CyMIRA: The Cytonuclear Molecular Interactions Reference for *Arabidopsis*

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ABSTRACT

The function and evolution of eukaryotic cells depends upon direct molecular interactions between gene products encoded in nuclear and cytoplasmic genomes. Understanding how these cytonuclear interactions drive molecular evolution and generate genetic incompatibilities between isolated populations and species is of central importance to eukaryotic biology. Plants are an outstanding system to investigate such effects because of their two different genomic compartments present in the cytoplasm (mitochondria and plastids) and the extensive resources detailing subcellular targeting of nuclear-encoded proteins. However, the field lacks a consistent classification scheme for mitochondrial- and plastid-targeted proteins based on their molecular interactions with cytoplasmic genomes and gene products, which hinders efforts to standardize and compare results across studies. Here, we take advantage of detailed knowledge about the model angiosperm *Arabidopsis thaliana* to provide a curated database of plant cytonuclear interactions at the molecular level. CyMIRA (Cytonuclear Molecular Interactions Reference for *Arabidopsis*) is available at http://cymira.colostate.edu/ and https://github.com/dbsloan/cymira and will serve as a resource to aid researchers in partitioning evolutionary genomic data into functional gene classes based on organelle targeting and direct molecular interaction with cytoplasmic genomes and gene products. It includes 11 categories (and 27 subcategories) of different cytonuclear complexes and types of molecular interactions, and it reports residue-level information for cytonuclear contact sites. We hope that this framework will make it easier to standardize, interpret and compare studies testing the functional and evolutionary consequences of cytonuclear interactions.

Keywords: chloroplast, cytonuclear coevolution, mitochondria, OXPHOS, photosynthesis

INTRODUCTION

The endosymbiotic history of eukaryotes has resulted in cells that are operated under divided genetic control between nuclear and cytoplasmic (i.e., mitochondrial and plastid) genomes. Core eukaryotic functions depend on integration and coevolution between these genomic compartments. The level of integration extends down to direct molecular interactions within multisubunit enzyme complexes (Rand, et al. 2004). For example, the major enzymes in mitochondria and plastids such as oxidative phosphorylation (OXPHOS) complexes, photosynthetic machinery, and ribosomes are 'chimeric' in the sense that they are composed of gene products from both nuclear and cytoplasmic genomes. This organization reflects an evolutionary history in which many of the genes ancestrally present in cytoplasmic genomes have been replaced by a combination of gene transfer to the nucleus and substitution by existing nuclear genes (Sloan, et al. 2018). There are also extensive interactions between cytoplasmic RNAs and nuclear-encoded proteins that are responsible for post-transcriptional processes, such as transcript end-processing, intron splicing, RNA editing, base modifications, and tRNA aminoacylation (Germain, et al. 2013; Salinas-Giegé, et al. 2015). Furthermore, many nuclear-encoded proteins must directly interact with the cytoplasmic genomes themselves to mediate processes of DNA replication, repair, recombination, and transcription (Zhang, et al. 2016; Gualberto and Newton 2017).

The intimacy of these interactions has made them an attractive arena for studying molecular coevolution, especially because they can elucidate the consequences of genes evolving in very different genomic contexts (e.g., differences in mutation rates, replication and expression mechanisms, frequency of recombination, effective population sizes, and modes of inheritance). Not surprisingly, disruption of cytonuclear interactions can have significant functional consequences, and genetic incompatibilities between nuclear and cytoplasmic genomes contribute to reproductive isolation in many systems (Burton, et al. 2013; Hill 2015; Sloan, et al. 2017). It is possible that cytonuclear incompatibilities evolve at a faster pace than nuclear-nuclear incompatibilities because of the differences in genome evolution and the conflicting genealogical histories that can often distinguish these compartments (Burton and Barreto 2012; Toews and Brelsford 2012).

To test such hypotheses, it is often useful to compare nuclear-encoded proteins that are involved in direct cytonuclear molecular interactions against relevant 'control' proteins. For example, classic studies in animals have taken advantage of OXPHOS complex II (succinate dehydrogenase), which is entirely nuclear-encoded, in order to make comparisons with the other OXPHOS complexes, which are all chimeric (Ellison and Burton 2006). In the current genomic era, it has become increasingly popular for evolutionary studies to partition nuclear gene content into categories based on whether they are targeted to mitochondria/plastids and whether they are involved in direct molecular interactions with cytoplasmic genomes and gene products within these organelles (Barreto and Burton 2013; Rogell, et al. 2014; Pett and Lavrov 2015; Sloan, et al. 2015; Zhang, et al. 2015; Adrion, et al. 2016; Rockenbach, et al. 2016; Weng, et al. 2016; Zhang, et al. 2016; Eslamieh, et al. 2017; Havird, et al. 2017; Sharbrough, et al. 2017; Barreto, et al. 2018; Forsythe, et al. 2018; Morales, et al. 2018; Ferreira, et al. 2019; Li, et al. 2019; Yan, et al. 2019; Zaidi and Makova 2019). Such approaches are an effective means to investigate the evolutionary effect of organelle targeting and molecular interactions. Because plants contain two endosymbiotically derived organelles, they are an especially appealing system in which to study such questions. However, comparing across studies can be challenging because of the variable

ways in which authors classify and partition gene sets. Although there are many excellent databases with gene-specific information on subcellular targeting in plants (Table 1), none of these provide comprehensive information about direct cytonuclear interactions at the level of protein subunits and amino-acid residues. To address this limitation, we have taken advantage of the extensive work on cytonuclear biology in the model angiosperm *Arabidopsis thaliana* to create the Cytonuclear Molecular Interactions Reference for *Arabidopsis* (CyMIRA).

MATERIALS AND METHODS

Curation of mitochondrial and plastid targeting databases.
To identify mitochondrial- and plastid-targeted genes, we integrated predictions from nine existing databases (Table 1). Based on these datasets, we classified all nuclear-encoded proteins in the *A. thaliana* Araport11 genome annotation into five targeting categories: mitochondrial, plastid, dual (both mitochondrial and plastid), other, or unknown. Because of the cytonuclear focus of this project, in cases where organelle-targeted proteins were known to have additional subcellular localizations, we still classified them based on their mitochondrial/plastid targeting status alone. To classify a protein as having an organellar localization, we required it to be identified as such in at least two different databases. Because it is well documented that many plant proteins play a dual functional role in both the mitochondria and plastids (Carrie and Small 2013), we assigned genes to the dual-targeted category as long as there were at least two databases supporting targeting to the mitochondria and at least two supporting targeting to the plastids. It was possible (although not required) for these to be the same two databases because the selected databases explicitly classify some genes as dual targeted. Some of these automated database classifications were subsequently refined based on manual curation of direct molecular interactions as described below.

Curation of direct cytonuclear molecular interactions
We conducted a literature-based curation to generate a resource that could distinguish nuclear proteins that are simply targeted to mitochondria and plastids from those that are involved in direct and intimate interactions with cytoplasmic genomes or their gene products. We assigned genes to 11 types of cytonuclear enzyme complexes and molecular interactions, which are further divided into 27 subcategories (Table 2).

Because of the manual nature of this curation, our classifications often required judgment calls and special considerations. With respect to major multi-subunit enzymes, we aimed to restrict our classification to the core complex, excluding proteins such as assembly factors involved in more transient interactions (e.g., Lu 2016; Ligas, et al. 2019).

