certaines organelles maternelles sont dupliquées (par exemple l'apicoplaste ou l'appareil de Golgi), tandis que les autres sont néo-synthétisées. De plus, lors de cette phase, les différentes organelles maternelles vont subir une réorganisation spatiale impliquée dans les prochaines phases du cycle. La ségrégation et la synthèse de novo, sont finement organisées et coordonnées avec la progression du cycle cellulaire (**Figure 14**). Lors de la phase G1, il y a production des protéines et des organelles nécessaires à la synthèse d'ADN en phase S. A la fin de la phase G1, la duplication de l'ADN est initiée lors de la phase S<sup>114</sup>. L'étape de réplication de l'ADN est suivie de près par la mitose.

#### 2) <u>Mitose et cytokinèse</u>

Les apicomplexes utilisent une mitose dite fermée. C'est-à-dire que l'enveloppe nucléaire reste pratiquement intacte pendant tout le processus de ségrégation des chromosomes<sup>112</sup>.

Afin d'assurer la fonctionnalité des futures cellules filles, il est nécessaire d'avoir une répartition équitable des organelles au sein de celles-ci. Le processus de cytokinèse, lié au bourgeonnement des cellules filles, est initié lors de la fin de la phase S et chevauche donc le cycle de réplication d'ADN<sup>114</sup>. La formation des cellules filles par bourgeonnement se fait grâce à l'assemblage des éléments du cytosquelette cortical. Cela permet par la suite de séparer toutes les organelles directement dans les cellules filles. La coordination entre la phase de croissance et de synthèse d'organelles et la mitose/cytokinèse est assurée par les centrosomes (un autre MTOC des tachyzoites), qui ont un rôle essentiel dans l'incorporation du matériel maternel dans les cellules filles. Une fois les cellules filles formées, la membrane de la cellule mère disparait, laissant alors place à deux tachyzoïtes néosynthétisés pouvant entamer à leur tour un cycle de réplication.



*Figure 15: Réplication des organelles durant le cycle cellulaire de T. gondii (adapté de*<sup>115</sup>)

#### C. Sortie

Après plusieurs cycles réplicatifs, les parasites néosynthétisés doivent pouvoir se disperser afin d'envahir de nouvelles cellules. La sortie des parasites de la cellule hôte est aussi nommée egress. C'est un processus dépendant de plusieurs facteurs<sup>64</sup> comme la sécrétion des micronèmes, la protrusion du conoïde et l'activation du mécanisme de déplacement par glissement dépendant du moteur d'actine/myosine<sup>116</sup>.

Récemment, il a été montré que *T. gondii* peut percevoir des changements environnementaux comme des flux d'ions potassium K<sup>+</sup> et calcium Ca<sup>2+</sup> ou des signaux de danger de la cellule hôte, et que ceux-ci pouvaient agir en tant que, signaux d'activation de la sortie du parasite<sup>117,118</sup> (**Figure 16**).

Concernant une activation émanant d'un signal de danger de la cellule hôte, cela proviendrait notamment de la liaison entre la cellule hôte infectée et les récepteurs des cellules T cytotoxiques conduisant à un mécanisme de destruction de la cellule et des parasites qui lui sont associés<sup>119</sup>. De même, un défaut dans les pompes Na<sup>+</sup>/K<sup>+</sup> de l'hôte qui ferait diminuer la concentration intra cytoplasmique de K<sup>+</sup> de la cellule hôte serai perçu comme un signal de danger<sup>118</sup>.

Parmi les paramètres intrinsèques aux parasites, on retrouve plusieurs signaux impliqués dans le déclanchement de la sortie du parasite. Par exemple, la multiplication des parasites au sein de la PV entraîne une baisse de pH, ce qui participerai à la sortie de la cellule par le parasite<sup>116,117</sup>.

Plusieurs flux d'ions sont impliqués dans les différentes étapes de la sortie de *T. gondii* (Figure 16). En effet, l'augmentation de la concentration intracellulaire de Ca<sup>2+</sup> par décharge des stocks intracellulaires de Ca<sup>2+</sup> (du ER et de l'IMC)<sup>118,119</sup>, va engendrer la sécrétion de MICs ainsi que l'activation du glideosome. De plus, une baisse de pH favorise la liaison membranaire et l'activité d'une protéine acidophile de micronèmes : la protéine de type perforine 1 (PLP1)<sup>117,118,120</sup>. Elle contient un domaine d'attaque membrane/perforine (MACPF) typique des protéines capable de former des pores, et qui une fois sous forme d'oligomère va pouvoir s'insérer dans la membrane de la PV et de la membrane plasmique de la cellule hôte<sup>121</sup>. Le pore ainsi formé entraine par conséquent la perméabilisation de la membrane d'intérêt.

La sécrétion des micronèmes est aussi régulée par un autre messager secondaire : la production en guanosine monophosphate cyclique (cGMP). En effet cela entraine une cascade d'activation dont celle de la protéine kinase G (PKG) qui est à l'origine de la production d'Inositol triphosphate (IP3) et de diacylglycerol (DAG)<sup>122,123</sup>. L'IP3 va alors stimuler la libération de Ca<sup>2+</sup> par l' ER alors que le DAG sera à l'origine de la fusion des micronèmes avec la membrane plasmique du parasite<sup>116</sup>. Ce phénomène est impliqué dans de nombreux mécanismes en cascade aboutissant à la sécrétion de micronèmes afin de libérer des facteurs fragilisant les membranes et permettant la mobilité des parasites.



Figure 16: Activation de la sortie de la cellule hôte par T. gondii (Adapté de<sup>117</sup>)

- (A) Vue d'ensemble des stimuli impliqués dans le phénomène de sortie.
- (B) Résumé des signaux des messagers secondaires menant à la sortie du parasite.

# Chapitre V : métabolisme au sein de l'apicoplaste de T. gondii

Cette organelle est cruciale pour la survie des formes tachyzoïtes du parasite. En conséquence, l'utilisation de drogues ciblant spécifiquement les capacités intrinsèques de l'organelle à répliquer ou exprimer son propre génome entraine la mort du parasite<sup>124</sup>. L'apicoplaste héberge notamment des voies métaboliques que l'on retrouve généralement au sein des chloroplastes telles que les biosynthèses de l'hème, des acides gras, des centres fer/soufre et des isoprenoides<sup>125,126</sup> (**Figure 17**), que je détaillerai plus loin.



Figure 17: Fonctions biologiques principales hébergées par l'apicoplaste<sup>127</sup>.

#### A. Apicoplaste et mort retardée

L'administration de traitements qui interfèrent avec les mécanismes de traduction bactériens (comme le chloramphénicol ou les macrolides)<sup>48</sup> conduit à une mort retardée (ou « delayed death ») du parasite dont il a été montré qu'elle était due à un effet sur l'apicoplaste<sup>128,129</sup>. Ce phénotype particulier est dû au fait que le traitement n'impacte pas drastiquement les parasites se développant au sein d'une même vacuole lors du premier cycle lytique, par contre ces parasites-là ne pourront se diviser

efficacement sans apicoplaste après une nouvelle re-invasion<sup>130,131</sup>.

Cette mort ne dépend pas de la dose d'antibiotiques administrés<sup>131</sup>. Le phénotype de mort retardée est la conséquence d'un dysfonctionnement ou d'une absence d'apicoplaste pouvant entrainer une déficience métabolique<sup>89,125</sup>. Cependant, elle est sans effet dans un premier temps car la grande connectivité des parasites se développant au sein d'une même vacuole permet probablement le partage de métabolites qu'ils génèrent<sup>66</sup>.

#### B. Voie de synthèse des acides gras

Parmi les voies métaboliques hébergées par l'apicoplaste, on retrouve donc la voie de biosynthèse des acides gras<sup>99</sup>. Le métabolisme des lipides est crucial pour le développement des parasites, ils permettent entre autres la synthèse des membranes, de molécules de signalisation, et constituent aussi une réserve d'énergie<sup>132</sup>. La synthèse des lipides au sein des parasites diverge partiellement de celle de l'hôte humain.

En effet, trois voies biochimiques de synthèse des acides gras sont codées par le génome de plusieurs parasites protozoaires comme les apicomplexes ou d'autres parasites protozoaires comme les Kinetoplastidés. Les synthèses d'acides gras de type I et II (FASI et FASII) permettent la production d'acides gras de novo, qui peuvent ensuite subir une élongation par une voie spécifique (FAE). Les voies FASI et FASII sont différentes de par leur architecture puisque les diverses étapes de la voie FASI sont assurées par une seule enzyme ayant plusieurs sites actifs, contrairement à FASII pour laquelle chaque étape enzymatique est effectuée par une protéine dédiée<sup>128</sup>.

Toutes ces voies ne sont pas présentes dans les mêmes organelles voire les mêmes organismes. La voie FASII (dite procaryote) est hébergée par l'apicoplaste de *P. falciparum* et *T. gondii* par exemple. La voie FASI est retrouvée dans le cytosol chez la plupart des eucaryotes dont l'Homme. Des protéines potentiellement impliquées dans cette voie sont également généralement présentes au sein des apicomplexes. C'est cependant la seule retrouvée chez *Theileria sp* et *Babesia bovis*, qui sont des parasites ne se développant pas dans une PV mais dans le cytosol de leur cellule hôte, facilitant donc l'accès aux nutriments de cette cellule<sup>129,133</sup>. C'est également la seule trouvée *Cryptosporidium* qui, bien que se développant dans une PV, est dépourvu d'apicoplaste<sup>129</sup>.

Tous les mécanismes de synthèse des acides gras suivent une séquence de réaction enzymatique similaire. En effet, les chaînes d'acide gras sont formées par addition séquentielle d'unité composées de deux carbones dérivés de l'acétyl CoA (**Figure 18**).

Les produits de la voie FASII issus de l'apicoplaste sont alors exportés vers le ER afin d'y être allongés et sont ensuite redirigés vers l'apicoplaste afin d'être incorporés dans les membranes de l'organelle<sup>134</sup>.



Figure 18: Mécanisme de synthèse des acides gras commun aux trois voies de biosynthèse<sup>136</sup>

Cet acheminement de lipides peut être partiellement facilité par les interactions membranaires entre l'apicoplaste et le ER<sup>135</sup>.

Le système FASII est requis pour la synthèse d'acide gras pouvant être importants dans la composition des lipides membranaires comme l'acide myristique (C14 :0) et l'acide palmitique (C16 :0)<sup>134,136</sup>.

Bien que les parasites aient la possibilité d'acquérir des précurseurs lipidiques de l'hôte, des études génétiques chez *T. gondii* ont montré que la présence de la voie FASII à l'apicoplaste est essentielle à l'intégrité de l'organelle ainsi qu'à la survie des tachyzoïtes 133,137.

## C. Voie de synthèse des isoprenoïdes

La seconde voie de biosynthèse présente à l'apicoplaste est la voie de synthèse des isoprénoïdes, qui forment une classe extrêmement variée de composants naturels essentiels. Ils le sont notamment pour la biogénèse des membranes de cellules eucaryotes par production de stérols tel que le cholestérol<sup>138,139</sup>. De même, chez les organismes apicomplexes, ils interviennent dans la formation de dolichols des ancres GPI (glycosylphosphatidyl inositol) des protéines membranaires<sup>124,140</sup>. Par ailleurs, les isoprenoïdes sont aussi impliqués dans des processus de signalisation cellulaire, de modifications des protéines (prénylation) ainsi que des modification d'ARNt et dans le transport des électrons dans la mitochondrie en fournissant des précurseurs pour la synthèse d'ubiquinones<sup>125,126,140</sup>.

Ces composés isoprenoïdes sont constitués d'unités successives d'isomères précurseurs que sont le isopentényl-pyrophosphate (IPP) et le diphosphate de diméthylallyle (DMAPP) qui, dans le cytosol les cellules animales et végétales, sont synthétisés par la voie du mévalonate<sup>126</sup>. Au contraire, dans les

bactéries et les chloroplastes, l'IPP et le DMAPP sont issus de la voie MEP/DOXP qui est indépendante du mévalonate. De même, les apicomplexes ont perdu la voie du mévalonate, mais utilisent la voie MEP/DOXP qui se trouve dans l'apicoplaste<sup>131,132,140</sup>.

Les isoprénoïdes sont issus de l'assemblage d'unités isoprène à 5 carbones, et ceux-ci sont en général l'IPP et le DMAPP<sup>126</sup>. C'est l'association de ces deux composés qui forme ainsi du géranylpyrophosphate (GPP). Celui-ci peut ensuite, par ajouts successifs d'une molécule d'IPP donner du farnésyl-pyrophosphate (FPP), puis du géranylgéranyl-pyrophosphate (GGPP) (**Figure19**). Le GPP tout comme le FPP peuvent servir à l'isoprénylation de protéines importantes pour les voies de signalisation<sup>131</sup>. Chez les formes sanguines de *P. falciparum*, il a été démontré biosynthèse des isoprénoïdes est la seule fonction essentielle de l'apicoplaste<sup>141</sup>.

C'est la fonction de prénylation qui est importante, notamment pour l'association aux membranes de protéines impliquées dans le trafic vésiculaire<sup>142</sup> et l'acquisition de nutriments. Chez le stade tachyzoïte de *Toxoplasma* la voie de synthèse des isoprénoïdes hébergée par l'apicoplaste est également essentielle<sup>143</sup>.

Comme les composants de la voie MEP/DOXP des parasites présents dans l'apicoplaste diffèrent de ceux présents à la voie MEP des hôtes<sup>140</sup>, ils sont une cible intéressante pour le développement de traitements antiparasitaires<sup>144</sup>.





#### D. Voie de synthèse de l'Hème

Une troisième voie biochimique essentielle et pour laquelle l'apicoplaste joue un rôle important est la biosynthèse de l'hème<sup>145</sup>. Cette voie est atypique chez les apicomplexes puisqu'elle n'est pas entièrement localisée dans une seule organelle. En effet, on retrouve des composants de la voie aussi bien dans la mitochondrie et le cytosol que l'apicoplaste<sup>124–126</sup>.

Cela est très différent de la biosynthèse de l'hème des cellules animales qui se déroule exclusivement à la mitochondrie<sup>146</sup>. De même dans les plantes cette voie est presque entièrement plastidique<sup>147</sup>. Les origines phylogénétiques des apicomplexes comprenant des organelles endosymbiotiques issues de cyanobactéries et de plastes expliquent la complexité de cette voie de biosynthèse<sup>126,148</sup>.

L'hème est un groupement prosthétique, complexé avec du fer, constitué de quatre cycles de pyrrole<sup>124,125,132</sup>. Cette structure particulière permet à l'hème d'accueillir un gaz tel que l'oxygène. Les protéines à hème sont ainsi impliquées dans le transport et la réduction de l'oxygène, le transfert d'électrons ainsi que d'autres processus biologiques importants<sup>149</sup>.

Les enzymes impliquées dans les dix étapes de biosynthèse de l'hème sont donc présentes dans les apicomplexes *P. falciparum* et *T. gondii*<sup>148,150</sup>, bien que réparties dans différents sous-compartiments cellulaires (**Figure 20**). La synthèse de l'hème débute et finit dans la mitochondrie, mais des étapes intermédiaires essentielles se déroulent dans le cytoplasme et l'apicoplaste.

En conséquence de tous ces changements de compartiments chez les apicomplexes, plusieurs intermédiaires de la voie de biosynthèse de l'hème doivent traverser les membranes de l'apicoplaste et de la mitochondrie. Ceci est rendu particulièrement difficile par les chaines latérales incapables de traverser des bicouches lipidiques, et demande donc l'implication d'un mécanisme de transport non connu à ce jour.

Chez *Plasmodium*, bien que l'hème en tant que cofacteur soit essentiel pour les stades hépatiques et dans l'hôte moustique, cela n'est pas le cas pour les stades sanguins<sup>151</sup>. Pour *Toxoplasma*, il a été récemment montré que la voie de biosynthèse de l'hème est essentielle à la viabilité des tachyzoites<sup>152</sup>, notamment la partie de la voie située dans l'apicoplaste<sup>153</sup>.



Figure 20: Synthèse de l'hème et métabolisme de T. gondii (adapté de <sup>123,147</sup>)

(1) Assemblage d'une glycine et du succinyl-CoA afin de générer du 5aminolevulinate (ALA) par la d-aminolevulinate synthase (ALAS).

Coproporphyrinogen

III oxydase

CPO

6

Protoporphyrinogen

oxydase PPO

7

Ferrochélastase

FC

(8)

Heme lyase

CCHL

Holo cytochrome-c

(9)

(2) La condensation de deux molécules ALA par la ALA-déhydratase (ALAD) aboutit à la formation de molécules porphobilinogenes.

Nouvelle (3) condensation de 4 porphobilinogenes grâce à l'action de la porphobilinogene désaminase (PBGD) menant à la formation d'un tétrapyrrole linéaire.

Réarrangement (4) spatial d'un centre pyrrole par l'uroporphyrinogene synthase (UROS) dormant un tétrapyrrole cyclique.

Délétion d'un (5) groupement carboxyle par l'uroporphyrinogen décarboxylase (UROD) permettant la production d'une molécule de coproporphyrinogene.

Décarboxylation (6) oxydative grâce à la coproporphyrinogene oxydase (CPO).

Réaction (7) d'oxydation par la protoporphyinogene oxydase (PPO).

(8) Chélation par la ferrochelatase (FeCH) permettant l'ajout d'un atome de fer liant les quatre cycles pyrrole.

Liaison de l'hème (9) aux cystéines de l'apocytochrome-c qui sera alors actif dans le transfert d'énergie de la chaine respiratoire.

## E. Biosynthèse des protéines à centre Fer-soufre

La dernière voie métabolique pour laquelle l'apicoplaste joue potentiellement un rôle est la voie de biosynthèse des protéines à centre fer-soufre [Fe-S]<sup>122</sup>.

Les centres fer-soufre sont des cofacteurs très anciens et donc très répandus, tant chez les eucaryotes que les procaryotes. Ils ont un rôle clé pour des protéines impliquées dans des processus métaboliques essentiels et variés parmi lesquels: le transfert d'électrons, la stabilisation de structures protéiques et la régulation de gènes<sup>154</sup> (**Figure 21**).



Figure 21: Structures et fonctions des principaux centres fersoufre dans la nature<sup>157</sup>.

Les organismes procaryotes et eucaryotes ont tous au moins une voie dédiée à la biosynthèse des centres [Fe-S]. L'acquisition par les eucaryotes de ces voies de synthèse suite à des endosymbioses a donné lieu à des systèmes d'assemblage distincts mais pouvant être interdépendants<sup>155,156</sup>.

Ainsi, chez les eucaryotes, ces centres sont assemblés et associés à des apoprotéines spécifiques par des voies de biosynthèse distinctes, mais avec des mécanismes d'action comparables, localisées dans différents compartiments cellulaires<sup>157</sup>.

Cette fonction de biosynthèse est ainsi assurée par la voie ISC (pour « iron sulfur cluster ») dans les mitochondries. Ce système est indirectement lié fonctionnellement à la machinerie CIA (pour « cytosolic iron/sulfur cluster assembly »), qui est impliquée dans la maturation des apoprotéines cytosoliques et nucléaires.

Le système SUF (pour « sulfur utilisation factors ») se trouve quant à lui généralement dans les organismes porteurs de plastes et assure la maturation des apoprotéines dans les plastes.

Les enzymes d'assemblage impliquées dans cette voie et adressées au plaste ne sont pas seulement présentes dans des organismes végétaux comme *Arabidopsis thaliana*<sup>155</sup>, mais ont été par la suite découvertes dans l'apicoplaste de *P. falciparum*, qui est le seul apicomplexe où des études fonctionnelle avaient été effectuées au moment de commencer ma thèse. Elles ont montrés que la voie SUF est potentiellement essentielle pour l'homéostasie de l'organelle et la viabilité des stades sanguins de *Plasmodium*<sup>156,158,159</sup>.

# Chapitre VI : voies de synthèse des protéines à centre Fer-Soufre

L'hypothèse concernant un possible système d'agrégation spontanée du fer et du soufre en grappe formant alors des centres [Fe-S], fut émise dès 1989 lors de recherches sur les cofacteurs acquis par la nitrogénase de la bactérie *Azotobacter vinelandii*<sup>160</sup>.

Ces groupements prosthétiques sont des cofacteurs servant à catalyser des processus biologiques essentiels (**Figure 21**) et semblent avoir été exploités tôt au cours de l'évolution<sup>161</sup>. En effet, des analyses phylogénétiques ont permis de déterminer que les protéines à centre [Fe-S] sont parmi les plus anciennes ce qui explique aussi leur large distribution dans l'arbre du vivant. Ils s'avèrent être présents dans les trois différents domaines du vivant : eucaryote, procaryote et archaea<sup>162</sup>.

Leur origine remonterait à environ 2.5 milliards d'années avant que l'atmosphère soit constituée majoritairement d'oxygène  $(O_2)^{163}$ . A cette époque, le fer et le soufre étaient des composants abondants de l'environnement anoxique dans laquelle les organismes vivaient.

Le changement de composition de l'atmosphère devenant donc riche en O2 a alors entrainé l'oxydation de nombreux composés tels quel fer et le soufre et par conséquent en a diminué la disponibilité. Ce changement atmosphérique a engendré l'apparition des dérivés réactifs à l'oxygène (ROS) pouvant être délétères au développement des micro-organismes sensibles à l'utilisation de l'O<sub>2</sub><sup>164</sup>. Pour faire face à l'augmentation de l'O<sub>2</sub>, diverses stratégies ont été mises en place notamment pour protéger les groupes [Fe-S] comme l'utilisation des métalloprotéines (des enzymes piégeant les radicaux libres) de type superoxyde dismutase (SOD)<sup>165</sup>. Cette théorie de l'évolution concernant les groupements [Fe-S] a été appuyée par une étude comparant l'utilisation de ces centres [Fe-S] dans 400 espèces procaryotes ayant des modes de vie et environnements en O<sub>2</sub> différents<sup>166</sup>. En effet, il semble que le nombre de protéines [Fe-S] d'un organisme soit en corrélation avec la taille du génome et la capacité de l'organisme à utiliser l'O2. Cela expliquerait donc pourquoi la quantité de protéines à centres [Fe-S] est bien plus élevée au sein de bactéries anaérobies par comparaison avec les bactéries aérobies<sup>166</sup>. Les connaissances accumulées au fil des années sur le sujet, sont plus avancées concernant la biogénèse des centres [Fe-S] bactériens et mitochondriaux par rapport à celle prenant place dans les plastes, et encore moins de recherches ont été menées concernant le plaste particulier des apicomplexes<sup>167,168</sup>.

#### A. Les centres [Fe-S]

Les formes libres de fer ( $Fe^{2+/3+}$ ) et en moindre mesure de soufre ( $S^{2-}$ ), sont toxiques pour les cellules. En effet elles peuvent donner ou accepter un électron des molécules voisines, elles vont alors endommager des composants cellulaires ou générer des ROS. Il a donc été nécessaire pour les organismes de développer au cours de l'évolution des mécanismes permettant de réguler les quantités de fer et de soufre libre afin de se protéger.

Les centres fer-soufre sont de composition variable mais retrouvés le plus couramment sous la forme [2Fe-2S] et la forme [4Fe-4S], respectivement de géométrie rhombique et cubique (**Figure 21**). Concernant la forme [2Fe-2S] les atomes de soufre, se situent dans le même plan que les deux atomes de fer. Alors que la structure de type cubique lie de manière covalente les atomes de fer et ceux de soufre de façon à ce qu'ils soient alternés<sup>169,170</sup>. Le point commun de ces deux formes est l'interaction avec des résidus soufrés de cystéines.

Il existe également un autre type de centre [2Fe-2S] : le type Rieske, nommé en rapport à la protéine éponyme du complexe III de la chaine respiratoire mitochondriale. Il semble que ce troisième type de centre ait un potentiel redox plus élevé du fait de l'interaction non pas avec des résidus soufrés de quatre cystéines, mais de deux cystéines et deux histidines.

Une protéine peut intégrer plusieurs centres [Fe-S] ou même interagir avec différents types de centres [Fe-S]. C'est notamment le cas de la biotine synthase, qui intègre aussi bien un [2Fe-2S] qu'un [4Fe-4S] ainsi que de la succinate déshydrogénase qui peut se lier aux trois différents types de centres<sup>167</sup>.

#### B. Transfert d'électron et rôle des centres [Fe-S]

Les centres [Fe-S] sont des catalyseurs, impliqués la majeure partie du temps, dans des réactions d'oxydoréduction. Les mécanismes faisant intervenir des centres [Fe-S] et n'impliquant pas nécessairement d'échange d'ions, sont notamment des mécanismes de régulation de l'expression des gènes au niveau transcriptionnel. On retrouve des exemples de ces régulations chez les levures (avec Aft1), les mammifères (avec la régulation des gènes du métabolisme du fer par IRP1/2)<sup>171</sup> et chez les bactéries (avec le système de répresseur IscR)<sup>172,173</sup>.

Concernant les réactions redox impliquant des protéines à centre [Fe-S], on les retrouve dans les chaînes de transfert d'électrons telles que la respiration et la photosynthèse ; tout comme dans des réactions enzymatiques impliquées dans la réparation de l'ADN ou la synthèse de cofacteurs.

Plus précisément, de nombreuses protéines à centres [Fe-S] sont retrouvées au niveau de la chaîne de transport d'électrons mitochondriale : le complexe I comportant pas moins de 8 centres [Fe-S], ainsi que le complexe III avec la protéine Rieske.

De même, au sein de la chaîne de transport d'électrons chloroplastique on retrouve des centres [Fe-S] en interaction de nombreuses protéines telles que la ferrédoxine ou le photosystème I.

Un des rôles principaux des centres [Fe-S] est de préserver les cellules et aussi de servir de senseur pour les ROS qui sont toxiques<sup>164</sup>. Les voies qui régulent l'homéostasie des ROS sont donc essentielles

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à de nombreux organismes.

Le fait de trouver de multiples protéines à centre [Fe-S] impliquées dans des fonctions variées mais conservées et essentielles d'organismes éloignés phylogénétiquement illustre le rôle important qu'on eut les groupements [Fe-S] au cours de l'évolution.

#### C. Biochimie de la synthèse des centres [Fe-S]

Les différents organismes, ou les différents compartiments subcellulaires des eucaryotes ont des répertoires de protéines à centre [Fe-S] pouvant varier. Il est donc légitime de penser que les voies de synthèses sont différentes selon les organismes et organelles considérés. Comme mentionné précédemment, on retrouve donc quatre machineries spécifiques de biosynthèse :

- la voie NIF (pour « NItrogene Fixation »), première voie découverte chez les bacteries<sup>160</sup>.

- la voie ISC (pour « iron sulfur cluster ») retrouvée dans les bactéries et les mitochondries.

- le système SUF (pour « sulfur utilisation factors ») se trouvant généralement dans les bactéries et les plastes.

 - la machinerie CIA (pour « cytosolic iron/sulfur cluster assembly »), présente chez les eucaryotes et liée de façon fonctionnelle à la voie ISC et impliquée dans la maturation d'apoprotéines cytosoliques et nucléaires.

Or, malgré des localisations différentes, au sein d'organelles spécialisées, la biosynthèse des protéines à centres fer-soufre nécessite une machinerie cellulaire complexe et coordonnée faisant intervenir de nombreuses protéines spécialisées et mais des étapes généralement conservées (**Figure 22**)<sup>174</sup>.



Figure 22: Schéma général de la voie de biosynthèse des centres [Fe-S] <sup>173</sup>

par l'action d'une sulfur transférase). Le donneur de fer n'est, à ce jour pas connu. L'assemblage des atomes de fer et de soufre en centre [Fe-S] est opéré par une protéine d'assemblage (« scaffold »). Le groupement est ensuite transféré jusqu'à l'apoprotéine cible grâce à des navettes protéiques dites protéines de transfert ou de transport (« carrier »). Lorsque l'apoprotéine reçoit le groupement [Fe-S] elle passe alors de sa forme immature à la forme mature : holoprotéine<sup>154,169</sup>.

#### 1) Les cystéines désulfurases

Les premiers acteurs des voies de biosynthèse des centres [Fe-S] sont les cystéines désulfurases. Elles peuvent être classées par homologie de séquence du motif déterminant la spécificité catalytique: - le groupe I (comprenant les protéines NifS et IscS décrites par la suite), possédant un motif SSGSACTS. - le groupe II (comprenant SufS et CsdA décrites elles aussi par la suite) possédant un motif RXGHHCA<sup>175</sup>.

Malgré des divergences structurelles entre ces deux groupes, la fonction d'une cystéine désulfurase reste inchangée : elle permet de libérer le soufre lié à une cystéine afin de le rendre disponible pour l'assemblage avec les atomes de fer.

La réaction peut notamment impliquer en premier lieu la formation d'une base de Schiff, c'est-à-dire une double liaison C=N entre une cystéine libre et le groupement aldéhyde d'une coenzyme : le phosphate de pyridoxal (PLP)<sup>175</sup>.

Le tout est suivi par l'attaque nucléophile de la cystéine-PLP engendré par le site actif d'un groupe cystéinylthiol. En effet, les groupes thiols confèrent aux cystéines des fonctions spécialisées telles que : la nucléophilie, la forte affinité pour les métaux, ainsi que la formation de ponts disulfures<sup>176</sup>. L'attaque nucléophile de la cystéine-PLP permet la formation d'un persulfure de cystéine (qui est un dérivé de la L-cystéine ayant un atome de soufre supplémentaire lié au groupe cystéinylthiol) permettant à son tour la libération d'une L-alanine<sup>177</sup>. Enfin le persulfure peut alors être transféré à un résidu cystéine d'une protéine ne contenant pas au préalable de centre [Fe-S], telle qu'une protéine d'assemblage.

#### 2) <u>Les protéines d'assemblage et protéines chaperonnes</u>

Ces protéines ont pour fonction de permettre l'assemblage en centre [Fe-S] des différents atomes libres de soufre et de fer.

Tout comme les cystéines désulfurases, elles peuvent être elles aussi distinguées en deux groupes (Utype scaffold et A-type scaffold) en fonction des motifs qu'elles contiennent, menant tous deux à la réduction du persulfure en sulfure pouvant alors être assemblé avec les atomes de fer pour former un centre [Fe-S]<sup>178</sup>. Afin que cette étape d'assemblage soit réalisée, il est nécessaire que des donneurs d'électrons interviennent (tels que la ferrédoxine mitochondriale pour la voie ISC).

Les protéines de type A comportent des résidus conservés dans leur région C-terminale : C-X<sub>42-44</sub>-D-X<sub>20</sub>-C-G-C. On peut regrouper sous cette appellation des protéines donnant le centre [Fe-S] à des protéines de type U, ou encore des protéines chaperonnes.

Concernant les protéines d'assemblage de type U, la première caractérisée et la plus connue de toutes est NifU<sup>160</sup>. Elles contiennent des domaines (3 pour NifU) permettant la formation de centres [Fe-S] pouvant ensuite être transférés vers une apoprotéine. On retrouve dans ce groupe des protéines

comprenant une partie similaire au domaine C-terminal de NifU chez les cyanobactéries, les plantes et les eucaryotes supérieurs<sup>175</sup>, ce qui atteste encore une fois de la conservation évolutive de ce type de machinerie.

Il reste néanmoins un point non élucidé de cette étape d'assemblage pour les différents mécanismes de biosynthèse des centres [Fe-S] : d'où provient le fer et comment celui-ci est-il intégré aux atomes de soufre ? Néanmoins, les connaissances concernant le fonctionnement et la structure des protéines d'assemblage ont avancé ces dernières années.

En effet, nous savons désormais que les protéines d'assemblage de la voie SUF fonctionnent en complexe (SufB, SufC et SufD) contrairement aux voies ISC et CIA ne comprenant qu'une seule protéine principale (respectivement IscU et NBP35)<sup>179</sup>.

Par la suite, l'intervention de protéines chaperonnes et de co-chaperonnes hydrolysant l'ATP en ADP fait alors retourner la protéine d'assemblage sous la forme immature dissociée du centre [Fe-S], qui sera lui alors associé à une protéine de transport<sup>175,178</sup>.

#### 3) <u>Les protéines de transport</u>

Une fois le centre [Fe-S] assemblé par les protéines d'assemblage, il doit être transféré à une apoprotéine. Les protéines impliquées dans ce transfert sont nommées transporteurs de type A canoniques (ATC). Il en hésite un grand nombre et, par exemple, *Escherichia coli* en possède trois différentes (IscA, SufA et ErpA décrites plus précisément dans la prochaine partie), toutes proches phylogénétiquement. Initialement ces protéines n'ont pas été décrites comme spécifique au transport puisqu'il leur est aussi possible de contribuer à la création du centre [Fe-S] en plus de le transférer à une apoprotéine<sup>180</sup>.

Or, il est maintenant établi que ces protéines appartiennent à une catégorie à part entière de la machinerie de biosynthèse des centres [Fe-S]. Les ATC peuvent lier le centre [Fe-S] grâce à un motif de trois résidus cystéines, et le transfert du centre d'une protéine d'assemblage vers une protéine de transport est non réversible<sup>172,173</sup>.

Il existe aussi des protéines de transport non usuelles, pour lesquelles il y a encore des nombreux débats. On retrouve notamment la classe de protéine NfuA présente chez *E.coli*, résultant en une fusion du domaine Nfu avec un domaine N-terminal dégénéré des ATC (ATC\*) donc dépourvu des trois résidus cystéine qui lient le centre [Fe-S]<sup>181</sup>. Il semble que le domaine ATC\* améliore l'efficacité du transfert des centres [Fe-S] en conditions de stress<sup>181</sup>. Il est parfois difficile de déterminer l'implication directe d'une protéine dans le transfert sans test d'activité *in vitro* c'est pour cela que des protéines homologues ont été classées comme protéines d'assemblages dans certains organismes et de transfert pour d'autres. C'est par exemple le cas pour Nbp35/ApbC pour qui on a assigné un rôle dans

l'assemblage chez *S. enterica* alors que son homologue est décrite en tant que protéine de transport chez les archae<sup>182</sup>.

De plus, il existe au sein des mitochondries, une autre famille de transporteurs nécessaire au fonctionnement de la voie cytosolique (CIA) : les transporteurs ABC mitochondriaux (ATM). On en retrouve aussi bien chez la levure (avec Atm1)<sup>183</sup> que chez les mammifères (ABCB7)<sup>184</sup> ou chez les végétaux (ATM1-ATM2-ATM3)<sup>179</sup>. Ce sont des transporteurs intramembranaires permettant le passage de facteurs (encore non identifiés) contenant des atomes de soufres dont la voie CIA se sert comme précurseur pour synthétiser *de novo* des clusters [Fe-S].

La finalité de ces groupes de protéines de transport reste le fait de transférer le groupement [Fe-S] à une apoprotéine qui est la cible finale nécessitant le cluster.

#### 4) Les apoprotéines cibles des centres [Fe-S]

Comme vu précédemment, dans une ultime étape, les centres [Fe-S] vont être incorporés dans protéines sous forme « apo » non mature, afin de les rendre stables et matures (sous forme « holo »). Comme évoqué plus haut, les apoprotéines, cibles finales des centres [Fe-S], sont impliqués dans de très nombreuses fonctions cellulaires.

Les fonctions cellulaires qui sont dépendantes de la biosynthèse des centres [Fe-S] diffèrent en fonction des organismes et des voies étudiées, mais on retrouve globalement des fonctions similaires pouvant être impactées.

La voie mitochondriale ISC, qu'elle soit bactérienne<sup>173</sup>, végétale<sup>155</sup>, ou pour d'autres eucaryotes<sup>157</sup>, alimente des protéines impliquées dans:

- La synthèse de cofacteurs (tels que la lipoate synthase) ;
- Le fonctionnement des complexes I et II de la chaine respiratoire et le transfert d'électrons
- L'approvisionnement en énergie par le cycle TCA (grâce à l'aconitase impliquant un centre [Fe-S]).

Concernant la voie CIA, elle génère des protéines impliquées dans la synthèse et réparation de l'ADN, les modifications post-traductionnelles et la synthèse d'acides aminés. De plus, elle permet aussi la fonction de senseurs de l'environnement tels que les protéines humaines IRP1-2 impliquées dans homéostasie du fer, tel que vu précédemment, avec l'apport d'énergie par le cycle TCA (la forme holoprotéine de IRP1 étant l'aconitase).

La voie SUF, hébergée notamment par les plastes, permet la synthèse de protéines [Fe-S] impliquées dans des fonctions vitales telles que :

- L'assimilation de nutriments (comme l'azote et le soufre) ;
- Le fonctionnement de différentes voies de biosynthèse ; acides gras / isoprenoïdes / hème
- La conversion du pyruvate en Acétyl-CoA (notamment par le biais de la sous-unité E2 de la pyruvate déhydrogénase (PDH), qui contient un centre [Fe-S]) ;
- La photosynthèse (photosystème I).

Ainsi, les centres [Fe-S] sont nécessaires à une grande partie des organismes, puisqu'ils gouvernent des fonctions cellulaires diverses et indispensables au bon développement de ces êtres vivants.

D. Organisation et régulation de la voie de synthèse des protéines à centres [Fe-S] Du fait de l'hétérogénéité des organismes abritant les voies de biosynthèse des protéines à centres

[Fe-S], il est logique de penser que divers mécanismes de régulations de ces voies ont été développés au cours de l'évolution.

#### 1) <u>Au sein des bactéries</u>

Le modèle bactérien le plus étudié concernant la biosynthèse des centres [Fe-S] est *E.coli* pour lequel il existe seulement deux des trois machineries bactériennes (ISC, SUF) organisées en opéron. Ainsi, la voie ISC est régie par l'opéron *iscRSUA-hscBA-fdx* ; alors que la voie SUF est, elle, sous contrôle de l'opéron *sufABCDSE* (**Figure 23**)<sup>172,174</sup>. Ces deux opérons codent respectivement pour les complexes de cystéines désulfurases (IscS et SufS/E), la protéine d'assemblage IscU (dont l'action est facilitée par une interaction avec les protéines chaperonnes et co-chaperonnes : HscB/A) et le complexe d'échafaudage SufBC2D. De plus, les protéines de transport IscA et SufA sont elles aussi codées par les opérons, tout comme la ferrédoxine (fdx) permettant de fournir les électrons nécessaires à la voie ISC<sup>174</sup>.

Le facteur de transcription *iscR* présent sur l'opéron *isc*, ainsi que le petit ARN non codant *RyhB*, contrôlent la transcription des gènes *isc* et *suf* chez *E. coli* ce qui permet aussi une autorégulation du répresseur<sup>175</sup>. Les voies ISC et SUF sont réprimées en condition anaérobie mais fortement exprimées en réponse aux ROS. En effet, la protéine IscR contient trois cystéines pouvant se lier à un cluster [Fe-S]. Ce centre [Fe-S] assure une fonction de senseur du stress oxydatif (par le régulateur OxyR) et de la disponibilité en nutriments (par le régulateur de fer FUR). Qu'elle soit sous forme apo ou holo, iscR a la capacité de lier l'ADN et est impliquée dans une boucle de régulation.

La forme holo agit comme répresseur de l'opéron de la voie ISC jusqu'à ce que la présence de la forme Apo-IscR soit grandement réduite. La répression est alors atténuée et la protéine IscR peut être à nouveau synthétisée, la boucle d'autorégulation peut alors recommencer.

L'activation de la voie SUF est dépendante du niveau d'expression de la forme Apo-IscR qui lorsqu'elle

est en grande quantité engendre, tout comme la présence d'OxyR ou une limitation en fer, la transcription de l'opéron *suf*.

Cette régulation sur la base d'opéron est importante pour la croissance optimale des bactéries et pour une réponse efficace aux stress cellulaires.





#### 2) Importance des protéines à centre [Fe-S] pour les cellules humaines

Les voies ISC et CIA sont présentes et indispensables aux cellules humaines. La machinerie ISC se situe dans les mitochondries (organelles nécessaires au bon fonctionnement de la cellule), or le fer présent dans ces organelles peut engendrer des dommages en favorisant la génération de ROS. Il est donc nécessaire d'avoir une régulation du fer mitochondrial.

La voie ISC est gouvernée par l'action d'un complexe faisant intervenir : la cystéine de sulfurase NFS1 et sa protéine stabilisatrice ISD11, la protéine d'assemblage ISCU, des protéines carrières de type A et la Frataxine (fxn) participant au transfert du soufre de NFS1 vers ISCU<sup>185</sup>. Par la suite c'est l'action de chaperonne/co-chaperonne (analogues aux HscA/HscB bactériennes) HSPA9/HSC20, qui va aboutir à l'apport du centre [Fe-S] à l'apoprotéine cible<sup>185</sup>.

De nombreuses recherches sont portées sur la Frataxine du fait de son implication dans l'ataxie de Friedreich, une pathologie neurodégénérative grave, causée par une déficience en cette protéine<sup>185</sup>. Il est maintenant établi qu'une déficience en Frataxine induit de très nombreuses conséquences comme la perturbation des transports de fer intra et extracellulaires : ferritines (FRTs) et ferroportines (FPN)<sup>186</sup>. Le tout aboutit à une réduction de l'efficacité de la voie ISC ainsi qu'à un dysfonctionnement de la régulation de l'homéostasie cellulaire par accumulation de fer intra cellulaire (**Figure 24**)<sup>186,187</sup>. Ce phénomène augmente alors les dommages oxydatifs (ROS) délétères pour la cellule.

Ainsi, il est suggéré que la Frataxine pourrait fonctionner comme un régulateur du métabolisme du fer mitochondrial, permettant de favoriser soit la voie de synthèse de l'hème, soit la voie ISC. D'autres protéines importantes sont impliquées dans la régulation du fer : IRP1 et IRP2 en régulant l'expression de protéines des machineries ISC et de synthèse de l'hème<sup>186,188</sup>. IRP1 a pour caractéristique d'être bi-fonctionnelle : en présence de fer, elle se complexe avec un centre [Fe<sub>4</sub>S<sub>4</sub>] et devient l'aconitase, alors qu'en absence de fer la forme apoprotéine se réarrange structurellement pour devenir un élément régulateur. En effet, lorsque le taux de fer dans la cellule est bas, les protéines IRPs se lient à différents éléments de réponse au fer (IRE) présents sur les ARNm de protéines liées au métabolisme du fer. Deux possibilités de liaison s'offrent aux IRPs<sup>186</sup> :

une liaison avec un IRE à l'extrémité 5'UTR réprimant la traduction de l'ARNm
une liaison en 3' UTR qui semble augmenter la traduction.



Figure 24: Régulation de l'homéostasie du fer des cellules eucaryotes (adapté de 186,188).

#### 3) Importance des centres [Fe-S] chez les plantes

Les organismes photosynthétiques (*i.e* les plantes comme que *Arabidopsis thaliana*, les algues) sont particulièrement riches en protéines à centre [Fe-S]. Ils abritent plusieurs voies de biosynthèse des protéines à centre [Fe-S] au sein de différents compartiments cellulaires. Les voies étant localisées dans différents compartiments : les plastes (voie SUF) ; les mitochondries (voie ISC) ; le cytosol (voie CIA), cela implique un moyen d'adressage spécifique des protéines vers les voies SUF et ISC. La compartimentation des machineries, tout comme la vulnérabilité due à une exposition à l'oxygène (particulièrement pour les chloroplastes) et la toxicité des nutriments libres Fe<sup>2+/3+</sup> et S<sup>2</sup> sont surement à l'origine de la complexité des mécanismes de régulation des voies de biosynthèse des centres [Fe-S]<sup>178</sup>.

L'héritage cyanobactérien des chloroplastes, où se déroulent les mécanismes de photosynthèse et de synthèse de l'hème, confère un système spécifique d'assemblage des centres [Fe-S] : la voie SUF<sup>155</sup>. De ce fait certaines protéines impliquées dans cette voie ont des homologies de séquence et d'activité avec des protéines bactériennes, même si la machinerie propre aux eucaryotes a pu se complexifier comme pour la protéine SufE qui a trois isoformes chez *A.thaliana*.

De multiples protéines de synthèse de centres [Fe-S] sont importantes pour la suivie de la plante ; ainsi leur absence engendre un phénotype de mort, ou une anomalie morphologique prononcée (chlorose et retard de croissance). C'est notamment le cas pour des protéines de la voie SUF comme HCF101/ AtSufB/ AtSufC<sup>168</sup>/ AtSufD<sup>189</sup>. De même, concernant la voie ISC, *Arabidopsis*, possède un homologue de la protéine Frataxine (nommée FH) qui comme pour les cellules animales est indispensable au développement de l'organisme. En effet, une déficience partielle en FH entraine une diminution de l'activité des protéines à centre [Fe-S] mitochondriales (aconitase et succinate déhydrogénase) et une hypersensibilité aux ROS, alors qu'une déplétion totale en FH cause la mort de l'embryon<sup>178</sup>.

En raison du besoin élevé en centres [Fe-S] des mitochondries et chloroplastes, ainsi que des phénotypes graves impliqués par une déficience dans les protéines à centres [Fe-S], une fine régulation de l'absorption et de l'assimilation de ces nutriments est nécessaire. Cependant, la régulation de l'homéostasie du fer et du soufre n'est pas complétement connue. Il semble que l'expression des gènes des voies ISC/CIA et ceux de la voie SUF puissent être activés indépendamment. Cela pourrai s'expliquer par le fait que les gènes de la voie mitochondriale ISC sont liés à ceux de la voie cytosolique CIA formant alors un seul et même groupe contrairement aux gènes de la voie SUF formant un groupe fonctionnel à part entière<sup>179</sup>. De plus ces deux groupes semblent être régulés différemment et en fonction de signaux externes à la plante.

En effet, chez les plantes supérieures, il s'avère que l'expression des protéines à centres [Fe-S] peut être adaptée en fonction du taux d'absorption de Fe, ainsi seules quelques protéines essentielles se verront maintenues<sup>179</sup> (**Figure 25**). C'est notamment le cas pour le photosystème I et le complexe I dont leur expression est abaissée lorsque les plants poussent dans des conditions pauvres en Fe<sup>190</sup>, incitant possiblement un recyclage du Fe déjà présent. De plus une autre source de Fe vient des centres [Fe-S] qui libèrent du Fe lorsqu'ils sont endommagés. Au vu de la toxicité du Fe libre, il est alors impératif de le mobiliser afin de le réutiliser ou de le stocker grâce à la ferritine.

De même, les gènes ISC et SUF peuvent être régulés à la baisse lors d'une hypoxie ou lors d'une infection par un pathogène comme *Pseudomonas syringae*. En effet, lors d'une infection par un

pathogène, les centres [Fe-S] peuvent être détruits, en raison du stress oxydatif engendré par les ROS libérés afin de combattre l'infection, et leur expression peut être également diminuée afin de limiter la quantité de Fe libérée et enrailler l'augmentation des dégâts oxydatifs<sup>179,189</sup>.

Pareillement, en cas d'hypoxie il semble que les centres [Fe-S] aient une durée de vie plus longue ce qui nécessite moins de biosynthèse de ces centres<sup>179</sup>.



Figure 25: Exemples d'impacts liés à l'expression de protéines à centres [Fe-S] chez les plantes

#### 4) <u>Ce qui est connu chez les apicomplexes</u>

Le phylum des apicomplexes auquel appartient *T. gondii*, mais aussi *P. falciparum* (un des agents du paludisme). Comme la plupart des eucaryotes, ces apicomplexes semblent coder pour des enzymes prédites pour participer à la biosynthèse de protéines à centres [Fe-S] (**Annexes 1 à 3**). Le travail de recherche sur les protéines [Fe-S] au sein de ces parasites est récent et a été jusqu'à présent essentiellement focalisé sur *P. falciparum*.

En ce qui concerne les autres membres du phylum, on peut trouver des informations sur la machinerie [Fe-S] de *Chromera velia* qui est génétiquement apparentée au phylum des apicomplexes<sup>191</sup> mais n'est autre qu'une algue vivant associées aux coraux de la grande barrière de corail australienne. Le séquençage de son génome a révélé des voies provenant des parasites et des algues (elle contient un plaste photosynthétique) et elle est souvent considérée comme modèle pour l'étude des apicomplexes. A contrario, au sein du même phylum on retrouve des organismes dépourvus d'apicoplaste comme *Cryptosporidium parvum* qui est utile afin de comprendre les spécificités liées à la présence de l'apicoplaste.

Par comparaison avec les prédictions faites pour différents organismes modèles d'apicomplexes et apparentés (**Annexes 1 à 3**), comprenant *T. gondii/ P. falciparum/ C. velia/ C. parvum* il apparait clairement que les apicomplexes comportent les principaux composants pour la synthèse des centres [Fe-S], Cela est valable pour les voies mitochondriales (ISC), cytoplasmique (CIA) et plastidique (SUF). En effet, il semble que ces quatre organismes comportent tous les composants de la voie CIA par homologie avec *A. thaliana* (**Annexe 1**). De plus, concernant la voie mitochondriale, il semble que la

majorité des composants de la voie sont présents pour les quatre apicomplexes étudiés (**Annexe 2**). Il subsiste néanmoins quelques divergences comme la possible absence d'homologues des IscA1 à 4 chez *C. parvum* alors qu'ils semblent être en partie présents pour les trois autres modèles. La plus grande disparité survient avec les prédictions concernant la voie SUF (**Annexe 3**). En effet, *C. parvum* ne semble pas posséder d'homologue de cette voie contrairement aux autres organismes, ce qui est tout à fait cohérent avec l'absence d'apicoplaste. Cependant, si l'on associe la voie SUF à la présence de l'apicoplaste, les différences fonctionnelles entre le plaste photosynthétique de *C. velia* et l'apicoplaste dépourvue de photosynthèse de *T. gondii* et *P. falciparum*, ne semble pas impliquer ou se répercuter sur la présence de protéines putatives de la voie SUF.

Bien que l'apicoplaste ne soit pas photosynthétique, il abrite plusieurs voies métaboliques indispensables aux parasites dont certaines sont prédites pour contenir des enzymes nécessitant des centres [Fe-S]<sup>192</sup>. C'est notamment le cas pour la lipoate synthase LIPA de la voie de synthèse de l'acide lipoïque ainsi que les protéines IspG-IspH nécessaires à la biosynthèse des isoprénoïdes.

Il s'avère que la voie DOXP des isoprénoïdes de *P. falciparum*, est la cible d'un anti-malarique (la fosmidomycine) ; c'est en fait la seule voie métabolique de l'apicoplaste qui est essentielle pour les stades sanguins du parasite. Par exemple, la supplémentation du milieu en isopentényle pyrophosphate (IPP)<sup>156</sup> permet aux parasites de survivre malgré l'absence d'apicoplaste. Il est donc naturel de supposer que des protéines à centre Fe-S (issus potentiellement de la voie SUF) nécessaires à la biosynthèse des isoprénoïdes ont une importance considérable pour les parasites, tout en étant absentes de l'hôte mammifère.

Par conséquent, une grande partie des études faites chez *P. falciparum* sont focalisées sur la voie plastidique SUF. Ce qui a permis de confirmer la localisation à l'apicoplaste de cette voie et de caractériser les premières interactions protéines-protéines avec le complexe SufS-SufE<sup>193</sup>.

De plus, il a été démontré par des études fonctionnelles, que la voie SUF lorsqu'elle est perturbée entraine une mort des parasites au stade sanguin de *P. falciparum*<sup>156</sup> ce qui n'est pas le cas lorsque ces parasites sont supplémentés en IPP. Cela semble confirmer l'importance de cette voie sur la synthèse des isoprenoides et le développement du stade sanguin. Dans un même temps, il apparait que ces mêmes parasites ne contiennent plus d'apicoplaste ni le génome qu'il héberge, ce qui n'est pas le cas lorsque l'on inhibe seulement la voie des isoprénoïdes. Cela suggère alors que la voie SUF ne sert pas seulement à fournir des centres Fe-S à la voie MEP mais est aussi impliquée dans le maintien de l'apicoplaste chez *P. falciparum*.

Le fait que l'apicoplaste n'ait pas de fonction photosynthétique, contrairement aux chloroplastes, implique alors très probablement des différences dans la machinerie SUF. Ainsi, de par l'absence de

photosystèmes dans l'apicoplaste par exemple, une protéine comme HCF101, permettant notamment le transfert de centre [Fe-S] vers le photosystème I chez les plantes, a une fonction inconnue chez les apicomplexes. Les apicomplexes comportent des homologues d'HCF101 (**Annexe 3**), or, il s'avère que les homologues présents chez *T. gondii* et *P. falciparum* ne possèdent pas de peptide signal, ou de domaine bipartite permettant un adressage spécifique à l'apicoplaste et auraient alors une localisation cytosolique. Ces protéines, qui sont aussi présentes au seins d'organismes n'ayant pas de plastes<sup>125,194</sup> (dont Cryptosporidium), ont peut-être une fonction originelle cytosolique et se seraient spécialisées dans une fonction liée au chloroplaste plus tard dans l'évolution.

Une autre protéine de la même famille que HCF101, Nbp35 (concernant la voie ISC) semble elle aussi être présente chez les apicomplexes, comme chez toutes les cellules eucaryotes<sup>194,195</sup>. La protéine Nbp35 de *T. gondii* semble être localisée à la mitochondrie grâce à un domaine d'adressage en N-terminal<sup>156</sup>. De plus elle semble être indispensable au bon développement du parasite mais non impliquée dans la biosynthèse des centres [Fe-S] mitochondriaux<sup>194,195</sup>. Concernant le rôle de Nbp35 de *T. gondii* au vu de sa localisation, il a été émis l'hypothèse d'une implication dans la maturation des protéines à centre [Fe-S] cytosoliques se faisant à la face cytosolique de la membrane externe mitochondriale.

Malgré le peu d'informations disponibles sur les voies de synthèse des centres [Fe-S] chez *T. gondii*, il est intéressant de noter que ce parasite semble comporter certaines originalités par rapport aux modèles canoniques eucaryotes, dont certaines pourraient être exploitées pour de futures approches thérapeutiques. En effet, étant donné l'importance de ce type de voies métaboliques pour les organelles qui les hébergent, ainsi que leur implication dans de nombreuses fonctions vitales, il est probable que les voies de synthèse des centres [Fe-S] aient une importance majeure dans la croissance de *T. gondii*. Cependant, au moment où j'ai commencé ma thèse, aucune caractérisation n'avait été effectuée chez ce parasite. Or, depuis, la voie cytoplasmique a récemment été montrée comme étant essentielle pour les tachyzoïtes<sup>195</sup>. Lors de ce projet de thèse, je me suis intéressée plus particulièrement aux deux voies de synthèse des centres [Fe-S] hébergées par les organelles d'origine endosymbiotique (mitochondrie et plaste) de *T. gondii* afin d'élucider leur contribution respective au développement des tachyzoïtes.

# <u>Résultats</u>

# *Chapitre I : identification et caractérisation de deux protéines putatives des voies de biosynthèse Fe-S chez T. gondii*

#### A. Introduction

Bien que les groupements prosthétiques [Fe-S] soient essentiels à la vie de nombreux organismes, leur synthèse et assemblage étaient relativement peu étudiés chez *T. gondii*.

Une analyse par recherches d'homologues entre *T. gondii* et la plante *A. thaliana* (qui comporte les trois voies, cytoplasmique, mitochondriale et plastidique), à l'aide de la base de données ToxoDB, nous a permis d'identifier les composants de ces machineries chez le parasite (**Annexes 1 à 3**). Nous avons ensuite utilisé l'outil bio-informatique MétalPrédator<sup>196</sup> grâce auquel plus d'une soixantaine de protéines candidates (**Annexe 4**), possédant un possible centre [Fe-S], ont été révélées. Parmi celle-ci, on trouve, comme chez d'autres eucaryotes, des protéines impliquées dans d'importantes fonctions cellulaires telles que les ADN et ARN polymérases ou encore des protéines impliquées dans le contrôle redox et le transfert d'électrons.

La base de données ToxoDB comporte des informations concernant la localisation<sup>197</sup> (données de protéomique spatiale par « hyperplexed localization of organelle proteins by isotope tagging » (hyperLOPIT) et l'essentialité<sup>198</sup> (données de crible CRISPR à l'échelle du génome) de nombreux candidats.

