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# Inheritance of chloroplast and mitochondrial DNA in alloplasmic forms of the genus *Daucus*

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Abstract The inheritance of mitochondrial (mt) and chloroplast (ct) DNA in the progeny from interspecific crosses between the cultivated carrot (Daucus carota sativus) and wild forms of the genus Daucus was investigated by analysis of mt and ct RFLPs in single plants of the parental and filial generations. We observed a strict maternal inheritance of the organellar DNAs in all interspecific crosses examined. Previous studies on putative F<sub>2</sub> plants from a cross between Daucus muricatus × D. carota sativus suggested paternal inheritance of ctDNA. Our reinvestigation of this material revealed that the mtDNA of the putative F<sub>2</sub> plants differed from the mtDNA of both putative parents. Therefore, our data suggest that the investigated material originated from other, not yet identified, parents. Consequently, the analysis of this material cannot provide evidence for a paternal inheritance of ctDNA.

**Key words** Daucus · Carrot · Chloroplast DNA · Mitochondrial DNA · Cytoplasmic male sterility

# Introduction

Since the discovery, at the beginning of this century, that plastids in angiosperms are inherited in a non-Mendelian manner investigations on plastid transmission have been carried out in nearly 60 species. A maternal inheritance of chloroplast (ct) genes was found in most cases though in about 20% of these species a biparental mode of inheritance has been observed (Smith 1988).

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Angiosperms transmitting plastids via the pollen have been classified by Hagemann (1992) into three groups: the *Oenothera*-type, with a predominantly maternal transmission, the *Pelargonium*-type, with more or less equal contribution of plastids by the maternal and paternal parent, and the *Medicago*-type, with predominantly paternally transmitted plastids.

Compared to chloroplasts even less is known about the transmission of mitochondria in intra- and interspecific crosses of higher plants. The maternal inheritance of the phenotype of cytoplasmic male sterility (cms) can be taken as an indication of maternal transmission of mitochondrial (mt) genes in angiosperms (Hanson and Conde 1985). Maternal transmission of mitochondria was directly demonstrated by the inheritance of the restriction fragment pattern of mtDNAs first in interspecific crosses within the genus Zea (Conde et al. 1979) and later for several other specific (e.g. Vedel et al. 1981; Samoilov et al. 1986), including species which show a biparental or paternal inheritance of chloroplasts (Schmitz 1988; Schumann and Hanock 1989). In gymnosperms, which transmit their chloroplast genes via the paternal parent, mtDNA is transmitted maternally in the genera Pinus (Neale and Sederoff 1989; Wagner et al. 1991) and Picea (Sutton et al. 1991), but paternally in Sequoia and Calocedrus (Neale et al. 1989, 1991). A paternal contribution of mitochondria to the progeny has also been reported for angiosperms. A paternal pattern of restriction fragments of mtDNA was found in Oenothera berteriana × Oe. odorata hybrids (Brennicke and Schwemmle 1984). Soliman et al. (1987) reported the presence of paternal and maternal organellar (mt and ct) DNAs in hybrids between Hordeum and Secale. Erickson and Kemble (1990) demonstrated a paternal transmission of mitochondria in the dicotyledoneous species Brassica napus. Biparental inheritance leading to heteroplasmy was found in 10% of the F<sub>1</sub> progeny, whereas plants of the subsequent F<sub>2</sub> generation contained either maternal or paternal mtDNA. Paternal inheritance of mtDNA, but maternal inheritance of ctDNA, occurs in bananas (Fauré et al. 1994).

Kiang et al. (1994) observed paternal inheritance of organellar DNAs in intergeneric hybrids between Festuca and Lolium. In the case of mtDNA, final conclusions on a possible paternal inheritance may require more thorough investigations: Kück et al. (1993) found "maternal" and "paternal" mtDNA fragments in hybrids resulting from crosses between different Triticale lines. However, they could also detect substoichiometric amounts of the "paternal" fragments in the DNA of the maternal parent by PCR amplification. Thus, a differential amplification of subgenomic mtDNA molecules, depending on the nuclear background, may produce new types of mtDNA in hybrids in the absence of paternal or biparental inheritance (Escote-Carlson et al. 1990; Mackenzie and Chase 1990). The reported data suggest that exceptions from the more common maternal transmission of mtDNA and ctDNA need to be taken into account. In particular, a biparental inheritance of mt genes with a low input by the paternal parent would have consequences for breeding programs because it would not be easily detectable and would lead to unstable expression of cytoplasmic male sterility and other traits which depend on organellar genes.

