Chapter 8

Seed Plant Mitochondrial Genomes: Complexity Evolving

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Summary

Complete mitochondrial genome sequences are now available for representatives of all major clades of land plants except for the ferns (monilophytes). More than 30 chondrome sequences have been determined for flowering plants alone. Given that a well-founded understanding of land plant phylogeny has developed over the recent years, we can now confidently trace the molecular evolution of plant mitochondrial genomes with respect to their numerous interesting features: an ongoing endosymbiotic gene transfer to the nucleus, the gains, losses and occasional disruptions of introns, the acquisition of foreign DNA sequences and the emergence of the pyrimidine conversion type of RNA editing. This review attempts to put the insights from several independent studies addressing the molecular evolution of these features and our insights from the growing list of completed plant chondrome sequences into a modern phylogenetic perspective on land plants.

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I. Introduction

Flowering plants (angiosperms) are unique among all eukaryotes in having very large and complex mitochondrial genomes. Already 30 years ago, it was recognized that the mitochondrial DNAs (mtDNAs) in the Cucurbitaceae, for example in muskmelon (Ward et al. 1981), may be larger than 2 mega base pairs (Mbp) and thus even exceed in size the genomes of many free-living bacteria. The compact and streamlined animal mitochondrial genomes (chondromes) are one to two orders of magnitude smaller and starkly contrast their angiosperm counterparts in almost every aspect. Note, that the term "chondriome" has previously been used ambiguously to describe either the mitochondrial genome of a species or the entirety of the dynamic population of all mitochondria in a cell (Logan 2010). This issue of confusion was recently addressed, suggesting that "chondriome" is now restricted to the latter sense whereas chondrome (without i) is used equivalently to mitochondrial genome (Knoop et al. 2010).

The mitochondrial genome of humans was the first chondrome to be determined in its complete sequence in 1981 and this was an early milestone on the path to what has later become known as the genomics era of biology (Anderson et al. 1981). The simple circular structure and small size (of only 16 kilo base pairs; Kbp) of the human mitochondrial DNA turned out to be prototypical not only for other mammals but also for animals (metazoa) at large. One has to dig deep into the phylogeny of metazoa to find (few) exceptions to the simple design of animal mtDNA encoding a standard set of 13 protein subunits of respiratory chain complexes (RCCs) plus 2 rRNAs and 22 tRNAs (Burger et al. 2009; Lavrov 2007; Signorovitch et al. 2007).

In contrast, many studies over the last three decades have revealed that a number of oddities have affected the evolution of flowering plant chondromes. Flowering plants represent the evolutionary most successful plant clade dating back in origin to the early cretaceous some 145 million years ago and comprising more than 250,000 extant species. The molecular peculiarities of angiosperm plant chondromes include (1) frequent mtDNA recombination producing alternative, co-existing DNA arrangements, (2) promiscuous DNA inserts originating from the chloroplast and nuclear genomes, (3) disruptions of genes creating the need for rejoining genetic information at the RNA level by trans-splicing, (4) frequent RNA editing of mitochondrial transcripts through site-directed pyrimidine (C/U) conversions and (5) an ongoing endosymbiotic gene transfer (EGT) into the nucleus, which makes plant chondrome gene complements highly variable. In addition, at least some plant chondromes seem to be prone to accept insertions of horizontally transferred sequences originating from other, distant taxa (Bergthorsson et al. 2003; Won and Renner 2003). In fact, horizontal gene transfer (HGT) may have had a significant influence on shaping certain angiosperm chondromes, such as the one of the early-branching species *Amborella trichopoda* (Bergthorsson et al. 2004 and J. Palmer, pers. communication). A separate chapter in this volume (Chap. 10) is exclusively dedicated to horizontal gene transfer and, therefore, I will only briefly allude to this issue here.

II. Complete Plant Chondrome Sequences

The mtDNA of the liverwort *Marchantia polymorpha* was the first land plant chondrome sequence to be completely determined nearly 20 years ago (Oda et al. 1992b).

Abbreviations: bp – Base pairs; CMS – Cytoplasmic male sterility; cpDNA – Chloroplast DNA; EGT – Endosymbiotic gene transfer (from endosymbiotic organelles to the nucleus); HGT – Horizontal gene transfer; HT-clade – hornwort-tracheophyte clade; Kbp – Kilo base pairs (10^3 bp); LGT – Lateral gene transfer; Mbp – Mega base pairs (10^6 bp); mRNA – Messenger RNA; mtDNA – Mitochondrial DNA; NLE-clade – non-liverwort embryophyte clade; ORF – Open reading frame; RCC – Respiratory chain complex; rRNA – Ribosomal RNA; SNP – Single nucleotide polymorphism; tRNA – Transfer RNA

Sequencing of the mtDNA of the model plant *Arabidopsis thaliana* (Brassicaceae) was completed 5 years later (Unseld et al. 1997) and this was followed by complete sequencing of several other angiosperm chondromes, mainly from crop species of agricultural importance (Table 8.1). Significant economical interest in studies of crop plant mtDNAs comes from an aspect of immediate practical, agronomical relevance in plant breeding: the phenomenon of cytoplasmic male sterility (CMS), which is of utmost importance for hybrid seed production. After experiencing a disastrous susceptibility of the widely used CMS-T varieties, harbouring the 'Texas' cytoplasm, of maize (*Zea mays*) to the fungal pathogen *Bipolaris maydis* in 1970, early groundbreaking research demonstrated that mtDNA rearrangements are correlated with the expression of the CMS phenotype (Levings and Pring 1976; Pring et al. 1977; Timothy et al. 1979). Some mitochondrial DNA recombinations turned out to be associated with the accidental creation of chimeric open reading frames (ORFs), which upon expression result in specific defects in mitochondrial function that become phenotypically apparent as defects in pollen maturation (Hanson and Bentolila 2004; Kubo and Newton 2008). Another chapter in this volume (Chap. 12) deals extensively with such mutations in plant mitochondrial genomes.

Several studies of flowering plant mtDNAs have shown that significant variation at the genus or species levels is not restricted to maize (Sederoff et al. 1981), but is also found, for example, in the evening primrose *Oenothera berteriana* (Brennicke and Blanz 1982), *Arabidopsis thaliana* (Ullrich et al. 1997) or the genera *Fagus* (Tomaru et al. 1998) and *Solanum* (Scotti et al. 2004). Several complete mtDNA sequences have recently been determined for different cultivars, sub-species or very closely related species of rice (*Oryza sativa*), maize (*Zea mays*), wheat (*Triticum aestivum*) and beet (*Beta vulgaris*), now providing a full view on mtDNA variability at these very low taxonomic levels. Immediately obvious – already from simply comparing the mtDNA sizes (Table 8.1) – are the vast expansions or reductions of chondrome sizes leading to significant mtDNA variability among the closely related taxa. One interesting exception is the near-identity of the recently determined chondrome of a winter wheat cultivar with its spring wheat cultivar counterpart, distinguished by only 10 minor indels and 7 SNPs (Cui et al. 2009). This, however, is in sharp contrast to a much larger chondrome containing vastly extended intergenic regions in the wheat CMS line Ks3 (Liu et al. 2011).

The total number of 22 complete chondrome sequences now available for the four genera *Beta, Oryza, Triticum* and *Zea* alone currently exceeds the number of 12 complete mtDNA sequence available for all other angiosperm genera – in fact even those of all other seed plant (spermatophyte) genera, given that the mtDNA of *Cycas taitungensis* is currently the only one representing the gymnosperms (Table 8.1).

Point mutations (SNPs, single nucleotide polymorphisms) are the prevailing differences at the species, genus or even higher taxonomic levels in animal mtDNAs, which are highly conserved in their simple, circular and non-recombining structure. Basically, the opposite is the case in plants: Structural rearrangements involving DNA recombinations dominate over very few SNPs that are only rarely discovered in the slowly evolving plant mtDNA sequences. By and large, the title of a late 1980s publication "Plant mitochondrial DNA evolves rapidly in structure but slowly in sequence" (Palmer and Herbon 1988) is essentially still correct, at least for angiosperms. However, it must be noted that some plant lineages have been discovered to show substantially elevated levels of mitochondrial primary sequence evolution (Adams et al. 1998b; Cho et al. 2004; Parkinson et al. 2005; Sloan et al. 2010b; Vangerow et al. 1999).

