Studies on the manifold effect of certain genes in Drosophila melanogaster

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Introduction

The modern theories of the structure of the hereditary material are corpuscular theories. According to these theories the hereditary material is divided into a number of autonomous units which we call genes. Our knowledge of the laws of transmission of the genes is at the present time rather considerable; the other side of the matter, however, the question as to the connexion between the genes and the characters of the developed organism has no yet been made the subject of special treatment or only been touched upon passim.

Discontinuity of the hereditary material was postulated already by the theoreticians of the pre-Mendelian period. The units composing the hereditary material (DARWIN's gemmulae, WEISSMANN's determinants, DE VRIES' pangenes) were usually considered as representatives or germs of definite organs, cells, or even parts of cells. These views were transferred unconciously, in a considerable degree, to the genes. Thus in the same way the genes were also often considered to be germs of certain organs or parts of the body.

However the discovery of polygenous characters, especially the phenomenon of polymeria discovered by Nilsson Ehle, made it necessary to recognize, that at least a great many characters are determined not by one but several and even many genes. Now it has already become very probable that every character is determined by many genes (MORGAN 1919, p. 240).

On the other hand more and more instances become known when one gene acts on the characters of different parts of the body which often are without a clear functional connection with one another. For such genes PLATE (1910, 1913) proposed the term "pleiotrop" applied chiefly by German and Scandinavian authors. At the present time some of the highest authorities in the field of genetics have come to the conclusion that the pleiotropism of the genes is not an exception but rather the general rule. According to these views the development of any part of the body does not depend on any separate genes, but on the entire genotype as a whole. (MORGAN 1919, p. 240, JOHANNSEN 1923, p. 139). From such a view there follows a series of consequences of very great theoretical importance. MORGAN (1924) thinks that "Perhaps the most significant fact, that a study of the mutant genes of *Drosophila* has brought to light, relates to the manifold effects produced by each gene".

Until now, however, the presence of manifold effects is established but for a few genes only. In their investigations geneticists start from the characters as such and avail themselves of the genes as symbols which may explain the way of hereditary transmission of the given character. It seems to me that the solution of the question may be approached in a different way. The present work is an attempt at studying the manifold effect of the genes starting from the already known and investigated genes on the one hand and from a definite organ on the other. Here the subject of study is the question, whether certain genes, which until now have only been known to manifest themselves in the external characters of the organism, affect one of the interior organs, viz. the sexual apparatus. It has to be established, whether such an influence exists at all and whether a manifold effect is manifested by all, or at any rate, by many genes or such genes are exceptions.

For the subject of this work there have been chosen the mutants of *Drosophila melanogaster*. The sexual apparatus of this fly has been studied in order to find the difference in the structure of the system of these organs in different mutants.

Literature account

The phenomenon of the manifold effect of the genes was known already to MENDEL (1865), who points out, that in the pea white colour of the flowers is accompanied by light colour of the seed coat, while plants with coloured flowers always have gray or red seed coats and reddish stems at the leaf axils. Subsequent experiments confirmed the correctness of MENDEL's observation. Moreover the mentioned gene, now designated $\mathbf{A}_1$, is at the same time the chief factor for the form of seed "indent" (WELLENSICK 1925). In the pea several more genes are known showing clearly expressed manifold effect. Thus the same gene causes the character of the surface of seeds "smooth" or "wrinkled", as well as the shape of the starch granules in the seeds, their sugar contents and absorptive capacity for water (KAPPERT 1920). The gene **B** is the factor of both the colour of the flower and the structure of the hilum. Moreover the factor B is probably identical with the factor of the colour of the seed (WELLENSICK 1925).

In the bean the same gene influences the colour and shape of the seed (JOHANNSEN 1911) as well as their colour and size (SAX 1923). In flax TAMMES (1913, 1915) discovered a genetic dependence between

the colour of the petals, their shape, the colour of the anthers, that of the seed and probably also the shape of the seed and its capacity to germinate. According to SAUNDERS (1920) in the *Mathiola incana* the same gene manifests an influence on the colour of the petals and hairiness of the stem.

NILSSON-EHLE (1909, 1914) showed, that in oats the genes controling the presence or the absence of the ligula at the same time cause a sharp alteration of the shape of the panicle. There is another even more interesting instance. In oats the gene **G** causes a yellow colour of the seed, **g** a white one. But at the same time **G** is a factor suppressing the awns and so **GG** plants are always less awned than **gg** ones. This instance presents an interest in one more respect, as the yellow colour of the seed produced by **g** is hypostatic for the black colour of the seed produced by another gene **S**. Therefore the oats **SS GG** and **SSgg** have both black seeds but **SSgg** is more awned. So in this case the effect of **g** is displayed only in the awns. This instance is very indicative since it shows, that the manifoldness of the effect of a gene often escapes our notice only because a part of its manifestations is not perceived owing to the action of other genes.

According to RASMUSON (1921) in *Godetia* the same gene acts upon the colour of the flowers and their size. In *Aquilegia vulgaris* (KRISTOFFERSON 1922) the same gene changes the colour of the flowers causing at the same time the colour of the leaves in one case on both sides of them, in other case on their underside only. Likewise the same gene causes a change of the colour of the leaf and the microscopic structure of the seed coat. Lastly the same gene influences the colour of the flower and the mean weight of the seed of this flower. Instances of manifold effect are known also in willows (HERIBERT NILSSON 1918), *Antirrhinum majus* (BAUR 1919, 1924) and in *Lupinus angustifolius* (HALLQUIST 1921).

Among animals not many instances of this kind are known. An exception is however *Drosophila*. In *Drosophila* there have been already described a great many cases of manifold effect and this phenomenon is much better known than in any other organism. There is a whole series of mutants characterised by a complex of features pertaining to different parts of the body. So the rudimentary fly differs from the normal by inferior length of the wings and the shape of the hind legs; moreover, the rudimentary one is almost quite sterile. Club causes both an alteration of the wing and the absence of sternopleural bristles. Cut

changes the shape of the wing and arista; vestigial shortens the wing and changes the location of one of the bristles on the scutellum; dachs has legs with four tarsal joints instead of five, the legs are in general shorter but besides that in this mutant there is observed a deviation in the venation; tan is distinguished by a change in the colour of the body and the loss of positive phototropism peculiar to the normal fly and all their mutants. In everyone of these instances all the enumerated alterations are without any doubt the result of the change of one and the same gene, as in crossing they are always inherited together (MORGAN 1916, MORGAN, STURTEVANT, MULLER, BRIDGES 1923). A whole series of mutants differ from the normal fly, besides certain morphological characters, by a general weakening of the viability or the sterility of one of the sexes. The viability of some mutants is so strongly reduced that they must be considered as semi-lethals as they generally seldom hatch from the pupae. In the mutants fused (alteration of the venation), rudimentary (length of the wings), morula (form of eye facettes), reduced (size of the bristles), dwarf (size of the body) and cleft (size of the wings and alteration of the venation), besides the indicated alterations of different organs of the body, is sterility observed in one of the sexes. As LYNCH's (1919) experiments have shown, the sterility in all these cases is due to the same gene as the external morphological characters.

PEARL, PARKER and GONZALEZ (1923) and GONZALEZ (1923) by way of experiments carried out with the greatest exactness have shown, that many mutants, besides variations in the colour of the body, eyes, length of wings and like characters, are distinguished by a diminished duration of life. So is for instance the imaginal life of vestigial on the average three times as short as that of the wild type. In this case the duration of life again depends on the same gene as the morphological characters of the mutant.

There is no doubt that a careful investigation will bring to light an enormous number of cases of manifold effect of the same gene. It is at any rate very probable that by this and no other way there will be explained many cases of a mysterious connexion existing between characters of an apparently quite different nature, which long since were pointed out by different authors in zoological and botanical literature. As an instance connection may be reminded existing in cats between the colour of the eyes on the one hand and deafness on the other, pointed out by DARWIN, as well as the development of hairs and teeth in doogs &c.

Materials and methods

As a material we availed ourselves of the culture of *Drosophila melanogaster* brought to Russia by prof. H. U. MULLER in August 1923 and received from the Institute of Experimental Biology in Moscou through the kindness of prof. A. S. SEREBROVSKY and prof. S. S. TCHETVERIKOV.

The cultures were conducted at the $t^0 = 25\ ^0C$ in glass cylinders having an inner dimension of $9{\cdot}5 \times 3{\cdot}8$ cm. Into each cylinder there was poured about 20 cb. cm. of nutritive medium composed of 2 ltr. water, 1 klg. raisins and 40 gr. agar-agar.

The investigation of the sexual apparatus of the wild type and the mutants showed the existence of a difference between them in a series of characters, as it has been pointed out already in my preliminary communication (DOBZHANSKY 1924). For the study of the inheritance of these differences between the mutants there were chosen but two characters viz. the colour of the testicles and the shape of the spermatheca, as these characters are the most resistant to external conditions.

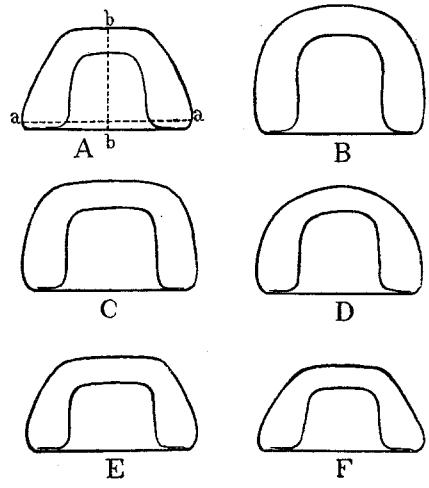

Fig. 1. Spermathecae: A = wild type, B = yellon white, C = ebony, D = bar forked, E = ivory, F = tan[2]

The investigation of the colour ot the testicles was performed by dissecting freshly killed flies in a drop of physiological solution. The investigation of the shape of the spermatheca was made with difficulty on freshly killed flies, as the epithelial layer covering the receptacles is not transparent enough. Therefore the flies were macerated in a solution of 20 % KOH. The solution was brought to the boiling point and immediatly after that cooled. Then the flies were gradually (during no less than one hour) transferred into a solution of KOH of lower concentration and at last into pure water. After having been washed the spermathecae were taken out together with the chitinous intima of the vagina and the external sexual parts. The prepared parts were put into a drop of water on a glass and covered with a cover glass. As

the receptacle has aproximately the shape of a hemisphere and measurements were taken of its diameters (Fig. 1, aa) and height (Fig. 1, bb) it must for investigation be placed in such a position that the plane of its bottom be parallel to the optic axis of the microscope. This was achieved by slightly pushing the cover glass with a needle. With a little practice it is not difficult to give the receptacle the desired position and it seldom happens that it is deformed or spoiled. Of the spermatheca placed in the right position there was made a drawing with the aid of a drawing apparatus of ABBE and then measured on paper. In each fly there was drawn one of her two receptacles. Measurements aa and bb (v. above) were taken an the index $\frac{a}{b}$ calculated, which served as a measure of the form of the spermatheca. Since there might arise a suspicion that the index $\frac{a}{b}$ measured in macerated flies differed from that in the living fly, these indices were compared in 25 individuals of the macerated and as many of the living flies, for wild type and the yellow white. The difference of the obtained mean values was smaller than the probable error of this difference.

For this work there were altogether investigated testicles in about 4000 flies and spermathecae in 13100 flies.

Colour of testicles

The testicles of *Drosophila melanogaster* have the appearance of a pair of spirally wound thick braids; the inner end of the spiral passes into a tube (vas deferens) forming in its middle a spindle-like extension filled with sperma (vesicula seminalis). The pair of vasa deferentia join and form a very short and narrow channel discharging itself into the extended frontal part of the azygos vas deferens.

The examination of the testicles of different mutants showed that according to the colour of this organ all the studied mutants fall into two groups: those having transparent testicles an those whose testicles are yellow. To the first group belong yellow white, white, ivory and star curly eosin; to the second — wild type and all the other mutants which I investigated.

In yellow white and white the testicles and vasa deferentia are always transparent. The tunic of the testicles is devoid of any colour and when light passes through it appears almost glassy. Only in individuals in the brunt of sexual activity inside the testicles and especially

in the vesiculae seminales a grayish accumulation of sperma is observed which gives them a dirty grayish colour. Not a single of the 200 dissected specimens of yellow white and white was observed with a slightest trace of yellow in the membrane of the testicles. In ivory and eosin star curly (200 specimens were dissected) the testicles proved of the same colour as in yellow white and white but in these mutants the tunic of the testicles sometimes happened to be of a very pale lemon-yellow colour. These differences are, however, so insignificant that they can be noticed only when very attentively examined.

The testicles and the pair of vasa deferentia in the wild type and all the other mutants are of a bright amber yellow colour. This colour is due exclusively to the colour of the tunic of the testicles and vasa deferentia, but the cells inclosed under it are as colourless as in white. As to the cause of the colour of the tunic it appears to be due to its being impregnated with diffused pigment. I failed to detect in it any granular pigment, neither when examining it in vivo nor on cuts. The yellow colour of the testicles of wild type and the other mutants varies very slightly and only in freshly hatched specimens it is less intense. Thus the difference of colour of the testicles between white, ivory and eosin on the one hand and wild type and the rest of mutants on the other is always a distinct one.

Inheritance of colour of testicles

In order to clear up the question as to the genetic nature of the variations in the colour of the testicles a series of crossings of mutants with transparent testicles to wild type was undertaken. When yellow white was crossed to wild type the transparency of the testicles behaved as a recessive sex linked character and there appeared a complete linkage of the gene of the testicle colour with the gene white (v. table 1).

Table 1

	gene-ration	Pellucid testicles				Yellow testicles			
		wild	yellow white	yellow	white	wild	yellow white	yellow	white
yellow white ♀ × wild ♂	F_1	—	50	—	—	—	0	—	—
	F_2	0	150	0	4	100	0	2	0
wild ♀ × yellow white ♂	F_1	0	—	—	—	50	—	—	—
	F_2	0	142	0	1	100	0	2	0
Total		0	342	0	5	250	0	4	0

Thus all males with red eyes always had also yellow testicles, while all the testicles in white eyed males were transparent. From white and yellow individuals obtained in these experiments there were bred separate cultures of these mutants and afterwards 100 white and 50 yellow examined. All the white eyed proved to have transparent testicles and all the yellow — yellow ones, quite identical in their colour with those of wild type.

Table 2

	gene-ration	Pellucid testicles		Yellow testicles	
		eosin	no eosin	eosin	no eosin
eosin star curly ♀ × wild ♂	F_1	52	—	0	—
	F_2	115	0	0	150
wild ♀ × eosin star curly ♂	F_1	—	0	—	50
	F_2	150	0	0	100
Total		317	0	0	300

When eosin star curly were crossed to wild type (table 2) the transparency of the testicles proved to be completely linked with the eosin colour of the eyes: all obtained forms not containing eosin (wild, star, curly, star curly) had yellow testicles and all forms with eosin (eosin, eosin star, eosin curly, eosin star curly) had transparent testicles.

In crosses of white to wild type (table 3) and ivory to wild type (table 4) the transparency of the testicles also proved completely linked with the colour of the eyes: all white and all ivory had transparent and all non-white and non-ivory had amber yellow testicles.

Table 3

	gene-ration	Pellucid testicles		Yellow testicles	
		white	wild	white	wild
white ♀ × wild ♂	F_1	50	—	0	—
	F_2	200	0	0	150
	F_{12}	100	0	0	75
wild ♀ × white ♂	F_1	—	0	—	50
	F_2	50	0	0	50
Total		400	0	0	325

In crosses of white to ivory all the males in generations F_1 and F_2 had transparent testicles.

