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CLASSE DES SCIENCES MATHÉMATIQUES ET NATURELLES SÉRIE B: SCIENCES NATURELLES (I)

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### Studja nad rasą mozajkową gatunku Petunia violacea. – Studies on a mosaic strain of Petunia violacea.

#### Mémoire

#### de M. E. MALINOWSKI m. c. et M<sup>lle</sup> A. SMOLSKA,

présenté dans la séance du 5 octobre 1931, par M. E. Malinowski m. c.

(Planches 16-20).

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#### Introduction

Since 1914 our Institute (Institute of Genetics, Skierniewice, Poland) has been engaged in the study of variegated colouration in *Petunia violacea* Lindl. We did isolate a strain showing some features unknown in the mosaic types of other plants. A characteristic trait of this strain is the distinct positive correlation existing between the amount of pigment and flower size and chiefly in this fact our case differs from other cases of patching in the flowers.

However some correlation phenomena between patching and other characters have been observed in Lathyrus and Maize. It

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has been shown by Emerson (2) that when aberrant seeds of maize occur in which recessive aleurone and endosperm characters are contributed by the female parent and the corresponding dominant characters by the male parent, spots of the recessive aleuron colour are in the great majority of cases underlaid by the recessive type of endosperm if the genes for these aleurone and endosperm characters are genetically linked. The correspondence in the outline between the colourless aleurone and the underlying waxy endosperm is srickingly exact. Punnett (5) reports that in *Lathyrus odoratus* in general habit of growth the patched plant is intermediate between the red and the normal. The normal shoots bearing purple flowers are more luxuriant in their habit and exhibit a brighter green colour than the patched ones.

The mosaic strain of *Petunia* has been obtained by the senior writer from the firm Vilmorin-Andrieux in Paris with some seeds of a normal, non-variegated garden variety. This strain has a large scale of variation regarding the colour distribution (from self-purple to mosaic) and the size and shape of flowers.

There are several theories as to the nature of patching and as to the inheritance of this character. For all of them however a sufficient cytological foundation is required. As one might expect and as the investigations carried out in this Institute seem to show the chromosomes play a decisive rôle as to the elucidation of the problem. It is probable that we have to deal here with a kind of segregation the mechanism of which is not sufficiently known.

Cytological investigations based on the material of our Institute have been started also by M. Skalińska some years ago (1927). The methods adopted in those previous researches have not been however sufficiently precise and therefore the senior writer decided to examine the problem anew by using stronger glasses. The cytological work has been entrusted to Miss A. Smólska and the results of those researches are given in the cytological part of this paper.

The cytological laboratory of our Institute having not been completed until recently, the great part of the cytological work has been conducted in Prof. Z. Wóycicki's laboratory at the University of Warsaw. We are greatly obliged to Prof. Z. Wóycicki for his kind assistance.

#### Studies on a mosaic strain of Petunia violacea

### I. Genetics (by E. Malinowski)

#### 1. Variability in colour distribution and corolla sizes of the mosaic strain ot Petunia violacea

The strain in question shows a wide variation in colour distribution, ranging from self-purple flowers (fig. 2, 1) on one hand to those in which the pigment is confined to the »eye« round the throat (fig. 1, 1) on the other hand. Between those two extreme types there are many gradations regarding the colour distribution as well as the size and shape of flowers. The sizes of corolla diminish along with the decrease of purple pigment.

We may group the various types composing this strain into 11 classes, the flowers of which are represented in the fig. 1



Fig. 1. The first seven classes of flowers of the mosaic strain of *Petunia* violacea. The first four classes are called in this paper small mosaic flowers.

and 2. The larger flowers have on an average more pigment. The correlation table I concerns these two variables. The coefficient of correlation equals + 0.837.

The shapes of small white flowers are a little different from those of large purple ones. In the former case the corolla spreads

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rapidly whilst in the latter it widens gradually. In addition,



Fig. 2. The remaining four classes of flowers of the mosaic strain of *Petunia violacea*. The class eleventh has large self-purple flowers.

TABLE I.

Correlation table for corolla diameter and amount of pigment.

eur hoge		GARANY.	F 1	o w	e r	с	l a	s s	es	3	Cinar
A Permit	1	2	. 3	4	5	6	7	8	9	10	11
Corolla di anti di ant		8 12 28 7	$\begin{array}{c}1\\11\\25\\6\end{array}$	1 4 11 14	2 9 22 25 8	$5 \\ 15 \\ 15 \\ 2$		7 4 1 2	$     \begin{array}{c}       1 \\       18 \\       16 \\       9 \\       5     \end{array} $	1 2	

#### Studies on a mosaic strain of Petunia violacea

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we can see a protuberance on the lower side of the corolla tube in the case of small flowers.

Very often we find two or more types of flowers on the same individual. These types may be extreme ones; they may belong for instance to the classes 1 and 11, or 2 and 10, or 3 and 9 and so on. No regularity in occurrence of different types



Fig. 3. Four flowers of the mosaic strain of *Petunia violacea* showing sectorial distribution of pigment (sectorial chimeras).

in one individual could be found out, no prevalence of a combination over any other one was observed. Occasionally it has been remarked that three or more flower types were appearing in the same plant. Such individuals may be regarded as sectorial chimeras, the different kinds of flowers being distributed usually on different shoots. Sometimes one half of the plant bears selfpurple flowers and the other half — mosaic ones, or there is a sector bearing flowers differing from those of the remaining part of the plant. In all those individuals, occasionally, flowers appear which show a sectorial distribution of pigment. Such flowers have always in the white sector smaller petals than in the purple one. Some of them are shown in the fig. 3.

#### E. Malinowski and A. Smólska:

It has been already pointed out that a positive correlation exists between the quantity of purple pigment and the size of flowers. This does not exclude the possibility of the appearance of a certain percent of individuals with self-purple flowers of medium size. And on the other hand we could observe some plants with an intermediate flower size and a purple colour limited round the throat. The diameter of purple flowers (of the 11-th class) did not reach however 3 cm. in our material and the diameter of small mosaic flowers (classes from 1-st to 4-th, see fig. 1) did not exceed 3 cm. The measurements of the corolla diameter have been made in the following lines: Nr. 28 of 1929 (in the individuals with self-purple flowers) and Nr. 25, 26 and 27 of 1929 (in the plants with small mosaic flowers). It follows from the fig. 4 that the flowers of the class 11-th are larger



Fig. 4. Diagram showing variability in corolla diameter of two extreme flower types namely small mosaic flowers of classes 1—4 and large selfpurple ones of class 11.

than those of the classes 1, 2, 3 and 4-th and that such two categories of flowers do not overlap each other as far as the diameter of the corolla is concerned.

The mosaic strain, we deal with, is self-incompatible. The selection experiments for detecting the genetical behaviour of various types, making up a mosaic series, must start therefore from the intercrossing of two plants exhibiting the same phenotype.

In our experiments the progeny raised from individuals with large purple flowers had, on an average, larger flowers and more pigment than the offspring obtained from small mosaic flowers.

We shall obtain an idea of the influence of selection by examining the table II, representing the frequency of particular flower types in 26 lines. Each line is a progeny of two plants having had flowers of the same type.

#### TABLE II.

Showing the results of selection of extreme flower types of the mosaic strain.

No of the	a coreli	F	1	0 W	е 1	c c	- 1 -	a s	s e	s	og er eom	otal oer of iduals
line	1	2	3	4	5	6	7	8	9	10	11	Tc numl indiv
$\begin{array}{c} 7/1931\\ 28/1929\\ 49/1929\\ 47/1929\\ 48/1929\\ 44/1929\\ 45/1929\\ 45/1929\\ 36/1929\\ 36/1929\\ 37/1929\\ 38/1929\\ 5/1931\\ 41/1929\\ 43/1929\\ 43/1929\\ 42/1929\\ 6/1930\\ 7/1930\\ 6/1931\\ 3/1930\\ 42/1930\\ 5/1930\\ 27/1929\\ 32/1929\\ 25/1929\\ 2/1931\\ \end{array}$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c} 1 \\ 10 \\ 2 \\ 2 \\ 1 \\ 2 \\ - \\ 2 \\ - \\ 2 \\ - \\ - \\ - \\ - \\ -$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c} 2\\ 32\\ 10\\ 6\\ 11\\ 15\\ 4\\ 16\\ 1\\ 3\\ 8\\ -\\ 3\\ 57\\ 17\\ 2\\ -\\ -\\ 67\\ 10\\ 1\\ 9\\ 4\\ 14\\ 1\end{array}$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c}1\\9\\7\\4\\4\\13\\3\\11\\-2\\4\\-4\\9\\15\\2\\-\\-\\21\\2\\-\\3\\-\\4\\2\end{array}$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c} 5\\ 3\\ 3\\ 2\\ 0\\ 5\\ 7\\ 5\\ 1\\ 9\\ 1\\ -2\\ 1\\ 3\\ 4\\ 7\\ 8\\ 1\\ -1\\ -4\\ 7\\ 2\\ 1\\ 8\\ 4\\ 9\\ 1\end{array}$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c} 67\\ 317\\ 64\\ 24\\ 59\\ 19\\ 24\\ 36\\ 6\\ 5\\ 33\\ 13\\ 71\\ 197\\ 96\\ 38\\ 18\\ 11\\ 6\\ 48\\ 4\\ 1\\ 5\\ 4\\ 6\\ 5\end{array}$	$\begin{array}{c} 85\\ 426\\ 128\\ 52\\ 89\\ 69\\ 46\\ 99\\ 8\\ 16\\ 48\\ 16\\ 110\\ 555\\ 181\\ 60\\ 18\\ 11\\ 60\\ 18\\ 11\\ 6\\ 396\\ 54\\ 17\\ 71\\ 23\\ 171\\ 64 \end{array}$

In the majority of those lines the individuals of the type eleventh, with large self-purple flowers, are prevailing. Such lines arose from plants with large self-purple flowers. In five lines only we may observe the numerical prevalence of individuals with small mosaic flowers of the first, second and third class. Such lines have arisen from plants with small mosaic flowers. The line 3/30 is an intermediate one in which the largest number of plants is found in the fifth class of our classification.

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This line is a progeny of the second and fifth types crossed with one another. The lines 6/30 and 7/30 are composed of few plants all of which possess large purple flowers of the eleventh class. Some of those individuals however give branches bearing flowers of the tenth and ninth classes. Sometimes solitary flowers belonging to such classes appear among the self-purple flowers. Those two lines were got from plants with large selfpurple flowers.

The generalisation of Chittenden (Bibiographia Genetica III) that a mosaic may be said to give a majority of plants like itself, or in neighbouring classes of mosaic, with relatively fewer in classes remote from parental type, holds good in our case.

#### 2) Crosses between the mosaic strain and a normal variety of *P. grandiflora* Hort.

This cross has been made in order to learn if mosaic may be associated with morphological types of flowers other than those of P. violacea and with other colours than the purple one. For this purpose the mosaic strain of P. violacea has been crossed to P. grandiflora Hort. var. Admiration. This variety posseses giant flowers of a dark violet colour and white stripes.

The  $F_1$  generation of this cross has been an intermediate one as to the sizes and shapes of the corolla. Anyhow all the flowers have been self-purple. No one trace of mosaic has been observed in the numerous  $F_1$ -plants. In  $F_2$  a segregation took place but the plants showing mosaic distribution of pigment have been very scarce. Among the 244 plants of  $F_2$  were 7 individuals only with mosaic flowers. The scale of variation of the corolla diameter in  $F_{2}$  is shown in the Table III. The frequency polygon is bimodal. One mode (between 56 and 60 mm.) is corresponding to F, and the second one (between 71 and 75 mm) — to the parental variety with giant self-violet flowers. The corolla size of the mosaic strain of P. violacea was represented in  $F_2$  by only few individuals and the mode which would correspond to this strain was lacking. For the sake of comparison the figures are given concerning the diameter of the corolla of the parental variegated strain, grown in 1927 side by side with the  $F_2$  generation. The mode of this strain lies between 36 and 30 mm. (Table III, p. 196).

Mosaic has appeared in  $F_2$  on plants with relatively small flowers (*P. violacea* type) as well as on those with giant ones (*P. grandiflora* type). The latter combination is a new one. It comprises the giant flower size and the dark colour of the parental *P. grandiflora* and in addition one of the characters of *P. violacea* namely that of mosaic. A description of the 7 plants in question is given below.

1) A plant with two types of flowers namely: a) self-violet ones of about 60 mm. in diameter and b) violet with patched margins being about 7 mm. smaller than the former ones.

2) A plant with: a) large self-violet flowers of about 60 mm in diameter and b) smaller flowers of about 56 mm in diameter with corolla margins patched with violet.

3) A plant all flowers of which are variagated but having a difference in size as well as in the amount of pigment between the particular flowers. The larger flowers (of about 65 mm.) have more pigment whilst the smaller ones (of about 48 mm.) have the self-purple area limited round the throat and along the main veins, the remaining of the petals being patched with purple on a white background.

4) A plant with two types of flowers namely: a) self-violet ones of about 65 mm. in diameter and b) patched ones with a violet pigment on a white background (of about 45 mm. in diameter).

5) A plant with: a) self-violet flowers (of about 65 mm. in diameter) and others with b) patched margins (of about 50 mm. in diameter).

6) The scale of variation concerning mosaic is larger than in all other  $F_2$  plants. There are the following types: a) large selfpurple (of about 51 mm.), b) flowers with mosaic margins (of about 47 mm.), c) small flowers of about 40 mm. in diameter with a large mosaic area, d) flowers mosaic for purple and violet. These last flowers represent a peculiar type of variegation which appeared only once in the  $F_2$  generation.

7) There are two types of flowers namely; a) large selfpurple of about 55 mm. in diameter and b) smaller ones of about 48 mm. with mosaic margins.

In the above descriptions we pointed out only the extreme types of flowers in each separate plant. In every one of these seven plants there were intermediate forms of flowers.

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	Pet. violacea     1928.     41     34       The new mosaic strain in     1928	18 23	soda Roman Alter alter A	Variability in corolla	Alence altern atte	Pet. violacca 1927	erren orgens ore	A long to the second se	Variability in corolla sizes of I
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	a liew		0	IV.	Success	17	35	m e	$F_2$ 0
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TABLE III.