Evolutionarily successful, beautiful and unmatched in importance for animal and human existence as they are, angiosperms represent even less than only the last third of plant evolution on this planet, which presumably dates back to Ordovician times. After the milestone mtDNA sequencing of *Marchantia polymorpha* it actually took as

Table 8.1. Completed land plant (embryophyte) mtDNA sequences and those of two charophyte algae discussed as most closely related to embryophyte lineage. Sizes of chondrome "master-circles", database accessions and key papers are indicated in most cases. The asterisks indicate that the true physical structure of the lycophyte chondromes is particularly unclear, but assumed to be network-like due to rampant recombination. For the *Isoetes engelmannii* chondrome (submitted as five partially redundant fosmid clones under database accessions FJ010859, FJ536259, FJ390841, FJ176330 and FJ628360), the net sequence complexity is indicated, for *Selaginella moellendorffii* the approximate sum of single-copy coding islands (~100 Kbp) plus 10 extended recombinationally active repeats (~50 Kbp) is given. A permanently updated list of Virdiplantae mtDNAs (i.e., including chlorophyte algae) is found at http://www.ncbi.nlm.nih.gov/genomes/GenomesGroup.cgi?taxid=33090&opt=organelle. Complete mtDNA sequences have been determined for closely related species/subspecies/varieties/cultivars and/or fertile and male infertile CMS lines in the agronomically relevant genera *Oryza, Triticum, Zea* and *Beta*. *Oryza sativa* cultivar PA64S[a] is in fact "*indica*-like", but its cytoplasm is of *japonica* type. The mtDNAs of bamboo (*Bambusa oldhamii*, Bambusoidae, BEP clade) and tomato (*Solanum lycopersicum*, Solanales) are deposited in the database under accessions EU365401 and FJ374974, but are annotated to contain undetermined gaps and are, therefore, not further discussed in this chapter

Taxonomy	*Species*	mtDNA size	DB accessions	Publication(s)
Streptophyte algae, Charophyte				
Charales	*Chara vulgaris*	68	AY267353/NC_005255	(Turmel et al. 2003)
Coleochaetales	*Chaetosphaeridium globosum*	57	AF494279/NC_004118	(Turmel et al. 2002a)
Marchantiophyta (liverworts)				
Marchantiales	*Marchantia polymorpha*	187	M68929/NC_001660	(Oda et al. 1992b)
Pleuroziales	*Pleurozia purpurea*	169	FJ999996/NC_013444	(Wang et al. 2009)
Bryophyta (mosses)				
Funariales	*Physcomitrella patens*	105	NC_007945	(Terasawa et al. 2007)
Anthocerotophyta (hornworts)				
Dendrocerotales	*Megaceros aenigmaticus*	185	EU660574/NC_012651	(Li et al. 2009)
Notothyladales	*Phaeoceros laevis*	209	GQ376531/NC_013765	(Xue et al. 2010)
Lycophyta (lycophytes)				
Isoetales	*Isoetes engelmannii*	58[b]	FJ010859 et c.[b]	(Grewe et al. 2009)
Selaginellales	*Selaginella moellendorffii*	~150[b]	JF338143-JF338147[b]	(Hecht et al. 2011)
Spermatophyta (seed plants)				
Gymnosperms – Cycadophyta/Cycadales				
Cycadaceae	*Cycas taitungensis*	415	NC_010303	(Chaw et al. 2008)
Angiosperms				
Monocots: Liliopsida/Poales/Poaceae				
BEP clade				
Ehrhartoidae	*Oryza sativa*	435–491		
	ssp. *japonica* Nipponbare-N	491	BA000029	(Notsu et al. 2002)
	ssp. *japonica* Nipponbare-S	491	DQ167400	(Tian et al. 2006)
	ssp. *japonica* PA46S[a]	491	DQ167807	(Tian et al. 2006)
	ssp. *indica* 93-11	492	DQ167399	(Tian et al. 2006)
	ssp. *indica* LD-CMS	435	AP011077	(Fujii et al. 2010)
	Oryza rufipogon CW-CMS	559	AP011076	(Fujii et al. 2010)
Pooidae	*Triticum aestivum*	453–658		
	cv. Chinese Spring	453	AP008982	(Ogihara et al. 2005)
	cv. Chinese Yumai	453	EU534409	(Cui et al. 2009)
	K-type CMS line Ks3	658	GU985444	(Liu et al. 2011)

(continued)

Table 8.1. (continued)

Taxonomy	*Species*	mtDNA size	DB accessions	Publication(s)
PACCAD clade/Panicoidae				
Andropogoneae	*Sorghum bicolor*	469	DQ984518	
	Zea mays	536–740		
	ssp. *mays* NB	570	AY506529/NC_007982	(Clifton et al. 2004)
	ssp. *mays* NA	701	DQ490952	(Allen et al. 2007)
	ssp. *mays* CMS-C	740	DQ645536	
	ssp. *mays* CMS-S	557	DQ490951	
	ssp. *mays* CMS-T	536	DQ490953	
	ssp. *parviglumis*	681	DQ645539	Allen et al., unpublished
	ssp. *perennis*	570	DQ645538	
	Zea luxurians	539	DQ645537	
	Tripsacum dactyloides	704	DQ984517	
Eudicotyledons/core eudicotyledons				
Caryophyllales				
Caryophyllaceae	*Silene latifolia*	253	HM562727/NC_014487	(Sloan et al. 2010a)
Amaranthaceae	*Beta vulgaris*	369–501		
	ssp. *vulgaris* TK81-0	369	BA000009/NC_002511	(Kubo et al. 2000)
	ssp. *vulgaris* TK81-MS	501	BA000024	(Satoh et al. 2004)
	ssp. *maritima* A	365	FP885845/NC_015099	(Darracq et al. 2011)
	ssp. *maritima* B	368	FP885834	
	ssp. *maritima* G	269	FP885871	
Asterids/Lamiids				
Lamiales	*Boea hygrometrica*	510	JN107814	(Zhang et al. 2012)
Solanales	*Nicotiana tabacum*	431	BA000042/NC_006581	(Sugiyama et al. 2005)
Rosids				
Vitales	*Vitis vinifera*	773	FM179380/NC_012119	(Goremykin et al. 2009)
Fabids				
Fabales	*Vigna radiata*	401	HM367685/NC_015121	(Alverson et al. 2011)
Malpighiales	*Ricinus communis*	503	HQ874649/NC_015141	(Rivarola et al. 2011)
Cucurbitales	*Citrullus lanatus*	379	GQ856147/NC_014043	(Alverson et al. 2010)
	Cucurbita pepo	983	GQ856148/NC_014050	(Alverson et al. 2010)
	Cucumis melo	>2,700	JF412792	(Rodríguez-Moreno et al. 2011)
	Cucumis sativus	>1,600	HQ860792	(Alverson et al. 2011)
Malvids/Brassicales				
Caricaceae	*Carica papaya*	477	EU431224/NC_012116	unpublished
Brassicaceae	*Arabidopsis thaliana*	367	Y08501/NC_001284	(Unseld et al. 1997)
	Brassica napus	222	AP006444/NC_008285	(Handa 2003)

many as 15 years until the second chondrome sequence of a non-angiosperm plant became available, the one of the "model moss" *Physcomitrella patens* (Terasawa et al. 2007). Only very recently, the first complete mtDNA sequences (see Table 8.1) of a gymnosperm, *Cycas taitungensis* (Chaw et al. 2008), a hornwort, *Megaceros aenigmaticus* (Li et al. 2009), and a lycophyte, *Isoetes engelmannii* (Grewe et al. 2009), became available. Somewhat earlier, the chondrome sequences of the charophyceaen algae *Chara vulgaris* and *Chaetosphaeridium globosum* had been determined (Turmel et al. 2002a, 2003), which are among those algal taxa being discussed most closely related to land plants and thus provide well-suited outgroup taxa for rooting the land plant (embryophyte) phylogeny. Chapters 3 and 6 of this volume deal with algal chloroplast and mitochondrial genomes in detail.

Molecular phylogenetic studies (e.g. Qiu et al. 2006), occasionally based on individual mitochondrial loci with wide taxon sampling,

have meanwhile established a well-supported overall plant phylogeny (see Fig. 8.1b). This modern concept rejects a monophyly of bryophytes (liverworts, mosses and hornworts) and also confidently defines the relationships of non-seed vascular plants. The clade of monilophytes comprising true ferns, horsetails and whisk ferns (Pryer et al. 2001), is well confirmed and sister to the seed plants (spermatophytes) comprising angiosperms and gymnosperms. Jointly, the spermatophytes and monilophytes constitute the clade of euphyllophytes. The euphyllophytes are the sister clade of lycophytes (comprising club mosses, spike mosses and quillworts), which represent the most ancient surviving lineage of vascular plants (tracheophytes). Hornworts are now considered to be the sister clade of tracheophytes, among other evidences supported by mitochondrial intron patterns (Groth-Malonek et al. 2005), as I will discuss below. No formal name has as yet been suggested for the joint hornwort + tracheophyte clade (provisionally designated the HT clade), mainly because a representative, name-giving morphological synapomorphy yet remains to be identified (although hornworts are, like tracheophytes, characterized by an enduring diploid sporophyte developmental phase). Mosses are the sister group to the HT clade and jointly this is the "Non-Liverwort Embryophyte" (NLE) lineage, sister to the liverworts. Hence, this phylogenetic topology places the root of land plant evolution between liverworts and all other plants in the NLE clade (Fig. 8.1b). Among the major land plant groups, a full chondrome sequence is still lacking for the monilophyte (i.e., ferns sensu lato) clade.

