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The heredity of specific traits in the hybrid *Mirabilis jalapa* × *Mirabilis longiflora*

by

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The genus *Mirabilis*, in particular the species *M. jalapa* and *M. longiflora* have been the subject of many investigations. The great morphological differences between these two species and especially the difference in the length of the flower tube have for long attracted the attention of genetists.

The first crosses between *M. jalapa* and *M. longiflora* were obtained as early as the 18th and the 19th century by Kölreuter (1764), Gärtner (1849), Lecoq (1862), and Naudin (1863).

Even those early investigators noticed that hybrids between these two species could be obtained only when *M. jalapa* was the maternal plant.

The first more detailed analysis of the hybrids *M. jalapa* × *M. longiflora* was carried out by Correns (1902) who described the manner in which the flower colour, the tube length, and the pollen size were inherited in the F_1 progeny of these species.

A still more complete analysis of the inheritance of some specific traits accounting also for the F_2 generation of this hybrid was carried out by Prakken (1944). He studied in particular the heredity of the length of the flower tube, the flower colour, and the pubescence.

The cytological study of the genus *Mirabilis* is rather difficult. The originally established chromosome number for some species in this genus has been subsequently corrected more than once.

The course of meiosis in the F_1 hybrids *M. jalapa* × *M. longiflora* and in the parental species was studied and compared by Showalter (1935) and Prakken (1944). According to Showalter the reduction divisions in both pure species and in the F_1 hybrid are strongly disturbed. However, Prakken is of the opinion that in the pure species meiosis proceeds regularly and undisturbed, and that disturbances in the reduction divisions of the F_1 hybrids are few.

Earlier descriptions of the heredity of specific traits in the hybrids *M. jalapa* × *M. longiflora* were restricted to only a few of the numerous

traits distinguishing these interesting species, whereas some results of the cytological investigations were contradictory. For this reason I have thought useful to repeat in greater detail the genetic analysis of the differences between the two species and to extend the investigation over a greater number of morphological traits and some physiological traits.

Meiosis in *M. jalapa* and in the F_1 hybrid *M. jalapa* × *M. longiflora* were also studied.

MATERIAL AND METHODS

The plants used for the crosses were obtained from seeds of plants grown for many generations in the Botanical Garden in Warsaw.

M. jalapa was the maternal plant, for, as has been mentioned, all reciprocal crosses were unsuccessful.

The setting of seeds when *M. jalapa* was pollinated with pollen of *M. longiflora* was very poor.

Although very many flowers were pollinated one seed only was found and from this seed one F_1 plant was grown. This cross was obtained by A. Doroszewska from whom I received the F_1 plant and some seeds for F_2. The whole F_2 generation was the progeny of this one F_1 plant. The seeds for F_2 were obtained by spacial isolation of the F_1 plant, since the setting of seeds under the usual isolating bags was much lower.

Numerous flowers of *M. jalapa* were also pollinated with pollen of the F_1 hybrid, but only two seeds were obtained from which one plant germinated.

From the reciprocal backcross not one seed was obtained.

Similarly all attempts at backcrosses with *M. longiflora* were unsuccessful.

Except for the F_1 plant all the plants of *M. jalapa*, *M. longiflora*, and the F_2 generation were grown close to each other on the same plot under similar conditions. The measurements were carried out during two successive seasons.

For the examinations of meiosis in pollen mother cells the buds were fixed in Navaschin's fixative according to Randolph's modification, embedded in paraffin, cut into sections 15 μ thick, and stained with crystal violet.

Pollen fertility was calculated after staining with aceto-carmine. About 400 pollen grains from each plant were examined and the percentage of grains with well stained cytoplasm and nuclei was counted.

CYTOLOGICAL ANALYSIS

The course of meiosis was examined in PMCs of *M. jalapa* and the F_1 hybrid.

Conformably with what was reported by Showalter and Prakken the chromosome number is n = 29 (Fig. 1).

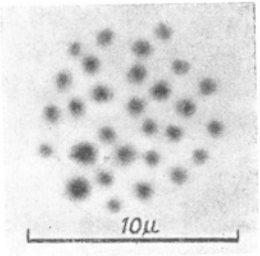

Fig. 1. Metaphase of the first meiotic division with 29 bivalents in *M. jalapa* — polar view

The course of meiosis in *M. jalapa* was not entirely regular. In the 30 examined PMCs in the stages of metaphase I, anaphase I, or telophase I such disturbances as single univalents and lagging chromosomes were found in three instances (Fig. 2).

In the F_1 hybrid the disturbances of meiosis are more frequent. In the 32 examined PMCs at the stages of metaphase I, anaphase I, or telophase I irregularities of meiosis occurred in as many as 17 cells (Fig. 3).

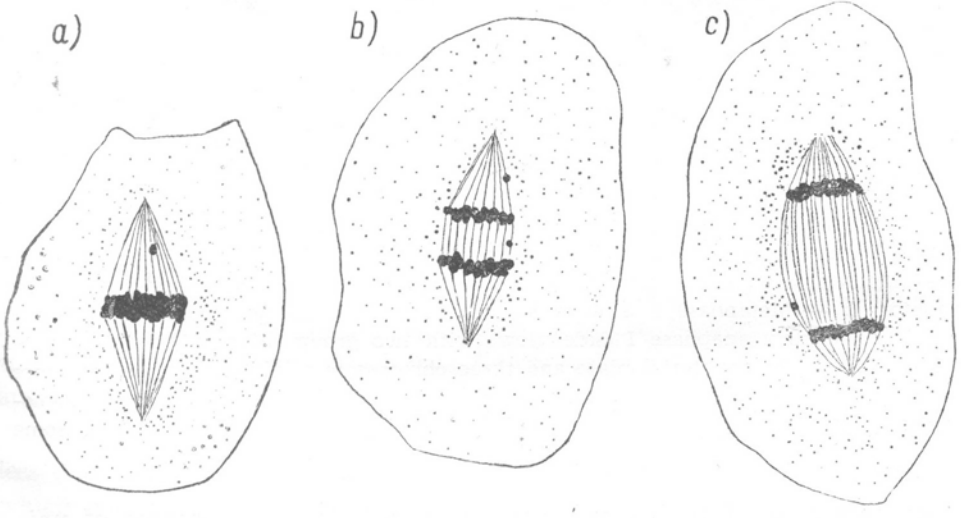

Fig. 2. Disturbances of meiotic divisions in *M. jalapa*. *a* — Metaphase I (side view) with a single chromosome, probably a univalent, lying between the equator and the pole of the spindle; *b* — Anaphase I (side view) with two chromosomes lying separately; *c* — Late anaphase I (side view) with a chromosome lagging in the spindle (× 3000)

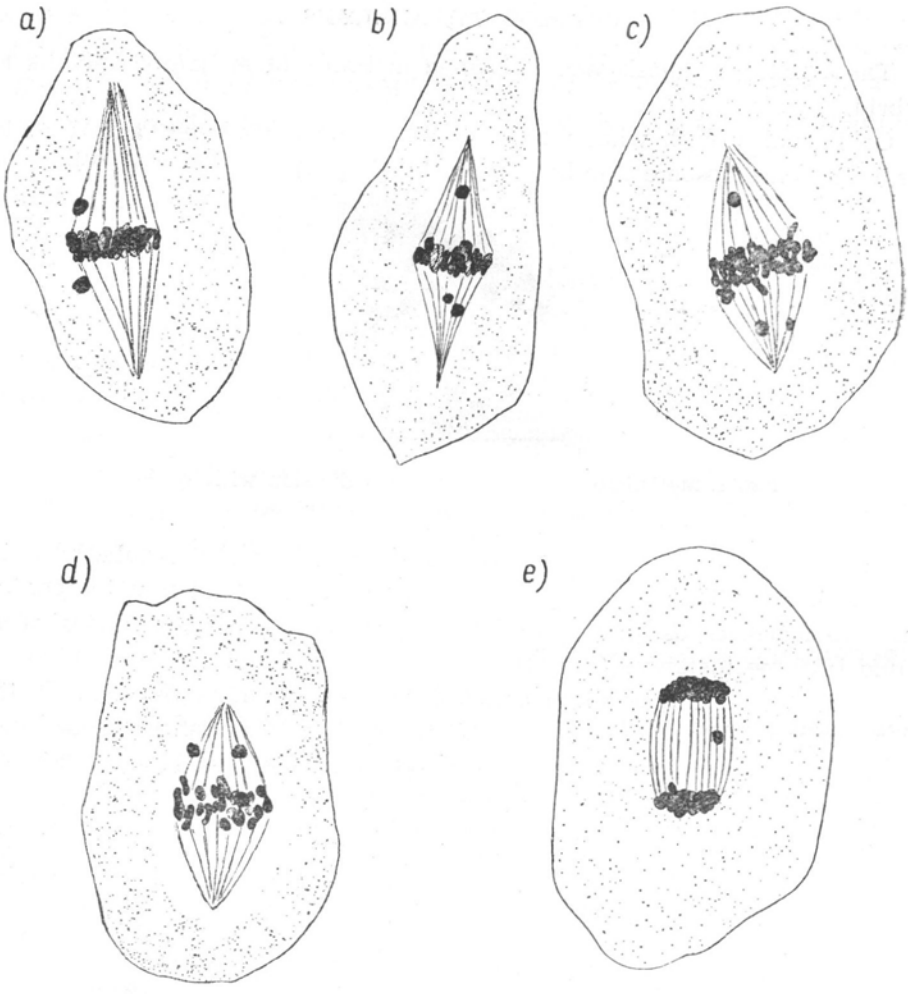

Fig. 3. Disturbances of meiotic divisions in the F_1 hybrid *M. jalapa* × *M. longiflora*. *a* — Methaphase I (side view) with two large chromosomes on either side of the equator; *b* — Metaphase I (side view) with three univalents, two large and one small; *c* — Early anaphase I (side view) with two groups of segregating chromosomes still on the equatorial plate and three chromosomes lying apart already close to the poles of the spindle; *d* — early anaphase I (side view) with two large chromosomes lying far from the others; *e* — Telophase I (side view) with a chromosome lagging on the spindle (× 3000)

In metaphase I the disturbances consisted in the presence of univalents, usually two large ones, lying at some distance from the other chromosomes grouped on the equatorial plate of the spindle. In anaphase I and in telophase I there were chromosomes, probably univalents, lagging on the equatorial plate of the spindle.

GENETICAL ANALYSIS

The following traits were measured and defined for the genetic analysis:

1. Length of flower tube.
2. Length of style.
3. Length of the lobe of the corolla.
4. Width of the lobe of the corolla.
5. Length of the lobe of the calyx.
6. Width of the lobe of the calyx.
7. Growth habit.
8. Morphology of leaves.
9. Pubescence on stems, leaves, and flowers.
10. Colour of stems.
11. Colour of flowers.
12. Date of flowering.
13. Time of anthesis.
14. Pollen fertility.

