

Observations on chromosome numbers and biosystematics in *Dahlia* (Asteraceae, Heliantheae) with an account on the identity of *D. pinnata*, *D. rosea*, and *D. coccinea*

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The chromosome numbers in *Dahlia* (Asteraceae, Heliantheae) are surveyed, and counts made on species grown in the Botanic Garden, University of Copenhagen, are given. Next a biosystematic study of species within *Dahlia* sect. *Dahlia* is presented. It is concluded that taxa with the same chromosome number can be brought to hybridize without specific barriers (some diploids possibly excepted). Based on this conclusion, it is demonstrated that the original European introduction of dahlias from Mexico consisted of two tetraploid ($2n = 64$) hybrids and a native, diploid ($2n = 32$) *D. coccinea* with scarlet rays. One of the hybrids was named *D. pinnata* which designation is consequently not applicable for the native species, currently known under that name. Instead, the new designation *D. sorensenii* is formally established. The other hybrid, *D. rosea*, is a synonym of *D. pinnata*.

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Introduction

The first taxa of *Dahlia* were established by Cavanilles (1791, 1796) as *D. pinnata*, *D. rosea*, and *D. coccinea*, being based on material sent from Mexico and grown in the Madrid Botanical Garden. A decade later, Thouin (1804) published an account on dahlia cultivation, including a coloured plate of Cavanilles' taxa, and from that date the genus caught great interest. The dahlias were considered by a number of contemporary authors (e.g., Sims 1804, Salisbury 1808, Willdenow 1809, Sabine 1818), but although most of them tried hard to understand what Cavanilles had actually described, this turned out to be very problematic. Many authors had access to seed propagated dahlias sent to various European botanical institutions from Madrid. Naturally, all took the Cavanilles' taxa to be true-breeding native spe-

cies, but in reality, *D. pinnata* and *D. rosea* were prone to segregate many new 'types' from seed propagation. At the same time, several authors had achieved plants of *D. coccinea* with yellow and orange rays, forms which deviated from the original scarlet type. All workers were thus misled by the fact that their dahlias did not fit with Cavanilles' diagnoses, and inevitably his work therefore became widely discredited. This injustice against Cavanilles led to many superfluous alterations of the original names.

The 19th century saw little interest in the native *Dahlia* species. The majority have been described after 1935 by E. E. Sherff and Paul D. Sorensen, the only workers who have studied the botany of the genus in detail. A firm taxonomic understanding of *Dahlia* was lacking until Sherff initiated his studies around 1930, ending up with a contribution to the North American

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Flora (Sherff 1955, see also Sherff 1959). It was then left for Sorensen (1969) to monograph the genus, while some additions later have been given by him (Sorensen 1980, 1987). The taxonomy is well rounded off by the latter author, and we consider Sherff's contribution to be partly out of date.

In 1969, Sorensen recognized 27 species, while *D. tubulata* was added in Sorensen (1980) and *D. congestifolia* P. D. Sorensen in Sorensen (1987). The species are placed in four sections (Sorensen 1969): sect. *Pseudodendron* Sherff (the tree-dahlias, 3 spp.), sect. *Epiphyllum* Sherff (1 sp., *D. macdougalii* Sherff), sect. *Entemophyllon* P. D. Sorensen (6 spp., incl. *D. congestifolia*), and sect. *Dahlia* (19 spp., incl. *D. tubulata*). The vast majority are endemic to Mexico.

Based on the flavonoid patterns in *Dahlia*, Giannasi (1975a, b) could sustain the taxonomy of Sorensen (1969), i.e., all his species are characterized by specific flavonoids or at least by a unique combination of these. Lam (1973) likewise found that specific polyacetylenes characterized the species which he studied.

In Copenhagen, there has been a collection of wild dahlias since 1958, where Hjerting brought back the first native species from Mexico. He has later collected there in 1983, 1984, 1988, 1991, 1993, and 1995. Our biosystematic study began in 1988.

The collection has been widely used for the studies of dahlia polyacetylenes by Lam & collaborators (e.g., Lam 1973, 1990, Neuschil et al. 1992). A joint poster by Hansen et al. (1994) on dahlia biosystematics, polyacetylenes, and the origin of cultivars was presented at the Kew Compositae Conference 1994.

Several new *Dahlia* species are currently being described in a co-work between Sorensen, Hjerting, and Hansen. In the present paper we contribute with some observations on *Dahlia* chromosome numbers and biosystematics. Using the latter as a reference, we finally document the nature of Cavanilles' original taxa. Sorensen (1969) concluded that *D. pinnata* Cav. equates to the native species described in Sorensen (1969: 359-365), but we demonstrate that Cavanilles rather diagnosed a taxon of hybridogene origin. The wild species has, in fact, never been given a name, but we formally establish the designation *D. sorensenii* for it here (see end of paper), and to this name we refer in the text; a more cumbersome reference would be: '*D. pinnata* Cav. sensu Sorensen, as to descr.'

The present paper is a short version of our original manuscript. We hope to publish more detailed accounts on aspects like ray colour designation and the early history of the cultivated dahlia (c. 1570-1836) elsewhere in the near future.

Materials and methods

All collections used for the biosystematic study (Tab. 1) are from the nature of Mexico, the majority being collected by Hjerting between 1958 and 1988. Paul Sorensen has kindly offered some additional numbers. In 1989, about 50 collections were in cultivation, while another fifty ones were added by Hjerting in 1991 and 1993. The latter numbers have hitherto mainly functioned as 'spare' collections for the biosystematic study, but many have been counted for chromosomes (Tab. 2).

The self-sterility tests were done on pot plants placed in greenhouses (one pot per section) to avoid pollination by insects.