III. Evolving Gene Complements in Seed Plant Chondromes

A. The Protein-Coding Gene Complement Affected by Endosymbiotic Gene Transfer

The chondrome of the liverwort *Marchantia polymorpha* (Oda et al. 1992b) turned out be about 11 times as large as the one of humans (Anderson et al. 1981). This is in part explained by the presence of several genes that are never encoded in animal mtDNAs as well as many introns disrupting coding regions, which I will discuss in the following section. With 73 genes encoded in the chondrome of *Marchantia* and the recently sequenced chondrome of the rather distantly related liverwort species *Pleurozia purpurea* (Wang et al. 2009), the liverworts hold the record for mitochondrial gene complements among land plants. The land plant chondrome gene complement includes genes for rRNAs, tRNAs, subunits of the RCCs I (*nad* genes), II (*sdh*), III (*cob*), IV (*cox*) and V (*atp*), subunits of a cytochrome c maturation pathway (*ccm*), ribosomal proteins (*rpl* and *rps*) and a subunit of a twin-arginine translocase (*tat*C).

One glaring exception in the liverworts is that *nad*7, a "core" RCC I subunit gene, is degenerated into a pseudogene and was functionally established as a nuclear gene after endosymbiotic gene transfer (Kobayashi et al. 1997). This is a particular surprising case, because although *nad*7 is degenerated, it is retained as a pseudogene in both marchantiid (like *Marchantia*) and jungermanniid (like *Pleurozia*) liverwort chondromes. However, a functional *nad7* gene still exists in the mtDNA of *Haplomitrium*, which represents the most ancient (and phylogenetically somewhat isolated) liverwort lineage, sister to the two large clades of marchantiid and jungermanniid liverworts (Groth-Malonek et al. 2007b).

Aside from an apparent loss of *rpl14* (conserved in algal chondromes) in the land plant stem lineage (Node O in Fig. 8.1b) or the later loss of *rps8* as a likely synapomorphy in the NLE stem lineage (Node A in Fig. 8.1b), *nad7* in the liverworts may actually represent the most ancient case of functional endosymbiotic gene transfer (EGT) in land plant evolution. Another example for the transfer of a gene encoding an RCC core component had been described earlier for the *cox*2 gene (encoding a subunit of cytochrome c oxidase, RCC IV) in the "legumes" (Fabaceae; Adams et al. 1999; Daley et al. 2002;

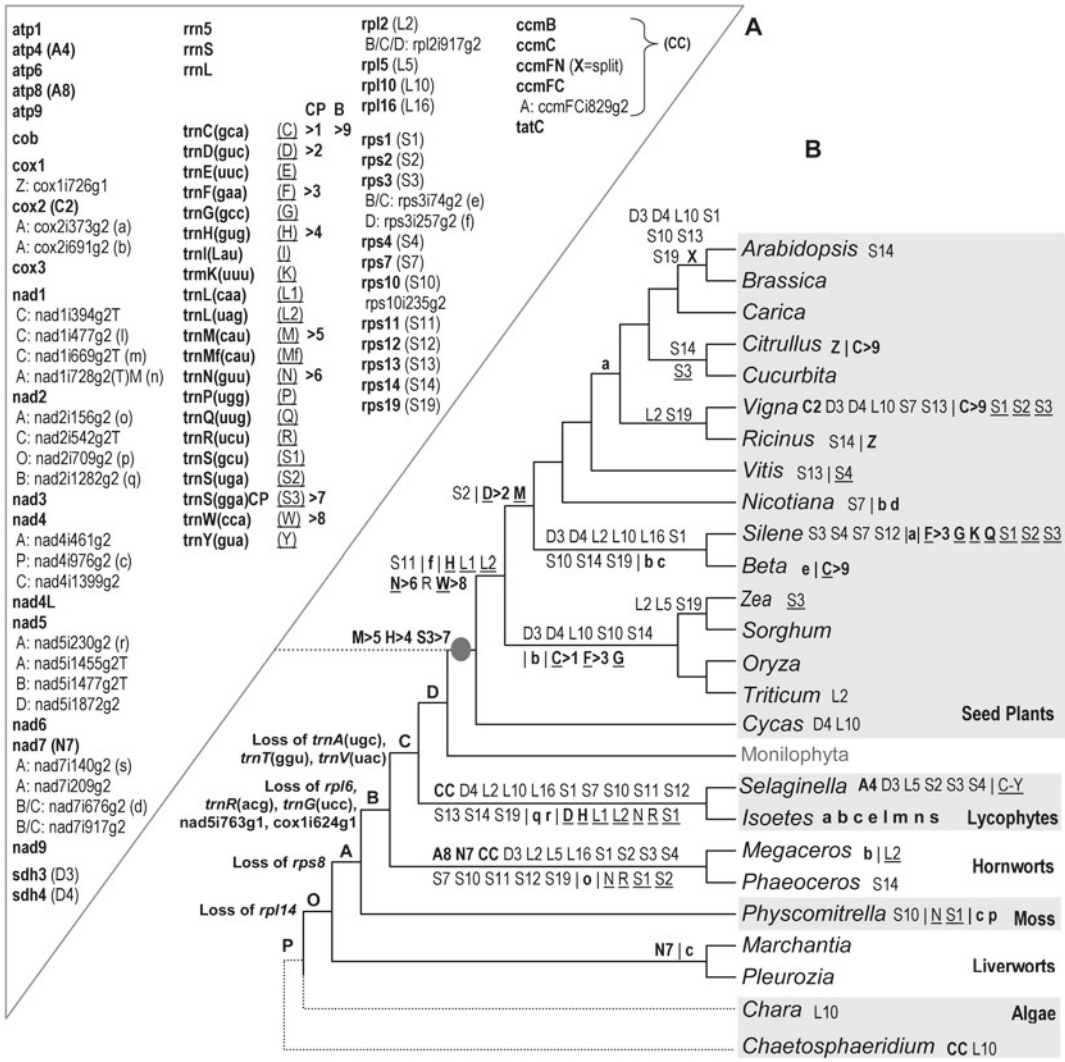

Fig. 8.1. (**a**) The ancestral gene complement of seed plant mtDNAs most likely contained genes for 20 protein subunits (first column) of respiratory chain complexes I (*nad*), II (*sdh*), III (*cob*), IV (*cox*) and V (*atp*), for 3 rRNAs and 20 tRNAs (*rrn* and *trn* genes, second column), for 15 proteins of the large and small ribosomal subunit (*rpl* and *rps*, third column) and for five genes involved in cytochrome c maturation (*ccm*) and a twin-arginine translocase subunit (*tatC, fourth column*). Introns are listed below the respective gene following a recently proposed nomenclature (Dombrovska and Qiu *2004*; Knoop *2004*). Capital letters indicate intron origins along the backbone nodes of plant phylogeny as depicted in the cladogram in B (O: Origin of embryophytes; A: NLE clade; B: HT clade; C: Tracheophytes; D: Euphyllophytes; P: a possible clade uniting the alga *Chara* and the embryophytes). The letter "X" indicates a split of ccmFN in the Brassicaceae and "Z" indicates independent gains of the "rampant invader" group I intron cox1i726g1 via HGT (in *Citrullus and Ricinus*). Letters in parentheses behind genes and introns denote losses from chondromes (small letters for introns, underlined capital letters for *trn* genes). Gain of chloroplast tRNA genes (CP) are indicated with ">" followed by an arbitrary number as given in the subsequent column. The source of the *trnC* xenologue "C > 9" (in *Beta, Citrullus* and *Vigna*), which is similar to bacterial (B) homologues, is as yet unidentified. (**b**) A cladogram based on a modern understanding of plant phylogeny is shown. It includes all embryophyte taxa, for which complete mtDNA sequences have been determined. For simplicity, only genus names and only one terminal branch is shown, where multiple chondrome sequences of very closely related taxa have been determined (*Beta, Oryza, Triticum, Zea*). Losses of protein-coding genes, introns and tRNA genes, the functional replacement of lost tRNA genes, the disruption of *ccmFN* (X) and the gain of intron cox1i726g1 (Z) are indicated at the backbone nodes, along the branches or after the genus names. Different types of sequence losses and acquisitions are separated by vertical lines. The labels are used as in A with rare events highlighted in *bold*.