Cela nous a permis de voir que la plupart des composants des trois voies de biosynthèses hypothétiques, ISC/SUF/CIA, semblent être indispensables au parasite. De même, la localisation suggérée (plaste/mitochondrie/cytoplasme) de leurs composants est généralement semblable à celle des homologues végétaux (avec tout de même quelques exceptions, comme TgHCF101).

Au début de ce projet, aucune étude fonctionnelle n'avait été réalisée sur les voies de synthèse [Fe-S] de *T. gondii*. Depuis, l'étude de l'équipe de Giel Van Dooren<sup>195</sup> est parue, décrivant la caractérisation de la protéine TgNbp35 et l'importance de la voie CIA pour la survie du parasite.

De notre côté, nous avons voulu évaluer les contributions respectives des deux voies de synthèse des centres [Fe-S], hébergées par les organelles d'origine endosymbiotique du parasite, pour lesquelles nous avons généré plusieurs mutants spécifiques.

Ainsi, les candidats dont nous avons commencé l'étude sont : pour la voie SUF, la cystéine désulfurase SufS, son partenaire putatif SufE, ainsi que l'ATPase SufC ; pour la voie ISC, la cystéine désulfurase IscS et la protéine d'assemblage IscU. Nous avons pu obtenir rapidement des mutants pour les candidats SufS et IscU dont nous avons poursuivi en priorité l'étude approfondie. L'analyse fonctionnelle de ces deux protéines est décrite sous forme de manuscrit, intitulé « Differential contribution of two organelles of endosymbiotic origin to iron-sulfur cluster synthesis and overall, in Toxoplasma » et tel qu'il a été soumis à Plos Pathogens. Pour un soucis de cohérence concernant la nomenclature des protéines composants les voies de biosynthèse SUF et ISC, avec le récent papier de Gil Van Dooren<sup>195</sup>, les mutants auparavant nommés TgSufS et TgIscU sont alors renommés dans cet article respectivement: TgNFS2 et TgISU1.

B. Differential contribution of two organelles of endosymbiotic origin to iron-sulfur cluster synthesis and overall, in Toxoplasma.

#### Differential contribution of two organelles of endosymbiotic origin to iron-1 2 sulfur cluster synthesis and overall fitness in Toxoplasma

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- 9
- 10 Abstract

11 Iron-sulfur (Fe-S) clusters are one of the most ancient and ubiquitous prosthetic groups, and they are 12 required by a variety of proteins involved in important metabolic processes. Apicomplexan parasites have inherited different plastidic and mitochondrial Fe-S clusters biosynthesis pathways through 13 14 endosymbiosis. We have investigated the relative contributions of these pathways to the fitness of 15 Toxoplasma gondii, an apicomplexan parasite causing disease in humans, by generating specific mutants. Phenotypic analysis and quantitative proteomics allowed us to highlight notable differences 16 17 in these mutants. Both Fe-S cluster synthesis pathways are necessary for optimal parasite growth in vitro, but their disruption leads to markedly different fates: impairment of the plastidic pathway 18 19 leads to a loss of the organelle and to parasite death, while disruption of the mitochondrial pathway 20 trigger differentiation into a stress resistance stage. This highlights that otherwise similar biochemical 21 pathways hosted by different sub-cellular compartments can have very different contributions to the 22 biology of the parasites, which is something to consider when exploring novel strategies for 23 therapeutic intervention.

24

#### 25 Author summary

26 Toxoplasma gondii is a ubiquitous unicellular parasite that harbours two organelles of endosymbiotic 27 origin: the mitochondrion, and a relict plastid named the apicoplast. Each one of these organelles 28 contains its own machinery for synthesizing iron-sulfur clusters, which are important protein co-29 factors. In this study, we show that interfering with either the mitochondrial or the plastidic iron-30 sulfur cluster synthesizing machinery has a profound impact on parasite growth. However, while 31 disrupting the plastidic pathway led to an irreversible loss of the organelle and subsequent death of 32 the parasite, disrupting the mitochondrial pathway led to conversion of the parasites into a stress 33 resistance form. We used a comparative quantitative proteomic analysis of the mutants, combined 34 with experimental validation, to provide mechanistic clues into these different phenotypic outcomes. 35 Although the consequences of disrupting each pathway were manifold, our data highlighted distinct 36 changes at the metabolic level. For instance, the plastidic iron-sulfur cluster synthesis pathway is 37 likely important for maintaining the lipid homeostasis of the parasites, while the mitochondrial 38 pathway is clearly crucial for maintaining their respiratory capacity. Interestingly, we have discovered 39 that other mutants severely impacted for mitochondrial function, in particular the respiratory chain, 40 are able to survive and initiate conversion to the stress resistance form. This illustrates a different 41 capacity for T. gondii to adapt for survival in response to distinct metabolic dysregulations. 42 Keywords: iron-sulfur cluster, Toxoplasma, differentiation, bradyzoite, apicoplast, mitochondrion 43

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45 Short title: Iron-sulfur cluster synthesis in Toxoplasma
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#### 46 Introduction

47

Endosymbiotic events were crucial in the evolutionary timeline of eukaryotic cells. Mitochondria and plastids 48 evolved from free-living prokaryotes that were taken up by early eukaryotic ancestors and transformed into 49 permanent subcellular compartments that have become essential for harnessing energy or synthesizing 50 essential metabolites in present-day eukaryotes [1]. As semiautonomous organelles, they contain a small 51 genome, but during the course of evolution a considerable part of their genes have been transferred to the 52 cell nucleus. Yet, they rely largely on nuclear factors for their maintenance and expression. Both organelles are 53 involved in critically important biochemical processes. Mitochondria, which are found in most eukaryotic 54 organisms, are mostly known as the powerhouses of the cell, owing to their ability to produce ATP through 55 respiration. Importantly, they are also involved in several other metabolic pathways [2], including the synthesis 56 of heme groups, steroids, amino acids, and iron-sulfur (Fe-S) clusters. Moreover, they have important cellular 57 functions in regulating redox and calcium homeostasis. Similarly, plastids that are found in plants, algae and 58 some other eukaryotic organisms, host a diverse array of pathways that contribute greatly to the cellular 59 metabolism [3]. While often identified mainly as compartments where photosynthesis occurs, plastids host other 60 important metabolic pathways. For example, they are involved in the assimilation of nitrogen and sulfur, as 61 well as the synthesis of carbohydrates, amino acids, fatty acids and specific lipids, hormone precursors, and also 62 Fe-S clusters. The best-characterized plastid is arguably the plant cell chloroplast, but not all plastids have 63 photosynthetic function, and in higher plants they are in fact a diverse group of organelles that share basal 64 metabolic pathways, but also have specific physiological roles [4]. 65

66

67 The phylum Apicomplexa comprises a large number of single-celled protozoan parasites responsible for serious 68 disease in animals, including humans. For example, this phylum includes parasites of the genus Plasmodium 69 that are responsible for the deadly malaria, and Toxoplasma gondii a ubiquitous parasite that can lead to a 70 severe pathology in immunocompromised individuals. Apicomplexan parasites evolved from a photosynthetic 71 ancestor and many of them still retain a plastid [5,6]. This plastid, named the apicoplast, originated from a 72 secondary endosymbiotic event [7,8]. It has lost its photosynthetic properties as the ancestors of Apicomplexa 73 switched to an intracellular parasitic lifestyle [9]. The apicoplast nevertheless still hosts four main metabolic 74 pathways [10,11]: a so-called non-mevalonate pathway for the synthesis of isoprenoid precursors, a type II 75 fatty acid synthesis pathway (FASII), part of the heme synthesis pathway, and a Fe-S cluster synthesis 76 pathway. As the apicoplast is involved in these important biological processes for the parasite, and as they 77 markedlydiffer from those of the host (because of their algal origin), that makes it a valuable potential drug 78 target. Apicomplexan parasites also generally contain a single tubular mitochondrion, although its aspect may 79 vary during parasite development [12,13]. The organelle is an important contributor to the parasite's 80 metabolic needs [14]. It classically hosts tricarboxylic acid (TCA) cycle reactions, whichare the main source of 81 electrons that feeds the mitochondrial electron transport chain (ETC) which generates a proton gradient used 82 for ATP production. It also contains additional metabolic pathways, like a Fe-S cluster synthesis pathway and 83 part of the heme synthesis pathway operating in collaboration with the apicoplast. The latter reflects obvious 84 functional links between the organelles and potential metabolic interactions, which is also illustrated by their 85 physical connection during parasite development [15,16]. 86

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88

Fe-S clusters are simple and ubiquitous cofactors involved in a great variety of cellular processes. Astheir name

implies, they are composed of iron and inorganic sulfur whose chemical properties confer key structural or electron transfer features to proteins in all kingdoms of life. They are important to the activities of numerous

91 proteins that play essential roles to sustain fundamental life processes

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92 including, in addition to electron transfer and exchange, iron storage, protein folding, oxygen/nitrogen stress 93 sensing, and gene regulation [17]. The synthesis of Fe-S clusters and their insertion into apoproteins requires 94 complex machineries and several distinct pathways have been identified in bacteria for synthesizing these 95 ancient cofactors [18]. They include the ISC (iron-sulfur cluster) pathway for general Fe–S cluster assembly [19], 96 and the SUF (sulfur formation) pathway [20] that is potentially activated in oxidative stress conditions [21]. 97 Eukaryotes have inherited machineries for synthesizing Fe-S cluster through their endosymbionts [22]. As a 98 result, organisms with both mitochondria and plastids, like land plants, use the ISC pathway for assembling Fe-S clusters in the mitochondria and the SUF pathway for Fe-S clusters in the plastids [23]. Additional protein 99 components that constitute a cytosolic Fe-S cluster assembly machinery (CIA) have also been identified: this 100 pathway is important for the generation of cytosolic, but also of nuclear Fe-S proteins, and is highly dependent 101 102 on the ISC mitochondrial pathway for providing a sulfur-containing precursor [24]. 103

104

105 Like in plants and algae, apicoplast-containing Apicomplexa seem to harbour the three (ISC, SUF and CIA) Fe-S 106 cluster synthesis pathways. Although the CIA pathway was recently shown to be important for Toxoplasma 107 fitness [25], investigations in apicomplexan parasites have been so far almost exclusively focused on the 108 apicoplast-located SUF pathway [26–30] and mostly in Plasmodium species. The SUF pathway was shown to be 109 essential for the viability of malaria parasites during both the erythrocytic and sexual stages of development, 110 and has thus been recognized as a putative avenue for discovering new antiparasitic drug targets (reviewed in 111 [31]). Contrarily to the ISC pathway, which is also present in the mammalian hosts of apicomplexan parasites, 112 the SUF pathwaymay indeed yield interesting specificities that may be leveraged for therapeutic intervention. 113 However, very little is known about Fe-S clusters synthesis in other apicomplexan parasites, including T. gondii. 114 For instance, out of the four known metabolic pathways hosted by the apicoplast, Fe-S synthesis was the only 115 one remaining to be functionally investigated in T. gondii, while the others were all shown to be essential for 116 the tachyzoite stage of the parasite (a fast replicating developmental stage responsible for the symptoms of 117 the disease) [32–35]. Here, we present the characterization of two T. gondii mutants we generated to 118 specifically impact the plastidic and mitochondrial SUF and ISC pathways, respectively. Our goal was to assess 119 the relative contributions of these compartmentalized pathways to parasite development and fitness. 120

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Results

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TgNFS2 and TgISU1 are functional homologs of components of the Fe-S cluster synthesis pathways 125

Fe-S cluster biosynthesis pathways in the mitochondrion and the plastid follow a similar general pattern: 126 cysteine desulfurases (NFS1, NFS2) produce sulfur from L-cysteine, scaffold proteins (ISU1, SufB/C/D) provide a 127 molecular platform allowing iron and sulfur to meet and form a cluster, and finally carrier proteins (like IscA 128 or SufA) deliver the cluster to target apoproteins [23]. The cytosolic CIA pathway, which is responsible for the 129 de novo formation of Fe-S clusters to be incorporated in cytosolic and nuclear proteins, is dependent on the 130 ISC pathway, as its first step requires the import of a yet unknown sulfur-containing precursor that is 131 translocated to the cytosol from the mitochondrion [24]. To get a general overview of the predicted 132 components for the Fe-S cluster machinery in T. gondii, we conducted homology searches in the ToxoDB.org 133 database [36], using well-characterized proteins from plants (Arabidopsis thaliana) belonging to the SUF, ISC 134 and CIA pathways (Table S1). Data from global mapping of protein subcellular location by hyperLOPIT spatial 135 proteomics [37] was in general in good accordance with the expected localization of the homologs 136

137 (with the noticeable exception of members of the NBP35/HCF101 ATP-binding proteins). Overall, our 138 search revealed that T. gondii appeared to have a good conservation of all the main components of 139 the three ISC, SUF and CIA Fe-S synthesis pathways (Table S1, Figure 1A). Additional information 140 available on ToxoDB.org such as scores from a CRISPR/Cas9-based genome-wide screening [38], 141 highlighted that most components of the three pathways are predicted to be important for parasite 142 fitness. This suggests several Fe-S proteins localizing to the endosymbiotic organelles, but also the 143 cytosol/nucleus, are essential for the optimal growth of tachyzoites. In order to verify this, our aim 144 was to specifically interfere with the apicoplast-localized SUF pathway or the mitochondrion-145 localized ISC pathway in T. gondii tachyzoites. More precisely, we wanted to target the homologs of 146 A. thaliana NFS2 and ISU1, which are both central (and presumably essential) to their respective 147 pathways (Figure 1A): NFS2 is a cysteine desulfurase that provides the inorganic sulfur part of 148 plastidic Fe-S clusters, while ISU1 is a scaffold protein important for cluster assembly in the 149 mitochondrial pathway. Interfering with these key players of the upstream machinery would likely 150 lead to a comparable disruption of the respective Fe-S cluster biogenesis pathways hosted by each 151 organelle [39]. 152 As a first step, we sought to determine whether TgNFS2 (TGGT1 216170) and TgISU1 153 (TGGT1 237560) were real functional homologs by performing complementation assays of bacterial 154 mutants. In many bacteria, the ISC machinery is the primary system for general Fe-S cluster 155 biosynthesis, while the SUF system plays a similar general role, but is mostly operative under stress 156 conditions (like iron limitation or oxidative stress). In Escherichia coli, both pathways are partially 157 redundant, but their individual disruption results in slowed bacterial growth, especially when limiting 158 iron availability with a specific chelator [40]. Expression of the predicted functional domains of 159 TgNFS2 and TgISU1 in mutant strains for the corresponding E. coli proteins (named SUFS and ISCU, 160 respectively) improved bacterial growth, in the presence of an iron chelator or not (Figure 1B). The 161 complementation seemed partial as complemented strains remained more sensitive to the iron 162 chelator than the wild-type strain. Yet, and although stationary phase was reached earlier than for 163 the wild-type bacteria, contrarily to the mutants the complemented strains showed a bacterial 164 density close to that of the WT at stationary phase. This suggests TgNFS2 and TgISU1, in addition to a 165 good sequence homology with their bacterial homologues (Figure S1), have a conserved function. 166 We next determined the sub-cellular localizations of TgNFS2 and TgISU1 by epitope tagging of the 167 native proteins. This was achieved in the TATi ΔKu80 cell line, which favors homologous 168 recombination and would allow transactivation of a Tet operator-modified promoter we would later 169 use for generating a conditional mutant in this background [41–43]. A sequence coding for a C-170 terminal triple hemagglutinin (HA) epitope tag was inserted at the endogenous TgNFS2 or TgISU1

- 171 locus by homologous recombination (Figure S2). Using the anti-HA antibody, by immunoblot we
- detected two products for each protein (Figure 2A, B), likely corresponding to their immature and
- 173 mature forms (ie after cleavage of the transit peptide upon import into the organelle). Accordingly,
- 174 the analysis of TgNFS2 and TgISU1 sequences with several subcellular localization and N-terminal
- 175 sorting signals site predictors confirmed they likely contained sequences for plastidic and
- 176 mitochondrial targeting [44], respectively, although no consensus position of the exact cleavage sites
- could be determined. Immunofluorescence assay (IFA) in T. gondii tachyzoites confirmed HA-tagged
   TgNFS2 and TgISU1 co-localize with markers of the apicoplast and the mitochondrion, respectively
- 179 (Figure 2C, D).
- NFS2 is a cysteine desulfurase whose activity is enhanced by an interaction with the SUFE protein
  [45]. Similar to plants that express several SUFE homologues [46], there are two putative SUFE-like
- 182 proteins in T. gondii (Table S1), one of which was already predicted to reside in the apicoplast by

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183 hyperLOPIT (TgSUFE1, TGGT1\_239320). We generated a cell line expressing an HA-tagged version of

the other, TgSUFE2 (TGGT1\_277010, Figure S3A, B, C), whose localization was previously unknown.

185 Like for TgNFS2, several programs predicted a plastidic transit peptide, which was confirmed by

186 immunoblot analysis (detecting TgSUFE2 immature and mature forms, Figure S3D). IFA showed

187 TgSUFE2 co-localizes with an apicoplast marker (Figure S3E). This further confirms that the initial

188 steps of Fe-S cluster biogenesis in the apicoplast are likely functionally-conserved.

189

190 Disruption of either the plastidic or the mitochondrial Fe-S cluster pathway has a profound impact191 on parasite growth

192 In order to get insights into plastidic and mitochondrial Fe-S biogenesis, we generated conditional

193 mutant cell lines in the TgNFS2-HA or TgISU1-HA-expressing TATi ΔKu80 background [43].

194 Replacement of the endogenous promoters by an inducible-Tet07SAG4 promoter, through a single

195 homologous recombination at the loci of interest (Figure S4), yielded TgNFS2 and TgISU1 conditional

196 knock-down cell lines (cKD TgNFS2-HA and cKD TgISU1-HA, respectively). In these cell lines, the

addition of anhydrotetracycline (ATc) can repress transcription through a Tet-Off system [47]. For
 each cKD cell line several transgenic clones were obtained and were found to behave similarly in th

198 each cKD cell line several transgenic clones were obtained and were found to behave similarly in the

initial phenotypic assays we performed, so only one was analysed further. Transgenic parasites weregrown for various periods of time in presence of ATc, and protein down-regulation was evaluated.

201 Immunoblot and IFA analyses of cKD further -HA and cKD TgISU1-HA parasites showed that the

addition of ATc efficiently down-regulated the expression of TgNFS2 (Figure 3A, C) and TgISU1

203 (Figure 3B, D), and most of the proteins were undetectable after two days of incubation.

We also generated complemented cell lines expressing constitutively an additional copy of TgNFS2 and TgISU1 from the uracil phosphoribosyltransferase (UPRT) locus from a tubulin promoter in their respective conditional mutant backgrounds (Figure S5A, B). We confirmed by semi-quantitative RT-PCR (Figure S5C) that the transcription of TgNFS2 and TgISU1 qenes was effectively repressed in the cKD cell lines upon addition of ATc, whereas the corresponding complemented cell lines exhibited a high transcription level regardless of ATc addition (due to the expression from the strong tubulin promoter).

211 We next evaluated the consequences of TgNFS2 and TgISU1 depletion on T. gondii growth in vitro. 212 First, to assess the impact on the parasite lytic cycle, the capacity of the mutants and complemented 213 parasites to produce lysis plaques was analyzed on a host cells monolayer in absence or continuous 214 presence of ATc for 7 days (Figure 4A, B). Depletion of both proteins completely prevented plaque 215 formation, which was restored in the complemented cell lines. To assess whether this defect in the 216 lytic cycle is due to a replication problem, all cell lines were preincubated in absence or presence of 217 ATc for 48 hours and released mechanically, before infecting new host cells and growing them for an 218 additional 24 hours in ATc prior to parasite counting. We noted that incubation with ATc led to an 219 accumulation of vacuoles with fewer parasites, yet that was not the case in the complemented cell 220 lines (Figure 4C, D). Overall, these data show that either TgNFS2 or TgISU1 depletion impacts parasite 221 growth.

222 Then, we sought to assess if the viability of the mutant parasites was irreversibly affected. We thus

223 performed another series of plaque assays, but at the end of the 7-day incubation, we washed out

the ATc, incubated the parasites for an extra 7 days in the absence of ATc and evaluated plaque

formation (Figure 4E). In these conditions, cKD TgNFS2-HA parasites displayed very small plaques

226 suggesting their viability was irreversibly impacted. In contrast, cKD TgISU1-HA parasites showed

227 plaques, suggesting parasite growth had at least partly resumed after ATc washout, while host cell

lysis remained limited if the drug was kept continuously during the same period of time. This
 suggests that although depletion of TgISU1 has a marked impact on parasite growth, it is not
 completely lethal.

231 We performed IFAs to assess possible morphological defects that may explain the impaired growths 232 of cKD TgNFS2-HA and cKD TgISU1-HA parasites. We stained the apicoplast and mitochondrion of 233 parasites kept in the continuous presence of ATc for several days. cKD TgNFS2-HA parasites managed 234 to grow and egress after three days and were seeded onto new host cells, where there were kept for 235 two more days in the presence of ATc. During this second phase of intracellular development, and in 236 accordance with the replication assays (Figure 4C), growth was slowed down considerably. Strikingly, 237 while the mitochondrial network seemed normal, we noticed a progressive loss of the apicoplast 238 marker TgCPN60 (Figure 5A), which was quantified (Figure 5B). As this could reflect a specific impact 239 on this protein marker rather than a loss of the organelle, we also stained the parasites with 240 fluorescent streptavidin, which mainly detects the biotinylated apicoplast protein acetyl-CoA 241 carboxylase [48], confirming a similar loss of signal (Figure S6). This suggests there is a general impact 242 of TgNFS2 depletion on the organelle. The growth kinetics we observed for this mutant are 243 consistent with the "delayed death" effect observed in apicoplast-defective parasites [6,49,50]. On 244 the other hand, we were able to grow cKD TgISU1-HA parasites for five days of continuous culture: 245 they developed large vacuoles and showed little sign of egress from the host cells (Figure 5C). Both 246 the mitochondrion and the apicoplast appeared otherwise normal morphologically. These large 247 vacuoles could reflect a defect in the parasite egress stage of the lytic cycle [51]. We thus performed 248 an egress assay on cKD TgISU1-HA parasites that were kept for up to five days in the presence of ATc, 249 and they were able to egress normally upon addition of a calcium ionophore (Figure 5D). These large 250 vacuoles are also reminiscent of cyst-like structures [52], so alternatively this may reflect 251 spontaneous stage conversion. Cysts are intracellular structures that contain the slow-growing form 252 of T. gondii, called the bradyzoite stage (which is responsible for the chronic phase of the disease), 253 and they may appear even during in vitro growth in particular stress conditions [53]. Yet, this mutant 254 cell line was generated in a type IT. gondii strain, which is associated with acute toxoplasmosis in the 255 mouse model [54], and typically does not spontaneously form cysts. So, to be confirmed this 256 hypothesis needed further investigations, as we will see later in the manuscript.

In any case, our data show that interfering with the plastidic and mitochondrial Fe-S protein
pathways both had important consequences on parasite growth, but had a markedly different impact
at a cellular level.

260

261 Use of label-free quantitative proteomics to identify pathways affected by TgNFS2 or TgISU1262 depletion

263 There is a wide variety of eukaryotic cellular processes that are depending on Fe-S cluster proteins.

264 To get an overview of the potential T. gondii Fe-S proteome, we used a computational tool able to

265 predict metal-binding sites in protein sequences [55], and performed subsequent manual curation to

refine the annotation. We identified 64 proteins encompassing various cellular functions or

metabolic pathways that included, beyond the Fe-S synthesis machinery itself, several DNA and RNA
 polymerases, proteins involved in redox control and electron transfer, and radical S-

269 adenosylmethionine (SAM) enzymes involved in methylation and methylthiolation (Table S2).

270 HyperLOPIT data or manual curation helped us assign a putative localization for these candidates. A

271 considerable proportion (19%) of these were predicted to localize to the nucleus, where many

272 eukaryotic Fe-S proteins are known to be involved in DNA replication and repair [56]. Yet, strikingly,

273 most of the predicted Fe-S proteins likely localize to the endosymbiotic organelles. Several (19%) are 274 predicted to be apicoplast-resident proteins, including radical SAM enzymes lipoate synthase (LipA) 275 [57] and MiaB, a tRNA modification enzyme [58], as well as the IspG and IspH oxidoreductases of the 276 non-mevalonate isoprenoid pathway [59]. Finally, for the most part (43%), candidate Fe-S proteins 277 were predicted to be mitochondrial, with noticeably several important proteins of the respiratory 278 chain (SDHB, the Fe-S subunit of the succinate dehydrogenase complex, Rieske protein and 279 TgApiCox13) [60–62], but also enzymes involved in other metabolic pathways such as heme or 280 molybdopterin synthesis. CRISPR/Cas9 fitness scores [38] confirmed many of these putative Fe-S 281 proteins likely support essential functions for parasite growth.

282 We sought to confirm these results experimentally. Thus, in order to uncover the pathways primarily 283 affected by the depletion of TgISU1 and TgNFS2, and to identify potential Fe-S protein targets, we 284 conducted global label-free quantitative proteomic analyses. Like most plastidic or mitochondrial 285 proteins, candidate Fe-S acceptors residing in these organelles are nuclear-encoded and thus need to 286 be imported after translation and have to be unfolded to reach the stroma of the organelle. This not 287 only implies the addition of the Fe-S cofactor should happen locally in the organelle, but also that this 288 may have a role in proper folding of these proteins. We thus assumed that disrupting a specific 289 pathway may have a direct effect on the stability and expression levels of local Fe-S proteins. Cellular 290 downstream pathways or functions may also be affected, while other pathways may be upregulated 291 in compensation. Parasites were treated for two days with ATc (TgISU1-HA) or three days (cKD TgNFS2-HA, as it takes slightly longer to be depleted, Figure 3A), prior to a global proteomic analysis 292 293 comparing protein expression with the ATc-treated TATi ΔKu80 control. For each mutant, we 294 selected candidates with a log2(fold change) ≤-0.55 or ≥0.55 (corresponding to a ~1.47-fold change in 295 decreased or increased expression) and a p-value <0.05 (ANOVA, n=4 biological replicates) (Tables S3 296 and S4, Figure 6A, B). To get a more exhaustive overview of proteins whose amounts varied 297 drastically, we completed this dataset by selecting some candidates that were consistently and 298 specifically absent from the mutant cell lines or only expressed in these (Tables S3 and S4).

299 Overall, depletion of TgISU1 led to a higher variability in protein expression and while the pattern of 300 expression was essentially specific for the respective mutants, a number of shared variant proteins 301 were found (Figure 6C, Table S5). For instance, common lower expressed candidates include a SAM 302 synthase, possibly reflecting a general perturbation of SAM biosynthesis upon loss of function of Fe-303 S-containing radical SAM enzymes [63]. Using dedicated expression data [64,65] available on 304 ToxoDB.org we realized that, strikingly, many of the common variant proteins were stage-specific 305 proteins (Table S5). For instance, the protein whose expression went down the most is SAG-related 306 sequence (SRS) 19F. The SRS family contains GPI-anchored surface antigens related to SAG1, the first 307 characterized T. gondii surface antigen, and whose expression is largely stage-specific [66]. This 308 protein, SRS19F, may be most highly expressed in stages present in the definitive host [65,67]. 309 Conversely, SRS44, also known as CST1 and one of the earliest marker of stage conversion to 310 bradyzoites [68], was upregulated in both mutants. Several other bradyzoite proteins whose 311 expression increased included Ank1, a tetratricopeptide-repeat protein highly upregulated in the 312 cyst-stages but not necessary for stage conversion [69], aspartyl protease ASP1, an α-galactosidase, 313 as well as several dense granule proteins (GRA). Dense granules are specialized organelles that 314 secrete GRA proteins that are known to participate in nutrient acquisition, immune evasion, and host 315 cell-cycle manipulation. Many GRA have been characterized in the tachyzoite stage, but several are 316 stage-specific and expressed in bradyzoites [70]. It should be noted that bradyzoite-specific proteins 317 were generally much strongly expressed upon TgISU1 depletion than TgNFS2 depletion. 318 Nevertheless, altogether these results show that altering either the plastidic or the mitochondrial Fe-

- 319 S cluster synthesis pathway led to an initial activation of the expression of some markers of the
- 320 bradyzoite stage, whose involvement in the stress-mediated response is well documented [53].

321

322 Depletion of TgNFS2 has an impact on the apicoplast, but also beyond the organelle

323 We next focused on proteins that varied specifically upon depletion of TgNFS2 (Table S3). Using the 324 hyperLOPIT data available on ToxoDB.org, we assessed the putative localization of the candidates 325 (Figure 6D, Figure S7A) and we also defined putative functional classes based on manual curation (Figure 6A, Figure S7B). Surprisingly, few apicoplast proteins were impacted. This could reflect a 326 327 limited impact on apicoplast Fe-S apoproteins, but this is in contradiction with the late, yet 328 pronounced, effect we see on the organelle in the absence of TgNFS2 (Figure 5A, B). There might also 329 be a bias due to an overall low protein abundance: less than half of the apicoplast candidates of the 330 predicted Fe-S proteome (Table S2) were robustly detected even in the control for instance, including 331 our target protein TgNFS2. Finally, of course it is possible that depletion of Fe-S clusters, while 332 impacting the functionality of target proteins, did not have a considerable effect on their abundance. 333 We sought to verify this for apicoplast stroma-localized LipA, a well-established and evolutionarily-334 conserved Fe-S cluster protein, which was found to be only marginally less expressed in our analysis 335 (Table S3). LipA is responsible for the lipoylation of a single apicoplast target protein, the E2 subunit 336 of the pyruvate dehydrogenase (PDH) [32]. Using an anti-lipoic acid antibody on cKD TgNFS2-HA 337 protein extracts, we could already see a marked decrease in lipoylated PDH-E2 after only one day of 338 ATc incubation (Figure 7A). This was not due to a general demise of the apicoplast as it considerably 339 earlier than the observed loss of the organelle (Figure 5A, B), and levels of the CPN60 apicoplast 340 marker were clearly not as markedly impacted (Figure 7A). This is also unlikely to reflect a general 341 decrease of TgPDH-E2 levels upon TgNFS2 knock-down, as our quantitative proteomics data, which 342 was performed after 3 days of ATc incubation, show the same amount of unique peptides for TgPDH-343 E2 ( $32 \pm 2.5$  for the control and  $32.25 \pm 2.75$  for the mutant, ~60% of sequence coverage). This 344 finding suggests apicoplast Fe-S-dependent activities may be specifically affected in our mutant, 345 which would happen before observing the general demise and loss of the organelle. Long term 346 incubation of cKD TgNFS2-HA parasites with ATc and co-staining with apicoplast and inner membrane 347 complex (IMC) markers, revealed general cell division defects, including organelle segregation 348 problems and an abnormal membranous structures (Figure 7B). Overall, this suggests impacting the 349 Fe-S cluster synthesis pathway in the apicoplast had important metabolic consequences beyond the 350 organelle itself.

351

352 Depletion of TgISU1 impacts the mitochondrial respiratory chain

353 We also analyzed the proteins whose abundance changed upon TgISU1 depletion (Table S4). Again, 354 we used hyperLOPIT data to determine the localization of variant proteins (Figure 6E, Figure S8A) and we also inferred their potential function from GO terms or manual curation (Figure 6B, Figure S8B). 355 356 Depletion of TgISU1 had a notable impact locally, as numerous mitochondrial proteins were found in 357 lower abundance. Remarkably, most of these proteins were identified as members of the 358 mitochondrial respiratory chain: while our proteomic study detected peptides corresponding to as 359 much as 92% of the hyperLOPIT-predicted mitochondrial membrane and soluble proteins, 12% of 360 these were found to be significantly less expressed upon TgISU1 depletion, 60% of which are known 361 mitochondrial ETC components (Figure 6A, Figure 8A, Table S4). This suggests a specific effect of 362 TgISU1 depletion on the mitochondrial ETC. This ETC comprises four complexes in Apicomplexa 363 (which typically lack complex I), in which several Fe-S proteins have important function. As

364 mentioned earlier, they include the Fe-S subunit of the succinate dehydrogenase complex (SDHB, 365 part of complex II), the Rieske protein (part of complex III) and TgApiCox13 (part of complex IV) [60-366 62]. Not only these three Fe-S cluster proteins were found to be less expressed upon TgISU1 367 depletion, but about 60% and 80% of complexes III and IV components (including recently 368 characterized parasite-specific subunits [61,62]), respectively, were also significantly less abundant 369 (Table S4, Figure 8A). The impact on components of complexes III and IV beyond their respective Fe-370 S-dependent subunits is not surprising: as shown by others in T. gondii depletion of selected members of a mitochondrial ETC complex can result in stalled assembly or impaired stability of the 371 372 whole complex [60-62,71].

373 We sought to verify the impact of TgISU1 depletion on proteins of the mitochondrial respiratory 374 chain by tagging two candidates, TgSDHB and TgApiCox13. In order to do this, due to the lack of 375 efficient selectable marker in the cKD TgISU1-HA cell line, we first had to generate a new 376 independent cKD TgISU1 untagged mutant from the TATi ΔKu80 cell line (Figure S9A, B). In this cell 377 line, we verified proper regulation of TgISU1 expression by ATc (Figure S9C) and impact of TgISU1 378 depletion on parasite growth (Figure S9D). In this cKD TgISU1 mutant, a sequence coding for a C-379 terminal triple HA epitope tag was inserted at the endogenous TgSDHB or TgApiCox13 locus by 380 homologous recombination (Figure S10). We then incubated these parasites with ATc for three days 381 and used an anti-HA antibody to detect and quantify the proteins of interest by IFA (Figure 8B) and 382 immunoblot (Figure 8C). In accordance with the quantitative proteomics data, both TgSDHB and 383 TgApiCox13 were found to be less expressed in absence of TgISU1.

384 This suggested the mitochondrial membrane potential and consequently the respiratory capacity of 385 the mitochondrion were likely altered in the absence of a functional mitochondrial Fe-S cluster 386 synthesis pathway. To verify this, we performed flow cytometry quantification using JC-1, a 387 monomeric green fluorescent carbocyanine dye that accumulates as a red fluorescent aggregates in 388 mitochondria depending on their membrane potential (Figure 8D). Depletion of TgISU1 led to a 389 marked decrease of the parasite population displaying a strong red signal (Figure 8D). The effect was 390 maximal after two days of ATc treatment and not further increased by a four-day treatment, which is 391 consistent with the quantitative proteomics data already showing strong impact on proteins from 392 complexes II, III and IV after only two days of ATc treatment. It should be noted that although we 393 believe the drop in mitochondrial membrane potential is likely due to a specific alteration of the 394 respiratory chain, it may also be due to a loss of parasite viability. Reassuringly, our results are in line 395 with the recent findings obtained by Aw et al., who generated a mutant of mitochondrial Fe-S cluster 396 synthesis (by depleting TgNFS1), and observed a sharp decrease in TgSDHB abundance and a clear 397 drop in mitochondrial  $O_2$  consumption rate [25].

398 Concomitantly to the lesser expression of mitochondrial respiratory chain subunits, the proteomics 399 analysis revealed TgISU1 depletion induced a significant increase in cytosolic enzymes involved in 400 glycolysis, as well as its branching off pentose phosphate pathway (Figure 8A, B, Table S4). The 401 upregulation of glycolytic enzymes potentially reflects a metabolic compensation for mitochondrial 402 defects in energy production due to the impairment of the respiratory chain. Other proteins whose 403 abundance was markedly decreased were predicted to be cytoplasmic or nuclear, including proteins 404 involved in DNA repair and replication (Table S4), which is perhaps unsurprising as the cytosolic CIA 405 Fe-S cluster assembly pathway is supposedly dependent from the ISC pathway [24]. Finally, the 406 changes in abundance of several RNA-binding proteins involved in mRNA half-life or 407 transcription/translation regulation may also reflect adaptation to a stress (Table S4).

408

## 409 Depletion of TgISU1 initiates conversion into bradyzoites

410 Another feature highlighted by the quantitative proteomics analysis of the TgISU1 mutant is indeed 411 the change in the expression of stage-specific proteins (Table S4). The expression of several 412 bradyzoite-specific proteins including GRAs and proteins of the SRS family, was strongly increased. At 413 the same time, some tachyzoite-specific SRS and GRA proteins were found to be less expressed. This 414 was supporting the idea that intracellularly developing parasites lacking TgISU1 may convert into 415 bona fide cyst-contained bradyzoites, as suggested by our initial morphological observations (Figure 416 5C). To verify this experimentally, we used a lectin from the plant Dolichos biflorus (DBL), which 417 recognizes the SRS44/CST1 glycoprotein that is exported to the nascent wall of differentiating cysts 418 [68]. We could see that during continuous growth of cKD TgISU1-HA parasites in the presence of ATc, 419 there was an increasing number of DBL-positive structures (Figure 9A). This was quantified during the 420 first 48 hours of intracellular development (Figure 9B) and, interestingly, was shown to mimic the 421 differentiation induced by nitric oxide, a known factor of stage conversion [72], and a potent 422 damaging agent of Fe-S clusters [73]. We combined RNAseq expression data for tachyzoite and 423 bradyzoite stages [65] to establish a hierarchical clustering of the SRS proteins detected in our 424 quantitative proteomics experiments for the two mutants (Figure 9C). This clearly confirmed a strong 425 increase in the expression of bradyzoite-specific SRS in the TgISU1 mutant. As mentioned earlier, 426 some were also upregulated in the TgNFS2 mutant but in much lesser proportions. The strongest 427 increase in bradyzoite-specific SRS expression upon TgNFS2 depletion was for SRS44/CST1, which 428 happens to be the protein DBL preferentially binds to [68]. However, contrarily to the TgISU1 mutant, 429 labelling experiments did not indicate any detectable increase in DBL recruitment in the TgNFS2 430 mutant (Figure 9B), confirming that impairing the plastidic Fe-S center synthesis pathway does not 431 trigger full stage conversion.

432 Stage conversion is a progressive process that happens over the course of several days, as it involves 433 the expression of distinct transcriptomes and proteomes [53]. Markers for specific steps of in vitro 434 cyst formation had been previously described [74], so we have used several of these to check the 435 kinetics of stage conversion in the TgISU1-depleted parasites. We kept the cKD TgISU1-HA parasites 436 for up to 14 days in the presence of ATc and tested for the presence of SAG1 (tachyzoite maker), DBL 437 (early bradyzoite marker), P18/SAG4 (intermediate bradyzoite marker) and P21 (late bradyzoite 438 marker) (Figure 9D). After 7 days of ATc treatment, the DBL-positive cyst contained parasites that 439 were still expressing SAG1 and not yet SAG4, whereas after 14 days parasites with SAG4 labelling 440 were found, but there was still a residual SAG1 expression; expression of late marker P21 was, 441 however, never detected. This suggests stage conversion of these parasites progresses beyond the 442 appearance of early cyst wall markers, but not only it does so with slow kinetics, but it seems 443 incomplete. In fact, observation of DBL-positive cysts showed a marked decrease in their mean size 444 between the 7 and 14 days timepoints (Figure 9D). This suggests incomplete conversion may be 445 leading to subsequent reactivation/reinvasion events. The smaller cyst size may also suggest a lack of 446 fitness in the long term for TgISU1-depleted parasites.

447

Lack of lethality and initiation of stage conversion are features shared by other mitochondrialmutants

450 As impairment of the mitochondrial ETC and stage conversion are the two main features observed

451 for the TgISU1 mutant, it raised the possibility the former may be involved in triggering the latter. We

452 thus sought to evaluate in more details viability and differentiation of other mitochondrial mutants.

453 We used the ATc-regulatable cKD cell line for TgQCR11 [62], a complex III subunit found less

abundant in absence of TgISU1 (Figure 8A), and which was found by others to be essential for
mitochondrial respiration and parasite growth [61,62]. We also included in our study an ATcregulatable cKD cell line for TgmS35, a mitoribosomal protein whose depletion impacts organelle

457 morphology and function (including mitochondrial respiration), and overall parasite fitness [75].

458 Like for TgISU1 (Figure 4E), we assessed whether or not the fitness phenotype of these mutants was 459 reversible by performing plaque assays in the presence of ATc for 7 days, and then monitored plaque 460 formation for another 7 days upon drug removal (Figure 10A). The TgQCR11 mutant behaved very 461 similarly to the TgISU1 mutant, with virtually no plaques formed when incubated with ATc, while it 462 was able to reactivate the lytic cycle upon ATc washout. The TgmS35 mutant seemed less affected by 463 protein depletion: not only it generated small plaques after 7 days in the presence of ATc, but 464 whether or not the drug was washed out, prolonged incubation led to large lysis plaques in the host 465 cells. Overall, this experiment showed that mitochondrial mutants, whether they are affected in a 466 metabolic or more structural function, remain essentially viable. The similarity between the TgISU1 467 and the TgQCR11 mutant suggested the latter may be switching to a slow-growing but still viable 468 bradyzoite stage. The slowed-down, but less hampered progression through the lytic cycle of the 469 TgmS35 mutant suggested it might retain more tachyzoite-like growth kinetics.

470 To investigate the ability of these mutants to form cysts, we performed IFAs with specific bradyzoite 471 markers, like we did previously for the cKd TgISU1-HA cell line (Figure 9A, B). We first looked for the 472 recruitment of DBL to parasite-containing vacuoles during the first 48 hours of protein depletion, 473 (Figure 10B, C). As a control, we also treated TATi ΔKu80 parasites with atovaguone, an inhibitor of 474 the mitochondrial ETC that was previously shown to trigger stage conversion [76]. Interestingly, like the atovaquone-treated TATi ΔKu80 parasites and the TgISU1 mutant (Figure 9A and B), treatment of 475 476 both TgQCR11 and TgmS35 mutants with ATc seemed to trigger stage conversion, as illustrated by an 477 increase in DBL staining of vacuoles over time (Figure 10B and C). When then tried to evaluate 478 conversion over a longer period by keeping the parasites for up to 14 days in the presence of ATc 479 (Figure 10D). For the TgmS35 mutant, this was achieved by using very low doses of parasite 480 inoculum, which allowed preserving some host cells in spite of the extensive lysis caused by the 481 parasites. Like for the TgISU1 mutant, even long term parasite did not allow complete disappearance 482 of the SAG1 tachyzoite marker in the TgQCR11 and TgmS35 mutants, and staining of the late 483 bradyzoites marker P21 was not observed. However, while a few DBL-labelled cysts remained in the 484 TgmS35 culture after 14 days of ATc treatment, they very rarely showed staining with the 485 intermediate bradyzoite marker P18/SAG4. On the contrary, substantial staining was observed upon 486 long term depletion of TgQCR11, like we observed for the TgISU1 mutant.

In conclusion, our findings suggest that interfering with general function like mitochondrial
translation, or targeting more specifically the mitochondrial ETC, does not irreversibly impair parasite
viability and instead leads to an initiation of stage conversion into bradyzoites, although it may not
necessarily be complete.

491

492 Discussion

Because of their origin and metabolic importance, the two apicomplexan endosymbiotic organelles
have gathered considerable interest as potential drug targets [77,78]. It may be obvious, as for
example the plastid hosts several metabolic pathways which are not present in the mammalian hosts
of these parasites. Yet, even for conserved housekeeping functions or, in the case of the
mitochondrion early phylogenetic divergence, there may still be enough molecular differences to
allow selective chemical inhibition. In fact, several drugs used for prophylactic or curative treatments

499 against Apicomplexa-caused diseases are already targeting these organelles [79]. They are essentially 500 impacting the organellar protein synthesis by acting on the translation machinery [80], although the 501 mitochondrial ETC inhibitor atovaquone is also used to treat malaria and toxoplasmosis [81]. One 502 main difference when targeting Plasmodium and Toxoplasma by drugs is that the latter easily 503 converts into the encysted bradyzoite resistance form. It has been known for some time that 504 treatment of tachyzoites with mitochondrial inhibitors triggers stage conversion [72,76,82]. This may 505 be efficient to counteract the acute phase of toxoplasmosis, but at the same time may favour 506 persistence of the parasites in the host.

507 Here we characterized Fe-S synthesis pathways which are very similar biochemically, but are located 508 into two distinct endosymbiotic organelles, and whose inactivation has drastically different 509 consequences for parasite fitness. Fe-S clusters are ancient, ubiquitous and fundamental to many 510 cellular functions, but their synthesis by distinct biosynthetic pathways was inherited by plastids or 511 by the mitochondrion through distinct bacterial ancestors, and have thus specialized into adding 512 these cofactors to different client proteins [22]. A key function of Fe-S clusters, owing to their mid-513 range redox potential, is electron transfer and redox reactions, mainly as components the respiratory 514 and photosynthetic ETCs. They also have important functions in stabilizing proteins, redox sensing, or 515 catalysis through SAM enzymes. Several of these are not retained in Apicomplexa, whose plastid has 516 lost its photosynthetic ability for example. Nevertheless, our prediction of the T. gondii Fe-S proteins repertoire suggests many key functions associated with the apicoplast or the mitochondrion are 517 518 likely to be affected by a perturbation of Fe-S assembly (Table S2).

519 For the apicoplast, these include lipoic acid or isoprenoid synthesis. Inactivation of the apicoplast-520 located TgNFS2 had a late but marked effect on the organelle itself, as it led ultimately to a partial 521 loss of the apicoplast, which is consistent with the phenotype observed when disrupting the SUF 522 pathway in Plasmodium [26]. IspG and IspH, which are key Fe-S-dependent enzymes of the non-523 mevalonate isoprenoid synthesis pathway [59], were only found marginally less expressed in our 524 quantitative analysis after TgNFS2 depletion. However, our proteomics dataset provided indirect 525 clues that their function may be impacted. Isoprenoid synthesis is vital for T. gondii tachyzoites [33], 526 and it has implication beyond the apicoplast, as prenylated proteins or isoprenoid precursors are 527 involved in more general cellular processes including intracellular trafficking or mitochondrial 528 respiration [83]. Isoprenoids are for instance important for synthesizing ubiquinone/coenzyme Q. 529 and the single predicted mitochondrial candidate that was significantly less expressed upon TgNFS2 530 depletion is a putative UbiE/COQ5 methyltransferase, involved in synthesis of this co-factor [84]. 531 Isoprenoids are also important for dolichol-derived protein glycosylation and 532 glycosylphosphatidylinositol (GPI)-anchor biosynthesis, and interestingly the three putative rhoptry-533 localized candidates significantly less expressed in the TgNFS2 mutant (Table S3) are predicted to be 534 GPI-anchored and/or glycosylated. Overall, this might be an indication that TgNFS2 depletion impacts 535 isoprenoid synthesis in the apicoplast, which in turn would impact other metabolic pathways. 536 Impairing isoprenoid synthesis does not, however, necessarily lead to a loss of the organelle [26]. 537 There may thus be another explanation for this phenotype. Interestingly, we could show that 538 perturbing the SUF pathway, which is supposedly important for Fe-S-containing enzyme LipA, impacts the lipoylation of the E2 subunit of the apicoplast-located PDH (Figure 7A). The PDH complex 539 540 catalyzes the production of acetyl-CoA, which is the first step of the FASII system, and perturbation of 541 either the PDH or other steps of the FASII system leads to a loss of the organelle and severely impairs 542 fitness of the parasites [33,85]. Interestingly, long term depletion of TgISU1 leads to cell division

- problems, and affects membrane compartments such as the IMC (Figure 7B), which are defects
- 544 previously observed in parasites where the FASII system has been genetically- or chemically-

545 disrupted [86-88]. Our quantitative proteomic analysis shows potential compensatory mechanisms 546 may be used by the parasites in response this early perturbation of the apicoplast lipid metabolism 547 that precedes organelle loss. Tachyzoites are indeed known to be able to use exogenous lipid sources 548 to adapt metabolically [85,87] and, interestingly, upon depletion of TgNFS2 we observed a pattern of 549 overexpression for ER-located enzymes involved in the synthesis of several phospholipids and 550 ceramides (Figure 6A and D, Table S3). These lipids are usually synthesized in the ER from apicoplast-551 generated precursors, as both organelles cooperate for FA and phospholipid (PL) synthesis [89]. Yet, 552 the ER-localized PL-synthesis machinery can also use FA scavenged from the host [90]. The increased 553 expression of ER-localized lipid-related enzymes may thus reflect an increased synthesis, potentially 554 from exogenous lipid precursors, in compensation for a defect in the apicoplast-localized machinery. 555 In spite of this potential compensation mechanism, it seems the alteration of the SUF pathway in T. 556 gondii has such a profound impact that it ultimately leads to the irreversible demise of the parasites 557 (Figure 4E). It would be interesting to use recently described approaches like stable isotope labelling 558 of lipid precursors combined to lipidomic analysis [87], to investigate in the SUF pathway mutant the 559 potential changes in de novo synthesis of FA or in lipid scavenging from the host.

560 In the mitochondrion, important pathways potentially involving Fe-S proteins include the respiratory 561 ETC, the TCA cycle, as well as molybdenum and heme synthesis (Table S2). Accordingly, perhaps the 562 most obvious consequence of disrupting the ISC pathway was the profound impact on the mitochondrial respiratory capacity, as evidenced experimentally by measuring the mitochondrial 563 564 membrane potential (Figure 8D), and supported by quantitative analyses showing a clear drop in 565 expression of many respiratory complex proteins (Figure 8A, B, and C, Table S4). This is also in line 566 with the recent description of another mitochondrial Fe-S cluster synthesis mutant that showed a 567 marked alteration of its respiratory capacity [25]. Although the mitochondrion, through the TCA cycle 568 and the respiratory chain/oxidative phosphorylation, contributes to energy production in tachyzoites 569 [91], the glycolytic flux is also believed to be a major source of carbon and energy for these parasites 570 [92]. Thus, rather coherently, as highlighted by our quantitative proteomic analysis, disruption of the 571 ISC pathway led to a potential overexpression of glycolytic enzymes concurrently with the lower 572 expression of mitochondrial ETC components (Figure 6B, Table S4). The possible overexpression of 573 enzymes of the pentose phosphate pathway, which is branching off from glycolysis and is providing 574 redox equivalents and precursors for nucleotide and amino acid biosynthesis, is also potentially 575 indicative of a higher use of glucose in these conditions. The metabolic changes encountered by ISC-576 deficient parasites do not cause their rapid demise, as they are able to initiate conversion to the 577 bradyzoite stage, which has been suggested to rely essentially on glycolysis for energy production 578 [93]. Our analysis of the viability of other mitochondrial mutants confirmed results obtained by 579 others showing that the organelle, and in particular the ETC, seem important for parasite fitness 580 [61,62,75]. Yet, perhaps because of their metabolic flexibility, we have shown that mutant parasites 581 seem to retain the ability to survive as tachyzoites, or initiate a switch to bradyzoites.

582 The inactivation of the ISC pathway likely has consequences on other important cellular 583 housekeeping functions besides mitochondrial metabolism. In other eukaryotes, the ISC pathway provides a yet unknown precursor molecule as a sulfur provider for the cytosolic CIA Fe-S cluster 584 585 assembly pathway [24]. The ISC pathway thus not only governs the proper assembly of mitochondrial 586 Fe-S proteins, but also of cytoplasmic and nuclear ones. Our quantitative proteomics data suggests it 587 is also the case in T. gondii, as several putative nuclear Fe-S proteins involved in gene transcription 588 (such as DNA-dependent RNA polymerases) or DNA repair (like DNA endonulease III) were found to 589 be impacted by TgISU1 depletion. The CIA pathway has recently been shown to be important for 590 tachyzoite proliferation [25], and several of the cytoplasmic or nuclear Fe-S cluster-containing 591 proteins are likely essential for parasite viability. It is thus possible that, in spite of their conversion to

a stress-resistant form, the long-term viability of TgISU1 parasites could be affected beyond recovery.
 In vivo experiment in the mouse model may be used to assess this.

594 The transition from tachyzoite to bradyzoite is known to involve a considerable change in gene 595 expression [64,65], and it takes several days of in vitro differentiation-inducing conditions to obtain 596 mature cysts [94,95]. Quantitative proteomic analysis showed that TgISU1-depleted parasites rapidly 597 display a high expression of bradyzoite-specific surface antigens and GRA markers (Table S4, Figure 598 9C). In all the mitochondrial mutants investigated in this study, long term perturbation of the 599 organelle led to the appearance of parasite-containing structures with typical cyst-like morphology 600 (Figure 5, Figure 9, Figure 10). However, using specific antibodies against early or late bradyzoite 601 markers, the differentiating parasites never appeared to reach a fully mature bradyzoite stage 602 (Figures 9 and 10). Also, contrarily to the ETC mutants (TgQCR11 and TgISU1), the mitochondrial 603 translation mutant (TgmS35), while seemingly initiating conversion to bradyzoite, largely continued 604 to thrive with almost tachyzoite growth dynamics (Figure 10A). However, as the mitochondrion 605 encodes three proteins that are subunits of mitochondrial ETC complexes III (cytochrome b) and IV 606 (Coxl and III), this mutant should also be supposedly impacted for ETC function. This apparent 607 discrepancy might then be explained by a looser control of down-regulation of protein expression, or 608 by compensatory mechanisms that may be specifically at play in this particular mutant. It is also 609 possible that more directly targeting the ETC is a much stronger inducer of differentiation, and thus 610 different mitochondrial mutants may behave differently regarding stage conversion. Importantly, 611 one main reason potentially explaining the incomplete differentiation of these mitochondrial 612 mutants is that they were generated in a type IT. gondii strain that typically does not form cysts: 613 type I tachyzoites may upregulate specific bradyzoite genes and, according to some reports, produce 614 bradyzoite-specific proteins or cyst wall components, but they are largely incapable of forming 615 mature bradyzoite cysts [96]. This calls for further investigations, and in particular generating similar 616 mitochondrion-related mutants in more cystogenic type II parasites, which could be very insightful.

617 Our quantitative proteomics analysis shows that SUF-impaired parasites also seem to initiate an 618 upregulation of some bradyzoite markers early after TgNFS2 depletion. Yet, these parasites did not 619 display the hallmarks of bradyzoite morphology. They did not progress towards stage conversion and 620 instead they displayed considerable perturbation of the cell division process (Figure 7B), and 621 eventually died. Both the apicoplast and the mitochondrion have established a close metabolic 622 symbiosis with their host cell, so there are likely multiple mechanisms allowing these organelles to 623 communicate their status to the rest of the cell. This raises the question as to why mitochondrion, 624 but not apicoplast, dysfunction can lead to differentiation into bradyzoites. This may be due to 625 differences in the kinetics or the severity of apicoplast-related phenotypes that may not allow stage 626 conversion (which is typically a long process) to happen. Alternatively, there might be differentiation 627 signals specifically associated to the mitochondrion. In fact this organelle is increasingly seen as a 628 signalling platform, able to communicate its fitness through the release of specific metabolites, 629 reactive oxygen species, or by modulating ATP levels [97]. Interestingly, it was shown in other 630 eukaryotes that mitochondrial dysfunctions, such as altered oxidative phosphorylation, significantly 631 impair cellular proliferation, oxygen sensing or specific histone acetylation, yet without diminishing 632 cell viability and instead may lead to quiescent states [98-100]. Consequences of mitochondrial 633 dysfunction include a restricted energy supply and thus constitutes a metabolic challenge that can 634 trigger important cellular adaptations that ultimately determine eukaryotic cell fate and survival. Our 635 results suggest that this is also possibly the case for T. gondii. It is for instance quite interesting to see 636 that altering the respiratory activity of the organelle, whether it is by generating specific mutants or 637 by the use of drugs such as atovaquone, seems to lead to a similar differentiation phenotype.

