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Review

Mitochondria in parasitic plants

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ABSTRACT

Plant mitochondrial genomes are renowned for their structural complexity, extreme variation in size and mutation rates, and ability to incorporate foreign DNA. Parasitic flowering plants are no exception, and the close association between parasite and host may even enhance the likelihood of horizontal gene transfer (HGT) between them. Recent studies on mistletoes (*Viscum*) have revealed that these parasites have lost an exceptional number of mitochondrial genes, including all complex I genes of the respiratory chain. At the same time, an altered respiratory pathway has been demonstrated. Here we review the current understanding of mitochondrial evolution in parasitic plants with a special emphasis on HGT to and from parasite mitochondrial genomes, as well as the uniquely altered mitochondria in *Viscum* and related plants.

1. Introduction

Plant mitochondria are involved in a variety of key cellular processes such as programmed cell death, stress response and anti-microbial defense, but their primary function is to generate ATP by oxidative phosphorylation and produce metabolic intermediates for various cellular processes. Thus, these organelles house key metabolic pathways such as the mitochondrial tricarboxylic acid (TCA) cycle, the mitochondrial electron transport chain (ETC) and the Fe-S cluster biogenesis machinery (Millar et al., 2011; Rao et al., 2017). A number of ETC proteins are encoded by genes located in the mitochondrial genome (mitogenome), and these genes have been considered essential to mitochondrial function (e.g. Adams and Palmer, 2003). Recent work in a group of parasitic plants has begun to challenge this long-held view and to suggest that these genes may be dispensable in plants as they have been shown to be in unicellular eukaryotes such as bakers's yeast, *Saccharomyces cerevisiae* (Maclean et al., 2018; Petersen et al., 2015a; Senkler et al., 2018; Skippington et al., 2015).

Compared to most other eukaryotes, the mitogenomes of plants and flowering plants (angiosperms) in particular are remarkably divergent in terms of size, structure, mutation rate, RNA editing, and ability to incorporate foreign DNA. These features have been described and reviewed in a number of papers (Gualberto and Newton, 2017; Johnston, 2019; Knoop, 2012; Kozik et al., 2019; Mower et al., 2012a,b; Sloan, 2015; Yurina and Odintsova, 2016), and in the present volume an updated review focusing on gene and intron divergence among angiosperms can be found (Mower, this issue). Our understanding of plant mitochondrial evolution is limited by existing sequence data, with the number of complete mitogenomes for angiosperms far lower than the number of complete plastid genomes (plastomes) (142 species with complete mitogenomes versus 4445 species with complete plastomes, NCBI 18 NOV 2019). The main reason for the lack of complete mitogenome data is the structural diversity of the mitogenome. Although many angiosperm mitogenomes are visualized as one circular chromosome – the "master chromosome" (Palmer and Shields, 1984) or "master circle" (Lonsdale et al., 1984) – increasing evidence suggests that plant DNA primarily exists *in vivo* as a dynamic, recombining collection of circular and non-circular (linear, branched) forms (see e.g., Gualberto and Newton, 2017; Kozik et al., 2019). While there is extensive diversity in intergenic regions within plant mitochondria, the overall gene complement appears to be largely conserved both in content and amount of sequence divergence.

Given the fundamental nature of mitochondrial function and the essential role of the mitochondrial genes, a parasitic lifestyle (altered source of carbon, nitrogen and other nutrients) might not be expected to influence mitogenome evolution substantially. Accordingly, parasitic plants examined to date do not appear to differ substantially from other plants in their mitogenome gene content, aside from a possibly higher frequency of putatively horizontally transferred genes. However, recent findings of highly divergent mitogenomes and strongly altered

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respiratory function in mistletoes (*Viscum*) (Maclean et al., 2018; Petersen et al., 2015a; Senkler et al., 2018; Skippington et al., 2015) have led to increased interest in mitochondrial evolution in parasitic plants.

Parasitism has evolved in almost all major groups of plants (e.g. rhodophytes, chlorophytes, bryophytes, lycophytes, monilophytes, gymnosperms, angiosperms) (see e.g. Figueroa-Martinez et al., 2015; Merckx and Freudenstein, 2010; Preuss et al., 2017; Westwood et al., 2010 and references therein), but in the present review we will focus on aspects of mitochondrial evolution in parasitic angiosperms. Parasitic angiosperms take up nutrients and water from their host, and they have adopted at least a partially heterotrophic lifestyle. These plants are typically classified by whether they require a host to complete their life cycle (obligate parasites) or not (facultative parasites), and by whether they have some photosynthetic activity (hemiparasites) or have lost it completely (holoparasites). The term parasitic angiosperm is mostly applied to those parasites having another plant as the direct host, whereas those feeding on a fungal host are referred to as mycoheterotrophs. While many plants have fungal associations that are important for obtaining water and inorganic nutrients (in exchange for the plant's carbon), mycoheterotrophs have reversed the direction of carbon flow and may indirectly obtain carbon from another plant via the fungus.

The evolution of parasitism and mycoheterotrophy has occurred repeatedly among angiosperms (see Table 1). With the inclusion of the family Balanophoraceae in the order Santalales, the number of parallel evolutionary events leading to parasitism is at least 12 (Barkman et al., 2007; Su et al., 2015; Westwood et al., 2010). Within the 12 parasitic lineages of angiosperms, holoparasitism has evolved at least 10 times. While the majority of the parasites are eudicots (the rest being magnoliids), full mycoheterotrophy (i.e. with a complete lack of photosynthesis) is most common among monocots, having evolved within at least seven monocot families including orchids, but in only three eudicot families (Graham et al., 2017; Merckx and Freudenstein, 2010; Westwood et al., 2010). The exact number of times that mycoheterotrophy has evolved is unclear since the trophic status for many mycorrhizal partnerships has not been determined. Thus, full mycoheterotrophy is thought to have evolved independently more than 50 times (Graham et al., 2017; Merckx and Freudenstein, 2010), but many of the events may have occurred within clades already being partially mycoheterotrophic. Generally, the recurrent development of parasitism and mycoheterotrophy provides an excellent framework for comparative evolutionary studies.