1. Length of flower tubes

The fused petals of the corolla of the flowers in *Mirabilis* form a narrow tube expanding at the end in five radially arranged lobes.

The length of the flower tube is the main specific trait distinguishing *Mirabilis jalapa* and *Mirabilis longiflora*. The tubes were measured from the end of the ovary to the point at which they form lobes (Fig. 4).

Table I lists the lengths in millimetres of flower tubes in the parental species, F_1 and F_2.

The row marked *Mj* lists the flower tube lengths in *M. jalapa* with white and red flowers only. The flower tube lengths in these two varieties are approximately the same averaging at about 31.1 mm. The parental plant in this investigation was *M. jalapa* with red flowers. The variety with variegated flowers which has flower tubes shorter than 30.0 mm., average about 25.0 mm., was not considered.

The average length of flower tubes in F_1 was 53.9 mm. and was much less than the arithmetic mean of tube lengths for the two parental species, which was 79.0 mm. This means that F_1 is distinctly shifted towards *M. jalapa*.

In the F_2 generation flower tubes were measured in 252 plants, ten flowers in each. In this generation the variation practically did not extend beyond the variation range in F_1 on the side of *M. longiflora*. Not one

plant was found in which the mean length of flower tubes from ten flowers was more than 65.0 mm., whereas the average length of tubes in individual plants of *M. longiflora* ranged 115.0 to 130.0 mm., and the

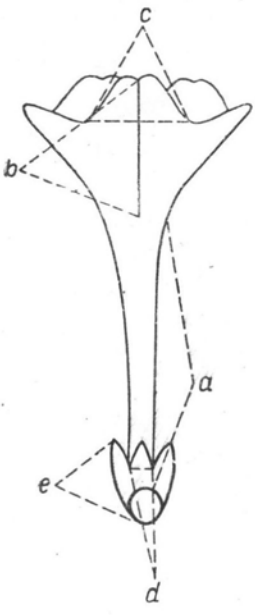

Fig. 4. Schematic diagram of *Mirabilis* flowers with the traits measured in the investigation marked in: *a* — Length of flower tube; *b* — Length of the lobe of the corolla; *c* — Width of the lobe of the corolla; *d* — Width of the lobe of the calyx; *e* — Length of the lobe of the calyx

length of tubes in individual flowers was 105.00 to 140.00 mm. On the other hand in the F_2 generation there were 23 plants with flower tubes of the same average length as in *M. jalapa*.

As is to be seen from these data the variation in the F_2 generation has a continuous character and a normal distribution, but is distinctly shifted towards the smaller values. Including the variation in *M. jalapa* the variation in F_2 does not attain the values for the other parental species. The average of the tube lengths for the whole of the F_2 generation is even lower than in F_1 which also is very characteristic.

Since the growth of plants essentially consists in the multiplication of living matter it is more convenient to express the relations here considered on a graph with a logarithmic scale.

Fig. 5 shows on the logarithmic scale the mean lengths of the flower tubes plotted against the number of plants in intervals of 0.02 log.

The graph with the logaritmic scale has been plotted so as to check whether the abnormal shift of the variation in F_1 and F_2 towards *M. jalapa* was not caused by some error in the choice of the arithmetic scale.

However, as is to be seen, even on the logarithmic graph the variation of the flower-tube length is shifted in F_2 towards *M. jalapa*, though in this case the shift is not as marked as in the table.

Table 1

Length of flower tubes in mm

Class values	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	N	$\bar{x}$	S	$s_{\bar{x}}$
M.j.		2	10																				12	31,1	2,0	0,56
M.l.																				1	3	1	5	122,9	4,8	2,1
F_1							1																1	53,9		
F_2		5	18	55	72	52	33	14	3														252	43,6	7,2	0,45

Table 2

Length of the lobe of the calyx in mm.

Class values	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	N	$\bar{x}$	S	$s_{\bar{x}}$
M.j.									3	5	1					9	16,1	0,57	0,19
M.l.								3	2							5	14,9	0,34	0,15
F_1					1											1			
F_2	1	21	38	47	33	42	17	12	13	9	6	5	7	1		252	12,0	2,7	0,17

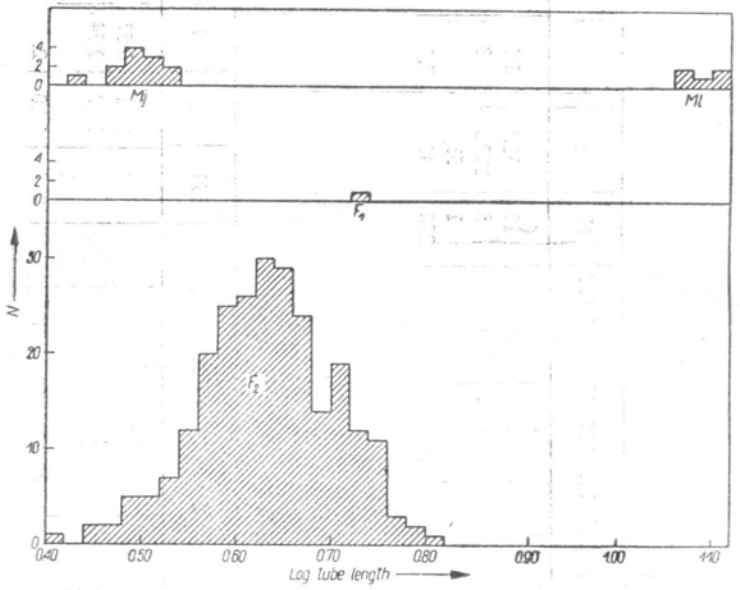

Fig. 5. Frequency histogram of the logarithm of the average flower tube lengths in *M. jalapa*, *M. longiflora*, F_1, and F_2

2. Length of style

The great difference in the length of flower tubes between the two parental species is associated with a similar difference in the length of the styles.

The average lengths of styles for five flowers in each of nine *M. jalapa* plants ranged 44.0 to 55.2 mm., the average for the nine plants being 47.7 mm.

The corresponding values for five *M. longiflora* plants were respectively 127.8 to 137.2 mm. and 132.8 mm.

The average length of styles for 100 flowers in the F_1 plant was 67.2 mm.

In the F_2 generation the length of styles was measured in 198 plants, in five flowers on each. The average length of styles in the particular plants ranged 40.0 to 90.0 mm.

The variation range of this trait in the parental species and the hybrids is shown on the logarithmic graph (Fig. 7). This graph resembles the one in fig. 5.

The variation in the F_2 generation is continuous and has a normal distribution, but similarly as in the case of the flower tube lengths it is shifted towards lower values including on one side the variation of

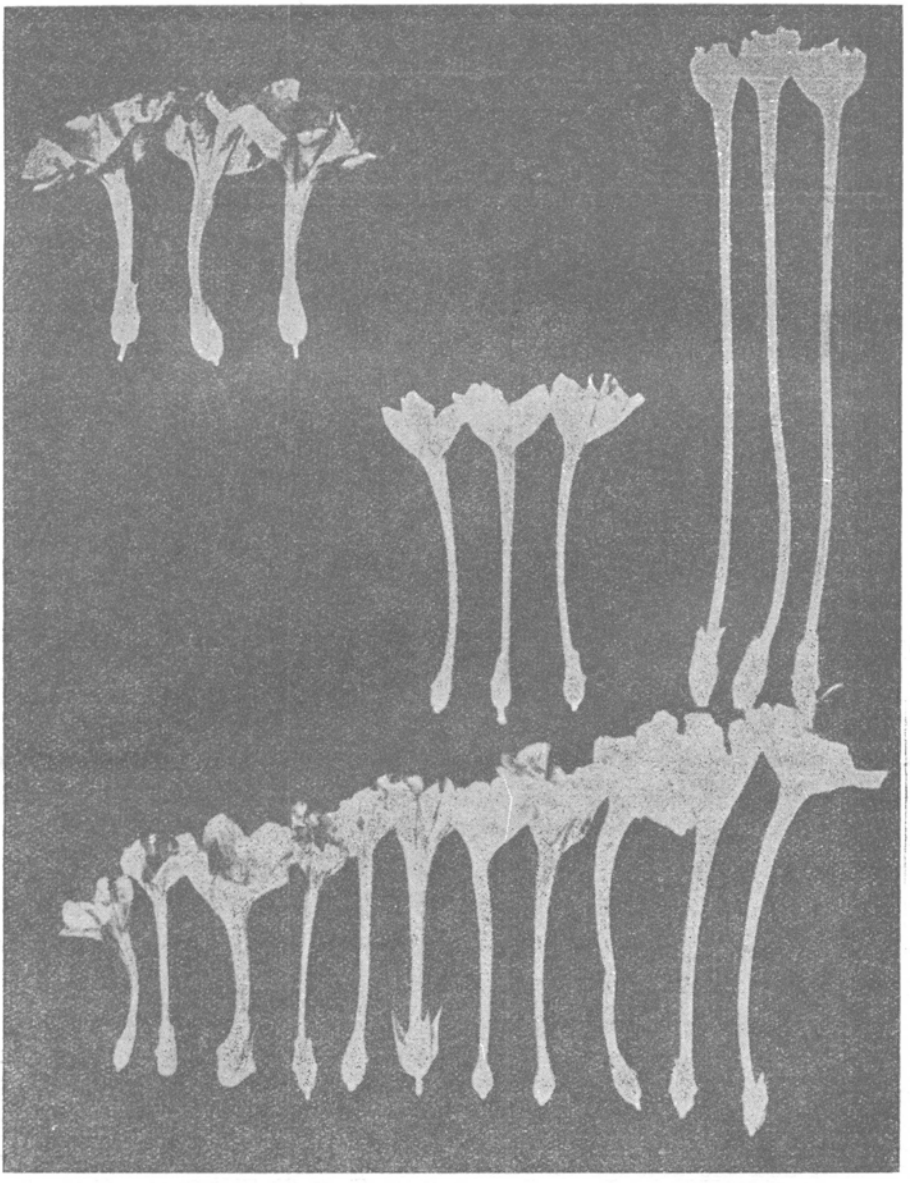

Fig. 6. Photograph of flowers of *M. jalapa* (top left), *M. longiflora* (top right), F_1 (middle), and F_2 (bottom). The first flower on the left in the bottom row is from the F_2 plant with the shortest flower tube and the first flower on the right is from the F_2 plant with the longest flower tube

M. jalapa and not extending on the other to the variation of *M. longiflora*. However, the difference between the variations in *M. longiflora*

