Cytogenetic Studies in the Artificially Raised Interspecific Hybrids of *Papaver*.**X. On the chromosome behaviours in the PMCs of a triploid F_1 plant between *Papaver* No. 41,8 and *P. bracteata*¹**

By

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(With 15 Text-Figures)

*Received March 23, 1943***Introduction**

In 1936 (YASUI, 1936) I mentioned that the tetraploid *Papaver* (Ped. No. 41,8) is to be regarded either as an F_1 plant of *P. orientale* and *P. bracteata* or as a derivative from such a hybrid, and provisionally designated the chromosome constitution as $O_1O_2O_3B$, namely that of F_1 plant of *P. orientale* and *P. bracteata*. This *Papaver* No. 41,8 was highly selfsterile, only few seeds being obtained. The external characters of the S_1 plants resembled those of the parent and were alike to each other. Also this S_1 plants resembled *P. bracteata* more than the F_1 plant mentioned above. These facts led me to the conclusion that the plant *P. (Papaver)* No. 41,8 is not of a hybrid nature like $O_1O_2O_3B$, but probably an amphidiploid derived from a hybrid between *P. bracteata* and an unknown *Papaver* having 7 haploid chromosomes. A further study of the relationship between this plant and *P. bracteata* was made in the F_1 plant of No. 41,8 and *P. bracteata* and the results were found mostly in accord with the above consideration and also some data were obtained with regard to the relationship between 2 chromosome complements in No. 41,8.

The material for the present study was fixed with NAVASHIN's fluid, the paraffin sections were stained either with HEIDENHAIN's iron-alum haematoxylin or the NEWTON's gentian violet. All the drawings were made, by the use of camera lucida with Zeiss objective H. I. $\times 100$, N. A. 1.3 and Ocular K. 12.

Observation

1. The external characters of the F_1 plant. As far as I have examined they resembled mostly those of the female parent, while the stem of the F_1 plant was stiff and stout as in the male parent. These will be seen in Table 1 and Fig. 1.

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Fig. 1. Parent plants and F_1 plants. A, female parent, tetraploid *Papaver* (Ped. No. 41,8); B, male parent, *P. bracteata*; C, F_1 plant; D, top view of the flower C, enlarged, ca. $\times 2/3$ nat. size,

Table 1. External characters in *Papaver* Ped. No. 41,8 (the female parent), *P. bracteata* (the male parent) and the F₁ plant.

	Female parent	Male parent	F ₁ plant
Stem	Slender and shorter than the male parent	Stronger and taller than the female parent, stiff	Intermediate, but somewhat stiff as in the male parent
Leaf	Pale green	Deep green	Deep green
Size of flower	Smaller than that of the male plant	Large and elegant	Like the male parent
Colour of the petal	Scarlet red	Deep crimson red	Red, margin whitish
Eye spot on the petal	Blackish purple on the ventral surface, white on the dorsal surface	Blackish purple on both sides	Like the female parent
Shape of the stigma	Pointed	Rather flat	Pointed as in the female parent

2. The somatic cells and chromosomes in the F₁ plant. A. The resting nucleus. In the fixed material some somatic cells of the young carpel showed no conspicuous nucleolus but many well stained dots on the hardly stained fine threads, the chromonemata, (Fig. 2, *a*), while the cells of young ovules in the same ovary showed generally a large nucleolus with a large room ('hof') around it; besides there were smaller nucleoli and some well stained dots (Fig. 2, *b*). These differences in the structure of the nucleoli in these two kinds of cells may depend upon the difference of the lengths of the interkinetic stage, there being no sufficient time for accumulation of the nucleolar substances to form a large nucleolus, when the interkinesis is short.

B. The room formation. In the nucleus which has large nucleolus there generally appears a room ('hof') around the nucleolus in fixed material as I have already described and discussed in other cases (YASUI, 1941). This room formation shows that the karyolymph or the continuous phase in the nuclear cavity and also the nucleolus have a surface membrane. So that when the nucleus is fixed the shrinkage of these substances result in the formation of a room between the nucleolus and the karyolymph. In the early prophase in the living state the connection between the nucleoli and the chromonemata is not clear due to the lack of space between the nucleolus and karyolymph, but when the material was fixed and the room was formed in the nucleus those chromosomes or chromonemata, probably nucleolar chromosomes, which were connected closely with the nucleolus are pulled in by the shrinkage of the nucleolus, thus showing the connection between the nucleolus and chromonemata clearly. The small dot on the upper right part of the nucleolar surface in Fig. 2, *b* shows a part of a chromosome where the latter attaches to the nucleolus, the connexion-thread in the room being out of the focus. Those chromosomes or chromonemata which are slightly connected with

the nucleolus detach easily from the nucleolus when the room was formed, and leave no trace of the attachment on the nucleolus. Therefore the lack of connection between the nucleolus and chromosomes or chromonemata in the fixed material does not mean that there is no relationship between these two.