Table 4

	gene-ration	Pellucid testicles		Yellow testicles	
		ivory	wild	ivory	wild
ivory ♀ × wild ♂	F_1	50	—	0	—
	F_2	100	0	0	100
	F_{12}	78	0	0	92
wild ♀ × ivory ♂	F_1	—	—	—	59
	F_2	150	0	0	100
Total		378	0	0	351

Thus there can be no doubt that the genes **w**, $\mathbf{w^{iv}}$ and $\mathbf{w^e}$ cause an alteration of the colour of the eyes peculiar to the normal fly and at the same time produce pellucidness of the tunic of the testicles.

The form of the spermatheca

The female *Drosophila melanogaster* has two spermathecae located in the cavity of the body and connected with the vagina by a narrow channel. Each spermatheca represents a more or less hemispherical rather dense chitinous capsule whose bottom is bent inward in the shape of a truncated cone (fig. 1). The diameter (aa) of the spermatheca in all flies which I examined varies from 63 to 95 μ and the hight (bb) from 37 to 58 μ. The absolute size of the spermatheca considerably varies with the size of the flies, which in its turn depends on more or less abundant feeding during the larval stage. Thus the size of the spermatheca even in specimens belonging to the same culture differs in those which hatched first from those which hatched the last. In contrast with such a discrepancy of the absolute sizes of the spermatheca, its index, viz. the value obtained by dividing the diameter by the hight $\left(\frac{a}{b}\right)$ is of remarquable constancy and very characteristic of every separate mutant. This finds its explanation in the fact that the diameter and the height of the spermatheca are strongly correlated and change proportionally under the influence of external conditions. The constancy of the index $\frac{a}{b}$ for each mutant is illustrated in the table 5, where

the results are given of repeated measurings of the index $\frac{a}{b}$ for wild type, cinnabar and tan[2], made in different years on material from cultures very widely differing in quantity of food.

Table 5

	Date	Culture Nr.	Nutrition	Mean	σ	c	Limits	n
wild type	VIII. 923	19	poor	1·727 ± 0·011	0·098	5·7	1·45—1·97	87
	III. 924	408	abundant	1·710 ± 0.009	0·086	5·0	1·50—1.89	102
	VIII. 925	1982	poor	1·737 ± 0·012	0·075	4·3	1·58—1·91	36
	VIII. 925	1983	abundant	1·719 ± 0·010	0·060	3·5	1·58—1·83	36
		Total		1·721 ± 0·005	0·086	5·0	1·45—1·97	261
cinnabar	XII. 923	208	poor	1·385 ± 0·008	0·082	5·9	1·21—1·54	100
	I. 925	1022	abundant	1·388 ± 0·007	0·070	5·0	1·22—1·56	112
	VIII. 925	2002	abundant	1·394 ± 0·013	0·078	5·6	1·27—1·61	36
		Total		1·390 ± 0·005	0·073	5·3	1·21—1·61	248
tan[2]	VI. 925	1799	abundant	1·909 ± 0·012	0·082	4·3	1·79—2·12	50
	VII. 925	1903	abundant	1·898 ± 0·014	0·068	3·6	1·74—2·08	25
	VII. 925	1904	poor	1·890 ± 0·020	0·101	5·3	1·67—2·04	50
		Total		1·901 ± 0·008	0·084	4·4	1·67—2·12	100

A general summary of the data of the size and variability of the index of the spermatheca is given on table 6. We see that some mutants in the shape of the spermatheca differ rather strongly from wild type and one another. The index of the spermatheca is lowest in yellow white (Fig. 1B) and cinnabar, in other words these mutants have the most convex spermatheca. The highest index of the spermatheca is found in tan[2] (Fig. 1F) and ivory (Fig. 1E), in other words, these mutants are characterised by the most flattened spermatheca. Wild type (Fig. 1A) occupies a place between these extreme forms, being somewhat nearer to tan[2] than to yellow white. Comparing the range of variation for different mutants we see that most of these variation curves are transgressive, but between the extreme forms a rather considerable hiatus is observed. Of the greatest interest is the question as to the number of mutants differing in the shape of their spermatheca from the wild type. Considering the difference between two mean values as certain, if it is greater than 3 m_{diff}, we must re-

cognize that only two of the investigated mutant forms, viz. star and singed do not differ in the shape of their spermatheca from wild type. Besides star and singed only black purple and vermilion dusky differ inconsiderably from wild type, while there exists a sufficiently great difference between the rest of the investigated mutants.

Table 6

	Mean	σ	c	Limits	n
yellow white	1·358 ± 0·007	0·073	5·4	1·22—1·49	100
cinnabar	1·390 ± 0·005	0·072	5·2	1·21—1·61	248
curly	1·425 ± 0·009	0·088	6·2	1·23—1·60	100
yellow	1·451 ± 0·007	0·096	6.6	1·23—1·68	192
white	1·529 ± 0·008	0·100	6·5	1·27—1·78	144
eosin	1·536 ± 0·007	0·087	5·7	1·35—1·77	178
eosin star curly	1·537 ± 0·008	0 090	5·9	1.33—1·79	123
ebony	1·608 ± 0·006	0·097	6.0	1·36—1·87	250
sooty	1·611 ± 0·006	0·088	5·5	1·41—1·88	211
yellow ivory	1·616 ± 0·009	0·095	5·9	1·37—1·84	100
bar forked	1·621 ± 0 015	0·109	6·7	1·40—1·88	53
black purple	1·679 ± 0·009	0·091	5·4	1·45—1·93	103
star	1·715 ± 0·008	0 085	5·0	1·52—1·88	118
wild type	1·721 ± 0·005	0·086	5·0	1·45—1·97	261
singed	1·726 ± 0·010	0·099	5·7	1·51—1·94	100
vermilion dusky	1·763 ± 0·009	0·091	5·2	1·53—1·94	100
dumpy	1·824 ± 0·009	0·097	5·3	1·64—2·04	115
dumpy vortex black purple	1·868 ± 0·008	0·080	4·3	1·70—2·17	103
ivory	1·893 ± 0·006	0·110	5·8	1·62—2·13	328
tan_2	1·902 ± 0·008	0·084	4·4	1·67—2·12	100

Among the data given in the table 6, those on the shape of the spermatheca of some multiple allelomorphs are of great interest. The members of the triple allelomorph wild-sooty-ebony clearly differ from each other by the colour of their bodies. However, in the shape of their spermatheca sooty and ebony are quite indistinguishable from each other (the index of sooty being equal to 1·611 ± 0·006, that of ebony — 1·608 ± 0·006) while they clearly differ from wild type. The relation in the series wild-eosin-ivory-white are still more peculiar. The members of this series can be very well distinguished from each other by the colour of their eyes; wild type is known to have red eyes, while the eyes of eosin and ivory are lighter, and white at last has

white eyes. If we dispose these four forms in a row according to the shape of their spermatheca we will obtain the following order:

ivory	wild type	eosin	white
$1{\cdot}893 \pm 0{\cdot}006$	$1{\cdot}721 \pm 0{\cdot}005$	$1{\cdot}536 \pm 0{\cdot}007$	$1{\cdot}529 \pm 0{\cdot}008$

that is: ivory deviates from wild type in the opposite direction compared to eosin and white and, moreover, eosin and white are alike in the shape of the spermatheca. It must be reminded here that eosin, ivory and white, as an examination of the colour of the testicles shows, have testicles of the same colour, but very sharply differ from wild type. Thus, if in these cases variation of the colour of the eyes, the tunic of the testicles and the shape of the spermatheca are due to the same gene, it must be admitted that the alterations produced by this gene in different parts of the body are far from proceding parallely and hand in hand. The spermathecae of the various mutants differ from each other not only by the value of the index, but also by some other characters. First of all, the index, though it is a value by which the shape of this organ is well characterised, nevertheless does not characterize it exhaustively. There exist other differences in the shape of the spermatheca not to be expressed in terms of numbers, though perceived by the practiced eye. So ebony and bar forked have the same index of the spermatheca and nevertheless the shape of this organ is different in this mutant. The spermatheca of bar forked (fig. 1D) in the optical cut approaches the form of a semicircle. The form of the spermatheca in ebony in the optical cut approaches a trapeze (fig. 1C). Similar differences are observed between yellow white and cinnabar (fig. 1B). These differences are rather constant, indeed, but in crossings of mutants, made for the purpose of establish the genetic nature of these differences, they could not, however, be ascertained with great exactness.

Inheritance of the form of the spermatheca. General remarks

In the preceding chapter we have shown that the spermathecae in various mutants differ more or less sharply from one another and wild type. The most reliable expression of these differences is the index of the spermatheca which caracterizes the form of this organ. The task of our further investigation is to clear up the question, whether the different forms of the spermatheca are due to the same genes as

the external differences of the mutants or whether the form of spermatheca and the external characters depend on different genes.

If any mutant differs from wild type by certain external characters (e. g. colour of the eyes, colour of the body etc.) differing at the same time by the form of the spermatheca, the genetic nature of these differences must be established by the crossing of this mutant to wild type. If in the segregation taking place in F_2 a linkage of the external characters with those of the spermatheca is always observed, we will be justified in concluding that all these characters are manifestations of one and the same gene. However, the practical solution of this question is not so easy as it was in the case of the colour of the testicles. The difficulty is due to the fact, that the differences in the size of the spermatheca observed between the mutants and wild type amount only to differences of mean values. Therefore the only criterion allowing to form an opinion on the presence of absolute linkage between the characters of the spermatheca and the external characters is the determination of the mean values of the index of the spermatheca in the compared forms before and after crossing.

Let us take for instance the mutant ebony. Ebony differs from wild type in no less than two characters: the body of ebony is black and the index of spermatheca is equal to $1{\cdot}608 \pm 0{\cdot}006$ on the average; the body of wild type is gray and the index of the spermatheca is $1{\cdot}721 \pm 0{\cdot}005$. On the genetic nature of these distinctions there may be expressed three suppositions, which can be tested only by way of crossing.

1. The colour of the body and the form of the spermatheca are determined by the same gene. Designating this gene as **E** and **e**, we must represent the cross of wild type ebony as follows:

$$\begin{array}{ll} P & \ldots\ldots\ldots \quad E \times e \\ F_1 & \ldots\ldots\ldots \quad E \\ F_2 & \ldots\ldots\ldots \quad 3E + 1e \end{array}$$

Let us breed from the flies obtained in F_2 the homozygous wild type. The homozygous wilds obtained after crossing will differ from ebony by the form of the spermatheca as sharply as before crossing. Hence in this case the mean values of the index of the spermatheca for wild and for that of ebony will not change after crossing.

2. The colour of the body and form of the spermatheca depend on different genes. The genes **E**, **e** determine the colour of the body

but have no influence on the spermatheca. Let the gene determining the form of the spermatheca be called **X**, **x** and wild type be designated as **EX** and ebony as **ex**. The results of crossing will be different and depend on the genes **E** and **X** being linked or not.

A. The genes **E** and **X** are not linked. The cross of wild type × ebony may be represented as follow:

$$\begin{array}{ll} P & EX \times ex \\ F_1 & EX \\ F_2 & 3E\ (3X + x) : 1e\ (3X + x) \end{array}$$

Here in F_2 ebony and wild type being different in colour will be alike in the form of spermatheca. So if the colour of the body and the form of the spermatheca depend on different genes which are not linked, the difference between the mean values of the index of the spermatheca for ebony and for wild type in F_2 must become equal to zero.

B. The genes **E** and **X** are linked. The result of the cross wild type × ebony will be the following:

$$F_2 \quad 3E\ (3n\ X + x) : 1e\ (3X + nx)$$

where the coefficient n will be the greater the closer is the linkage of **E** and **X**. In this case the homozygous wild type and ebony which we isolated after crossing, will differ in the form of the spermatheca less markedly, than they did befor crossing.

If the population obtained in F_2 is allowed to propagate, and if the mating within this population takes place at random, then in each generation, as has been shown by Jennings (1917), the percentage of individuals **Ex** and **eX** will increase at the expence of the decreasing percentage of the individuals **EX** and **ex**. In other words, the value of the coefficient n will decrease with each generation, tending to become equal to 1. Thus the expression $3E\ (3n\ X + x) : 1e\ (3X + nx)$ will have the tendency to become $3E\ (3X + x) : 1e\ (3x + x)$. When we study the spermatheca of wild type and ebony in such a population, we shall observe a decrease of the difference of the mean values with each generation until this difference practically disappears. The disappearance of this difference will take place the more rapidly the greater is the percentage of crossing-over between the genes **E** and **X**.

3. The gene **E, e** acts on the colour of the body as well as on the form of the spermatheca. The difference of the form of the spermatheca between wild type and ebony does not, however, depend ex-

clusively on the gene **E, e** but also on a special gene **Z, z**, which alters only the form of the spermatheca and has no perceptible influence whatever on the colour of the body. Let wild type be called **E Z** and ebony **e z**. The result of crossing wild type × ebony will be as follows:

$$F_2 \ldots\ldots 3\,E\,(3\,n\,Z + z) : 1\,e\,(3\,Z + n\,z),$$

where $n = 1$, if the genes **E** and **X** are not linked. Since wild type and ebony obtained after crossing have interchanged the genes **Z — z** modifying the form of spermatheca, their spermathecae will differ less obviously than before crossing. After crossing there will take place some approachment of the mean values of the index of the spermatheca for ebony and wild type, but this approachment will not attain identity, since the genes **E, e** by themselves cause unequality of the spermatheca of wild type and ebony. If the population obtained in F_2 propagates, the spermatheca of ebony, no matter what the number of generations of the cross, will not become equal to that of wild type.

Thus the possible linkage of the gene producing external characters with the hypothetical genes ruling the form of spermatheca makes it impossible to confine oneself to the analysis of the two first generations of hybrids. Therefore in some of the experiments the individuals obtained in F_2 were again crossed to each other during a series of generations. For this purpose there were in each generation brought together the heterozygous dominant specimens of one sex with the recessive specimens of the other. From time to time out of this hybrid population there were taken several pairs of dominant and several pairs of recessive individuals from which a separate progeny was obtained. When the cultures obtained in this way became homozygous, the spermathecae in the flies of each culture were investigated separately.

Ebony × wild type (v. table 7)

Ebony ♀ × wild ♂ and wild ♀ × ebony ♂ were crossed. The body of ebony is black, that of wild type yellowish gray. The spermatheca of ebony has an average index $1{\cdot}608 \pm 0{\cdot}006$, that of wild $-1{\cdot}721 \pm 0{\cdot}005$. Notwithstanding its insignificance this difference is quite certain (v. table 7). In F_1 the hybrid **E e** are of an intermediate colour of the body, nearer to wild than to ebony so that in this case the colour of wild may be referred to as not being completely dominant. The spermatheca of F_1 obtained by this crossing also

proved to be intermediate in its form between the parents (v. table 7 **E e**) with regard to the range of variation as well as to its mean size. However here wild could not be said to dominate over ebony, since the mean size of the index of the spermatheca in F_1 is $1{\cdot}620 \pm 0{\cdot}010$, and consequently even nearer to ebony than to wild type. Reciprocal crossing produce similar results: in crosses of ebony ♀ × wild ♂ in F_1 gave a somewhat greater mean value (culture Nr. 500) than crosses of wild ♀ × ebony ♂ (cultures Nr. 499 and 504); this difference is, however, so insignificant that it is hardly possible to attribute to it any importance at all.