638 More generally, the environmental or metabolic cues that drive specific gene expression to induce a 639 functional shift leading to conversion into bradyzoites are not fully identified. Moreover, how these 640 stimuli are integrated is also largely unknown. A high-throughput approach has allowed the recent 641 identification of a master transcriptional regulator of stage conversion [101], but how upstream 642 events are converted into cellular signals to mobilize the master regulator is still an important, yet 643 unresolved, guestion. Translational control [102] may play a role in regulating this factor in the 644 context of the integrated stress response [103]. In fact, an essential part of the eukaryotic cell stress 645 response occurs post-transcriptionally and is achieved by RNA-binding proteins [104]. Interestingly, 646 among the proteins significantly less abundant in the spontaneously-differentiating TgISU1 mutant 647 were many RNA-binding proteins. They include components of stress granules (PolyA-binding 648 protein, PUF1, Alba1 and 2, some of which are linked to stage conversion [105–107]), which are 649 potentially involved in mRNA sequestration from the translational machinery, but also two regulators 650 of the large 60S ribosomal subunit assembly, as well as the gamma subunit of the eukaryotic 651 translation initiation factor (eIF) complex 4 (known to be down-regulated in the bradyzoite stage 652 [108]). Variation in these candidates may have a considerable impact on the translational profile and 653 on the proteostasis of differentiating parasites, and how they may help regulating stage conversion 654 in this context should be investigated further. Understanding the mechanisms that either lead to 655 encystment or death of the parasites is crucial to the development of treatments against 656 toxoplasmosis. This question is key to the pathology, because long term persistence of bradyzoites 657 and their resistance to current treatments makes them a durable threat for their human hosts. 658 Comparative studies of stress-induced or spontaneously differentiating conditional mutants may 659 bring further insights on how the parasites integrate upstream stresses or dysfunctions into global 660 regulation of stage conversion.

661

### 662 Materials and methods

Parasites and cells culture. Tachyzoites of the TATi ΔKu80 T. gondii strain [43], as well as derived

transgenic parasites generated in this study, were maintained by serial passage in human foreskin

665 fibroblast (HFF, American Type Culture Collection, CRL 1634) cell monolayer grown in Dulbecco's

666 modified Eagle medium (DMEM, Gibco), supplemented with 5% decomplemented fetal bovine

serum, 2-mM L-glutamine and a cocktail of penicillin-streptomycin at 100  $\mu$ g/ml. The TgQCR11 [62]

and TgmS35 [75] conditional mutants cell lines were generously provided by the Sheiner laboratory.

669 Bioinformatic analyses. Sequence alignments were performed using the MUltiple Sequence

670 Comparison by Log-Expectation (MUSCLE) algorithm of the Geneious 6.1.8 software suite

671 (<u>http://www.geneious.com</u>). Transit peptide and localization predictions were done using IPSORT

672 (http://ipsort.hgc.jp/), Localizer 1.0.4 (http://localizer.csiro.au/), and Deeploc 1.0

673 (http://www.cbs.dtu.dk/services/DeepLoc-1.0/) algorithms.

674 The putative Fe-S proteome was predicted using the MetalPredator webserver

675 (http://metalweb.cerm.unifi.it/tools/metalpredator/) [55]. The whole complement of T. gondii

676 annotated proteins was downloaded in FASTA format from the ToxoDB database (https://toxodb.org

[36], release 45) and used for analysis in the MetalPredator webserver. Additional manual curation

678 included homology searches for known Fe-S proteins from plants (see appendix A in [109]), and

679 search for homologues in the Uniprot database (<u>https://www.uniprot.org</u>) that were annotated as

- 680 containing a Fe-S cofactor. For proteomics candidates, annotations were inferred from ToxoDB,
- 681 KEGG (<u>https://www.genome.jp/kegg/</u>)
- and the Liverpool Library of Apicomplexan Metabolic Pathways (<u>http://www.llamp.net/</u> [110]).

- 683 N-glycosylation predictions were done with the GlycoEP webserver
- 684 (http://crdd.osdd.net/raghava/glycoep/index.html). GPI anchor predictions were done with the
- 685 PredGPI (http://gpcr.biocomp.unibo.it/predgpi/) and GPI-SOM (http://gpi.unibe.ch/) webservers.
- 686 Candidate variant proteins identified by quantitative proteomics were mapped on the graphic
- 687 representation of the high-resolution spatial proteome map of T. gondii using the hyperLOPIT dataset
- 688 [37] (<u>https://proteome.shinyapps.io/toxolopittzex/</u>).

689 Heterologous expression in E. coli. Constructs for designing recombinant proteins were defined by 690 aligning TgNFS2 and TgISU1 amino acid sequences with their E. coli counterparts. For TgNFS2, a 1,438 691 bp fragment corresponding to amino acids 271-699, was amplified by polymerase chain reaction 692 (PCR) from T. gondii cDNA using primers ML4201/ML4012 (sequences of the primers used in this 693 study are found in Table S6). For TgISU1, a 393 bp fragment corresponding to amino acids 64-194, 694 was amplified by PCR from T. gondii cDNA using primers ML4204/ML4205. The fragments were 695 cloned into the pUC19 (Thermo Fisher Scientific) using the HindIII/BamHI and SphI/BamHI restriction 696 sites, respectively. E. coli mutants from the Keio collection (obtained from the The Coli Genetic Stock 697 Center at the University of Yale: stain numbers JW1670-1 for SufS, JW2513-1 for IscU), were 698 transformed with plasmids for expressing recombinant TgNFS2 and TgISU1 and selected with 699 ampicillin. For growth assays [40], overnight stationary phase cultures were adjusted to the same 700 starting OD<sub>600</sub> of 0.6 in salt-supplemented M9 minimal media containing 0.4% glucose and varying 701 amounts of the 2,2[-Bipyridyl iron chelator (Sigma-Aldrich). Parental E. coli (strain K12) were 702 included as a control. Growth was monitored through  $OD_{600}$  measurement after 7, 14 and 24 hours at 703 37°C in a shaking incubator.

- 704 Generation of HA-tagged TgNFS2, TgSUFE2 and TgISU1 cell lines. The ligation independent strategy 705 [42] was used for C-terminal hemagglutinin (HA)<sub>3</sub>-tagging of TgISU1. A fragment corresponding to the 706 3' end of TgISU1 was amplified by PCR from genomic DNA, with the Q5 DNA polymerase (New 707 England BioLabs) using primers ML4208/ML4209 and inserted in frame with the sequence coding for 708 a triple HA tag, present in the pLIC-HA<sub>3</sub>-chloramphenicol acetyltransferase (CAT) plasmid. The 709 resulting vector was linearized and 40  $\mu$ g of DNA was transfected into the TATi  $\Delta$ Ku80 cell line to 710 allow integration by single homologous recombination, and transgenic parasites of the TgISU1-HA 711 cell line were selected with chloramphenicol and cloned by serial limiting dilution. 712 For TgNFS2 and TgSUFE2, a CRISPR-based strategy was used. Using the pLIC-HA<sub>3</sub>-CAT plasmid as a
- template, a PCR was performed with the KOD DNA polymerase (Novagen) to amplify the tag and the
   resistance gene expression cassette with primers ML3978/ML3979 (TgNFS2) and ML4023/ML4162
- 715 (TgSUFE2), that also carry 30[bp homology with the 3[ end of the corresponding genes. A specific
- right single-guide RNA (sgRNA) was generated to introduce a double-stranded break at the 3[ of the
- 717 respective loci. Primers used to generate the guides were ML3948/ML3949 (TgNFS2) and
- 718 ML4160/ML4161 (TgSUFE2) and the protospacer sequences were introduced in the Cas9-expressing
- pU6-Universal plasmid (Addgene, ref #52694) [38]. Again, the TATi ΔKu80 cell line was transfected
- 720 and transgenic parasites of the TgNFS2-HA or TgSUFE2-HA cell lines were selected with
- 721 chloramphenicol and cloned by serial limiting dilution.

Generation of TgNFS2 and TgISU1 conditional knock-down and complemented cell lines. The
 conditional knock-down cell for TgNFS2 and TgISU1 were generated based on the Tet-Off system

- vising the DHFR-TetO7Sag4 plasmid [111].
- For TgISU1, a 930 bp 5' region of the gene, starting with the initiation codon, was amplified from
- 726 genomic DNA by PCR using Q5 polymerase (New England Biolabs) with primers ML4212/ML4213 and

727 cloned into the DHFR-TetO7Sag4 plasmid, downstream of the anhydrotetracycline (ATc)-inducible

728 TetO7Sag4 promoter, yielding the DHFR-TetO7Sag4-TgISU1 plasmid. The plasmid was then linearized

729 and transfected into the TgISU1-HA cell line. Transfected parasites were selected with

730 pyrimethamine and cloned by serial limiting dilution. A similar approach was used to generate an

731 independent cKD TgISU1 cell line, but starting from the TATi ΔKu80 cell line instead of the TgISU1-HA

732 cell line, to allow subsequent tagging of mitochondrial candidates.

733 For TgNFS2, a CRISPR-based strategy was used. Using the DHFR-TetO7Sag4 plasmid as a template, a 734 PCR was performed with the KOD DNA polymerase (Novagen) to amplify the promoter and the

735

resistance gene expression cassette with primers ML4154/ML4155 that also carry 30[bp homology 736

with the 5[ end of the TgNFS2 gene. A specific sgRNA was generated to introduce a double-stranded 737 break at the 5[ of the TgNFS2 locus. Primers used to generate the guide were ML4156/ML4157 and

738 the protospacer sequences were introduced in the pU6-Universal plasmid (Addgene ref#52694) [38].

739 The TgNFS2-HA cell line was transfected with the donor sequence and the Cas9/guide RNA-

740 expressing plasmid and transgenic parasites were selected with pyrimethamine and cloned by serial

741 limiting dilution.

742 The cKD TgNFS2-HA and cKD TgISU1-HA cell lines were complemented by the addition of an extra

743 copy of the respective genes put under the dependence of a tubulin promoter at the uracil

744 phosphoribosyltransferase (UPRT) locus. TgNFS2 (2097 bp) and TgISU1 (657 bp) whole cDNA

745 sequences were amplified by reverse transcription (RT)-PCR with primers ML4576/ML4577 and

746 ML4455/ML4456, respectively. They were then cloned downstream of the tubulin promoter

747 sequence of the pUPRT-TUB-Ty vector [43] to yield the pUPRT-TgNFS2 and pUPRT-TgISU1plasmids,

respectively. These plasmids were then linearized prior to transfection of the respective mutant cell 748

749 lines. The recombination efficiency was increased by co-transfecting with the Cas9-expressing pU6-

750 UPRT plasmids generated by integrating UPRT-specific protospacer sequences (with primers

751 ML2087/ML2088 for the 3', and primers ML3445/ML3446 for the 5') which were designed to allow a

752 double-strand break at the UPRT locus. Transgenic parasites were selected using

753 5-fluorodeoxyuridine and cloned by serial limiting dilution to yield the cKD TgNFS2-HA comp cKD 754 TgISU1-HA comp cell lines, respectively.

755 Generation of HA-tagged TgSDHB and TgApiCox13 cell lines. A CRISPR-based strategy was used.

756 Using the pLIC-HA<sub>3</sub>-CAT plasmid as a template, a PCR was performed with the KOD DNA polymerase

757 (Novagen) to amplify the tag and the resistance gene expression cassette with primers

758 ML5116/ML5117 (TgSDHB) and ML5114/ML5115 (TgApiCox13), that also carry 30[bp homology with

759 the 3[ end of the corresponding genes. A specific sgRNA was generated to introduce a double-

760 stranded break at the 3[ of the respective loci. Primers used to generate the guides were

761 ML4986/ML4987 (TgSDHB) and ML4984/ML4985 (TgApiCox13) and the protospacer sequences were

762 introduced in the Cas9-expressing pU6-Universal plasmid (Addgene, ref #52694) [38]. The cKD TgISU1

763 cell line was transfected and parasites were selected with chloramphenicol and cloned by serial 764 limiting dilution.

765 Immunoblot analysis. Protein extracts from  $10^7$  freshly egressed tachyzoites were prepared in 766 Laemmli sample buffer, separated by SDS-PAGE and transferred onto nitrocellulose membrane using 767 the BioRad Mini-Transblot system according to the manufacturer's instructions. Rat monoclonal 768 antibody (clone 3F10, Roche) was used to detect HA-tagged proteins. Other primary antibodies used 769 were rabbit anti-lipoic acid antibody (ab58724, Abcam), mouse anti-SAG1 [112], rabbit anti-CPN60 770 [113] and mouse anti-actin [114]. Protein quantification was performed by band densitometry using 771 FIJI (https://imagej.net/software/fiji/).

772 Immunofluorescence microscopy. For immunofluorescence assays (IFA), intracellular tachyzoites 773 grown on coverslips containing HFF monolayers, were either fixed for 20 min with 4% (w/v) 774 paraformaldehyde (PFA) in PBS and permeabilized for 10 min with 0.3% Triton X-100 in PBS or fixed 775 for 5 min in cold methanol (for the use of cyst-specific antibodies). Slides/coverslips were subsequently blocked with 0.1% (w/v) BSA in PBS. Primary antibodies used (at 1/1,000, unless 776 777 specified) to detect subcellular structures were rabbit anti-CPN60 [113], mouse monoclonal anti-F1-778 ATPase beta subunit (gift of P. Bradley), mouse monoclonal anti-GRA3 [115], rabbit anti-TgHSP28 779 [116], rabbit anti-GAP45 [117], mouse monoclonal anti-SAG1 [112], anti SAG4/P18 (diluted 1/200, T8 780 3B1) and anti P21 (diluted 1/200, T8 4G10) [118]. Rat monoclonal anti-HA antibody (clone 3F10, 781 Roche) was used to detect epitope-tagged proteins. Staining of DNA was performed on fixed cells by 782 incubating them for 5 min in a 1 µg/ml 4,6-diamidino-2-phenylindole (DAPI) solution. All images were 783 acquired at the Montpellier RIO imaging facility from a Zeiss AXIO Imager Z1 epifluorescence 784 microscope driven by the ZEN software v2.3 (Zeiss). Z-stack acquisition and maximal intensity 785 projection was performed to visualize larger structures such as in vitro cysts. Adjustments for 786 brightness and contrast were applied uniformly on the entire image.

787 Plaque assay. Confluent monolayers of HFFs were infected with freshly egressed parasites, which 788 were left to grow for 7[days in the absence or presence of ATc (added to a final concentration of 1 789  $\mu$ g/ml). They were then fixed with 4% v/v PFA and plaques were revealed by staining with a 0.1% 790 crystal violet solution (V5265, Sigma-Aldrich). For the washout experiments, after 7 days the culture 791 medium was removed from the wells and one gentle wash was performed with Hanks' Balanced Salt 792 Solution (HBSS), taking care not to disturb the cells; then new DMEM medium containing or not ATc 793 was added for another 7-day incubation, before termination of the experiment by PFA fixation and 794 crystal violet staining.

Egress assay. T. gondii tachyzoites were grown for 40 (without ATc) or 120 (with ATc) hours on HFF
cells with coverslips in 24-well plates. The infected host cells were incubated for 7 min at 37°C with
DMEM containing 3[μM of calcium ionophore A23187 (C7522, Sigma-Aldrich) prior to fixation with
4% PFA. Immunofluorescence assays were performed as previously described [119]: the parasites
and the parasitophorous vacuole membrane were labelled with anti-GAP45 and anti-GRA3,
respectively. The proportion of egressed and non-egressed vacuoles was calculated by counting 250
vacuoles in three independent experiments. Data are presented as mean values ± SEM.

802 Semi-quantitative RT-PCR. Total mRNAs of freshly egressed extracellular parasites from the cKD 803 TgNFS2-HA, cKD TgISU1-HA and their respective complemented cell lines, as well as cKD TgISU1 804 (incubated with or without ATc at 1.5  $\mu$ g/mL for 3 days) were extracted using Nucleospin RNA II Kit 805 (Macherey-Nagel). The cDNAs were synthesized with 450 ng of total RNA per RT-PCR reaction using 806 High-Capacity cDNA Reverse Transcription Kit (Applied Biosystems). Specific primers for TgNFS2 807 (ML4686/ML4687), TgISU1 (ML4684/ML4685) and, as a control, Tubulin  $\beta$  (ML841/ML842) or actin 808 (ML843/ML844) were used to amplify specific transcripts with the GoTag DNA polymerase 809 (Promega). PCR was performed with 21 cycles of denaturation (30 s, 95 °C), annealing (20 s, 55 °C),

810 and elongation (30 s, 72 °C).

811 Mitochondrial membrane potential measurement. Parasites grown for the indicated time with or

812 without ATc were mechanically released from their host cells, purified on a glass wool fiber column,

813 washed and adjusted to  $10^7$  parasites/ml in phenol red-free medium, and incubated in with 1.5  $\mu$ M

of the JC-1 dye (5,5',6,6'-tetrachloro-1,1',3,3'-tetraethylbenzimidazolylcarbocyanine lodide, T3168,

815 Invitrogen) for 30 min at 37°C, washed phenol red-free medium and analyzed by flow cytometry or

816 microscopy. Flow cytometry analysis was performed on a FACSAria III flow cytometer (Becton

Dickinson). An unstained control was used to define gates for analysis. 50,000 events per condition
were collected and data were analysed using the FlowJo Software.

819 Quantitative label-free mass spectrometry. Parasites of the TATi ΔKu80 and cKD TgISU1-HA cell lines 820 were grown for two days in the presence of ATc; parasites of the cKD TgNFS2-HA were grown for 821 three days in the presence of ATc. Then they were mechanically released from their host cells, 822 purified on a glass wool fiber column, washed in Hanks' Balanced Salt Solution (Gibco). Samples were 823 first normalized on parasite counts, but further adjustment was performed after parasite pellet 824 resuspension in SDS lysis buffer (50 mm Tris-HCl pH8, 10 mm EDTA pH8, 1% SDS) and protein quantification with a bicinchoninic acid assay kit (Abcam). For each condition, 20 µg of total proteins 825 826 were separated on a 12% SDS-PAGE run for 20 min at 100 V, stained with colloidal blue (Thermo 827 Fisher Scientific), and each lane was cut in three identical fractions. Trypsin digestion and mass 828 spectrometry analysis in the Q Exactive Plus mass spectrometer (Thermo Fisher Scientific) were 829 carried out as described previously [120].

830 For peptide identification and quantification, the raw files were analyzed with MaxQuant version 1.6.10.43 using default settings. The minimal peptide length was set to 6. Carbamidomethylation of 831 832 cysteine was selected as a fixed modification and oxidation of methionine, N-terminal-833 pyroglutamylation of glutamine and glutamate and acetylation (protein N terminus) as variable 834 modifications. Up to two missed cleavages were allowed. The files were searched against the T. 835 gondii proteome (March 2020 -https: //www.uniprot.org/proteomes/UP000005641-8450 entries). 836 Identified proteins were filtered according to the following criteria: at least two different trypsin 837 peptides with at least one unique peptide, an E value below 0.01 and a protein E value smaller than 838 0.01 were required. Using the above criteria, the rate of false peptide sequence assignment and false 839 protein identification were lower than 1%. Peptide ion intensity values derived from MaxQuant were 840 subjected for label-free quantitation. Unique and razor peptides were considered [121]. Statistical 841 analyses were carried out using R package software. ANOVA test with threshold of 0.05 was applied 842 to identify the significant differences in the protein abundance. Hits were retained if they were 843 quantified in at least three of the four replicates in at least one experiment. Additional candidates 844 that consistently showed absence or presence of LFQ values versus the control, and mean LFQ was 845 only considered if peptides were detected in at least three out of the four biological replicates.

846 Statistical analysis for phenotypic assays. Unless specified, values are usually expressed as means ±

standard error of the mean (SEM). Data were analysed for comparison using unpaired Student's

848 t-test with equal variance (homoscedastic) for different samples or paired Student's t-test for similar

- 849 samples before and after treatment. For comparisons with of ratios of groups of samples with a
- 850 reference set to 1, analysis of variance (ANOVA) was used.
- Data availability. All raw MS data and MaxQuant files generated have been deposited to the
- 852 ProteomeXchange Consortium via the PRIDE partner repository
- 853 (https://www.ebi.ac.uk/pride/archive) with the dataset identifier PXD023854.
- 854

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- 864
- 865 Conflict of Interests
- 866 The authors declare that they have no conflict of interest.
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- 1215 Figure legends
- 1216

# Figure 1. TgNFS2 and TgISU1 are functional homologs of components of iron-sulfur clustersynthesis pathways.

1219A) Putative Fe-S cluster synthesis pathways and associated molecular machinery in Toxoplasma. B)1220Functional complementation of bacterial mutants for IscU (top) and SufS (bottom). Growth of 'wild-1221type' (WT) E. coli K12 parental strain, bacterial mutant strains and strains complemented ('comp') by1222their respective T. gondii homologues ('comp'), was assessed by monitoring the optical density at1223600 nm in the presence or not of an iron chelator (2,2'-bipyridyl, 'chel'). Values are mean from n=31224independent experiments ±SEM. \* denotes  $p \le 0.05$ , Student's t-test.

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### 1227 Figure 2. TgNFS2 and TgISU1 localize to the apicoplast and the mitochondrion, respectively.

1228 Detection by immunoblot of C-terminally HA-tagged TgNFS2 (A) and TgISU1 (B) in parasite extracts 1229 reveals the presence of both precusor (p) and mature (m) forms of the proteins. Anti-actin (TgACT1) 1230 antibody was used as a loading control. Immunofluorescence assay shows TgNFS2 co-localizes with 1231 apicoplast marker TgCPN60 (C) and TgISU1 co-localizes with mitochondrial marker F1  $\beta$  ATPase (D). 1232 Scale bar represents 5  $\mu$ m. DNA was labelled with DAPI. DIC: differential interference contrast.

1233

# 1234 Figure 3. Efficient down-regulation of TgNFS2 and TgISU1 expression with anhydrotetracyclin (ATc).

A) Immunoblot analysis with anti-HA antibody shows efficient down-regulation of TgNFS2 after 48h
 of incubation with ATc. Anti-SAG1 antibody was used as a loading control. B) Immunoblot analysis
 with anti-HA antibody shows efficient down-regulation of TgISU1 after 24h of incubation with ATc.

1238 Anti-SAG1 antibody was used as a loading control. C) and D) Immunofluorescence assays show

1239 TgNFS2 and TgISU1 are not detectable anymore after 48h of incubation with ATc. Scale bar

1240 represents 5 µm. DNA was labelled with DAPI. DIC: differential interference contrast.

1241

1242 Figure 4. Depletion of TgNFS2 or TgISU1 affects in vitro growth of the tachyzoites. Plaque assays 1243 were carried out by infecting HFF monolayers with the TATi ΔKu80 cell line, the cKD TgNFS2-HA (A) or 1244 the cKD TgISU1-HA (B) cell lines, or parasites complemented with a wild-type version of the 1245 respective proteins. They were grown for 7 days ± ATc. Measurements of lysis plaque areas are shown on the right and highlight a significant defect in the lytic cycle when TgNFS2 (A) or TgISU1 (B) 1246 1247 were depleted. Values are means of n=3 experiments ± SEM. Mean value of TATi ΔKu80 control was set to 100% as a reference. \*\*\*\* denotes p ≤ 0.0001, Student's t-test. Scale bars= 1mm. TgNFS2 (C) 1248 1249 and TgISU1 (D) mutant and complemented cell lines, as well as their parental cell lines and the TATi 1250 ΔKu80 control, were grown in HFF in the presence or absence of ATc for 48 hours, and subsequently allowed to invade and grow in new HFF cells for an extra 24 hours in the presence of ATc. Parasites 1251 1252 per vacuole were then counted. Values are means  $\pm$  SEM from n=3 independent experiments for 1253 which 200 vacuoles were counted for each condition. E) Plaque assays for the TgNFS2 and TgISU1 1254 mutants were performed as described in A) and B), but ATc was washed out after 7 days (7 days+7 1255 days-) or not (14 days+), and parasites were left to grow for an extra 7 days. Plaque area was 1256 measured. Data are means  $\pm$  SEM from three independent experiments. \*\*\* p  $\leq$  0.001, Student's 1257 t-test. Arrowheads show plaques forming in the TgISU1 upon ATc removal. Scale bar= 1mm.

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#### 1258

#### 1259 Figure 5. Impact of TgNFS2 and TgISU1 depletion on intracellular tachyzoites.

1260 A) Depletion of TgNFS2 impacts the apicoplast. cKD TgNFS2-HA parasites were kept in the presence 1261 of ATc and the aspect of the apicoplast and mitochondrion was evaluated by microscopic observation 1262 using specific markers (CPN60 and F1ß ATPase, respectively). After 72 hours, parasites egressed and were used to reinvade new host cells for subsequent timepoints. Scale bar represents 5 µm. DNA was 1263 labelled with DAPI. DIC: differential interference contrast. B) Quantification of apicoplast loss in 1264 1265 vacuoles containing cKD TgNFS2-HA parasites after 72 to 120 hours of incubation with ATc. Data are mean values from n=3 independent experiments  $\pm$ SEM. \*\* p  $\leq$  0.01, \*\*\*\* p  $\leq$  0.0001, Student's t-test. 1266 1267 C) Depletion of TgISU1 does not impact mitochondrial and overall parasite morphologies, but affects 1268 parasite growth. cKD TgISU1-HA parasites were grown in the presence of ATc for up to five days and 1269 the aspect of the apicoplast and mitochondrion was evaluated by microscopic observation using 1270 specific markers described in A). Growth in the presence of ATc was continuous for up to five days. 1271 Scale bar represents 5 μm. DNA was labelled with DAPI. DIC: differential interference contrast. D) 1272 Egress is not affected by TgISU1depletion. An egress assay was performed using calcium ionophore 1273 A23187. On the left are representative images of vacuoles containing parasites that egressed 1274 normally or did not. GRA3 (parasitophorous vacuole marker) staining is shown in green and GAP45 (parasite periphery marker) in red. Scale bars=  $10[\mu m$ . On the right is the quantification of egress for 1275 1276 cKD TgISU1-HA parasites kept in the presence of ATc or not. Mean values ± SEM from n=3 1277 independent biological experiments are represented.

1278

1279 Figure 6. Change in protein expression induced by TgNFS2 and TgISU1 depletion. Volcano plots 1280 showing the protein expression difference based on label-free quantitative proteomic data from 1281 TgNFS2 (A) and TgISU1 (B) mutants grown in the presence of ATc. X-axis shows log2 fold change 1282 versus the TATi  $\Delta$ Ku80 control grown in the same conditions, and the Y-axis shows -log10(p value) 1283 after ANOVA statistical test for n=4 independent biological replicates. Selected variant protein 1284 categories are highlighted in color. C) Venn diagram representation of the shared and unique 1285 proteins whose expression is affected by the depletion of TgNFS2 and TgISU1. D) and E): mapping of 1286 less or more abundant candidates in the TgNFS2 and TgISU1 mutants, respectively, on the spatial 1287 proteome map representation of the hyperLOPIT data highlighting clusters denoting putative 1288 subcellular localization. Full details available at: https://proteome.shinyapps.io/toxolopittzex/.

1289

1290 Figure 7. TgNFS2 depletion impacts apicoplast-related pathways and has deleterious effects on 1291 parasite replication. A) A decrease in the lipoylation of the E2 subunit of pyruvate dehydrogenase 1292 (TgPDH-E2), which depends on the Fe-S-containing lipoyl synthase called LipA in the apicoplast, was 1293 observed by immunoblot using an anti-lipoic acid antibody on cell extracts from cKD TgNFS2-HA 1294 parasites kept with ATc for an increasing period of time. TgCPN60 was used as a control for 1295 apicoplast integrity. TgSAG1 was used as a loading control. Decrease of lipoylated TgPDH-E2 was 1296 quantified by band densitometry and normalized with the internal loading control. Data represented are mean  $\pm$ SEM of n=3 independent experiments. \*\* p  $\leq$  0.01, \*\*\* p  $\leq$  0.001 ANOVA comparison. B) 1297 1298 cKD TgNFS2-HA parasites that were grown in the presence of ATc for 5 days were co-stained with 1299 anti-TgIMC3 (to outline parasites and internal buds) and anti-CPN60 (an apicoplast marker), which 1300 highlighted abnormal membrane structures and organelle segregation problems. Scale bar 1301 represents 5  $\mu$ m. DNA was labelled with DAPI. DIC: differential interference contrast. 1302

Figure 8. TgISU1 depletion impacts the mitochondrial respiratory chain. A) Schematic
 representation of the T. gondii mitochondrial respiratory chain; listed are the subunits of the
 different complexes that were found less abundant upon TgISU1 depletion; Fe-S proteins are
 highlighted in green. SDH: succinate dehydrogenase; CoQ: coenzyme Q B) Immunofluorescence
 analysis of cKD TgISU1 parasites expressing HA-tagged TgSDHB (top) or TgApiCox13 (bottom)

showing a decrease in expression in the HA-tagged candidates after 3 days of incubation with ATc. 1308 1309 Images were taken with the same exposure time for similar channels. TgHSP29 was used as a 1310 mitochondrial marker. Scale bar represents 10 µm. DNA was labelled with DAPI. C) Immunoblot 1311 analysis of TgSDHB (top) and TgApiCox13 (bottom) levels upon depletion of TgISU1 after 3 days of 1312 incubation with ATc. TgACT1 was used as a loading control. Protein levels were quantified by band 1313 densitometry and normalized with the internal loading control. Data represented are mean ±SEM of n=5 independent experiments. \*\* p  $\leq$  0.01, \*\*\* p  $\leq$  0.001, ANOVA comparison. D) Impact of TgISU1 1314 1315 depletion on the parasite mitochondrial membrane potential was measured by JC-1 labelling. cKD 1316 TgISU1-HA parasites were grown or not in the presence of ATc, mechanically released from their host cells and labelled with the JC-1 dye. This dye exhibits potential-dependent accumulation in the 1317 1318 mitochondrion, indicated by a switch from green fluorescence for the monomeric form of the probe, 1319 to a concentration-dependent formation of red aggregates (inset, DNA is labelled with DAPI and 1320 shown in blue, scale=1µm). Parasites were then analysed by flow cytometry. Unlabelled parasites (no 1321 JC-1) was used as a control for gating. Numbers represent the percentage of cells in each of the 1322 subpopulations (P1, P2, P3). One representative experiment out of n=3 biological replicates is shown.

1323

## 1324 Figure 9. Depletion of TgISU1 triggers parasite differentiation.

1325 A) cKD TgISU1-HA parasites were grown in the presence of ATc and labelled with anti-TgIMC3 (to 1326 outline parasites) and a lectin of Dolicos biflorus (DBL) to specifically outline nascent cyst walls. Scale 1327 bar represents 10 µm. DNA was labelled with DAPI. DIC: differential interference contrast. B) 1328 Quantification of DBL-positive vacuoles after 24 hours or 48 hours of culture of 1) the cKD TgISU1-HA 1329 and cKD TgNFS2-HA mutants in the presence or absence of ATc 2) the Tati ΔKu80 cell line, as a 1330 negative control, 3) the Tati  $\Delta$ Ku80 cell line in the presence of 100 $\mu$ M nitric oxide (NO), as a positive 1331 control. Data are from n=3 independent experiments. Values are mean  $\pm$ SEM. \* p  $\leq$  0.05, \*\* p  $\leq$  0.01, 1332 Student's t-test C) Clustering of bradyzoite (Bz) or tachyzoite (Tz)-specific proteins of the SRS family 1333 shows specific enrichment of bradyzoite proteins upon TgISU1 depletion. D) The cKD TgISU1-HA 1334 mutant was grown for up to 14 days in the presence of ATc and labelled for tachyzoite marker SAG1, 1335 or intermediate (P18/SAG4) or late (P21) bradyzoite markers. Scale bar represents 10 µm. DNA was 1336 labelled with DAPI. DIC: differential interference contrast. E) Measurement of the cyst area size after 1337 growing the cKD TgISU1-HA mutant for 7 and 14 days in the presence of ATc and labelling the cyst wall with DBL and measuring the surface of 60 cysts per condition. Mean ±SD is represented. One 1338 1339 representative experiment out of three independent biological replicates is shown. \*\*\*\* denotes p ≤ 1340 0.0001, Student's t-test.

1341

1342 Figure 10. Other mitochondrial mutants remain viable and initiate stage conversion. A) Plaque 1343 assays for the TgQCR11 and TgmS35 mutants were performed by infecting HFF monolayers with cKD 1344 cell lines and letting them grow in absence (7 days -) or presence of ATc (7 days +), after 7 days ATc 1345 was washed out (7 days+7 days-) or not (14 days+), and parasites were left to grow for an extra 7 1346 days. Plaque area was measured. Data are means  $\pm$  SEM from three independent experiments. \*  $p \leq$ 0.05, \*\*  $p \le 0.01$ , \*\*\*  $p \le 0.001$ , \*\*\*\*  $p \le 0.0001$ , Student's t-test. Arrowheads show small plaques. 1347 1348 Scale bar= 1mm. B) Tati  $\Delta$ Ku80 parasites were grown in the presence of atovaquone and cKD TgQCR11 and TgmS35 parasites were grown in the presence of ATc for up to two days. They were 1349 1350 labelled with anti-TgIMC3 (to outline parasites) and Dolicos biflorus lectin (DBL) to specifically outline 1351 nascent cyst walls. Scale bar represents 10 µm. DNA was labelled with DAPI. DIC: differential 1352 interference contrast. C) Quantification of DBL-positive vacuoles after 24 hours or 48 hours of culture 1353 of 1) the cKD TgQCR11 and cKD TgmS35 mutants in the presence or absence of ATc 2) the Tati  $\Delta$ Ku80 1354 cell line in the presence or not of  $1\mu$ M atovaquone. Data are from n=3 independent experiments. Values are mean ±SEM. \*\*  $p \le 0.01$ , \*\*\*  $p \le 0.001$ , Student's t-test. D) The cKD TgQCR11 and cKD 1355 1356 TgmS35 mutants were grown for up to 14 days in the presence of ATc and labelled for tachyzoite 1357 marker SAG1, or early (P18/SAG4) or late (P21) bradyzoite markers. Scale bar represents 10 µm. DNA was labelled with DAPI. DIC: differential interference contrast. 1358 1359

1360	Sunnlemental table legends
1361	Suppemental table legends
1362 1363 1364 1365 1366	Table S1. Predicted Toxoplasma homologues of the iron-sulfur cluster synthesis machinery.Homology searches were conducted in ToxoBD.org using Arabidopsis thaliana proteins as a query.Putative subcellular localization was obtained from the hyperLOPIT data available on ToxoDB.org, orby manual annotation. CRISPR fitness score data was obtained from ToxoDB.org.
1367	Table S2. Predicted Toxoplasma iron-sulfur proteome. The Toxoplasma predicted whole proteome
1368 1369	was obtained from the ToxoDB.org database and searched for putative iron-sulfur-containing proteins with the MetalPredator web server ( <u>http://metalweb.cerm.unifi.it/tools/metalpredator/</u> ).
1370	Putative subcellular localization was obtained from the hyperLOPIT data available on ToxoDB.org, or
1371	by manual annotation. CRISPR fitness score data was obtained from ToxoDB.org.
1372	
1373	Table S3. Proteins with lower or higher expression upon depletion of TgNFS2 as found by label- free quantitative proteomics.
1374	For each protein candidate (with www.ToxoDB.org and www.Uniprot.org identifier),
1375	log <sub>2</sub> of the different ratio were calculated between the mean MaxQuant LFQ values
1376	('moyLFQ') found for the TgISU1 ('Mito') and TgNFS2 ('Apicoplast') mutants, and the TATi $\Delta$ Ku80
1377	control ('CTRL')log <sub>10</sub> (pvalue) is also provided. Putative subcellular localization was obtained from
1378	the hyperLOPIT data available on ToxoDB.org, or by manual annotation. CRISPR fitness score and
1379	transcriptomic data for tachyzoites (Tz) and bradyzoites (Bz) were obtained from ToxoDB.org.
1380	
1381	Table S4. Proteins with lower or higher expression upon depletion of TgISU1 as found by label- free quantitative proteomics.
1382	See legend of Table S3. Candidates from the Fe-S proteome (Table S2) that
1383	were found to have a lower expression upon TgISU1 depletion are highlighted in red.
1384	
1385	Table S5. Common proteins with lower or higher expression upon depletion of TgNFS2 or TgISU1,
1386	as found by label-free quantitative proteomics. See legend of Table S3.
1387	
1200	Table SC. Oliver well estides used in this study.

1388 Table S6. Oligonucleotides used in this study.





**Figure 2**: TgNFS2 and TgISU1 localize to the apicoplast and the mitochondrion, respectively.

Figure 3: Efficient down-regulation of TgNFS2 and TgISU1 expression with anhydrotetracyclin (ATc).



Figure 4: Depletion of TgNFS2 or TgISU1 affects in vitro growth of the tachyzoites .





number of vacuoles

Résultats – Chapitre I – Figures du papier

Α

cKD TgNFS2-HA \*\*\*\* 120 Merge: Apico Mito DAPI DIC Vacuoles 100no apicoplast loss with apicoplast loss 80-60. 40-20-0 72h 1201 24h cKD TgNFS2-HA ATc 72h 120h 96h С D cKD TgISU1-HA continuous culture GRA3 % 120 Merge: Apico Mito DAPI DIC 100-Vacuoles 80. egressed 60non-egressed egressed 40. GRA3 20. т 100 cKD TgISU1-HA cKD TgISU1-HA no ATc 40h + ATc 120h non-egressed 96h 120h

В

Figure 5: Impact of TgNFS2 and TgISU1 depletion on intracellular tachyzoites.

reinvasion

92



Figure 6: Change in protein expression induced by TgNFS2 and TgISU1 depletion.


Figure 7: TgNFS2 depletion impacts apicoplast-related pathways and has deleterious effects on parasite replication.

В







#### Figure 8: TgISU1 depletion impacts the mitochondrial respiratory chain.



Figure 9: Depletion of TgISU1 triggers parasite differentiation.



Figure 10: Other mitochondrial mutants remain viable and initiate stage conversion.

[		Protein name	Gene ID (A. thaliana )	Uniprot ID (A. thaliana )	Gene ID (T. gondii)	BLAST E value	Localization (HyperLOPIT)\$	CRISPR Fitness score¤	proposed function
		NFS2	AT1G08490	Q93WX6	TGGT1_216170	1,00E-105	Apicoplast	-3.95	cysteine desulfurase
		SUFE1	AT4G26500	Q84W65	TGGT1_239320	4,00E-14	Apicoplast	0.1	neroscary for NES2 activity
		SUFE2	AT1G67810	Q9FGS4	TGGT1_277010	6,00E-04	N/A	-3.31	
		SUFB	AT4G04770	Q9ZS97	TGGT1_300650	9,00E-110	N/A, apicoplast genome-encoded	N/A	part of SUFB/C/D transfer complex, encoded by the apicoplast genome
÷		SUFC	AT3G10670	Q9CAF5	TGGT1_225800	3,00E-81	Apicoplast	-5.57	part of SUFB/C/D transfer complex, ATPase
	Plastid SUF	SUFD	AT1G32500	Q9LQK7	TGGT1_273445	2,00E-21	Apicoplast	-5.29	part of SUFB/C/D transfer complex, co-factor
	pathway	NFU1	AT4G01940	Q93W77	TGGT1_221922	7,00E-22	Apicoplast/ER	-0.76	Fe.S carrier
Ĕ		SUFA/CpISCA	AT1G10500	Q9XIK3	TGGT1_297925	9,00E-25	N/A	-4.01	
20		GRXS14	AT3G54900	Q84Y95	TGGT1_247580	1,00E-21	Rhoptry	-0.07	Clutaradovins
Ľ		GRXS16	AT2G38270	Q8H7F6	TGGT1_238070	3,00E-24	Cytoplasm	-0.65	Ulutareuthins
Ī		HCF101	AT3G24430	Q6STH5	TGGT1_318590	2,00E-40	Cytoplasm	-3.24	assembly of Fe-S cluster on selected proteins , ATP dependent
^ 		Frd	AT4G14890	023344	TGGT1_215070	8,00E-35	Apicoplast	-4.35	Ferredoxin
וא		NFS1	AT5G65720	049543	TGGT1_211090	3,00E-174	Mitochondrion	-3.54	cysteine desulfurase
2		ISD11	AT5G61220	Q8L9E3	TGGT1_254800	0.006	Mitochondrion	-3.51	necessary for NFS1 activity
5		ISU1	AT4G22220	049627	TGGT1_237560	8,00E-52	Mitochondrion	-5.99	Fe-S cluster scaffold
5		FH (frataxin)	AT4G03240	Q9ZR07	TGGT1_262810	1,00E-08	Mitochondrion	-3.34	putative Fe donor , regulator of NFS1
		HSCA	AT4G37910	Q8GUM2	TGGT1_251780	0.00	Mitochondrion	-5.09	Chaperone
=		HSCB	AT5G06410	Q8L7K4	TGGT1_288685	1,00E-14	Mitochondrion	-2.92	co-chaperone
Ľ	Mitochondrion ISC	NFU4	AT3G20970	Q9LIG6	TGGT1 212930	3,00E-29	Mitochondrion	-1.03	To Counting
5	pathway	ISCA	AT2G16710	Q8LBM4	TGGT1 213810	1,00E-21	Mitochondrion	-4.52	re-s carrier
2		GRXS15	AT3G15660	Q8LBK6	TGGT1 268730	5,00E-14	Mitochondrion	-2.13	Glutaredoxin
ມ		MGE 1	AT5G55200	Q9FLP3	TGGT1_265220	3,00E-23	Mitochondrion	-5.29	co-chaperone
5					TGGT1_236000	3,00E-23	Mitochondrion	0.2	Mitochondrial ferredoxin
		MFdx1/2	AT4G05450/AT4G21090	Q9M0V0/Q8S904	TGGT1 240670	8,00E-40	Mitochondrion	-2.45	Mitochondrial ferredoxin
-		ADRX	AT4G32360	Q8W3L1	TGGT1 261030	2,00E-60	Mitochondrion	-3.66	Adrenodoxin reductase
Ĭ		ATM3	AT5G58270	Q9LVM1	TGGT1 269000	3,00E-146	Mitochondrion	-4.96	transporter of S precursor needed for cytosolic Fe-S assembly
		ATR3	AT3G02280	Q6NPS8	TGGT1 249320	4,00E-27	Mitochondrion	-3.87	reductase
2		DRE2	AT5G18400	Q8L7Z3	TGGT1 216900	8,00E-27	Cytoplasm	N/A	electron transfer
2	Cytoplasm CIA	NBP35	AT5G50960	Q8H1Q2		4,00E-96	Mitochondrion	-4.81	Fe-S custer scaffold, mitochondrial but is involved in the CIA pathway
ע	pathway	CIA1	AT2G26060	080990	 TGGT1 215740	2,00E-25	Nucleus	-4.92	
וו		AE7	AT1G68310	Q9C9G6		8,00E-21	N/A	-4.52	
וע		MET18	AT5G48120	Q6NPS8		3,00E-06	Cytoplasm	-5.39	formation of a complex and association with target Fe-S proteins
:		NAR1	AT4G16440	Q94CL6	 TGGT1 242580	9,00E-30	Mitochondrion	-4.36	
0					-		\$ inferred from (published data or	¤ fitness score data from whole genome	
							HyperLOPIT prediction -Barylyuk K et al Cell	CRISPR screen (Sidik SM et al. Cell 2016)	
-							Host & Microbe 2020-)	. ,	

chinerv 2 2 Ğ 5 -sulfu ċ iro ٩ 4 f 2 Ъ S Table

ToxoDB ID	CRISPR Fitness score ¤	Predicted location \$	Product Description	Cellular process
TGGT1_209770	-4.09	nucleus	putative helicase	DNA repair and replication
TGGT1 215550	-2.4	-	exonuclease V	DNA repair and replication
TGGT1 216870	-4.33	nucleus	DNA excision repair helicase	DNA repair and replication
TGGT1 258030	-4.45	nucleus (HyperLOPIT)	DNA polymerase	DNA repair and replication
TGGT1 264670	-0.2	nucleus	DNA polymerase	DNA repair and replication
TGGT1 297840	-4.86	nucleus	DNA primase large subunit	DNA repair and replication
TGGT1_201010	-0.96	nucleus (Hyperl OPIT)	DNA diversitiase (andenuclease-like	DNA repair and replication
TGGT1_313470	0.24	nucleus	DNA givessilas/endonuclease-like	DNA repair and replication
TCGT1_215070	4.35	anicoplast (Hyperl OPIT)	forcedoxia (ED)	Electron transfor
TGGT1_215070	-4.33	mitochondrion (HyperLOFT)	Terrodoxin (FD)	
TGGT1_230000	0.2	mitochondhon (hyperLOPT)		
1GG11_240670	-2.45	milochondrion (HyperLOPTI)		
TGGT1_265230	-2.37	mitochondrion	electron transfer flavoprotein-ubiquinone oxidoreductase	Electron transfer
TGGT1_231390	-0.08		neske [zie-zs] doman-containing potein	Mitochondhai respiratory chain
TGGT1_320220	-5.76	mitochondrion (HyperLOPIT)	putative ubiquinoi cytochrome c oxidoreductase	
1GG11_254030	-4.26	mitochondrion (HyperLOPII)	NEET family, zinc finger CDGSH-type domain-containing protein, TgApiCox13	Mitochondrial respiratory chain
TGGT1_215280	-2	mitochondrion (HyperLOPIT)	succinate dehydrogenase	Mitochondrial respiratory chain/TCA cycle
TGGT1_267330	-3.5	mitochondrion (HyperLOPIT)	fumarate hydratase	TCA cycle
TGGT1_226730	-4.73	mitochondrion (HyperLOPIT)	aconitate hydratase ACN/IRP	TCA cycle/iron sensor
TGGT1_211090	-3.54	mitochondrion (HyperLOPIT)	IscS desuphurase	Fe-S cluster biosynthesis
TGGT1_212930	-1.03	mitochondrion (HyperLOPIT)	NifU-like protein	Fe-S cluster biosynthesis
TGGT1_213810	-4.52	mitochondrion	IscA	Fe-S cluster biosynthesis
TGGT1_216170	-3.95	apicoplast (HyperLOPIT)	SufS subfamily cysteine desulfurase	Fe-S cluster biosynthesis
TGGT1_216900	-2.88	mitochondrion (HyperLOPIT)	Anamorsin/DRE2-like	Fe-S cluster biosynthesis
TGGT1_221922	-0.76	apicoplast/ER (HyperLOPIT)	NifU family domain-containing protein	Fe-S cluster biosynthesis
TGGT1 237560	-5.99	mitochondrion (HyperLOPIT)	IscU	Fe-S cluster biosynthesis
TGGT1 239320	0.1	apicoplast (HyperLOPIT)	SufE-like, BolA family protein	Fe-S cluster biosynthesis
TGGT1 242580	-4.36	mitochondrion (HyperLOPIT)	Nar1-like Fe-hydrogenase	Fe-S cluster biosynthesis
TGGT1 273445	-5.29	apicoplast (HyperLOPIT)	SufD	Fe-S cluster biosynthesis
TGGT1 280730	-4.81	mitochondrion (HyperLOPIT)	Mrp/NBP35 subfamily of P loop NTPases	Fe-S cluster biosynthesis
	-4.01	apicoplast	SufA	Fe-S cluster biosynthesis
TGGT1 300650	N/A (apicoplast-encoded)	apicoplast	SufB	Fe-S cluster biosynthesis
TGGT1_318590	-3.24	cytoplasm (HyperLOPIT)	Mrn/NBP35 subfamily of P loop NTPases_HCF101-like	Fe-S cluster biosynthesis
TGGT1_230070	2 11	cytoplasm	Rold 2 family protein	GRX-interacting/Fe-S cluster biosynthesis
TGGT1_227150	1 30	anicoplast (Hyperl OPIT)	outation glutaredoxin (GPX)	Redox reactions/Fe-S cluster biosynthesis
TGGT1_227130	-0.65	cytoplasm (HyperLOPIT)	putative glutaredoxin (GRY)	Redox reactions/Fe-S cluster biosynthesis
TGGT1_238070	-0.03		putative glutanedovin (GN)	Redox reactions/Fe-S cluster biosynthesis
TGGT1_247580	-0.07	rhoptry (HyperLOPTT)	putative glutaredoxin (GKX)	Redox reactions/Fe-S cluster biosynthesis
TGGT1_208730	-2.13		putative glutaredoxin (GRA)	Redox reactions/Fe-3 cluster biosynthesis
TGGT1_279400	1	cytoplasm (HyperLOPIT)	putative giutaredoxin (GRX)	Redox reactions/Fe-S cluster biosynthesis
1GG11_288640	2.29	mitochondrion	radical S-adenosyi-L-methionine (SAVI)-like, coproporphyrinogen denydrogenase, CPDH	Heme biosynthesis
IGG11_227420	-6.01	apicoplast (HyperLOPIT)	4-hydroxy-3-methylbut-2-enyl diphosphate reductase, IspH/LytB	Isoprenoid biosynthesis, MEP pathway
TGGT1_262430	-4.41	apicoplast (HyperLOPIT)	4-hydroxy-3-methylbut-2-en-1-yl diphosphate synthase, lspG/GcpE	Isoprenoid biosynthesis, MEP pathway
TGGT1_226400	-0.97	apicoplast (HyperLOPIT)	lipoic acid synthase LIPA	Lipoic acid synthesis
TGGT1_213780	-2.92	mitochondrion	radical S-adenosyl-L-methionine (SAM)-like, Molybdopterin cofactor synthesis protein 1, MOCS1	Molybdopterin synthesis
TGGT1_207620	-1.15	mitochondrion (HyperLOPIT)	pyridine nucleotide-disulfide oxidoreductase domain-containing protein	Oxidative stress response
TGGT1_249630	1.63	mitochondrion (HyperLOPIT)	glutathione S-transferase domain-containing protein	Oxidative stress response
TGGT1_304660	0.74	mitochondrion (HyperLOPIT)	glutathione S-transferase domain containing protein	Oxidative stress response
TGGT1_255910	1.64	mitochondrion (HyperLOPIT)	NEET family, zinc finger CDGSH-type domain-containing protein	Regulation of iron and reactive oxygen metabolism
TGGT1_260870	0.92	mitochondrion (HyperLOPIT)	NEET family, zinc finger CDGSH-type domain-containing protein	Regulation of iron and reactive oxygen metabolism
TGGT1_204540	-0.22	-	DUF367 domain-containing protein	rRNA biogenesis?
TGGT1_209790	-1.82	mitochondrion (HyperLOPIT)	radical S-adenosyl-L-methionine (SAM)-like	rRNA methytransferase
TGGT1_252465	-4.12	mitochondrion	radical S-adenosyl-L-methionine (SAM)-like	rRNA methytransferase
TGGT1_238190	-4.42	nucleus (HyperLOPIT)	DNA-directed RNA polymerase	Transcription
TGGT1_249560	-4.38	-	DNA-directed RNA polymerase	Transcription
TGGT1_261540	-3.54	nucleus (HyperLOPIT)	DNA-directed RNA polymerase	Transcription
TGGT1_267390	-5.2	nucleus (HyperLOPIT)	DNA-directed RNA polymerase	Transcription
TGGT1_313120	-4.48	-	DNA-directed RNA polymerase	Transcription
TGGT1_216790	-4.11	nucleus (HyperLOPIT)	putative ATP-binding cassette sub-family E member 1	Translation
TGGT1_261060	-1.94	-	diphthamide biosynthesis protein 2-related	Translation
TGGT1 272270	0.41	-	radical S-adenosyl-L-methionine (SAM)-like, demethylwyosine synthase	tRNA modification
TGGT1 273140	-0.23	apicoplast	radical S-adenosyl-L-methionine (SAM)-like methylthiotransferase, MiaB/RimO family protein	tRNA modification
TGGT1 305480	-3.28	mitochondrion (HyperLOPIT)	elongator complex protein ELP3	tRNA modification
TGGT1 314000	1.1	nucleus (HyperLOPIT)	putative peptide methionine sulfoxide reductase msrB	tRNA modification
TGGT1 315958	0.66	-	radical S-adenosyl-L-methionine (SAM)-like, demethylwyosine synthase	tRNA modification
TGGT1 213870	-4.83	cvtoplasm (HyperLOPIT)	UBA/TS-N domain-containing protein	Ubiquitin associated