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Several mosaic plants of the  $F_2$  generation were intercrossed in order to get a  $F_3$  generation and in such a way six  $F_3$ 



Fig. 5. Flowers of new mosaic strain of *Petunia* obtained in a cross with *P. grandiflora.* 1 flower of class 1 showing the smallest sizes and smallest amount of pigment; 3 flower of class 3 (intermediate class); 5 giant self-violet flower of class 5.

lines have been obtained all being more or less heterogenous as to the flower type. Two of these lines proved more uniform as to the morphological type of flowers and as to the colour. They

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reproduced namely the type of *P. grandiflora* but without white stripes. These two lines have been raised from seeds obtained after an intercrossing of the first and second of the above described plants. As there is no visible difference between these two lines they can be and will be treated in conjunction in this paper.



Fig. 6. Flowers of new mosaic strain, showing sectorial distribution of pigment.

They may be looked upon as a new mosaic strain, differing from the mosaic P. violacea in the size of the flowers which are larger here and in the colour of the flowers which are of a dark violet tint instead of being purple. But the successive degrees in the mosaic distribution of the pigment characteristic of the parental strain occur here also quite distinctly. Fig. 5 shows three

#### Studies on a mosaic strain of Petunia violacea

flowers of this new variegated strain. The first is a large selfviolet one, the second being of an intermediate size, shows variegation and the third is a small one with a violet pigment confined round the throat. This last flower represents the extreme form of the scale of variation. Anyhow the above mentioned specimens have many intermediate forms between one another. We find in the Table IV (p. 196) the figures showing the variability of the corolla diameter concerning both strains: the new

#### TABLE V.

The correlation table for corolla sizes and amount of pigment of the new mosaic strain.

	C RANÉ I SA A da		Flo	wer cla	sses	
		1	2	3	4	5
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in cı	7.0 ,,		lia.a. ite se tVesti	2	5	51
leter	6.5 ,,	i wa i	NBA I	14	8	21
diam	6.0 ,,	ion son Groot in	5	10	8	8
rolla	5.5 ,,	1	8	7	2	0110-0
Coi	5.0 ,,		5	5		ew o n wiste
	4.5 ,,	1	5	3	e oliqui	de la

mosaic one and the parental one. These figures refer to the plants got in 1928 and which had been growing side by side in our experimental garden.

It is evident from what has been said that the patching has been transferred from a strain with a relatively small flowers and purple pigment to a strain with giant flowers and a violet pigment. In all we obtained in 1928 150 individuals making up together the new mosaic strain. Such was the number of plants of the two  $F_3$  lines, referred to above. The sectorial chimeras appeared only in 10 individuals of the new mosaic strain. Fig. 6 shows some  $F_3$  flowers with a sectorial distribution of violet pigment.

Thus, all peculiarities of the parental strain concerning patching reappeared in the  $F_s$  lines.

We have grouped the various flowers of the new variegated strain into five classes only. The first is the class with giant self-violet flowers (fig. 5, 5), the fifth possess the smallest amount of pigment and the smallest sizes of flowers (fig. 5, 1). The correlation existing between the diameter of the corolla and the amount of pigment is shown in the Table V (p. 199). Coefficient of correlation equals  $\pm 0.575$ .

Selection experiments, conducted with a view to isolate the extreme types of flowers, have had results being analogous to those obtained in the mosaic strain of *Petunia violacea*.

The material for cytological purposes has been taken from plants grown in our Institute in 1929. In the following pages the term »self-purple flowers« refers to the class 11 of our classification and the term »small mosaic flowers« to the class 1.

#### II Cytology (by A. Smólska).

The puzzling phenomenon of anthocyanin variegation in Pe-tunia has been recently subjected to caryological investigations by M. Skalińska (7) and E. Malinowski (4). Skalińska assumes that the unequal division of chromatic substance in meiosis is responsible for the mosaic segregation in *Petunia*; this unequal chromatic division is supposed to occur also in somatic mitoses. Malinowski is inclined to believe that in the small mosaic flowers the chromosomes are, on an average, shorter that in the large self-purple ones.

#### 1) Methods

K a g a w a's (3) method applied in this work permitted to identify the particular chromosomes in the two extreme forms of flowers of the mosaic strain in question. I used this method for the measuring of the somatic chromosomes.

The chromosome length in meiosis has been determined in another way. The method adopted in such a case consisted in projecting the chromosomes on the opaque screen of a large photomicrographic Zeiss apparatus and in measuring them on the screen.

The fixing reagents used in the actual work have been the following ones: Benda's reagent without acetic acid, Flemming's

#### Studies on a mosaic strain of Petunia violacea

fluid (stronger solution) with a very small quantity of acetic acid (less than in Flemming's formula) and Mottier's fluid with a very small quantity of acetic acid. The chromosomes have been stained with Heidenhain's Iron-Haematoxylin.

As to the somatic cells Benda's fluid, without acetic acid, proved to be the best fixing reagent because it did not lead to any swelling in the chromosomes, which showed always the same thickness however cell layer having been examined. The use of Fleming's solution on the contrary has brought as a result a swelling of the chromosomes being placed in the superficial cell layers. But such a swelling had no apparent influence on the chromosome length.

#### 2) The somatic chromosomes

In comparing several drawings of the equatorial plates some differences in general appearence have been noticed. A more detailed examination of equatorial plates in various cell layers of the flower buds, in various buds and in material fixed in various reagents, has shown that those differences have been due to deformations especially a swelling of the chromosomes produced by different reagents or by the same reagent which when penetrating particular cells, could modify the degree of solution. Only those plates which have been obtained from material fixed in Benda's fluid without acetic acid did not show any swelling, whatever bud, tissue or flower level is examined.

The equatorial plates of two extreme flower types did not show on a superficial examination any visible differences in general appearence. For this reason the measurements of the somatic chromosomes have been performed with the most exact method so far employed, namely the method of F. Kagawa(3).

Kagawa's method leads to an exact measuring of the length of a curved chromosome which is not lying in one plane. With this method the measurements of 25 chromosome complements have been performed.

At first each complement has been drawn with the help of a camera lucida (obj. Zeiss Apochr. 1.20, aper. 1.3 and eyepiece Zeiss Komp. 30). These drawings have been magnified 2.5-fold with a photographic apparatus. After it the chromosomes have been brought to one plane. The measurements of the chromosome dra-

wings have been performed with compasses; the distance between the points of its two branches has been changing from complement to complement but it has been always corresponding to  $1/4 \mu$ . For the complements shown in the Fig. 7 (13, 14, 16) for instance the distance of 0.30 cm corresponded to  $1/4 \mu$ , for the Fig. 7 (15), Fig. 8 (19, 21, 22) this distance has been 0.31 cm, for the Fig. 8 (25, 26) 0.32 cm and for the Fig. 7 (10), Fig. 8 (20) etc. it amounted to 0.33 cm. These slight differences are due to the fact that both the camera lucida and the drawing table, did not always assume strictly the same position and the scale of magnification of our drawings changed from case to case. In each case it has been verified and a section exactly corresponding to  $1/4 \mu$  has been computed.

The flower buds for fixing have been taken either from plants exhibiting exclusively large self-purple flowers or from those only bearing small mosaic flowers.

The fundamental number of chromosomes is 14 for both extreme types of flowers, viz., large self-purple and small mosaic. Occasionally however other numbers occurred namely: 16 and 18 chromosomes on the one hand and 12 and 10 on the other. The occurrence of these numbers is irregular and rather rare; one could conclude that the complexes of such cells do not occur and that this phenomenon therefore has nothing to deal with the mosaic segregation.

A characteristic feature of the somatic chromosomes is a bifurcation of their ends. But this phenomenon is not bound to particular chromosome sizes. Some of the chromosome complements under discussion are shown in the Fig. 7 and 8 in the text.

In addition to the bifurcation of their ends another characteristic feature of these chromosomes is their regular outlines and relative elongation. Tickened ends of some chromosomes shown in Fig. 8 (19) (sizes 2.9, 2.5) and in Fig. 8 (20) (sizes 2.9, 2.7, 2.5) are signs of a commenced bifurcation. We do not see, however, this bifurcation because of an insufficient decolouration of the slides. The shapes as we can judge through the Fig 7 and 8 in the text, are diverse. For instance the chromosome 3.1 (Fig. 7, -10, 14, 15 etc.) in the above mentioned Fig. 7 assumes various shapes. Such shapes are not characteristic of a definite chromosome size.

It has been pointed out that 25 chromosome complements have been measured, 10 belonging to the large self-purple flowers

and 15 to the small mosaic ones. Figures representing microns and concerning the length of chromosomes of those 25 complements are shown in Tables VI and VII (p. 206). The chromosomes which sizes are shown in these Tables have been set in pairs not only according to their length their shapes and the bifurcation of their ends have also been taken into consideration. The shapes of chromosomes of 16 complements are shown in Fig. 7 and 8 in the text. Eight complements (Fig. 7, -9-16) belong to the selfpurple flowers and eight (Fig. 8, -19-26) to the small mosaic type. As we may see in the fig. 7 (15) there have been put together in the seventh complement the chromosomes 3.7 and 3.4 in the first pair and the chromosomes 3.6 and 3.3 in the second one chiefly according to their shapes (the chromosomes of the first pair are bifurcated and those of the second show no traces of division). According to the absolute length we would had been led to set 3.7 with 3.6 to form the first pair and 3.4 with 3.3 to form the second one. For the same reason the chromosomes 3.7 and 3.0 (Fig. 8 in the text, fig. 24) have been put in one pair and the chromosomes 3.6 and 3.0 in the other. Relying upon their length, the combinations would have been 3.7 and 3.6 for the first pair and 3.0 and 3.0 for the second. In each column from I to VII, Tables VI and VII) we see pairs of figures which refer to pairs of chromosomes. The difference between the length of chromosomes in one pair are very small and for the most part they do not exceed  $0.1 \,\mu - 0.2 \,\mu$ . Some dimensions are always lacking in each complement but often the same chromosome length is repeated three or even fourfold in the same.

The largest figure in column I Tabl. VI (self-purple flowers) is 3.8 and the smallest 3.0. The figures of column I refer to the largest pair of chromosomes which we may call pair I. In the 10 pairs of this column the figure 3.5 in repeated 7 times, what makes  $35^{\circ}/_{\circ}$  and other figures only reach  $5^{\circ}/_{\circ}$ ,  $10^{\circ}/_{\circ}$  and  $20^{\circ}/_{\circ}$ . The figure 3.5 is the mode of our scale of variation and therefore one may assume that this figure represents the length of the first pair of chromosomes. The modal values for the chromosome pairs of the self-purple flowers will be 3.5, 3.3, 3.0, 2.8, 2.6, 2.5 and 2.3 respectively. For small mosaic flowers we obtain the following modes: 3.4, 3.2, 3.1, 2.9, 2.7, 2.4 and 2.2. This may be seen in Tables VIII and IX, in which the chromosomes Bulletin III. B. 1, 1931.

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Fig. 7. Somatic chromosomes of the large self-purple flowers drawn with Kagawa's method.



Fig. 8. Somatic chromosomes of the small mosaic flowers drawn with Kagawa's method.

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#### TABLE VI.

Chromosome sizes of 10 complements of self-purple flowers. The figures represent microns. Horizontal lines separate complements from different buds.

osome		Columns corresponding to chromosome pairs								
Chrom	I	П	III	IV	v	VI	VII			
1	3.7-3.6	3.3-3.3	3.1-3.0	2.9-2.8	2.8-2.8	2.7-2.6	2.5-2.4			
2 3	3.5 - 3.5 3.5 - 3.5	3.1 - 3.1 3.3 - 3.2	3.3 - 3.0 3.0 - 3.0	3.0-2.6 3.0-2.9	2.8 - 2.7 2.9 - 2.9	2.5-2.5 28-2.8	$2 \cdot 3 - 2 \cdot 3$ $2 \cdot 7 - 2 \cdot 6$			
4	3.7-3.5	3.2-3.0	3.1 3.0	3.0-3.0	3.1-2.9	2.7-2.7	2.4-2.3			
5 6 7	$\begin{vmatrix} 3.8 - 3.4 \\ 3.6 - 3.3 \\ 3.7 - 3.4 \end{vmatrix}$	$\begin{vmatrix} 3 \cdot 3 - 3 \cdot 2 \\ 3 \cdot 3 - 3 \cdot 3 \\ 3 \cdot 6 - 3 \cdot 3 \end{vmatrix}$	2.9-2.9 3.1-3.1 3.3-3.1	$\begin{array}{c} 2.8 - 2.6 \\ 3.1 - 2.8 \\ 3.1 - 2.9 \end{array}$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{c} 2.5 - 2.4 \\ 2.5 - 2.3 \\ 2.8 - 2.6 \end{array}$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$			
8 9 10	$\begin{vmatrix} 3.7 - 3.5 \\ 3.5 - 3.3 \\ 3.6 - 3.0 \end{vmatrix}$	$\begin{vmatrix} 3.0 - 2.9 \\ 3.1 - 3.0 \\ 2.7 - 2.7 \end{vmatrix}$	$2 \cdot 9 - 2 \cdot 8$ $3 \cdot 0 - 2 \cdot 9$ $2 \cdot 7 - 2 \cdot 7$	$\begin{array}{c} 2.8 - 2.8 \\ 2.8 - 2.5 \\ 2.7 - 2.7 \end{array}$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{c} 2.7 - 2.6 \\ 2.5 - 2.5 \\ 2.4 - 2.4 \end{array}$	$\begin{array}{c} 2 \cdot 3 - 2 \cdot 1 \\ 2 \cdot 4 - 2 \cdot 3 \\ 2 \cdot 3 - 2 \cdot 2 \end{array}$			

#### TABLE VII.

Chromosome sizes of 15 complements of small mosaic flowers. The figures represent microns. Horizontal lines separate complements from different buds.