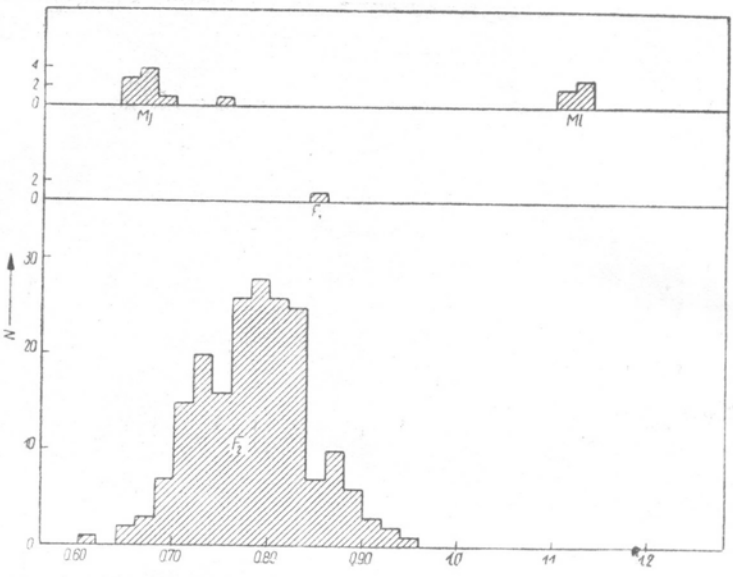

Fig. 7. Frequency histogram of the logarithm of the average style lengths in *M. jalapa*, *M. longiflora*, F_1, and F_2

and in the F_2 hybrids is somewhat smaller in the case of the length of styles than of the flower tubes.

3. Length of the lobe of the corolla

The lobes were measured from the point at which the flower tubes began to expand suddenly (fig. 4 b).

So far as the length of the lobe is concerned *M. jalapa* and *M. longiflora* differ only slightly. On the average the lobes in *M. longiflora* are somewhat shorter.

The lobes of ten flowers in each of nine *M. jalapa* plants were measured and the average lengths for the particular plants ranged 19.50 to 24.00 mm. The average length of the lobe for all the nine plants was 22.06 mm.

The average lengths of lobes in five *M. longiflora* plants ranged 17.30 to 20.90 mm. The average length of lobes of all the five plants was 19.30 mm.

The average length of lobes of 100 flowers in the F_1 plant was 23.50 mm.

In the F_2 generation the lobes were measured in 252 plants, in ten

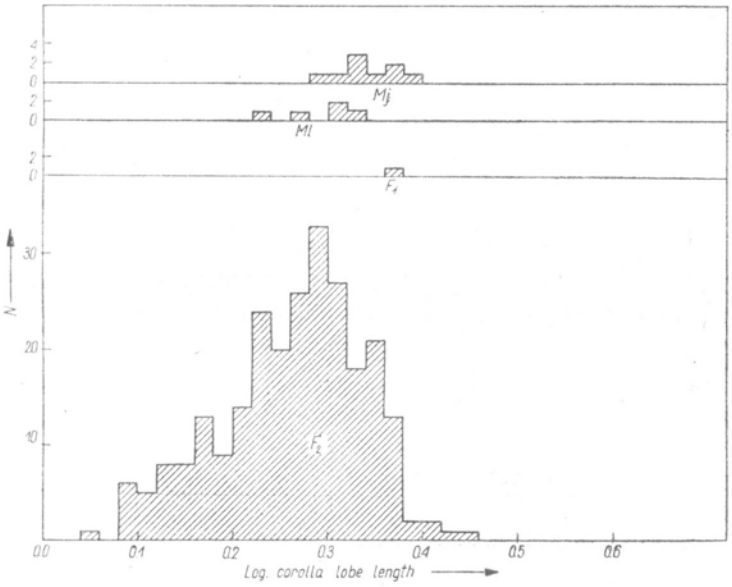

Fig. 8. Frequency histogram of the logarithm of the average lengths of the corolla lobes in *M. jalapa, M. longiflora,* F_1, and F_2

flowers on each. The average length of lobes for the particular plants ranged 11.10 to 28.00 mm. This means that the variation in F_2 extends somewhat beyond the variation in the two parental species.

The variation ranges of the lobe length in the parental species and the hybrids are illustrated by the logarithmic graph in fig. 8.

4. Width of the lobe of the corolla

The difference between *M. jalapa* and *M. longiflora* in the width of the lobes is well marked.

The average widths of the lobes of ten flowers in each of nine *M. jalapa* plants ranged 21.40 to 26.60 mm.

The corresponding average values for the lobes of the flowers in five *M. longiflora* plants were 15.00 and 17.50 mm.

The average width of lobes of 100 flowers in the F_1 plant was 18.00 mm.

In the F_2 generation the width of lobes was measured in 252 plants, in ten flowers on each. The average width in the particular plants ranged 9.20 to 23.00 mm.

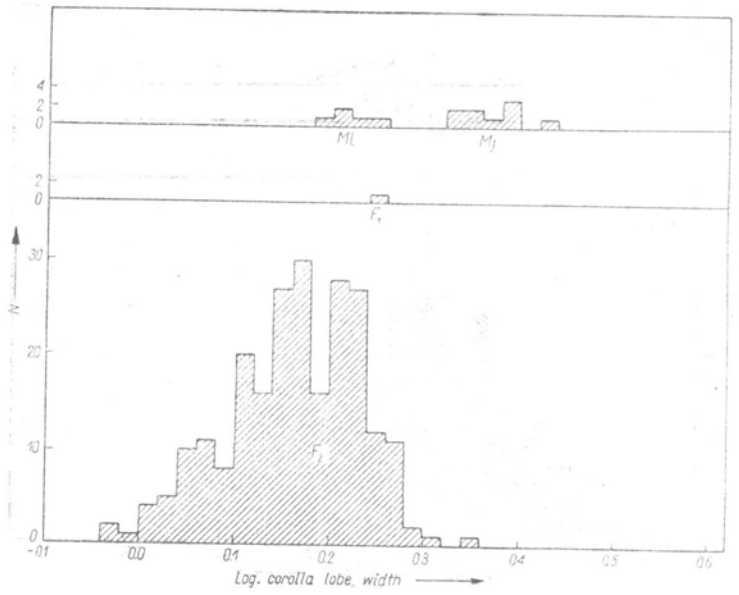

Fig. 9. Frequency histogram of the logarithm of the average widths of the corolla lobes in *M. jalapa*, *M. longiflora*, F_1, and F_2

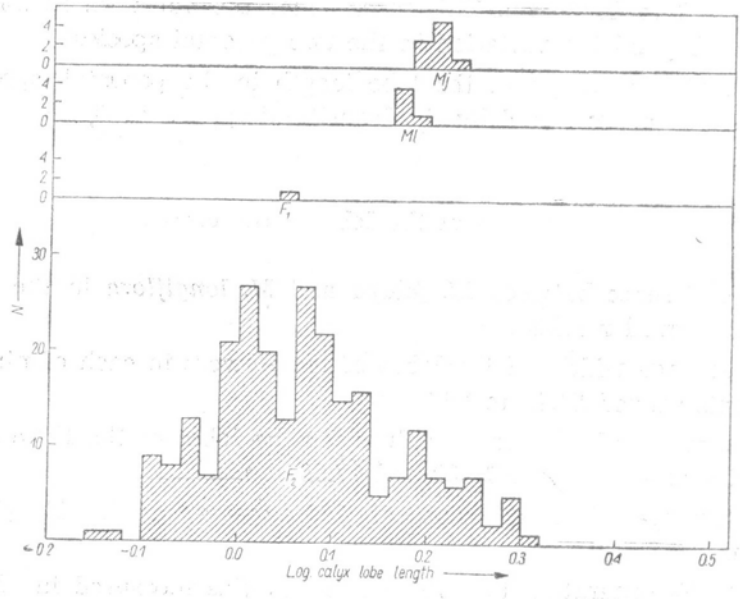

Fig. 10. Frequency histogram of the logarithm of the average lengths of the calyx lobes in *M. jalapa*, *M. longiflora*, F_1, and F_2

These values indicate a certain degree of transgression beyond the values of *M. longiflora*. The transgression is clearly visible on the logarithmic graph in fig. 9.

5. Length of the lobe of the calyx

(Morphologically this is not the true calyx but calyx-like bractlets)

The difference between the lengths of the lobes of the calyx in the two parental species is small.

Table 2 shows the variation of this trait in *M. jalapa*, *M. longiflora*, F_1 and F_2.

The well marked transgression in the F_2 generation proves that the length of the lobes of the calyx is controlled by many polymerous genes. The transgression in F_2 with regard to both parental species especially visible on the side of *M. longiflora*, is also reflected by the graph showing the range of variation of this trait on the logarithmic scale (Fig. 10).

6. Width of the lobe of the calyx

Although the difference in the lengths of lobes between *M. jalapa* and *M. longiflora* is small the two species distinctly differ by the width of the lobes. In *M. jalapa* they are much wider than in *M. longiflora*.

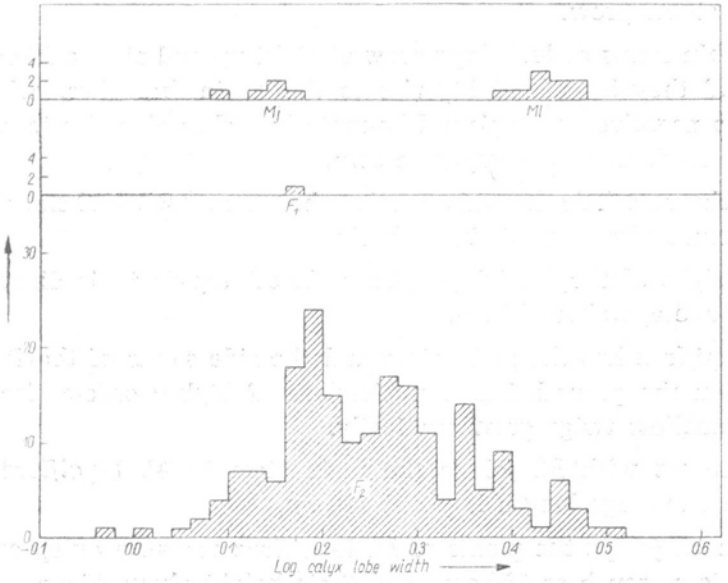

Fig. 11. Frequency histogram of the logarithm of the average widths of the calyx lobes in *M. jalapa*, *M. longiflora*, F_1, and F_2

Err.: The signes Mj and Ml on the fig. 11 should be interchaned.

In order to obtain greater values the widths of all the lobes in each flower were added up and the average total width of the lobes in five flowers, i.e. the average circumference of the calyx of five flowers, of every plant was compared.

