

CYTOTAXONOMICAL STUDIES IN THE *CHRYSANTHEMUM LEUCANTHEMUM* COMPLEX

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The Ox-eye Daisy is very polymorphic and a large number of infraspecific taxa have been described by various authors (see, e.g. Briquet & Cavillier, 1916, 86-88, and Horvatić, 1935). The polymorphy undoubtedly is most striking when material from various parts of the whole range is considered. In a small area like Denmark the variation appears to be moderate. In the years 1949-56, we have collected material in various European countries for experimental cultivation and chromosome studies. In this material we were able to confirm the euploid series of chromosome numbers, $2n = 18, 36$ and 54 found by Dowrick (1952) in material from botanical gardens. The three cytotypes, however, apparently rarely occurred in the same area, suggesting three geographically distinct series of races. Dowrick (1952) states that there are no significant changes in form, apart from size and growth-rate, with increase in the degree of polyploidy and does not consider the cytotypes to be separate species. In our experiments, however, it is quite apparent that most diploids differ from the tetraploids in life-form (duration of life) and in some morphological characters. A taxonomic separation between the cytotypes, therefore, is not at all out of the question but an exhaustive systematic treatment must be postponed until more cultivation experiments and observations can be taken into consideration. The present paper only touches on some of the more important taxonomical questions. It is hoped that the differences which are reported below may prove stimulating and invite further studies. We should very much like to receive information which might complete our present knowledge of the distribution and should further be grateful to anyone who would supply us with seed collected in nature, accompanied by some notes about the habitat and the locality.

CHROMOSOME COUNTS PUBLISHED BY PREVIOUS WRITERS

The tetraploid number $2n = 36$ was first reported by Tahara (1915, 1921) who studied plants of unknown origin. It was further found by Orth, in 1926 (Tischler, 1950), by Shimotomai (1938) in material from Innsbruck and Kaiserstuhl, by Cooper and Mahony (1935) in var. *pinnatifidum* from N. America, and by Dowrick (1952) in garden material. The diploid number, $2n = 18$, also reported by Dowrick, was first found by Polya (1950) in Hungarian material from the province Hajdú-Bihar (along a railway bank). Quite recently Duckert and Favarger (1956) found $2n = 18$ in var. *alpicola* Gremlí from the Jura. The hexaploid number was found by Dowrick (1952) in garden material.

CHROMOSOME COUNTS IN THE PLANTS USED FOR EXPERIMENTAL CULTIVATION

1. *Diploids*. Nine diploid strains were studied (see Table 1). In one of these, No. 3490 from Denmark, a small fragment chromosome occurred. During diakinesis it was frequently attached to the end of a rod-shaped bivalent. Duckert & Favarger (1956) found a rather high frequency of meiotic irregularities in the diploid var. *alpicola*. In