Three methods have been adopted for pollination experiments: 1) Hand-pollination made during Sept.-Oct.) on indoor pot plants. Heads for pollen donation were cut and placed 2-3 days in water, after which plenty of pollen is set free on the summit of the anther tube. Pollen was then brushed onto the exposed maternal styles, and subsequently the pollinated head was bagged to protect it from foreign pollen. Later in the project, the heads have instead been repeatedly pollinated without any bagging. 2) Outdoor (open) pollination with two to six parental plants being placed 100-200 m away from other dahlias. 3) Outdoor (open) pollination with all the collections being placed together in general beds. Two areas have been used, the one in Taastrup, W. of Copenhagen (main collections), the other in the Botanic Garden (additional main collections, hybrids). In 1989 10 seed offsprings (harvested between 1985 and 1988) of c. 40 original collections were raised in Taastrup to test the impact of 'spontaneous' field hybridization. From this and other similar experiments, several hybrids were achieved and later hybridized further by the use of methods 1, (2), and 3. Altogether c. 2500 offsprings, originating from about 300 different experiments, have been tested during the years.

Most cytological studies were made on root-tips taken from germinating seeds or from cuttings. The tips were pretreated for 3 hours in 0.1 per cent colchicine followed by 30 minutes in Clarke's solution, then macerated in 1 N HCL for 8 minutes, transferred to Schiff's reagent for 15-120 minutes, and finally squashed before microscopy. For PMC counts a drop of orceinacetic acid was placed on a slide; the anthers (in a representative stage) were placed in the drop and prepared under the microscope; another drop of orceinacetic acid was added, the slide heated to max. 60 °C, and the anthers then squashed before microscopy.

In the text, a 'formula' is sometimes used for the citation of particular collections. *D. coccinea*, 7000, 2n = 32, rays scarlet may, for example, be abbreviated to COC 7000^{scarlet,32}. The ray colours are indicated only for *D. coccinea*, using four gross designations: yellow,

Tab. 1. List of the native *Dahlia* seed collections (all from Mexico) used in the present study. Unless otherwise specified, the numbers refer to Hjerting. In brackets the approximate number of collections actively maintained in 1995.

sect. *Dahlia*

D. apiculata (Sherff) Sorensen (2): - 7343: Puebla State, c. 26 km from Tehuacán on road to Esperanza. Rocky humid slope. 2250 m. 9.10. 1991. - 7347: Puebla State, c. 10 km along road from Coxcatlán towards Zoquitlán, turning off the Tehuacán-Oaxaca road. 1900 m. 10.10. 1991.

D. australis (Sherff) Sorensen (12): - 7098: Puebla State, road from Tehuacán to Oaxaca, turning off at Coxcatlán and going 20 km towards Zoquitlán. 2640 m. 23.10. 1983. - 7155: Oaxaca State, 16 km N. of Ixtlán de Juárez towards Tuxtepec. 2850 m. 16.10. 1984. - 7163: Oaxaca State, road from Oaxaca to Puerto Ángel, turning off at San José Pasífico and going 2.5 km towards La Fábrica. 2610 m. 18.10. 1984. - 7250: Oaxaca State, road from Tlaxiaco to Putla. 2300 m. 17.9. 1988. - 7316: Oaxaca State, 10 miles from Oaxaca along route 175 towards Tuxtepec, near km 196 from Tuxtepec. 2540 m. 26.9. 1991. - 7322: Oaxaca State, 19 miles from Oaxaca along route 175 towards Tuxtepec, km 180.1 from Tuxtepec. 2370 m. 26.9. 1991. - 7328: Oaxaca State, 41 miles from Oaxaca along route 175 towards Tuxtepec, km 146 from Tuxtepec. 2360 m. 26.9. 1991. - 7329: Oaxaca State, 43 miles from Oaxaca along route 175 towards Tuxtepec, km 143 from Tuxtepec. 2550 m. 26.9. 1991. - 7330: Oaxaca State, 44 miles from Oaxaca along route 175 towards Tuxtepec, km 141 from Tuxtepec. 2630 m. 26.9. 1991.

D. brevis P. D. Sorensen (0): - 1396: Same locality as *D. merckii* 1395 (see below). 4.9. 1958. Perished in culture c. 1965.

D. coccinea Cav. (25): - 1422: Querétaro State, road from San Juan del Río to Querétaro going north towards Bernal, Cerro Galeras. 2050 m. 5.9. 1958. - 1535: Michoacán State, near Chilchota. 1600 m. 21.9. 1958. - Inst. Biol. (52): Distrito Federal, Pedregal de San Ángel, coll. M. Pantí s.n. 1982. - 7000: Durango State, 28 km beyond San Juan Capistrano on track to Santa Lucía de la Sierra. 2490 m. 21.9. 1983. - 7051: Guerrero State, 31 km from Taxco on road to Zacualpan. 2400 m. 7.10. 1983. - 7058: Hidalgo State, 85 km from Pachuca on road to Tampico, El Banco. 1840 m. 11.10. 1983. - 7128: Morelos State, road from Cuernavaca to Toluca, 8 km from turning off route 95 towards Lagunas de Zempoala. 2600 m. 28.10. 1983. - 7162: Oaxaca State, 26 km S. of Miahuatlán on road to Puerto Ángel. 2300 m. 18.10. 1984. - 7207: Mexico State, about 6.5 km towards San Pedro Tenayac from junction with Temascaltepec-Valle de Bravo road. 1860 m. 6.11. 1984. - 7305: Mexico State, near Ixtapan de la Sal on road from Toluca. 1800 m. 21.9. 1991. - 7337: Chiapas State, c. 33 km along road from San Cristóbal de las Casas to Palenque, after turning from route 190. Stony wayside. 2200 m. 30.9. 1991. - 7342: Puebla State, c. 27 km from Tehuacán on road to Esperanza, route 125. Rocky humid slope. 2250 m. 9.10. 1991. - 7348: Morelos State, road from Cuernavaca to Toluca, 5.8 km from turning off highway 95 towards Lagunas de Zempoala. 2500 m. 12.10. 1991. - 7370: Hidalgo State, road from Pachuca to Zimapán, between km 139 and km 151. 2200 m. 17.10. 1991. - 7372, 7373, 7374 & 7375: Hidalgo State, c. 1.5 km S. of Minas Viejas on route 85 from Ixmiquilpán to Tamazunchale. 17.10. 1991. - 7379: Querétaro State, road from Tamazunchale via A.M. Terrazas to Jalpán, between El Lobo and La Lagunita, km 225.5. 1550 m. 18.10. 1991. - 7383: San Luis Potosí State, km 216 on road from Rio Verde to San Luis Potosí. 1950 m. 19.10. 1991.