The close association between parasitic plants and their hosts, either via a haustorial structure or as endoparasites within host tissue, makes them excellent candidates for studying horizontal gene transfer (HGT). Mitochondria are potentially well suited to incorporating foreign DNA into their genomes due to an active DNA uptake system (Koulintchenko et al., 2003) and their propensity to fuse and split and recombine their genomes (Arimura et al., 2004; Logan, 2006). The phenomenon of HGT between plants, first detected in mitochondria (Bergthorsson et al., 2003), has been a research focus for the past 15 years and a subject of reviews spanning angiosperms (Bock, 2010; Mower et al., 2012a; Renner and Bellot, 2012; Richardson and Palmer, 2007; Sanchez-Puerta, 2014; Wickell and Li, 2020) and focusing on parasites in particular (Davis and Xi, 2015). While the increasing amount of data from nuclear genomes has broadened our appreciation of HGT in parasitic plants, the mitogenome is still largely unexplored for what is likely a prevalent process. Newer studies are hinting at both the incorporation of massive amounts of host sequence into parasite mitogenomes, as well as a surprising absence of transfers, so that the expected occurrence of HGT in parasitic genomes remains unclear.

Here we briefly summarize the current data available and evidence for mitochondrial evolution in parasitic and mycoheterotrophic angiosperms, and then focus on two aspects of parasite mitochondria that appear to differ from most other plants, namely elevated HGT and the curious case of an altered mode of respiration in *Viscum*.

2. Parasitic mitogenomes

There are remarkably few completely sequenced and assembled mitogenomes from parasitic and mycoheterotrophic plants (Table 1). The first published mitogenome for a parasitic plant was the small and very divergent mitogenome of *Viscum scurruloideum* (Skippington et al., 2015), followed soon after by the mitogenome of *V. album* (Petersen et al., 2015a). Remarkably, both species lack *nad* genes encoding complex I subunits of the electron transport chain (see Section 4) and most of their remaining mitochondrial genes appear highly divergent compared to homologous genes in other angiosperms (Petersen et al., 2015a; Skippington et al., 2015, 2017).

Although the differences in size and structure of the mitogenomes in Table 1 may appear vast, the diversity is consistent with known flowering plant mitogenome diversity (Mower et al., 2012a), which include sizes up to 11.3 Mb and chromosome numbers exceeding one hundred (Sloan et al., 2012).

Data from the few complete mitogenomes suggests no evolutionary correlation between the type of parasitic lifestyle and mitogenome size and structure. Although this may be expected, it should be emphasized that mitogenome structure is particularly problematic to determine, and the data listed here are results of individual researchers' preferred methods of assembly and visualization. Given that plant mitochondrial DNA primarily exists *in vivo* as a dynamic collection of non-circular (linear, branched) forms and that these configurations are shaped by recombination between/across repeated sequences (see, e.g. Johnston, 2019; Kozik et al., 2019), both chromosome numbers and genome sizes should be considered approximations.

In addition to the complete mitogenomes, larger but partial mitogenome assemblies have been produced for a few parasite species, and for additional species more or less complete gene surveys (protein coding genes and ribosomal RNA genes) have been reported (Table 1). However, the availability of the gene data varies considerably: the raw data may or may not be publicly available, and the genes reported may or may not be available either. Nevertheless, from the twelve evolutionary lineages of parasitic plants, nine now have at least some gene complement data, whereas only three mycoheterotrophic lineages have data, but from complete mitogenomes. Raw sequence data is accumulating as part of genome assembly projects and genome skimming, which provide opportunities to assemble partial or entire mitogenomes. For parasites, recent genomic work includes genomes of two *Cuscuta* species (Sun et al., 2018; Vogel et al., 2018), *Santalum* (Santalaceae) (Mahesh et al., 2018) and *Striga* (Orobanchaceae) (Yoshida et al., 2019).

Gene content in both parasites and mycoheterotrophs appears to be generally conserved compared to other angiosperms, consistent with the unremarkable variation in size and structure. The exception to this pattern is the gene content of *Viscum* and *Phoradendron*, both members of Viscaceae, a family that also seems to have unusually high sequence divergence in the mitochondrial genes that are still present. While it seems that gene content is largely conserved across parasites, the origin of some of those genes or the presence of extra copies appears to be due to HGT, which appears to be enhanced by parasitism (see Section 3).

3. Parasitic plants and HGT

While HGT has been defined to include movement of genetic material between genomic compartments such as the nucleus and mitochondrion (e.g. Mower et al., 2012a), here we define HGT in plants to be the movement of genetic material between species by a means other than sexual reproduction (i.e. the fusion of gametes of close relatives). In a parasitic context, this exchange could arise as a result of cell-to-cell contact or the uptake of DNA from lysed cells or vascular fluid as in, e.g., grafting experiments (Stegemann and Bock, 2009; Stegemann et al., 2012). The persistence of any incorporated DNA then depends on its eventually entering a meristem and the subsequent production of

Table 1
List of lineages of parasitic and mycoheterotrophic angiosperms and species with published mitogenome data.