The average circumference of the calyx in nine *M. jalapa* plants ranged 24.2 to 31.2 mm. and in five *M. longiflora* plants 13.0 to 15.0 mm.

The analogical average for 20 flowers of the F_1 plant was 14.8 mm. The average circumferences of the calyx of 198 F_2 plants ranged 9.3 to 32.2 mm.

The graph in fig. 11 shows these values on the logarithmic scale.

7. Growth habit

M. jalapa and *M. longiflora* strikingly differ in their growth habits. These differences consist in the direction of growth of the main stem, the direction of the main branchings, the number and the thickness of the main branches, the number of nodes, and the length of internodes.

The most important of these traits is the direction in which stems grow and that trait was studied in greater detail. Further on in this paper when referring to the growth habit I am thinking only of the direction in which stems grow.

The main stems of *M. jalapa* grow straight up and at 2 to 10 cm. above the ground they branch giving rise to the main branches, which also manifest a negative geotropism. The main branches give rise to numerous ramifications forming a compact crown.

It is characteristic for this species that above 2 to 10 cm. the main stem becomes almost undistinguishable.

The height of the *M. jalapa* plants almost equals their diameter and is on the average about 70 cm.

M. longiflora has the main stem and the side stems of the first order creeping on the ground. The ramifications of higher orders rise slightly and the smallest twigs grow vertically.

In contrast with *M. jalapa* the main stem in *M. longiflora* is very distinct. Its average length is about 120 cm.

Unlike *M. jalapa* the plants of *M. longiflora* are very outspread. Their diameter is as much as 150 cm., and their height about 40 cm.

The F_1 plant is very vigorous. Its growth habit is semi-prostrate resembling more *M. longiflora* than *M. jalapa*. Most main branches lie on the ground but some of them rise sligthly.

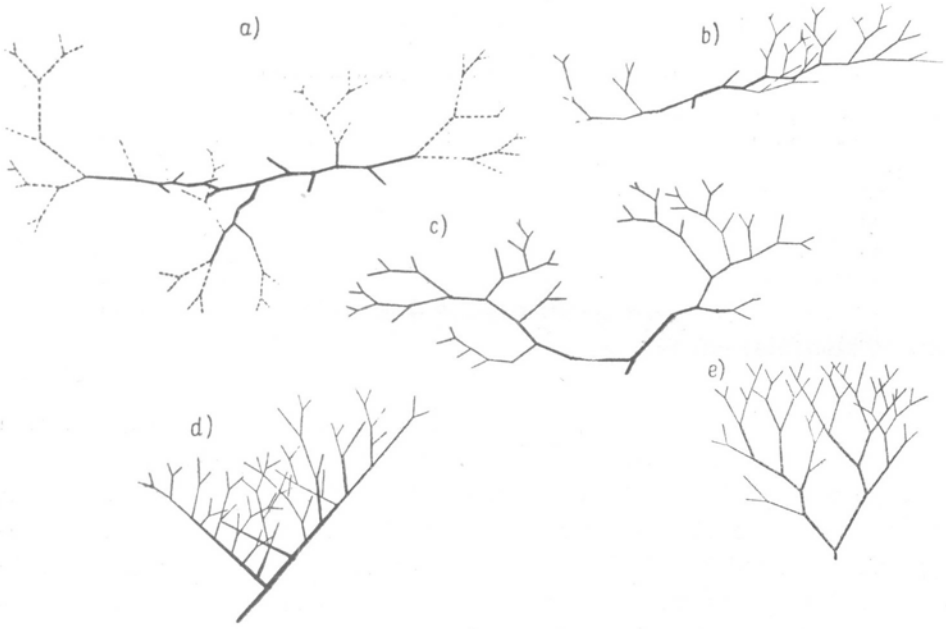

Fig. 12. Schematic diagram of the growth habits in the F_2 generation of the hybrid *M. jalapa* × *M. longiflora*. *a* — Growth habit of type I F_2 plants and of *M. longiflora*; *b* — Growth habit of type type II F_2 plants and of the F_1 plant; *c* — Growth habit of type III F_2 plants; *d* — Growth habit of type IV F_2 plants; *e* — Growth habit of type V F_2 plants and of *M. jalapa*

In the F_2 generation of 274 individuals the following types of growth habits were distinguished (Fig. 12):

I. Growth habit as in *M. longiflora*.
II. Growth habit semi-prostrate, resembling *M. longiflora*, more or less as in the F_1 plant.
III. Growth habit intermediate.
IV. Growth habit approaching *M. jalapa*, the main stem not vertically upright as in *M. jalapa* but usually a little slanting.
V. Growth habit as in *M. jalapa*.

The numbers of plants in the particular classes are listed in table 3. The mutual ratio of the numbers in the particular classes is approximately 3 : 6 : 4 : 2 : 1.

The deviations of this ratio from the theoretical values are very small. The values of X^2 is 1.00, which for four degrees of freedom makes the value p between 90 and 95 per cent.

The segregation as shown by the ratio stated above leads to the conclusion that the trait of the growth habit is determined by two indepen-

Table 3

The inheritance of the growth habit

Class values	I	II	III	IV	V	N
M. j.					+	
M. l.	+					
F_1		1				
F_2 Observed	49	97	74	36	18	274
Expected	51.4	102.8	68.5	34.2	17.1	274
Ratio	3	6	4	2	1	

dent pairs af alleles. The genes *A* and *B* determine the prostrate growth habit, whereas their alleles *a* and *b* determine the upright growth habit. The gene *B* of the prostrate growth habit is dominant over the gene *b*, but neither gene of the other pair is dominant over its allele. Consequently *M. longiflora* is homozygous with regard to both the prostrate growth habit genes and its genotype is *AABB*, whereas *M. jalapa* is homozygous with regard to both the upright growth habit genes and has the genotype *aabb*. The F_1 hybrid is a double heterozygote with the genotype *AaBb*.

The F_2 plants with the prostrate growth habit (type I) as in *M. longiflora* are, thus, homozygous with regard to the gene *A* and homozygous or heterozygous with regard to the gene *B*, since the gene *b* would not manifest itself phenotypically in the presence of gene *B*.

The F_2 plants with the semi-prostrate growth habit (type II) have the gene *A*, the gene *a* manifesting itself phenotypically, and the gene *B* in the homozygous or heterozygous state.

The F_2 plants with the intermediate growth habit (type III) may have the genes *A* and *b* or the genes *a* and *B* in the homozygous state or they may be homozygous with regard to the gene *a* and heterozygous with regard to the gene *B*.

The plants with a growth habit similar to *M. jalapa* (type IV) have only one gene of the prostrate growth habit. It is not the gene *B* since owing to its being dominant over the gene *b* the effect would be the same as if there were two genes of the prostrate growth habit. These plants are heterozygous with regard to gene *A* and homozygous with regard to gene *b*.

The F_2 plants with the upright growth habit as in *M. jalapa* (type V) have genes *a* and *b* in the homozygous state.

The genotype formulae and relations corresponding to the classes of growth habits distinguished in F_2 are, therefore, the following:

I. 1 *AABB*, 2 *AABb*

II. 2 *AaBB*, 4 *AaBb*

III. 1 *AAbb*, 1 *aaBB*, 2 *aaBb*

IV. 2 *Aabb*

V. 1 *aabb*

The other differences in the growth habit, such as the number of nodes, the length of internodes, and the number and the thickness of side stems, are not sufficiently distinct for a detailed anylysis.

8. Morphology of leaves

The leaves of *M. jalapa* and *M. longiflora* are strikingly different. However, the difference results from the summing of many, more or less independent minor traits difficult to define.

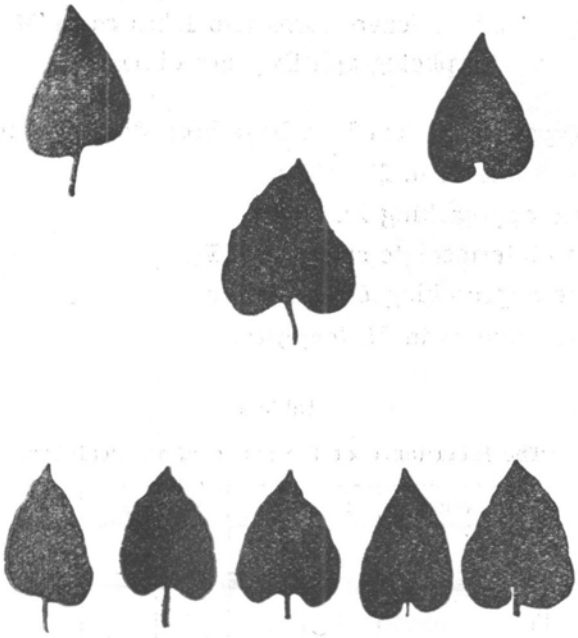

Fig. 13. Protograph showing the shapes of the leaf base in *M. jalapa*, *M. longiflora*, F_1, and F_2. Top row: left *M. jalapa*, right *M. logiflora*, in the middle a leaf of the F_1 plant. Bottom row: leaves of F_2 plants

These differences are:

Mirabilis jalapa	*Mirabilis longiflora*
1. Base of leaf obtuse.	1. Base of leaf cordate.
2. Base of leaf usually oblique.	2. Base of leaf symmetrical.
3. Venation pinnate usually asymmetrical at base.	3. Venation pinnate usually symmetrical at base.
4. The tapering of leaves not gradual, at first slow then sudden.	4. The tapering of leaves gradual.
5. Leaf tip sharply acute.	5. Leaf tip not sharply acute.

There are, moreover, some differences in the size of leaves, the length of petioles, the length to width ratio, and the kind and the distribution of the pubescence. The last mentioned trait will be discussed further on (page 630).

The difference in the shape of the leaf base is rather pronounced (Fig. 13).

The F_1 plant has leaves with the base shaped intermediately between the parental species. The leaves have two lobes as in *M. longiflora*, but as is to be seen on the photograph they are different.

In F_2 five types of the leaf base have been discriminated:

1. Leaf base same as in *M. jalapa*.
2. Leaf base approaching *M. jalapa*.
3. Leaf base intermediate same as in F_1.
4. Leaf base approaching *M. longiflora*.
5. Leaf base same as in *M. longiflora*.

Table 4

The inheritance of the shape of the leaf base

Class values	I	II	III	IV	V
M.j.	+				
M.l.					+
F_1			1		
F_2	39	55	41	54	55

However, these classes have been discriminated artificially and probably the variation in F_2 actually is continuous.

The more accurate analysis of the manner in which the shape of the leaf base is inherited has been made impossible by the great phenotypical variation, so that in one plant there could be simultaneously leaves with the base shaped according to two, three, or even four of the discriminated types.

