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Studies on the Control of Diploid-like Meiosis in Polyploid Taxa of *Chrysanthemum* II. Octoploid *Ch. ornatum* Hemsley

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In native Japanese species of *Chrysanthemum*, polyploidy has played an important role in evolution, and has given rise to tetraploids, hexaploids, octoploids, and decaploids. Despite these frequent polyploidy, a diploid-like meiotic behaviour characterises all polyploid species. In a previous paper (Watanabe 1981), it was suggested that the most likely control system for bivalent formation in hexaploid *Ch. japonense* Nakai although all of the constituent genomes of this species were sufficiently homologous to be able to pair with each other, was the restriction of pairing initiation at one site only per chromosome. One of the analytical methods to verify such genetic control system in high polyploids, is to analyse the chromosomal association in induced depolyploidized progenies, especially, polyhaploids. By the technique of ovary culture the polyhaploid of 8x and the F_1-hybrids of $2x \times 8x$ have been obtained (Watanabe 1977 b).

The purpose of this article is to verify the control system of diploid-like meiosis in octoploid *Ch. ornatum* Hemsley through the analyses of chromosome morphology, chromosome behaviour and external morphology in these polyhaploid and F_1-hybrids.

Materials and methods

Chrysanthemum ornatum Hemsley is a stable octoploid and occurs in South-Western parts of Kyushu, Koshiki Isl. and Yakushima Isl. *Ch. Makinoi* Matsumura et Nakai is a stable diploid and occurs widely in Honshu and Shikoku of Japan. *Ch. boreale* Makino is a stable diploid and is found in Japan, Korea, Manchuria and Northern parts of China. Plants were collected from their native localities as follows and were classified according to Kitamura's system (1967).

In Kaneko's paper (1961) and my previous papers (1977a, b), the chrysanthemums collected from Yakushima Isl. were identified as *Ch. japonense* var. *octoploid* which was taxonomically normen nudum. In this paper it is treated as *Ch. ornatum* Hemsley (Yakushima Isl. strain).

Ch. ornatum (Akune strain), Akune, Kagoshima Pref.

Ch. ornatum (Yakushima Isl. strain), Yakushima Isl., Kagoshima Pref.

Ch. Makinoi, Nukushina, Hiroshima Pref.

Ch. boreale, Koyaguchi, Wakayama Pref.

All methods used were identical to those reported by Watanabe (1981).

Results

1. *Ch. ornatum* Hemsley (Akune strain)

Ch. ornatum (Akune strain)

Ch. ornatum (Akune strain) with 2n=8x=72 was used in hybridization with the diploid *Ch. Makinoi.*

Table 1. Measurements of the somatic chromosomes of *Ch. ornatum* (Akune strain)

Chromosomes	Length in μm	Relative length	Arm ratio (long/short)
1	2.3+2.8=5.1	7.0	1.2
2	1.7+3.2=4.9	6.7	1.9
3	2.4+2.4=4.8	6.6	1.0
4	2.0+2.8=4.8	6.6	1.4
5	2.0+2.7=4.7	6.4	1.4
6	1.6+3.1=4.7	6.4	1.9
7	2.0+2.5=4.5	6.2	1.3
8	1.8+2.7=4.5	6.2	1.5
9	1.7+2.8=4.5	6.2	1.7
10	1.6+2.9=4.5	6.2	1.8
11	1.5+3.0=4.5	6.2	2.0
12	2.2+2.2=4.4	6.0	1.0
13	2.2+2.2=4.4	6.0	1.0
14	2.1+2.3=4.4	6.0	1.1
15	1.8+2.6+4.4	6.0	1.4
16	2.1+2.2=4.3	5.9	1.1
17	2.0+2.3=4.3	5.9	1.2
18	2.0+2.3=4.3	5.9	1.2
19	1.9+2.4=4.3	5.9	1.3
20	1.7+2.6=4.3	5.9	1.5
21	1.6+2.7=4.3	5.9	1.7
22	1.6+2.7=4.3	5.9	1.7
23	1.5+2.8=4.3	5.9	1.9
24*	0.8+3.5=4.3	5.9	4.4
25	2.0+2.2=4.2	5.8	1.1
26	2.0+2.2=4.2	5.8	1.1
27	2.0+2.2=4.2	5.8	1.1
28	2.0+2.2=4.2	5.8	1.1
29	2.0+2.2=4.2	5.8	1.1
30	1.8+2.4=4.2	5.8	1.3
31	1.8+2.4=4.2	5.8	1.3
32	1.4+2.8=4.2	5.8	2.0
33*	1.2+3.0=4.2	5.8	2.5
34*	1.1+3.1=4.2	5.8	2.8
35	1.9+2.2=4.1	5.6	1.2
36	1.9+2.2=4.1	5.6	1.2

Table 1. (continued)

Chromosomes	Length in μm	Relative length	Arm ratio (long/short)
37	1.7+2.4=4.1	5.6	1.4
38	1.7+2.4=4.1	5.6	1.4
39	1.5+2.6=4.1	5.6	1.7
40	0.8+3.3=4.1	5.6	4.1
41	2.0+2.0+4.0	5.5	1.0
42	2.0+2.0=4.0	5.5	1.0
43	1.9+2.1=4.0	5.5	1.1
44	1.8+2.2+4.0	5.5	1.2
45	1.7+2.3=4.0	5.5	1.4
46	1.3+2.7=4.0	5.5	2.1
47	1.9+2.0=3.9	5.3	1.1
48	1.5+2.4=3.9	5.3	1.6
49	0.8+3.1=3.9	5.3	3.9
50	1.8+2.0=3.8	5.2	1.1
51	1.8+2.0=3.8	5.2	1.1
52	1.4+2.4=3.8	5.2	1.7
53*	1.2+2.6=3.8	5.2	2.2
54	1.0+2.8=3.8	5.2	2.8
55	0.6+3.2=3.8	5.2	5.3
56	1.8+1.9=3.7	5.1	1.1
57	1.8+1.9=3.7	5.1	1.1
58	1.8+1.9=3.7	5.1	1.1
59	1.6+2.1=3.7	5.1	1.3
60*	1.1+2.6=3.7	5.1	2.4
61	0.9+2.8=3.7	5.1	3.1
62	0.8+2.9=3.7	5.1	3.6
63	1.6+2.0=3.6	4.9	1.3
64	1.4+2.2=3.6	4.9	1.6
65	0.8+2.8=3.6	4.9	3.5
66*	1.2+2.3=3.5	4.8	1.9
67	0.8+2.6=3.4	4.7	3.3
68	0.6+2.8=3.3	4.7	4.7
69	1.4+1.9=3.3	4.5	1.4
70	1.4+1.6=3.0	4.1	1.1
71	0.4+2.6=3.0	4.1	6.5
72	1.4+1.4=2.8	3.8	1.0