In F_2, owing to the different colour of the body between the forms of the composition **E E** and **E e**, apart individuals were set probably representing homozygous wild type. Examination of the spermathecae was made only in wild (**E E**) and ebony (**e e**). The mean value of the index for wild proved to be $1{\cdot}735 \pm 0{\cdot}011$, i. e. identical with that observed before the cross, while ebony in F_2 had a mean value of $1{\cdot}552 \pm 0{\cdot}012$ i. e. compared with P the index not only had not increased, but on the contrary somewhat decreased. The difference between the means for ebony from P and from F_2 is $1{\cdot}608 - 1{\cdot}552 = 0{\cdot}056 \pm 0{\cdot}013$. The difference between wild and ebony in F_2 is $0{\cdot}183 \pm 0{\cdot}016$, that is to say, certain. The results obtained in F_2 from the described cross demonstrate that the colour of the body and form of the spermatheca in ebony are dependent on one gene or on closely linked genes.

In order to verify this conclusion the crossings were continued. The heterozygous wild (**E e**) obtained in F_2 was crossed to ebony (**e e**), and so were these obtained in F_3, F_4 etc.; thus the crossing was carried on to F_{31}. In F_{12} from this crossing there were examined the spermathecae of ebony obtained in the cultures Nr. 800 and 801. Besides, from culture Nr. 800 3 ♀♀ and 5 ♂♂ of heterozygous wild type (**E e**) were taken in whose offspring the homozygous wild (**E E**) were selected. The result was culture Nr. 845, which produced exclusively individuals of the composition **E E**. The examination of the spermathecae of ebony and wild type obtained in this way showed, that the difference between them had persisted: $0{\cdot}131 \pm 0{\cdot}014$. However, an examination of table 7 shows that the mean values in F_{12} are higher than those observed both in P and F_2, for wild type as well as especially for ebony. This increase may be best explained as a result of the influence of some external factors, acting on the cultures at that time.

Table 7. Ebony × wild type

		Culture Nr.	Mean	σ	c	Limits	n
P	E E		1·721 ± 0·005	0·086	5·0	1·45—1·97	261
	e e		1·608 ± 0·006	0·097	6·0	1·36—1·87	250
F_1	E e	499	1·618 ± 0·021	0·115	7·1	1·38—1·87	30
		500	1·656 ± 0·014	0·100	6·0	1·46—1·92	50
		504	1·594 ± 0·014	0·102	6·4	1·42—1·88	50
		Total	1·620 ± 0·010	0·110	6·8	1·38—1·92	130
F_2	E E	593	1·727 ± 0·013	0·095	5·5	1·54—1·92	47
		597	1·744 ± 0·017	0·096	5·5	1·54—2·00	33
		Total	1·735 ± 0·011	0·096	5·6	1·54—2·00	80
	e e	593	1·556 ± 0·016	0·115	7·4	1·38—1·84	49
		597	1·548 ± 0·017	0·109	7·0	1.37—1·74	42
		Total	1·552 ± 0·012	0·110	7·1	1·37—1·84	91
F_{12}	E E	845	1·761 ± 0·012	0·086	4·9	1·58—1·92	50
	e e	800	1·626 ± 0·010	0·087	5·3	1·48—1·79	69
		801	1·635 ± 0·016	0·110	6·7	1·39—1·92	47
		Total	1·630 ± 0·008	0·091	5·5	1·39—1·92	116
F_{18}	E E	1118	1·732 ± 0·020	0·098	5·7	1·53—1·95	23
	e e	1119	1·642 ± 0·021	0·091	5·5	1·45—1·81	19
		1158	1·578 ± 0·019	0·075	4·7	1·48—1·76	16
		1159	1·618 ± 0·014	0·070	4·3	1·48—1·74	25
		Total	1·615 ± 0·011	0·083	5·2	1·45—1·81	60
F_{31}	E E	2317	1·724 ± 0·019	0·094	5·5	1·50—1·88	25
		2319	1·734 ± 0·016	0·081	4·7	1·57—1·85	25
		2422	1.736 ± 0.023	0·115	6·6	1·53—1·91	25
		2423	1·760 ± 0·015	0·076	4·3	1·50—2·00	25
		Total	1·739 ± 0·010	0·096	5·5	1·50—2·00	100
	e e	2153	1·587 ± 0 016	0·080	5·0	1·48—1·86	25
		2159	1·632 ± 0·018	0·089	5·5	1·50—1·82	25
		2203	1·594 ± 0·013	0·063	4·0	1·46—1·75	25
		2204	1·570 ± 0·016	0·078	5·0	1·40—1·75	25
		Total	1·596 ± 0·008	0·083	5·2	1·40—1·86	100

In F_{18} a selection of homozygous wild and ebony was again made. The results obtained by the examination of the spermathecae proved very near to those observed in F_{12}. The difference of the mean values is $0{\cdot}117 \pm 0{\cdot}023$. As before any coincidence of the variation curves of ebony and wild type is out of the question.

In F_{31} out of a mixture of **Ee** and **ee** were set apart 4 ♀♀ and 4 ♂♂ **Ee** and 4 ♀♀ and 4 ♂♂ **ee**. 4 parallel cultures of each of these forms were founded. In three generations there was made a selection of homozygous wild type after which were obtained 4 cultures of homozygous wild (Nr. 2317, 2319, 2422, 2423) and four cultures of ebony (Nr. 2153, 2159, 2203, 2204). The examination of the spermathecae of these flies showed that in spite of such prolonged crossing the colour of the body and form of the spermatheca had remained linked. The difference of $M_{wild} - M_{eb} = 0{\cdot}143 \pm 0{\cdot}013$. The range of variation also had remained different (wild 1·50—2·00, ebony 1·40—1·86). It is a fact of essential importance, that the results from the different cultures proved to be very near to one another. If, however, the colour of the body and form of the spermatheca were dependent on different genes, the population in F_{31} excepting cases of a very close linkage between the genes, would already contain a considerable quantity of products of interchange between the genes. Thus we might justly expect that one at least of the individuals of ebony which we had selected would have produced offspring having a spermatheca of a shape reminding of the average of wild or the reverse. Nothing of the kind was observed, therefore, we must recognize the probability of the conclusion, that in this case the colour of the body and form of the spermatheca are dependent either on the same gene or on genes very closely linked together.

Sooty × wild type (v. table 8)

The gene sooty (e^s) is allelomorphous with ebony (e) and wild type (E). The colour of the body of sooty is considerably darker than that of wild, but lighter than that of ebony. In the shape of the spermatheca sooty is identical with ebony but different from wild. Thus the crossed forms are in this case identical as to the form of the spermatheca with the preceeding cross.

In F_1 the colour of the body is almost identical with wild type; the heterozygous Ee^s are on the whole only a little darker than the homozygous **EE**. The form of the spermatheca in F_1 from the cross

under consideration proved intermediate but obviously nearer to sooty than to wild ($M = 1{\cdot}634 \pm 0{\cdot}008$). It is interesting to note that the heterozygous Ee^s and Ee have identical mean values (for Ee $M = 1{\cdot}620 \pm 0{\cdot}010$).

Table 8. Sooty × wild type

		Culture Nr.	Mean	σ	c	Limits	n
P	E E		1·721 ± 0·005	0·086	5·0	1·45—1·97	261
	$e^s e^s$		1·611 ± 0·006	0·088	5·5	1·41—1·88	211
F_1	E e^s	1070	1·634 ± 0·008	0·081	5·0	1·45—1·80	108
F_2	E E	1814	1·689 ± 0·010	0·093	5·5	1·46—1·92	86
	$e^s e^s$	1824	1·572 ± 0·008	0·079	5·0	1·41—1·73	97
F_{16}	E E	2152	1·734 ± 0·014	0·069	4·0	1·60—1·87	25
		2156	1·742 ± 0·014	0·070	4·0	1·62—1·91	25
		2225	1·712 ± 0·019	0·094	5·5	1·52—1·88	25
		2226	1·776 ± 0·016	0·080	4·5	1·59—1·88	25
		Total	1·741 ± 0·008	0·082	4·7	1·52—1·91	100
	$e^s e^s$	2032	1·560 ± 0·014	0·067	4·3	1·45—1·77	25
		2033	1·594 ± 0·017	0·086	5·4	1·42—1·77	25
		2150	1·550 + 0·016	0·082	5·3	1·43—1·76	25
		2151	1·602 ± 0·017	0·084	5·2	1·43—1·79	25
		Total	1·576 ± 0·008	0·083	5·3	1·42—1·79	100

The flies obtained in F_2 were not directly examined since it is impossible, as mentioned above, to distinguish individuals Ee^s from those EE by their outward appearance, and therefore only the mixture of homozygous and heterozygous wild underwent examination. The heterozygous wild is, however, in the form of its spermatheca so near sooty, that such an examination would hardly lead to clear results. Therefore, from the individuals obtained in F_2 mass cultures were founded where for 8 generations the homozygous wild type was selected. This selection from a mass culture is no easy task since it is difficult to make sure that all individuals are homozygous. From sooty obtained in there also 5 pairs of flies which served as progenitors to mass cultures of sooty were picked out. It resulted from the examination of the spermathecae obtained in this way that the difference

between them in the form was found to have persisted: $M_w - M_s = 0{\cdot}117 \pm 0{\cdot}013$. Attention is drawn by the decrease of the mean value in wild type: $1{\cdot}689 \pm 0{\cdot}010$ instead of $1{\cdot}721 \pm 0{\cdot}005$. This decrease is in the first place mathematically not certain and, moreover, it has most probably to be explained as resulting from the presence in the examined material of several individuals of the composition **Ee^s**. The mean value for sooty in F_2 also proved lower than in the P generation: $1{\cdot}572 \pm 0{\cdot}008$ in F_2 instead of $1{\cdot}611 \pm 0{\cdot}006$ in P.

2 females of wild type obtained in F_2 were mated to males of sooty obtained in the same generation. The same was done in F_3, F_4 etc. until F_{16}. From F_{16} there were picked out 5 ♀♀ and 5 ♂♂ sooty and wild type and founded 5 parallel cultures of each of these forms. Thus each culture had for its progenitor one single ♀ and one single ♂. In the cultures of wild type there were selected the homozygous wild type for 3 generations after which the homozygous wild and sooty were examined. The difference of their mean values in F_{16} appeared equal to $0{\cdot}165 \pm 0{\cdot}011$. Sooty had in F_{16} the same index ($1{\cdot}576 \pm 0{\cdot}008$) as in F_2, but somewhat lower than in P. The mean value of wild type in F_{16} was $1{\cdot}741 \pm 0{\cdot}008$ i. e. almost equal to P.

The mentioned facts speak in favour of the characters of colour of the body and form of the spermatheca being dependent on one and the same gene or genes closely linked to each other.

Cinnabar × wild type (v. table 9)

Cinnabar differs from wild type by the bright cinnabar-red colour of the eyes. The spermatheca of cinnabar sharply differs from that of wild; the mean value of the index $\frac{a}{b}$ is for cinnabar $1{\cdot}390 \pm 0{\cdot}005$ and for wild type $1{\cdot}721 \pm 0{\cdot}005$. The variation curves are rather feebly transgressing.

The heterozygous **Cn cn** have somewhat brighter eyes than **Cn Cn** but this difference is so insignificant, that a distinction of these forms is impossible. In F_1 obtained by a cross of cinnabar ♀ × wild ♂ (cultures Nr. 1108 and 1110) and of wild ♀ × cinnabar (Nr. 311, 1063) the spermatheca proved of an intermediate form, but somewhat nearer to cinnabar than to wild. The mean value of the index in F_1 is $1{\cdot}482 \pm 0{\cdot}007$.

Table 9. Cinnabar × wild type

		Culture Nr.	Mean	σ	c	Limits	n
P	Cn Cn		1·721 ± 0·005	0·086	5·0	1·45—1·97	261
	cn cn		1·390 ± 0·005	0·072	5·2	1·21—1·61	248
F_1	Cn cn	311	1·446 ± 0·019	0·096	6·6	1·30—1·64	25
		1063	1·497 ± 0·012	0·100	6·7	1·32—1·68	64
		1108	1·470 ± 0·019	0·102	6·9	1·28—1·68	28
		1110	1·493 ± 0·010	0·076	5·1	1·34—1·63	56
		Total	1·482 ± 0·007	0·095	6·4	1·28—1.68	173
F_2	Cn cn + Cn Cn	1117	1·548 ± 0017	0·090	5·8	1·35—1·72	27
		1124	1·555 ± 0·022	0·130	8·4	1·35—1·84	42
		Total	1·552 ± 0·013	0·109	7·0	1·35—1 84	69
	cn cn	1205	1·431 ± 0·017	0·095	6·6	1·25—1·61	33
		1219	1·442 ± 0·014	0·104	7·2	1·16—1·61	59
		1233	1·446 ± 0·013	0·070	4·8	1·28—1·58	30
		Total	1·441 ± 0·009	0·096	6·7	1·16—1·61	122
F_3	Cn Cn	1325	1·637 ± 0·017	0·102	6·3	1·43—1·84	35
		1391	1·650 ± 0·013	0·071	4·3	1·45—1·80	33
		Total	1·644 ± 0·011	0·090	5·5	1·43—1·84	68
	cn cn	1319	1·375 ± 0·009	0·068	4·9	1·22—1·55	53
		1326	1·378 ± 0·010	0·068	4·9	1·22—1·52	41
		Total	1·377 ± 0·007	0·067	4·9	1·22—1·55	94
F_{12}	Cn Cn	1849	1·626 ± 0 012	0·073	4·5	1·50—1·83	35
		1850	1·664 ± 0·014	0·082	4·9	1·45—1·85	35
		1932	1·587 ± 0·017	0·083	5·3	1·43—1·76	25
		1933	1·630 ± 0·015	0·076	4·7	1·49—1·80	25
		1935	1·610 ± 0·015	0·077	4·8	1·45—1·80	25
		Total	1·627 ± 0·007	0·083	5·1	1·43—1·85	145
	cn cn	1780	1·453 ± 0·009	0·066	4·6	1·30—1·58	50
		1847	1·391 ± 0·011	0·074	5·3	1·22—1·60	49
		1848	1·445 ± 0·010	0·068	4·7	1·29—1·59	50
		Total	1·430 ± 0·006	0·075	5·2	1·22—1·60	149

F_2 was obtained from cinnabar ♀ × wild ♂ only. Cinnabar on the one hand and a mixture of **Cn cn** and **Cn Cn** on the other were examined. Cinnabar had an average index of 1·441 ± 0·009, i. e. somewhat higher than before the crossing (the difference between the means is as much as 0·051 ± 0·010); this difference is mathematically certain. The mixture of **Cn cn** and **Cn Cn** gave a mean value of 1·552 ± 0·013. Taking into consideration that in this mixture the number of **Cn cn** is in relation to **Cn Cn** as 2 : 1, and starting from the data for P and F_1 and on the assumption that the shape of the spermatheca and the colour of the eyes are due to one gene, we are able to calculate the expected mean value for our mixture — 1·562, which coincides with what we actually observe. The obvious increase of the mean value observed in cinnabar does not, however, allow to ascribe the alteration of the colour of the eye and of the form of the spermatheca to one gene exclusively. These characters are dependent either on different but linked genes, or the gene of cinnabar affects the form of the spermatheca, moreover one or several more genes are present modifying the form of this organ independently of cinnabar. Only by means of continuing the crossing it is possible to get nearer to the solution of this alternative.