One of the largest classes of genes involved in plant cytonuclear interactions is the RNA-binding pentatricopeptide repeat (PPR) family (Schmitz-Linneweber and Small 2008). These proteins are overwhelmingly targeted to the mitochondria and plastids where they play diverse roles in RNA processing and maturation. We classified six specialized PPRs as components of the mitochondrial ribosome (Waltz, et al. 2019) or as functioning in tRNA end processing (Gobert, et al. 2010). The remaining PPRs were assigned to their own category. Even though many PPRs still lack detailed functional characterization, we considered these examples of direct cytonuclear interactions because of their near universal role in binding cytoplasmic transcripts. A total of 109 PPRs (24%) were not identified as mitochondrial or plastid targeted based on our

automated database curation. In these cases, we reassigned their targeting classification using The Arabidopsis Information Resource (TAIR) Gene Ontology (GO) cellular component designations (Berardini, et al. 2015). As a result, all PPRs were assigned as mitochondrial and/or plastid targeted, with the exception of only nine genes (AT1G06150, AT1G77150, AT2G20720, AT3G13150, AT3G47530, AT3G58590, AT5G09320, AT5G15300, AT5G44230), which we excluded from the direct-interaction dataset. A large portion of PPR genes function as specificity factors in C-to-U RNA editing of organellar transcripts. Therefore, RNA editing interactions are effectively subsumed within the PPR category. Although other types of nuclear proteins have been found to function in RNA editing (Sun, et al. 2016), we are not aware of any evidence that these directly bind to organellar transcripts, so they were not classified as directly interacting.

Mitochondrial transcription termination factors (mTERFs) are another sizeable family of organelle-targeted nucleic-acid binding proteins (Shevtsov, et al. 2018). Similar to how we handled PPRs, we defined mTERFs as their own subcategory within the transcription and transcript maturation category, even though many individual mTERF genes await functional characterization.

Although our manual curation of direct cytonuclear interactions overwhelmingly agreed with general subcellular targeting predictions from our database summary, there were 189 genes (21%, including 100 PPRs; see above) for which the automated targeting predictions did not include the organelle(s) found in our manual analysis. In such cases, we updated the original automated targeting call by adding the location of direct cytonuclear interactions (but we did not remove other predicted localizations from the automated call set).

As a companion to this curated interaction dataset, we also made use of the TAIR Interactome v 2.0 (Geisler-Lee, et al. 2007), which identifies proteins with direct physical interactions. We used all pairwise interactions to create a list of partners for each Araport11 protein (File S1). For organelle-targeted proteins, lists were further refined to include interacting partners that are targeted to the same subcellular compartment.

Identification of direct cytonuclear contact sites within multisubunit enzyme complexes
In some cases, nuclear-encoded proteins may form part of a cytonuclear enzyme complex but still not physically contact a cytoplasmic gene product within the complex. Therefore, to identify direct cytonuclear interactions at the level of subunits and amino-acid residues, we mapped *A. thaliana* protein sequences to reference structures of 13 multisubunit enzyme complexes that are involved in OXPHOS, photosynthesis, protein translation, and fatty acid biosynthesis. Reference structures for these complexes were searched in the Protein Data Bank (PDB) and were chosen based on their completeness and relatedness to *A. thaliana* (File S1). We identified cytonuclear contact residues in these structures using the "find clashes/contacts" tool in Chimera version 1.12 (Pettersen, et al. 2004) with default contact settings except that VDW overlap was changed to ≥ -1 to increase the sensitivity of detecting contacts. We determined homologous genes and residues in *A. thaliana* by querying the structural reference sequences with TAIR BLAST 2.2.8, and we aligned the resulting hits with MUSCLE as implemented in MEGA 7 (Kumar, et al. 2016) to identify the corresponding contact residues in *A. thaliana* genes.

RESULTS AND DISCUSSION

CyMIRA is a detailed curation of *A. thaliana* cytonuclear interactions at the molecular level, which is available as supplementary material with this paper (File S1). Future updates will be disseminated via GitHub (https://github.com/dbsloan/cymira), and we have also generated a queryable web interface to extract specific subsets of the data: http://cymira.colostate.edu/.

Our initial automated predictions of organelle targeting based on nine existing databases (Table 1) identified a total of 4,130 nuclear-encoded protein-coding genes (1,256 mitochondrial-localized, 2,468 plastid-localized, and 406 dual-localized). The sampled databases differed greatly in their number of organelle-targeting predictions, and very few genes shared the same prediction across all nine databases (Figure 1). Because we limited our classification to predictions shared by at least two databases, there were thousands of genes that were excluded because they had a mitochondrial or plastid targeting prediction in only a single database (Figure 1). As such, taking the full union of predictions across all nine databases would have massively exceeded typical estimates of mitochondrial and plastid proteome content.

Subsequent manual curation of proteins with direct cytonuclear interactions led to the inclusion of 138 new genes and changed the prediction for six genes that were initially identified as targeting just one organelle to dual targeting. As a result, our final organelle targeting count was 4,268 with 1,337 mitochondrial, 2,495 plastid, and 436 dual. Of these, 910 were classified as being involved in direct cytonuclear molecular interactions, meaning that they are components of chimeric cytonuclear enzyme complexes or directly interact with cytoplasmic DNA and/or RNA transcripts (Table 2). The majority of genes involved in these direct cytonuclear interactions were characterized as exclusively mitochondrial (535) or plastid (293), but there are also 82 dual targeted genes in this group, many of which are involved in DNA recombination/replication/repair, tRNA aminoacylation, and post-transcriptional RNA modifications (File S1).

Many studies have begun taking advantage of protein structural data to specifically investigate molecular evolution at the physical interface between contacting cytoplasmic and nuclear gene products (Osada and Akashi 2012; Havird, et al. 2015; Zhang, et al. 2015; Havird and McConie 2019; Yan, et al. 2019). We therefore used structural data from 13 protein complexes (Figure 2) to identify which nuclear subunits actually contact cytoplasmically encoded subunits within these complexes and their specific interacting amino acid positions (File S1). However, the efficacy of this structural mapping approach varied greatly depending on the completeness and phylogenetic relatedness of the reference structures. For many photosynthetic complexes, reference structures are available from angiosperms or even *A. thaliana* itself, but other complexes required use of structures from anciently divergent species, including bacteria and mammals (File S1), making inference of residue homology tenuous. Furthermore, even when structures from close relatives were available, they were sometimes known to be missing certain subunits (van Bezouwen, et al. 2017; Laughlin, et al. 2019). Therefore, we did not analyze many subunits within these complexes because of their absence from reference structures or low level of sequence similarity, designating them simply as not available ("NA"). Some additional subunits were classified only as "likely" or "not likely" to be involved in direct cytonuclear interactions because of low confidence in the reference mapping. Despite these limitations, structural data suggest that most nuclear-encoded proteins within these chimeric complexes do physically contact cytoplasmic gene products (91% of those for which assignments were made).

Our goal in generating CyMIRA is to provide a standardized partitioning of plant nuclear gene content based on cytonuclear interactions at a molecular level to improve consistency

across evolutionary genomic studies. One obvious need that will arise is to extend this *A. thaliana* annotation to genomic datasets from non-model plant species that lack the same level of functional data. Because of the extensive history of gene and whole-genome duplication and the associated process of neofunctionalization in plants (Panchy, et al. 2016), we recommend against relying solely on homology searches when porting the CyMIRA annotations to other species. Instead, we suggest combining such information with tools that perform *in silico* predictions of organelle targeting to increase confidence in assignments (Bannai, et al. 2002; Small, et al. 2004; Emanuelsson, et al. 2007; Sperschneider, et al. 2017).