osome	and a	Columns corresponding to chromosome pairs								
Chrom comple	I	Π	III	IV	V	VI	VII			
$\begin{array}{c}1\\2\\3\\4\end{array}$	3.4 - 3.0 3.4 - 2.9 3.5 - 3.4 3.6 - 3.4	3.1 - 3.0 2.9 - 2.8 3.3 - 3.2 3.2 - 3.2	$2 \cdot 9 - 2 \cdot 5  2 \cdot 9 - 2 \cdot 8  3 \cdot 1 - 3 \cdot 0  3 \cdot 2 - 3 \cdot 1$	$\begin{array}{c} 2.7 - 2.7 \\ 2.9 - 2.7 \\ 3.0 - 2.9 \\ 2.9 - 2.7 \end{array}$	$\begin{array}{c} 2.7 - 2.4 \\ 2.7 - 2.5 \\ 2.9 - 2.9 \\ 2.8 - 2.5 \end{array}$	$\begin{array}{c} 2 \cdot 5 - 2 \cdot 4 \\ 2 \cdot 6 - 2 \cdot 6 \\ 2 \cdot 7 - 2 \cdot 6 \\ 2 \cdot 7 - 2 \cdot 6 \\ 2 \cdot 7 - 2 \cdot 6 \end{array}$	$\begin{array}{c} 2 \cdot 4 - 2 \cdot 1 \\ 2 \cdot 2 - 2 \cdot 2 \\ 2 \cdot 3 - 2 \cdot 2 \\ 2 \cdot 6 - 2 \cdot 5 \end{array}$			
5 6 7 8 9 10	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{r} 3 \cdot 4 - 3 \cdot 4 \\ 3 \cdot 6 - 3 \cdot 0 \\ 3 \cdot 1 - 2 \cdot 8 \\ 2 \cdot 7 - 2 \cdot 7 \\ 3 \cdot 1 - 3 \cdot 0 \\ 3 \cdot 2 - 3 \cdot 2 \end{array}$	$\begin{array}{c} 3 \cdot 4 - 3 \cdot 3 \\ 3 \cdot 0 - 3 \cdot 0 \\ 3 \cdot 1 - 2 \cdot 8 \\ 2 \cdot 5 - 2 \cdot 5 \\ 3 \cdot 1 - 2 \cdot 6 \\ 3 \cdot 2 - 3 \cdot 1 \end{array}$	$\begin{array}{c} 3 \cdot 3 - 3 \cdot 3 \\ 2 \cdot 9 - 2 \cdot 8 \\ 3 \cdot 0 - 2 \cdot 9 \\ 2 \cdot 5 - 2 \cdot 5 \\ 2 \cdot 9 - 2 \cdot 7 \\ 2 \cdot 8 - 2 \cdot 6 \end{array}$	$\begin{array}{c} 3.1 - 2.7 \\ 2.7 - 2.7 \\ 2.8 - 2.6 \\ 2.4 - 2.3 \\ 2.6 - 2.6 \\ 2.8 - 2.7 \end{array}$	$\begin{array}{c} 2 \cdot 5 - 2 \cdot 4 \\ 2 \cdot 5 - 2 \cdot 5 \\ 2 \cdot 4 - 2 \cdot 4 \\ 2 \cdot 4 - 2 \cdot 4 \\ 2 \cdot 5 - 2 \cdot 4 \\ 2 \cdot 5 - 2 \cdot 4 \\ 2 \cdot 5 - 2 \cdot 4 \end{array}$	$\begin{array}{c} 2 \cdot 5 - 2 \cdot 4 \\ 2 \cdot 3 - 2 \cdot 2 \\ 2 \cdot 2 - 2 \cdot 2 \\ 2 \cdot 2 - 2 \cdot 2 \\ 2 \cdot 2 - 2 \cdot 1 \\ 2 \cdot 4 - 2 \cdot 1 \\ 2 \cdot 4 - 2 \cdot 2 \end{array}$			
11 12	$\begin{vmatrix} 3.6 - 3.4 \\ 3.9 - 3.7 \end{vmatrix}$	$\begin{vmatrix} 3.5 - 3.4 \\ 3.2 - 3.1 \end{vmatrix}$	$3 \cdot 4 - 3 \cdot 0$ $3 \cdot 0 - 3 \cdot 0$	$\begin{array}{c c} 2 \cdot 9 - 2 \cdot 7 \\ 2 \cdot 9 - 2 \cdot 6 \end{array}$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{ c c c c } 2.7 - 2.6 \\ 2.5 - 2.4 \end{array}$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$			
13	4.2-3.8	3.8-3.4	2.9 - 2.7	2.6 - 2.4	2.42.4	2.2-2.2	2.2-2.1			
14 15	3.5-2.8 4.2-3.7	$\begin{vmatrix} 3.0 - 2.8 \\ 3.8 - 3.5 \end{vmatrix}$	2.8 - 2.8 3.2 - 3.1	$\left \begin{array}{c} 2.7 - 2.7 \\ 3.0 - 3.0 \end{array}\right $	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$			

have been classified according to their size, the class interval being 0.1.

The difference between the chromosome complements of two extreme flower forms, which strikes us at first sight is that the scale of variability in self-purple flowers ranges from 3.5 to 2.3and in the small mosaic ones from 3.4 to 2.2.

Let us group the supposed chromosome sizes (modes) into two series, one of which will include odd numbers  $(3\cdot 5 - -3\cdot 3)$  $-3\cdot 1 - 2\cdot 9 - 2\cdot 7 - 2\cdot 5 - 2\cdot 3$ ) and the other even numbers  $(3\cdot 4)$  $-3\cdot 2 - 3\cdot 0 - 2\cdot 8 - 2\cdot 6 - 2\cdot 4 - 2\cdot 2)$ . The difference between the actual numbers found in two extreme types of flowers and the above two series, lies in an interchange of the three middle classes. The actual series are as follows:

1) 3.5, 3.3, 3.0, 2.8, 2.6, 2.5, 2.3 for self-purple flowers

2) 3.4, 3.2, 3.1, 2.9, 2.7, 2.4, 2.2 for small mosaic flowers.

Having set in pairs the chromosomes exclusively according to their length, the results obtained would differ from those presented in Tables VIII and IX. The modal value for chromosome length will undergo some alteration and in some cases two modes will appear: it is shown in Tables X and XI. For instance in column III of the Table X (for self-purple flowers) besides 3.0 appears 3.1 and in column II of the Table XI for mosaic flowers, besides 3.2 appears 3.0. In spite of these facts the lowest and the highest modal values remain unaltered for both flower types.

The figures obtained may be tabulated still in other way. We may take into consideration only the frequency of occurrence of a given figure and bring no attention to the chromosome pair which it represents. In such a case we shall get the results (the last row of the Tables X and XI).

In the Table X are given all figures found in 140 chromosomes of the self-purple flowers and in the Table XI those for 140 chromosomes of the mosaic flowers. The figures 3.5, 3.3, 3.1, 3.0, 2.8, 2.6, 2.3 are characteristic of the self-purple flower type and the figures 3.4, 3.2, 2.9, 2.7, 2.5, 2.4, 2.2 for the mosaic one. There is not a very large difference between the first tabulation and the third one; only the figures 3.1 and 2.5 have been exchanged. But the scale of variability remains unaltered in all three cases.

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TABLE X.

### Studies on a mosaic strain of Petunia violacea 209

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In addition to the above measurements I have made some new measurements of other 5 complements, these last complements being obtained from material fixed in Benda's fluid without acetic acid<sup>1</sup>). The results then obtained have been tabulated together with the preceeding ones (Tab. XII). In comparing the Tables IX and XII we see that there are only slight differences in chromosome pairs III and IV. In the last case namely the variability of chromosome length exhibits two modal values 3.1 and 3.0 for the 3-d and 2.9 and 2.7 for the 4-th chromosome pair.

If we would take into consideration only the frequency of occurrence of a given figure, the chromosome sizes of our 5 chromosome complements would give a frequency distribution shown in Table XIII. In this frequency table the chromosome size 3.4occurs nearly as frequently as the chromosome size 3.5, but the chromosome size 2.2 appears much more frequently than 2.3. It is self-evident that the results obtained on the measuring of 5 complements cannot be separately taken into consideration but it is worth mentioning that these results are the nearest to those arrived at for the chromosomes in diakinesis.

#### 3) The chromosomes in meiosis

In order to verify the results obtained for the somatic chromosomes it was necessary to measure the chromosomes in meiosis. The most suitable stage proved to be that of a not very late diakinesis (Plates 16, 17, 18). At this stage, in *Petunia*, the chromosomes still remain elongated and are more convenient for measuring than at a late diakinesis at which they are becoming ovated and mostly superposed. It was howevor impossible to find out even a very limited number of complements in which all chromosomes could be measured with the Kagawa's method. They are lying obliquely or vertically, they overlap each other or are superposed and in such cases it is impossible to determine exactly the limits of particular chromosomes. It has been decided therefore to reproduce the chromosome complements from relatively rare pairs lying entirely in the plane of the microscope and which

<sup>1</sup>) The material treated with Benda's fluid shows the slightest deformations, so one can assume that the measurements concerning this material are more exact.

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ends have not been superposed. It is self-evident that in order to meet all pairs making up the set of chromosomes in question, it was necessary to examine very many pairs placed by mere chance in the plane of the microscope. Another difficulty met with, was that diakinesis proceeds irregularly so that in the upper part of the anther we can have an early stage and in the lower part a late one. It was necessary therefore to limit as far as possible the space in which the cells had to be examined. To be sure that the proper stage had been found out I have only examined cells taken from the part where many cells with identical smallest chromosomes had occurred. Such chromosomes have been relatively easily recognisable.

For self-purple flowers I have picked out a hundred of such pairs which have been drawn with the help of a camera lucida. All of them have been chosen from the same microsporagium. For the small mosaic flower type, 46 pairs only have been found in one microsporangium. The said pairs have been drawn and subsequently the drawings have been enlarged 2.5 fold with the help of a photographic apparatus. Thereafter the magnified drawings have been measured with compasses, the distance between their branches being 3.7 mm. The figures obtained from the measurements of 100 chromosome pairs of the self-purple flower type have revealed a variation ranging from 5.20 to 3.25. The relation between those figures is corresponding approximately to the relation 3.5:2.2 found in the somatic complements. The numbers have not been however precise enough to allow an identification of the chromosomes at diakinesis with those in somatic mitoses. This may be possibly attributed to the difficulty of delineating exactly the sizes of chromosomes with the help of a camera lucida. Our eye wavers slightly over the eyepiece when the pencil is following the outlines of the chromosome and often as far as our case is concerned the same end of a given chromosome could be traced at different points more or less distant from one another. Such distance however never exceeds 1 mm. Such fluctuations are rather slight but when one is dealing with so small sizes as those of the chromosomes of Petunia they suffice to bring about a considerable error particularly after the enlarging of the drawings.

After many trials concerning the various ways the method which I adopted consisted in projecting the image of the chromosomes on an opaque screen of a large Zeiss microphotographic apparatus with a strong lamp and a 130.5 cm. long camera. The magnification attained in this way corresponds exactly to the photographs shown in Plates 16, 17 and 18. The chromosome length has been measured in the following way. After inverting the opaque screen of the apparatus its rough surface outside the outlines of the chromosomes have been drawn on it with a hard and very sharp pencil. On the drawing thus obtained a line through the middle of the chromosome has been traced from one end to the other and this line has been measured with compasses, the distance between the points of its branches being one millimeter. The opening of the compasses has been often verified on the same, 20 mm. long scale. One chromosome has been thus measured many times and the only figure chosen has been the one repeating itself at least in 50% of cases. For instance, for the chromosome pair represented in Plate 16, Fig. 5 the following dimensions have been obtained: for the left chromosome 12.0, 12.0, 12.0, 12.0, 12.0, 12.0, 12.0, 12.4, 12.0, 12.4, 12.0, 12.6 and for the right one 8.4, 8.8, 8.0, 9.0, 8.4, 8.2, 8.8, 9.0, 8.4, 9.4, the number 12.0 occurred in 75% of cases and for the second one the number 8.8 has been repeated in 52% of cases. In this way for the chromosome pair in question the sizes 12.0 and 8.8 have been kept. For the pair represented in Plate 16, Fig. 10 the following numbers have been obtained: for the left chromosome 10.8, 10.8, 10.4, 10.8, 10.1, 10.2, 10.8, 10.8, 10.8, 9.9, 10.4, 10.5, 10.4, 10.8, 10.6, 10.8, 10.8, or 10.8 in 52% of cases, for the right one 11.6, 10.8, 11.2, 11.2, 11.4, 10.8, 11.2, 11.8, 11.2, 11.6, 11.2, 11.2, 11.2, 11.7, 11.2, 11.8, 11.2 or 11.2 in 52% of cases. Thus the length of the chromosomes of this pair may be estimated for 10.8 and 11.2 respectively. With such a method 60 pairs of chromosomes for the self-purple flower type have been measured and 45 pairs for the small mosaic type.

All pairs subjected to measurements have been subsequently photographed and all those photographs are shown in fig. 1— 105 (Plates 16, 17 and 18). Each photograph represents correctly the relation between the length of chromosomes in one pair but

we cannot always compare the pairs between them because the reprints may be stronger in one case than in the other. On the photographic reprints therefore the measurements of the chromosomes cannot be made. If in some of the figures of the Plates 16, 17 and 18 the ends of the chromosomes are not very distinct this is also due to the fault of the photograph. For instance, the figures 13 and 130 (Pl. 20) represent the same chromosome pair but in the latter case, the photograph has been made particularly carefully and this may account for a better distinctness of chromosome outlines.

As a rule, the chromosomes composing one pair are differing more or less in their length. The pairs exhibiting striking diffe rences (Fig. 5, 6, 7, 12 etc.) have been less numerous than the ones showing smaller differences (Fig. 9, 11, 18, 24 etc.). The most numerous pairs exhibit a slight difference in chromosome length (Fig. 4, 10, 15, 16, 25, 33 etc.) but this difference is however such that it may be perceived at the first sight, what has been always confirmed by the measurements. The pairs with equal chromosomes occasionally occur and they concern only the largest and the smallest chromosomes. The phenomenon of unequal chromosome sizes of one pair cannot be looked upon as a result of a separate contraction of the conjugating chromosomes because such unequal pairs occur also in the metaphase and even in the anaphase where the contraction of chromosomes is already completed. Fig. 126, Plate 20 shows two chromosomes at the metaphase, exhibiting marked differences in their length. One cannot explain the differences in chromosomes of one pair in assuming an unequal division of chromatic substance belonging to two previously joint chromosomes, what has been proposed by Skalińska (1927). The joining together of the chromosomes do not occur. The chromosomes emerge in the form of very long and slender threads of granular structure (Fig. 127, Plate 20) and from these first stages they remain mostly separated (Fig. 1-105), their ends only being sometimes connected. Often they do not touch each other and only seldom they cross in one point. We have to deal here with a conjugation of chromosomes being unequal from their very beginning.