* Chromosome with satellites.

The chromosomes of *Ch. ornatum* (Akune strain), at mitotic metaphase, vary in length from 5.1 μm to 2.8 μm and in arm ratio from 1.0 to 6.5 (Fig. 1–A and Table 1). The seventy-two chromosomes are arranged in order of size in Fig. 2–A. Six chromosomes had minute satellites. Three were medium-sized subterminal chromosomes (Chromosomes 24, 33 and 34) and the rest were small subterminals (Chromosomes 53, 60 and 66). Seven extreme subterminal chromosomes with arm ratios of 3.5–6.5 (Chromosomes 40, 49, 55, 62, 65, 68 and 71) were distinguishable. Karyomorphologically *Ch. ornatum* (Akune strain) seems not to be an auto-octoploid.

The following meiotic configurations were frequently observed; 3 IV+30 II,

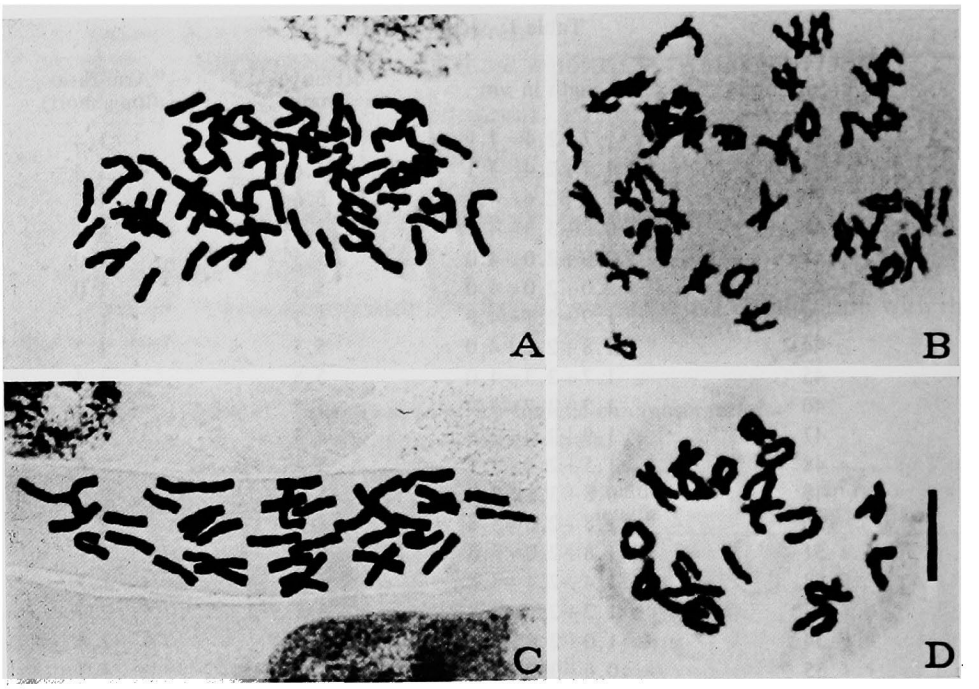


Fig. 1. Mitotic and meiotic chromosomes of *Ch. ornatum* (Akune strain) (A and B) and its androgenetic polyhaploid (C and D). A, mitotic chromosomes. 2n=8x=72. B, meiotic chromosomes 1IV+33II+2I. C, mitotic chromosomes 2n=4x=1=37. D, meiotic chromosomes. 18II +1I. Scale 10 μm.

2 IV+32 II, 2 IV+31 II+2 I, 1 IV+34 II, 1 IV+33 I+2 I, 36 II and 35 II+2 I (Fig. 1–B). The frequency of bivalent formation was 95.5%.

The parental species *Ch. ornatum* (Akune strain) and *Ch. Makinoi* can be distinguished from one another by many characters, —the basal shape of leaves (truncate / cuneate), the number of leaf teeth (less / more), the shape and depth of marginal teeth (more obtuse and lobate / less), the depth of incision of leaves (shallow / deep), the hair color on the reverse side of the leaves (silver-white / ashen) and the length of the outer involucral bracts (short / long). In each comparison the form of *Ch. ornatum* (Akune strain) is given first.

Ch. Makinoi (♀)×*Ch. ornatum* (Akune strain) (♂)

In this cross, 1968 disc florets of 12 heads were pollinated and cultivated on the artificial medium. Eight ovaries developed and were germinated, representing only about 0.4% seed set. Of these, one had 2n=5x+2=47 and three had 2n=5x+1=46, and were accepted as being aneuploid F_1-hybrids. One plant with 2n=4x+1=37 was probably an androgenic aneuploid. Two plants were diploid and were doubtless due to selfing. One died before it could be karyotyped.