A further complication in expanding to evolutionary studies across species is that the landscape of cytonuclear integration and interactions is rapidly shifting in plants. Unlike many eukaryotes in which the gene content in cytoplasmic genomes has reached a period of long-term stasis (Johnston and Williams 2016; Janouškovec, et al. 2017), flowering plants remain highly active in the process of endosymbiotic gene transfer to the nucleus (Timmis, et al. 2004). For example, our CyMIRA annotations do not include OXPHOS complex II because this is entirely nuclear-encoded in *A. thaliana*. In contrast, many other angiosperms have retained functional complex II genes (*sdh3* and/or *sdh4*) in their mitochondrial genomes. Ribosomal subunits are also subject to ongoing functional transfers to the nucleus, resulting in substantial heterogeneity in cytoplasmic gene content across angiosperms (Adams, et al. 2002). Therefore, species-specific additions and deletions to this dataset, even at the whole complex level, should be considered based on the retained cytoplasmic gene content in each lineage. Although this continued need for refinement across phylogenetic scales undoubtedly poses a challenge for future studies, the dynamic nature of cytoplasmic genomes in plants is also one of the strongest motivations for studying cytonuclear interactions in these systems.

In summary, the proliferation of plant genomic resources makes this an exciting time to take studies of cytonuclear biology to a genome-wide level, and methodological consistency will be key to the efficacy of such efforts. We hope that CyMIRA will serve as useful community resource in this respect.

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Table 1. Set of nine databases with information on subcellular localization of proteins in plants that were used for automated curations of targeting predictions. Counts reflect number of genes in each targeting category.

	Targeting Predictions			
Database	**Mito**	**Plastid**	**Dual**	**Reference**
SUBA predicted	2370	2644	97	(Hooper, et al. 2017)
eSLDB	848	4427	69	(Pierleoni, et al. 2007)
PA-GOSUB	985	730	14	(Lu, et al. 2005)
SUBA experimental	1217	2128	785	(Hooper, et al. 2017)
SWISS PROT	311	657	20	(Boutet, et al. 2007)
TAIR	397	1598	266	(Reiser, et al. 2017)
LocDB	446	1527	234	(Rastogi and Rost 2011)
PPDB	327	1570	73	(Sun, et al. 2009)
Organelle DB	512	276	11	(Wiwatwattana, et al. 2007)

Table 2. List of functional categories used in manual curation of direct cytonuclear interactions. Counts reflect number of genes in each targeting category. Key references are listed by category. More extensive literature references are provided in Table S1.

Category	Subcategory	Mito	Plastid	Dual	Key Reference(s)
ACCase		**0**	**4**	**0**	(Sasaki and Nagano 2004)
Chlororibosome		**0**	**42**	**0**	(Bonen and Calixte 2006; Sloan, et al. 2014)
	Large subunit	0	31	0	(Bieri, et al. 2017)
	Small subunit	0	11	0	(Tiller, et al. 2012)
Clp protease		**0**	**15**	**0**	(Nishimura and van Wijk 2015)
DNA-RRR		**11**	**8**	**17**	(Zhang, et al. 2016; Gualberto and Newton 2017)
TAT complex		**1**	**0**	**0**	(Carrie, et al. 2016)
Mitoribosome		**88**	**0**	**0**	(Waltz, et al. 2019)
	Large subunit	41	0	0	
	Small subunit	47	0	0	
OXPHOS		**91**	**0**	**0**	(Senkler, et al. 2017)
	Complex I	48	0	0	
	Complex III	14	0	0	
	Complex IV	14	0	0	
	Complex V	15	0	0	
Photosynthesis		**0**	**67**	**0**	
	ATP synthase	0	3	0	(Friso, et al. 2004)
	Cytochrome b6f	0	2	0	(Friso, et al. 2004)
	NDH	0	18	0	(Shikanai 2016)
	PSI	0	18	0	(Jensen, et al. 2007)
	PSII	0	22	0	(van Bezouwen, et al. 2017)
	Rubisco	0	4	0	(Izumi, et al. 2012)
PPR		**308**	**110**	**36**	(Cheng, et al. 2016)
Transcription and transcript maturation		**33**	**46**	**5**	
	Intron splicing	7	7	1	(de Longevialle, et al. 2010)
	mTERF	17	11	0	(Shevtsov, et al. 2018)
	RNA polymerase	1	1	1	(Kühn, et al. 2007)
	rRNA base modification	1	2	0	(Yu, et al. 2008)
	Sigma factor	0	6	0	(Zhang, et al. 2015)
	Transcript end processing	5	5	3	(Perrin, et al. 2004; Stoll and Binder 2016)
	tRNA base modification	2	14	0	(Chen, et al. 2010)
tRNA aminoacylation		**3**	**1**	**24**	(Duchêne, et al. 2005)
Total		**535**	**293**	**82**	

Table S1: Full list of references used for manual curation of cytonuclear complexes

Category	References
ACCase	Konishi and Sasaki 1994; Sasaki and Nagano 2014; Rockenbach et al. 2016; Salie and Thelen 2016; Sudianto and Chaw 2019
Chlororibosome	Bonen and Calixte 2005; Tiller et al. 2012; Sloan et al. 2014; Bieri et al. 2017; Boerema et al. 2018
Clp protease	Nishimura et al. 2015; Nishimura and Wijk 2015; Rockenbach et al. 2016; Williams et al. 2019
DNA-RRR	Zaegel et al. 2006; Lamesch et al. 2012; Cupp and Nielsen 2014; Zhang et al. 2015; Gualberto and Newton 2017; Córdoba et al. 2019
TAT complex	Lamesch et al. 2012; Carrie et al. 2016
Mitoribosome	Bonen and Calixte 2005; Waltz et al. 2019
OXPHOS	Millar et al. 2004; Lu et al. 2005; Meyer et al. 2008; Klodmann et al. 2010; Klodmann et al. 2011; Lamesch et al. 2012; Senkler et al. 2017; Huang et al. 2019; Ligas et al. 2019
Photosynthesis	Kurisu et al. 2003; Friso et al. 2004; Nelson et al. 2004; Jensen et al. 2007; Izumi et al. 2012; Shikanai 2016; Bezouwen et al. 2017; Laughlin et al. 2019
PPR	Lurin et al. 2004; Toole et al. 2008; Fujii et al. 2010; Cheng et al. 2016
Transcription and transcript maturation	Hess and Borner 1999; Walter et al. 2002; Gu et al. 2003; Perrin et al. 2004; Kuhn et al. 2007; Schmidt von Braun et al. 2007; Yu et al. 2008; Canino et al. 2009; Delannoy et al. 2009; Chen et al. 2010; Falcon de Longevialle et al. 2010; Gobert et al. 2010; Placido et al. 2010; Richter et al. 2010; Babiychuk et al. 2011; Bryant et al. 2011; Gerdes et al. 2011; Sharwood et al. 2011; Apitz et al. 2014; Brown et al. 2014; Cohen et al. 2014; Schmitz-linneweber et al. 2015; Zhang et al. 2015; Stoll and Binder 2016; Wang et al. 2016; Shevtsov et al. 2018; http://seve.ibmp.unistra.fr/plantrna
tRNA aminoacylation	(Mireau et al. 1996; Akashi et al. 1998; Menand et al. 1998; Uwer et al. 1998; Souciet et al. 1999; Peeters et al. 2000; Duchene et al. 2001; Berg et al. 2005; Duchene et al. 2005; Pujol et al. 2007; Pujol et al. 2008; Hopper et al. 2011)