D. merckii Lehm. (7): - 1395: Mexico State, road from Mexico City to San Juan del Río, km. 167 near Calpulalpan, San Martín. 3100 m. 4.9. 1958. - 7079: Mexico State, near Lagunas de Zempoala. 2900 m. 19.10. 1983. - 7180: Puebla State, route 129 from Puebla to Teziutlán. 2350 m. 30.10. 1984.

D. rudis P. D. Sorensen (1): - 7352: Mexico State, road from Cuernavaca to Toluca, just inside the entrance to Parque Nacional Lagunas de Zempoala. 2700 m. 12.10. 1991.

D. sherffii P. D. Sorensen (6): - 1235: Chihuahua State, Majalca, 40 miles NW. of Chihuahua. 14.8. 1958. 2100 m. - 7266: Chihuahua State, NW. slope of Sierra Mohinoa. 2870 m. 9.10. 1988. - 7269: Chihuahua State, 18 km from Vergel towards Parral. 2650 m. 10.10. 1988. - 7272: Chihuahua State, Río Verde, between Vergel and Parral. 2400 m. 10.10. 1988. - Spooner s.n.: Chihuahua State, Bahuichivo railway station. 11.10. 1988. - 7402: Chihuahua State, c. 20 km from Vergel towards Parral. 2550 m. 26.10. 1991.

D. sorensenii H. V. Hansen & Hjert. (5): - Sorensen 6490: Mexico State: 1.5 miles N. of Villa Guerrero. Sept. 1966. - Sorensen 6519: Intraspecific cross between two wild populations. April 1967. - 7308: Mexico State, near Coatepec S. of Toluca. 2200 m. 21.9. 1991.

D. tubulata P. D. Sorensen (1): - 7069: Coahuila State, 8 km above Los Lirios, E. of Saltillo. 2550 m. 14.10. 1983.

sect. *Pseudodendron*

D. imperialis Roezl ex Ortgies (5)

D. tenuicaulis P. D. Sorensen (2): - 1722: Oaxaca State, Sierra de Juárez, road from Oaxaca to Ixtlán de Juárez, 13.5 miles from Oaxaca-Tehuantepec highway. 2700 m. 21.10. 1958.

sect. *Entemophyllon*

D. dissecta S. Watson (1)

Tab. 2. Chromosome numbers for collections of *Dahlia* grown in Copenhagen and some of their hybrids. * the father has been verified from 'inferential evidence'. (h) = PMC count. Three counts made by Dr Hong Ding, University of Auckland, and two made by Prof. Sorensen are cited by permission.

Species	chromosome-number ('n')	year of investigation
<i>D. apiculata</i>		
- 7343	16	1995
- 7347	16	1994 (Sorensen)
<i>D. australis</i> (AUS)		
- 7098	32	1990
- 7155	32	1992
- 7163	16 (h)	1994 (Sorensen)
- 7250	16	1994
- 7316	32 (h)	1994
- 7322	16 (h)	1994
- 7328	16 (h)	1994
- 7329	32 (h)	1994
- 7330	32 (h)	1994
(AUS 7163 × COC 7051*)	16 (h)	1994
((AUS 7163 × COC 7051) × 4n), see text	32 (h)	1995
<i>D. brevis</i> 1396	16	1959
<i>D. coccinea</i> (COC)		
- 1422 (scarlet)	16	1959
- 1535 (scarlet)	16	1959
- 7000 (scarlet)	16	1991
- 7051 (yellow)	16	1994
- 7058 (dark red)	32	1993
- 7128 (yellow)	32	1990
- 7162 (orange)	32 (h)	1994
- 7207 (orange)	16	1991
- 7305 (orange-red)	16 (h)	1995
- 7337 (orange)	32 (h)	1995
- 7342 (orange-red)	32 (h)	1995
- 7348 (yellow)	32 (h)	1995
- 7370 (dark red)	32 (h)	1995
- 7372 (dark red)	32 (h)	1995
- 7373 (dark red)	32 (h)	1994
- 7374 (dark red)	32	1994 (Hong Ding)
- 7375 (dark red)	32	1993
- 7379 (dark red to blackish red)	32	1995
- 7383 (dark red)	32	1995
- Inst. Biol. (52) (orange)	16	1994 (Hong Ding)
(COC 1422 × SHE 7272)	16 (h)	1994
(COC 7000 × TUB 7069)	16	1992
(COC 7058 × AUS 7155*)	32	1992
(COC 7162 × AUS)	32 (h)	1994
<i>D. merckii</i> (MER)		
- 1395	18	1959
- 7079	18	1994
- 7180	18	1994
<i>D. rudis</i> 7352	16	1993
<i>D. sherffii</i> (SHE)		
- 1235	32	1959
- 7266	16	1994 (Hong Ding)
- 7269	16	1991
- 7272	16	1994
- 7402	32 (h)	1995
- Spooner s.n.	32	1990
(SHE 7269 × AUS 7163)	16 (h)	1995
((SHE 1235 × COC 7058*) × AUS 7155)	32	1991
((SHE 1235 × COC 7058*) × AUS, 7155) × SOR, Sor. 6490)	32	1991
<i>D. sorensenii</i> (SOR) Sorensen 6519	32	1990
<i>D. tenuicaulis</i> 1722	16	1959
<i>D. tubulata</i> (TUB) 7069	16	1990

orange, scarlet, and dark red. All other species used in our biosystematic study roughly spoken have purple or purple-violet rays.