Lineage (parasitic species[1])	Species with data[2]	Parasite type[3]	Mt data[4]	Mitogenome size (bp) [chromosomes]	Reference
Parasites					
Santalales (> 2300)	*Viscum scurruloideum*	hemi	complete	65,873 [1 circular, 1 linear]	(Skippington et al., 2015)
	Viscum album	hemi	complete	565,432 [1 linear]	(Petersen et al., 2015a,b)
	Viscum minimum	hemi	genes		(Petersen et al., 2015a,b)
	Viscum crassulae	hemi	genes		(Petersen et al., 2015a,b)
	Phoradendron liga	hemi	genes		(Zervas et al., 2019)
	Lophophytum mirabile	holo	complete	821,919 [54 circular]	(Sanchez-Puerta et al., 2017)
	Langsdorffia hypogaea	holo	genes		(Zervas et al., 2019)
	Loranthus europaeus	hemi	genes		(Zervas et al., 2019)
	Osyris alba	hemi	genes		(Zervas et al., 2019)
Orobanchaceae (> 1900)	*Castilleja paramensis*	hemi	complete	495,499 [1 circular]	(Fan et al., 2016)
	Bartsia pedicularoides	hemi	partial	> 414,794	(Fan et al., 2016)
	Schwalbea americana	hemi	genes		(Fan et al., 2016)
	Orobanche crenata	holo	genes		(Fan et al., 2016)
	Orobanche gracilis	holo	genes		(Fan et al., 2016)
	Phelipanche ramosa	holo	genes		(Fan et al., 2016)
	Lathraea squamaria	holo	genes		(Zervas et al., 2019)
	Lathraea clandestina	holo	genes		(Zervas et al., 2019)
Cuscuta (> 200)	*Cuscuta gronovii*	holo	partial	> 212,123	(Park et al., 2015)
Rafflesiaceae (37)	*Rafflesia lagascae*	holo	partial	> 320,255	(Molina et al., 2014)
	Rafflesia cantleyi	holo	genes		(Xi et al., 2013)
	Rafflesia tuan-mudae	holo	genes		(Xi et al., 2013)
	Sapria himalayana	holo	genes		(Xi et al., 2013)
Krameria (23)	*Krameria lanceolata*	hemi	genes		(Zervas et al., 2019)
Cassytha (19)	*Cassytha pubescens*	hemi	genes		(Zervas et al., 2019)
Cytinaceae (12)	*Cytinus hypocistis*	holo	genes		(Zervas et al., 2019)
Hydnoraceae (10)		holo			
Apodanthaceae (10)		holo			
Lennoaceae (4)	*Pholisma sonorae*	holo	genes		(Zervas et al., 2019)
Mitrastemon (2)		holo			
Cynomorium (1)	*Cynomorium coccineum*	holo	complete	1,106,389 [49 circular]	(Bellot et al., 2016)
Mycoheterotrophs					
Orchidaceae[5] (220)	*Gastrodia elata*	myco	complete	1,340,105 [12 circular, 7 linear]	(Yuan et al., 2018)
Thismiaceae (60)		myco			
Burmanniaceae (56)		myco			
Triuridaceae (45)		myco			
Corsiaceae (27)		myco			
Gentianaceae[5] (25)		myco			
Ericaceae[5] (16)	*Monotropa hypopitys*	myco	complete	801,116 [1 circular, 1 linear]	(Shtratnikova et al., 2019)
Epirixanthes (7)	*Epirixanthes elongata*	myco	complete	365,168 [1 circular]	(Petersen et al., 2019)
Petrosavia (2)		myco			
Geosiris (1)		myco			

[1] Species numbers from Nickrent: The Parasitic Plant Connection (https://parasiticplants.siu.edu/) and (Merckx and Freudenstein, 2010).
[2] The list does not include species with a few genes sequenced e.g. in phylogenetic analyses.
[3] Hemi = hemiparasite, holo = holoparasite, myco = mycoheterotroph (full).
[4] Data is categorized as complete for completely sequenced mitogenomes, partial when larger contigs were assembled, and genes when the gene complement (at least protein coding genes) is reported.
[5] In Orchidaceae, Gentianaceae and Ericaceae mycoheterotrophy has evolved more than once.

reproductive structures (flowers). While this is often the assumed route for HGT involving parasitic plants, other mechanisms of HGT may also be invoked to explain the presence of foreign DNA, such as illegitimate pollination (probably more likely when plants are more closely related) or epiphytic interactions (Rice et al., 2013; Richardson and Palmer, 2007).

Inferences of HGT are typically through phylogenetic analysis, where the supposed foreign DNA sequences are statistically supported as grouping with a different group of organisms than the known close relatives of the sample, though this is not without difficulties surrounding phylogenetic analysis and other mechanisms causing incongruencies in trees (Andersson, 2005; Richards et al., 2003; Smith et al., 1992). Given that our ability to detect HGT relies on differences between sequences, HGT is more easily detected when host and recipient are more distantly related, and probably overlooked when they are closely related (Richardson and Palmer, 2007). This is especially true for HGT events involving plant mitochondrial genes, where highly conserved sequences can limit the number of characters available to confidently determine where putatively foreign DNA may have come from, or if it is indeed foreign (Richardson and Palmer, 2007). Since parasites often live in close association with (i.e. parasitize) distantly related plants and probably have more opportunities for exchange than autotrophic plants, we might expect to more easily detect HGT between parasites and their hosts.

The early indications of HGT between multicellular plants were detected in mitochondria, with the strange phylogenetic distribution of *cox1* introns (Cho et al., 1998) and then three mitochondrial genes inferred to have been transferred between angiosperms (Bergthorsson et al., 2003) and one from angiosperms to *Gnetum* (Won and Renner, 2003). Perhaps it is not surprising that the first indications of HGT were found in mitochondria given the greater sequence availability at that time compared to the nuclear genome, but what stands out is that even though plastomes have many more sequences available than mitogenomes, there is almost no indication of HGT between plastomes (Sanchez-Puerta, 2014). This difference is partly attributed to the propensity for mitochondrial fusion (Arimura et al., 2004) and active DNA uptake (Koulintchenko et al., 2003), and could be related to gene order and the length and content of intergenic regions in plant mitochondria, which are so dynamic (Mower et al., 2012b; Sanchez-Puerta, 2014). Foreign DNA is probably more likely to be incorporated and retained if

Table 2
Inferred horizontal gene transfers in parasitic plants.