Figure 1: Summary of nine existing databases on subcellular protein targeting plants that were used to generate our automated targeting predictions.
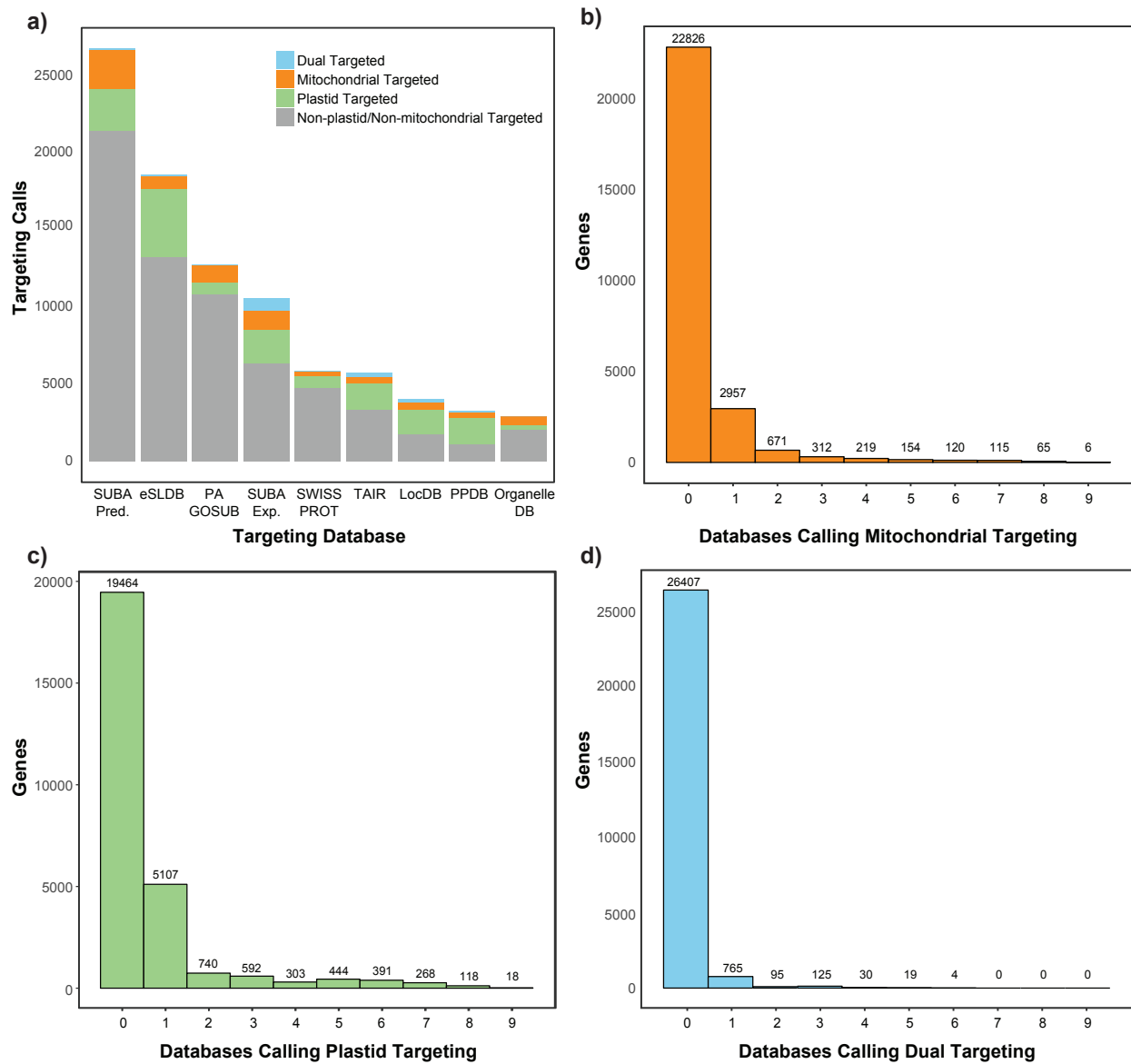
Figure 2: Chimeric cytonuclear protein complexes showing cytoplasmic-encoded, nuclear-encoded, and nuclear contact residues. Plastid-encoded residues are in green, mitochondrial-encoded residues are in purple, nuclear-encoded non-contact residues are in yellow, and nuclear-encoded contact residues are in red. Amino acids are shown as spheres, RNA is shown as ribbons. PDB accessions for reference structures: PSI: 2O01, PSII: 5MDX, rubisco: 5IU0, ACCase: 2F9Y, NDH: 6NBY, B6F: 1VF5, plastid ATPase: 6FKF, chlororibosome: 5MMM, CI: 5LNK, CIII: 1BGY, CIV: 1V54, mitochondrial ATPase: 5ARA, and mitoribosome: 3J9M.
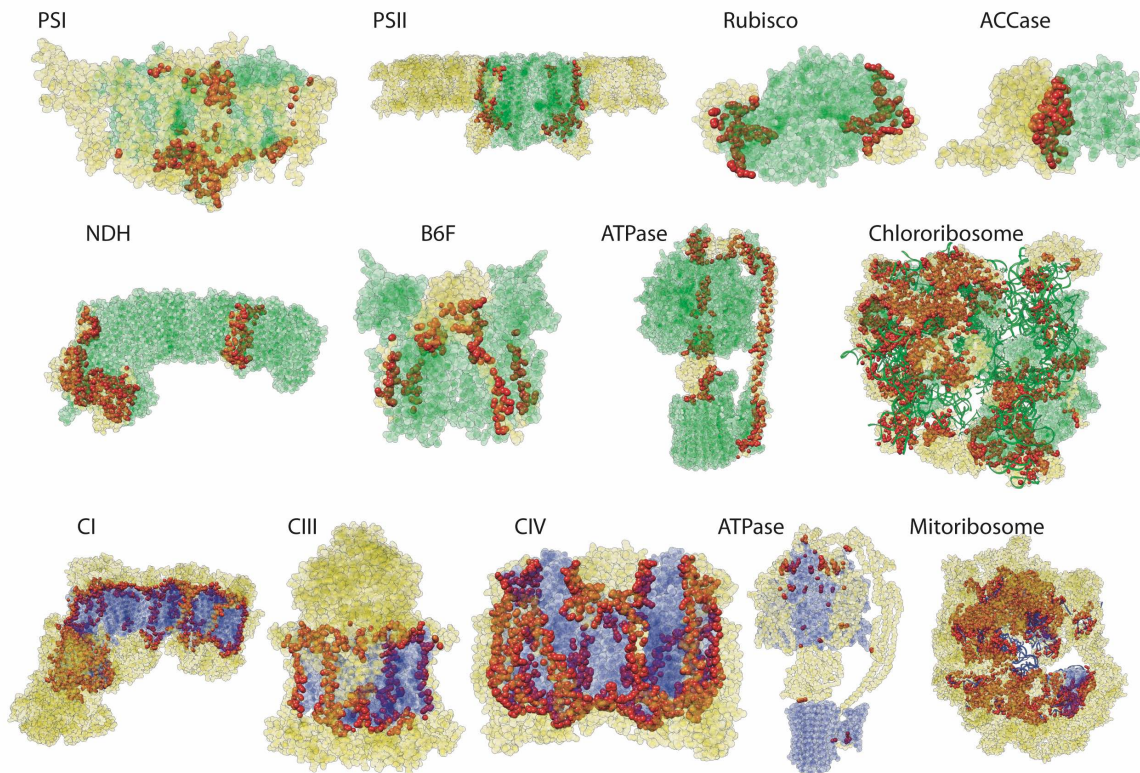
REFERENCES

Adams KL, Qiu YL, Stoutemyer M, Palmer JD. 2002. Punctuated evolution of mitochondrial gene content: high and variable rates of mitochondrial gene loss and transfer to the nucleus during angiosperm evolution. Proceedings of the National Academy of Sciences of the United States of America 99:9905-9912.