We have chosen the genus Daucus for our studies on organellar transmission in interspecific crosses since cytoplasmic male sterility is extensively used in the breeding of carrot (D. carota sativus) (reviewed in Börner et al. 1995). Furthermore, one of the rare cases of exclusively paternally transmitted plastids in angiosperms was reported for progenies of crosses between D. muricatus and D. carota sativus (Boblenz et al. 1990). In the present paper we provide evidence for the maternal mode of organellar inheritance in several crosses between carrot cultivars and closely related species/subspecies of the genus Daucus.

#### Material and methods

# Plant material

The plant material was obtained from the *Daucus* collection and breeding program of the Institute for Breeding Methods in Vegetables, Quedlinburg (Germany). Table 1 presents a compilation of the crosses analyzed in the present study. Furthermore, we investigated the progeny of several backcross generations resulting originally from a cross between *D. carota gummifer* × *D. carota sativus*.

Table 1 Material analyzed in this study. (BC = backcross generation, Sa = male-sterile line with 'brown-anther' type of cms; LSR = cv 'Lange Rote Stumpfe', Luw = cv 'Luwal', Vit = 'Vitaminaya')

No. Cross Generation 1 D. muricatus (29/78) D. carota sativus (Vit) D. gingidium D. carota sativus  $BC_2F_3$ 3 D. carota libanotifolia  $BC_2F_2$ D. carota sativus 4 D. carota gummifer D. carota sativus (Vit) X  $\mathbf{F}_{\mathbf{1}}$ 5 D. carota gummifer × D. carota sativus (LSR) 6 D. carota gummifer × D. carota sativus  $BC_3F_3$  $BC_{3,4,5,6}F_2$ 7 D. carota commutatus X D. carota sativus (Vit) 8 D. carota sativus (Sa 409) × D. carota commutatus D. carota maximus D. carota sativus (Luw) X 10 D. carota maximus (Sa 906) D. carota maximus

In the BC3F<sub>2</sub> generation, three male-sterile plants ("gum 1-3") were selected and used as female parents in crosses with two cultivars and a maintainer line of *D. carota sativus* (Fig. 1).

In addition, single plants of three populations of D. muricatus (74A, 74B, 29/78) were included. These populations originated from three different seed samples obtained from the Istituto Edorto Botanico dell' Universita di Torino/Italy, Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben/Germany, and Hortus Botanicus Coimbra/Portugal, respectively. The investigations on organellar inheritance in the progenies of the cross D. muricatus "29/78"  $\times D$ . carota sativus cv 'Vitaminaya' were undertaken on the same plant material which had been used previously in the study of Boblenz et al. (1990): five hybrid plants of this cross were self pollinated and the DNAs were isolated from single  $F_2$  plants.

All crosses were performed manually taking advantage of protandry or male sterility. Except for crosses nos. 1–3 (Table 1), the interspecific hybrids were obtained by the crossing of defined single plants which in turn also served as a source of DNA.

All plants were grown in pots under greenhouse conditions.

Crosses examined for transmission of mtDNA. D. gingidium × D. carota sativus; D. carota libanotifolia × D. carota sativus, D. carota gummifer × D. carota sativus, D. carota commutatus × D. carota sativus, D. carota sativus, D. carota sativus, D. carota sativus × D. carota sativus × D. carota maximus × D. carota sativus, D. carota sativus × D. carota maximus.

Crosses analyzed for transmission of ctDNA. D. carota maximus  $\times$  D. carota sativus, D. carota sativus  $\times$  D. carota maximus and D. carota sativus  $\times$  D. carota commutatus.

