Against the traffic
The first evidence for mitochondrial DNA transfer into the plastid genome

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Transfer of DNA between different compartments of the plant cell, i.e., plastid, mitochondrion and nucleus, is a well-known phenomenon in plant evolution. Six directions of inter-compartmental DNA migration are possible in theory, however only four of them have been previously reported. These include frequent cases of mitochondrion and plastid to nucleus transfer, plastid to mitochondrion transfer, and rare nucleus to mitochondrion migrations. The connection between the plastid and mitochondrial genomes in flowering plants has been viewed as a one way road. Contrary to these observations we found that a sequence widespread in the carrot mitochondrial genome, designated as *Dc*MP, was transferred to the plastid genome of a carrot ancestor. Interestingly, *Dc*MP was integrated into a tRNA promoter of the plastid *trnV* gene, replacing the original promoter sequence. The rearrangement of the plastid genome is specific for carrot and closely related species belonging *Scandiceae* clade. The structure of the sequence and the presence of a 6 nt target site duplication led us to speculate that the transfer was a result of a transposition event of a non-LTR retrotransposon. These findings open interesting questions about the evolution of organellar genomes and mobile genetic elements and provide a useful plastid marker to phylogenetically delineate species relationships within the *Scandiceae* clade.

Introduction

Inter-compartmental DNA migration is a well-known phenomenon in plant cell evolution and has contributed significantly to genome evolution by relocating and refashioning genes and consequently contributing to genetic diversity. DNA transfer among the plastid, mitochondrial and nuclear genomes resulted in a functional relocation of organellar genes early in organelle evolution.[1-6] In contrast, almost all reported recent inter-compartmental DNA transfers gave rise to non-coding sequences or pseudogenes.[1] Six directions of the inter-compartmental DNA migration are possible in theory, and four of them have been previously reported in angiosperms. Transfers of DNA from the mitochondria and from the plastid to the nucleus are the most common reported transfers.[7,8] Transfers of DNA from the plastid to the mitochondrion have also been frequently observed. Cases of nuclear DNA transfer to the exceptionally large mitochondrial genomes of Fabaceae and Cucurbitaceae were also reported.[9,10] In contrast, no evidence of DNA transfer from the nucleus or the mitochondrion to the plastid has been reported in angiosperms. Smith[11] investigated evidence for the presence of mitochondrial DNA in the plastid genome of 42 species including 11 angiosperms and did not find any mtDNA-like sequences. Forces driving inter-comparmal DNA transfer are still unclear. Plant mitochondria actively import DNA via a permeability transition pore complex.[12] In contrast, the relative absence of nuclear and mitochondrial DNA in the plastome could reflect the lack of a DNA uptake system, due to the integrity of the plastid membrane. Escape of DNA from organellar genomes to the nuclear genome seems to coincide with the degradation of organelle DNA.[1] Both mobile elements and integration of DNA by nonhomologous end-joining (NHEJ) repair of double-strand breaks (DBSs) are important components of the DNA transfer machinery. In our recent paper[13] we provided evidence that a sequence designated *Dc*MP (*D. carota* mitochondrial-plastid), was transferred from the mitochondrial genome to the plastid genome of the carrot ancestor. Here we discuss a hypothetical mechanism explaining this event. To date, this represents the first evidence for this direction of DNA transfer. Given the large amount of available angiosperm sequence data, this strongly suggests that this is a rare event. However, the increasing availability of new organellar and nuclear genome sequences could reveal similar events in other species, and this could elucidate the mechanism that makes the uptake of DNA by the plastid genome such a rare event.
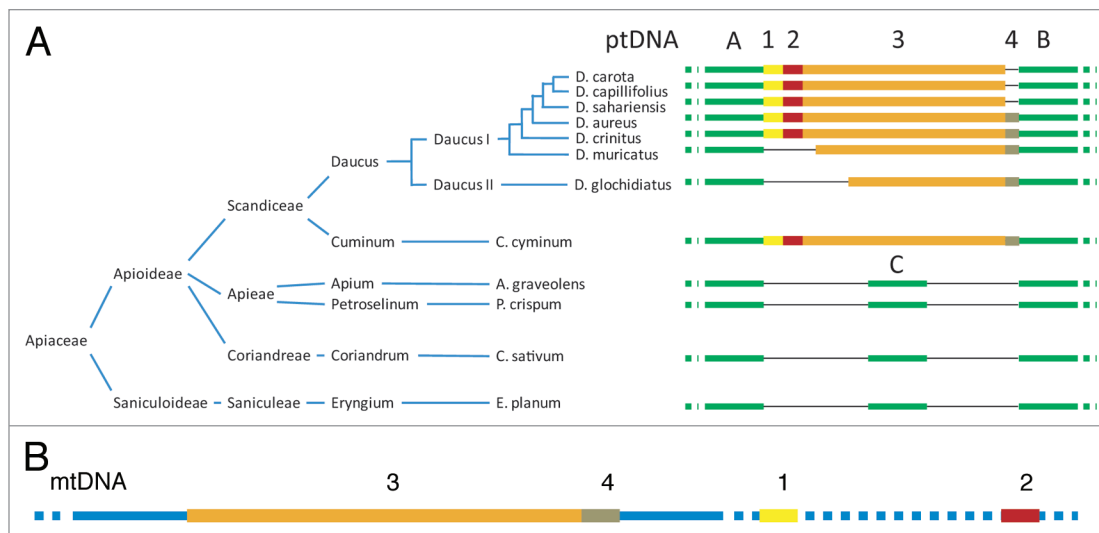
Figure 1. Presence of *Dc*MP insertion variants in the plastid genome of Apiaceaeous species according to the reconstructed phylogeny.[15,16] (**A**) Yellow, red, orange and brown segments 1 to 4 represents the region of plastid (pt) DNA transferred from the mitochondrial genome (dubbed *Dc*MP). It has likely been transferred in a single event with the present organization of the transferred sequences in the carrot mitochondrial genome depicted in (**B**) Green lines A and B denote conserved plastid sequences flanking the insertion; green line C represents the 339 nt region that have been deleted in the Scandiceae plastid genomes; thin black lines denote missing regions. (**B**) Blue lines denote mitochondrial sequences of carrot; colored segments represent the *Dc*MP regions 1–4; dashed lines represent mtDNA segments separating regions 1–4. The scheme is not drawn to scale.