Adrion JR, White PS, Montooth KL. 2016. The roles of compensatory evolution and constraint in aminoacyl tRNA synthetase evolution. Molecular Biology and Evolution 33:152.

Akashi K, Grandjean O, Small I. 1998. Potential dual targeting of an Arabidopsis archaebacterial-like histidyl-tRNA synthetase to mitochondria and chloroplasts 1. FEBS Lett. 431:39–44.

Apitz J, Schmied J, Lehmann MJ, Hedtke B, Grimm B. 2014. GluTR2 complements a hema1 mutant lacking glutamyl-tRNA reductase 1, but is differently regulated at the post-translational level. Plant Cell Physiol. 55:645–657.

Babiychuk E, Vandepoele K, Wissing J, Garcia-Diaz M, Rycke R De, Akbari H. 2011. Plastid gene expression and plant development require a plastidic protein of the mitochondrial transcription termination factor family. PNAS 108:6674–6679.

Bannai H, Tamada Y, Maruyama O, Nakai K, Miyano S. 2002. Extensive feature detection of N-terminal protein sorting signals. Bioinformatics 18:298-305.

Barreto F, Watson E, Lima T, Willett C, Edmands S, Li W, Burton R. 2018. Genomic signatures of mitonuclear coevolution across populations of Tigriopus californicus. Nature ecology & evolution 2:1250-1257.

Barreto FS, Burton RS. 2013. Evidence for Compensatory Evolution of Ribosomal Proteins in Response to Rapid Divergence of Mitochondrial rRNA. Molecular Biology and Evolution 30:310-314.

Berardini TZ, Reiser L, Li D, Mezheritsky Y, Muller R, Strait E, Huala E. 2015. The Arabidopsis information resource: Making and mining the "gold standard" annotated reference plant genome. Genesis 53:474-485.

Berg M, Rogers R, Muralla R, Meinke D. 2005. Requirement of aminoacyl-tRNA synthetases for gametogenesis and embryo development in Arabidopsis. plan J.:866–878.

Bezouwen LS Van, Caffarri S, Kale RS, Kou R, Thunnissen AWH, Oostergetel GT, Boekema EJ. 2017. Subunit and chlorophyll organization of the plant photosystem II supercomplex. Nat. Plants 17080:1–11.

Bieri P, Leibundgut M, Saurer M, Boehringer D, Ban N. 2017. The complete structure of the chloroplast 70S ribosome in complex with translation factor pY. The EMBO Journal 36:475-486.

Boerema AP, Aibara S, Paul B, Tobiasson V, Kimanius D, Forsberg BO, Wallden K, Lindahl E, Amunts A. 2018. Structure of the chloroplast ribosome with chl-RRF and hibernation-promoting factor. Nat. Plants 4:212–217.

Bonen L, Calixte S. 2006. Comparative analysis of bacterial-origin genes for plant mitochondrial ribosomal proteins. Molecular Biology and Evolution 23:701-712.

Boutet E, Lieberherr D, Tognolli M, Schneider M, Bairoch A. 2007. UniProtKB/Swiss-Prot. Methods Mol Biol 406:89-112.

Brown GG, Francs-small CC, Ostersetzer-biran O. 2014. Group II intron splicing factors in plant mitochondria. Front. Plant Sci. 5:1–13.

Bryant N, Lloyd J, Sweeney C, Myouga F, Meinke D. 2011. IDentification of nuclear genes encoding chloroplast-localized proteins required for embryo development in Arabidopsis. Plant Physiol. 155:1678–1689.

Burton RS, Barreto FS. 2012. A disproportionate role for mtDNA in Dobzhansky-Muller incompatibilities? Molecular Ecology 21:4942-4957.

Burton RS, Pereira RJ, Barreto FS. 2013. Cytonuclear genomic interactions and hybrid breakdown. Annual Review of Ecology, Evolution, and Systematics 44:281-302.

Canino G, Bocian E, Barbezier N, Echeverrı M, Forner J, Binder S, Marchfelder A. 2009. Arabidopsis encodes four tRNase Z enzymes. Plant Physiol. 150:1494–1502.

Carrie C, Small I. 2013. A reevaluation of dual-targeting of proteins to mitochondria and chloroplasts. Biochimica et Biophysica Acta-Molecular Cell Research 1833:253-259.

Carrie C, Weißenberger S, Soll J. 2016. Plant mitochondria contain the protein translocase subunits TatB and TatC. Journal of Cell Science 129:3935-3947.

Chen P, Jäger G, Zheng B. 2010. Transfer RNA modifications and genes for modifying enzymes in Arabidopsis thaliana. BMC Plant Biology 10:201.

Cheng S, Gutmann B, Zhong X, Ye Y, Fisher M, Bai F, Castleden I, Song Y, Song B, Huang J. 2016. Redefining the structural motifs that determine RNA binding and RNA editing by pentatricopeptide repeat proteins in land plants. The Plant Journal 85:532-547.

Cohen S, Zmudjak M, Francs-small CC, Malik S, Shaya F, Keren I, Belausov E, Many Y, Brown GG, Small I, et al. 2014. nMAT4, a maturase factor required for nad1 pre-mRNA processing and maturation , is essential for holocomplex I biogenesis in Arabidopsis mitochondria. plan J. 78:253–268.

Córdoba JP, Fassolari M, Marchetti F, Soto D, Pagnussat GC, Zabaleta E. 2019. Different Types of CA Domains Are Present in Complex I from Immature Seeds and Adult Plants in Arabidopsis thaliana. Japanese Soc. Plant Physiol.

Cupp JD, Nielsen BL. 2014. Mitochondrion Minireview : DNA replication in plant mitochondria. Mitochondrion 19:231–237.

de Longevialle AF, Small ID, Lurin C. 2010. Nuclearly encoded splicing factors implicated in RNA splicing in higher plant organelles. Molecular Plant 3:691-705.

Delannoy E, Le Ret M, Faivre-Nitschke E, Estavillo GM, Bergdoll M, Taylor NL, Pogson BJ, Small I, Imbault P, Gualberto JM. 2009. Arabidopsis tRNA adenosine deaminase arginine edits the wobble nucleotide of chloroplast tRNA Arg (ACG) and Is essential for efficient chloroplast translation. Plant Cell 21:2058–2071.

Duchêne A-M, Giritch A, Hoffmann B, Cognat V, Lancelin D, Peeters NM, Zaepfel M, Maréchal-Drouard L, Small ID. 2005. Dual targeting is the rule for organellar aminoacyl-tRNA synthetases in *Arabidopsis thaliana*. Proceedings of the National Academy of Sciences 102:16484-16489.