Unless otherwise indicated, the hybrid data refer to observations made on plants grown in the general beds and with access to partners of equal as well as 'opposite' ploidity.

Chromosome numbers in *Dahlia*

The species in sect. *Entemophyllon* have $2n = 34$, while $2n = 32$ for the tree-dahlias (Sorensen 1969). No count exists for *D. macdougallii*. In sect. *Dahlia* $2n = 32$ or 64 with the exception of *D. merckii* Lehm. which is unique by having $2n = 36$ (Sorensen 1969 & Tab. 2). Our diploid count for *D. sherffii* was not reported by Sorensen (1969). The standard chromosome book references concur with his general observations. Only Sundberg et al. (1986) have given a surprising report of $2n = 24$ for *D. australis*; this breaks an otherwise very regular pattern of chromosome numbers in the genus. The count of Sundberg et al. for 'cf. *D. apiculata*' ($2n = 36$) may warrant verification.

Biosystematics

A biosystematic study of *Dahlia* is rather difficult to perform in Denmark, since the wild species are not adapted to our long day conditions and climate. These problems have especially concerned the important species *D. coccinea*, while *D. apiculata*, *D. rudis*, *D. dissecta*, and the tree-dahlias seldom flower with us.

For crossing experiments, indoor hand-pollination was usually tried first, but it often shows up to be a trial-and-error method (Tab. 3). Furthermore, the method may be inapplicable, since many collections are not well suited for indoor growth. The outdoor isolated pollination method (2) was optimized, once the ploidity of the various collections had been verified, but during the warm summers 1993-1995 many arrangements have failed to give results. The open field pollination method (3) is often a more safe alternative. In this case, the pollen donor must be verified from 'inferential evidence', but that rarely constitutes a problem for two-species hybrids. However, a general restraint on the project has been the rather limited access to diploid collections which besides are the most sensitive to climatic fluctuations. All potential hybrids must be brought into flower, before their intermediate morphology can be verified.

Because of these many shortcomings, a few compatible parents (in Tab. 3) still await to be mated, but the general conclusions are clear by now. One major aspect of our study has been to reconstruct the cultural history

Tab. 3. Two-species hybrids achieved in the project. 'Intraspecific hybridization' is indicated only for *Dahlia coccinea*. Boldfaced taxa are diploid, all other ones tetraploid. In the column 'indoor hand-pollinated', the fraction indicates the number of experiments and the outcome (e.g., 2/1 = two different plants pollinated, one cross being successful; one to many heads may have been pollinated per plant). () = number of hybrids grown to maturity. If an experiment instantly lead to success, no repetition has usually been made. - = no experiments. Indoor pollination has not been extensively used since 1991. In the column 'outdoor isolated', 1/1 means that one group of plants has been isolated with success and given the number of hybrids indicated in brackets; tests which have failed completely (i.e., from lack of appropriate flowering) are not included. In the column 'outdoor open pollination', the numbers refer to the sum of individuals hitherto achieved. n = approx. number of offsprings tested during the years; the maternal taxa have generally had access to all potential partners included within the table. - Note: Collection 1560 (see Lam 1973) is a yellow-rayed, naturally (?) occurring hybrid (*D. coccinea*_{yellow, 64} with introgression from *D. sorensenii*) which has been widely used in the study as a 'substitute' for the late flowering COC 7128. The many hybrids achieved with 1560 are not included.

maternal	paternal	indoor hand-pollinated	outdoor isolated	outdoor open pollination	n
<i>australis</i> 7078, 7155	COC 7000	1/0	-	0	120
	COC 7058	-	-	2	
	COC 7128	2/0	-	0	
	SHE	3/0	1/1 (2)	0	
	SOR	2/0	-	>5	
	TUB	3/0	-	0	
<i>australis</i> 7163	COC 7051	-	-	1	20
<i>coccinea</i> 1422	SHE 7272	-	1/1 (1)	-	70
<i>coccinea</i> 7000	AUS	3/0	-	0	70
	COC 7128	2/0	-	0	
	SHE	2/0	-	0	
	SOR	4/0	3/0	0	
	TUB	1/1 (>5)	see text	0	
<i>coccinea</i> 7058	AUS	-	-	5	30
	COC 7128	-	-	0	
	SHE	-	-	0	
	SOR	-	-	2	
	TUB	-	-	0	
<i>coccinea</i> 7128	AUS	1/1 (2)	-	1	30
	COC 7000	1/0	-	0	
	COC 7058	-	-	0	
	COC 7162	-	-	2(?)	
	SHE	-	-	0	
	SOR	1/0	-	2	
	TUB	2/0	-	0	
<i>coccinea</i> 7162	AUS	-	-	1	15
<i>coccinea</i> 7375	AUS	-	-	1	30
	COC 7128	1/1 (>20)	-	1	
	SOR	1/1 (>20)	-	1	
<i>sherffii</i> 1235, Spooner s.n.	AUS	-	1/1 (1)	0	60
	COC 7000	-	-	0	
	COC 7058	-	-	5	
	COC 7128	1/0	-	0	
	SOR	1/1 (4)	-	2	
	TUB	1/0	-	0	
<i>sherffii</i> 7269	AUS 7163	1/1 (1)	-	-	25
<i>sorensenii</i> 6490, 6519	AUS	2/1 (1)	-	3	110
	COC 7000	4/0	3/0	0	
	COC 7058	4/0	-	0	
	COC 7128	1/1 (1)	-	1	
	SHE	1/1 (1)	-	0	
	TUB	3/0	-	0	
<i>sorensenii</i> 7308	COC 7375	-	-	1	10
<i>tubulata</i> 7069	most other species	1-3/0	see text	0	80
<i>rudis</i> 7352	most other species	-	-	0	10
<i>merckii</i> 1395, 7180 a.o. (2n = 36)	most other species	1-2/0	-	0	140