Moreover, in various years the same plant could be classified according to the shape of its leaf base to different, though not extremely different, classes, which proves how strongly the shape of the leaf base fluctuated.

The symmetry or the asymmetry of the leaf base is not related with its shape.

The manner in which the leaf blade tapers off is very difficult to define, but probably is not strictly related with the shape of the leaf base.

M. jalapa has larger leaves than *M. longiflora*. In ten *M. jalapa* plants the average length of the leaves from the seventh internode ranged

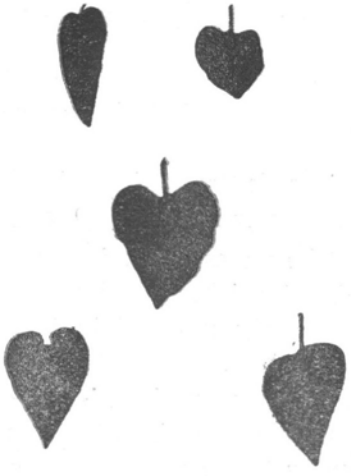

Fig. 14. Photograph showing the leaves in *M. jalapa* (top. left), *M. longiflora* (top right), F_1 (middle), and the extreme forms in F_2 (bottom row)

89 to 138 mm. The analogical averages in five *M. longiflora* plants ranged 65 to 83 mm. In the F_1 plant the average length of leaves was 81 mm. The corresponding values for the F_2 plants were 36 to 123 mm.

The petioles are much longer in *M. jalapa* than in *M. longiflora*. The average length of petioles in the former species was ± 20 mm. and in the latter ± 1 mm.

The F_1 plant has petioles of the same length as in *M. jalapa*, whereas in the F_2 generation there were plants with petioles as long as in *M. jalapa* and of the intermediate lengths, but no plants with petioles as short as in *M. longiflora*.

The leaves of *M. jalapa* and *M. longiflora* also differ in the width to length ratio.

In *M. jalapa* the ratio is somewhat lower and for the particular leaves varied within the range 0.450 to 0.750 and in *M. longiflora* within the range 0.650 to 0.900. The corresponding values in the F_1 plant were 0.650 to 0.800.

In the F_2 generation the variation is in a continuous series ranging from one parental species to the other. There are, moreover some plants with leaves much narrower than in *M. jalapa* and wider than in *M. longiflora.*

In the plants with the narrowest leaves the width to length ratio was 0.410 and in those with the widest leaves it was 1.071. Fig. 14 shows leaves of the F_2 plants with the narrowest and the widest leaves (bottom row), a leaf of the F_1 plant (middle row), and one leaf from each of the parental species (top row).

All the details here described show that the morphological differences between the leaves of the two species are very complex. The variations of these traits fluctuate very strongly and the traits are, therefore, unssuitable for a detailed analysis.

9. Pubescence on stems, leaves, and flowers

The degree and the kind of pubescence on the stems, the leaves, and the flowers in *M. jalapa* and *M. longiflora* are very different.

The stems of *M. jalapa* are covered with short, downy, almost appressed hairs. The distribution of the pubescence is not uniform. The hairs are mainly grouped in two strips stretching along the stem on its opposite sides.

The average length of hairs ranges 300 to 800 μ. In the dense strips of pubescence the distances between the hairs in the lengthwise rows usually is from 100 to 300 μ. The analogical distances in the parts with less dense hairs are 600 to 2000 μ.

The hairs in *M. jalapa* and the manner in which they grow on the stems are shown in fig. 15 a.

The stems of *M. longiflora* are covered by uniformly distributed, upright glandular hairs.

The length of these hairs is usually from 150 to 900 μ. The distances between the hairs in the lengthwise rows average at 100 to 500 μ.

Owing to the large number of the glandular hairs the stems of *M. longiflora* are distinctly sticky. Among the glandular hairs ending with the spherical secreting cell there are occasionally some non-glandular hairs ending with a long thin cell as in *M. jalapa* and other as if intermediate hairs ending with slightly swollen club-like cells.

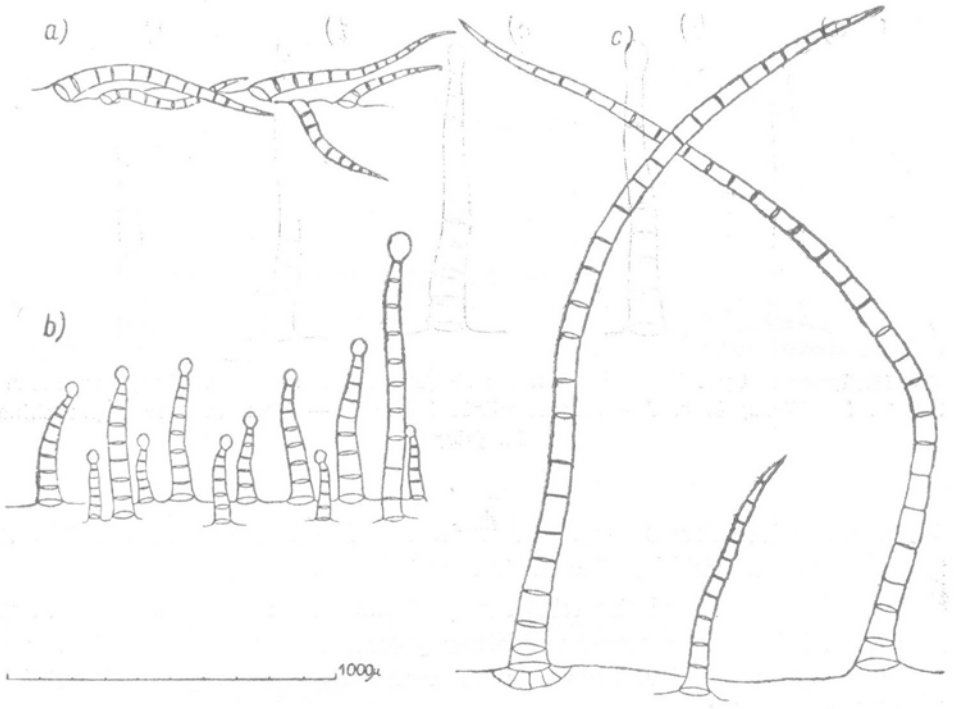

Fig. 15. The size, the shape, and the position of hairs on stems. *a* — *M. jalapa*; *b* — *M. longiflora*; *c* — One of the F_2 plants

The glandular hairs of *M. longiflora* and their arrangement on the stem is shown in fig. 15 b.

In the F_1 hybrid the distribution of pubescence on the stems is not uniform. Most of the hairs are grouped as in *M. jalapa* in two opposite strips. However, the difference between the density of hairs in the denser strips and the other parts of the stem is not as great as in *M. jalapa*. The hairs are not glandular but less appressed than in *M. jalapa*.

The length of hairs is usually from 150 to 800 µ. Some hairs are longer, up to 1200 µ long, and upright. Occasionally there are hairs with a swollen end cell.

In the F_2 hybrids the pubescence on the stems is very varied. There are individuals with hairs distributed as in *M. jalapa* and others with the hairs as uniformly distributed as in *M. longiflora*, as well as the full series of intermediate distributions. The pubescence could be appressed as in *M. jalapa* upright as in *M. longiflora*, and of many intermediate types. The cell at the end of hairs also are of various kinds: there are cells sharply tapering as in *M. jalapa* (Fig. 16 e), swollen and almost as spherical as the cells of the glandular hairs in *M. longiflora* (Fig. 16 a), or of all

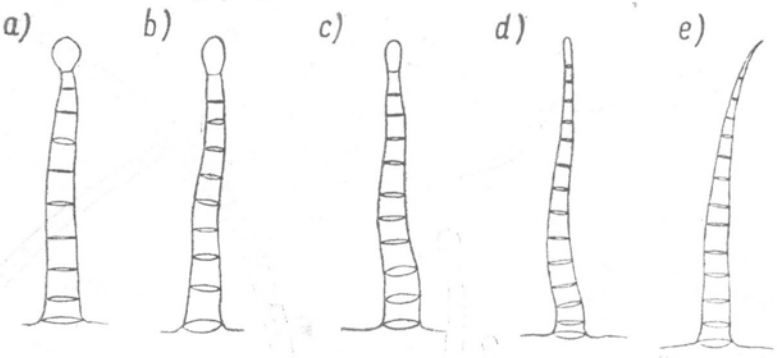

Fig. 16. Types of tip cells of hairs in the F_2 generation. *a* — Hair of type approaching *M. longiflora; b, c, d* — Intermediate hairs; *e* — Hair of type approaching *M. jalapa*

the intermediate forms (Fig. 16 b, c, d). The hairs of all these different types may occur side by side on the same plant.

However, even the hairs with the most rounded cells at the tip are not glandular, because the stems and other organs having this kind of pubescence are never sticky. This circumstance was already pointed out by Prakken (1944).

The absence of secreting cells at the tips of hairs leads to the conclusion that the type of pubescence characteristic for *M. longiflora* is not segregated in the F_2 generation, though among the 150 examined individuals there were 20 with hairs of a similar kind and similarly distributed as in *M. jalapa*. In 26 other individuals the stems were uniformly covered with hairs. Very often a stem was covered with two kinds of pubescence: upright bristly hairs covered more or less uniformly the whole stem, whereas the appressed, shorter, downy hairs were mainly grouped in two opposite strips.

In the plants of the F_2 generation the pubescence on the stems often was less dense and longer than in the parental species. An extreme example of this kind of pubescence was supplied by the plant in which the length of the longest hairs ranged 700 to 3000 μ. The longest hairs of this plant were about four times longer than the hairs in either *M. jalapa* or *M. longiflora* (Fig. 15 c).

The pubescence of leaves in both parental species shows similar differences concerning distribution, morphological characters of different kinds of hairs and position of hairs on the surface of the blade.

In F_1 the distribution of the hairs is similar to that in *M. jalapa* and other traits are more or less intermediate.

In F_2 a distinct segregation was observed but in any plant the type of

appressed hairs typical for *M. jalapa* was found. Also the giandular type of hairs of *M. longiflora* was not reconstructed.

The type of pubescence on floral tubes was in parental species, F_1 and F_2 hybrids more or less similar to that described for the stems. However, the pubescence of the calyx and its inheritance was almost the same as in the case of leaves.

10. Colour of stems

In *M. longiflora* the main and the secondary stems have green internodes and reddish nodes. The reddish colour of the nodes is caused by anthocyanin in the epidermal cells and also in some of the neighbouring collenchyma cells.

Anthocyanin present in the flowers of *M. longiflora* causes the pale pink-violet colour of the inside of the flower tubes and the red-violet ring at the point where the tube widens to form lobes.