Several cinnabar females obtained in F_2 were crossed to heterozygous males of wild type and the same repeated in F_3, F_4 and so on as far as F_{12}. In F_3 there were picked out 2 ♀♀ cinnabar and 2 ♀♀ wild type which were put into cylinders provided with food. For three generations in the offspring of the wild type there was made a selection of the homozygous wild obtained in the cultures Nr. 1325 and 1391. Their examinaton showed that the mean value of the index for wild type had decreased after crossing with cinnabar and had become equal to 1·644 ± 0·011. The difference between P and F_3 in this respect is 0·077 ± 0·012, i. e. quite certain. On the other hand cinnabar has in F_3 a mean value of 1·377 ± 0·007, i. e. the same as in P, but lower than in F_2. The difference between wild type and cinnabar in F_3 is 0·267 ± 0·013, i. e. it indubitably exists. The decrease of the index of cinnabar observed in F_3 in comparison with F_2 can be explained either by accidental causes (influence of external conditions) or, and this is more probable, by a fortuitous choice of individuals of cinnabar which had in F_3 the same composition as before the cross, i. e. such as had not received the genes modifying the form of the spermatheca in the plus direction.

In F_{12} 4 ♀♀ and 4 ♂♂ of wild type were picked out and placed in pairs in separate cultures. In the same way there were picked out 4 pairs of cinnabar. In the cultures of wild type the **Cn Cn** were carefully selected for 8 generations. Such a prolonged selection is justified by the intention to exclude any possibility of the presence in the cultures of individuals of the composition **Cn cn.** The examination of cinnabar gave a mean value of the index of $1{\cdot}430 \pm 0{\cdot}006$. In wild type the mean value proved to be as much as $1{\cdot}627 \pm 0{\cdot}007$. The difference between them is $0{\cdot}197 \pm 0{\cdot}009$; the spermathecae of cinnabar and wild type had, accordingly remained obviously different, in spite of 12 generations of crosses. On the other hand the examination of the mutant after crossing reveals an obvious approach of their mean values in comparison to P. This approach is exhibited with particular clearness when we compare the variation curves of cinnabar and wild type before crossing with the curves of the same mutants after crossing.

The deduction to be made from the described facts is as follows. The gene cinnabar either acts on the colour of the eyes together with the form of the spermatheca, but there exists in addition another gene (or genes) modifying the form of the spermatheca, or the colour of the eyes and form of the spermatheca are dependent on different but closely linked genes.

Dumpy vortex black purple × wild type

The homozygous dumpy vortex black purple has a mean value of the index $\frac{a}{b}$ of $1{\cdot}868 \pm 0{\cdot}008$, i. e. considerably higher than that of wild type, which is $1{\cdot}721 \pm 0{\cdot}005$. By crossing (dumpy vortex black purple ♀ × wild type ♂) F_1 ♀ × dumpy vortex black purple ♂ there were obtained along with the form entering into the crossing also products of crossing-over: dumpy on the one hand and black purple on the other. Altogether there were obtained 3 ♀ and 5 ♂ dumpy and 2 ♀ and 2 ♂ black purple. They were picked out and the homozygous forms in their progeny were selected. The examinations of the spermathecae showed that the mean value of the index for dumpy is $1{\cdot}824 \pm 0{\cdot}009$, i. e. almost the same as for dumpy vortex black purple. The spermatheca of black purple has $M = 1{\cdot}679 \pm 0{\cdot}009$ (table 6) i. e. lower than both crossed forms.

Eosin star curly × wild type

Eosin star curly represents a system of balanced lethals. One of the second chromosomes contains a dominant and lethal, when homozygous, gene curly (Cy) assoicated with $C_{II\,L}$ and $C_{II\,R}$, genes that do not allow crossing-over in the second chromosome (WARD, 1923, MORGAN, BRIDGES, STURTEVANT, 1925, p. 223).

The chromosome, which is homologue to that which carries curly, contains a dominant and lethal, when homozygous, gene star (S). In the sex-chromosome there is a gene eosin (w^e). The index of the spermatheca of eosin star curly is on the average equal to $1{\cdot}537 \pm 0{\cdot}008$. Eosin star curly ♀ was crossed to wild type ♂ and the eosin, star and curly obtained in F_2 picked out. Then eosin ♀ was mated to wild type ♂ and in F_2 picket out ♀♀ and ♂♂ eosin, which served as ancestors of a pure culture of eosin. A male curly was mated to a female wild type and after that the obtained ♀♀ and ♂♂ of curly cultured in an unbalanced condition. Star was treated in just the same way as curly.

When the spermathecae of eosin were examined it appeared that their index was on the average equal to $1{\cdot}536 \pm 0{\cdot}007$, i. e. the same as that for eosin star curly on the one hand and the same as for white on the other (v. table 6). Out of the cultures of star and curly females were taken with clearly expressed characters of star and curly respectively. The spermatheca of star proved to be alike with that of wild type ($M = 1{\cdot}715 \pm 0{\cdot}008$), while the spermatheca of curly differed from that of eosin star curly and even more sharply from that of wild type: the mean value of the index $\frac{a}{b}$ in curly is $1{\cdot}425 \pm 0{\cdot}009$ (v. table 6).

The difference of the spermathecae of curly and wild type is dependent on some gene lying in the second chromosome which contains curly. It is difficult to establish, whether this gene is identical with the gene curly or independent of it, since the chromosome containing curly contains two more suppressors of crossing-over and perhaps some other genes cinnabar$_2$, according to WARD (1923). As to eosin, the form of the spermatheca, probably, is here dependent either on eosin, or on a gene located not very far from eosin in the same chromosome.

Yellow white × wild type (v. table 10)

Yellow white ♀ × wild ♂ (cultures N 69, 1867) and wild ♀ × yellow white ♂ (culture 68) were crossed. Yellow white differs from wild type by its eyes being white and the colour of the body yellow. The spermatheca of yellow white is the most convex of all the mutants I know. The mean value of the index $\frac{a}{b}$ is for yellow white $1{\cdot}358 \pm 0{\cdot}007$ and the variation curves of yellow white and wild type show almost no transgression (v. table 10).

In F_1 the colour of the body and eye of wild type at sight completely dominates over yellow white. The index of the spermatheca is $1{\cdot}627 \pm 0{\cdot}007$, i. e. it is intermediate between the parental forms but obviously nearer to wild type. Thus the form of the spermatheca of wild type partly dominates over yellow white. Reciprocal crosses give the same results.

F_2 was obtained only from yellow white ♀ × wild ♂. The heterozygous females **YyWw** had a spermatheca of the same form as in F_1; the mean value of the index $\frac{a}{b}$ is $1{\cdot}643 \pm 0{\cdot}007$. The homozygous yellow white reared in the same cultures (v. table 10) as the above described **Yy Ww** have a mean index of $1{\cdot}463 \pm 0{\cdot}007$. Thus, the wild type and yellow white obtained in F_2 are clearly distinguishable from each other: the difference between the indices is $0{\cdot}180 \pm 0{\cdot}010$. However, when we compare the spermathecae of yellow white obtained in F_2 with those before crossing (P), we notice at once that the index $\frac{a}{b}$ has obviously increased $M_{F2}—M_P = 0{\cdot}105 \pm 0{\cdot}010$. After crossing, the spermathecae of yellow white and wild type have, accordingly, become considerably more alike one another than they were before crossing. This approach however by no means reaches complete identity. A similar conclusion has to be drawn from the comparison of the variation range of yellow white in F_2 with that of yellow white in P (v. table 10). We see that the range of variation in the minus direction is the same in both yellow whites: 1·22 before crossing and 1·19 in F_2. But instead there has occurred a considerable displacement of the variation curve in the plus direction; the extreme plus variation before the cross was 1·49; in F_2 we see already 1·74. The variation curves of yellow white and wild type belonging to F_2 are already considerably more transgressive.

Table 10. Yellow white × wild type

		Culture Nr.	Mean	σ	c	Limits	n
P	YY WW		1·721 ± 0·005	0·086	5·0	1·45—1·97	261
	yy ww		1·358 ± 0·007	0·073	5·4	1·22—1·49	100
F_1	Yy Ww	68	1·640 ± 0·012	0·075	4·6	1·50—1·86	38
		69	1·600 ± 0·011	0·086	5·4	1·40—1·78	63
		1867	1·650 ± 0·010	0·072	4·3	1·45—1·83	50
		Total	1·627 ± 0·007	0·085	5·2	1·40—1·86	151
F_2	yy ww	114	1·434 ± 0·010	0·095	6·6	1·19—1·74	84
		1950	1·468 ± 0·021	0·087	5·9	1·27—1·59	18
		1951	1·493 ± 0·015	0·070	4·7	1·36—1·64	21
		1952	1·495 ± 0·018	0·082	5·5	1·34—1·62	20
		1953	1·506 ± 0·020	0·079	5·3	1·39—1·65	16
		1958	1·486 ± 0·017	0·086	5·8	1·30—1·60	25
		Total	1·463 ± 0·007	0·095	6·5	1·19—1·74	184
	Yy Ww	114	1·614 ± 0·011	0·104	6·5	1·33 - 1·86	87
		1950	1·680 ± 0·016	0·082	4·9	1·55—1·80	25
		1951	1·700 ± 0·015	0·075	4·4	1·53—1·85	25
		1952	1·644 ± 0·015	0·073	4·4	1·54—1·82	25
		1958	1·650 ± 0·018	0·091	5·5	1·46—1·82	25
		Total	1·643 ± 0·007	0·096	5·9	1·33—1·86	187
	YY WW	135	1·668 ± 0·017	0·100	6·0	1·48—1·90	35
F_3	yy ww	311	1·465 ± 0·012	0·113	7·7	1·22—1·72	91
		400	1·516 ± 0·014	0·095	6·3	1·31—1·68	46
		Total	1·483 ± 0·009	0·104	7·0	1·22—1·72	137
	YY WW	401	1·679 ± 0·019	0·107	6·4	1·52—1·96	32
F_8	yy ww	482	1·514 ± 0·014	0·096	6·4	1·31—1·69	47
		483	1·494 ± 0·013	0·093	6.2	1·30—1·75	52
		Total	1·504 ± 0·010	0·096	6·4	1·30—1·75	99
	YY WW	484	1·641 ± 0·010	0·104	6·3	1.40—1·93	100

Several ♀♀ and ♂♂ of wild type obtained in the culture Nr. 114 were isolated and in their offspring selected the homozygous wild type obtained in culture Nr. 135[1]. Examination of the flies produced in

[1] On table 10 the culture Nr. 135 is placed in the column F_2 although with regard to culture Nr. 114 it is already F_4. By placing here the homozygous wild type in

this culture showed that the mean value of the index for them was $1{\cdot}668 \pm 0{\cdot}017$, i. e. that the index for the homozygous **YYWW** had most probably somewhat decreased after the crossing although by no means as much as to coincide with yellow white.

From the flies reared in culture Nr. 114 there were taken 3 ♀♀ of wild type and crossed to 2 ♂♂ yellow white taken from the same culture. The same was done with the offspring and the crossing thus carried on to F_8. In F_6 and F_8 several individuals of wild type were isolated and in their offspring selected the homozygous wild type. Among these generations several pairs of yellow white which gave pure cultures were likewise picked out. Examination of the homozygous wild type obtained in this way showed that the index of their spermatheca is on the average lower than it was in wild type before crossing. For the isolated individuals of F_6 it was $1{\cdot}679 \pm 0{\cdot}019$ and those of F_8 $1{\cdot}641 \pm 0{\cdot}010$. On the other hand the isolated yellow white of these generations had an index of the spermatheca which was considerably higher than before the crossing: in F_6 — $1{\cdot}483 \pm 0{\cdot}009$ and in F_8 — $1{\cdot}504 \pm 0{\cdot}010$. The difference between the spermathecae in wild type and yellow white, however, persisted: in F_6 the difference was $0{\cdot}196 \pm 0{\cdot}021$ and in F_8 it was $0{\cdot}137 \pm 0{\cdot}014$. Thus notwithstanding the fact, that the spermathecae in wild type and yellow white after crossing had become considerable more alike, this similarity did not attain identity.

From the foregoing description of the results of crossing it follows, that the difference in the form of the spermatheca between yellow white and wild type is dependent on some genes (or one gene) closely linked to the genes yellow and white or partly on yellow or white themselves and partly on genes independent of them, which modify the form of the spermatheca.

In F_2 of the described cross 3 ♀♀ and 6 ♂♂ white and 1 ♀ and several ♂♂ yellow were obtained. They were isolated and became the ancestors of pure cultures of white and pure cultures of yellow. The index for the spermatheca was $1{\cdot}529 \pm 0{\cdot}006$ in white and $1{\cdot}451 \pm 0{\cdot}007$ in yellow. Not a single of the three obtained ♀♀ white had offspring whose index for the spermatheca exceeded $1{\cdot}550 \pm 0{\cdot}020$. Thus it proved that white as well as yellow have a

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the column of F_2 I wish to point out that the wild type from which it originated was isolated from the others in F_2 of the described cross.

spermatheca which clearly differs from that of wild type. This fact is an evidence that the genes white and yellow in themselves act upon the form of the spermatheca. These genes are located very close to each other in the left end of the sex-chromosome and if their action on the form of the spermatheca were denied it would be necessary to assume, that very near each of them there lies a gene not manifesting itself in the exterior of the organism but acting upon the form of the spermatheca. This possibility cannot be ruled out a priori, but its probability seems to me very small.

White × wild type (v. table 11 and 12)

White ♀ was crossed to wild type ♂. In F_1 (v. table 11) the heterozygous females **Ww** have an index of the spermatheca of $1{\cdot}595 \pm 0{\cdot}010$ on the average, i. e. an intermediate one between the parental forms.

In F_2 the heterozygotes are identical with F_1 as to the form of the spermatheca, its mean value being $1{\cdot}576 \pm 0{\cdot}007$. The female white on the contrary have a considerably more convex spermatheca: the mean value of the index is $1{\cdot}483 \pm 0{\cdot}007$. The difference between **Ww** and **ww** is in F_2 $0{\cdot}093 \pm 0{\cdot}010$, i. e. quite certain. When we compare white before crossing with white of F_2 we see, that neither the mean values nor the range of variation show any displacement in the direction of wild type after crossing. From an examination of these data it follows that the colour of the eyes and form of the spermatheca are closely linked together. In order to test the strength of this linkage crossing was continued.