Daucus carota Mitochondrial-Plastid (*Dc*MP) Region

Following the evidence provided by Goremykin and colleagues[14] that a region in the *Vitis vinifera* mitochondrial genome was similar to a fragment of the carrot plastid genome, we identified that this region was part of a DNA segment designated as *Dc*MP that was likely transferred from the mitochondrial to the plastid genome of carrot.[13] This was the first time that DNA transfer from the mitochondrion to the plastid was reported in flowering plants. Our evidence indicated that the transferred segment was at least 1,452 nt-long. Currently, it resides in mitochondrial genomes of a wide range of Apiaceae species, but its presence in the plastid genome is restricted to the genus Daucus and their close relatives including cumin (*Cuminum cyminum*), indicating that the transfer took place in their common ancestor. This observation suggests that *Dc*MP could be a characteristic of species belonging to the tribe Scandiceae[15,16] (**Fig. 1A**). The insertion into the plastid genome was accompanied by a deletion of 339 nt sequence (**Fig. 1A,** segment C), which was present in the empty insertion site of all examined non-Scandiceae species. The *Dc*MP region was apparently transferred as a contiguous sequence from the mitochondria to the plastid but at present it is highly rearranged in the investigated mitochondrial genomes (**Fig. 1B**). The position of the *Dc*MP segments 3 and 4 is conserved across the mitochondrial genomes of all investigated Apiaceae species. In the carrot mitochondrial genome segments 1 and 2 are physically separated from 3 and 4 and located ca. 5 kb and over 80 kb downstream, respectively, relative to *Dc*MP 3 and 4 (**Fig. 1B**). Notably, only *Dc*MP segment 2 has homology to other plant mitochondrial genomes—it is a fragment of the *cox1* gene. It is therefore likely that the presence of the *Dc*MP segments 1, 3 and 4 in the carrot mitochondrial genome resulted from a DNA transfer of unknown origin, common to Apiaceae, which predated the transfer from the mitochondria to the plastid. The observed fragmentation of the *Dc*MP region in mtDNA can be explained by a high level of recombination activity often observed in plant mitochondrial genomes, and resulting in the intragenomic reshuffling of DNA segments.