The colour of the stems in *M. jalapa* differs in the particular varieties. The stems of the variety with white or yellow flowers are all green and contain no anthocyanin.

The stems of the variety with red or pink flowers have red nodes, usually more intensely red than the nodes in *M. longiflora*, and green often red-streaked internodes.

The hybrid of this investigation was obtained by crossing a *M. longiflora* plant with a *M. jalapa* plant of the red-flower variety. Thus, both parental plants have red nodes and green internodes.

The F_1 plant has stems with red nodes and distinctly pink-streaked internodes.

In the F_2 generation the plants with stems coloured in a similar way as in both parental plants predominated. However, there were also some plants with much more intensely coloured stems and others with stems coloured less intensely than in the parental plants.

Among 240 examined F_2 plants the following three degrees in the intensity of the red colour of stems were discriminated:

I. Plants with more or less the same colour of stems as in the parental plants $n = 118$.

II. Plants with stems less intensely coloured than in the parental plants, $n = 45$. This group included plants with:

a) nodes and internodes all green, $n = 2$, and

b) green-brown nodes and green internodes, $n = 43$.

III. Plants more intensely coloured than the parental plants, $n = 77$. This group included plants with:

a) the whole stems intensely red, $n = 15$,

b) stems all pink, n = 12, and

c) nodes and all internodes, except for the last three or four, red, n = 50.

The great phenotypic variability of this trait has made its detailed analysis difficult and the manner in which the trait is inherited is not discussed here.

11. Colour of flowers

The flowers in *M. longiflora* are white, except for the inside of the flower tube, which according to the Horticultural Colour Charts is cyclamen purple 30, and the ring the colour of which is orchid purple 31.

M. jalapa has flowers of different colours — yellow, red, or white.

The progeny obtained by crossing the varieties with differently coloured flowers often have flowers of very peculiar red or orange-red tones.

The *M. jalapa* plant used as the parental plant for the F_1 generation had red — magenta red 27 — flowers with the inside of the tube and the ring somewhat more violet in tone — i.e. rhodamine purple 29.

The colour of the flowers in the F_1 plant is mauve 633 with the inside of the tube and the ring cyclamen purple 30.

The segregation in F_2 was highly complicated. In all flowers independently of the colour of the lobes the colour of the inside of the tube and of the ring was cyclamen purple, rhodamine purple, or orchid purple.

The colours of the lobes were of different tones and different intensities.

An additional difficulty in the classification of flower colours was that in about 20 per cent of the F_2 plants the colour at the base of lobes was of a different shade than in the upper part of the lobes.

For the sake of simplicity in the descriptions of the colour of the lobes the difference in colour at the lobe base is here disregarded.

Among 153 examined F_2 plants not one with white lobes as in *M. longiflora* was found.

In only one plant the colour of the lobes was magenta 27, i.e. the same as in the parental *M. jalapa* plant.

The conclusion to be drawn from this result is that the colour of lobes is determined by more than two pairs of genes.

About 15/16 of the plants in the F_2 generation had violet-pink flowers with various proportions between these two colours. The flowers ranged from very distinctly violet as in the F_1 plant to almost pure pink or red with only small additions of violet tones. All these colours were of various intensities ranging from almost white to very dark.

About 1/16 of the F_2 plants had flowers of various colours without any violet tones. There were ten such plants and their colours were as follows:

magenta 27 (red)	1 plant
magenta rose 027 (dirty red)	6 plants
jasper red 18 / claret rose 21 (red-orange)	2 plants
crimson (warmer red than magenta) .	1 plant.

The occurrence of these colours in the F_2 generation can be explained by assuming as did Marryat (1909), that the colour of the lobes in *M. jalapa* is determined by two pairs of genes.

According to this supposition the *M. jalapa* plants with red flowers are heterozygous or homozygous with regard to the gene *R* responsible for the red colour and homozygous or heterozygous with regard to the gene *Y* responsible for the yellow colour. The red colour cannot appear without at least one gene *Y*, so that even when there are two *R* genes the colour of the flower is white as long as a *Y* gene is missing.

According to Marryat the genotype of *M. jalapa* can be as follows:
when the colour of flowers is magenta the genotype is *Y y R R*,
when the colour of flowers is crimson the genotype is *Y Y R R*,
when the colour of flowers is various shades of orange-red the genotype is *Y Y R r*,
when the colour of flowers is magenta rose the genotype is *Y y R r*.

The presence in the F_2 generation of plants with flowers of these colours indicates that the original F_1 plant must have in its genotype the gene *Y* of *M. jalapa*.

If the genotype of *M. longiflora* only has the same genes as the white variety of *M. jalapa*, then the above-mentioned types would have to be much more numerous and there also would have to be a large proportion of plants with yellow and white flowers. This would also leave unexplained the presence of violet tones not occurring in *M. jalapa*.

This circumstance makes it necessary to accept Prakken's assumption that *M. longiflora* has genes determining the violet colour of petals which cannot manifest themselves owing to the absence of colour intensity factors present in the genotype of *M. jalapa*.

The fact that all the plants without any violet tones in the colour of their flowers only amounted to 1/16 of the whole F_2 population leads to the conclusion that in the genotype of *M. longiflora* there are at least two independent pairs of genes V_1 V_1 and V_2 V_2, which confirms Prakken's supposition. These genes are not allelomorphic with regard to the previously mentioned genes of *M. jalapa*.

According to these assumptions the parental plants probably have the following genotypes:

M. jalapa	*M. longiflora*
$Y\ y\ R\ R\ v_1\ v_1\ v_2\ v_2$	$y\ y\ r\ r\ V_1\ V_1\ V_2\ V_2$

Moreover, the genotype of *M. jalapa* must contain various colour intensity factors $I_1\ I_1\ I_2\ I_2\ I_3\ I_3$. The presumable genotype of the F_1 plant is $Y\ y\ R\ r\ V_1\ v_1\ V_2\ v_2$, whereas the 1/16 of the F_2 plants without the violet tones in the flowers do not contain the V_1 and V_2 genes and have various combinations of the *Y* and *R* factors.

Probably there are many other genes responsible for the different shades of the lobe base or of the apical parts of the lobes and possible determining the lack of uniformity in the distribution of various pigments in the lobes. However, a detailed analysis of these factors would be extremely complicated and has not been considered.

12. Date of flowering

Under optimum conditions the two *Mirabilis* species of this investigation begin to flower almost simultaneously.

In various years *M. jalapa* begins to flower between the middle of July and the first days of August.

In 1959 ten *M. jalapa* plants flowered between July 17 and 23. In the much less sunny summer of 1960 these plants began flowering between July 31 and August 8.

In 1960 five plants of *M. longiflora* began flowering between August 5 and 10.

However, the difference in the date of flowering between the two species is so small only when the insolation is sufficient. *M. longiflora* is much more sensitive to the intensity of light.

The usual difference in the flowering date between the two species when they grow on a well shaded stand is about one month. Sometimes the *M. longiflora* plants do not flower at all, whereas the delay in the flowering of *M. jalapa* is only about two weeks.

In the further comparisons of the flowering dates only the optimum conditions have been considered.

The F_1 plant flowers approximately on the same date as *M. jalapa* and *M. longiflora.*

In 1960 the F_1 plant flowered on July 29. In the same year the first F_2 plants flowered on July 19 and the last on September 22.

Table 5

Dates at which the plants flowered

Class values	19 VII	25 VII	31 VII	6 VIII	12 VIII	18 VIII	24 VIII	30 VIII	5 IX	11 IX	17 IX	23 IX	N
M.j.			9	1									10
M.l.			1	4									5
F_1		1											1
F_2	5	9	14	41	38	15	9	3	6	3	9		152

Table 5 lists the number of plants flowering at different dates.

This table shows very clearly the great differences in the beginning of the flowering of various plants. These differences would be even greater if on the night of September 24 the temperature did not drop below —1 C so that most of the plants were frosted. In this way ten F_2 plants did not flower at all.

So great differences in the date of flowering of F_2 plants can not only be due to the large number of plants in this generation as compared to the numbers of the parental species.

13. Time of anthesis

The genus *Mirabilis* has one-day flowers opening in the afternoon and withering the same night.

Under the same environmental conditions the time of anthesis is different in the various species and varieties.

On any particular day the time of anthesis is influenced by various factors, such as the temperature, the insolation, air humidity etc. The influence of temperature on the time of anthesis is the strongest.

On cold days at the end of the summer the flowers open much later and in plants which even on warm days flower late in the day on cold days they often do not open at all.

On heavily clouded days the rate of anthesis also is retarded but clouds never stop the opening of flowers.

The flowers of *M. longiflora* open between $4^h15'$ and $5^h30'$ p.m. depending on the prevailing weather conditions.

The flowers of the white variety of *M. jalapa* open between 6 and $7^h30'$ p.m. and of the red variety even later, between $6^h30'$ and 8 p.m. (sometimes they do not open at all).

The flowers of the F_1 plant open between $5^h30'$ and $6^h30'$ p.m.

On any given day the differences between the time of anthesis in the

particular plants of *M. longiflora* or in the particular plants of the *M. jalapa* varieties are insignificant.

On the other hand, the time of anthesis in the particular plants of the F_2 generation on any given day differ strikingly. In the plants flowering earliest in the day the flowers open approximately at the same time as in the parental plant opening its flowers earliest, i.e. at the same time as *M. longiflora*. The last F_2 plants flower somewhat later than the late flowering parent, i.e. later than *M. jalapa*.

Observations indicate that the hour of anthesis in any given F_2 plant is not accidental. The F_2 plants flowering earliest on some one day also flower earliest on any other day and, similarly, the plants in which the flowers on one day open at an intermediate or late hour also flower at an intermediate or late hour on all other days.

Although the anthesis time of a particular plant is different on different days, there is a rather well established sequence in the flowering of the particular plants of the F_2 generation which persists from day to day.