#### DNA isolation

Total cellular DNA was extracted from leaf or root material according to the CTAB method of Rogers and Bendich (1985). DNAs were

### D.carota gummifer x D. carota sativus

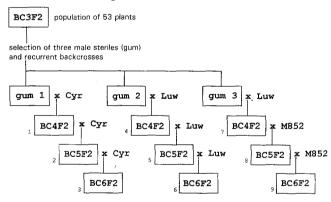


Fig. 1 Schematic representation of the crosses performed between male-sterile plants carrying the "gummifer" cytoplasm and cultivars (Cyr = cv 'Cyrano', Luw = cv 'Luwal') and a maintainer line (M852) of D. carota sativus

digested with different restriction enzymes following the recommendations of the supplier (Amersham, Braunschweig, Germany). DNA endonuclease digests were resolved on 0.8% agarose gels, transferred to Hybond N-filters (Amersham) and analyzed by Southern hybridization (Sambrook et al. 1989).

MtDNA was prepared according to the DNase-method of Chase and Pring (1986), digested with BamHI and electrophoretically separated on a 0.8% TEA-agarose gel. An 11.2-kb fragment was eluted from the agarose gel using the Qiaex-Gel-Extraction Kit following the protocol recommended by the supplier (Diagen, Düsseldorf, Germany) and served as a hybridization probe.

MtDNA was also isolated from 5 g of root material using the 'mini'-preparation method described by Steinborn et al. (1992).

#### Analysis of mtDNA

For Southern-hybridization experiments two sources of mtDNA probes were used: (1) a set of mitochondrial genes: coxI, coxIII (Hiesel et al. 1987), cob (Schuster and Brennicke 1985), atpA (Schuster and Brennicke 1986) and rrn26 (Manna and Brennicke 1985) from Oenothera berteriana, cox II from Zea diploperennis, and (2) an 11.2-kb BamHI-fragment which originated from the mtDNA of the male-fertile carrot line M 509. The DNA probes were radioactively labelled according to Feinberg and Vogelstein (1983) using the 'Megaprime DNA Labelling System' (Amersham, Braunschweig, FRG).

For restriction endonuclease analysis, mtDNA was prepared as described by Steinborn et al. (1992). After digestion with *EcoRI*, restriction overhangs were radioactively end-labelled and electrophoretically separated. Restriction-fragment patterns of mtDNA were visualized by autoradiography after drying the agarose gel.

#### Analysis of ctDNA

Total ctDNA of *D. carota sativus* (line Sa 46017, Scheike et al. 1992) or a 1.3-kb *Bgl*-II fragment served as ctDNA probes in the hybridizations. The 1.3-kb fragment was isolated from digested ctDNA of the carrot line Sa 90 exhibiting the 'brown-anther' phenotype of male sterility.

DNA of phage *Lambda* digested with *HindIII* or *EcoRI* served as a size marker in all electrophoretic separations.

# **Results**

# Inheritance of organellar DNA in interspecific crosses

Southern hybridization experiments, with total DNA from leaves of parental plants and from the offspring of interspecific crosses and ctDNA- or mtDNA-specific probes, revealed in all cases a maternal inheritance of ct and mt RFLPs. The maternal transmission of ctDNA was demonstrated for the cross D. carota sativus  $\times$  D. carota maximus by using radioactively labelled ctDNA as a probe. Fragments of 1.3kb and approximately 1.75 kb could be observed in the BglII-pattern of the maternal parent and all four investigated F<sub>1</sub> hybrid plants. These fragments are not present in the ctDNA pattern of the paternal parent, D. carota maximus. In contrast, the pattern of D. carota maximus contained fragments of about 1.8 kb and 1.9 kb which are lacking in the maternal pattern and in the patterns of plants from the offspring of this cross (Fig. 2).