The chromosomes of the androgenic aneuploid with 2n=4x+1=37, at mitotic metaphase, vary in length from 8.3 μm to 4.0 μm and in arm ratio from 1.0 to 5.1 (Fig. 1–C). The thirty-seven chromosomes are arranged in order of size in Fig. 2–B. Three chromosomes had minute satellites. Two of them were medium-sized subter-

minal chromosomes (Chromosomes 18 and 22) and the third a small subterminal (Chromosome 30). Three extreme subterminal chromosomes with arm ratios of 3.7–5.1 (Chromosomes 26, 36 and 37) were distinguishable. Karyomorphologically

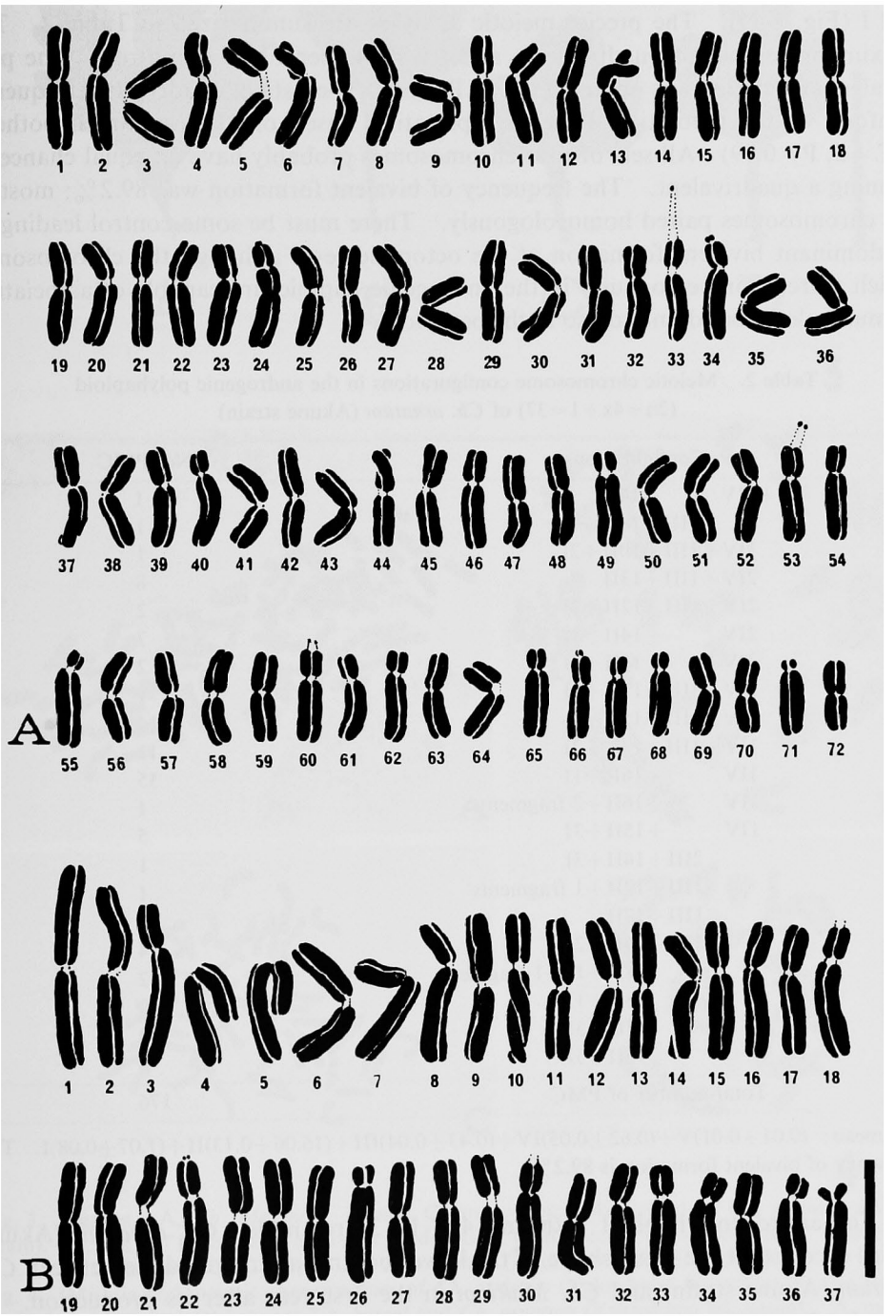


Fig. 2. Somatic karyptype. A, *Ch. ornatum* (Akune strain). B, its androgenic polyhaploid. Scale 5 μm.

this plant seems not to be the autotetraploid of *Ch. Makinoi* but is more likely to be derived androgenically from *Ch. ornatum* (Akune strain).

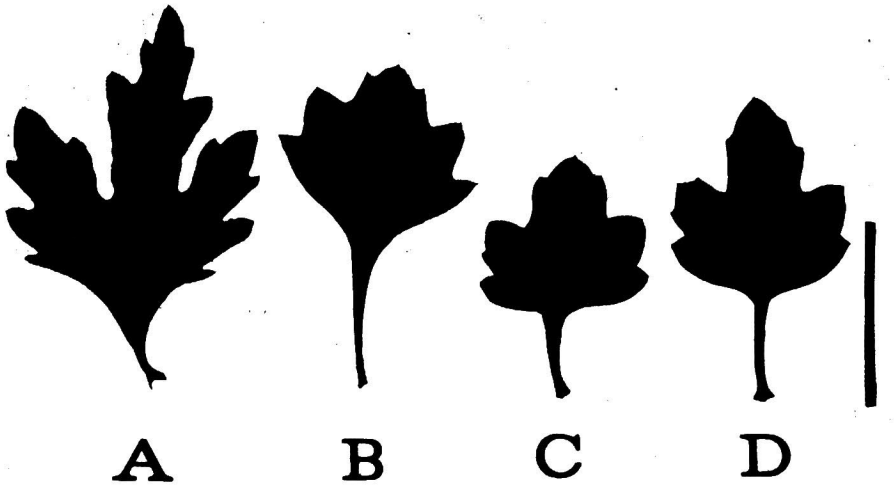
In this aneuploid, the following meiotic configurations were frequently observed; 1 IV+1 III+15 II, 1 IV+1 III+14 II+2 I, 1 IV+16 II+1 I, 1 III+17 II and 18 II +1 I (Fig. 1-D). The precise meiotic analyses are summarized in Table 2. The maximum number of quadrivalents and trivalents per PMC was three. One pentavalent association was observed in two PMCs. The data of quadrivalent frequency conform to the theoretical Poisson expectation based on the random hypothesis (d.f.=2, P=0.09) All sets of four chromosomes probably have an equal chance of forming a quadrivalent. The frequency of bivalent formation was 89.2%: most of the chromosomes paired homoeologously. There must be some control leading to predominant bivalent formation at the octoploid level although the chromosomes which paired homoeologously in the androgenic haploid are capable of associating as multivalents but do not do so in the octoploid.

