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CYTO-GENETICAL STUDIES OF THE CROSS BETWEEN THE SQUASH (*CUCURBITA MAXIMA*, DUCH.) AND PUMPKIN (*C. PEPO*, L.)

(番南瓜與南瓜之雜交及其染色體之研究)

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CYTO-GENETICAL STUDIES OF THE CROSS BETWEEN THE SQUASH (*CUCURBITA MAXIMA*, DUCH.) AND PUMPKIN (*C. PEPO* L.)

H. W. Li*

Historical Remarks

The genetical relations of the cucurbits have been studied very thoroughly by Vavilov (Babcock and Clausen, pp. 436, 1927) who reports that the genera of Cucurbitaceae differ in the character of their pollen, in chromosome number, and in their behavior towards parasites. Over a thousand crosses were made between different forms of watermelons, canteloupes, and squashes; and it was found that none of these genera would intercross, whereas crosses between varieties and species within a genus were successful. Sagaret (1826) and Naudin (1856, 1859) made extensive hybridization studies with some species belonging to the family Cucurbitaceae (Hayes and Garber, 1926). Naudin in a special classification made on the basis of genetical behavior placed both pumpkin and summer squash in *C. pepo*, and all the forms which cross readily he placed in the same species group. Bailey (1890) as the result of many artificial pollinations concludes that "the field pumpkins and the summer and fall types of bush squashes (*C. pepo*) do not cross with the running squashes of the Hubbard, Marblehead, Boston Morrow, Turban, and Mammoth types (*C. maxima*)." The diploid number of chromosomes for several species of Cucurbitaceae has been reported by Kozhukhov (1924-1925). The number was found to be 40 in two varieties and 42 in one variety of *C. pepo* and 48 in *C. maxima* (Hayes and Garber, 1926). Sinnott and his co-workers (1922 a and b, 1927, 1930, 1931) made careful studies in *C. pepo* on the inheritance of the shape and the body color of the fruit and on the inheritance of some other quantitative characters. Whitaker (1932) was successful in obtaining fertile hybrids between the gourd and pumpkin, both belonging to *C. pepo*.

Material and Methods

In the spring of 1933, Mr. L. N. Wang of the Bureau of Agriculture and Forestry of Honan Province gave the author some hybrid seeds of the cross between the squash (*C. maxima*) and pumpkin (*C. pepo*) that he had obtained the previous year. All the seeds (about 10) failed to germinate. Some ten plants, however, grew successfully to maturity in Mr. Wang's own garden. These plants were obtained by sowing a handful of seeds, the number of which is unknown. Through the kindness of Mr. Wang, the author was permitted to make cytological studies of and artificial pollinations with these plants.

In making cytological studies, aceto-carmine smears were tried. Due to the minuteness of the chromosomes and to the inability of the chromosomes to take up enough stain, the method was not satisfactory. For cut sections, the anthers were fixed in either Navashin's or Allen's modified Bouin's solution. Both gave satisfactory results. The paraffin sections were cut ten microns

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*Professor of Plant Breeding, Honan University, Kaifeng thick and were stained with Newton's iodine-gentian-violet stain. The drawings were made with the aid of an Abbe camera lucida. All magnifications are about 4000 times unless otherwise stated. All drawings were made at table level.

Description of the F_1 Plants

Many of the F_1 seeds failed to germinate. Apparently, they do not manifest any hybrid vigor. The F_1 plants also show no signs of any heterosis. The most interesting thing that strikes one's attention is the fact that many of the anthers of the F_1 plant do not dehisce at all. Some of them do dehisce with the liberation of only a few pollen grains, however. As a result, repeated self-pollination is a complete failure. Nevertheless, by using an F_1 plant as the female parent and either of the parents as the pollen parent, fruits can be obtained. Many of the morphological characters of the F_1 plants are intermediate between those of the two parents, such as the shape of the fruit, the depth of the grooves on the fruit, the pentagonal ridges of the peduncle, and the size and shape of the anthers (Plate 2 and Appendix 1).

When the pollen grains of the F_1 plant are examined under the microscope, it can be found that most of them (96 per cent) are non-viable. They also vary tremendously in size. This is a great divergence from the pollen grains of both parents used (Plate 3 and Appendix 1). The abundance of abortive seeds in the fruits obtained through back-crosses signifies that some disturbance has occurred in the ovules as well. In one of the batches of seeds planted, only 11 seedlings from 66 (F_1 x squash) seeds and, in another case, only 10 seedlings from 139 (F_1 x pumpkin) seeds were obtained. Many of the F_2 seeds were empty. Some had no embryo. Others were without cotyledon. Still others had poorly developed embryo and cotyledon. All these facts point to the conclusion that some disturbance had happened during both micro - and macro-sporogenesis.

Results from Cytological Studies

The haploid number of chromosomes of both the squash and pumpkin is 21 (Plate 4, Figs. 1 and 2). Some of the metaphase figures of meiotic mitosis in the F_1 have 21 pairs (Plate 4, Fig. 4). Others, however, have varying numbers. One has 28 complements (Plate 4, Fig. 3), 12 of which might be univalents. The diakinetic figures of the hybrid (Plate 4, Figs. 6 and 7) are found to have many of their chromosomes with a terminal chiasma. A few show an interstitial chiasma. Only one clear figure of the diplotene stage in the hybrid plant was observed, and in this figure one pair of chromosomes had interstitial chiasmata (3 in number). Other chromosome pairs in the same complex do not seem to show such a close association. On the contrary, the early diakinetic stages of squash (Plate 4, Figs. 5a and 5b) show no exception in this respect. All the members of the chromosome pairs show an interstitial chiasma. It is unfortunate indeed that, on account of the minuteness of the chromosomes, the details of chiasma formation are difficult to determine and so are left out of the discussion.

From the above observation, two hypotheses can be stated concerning the behavior of the hybrid chromosomes: 1. Some of the chromosomes coming from both parents might pair and form regular chiasmata in early prophase, but during late prophase and thereafter terminalization might go on more rapidly in some of the chromosomes than in others. This is especially true for the shorter chromosomes. 2. It might be possible, too, that some of the chromosomes of the two parents have homologous ends only. Thus only terminal chiasmata are formed. It seems that the second hypothesis might be more correct judging from the observation stated earlier. However, either of these hypotheses would explain the cytological findings in the hybrid. With both terminal-chiasma- and interstitial chiasma-forming chromosomes present in the hybrid, it is easy to explain why there is lagging and precocious separation of the chromosomes in the anaphase stage during meiosis of the hybrid (Plate 5, Figs. 11, 12, and 13). Chromosomes with terminal chiasmata would separate much more easily than chromosomes with interstitial chiasmata (Darlington, 1932, p. 111). With precociously separating and lagging chromosomes we could expect the formation of micronuclei. Indeed, micronuclei are of frequent occurrence in the dyad stage (Plate 5, Fig. 8) and in the tetrad stage (Figs. 9 and 10). The second meiotic division is regular, as expected when the entire chromosome complement is present. Microspores thus obtained from either a surplus or deficient chromosomal complement are apt to be non-viable. Many of the young microspores are found to be shriveled, even in the tetrad stage. Others degenerate later. Some of the chromosomes, however, do separate regularly (Plate 5, Fig. 13). Four per cent of the pollen grains were found to be viable. Macrosporogenesis, although not studied, doubtless behaves in the same way for many of the seeds obtained by back-crossing are abortive and non-viable.

The chromosome number of three plants in the F_2 population was determined. All of them have 21 pairs. The behavior of the chromosomes during the anaphase in the meiosis of these plants resembles closely that seen in the hybrid. We find again precocious separation and lagging of chromosomes.

Results from Genetical Studies

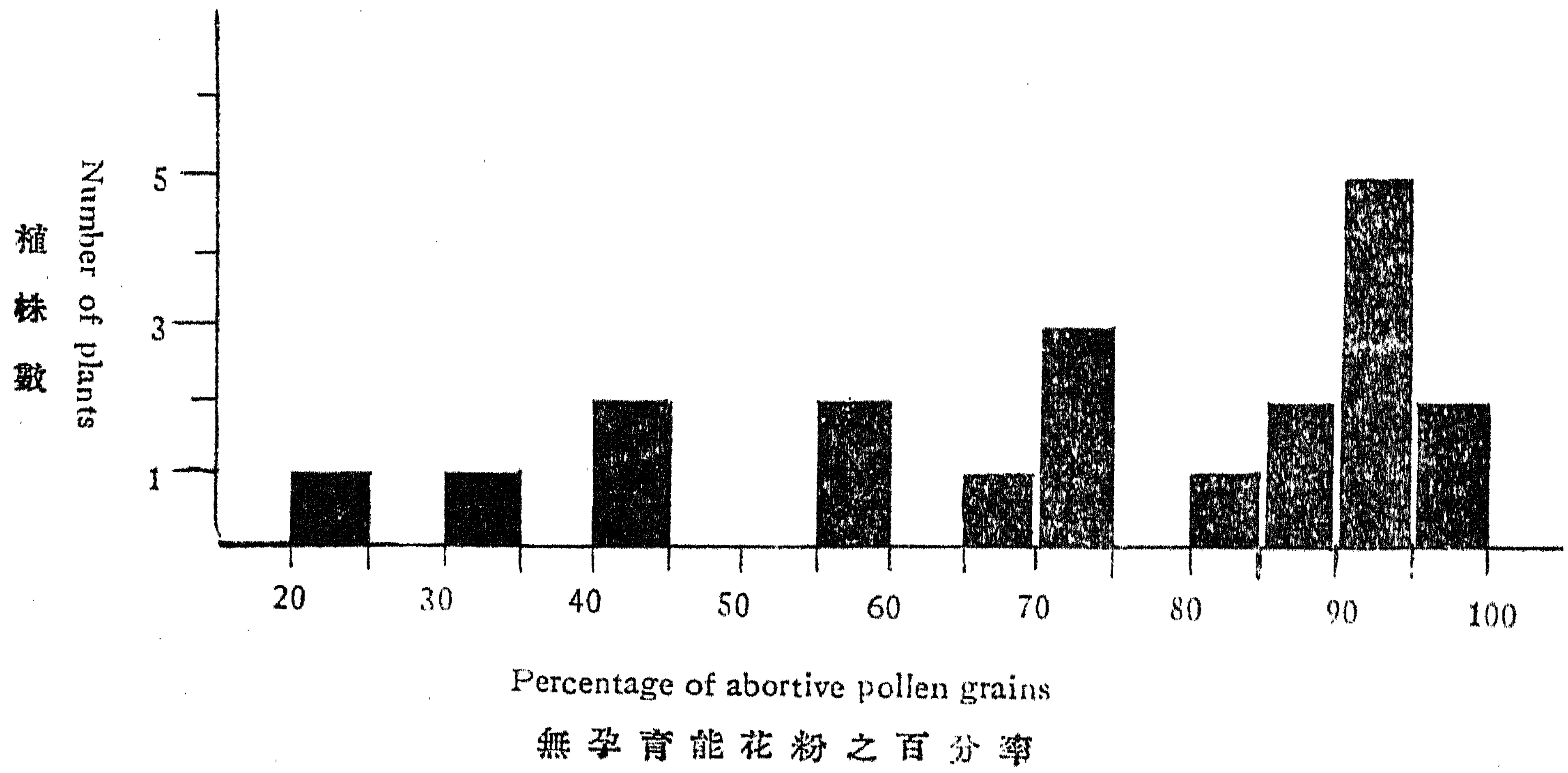
The F_2 or rather the seeds of the back-cross were germinated in the petridish and were later transplanted to the flats in the greenhouse. The seeds obtained by using squash pollen have a much higher percentage of germination than those obtained by using pumpkin pollen, 16 per cent and 7 per cent respectively. We find plumper seeds in the fruit obtained by back-crossing F_1 to the squash parent than by back-crossing to the pumpkin parent. This is coupled with the fact that the viability of the F_1 seeds is very poor as already stated. Seeds having their nuclei and cytoplasm from the same origin seem to survive more consistently than seeds having their nuclei and cytoplasm from a different origin. This tends to suggest the hypothesis of the inter-relationship between nucleus and cytoplasm.