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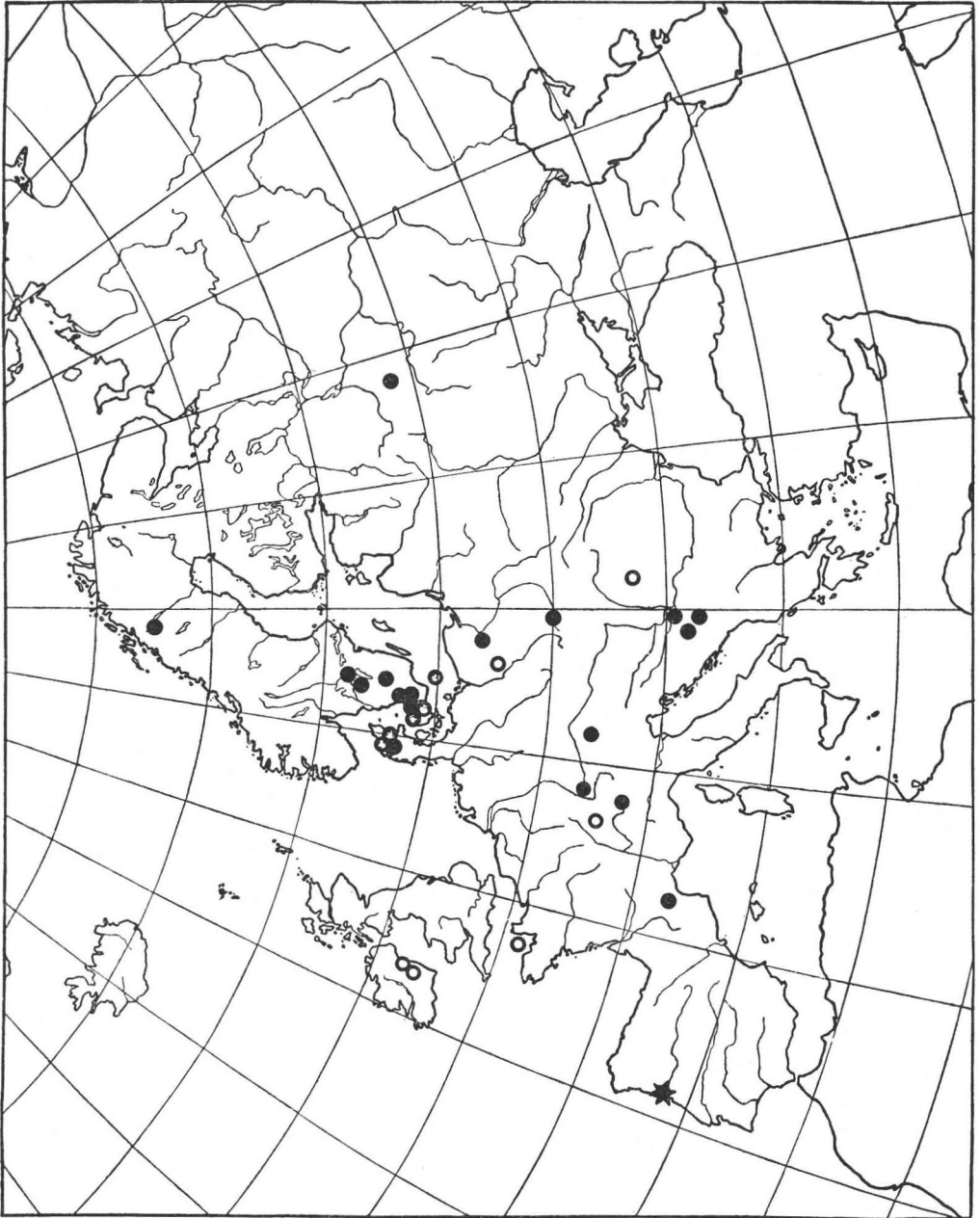


Fig. 1. Distribution in Europe of the three cytotypes in the *Chrysanthemum leucanthemum* complex. Rings : Diploids (*C. leucanthemum* L.); Solid dots : Tetraploids (*C. irtutianum* Turcz.). Asterisk : Hexaploids (*C. pallens* Gay).

culture the diploid plants were frequently short-lived perennials and flowered in the first year of cultivation. After luxuriant flowering in the second summer, they died or were very much weakened and died after the third summer. None of the diploid strains was perennial, when cultivated in the experimental field. In nature the diploid population in Naesby Dale (No. 2733) was covering the hill slopes one year (Böcher, Christensen and Christiansen 1946, Fig. 3 and Plate 6, Fig. 1) while some few years later the plants in the same spot were scattered and of subordinate importance.

TABLE 1.