Table 2. Meiotic chromosome configurations in the androgenic polyhaploid (2n=4x+1=37) of *Ch. ornatum* (Akune strain)

Configurations	No. PMC
1V+1IV +14II	1
1V +1III+14II+1I	1
3IV+1III+10II+2I	1
2IV+1III+13II	8
2IV+1III+12II+2I	2
2IV +14II+1I	7
2IV +13II+3I	2
1IV+3III+11II+2I	1
1IV+1III+15II	14
1IV+1III+14II+2I	11
1IV +16II+1I	35
1IV +16II+2 fragments	1
1IV +15II+3I	5
2III+14II+3I	1
1III+17II+1 fragments	1
1III+17II	28
1III+16II+2I	4
18II+1I+1 fragment	2
18II+1I	39
17II+3I	9
16II+5I	3
Total number of PMC	176

mean; (0.01 ± 0.01)V+(0.62 ± 0.05)IV+(0.43 ± 0.04)III+$(16.06+0.13)$II+(1.07 ± 0.08)I. The frequency of bivalent formation is 89.2%.

The androgenic haploid with 2n=4x+1=37 resembled *Ch. ornatum* (Akune strain) except that the basal shape of the leaves became an intermediate between *Ch. ornatum* (Akune strain) and *Ch. Makinoi* in the first year after its production. It might be due to the cytoplasmic effects of the female parent, *Ch. Makinoi* (Fig. 3-B). After the second year of its production, the basal shape of the leaves of this plant



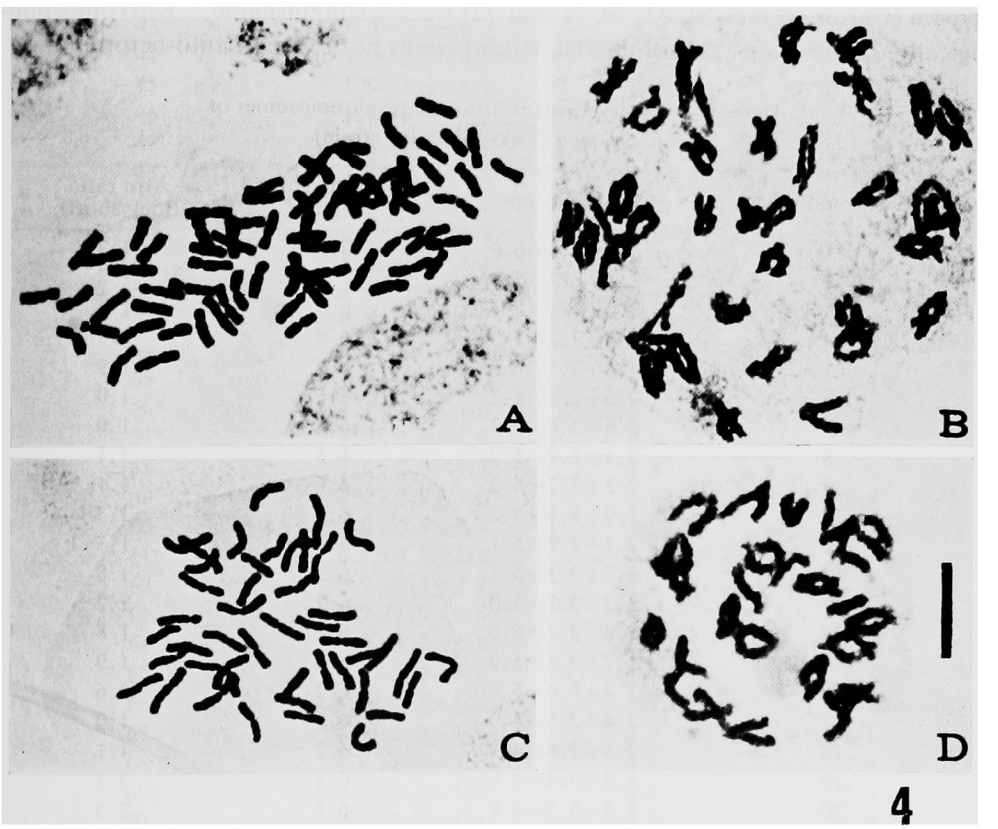


Fig. 3. Leaves. A, *Ch. Makinoi*. B, and C, androgenic polyhaploid of *Ch. ornatum* (Akune strain). B: the leaf in the first year of its producetion, C: the leaf in the second year. Note to the change of basal shape. D, *Ch. ornatum* (Akune strain). Scale 2.5 cm.

Fig. 4. Mitotic and meiotic chromosomes of *Ch. ornatum* (Yakushima Isl. strain) (A and B) and the F_1-hybrid (C and D) between *Ch. boreal* and *Ch. ornatum* (Yakushima Isl. strain). A, mitotic chromosomes. 2n=8x=72. B, meiotic chromosomes. 36II. C, mitotic chromosomes. 2n=5x=45. D, meiotic chromosomes. 2III+18II+3I. Scale 10μm.

completely resembled the *Ch. ornatum* (Fig. 3-C). Plant mass of this haploid was smaller than that of the parental *Ch. ornatum*.