Many of the F_2 seedlings were abnormal. Some of them have coalescent cotyledons. Others have deformed leaves. Only thirty-nine plants were finally transplanted to the field. Most of these plants were about as vigorous as those of the parents growing side by side with them. A few of the F_2 seedlings had a very weak growth and died before they bore any fruit. Many bore fruit as early as the parents. A few of them had such a weak growth that, though they were able to survive, they were unable to bear a single fruit. The anthers in some of the plants failed to dehisce as in the F_1 plants. Thus self-pollination was again impossible in many of the plants even after repeated trials. Consequently, back-crossing was again resorted to. Since the number of the F_2 population was very small, any attempt to make a genetical interpretation would be inference only. The detailed description of the morphological characters of the parents and the F_1 and F_2 plants is found in Appendix 1. The individual characters concerned will be discussed one by one.

Percentage of non-viable pollen grains — The pollen grains from the male flower that was ready to open were counted under the microscope after being stained with iodine solution. At least 300 grains were counted and the percentage calculated. For the percentage of non-viable grains, we find 4 per cent in the squash, 10.21 per cent in the pumpkin, and 96 per cent in the hybrid. In the F_2 plants the percentage varies from 20 to almost 100 with a unimodal curve skewing toward the right (Fig. 16). This indicates, of course, the persistence of the non-homology of the chromosomes even after back-crossing for another generation.

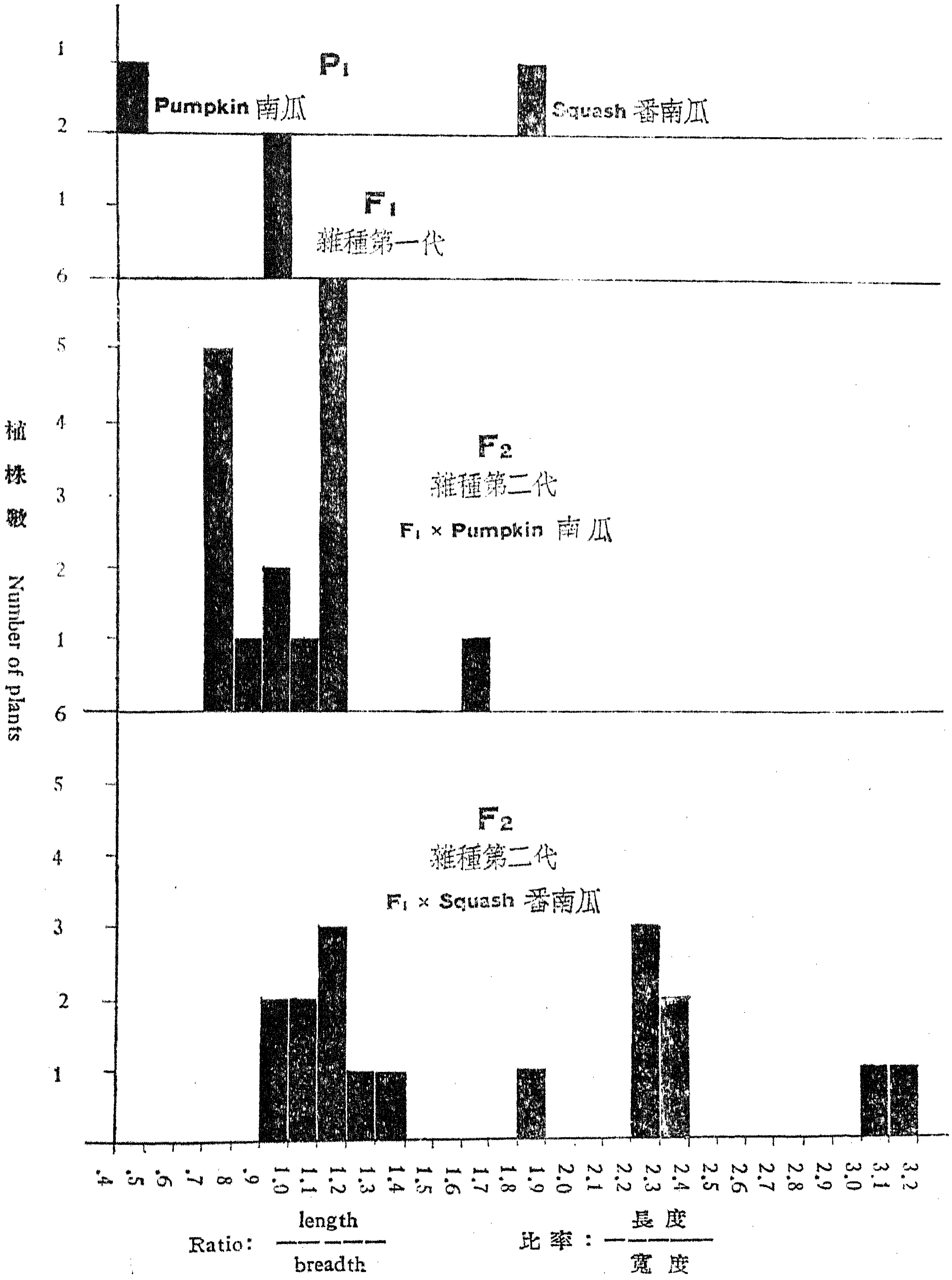
Fig. 16 Percentage of abortive pollen grains in F_2 generation

圖十六 在雜種第二代時無孕育能花粉粒之百分率



Diameter of the pollen grains — The unit used is the micrometer unit. Each unit is equivalent to .015 mm. The pollen grain of the squash is about one unit larger than that of the pumpkin, being 10 and 9 respectively. The size is rather uniform in both parents as indicated under the *large* and *small* column in Appendix 1. The average size of the F_1 pollen is 10 units, but it varies from 7 units to 15. In examining the size of the pollen grains of the F_2 plants, it is observed that the average diameter ranges from 8 to 10 units. Some plants show very little variation in size, while others do to a great degree. Some of the huge pollen grains observed reach a size of 15 units. It seems that the more irregular the meiotic division is, the greater is the number of the non-viable pollen grains, and there is more variation in the size of the grains.

Fig. 17 Inheritance of shape of fruit 圖十七 果實形狀之遺傳



Shape of the fruit — The fruit of the squash is decidedly oblong in shape. The pumpkin, however, is clearly a disk type. Though both parents come from commercial stock, there is very little variation in these respective shapes. The hybrid has a round fruit, a blend of its two parents (Plate 1). In the F_2 there is a great variation in the shape of the fruit. Besides the oblong, disk, and round types, there are conical, egg, and dumb-bell types, etc. If we represent these types by the ratio of the length to the breadth and make a graphical representation, we can get a better picture of the segregation of this characteristic among the F_2 population (Fig. 17). The shape of the fruit from the plants that are back-crossed to the pumpkin parent is seen to be either disk or globular with the exception of one plant only; about half the plants have disk-shaped fruit and the other half globular. That exception has an egg-shaped fruit. The graph, therefore, centers around the type of the hybrid plant. On the other hand, about half the plants resulting from the back-cross to the squash parent have globular fruit like that of the hybrid parent and the other half have oblong fruit like that of the squash parent. From this, it seems that the shape of fruit is governed by a major factor, and that neither disk nor oblong is dominant over the other. Thus, when types such as the conical, egg, and dumbbell segregate in the F_2 population, other modifying factors seem to be present. However, the data do not permit us to offer further explanations.

Leaf lobes — The leaf lobes of the squash are round and those of the pumpkin are pointed. The F_1 plant is assumed to have a pointed leaf lobe. Nine of the plants from back-crossing the F_1 to the squash have pointed leaf lobes; the other ten have round lobes. All of the plants that are obtained from back-crossing the F_1 to the pumpkin parent have pointed leaf lobes. This seems to be a simple Mendelian segregation with pointed leaf lobes dominant over round.

Owing to the small number of individuals in the F_2 population, it is hard to explain the mode of inheritance of the characters listed in Appendix 1; but the most interesting thing is the segregation of color in the mature fruit. Besides the cream-yellow color of the squash, the reddish-brown color of the pumpkin, and the brown color of the hybrid, there are red, orange, cream, white, and black colors appearing in the F_2. This indicates an interaction of factors; but how it comes about, it is again difficult to explain with such a small F_2 population.

Some abnormalities appear in the F_2 population. Plants 21 and 24 (both obtained by back-crossing F_1 to the pumpkin parent) besides their normal male and female flowers have perfect flowers present. The calyx tube of such flowers is enlarged at the base in such a way as to resemble an ovary. Both anthers and stigma are present side by side, but they are very much deformed. The ovules are attached to the style-like placenta just inside the calyx. The edges of the leaves of plants 24 and 29 are rolled up as if permanent wilting has occurred, but in other respects they appear to be healthy.