Nugent and Palmer 1991). Like *nad7* in the liverworts, the *cox2* EGT in Fabaceae could actually be a unique one-time event in plant evolution, among the completely sequenced angiosperm chondromes only represented by the mung bean *Vigna radiata* (Alverson et al. 2011; labelled C2 in Fig. 8.1). Only two further core RCC protein subunit genes have recently been shown to be subject to rare EGT: The *atp8* gene is absent from the *Allium* and hornwort chondromes (Adams et al. 2002b; Li et al. 2009; Xue et al. 2010) and the *atp4* gene is lacking from the mtDNA of the lycophyte *Selaginella moellendorffii* (Hecht et al. 2011); labelled A8 and A4, respectively, in Fig. 8.1.

Many more examples for ongoing, frequent and independent EGT in angiosperms have earlier been recognized for mitochondrial ribosomal protein genes. For example, when *rps10*, the mitochondrial gene for protein S10 of the small ribosomal subunit, was identified in angiosperms, it was immediately obvious that it occurred only sporadically among flowering plant mtDNAs (Knoop et al. 1995; Zanlungo et al. 1994). A subsequent study showed numerous independent EGTs of *rps10* among angiosperms (Adams et al. 2000) and a very similar picture emerged for the *sdh* genes encoding RCC II (succinate dehydrogenase) subunits (Adams et al. 2001). Ultimately, a comprehensive survey of 280 angiosperm genera revealed that all *rpl* and *rps* as well as the *sdh* genes are frequently and independently lost from mtDNAs. Interestingly, this is not the case for the *ccm* genes and the other "core" RCC genes encoding subunits of complexes I, III, IV and V (Adams et al. 2002b). Between 42 and 6 independent gene losses were observed and ranking genes according to the number of independent EGT events results in the following order: *rps7* > *rpl2* > *sdh3* > *rps19* > *rps1* > *rps13* > *rps14* > *rps10* > *sdh4* > *rpl5* > *rpl16* > *rps11* > *rps2* > *rps3* > *rps4* > *rps12*. Not included in the taxonomically wide survey at that time was *rpl10,* previously annotated as open reading frames (ORFs) of varying sizes (in different species), which were only recently recognized as encoding ribosomal protein L10 (Kubo and Arimura 2010; Mower and Bonen 2009). The frequent losses of *rpl, rps* and *sdh* gens among flowering plants are reflected in the current sampling of complete angiosperm chondromes and also supported by independent losses in the hornwort and lycophyte lineages (Fig. 8.1b). Also, these genes were frequently lost from algal mitochondrial genomes (Chap. 3) and even from mitochondrial DNAs in eukaryotes at large (V.K., unpublished). Together with the complete mtDNA sequence of the gymnosperm *Cycas taitungensis* (Chaw et al. 2008), the available data now allow us to reasonably hypothesize on the likely mitochondrial gene complement of the last common ancestor of the seed plant stem lineage (Fig. 8.1a).

A more puzzling picture emerges for the three genes involved in cytochrome c maturation – *ccmB, ccmC* and *ccmF* – which are highly conserved among angiosperms and were never found missing from their chondromes in the above-mentioned large-scale survey (Adams et al. 2002b). The *ccmF* reading frame is originally continuous in protists and in the alga *Chara vulgaris,* but disrupted into separate ORFs covering the N- and C-terminal parts (*ccmFN* and *ccmFC*) in land plants. A subsequent second disruption of *ccmFN* (labelled X in Fig. 8.1) has occurred later in evolution in the Brassicaceae. In striking contrast to the survey on angiosperms, the entire suite of *ccm* genes is lost surprisingly often and several times independently from the chondromes of protists (V.K., unpublished), algae (including the Charophyceae *Chaetosphaeridium globosum*), hornworts and lycophytes (Fig. 8.1b). Possibly, alternative "backup" pathways of cytochrome c biogenesis (Allen et al. 2008; Giegé et al. 2008) have been retained in these basal lineages, but not in the seed plants, which could allow for loss of the *ccm* pathway. Perhaps more likely, unrecognized functional adaptations of Ccm protein assembly or interactions in seed plant mitochondria preclude the re-targeting of nuclear-encoded *ccmB, ccmC* and *ccmF* gene products after EGT, similar to the core

RCC subunits that are universally retained in the chondrome.

Altogether, the *rpl, rps* and *sdh* genes and, to a lesser extent the *ccm* genes in more ancient clades, appear to be subject to frequent, independent EGTs, whereas only three deep gene losses – of *rpl14*, *rps8* and *rpl6* – seem to be singular synapomorphies along the backbone of plant phylogeny, together with five losses of tRNA genes (Fig. 8.1b).

It should be noted that the loss of a gene from the mitochondrial compartment does not necessarily imply its functional transfer to the nucleus. Takeover of the homologous chloroplast gene after its transfer into the nuclear genome has occurred for several ribosomal protein genes, including *rps8, rps13* and *rpl10* (Adams et al. 2002a; Kubo and Arimura 2010; Mower and Bonen 2009). Such gene substitutions can also occur in the opposite direction: the chloroplast ribosomal protein S16 is provided by a nuclear gene of mitochondrial origin (Ueda et al. 2008).

B. The tRNA Gene Complement Affected by Loss and Replacement

Contrary to the EGT of protein-coding genes, the loss of tRNA genes from mitochondrial genomes is not accompanied by a corresponding establishment of gene copies in the nuclear genomes, followed by subsequent reimport of the gene product. Instead, tRNA genes lost from mitochondrial genomes are generally replaced by import of their cytosolic counterparts (Duchêne et al. 2009). The import of tRNAs into plant mitochondria has been studied biochemically, mostly using wheat, *Triticum aestivum* (Glover et al. 2001), or potato, *Solanum tuberosum* (Delage et al. 2003), as model systems. For example, tRNA-Gly(UCC) is known to be imported from the cytosol (Brubacher-Kauffmann et al. 1999), obviously to compensate for the loss of the mitochondrial *trnG*(ucc) gene, which may date back to the stem lineage of the HT clade (Fig. 8.1b, node labelled B). In contrast, a mitochondrial *trnG*(gcc) gene encoding the isoacceptor tRNA-Gly(GCC) addressing GGY glycine codons is present in most plants but not in monocots and white campion (*Silene latifolia,* Caryophyllaceae) or the spikemoss *Selaginella moellendorffii*, respectively, which both represent interesting cases of massive tRNA gene loss from plant chondromes (Hecht et al. 2011; Sloan et al. 2010a). These independent losses of *trnG*(gcc) may be facilitated by functional replacement through superwobbling of the (imported) tRNA-Gly(UCC), which can read all GGN glycine codons, as has recently been shown for the tRNA-Gly pair of chloroplasts (Rogalski et al. 2008).

Seed plant evolution, however, has brought about an alternative to mitochondrial tRNA import from the cytosol to compensate for loss of original native mitochondrial tRNAs. Chloroplast tRNA gene copies have been integrated into seed plant chondromes and can complement their original bona fide mitochondrial counterparts. One must assume that such a newly acquired chloroplast tRNA gene co-exists with its native mitochondrial counterpart in an evolutionary transition phase allowing for gradual functional take-over. This indeed appears to be the case for *trnM, trnH* and *trnS(gga)* in the chondrome of the gymnosperm *Cycas taitungensis*. Taken together with data from the other complete mtDNA sequences, this suggests that the gain of these three chloroplast xenologues were the first events of this kind in the seed plant lineage (labelled H>4, M>5, S3>7 in Fig. 8.1). The native mitochondrial *trnH* gene was subsequently lost early in angiosperm evolution, whereas *trnM* has continued to co-exist with its chloroplast homologue in monocots and was lost only later in the eudicot clade (Fig. 8.1b). Similar to *trnH*, the native mitochondrial tRNA genes *trnL*(caa), *trnL*(uag) and *trnR*(ucu) appear to be lost in the angiosperm stem lineage. These three losses, however, are not accompanied by replacement with chloroplast homologues. Finally, two further complete tRNA gene replacements by chloroplast homologues (without the native mitochondrial genes remaining present) have taken place for *trnN* and *trnW* along the (phylogenetically long) branch to extant angiosperms

(labelled N>6, W>8 in Fig. 8.1). It will be interesting to see whether any of the six native mitochondrial genes apparently lost early in angiosperm evolution (*trnH, trnL*(caa), *trnL*(uag), *trnN, trnR* and *trnW*) will show up in the future in the chondrome sequence of a basal angiosperm lineage predating the monocot-eudicot split, such as the *Amborella trichopoda* mtDNA currently being sequenced (J. Palmer, personal communication). Later in angiosperm evolution, the replacement of the original mitochondrial *trnD* gene by its chloroplast homologue appears to be a eudicot-specific event. The *trnC* and *trnF* replacements (labelled C>1, D>2, F>3 in Fig. 8.1b) as well as the unsubstituted loss of *trnG*(gcc) may well turn out to be synapomorphies of the monocot clade.