ToxoDB ID	Uniprot ID	Mito/Ctrl (log2)	Apicoplast/Ctrl (log 2)	Apicoplast/Mito (log 2)	moyCtrl-LFQ	moyMito-LFQ n	noyApicoplast-L	Fpvalue (log1	CRISPR score Localization\$	Tz expression Bz	expression Bz/Tz	Protein	Reference	Cellular function
FGGT1_301180	S7VPV0	-2.68365406990051	-2.68964028358459	-0.00598621973767877	479318250	74604250 7	42953333.3	1.396378755	1.62 PM - peripheral 1	24.41	27.71 1.13519049569848	SAG-related seqence SRS19F, potentially sporozoite-specific		SRS
FGGT1_410610	S7VXS4	0.636475384235382	-1.3603196144104	-1.99679493904114	189356666.7	29436000 7	37536666.7	1.308788537	S N/A N/A	N/A	N/A N/A	Protein kinase domain-containing protein		Unknown
GGT1 313690	S7UUJ6	-0.698630213737488	-1.35542297363281	-0.65679258108139	87798250	54097500 3	43133333.3	1.494558215	1 -4.61 apicoplast	22.68	11.22 0.494708994708995	Sel1 repeat-containing protein		Unknown
GGT1 295690	A0A125YN53	-0.851312875747681	-1.27982342243195	-0.428510516881943	68255500	378326666.7	28110750	2.190474510	1 -3.62 mitochondrion - membra	15.24	30.36 1.99212598425197	Ubiquinone/menaquinone biosynthesis methyltransferase UbiE/COQ5. Ubiquinone metabolism		Mitochondrial respiratory cha
GT1 294790	AOA125YPS7	0.0454948879778385	-1.01879191398621	-1.06428694725037	1132435000	1168715000	558890000	2.620073556	-0.59 rhoptries 2	223.84	155.98 0.696837026447462	hypothetical protein		Unknown
GT1 257470	S7WF44	-0.30433064699173	-1.01018738746643	-0.705856740474701	40609750	32886500	20162000	1.578788995	-3.01 PM - peripheral 2	9.12	4.66 0.510964912280702	Cytoskeleton component, TgMyoJ	PMID: 28593938	Basal complex constriction
T1 214140	\$7VZ47	-0.334176927804947	-0.868143498897552	-0.533966481685638	83101000	65918750	45527000	1.408228039	-1.87 nucleus - chromatin	17.3	4.44 0.256647398843931	Part of the AP2IX-4 complex, transcriptionally regulating cell cycle progression	PMID: 32938695	RNA-interacting/regulating
T1 266970	S7UHF3	-0.694063067436218	-0.86726039648056	-0.173197358846664	787715000	486895000	431815000	1.531296968	4 0.67 PM - peripheral 2	71.92	9.92 0.137931034482759	Ubiouitin domain-containing protein		Unknown
T1 246630	S7W9K7	-1.11214685440063	-0.862397491931915	0.249749451875687	384143333.3	1777066666.7 2	11293333.3	2.365318059	-5.32 nucleus - non-chromatin	13.76	9.78 0.710755813953488	DNA-directed RNA polymerase		RNA-interacting/regulating
GT1 248290	S7V0K5	0.0490309000015259	-0.858825862407684	-0.907856643199921	53483750	553326666.7	29491000	2.245445489	<ul> <li>-2.75 nucleus - chromatin</li> </ul>	6.85	3.04 0.443795620437956	WD domain-containing protein		Unknown
	\$7WD02	-0.186314895749092	-0.850665152072906	-0.664350271224976	52035750	45731500 2	88553333.3	1.436783909	7 -4.39 nucleolus	5.16	3.06 0.593023255813953	Putative origin recognition complex subunit-like		DNA repair and replication
GT1 258660	A0A125YKF2	0.0850631222128868	-0.806744635105133	-0.891807675361633	1248145000	1323950000	713527500	1.544512510	2 0.28 rhoptries 2	651.89	270.27 0.41459448679992	ROP6	PMID: 10634041, 16969065	Unknown
GGT1 212270	A0A125YX33	-0.195551857352257	-0.804212391376495	-0.608660578727722	745772500	651237500	427085000	2.607061147	E -3.05 micronemes	199.78	189.69 0.949494443888277	hypothetical protein		Unknown
GGT1 240690	A0A125YNS1	-0.868883609771729	-0.798904955387115	0.0699787363409996	2131000000	1166872500	1224867500	2.106526136	-4.44 cvtosol	87.18	36 0.412938747419133	Methionine adenosyl transferase. Methionine metabolism		Amino acid metabolism
GGT1 294430	\$7UIK2	-0.61689430475235	-0.785761833190917	-0.168867528438568	83244750	542816666.7	48285750	2.327338457	1 -3.87 nucleolus	9.42	11.23 1.19214437367304	SDA1-like. potentially involved in 60S pre-ribosomal subunits export and maturation		Ribosome biogenesis
GGT1_267140	S7UH64	-0.734389245510101	-0.782125234603882	-0.0477358922362328	868610000	522097500	505105000	2.607596158	0.57 PM - peripheral 1	17.24	3.58 0.207656612529002	SAG-related sequence SRS38B		Tz SRS
GT1_289620	S7UPV8	-1.10120224952698	-0.771169424057007	0.330032765865326	496205000	231295000	290747500	2.062313318	0.95 micronemes	108.52	88.69 0.817268706229267	Cathensin C.	PMID: 17164247	Catabolism/peptidase
T1 271050	A0A125YVU5	0.0715482905507088	-0.740416765213013	-0.811965107917786	67279500000	70700250000	40271250000	2.056658267	1.72 PM - nerinheral 1	3261 16	585.01 0.179387089256584	SAG-related sequence SRS34A		Tz SRS
GT1 315410	S7ULI3	0.0838769376277924	-0.701882064342499	-0.785758852958679	503530000	533672500	309555000	2.226924657	1.35 PM - nerinheral 1	2 95	10.29 3.48813559322034	SAG-related sequence SRSS3F		Bz SRS
GT1 261410	\$7W6W5	.0 758374014170242	-0 701039254665375	0.0573350414633751	100007750	505072500	21263332 2	1 97782000	-2.85 N/A	19.86	20.45 1.02970795568982	Protein-twroine-nhoshatase		Unknown
ST1 265010	\$7UHV6	.0.00424213842012	5 _0 70091599750070	-0.606371521949769	66180000	61990500	£12000000.0 AN718250	1 970031/00	3 -2.03 m/n	20.00	20.43 1.02370733300363	Gutamate Skinase Glutamate metabolism		Amino acid metabolism
GT1 200010	5701110	0.0040401000000000000000000000000000000	-0.605055010031054	.0 /1169727/11/00	130005000	1066720200	90101000	1 2007606499	1.06 nucleur, non chromatin	23.03	20.001000002/10/00000	DNA recognition motif.containing protein		PMA.interaction/comulation
GT1 22103/U	5711157	-0.204200400018393	-0.093933612951001	-0.41108/3/411499	125500000	0001c000 7	00191000 07116666 7	3 UC3EJJJJJ T'322/02002	c 1.90 HUCIEUS - HUH-CRIOMATIN	23.39	12 70 0 715340053555	hundhatiral protein		Linknown
CT1_2219/U	3/UL32	-0.400/30033310925	-0.00/01/301545503	-U.130021240023993	12/580000	30310000 /	52110000./	3.003323292	-1.03 N/A	19.28	13./3 0./13248902055002	nypotneticar protein		Unknown
GT1_295770	AUA125TKK/	-0.191406942429543	-0.6/22164154052/3	-0.480/4948/8/6892	843262500	/3845/500	529182500	2.202811/1/	S U.7 micronemes	50.45	55.10 1.095359/62140/3	Chitinase-like protein CLP1		Unknown
GT1_225320	5/W5U8	-0.1156/5926208496	-0.058113058428192	-0.542437732219696	428065000	395082500	2/120/500	2.04/882556	S U.64 moptries 2	99.15	57.64 0.581341401916288	Nypothetical protein		Dihanana kiranania
311_224970	5/UW05	-1.148842930/93/6	-0.639941155910492	0.508901/7488327	34//03333.3	156836666./ 2	231/3333.3	2.898288488	s U nucleoius	15.52	8.5 0.628698224852071	Nop52 protein-like. Ribosome biogenesis		Ribosome biogenesis
11_315150	S/ULH3	-0.52618354558944/	-0.63051/125129/	-0.104333661496639	261640000	181680000	169005000	1.446518659	<ul> <li>-1.99 nucleus - non-chromatin</li> <li>2.20 FB</li> </ul>	18.75	15.18 0.8096	Putative eukaryotic initiation factor-4E		RNA-interacting/regulating
311_254490	S/UN3/	0.2961496/10///28	-0.62020/0/1304321	-0.910350/4238205	150695000	192400000	101942250	3.122195720	t -3.29 EK	15.44	6.84 0.5089285/14285/1	Seit repeat-containing protein		Unknown
511_319720	S7UK66	-0.767558872699738	-0.617857038974761	0.149701848626137	55649750	32689250	36263500	2.411698341	-4.4/ nucleus - chromatin	8.86	1.85 0.208803611738149	hypothetical protein		Unknown
11_208850	A0A125YN91	0.0051477048546075	8 -0.610444962978363	-0.6155925989151	325922500	327087500	213477500	3.106467723	8 2.25 PM - peripheral 1	6.47	2.04 0.315301391035549	SAG-related sequence SRS11		Tz SRS
GT1_247020	A0A125YL37	-0.401611328125	-0.599947571754456	-0.198336243629456	254642500	192767500	168007500	1.436465978	6 -1.73 nucleus - chromatin	40.51	44 1.08615156751419	Putative high mobility group protein b1		Unknown
ST1_290200	S7VXT3	-0.544718444347382	-0.593576848506927	-0.0488584935665131	8902700000	6103025000	5899800000	2.863051414	<ul> <li>-0.87 nucleus - non-chromatin</li> </ul>	272.64	66.42 0.243617957746479	NAD/NADP octopine/nopaline dehydrogenase		Amino acid metabolism
GT1_234470	S7W4G9	-0.287438690662384	-0.590273201465607	-0.302834630012512	70760500	57978000 4	70003333.3	1.641103386	8 2.1 nucleus - non-chromatin	9.33	15.62 1.67416934619507	hypothetical protein		Unknown
GT1_294980	AOA125YGY1	-1.74661135673523	-0.588016211986542	1.15859508514404	355287500	105876000	236357500	2.332672357	2.06 dense granules	10.47	2.88 0.275071633237822	hypothetical protein		Unknown
GT1_320230	S7VYJO	-0.228917509317398	-0.581449389457703	-0.352531909942627	141455000	120700000	94533250	1.507229447	0.31 PM - peripheral 1	0.5	10.94 21.88	SAG-related sequence SRS15C		Bz SRS
GT1_233460	A0A125YG48	-0.179791614413261	-0.569025218486786	-0.389233648777008	2,30E+15	2,03E+15	1,55E+16	1.482438325	<ul> <li>-0.07 PM - peripheral 1</li> </ul>	4153.25	314.87 0.0758129175946548	SAG-related sequence SRS29B		Tz SRS
GGT1_226860	S7W5K4	0.128666505217552	-0.563585937023163	-0.692252457141876	919115000	1004852500	621890000	1.529967188	8 1.88 PM - peripheral 1	77.76	101.33 1.3031121399177	SAG-related sequence SRS67		SRS
GGT1_224330	S7UW24	-0.74552583694458	-0.560373246669769	0.185152485966682	130650000	77926250	88597250	1.877975225	4 0.18 cytosol	35.55	30.44 0.856258790436006	Proteasome activator pa28 beta subunit		Catabolism/peptidase
o LFQ values in	TgNFS2 mutant													
GGT1_203320	S7WAU3	0.37899408744	N/A	N/A	12572333.3	16349500	C	N/A	-2.09 N/A	11.01	2.95 0.2679382379	E3 ubiquitin-protein ligase, Zinc finger protein		Unknown
GGT1_258480	S7UZ70	-0.160527614386435	N/A	N/A	23820333.3	21312000	C	N/A	0.03 nucleus - chromatin	54.43	70.56 1.29634392798	hypothetical protein		Unknown
GT1_262480	S7UXR9	-0.21345274075	N/A	N/A	102622333.3	88508750	C	N/A	-1.01 N/A	167.28	307.22 1.8365614538498	Robl_LC7 domain-containing protein, may modulate specific dynein functions		Unknown
GGT1_301160	S7UHG9	-0.126331253	N/A	N/A	72831666.6	66725333.3	C	N/A	0.6 PM - peripheral 1	21.68	27.25 1.25691881918819	SAG-related sequence SRS19C, potentially sporozoite-specific		SRS
No LFQ values in	TgNFS2 and TgISU1	nutants, but LFQ values	in control											
GGT1_285860	S7UNY4		0	0 N/A	66018000	0	C	N/A	1.72 PM - peripheral 1	9.39	1.97 0.209797657082002	SAG-related sequence SRS20C		Tz SRS
GGT1_272770	S7V3A5		0	0 N/A	23139666.6	0	C	N/A	-4.32 N/A	45.86	46.47 1.01330135194069	Ltv1 Low temperature viability protein-like motif		Ribosome biogenesis
GGT1_251410	S7V016		0	0 N/A	16610000	0	C	N/A	0.25 N/A	19.7	6.9 0.350253807106599	Tetratricopeptide repeat-containing protein		Unknown
GGT1_275420	\$7W518		0	0 N/A	13814666.6	0	C	N/A	-2.47 N/A	26.2	14.09 0.537786259541985	Histone demythylase/N1-acetylpolyamine oxidase (polyamine salvage)		Unknown
GGT1 255310	S7W160		0	0 N/A	9955600	0	C	N/A	0.7 nucleus - non-chromatin	59.36	10.41 0.175370619946092	CCCH zinc finger-containing hypothetical protein		Unknown
									¥ fitness \$ inferred from	# RNAsen				
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									from whole Hyperi OPIT nediction -	Hehl AB et al				
									renome Randwik K et al Cell	DMC				
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									UKISPK HOST & MICFODE 2020-)	Genomics				
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									SM et al. Cell					
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ToxoDB ID	Uniprot ID	Mito/Ctrl (log2)	Apicoplast/Ctrl (log 2)	Apicoplast/Mito (log 2)	moyCtrl-LFQ	moyMito-LFQ r	noyApicoplast-LFQ pvalue (log10)	CRISPR score#	Localization\$	Tz expression# Bz exp	expression#	Bz/Tz F	Protein	Reference	Cellular function
TGGT1_216140	A0A125YUL1	5.34013509750366	5.2523341178894	-0.0878007486462593	15598400	631860000	594552500 5.84068965911	165	1.75 N/A	139.62	1142.46	8.1826385904	WK1, expressed in Bz, do not participate in differentiation	PMID: 29180989	Unknown
TGGT1_264660	S7VP87	3.99073934555054	2.98403120040894	-1.00670802593231	107631333.3	171108250	85157250 2.28895807266	35	0.85 dense granules	140.35	725.26	5.1675097969	Bz cyst wall protein CST1 (initially annotated as SAG-related sequence SRS44)	PMID: 24385904	Bz SRS
TGGT1_309930	S7W7S4	3.42434287071228	1.81320333480835	-1.61113965511322	21157700	227142500	74352750 3.56172108650	108	-1.13 dense granules	107.99	243.45	2.2543754051	SRA56, higher expression in Bz	PMID: 32374791	Bz GRA
TGGT1_201840	S7UV48	2.34287166595458	1.76575911045074	-0.577112555503845	143747500	729247500	488817500 2.87034058570	162	-0.36 endomembrane vesi	ic 105.67	250.07	2.3665184063	SP1, VAC-localized, upregulated in Bz	PMID: 25240600, PMID: 32051238	Catabolism/peptidase
TGG11_225850	5/W5H3	1.0085084458524	1.308558225631/1	0.300049751996994	85/7/250	1/2569250	212465000 1.41557823867	98	-5.U2 EK	22.66	25.0	1.103/069/2t1	VIZS metalio peptidase, round in MAGLIP Tiuren 1.3. eleke ekuesidear (CANAR). M. Churen kingustearin	PMID: 32374791	Catabolism/peptidase
TGGT1_253030	570105	0.408014540000502	1.30314433374077	0.894529819488525	141083750	225206666 7	3036222300 2.20001/90000	98	-0.92 N/A	12.26	34.03	4.8298403825	Seperal cubstrate transporter		Channel/transporter
TGGT1_245380	570071	2 09510111808777	1 21698665618896	-0.878114461898804	125750000.7	543865000	295905000 1 84367239475	10	-0.79 dense granules	30.5	38.27	1 2547540981	perierar souscare cransporter Putative GRA: nossibly unregulated in Rz	PMID: 25240600	GRA
TGGT1_257510	57U7E3	0.360445111989975	1.20049738883972	0.840052247047424	32134000	4125433333	73850000 2.13097953796	187	-0.29 FR	86.37	27.4	0.3182818108	Diacylelycerol choline nhosohotransferase. Phosohatidylcholine metabolism	PMID: 24429285	Lipid metabolism
TGGT1 233480	S7WBY8	-0.574986755847931	1.15701198577881	1.73199880123138	1377250000	924537500	3071200000 2.16469097137	151	1.51 PM - peripheral 1	2756.33	211.09	0.0765837182	AG-related sequence SRS29C		Tz SRS
TGGT1_219240	S7V235	0.724526345729828	1.12648010253906	0.401953667402267	298015000	492427500	650642500 2.95005321502	86	1.31 N/A	14.32	25.4	1.7737430167	Peptidyl-tRNA hydrolase PTH2 domain-containing protein		RNA-interacting/regulating
TGGT1_240860	A0A125YWP8	0.365964740514755	1.05630147457123	0.69033670425415	324492500	418187500	674812500 1.91257560253	43	-2.54 ER	54.54	37.93	0.6954528786	I-acylGlycerol-3-phosphate O-acyltransferase, AGPAT. Production and recycling of phospholipids		Lipid metabolism
TGGT1_316250	S7ULD1	-1.14098143577576	1.05221843719482	2.19319987297058	165567500	75076750	343340000 2.64816331863	103	1.15 dense granules	120.86	75.83	0.6274201555	GRA45, involved in translocation of dense granule effectors. Higher expression in Tz	PMID: 30377279	Tz GRA
TGGT1_215490	S7W572	0.0471646934747696	1.03256356716156	0.985398828983307	23275500	24049000	476136666.7 2.99689245223	199	-3.91 Golgi	105.57	126.41	1.1974045656	NPT1, Arginine transporter	PMID: 28205520	Channel/transporter
TGGT1_283710	A0A125YW31	0.301033645868301	1.02287518978119	0.721841633319855	225092500	277320000	457380000 1.69656848907	171	-1.09 ER	162.1	35.95	0.221776681(	iphingosine N-acyltransferase. Sphingomyelin metabolism		Lipid metabolism
TGGT1_231000	S7V288	0.346877008676529	1.01494872570038	0.668071687221527	30495250	38784000	61625750 2.13672828674	116	-2.33 Golgi	23.51	14.02	0.5963419821	TART domain-containing protein, potentially lipid-binding		Lipid metabolism
TGGT1_247195	S7V0Y7	0.29553285241127	1.00723934173584	0.711706459522247	177170000	217447500	356122500 1.30818748474	21	-3.31 micronemes	46.46	22.43	0.4827808867	VIC15		Unknown
TGGT1_315940	S7UM44	0.224215164780617	0.965925693511963	0.741710543632507	45058750	52635000	88014000 1.56165206432	143	0.39 ER	17.82	9.89	0.5549943883	Putative lipase maturation factor		Lipid metabolism
TGGT1_209800	ADA125YSC6	1.90726351737976	0.965333998203278	-0.941929459571838	166654250	625115000	325395000 2.00076079368	i91	1.1 PM - integral	30.64	16.54	0.5398172323	NT-1, PM-localized formate/lactate transporter	PMID: 30237165	Channel/transporter
TGG11_236890	AUA125YNW9	2.1108283996582	0.945395052433014	-1.10543528/02054	151412500	654010000	2915//500 4.42215/28/59	'bb	2.1 dense granules	1/6.9/	18/.4/	1.0590495564	SKA37, expressed in 12 and 82 Notifice and exited to express Ministrate and electronicity and block	PMID: 32374791	GKA
TGG11_301210	S/UHHb	0.55/322382926941	0.9944646894931793	0.38/324512004852	385626666.7	56/463333.3	/4222250 1.41558363628	187	-1.91 PW - Integral	24.97	25.14	1.0060072086	vrioine nucleotide transnyorogenase. Nicotinate and nicotinamide metabolism		NAD/NADP synthesis
TGGT1 205410	HUR123128/	1 50710455710004	0.536544041/265/5	0.003/49814033508	42112750	120001/2500	21622250 1 55205102105	M3	2.17 CK	200.76	514.0t	1.0308284061	vyposiecical protein		Unknown
TGGT1 262700	570130	1 7853051424025	0.021200000820897	-0.070214050506068	43113/30	246032200	136447500 2 27276250749	45 M	1.63 dense granuler	4.32	510 51	1 9839777067	yponicical protein IRAS8 higher evenession in Rz	PMID: 32374791	Rz GRA
TGGT1 289880	S7UP43	0.231316551566124	0.883353173732758	0.652036726474761	12217300	155880000	244947500 1 437202539748		1.8 Golgi	Δ1 79	36.70	0.8803541517	Protein with Aloha /Beta hydrolase fold		Unknown
TGGT1 283720	A0A125VSI 5	0.110573157668114	0.866523087024689	0.75594991445541/	82739000	89329750	150855000 1 76293551921	144	-0.78 Golgi	41.75	30.75 7 70	0.187741437/1	ratementrane 9 superfamily member		Channel/transporter
TGGT1 241820	S7URK6	0.039458267390728	0.865334928035736	0.825876772403717	55600000	571416666.7	101290000 2.33807277679	43	-0.5 Golei	71.65	59.33	0.8286113040	woothetical protein		Unknown
TGGT1 300350	S7VP37	0.604513168334961	0.825931489467621	0.221418380737305	134677500	204772500	238740000 1.65349471569	161	0.45 ER 2	14.27	11.09	0.77715487010	Vyteine desulfurase. Folate metabolism		Folate metabolism
TGGT1 276190	S7UNK3	-0.397864103317261	0.82391345500946	1.22177755832672	18566250	140914333.3	32866000 1.69035327434	i4	-3.94 ER	10.61	1.6	0.1536286522	Diacylglycerol choline phosphotransferase. Phosphatidylcholine metabolism		Lipid metabolism
TGGT1_284780	\$7W2W0	0.175652027130127	0.822377800941467	0.646725714206696	96854750	109395000	171270000 1.44623470306	196	0.73 Golgi	50.65	42.46	0.8383020730	usaric acid resistance-domain containing protein		Unknown
TGGT1_260520	S7UYP6	1.14152121543884	0.820777893066406	-0.320743381977081	110010250	242697500	194317500 4.66463279724	21	1.9 dense granules	79.49	79.5	1.0001258019	IST6/GRA53, expressed in Bz	PMID: 32374791	Bz GRA
TGGT1_290940	S7UQ27	0.151469677686691	0.803147971630096	0.651678323745728	223847500	248627500	390592500 1.86565268039	103	-0.5 Golgi	63.7	37.66	0.59120879121	Fransmembrane 9 superfamily member		Channel/transporter
TGGT1_226580	A0A125YY97	-0.236971154808998	0.786019504070281	1.02299070358276	969895000	822980000	1672400000 2.44299602508	45	-4.07 ER	58.07	129.53	2.2305837781	nypothetical protein		Unknown
TGGT1_224820	S7W544	0.635936498641968	0.772736489772797	0.136799976229668	43562000	67693000	74426000 2.03762745857	139	0.71 mitochondrion - mer	m 16.22	31.56	1.9457459926	nypothetical protein		Unknown
TGGT1_201630	S7WB62	1.03427338600159	0.771023631095886	-0.263249695301056	114534000	234575000	195450000 2.34060287475	86	1.65 rhoptries 1	53.39	64.24	1.203221577(	Phosphatase TgPPM3H	PMID: 28556455	Unknown
TGGT1_260310	A0A125YUY7	0.992248356342316	0.769039690494537	-0.223208665847778	59250000	117865000	100970000 1.49347734451	194	0.69 Golgi	10.6	2.68	0.252830188€	ATP-binding cassette transporter ABC.B1		Channel/transporter
TGGT1_222410	S7UKA3	0.419835209846497	0.743056118488312	0.323220819234848	48989000	65536250	81993750 1.39320933818	117	-3.63 ER	37.77	21.48	0.5687053216	Putative lipase maturation factor		Lipid metabolism
TGGT1_261480	S7UXZ9	0.149466797709465	0.729111313819885	0.579644501209259	97893500	108579500	162270000 1.33295309543	i1	-4.8 ER	30.33	9.21	0.3036597428	Phosphatidylserine synthase 2. Phosphatidylethanolamine and phosphatidylserine metabolism	PMID: 26565995	Lipid metabolism
TGG11_202620	S/UVJ3	0.232138/9/6408	0.728111624/1//12	0.4959/28419/80/3	102234000	120081500	16934/500 1.309/51/4903	5/ NOC	0.94 dense granules	124.66	1/9.63	0.0020441024	typothetical protein		Unknown
TGGT1_292020	S/UNY5	0.661832/4984359/	0.724787890911102	0.062955250474472	92529750	146390500	152920000 1.70618069171	Ub	-3.64 micronemes	3.94	3.4	0.86294416240	SUL2 and GUL3 Tyrosine-protein kinase eprini type A/B receptor-like	DMID: 35340500	Receptor
TGGT1_249180	RUH1231712	.0 170522002772898	0.713443007403701	0.82420016552312	4202873000	567645000	1040405000 1 21227700851	i03	N/A INCIDEUS - NOTI-CITOTI	51 75	22.7/	0.203304304.0	Distance of the control of the contr	PMID. 23240000	Catabolism/nentidase
TGGT1_221170	A0A125VGK5	-0.170322093772888	0.600126362800508	0.87420910337312	10/1055000	1005750000	1600175000 1.31332750831	195	1.78 FP	224.2	50.74 608.04	2 6001707041	vicative CHAX metallo endopeptidase informed in the cleavage of isophenylated proteins		Unknown
TGGT1_208370	570176	0.551288843154907	0.690403342247009	0.139114439487457	1300725000	1905075000	2099025000 1.83155822753	106	1.79 dense granules	46.22	127.59	2.7604932929	SRA46. higher expression in Bz	PMID: 30377279	Bz GRA
TGGT1_200370	S7V482	1.61908733844757	0.660394430160522	-0.958692967891693	790772500	2429100000	1249827500 3.51634883880	15	1.25 dense granules	870.6	2433.61	2.7953250631	VAG1 cvst matrix antigen. Unrepulated in Bz	PMID: 7808478	Bz GRA
TGGT1 251490	S7V032	0.734762012958527	0.653240978717803	-0.0815209597349167	24537250	40833000	385896666.7 1.33415234088	198	0.11 nucleus - chromatin	22.45	32.28	1.4378619153	ACR.COG2135 domain-containing protein		Unknown
TGGT1_222090	A0A125YWQ8	0.0456425286829472	0.632726669311523	0.587084233760834	89639250	92520500	138985000 1.36657249927	21	1.14 ER	62.64	60.5	0.9658365261	RabS interacting motif-containing		Unknown
TGGT1_240060	S7W054	0.515200436115265	0.620320975780487	0.105120435357094	1149740000	1643200000	1767400000 1.39700818061	129	1.44 dense granules	150.62	34.68	0.2302483069	Dense granule protein TgIST	PMID:27503074	Tz GRA
TGGT1_217530	S7WHL7	-1.20679974555969	0.606696426868439	1.81349611282349	113804250	49303250	173297500 1.70100963115	i92	2.13 dense granules	37.34	113.45	3.0382967327	nypothetical protein		Unknown
TGGT1_225120	S7UW30	1.42969179153442	0.605309188365936	-0.824382662773132	59675750	160760000	90785000 3.48011136054	193	0.64 dense granules	192.72	160.82	0.8344748858	Putative GRA, expressed in Tz and Bz		GRA
TGGT1_259200	S7WEL3	-0.381515145301819	0.601512372493744	0.983027517795563	75658750	58078000	114797500 2.53040385246	.77	-1.46 PM - integral	5.14	1.73	0.3365758754	Na+/H+ exchanger NHE1	PMID: 15173192	Channel/transporter
TGGT1_251540	A0A125YWK4	1.41529583930969	0.581027448177338	-0.834268450737	722317500	1926525000	1080525000 2.80179762840	.7	1.52 dense granules	252.54	528.97	2.09459887540	SRA9, higher expression in Bz	PMID: 32374791	Bz GRA
TGGT1_220890	ADA125YXQ8	-0.368621647357941	0.578576683998108	0.947198331356049	247175000	191442500	369125000 2.58145761489	168	2.06 PM - peripheral 2	40.64	61.15	1.5046751968	hypothetical protein	D #D 4 0000000	Unknown
IGGT1_223920	S/UWM8	-0.050005380064249	0.56/113816738129	0.617119252681732	4149875000	4008500000	6148275000 1.44249820709	29	-4.41 rhoptries 1	166.59	85.27	0.5118554535	Rhoptry protein RUN3	PMID: 16002398	Unknown
TGGT1_294040	5/UHH8	-U.2/UU9U222358704	0.55/809255542/55	0.82/9594//901459	b//93250	56218/50	99/98000 1.81365442276	101	-2.72 EK	29.86	18.17	0.0085063630	vulative Auct eniuopiasmic reticulum protein retention receptor 2 (KDELK2)	DMID: 25240600	Receptor
TGGT1 244570	AURIZOYWKD S7VMIA7	0.38283/286950084	0.30092011/909015	-0.420932159158249	13/0425000	5103/50000	£2350300000 2.26548218/2/	10	1.43 DELISE BLAUTIER	215.45	69.65	0.3204955255	aucuserorphosphate Erdenyorogenase. Perilose phosphate pathway. Upregulated in 12	rw11D: 20240000	Temose phosphate pathway
TGGT1 244550	A0A125V706	0.746073246002107	0.554047405719757	-0.192025780677705	42333730	118201500	1035495000 1 73877303057	08	1.52 PM - perinheral ?	71.69	4.t 97 n	1.14479006821	mmune manned protein 1. TeIMP1	PMID: 27888074	Unknown
TGGT1 293810	A0A125Y737	0.956510066986083	0.551496088504791	-0.40501394867897	473395000	918675000	693810000 2.64519810676	575	-0.6 cvtosol	31.19	160.41	5.1429945495	Carboxwiryl-carboxyohosohonate phosohorylmutase. Phosohonate and phosohinate metabolism. Horeevlated in Rz	PMID: 25240600	Organophosphorus commund synthesis
TGGT1 275460	S7UQV5	0.849380552768707	0.550823330879211	-0.298557192087173	88701000	159815000	129940000 2.84133386611	138	2.32 dense granules	63.43	83.31	1.3134163644	Putative GRA expressed in Tz and Bz	PMID: 25240600	GRA
LFQ values in Tgl	VFS2 mutant only														
TGGT1_223125	S7VTV9	N/A	N/A	N/A	0	0	50273333.3 N/A		-4.91 Apicoplast	169.16	122.28	0.7228659257	Plastid Ubiquitin-like PUBL protein	PMID: 28655825	Plastid protein import
No LFQ values in	control, but LFQ v	alues in TgNFS2 and TgI	SU1 mutants												
TGGT1_224190	S7UVS1	N/A	N/A	-0.11271425367	0	20276333.3	21924000 N/A		-5.24 Golgi	46.22	11.84	0.2561661618	ipid flippase TgFLP2	BioRxiv: 10.1101/2020.06.19.160341	Lipid metabolism
TGGT1_317705	S7UFF2	N/A	N/A	-0.75161181616	0	26330333.3	44331666.6 N/A		-0.45 N/A	103.44	104.55	1.0107308584	noyl-CoA hydratase/isomerase family protein		Lipid metabolism
TGGT1_261650	S7UY15	N/A	N/A	0.20880937503	0	57346750	49619333.3 N/A		1.61 PM - peripheral 2	110.47	389.39	3.52484837510	yst wall protein IgCST4	PMID: 31040239	Bz cyst wall protein
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lense une entorement     4.32 lense une entorement     4.31 lense une entorement     4.32 lense une entorement     4.33 lense une entorement     4.34 lense une entorement     4.34 lense une entorement     4.34 lense une entorement     4.34 lense une entorement     4.35 lense entorement     4.35 lense entorement     4.35 lense entorement     4.37 lense unenorthom     4.38 lense enorthom     4.39 len</td> <td>b         170.1.1           b         217.1.3           b         217.5.7.3           b         21.5.7.5           b         36.3.3           b         116.06           b         116.06           b         21.9.4.7.5           b         21.9.4.7.5           b         21.9.4.7.5           b         21.9.4.7.5           b         21.9.4.7.5           b         22.9.4.6.5           b         22.9.4.6.5           b         13.9.2.2.5           b         13.9.2.2.5           b         14.7.4.8.6.5           b         14.7.4.8.6.5           b         14.7.4.8.6.5           b         14.7.4.8.6.5           b         14.7.4.8.6.5           b         14.6.6.6.5.9.5           b         14.6.6.5.9.5           b         14.6.6.5.9.5           b         14.9.7.5.7           b         14.9.7.5.7           b         14.9.7.5.7           b         14.9.7.5.7           b         14.9.7.5.7.7.7.7.7.7.7.7.7.7.7.7.7.7.7.7.7</td> <td>600.36.2.179244255(C-singlets with complexIV         123.97 1.5054425(C-singlets with complexIV         123.97 1.5054425(C-singlets with complexIV         123.60 0.51292077 [Exc3:6]         124.60 0.77022377 [Exc3:6]         124.60 0.51292077 [Exc3:6]         124.60 0.51292077 [Exc3:6]         124.60 0.51292077 [Exc3:6]         124.60 0.51292077 [Exc1:6]         124.60 0.51292077 [Exc1:6]         124.60 0.51292077 [Exc1:6]         124.60 0.51292077 [Exc1:1]         125.00 0.559374567 [Exc1:6]         125.00 0.559374567 [Exc1:6]         125.00 0.55937457 [Exc1:6]         125.00 0.5593757 [Exc1:6]         126.00 0.5593757 [Exc1:6]         126.00 0.5593757 [Exc1:6]         126.00 0.5593757 [Exc1:6]         128.00 0.4766000231 [Exc1:7]         128.10 0.5593757 [Exc1:6]         128.10 0.559375757 [Exc1:6]         128.10 0.55937577 [Exc1:6]         128.10 0.55937</td> <td>t of this complex is down-regulated in Bz t of this complex is down-regu</td> <td>Mitobio           Mitobio           <td< td=""></td<></td>   | 144880000<br>4933320<br>4933320<br>4933320<br>493536667,
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       64.7           17.1         15.1           17.1         15.1   | 600.36.2.173944555 (C-singtest with complex IV<br>27.397 1.505/dx17 [Foots6<br>156.96 0.77402364 F[costs]<br>25.46 0.51359077 [Foots6<br>25.48 0.5439775 [Foots6<br>25.48 0.5439775 [Foots6<br>25.48 0.5439775 [Foots6<br>25.48 0.5439775 [Foots6]<br>25.48 0.5439775 [Foots6<br>25.48 0.5439775 [Foots6]<br>25.48 0.5439775 [Foots6]<br>25.48 0.5439775 [Foots6]<br>25.48 0.5439775 [Foots6]<br>25.48 0.5439775 [Foots6]<br>25.48 0.5439775 [Foots6]<br>25.48 0.54397452 [Foots6]<br>25.48 0.54397452 [Foots6]<br>25.48 0.54397452 [Foots6]<br>25.48 0.54397452 [Foots6]<br>25.48 0.5439752 [Foots6]<br>25.48 0.54397452 [Foots6]<br>25.49 0.54397452 [Foots6]<br>25.49 0.54397452 [Foots6]<br>25.49 0.54397452 [Foots6]<br>25.49 0.54397452 [Foots6]<br>25.49 0.54397452 [Foots6]<br>25.49 0.54397452 [Foots6] [Foots6]<br>25.49 0.54397452 [Foots6] [Foo   | t of this complex is down-regulated in Bz t of this complex is down-regu   | Mitchio           Mitchio <td< td=""></td<>  |
| 1.00         1.00 <td< td=""><td>Lang 22 (2002)<br/>Lang 22 (2002)</td><td>2.0054292411804<br/>2.0054292411804<br/>3.005295550511<br/>1.8251050515071<br/>1.4691950515937<br/>1.4691950515937<br/>1.4691950515937<br/>1.4691950515937<br/>1.4691950515937<br/>1.4591950515937<br/>1.4591950515937<br/>1.4591950515937<br/>1.591951755214<br/>1.512614517553<br/>0.24974945157585<br/>0.5157159211583<br/>1.389591259531<br/>1.389591259531<br/>1.389591259531<br/>1.389591259531<br/>1.389591259531<br/>1.389591259531<br/>1.389591259531<br/>1.389591259531<br/>1.389591259531<br/>1.389591259531<br/>1.39595125931<br/>1.39595125931<br/>1.39595125931<br/>1.39595125931<br/>1.39595125931<br/>1.39595125931<br/>1.39595125931<br/>0.45919545402535<br/>0.4794543159259<br/>0.4551551585475<br/>0.475554450253<br/>0.4755545402535<br/>0.4755545402535<br/>0.4755545402535<br/>0.4755545402535<br/>0.4755545402535<br/>0.4755545402535<br/>0.4755545402535<br/>0.4755545402535<br/>0.4755545402535<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4755545402555<br/>0.4257212455741<br/>0.4255544025554<br/>0.4255544025552<br/>0.4257212455741<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.4255544025554<br/>0.42555440255544550<br/>0.425554402555445504<br/>0.425554402555445504<br/>0.42555440</td><td>12713700<br/>3710950<br/>31710950<br/>140895000<br/>1138042<br/>347753333<br/>341655575<br/>6474755<br/>343413333<br/>34962000<br/>12785000<br/>6401375<br/>34343333<br/>34962000<br/>13559500<br/>35233500<br/>35233500<br/>35233500<br/>35233500<br/>35233500<br/>35233500<br/>35233500<br/>35233500<br/>35233500<br/>35233500<br/>35233500<br/>35233500<br/>3533500<br/>3533500<br/>3533500<br/>3533500<br/>3533500<br/>3533500<br/>3533500<br/>3533500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>35355500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>35355500<br/>35355500<br/>3535500<br/>3535500<br/>3535500<br/>35355500<br/>35355500<br/>35355500<br/>35355500<br/>35355500<br/>35355500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>3535500<br/>353550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        1588           15500         1568           15500         1568           15500         1568           15500         1568           1568         1568           1569         1570           15000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1570           150000         1520           150000         1520           150000         1520           150000         1520           150000         1520           150000         1520      1500000         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1.91</td><td>NBUA433<br/>NBUA433<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PARLASS<br/>PAR</td><td>-0.4 intochendrion           -0.3 intochendrion           -3.2 idense grandes           -2.8 intochendrion           -2.8 intochendrion           -3.8 intochendrion           -3.8 intochendrion           -3.9 intochendrion           -3.5 intochendrion           -3.6 intochendrion           -3.6 intochendrion           -3.6 intochendrion           -3.7 ippicplast           -4.6 ispicplast           -4.7 ispicplast           -5.8 intochendrion           -5.9 intochendrion           -5.9 intochendrion           -5.9 intochendrion</td><td>b         170.1.1           170.1.1         170.1.1           125.7.7.2         36.3.3           13.3         16.0.5           14.4         3.4.4.3           15.0.5         116.0.5           14.4         3.4.3           110.0.5         21.9.4.7           110.0.1         3.4.4           12.9.7.7         3.2.2.2           12.9.7.7         3.2.2.2           12.9.7.8         3.2.2.2           12.9.7.8         3.4.4.4           13.2.2.2         2.8.4           14.2.4.2         3.4.4           14.2.4.2         3.4.4           14.4.4         14.4.4           14.2.2         2.8.4           14.1.1         3.4.4           14.2.2         2.8.4           14.4.4         14.4           14.4         14.4           14.4         14.4           14.4         14.4           14.4         14.4           14.4         14.4           14.4         14.4           15.4         14.4           15.5         14.4           15.5         14.4           15.5         14.4     <td>600.36.2.173944255(C-singlets with complexIV         125.97       1.5504425(C-singlets with complexIV         125.86       0.51295977 [Eox36         125.86       0.51295977 [Eox36         125.86       0.51295977 [Eox36         126.80       0.51295977 [Eox36         126.80       0.512977 [Eox36         126.80       0.512977 [Eox36         126.80       0.512977277 [Ox4-directed BVA polymerase         120.77212277 [Ox4-directed BVA polymerase       0.77712407 [Eox17]         120.70       0.559774527 [Eox17]         121.70       0.425971257 [Eox17]         125.10       0.559774527 [Eox17]         125.10       0.559774527 [Eox18]         126.61       0.1259757 [Eox18]         126.61       0.529795857 [Eox18]</td><td>t of this complex is down-regulated in Bz t of this complex is down-regu</td><td>Mitchio           Mitchio           <td< td=""></td<></td></td></td></td<>  | Lang 22 (2002)<br>Lang 22 (2002)                                       | 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<td>-0.4 intochendrion           -0.3 intochendrion           -3.2 idense grandes           -2.8 intochendrion           -2.8 intochendrion           -3.8 intochendrion           -3.8 intochendrion           -3.9 intochendrion           -3.5 intochendrion           -3.6 intochendrion           -3.6 intochendrion           -3.6 intochendrion           -3.7 ippicplast           -4.6 ispicplast           -4.7 ispicplast           -5.8 intochendrion           -5.9 intochendrion           -5.9 intochendrion           -5.9 intochendrion</td> <td>b         170.1.1           170.1.1         170.1.1           125.7.7.2         36.3.3           13.3         16.0.5           14.4         3.4.4.3           15.0.5         116.0.5
          14.4         3.4.3           110.0.5         21.9.4.7           110.0.1         3.4.4           12.9.7.7         3.2.2.2           12.9.7.7         3.2.2.2           12.9.7.8         3.2.2.2           12.9.7.8         3.4.4.4           13.2.2.2         2.8.4           14.2.4.2         3.4.4           14.2.4.2         3.4.4           14.4.4         14.4.4           14.2.2         2.8.4           14.1.1         3.4.4           14.2.2         2.8.4           14.4.4         14.4           14.4         14.4           14.4         14.4           14.4         14.4           14.4         14.4           14.4         14.4           14.4         14.4           15.4         14.4           15.5         14.4           15.5         14.4           15.5         14.4     <td>600.36.2.173944255(C-singlets with complexIV         125.97       1.5504425(C-singlets with complexIV         125.86       0.51295977 [Eox36         125.86       0.51295977 [Eox36         125.86       0.51295977 [Eox36         126.80       0.51295977 [Eox36         126.80       0.512977 [Eox36         126.80       0.512977 [Eox36         126.80       0.512977277 [Ox4-directed BVA polymerase         120.77212277 [Ox4-directed BVA polymerase       0.77712407 [Eox17]         120.70       0.559774527 [Eox17]         121.70       0.425971257 [Eox17]         125.10       0.559774527 [Eox17]         125.10       0.559774527 [Eox18]         126.61       0.1259757 [Eox18]         126.61       0.529795857 [Eox18]</td><td>t of this complex is down-regulated in Bz t of this complex is down-regu</td><td>Mitchio           Mitchio           <td< td=""></td<></td></td>  | 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      SH318377</td> <td>4.04 intechnolsion     4.32 iemes gandes     4.34 iemes gandes     4.35 iemes gandes     4.36 iemes gandes     4.36 iemes gandes     4.36 iemes     4.37 incloses non-chrom     4.37 incloses non-chrom     4.37 incloses non-chrom     4.38 incluses non-chrom     4.39 incluses     4.39 incluses     4.39 incloses     4.41 iemes     4.51 intechnolise     4.51 intechnolise     4.52 intechnolise     4.53 intechnolise     4.54 intechnolise     4.54 intechnolise     4.54 intechnolise     4.54 intechnolise     4.55 intechnolise</td> <td>170.1.1         170.1.1           170.1.1         170.1.1           182.17.7.7         36.3.3           144.38         14.9.9           116.05         116.05           116.05         119.08           117.1         28.13           22.8.12         119.8           117.10         28.13           22.8.45         119.9           117.20         110.8           117.20         110.8           117.20         110.8           117.20         110.8           117.20         110.8           117.20         110.8           117.20         110.8           117.20         111.1           117.20         111.1           117.20         111.1           118.6         114.6           119.10         114.6           111.10         114.6           111.10         114.6           111.10         114.6           111.11         114.6           111.11         114.6           111.11         114.0           1111.11         114.0           1111.11         114.0           1111.11         11</td> <td>600.36.2.173944255(C-singlets with complexIV           123.971 L505442           123.971 L505442           123.68 0.5130977 [Eox35           123.68 0.5130977 [Eox35           123.68 0.5130977 [Eox35           134.62 2.880743024 [Pox150 [Eox35           123.68 0.5130977 [Eox35           134.62 2.880743024 [Pox150 [Eox35           136.80 0.5487772277 [M-64resci BNA polymerase           124.70 0.053877588 [GMA5           124.80 0.53772727 [M-64resci BNA polymerase       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4.39 anclues     5.7 PM - propheral     1     4.6 grante-     4.7 grante-     4.8 grante-</td><td>170.1.1         170.1.1           170.1.1         170.1.1           125.7.7.2         36.3.3           14.9.9         14.9.9           116.00         116.00           116.01         12.9.9           117.1         28.3           118.00         13.2           119.00         13.2           119.00         13.2           119.00         13.2           119.00         13.2           119.00         13.2           119.00         13.2           110.00         13.2           110.00         13.2           111.00         12.5           111.00         12.5           111.00         13.4           111.00         13.4           111.00         13.4           111.00         13.4           111.00         13.4           111.00         13.4           111.00         13.3           111.00         13.3           111.00         14.3           111.00         14.3           111.00         11.00           111.00         11.00           1111.00         11.00      <tr< td=""><td>600.36.2.173944255(C-singleste with complex IV           123971 L5054425(C-singleste with complex IV           12398.1.505442           1236.0.51205977 [Ecx20           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.51206           1237.0.51207           1238.0.5277277.0.14.4764421 protein           1239.0.55557597           1239.0.55557557           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.539577           1239.0.539577           1239.0.539577           1230.</td><td>e metabolium e met</td><td>Mitchin           0000         Nitchin           Mitchin         Mitchin           Mitchin         Mitchin           Mitchin         Mitchin           Mitchin         Mitchin           Mitchin         BiA-Arine           Mitchin         Mitchin           Mitchin         BiA-Arine           Mitchin         Mitchin           Mitchin         BiA-Arine           Mitchin         Mitchin           Mitchin         Arine a           Mitchin         BiA-Arine a           Mitchin</td></tr<></td></td<> | 4.04 intechendrion     4.32 elems grantes     4.34 elems grantes     4.35 elems     4.34 elems     4.35 elems     4.35 elems     4.35 elems     4.38 anclues     4.38 anclues     4.38 anclues     4.38 anclues     4.39 anclues     5.7 PM - propheral     1     4.6 grante-     4.7 grante-     4.8 grante-  | 170.1.1         170.1.1           170.1.1         170.1.1           125.7.7.2         36.3.3           14.9.9         14.9.9           116.00         116.00           116.01         12.9.9           117.1         28.3           118.00         13.2           119.00         13.2           119.00         13.2           119.00         13.2           119.00         13.2           119.00         13.2           119.00         13.2           110.00         13.2           110.00         13.2           111.00         12.5           111.00         12.5           111.00         13.4           111.00         13.4           111.00         13.4           111.00         13.4           111.00         13.4           111.00         13.4           111.00         13.3           111.00         13.3           111.00         14.3           111.00         14.3           111.00         11.00           111.00         11.00           1111.00         11.00 <tr< td=""><td>600.36.2.173944255(C-singleste with complex IV           123971 L5054425(C-singleste with complex IV           12398.1.505442           1236.0.51205977 [Ecx20           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.51206           1237.0.51207           1238.0.5277277.0.14.4764421 protein           1239.0.55557597           1239.0.55557557           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.539577           1239.0.539577           1239.0.539577           1230.</td><td>e metabolium e met</td><td>Mitchin           0000         Nitchin           Mitchin         Mitchin           Mitchin         Mitchin           Mitchin         Mitchin           Mitchin         Mitchin           Mitchin         BiA-Arine           Mitchin         Mitchin           Mitchin         BiA-Arine           Mitchin         Mitchin           Mitchin         BiA-Arine           Mitchin         Mitchin           Mitchin         Arine a           Mitchin         BiA-Arine a           Mitchin</td></tr<>   | 600.36.2.173944255(C-singleste with complex IV           123971 L5054425(C-singleste with complex IV           12398.1.505442           1236.0.51205977 [Ecx20           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.512058           1237.0.51206           1237.0.51207           1238.0.5277277.0.14.4764421 protein           1239.0.55557597           1239.0.55557557           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.5395757           1239.0.539577           1239.0.539577           1239.0.539577           1230.   | e metabolium e met   | Mitchin           0000         Nitchin           Mitchin         Mitchin           Mitchin         Mitchin           Mitchin         Mitchin           Mitchin         Mitchin           Mitchin         BiA-Arine           Mitchin         Mitchin           Mitchin         BiA-Arine           Mitchin         Mitchin      
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NB45 NB45 NB45 NB45 NB45</td> <td>4.0 a introchendrion     4.32 dense grantes     4.34 dense grantes     4.35 dense grantes     4.37 locatives - mon-thom     4.37 locatives - mon-thom     4.38 locatives - mon-thom     4.38 locatives - mon-thom     4.39 locatives - dense     4.39 locatives     4.41 locations - men     4.55 lintschendrion - men     4.55 lintsch</td> <td>b         170.1           170.1         170.1           212,7,7,2         36.3           36.3         36.3           116.00         116.00           bit         13.3           110.01         110.01           110.01         110.01           110.01         110.01           110.01         110.01           110.01         110.01           110.01         110.01           110.01         100.82           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02</td> <td>600.36.2.173944555(C-singtest with complex IV<br/>27397 1.505645(T) (Flocks)<br/>156.96 0.774023044 T[costs)<br/>156.96 0.774023044 T[costs)<br/>156.96 0.774023047 [costs]<br/>156.96 0.774023047 [costs]<br/>156.96 0.77402304 [costs]<br/>156.96 0.058977588 (GMAS<br/>5.20 0.26885740 (Psochistical protein<br/>8.94 0.67772227) (TM-detected NM polymerase<br/>8.0.877742027) [Costs]<br/>156.06 0.259775227] (TM-detected NM polymerase<br/>8.0.877742027) [Costs]<br/>157.96 0.42581758 (GMAS<br/>150.90 0.2597527) [Costs]<br/>159.00 4.259875207 [Costs]<br/>159.00 4.259875207 [Costs]<br/>159.00 4.259875267 [Costs]<br/>159.00 4.259875267 [Costs]<br/>159.00 4.25987527] 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  | 4.0 a introchendrion     4.32 dense grantes     4.34 dense grantes     4.35 dense grantes     4.37 locatives - mon-thom     4.37 locatives - mon-thom     4.38 locatives - mon-thom     4.38 locatives - mon-thom     4.39 locatives - dense     4.39 locatives     4.41 locations - men     4.55 lintschendrion - men     4.55 lintsch  | b         170.1           170.1         170.1           212,7,7,2         36.3           36.3         36.3           116.00         116.00           bit         13.3           110.01         110.01           110.01         110.01           110.01         110.01           110.01         110.01           110.01         110.01           110.01         110.01           110.01         100.82           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02           110.01         10.02   | 600.36.2.173944555(C-singtest with complex IV<br>27397 1.505645(T) (Flocks)<br>156.96 0.774023044 T[costs)<br>156.96 0.774023044 T[costs)<br>156.96 0.774023047 [costs]<br>156.96 0.774023047 [costs]<br>156.96 0.77402304 [costs]<br>156.96 0.058977588 (GMAS<br>5.20 0.26885740 (Psochistical protein<br>8.94 0.67772227) (TM-detected NM polymerase<br>8.0.877742027) [Costs]<br>156.06 0.259775227] (TM-detected NM polymerase<br>8.0.877742027) [Costs]<br>157.96 0.42581758 (GMAS<br>150.90 0.2597527) [Costs]<br>159.00 4.259875207 [Costs]<br>159.00 4.259875207 [Costs]<br>159.00 4.259875267 [Costs]<br>159.00 4.259875267 [Costs]<br>159.00 4.25987527] [Costs]<br>150.00 4.2598742] [Costs]<br>150.00 4.259742] [Costs]<br>150.00  | t of this complex is down-regulated in Bz t of this complex is down-regu   | Mitchio           Mitchio      Mitchio  
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   | 600.36.2.173944255(C-singlate with complex IV           20.39.1.15054425(C-singlate with complex IV           20.39.1.15054425(C-singlate with complex IV           20.36.0.5129977[Eox35]           20.36.0.5129977[Eox35]           20.36.0.5129977[Eox35]           20.36.0.5129977[Eox35]           20.36.0.5129977[Eox35]           20.36.0.5129977[Eox36]           20.36.0.5129977[Eox37]           20.40.0.53877588[GMA5           20.37272727[OM-d-free/cold PA polymerase           20.3727272[OM-d-free/cold PA polymerase           20.3727372[CM-d-free/cold PA polymerase           20.372737[CM-d-free/cold PA polymerase           20.3.37357[Sfree/cold Pa polymerase           20.472802021 [FgCR17           21.3.3.0.338757[Sfree/cold Pa polymerase           21.66.1111232[A Pin-chingroprotein           21.66.111232[A Pin-chingroprotein           21.66.111232[A Pin-chingroprotein           21.66.111232[A Pin-chingroprotein           21.66.11232[A Pin-chingroprotein  | e metabolium e metabolium t of this complex is down-regulated in B:  | Mitchin           000000000000000000000000000000000000   
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   | 4.04 intechendrion     4.32 lense grankes     4.32 lense grankes     4.32 lense grankes     4.32 lense grankes     4.34 lense grankes     4.36 lense grankes     4.37 lencleus     5.7 PM - peripheral 1     4.4 lense     4.36 lense     4.36 lense     4.36 lense     4.36 lense     4.36 lense     4.37 lencleus     4.36 lense     4.37 lense     4.38 lense     4.37 lense     4.38 lense     4.  | 170.1.1         170.1.1           170.1.2         170.1.1           182.17,77         38.3.3           18.10,70         116.05           116.05         116.05           116.05         116.05           116.05         116.05           116.05         116.05           110.01         124.42           110.01         13.2           110.01         13.2           110.01         13.2           110.01         14.64           110.02         14.64           110.02         14.64           110.02         14.64           110.02         14.64           111.03         14.64           112.55         14.64           113.2         14.64           115.04         14.64           115.04         14.64           116.05         15.64           117.05         19.00           118.06         65.93           119.03         131.44           110.05         131.44           111.11         121.55           111.11         121.55  | 600.36.2.173944255(C-nignets with complex IV           27.397 1.55054271 (Flocks)           156.96 0.774023044 (Flocks)           125.46 0.51350977 (Flocks)           125.46 0.51350977 (Flocks)           125.46 0.51350977 (Flocks)           125.46 0.51350977 (Flocks)           126.47 0.5135077 (Flocks)           126.47 0.533577 (Flocks)           126.47 0.533577 (Flocks)           127.47 0.60 0.5335775387 (Flocks)           127.47 0.412315781 (Flocks)           127.48 0.412315781 (Flocks)           127.40 0.425357857 (Flocks)           127.40 0.42535757 (Flocks)           128.41 0.42539757 (Flocks)           128.41 0.42339757 (Flocks)           128.41 0.42339757 (Flocks)           128.41 0.42337577 (Flocks)           128.41 0.424374447 (Flocks)           128.41 0.4434247 (Flocks)           128.41 0.44447 (Flocks)           128.41 0.44447 (Flocks)      <  
  | e metabolism e metabolism t of this complex is down-regulated in Bz e metabolism   | Mitchin           Mitchin <td< td=""></td<>  |
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   | 4.04 introchendrion     4.32 idense grandes     4.35 idense grandes     4.55 introchendrion     5.04 idense grandes     4.55 introchendrion     5.7 PM - preprieval     1.38 inclusive .mon-chrom     4.39 introchendrion     5.7 PM - preprieval     1.55 introchendrion     4.40 inclusive .mon-chrom     4.55 introchendrion     4.60 inclusive     4.60 inclusive     4.61 i  | 170.1.1         170.1.1           170.1.1         170.1.1           125.7.7.2         36.3.3           16.0.0         116.00           111.0.0         12.9.4           121.3         28.1.3           121.4         29.9.4           110.0         11.0.0           110.0         28.1.3           28.1.1         29.2.4           121.2         28.4.4           121.2         28.4.4           121.2         28.4.4           122.5         28.4.4           124.2         28.4.4           125.4.5         45.4.4           125.4.5         45.4.4           125.4.5         45.4.4           125.5         45.4.4           126.5         55.9.5           126.5         55.9.5           126.5         55.9.5           126.6         53.4.4           127.7         72.7           127.7         72.7  
   | 600.36.2.129244255(C-singstex with complex IV           20.39 I L5054425(C-singstex with complex IV           20.39 I L50544217[Costs]           20.48 0.51292977[Costs]           20.48 0.5129277[Costs]           20.49 0.5729277[Costs]           20.49 0.5729277[Costs]           20.48 0.5729277[Costs]           20.48 0.5729277[Costs]           20.412811578[hypothetical protein           20.39 0.56557297[CpGC11]           20.412811578[hypothetical protein           20.412811578[hypothetical protein           20.40 0.55895527[Sorren entablem, Series/pyruste transminace           21.39 0.40495771[CpGC12]           20.40 0.54895527[Sorren entablem, Series/pyruste transminace           21.43 0.4124124017[CpGC14]           20.41 0.54895527[Sorren entablem, Series/pyruste transminace           21.43 0.4124124017[CpG14]           21.43 0.4124142017[CpG14]           21.43 0.4124142017[CpG14]           21.43 0.41241[hypothetical protein           21.44 0.42245524[hypothetical protein           21.44 0.   | PMID: 18936550<br>PMID: 18936550<br>PMID: 30377279<br>PMID: 17164247<br>BioRviv DOI: 10.1101/20<br>BioRviv | Mitchio           Mitchio <td< td=""></td<>  |
| 100         L-009835805132           101         L-009835805132           102         L-260739387413           102         L-260740740718           102         L-260740740718           103         L-260740740718           103         L-260740740718           103         L-260740740718           103         L-2707553952542           103         L-2707553952542           104         L-11474353765           105         L-26074724724284155           105         L-26074724724284155           104         L-114743537151           105         L-260747247248415           105         L-2607472472434155           104         L-270755501441           104         L-270755501441           105         L-260747242434155           105         L-260747242434155           104         L-270755801441           10407455546144         L-27074242434155   
   
   | Lang 722 702 1<br>Characterized States 1<br>Constraints                       | 2.0054329211804<br>2.005429211804<br>2.807593585611<br>1.8251060518971<br>1.4691906513974<br>1.4691906513974<br>1.4691906513974<br>2.159198271<br>2.159199737058<br>2.159199737058<br>0.2997945137587<br>0.2997945137587<br>0.2997945137587<br>0.2997945137587<br>0.2997945137587<br>0.2997945137587<br>0.2997945137587<br>0.2997945137587<br>0.29979451358502<br>0.75014551758<br>0.75014551758<br>0.7401451758<br>0.7401451758<br>0.7401451758<br>0.7401451758<br>0.7401451758<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851929<br>0.4751651851245552<br>0.47516519219<br>0.4751551851245552<br>0.4751651223<br>0.475165124523<br>0.4751651245352<br>0.4751651245352<br>0.4751651245352<br>0.4751651245352<br>0.4751651245352<br>0.4751651245352<br>0.4751651245352<br>0.4751651245352<br>0.4755549211671<br>0.47515549211671   | 12713705<br>37109500<br>14089000<br>1138042<br>347763333<br>4716355755<br>6474755<br>384143333<br>4962030<br>12786000<br>64313152<br>103365000<br>6431375<br>30355000<br>64373750<br>22431000<br>10357550<br>5351555<br>536155<br>536155<br>536497<br>31009972<br>335567500<br>554897<br>31009972<br>335567500  | 00000 0000 0000 0000 0 0000 0 1568 0 1568 0 1777 0 0000 0 12500 0 0000 0 1777 0 0 0 0 0 0 0 0 0 0 0 0   
   