More work should be done on such crosses in order that more conclusive evidence than given in this paper can be shown.

Summary

The squash and pumpkin can be crossed when the squash is used as the female parent. The reciprocal cross, however, is not successful.

The F_1 plant shows no signs of heterosis.

The haploid number of chromosomes for both parents is 21. The hybrid plant has 42 chromosomes as the diploid number. Only 4 per cent of the pollen grains of the hybrid plant are fertile, and they vary greatly in size.

The first meiotic division in microsporogenesis shows much abnormality. Precocious division and lagging of chromosomes during anaphase resulted in the formation of extra microspores and non-viable grains. This irregular separation of the chromosomes is attributed to the non-homology between some of the chromosomes of the two parents. On account of this non-homology, some pairs of chromosomes form an interstitial chiasma and other chromosomes form a terminal chiasma during late prophase. This accounts, perhaps, for the irregular meiotic division of the hybrid plant.

Genetical studies have disclosed simple Mendelian inheritance for shape of fruit, oblong and disk, with neither one dominant over the other; and for leaf lobe, the pointed is seen to be dominant over the round.

Acknowledgment

The author is indebted to Mr. L. N. Wang for furnishing the material for this study and to Dr. J. Theron Illick of the University of Nanking for reading the manuscript.

Appendix 1 — Detailed Description of the Characters of the Parents and Their Subsequent Progenies*
附 錄 一　親代及其後代性狀上之詳細說明 *

Plants 植 株	% of abortive pollen grain 無孕育能花粉粒之百分率	diameter of pollen grain unit .015 mm. 花粉粒之直徑(以.015糎爲單位)			Shape of fruit 果 形		peduncle 果 柄	leaf lobes 葉之裂片	markings on the leaf 葉身上之斑紋	sepal 萼 片	color of the mature fruit 成熟果實之色澤	fruit groove 果實溝紋
		average units 平均數	large units 最大	small units 最小	ratio: $\frac{\text{length}}{\text{breadth}}$ 比率: $\frac{長度}{寬度}$							
Squash 番南瓜	4.00	9.55	10	8	1.78	oblong 長圓形	round 圓	rounded 圓	absent 無	flap-like 指 狀	cream-yellow 乳酪黃色	absent 無
Pumpkin 南瓜	10.21	8.59	9	8	0.44	disk 盤 形	obtusely pentagonal, deeply ridged 甚有稜脊	pointed 尖	present 有	leaf-like 葉 狀	brown 褐 色	deep 深
F1 雜種第一代	95.66	10.00	13	7	0.85	round 圓 形	moderately ridged 稍有稜脊	,,	,,	flap-like 指 狀	light brown 淡褐色	medium dept 中 度
雜種第二代 1					2.29	oblong 長圓形	round 圓	,,	,,	,, ,,	orange 橘 色	absent 無
2					1.14	round 圓 形	lightly ridged 微有稜脊	,,	,,	,, ,,	cream-white 乳白色	shallow 淺
3	91.38	9.55	12	8	1.30	round 圓 形	,, ,,	round 圓	absent 無	,, ,,	,, ,,	,,
4	70.32	8.58	11	7	1.05	round 圓 形	,, ,,	,,	present 有	leaf-like 葉 狀	,, ,,	,,
5	23.30	10.20	11.5	9	.90	disk 盤 形	,, ,,	pointed 尖	,,	spatula-like 匙 狀	orange 橘 色	,,
6					1.00	round 圓 形	,, ,,	,,	absent 無	flap-like 指 狀		,,
7					1.15	round 圓 形	,, ,,	round 圓	present 有	leaf-like 葉 狀	red 紅 色	,,
8					.91	round 圓 形	,, ,,	pointed 尖	,,	,, ,,	cream-white 乳白色	,,
9	98.79	8.85	11	7.5	2.30	oblong 長圓形	,, ,,	round 圓	absent 無	flap-like 指 狀	,, ,,	absent 無
10	80.95	8.15	9	7	3.08	oblong 長圓形	,, ,,	pointed 尖	,,	leaf-like 葉 狀	orange 橘 色	,,
11												
12	93.40	12.31	15	11	1.78	oblong 長圓形	,, ,,	round 圓	absent 無	spatula-like 匙 狀	cream-white 乳白色	absent 無
13					2.21	oblong 長圓形	round 圓	,,	present 有	flap-like 指 狀		,,
14												
15	68.93	9.89	11	8	1.90	round 圓 形	lightly ridged 微有稜脊	pointed 尖	present 有	flap-like 指 狀	cream-white 乳白色	shallow 淺
16					3.03	oblong 長圓形	,, ,,	round 圓	absent 無	,, ,,	red 紅 色	absent 無
17					2.19	oblong 長圓形	round 圓	pointed 尖	,,	,, ,,	cream-white 乳白色	,,

(F1 × Squash 番南瓜)

	18					1.10	round 圓 形	lightly ridged 微有稜脊	pointed 尖	absent 無	flap-like 指 狀		medium dept 中 度
	19	87.78	8.57	15	7	2.15	oblong 長圓形	,, ,,	round 圓	,,	spatula-like 匙 狀		absent 無
雜種第二代 (F_1 × Pumpkin 南瓜)	20					1.61	egg 卵 形	moderately ridged 稍有稜脊	pointed 尖	,,	flap-like 指 狀		,,
	21	19.67	9.08	14	7	.95	egg 卵 形	deeply ridged 甚有稜脊	,,	present 有	spatula-like 匙 狀	orange 橘 色	shallow 淺
	22							round 圓 形	,,	absent 無	flap-like 指 狀		
	23					1.13	conical 圓錐形	deeply ridged 甚有稜脊	,,	present 有	leaf-like 葉 狀	orange 橘 色	medium dep 中 度
	24	93.00	10.02	13	8	.66	disk 盤 形	,, ,,	,,	,,	,, ,,	dark brown 深褐色	deep 深
	25	42.85	10.00	12	8	1.09	round 圓 形	moderately ridged 稍有稜脊	,,	absent 無	flap-like 指 狀	,, ,,	shallow 淺
	26	86.30	10.02	13	9	.94	round 圓 形	deeply ridged 甚有稜脊	,,	present 有	leaf-like 葉 狀	brown 褐 色	medium 中 度
	27	99.57	7.75	9	7	.72	disk 盤 形	moderately ridged 稍有稜脊	,,	,,	flap-like 指 狀	,,	shallow 淺
	28					.67	disk 盤 形	,, ,,	,,	absent 無	,, ,,	orange 橘 色	absent 無
	29	93.05	10.07	13	9	1.13	conical 圓錐形	,, ,,	,,	present 有	leaf-like 葉 狀	tan 黃褐色	shallow 淺
	30	91.97	11.00	13	9	1.12	conical 圓錐形	,, ,,	,,	,,	flap-like 指 狀	brown 褐 色	,,
	31					.75	disk 盤 形	lightly ridged 微有稜脊	,,	,,	,, ,,	orange 橘 色	,,
	32	56.20	10.57	12	10				,,	absent 無	spatula-like 匙 狀		,,
	33	57.57	10.00	12	9	1.07	conical 圓錐形	moderately ridged 稍有稜脊	,,	present 有	flap-like 指 狀	red 紅 色	medium 中 度
	34							lightly ridged 微有稜脊	,,	absent 無	,, ,,	blackish green 深青色	
	35	30.96	8.60	13	7	.66	disk 盤 形	deeply ridged 甚有稜脊	,,	present 有	leaf-like 葉 狀	brown 褐 色	medium 中 度
	36	70.27	8.81	10	8	.70	disk 盤 形	moderately ridged 稍有稜脊	,,	,,	flap-like 指 狀	tan 黃褐色	shallow 淺
	37	70.70	8.75	11	7	1.09	round 圓 形	deeply ridged 甚有稜脊	,,	,,	,, ,,	brown 褐 色	,,
	38	44.79	10.55	13	9	.85	round 圓 形	moderately ridged 稍有稜脊	,,	,,	spatula-like 匙 狀	red 紅 色	,,
	39							lightly ridged 微有稜脊	,,	absent 無	flap-like 指 狀		,,

*Omissions signify either that the plant died before the record was taken or that it was impossible for practical reasons to take a record

*缺 明者，以株植在記載前，即已夭折。

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Description of the Plates

圖版說明

Plate 1. Shape of fruit 版一 果實之形狀
Plate 2. Types of seeds and anthers 版二 種子及花藥之式樣
Plate 3. Pollen grains 版三 花粉粒

Plate 4. 版四

Fig. 1 — Polar view of the metaphase plate of squash showing 21 chromosomes
圖一 番南瓜分裂中期,從其極端觀之圖形,表明二十一染色體.
2 — The same for pumpkin, also showing 21 chromosomes
圖二 同樣表明南瓜之二十一染色體。
3 — The same for F_1 having 28 complements, 12 of which might be univalents
圖三 同樣表明F_1染色體有二十八雙組數,其中十二個爲單價.
4 — The same for F_1 but having also 21 pairs of chromosomes
圖四 同樣表明F_1 亦有二十一對染色體者.
5 — Early diakinetic figure of squash; a and b are from two different levels of one cell
圖五 番南瓜早期減數分裂之圖形;a及b爲同一細胞,從不同之二平面,觀察之圖形,
6 — Diakinetic figure of F_1 (x 3100)
圖六 雜種第一代之早期減數分裂圖形.(x 3100)
7 — The same as Fig. 6
圖七 與圖六同.