The case of the *trnC* genes encoding tRNAs for cysteine is particularly interesting in that it may represent a different type of gene replacement in angiosperm chondromes. Initially observed for *Beta vulgaris* (Kubo et al. 2000), a novel *trn*C gene (labelled C>9 in Fig. 8.1) has replaced the native copy in the sugarbeet mtDNA. Interestingly, this gene also co-exists as a second paralogue copy with the original mitochondrial *trnC* gene in *Vigna radiata* and *Citrullus lanatus.* Surprisingly, this novel and sporadically occurring *trnC* is most closely related to bacterial (Chloroflexi) homologues (V.K., unpublished observation). Possibly, this may be a particularly intriguing case of horizontal gene transfer involving a prokaryotic source organism and sporadically affecting distantly related angiosperms, similar to the case of group I intron cox1i726g1 outlined below.

IV. Plant Mitochondrial Intron Stasis and Dynamics

One of the striking outcomes of mitochondrial DNA studies in different land plant clades is the generally high conservation of introns within plant clades (including the liverworts as the presumably most ancient embryophytes), but the strikingly different patterns of intron occurrence in different plant clades. The latter in particular contrasts the much more widely conserved introns in embryophyte chloroplast genomes (see Chap. 5). In the superset of 74 mitochondrial introns now identified in total in bryophyte chondromes, several introns are differentially shared between two of the three bryophyte classes, but not a single one is universally shared between liverworts, mosses and hornworts (Knoop 2010).

A nomenclature has been proposed for naming of organelle introns, which uses the name of the gene in question, the upstream nucleotide position in the continuous reading frame (using the *Marchantia polymorpha* homologue as a reference) and the notation g1/g2 to indicate a group I or group II intron (Dombrovska and Qiu 2004; Knoop 2004), which I will use here to denote intron orthologues.

A. Mitochondrial Intron Conservation Within Plant Clades

Several phylogenetic studies employing wide taxon sampling have shown that plant mitochondrial introns are widely conserved within ancient plant clades, such as introns nad5i753g1 and cox1i624g1 in liverworts and mosses (Beckert et al. 1999; Volkmar and Knoop 2010), nad2i156g2 and cobi420g1 among mosses (Beckert et al. 2001; Wahrmund et al. 2010) or nad4i548 exclusively among liverworts (Volkmar et al. 2011). All of these introns were found nearly universally conserved within the respective bryophyte clades, with only very rare exceptions (atp1i989g2 and atp1i1050g2 in *Treubia lacunosa* and nad5i753 in *Takakia ceratophylla*) indicating secondary losses (Knoop 2010). Evidence for the stability of mitochondrial introns in the early plant clades now also comes from the full chondrome sequence of the liverwort *Pleurozia purpurea* to complement the one of *Marchantia polymorpha* (Wang et al. 2009). Of 32 introns in the *Marchantia* mtDNA (25 group II, 7 group I), all but one are conserved in *Pleurozia,* which only lacks rrnSi1065g2 in the small subunit ribosomal RNA gene. The extraordinary

degree of intron conservation in this ancient plant clade even includes the two introns in *nad7,* which are surprisingly retained in the *nad7* pseudogene present in marchantiid and jungermanniid liverworts (Groth-Malonek et al. 2007b). Intron variability is slightly larger among hornworts, where four of 34 introns are missing in *Megaceros aenigmaticus* compared to *Phaeoceros laevis* (Li et al. 2009; Xue et al. 2010). Similarly, a somewhat higher variability of mitochondrial introns is seen in the two lycophyte mtDNA genomes recently determined (Grewe et al. 2009; Hecht et al. 2011). With 37 introns in total, *Selaginella moellendorffii* has the intron-richest plant chondrome identified so far. Two of its three group I introns and 24 of its 34 group II introns are conserved in *Isoetes engelmannii*. An exhaustive view is currently missing for monilophyte mtDNAs, due to the lack of a complete fern chondrome sequence. However, two introns – atp1i361g2 occurring exclusively in monilophytes and nad5i1242g2 shared only with lycophytes – have been investigated for phylogenetic purposes and independent secondary losses have become apparent in the fern lineage (Vangerow et al. 1999; Wikström and Pryer 2005). I will not elaborate here further on non-seed plant introns, given that the previous chapter (Chap. 7) is also devoted to this issue, but will rather concentrate on spermatophytes in the following.

The *Cycas taitungensis* mtDNA sequence (Chaw et al. 2008), as the first gymnosperm addition to the set of sequenced spermatophyte chondromes, harbours all angiosperm mitochondrial introns hitherto identified as conserved in seed plants at large. Mitochondrial intron conservation between angiosperms and the gymnosperm *Cycas* also includes the five *trans*-arranged group II introns in three *nad* genes (*nad1*, *nad2* and *nad5*) that trace back to cis-spliced ancestors in early plant evolution (Groth-Malonek et al. 2005; Malek et al. 1997; Malek and Knoop 1998). Among the completely sequenced angiosperm chondromes, the full set of 25 mitochondrial introns (Fig. 8.1) is present in the *Vitis vinifera* mtDNA. Other angiosperm mtDNAs show occasional rare secondary losses of introns nad4i976g2, nad7i676g2, rps3i74 (Labels c, f, g in Fig. 8.1) and more frequent independent losses of cox2i373g2 and cox2i691g2 (Labels a, b in Fig. 8.1). Loss of nad4i976g2 has been investigated as a phylogenetic marker in Caryophyllales (Itchoda et al. 2002) and nad1i477g2 has additionally been reported to be lost in the Geraniaceae (Bakker et al. 2000). *Silene latifolia* has the intron-poorest among the fully sequenced angiosperm chondromes, due to lack of three of the above introns and the absence of three ribosomal protein genes (*rpl2, rps3* and *rps10*), which carry conserved introns in angiosperms mtDNAs (Fig. 8.1b).

Taken together, the mitochondrial intron history in seed plants is largely explained by ancient group II intron gains (and their disruptions in five cases; see also below), prior to diversification of seed plants and some later secondary losses. One glaring exception, however, concerns the only known example of a seed plant mitochondrial group I intron, originally identified in the *cox1* gene of *Peperomia polybotrya* (Vaughn et al. 1995). This particular group I intron (cox1i726g1) apparently originates from a fungal donor and seems to have been acquired several times independently in angiosperm evolution as a "rampant invader" of the *cox1* gene (Adams et al. 1998a; Cho et al. 1998; Cho and Palmer 1999; Sanchez-Puerta et al. 2008; Seif et al. 2005). The actual extent of independent primary acquisitions by HGT from fungi or between flowering plants vs. independent later losses of cox1i726g1 has been questioned, however, and needs further investigation (Cusimano et al. 2008); see also Chap. 10 in this volume. Among the fully sequenced plant chondromes, cox1i726g1 is present in the mtDNAs of *Citrullus lanatus* and *Ricinus communis* (Label Z in Fig. 8.1). Interestingly, an endonuclease ORF, otherwise frequently found in mobile group I introns, is only sporadically present in cox1i726g1. In contrast, all three endonuclease reading frames in the *Marchantia polymorpha* chondrome

are embedded in group I introns disrupting the *cox1* gene in other locations (cox1i395g1, cox1i730g1 and cox1i1116g1). Mysteriously, *cox1* in particular seems to be a prime target for group I intron invasion with a total of 11 different group I intron insertion sites identified among charophyceaen algae, bryophytes and lycophytes.