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   | 4.04 intechendrion     4.32 dense grantes     4.32 dense grantes     4.32 dense grantes     4.32 dense grantes     4.35 anticolus     4.34 dense grantes     4.35 anticolus     4.35 anticolus     4.35 anticolus     4.35 anticolus     4.35 anticolus     4.37 Marchaeles     4.38 anticus     4.38 anticus     4.39 anticus     4.39 anticolus     4.4 anclus  | 170.1.1<br>170.1.1<br>170.1.1<br>170.1.1<br>170.1.1<br>170.1.1<br>170.1.1<br>180.1.1<br>180.1.1<br>180.1.1<br>180.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.1.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190.0.1<br>190  | 600.36.2.173944255(C-singlets with complex IV           27.397 I.50504217 [Focks6           156.96 0.774023044 [Focks6]           156.96 0.774023047 [Focks6]           156.96 0.774023047 [Focks6]           156.96 0.774023047 [Focks6]           156.96 0.774023047 [Focks6]           156.96 0.0538775836 (FAAS           150.06 0.0538775836 (FAAS           150.07 0.053877586 (FAAS           150.08 0.057727277 (FAAS           150.08 0.0577727277 (FAAS           160.077122027 (FAAS           150.0         0.55973466 (FaASAAB, NASA Polymerase           150.0         0.55973426 (FaASAB, NASA Polymerase           150.0         0.559374507 (FaCR FIL           150.0         0.440580237 (FaCR FIL           151.0         0.053875587 (Facrie metabolism, Serie/pryoutet transminse           121.6         1111234 (Facrie Metabolism, Serie/pryoutet transminse           123.0         0.139375386 (Facrie Metabolism, Methorine aderosy (transferase           152.0         0.032373686 (Facrie Metabolism, Serie / pryotimets methyltransferase Ub2/COCS. Ubiguiton           150.0         0.132373546 (Ubiopalong metabolism, involved in regulating stage conver  
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Hopeiiiiiii</td>   | 600.36.2.173944255(Co-migrates with complex IV           20.39.1.51054217 (Fig.Os/B)           116.96.80.774023644 (Fig.Os/B)           116.96.80.774023644 (Fig.Os/B)           116.96.80.774023644 (Fig.Os/B)           116.96.81.7740237445 (Fig.Os/B)           116.96.81.7740237417 (Mos/S) 4/like, Elevient to be involved in the generation of 285 rRNA           70.08.0338775438 (Fig.As/B)           117.86.04.1371127721701/M-directed BNA polymerase           120.91.04557712721701/M-directed BNA polymerase           120.91.0455771120171201711           150.91.0455781 (Spotherical protein           130.91.045577575 (Fig.GNLT)           156.60.0.476680201 (Fig.GNLT)           157.81.03503851 (Fig.Esc)           131.80.0360375561 (Fig.Esc)           131.80.0360375561 (Fig.Esc)           131.80.0360375561 (Fig.Esc)           131.80.0360375561 (Fig.Esc)           133.80.0360375561 (Fig.Esc)           133.80.036037561 (Fig.Esc)           133.80.0360375761 (Fig.Esc)           133.80.036047575 (Fig.Esc)           133.80.036047575 (Fig.Esc)  | e metabolum<br>PMID: 18936550<br>PMID: 30377279<br>PMID: 30377279<br>PMID: 17164247<br>BioRiv DOI: 10.1101/20<br>BioRiv DOI: 10.1101/20<br>BioRiv DOI: 10.1101/20<br>BioRiv DOI: 10.1101/20<br>BioRiv DOI: 10.1101/20<br>BioRiv DOI: 10.1101/20  | Mitchio           Mitchio      Hopeiiiiiii   
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   | 4.04 intechendrion     4.12 dense granules     4.22 dense granules     4.22 dense granules     4.24 dense granules     4.26 intechendrion - solut     4.38 inclusus - non-chrome     4.39 microseneme     4.39 microseneme     4.39 microseneme     4.39 microseneme     4.39 microseneme     4.30 microseneme     4.31 microseneme     4.31 microseneme     4.31 microseneme     4.31 microseneme     4.31 microseneme     4.32 mitochendrion     4.31 microseneme     4.32 microseneme     4.31 microseneme   | 170.1.1 (1.1 (1.1 (1.1 (1.1 (1.1 (1.1 (1.1  
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<td>170.11.170.11<br/>212.57.75.10<br/>241.25.25.10<br/>16.05.10<br/>16.05.10<br/>16.05.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.11.10<br/>10.</td> <td>600.36.2.173944255(C-singstate with complex IV           20.39.1.5105425(C-singstate with complex IV           20.39.1.5105425(C-singstate with complex IV           20.39.1.5105425(C-singstate with complex IV           20.36.0.512597(Ecox3b           20.36.0.512597(Ecox3b           20.36.0.512597(Ecox3b           20.36.0.512597(Ecox3b           20.36.0.512597(Ecox3b           20.40.0.5127127(DN-51446) Eebeval to be involved in the generation of 285 rBNA           70.08.0.50377227(DN-51456) Eebeval to be involved in the guineration of 285 rBNA           20.40.0.512727(DN-51456) Eebeval to be involved in the guineration of 285 rBNA           20.40.0.512727(DN-51456) Eebeval to be involved in regulating stage conversion           20.40.0.5127127(DN-51456) Epiceta           20.40.0.5127127(DN-144640000, involved in regulating stage conversion           20.40.0.5127127(DN-14560000) Epiceta           20.40.0.5027127(DN-1456000000000000000000000000000000000000</td> <td>e metaboliom</td> <td>Mitchio           202.08.17.252163         Mitchio           Mitchio         Mitchio</td>   | 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   | Mitchio           202.08.17.252163         Mitchio           Mitchio         Mitchio   |
| 100         U.2009833855132           100         U.200983385132           100         U.200983785132           100         U.250739387413           100         U.25073917           100         U.2507491           100         U.25074913918743           100         U.2507491401916           100         U.2507491401916           100         U.2507491401916           100         U.2507491401916           100         U.2507491401916           101         U.2707539552144           101         U.270753955141           101 <td>Lang 722 702 11<br/>60642688439 11<br/>60642688439 12<br/>2184371642 2<br/>2074071407318 1<br/>2397493391915 0<br/>602278072354 0<br/>602278072354 1<br/>107553925124 1<br/>11<br/>77553925124 1<br/>11<br/>77553925124 1<br/>11<br/>77553925124 1<br/>11<br/>77553925124 1<br/>11<br/>7755392512 1<br/>11<br/>11<br/>11<br/>11<br/>11<br/>11<br/>11<br/>11<br/>11</td> <td>2.0054372411804<br/>12.0054254211804<br/>12.837555555611<br/>12.83756555527<br/>1.469199050139374<br/>1.2697695755827<br/>1.269793775214<br/>13.819611282349<br/>0.5969017768827<br/>2.1951987797058<br/>0.26970455157587<br/>0.26970455157587<br/>0.3300237656525<br/>0.5151758215881<br/>1.385951285614<br/>0.7360515758<br/>1.385951285614<br/>0.7360515758<br/>0.74145517588<br/>1.385951292634<br/>0.745695159256<br/>0.74145517588<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.7414551758<br/>0.741455555555555555555555555555555555555</td> 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3.68559<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.19595<br/>2.1955<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.19555<br/>2.1955</td>
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solut     4.66 intechendrion - solut     4.67 intechendrion     4.7 inacleus - non-chrome     4.67 intechendrion     4.67 inacleus - non-chrome     4.68 intechendrion     4.64 inacleus - chromatin     4.64 intechendrion     4.64 intechendrion     4.64 intechendrion     4.64 intechendrion     4.65 intechendrion     4.64 intechendrion     4.65 intechendrion</td> <td>170.11.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170.12.<br/>170</td> <td>600.36.2.173944255(C-singtracts with complex IV           20.391 1.615044217 [Costs]           156.96 0.7740230447 [Costs]           125.86 0.51350977 [Costs]           126.86 0.51350977 [Costs]           126.86 0.51350977 [Costs]           126.86 0.51350977 [Costs]           126.87 0.5135077 [Costs]           126.88 0.5135077 [Costs]           127.86 0.513578 [Costs]           127.86 0.41251372[Costs]           127.86 0.41251372[Costs]           127.86 0.41251372[Costs]           128.0 0.475050007 [Cost:11           126.0 4.4251372[Costs]           127.86 0.4258357[Sost:ne metabolism, Serine/pyrouste transminuse           127.46 0.42583757[Sost:ne metabolism, Serine/pyrouste transminuse           128.0 4.42583257[Sost:ne metabolism, Serine/pyrouste transminuse           128.10 0.42583757[Sost:ne metabolism, Serine/pyrouste transminuse           128.3 0.4358742[Cost:N           128.3 0.4358745[Cost:N           128.3 0.4358745[Cost:N           128.3 0.4358745[Cost:N           128.3 0.4358745[Cost:N           128.3 0.4358745[Cost:N           128.3 0.4358745[Cost:N           128.3 0.435874</td> <td>e metabolium</td> <td>Mitchio           Q20.08.17.252163         Mitchio           Mitchio         Mitchio           Mitchio         Mitchio           Q20.08.17.252163         Mitchio           Mitchio         Bitchio           Q20.08.17.252163         Mitchio           Q20.08.17.252164         Mitchio           Q20.08.17.253464/1         Mitchio           Q20.08.18.253464/1         Mitchio           Q20.08.18.253464/1<!--</td--></td>  
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   | 1224977500 3.2077<br>14.970000 5.49456<br>190755000 5.00915<br>173297500 1.70100<br>2317333 2 .89533<br>2333130 2.64516<br>93131205 2.2553<br>12037333 2 .395331<br>2365311<br>2365311<br>2365311<br>246531000 1.64531<br>57558000 0.46351<br>1246670500 3.17922<br>22790000 3.68593<br>1372475000 3.11922<br>1246670500 2.43951<br>1372475000 3.18592<br>1224667500 2.16552<br>158570000 3.68559<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.19595<br>2.1955<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.19555<br>2.1955   | 70234232<br>97824559<br>97824559<br>9782559<br>9782559<br>9782559<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>978255<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>978255<br>9782555<br>9782555<br>9782555<br>9782555<br>978255<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>978255<br>9782555<br>978255<br>9782555<br>9782555<br>978255<br>9782555<br>9782555<br>9782555<br>9782555<br>978255<br>978255<br>9782555<br>978255<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>978255<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9782555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>9775555<br>97755555<br>97755555<br>97755555<br>97755555<br>97755555<br>97755555<br>97755555<br>9775555555<br>977555555<br>9775555555555  
   | 4.04 intechendrion     4.12 dense granules     4.12 dense granules     4.12 dense granules     4.12 dense granules     4.14 dense granules     4.66 intechendrion - solut     4.66 intechendrion - solut     4.67 intechendrion     4.7 inacleus - non-chrome     4.67 intechendrion     4.67 inacleus - non-chrome     4.68 intechendrion     4.64 inacleus - chromatin     4.64 intechendrion     4.64 intechendrion     4.64 intechendrion     4.64 intechendrion     4.65 intechendrion     4.64 intechendrion     4.65 intechendrion  | 170.11.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170.12.<br>170  | 600.36.2.173944255(C-singtracts with complex IV           20.391 1.615044217 [Costs]           156.96 0.7740230447 [Costs]           125.86 0.51350977 [Costs]           126.86 0.51350977 [Costs]           126.86 0.51350977 [Costs]           126.86 0.51350977 [Costs]           126.87 0.5135077 [Costs]           126.88 0.5135077 [Costs]           127.86 0.513578 [Costs]           127.86 0.41251372[Costs]           127.86 0.41251372[Costs]           127.86 0.41251372[Costs]           128.0 0.475050007 [Cost:11           126.0 4.4251372[Costs]           127.86 0.4258357[Sost:ne metabolism, Serine/pyrouste transminuse           127.46 0.42583757[Sost:ne metabolism, Serine/pyrouste transminuse           128.0 4.42583257[Sost:ne metabolism, Serine/pyrouste transminuse           128.10 0.42583757[Sost:ne metabolism, Serine/pyrouste transminuse           128.3 0.4358742[Cost:N           128.3 0.4358745[Cost:N           128.3 0.4358745[Cost:N           128.3 0.4358745[Cost:N           128.3 0.4358745[Cost:N           128.3 0.4358745[Cost:N           128.3 0.4358745[Cost:N           128.3 0.435874  
  | e metabolium   | Mitchio           Q20.08.17.252163         Mitchio           Mitchio         Mitchio           Mitchio         Mitchio           Q20.08.17.252163         Mitchio           Mitchio         Bitchio           Q20.08.17.252163         Mitchio           Q20.08.17.252164         Mitchio           Q20.08.17.253464/1         Mitchio           Q20.08.18.253464/1         Mitchio           Q20.08.18.253464/1 </td  |
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   | PMID: 18936550<br>PMID: 30377279<br>PMID: 17164247<br>BioRwir DDI: 10.1101/20<br>BioRwir DDI: 10.1101/20<br>BioRwir DDI: 10.1101/20<br>BioRwir DDI: 10.1101/20<br>BioRwir DDI: 10.1101/20<br>BioRwir DDI: 10.1101/20<br>BioRwir DDI: 10.1101/20  | Mitchin           0.17,252163         Mitchin           Mitchin         Mitchin      Mitchin           Mitchin   |
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   | 4.04 intochondrion<br>4.32 dense grandes<br>4.32 dense grandes<br>4.32 dense grandes<br>4.36 intochondrion - solut<br>4.36 intochondrion - solut<br>5.3 micronemes<br>0.57 PM - peripheral 1<br>0.67 mitochondrion - men<br>1.55 mitochondrion - men<br>4.54 mitochondrion - men<br>0.11 (crosol<br>4.49 mackeus - chromatin<br>3.48 mitochondrion - men<br>2.54 mitochondrion - men<br>2.54 mitochondrion - men<br>2.54 mitochondrion - men<br>3.54 mitochondrion - men<br>3.55 mitocho | 170.11<br>215.77<br>241.33<br>36.33<br>14.94<br>116.05<br>21.94<br>ati<br>104.17<br>28.5<br>190.84<br>ati<br>274.55<br>mb<br>109.82<br>310.84<br>31.22<br>208.45<br>31.22<br>208.45<br>83.66<br>83.66   | 600.36.2.173944255(C-singtrate with complex IV           20.39 I L50544217[Costs]           21.36 I 0.31269971[Costs]           21.36 I 0.3126971[Costs]           21.372512[Costs]           21.372512[Costs]           21.372512[Costs]           21.372512[Costs]           21.372512[Costs]           21.372512[Costs]           21.372512[Costs]           21.372512[Costs]           21.372512[Costs]           20.4727122027[Costs]           21.37252[Costs]           21.37252[Costs]           21.37252[Costs]           21.37252[Costs]           21.37252[Costs]           21.37252[Costs]           21.37252[Costs]           21.37252[Costs]           21.38.342532[Costs]           21.39.342532[Costs]           21.39.342532[Costs]           21.39.342532[Costs]           21.39.342532[Costs]           21.342532[Costs]           21.3425332[Costs] <t< td=""><td>PMID: 18036550<br/>PMID: 30377279<br/>PMID: 7164247<br/>Bohwy COI: 10.101/20<br/>Bohwy COI: 10.101/20<br/>Bohwy COI: 10.101/20<br/>Bohwy COI: 10.101/20<br/>Bohwy COI: 10.101/20<br/>Bohwy COI: 10.101/20</td><td>Mitchio           Q20.08.17.252163         Mitchio           Mitchio         Mitchio           Mitchio         Mitchio           Q20.08.17.252163         Mitchio           Q20.08.17.252163         Mitchio           Q20.08.17.252164         Mitchio           Q20.08.17.253464/1         Mitchio           Q20.08.18.253464/1         Mitchio</td></t<>   | PMID: 18036550<br>PMID: 30377279<br>PMID: 7164247<br>Bohwy COI: 10.101/20<br>Bohwy COI: 10.101/20<br>Bohwy COI: 10.101/20<br>Bohwy COI: 10.101/20<br>Bohwy COI: 10.101/20<br>Bohwy COI: 10.101/20  
   | Mitchio           Q20.08.17.252163         Mitchio           Mitchio         Mitchio           Mitchio         Mitchio           Q20.08.17.252163         Mitchio           Q20.08.17.252163         Mitchio           Q20.08.17.252164         Mitchio           Q20.08.17.253464/1         Mitchio           Q20.08.18.253464/1         Mitchio  |
| Name         L-2049823855132           Name         L-2049823855132           Name         L-204973938743           Name         L-204973938743           Name         L-204973938743           Name         L-204973938743           Name         L-204973938743           Name         L-204973938743           Name         L-204974743748           Local         L-2019717           Local         L-2019174           Local         Local           Local         Local           Local         Local           Local         Local           Local         Local           Loca   
   
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   | 4.04 imtochondrion     4.12 dense granules     4.12 dense granules     4.12 incluois     0.43 dense granules     4.13 incluois     4.16 dense granules     4.16 dense granules     4.16 dense granules     4.17 incluois     4.15 imtochondrion     4.15 imtochondrion     4.15 imtochondrion     4.15 imtochondrion     4.16 dense     4.17 incluois     4.11 incluois     4.11 incluois     4.17 incluois     4.1  | 170.11<br>1215.72<br>241.33<br>36.31<br>14.94<br>116.05<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.94<br>21.9  | 600.36 : 2.179244255 (C-singtrace with complex IV           21.39 : 1.50544251 (Fjordsh           156.96 (D.774023084 / Fjordsh           157.96 (D.77402308 / Fjordsh           157.97 (D.7740 / Fjordsh           158.90 (D.7750 / Fjordsh           159.90 (D.7750 / Fjordsh            150.90 (D.7550 / Fjordsh            17  
  | PMID: 18036550<br>PMID: 30372279<br>PMID: 30372279<br>Bolikiv DOI: 10.101/20<br>PMID: 2345456<br>Bolikiv DOI: 10.101/20<br>Bolikiv DOI: 10.101/20<br>Bolikiv DOI: 10.101/20<br>Bolikiv DOI: 10.101/20  | Mittochio           202.08.17.252163         Mittochio           Mittochio         Mittochio <td< td=""></td<>   |
| 100         U.200983365313           100         U.200983365313           100         U.200983365313           100         U.25073938743           100         U.25073938743           100         U.25073938743           100         U.25073938743           100         U.25073938743           100         U.25073938743           100         U.250749376030           100         U.250749740740718           100         U.2708051288           100         U.2708051288           100         U.2708051288           100         U.2708051288           100         U.27080512883           100         U.27080512884           100         U.27080512884           100         U.27080512884           100         U.27080512884           100         U.27080512845           100         U.27080512   
   
   | 1.4447/27/27/03         1           1.51610851288         1           66942686439         1           1.941155910492         0           2.1243719482         2           074071407318         1           1.159327401331951         0           0.1169424067007         0           0.92780275345         0           0.827802782542         1           7/8553927655         1           1351760149002         1           1351760149002         1           1351760149002         1   | 2.0054292411804<br>12.805925855611<br>12.8251055515071<br>12.8251056515927<br>12.697954759827<br>12.697954759827<br>12.697954759214<br>13.81561128234<br>0.509907748827<br>21.9519967375551<br>0.2697045129513<br>0.2697045129513<br>0.2697045129513<br>0.269704512981<br>1.189651565565<br>1.280245165758<br>1.280245165758  |
12713750<br>37109500<br>14089000<br>1138042<br>307763333<br>40750333<br>4095020<br>647455<br>100355000<br>6430125<br>100355000<br>1425000<br>6430125<br>100355000<br>6430125<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>35890000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000000<br>3590000<br>3590000<br>3590000<br>3590000<br>359000<br>359000<br>359000<br>3590000<br>3590000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>359000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>359000<br>359000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>3590000<br>35900000<br>3590000<br>3590000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>3590000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>35900000<br>3590000000000   | 0000<br>57500<br>55000<br>50000<br>10000<br>15500<br>15500<br>1777<br>15000<br>10000<br>12500<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>10000<br>100000<br>100000<br>100000<br>100000<br>10000<br>10000<br>10000<br>10000<br>10000   
  | 149880000           \$8025000           49303250           2275076750           5683666.7         22           73074300           231295000           306770000           931770000           1858275000           1855225000  
   | 122497500 3.4075<br>144970000 5.40455<br>190755000 5.00519<br>173397500 1.71000<br>2377333.3 2.49828<br>34340000 2.46416<br>9831820 3.2255<br>24904700 2.6631<br>24974700 2.6631<br>24974700 2.6631<br>24974700 2.6631<br>24954700 2.4631<br>24954700 2.4631<br>249547000 2.4631<br>24954700 2.46317000000000000000000000000000000000000   | 708244324<br>373425659<br>43740847<br>963115692<br>963115692<br>903573608<br>905992126<br>333185403<br>905992126<br>3331825256<br>406950806<br>50637512<br>9668122986<br>665122986<br>665122986<br>665122986<br>5292458884<br>597747803  
   | 4.04 mitschondrion<br>4.32 dense grantes<br>2.82 nucleos grantes<br>2.65 mitschondrion - solu<br>4.63 nucleus - non-chrom<br>5.21 micsonemes<br>0.57 PM - peripheral 1.<br>0.67 mitschondrion - men<br>1.56 mitschondrion - men<br>1.56 mitschondrion - men<br>1.56 mitschondrion - men<br>2.43 mitschondrion - men<br>2.54 mitschondrion - men  | 170.11<br>1215.77<br>241.33<br>36.31<br>34.49<br>116.05<br>21.94<br>21.94<br>21.94<br>22.55<br>100.84<br>ath 274.55<br>mb 137.96<br>mb 142.43<br>31.21  | 600.36.2.173944255(C-singtacts with complex IV           213.971         1.50546           213.971         6.50546           213.971         6.50546           213.976         5.50547           213.66         0.1359977           213.66         0.1359977           213.66         0.1359977           213.67         0.135977           213.67         0.135977           213.67         0.135977           213.67         0.135977           213.78         0.645977           213.78         0.645977           214.79         0.645977           213.79         0.13597           214.79         0.055977           213.79         0.055977           214.79         0.055977           214.79         0.055977           214.79         0.055977           215.40         0.055977           214.79         0.055977           215.40         0.055977           215.40         0.055977           215.40         0.055977           215.40         0.055977           215.40         0.055977           215.40         0.055977           215.40  
  | PMID: 18036550<br>PMID: 30377279<br>PMID: 17160247<br>BioRwir DOI: 10.1101/20<br>BioRwir DOI: 10.1101/20<br>BioRwir DOI: 10.1101/20<br>BioRwir DOI: 10.1101/20   | Mitochio           0.17,252163         Mitochio           Mitochio         Mitochio           Dialogia         Mitochio           Mitochio         Mitochio           Dialogia         Mitochio           Dialogia         Mitochio           Dialogia         Mitochio           Dialogia         Mitochio  |
| Name         U.2009833855132           1.2007878         Control Status           1.200788         Control Status           1.2007888         Control Status           1.2007888         Control Status           1.2007888         Control Status           1.20078888 <td>1449/32/3703         1           15610851288         1           66942668439         1           12143719462         2           21243719482         2           2074071407318         1           1159410407319         0           21943719482         2           2074071407318         1           1169420657007         0           2798610339628         1           767553925342         0           06272471228         1           47483587265         1           31760149002         1</td> <td>2.0554/292411804<br/> 1.8076295526511<br/> 1.8076295526511<br/> 1.82510623156071<br/> 1.4667996479827<br/> 1.46919906139374<br/> 1.71697437763214<br/> 1.81349611382349<br/> 0.50890177488377<br/> 2.19319987297058<br/> 1.67770127105713<br/> 0.249749451875687<br/> 0.30022756857361<br/> 0.30022756857361<br/> 0.30022756857361<br/> 0.730801624955614<br/> 0.730801624955614<br/> 0.730801624955614<br/> 1.3245256407978<br/> 1.2422154045155<br/></td> <td>12713700<br/>37109500<br/>14089000<br/>1138042<br/>34776333.3<br/>1655675<br/>38414333.3<br/>4962050<br/>12786000<br/>6430125<br/>100365000<br/>18589000<br/>35890000<br/>6437250</td> <td>00000<br/>57500<br/>75000<br/>00000<br/>10000<br/>1568<br/>57500<br/>1568<br/>1777<br/>15000<br/>10000<br/>12500<br/>10000<br/>10000<br/>10000<br/>10000<br/>10000</td> <td>149880000 58025000 49303250 56836666.7 22 75076750 3074300 77706666.7 23 231295000 306770000 93177000 1828175000 1828175000</td> <td>1224977500 8.42077<br/>1414970000 5.49456<br/>190755000 5.00319<br/>173297500 1.701000<br/>9818250 2.6885<br/>9818250 3.22555<br/>1129333.3 2.36531<br/>290747500 2.68213<br/>918685000 1.74634<br/>675580000 1.74634<br/>675580000 1.74634<br/>6.60939<br/>2186000000 3.60093<br/>4155500000 5.4807<br/>7283850000 4.30391</td> <td>708244324<br/>739425559<br/>963115692<br/>963115692<br/>948838806<br/>933165403<br/>330573608<br/>90590126<br/>33182526<br/>406950006<br/>520637512<br/>063854218<br/>966512986<br/>6512986</td> <td>-4.04 mitochondrion<br/>-4.32 dense granules<br/>-2.82 inucleolus<br/>-2.66 mitochondrion - solu<br/>-3.81 miconemes<br/>-0.71 Miconemes<br/>-0.71 Micondrion - men<br/>-0.71 micondrion - men<br/>-2.51 mitochondrion - men<br/>-2.51 mitochondrion - men<br/>-2.54 mitochondrion - men<br/>-2.54 mitochondrion - men</td> <td>170.11<br/>125.72<br/>36.33<br/>14.94<br/>116.05<br/>109.417<br/>104.17<br/>22.93<br/>104.17<br/>104.17<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.83<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85<br/>109.85</td> <td>600.36.2.173944255(C-singtrate with complex IV           20.39 11.615642171 [focts/sh           116.96.80.7740230841 [focts/sh           126.86.0.15109797 [focts/sh           126.86.0.1510977 [focts/sh           126.86.0.1510977 [focts/sh           126.86.0.1510977 [focts/sh           126.86.0.0.150077 [focts/sh           126.86.0.0.150077 [focts/sh           126.87.0.150078 [focts/sh           126.87.0.150078 [focts/sh           127.07.01.0.100078 [focts/sh           127.000.0.100078 [focts/sh           128.0.0.0.1000078 [focts/sh           128.0.0.0.1000078 [focts/sh           128.0.0.0.1000078 [focts/sh           128.0.0.0.1000078 [focts/sh           128.0.0.0.10000078 [focts/sh           128.0.0.0.10000078 [focts/sh           128.0.0.0.100000000000000000000000000000</td> <td>PMID: 18036550<br/>PMID: 30377279<br/>PMID: 17164247<br/>Bohwy OOI: 10.101/20<br/>Bohwy OOI: 10.101/20<br/>Bohwy OOI: 10.101/20<br/>Bohwy OOI: 10.101/20<br/>Bohwy OOI: 10.101/20</td> <td>Mitchio           202.06.17.252163         Mitchio           Mitchio         Mitchio           Mitchio         Mitchio           Mitchio         Mitchio           Mitchio         Mitchio           Mitchio         Mitchio           Mitchio         Mitchio           RAMA         Biolitic           RAMA         Mitchio           Q20.06.18.25366W1         Mitchio           Q20.06.18.253466W1         Mitchio           Q20.06.18.253466W1         Mitchio           Q20.06.18.253466W1         Mitchio</td>   
   
  | 1449/32/3703         1           15610851288         1           66942668439         1           12143719462         2           21243719482         2           2074071407318         1           1159410407319         0           21943719482         2           2074071407318         1           1169420657007         0           2798610339628         1           767553925342         0           06272471228         1           47483587265         1           31760149002         1  | 2.0554/292411804<br>1.8076295526511<br>1.8076295526511<br>1.82510623156071<br>1.4667996479827<br>1.46919906139374<br>1.71697437763214<br>1.81349611382349<br>0.50890177488377<br>2.19319987297058<br>1.67770127105713<br>0.249749451875687<br>0.30022756857361<br>0.30022756857361<br>0.30022756857361<br>0.730801624955614<br>0.730801624955614<br>0.730801624955614<br>1.3245256407978<br>1.2422154045155<br>   | 12713700<br>37109500<br>14089000<br>1138042<br>34776333.3<br>1655675<br>38414333.3<br>4962050<br>12786000<br>6430125<br>100365000<br>18589000<br>35890000<br>6437250  
   | 00000<br>57500<br>75000<br>00000<br>10000<br>1568<br>57500<br>1568<br>1777<br>15000<br>10000<br>12500<br>10000<br>10000<br>10000<br>10000<br>10000  
   | 149880000 58025000 49303250 56836666.7 22 75076750 3074300 77706666.7 23 231295000 306770000 93177000 1828175000 1828175000  | 1224977500 8.42077<br>1414970000 5.49456<br>190755000 5.00319<br>173297500 1.701000<br>9818250
2.6885<br>9818250 3.22555<br>1129333.3 2.36531<br>290747500 2.68213<br>918685000 1.74634<br>675580000 1.74634<br>675580000 1.74634<br>6.60939<br>2186000000 3.60093<br>4155500000 5.4807<br>7283850000 4.30391  | 708244324<br>739425559<br>963115692<br>963115692<br>948838806<br>933165403<br>330573608<br>90590126<br>33182526<br>406950006<br>520637512<br>063854218<br>966512986<br>6512986   
   | -4.04 mitochondrion<br>-4.32 dense granules<br>-2.82 inucleolus<br>-2.66 mitochondrion - solu<br>-3.81 miconemes<br>-0.71 Miconemes<br>-0.71 Micondrion - men<br>-0.71 micondrion - men<br>-2.51 mitochondrion - men<br>-2.51 mitochondrion - men<br>-2.54 mitochondrion - men<br>-2.54 mitochondrion - men  | 170.11<br>125.72<br>36.33<br>14.94<br>116.05<br>109.417<br>104.17<br>22.93<br>104.17<br>104.17<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.83<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85<br>109.85  | 600.36.2.173944255(C-singtrate with complex IV           20.39 11.615642171 [focts/sh           116.96.80.7740230841 [focts/sh           126.86.0.15109797 [focts/sh           126.86.0.1510977 [focts/sh           126.86.0.1510977 [focts/sh           126.86.0.1510977 [focts/sh           126.86.0.0.150077 [focts/sh           126.86.0.0.150077 [focts/sh           126.87.0.150078 [focts/sh           126.87.0.150078 [focts/sh           127.07.01.0.100078 [focts/sh           127.000.0.100078 [focts/sh           128.0.0.0.1000078 [focts/sh           128.0.0.0.1000078 [focts/sh           128.0.0.0.1000078 [focts/sh           128.0.0.0.1000078 [focts/sh           128.0.0.0.10000078 [focts/sh           128.0.0.0.10000078 [focts/sh           128.0.0.0.100000000000000000000000000000   
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  | -4.04 mitochondrion<br>-4.32 dense granules<br>-2.82 nucleolus<br>0.48 dense granules<br>-2.66 mitochondrion -solu<br>-1.38 nucleus - non-chromu<br>-5.2 mitochondrion<br>0.57 PM - peripheral 1<br>0.67 mitochondrion - men<br>-2.47 nucleus - non-chromu<br>-2.53 mitochondrion - men  | 170.11<br>125.72<br>36.33<br>14.94<br>116.05<br>109.41<br>104.11<br>104.11<br>104.12<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43<br>100.43  
   | 600.36         2.173944255(Co-singutate with complex IV           2139 II L505464         1760350           115.68         0.51409577 [Efock3b           115.68         0.51409777 [Efock3b           115.68         0.51407977 [Efock3b           0.54307         10.6455           0.54307         10.6455           0.54307         10.6455           0.54307         10.6455           0.54307         10.6455           0.64307         10.6455           0.64307         10.6455           0.64307         10.6455           0.64307         10.6455           0.64101         10.6456           0.64101         10.6456           0.64101         10.6456           0.64101         10.6456           0.64101         10.6456           0.64101         10.6456           0.64101         10.6456           0.64101         10.6456           0.64101         10.6456           0.64101         10.6456           0.64101         10.6456           0.64101         10.6456           0.64101         10.6456           0.64101         10.64567           0.64111   | PMID: 18036550<br>PMID: 30377279<br>PMID: 30377279<br>PMID: 17165247<br>BioRwir 2001: 10.1101/20<br>PMID: 2345455<br>BioRwir 2001: 10.1101/20  | Mitocho           202.08.17.252163         Mitocho           Mitocho         Mitocho   |
| 1100         1.2.9093853855133           1200         1.2.9093853855132           1200         1.3.82052302360553           1200         1.3.82052302360553           1200         1.3.82052302360553           1200         1.3.82052302360553           1200         1.3.8205230236053           1201         1.4.71516051288           1201         0.4.71516051288           1201         0.4.71516051288           1201         0.5.2134719482           1201         0.5.2134719482           1205         0.5.2134719415511069           1206         0.4.721471497318           1206         0.4.71149741571109           1206         0.7111694140571070           1208         0.71179681031925           1204         0.71175951095325342   
   
   | 1.100/72/73/03         1.           1.51610851288         1.           1.696426868439         1.           9941155910492         0.           212843719482         2.           2.07/407/1407318         1.           1.169424057007         0.           0.27986103295345         0.           2.798610329628         1.           7675539255142         0.   | 2.055429411804<br>1.807629552611<br>1.82510526316071<br>1.82510526316071<br>1.7160743776321<br>1.71607437763214<br>1.81349611282499<br>0.58090177488327<br>2.13319967297058<br>1.6777012710513<br>0.249749451875687<br>0.330023705685366<br>0.515177982215881<br>1.1389691829644  | 127137500<br>371095000<br>140890000<br>11380425<br>347763333.3<br>16556755<br>38414333.3<br>49620500<br>12786000<br>64301255<br>100365000  
  | 10000<br>10000<br>10000<br>10000<br>14250<br>1568<br>1568<br>157500<br>16500<br>1777<br>15000<br>10000<br>12500<br>10000   
  | 1498800000<br>580250000<br>49303250<br>56836666.7 22<br>75076750<br>30743000<br>77706666.7 21<br>231295000<br>599765000<br>306770000<br>4961950000   
   | 1224977500 3.42077<br>414970000 5.49456<br>190755000 5.0919<br>173297500 1.70100<br>223173333.3 2.89828<br>343340000 2.68816<br>98318250 2.2555<br>11129333.3 2.365311<br>290747500 2.06231<br>91865000 1.74634<br>6.755580000 3.17922<br>827930000 1.61944  | 708244324<br>739425659<br>95311569<br>848838806<br>83385640<br>30357308<br>805992126<br>331825256<br>406950006<br>520637512  
   | -4.04 mitochondrion<br>-4.32 dense granules<br>-2.82 nucleolus<br>0.48 dense granules<br>-2.66 mitochondrion -solu<br>-1.38 nucleus - non-chromi<br>-5.2 micronemes<br>0.57 PM - peripheral 1<br>0.67 mitochondrion<br>-2.47 nucleus - non-chromi  | 170.11<br>1215.73<br>241.33<br>36.31<br>14.94<br>116.05<br>104.17<br>21.94<br>116.05<br>21.94<br>117.78<br>104.17<br>28.55<br>190.84<br>ati 274.55  | 600.36.2.173944255(Co-ingrates with complex IV           213.971         15.05640           15.69.60         0.774023044           15.69.60         0.774023044           15.69.60         0.774023044           15.69.60         0.774023044           15.69.61         0.774023044           15.69.62         2.8807431044           15.69.62         2.8807431044           15.69.62         2.8807433044           15.69.62         2.8807433044           16.69.62         2.8807433044           16.69.62         2.8807433044           16.69.62         2.8807433044           16.69.62         2.8807433044           16.79.712434         GAME           16.90.638777221         10.0114           17.60.410151128         GAME           17.60.410111                             
   | РМП: 18336550<br>РМП: 1337279<br>РМП: 17160247<br>Волжу DOI: 10.1101/20<br>РМП: 245455   | Mitocho<br>200.08.17.252163 Mitocho<br>Mitocho<br>Unineer<br>RRA-inte<br>E GRA<br>Uninicer<br>RRA-inte<br>Catalon<br>Unineer<br>RRA-inte<br>Catalon<br>Unineer<br>RRA-inte<br>Catalon<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-inte<br>RRA-int |
| 1100         1.2/9993853855133           1200         1.2/9993853855132           1200         1.382052302360533           1201         1.2289930768011           1213         4.0536347905076           12243         0.65114147927703           12569         0.560447914053076           12569         0.56044714501042           12751         0.54374071407318           10053         0.65394115501042           10053         0.65394115501042           10053         0.65394124307407           10053         0.6239749131051           10054         0.47692278027354344007107318           10053         0.47692278027354344           10054         0.47692278027364501396525  
   
   | L140+7275703 1.<br>151610651288 1.<br>696426868439 1.<br>211843719482 0.<br>211843719482 2.<br>074071407318 1.<br>12397491931915 0.<br>1169424057007 0.<br>6922780275345 0.<br>2798610329528 1.  | 2.0554292411804<br>1.8076295525011<br>1.8076295525011<br>1.26576964759827<br>1.71697437753214<br>1.8134961128249<br>0.5090177488327<br>2.19319987297058<br>1.67720127105713<br>0.24974451875687<br>0.33002375685136   | 127137500<br>371095000<br>140890000<br>11380425<br>347763333.3<br>16556750<br>6747650<br>384143333.3<br>49620500<br>127860000<br>64301250  
  | 20000<br>27500<br>5000<br>5000<br>1568<br>57500<br>1568<br>57500<br>1568<br>1777<br>15000<br>10000<br>12500  
  | 1498800000 580250000 49303250 56836666.7 22 75076750 30743000 77706666.7 21 231295000 599765000 306770000  
   | 1224977500 3.42077<br>414970000 5.49456<br>190755000 5.0919<br>173297500 1.70100<br>223173333 3 2.89820<br>43340000 2.64816<br>93818250 3.22555<br>111293333 2 2.65311<br>290747500 2.02531<br>91865000 1.74634<br>675550000 3.179222  | 708244324<br>739425659<br>963115692<br>84883806<br>331863403<br>303573608<br>805992126<br>331825256<br>408950806<br>520637512  
   | 4.04 mitochondrion     4.32 dense granules     4.32 nucleolus     0.48 dense granules     4.66 mitochondrion - solu     1.38 nucleus - non-chrom:     5.2 micronemes     0.57 PM - peripheral 1     0.67 mitochondrion   | 170.11<br>mbr 215.73<br>241.33<br>36.31<br>14.94<br>116.05<br>bble 21.94<br>atli 13.2<br>104.17<br>28.5<br>190.84   | 600.36.2.173944255(C-singtrate with complex IV           27.397 1.650542717 [Ecos3b           25.480 5.17505278           25.480 5.1505977 [Ecos3b           25.480 5.1505977 [Ecos3b           25.480 5.1505977 [Ecos3b           26.480 5.480749124(hypothetical protein           26.480 5.491757238           26.380745124(hypothetical protein           26.40 6.05377252727           26.40540 [hypothetical protein           26.40 6.077272727           27.4010247           27.4010247           28.0 4.07727277           27.4010247           28.0 4.07727277           28.0 4.07727277           28.0 4.0772727           28.0 4.0772727           28.0 4.0772727           28.0 4.0772727           28.0 4.0772727           28.0 4.0772727           28.0 4.0772727          
28.0 4.0772727           28.0 4.0772727           28.0 4.0772727           28.0 4.077277           28.0 4.0772727           28.0 4.0772727           28.0 4.077277           28.0 4.077277           28.0 4.077277           28.0 4.077277           28.0 4.077277           28.0 4.077277           28.   | PMID: 18036550<br>PMID: 30377279<br>PMID: 171651277<br>BioRay DOI: 10.1101/20  | Mitochin<br>200.08.17.252163 Mitochin<br>Mitochin<br>Mitochin<br>Mitochin<br>Il Mitochin<br>Rivi-Inte<br>Foreita<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Uninover<br>Rivi-Inte<br>Carateou<br>Rivi-Inte<br>Rivi-Inte<br>Carateou<br>Rivi-Inte<br>Rivi-Inte<br>Carateou<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte<br>Rivi-Inte   |
| 1100         1.2/9993853855133           1200         1.2/9993853855133           1200         1.22647390336413           12754         0.23607390386013           1230         0.2596930768013           12384         0.1612184792075703           1241         0.053634379050076           12757         0.05664379050076           12761         0.473151051288           0.0666942688439         0.6666942688439           127757         0.5521843719482           127576         0.5521843719482           12510         0.43074071407318           12689         0.77116943491391315           12689         0.771149431931309   
   
   | 1151610851288 1.<br>1150610851288 1.<br>115060426868439 1.<br>121843719482 2.<br>1074071407318 1.<br>12397491931915 0.<br>1169424057007 0.<br>1169424057007 0.   | 2.058429411804<br>1.8076295826611<br>1.25676964759827<br>1.26676964759827<br>1.71697437763214<br>1.71697437763214<br>1.81346511282349<br>0.50890177488377<br>2.9319987297058<br>1.67720127105713<br>0.38003276586336<br>0.38003276586336  | 127137500<br>371095000<br>140890000<br>34776333.3<br>15556750<br>6747650<br>38414333.3<br>49620500<br>137970000  
  | 000000<br>57500<br>57500<br>50000<br>00000<br>04250<br>1568<br>57500<br>1777<br>05000<br>00000   
  | 1498800000<br>580250000<br>49303250<br>56836666.7 22<br>75076750<br>30743000<br>77706666.7 21<br>231295000<br>50075500   
   | 1224977500 3.42077<br>4149700000 5.49456<br>1907550000 5.00919<br>173297500 1.70100<br>23173333 2.89828<br>343340000 2.64816<br>98318250 3.25555<br>11293333 2.365311<br>290747500 2.06231<br>918656500 1.75754  | 708244324<br>739425659<br>963115692<br>84883806<br>331863403<br>303573608<br>805992126<br>331825256<br>409050905   
   | 4.04 initochondrion     4.32 dense granules     4.32 dense granules     4.38 dense granules     4.48 dense granules     4.66 initochondrion - solu     1.38 nucleus - non-chrom     5.2 micronemes     0.57 DM - oppide=1*   | 170.11<br>nbi 215.73<br>241.35<br>36.31<br>14.94<br>116.05<br>ble 21.94<br>ati 13.2<br>104.17   | 600.36:2:179244255(Co-migrates with complex IV           213:91:1605442117[consb           126:86:0:17082356417[consb           126:86:0:1286397[r][consb           126:46:1286398417[consb           126:46:1286398417[consb           126:46:1286398417[consb           126:46:1286398417[consb           126:46:1286398417[consb           126:46:1286398417[consb           126:46:1286398417[consb           126:46:1286388416           126:46:1286388416           126:46:1286388416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416          
128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:128638416           128:46:   | PMID: 18036550<br>PMID: 30377279<br>PMID: 17164247   | Mitocho<br>20.08.17.252163 Mitocho<br>Mitocho<br>Unknow<br>RNA-inte<br>Gatalosi<br>Catalosi<br>National Catalosi<br>National Catalosi  |
| 1100         1.2/9993853855133           1200         1.2/9993853855133           1200         1.3806530236053           1275         1.226473793387413           1280         1.230930768013           1238         1.621149725703           1238         1.611591149725703           1762         0.437151610851288           15556         0.06669426864139           17757         1.65218437194307           10521843719432         1.052143719442           10530         0.4537447107318           1053         0.45374471047318  
   
   | 12109/192/19703         1.           1151610851288         1.           16696426868439         1.           9941155910492         0.           121843719482         2.           1074071407318         1.           2397491931915         0.   | 2.00584292411804<br>1.80762958526611<br>1.82510626316071<br>1.26676964759827<br>1.46919906139374<br>1.71697437763214<br>1.81349611282349<br>0.50990177488327<br>2.19319987297058<br>1.67720127105713<br>0.249749451875687   | 127137500<br>371095000<br>140890000<br>11380425<br>347763333<br>16556750<br>6747650<br>384143333.3   
  | 00000<br>57500<br>57500<br>50000<br>00000<br>04250<br>1568<br>57500<br>76500<br>1777   
  | 1498800000<br>580250000<br>49303250<br>56836666.7 22<br>75076750<br>30743000<br>77706666.7 21  
   | 1224977500 3.42077<br>4149700000 5.49456<br>1907550000 5.0939<br>173297500 1.70100<br>12317333.3 2.89828<br>343340000 2.64816<br>98318250 3.25555<br>11293333.3 2.36531  | 708244324<br>739425659<br>963115692<br>848838806<br>331863403<br>303573608<br>805992126  
   | -4.04 mitochondrion<br>-4.32 dense granules<br>-2.82 nucleolus<br>0.48 dense granules<br>-2.66 mitochondrion - solu<br>-1.38 nucleus - non-chroma  | 170.11<br>nbi 215.73<br>241.35<br>36.31<br>14.94<br>116.05<br>ible 21.94<br>atli 13.2   | 600.36:2:173944255(Co-migrates with complex IV           213:971 L505642           213:971 L505642           215:86:012709771 [GroxNo           215:86:012709771 [GroxNo           215:86:012709771 [GroxNo           216:86:012709771 [GroxNo           216:86:01270971 [GroxNo           216:86:01270971 [GroxNo           216:88:01270971 [GroxNo           216:88:01270971 [GroxNo           216:88:01270971 [GroxNo           216:89:01270971 [GroxNo           216:80:01270971 [GroxNo           216:80:0127071 [GroxNo           216:80:0127071 [GroxNo           216:80:0127071 [GroxNo           216:80:0127071 [GroxNo           216:80:012701 [GroxNo           216:80:012701 [GroxNo   
  | PMID: 18036550<br>PMID: 30377279   | Mitocho<br>220.08.17.252163 Mitocho<br>Mitocho<br>Mitocho<br>Christian<br>RNA-Inte<br>Frank<br>Ukristow<br>RNA-Inte<br>RNA-Inte<br>RNA-Inte  |
| 1.33         1.3299382385133           1.329938238513         2.3007482264175           1.5551         0.382052302360535           2.57754         0.22647393387413           1.329939768013         0.329930768013           1.3293         0.3296930768013           1.5218479275705         0.63194179275705           0.633941155010085         0.660642668439           1.5218471479427         1.552184719482           1.55218471479473183         1.552184714743738  
   
   | 1151610851288         1.           1151610851288         1.           1696426868439         1.           9941155910492         0.           121843719482         2.           1074071407318         1.   | 2.00584292411804<br>1.80762958526611<br>1.82510628316071<br>1.26676964759827<br>1.46919906139374<br>1.71697487763214<br>1.81349611282349<br>0.50890177488327<br>2.19319987297058<br>1.67720127105713  | 127137500<br>371095000<br>140890000<br>11380425<br>347763333.3<br>16556750<br>6747650  
  | 000000<br>57500<br>75000<br>50000<br>00000<br>00000<br>00000<br>1568<br>57500<br>76500   
  | 1498800000<br>580250000<br>49303250<br>56836666.7 22<br>75076750<br>30743000   
   | 1224977500 3.42077<br>4149700000 5.49456<br>1907550000 5.0919<br>173297500 1.70109<br>2317333.3 2.89828<br>343340000 2.64816<br>98318250 3.22555   | 708244324<br>739425659<br>437408447<br>963115692<br>848838806<br>331865403<br>303573608  
   | -4.04 mitochondrion<br>-4.32 dense granules<br>-2.82 nucleolus<br>0.48 dense granules<br>-2.66 mitochondrion - solu  | 170.11<br>nbi 215.73<br>241.35<br>36.31<br>14.94<br>116.05<br>bbe 21.94   | 60.35.2.179244255(C-singtrate with complex IV<br>27.397 1.505/45171 [fcos/sb<br>156.96 0.774023084 [fcos/sb<br>126.86 0.51807977 [fcos/sb<br>126.46 2.3807493045] /hypothetical protein<br>8.88 0.948775218(f6A45)<br>8.88 0.94877538(f6A45)<br>6.32 0.28887538(f6A45)   
  | PMID: 18036550<br>PMID: 30377279   | Mitocho<br>20.08.17.252163 Mitocho<br>Mitocho<br>Mitocho<br>Unknow<br>RNA-inte<br>2 GRA<br>Upknow  |
| 0.3.299383855133           0.3.299383855133           0.3.209383855133           0.38201742           0.382052302360535           7755           0.26473793387413           229           0.3299930788013           2282           0.3299930788013           52384           0.161218479275703           77521           0.437151610851288           55960           0.66696426868439           93376           0.4399411559104922           77571           0.251843714007  
   
   | 1151610851288         1.           1696426868439         1.           9941155910492         0.           121843719482         2.   | 2.00584292411804<br>1.80762958526611<br>1.82510626316071<br>1.2667694759827<br>1.46919906139374<br>1.71697437763214<br>1.81249611282349<br>0.50890177488327<br>2.19319697297058   | 127137500<br>371095000<br>140890000<br>11380425<br>347763333.3   
  | 000000<br>57500<br>75000<br>50000<br>00000<br>00000<br>04250<br>1568<br>57500  
  | 1498800000<br>580250000<br>49303250<br>56836666.7 22<br>75076750   
   | 1224977500 3.42077<br>4149700000 5.49456<br>1907550000 5.0919<br>173297500 1.70100<br>23173333.3 2.89828<br>343340000 2.64945  | 708244324<br>739425659<br>437408447<br>963115692<br>848838806<br>331863403   
   | -4.04 mitochondrion<br>-4.32 dense granules<br>-2.82 nucleolus<br>0.48 dense granules  | 170.11<br>nbr 215.73<br>241.35<br>36.31<br>14.94<br>116.05  | 603 85.2 1739244256 Co-migrates with complex IV<br>273.97 1.510924171 [75:0x86<br>166.98 0.7740230841 [75:0x56<br>123.68 0.511465/971 [75:0x56<br>104.6.2 8.289734971 [75:0x76]<br>104.6.2 8.28973404 [fworth-ficial protein<br>8.88 0.5949775101 [void-34.88, believed to be involved in the generation of 285 rRNA<br>70 06 10 ref977456 (feads  
  | PMID: 18036550   | Mitochov<br>200.08.17.252163 Mitochov<br>Mitochov<br>Mitochov<br>Mitochov<br>Rakow<br>RNA-Inte   |
| 1403         U.3.24993853855133           12851         0.240047842264175           75751         0.382052302360533           77754         0.226473793387413           12829         0.32969930768013           73438         -0.053634379059076           52384         0.161218479275703           52384         0.616218479257503           52384         0.606596426868439           55969         0.606596426868439  
   
   | 151610851288 1.<br>1696426868439 1.  | 2.00584292411804<br>1.80752958526611<br>1.82510626316071<br>1.26676964759827<br>1.46919906139374<br>1.71697437763214<br>1.81349611282349  | 127137500<br>371095000<br>140890000<br>11380425  
  | 57500<br>57500<br>50000<br>50000<br>50000<br>50000<br>50000  
  | 1498800000<br>580250000<br>49303250  
   | 1224977500 3.42077<br>4149700000 5.49456<br>1907550000 5.00919<br>173297500 1.70100  | 708244324<br>739425659<br>437408447<br>963115692   
   | -4.04 mitochondrion<br>-4.32 dense granules  | 170.11<br>nbi 215.73<br>241.35<br>36.31   | 603.82.1739244255(Co-migrates with complex IV<br>273.971.16305421171 [Cox68<br>166.98 (0.7740230641 [Cox56<br>123.88 (0.5134507971 [Cox56<br>104.6 2.280749104[hypothetical protein  
  | PMID: 18036550   | Mitochor<br>220.08.17.252163 Mitochor<br>Mitochor<br>Mitochor<br>Mitochor<br>Mitochor<br>Unknowr   |
| U.329693853855133           28851         0.240047842264175           75751         0.382052302360535           97754         0.226473793387413           2829         0.32969930768013           73438         -0.056364379059076           62384         0.161218479275703           7621         0.437151610851288  
   
   | 151610851288 1.  | 2.00584292411804<br>1.80762958526611<br>1.82510626316071<br>1.26676964759827<br>1.46919906139374<br>1.71697437763214  | 127137500<br>371095000<br>140890000  
  | 57500<br>57500<br>50000<br>50000   
  | 1498800000<br>580250000  
   | 1224977500 3.42077<br>4149700000 5.49456<br>1907550000 5.00919   | 708244324<br>739425659<br>437408447  
   | -4.04 mitochondrion  | 170.11<br>nbi 215.73<br>241.35  | 600 36 2.179244255(co-migrates with complex IV<br>273 97 1.610546117/TgCox6b<br>166 98 0.77402304/TgCox5b<br>123 68 0.512405797/TgCox2b  
  | PMID: 18036550   | Mitochoi<br>020.08.17.252163 Mitochoi<br>Mitochoi<br>Mitochoi<br>Mitochoi  |
| J.Lo.3         U. 3.2/96938538355133           28851         0.240047842264175           75751         0.382052302360535           97754         0.226473793387413           2829         0.32969930768013           93438         -0.053634379059076           75340         1.61218470272772   
   
   | / 106/9//0/10  | 2.00584292411804<br>1.80762958526611<br>1.82510626316071<br>1.26676964759827<br>1.46919906139374  | 127137500  
  | 00000<br>57500<br>75000<br>50000   
  | 1498800000   
   | 1224977500 3.42077   | 708244324 739425659  
   | CONTRACTOR OF A CONTRACT OF A CONTRACT. CONTRACT OF A CONT   | 170.11  | 600.36(2.179244255(Co-migrates with complex IV<br>273.97) 1.610546117/TgCox6b<br>166 98(1) 77027804/TeCox5b  
  |  | Mitocho<br>020.08.17.252163 Mitocho<br>Mitocho<br>Mitocho  |
| 0.329693853855133           0.240047842264175           0.240047842264175           0.382052302360535           0.754           0.32969930768013   
   
   | 36343790590763 1.  | 2.00584292411804<br>1.80762958526611<br>1.82510626316071  |  
  | 00000<br>57500   
  | 509087500  
   |  |  
   | -0.87 mitochondrion  |   | 600.36 2.179244255( Co-migrates with complex IV  
  |  | Mitochor<br>220.08.17.252163 Mitochor  |
| 0.329693853855133           0.240047842264175           0.382052302360535           07754         0.226473793387413  
   
   | 69930768013 1  | 2.00584292411804<br>1.80762958526611  | 36075750   
  | 00000  
  | 127953750  
   | 453382500 4.056970   | 059631348  
   | -0.62 mitochondrion - men  | mbr 275.49  |  
  | BiorXiv DOI: 10.1101/202   | Mitochor   |
| 0.329693853855133<br>0.240047842264175<br>0.283053203260525  
   
   | 473793387413 1.  | 2 00594202411904  | 124050000  
  | 00000  
  | 414592500  
   | 1451350000 2.95316   | 48159027   
   | -4.82 mitochondrion - men  | mbr 179.18  | 157.89 0.881180935 TgApiCox23, component of the cytochrome c oxidase   
  | PMID: 30204084   | 720.06.17.232103 WILLOCHON   |
| 0.329693853855133  
   
   | 047842264175 1.  | 1.87776350975037  | 87515000   
  | 50000  
  | 281242500  
   | 1033580000 3.78846   | 740722656  
   | 2.06 mitochondrion - men   | mbr 186.82<br>mbr 188.35  | 64.13 0.343271598; TgApiCox18, component of the cytochrome c oxidase<br>335 67 1 782160870 Co-migrates with complex IV   
  | PMID: 30204084<br>BiorXiv DOI: 10.1101/202   | Mitochor<br>120.08.17.252163 Mitochor  |
| 0.0000000000000000000000000000000000000  
   
   | 693853855133 1.  | 1.99816453456879  | 96723750   
  | 37500  
  | 304280000  
   | 1215572500 5.61110   | 44883728   
   | -3.62 mitochondrion - men  | mbr 91.53   | 69.44 0.758658363 TgCox2a  
  | PMID: 18036550   | Mitochor   |
| 0.244057461619377  
   
   | 057461619377 1.  | 1.93211710453033  | 328642500  
  | 25000  
  | 1019922500   
   | 3892175000 6.47439   | 861297607  
   | -3.64 mitochondrion - men  | mbr 174.57  | 180.69 1.035057570 TgApiCox25, component of the cytochrome c oxidase   
  | PMID: 30204084   | Mitocho  |
| 73523 -0.588016211986542<br>10513 0.220656126737595  
   
   | 8016211986542 1.   | 1.15859508514404  | 35528750   
  | 37500<br>75000   
  | 105876000  
   | 236357500 2.33267  | 23575592<br>770446777  
   | -2.67 dense granules<br>1.62 mitochondrion - men   | 11.71<br>nbr 168.69   | 3.29 0.2809564474 hypothetical protein<br>251.61 1.4915525520 TeApiCox26, component of the cytochrome c oxidase  
  | PMID: 30204084   | Unknown  |
| 15247 0.206179112195969  
   
   | 179112195969 1.  | 1.95323729515076  | 235372500  
  | 25000  
  | 701195000  
   | 2715325000 5.27640   | 676498413  
   | -3.68 mitochondrion - men  | mbr 163.47  | 238.96 1.461797271(TgApiCox30, component of the cytochrome c oxidase   
  | PMID: 30204084   | Mitochor   |
| 44824 0.363219082355499  
   
   | 219082355499 2   | 2.1305205821991   | 321035000  
  | 50000  
  | 943065000  
   | 4129450000 5.472465  | 599197388  
   | -4.18 mitochondrion - men  | nbr 177.4   | 125.67 0.708399098( TgApiCox35, component of the cytochrome c oxidase  
  | PMID: 30204084   | Mitocho  |
| 38586 0.42625567317009   
   
   | 25567317009 2.   | 2.27768969535828  | 10136250   
  | 52500  
  | 28089250   
   | 136205000 3.64148  | 139953613  
   | 0.62 mitochondrion - solu  | ible 27.8   | 10.38 0.3733812945 hypothetical protein  
  | PWID: 30204064   | Unknown  |
| 0.0910109505057335   
   
   | 0109505057335 1.   | 1.95628654956818  | 62922000   
  | 0000   
  | 172702500  
   | 670192500 5.28431  | 558609009  
   | A C 4 mala second size a second  |   | 265.78 1.437736665 TgApiCox24, component of the cytochrome c oxidase   
  | PMID: 30204084   | Mitochor   |
| -0.160373404622078   
   
   | 0373404622078 1  | 1.92393124103546  | 205223333.3  
  | 4839   
  |  
   |  |  
   | 1.15 mitochondrion - men   | mbr 184.86  | 1.54 0.044214757 Serine C-palmitoyltransferase. Vitamin B6-dependent enzyme, Sphingomyelin and d   
  | ceramide metabolism  | Lipid met  |
| 52332 0.545931994915009  
   
   | 1931994915009 2.   | 2.64000701904297  |  
  | 35000  
  | 33936666.7   
   | 183632500 3.465419   | 976928711  
   | 0.19 ER<br>1.15 mitochondrion - men  | 34.83   | 99.39 0.869705985/TgApiCox16, component of the cytochrome c oxidase  
  |  | WILCOCHOT  |
| 02539 0.14161604642868   
   
   | 031004015000   |   | 95418500   
  | 33000  
  | 223487500<br>83936666.7  
   | 1393075000 4.13905<br>183632500 3.465419   | 143737792<br>976928711   
   | -4.47 mitochondrion - men<br>0.19 ER<br>1.15 mitochondrion - men   | nbi 114.28<br>34.83<br>nbi 184.86<br>nbi 187.46   | 1J20.01 Z.J02000J00; COMINERATES WITH COMPLEX BY   
  | PMID: 30204084   | Altochor   |
| 0051 -2.68964028358459   
   
   | .61604642868 2.<br>1630379676819 2.  | 2.37358379364014  | 150235000<br>62566500<br>95418500  
  | 50000<br>55000   
  | 319802500<br>144680250<br>223487500<br>83936666.7  
   | 1657302500 5.022774<br>783547500 4.65023<br>1393075000 4.13905<br>183632500 3.465419   | 46963501<br>279190063<br>143737792<br>976928711  
   | -5.76 mitochondrion - men<br>0.07 mitochondrion<br>-4.47 mitochondrion - men<br>0.19 ER<br>1.15 mitochondrion - men  | nbi 45.72<br>645.83<br>nbi 114.28<br>34.83<br>nbi 184.86  | 17.65 (0.386045494) SDH, complex II subunit<br>1526.01 2.362866388! Co-migrates with complex IV  
  | BiorXiv DOI: 10.1101/202<br>PMID: 30204084   | 20.08.17.252163 Mitocho<br>Mitocho<br>Mitocho  |
| Apicoplast,           2)         Apicoplast,           31553         0.00419202           30051         -2.6896402           202539         0.14161604           56272         0.32463037           52322         0.54593196           15173         -0.1603734           2049         0.09101095           385632         0.31155487  
   
   | 93195<br>03734<br>01095<br>55487<br>25567  | 9676819<br>4915009<br>04622078<br>05057335<br>18950119<br>1317009   | 04622078 1.92393124103546<br>005057335 1.95628654956818<br>18950119 2.17671942710876<br>317009 2.27768969535828  
  | 4915009         2.64000701904297         95411           04622078         1.9393124103546         20522333.3           05057335         1.95628654956818         62922           8950119         2.17671942710876         210343           317009         2.27768969535828         10134   
  | 05057335         1.95628654956818         629220000           18950119         2.17671942710876         2103450000           1317009         2.27768969535828         101362500  
   | 05057335 1.95628554956818 629220000 172702500<br>8950119 2.17671942710876 2103450000 577380000<br>317009 2.27768969535828 101362500 28089250   | dS057335         1.9565854956518         620220000         172702500         67019500         528431           8850119         2.17671942710876         2103450000         577380000         2610475000         456103           317009         2.2776890553528         101362500         2808250         13625000         364148  
   | 28950119         2.17671942710876         2103450000         577380000         2610475000         4.56103849411011           317009         2.27768969535828         101362500         28089250         136205000         3.64148139953613   | 217009 2.27768969535828 101362500 28089250 13620500 3.6414813953613 0.62 mitochondrion - solu   | 495500         2.6400703004097         954185000         232487500         1390514277972         -4.47 imfachondion - member         114.28           0.622078         1.92393124103566         20522333.3         483936666.7         1383632003 1.45619622711         0.19 ER         34.8         34.8           0.620735         1.55826456466818         6.3232000         1.7720306         670032500 1.248135864000         1.15 imfachondrion - member         194.48           9890119         2.17871542710876         2.20447500         5.2481358641011         -4.61 imfachondrion - member         194.86           9890119         2.17871542710876         2.20447500         2.54017500 1.5481358640101         -4.61 imfachondrion - member         194.86          
9890119         2.17871542710876         2.20447500         2.54017500 1.5481358640101         -6.21 imfachondrion - member         194.96           10.109         2.17871542710876         2.20447500         2.54017500 1.5401354841111         -6.21 imfachondrion - subber         127.8  | 04522078         152293124103545         20252333.3         44399666.7         18353200 3.4654397622711         0.19 FR         34.83         1.5.40.044214757.5minc 6.paimlong/transmine/secondent enzyme, Sphingsmyelin and dispositional secondent enzyme enzy   | National System         System <t< td=""></t<>   |

# **Table S4 bis:** Proteins with higher expression upon depletion of TgISU1 as found by label-freequantitative proteomics.