Lineage	Parasite	Transfer[1]	Partner[2]	References
Santalales	?	mito? – > mito?	*Botrychium* (fern)	(Davis et al., 2005)
	?	cp/mito? – > mito	*Amborella*	(Rice et al., 2013)
	Viscum album	mito < – mito?	Ericales? Santalales?	(Skippington et al., 2017)
	Lophophytum mirabile	mito < – mito	Fabaceae	(Choi et al., 2019; Kovar et al., 2018; Sanchez-Puerta et al., 2017, 2019)
Orobanchaceae	*Bartsia* (?)	mito? – > mito?	*Plantago*	(Mower et al., 2004)
	Phelipanche	mito? < – cp/mito?	*Orobanche*	(Park et al., 2007)
	Cistanche deserticola	mito? < – cp/mito?	*Haloxylon ammodendron*	(Li et al., 2013)
	Bartsia (?)	mito? – > mito	*Geranium*	(Park et al., 2015)
	Orobanche coerulescens	mito? < – mito?	Asteraceae	(Kwolek et al., 2017)
	Aphyllon epigalium	mito < – cp/mito?	*Galium*	(Schneider et al., 2018)
	?	mito – > mito	*Physochlaina orientalis*	(Gandini et al., 2019)
	Striga hermonthica	nuc < – nuc	Poaceae	(Yoshida et al., 2010)
	Phelipanche	nuc < – nuc	Fabaceae	(Zhang et al., 2013)
	Orobanche aegyptiaca	nuc < – nuc	Brassicaceae	(Zhang et al., 2014)
	Phelipanche, *Orobanche*	nuc < – nuc	Brassicaceae	(Sun et al., 2016)
	Phelipanche aegyptiaca, *Striga hermonthica*, *Triphysaria versicolor*	nuc < – nuc	(multiple angiosperms)	(Yang et al., 2016)
	Orobanche minor, *Aeginetia indica*	nuc < – nuc	Fabaceae, Poaceae	(Kado and Innan, 2018)
	Striga asiatica	nuc < – nuc	Poaceae	(Yoshida et al., 2019)
Cuscuta	*C.* sp.	mito – > mito	*Plantago*	(Mower et al., 2010, 2004)
	C. gronovii	mito – > mito	*Geranium*	(Park et al., 2015)
	C. pentagona, *C. suaveolens*	nuc? < – nuc?	?	(Jiang et al., 2013)
	C. pentagona	nuc < – nuc	Fabaceae	(Zhang et al., 2013)
	C. australis	nuc < – nuc	Brassicaceae	(Zhang et al., 2014)
	C. campestris	nuc < – nuc	(multiple orders)	(Vogel et al., 2018; Yang et al., 2019)
Rafflesiaceae	*Rafflesia*, *Sapria*	mito? < – mito?	*Tetrastigma*	(Davis and Wurdack, 2004)
	Rafflesia pricei, *Rhizanthes lowii*	mito < – mito?	*Tetrastigma diepenhorstii*	(Barkman et al., 2007)
	Rafflesia cantleyi, *R. tuan-mudae*, *Sapria himalayana*	mito < – mito	Vitaceae	(Xi et al., 2013)
	Rafflesia cantleyi	nuc/mito < – nuc/mito	*Tetrastigma rafflesiae*	(Xi et al., 2012)
	Rafflesia lagascae	nuc/mito < – cp/nuc/mito?	Vitaceae, others	(Molina et al., 2014)
Apodanthaceae	*Apodanthes casearia*e, *Pilostyles thurberi*	mito? < – mito?	Ericales, Fabales	(Nickrent et al., 2004)
	Pilostyles thurberi	mito? < – mito?	Fabaceae	(Barkman et al., 2007)
Mitrastemon	*M. yamamotoi*	mito? < – mito?	Fagaceae	(Barkman et al., 2007)
Cynomorium	*C. coccineum*	mito? < – mito?	Sapindales (?)	(Barkman et al., 2007)
	C. coccineum	mito/nuc < – mito?	Sapindales, Caryophyllales	(Bellot et al., 2016; Cusimano and Renner, 2019)
Orchidaceae	Orchidaceae, Epidendroideae	mito < – mito?	fungus (Ustilaginales?)	(Sinn and Barrett, 2019)

[1] Source genome, direction of transfer and destination genome (mito = mitogenome, nuc = nuclear genome, cp = plastome). Question marks indicate uncertainty or lack of evidence for genomic location, e.g. when a mitochondrial gene is transferred, but may actually be present in the recipient's nucleus.
[2] Partner here may or may not be a host. While it is likely that HGT involving parasitic plants occurs via the parasitic interaction, it is possible that it also occurs by another mechanism (e.g. illegitimate pollination, wounding, epiphytic interactions, etc.).

there is little restriction on genome and intergenic spacer sizes (e.g. Marienfeld et al., 1999). Indeed, more recent work suggests a correlation between genome size and the amount of putatively foreign DNA (Gandini and Sanchez-Puerta, 2017).

It soon became evident that parasitic plants were likely candidates for these HGT events, with inferred transfers of mitochondrial genes from parasites to hosts (Mower et al., 2004) and hosts to parasites (Davis and Wurdack, 2004; Nickrent et al., 2004). Over the last 15 years, examples of HGT involving parasitic angiosperms have continued to accumulate (Table 2). Recent studies are revealing extensive transfers into parasite nuclear genomes, sometimes putatively functional, which were harder to detect prior to the increase in accessible sequence data. So far, it is unclear whether there are HGT events from parasite nuclear genomes into their hosts, with the only evidence for transfers in that direction coming from mitochondrial genes. Of the putative twelve lineages in which plant parasitism has evolved in angiosperms, seven have been shown to be involved in some kind of HGT (see Table 2). The remaining five lineages (*Krameria*, *Cassytha*, Cytinaceae, Hydnoraceae and Lennoaceae) have either not been investigated for HGT or are lacking evidence. The extent of HGT within parasitic angiosperm mitochondria remains largely unexplored, with some of the larger lineages (e.g. Santalales) having only a few assembled mitogenomes, and most of the others without any (see Table 1).