of dahlia by the use of extant material, for which purpose we have simply tried to mate all available species pairwise. There has been no demand for invoking the traditional biosystematic method (with its series of controlled crosses, staining of F1 pollen etc.). Furthermore, this method has recently been rather discredited. As demonstrated by Seberg (1989), crossing ability does not necessarily imply a very close relationship between two parental species, interfertility being plesiomorphic relative to intersterility.

Self-sterility tests

Sorensen (1969: 406) concluded that most dahlia species are self-incompatible, while Lawrence's remarks on this question were somewhat ambiguous (Lawrence 1929, 1931a, 1932, 1970).

According to our tests, performed on indoor plants, *D. merckii* is perfectly self-fertile. All other species tested are generally self-sterile, but late in the season a few achenes (cypselas) may now and then ripen on some of the diploid taxa.

From these observations, one would expect *D. merckii* to be self-fertile also in the open field. In reality, this seems to count for most diploid taxa. Single specimens of *D. australis* (7250), *D. coccinea* (1422, 7000), *D. merckii* (1395, 7180), and *D. tubulata* (7069) have often been planted in isolation or at least far removed from partners, and all have repeatedly been shown to self-fertilize.

We surmise that the tetraploid taxa are practically self-sterile when being grown in the general beds or in outdoor isolation, but there may be exceptions to this.

Biosystematic conclusions and discussions

The following conclusions on interspecific hybridization are based on the six most common members of sect. *Dahlia* (Tab. 3). They count for field pollination under optimal conditions:

1. Diploid species ($2n = 32$), or the diploid stock of species which also includes tetraploid forms, can be brought to cross, although often with difficulty and some strains possibly excepted.

Only four diploid interspecific hybrids have been achieved during the years, but notably they involve all available species (*D. australis*, *D. coccinea*, *D. sherffii*, and *D. tubulata*). We therefore ascribe some of the problems with raising diploid hybrids to the difficulties outlined above. On the other hand, much tested strains like AUS 7250, COC 7000, and TUB 7069 have never hybridized in the general beds, documenting their general unwillingness to cross at all (cf. Tab. 3).

(COC 7000^{scarlet} × TUB 7069) was raised back in 1988. All efforts for achieving the reciprocal cross have failed, and hence there is an obvious crossing barrier between the parents, to be broken only by chance from enforced indoor hybridization. The seven offsprings remain completely sterile. They expose definite hybrid vigor, being up to 2.5 m tall, while the parents rarely exceed 1.5 m in height. On the other hand, three further offsprings were retarded and soon perished.

(AUS 7163 × COC 7051^{yellow}) is also taller than its parents. It is partly fertile, but among the hundreds of achenes sown out since 1990, the majority have been poorly developed and failed to germinate.

For (COC 1422^{scarlet} × SHE 7272) and (SHE 7269 × 7163 AUS) no certain data on fertility are available.

2. Tetraploid species ($2n = 64$), or tetraploid stocks of species which also include diploids, cross freely as do their hybrids of any complexity. Furthermore, unlike the diploid counterparts, all tetraploid hybrids are perfectly fertile.

This conclusion is firmly documented. 'Complex' hybrids, involving all the four tetraploid species, have been achieved without problems (cf. Tab. 2, further information on these secondary hybrids is not included).

The conditions for raising tetraploid two-species hybrids have varied considerably. Maternal plant(s) will be especially prone to hybridize outdoors when 1) they are tall growing and flower profoundly throughout the season (like *D. sorensenii*); 2) only one well flowering specimen of a collection has been retained in the general beds, since it has then been forced to cross with foreigners (like SHE 1235 & Spooner s.n., COC 7058); 3) two well flowering parents have been planted in juxtaposition, since pollination predominantly takes place between neighbouring plants.

3. Diploid species cannot cross with tetraploids, but see below under 'alternative hybrid pathways'.

4. *D. merckii* cannot cross at all. Although the self-fertility of the species possibly interferes, it seems safe to make this conclusion, cf. Lawrence (1970) and Sorensen (pers. comm.). *D. merckii* is undoubtedly well nested within the genus, but has several autapomorphies, among others the deviating $2n = 36$.

From these conclusions one may assume that the sect. Entemophyllon members ($2n = 34$) cannot mate with other dahlias. But since the tree-dahlias like most sect. *Dahlia* members have $2n = 32$, it might be theoretically possible to cross representatives of these two sections. However, already within sect. *Dahlia* it would appear difficult to mate the remaining diploid species (which commonly are morphologically very distinct) with those already studied. In contrast, the two remaining tetraploid species within the section, viz., *D. atropurpurea* P. D. Sorensen and *D. barkerae* Knowles & Westc. (Sorensen 1969), should cross freely with the other tetraploids.

Intraspecific hybridization

When populations of tetraploid dahlia species are grown together in the outdoor beds, approximately one tenth of their offsprings will be interspecific hybrids, but the fraction varies much with the growth conditions. The remaining c. 90 per cent breed true in the sense that they at most exchange pollen with other collections of the same species ('intraspecific hybridization'). The latter is about as common as interspecific hybridization which would also be expected, since all the tetraploids mate freely.