2. *Ch. ornatum* Hemsley (Yakushima Isl. strain)

Ch. ornatum (Yakushima Isl. strain)

Ch. ornatum (Yakushima Isl. strain) with 2n=8x=72 was used in hybridization with the diploid *Ch. boreale*.

The chromosomes of *Ch. ornatum* (Yakushima strain), at mitotic metaphase, vary in length from 6.0 μm to 3.2 μm and in arm ratio from 1.0 to 4.6 (Fig. 4-A and Table 3). The seventy-two chromosomes are arranged in order of size in Fig. 5-A. Ten chromosomes had minute satellites. One was a large submedian chromosome (Chromosome 4), one a medium-sized submedian (Chromosome 22), one a medium-sized median (Chromosome 32), one a medium-sized subterminal (Chromosome 34), one a small submedian (Chromosome 40) and five small subterminals (Chromosomes 53, 56, 57, 61 and 69). Five extreme subterminal chromosomes with arm ratios of 3.7–4.6 (Chromosomes 54, 62, 70, 71 and 72) were distinguishable. Karyomorphologically *Ch. ornatum* (Yakushima Isl. strain) seems not to be an auto-octoploid.

Table 3. Measurements of the somatic chromosomes of *Ch. ortanum* (Yqkushima Isl. strain)

Chromosomes	Length in μm	Relative length	Arm ratio (long/short)
1	2.7+3.3=6.0	7.5	1.2
2	2.7+3.2=5.9	7.3	1.2
3	2.2+3.1=5.3	6.6	1.4
4*	2.1+3.2=5.3	6.6	1.5
5	1.8+3.5=5.3	6.6	1.9
6	2.6+2.6=5.2	6.5	1.0
7	2.6+2.6=5.2	6.5	1.0
8	2.5+2.7=5.2	6.5	1.1
9	2.5+2.7=5.2	6.5	1.1
10	1.9+3.3=5.2	6.5	1.7
11	2.2+2.9=5.1	6.3	1.3
12	1.8+3.3=5.1	6.3	1.8
13	2.3+2.7=5.0	6.2	1.2
14	1.8+3.2=5.0	6.2	1.8
15	1.7+3.3=5.0	6.2	1.9
16	1.4+3.6=5.0	6.2	2.6
17	2.4+2.5=4.9	6.1	1.0
18	2.3+2.6=4.9	6.1	1.1
19	1.5+3.4=4.9	6.1	2.3
20	1.4+3.5=4.9	6.1	2.5
21	2.3+2.5=4.8	6.0	1.1
22*	2.1+2.7=4.8	6.0	1.3
23	2.0+2.8=4.8	6.0	1.4
24	1.9+2.9=4.8	6.0	1.5
25	1.4+3.4=4.8	6.0	2.4
26	2.3+2.4=4.7	5.8	1.0

Table 3. (continued)

Chromosomes	Length in μm	Relative length	Arm ratio (long/short)
27	2.2+2.5=4.7	5.8	1.1
28	2.2+2.5=4.7	5.8	1.1
29	2.1+2.6=4.7	5.8	1.2
30	2.1+2.6=4.7	5.8	1.2
31	1.9+2.8=4.7	5.8	1.5
32*	2.1+2.4=4.5	5.6	1.1
33	1.9+2.6=4.5	5.6	1.4
34*	1.6+2.9=4.5	5.6	1.8
35	1.2+3.3=4.5	5.6	2.8
36	2.0+2.4=4.4	5.5	1.2
37	1.9+2.5=4.4	5.5	1.3
38	1.8+2.6=4.4	5.5	1.4
39	1.8+2.6=4.4	5.5	1.4
40*	1.8+2.6=4.4	5.5	1.4
41	1.7+2.7=4.4	5.5	1.6
42	1.8+2.5=4.3	5.3	1.4
43	1.3+3.0=4.3	5.3	2.3
44	2.0+2.2=4.2	5.2	1.1
45	1.9+2.3=4.2	5.2	1.2
46	1.8+2.4=4.2	5.2	1.3
47	1.8+2.4=4.2	5.2	1.3
48	1.6+2.6=4.2	5.2	1.6
49	1.4+2.8=4.2	5.2	2.0
50	1.3+2.9=4.2	5.2	2.2
51	1.6+2.5=4.1	5.1	1.6
52	1.1+3.0=4.1	5.1	2.7
53*	0.8+3.3=4.1	5.1	4.1
54	0.8+3.3=4.1	5.1	4.1
55	1.3+2.7=4.0	5.0	2.1
56*	1.1+2.9=4.0	5.0	2.6
57*	1.0+3.0=4.0	5.0	3.0
58	1.6+2.3=3.9	4.8	1.4
59	1.0+2.9=3.9	4.8	2.9
60	1.0+2.9=3.9	4.8	2.9
61*	0.8+3.1=3.9	4.8	3.9
62	0.7+3.2=3.9	4.8	4.6
63	1.9+1.9=3.8	4.7	1.0
64	1.9+1.9=3.8	4.7	1.0
65	1.4+2.4=3.8	4.7	1.7
66	1.4+2.4=3.8	4.7	1.7
67	1.8+1.9=3.7	4.6	1.1
68	1.0+2.6=3.6	4.5	2.6
69*	0.8+2.6=3.4	4.2	3.3
70	0.7+2.7=3.4	4.2	3.9
71	0.7+2.6=3.3	4.1	3.7
72	0.6+2.6=3.2	4.0	4.3

* Chromosome with satellites.

In meiosis the main chromosome configuration was 36 II but 3 IV+30 II, 2 IV+32 II, 1 IV+34 II and 35 II+2 I were rarely observed. The frequency of bivalent formation was 98.6%. Chromosome association in this strain is primarily as bivalents (Fig. 4–B).