B. Intron Gains and Losses Along the Backbone of Plant Phylogeny

A "gymnosperm-specific" mitochondrial intron, rps3i257g2, was found secondarily lost in some gymnosperms (Ran et al. 2010; Regina et al. 2005; Regina and Quagliariello 2010) but is present in the *rps3* gene of *Cycas taitungensis*. This adds one intron to the set of 25 introns conserved between the gymnosperm and angiosperms (not considering the additional intron cp-trnVi39g2 in the *trnV* gene as part of a promiscuous chloroplast insert in the cycad's mtDNA). Gain of intron rps3i257g2 could alternatively be a synapomorphy of gymnosperms. However, is the intron was recently identified in the mtDNA of the fern *Gleichenia dicarpa* (F. Grewe and V.K, unpublished observation), making its early gain and later secondary loss in the angiosperm clade more likely. Like rps3i257g2, none of the other 25 mitochondrial introns conserved among seed plants is specific for this clade – all 26 spermatophyte mitochondrial group II introns appear to be early evolutionary gains along the backbone of early non-seed plant evolution more than 300 million years ago (indicated by capital letters A, B, C, D in Fig. 8.1). The two spermatophyte introns of the *cox2* gene, for example, can be traced back down to the common ancestor with the mosses (node A in Fig. 8.1). Secondary losses have been found for cox2i691g2 in *Megaceros* and for both *cox2* introns in *Isoetes* (labels a, b in Fig. 8.1). Both *cox2* introns, however, exist in *Selaginella*, where coxi373g2 is uniquely found in a trans-splicing arrangement (Hecht et al. 2011, see below). The origins of intron gains remain somewhat unclear only in those few cases, where the respective gene is entirely lacking from the mtDNA in early clades (*nad7* and *rps3* in the hornworts, *rpl2* in hornworts and lycophytes). Similar to the two *cox2* gene introns, the single maturase-containing (label M in Fig. 8.1a) mitochondrial intron nad1i728 of seed plants traces back to the common ancestor with mosses in the NLE lineage (Qiu et al. 1998); node A in Fig. 8.1b. The three other introns in *nad1* were obviously gained in the earliest tracheophytes (label C in Fig. 8.1), since all of them are shared with *Selaginella moellendorffii* in cis-splicing arrangements (however, with all but the first one secondarily lost in *Isoetes engelmannii*).

C. Maturases and cis-to-trans Conversions in Mitochondrial Introns

Group II intron nad1i728 is not only interesting as the only mitochondrial intron carrying a maturase reading frame (mat-r) that is highly conserved among seed plants, but is also unique under two further aspects. Firstly, intron nad1i728g2 is conserved in mosses, hornworts and the lycophyte *Selaginella moellendorffii* (Dombrovska and Qiu 2004; Hecht et al. 2011), but the (functional) maturase ORF has been lost (several times independently) in all non-seed plant taxa. However, extensive homologies with the mat-r reading frame disrupted by frame shifts are readily detectable in nad7i28g2 of hornworts and two *Takakia* species, probably representing the most basal-branching extant moss genus. Interestingly, mat-r is entirely lost from nad1i728g2 in the *Selaginella moellendorffii* chondrome, where we now found the first example of a bona fide mitochondrial gene, *nad4L,* inserted into nad1i728g2 (Hecht et al. 2011). Notably, other maturases in the mitochondrial genomes of the liverwort *Marchantia polymorpha* (nine maturase ORFs) or the moss *Physcomitrella patens* (two maturase ORFs) are not particularly closely related to mat-r in nad1i728g2 of seed plants. Yet more importantly, no traces of nuclear-encoded maturases are found in the genomes of *Physcomitrella patens* (Rensing et al. 2008) or *Selaginella*

moellendorffii (Banks et al. 2011). In contrast, four maturases are encoded in the *Arabidopsis thaliana* nuclear genome and involved in the splicing of different sets of mitochondrial introns (Keren et al. 2009). Overall, maturases seem to be on the way out in NLE chondrome evolution, but the evolutionary origin of the four nuclear maturases in angiosperms like *Arabidopsis* and the nature of possible alternative proteinaceous splicing factors in *Physcomitrella* or *Selaginella* remains mysterious at present.

Secondly, nad1i728g2 it is the only clearly documented example with multiple, independent transitions from cis- to trans-splicing among flowering plants. The nad7i728g2 intron can get disrupted either 5′ or 3′ of its maturase reading frame and at least ten such independent disruption events have been found for the upstream and at least five for the downstream breakage among angiosperms (Qiu and Palmer 2004). It is certainly tempting to speculate that Mat-r may aid in the transition from cis- to trans-splicing. The numerous independent cis-to-trans conversions of nad1i728g2 contrast the single-event disruptions leading to the five trans-splicing group II introns, which appear to be universally conserved among seed plants. These introns originated early in plant phylogeny (Groth-Malonek et al. 2005; Malek et al. 1997; Malek and Knoop 1998) and all five (nad1i394g2, nad1i669g2, nad2i542g2, nad5i1455g2 and nad5i1477g2) are present as cis-splicing orthologues in *Selaginella moellendorffii* (Hecht et al. 2011) and ferns (our unpublished observations), which suggests their disruption early in the spermatophyte stem lineage. It is interesting to note, however, that four other mitochondrial introns have acquired trans-splicing status in *Selaginella moellendorffii* (atp9i21g2, cobi787g2, cox2i373g2 and cox1i1305g1), including the trans-splicing group I intron previously identified as the first example of its kind in *cox1* of *Isoetes engelmannii* (Grewe et al. 2009). Of these, only cox2i373g2 has been reported as trans-splicing in onion (Kim and Yoon 2010), obviously resulting from an independent cis-to-trans conversion in plant evolution.

Significantly, *Isoetes* has no trans-splicing introns other than cox1i1305g1 and the average cis-splicing intron sizes are five times smaller than in *Selaginella*. Hence, disruption of mitochondrial introns into trans-splicing configurations largely seems to be an (irreversible) chance process, solely dependent on recombination hitting sufficiently large intron sequences at splicing-compatible sites. These two factors (size expansion and recombinational activity) may have increased the chances for evolution of trans-splicing introns in tracheophyte mitochondria, where a total of ten examples (9 group II, 1 group I) are now known. However, examples of trans-splicing group II introns are also known for the mitochondrial *nad3* gene of the alga *Mesostigma viride* (Turmel et al. 2002b), the chloroplast *psaA* gene in *Chlamydomonas reinhardtii* (Choquet et al. 1988), three chloroplast genes (*psaC, petD* and *rbcL*) in the alga *Floydiella terrestris* (Brouard et al. 2010) and notably the chloroplast *rps12* gene, where trans-splicing probably goes back to an ancient gene disruption in the land plant lineage (Hildebrand et al. 1988; Kohchi et al. 1988). Interestingly, trans-splicing group I introns unrelated to the ones in the lycophytes have also been found in the *cox1* genes of the entomoparasitic alga *Helicosporidium sp.* (Pombert and Keeling 2010) and in the primitive metazoan *Trichoplax adhaerens* (Burger et al. 2009).

V. Evolving Structural Complexity in Plant Chondromes

The independent gene losses from chondromes in the plant lineage may suggest that the extent of coding sequences may vary significantly. However, this is actually not the case, mainly because most genes affected by EGT encode rather small proteins and the tRNA genes lost from the chondrome are particularly small. Without introns and with compact intergenic regions, ca. 40 Kbp of

DNA sequence could essentially be sufficient to accommodate the coding regions, even in plant mtDNAs which have not experienced extensive gene losses.

A. Moderate Early Structural Chondrome Evolution in Bryophytes

Early plant mitochondrial genome evolution has largely seen a gain in the size of intergenic regions and a differential gain of introns as discussed above. Comparing the chondromes of mosses, liverworts and hornworts, extensive gene syntenies retaining ancestral gene arrangements are identified (Li et al. 2009; Wang et al. 2009; Xue et al. 2010). The simple circular-mapping genomes of the bryophytes lack co-existing alternative gene arrangements. However, rare recombinational activity has left recognizable traces on evolutionary timescales. The *Pleurozia purpurea* mtDNA (Wang et al. 2009) carries four sequence repeats of sizes between 187 and 660 bp (see Chap. 7). One of these has been studied over a wider liverwort sampling: A large portion of group II intron cobi783g2 was apparently copied into the intergenic region between *nad5* and *nad4* (Groth-Malonek et al. 2007a). A retro-splicing and transposition event is suggested from the precise end of sequence similarity precisely coinciding with the upstream splice site. However, the intron sequence is mysteriously inverted relative to the direction of transcription in the *nad5-nad4-nad2* gene cluster. The molecular evolution of one further chondrome region in liverworts has been studied in detail, the *trnA-trnT-nad7* cluster. Here, an inversion of *trnT* in the intergenic *trnA-nad7* region and independent losses of *trnT* from the chondromes were observed during diversification of the liverworts (Wahrmund et al. 2008). However, such genomic changes seem to be rare exceptions rather than the rule in mitochondrial DNA evolution in the early plant clades such as liverworts and mosses (Yin-Long Qiu, pers. comm. and see previous Chap. 7).