Functional Replacement of a tRNA^Val Initiation Site

The *Dc*MP sequence integrated into the plastid genome just upstream of the tRNA^Val gene (*trnV*), located in the large inverted repeat. Interestingly, Manna et al.[17] investigated the expression level of *trnV* during carrot embryogenesis and identified three putative plastid *trnV* promoters: P1, P2 and P3 (**Fig. 2**). They observed that the three promoters mapped to a region of minor conservation when compared with the tobacco and maize plastid genomes, where two putative *trnV* promoters P4 and P5 were previously identified[18] (**Fig. 2**). Promoters P1, P2 and P3 are located 105, 41 and 16 nt upstream of *trnV*, respectively. They suggested that these three promoters were responsible for the differential expression of *trnV* during embryogenesis. Our findings revealed that all three promoters were in fact a part of the integrated *Dc*MP sequence (**Fig. 2,** shaded sequence), while P4 and P5 were located at the 3' end of the 339 nt DNA fragment that was replaced by *Dc*MP in the carrot plastid genome (**Fig. 2,** rectangular box; **Fig. 1A,** segment C). A comparison of the carrot, tobacco (*Nicotiana tabacum*), and parsley (*Petroselium crispum*) plastid genomes in
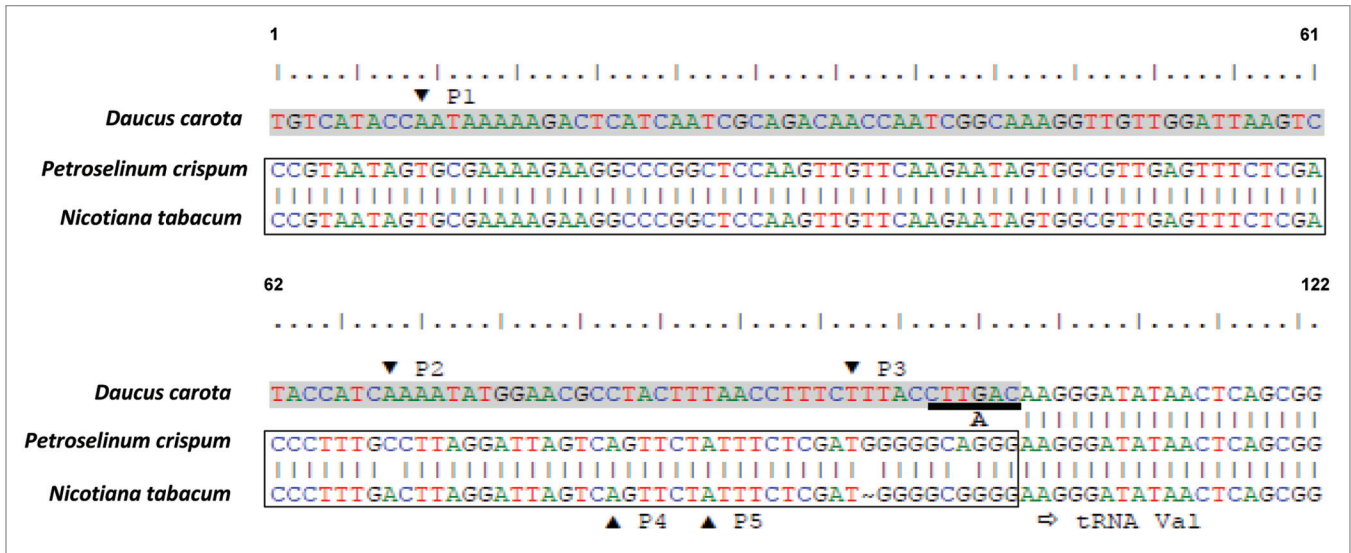
Figure 2. Nucleotide sequence upstream of the plastid *trnV* gene in *D. carota*, *P. crispum* and *N. tabacum*. Shading indicates the 3' end of *Dc*MP plastid region present only in *D. carota*. The rectangular box represents the 3' end of the 339 nt DNA fragment replaced by *Dc*MP in the *D. carota* plastid genome. P1, P2, P3: putative promoters of the *D. carota* trnV.[17] P4, P5: putative promoters of the *P. crispum* and *N. tabacum* trnV.[18] Horizontal arrow indicates the 5' end of *trnV*. Underlined sequence A represents the unit of the *Dc*MP direct repeat.