ToxoDB ID	Uniprot ID	Mito/Ctrl (log2)	Apicoplast/C	C Apicoplast/Mit	moyCtrl-LFQ	moyMito-LFQ	moyApicoplast-LF	pvalue (-log10)	CRISPR score	Localization\$	Tz expression B	Iz expression Bz	/Tz P	Protein	Reference	Cellular function
TGGT1_216140 TGGT1 264660	S7VP87	3.990739345550	5 2.984031200	-1.0067080259	107631333.3	171108250	85157250	2.28895807266235	0.85	cytosoi dense granule	139.62	725.26 5.3	182638 P 167509 B	kv.k., expressed in 62 but does not participate in differentiation kz cyst wall protein CST1 (initially annotated as SAG-related sequence SRS44)	PMID: 18061287, 29180989 PMID: 24385904	Bz SRS
TGGT1_309930	\$7W754	3.424342870712	2 1.813203334	48-1.6111396551	21157700	227142500	74352750	3.56172108650208	-1.13	dense granule	107.99	243.45 2.3	254375 0	SRA56, higher expression in Bz	PMID: 32374791	Bz GRA
TGGT1_201840 TGGT1_222370	S7UV48 S7UKA0	2.342871665954	5 1.765759110 5 0.210089251	0.5771125555 -2.0920438766	143747500	729247500	488817500	2.87034058570862 2.58790993690491	-0.36	VAC PM-nerinhera	41.23	250.07 2.3	366518 A 406985 S	ISP1, VAC-localized, upregulated in Bz AG-related sequence SRS13, upregulated in Bz	PMID: 25240600, 32051238 PMID: 25240600	Catabolism/peptidase Bz SRS
TGGT1_236890	A0A125YNW9	2.110828399658	2 0.945395052	24-1.1654332876	151412500	654010000	291577500	4.42215728759766	2.1	dense granule	176.97	187.42 1.0	059049 0	RA37, expressed in Tz and Bz	PMID: 32374791	GRA
TGGT1_215910	S7ULS1	2.095101118087	7 1.216986656	51-0.8781144618	127292500	543865000	295905000	1.8436723947525	-0.79	dense granule	30.5	38.27 1.3	254754 h	rypothetical protein, potentially upregulated in Bz Munctional dihedrafalate reductors themiskidae custbara. Falate metabolism, Upregulated in	PMID: 25240600	Unknown Folata matabolism
TGGT1_209800	A0A125YSC6	1.907263517379	7 0.965333998	32-0.9419294595	166654250	625115000	325395000	2.00076079368591	1.1	Golgi	30.64	16.54 0.5	539817 F	NT-1, PM-localized formate/lactate transporter	PMID: 30237165	Channel/transporter
TGGT1_260190	S7UYL3	1.793227672576	9 -0.09037586	3 -1.8836036920	75933500	263177500	713226666.7	3.34536695480347	-0.01	micronemes	41.77	2174.63 52	.06200 N	VIC13, upregulated in Bz	PMID: 25240600, 30635773	Stress response
TGGT1_268/90 TGGT1_318750	A0A125YRB3	1.675514221191	4 0.535255193	37-0.8673796057	209590000	669500000	303737500	2.53529977798462	-0.15	cytosol	261.86	1495.09 22	983922 C	akasa, nigner expression in Bz Jeoxyribose-phosphate aldolase, upregulated in Bz. Pentose phosphate pathway	PMID: 32374791 PMID: 18950626	Pentose phosphate pathway
TGGT1_270240	S7V482	1.619087338447	5 0.660394430	01-0.9586929678	790772500	2429100000	1249827500	3.51634883880615	1.25	dense granule	870.6	2433.61 2.3	795325 N	MAG1, cyst matrix antigen, upregulated in Bz	PMID: 7808478	Bz GRA
TGGT1_305610 TGGT1_225120	S7UI56 S7UW30	1.59219455/189	9 0.921980559 4 0.605309188	8-0.6702140569 3-0.8243826627	43113/50 59675750	129991250	81688250 90785000	1.55295193195343 3.48011136054993	-0.34	N/A dense granule	4.32	17.29 4.0	002314 h 834474 P	iypothetical protein Putative GRA, expressed in Tz and Bz		GRA
TGGT1_251540	A0A125YWK4	1.415295839309	6 0.581027448	31-0.8342684507	722317500	1926525000	1080525000	2.8017976284027	1.52	dense granule	252.54	528.97 2.0	094598	RA9, higher expression in Bz	PMID: 32374791	Bz GRA
TGGT1_207140	\$7UQK0	1.343899846076	9 -0.32928487 5 0 460271656	6-1.6731846332	336565000	854325000	267882500	3.37630128860474	0.28	PM-periphera	16.51	90.84 5.	502119 S 230180 P	AG-related sequence SRS49B, upregulated in Bz	PMID: 18347037	Bz SRS Co A synthesis
TGGT1_222110	\$7UL75	1.232611417770	3 0.244350627	7(-0.9882607460	60496750	142162500	71662000	1.52858543395996	1.73	N/A	33.01	36.8 1.:	114813 P	Protein ith putative protein-protein interaction domain implicated in the ubiquitin-proteasome (	pathway	Unknown
TGGT1_320170	A0A125YHU8	1.208315014839	1-0.20355731	2-1.4118723869	145980000	337312500	126770000	5.57573556900024	1.4	PM-periphera	1.67	3.94 2.3	359281 S	AG-related sequence SRS16E	DA410- 22224201	Bz SRS
TGGT1_202900	S7UVM4	1.141521215458	9 0.046338692	2-1.0936712026	70739500	155897500	73048500	2.82374453544617	0.89	N/A	15.92	21.39 1.3	343592 Z	Sing Gradina Si, cyst wall component but potentially expressed in 12 and 62	PIWID. 52574791	Unknown
TGGT1_218950	A0A125YUS9	1.125295400619	5 0.491882681	18-0.6334127187	260293333.3	56782000	36604500	1.48080444335938	-4.19	nucleolus	4.58	8.51 1.1	858078 h	ypothetical protein		Unknown
TGGT1_239480 TGGT1_225790	ADA125YFI3	1.087163329124	4 0.287885665	8-1.4526190757 58-0.7992775440	705570000	1499025000	861395000	3.36608600616455	-1.65	cytoskeleton	17.24	258.27 1.6	613179 T	iucieic acio binding		Oxidative stress response
TGGT1_247440	S7V110	1.060543060302	7 0.428419858	3-0.6321232318	502062500	1047160000	675655000	2.49267792701721	1.72	dense granule	127.15	144.59 1.3	137160 0	RA33, expressed in Tz and Bz		GRA
TGGT1_201630 TGGT1_243350	\$7WB62 \$7UFF5	1.034273386001	5 0.771023631 5 0.355264514	L(-0.2632496953 16-0.6590728163	114534000	234575000	195450000	2.34060287475586	1.65	rhoptries1 endomembra	53.39	64.24 1.3	203221 P 991550 C	hosphatase TgPPM3H Samma-elutamul hydrolase. Folate synthesis	PMID: 28556455	Unknown Folate metabolism
TGGT1_225850	S7W5H3	1.008508443832	4 1.308558225	50.30004975199	85777250	172569250	212465000	1.41337823867798	-5.02	ER	22.66	25.01 1.:	103706 N	/128 metallo peptidase, found in MAG1 IP	PMID: 32374791	Catabolism/peptidase
TGGT1_260310	A0A125YUY7	0.992248356342	3 0.769039690	0.2232086658	59250000	117865000	100970000	1.49347734451294	0.69	Golgi RM. parinhara	10.6	2.68 0.2	252830 A	IBC transporter		Channel/transporter
TGGT1_321400	A0A125YWK6	0.982857286930	0 0.556925117	79-0.4259321391	1570425000	3103750000	2310300000	2.26548218727112	1.49	dense granule	213.45	69.69 0.3	326493	Slucose-6-phosphate 1-dehydrogenase. Pentose phosphate pathway. Upregulated in Tz	PMID: 25240600	Pentose phosphate pathway
TGGT1_320190	A0A125YJX4	0.981666922569	2 0.155521601	4-0.8261454105	1192672500	2355225000	1328427500	1.49226236343384	0.44	PM-periphera	91.39	1154.67 12	.63453 S	AG-related sequence, upregulated in Bz	PMID: 25240600	Bz SRS
TGGT1_209985 TGGT1 293810	S/VX11 A0A125YZ37	0.976530194282	5-0.45/78107 0 0.551496088	6-1.4343113899 35-0.4050139486	473395000	204560000 918675000	75692000 693810000	3.29283/619/8149 2.64519810676575	-0.6	rhoptries1 cytosol	25.56	394.84 15	142994 C	ICUP26 protein kinase, upregulated in Bz Carboxyvinyl-carboxyphosphonate phosphorylmutase. Phosphonate and phosphinate metabolic	PMID: 25240600 PMID: 25240600	Unknown Organophosphorus compound synthe
TGGT1_320630	A0A125YIW2	0.953933715820	3 0.546553850	01-0.4073798656	78827250	152700000	115134500	1.7426530122757	0.01	dense granule	43.27	20.15 0.4	465680 0	holine kinase. Phosphatidylcholine metabolism		Lipid metabolism
TGGT1_249670	\$7W8W7 \$7W4F8	0.942174971103	6 0.340112239 8 0 249006509	01-0.6020625829	918395000	1764625000	1162555000	2.30851101875305	0.95	VAC	119.14	164.29 1.	378965 C	Cathepsin B	PMID: 12000756	Catabolism/peptidase Folate metabolism
TGGT1_248320	S7WGM8	0.925476014614	1 0.155468329	0.7700075507	253552500	481575000	282402500	4.60057687759399	-5.17	mitochondrio	18.9	20.83 1.	102116 N	Aitochondrial carrier		Channel/transporter
TGGT1_226072	\$7WCJ8	0.923117280006	4 0.477917939	0.4451993405	373295000	707845000	519900000	3.87257528305054	-0.32	endomembra mitochorde	83.25	44.39 0.5	533213 5	ier/Thr phosphatase family		Unknown
TGGT1_215980	A0A125YHJ3	0.900917112827	3 0.307252794	0.4659844148 1-0.5936642885	6087125000	11366200000	7531900000	+.,/002062931519 2.16732835769653	2.11	dense granule	864.56	28.68 0.	, ozoza N 678576 C	Recention and cattlet	PMID: 30362762	GRA
TGGT1_249580	S7V071	0.858355581760	4 1.221336603	310.36298105120	129790666.7	235306666.7	302623333.3	1.72367322444916	0.47	PM-integral	12.36	9.56 0.	773462	seneral substrate transporter	PMID: 25240600	Channel/transporter
IGGT1_292280 TGGT1_289180	A0A125YQN8 A0A125YMW4	0.857272028923	U 0.547212958 0 0.220799431	s: -0.3100590705	442180000 103410333 3	801057500 186405000	646140000 120512250	2.91627240180969 1.32925546169781	N/A	PM-periphera mitochondrio	1.38 39.89	3.57 2.	586956 S 211581 T	AG-related sequence SRS36D		Bz SRS Oxidative stress response
TGGT1_275460	S7UQV5	0.849380552768	7 0.550823330	0.2985571920	88701000	159815000	129940000	2.84133386611938	2.32	dense granule	63.43	83.31 1.	313416 P	rutative GRA expressed in Tz and Bz	PMID: 25240600	GRA
TGGT1_318490	A0A125YG85	0.835339546203	6 0.352327853	34-0.4830117821	87276250	155725000	111418500	2.25274872779846	0.66	N/A	24.05	53.9 2.2	241164 S	AM-dependent RNA methylase		RNA-interacting/regulating
TGGT1_231920	\$7WJ25	0.805483222007	7 0.520373404	4(-0.2851098179	4093350000	7154075000	5871200000	1.8788537979126	0.25	cytosol	102.79	114.04 1.3	109446 F	olate metabolism, Sepiapterin reductase		Folate metabolism
TGGT1_209100	\$7V\$99	0.797917187213	8-0.02834147	0-0.8262586593	369992500	643265000	362795000	3.78961324691772	-3.3	nucleus-chror	51.37	39.14 0.1	761923 p	rotein-protein interaction domain implicated in the ubiquitin-proteasome pathway		Catabolism/peptidase
TGGT1_270650 TGGT1_275440	S7UQL8	0.751828312873	9 0.414762765 8 0.514736950	0.3704181313 0-0.2370914518	298690000	4858925000	4122575000	2.76742005348206 3.88083076477051	1.91	N/A dense granule	1423.05	882.84 0.6	620385 C	Jeoxyribose-phosphate aldolase, upregulated in BZ. Pentose phosphate pathway SRA6, higher expression in Tz	PMID: 7637717	Tz GRA
TGGT1_293470	A0A125YZ06	0.746073246002	1 0.554047405	57-0.1920257806	705282500	1182915000	1035495000	1.73872303962708	1.52	PM-periphera	71.69	82.07 1.3	144790 li	mmune mapped protein 1, TgIMP1	PMID: 27888074	Unknown
TGGT1_263130 TGGT1_251490	\$7WDG5 \$7V032	0.745062172412	8 -0.07751032 5 0 653240978	7-0.8225725293 3-0.0815209597	2625300000 24537250	4400125000	2487975000 385896666 7	3.07843971252441 1.33415234088898	1.86	cytosol nucleus-chror	41.89	29.53 0.3	704941 2 437861 5	-methylcitrate synthase. CoA synthesis //S response associated pentidase (SRAP)		CoA synthesis DNA repair and replication
TGGT1_226720	S7UXF7	0.730272769927	9 0.253851383	39-0.4764214158	740542500	1228525000	883012500	3.29289603233337	0.29	cytosol	43.01	133.54 3.	104859 T	ranslin, involved in RNA-induced silencing complex		RNA-interacting/regulating
TGGT1_271610	S7V4N7	0.726739645004	2 0.102258473	36-0.6244811415	356080000	589275000	382235000	2.83289170265198	0.85	PM-periphera	134.19	332.47 2.4	477606 P	Pyrroline-5-carboxylate reductase, upregulated in Bz. Proline metabolism		Amino acid metabolism
TGGT1_219240 TGGT1_283780	57W2U8	0.724526545725	4 0.167988330	1-0.5485450029	1797300000	2953375000	2019250000	1.90095794200897	-2.52	cytosol	202.81	870.59 4.3	292638 P	homoscy-trive nyurolase Phosphoglucose isomerase, upregulated in Bz. Glycolysis		Glycolysis/gluconeogenesis
TGGT1_320490	S7VSP7	0.709642231464	3 0.492255151	12-0.2173871397	57129500	93429500	80360750	2.28308367729187	0.13	dense granule	42.36	36.86 0.1	870160	4-acyl phosphatidylethanolamine phospholipase D, hydrolyzes N-acyl-phosphatidylethanolamine	nes (NAPEs) to produce N-acyleth	Lipid metabolism
TGGT1_270320 TGGT1 208560	AUA125YP66 AUA125YPP8	0.709304511547	0 0.199646592 5 0.124433577	21-0.5096579790 7(-0.5841082930	603105000	2894550000 985565000	2033100000 657432500	1.48/1244430542 3.26823425292969	-3.49	rhoptries1 apicoplast	226.23	83.8 U. 38.94 O.	370419 C 557959 C	aRA protein PPM3C, part of the MYR1 complex, higher expression in Tz	PMID: 32075880	Tz GRA Channel/transporter
TGGT1_244550	S7VMW7	0.702784597873	6 0.556319057	79-0.1464655101	42335750	68907500	62255250	1.49713885784149	-0.35	ER	13.19	4.6 0.3	348749 h	ypothetical protein		Unknown
TGGT1_272380	\$7V3W6	0.701357543468	4 0.470330685	5-0.2310268282	66783500	108592250	925236666.7 2670775000	1.3892320394516	1.71	micronemes cutosol	101.05	72.36 0.3	716081 h 086300 6	iypothetical protein		Unknown Pentose phosphate pathway
TGGT1_239820	A0A125YMY8	0.690705537796	0 0.250900506	59-0.4398051500	4736125000	7644450000	5635750000	2.51304864883423	1.00	nucleus-non-c	399.27	270.48 0.6	677436 P	hosphoglycerate dehydrogenase. De novo serine synthesis		Amino acid metabolism
TGGT1_239680	\$7W6G6	0.688606560230	2 0.237206757	70-0.4513998329	52443000	84523750	61815000	1.63691902160645	-3.24	apicoplast	30.02	15.93 0.9	530646 h	whether a second se	DMID: 27274701	Unknown
TGGT1_309780 TGGT1_285980	S7US82	0.672067165374	7 0.135590150	0.5364191731 0.5364769697	1486675000	2368800000	1633175000	2.10460473944319	1.18	cytosol	146.05	635.64 4.3	352208	annoo, expressed in 12 and 62 Slucosephosphate-mutase GPM1, glycogen metabolism/Pentose Phosphate Pathway, upregulai	PMID: 25240600	Pentose phosphate pathway
TGGT1_292300	S7UPT9	0.671504974365	2 0.144547000	0.5269579887	19239250	30643000	21266750	1.40334987640381	-1.53	mitochondrio	10.99	3.69 0.3	335759 N	Mitochondrial RNA pol III	PMID: 30204084	RNA-interacting/regulating
TGGT1_281620 TGGT1_219130	S7UV92 S7V1M4	0.662798225879	3 0.513610363 6 0.048404552	30-0.1522090435 20-0.6143934726	399825000 82149500	634310000 130055000	5/0/9/500 84952500	4.56814/659301/6 1.51844131946564	-3.03	nucleus-chror apicoplast	26.96	13.05 0.4	484050 A 292221 N	Ndo/keto reductase family. Folate or Lipid metabolism IADPH-elutathione reductase		Polate metabolism Oxidative stress response
TGGT1_292020	S7UNY5	0.661832749843	5 0.724787890	0.06295523047	92529750	146390500	152920000	1.70618069171906	-3.64	micronemes	3.94	3.4 0.1	862944	GCC2 and GCC3 Tyrosine-protein kinase ephrin type A/B receptor-like		Unknown
TGGT1_312600 TGGT1_247510	S7UTP6 A0A125YGG2	0.658649623394	0 0.315898597	72-0.3427510261 12-0.2010122239	4387800000	6926600000 19200750000	5461875000	2.4046459197998 2.58831810951233	-4.77	cytosol cytosol	228.21	2247.84 9.1	849875 H 424237 P	ISP21, upregulated in Bz Phosohofructokinase-2/fructose bisohosobatase-2. Glycolysis. Glyconeogenic enzyme	PMID: 26269956	Stress response Glycolysis/glyconeogenesis
TGGT1_202300	S7W3F8	0.654201805591	5 0.336286842	28-0.3179149627	483032500	760170000	609830000	2.8143048286438	0.42	cytosol	17.74	38.87 2.3	191093	lucleoside-triphosphate pyrophosphatase. Pyrimidine metabolism		Nucleic acid synthesis
TGGT1_223110	A0A125YWQ0	0.653622150421	1-0.02705298	3-0.6806752085	1264467500	1989150000	1240977500	2.32521271705627	-1.03	nucleus-chror	90.37	206.35 2.2	283390 0	Bycolipid transfer protein. Sphingomyelin metabolism		Lipid metabolism
TGGT1_222100	S7W608	0.648304150354	8 0.185486599	0.4568351507	1165575000	1819275000	1325492500	2.00795388221741	-0.84	PM-periphera	103.42	235.71 2.0	068901 P	yrroline-5-carboxylate reductase. Proline metabolism		Amino acid metabolism
TGGT1_410610	S7VXS4	0.636475384235	3 -1.36031961	4 - 1.9967949390	189356666.7	29436000	737536666.7	1.30878853797913	N/A	N/A	N/A	N/A N/	A P	Protein kinase domain-containing protein		Unknown
TGGT1_233310 TGGT1_224820	S7V314 S7W544	0.635936498641	/ 0.2234935/6 9 0.772736489	50-0.4126641452 970.13679997622	139385000 43562000	216630000 67693000	162/40000 74426000	3.299/4484443665 2.03762745857239	1.38	195 proteasor mitochondrio	28.68	32.1/ 1.3	121687P 945745h	reptidase ivoothetical protein		Catabolism/peptidase
TGGT1_315130	\$7VV27	0.635259866714	4 0.252323120	08-0.3829367160	172593333.3	268075000	205580000	2.75814509391785	-2.44	nucleus-chror	61.14	66.29 1.0	084232 P	rotein-L-isoaspartate(D-aspartate) O-methyltransferase (protein repair)		Stress response
TGGT1_230950 TGGT1_278890	S7V292 S7WFM4	0.631697654724	1-0.26901000	17-0.9007077217	187093333.3 38300000	28988000 594733333 3	155266666.7 47005750	1.36878025531769	-5.08	nucleolus Golei	6.23	3.47 0.	556982 A 683318 P	Irmadillo repeat-containing hypothetical protein Putative Golei membrane protein whith a notential role in vesicle transport		Unknown Unknown
TGGT1_264880	S7UFR9	0.625782608985	9 -0.12592433	13-0.7517070174	44587250	68800250	40860500	1.90400576591492	-2.77	195 proteasor	19.52	13.48 0.6	690573 N	IEDD8-activating enzyme		Catabolism/peptidase
TGGT1_300350	\$7VP37	0.604513168334	9 0.825931489	0.22141838073	134677500	204772500	238740000	1.65349471569061	0.45	ER cutoso <sup>1</sup>	14.27	11.09 0.	777154	ysteine desulfurase. Folate metabolism		Folate metabolism
TGGT1_299780	A0A125YGU0	0.592484176158	9 0.191560044	18-0.4009241461	533740000	804795000	609530000	1.68315982818604	1.13	dense granule	47.5	26.54 0.5	347578 P	Potentially a GRA. Important for in vivo fitness	PMID: 31481656	Tz GRA
TGGT1_286750	A0A125YUI3	0.591726303100	5 0.163417354	1-0.4283089041	1314025000	1980300000	1471625000	3.0101056098938	0.51	mitochondrio	62.78	65.24 1.0	039184 P	Potentially involved in translational regulation		Unknown
IGGT1_309210 TGGT1_318560	S7W128 S7UKA1	0.584580779075	6 0.070281155 9 0.524277091	-0.5142995119 L(-0.0571809150	18584250000	27869000000 277537500	19512000000 266752500	3.64621877670288 3.71216702461743	0.17	cytosol mitochondrio	209.5 23.08	377.03 1.	/99665 R 453639 A	tedox metabolism, peroxiredoxin 6 XTPase/histidine kinase/DNA gyrase B/HSP90 domain		Uxidative stress response Unknown
TGGT1_315320	S7UMK1	0.573760330677	0 0.080777689	8 -0.4929825961	11248000000	16741500000	11895750000	4.20507669448853	-0.48	PM-periphera	212.17	99.47 0.4	468822 5	AG-related sequence SRS52A, upregulated in Tz	PMID: 25240600	Tz SRS
TGGT1_258100	S7W7F7	0.572838544845	5 -0.04256305 4 0 509810507	0-0.6154015660	341657500	508197500 621390000	331725000	1.51949381828308 1.65090990066539	-2.01	mitochondrio dense arcoulo	38.69	44.32 1.3	145515 P	Putative flavinator of succinate dehydrogenase. Mitochondrial iRA32. bieher expression in Tz	PMID: 30204084 PMID: 27486190	Mitochondrial respiratory chain
TGGT1_221470	S7UKF9	0.566366016864	7 0.297653228	3(-0.2687127590	4246250000	6287800000	5219250000	1.87728798389435	-1.492	cytosol2	170.43	223.21 1.	309687 h	ypothetical protein		Unknown
TGGT1_201150	\$7W884	0.565702497959	1 0.477401047	79-0.0883014500	99374500	147085000	138352500	1.82954502105713	-1.57	Golgi catoro!N	14.17	8.45 0.5	596330 H	Heavy metal translocating P-type ATPase		Channel/transporter
TGGT1_201380 TGGT1_273110	57W4/1 \$7V3C4	0.565033972263	or J. J. 23435086 3 -0.28116279	n -0.5416343212 8 -0.8461967110	120373000	904977500 178082500	621/12500 99058250	2.0080/118835449 1.77262341976166	-2.84	vytosol2 N/A	112.46	43.39 0.3	365826 S 3125 S	Informate prosynthesis. Chorismate synthase AG-related sequence SRS30D		Bz SRS
TGGT1_205720	A0A125YQL8	0.562255680561	0 0.400461107	74-0.1617945730	135225000	199670000	178487500	1.43205583095551	0.09	N/A	12.51	21.12 1.0	688249 A	denosine deaminase. Purine metabolism		Nucleic acid synthesis
IGGT1_301210 TGGT1_286630	S7UHH6 S7VWS3	0.557322382926	9 0.944646894 2 0.255169510	150.38732451200 06-0.3021084070	385626666.7 5698900000	567463333.3 8385875000	74222250 680150000	1.41358363628387 1.54473638534546	-1.91	PM-integral apicoplast?	24.97 224.43	25.12 1.0	UU6007 P 094377 P	yrridine nucleotide transhydrogenase. Nicotinate and nicotinamide metabolism Redox metabolism, Peroxiredoxin		NAD/NADP synthesis Oxidative stress response
TGGT1_250880	\$7V031	0.552533090114	5 0.422195553	37-0.1303375363	1236450000	1813450000	1656800000	3.40366363525391	1.37	cytosol	42.54	27.35 0.0	642924 P	Purine metabolism, Adenosine kinase		Nucleic acid synthesis
TGGT1_208370	\$7UJT6	0.551288843154	9 0.690403342	2.0.13911443948	1300725000	1906075000	2099025000	1.83155822753906	1.79	dense granule	46.22	127.59 2.3	760493	iRA46, higher expression in Bz	PMID: 30377279	Bz GRA
	57 1122	5.551130314608			304/4000	14132/300	11220230	2.302-3000364204	0.0/		JØ.10	43.49 U.				
LFQ values in TgISU	J1 mutant only	N/A	N/A	N/A		40005222		N/A		N/A		F.4.70	10104-	AG related regulates SPS/AE		D+ CDC
TGGT1_225230	57W551 \$7W583	N/A	N/A	N/A	0	49895333,3 25276250	0	N/A	-0.64	nucleus - chro	98.56	54.38 20 26.39 0.1	.29104 S 267755 h	ypothetical protein		Unknown
TGGT1_237460	\$7UQ46	N/A	N/A	N/A	0	20884250	0	N/A	-0.96	PM - peripher	25.2	4.33 0.3	171825 h	ypothetical protein, contains a Derlin1- motif		Unknown
TGGT1 253330	S/UNB5 S7UMR4	N/A N/A	N/A N/A	n/A N/A	0	4/188333,3 17996000	0	n/A N/A	-1.78	rnoptries 2 PM - perinher	129.93	34.68 0.3	266912 h 1.13907 P	iypotneticai protein kradyzoite pseudokinase 1. (TgBPK1), cvst wall component	PMID: 23291621	unknown Bz GRA
TGGT1_280570	A0A125YZ54	N/A	N/A	N/A	0	590860000	0	N/A	-0.48	N/A	1781.61	12466.81 6.9	997496 S	AG-related sequence SRS35A	-	Bz SRS
No LEO valuer in	antrol, but 150	lues in TelCIII	d TeNES?	ants									_			
TGGT1_224190	\$7UV\$1	N/A	N/A	-0.1127142536	0	20276333.3	21924000	N/A	-5.24	Golgi	46.22	11.84 0.3	256166 L	ipid flippase TgFLP2	BioRxiv: 10.1101/2020.06.19.16	Lipid metabolism
TGGT1_317705	S7UFF2	N/A	N/A	-0.7516118161	0	26330333.3	44331666.6	N/A	-0.45	N/A	103.44	104.55 1.0	010730 E	noyl-CoA hydratase/isomerase family protein		Lipid metabolism
16611_261650	s/UY15	N/A	N/A	0.20880937503	0	57346750	49619333.3	n/A	1.61	r-m - peripher	110.47	369.39 3.5	524848 (	.yst waii protein TgCS14	PMID: 31040239	BZ CySt wall protein
										\$ inferred from						
									¤ fitness	(published						
									score data	data or	# DAL					
									genome	prediction -	# KNASEQ data from					
									CRISPR	Barylyuk K et	Hehl AB et al					
									screen (Sidik SM et al. Cell	al Cell Host & Microhe	BMC Genomics					
									2016)	2020-)	2015					

**Table S5:** Common proteins with lower expression upon depletion of TgNFS2 or TgISU1, as found by label-free quantitative proteomics.

ToxoDB ID	Uniprot ID	Mito/Ctrl (log2)	Apicoplast/Ctrl (log 2)	Apicoplast/Mito (log 2)	moyCtrl-LFQ	moyMito-LFQ	moyApicoplast-LF	FQ pvalue (log10)	CRISPR score¤	Localization\$	Tz expression#	Bz expression# Bz/Tz	Protein	
TGGT1_301180	S7VPVO	-2.68365406990051	-2.68964028358459	-0.00598621973767877	479318250	7460425	) 742953333.3	1.39637875556946	1.62	PM - peripheral 1	24.4	1 27.71 1.1351	0495€ SAG-related seqence SRS19F, potentially sporozoite-specific	SRS
TGGT1_313690	S7UUJ6	-0.698630213737488	-1.35542297363281	-0.65679258108139	87798250	5409750	) 343133333.3	1.4945582151413	-4.61	apicoplast	22.6	8 11.22 0.4947	8994 Sel1 repeat-containing protein	Unknown
TGGT1_295690	AOA125YN53	-0.851312875747681	-1.27982342243195	-0.428510516881943	68255500	378326666.7		28110750 2.19047451019287	-3.62	mitochondrion - membranes	15.2	4 30.36 1.9921	159842 Ubiquinone/menaquinone biosynthesis methyltransferase UbiE/COQ5. Ubiquinone metal	ooli Mitochondrial respiratory chain
TGGT1_266970	S7UHF3	-0.694063067436218	-0.86726039648056	-0.173197358846664	787715000	48689500	)	431815000 1.53129696846008	0.67	PM - peripheral 2	71.9	2 9.92 0.1379	1034 <sup>4</sup> Ubiquitin domain-containing protein	Unknown
TGGT1_246630	S7W9K7	-1.11214685440063	-0.862397491931915	0.249749451875687	384143333.3	177706666.7	211293333.3	2.36531805992126	-5.32	nucleus - non-chromatin	13.7	6 9.78 0.7107	58139 DNA-directed RNA polymerase	RNA-interacting/regulating
TGGT1_240690	AOA125YNS1	-0.868883609771729	-0.798904955387115	0.0699787363409996	213100000	116687250	) 1	1224867500 2.10652613639832	-4.44	cytosol	87.1	8 36 0.4129	87474 Methionine adenosyl transferase. Methionine metabolism	Amino acid metabolism
TGGT1_294430	S7UIK2	-0.61689430475235	-0.785761833190917	-0.168867528438568	83244750	542816666.7		48285750 2.32733845710754	-3.87	nucleolus	9.4	2 11.23 1.1921	4373¢ SDA1-like, potentially involved in 60S pre-ribosomal subunits export and maturation	Ribosome biogenesis
TGGT1_267140	S7UH64	-0.734389245510101	-0.782125234603882	-0.0477358922362328	868610000	52209750	)	505105000 2.60759615898132	0.57	PM - peripheral 1	17.2	4 3.58 0.2076	66125 SAG-related sequence SR5388	Tz SRS
TGGT1_289620	S7UPV8	-1.10120224952698	-0.771169424057007	0.330032765865326	496205000	23129500	)	290747500 2.06231331825256	0.95	micronemes	108.5	2 88.69 0.8172	87062 Cathepsin C	Catabolism/peptidase
TGGT1_261410	S7W6W5	-0.758374214172363	-0.701039254665375	0.0573350414633751	100997250	5970575	0 621263333.3	1.92283999919891	-2.85	N/A	19.8	6 20.45 1.0297	17955€ Protein-tyrosine-phosphatase	Unknown
TGGT1_224970	S7UWG5	-1.14884293079376	-0.639941155910492	0.50890177488327	347763333.3	156836666.7	223173333.3	2.89828848838806	0	nucleolus	13.5	2 8.5 0.6286	8224 Nop52 protein-like. Ribosome biogenesis	Ribosome biogenesis
TGGT1_319720	S7UK66	-0.767558872699738	-0.617857038974761	0.149701848626137	55649750	3268925	)	36263500 2.41169834136963	-4.47	nucleus - chromatin	8.8	6 1.85 0.2088	13611, hypothetical protein	Unknown
TGGT1_294980	AOA125YGY1	-1.74661135673523	-0.588016211986542	1.15859508514404	355287500	10587600	)	236357500 2.3326723575592	2.06	dense granules	10.4	7 2.88 0.2750	16337 hypothetical protein	Unknown
TGGT1_224330	S7UW24	-0.74552583694458	-0.560373246669769	0.185152485966682	130650000	7792625	)	88597250 1.87797522544861	0.18	cytosol	35.5	5 30.44 0.8562	8790 <sup>,</sup> Proteasome activator pa28 beta subunit	Catabolism/peptidase
No LFQ values in	TgNFS2 and TgIS	6U1 mutants, but LFQ va	lues in control											
TGGT1_285860	S7UNY4		0	0 N/A	66018000		)	0 N/A	1.72	PM - peripheral 1	9.3	9 1.97 0.2097	7657(SAG-related sequence SRS20C	Tz SRS
TGGT1_272770	S7V3A5		0	0 N/A	23139666.6	i	)	0 N/A	-4.32	N/A	45.8	6 46.47 1.0133	1351 Ltv1 Low temperature viability protein-like motif	Ribosome biogenesis
TGGT1_251410	S7V016		0	0 N/A	16610000		)	0 N/A	0.25	N/A	19.	7 6.9 0.3502	38071 Tetratricopeptide repeat-containing protein	Unknown
TGGT1_275420	S7W518		0	0 N/A	13814666.6	i	)	0 N/A	-2.47	N/A	26.	2 14.09 0.5377	62599 Histone demythylase (polyamine salvage)	Unknown
TGGT1_255310	S7W160		0	0 N/A	9955600		)	0 N/A	0.7	nucleus - non-chromatin	59.3	6 10.41 0.1753	106199 CCCH zinc finger-containing hypothetical protein	Unknown
									¤ fitness score data	\$ inferred from (published data or	# RNAseq data from	n		
									from whole genome	HyperLOPIT prediction - Barylyuk K	Hehl AB et al BM	c		
									CRISPR screen (Sidik	et al Cell Host & Microbe 2020-)	Genomics 201	5		
									SM et al. Cell 2016)					

	ToxoDB ID	Uniprot ID	Mito/Ctrl (log2)	Apicoplast/Ctrl (log 2)	Apicoplast/Mito (log 2)	moyCtrl-LFQ mo	oyMito-LFQ moyApicop	last-LFQ pvalue (log10)	CRISPR scoreX Localiza	tion\$ Ta	'z expression# E	Bz expression# B	z/Tz	Protein	Reference	
	TGGT1_216140	AOA125YUL1	5.34013509750366	5.2523341178894	-0.0878007486462593	15598400	631860000	594552500 5.84068965911865	1.75 cytosol		139.62	1142.46 8	.18263859045982	ANK1, expressed in Bz but does not participate in differentiation	PMID: 18061287, 29180989	Unknown
	TGGT1_264660	S7VP87	3.99073934555054	2.98403120040894	-1.00670802593231	1076313333	171108250	85157250 2.28895807266235	0.85 dense g	ranules	140.35	725.26 5	.16750979693623	Bz cyst wall protein CST1 (initially annotated as SAG-related sequence SRS44)	PMID: 24385904	Bz SRS
S S	TGGT1_309930	\$7W7\$4	3.42434287071228	1.81320333480835	-1.61113965511322	21157700	227142500	74352750 3.56172108650208	-1.13 dense g	ranules	107.99	243.45 2	.2543754051301	GRA56, higher expression in Bz	PMID: 32374791	Bz GRA
l pi	TGGT1_201840	S7UV48	2.34287166595458	1.76575911045074	-0.577112555503845	143747500	729247500	488817500 2.87034058570862	-0.36 VAC		105.67	250.07 2	.36651840635942	ASP1, VAC-localized, upregulated in Bz	PMID: 25240600, 32051238	Catabolism/peptidase
n	TGGT1_236890	AOA125YNW9	2.1108283996582	0.945395052433014	-1.16543328762054	151412500	654010000	291577500 4.42215728759766	2.1 dense g	ranules	176.97	187.42 1	.05904955642199	GRA37, expressed in Tz and Bz	PMID: 32374791	GRA
fo	TGGT1_215910	S7ULS1	2.09510111808777	1.21698665618896	-0.878114461898804	127292500	543865000	295905000 1.8436723947525	-0.79 dense g	ranules	30.5	38.27 1	.25475409836066	hypothetical protein, potentially upregulated in Bz	PMID: 25240600	Unknown
, a	TGGT1_249180	AOA125YXY2	1.96048045158386	0.713445067405701	-1.24703538417816	4262875000	16590750000	6989900000 6.14134836196899	N/A nucleus-	-non-chromatin	133.2	38.57 0.	.289564564564565	Bifunctional dihydrofolate reductase-thymidylate synthase. Folate metabolism. Upregulated in Tz	PMID: 25240600	Folate metabolism
Ú Ú	TGGT1_209800	AOA125YSC6	1.90726351737976	0.965333998203278	-0.941929459571838	166654250	625115000	325395000 2.00076079368591	1.1 Golgi		30.64	16.54 0	539817232375979	FNT-1, PM-localized formate/lactate transporter	PMID: 30237165	Channel/transporter
SIS	TGGT1_268790	S7V4L0	1.78530514240265	0.917925596237183	-0.867379605770111	72217500	248927500	136447500 3.3732635974884	1.63 dense g	ranules	261.86	519.51 1	.98392270678989	GRA58, higher expression in Bz	PMID: 32374791	Bz GRA
Ĕ	TGGT1_270240	S7V482	1.61908733844757	0.660394430160522	-0.958692967891693	790772500	2429100000	1249827500 3.51634883880615	1.25 dense g	ranules	870.6	2433.61 2	.79532506317482	MAG1, cyst matrix antigen, upregulated in Bz	PMID: 7808478	Bz GRA
ō	TGGT1_305610	S7UI56	1.59219455718994	0.921980559825897	-0.670214056968688	43113750	129991250	81688250 1.55295193195343	-0.34 N/A		4.32	17.29 4	.00231481481481	hypothetical protein		Unknown
-S2	TGGT1_225120	S7UW30	1.42969179153442	0.605309188365936	-0.824382662773132	59675750	160760000	90785000 3.48011136054993	0.64 dense g	ranules	192.72	160.82 0	.834474885844749	Putative GRA, expressed in Tz and Bz		GRA
N.	TGGT1_251540	AOA125YWK4	1.41529583930969	0.581027448177338	-0.834268450737	722317500	1926525000	1080525000 2.8017976284027	1.52 dense g	ranules	252.54	528.97 2	.09459887542568	GRA9, higher expression in Bz	PMID: 32374791	Bz GRA
Ш	TGGT1_260520	S7UYP6	1.14152121543884	0.820777893066406	-0.320743381977081	110010250	242697500	194317500 4.66463279724121	1.9 dense g	ranules	79.49	79.5 1	.00012580198767	CST6/GRA53, cyst wall component but potentially expressed in Tz and Bz	PMID: 32374791	GRA
of	TGGT1_201630	S7WB62	1.03427338600159	0.771023631095886	-0.263249695301056	114534000	234575000	195450000 2.34060287475586	1.65 rhoptrie	51	53.39	64.24 1	.20322157707436	Phosphatase TgPPM3H	PMID: 28556455	Unknown
uo	TGGT1_225850	S7W5H3	1.0085084438324	1.30855822563171	0.300049751996994	85777250	172569250	212465000 1.41337823867798	-5.02 ER		22.66	25.01 1	.10370697263901	M28 metallo peptidase, found in MAG1 IP	PMID: 32374791	Catabolism/peptidase
leti	TGGT1_260310	AOA125YUY7	0.992248356342316	0.769039690494537	-0.223208665847778	59250000	117865000	100970000 1.49347734451294	0.69 Golgi		10.6	2.68 0	252830188679245	ABC transporter		Channel/transporter
epl	TGGT1_294200	AOA125YWK6	0.982857286930084	0.556925117969513	-0.425932139158249	1570425000	3103750000	2310300000 2.26548218727112	1.49 dense g	ranules	213.45	69.69 0	.326493323963457	Glucose-6-phosphate 1-dehydrogenase. Pentose phosphate pathway. Upregulated in Tz	PMID: 25240600	Pentose phosphate pathway
þ	TGGT1_293810	A0A125YZ37	0.956510066986083	0.551496088504791	-0.40501394867897	473395000	918675000	693810000 2.64519810676575	-0.6 cytosol		31.19	160.41 5	.14299454953511	Carboxyvinyl-carboxyphosphonate phosphorylmutase. Phosphonate and phosphinate metabolism, upregula	PMID: 25240600	Organophosphorus compound synthesis
JOC .	TGGT1_249580	\$7\071	0.858355581760406	1.22133660316467	0.362981051206589	129790666.7 23	5306666.7 302623333.	3 1.72367322444916	0.47 PM-inte	gral	12.36	9.56 0.	.773462783171521	General substrate transporter	PMID: 25240600	Channel/transporter
'n	TGGT1_275460	S7UQV5	0.849380552768707	0.550823330879211	-0.298557192087173	88701000	159815000	129940000 2.84133386611938	2.32 dense g	ranules	63.43	83.31 1	.3134163644963	Putative GRA expressed in Tz and Bz	PMID: 25240600	GRA
uo	TGGT1_293470	A0A125YZ06	0.746073246002197	0.554047405719757	-0.192025780677795	705282500	1182915000	1035495000 1.73872303962708	1.52 PM-peri	pheral2	71.69	82.07 1	.14479006834984	Immune mapped protein 1, TgIMP1	PMID: 27888074	Unknown
ssi	TGGT1_251490	\$7\032	0.734762012958527	0.653240978717803	-0.0815209597349167	24537250	40833000 385896666.	7 1.33415234088898	0.11 nucleus-	chromatin	22.45	32.28 1	.43786191536748	SOS response associated peptidase (SRAP)		DNA repair and replication
ore	TGGT1_219240	S7V235	0.724526345729828	1.12648010253906	0.401953667402267	298015000	492427500	650642500 2.95005321502686	1.31 N/A		14.32	25.4 1	.77374301675978	Aminoacyl-tRNA hydrolase		RNA-interacting/regulating
exl	TGGT1_244550	S7VMW7	0.702784597873688	0.556319057941437	-0.146465510129929	42335750	68907500	62255250 1.49713885784149	-0.35 ER		13.19	4.6 0	.348749052312358	hypothetical protein		Unknown
er	TGGT1_292020	S7UNY5	0.661832749843597	0.724787890911102	0.062955230474472	92529750	146390500	152920000 1.70618069171906	-3.64 microne	mes	3.94	3.4 0	.862944162436548	GCC2 and GCC3 Tyrosine-protein kinase ephrin type A/B receptor-like		Unknown
gh	TGGT1_224820	S7W544	0.635936498641968	0.772736489772797	0.136799976229668	43562000	67693000	74426000 2.03762745857239	0.71 mitocho	indrion-membranes	16.22	31.56 1	.94574599260173	hypothetical protein		Unknown
iq	TGGT1_300350	S7VP37	0.604513168334961	0.825931489467621	0.221418380737305	134677500	204772500	238740000 1.65349471569061	0.45 ER		14.27	11.09 0	.777154870357393	Cysteine desulfurase. Folate metabolism		Folate metabolism
/ith s.	TGGT1_301210	S7UHH6	0.557322382926941	0.944646894931793	0.387324512004852	385626666.7 56	7463333.3	74222250 1.41358363628387	-1.91 PM-inte	gral	24.97	25.12 1	.00600720865038	Pyridine nucleotide transhydrogenase. Nicotinate and nicotinamide metabolism		NAD/NADP synthesis
nic v	TGGT1_208370	S7UJT6	0.551288843154907	0.690403342247009	0.139114439487457	1300725000	1906075000	2099025000 1.83155822753906	1.79 dense g	ranules	46.22	127.59 2	.76049329294678	GR446, higher expression in Bz	PMID: 30377279	Bz GRA
ein																
ote ote	No LFQ values in co	ntrol, but LFQ valu	es in TgNFS2 and TgISU	1 mutants												
bud	TGGT1_224190	\$7UV\$1	N/A	N/A	-0.11271425367	0	20276333.3	21924000 N/A	-5.24 Golgi		46.22	11.84 0	256166161834704	Lipid flippase TgFLP2	BioRxiv: 10.1101/2020.06.19.160341	Lipid metabolism
ve	TGGT1_317705	S7UFF2	N/A	N/A	-0.75161181616	0	26330333.3	44331666.6 N/A	-0.45 N/A		103.44	104.55 1	.01073085846868	Enoyl-CoA hydratase/isomerase family protein		Lipid metabolism
ati	TGGT1_261650	S7UY15	N/A	N/A	0.20880937503	0	57346750	49619333.3 N/A	1.61 PM - per	ripheral 2	110.47	389.39 3	.52484837512447	Cyst wall protein TgCST4	PMID: 31040239	Bz cyst wall protein
on																
nar C																
e qu									¤ fitness score data \$ inferre	ed from (published data	# RNAseq data from					
<b>S5</b>									from whole genome or Hype	rLOPII prediction -	Hehl AB et al BMC					
l-fi									CRISPR screen (Sidik Barylyuk	k K et al Cell Host &	Genomics 2015					
<b>ab</b> ibe									SM et al. Cell 2016) Microbe	e 2020-)						
E e																

Résultats – Chapitre I – Tables supplémentaires

Primer name	Primer sequence
ML687	GTTTGAATGCAAGGTTTCGTGCTGTCG
ML841	ATGTTCCGTGGTCGCATGT
ML842	TTCATGTTGTTGGGAATCCAC
ML843	GCGCGACATCAAGGAGAAGC
ML844	CATCGGGCAATTCATAGGAC
ML1041	CGGATCATTTGAAAACATCGTGAGGCTGG
ML1476	CAGCGTAGTCCGGGACGTCGTAC
ML1771	CTGCTTTCGTCTGTCTTC
ML1774	TACGACTCACTATAGGGC
ML2087	AAGTGCTCCCACGTCCCTCACCAT
ML2088	AAAAATGGTGAGGGACGTGGGAGC
ML2866	CGTTCATTCGAAACAAGGAC
ML3445	aagtCAGGGCTTCTAAAATGGCGC
ML3446	aaaaGCGCCATTTTAGAAGCCCTG
ML3948	aagtGCATCGTGCTGGCGTGGAATG
ML3949	aaaaCATTCCACGCCAGCACGATGC
ML3978	GTAGGCGCGCTGAAAATTTACAAAGCAGCTACCCGTACGACGTCC
ML3979	CTCCGAATATGCCGCCGATAAACGCTGCTTCTAGAACTAGTGGATCCCC
ML3982	CCAGCCAGGTTTGAGGCAGGAAC
ML4012	GCCGGATCCCTAGCTGCTTTGTA
ML4023	CTGCTGCGAGTGCGGACAAGGGCAAAGTCTACCCGTACGACGTCC
ML4101	CTCTCCTGGATAATCAGCTCGAGG
ML4154	TTGTGTCAGCGGTGGCTTTGCGTGCTTCCCAAGCTTCGCCAGGCTGTA
ML4155	GAGAAGGAAGGCAACGGCGCCAGAAGCCATAGATCTGGTTGAAGACAGAC
ML4156	aagtGAAGATGCCCTGGAAGAACCG
ML4157	aaaaCGGTTCTTCCAGGGCATCTTC
ML4158	GTTGACGAGATGTTTCCGCG
ML4159	GTAAAGCCTCGGCTCCTCG
ML4160	aagtGTTTTCCCCAGAGTACAGTTG
ML4161	aaaaCAACTGTACTCTGGGGAAAAC
ML4162	TACACGTTCTGCGTCTTTGCCTTGTCTCGCTCTAGAACTAGTGGATCCCC
ML4201	GCCAAGCTTCATGAAAGAACAGGACGAAATG
ML4204	CTTGCATGCAATGCGACGGTACAGCAAAAAAG
ML4205	CGGGGATCCTTAGGTTGTCTTCTGCTTC
ML4208	TACTTCCAATCCAATTTAATGCGCAAGACATGCGATGACGCCC
ML4209	TCCTCCACTTCCAATTTTAGCCTGGGCAGGTGCAGCGGATGC
ML4212	TTTAGATCTATGGCGCTGACACGCG
ML4213	TTTGCGGCCGCCCACATCGCTGCATCTTTC
ML4387	GAGGACCTCAAAAGCTAG
ML4388	TCAGAACTGCGGGCAATC
ML4455	TTTAGATCTATGGCGCTGACACGCGTTC
ML4456	tttCCTAGGCTGGGCAGGTGCAGCGGATG
ML4576	TTTGAATTCATGGCTTCTGGCGCCGTTG
ML4577	gggGCTAGCGCTGCTTTGTAAATTTTCAG
ML4684	
ML4685	TTGATGAGTTCCGTGGCG
ML4686	
ML4687	GCGACAAGATTGATACCGTC
ML4984	aagtGCATGGTTAATTCCCCATGGA
ML4985	aaaaTCCATGGGAATTAACCATGC
ML4986	aagtGACCTCGGCTCGCCGTACACT
ML4987	aaaaAGTGTACGGCGAGCCGAGGTC
ML5006	ACGGCACTCACTTGTGGG
ML5013	TGCGTTTGTCTCTAGCAC
ML5114	GGCGTCGCCTCCACGTACCTGATGCATGGTTACCCGTACGACGTCCCGGA
ML5115	AACCGGGTGAGAGACCACCAGGGCCTCACCGGCGGCCGCTCTAGAACTAG
ML5116	AAGCTCGCGAAGGACCTTGGCCTCGCTGCGTACCCGTACGACGTCCCGGA
MT.5117	IGCATGCCTAGGTCCCCACATCGACTGCTCGGCCGCCCCCTCTAGAACTAG

# Table S6. Oligonucleotides used in this study.



**Figure S1. Alignment of SufS/NFS2 and IscU/ISU1 homologs**. TgNFS2 (A) and TgISU1 (B) homologs werealigned to their counterparts from plant (*Arabidopsis thaliana*) and bacteria (*Escherishia coli*). Key conserved cysteine residue for cysteine desulfurase activity is indicated.