B. Origins of Plant Chondrome Complexity Predate Seed Plant Age

The mtDNA of the liverwort *Marchantia polymorpha* maps as a simple, circular and non-recombining genome (Oda et al. 1992a), thus starkly contrasting the high degree of recombinational activity that was already well documented for flowering plant chondromes at that time (Brennicke et al. 1985; Brennicke and Blanz 1982; Manna and Brennicke 1986; Palmer and Shields 1984; Schuster and Brennicke 1987a; Stern and Palmer 1984). Complex mtDNA structures created through frequent recombination in repeated sequences and thus leading to multipartite chondromes clearly appear to be the rule among flowering plants. Depending on the numbers (and orientation) of recombinationally active repeat sequences, plant mitochondrial genomes range from the simple tripartite structures of spinach (Stern and Palmer 1986) or turnip (Palmer and Shields 1984) to highly complex multipartite ones, as for example characterized in maize, tobacco or wheat (Allen et al. 2007; Lonsdale et al. 1984; Ogihara et al. 2005; Sugiyama et al. 2005). With its two pairs of repeated sequences, the mitochondrial genome of the model angiosperm *Arabidopsis thaliana* as the first completely sequenced flowering plant mtDNA is at the lower end of recombinational complexity (Klein et al. 1994; Unseld et al. 1997). Angiosperm mtDNAs are mostly displayed in the form of a so-called, and often entirely hypothetical, "master-circle" comprising the full chondrome sequence complexity including all repeated sequences in one large circular molecule and potentially giving rise to co-existing subgenomic structures via recombination. In contrast, unicircular non-recombining chondromes such as the one of *Brassica hirta* (Palmer and Herbon 1987) – structurally similar to the ones of *Marchantia* or the charophyceaean green algae – seem to be rare exceptions and secondary re-simplifications of angiosperm chondrome structures.

Significantly complicating the outcome of plant mtDNA recombination, the recombination

event can be followed by shifts in the stoichiometries of the recombination products (Kmiec et al. 2006; Small et al. 1989; Woloszynska 2010). Hence, one product of DNA recombination may become dominant in stoichiometry over another, which may persist at a low level or vanish altogether. Small circular, supercoiled molecules presumably resulting from such processes had been reported very early for several plant taxa (Brennicke and Blanz 1982; Dale 1981; Dale et al. 1983).

Like in *Marchantia*, simple circular genomes of comparable sizes have been identified in all other bryophytes as well (Table 8.1). It should be noted, however, that it remains questionable whether such circular DNA genomes truly exist in vivo or whether other physical forms, such as overlapping linear or branched DNAs, might prevail in mitochondria and possibly even in chloroplasts (Bendich 1993; Bendich 2007; Oldenburg and Bendich 1998, 2001; Yamato et al. 1992).

Completely contrasting the circular mapping chondromes of bryophytes, recombination events in lycophytes are so numerous that creation of a potential "master-circle" encompassing the full chondrome complexity seemed futile. More than 20 specific recombination breakpoints each have been identified in the mtDNAs of *Isoetes engelmannii* and *Selaginella moellendorffii,* which led to creation of network-like maps linking single-copy sequence islands across recombination breakpoints and repeated sequences (Grewe et al. 2009; Hecht et al. 2011). Long sequence repeats of up to more than 7 Kbp in *Selaginella* are strongly reminiscent of the recombinationally active repeated sequences in flowering plant chondromes and suggest the origin of frequent chondrome recombination producing multipartite structures to lie in the tracheophyte stem lineage. A notable feature of the large sequence repeats in *Selaginella moellendorffii* are numerous microsatellite repeat motifs, which vary in copy number between repeat environments (Hecht et al. 2011).

C. Nuclear-Encoded Proteins Determine Plant Chondrome Recombination

Large sequence repeats extending over several Kbp in the flowering plant chondromes obviously mediate reversible homologous recombination events, which predominantly create alternative sequence arrangements co-existing in (near-) equilibrium. Shorter sequence motifs (< ca. 500 bp), in contrast, seem to be the substrates for rare recombination events, which create sequence arrangements that appear sub-stoichiometrically (Arrieta-Montiel and Mackenzie 2011). In extreme cases, such "sublimons" exist at very low amounts that go nearly unnoticed in gel electrophoresis (as "ghost bands"), because they are covered up by the dominating chondrome arrangements. Most important is the observation that such sublimons can experience substoichiometric shifting (Small et al. 1989). Several nuclear-encoded factors have now been recognized that control recombination events in plant mitochondrial genomes, mainly by suppressing recombination on short sequence stretches. The *Arabidopsis thaliana* MSH1 gene (named so as a homologue of the bacterial MutS and earlier described as *chm* for chloroplast mutator), in particular, results in dramatic alterations in mtDNA conformation upon gene inactivation (Abdelnoor et al. 2003; Arrieta-Montiel et al. 2009). Other proteins found to be involved in mtDNA maintenance are OSB1, the "organellar single-stranded DNA-binding protein" and *RecA* homologues targeted to mitochondria. Double knockouts of MSH1 and RECA3 in *Arabidopsis* show particularly significant alterations in the mtDNA and, interestingly, the resulting plants also exhibit significant changes in nuclear transcript profiles and show thermotolerance (Shedge et al. 2007, 2010). In the moss *Physcomitrella patens,* the mitochondrial RECA1 protein likewise seems to suppress rather than promote recombination between short stretches of similar sequences (Odahara et al. 2009). Strangely though, a *RecA*-like DNA recombination activity has been identified

biochemically in soybean mitochondria (Manchekar et al. 2006). Homologues of MSH, OSB and RECA are easily identified in all available genome sequences of the plant lineage and it will be particularly interesting to elucidate their role in taxa such as the lycophytes, which display tremendous amounts of chondrome recombination.

D. When mtDNA Recombination Matters: Mitochondrial Mutants

As outlined earlier, the most dramatic mutant phenotype associated with mitochondrial malfunction in plants is cytoplasmic male sterility (CMS). Pollen biogenesis appears to be the major bottleneck revealing even those mitochondrial defects that do not become apparent in the vegetative phases of plant development. This may well be related to the dramatic reduction in mtDNA amounts during pollen biogenesis that was recently uncovered (Wang et al. 2010). The emergence of CMS phenotypes is accompanied by recombinations in the mitochondrial DNA (and/or their rise to stoichiometrical dominance), which create chimeric reading frames encoding protein products with deleterious effects (Budar and Pelletier 2001; Fujii et al. 2010; Janska et al. 1998; Kubo and Newton 2008). Mitochondrial mutations such as CMS or the non-chromosomal stripe (NCS) mutants of maize will be dealt with in a separate chapter (Chap. 12) of this volume.

E. Foreign Sequences in Plant Chondromes

Nearly 30 years ago, it was first recognized in maize that the two endosymbiotic organelles in the plant cell share common sequences, owing to the fact that chloroplast DNA fragments are integrated into mtDNA (Stern and Lonsdale 1982). Soon afterwards, the term “promiscuous DNA” was coined (Ellis 1982). Since then, numerous reports have documented that such promiscuous chloroplast DNA fragments are transferred quite frequently into flowering plant mitochondrial genomes. For example, a total of more than 68 Kbp of chloroplast DNA sequence inserts are present in the *Vitis vinifera* mtDNA (Goremykin et al. 2009). Likewise, large chloroplast DNA inserts were found in the chondrome of the gymnosperm *Cycas taitungensis* (Wang et al. 2007). Similarly, several sequences clearly originating from the nuclear genome, mostly retrotransposon fragments of different sizes, are frequently identified in seed plant chondromes (Knoop et al. 1996; Schuster and Brennicke 1987b). It should be kept in mind that chloroplast-derived promiscuous sequences are easily recognized but that this is naturally much more difficult for promiscuous DNA originating from the much more variable plant nuclear genome. In fact, large parts of intergenic sequences in plant chondromes may ultimately be recognized as nuclear in origin, once nuclear genome sequences of the respective or closely related taxa become available.

So far, there is no report on promiscuous DNA (i. e., nuclear or chloroplast DNA insertions) in bryophyte chondromes. Recently, however, such insertions of chloroplast and nuclear DNA were identified in the mtDNA of the lycophyte *Isoetes engelmannii* (Grewe et al. 2009), demonstrating that the propensity of plant chondromes to accept promiscuous DNA sequence integrations originated with the tracheophyte lineage. Most of the insertions of foreign DNA into plant chondromes are non-functional. However, as outlined above, seed plants have occasionally made use of chloroplast tRNA genes inserted into their chondromes to complement the sets of cytosol-imported and remaining native mitochondrial tRNAs.