C. Chromosome formation. These region of well stained dots in the resting nucleus mentioned above should represent either the nucleolar substances attached to the chromonemata or the so-called heterochromatic region of the chromosomes where the spirals of the chromosomes in the previous division did not stretch out in the interkinesis and held the nucleolar substances. In the prophase, in which the chromosome formation or the rearrangement of the chromonemata-composition begins, it starts from these deeply stained region; namely the compactness and the staining capacity in the region were gradually decreased. These phenomena are due probably to the dispersion of the nucleolar substances from the compact region to other part. With the progress of the processes the deep stained dots disappear and the staining capacity of the whole chromosomes increases, so that the chromosomes become smooth looking deep stained threads. In the early prophase the nucleolus looks soft and sticky so that when the attached chromosome detaches from the latter they often tear off some pieces of the nucleolar substance. Such pieces of the nucleolar substance generally become gradually smaller and disappear in the progress of the mitotic stage, but some of them

FIG. 2. Somatic cells of the F_1 plant. *a*, cell showing the nucleus having a small nucleolus (*n*) with no room around it; *b*, the nucleus showing a nucleolus (*n*) with a large room around it; *c*, an equatorial plate. $\times 1270$.

remain attached to the chromosome until metaphase. These data led to the view that the chromonemata get material which serves for the rearrangement of the chromonemata-composition: the change of the staining

capacity means the change of the charge, and the contraction of the chromonemata, the enlargement of the diameter of the spiral, must be the result of the molecular or micellar rearrangement in the chromonemata.

In the several cells in the tissue of the ovary there were some alike chromosomes gathering around a remaining piece of the nucleolus (Fig. 2, *c*, 1, 2 and 3). Besides we have found that certain alike chromosomes were situated nearer to each other than to others, especially they approached with their second constrictions (Fig. 2, *c*, 14–16 and 18–20). This is one of the cases that homologous chromosomes come together in the somatic nucleus. I have discussed already of such situation (Yasui, 1935). In this case a certain condition in the nucleus leading to the elongation of the duration of the prophase has a roll for the approaching of the homologous chromosomes.

D. Chromosome constitution. The chromosome number in the F_1 plant cell is 21, the sum of the haploid numbers of the parent plants. We can classify the chromosomes in the somatic metaphase as is shown in Table 2.

Table 2. The structure of the metaphase chromosomes in the somatic cells

No.	Relative length	Region of the 1st constriction	Presence (+) or absence (—) of 2nd constrict.	Presence (+) or absence (—) of sat. or knob	No. of the chromosomes in Fig. 2, <i>c</i>
1	Long (L)	Median	+	—	9\
2	L	„	+	—	20\}
3	L	Submedian	+	—	11\}
4	L	„	+	—	13\}
5	L	Subterminal	+ distal pt. in long arm	—	10\}
6	L	„	+ „	—	12\}
7	L	„	—	+ at the distal end of long arm	17\}
8	L	„	—	+ „	21\}
9	L	„	—	+ „	18\}
10	L	„	—	+ „	19\}
11	Long but shorter than L (l)	Submedian	—	+ „	14\}
12	l	„	—	+ „	15\}
13	l	„	—	+ „	16\}
14	l	Subterminal	+ in the long arm	—	8
15	l	Submedian	—	—	5
16	Median (M)	„	—	+ at the distal ends of both arms	6\}
17	M	„	—	+ „	7\}
18	M	Subterminal	—	+ at the distal end of the longer arm	1\}
19	M	„	—	+ „	2\}
20	M	„	—	+ „	3\}
21	M	Median	—	+ at the distal ends of both arms	4

Homologous chromosomes, though not completely in some sets, are bracketed in the table. Thus we can find 6 sets of 2 like chromosomes, 2 sets of the 3 like, and 3 chromosomes with no homologous partners in the $2n$ (sporophytic) complement of the F_1 plant.