The numbers obtained with the above method and concerning

the length of particular pairs of chromosomes at diakinesis are shown in Tables XIV and XV.

#### TABLE XIV.

Sizes of 60 chromosome pairs in diakinesis of self-purple flowers. The successive slides in one row are indicated by capital letters and the successive cells in those slides — by small letters.

$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	Figures in Plates I and II	Chromosome length in mm	Position of a given pair	Figures in Plates I and II	Chromosome lenght in mm	Position of a given pair
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{c} 1\\ 2\\ 3\\ 4\\ 5\\ 6\\ 7\\ 8\\ 9\\ 10\\ 11\\ 12\\ 13\\ 14\\ 15\\ 16\\ 17\\ 18\\ 19\\ 20\\ 21\\ 22\\ 23\\ 24\\ 25\\ 26\\ 27\\ 28\\ 29\\ 30\\ \end{array}$	$\begin{array}{c} 100-88\\ 92-88\\ 92-88\\ 120-132\\ 100-104\\ 120-88\\ 108-88\\ 108-88\\ 108-88\\ 108-88\\ 108-88\\ 108-88\\ 108-88\\ 108-112\\ 140-120\\ 100-88\\ 108-112\\ 140-120\\ 100-92\\ 108-98\\ 116-100\\ 108-88\\ 128-124\\ 108-88\\ 128-124\\ 108-88\\ 128-124\\ 108-88\\ 140-152\\ 132-128\\ 108-96\\ 116-104\\ 96-88\\ 116-100\\ 140-128\\ 96-104\\ 140-128\\ 96-104\\ 140-128\\ 140-140\\ \end{array}$	Ba Bb Bc Cb Cc Cg Db Ea Fa Fb Fc Fd Fc Ff Fh Gd Ha Hb He Hf Ia Ic If Ig Ih Ja Jc Ka Lb	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c} 12\cdot 4 - 12\cdot 8\\ 8\cdot 4 - 9\cdot 2\\ 10\cdot 0 - 10\cdot 4\\ 10\cdot 8 - 11\cdot 6\\ 14\cdot 0 - 12\cdot 8\\ 12\cdot 8 - 12\cdot 4\\ 8\cdot 8 - 10\cdot 4\\ 8\cdot 8 - 9\cdot 6\\ 12\cdot 0 - 9\cdot 2\\ 10\cdot 0 - 10\cdot 4\\ 10\cdot 8 - 11\cdot 2\\ 10\cdot 0 - 10\cdot 4\\ 10\cdot 8 - 11\cdot 2\\ 10\cdot 0 - 9\cdot 2\\ 10\cdot 0 - 10\cdot 4\\ 10\cdot 8 - 11\cdot 2\\ 10\cdot 0 - 9\cdot 2\\ 10\cdot 0 - 10\cdot 4\\ 10\cdot 8 - 12\cdot 0\\ 9\cdot 6 - 8\cdot 8\\ 9\cdot 2 - 12\cdot 0\\ 8\cdot 8 - 9\cdot 6\\ 14\cdot 0 - 11\cdot 6\\ 13\cdot 2 - 12\cdot 0\\ 9\cdot 6 - 8\cdot 8\\ 9\cdot 2 - 12\cdot 0\\ 9\cdot 6 - 10\cdot 4\\ 14\cdot 0 - 15\cdot 2\\ 9\cdot 2 - 9\cdot 6\\ 14\cdot 0 - 12\cdot 8\\ 9\cdot 6 - 8\cdot 8\\ 9\cdot 6 - 10\cdot 8\\ 12\cdot 0 - 11\cdot 6\\ 10\cdot 8 - 11\cdot 2\\ 8\cdot 8 - 9\cdot 6\end{array}$	Lf Na Nb Nc Oa Oc Pa Pb Pd Pe Pf Pg Qd Qf Ra Rb Sa Sb Sc Sd Sf Ta Tb Va Vb Vc Vd Wa Xa

The numbers which come into play in these Tables are tabulated in Tables XVI and XVII.

The chromosomes 14.0 and 8.8 only have been found doubled in some pairs. Namely the former one (14.0) has been doubled in the self-purple flower type (in the chromosome pair Fig. 30)

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TA	B	LE	X	V

Sizes of 45 chromosome pairs in diakinesis of small mosaic flowers. The successive slides in one row are indicated by capital letters (except the slides 29<sup>th</sup> and 30<sup>th</sup>) and the successive cells in those slides — by small letters.

Figures in Plates II and III	Chromosome length in mm	Position of a given pair	Figures in Plates II and III	Chromosome length in mm	Position of a given pair
	$ \begin{array}{c} 15.0 - 11.6 \\ 14.0 - 13.2 \\ 8.8 - 9.6 \\ 8.8 - 8.8 \\ 13.6 - 12.8 \\ 9.6 - 10.4 \end{array} $	Pa Pb Ra Sa Ua	84 85 86 87 88	$ \begin{array}{r} 12.0 - 14.0 \\ 12.4 - 14.0 \\ 12.0 - 9.6 \\ 13.6 - 12.4 \\ 8.8 - 8.8 \\ \end{array} $	Kb Kd Ma Mb
67 68 69 70	$\begin{array}{r} 3.6 - 10.4 \\ 8.4 - 7.2 \\ 12.0 - 11.6 \\ 10.0 - 10.4 \\ 8.8 - 10.0 \end{array}$	29 <sup>th</sup> a 30 <sup>th</sup> a Ba	89 90 91 92	$ \begin{array}{c} 12.0 - 12.8 \\ 8.8 - 9.6 \\ 8.8 - 8.8 \\ 8.8 - 9.6 \\ 12.0 - 11.6 \\ \end{array} $	Mc Na Nb Nc
$71 \\ 72 \\ 73 \\ 74$	$\begin{array}{c} 8.8 - 9.6 \\ 9.6 - 8.8 \\ 9.6 - 8.8 \\ 10.4 - 14.0 \end{array}$	Bo Da Ea Fa	93 94 95 96 97	$ \begin{array}{c} 12.0 - 11.6 \\ 8.8 - 10.4 \\ 8.8 - 9.6 \\ 13.6 - 12.8 \\ 9.6 \\ 10.8 \end{array} $	Ne Nf Oa Ob
75 76 77 78	$ \begin{array}{c} 10.0 - 8.8 \\ 8.8 - 8.8 \\ 12.0 - 8.8 \\ 8.8 - 9.6 \end{array} $	Ga Gb Ha Hb	$     \begin{array}{r}       98 \\       99 \\       100 \\       101     \end{array} $	$ \begin{array}{r} 56-108\\ 88-100\\ 88-88\\$	Pa Qa Qb Bh
79 80 81 82 83	$ \begin{array}{r} 8.8 - 8.8 \\ 8.8 - 8.8 \\ 10.8 - 9.6 \\ 10.4 - 13.2 \\ 8.8 - 8.8 \end{array} $	Hc Hd He Hf Ka	$     \begin{array}{r}       102 \\       103 \\       104 \\       105     \end{array} $	$\begin{array}{c} 10.0-10.4\\ 10.8-11.2\\ 8.8-9.6\\ 10.8-11.6\end{array}$	Ta Va Wa Xa
at an atternet	A topstrate	1 1 80	all	1 1-51-611	19 9/20-1

#### TABLE XVI

The figures characterizing chromosomes in meiosis of the self-purple flowers. Chromosome sizes in mm.  $(15\cdot2) - 14\cdot0 - 14\cdot0 - 13\cdot2 - 12\cdot8 - 12\cdot4 - 12\cdot0 - 11\cdot6 - 11\cdot2 - 10\cdot8 - 10\cdot4 - 10\cdot0 - 9\cdot6 - 9\cdot2 - 8\cdot8 - (8\cdot4)$ Corresponding figures in  $\mu$   $(3\cdot8) - 3\cdot5 - 3\cdot5 - 3\cdot3 - 3\cdot2 - 3\cdot1 - 3\cdot0 - 2\cdot9 - 2\cdot8 - 2\cdot7 - 2\cdot6 - 2\cdot5 - 2\cdot4 - 2\cdot3 - 2\cdot2 - (2\cdot1)$ 

#### TABLE XVII

The figures characterizing c	hromosomes in meiosis of the small mosaic flowers.
Chromosome sizes in mm.	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$
Corresponding figures in $\mu$	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$
#### Studies on a mosaic strain of Petunia violacea

and the latter (8.8) in the small mosaic type (in the chromosome pairs Fig. 64, 76 etc.). In comparing the successive numbers in each of the above two series, one is struck by the fact that the differences between them are equal to 0.4 mm with the exception of numbers 15.2, 16.0 and 7.2. In addition, those two series have 12 numbers in common and they differ only in the extreme figures.

The question arises whether the numbers in Tables XVI and XVII correspond to the sizes of somatic chromosomes. We cannot compare the figures directly and the only method which may be applied is to find out the relations corresponding to the ratios 3.5:2.3, 3.4:2.2 and so on. It has been found that the ratio 14.0:9.2 corresponds to that of 3.5:2.3 an the ratio 13.6:8.8 to that of 3.4:2.2. In this way all figures have been compared with the sizes of the somatic chromosomes and the relations established are shown in Tables XVI and XVII.

The differences between the successive figures are equal to 0.4 mm, what corresponds to the difference of 0.1  $\mu$  in somatic chromosomes. In brackets are comprised such figures for which there are no corresponding modal values in the somatic complements. Setting apart the figures in brackets and taking into consideration only the remaining ones we shall find an important difference between the two extreme types of flowers. In the large self-purple flowers namely the chromosome 3.4 is lacking and in the small mosaic flowers the chromosome 2.3 is absent. The figure 15.2 has been met with twice only and the figure 8.4 only once in 60 chromosome pairs examined in self-purple flower type. Each of the figures 16.0, 8.4 and 7.2 has been found once in 44 pairs of the small mosaic flowers. These aberrant figures may be accounted for an error which, of course, is always possible but they may also be real ones (corresponding sizes have been met with in somatic chromosomes too) particularly when we take into consideration the presence of satellites which will be referred to, later on.

In comparing the above figures with those obtained for the somatic complements we find a notable conformity between them especially when we compare the meiotic complements with the figures of the Tables X, XI and XIII. There is however a difference between those two results, namely in the somatic

complements the two extreme chromosome sizes (3.5, 2.3 and 3.4, 2.2) are prevailing and in the meiotic complements only one of them 14.0 (3.5) and 8.8 (2.2). We must however take into consideration that the measurements of meiotic complements 1) have been made on slides got from plants grown one year later and 2) have been obtained from one bud and not from several ones.

Let us try now to draw a parallel between the morphological and the cytological phenomena. In the small mosaic flowers the chromosome 8.8 is doubled and the chromosome 9.2 is absent; this corresponds to the presence of small corolla and to the absence of large corolla. In the large self-purple flowers the chromosome 14.0 (3.5) is doubled and the chromosome 13.6 (3.4) is absent; this corresponds to the presence of purple colour distributed all over the corolla surface and to the absence of mosaicism. We may suppose that owing to the presence of the doubled chromosome 14.0 (3.5) in the complements of the selfpurple flower type this type gives rise to a progeny with a high percent of self-purple flowers and that this percent increases in the subsequent generations. The presence of two different chromosomes 9.2 (2.3) and 8.8 (2.2) characterizing the corolla sizes as one may suppose will lead to a variability in the corolla sizes. In the progeny of small mosaic flowers the percent of plants with small corolla will increase from generation to generation, owing to the presence of doubled chromosome 8.8 (2.2), whilst owing to the presence of different chromosomes: 14.0 (3.5) and 13.6 (3.4) as one may suppose we shall have to deal with a variability in the colouration of the corolla.

In the large self-purple flowers the self-purple colouration (two chromosomes 14.0) is associated to the large corolla sizes (chromosome 9.2) and in the small mosaic flowers the mosaicism (the chromosome 13.6) accompanies the small corolla sizes (two chromosomes 8.8). If, as we have assumed, the gene of selfpurple colour is located in the chromosome 14.0 (3.5) and that of white colour in the chromosome 13.6 (3.4) one may consider those two chromosomes as homologous ones. For the same reason the chromosomes 9.2 (2.3) and 8.8 (2.2) would be homologous.

From the data presented in Tables XIV and XV it is seen that the same chromosome pairs occur several times but in spite of

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this fact in the self-purple flower type 25 combinations of 14 different chromosomes and in the small mosaic flowers 20 of the same combinations have been met with. This is shown in Tables XVIII and XIX. The largest chromosomes combine for the most part with large ones and the smallest ones conjugate with chromosomes which do not differ notably from them. The combinations of the largest chromosomes with the smallest ones do not appear.

If we assume that the chromosomes 14.0 (3.5) and 13.6 (3.4) are homologous ones and that the same holds good for the chromosomes 9.2 (2.3) and 8.8 (2.2) then, in our case, the following pairs of homologous chromosomes would come into play:

14.0		13.6	
13.2	10	12.8	
12.4		12.0	
11.6		11.2	
10.8	TIL	10.4	1 2.1
10.0	1 (1) 	9.6	1.00
9.2	()-7 <u>-</u> () 	8.8	1 8.9
	$ \begin{array}{r} 14.0 \\ 13.2 \\ 12.4 \\ 11.6 \\ 10.8 \\ 10.0 \\ 9.2 \end{array} $	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$

It is surprising that in the Table XVIII the combinations of such kind appear only twice (the pair  $13\cdot2-12\cdot8$  and  $9\cdot2-8\cdot8$ ) and in the Table XIX they do not appear at all. The phenomena of conjugation of unequal chromosomes are produced firstly by the fact that almost all chromosomes of the complements examined (Tables XVI and XVII) are differing from one another as far as their sizes are concerned and, secondly, by the non-conjugation or by the occurence of isolated cases of conjugation of homologous chromosomes. The differences in sizes of conjugating chromosomes are comprised in the limits of  $0\cdot1 \mu - 0\cdot8 \mu$  for the large flower type and in the limits of  $0\cdot1 \mu - 0\cdot9 \mu$  for the small flower type (Table XX). This may be seen from the comparison of the Tables XVIII and XIX with the photographs fig. 1-105 (Plates 16, 17, 18).

The most frequent combinations are those between the chromosomes differing in  $0.1 \mu$ ,  $0.2 \mu$  and  $0.3 \mu$  (Table XX).

The conjugation of chromosomes of equal size in exceptional and the bivalent formed of two chromosomes differing more than in  $0.3 \mu$  are rather rare. This indicates that there must be

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#### TABLE XVIII.