The parental species *Ch. ornatum* (Yakushima Isl. strain) and *Ch. boreale* can be distinguished from one another by many characters, —the number of head (less / more), the number of ray and disc florets (more / less) and their size (larger / smaller), the color of ray florets (white / yellow), the size of laminae (smaller / larger), the number of leaf teeth (less / more) and the presence of pseudostipules and rhizome (present / absent). In each comparison the form of *Ch. ornatum* (Yakushima Isl. strain) is given first.

Ch. boreale (♀)×*Ch. ornatum* (Yakushima Isl. strain) (♂)

In this cross, 3901 disc florets of 52 heads were pollinated and cultivated on the artificial medium. Five ovaries developed and were germinated, representing only about 0.1% seed set. Of these, three plants had 2n=5x=45 and were presumably hybrids. Two plants were diploids and doubtless due to selfing. The reciprocal cross failed completely although 435 disc florets of 3 heads were pollinated and cultivated in the same manner.

The chromosomes of the F_1-hybrid with 2n=5x=45, at mitotic metaphase, vary in length from 7.5 μm to 3.5 μm and in arm ratio from 1.0 to 3.7 (Fig. 4–C). The forty-five chromosomes are arranged in order of size in Fig. 5–B. Four chromosomes had minute satellites. One was a large submedian chromosome (Chromosome 6), one a medium-sized median (Chromosome 16), one a medium-sized subterminal (Chromosome 26) and one a small subterminal (Chromosome 38). Five extreme subterminal chromosomes with arm ratios of 2.9–3.3 (Chromosomes 36, 42, 43, 44 and 45) were distinguishable.

The following meiotic configurations were frequently observed; 1 IV+19 II+3 I, 2 III+17 II+5 I, 1 III+19 II+4 I, 21 II+3 I and 20 II+5 I. The precise meiotic data have been reported previously (Watanabe 1977a). The maximum number of quadrivalents and trivalents per PMC were one and five, respectively. In no less than 42 out of the 58 cells there must be some intra-genomic pairing. The excess of bivalent formation suggests that there must be a limited segmental homology perhaps due to interchange or duplication, between essentially the non-homologous members of the five basic sets of the F_1-hybrid. At least two basic sets among four derived from *Ch. ornatum* (Yakushima Isl. strain) must have paired homoeologously. Consequently there must again be some control leading to predominant bivalent formation at the octoploid level although the chromosomes which paired homoeologously in the F_1-hybrid are capable of associating as multivalents but do not do so in the octoploid.

All F_1-hybrids had rhizomes and white ray florets and they had leaves both with and without pseudostipules. The F_1-hybrids resembled *Ch. ornatum* (Yakushima Isl. strain) more than *Ch. boreale* in their quantitative characters (Fig. 6).