One ♀ wild type of F_2 (culture Nr. 994) was crossed to ♂ white of the same generation (culture Nr. 988). In the obtained F_3 ♀ wild was again crossed to ♂ white. The same was done in F_4, F_5 etc. until F_{19}. In F_{12} from this cross out of the obtained hybrids 2 ♀♀ and 2 ♂♂ wild type and 2 ♀♀ and 2 ♂♂ white were taken. They were placed in pairs into different cultures and among the offspring of wild type the homozygous **WW** were selected for 3 generations. In this way there were obtained two cultures of homozygous wild type (1857 and 1860, v. table 11) and two cultures of white (1862 and 1937). The examination of the spermatheca of white showed, that the form of the spermatheca peculiar to white before the crossing had persisted in its purity as far as F_{12}. The mean value of the index of white was $1{\cdot}500 \pm 0{\cdot}008$. Wild type has in F_{12} a spermatheca identical with

Table 11. White × wild type

		Culture Nr.	Mean	σ	c	Limits	n
P	W W		1·721 ± 0·005	0·086	5·0	1·45—1·97	261
	w w		1·529 ± 0·008	0·100	6·5	1·27—1·78	144
F_1	W w	932	1·608 ± 0·012	0·096	6·0	1·40—1·84	60
		933	1·568 ± 0·015	0·079	5·0	1·42—1·72	27
		Total	1·595 ± 0·010	0·094	5·9	1·40—1·84	87
F_2	W w	936	1·584 ± 0·024	0·120	7·6	1·40—1·87	24
		981	1·590 ± 0·018	0·099	6·2	1·35—1·77	29
		982	1·605 ± 0·015	0·100	6·2	1·42—1·84	43
		988	1·550 ± 0·027	0·100	6·4	1·46—1·80	14
		994	1·553 ± 0·015	0·085	5·5	1·38—1·73	29
		1001	1·590 ± 0·015	0·080	5·0	1·42—1·74	30
		1002	1·546 ± 0·016	0·102	6·6	1·35—1·79	39
		Total	1·576 ± 0·007	0·101	6·4	1·35—1·87	208
	w w	936	1·494 ± 0·019	0·126	8·4	1·22—1·70	42
		981	1·452 ± 0·019	0·078	5·4	1·36—1·66	18
		982	1·480 ± 0·016	0·093	6·3	1·18—1·68	35
		988	1·500 ± 0·022	0·115	7·7	1·27—1·69	28
		994	1·460 ± 0·019	0·099	6·8	1·20—1·64	28
		1001	1·485 ± 0·018	0·111	7·5	1·24—1·74	40
		1002	1·465 ± 0·016	0·097	6·6	1·29—1·70	37
		Total	1·483 ± 0·007	0·113	7·6	1·18—1·74	228
F_{12}	W W	1857	1·688 ± 0·011	0·075	4·4	1·52—1·83	50
		1860	1·676 ± 0·012	0·086	5·1	1·50—1·90	50
		Total	1·682 ± 0·008	0·081	4·8	1·50—1·90	100
	w w	1862	1·485 ± 0·014	0·084	5·7	1·34—1·69	33
		1937	1·507 ± 0·010	0·083	5·5	1·33—1·69	68
		Total	1·500 ± 0·008	0·083	5·5	1·33—1·69	101
F_{19}	W W	2437	1·696 ± 0·016	0·080	4·7	1·56—1·83	25
		2439	1·706 ± 0·017	0·087	5·1	1·55—1·92	25
		2520	1·666 ± 0·022	0·108	6·5	1·47—1·87	25
		2521	1·664 ± 0·015	0·077	4·6	1·50—1·82	25
		Total	1·683 ± 0·009	0·091	5·4	1·47—1·92	100
	w w	2339	1·504 ± 0·015	0·075	5·0	1·37—1·67	25
		2401	1·528 ± 0·017	0·087	5·7	1·33—1·70	25
		2504	1·500 ± 0·021	0·106	7·0	1·35—1·69	25
		2505	1·500 ± 0·017	0·087	5·8	1·30—1·71	25
		Total	1·508 ± 0·009	0·091	6·0	1·30—1·71	100

that before the crossing or a little more convex. The mean value of the index for the spermatheca of wild type in F_{12} is $1{\cdot}682 \pm 0{\cdot}009$. The difference between wild type and white in F_{12} is $0{\cdot}182 \pm 0{\cdot}004$, i. e. undoubtedly certain.

In F_{19} of the mixture of white and wild type 5 ♀♀ and 5 ♂♂ white and as many wild type were taken and distributed among separate cultures. From the offspring of wild type homozygous wild were selected for 3 generations. In this way were obtained the cultures Nr. 2437, 2439, 2520, 2521 of wild type and Nr. 2339, 2401, 2504, 2505 of white (v. table 11). Examination showed that the index for wild type is on the average $1{\cdot}683 \pm 0{\cdot}009$, and for white $1{\cdot}508 \pm 0{\cdot}009$. Wild type has after crossing a somewhat lower index of the spermatheca than before, the difference between the mean values amounting to $0{\cdot}038 \pm 0{\cdot}010$ can, however, scarcely be considered as certain. White, also has in F_{19} a lower index of the spermatheca than before crossing, however, this difference too is not certain. Thus the difference between white and wild type was persistent notwithstanding 19 generations of crosses and the amount of this difference did no suffer any decrease. Accordingly the form of the spermatheca of white is dependent either on the gene white or on genes very closely linked to it. In order to test the strength of linkage of these supposed genes to white, one more experiment was made in which the way of crossing was somewhat altered. One of the heterozygous ♀♀ of wild type, obtained in F_2 was crossed to ♂ white from the original culture of white. Out of the obtained offspring a heterozygous ♀ of wild type was again taken and crossed to a white ♂ from the original culture. The same was done in the following generations and the crossing continued in this way for 15 generations. If the gene white does not act on the form of the spermatheca and the observed difference in the form of this organ between white and wild type is due to some gene independent of white, the experiment conducted in this way sooner or later must result in yielding a wild type fly with a spermatheca peculiar to white; 15 generations during which the experiment was carried on in this way are quite sufficient for saturating wild type with the supposed modificators brought in with the male white in each generation. In the fifteenth generation of such crossing 5 ♀♀ and 5 ♂♂ of wild type placed in pairs into different cultures were taken from the culture. During 3 generations there was continued the selection of the homozygous wild type, after which the culture 2184, 2186, 2187, 2307

and 2306, containing homozygous **WW** were obtained. The results of examination of the flies from these cultures are given on table 12. The index of the spermatheca, as shown by the table, is $1{\cdot}635 \pm 0{\cdot}006$ and not in a single of the cultures there was found a population whose index of the spermatheca was lower than $1{\cdot}604 \pm 0{\cdot}020$ (culture Nr. 2306). The difference between these wild type and white is $0{\cdot}106 \pm 0{\cdot}011$, i. e. still quite certain. Likewise the range of variation of the obtained wild type (table 12) is, without doubt, nearer to pure wild type than to white. On the other hand some dislocation, and a certain one, of the mean value of the index of the spermatheca peculiar to wild type, can be indubitably observed here in the direction of white. This forces on us the assumption, that the differences between white and wild type partly depend on modifying genes not identical with the gene of white.

Table 12. Wild type from white × wild type (s. Text).

Culture Nr.	Mean	σ	c	Limits	n
2184	1·628 ± 0·017	0·083	5·1	1·48—1·79	25
2186	1·678 ± 0·013	0·063	3·8	1·55—1·80	25
2187	1·652 ± 0·016	0·080	4·9	1·48—1·85	25
2306	1·604 ± 0·020	0·101	6·3	1·46—1·80	25
2307	1·614 ± 0·021	0·104	6·4	1·40—1·83	25
Total	1·635 ± 0·008	0·093	5·7	1·40—1·85	125

Yellow × wild type (v. table 13)

Yellow ♀ was crossed to wild ♂. In F_1 the spermatheca of the flies are of a form intermediate between wild type and yellow. The mean value of the index of the spermatheca is $1{\cdot}597 \pm 0{\cdot}014$. In the heterozygous wild type with regard to the form of the spermatheca are identical with wild type in F_1: the mean value is $1{\cdot}603 \pm 0{\cdot}009$. The index of the spermatheca of yellow is in F_2 on the average $1{\cdot}468 \pm 0{\cdot}008$, i. e. identical with yellow before the crossing. The difference between wild type and yellow in F_2 is $0{\cdot}135 \pm 0{\cdot}012$, i. e. quite certain. The individuals of yellow and wild type whose spermathecae were measured originated from the same cultures (v. table 13).

From the wild type obtained in F_2 from this crossing 4 ♀♀ and 4 ♂♂ were taken and placed in pairs into different cultures.

Among the offspring there the homozygous wild type were selected for 2 generations. In this way there were obtained the cultures 2298, 2299, 2326, 2327 containing YY individuals. Their examination showed that as to the form of the spermatheca they were very near to wild type before crossing and there was observed some change in the mean value of the index of the spermatheca towards yellow. The mean value for these YY is 1·670 ± 0·008 differing from YY before the crossing by 0·051 ± 0·010.

Table 13. Yellow × wild type

		Culture Nr.	Mean	σ	c	Limits	n
P	YY		1·721 ± 0·005	0·086	5·0	1·45—1·97	261
	yy		1·451 ± 0·007	0·096	6·6	1·23—1·68	192
F_1	Yy	1868	1·597 ± 0·014	0·088	5·5	1·42—1·79	40
F_2	yy	1954	1·470 ± 0·012	0·061	4·2	1·35—1·58	25
		1955	1·466 ± 0·019	0·097	6·6	1·31—1·63	25
		1956	1·492 ± 0·018	0·088	5·9	1·30—1·63	25
		1957	1·450 ± 0·014	0·071	4·9	1·33—1·62	25
		Total	1·468 ± 0·008	0·082	5·6	1·30—1·63	100
	Yy	1954	1·636 ± 0·016	0·079	4·8	1·48—1·82	25
		1955	1·622 ± 0·018	0·090	5·5	1·52—1·81	25
		1956	1·578 ± 0·017	0·085	5·4	1·46—1·75	25
		1957	1·576 ± 0·018	0·091	5·8	1·43—1·75	25
		Total	1·603 ± 0·009	0·091	5·7	1·43—1·82	100
	YY	2298	1·682 ± 0·011	0·056	3·4	1·60—1·85	25
		2299	1·666 ± 0·013	0·064	3·8	1·54—1·82	25
		2326	1·660 ± 0·016	0·079	4·8	1·43—1·81	25
		2327	1·672 ± 0·020	0·098	5·9	1·48—1·90	25
		Total	1·670 ± 0·008	0·076	4·6	1·43—1·90	100

The described results serve as an evidence, that the difference in the form of the spermatheca between yellow and wild type depends either on the gene yellow or on a gene closely linked to it. In order to explain the decrease of the index of the spermatheca observed in wild type after the crossing there the existence of a special gene independent of yellow which modificates the form of the spermatheca must be assumed.

Ivory × wild type (v. table 14)

Ivory ♀ was crossed to wild type ♂. The spermatheca of ivory differs from that of wild type by a considerably higher index: the mean value for ivory is 1·893 ± 0·006. The spermatheca of the hybrids (F_1) proves to be intermediate between the parental forms; the mean value of their index is 1·814 ± 0·014.

Table 14. Ivory × wild type

		Culture Nr.	Mean	σ	c	Limits	n
P	WW		1·721 ± 0·005	0·086	5·0	1·45—1·97	261
	w^{iv} w^{iv}		1·893 ± 0·006	0·110	5·8.	1·62—2·13	328
F_1	W w^{iv}	310	1·814 ± 0·014	0·110	6·1	1·59—2·05	63
F_2	W w^{iv}	353	1·785 ± 0·010	0·103	5·8	1·51—2·04	100
	w^{iv} w^{iv}	353	1·865 ± 0·010	0·105	5·6	1·59—2·08	103
	WW	403	1·713 ± 0·022	0·121	7·1	1·53—1·95	29
F_{10}	WW	847	1·754 ± 0·017	0·116	6·6	1·53—2·01	49
	w^{iv} w^{iv}	848	1·839 ± 0·021	0·125	6·8	1·59—2·13	37
F_{18}	WW	1098	1·720 ± 0·010	0·096	5·6	1·47—1·92	87
	w^{iv} w^{iv}	1022	1·897 ± 0·009	0·087	4·6	1·65—2·06	100

In F_2 the heterozygous wild type (Ww^{iv}, table 14) has an index which is on the average 1·785 ± 0·010. The difference from the heterozygous wild type of F_1 is not certain (0·029 ± 0·017). Ivory has in the generation F_2 a spermatheca similar to ivory from P, or perhaps a little more convex one. The mean value of the index is for ivory in F_2 1·865 ± 0·010. The difference $M_P - M_{F_2} = 0·028 \pm 0·012$ is, however, not certain. On the other hand there exists undoubtedly a difference between heterozygous wild type and ivory in F_2 0·080 ± 0·014.

From wild type obtained in F_2 several ♀♀ and ♂♂ were selected and among their offspring selected the homozygous wild type. From it resulted the culture Nr. 403, which was examined. The spermatheca of the obtained homozygous **WW** had on the average an index of 1·713 ± 0·022, i. e. identical with wild type before crossing.

The crossing was continued beyond F_2. Among the flies obtained in F_2 several ♀♀ wild type were picked out and crossed to ♂♂ ivory obtained in the same generation. In F_3, F_4, F_5 etc. the same was

repeated as in F_2 and in this way the crossing was continued to F_{13}. In F_{10} and F_{13} of the mixture several ♀♀ and ♂♂ wild type and ivory were picked out and distributed among different cultures. After selection of the homozygous wild type the obtained cultures were examined. In F_{10} the average index of the spermatheca was $1{\cdot}754 \pm 0{\cdot}017$ for wild type and $1{\cdot}839 \pm 0{\cdot}021$ for ivory. This difference $0{\cdot}085 \pm 0{\cdot}027$ is mathematically at the limit of certainty which finds its explanation in the small number of examined specimens. The difference between wild type from F_{10} and wild type from P and between ivory from F_{10} and ivory from P are, on the contrary, mathematically certain. In F_{13} the average index of the spermatheca for wild type is $1{\cdot}720 \pm 0{\cdot}010$ i. e. it coincides with that of wild type before crossing, and the average index for ivory is $1{\cdot}897 \pm 0{\cdot}009$, i. e. it coincides with that of ivory before crossing. The difference between wild type and ivory in F_{13} is $0{\cdot}177 \pm 0{\cdot}013$, i. e. it is quite certain and at the same time as considerable as the difference observed between the mutants before crossing.

Tan^2 × wild type (v. table 15)

According to MORGAN, BRIDGES, STURTEVANT 1925, p. 237, the mutant tan^2 differs from wild type by a more yellowish colour of the body, particularly the antennae and by the absence of positive phototropism, peculiar to wild type of *Drosophila melanogaster* and its mutants. Tan^2, an allelomorph of tan, according to the mentioned authors possesses the same characters as tan, but more feebly expressed than in the latter. Besides tan^2 is "not indifferent to light". The culture which I received under the name of tan^2 consisted of flies coloured more lightly than wild type, with light antennae but with very feebly expressed positive phototropism. In addition to this all the tan^2 of my cultures sharply differ from wild type by the character of their arista. In wild type the arista is branched after the fashion of a plume; in my tan^2 it looks like a simple unbranched bristle. The length of the unbranched arista in my tan^2 is not less than in wild type. This character of the arista is a sex linked hereditary character. Therefore I suppose the described condition of arista to be one of the characters of tan^2. In crossing tan^2 × wild type for separating the hybrids I availed myself of this very form of the arista. In the form of its spermatheca tan^2 differs from wild type in that it is much more flattened. The index of the spermatheca is for tan^2 $1{\cdot}902 \pm 0{\cdot}008$.

Tan^2 ♀ was crossed to wild type ♂. The spermathecae of the hybrids proved to be almost identical with those of wild type; their index is on the average 1·760 ± 0·009 (v. table 15). The difference between Tt^2 and TT is thus 0·039 ± 0·010, i. e. near the limit of certainty. The form of the spermatheca in wild type, accordingly shows almost complete dominance over tan^2; this is the only case of complete dominance in the characters of the form of spermatheca which I have observed.