3. Chromosome behaviours in the PMCs of the F_1 plant. In the most cases chromosome assortment in the meiotic prophase can be shown by the formula $6_{II} + 2_{III} + 3_I = 21$. The latter conforms to the data which are shown in the metaphase of the somatic mitosis (Fig. 2, *c*) and in Table 2. The structure and the configuration of the chromosomes are shown in Table 3.

Table 3. The association and assortment of the chromosomes in the later prophase (diplotphase) of the PMCs in the F_1 plant.

Valency	Configuration
Trivalent No. 1	Chain (Fig. 3, <i>c</i>). This is connected with larger nucleolus.
Trivalent No. 2	Two of 3 components form a ring which often interlocks with the bivalent No. 3 (<i>g</i> in Fig. 3, <i>a</i>). The third component chromosome attaches with one of its distal ends to the distal part of one component of the ring portion, and with another end to the smaller nucleolus (Fig. 3, <i>b</i>).
Bivalent No. 1	Chain, each chromosome attaches to the larger nucleolus with its secondary constriction near the distal end, and to each other with the another distal end (Fig. 3, <i>f</i>).
Bivalent No. 2	Chain, each chromosome attaches to the larger nucleolus with the satellited end and attaches to each other with other end.
Bivalent No. 3	Chain, one chromosome attaches to larger nucleolus with its satellite and joins with other non-satellited chromosome by the non-satellited end (Fig. 3, <i>g</i>). The latter chromosome is sometimes furnished with a satellite as in its companion, but even in this case this satellite detaches earlier from the nucleolus than that of the companion. (<i>g</i> in Fig. 3, <i>a</i>).
Bivalent No. 4	Chain, long necked satellites of both chromosomes synapse to each other without synapsis of the necks, and the adjacent distal portion of one component chromosomes attaches to an interstitial portion of the other component (Fig. 3, <i>d</i>). The latter synapsed regions detach from each other earlier than the separation of the synapsed satellites (<i>d</i> in Fig. 3, <i>a</i>).
Bivalent No. 5	Ring, this shows no connection with either larger or smaller nucleolus (Fig. 3, <i>h</i>).
Bivalent No. 6	Ring, each chromosome has a satellite which attaches to the smaller nucleolus at different points (Fig. 3, <i>e</i>).
Univalent No. 1	The chromosome attaches to the larger nucleolus with the second constriction (Fig. 3, <i>i</i>).
Univalent No. 2	The chromosome attaches to the smaller nucleolus.
Univalent No. 3	Same as No. 2.

As we see in Table 3 the chromosome structure as well as the configurations show us that in this F_1 plant the component chromosomes of trivalents as well as of bivalents are not thoroughly homologous to each other.

In the 1st meiotic division we have found 3 divided univalents at the equator, after the bi- and trivalent chromosomes had separated

from each other and proceeded to the poles, though not all of the bivalents separated simultaneously (Figs. 5 and 6). Sometimes one component of the trivalent is detached from the other two, so that there are found 4 or 5 instead of 3 univalents at the equator. Generally 2

Fig. 3. a, PMC in a later prophase, and the individual chromosomes from PMCs in the similar stage, somewhat diagrammatized. *n*, nucleolus; *a*, a PMC showing a nucleus in later prophase, $\times 1270$; *b-i*, chromosomes in the later prophase (diplophase); *b* and *c*, trivalents; *d-h*, bivalents; *d* and *g*, which resemble the bivalents *d* and *g* in *a* respectively; *i*, a univalent.

component chromosomes of the trivalent go to one pole and the third to the other without division of the sister chromatids, while in some cases 3 chromosomes of these trivalents are distributed longitudinally along the axis of the spindle and causes an incomplete 1st division, a bridge being formed between the daughter chromosome groups in the interkinesis (Figs. 12 and 13). In some PMCs we found a fragment chromosome during meiosis (the small spot at right end of the upper daughter chromosome group in Fig. 5 shows such a fragment). Such a fragment was also found in the meiosis of the PMCs of the mother plant (YASUI, 1937). Here I wish to mention that the configuration of the bivalent like *d* in Fig. 3 suggests that a fragment and a larger chromosome can be derived by a crossing over of the chromonemata.

The distribution of the chromosomes in the 1st division is not regular, so that the chromosome numbers in the daughter nuclei are often different, and incomplete nuclear division results in the formation of the restitution nuclei. In some PMCs the early stage of the middle lamella formation was observed in the interkinesis (Fig. 8), but no complete cytokinesis took place generally and the substances of the phragmoplast remained at the equator of the 1st division as fine granules in the fixed condition (Figs. 9 and 13).