Duchene A, Peeters N, Dietrich A, Cosset A, Small ID, Wintz H, Glyrs P. 2001. Overlapping destinations for two dual targeted glycyl-tRNA synthetases in arabidopsis thaliana and Phaseolus vulgaris. J. Biol. Chem. 276:15275–15283.

Ellison CK, Burton RS. 2006. Disruption of mitochondrial function in interpopulation hybrids of *Tigriopus californicus*. Evolution 60:1382-1391.

Emanuelsson O, Brunak S, von Heijne G, Nielsen H. 2007. Locating proteins in the cell using TargetP, SignalP and related tools. Nat Protoc 2:953-971.

Eslamieh M, Williford A, Betrán E. 2017. Few nuclear-encoded mitochondrial gene duplicates contribute to male germline-specific functions in humans. Genome Biology and Evolution 9:2782-2790.

Ferreira dCJ, Lucas J, Deniot G, Falentin C, Filangi O, Gilet M, Legeai F, Lode M, Morice J, Trotoux G. 2019. Cytonuclear interactions remain stable during allopolyploid evolution despite repeated whole-genome duplications in Brassica. Plant Journal In Press.

Forsythe ES, Nelson ADL, Beilstein MA. 2018. Biased gene retention in the face of massive nuclear introgression obscures species relationships. bioRxiv.

Friso G, Giacomelli L, Ytterberg AJ, Peltier JB, Rudella A, Sun Q, van Wijk KJ. 2004. In-depth analysis of the thylakoid membrane proteome of Arabidopsis thaliana chloroplasts: new proteins, new functions, and a plastid proteome database. The Plant cell 16:478-499.

Fujii S, Bond CS, Small ID. 2010. Selection patterns on restorer-like genes reveal a conflict between nuclear and mitochondrial genomes throughout angiosperm evolution. PNAS 108:1723–1728.

Geisler-Lee J, O'Toole N, Ammar R, Provart NJ, Millar AH, Geisler M. 2007. A predicted interactome for Arabidopsis. Plant Physiol 145:317-329.

Gerdes S, Yacoubi B El, Bailly M, Blaby IK, Blaby-haas CE, Jeanguenin L, Lara-núñez A, Pribat A, Waller JC, Wilke A, et al. 2011. Synergistic use of plant-prokaryote comparative genomics for functional annotations. BMC Genomics 12:1–16.

Germain A, Hotto AM, Barkan A, Stern DB. 2013. RNA processing and decay in plastids. WIREs RNA 4:295-316.

Gobert A, Gutmann B, Taschner A, Gössringer M, Holzmann J, Hartmann R, Rossmanith W, Giegé P. 2010. A single Arabidopsis organellar protein has RNase P activity. Nature Structural & Molecular Biology 17:740-744.

Gu W, Jackman JE, Lohan AJ, Gray MW, Phizicky EM. 2003. tRNA His maturation: An essential yeast protein catalyzes addition of a guanine nucleotide to the 5' end of tRNA His. Genes Dev. 17:2889–2901.

Gualberto JM, Newton KJ. 2017. Plant mitochondrial genomes: dynamics and mechanisms of mutation. Annual Review of Plant Biology 68:225-252.

Havird JC, McConie HJ. 2019. Sexually antagonistic mitonuclear coevolution in duplicate oxidative phosphorylation genes. Integrative & Comparative Biology In Press.

Havird JC, Trapp P, Miller C, Bazos I, Sloan DB. 2017. Causes and consequences of rapidly evolving mtDNA in a plant lineage. Genome Biology and Evolution 9:323-336.

Havird JC, Whitehill NS, Snow CD, Sloan DB. 2015. Conservative and compensatory evolution in oxidative phosphorylation complexes of angiosperms with highly divergent rates of mitochondrial genome evolution. Evolution 69:3069-3081.

Hess WR, Borner T. 1999. Organellar RNA Polymerases of Higher Plants. Int. Rev. Cyrology 190:7674–7696.

Hill GE. 2015. Mitonuclear ecology. Molecular Biology and Evolution 32:1927-1937.

Hooper CM, Castleden IR, Tanz SK, Aryamanesh N, Millar AH. 2017. SUBA4: the interactive data analysis centre for Arabidopsis subcellular protein locations. Nucleic Acids Research 45:D1064-D1074.

Huang S, Braun H-P, Gawryluk RMR, Millar AH. 2019. Mitochondrial complex II of plants: subunit composition, assembly and function in respiration and signaling. Plant J.

Izumi M, Tsunoda H, Suzuki Y, Makino A, Ishida H. 2012. RBCS1A and RBCS3B, two major members within the Arabidopsis RBCS multigene family, function to yield sufficient Rubisco content for leaf photosynthetic capacity. Journal of Experimental Botany 63:2159-2170.

Janouškovec J, Tikhonenkov DV, Burki F, Howe AT, Rohwer FL, Mylnikov AP, Keeling PJ. 2017. A new lineage of eukaryotes illuminates early mitochondrial genome reduction. Current Biology 27:3717-3724.

Jensen PE, Bassi R, Boekema EJ, Dekker JP, Jansson S, Leister D, Robinson C, Scheller HV. 2007. Structure, function and regulation of plant photosystem I. Biochimica et Biophysica Acta 1767:335-352.

Johnston IG, Williams BP. 2016. Evolutionary inference across eukaryotes identifies specific pressures favoring mitochondrial gene retention. Cell Systems 2:101-111.

Klodmann J, Senkler M, Rode C, Braun H. 2011. Defining the protein complex proteome of plant mitochondria. Plant Physiol. 157:587–598.

Klodmann J, Sunderhaus S, Nimtz M, Jansch L, Braun HP. 2010. Internal architecture of mitochondrial complex I from Arabidopsis thaliana. Plant Cell 22:797–810.

Konishi T, Sasaki Y. 1994. Compartmentalization of two forms of acetyl-CoA carboxylase in plants and the origin of their tolerance toward herbicides. PNAS 91:3598–3601.

Kumar S, Stecher G, Tamura K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33:1870-1874.

Kühn K, Bohne A, Liere K, Weihe A, Börner T. 2007. Arabidopsis phage-type RNA polymerases: accurate in vitro transcription of organellar genes. Plant Cell 19:959-971.

Kurisu G, Zhang H, Smith JL, Cramer WA. 2003. Structure of the cytochrome b6f complex of oxygenic photosynthesis: tuning the cavity. Science (80-.). 302:1009–1015.

Lamesch P, Berardini TZ, Li D, Swarbreck D, Wilks C, Sasidharan R, Muller R, Dreher K, Alexander DL, Garcia-Hernandez M, et al. 2012. The Arabidopsis Information Resource (TAIR): Improved gene annotation and new tools. Nucleic Acids Res. 40:1202–1210.

Laughlin T, Bayne A, Trempe J, Savage D, Davies K. 2019. Structure of the complex I-like molecule NDH of oxygenic photosynthesis. Nature 566:411-414.

Li C, Sun X, Conover J, Zhang Z, Wang J, Wang X, Deng X, Wang H, Liu B, Wendel J. 2019. Cytonuclear coevolution following homoploid hybrid speciation in *Aegilops tauschii*. Molecular Biology and Evolution 36:341-349.

Ligas J, Pineau E, Bock R, Huynen M, Meyer E. 2019. The assembly pathway of complex I in *Arabidopsis thaliana*. Plant Journal 97:447-459.