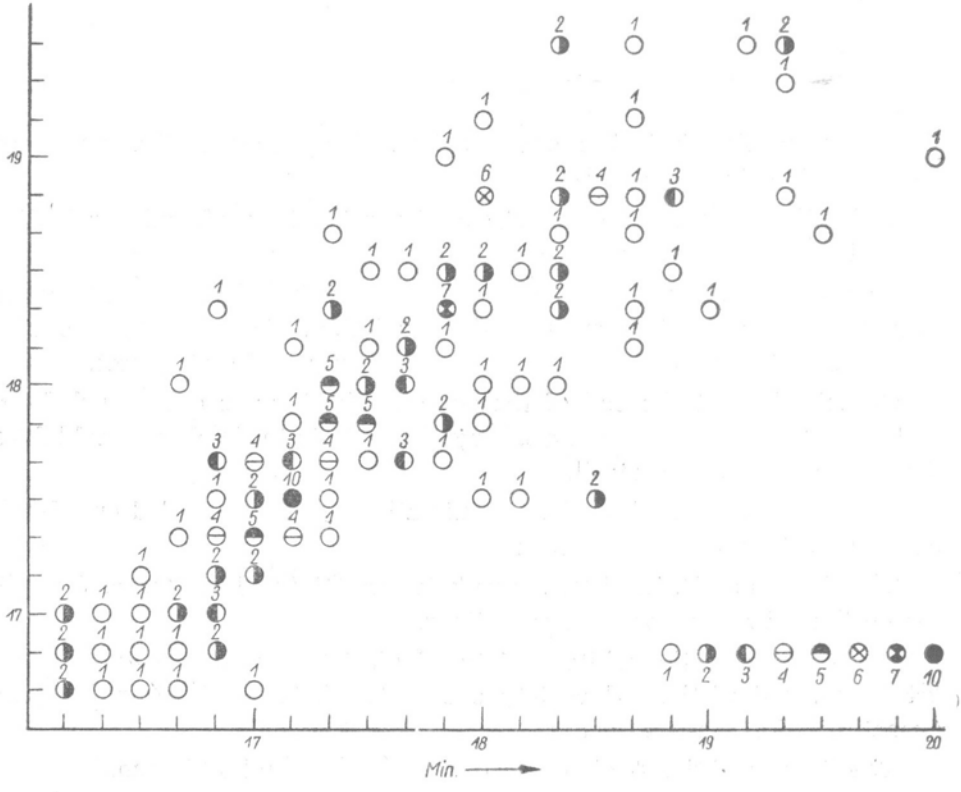

Fig. 17. Relation between the times of anthesis in F_2 plants on two different days

Since the time of the day at which the flowers open depends on many factors, the differences in the sequence of the opening of flowers among the plants of the F_2 generation increase with any increase of the number of factors by which one day differs from another.

Fig. 17 shows the relationship between the recorded times of anthesis of F_2 plants on two days with a similar insolation which differed markedly only in the prevailing temperatures. The maximum temperature was 26°C on September 20 and 23°C on September 21. The points on the graph in fig. 17 represent the particular plants. The position of the points with regard to the x-axis corresponds to the time of the day at which the flowers of a plant opened on September 20 and their position with regard to the y-axis corresponds to the time on which the flowers opened on September 21. The distribution of the points on the graph is ordered which proves that the time of the day at which the plants of the F_2 generation flowered was not accidental.

The differences in the time of anthesis might have been caused by various environmental conditions in the different parts of the experimental plot. However, this does not seem to be the case, since in seven *M. jalapa* plants of the red variety distributed at random over the whole field among the F_2 plants the flowers opened almost simultaneously.

It seems, therefore, that the time of anthesis is determined genetically and that this trait is inherited in a similar way as any other quantitative trait.

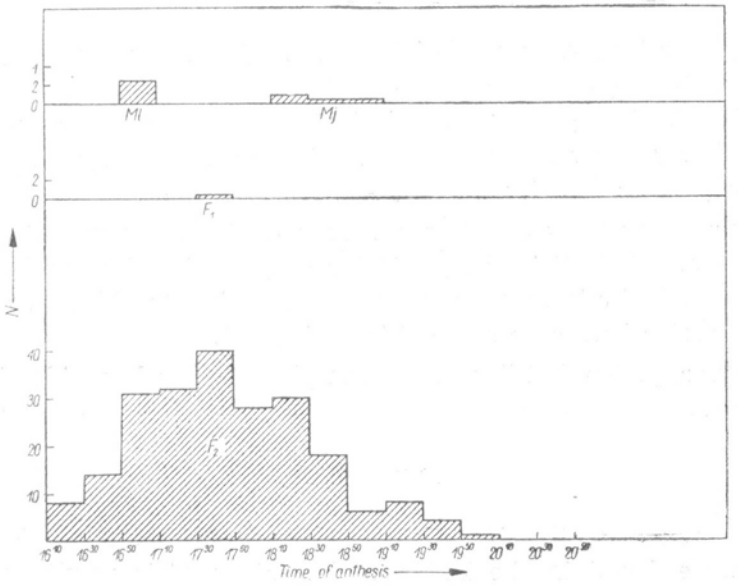

Fig. 18. Frequency histogram of the average time of the day at which anthesis occurs in *M. jalapa*, *M. longiflora*, F_1, and F_2

The numbers of plants flowering at intervals of ten minutes on September 20, 1960, are shown in fig. 18. As is to be seen the frequency distribution in this graph is essentially similar to the other graphs illustrating the distribution of the other quantitative traits.

14. Pollen fertility

The pollen fertility in *M. jalapa* is normal ranging in the plants from 87 to 96 per cent, average 91 per cent.

In *M. longiflora* the pollen fertility is reduced and ranges in the five examined plants between 64 and 87 per cent, average 71 per cent.

The pollen fertility in the F_1 plant is 16 per cent, whereas in 195 examined F_2 plants it ranges between 1 and 82 per cent. The results of the pollen fertility counts are listed in Table 6.

Table 6

Pollen fertility in percents

Class values	0	10	20	30	40	50	60	70	80	90	100	N
M.j.								6	4			10
M.l.							3	1	1			5
F_1		1										1
F_2	28	61	42	20	20	11	4	8	1	0		195

The greatest number of F_2 plants are in the same class of pollen fertility as the F_1 plant. In 54 per cent of F_2 plants pollen fertility was higher than in the F_1 plant and only in 14 per cent of plants pollen fertility was lower. Only in one plant, i.e. in about 0.5 per cent of the F_2 population, pollen fertility was more than 80 per cent.

The pollen fertility counts were very difficult because of the great variability of this trait in the particular flowers of a plant with similarly developed and similarly coloured anthers. Owing to this large number of pollen grains had to be counted in each plant.

Moreover, pollen fertility of a given plant differed considerably from year to year.

DISCUSSION

In the course of this investigation distrubances of the reduction divisions were found in the PMCs of *M. jalapa*. This result contradicts Prakken's report about the regular course of meiosis in both *M. jalapa* and *M. longiflora*.

However, it seems that in the F_1 plant disturbances of meiosis are more frequent than in *M. jalapa*. This again contradicts the results obtained by Showalter who found that the percentage of disturbed meioses in the F_1 hybrid was approximately the same as in the parental species.

The rather frequent disturbances of microsporogenesis in the F_1 plant are however insufficient to explain the very low pollen fertility in this plant. It seems that besides the visible chromosome disturbances the pollen sterility must also be caused by gene sterility or cryptic structural hybridity.

One point already emphasized by Schowalter must be stressed here. The anthers in the flowers of the F_1 hybrid produce much less pollen than in the parental species, owing to the degeneration of PMCs beginning before meiosis, which must be caused by gene sterility.

In the F_2 generation there is a certain increase in the pollen fertility as compared to F_1, which is reflected by that 54 per cent of the F_2 plants have a pollen fertility higher than in F_1 and only in 14 per cent of plants pollen fertility is lower than in F_1.

The higher fertility of gametes in F_2 is a rather frequent phenomenon. It is reported by e.g. Clausen in the genus *Viola* (1926, 1930), Müntzing in the cross *Galeopsis tetrahit* × *G. bifida* (1930), and Anderson in the cross *Nicotiana langsdorffii* × *N. alata* (1936). According to those authors the higher pollen fertility in F_2 is caused by the segregation of some factors responsible for the sterility of gametes in the heterozygous condition only.

However, as compared with the parental species the pollen fertility of the F_2 plants is very much reduced.

The very low setting of seeds in the F_1 and F_2 generations does not seem to be caused by the reduced pollen fertility, though this often is the case in other interspecific hybrids, e.g. in the cross *Aquilegia vulgaris* × × *A. ecalcarata* (Prażmo 1960). Out of nine plants in the F_2 generation with pollen fertility of more than 70 per cent five did not set seeds at all and four developed one to five seeds.

The plant on which 34 well developed seeds were collected — this was the highest number of well developed seeds collected on any one of the F_2 plants — only had 24 per cent of good pollen grains. Unfortunately, owing to great technical difficulties the exact correlation between the setting of seeds and pollen fertility has not been calculated.

There are very good reasons to suppose that the factors determining the length of styles are to some extent independent of the factors responsible for the length of the pollen tube. If this was the case, a certain number of F_2 plants with very long styles would produce disproportionately short pollen tubes. Then the failure in the setting of seeds in such plants

would be primarily caused by the pollen tubes not reaching to the ovules, thus making fertilization impossible. This probably is the reason why all attempts at the cross *M. longiflora* ♀ × *M. jalapa* ♂ always fail. However, this does not seem to be of significance, since on the whole the F_2 plants with short styles do not set more seeds than the plants with long styles, as they would if the low rate in the setting of seeds in the F_2 generation was primarily caused by the too short pollen tubes.

A low seed fertility in the F_1 and F_2 generations is very common in similar interspecific crosses. The hybrid *M. jalapa* × *M. longiflora* resembles under many regards other hybrids of this kind.

Very characteristic is the polymerous segregation of quantitative traits — e.g. the flower tube length, the style length, the length and the width of lobes etc. — and the Mendelian segregation of other traits — e.g. the colour of flowers, the growth habit. However, the inheritance of the flower tube length is rather unusual. Although in F_2 the variation of the tube length has the normal frequency distribution the curve is shifted towards one of the parental species so that the variation in F_2 includes the variation in *M. jalapa* but does not extend to *M. longiflora*.

This deviates from the normal variation for which there usually are only two alternatives: either in the F_2 generation there are in approximately equal numbers individuals having the particular quantitative trait developed in the extreme forms as in the parental species (e.g. plants with flower tubes as short as in *M. jalapa* or as long as in *M. longiflora*), or the F_2 plants resemble with regard to the trait in question neither parental species.

Inheritance is according to the latter alternative when a given trait is determined by a very large number of polymerous factors. Then the probability that individuals with the trait expressed in the extreme form will appear is so small as to become practically an impossibility.

In experiments with the genus *Nicotiana* Smith (1937) crossed species which differed, similarly as the *Mirabilis* species, in the length of flower tubes. The average length of the short tubes in *Nicotiana langsdorffii* was about 18 mm., whereas the average length of the much longer tubes in *Nicotiana Sanderae* is about 70 mm. In the F_1 generation the length of the flower tubes was intermediate and in the F_2 generation the variation exceeded the variation in F_1, but extended to neither of the two possibilities represented by the parentals species. The length of the flower tubes was 23 mm. in the F_2 plant with the shortest tubes and 55 mm. in the plant with the longest tubes. This is the simplest example of inheritance dependent on a large number of polymerous genes.