Cult. No.	2n	Country	Station	Habitat	Pollen diameter in μ									
					21	24	27	30	33	36	39	42	45	
3718	18	Poland	Puszczykowo (district Poznan)*											
3136	18	Eire	Scraw Bog	Meadow		2	34	60	4					
3140	18	Eire	Edenderry	Gravel-pit		5	12	63	18	2				
3276	18	Jersey	Grosnez Castle	Windyslope	3	8	24	63	2					
2668	18	Denmark	Kongerslev, North Jutland	Grassland			11	48	39	2				
2733	18	Denmark	Naesby Dale, North Jutland	Pasture		2	7	39	42	10				
3490	18	Denmark	Lumsås, N. Zealand	Roadside		1	11	73	15					
4683	18	Denmark	Copenhagen, N. Zealand	Lawns, Botanical garden			4	34	52	10				
4685	18	Denmark	Almindingen, Isle of Bornholm†	Forest meadow		20	57	22	1					
1648	36	France	Col de Babourade at Quillan	Dry grassland			2	21	48	27	2			
1868	36	Switzerland	Col de Pillon	Altitude 1600–1700 m.		3	7	25	33	26	5		1	
3580	36	Poland	Tatra*					4	36	58	2			
3699	36	Poland	Bydgoszcz*				3	15	27	52	3			
3893	36	Yugoslavia	Pàle at Sarajevo	Montane meadow				4	24	60	12			
3903	36	Yugoslavia	Ilidza	Meadow			2	32	62	4				
3942	36	Yugoslavia	Doboj	Forest meadow		1	1	9	27	57	4		1	
4180	36	U.S.S.R.	Zagorsk‡				1	14	48	34	3			
3581	36	Sweden	Småland*				1	3	20	64	11	1		
4527	36	Sweden	Abisko	Railway station										
4690	36	Sweden	Billingen, V-Götland	Grassland, south-facing slope				8	28	58	6			
4702	36	Sweden	Hallandsåsen at Båstad	Roadside		2	3	8	15	61	11			
4719	36	Sweden	Söderåsen	Roadside			1	10	27	49	12	1		
	36	Sweden	Mösseberg, V-Götland	Grassland			4	30	51	15				
4684	36	Denmark	Spöttrup, N. Jutland	Cultivated grassland		3	18	44	20	12	2	1		
	36	Denmark	Birkerød, N. Zealand	Railway slope		1	10	61	28					
3700	54	Portugal	Porto*					9	36	45	7	1	2	
			Type of <i>C. leucanthemum</i> L. Herb. Cliffortianum, British Museum, see Plate 6, fig. 1			1	6	58	33	2				
			<i>C. leucanthemum</i> in the Linnean Herbarium, see Plate 6, fig. 2 (= <i>C. irtucianum</i> s.l.)					2	28	53	14	2	1	

* Seeds of wild origin obtained through botanical gardens. † Collected by Dr. Anna Frandsen. ‡ Collected by Dr. Morten Lange.

2. *Tetraploids*. Fifteen strains were counted in root tip mitoses and one (from Mösseberg) in meiotic divisions (Table 1). Meiosis appeared to be completely regular and no multivalent formation could be detected. Most strains were raised from seeds. Among these one from Småland (No. 3581) deviated by producing flowering heads on 5 out of 15 plants the first summer and by being inclined to die after flowering the second summer (10 out of 15). In the other 8 strains (1648-4180), the first-year plants remained vegetative, five of them being clearly perennials, whereas the rest, which flowered for the first time in the summer of 1956, are apparently perennials forming vigorous new basal shoots in the autumn.

3. *Hexaploids*. In one strain from Portugal (No. 3700) the number $2n = 54$ was counted. It belongs to subsp. *pallens* (Gay) Briq. & Cavill. The seedlings deviated by being much larger than those of the tetraploid strains. None of the plants showed any crowding of the basal leaves, as is usually the case with diploids and tetraploids, and they flowered abundantly in August the first year. After flowering most of the plants survived and flowered again in the next two summers.

POLLEN SIZE

In Table 1 all pollen measurements are put together. It appears that the diploid and tetraploid number to some extent corresponds to two different pollen sizes. However, a great overlapping exists, for which reason pollen size cannot be used in a simple way as a character by which herbarium material can be divided. In the two Danish tetraploids the pollen diameters are remarkably low. The hexaploid (No. 3700) has pollen of about the same size as the tetraploids, and this is also the case with some herbarium material of subsp. *pallens* from Southern Europe.

DISTRIBUTION OF DIPLOIDS AND TETRAPLOIDS

In Fig. 1 all stations for *Chrysanthemum leucanthemum* s.l. with known chromosome number are summarised. From the map and some additional pollen measurements from various stations (e.g., several from the British Isles) we are inclined to draw the conclusion that the diploids are prevailing in the north-west and the tetraploids in the north and east and in the mountains in the south, whereas both types occur intermixed in Central Europe. A distribution like this suggests two series of races, one diploid and with atlantic distribution and another tetraploid with continental-montane distribution. Much more material, however, is required in order to establish the distribution and frequency-limits of the two series. In Denmark, Eire, Jersey and, according to Duckart & Favarger, also in the Jura, the diploids frequently occur in natural plant communities whereas tetraploids, at least in Denmark, may have been introduced recently by man. In south-east Europe things may be quite different; tetraploids in Yugoslavia grew in natural meadows whereas the diploid found by Polya occurred along a railway.