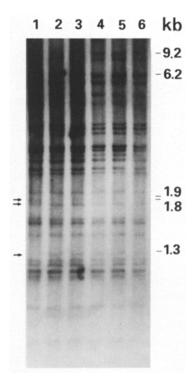


Fig. 2 Southern hybridization, cross *D. carota sativus* (Sa 906)  $\times$  *D. carota maximus. Bgl*II-digested total DNA probed with ctDNA of *D. carota sativus. Lane 1, D. carota maximus, lane 2, D. carota sativus* (Sa 906); *lanes 3*–6,  $F_1$  plants *Arrows* indicate the position of parent-specific fragments

All further studies were performed in a similar way by hybridizing total DNA with organelle-specific gene probes, revealing RFLPs between ctDNA or mtDNAs of the maternal and paternal parent. Total DNAs of single plants of the investigated progenies were analyzed under the same conditions as parental DNAs and found to exhibit the maternal pattern. Hybridization patterns of the parental parent were clearly different from those of the progenies and the maternal parent. Examples are shown in Figs. 3 and 4.

Our data contrast with the results of Boblenz et al. (1990) who reported on the paternal inheritance of ctDNA in the interspecific cross *D. muricatus* "29/78" × *D. carota sativus* cv 'Vitaminaja'. Therefore, we included the same plant material as used by Boblenz et al. (1990) in our investigation. The results are summarized in Table 2.

# Re-investigation of the progeny of a putative cross

Total DNAs from plants of the putative maternal species D. muricatus (populations "29/78", "74A", "74B"), of the putative paternal cultivar (cv 'Vitaminaya' of D. carota sativus), and of the  $F_2$  generation, were digested with EcoRI, HindIII and BgIII and analyzed in Southern-hybridization experiments. Using radioactively labelled ctDNA as a probe, identical ctDNA fragment

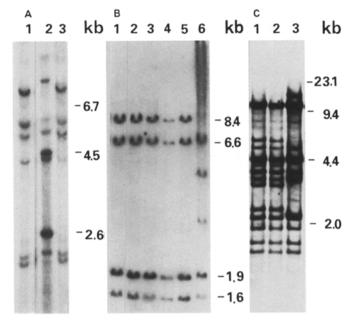


Fig. 3 A Southern hybridization, cross D. carota maximus  $\times$  D. carota sativus cv Luwal. EcoRI-digested total DNA hybridized with a 'composite' probe consisting of coxI, coxIII, coxIII and atpA. Lane 1,  $F_1$  plant; lane 2, D. carota sativus cv 'Luwal', lane 3, D. carota maximus. B Southern hybridization, cross D. carota gummifer  $\times$  D. carota sativus cv 'Vitaminaya'. HindIII-digested total DNA probed with a 11.2-kb BamHI fragment of mtDNA. Lane 1, D. carota gummifer; lanes 2–5,  $F_1$  plants; lane 6, D. carota sativus cv 'Vitaminaya'. C Southern hybridization, cross D. carota gummifer  $\times$  D. carota sativus cv 'Vitaminaya'. BamHI-digested total DNA hybridized with atpA. Lane 1, D. carota gummifer; lane 2,  $F_1$  plant; lane 3, D. carota sativus cv 'Vitaminaya'

profiles were observed in lanes containing DNA from the F<sub>2</sub> plants and the putative paternal parent. Clearly different patterns were obtained in lanes with ctDNA of the putative maternal parent, *D. muricatus* (shown for EcoRI in Fig. 5 A, for HindIII in Fig. 5 B; BglII not shown). In the case of D. muricatus, DNA from single plants of three populations of different origin were analyzed. The ctDNA patterns differed between the populations, but were identical within a population (shown for HindIII-digested DNA in Fig. 5 B). None of the D. muricatus ctDNAs displayed a pattern identical with that of the  $F_2$  plants.