Plate 5 版五

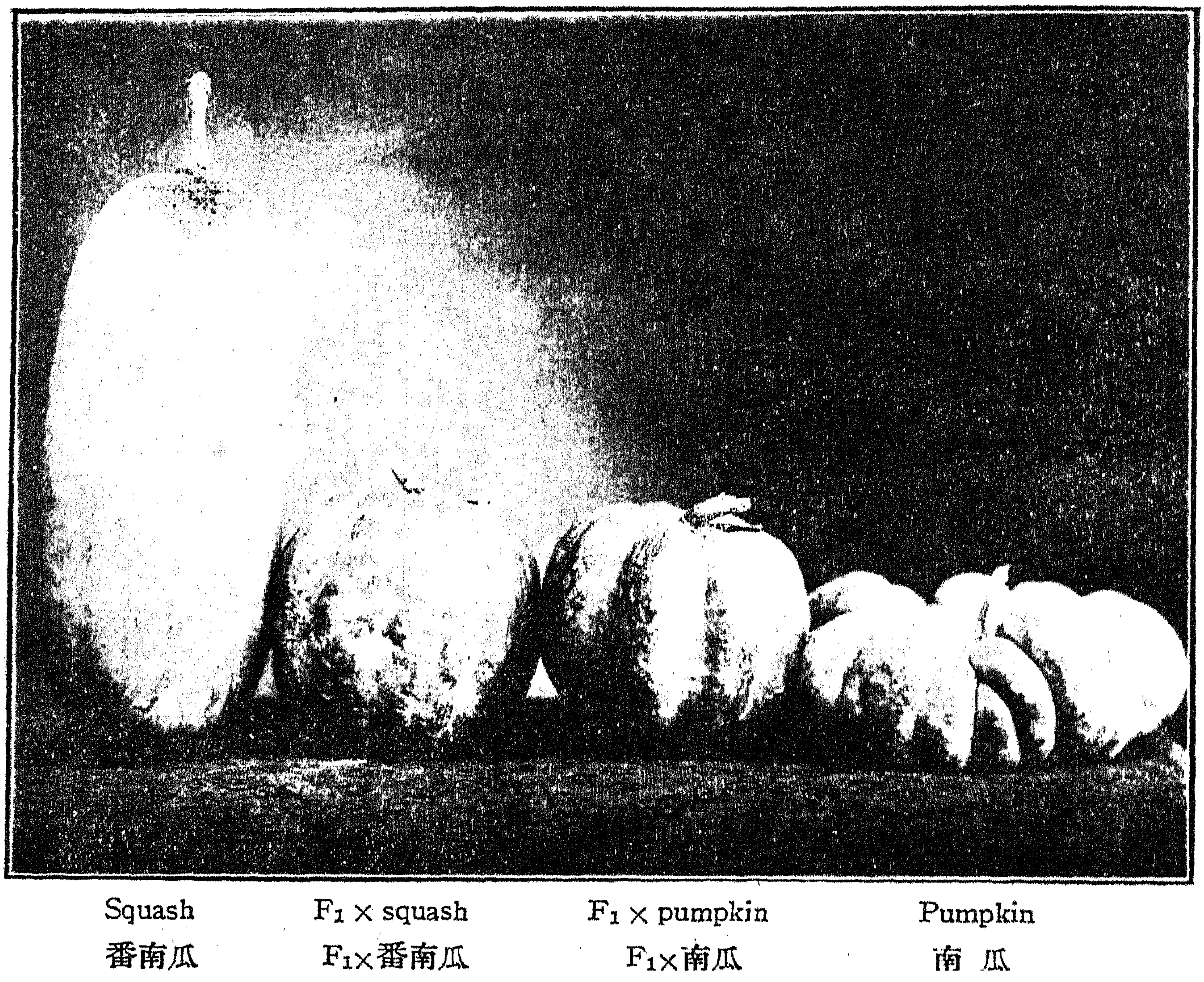
Fig. 8 — Dyad stage of F_1;notice the two micronuclei (x 700)
圖八 雜種第一代之雙染體時期.注意二小核 (x 700)
9 and 10 — Tetrad stage of F_1 showing the extra microspores and the difference in size among them (x 380)
圖九及十 雜種第一代之四染體時期,表明另外之小胞子及其大小之差異.(x 380)
11 — Anaphase figure of F_1, side view. Notice lagging and precocious separation of chromosomes
圖十一 雜種第一代分裂後期之側面觀圖形.注意染色體分離之提早及落後。
12 — Telophase of F_1, showing the lagging of chromosomes (lagging chromosomes are made dark so as to show the contrast)
圖十二 雜種第一代之分裂末期,表明染色體之分離落後.(落後之染色體爲黑色以示區別)
13 — Early anaphase of F_1, side view. Not all the chromosomes are represented in this figure. Notice the more or less regular separation of the F_1 chromosomes
圖十三 雜種第一代分裂早後期之側面觀圖形.未將所有之染色體表示.注意雜種第一代染色體之分離,頗有規則。

Plate 6 版六

Fig. 14 — Metaphase figure of squash, side view. (Chromosomes are drawn separately at four different levels). Notice the type of chiasma formation. Four chromosomes are not found in this drawing.
圖十四 番南瓜分裂中期之側面觀.(染色體係由四種不同之平面觀察而繪圖,注意打紐之構成,有四染色體不在圖內.
15 — a and b, the same for pumpkin
圖十五 a及b,同樣表明南瓜