TAXONOMY

The hexaploid subsp. *pallens* in our opinion deviates so much, that it seems natural with Gay in Perreymond (1833) to regard it as a separate species (*C. pallens* Gay). The diploid and tetraploid series of races might also be regarded as two species, but a clear-cut morphological distinction is made very difficult because some diploid varieties (e.g., var. *alpicola* Gremlé) approach the tetraploids morphologically. However, the majority of tetraploids can be clearly distinguished; they correspond to subsp. *montanum* (All.)

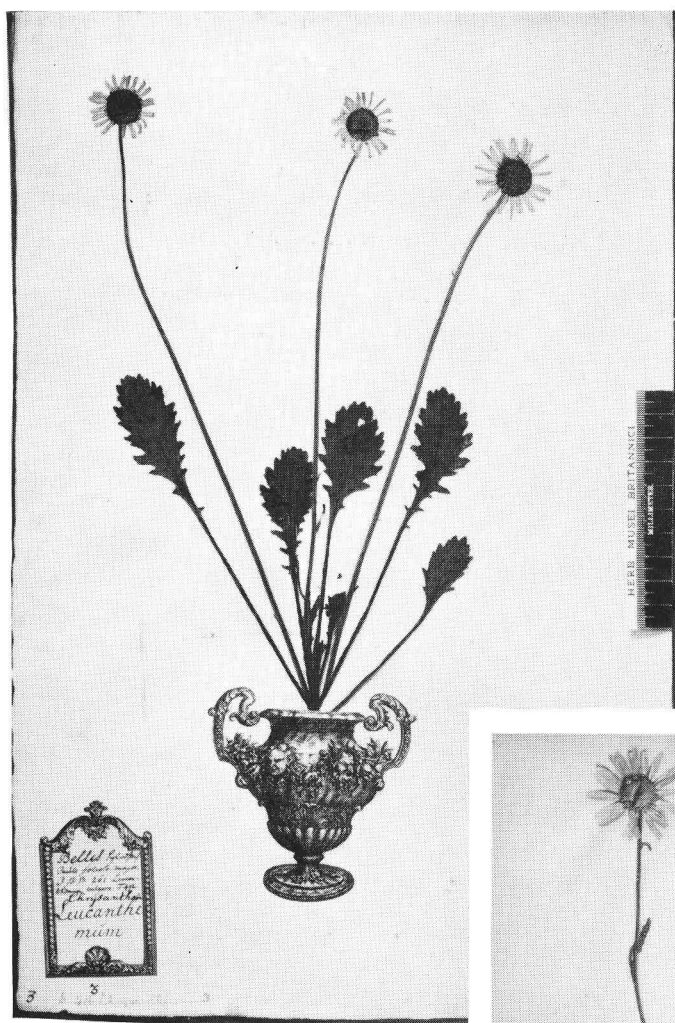


Fig. 1.
Type specimen
of *Chrysanthemum*
leucanthemum L.
in British Museum.



Fig. 2.
The specimen of *Chrysanthemum*
leucanthemum in the Linnean Herbarium
(= *C. ircutianum* Turcz. s.l.).

PLATE 5.



Fig. 1. Cultivated specimen of No. 3170 from Edenderry, Eire. Diploid series (= *C. leucanthemum* L. s. str.).

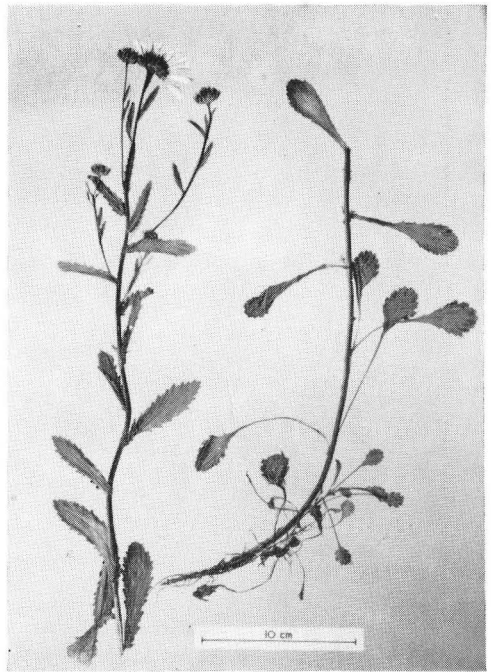


Fig. 2. Cultivated specimen of No. 7180 from Zagorsk, U.S.S.R. Tetraploid series (= *C. ircutianum* Turcz. s.l.).