For mycoheterotrophs, there is almost no indication of HGT so far, though this may be associated with possible barriers between angiosperms and fungi that might explain the lack of detected HGT (Richards et al., 2009). There are only a few putative transfers between fungi and angiosperms, such as the previously mentioned *cox1* intron (Vaughn et al., 1995) and some mitochondrial plasmids (Handa, 2008; Warren et al., 2016). A recent discovery of two putative mitochondrial HGT events between fungi and orchids suggested the transfers occurred into the ancestors of those plants (Sinn and Barrett, 2019). Since orchids are dependent on fungi for at least a part of their lifecycle and should have ample opportunity for exchange through their evolution, the finding of evidence for only a few events suggests that genetic exchanges between plants and fungi are rarely successfully retained in plant mitochondria. It seems unlikely that mycoheterotrophs will show elevated rates of plant-plant HGT, given HGT would likely require two plant-fungal HGT events. If a plant-fungal interaction is an effective corridor for HGT, we might also expect HGT between land plants that rely on mycorrhizal partners, and not just those that rely on fungi for a carbon source.

While parasites have been shown to exchange RNA with their hosts across the haustorial connection (e.g. Kim et al., 2014), the majority of putative HGT events in angiosperms appear to be via pieces of DNA, based on the presence of introns, lack of RNA editing and the size of pieces with syntenic genes that are incorporated (Dunning et al., 2019;

Kado and Innan, 2018; Mower et al., 2010; Yang et al., 2016, 2019; Zhang et al., 2014; Zhang et al., 2013). One of the hypotheses for how DNA could be incorporated into mitochondria is that of mitochondrial fusion, whereby entire mitochondrial chromosomes recombine with recipient mitochondrial DNA (Bock, 2010; Rice et al., 2013). Evidence for this mechanism includes the bizarre case of the *Amborella* mitogenome, where almost two full moss mitogenomes have been differentially incorporated along with large amounts of green algal and flowering plant sequences (Bergthorsson et al., 2004; Rice et al., 2013; Taylor et al., 2015). For parasites, an outstanding example is that of *Lophophytum*, where approximately 80% of the genes and 60% of the mitogenome sequence is thought to have been incorporated from its host (Sanchez-Puerta et al., 2017, 2019). This mechanism does not appear to explain other cases, however, where apparently only a few genes are inferred to have been transferred, such as in *Viscum* (Skippington et al., 2017). How prevalent the mitochondrial fusion mechanism is across parasite mitochondria remains to be explored as more genomes are assembled.

Based on the limited survey of parasite sequences to date, it is difficult to detect a consistent association between the amount of HGT and the form of parasitism. Looking at holoparasites vs. hemiparasites, it appears that the only examples of large-scale incorporation of foreign genes/sequences into mitochondria are from holoparasites such as *Rafflesia* (Xi et al., 2013) and *Lophophytum* (Sanchez-Puerta et al., 2017), and not in hemiparasites investigated to date. The amount of HGT across holoparasites is not consistent though, with intermediate levels of HGT found in *Cynomorium* (Bellot et al., 2016; Cusimano and Renner, 2019) and apparently lower levels in Apodanthaceae (Nickrent et al., 2004) and Orobanchaceae (Kwolek et al., 2017; Schneider et al., 2018). The few hemiparasites for which mitochondrial data has been examined show little to no evidence of HGT events in their mitochondria, e.g. *Viscum* (Skippington et al., 2017). In the case of a better-studied stem parasite, *Cuscuta*, there is evidence for substantial nuclear HGT with functional significance (Yang et al., 2019) and mitochondrial genes transferred to other plants (Mower et al., 2010; Park et al., 2015), but apparently no clear HGT events into the mitogenome (B. Anderson, K. Krause, G. Petersen, unpublished). Other aspects of parasite biology may be important in understanding how likely they are to be involved in HGT, such as whether they live inside their hosts (e.g. *Rafflesia*) or primarily interact via haustorial connections (e.g. *Cuscuta*). The relative dependence of the parasite on its host from germination through the development of a connection, the extent of cellular interaction during that process, and which plant organs are involved could also affect how much opportunity there is for genetic exchange and how likely that exchange is to be incorporated in reproductive material. A survey of four species in the Orobanchaceae showed that frequency of HGT increased with relative dependence on the host, possibly explained by both earlier contact and the type of haustorial connection (phloem or not) in more dependent parasites (Yang et al., 2016). More surveys of the prevalence of mitochondrial HGT across different types of parasitism may help to clarify whether there is any correlation between the type of parasitism and the amount of detected HGT.

So far, most detected mitochondrial transfers into parasites typically result in pseudogenization of the extra foreign genes or more rarely replacement of recipient mitochondrial genes (Mower et al., 2012a). A particularly striking exception to the typical pseudogenization of foreign gene copies is the previously mentioned case of *Lophophytum*, where 26 genes have likely been replaced by host-derived copies (Sanchez-Puerta et al., 2017). Two other potential scenarios are 1) the reintroduction of mitochondrial genes that had been lost from the recipient (e.g. to the nucleus), termed recapture HGT; and 2) coexistence and gene conversion with the recipient's copy, or chimeric HGT (Bergthorsson et al., 2003; Sanchez-Puerta, 2014). Examples of these two scenarios involving parasitic plants include the recapture of *rps4* and *rps14* into *Geranium* species from *Cuscuta* (Park et al., 2015), and gene conversion between recipient (*Plantago*) and donor (*Cuscuta*) *atp1* copies (Mower et al., 2010). The conversion scenario in particular has been suggested as a mechanism for generating mitochondrial diversity (Hao et al., 2010; Mower et al., 2010), although examples such as *atp1* in *Ternstroemia* indicate few amino acid changes as a result of chimerism (Hao et al., 2010). Given the conserved nature and function of plant mitochondrial genes (Mower et al., 2012a), it may be that transfers of similarly conserved genes, even following conversion or replacement, will have limited impact on the biology of the organism, but this remains unclear. In contrast, nuclear transfers have been shown to likely be functional and potentially adaptive for parasites (e.g. Yang et al., 2019). In the search for evolutionarily significant HGT in parasites, it appears that the nuclear genome holds the most promise. Surveying mitogenomes nevertheless remains an important area to explore given functional anomalies detected in *Viscum* (see Section 4) and the lack of knowledge around what determines plant mitogenome size and the apparently correlated incorporation of foreign (as well as intracellular) DNA.