The frequency of occurence of combinations of particular chromosome sizes in self-purple flowers.

「「「「「」」	The combi- ning sizes in mm	The figures in $\mu$	Differences in $\mu$	The pairs shown in Plates I and II
the second se	$\begin{array}{c} 14.0-14.0\\ 14.0-12.8\\ 14.0-12.0\\ 14.0-11.6\end{array}$	$\begin{array}{r} 3.5 - 3.5 \\ 3.5 - 3.2 \\ 3.5 - 3.0 \\ 3.5 - 2.9 \end{array}$	0·0 0·3 0·5 0·6	fig. 30 > 27, 29, 35, 55 > 8, 11, 14, 46 > 50
	$13 \cdot 2 - 12 \cdot 8$ $13 \cdot 2 - 12 \cdot 0$	3·3-3·2 3·3-3·0	0·1 0·3	» 22 » 3, 51
	$12.8 - 14.0 \\ 12.8 - 13.2 \\ 12.8 - 12.4$	3.2-3.1	0.1	» 18, 31, 36
	12.4-12.8	01	1 b	1
	$12 \cdot 0 - 14 \cdot 0$ $12 \cdot 0 - 13 \cdot 2$ $12 \cdot 0 - 11 \cdot 6$ $12 \cdot 0 - 10 \cdot 8$ $12 \cdot 0 - 9 \cdot 2$ $12 \cdot 0 - 8 \cdot 8$	$3 \cdot 0 - 2 \cdot 9$ $3 \cdot 0 - 2 \cdot 7$ $3 \cdot 0 - 2 \cdot 3$ $3 \cdot 0 - 2 \cdot 2$	0·1 0·3 0·7 0·8	<ul> <li>58</li> <li>45</li> <li>7, 39, 48</li> <li>5, 12</li> </ul>
	$\begin{array}{c} 11.6-14.0\\ 11.6-12.8\\ 11.6-10.8\\ 11.6-10.8\\ 11.6-10.4\\ 11.6-10.0\end{array}$	2.9-2.7 2.9-2.6 2.9-2.5	0·2 0·3 0·4	<ul> <li>» 34</li> <li>» 24</li> <li>» 13, 26</li> </ul>
	11.2-10.8	2.8-2.7	0.1	» 10, 42, 59
	$\begin{array}{c} 10.8 - 12.0 \\ 10.8 - 11.6 \\ 10.8 - 11.2 \\ 10.8 - 9.6 \\ 10.8 - 8.8 \end{array}$	2.7-2.4 2.7-2.2	0·3 0·5	<ul> <li>* 16, 23, 57</li> <li>* 6, 17, 20</li> </ul>
	$\begin{array}{c} 10.4 - 10.0 \\ 10.4 - 9.6 \\ 10.4 - 8.8 \end{array}$	2.6-2.5 2.6-2.4 2.6-2.2	0·1 0·2 0·4	<ul> <li>» 4, 19, 33, 40, 41, 44</li> <li>» 28, 52</li> <li>» 37</li> </ul>
	$\begin{array}{c} 10.0 - 11.6 \\ 10.0 - 10.4 \\ 10.0 - 9.2 \\ 10.0 - 8.8 \end{array}$	2.5-2.3 2.5-2.2	0·2 0·3	» 15, 43 » 1, 9
	$\begin{array}{c} 9.6 - 10.8 \\ 9.6 - 10.4 \\ 9.6 - 9.2 \\ 9.6 - 8.8 \end{array}$	$2\cdot 4 - 2\cdot 3$ $2\cdot 4 - 2\cdot 2$	0·1 0·2	<ul> <li>54</li> <li>25, 38, 47, 49, 56, 60</li> </ul>
	9.2- 8.8	2.3-2.2	0.1	» 2

#### TABLE XIX.

The frequency of occurrence of combinations of particular chromosome sizes in small mosaic flowers.

The combin- ing sizes in mm	The figures in $\mu$	Differences in $\mu$	The pairs shown in Plates II and III.
$\begin{array}{c} 14 \cdot 0 - 13 \cdot 2 \\ 14 \cdot 0 - 12 \cdot 4 \\ 14 \cdot 0 - 12 \cdot 0 \\ 14 \cdot 0 - 10 \cdot 4 \end{array}$	$3 \cdot 5 - 3 \cdot 3$ $3 \cdot 5 - 3 \cdot 1$ $3 \cdot 5 - 3 \cdot 0$ $3 \cdot 5 - 2 \cdot 6$	$0.2 \\ 0.4 \\ 0.5 \\ 0.9$	fig. 63 * 85 * 84 * 74
$\begin{array}{r} 13.6 - 12.8 \\ 13.6 - 12.4 \end{array}$	$3\cdot 4 - 3\cdot 2$ $3\cdot 4 - 3\cdot 1$	$\begin{array}{c c} 0.2\\ 0.3 \end{array}$	» 65, 96 » 87
$   \begin{array}{r} 13 \cdot 2 - 14 \cdot 0 \\     13 \cdot 2 - 10 \cdot 4 \\   \end{array} $	3.3-2.6	0.7	» 82
$   \begin{array}{r}     12.8 - 13.6 \\     12.8 - 12.0 \\     \hline   \end{array} $	3.2-3.0	0.5	» 89
12.4 - 14.0 12.4 - 13.6	Line 100 (re)	AG 404	o 1996 of the section
$\begin{array}{c} 12 \cdot 0 - 14 \cdot 0 \\ 12 \cdot 0 - 12 \cdot 8 \\ 12 \cdot 0 - 11 \cdot 6 \\ 12 \cdot 0 - 9 \cdot 6 \\ 12 \cdot 0 - 8 \cdot 8 \end{array}$	3.0-2.9 3.0-2.4 3.0-2.2	0·1 0·6 0·8	<ul> <li>68, 93</li> <li>86</li> <li>77</li> </ul>
$\frac{11.6-12.0}{11.6-10.8}$	2.9-2.7	0.2	<ul> <li>105</li> </ul>
11.2-10.8	2.8-2.7	0.1	» 103
$\begin{array}{c} 10.8 - 11.6 \\ 10.8 - 11.2 \\ 10.8 - 9.6 \end{array}$	2.7-2.4	0.3	81, 97
$\begin{array}{c} 10.4 - 14.0 \\ 10.4 - 13.2 \\ 10.4 - 10.0 \\ 10.4 - 9.6 \\ 10.4 - 8.8 \end{array}$	2.6 - 2.5 2.6 - 2.4 2.6 - 2.2	0·1 0·2 0·4	<ul> <li>69, 102</li> <li>66</li> <li>94</li> </ul>
$\begin{array}{c} 10 \cdot 0 - 10 \cdot 4 \\ 10 \cdot 0 - 8 \cdot 8 \end{array}$	2.5-2.2	0.3	» 70, 75, 98
$\begin{array}{r} 9.6-10.8\\ 9.6-10.4\\ 9.6-8.8\end{array}$	2.4-2.2	0.2	» 63, 71, 72, 73, 78, 90, 92, 95, 104
$\begin{array}{r} 8.8 - 12.0 \\ 8.8 - 10.4 \\ 8.8 - 10.0 \\ 8.8 - 9.6 \\ 8.8 - 8.8 \end{array}$	2.2-2.2	00	<ul> <li>64, 76, 79, 80, 83, 88, 91, 99, 100, 101</li> </ul>

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#### TABLE XX.

The frequency of occurrence of particular differences between the chromosomes of one pair.

Flower type	The differences in $\mu$ between the conjugating chromosomes													
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9				
large self-purple	1	7	4	6	2	2	.1 .	1	1					
small mosaic	1	3	6	3	2		1	• 1	1	1				

difficulties in the conjugation of chromosomes of such sizes. This conclusion is confirmed by the behaviour of chromosomes in anaphase.

Some abnormal processes occur namely in a certain percent of cases in the anaphase (Plates 19, 20) and they concern the following phenomena: 1) a precoce disjunction of the chromosomes of one pair (fig. 111, 112) and 2) a non-disjunction of chromosomes and their passing as bivalents to one pole (fig. 113, 114, 115, 116). Both phenomena may occur simultaneously in one cell (fig. 117). The most frequent are, besides normal cases (fig. 106, 107, 108, 109, 110), such images in which slight abnormalities occur (fig. 118, 119, 120). In fig. 121, 122, 123, 124 we see notable abnormalities so that the chromosomes are becoming scattered along the spindle. The figures with solitary chromosomes at the pole in about  $5^{\circ}/_{\circ}$  and finally the figures with the chromosomes scattered along the spindle appear in about  $30^{\circ}/_{\circ}$  of cases.

The important point is that all non-disjoint pairs have been composed (as one can judge from observations only because the measurements have not been made) of equal or nearly equal chromosomes (fig. 113, 114, 115, 116, 117). The non-disjoint pairs are corresponding probably to the pairs of equal or nearly equal chromosomes in diakinesis, because the frequency of their occurence in diakinesis and in anaphase is nearly the same. All solitary chromosomes found at the poles in the anaphase are either very large (fig. 111) or very small (fig. 112), what indicates that the precoce disjunction occurs in pairs composed of chromosomes

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exhibiting notable differences (there are however exceptions in which the chromosomes showing notable differences do not disjoin, what may be seen in fig. 126). The frequency of occurence of this phenomena corresponds more or less to the frequency of occurence of pairs with notable differences in diakinesis. The dispersion of chromosomes along the spindle is probably due to the simultaneous presence of pairs showing small differences in chromosome length and also those showing large differences. Thus the anaphase shows that the conjugation of identical chromosomes as well as those exhibiting notable differences are abnormal processes leading to disturbances in meiosis.

A very characteristic trait of the chromosomes in diakinesis is the occurrence at this stage of peculiar satellites. The satellites are smaller or larger portions of chromatic substance linked with chromosomes at various points (Plates 16—18, fig. 3, 4, 16, 26, 30, 39, 65, 68, 74, 80, 81, 87, 91, 92, 94, 102, 104). They are very common in diakinesis in both large self-purple and small mosaic flower types. At the early stages of diakinesis they have not been observed, whilst in the middle stages (see Plates 16, 17 and 18) they are very common. In the late diakinesis they are already separated from the chromosomes.

The satellites are composed of one or more granules of chromatin, the dimensions of which seem to be equal or nearly so. Small satellites composed of one granule are seen in fig. 129 (between the ends of a chromosome), fig. 128 (two satellites side by side); fig. 9, 23, 63, 65 (simple satellite on a complex one); fig. 76.

The chromosomes themselves as one can judge from the photographs, Plates 16, 17, 18, 20, seem also to be composed of granules. This granular structure may be seen in fig. 130. In the lower end of the left chromosome shown in this figure we see 2 granules and, immediately above, two other ones under which as the preparation shows, the next pair of granules is lying. The granular structure is seen also in fig. 127 (chromosomes at an early diakinesis) and in fig. 125 (three granules in the bifurcated upper end of a somatic chromosome). The granular structure makes the outlines of the chromosomes irregular in many cases. The sizes of simple satellites correspond to the sizes of granules of chromosomes.

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The presence of satellites is not bound up with definite chromosome sizes, and their position and structure seem to show that we have to deal with a phenomenen of expulsion of chromatic substance which is superfluous or not harmonizing with the remainder of the chromosome.

All phenomena described above like: unequal chromosomes in diakinesis, dispersion of chromosomes along the spindle in the anaphase, non-disjunction of chromosomes and their passing as bivalents to one pole of the dividing cell, occurrence of satellites and so on may also be seen in *Pet. nyctaginiflora*, which do not show any traces of mosaic autocyanin-distribution in its flowers.

The above described cytological investigations may be summarized as follows:

1) The chromosome sizes for two extreme flower types of the mosaic strain of *Petunia violacea* are as follows:  $3\cdot 5\mu$ ,  $3\cdot 5\mu$ ,  $3\cdot 3\mu$ ,  $3\cdot 2\mu$ ,  $3\cdot 1\mu$ ,  $3\cdot 0\mu$ ,  $2\cdot 9\mu$ ,  $2\cdot 8\mu$ ,  $2\cdot 7\mu$ ,  $2\cdot 6\mu$ ,  $2\cdot 5\mu$ ,  $2\cdot 4\mu$ ,  $2\cdot 3\mu$ ,  $2\cdot 2\mu$  for the self-purple flower type and  $3\cdot 5\mu$ ,  $3\cdot 4\mu$ ,  $3\cdot 3\mu$ ,  $3\cdot 2\mu$ ,  $3\cdot 1\mu$ ,  $3\cdot 0\mu$ ,  $2\cdot 9\mu$ ,  $2\cdot 8\mu$ ,  $2\cdot 7\mu$ ,  $2\cdot 6\mu$ ,  $2\cdot 5\mu$ ,  $2\cdot 4\mu$ ,  $2\cdot 2\mu$ ,  $2\cdot 2\mu$  for the mosaic flower type. In the former one the chromosome  $3\cdot 5$  is doubled and this condition might be considered as being responsible for the self-purple colour (the chromosome  $3\cdot 4$  determining the white colour is lacking). In the latter type the chromosome  $2\cdot 2$  is doubled and this may be accounted for the presence of small corolla (the chromosome  $2\cdot 3$  responsible for large corolla is absent).

2) The conjugating chromosomes in diakinesis are, as a rule, unequal. As one can judge from the annexed photographs the chromosomes in diakinesis do not touch each other in the great majority of cases.

3) The most frequent chromosome combinations in diakinesis are such that the differences between chromosome sizes of particular bivalents are equal to  $0.1 \,\mu$ ,  $0.2 \,\mu$  and  $0.3 \,\mu$ . The conjugation of chromosomes of equal size is exceptional and the bivalents formed of two chromosomes differing more than in  $0.3 \,\mu$  are less common. This indicates that there must be difficulties in the conjugation of chromosomes of such sizes.

4) The images observed in anaphase are corresponding to those in diakinesis. Some abnormal processes occur in the ana-

#### Studies on a mosaic strain of Petunia violacea

phase in certain percent of cases and they concern the following phenomena: 1) a precoce disjunction of chromosomes of one pair and 2) a non-disjunction of chromosomes and their passing as bivalents to one pole.

5) The conjugation of unequal chromosomes in diakinesis as well as the sizes of chromosomes of two extreme flower types seem to indicate that the mosaic strain of *Petunia* is of a hybrid nature.