Due to the irregular distribution of the chromosomes derived from the divided univalents in the 1st division the 2nd meiotic division is more

Figs. 4–15. PMCs in the F_1 plant. 4, side view of the 1st metaphase; 5 and 6, later anaphase of the 1st division; one daughter chromosome group (upper) in 5 has a small fragment, chromosomes in black are derivatives of bi- and tri-valents, the outlined are the separating univalents; 7, interphase, phragmoplast and the early stage of the MLI formation after the 1st division are seen; 8, 2nd metaphase; 9, a side view of the 2nd metaphase, at the equator of the 1st division the residue of the phragmoplast is seen; 10, the 2nd anaphase, 3 chromosomes (outlined) derived from the univalents are shown at the equator; 11, a tetrad; 12, later anaphase of the 1st division, a chromosome bridge disturbing the daughter nuclei formation is seen; 13, metaphase of the 2nd division, a chromosome bridge between the daughter nuclei and the residue of the phragmoplast between the nuclei are seen; 14, tetrad, the chromosome bridge of the 1st division is still remaining, 3 miniature nuclei besides 4 large nuclei are shown; 15, tetrad, each of 2 microspores having one miniature nucleus besides a large nucleus, and one microspore having 2 miniature nuclei and a large nucleus are seen.

irregular than the 1st. Table 4 shows an example which was observed in a single flower. Chromosome bridges, extranuclear chromosomes and the miniature nuclei were often found (Figs. 14 and 15).

Table 4. Number of the PMCs in the interkinesis and the tetrad with or without extranuclear chromosomes.

Number of the extranuclear chromosomes	Number of the pollen mother cells			
	Interkinesis		Tetrad	
	Absolute No.	Per cent	Absolute No.	Per cent
0	103	70.55	22	30.99
1	41	28.08	28	39.44
2	2	1.37	8	11.27
3	0	0.00	8	11.27
4	0	0.00	4	5.63
5	0	0.00	1	1.41
Total	146	100.00	71	100.01

The pollen grains were almost sterile, but the sporadic seed formation in the case of the back crosses with the pollen grains of the male parent shows that some egg cells were fertile.

Discussion

1. Chromosome constitution of the mother plant (*Papaver* No. 41,8). The chromosome constitution in the PMCs of the F_1 plant between No. 41, 8 plant and *P. bracteata* is as a rule

$$6_{II} + 2_{III} + 3_I \quad (1)$$

and in rare cases

$$4_{II} + 2_{III} + 1_{IV} + 3_I \quad (2)$$

The chromosome association in the PMCs of the mother plant is 14_{II} , while the haploid chromosome complement shows the constitution

$$2_{II} + 1_{III} + 7_I \quad (3) \text{ (YASUI, 1937).}$$

The basic chromosome number in *Papaver* is 7 or 11, so that 14 chromosomes of the haploid complement in the mother plant ought have been derived from 2 complements each having 7 component chromosomes. Therefore in the formula (3) each chromosome in the bivalent must belong either to a basic complement, one chromosome in the trivalent to one basic complement and the remaining two to the other basic complement, and some of 7 univalents to one basic complement and the remaining to the other. Now

$$\begin{aligned} & 2_{II} + 1_{III} + 7_I \text{ (the haploid complement of the mother plant)} \\ + & 7 \text{ haploid } bracteata \text{ chromosomes} = \\ & 2_{III} + 1_{IV} + 4_{II} + 3_I \text{ \{formula (2)\}, or} \\ & 2_{III} + 6_{II} + 3_I \text{ \{formula (1)\}.} \end{aligned}$$

The formula $2_{III} + 1_{IV} + 4_{II} + 3_I$ shows that each of the two bivalents in the formula (3) synapses with one *bracteata* chromosome, thus forming 2 trivalents; one trivalent synapses with one *bracteata* chromosome forming one quadrivalent, and the remaining 4 *bracteata* chromosomes

synapse with certain 4 chromosomes of the 7 univalents in the formula (3) thus forming 4 bivalents, the remaining 3 univalents being left as univalents. Then 6_{II} in the formula $2_{III} + 6_{II} + 3_I$ must be the result of the splitting of the quadrivalent in the formula $2_{III} + 1_{IV} + 4_{II} + 3_I$ to form 2 bivalents. Such a case is easily conceivable, the configuration of the trivalent in the mother plant is generally in a ring shape (YASUI, 1937) which means that the 2 components of this trivalent are homologous to each other, but both ends of the remaining one must be homologous with one end in each of 2 homologous chromosomes just mentioned, so