4. Divergent mitochondria in the family Viscaceae

4.1. Altered oxidative phosphorylation system

Mitogenomes of *Viscum* and *Phoradendron* (both Viscaceae) are exceptional among angiosperms in terms of gene loss (Mower, this issue; Petersen et al., 2015a; Skippington et al., 2015, 2017; Zervas et al., 2019). They have functionally lost all nine *nad* genes, which unequivocally form the mitochondrial complement of genes encoding complex I of the electron transport chain (ETC) in all other angiosperms sequenced to date (Mower, this issue). While small fragments of most *nad* genes can still be identified in the mitogenome of *Viscum album*, no recognizable gene sequences are left in *V. scurruloideum* (Petersen et al., 2015a; Skippington et al., 2015, 2017). Gene surveys, but no completely assembled mitogenomes, of two other species of *Viscum* (*V. minimum* and *V. crassulae*) and a species of *Phoradendron* also suggest the presence of only a few *nad* gene fragments, but other representatives of the Santalales appear to have a normal *nad* gene complement (Petersen et al., 2015a; Zervas et al., 2019).

The only other known cases of *nad* gene loss from the mitogenome among land plants are the several independent losses of *nad7* in some species of liverworts, hornworts, mosses (Bell et al., 2014; Goryunov et al., 2018; Groth-Malonek et al., 2007; Li et al., 2009; Liu et al., 2014; Villarreal et al., 2018; Xue et al., 2010) and the lycophyte *Huperzia* (Liu et al., 2012). In the liverwort *Marchantia*, the *nad7* gene has been functionally transferred to the nuclear genome (Kobayashi et al., 1997) and it is possible that one ancient transfer has made several subsequent mitochondrial losses possible. Further losses of one or a few mitochondrial *nad* genes, including *nad7*, have occurred among chlorophyte algae (see e.g., Mower et al., 2012b; Sloan et al., 2018; Turmel et al., 2010 and references therein).

Outside the plant lineage, complete loss of all mitochondrial *nad* genes has been observed in a few eukaryotic lineages. However, all cases reported so far concern unicellular species. Examples are mostly found in anaerobic organisms where the mitogenomes may be lost completely (Müller et al., 2012), but also in some facultative aerobic organisms including fungi (e.g, the cryptomycotan *Rozella* and some saccharomycetes) and alveolates (e.g., *Plasmodium* and *Chromera*) (e.g., Flegontov et al., 2015; Gabaldón et al., 2005; James et al., 2013; Pramateftaki et al., 2006; Vaidya and Mather, 2009; van Dooren et al., 2006). Since complete loss is consistently associated with loss of nuclear complex I genes, these organisms all rely on alternative means of respiration, and it was thought a similar alternative pathway may be what allows *Viscum* to survive without mitochondrial *nad* genes (Petersen et al., 2015a; Skippington et al., 2015).

Since *Viscum* species are the very first multicellular eukaryotes reported to lack all complex I genes in the mitogenome, their mode of respiration is of considerable interest. How do *Viscum* species produce sufficient amounts of ATP to drive basic cellular functions? Recently, the composition and function of the oxidative phosphorylation (OXPHOS)

system in *V. album* was investigated biochemically (Maclean et al., 2018; Senkler et al., 2018; see also comments in Busch, 2018; da Fonseca-Pereira et al., 2018). Mitochondria were isolated from buds and leaves of *V. album* (Maclean et al., 2018; Senkler et al., 2018). Protein complexes of the isolated organelles were systematically analyzed by blue-native gel electrophoresis in combination with protein identification by mass spectrometry. It was confirmed at the protein level that mitochondrial complex I is very likely absent, as no subunits or activity could be detected. This suggests that the mitochondrial complex I genes have probably not been replaced by functional nuclear copies of these genes. The other complexes of the OXPHOS system (complexes II to V) are present in the mitochondria of *V. album*, but at comparatively lower abundance than in mitochondria of other angiosperms like *Arabidopsis* or potato (Fig. 1) (Maclean et al., 2018; Senkler et al., 2018). Interestingly, complexes III and IV form very stable supermolecular assemblies.

Contrasting the absence of complex I, alternative oxidoreductases, like the alternative NAD(P)H dehydrogenases and alternative oxidase, are abundant in *V. album* mitochondria. As a result, even in the absence of complex I, the mitochondria of *V. album* appear to contain a functional, albeit remodeled, OXPHOS system. Electrons enter the respiratory chain via complex II or via the alternative NAD(P)H dehydrogenases (Fig. 1). The second half of the respiratory chain appears to be fully functional as evidenced by the presence of supercomplexes formed by complexes III and IV and of the alternative oxidase. Due to the absence of complex I, which largely contributes to the formation of the proton gradient across the inner mitochondrial membrane, and the low abundance of mitochondrial ATP synthase (Fig. 1), it is likely that mitochondrial ATP production is low in *V. album*. Extra-mitochondrial ATP-producing processes may have evolved to compensate for this. These metabolic adaptations may include enhanced glycolysis (Maclean et al., 2018) or increased ATP formation by the plastids (Senkler et al., 2018), although it is uncertain to what extent it would contribute to cytosolic ATP content (Gardeström and Igamberdiev, 2016). In conclusion, the loss of complex I in *V. album* appears to be accompanied by a reorganization of the cellular bioenergetic network, a phenomenon previously undocumented in photosynthesizing species. This metabolic adaptation remains a fruitful avenue for future investigations.

The OXPHOS system is the major protein component of the mitochondrial cristae membranes (Fuchs et al., 2020) and ATP synthase dimers have been shown to be important for cristae formation (Hahn et al., 2016). Therefore, a remodeled OXPHOS system might be expected to influence cristae morphology. Interestingly, ATP synthase dimers could not be detected in *V. album* (Senkler et al., 2018), but the cristae morphology appears normal, though fewer cristae per mitochondria were observed (Maclean et al., 2018; Senkler et al., 2018). These observations suggest that the number of cristae per mitochondrion reflects the abundance of the OXPHOS system.