6) A very characteristic trait of chromosomes in diakinesis is the occurrence at this stage of peculiar satellites.

The satellites are smaller or larger portions of chromatic substance linked with chromosomes at various points. The position and the structure of satellites seem to show that we have to deal here with an expulsion of chromatic substance.

### III. Discussion (by E. Malinowski)

The results of cytological investigations as well as the selection experiments concerning the extreme flower types of the mosaic strain of *Petunia violacea* seem to show that the strain in question is a heterozygous one and that we have to deal here with a kind of segregation which may be called "mosaic segregation".

Had we disregarded the correlation between the corolla sizes and the amount of pigment we could assume, as it has been made previously, that:

the chromosome  $3.5 \mu$  is responsible for large flowers

\* \*

«	$2\cdot 3 \mu$	«	«	«	self-purple colour
«	3·4 µ	«	«	«	small flowers
«	$2\cdot 2 \mu$	«	«	«	mosaicism.

But if we take into consideration the fact of an association existing between small corollas and mosaic distribution of pigment we shall be compelled to alter more or less the above hypothesis.

The case seems to be a complex one and a simple scheme would hardly correspond to all the facts observed in our experiments, but the following interpretation appears to be conform to the essential phenomena.

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The following characters are located in the chromosome 2.3: uniform distribution of pigment, corolla sizes of about 30 mm. in diameter and corolla shapes characteristic of large self-purple flowers. In the chromosome 3.5 is located the gene increasing the corolla diameter of about 20 mm. (viz. in such case the flowers would have about 50 mm. in diameter). As concerns the purple pigment it is located in some other chromosome (out of 3.5 and 2.3).

In the chromosome  $2\cdot 2$  the following characters are located: mosaic distribution of pigment characteristic of the class 1 (fig. 1) of our classification, flowers of about 10 mm. in diameter with corolla shapes characteristic of small mosaic flowers. In the chromosome  $3\cdot 4$  the gene increasing the corolla sizes is absent. The purple pigment (as well as in the large self-purple flowers) is located in a chromosome not being  $3\cdot 4$  or  $2\cdot 2$ . This character is common to both extreme flower types and it is independent of any of the four chromosomes which, according to our supposition, characterize these extreme types of flowers.

As concerns the intermediate types of flowers they may be caused by recombinations of the chromosomes in question. So, for instance, the self-purple flowers of 30 mm. in diameter may be due to the simultaneous presence in a homozygous condition of the chromosomes 2.3 and 3.4. On the other hand the mosaic flowers of 30 mm. in diameter may be caused by the presence of chromosomes 2.2 and 3.5.

Thus according to the scheme adopted the range of variation of self-purple flowers would extend from 30 mm, to 50 mm. and that of mosaic ones from 10 mm. to 30 mm, what would approximately correspond to the actual sizes found in our experiments.

The above outlined hypothesis implies that the factor for purple colouration is independent of both chromosome pairs  $2\cdot 2 - 2\cdot 3$  and  $3\cdot 4 - 3\cdot 5$ . This is confirmed by our crossing experiments between the mosaic strain in question and *Petunia* grandiflora. We did isolate in subsequent generations of this cross a mosaic strain showing dark violet pigment instead of a purple one. This new mosaic strain presents a combination of mosaicism, of dark violet colouration and of giant corolla sizes. The first feature comes from the mosaic strain of *Petunia violacea* and the others from the variety Admiration of *Petunia grandiflora*.

Pl. 16.



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Pl. 17.



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71	72	<b>10</b> 73	<b>12</b> 74	75
0	0	X	4	SAL .
76	77	78	79	80
0.	1	SV.	0	*
81	82	83	84	85
A	-	5	X.	íu.
86	87	88	89	90
0.	5	0	5	Q
91	92	93	94	95
6	97	8	0	6
20	51	98	99	100
42	~	-0	62	15
101	102	103	104	105

E. Malinowski and A. Smólska.

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Pl. 18.



Pl. 19.







Pl. 20.



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27. 20.

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### Appendix

The length of the somatic chromosomes was measured with a unit corresponding to  $0.25 \,\mu$ . According to the theory of Abbé the resolving power of the microscope in our case would be  $\delta = \frac{0.55}{2(1\cdot3)} = 0.2 \,\mu$ . Then two points showing between themselves a distance of  $0.20 \,\mu$  are distinguishable according to Abbé. But in our work the distance being 1/2 smaller than  $0.25 \,\mu$  has also been taken into consideration. We must quote however the recent researches of H. Siedentopf (6) who considers that the resolving power of the microscope is much greater than the one resulting when the theory of Abbé is applied.

From the Institute of Genetics, Skierniewice, Poland.

#### Literature.

Bigs 28. -- William Million William Digital Million (1990) -- William William William William

1. R. J. Chittenden. Vegetative segregation. Bibliographia Genetica. III. -2. R. A. Emerson. Genetic evidence of aberrant chromosome behaviour in Maize endosperm. Amer. Journal of Botany. 8. 1921. -3. F. Kagawa. Cytological studies on Triticum and Aegilops I. Size and shape of somatic chromosomes. La Cellule. 37. 1927. -4. E. Malinowski. Variegation and chromosomes in *Petunia*. Journal of Heredity. 1928. -5. R. C. Punnett. On a case of patching in the flower colour of the sweet pea. Journal of Genetics. 1922. -6. H. Siedentopf. On the quality of the image and resolving power in the microscope. Journal R. micr. Soc. 49. 1929. -7. M. Skalińska und A. Cuchtman. Karyologische Analyse einer polymorphen Rasse von *Petunia violacea*. Bibliotheca Univ. Liberae Poloniae. 19. 1927.

# Explanation of Plates 16-20.

Fig. 61. - - 15-0 (16-0) - 11-6

Plates 16-18. Bivalents at the middle diakinesis of the mosaic strain of *Petunia violacea*, photographed with the help of a large Zeiss microphotographic apparatus. Distention of the camera 130.5 cm. Obj. Zeiss Ap. 120, ap. 13. Eypiece Zeiss proj. 4. Material fixed in Flemming's strong solution with very small quantity of acetic acid and stained with Iron Haemat Figures 1-60 from self-purple flowers, figures 61-105 from small mosaic flowers. The bivalents of small mosaic flowers obtained from one microsporangium and the same is true for those of the self-purple flowers. In the

following lines the dimensions of particular chromosomes are given. For each figure in the above plates the sizes of chromosomes are given in the following order: 1) the difference between the chromosomes of one pair expressed in microns, 2) the length of each of two chromosomes expressed in mm.

Fig.	1	0.3 -	10.0 -	8.8.	e microse	Fig.	2	0.1 -	9.2 -	- 8.8.
Fig.	3	0.3 -	13.2 -	12.0.		Fig.	4	0.1 -	10.4 -	- 10.0.
Fig.	5. —	0.8 -	12.0 -	8.8.		Fig.	6. —	0.5 —	10.8 -	- 8.8.
Fig.	7. +	0.7 -	12.0 -	9.2.	ladamonid	Fig.	8. —	0.5 -	14.0 .	- 12.0.
Fig.	9. —	0.3 -	10.0 -	8.8.	Olt mi	Fig.	10	0.1 -	11.2 .	- 10.8.
Fig.	11. —	0.5 -	14.0 -	12.0.		Fig.	12. —	0.8 -	12.0 .	- 8.8.
Fig.	13. —	0.4 -	11.6 -	10.0.	m ow .m	Fig.	14	0.5 -	14.0 -	-12.0.
Fig.	15. —	0.2 -	10.0 -	9.2.		Fig.	16. —	0.3 -	10.8 -	- 9.6.
Fig.	17. —	0.5 -	10.8 -	8.8.		Fig.	18	0.1 -	12.8 .	- 12.4.
Fig.	19. —	0.1 -	10.4 -	10.0.	i AddA to	Fig.	20. —	0.5 -	10.8	- 8.8.
Fig.	21	0.3 -	14.0 -	15.2.		Fig.	22. —	0.1 -	13.2 -	- 12·8.
Fig.	23. —	0.3 -	10.8 -	9.6.		Fig.	24. —	0.3 -	11.6 -	- 10.4.
Fig.	25. —	0.2 -	9.6 -	8.8.		Fig.	26. —	0.4 -	11.6 .	<u> </u>
Fig.	27. —	0.3 -	14.0 -	12.8.		Fig.	28. —	0.2 -	10.4	- 9.6.
Fig.	29. —	0.3 -	14.0 -	12.8.		Fig.	30. —	0.0	14.0	- 14.0.
Fig.	31. —	0.1 -	12.8 -	12.4.		Fig.	32. —	0.2 -	9.2 .	- 8.4.
Fig.	33. —	0.1 -	10.4 -	10.0.		Fig.	34. —	0.2 -	11.6 .	- 10.8.
Fig.	35. —	0.3 -	14.0 -	12.8.		Fig.	36. —	0.1 -	12.8 .	- 12.4.
Fig.	37. —	0.4 -	10.4 -	8.8.		Fig.	38. —	0.2 -	9.6	- 8.8.
Fig.	39. —	0.7 -	12.0 -	9.2.		Fig.	40. —	0.1 -	10.4	<u> </u>
Fig.	41	0.1 -	10.4 -	10.0.		Fig.	42. —	0.1 -	11.2	<u> </u>
Fig.	43. —	0.2 -	10.0 -	9.2.		Fig.	44	0.1 -	10.4	- 10.0.
Fig.	45	0.3 -	12.0 -	10.8.		Fig.	46. —	0.5 —	14.0 .	-12.0.
Fig.	47. —	0.2 -	9.6 -	8.8.		Fig.	48. —	0.7 —	12.0	- 9.2.
Fig.	49. —	0.2 -	9.6 -	8.8.		Fig.	50. —	0.6 -	14.0	— 11·6.
Fig.	51	0.3 -	13.2 -	12.0		Fig.	52. —	0.2 -	10.4	— 9·6.
Fig.	53. —	0.3 -	14.0 -	15.2.		Fig.	54. —	0.1 -	9.6	- 9.2.
Fig.	55. —	0.3 -	14.0 -	12.0.		Fig.	56. —	0.2 -	9.6	- 8.8.
Fig.	57. —	0.3 -	10.8 -	9.6.		Fig.	58. —	0.1 -	12.0	- 11.6.
Fig.	59. —	0.1 -	11.2 -	10.8.		Fig.	60. —	0.2 -	9.6	- 8.8.
Fig.	61. —		15.0 (16	.0) —	11.6	Fig.	62. —	0.2 -	14.0	- 13·2.
Fig.	63. —	0.2 -	9.6 -	8.8.		Fig.	64. —	0.0	8.8	- 8.8.
Fig.	65. —	0.2 -	13.6 -	12.8.		Fig.	66. —	0.2 -	10.4	- 9.6.
Fig.	67. —	0.3 -	8.4 -	7.2.		Fig.	68. —	0.1 -	12.0	— <b>11</b> ·6.
Fig.	69. —	0.1 -	10.4 -	10.0.		Fig.	70. —	0:3 -	100	- 8.8.
Fig.	71. —	0.2 -	9.6 -	- 8.8.		Fig.	72. —	0.2 -	9.6	- 8.8.
Fig.	73. —	0.2 -	9.6 -	. 8.8.		Fig.	74. —	0.9 -	14.0	- 10.4.
Fig.	75. —	0.3 -	10.0 -	8.8.		Fig.	76. —	0.0 -	8.8	- 8.8.
Fig.	77	0.8 -	12.0 -	8.8.		Fig.	78. —	0.2 -	9.6	- 8.8.
Fig.	79. —	0.0 -	8.8 -	8.8.		Fig.	80	0.0	8.8	- 8.8.
Fig.	81	0.3 -	10.8 -	9.6.		Fig.	82	0.7	13.2	- 10.4.
Fig.	83	00 -	8.8 -	- 8.8.		Fig.	84	0.5 -	14.0	- 12.0.

T1.	07 0.1 110 10.1	0.0 0.0t 0.0 10
Fig.	85 0.4 - 14.0 - 12.4.	Fig. 86. $-0.6 - 12.0 - 9.6$ .
Fig.	87 0.3 - 13.6 - 12.4.	Fig. $88 0.0 - 8.8 - 8.8$ .
Fig.	89 0.2 - 12.8 - 12.0.	Fig. 90. $-0.2 - 9.6 - 8.8$ .
Fig.	91 0.0 - 8.8 - 8.8	Fig. 92. $-0.2 - 9.6 - 8.8$ .
Fig.	93. $-0.1 - 12.0 - 11.6$ .	Fig. 94. $-0.4 - 10.4 - 8.8$ .
Fig.	95 0.2 - 9.6 - 8.8.	Fig. 96. $-0.2 - 13.6 - 12.8$ .
Fig.	97 0.3 - 10.8 - 9.6.	Fig. 98. $-0.3 - 10.0 - 8.8$ .
Fig.	99 0.0 - 8.8 - 8.8	Fig. 100. $-0.0 - 8.8 - 8.8$ .
Fig.	101 0.0 - 8.8 - 8.8.	Fig. 102. $-0.1 - 10.4 - 10.0$ .
Fig.	103 0.1 - 11.2 - 10.8.	Fig. 104. $-0.2 - 9.6 - 8.8$ .
Fig.	105 0.2 - 11.6 - 10.8.	

Plate 19. Anaphase of self-purple flowers photographed with obj. Zeiss Ap. 120, ap. 1·32, eyepiece 10 comp. Camera distention 71·8 cm. Fixed in Flemming's str. solut. with a very small quantity of acetic acid. Stained with Iron Haemat. Fig. 106—109 early normal anaphase. Fig. 110 normal late anaphase. Fig. 111 early anaphase with one large chromosome aside. Fig. 112 early anaphase with one small chromosome aside. Fig. 113—115 early anaphase. In each case a pair of chromosomes are aside. Fig. 116 early anaphase with one pair of chromosomes at the pole. Fig. 117 early anaphase with one pair of chromosomes and one solitary chromosome at the pole.