Figure 3. Structure of the plastid *D. carota Dc*MP sequence. ORF were detected using Open Reading Frame Finder (http://www.ncbi.nlm.nih.gov/gorf/gorf.html). The sequence was oriented according to 5'-3' (indicated by arrows) ORF orientation is in opposite direction as related to other figures. Thick vertical blue lines indicate target site duplication (TSD). Thin red vertical lines indicate relative position of P1, P2 and P3 *tnrV* promoters. Red box indicates the region comprising partial sequence of *cox*1 gene. The scheme is drawn to scale.

this region revealed that P4 and P5 are conserved in parsley. This strongly suggests that with the integration of *Dc*MP into the plastid genome, the conserved promoter region upstream of a *trnV*[18] was replaced with a functional substitute, resulting in the modified expression pattern of *trnV*.

Sequence Analysis of the Plastid *Dc*MP Variant and a Possible Mechanism for the *Dc*MP Transfer

Analysis of the plastid *Dc*MP sequence, the structure of which likely represents the organization of the transferred contiguous sequence, could suggest its possible mode of integration. Annotation of *Dc*MP sequence was performed using Open Reading Frame Finder (http://www.ncbi.nlm.nih.gov/gorf/gorf.html) website. Investigation of repeat sequences was carried using blastn. In order to detect sequences flanking the plastid *Dc*MP

region with homology to sequences flanking the mitochondrial *Dc*MP region, the sequence of the plastid genome was queried against a local database containing the carrot mitochondrial genome.

Sequence annotation identified three putative ORFs (Open Reading Frame), ORFa and ORFb of 153 and 408 nt respectively (**Fig. 3**) both with similarity to a *gag* domain annotated in *Vitis vinifera*, and the third ORF, ORFc of 144 nt (**Fig. 3**) with moderate similarity to a reverse transcriptase annotated in *Medicago truncatula*. Further characterization of the *Dc*MP region in the plastid revealed the presence of a 6 nt direct repeat (CTTGAC), immediately flanking *Dc*MP (**Fig. 3**, blue vertical lines), i.e., the repeats were present directly upstream of *Dc*MP1 and directly downstream of *Dc*MP4. These characteristics suggest that the *Dc*MP might be a non-LTR retrotransposon and the direct repeats