4.2. Additional gene losses

In addition to the loss of *nad* genes in *Viscum* and *Phoradendron*, numerous ribosomal protein genes have also been lost (Petersen et al., 2015a; Skippington et al., 2015, 2017; Zervas et al., 2019), but this is not uncommon among plants (e.g., Petersen et al., 2017; Sloan et al., 2012; Zhu et al., 2014). More intriguing is the absence in some Viscaceae of *matR* and *ccmB*, which are present in all other sequenced angiosperm mitogenomes (Mower, this issue; Petersen et al., 2015a; Skippington et al., 2015, 2017; Zervas et al., 2019). Both genes are absent from the mitogenome of *V. scurruloideum* and gene surveys of two more species of *Viscum* (*V. minimum* and *V. crassulae*) and *Phoradendron liga*[1] suggest absence in those species as well (Petersen et al., 2015a; Skippington et al., 2015, 2017; Zervas et al., 2019). In *V. album*, however, the genes are both present (Petersen et al., 2015a; Skippington et al., 2017). Thus, the genes have either been lost at least twice or lost once in a common Viscaceae ancestor to be gained later in *V. album* or a lineage leading to it. In contrast to most mitochondrial genes in Viscaceae being exceptionally divergent from other angiosperms, the *matR* and *ccmB* genes found in *V. album* are both quite normal (Petersen et al., 2015a; Skippington et al., 2017), and Skippington and coworkers (2017) favor a hypothesis of gain through HGT. Whether the genes are functional still needs to be determined, but if other Viscaceae species can survive without these genes being located in the mitogenome, *V. album* should not need horizontally transferred copies to function.

So how do species of *Viscum* and *Phoradendron* cope with loss of *matR* and *ccmB* from their mitogenome? Their conservation in all other angiosperms suggests that they are indispensable without an alternative. Two evident options are that the plants use an alternative gene or pathway as they do to cope with the loss of *nad* genes, or that the genes have been functionally transferred to the nucleus. For *matR* Skippington and coworkers (2015) favor the former. They argue that the maturase encoded by *matR* could be substituted by a nuclear-encoded homologous protein. However, for *ccmB* they favor the latter. The *ccmB* gene is involved in mitochondrial biogenesis of cytochrome *c* together with three more mitochondrial *ccm* genes and several nuclear genes (Sanders et al., 2010), so it is arguably more likely to be transferred and still functional, given the remaining mitochondrial *ccm* genes are most likely functional (Skippington et al., 2015). However, in other eukaryote lineages including chlorophyte algae, an alternative cytochrome *c* biogenesis pathway operates (Allen et al., 2008; Babbitt et al., 2015). To our knowledge this pathway has not been found in land plants, although functional loss of all mitochondrial *ccm* genes has occurred repeatedly. In some liverworts (Liu et al., 2011), hornworts (Li et al., 2009; Xue et al., 2010), lycophytes (Grewe et al., 2009; Hecht et al., 2011; Liu et al., 2012) and ferns (Guo et al., 2017; Wolf et al., 2015), all mitochondrial *ccm* genes have been lost completely or pseudogenised. An attempt to identify *ccm* genes in the nuclear genome of the lycophyte *Selaginella* did not recover any of the genes, and in the fern *Ophioglossum* no transcripts of *ccm* genes were detected (Banks et al., 2011; Guo et al., 2017), suggesting that an alternative pathway might exist. Among angiosperms, additional cases of *ccm* gene pseudogenisation are possible for *Silene conica* (Sloan et al., 2012) and in the Convolvulaceae, where the *ccmFc* gene appears to be pseudogenised in *Ipomoea* (Hoshino et al., 2016) and *Cuscuta* (B. Anderson, K. Krause, G. Petersen, unpublished). In light of the altered respiratory pathway used in the Viscaceae, it seems possible that some alternative genes or pathways may also exist for cytochrome *c* biogenesis both in this family and possibly other land plants.

4.3. Elevated substitution rates

Coupled with the loss of complex I genes, most other mitochondrial genes in *Viscum* and *Phoradendron* are highly divergent from those of most other angiosperms (Petersen et al., 2015a; Skippington et al., 2015, 2017; Zervas et al., 2019). Petersen et al. (2015a) initially failed to identify some of the most divergent genes and questioned the functionality of others because of this high divergence. However, copies of supposedly missing genes were later found in a re-analysis by Skippington and coworkers (2017), who argued for the functionality of most genes. Subsequently, proteome studies of *V. album* confirmed functionality of the genes in that species (Maclean et al., 2018; Senkler et al., 2018), and transcriptome data for both *Viscum* and *Phoradendron* show the presence of transcripts from most of the mitochondrial genes, providing supporting evidence for functionality (Zervas, 2018). That high sequence divergence alone does not necessarily alter mitochondrial function have also been shown in the two species of the autotrophic genus *Silene* (Havird et al., 2019).

The divergent protein-coding genes of *Viscum*, including genes for

[1] In Zervas et al. (2019) Fig. 1 *ccmB* is erroneously marked as present in *Phoradendron*.