that we have the configuration like $\begin{array}{c} 1/2 \cdot 2 \\ | \\ 1 \backslash 2 \cdot 2 \end{array}$, therefore when this trivalent

synapses with another chromosome 1—2 the configuration must be a quadrivalent in chain like 1—2·2—1·1—2·2—2, or $\begin{array}{c} 1-2 \\ | \\ 1-2 \end{array}$ and 1—2·2—2, namely a ring and a chain bivalents. The former case fits the formula (2) and the latter the formula (1).

Thus we see that the haploid chromosome complement in No. 41, 8 (the mother plant) contains one complete set which is homologous with the *bracteata* complement (*B*-complement) and in the remaining 7 chromosomes 3 have their partners in the *B*-complement, another is partially homologous with one chromosome in its own set (this set may be called *A*-complement) and also one chromosome in the *B*-complement, while the remaining 3 are not homologous to neither of other 2 complements. The above consideration of the relationship among the chromosome complements in the F_1 plant will be shown in Table 5. For the sake

Table 5. Derivation of the chromosome complements and the association of the chromosomes in PMC of F_1 plant between *Papaver* No. 41,8 and *P. bracteata*.

No.	1	2	3	4	5	6	7	
Derivation								
<i>P. bracteata</i>	B_1	B_2	B_3	B_4	B_5	B_6	B_7	 <i>B</i> -complement
	(B) ₁	(B) ₂	(B) ₃	(B) ₄	(B) ₅	(B) ₆	(B) ₇	(<i>B</i>)-complement
<i>Papaver</i> No. 41,8								
	A_1	A_2	A_3	A_4	A_5	A_6	A_7	 <i>A</i> -complement

B_1-7 , (B)₁₋₇, and A_1-7 are the provisional designation of the chromosomes; vertical full line connection shows the association of the chromosomes; chromosomes bounded by dotted lines are the constituents of the trivalent in the formula (3).

of convenience I have numbered the chromosomes 1—7 in each complement. Nos. 1 and 2 in each complement are the members which synapse to form trivalents, Nos. 3s are third chromosomes which are homologous to each other, Nos. 4—7 in *B* and (*B*) (the *bracteata* complement in the

mother plant) are homologous respectively, No. 4 of *A*-complement is the chromosome which has two ends homologous to one end of the third chromosome, Nos. 5–7 in *A*-complement are those which have homologous chromosome neither in *B*- nor in (*B*)-complement.

Thus we can consider that No. 41, 8 has 2 primary complements in its haploid condition, and one—(*B*)-complement—of the two can produce by itself a viable plant and is homologous with *bracteata* complement (*B*-complement), while the other chromosomes (*A*-complement) can not form a complete basic complement as the former, because in the *A*-complement there is at least one chromosome (A_4) whose both ends are homologous to each other and also homologous with one end of another chromosome (A_3) belonging to one and the same complement; therefore the *A*-complement has no true fourth chromosome.

Consequently the *n*(haploid or gametic) chromosome-complement of No. 41, 8 is not complete diploid, though it appears to be so from the number of constituent chromosomes. Such a plant may be called "pseudopolyploid". It is quite possible that such a plant exists in nature, and such a chromosome constitution can have a roll for the duplication of the chromosome complements, thus leading to the formation of a pseudotetraploid or pseudopolyploid.

The derivation of No. 41, 8 is unknown, so that the derivation of the *A*-complement is also unknown. Consequently whether this chromosome complement is perfectly homologous with O_1 -complement in *P. orientale* or not, can not be determined now. The investigation on the pentaploid F_1 plant between No. 41, 8 and *P. orientale*, which was raised already, will give some data for the solution of the above problem. However, if these two complements, O_1 - and *A*-chromosome complement, are homologous to each other then *P. orientale* is another example of a pseudopolyploid (pseudohexaploid).

In Table 5 we can find out that (*B*)- or *B*-chromosome complement is composed of two groups, one having 3 and another 4 chromosomes, and that chromosomes in the former group have their partners in the *A*-complement but those in the latter has none. However, there is no evidence whether this grouping is a natural one. In other places (YASUI, 1936, 1937 etc.) I have considered that 7 basic chromosomes in *Papaver* were derived from 2 primary chromosome sets, one having 3 and the other 4 chromosomes. I will call these primary sets as Chelidonoid- and Corydaloid-sets respectively after SUGIURA's consideration about the chromosome constitution in Papaveraceae (SUGIURA, 1940).