represent target site duplication (TSD)[19] created as a result of the *Dc*MP integration following its mobilization from a donor site localized in the mitochondrial genome. It has been shown that some non-LTR elements may specifically target RNA polymerase III dependent genes, such as tRNA genes. Recently, Wenke et al.[20] described a group of non-LTR retrotransposons targeting tRNA genes in *Dictyostelium discoideum*. Integration of non-LTR elements can alter genome structure and function and has been associated with genome rearrangements,[21] deletions[22,23] and in some cases it resulted in modified expression of adjacent genes.[24,25] Alternative mechanisms could have involved homologous recombination by microhomology or transfer of a group I intron. Homologous recombination would require that regions of plastome have homology to the recombinant DNA fragment. However, since we found no
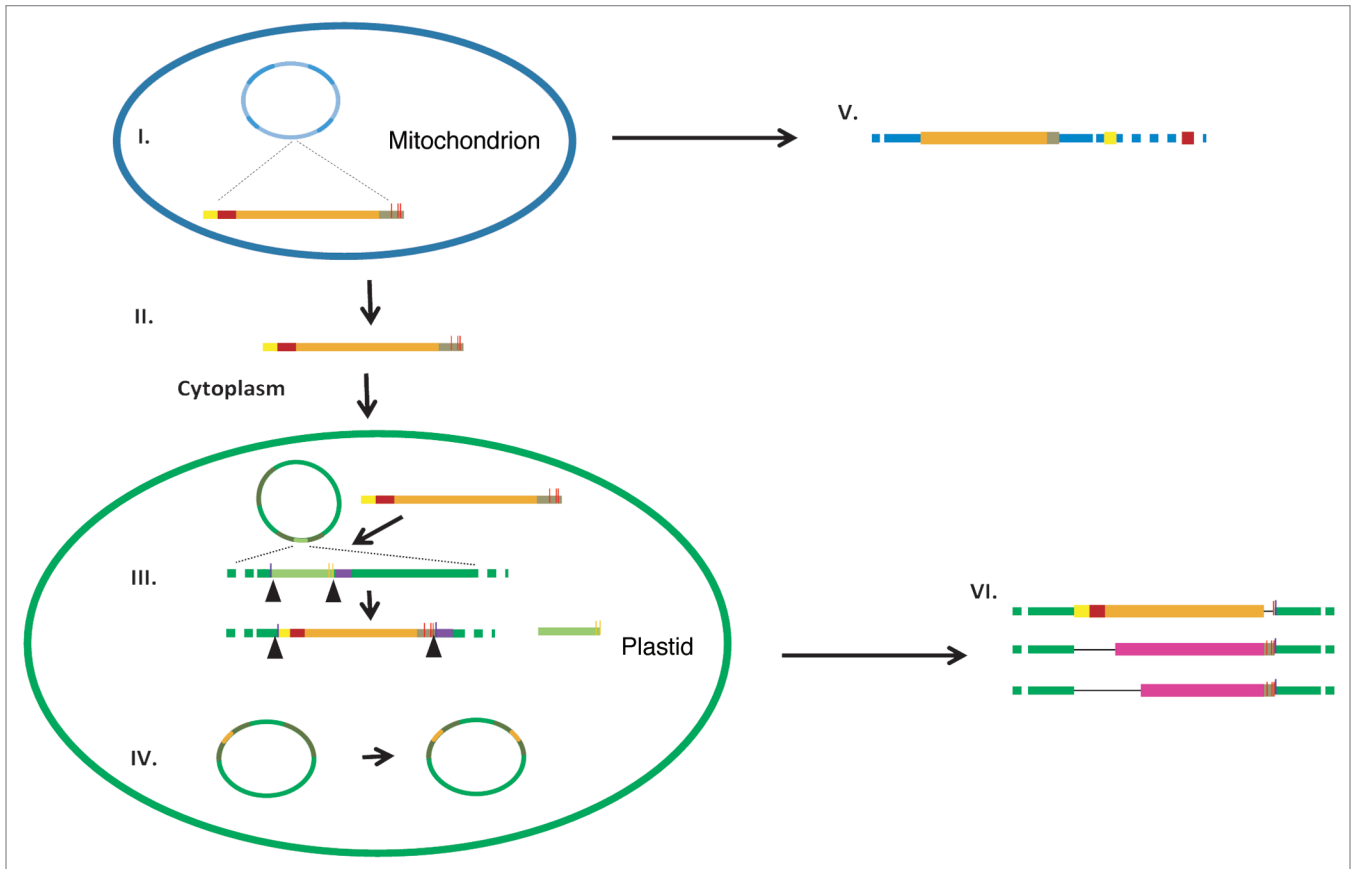
Figure 4. A schematic representation of the hypothetical mitochondrial to plastid genome transfer of *Dc*MP in the carrot ancestor. (**I**) Transcription of a chimeric segment (*Dc*MP) comprising non-LTR fragments and Mt-specific regions (including *cox*1, red segments); (**II**) Migration of *Dc*MP transcript to the cytoplasm and into the plastid; (**III**) Integration of *Dc*MP and deletion of the ancestral Pt-specific segment (light green segment) including creation of a target site duplication (blue vertical lines) and replacement of the conserved promoters P4 and P5 (yellow vertical lines) with P1, P2 and P3 (red vertical lines) upstream of *trnV* (violet segment), the reverse transcription step is not shown; (**IV**) Copy correction in the inverted repeat (IR, dark green segments); (**V**) Mt genome reshuffling and deletions of *Dc*MP; (**VI**) Accumulation of lineage-specific deletions in the *Dc*MP region. The scheme is not drawn to scale.