Lu P, Szafron D, Greiner R, Wishart DS, Fyshe A, Pearcy B, Poulin B, Eisner R, Ngo D, Lamb N. 2005. PA-GOSUB: a searchable database of model organism protein sequences with their predicted Gene Ontology molecular function and subcellular localization. Nucleic Acids Research 33:D147-153.

Lu Y. 2016. Identification and roles of photosystem II assembly, stability, and repair factors in Arabidopsis. Frontiers in Plant Science 7:168.

Lurin C, Andrés C, Aubourg S, Bellaoui M, Bitton F, Bruyère C, Caboche M, Debast C, Gualberto J, Hoffmann B, et al. 2004. Genome-wide analysis of arabidopsis pentatricopeptide repeat proteins reveals their essential role in organelle biogenesis. Plant Cell 16:2089–2103.

Menand B, Marechal L, Sakamoto W, Dietrich A, Wintz H. 1998. A single gene of chloroplast origin codes for mitochondrial and chloroplastic methionyl – tRNA synthetase in Arabidopsis thaliana. PNAS 95:11014–11019.

Meyer EH, Taylor NL, Millar AH. 2008. Resolving and identifying protein components of plant mitochondrial respiratory complexes using three dimensions of gel electrophoresis. J. Proteome Res. 7:786–794.

Millar AH, Eubel H, Ja L, Kruft V, Heazlewood JL. 2004. Mitochondrial cytochrome c oxidase and succinate dehydrogenase complexes contain plant specific subunits. Plant Mol. Biol. 56:77–90.

Mireau H, Lancelin D, Small ID. 1996. The same arabidopsis gene encodes both cytosolic and mitochondrial alanyl-tRNA synthetases. Plant Cell 8:1027–1039.

Morales H, Pavlova A, Amos N, Major R, Kilian A, Greening C, Sunnucks P. 2018. Concordant divergence of mitogenomes and a mitonuclear gene cluster in bird lineages inhabiting different climates. Nature ecology & evolution 2:1258-1267.

Nelson N, Ben-shem A, Wise TGS. 2004. The complex architecture of oxygenic photosynthesis. Mol. Cell Biol. 5:1–13.

Nishimura K, Apitz J, Friso G, Kim J, Ponnala L, Grimm B, Wijk KJ Van. 2015. Discovery of a unique Clp component , ClpF , in chloroplasts: A proposed binary ClpF-ClpS1 adaptor complex functions in substrate recognition and delivery. Plant Cell 27:2677–2691.

Nishimura K, van Wijk KJ. 2015. Organization, function and substrates of the essential Clp protease system in plastids. Biochimica et Biophysica Acta-Bioenergetics 1847:915-930.

Osada N, Akashi H. 2012. Mitochondrial-nuclear interactions and accelerated compensatory evolution: evidence from the primate cytochrome C oxidase complex. Molecular Biology and Evolution 29:337.

Panchy N, Lehti-Shiu M, Shiu S. 2016. Evolution of gene duplication in plants. Plant Physiology 171:2294-2316.

Peeters NM, Chapron A, Giritch A, Grandjean O, Lancelin D, Lhomme T, Vivrel A, Small I. 2000. Duplication and quadruplication of Arabidopsis thaliana cysteinyl- and asparaginyl-tRNA synthetase genes of organellar origin. J. Mol. Evol. 50:413–423.

Perrin R, Lange H, Grienenberger JM, Gagliardi D. 2004. AtmtPNPase is required for multiple aspects of the 18S rRNA metabolism in Arabidopsis thaliana mitochondria. Nucleic Acids Research 32:5174-5182.

Pett W, Lavrov DV. 2015. Cytonuclear interactions in the evolution of animal mitochondrial tRNA metabolism. Genome Biology and Evolution 7:2089-2101.

Pettersen EF, Goddard TD, Huang CC, Couch GS, Greenblatt DM, Meng EC, Ferrin TE. 2004. UCSF Chimera—a visualization system for exploratory research and analysis. Journal of Computational Chemistry 25:1605-1612.

Pierleoni A, Martelli PL, Fariselli P, Casadio R. 2007. eSLDB: eukaryotic subcellular localization database. Nucleic Acids Research 35:D208-212.

Placido A, Gobert A, Gallerani R, Mare L, Giege P. 2010. Plant mitochondria use two pathways for the biogenesis of tRNA His. Nucleic Acids Res. 38:7711–7717.

Pujol C, Bailly M, Kern D, Marechal L, Becker H, Duchene A. 2008. Dual-targeted tRNA-dependent amidotransferase ensures both mitochondrial and chloroplastic Gln-tRNA Gln synthesis in plants. PNAS 105:6481–6485.

Pujol C, Maréchal-drouard L, Duchêne A. 2007. How can organellar protein N-terminal sequences be dual targeting signals? In silico analysis and mutagenesis approach. J. Mol. Biol. 369:356–367.

Rand DM, Haney RA, Fry AJ. 2004. Cytonuclear coevolution: the genomics of cooperation. Trends in Ecology & Evolution 19:645-653.

Rastogi S, Rost B. 2011. LocDB: experimental annotations of localization for Homo sapiens and Arabidopsis thaliana. Nucleic Acids Research 39:D230-234.

Reiser L, Subramaniam S, Li D, Huala E. 2017. Using the Arabidopsis Information Resource (TAIR) to Find Information About Arabidopsis Genes. Curr Protoc Bioinformatics 60:1 11 11-11 11 45.

Richter U, Ku K, Okada S, Brennicke A, Weihe A, Bo T, Botanik M. 2010. A mitochondrial rRNA dimethyladenosine methyltransferase in Arabidopsis. Plant J. 1:558–569.

Rockenbach KD, Havird JC, Monroe JG, Triant DA, Taylor DR, Sloan DB. 2016. Positive selection in rapidly evolving plastid-nuclear enzyme complexes. Genetics 204:1507-1522.

Rogell B, Dean R, Lemos B, Dowling DK. 2014. Mito-nuclear interactions as drivers of gene movement on and off the X-chromosome. BMC Genomics 15:330.

Salie MJ, Thelen JJ. 2016. Regulation and structure of the heteromeric acetyl-CoA carboxylase. Biochim. Biophys. Acta 1861:1207–1213.

Salinas-Giegé T, Giegé R, Giegé P. 2015. tRNA biology in mitochondria. International Journal of Molecular Sciences 16:4518-4559.

Sasaki Y, Nagano Y. 2004. Plant acetyl-CoA carboxylase: structure, biosynthesis, regulation, and gene manipulation for plant breeding. Bioscience, Biotechnology, and Biochemistry 68:1175-1184.

Schmidt von Braun S, Sabetti A, Hanic-joyce PJ, Gu J, Schleiff E, Joyce PBM. 2007. Dual targeting of the tRNA nucleotidyltransferase in plants: not just the signal. J. Exp. Bot. 58:4083–4093.Schmitz-Linneweber C, Small I. 2008. Pentatricopeptide repeat proteins: a socket set for organelle gene expression. Trends in Plant Science 13:663-670.

Schmitz-Linneweber C, Lampe M, Sultan LD, Ostersetzer-biran O. 2015. Organellar maturases: A window into the evolution of the spliceosome. BBA - Bioenerg. 1847:798–808.

Senkler J, Senkler M, Braun HP. 2017. Structure and function of complex I in animals and plants–a comparative view. Physiologia Plantarum 161:6-15.

Senkler J, Senkler M, Eubel H, Hildebrandt T, Lengwenus C, Schertl P, Wagner S, Wittig I, Braun H. 2017. The mitochondrial complexome of Arabidopsis thaliana. Plant J. 89:1079–1092.