Plate 1. 版一

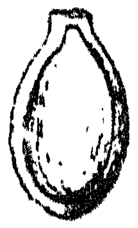
Shape of fruit
果實之形狀



Squash 番南瓜 F₁ × squash F₁×番南瓜 F₁ × pumpkin F₁×南瓜 Pumpkin 南瓜

Plate 2. 版二

Types of seeds and anthers (about natural size)
種子及花藥式樣（約與天然之大小相近）



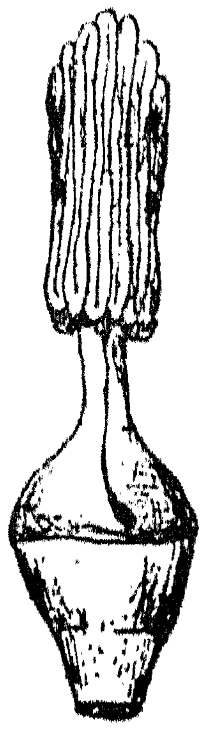
Squash
番南瓜

Pumpkin
南瓜

F_1 雜種第一代

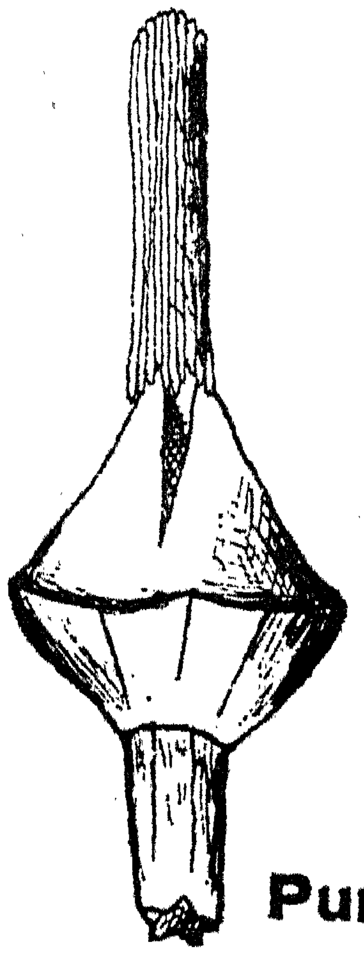
F_1 × **Squash** 番南瓜

F_1 × **Pumpkin** 南瓜



Squash
番南瓜

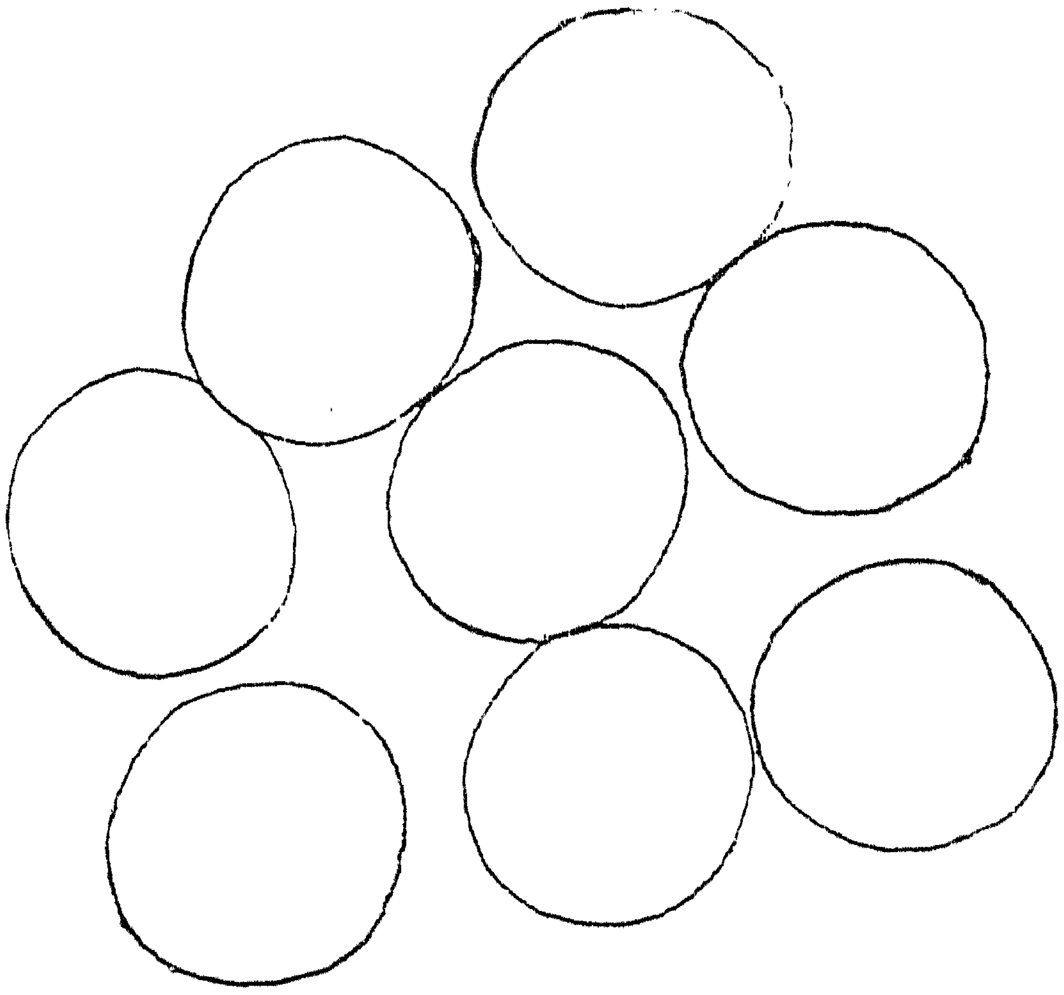
F_1 雜種第一代



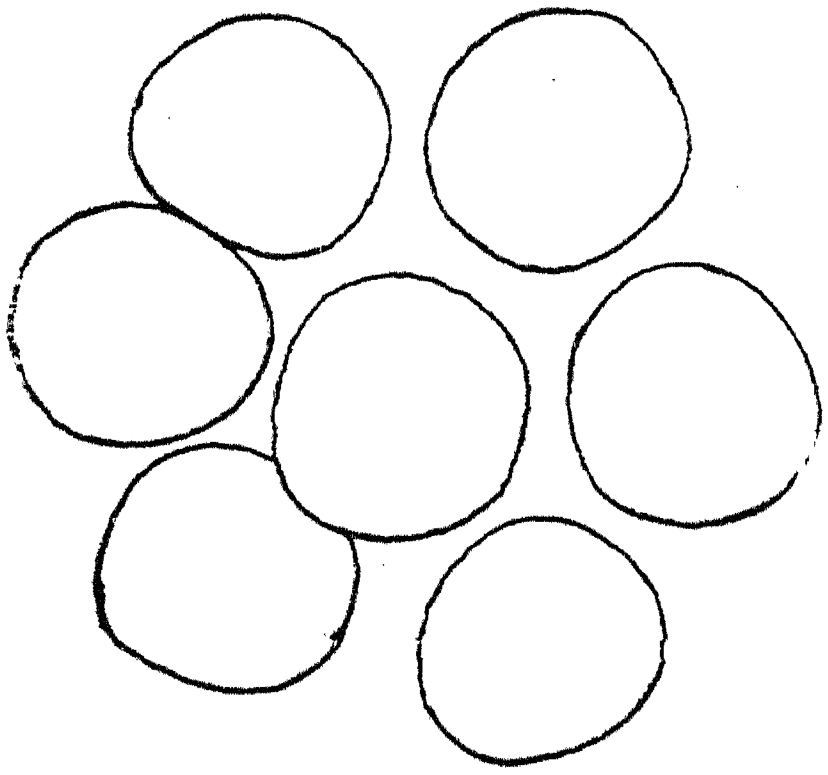
Pumpkin
南瓜

Plate 3. 版三

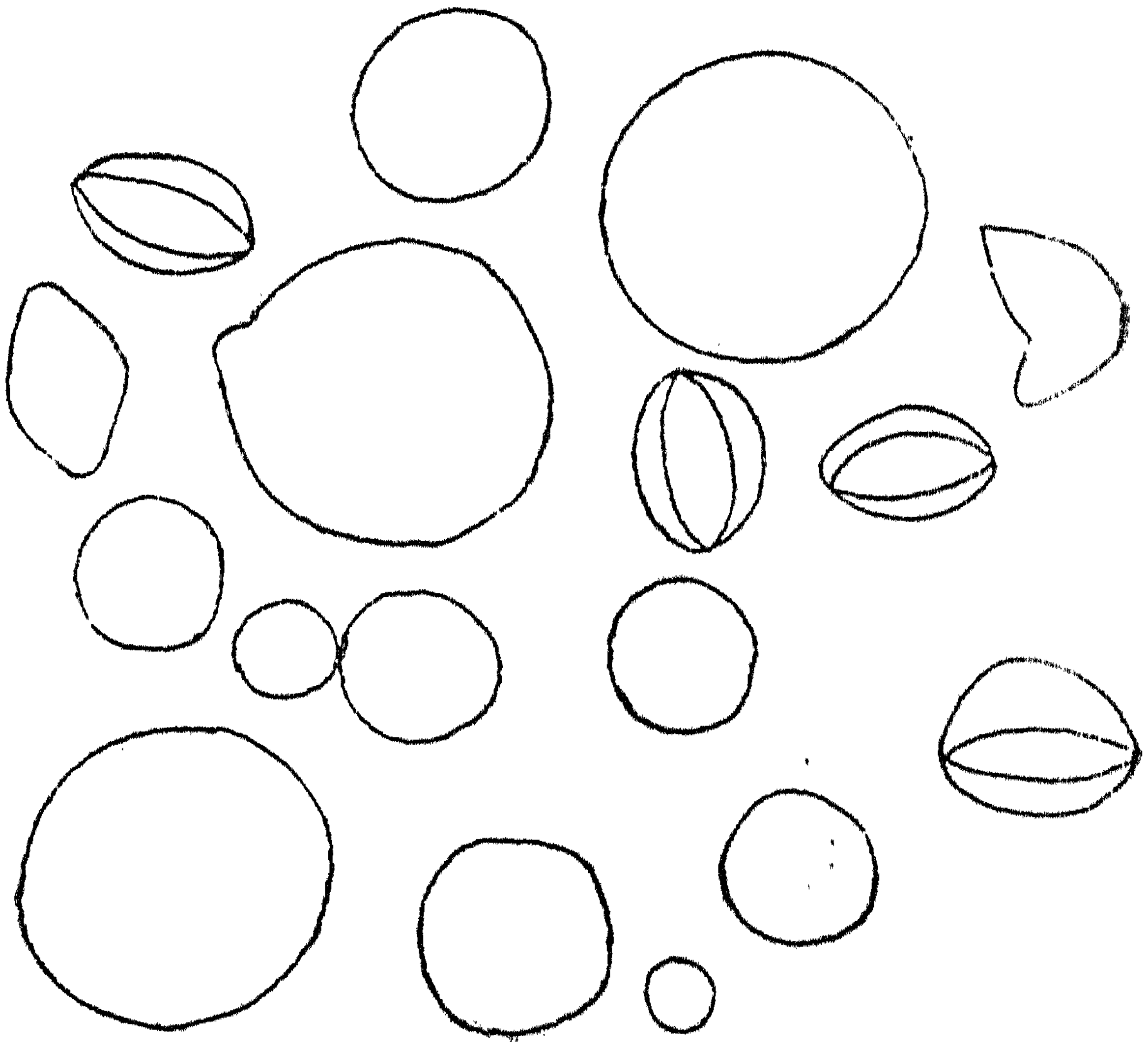
Pollen grains (×112)
花紛粒 (放大112倍)



Squash
番南瓜

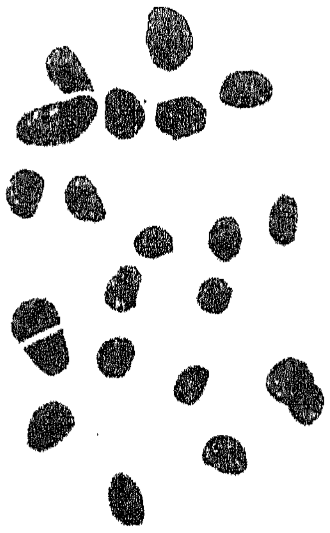


Pumpkin
南瓜

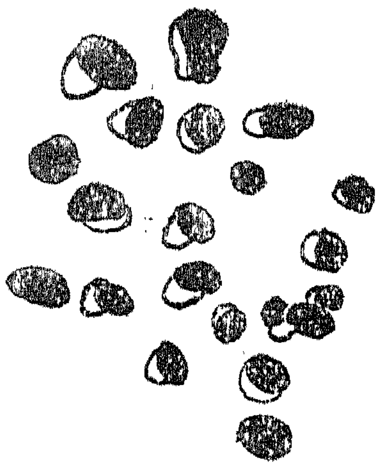


F_1
雜種第一代

Plate 4. 版四



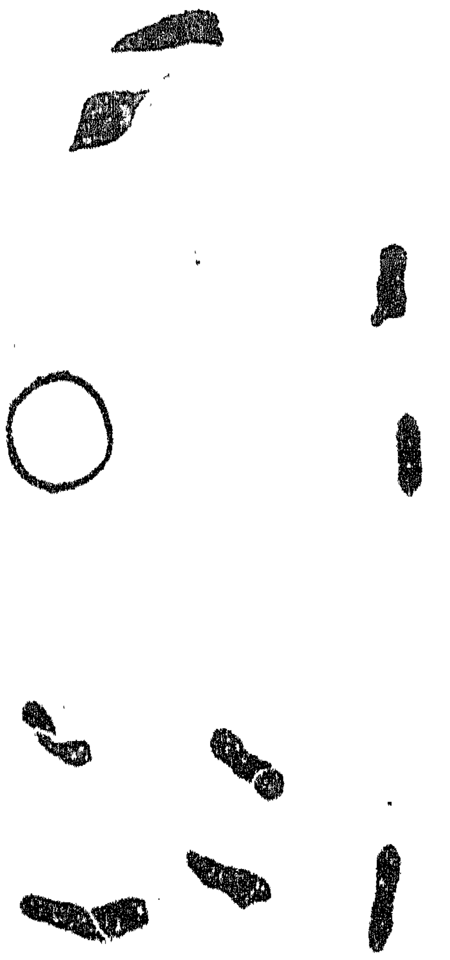
1



2

3

5a



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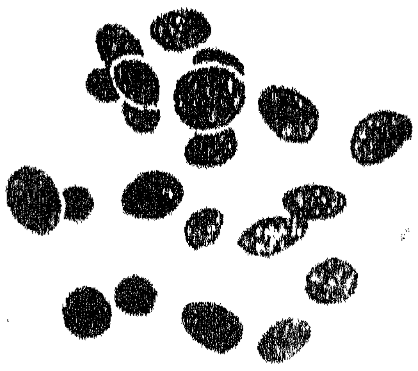