Finally, plant chondromes seem to accept foreign DNA insertions not only from the other two genetic compartments in the same plant cell but also from mitochondria of other species via horizontal gene transfer (HGT). Following the two initial reports on mitochondrial HGT in angiosperms (Bergthorsson et al. 2003) and gymnosperms (Won and Renner 2003), numerous further cases have been identified where certain plant mitochondrial sequences seem to originate from HGT. The identification of horizontal gene

transfer events is complicated by the fact that HGT events do not necessarily affect complete genes but that transfer of gene parts may create gene chimaeras in the target genome (Hao et al. 2010). A separate chapter in this volume (Chap. 10) is specifically dedicated to the issue of horizontal gene transfer. From a phylogenetic perspective, it is interesting to note that one example of HGT into a fern chondrome has been reported (Davis et al. 2005), but so far no cases of HGT into bryophyte chondromes are known.

Similar to integration of promiscuous DNA into plant mitochondrial DNA, the high recombinational activity arising with the earliest tracheophytes may also be a prerequisite for integration of foreign sequences via HGT. The inherent dynamics of plant mitochondria with their propensity for fission and fusion may likewise be an underlying cause for their apparent readiness to acquire foreign DNA (Logan 2010; Scott and Logan 2011). The chloroplast genome of plants, in contrast, seems to be largely immune against insertions of DNA from foreign sources. Possibly, this difference is simply related to the higher structural integrity of the plastids and their unwillingness to participate in membrane fusion events or, alternatively, to the lack of recombination owing to the absence of double-strand DNA break repair mechanisms (Kohl and Bock 2009). However, it should be noted that one report in the literature documents a likely origin of *rpl36* in the ancestor of cryptophyte and haptophyte plastids via HGT (Rice and Palmer 2006).

VI. Evolving RNA Editing

A separate chapter in this volume (Chap. 13) is dedicated to plant organelle RNA editing and I will therefore cover this phenomenon here only very briefly from a phylogenetic perspective. There seems to be no doubt that the cytidine-to-uridine conversion type of RNA editing in chloroplasts and mitochondria originated with land plants. Only one clade of plants, the marchantiid ("complex-thalloiid") liverworts, has apparently secondarily lost RNA editing altogether (Groth-Malonek et al. 2007b). RNA editing frequencies among the other plant clade vary widely, from only nine sites in the mitochondrial transcriptome of the moss *Funaria hygrometrica* (Rüdinger et al. 2011) to more than 2,000 editing events in the lycophyte *Selaginella moellendorffii* (Hecht et al. 2011). Editing frequencies correlate well with the size of a particular subfamily of nuclear-encoded pentatricopeptide repeat (PPR) proteins carrying a terminal extension called "DYW domain", which has remote similarity to deaminases (Rüdinger et al. 2008; Salone et al. 2007). One highly puzzling phenomenon is that the canonical C-to-U editing in the organelles is accompanied by massive amounts of additional "reverse" U-to-C pyrimidine conversions in hornworts (Kugita et al. 2003; Yoshinaga et al. 1996), in the lycophyte *Isoetes engelmannii* (Grewe et al. 2010) and in ferns (Vangerow et al. 1999). Hence, the emergence of the tracheophyte lineage or the hornwort-tracheophyte transition phase of plant evolution also seems to have been accompanied by a major shift in RNA editing biochemistry. This is somewhat similar to the sudden occurrence of massive independent mitochondrial gene losses in hornworts and tracheophytes (due to increased EGT activity) or the emergence of frequent chondrome recombination in the vascular plant stem lineage.

VII. Perspectives

The origins of the oddities in plant mitochondrial genomes seem to coincide with major changes in lifestyle during land plant evolution. Early plant evolution under a bryophyte-type of developmental organization was characterized by a dominating haploid gametophyte stage and a fully gametophyte-dependent diploid sporophyte phase. This bryophyte lifestyle correlates with retention of an ancestral, circular and largely non-recombining structure of the mtDNA, similar to the mtDNAs in green algae of the Charophyceae, which are most closely related to the plant

lineage. The transition from algal to land plant life came with a moderate expansion of intergenic regions but, most notably, with a dramatic gain and loss of introns. Among 74 introns now identified in bryophyte mitochondrial genes, not a single one is conserved across all three bryophyte classes (liverworts, mosses and hornworts) an observation that implies numerous gains and losses in early plant genealogy. Strikingly, once established in evolution, the mitochondrial introns remain surprisingly stable within the three bryophyte clades again suggesting that cladogenic events (but not diversification within the clades) trigger larger events of molecular evolution in plant mitochondria. It is tempting to speculate on the biological sources for the differential intron gains in early plant mitochondrial evolution. Symbiotic, mycorrhiza-like interactions of bryophytes with endophytic fungi are now increasingly well characterized (Jakucs et al. 2003; Kottke et al. 2003; Kottke and Nebel 2005; e.g. Read et al. 2000; Russell and Bulman 2005). Varying intimate contacts between fungi and bryophyte ancestors early after the conquest of land habitats by plants may have played a role in HGT of mitochondrial introns via retro-splicing and may at the same time explain why the mitochondrial, but not the chloroplast, genomes are affected by such differential intron invasions.

The mitochondrial intron dynamics surprisingly contrasts the overall conservative evolution of the bryophyte chondromes with extensive gene syntenies being retained between liverworts and mosses and, to a large extent, also in hornworts. The latter clade is now assumed to be the sister group to tracheophytes. One feature which sets hornwort chondromes apart from the other bryophytes is the sudden increase in endosymbiotic gene transfer activity, which results in numerous tRNA, ribosomal protein, succinate dehydrogenase and cytochrome c maturation genes lacking from their mtDNAs. What is very surprising though is that frequent EGT affecting the same types of genes has obviously independently and in parallel occurred in the lycophytes. Hence, the bryophyte-tracheophyte transition seems to coincide with a massive increase in EGT, making it all the more striking that the above genes have survived in the chondrome along the stem lineage leading to modern euphyllophytes.

The conserved circular mtDNAs of the hornworts couldn't be more contrasted than by the heavily recombining and rearranging mtDNAs of the lycophytes. Possibly, the dominating diploid sporophytic phase of emerging tracheophytes is causally connected to this difference, in that nuclear genetic control of mtDNA structure is somehow relaxed or disturbed when two alleles of relevant nuclear factors coexist for a longer time in development. However, it must be kept in mind that the two hitherto investigated lycophyte taxa with heavily recombining mtDNAs, *Isoetes* and *Selaginella*, are heterosporous. Rather than an enduring diploid phase, it may thus actually have been the emerging sexuality (giving rise to different gametes and gametophytes), which could be the key to the emergence of heavily recombining mitochondrial DNAs. The mitochondrial genome of a first isosporous lycophyte (*Huperzia*, Yin-Long Qiu, pers. comm. and see previous chapter) and the comparisons of hetero- and isosporous monilophyte mtDNAs will clearly shed more light on these considerations in the future.

The predisposition to acquire foreign DNA seems to fully coincide with the gain of recombinational activity in early vascular plant mtDNAs. No nuclear or chloroplast DNA inserts have hitherto been identified in bryophyte mtDNAs, but both types of promiscuous DNA were found in the *Isoetes engelmannii* chondrome. As yet, we do not have a complete chondrome sequence available for a monilophyte, the sister clade of seed plants. Our own preliminary data (Felix Grewe and V.K., unpublished) for the fern *Gleichenia dicarpa* hint to extraordinary mtDNA recombination even exceeding what has previously been found in lycophytes. In addition, the massive insertion of nuclear retrotransposon sequences and other mobile DNAs has occurred, while intron insertion patterns are very seed plant-like. Hence, the

origin of euphyllophytes seems to come with an emerging stasis in mitochondrial intron distributions, which continues in the two sister clades monilophytes and seed plants. It is very fortunate that the changes in chondrome make-up along plant phylogeny can soon be correlated with nuclear genome information for all those important taxonomic groups, where full genome information is currently still lacking, such as liverworts, hornworts and monilophytes.

Overall, we now have a clear view of the likely state of the ancestral seed plant chondrome, at least with respect to its gene and intron composition. The diversity among seed plant chondromes – as it keeps being unearthed by mitochondrial genomics efforts – will mainly be attributable to a combination of five factors: (1) the amount of endosymbiotic gene transfer, (2) the integration of promiscuous DNA sequences originating from the chloroplast and nucleus, (3) the amount of horizontal gene transfer integrating sequences from mtDNAs of other species, (4) the amount of recombinational activity and (5) the acceleration or deceleration of evolutionary rates. However, given that plant mitochondria have often proven to be "more unique than ever" (Rasmusson et al. 2008), some exciting surprises may still wait for us further down the road.

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