**Figure S2. Generation of HA-tagged TgNFS2 and TgISU1 cell lines.** A) Schematic representation of the strategy for expressing HA-tagged versions of TgNFS2 (left) and TgISU1 (right) by homologous recombination at the native locus of the corresponding gene of interest . Chloramphenicol was used to select transgenic parasites based on their expression of the Chloramphenicol acetyltransferase (CAT). B) Diagnostic PCR for verifying correct integration of the construct. The amplified fragments correspond to theblue or red arrows in A), and specific primers used were ML3982/ML1476 (TgNFS2) and ML4208/ML1476 (TgISU1).



**Figure S3. HA-tagging of TgSUFE2 shows it is an apicoplast protein.** A) Sequence alignment of TgSUFE2 (TGGT1\_277010) with plant (*A. thaliana*) and bacterial (*E. coli*) homologues. B) Schematic representation of the strategy for expressing an HA-tagged version of TgSUFE2 by double homologous recombination at the native locus. Chloramphenicol was used to select transgenic parasites based on their expression of the Chloramphenicol acetyltransferase (CAT). C) Diagnostic PCR for verifying correct integration of the construct. The amplified fragment corresponds to the red arrows in B), and specific primers used were ML4101/ML1476. D) Detection by immunoblot of C-terminally HA-tagged TgSUFE2 in parasite extracts reveals the presence of both precusor and mature forms of the protein. Anti-actin antibody (TgACT1) was used as a loading control. E) Immunofluorescence assay shows TgSUFE2 co-localizes with apicoplast markerTgCPN60. Scale bar represents 5  $\mu$ m. DNA was labelled with DAPI. DIC: differential interference contrast.



**Figure S4. Generation of TgNFS2 and TgISU1 conditional mutants.** A) Schematic representation of the strategy for generating TgNFS2 (top) and TgISU1 (bottom) conditional knock-down cell lines by homologous recombination at the native locus. Pyrimethamine was used to select transgenic parasites based on their expression of Dihydrofolate reductase (DHFR). B) Diagnostic PCR for verifying correct integration of the

construct. The amplified fragments confirming 5' and 3' integration correspond to the blue and red arrowsdisplayed in A), respectively, and specific primers used were: ML4158/ML687 (TgNFS2 5' integration),

ML1041/ML4159 (TgNFS2 3' integration), ML1774/ML4388 (TgISU1 5' integration), ML1771/ML4387(TgISU1 3' integration).



**Figure S5. Generation of TgNFS2 and TgISU1 complemented cell lines.** A) Schematic representation of the strategy for generating TgNFS2 and TgISU1 complemented cell lines by integrating an extra copy of the gene of interest (GOI) by double homologous recombination at the *Uracil Phosphoribosyltransferase* (*UPRT*) locus. Negative selection with 5-fluorodeoxyuridine (FUDR) was used to select transgenic parasites based on their absence of UPRT expression. B) Diagnostic PCR for verifying correct integration of the construct.

The amplified fragments confirming integration correspond to the red arrows displayed in A), and specific primers used were: ML2866/ML4686 (TgNFS2 integration), ML2866/ML4455 (TgISU1 5' integration). C) Semi-quantitative RT-PCR analysis from cKD TgNFS2-HA, cKD TgISU1-HA and their respective complemented cell lines grown for three days in the presence or absence of ATc, using specific primers couples ML4686/ML4687 (*TgNFS2*) and ML4684/ML4685 (*TgISU1*). It shows complemented cell lines express high levels of the corresponding mRNA. Specific *β*-tubulin primers (ML841/ML842) were used as controls.



Figure S6. Quantification of apicoplast loss upon TgNFS2 depletion using streptavidin. Percentage of cKD TgNFS2-HA parasites-containing vacuoles displaying a loss of apicoplast signal when labeled with streptavidin-Fluorescein Isothiocyanate after culture in the presence or absence of ATc for 120 hours. Dataare mean values from n=3 independent experiments  $\pm$ SEM. \*\*\*\*  $p \le 0.0001$ , Student's *t*-test. Inset : typicalstreptavidin labeling of the apicoplast (green) in a tachyzoites-containing vacuole, the inner membrane complex was stained with anti-TgIMC3 (red) and the DNA with DAPI (blue); scale bar=5µm.



Figure S7. Quantitative proteomics shows depletion of TgNFS2 does not have a global impact on the apicoplast, but may suggest compensatory response from other cellular pathways in response to specific apicoplast-related lipid synthesis defects. Classification of variant proteins according to their putative cellular localization (A) and function (B). N/A: not available; ER: endoplasmic reticulum; PM: plasma membrane; VAC: vacuolar compartment; GRA: dense granule protein; SRS: SAG-related sequence. In particular, the increased expression of ERlocated lipid metabolism enzymes suggests possible compensation for loss of apicoplastrelated lipid synthesis function.



Figure S8. TgISU1-depleted parasites show a marked decrease in proteins related to mitochondrial respiration, and a strong increase in bradyzoite-specific dense granules proteins and surface antigens. Classification of variant proteins according to their putative cellular localization (A) and function (B). N/A: not available; ER: endoplasmic reticulum; PM: plasma membrane; VAC: vacuolar compartment; GRA: densegranule protein; SRS: SAG-related sequence. A large proportion of components of complexes II, III and IV of the mitochondrial respiratory chain, which involve Fe-S proteins, were found to be less abundant.

Conversely, the abundance of many bradyzoite-specific dense granule proteins of plasma membrane-located surface antigens increased.



**Figure S9. Generation of a tag-free cKD TgISU1 cell line.** A) Schematic representation of the strategy forgenerating the conditional knock-down cell line by homologous recombination at the native locus.

Pyrimethamine was used to select transgenic parasites based on their expression of Dihydrofolate reductase (DHFR). B) Diagnostic PCR for verifying correct integration of the construct. The amplified fragments confirming 5' and 3' integration correspond to the blue and red arrows displayed in A), respectively, and specific primers used were ML1774/ML4388 (5' integration), and ML1771/ML4387 (3' integration). C) Semi-quantitative RT-PCR analysis of the cKD TgISU1 cell line grown for up to three days inthe presence or absence of ATc, using specific primers couple ML4684/ML4685, showing effcient down- regulation of *TgISU1* expression. Specific *actin* primers (ML843/ML844) were used as controls. D) Plaque assays were carried out by infecting HFF monolayers with the newly generated cKD TgISU1 cell line or the original cKD TgISU1-HA mutant cell line as a control. They were grown for 7 days ± ATc. Measurements of lysis plaque areas are shown on the right and confirm a significant defect in the lytic cycle in the two

mutant cell lines upon ATc addition. Values are means of n=3 experiments ± SEM. \*\*\*\* denotes  $p \le 0.0001$ , ANOVA. Scale bar= 1mm.



**Figure S10. Tagging of mitochondrial candidates in the cKD TgISU1 background.** A) Schematic representation of the strategy for expressing HA-tagged versions of TgSDHB and TgApiCox13 by homologous recombination at the native locus of the corresponding gene of interest. Chloramphenicol was used to select transgenic parasites based on their expression of the Chloramphenicol acetyltransferase (CAT). B) Diagnostic PCR for verifying correct integration of the construct. The amplified fragment corresponds to the red arrows in A), and specific primers used were ML1476/ML5013 (TgSDHB), ML1476/ML5006 (TgApiCox13).

С.

Dans cette étude, nous avons mis en évidence la présence de voies de biosynthèse des protéines fersoufre au sein de la mitochondrie (ISC) et de l'apicoplaste (SUF) de *T. gondii*. Nous avons aussi découvert qu'impacter ces voies par dérégulation d'une de leurs protéines clés (TgSufS pour la voie plastidique et TgIscU pour la voie mitochondriale), mène à une perturbation du cycle replicatif du parasite. Cependant, la dérégulation de ces protéines n'aboutit pas à des phénotypes équivalents.

Ainsi, la protéine SufS est essentielle à la survie du parasite. En effet, sa déplétion semble entrainer une perte de l'apicoplaste, quoi que partielle et tardive, ainsi que des défauts visibles et irréversibles dans le cycle replicatif du parasite jusqu'à engendrer la mort. La perturbation de la cystéine désulfurase SufS semble impacter directement la voie de biosynthèse des protéines à centres [Fe-S] de l'apicoplaste. Nous avons par exemple démontré que LipA, une protéine responsable de la lipoylation de la sous-unité E2 de la pyruvate déshydrogénase (PDH) plastidique n'était plus fonctionnelle. Etant donnée l'importance de la PDH pour la voie de synthèse de l'acétyl coA, qui est notamment un précurseur important de la synthèse des acides gras, on peut supposer que cela peut conduire à de graves disfonctionnements métaboliques, notamment par rapport au maintien de l'homéostasie lipidique du parasite.

A contrario, perturber l'expression de la protéine d'assemblage IscU n'engendre pas de phénotype particulier visible au niveau subcellulaire, mais ralentit la croissance de façon réversible. Nous avons montré que la capacité respiratoire des parasites est fortement impactée, ce qui peut être expliqué par le fait que trois protéines à centres [Fe-S] font partie des complexes II, III et IV, (sous-unité Fe-S du complexe succinate déshydrogénase, protéine Rieske et TgApiCox13). L'analyse de protéomique quantitative a démontré que trois protéines à centres [Fe-S], respectivement des complexes II, III et IV, ainsi que la plupart des composants des complexes III et IV sont spécifiquement impactés par la perte d'IscU. Comme l'ont montré d'autres études<sup>85,199</sup> réalisées sur T. gondii, la déplétion d'un membre d'un complexe de la chaîne respiratoire mitochondriale peut entraîner une altération dans l'assemblage ou la stabilité du complexe. De façon intéressante, l'analyse protéomique a également suggéré que la perte de la capacité respiratoire pourrait être compensée par une augmentation de la capacité glycolytique des parasites pour générer de l'ATP. Par conséquent, contrairement à ce que l'on observe pour le mutant SufS, le stress métabolique subit par les parasites n'est pas léthal et semble déclencher un processus de différenciation, identifié à l'aide de marqueurs spécifiques ainsi que par l'analyse protéomique. Comme mentionné dans l'introduction de ce manuscrit, les formes tachyzoïtes de T. gondii ont la capacité de se différencier en formes bradyzoïtes, qui ont une croissance ralentie et sont contenues dans des kystes pouvant persister et survivre dans des conditions défavorables. Cette capacité à former des kystes diffère en fonction des souches et en l'occurrence le mutant IscU a été

généré dans une souche de type I qui est peu propice à la différenciation. Il est donc particulièrement marquant de voir que la perte d'IscU entraîne une différentiation spontanée dans ce contexte. La question est maintenant de savoir si ce phénomène est général pour les mutants métaboliques mitochondriaux, ou spécifique au mutant IscU. De plus, il est nécessaire de garder à l'esprit que la voie mitochondriale de synthèse des centres [Fe-S] est importante également pour la fonction de protéines [Fe-S] cytoplasmiques et nucléaires, dont certaines pourraient jouer un rôle dans le déclenchement de la différenciation.

Il reste donc de nombreuses inconnues concernant le fonctionnement et l'impact de ces deux voies de biosynthèses. Le stress engendré par la perturbation de la voie mitochondriale nécessite d'être étudié de façon approfondie afin de comprendre les mécanismes moléculaires qui sont impliqués. De plus, le mutant IscU pourrait être un bon modèle pour identifier de nouveaux facteurs de différenciation.

De même, une meilleure compréhension de l'implication de la voie SUF sur le fonctionnement des voies métaboliques importantes de l'apicoplaste pourrait ouvrir des perspectives intéressantes pour le développement de nouvelles cibles thérapeutiques anti-parasitaires.

De ce point de vue, comme décrit dans le chapitre suivant, nous avons cherché à mieux caractériser les perturbations métaboliques liées à la perte de la voie SUF. Pour cela, nous avons généré un nouveau mutant pour cette voie afin de l'analyser en détail en parallèle du mutant SufS.

# Chapitre II : Caractérisation de l'ATPase SufC

# A. Conservation de la fonction ATPase au cours de l'évolution.

Comme vu dans l'introduction de ce manuscrit, les protéines d'assemblage telles que IscU ou le complexe SufB/C/D, permettent l'interaction du fer et du soufre afin de former le centre [Fe-S]. Notre analyse bio-informatique a permis d'identifier une ATPase putative potentiellement homologue de SufC (TGGT1\_225800). La protéine putative SufC de *T. gondii* est prédite comme étant plastidique à 95% d'après l'algorithme Deeploc V1.0 (http://www.cbs.dtu.dk/services/DeepLoc/). Par rapport à la SufC bactérienne, la protéine de *T. gondii* possède une extension en N-terminale (**Figure 26**) qui comporte probablement la séquence d'adressage au plaste ainsi qu'une extension C-terminale riche en acides aminés chargés (D, E, R) dont la fonction reste inconnue.

	(d.					12			~~ <u>*</u>			10		
TgSufC TGGT1_225800 FcSufC EGT68402	MAS	LPVE	FLVE	LDRV	VKHH	VWLR	RLR	CLL	VSP	FVS	LSV	LPVL	LPF	LFN
		5 <b>0</b>		6	p		70	6			60			eò.
TgSufC TGGT1_225800 EcSufC EGT58402	FVT	SPDI	[VPS	SAL	TLKS	TSAF	LSS	PAS	RFS	SPPI	SPL	SCVS	SRP	SLS
			190			19D			120			130		
TgSufC TGGT1_225800 EcSufC EGT68402	PSS	SASS	SAPS	SPSS	SASL	GVRF	PHFI	SVP	AAS	GTE	LAA	SLSS	TTS	SFI
	140			150			100			170			180	
TgSufC TGGT1_225800 EcSufC EGT68402	GSS	SSTF	RPAL	NRDS	SACR	QTVS	SFPA	RLS	PTI	FPL	SPD	TEDG	RGS	FSD
		190			200			210			220			230
TgSufC TGGT1_225800 EcSufC EGT68402	LQQ	LRDS	SREE	RFA	ALKS	MREÇ	DETE	PRFQ	AED	WTP	DQP	LLEI MLSI	KDL KDL	RVE HVS
			240			250			.26 Walker		>	270		
TgSufC TGGT1_225800 EcSufC EGT68402	ABE VED	DGQE KZ	ILK	GVNI GLSI	TIM AVR	<u>PGEV</u> PGEV	HA1	MG R MG P	<u>NGS</u> NGS	GKS	TLS	KV <mark>LA</mark> AT <b>LA</b>	GYP Gre	SYK DYE
TgSufC TGGT1_225800	VTA	GEVF	YKG	LDLI	ELP	IDNR	GLA	GLE	LAF	'QYP	IEI	PLVS	NLE	FLR
EcSuIC EGT68402	VTG	GTVI	SFKG	KDLI	ALS	PEDR 340	AGE	GIF	MAE	'QYP	VEI	PGVS	NQF	FLQ
TgSuIC TGGT1_225800	VAF	NER	KWK	KEPI	EVVS	YEFR	ELV	EGR	LKE	VGI	DPS	FLDR	PLN	YGF
EcSuIC EGT68402	'Т' <b>А</b> Ц. 370	NAVE	SYR	GQE'	LDR	EDEC		IBER	IAI.		PED	LLTR	SVN 410	VGE
ToSulC TGGT1 225800	ABC B	EKK F		T.OM	VID	PELV	Walker 8		SGI	DVD	SFN	TTAN	ATK	RFS
EcSufC EGT68402	SGG	EKKF	NDI	LÕM	VLE	PELO	ILD	ESD 440	SGĪ	DID	ALK	VVAD	GVN	SLR
TgSufC TGGT1_225800	KRK	GKS	LVT	THYF	KLL	DVLC	PHK	THV	MHA	GKI	VIS	GSMD	TAG	OIE
EcSuIC EGT68402	DGK	RSE	IIV	THY	DRIL	DY IK	PDY	VHV	LYC	GRI	VKS	GDFT	IVK	ÕLE
TgSufC TGGT1_225800 EcSufC EGT68402	AEG EQG	FQA Yğw	VGA T	AAEC	EEE EQQ	EERD	RRE	DEG	ERE	EHE	GED	EAES	LLS	PSA
		510		515										
TgSufC TGGT1_225800 EcSufC EGT68402	AGG	GRRN	JLDR	LL										

Figure 26: Alignement de séquences codant pour l'ATPase SufC de E. coli ainsi que son homologue putatif chez T. gondii

Walker A : domaine catalytique de liaison aux nucléotides permettant l'hydrolyse de l'ATP ; Q loop et motif H : motifs catalysant l'hydrolyse de l'ATP ; ABC signature : motif représentatif des transporteurs de la famille ABC (ATP-binding-cassette) ; Walker B : domaine d'hydrolyse de l'ATP contenant un aspartate pouvant intéragir avec du magnésium ; D loop: boucle participant au contrôle de l'hydrolyse de l'ATP.

Dans un premier temps, afin de vérifier la fonction de cette protéine candidate, nous avons effectué la complémentation d'un mutant bactérien de *E. coli* avec la séquence codant pour le domaine fonctionnel de la protéine putative TgSufC (acides aminés 220 à 518). Les cinétiques de croissance bactériennes ont été réalisées dans un milieu minimum en présence de différentes concentrations en chélateur de fer (2,2'-bipyridyl). L'expression du domaine ATPase a permis de restaurer la croissance bactérienne que cela soit en présence ou non de chélateur. Cela suggère que TGGT1\_225800 (que nous appelons désormais TgSufC), n'est pas uniquement similaire par sa séquence mais bien un homologue fonctionnel de SufC (**Figure 27**).



Figure 27: Cinétique de croissance des bactéries E. coli mutantes et complémentées.

WT : souche de E. coli K12 ; ΔSufC : souche bactérienne K12 délétée en SufC ; ΔSuf C comp : souche mutante complémentée ; chel (chélateur de fer) : 2,2'-bipyridyl.

# B. Localisation et impact sur le cycle lytique de *T. gondii*.

#### 1) <u>Localisation de la protéine TgSufC</u>

Afin de commencer à caractériser cette protéine nous avons voulu déterminer sa localisation pour vérifier si elle était adressée à l'apicoplaste. Aude Cerutti, la post-doctorante de l'équipe, a généré une souche transgénique dans laquelle une séquence codant pour une étiquette triple hémagglutinine (HA) a été insérée en 3' du gène (**Figure 28 A**). L'intégration de la construction a été vérifiée par PCR (**Figure 28 B**). Par microscopie en immunofluorescence, à l'aide d'anticorps anti-HA, nous avons pu confirmer la localisation de TgSufC à l'apicoplaste (**Figure 28 C**).



Figure 28: Génération d'un mutant TgSufC étiqueté triple HA

**A** : schéma représentant la stratégie pour obtenir une protéine TgSufC exprimant un triple tag Ha en C-term par recombinaison homologue au locus natif du gène d'intérêt. Sélection des parasites transgéniques positifs par chloramphénicol acétyltransférase (CAT). **B** : PCR diagnostic afin de vérifier intégration de la construction, avec un fragment correspondant aux flèches rouges en (A) de 923 pb amplifié avec les amorces ML3984 et ML1476. **C** : Immunofluorescence de vérification de l'expression et de la localisation de la protéine étiquetée TgSufC-HA

#### 2) <u>Genèse d'un mutant conditionnel de TgSufC</u>

Nous avons démontré précédemment que perturber la biogénèse des protéines à centres [Fe-S] en diminuant drastiquement l'expression de la cystéine désulfurase TgSufS induit un défaut dans le cycle lytique de parasite. Nous nous sommes alors demandé si perturber l'expression de TgSufC impacterait de façon similaire le développement du parasite.

Nous avons entrepris de générer un mutant conditionnel en remplaçant le promoteur natif par un promoteur SAG4 régulable par l'anhydrotétracycline (ATc) (**Figure 29 A**). Dans cette souche (cKDSufC), qui a été générée par la post-doctorante Aude Cerutti, le remplacement de promoteur a été vérifié par PCR (**Figure 29 B**).

Par la suite, des immunoblots nous ont permis de vérifier la régulation de l'expression de la protéine. Avant le remplacement du promoteur, nous avons pu voir que deux produits sont détectés. Ils correspondent très probablement à la forme précurseur (à ~50kDa, avant le clivage de peptide transit) ainsi qu'à la forme mature (à 38kDa) présent dans la matrice de l'apicoplaste (**Figure 29 C**). De plus, notre lignée étant taguée HA, une analyse par immunofluorescence nous a permis de vérifier la bonne régulation, par ajout ou non d'ATc, du marquage HA en C-terminal de notre protéine d'intérêt TgSufC (**Figures 29 C et D**).



Figure 29: Génération d'une lignée de parasites mutants conditionnels cKD TgSufC-HA

*A* : schéma représentant la stratégie pour obtenir un mutant conditionnel (cKD) TgSufC par recombinaison homologue au locus natif du gène d'intérêt. Sélection des parasites transgéniques positifs par expression de la Dihydrofolate réductase (DHFR) qui leur confère une résistance à la pyriméthamine. *B* : PCR diagnostic afin de vérifier intégration de la construction. Le fragment correspondant aux flèches bleues en (A) pour l'intégration 5' et aux flèches rouges en (A) pour l'intégration 3'. Respectivement réalisés par les couples d'amorces ML4111/ML687 (TgSufC 5' intégration de 1273 pb) et ML1041/ML4112 (TgSufC 3' intégration de 1158 pb). *C* et *D* : Vérification de l'expression et de la régulation de la protéine cKD TgSufC-HA par immunoblot (*C*) et immunofluorescence (*D*). Utilisation, pour le western blot, comme contrôle d'expression de la lignée parentale TATi, la lignée mutante (cKD TgSufC-HA) mise en culture sur une cinétique de 3 jours dans du milieu contenant ou non l'anhydride de tétracycline (ATc). Marquage de la protéine de surface P30 comme expression control. Concernant l'IFA, utilisation de la lignée mutante (cKD TgSufC-HA) ainsi que de la lignée comprenant construction de complémentation (cKD TgSufC-HA comp) après 24h de culture dans du milieu avec ou sans ATc. La Fluorescence rouge indique un marquage du tag HA (régulé par l'ATc) alors qu'une fluorescence verte indique la présence du tag Ty (issu de la complémentation et non régulé par l'ATc).

Dans un même temps, nous avons voulu nous assurer de la spécificité des futures analyses phénotypiques. Nous avons donc généré une lignée complémentée exprimant au locus *UPRT* (*uracile phosphoribosyltransférase*) une copie supplémentaire de *TgSufC*. Ainsi les phases initiales de l'analyse décrites ci-après ont pu être réalisées sur la souche mutante (cKD TgSufC) mais aussi, servant de contrôle, sur la souche Tati∆ku80 (dont est issues la lignée mutante) qui permet la régulation par l'ATc ainsi que sur la souche complémentée (**Figure 30**). L'expression et la bonne localisation à l'apicoplaste de la copie additionnelle de TgSufC, étiquetée avec un épitope Ty, a été vérifiée par immunofluorescence (**Figure 29 D**).



Figure 30: Génération de la lignée complémentée de TgSufC

*A*: schéma représentant la stratégie pour obtenir une lignée complémentée (cKD TgSufC-HA comp) par addition d'une extracopie, du gène codant pour SufC, par recombinaison au locus Uracil phosphoribosyltrasferase (UPRT). Nous avons utilisé la CAS9 couplé à des ARNg spécifiques (flèches jaunes) pour perturber le gène de l'UPRT. La perte de l'UPRT engendre une résistance à la 5-fluorodeaxyuridine (FUDR), nous permettant de sélectionner les parasites transgéniques. *B*: PCR de vérification de la complémentation par les amorces : ML801/4816 (gène SufC, flèches vertes) ; ML1432/1433 (UPRT natif flèches bleues) et ML3636/3190 (promoteur tubuline et début du gène SufC, flèches roses).

### C. La perturbation de l'expression de SufC impacte la réplication du parasite.

#### 1) Impact de la perte de TgSufC sur la croissance et la réplication

Dans le but de mesurer et comprendre l'impact de la déplétion de SufC sur le cycle lytique de *T. gondii in vitro*, nous avons réalisé des expériences de plage de lyse (**Figure 31 A**). Ce test permet d'évaluer le bon déroulement du cycle lytique du parasite. En effet, le développement (les étapes d'invasion/réplication/sortie) sur un tapis de cellules hôtes confluentes va créer des plages de lyses quantifiables et mesurables. Après un traitement de 7 jours (en présence ou absence d'ATc dans le milieu de culture), les plages de lyse sont dénombrées et leur aire est mesurée (**Figure 31 B**). Le résultat est semblable à celui obtenu précédemment avec TgSufS : la condition comprenant la lignée mutante inductible en présence d'ATc ne montre aucune plage de lyse contrairement aux diverses autres conditions. Cela suggère donc que perturber l'expression de SufC induit un défaut dans le cycle lytique du parasite.



Figure 31: Régulation de l'expression de SufC et impact sur le cycle lytique de T. gondii.

**A** : Test de plage de lyse avec les parasites issus de la lignée mutante conditionnelle et de la lignée complémentée en présence ou absence d'anhydride de tétracycline (ATc) pendant sept jours consécutifs. **B** : dénombrement des plages de lyse pour chaque condition de cultures. Test de Student \*\* p<0.01 n=3

Une perturbation du cycle lytique peut avoir lieu à une ou plusieurs de ses étapes qui sont l'invasion de la cellule hôte, la réplication au sein de la cellule hôte, pour terminer avec la sortie ce qui entraine la lyse de la cellule hôte. Le mutant SufS était perturbé au niveau de la réplication, nous avons donc voulu évaluer si c'était également le cas pour le mutant SufC (**Figure 32**).

Pour cela après 48h de préincubation en présence ou non d'ATc, les parasites sont utilisés pour

réenvahir des cellules hôtes toujours dans les mêmes conditions. Nous effectuons ensuite des marquages en immunofluorescence afin de d'identifier et de quantifier le nombre de parasites par vacuoles 24h post ré-invasion. Comme représenté dans la **figure 32** ci-dessus, pour les trois conditions



Figure 32: Test de réplication et décompte de parasites par vacuoles

Les valeurs représentées sont la moyenne +/- erreur type. Les comptages sont réalisés sur un total de 200 vacuoles pour chaque condition.

contrôles (WT +ATc/ HA +ATc/ cKD -ATc) ainsi que pour la souche complémentée, la plupart des vacuoles contiennent en majorité 4 parasites. Au contraire, lorsque la protéine SufC est déplétée par ajout d'ATc, les vacuoles contiennent en majorité 1 ou 2 parasites, ce qui indique un ralentissement ou une perturbation du cycle replicatif des parasites.

#### 2) <u>TgSufC est importante pour l'intégrité de l'apicoplaste.</u>

Comme nous l'avons démontré précédemment, la protéine TgSufC, tout comme TgSufS, est localisée à l'apicoplaste. Il est donc possible que l'impact sur le cycle réplicatif soit dû à un défaut au niveau de cette organelle essentielle à la survie des tachyzoïtes. De plus, la perte de viabilité des mutants TgSufS et TgSufC est compatible avec le phénotype de 'mort retardée' qui est caractéristique de défauts de l'apicoplaste (d'où la nécessité de pré-incuber les parasites pendant 48h avec l'ATc avant d'observer les défauts de croissance). Ainsi, pour évaluer s'il y a ou non une perte d'intégrité de l'apicoplaste, nous avons réalisés des quantifications de l'organelle par immunofluorescence sur des parasites incubés jusqu'à cinq jours avec de l'ATc. Nous avons utilisé comme marquage de l'apicoplaste un anticorps dirigé contre la chaperonine CPN60 (**Figure 33 A et B**). On note la perte progressive de l'organelle suite à la déplétion de TgSufC, mais elle semble lente et incomplète. Après cinq jours d'incubation, près de la moitié des vacuoles comportent des parasites ayant perdu leur apicoplaste. Ce résultat a été confirmé avec un deuxième marquage indépendant utilisant de la streptavidine fluorescente, qui reconnaît essentiellement l'acetyl-CoA carboxylase (ACC) une protéine de l'apicoplaste naturellement biotinylée (**Figure 33 C et D**).





A et C : immunofluorescences évaluant la perte de l'apicoplaste à l'aide de différents marquages : la protéine de lumen CPN60 (reconnue de façon spécifique par un anticorps) et la protéine ACC (protéine biotinylée majoritairement reconnues par la streptavidine couplée à un fluorochrome). B et D : Représentations graphiques du dénombrement de vacuoles comportant des parasites ayant un apicoplaste présent ou une perte d'apicoplaste à partir des immunofluorescences, décrites respectivement en A et C. 40 vacuoles ont été comptées par conditions et utilisation du test statistique « T-test » de Student: ns : non significatif, \* P<0.05, \*\*\*\* P<0.0001.

#### D. SufS et SufC : un impact sur les lipides et les membranes ?

# <u>La dérégulation de la voie SUF entraine une perturbation de lipoylation de la sous-unité</u> <u>E2 de la PDH apicoplastique</u>

Une des protéines classiquement connues comme possédant un centre [Fe-S] et résidant dans l'apicoplaste est la lipoyl synthase LipA. Dans l'organelle, elle a pour substrat la sous-unité E2 de la pyruvate dehydrogénase (PDH)<sup>200</sup>, dont elle assure la lipoylation (ajout d'un acide lipoïque), qui est essentielle à sa fonction. Nous avons utilisé un anticorps spécifique de l'acide lipoïque pour évaluer par immunoblot l'impact de la perte de TgSufC sur la lipoylation de LipA. Nous avons pu voir que la lipoylation de PDH-E2 est rapidement affectées en présence d'ATc (**Figure 34**). Contrairement à d'autres protéines lipoylées du parasite, comme les sous-unités E2 de la « branched-chain alpha-keto dehydrogenase » (BCDH) et de la «  $\alpha$ -ketoglutarate dehydrogenase » (KGDH)<sup>201</sup>, qui sont mitochondriales et ne sont pas affectées. La diminution de la lipoylation de la PDH-E2 semble spécifique car elle est antérieure aux pertes partielles de l'apicoplaste lui-même, comme montré avec le marqueur Cpn60 dont les quantités varient peu (**Figure 34**).

L'apicoplaste est connu pour être le siège de nombreuses voies métaboliques indispensables au bon fonctionnement du parasite. Parmi celles-ci se trouve la voie FASII de synthèse d'acide gras. Cette voie de biosynthèse dépend de précurseurs comme l'acetyl-CoA, lui-même synthétisé grâce à la PDH. Le mutant TgSufS nous avons que (voir précédemment caractérisé chapitre I) est lui aussi impacté pour



*Figure 34: Immunoblot attestant de l'état de lipoylation de la sous unité E2 de la pyruvate déhydrogénase (PDh) chez T. gondii.* 

la lipoylation de la PDH-E2. L'analyse de protéomique quantitative, faite sur ce mutant, a montré une augmentation de l'expression qu'un certain nombre d'enzymes localisées dans l'ER et impliquées dans la synthèse de plusieurs phospholipides et céramides. Ces lipides sont généralement synthétisés dans le ER à partir précurseurs issus de l'apicoplaste, ces précurseurs peuvent également être récupérés à partir de la cellule hôte, donc cela peut clairement indiquer un mécanisme compensatoire.

Par conséquent nous pouvons supposer que les deux mutants de protéines impliqués dans la biosynthèse des centres [Fe-S] (TgSufS et TgSufC) se comportent de manière similaire. Les protéines à

centre [Fe-S] de l'apicoplaste semblent donc nécessaires au parasite puisque leur dysfonctionnement pourrait entrainer des perturbations d'autres voies biologiques indispensables, en particulier l'homéostasie lipidique des parasites.

Afin d'évaluer l'importance de cette voie SUF sur la biosynthèse des lipides et donc de façon concomitante la formation des membranes de *T. gondii*, une analyse lipidique spécifique de l'apicoplaste a été menée par nos collaborateurs de l'institut de bioscience de Grenoble. Dans un même temps, nous avons a effectué des analyses complémentaires par microscopie électronique à transmission et en microscopie photonique afin de voir si nos mutants peuvent être associés à un phénotype morphologique spécifique attestant de dysfonctions au niveau lipidique, lors de la formation des membranes nécessaires au développement du parasite.

#### 2) Analyse morphologique et lipidomique et de T. gondii.

#### a) Intégrité membranaire des mutants TgSufS et TgSufC.

Lors des précédentes analyses en microscopie des mutants apicoplastiques (TgSufS et TgSufC) il nous a semblé voir une division non synchronisée des parasites au sein des vacuoles. Afin de vérifier cela, nous avons effectué un marquage du complexe membranaire interne (IMC), permettant de visualiser le stade de division des parasites, notamment l'initiation de la formation des cellules filles (Figure 35 A et B). Il semble en effet que les mutants, lorsqu'ils sont déplétés de leur protéine d'intérêt respective, aient un problème précoce dans la synchronisation de la division au sein d'une même vacuole et, plus tard, dans la formation de l'IMC. L'effet est particulièrement marqué pour le mutant TgSufC qui au bout de seulement deux jours de traitement à l'ATc contient approximativement 80% de vacuoles comportant des parasites asynchrones. Nous avons également évalué l'effet à plus long terme au niveau morphologique (nous avons vu précédemment par exemple que l'apparition du phénotype de perte de l'apicoplaste est progressive et arrive tardivement). Nous avons donc décidé de refaire une analyse de l'IMC après sept jours de traitement à l'ATc (Figure 35 C). En plus du défaut de synchronisation de la division des parasites, il semble que le complexe membranaire interne s'élargisse et perde son intégrité, accompagné d'un défaut de ségrégation du noyau tout comme d'une perte importante de l'apicoplaste (que nous avions auparavant décrite). Une analyse ultrastructurale par microscopie électronique du mutant TgSufS (Figure 35 D), après quatre jours de traitement à l'ATc, a également révélé de nombreuses malformations dans la continuité du réseau membranaire (membrane plasmique et IMC). De façon intéressante, ce phénotype rappelle celui observé dans le mutant de l'acyltransférase TgATS2<sup>200</sup>, impliquée dans la synthèse d'acide phosphatidique dans l'apicoplaste, un précurseur de la synthèse de nombreux autres phospholipides. Ainsi, il semblerait que dépléter les tachyzoïtes des protéines TgSufS et TgSufC, engendre potentiellement un défaut de

synthèse lipidique conduisant à de multiples perturbations membranaires, impactant à leur tour la division cellulaire et la biogenèse d'organelles.



#### Figure 35: Analyses morphologiques des membranes de T. gondii : déplétion de TgSufC/SufS et défauts membranaires.

**A**: Immunofluorescence de l'IMC par marquage de la protéine IMC3 (en rouge) attestant d'une désynchronisation de la division des parasites mutants TgSufS et TgSufC après deux jours de traitement à l'ATc. L'ADN est marqué en bleu avec le DAPI. Echelle= 5μm. **B**: Quantification de vacuoles comportant des divisions asynchrones de cellules filles, sur la base du marquage IMC3 montré en **A**. Les valeurs sont la moyenne +/- erreur standard. n=3. **C**: Immunofluorescence effectuée après sept jours de traitement + ATc par marquage du complexe membranaire interne (protéine IMC3, en rouge) ; du noyau (DAPI, en bleu) ainsi que de l'apicoplaste (protéine ATRX1, en vert). Echelle=5 μm. **D**: Analyse par microscopie électronique des mutants TgSufS et Tg SufC après quatre jours +ATc. Les défauts dans la séparation et continuité des membranes sont indiqués par des flèches vertes sur les images initiales (images du haut) ainsi que sur le zoom qui en découle (images du bas).

b) Biosynthèse des acides gras et analyse lipidomique pour le mutant TgSufC.

Au vu des défauts membranaires observés précédemment et parce-que l'apicoplaste contient la voie FASII de biosynthèse des acides gras, nous avons, avec l'aide de nos collaborateurs de Grenoble, voulu savoir si ces perturbations pouvaient être corrélées avec un défaut dans la synthèse d'acides gras. Les résultats préliminaires de l'analyse lipidomique, du mutant TgSufC montrent que la proportion de certains acides gras fluctue lors de la déplétion de la protéine TgSufC, mais n'est pas altérée pour les parasites complémentés (**Figure 36 A**). De plus, en comparant les quantités de chaque catégorie d'acide gras (**Figure 36 B**), il semble que la quantité d'acide gras à chaine courte diminue lors de la déplétion de TgSufC contrairement à la quantité d'acides gras à chaine longue. Les acides gras à chaine courte sont synthétisés dans l'apicoplaste avant d'être distribués dans l'ER pour des étapes d'élongation. Cette analyse pointe donc vers un défaut de synthèse de précurseurs lipidiques dans l'apicoplaste lorsque la voie de synthèse des protéines [Fe-S] apicoplastique est perturbée. Cependant, l'effet observé avec ces résultats préliminaires (qui doivent être confirmés par l'analyse du mutant TgSufS), est modeste. Ceci pourrait en fait refléter une compensation par le parasite avec l'import de précurseurs lipidiques de la cellule hôte. Des expériences de marquage métabolique de précurseurs lipidiques de l'hôte qui sont en cours nous permettront d'évaluer ceci.

![](_page_142_Figure_1.jpeg)

Figure 36: analyse du répertoire lipidique de TgSufC

**A** : Graphique représentant l'abondance des acides gras cours (C12 à C17) et longs (C18 à C24) lors d'une incubation en absence ou présence d'ATc pendant 5 jours. Quantité d'acide gras relevée pour  $10^6$  parasites mutants cKD TgSufC (en haut) ou complémentés (en bas) ; n =3. **B** : Ratio des quantités d'acide gras cours et longs par comparaison des conditions + et – ATc du mutant conditionnel (graphique du haut) et du complémenté (graphique du bas) ; utilisation du T-test de student, ns = non significatif et \*\*\*\* p< 0.0001 n=3.

# E. Production d'un nouvel anticorps dirigé contre l'apicoplaste de T. gondii

# 2) <u>Production et purification de protéines recombinantes de la machinerie [Fe-S]</u>

Nous avons voulu essayer de générer des protéines recombinantes correspondant aux candidats des voies de synthèse de centres [Fe-S] de la voie SUF que nous avions choisi d'étudier. Ceci afin éventuellement d'en étudier l'activité enzymatique.

La spécificité de la voie SUF (à l'apicoplaste et donc absente de l'Homme), et les activités enzymatiques de certaines protéines (cystéine désulfurase pour TgSufS, éventuellement potentialisée par TgSufE, une activité d'ATPase concernant TgSufC) en font des cibles thérapeutiques potentielles. De plus on a pu voir que grâce à la complémentation de mutants de *E. coli* par l'homologue de *T. gondii*, que l'activité de ces protéines semble être conservée. Il faut cependant noter que la sensibilité à l'oxygène de certains centres [Fe-S] peut rendre difficile l'expression et l'étude biochimique de certaines protéines [Fe-S] (nécessitant potentiellement de travailler dans des conditions anaérobies).

Nous avons cloné le fragment contenant le site actif putatif de chaque protéine d'intérêt dans le plasmide pET15b. Ce plasmide nous permettant d'exprimer une protéine étiquetée en N-term avec un six His, dont l'expression est mise sous le contrôle du promoteur Lac de l'opéron lactose. L'expression protéique peut donc être induite par ajout isopropyl β-D-1-thiogalactopyranoside (IPTG), un analogue d'allolactose.

Les constructions pour TgSufS/TgSufE et TgSufC ont été transformées dans des bactéries BL21 permettant l'expression, qui est induite par ajout de 0.5mM d'IPTG. Afin de voir si les protéines sont correctement exprimées, différentes conditions de cultures sont expérimentées (comme par exemple une culture à 37°C ou 16°C). Après dépôt sur gel de polyacrylamide des fractions issues des cultures (**Figure 37**) il s'avère que l'on obtient les différentes protéines exprimées aux tailles attendues (TgSufS : 53kDa, TgSufE : 18kDa, TgSufC 34kDa). Or, il apparait que la protéine TgSufS n'est pas soluble, contrairement aux protéines TgSufE et TgSufC. De plus, la production de TgSufE reste faible et n'a d'intérêt que dans le contexte de l'étude de SufS. Par conséquent, il nous a semblé judicieux de nous concentrer sur TgSufC.

		TgS	SufS			TgSufC						TgSufE							
kDa	Da Ni		i <u>37°C</u>		i 16°C		Ni		i <u>37°C</u>		i 16°C		Ni		i <u>37°C</u>		i <u>16°C</u>		
КDа	С	S	С	S	С	S	С	S	С	S	С	S	С	S	С	S	С	S	
70 — 55 — 40 —			-					A STATE					and the second				2	1	and a local
35 —	1						-	No.		調理		a state		Ser. Ja					
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15 —		-				- and the								-	A STATE OF				

Figure 37: Expression des protéines recombinantes TgSufS/C/E Tailles attendues TgSufS= ~53kDa ; TgSufC=~38kDa ; TgSufE=~18kDa ; C : culot ; S : surnageant ; Ni : non induit ; i : induit

C'est donc dans le but d'analyser l'activité ATPase de cette protéine que nous avons créé des lignées bactériennes contenant une mutation au site actif de TgSufC afin d'attester de la spécificité des futurs résultats. Deux lignées sont créées, une contenant une mutation changeant la lysine (K40) par un autre acide aminé proche chimiquement : l'arginine (K40R), contrairement à la seconde lignée pour laquelle nous avons remplacé la lysine par un acide aminé très éloigné chimiquement : l'alanine (K40A).
Avant toute expérience sur ces protéines recombinantes, il est nécessaire de les purifier à partir des fractions solubles issues des cultures bactériennes. Pour cela, nous nous sommes servis du tag triple histidines en N-terminal de nos protéines qui nous permet d'effectuer une chromatographie d'affinité sur colonne de nickel.

Après migration sur gel de poly acrylamide et coloration au bleu de coomassie, nous avons vu que la protéine d'intérêt est éluée de façon efficace (**Figure 38 A**).

Les sels et l'imidazole contenus dans la solution d'élution, ont alors été éliminés par dialyse avant qu'un dosage protéique soit effectué (**Figure 38 B**). Notre extrait protéique n'était pas complétement pur, mais la bande majoritaire est celle correspondant à notre protéine d'intérêt, que nous avons obtenu à une concentration de  $\sim 2\mu g/\mu L$ .



Figure 38: Gels de coomassie post- purification et dialyse de TgSufC

**A**: gel de coomassie avec les différentes fractions de purification de la protéine recombinante TgSufC. La section flowthrough représente l'éluât issu du passage de la culture bactérienne sur la colonne de nickel ; les fractions suivantes sont issues respectivement du 1<sup>er</sup> lavage de la colonne ainsi que des élutions n°2 à n°8 à concentration constante d'imidazole. **B**: Gel de coomassie ayant permis le dosage de TgSufC suite à la dialyse. La gamme standard permettant le dosage des protéines est faite avec de l'albumine de sérum bovin (BSA), diluée à des concentrations comprises entre 0.5 et 2 µg/µL ; 15µL de protéine purifiée sont déposés afin de déterminer la concentration qui se révèle alors être de ~2µg/µL dans notre échantillon final de protéine TgSufC.

#### 3) <u>Activité de TgSufC.</u>

Lors de l'étape de purification de la forme mutée K40R était toujours soluble mais ne semblait pas être retenue par la colonne de nickel, par contre la forme K40A a été obtenue de façon similaire à la forme sauvage, à une concentration finale de 0.5  $\mu$ g/ $\mu$ L. L'activité ATPase de la protéine TgSufC non mutée a été étudiée à l'aide d'un test colorimétrique au vert de malachite (le vert de malachite forme une couleur vert foncé avec le phosphate libéré par l'hydrolyse de l'ATP). Le test a été mené dans un premier temps uniquement avec la forme non mutée du site actif de TgSufC puis par la suite avec la forme mutante K40A servant de contrôle négatif afin de nous assurer de la spécificité des mesures. Afin de voir une potentielle variation de l'activité ATPase le test a été effectué sur deux paramètres de façons indépendantes (Figure 39 A). Dans un premier temps, j'ai fait varier la concentration en ATP (de 0.05mM à 25mM) afin que le paramètre constant soit la concentration en protéine purifiée TgSufC à 1.8µg/µL. Inversement, le test est aussi mené en faisant varier la concentration en protéine (de  $0.1\mu g/\mu L$  à  $3\mu g/\mu L$ ) avec une valeur constante d'ATP de 0.05 mM. Il s'est avéré que l'activité de la protéine SufC semble être à son maximum (mesure formant un plateau) quelle que soit la concentration en ATP testée pour 1.8µg de protéine. Nous avons donc décidé de faire varier la concentration en protéine pour laquelle on observe une courbe d'absorbance presque linéaire jusqu'à arriver à un plateau prenant effet à partir de 2µg de protéine (ce qui concorde avec la courbe l'activité précédente).



Figure 39: courbes d'activité de TgSufC d'après un test colorimétrique au vert de malachite.

**A**: Courbes d'absorbance représentatives de l'activité de TgSufC dépendante : en bleu de la concentration en ATP mais avec une concentration fixe en protéine de 1.8μg/μL ; en violet de la concentration en protéine d'intérêt avec une concentration fixe en ATP de 0.05 mM. En pointillés sont représentées les courbes de tendances. **B** : Courbes d'absorbance liées à l'activité de la forme native (en orange) et mutante (en vert) de TgSufC ainsi que de l'activité résultant de la différence des deux précédentes courbes en bleu (native-mutante). Toutes les mesures sont relevées après 30 min de réaction à 37°C. Chaque point est la représentation d'un triplicata technique.

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A ce moment, il nous semble donc que la protéine native SufC comporte une activité mesurable d'environ 150 $\mu$ M de phosphate inorganique (Pi) consommé en 30 min (ce qui équivaut à 5 $\mu$ M /min). Or, lorsque ce test est effectué avec la protéine wt ainsi que la forme K40A mutée au site actif putatif, on remarque que l'activité ATPase présumée est présente et presque similaire pour les relevés de chaque conditions (**Figure 39 B**). Nous ne pouvons donc pas attester de la spécificité des mesures relevées précédemment. Il semble que soit la mutation n'est pas fonctionnelle, soit plus vraisemblablement que la protéine recombinante que nous avons produite n'est pas ou peu active.

#### 4) <u>Un nouvel anticorps polyclonal de lapin dirigé contre l'apicoplaste.</u>

La protéine recombinante étant produite en quantité considérable, et comme nous avons montré que la protéine TgSufC est localisée à l'apicoplaste, nous avons décidé alors de l'utiliser pour produire un anticorps polyclonal dirigé contre cette organelle, réactif qui peut s'avérer utile pour nos études futures.

Pour cela nous avons fourni, à la plateforme d'animalerie du CRBM (Centre de Recherche en Biologie cellulaire de Montpellier), des aliquots de protéine purifiée de 100µg chacun. Par la suite, chaque sérum récolté au cours de l'immunisation est testé par immunoblot et immunofluorescence. D'après les immunofluorescences effectuées, nous confirmons que l'anticorps reconnait bien l'apicoplaste (**Figure 40**).



Figure 40: Vérification par IFA de l'action de l'anticorps anti-TqSufC.

Noyau marqué par DAPI, utilisation du Sérum S6 à 1/200, CPN60 marqueur de l'apicoplaste à 1/2000.

L'analyse du sérum anti-TgSufC par immunoblot a révélé par contre des

réactions croisées avec des protéines non spécifiques en plus de la bande correspondant à notre protéine d'intérêt (aux alentours de 34kDa). Malgré ce problème, il faut retenir que nous avons réussis à créer une protéine recombinante nous ayant permis de produire un anticorps dirigé contre l'apicoplaste qui est d'ores et déjà fonctionnel en immunofluorescence.

#### F. Conclusion

Dans ce chapitre, nous avons pu mettre en évidence que la voie SUF à l'apicoplaste de *T. gondii* contient la protéine TgSufC une ATPase putative. Nous avons confirmé que la protéine de toxoplasme est bien une homologue fonctionnelle de la SufC bactérienne. Malheureusement, la création d'une protéine recombinante contenant le site actif putatif de notre protéine d'intérêt ne nous a pas permis de mesurer l'activité enzymatique de TgSufC. L'activité ATPase des homologues de TgSufC est liée à l'action concomitante de plusieurs régions ou domaines protéiques permettant l'hydrolyse de l'ATP (les domaines Walker A et B, ainsi que les différentes boucles qui semblent catalyser et stabiliser la réaction). Il serait intéressant et nécessaire de créer de nouvelles constructions de protéines recombinantes wt et mutantes pour une ou plusieurs régions du site actif putatif, car une protéine active pourrait être utile pour cribler des inhibiteurs spécifiques par exemple.

Nous avons pu apporter un nouvel outil au laboratoire en créant un anticorps polyclonal de lapin, anti apicoplaste. Il s'est avéré que l'anticorps, issus des différents sérums d'immunisation, ne semble pas complétement spécifique de notre protéine et difficile à utiliser pour un marquage en immunoblot puisque des réactions croisées sont présentes. Le signal précis et localisé à l'apicoplaste obtenu par immunofluorescence semble cependant indiquer que notre anticorps peut être utile au laboratoire pour des analyses par immunofluorescences. Afin de pouvoir offrir la possibilité d'utilisation en immunoblot, il est par contre maintenant nécessaire de purifier le sérum.

Concernant la caractérisation phénotypique du mutant TgSufC, il s'est avéré que l'on obtient un phénotype similaire au premier mutant de la voie apicoplastique SUF que nous avons décrit (**Figure 41**). Ainsi, interférer avec l'expression de protéines impliquées dans les premières étapes de la voie SUF telles que TgSufS et TgSufC, impacte directement le cycle lytique des parasites. Nous avons pu voir que ce dysfonctionnement de cycle semble être dût à un défaut de réplication. Concernant les mutants SUF, il y a un défaut de réplication, ainsi qu'une perturbation morphologique des compartiments membranaires comme l'IMC et, plus tardivement, de l'apicoplaste lui-même. Ces phénotypes pourraient être dus à une perturbation de l'homéostasie lipidique, dépendant elle-même au niveau de l'apicoplaste de la protéine [Fe-S] LipA, qui régule la fonction de la PDH, génératrice d'acétyl-CoA (précurseur de la voie FASII).



Figure 41: schéma résumant les phénomènes observés lors de l'absence des protéines TgIscU (mitochondrie), TgSufS ou TgSufC (apicoplaste).

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# Matériels et méthodes

#### Culture de parasites :

Les stades tachyzoites de toutes les souches utilisées (Tati  $\Delta$ ku80 et souches dérivées mutantes et complémentées) ont été maintenues en culture par passages successifs sur une monocouche de fibroblastes humains par passages successifs. Le milieu de culture étant du milieu Dulbecco « Eagle medium » supplémenté avec 10% de sérum de veau fœtal décomplémenté, 2-mM de L-glutamine ainsi qu'un mélange pénicilline / streptomycine à 100µg/mL.

#### Expression hétérologue de TgSufC chez E. coli :

D'après l'alignement de séquence des acides aminés de TgSufC (TGGT1\_225800) avec son homologue chez *E. coli* le fragment d'intérêt fait 900bp. Il a été amplifié par PCR à partir de l'ADNc de *T. gondii* l'aide des amorces ML4009/ML4010 (voir **annexe 5** pour les séquences). Les fragments ont été clonés dans le plasmide pUC19 (de Thermo Fisher Scientific) par restriction des enzymes BamHI/HindII. La souche *E. coli* mutante (SufC JW1672) a été obtenue à partir de la collection Keio et issue de « The Coli Genetic Stock Center » de l'université de Yale. La transformation a été faite avec le plasmide contenant le fragment d'intérêt TgSufC et les bactéries ont été sélectionnées avec de l'ampicilline.

#### Test de croissance bactérienne :

Les bactéries sont laissées à 37°C pendant une nuit dans du milieu LB complet. Le lendemain, les cultures sont ajustées à la même concentration de départ (DO600 nm de 0.6) dans du milieu minimum M9 contenant 0.4% de glucose contenant ou non le chélateur de fer 2,2'-Bipyridil (Sigma Aldrich) à différentes concentrations. La croissance est mesurée en notant la DO600 à 7, 14 et 24h post incubation à 37°C.

#### Génération de lignée étiquetée TgSufC-HA :

Lignée étiquetée créée grâce à la technique Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR). En utilisant le plasmide pLIC-HA-CAT. Grace aux amorces ML4048 / ML3981 utilisées pour faire une PCR avec la KOD DNA polymérase (Novagen) afin de d'amplifier un fragment comprenant le tag triple HA ainsi que la cassette de résistance au chloramphénicol, entouré par des séquences homologues de 30 bp de part et d'autre de la zone de recombinaison dans la région 3' du gène d'intérêt. De plus, nous avons utilisé les amorces ML3952/ML3953 afin de générer un guide ARN permettant de couper les deux brins d'ADN au locus d'intérêt. Ces séquences ont été intégrées au plasmide pU6-Universal<sup>198</sup> (Addgen #52694) exprimant la Cas9. La séquence donneuse et le plasmide exprimant l'ARN guide et la Cas9 ont été co-transfectés dans la lignée parentale TATi ΔKu80 et les parasites transgéniques, issus de la transfection, ont été sélectionnés par traitement au

chloramphénicol puis clonés par dilutions en série. L'intégration de la construction a été vérifiée grâce aux amorces ML3980 / ML3984 / ML3986 / ML1476.

Génération de lignée mutante conditionnelle (cKD TgSufC) et complémentée (cKD TgSufC comp) : La lignée du mutant conditionnel TgSufC (cKD TgSufC) dont l'expression est régulée grâce au système Tet-Off a été générée grâce au plasmide DHFR-TetO7Sag4 et à la stratégie CRISPR. La séquence donneuse a été obtenue par PCR avec la KOD polymérase, permettant d'amplifier la séquence TetO, le promoteur régulable et la cassette résistance avec les amorces ML4107/ML4108 entourée de deux séquences de 30 pb d'homologie avec la région de part et d'autre de la zone ciblée, à l'extrémité 5' du gène TgSufC. Dans un même temps nous avons généré un guide ARN à l'aide des amorces ML4409/ML4410 inséré dans le plasmide pU6-Universal (Addgen #52694) permettant la coupure double brin au locus cible. Une fois la transfection effectuée les parasites transgéniques sont sélectionnées en fonction de leur résistance à la pyriméthamine et clonés par dilutions en série.