Now if the 2 groups in the *B*-complement mentioned above were natural ones the Chelidonoid-set in the *B*-complement have 3 chromosomes homologous with those in *A*-complement, and the Corydaloid-set has no homologous ones, but if the above grouping were an artificial one, the

each primary set of *B*-complement has one or two homologous chromosomes in the primary sets of *A*-complement respectively, in other words the Chelydonoid- and Corydaloid-sets have some homologous chromosomes in them. The latter consideration is rather inconceivable.

2. Relationship between the chromosomes and the nucleolus. We find generally 2 nucleoli, one large and another small, in the meiotic prophase of the PMCs. If every chromosome complement had to have one nucleolus then this F_1 plant must have 3 instead of 2 nucleoli. While, several authors mentioned already the cases of a decrease of the number of nucleoli due to their fusion. The present case in *Papaver* will be one of such cases.

There are two homologous and one non-homologous chromosome complements in the F_1 plant, so that if each one could have one special nucleolus we will have two nucleoli of the same kind and one of different kind in a nucleus; consequently it seems probable that the 2 same kind nucleoli just mentioned will form a larger nucleolus by their fusion and the third one will remain as a smaller one, but the determination will be postponed until we will have more data.

Recently HAGA (1942) described a satellite chromosome in *Paris* and mentioned that "the length of the connecting filament and the size of the satellite determined passively by the developing nucleolus" But the data observed in the F_1 plant now concerned show that the size of the satellite and the connecting filament are determined by the contraction of the chromonemata by which the chromosome detaches from the nucleolus in the prophase, and the nucleolus in this stage is in the process of deformation and not of development or the accumulation of the substances.

Summary

1. The chromosome number in the F_1 plant between *Papaver* No. 41, 8 (a *bracteata* like tetraploid *Papaver*) and *P. bracteata* is 21 which is the sum of the gametic chromosome numbers of the parents. The chromosome association in the meiotic phases of the PMCs is generally $2_{III} + 6_{II} + 3_I$, but rarely $2_{III} + 4_{II} + 1_{IV} + 3_I$. The 2_{II} in 6_{II} of the former formula is derived from 1_{IV} of the latter.

2. *Papaver* No. 41, 8 has 28 chromosomes which synapse to form 14 gemini in the PMCs, while the haploid complement has the constitution $2_{II} + 1_{III} + 7_I$ (YASUI, 1937). This fact together with the above mentioned data led to the following conclusions as to the relationship between the basic chromosome complements in *Papaver* No. 41, 8: 1), the haploid chromosome complement of No. 41, 8 consists of the 2 basic complements, (*B*) and *A*; 2), (*B*)-complement is homologous to the haploid complement of *P. bracteata* (*B*-complement); 3), three (A_{1-3}) of 7 chromo-

somes in *A*-complement have homologous chromosomes—(*B*)₁₋₃ and *B*₁₋₃ in Table 5—either in (*B*)- or *B*-complement; 4), the fourth chromosome (*A*₄ in Table 5) has homologous ends which is homologous to one end of the third chromosome in all these three kinds of complements; 5), the remaining three of the *A*-complement have no homologous chromosomes in (*B*)- or *B*-complement (cf. Table 5).

3. *Papaver* No. 41, 8 is a tetraploid in terms of chromosome numbers, but it is an incomplete tetraploid in the sense of the chromosome constitution, because on one hand in one (*A*-complement) of 2 basic chromosome complements one component chromosome is lacking, so that it is incomplete, and on the other hand one chromosome is added which is duplicated by one part of another component chromosome.

4. The structure of the synapsed chromosomes in the *F*₁ plant and the relationship between the chromosomes and the nucleoli were discussed.

5. The irregular behaviours of the chromosomes in the meiosis of the PMCs of the *F*₁ plant result in high abortion of the pollen grains, but the sporadic seed formation by the back cross with the pollen grains of the male parent shows that some egg cells are fertile.

Here the writer wishes to express her best thanks to Prof. Fujii for his valuable advice throughout the course of the work. The expence of carrying out this study were partly defrayed out of a grant from the Science Research Fund of the Department of Education.

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