Table 15. Tan^2 × wild type

		Culture Nr.	Mean	σ	c	Limits	n
P	TT		1·721 ± 0·005	0·086	5·0	1·45—1·97	261
	t^2t^2		1·902 ± 0·008	0·084	4·4	1·67—2·12	100
F_1	Tt^2	2046	1·782 ± 0·015	0·073	4·1	1·65—1.92	23
		2047	1·763 ± 0·016	0·086	4·9	1·61—1·93	27
		2063	1·749 ± 0·014	0·096	5·5	1·55—1·92	50
		Total	1·760 ± 0·009	0·090	5·1	1·55—1·93	100
F_2	TT	2334	1·701 ± 0·016	0·100	5·9	1·52—1·94	39
		2335	1·705 ± 0·016	0·094	5·5	1·52—1·88	36
		2418	1·704 ± 0·018	0·091	5·4	1·54—1·95	25
		Total	1·703 ± 0·010	0·096	5·7	1·52—1·95	100
	t^2t^2	2332	1·873 ± 0·015	0·108	5·8	1·62—2·29	50
		2333	1·911 ± 0·022	0·110	5·8	1·69—2·12	26
		2416	1·926 ± 0·025	0·137	7·1	1·69—2·16	25
		Total	1·896 ± 0·012	0·118	6·2	1·62—2·29	101

F_2 obtained by this crossing remained unexamined owing to my departure from Leningrad. Instead of it F_3 was studied. From the flies obtained in F_3 there were taken 4 ♀♀ and 4 ♂♂ with branched arista (wild type) and as many with unbranched arista (tan^2). These flies were introduced in pairs into different cultures and in the cultures of wild type the homozygous wild type during two generations were selected. The cultures of flies with unbranched arista produced identical offspring. Thus in the cultures 2334, 2335, 2418 there were obtained homozygous wild type (all of them with branched arista and clearly expressed phototropism and in the cultures 2332, 2333, 2416 — tan^2 — all with bristle-like arista and feebly expressed phototropism.

The examination of wild type showed that the index of their spermatheca was 1·703 ± 0·010 on the average, i. e. remained the same as it had been before the crossing. The individuals with bristle-like arista had a spermatheca with an index of 1·896 ± 0·012 i. e. such a one as the spermatheca of tan^2 had been before the crossing. Among the tan^2 obtained in this cross one individual had a spermatheca with the index 2·27 and two even with 2·29 — the maximal indices of the spermatheca which I observed during the whole of my work.

The mentioned facts are an evidence that the form of the spermatheca peculiar to tan^2 depends either on the gene tan^2 or on a gene closely linked to it.

Yellow × white (v. table 16)

Both yellow and white have a spermatheca which is considerably more convex than that of wild type: for yellow M = 1·451 ± 0·007, for white M = 1·529 ± 0·008, for wild type M = 1·721 ± 0·005. The genes **y** and **w** are both located in the x chromosome, being within a distance of only 1·5 units from each other. If the difference in the form of spermatheca between white and wild and between yellow and wild are due, as we suppose, to the same genes as the external characters of these mutants, the wild type flies resulting from the crossing of yellow × white must have a more convex spermatheca than both parental forms. Thus, if our assumption be right we must in crossing two forms (yellow and white) with strongly convex spermatheca, obtain as a result individuals with flattened spermathecae.

Yellow ♀ was crossed to white ♂. The females resulted from this crossing (F_1 culture N 2152) were all of the composition **Yy Ww** (v. table 16). The examination of the spermathecae of these females showed, that their index was 1·594 ± 0·009, i. e. actually higher than that of both parental forms. The difference between **Yy Ww** females and pure **yy WW** is 0·065 ± 0·012, i. e. it is certain. It is interesting to note that the spermatheca in **Yy Ww** females obtained in the described experiment proved almost identical with the spermatheca in **Yy Ww** females obtained in the cross of yellow white × wild type (v. table 10). Among the flies obtained through the described crossing in F_2 several individuals yellow white and several male wild type were found. These individuals were set apart and from them were obtained cultures of homozygous yellow white and homozygous wild type flies. After examining wild type obtained in this way, I found that the index of

their spermatheca is on the average 1·676 ± 0·009, i. e. only a little lower than the index observed in the flies of the original line of wild type (the difference being 0·045 ± 0·010). The spermatheca in yellow white proved on the contrary more convex than in white as well as in yellow. The mean value of the index was 1·405 ± 0·009. Comparing the variation curves of the obtained wild type and yellow white (table 16) we see, that they are almost intransgressive. All these results are best explained by the assumption that the genes w and y determine both the colour of the eyes and body as well as the form of the spermatheca.

Table 16. Yellow × white

		Culture Nr.	Mean	σ	c	Limits	n
P	yy WW		1·451 ± 0·007	0·096	6·6	1·23—1·68	192
	YY ww		1·529 ± 0·008	0·100	6·5	1·27—1·78	144
F_1	Yy Ww	2152	1·594 ± 0·009	0·086	5·4	1·48—1·81	100
F_2	YY WW	2514	1·622 ± 0·014	0·071	4·4	1·51—1·77	25
		2517	1·686 ± 0·019	0·093	5·5	1·53—1·92	25
		2519	1·716 ± 0·019	0·093	5·4	1·57—1·88	25
		2658	1·680 ± 0·021	0·106	6·3	1·52—1·90	25
		Total	1·676 ± 0·009	0·098	5·8	1·51—1·92	100
	yy ww	2523	1·388 ± 0·017	0·085	6·1	1·24—1·62	25
		2524	1·428 ± 0·022	0·110	7·7	1·24—1·64	25
		2529	1·398 ± 0·017	0·086	6·1	1·19—1·56	25
		2530	1·406 ± 0·013	0.067	4·8	1·29—1·56	25
		Total	1·405 ± 0·009	0·089	6·4	1·19—1·64	100

Yellow × cinnabar (table 17).

Both the crossed forms are distinguished by a strongly convex spermatheca. As in the preceding experiment (crossing of yellow × white) it must be expected that the result here will be the appearance of a form bearing the character of wild type in its exterior as well as in the structure of the spermatheca.

Yellow ♀ was crossed to cinnabar ♂. In F_2 there were selected the individuals with the characters cinnabar eye and yellow body

(**yy cncn**) on the one hand and the external characters of wild type on the other. Among their offspring during six generations the selection of the homozygous wild type was carried on.

The examination of the yellow cinnabar flies showed, that their spermatheca is at any rate of no less convexity than that of homozygous cinnabar; the mean value of the index being $1{\cdot}383 \pm 0{\cdot}008$. The obtained homozygous wild type (**YY CnCn**) had an index of the spermatheca equal to $1{\cdot}577 \pm 0{\cdot}008$. This index is not only considerably higher than the index peculiar to cinnabar (the difference between the mean values being $0{\cdot}187 \pm 0{\cdot}009$) but than the index of yellow (the difference of their mean values being $0{\cdot}126 \pm 0{\cdot}011$). However, a comparison of the spermatheca of wild type obtained in the described experiment with wild type from the original cultures shows us, that the former is perceptibly more convex than the latter, the difference of their mean values being $1{\cdot}721 - 1{\cdot}577 = 0{\cdot}144 \pm 0{\cdot}010$, i. e. certain. If we compare the variation curves of the obtained forms of **yy cncn** and **YY CnCn**, we see, that there is wide difference between them; the value of this difference is at any rate several times greater than the difference between the spermatheca of the parental forms of yellow and cinnabar.

Table 17. Yellow × cinnabar

		Culture Nr.	Mean	σ	c	Limits	n
P	yy CnCn		1·451 ± 0·007	0·096	6·6	1·23—1·68	192
	YY cncn		1·390 ± 0·005	0·072	5·2	1·21—1·61	248
F_2	YY CnCn	2511	1·614 ± 0·016	0·082	5·1	1·48—1·86	25
		2532	1·554 ± 0·016	0·078	5·0	1·42—1·73	25
		2602	1·586 ± 0·018	0·092	5·7	1·43—1·73	25
		2605	1·552 ± 0·014	0·068	4·4	1·40—1·71	25
		Total	1·577 ± 0·008	0·084	5·3	1·40—1·86	100
	yy cncn	2302	1·358 ± 0·016	0·082	5·9	1·20—1·52	25
		2303	1·372 ± 0·014	0·069	4·3	1·24—1·55	25
		2410	1·412 ± 0·016	0·078	5·5	1·21—1·52	25
		2412	1·390 ± 0·017	0·087	6·7	1·19—1·55	25
		Total	1·383 ± 0·008	0·082	5·9	1·19—1·55	100

These results find their simplest explanation in the assumption, that the genes cinnabar and yellow alter not only the colour of the eyes and body but also the form of the spermatheca. However, the difference between the indices of the spermatheca in wild type originated from the cross of yellow × cinnabar and wild type from the original cultures forces us to recognise, that in the discussed cross besides the genes of yellow and cinnabar, other genes which are independent of them and modify the form of the spermatheca are playing a rôle. With regard to this it is not without interest to note, that in crosses of yellow × wild type (v. table 13) and cinnabar × wild type (v. table 9) genes modifying the form of the spermatheca also played a certain role.

Ivory × yellow white (table 18)

In the form of the spermatheca these two mutants are most distant from each other. The mean value of the index of the spermatheca is for ivory $1{\cdot}893 \pm 0{\cdot}006$ and $1{\cdot}358 \pm 0{\cdot}007$ for yellow white. The variation curves of both mutants are not transgressive, the hiatus between them being considerable (v. table 18).

Ivory was crossed to yellow white ♂ and white yellow ♀ to ivory ♂. The results in both cases were alike; in both reciprocal crossings the females obtained in F_1 are phenotypically ivory (genetically **Yy w^{iv}w**) and the index of their spermatheca was $1{\cdot}641 \pm 0{\cdot}006$, i. e. almost exactly intermediate between the parental forms.

F_2 was obtained from white yellow ♀ × ivory ♂ only. The heterozygous female ivory (**Yy w^{iv}w**) here too has an index of the spermatheca of $1{\cdot}642 \pm 0{\cdot}008$, i. e. exactly coinciding with that observed in heterozygous ivory of F_1. We noticed, however, in ivory of F_2 some alterations; these alterations consisted in the range of variability in comparison with F_1. The limits of variability of the index of the spermatheca of **Yy w^{iv}w** in F_1 is 1·40—1·87 and in F_2 it is 1·42—1·96; a more obvious evidence of the increase of variability is the coefficient of variability. In F_1 it is $5{\cdot}7 \pm 0{\cdot}28$ and in F_2 — $7{\cdot}6 \pm 0{\cdot}36$. Their difference is $1{\cdot}9 \pm 0{\cdot}46$, i. e. it must be recognised as certain.

Yellow white in F_2 of the described cross has an index of the spermatheca amounting to $1{\cdot}520 \pm 0{\cdot}009$. The difference between heterozygous ivory and yellow white is here $0{\cdot}122 \pm 0{\cdot}011$, i. e. it doubtlessly exists. However, comparing the spermatheca of yellow white before crossing ($1{\cdot}358 \pm 0{\cdot}007$) and in F_2 ($1{\cdot}520 \pm 0{\cdot}009$), we notice

a sharp increase of the mean value after crossing. The variation curve of the spermathecae of yellow white in F_2 is obviously bimodal; the extreme minus variants almost coincide with those observed before the crossing (1·26 instead of 1·22) but the right hand side of the variation curve has made a sharp move in the plus direction (1·77 instead of 1·49).

Table 18. Ivory × yellow white

		Culture Nr.	Mean	σ	c	Limits	n
P	YY $w^{iv}w^{iv}$		1·893 ± 0·006	0·110	5·8	1·62—2·13	328
	yy ww		1·358 ± 0·007	0·073	5·4	1·22—1·49	100
F_1	Yy $w^{iv}w$		1·641 ± 0·006	0·093	5·7	1·40—1·87	212
F_2	Yy $w^{iv}w$	538	1·677 ± 0·014	0·103	6·1	1·42—1·95	52
		539	1·627 ± 0·017	0·152	9·3	1·43—1·92	80
		585	1·678 ± 0·027	0·130	7·7	1·45—1·96	23
		586	1·613 ± 0·017	0·103	6·4	1·45—1·95	35
		587	1·655 ± 0·022	0·125	7·6	1·43—1·93	33
		Total	1·642 ± 0·008	0·123	7·5	1·42—1·96	223
	yy ww	538	1·542 ± 0·009	0·081	5·3	1·34—1·77	81
		585	1·459 ± 0·017	0·091	6·2	1·26—1·63	29
		Total	1·520 ± 0·009	0·090	5·9	1·26—1·77	110
F_{10}	YY $w^{iv}w^{iv}$	1082	1·684 ± 0·012	0·097	5·8	1·52—2·00	69
		1083	1·659 ± 0·018	0·102	6·1	1·52—1·92	33
		Total	1·676 ± 0·009	0·099	5·9	1·52—2·00	102
	yy ww	1086	1·540 ± 0·014	0·086	5·6	1·33—1·71	36
		1087	1·551 ± 0·010	0·088	5·7	1·34—1·77	71
		Total	1·548 ± 0·008	0·088	5·7	1·33—1·77	107

Homozygous ivory was not sorted out from the population in F_2. The crossing was continued by mating heterozygous female **Yy $w^{iv}w$** to male **yw** as far as F_{10}. In F_{10} from the mixture the heterozygous **Yy $w^{iv}w$** on the one hand and yellow white on the other were picked out and placed in different cultures. In the offspring of **Yy $w^{iv}w$** during three generations the homozygous ivory (**YY $w^{iv}w^{iv}$**) were selected after which ivory as well as yellow white were examined. The spermatheca of yellow white in F_{10} proved very near those of yellow white in F_2 the mean value of their indices was 1·548 ± 0·008.

The result of the examination of the homozygous ivory was an unexpected one. The mean value of their index proved to be $1{\cdot}676 \pm 0{\cdot}009$, i. e. only a little higher than the one observed in heterozygous flies **Yy w^{iv}w** in F_2 ($1{\cdot}642 \pm 0{\cdot}008$) and lower than in wild type ($1{\cdot}721 \pm 0{\cdot}005$). So ivory characterized before crossing by a more flattened spermatheca than in wild type, after crossing with yellow white acquired a more convex spermatheca than wild type. However, notwithstanding such a considerable approach of the mean values, yellow white and ivory of F_{10} persist to clearly differ from one another by the form of the spermatheca; the difference of the mean values is here $0{\cdot}128 \pm 0{\cdot}012$.

The preceding facts suggest the idea, that the difference in the form of the spermatheca observed in ivory and yellow white before the crossing depends on special genes, determining the form of these organs, not identical ones with white and yellow, but linked to them. Such a conclusion may, however, appear to be in some contradiction with the results of the cross ivory × wild type; in the latter case we were forced to recognize that the differences in the form of the spermatheca between ivory and wild type are dependent either on the gene w^{iv} or a gene very closely linked to it. Therefore there may be advanced another theory for explaining the results of the cross yellow white × ivory. The genes **y** and **w** act on the form of the spermatheca tending to increase its convexity (resp. to diminish the index of the spermatheca); reversely, the genes **Y** and $\mathbf{w^{iv}}$ diminish the convexity of the spermatheca (resp. increase its index). However the manifold action of the genes **Y**, **y** and **w**, $\mathbf{w^{iv}}$, **W** in our cross of yellow withe × ivory is masked owing to the presence of special genes modifying the form of the spermatheca and independent of **Y** and **W**. From this point of view our original culture of yellow white contained besides the genes **y** and **w** one or several more genes modifying the form of the spermatheca in the minus direction and our original culture of ivory contained besides the gene $\mathbf{w^{iv}}$ one or several more genes modificating the form of the spermatheca in a plus direction. The interchange of these genes which takes place at the crossing produces the approachment of the indices of the spermathecae observed in our experiments.

We have already applied the above mentioned hypothesis to the crosses of cinnabar × wild type, yellow white × wild type, white × wild type and yellow × wild type. In all the enumerated cases after the crossing there also was observed a greater or lesser

approaching of the indices of the crossed forms, which might be explained by the action of modifying genes. In the case, however, of yellow white × ivory this approachment is the nearest; here the supposed manifold effect of the genes yellow and white is the least clear and the application of the hypothesis of manifold effect to this case is most contestable. Therefore a support received by this theory from a detailed analysis of this case will make it more probable for all other cases.