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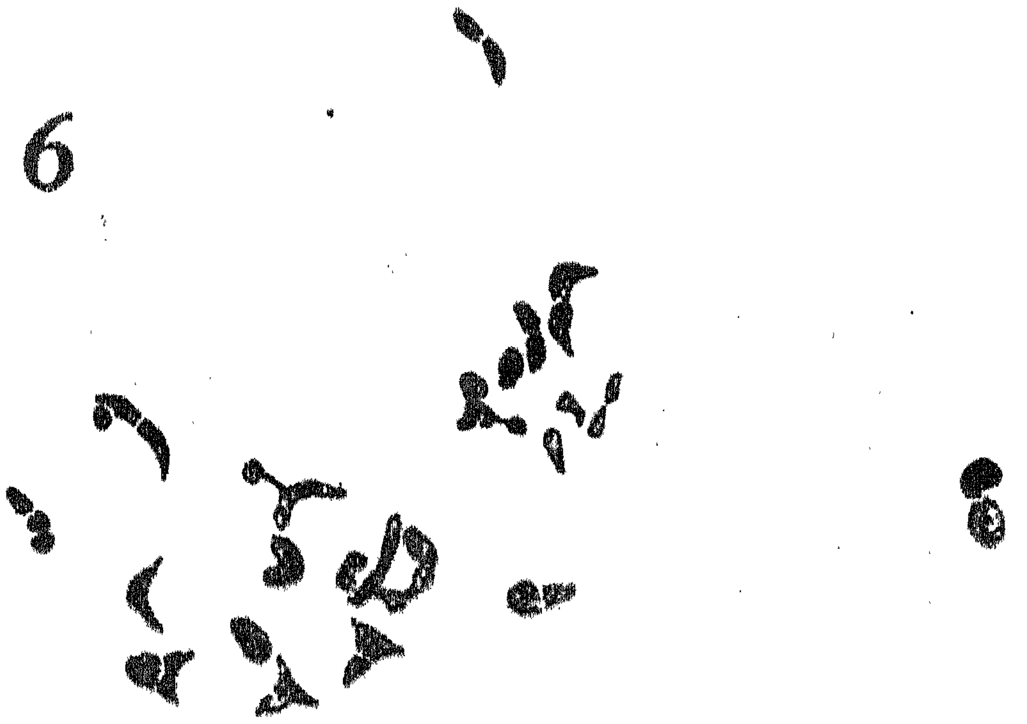

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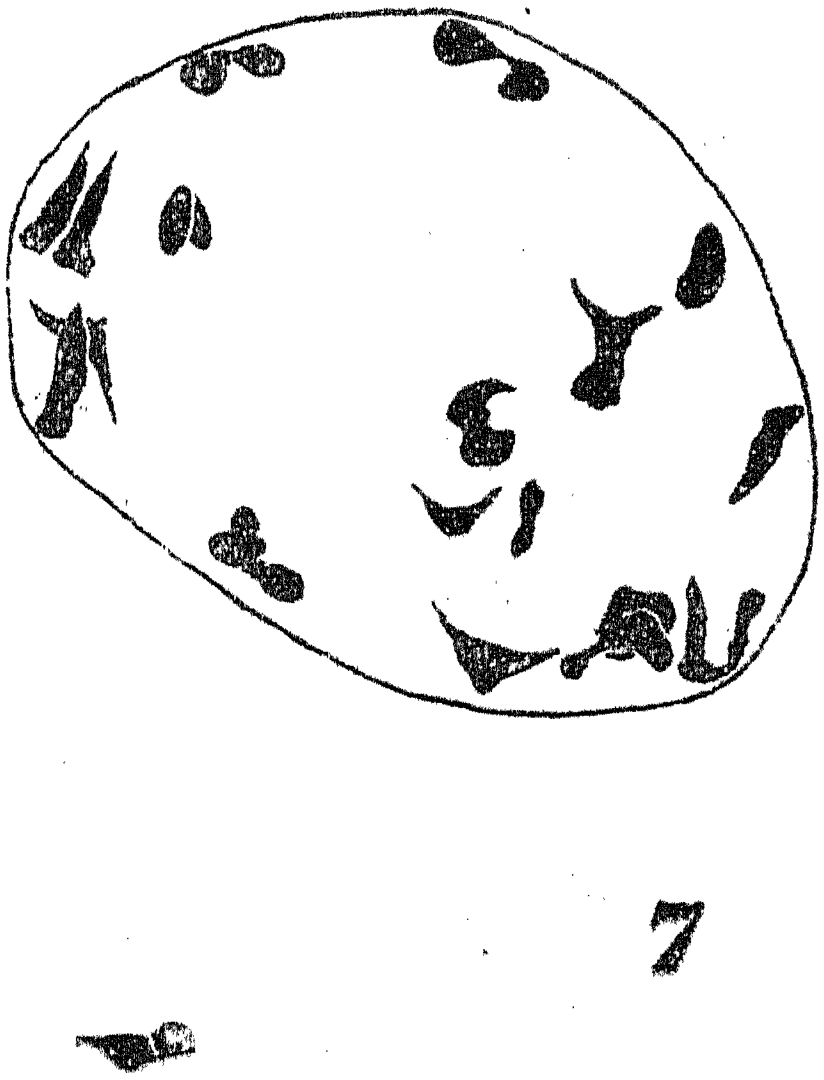

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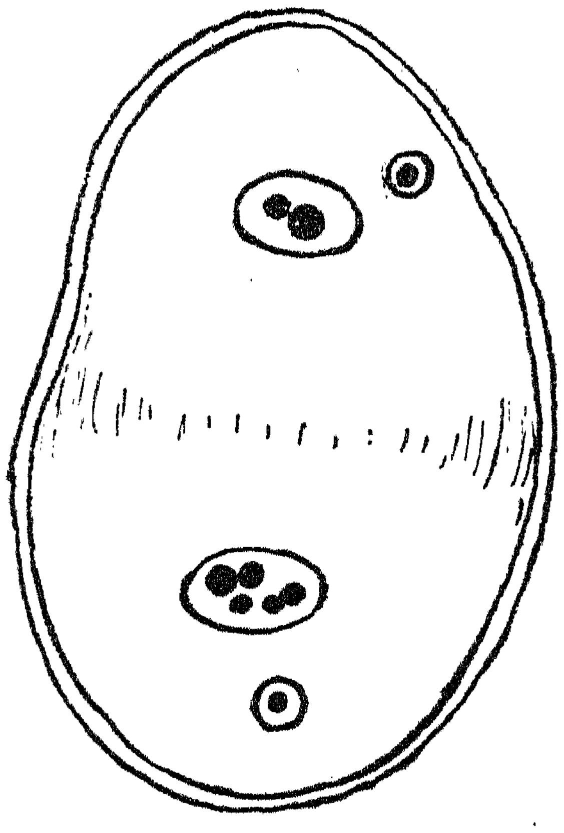
Plate 5. 版五



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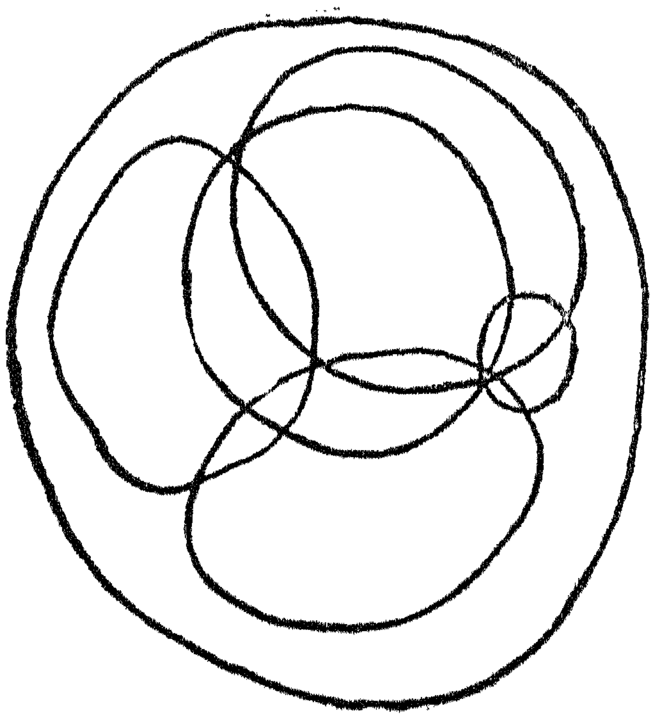

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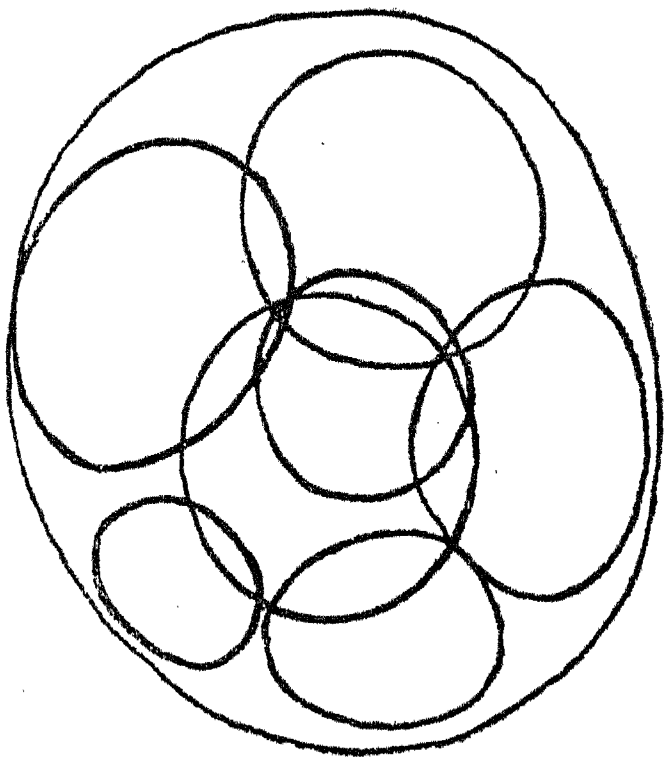