The diploid taxa constitute a more interesting group. Morphologically distinct strains like AUS 7250 (disc yellow, in all other *D. australis* grown by us it is blackish) and COC 7000 breed true in the strictest sense, i.e., they do not even exchange genes with other diploid members of the same species. In contrast, almost identical collections like SHE 7266/SHE 7272 and COC 1422/1535 can be 'crossed' pairwise quite easily. There is thus provisional evidence for concluding that the morphologically distinct diploid collections tend to never mate at all, while the less distinct ones are more willing to exchange genes.

Alternative hybrid pathways

During his pioneer studies around 1930, W. J. C. Lawrence was in rare cases able to cross a genuine diploid *D. coccinea* with the always tetraploid garden dahlia after two alternative pathways (Lawrence & Scott-Moncrieff 1935, Lawrence 1970):

- a. diploid \times tetraploid = triploid (the offspring sterile) or
- b. diploid \times tetraploid = tetraploid (the offspring fertile).

Sorensen (pers. comm.) has from hand-pollination obtained a few two-species hybrids, presumably following route b, but our amplified tests document that chromosome doublings must be very rare events. There is only one verified example: (AUS 7163 \times COC 7051) was crossed indoors with *D. sorensenii* in 1990, and although most heads withered, two tetraploid hybrid plants were raised and grown to maturity. A few additional ones were obtained outdoors in 1994 (with a father of 'complex' origin). These unusual events clearly pertain to the fact that the mother had been submitted solely (1990) or mainly (1994) to tetraploid partners, leading to a few 'forced' cases of chromosome doubling. SHE 7266 also appears to have doubled in the general beds (1993, no counts available; the offsprings are more stout in habit than their mother). However, we have not observed any further events of chromosome doubling within our material, and no triploid hybrids have been encountered by us. We therefore conclude that the alternative pathways in practice can be disregarded.

Ray colour genetics

Lawrence studied about eight native species of *Dahlia* which he arranged into two groups according to their ray colours (Lawrence 1929, Lawrence 1931a, Lawrence & Scott-Moncrieff 1935). Group 1 has ivory-purple rays governed by the flavonoid ray factor I (ivory, commonly denoted as 'white' or 'whitish') and the anthocyanic ray factor A (purple), while group 2 has yellow-orange-red rays governed by the corresponding factors Y and B. See Bate-Smith et al. (1955) for further elaboration of the generalized terms 'anthocyanic' and 'flavonoid' and compare with Giannasi (1975a, b). The anthocyanic colours overlie and mask the weaker flavonoid colours, except when the former ones are bottom recessive (I_xA_0 is thus 'whitish', while Y_xB_0 is yellow). Plants without the ability to develop flavonoids will lack vigor and may possibly perish.

In diploid native species, factors IA resp. YB are present in max. four dominant doses (I_4A_4 or Y_4B_4), while in the tetraploids the ray factors are assumed to occur in max. eight doses. As indirect evidence for this consider the data for *D. coccinea* in Tab. 2. All the dark red collections are tetraploids, while all the scarlet ones are diploids. Consequently, in *D. coccinea* there is a correlation between the depth of the 'red' ray pigmentation and the number of dominant ray colour factors. The same may apply to yellow *D. coccinea* (Y_xB_0), but we have not had enough material to investigate this aspect. Orange forms may be either diploid or tetraploid (Tab. 2). Their Y_x/B_x ratio must be relatively high, enabling factor Y to partly 'dilute' the influence of B (see Lawrence & Scott-Moncrieff (1935) for details).

We know today that only *D. coccinea* and the always yellow-rayed *D. tenuis* B. L. Rob. & Greenm. definitely belong to the YB group of native species, but according to Giannasi (1975b) *D. cardiophylla* S. F. Blake & Sherff may also belong here. All other species fall into the IA series (see Giannasi [1975b] for notes on *D. rudis* and *D. atropurpurea*). Only within four of these, ivory populations have been reported (Sorensen 1969), but *D. dissecta* strain 7371 also has this colour. Such rays may be bottom recessive for ray factor A, but the case is probably more complex; otherwise, ivory rays should be further distributed within the AI series than presently known. With respect to anthocyanic colour intensity, rays of *D. tubulata* 7069₃₂ and *D. australis* 7250₃₂ are more faintly tinged than those of *D. sorensenii*₆₄, but within *D. sherffii* the overall variation is continuous (data not included). *D. rudis* 7352₃₂ and all *D. australis* (except 7250) have a very deep pigmentation. In the AI series, any possible correlation between the number of A factors and the ray colour intensity therefore may be obscured by the existence of several 'types' of A (and I) pigments. Likewise, the ray colour of *D.*

tenuis is different from that found in any yellow form of *D. coccinea* (as noted by Hjerting in the field). These observations are in accordance with Giannasi (1975a,b), who found that the ray chemistry of native dahlia species is much more complex than presented here, albeit not with respect to anthocyanins.

When ray factors IA are mixed with YB, the IAYB hybrid will achieve reddish rays, since red weights more than purple in the cross (Lawrence 1931a, Lawrence & Scott-Moncrieff 1935). The intensity will, however, vary with the number of B factors, and it is therefore usually easy to verify the paternal ploidy of such hybrids.

IAYB forms mix four very different colours, and since the outcome may principally vary between $I_{1,4}A_{1,4}Y_{1,4}B_{1,4}$, there will be 256 theoretical hybrid combinations (4^4) plus forms where one or more factors are bottom recessive (X_0 , for details we refer to Lawrence). A host of colours have been observed during our study, amplified from the use of the deeply pigmented *D. australis*.