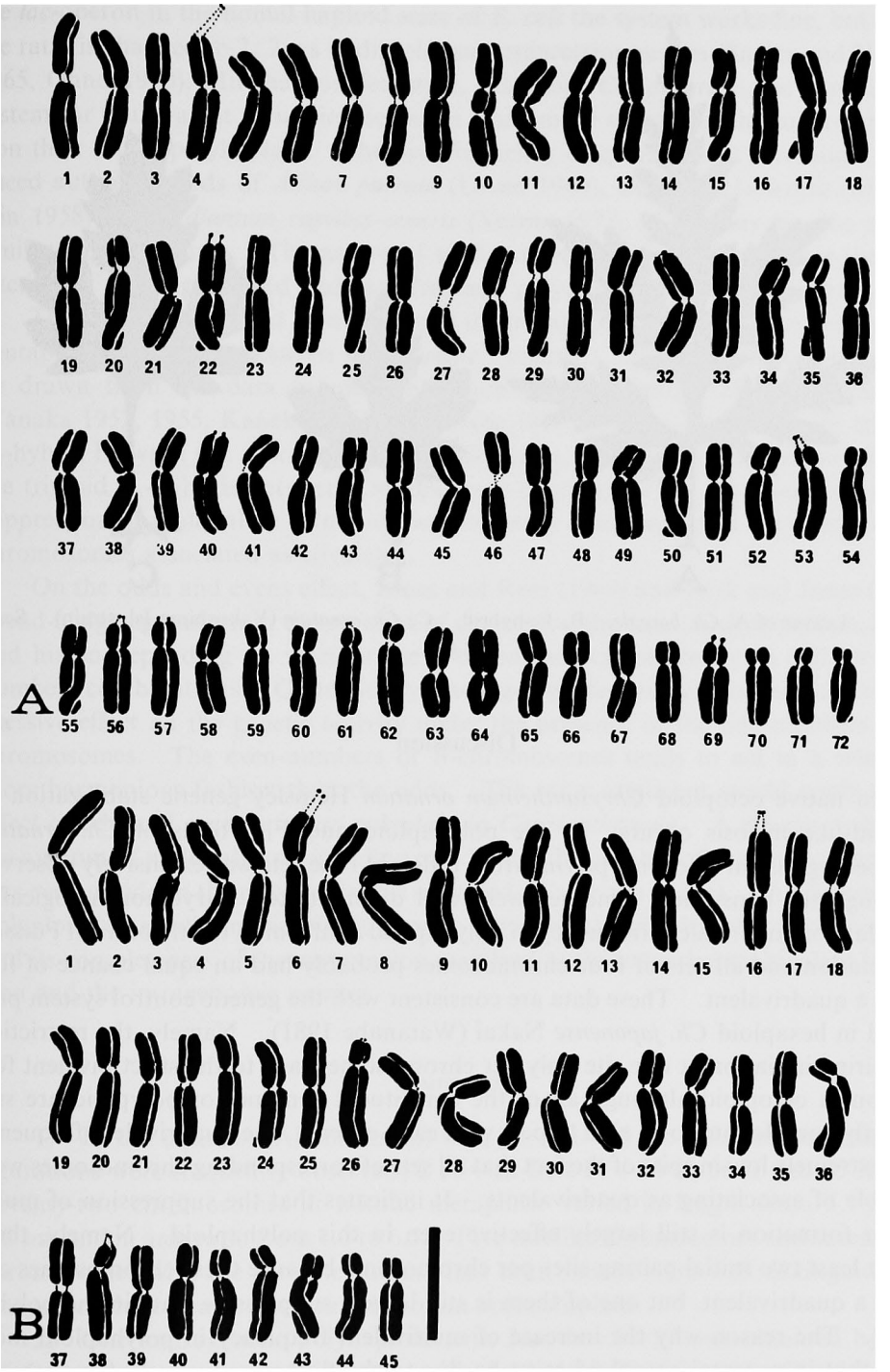


Fig. 5. Somatic karyotype. A, *Ch. ornatum* (Yakushima Isl. strain). B, F_1-hybrid between *Ch. boreale* and *Ch. ornatum* (Yakushima Isl. strain). Scale 5 μm.

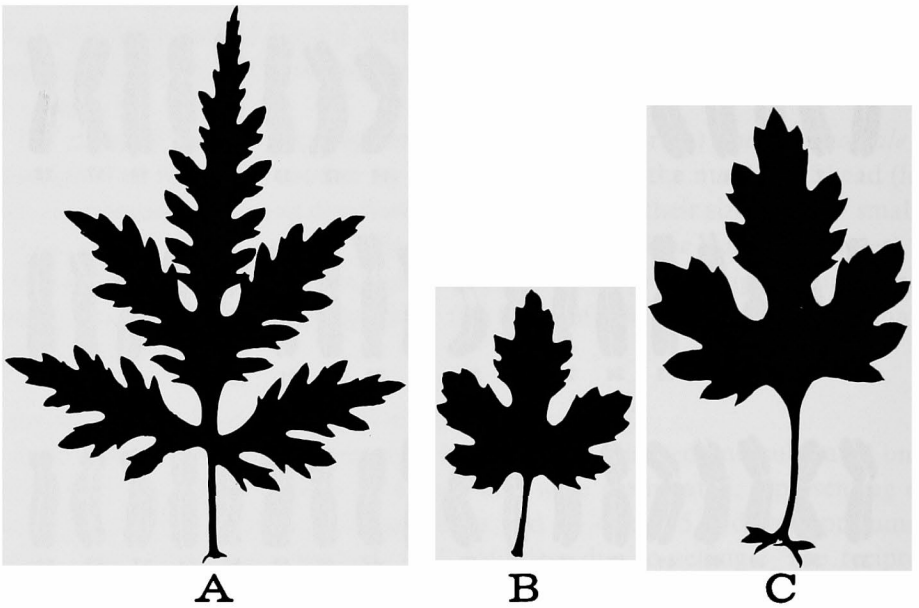


Fig. 6. Leaves of A, *Ch. boreale*. B, F_1-hybrid. C, *Ch. ornatum* (Yakushima Isl. strain). Scale 2.5 μm.

Discussion

In native octoploid *Chrysanthemum ornatum* Hemsley genetic stabilization of diploid-like meiosis occurs. In the polyhaploid and F_1-hybrids of *Ch. ornatum* homoeologous chromosome pairing from different base sets was extensively observed although the constituent genomes were well differentiated, karyomorphologically. The data of quadrivalent frequency in polyhaploid conform to the theoretical Poisson expectation and all sets of four chromosomes probably had an equal chance of forming a quadrivalent. These data are consistent with the genetic control system proposed in hexaploid *Ch. japonense* Nakai (Watanabe 1981). Namely, the restriction of pairing initiation at one site only per chromosome leads to the strict bivalent formation in octoploid although all of the constituent genomes of polyploid are sufficiently homologous to be able to pair with each other. The quadrivalent frequency was extremely low in spite of the fact that all sets of corresponding chromosomes were capable of associating as quadrivalents. It indicates that the suppression of multivalent formation is still largely effective even in this polyhaploid. Namely, there are at least two initial pairing sites per chromosome because these chromosomes can from a quadrivalent, but one of them is still largely suppressive state in the polyhaploid. The reason why the increase of multivalent frequency in polyhaploid more than that in parental octoploid must be due to the dosage reduction of suppressive gene although it is partly due to the effect of extra one autosome. Such dosage effect may be comparable with that in the *lac*-operon system of *Escherichia coli*. It has been shown that the rate of synthesis of β-galactosidase varies reciprocally with the first power level of the repressor. At 1 : 1 dosage ratio of the repressor gene and

the *lac*-operon in the nomal haploid state of *E. coli* the system works fine, but when the ratio is changed to 2: 2, as in diploid, superrepression results (Sadler and Novick 1965, Ohno 1970). In the doubled state, octoploid *Ch. ornatum*, the suppression system for multivalent formation seems to work more strictly by the super-suppression than in the polyhaploid. The low frequency of quadrivalent formation in induced autotetraploids of *Allium porrum* (Levan 1940), *Dactylis glomerata* (McCollum 1958) and *Adiantum capillus-veneris* (Verma 1977, 1978) may be due to the similar control system. The nature of such suppressive gene should serve the production of stable polyploid and very frequent polyploidy in chrysanthemums.

The extensive trivalent formation and the intragenomic pairing were observed in pentaploid F_1-hybrids between *Ch. boreale*×*ornatum*. Similar conclusions are to be drawn from the data in other odd-numbered polyploids of *Chrysanthemum* (Tanaka 1952, 1955, Kaneko 1961. Watanabe 1977a, 1981). Especially, in triploid F_1-hybrid between *Ch. wakasaense* 4x×*Makinoi* 2x, polyhaploid *Ch. indicum* 6x and the triploid B_1-hybrids between *Ch. japonense* 6x×*boreale* 2x, the release from the suppression of multivalent formation was occurred completely and two-thirds of the chromosomes associated as trivalents.