Plate 20. Fig. 118—124 anaphase and fig. 126 metaphase from self-purple flower type. Photographed with obj. Ap. 120, ap. 1·32, eyepiece 10 comp. Zeiss. Camera distention 71·8 cm. Photographs fig. 125 and 127—130 made with obj. Ap. 92, ap. 1·4 and eyepiece Homal IV. Camera distention 71·8 cm. Phot. of fig. 131 made with a smaller camera distention. Fig. 118—120 early anaphase showing slight abnormalities. Fig. 121—124 irregular anaphase with chromosomes scattered along the spindle. Fig. 125 granular structure seen in bifurcated ends of the somatic chromosome. Fig. 126 metaphase. Chromosomes showing notable differences in their length. Fig. 127 chromosome pair at an early diakinesis. Fig. 128 chromosome pair at a middle diakinesis. The right chromosome with two satellites. Fig. 129 chromosome pair at a middle diakinesis. Satellite between chromosome ends. Fig. 130 chromosome pair at a middle diakinesis. Fig. 131 chromosome pair at a middle diakinesis.

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### Badania nad mieszańcami gatunków tetraploidalnych pszenicy. – Crossing experiments on tetraploid species of wheat.

#### Mémoire

#### de M. K. KANIEWSKI,

présenté dans la séance du 9 novembre 1931, par M. E. Malinowski m. c.

In this paper I draw the attention to some characters of wheat which so far have not been described and I try to interpret in terms of factors some specific differences concerning tetraploid wheats.

The researches here reported have been carried out in the Institute of Genetics (Skierniewice, Poland) under Professor E. Malinowski, to whom I am indebted for much valued advice.

#### I. Crosses between Triticum polonicum and Tr. dicoccum

#### a) The parental forms

Triticum polonicum is characterized by long glumes (Fig. 1, A, 1). The empty glumes are longer than the flowering ones. Both empty and flowering glumes of each pair are unequal as to their length. Longer empty glume of a given spikelet is accompanied by shorter flowering glume and vice versa at the side of the shorter empty glume we find longer flowering glume. The middle flower is lower than the top of empty glumes. In all other species of wheat the empty as well as the flowering glumes are much shorter than in Tr. polonicum and the middle flower of a spikelet grows higher than empty and even flowering glumes.



Fig. 1. Spikelets and glumes from the cross Tr. polonicum  $\times$  Tr. dicoccum. A 1-3 Tr. polonicum: A 1—spikelet; A 2—empty glume (outer half); A 3 empty glume (inner half); A 4—6 Tr. dicoccum: A 4—spikelet; A 5—empty glume (outer half); A 6—empty glume (inner half). B 1–3 F<sub>1</sub>: B 1—spikelet; B 2—empty glume (outer half); B 3—empty glume (inner half). C 1–5 »po-

#### Crossing experiments on wheat

lonicum« type of F<sub>1</sub>: C1-spikelet; C2-empty glume (outer part); C3-empty glume (inner half); C 4, 5-two empty glumes of one spikelet. D 1-5
»dicoccum« type of F<sub>2</sub>: D1-spikelet; D2-empty glume (outer half); D3-empty glume (inner half); D 4, 5-two empty glumes of one spikelet.

Triticum polonicum, used in this cross, may be described as follows. The ears are relatively long, bearded. Their awns were of a grey colour, but some were dark or even black. Glumes lanceolate (Fig. 1, A, 2). Ribs are very distinct, even conspicuous. Tooth is straigth. Colour of the glumes is grey, often with bluish tint. Spikelets are broad (Fig. 1, A, 1).



Fig. 2. Transverse section of empty glume of Tr. polonicum: a - b height of the keel; a-d width of empty glume (outer half); a-f width of empty glume (inner half).

#### K. Kaniewski:

Fig. 2 shows the cross section of an empty glume. At c and e are ribs. From a to b there is the cross section of the keel. The outer part of the keel  $(z_1)$  contains a vascular bundle, the inner one  $(z_2)$  is made up of parenchyma. The ribs as well as the keel are covered by scabrid hairs (fig. 3—1, 2 and fig. 4—1, 2), which are larger in the upper part of empty glumes. The last rib of the glume (the most distant from the keel) is the largest. A corresponding rib may be found also in *Tr. durum* and *Tr. dicoccum*, though other ribs may be absent in those species.



Fig. 3. Scabrid hairs on the upper part of empty glumes: 1, 2 – Tr. polonicum; 3, 4 – dicoccum; 5, 6 – polonicoid; 7, 8 – Tr. durum. Odd numbers refer to the scabrid hairs on the keel and even numbers – to those of the main rib.

It is why the comparison we make is only for those scabrid hairs being on the above said rib. Empty and flowering glumes may be easily detached without any damage from the spikelet. They are fragil. Rachis of the loose *Tr. polonicum* is tough. Its grain is long and white.

Triticum dicoccum used in our crosses has compact squareheadlike ears. Empty glumes are much shorter than in Tr. polonicum (Fig. 1, A, 4, 5). Flowering glumes are longer than empty ones. Middle flowers of the spikelets grows higher than empty glumes and generally also higher than flowering ones.

Both empty glumes of a spikelet have an equal length and it is the same for flowering glumes. The spikelets are narrow, the empty and flowering glumes are laying close together. Ears compressed, narrower across the face than the 2-rowed profil, they are of a white colour, beardless or with short awns confined to flowering glumes. Empty glumes are short, broad and thick (Fig. 1, A, 5). Apical teeth are small. On the cross section of empty glumes there is only one salient rib (Fig. 6, 1). Empty glumes are elastic and pubescent. The glumes cannot be detached undamaged from the spikelet. The keels are thick and shorter than in *Tr. polonicum* (Fig. 6, 1). Scabrid hairs appear only in the upper part of glumes on their keel and ribs (Fig. 3-3, 4). Rachis is fragil, grain is reddish.



Fig. 4. Scabrid hairs on the middle part of empty glumes: 1, 2 - Tr. polonicum; 3, 4--Tr. durum. Odd numbers refer to the scabrid hairs on the keel whilst even numbers — to those of the main rib.

#### b) The $F_1$ generation

The  $F_1$  plants were intermediate as to the principal characters. Tables I, II, III, IV, and V contain data as to some characters of the  $F_1$  plants. Ears are beardless or slightly bearded (Fig. 1, B, 1). The middle flowers are at the same height as empty and flowering glumes. Spikelets are narrow and pubescent; apical teeth are intermediate. The thickness of the glume is intermediate (Fig. 6, 2). The keels are prominent, higher and thicker than in *Tr. polonicum* (Fig. 6, 2). Scabrid hairs are on the keels and ribs.

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ed and	ren	13	19		REI.	28	10	19 1 (12)	14	and a		183		ab	8 m	19	189	in the	ALA ALA	1. IN	6 th	144	I	len	T.gtl	A I 1 O	3 f
rag Eastan	x	9.2	6	9.9	10	10.5	11	11.5	12	12.5	13	13.5	14	14.5	15	15.5	16	16.5	17	17.5	18	18.5	19	19-5	20	20.5	21
Tr. polonicum	168	ei	88	12	1		(h				1	86		H	ale	10	19.3		E.	Et.	20	19	3	N	da		
Tr. dicoccum	1	1	6	17	4					日		14	140. 130	1 AN	946 146					100 L							
F <sub>1</sub>		d			1.15	in		94	197	10	19	R	1.65%		in the			2	1		1				10		
»polonicum« of F,				1	198		91	ST T		19	19.7		22.5	NAR Brit	19. I			1	and and	121	1.R	1	2	54	3	4	3
intermediate type of F <sub>2</sub>	11	ad.	1	4	ler	R		I	4	2	6	10	21	15	26	14	37	16	31	16	37	13	24	8	4	2	6
»dicoccum« of F <sub>2</sub>	1	2	4	5	16	17	29	19	15	7	3	ari ari	12		0 10	ET.	q i	19	P.I.O	U DI	SI SI	1	111	W.C.	10		

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	-	121	1100		2.4.2	-		1000	35.8.2	1				201	112		.200		10124		1.5.5	U	
1:1	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Tr. polonicum	1	3	1	2	7	7	6	4	7	2	2						1						
Tr. dicoccum									1	77				- Maria									
F <sub>1</sub>					No.				1	1				The second									
»polonicum« of $F_2$		1		2	5	2	2	4	11	8	5	6	4	7	6	4	3	2	3	4	3	2	1
intermediate type	1			1	2	5	5	15	15	28	28	22	31	28	16	16	18	15	13	14	.2	9	5
»dicoccum« of F <sub>2</sub>	GD	10			-		100	1	3	2	1	4	11	9	5	10	10	14	7	6	6	2	5

TAB Length

s why the compadie	36.5	38.5	40.5	42.5	44.5	46.5	48.5	50.5	52.5	54.5	56.5	58.5	60-5	62.5	64.5	66.5	6.89
Tr. polonicum			01	A DI		103				NS II	184	10 Å	2	HA.	100	1	
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intermediate type of $F_2$		8 3	1	1	4	2	2	5	5	8	8	16	17	12	14	15	21
»dicoccum« of F2	1		1	4	5	3	5	4	5	6	10	9	9	10	11	8	9

Crossing experiments on wheat

LEI.		
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### LE II.

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#### LE III. of ears.

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#### c) The F<sub>2</sub> generation

As in many crosses in which Tr. polonicum was one of the parental forms, so in this one three relatively distinct types appeared in the F<sub>2</sub> generation namely: polonicum, intermediate and dicoccum in the proportion of 1:2:1. Our classification into three classes has been based on the length of the glumes compared with the one of middle flowers. In such a case we did act as Liepin did. We classed as »polonicum« such plants in which the middle flower in spikelets was lower than the top of empty glumes and we regarded as »dicoccum« such plants in which the empty as well as the flowering glumes were much shorter and the middle flowers were growing higher than empty glumes. We shall designate the first type by the letters PP and the second one by the letters pp. In the intermediate class of  $\mathbf{F}_{\circ}$  plants (Pp) empty glumes have been on the same level as the middle flowers. In our case the actual numbers were as follows: 120 individuals of the polonicum type, 324 intermediate plants and 145 individuals of the dicoccum type.

Let us consider particular characters of the  $F_1$  plants.

The frequency polygone concerning the glume length is trimodal in the  $F_2$  generation. The glumes corresponding to Tr. *polonicum* were shorter than in the parental *polonicum* and the glumes corresponding to Tr. *dicoccum* were longer than in the parental *dicoccum* (Table I). Analogous results were obtained previously by many writers in cases when Tr. *polonicum* was used for crossing experiments with other tetraploid species.

The ear density of the  $F_2$  generation is shown in Table II. We see in this Table that the *polonicum* type in  $F_2$  has surpassed the density of the parental *polonicum* but it did not reach the degree of density of the parental *dicoccum*. As to the *dicoccum* type in  $F_2$  we see that its density is smaller than in the parental *dicoccum*.

The average length of ears of the *polonicum* type has diminished in  $F_2$  as compared to the parental *polonicum* and the average length of ears of the *dicoccum* type has increased (Table III).

The data concerning the number of spikelets of particular ear types in  $F_2$  are shown in Table IV. Taking into considera-

#### TABLE IV.

The number of spikelets in ears

ery soft bone	15	16	17	18	19	20	21	22	23	24	25	26	М	N
Tr. polonicum	2	3	9	7	11	8	1	1					18.31	42
Tr. dicoccum									9	16	3	1	23.87	29
F <sub>1</sub>			10		1				1					
$\sim$ polonicum « of F <sub>2</sub>	2	3	1	1	ō	17	13	14	13	11	5	1	21.43	86
»dicoccum« of F2		5	8	14	18	16	20	12	9	9	4		20.32	115
			ta		1			1		17-12-14				

tion the average values given in Tables I and II we see that in  $F_2$  in the limits of the *polonicum* type the density of ears has increased and the length of glumes has decreased whilst within the *dicoccum* type the density of ears has decreased and the length of glumes has increased. The correlation coefficient between the glume-length and ear-density (Table VI) is rather low (-0,33).

When we compare the parental types with the corresponding  $F_2$  types we see that the shift observed in  $F_2$  and concerning the ear density is greater than the shift of the glume length We possibly may explain this in assumming that:

1) a certain essential glume length is determined by the factor linked with the type of the ear and the modifications brough about by additional factors of glume length are comparatively small,

2) the ear density is determined only by cummulative factors independent of the type of the ear.

The glumes of the type pp may be shorter or longer but they are always short as compared to those of the PP individuals, whilst as concerns the density of the ear such correlation does not exist. In the pp as well as in the PP types the ears may be either loose or compact.

The spikelets of the parental *dicoccum* type were narrow. In  $F_2$  in the limits of the *dicoccum* type individuals appeared with broad spikelets (Fig. 1, D, 1). The glumes of the *dicoccum* type in  $F_2$  exhibited also some modifications when compared to the parental

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TABLE ٧.

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dicoccum. The thickness of glumes decreased in many individuals (Fig. 7-1, 4). Plants with fragil glumes appeared, some of them being exceptionally hard. Among the pliable glumes some were very soft. Some plants have narrower glumes (Fig. 1, D, 2, 3). Apart the glumes with a curved keel others appeared with a more straightened one (Fig. 1, D, 4, 5). I noticed that the height of the keel had increased in the majority of cases (Table V). In many

#### TABLE VI.

Correlation between ear density and glume length in  $F_2$  ear density

glume length	17-21-9	22-26.9	27-31.9	32 36-9	37-41.9	42-46.9	47-51-9
28.0-32.9	2	2	2	2		a 1	
23.0 - 27.9	5	23	20	10	1	1	
18.0-22.9	2	28	51	24	13	3	
13.0-17.9	3	42	78	56	12	5	
8.0—12.9		6	32	47	24	8	1

#### TABLE VII.

Correlation between ear density and glume length in the parental varieties ear density

glume lenght	17 - 21 9	22 26.9	27-31.9	32-36.9	37 - 41.9	42 46.9	47 - 51-9	52 - 56.9	57 - 61.9	6266.9
33.0 - 37.9	2						1			11Te
28.0 - 32.9	8	11	badda wor n	pon si mol :	g turno micran	olog .	1011 J	an An	gmai	1. BU
23.0 - 27.9	4	15	2	i Sa	(brid)	holes	ofba	did	incit a	ppeal
18.0-22.9	- lenast	and the	( dia a	Rodi		Congress maine	dig a di	dood h	States -	addaa addaa
13.0 - 17.9	kanala kanala	dando i	period for 1	bioma	dante	viloti.	city	ener o Philippi	ing list	undat
8.0 - 12.9	palare	hevel a	ie/ei	Aure	stonte	019	97 81	10	14	5

plants scabrid hairs appeared on the keel and on the whole surface of empty glumes. One could observe keels which were more narrow than those of the parental variety and also some which were thicker than in the parental *dicoccum* (Fig. 7-4,



Fig. 5. Empty and flowering glumes detached from the spikelets. Upper row — Tr. polonicum; lower row — Tr. durum.