The so-called garden dahlia is an IAYB plant which has been submitted to breeding. Only Lawrence has presented a theory for its descendance (see, e.g., Lawrence 1931a, 1970): His postulate was that some native diploid IA species had crossed with some native diploid YB species; the resulting IAYB hybrid was presumably sterile. A chromosome doubling (to $2n = 64$) gave origin to the first primitive garden forms, while at the same time restoring full fertility in these.

Lawrence was not familiar with any tetraploid native species, but clearly the order of events must have been opposite to that proposed by him. Populations of tetraploid AI resp. YB species occur already in the nature, and since they cross without any barriers, it was no problem for the indians to achieve the first IAYB hybrids back in old Mexico (see below). Sorensen (1969) has later shown that all garden forms descend from only two species, viz., *D. sorensenii* (IA) and *D. coccinea* (YB). Both species are very prosperous and besides common in the vicinity of Mexico City.

Lawrence's idea of partial sterility for diploid IAYB hybrids (Lawrence 1931a) has been sustained by our study. In contrast, all tetraploid IAYB (and interspecific IA × IA) hybrids are perfectly fertile, since in the hybrid meiosis each parent will have an identical partner, and the tetraploids therefore tend to be 'functional diploids' (cf. Lawrence 1931b).

The data suggest that tetraploid lines have evolved independently within the specific limits of six sect. *Dahlia* species. Diploid forms of *D. atropurpurea*, *D. barkerae*, and *D. sorensenii* may await to be detected, or they could be extinct by now. It is thus postulated that the mutual crossing ability among the tetraploid taxa is a secondary phenomenon which lends no phylogenetic information. Our results further document that species populations with different ploidy level cannot be

brought to 'cross'. The problem is, however, that within the three species concerned (*D. australis*, *D. coccinea*, and *D. sherffii*), the morphology is continuous (Sorensen 1969 and pers. obs.). The scarlet and dark red forms of *D. coccinea* (discussed above) make no exception to this, because when the yellow and orange types are added, there is a continuous variation also within that species.

The identity of Cavanilles' taxa

Lawrence and Sorensen have both illuminated on this problem, but they reached rather deviating conclusions. According to Lawrence (1970) *D. pinnata* was of hybridogone origin (no parents indicated), while Sorensen (1969, 1970) took *D. pinnata* to represent the wild species described in Sorensen (1969), notwithstanding that Cavanilles presumably diagnosed a domesticated plant. According to Sorensen, it was only after the introduction to Madrid that 'the native *D. pinnata*' (i.e., *D. sorensenii*) came to cross with *D. coccinea*.

The latter taxon was a 'single-flowered' plant, and from Cavanilles' aptly chosen epithet, we safely deduce this to have been a native diploid form with scarlet rays. The plant was later colour illustrated by Willdenow (1809: Tab. 96), having a striking resemblance with COC 7000.

In contrast, *D. pinnata* and *D. rosea* were both tetraploids, as also acknowledged by Lawrence as well as Sorensen. *D. pinnata* had 4 to 5 series of 'rays', while *D. rosea* was 'single-flowered'. Our historical tracing documents that these plants were very prone to segregate new 'types' from seed-propagation, notwithstanding that their number must have been very limited. Consequently, the constitution of *D. pinnata* and *D. rosea* was IAYB, since had it been IA, the potential for variation would have been much less pronounced.

Native dahlia hybrids are rarely seen in the nature of Mexico. Presumably, therefore, the first IAYB plants originated in the old Mexican gardens. The indians simply had to bring specimens of *D. sorensenii* and *D. coccinea* into cultivation, after which hybridization would take place immediately. There was no demand for any 'controlled' domestication, since hosts of hybrids would be achieved from plain seed propagation. Nevertheless, the indians must have nursed their dahlias rather intensively. A 'semi-double' as well as a 'perfectly double' form were illustrated already by Hernandez around 1570 (Sorensen 1970), and these could not have originated by chance in the old Mexican gardens. The dahlias were therefore well domesticated at least three centuries before Cavanilles established the genus!

The 'double-flowered' condition is a trait usually linked with hybrid vigor. What Sorensen (1969) indi-