Briq. & Cavill. although in some of the strains the small membranous calyx or crown may be rudimentary or even missing. This character, which has been used as a primary distinguishing feature by all previous taxonomists, does not correspond to the chromosomal differences and may therefore be regarded as a secondary one. It is possible on the basis of our experimental cultivations to describe two species, one covering most diploids and the other most of the tetraploids. The position of var. *alpicola* and a similar diploid race from Denmark as well as of the tetraploid var. *pinnatifidum* deserves a closer study, but it may prove correct to attach them to the diploid and tetraploid species respectively. The correct names for the two species seem to be *C. leucanthemum* L. and *C. ircutianum* Turcz.

Chrysanthemum leucanthemum L. (s. str.) 1753, *Species Plantarum*, 888 Syn.: *Leucanthemum vulgare* Lamk. subsp. *triviale* Briq. & Cavill. Diagnosis in Linnaeus, 1737, *Hortus Cliffortianus*. Type in British Museum (Natural History) (see Plate 6, Fig. 1). The type specimen is defective without any stem leaves. The pollen-size corresponds very well to that of the diploid strains (Table 1) and the basal leaves have to a great extent alternate, not opposite teeth or lobes. Thus it has two of the most important characters of our diploid series. The specimen in the Linnean Herbarium (No. 1012.7) which is shown on Plate 6, Fig. 2, belongs to a later collection. Its pollen-size (Table 1) and the regularly toothed stem leaves agree very well with corresponding features in our tetraploid plants.

The more important characters of *C. leucanthemum* L. are the following: Diploid, with small pollen, *c.* 27–33 μ in diameter (including spines on the surface). Lower leaves frequently subpinnatifid, more or less spatulate with irregular alternating lobes or teeth; upper leaves linear-lanceolate with pinnatifid bases not very regularly toothed. One or; few heads, 4–7 cm. in diameter (discs 1.5–2.7 cm. in diameter). Ray-florets with a limb 0.3–0.7 cm. broad and usually without crown or with this rudimentary or unilateral. Inclined to be a short-lived perennial at least in culture. Frequent in north-west Europe. Variable, including several subspecies and varieties.

Chrysanthemum ircutianum Turcz. (s.l.), 1846, *Bull. Soc. Nat. Mosc.*, **29**, II, 177 and *Cat. Pl. Baic. Dah.*, 605. Syn. *Leucanthemum ircutianum* (Turcz.) DC., *Prodromus*, **6**, 47, and Ledebour, *Flora Rossica* **2**, 543. Type: In pratis graminosis prope Irkutsk. In the descriptions this species is stated to be closely related to *Chrysanthemum montanum* sensu All., 1785, *Flora Pedemont.*, **1**, 190, tab. 37, fig. 2, from which it is distinguished by its upper leaves which are obtuse or subacute, not mucronate, and by the ray-florets which are longer. We have studied these characters in material of *C. ircutianum* in the Botanical Museum of Copenhagen and have been unable to separate this species from specimens of *C. leucanthemum* subsp. *montanum* or from our tetraploid specimens. (*C. montanum* L. is quite a different species.)

This species has the following important characters: Tetraploid, with larger pollen grains, *c.* 30–39 μ in diameter. Lower leaves spatulate to spatulate-lanceolate, regularly toothed and not lobed; upper leaves lanceolate (oblong-lanceolate to linear-lanceolate) regularly and mostly closely toothed, not or slightly pinnatifid at the base. Heads frequently more than one, 5–7.5 cm. (discs 1.5–3.0 cm.) in diameter. Ray-florets with a limb 0.4–0.8 cm. broad and frequently with a more or less distinct crown. Perennial, occurring in north-east Europe and Siberia as well as in European mountains. Variable, including several subspecies and varieties.

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