We analyzed the mtDNA in the same way. Figure 6 A shows Southern hybridizations between total DNAs and a mtDNA fragment of 11.2kb. As with ctDNA, RFLPs could be observed between the D. muricatus populations but identity of the restriction fragment pattern within the populations. All F<sub>2</sub> plants had the same pattern which differed from the mtDNA of all investigated D. muricatus plants. However, in striking contrast to the situation with ctDNA, the pattern of the paternal mtDNA was also distinctly different from the pattern of  $F_2$  plants and of the D. muricatus populations (lane 11, Fig. 6 A). During the course of this study, we found a variability of mtDNA within the cv 'Vitaminaya' which served as putative paternal parent in the investigated cross. Four different restriction fragment profiles of mtDNA were evident (Steinborn et al. 1992). Additional types could not be detected within the material used in the breeding program. Since only one type of mt genome should have been present in the putative paternal parent, we compared the four types of mtDNAs present in cv 'Vitaminaya' with the mtDNAs of the F<sub>2</sub> plants. All types of mtDNA of cv 'Vitaminaya' were found to differ from the mtDNA of the F<sub>2</sub> generation. Figure 6 B depicts the restriction-fragment patterns of EcoRI-digested, radioactively end-labelled mtDNAs. Lanes 1-3 represent three out of the four types of mtDNA of cv 'Vitaminaya'. Lanes 3–5 show mtDNAs of the same type isolated from three different plants of cv

Fig. 4 Southern-blot analysis of BamHI-digested total cellular DNAs probed with coxI, coxII, coxIII, atpA, and rrn26. Lanes 1-9, single plants derived from different backcross generations (lane number corresponds to the numbers indicated in Fig. 1). Lane 10, D. carota gummifer (maternal parent); lane 11, single plant of the BC<sub>3</sub>F<sub>3</sub> resulting from selfing the BC<sub>3</sub>F<sub>2</sub> (Fig. 1); lane 12, M852; lane 13, cv 'Cyrano' lane 14, cv 'Luwal'. Asterisks indicate bands typical for the pattern of paternal parents (lanes 12, 13, 13, 14). M = sizemarker

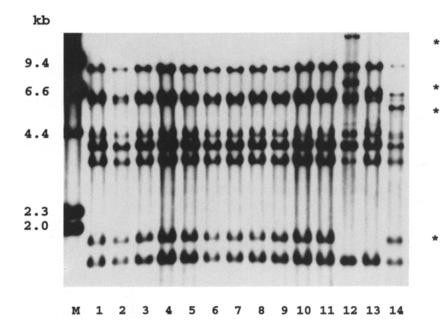


Table 2 Maternal transmission of plastid DNA in interspecific crosses of the genus Daucus: plants of all progenies listed in this table showed the restriction-fragment patterns of the maternal parent. Especially indicated are those cases in which fragments were observed only in the paternal pattern and not in the pattern of the maternal parent and of the hybrids. ("cross no." = as in Table 1; "plant no." = number of plants studied in the filial or backcross generation; "enzyme" = restriction endonuclease used to digest the DNA; "probe" = chloroplast (ct) or mitochondrial (mt) probe used in Southern hybridization. If more than one probe is listed, these probes were used together. In cross no. 10 restriction-fragment profiles of purified mtDNA were studied)

| Cross<br>no. | Plant.<br>no. | Enzyme          | Probe  |                    | Paternal     |
|--------------|---------------|-----------------|--------|--------------------|--------------|
|              |               |                 | ct     | mt                 | fragment (s) |
| 2            | 4             | EcoRI           |        | coxI, coxII        | +            |
| 2            | 4             | rnr             |        | cob                |              |
| 3            | 4             | EcoRI           |        | coxI, coxII<br>cob | +            |
| 4            | 9             | BamHI           |        | atpA               |              |
|              | 9             | HindIII         |        | 11.2 kb            |              |
| 5            | 4             | BamHI           |        | atpA               |              |
| 6            | 9             |                 |        | coxI, coxII        | +            |
|              |               |                 |        | coxIII, $atpA$     |              |
|              |               |                 |        | rrn26s             |              |
| 7            | 10            | $Hin { m dIII}$ |        | 11.2 kb            |              |
| 8            | 3             | $Bgl\Pi$        | 1.3 kb |                    |              |
|              | 10            | HindIII         |        | 11.2 kb            | +            |
| 9            | 1             | $Bgl \Pi$       | 1.3 kb |                    | +            |
|              | 6             | $Eco{ m RI}$    |        | coxI, $coxII$      | +            |
|              |               |                 |        | coxIII, atpA       |              |
| 10           | 4             | $Bgl \Pi$       | ctDNA  |                    | +            |
|              | 4             | EcoRI           |        | mtDNA              | +            |
|              | 4             | XbaI            |        | mtDNA              | +            |