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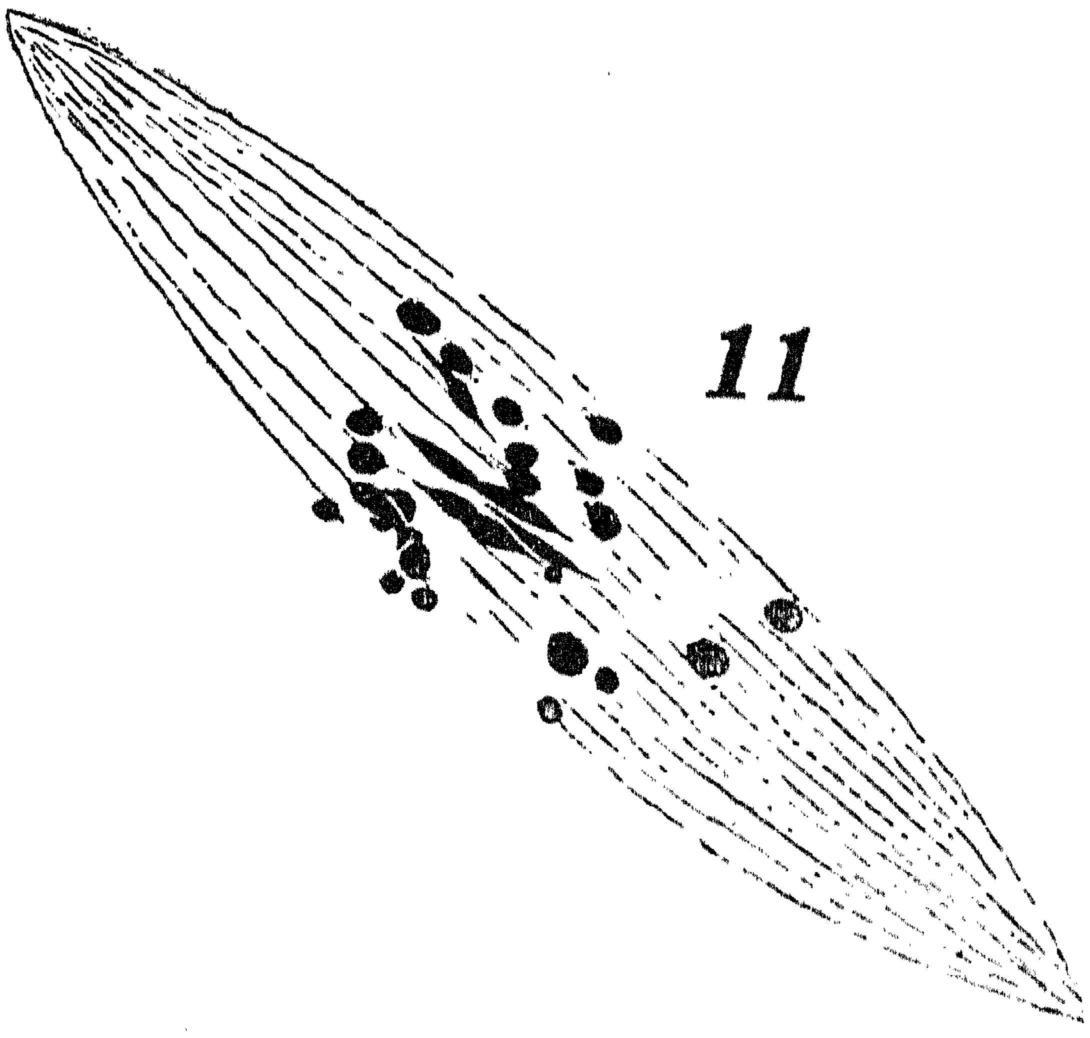

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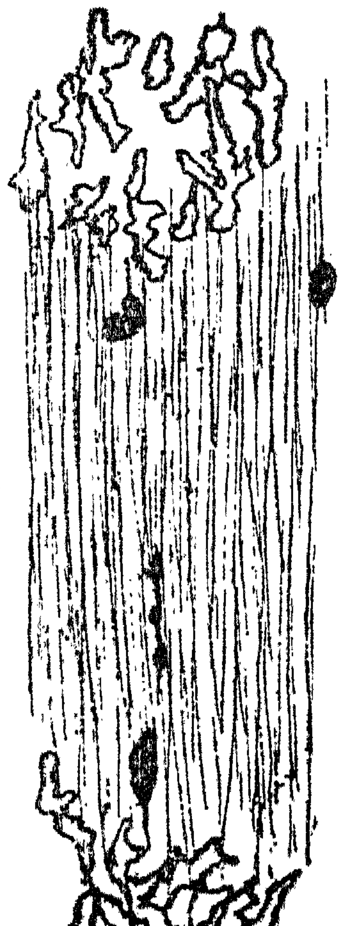

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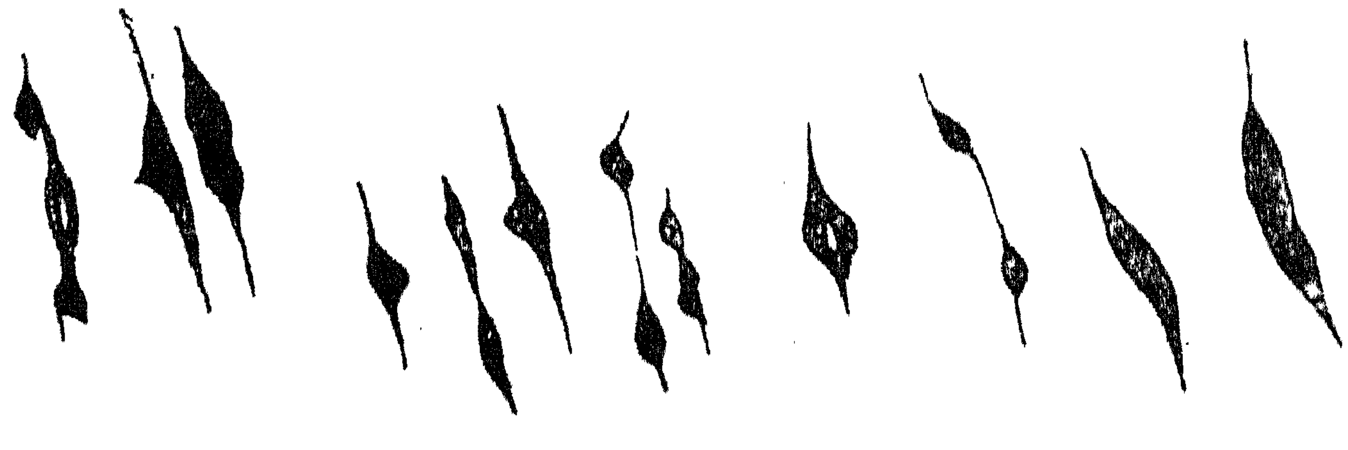

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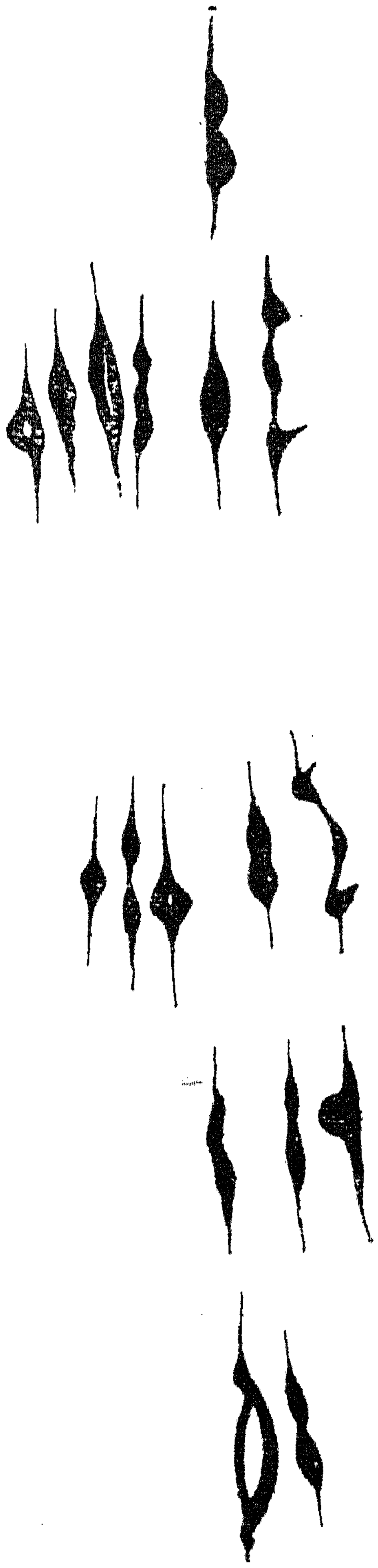
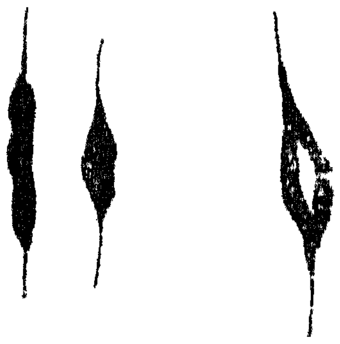
Plate 6. 版六

14



15a



15b

番南瓜與南瓜之雜交及其染色體之研究

李先聞

以往研究之回顧

Vavilov 氏 (1927) 對瓜類遺傳,曾作澈底之研究.凡葫蘆科各屬之花粉性狀,染色體數目,及其對於寄生物之習性,俱有報告.彼等曾將外形不同之西瓜,甜瓜,及番南瓜,作一千以上之雜交;其結果無一能與異屬交配者.而品種間及同屬異種間相交,則俱能配合. Sagaret 氏 (1826) 及 Naudin 氏 (1856,1859) 以葫蘆科中之數種 (Species) 作大規模雜交之研究.Naudin 氏根據遺傳上之特性,爲之分類.將南瓜與夏季番南瓜同歸入於 C. pepo 一類.其同屬一類者,彼此間俱易於配合. Bailey 氏 (1890) 從多數人工交配之結果,斷定南瓜及夏季與秋季之叢性番南瓜 (C. pepo) 不能與蔓性番南瓜 (C. Maxima) 之 Hubbard, Marblehead, Boston Marrow, Turban 及 Mammoth 配合. Kozhukhov 氏 (1924-1925) 曾報告葫蘆科內有數種 (Species), 其染色體爲雙價數,在 C. pepo 種內,已發現二品種之染色體爲雙價數,各爲四十,而另一品種則爲四十二, 在 C. Maxima 則爲四十八.

Sinnott 氏及其助理 (1922, 1927, 1930, 1931) 對於南瓜果形與果皮色及他種數量遺傳之性狀,曾作精密之研究. Whitaker 氏 (1932) 將同屬於 C. pepo 之南瓜與葫蘆 (gourd) 雜交,結果得到受精之雜種.

材料及方法

民國二十二年春,著者蒙河南省農林局王陵南君惠贈其上年所得之南瓜與番南瓜雜交種子.惜其所贈之種子,悉數未能發芽.惟王君自種者,得成長十株,復蒙王君好意,允將此等材料,供著者作細胞上及遺傳上之研究.