Demonstration of genes modifying the form of the spermatheca

In F_{10} of the cross yellow white × ivory we obtained yellow white whose index of the spermatheca was $1{\cdot}548 \pm 0{\cdot}008$. Let us designate this line of yellow white as yellow white B in distinction from the original line of yellow white which we will designate as yellow white A ($M = 1{\cdot}358 \pm 0{\cdot}007$). Likewise let us designate as ivory B the ivory with the index of the spermatheca $1{\cdot}676 \pm 0{\cdot}009$ which we obtained in the mentioned cross, and the original line of ivory ($M = 1{\cdot}893 \pm 0{\cdot}006$) as ivory A. According to the exposed theory the difference in the form of the spermatheca between yellow white A and yellow white B as well as the difference between ivory A and ivory B depends on special genes modifying the form of this organ. In order to test this theory there were crossed yellow white A × yellow white B and subsequently picked out the extreme forms appeared in F_2; likewise there were crossed ivory B × wild type.

Yellow white A × yellow white B (v. table 19)

Yellow white B was crossed to yellow white A. The first generation of hybrids (F_1) had a spermatheca intermediate between the parental forms, as to the frequency polygon and average value of the index; the latter proved to be $1{\cdot}488 \pm 0{\cdot}009$. In F_2 there was obtained a population (consisting, of course, only of yellow white flies) which had similar indices as in F_1. The mean value of the index in F_2 was $1{\cdot}488 \pm 0{\cdot}008$, i. e. coinciding with that observed in F_1 with almost curious exactness. The variability of the form of the spermatheca observed in F_2 is however considerably greater than in F_1. The coefficient of variability in F_1 is $5{\cdot}4 \pm 0{\cdot}44$ and $8{\cdot}0 \pm 0{\cdot}40$ in F_2. The difference of the coefficients of variability is $2{\cdot}6 \pm 0{\cdot}59$, i. e. certain. The increase of variability in F_2 in comparison with F_1 is also obvious when the variation curves observed in these generations are compared with each other.

Table 19. Yellow white A × yellow white B

	Line	Culture Nr.	Mean	σ	c	Limits	n
P	A		1·358 ± 0·007	0·073	5·4	1·22—1·49	100
	B		1·548 ± 0·008	0·088	5·7	1·33—1·77	107
F_1		1185	1·481 ± 0·012	0·081	5·5	1·30—1·64	49
		1186	1·502 ± 0·014	0·072	4·8	1·32—1·62	25
		Total	1·488 ± 0·009	0·079	5·4	1·30—1·64	74
F_2		1216	1·500 ± 0·013	0·129	8.6	1·24—1·77	95
		1223	1·477 ± 0·012	0·120	8·1	1·27—1·78	102
		Total	1·488 ± 0·008	0·119	8·0	1·24—1·78	197
F_3—F_6		Selection					
F_7	C	1638	1·715 ± 0·009	0·098	5·7	1·50—2·00	114
	D	1639	1.371 ± 0·008	0·063	4·6	1·25—1·55	63
		1716	1·400 ± 0·016	0·080	5·7	1·26—1·54	25
		Total	1·379 ± 0·008	0·073	5·3	1·25—1·55	88

The results obtained in the described cross represent a typical instance of blended inheritance so often observed in studying the inheritance of quantitative characters. The further task of the analysis of this cross consists in the attempt at singling out the extreme forms in all their purity by way of carrying out selection in the population of F_2. The studied character — the form of the spermatheca — is very unfavourable to experiments of this kind. In the first place it is impossible to investigate the spermatheca without dissecting the fly. Accordingly, the individual value of the picked out specimen can be determined only after its death. Secondly the studied character exists only in the female and, consequently, the male used in the selection always remains uncertain. In order to carry out the selection we had therefore to take recourse to very complicated and toilsome technics, consisting in the following.

There were used 20 cylinders with food and in each of them placed 1 ♀ and 1 ♂, taken at random from the population obtained in F_2 of yellow white A × yellow white B. After all these females had layed a sufficient quantity of eggs, they were killed and macerated, each of them separately, in KOH. Then in each female were examined both

their spermathecae. In this way the mothers of the 20 founded cultures became certain. Among the females taken for selection there occured the following extreme forms; one female had an average index of 1·675; one female of 1·450 and one of 1·455. In order to prevent any possible unfavourable influence of the unknown male on the experiment we proceeded in the following way. As soon as a sufficient number of flies had hatched in the cultures, but of each of them there were taken 15—20 flies and their spermatheca subjected to examination. Thus, for every one of the cultures the mother and part of her progeny became certain. In two cases the obtained results were favourable. The culture Nr. 1308 had for mother a female with a spermatheca of 1·675 and had yielded a progeny with 1·627 $\pm$ 0·018 on the average. In culture Nr. 1310 the mother's spermatheca was 1·455 and that of her progeny 1·454 $\pm$ 0·021. The culture 1308 became the starting point of the plus line, and the culture 1310 that of the minus line. The selection begun in this way in the generation F_2 was continued through 4 more generations. In each generation there were studied 10 cultures of the plus line and as many of the minus line. In F_6 the selection was made for the last time and the obtained F_7 made the subject of a detailed investigation of a larger number of individuals.

The plus line (culture Nr. 1638 table 19) had on the average the index 1·715 $\pm$ 0·009 of the spermatheca and the minus line (cultures Nr. 1639 and 1716) — 1·379 $\pm$ 0·008 on the average. As can be seen from table 19, the resulted populations were very different; the variation curves are only slightly transgressive. Farther on the plus line will be designated as yellow white C and the minus line as yellow white D. Comparing yellow white D with yellow white A (the original american line) we see that they are almost alike; the difference between their mean values is 0·021 $\pm$ 0·011 i. e. mathematically uncertain. Thus, by way of selection one of the parental forms was singled out in its purity. The line yellow white C in the form of its spermatheca coincides with wild type; in the plus direction the selection not only singled out the parental form but even went beyond it.

Yellow white C $\times$ wild type (v. table 20)

The mean values of the index of the spermatheca for the crossed forms are 1·721 $\pm$ 0·005 for wild type and 1·715 $\pm$ 0·009 for yellow white C, i. e. they coincide with each other. According to our theory

the genes **y** and **w** besides altering the colour of the eyes and body peculiar to the wild fly, also alter the form of the spermatheca in the direction of decrease of its index. From this point of view the uniformity of the spermatheca of yellow white C and wild type is explained by the presence in the line yellow white C besides of the genes **y** and **w** of one or several more genes modifying the form of the spermatheca in the sense of an increase of the index. Let us designate this hypothetical gene as **X—x**. The genotypical composition of our line yellow white C must accordingly be expressed by the formula **yy ww xx**; and the genotypical composition of wild type by **YY WW XX**. The effect of the genes **y** and **w** modifying the form of the spermatheca in our line yellow white C is neutralized by the effect of the plus modifier **x** owing to which the spermatheca of **yy ww xx** becomes phenotypically identical with that of **YY WW XX**.

Table 20. Yellow white C × wild type

		Culture Nr.	Mean	σ	c	Limits	n
P	YY WW		1·721 ± 0·005	0·086	5·0	1·45—1·97	261
	yy ww	C	1·715 ± 0·009	0·098	5·7	1·50—2·00	114
F_1	Yy Ww	1779	1·788 ± 0·009	0·074	4·1	1·55—1·92	67
F_2	Yy Ww	1864	1·762 ± 0·020	0·099	5·6	1·60—2·00	25
		1958	1·760 ± 0·021	0·107	6·1	1·55—1·96	25
		1959	1·778 ± 0·018	0·091	5·1	1·65—1·96	25
		Total	1·768 ± 0·012	0·100	5·7	1·55—2·00	75
	yy ww	1864	1·608 ± 0·019	0·094	5·9	1·38—1·87	25
		1958	1·549 ± 0·018	0·107	6·9	1·35—1·79	35
		1959	1·557 ± 0·020	0·105	6·7	1·28—1·75	29
		Total	1·567 ± 0·011	0·108	7·0	1·28—1·87	89
	YY WW	2312	1·826 ± 0·031	0·155	8·5	1·52—2·08	25
		2313	1·782 ± 0·015	0·077	4·3	1·62—1·89	25
		2314	1·804 ± 0·022	0·108	6·0	1·64—2·04	25
		2315	1·760 ± 0·020	0·100	5·7	1·55—2·00	25
		Total	1·793 ± 0·012	0·117	6·5	1·52—2·08	100

If our assumption is right, then in crossing **yy ww xx** to **YY WW XX** we must already in F_2 obtain an interchange of the genes **x** and **X** (the genes **y** and **w** are closely linked; crossing over we leave without

consideration). Therefore in F_2 along with **yywwxx** there must arise the forms **yywwXx** and **yywwXX** i. e. part of the yellow white obtained in F_2 has become free of the modificator **x** owing to its being exchanged against **X**. But the individual of the structure **yywwXX** has a more convex spermatheca (resp. with a lower index) than wild type. Therefore it must be expected that from the crossing would result a yellow white population with an index of the spermatheca which is on the average lower than in our line of yellow white C. On the other hand wild type which had before crossing the structure **YYWWXX** will after crossing represent a population where the genotypes **YYWWxx**, **YYWWXx** and **YYWWXX** will be mixed. Owing to the apparition in the genotype of the genes **x** modifying the form of the spermatheca in a plus direction, wild type resulting from the crossing must have an index of the spermatheca which is on the average higher than in the original wild type. In other words, notwithstanding the form of the spermatheca in the crossed yellow white C and wild type being equal, we must obtain in F_2 yellow white and wild type with different form of the spermatheca and moreover yellow white will have a more convex spermatheca than wild type.

Yellow white C ♀ was crossed to wild type ♂. In F_1 were obtained flies **YyWwXx** (wild type), whose spermatheca were on the average less convex than those of each of the crossed parents: the mean value of the index of the spermatheca was $1{\cdot}788 \pm 0{\cdot}009$. The difference between the spermathecae in F_1 and wild type is $0{\cdot}067 \pm 0{\cdot}010$, i. e. certain (v. table 20).

In F_2 the heterozygous wild type had on the average the same index of the spermatheca as in F_1 viz. $1{\cdot}768 \pm 0{\cdot}012$. Yellow white obtained in F_2 showed considerably more convex spermathecae. The mean value of their index was $1{\cdot}567 \pm 0{\cdot}011$. The difference between the mean values of F_2 wild type and yellow white is $0{\cdot}201 \pm 0{\cdot}016$ i. e. it indubitably exists. The variation curves of the compared forms are obviously different.

Out of the heterozygous wild type obtained in F_2 from the described crossing, there were taken 4 ♀♀ and 4 ♂♂ which were placed in pairs in different cultures. In their progeny there was made a selection of the homozygous wild type for 5 generations. Their examination (table cultures Nr. 2312, 2313, 2314 and 2315) showed that the index of their spermatheca was on the average $1{\cdot}793 \pm 0{\cdot}012$, i. e. perceptibly higher than it was in wild type before the cross (the difference of the mean

values being $0{\cdot}072 \pm 0{\cdot}013$) and considerably higher than in yellow white obtained in F_2 (the difference being $0{\cdot}226 \pm 0{\cdot}016$).

Thus, as a result of crossing yellow white C to wild type, which are identical as to the form of their spermatheca, we obtained yellow white and wild type obviously differing in the form of this organ, in other words the advanced assumption received complete confirmation. It follows that 1) there exist genes (or a gene) independent of y and w modifying the forms of the spermatheca 2) the difference in the form of the spermatheca between yellow white and wild type depends either on the very genes y and w, or on some gene very closely linked to y and w.

Ivory B × wild type (v. table 21)

The mean values of the index of the spermatheca for the crossed forms are in wild type $1{\cdot}721 \pm 0{\cdot}005$ and in ivory B $1{\cdot}676 \pm 0{\cdot}010$, i. e. ivory has a lower index than wild type. Yet the original line ivory A is characterized by a higher index than wild type ($M = 1{\cdot}893 \pm 0{\cdot}006$). If the gene w^{iv} as a matter of fact, modificates the form of the spermatheca tending to increase its index in comparison with the wild fly, then the unusually low index observed in ivory B is explained by the presence in this line of some gene (or genes) modifying the index of the spermatheca in the minus direction and neutralizing the action of w^{iv}. If this is so, to the case of crossing ivory B × wild type there may be applied the same argument as to the cross yellow white C × wild type. In other words, in F_2 from ivory B × wild type we must obtain ivory whose spermatheca is characterized by a higher index than the spermatheca of wild obtained from the same crossing.

Ivory B ♀ was crossed to wild type ♂. The flies in the generation F_1 had a more convex spermatheca than each of the parental forms. The mean value of the index of the spermatheca for F_1 is $1{\cdot}615 \pm 0{\cdot}010$. The difference between the mean values for F_1 wild type and parental ivory B is $0{\cdot}061 \pm 0{\cdot}014$, i. e. certain.

Now, ivory in F_2 is characterized by a much higher index of the spermatheca; the mean value of the index for ivory is $1{\cdot}728 \pm 0{\cdot}010$. This index is considerable higher than that of wild type (the difference is $0{\cdot}130 \pm 0{\cdot}013$) and somewhat higher than the index of ivory B (the difference is $0{\cdot}052 \pm 0{\cdot}014$).

Table 21. Ivory B × wild type

		Culture Nr.	Mean	σ	c	Limits	n
P	WW		1·721 ± 0·005	0·086	5·0	1·45—1·97	261
	$w^{iv}w^{iv}$	B	1·676 ± 0·010	0·099	5·9	1·52—2·00	102
F_1	Ww^{iv}	1947	1·615 ± 0·010	0·083	5·1	1·39—1·81	74
F_2	Ww^{iv}	2174	1·650 ± 0·012	0·082	5·0	1·48—1·83	44
		2175	1·534 ± 0·015	0·073	4·8	1·41—1·67	25
		2176	1·577 ± 0·017	0·095	6·0	1·38—1·75	31
		Total	1·598 ± 0·009	0·095	5·9	1·38—1·83	100
	$w^{iv}w^{iv}$	2174	1·741 ± 0·014	0·099	5·7	1·50—2·00	50
		2175	1·730 ± 0·019	0·095	5·5	1·54—1·90	25
		2176	1·702 ± 0·018	0·088	5·2	1·53—1·87	25
		Total	1·728 ± 0·010	0·097	5·6	1·50—2·00	100
	WW	2323	1·596 ± 0·021	0·105	6·6	1·40—1·84	25
		2324	1·472 ± 0·015	0·077	5·2	1·33—1·67	25
		2326	1·562 ± 0·018	0·089	5·7	1·41—1·70	25
		2427	1·480 ± 0·021	0·107	7·2	1·31—1·62	25
		Total	1·528 ± 0·011	0·105	6·9	1·31—1·84	100

In F_2 of Ww^{iv} obtained from the described crossing there were taken 4 ♀♀ and 4 ♂♂ which were placed in pairs in different cultures. In their offspring there were during 2—3 generations selected the homozygous wild type. The examination of these wild type showed that their spermatheca is characterized by a very low index 1·528 ± 0·011.

Thus, notwithstanding the fact that in P the index of the spermatheca of ivory B was lower than in wild type, it had for ivory become after crossing considerably higher than in wild type. It follows that: 1) there exist genes (or a gene) independent of W and w^{iv}, modificating the index of the spermatheca in the minus direction; 2) the difference in the form of the spermatheca observed between ivory and wild type depends either on the action of the gene w^{iv} itself or on an gene very closely linked to it.