Sharbrough J, Havird JC, Noe GR, Warren JM, Sloan DB. 2017. The mitonuclear dimension of Neanderthal and Denisovan ancestry in modern human genomes. Genome Biology and Evolution In Press.

Sharwood RE, Halpert M, Luro S, Schuster G, Stern DB. 2011. Chloroplast RNase J compensates for inefficient transcription termination by removal of antisense RNA. RNA 17:2165–2176.

Shevtsov S, Nevo-Dinur K, Faigon L, Sultan LD, Zmudjak M, Markovits M, Ostersetzer-Biran O. 2018. Control of organelle gene expression by the mitochondrial transcription termination factor mTERF22 in Arabidopsis thaliana plants. PLoS One 13:e0201631.

Shikanai T. 2016. Chloroplast NDH: A different enzyme with a structure similar to that of respiratory NADH dehydrogenase. Biochimica et Biophysica Acta 1857:1015-1022.

Sloan DB, Fields PD, Havird JC. 2015. Mitonuclear linkage disequilibrium in human populations. Proceedings of the Royal Society B: Biological Sciences 282:20151704.

Sloan DB, Havird JC, Sharbrough J. 2017. The on-again, off-again relationship between mitochondrial genomes and species boundaries. Molecular Ecology 26:2212-2236.

Sloan DB, Triant DA, Wu M, Taylor DR. 2014. Cytonuclear interactions and relaxed selection accelerate sequence evolution in organelle ribosomes. Molecular Biology and Evolution 31:673-682.

Sloan DB, Warren JM, Williams AM, Wu Z, Abdel-Ghany SE, Chicco AJ, Havird JC. 2018. Cytonuclear integration and co-evolution. Nature Reviews Genetics 19:635-648.

Small I, Peeters N, Legeai F, Lurin C. 2004. Predotar: A tool for rapidly screening proteomes for N-terminal targeting sequences. Proteomics 4:1581-1590.

Sperschneider J, Catanzariti AM, DeBoer K, Petre B, Gardiner DM, Singh KB, Dodds PN, Taylor JM. 2017. LOCALIZER: subcellular localization prediction of both plant and effector proteins in the plant cell. Sci Rep 7:44598.

Souciet G, Menand B, Ovesna J, Cosset A, Dietrich A, Wintz H. 1999. Characterization of two bifunctional Arabdopsis thaliana genes coding for mitochondrial and cytosolic forms of valyl-tRNA synthetase and threonyl-tRNA synthetase by alternative use of two in-frame AUGs. FEBS 854:848–854.

Stoll B, Binder S. 2016. Two NYN domain containing putative nucleases are involved in transcript maturation in Arabidopsis mitochondria. Plant Journal 85:278-288.

Sudianto E, Chaw S-M. 2019. Two independent plastid accD transfers to the nuclear genome of Gnetum and other insights on acetyl-CoA carboxylase evolution in gymnosperms. Genome Biol. Evol.:1–30.

Sun Q, Zybailov B, Majeran W, Friso G, Olinares PD, van Wijk KJ. 2009. PPDB, the Plant Proteomics Database at Cornell. Nucleic Acids Research 37:D969-974.

Sun T, Bentolila S, Hanson M. 2016. The unexpected diversity of plant organelle RNA editosomes. Trends in Plant sScience 21:962-973.

Tiller N, Weingartner M, Thiele W, Maximova E, Schöttler MA, Bock R. 2012. The plastid-specific ribosomal proteins of Arabidopsis thaliana can be divided into non-essential proteins and genuine ribosomal proteins. The Plant Journal 69:302-316.

Timmis JN, Ayliffe MA, Huang CY, Martin W. 2004. Endosymbiotic gene transfer: Organelle genomes forge eukaryotic chromosomes. Nature Review Genetics 5:123-135.

Toews DP, Brelsford A. 2012. The biogeography of mitochondrial and nuclear discordance in animals. Molecular Ecology 21:3907-3930.

Toole NO, Hattori M, Andres C, Iida K, Lurin C, Schmitz-linneweber C, Sugita M, Small I. 2008. On the expansion of the pentatricopeptide repeat gene family in plants. Mol. Biol. Evol. 25:1120–1128.

Uwer U, Willmitzer L, Altmann T. 1998. Inactivation of a glycyl-tRNA synthetase leads to an arrest in plant embryo development. Plant Cell 10:1277–1294.

van Bezouwen L, Caffarri S, Kale R, Kouřil R, Thunnissen A, Oostergetel G, Boekema E. 2017. Subunit and chlorophyll organization of the plant photosystem II supercomplex. Nature Plants 3:17080.

Walter M, Kilian J, Kudla È. 2002. PNPase activity determines the efficiency of mRNA 3'-end processing, the degradation of tRNA and the extent of polyadenylation in chloroplasts. Eur. Mol. Biol. Organ. 21:6905–6914.

Waltz F, Nguyen T, Arrivé M, Bochler A, Chicher J, Hammann P, Kuhn L, Quadrado M, Mireau H, Hashem Y. 2019. Small is big in Arabidopsis mitochondrial ribosome. Nature Plants 5:106-117.

Wang S, Bai G, Wang S, Yang L, Yang F, Wang Y. 2016. Chloroplast RNA-binding protein

RBD1 promotes chilling tolerance through 23S rRNA processing in Arabidopsis. PLoS Genet. 1:1–21.

Weng ML, Ruhlman TA, Jansen RK. 2016. Plastid-nuclear interaction and accelerated coevolution in plastid ribosomal genes in Geraniaceae. Genome Biology and Evolution 8:1824-1838.

Williams AM, Friso G, Wijk KJ Van, Sloan DB. 2019. Extreme variation in rates of evolution in the plastid Clp protease complex. Plant J.:1–17.

Wiwatwattana N, Landau CM, Cope GJ, Harp GA, Kumar A. 2007. Organelle DB: an updated resource of eukaryotic protein localization and function. Nucleic Acids Research 35:D810-814.

Yan Z, Ye G, Werren J. 2019. Evolutionary rate correlation between mitochondrial-encoded and mitochondria-associated nuclear-encoded proteins in insects. Molecular Biology and Evolution In Press.

Yu F, Liu X, Alsheikh M, Park S, Rodermel S. 2008. Mutations in SUPPRESSOR OF VARIEGATION1, a factor required for normal chloroplast translation, suppress var2-mediated leaf variegation in Arabidopsis. Plant Cell 20:1786-1804.

Zaegel V, Guermann B, Le Ret M, Andres C, Meyer D, Erhart M, Canaday J, Gualberto JM, Imbault P. 2006. The plant-specific ssDNA binding protein OSB1 Is involved in the stoichiometric transmission of mitochondrial DNA in Arabidopsis. Plant Cell 18:3548–3563.

Zaidi A, Makova K. 2019. Investigating mitonuclear interactions in human admixed populations. Nature ecology & evolution 3:213-222.

Zhang J, Ruhlman TA, Sabir J, Blazier JC, Jansen RK. 2015. Coordinated rates of evolution between interacting plastid and nuclear genes in Geraniaceae. The Plant cell 27:563-573.

Zhang J, Ruhlman TA, Sabir JS, Blazier JC, Weng ML, Park S, Jansen RK. 2016. Coevolution between nuclear-encoded DNA replication, recombination, and repair genes and plastid genome complexity. Genome Biology and Evolution 8:622-634.