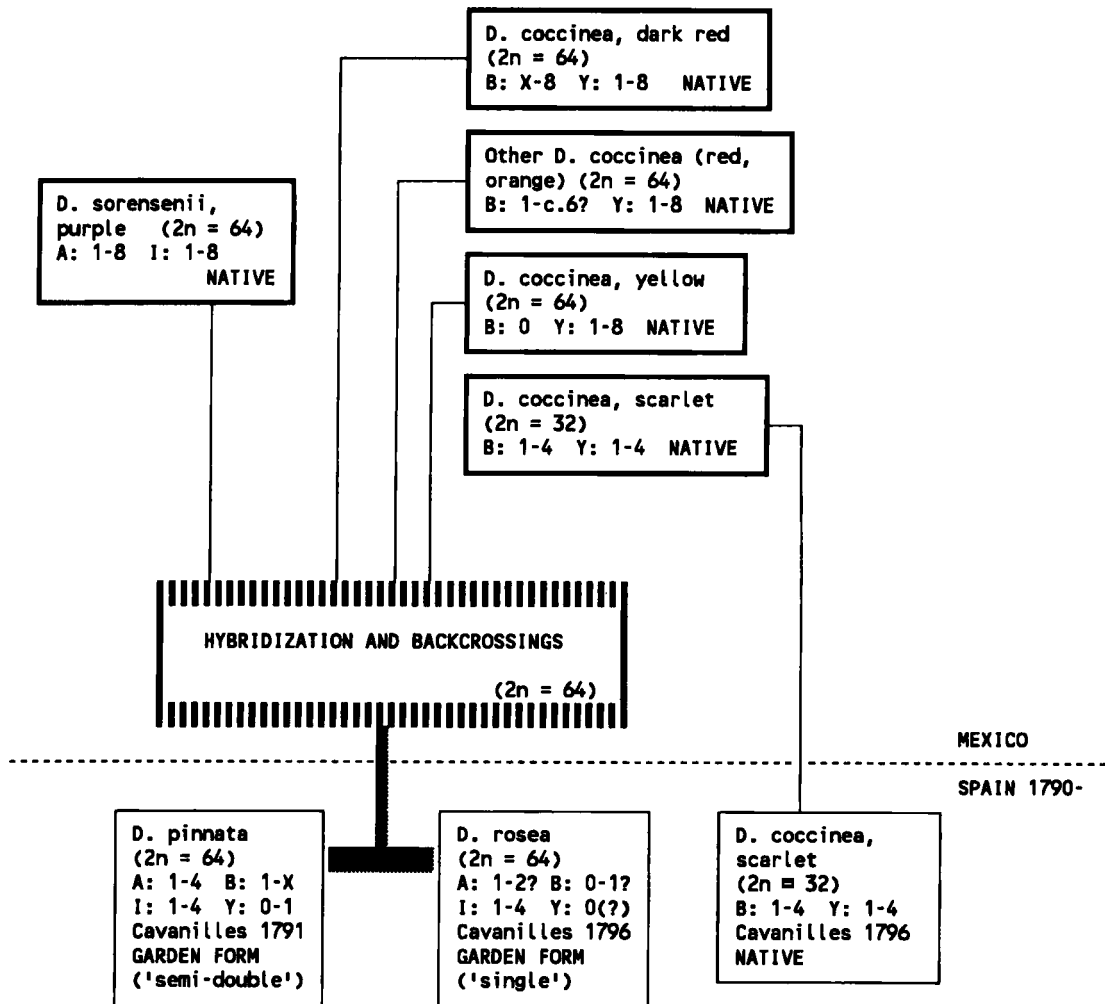


Fig. 1. The early history of the cultivated dahlia.

rectly postulated was, however, that prolonged infra-specific selection on 'the native *D. pinnata*' had led to 'semi-double' forms like the one described by Cavanilles. But even if we accept this as a remote possibility, it would not count for the dahlias, since the Indians should then have kept *D. sorensenii* and *D. coccinea*₆₄ isolated for many generations. They had no purpose for doing that and could not have managed such a task.

Sorensen emphasized that Cavanilles attributed only one ray colour, 'purple' or literally spoken 'coeruleo-rubens', to his *D. pinnata*. Truly, many colours would have been expected for an IAYB taxon, but since Cavanilles at most had a few plants on which to base his diagnoses, there would be little, if any, detectable variation to describe. It was only from seed propagation that the potential for segregating new forms could reveal itself.

D. pinnata originated in Mexico from hybridization

(and cases of backcrossing) between two native *Dahlia* species (Fig. 1). The origin of *D. rosea* is also quite obvious. Already Willdenow (1809) concluded that it was simply a form of *D. pinnata*. His view soon came to be accepted, but as time passed, the identity of both taxa became highly confounded. *D. pinnata* mainly segregated 'single-flowered' offsprings from seed-propagation ('doubleness' is the recessive state, Lawrence 1970), and the authors which succeeded Cavanilles therefore mostly had access to 'single' forms of dahlia. The original *D. rosea* may have been a seed segregate harvested in Mexico on a type resembling *D. pinnata*, or both its parents may have been 'single-flowered'. *D. rosea* was a light coloured type, presumably being almost recessive for anthocyanin.

The diploid specimen(s) of *D. coccinea* were unable to cross with the Madrid tetraploids, and hence it/they

played no role for the development of the European garden dahlia (Fig. 1). It is not known when the first tetraploid forms of *D. coccinea* came to Europe, but Humboldt may have introduced them in 1804 (data not included).

The native taxon, currently known as *D. pinnata*, has never been named, but we formally do this below.

***Dahlia sorensenii* H. V. Hansen & Hjert.**

Herba perennis, 10-18 dm. alta. Folia media pinnatifida vel pinnata ad bipinnata; petiolus saepe alatus pinnis basilaribus decurrentibus; pinnis superne rugatis. Capitula grandis, involucrium usque ad 2.5 cm. latum. Flosculi ligulati maximam partem purpurei. Crescet in Mexico.

Type: 'Federal District, Sierra de Ajusco, 8500 ft. Sept. 6th, 1905', C.G. Pringle 13546 (C, holotype!, CAS, GH, MICH, US, isotypes, n.v.).

Syn.: *Dahlia pinnata* Cav. sensu P. D. Sorensen non Cav., as to descr. (Sorensen 1969: 359-365).

Note: It is an odd task to name this species which was described so well by Sorensen (1969), but wrongly applied to *D. pinnata* (in accordance with Sherff (1955)). However, it gives us the opportunity to acknowledge Paul Sorensen by naming the species after him. As to the choice of type, the situation is also peculiar. Until 1969, there was no historical evidence to rely on, not even in Sherff (1955). It therefore seems logic to select a type specimen from among the citations in Sorensen (1969), and we have chosen Pringle 13546. Sorensen did not quote the sheet at C, but it was later (1970) determined by him.

D. pinnata is a hybrid taxon, and the synonyms given by Sorensen (1969: 359-360, sub *D. pinnata*) all pertain to this. With respect to Sorensen's list of 'Doubtful, Excluded and Rejected Names' we have two comments:

Dahlia juarezii Van der Berg: This name was based on hybrid material, not on a genuine *D. coccinea*.

Dahlia rosea Cav. is a synonym of *D. pinnata*.

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