'Vitaminaya' as examples of the reproducibility of the fragment pattern obtained. Lanes 6–9 contain mtDNAs of four  $F_2$  plants, and lane 10 contains mtDNA of D. muricatus population "29/78". The fragment pattern of the  $F_2$  plants clearly differs from the pattern of all putative parents. This result is neither compatible with an exclusively paternal nor with an exclusively maternal inheritance of mtDNA in this material.

#### Discussion

Two types of cms are commonly used in the hybrid breeding of carrots, the 'brown-anther' and the 'petaloid' type (e.g. Scheike et al. 1992). In the search for new types of cms systems, interspecific crosses have been performed on a large scale between the cultivated carrot, *D. carota sativus*, and wild species and subspecies (Nothnagel 1992, and unpublished). A new type of cytoplasmic male sterility was found in plants with the "gummifer" cytoplasm (Nothnagel 1992; Börner et al. 1995; Fig. 1). The usefulness of cms in breeding depends on its uniparental maternal inheritance (Kaul 1988).

A biparental inheritance of organellar, in particular mitochondrial, genes would lead to unstable expression of the male-sterile phenotype. Therefore, the observation of paternal transmission of ctDNA in one of the

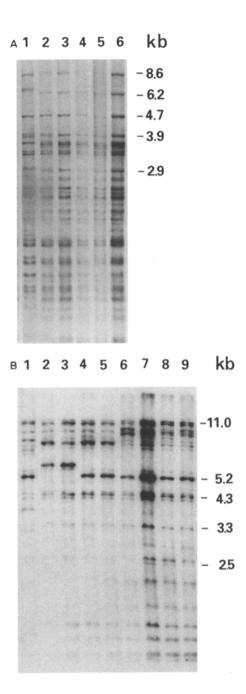


Fig 5A,B Southern hybridization, cross D. muricatus  $\times$  D. carota sativus cv 'Vitaminaya'. EcoRI- (A) and HindIII- (B) digested total DNA probed with ctDNA of D. carota sativus. A Lane 1. D. muricatus; lane 2, D. carota sativus cv 'Vitaminaya', lanes 3-6,  $F_2$  plants. Lanes 1 to 5, three origins of D. muricatus (lane 1, 74A; lanes 2, 3, two plants of 74B; lanes 4, 5, two plants of 29/78); lane 6, D. carota sativus cv 'Vit-

aminaya'; lanes 7 to 9, three F<sub>2</sub> plants

crosses from the breeding program mentioned above, D. muricatus  $\times$  D. carota sativus (Boblenz et al. 1990), led to further analyses or organellar inheritance in this material and several other interspecific crosses.

We used the same  $F_2$  generation as Boblenz et al. (1990) in our studies on the hybrids of the putative cross D. muricatus  $\times$  D. carota sativus. Our results, reported in this paper, in agreement with previous observations,

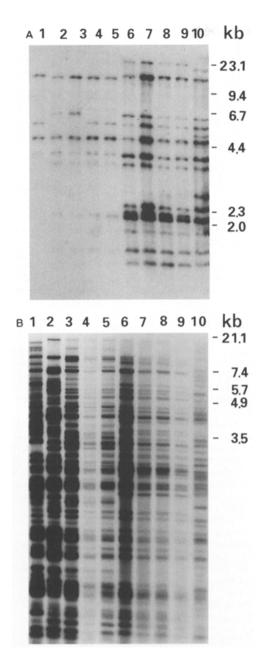


Fig. 6 Southern hybridization, cross D. muricatus × D. carota sativus cv 'Vitaminaya'. HindIII-digested total DNA probed with a 11.2-kb BamHI fragment of mtDNA. Lanes 1-6, three origins of D. muricatus (lane 1, plant of 74A; lanes 2, 3, two plants of 74B; lanes 4,5, two plants of 29/78); lanes 6-9, F<sub>2</sub> plants; lane 10, D. carotaa sativus cv 'Vitaminaya'. B Restriction fragment pattern of mtDNAs digested by EcoRI; cross D. muricatus × D. carota sativus cv 'Vitaminaya'. Lanes 1-5, single plants of the population of the paternal parent D. carota sativus cv 'Vitaminaya'; lanes 6-9, F<sub>2</sub> plants; lane 10, D. muricatus