The supposition may be advanced that, in view of the very low

pollen and seed fertility in the F_1 plant, the unusual manner in which the length of the flower tube was inherited in the cross *M. jalapa* × *M. langiflora* is caused by that some genotypes are not eliminated at random. However, the improbability of this kind of elimination is demonstrated by the normal segregation of most other traits in the F_2 generation, in particular by the almost ideal segregation of the various types of the growth habit.

The absence in the F_2 generation of the cross *M. jalapa* × *M. longiflora* of plants with long flower tubes of the *M. longiflora* type may have various causes.

One highly probable explanation is that it is simply the result of cytoplasmic heredity, since *M. jalapa* was here the maternal plant. Unfortunately the supposition can only be checked by measurements of the flower tube lengths in the second generation of the reciprocal cross. This, however, is very difficult, if not impossible, since in spite of repeated attempts by many workers such crosses have never been successful.

This explanation for the abnormal variation of the flower tube length in the F_2 generation has been advanced by P r a k k e n who also thought it highly probable that the absence of plants with long flower tubes of extreme lengths was caused by the large number of polymerous factors determining this trait. However, this opinion does not seem to be justified, since when the numerous polymerous factors are assumed it is impossible to explain the presence of plants with the short flower tubes similar to the flower tubes in *M. jalapa*.

The most plausible explanation of this phenomenon seems to be the presence in the genotype of *Mirabilis jalapa* of inhibitors caunteracting the factors responsible for the elongation of the flower tube in *M. longiflora*.

Let us assume that the difference between the length of flower tubes in *M. jalapa* and in *M. longiflora* is determined by a certain number of independent loci and let there be three such loci.

Let us assume, moreover, that *M. jalapa* is homozygous with regard to the genes $l_1\ l_2\ l_3$, whereas *M. longiflora* is homozygous with regard to their alleles $L_1\ L_2\ L_3$.

The genes represented by the small letters have no influence on the lengthening of the flower tube, whereas each of the alleles represented by the capitals increases the length of the flower tube adding to it some fixed amount or multiplying it by some fixed factor.

Besides the genes just mentioned let us assume that in the genotype of *M. jalapa* there are the inhibitors $I_1\ I_2\ I_3$. Then the genotype of *M. jalapa* would be $l_1\ l_1\ l_2\ l_2\ l_3\ l_3\ I_1\ I_1\ I_2\ I_2\ I_3\ I_3$ and the genotype of *M. longiflora* $L_1\ L_1\ L_2\ L_2\ L_3\ L_3\ i_1\ i_1\ i_2\ i_2\ i_3\ i_3$.

Finally let us assume that when *M. jalapa* is crossed with *M. longiflora* each of the inhibitor genes acts so as to prevent the manifestation of the effects of any of the two pairs of genes L_1 and L_2. Each of the inhibitors can also inhibit all these four genes simultaneously. However, the inhibitors do not affect the third pair of genes $L_3\,L_3$. The genotype of the F_1 generation would then be $L_1\,l_1\,L_2\,l_2\,L_3\,l_3\,I_1\,i_1\,I_2\,i_2\,I_3\,i_3$.

Thus the flower tubes in the F_1 generation would be longer than the average tubes in *M. jalapa* and shorter than the arithmetic mean or the geometric mean length of tubes in the two parental species.

The plants with flower tubes as short as in *M. jalapa* would then constitute $\frac{1009}{4096}$ of all the plants in the F_2 generation. These would be those plants homozygous for l_3 do not have at the same time any L_1 or L_2 genes together with i_1, i_2, i_3 in homozygous condition.

The plants with flower tubes as long as in *M. longiflora* can have none of the $l_1\,l_2\,l_3$ and of the $I_1\,I_2\,I_3$ genes and, according to the probability for six segregating genes, would constitute 1/4096 of the whole F_2 population. The probability that such a plant would appear in a population of the size obtained in this investigation is extremely small.

The probability of the occurrence in F_2 of plants with flower tubes much longer than in F_1 also is very small.

The plants with the longest flower tubes that can actually be found in the F_2 generation can have tubes not much longer than the tubes in F_1. Such plants would be homozygous with regard to the gene L_3 which is not affected by the inhibitors.

The model here described undoubtedly greatly simplifies the actually existing conditions, but it may reflect them more or less accurately.

In many interspecific and intervarietal crosses the presence in one group of genes inhibiting the effect of genes from the other group has often been observed. Such inhibitors were found e.g. by Clausen and Hiesey (1958) in crosses between two subspecies of *Potentilla glandulosa*. One of the subspecies used for the cross had incised petals, whereas the petals in the other subspecies were entire in the usual way. On the ground of an analysis of the F_1 generation and of the segregation in F_2 and F_3 Clausen and Hiesey reached the conclusion that this trait was controlled by at least three independent pairs of genes: one pair of genes *NN* causing incision and two pairs of incision inhibitors $I_1\,I_1$ *and* $I_2\,I_2$.

The plant with incised petals used for the cross contained no inhibitor genes and was homozygous with regard to the incision gene *N*, which in the absence of the inhibitors was dominant. The plant with entire petals contained no incision genes and was homozygous with regard to the genes I_1 and I_2.

In the cross described by Clausen and Hiesey the inhibition of the incision gene had different intensities according to the number of the inhibitors present in the genotype.

In the model here described the situation is different. The effect of one inhibitor is as strong as of all of them acting together.

There can also be other reasons for the untypical segregation of the flower tube length in the plants of the F_2 generation of the cross *M. jalapa* × *M. longiflora*.

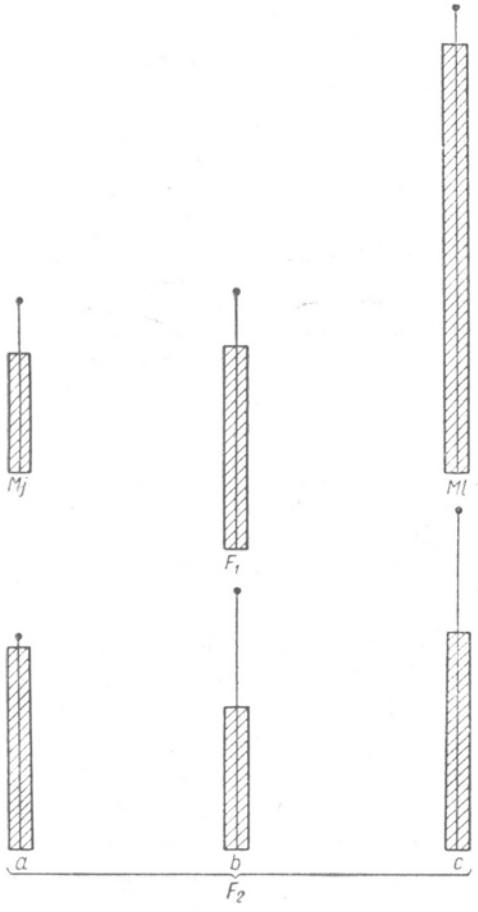

Fig. 19. Examples of plants having flowers with unadiusted flower tube and style lengths. *a* — Schematic diagram of a flower in a F_2 plant with the style too short as compared to the length of the flower tube; *b,c* — Schematic diagrams of flowers in F_2 plants with styles too long as compared to the length of the flower tubes. The flowers of *M. jalapa*, *M. longiflora* (top row), and the F_1 plant (middle row) are shown for comparison

Smith's (1937) work on the influence of an additional chromosome on the size of the corolla in *Nicotiana* has demonstrated that in the genotype of the species with the short flower tube there are also "factors elongating the tube", whereas in the genotype of the species with long flower tubes there are "factors of the short tube length".

The assumption that in the genotype of *M. longiflora* there are certain factors "of the short tube length" as well as recessive inhibitors corresponding to these factors in the homozygous state also explains the unusual segregation in F_2.

Another observation made in this investigation on the cross *M. jalapa* × *M. longiflora* is that, in spite of the correlation between the lengths of the flower tube and the style clearly marked for the F_2 generation as a whole, there also are in this generation single plants in which the length of the style is as if unadjusted to the length of the tube (Fig. 19).

In some instances there is a certain "unadjustment" between the length of the style and the length of stamens. In both parental species stigma is on average 2 to 10 mm above the anthers. However, in F_2 there are plants which have anthers on the same level as the stigma and even in a few plants the anthers are above the stigma.

The circumstance that such a physiological trait as the time of the day at which anthesis takes place is determined genetically also seems of significance. The genetical determination of this trait is indicated by the constant and approximately uniform differences in the time at which the flowers open in *M. jalapa* and *M. longiflora* as well as the essentially unchanging order in which anthesis occurs in the particular plants of the F_2 generation. The segregation with regard to this physiological trait is polymerous, similarly as in the case of other quantitative traits.

The stability of the time of the day at which the flowers open in the various *Mirabilis* species has long attracted attention and this peculiarity is even reflected in their popular name tour o'clock.

This investigation on the heredity of the specific traits in the cross *M. jalapa* × *M. longiflora* has shown that, in spite of the great morphological differences between the two species, especially striking in the case of the size of flowers, a genetic analysis is possible. The results reported here may serve as a contribution to the studies on the genetic principles underlying interspecific differences and on the speciation processes.

CONCLUSIONS

1. The haploidal chromosome number in the species *Mirabilis jalapa* and *M. longiflora* is $n = 29$.

Numerous PMCs were examined in *M. jalapa* and a few univalents were found.

2. In metaphase I of the hybrid *M. jalapa* × *M. longiflora* there are usually one or two pairs of univalents, though often there are 29 bivalents. Usually the two largest chromosomes of the *Mirabilis* karyotype fail to conjugate with each other.

3. The strongly reduced pollen fertility in the F_1 hybrid is about 16 per cent. The setting of seeds is also greatly reduced.

4. In spite of the very low fertility of the F_1 hybrid most of the traits characteristic for the parental species segregate regularly in F_2.

5. The majority of the investigated morphological traits — such as the lengths of the flower tube, the style, the lobes of the corolla and of the calyx, as well as the widths of the lobes — manifest a continuous, sometimes transgressive variation caused by the segregation of numerous polymerous factors.

6. The length of the style and the length of the flower tube are inherited in a way giving a continuous variation in the F_2 generation. The range of the variation includes *M. jalapa*, but does not extend to the variation of the other parental species only slightly exceeding on the side of *M. longiflora* the variation in F_1.

The pubescence is inherited in a similar manner.

7. One of the physiological traits — the time of the day at which anthesis occurs — also manifests a continuous variation in F_2. This proves that the trait is controlled by numerous polymerous factors.

8. Such traits as the colour of flowers and the growth habit of stems manifest the typical Mendelian segregation.

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