La lignée mutante conditionnelle générée est ensuite utilisée pour y insérer une copie ectopique du gène d'intérêt sous contrôle d'un promoteur tubuline au locus UPRT (uracyl phosphoribosyltransférase) afin de créer une lignée complémentée. Le cDNA de TgSufC a été amplifié par transcription reverse (RT-PCR) en utilisant les amorces ML 4815/ ML4816. Cette séquence a alors été clonée en aval de la séquence codant pour le promoteur *tubuline* du plasmide pUPRT-TUB-Ty. Le plasmide alors généré a été linéarisé par action des enzymes de restriction BamHI et Apal. Dans un même temps les couples d'amorces ML3445/ML3446 et ML 2087/ML 2088 ont été insérés dans le plasmide pU6-universal pour générer les ARN guides permettant respectivement l'intégration en 5' et 3' du locus UPRT. Après cotransfection des plasmides dans la lignée mutante conditionnelle, les parasites complémentés (cKD TgSufC-HA comp) ont été sélectionnés grâce à leur résistance à la 5fluorodésoxyuridine.

#### Test de plage de lyse :

Une monocouche de HFF est infectée avec des parasites fraichement égressés et laissés pendant 7 jours en culture en présence ou en absence d'ATc. Les parasites sont par la suite fixés avec une solution à 4% de paraformaldéhyde (PAF) et colorés grâce à une solution à 0.1% de Crystal violet (Sigma AldrichV5265).

#### Immunoblot (IB) :

Les parasites fraichement extracellulaires sont sédimenter par centrifugation et resuspendus dans du tampon de Laemmli. Ils seront par la suite déposés sur gel de polyacrylamide où les protéines seront séparées par électrophorèse en présence de SDS SDS-PAGE) et transférés sur membrane de nitrocellulose grâce au système « Mini-transblot » (BioRad). Par la suite, la membrane est bloquée avec

du TNT 1X (15 mM Tri-HCl; 140 mM NaCl; Tween 0.05%, pH = 8) supplémenter avec 5% p/v de lait écrémé en poudre (Régilait). Les anticorps primaires utilisés pour la détection des protéines d'intérêt sont : un monoclonal de rat anti-HA (clone 3F10, Roche), l'anticorps de lapin anti-acide lipoïque (ab58724 de Abcam), un anticorps de souris anti-sag1<sup>202</sup> ainsi qu'un anticorps de lapin anti-CPN60<sup>105</sup> et un anticorps de souris anti-actine<sup>203</sup>.

#### Immunofluorescence (IFA) :

Des lamelles recouvertes d'une monocouche de HFF sont infectées par des parasites fraichement égréssés afin que ceux-ci puissent s'y multiplier. Elles seront ensuite fixées pendant 20 minutes avec une solution de PBS contenant 4% paraformaldéhyde (PFA), puis les membranes sont perméabilisées avec une solution à 0.3% de Triton X-100 et bloquées avec une solution PBS contenant 0.1% p/v d'albumine bovine (BSA). L'incubation des anticorps primaires et secondaires se fait dans du PBS + BSA. Les images ont pu être acquises grâce à la plateforme de microscopie MRI sur les microscopes Zeiss AXIO imager Z1 ainsi que le Leica Thunder

#### Production de protéines recombinantes :

Amplification sur cDNA de *T. gondii* des fragments correspondant aux domaines fonctionnels (sur la base d'un alignement avec la séquence d'*E. coli*) de nos trois protéines d'intérêts avec la polymérase Q5 (New England Biolabs) et les amorces :

- Pour TgSufC : ML4009/M4010
- Pour TgSufS : ML4011/ML4012
- Pour TgSufE : ML4013/ML4014

Les différentes constructions obtenues par transformation et cultures bactériennes sont ensuite digérées par les enzymes de restriction Ndel/BamHI afin d'être liée au plasmide pET15b digéré lui aussi par ces mêmes enzymes.

Concernant les constructions permettant de muter le site actif de la protéine TgSufC, elles ont été générées à partir du plasmide pET15b-TgSufC par mutagenèse dirigée (kit Qickchange, Qiagen) à l'aide des amorces suivantes :

- Pour le remplacement de la lysine en arginine (K40R) : ML4163/ML4164.
- Pour le changement de lysine en alanine (K40A) : ML4184/ML4185.

Toutes les constructions sont vérifiées par séquençage puis transformées dans la souche BL21 d'*E. coli* permettant l'expression. Ensuite, les cultures bactériennes sont pré-ensemencées sur la nuit dans 10 mL de milieu LB complet. Le lendemain les cultures et ajustées à une densité optique à 600nm de 0,6.

L'induction de la production des protéines d'intérêt se fait alors par ajout de 0.5M d'IPTG dans le milieu de culture pour une incubation à 37°C ou 16°C.

Suite à l'induction pendant 3h à 37°C ou sur une nuit à 16°C, la culture est centrifugée. Les culots sont resuspendus dans du tampon de lyse (10mM Tris HCL pH 8 + 50mM NaH2PO4 + 0.5% triton TX10) puis soniqués par pulse de 1 min à amplitude de 60% fait avec le sonicateur 450-D de chez Branson. Les extraits sont centrifugés pour séparer les fraction solubles et insolubles, et peuvent alors être soit déposés sur gel de polyacrylamide soit, pour la fraction soluble, utilisés pour la purification sur colonne de nickel.

#### Purification de protéine recombinante sur colonne de nickel :

La colonne de chromatographie d'affinité est obtenue par utilisation de résine contenant de l'acide nitrilotriacétique ainsi que du nickel (résine NiNTA, Qiagen). Apres filtration de la fraction soluble contenant la protéine d'intérêt, des lavages sont effectués avec une solution contenant de l'imidazole (50mM NaH2PO4 + 300mM NaCl+ 20 mM Imidazole). Enfin, la protéine d'intérêt est récupérée dans un tampon d'élution (50mM NaH2PO4 + 300mM NaCl +250mM imidazole). Des élutions successives sont effectuées puis déposées sur gel de polyacrylamide afin d'être analysées par coloration au bleu de coomassie. La colonne est ensuite lavée avec un tampon de décapage (« stripping buffer » : 500mM NaCl + 100mM EDTA à pH8.0) puis incubée avec une solution rechargée en nickel (solution à 100mM de Nikel) dont l'excédent est enlevé par lavage à l'eau distillée. Elle peut alors être ré-utilisée ou stockée à l'aide d'une solution à 20% v/v d'éthanol.

#### Traitement des élutions par dialyse :

Le traitement par dialyse visant à éliminer le surplus de sels et d'imidazole, subvient après avoir vérifié la présence et la concentration de la protéine d'intérêt dans les solutions d'élution. La membrane de dialyse (ayant une limite d'exclusion « Cut off » de 8 kDa) est hydratée avec le tampon (100mM Tris pH7.5 + 50mM NaCl) avant d'y insérer les élutions contenant la protéine d'intérêt. La membrane de dialyse est alors laissée une nuit entière sous agitation à 4°C dans du tampon. Le jour suivant, la solution contenant la protéine d'intérêt est récupérée, dosée à l'aide du kit de dosage BiCinchoninic acid (BCA, thermo scientific) puis congelée à -20°C.

#### Test d'activité au vert de malachite<sup>204</sup> :

Les solutions utilisées sont préparées séparément et la solution de vert de malachite peut être stockée à l'abris de la lumière :

 Solution stock de vert de malachite : 0.44g de vert de malachite (Sigma) dans 360mL d'acide sulfurique 3M.

- « Dye reagent » : solution à 7.5% poid/volume d'ammonium molybdate (Sigma) à la quelle est ajoutée 10mL de solution stock de vert de malachite ainsi que 11% v/v de tween 20%.
- « Mix Dye reagent » : composé de 40μL de « Dye reagent » dans un volume final de 180μL.

Une courbe étalon est obtenu à partir d'un gradient de concentration de phosphate inorganique (Pi de chez Enzolife, entre 1 et 80 µM dans 160µL) auquel est ajouté 40µL de « Dye reagent ». Apres incubation de 10 minutes à 37°C l'absorbance est mesurée à une longueur d'onde de 620nm avec le lecteur d'absorbance Sunrise, ainsi que le logiciel Magellan<sup>™</sup> de la marque Tecan.

L'activité de la fraction issue de la dialyse est obtenue par dépôt de 0,05µg à 1,8µg de protéine purifiée dans 100µL de tampon de réaction ajusté en ATP (5mM de MgCl2 + ATP (de 0,05 à 2mM) + 25 mM de tris pH 7.5). Après 30 min d'incubation à 37°C, la réaction est stoppée avec 50mM EDTA. 20µL de la réaction sont alors prélevés et ajoutés à 80µL de « Mix Dye reagent », après 5 min d'interaction l'absorbance à 630 nm est mesurée sur le Tecan Sunrise.

# Création d'un anticorps polyclonal de lapin par immunisation (réalisée par l'animalerie du CRBM de Montpellier) :

La protéine recombinante TgSufC est obtenue par purification sur colonne de Ni-NTA, puis les fractions d'élution sont séparées sur gel de polyacrylamide préparatif pour une étape supplémentaire de purification. La bande correspondant à la protéine d'intérêt est découpée et la protéine est récupérée par électro-élution. La protéine est resuspendus afin d'obtenir 400µL de PBS contenant 100µg de protéine recombinante purifiée. Ce volume est ensuite supplémenté avec 400µL d'adjuvant de Freund. Trois injections sont alors effectuées sur le lapin, les deux premières à une semaine d'intervalle et la troisième est faite trois semaines après. S'en suivent trois prélèvements de 20mL à une semaine d'intervalle chacun. Par la suite un cycle d'une injection suivit de trois prélèvements est répété jusqu'à obtenir un septième prélèvement après lequel nous avons demandé l'arrêt du protocole d'immunisation par saignée totale du lapin, effectuée sous anesthésie au Pentobarbital, et la mise à mort est engendrée par injection au cœur de Doléthal.

Les différents lots de sérums obtenus sont alors testés à diverses concentrations (1/200 et 1/500) en immunoblot et en immunofluorescence. Par la suite, afin d'essayer d'atténuer la présence de réactions croisées, une partie du sérum issus de la saignée totale est purifiée par incubation prolongée sur membrane contenant un dépôt protéique issus de parasites de la lignée mutante cKD TgSufC.

#### Microscopie électronique à transmission :

Les parasites sont cultivés au sein de flasques contenant des fibroblastes humains (HFF) dans du milieu Dulbecco « Eagle medium » contenant 10% de sérum de veau fœtal décomplémenté, 2-mM de Lglutamine ainsi qu'un mélange pénicilline / streptomycine à 100µg/mL et supplémenté ATc ou non.

Après trois jours de culture en flasque les parasites extracellulaires sont alors mis en incubation sur des lamelles de verre contenant une monocouche de HFF. Deux jours post infection des lamelles, celleci seront fixées deux heures à température ambiante à l'aide d'une solution contenant 0,1M de cacodylate et 2,5% de glutaraldéhyde. Elles sont ensuite conservées à 4°C avant inclusion, découpe et observation fait par Laurence BERRY.

#### Analyse lipidomique par GC-MS :

- Extraction lipidique : Prélèvement de tachyzoïtes (~10<sup>8</sup> cellules), des lignées mutantes (cKD TgSufS-HA /cKD TgSufC-HA) et complémentées (cKD TgSufS HA-comp /cKD TgSufC HA-comp) sont cultivés en présence de tétracycline pendant cinq jours. Par la suite les parasites fraichement égressés, sont plongés dans un bain de carboglace /éthanol afin d'arrêter leur métabolisme et les lipides sont extraits dans un mélange de chloroforme/méthanol/eau (2 :1 :0,8, v/v/v contenant 10 nmol d'acide tridécanoïque C13 :0 comme standard interne d'extraction) pour l'analyse des lipides totaux.

- Quantification des lipides : l'extrait est séché dans un concentrateur (sous vide). L'aliquot séché est ensuite dissous dans une solution de chloroforme/méthanol (2 :1, v/v). Les esters méthyliques des acides gras ont alors été analysés par GC-MS et identifiés par spectrométrie de masse et leur temps de rétention par rapport aux standards. Les identifications de lipides ont été effectuées à l'aide du logiciel Mass hunter Quantification (Agilent).

## Discussion

Lors de leur évolution en tant que parasites intracellulaires obligatoires, les espèces présentes dans le phylum des apicomplexes ont adaptés leur métabolisme<sup>90</sup>, et tout particulièrement celui présent à l'apicoplaste (ayant notamment perdu sa capacité photosynthétique). L'importance des pathologies engendrées par les parasites de ce phylum, au niveau vétérinaire (donc agronomique) ainsi qu'en santé humaine, est la source de nombreuses études. Bien que le parasite *T. gondii* soit étudié depuis de nombreuses années, il reste de multiples inconnues dans les processus cellulaires et moléculaires fondamentaux. Par exemple, l'importance des mécanismes hébergés ou gouvernés par l'apicoplaste, ainsi que les ceux permettant le passage vers la forme latente du parasite sont encore très peu compris et pourtant essentiels à la survie des parasites.

L'apicoplaste et la mitochondrie sont des hauts lieux du métabolisme de *T. gondii*. Leur origine endosymbiotique en fait des organelles abritant des voies métaboliques spécifiques, car parfois absente des hôtes du parasite, donc particulièrement intéressantes pour la recherche de potentielles cibles de traitements anti-parasitaires. Le principal objectif de ma thèse était de confirmer la présence de nouvelles voies biochimiques essentielles dans ces organelles, les voies de biosynthèse des centres [Fe-S] et d'évaluer leur importance pour le développement du parasite.

Nous avons pu mettre en lumière que deux voies distinctes de biosynthèses des centres [Fe-S] sont présentes à la mitochondrie et à l'apicoplaste de *T. gondii*, respectivement la voie ISC et SUF. La déplétion de protéines clés impliquées dans ces voies a entrainé deux devenirs cellulaires très différents. Le parasite développe des problèmes de réplication menant à un phénotype de mort retardée lorsque l'on cible la voie apicoplastique (SUF), contrairement à un impact de la voie mitochondriale (ISC) qui semble conduire à la survie des parasites par différenciation en forme latente.

Il apparait donc que malgré un mécanisme de synthèse et d'assemblage des centres [Fe-S] présentant des similarités biochimiques entre les deux voies, hébergées dans deux compartiments d'origine endosymbiotique distincts, elles semblent impliquées dans des processus biologiques très différents. Cela est probablement dû au fait de la diversité des fonctions biologiques des protéines à centre [Fe-S] dépendant respectivement de ces voies.

# Machinerie des protéines à centre fer-soufre, métabolisme mitochondrial et différenciation.

Il est établi que chez les hôtes intermédiaires du parasite, lors d'un stress intense causé par le système immunitaire, les formes tachyzoïtes de *T. gondii* peuvent se différencier en forme enkystée (ou bradyzoïte). Cette forme de développement latent est particulièrement résistante aux traitements et peut entrainer des réactivations ainsi qu'une toxoplasmose aigüe chez les individus immunodéprimés. Un certain nombre de stress spécifiques aboutissant à la différenciation peuvent être reproduits *in vitro* (pH alcalin, choc thermique, privation en nutriments...).

Le passage de la forme hautement infectieuse et multiplicative à la forme latente du parasite s'accompagne de nombreux changements métaboliques et morphologiques, dus à l'expression de répertoires protéiques spécifiques, dont la régulation au niveau transcriptomique est encore mal connue<sup>27</sup>. Parmi ces changements, on retrouve notamment ceux de la vacuole parasitophore, qui se modifie afin de devenir une paroi de kyste comportant de nombreuses glycoprotéines, ainsi que les changements métaboliques tels qu'une production d'énergie, effectuée essentiellement au niveau glycolytique plutôt que par respiration mitochondriale.

Un facteur de transcription contrôlant l'entrée en phase latente a récemment été identifié par l'équipe de S. Lourido<sup>205</sup>. Ainsi, l'expression du gène « Bradyzoite – formation Deficient 1 » (BFD1) s'avère suffisante pour engendrer la différenciation même en absence de stress. BFD1 se lie a de nombreux sites de transcription correspondant à des gènes surexprimés lors de la différenciation ainsi qu'a son propre promoteur. BFD1 est un régulateur majeur des programmes transcriptionnels impliqués dans de la différenciation en formes bradyzoïtes. Mais il reste notamment à déterminer quelles sont les voies de régulation en amont qui permettent de transduire les signaux de stress et déclencher l'expression de BFD1 lui-même.

Il y a peu d'exemples de mutants de *T. gondii* se différenciant spontanément en bradyzoïtes, en particulier dans une souche de type I, qui est peu kystogène. Le mutant IscU, que nous avons généré, constitue donc une souche transgénique intéressante qui pourrait apporter des informations sur les éléments régulateurs de la différenciation.

Il y a plusieurs raisons qui peuvent expliquer la différenciation de ce mutant lors de la déplétion d'IscU. En premier lieu, il est possible que des protéines [Fe-S] dépendantes de la voie ISC soient impliquées dans l'expression de régulateurs de la différenciation. La voie ISC se situe dans la mitochondrie, mais il a été montré chez d'autres eucaryotes de celle-ci dépendent que de nombreuses protéines [Fe-S]

cytoplasmiques ou du noyau (où se trouvent la plupart des facteurs modulateurs de l'expression génique) qui sont générées par la voie CIA. Une autre explication est que lorsque la voie ISC est impactée, cela génère un stress métabolique qui serait un des signaux reconnus pour engendrer la différenciation. Comme on l'a montré, la capacité respiratoire mitochondriale du mutant IscU est fortement diminuée. Or, de façon intéressante l'Atovaquone et d'autres composés ciblant le métabolisme mitochondrial ont été montrés comme étant des déclencheurs de la différenciation in vitro<sup>206</sup>. La conversion en bradyzoïtes pourrait donc être une réponse adaptative générale à une diminution des activités mitochondriales. Il serait intéressant d'analyser plusieurs mutants mitochondriaux générés dans le passé et connus pour être affectés dans leur croissance, pour voir s'ils ne se différencient pas eux aussi en bradyzoïtes. On ne connait en tout cas pas pour l'instant la ou les molécules (potentiellement un ou des métabolites liés au métabolisme énergétique mitochondrial) susceptible(s) d'enclencher la signalisation pour la conversion en bradyzoïtes.

Le mutant TgIscU peut également être utilisé comme outil pour essayer d'identifier de nouveaux gènes gouvernant la différenciation. D'après l'analyse en protéomique quantitative de ce mutant, de multiples protéines semblent impactées (sur ou sous-exprimées) lors de la déplétion en TgIscU. Parmi elles se trouvent plusieurs candidats pouvant éventuellement jouer un rôle dans la régulation traductionnelle ou transcriptionnelle. On trouve par exemple une sous-unité d'un facteur initiateur de la traduction, des protéines homologues de régulateurs de l'assemblage de sous-unités ribosomales, des protéines à motif de liaison à l'ARN, etc....

Parmi ces candidats, ceux étant sur-exprimés dans le mutant, pourraient potentiellement être des activateurs de la différenciation, tandis que ceux qui sont sous-exprimés pourraient être des répresseurs. De façon intéressante, plusieurs des candidats (eIF4G, PABP, Pumillio) sont des composants potentiels des « granules de stress », qui sont des structures séquestrant les complexes ARNm/ribosomes sous forme inactive en réponse au stress<sup>207</sup>. Le contrôle traductionnel est un des mécanismes de réponse au stress le plus précoce et pourrait se trouver en amont de la régulation transcriptionnelle par BFD1. Il faudrait réaliser des études fonctionnelles de ces candidats en générant des mutants conditionnels dans une souche de type II afin de déterminer leur implication dans le processus de différenciation.

Le mutant TgIscU peut donc être un outil d'étude qui pourrait mener à une meilleure compréhension des mécanismes moléculaires permettant d'induire la persistance de *T. gondii*.

### La voie SUF est importante pour l'homéostasie lipidique.

La perturbation de la voie de biosynthèse des centres [Fe-S] de la mitochondrie ne semble pas entrainer de défaut morphologique particulier pour les parasites, y compris au niveau de l'organelle. Par contre, concernant la voie SUF, on a pu voir que lorsque l'expression des protéines de l'apicoplaste TgSufS et TgSufC est impactée, alors les parasites ont des conséquences visibles aux niveaux morphologique et cellulaire. En effet, nous avons démontré qu'une perturbation dans l'expression de ces protéines entraine un défaut de réplication ainsi qu'une perte d'apicoplaste. Pour l'organelle, ce phénomène est malgré tout assez tardif et ne reste que partiel. De façon plus précoce nous avons pu observer des perturbations du processus de division et une altération de la pellicule des parasites. La pellicule est constituée d'un complexe tri-membranaire, comportant la membrane plasmique externe ainsi que l'IMC, lui-même constitué de deux membranes très proches l'une de l'autre. Ces composants membranaires ont un rôle essentiel dans la structure et la motilité des parasites.

Or, l'apicoplaste, qui héberge aussi la voie de biosynthèse FASII, est une organelle cruciale pour le maintien de l'homéostasie lipidique des tachyzoïtes<sup>133,137</sup>. Nous avons montré, avec le défaut de lipoylation de la sous-unité E2 de la PDH dans les mutants apicoplastiques de TgSufS et TgSufC, que la fonction de la protéine [Fe-S] LipA est altérée par les déplétions de ces protéines. La PDH a un rôle important pour générer l'acetyl-CoA, un précurseur essentiel de la voie de synthèse des acides gras dans l'organelle. Il a récemment été montré que les différentes sous-unités de la PDH sont importantes pour la croissance des parasites et la synthèse d'acides gras<sup>200</sup>. La caractérisation phénotypique de plusieurs mutants déficients pour la synthèse d'acides gras dans l'apicoplaste montre des défauts au niveau de la pellicule et de la division cellulaire<sup>208,209</sup>. De plus, l'utilisation du Triclosan<sup>210</sup>, un inhibiteur de la voie FASII de l'apicoplaste, conduit également à des défauts de formation de la pellicule, engendrant des problèmes de division cellulaire. Il nous faut étudier plus en détail les conséquences morphologiques de la perte de TgSufS et TgSufC, mais il semblerait que nous observions un phénotype similaire.

Les analyses lipidomiques des mutants SufS et SufC semblent indiquer une diminution des acides gras à chaine courte (ceux générés dans l'apicoplaste), alors que ceux à chaine longue (ceux fabriqués dans l'ER à partir de précurseurs de l'apicoplaste ou issus de la cellule hôte) ne varient pas. Cela semble donc confirmer que la perturbation de la voie de synthèse des centres [Fe-S] de l'apicoplaste impacte fortement la synthèse de lipides dans l'organelle. En compensation, les parasites pourraient utiliser plus de précurseurs en provenance de la cellule hôte. C'est d'ailleurs ce qui semble ressortir de

l'analyse en protéomique quantitative du mutant SufS, qui montre une augmentation de l'expression de plusieurs enzymes de l'ER potentiellement impliquées dans la prise en charge des lipides de l'hôte. Des expériences de marquages de précurseurs lipidiques de l'hôte et d'analyse lipidomique, effectuées sur les deux mutants SufS et SufC par nos collaborateurs de l'IAB de Grenoble devraient bientôt nous permettre d'en savoir plus à ce sujet.

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# *La voie SUF, au carrefour de plusieurs voies métaboliques importantes dans l'apicoplaste ?*

L'origine de l'apicoplaste et les voies métaboliques importantes qu'il héberge, en font une cible particulièrement intéressante pour la recherche de nouveaux traitements anti-parasitaires. Notre étude concernant la voie SUF nous a permis, en plus d'attester de sa présence chez T. gondii, de mettre en évidence son importance pour l'intégrité de l'apicoplaste, avec un possible impact de la voie FASII de synthèse de lipides. Mais du fait des nombreuses voies indispensables hébergées dans cette organelle, il se peut également que la voie FASII ne soit pas la seule à subir des dysfonctions lorsque la voie SUF est impactée. En effet, il s'avère que l'apicoplaste héberge, entre autres, la voie de biosynthèse des isoprénoïdes non dépendante du mévalonate (MEP/DOXP) qui est essentielle aux tachyzoïtes<sup>143</sup>. Les isoprénoïdes sont des précurseurs essentiels aux membranes des cellules eucaryotes par production de composés servant à la formation de protéines membranaires et ancres GPI<sup>124,140</sup>. Les parasites apicomplexes les produisent d'une façon différente de leurs hôtes mammifères : en utilisant la voie du MEP, qui est une alternative à la voie du mévalonate, et que l'on retrouve également dans les plastes des plantes et dans certaines bactéries<sup>131,132,140</sup>. Or, il s'avère que deux protéines importantes pour cette voie sont des protéines à centres [Fe-S] : IspG et IspH. Par homologie de séquences et prédictions de fonction, on voit que les apicomplexes P. falciparum et T. gondii, ainsi que l'algue C. velia (très proche génétiquement des apicomplexes), comportent des protéines prédites comme similaires (Figure 41).

FONCTIONS	PROTEINES BACTERIENNES ( <i>E.coli</i> )	HOMOLOGUES VEGETAUX ( <i>A.thaliana</i> )	HOMOLOGUES CHROMERIDE ( <i>C.velia</i> )	HOMOLOGUES APICOMPLEXES ( <i>P.falciparum</i> )	HOMOLOGUES APICOMPLEXES (T.gondii)
4-hydroxy-3- methylbut-2-enyl diphosphate reductase	lspH (BAB96598 )	lspH (At4g34350)	Cvel_2579	lspH/LytB (PF3D7_0104400)	TGME49_227420
4-hydroxy-3- methylbut-2-en-1- yl diphosphate synthase	lspG (BAA16402)	ISPG (At5g60600)	Cvel_23671	IspG/GcpE (PF3D7_1022800)	TGME49_262430

Figure 42: Protéines homologues putatives d'IspG et IspH de E. coli chez différents organismes végétaux et apicomplexes.

IspG et IspH sont connues pour être des cibles de stratégies antibactériennes<sup>211,212</sup> visant à perturber les protéines à centres [Fe-S]. Ce métabolisme est crucial pour les apicomplexes : la voie de synthèse des isoprénoïdes est par exemple la seule fonction de l'apicoplaste qui est essentielle pour la survie des stades érythrocytaires de *P. falciparum*<sup>141</sup> par exemple et elle est importante pour les tachyzoïtes de *T. gondii*<sup>143</sup> également. En plus de la dérégulation de l'homéostasie lipidique entraînée par la perturbation de la voie SUF, des effets sur la fonction des protéines homologues putatives d'IspH et G (respectivement : TGME49\_227420 et TGME49\_262430) pourraient également contribuer au phénotype léthal observé. Cela renforcerait d'autant plus l'intérêt d'essayer de développer des inhibiteurs de la voie SUF pour découvrir de nouvelles approches thérapeutiques contre les apicomplexes responsables de la malaria<sup>213,214</sup> et de la toxoplasmose .

## Conclusion

Au cours de ma thèse j'ai donc pu mener à bien l'objectif principal qui était de caractériser de nouvelles voies de biosynthèse au sein d'organelles d'origines endosymbiotiques et d'évaluer leur impact sur le développement du parasite.

Le chemin reste long puisque nous somme uniquement au début de l'étude de ces voies, mais d'après les différences biologiques observées, elles peuvent être de très bons outils pour l'identification de nouveaux candidats thérapeutiques. L'étude de la voie ISC pourrait alors permettre d'identifier les mécanismes liés à l'entrée en phase latente des parasites. Cela rendrait lors possible l'étude de cibles potentielles pour des nouvelles molécules pharmaceutiques permettant, dans l'idéal, le traitement de la toxoplasmose chronique. Quant à l'étude approfondie de la voie SUF, elle pourrait permettre d'identifier de nouvelles thérapeutiques impliquées dans la lutte contre la toxoplasmose aigüe.

# Annexes :

Annexe 1: Tableau répertoriant les protéines impliquées dans la voie de biosynthèse des centres Fe-S à la mitochondrie (ISC), au sein d'espèces représentatives de l'évolution. Protéines en italique = non caractérisées

910								ISC										VOIE
Transport mitochondrial (carriere)	Possible donneur d'electron	Glutaredoxine	Liaison fer	Facteur de transcription regulateur	Assemblage de cluster	Assemblage de cluster	Assemblage de cluster	Assemblage de cluster	Assemblage de cluster	Assemblage de cluster	Assemblage de cluster	Assemblage de cluster	Assemblage de cluster	Assemblage de cluster	Assemblage de cluster	Cysteine désulfurase partenaire	Cysteine désulfurase	FONCTIONS
/	CyaY (BAE77494) <sup>22</sup>	GrxD; ydhD (BAA15420) <sup>18</sup>	lscX ; yfhJ (BAA16414) <sup>17</sup>	IscR; yfhP (BAA16425) <sup>16</sup>	1	/	IscA (BAA16422) <sup>7</sup>	1	I	1	1	NfuA; yhgl (BAE77877)	/		ISCU (BAA16423) <sup>7</sup>	1	ISCS (BAA16424) <sup>1</sup>	PROTÉINES E. coli
Mitoferrine 1 (HGNC:29786) <sup>25</sup>	Frataxin (FXN; FRDA) (HGNC:3951) <sup>23</sup>	GLRX5 (HGNC:20134) <sup>19</sup>	1	1	ISCA2; HBLD1 (HGNC:19857) <sup>14</sup>	1	ISCA1;HBLD2 (HGNC:28660) <sup>14</sup>	1	1	1	1	NFU1;HIRIP5 (HGNC:16287) <sup>12</sup>	1	1	ISCU; NIFUN (HGNC:29882) <sup>8</sup>	ISD11; LYRLM4 (HGNC:21365) <sup>6</sup>	NFS1 (HGNC:15910) <sup>2</sup>	HOMOLOGUES H. sapiens
(At1g07030)	frataxine (FH) (At4g03240) <sup>24</sup>	GRXS15 (At3g15660) <sup>20</sup>	1	/	IsA4; IscA4 (At5g03905)	IsA3; IscA3 (At2g36260)	(At2g16710) <sup>15</sup>	NFU5;NIFU5 (At1g51390) <sup>13</sup>	NFU4; NIF4 (At3g20970) <sup>13</sup>	NFU3 (At4g25910) <sup>13</sup>	NFU2; NiFU2 /CnfU (At5g49940) <sup>13</sup>	NFU1; NiFU1(At4g01940) <sup>13</sup>	Isu3; IscU3 (At4g04080) <sup>11</sup>	Isu2; IscU2 (At3g01020) <sup>11</sup>	Isu1; IscU1 (At4g22220) <sup>9</sup>	Isd11; MAF19; Lyrm4 (At5g61220)	NFS1; NifS1 (At5g65720) <sup>3</sup>	HOMOLOGUES A. thaliana
(cgd2_1030)	1	Glutaredoxine-like 2 (cgd6_3970)	1	1	1	1	1	1	ĺ	1	1	1	1	(cgd6_1050)4	1	(cgd6_310)	NifS-like/IscS (cgd4_3040) <sup>4</sup>	HOMOLOGUES C. parvum
/	(Cvel_31480)	Glutaredoxine 5 (Cvel_22872)	lscX (Cvel_14554)	1	IscA1-like (Cvel_28660) / IscA- like 2 (Cvel_9596)	1	(Cvel_28660)	1	NifU-like (Cvel_5443)/ Cvel_1427	I	1		/	NfuN (Cvel_5443)	NifU-like (Cvel_31875)	(Cvel_33324)	Cysteine désulfurase (Cvel_27718)	HOMOLOGUES C. velia
(PF3D7_0905200)	1	GRXS15/GLP2 (PF3D7_0606900) <sup>21</sup>	lscX / YfhJ (PF3D7_1361600)	1	lscA1 (PF3D7_0207200)	/	IscA2 (PF3D7_0322500) / (PF3D7_0207200)	1		1	1	NifU (PF3D7_0921400)	1	NFU1 (PF3D7_0930900)	lscU1 (PF3D7_1454500)	lsd11 (PF3D7_1311000) <sup>5</sup>	ISCS /NFS1 (PF3D7_0727200) <sup>5</sup>	HOMOLOGUES P. falciparum
1	CyaY (TGME49_262810)	(TGME49_268730)	1	1	HesB-like protéine (TGME49_297925)		lscA (TGME49_213810)			1			1	Protéine famille NifU (TGME49_212930) / (TGME49_221922)	IscU (TGME49_237560) <sup>10</sup>	1	(TGME49_211090)	HOMOLOGUES T. gondii

#### Annexe 1 : Suite. Protéines en italique = non caractérisées

VOIE	FONCTIONS	PROTEINES E. coli	HOMOLOGUES H. sapiens	HOMOLOGUES A. thaliana	HOMOLOGUES C. parvum	HOMOLOGUES C. velia	HOMOLOGUES P. falciparum	HOMOLOGUES T. gondii
	Sulphydryl oxydase FAD dependent	1	GFER; ALR; HERV1 (HGNC:4236) <sup>26</sup>	ERV1 ; ALR (At1g49880) <sup>27</sup>	Proteine famille ERV/ALR (cgd6_2470)	ALR (Cvel_1351)	ERV1 (PF3D7_0110200) <sup>28</sup>	Proteine famille Erv1/Alr (TGME49_210787)
-	Assemblage de cluster/ modification ARNt	YgfZ (BAE76963) <sup>29</sup>	IBA57 (HGNC:27302) <sup>14</sup>	lba57 (At4g12130) <sup>30</sup>	/	1	(PF3D7_1452200)	YgfZ (TGME49_267560)
	Transfert electron/ adrenoxine oxidoreductase	Ygfk (BAE76944) <sup>31</sup>	FDXR ; ADXR (HGNC:3642) <sup>32</sup>	ADXR; MFDR (At4g32360) <sup>33</sup>	mtFNR (cgd8_2710) <sup>34</sup>	(Cvel_14280)	ADRX (PF3D7_1139700)	(TGME49_261030)
	Ferrédoxine/adrenoxine (apport Fe/ transport electron)	Fdx (BAA16415) <sup>7</sup>	FDX1 (HGNC:3638) <sup>35</sup> et FDX2 (HGNC:30546)	ADX1; MDFX2 (At4g21090) <sup>33</sup>	Fd1 ; mtFd -II (cgd6_3000) <sup>34</sup>	(Cvel_14675)	(PF3D7_1214600)	(TGME49_240670)
	Ferredoxine/adrenoxine (apport Fe/ transport électrons)	/	/	ADX2; MDFX1 (At4g05450) <sup>33</sup>	/	(Cvel_17684)	/	(TGME49_236000)
ISC	Co-chaperonne	1	GRPEL1 (HGNC:19696) <sup>36</sup>	MGE1a; MGE2 (At4g26780) <sup>37</sup>	GrpE (cgd5_3510)	GrpE (Cvel_17825)	MGE1/GrpE homologue (PF3D7_1124700)	GrpE (TGME49_265220)
	Co-chaperonne	/	GRPEL2 (HGNC:21060)	MGE1b; MGE1 (At5g55200) <sup>37</sup>	1	/	/	1
	DnaK-like co-chaperonne liant le motif LYR	HscB; yfhE; Hsc20 (BAA16421) <sup>7</sup>	HSCB; DNAJC20 (HGNC:28913) <sup>38</sup>	HscB (At5g06410) <sup>39</sup>	DNAJ (cgd3_2810)	HscB (Cvel_13897)	HscB (PF3D7_0920100)	HscB (TGME49_288685)
-	DnaJ-like chaperonne	HscA (BAA16420) <sup>7</sup> /DnaK (BAB96589) / HscC (BAA35297)/ yegD (BAA15927)	HSPA9; mortaline (HGNC:5244) <sup>40</sup>	AtHscA1; mtHSC70-1 (At4g37910) <sup>41</sup>	Hsp70 (cgd3_3440) <sup>42</sup>	chaperonne DnaK (Cvel_27211)	HscA (PF3D7_1134000)	Heat shock protein (TGME49_251780)
	Complexe I : assemblage	/	NUBPL ;Ind1 (HGNC:20278) <sup>43</sup>	INDL; IND1-like; INDH (At4g19540) <sup>44</sup>	/	Nubp1 (Cvel_19821)/ homologue mrp (Cvel_1712), (Cvel_23131)	(PF3D7_1128500)	Proteine famille MRP (TGME49_318590)
	DnaJ-like chaperonne	1	/	AtHscA2; mtHSC70-2 (At5g09590) <sup>45</sup>	1	1	1	/
	ABC transporteur mitochondrial	CydD (BAA35612) <sup>46</sup> / MsbA (BAA35658)	ABCB6; MTABC3 (HGNC:47) <sup>47</sup> / ABCB7 (HGNC:48) <sup>48</sup>	ABCB23; Atm1 (At4g28630) <sup>49</sup>	/	/	/	1
ISC /CIA	ABC transporteur mitochondrial	/	ABCB8;MABC1 (HGNC:49) <sup>50</sup>	ABCB24; Atm2 (At4g28620) <sup>49</sup>	1	/	/	/
	ABC transporteur mitochondrial	/	ABCB9; KIAA1520 (HGNC:50) <sup>51</sup>	Atm3; Sta1; ABCB25 (At5g58270) <sup>52</sup>	ATM1like; CpABC (cgd1_1350) <sup>53</sup>	ABC transporteur famille B (Cvel_10118)	ATM3/MDR2 (PF3D7_1447900) <sup>54</sup>	(TGME49_269000)

Annexe 2: Tableau répertoriant les protéines impliquées dans la voie de biosynthèse des centres Fe-S cytoplasmique (CIA), au sein d'espèces représentatives de l'évolution. Protéines en italique = non caractérisées

VOIE	FONCTIONS	PROTEINES E. coli	HOMOLOGUES H. sapiens	HOMOLOGUES A. thaliana	HOMOLOGUES C. parvum	HOMOLOGUES C. velia	HOMOLOGUES P. falciparum	HOMOLOGUES T. gondii
	Transport électron	/	CIAPIN1; Anamorsine (HGNC:28050) <sup>55</sup>	Dre2; Ciapin1 (At5g18400) <sup>56</sup>	Anamorsine (cgd6_4130)	Homologue anamorsine (Cvel_5527)	Dre2/MAL8P1 (PF3D7_0824600)	(TGME49_216900)
	Transport électron	1	NDOR1; NR1 (HGNC:29838) <sup>57</sup>	Tah18; Atr3 (At3g02280) <sup>58</sup>	(cgd4_1330)	(Cvel_6121)	(PF3D7_1450300)	(TGME49_249320)
	Adaptateur entre voie CIA et / apoprotéine / ADN réparation /		MMS19 (HGNC:13824) <sup>59</sup>	Met18; Mms19 (At5g48120) <sup>60</sup>	MM519 (cgd4_180)	MMS19 (Cvel_16316)	MMS19-like (PF3D7_0505000)	(TGME49_222230)
	Assemblage/transfert de cluster	/	CIAO1 (HGNC:14280) <sup>61</sup>	Cia1; emb1345 (At2g26060) <sup>62</sup>	1	(Cvel_5245)	CiaO1/CIA1 (PF3D7_1209400)	CIAO1 (TGME49_313280)
CIA	Facilite transfert cluster à IRP1	1	FAM96A/CIAO2A (HGNC:26235) <sup>63</sup>	1	1	1	1	1
	Assemblage de cluster	1	FAM96B; CIAO2B; MIP18 (HGNC:24261) <sup>63</sup>	Cia2; AE7; MEP18; (At1g68310) <sup>62</sup>	(cgd7_5070)	MIP18 (Cvel_1059)	Ae7 /CIA2 (PF3D7_0703100)	Hypothetical (TGME49_306590)
	Assemblage/transfert de cluster	1	NARF (HGNC:29916) / CIAO3; NARFL (HGNC:14179) <sup>64</sup>	Nar1; Gollum (At4g16440) <sup>65</sup>	Narf-like (cgd1_190)	NarfL (Cvel_25862)	Nar1 (PF3D7_0614200)	(TGME49_242580)
	Assemblage de cluster	1	NUBP1 (HGNC:8041) <sup>66</sup>	Nbp35 (At5g50960) <sup>67</sup>	Nubp1 (cgd8_3140)	Nubp1 (Cvel_19821)	Nbp35 (PF3D7_0910800)	Nbp35 (TGME49_280730)
	Assemblage de cluster	CFD1; DRE3 (S000001265)	CFD1; NUBP2 (HGNC:8042) <sup>68</sup>	1	1	1	1	1

Annexe 3: Tableau répertoriant les protéines impliquées dans la voie de biosynthèse des centres Fe-S apicoplastique (SUF), au sein d'espèces représentatives de l'évolution. Protéines en italique = non caractérisées

VOIE	FONCTIONS	PROTÉINES E. coli	HOMOLOGUES H. sapiens	HOMOLOGUES A. thaliana	HOMOLOGUES C. parvum	HOMOLOGUES C. velia	HOMOLOGUES P. falciparum	HOMOLOGUES T. gondii
	Carriere Type A : transport	SufA; ydiC (BAA15453) <sup>69</sup>	/	SufA1; CpIscA (At1g10500) <sup>15</sup>	1	1	SufA (PF3D7_0522700) <sup>70</sup>	HesB-like (TGME49_297925)
SUF	Assemblage de cluster	SufB; ynhE (BAA15454) <sup>69</sup>	1	SufB; NAP1; ABCI8 (At4g04770) <sup>71</sup>	1	Ycf24 (Cvel_4495)	SufB (PF3D7_API04700) <sup>72</sup>	ycf24 (TGME49_300650 )
	Protéine assemblage / ATPase de la cassette de liaison à l'ATP	SufC; ynhD (BAA15455) <sup>69</sup>	1	SufC; NAP7; ABCI6 (At3g10670) <sup>73</sup>	1	Ycf16 (Cvel_14)	SufC (PF3D7_1413500) <sup>72</sup>	(TGME49_225800) <sup>10</sup>
	Protéine assemblage /apport Fe (proposée)	SufD; ynhC (BAA15456) <sup>69</sup>	7	SufD; NAP6; ABCI7 (At1g32500) <sup>74</sup>	1	ABCI7 (Cvel_17786)	SufD (PF3D7_1103400)	SufB/D (TGME49_273445)
	Cysteine désulfurase	SufS ; csdB; ynhB (BAA15457) <sup>1</sup>	1	CpSufS; NFS2; CpNifS1 (At1g08490) <sup>3</sup>	1	(Cvel_2564)	SufS (PF3D7_0716600) <sup>5</sup>	SufS (TGME49_216170) <sup>10</sup>
	Activateur de désulfurase NFS1/NFS2	SufE; ynhA (BAE76500) <sup>75</sup>	1	SufE1/E2; CpSufE1 (At4g26500) <sup>76</sup>	1	SufE-like (Cvel_21762)	SufE (PF3D7_0206100) <sup>5</sup>	SufE (TGME49_277010)
	Activateur de désulfurase NFS2	1	1	SufE2; CpSufE2 (At1g67810) <sup>77</sup>	1	1	1	1
	Quinolate synthase A / activateur de désulfurase NFS2	NadA (BAA35409) <sup>78</sup>	1	SufE3; CpSufE3; QS (At5g50210) <sup>77</sup>	1	1	1	1
	Non Carriere Type A : transport, facteur adressage	T	1	NIFU3; CNFU3; NFU3 (At4g25910) <sup>79</sup>	/	NifU-like 2 (Cvel_22466)	SufU/NifU-like (PF3D7_0921400)	Protěine famille NifU (TGME49_212930)
	Glutaredoxine	GrxD ; ydhD (BAA15420) <sup>18</sup>	1	GRXS14; CXIP1 (At3g54900) <sup>80</sup>	glutaredoxine-like 2 (cgd6_3970)	Glutaredoxine-5 (Cvel_22872)/ Glutaredoxine-3 (Cvel_1427)	GLP1; GRXS14 (PF3D7_0304500) <sup>21</sup> / GLP2; GRXS16 (PF3D7_0606900) <sup>21</sup>	(TGME49_247580)/ (TGME49_268730)
	Glutaredoxine	1	1	GRXS16 ; CXIP2 (At2g38270) <sup>81</sup>	1	Peroxiredoxine 2E2 (Cvel_1315)	1	(TGME49_238070)
	Possible protéine assemblage / transport	Mrp (BAE76591) <sup>82</sup>	MARCKSL1/MRP (HGNC:7142) <sup>83</sup>	HCF101 (At3g24430) <sup>84</sup>	1	Homologue mpr (Cvel_17212) / (Cvel_19821)/ (Cvel_23131)	HCF101 (PF3D7_1128500)	Protéine famille MRP ; HCF101 (TGME49_318590) <sup>85</sup>
	Possible ferredoxine / transfer electron	Fpr (BAE77386) <sup>86</sup>	7	FD1 (At1g10960) <sup>87</sup> ; FD2 (At1g60950); FD3 (At2g27510); FD4 (At5g10000)	1	(Cvel_10809)	Frd/FD (PF3D7_1318100) <sup>88</sup>	FD (TGME49_215070) <sup>88</sup>
	Reductase	FNR; niR (BAA14927) <sup>89</sup>	1	DFRA (At5g42800) <sup>90</sup>	1	(Cvel_4823)	FNR (PF3D7_0623200) <sup>88</sup>	Protěine famille BolA (TGME49_239320) / (TGME49_298990)

ToxoDB ID	CRISPR Fitness score ¤	Predicted location \$	Product Description	Cellular process
TGGT1_209770	-4.09	nucleus	putative helicase	DNA repair and replication
TGGT1_215550	-2.4	-	exonuclease V	DNA repair and replication
TGGT1_216870	-4.33	nucleus	DNA excision repair helicase	DNA repair and replication
TGGT1_258030	-4.45	nucleus (HyperLOPIT)	DNA polymerase	DNA repair and replication
TGGT1_264670	-0.2	nucleus	DNA polymerase	DNA repair and replication
TGGT1 297840	-4.86	nucleus	DNA primase, large subunit	DNA repair and replication
TGGT1 305920	-0.96	nucleus (HyperLOPIT)	DNA glycosylase/endonuclease-like	DNA repair and replication
TGGT1 313470	0.24	nucleus	DNA glycosylase/endonuclease-like	DNA repair and replication
	-4.35	apicoplast (HyperLOPIT)	ferrodoxin (FD)	Electron transfer
TGGT1 236000	0.2	mitochondrion (HyperLOPIT)	ferrodoxin (FD)	Electron transfer
	-2.45	mitochondrion (HyperLOPIT)	ferrodoxin (FD)	Electron transfer
TGGT1_265230	-2.37	mitochondrion	electron transfer flavoprotein-ubiquinone oxidoreductase	Electron transfer
TGGT1 251390	-0.08	mitochondrion	rieske [2fe-2s] domain-containing protein	Mitochondrial respiratory chain
TGGT1_320220	-5.76	mitochondrion (Hyperl OPIT)	nutative ubiquinol cytochrome c oxidoreductase	Mitochondrial respiratory chain
TGGT1_254030	-4.26	mitochondrion (HyperLOPIT)	NFET family zinc finger CDGSH-type domain-containing protein TgAniCox13	Mitochondrial respiratory chain
TGGT1_215280	-2	mitochondrion (HyperLOPIT)	surchinate debudrogenase	Mitochondrial respiratory chain/TCA cycle
TGGT1_267330	-3.5	mitochondrion (HyperLOPIT)	Successful and the second se	
TGGT1_207330	-4.73	mitochondrion (HyperLOPIT)		TCA cycle/iron sensor
TCCT1_211000	2 54	mitochondrion (HyperLOPIT)		Fo S objector biographical
TCCT1_211090	-3.34	mitochondrion (HyperLOPIT)	Isco desupriorase	Fe-S cluster biosynthesis
TGGT1_212930	-1.03	milochondrion (HyperLOPT)	NiTU-like protein	Fe-S cluster biosynthesis
TGGT1_213810	-4.52	mitochondrion		Fe-S cluster biosynthesis
IGGI1_216170	-3.95	apicoplast (HyperLOPIT)	SutS subfamily cysteine desulturase	Fe-S cluster biosynthesis
TGGT1_216900	-2.88	mitochondrion (HyperLOPIT)	Anamorsin/DRE2-like	Fe-S cluster biosynthesis
TGGT1_221922	-0.76	apicoplast/ER (HyperLOPIT)	NifU family domain-containing protein	Fe-S cluster biosynthesis
TGGT1_237560	-5.99	mitochondrion (HyperLOPIT)	IscU	Fe-S cluster biosynthesis
TGGT1_239320	0.1	apicoplast (HyperLOPIT)	SufE-like, BolA family protein	Fe-S cluster biosynthesis
TGGT1_242580	-4.36	mitochondrion (HyperLOPIT)	Nar1-like Fe-hydrogenase	Fe-S cluster biosynthesis
TGGT1_273445	-5.29	apicoplast (HyperLOPIT)	SufD	Fe-S cluster biosynthesis
TGGT1_280730	-4.81	mitochondrion (HyperLOPIT)	Mrp/NBP35 subfamily of P loop NTPases	Fe-S cluster biosynthesis
TGGT1_297925	-4.01	apicoplast	SufA	Fe-S cluster biosynthesis
TGGT1_300650	N/A (apicoplast-encoded)	apicoplast	SufB	Fe-S cluster biosynthesis
TGGT1_318590	-3.24	cytoplasm (HyperLOPIT)	Mrp/NBP35 subfamily of P loop NTPases, HCF101-like	Fe-S cluster biosynthesis
TGGT1_230070	2.11	cytoplasm	BolA2 family protein	GRX-interacting/Fe-S cluster biosynthesis
TGGT1 227150	1.39	apicoplast (HyperLOPIT)	putative glutaredoxin (GRX)	Redox reactions/Fe-S cluster biosynthesis
TGGT1 238070	-0.65	cytoplasm (HyperLOPIT)	putative glutaredoxin (GRX)	Redox reactions/Fe-S cluster biosynthesis
	-0.07	rhoptry (HyperLOPIT)	butative glutaredoxin (GRX)	Redox reactions/Fe-S cluster biosynthesis
TGGT1 268730	-2.13	mitochondrion (HyperLOPIT)	butative glutaredoxin (GRX)	Redox reactions/Fe-S cluster biosynthesis
	1	cvtoplasm (HyperLOPIT)	butative glutaredoxin (GRX)	Redox reactions/Fe-S cluster biosynthesis
TGGT1_288640	2 29	mitochondrion	radical S-adenosyl-L-methionine (SAM)-like_conconcribyringen debydrogenase_CPDH	Heme biosynthesis
TGGT1_227420	-6.01	apicoplast (HyperLOPIT)	A-hydroxy-3-methylbit-2-envl dinboshate reductase IshH/lytB	Isoprenoid biosynthesis MEP pathway
TGGT1_262430	-4.41	anicoplast (HyperLOPIT)	A hydroxy-3-methylatiz 2 en 1-yl diplochet cadada jan 1917 275	Isoprenoid biosynthesis, MEP pathway
TGGT1_202400	-0.97	apicoplast (HyperLOTT)	linois cuid synthesia IIBA	Lippic acid synthesis
TCCT1 212790	2.02	mitechandrian	npole actu synthase Lin A	Molyhdenterin overtheoio
TCGT1_213780	1 15	mitochondrion (Hyport OPIT)	Tautical Statehosystemethionine (SAM) rike, Moryodopterin Coractor synchesis protein 1, MOCS1	Ovidativo stross rosponso
TGGT1_207020	-1.15	mitochondhon (HyperLOPIT)	pyriane nacieotide assume oxidoreductase doman-containing protein	
TGGT1_249630	0.74	mitochondhon (HyperLOPIT)	glutatione S-transferase domain-containing protein	
TGGT1_304660	0.74	milochondrion (HyperLOPIT)	glutatnione S-transferase domain containing protein	Oxidative stress response
1GG11_255910	1.64	mitochondrion (HyperLOPIT)	NEE I Tamily, zinc Tinger CDGSH-type domain-containing protein	Regulation of Iron and reactive oxygen metabolism
TGGT1_260870	0.92	mitochondrion (HyperLOPIT)	NEL I Tamily, zinc Tinger CDGSH-type domain-containing protein	Regulation of Iron and reactive oxygen metabolism
IGG11_204540	-0.22	-	DUF36/ domain-containing protein	rRNA biogenesis?
TGGT1_209790	-1.82	mitochondrion (HyperLOPIT)	radical S-adenosyl-L-methionine (SAM)-like	rRNA methytransferase
TGGT1_252465	-4.12	mitochondrion	radical S-adenosyl-L-methionine (SAM)-like	rRNA methytransferase
TGGT1_238190	-4.42	nucleus (HyperLOPIT)	DNA-directed RNA polymerase	Transcription
TGGT1_249560	-4.38	-	DNA-directed RNA polymerase	Transcription
TGGT1_261540	-3.54	nucleus (HyperLOPIT)	DNA-directed RNA polymerase	Transcription
TGGT1_267390	-5.2	nucleus (HyperLOPIT)	DNA-directed RNA polymerase	Transcription
TGGT1_313120	-4.48	-	DNA-directed RNA polymerase	Transcription
TGGT1_216790	-4.11	nucleus (HyperLOPIT)	putative ATP-binding cassette sub-family E member 1	Translation
TGGT1_261060	-1.94	-	diphthamide biosynthesis protein 2-related	Translation
TGGT1_272270	0.41	-	radical S-adenosyl-L-methionine (SAM)-like, demethylwyosine synthase	tRNA modification
TGGT1_273140	-0.23	apicoplast	radical S-adenosyl-L-methionine (SAM)-like methylthiotransferase, MiaB/RimO family protein	tRNA modification
TGGT1 305480	-3.28	mitochondrion (HyperLOPIT)	elongator complex protein ELP3	tRNA modification
TGGT1 314000	1.1	nucleus (HyperLOPIT)	putative peptide methionine sulfoxide reductase msrB	tRNA modification
TGGT1 315958	0.66	-	radical S-adenosyl-L-methionine (SAM)-like, demethylwyosine synthase	tRNA modification
TGGT1_213870	-4 83	cytoplasm (HyperLOPIT)	IIBA/TS-N domain-containing protein	Libiquitin associated

Amorces	Séquences
ML801	GAAGACATCCACCAAACGG
ML1432	GAAGAACGACGCTGCAAAC
ML1433	TTGCCATGTCAAGTTCCTACC
ML1476	CAGCGTAGTCCGGGACGTCGTAC
ML 2087	GCTCCCACGTCCCTCACCAT
ML 2088	ATGGTGAGGGACGTGGGAGC
ML3190	TCCCGTTACAGGTGTACGGG
ML3445	CAGGGCTTCTAAAATGGCGC
ML3446	GCGCCATTTTAGAAGCCCTG
ML3952	aagtGTTGAGGTACGATGTGAACAT
ML3953	aaaaATGTTCACATCGTACCTCAAC
ML3980	GCGGCAGACGCAATCTAGACCGCCTGCTCTACCCGTACGACGTCC
ML3981	GGTTTGGCATGAAATTACTGTTACACCGCTCTAGAACTAGTGGATCCCC
ML3984	CGATCTGAGTGCACAGCGAGCC
ML3986	CGATTCTTCGGTAGCAATCCAAGAC
ML4009	AGCCATATGCCGCTCCTCGAGATCAAAG
ML4010	GCCGGATCCTTAGAGCAGGCGGTCTAG
ML4011	AGCCATATGAAAGAACAGGACGAAATG
ML4012	GCCGGATCCCTAGCTGCTTTGTA
ML4013	AGCCATATGGGCGACAAGGAGATCCTC
ML4014	GCCGGATCCTCAGACTTTGCCCTTGTCC
ML4048	GCGGCAGACGCAATCTAGACCGCCTGCTCtacccgtacgacgtcccggac
ML4107	TCTGTCTTCCGCGAACCTGAGTTCCGCTTGAAGCTTCGCCAGGCTGTA
ML4108	CTCAACAAGGAACACTGGTAGCGACGCCATAGATCTGGTTGAAGACAGAC
ML4163	GGAAAGGGTAGATCTTCCCGATCCGTT
ML4164	AACGGATCGGGAAGATCTACCCTTTCC
ML4184	AACGGATCGGGAGCATCTACCCTTTCC
ML4185	GGAAAGGGTAGATGCTCCCGATCCGTT
ML4409	aagtGTTCCGCTTGATGAGAAGGCG
ML4410	aaaaCGCCTTCTCATCAAGCGGAAC
ML 4815	TTTAGATCTATGGCGTCGCTACCAGTG
ML 4816	TTTCCTAGGGAGCAGGCGGTCTAGATTG

Annexe 5 : Séquences génomique des amorces utilisées pour le projet TgSufC.

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