showed that the  $F_2$  plants contained ctDNA exhibiting the same restriction-fragment pattern as the putative paternal parent which is clearly different from that of the maternal parent. The mtDNA of these  $F_2$  plants was, however, different from the mtDNA of both the maternal and the paternal parent. This result excludes an exclusively maternal or paternal transmission of

mitochondria. In the case of biparental inheritance, one would expect to find a mixture of the parental fragments or else, due to sorting out of the mitochondria during ontogenesis, the maternal or the paternal pattern, as reported for biparental inheritance in Brassia napus (Erickson and Kemble 1990). It is known from studies on somatic hybrids that mtDNAs may recombine leading to new types of restriction-fragment profiles (Medgyesy 1990). If recombination were also to occur in the case of the biparental transmission of mitochondria during sexual propagation, new types of mtDNA in the filial generation would be expected. But even biparental inheritance of mitochondria and recombination of the involved mtDNAs could hardly explain our observation of identical restriction fragment profiles in all F<sub>2</sub> plants. An alternative explanation would be that the new combination of nuclear alleles in the hybrids is responsible for the altered restriction-fragment pattern. Such an influence of the nuclear genome on mtDNA was suggested by Kiang et al. (1994) for Festuca-Lolium hybrids (see also Escote-Carlson et al. 1990; Mackenzie and Chase 1990). Since neither we nor Boblenz et al. (1990) could analyze the original parental plants, the most plausible explanation of the striking mtDNA pattern would be that hitherto unknown parents were crossed to produce the investigated F<sub>2</sub> plants and that the true maternal parent had the pattern of ctDNA and mtDNA that we found in the  $\bar{F}_2$  plants. Thus, the reported paternal inheritance of ctDNA in the cross D. muricatus × D. carota sativus remains doubtful. We tried to reproduce the cross between D. muricatus and D. carota sativus, but so far no hybrid seeds has been obtained; a fertilization of D. muricatus with pollen from D. carota sativus seems not to be feasible. Therefore, our results strongly suggest than neither we nor Boblenz et al. (1990) had the correct paternal idiotypes in our hands. The putative "F<sub>2</sub>" plants most probably did not result from a cross between D. muricatus and D. carota sativus, but from a cross with a hitherto unidentified maternal parent with the ctDNA and mtDNA observed in the "F<sub>2</sub>" plants.

Table 2 compiles the data from our investigations on all other interspecific crosses. We did not find any indication for a paternal inheritance of ctDNA and mtDNA. In all cases where the paternal pattern of organellar DNA contained one or more specific bands. we could role out the transmission of these bands to the progeny. This would also exclude biparental inheritance of the respective organellar DNA. If such a specific paternal fragment were not to exist, then a maternal transmission of the organelle would be obvious, but a paternal contribution cannot be excluded yet with sufficient probability. Kiang et al. (1994) observed a paternal transmission of organellar DNAs in backcross hybrids but not in the F<sub>1</sub> hybrids of Festuca pratensis and Lolium perenne. Hence, the degree of paternal transmission of mitochondria might depend on the nuclear background. We checked plants of several backcross generations originating from a cross between D. carota gummifer and

D. carota sativus. All these plants contained the maternal pattern of mtDNA (Figs. 1, 4). This cytoplasm leads to a new type of male sterility with flowers entirely lacking anthers (Börner et al. 1995).

Summarizing, we did not find any evidence for paternal or biparental transmission of chloroplasts and mitochondria in the investigated crosses. Our results indicate uniparental, maternal inheritance of organellar DNA in interspecific crosses within the genus *Daucus*.

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