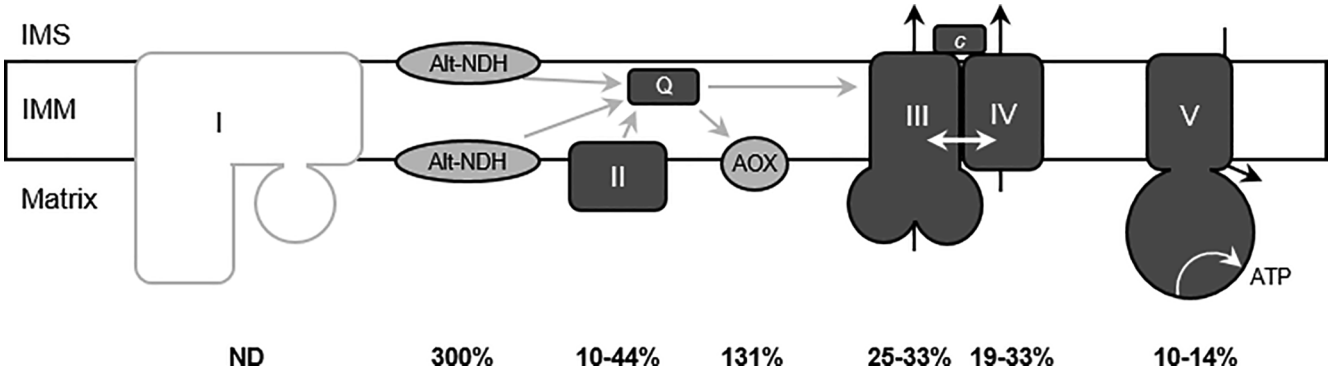

Fig. 1. Representation of the OXPHOS system in *Viscum album*.
OXPHOS complexes are shown in dark grey and labelled with roman numbers. Complex I is shown in white as it was not detected. The alternative pathways are shown in light grey. Electron transport and proton transport are represented with grey and black arrows, respectively. The white double headed arrow indicate the occurrence of a stable supercomplex. Numbers under each complex indicate the relative amount of the respective complex in *Viscum* as compared to *Arabidopsis* (Maclean et al., 2018). IMS: intermembrane space, IMM: inner mitochondrial membrane, Alt-NDH: alternative NAD(P)H dehydrogenases, Q: quinone pool, AOX: alternative oxidase, *c*: cytochrome *c*, ND: not detected.

OXPHOS complexes II–V, cytochrome *c* biogenesis and ribosomal proteins, have highly elevated synonymous as well as non-synonymous substitution rates, and most appear to evolve under relaxed selection compared to other angiosperms (Skippington et al., 2015, 2017). Since this pattern resembles evolution of still functional plastome genes in parasitic and mycoheterotrophic plants with reduced photosynthesis (see Wicke and Naumann, 2018 and references therein), the elevated substitution rates and relaxed selection in *Viscum* mitochondria might be associated with the parasitic lifestyle (Petersen et al., 2015a; Skippington et al., 2015; Zervas et al., 2019). Theoretically, increased substitution rates may be beneficial to parasites evolving under a co-evolutionary host-parasite arms race (e.g., Haraguchi and Sasaki, 1996). Under such a model, the elevated substitution rates are expected to affect all genomic compartments, and a study based on nuclear, plastid and mitochondrial genes from representatives of all 12 lineages of parasitic plants and their assumed closest autotrophic relatives did find a general increase in most parasitic lineages (Bromham et al., 2013). Using mitochondrial sequence data from seven clades of parasites and a more comprehensive phylogenetic sampling of autotrophic taxa, Zervas and coworkers (2019) also detected slightly to moderately increased substitution rates in some of the parasites and a significantly large increase for *Viscum* and *Phoradendron*. However, they did not find any statistically significant differences between autotrophs, hemiparasites and holoparasites in general, since some autotrophic lineages of angiosperms also have highly elevated substitution rates for mitochondrial genes (Sloan, 2015; Zervas et al., 2019). Previously published phylogenies for species of Viscaceae and other members of the order Santalales tend to show a pattern of long branches for Viscaceae although rates have not been quantified (e.g., Der and Nickrent, 2008; Le et al., 2018; Matsubara et al., 2003; Maul et al., 2019; Nickrent et al., 2019; Petersen et al., 2015b; Su et al., 2015). Some of these phylogenies are based on combinations of data from two or more genomic compartments, but it does appear that both plastid and nuclear sequences from the Viscaceae evolve slightly faster than in other Santalales, with the exception of plastid sequences from holoparasites. The potentially increased substitution rate in the nuclear and plastid genomes is, however, orders of magnitude smaller than the increase in the mitogenome, and since most other members of the Santalales are also parasitic, a host-parasite arms race is unlikely to account for the highly elevated mitochondrial substitution rate in Viscaceae. Further studies including a much denser taxon sampling in the Santalales are needed in order to understand the peculiar, and so far unique, molecular evolution of the mitogenome within the clade.

5. Future prospects

The scarce amount of mitogenomic data currently available from parasitic and mycoheterotrophic species is likely to be soon supplemented by large amounts of data from ongoing and future genome sequencing projects. We anticipate that we will soon have data from all clades of parasites, and thus be able to investigate much more precisely whether any general correlation exists between parasitism and mitochondrial evolution. Genome sequencing projects will also provide valuable sources of data for non-parasites, allowing for much denser taxon sampling in future studies trying to identify sources of HGT.

The physical mechanisms underlying the transfer of DNA between parasites and hosts, and the incorporation of foreign DNA into mitochondrial and nuclear genomes, remain poorly understood and deserve future attention. While furthering our understanding of species interactions in general, increased knowledge may be useful for controlling parasitic plants, which include extremely harmful agricultural pests such as broomrape and witchweed.

In addition to genome sequencing projects, efforts should be made to investigate the fascinating physiology of parasitic plants. Biochemical investigations of the mitochondria from parasites should be performed to better understand the metabolic changes in organisms that opted for a parasitic life strategy. In the context of known HGT of mitochondrial genes, might the genes acquired through HGT possibly give a metabolic advantage to the parasite?

Currently, the altered mitogenome and respiratory pathway used by species of Viscaceae have no parallels among other parasites, and thus may not be related to the parasitic lifestyle at all. If the modifications remain unique, further studies into the origin and evolution of the modified respiratory machinery may help elucidate a possible correlation. Such studies requires a much denser sampling of data from the Viscaceae as well as from closely related families in the Santalales.

In plastomes of *Viscum* and other species in the Santalales, the *ndh* genes that code for the plastid NADH dehydrogenase complex involved in cyclic electron transport complex are either lost or pseudogenized (Petersen et al., 2015b). Although these genes are consistently the first to be lost from the plastome in parasitic lineages and are observed to be lost in other clades of autotrophic plants (see Wicke and Naumann, 2018 and references therein), it is tempting to speculate whether the mitochondrial complex I loss is in any way related to the plastid *ndh* loss. Establishing the impact of these losses on plant energy metabolism will require thorough studies of the metabolism of *Viscum* cells, mitochondria and plastids.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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