1, 3). The tooth characteristic of the *dicoccum* type appeared rather rare; in the majority of cases the plants had teeth of the parental *polonicum*. Individuals with bearded ears appeared in  $F_2$  (sometimes awns were black). I observed also plants with tough rachis. As to the *polonicum* type of  $F_2$  we may say that
#### Crossing experiments on wheat

in the majority of cases the plants differed in many characters from the parental *polonicum*. I shall enumerate some of those differences. The tooth of the *dicoccum* type was more frequently met with than that of the *polonicum* type. Empty glumes often had curved keel (Fig. 1, C, 4, 5) what has not been observed in parental *polonicum* type. The width of glumes was often increased (Fig. 1, C, 2, 3). Individuals appeared with glumes thicker than in the parental variety (Fig. 7, 2). The heigth of the keel had often decreased (Table V). Apart thin keels there appe-



Fig. 6. Transverse section of empty glumes: 1-Tr. dicoccum;  $2-F_1$ ; 3-Tr. polonicum.

ared also thick ones (Fig. 7, 2). Scabrid hairs often did not appear at all. A great deal of plants had pliable glumes, such pliantness being a character antagonistic to the characteristic fragility of the parental *polonicum*. Individuals with a fragile rachis appeared. Beardless plants were also observed.

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# II. Crosses between a polonicum-like form and Tr. durum

a) The parental forms

For this cross a *polonicum* type was used which probably derived from the crossing of a typical *Tr. polonicum* with *Tr.* 



Fig. 7. Transverse sections of empty glumes observed in F<sub>1</sub> of the cross Tr. polonicum × Tr. dicoccum. 1, 3, 4-glumes of the dicoccum type: 1-glume ppddEEGG, 3-glume ppDDEEGG, 4-glume ppddee GG(?), 2-glume of the \*polonicum« type (PPDDeegg).

*dicoccum.* This type was obtained by our Institute from the late Professor K. Miczyński several years ago. In our crosses between *Tr. polonicum* and *Tr. dicoccum* we got a similar type (Fig. 1, C 1-5).

The parental form resembling *Tr. polonicum* and used in the actual cross may be characterized as follows:

1) Ears compact, squarehead-like.

2) Rachis fragile, while in Tr. polonicum it has been tough.

3) Spikelets narrow (Fig. 8, A 1).

4) Empty glumes are long (average lengths for three years were: 20.31, 18.98, 18.83) but shorter than those of Tr. polonicum.

5) Glume width is greater (Fig. 8, A 2, 3) than in Tr. polonicum. Glume thickness is also greater (Fig. 9, 2).

6) The keel of empty glumes is more curved (Fig. 8, A 2) whilst in Tr. polonicum it is more straight and the glumes have been lanceolate.

7) Ribs are not so salient (Fig. 9, 2) as in Tr. polonicum.

8) The keel is not so high but is thicker (Fig. 9, 2) than in Tr. polonicum. It is very similar to that of Tr. dicoccum but it is smaller.

9) Typical scabrid hairs did not occur but some imperfect hairs were seen at the top of empty glumes (Fig. 3, 5, 6).

10) Empty and flowering glumes could not be detached undamaged from the spikelets.

11) The tooth of empty glumes is curved. Such a curved tooth is characteristic of certain varieties of Tr. dicoccum (Fig. 8, A 2).

12) Grain is long like in Tr. polonicum.

13) Empty glumes are pubescent.

As concerns Tr. durum the following characters have been noticed:

1) Ear long and loose, bearded. Awns black.

2) Spikelets broad (Fig. 8, A 4).

3) Empty glumes are more straightened (Fig. 8, A 5), are yellow or bluish-grey.

4) The width of the glumes is smaller (Fig. 8, A 5, 6) than in Tr. dicoccum.

5) The tooth is straight like in Tr. polonicum.

6) The ribs are more salient than in Tr. dicoccum (Fig. 9, 1).

7) The keel differs from that of Tr. dicoccum (Fig. 9, 1). It resembles the keel of Tr. polonicum but is higher and thicker. The width of the keel is usually the same in Tr. durum and in Tr. dicoccum though sometimes the keel of Tr. dicoccum is wider.

type of  $F_{i}$ : D1 + epikelet <math>D2 - empty where (outer half); D3 - empty where (anger half); D4 + empty elements (ranger half); D5 + empty elements



Fig. 8. Spikelets and glumes from the cross Tr. polonicoides  $\times$  Tr. durum. A 1-3 polonicoid: A 1-spikelet; A 2-empty glume (outer part); A 3-empty glume (inner part). A 4-6 Tr. durum: A 4-spikelet; A 5-empty glume (outer half); A 6-empty glume (inner half). B 1-3 the F<sub>4</sub> generation: B 1-spikelet; B 2-empty glume (outer half): B 3-empty glume (inner half). C 1-5 \*polonicum\* type of F<sub>2</sub>: C 1-spikelet; C 2-empty glume (outer half); C 3-empty glume (inner half); 4, 5-two empty glume (outer half); D 3-empty glume (inner half); D 4, 5-two empty glumes from one spikelet. 8) Scabrid hairs appear on the keel and on the thickest ribb (Fig. 3-7, 8 and Fig. 4-3, 4). In other places of empty glumes those hairs are less developped.



Fig. 9. Transverse sections of empty glumes of Tr. durum (1), of Tr. polonicoides (2) and of F<sub>1</sub> (3).

9) Empty glumes of Tr. durum are thinner than those of Tr. dicoccum (Fig. 9, 1).

10) Empty and flowering glumes may be easily detached undamaged from the spikelet (Fig. 4) what does not happen in the case of Tr. dicoccum.

11) Rachis is tough.

12) Grain is similar to that of Tr. dicoccum.

### b) The $F_1$ generation

The spikelets of  $F_1$  plants were narrow (Fig. 8, B 1), the glumes were intermediate as to their length, their thickness being also intermediate (Fig. 9, 3). The apical tooth is intermediate.

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The keel is lower than in the parental durum (Fig. 9, 3) and broader than in Tr. polonicum but narrower than in Tr. durum. Scabrid hairs occur on the keel and on the main rib.

## c) The $F_2$ generation

In the  $F_2$  generation three types were distinguishable namely: »durum«, intermediate and »polonicum«. The division into



Fig. 10. Transverse sections of empty glumes observed in F<sub>2</sub> of the cross polonicoid X Tr. durum. 1-3-glumes of the \*durum« type; 1 glume ppDD eegg, 2-glume ppddeeGG (?), 3-glume ppDDEEGG, 4-glume of the \*polonicum < type PPddEEGG.

those three types was based upon the same characters as the ones taken into consideration in the first cross. The proportion 1:2:1 between the three types in question was observed.

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I shall describe some characters observed in the  $F_2$  generation within the limits of *»durum«* as well as *»polonicum«* type.

In the limits of *adurum* type individuals with narrow spikelets appeared (Fig. 8, D 1); individuals were observed with empty glumes broader than those in parental *durum* (Fig. 8, D 2); individuals appeared with keels more curved (Fig. 8, D 4, 5). In many cases the width of empty glumes had increased. One could often see that the thickness of empty glumes has increased and that it was equal to the one of the parental *dicoccum* (Fig. 10 – 1, 3). Individuals appeared with keels broader and other with keels thinner (Fig. 10 – 3, 2) than in the parental *durum*. In the majority of cases the height of keel has diminished. Some plants possessed fragile rachis.

In the limits of the *»polonicum«* type individuals appeared with broad spikelets (Fig. 8, C 1). The width of empty glumes often was becoming smaller and their keel in many cases was straightened (Fig. 8–C 2, 4, 5). The consequence of it was that the empty glumes in some plants became lanceolate. I noticed glumes as thick as those of *Tr. polonicum* (Fig. 10, 4). Many plants exhibited a keel higher than in the parental type (Fig. 10, 4). Many individuals were observed with fragile glumes. Scabrid hairs appeared on the keel and on the ribs of many plants Some individuals were also obtained with tough rachis.

#### **III.** Discussion

From the data given above it is seen that both *PP* and *pp* types are complex ones. We do not know whether the characters composing those types are determined in each case by one or by many genetical factors. If there is one factor its effect would be manifold. If many factors are involved then such factors are linked.

The type PP included in Tr. polonicum may be characterized as follows:

1) The middle flower in the spikelet is lower than the tops of empty glumes.

2) The empty glumes in a spikelet are unequal as to their length and the same is for the flowering glumes.

3) Both empty and flowering glumes are long.

4) The back line of empty glumes is relatively straight.

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5) The keel is low (we may assume that in this case the keel is absent and that we have to deal only with the central nerve).

6) Empty glumes are thinner than in the case of *pp* type.

7) Glumes are narrow.

The type pp included in *Tr. durum* and in *Tr. dicoccum* may be described as follows:

1) The middle flower in a spikelet grows higher than empty glumes do.

2) The empty glumes in a spikelet are equal as to their lenght.

3) Both empty and flowering glumes are relatively short.

4) The back line of empty glumes is curved.

5) The keel is higher than in PP type because the glume is thicker.

6) Glumes are thicker than in the case of PP type.

7) Glumes are narrow, but a little broader than in PP.

The above two complexes of characters making up what we have called types PP and pp may be accompanied by various other characters. According to the characters involved we have to deal with different forms and among those various forms appearing in  $F_2$  of our crosses four principal types were clearly distinguishable. Such types correspond to four species of wheat namely: Tr. polonicum, Tr. dicoccum, Tr. durum and a new form which I propose to call *»polonicoid«* and which differs from Tr.polonicum in the same characters in which Tr. dicoccum differs from Tr. durum. In the  $F_2$  generation of the crosses Tr. polonicum  $\times Tr.$  dicoccum we observe Tr. durum and polonicoids and in the crosses Tr. durum  $\times$  polonicoid we distinguish Tr.polonicum and Tr. dicoccum.

We may assume that besides PP and pp the following factors were involved in our crosses:

A — factor or a group of factors elongating the essential glume length. This factor elongates the glumes more in *PP* than in *pp* type.

a — absence of this factor or factors.

B — factor or factors widening the essential width of glumes.

b — absence of B.

C — factor or factors straightening the back line of empty glumes.

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c — in the case of absence of such factor or factors the back line of empty glumes is curved.

D — factor or factors increasing the essential glume thickness. This factor increases more the thickness in the case of pp type. d — absence of D.

E — factor or factors determining the fragility of glumes as contrasted to elasticity. Fragile glumes can be easily detached undamaged from the spikelet. The outer half of such glumes has its edge folded inwards. Such folding occur in the upper part of the glume (Fig. 11, 2 and 4). Ribs and scabrid hairs are larger than in the case of absence of E.



Fig. 11. Cross sections made in the upper part of empty glumes in order to show their folded edges: 1 - polonicoid; 2-durum; 3-dicoccum; 4-polonicum.

e — glumes are elastic. They cannot be easily detached undamaged from the spikelet. The edge of the outer half of empty glume is not folded (Fig. 11, 1 and 3). Ribbs and scabrid hairs are smaller than in the case of presence of E.

F — In the case of presence of such factor or factors the apical tooth of empty glumes is curved.

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f — apical tooth is straight and acute.

G — factor or factors increasing the height of the keel.

g — absence of G (in such case we may have to deal either with a keel of *dicoccum* or with that of *polonicoid*).

H — empty glumes are pubescent. Empty glumes pubescent and fragile were not observed.

h — absence of H.

I - ears are narrow.

i - absence of I.

K — ears are loose.

k — ears are dense.

L — ears are squarehead-like.

l — absence of L.

M — ears are beardless.

m — ears are bearded.

N — Rachis is fragile. This character seems to be linked to the elastic glumes.

n — rachis is tough. This character seems to be linked to the fragile glumes.

The genetical constitution of the four types mentioned above would be as follows:

Tr. polonicum L. - PPAAbbCCddEEffGGhhiiKKllmmnn,

Tr. dicoccum Schübl.— ppaaBBccDDeeFFggHHIIkkLLMMNN, Tr. durum Desf. — ppAAbbCCddEEffGGhhiiKKllmmnn,

polonicoid form — PPaaBBccDDeeFFggHHIIkkLLMMNN.

Tr. turgidum contains probably pp factors differing from corresponding factors of *dicoccum* and *durum*. We may call them  $p_1p_1$ . It is possible that some forms classed by botanists as *dicoccum* contain the factors  $p_1p_1$  instead of pp.

The factors PP and pp do not seem to influence the shapes of the keel. The essential morphological elements of the keel are the thickness and the height. The thickness of the keel corresponds to the thickness of the glume (Watkins, 5). It is associated to a certain extent to the fragility of the glumes. In comparing two glumes of equal thickness we always find that the keel of a fragile glume is thicker than that of an elastic one. The keel of one and the same type is higher on the thick glumes than on the thin ones. The keels of *dicoccum* and *polonicoides* are very much similar, the former being thicker because the glumes are thicker in *dicoccum*.

Strictly speaking neither *dicoccum* nor *polonicoid* have any keel. The keels occur only in *durum* and *polonicum* types.

On the other hand the keels of *durum* and *polonicum* are resembling very much to each other. The same factor G determines the keel of *polonicum* and of *durum*. But the factor Gtransferred to *dicoccum* produces longer keel because the thickness of glumes of *dicoccum* is greater (Fig. 7, 3 and Fig. 10, 3).

The keel of *durum* type after being transferred to *polonicoides* becomes similar to that of *polonicum* and the only difference I noticed is that such a keel is a little higher than the one of the parental *polonicum* (probably because empty glumes of the *polonicoid* form are thicker than those of *Tr. polonicum*).

In the crosses between the *polonicoid* form and Tr. vulgare (Malinowski, 4) such types as Tr. dicoccum and Tr. Spelta appear in  $F_2$ . Such types do not occur in the crosses between Tr. polonicum and Tr. vulgare. We know that Tr. Spelta and Tr. dicoccum appear in the crosses between Tr. dicoccum and Tr. vulgare but they do not occur in the crosses between Tr. durum and Tr. vulgare. It follows from those data that polonicoid form and Tr. dicoccum have in common some characters and that such characters are lacking in Tr. polonicum and in Tr. durum.

From the Institute of Genetics, Skierniewice, Poland.

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