On the odds and evens effect, Jones and Rees (1969) and Kirk and Jones (1970) found a zig-zag pattern in the amount of chiasmata, the total nuclear protein, RNA and histon depending on whether the B-chromosomes are present in odd- or even-numbers combinations. Quite clearly, the zig-zag effect in rye may be due to a repressive effect on the genetic activity under the presence of the odd-numbers of B-chromosomes. The even-numbers of B-chromosomes tends to act in a relatively more harmonious fashion than the odds. The same argument would apply to the effect of odd and even-numbers polyploid in *Chrysanthemum*. A zig-zag pattern in the amount of multivalents depending on whether the number of constituent genomes was even or odd in the polyploids was observed (Watanabe 1977a). In odd-numbers polyploid, especially in triploid, it may be repressed the activity of suppressive gene and its completeness of the suppression may lead to the extensive multivalent formation and the intragenomic pairing.

Summary

1) In *Ch. ornatum* (Akune strain) with 2n=8x=72 the following meiotic configurations were frequently observed; 2 IV+32 II, 1 IV+34 II, 36 II and 35 II+2 I. Seventy-two chromosomes at mitotic metaphase varied in length from 5.1 μm to 2.8 μm and in arm ratio from 1.0 to 6.5. Five satellite chromosomes and seven small chromosomes with the extreme subterminal centromeres were well distinguishable. Karyomorphologically this strain is not an autooctoploid.

2) One androgenetic polyhaploid with 2n=4x+1=37 was obtained by artificial ovary culture after hybridization with the diploid *Ch. Makinoi*. The following meiotic configurations were frequently observed; 1 IV+1 III+15 II, 1 IV+1 III+14 II+2 I, 1 IV+16 II+1 I, 1 III+17 II and 18 II+1 I. A pentavalent association and a chromosome fragment were also observed rarely. The chromosomes derived from *Ch. ornatum* (Akune strain) paired homoeologously. The data of quadrivalent

frequency conform to the theoretical Poisson expectation based on the random hypothesis.

3) In *Ch. ornatum* (Yakushima Isl. strain) with 2n=8x=72, 36 II was the main meiotic configuration and 3 IV+30 II, 2 IV+32 II, 1 IV+34 II and 35 II+2 I were rarely observed. Seventy-two chromosomes, at mitotic metaphase, varied in length from 6.0 μm to 3.2 μm and in arm ratio from 1.0 to 4.6. Ten satellites chromosomes and five small chromosomes with extreme subterminal centromers were well distinguishable. Karyomorphologically this strain is not an autooctoploid.

4) Three F_1-hybrids with 2n=5x=45 between diploid *Ch. boreale* and *Ch. ornatum* (Yakushima Isl. strain) were obtained by ovary culture. The following meiotic configurations were frequently observed; 1 IV+19 II+3 I, 5 III+12 II+6 I, 2 III+17 II+5 I, 21 II+3 I and 20 II+5 I. The chromosomes derived from *Ch. ornatum* (Yakushima Isl. strain) paired homoeololgously.

5) The genetic control system for the suppression of multivalent formation in octoploid, its polyhaploid and pentaploid F_1-hybrid must be the restriction of pairing initiation at one of two sites per chromosome. This restriction seems to be under the polygenic control which leads to the super-suppression in accompany with the increase of gene dosage. This system tends to act in a relatively more harmonious fasion in the even-numberd polyploid than in the odds.

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Literature Cited

Jones, R. N. and Rees, H. 1969. An anomalous variation due to B chromosomes in rye. Heredity **24**: 265–271.

Kaneko, K. 1961. Cytogenetical studies on three high polyploid species of *Chrysanthemum*. Jour. Sci. Hiroshima Univ. Ser. B, Div. 2, **9**: 59–98.

Kirk, D. and Jones, N. 1970. Nuclear genetic activity in B-chromosome rye, in terms of the quantitative interrelationships between nuclear protein, nuclear RNA and histon. Chromasoma (Berl.) **31**: 241–254.

Levan, A, 1940. Meiosis in *Allium porrum*, a tetraploid species with chiasma localization. Hereditas **26**: 452–462.

McCollum, G. D. 1958. Comparative studies of chromosome pairing in natural and induced tetraploid *Dactylis*. Chromosoma (Berl.) **9**: 571–605.

Ohno, S. 1970. Evolution by Gene Duplication. Springer-Verlag. New York Inc. p. 150.

Sadler, J. R. and Novick, A. 1956. The properties of repressor and the kinetics of its action. Jour. Mol. Biol. **12**: 305–327.

Tanaka, R. 1952. Cytologische Untersuchungen über die triploiden F_1-Artbastard von *Chrysanthemum Makinoi* (2n=18)×*Ch. Wakasaense* (2n=36) und einen triploiden Mutant von *Ch. Makinoi*. Jour. Sci. Hiroshima Univ. Sre. B, Div. 2, **6**: 45–49.

— 1955. Über die polyploiden Nachkommen und abnormen F_1-Bastarde bei *Chrysanthemum indecum* var. *hexaploid* (2n=45)×*Ch. lavandulaefolium* (2n=18). Japan. J. Genetics **30**: 17–23.

Verma, S. C. 1977. Chromosomal association in autotetraploid and autotriploid *Adiantum capillus-veneris*. Nucleus **20**: 99–105.

— 1978. Pairing restriction and non-homologous pairing in autoploids of *Adiantum capillus-veneris*. Cytologia **43**: 515–523.

Watanabe, K. 1977a. The control of diploid-like meiosis in polyploid taxa of *Chrysanthemum* (Compositae). Japan. J. Genetics **52**: 125–121.

— 1977b. Successful ovary culture and production of F_1-hybrids and androgenic haploids in Japanese *Chrysanthemum* species. Jour. Herdity **68**: 317–320.

— 1981. Studies on the control of diploid-like meiosis in polyploid taxa of *Chrysanthemum* 1. Hexaploid *Ch. japonense* Nakai. Cytologia **46**: 459–498.