作細胞方面之研究時,曾試用醋洋紅 (Aceto-Carmine) 染色,但以染色體細小,及其他不明白之原因,不能將其充分染色.故此法未能滿意.爲切片計,將花藥固定於Navashin's或Allen's Modified Bouin's溶液內,俱得滿意之結果.白蠟切片,切至百分之一糎厚,並用 Newtons iodine-genetion-violet 色料染色,畫圖用顯微鏡繪圖器 (Abbe camera lucide) 爲助,其各種圖形,除另有說明外,均放大四千倍.

雜種第一代植株之描述

雜交種第一代之種子,多數不能發芽,而雜種第一代之植株,似乎無雜交勢之表徵.其最堪引人注意者,即第一代植株之花藥,全不能裂開;縱有裂開者,亦僅放出少量之花粉而已.其自交之結果,則全歸失敗惟如將雜種第一代之植株作爲母本,而用任何親代之植株爲父本,均能配合結實.第一代植株形態上之性狀,多介于兩親之間,如果實形狀及其溝紋之深度,果柄上五角形之棱脊,及花藥之形狀與大小(版二及附錄一).

若將第一代之花粉粒以鏡檢之,大多數之花粉粒 (96%) 缺乏生機.彼此之大小,差異甚大,而與兩親之花粉粒亦有歧異. (版三及附錄一) 由回交所得之果實,內含有許多不充實之種子,此足以表明胚珠內亦有擾亂之現象.從66粒 (F_1 × 番南瓜) 種子中,僅得十一粒能發芽者.又從139粒 (F_1 × 南瓜) 種子中,僅得十株.雜種第二代之種子,大半空虛.有則無胚,有則無子葉,亦有雖有胚胎及子葉而發育不良者.凡此種種事實,俱可用以推斷大胞子形成 (Macrosporogensis) 及小胞子形成 (Microsporogensis) 均有擾亂情形之存在.

細胞上研究之結果

番南瓜與南瓜染色體之單數 (Haploid number) 爲21, 在減數分裂

中期時,有則染色體數爲21對,但亦有變異者.有一則具28染色體之組合(Complements),其中之十二爲單價者(Univalent),在雜種之初期分裂(版四圖六及七),染色體多行對頭打紐(Terminal Chiasma),亦間有行中間打紐者(Interstitial Chiasma).在分裂初期之Diplotene stage祇觀察得一個清楚之圖形,而在此圖形中,有一對染色體,爲中間打紐,(打三紐);其餘各對染色體在此圖形中者,似無如此現象.反之在番南瓜之初期分裂時之Diakinetic stage(版四,圖5a及b),各染色體完全有打紐現象.其各對染色體均表顯爲中間打紐.因染色體細小,難以檢定,而打紐之詳情,未能有所論及,實爲憾事.

從以上觀察,關於雜種染色體之特性,有兩種推論.(1)染色體有從兩親來者,可以成對,並於早分裂初期Early Prophase成有規則之打紐,但當晚初期,於'頂端紐化'(Terminalization)後,則染色體中有進行較速者,尤以染色體短者爲然.(2)此或因兩親之染色體,僅頂端部分均一(Homologous),是以僅成頂端打紐.第二個推論,從上述之觀察,比較上較爲真確.但無論如何,此兩種推論,均足解釋雜種在細胞學上,其染色體有對頭打紐及中間打紐之現象.故於雜種分裂後期(Anaphase),染色體之分離,爲何落後及提早之理由,均易於解釋(版五,圖11,12及13).以對頭打紐之染色體,較中間打紐者,分離大爲易易.又以染色體分離,提早及落後,則吾人可期多數小細胞核(Micronuclei)之造成,此等情形,確常於二分子時期(Dyad stage)(版五,圖八)及於四分子時期Tetrastage(圖九及十)存在.當所有染色體組合(Complements)呈現後,則第二次之分裂爲有規則.是以從過剩或不足之組合,則易失其生機.許多幼小之小胞子呈皺縮態,即於四分子時期,亦復如是.其餘之小胞子,後即死滅.但染色體亦有分離爲有規則者(版五,圖十三).但花粉粒能孕育者,僅百分之四耳.又對於大胞子形成(Macrosporogensis)雖未加以研究,但亦與此彷彿,可無庸置疑,因從回交所得之種子,大多發育不全而多無孕育能力也.

第二代之植株中,三株之染色體均爲21對,而此等植株之染色體,

於減數分裂後期之特性,與在第一代雜種所見者,極爲相似.吾人於此又發現染色體提早或落後分離之現象.

遺傳上研究之結果

將雜種第二代或卽囘交所得之種子,置於培養皿中發芽,旋卽轉置於温室內之木匣中.其用番南瓜花粉雜交所得之種子,較用南瓜花粉所得者,發芽率爲高.前者爲百分之十六,後者爲百分之七.吾人又發現雜種第一代與番南瓜親本囘交所得之種子,較其用南瓜親本者爲肥滿.此則與雜交種第一代之種子萌芽力,極爲不良之事實符合.種子之細胞核及細胞質來自同源者,似較來自異源者之發芽力爲優.由此吾人可引申細胞核與細胞質有相互關係之假設.

雜種第二代之幼苗,多爲奇特者.有則兩子葉合爲一體,有子葉呈畸形者.最後移植於田間者,僅三十九株.大多數之植株,與栽培於其旁之親本,生長同樣健旺,雜種第二代有少數植株,生長極爲柔弱,於結果前,卽已夭折.然大多數之植株,仍能與親本同時結果.少數因生長柔弱,雖能苟延生命,但不結果.又少數植株之花藥,不能開裂,一如雜種第一代植株.故在多數植株,自交爲不可能.結果仍須有賴乎囘交.因雜種第二代之總數甚少,故關於遺傳上之解釋,僅能作一種推論而已.雜種第一代及第二代植株形態上之描述,可參考附錄一.其性狀於此亦逐一加以討論.

不能孕育花粉粒之百分率: 從已開放之雄花,取其花粉粒,用碘溶液染色後,以鏡檢之,每種至少數三百粒,然後再計其百分率.其不能孕育之花粉粒的百分率,在番南瓜爲4.0%,在南瓜爲10.21%,而在雜種,則有96%.至於雜種第二代,則其百分率爲自20%直至100%.繪成弧線後,有向右傾斜狀況(圖十六).此則可表明在囘交後之次代,其染色體仍固持其分裂時奇特之情形.

花粉粒之直徑: 所用之單位爲測微計上之單位,每單位相當

於 .015 糎.番南瓜花粉粒之直徑,約較南瓜者大一單位.前者爲十單位,後者爲九單位.在附錄一所示花粉粒之大小二項,可知兩親花粉粒之大小,各自比較均一.至於雜種第一代之花粉粒之直徑,平均爲十單位,但其變異,則自七單位直至十五單位.再檢查雜種第二代花粉粒之大小,其平均直徑自八至十單位.植株中有數株花粉粒大小之變異甚小.有數株則甚大.其最大之花粉粒,有達十五單位者.減數分裂愈不規則,則無孕育力之花粉粒似愈多,而其大小之變異亦隨之而增.

果形: 番南瓜之果形,爲長圓形.而南瓜之果形,則爲盤狀.兩親雖來自普通栽培種,但兩種之果形,則各無甚變異.其雜種第一代之果實,則爲圓形(版一).在雜種第二代,果形之變化甚多,除原有之長圓形,盤形,及圓形外,又另有圓錐形,卵形及啞鈴形等.倘吾人將此等果形,用其長度與寬度之比率,作一圖形之表示,則吾人於其第二代分離情形,更可得一具體之印象(圖十七).其與南瓜親本回交所得之植株,除一株之外其一半之植株之果形,屬於盤形,一半爲圓形.在另一方面,其用番南瓜回交者,則約有一半植株之果實爲圓形,有如雜種第一代之果實.一半植株之果實,則爲長橢圓形,有如番南瓜之親本.由此吾人可知果實之形狀,似爲一主要因子(Major factor)所轄制,盤形與長圓形二者似爲不完全顯性,在雜種第二代所分離出之圓錐形,卵形,及啞鈴形,似有其他修改因子(Modifying factors)之存在.但就所得之記載,不容吾人作更進一步之解釋.

葉身: 番南瓜之葉的裂片爲圓形,而南瓜則尖形.雜種第一代葉之裂片亦爲尖形.雜種第一代與番南瓜回交,有九株爲尖形,另十株爲圓形.若與南瓜回交,則所得植株葉之裂片,全爲尖形.此種遺傳現象殆爲簡單門得爾之遺傳事實,尖形葉爲顯性.

因雜種第二代之植株不多,故對於列在附錄一之性狀,其遺傳情形,難以解釋.但其最有意義者,即成熟果實之色澤分離,除番南瓜之乳酪黃色,南瓜之紅褐色,及雜種之褐色外,另分離出紅色,橘色,乳色,白色,及黑色.此則表示因子之相互作用.但此等色澤,究何由分離,則以雜種

第二代之植株數太少,故亦難於解釋也.

在雜種第二代之植株中,則有不爲常態者,植株21與24株(皆得自雜種第一代與南瓜回交者)除有通常之雄花及雌花外,另有完全花之出現.此等完全花之萼筒,於底部擴大,有如子房,花藥與柱頭靠近,而皆呈畸形.其胚珠適與在花萼內之花柱狀之胎座相接.植株24與29之葉緣捲起,有爲永久凋萎狀者,但其他植株,則爲健全者.

此等雜交必需繼續研究.如是則較現在所顯示之事證,必更能確實也.

摘要

舉行番南瓜與南瓜雜交試驗時,若以番南瓜作爲母本,則可得受精之雜種,若作爲父本,則否.

雜種第一代,似無雜種健全性之表現.父母本既各具染色體21對,則雜種當亦有染色體四十二個.雜種第一代所產生之花粉,其有孕育能力者,僅百分之四耳.且花粉粒之大小亦不一致.

當初期減數分裂時,小胞子之形成(Microsporogensis)異乎尋常.於分裂後期時(Anaphase)因染色體分離提早或落後,結果有特多之小胞子(Microspore)及無孕育能力花粉粒之形成.染色體分離,所以不規則者,因二親之染色體,有者不相一致,因此等染色體有成中間打紐(Interstitial Chiasma)及對頭打紐(Terminal Chiasma)之現象.

從遺傳方面之研究,得知果實形狀及葉之裂片形狀,俱係按照門得爾氏遺傳率之性狀.於果形方面,則長圓形及盤形,爲不完全顯性.至於葉之裂片,則似以尖形者爲顯性.

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