homology between sequences flanking the mitochondrial *Dc*MP and the plastid genome[13] we find this possibility unlikely. In addition, homologous recombination is an unlikely mechanism for replacing a functional promoter. A second alternative mechanism could have involved group I introns which catalyze their own splicing and function as mobile elements, such as those found in the tRNA[Leu] genes of ptDNA.[26] Also group I introns are present in the mithocondrial *cox1* gene and are involved in horizontal gene transfer. The structure of *Dc*MP does not support this hypothesis. In fact *Dc*MP has almost no internal homology (11 nt maximum), excluding the possibility of the characteristic folding exhibited by group I introns. Interestingly, the *D. carota* mt genome lacks the *cox1* group I intron as reported

by Sanchez-Puerta et al.[27] for many other angiosperm species.

Considering the structure of the *Dc*MP region and the functionality of its sequence proposed by Manna et al.,[17] we speculate that it represents a non-LTR element, and that a retrotransposition event likely caused its integration into the mitochondrial genome from an unknown source, which was then followed by the reported transfer to the plastid genome. At present, it is difficult to speculate about the exact mechanism accounting for the transfer and integration of *Dc*MP into the organellar genomes. If the current non-contiguous organization of the *Dc*MP region in the carrot mitochondrial genome is shared by many Apiaceae, this migration event likely was much older than the transfer to the plastid genome, which has been restricted

to a much narrower group of closely related species. Moreover, the fragmentation of *Dc*MP in the mitochondria likely predated the transfer into plastids based upon its apparent rearrangements observed in the mitochondrial genome and described above. However, the presence of the *cox1* gene fragment in the region that migrated into the plastid genome suggests that the donor sequence must have originated in the mitochondrial genome. A possible scenario could have involved retrotransposition into the mitochondrial genome, mtDNA re-arrangements and acquirement of the *cox1* sequence transcription from a chimeric mitochondrial donor sequence and reverse transcription, and finally transfer into the plastid and integration of the new copy comprising both retroelement-specific and mitochondrial

sequences (**Fig. 4**). The scenario involving retrotransposition gains some support from the fact that a retroelement-related ORF coding for reverse transcriptase had already been found in the plastome of green alga.[28]

In our scenario, following transcription, retrotransposon RNA migrates into the cytoplasm and proliferates via a 'copy and paste' mechanism requiring an RNA intermediate. Here the proteins required for transposition are produced (**Fig. 4I**). Although the mechanism of this migration is not clear, it is worth mentioning that cases of out-of-mitochondria transcript translocation have been well evidenced for animal cells.[29-31] A horizontal transfer scenario would require that the RNA copy was transported into the plastid (**Fig. 4II**). The mechanism leading to this event is unknown, but previous studies revealed that stress conditions such as heat shock could cause pore formation in the plastid envelope and allow entry of DNA.[32] Related research also demonstrated that plastids were actively able to import mRNA.[33] We observed that, in the plastid genome *Dc*MP integrated upstream of the *trnV* creating a deletion of the ancestral plastid sequence and a target site duplication (TSD) (**Fig. 4III**). It was not possible to identify the integration region in the mitochondrial genome, due to extensive rearrangements it underwent subsequent to insertion (**Fig. 4V**). The functional replacement of promoter activity upstream of the *trnV* avoided negative selection and we speculate that its transfer into the inverted repeat (IR), followed by a copy correction mechanism, that duplicated the introduced *Dc*MP into the other inverted repeat (**Fig. 4IV**), resulted in a stable integration into the plastid genome. After the integration, deletion events could have occurred within other species of Daucus or Cuminum, both members of the Scandiceae clade (**Figs. 1A and 4VI**).

Significance and Applications

The data discussed here provide new insights in the dynamics of inter-compartmental DNA migration. The structure of the *Dc*MP sequence, along with its functional aspects, provides a plausible scenario for the evolution of organellar genomes, including integration of mobile genetic elements, and suggests a mechanism for that process. As revealed by studies in plants[34] and other organisms,[25] transposable elements are very powerful markers to trace ancestor history. Considering the stability of the plastid genome, the presence of the *Dc*MP region in members of the Scandiceae makes it a candidate marker to delineate relationships in this clade.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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