Conclusions

The purpose of the crossings was to clear up the question wether the external characters of mutants (as f. i. the colour of the body, eyes etc.) in their hereditary transmission are linked to the characteristics of the spermatheca. In the crosses ebony × wild type, sooty × wild type, tan^2 × wild type and, perhaps, ivory × wild type this linkage appeared to be complete. Wild type, ebony, sooty, tan^2 obtained in F_2 and more distant generations of the crossings invariably proved identical with wild type, ebony, sooty and tan^2 before crossing.

In all these cases, consequently, the external characters of the mutants and the shape of their spermatheca was due either to the same genes or to closely linked genes.

In the crosses of cinnabar × wild type, yellow white × wild type, white × wild type, yellow × wild type and ivory × yellow white the results proved somewhat different. Here as in the above mentioned crosses the differences which existed in the form of the spermatheca before hybridization had persisted after it. The extent of these differences proved, however, to be less after hybridization than before it. As a result of crossing in these cases there was observed some approachment, which remained however of very different degrees. Those cases may be explained in the following way: 1) The external characters of mutants and the form of the spermatheca are due to different but linked genes. The approachment of the mean values of the index for the spermatheca observed as a result of crossing, is to be explained by crossing over between the genes of the external characters and those of the form of the spermatheca. 2) The external characters of mutants and the form of the spermatheca are dependent on different but so closely linked genes, that a crossing over between them is practically untraceable. Besides there exist special genes which modificate the form of the spermatheca and are independent of the former or very loosely linked to them. The interchange of these genes taking place in crossing causes the observed approachment between the mean values. 3) The external characters of mutants and the form of their spermatheca is dependent on the manifold action of the same gene. Besides there exist special genes which modificate the form of the spermatheca and are independent of the fundamental genes. The interchange of these genes causes the approachment of the mean values after crossing.

The applicability of the first of these explanations was tested by way of experiment. The line yellow white B resulting from the cross ivory × yellow white had a spermatheca more alike that of wild type than it was before crossing. By way of selection we succeded in rearing the line yellow white C, whose spermatheca was identical with that of wild type. However when yellow white C was crossed to wild type, yellow white and wild type obtained in F_2 proved obviously different. The crossing of the line ivory B, obtained from the cross ivory × yellow white to wild type gave quite similar results. Thus it became clear that the external characters of mutants and the form of their spermatheca are linked together, while the approachment of the mean values observed in some crosses is explained by the presence of special modifying genes.

So the first of the three proposed explanations of the results of the crossing proves inadequate. There remains the alternative: the difference in the form of the spermatheca between the mutants is either due to the manifold effect of the same genes on which are depending the external characters of mutations, or it is caused by different but very closely linked genes. These two assumptions cannot bè practically tested by way of experiment, since very close linkage is on the limit of absolute linkage. This is true particularly in regard to the quantitative characters, to which belongs the size of the spermatheca, but this is true also with regard to the qualitative characters and the discussed colour of the testicles is one of them.

There may be, however, advanced an argument which indirectly speaks in favour of the fact that in the above examined cases we are dealing with the manifold effect of one gene and not a close (or absolute) linkage of different genes. Of the 19 mutants investigated besides wild type (v. table 6) only two (star and singed) do not differ in the form of their spermathecae from wild type. In all cases which were tested by crossing it became clear that the differences in the form of the spermatheca depended on the same genes as the external characters of mutant or on genes closely linked to them. The assumption that in all these experiments we met fortuitously with pairs of such linked genes seems to me absolutely improbable, therefore I should think it much more likely that in all these cases we are dealing with the manifold effects of genes.

Discussion of results

The above exposed facts show that in the investigated cases the external characters of mutants (colour of the eyes, body, shape of the wings etc.) and those of their sex apparatus are very closely linked. In all sufficiently studied cases this linkage seems to be absolute. Thus there arises the dilemma: the studied genes have a manifold effect or else we have to do with the linkage of genes. We had advanced a consideration of a practical nature which inclined us to the assumption that it is the manifold effect of the genes and not absolute linkage which explains the described phenomena.

There is one more consideration a purely theoretical one, not permitting in our opinion to adept the hypothesis of the absolute linkage of the genes. Hereditary unit or gene is called strictly speaking, the cause contained in the sex cell, which produces by its presence the appearance of a certain character or characters in an organism hereditarily transmitted as an indissoluble whole. Therefore, if there exists a complex, whatever be its extent, relating even to the most various parts of the body but transmitted as a unit, to explain the hereditary transmission of this complex by assuming the existence of more than one single gene seems to me a methodological paradox.

The view we have just uttered is in contradiction with the opinion of several authors, who hold, that the appearance of two characters may be ascribed to the action of one gene only then if there exists between these characters a clearly expressed organic connection. In our case this requirement is not fullfilled. Even with regard to the connection between the colour of the eyes and that of the testicles (v. white, ivory and eosin) there can be shown no direct interdependence between these organs. The fact is that the colour of the testicles and eyes in *Drosophila* are of a quite different nature; in the eyes we have large grained pigment, in the tunic of the testicles there is instead observed a diffused pigmenting substance. The loss of pigment in the eyes is not accompanied by an inpoverishment of pigment in the integument of the body and inversely, the mutants with a lighter colour of the body than wild type (e. g. the yellow body of yellow) but normal eyes, have testicles which are as intensely coloured as those of wild type. Even less there can be pointed out a functional dependence between characters of such a kind as the colour of the body and the form of the chitinous spermatheca. The presence of a plain func-

tional (ontogenetic) connection between the characters does not, however, seem to me necessary in order to adept the assumption that these characters are due to one and the same gene.

Let us illustrate our idea by an instance. In *Antirrhinum majus* the zygomorphous form of the flower is connected with a bilaterally symmetrical seed capsule. These two characters are dependent on the action of one and the same gene (BAUR, 1919) and between them there is a plain ontogenetic connection: the form of the ovary is to a certain degree determined already during the bloom and therefore it is clear that the form of the flower can change the form of the ovary. Here there exists a common cause to which are due both characters of the peloric flower, the form of the flower as well as that of the seed capsule. We do not know the nature of this cause but only its effect on the organism in a comparative by advanced state of development. Here „phenokritischer Gabelpunkt", according to HAECKER's terminology, lies in the ontogenesis at so inconsiderable a depth, that the connection between the characters can be clearly perceived. It is, however, quite possible to imagine also such conditions when „phenokritischer Gabelpunkt" is liying in the ontogenesis much deeper; and the farther it moves into the depth of individual development the more difficult it is to discover it and, consequently, less and less evident becomes the functional connection between the characters. The causes, however, which are responsible for the appearance of one or another hereditary character are present already in the sex cells and the sex cells of hereditarily different individuals are already different. The question as to when these differences in the ontogenesis become perceptible for our eye, is already a question of the physiology of development and not of the science of heredity in the strict sense of the word. Thus the existence of functional connection between characters dependent on the same gene is doubtless, but the requirement that it should lie in the ontogenesis so superficially as to be easely perceptible has no foundation. As long as we do not know the intrinsic nature of the gene the only criterion allowing to form an opinion as to wether a character depends on one or several genes are exclusively genetical data, and not the data of the physiology of development.

One more argument may be advanced against the manifold effect of the gene in our case. The allelomorphous characters — the colour of the eyes of wild type, eosin, ivory and white arrange themselves in a line in the just mentioned order in accordance with the degree of

impoverishment in pigment and the dominance of the one over the other (each preceding dominates over the following). The investigation of the form of the spermatheca in the respective mutants has, however, shown, that beeing arranged according to the decrease of the index of the spermatheca, they follow one after other in this order: ivory, wild type, eosin, white, while the last two have similar spermathecae. The colour of the testicles in wild type is yellow, whereas in eosin, ivory and white the testicles are transparent. Likewise the allelomorphous colour of the body: wild type, sooty, ebony may be arranged in the mentioned order according to the impoverishment of the integuments in pigment. Sooty and ebony are however indistinguishable from each other by the form of the spermatheca. Finally it was shown by the crosses that the form of the spermatheca in heterozygous individuals is always more or less intermediate between the parental forms, while the external characters of the respective mutants not infrequently seem to display a complete dominance. Thus, between the external characters of mutants and the characters of their sex apparatus there is no complete correspondency. But this circumstance is in our opinion no serious argument against the possibility of attributing these characters to the effect of one gene with manifold effect. In his classical work "Physical basis of heredity" MORGAN (1919, p. 37) says: "In all these series it is the same organ that is mainly affected by the different allelomorphs, which seems "natural", but was not necessarily to have been expected".

Thus it is theoretically quite admissible that various mutations of the same gene would act even on different parts of the organism. The more it is possible that the repeated alterations of the same gene the alterations which it causes will take different directions in different parts of the body, or that the alteration of one of the characters may be out of proportion whith that in another. A phenomenon of this kind we ascertained by the investigation of the sex apparatus of the mutants of *Drosophila melanogaster*, but it was already known before. So out of two mutations of the gene singed in *Drosophila melanogaster*, singed alters the shape of the bristles and in addition renders the females sterile, while singed^2 causes almost the same alteration of the bristles as singed, but the female proves fertile (MORGAN, BRIDGES, STURTEVANT 1925).

But the most remarquable case of this kind is that discovered by MULLER and ALTENBURG (ALTENBURG and MULLER 1920, MULLER 1922). The mutations of the gene truncate give rise to alterations in the

shape of the wing, lethal effect, alterations in the arrangement of the bristles on the thorax and a combination of these characters.

The adoption of the existence of genes with manifold effect does not lead to theoretical difficulties. The conception of the gene, the hereditary unit, stands in no logical connection with any theories on the teachings of development. The preformational as well as the epigenetical ideas are equally in harmony with the modern conception of the gene. On the other hand there exist no empirical data whatever which would lead us to the conception of the gene at the representative of a definite part of the body. Therefore, whenever there is observed in an experiment an absolute linkage of characters there can be spoken only of the manifold effect of one gene but not of the presence of absolutely linked genes.

The assumption of the existence of manifold effect of the genes removes a series of difficulties confronting modern genetics. In the place there must definitely fall away the assertion so often repeated, by non geneticists at least, that Mendelism studies the heredity only of "superficial" qualities of the organism having no importance for his life, while "fundamental" qualities are without the scope of Mendelism. It has been declared that we know rather a good deal about the genes of "the colour of the eyes", "the shape of the bristles" and "superficial characters" of this sort, but that we do not know anything about the genes of the heart, the intestine etc.

PLATE (1913) even declared that we shall never know anything of these genes having such an importance for the life of the individual, since there do not exist individuals without heart, intestine etc. Considerations like these are entirely based upon the preconceived idea that each gene determines a certain part of the body an that in its absense this part cannot develop. It was pointed out above that there existed genes modifying the structure of such an important (even the most important) part of the body as the sex apparatus. Even more, part of these genes were most probably identical with those determining these "superficial" structures — the colour of the eyes, body etc. As has been pointed out by MORGAN (1919, p. 238) we designate in calling a gene "white" only that the transition of the gene **W** in the state **w** causes in the organism a series of alterations, of which the most obvious is the change of the colour of the eyes from red to white. This is however far from exhausting the subject. As MORGAN (l. c.) points out, the individual **ww** differ from **WW** also by its lesser viability and

decreased fertility. We may add to it the differences in the form of the spermatheca and colour of the testicles. It sems to me even more than probable, that a careful investigation will reveal a whole series of other differences between **ww** and **WW** individuals. The same relates, of course, not to the gene **w** only, but to many other and most probably even to all genes.

However, we would be mistaken in supposing that having actually studied all the alterations caused in the organism by the transition of the gene **W** into **w** we would obtain full knowledge of the whole totality of the effect of this gene on the organism. Having designated the totality of effects of the gene **W** on the organism as **A** and the totality of the effects of **w** as **B** we will be bound to acknowledge, that in comparing the individuals **WW** with those **ww** we will be able to study only the difference **A—B** but not to obtain any idea either of **A** or of **B** as such. The fact, however, that the mutation of a single gene is followed by a series of alterations in different parts of the body forces upon us the conclusion, that the importance of every gene, no matter how insignificant its external effect may appear, is very great. This view is supported by the fact, that in all cases of deficiency of genes we know of up to the present time, i. e. in all cases of loss of genes, a homozygous organism with regard to deficiency proves unviable (MORGAN, BRIDGES, STURTEVANT 1925).

Recent investigations, particularly those of *Drosophila*, have shown, that in all cases when some character which at first seemed to be dependent on one gene is studied with more detail, it proves that the genetic nature of this character is complicated. Usually there are one or a few chief genes and several or many modifying genes. Such are the cases of beaded (MULLER 1918), truncate (ALTENBURG and MULLER 1920), notch (MORGAN 1919), dichaete (STURTEVANT 1918), reduced (PAYNE 1920), vortex (BRIDGES and MOHR 1919) and some others. The relations become particularly complicated in those cases when the modifying genes have a specific effect on one of the allelomorphs of the "chief gene" such a one as takes place in the case of the specific modifiers for eosin described by BRIDGES (1919). Under the condition that each gene acts only on one definite part of the body the number of genes we must adopt in order to explain the hereditary transmission of the external characters only of *Drosophila* is enormous. Now the adoption of the manifold effect of the gene removes this difficulty, since the gene being the modificator of one character may at the same time

determine a series of characters in other parts of the body. NILSSON-EHLE was the first to point out this possibility as early as 1909 (NILSSON-EHLE 1909). In our experiments the investigation of the form of the spermatheca has shown that its hereditary transmission depends on a whole series of genes, the majority of which proved, however, to be already known genes, causing certain external features as the colour of the eyes, body, length of wings etc. A similar case was established in *Drosophila* by ALTENBURG and MULLER (1920), who showed that the genes black (black body), bar (form of the eye) and Star (form of the facettes) act as modifying genes on the character truncate (truncate wing). BRIDGES and MOHR (1919) found that the gene streak (black streak on the back of the thorax) is at the same time a gene modifying vortex (arrangement of the bristles on the thorax). All these facts are evidences of nothing else but of the genes black, bar, star and streak having a clearly expressed manifold effect.

In those cases when we observe a manifold effect of a gene one the characters produced by it is more sharply expressed than the rest. Just so it is in our case: our mutants as a rule differed very sharply in their external characters, while the difference between them in the form of the spermatheca proved rather inconsiderable and in the majority of cases amounted to differences between the mean values. It seems to me, however, that it would be wrong to draw from it the inference that one of the characters depending on the given gene is the chief character, while the rest of them are secondary or accessory. In the first place in some cases, or even generally, it is difficult to point out which of the differences observed between the mutant and wild type is the sharper. So white differs from wild type by two very obvious characters: white has white eyes and transparent testicles while the eyes of wild type are red and the testicles of a bright yellow colour. Both differences are equally sharp and therefore each of them may be rightly considered as the chief difference. Besides, in my opinion it is altogether impossible to conclude on the importance or subordinateness of differences with regard to genetics from the mere fact, that one of them is obvious and the other discovered only with difficulty.

If it had been our purpose to distribute the genes known in *Drosophila* according to the organs whose characters are determined by them i. e. to point out the genes connected in the first place with the eyes, then other genes connected chiefly with the wings and so on, such a classification would have no other but a mnemotechnical meaning. To

me it seems to be the most probable that every gene acts on all parts of the body and that each part develops under the action of the totality of the genes. There exist no genes determining some part of the body only.

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